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Seasonal inhibitory effects of marine plants on sea urchins: structuring communities the algal way

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Abstract Natural and manipulative experiments were used to evaluate the effect of algal cover on sea urchin (*Strongylocentrotus polyacanthus*) distribution on submarine pinnacles at Shemya Island in the western Aleutian Archipelago. In July, pinnacle tops had dense kelp stands with low densities of sea urchins. In subsequent months, urchin densities increased as annual algal cover declined. In the summer, removal of specific combinations of macroalgae from the pinnacle tops resulted in an increase in urchin density. Artificial structures that imitated certain common seaweeds were placed on pinnacle tops and inhibited urchin movement. Clod cards that were used to measure relative abrasion rates on vegetated and cleared pinnacles demonstrated that algae cause a significant amount of abrasion. This study showed that the physical structure of the dominant annual alga, *Desmarestia viridis*, is capable of limiting sea urchin distribution, movement, and grazing. In this study, a potential food source actively controlled herbivore distribution and was the primary cause for the persistence of isolated kelp communities surrounded by barrens dominated by sea urchin grazing.

Key words Plant-herbivore interactions · Urchin mobility · Algal abrasion

Introduction

Although plants are conspicuous members of most ecosystems, their role in determining and maintaining the structure of communities is still a matter of debate (Hairston et al. 1960; Slobodkin et al. 1967; Power 1992;

Estes et al. 1998). In general, the argument for the importance of a particular plant species for community structure depends on one of three mechanisms. First, a plant species may be a dominant competitor, outcompeting most other sessile species for space or other resources. Second, plants can determine the structure of communities by modifying the physical environment (Reed and Foster 1984; and see Tilman 1997 for a review). Third, a plant species may structure communities through trophic interactions with herbivores (John et al. 1992; and Crawley 1997 for a review). In the work reported here, I investigated the importance of plant-herbivore interactions in structuring marine benthic communities on Shemya Island, Alaska.

Most explorations of plant-herbivore interactions in a community context have emphasized either the negative effects of herbivores on plants, or the positive effects of plants for herbivores. Herbivores can reduce individual fitness, as well as the population distribution and dispersion of plants (Dowd and Hay 1980; Hay 1981; Mole 1994; Karban and Niho 1995; McCook 1997). In extreme cases, the removal of the majority of the plant community by herbivores can completely alter ecosystem structure (Arnold 1976; Chapman 1981; Watanabe and Harrold 1981; Schiel 1982; Dean et al. 1984). Conversely, with bottom-up community control, increases in host plant abundance or the “quality” of a host plant can cause increases in herbivore densities by supplying food, refuge, or both (Dayton 1975; Ayling 1978; Dowd and Hay 1980; Hay and Fuller 1981; Vasquez et al. 1984; Dearn 1987; Branch et al. 1992; Eubanks et al. 1997). These two types of interactions, however, are only a subset of the possible alternatives (Table 1). In particular, individual plant fitness and population densities can also be enhanced by herbivore presence (however, see critique in Crawley 1997). Positive results of these interactions include increasing propagule dispersal, and increasing growth and biomass following herbivory (Paige and Whitman 1987; Steneck et al. 1991; Horn 1992; Santelices 1992; Littler et al. 1995). Finally, another plant/herbivore interaction is a reduction in herbivore density by

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Table 1 Possible interactions between plants and herbivores with effects being either positive (+) or negative (-). The list of studies is not exhaustive

Controlling species	Recipient species	Net effect	Examples	Studies
Herbivore	Plant	-	1. Tissue damage from herbivory. This can limit distribution and dispersion, and reduce fitness of plant	Dowd and Hay 1980; Hay 1981; Mole 1994; Karbon and Niho 1995; McCook 1997
Herbivore	Plant	+	1. Enhance propagule dispersal	Horn 1992; Santelices 1992
		+	2. Increase in plant biomass	Steneck 1991; Littler et al. 1995
Plant	Herbivore	+	1. Supply food to herbivores	Ayling 1978; Vasquez et al. 1984
		+	2. Offer refuge to herbivores	Dayton 1975; Dearn 1987; Eubanks et al. 1997
		+	3. Supply food and refuge	Dowd and Hay 1980; Hay and Fuller 1981; Branch et al. 1992
		+	4. Pollination/nectar reward	
Plant	Herbivore	-	None found in literature where plant is a potential food source	

plant populations. While this pattern has been shown to result from non-food plants that interfere with host-searching behavior by herbivorous insects (e.g., Root 1972), such a pattern involving host plants and their own herbivores is not known. In this paper, I present evidence for a strong interaction of this last type using sea urchins and a potential macroalgal food, and describe the importance of the interaction in structuring the subtidal communities of Shemya Island, in the Aleutian Archipelago.

In the Aleutian Islands, much of the nearshore subtidal habitats can be classified as sea urchin barren grounds (areas devoid of foliose macroalgae and dense with sea urchins) or kelp forests. The presence of one community type or the other is generally controlled by the presence or absence of the top predator, the sea otter (*Enhydra lutris*). The trophic interactions between otters, urchins, and algae in the western Aleutians have been well documented (Estes and Palmisano 1974; Estes et al. 1978, 1998; Estes and Duggins 1995). With few exceptions (Estes and Duggins 1995; Konar 1998), islands where sea otter density is high have relatively few and small sea urchins, whereas algal cover is high. Conversely, islands where sea otters are rare or absent have many large sea urchins, whereas algal cover is low.

Study system

Shemya Island, part of the Semichi Island group, was one of the last islands in the Aleutian Archipelago to be recolonized by sea otters. The slow recovery of sea otters at this island has allowed kelp forest reinvasion; however, much of the north side is still dominated by barren grounds. This study focuses on submarine, rocky pinnacles that have isolated kelp stands on the tops and barren grounds on the sides and bases (Fig. 1). It is particularly curious that isolated kelp stands exist while surrounded by extensive barren grounds because many studies have shown that sea urchins in barren grounds will migrate into areas of higher foliose algal cover (Mattison et al. 1977) and overgraze the foliose algal

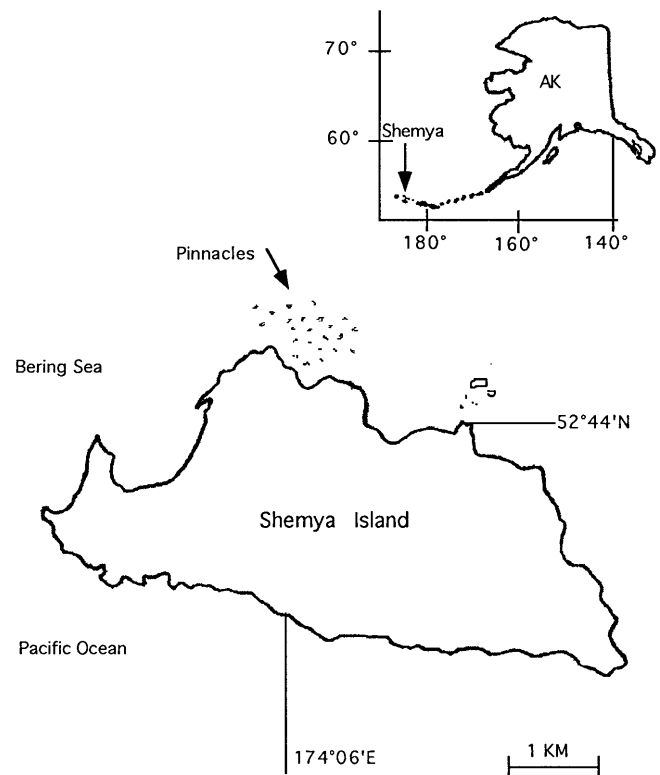


Fig. 1 Map showing location of Shemya Island in the Aleutian chain of Alaska and location of pinnacles within Shemya. Pinnacle tops, which were used in all work except for the two artificial structure experiments, ranged between 3–13 m water depth. Boulders, which were used in the two artificial structure experiments, were interspersed among the pinnacles

communities (Harrold and Reed 1985; Andrew and Underwood 1993). There are multiple possible explanations for the maintenance of kelp patches adjacent to barren grounds, including physical forces and biotic interactions. The major goal of this study was to determine which of these factors allow the continued existence of kelp forests in close proximity to urchin barren grounds.

To examine this question, I used a combination of direct observations and field experiments. In particular, I addressed the following hypotheses concerning the maintenance of this community boundary: (1) urchins would not encroach into the kelp stands on the tops of the pinnacles because there was a specific algal species producing chemical deterrents that were inhibiting urchin movement (some species inhabiting pinnacle tops are known to produce compounds that inhibit herbivory; Eppley and Bovell 1958); (2) urchins within this system were sedentary and did not move between the tops, sides, and bases of the pinnacles (subsequently, tops, sides, and bottoms will be referred to as habitat types); (3) a specific algal species or a combination of various algae might be inhibiting sea urchin movement onto the tops of the pinnacle; (4) physical structure was deterring urchin encroachment into the kelp stands on the tops of the pinnacles, and (5) higher current flows on the tops of pinnacles prevent urchins from invading and foraging.

Materials and methods

Study pinnacles

The study pinnacles on the north side of Shemya Island were at least 7 m from the tops to the bases, with a horizontal surface area of least 16 m² on the tops. The tops ranged between 3 and 13 m water depth. Similar to the tops, the bases were also horizontal and between the pinnacles. Large boulders, approximately 2 m round with horizontal tops were abundant around the pinnacles. The algal community on the tops of the pinnacles was dominated by brown algal species. These included annuals (*Alaria fistulosa*, *Desmarestia ligulata*, *D. viridis*) and perennials (*Laminaria dentigera*, *Agarum cribrosum*, and *Thalassiphyllum clathrus*). The algal community on the sides and bases was dominated by encrusting coralline algae.

Temporal trends in community structure

To document temporal changes in sea urchin density and algal cover on the tops of the pinnacles, I visually estimated percentage cover of total foliose algae (using methods of Dethier et al. 1993) and enumerated sea urchins present on the pinnacles from late summer to early fall. One haphazardly placed 0.25-m² quadrat was quantified in the central top area of approximately 26–32 pinnacles each month from July to October 1995.

Sea urchin feeding preferences and movement

To explain the lack of sea urchin encroachment into the kelp stands on the tops of my study pinnacles and to test the possibility of chemical deterrence, I conducted a series of experiments. An experiment to test if any of the algal species was producing chemical deterrents was conducted by determining if urchins would move toward and climb on the algal species found on the tops. This was done in June 1996. For this, I anchored clumps of the algal species most commonly found on pinnacle tops, *A. fistulosa*, *A. cribrosum*, *D. viridis*, *D. ligulata*, *T. clathrus*, and mixtures of various filamentous red algal species, to the centers of individual 0.25-m² quadrats within barren grounds. These quadrats were first cleared of all sea urchins. Two control treatments were used: quadrats cleared of urchins (to determine encroachment rate when no algae were present) and undisturbed quadrats (to determine natural variation in urchin density over the 1.5-h time interval of this

experiment). Treatments and controls were randomly placed but were at least approximately 5 m apart. All treatments and controls were resampled after 1.5 h on a second dive by counting all the urchins in the 0.25-m² quadrats. Preliminary trials showed that 1.5 h was long enough to allow for some urchin movement, and was generally the longest surface dive interval that could be accomplished (during longer surface intervals, the sea state often changed and a second dive was not possible). Over a 3-week period, 14 replicates of each species and control treatment were attempted, but there was some loss of replicates because surge-induced water movement removed some of the nails that marked the quadrats and held the cable-ties attaching the algae to the substrate.

To verify that *D. viridis* (the most likely inhibitor alga because of its abundance and morphology) is a potential food source, an in situ feeding experiment was done on Amchitka Island in August 1999. For this, thalli of individual plants were trimmed underwater so they were the same approximate size (30 cm) and either cable-tied to a brass bar or placed in a 20×20 cm plastic cage with 3-mm mesh sides. There were four replicates of each treatment. Both bars and cages were left in a barren ground for 40 h. At that time, the lengths of all individual thalli were remeasured underwater. These plants were never brought to the surface because air would cause the sulfuric acid naturally found in the plants to make them quickly decay.

Another test of sea urchin mobility was undertaken to determine if urchins in this system were sedentary or mobile. Specifically, I wanted to determine if urchins moved from one habitat type (foliose algal covered tops, barren sides, and barren bases) to another. Pinnacles chosen for this study had a minimum vertical relief of 10 m. In August and October 1996, 100 sea urchins from each habitat type were tagged through the periproct with 2-cm floy tags (totaling 300 urchins per pinnacle) on two replicate pinnacles. The urchin tags at each habitat were color coded so that the original habitat type of each urchin could be determined. Urchins were not moved during the tagging process. After 2 days, all tagged sea urchins were counted and their locations recorded. From the total number of tagged urchins actually recovered, a percentage was calculated to quantify the minimum number of urchins that moved from one habitat type to another. This was done once in the summer (August) and once in the fall (October) to determine if there were short-term temporal differences. Foliose algal cover was less in the fall than in the summer and foliose algal cover might be influencing mobility between habitat types (see Results; Fig. 2).

Algal clearings

To determine whether a specific algal species or a cover combination of various algae was influencing sea urchin density on pinnacle tops, I removed various combinations of algae from the tops of 20 pinnacles and compared subsequent changes in sea urchin abundance with other pinnacles from which the algae were not removed. By removing specific algal genera, I wanted to determine if sea urchins could be induced to encroach onto the pinnacle tops. Four spatial blocks of five replicate pinnacles each were cleared of different algal genera in June 1996. Within each block, each pinnacle was randomly assigned to one of five treatments cleared of (1) *A. fistulosa*, (2) *Desmarestia* spp., (3) all annual algae, (4) all foliose algae, or (5) controls with no algae removed. These treatments were chosen because I wanted to test whether either of the two dominant annual algae (*A. fistulosa*, *Desmarestia* spp., or a combination of the two as in the all annual algal clearing) was exerting a significant influence on sea urchin distribution. I also wanted to explore how the extreme case, a total foliose algal cover removal, would affect urchin distribution. Control pinnacles were used to monitor natural changes in urchin and algal density through the summer and early fall. Pinnacle tops were monitored for changes in urchin density and algal cover every 4 weeks from June 1996 to November 1996 using six haphazardly placed 0.25-m² quadrats on each pinnacle. Clearings were initiated at the

beginning of June and maintained at weekly intervals through June. After this time, sea urchins had moved onto the pinnacle tops in sufficient numbers to maintain the all foliose algae removal treatments, and thus future clearings on these pinnacles were unnecessary. In addition, urchins also created foliose algal barrens on the annual algae and *Desmarestia* spp. removal treatments, so it was also unnecessary to maintain any of these clearings after June.

Artificial algal experiments

To determine if physical structure was deterring sea urchin encroachment into the kelp stands on pinnacle tops, I placed artificial plants on boulders and monitored for subsequent sea urchin mobility. I used boulders instead of pinnacles because erecting artificial algal beds on a smaller scale was logistically simpler. I do not believe that this scaling-down influenced the results because I was interested in the effects of artificial structure versus no structure on urchin mobility. If anything, the currents would have been slower on the tops of boulders and the artificial algae would not sway as much as would have been expected at the tops of the pinnacles. The boulders used were common between the larger pinnacles in a water depth of 13 m. They had at least 4 m² of horizontal surface area and 1.5-m vertical relief. Individual boulders were randomly assigned to one of four treatments: two treatments had two different types of artificial structures added to boulders cleared of urchins, one treatment was a control with no structure additions to boulders cleared of urchins, and one treatment was a control with no structural additions and no urchins removed. One type of artificial structure was surgical tubing. This was used to imitate the morphology of *A. fistulosa* (without sporophylls). Each artificial plant comprised eight surgical tubing "stipes" (3 mm outside diameter), approximately 1 m tall, cable-tied together. The surgical tubing was positively buoyant so the majority of the plant was suspended above the substrate. Another artificial structure was polyethylene surveyors flagging. This was used to imitate *D. viridis* and *D. ligulata* morphology (size and buoyancy). Each of these artificial plants consisted of 20 flexible flagging "branches" (approximately 20 cm long, 2 cm wide, and less than 1 mm thick), which were cable-tied together. The flagging did not float, so the majority of the plant rested on the substratum and moved with the swell. On manipulated boulders, all foliose algae and urchins were removed and the artificial plants were nailed to the substrate at the approximate densities of the natural algal cover found on pinnacle tops (approximately 60% cover). Unmanipulated boulders (no structures added) were monitored for changes in urchin density. Boulders that had the algae removed and no structures added were also monitored to determine how many urchins would move to the tops of the boulders in the absence of structures. Manipulations were initially set up in August 1996. The tops of the boulders were resampled for sea urchin density by counting the sea urchins in four haphazardly placed 0.25-m² quadrats 1 week after the experiment was set up.

To determine the influence of plant (or artificial structure) density on sea urchin abundance, I conducted experiments in June 1997 similar to those just described using artificial structures mimicking *Desmarestia* spp. In these experiments, I varied the density of artificial plants made from surveyors flagging, to produce total covers of 100, 75, 50, 25, and 0%. Three replicates of each treatment were set up on boulders that were initially cleared of all algae and sea urchins. Two sets of controls (with and without sea urchin removal) were also used to monitor changes in sea urchin abundance as in the other experiments. All treatments were sampled after 1 week for sea urchin encroachment by counting the number of urchins in three haphazardly placed 0.25-m² quadrats on the tops of the boulders.

Abrasion experiments

Clod cards were used to measure the physical abrasion from foliose macroalgae due to water motion and also relative water mo-

tion between the tops and bases of the pinnacles. Typically, clod cards have been used to measure only relative erosion due to water motion (Denny 1985). In my study, some of the clod cards were inside an algal bed so their weight loss was primarily due to the mechanical rubbing of the algae in conjunction with water motion. The clod cards used in my study were similar to those described by Doty (1971). The "clods" were a mixture of plaster of Paris and latex paint that were molded and hardened in ice cube trays. Once hard, each clod was glued to a small (8 cm×4 cm×2 mm thick) piece of PVC sheet and placed in a seawater aquarium to cure for approximately 1 week. They were then removed from the seawater, dried, and weighed. They were reweighed daily until a constant weight was reached. This usually took approximately 1 week. Once fully dried, each clod card was attached to the top of a flat cement brick (40×20×6 cm thick) by cable-ties and then placed in the field. All clods for an experiment were made from one batch in order to minimize variation in the experimental material. Treatment/handling controls were taken into the field and then returned to the laboratory seawater aquarium for the duration of the experiment. This accounted for scour due to the handling and transporting of the cards and simple dissolution. The mean weight that was lost from the control clod cards was subtracted from the actual weight loss in each of the treatments (there was extremely little variance in the weight loss of the control clod cards: ±0.0). This experiment was conducted in the summer (June 1997) when sea conditions were relatively calm, to ensure that few clod cards would be destroyed by extreme swell-induced water motion.

This clod card experiment had three treatments. First, the clods were placed on the tops of pinnacles underneath the overstory algae and directly adjacent to the understory algae. In the second treatment, cards were placed on pinnacles with the foliose algae removed. In the final treatment, the cards were placed at the bases of pinnacles that had no foliose algae and were at a deeper water depth than the tops (5 vs 12 m). Nine clod cards were used for each experimental treatment. However, five were lost from the pinnacle tops and three from the pinnacle bases. After 2 weeks, all the clod cards were collected, brought to the laboratory, dried and weighed until a constant weight was reached.

Results

Temporal trends in community structure

Algal cover and sea urchin densities were inversely correlated over time from late summer to early fall on pinnacle tops. Between July and October 1995, foliose macroalgal cover decreased (Fig. 2), primarily by the attrition of the annual algae. During this time period, annual algal individuals became thinner and appeared less healthy than their perennial neighbors and by October, most of these annual plants had died and fallen off the pinnacles (personal observation). A corresponding increase in sea urchin density was observed with this decrease in algal cover. Greatest algal cover and lowest urchin densities occurred in July, whereas lowest algal cover and greatest urchin densities occurred in October.

Sea urchin feeding preferences and movement

Algal feeding trials using different algal species revealed that sea urchins would climb on all species, although at significantly different levels (ANOVA, $F=9.21$, $df=8,85$, $P<0.001$; Fig. 3). *A. fistulosa* and *T. clathrus* attracted

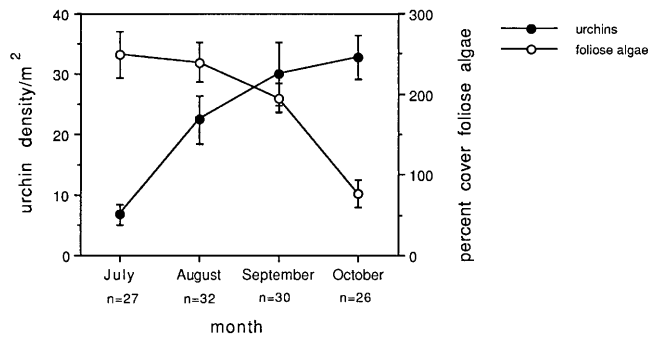


Fig. 2 Trends in sea urchin density and foliose algal percent cover (± 1 SE) from the end of summer to the beginning of fall 1995 on pinnacle tops (n the number of pinnacles sampled each month)

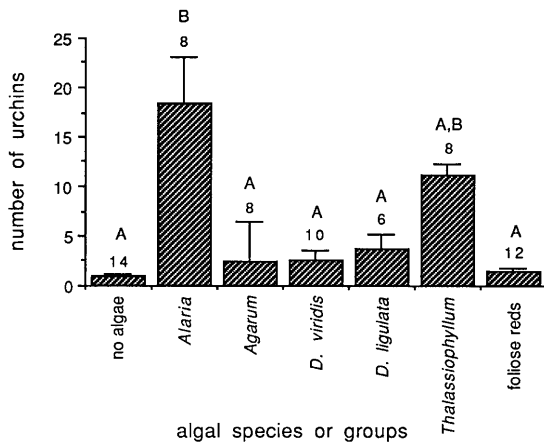


Fig. 3 Density (± 1 SE) per 0.25 m² of sea urchins that climbed onto various algal species 1.5 h after the experimental set-up. The areas covered by each algal treatment were identical. The value above the SE bar is the sample size. Letters denote non-significance groupings among treatments using a post hoc Scheffé F -test ($P < 0.05$). In controls where no urchins were removed ($n = 14$), initial densities were 11.8 ± 1.9 , and 11.2 ± 1.7 after 1.5 h

the highest numbers of sea urchins. There were significantly more urchins on *A. fistulosa* than in the controls or most of the other treatments (except *T. clathrus*; post hoc Scheffé F -test, $P < 0.05$). Quadrats with the other algal species, *Thalasssiophyllum*, *Agarum*, *D. ligulata*, *D. viridis*, and foliose reds all contained more urchins than did control quadrats, which had urchins removed and nothing added, but these differences were not significant (post hoc Scheffé F -test, $P < 0.05$). There were no differences in the control quadrats between the initial sea urchin densities (11.8 ± 1.9) and the final (1.5 h) densities (11.2 ± 1.7).

The in situ feeding experiment demonstrated that *D. viridis* is a potential food source for sea urchins. All individuals that were placed on the sea floor attached to brass bars were completely eaten by urchins, so that re-measurement of thallus length was impossible. In fact, immediately upon placing the bars on the substrate, the

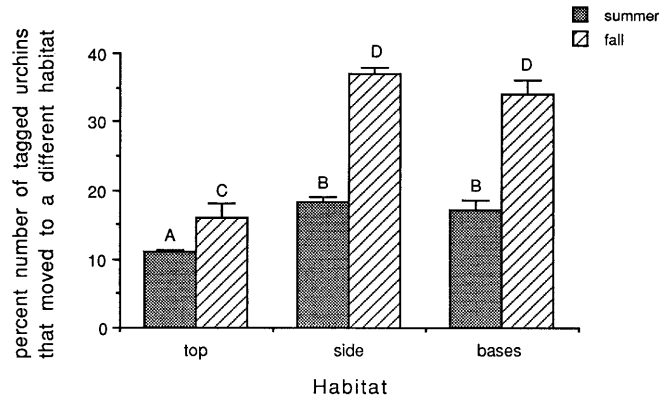


Fig. 4 Mean percent number of tagged sea urchins (± 1 SE) from each habitat that moved within 48 h to a different habitat in both summer and fall ($n = 2$ pinnacles with 300 urchins tagged on each pinnacle). Letters denote non-significant differences within each season using a post hoc Scheffé F -test ($P < 0.05$)

Table 2 Two-way ANOVA of the effect of season (fall, summer) and orientation (top, side, base) on the number of tagged emigrants. This experiment was conducted on two pinnacles at Shemya Island in each season (fall and summer) of 1996

Source	<i>df</i>	MS	<i>F</i> -ratio	<i>P</i>
Season	1	540	144.8	<0.001
Substrate	2	229	61.5	<0.001
Season×Substrate	2	57	15.4	0.004
Error	6	4		

urchins began climbing on the algae. The control plants, which were placed in plastic cages, were all intact and approximately the same size (30 cm) after 40 h.

The 48-h movement experiment demonstrated that sea urchins were very mobile in the fall and summer and on all different habitat types (Fig. 4). Movement was lowest on the tops of the pinnacles in the summer, when 10% of the urchins tagged on the tops moved to a different habitat. A two-way ANOVA showed that the amount of emigration varied significantly with habitat type and season and that there was a highly significant interaction effect (Table 2). In both seasons, significantly more urchins moved away from the sides and bases of the pinnacles than the tops (post hoc Scheffé F -test, $P < 0.05$). There were also significantly more urchins moving between habitats in the fall than in the summer (post hoc Scheffé F -test, $P < 0.05$). This implies that sea urchins are not sedentary in this system but do in fact move between habitat types.

Algal clearings

Throughout this experiment, large differences were seen in foliose algal cover. This was expected at the beginning of the experiment because different pinnacles were cleared of various algal genera. However, these clearings were not maintained after June and significant differ-

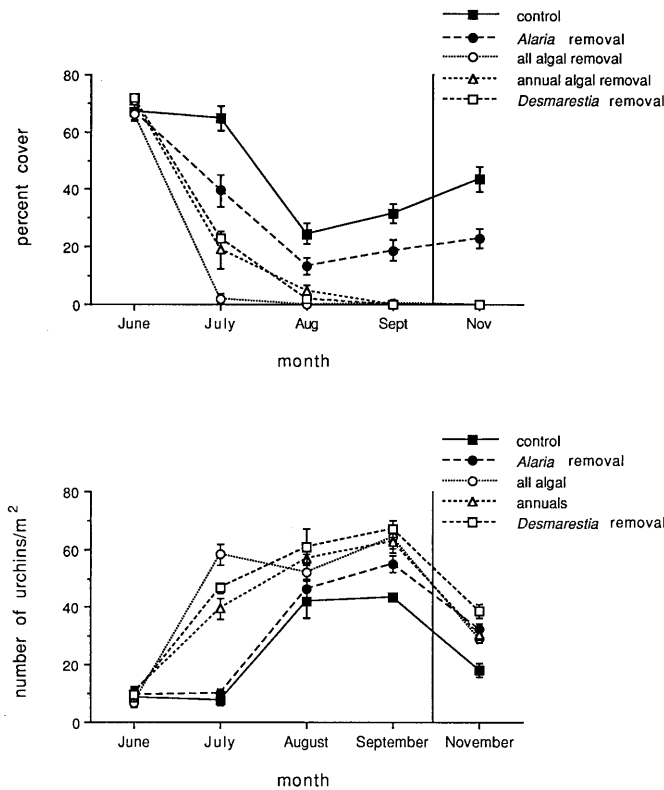


Fig. 5 **A** Mean (± 1 SE) percent cover of foliose algae in each of the treatments and controls in the algal removal experiments. Removals were done on four replicate pinnacles for each treatment. The *line* indicates a break in time. **B** Density (± 1 SE) of sea urchins in each of the treatments and controls in the algal removal experiments. Removals were done on four replicate pinnacles for each. The *line* indicates a break in time

ences were found through the end of the experiment in November. At this time, foliose algal cover varied significantly with treatment (ANOVA, $F=70.33$, $df=4,115$, $P<0.001$; Fig. 5A), with more algal cover on the controls than on any of the other treatments, including the *Alaria* removals (post hoc Scheffé F -test, $P<0.05$). Also at this time, the *Alaria*-cleared pinnacles had more foliose algal cover than any of the other removal treatments ($P<0.05$). Although by August, the foliose algal cover on control and *Alaria*-cleared pinnacles had decreased due to the natural dieback of the annual algae, they never reached the virtually barren state that was found in the other treatments. By September and November, algal cover was increasing in the control and *Alaria* clearings. The following summer (1 year after set-up), the sites were revisited and the treatment and control pinnacles could not be distinguished (personal observation). No data were taken at this time, but it was obvious that these small kelp stands had not been permanently deforested. No sampling was done in October because of high seas.

In July, the month after the algal clearing experiment was set up, sea urchin abundance on the tops of treatment and control pinnacles varied significantly depending on which algal species was or were cleared

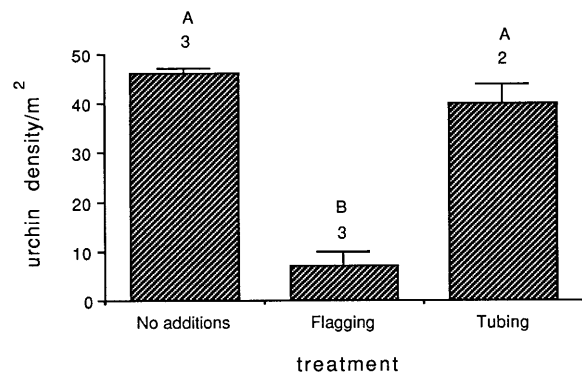


Fig. 6 Density (± 1 SE) of sea urchins on boulders with various structural treatments after 1 week. The value above the SE bar is the number of replicate boulders for each treatment. Identical *let*-ters above the SE bars denote non-significant differences among treatments using a post hoc Scheffé F -test ($P<0.05$). In controls from which urchins were not removed ($n=3$), initial densities were 11.7 ± 0.2 , and after 1.5 h, densities were 11.8 ± 0.6

(ANOVA, $F=76.41$, $df=4,115$, $P<0.001$; Fig. 5B). At this time, more urchins were found on the tops of pinnacles from which I had removed all the algae, all annuals, or *Desmarestia* spp. compared to the controls (post hoc Scheffé F -test, $P<0.05$) and those in which only *A. fistulosa* was removed ($P<0.05$). In August, after foliose algal cover had declined on the control and *Alaria* removal pinnacles due to natural senescing of annual algae (Fig. 5A, and also see Fig. 2 for this trend), sea urchin densities had increased on the control and *Alaria* removals, but the numbers were typically never as high as in the other treatments (ANOVA, $F=5.955$, $df=4,115$, $P<0.001$). At this time, there were significantly fewer urchins in the controls than on any of the other treatments (except for *Alaria* removals; post hoc Scheffé F -test, $P<0.05$). Likewise, there were significantly fewer urchins on the *Alaria* removals than on any of the other removal treatments (except for the all algal removal; $P<0.05$). These trends continued on all the pinnacles, with sea urchin densities remaining high through September, after which they declined.

Artificial algal experiments

Significant differences were found in the amount of sea urchin encroachment into algal-cleared areas depending on the presence or absence of artificial structures (ANOVA, $F=65.64$, $df=4,9$, $P<0.001$; Fig. 6). Specifically, surveyors flagging (simulating *Desmarestia* spp.) significantly deterred urchin encroachment, with far fewer sea urchins on boulders with flagging than on the control boulders (post hoc Scheffé F -test, $P<0.05$) or on those with surgical tubing ($P<0.05$). In contrast, surgical tubing (simulating *A. fistulosa* without sporophylls) did not deter urchin movement: there was no significant difference in urchin density between boulders with surgical tubing and those without it ($P<0.05$). Unfortunately, only

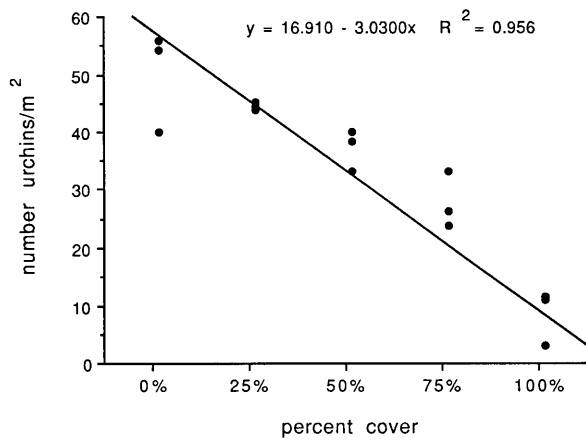


Fig. 7 Sea urchin density (with regression) on boulders with various percent covers of surveyors flagging after 5 days ($n=3$ for each treatment). In controls from which urchins were not removed, initial densities were 11.9 ± 0.9 (SE) and after 5 days, densities were 12.1 ± 0.6

two replicates of the surgical tubing were successful so these results may be biased. However, it did appear that urchin movement was completely unhampered on the two boulders with this treatment (personal observation). There was also no significant difference between these treatments and the unmanipulated controls, which had mean initial densities of 11.7 ± 0.2 and mean final (1 week) densities of 11.8 ± 0.6 . Further experiments showed that the strength of the deterrent effect of artificial algae (flagging) was strongly dependent on density, with a strong negative correlation between the amount of artificial cover and sea urchin distribution on boulders ($R^2=0.956$; Fig. 7). This relationship appears linear, indicating that there is no minimum threshold cover that results in a strong behavioral response from the urchins.

Abrasion experiments

Clod cards revealed that algal cover on pinnacles had a large effect on the relative abrasion that is likely to be experienced by sea urchins. After 2 weeks, clod cards had lost significantly more weight on the tops of pinnacles with algae than on those from which the foliose algae were removed or at the base of the pinnacles, which naturally had no foliose algae (ANOVA, $F=39.32$, $df=2,11$, $P<0.001$; post hoc Scheffé F -test, $P<0.05$; Fig. 8). These data suggest that during calm periods, algal cover but not water depth has an effect on relative abrasion.

Discussion

The results of this study indicate that a plant-herbivore interaction between a potential food source (the brown annual alga, *Desmarestia* spp.) and the dominant herbi-

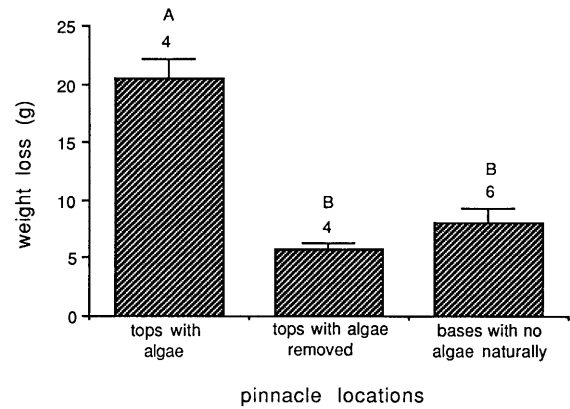


Fig. 8 Mean (\pm SE) weight loss of clod cards after 2 weeks at various locations on pinnacles. The value above the SE bar is the number of replicate clod cards. Identical letters above these numbers denote non-significant differences among treatments using a post hoc Scheffé F -test ($P<0.05$). Weight loss in the controls ($n=9$) was 1.2 ± 0.0 g

vore (sea urchin) is the major interaction distinguishing the pinnacle community from the surrounding bottom system at Shemya Island, Alaska. The plant-herbivore interaction in this study differs sharply from others previously proposed to control community structure. Here, a potential food source (*Desmarestia*) had negative effects on urchin distribution and abundance on the tops of pinnacles. In the summer, these tops had few urchins and lush kelp stands, whereas the sides and bases of pinnacles were dense with urchins and had little or no foliose macroalgae. When annual algal cover began to decrease on the pinnacle tops in the early fall due to natural attrition, sea urchin densities increased (Fig. 2). The annual algae were apparently senescing rather than being grazed by invertebrates because these plants would begin to decay and then fall off the pinnacle tops, landing at the bases where they were quickly eaten by the urchins (personal observation). In the fall, the increase in urchins on the tops of the pinnacles never resulted in urchin densities as high as those found naturally on the sides and bases of the pinnacles (8.2 ± 0.9 on tops vs 12.5 ± 0.6 and 21.3 ± 0.8 on sides and bases, respectively). My study of urchin movement into kelp forests from barren grounds differs from previous studies of urchin mobility in which unhindered urchin encroachment has been documented (Arnold 1976; Chapman 1981; Watanabe and Harrold 1981; Schiel 1982; Dean et al. 1984).

I examined five possible explanations for the lack of sea urchin encroachment from barren grounds into kelp stands on the pinnacle tops at Shemya Island. First, urchins did not encroach into the kelp stands on the tops of the pinnacles because a specific algal species was producing a chemical deterrent that inhibited their movement. Second, urchins within this system were sedentary and movement to the tops of the pinnacles was limited. Third, a specific algal species or a combination of various algae was inhibiting sea urchin movement onto the

tops of the pinnacles. Fourth, some physical structure was deterring urchin encroachment into the kelp stands on the tops of the pinnacles. Finally, higher current flows on the tops of pinnacles were preventing urchins from invading and foraging.

Inhibition caused by chemical deterrence

Certain algal species are rarely fed upon by sea urchins (Vadas 1977; Himmelman 1984; Lemire and Himmelman 1996) and others are known to produce secondary metabolites that reduce urchin grazing (Steinberg 1984; Hay and Fenical 1992). *Desmarestia* spp. contain sulfuric acid, a chemical that has been shown to deter herbivores (Eppley and Bovell 1958; Thompson 1988). However, in my study, urchins climbed on all the foliose algal species found on the tops of the pinnacles, including *Desmarestia* spp., when the alga was anchored to the substrate of a barren ground (Fig. 3). In fact, urchins readily fed on *D. viridis* when it was anchored down in barren grounds for 40 h and could not undulate with the prevailing swell. In addition, the canopy-forming kelp, *A. fistulosa* attracted a substantial number of urchins within 1.5 h of observations. Given the abundance of these and other algal species on the pinnacle tops, and the attraction that urchins have to algae when the algae are anchored in barren grounds and not allowed to move, that sea urchins did not move from the barren sides and bases of the pinnacles to the tops where food was very abundant was perplexing.

Immobile urchins

In some situations, sea urchins have been shown to be very immobile (Mattison et al. 1977; Himmelman 1984). However, this was not the case for the sea urchins in this study. When sea urchins present on the tops, sides, and bases of pinnacles were tagged and monitored over a 48-h period, they were found to move between habitats (Fig. 4). In the summer, sea urchins moved between all of the pinnacle habitats. In the fall, as annual algal cover naturally decreased, urchin mobility increased on all habitat types. This increase in urchin movement as algal cover decreased lends support to the idea that the inhibition is algal related. The question, however, that still remains is why so few of the urchins from the barren grounds moved to the tops of the pinnacles where food is more abundant.

Inhibition caused by a specific algal species

An algal removal experiment demonstrated that large, dense *Desmarestia* thalli deterred urchin movement. Urchin densities increased on the tops of pinnacles when this species was removed. The fact that urchins would climb and feed on *Desmarestia* when it was secured to

the seafloor, but they would not enter kelp stands that had naturally occurring *Desmarestia* suggested the possibility that the inhibition was related to algal structure.

Inhibition caused by structure

Another hypothesis to explain the lack of sea urchin movement was that some type of physical structure on the top of the pinnacles was deterring urchin movement. My use of artificial plant structures clarifies that the physical barrier produced by *Desmarestia* is the mechanism reducing sea urchin densities, rather than chemical or other effects. I propose that *A. fistulosa* (with sporophylls) clearings did not deter sea urchin encroachment to the same extent as *Desmarestia* spp., because *Desmarestia* spp. were far more dense (47.8 ± 9.7 versus 15.5 ± 1.1 for *Desmarestia* spp. and *A. fistulosa* percent cover, respectively). When the effects of algal percentage cover on herbivore densities were tested experimentally with artificial *Desmarestia* structures, I found that there was a strong negative correlation between the amount of artificial cover and sea urchin density on the tops of the boulders (Fig. 7).

Increased water flow on the tops of pinnacles

Clod cards demonstrated that abrasion caused by water motion was not significantly higher on the tops of pinnacle than at the bases. However, algae sweeping the substrate caused a significant amount of abrasion on the tops of the pinnacles. The relative amount of abrasion of clod cards on pinnacle tops with and without algae suggests that mechanical abrasion might be a mechanism by which the algae prevent urchin encroachment. Whether it is as a physical barrier or through their mechanical abrasion, algae appear to be the dominant structuring force in this system.

The *Desmarestia* paradox

The tops may possibly not be a good habitat for urchins due to abiotic factors such as excessive wave action and higher current flows. In other studies, the distribution of urchins was found to be restricted by wave action and exposure (Lissner 1980, 1983; Cowen et al. 1982; Himmelman 1984; Ebeling et al. 1985). In the summer and fall, when wave action is limited, I found that, for strictly abiotic reasons, pinnacle tops were not an unacceptable habitat for sea urchins. This conclusion is based on removal experiments, which revealed that urchins would move in calm seasons to the tops of all treatments when *Desmarestia* spp. were removed (Fig. 5 upper graph). This shows that pinnacle tops are acceptable to urchins if *Desmarestia* spp. are absent. Supporting this, clod cards revealed that there were no differences in the amount of relative abrasion due to swell at the tops of

the cleared pinnacles compared to the bases of the pinnacles. The interesting paradox of these data is that when seas are calm, sea urchins will climb and feed on *Desmarestia* when it is anchored to the substrate in the barren ground and not allowed to move. At this same time, urchins will also climb to the tops of the pinnacles when *Desmarestia* is removed, so, in the summer and fall, pinnacle tops are an acceptable habitat for the urchins. Thus, both *Desmarestia* and the habitat location (tops), by themselves, do not deter urchin movement: the deterrent influence is a result of the interaction between plant and habitat.

The mechanism governing this negative plant-herbivore interaction appears to be driven by the structure of the dominant alga (*Desmarestia viridis*), which is also a potential food source. While previous work has not documented the community-wide effects of this interaction, other studies have suggested its existence. In one study, the movement of algal fronds by wave action was shown to deter urchin grazing (Himmelman 1984). Himmelman noticed that the delicate structure of *D. viridis* allowed it to be washed about by even the slightest water motion and that at his site, while sea urchins were more abundant and relatively evenly distributed on vertical reef faces during the summer, urchins were noticeably absent on those surfaces when *D. viridis* was swept about by the wave surge. In the same study, a similar urchin-free zone was observed around other algae (*Alaria esculenta*, *A. cribrosum*, and *D. aculeata*) when they were being swept by waves. Similarly, Velimirov and Griffiths (1979) found that ocean swell caused *L. pallida* to scour a halo on the substrate around itself that prevented algal colonization and urchin movement.

Implications

The interactions that I document in this system have important implications for studies of plant-herbivore interactions and the regulation of community structure. First, a potential food source may be able to actively control herbivores through biomechanical interactions. Most studies of community structure focus solely on trophic interactions and competition and those researchers studying physical forces on individual species rarely consider effects on other community members (Sousa and Connell 1992; Gaylord et al. 1994; Shaughnessy et al. 1996). This study has shown that a marine benthic community can be structured by a combination of both physical and biotic factors. Second, the abiotic factors interacting with species at one trophic level can propagate to higher and lower trophic levels. This type of community influence may be accomplished not only through the typical routes of competition or trophic interactions. Rather, "bottom-up control" can be achieved through the physical barriers produced by a primary producer, thus limiting the feeding effects of an otherwise controlling herbivore. Although some aspects of plant-herbivore interactions have been well documented in the literature, this

study presents a new type of interaction, where a potential food source (plants) controls the distribution of a recipient herbivore population.

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