

THE STABILITY OF BOUNDARY REGIONS BETWEEN KELP BEDS AND DEFORESTED AREAS

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Abstract. Two distinct organizational states of kelp forest communities, foliose algal assemblages and deforested barren areas, typically display sharp discontinuities. Mechanisms responsible for maintaining these state differences were studied by manipulating various features of their boundary regions. Urchins in the barren areas had significantly smaller gonads than those in adjacent kelp stands, implying that food was a limiting resource for urchins in the barrens. The abundance of drift algae and living foliose algae varied abruptly across the boundary between kelp beds and barren areas. These observations raise the question of why urchins from barrens do not invade kelp stands to improve their fitness. By manipulating kelp and urchin densities at boundary regions and within kelp beds, we tested the hypothesis that kelp stands inhibit invasion of urchins. Urchins that were experimentally added to kelp beds persisted and reduced kelp abundance until winter storms either swept the urchins away or caused them to seek refuge within crevices. Urchins invaded kelp bed margins when foliose algae were removed but were prevented from doing so when kelps were replaced with physical models. The sweeping motion of kelps over the seafloor apparently inhibits urchins from crossing the boundary between kelp stands and barren areas, thus maintaining these alternate stable states. Our findings suggest that kelp stands are able to defend themselves from their most important herbivores by combining their flexible morphology with the energy of wave-generated surge. The inhibitory influence of this interaction may be an important mechanism maintaining the patchwork mosaics of barren areas and kelp beds that characterize many kelp forest ecosystems.

Key words: *Alutian Islands; boundary stability; grazing; kelp; sea urchins; Strongylocentrotus polyacanthus.*

INTRODUCTION

Thirty years ago, Lewontin (1969) raised the question of whether biological communities are globally stable or take multiple stable states. Five years later, Sutherland (1974) presented empirical evidence for multiple stable states in the marine fouling community at Beaufort, North Carolina, and argued that other systems behave in a similar manner. Although ecologists have since debated the evidence needed to demonstrate multiple stable-state communities (Connell and Sousa 1983, Peterson 1984), there are now many examples showing that different organizational states of the same species do exist in nature (Holling 1973, Noy-Meir 1975, May 1977, Dayton and Tegner 1984, Ash 1988, Knowlton 1992, Law and Morton 1993, Maron and Jefferies 1999, Petraitis and Dudgeon 1999, Scheffer et al. 2001).

How and why multiple stable communities occur is less clear. To answer these questions, one must understand both the generation and maintenance of the alternative states (Petraitis and Latham 1999). Mosaics

of alternate stable-state communities should develop where forces capable of driving a community beyond its domain of attraction are localized and spatially asynchronous. Such events, including avalanches, fires, treefall gaps, seed masts, and physical disturbance from wave-borne rocks and logs, are probably ubiquitous in nature. Alternate domains of attraction in systems with multiple stable states are separated by unstable equilibria (May 1977, Scheffer et al. 2001) that should create sharp transitions in space and time. Thus, one approach to understanding multiple stable communities is to focus on their boundaries.

Numerous studies, done mostly at temperate latitudes in the northern hemisphere, indicate that kelp forests exist in two organizational states: one dominated by lush kelp assemblages (hereafter termed “kelp beds”) and the other by intense sea urchin grazing and a dearth of foliose algae (hereafter termed “barren areas”) (see Dayton 1984, Harrold and Pearse 1987, Witman and Dayton 2000 for reviews). Both organizational states contain the same species, although the rate of plant tissue loss to herbivory by sea urchins is low in kelp beds and high in barren areas (Steinberg et al. 1995, Estes et al. 1998). Variation in sea urchin behavior (and not abundance per se) is often the driving force in determining which of these states occurs at any place or time. Sea urchins in kelp beds are typically

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weakly motile or sessile, employing a sit-and-wait foraging strategy in which they consume detrital fallout (hereafter termed "drift") from the kelp canopy (Pearse 1980, Duggins 1981, Cowen et al. 1982, Keats et al. 1984, Ebeling et al. 1985, Harrold and Reed 1985, Rogers-Bennett et al. 1995, Konar 2000a). In barren areas, these herbivores move extensively in their quest for food, destroying kelps and other foliose algae in the process (Russo 1979, Cowen et al. 1982, Harris et al. 1984, Harrold and Reed 1985, Scheibling 1986, Rogers-Bennett et al. 1995). While sea urchin predators can drive shallow reef environments from one state to the other, especially in the northern hemisphere (Estes and Palmisano 1974, Dayton 1984, Harrold and Pearse 1987, Foster and Schiel 1988, Steinberg et al. 1995), smaller scale mosaics (from meters to hundreds of meters across) of kelp beds and barren areas characterize many kelp forests (Duggins 1983, Watson 1993). These mosaics often exist within what appear to be uniform habitats, and switches between states in specific patches of habitat occur through time (Ebeling et al. 1985, Harrold and Reed 1985, Konar 2000a). Ebeling et al. (1985) found that episodic storms drove this system from one state to another, contingent on the starting point (i.e., storms drove kelp forests to urchin barrens and visa versa) although they did not attempt to explain the abrupt spatial transitions between kelp forests and barren areas. In some cases these boundary regions are transitory as actively grazing sea urchins form "fronts" that invade the kelp beds (Leighton 1971, Camp et al. 1973, Witman 1985), whereas in other cases they persist for long periods (Mattison et al. 1977).

Despite this extensive evidence for multiple stable states in kelp forest communities, the transitional dynamics between kelp forests and barren areas are poorly understood. Here we examined why sea urchins in barren areas at the margins of kelp patches did not invade the adjacent kelp beds. First, we investigated the possibility that urchins at the border regions are not food limited and do not move into kelp areas for this reason. Our findings did not support this idea. We next hypothesized that the kelps somehow prevented urchin intrusions, and tested that hypothesis by manipulating kelp and urchin populations at the border regions and within established kelp beds. A strong inhibitory effect by the kelps in the border regions was demonstrated. We also conducted a series of related experiments and measurements to clarify the inhibitory mechanism.

THE SYSTEM

Our work was done in the western Aleutian archipelago of the North Pacific Ocean. Whether rocky reef systems in this region exist as barren areas or kelp beds depends largely on whether or not sea otters (*Enhydra lutris*) are present. Sea otters consume sea urchins (*Strongylocentrotus polyacanthus*), thereby limiting their size and population density, and preventing the development of barren areas (Estes and Palmisano

TABLE 1. Changes in kelp abundance at Adak and Shemya Island (in the Semichis) between 1987 (when sea otters were absent from the Semichis and abundant at Adak) to 1997 (when sea otter population density was similar at both islands).

Island	Date			
	1987		1997	
	<i>n</i>	Percentage w/o kelps	<i>n</i>	Percentage w/o kelps
Adak	786	20.9	780	71.9
Semichi	845	87.5	840	64

Notes: The analysis is based on counts of kelp plants in randomly placed 0.25 m²-quadrats at 35 randomly selected sites in the Semichi Islands and 45 similarly selected sites at Adak Island (see Estes and Duggins [1995] for details of sampling procedures). Number of quadrats sampled = *n*; "percentage w/o kelps" refers to the percentage of these quadrats in which no kelps were counted.

1974). The state change is abrupt for both increasing (Estes and Duggins 1995) and declining (Estes et al. 1998) otter numbers. Furthermore, after making thousands of dives at dozens of islands in the Aleutian archipelago, it was apparent that when kelp forests and barren areas co-occur in these transitional communities, they always do so as a distinct patchwork mosaic with one state or the other predominating over the larger scale of entire islands. Thus, our efforts to understand the mechanisms of change have focused on these mosaics, and especially the boundary regions between them.

The work reported here was done at Shemya (52°43' N, 174°07' E) and Adak (51°84' N, 176°64' W) islands in the Aleutian archipelago. Shemya Island was recolonized by sea otters in the late 1980s or early 1990s and supported a small population during the time of our study (Konar 2000b). The reef habitat around Shemya was mostly barren areas, interspersed with small foliose algal beds formed by the perennial kelps, *Agarum cribrosum*, *Thalassiophyllum clathrus*, *Laminaria dentigera*, and *L. yezoensis*, and during summer the annual species *Desmarestia viridis*, *D. ligulata*, and the surface canopy-forming kelp, *Alaria fistulosa*. The boundaries between kelp stands and barren areas are sharp and persist over time intervals of weeks to months. Adak Island supported an abundant sea otter population from the early 1960s through the 1980s (Kenyon 1969), during which time the reef habitats surrounding the island were kelp dominated (Estes and Duggins 1995). Increased predation by killer whales drove this population sharply downward during the 1990s. By 1999, when the work reported herein was done, both otter densities (Doroff et al. 2003) and the kelp forest community at Adak and Shemya (Estes et al. 1998, Table 1) were similar.

Our focus here is on how the mosaics of kelp stands and urchin barrens are maintained. While prior experiments have demonstrated that urchin grazing prevents

kelps from invading the barren areas (Paine and Vadas 1969, Duggins 1981, Harrold and Pearse 1987), the factor or factors that prevent sea urchins from invading the adjacent kelp beds were unclear. In most cases, there was no evident variation in the physical habitat (i.e., depth, substrate type, or water movement) between these community states.

METHODS

The community and study sites

Except for descriptions of the transitions between kelp beds and barren areas (described in the following paragraph), all of our research was done in a mosaic of kelp beds and barren areas on the southwest shore of Shemya Island. The percent cover of major algal taxa in three distinct beds was visually estimated (Dethier et al. 1993) in randomly placed 0.25-m² quadrats. Brown algae were identified to species and grouped as annuals or perennials, while foliose red algae and encrusting coralline algae were grouped, but not identified to species. Our characterization of these kelp beds was based on a sample of 54 quadrats, taken from between 8 and 13 m water depth during June–August 1996.

Transitions between kelp beds and barren areas

To quantify the nature of transitions between kelp beds and barren areas, we located three small kelp beds in the Kuluk Bay region of Adak Island. The species composition and mosaic nature of these beds were similar to those that occurred at Shemya Island (B. Konar, *personal observation*). Border regions were located haphazardly, and contiguous 0.25-m² quadrats were sampled perpendicularly across each border. All foliose brown algae were identified to species and counted, sea urchins were counted, and percent covers estimated for foliose red algae. For each of these variables, we used a randomized block design (in vs. out of kelp stands and distance from border as treatments, beds as blocks) to assess statistically significant spatial patterns between and within the alternate community state.

Algal drift measurements

Drift algae are known to influence the foraging behavior of sea urchins, and thus their tendency to overgraze kelp beds (Ebeling et al. 1985, Harrold and Reed 1985, Konar 2000a). The abundance and species composition of drift algae were measured along transects run perpendicular to the kelp bed–urchin barren interface to determine how this potential food source for urchins varied across the border between these two community states. Drift algae were quantified 3 m into the kelp bed and 3 m into the urchin barren by collections from six haphazardly placed 10-m² circular plots in each habitat. Only horizontal, rocky substrates were sampled. The drift algae were weighed to the nearest gram (wet mass). Brown algae were identified to species and grouped as perennials or annuals.

Urchin gonad indices

Echinoderm gonads, besides producing gametes, serve the added function of energy storage (Lares and Pomoroy 1998, Russell 1998). Thus, gonad size varies both seasonally and with food availability (Hagen 1998, Konar 1998, Meidel and Scheibling 1999, Vadas et al. 2000). Gonadal indices of sea urchins ([gonad mass/total wet mass] × 100; Gonor 1972) were measured from individuals distributed across the kelp bed–barrens border as a relative measure of fitness variation between the two community states and at their interface. Although fitness is defined by both growth and reproductive output, we selected this simple measure because we were interested in the degree to which food might be limiting to sea urchins across the barren–kelp forest interface at the time of our study.

Twelve urchins of varying test diameters were haphazardly collected 1 m into the kelp beds, 1 m into the barren grounds, and at the points of transition from kelp to barren areas. Only sea urchins >40 mm test diameter were used in this analysis, because studies elsewhere show that smaller individuals of a similar species, *S. purpuratus*, have proportionally smaller gonads (Gonor 1972). The urchins were weighed and dissected to determine gonad mass. These measurements were taken in June 1997.

Urchin additions and algal removals

We conducted an experiment to determine if sea urchins could generate and maintain barren areas within established kelp beds. Four replicate 100-m² blocks were established within kelp beds. Each block was divided into four 5 × 5 m plots, which served as our experimental units. Urchin density and algal cover were monitored monthly in each block using six randomly placed 0.25-m² quadrats. Both the manipulations and measurements were located sufficiently far from the block borders to avoid interactions with treatments in the adjacent blocks. Measurements were taken from July through November of 1996 (no sampling was done in October because of persistent inclement weather), and in August 1997. The experimental units were subjected to the following treatments, assigned at random in each block.

Foliose algae removed/urchins added.—The purposes of this treatment were to determine if high urchin densities could persist within a kelp bed when the foliose algae were removed, and if so, whether or not these cleared patches were maintained as barren areas. To make this determination, all foliose algae were removed and urchins were added (from the nearby barrens) at a density of 68.0 individuals/m² (average density in the nearby barrens).

Foliose algae removed/no urchins added.—The purposes of this treatment were to determine if urchins moved from within or through the kelp bed into a cleared area, and if not, to measure recovery of the

foliose algae relative to Treatment 1. To make this determination, all foliose algae were removed from the experimental units, but urchins were not added.

Foliose algae not removed/urchins added.—The purposes of this treatment were to determine if urchins could remove the foliose algae from within an established kelp bed, and if so, to chronicle the development and persistence of the resulting urchin barren. To make this determination, urchins were added to the experimental units at a density of 68.0 individuals/m², but the foliose algae were not removed.

Unmanipulated control.—These were included to determine the natural variation of urchin and foliose algal abundance over the course of the experiment.

We analyzed these data as a three-way model (urchins present/absent \times foliose algae present/absent \times areas). The ANOVAs were run separately for each time period in order to make explicit changes through time evident.

Invasion of urchins into kelp beds

Foliose algae were removed from kelp beds at their interface with barren areas to determine if the algae inhibited sea urchin invasion. Here again, the experimental units were 5 \times 5 m quadrats, extending into the kelp bed from the barren area interface. Twelve experimental units were established, and the treatments were assigned randomly among them. Urchin densities were measured from six randomly placed 0.25-m² quadrats in each experimental unit and the adjacent urchin barren. Measurements were taken immediately prior to the manipulations and 10 d later. These experiments were initiated in June 1997 and consisted of the following four treatments, each replicated three times.

Total algal removals.—This treatment was undertaken to determine if urchins would invade the kelp bed when all of the foliose algae were removed from its border. A strong initial response was obtained, and hence the following treatments were added to refine our understanding of the mechanisms.

Removal of annuals only.—Only the annual algae (*Alaria fistulosa* and *Desmarestia* spp.) were removed. This was done to determine the role of annual vs. perennial algae in inhibiting sea urchin invasions.

Structural replacements of the foliose algae.—All foliose algae were removed, but they were replaced with clumps of surveyor's flagging that were nailed to the substrate in similar densities to the algae. These "artificial plants" were added to recreate the physical presence of foliose algae, but without any of their biological properties, to determine if algal structure alone could prevent sea urchins from invading the kelp beds. While these models are dissimilar in form to many of the foliose algae (the morphology of which also varies substantially both within and among species), they are similar to most of these algae in their flexibility and movement with wave-induced surge.

Unmanipulated controls.—These were done to monitor natural fluctuations in urchin density at the kelp bed margins and on the periphery of the barren grounds during the course of the experiment.

Nested ANOVAs (quadrats nested within experimental units nested within sites) were conducted on urchin densities in the kelp beds and barren areas immediately before the manipulations to determine if the availability of urchins varied among treatment areas. The same analyses were conducted on urchin densities 10 d after the manipulations to determine if there were significant treatment effects.

Algal abrasion

The previously described algal removal experiments showed that both fleshy macroalgae and the surveyor's tape-models inhibited sea urchins from invading the kelp beds. We suspected that wave-induced abrasion was the mechanism causing this inhibition. Because the kelp beds were comprised of several common macroalgal species, we wished to determine whether these varied in abrasive function, and if so, which ones caused the most abrasion. Dissolution rates of clod cards (Denny 1985) were used for this purpose.

Our clod cards, similar to those described by Doty (1971), were a mixture of plaster of paris and latex paint that were molded and hardened in ice cube trays. Once hard, the clod cards were glued to a small sheet of PVC and placed in a seawater aquarium for one week to cure. They were then removed from the seawater, dried, and weighed at successive times until a constant value was attained. Each clod card then was attached by a cable tie to a cement brick (40 \times 20 \times 6 cm) and placed in the field. The clod cards used for each experiment were made from a single batch in order to eliminate variation between the relative amounts of plaster of paris and latex paint used. Treatment/handling controls were taken into the field and then returned to the seawater aquarium.

Field measurements were made during July 1997, a period when sea conditions were relatively calm. Clod cards were haphazardly placed in the field under naturally occurring patches of *Alaria fistulosa*, *Desmarestia viridis*, *Agarum cribrosum*, or *Laminaria dentigera* that were intermixed within the same kelp stand. One clod card was placed under each patch. Additional cards were placed in cracks in the substratum. Each treatment was replicated four times. After four days, all the cards were collected and returned to the laboratory, and dried until a constant mass was attained. Mass loss by the control cards was subtracted from mass loss by the various treatment cards to obtain an index of abrasion.

Unless otherwise stated, standard parametric statistical analyses were used. Enumeration data were $\ln + 1$ transformed, and percent cover data were arcsine square-root transformed prior to analysis.

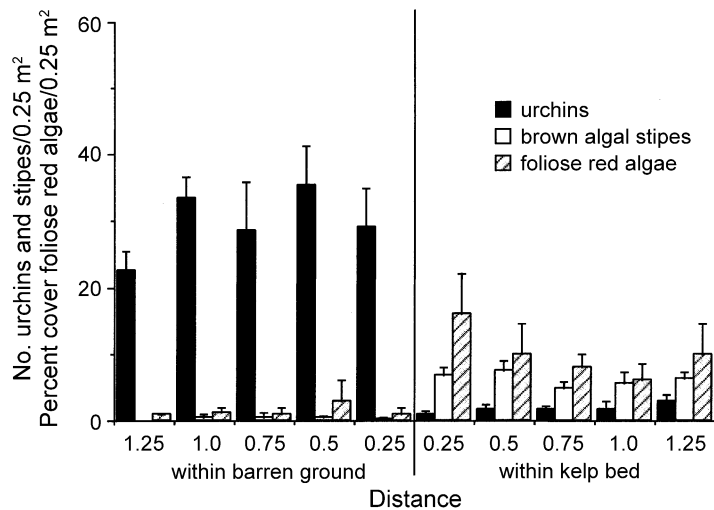


FIG. 1. Number of urchins and brown algal stipes and percent cover of foliose red algae in 0.25-m² quadrats placed along a contiguous transect from 1.25 m within the kelp bed to 1.25 m within the barren area at the study site in the Aleutian archipelago. Values are means and 1 SE.

RESULTS

The community

The percent algal cover in kelp beds at Shemya Island varied substantially among species. Perennial brown algae (*Agarum cribrosum*, *Thalassiophyllum clathrus*, *Laminaria dentigera*, and *L. yezoensis*) contributed most of the canopy cover ($52.4 \pm 3.4\%$ [mean ± 1 SE]), followed by annual brown algae (*Alaria*, $10.9 \pm 1.9\%$ and *Desmarestia*, $3.0 \pm 0.9\%$), foliose red algae ($20.9 \pm 2.5\%$), and encrusting coralline algae ($11.7 \pm 2.5\%$). Foliose algae of all kinds were absent from the adjacent barrens where the substratum was covered almost entirely with encrusting coralline algae and occasional small (<0.25 m²) patches of the encrusting green alga, *Codium setchelli*.

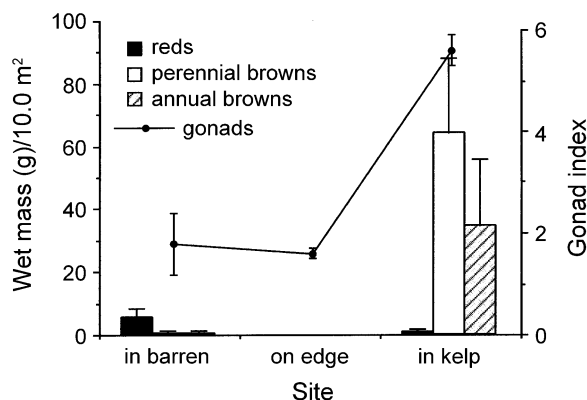


FIG. 2. Drift algal abundance and sea urchin gonadal indices (mean ± 1 SE) across the barren-area-kelp-bed interface in 15 m water depth on the Pacific Ocean side of Shemya Island, Alaska. Drift algae were quantified 1.0 m into the barren area and 1.0 m into the kelp bed from the barren-kelp-bed interface using six randomly placed 10-m² circular plots in each habitat. Gonads were quantified by sampling 12 urchins in each habitat and along the interface.

Transitions between kelp beds and barren areas

The borders between kelp beds and barren areas at Adak Island were sharply defined (Fig. 1). Sea urchins were abundant from the edge of the border outward into the urchin barren, but urchin density declined abruptly from the border into the kelp beds. Similarly, kelp density and red algal cover varied sharply over the same gradient, but in the opposite direction. All of these variables differed significantly between the kelp stands and adjacent barren areas (urchins, $F_{1,44} = 329.7$; kelp stipes, $F_{1,44} = 221.6$; foliose red algae, $F_{1,44} = 30.5$; $P < 0.01$ for each). None of these variables differed significantly among the five distances from the borders across the kelp beds (urchins, $F_{4,20} = 0.692$, $P = 0.606$; kelp stipes, $F_{4,20} = 0.836$, $P = 0.518$; foliose red algae, $F_{4,20} = 0.421$, $P = 0.792$) or the barren areas (urchins, $F_{4,20} = 1.049$, $P = 0.407$; kelp stipes, $F_{4,20} = 0.478$, $P = 0.751$; foliose red algae, $F_{4,20} = 0.387$, $P = 0.815$).

Drift algae

The abundance of drift algae also varied sharply across the kelp bed-urchin barren interface (7.1 ± 3.5 g wet mass/10 m² in barren area vs. 99.5 ± 41.9 g/10 m² in kelp bed, Fig. 2). This difference was highly significant ($t = 5.02$, $df = 10$, $P < 0.001$). Most drift in the barrens was red algae (81.7% of the total). In contrast, most drift in the kelp bed was perennial (64.1% of the total) and annual (34.9% of the total) brown algae.

Urchin gonad indices

The relative size of sea urchin gonads also varied sharply across the barren-area-kelp-bed interface (Fig. 2). These were significantly less at the kelp-barren interface and 1 m into the barren ground (1.8 ± 0.3 and 1.6 ± 0.1 , respectively) than they were only 1 m into the kelp bed (5.6 ± 0.6 ; ANCOVA: Area, $F_{2,32} = 24.97$,

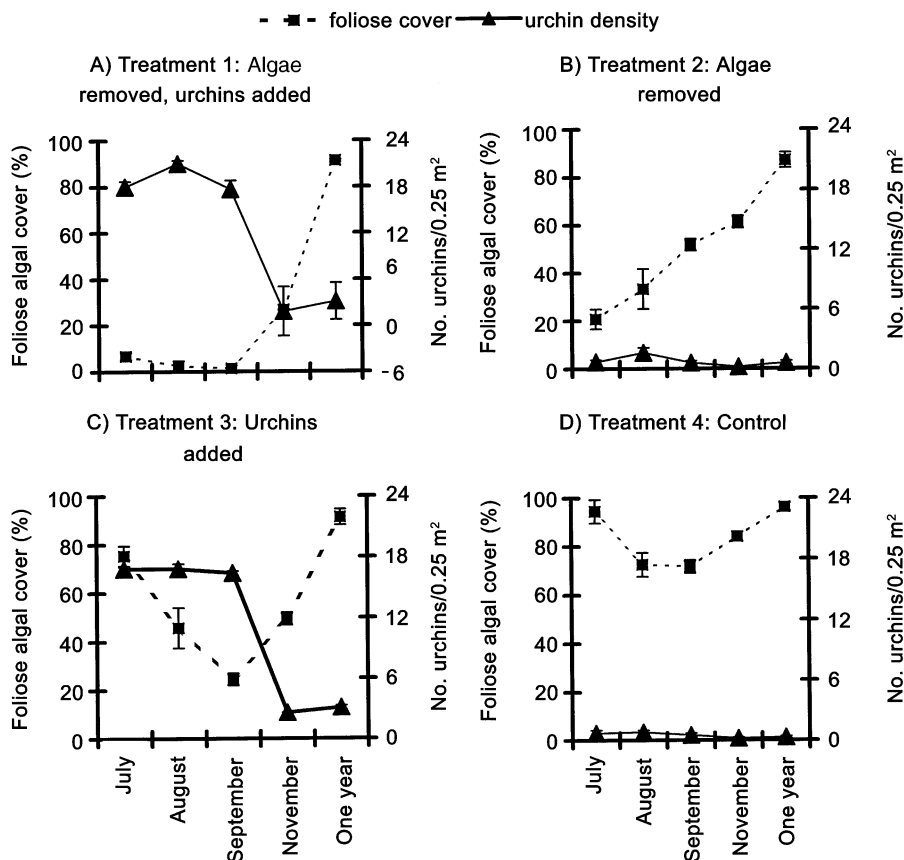


FIG. 3. Urchin density (mean \pm 1 SE) and mean percent cover foliose algae at the various algal removal and urchin addition manipulations. The design of this manipulation consisted of four replicate 100-m² manipulation blocks that were set up in three separate kelp beds on the Pacific Ocean side of Shemya Island, Alaska, between 8 and 13 m water depth.

$P < 0.001$; Urchin mass a covariate, $F_{1,32} = 7.291$, $P = 0.011$).

Urchin additions and algal removals within the kelp beds

Urchins added to both cleared and uncleared areas within the kelp beds remained at high densities (65.6 to 84.0 urchins/m², respectively) from July 1996 when the translocations were initiated, until the first winter storms in October (Fig. 3a, c). Highly significant urchin treatment effects on urchin densities for the period of July through September reflect this pattern (Table 2). By November, urchin densities had declined in both urchin addition treatments (0.8 to 10.4 urchins/m², respectively), and all of those that remained occurred in cracks and crevices within the substrate. At this point, urchin densities did not vary significantly among treatments (Table 2). This pattern remained unchanged through August 1997, although by that time significant treatment effects again had developed because of increases in both urchin addition treatments (Fig. 3a, c). Urchin densities in the other treatment plots (Foliose algae removed/no urchins added, and Unmanipulated controls) remained low throughout the study (Fig. 3b,

d). Site effects on urchin density were statistically significant during two of the sample periods (Table 2). Interaction effects were similarly small and inconsistent through time (Table 2).

Foliose algal cover in the control plots remained largely unchanged through the study, ranging between 71.7% and 96.3% (Fig. 3d). When all foliose algae were removed and urchins were not added, foliose cover increased by ~20% after one month (by August) and increased steadily thereafter to ~90% of the initial value one year later (Fig. 3b). When sea urchins were added to otherwise unmanipulated kelp beds, they actively grazed the plots, causing the foliose algal cover to decline from 75.4% to 24.5% between July and September (Fig. 3c). Defoliation continued until the first winter storms, at which time most of the urchins disappeared and foliose algal cover increased to 49.5% by November 1996 and 91.3% by August 1997. Urchins added to cleared areas prevented foliose algal recovery from July through September (Fig. 3a). Most of these urchins disappeared or retreated to cryptic habitats with the onset of winter storms in October, whereupon foliose algal cover increased (to 26.6% by November and to 91.3% by August 1997). After one year,

TABLE 2. Summary of statistical results, reported by time periods, from the experimental addition of sea urchins into kelp forests at Shemya Island, Alaska.

Effect	df	Month			
		July		August	
		F	P	F	P
Sea urchin density					
Kelp	1, 3	1.38	0.325	4.46	0.125
Urchin	1, 3	1032.56	<0.001	517.29	<0.001
Site	3, 16	4.08	0.025	2.42	0.104
Kelp × Urchin	1, 3	0.05	0.831	0.003	0.961
Kelp × Site	3, 16	1.13	0.367	1.06	0.394
Urchin × Site	3, 16	0.78	0.524	1.16	0.357
Kelp × Urchin × Site	3, 16	0.87	0.475	1.85	0.179
Percent cover foliose algae					
Kelp	1, 3	38.22	0.009	87.07	0.003
Urchin	1, 3	0.54	0.517	11.67	0.042
Site	3, 16	1.17	0.354	7.87	0.002
Kelp × Urchin	1, 3	0.14	0.732	0.05	0.841
Kelp × Site	3, 16	16.51	<0.001	4.05	0.026
Urchin × Site	3, 16	0.64	0.598	17.81	<0.001
Kelp × Urchin × Site	3, 16	1.79	0.189	2.6	0.088

Notes: Data were analyzed as a $2 \times 2 \times 4$ factorial experiment, with Kelp (+ or - at beginning of experiment) and Urchin (+ or - at beginning of experiment) as fixed effects and Site as a random effect. The ANOVAs were conducted on sea urchin densities ($\ln + 1$ transformed) and percent cover of foliose algae (arcsine square-root transformed).

the percent covers of foliose algae in all the manipulated treatments had returned to their initial values and were not significantly different from the controls (Fig. 3). These patterns are reflected by highly significant algal and urchin treatment effects on foliose algal cover for each sample period from July–November 1996 and statistically insignificant effects by summer 1997 (Table 2). Site effects were mostly insignificant through the summer months of 1996. Site effects were highly significant in November 1996 and summer 1997. Interaction effects were small and inconsistent through time (Table 2).

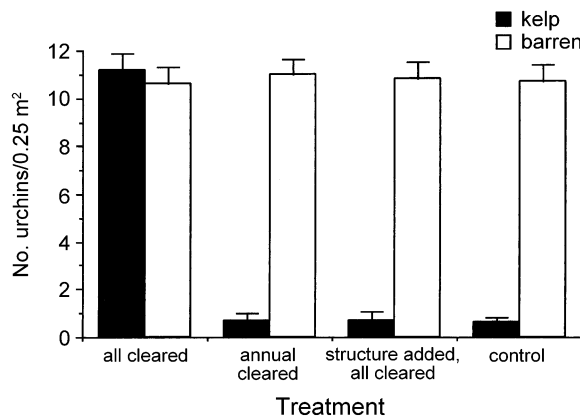


FIG. 4. Sea urchin densities following kelp manipulations at the kelp-bed–barren-area interface on Shemya Island, Alaska. After 10 d, three replicate treatments were surveyed for urchin densities using six randomly placed 0.25-m² quadrats in each treatment and adjacent barren area. Values are means and 1 SE.

Inhibition of urchin invasions across the kelp bed border

Sea urchin densities did not differ significantly among treatment plots prior to the manipulations, thus demonstrating the preexperimental homogeneity of our experimental units (Table 3). Likewise, the absence of significant treatment effects in the adjacent barren areas demonstrates that all of the plots were similar in terms of available sea urchins (Table 3). However, the various treatment manipulations strongly influenced subsequent sea urchin density. Sea urchins quickly occupied areas that were cleared of all foliose algae at the kelp–barren interface (Fig. 4). Within ten days, urchin densities in these plots increased from low values to those occurring in the adjacent barrens (42.4 ± 2.8 urchins/m² vs. 44.8 ± 2.8 urchins/m², respectively). During the same time period, urchin densities in the kelp bed margins did not change notably when only the annual algae were removed, when all algae were removed and surveyor's flagging was added, or in the unmanipulated treatments (Fig. 4).

Algal abrasion

The rate of mass loss varied significantly across the various algal species (Table 4; ANOVA: $F = 19.62$, $df = 4, 15$, $P < 0.001$). The loss rate was greatest for clod cards placed under the two annual species, *Alaria fistulosa* (19.7 ± 0.6 g) and *Desmarestia viridis* (17.8 ± 1.8 g), and the perennial kelp *Agarum cribrosum* (15.0 ± 1.1 g); less for cards placed under *Laminaria dentigera* (6.9 ± 1.0 g); lower yet for cards placed in substrate cracks and crevices (3.1 ± 1.0 g); and lowest for the laboratory controls (1.4 ± 0.05 g; $n = 5$, Scheffé

TABLE 2. Extended.

Month						
September		November		One year		
<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	
10.93	0.046	0.001	0.977	0.002	0.986	
771.93	<0.001	7.62	0.07	235.33	0.001	
1.77	0.193	12.51	<0.001	0.672	0.582	
0.002	0.963	0.36	0.59	1.1	0.372	
0.089	0.965	1.507	0.251	0.91	0.458	
1.36	0.29	22.756	<0.001	0.257	0.855	
0.28	0.836	1.884	0.173	0.253	0.858	
17.77	0.024	28.29	0.013	3.254	0.169	
258.97	<0.001	21.48	0.019	2.349	0.223	
1.66	0.217	20.65	<0.001	40.57	<0.001	
10.09	0.05	0.55	0.512	0.353	0.594	
7.5	0.002	1.61	0.226	4.07	0.025	
1.9	0.17	11.73	<0.001	4.61	0.016	
3.21	0.051	3.63	0.036	2.16	0.133	

multiple range test, $P < 0.05$). An expanded analysis including data from the crevice treatments and laboratory controls showed that loss rates under *L. dentigera* were significantly elevated (ANOVA: $F = 64.09$, $df = 5, 19$, $P < 0.001$, Scheffé multiple range test, $P < 0.05$).

DISCUSSION

Alternate stable states in kelp forest communities

Many complex systems may be characterized by multiple equilibria because of the nonlinear nature of their forcing functions (Scheffer et al. 2001). Kelp beds and barren areas in northern hemisphere kelp forests seem to provide a particularly good example of alternate stable states for biological communities. Spatio-temporal discontinuities in these states have been demonstrated in numerous studies, but the essential role of history in understanding these systems (Lewontin 1969, Sutherland 1974) only became clear following Ebeling et al.'s (1985) long-term study of Naples Reef. Other studies have shown a strong tendency for urchins

in barren areas to move toward food, which is abundant in the adjacent kelp beds (Mattison et al. 1977, Russo 1979, Konar 2000a), a behavior that seems inconsistent with stable boundary areas. The common explanation for boundary area stability has been that the kelp bed supplies enough drift algae to urchins at the edge of the barren area that these individuals need not move in search of food (Russo 1979, Harrold and Reed 1985). This was not the case in our study, as the abundance of drift algae declined to the typically low value of barren areas within a meter of the kelp bed border (Fig. 2). Food limitation for urchins living at the margin of the barren ground is further indicated by the abrupt decline in their gonadal indices at the kelp forest–barren interface (Fig. 2).

Our experiments show that macroalgae living at the border between kelp beds and barren areas deter invasions by sea urchins. When all foliose algae at the kelp bed margin were removed, urchin densities rapidly increased within the clearings (Fig. 4). Urchin invasions also were inhibited when the cleared algae were

TABLE 3. Summary statistics for nested ANOVAs conducted on sea urchin numbers measured immediately before and 10 days following the border manipulations.

Source	Initial			After 10 days		
	<i>F</i>	df	<i>P</i>	<i>F</i>	df	<i>P</i>
Barren area						
Treatment	0.958	3, 45	0.421	0.251	3, 45	0.86
Replicate(Treatment)	0.739	8, 45	0.657	1.41	8, 45	0.219
Quadrat(Replicate)	0.561	15, 45	0.889	0.995	15, 45	0.476
Kelp area						
Treatment	0.334	3, 45	0.799	90.03	3, 45	<0.001
Replicate(Treatment)	0.482	8, 45	0.862	0.537	8, 45	0.822
Quadrat(Replicate)	0.94	15, 45	0.53	1.115	15, 45	0.371

Notes: Results are reported separately for measurements taken from within the kelp forests and the adjacent barren areas. Data were $\ln + 1$ transformed prior to analysis.

TABLE 4. Mass loss (g; mean \pm 1 SE) of clod cards placed under different algal species.

Algae	Mean \pm 1 SE
<i>Alaria</i>	19.7 \pm 0.6 A
<i>Desmarestia</i>	17.8 \pm 1.8 A
<i>Agarum</i>	15.0 \pm 1.1 A
<i>Laminaria</i>	6.9 \pm 1.7 B
In crack	3.1 \pm 1.0 B

Notes: Four cards were placed under each experimental species and collected after four days. Similar letters to the right of the standard errors denote nonsignificant differences using a post hoc Scheffé *F* test, $P < 0.05$.

replaced with model kelp plants, thus demonstrating that some feature of the kelp's physical presence (as opposed to induced defenses) was likely the key mechanism. These observations led us to wonder why the same food species are beneficial in some circumstances and inhibitory in others.

Although sea urchins did not move naturally from barrens into kelp beds, those that were translocated across the boundary areas into the centers of the beds both persisted and defoliated the surrounding areas (Fig. 3), thus indicating that kelps living in the interior portions of the bed are vulnerable to urchin grazing, whereas those at the margin are not. Induced chemical defense by kelps in the border region is one possibility. While we did not test for this directly, we think it is unlikely for several reasons. One is that we have found very little variation in secondary metabolite levels (both phlorotannins and nonpolar compounds) in *Alaria* or *Laminaria* species collected from the western Aleutian archipelago (Estes and Steinberg 1988; P. D. Steinberg and J. A. Estes, unpublished data). Another is that sea urchins in barren areas readily consume even the most well defended kelp species (*Agarum* and *Thalassiophyllum*, Steinberg et al. 1995; *Desmarestia*, Konar 2000a). Finally, if individuals in the border areas were protected by chemical defenses, we would expect to find the most well defended species in these areas, which was not the case. We think it more likely that the pattern relates to differences in flow and the directionality of urchin attack between borders and interiors. Kelps living at the borders are vulnerable to attack from only one direction, whereas those living in the midst of translocated urchins are vulnerable to attack from all directions. Himmelman (1984) noted that sea urchins usually attacked individual kelps simultaneously from all sides and that the resulting large number of attacking urchins often anchored the plant to the seafloor, thus preventing its normal wave-induced motion from pummeling and thereby warding off attackers. Because kelp beds impart significant drag on their surrounding water mass (Duggins 1987, Eckman and Duggins 1993, Friedland and Denny 1995), the strength of surge-induced motion by kelps is probably less in the center of a kelp bed than it is at the border (Seymour et al. 1989).

Different algal species varied in their abrasive action (Table 4). We did not measure flow rate, and thus it is possible that some of the differences among species was a consequence of differential dissolution due to variable water flow rather than abrasion per se. However, we believe that the differences in the clod card mass loss were due to algal abrasion rather than differences in water flow around dissimilar algae because in another study done on Shemya Island, clod cards were found with significantly more abrasion under algae in kelp beds than in algal cleared kelp beds (20.5 g \pm 1.6 vs. 5.8 g \pm 0.5; Konar 2000a). In fact, mass loss of clod cards due to water motion alone was minimal. In general, annuals caused more abrasion than did perennials. Nonetheless, the perennials by themselves prevented urchins from invading the kelp beds. These findings explain why the borders we studied persisted through the winter when the annual algae were absent. The only alga that did not cause significant abrasion was *Laminaria dentigera*. This probably is because *L. dentigera* possess a long, thick stipe that holds its single blade above the substrate. Velimirov and Griffiths (1979) showed that abrasion patterns beneath *L. pallida* (a species with similar morphology) varied with plant size. Smaller plants (1–5-cm stipe length) in Velimirov and Griffiths' study abraded the substrate evenly with an area defined by the arc of their blade length whereas the abrasion beneath larger plants (20–150-cm stipe length) was less near their holdfasts. Most individual *L. dentigera* in the kelp beds we studied were large (50–75-cm stipe length).

The tendency for sea urchins to reside in cryptic habitats has been viewed largely as a means of predator avoidance (Himmelman and Steele 1971, Lowry and Pearse 1973, Nelson and Vance 1979, Bernstein et al. 1981, Witman 1985, McClanahan 1998), facilitated by urchins' ability to employ a sit-and-wait foraging strategy where drift algae is abundant. Algal abrasion may also contribute to this behavior, as our clod card experiments demonstrate that abrasion rate is lowest in cracks and crevices (Table 4). This interpretation is supported by the fact that all of the urchins we translocated into the kelp beds that survived the winter storms did so by residing in cryptic habitats. Barren areas persist through the winter, even in shallow water. However, when kelp beds are present, sea urchin density may be limited by the amount of cryptic habitat. Other factors (such as drift abundance) set higher density limits in these same habitats when kelps are absent.

Interaction variation as a mechanism for maintaining alternate stable communities

Our findings indicate that the same species of plants and herbivores may interact in qualitatively different ways depending on relationships between their behavior and initial abundance. This is of more general interest because consumer–prey interactions are essential organizational features of all natural communities.

Thus, historically mediated contingencies in the nature of consumer–prey interactions might lead to the broad occurrence of multiple stable communities. At the level of population regulation, these interactions take four possible forms, depending upon whether the prey and consumer populations are enhanced or reduced by their respective interactors. For plant–herbivore interactions specifically, both negative and positive effects of herbivores on plants are known. Negative effects occur in the numerous cases where plant tissue loss from herbivory reduces a plant's future fitness. Positive effects through overcompensation, though less well documented, are also possible. Examples include increased flowering and seed production in montaine shrubs (Paige and Whitman 1987), increased growth rates in encrusting coralline algae (Steneck et al. 1991), enhanced plant growth and primary production by ungulate grazing in African grasslands (Augustine and McNaughton 1998), and enhanced intertidal diatom populations by grazing limpets (Connor and Quinn 1984). Positive effects of plants on herbivores are ubiquitous in nature, occurring in all ecosystems fueled by photosynthesis. Negative effects of plant defenses on herbivores also are well known (Lindquist and Hay 1996, Bolser et al. 1998, Schnitzler et al. 1998, Witman and Dayton 2000). However, while herbivore fitness is often reduced relative to that of an herbivore feeding on undefended plants, the herbivores are generally thought to respond either through the evolution of resistance or by feeding on more palatable species. Chemically defended plants may create variation in herbivore abundance, with the herbivores aggregating around more palatable prey species. Our findings demonstrate the importance of physically mediated inhibition of herbivores by plants, the result being a very strong negative effect on herbivore population density by their preferred prey.

Density-dependent shifts in bottom-up forcing by plants on herbivores (from positive in barren areas to negative at the kelp bed's border) in turn changes the strength of top-down forcing by herbivores on plants (from weak in the kelp beds to strong in the barren areas), thus maintaining the two alternate community states. We know of only one other example of a consumer–prey role reversal causing such a shift in community state: Barkai and McQuaid's (1988) report of predator–prey switching between rock lobsters and whelks in South Africa. At normal densities, rock lobsters consume whelks and limit whelk populations, whelks consume mussels and other bivalves, and thus lobsters help maintain a mussel-dominated reef community. When lobster populations were reduced from overfishing or physical disturbance, whelk populations increased, thus causing mussel beds to decline. The superabundant whelks became lobster predators, so that when lobsters were reintroduced into the system, high mortality from whelk predation prevented them from becoming reestablished. These findings raise the ques-

tion of whether such density-dependent shifts in the qualitative nature of consumer–prey interactions is a common mechanism for the generation and maintenance of multiple stable-state communities. The answer most likely will come from studies of systems under strong top-down control and for which multiple organizational states are evident in space or time.

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