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Divergent succession and implications for alternative states on rocky intertidal shores

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Abstract

It has been hypothesized that rockweed stands and mussel beds in sheltered bays in the Gulf of Maine, USA, are alternative community states. As a test of this hypothesis, experimental clearings of different sizes were established in stands of the rockweed *Ascophyllum nodosum* (L.) Le Jolis to determine if successional changes in large clearings developed species assemblages distinctly different from the surrounding *A. nodosum* stands. Clearings ranging from 1 to 8 m in diameter were created at 12 sites in 4 bays on Swan's Island, Maine, in 1996 to mimic the effects of ice scour, and abundances of gastropods, barnacles, mussels and fucoid algae were monitored until 2002. ANOVAs and MDS showed strong effects of clearing size and divergent successional changes in large clearings. Large clearings were quickly filled in and remained dominated by the alga *Fucus vesiculosus* L. and the barnacle *Semibalanus balanoides* (L). There was no evidence for site-specific effects, and Mantel tests showed clearing size was a better predictor of species composition than geographic distances among sites. Results suggest that large pulse disturbances using clearings of 8 m in diameter can initiate divergent successional pathways and have a protracted effect on species composition. Results are also consistent with the hypothesis that mussel beds and rockweed stands in sheltered bays may be alternative community states.

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1. Introduction

It is well known that distinctly different assemblages of species often occur within the same habitat or under the same environmental conditions, and the

idea that these different assemblages represent alternative stable states has fascinated ecologists since the 1960s (Lewontin, 1969; May, 1977). Recently, it has been proposed that mussel beds and fucoid rockweed stands on sheltered shores of eastern North America may be alternative states (Petraitis and Latham, 1999) even though these distinctly different communities have long been viewed as being maintained by strong top-down control by consumers (Menge, 1976).

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The traditional paradigm assumes that the occurrence of rockweeds vs. mussels depends on the control of mussels by predators (Menge, 1976; Lubchenco and Menge, 1978; Bertness et al., 2002, 2004). Rockweeds are thought to be poorer competitors for space than mussels, and so rockweeds can dominate rocky shores only in places where mussels are controlled by predators. Predator efficiency is depressed in areas of wave surge, and thus, rockweeds are common on more protected shores.

However, both mussel beds and rockweed stands can occur in very close proximity on sheltered mid-intertidal shores (Lewis, 1964) and so appear to be good candidates for being alternative states (Petraitis and Latham, 1999). In sheltered bays of the Gulf of Maine, rockweed stands are dominated by the furoid *Ascophyllum nodosum* (L.) Le Jolis, and mussel beds are dominated by the mussel *Mytilus edulis* L. and the barnacle *Semibalanus balanoides* (L.). Rockweed stands and mussel beds provide distinct structural habitats (foundation species, sensu Dayton, 1971) that harbor different assemblages of species (e.g., Coleman, 1940; Wieser, 1952; Lewis, 1964; Stephenson and Stephenson, 1972; Tsuchiya and Nishihira, 1985) and typically persist from tens to hundreds of years (Reynolds, 1969; Åberg, 1992a,b).

Ice scour has been suggested as the trigger for the switch between these assemblages in sheltered bays (Petraitis and Dudgeon, 1999; Petraitis and Latham, 1999; Dudgeon and Petraitis, 2001; Petraitis et al., 2003), and while rare, ice scour events can clear large areas of the shore. In the southern Gulf of Maine, sea ice has occurred during approximately 86 winters in 380 years, and severe ice scour significantly affects species composition for years thereafter (Wetthey, 1985). In the northern Gulf of Maine, ice accumulates annually in sheltered bays and may remove as much as 50% of the standing crop of *A. nodosum* (Mathieson et al., 1982, S.R. Dudgeon, P.S. Petraitis, personal observation). In most years, ice does not scrape the surface clean; however, such major events occurred in the winters of 1978–1979, 2002–2003, and 2003–2004 (Markham, 1980, P.S. Petraitis, L. Ranquist, personal observation).

Here we use rockweed stands in sheltered bays to test three predictions that can be drawn from theory if the scale of a perturbation plays a role in the initiation of alternative states (Petraitis and Dudgeon, 2004b).

First, the scale of perturbation should have a significant effect on succession, and succession after a large perturbation should, on average, be quite different from succession after a small perturbation. Second, not all large perturbations would be expected to cause a change from one alternative state to another, and so successional pathways should vary from plot to plot after a large perturbation. This variation should be greater than the variation among successional pathways after a small perturbation. Third, the theory of alternative stable states does not preclude the possibility of site-specific differences (e.g., due to strong local consumer effects) but site-specific effects should be weaker than and uncorrelated with scale-dependent perturbation effects. The experiments described here examine the effects of the removal of *A. nodosum*, which was done to mimic ice scour, and do not consider the “mirror-image” manipulation of mussel beds in sheltered bays because theory suggests that good experimental tests of alternative stable states must show that different communities can occur in the same environment (Peterson, 1984). Changes in mussel beds, which is an important test, should be viewed as a separate experiment in a potentially different micro-habitat type (Petraitis and Dudgeon, 2004a), and such experiments are underway and will be reported elsewhere.

2. Methods

2.1. Study sites and sampling methods

Complete descriptions of research sites, establishment of the experimental clearings, and most of the sampling methods are reported elsewhere (Dudgeon and Petraitis, 2001; Petraitis et al., 2003). Briefly, 12 replicate sites in four bays on Swan’s Island, Maine, USA, were used. The bays are Mackerel Cove and Seal Cove, which are on the north side of the island, and Burnt Cove Harbor and Toothacker Cove, which are on the south side of the island. The experiment was established in the mid-intertidal zone, which is dominated by the rockweed *A. nodosum*. At each site, four experimental plots, which were 1, 2, 4 and 8 m in diameter clearings, and a control plot, which was not cleared, were established. It was not possible to make the clearings during the winter because of limited

access and dangerous conditions due to snow and ice. Thus, plots were originally scraped in July–August 1996, and re-scraped in February 1997 to mimic winter ice events.

The size range of the experimental clearings is within the normal range of major ice scour events, which occur infrequently on Swan's Island. For example, ice removed an average of 13% of the *A. nodosum* cover from the 12 replicate sites during the winter of 2002–2003 (range: 0–39%, P.S. Petraitis, unpublished data). At the three sites with the greatest damage, the average area of naturally created clearings was 25.4 m² (range: 2.4–78.5 m², $n=5$ clearings per site). Our experimental clearings were 0.8–50.3 m² in area.

Abundance and percent cover of the most common species were sampled at least once a year between 1996 and 2002 for a total of 10 times. The sampling times were summer 1996, spring and summer 1997, spring and summer 1998, spring 1999, spring and summer 2000, and summers of 2001 and 2002. Percent cover and densities were not sampled for all species on all dates. Here only the data from 1998 to 2002 are completely analyzed because the 1996 and 1997 data have been analyzed and reported in Petraitis et al. (2003). Data from 1997 are included in some graphs, in the MDS analysis, and the Mantel tests for comparisons of changes over time. Spring samples were taken between mid-May and mid-June, and summer samples were taken between late July and early August.

Mussels (*M. edulis* and *Modiolus modiolus* (L.) and gastropods (*Tectura testudinalis* (Müller), *Littorina littorea* (L.), *Littorina obtusata* L. and *Nucella lapillus* (L.)) were counted using five 50 × 50-cm quadrats per plot. Furoid algae (*A. nodosum* and *Fucus vesiculosus* L.) were counted in five 10 × 10-cm squares that were on the diagonal of each 50 × 50-cm quadrat because of the large number of recruits. The barnacle *S. balanoides* was counted in two 2 × 2-cm squares per 50 × 50-cm quadrat except in 1998 when one square per quadrat was used. Barnacle counts were divided into the current year's recruits and older individuals, which could be distinguished by differences in size and color.

Percent cover data were collected for fucoids, barnacles, and mussels. Cover was estimated by counting the most common space occupier in the

twenty-five 10 × 10-cm squares per 50 × 50-cm quadrat. Percent cover was thus calculated on the basis of 125 counts of presence/absence (25 squares per quadrat × 5 quadrats per plot). A category of "other cover" included all other species, which were rare and bare space. Data for *A. nodosum* percent cover are presented but were not analyzed because removal of the alga was a treatment effect. Quadrats were grouped in the center of each clearing, and the sampling in the uncleared controls was done within 2 m of the reference bolts.

Variables of interest were the densities and percent cover per plot, and so average densities and average percent cover per plot rather than per quadrat were used in the analyses. Note that counts per quadrat may not be independent because randomly placed quadrats overlapped in some plots, but the average of a plot, as long as the observations per plot were taken at random, provided an unbiased estimate of the parametric mean of the plot (Mood and Graybill, 1963, 142–153). There was the potential for problems with precision of the estimates because differences in the spatial spread and overlap of quadrats could have caused heterogeneity of variances, but we found no evidence for this.

The maximum number of averages was 420 (i.e., 5 clearing types per site × 12 sites × 7 sampling dates). Averages for densities and percent cover were $\log_{10}(x + 1)$ transformed for univariate and multivariate analysis because the distribution of averages tended to be right skewed. Visual inspection of transformed data and residuals indicated that the transformed data were normally distributed. Averages and confidence limits reported in the figures are back-transformed.

2.2. Univariate analyses

A mixed model ANOVA design was used to test for the effects of sampling date, clearing size, bay, sites nested with bay, and their interactions. The effects of bay, sites within bays, and interactions with these main effects were treated as random factors. A separate ANOVA was done for each variable. Slice tests (Winer, 1971) were used to examine differences among treatment levels within significant interaction terms. *M. modiolus* density was not analyzed because the mussel was only found at two sites in

Toothacker Cove. Multivariate and repeated measures ANOVAs were not used because of missing data, high dimensionality in multivariate space, and problems with multivariate normality. Preliminary analysis using principal components showed the first three components explained only 50% of the variation. Even though the PC analysis suggested that the response variables were weakly correlated, we were concerned that multiple ANOVAs could inflate the Type I error and thus used sequential Bonferroni tests (Sokal and Rohlf, 1995). SAS/STAT™ software was used to run the ANOVAs.

Variance components analyses were used to examine location-specific effects. If location-specific effects are important, then the variance components for bays, sites within bays, and their interactions should be large. Restricted maximum likelihood methods in SAS/STAT™ software were used to estimate variance components.

2.3. Multivariate analyses

Procrustes analysis, a type of MDS analysis, was used to examine the successional trajectories of different sized clearings in multivariate space. Procrustes analysis fits a candidate matrix to a target configuration (Cox and Cox, 1994). The spring 1997 data were used as the target configuration. Data from the remaining dates were used as the candidate matrices. Software provided with Cox and Cox (1994) was used to do the analysis. Gower's general index of dissimilarity was used to construct the distances among plots. All 60 plots (i.e., 12 sites \times 5 levels of clearing treatment) were included, giving a triangular matrix with 1770 entries for each date. Averages per clearing size (i.e., 0, 1, 2, 4, and 8 m) and per site (i.e., all 12 sites) were graphed for each date (i.e., 9 dates). If location-specific effects are unimportant, then the plot of site averages should show no pattern. Kruskal and Wish's (1978) multiple regression method was used to find meaningful axes in MDS space.

If large clearings are switching to an alternative state, then the changes in large clearings should not only diverge from controls but also be more variable than controls. We used 95% confidence ellipses to examine the spread of the data on the last sampling date. The MDS coordinates for the 2002 data grouped by clearing size were used to calculate the 95% con-

fidence limits on the major and minor axes (Sokal and Rohlf, 1995).

Mantel tests and randomization tests were used to test if the patterns seen in the Procrustes analysis were explained by the size of clearings or by the geographic distances among plots. For size of clearings, the absolute difference in diameter was used as the distance metric (e.g., distance between a 1-m plot and an 8-m plot was 7). The shortest water route between two plots was used for the matrix of geographic distance. Mantel tests are very sensitive to large differences in geographic distances, and so distances were transformed by using the reciprocal of distance to correct for this problem, which is the recommended transformation (Manly, 1997). Signs of these correlations are reversed so that they agree with the correlations based on clearing size. Correlations and z -statistics between matrices were calculated and tested using 1000 randomizations (Manly, 1997). Randomization tests were also used to test if clearing size or geographic distance was a better predictor of the pattern of similarity in the data matrices from each sampling date. The tests were carried out using 1000 randomizations of the standardized cross-products, which were used to calculate the null distribution.

3. Results

3.1. Univariate analyses

Periwinkle snails (*L. littorea* and *L. obtusata*), barnacles, and the fucoid *F. vesiculosus* were the most common species throughout the entire study. Average densities and 95% confidence limits for *L. littorea*, *L. obtusata*, and *F. vesiculosus* were 31.1 (28.7–33.7), 1.4 (1.2–1.6), and 4.4 (3.5–5.4) per 0.25 m², respectively. Average densities and confidence limits for newly recruited and older barnacles were 2.6 (2.3–2.9) and 0.7 (0.6–0.8) per 4 cm², respectively. All other species had densities of less than 1.2 individuals per 0.25 m². Largest overall averages for percent cover were 21.5% (17.7–25.9%) for bare surface, 7.6% (5.9–9.5%) for barnacles, and 4.3% (3.5–5.2%) for *F. vesiculosus*. Neither *A. nodosum* nor *M. edulis* accounted for more than 1% cover by the end of 5.5 years, although both were common in some plots (Fig. 1).

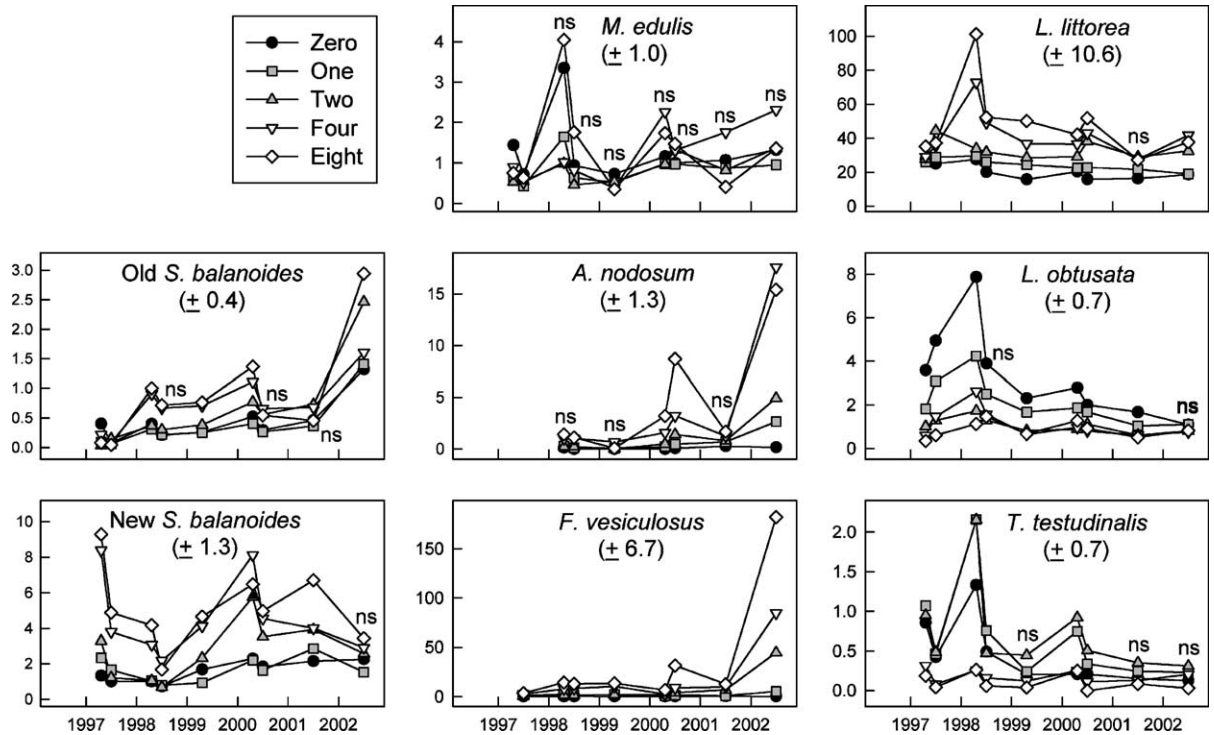


Fig. 1. Average densities for barnacles (*S. balanoides*), mussels (*M. edulis*), rockweeds (*F. vesiculosus*, *A. nodosum*), periwinkles (*L. littorea*, *L. obtusata*) and limpets (*T. testudinalis*). All averages, except for barnacles, are numbers per 0.25 m². Barnacles are numbers per 4 cm². Non-significant effects of clearing size based on slice tests are denoted by “ns.” Numbers in parentheses are average 95% confidence limits, which were estimated from the average range of all back-transformed confidence limits. Calculation of confidence limits used $t=2.2$ ($df=11$). 1997 data from Petraitis et al. (2003).

Sampling date was significant for all variables except *M. edulis* density (Tables 1 and 2). Some species increased in density and cover over time (e.g., algae) and others declined (e.g., herbivorous gastropods). The steady decline in *N. lapillus* from 1.3 per 0.25 m² in 1998 to 0.3 per 0.25 m² in 2002 was unexpected because *N. lapillus* is often found under algal canopies, which increased over time.

Clearing size and its interaction with sampling date had significant effects for most species (Tables 1 and 2). The periwinkle *L. littorea* and the barnacle *S. balanoides* tended to be significantly more common in 4- and 8-m clearings while the periwinkle *L. obtusata* and the limpet *T. testudinalis* tended to be more common in uncleared controls and in 1- and 2-m clearings (Fig. 1). Algal (*F. vesiculosus* and *A. nodosum*) and limpet densities showed significant clearing size by sampling date interactions. Algal densities increased over time with most of the individuals

being less than 2 cm in length. The differences due to clearing size increased over time for algae and declined over time for limpets (Fig. 1). Finally, drops in densities from spring to summer were seen for gastropods and barnacles (Fig. 1; see 1997, 1998, and 2000 in which both spring and summer samples were taken).

Barnacles and *F. vesiculosus* were the two dominant sessile species in terms of percent cover. Both species tended to be more common in larger clearings, but clearing size showed significant interactions with sampling date or bay for both species (Table 2, Fig. 2). By 2002, barnacles were >40% in the 4- and 8-m clearings in the north-facing bays (Mackerel Cove and Seal Cove) while *F. vesiculosus* was >60% in the 4- and 8-m clearings in the south-facing bays (Burnt Coat Harbor and Toothacker Cove). *F. vesiculosus* was >90% in many plots in the south-facing bays. Barnacle cover in 4- and 8-m clearings was often very

Table 1
ANOVAs for densities

Source	df	MS	F	P	MS	F	P	MS	F	P
	<i>L. littorea</i>				<i>L. obtusata</i>			<i>T. testudinialis</i>		
Date	6	0.438	3.67	0.0147	0.836	6.00	0.0014	0.455	9.67	< 0.0001
Size	4	2.247	8.39	0.0018	1.246	4.11	0.0252	0.507	5.26	0.0111
Date × Size	24	0.063	1.53	0.0859	0.060	1.99	0.0133	0.052	2.88	0.0003
Bay	3	0.520	0.30	0.8231	7.499	6.71	0.0065	0.752	1.75	0.2254
Bay × Date	18	0.119	1.74	0.0718	0.139	2.43	0.0096	0.047	1.66	0.0828
Bay × Size	12	0.268	1.47	0.1870	0.303	2.20	0.0376	0.096	1.23	0.3040
Bay × Date × Size	72	0.041	1.12	0.2758	0.030	1.07	0.3553	0.018	1.35	0.0569
Site(Bay)	8	1.581	7.69	< 0.0001	0.868	5.32	0.0001	0.389	4.62	0.0005
Date × Site(Bay)	48	0.064	1.74	0.0049	0.056	1.97	0.0007	0.024	1.78	0.0035
Size × Site(Bay)	32	0.178	4.83	< 0.0001	0.136	4.82	< 0.0001	0.074	5.55	< 0.0001
Residual	192	0.037			0.028			0.013		
	<i>N. lapillus</i>				New <i>S. balanoides</i>			Old <i>S. balanoides</i>		
Date	6	0.451	31.26	< 0.0001	1.123	3.82	0.0124	0.719	9.52	< 0.0001
Size	4	0.136	0.53	0.7158	1.897	12.40	0.0003	0.358	5.06	0.0127
Date × Size	24	0.033	1.11	0.3547	0.072	1.40	0.1387	0.025	1.26	0.2271
Bay	3	2.096	4.92	0.0205	2.264	0.81	0.5182	1.113	3.15	0.0700
Bay × Date	18	0.014	0.46	0.9578	0.294	3.55	0.0003	0.075	2.05	0.0306
Bay × Size	12	0.257	2.47	0.0207	0.153	0.69	0.7503	0.071	1.40	0.2193
Bay × Date × Size	72	0.030	1.08	0.3303	0.051	1.32	0.0681	0.020	1.03	0.4236
Site(Bay)	8	0.289	2.79	0.0188	2.628	10.89	< 0.0001	0.294	4.41	0.0006
Date × Site(Bay)	48	0.029	1.06	0.3808	0.070	1.82	0.0024	0.036	1.87	0.0016
Size × Site(Bay)	32	0.102	3.67	< 0.0001	0.210	5.43	< 0.0001	0.050	2.57	< 0.0001
Residual	192	0.028			0.039			0.019		
	<i>F. vesiculosus</i>				<i>A. nodosum</i>			<i>M. edulis</i>		
Date	6	5.019	17.44	< 0.0001	3.434	16.09	< 0.0001	0.548	1.26	0.3220
Size	4	19.778	15.38	0.0001	4.227	13.64	0.0002	0.185	0.40	0.8027
Date × Size	24	0.605	6.77	< 0.0001	0.351	4.12	< 0.0001	0.124	1.40	0.1378
Bay	3	11.846	4.79	0.0217	0.517	0.50	0.6972	11.055	3.39	0.0793
Bay × Date	18	0.288	2.83	0.0127	0.213	0.68	0.8134	0.434	1.66	0.0869
Bay × Size	12	1.286	1.80	0.0954	0.310	0.75	0.6939	0.460	0.65	0.7867
Bay × Date × Size	72	0.089	0.79	0.8713	0.085	0.96	0.5743	0.089	1.00	0.4875
Site(Bay)	8	1.739	2.31	0.0437	1.238	1.92	0.0760	3.337	3.78	0.0018
Date × Site(Bay)	48	0.125	1.11	0.3076	0.319	3.58	< 0.0001	0.262	2.95	< 0.0001
Size × Site(Bay)	32	0.739	6.56	< 0.0001	0.417	4.68	< 0.0001	0.711	8.02	< 0.0001
Residual	192	0.113			0.089			0.089		

Columns labeled *P* give uncorrected *P*-values with Bonferroni corrected *P*-levels for $P < 0.05$ shown in bold.

extensive during the first 3 years but declined as *F. vesiculosus* became more common (Fig. 2, for the rank correlation between *F. vesiculosus* and *S. balanoides*, Kendall's tau = -0.49, $P < 0.0001$, $n = 120$ pairs based on data from the 4- and 8-m clearings over all sampling dates).

For *M. edulis* percent cover, the significant interaction between clearing size and sampling date was due to exceptional recruitment of mussels into the uncleared controls in 2001. The average mussel

cover was 25% in uncleared controls in summer 2001 but was 0.5% (range: 0–2.8%) in all other plots in all other years.

ANOVA results and variance component analyses showed considerable site-specific variation. Nearly all tests for the effect of sites within bays and its interactions with sampling date and size were significant (Table 3). The major sources of variation were residual error (average = 39%), the interaction of clearing size × site with bays (average = 17%), and the main

Table 2
ANOVAs for percent cover

Source	df	MS	F	P	df	MS	F	P
	<i>S. balanoides</i>				<i>F. vesiculosus</i>			
Date	4	0.287	0.14	0.9630	6	4.638	13.66	<0.0001
Size	4	8.133	14.00	0.0002	4	10.041	7.93	0.0023
Date × Size	16	0.544	2.28	0.0143	24	0.395	4.50	<0.0001
Bay	3	4.839	1.32	0.3077	3	21.311	9.28	0.0023
Bay × Date	12	2.034	3.49	0.0024	18	0.341	2.46	0.0086
Bay × Size	12	0.584	1.16	0.3555	12	1.273	1.66	0.1230
Bay × Date × Size	47	0.239	1.20	0.2106	71	0.088	1.16	0.2206
Site(Bay)	8	2.121	2.63	0.0204	8	1.582	1.97	0.0796
Date × Site(Bay)	32	0.545	2.75	<0.0001	48	0.127	1.67	0.0086
Size × Site(Bay)	32	0.467	2.35	0.0004	32	0.758	9.96	<0.0001
Residual	122	0.198			186	0.076		
	<i>M. edulis</i>				Bare surface			
Date	4	2.780	25.71	<0.0001	4	1.815	3.93	0.0288
Size	4	0.482	6.95	0.0038	4	9.292	13.09	0.0002
Date × Size	16	0.597	8.94	<0.0001	16	0.381	1.80	0.0597
Bay	3	1.143	1.86	0.2587	3	1.471	0.78	0.5268
Bay × Date	12	0.109	0.52	0.8867	12	0.464	1.77	0.1136
Bay × Size	12	0.069	0.48	0.9076	12	0.714	1.59	0.1475
Bay × Date × Size	47	0.067	1.14	0.2814	47	0.212	1.17	0.2512
Site(Bay)	8	0.782	2.82	0.0134	8	1.388	2.96	0.0146
Date × Site(Bay)	32	0.202	3.44	<0.0001	32	0.233	1.28	0.1690
Size × Site(Bay)	32	0.135	2.31	0.0006	32	0.421	2.31	0.0006
Residual	122	0.059			122	0.182		

Columns labeled *P* give uncorrected *P*-values with Bonferroni corrected *P*-levels for *P*<0.05 shown in bold.

effect of sites nested with bays (average=15%). Very little of the total variance for most variables was due to bays or the interaction between clearing sizes and bays (Table 3). Densities of *N. lapillus*, *M. edulis*, *F. vesiculosus*, and percent cover by *F. vesiculosus* were the exceptions and reflected differences between north- and south-facing bays.

3.2. Multivariate analyses

Procrustes analysis showed clear separation based on clearing size but not on location of the sites (Fig. 3). The uncleared controls and 1-m clearings were grouped together in one corner and the 4- and 8-m clearings were grouped together in another corner. The 2-m clearings started out near the uncleared controls and 1-m clearings but drifted towards the 4- and 8-m cluster over time. Densities of barnacles, *F. vesiculosus*, mussels, and periwinkles were the most important variables separating the 0- and 1-m clearings from the 4- and 8-m clearings. Within each cluster, the

year-to-year shifts appeared to be due to percent cover of *F. vesiculosus* and densities of *A. nodosum*. The Procrustes plot based on averages by site showed no obvious pattern over time that could be attributed to site-specific effects.

Patterns of variation and covariation differed between treatments and control. The 95% confidence ellipses were larger for clearings than control plots, but the ellipses were equivalently sized among all clearing sizes. Direction of the major axis can be used to examine differences in patterns of covariation. The slope of major axis was negative for the control plots and positive for all clearing sizes.

Mantel tests and randomization tests showed significant but weak spatial autocorrelations (Table 4). All but one of the Mantel tests for correlations of species composition with either geographical distance or clearing size was significant and positive. Clearings that were similar in size and geographically close to each other tended to be more similar in species composition. Randomization tests comparing

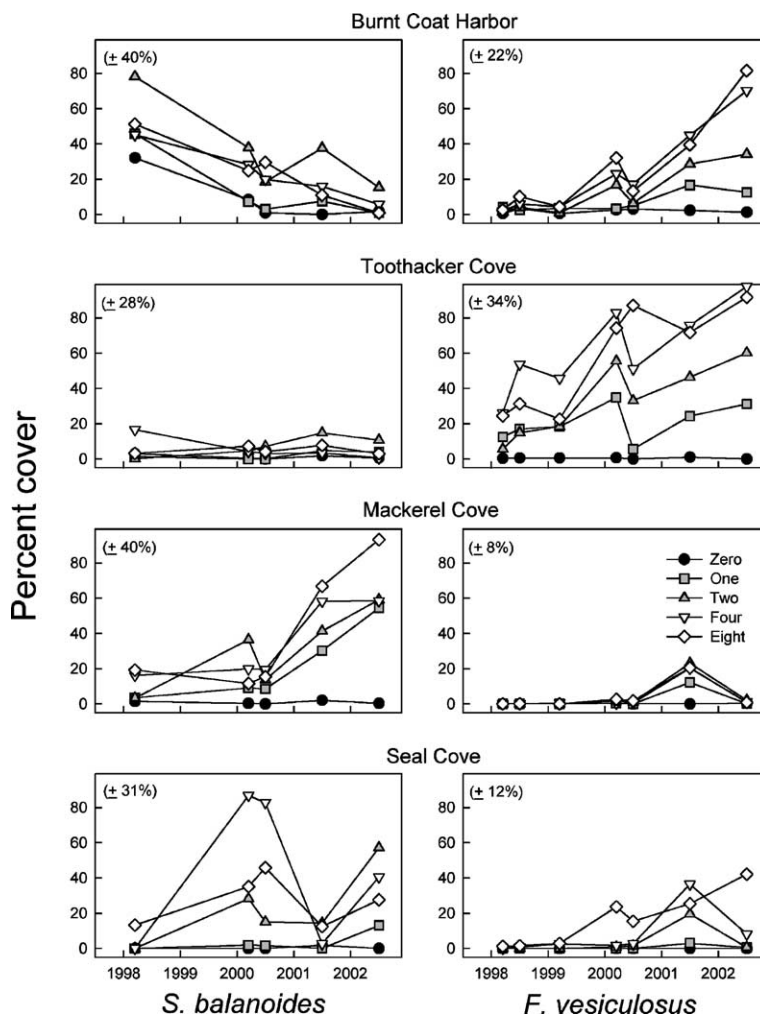


Fig. 2. Average percent cover by barnacles (*S. balanoides*) and rockweed (*F. vesiculosus*). See Fig. 1 for details about non-significance and confidence limits. Calculation of confidence limits used $t=4.3$ ($df=3$).

clearing size against geographical distance showed clearing size was a significantly better predictor of species composition than geographic distance on most sampling dates although correlations were small (average Mantel $r=0.171$ for clearing size and 0.132 for distance).

4. Discussion

We have focused on the successional changes in *A. nodosum* stands because divergent succession in sheltered bays would strongly contradict the current par-

adigm. Sheltered bays in the Gulf of Maine are often dominated by the rockweed *A. nodosum* even though mussels are a superior competitor for space. The most commonly accepted explanation for the occurrence of rockweeds in sheltered bays is strong and persistent consumer control of mussels (Menge, 1976; Bertness et al., 2002). If this explanation is correct, then one might expect succession to be deterministic and canalized across sites and clearing sizes (Berlow, 1997; Bertness et al., 2002).

Yet we found succession to be very idiosyncratic. Clearing size had a significant effect on the succession, and succession in large clearings was quite

Table 3
Variance components of random effects

Source	Variance components as percentages				
	Ll	Lo	Tt	Nl	
Bay	0.00	42.21	7.75	23.59	
Bay × Date	3.22	3.79	3.16	0.00	
Bay × Size	3.55	5.46	2.16	11.06	
Bay × Date × Size	1.41	0.45	3.90	0.00	
Site(Bay)	30.48	13.99	22.08	8.00	
Date × Site(Bay)	5.34	3.79	5.25	0.00	
Size × Site(Bay)	19.92	10.69	21.94	15.84	
Residual	36.08	19.61	33.76	41.50	
	nSb	oSb	Fv	An	Me
Bay	0.00	16.21	25.22	0.00	20.09
Bay × Date	9.38	5.77	3.06	0.00	3.21
Bay × Size	0.00	2.17	7.34	0.00	0.00
Bay × Date × Size	2.64	0.47	0.00	0.00	0.00
Site(Bay)	43.20	14.57	7.90	7.01	20.15
Date × Site(Bay)	4.22	7.56	1.05	21.92	9.67
Size × Site(Bay)	14.68	9.77	25.46	23.26	22.11
Residual	25.88	43.48	29.97	47.81	24.77
	pSb	pFv	pMe	pBare	
Bay	3.06	42.90	4.24	0.00	
Bay × Date	20.55	3.44	0.00	5.20	
Bay × Size	1.15	5.86	0.00	5.81	
Bay × Date × Size	2.38	0.73	0.55	1.78	
Site(Bay)	10.79	5.37	17.88	11.54	
Date × Site(Bay)	13.41	2.23	19.11	1.84	
Size × Site(Bay)	10.78	22.17	9.57	14.92	
Residual	37.87	17.30	48.64	58.90	

ANOVA results are in Tables 1 and 2, and bolded entries are significant. Codes for species: Ll=*L. littorea*, Lo=*L. obtusata*, Tt=*T. testudinialis*, Nl=*N. lapillus*, nSb=young of the year *S. balanoides*, oSb=older *S. balanoides*, Fv=*F. vesiculosus*, An=*A. nodosum*, Me=*M. edulis*, and Bare=other species. Species codes preceded by p are percent cover results; those without are density results.

different and more variable than succession in small clearings. In addition, geographic location of sites and plots within sites, which would be expected to reflect site-specific effects such as local consumer control, is a poor predictor of successional changes.

Our results also support the three predictions based on the theory of alternative states. The first prediction of scale-dependent effects is strongly supported by univariate and multivariate analyses. Overall, the species compositions of the 4- and 8-m clearings were similar to each other and markedly different from uncleared controls. Succession in these large clearings showed no signs of returning to *A. nodosum* stands. In

contrast, species composition in the 1-m clearings tended to be similar to the uncleared controls and in the 2-m clearings shifted from being similar to the control in 1997 to being similar to the 4- and 8-m clearings in 2002.

Scale-specific differences were largest for *F. vesiculosus*, barnacles, and herbivorous snails, which were consistently more abundant in larger clearings. *F. vesiculosus* was the most common space occupier in the 4- and 8-m clearings by the third year, and many individuals had multiple fronds that were greater than 15 cm in length. By the fifth and final year, 25% of the 4- and 8-m clearings had >90% cover with a median of 64%. Barnacle percent cover in larger clearings declined as *F. vesiculosus* occupied more space. Barnacles tended to be more common in north-facing bays, which were more protected, and *F. vesiculosus* were more common in south-facing bays, which faced the open ocean.

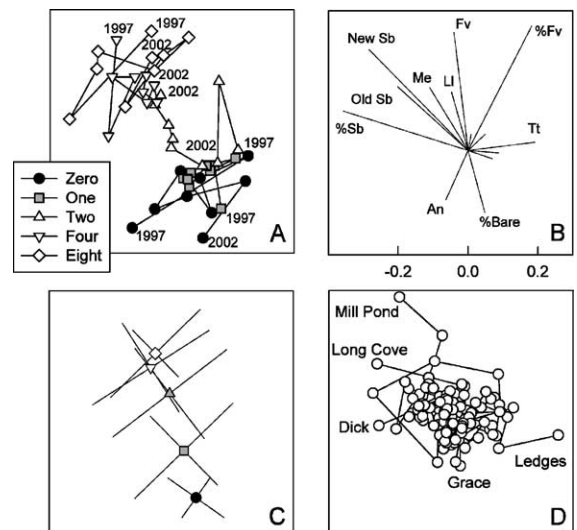


Fig. 3. Plots for Procrustes analysis. Panel A gives averages by clearing size. Years identify the initial and final position for each clearing size. Panel B shows Kruskal and Wish (1978) vectors that define the contributions of variables to the spread of points in Panel A. Lengths of vectors indicate R^2 values; numbers on axis denote lengths equal to R^2 of 0.2. Only the largest vectors are identified. Panel C gives the 95% confidence limits for the 2002 averages from Panel A. Panel D gives averages by site. Site names show positions in 1997 of those sites outside the cloud of points. Codes: New Sb=young of the year barnacles, Old Sb=older barnacles, %Sb=barnacle percent cover, Me=blue mussels, Ll=common periwinkle, Fv=*F. vesiculosus*, Tt=limpets, An=*A. nodosum*, and %Bare=percent "bare" space. 1997 data from Petraitis et al. (2003).

Table 4

Results of Mantel and randomization tests with Mantel correlations (r), z -statistics (z), and significance levels based on randomization tests (P)

Sampling date	Clearing size			Geographical distance			Comparison of r 's	
	r	z	P	r	z	P	z	P
Spring 1997	0.051	2.166	0.016	0.128	5.348	0.001	−3.182	0.007
Summer 1997	−0.068	−2.869	0.001	−0.031	−1.426	0.093	−1.443	0.155
Spring 1998	0.252	10.407	<0.001	0.137	5.698	0.001	4.708	0.000
Summer 1998	0.216	9.128	<0.001	0.164	6.891	0.001	2.237	0.057
Spring 1999	0.157	6.316	<0.001	0.158	6.630	0.001	−0.314	0.426
Spring 2000	0.253	10.304	<0.001	0.168	7.114	0.001	3.190	0.012
Summer 2000	0.308	12.770	<0.001	0.160	6.610	0.001	6.160	<0.001
Summer 2001	0.155	6.621	<0.001	0.166	6.943	0.001	−0.321	0.410
Summer 2002	0.216	9.123	<0.001	0.139	5.808	0.001	3.315	0.010

A. nodosum was also common in 4- and 8-m clearings after 4 years, although *A. nodosum* densities were an order of magnitude less than *F. vesiculosus*. The average density for *A. nodosum* was 1.02 plants per 0.25 m² with a range from 0 to 779 per 0.25 m², and the average and range are very similar to values reported elsewhere (Cervin et al., 2004). Most of the plants were quite small (<2 cm), which suggested they were only 1–2 years old (Dudgeon and Petraitis, 2005).

There were also seasonal differences. Limpets (*T. testudinalis*), periwinkles (*L. littorea* and *L. obtusata*), mussels (*M. edulis*), and barnacles (*S. balanoides*) had larger spring densities followed by smaller summer densities in years when both spring and summer samples were taken. Changes in gastropod densities were probably driven by the generally warmer and dry conditions during the summer, which caused snails to avoid the more open areas in clearings. Spring to summer declines in barnacle and mussel densities resulted from recruitment pulses followed by summer mortality (Dudgeon and Petraitis, 2001; Petraitis et al., 2003). Mussels recruit in the late summer (Petraitis, 1991), and thus, large densities seen in spring 1998 reflect the extraordinary recruitment in late summer 1997 (Petraitis, unpublished data on mussel recruitment from 1985 to 2004).

The second prediction concerning scale-dependent variability is weakly supported. If larger clearings were more likely to switch to an alternative state, then larger clearings should have more variable patterns of succession. However, the amount of variation did not change with clearing size although all clearing

sizes show more variation than the uncleared control plots. There is also a similar pattern seen in covariation with the control plots being quite different from the treatment plots.

Third, variance components, Procrustes analysis, Mantel tests, and randomization tests provide little evidence that location-specific effects had a larger effect on or were a better predictor of species composition and successional changes than clearing size. Variance component analyses showed that small-scale variation within sites was much larger than variation among bays or sites within bays (Table 3). Procrustes plots, Mantel tests, and randomization tests showed clearing size was a better predictor of species composition than geographic location (Table 4). It seems unlikely to us that site-specific effects such as local consumer control will provide an explanation for the broad pattern of mussels and rockweeds on sheltered shores.

Although our results are consistent with Petraitis and Latham's (1999) suggestion that large pulse disturbances can initiate divergent successional pathways, we have not resolved if divergence will lead to alternative community states. Part of the problem is that interpretation of experimental tests of the theory are difficult and contentious (Petraitis and Dudgeon, 1999, 2004a,b; Bertness et al., 2002) even though models of dynamical systems with multiple equilibria are easily constructed (e.g., Scheffer et al., 1993, 2001). The crucial step in both theory and experiment, however, is the initiation of a "switch" (Wilson and Agnew, 1992) that reinforces the establishment of an alternative state. This means that in sheltered bays, ice scour must be large enough to uncouple the

within-patch dynamics from the surrounding environment so that early successional events can set the stage for divergence (e.g., via priority effects and types of succession, Connell and Slatyer, 1977; Drake, 1991; Drake et al., 1996). The uncoupling of patch dynamics from the surrounding environment must also last long enough for mussels to become established because the switches envisioned by Wilson and Agnew (1992) usually involve the modification of the environment by one or more species. This suggests that a switch from rockweeds to mussels cannot occur until mussels reach sufficient size, biomass or age.

While after 5.5 years, our clearings show no signs of becoming mussel beds or returning to rockweed stands, two lines of evidence suggest that the divergence in succession will lead to an alternative state in some large clearings. First, effects of clearing size were often larger than differences among bays and sites within bays, and species composition showed very weak spatial autocorrelation. This suggests any site-specific effect such as local consumer control would be weak or at a very small spatial scale. One of the more striking examples is the pattern of *F. vesiculosus* cover. At the end of the experiment, the average differences in *F. vesiculosus* cover were 50% for control vs. 8 m clearings and <5% among bays for control plots (Fig. 2). Thus, the signature of a single pulse event is far more dramatic than the continued long-term and large-scale variation among bays.

Second, the species responses to the manipulation of clearing size were as large as the responses typically seen in experiments using enclosures. For example, Bertness et al. (2002: Fig. 6) reported a 55% difference in *F. vesiculosus* cover between controls and consumer exclusion cages in unmanipulated plots after 2.5 years. We saw a 51% difference between controls and 8-m clearings in south-facing bays after 3 years (average across all bays at 2 years was 39%; see Fig. 2, year 2000). The effect of a pulse disturbance making an 8-m clearing is comparable to the continuous press effect of a cage over 2.5 years and thus could be a potent force in maintaining divergence over long periods of time.

In addition, our results from the small clearings are consistent with comparable studies of succession in stands of *A. nodosum* done elsewhere. This suggests

that our experimental sites were not atypical of sites used by others, and more importantly, the pattern of succession in small clearings does not provide evidence against the switch to alternative states in large clearings. For example, both Bertness et al. (2002, 2004) and Cervin et al. (2004) observed slow increases in barnacles and *F. vesiculosus* in small clearings in *A. nodosum* stands when cages were not used. Bertness et al. (2002) followed plots in 1 × 1-m and 3 × 3-m clearings in Maine for 2.5 years, and Cervin et al. (2004) monitored 0.8 × 0.3-m clearings on the west coast of Sweden for 4 years. More striking are the results from 2 × 2-m clearings in *A. nodosum* stands that have been followed for 12 years on the Isle of Man (Jenkins et al., 2004). These plots became dominated by *Fucus* spp. (*F. serratus* and *F. vesiculosus*) within 2–3 years following removal of *A. nodosum*, and were still dominated by *F. serratus* after 12 years. Both Cervin et al. (2004) and Jenkins et al. (2004) concluded their plots would revert to domination by *A. nodosum* despite the lack of evidence. Collectively, these studies from both sides of the Atlantic are consistent with our results, which showed prolonged succession with *A. nodosum* remaining rare even in small clearings. We think it remains an open question if even small clearings will revert to *A. nodosum* stands in the near future.

The slow rate of succession in *A. nodosum* stands underscores the fact that historical events such as ice scour events can leave strong and long-term signatures and are likely to be an important factor in community organization. Given that *A. nodosum* and mussel assemblages develop slowly, it is possible that the current dominance by *F. vesiculosus* and barnacles in the large clearings is a transitory state, and these clearings will return to *A. nodosum* stands (e.g., see distinction of Berlow, 1997, between contingent and canalized succession). We suspect that the persistence of *F. vesiculosus* as a transitory state could be quite long given that the average percent cover by *F. vesiculosus* is 5% in old stands of *A. nodosum* (P.S. Petraitis, unpublished transect data) and major ice events occur on the order of 10–20 years. Indeed, experimental patches of *F. vesiculosus* within stands of *A. nodosum* that were established by Vadas in 1974 were still present in the mid-1990s (Vadas, 1992, S. Dudgeon, personal observation).

Finally, we think it is equally plausible that not only the current *F. vesiculosus*-barnacle assemblage but also *A. nodosum* stands and mussel beds are persistent, but not stable, states (Grimm and Wissel, 1997). Mussel beds and rockweed stands may occupy space for long periods of time through the persistence and longevity of established individuals rather than the recruitment of new individuals. Thus, the occurrence of rockweeds and mussels on sheltered shores may be more similar to the alternative states of fouling communities found by Sutherland (1974, 1978, 1981, 1990) in which established individuals held space until they were removed or died. This is a tantalizing idea and very different from the ecosystems with multiple stable points envisioned by Lewontin (1969) and May (1977).

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