



## Variation on a theme of herbivory: *Corallina*–hermit crab relationship on a temperate-subtropical rocky shore

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Elucidation of species interactions involving multiple processes is an important task in ecology, as different processes may operate in non-apparent, opposing directions. While herbivory is a major form of interspecific interaction affecting plants, calcareous algae are generally thought to be protected from herbivory due to  $\text{CaCO}_3$  deposition. However, field observations and experiments in temperate-subtropical intertidal rockpools showed that hermit crabs (Paguroidea, Decapoda) did not ingest *Corallina* but cut short its fronds. We tested the implications of this frond-cutting behaviour with field experiments where hermit crab density and *Corallina* frond length were artificially manipulated.

Hermit crab guts were fuller and contained more microscopic animals when *Corallina* fronds were shorter, suggesting that frond-cutting affects accessibility to food resources that exist in the basal part of algal mat. *Corallina* showed compensatory growth when fronds were artificially reduced in length/density, simulating the cutting by hermit crabs. Frond density increased, probably due to increased exposure to light of the basal part of *Corallina* coupled with a reduction in apical dominance.

The present study revealed a direct, non-trophic relationship between hermit crabs and *Corallina* in which the former affected the latter for gaining access to food resources. Overall, the combination of positive and negative effects of hermit crab led to a positive, facilitative effect on *Corallina*. In terms of the effect on algae or plants, this relationship is functionally analogous to herbivory, without involving direct consumption. We discuss the problem of extending the concept of ecological engineering to herbivory and herbivory-like phenomena and suggest the term 'pseudo-herbivory' to describe relations in which animals have non-trophic but herbivory-like effects on plants/algae, as seen in the hermit crab–*Corallina* relationship.

Interactions between species constitute one of the key issues for understanding the mechanics of species coexistence and community organisation (Tokeshi 1999, Begon et al. 2005). Species coexistence in both terrestrial and marine systems can be influenced either negatively or positively by diverse forms of interaction and a relationship between any two organisms may involve multiple interactions which could lead to opposing effects (Callaway and Walker 1997, Irving and Witman 2009). Given such variability in interactions, investigations into interspecific relations require a careful identification of different, sometimes unexpected, processes (Holzapfel and Mahall 1999, Kawai and Tokeshi 2004).

Among different kinds of species interactions observed in nature, herbivory represents a major, direct influence of animals upon the survival, biomass production and relative abundances of plants/algae (Lubchenco 1978, Lamberti and Resh 1983, de Mazancourt et al. 1998, Gruner et al. 2008). In shallow marine systems, ecological implications and importance of herbivory have been noted for both relatively large-sized 'grazers' such as mammals, fish, echinoids and gastropods (Heck and Valentine 2006) and non-typical, small-sized taxa with herbivorous or supposedly omnivorous tendencies (mesograzers; Hughes et al. 2004, Poore et al. 2009).

In rocky shore systems of cold temperate to subtropical latitudes, turf-forming calcareous algae are a ubiquitous component of intertidal assemblages (Masaki et al. 1982, Konar and Foster 1992) that provide habitats for micro and macro fauna (Akioka et al. 1999, Kelaher et al. 2001). In terms of interspecific interactions in rocky shore habitats, calcareous algae are considered unique in that they are largely avoided as food by herbivores due to their low calorific values and hard body structures which result from the deposition of calcium carbonate (Littler and Littler 1980). Although frequently recognized as a conspicuous group of sessile organisms in hard-substrate habitats (Dayton 1975), few studies have focused on the patterns and dynamics of interactions involving turf-forming calcareous algae. Documenting the occurrence and nature of such interactions is an important step for a better understanding of species coexistence and community organization in rocky intertidal systems.

In the rocky intertidal of Amakusa, southwestern Japan, a large proportion of tidepool habitats is occupied by a coralline alga *Corallina pilulifera* (Rhodophyta), which adds a complex three-dimensional structure to otherwise bare substrates. The present study was stimulated by our preliminary observation that, in the tidepools where *Corallina*

patches were abundant, hermit crabs were also abundant and appeared to cut, but not consume *Corallina* fronds. While hermit crabs are generally recognised as omnivores that feed on a variety of organic matters of both animal and plant origin (Hazlett 1981), there are no reports of either trophic or non-trophic linkages between hermit crabs and coral-line algae. On the other hand, the fact that hermit crabs are capable of adopting different feeding modes under different circumstances (Greenwood 1972, Gherardi 1994) may suggest a possibility of hitherto unknown relationship with apparently unpalatable and spatially dominant *Corallina* involving non-conventional interactions.

The objective of the present study is therefore to clarify the nature of interspecific relationships between hermit crabs and *Corallina*. Our primary goal was to examine the possible dual effects of hermit crabs frond-cutting behaviour on *Corallina* and on hermit crabs themselves. Specifically, we focused on (1) the relation between hermit crab abundance and *Corallina* conditions in terms of frond length and density, (2) the effect of frond-cutting behaviour on hermit crabs' feeding, and (3) the effect of frond-cutting on *Corallina*. We combined field observations with experiments using artificial tidepool habitats in the field to elucidate mechanistic relations.

## Material and methods

### Study site

The study was conducted in the intertidal zone (1.0–2.3 m a.s.l.) of a temperate-subtropical rocky shore on the Amakusa Shimoshima Island, southwestern Japan (32°32'N, 130°02'E). The water temperature on this shore ranged from 13 to 30°C, with the temperature in tidepools sometimes reaching 35°C in mid summer. The mean tidal difference in this area was relatively large, approximately 3.4 m. The tidepools used in the present study emerged for 3 to 7 h at daytime spring tide in summer.

*Clibanarius virescens* (Paguroidea; Crustacea) was by far the most abundant and dominant hermit crab species in the tidepools, followed by *Pagurus filholi* and *Pagurus lanuginosus*, which occurred sporadically. Hermit crabs inhabited tidepools only in the late spring–summer season and migrated to the subtidal at other times of year. Therefore the observation and experiments were undertaken between May and August 2005–2008.

### Relationship between crab density and *Corallina*

We investigated the relationship between hermit crab density and *Corallina* density/size through a combination of field observation and experiment. For field observation we chose a total of 32 tidepools for examining the densities of hermit crabs and *Corallina* in 2005–2007. In the present study, we used data from the same 32 tidepools at full moon spring tide of June and July in 2005–2007 for analysis. We counted the number of hermit crabs in each of the 32 tidepools and expressed their density as number of individuals per unit surface area of tidepool. Mean frond density and frond length (from the base to the apex) of *Corallina* were measured from three *Corallina* patches per pool using

a 25 × 25 mm quadrat. We subjected all data to logarithmic transformation (in the case of hermit crabs, log (density + 0.5) to deal with zero values; Yamamura 1999) before applying a regression analysis.

We used artificial tidepools to examine the relationship between hermit crab abundance and *Corallina* in June 2006. A total of forty earthenware containers (30 cm ø × 25 cm deep) was fixed in the intertidal substrate of a moderately exposed shore (1.5 m a.s.l.), simulating tidepools. In each container, we placed a stone (ca 15 cm ø × 8 cm tall) with a patch of *Corallina*. *Clibanarius virescens* individuals of medium to large body size (carapace length >80 mm) carrying a *Turbo stenogyrus* shell were collected from the field and acclimatised overnight in the running seawater system in the laboratory. We introduced them into the container at four different densities (0, 2, 6, 12 individuals per container; designated as zero, low, mid and high density treatments, respectively, each with 10 replications). These densities spanned the range naturally observed in tidepools (locally and seasonally, variable up to 25–30 individuals per 700 cm<sup>2</sup> on a local habitat scale). The length and density of *Corallina* fronds were not significantly different among treatments at the beginning of experiment (ANOVA with Scheffé's test,  $F_{3,28} = 1.024$ ,  $p = 0.867$  for length and  $F_{3,28} = 0.811$ ,  $p = 0.499$  for density). After two weeks of experimental period, we measured the length and density of coralline fronds as in the field observation. We analysed the data using ANOVA with Scheffé's test for a posteriori multiple comparisons.

### Effect of frond-cutting on hermit crab feeding

We examined experimentally the effect of different degrees of frond-cutting on the feeding of hermit crabs in August 2007, using the same artificial tidepools as above. In this experiment, *Corallina* fronds were cut artificially at different lengths (heights) as treatments (10 mm, short-cut; 20 mm, long-cut; no-cut), assuming that food availability for hermit crabs would be changed. As in the previous experiment, we placed medium-large *C. virescens* individuals in the artificial tidepools at the density of two individuals per pool for a week. This density of hermit crabs was too low to affect the algal length/abundance in the pool within a week, according to our preliminary (and previous) experiments. We also sampled hermit crabs from natural habitats for comparison.

After the experiment hermit crabs were fixed in 10% formalin and preserved in 70% alcohol. For examining gut fullness and contents, we removed foreguts immediately below the mouthpart. Gut fullness was estimated volumetrically and scored on a scale of 0 to 1.0. For gut content analysis, we opened the removed guts and photographed their contents with a digital camera under a microscope. We evaluated gut contents as proportions of different food items (excluding inorganic matter such as sand particles) by counting their numerical frequencies using a 0.125 µm grid on a computer screen. Proportional values were then weighed by multiplying gut fullness values. We used Kruskal–Wallis test with STP (simultaneous test procedure; Sokal and Rohlf 1995) for multiple comparisons and a  $\chi^2$ -test for gut fullness and gut contents data, respectively, for comparisons among treatments and between treatments and the field sample.

## Effects of frond-cutting on *Corallina* density

We evaluated experimentally the potential effects of different degrees of frond-cutting on the density of *Corallina* by simulating the cutting behaviour of hermit crabs. For this experiment we used patches of *Corallina* of similar sizes growing on rocks in a large, shallow tidepool (ca 100 m across, < 60 cm deep). We chose four patches on eleven rocks and subjected them to control and three different treatments: (1) cut at 10 mm height (short-cut); (2) cut at 20 mm (long-cut); (3) selective removal of fronds > 20 mm (partial removal). After the manipulation, frond density in partial removal treatment was lower than in other treatments (ANOVA with Scheffé's test,  $F_{3,40} = 36.050$ ,  $p < 0.0001$ , partial removal < control = short-cut = long-cut). After the experimental period of five weeks, we measured frond length and density for all treatments and calculated changes (%) in these as  $\frac{x_2 - x_1}{x_1} \times 100$  where  $x_1$  and  $x_2$  are measurements at the start and the end of experiment, respectively. The data were analysed by ANOVA with Scheffé's test.

## Results

### Relationship between crab density and *Corallina*

Data from the natural tidepools showed that frond length was negatively related to hermit crab density in all monthly data (June and July) of 2005–2007 (Fig. 1,  $p < 0.01$  for all regressions). In contrast, *Corallina* frond density in natural tidepools did not change significantly with crab density (Fig. 2, all regression slopes not significantly ( $p > 0.05$ ) different from zero). The results were essentially the same with untransformed data and even when zero density points were excluded from analysis. The experiment with artificial tidepools also confirmed the same trend, that frond length was significantly shorter in the high crab density treatment (Fig. 3a, ANOVA with Scheffé's test,  $F_{3,28} = 7.805$ ,  $p < 0.0001$ ; high < mid = zero = low). Further, the pattern for frond density in the experiment confirmed the field observation of no monotonic decline with crab density, but indicated significant variation among crab density treatments (Fig. 3b, ANOVA,  $F_{3,28} = 3.381$ ,  $p = 0.032$ ), mainly due to lower *Corallina* frond density in the zero crab density treatment than in the low crab density treatment. This difference in frond density was more clearly shown when the high crab density treatment that had apparently higher variance than other treatments was excluded from analysis (ANOVA,  $F_{2,21} = 5.326$ ,  $p = 0.013$ ; Scheffé's test,  $p = 0.019$  for zero-low treatments; mean  $\pm$  SD =  $24.7 \pm 6.3$  (zero),  $37.8 \pm 9.2$  (low),  $35.1 \pm 9.4$  (mid)). Pieces of fronds cut and left by hermit crabs were seen on the bottom of the artificial tidepools.

### Effect of frond-cutting on hermit crab feeding

Frond length remained the same in treatments throughout the experiment, with no detectable change (repeated ANOVA,  $F_{3,36} = 0.088$ ,  $p = 0.966$ ). Gut fullness of hermit crabs showed significant variation among treatments, with the highest level of fullness recorded in the short-cut

treatment (Fig. 4a, Kruskal–Wallis test,  $\chi^2 = 24.004$ , DF = 2,  $p < 0.0001$ ; STP, no-cut < long-cut < short-cut). In the no-cut treatment, the majority of hermit crabs had empty guts. Gut fullness of field-derived individuals ( $0.8 \pm 0.04$ , mean  $\pm$  SE) was similar to that of individuals in the short-cut and long-cut treatments (Mann–Whitney–Wilcoxon test,  $W = 384.500$ ,  $p = 0.495$  (short-cut);  $W = 342.000$ ,  $p = 0.068$  (long-cut)).

Detritus was the major component of gut contents in all treatments. Importantly, no *Corallina* fragments were recognised among gut contents. Proportions of different food items were significantly different between the no-cut and the short-cut treatment ( $\chi^2$ -test, DF = 3,  $\chi^2 = 43.169$ ,  $p < 0.0001$ ) and between the no-cut and the long-cut treatment ( $\chi^2$ -test, DF = 3,  $\chi^2 = 20.246$ ,  $p < 0.0001$ ), but not between the short-cut and the long-cut treatment ( $\chi^2$ -test, DF = 3,  $\chi^2$ -test = 4.301,  $p = 0.231$ ) (Fig. 4b). These differences were mainly due to a higher proportion of animal food in the short-cut and the long-cut treatment than in the no-cut treatment. Higher proportions of coarse sand were observed in the guts of cut treatments (about six times more in the short-cut treatment and four times more in the long-cut treatment than in the no-cut), suggesting that hermit crabs ingested the material deposited at the base of *Corallina* fronds. Field-derived individuals showed broadly similar feeding habits, but the proportions of items were statistically different from those of all experimental treatments ( $\chi^2$ -test,  $p < 0.0001$  for all tests), due mainly to a higher proportion of microscopic filamentous algae.

### Effects of frond-cutting on *Corallina* density

*Corallina* frond density at the end of a five-week experimental period was significantly different among treatments (Fig. 5a, ANOVA,  $F_{3,40} = 17.489$ ,  $p < 0.0001$ ), with the highest mean density recorded for the short-cut treatment and the lowest for the control (Scheffé's test,  $p < 0.0001$ , long-cut < short-cut, control < short-cut, control < partial removal). The long-cut treatment showed no significant difference in mean frond density compared with the control. It is notable that frond density in the partial removal treatment was higher than that in the control and not statistically different from the short-cut treatment, despite the fact that it was lower than in other treatments at the beginning of experiment (Material and methods). The partial removal treatment showed the largest change in frond density, followed by the short-cut treatment (Fig. 5b, ANOVA,  $F_{3,40} = 29.711$ ,  $p < 0.0001$  for all treatments; Scheffé's test, control = long-cut < short-cut < partial removal). Significant differences in frond length remained among treatments, though reduced in magnitude, until the end of experiment (ANOVA,  $F_{3,40} = 81.939$ ,  $p < 0.0001$ ; mean  $\pm$  SE,  $24.3 \pm 1.0$  mm (control),  $17.8 \pm 0.7$  mm (long-cut),  $9.7 \pm 0.2$  mm (short-cut),  $13.5 \pm 0.7$  mm (partial removal)).

## Discussion

### *Corallina* responses

Although herbivory in general implies negative impacts on plants, there are circumstances in which plants achieve more

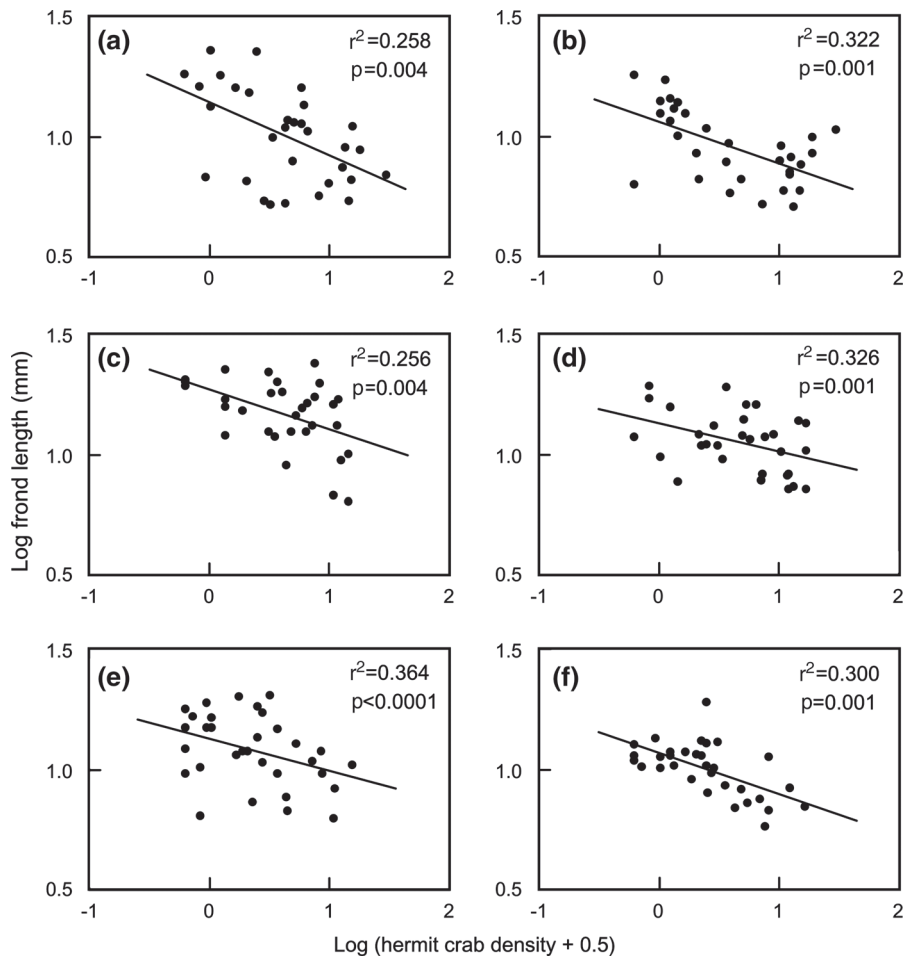


Figure 1. Relationship between hermit crab density (number of individuals per unit surface area of tidepool) and *Corallina* frond length in (a) June 2005, (b) July 2005, (c) June 2006, (d) July 2006, (e) June 2007 and (f) July 2007. Linear regressions are (a)  $y = 1.141 - 0.222x$ , (b)  $y = 1.060 - 0.172x$ , (c)  $y = 1.271 - 0.166x$ , (d)  $y = 1.123 - 0.118x$ , (e)  $y = 1.128 - 0.134x$  and (f)  $y = 1.072 - 0.172x$ .

growth after being damaged by herbivory, resulting in higher productivity and higher biomass (Lamberti and Resh 1983, Wilson 1992, Hjältén et al. 1993, de Mazancourt et al. 1998). In the present study, while hermit crabs had direct, negative effects on the frond length of *Corallina*, frond density was stimulated to increase by the cutting and partial removal of fronds. This response of *Corallina* to frond-cutting was similar to the cases of terrestrial plants where shoot numbers were stimulated to increase after receiving damages (Wilson 1992, Fox 1995). Compensatory growth has been variously linked to removal of apical dominance (Olson and Richards 1988, Wilson 1992, Hjältén et al. 1993), and/or increased availability of limiting resources such as light (Gold and Caldwell 1990) and nutrients (Lamberti and Resh 1983) to the remained parts of a plant.

While the phenomenon of apical dominance is not understood well in algae (Cooke et al. 2002), Yokoya and Handro (1996) suggested a possibility of hormonal control of growth in a rhodophyte *Grateloupia*. Although Akioka et al. (1999) described the occurrence of branched fronds of *Corallina* at high intensity of grazing, causal relationships were not clear and there was no concrete evidence of apical control of growth. In the present study, the fact that no compensatory growth (in terms frond density) was observed

in the long-cutting treatment suggests that apical dominance, if any, is weak in *Corallina*. Rather, the compensatory growth observed in this study is more likely to be a response to changes in micro-environmental conditions, particularly light availability, in different parts of the algal body. After hermit crabs cut or remove fronds of *Corallina*, the basal part of the alga remained intact and new fronds grew from it, while the old fronds did not significantly increase their length. This suggests that an increase in frond density was stimulated by increased light availability to the basal part of *Corallina*. Changes in nutrient availability, on the other hand, are a less likely explanation for the observed patterns, as nutrients do not generally constitute a major limiting factor for intertidal coralline algae (Wai and Williams 2005).

Responses of plants to herbivory are quite variable under different conditions, ranging from under- to over-compensation (Maschinski and Whitham 1989). Different levels of damage from herbivory constitute one of the factors that generate variation in plant responses (Hjältén et al. 1993). The present study on *Corallina* demonstrated that more compensatory growth occurred with a greater removal of fronds. Indeed, the largest increase in frond density was observed in the partial removal treatment where the largest amount of coralline fronds was removed. It appears that new fronds



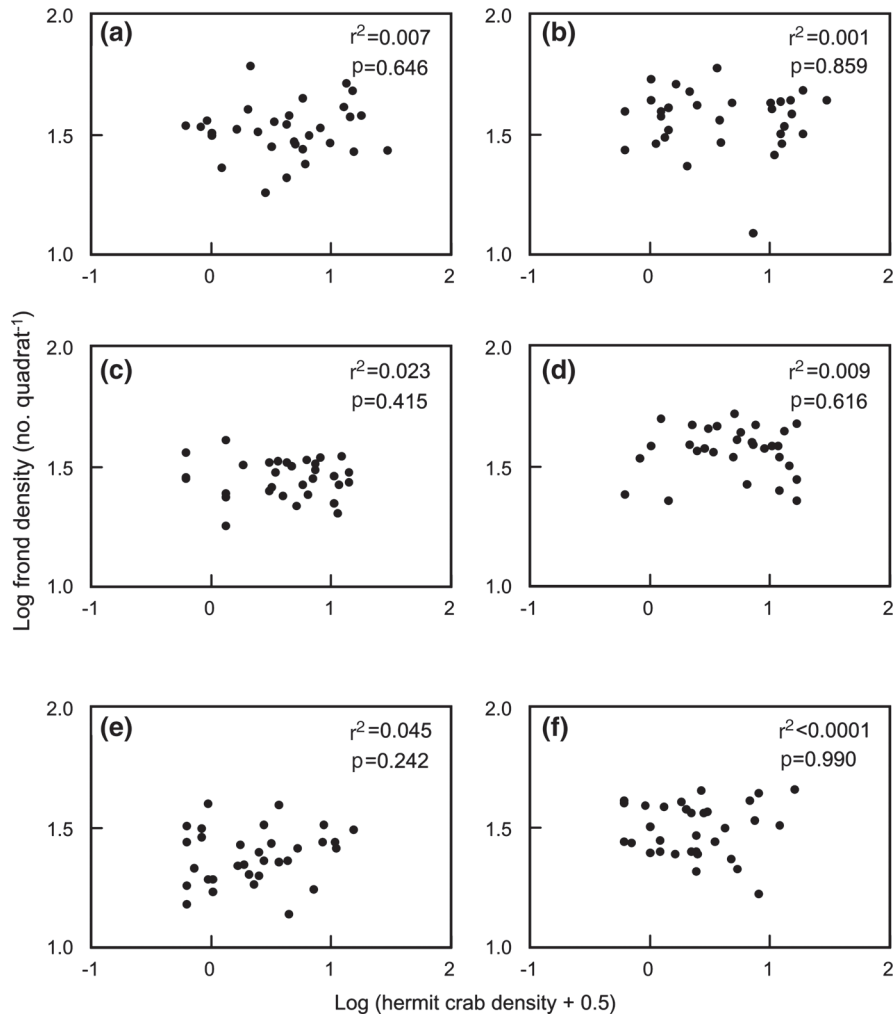


Figure 2. Relationship between hermit crab density and *Corallina* frond density (number of fronds per 625 mm<sup>2</sup>) in (a) June 2005, (b) July 2005, (c) June 2006, (d) July 2006, (e) June 2007 and (f) July 2007.

were stimulated to emerge when more of a limiting resource, light, became available to the basal part of *Corallina*.

The fact that the density of *Corallina* fronds was lower in the zero crab density treatment compared with the low density treatment may be related to the accumulation of sediments on fronds, which is considered to exert a negative impact on algae (Airoldi 1998). In this respect the presence of hermit crabs might have a positive effect on *Corallina* through their constant movements that prevent sediment accumulation on fronds. Indeed, it has been reported that removal of sediment by benthic organisms could enhance the abundance/productivity of algae (Pringle et al. 1993).

We hypothesise that the observed large variation in the relationship between hermit crab density and *Corallina* frond density results from a combination of two opposing forces, the immediate effect of hermit crabs' cutting activity, i.e. loss of long and old fronds, on the one hand and its delayed effect, i.e. enhanced growth of new fronds, on the other. In the short term, the loss may appear larger than the gain. This must largely account for the lack of a clear relationship between hermit crab density and *Corallina* frond density, as the timing and frequency of frond cutting are unknown (more so in the field than in the experiment).

In contrast, the artificial frond-cutting experiment allowed us to isolate the effects of different levels of frond-cutting by controlling the timing of cutting. Thus, the overall effect of hermit crabs on *Corallina* appears to be a positive one, as cutting would stimulate the renewal and increase of *Corallina* fronds, which may lead to their dominance in the sessile assemblages of tidepools.

### Coralline mats and hermit crab feeding

Aggregation of hermit crabs in intertidal habitats where mats of coralline and other algae occur has also been observed on a rocky shore of the Mediterranean (Benvenuto et al. 2003). Beds of turf-forming coralline algae are known to harbour a large amount of sediment and various micro- and macro-invertebrates within their complex structure (Akioka et al. 1999, Kelaher et al. 2001). Among organisms found in *Corallina* mats (listed by Akioka et al. 1999), foraminiferans were frequently observed in the guts of hermit crabs. The high proportion of coarse sand observed in the guts also indicated that hermit crabs obtained food from the algal mat in which sand and other non-organic as well as organic particles accumulate. Interestingly, the guts of field-collected hermit

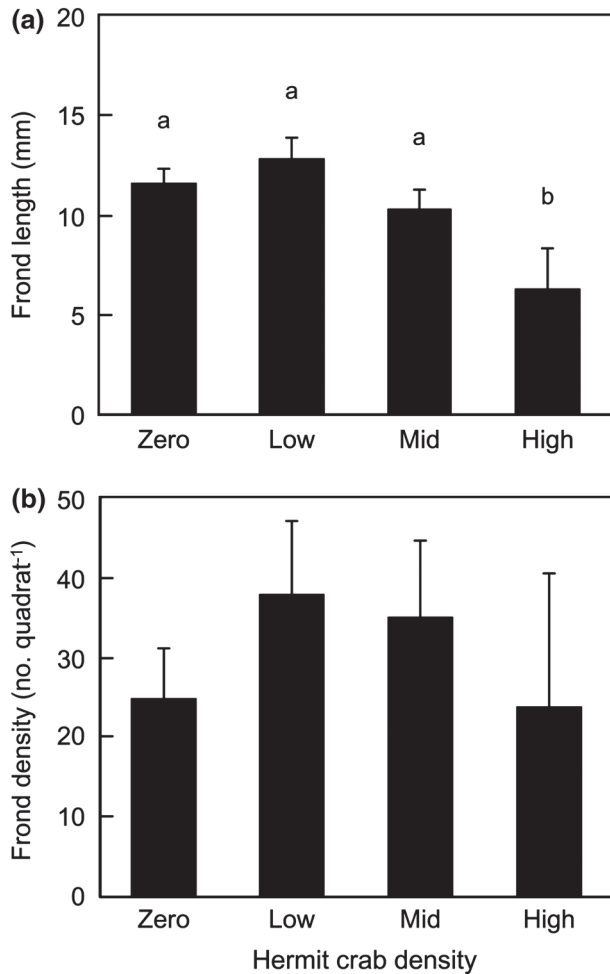


Figure 3. (a) Frond length, mean  $\pm$  1 SE and (b) frond density, mean  $\pm$  1 SD after the experiment. Different letters denote significant differences among means (tested by ANOVA with Scheffé's test).

crabs were as full as those in the short-cut treatment, suggesting that they increase their access to food by cutting fronds short. Kelaher (2003) reported that coralline frond length affected the amount of sediment trapped and the abundance and diversity of gastropod assemblages associated with algal turfs, with more sediment and gastropods being found in short-frond turfs than in long ones. This concurs with the present observation that hermit crabs gain more food under the short-cut treatment. Thus, cutting of algal fronds may be an adaptive behaviour on the part of hermit crabs, whereby the animal gains access to energetically valuable food and at the same time can expect to improve its supply by encouraging further accumulation of organic matter.

It is notable that there was no trace of *Corallina* in the guts of hermit crabs, although *Corallina* was observed to be 'clipped' by hermit crabs. This observation clearly indicated that hermit crabs cut *Corallina* not for direct consumption as in the case of herbivory. Given the poor nutritional value of calcareous algae (Littler and Littler 1980), it appears reasonable that hermit crabs did not ingest *Corallina*. This in turn suggests that the expected increased availability of non-coralline food after the frond-cutting compensates for the energetic cost of cutting *Corallina*.

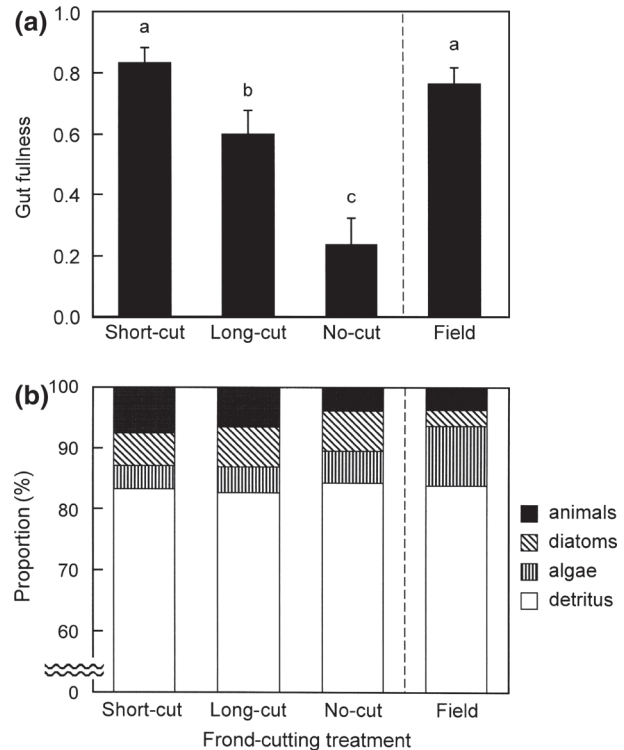


Figure 4. (a) Gut fullness, mean  $\pm$  1 SD and (b) gut contents in the experiment and field sampling (right). Different letters denote significant differences among means (tested by Kruskal–Wallis with STP).

Based mainly on the structure of feeding apparatus, *Clibanarius virescens* was described as detritivorous and macrophagous (Kunze and Anderson 1979). This was confirmed in the present study where the gut contents of *C. virescens* consisted of detritus and other materials including microscopic algae and animals. On the other hand, it is possible that the presence of animal material in the guts of detritivorous hermit crabs (Greenwood 1972) may as well indicate their propensity to take such high-protein food whenever opportunities arise to supplement their otherwise low nutritional diet.

### Herbivory-like relation

The present study has revealed a direct, non-trophic relationship between hermit crabs and *Corallina* in which hermit crabs cut fronds to gain access to food. The effect of hermit crabs on *Corallina* is functionally analogous to that of herbivory, involving the partial loss of algal body and inducing compensatory growth. It is also notable that the hermit crab's interaction with *Corallina* was not an accidental but a clearly targeted behaviour, similar to a herbivore consuming a particular species of plant. Therefore, there is no or little difference between the observed phenomenon and herbivory in terms of its mechanics and effect on the affected (algae/plants); animals target and impact directly on algae/plants in an initially negative way. The only difference concerns whether or not nutrients are extracted from the affected.

While non-trophic relations as demonstrated by hermit crabs in the present study may be described as ecosystem

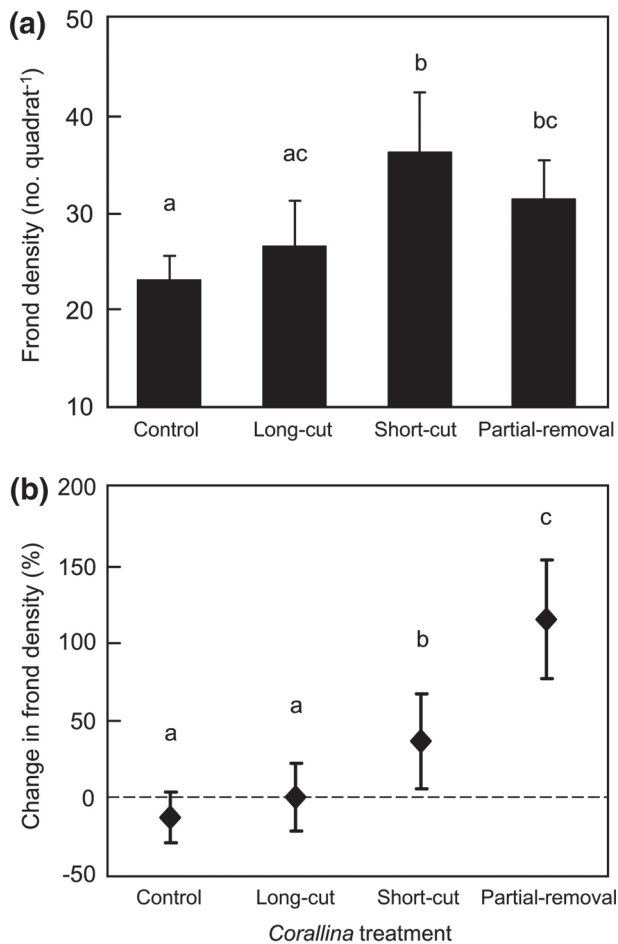


Figure 5. (a) Frond density, mean  $\pm$  1 SD and (b) change in frond density, mean  $\pm$  1 SD after the experiment. Different letters denote significant differences among means (tested by ANOVA with Scheffe's test).

engineering, this would raise a problem in relation to the concept of herbivory. The definition of physical ecosystem engineers as “organisms that directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials” (Jones et al. 1997) clearly applies to herbivores as well as to non-herbivores like hermit crabs, as both cause physical state changes (e.g. removal of branches) that would affect resource availability (e.g. space, epiphytic materials) to other organisms. Indeed, there is no herbivory which does not involve a physical state change in plants/algae. Therefore, if this definition of ‘ecosystem engineer’ is to be upheld, there seems to exist no option but to consider both herbivory and herbivory-like interactions as forms of ecosystem engineering. However, Jones et al. (1997) argued explicitly that the utilization of the living tissues of one organism as food by a consumer is not engineering. This contradictory definition of ecosystem engineering/engineers with regard to herbivory makes the situation more confusing for non-tropic relations that are functionally similar to herbivory, as two phenomena which bear the same consequences for associated organisms (i.e. the same ecosystem effects) would then be treated differently under this concept. Conversely, use of the term

‘ecosystem engineer’ to describe hermit crabs would obscure an important point concerning their herbivory-like effects on *Corallina*. Thus, it is debatable that elucidation of herbivory and herbivory-like phenomena is facilitated by the application of ecosystem engineering concept as is currently defined.

Such operational ambiguity of ecosystem engineering suggests that, where the affected is essentially a particular group of algae/plants rather than an unspecified range of physico-chemical environmental states, a term ‘pseudo-herbivory’ may allow a more precise description that helps draw our attention to herbivory-like effects on producers. Here, pseudo-herbivory is tentatively defined as relations in which animals exert herbivory-like effects on plants/algae without actually consuming them as food. Note that this does not replace ‘ecosystem engineering’; rather, it demarcates part of ‘ecosystem engineering’, which would merit a more specific designation than what ecosystem engineering as a broad and all-inclusive term implies. For example, a damselfish *Stegastes nigricans* selectively removed calcareous and other unpalatable algae in order to maintain their favoured rhodophyte *Polysiphonia* in its territory (Hata and Kato 2002). This ‘pseudo-herbivory’ on the calcareous/unpalatable algae contrasts with a typical example of ‘ecosystem engineering’ or bioturbation where a tropical freshwater fish *Prochilodus mariae* modifies its habitat by ingesting a large volume of sediments, which indirectly leads to changes in algal communities (Flecker 1996). Other cases of pseudo-herbivory may include birds which use live plant materials for nest construction (leaves used as bedding material, Clark and Mason 1985, Lafuma et al. 2001) or make a hole in living trees to nest or feed on insects (Tebich et al. 2004). These activities may affect the growth and survivorship of targeted plants, particularly when the abundances of their favoured plant(s) (for non-feeding purposes) are limited.

Therefore, pseudo-herbivory may not be an uncommon phenomenon in nature and its detection would depend on more attention being paid to deciphering the ramification of a particular behaviour, i.e. how different actions of animals affect their surrounding environments, particularly plants. Thus, plants/algae may experience herbivory-like situations even though they may not be directly consumed by animals. More research will be needed to clarify the mechanisms and implications of such complex relations as pseudo-herbivory for a broader understanding of interspecific relationships in ecological communities.

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