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Author(s): Mark D. Bertness, Geoffrey C. Trussell, Patrick J. Ewanchuk, Brian R. Silliman
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DO ALTERNATE STABLE COMMUNITY STATES EXIST IN THE GULF OF MAINE ROCKY INTERTIDAL ZONE?

MARK D. BERTNESS,¹ GEOFFREY C. TRUSSELL,² PATRICK J. EWANCHUK, AND BRIAN R. SILLIMAN

Department of Ecology and Evolutionary Biology, Box G-W, Brown University, Providence, Rhode Island 02912 USA

Abstract. It has recently been hypothesized that intertidal mussel beds and seaweed canopies in the Gulf of Maine are alternate community stable states or disturbance patch mosaics dominated by either seaweed or mussel communities. The community that occurs in a given site is proposed to be stochastic and dependent on the size of the original disturbance and subsequent recruit availability. Large disturbances are postulated to be dominated by mussel beds and barnacles with widely dispersed larvae, whereas smaller disturbances are dominated by seaweeds, with limited dispersal. Positive feedbacks are proposed to maintain these two communities.

We tested this hypothesis in a tidal estuary in central Maine. At eight mussel bed and eight seaweed canopy sites, we created 9-m² and 1-m² clearings and an unmanipulated control area, and in each plot established control, caged, and cage control quadrats. After three years of monitoring, our results do not support the alternate stable state hypothesis. Instead, they suggest that the occurrence of mussel beds and seaweed canopies is highly deterministic. Seaweed canopies dominate habitats with relatively little water movement, whereas mussel beds dominate habitats with high flows; and largely independent of disturbance size, mussel beds and seaweed canopies rapidly returned to their original community type, but only in the absence of consumers (crabs and snails). With consumers present, neither community showed significant signs of recovery, even after three years. In the presence of consumers, community recovery appears to be dependent on cracks and crevices providing refuges from consumers to seaweed and mussel recruits.

The idea that natural communities may represent stochastically determined alternate stable states has important implications for understanding and managing natural ecosystems, but the very existence of alternate stable states in nature has been difficult to establish. Our results suggest that intertidal seaweed canopies and mussel beds in tidal rivers in the Gulf of Maine are highly deterministic alternative community states under consumer control. More generally, since all proposed examples of alternate community stable states are based on indirect, inferential evidence, our results imply that stochastically determined alternate community stable states might be an interesting theoretical idea without a definitive empirical example.

Key words: *alternative community stable state; Ascophyllum nodosum; Carcinus maenus; consumer control of community pattern; disturbance theory; Fucus spp.; Littorina littorea; predation; Mytilus edulis; rocky intertidal; secondary succession; Semibalanus balanoides.*

INTRODUCTION

The idea that natural communities may have alternate stable states, where more than one distinctive and persistent type of community can occur in a given habitat, is an important concept. If alternate community stable states are common, they would be of considerable conceptual interest to ecologists and important for the management and conservation of natural ecosystems. Alternate stable states have been suggested to play an important role in structuring a wide variety of marine and terrestrial communities, including subtidal rocky bottoms (Simenstad et al. 1978, Barkai and Branch 1988, Johnson and Mann 1988), tropical coral

reefs (Knowlton 1992, Hughes 1994), tropical grasslands (Dublin et al. 1990), and temperate forests (Petraitis and Latham 1999). Unfortunately, there have not been rigorous experimental tests of the actual existence of alternate community stable states in any community (Connell and Sousa 1983, Petraitis and Latham 1999). Because of our good general understanding of temperate rocky shore communities, they are an ideal model system for a critical examination of alternate community stable state theory.

Rocky intertidal communities have long been important model systems for the exploration of the biological and physical forces that generate patterns in natural communities. Early studies clarified the roles of consumers (Paine 1966, Lubchenco 1978), competition for resources (Connell 1961, Buss and Jackson 1979), and physical disturbance (Dayton 1971, Sousa 1979) in the generation of community patterns within sites. More recent studies have addressed the causes of

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¹ E-mail: mark_bertness@brown.edu

² Present address: Marine Science Center, Northeastern University, East Point Nahant, Massachusetts 01908 USA.

among site variation, including identifying disturbance (Sousa 2001), larval recruitment (Underwood and Denley 1984, Gaines and Roughgarden 1985), nutrient supply (Menge 1992, Bustamante and Branch 1996), positive feedback (Bertness and Leonard 1997), and local hydrodynamic conditions (Denny et al. 1985, Leonard et al. 1998) as important larger scale community structuring forces.

There are many reasons why rocky intertidal habitats have been a model system for examining how natural communities are structured. They are relatively simple assemblages that are accessible and dominated by small, easily manipulated sessile plants and invertebrates, as well as slow-moving consumers that are often readily removed manually or effectively manipulated in the field with cages. Moreover, many of the organisms that dominate these habitats are short lived, making exploration of population and community dynamics over a number of generations feasible. While many of these characteristics of rocky intertidal communities are not found in more common habitats like forests and coral reefs, the lessons learned about natural community organization on rocky shores can often be extrapolated to other habitats where experimental work is less feasible (e.g., Paine 1966, Connell 1978, Lubchenco 1978).

One benefit from work on rocky shores is the increased understanding of the role played by natural disturbances in generating patterns in natural communities (Dayton 1971, Connell 1978, Paine and Levin 1981, Sousa 1985). As a consequence of this work and work in other systems (Pickett and White 1985), most natural communities are now viewed as nonequilibrium assemblages or mosaics of patches in varying stages of recovery from disturbance (see Sousa [2001] for a review of the marine literature). One of the most conceptually interesting ideas from studies of disturbance in natural communities is that communities can exist in more than one stable state that, once established, can persist indefinitely over many generations of the organisms making up the community. In this situation, the community that dominates a habitat following a disturbance is stochastic, the product of propagule availability when the space was made available and is maintained by positive feedbacks. This idea, commonly referred to as alternate community stable states, was initially proposed theoretically and elaborated on by Lewontin (1969) and Holling (1973). One of the first proposed examples was published on North Carolina fouling communities by Sutherland (1974). In Sutherland's example, recruitment panels placed out at different times were colonized by different taxa that resisted further invasion. Resistance to invasion was seen as evidence of stability, but since the communities that developed only persisted until the original recruits died, it is now recognized that Sutherland's example did not fit the definition of an alternate community stable state (Connell and Sousa 1983). Community sta-

bility and persistence over more than one generation of the organisms dominating the assemblage is required to be considered an alternate community stable state.

Long-term persistence through more than a generation has been one of the largest sticking points for most proposed examples of alternate community stable states (Connell and Sousa 1983, Peterson 1984). In communities dominated by long-lived organisms like corals and forest trees, with life spans much longer than the biologists that study them, intergenerational stability is difficult to establish (Knowlton 1992). In communities of shorter-lived organisms, however, intergenerational stability has been just as elusive to establish (Sousa 1985, Sousa and Connell 1985). In spite of these difficulties, the idea that natural communities may exist in alternate states has remained an issue of considerable interest and debate (see Petraitis and Latham [1999] for a recent discussion).

Recently, Peter Petraitis and his colleagues (Petraitis and Dudgeon 1999, Petraitis and Latham 1999) have suggested that alternate community stable states occur on rocky intertidal shores in New England. Rocky shores on the open coast in the Gulf of Maine, in habitats with low to moderate wave stress, are typically conspicuously dominated by dense canopies of the brown fucoid algae, *Ascophyllum nodosum*. *Ascophyllum* is a large, canopy-forming algae, that can reach two meters in length and live over 10 yr (Steneck and Dethier 1994). At middle intertidal elevations on New England shorelines, *Ascophyllum* can form dense canopies of 20–50 plants/m² that entirely dominate these habitats. At high tide, when these habitats are submerged, the air bladders of *Ascophyllum* float the plants over the substrate, forming a dense forest of plants, while at low tides, *Ascophyllum* individuals cover the substrate as a thick (10–30 cm) mat of plants draped over all middle intertidal surfaces. Wave-exposed sites on the open coast in the Gulf of Maine conspicuously lack an *Ascophyllum* canopy, but instead are often dominated by dense assemblages of the mussel *Mytilus edulis* and the barnacle *Semibalanus balanoides*. The absence of an *Ascophyllum* canopy at wave-exposed sites has been suggested to be due to the inability of *Ascophyllum* recruits to successfully remain attached to the substrate at high wave stresses (Vadas et al. 1990) and the failure of adult plants under high wave stresses.

Petraitis and his colleagues (Petraitis and Dudgeon 1999, Petraitis and Latham 1999) have proposed that *Ascophyllum* canopies and mussel beds can represent alternate community stable states on rocky shores in the Gulf of Maine (Fig. 1). More specifically, they hypothesize that rocky shores in the Gulf of Maine can be dominated by either seaweed canopies or mussel/barnacle beds and that disturbance history and stochastic processes, rather than the physical attributes of a habitat, can determine which of these two distinct communities dominate a habitat. They suggest that habitats with a history of low disturbance are dominated

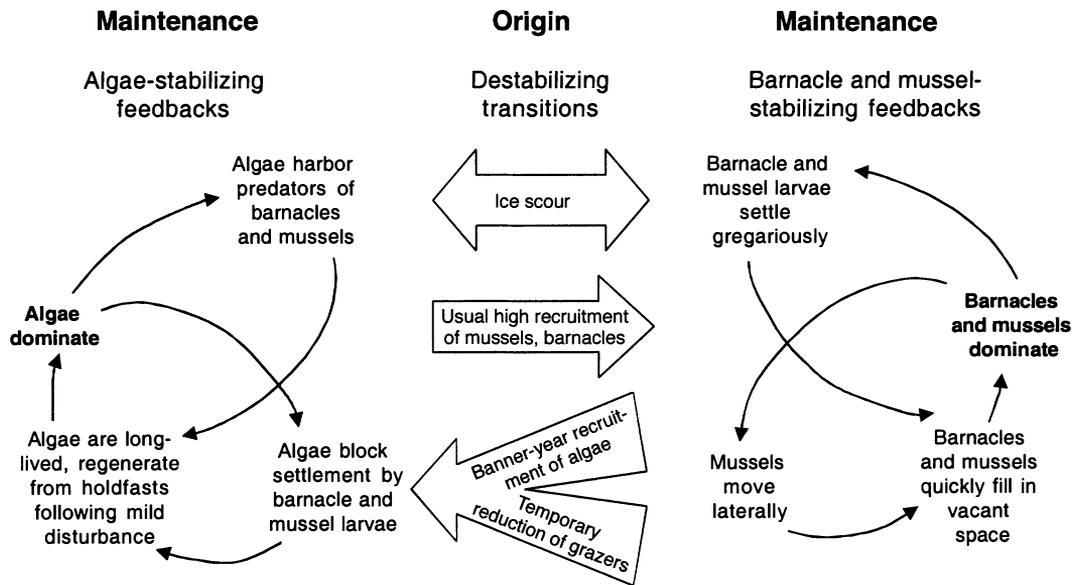


FIG. 1. Conceptual model of the *Ascophyllum* canopy–mussel bed alternate community stable state hypothesis proposed by Petraitis and Latham (1999).

by long-lived *Ascophyllum* canopies, whereas habitats with a history of recent large-scale disturbances are dominated by mussel/barnacle bed habitats. They further suggest that these two community types, once established, are maintained by positive feedback (Wilson and Agnew 1992). In both communities, snail and crab consumers refuged in established assemblages are proposed to limit further recruitment and thus maintain the stability of each community type. The maintenance of these community types is hypothesized to be scale dependent. Small disturbances in *Ascophyllum* canopies are proposed to be recolonized by *Ascophyllum*, which has extremely limited dispersal. Large disturbances, in contrast, are proposed to be colonized by mussel and barnacle recruits, which have much wider dispersal. Petraitis and his colleagues suggest that chronic disturbance by ice scouring mediates the occurrence of these hypothesized alternate community states. Large ice disturbances are suggested to lead to stable mussel/barnacle assemblages, whereas smaller disturbances in established seaweed canopies are suggested to typically be colonized and ultimately dominated by *Ascophyllum*. While this hypothesis has received considerable attention (Levinton 2001, Morgan 2001), to date it has been supported largely by indirect evidence of recruitment and consumer patterns that could potentially lead to mussel bed/seaweed canopy alternate stable states (Petraitis and Dudgeon 1999, Petraitis and Latham 1999, Dudgeon and Petraitis 2001).

The most conspicuous problem of the *Ascophyllum* canopy–mussel bed alternate stable state hypothesis in the Gulf of Maine is that it does not consider the more parsimonious and widely recognized (Gosner 1978, Vadas et al. 1990, Leonard et al. 1998) alternative hy-

pothesis that these communities are a deterministic product of different physical environments. *Ascophyllum* canopies are characteristic of wave-protected shores (Gosner 1978, Vadas et al. 1990, Leonard et al. 1998), whereas mussel bed–barnacle assemblages dominate shores that are typically associated with wave-exposed habitats (Menge 1976) or habitats with high water movement and larval and food fluxes (Leonard et al. 1998).

In this paper we present the results of an experiment designed to examine the hypothesis that mussel beds and *Ascophyllum* canopies can be alternate community stable states on rocky shores in the Gulf of Maine.

METHODS

We examined the generality of the seaweed canopy–mussel bed alternate stable state hypothesis on the Damariscotta River in central Maine. It is an ideal location for exploring this hypothesis. The Damariscotta River is a tidal estuary and its shores are lined with discrete, spatially segregated areas of dense *Ascophyllum* canopy and mussel/barnacle beds. Seaweed canopies and mussel beds are often found in adjacent habitats, very close together, but their occurrence is strongly correlated with local hydrodynamic conditions. Habitats that are exposed to low water flows are dominated by dense monospecific stands of *Ascophyllum*, whereas habitats exposed to high water flows, often just a few meters away, are characterized by intertidal mussel bed and barnacle assemblages (Leonard et al. 1998). The association between hydrodynamic conditions and intertidal community type along the estuary is striking. Mussel-bed-dominated intertidal habitats occur at any narrowing in the river where tidal flows are elevated.

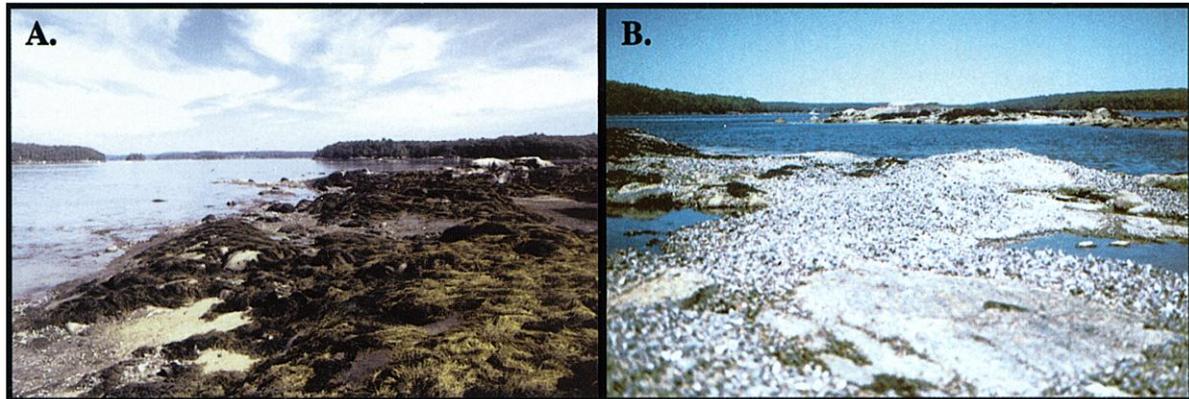


FIG. 2. (A) *Ascophyllum* canopy and (B) mussel bed habitats on the Damariscotta River in central Maine (USA).

Islands that occlude flow in the river and the mouths to inlets are typically dominated by mussel/barnacle beds. Just as predictably, however, nearby areas with lower flows are dominated by dense *Ascophyllum* canopies. Fig. 2 illustrates how dramatically different these habitats are in spite of their often close physical proximity. Habitats that are not clearly either mussel bed/barnacle assemblages or *Ascophyllum* canopies are not apparent in this or other nearby tidal rivers in Central Maine.

To test the alternate community stable state hypothesis in this system, in February 1999 we established eight study sites on the river with dense intertidal mussel beds and barnacles and eight study sites near the mussel bed sites that were dominated by dense *Ascophyllum* canopies. The sites were all located along a 10-km section of the estuary typically exposed to full strength seawater (Leonard et al. 1998). For seaweed canopy sites, we chose sites adjacent to our mussel bed sites and avoided habitats with extremely low water movement, typically characterized by sediment-covered surfaces under the canopy. We did this to maximize the probability of finding alternate community states in this system. Similarly, for mussel bed sites, we chose locations where nearby *Ascophyllum* canopies suggested that conditions were suitable for *Ascophyllum*. Snails (primarily *Littorina littorea*) and crabs (primarily *Carcinus maenas*), the dominant consumers in this system, were abundant at all the sites (Leonard et al. 1998).

At each site we replicated Petraitis and Dudgeon's (1999) experiment to test for the disturbance size-dependent occurrence of seaweed–mussel alternate community states. At the same intermediate tidal elevation at each site, we cleared one 3 × 3 m and one 1 × 1 m area of all plants and sessile animals. In the clearings, organisms were removed from the substrate with flat edged garden shovels and paint scrapers. Any remaining algal holdfasts were burned from the surface with a propane torch, so that no recolonization of the plots could be attributed to vegetative regrowth. While this

may not mimic the typical natural creation and recovery of ice-generated disturbance patches, where plants may regenerate from remaining holdfasts (Aberg 1992, McCook and Chapman 1991), it is intended to mimic the recovery from particularly severe ice disturbances that entirely denude surfaces (Petraitis and Dudgeon 1999). In addition to entirely denuding the cleared plots, *Ascophyllum* around the border of the bare patches that could potentially rest on the bare patch surfaces during low tides were also removed. Since *Ascophyllum* individuals at our study sites were commonly longer than 1.5 m, this was done to standardize the size of the bare areas and give them discrete edges. Because we cleared our plots so that no *Ascophyllum* would rest in them during low tide, our 3 × 3 m clearings were at least comparable in size to the 4 × 4 m plots used by Petraitis and Dudgeon (1999), since they only cleared plants attached within the plots, but did not remove surrounding plants that could rest in the plots. Our large 3 × 3 m clearings were therefore at or above the size threshold thought to be necessary to stimulate community switches in the system (Petraitis and Dudgeon 1999). In the middle of each clearing and in nearby unmanipulated habitats at each site, we cleared and marked three haphazardly placed 10 × 10 cm monitoring quadrats with individually numbered metal tags and corner bolts. At each site and disturbance treatment (3 m, 1 m, and unmanipulated), one of the quadrats was left as a control, one was covered with a stainless steel mesh (5 mm) consumer exclusion cage (20 × 20 × 4 cm [length × width × height]), and the remaining quadrat was covered with a stainless steel cage control, identical to the cage treatment, but without sides. We included a caging treatment to explore the role of consumers in the recovery of bare space, because previous work in this system had shown that both snail (Menge 1976, Lubchenco 1978, 1983) and crab (Leonard et al. 1998, 1999a) consumers can have enormous effects on the recruitment and persistence of primary space holders. We monitored this experiment by photographing the marked quadrats with color slide film in late spring

and fall of 1999, 2000, and 2001. One entire mussel bed site had to be abandoned after the first winter because it was destroyed by ice scouring. The quadrat slides were analyzed (for percent cover) by projecting them to their actual size, placing a clear plastic sheet with 100 random points over the photograph, and identifying the space occupant at each random point. This photographic method worked well to document changes in surface cover, but at *Ascophyllum* canopy sites when consumers were excluded, a dense canopy of algal recruits developed by the second year of the experiment (see *Results*). In these quadrats, photographs were useless for documenting changes in understory primary space occupiers. To examine patterns in the development of this understory community, in September 2001, we quantified understory space occupation in the field by placing a 10 × 10 cm grid with 100 sampling cells over each caged plot and identifying the occupants of each sampling cell.

We quantified the abundance and distribution of primary space holders in the intertidal communities at our study sites in July 2001. At each site, at both high intertidal and low intertidal elevations, we haphazardly tossed a 50 × 50 cm sampling quadrat subdivided into 100 5 × 5 cm cells 10 times at approximately two-meter intervals, and identified the occupant at the center of each cell. At the *Ascophyllum* canopy sites at each haphazard sampling location we also sampled the rock surface under the canopy (understory) using the same methods. High and low intertidal sampling heights at all sites corresponded to the elevation of the high and low intertidal borders of *Ascophyllum* canopy. For more detailed descriptive data of the intertidal community at these sites, including tidal height information and data on mobile organisms of importance like crabs and snails, see Leonard et al. (1998).

To quantify relative differences in water movement among the study sites, we used calcium sulfate (dental plaster) dissolution blocks. The dissolution rate of calcium sulfate is proportional to flow speed and has been widely used to estimate gross differences in water movement among sites (Thompson and Glenn 1994). We used chalk cylinders sealed on the sides with polyurethane, leaving an erosion surface that remained constant in area as the blocks dissolved (Sanford et al. 1994). Each chalk block was glued to a wire mesh backing so that they could be easily bolted to the substrate. Four blocks were deployed at identical low (0 m) tidal heights below the elevation of the algal canopy, separated by at least one meter at each site in June 1999 during spring tides. The mass of each chalk block was measured (± 0.01 g) before deployment and after four days of exposure was dried and masses remeasured.

To quantify differences among the study sites in the recruitment of benthic organisms with pelagic larval dispersal, we quantified annual barnacle recruitment at each study site in the 1-m and 3-m clearings and the

unmanipulated control plots. We used the annual spring recruitment of the northern acorn barnacle, *Semibalanus balanoides*, to examine within and among site variation in recruitment, since previous work has shown that recruitment variation in this species is representative of the other common benthic invertebrates in this system that have pelagic dispersal, i.e., the mussel *Mytilus edulis*, the periwinkle *Littorina littorea*, the green crab *Carcinus maenus* (Leonard et al. 1998). We quantified annual barnacle recruitment by counting metamorphosed barnacle recruits in the May photographs of the uncaged control quadrats at each site for 1999–2001. In cases where the control quadrats did not have enough bare space to estimate recruit density (i.e., when adult barnacle cover limited the access of juveniles from primary substrate space), nearby substrate with free space was haphazardly selected and photographed to estimate barnacle recruitment.

Variation in predation pressure by crabs at the study sites was determined by tethering 10 individual mussels (20–40 cm in length) at each site at mean low water (MLW) on bare rock surfaces and determining mortality over a single tide cycle (12 h). Mussels were tethered to the rock with a 5 cm length of nylon fishing line glued to the shell. This held the mussel in place long enough for it to attach to the rock by its own byssal threads. Tethered individuals were always placed more than one meter apart. While this technique surely overestimates the predation rate on mussels, it provides a reliable estimate of relative predation intensity among sites (see Leonard et al. [1998], [1999b] for discussion). Mussel mortality in these assays could be unambiguously attributed to crab predation because of the characteristic shell breaking patterns seen on the recovered shells (Elner 1978). We also directly observed crabs foraging on the rising tide, locating and crushing tethered mussels. Since the results of this experiment were similar to more extensive assays of predation, including both tethering and mark–recapture techniques, done earlier at nearby sites (Leonard et al. 1998), we did these assays only once.

STATISTICAL ANALYSES

Percent cover data from the alternate stable state experiment were analyzed with a three-way ANOVA that treated site type (high flow vs. low flow), clearing size (canopy, 1 m², 9 m²), and caging treatment (control, cage control, cage) as fixed effects. Analyses were conducted on arcsine square-root transformed data when necessary (Sokal and Rohlf 1981), and in all cases, transforming the data resulted in data that fit the assumptions of parametric statistics. Because we were interested in the final outcome of patch recovery, we only analyzed the final percent cover data, but still present the entire data set graphically to give readers a feel for the temporal course of patch recovery. Understory cover data from the consumer exclusion cages at the *Ascophyllum* canopy sites were analyzed for each

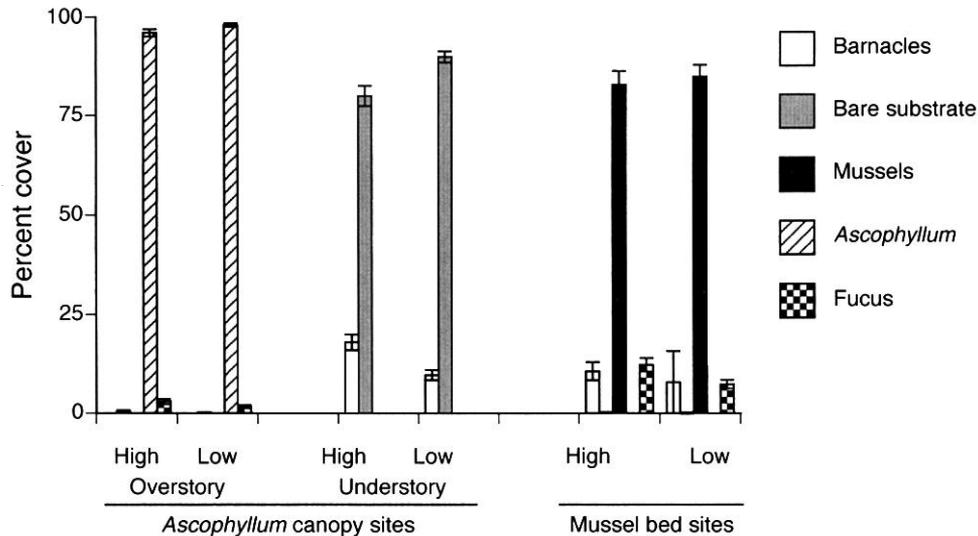


FIG. 3. Mean (± 1 SE) percent cover of sessile space holders at the eight mussel bed and eight *Ascophyllum* canopy sites used for the experiments. For all analyses on sessile species, the ANOVA revealed that only habitat type was significant, with no significant habitat type, or habitat type \times tidal elevation interaction: barnacles ($F_{1,220} = 29.95$, $P < 0.0001$), mussels ($F_{1,220} = 1006.94$, $P < 0.0001$); *Ascophyllum* ($F_{1,220} = 4942.34$, $P < 0.0001$). No significant effects were detected for percent cover of bare space ($P > 0.34$ in all cases). Understory sampling at the *Ascophyllum* canopy sites revealed that tidal elevation was significant for both the percent cover of barnacles ($F_{1,126} = 10.41$, $P = 0.0016$) and bare space ($F_{1,126} = 7.39$, $P = 0.008$).

species with a one-way ANOVA that considered clearing size as a fixed effect. Community composition data were analyzed with a two-way ANOVA that treated site type and tidal elevation as fixed effects. Understory data obtained at the *Ascophyllum* sites were analyzed with a one-way ANOVA that treated tidal elevation as a fixed effect. We analyzed the dissolution data with a one-way ANOVA that treated habitat type as a fixed effect. Barnacle recruitment data were analyzed with a two-way, repeated-measures ANOVA. Site type and clearing size were treated as fixed effects, and sampling year was considered a random, repeated effect. All statistical analyses were conducted with JMP software (Version 3.2.2, SAS Institute, Cary, North Carolina, USA). Any post hoc comparisons were performed using the linear contrast feature of JMP.

RESULTS

Quantification of study site characteristics

The abundance and distribution survey of sessile space-holding organisms illustrates the dramatic differences in the benthic communities among the study sites (Fig. 3). At *Ascophyllum* canopy sites, the *Ascophyllum* canopy covered $>95\%$ of the shoreline at both high and low tidal heights. The brown seaweed, *Fucus* spp., and unoccupied bare space accounted for the remaining space at the *Ascophyllum* canopy sites. The understory at *Ascophyllum* canopy sites was largely unoccupied bare space (Fig. 3). Over 80% of the rock surfaces under the canopy was bare, with 9.7% and 18% barnacle (*Semibalanus balanoides*) cover in the high and low canopy understory, respectively. In

sharp contrast to the large amount of bare space in the *Ascophyllum* canopy understory, bare space was extremely uncommon and not detected in our sampling at the mussel bed sites. At the mussel bed sites, at both high and low tidal heights, mussels occupied $>80\%$ of the available primary surface space with the rest of the space occupied by *Fucus* and barnacles.

Water movement over the study sites, measured by the dissolution of dental chalk blocks (Fig. 4) was over

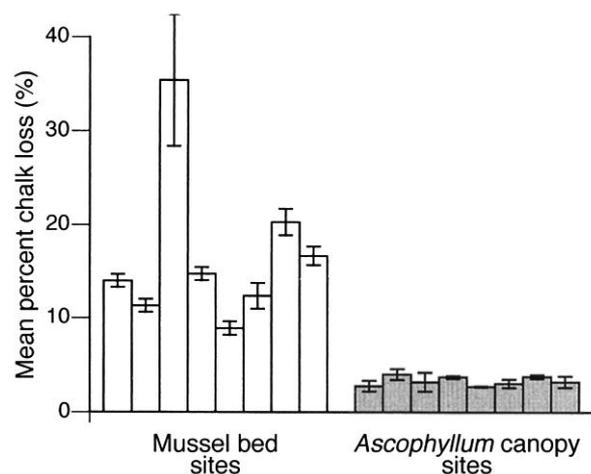


FIG. 4. Mean (± 1 SE) chalk block dissolution data from the eight mussel bed and eight *Ascophyllum* canopy sites used for our examination of disturbance-generated bare space recovery on the Damariscotta River. Percent loss of chalk block mass was significantly greater at the high-flow sites (ANOVA, $F_{1,58} = 57.42$, $P < 0.0001$). Blocks were deployed for four days; $N = 4$ blocks/site.

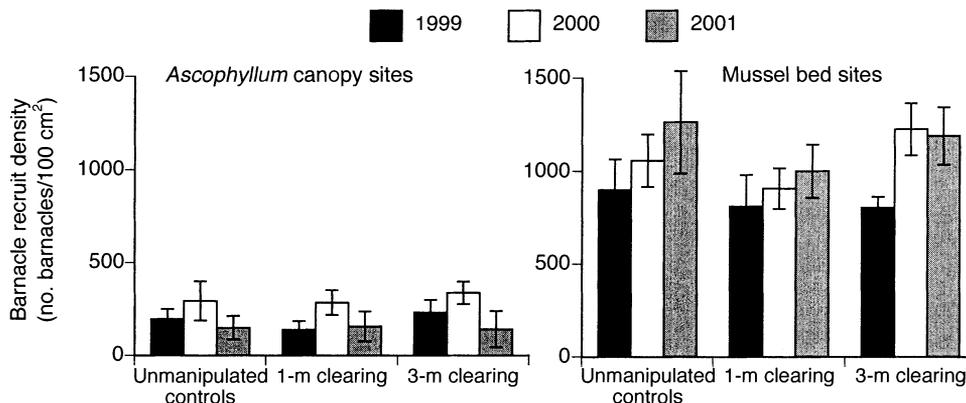


FIG. 5. Mean (± 1 SE) barnacle (*Semibalanus balanoides*) recruitment in unmanipulated control plots, 1-m clearings, and 3-m clearings at the mussel bed and *Ascophyllum* canopy sites during the three years of this study. Data were taken in May of each year in uncaged plots. Results of repeated-measures ANOVA revealed that barnacle recruitment was significantly greater at mussel bed vs. *Ascophyllum* sites ($F_{1,36} = 617.56$, $P < 0.0001$). In addition, a trend indicating a clearing-size effect on barnacle recruitment was detected ($F_{2,36} = 2.94$, $P = 0.066$). No habitat type \times clearing type interaction was detected ($F_{2,36} = 1.91$, $P = 0.162$). For interactions with sampling time, only the time \times habitat interaction was significant (Wilks' $\lambda = 0.76$, $F_{2,35} = 5.63$, $P = 0.008$). Thus, while barnacle recruitment was always greater at mussel bed vs. *Ascophyllum* canopy sites, the magnitude of this difference varied among years.

four times higher at the mussel bed sites than at the *Ascophyllum* canopy sites. In four days the blocks at the mussel bed site lost 15.5 ± 1.2 g, while the blocks from the *Ascophyllum* canopy sites lost only 3.9 ± 0.67 g.

Barnacle settlement showed strong variation among site types and some interannual variation (Fig. 5), but no significant variation among disturbance treatments or any significant interactions. Barnacle recruitment was four times higher at the mussel bed sites than at the *Ascophyllum* canopy sites. Other recruitment patterns that were expected, like higher barnacle recruitment in large clearings than in small clearings and unmanipulated plots due to grazing hallos (Petraitis and Dudgeon 1999), were not apparent in the data. We suspect that this was largely due to the intense predation pressure of small barnacles at our study sites by highly mobile crabs (Leonard et al. 1999b). There was a marginally significant patch size effect, but this was very small relative to habitat type effects.

Predation assays at the study sites showed that crab predation was two times greater at the *Ascophyllum* canopy sites than at the mussel bed sites (ANOVA, $F_{1,14} = 9.03$, $P = 0.0094$). At *Ascophyllum* canopy sites, $77.5 \pm 9.59\%$ of the tethered mussels were consumed by crabs in a single tidal cycle, while at the mussel bed sites $31.5 \pm 11.93\%$ of the tethered mussels were eaten. Clearly, predation by crabs, however, is high at both mussel bed and *Ascophyllum* canopy sites.

Recovery of experimental bare patches

Results of the patch recovery experiment have been striking (Figs. 6 and 7, Table 1). Without excluding consumers, very little recovery of the plots to their initial condition has occurred in three years. At sites initially dominated by either an *Ascophyllum* canopy or mussel beds, control quadrats in large and small

clearings and unmanipulated habitats have been colonized almost exclusively by barnacles. After three years, surfaces in control and cage control quadrats with consumers present were covered with only barnacles and bare space, with no conspicuous signs of recovery to their original condition. Removing consumers, however, had a dramatic effect on recovery. At mussel bed sites, in the absence of consumers, mussels rapidly recolonized plots in all disturbance treatments. By the end of the second field season, consumer exclusion cages at mussel bed sites were nearly all stainless steel mesh "baskets of mussel recruits." By the third year all caged quadrats at mussel bed sites, regardless of clearing size, were entirely dominated by dense mussel cover (Fig. 6).

Removing consumers had equally dramatic effects at *Ascophyllum* canopy sites (Fig. 7). At these sites, removing consumers lead to rapid recolonization of brown seaweeds, but the species identity of the algal recruits varied markedly among treatments. In both large and small canopy removal areas, after two field seasons removing consumers lead to cages entirely carpeted with *Fucus* recruits. As with the cages at the mussel bed sites, there was nothing subtle about this result, caged substrate in clearings in *Ascophyllum* canopies rapidly became dense *Fucus* monocultures in a habitat where *Fucus* was otherwise not common (Fig. 8). Cages placed in undisturbed *Ascophyllum* canopies, however, responded very differently. Excluding consumers under the *Ascophyllum* canopy lead to dramatic *Ascophyllum* recruitment. After two field seasons, *Ascophyllum* recruits dominated grazer-free habitats under the canopy, in spite of earlier reports that *Ascophyllum* is a weak recruiter (Vadas et al. 1990).

Closer examination of the recruitment of juvenile furoids and mussels into uncaged control quadrats was

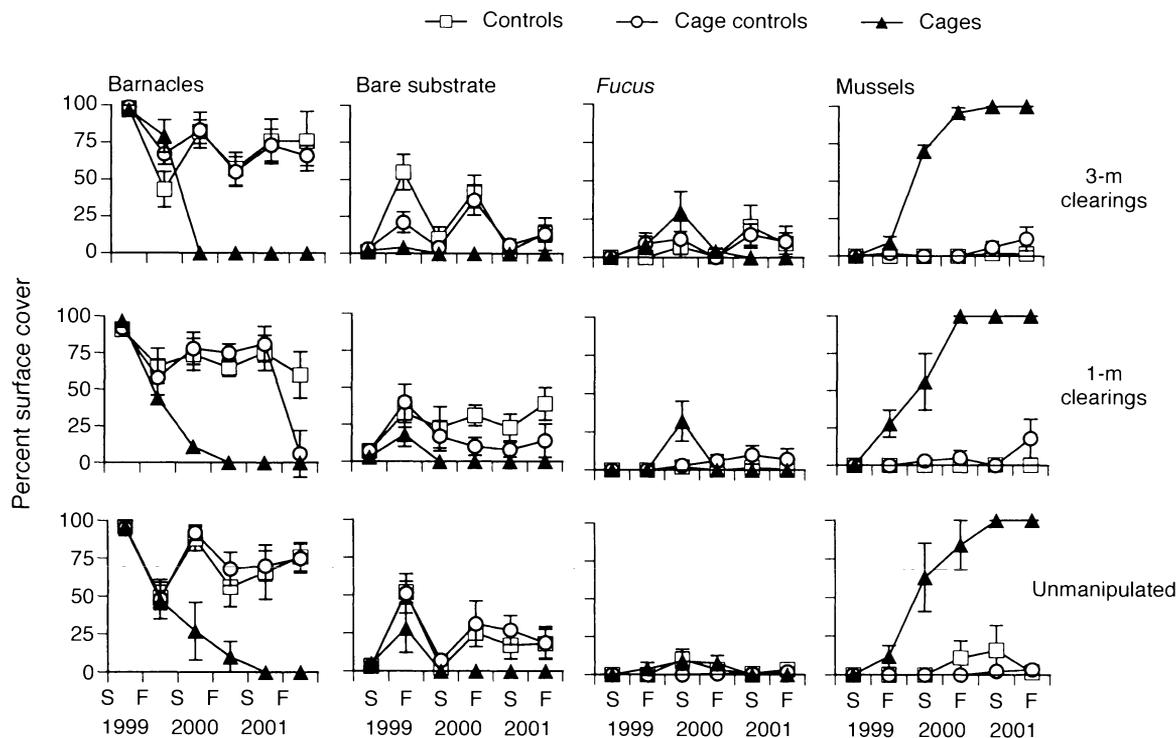


FIG. 6. Results of the disturbance-generated bare patch recovery experiment at mussel bed sites on the Damariscotta River. All data are means \pm 1 SE. Error bars are only shown when they are larger than the symbols. Data are given for spring and fall of 1999, 2000, and 2001.

particularly telling. Whereas no furoid or mussel recruits were observed in the first year of the experiment, by the end of the second year (September 2000), a modest number of both furoid and mussel recruits were seen in control (control and cage control) quadrats. While recruitment of these space holders was relatively rare, almost all recruits were found in conspicuous cracks or crevices, likely natural refuges from consumers. By the end of the second year of the experiment (September 2000), of a total of 53 furoid recruits found in the 48 uncaged control and cage control plots at sites initially dominated by an *Ascophyllum* canopy, 100% were found in unambiguous crevices, almost exclusively associated with the holes we had drilled in the substrate to mark quadrat corners. Similarly, in uncaged plots at sites that initially were mussel beds ($n = 48$), a total of 68 juvenile mussel recruits were found, 76% were found in obvious crevices. By the end of the third year of patch recovery (September 2001), furoid and mussel recruits were not as tightly associated with cracks and crevices. In control quadrats at the *Ascophyllum* canopy sites, a total of 130 furoid recruits were found, with 81.5% (106) found in crevices. In control quadrats at the mussel beds sites, of a total of 85 individual mussels counted, only 22% (19) were unambiguously associated with cracks and crevices. These data strongly suggest that natural recovery of disturbance patches in this system is dependent on substrate

heterogeneity providing consumer refuges for recruits (see also Lubchenco [1983]).

The understory community that developed at the *Ascophyllum* canopy sites where consumers were excluded had high densities of *Ascophyllum* and mussel recruits (Fig. 9). *Ascophyllum* recruits were particularly abundant in unmanipulated plots under intact *Ascophyllum* canopies. Without consumers under an intact canopy, >75% of the rock surface was covered with *Ascophyllum* recruits, typically at densities >25 recruits/cm². *Ascophyllum* recruits were also common in furoid canopies that developed in the absence of consumers in the 1-m² and 9-m² clearings. *Ascophyllum* recruit cover in caged areas of the small and large clearings (28% and 32% cover of recruits, respectively), however, was less than half that found under the canopy. More surprising was the recruitment of mussels to the *Ascophyllum* canopy sites when consumers were removed. In the 1-m² and 9-m² clearings, 25% and 20%, respectively, of the understory of grazer-free plots were covered with juvenile mussels. Mussel recruits were also found in the grazer-free plots under intact canopies, but at much lower densities (5% cover).

DISCUSSION

Our results suggest that intertidal mussel beds and *Ascophyllum* canopies on tidal rivers in the Gulf of Maine do not represent alternate community stable

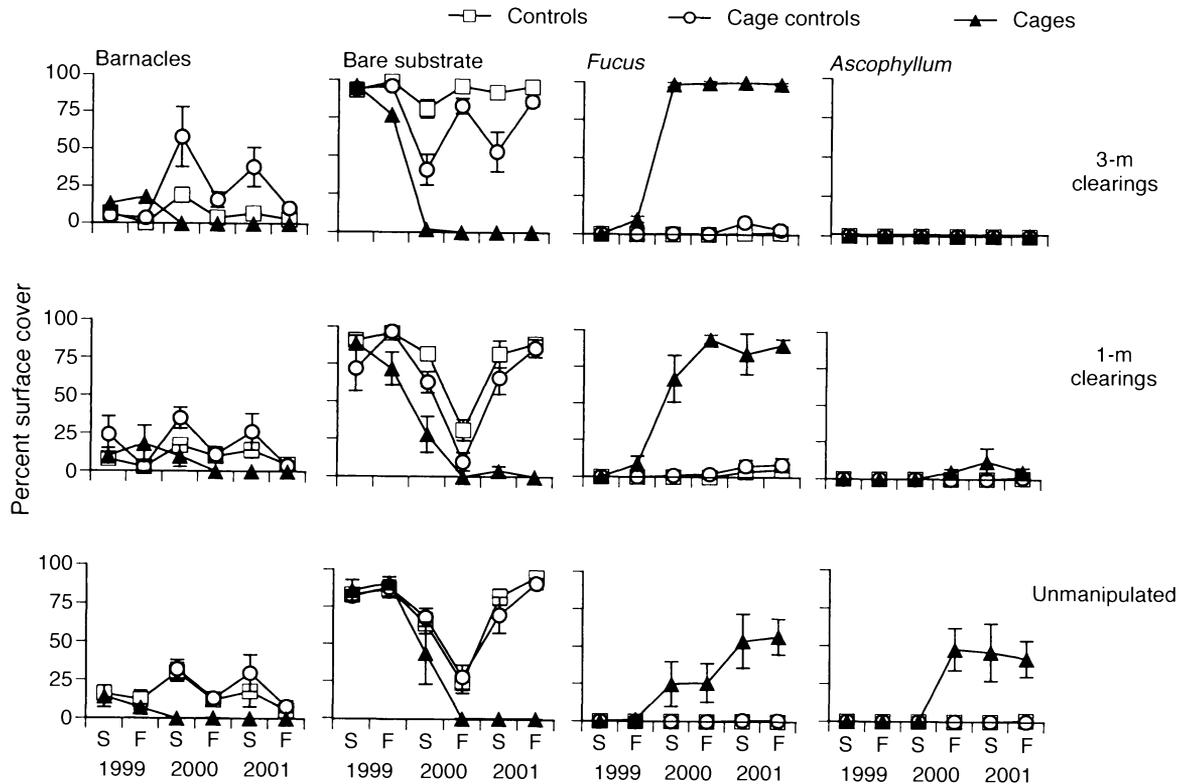


FIG. 7. Results of the disturbance-generated bare patch recovery experiment at *Ascophyllum* canopy sites on the Damariscotta River. All data are means \pm 1 SE. Error bars are only shown when they are larger than the symbols. Data are given for spring and fall of 1999, 2000, and 2001.

states. Instead we found compelling evidence of a high degree of community determinism controlled by intense consumer pressure and recruit supply patterns mediated by water flow.

Consumer control of alternate community states

Although our experiments were designed to explicitly test the hypothesis that mussel beds and seaweed canopies can represent alternate community stable states, our results suggest that these distinct community types are highly deterministic and that consumers powerfully control patch recovery and community structure in both of these community states. In both mussel bed and *Ascophyllum* canopy habitats, and in large and

small clearings and unmanipulated plots, very little patch recovery occurred in three years in the presence of consumers. After three full years of recovery, quadrats exposed to consumers at both mussel bed and seaweed canopy sites were dominated by barnacles and bare space, respectively, with little evidence of recovery to either of the initial starting states. Moreover, at both mussel bed and seaweed canopy sites, the size of the disturbance plot had surprisingly little effect on community development. This is not to say that consumer pressure, larval settlement, or physical stresses did not vary with plot size and influence the mortality patterns of these organisms (as in Petraitis and Dudgeon [1999]), but that these effects have not cumula-

TABLE 1. Summary of *P* values generated by a three-way ANOVA examining the effect habitat type (mussel bed vs. *Ascophyllum* canopy), patch size (canopy, 1-m, 3-m), and caging treatment (cage, cage control, control) on percent cover of mussels (*Mytilus edulis*), *Ascophyllum nodosum*, *Fucus* sp., and bare space.

Dependent variable, percent cover of:	Habitat (H)	Patch size (P)	Caging treatment (C)	H \times P	H \times C	P \times C	H \times P \times C
Mussels	<0.0001	0.9411	<0.0001	0.9252	<0.0001	0.2548	0.1923
Barnacles	<0.0001	0.2691	<0.0001	0.4542	<0.0001	0.8336	0.8987
<i>Ascophyllum</i>	0.0051	0.0061	0.0011	0.0061	0.0011	0.0005	0.0005
<i>Fucus</i>	<0.0001	0.0001	<0.0001	0.0041	<0.0001	0.0008	<0.0001
Bare space	<0.0001	0.5230	<0.0001	0.1358	<0.0001	0.7866	0.3684

Note: Values in bold type indicate results of high significance.

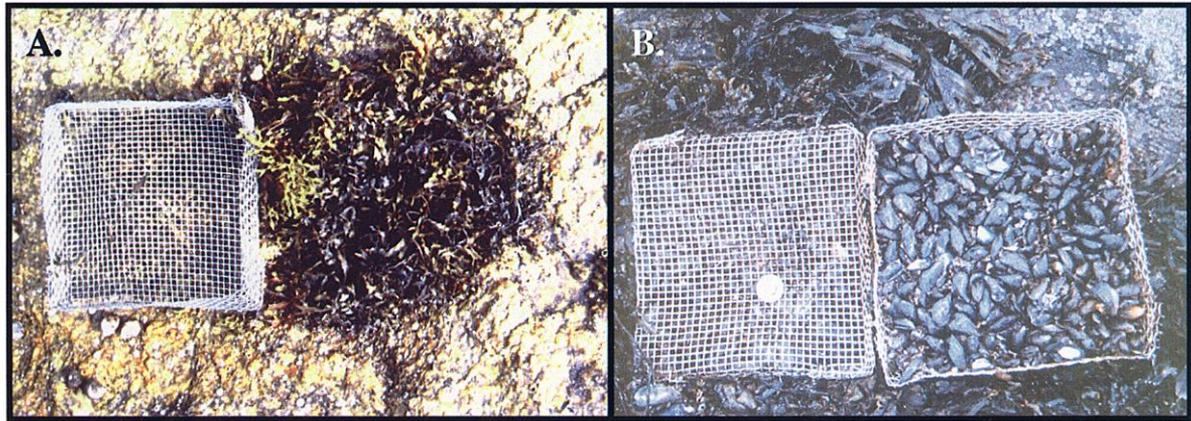


FIG. 8. Representative examples of the effect of removing consumers on bare patch recovery: (A) a dense *Fucus* canopy developing on otherwise bare rock in a 3-m² clearing at an *Ascophyllum* site; (B) a consumer exclusion cage at a mussel bed site full of mussel recruits.

tively influenced the trajectory or outcome of patch recovery. We suspect that the lack of pronounced recruitment patterns with patch size is likely due to the intense predation pressure of small barnacles and all other small animals at our study sites by highly mobile crabs (Leonard et al. 1999b). In more wave-exposed intertidal habitats where mobile consumers such as crabs are less abundant (Menge 1976) and less-successful consumers (Weissburg and Zimmer-Faust 1993), slow moving consumers such as snails are limited from foraging on open surfaces away from refuges due to physical stress (Menge 1978). In these systems this can lead to recruitment grazing halos around large bare patches and conspicuous differences in the cover of sessile organisms with patch size (Menge 1978, Petraitis and Dudgeon 1999).

The strength of consumer control in the recovery of our bare patches was striking. At mussel bed sites, mussel recruitment was seen in the first year of the experiment, but only when predators were excluded. By the end of the second year, mussel cover was >80% in all caged plots, and by the third year of the experiment a dense bed of mussels was found in every caged quadrat at mussel bed sites, independent of disturbance size treatment. When predators were present in control and cage control quadrats, mussels only began to appear (<10% cover) after three years of recovery. This high degree of consumer control was also seen at the *Ascophyllum* canopy sites. At these sites, even after three years, >90% of the uncaged quadrats were bare rock. By the end of the second year, however, algal cover was 100% in all clearing types when consumers were removed. Recovery of the algal canopy, however, was highly dependent on disturbance treatment. In both the 9-m² and 1-m² clearings, when consumers were excluded, *Fucus* cover of the substrate reached close to 100% by the end of the second year of the experiment. In contrast, in caged quadrats under unmanipulated *Ascophyllum* canopies, *Ascophyllum* recruitment

was intense, and by the end of the second year of the experiment *Ascophyllum* cover was ~50%, with the remaining space occupied by *Fucus*. This is consistent with work showing that *Ascophyllum* dispersal is largely limited to immediately under adult plants (Vadas et al. 1990, Dudgeon and Petraitis 2001). In three years of monitoring the mussel bed site clearings, we have not seen a single *Ascophyllum* recruit, which is also consistent with the low dispersal potential of *Ascophyllum*.

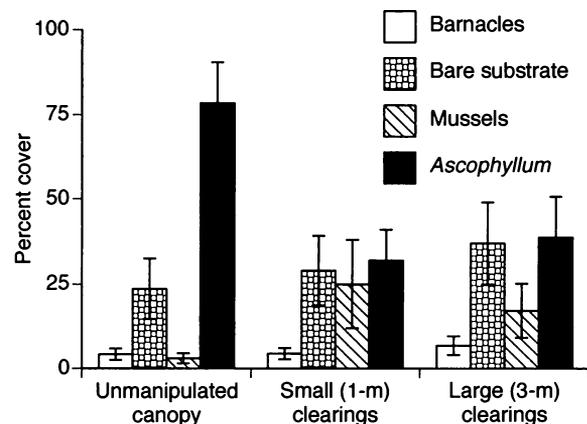


FIG. 9. Mean (± 1 SE) percent cover of understory organisms in consumer exclusion cages at the *Ascophyllum* canopy sites in September 2001, after three years of recovery. ANOVA revealed that for mussels ($F_{2,20} = 1.27$, $P = 0.302$), barnacles ($F_{2,20} = 0.29$, $P = 0.749$), and bare space ($F_{2,20} = 1.67$, $P = 0.214$) there was no significant effect of clearing size on percent cover. In contrast, there was a significant effect of clearing size on understory *Ascophyllum* percent cover ($F_{2,20} = 4.98$, $P = 0.018$). Post hoc linear contrasts revealed that percent cover of *Ascophyllum* was significantly greater in canopy vs. 1-m clearings ($P = 0.007$) and canopy vs. 3-m clearings ($P = 0.026$). There was no significant difference in *Ascophyllum* percent cover between 1-m and 3-m clearings ($P = 0.54$).

We should point out that these caging results appear to be highly replicable. Since doing the initial set of experiments described here, we have begun other experiments exploring the mechanisms underlying the initial results. To date we have found that caging substrate in either mussel beds or algal canopies always appears to result in a rapid return to the original state (M. D. Bertness, G. C. Trussell, P. J. Ewanchuk, and B. R. Silliman, *unpublished data*).

The role of predator refugia in recovery

The intense consumer control of the recovery of both mussel beds and *Ascophyllum* canopies that we have documented raises the question of how natural recovery occurs in these habitats. While temporal and spatial variation in the densities of snail and crab consumers is a possibility, one of the most conspicuous features of these communities is the ubiquity of snail and crab consumers (Leonard et al. 1998). The most important consumers in the system, the grazing snail, *Littorina littorea*, and the omnivorous green crab, *Carcinus maenus*, have high population densities that do not vary conspicuously from year to year or spatially on the spatial scale of our experiments. Physical refuges from consumers, however, such as cracks and crevices are common on rocky shores of the Gulf of Maine and could be critical in the typical recovery of intertidal landscapes from large disturbances. This was seen in our experiments when virtually all of the mussel and furoid recruits that initially colonized uncaged quadrats were found in conspicuous cracks and crevices. While increased larval recruitment to cracks and crevices could also be attributed to passive larval settlement (Butman 1987), the almost total reliance of successful recruits to these rock surface features and the rapid recruitment of both seaweeds and mussels to smooth surfaces when consumers were excluded, strongly suggests that consumer refugia were largely responsible for this result (Lubchenco 1983). The reliance of larval recruitment of mussels and *Ascophyllum* on cracks and crevices could also in part explain the slow recovery evident in our photographic monitoring quadrats. Our monitoring quadrats were intentionally placed on relatively smooth rock surfaces to make analyzing the photographs easier and more accurate. Large cracks and crevices were avoided, and this may have led to us underestimating the rate of recovery. Since the recovery of the 100-cm² treatment quadrats was generally similar to recovery of substrate in the entire plot, however, this does not appear to have been a very large bias. We have just set up a series of experiments at the sites with artificial substrates with and without heterogeneous surfaces to test the hypothesis that substrate heterogeneity stimulates and accelerates patch recovery.

Once mussels and furoid algae successfully recruit to cracks and crevices, the recruits themselves may provide refuge for further recruitment. The surface het-

erogeneity of dense mussel aggregations (Bertness and Grosholz 1985, Witman 1985) and algal holdfasts (Moreno 1995) are both known to potentially provide refuges from consumers, particularly to new recruits and vulnerable juveniles. This type of positive feedback could lead to cracks and crevices facilitating initial recruitment, with the recruits then facilitating further recruitment success. This could result in mussel beds and seaweed canopies expanding through positive feedback (sensu Wilson and Agnew 1992) out of natural cracks and crevices on to smooth rock surfaces.

Understory development: evidence for a trophic cascade?

Although our results show that consumers control the recovery of mussel beds and *Ascophyllum* canopies, the development of the understory community in caged plots at algal canopy sites suggests that in the absence of consumers all habitats in this tidal river system could become mussel beds. After three years, quadrats at algal canopy sites exposed to consumers were still primarily bare substrate (Fig. 7); whereas, when consumers were excluded, not only did a dense furoid canopy develop, but an understory community also emerged. While the natural understory habitat at these sites is dominated by bare space, without consumers the understory substrate is covered with mussels and *Ascophyllum* recruits (Fig. 8). *Ascophyllum* recruits densely cover the substrate in quadrats under the canopy, as predicted by the extremely localized dispersal of *Ascophyllum* propagules (Dudgeon and Petraitis 2001). *Ascophyllum* recruit densities under these cages were often >25 individuals/cm² (M. D. Bertness, G. C. Trussell, P. J. Ewanchuk, and B. R. Silliman, *personal observations*). The high cover and density of *Ascophyllum* recruits in the unmanipulated canopy plot cages may exploitatively usurp space and limit the recruitment of other sessile space holders like barnacles and mussels. This may explain the relative lack of mussels in the understory of caged canopy treatments in comparison to the mussel cover in the understory of small and large clearings after three years. The relatively high mussel recruitment to the understory of cleared plots when consumers were removed was striking. In both small and large canopy clearings, when consumers were excluded, mussels recruited to the algal canopy sites and covered 25% and 17%, respectively, of the understory space after three years (Fig. 8). This indicates that in the absence of consumers, even at low-flow sites with a low flux of potential recruits, mussels recruit to areas normally dominated by an *Ascophyllum* canopy. This suggests that the dominance of *Ascophyllum* beds in low-flow habitats may be the consequence of a trophic cascade, where intense snail and crab consumption along with low larval delivery leads to shorelines dominated by long-lived unpalatable seaweeds without mussels. We are continuing to maintain and monitor these caged plots to see if mussels ultimately dominate

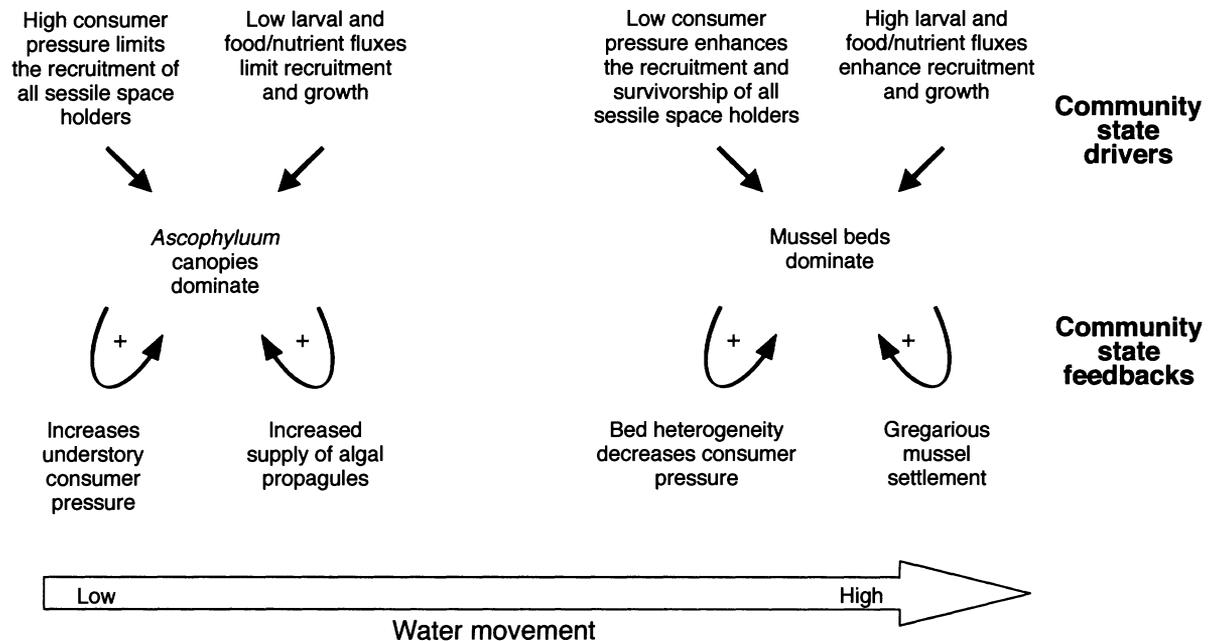


FIG. 10. Conceptual model of the deterministic generation and maintenance of *Ascophyllum* canopy-mussel bed alternate community states on Gulf of Maine rocky shores. At low-flow sites, intense consumer pressure by snails and crabs leads to habitats dominated by an unpalatable seaweed canopy, whereas at high-flow sites, low consumer pressure and high recruit supply lead to mussel bed habitats. Positive feedbacks in each community type lead to its expansion and persistence. If stochastically determined alternate stable states occur in this system, they are predicted to occur at intermediate-flow sites where consumer control and the predictability of larval recruitment are relaxed.

these consumer-free habitats and displace the *Ascophyllum* recruits.

Consumer-mediated alternate community states

Our results suggest that instead of representing alternate stable states mediated by stochastic events, mussel beds and *Ascophyllum* beds in Gulf of Maine rocky intertidal habitats are deterministic community types under the control of consumers and larval delivery (Fig. 10). Consumer-controlled alternate community states differ fundamentally from alternate community stable states, since community stable states are stochastically determined, whereas consumer mediated alternate community states are maintained by consumers (Connell and Sousa 1983). We suggest that mussel beds and *Ascophyllum* canopies on tidal rivers in the Gulf of Maine are best characterized as consumer-mediated alternate community states. In habitats with high water movement, consumer control of intertidal communities is reduced because consumer mobility (Menge 1978) and the ability to locate prey due to the dilution of chemical signals (Weissburg and Zimmer-Faust 1993) are severely limited. This leads to low consumer effectiveness and impact. At the same time, high water movement, by increasing larval and nutrient fluxes (Gaines and Bertness 1993), increases the recruitment and growth of benthic organisms (Sanford et al. 1994, Leonard et al. 1998), leading to high population densities of benthic space holders. As a consequence of

low consumer pressure and high recruitment, mussel beds dominate these habitats.

In habitats with little water movement, intense consumer pressure by snails and crabs leads to most of the primary rock substrate remaining bare, with the dominant feature of the habitat being a monospecific canopy of the unpalatable, long-lived seaweed, *Ascophyllum*. *Ascophyllum* dominates these habitats because it is relatively immune to consumer damage as an adult, and since once established it can live for over a decade (Steneck and Dethier 1994). The relatively low density of adult plants (~ 50 individuals/m²) in a typical *Ascophyllum* canopy, coupled with enormous localized reproductive output (Dudgeon and Petraitis 2001), means that even in the face of massive recruit mortality, the survival of just a few recruits in consumer refuge microhabitats annually could continuously replace the canopy. When we excluded grazers under the canopy we commonly saw 20–50 *Ascophyllum* recruits per square centimeter. Since these recruits were only visible when they exceeded one centimeter in height, this is likely a serious underestimate of initial recruit numbers. Nonetheless, this translates to a conservative estimate of potentially 200 000–500 000 recruits-m⁻²·yr⁻¹. Less than 0.001% of these potential recruits would have to survive annually to entirely replace the canopy. Cracks, crevices, and biotic structures like the edges of holdfasts and barnacles are likely refuges for fucoid recruits.

Once established, both *Ascophyllum* canopies and mussel beds generate positive feedbacks that can enhance their persistence, expansion, and stability. Once in place, *Ascophyllum* canopies increase the supply of *Ascophyllum* propagules (Dudgeon and Petraitis 2001), thus increasing the chances that new plants will become established. Furthermore, by providing refuge from physical stresses, such as heat and desiccation (Bertness et al. 1999), *Ascophyllum* canopies increase consumer pressure under the canopy, thus limiting the success of other space holders, like mussels and barnacles. In mussel beds, gregarious settlement and postsettlement movement of juvenile mussels lead to mussel beds increasing in size. In addition, dense beds of mussels protect juvenile mussels from consumers (Bertness and Grosholz 1985) and buffer individuals from thermal/desiccation (Bertness and Leonard 1997) and wave stresses (Denny et al. 1985). The strength of these feedbacks is likely responsible for how discrete and distinctive these disparate community types are on Maine rocky shores.

Do alternate community stable states exist on Gulf of Maine rocky shores?

Our results suggest that the occurrence of mussel beds and algal canopies on rocky shores in the Gulf of Maine is strongly deterministic and under consumer control. Over time our results suggest that large disturbance patches in mussel beds and *Ascophyllum* canopies will return to their initial states, aided by spatial refuges from consumers. Does this mean that stochastic alternate community stable states hypothesized by Petraitis and his colleagues (Petraitis and Dudgeon 1999, Petraitis and Latham 1999) do not exist in these habitats? Our results indicate that intertidal mussel beds and *Ascophyllum* canopies are more accurately viewed as deterministic community states controlled by consumers, but also shed light on where mussel beds and algal canopies may be alternate stable states.

The strong level of consumer control that we have documented in the tidal river system suggests that if stochastic mussel bed–*Ascophyllum* canopy alternate states occur, they would occur in a much smaller subset of rocky intertidal habitats exposed to intermediate tidal flows that would lead to intermediate consumer intensity and recruitment levels. Intermediate consumer levels would reduce the intensity of consumer control in these habitats, whereas intermediate recruitment rates would reduce the predictable supply of recruits to recovering bare patches. With both consumer and recruitment predictability reduced, stochastic processes could become more important. There is no obvious evidence that intermediate-flow habitats that could have alternate stable states indeed occur along the Damariscotta River. This is not particularly surprising, given that positive feedbacks appear to strongly act to maintain and expand mussel beds (through gregarious settlement) and *Ascophyllum* canopies (by massive

propagule production) once they are established (Fig. 10). In selecting study sites for this work we avoided extreme low-flow habitats in favor of more intermediate-flow habitats to increase the likelihood of our experiments detecting potential alternate states. The strong and extremely spatially predictable decoupling in tidal river systems between high larval recruitment and the growth of most filter feeders and algae, on the one hand, and reduced consumer pressure, on the other hand (Leonard et al. 1998), may restrict the habitats where alternate stable states are possible to a very limited subset of habitats. Within some *Ascophyllum* canopy habitats, usually associated with the mouths of small embayments or tidal restrictions that can locally accelerate flows, *Ascophyllum* canopies in the intertidal occasionally give way in the low intertidal to mussel beds typically associated with cracks and crevices. While this type of habitat is rare, it may be the habitat where mussel bed–*Ascophyllum* canopy alternate states occur.

Conditions where mussel bed–*Ascophyllum* canopy alternate states are possible may be more common in other Gulf of Maine habitats where water flow patterns, consumer pressure, and recruitment intensity are not as spatially predictable and tightly linked. This may be the case in the coastal bays and wave-sheltered shores studied by Petraitis and Dudgeon (1999). In these habitats, although mussel beds and *Ascophyllum* canopies superficially look like these habitats in tidal rivers, consumer densities, larval supply, and the flow patterns that can modulate the intensities of consumer pressure and larval fluxes may be less predictable. In comparison to tidal river systems, reduced consumer intensity and more episodic recruitment would seem to be necessary ingredients for stochastic alternate community stable states to be more common.

Our results also call into question proposed examples of alternate community stable states in other ecosystems. In virtually all other ecosystems where alternate community stable states have been proposed, they have been only supported by indirect, inferential mechanistic evidence, rather than by direct experimental proof (Connell and Sousa 1983). The advantage of examining the alternate stable state hypothesis in a rocky intertidal habitat is that it is relatively easy to experimentally test the idea at ecologically realistic spatial and temporal scales. This is not really the case in coral reef (Knowlton 1992, Hughes 1994), subtidal rocky bottoms (Simenstad et al. 1978, Johnson and Mann 1988, Barkai and Branch 1988), temperate forest (Petraitis and Latham 1999), or tropical grassland (Dublin et al. 1990) ecosystems where alternate community stable states have been proposed. In these systems, either the foundation species that create and define the habitat states are longer lived than the ecologists who study them (e.g., coral reefs and forest trees), making the direct critical evaluation of state shifts and stability virtually impossible, or the spatial scale that the community

states operate on is too large for practical experimentation. As a result, alternate stable states in these communities are based on indirect evidence consistent with an alternate stable state hypothesis, rather than direct experimental evidence. Unfortunately, without direct experimental testing, it is impossible to evaluate the relative importance of indirect mechanistic evidence in the generation and maintenance of alternate community states (Connell and Sousa 1983). As we have found for algal canopy–mussel bed alternate community states on rocky shores in the Gulf of Maine, coral reef, tropical grassland, and subtidal rocky bottom alternate community states may also be examples of highly deterministic consumer regulated alternate community states, rather than stochastically dictated alternate stable states. In each of these proposed examples of alternate community stable states, consumers play a major role in maintaining proposed community states, and the long-term maintenance and stability of these community states have not been experimentally examined.

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