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CONSUMER-CONTROLLED COMMUNITY STATES ON GULF OF MAINE ROCKY SHORES

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Abstract. Mussel beds and algal canopies on Gulf of Maine (USA) rocky shores have been hypothesized to represent stochastically determined community states, but we recently found that they were highly deterministic, consumer-controlled states in a tidal river. Mussel beds dominated high-flow habitats with high larval delivery and low consumer pressure, whereas algal canopies dominated low-flow habitats with high consumer pressure. In this paper we examine the alternative-community-state hypothesis on rocky shores on the open coast of Maine. We hypothesized that community states would be less deterministic due to reduced consumer pressure and more stochastic flow patterns.

At 10 mussel-bed and 10 seaweed-canopy sites on the open coast of central Maine, we created 9-m^2 and 1-m^2 clearings and an unmanipulated control area, each containing control (no caging), caged, and cage-control quadrats. Independent of disturbance patch size, mussel beds and seaweed canopies rapidly began to return to their original community type in the absence of consumers (crabs and snails). With consumers present, recovery of the original communities did occur, but at a much slower pace.

Our results suggest that mussel beds and algal canopies in the Gulf of Maine are deterministic consumer-controlled states, rather than being stochastically determined. If stochastic alternative community states exist in this system, they occur in a very restricted subset of habitats where the strong consumer control and determinism we have found in both tidal river and open coast habitats are relaxed.

Key words: alternative community states; Ascophyllum nodosum; *community ecology; consumer control of community pattern; disturbance theory; Gulf of Maine (USA) rocky shores;* Mytilus edulis; *predation; rocky intertidal; secondary succession; tidal-river cf. open-coast habitats.*

INTRODUCTION

The idea that natural communities can represent stochastically determined alternative states is important for our understanding of the dynamics and conservation of natural communities (Petraitis and Latham 1999). The alternative-community-state hypothesis proposes that communities can exist in more than one stable state, and that once established, can persist indefinitely over more than one generation of the organisms making up the community (Lewontin 1969, Holling 1973, Sutherland 1974, Connell and Sousa 1983). The community that dominates a habitat following a disturbance is proposed to be stochastic, the product of propagule availability when the space was made available, and is maintained by positive feedbacks (Wilson and Agnew 1992). Since being described, alternative stable states have been commonly invoked to explain community dynamics in a wide range of marine, freshwater, and terrestrial habitats, but generally have not been rigor-

ously tested (see Bertness et al. [2002] for examples and discussion).

Petraitis and colleagues (Petraitis and Latham 1999, Petraitis and Dudgeon 1999) have suggested that *Mytilus edulis* mussel beds and *Ascophyllum nodosum* (hereafter referred to by generic name only) seaweed canopies on rocky shores in the Gulf of Maine (USA) can represent alternative community stable states or disturbance patch mosaics dominated by either seaweed or mussel communities. They proposed that the community occurring at a given site is stochastic in origin 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, while smaller disturbances are dominated by *Ascophyllum* canopies having limited dispersal. Positive feedbacks were postulated to maintain these two communities. We recently tested the *Ascophyllum*-canopy/mussel-bed alternative-community-stable-state hypothesis on a tidal river in central Maine (Bertness et al. 2002). We found no evidence for stochastic alternative states. Instead we found that mussel beds and seaweed canopies rapidly returned to their original community type, but only in the absence of consumers (crabs and snails). When consumers were present, neither community showed significant signs of recovery, even after three

years. Thus, we found that in tidal-river habitats, mussel-bed and *Ascophyllum*-canopy habitats were highly deterministic alternative community states under strong top-down control.

Why did our conclusions differ from those of Petraitis and colleagues (Petraitis and Latham 1999, Petraitis and Dudgeon 1999)? Although we both worked in Gulf of Maine rocky intertidal habitats, our experiments were conducted in very different environments. We tested the *Ascophyllum* canopy/mussel bed alternative-community-state hypothesis in a tidal-river system because *Ascophyllum* canopies and mussel beds are very discrete habitats in this system, cover virtually all hard-substrate, middle-intertidal habitats, and often abut each other (Bertness et al. 2002). In contrast, Petraitis and colleagues (Petraitis and Latham 1999, Petraitis and Dudgeon 1999) worked in coastal, wave-protected bays. While rocky shorelines in tidal rivers and coastal habitats in the Gulf of Maine are both characterized by mussel beds and *Ascophyllum* canopies, they differ in a number of respects that could influence whether or not community states are stochastic or deterministic. In particular, predation pressure is known to be higher in wave-protected habitats than in wave-exposed habitats (Menge 1976, 1978). This suggests that the strong consumer control we found on community structure in the river system could be a consequence of working in this system. On tidal rivers in Maine, predation pressure by green crabs (*Carcinus maenas*) is particularly intense. Green crab predation on tethered juvenile mussels in intertidal habitats in the tidal river is extremely high, ranging from 30 to 95% per day (Leonard et al. 1998, Bertness et al. 2002). In addition, densities of grazing snails (*Littorina littorea*) are also much higher in tidal rivers than in coastal habitats. On the Damariscotta River where we did our work, snail densities of 200–400 individuals/m² are common, whereas in nearby open coast habitats, snail densities are rarely as high. Intense consumer pressure in tidal-river habitats may render the stochastic recruitment events postulated to drive the alternative states of little consequence.

A second difference between tidal-river and coastal habitats is spatial predictability of flow. In tidal rivers the spatial variation in flow is extremely predictable, because flow is almost exclusively tidally driven. In coastal habitats where the flow experienced by shoreline organisms is much more complex and driven by tides, currents, and local weather conditions, spatial variation in flow patterns is much less spatially predictable. Since local flow conditions can play a leading role in dictating larval supply patterns (Gaines and Bertness 1993, Sanford et al. 1994) and can dictate the effectiveness of consumers and thus control consumer pressure (Weissburg and Zimmer-Faust 1993), differences in the spatial predictability of flow could influence how deterministic communities are. Thus, our finding of strongly deterministic, consumer-controlled

communities in tidal river systems may not apply to coastal habitats with reduced consumer pressure and less spatially predictable water movement.

In this paper we present the results of an experiment to test the hypothesis that *Ascophyllum* canopies and mussel beds represent stochastic alternative community states in coastal habitats in the Gulf of Maine.

METHODS

Our study was conducted at several sites distributed across two well-studied rocky promontories (Chamberlain and Pemaquid Point) on the open coast of central Maine, USA (see Menge 1976, 1978, Bertness et al. 1999*a*). This area is representative of coastal rocky shores in the Gulf of Maine and is dominated by mussel (*Mytilus edulis*) beds and *Ascophyllum* canopies that are often in close proximity to one another. Exposed headlands are usually dominated by mussel beds, often intermixed with heavy barnacle and fucoid algal cover. Nearby wave-protected habitats, in contrast, are typically characterized by *Ascophyllum* canopies with bare space dominating understory rock surfaces. Spatial segregation between mussel-bed and *Ascophyllum*-canopy habitats is as striking as in the tidal-river habitats where we did our initial experiments.

To test the alternative-community-state hypothesis in this system, we performed the same experiment that we conducted in the tidal river (Bertness et al. 2002). In February 2001 we established 10 study sites in mussel-dominated habitats and 10 study sites in *Ascophyllum* canopy-dominated habitats. Sites were separated by >20 meters. At the same intermediate tidal elevation at each site, we cleared one 3 × 3 m (9 m²) and one 1 × 1 m (1 m²) area of all plants and sessile animals. In the clearings, all organisms were entirely removed from the substrate with flat-edged garden shovels and paint scrapers (see Bertness et al. [2002] for methods). *Ascophyllum* around the edge of the bare patches that could potentially rest on the bare patch surfaces during low tides was also removed to standardize the size of bare areas and ensure that they were 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 the nearby undisturbed control at each site, we marked three 10 × 10 cm monitoring quadrats that were initially scraped bare. One quadrat was left as a control, one was covered with a stainless-steel mesh consumer-exclusion cage, and one was covered with a stainless-steel sideless cage control (see Plate 1). We monitored this experiment photographically in late spring and fall of 2001 and 2002 (see Bertness et al. [2002] for methods). Two mussel-bed site replicates were lost to vandalism so we ended up with eight mussel-bed site replicates for our final analysis. In monitoring quadrats where a *Fucus* canopy developed, photographs could not be used to quantify understory primary space occupiers. Instead, we quantified understory space oc-
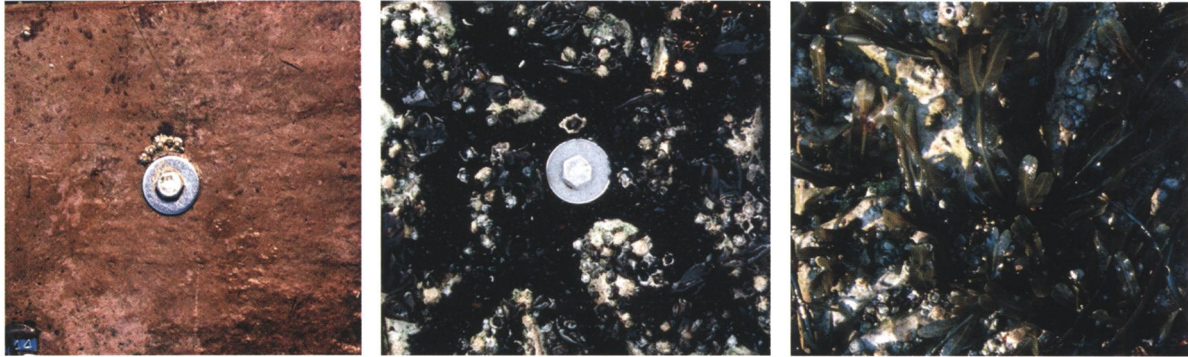
PLATE 1.   In the presence of consumers, natural recovery from disturbance was strongly dependent on crack and crevice refuges as illustrated by recovery on smooth and textured settlement tiles. Smooth tiles remained virtually bare after two years at Chamberlain in both mussel bed and seaweed canopy habitats (left), while over the same period of time, textured settlement tiles were heavily covered with mussels at mussel bed sites (center), and fucoid seaweeds at seaweed canopy sites (right). Photo credit: Mark Bertness.

cupation in the field in September 2002 by placing a 10 × 10 cm grid with 100 sampling cells over each caged plot and identifying the occupants of each sampling cell.

To describe the intertidal community at the study sites, we quantified (1) the abundance and distribution of primary space holders with standard quadrat-sampling techniques, (2) the relative differences in water movement among the study sites with calcium sulfate (dental plaster) dissolution blocks (for detailed methods and discussion see Bertness et al. [2002]), and (3) quantified recruitment patterns. Barnacle and mussel recruitment was quantified at each study site in the 1-m² and 9-m² clearings and the unmanipulated control plots. Barnacle recruitment was quantified by counting metamorphosed barnacle recruits in the May 2001 quadrat photographs. Mussel recruitment was quantified by bolting settlement substrates (plastic kitchen scrub pads [Lola plastic scourer]) to the rock surface in each treatment from May to October 2002 (see Bertness et al. [1999b] for methods). Mussel recruits from each collector were counted in the laboratory with a dissecting scope.

To examine variation in consumer pressure we quantified variation in the densities of grazing snails (*Littorina littorea*) and green crabs (*Carcinus maenas*) and the mortality of tethered mussels. Because we were ultimately interested in comparing the results of our open-coast study with our previous work in tidal-river habitats, we quantified consumer densities and pressure at our original tidal-river sites (Bertness et al. [2002]) and our open-coast sites. To quantify snail densities, we counted the number of snails (*L. littorea*) in 0.5 × 0.5 m sampling quadrats (*N* = 5 quadrats) haphazardly placed adjacent to each of our tidal-river and open-coast experimental sites in July 2002. To quantify variation in green crab density we used commercially available green crab traps (M&L Traps, Bristol, Rhode Island, USA). In July 2002, on two occasions, we de-

ployed five traps at mussel-bed sites and five traps at *Ascophyllum*-canopy sites on the open coast and tidal river. Traps were baited with raw chicken and deployed for 24 hours, and captured crabs were counted and measured (carapace width). To directly quantify crab predation intensity within and among our study sites we conducted a mussel-tethering experiment at our tidal-river and open-coast study sites. In July 2002 we tethered four individual mussels (20–40 cm in length) at each site (16 river and 18 open coast) and disturbance treatment (undisturbed controls, 1-m² and 9-m² clearings) on bare rock surfaces and recorded mussel mortality daily for two days. Mussels were tethered to the rock with a 5-cm length of nylon fishing line glued to the shell (see Bertness et al. [2002] for a complete description and discussion of this technique).

Statistical analyses

Descriptive data characterizing mussel-bed and *Ascophyllum*-canopy sites on the open coast was analyzed with two-way nested ANOVA that considered Habitat type (mussel bed vs. *Ascophyllum* canopy) as a fixed effect and Site as a random effect nested within Habitat type. Data on barnacle recruitment were analyzed with a three-way nested ANOVA that considered Location (open coast vs. river), Habitat type (mussel bed vs. *Ascophyllum* canopy), and Disturbance treatment (3-m², 1-m², undisturbed control) as fixed effects and Sites as a random effect nested within Habitat type. This model was also used for the tethering experiment but because of lost data we ended up with only six sites of each habitat type at each location. Data examining differences in consumer abundance (*L. littorea*, *Nucella lapillus*, *C. maenas*) were analyzed with a two-way nested ANOVA that considered Location (open coast vs. river) and Habitat type (mussel bed vs. *Ascophyllum* canopy) as fixed effects and Sites as a random effect nested within Habitat type as a random effect. Data from the alternative-state experiment were analyzed

with a three-way nested ANOVA that considered Habitat type (mussel bed vs. *Ascophyllum* canopy), Disturbance (3-m², 1-m², undisturbed control) and Caging treatments (control, cage control, caged) as fixed effects and Sites as a random effect nested within Habitat type. 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 allow readers to appreciate the time course of patch recovery. There has been discussion regarding the appropriate model for this experimental design (Petraitis and Dudgeon 2004, Bertness et al. 2004). Although we provide our perspective on these issues elsewhere, here we have used one of the models suggested by Petraitis and Dudgeon (2004) but point out that the results of this model and the model used for our previous experiments (Bertness et al. 2002) produced remarkably similar results.

All analyses were conducted using JMP software (SAS Institute 1996) for the Macintosh. In some cases it was necessary to transform data (either arc sine for percent cover or square root for counts) to meet the homogeneity assumption of ANOVA. Any post hoc comparisons were performed using the linear contrast feature of JMP. In some cases the loss of replicates resulted in the loss of entire sites or produced incomplete sites. These sites were dropped from the analyses, leaving us with a total of seven mussel-bed sites and seven *Ascophyllum*-canopy sites on the open coast.

RESULTS

Mussel-bed and Ascophyllum-*canopy site characteristics*

The mussel-bed and *Ascophyllum*-canopy communities at the study sites differed dramatically (Fig. 1a). At *Ascophyllum*-canopy sites, nearly half of the primary understory substrate space was bare with the rest covered with barnacles (*Semibalanus balanoides*), and *Fucus* spp. (hereafter referred to by generic name only). Mussel cover was <10% in the *Ascophyllum* understory (Fig. 1a). At mussel-bed sites, *Fucus* cover was >60% and mussel cover was >80% in the *Fucus* understory. The little remaining space at mussel-bed sites was bare (~10%), or covered with barnacles or *Ascophyllum* (Fig. 1a). Chalk dissolution data (Fig. 1b) indicated that flow velocities were over twice as high at mussel-bed sites compared to *Ascophyllum*-canopy sites (ANOVA, $F_{1,12} = 192.16$, $P < 0.0001$).

Barnacle and mussel recruitment patterns

Although barnacle recruitment (Fig. 2) differed significantly between *Ascophyllum* canopy sites and mussel-bed sites (ANOVA, $F_{1,12} = 7.07$, $P = 0.0208$) and among caging treatments (ANOVA, $F_{2,24} = 21.96$, $P < 0.0001$), we did not detect consistent significant differences in barnacle recruitment among disturbance treatments (ANOVA, $F_{2,24} = 1.55$, $P = 0.2334$). These
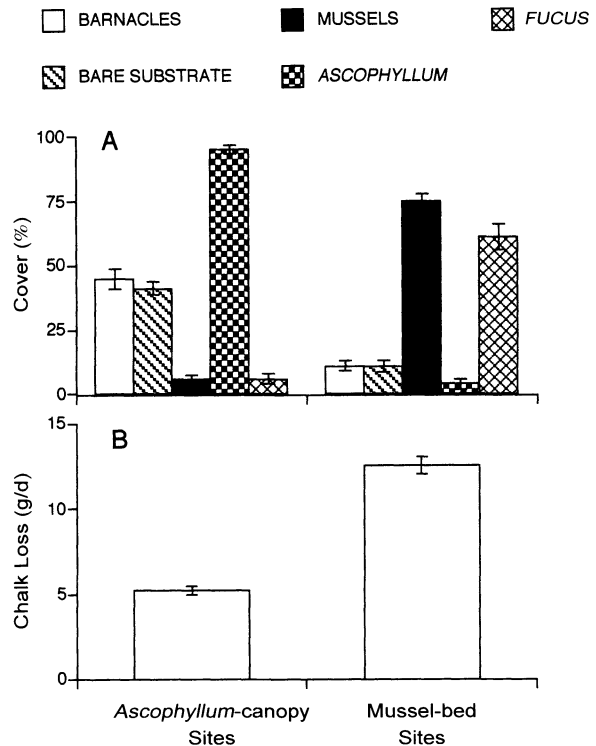

FIG. 1. Percent cover and flow-velocity data at mussel-bed and *Ascophyllam*-canopy sites on the open coast of Maine, USA. (A) Percent cover of sessile space holders; data are means ± 1 SE. For *Ascophyllum*-canopy sites, data for barnacles, bare space, and mussels were obtained from the canopy understory. At mussel-bed sites, a *Fucus* canopy was often present. Hence, mussel percent-cover data reflect a combination of over- and understory measurements whereas data for barnacles, bare space, and *Ascophyllum* are from the *Fucus*-canopy understory. Both mussel cover (ANOVA, $F_{1,12} = 293.20$, $P < 0.0001$) and *Fucus* cover (ANOVA, $F_{1,12} = 20.98$, $P = 0.0006$) were significantly greater at mussel-bed sites, whereas *Ascophyllum* cover (ANOVA, $F_{1,12} = 2230.88$, $P < 0.0001$), barnacle cover (ANOVA, $F_{1,12} = 13.94$, $P = 0.0029$), and bare space (ANOVA, $F_{1,12} = 8.12$, $P = 0.0146$) were significantly greater at *Ascophyllum*-canopy sites. (B) Chalk dissolution data from mussel-bed and *Ascophyllum*-canopy sites on the open coast of Maine. Calcium sulfate blocks were deployed for 48 hours; data are means ± 1 SE.

complex patterns arose primarily because disturbance treatments affected barnacle recruitment differently at *Ascophyllum*-canopy and mussel-bed sites (Habitat type × Disturbance treatment; ANOVA, $F_{2,24} = 8.79$, $P = 0.0014$) and the effects of disturbance treatment depended on caging treatment (Disturbance treatment × Caging treatment; ANOVA, $F_{4,48} = 3.52$, $P = 0.0134$).

At *Ascophyllum*-canopy sites, barnacle recruitment was lower in the 1-m² and 9-m² clearings compared to undisturbed control plots (linear contrast, both $P < 0.005$). Compared to uncaged plots, caging significantly increased barnacle recruitment in 1-m² (linear contrast, $P = 0.0224$) and undisturbed control plots (linear contrast, $P < 0.0001$), but not in 9-m² clearings
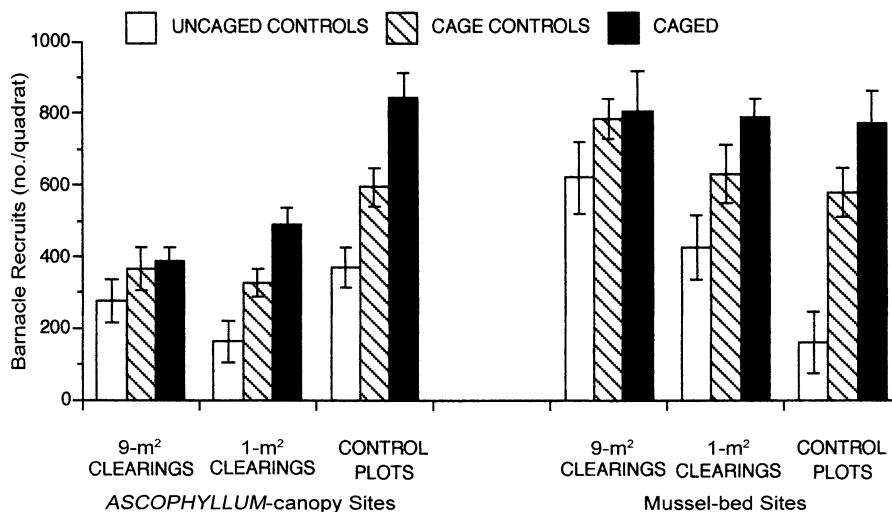
FIG. 2. Barnacle (*Semibalanus balanoides*) recruitment in unmanipulated control plots and two sizes of cleared plots with three different caging treatments at the mussel-bed and *Ascophyllum*-canopy sites in 2001 at the open-coast study sites (Maine, USA). Data are means ± 1 SE.

(linear contrast, $P = 0.41$). These results are consistent with consumers limiting barnacle recruitment under the canopy, but not in large clearings (Fig. 2).

At mussel-bed sites, barnacle recruitment in uncaged quadrats was significantly greater in 9-m² clearings than in undisturbed controls (linear contrast, $P = 0.0195$). Compared to uncaged controls, caging significantly increased barnacle recruitment in 1-m² plots (linear contrast, $P < 0.0047$) and in undisturbed control plots (linear contrast, $P < 0.0001$), but had no significant effect in 9-m² clearings (linear contrast, $P = 0.0999$). Again these results suggest that consumers were more important in undisturbed mussel beds than they were in large clearings.
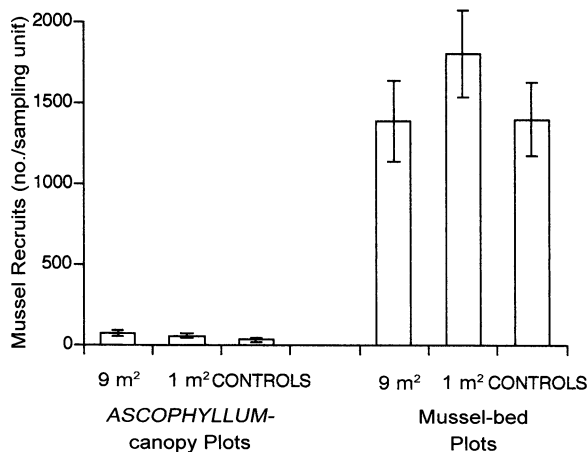

FIG. 3. Mussel (*Mytilus edulis*) recruitment in unmanipulated control plots and two sizes of cleared plots at the mussel-bed and *Ascophyllum*-canopy sites in 2002 at the open-coast study sites (Maine, USA). Data are means ± 1 SE.

Mussel recruitment (Fig. 3) differed significantly between *Ascophyllum*-canopy sites and mussel-bed sites (ANOVA, $F_{1,12} = 217.37$, $P < 0.001$), but not among patch types (ANOVA, $F_{2,24} = 2.31$, $P = 0.1212$), with no interaction between plot type and patch treatment (ANOVA, $F_{2,24} = 1.78$, $P = 0.1895$). Mussel recruitment was over 30 times higher at mussel-bed sites than at *Ascophyllum*-canopy sites (Fig. 3). Although we do not have comparable data from tidal-river sites, we do have mussel recruitment data from the large 9-m² clearings taken at the same time as the data in Fig. 3. These data show that mussel recruitment at mussel-bed sites was significantly greater compared to *Ascophyllum* canopy sites (ANOVA, $F_{1,12} = 19.86$, $P = 0.0008$). In the river the recruitment at mussel-bed sites was nearly 25 times greater (226.0 ± 59.3 recruits/pad) compared to *Ascophyllum*-canopy sites (5.1 ± 2.4 recruits/pad) (mean ± 1 SE). These data also illustrate the dramatic difference between mussel recruitment at open-coast and tidal-river habitats (ANOVA, $F_{1,12} = 33.62$, $P < 0.0001$). Mussel recruitment was 5 times higher in coastal habitats than tidal-river habitats. There was no significant interaction, indicating that differences in mussel recruitment between mussel-bed and *Ascophyllum*-canopy sites were similar on the open coast and in the river (ANOVA, $F_{1,12} = 0.90$, $P = 0.3615$).

Consumer densities

Densities of the herbivorous snail, *Littorina littorea*, were dramatically greater at river sites compared to coastal sites (ANOVA, $F_{1,12} = 96.67$, $P < 0.0001$) and greater at mussel-bed sites compared to *Ascophyllum*-canopy sites (ANOVA, $F_{1,12} = 41.71$, $P < 0.0001$). A significant Location × Habitat interaction revealed that the difference in *L. littorea* density between the two

community types was greater for river sites (ANOVA, $F_{1,12} = 16.17$, $P = 0.0017$). In the river, *L. littorea* density at *Ascophyllum*-canopy sites was 77 snails/m², but increased considerably to >290 snails/m² at mussel-bed sites. At open-coast sites, *L. littorea* density was <15 snails/m² at *Ascophyllum*-canopy sites, but just over 25 snails/m² at mussel-bed sites.

Densities of the green crab (*Carcinus maenas*) also were significantly greater at river sites compared to open-coast sites (ANOVA, $F_{1,12} = 68.73$, $P < 0.0001$) and greater at *Ascophyllum*-canopy sites compared to mussel-bed sites (ANOVA, $F_{1,12} = 36.39$, $P < 0.0001$). At river sites, we caught a mean of 11 crabs at *Ascophyllum*-canopy sites, but less than half that at nearby mussel-bed sites. At open-coast sites, we caught just over three crabs in *Ascophyllum*-canopy sites, but did not catch any crabs at mussel-bed sites. Green crabs from river sites also were significantly larger (47.8 ± 1.1 mm [mean ± 1 SE] carapace width) than from open-coast sites (40.6 ± 2.2 mm carapace width, ANOVA, $F_{2,140} = 4.46$, $P = 0.013$).

In contrast to periwinkles and green crabs, densities of the carnivorous whelk, *Nucella lapillus*, were much higher at open-coast than river sites (ANOVA, $F_{1,12} = 24.05$, $P = 0.0004$) and higher at mussel-bed sites than *Ascophyllum* sites (ANOVA, $F_{1,12} = 25.10$, $P = 0.0003$). A significant Location × Habitat interaction (ANOVA, $F_{1,12} = 12.06$, $P = 0.0046$) revealed, however, that differences in *Nucella* density between mussel-bed and *Ascophyllum* sites were only significant at the open-coast habitats location (linear contrasts, Open coast $P < 0.0001$, River $P = 0.2984$). On the open coast, *Nucella* density was 126.3 ± 20.7 snails/m² at mussel-bed sites and 3.3 ± 1.1 snails/m² at *Ascophyllum*-canopy sites (means ± 1 SE). In contrast, in the river *Nucella* density was 5.0 ± 1.1 snails/m² at mussel-bed sites and 0 ± 0.0 snails/m² at *Ascophyllum*-canopy sites.

Green crab predation pressure

Our tethering experiment revealed strong differences in crab predation, with mussel mortality rates being highest at river sites (ANOVA, $F_{1,10} = 184.95$, $P < 0.0001$) and within the *Ascophyllum* canopy (ANOVA, $F_{1,10} = 12.93$, $P = 0.0049$; Fig. 4). Patch size had no effect on mussel mortality rates (ANOVA, $F_{2,20} = 0.40$, $P = 0.6770$). The data also revealed an interaction between habitat type (mussel bed vs. *Ascophyllum* canopy) and patch size (ANOVA, $F_{2,20} = 3.58$, $P = 0.0469$) with predation rates being higher in undisturbed controls (linear contrast, $P = 0.0143$) and small clearings (linear contrast, $P = 0.0008$). Otherwise, there were no significant interactions ($0.35 \leq P \leq 0.94$). Mortality of tethered mussels in these experiments could be unambiguously attributed to crab predation because of the characteristic shell-breaking patterns seen on the recovered shells (Elner 1978). At *Ascophyllum*-canopy sites on the river, crabs ate nearly all (97%) of the
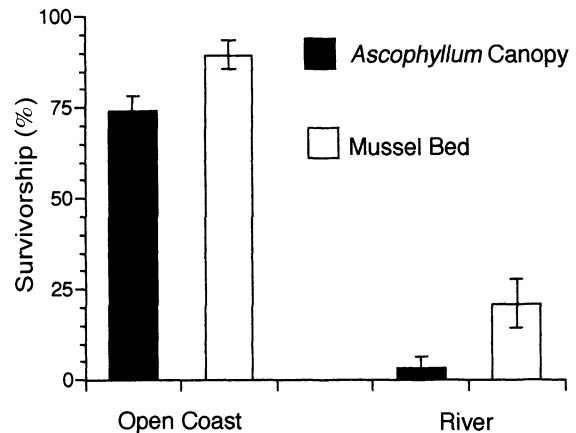

FIG. 4. Survivorship of tethered juvenile (2–3 cm long) mussels after two days in mussel-bed and *Ascophyllum*-canopy plots at tidal-river and open-coast sites (Gulf of Maine, USA) in July 2002. See *Results: Green crab predation pressure* for details. Overall, crabs consumed significantly more mussels in the river compared to the open coast, and significantly more mussels at *Ascophyllum*-canopy sites compared to mussel-bed sites. There was no significant effect of patch size on mussel survivorship, and there were no significant interactions.

tethered mussels in two days (Fig. 4). Although crab predation on tethered mussels at mussel-bed sites was high (79% mortality after two days), it was still significantly less than that recorded for river *Ascophyllum* sites (Fig. 4). In contrast to the river, crab predation on tethered mussels at open-coast sites was minimal. At *Ascophyllum*-canopy sites on the open coast, crabs consumed 29% of tethered mussels after two days, while at open-coast mussel-bed sites, crabs consumed only 10% of the tethered mussels (Fig. 4).

Recovery of experimental bare patches

Results of the patch-recovery experiment were striking (Figs. 5 and 6, Table 1). Without exclusion of consumers, recovery of plots to their initial condition was slow. At sites initially dominated by either an *Ascophyllum* canopy or mussel beds, uncaged control quadrats in large and small clearings and unmanipulated habitats were still dominated by unoccupied bare space after two years of recovery. However, unlike our results in the tidal river where virtually no recovery occurred after two years when consumers were present, bare patches on the open coast did begin to recover even in the presence of consumers. At mussel-bed sites, mussels covered 20–25% of surfaces exposed to consumers after two years (Fig. 5). At *Ascophyllum*-canopy sites, *Fucus* covered 20–40% of surfaces exposed to consumers after two years (Fig. 5).

As we found in our work in a tidal-river system, removing consumers had a dramatic affect on recovery. At mussel-bed sites, mussels rapidly recolonized plots in all disturbance treatments in the absence of consumers. By the end of the second field season, caged con-
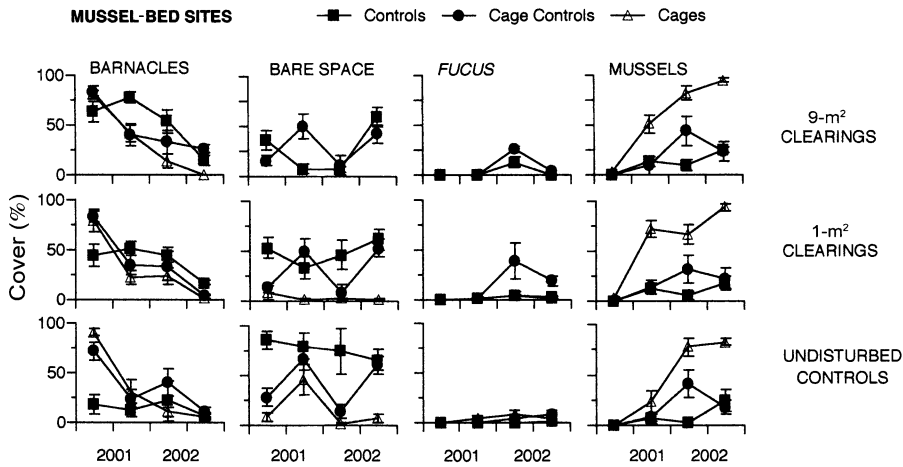
Fig. 5. Cover of sessile organisms in the bare-patch recovery experiment at mussel-bed sites on the open coast of Maine (USA). All data are means ± 1 SE. Error bars are only shown when they are larger than the symbols. Data are given for spring and fall of 2001 and 2002.

sumer-exclusion plots at mussel-bed sites were almost entirely covered by mussel recruits, regardless of disturbance treatment (Fig. 5).

Removing consumers had equally dramatic affects at *Ascophyllum*-canopy sites (Fig. 6). Removing consumers from small and large clearings in the *Ascophyllum* canopy led to rapid recolonization of brown seaweeds with a dense cover (75–85%) of *Fucus* spp. in two years. As with consumer-exclusion cages at the mussel-bed sites, there was nothing subtle about this result; caged substrate in clearings in *Ascophyllum* canopies became dense *Fucus* monocultures in two years in a habitat where *Fucus* was otherwise not common (Fig. 6). Cages in undisturbed *Ascophyllum* canopies, however, responded very differently. Excluding consumers under the *Ascophyllum* canopy led to comparatively modest (<25% cover) *Fucus* recruitment relative to the cleared plots, but nearly 50% mussel cover and significant *Ascophyllum* recruitment (Fig. 6). After two field seasons, mussel recruits covered nearly 50%

of the available space in grazer-free habitats under the canopy, but were entirely absent in uncaged plots under the canopy and rare in all quadrat types in the large and small clearings. Similarly, *Ascophyllum* recruits covered 16% of the available space in cages under the canopy, but were virtually absent in uncaged habitats under the canopy and in caged plots in small clearings, and entirely absent in all other quadrat types.

Examination of understory organisms in caged plots at the *Ascophyllum*-canopy sites revealed mussel and *Ascophyllum* recruitment, particularly in 1-m² clearings and undisturbed control plots (Fig. 7). Excluding consumers resulted in an understory with ~20% mussel cover in 1-m² clearings and 27% mussel cover in undisturbed control plots. However, due to high variability we were unable to detect significant patch-size effects for mussel cover (ANOVA, $F_{2,12} = 1.65$, $P = 0.2319$). In contrast, there were significant patch-size effects for *Ascophyllum* recruitment cover (ANOVA, $F_{2,12} = 7.93$, $P = 0.0064$), with undisturbed control
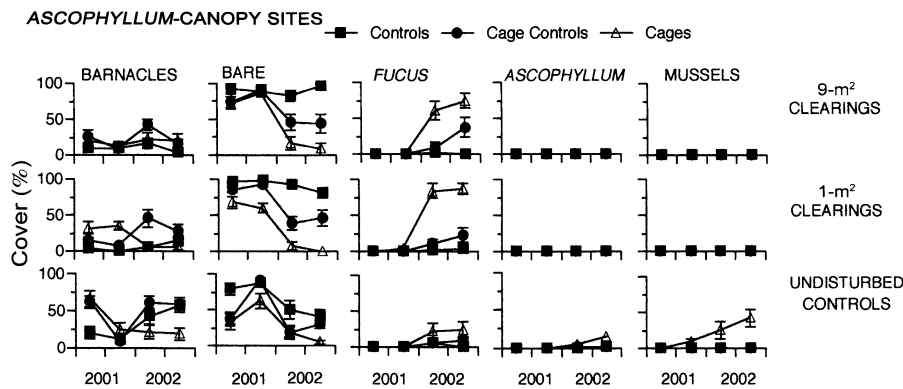

Fig. 6. Cover of sessile organisms in the bare-patch recovery experiment at *Ascophyllum*-canopy sites on the open coast of Maine (USA). All data are means ± 1 SE. Error bars are only shown when they are larger than the symbols. Data are given for spring and fall of 2001 and 2002.

TABLE 1. Summary of P values generated by a three-way nested ANOVA examining the effect of habitat type, patch size, and caging treatment on percent cover of mussels (*Mytilus edulis*), barnacles (*Semibalanus balanoides*), *Ascophyllum nodosum*, *Fucus* spp., and bare space.

Cover	Habitat, H†	Patch size, P‡	Caging treatment, C§	H × P	H × C	P × C	H × P × C
Mussels	<0.0001	0.5474	<0.0001	0.0597	<0.0001	0.2879	0.0312
Barnacles	<0.0001	0.0015	0.0057	<0.0001	0.7722	0.1785	0.0076
Ascophyllum	0.0001	0.0027	<0.0001	0.0027	<0.0001	0.0002	0.0002
Fucus	0.0004	0.0129	<0.0001	0.0201	<0.0001	0.0087	0.0002
Bare space	0.5182	0.6862	<0.0001	0.0199	0.0760	0.0980	0.2692

Note: Level of significance: $P < 0.05$.
† Mussel bed vs. *Ascophyllum* canopy.
‡ Undisturbed controls and 1-m^2 and 3-m^2 cleared plots.
§ Cage, cage control, or control.

plots having significantly more *Ascophyllum* cover than 1-m^2 clearings and 9-m^2 clearings (linear contrast, both $P < 0.005$). There was no *Ascophyllum* cover in 9-m^2 and 1-m^2 clearings, and 12% in undisturbed control plots (Fig. 7).

DISCUSSION

Our results reveal that mussel beds and *Ascophyllum* canopies on Gulf of Maine open coast rocky shores are consumer controlled deterministic community types. Together with similar results from tidal rivers, these findings suggest that if mussel beds and *Ascophyllum* seaweed canopies represent alternative community states on Gulf of Maine rocky shores, they do so in a much narrower set of habitats where the strong determinism we have found is relaxed and stochastic processes come into play.
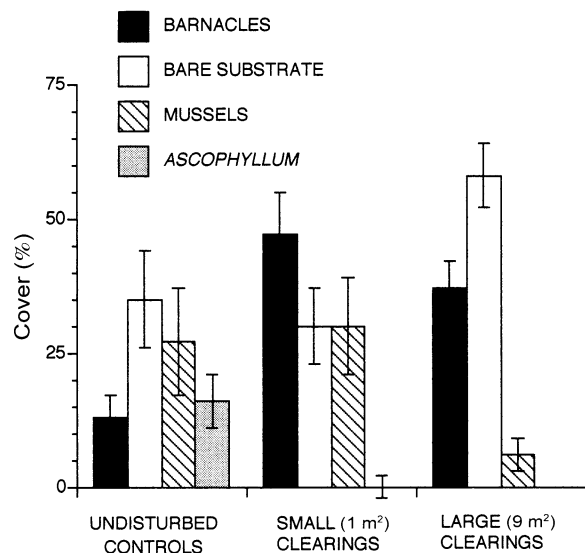

FIG. 7. Percent cover of understory organisms in consumer-exclusion cages at the *Ascophyllum*-canopy sites (Gulf of Maine, USA) in September 2002, after two years of recovery. Data are means ± 1 SE.

Consumer-driven alternative community states in open-coast habitats

We found no evidence for stochastically determined mussel-bed/*Ascophyllum*-canopy alternative states at open-coast sites. In habitats that were initially mussel beds, mussels dominated (>80% cover) in just two years small and large clearings and undisturbed controls when consumers were excluded (Fig. 5). With consumers present, mussel cover reached 20–30% in all plots by the second year of the experiment, suggesting that over time all mussel plots would ultimately return to mussel dominance even in the presence of consumers. Thus, the results of our test for stochastic community identity in these mussel-bed communities have shown that open-coast mussel-bed communities are highly deterministic and under consumer control.

In *Ascophyllum* canopies, two years after consumers were excluded, *Fucus* dominated (>75% cover) small and large clearings but not control plots under the *Ascophyllum* canopy (Fig. 6). When consumers were excluded under the canopy, mussels covered nearly 50% and *Ascophyllum* recruits covered 16% of the substrate after two years (Fig. 6). When consumers were not excluded from *Ascophyllum* canopies, neither mussels nor *Ascophyllum* were able to successfully recruit in two years—providing strong evidence that their recruitment is consumer limited. *Ascophyllum* recruits were found almost exclusively in control plots under the adult *Ascophyllum* canopy with slight recruitment in the small clearings and no recruits ever seen in the large clearings (Figs. 6 and 7). *Ascophyllum* dispersal is typically known to be limited to immediately under adult plants (Vadas et al. 1990, Dudgeon and Petraitis 2001). In three years of monitoring our open-coast mussel-bed sites, we have not seen a single *Ascophyllum* recruit, which is also consistent with the low dispersal potential of *Ascophyllum*.

Thus, as we found in the tidal-river system (Bertness et al. 2002), consumer pressure in wave-protected open-coast habitats limits the distribution of mussels

and leads to a community dominated by a long-lived canopy of *Ascophyllum* with an understory dominated by bare space. In habitats exposed to heavier wave action, consumer pressure by crabs is reduced and the delivery of mussel and barnacle recruits is increased. This leads to the dominance of mussels, the competitive dominant for space in coastal intertidal habitats in the Gulf of Maine (Menge 1976).

Comparison of open-coast and tidal-river systems

Although open-coast and tidal-river habitats share the same dominant species, the similarity of mussel-bed and *Ascophyllum*-canopy habitats in these systems is clearly superficial. Tidal rivers are characterized by extremely high predation rates and powerful consumer control of community development, while open-coast habitats are characterized by reduced consumer pressure and highly dynamic mussel populations. These differences between tidal-river and open-coast systems appear to be general in the Gulf of Maine (M. D. Bertness, *personal observation*).

Mussel beds in tidal rivers in central Maine are usually dominated by larger (>5 cm long) mussels, with juvenile mussels inconspicuously living deeply in the bed (Leonard et al. 1999, Bertness et al. 2002). Juvenile mussels are protected from both predators and physical stress by living in beds (Bertness and Grosholz 1985). In the tidal river, mussels rapidly recruited to predator-exclusion cages in about two years and grew to the sizes commonly seen in mussel beds (Bertness et al. 2002; M. D. Bertness, G. C. Trussell, P. J. Ewanchuk, B. R. Silliman, and C. M. Crain, *unpublished data*). Without excluding consumers in the tidal river, however, juvenile mussels are rare. In contrast, open-coast mussel beds characteristic of wave-exposed headlands in the Gulf of Maine are typically composed of small individuals, <3 cm long, and recruits (<1 cm long) are common. Both primary and secondary mussel recruitment (sensu Bayne 1964) are conspicuous in these open coast habitats. *Mytilus* settle initially (primary settlement) on algal turfs, and upon reaching 1–3 mm in length, they detach and passively drift until ultimately reattaching, typically with conspecifics (secondary settlement). In our work at open-coast sites (Bertness and Leonard 1997, Bertness et al. 1999*a*), whenever we have left empty drilled holes in rock surfaces, they rapidly (usually within a month) filled with small (<1 cm) mussel recruits (M. D. Bertness, *personal observation*). In contrast, at tidal-river sites, mussel recruits are always rare, almost never found unless explicitly looked for, and are found almost exclusively in mussel beds with adult congeners (Leonard et al. 1998). At river sites, abandoned drill holes never contain juvenile mussels (M. D. Bertness, *personal observation*). The small size of individuals in open-coast mussel beds reflects the fact that these systems are extremely dynamic. Predation by the whelk *Nucella lapilus* is intense at lower to middle tidal levels and is

capable of limiting mussel populations (Menge 1976). Wave disturbance also frequently results in mussels being ripped from the substratum (Menge 1976; M. D. Bertness, *personal observation*). As a result of these mortality sources, mussel beds on wave-exposed headlands are best envisioned as highly disturbed patch mosaics of juvenile mussels with a large supply of recruits. This is vastly different from mussel beds in tidal rivers, which are typically made up of large, older individuals that have reached a size refuge from predation and are characterized by lower levels of recruitment.

A second major difference between Maine coastal and tidal river systems is that herbivorous snails and predatory crabs are much more common in tidal-river than in coastal habitats. Densities of the major herbivorous snail, *Littorina littorea*, were on average 9 times higher in the river than at our open-coast sites, and green crab densities were more than twice as high at river sites than on the open coast. Our tethering experiment showed that consumer pressure by crabs was dramatically greater at river sites than at open-coast sites (Fig. 4). In contrast to periwinkles and green crabs, the predatory snail, *Nucella*, is much more abundant at open-coast sites than river sites and is almost entirely restricted to mussel-bed sites. At open-coast mussel-bed sites, *Nucella* is the most important consumer of mussels and barnacles (Menge 1976), whereas in mussel-bed habitats in tidal rivers *Nucella* is relatively rare and green crabs are the most important predators of mussels and barnacles (Leonard et al. 1998, 1999, Bertness et al. 2002). We have previously shown (Leonard et al. 1998) in the tidal-river habitat that *Nucella* is limited from *Ascophyllum*-bed habitats by green crab predation.

Differences in the availability of mussel recruits and the intensity of predation between coastal and river systems appear to account for many of the differences we found in the patch recovery process in these systems. One of the surprising things we found with bare-patch colonization in the river was the lack of strong patch-size effects on colonization (Bertness et al. 2002). Recruitment patterns that were expected, like higher barnacle recruitment in large clearings than in small clearings due to grazing halos (Petraitis and Dudgeon 1999), were not found. We speculated that this was due to the intense crab-predation pressure on small barnacles at our study sites (Leonard et al. 1999). On the open coast with reduced crab-predation pressure we did find, under certain conditions, the strong patch-size effects in barnacle recruitment (Fig. 3) found by Petraitis and Dudgeon (1999).

Recovery of disturbance-generated bare space on the open coast was also faster and less dependent on substrate spatial heterogeneity than in the river. In the river, even after three years of recovery, neither mussels nor fucoid algae had begun colonizing cleared plots in mussel beds and *Ascophyllum* canopies, respectively (Bertness et al. 2002). The few that did colonize were ex-

clusively restricted to crack-and-crevice refuges. Caging out consumers on the river, however, led to rapid invasion of mussels and fucoid algae (Bertness et al. 2002). In contrast, on the open coast with reduced consumer pressure, recovery was much quicker and recolonization was not conspicuously dependent on cracks and crevices. Excluding consumers accelerated the recovery process, but significant recovery occurred in two years even in the presence of consumers. In our open-coast experiments in *Ascophyllum*-canopy plots, *Fucus* cover in uncaged quadrats in the small and large clearing was 25–50% after two years of recovery, while in the mussel-bed plots mussel cover reached 25–35% in uncaged quadrats (Fig. 5). In the tidal-river system, no mussels or fucoid algae successfully colonized the smooth surfaces of our uncaged quadrats even after three years of recovery (Bertness et al. 2002).

In contrast to the rapid recolonization of open-coast plots by mussels and *Fucus*, *Ascophyllum* recruitment at open-coast sites has been slow in comparison to the tidal river. When consumers were excluded in our previous experiments in the tidal-river system, *Ascophyllum* recruitment was heavy under the *Ascophyllum* canopy. In some cases we counted over 50 *Ascophyllum* recruits/cm^2 in cages under the canopy (Bertness et al. 2002). On the open coast we have never observed these high densities of *Ascophyllum* recruits. In cages under the *Ascophyllum* canopy at the open coast the highest densities of *Ascophyllum* recruits we observed was 2–5 recruits/cm^2 (M. D. Bertness, G. C. Trussell, P. J. Ewanchuk, B. R. Silliman, and C. M. Crain, *unpublished data*). After two years of recovery at open-coast sites, *Ascophyllum* recruits covered less than half the space under cages (~25%, Fig. 6) compared to the coverage at river sites (~50%, Bertness et al. 2002). These findings are consistent with previous work suggesting that *Ascophyllum* recruitment is limited by wave action in coastal habitats (Vadas et al. 1990, Dudgeon and Petraitis 2001).

Stochastic or deterministic community states?

Together, our results from open-coast and tidal-river habitats suggest that intertidal mussel beds and *Ascophyllum* canopies are deterministic, consumer-driven, rather than stochastic alternative community states. In both habitats we found no evidence for stochasticity in the type of community that recolonized after a disturbance, regardless of the size of the disturbance. Moreover, while we found differences in the rate and degree of consumer control of recovery, the recovery of both community types in tidal-river and open-coast habitats was found to be under strong consumer control.

Our results do not mean that mussel beds and *Ascophyllum* canopies can never represent stochastic alternative community states in the Gulf of Maine. But our results have not been ambiguous, suggesting that the mussel beds and *Ascophyllum* canopies that dominate shorelines in the Gulf of Maine are usually de-

terministic community types. Intermediate habitats with low consumer pressure and episodic recruitment could potentially support stochastic community states, and these conditions may occur in the coastal wave-protected bay environment studied by Dudgeon and Petraitis (2001). Consumer control would need to be reduced, since intense consumer control of recruitment can eliminate the role played by propagule supply variation in influencing community structure. Episodic, stochastic recruitment would also be needed for mussel beds and *Ascophyllum* canopies to exist as alternative community states. In our work in tidal-river and coastal habitats, predictable recruitment patterns driven by spatial differences in flow eliminated the possibility of alternative community states.

The idea that natural communities can represent alternative stable states—where the community that persists at a particular location is the stochastic product of recruit supply during community development—is important for our basic understanding of natural communities, and for making intelligent decisions about their conservation and management. Our results have two important lessons for our understanding of alternative community states. First, our results show that hypothesized alternative stable states based on correlative data and evidence suggesting potential mechanisms for the maintenance of alternative states may not prove to be true under experimental scrutiny. This points to the importance of experimentally testing alternative-state scenarios before they are widely accepted. Second, our results suggest that communities are probably not easily characterized as either stochastic or deterministic. In the mussel-bed and *Ascophyllum*-canopy communities we have examined, we suspect that these communities are generally highly deterministic, but that there are probably some intermediate or transitional habitats where stochastic factors can dictate community composition at a given site. Given the strength of the determinism we have found in our examination of the alternative community states in this system, however, we suspect that habitats with stochastic community composition are relatively uncommon. Understanding when, where, and how frequently community composition is stochastic or deterministic will contribute a great deal to the debate about the importance of alternative community stable states in nature.

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