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Experimental confirmation of multiple community states in a marine ecosystem

Peter S. Petraitis · Elizabeth T. Methratta · Erika C. Rhile · Nicholas A. Vidargas · Steve R. Dudgeon

Abstract Small changes in environmental conditions can unexpectedly tip an ecosystem from one community type to another, and these often irreversible shifts have been observed in semi-arid grasslands, freshwater lakes and ponds, coral reefs, and kelp forests. A commonly accepted explanation is that these ecosystems contain multiple stable points, but experimental tests confirming multiple stable states have proven elusive. Here we present a novel approach and show that mussel beds and rockweed stands are multiple stable states on intertidal shores in the Gulf of Maine, USA. Using broad-scale observational data and long-term data from experimental clearings, we show that the removal of rockweed by winter ice scour can tip persistent rockweed stands to mussel beds. The observational data were analyzed with Anderson's discriminant analysis of principal coordinates, which provided an objective function to separate mussel beds from rockweed stands. The function was then applied to 55 experimental plots, which had been established in rockweed stands in 1996. Based on 2005 data, all uncleared controls and all but one of the small clearings were classified as rockweed stands; 37% of the large clearings were classified as mussel beds. Our results address the establishment of mussels versus rockweeds and complement rather than refute the current paradigm that mussel beds and rockweed stands, once established, are maintained by site-specific differences in strong consumer control.

Keywords *Ascophyllum nodosum* · Alternative stable states · *Fucus* · Mussels · Rocky intertidal shores

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Introduction

Small temporary changes in environmental conditions can unexpectedly tip an ecosystem from one community type to another, and such shifts in community composition are known to occur in semi-arid grasslands (van de Koppel et al. 1997; Suding et al. 2004), freshwater lakes and ponds (Scheffer et al. 1993; Carpenter et al. 1999; Chase 2003), coral reefs (Hughes 1994; Bellwood et al. 2004), and kelp forests (Simenstad et al. 1978; Estes et al. 1998). Often the shifts are rapid, and communities fail to return to the original state even when environmental conditions return to normal. These sudden switches are also intriguing because they are consistent with the theory that ecosystems can contain multiple stable points (Lewontin 1969; May 1977).

Tests for multiple stable states in natural ecosystems have often been inconclusive (Connell and Sousa 1983; Petraitis and Dudgeon 2004a; Suding et al. 2004; Schröder

et al. 2005) because the litmus test for multiple stable states in natural ecosystems must contain several distinct requirements that are rarely met. First, experimental manipulations must be used to show that the same site could be occupied by different self-replacing communities (Peterson 1984). In addition, the manipulations must be pulse perturbations (sensu Bender et al. 1984) that mimic a natural event in spatial extent, temporal duration and its effect on species in the system (Connell and Sousa 1983). While at first glance, these four criteria—same site, different communities, self-replacement, and natural pulse perturbations—are unambiguous, they have proven difficult to meet experimentally in field experiments (Connell and Sousa 1983; Petraitis and Dudgeon 2004a; Suding et al. 2004; Schröder et al. 2005).

Peterson (1984) argued very forcefully and convincingly that the requirement of using "the very same site" was critical because of undetected effects of environmental variation. On one hand, different species assemblages may occur as a mosaic of patches across what appears to be a uniform environment, yet it is possible such a patchwork reflects undetected environmental variation. On the other hand, the dominant species within communities are often ecosystem engineers, which have modified the environment. Thus, established multiple community states may appear to exist in different environments even though initial environmental conditions were identical. Protection against the unintended effects of environmental variation requires replicate plots spread over the same community type and over the same environment.

Similar problems arise in attempting to define different communities and natural perturbations because operational definitions require a priori knowledge about the amount of variation in species composition and disturbances within and between the presumed communities. Thus baseline data that characterize the variation among species assemblages and of disturbances should be used to define community types and appropriate experimental perturbations.

The most troublesome issue is stability (Sutherland 1981; Connell and Sousa 1983; Peterson 1984; Sousa and Connell 1985; Sutherland 1990; Grimm and Wissel 1997). In the context of dynamical systems, stability of multiple states is well defined and has either a "yes" or "no" answer (Lewontin 1969). In practice, ecologists must often use a proxy when evaluating stability of natural ecosystems, but there is little agreement on the best approach (Grimm and Wissel 1997).

Here we met the demands of same site, different communities, stability, and pulse perturbations and present a novel approach to test for multiple community states on sheltered rocky intertidal shores in the Gulf of Maine, USA. Mussel beds (*Mytilus edulis*) and stands of brown macroalgae known as rockweeds (*Ascophyllum nodosum* and *Fucus vesiculosus*) are the most common community types on sheltered shores, and these different communities often occur in close proximity as a mosaic of patches. Petraitis and Latham (1999) proposed that these distinct patches were different states in the same habitat, and ice scour, if sufficiently destructive, could tip an area from one type of patch to the other.

Data from a 9-year experimental manipulation and a large-scale observational study were used to test the hypothesis that ice scour alone could tip *A. nodosum* stands to a different community state. Our approach involved three steps. We first created experimental clearings of different sizes in 1996–1997 to mimic the effects of ice scour on *A. nodosum* stands. Next, observational data from persistent rockweed stands and mussel beds over a large area of the Gulf of Maine were collected to provide a priori definitions of different community types and used to define an independent benchmark for the different community states. Finally the function based on the benchmark data was used to assign each experimental plot to one of the community states and to assess ecological stability. In addition, data on succession changes from 1996 to 2005 afforded an opportunity to assess the divergent succession, which is a hallmark of alternative stable states (Schröder et al. 2005), and extensive natural ice scour during the winter of 2002–2003 allowed us to examine resilience of alternative assemblages.

We only focused on the switch from rockweeds to mussels and not the reverse switch from mussels to rockweeds because the traditional view is that rockweeds persist only in areas where predators control mussels. According to this view, mussel beds should not occur on sheltered shores where predators are common and active (Menge 1976; Lubchenco and Menge 1978; Bertness et al. 2004a). Thus a demonstration that mussel beds can form in areas dominated by rockweeds without the exclusion of predators meets Peterson's criteria and is a strong test of multiple stable states.

Finally, we will argue that our view of mussel beds and rockweed stands as multiple community states complements rather than opposes the traditional paradigm, which is based on consumer control of mussels. The traditional paradigm characterizes the maintenance of community states in different places that differ principally in hydrodynamic conditions. In contrast, on sheltered shores with a mosaic of rockweed stands and mussel beds, we think that a large-scale disturbance such as ice scour opens the system to a race between mussels and rockweeds for establishment. The outcome of this race depends in part on which species arrives first, but the outcome is far from certain. Once the critical point is reached at which either mussels or rockweeds are common enough to dominate the system, then positive feedbacks among the species maintain the status quo. Our view of rockweed stands and mussel beds as alternative stable states stresses the strong temporal component of establishment of these states.

Materials and methods

Benchmark sites

Benchmark sites were chosen to represent typical rockweed stands and mussel beds on rocky shores in sheltered bays and were spread across the Gulf of Maine. The straight-line distance from the most southwestern site (43°26.8′N, 70°20.7′W) to the most northeastern site (44°14.6′N, 68°18.0′W) was 186 km. Based on our impression prior to sampling, each site was assigned as mussel (*M. edulis*) beds (five sites) or one of three types of rockweed stands: "pure" *A. nodosum* (25 sites), "pure" *F. vesiculosus* (18 sites), or mixed *A. nodosum* and *F. vesiculosus* (four sites). Large mussel beds are rare in sheltered bays because of differences between rockweeds and mussels in longevity, and the low number of sites with mussel beds reflects this fact. Persistence of mussel stands is likely of the order of tens of years while the persistence of *A. nodosum* stands is likely of the order of hundreds of years (Åberg 1992; P. S. Petraitis, unpublished data), and *ceteris paribus*, longer-lived species will appear more common (for a similar line of reasoning on effects of long handling times on apparent diet, see Peterson and Bradley 1978; Fairweather and Underwood 1983; Petraitis 1990).

Experimental plots

The experimental plots were established in *A. nodosum* stands at 12 mid intertidal sites with three sites in each of four sheltered bays on Swan's Island, Maine. Two bays faced north, towards the mainland and two faced south towards the open sea. At each site, four circular clearings (1, 2, 4, and 8 m in diameter) were made, and an uncleared control plot was set up. Clearings were set up and initially scraped during the summer of 1996 and then re-scraped in February 1997 to mimic the effects of winter ice scour. Sizes of experimental clearings were well within the range of natural clearings (natural clearings created during the winter of 2002–2003 by ice scour averaged 25.4 m² and ranged from 2.4 to 78.5 m²; P. S. Petraitis, unpublished data). Detailed information on creation of the clearings, rationale for choice of clearing sizes, and descriptions and locations of the sites can be found elsewhere (Dudgeon and Petraitis 2001; Petraitis and Methratta 2006; Petraitis and Vidargas 2006; Petraitis et al. 2008).

Sampling

Data were collected on abundances of the most common species (16 variables), percentage cover by sessile species (14 variables), length of and number of bladders on *A. nodosum* (four variables), and presence/absence of other species (21 variables) in three 50-cm × 50-cm quadrats per plot. Benchmark sites were sampled in June–September 2005. Experimental plots were sampled in July–August 2005; only 55 of the original 60 plots were included in the analysis because of destruction of some plots and missing data. Average age of organisms was calculated using log-transformed data. Species were scored as 0 for annuals [i.e., log(1) = 0], 0.699 for species living 1–5 year [log(5) = 0.699], 1 for species living 10 years, 1.301 for species living 20 years, and 2 for species living for the order of 100 years.

Most of the methods used for sampling abundance and percentage cover data are also reported elsewhere (Petraitis and Methratta 2006; Petraitis and Vidargas 2006). Abundance data were collected for mussels (the blue mussel *M. edulis* and the ribbed mussel *Modiolus modiolus*) and gastropods (the limpet *Tectura testudinalis*, the common periwinkle snail *Littorina littorea*, smooth periwinkle *Littorina obtusata* and the dogwhelk *Nucella lapillus*), barnacles (*Semibalanus balanoides*), and fucoid algae (*A. nodosum and F. vesiculosus*) per quadrat. Barnacle counts were divided into the current year's recruits and older individuals. Fucoids and mussels were divided into young and old individuals (young fucoids <1 cm, young mussels <0.5 cm in length). Percentage cover data were collected for unoccupied space, and canopy and surface cover by fucoids, barnacles, mussels, the red alga *Chondrus crispus*, other algal species, and other sessile invertebrate species. The categories of other algal and sessile invertebrate species were aggregate groupings of all other species, which were usually rare or common in only a few quadrats.

For *A. nodosum* and *F. vesiculosus*, we also measured several additional variables: the distance from each quadrat to the three nearest individuals, which is an inverse index of abundance, and the length of the longest frond on three randomly chosen individuals per quadrat. For the three *A. nodosum*, we also counted the number of air bladders on the longest frond and calculated the average internode length.

Analyses

Data from quadrats were averaged giving two data matrices—a 52-site × 55-variable matrix for the benchmark data and a 55-plot × 55-variable matrix for the experimental data. Data were range-standardized using an aggregated data set of both matrices, which provided meaningful comparisons not only among variables (e.g., the one/zero range of presence/absence data has the same range as the maximum/minimum abundance of a common species) but also between the two data matrices.

For the benchmark data, the four categories of community states were assessed using canonical analysis of principal

coordinates (CAP analysis; Anderson and Robinson 2003; Anderson and Willis 2003). We used Euclidian distances and the default selection for the number of meaningful axes (i.e., *m*). Significance of the trace statistic and the first squared canonical correlation was tested by permutation (*n* = 9,999), and cross-validation of group assignment used "leave-one-out" allocation.

A function derived from the CAP analysis was then used to classify each experimental plot to one of the three algal categories (*A. nodosum* stands, *F. vesiculosus* or mixed stands) or as a mussel bed. Assignment was based on the distance to nearest group centroid and was done using PREDICTION, an unpublished program provided by M. J. Anderson.

Successional changes

Based on the assignments from the PREDICTION analysis, the experimental plots were divided post hoc into four groups, and successional changes in percentage cover by dominant space occupiers were examined. The four groups were all control plots, and plots ≥2 m in diameter that were classified as: (1) *F. vesiculosus* stands in north-facing bays, (2) *F. vesiculosus* stands in south-facing bays, or (3) *M. edulis* beds.

We followed changes in percentage surface cover by *M. edulis* and *S. balanoides*, and changes in percentage canopy cover by *A. nodosum* and *F. vesiculosus* from 1998 to 2005 (data available in Petraitis and Vidargas 2006; Petraitis et al. 2008). Averages and variances were calculated using arcsine transformed data, and back-transformed to averages and 95% confidence limits for presentation. Statistical analyses were not done because the groupings were created post hoc using the classification analysis, and testing for significant differences among these groups would be meaningless.

Results

The benchmark sites and experimental plots contained the same species and showed no difference in the average age of the species found (average = 5.5 years, median = 10 years). However, rockweed stands and mussel beds at the benchmark sites were distinctly different in composition, and the CAP analysis gave good and significant separation of the four groups (Fig. 1a). The analysis gave a surprisingly high dimensional solution (*m* = 10), and the first ten axes accounted for 73.3% of the variation. Even so, the separation of the groups was quite distinct on the first two axes, which accounted for 28.7% of the variation. Separation among the first two axes was largely due to the presence of rockweeds, mussels, barnacles, a predatory snail (*Nucella lapillus*) and two red algal species (see S1 in
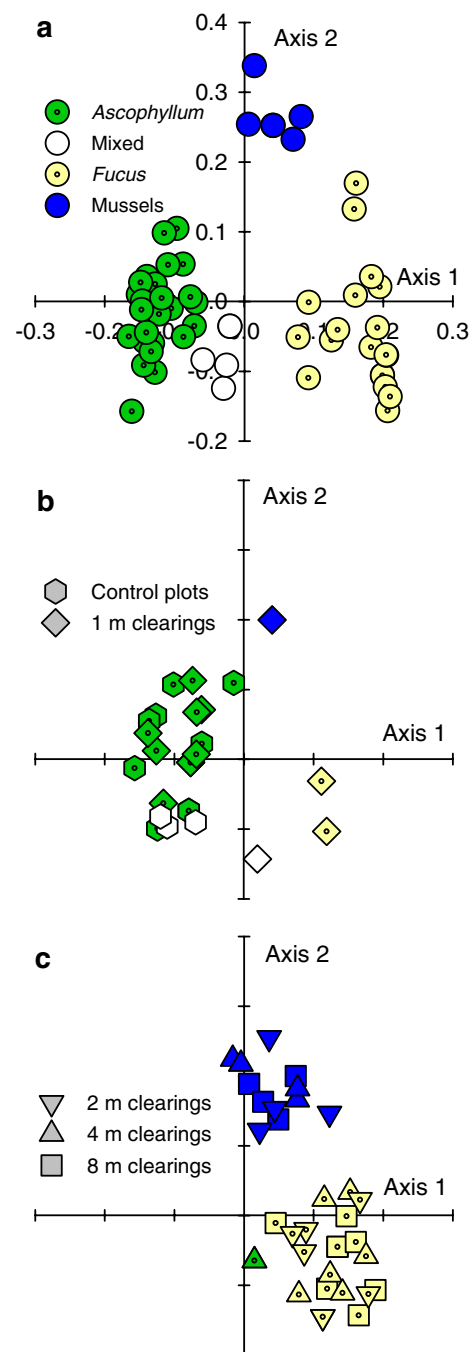

Fig. 1 Representation of benchmark sites and experimental plots as constrained multi-dimensional scaling ordination plots: **a** benchmark sites based on canonical analysis of principal coordinates, **b** assignment by PREDICTION analysis of uncleared control plots and small experimental clearings (1 m in diameter), **c** assignment of large experimental clearings (≥2 m in diameter). Axes and scale are the same in all panels

Electronic Supplementary Material). The first axis separates the three types of rockweed stands, and the second axis separates mussel beds from rockweed stands. Cross validation of group assignment was quite high with 86.5% of the sites being correctly assigned. All mussel sites and

85.1% of the rockweed sites were correctly assigned. Five rockweed sites were assigned to the wrong rockweed category (10.6%) and two *F. vesiculosus* sites were misclassified as mussel beds (4.3%).

Experimental plots were assigned to very distinct groups based on clearing size with a very sharp distinction between controls and 1-m clearings versus ≥2-m clearings (Fig. 1b, c). All the control plots and most of the 1-m clearings were classified as either pure *A. nodosum* or mixed rockweed stands (87.0%, n = 23). The remaining 1-m clearings were classified as *F. vesiculosus* stands (8.7%) or mussel beds (4.3%). All but one of the larger (≥2 m in diameter) clearings were classified as either *F. vesiculosus* stands (59.4%, n = 32) or mussel beds (37.5%). The remaining plot was a 4-m clearing that was classified as a pure *A. nodosum* stand.

The classification of the larger (≥2 m) clearings as either *F. vesiculosus* stands or mussel beds depended on the location of the sites. Fourteen of the 19 plots ≥2 m in diameter and classified as *F. vesiculosus* stands were in the south-facing bays, while all of the plots ≥2 m in diameter and classified as mussel beds were in north-facing bays (see S1).

Succession in the experimental plots followed two distinctly different pathways that can be clearly seen when the plots are grouped by their assignment. Large experimental plots classified as *F. vesiculosus* stands showed a consistent and large increase in cover by *F. vesiculosus* from 1998 to 2005 (Fig. 2). Neither *A. nodosum* nor mussels had become

established as a dominant species in these plots. On the other hand, large experimental plots classified as mussel beds showed a slower and somewhat variable increase in cover by mussels, which is reflected by the large confidence limits in 2004 and 2005. In 2005, four of the plots had >40% cover by mussels (range 41–75%). Not surprisingly, control plots had nearly 100% cover by *A. nodosum* from 1998 to 2005 with the exception of 2003 because of ice scour (see arrows in Fig. 2).

Barnacle cover, which was an important variable in the assignment of experimental plots to mussel beds and the different rockweed stands, did not show strong and consistent differences in successional patterns (S2). Large experimental plots classified as mussel beds tended to have an early spike in barnacle cover (2000–2002) followed by a decline. In contrast, barnacle cover was low in plots assigned to rockweed stands until 2004. We assumed the sharp increase in barnacle cover in 2004 was due to ice scour that removed rockweeds during the winter of 2002–2003 and allowed barnacle recruitment and growth during 2003–2004.

Both control plots dominated by *A. nodosum* and experimental plots dominated by *F. vesiculosus* showed declines in cover and larger confidence limits in 2003, which were due to ice scour during the winter of 2002–2003. Three of the 11 control plots that sustained the greatest damage by ice scour went from 100% cover by *A. nodosum* in 2002 to an average of 37% in 2003 (range 11.2–51.2%). In the plots

Fig. 2 Percentage cover (average ± 95% confidence interval) by *Ascophyllum*, *Fucus* and mussels in **a** control plots and large clearings (≥2 m in diameter) assigned as **b** mussel beds in north-facing bays, **c** *Fucus* stands in south-facing bays, and **d** *Fucus* stands in north-facing bays. *Arrows* show changes associated with severe winter ice damage in winter of 2002–2003
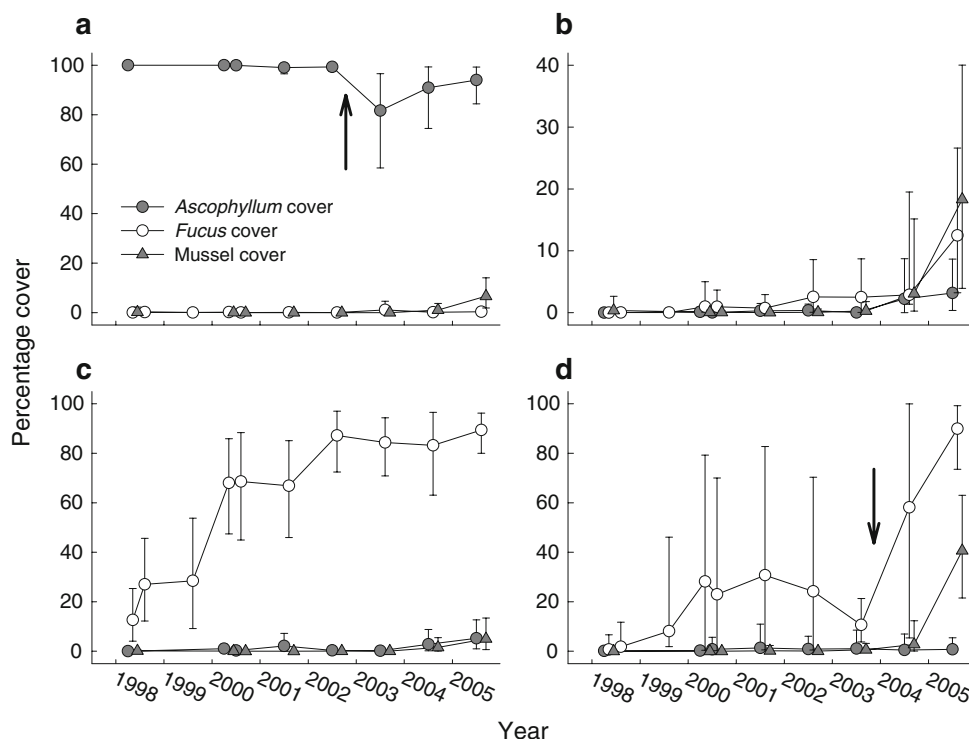
classified as *F. vesiculosus* stands, the three most damaged plots had an average of 88% cover in 2002 and declined to 46% in 2003 (range 16.8–74.4%).

There is also evidence that the *F. vesiculosus* and *A. nodosum* stands were resilient after the severe ice scour (Fig. 2). In large clearings that were classified as *F. vesiculosus* stands, there was a 5.7% decline in *F. vesiculosus* cover in 2002–2003 followed by an 11.4% increase in 2003–2004. Established stands of *A. nodosum* (i.e. the control plots) showed a 22.8% decline in *A. nodosum* cover in 2002–2003, and an 8.6% increase in 2003–2004. In both cases, the decline was correlated with the removal of rockweed by ice during the 2002–2003 winter (for control plots, $r = +0.69$, $n = 11$, $P = 0.019$; for large clearings, $r = +0.50$, $n = 19$, $P = 0.028$).

Discussion

Our results suggest that the community assemblages at sites in sheltered bays in New England can switch from rockweed stands to mussel beds after extensive clearing due to rare events of ice scour. Only one of the large clearings (≥ 2 m in diameter) reverted to an *A. nodosum* stand, and the rest developed into either mussel beds (37%) or *F. vesiculosus* stands (60%). In contrast, most small clearings (1 m in diameter) and all control plots remained *A. nodosum* stands. The combined weight of evidence from the classification of experimental clearings relative to benchmark sites, the successional patterns of mussels and rockweeds, and the resilience of rockweeds suggest that rockweed stands and mussel beds are indeed multiple stable states. In particular, it is quite striking that we were able to induce the formation of mussel beds without the use of cages in areas dominated by *A. nodosum* stands, which are thought to occur only in areas where mussel predators are present and active (Menge 1976; Bertness et al. 2002).

We believe our experiment is a strong test of the theory of multiple stable states and meets all four requirements of such tests. Our experiments show that "the very same site could come to be occupied by different, self-replicating communities" (Peterson 1984) and used pulse perturbations (i.e. one-time scraping of clearings) that matched the temporal and spatial scale of natural ice scour events (Connell and Sousa 1983; Sousa and Connell 1985).

Our pulse perturbation clearly matched the natural disturbance of ice scour. We mimicked the effects of a single ice scour event by scraping the clearings only in the first year. More importantly, our experimental clearings were scraped during winter and were well within the range of clearings that are created naturally by ice scour.

We addressed the issue of carrying out the experiment in the "same site" by using a large number of replicates that were all within established *A. nodosum* stands and spread over four bays. The "very same site" requirement is crucial because different community states could be due to undetected differences in environmental conditions and thus different communities reflect different environments rather than multiple stable states (Lewontin 1969; May 1977). Even switches at the very same site conceivably could be due to undetected environmental change over time. Thus, compelling tests, such as ours, need to be well replicated at a number of sites in the same environment under the assumption that randomization of treatment assignments with replication at a large number of sites in the same environment controls for undetected environmental variation (Petraitis and Dudgeon 2004a, b).

The fact that we found differences in where mussel beds and *F. vesiculosus* stands became established highlights why using a large number of replicates spread over a wide geographical area is so important. The establishment of mussel beds was only seen in large (≥ 2 m) clearings in north-facing bays while *F. vesiculosus* stands were found in both north-facing and south-facing bays. We have found no consistent north–south differences in consumers' activities and densities, or in recruitment of mussels (Petraitis and Dudgeon 1999, 2005; Dudgeon and Petraitis 2001; Petraitis and Methratta 2006).

However, it is possible that the success of *F. vesiculosus* in south-facing bays is related to its slightly greater abundances in the surrounding community. Dispersal distances of rockweeds are of the order of meters, and recruitment depends on nearby adults (Chapman 1995; Dudgeon et al. 2001). Nearby adults give rockweeds an advantage in their race with mussels for establishment. *F. vesiculosus*, while rare in *A. nodosum* stands, was initially more common in south-facing bays (14.7% cover) versus north-facing bays (2.9%; P. S. Petraitis, unpublished data from point-intercept transects done in 1999). In addition, *F. vesiculosus* cover in the large (≥ 2 m) clearings in 2005 is correlated with the background cover in 1999 (Kendall's $\tau = 0.35$, $n = 32$, $P = 0.0071$). While the initial difference among bays was small in absolute numbers, there was a sixfold advantage for *F. vesiculosus* in south-facing bays. Mussel beds may be a viable alternative state in south-facing bays, but they frequently lose the race.

The third criterion of defining "different" communities requires an independent assessment that accounts for natural variation between and within the community states. Our benchmark sites not only provide an independent assessment of the persistent community states, but also fully account for the variation within and between community states over a large spatial scale.

The final requirement of demonstrating stability of the system is the most vexing. The suggestion that a good criterion for stability is self-replication (Connell and Sousa

1983; Peterson 1984; Sousa and Connell 1985) is only one of many (e.g., Paine et al. 1985; Grimm and Wissel 1997; Paine and Trimble 2004). In fact, Grimm and Wissel (1997) grouped 163 definitions of ecological stability into six broad categories—persistence, constancy, resilience, resistance, elasticity, and domain of attraction. In particular, we think self-replacement, although desirable in some respects, may not be the best proxy for stability when considering multiple stable states because self-replacement cannot be used to distinguish between long-transient mid-successional stages, which may be self-replacing, and stable endpoints. Long-transient successional stages are likely to occur in systems with protracted bouts of tolerance (Connell and Slatyer 1977; Petraitis and Dudgeon 2004a). Moreover, the notion of an alternative state rests on the assumption that the state persists by inhibiting further change (i.e., resists invasion) until a pulse perturbation (usually a large one) shifts the biotic assemblage from one basin of attraction to another. For these reasons, we think a combination of different lines of evidence of stability, such as we have used, is more desirable.

Four lines of evidence indicate that the mussel beds and *F. vesiculosus* stands that became established in our large experimental clearings are ecologically stable based on Grimm and Wissel's (1997) definitions. First, most of the organisms in the large clearings are short-lived (average generation time = 5.5 years), and many organisms have turned over several times between 1997 and 2005. Thus the communities have shown self-replication (i.e., persistence) over a number of generations. Second, our classification analysis of the experimental plots shows that most of our large clearings are indistinguishable from the established and persistent rockweed stands and mussel beds found at the benchmark sites. Our experimental plots have arrived at recognized endpoints. Third, both the control plots with *A. nodosum* and the *F. vesiculosus* stands in large experimental clearings showed resilience to natural ice scour in 2002–2003. Finally, all but one of the large (≥2 m) clearings show no sign of re-colonization by *A. nodosum*, and many of the large clearings have entered a different basin of attraction.

Synthesis of community organization on New England rocky shores

Our hypothesis that mussel beds and rockweed stands are multiple stable states complements rather than opposes the commonly accepted explanation for the occurrence of mussels and rockweeds in the western North Atlantic, and provides a way to reconcile opposing views (Bertness et al. 2004b; Petraitis and Dudgeon 2004b). The current paradigm is that mussel beds and rockweed stands are maintained by strong top-down control that is very site specific

and greatly influenced by water motion (Menge 1976; Lubchenco and Menge 1978; Leonard et al. 1998; Bertness et al. 2002, 2004a). Mussels are better competitors than rockweeds for space, and so rockweeds can only persist in areas where mussel predators are common and active. Moreover, wave surge limits predator activity and lowers consumption rates. Taken together, the early experiments by Menge and Lubchenco (1978) and the later confirmation by others provide an explanation for why mussels dominate exposed shores and rockweeds dominate sites protected from wave surge.

Yet the continuum of hydrodynamic exposure is not a smooth curve but rather a fuzzy set of sites with huge variation in wave surge, and many sites can come to be dominated by either rockweed or mussel assemblages. In particular, our scenario of how the same site can develop into either a mussel bed or a rockweed stand transforms Lubchenco and Menge's (1978) spatial explanation into a temporal one (Fig. 3). Both scenarios involve top-down effects, but differ in how consumer control varies over time and space. Under Lubchenco and Menge's (1978) scenario, consumer control varies spatially as the effects of wave surge change from exposed to protected shores.
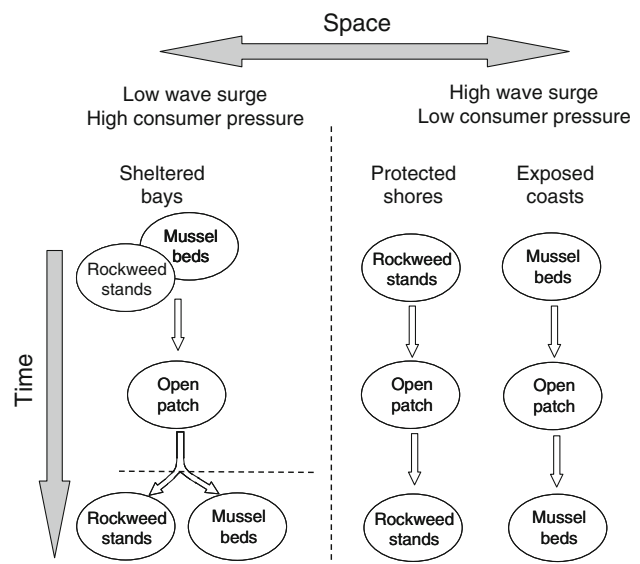

Fig. 3 Development of rockweed stands and mussel beds over time and space. On open coastal shores there is a gradient in wave surge from protected to exposed shores with predators of mussels showing an increase in activity as wave surge diminishes. Work by Lubchenco and Menge (1978) suggested that rockweeds are confined to protected shores where predators are active enough to eliminate mussels. In sheltered bays, both mussels and rockweeds occur as a mosaic of patches and our work suggests that development depends on which species becomes established first. The *horizontal dotted line* shows where a developing patch is "committed" to becoming a mussel bed or rockweed stand. The *vertical dotted line* shows the hypothetical boundary between the two kinds of development, but the transition could also be gradual or not linked to wave exposure alone

In contrast, we envision consumer control varying at a given site during succession and diverging depending upon which foundation species arrives first. Immediately following a disturbance, the capacity of consumers to exert control over succession varies with patch size (Petraitis and Dudgeon 1999; Petraitis et al. 2003). In large patches, succession becomes uncoupled from the surrounding community. Barnacles, mussels and *F. vesiculosus* have better recruitment in large, open areas well away from the canopy edge (Dudgeon and Petraitis 2001), and all three taxa have better success and more time to become established in large open patches than under or near established *A. nodosum* canopies. Barnacles may facilitate both rockweeds (Lubchenco 1983; Kordas and Dudgeon, unpublished data) and mussels (Chipperfield 1953; Seed 1969; Menge 1976; Petraitis 1990), and in large patches it is a race as to which species (*A. nodosum*, *F. vesiculosus* and mussels) will replace barnacles and become established first.

Once either mussels or rockweeds are large enough and common enough in a new patch, these foundation species cause the succession pathways to diverge because of habitat modification and increasing consumer control as the patch closes. In established stands, rockweeds modify the patch habitat by their presence en masse; the canopy blocks the arrival of mussel larvae and provides habitat and refuge for mussel predators (Lubchenco and Menge 1978; Bertness et al. 2004a). In contrast, mussels embedded in established beds not only resist attacks by predators (Petraitis 1987) but also modify the surface through the production of large amounts of pseudofeces so that rockweeds are unable to recruit (P. S. Petraitis and S. R. Dudgeon, unpublished data). These positive feedbacks keep rockweed stands as rockweed stands and mussel beds as mussel beds.

One interesting difference between these views is the direction of the causal arrow between rockweed canopy and mussel predators. Under site-specific top-down control, consumers are the indirect cause of the presence of rockweeds. In contrast, under the model of multiple stable states, the presence of rockweed canopy causes an enhancement of consumer pressure. Rockweeds provide the opportunity for predators to arrive and to keep mussels out of established rockweed stands. This difference points to the fact that these two views are complementary in which the site-specific driven consumer-pressure model is a special case of a more general framework of how communities may be organized in space and time with multiple stable states.

Recent meta-population models provide support for our more general framework (Shurin et al. 2004). Shurin et al. (2004) found that multiple stable states that depended on habitat modification by ecosystem engineers (what they called "biotic heterogeneity") would not be maintained in the system without some kind of abiotic heterogeneity.

Multiple stable states of mussels and rockweeds require both habitat modification and a gradient of an environmental factor such as wave surge which provides refuges for both mussels and rockweeds.

There remain two open questions—one spatial and the other temporal (Fig. 3). First, where is the break on the exposure gradient between the two scenarios? It is possible that our view is a thin slice on the sheltered end of the hydrodynamic gradient, but it is equally possible that multiple stable states comprise a larger subset of shores including moderately exposed ones. Properly designed and well-replicated experiments on more exposed shores have not been done and so this remains an open question (Petraitis and Dudgeon 2004b). Second, there must be a critical size and density at which rockweeds and mussels become ecosystem engineers and begin to modify the habitat and affect consumers. This break may itself be spatially dependent and thus will shift with latitude, exposure, the potential for growth by individuals, and recruitment patterns.

More tantalizing is the possibility that lack of recovery of the *A. nodosum* community state may reflect changing conditions over a much longer time scale. We think stands of *A. nodosum* may be relics that were established prior to the arrival of the herbivorous snail *L. littorea* in the Gulf of Maine in 1858 (Carlton 1982). Two observations suggest that this might be true. Juvenile *A. nodosum* are rare and very old adults are quite common (P. S. Petraitis, S. R. Dudgeon, personal observation). In addition, the survival of *A. nodosum* from zygote to 1 year is much less than 0.1% in the presence of *L. littorea*, which may contribute to *A. nodosum*'s typically poor recruitment (Dudgeon and Petraitis 2005). If *A. nodosum* stands are relics, then the community state may have, upon arrival of *L. littorea*, changed from a stable (i.e., high resistance, high resilience and high elasticity) to a nearly neutral one, and the community state for *A. nodosum* stands would appear as a very shallow bowl between the two deep stable valleys formed by *F. vesiculosus* stands and mussel beds.

Our experiments make clear how difficult it may be to detect multiple stable states under field conditions. Natural ecosystems have become increasingly fragile as an unintended consequence of human activity, and some systems—as diverse as lakes, coral reefs, grasslands, and fisheries—have experienced shifts in species composition which are dramatic and difficult to reverse (May 1977; Scheffer et al. 2001; Scheffer and Carpenter 2003). Yet in many cases it is still not clear if these changes are phase shifts due to undetected changes in environmental conditions or represent true multiple stable states. We suggest the question of phase shifts versus multiple stable states can be addressed by using experimental approaches such as ours that couple benchmark data to establish independent assessments of community states with monitoring to

assess environmental change. It remains an open question if multiple stable states are common in nature, but their occurrence implies that past events—both natural and anthropogenic ones—could play a profound role in structuring present-day assemblages.

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