Alternative state? Experimentally induced *Fucus* canopy persists 38 yr in an *Ascophyllum*-dominated community

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Abstract. Experimental tests of the hypothesis that ecological communities can exist in "multiple stable states" are rare, and some argue, impossible, because of the unlikelihood that any system will meet the necessary criteria. These are that alternative states (1) are in the same location, (2) experience the same environment, (3) persist for multiple generations, (4) resist repeated perturbations, and (5) result from a pulse manipulation. In 1974, we initiated an experiment testing the ability of *Ascophyllum nodosum*-dominated rocky intertidal communities to recover from complete canopy removal. Manipulations were monitored frequently for 5 yr after clearance and resurveyed again after a 35-yr hiatus. After clearance, *Ascophyllum* was replaced immediately by another fucoid alga, *Fucus* spp, which continued to dominate the space through 1979 despite regular annual recruitment by *Ascophyllum*. Observations in 2009 revealed that *Fucus* spp. still dominated the cleared plots. Surveys in 2011 and 2013 demonstrated that *Fucus* persisted in experimental plots and *Ascophyllum* persisted in adjacent, unmanipulated plots. All criteria for testing an alternative state were met. *Fucus* persisted through multiple generations of both fucoids, a steady annual rain of recruits of both species, a high frequency of storm-driven perturbations, and it resulted from a pulse manipulation. Likely mechanisms include poor *Ascophyllum* recruitment directly under the *Fucus* spp. canopy despite abundant recruitment in adjacent areas, self-maintenance by *Fucus* spp. through high recruitment and fast growth, and recruitment facilitation of *Fucus* by the barnacle *Semibalanus balanoides*. Several lines of evidence indicate that other possible mechanisms including indirect facilitation of fucoids through predation on competitors (mussels), and positive or negative effects of littorine grazing, are unlikely. Although prior results in Maine suggested that the mussel *Mytilus edulis* was an alternative stable state, the new results suggest that *Fucus* spp. was the alternative state to *Ascophyllum*. During the nearly four decades of this experiment, a number of important species including fucoids, littorine grazers, and mussels all declined in abundance, most likely due to climate change. The presumed impact of climate change makes prediction of the long-term response of this system difficult, but it already differs dramatically from its structure in the 1970s.

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INTRODUCTION

The idea that communities might display multiple equilibrial states (multiple stable points, alternative stable states) was first proposed by Lewontin (1969) and explored theoretically by Noy-Meir (1975), May (1977), Beisner et al. (2003), and others. Sutherland (1974) was the first

empiricist to suggest that results of experiments in his system, marine fouling communities, were consistent with this concept. The idea has persisted since, usually under the term "alternative stable states," but demonstrating such states empirically, particularly in a field setting, has been elusive (e.g., Schroder et al. 2005, Petraitis 2013).

Multiple stable states (MSS) are defined as differing "stable" configurations of community structure that exist under the same environmental conditions and persist until a major perturbation causes a transition to another state (Lewontin 1969, Sutherland 1974, 1981, Connell and Sousa 1983, Petraitis and Latham 1999). Because these criteria are at best difficult to meet, documenting the existence of MSS in natural communities has been a challenging and controversial issue. For example, many early proposed examples of MSS (e.g., Holling 1973, Sutherland 1974, 1981, Simenstad et al. 1978) were disputed by Connell and Sousa (1983) as not meeting the criteria necessary to qualify as truly stable states. These workers argued that three criteria must be met to demonstrate an alternative stable state. These are that evidence must be provided that (1) multiple community states are stable, that is, resist or are resilient to perturbations and are persistent; (2) the environment in which these states occur must be the same; and (3) the states should not be maintained via artificial intervention (e.g., removals, exclosures, additions). Other criteria were added by Peterson (1984) and Schroder et al. (2005): (4) The site should be able to sustain two or more alternative communities, (5) the existence of MSS must be demonstrated experimentally, since observations of alternate states could be explained in multiple ways independent of the conditions leading to MSS, and (6) the experiment should be a pulse (see summary in Petraitis 2013). In particular, the Connell and Sousa persistence criterion required that the test must be based on long-term information, spanning at least one turnover of all the populations or communities under investigation (Connell and Sousa 1983). Since many community dominants can live decades to hundreds and even thousands of years, an alternative and less stringent requirement is that states must persist through multiple generations (i.e., time from birth to reproductive maturity) of the longest-lived species (Paine and

Trimble 2004). Following the publication of Connell and Sousa (1983), a flurry of papers appeared discussing whether or not their "required" criteria were likely to ever be met, and proposing alternative or modified criteria (Peterson 1984, Sousa and Connell 1985, Sutherland 1990).

In the 1990s, research in shallow lakes highlighted the likelihood that MSS were common in lakes and other habitats, and posed a major challenge to conservation biologists and ecosystem managers (Scheffer et al. 1993, 2001, Scheffer and Carpenter 2003). Examples from a variety of habitats have been proposed as MSS including terrestrial systems in sub-Saharan Africa (Staver et al. 2011), kelp beds (Estes and Palmisano 1974, Simenstad et al. 1978, Estes et al. 1998), coral reefs (Bellwood et al. 1994, Hughes 1994), fouling communities (Sutherland 1981), and rocky intertidal shores (Petraitis and Dudgeon 1999, Petraitis and Latham 1999, Paine and Trimble 2004, Petraitis et al. 2009). However, despite these examples, the ubiquity of MSS in nature remains unclear.

The difficulty in demonstrating MSS was highlighted by Schroder et al. (2005). Using the three Connell and Sousa (1983) criteria, their own argument that experimental demonstration of MSS was a fourth necessary criterion, and focusing on long-term studies, these authors reviewed the literature through 2004 and found 35 relevant experimental studies across terrestrial, freshwater, and marine environments. Of these, 13 experiments demonstrated MSS, but only two (salt marsh, Handa et al. 2002, old field, Schmitz 2004) were field studies (Chase 2003 was a hybrid; a pond mesocosm done outdoors). This analysis does not enable determination of the question of whether MSS are truly rare, and thus perhaps primarily of theoretical interest, or whether they are common, and thus in some instances at least, may lead to seriously degraded habitats and ecosystems.

Petraitis and Latham (1999) suggested that their study of algal-dominated rocky intertidal systems qualified as an example of MSS. Specifically, they hypothesized that their system existed in two states, fucoid alga (*Ascophyllum nodosum*, *Fucus vesiculosus*)- and mussel (*Mytilus edulis*)-dominated patches. They proposed that these states were driven by ice scour during exceptionally cold New England winters, which could clear fucoids off rock surfaces through tidally

induced abrasion by ice floes (e.g., Wethey 1985, McCook and Chapman 1991, Scrosati and Heaven 2008). Subsequent successional processes were argued to lead to either fucoid recovery or a shift to mussels. They tested their hypothesis using an *Ascophyllum* clearance experiment on a sheltered island on the coast of Maine (Petraitis et al. 2009). They found that *Ascophyllum* clearances >2 m in diameter were taken over (i.e., reached >80% mean cover) either by *F. vesiculosus* (within ~4 yr), or more slowly (~7 yr) and at lower abundance (~13–19% mean cover), by *M. edulis*. In smaller clearances, *Ascophyllum* generally regained dominance within the seven-year duration of the experiment.

In 1974, BAM and JL initiated an *Ascophyllum* clearance experiment in a wave-protected cove at Nahant, MA, aimed at testing the resilience of this community to a simulated major perturbation. Based on similar experiments with macrophytes (e.g., Dayton 1975, Lubchenco 1980) and apparent high annual reproductive output, expectations were that full recovery might take several years. BAM and JL followed recovery trajectories in detail from 1974 to 1979, and plots were resurveyed by MESB and HML in 2011 and 2013. The resurvey was prompted in part by qualitative observations by BAM in 2009 (Fig. 1), suggesting that dominance patterns last observed in 1979 had persisted during the intervening 30 yr. Below, we address four questions: (1) What was the recovery status of the cleared areas after 36–38 yr? (2) Had community structure shifted into an alternative state? (3) Did suppression of barnacle recruitment in the first years of the experiment have a persistent effect? (4) Were changes in the abundance of sessile organisms related to changes in the abundance of consumers?

Results suggest that despite nearly four decades of recovery time, the experimentally induced shift from *Ascophyllum* to *Fucus* domination observed in the 1970s had not changed. That is, the almost immediate shift to an alternative state had persisted for decades, despite the occurrence of several severe winters, annual reproduction of all dominant species, and the passage of many generations of sessile invertebrates and fucoids. Finally, although barnacle recruitment suppression appeared to have persistent effects on aspects of community structure, major declines in the abundance of fucoids, mussels, and littorine
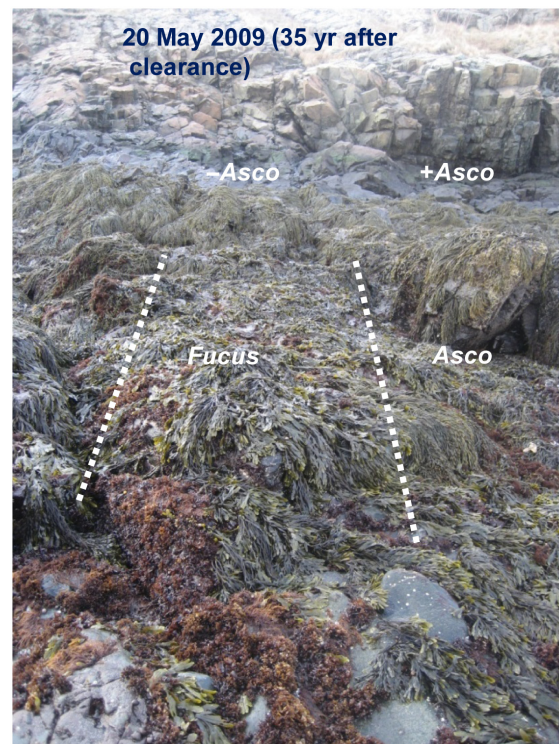

Fig. 1. Photograph of −*Ascophyllum nodosum*−*Semibalanus balanoides* treatment in 2009, 35 yr after the initial clearance. The area delineated by the dotted lines is dominated by *Fucus vesiculosus*. *Ascophyllum nodosum* covers the upper shore and the area to the right of the right dotted line.

snails since the 1970s are most consistent with previously reported, negative effects of climate change.

METHODS AND STUDY SITE

Study site

The research was conducted at Canoe Beach Cove, a rocky intertidal site adjacent to the Marine Science Center of Northeastern University in Nahant, MA (Fig. 2A). This wave-sheltered location has been dominated by the large fucoid alga *A. nodosum* (hereafter *Ascophyllum*) since at least the 1970s, and was a site used in previous experimental research by two of the authors (BAM, JL; Menge 1976, 1978*a*, *b*, Lubchenco and Menge 1978, Lubchenco 1983), and was used more recently by MESB and others at the MSC (e.g., Bryson et al. 2014).

Fig. 2. Photographs of Canoe Beach Cove study site and transect line. (A) A canopy of *Ascophyllum nodosum* covers most of the space in the mid- and upper intertidal zones. (B) Screws installed by BAM in 1974 (bent flathead screws) were relocated in 2009, and transect lines were re-established using lag screws (hexhead screw).

Experimental design

In March 1974, to test the community role of *Ascophyllum* and with the assistance of a marine biology undergraduate class, BAM initiated an *Ascophyllum* removal experiment. Three 2 m wide cross-shore (i.e., high to low intertidal) transects, 14–18 m in length, were laid out from the low to the high tide mark, marked at one-meter intervals with stainless steel screws (Fig. 2B), and sampled using 0.25-m^2 quadrats. We used standard methods to quantify percent cover of all sessile organisms (macrophytes, sessile invertebrates) and density of mobile and solitary sessile invertebrates. In the immediate aftermath of canopy removal, several species of encrusting and foliose algae and invertebrates (e.g., coralline algae, *Chondrus crispus,* several species of colonial invertebrates) suffered heavy mortality, so we also kept track of live and dead covers of these groups. Percent cover estimates in the 1970s were based on counts of randomly placed dots on a 0.5 × 0.5 m plexiglass panel (Menge 1976), and in the 2010s on visual estimates using a 0.5 × 0.5 m frame quadrat divided into 10 × 10 cm subquadrats (see Dethier et al. 1993 for a comparison of these methods). When taxa were especially abundant, counts were made using subquadrats, and densities were adjusted to a 0.25-m^2 basis.

After initial pre-treatment surveys, all *Ascophyllum* (abbreviated as *Asco* in treatments) were removed from two of the three transects with scrapers. To test the potential role of barnacles as facilitators of recruitment and recovery, an additional treatment, removal of the barnacle *Semibalanus balanoides* (*Sbal* in treatments), was applied to one of the two canopy removal transects, establishing three treatments: a control transect (+*Asco*+*Sbal*), a canopy removal transect (−*Asco*+*Sbal*), and a canopy and barnacle removal transect (−*Asco*−*Sbal*). Other invertebrates and algae beneath the canopy were left undisturbed. In the −*Asco*−*Sbal* treatment, barnacle recruits were removed annually with scrapers, steel brushes, and by foot stomping. To avoid affecting fucoid recruitment, we were careful to remove just barnacles. If fucoids were attached to barnacle shells, we left the barnacles and removed them at a later date if possible. On the upper shore, mussels and barnacles were densely interwoven with recruiting fucoid holdfasts, and to avoid damage to the fucoids, we abandoned barnacle reduction efforts after the first three years of the experiment (1974–76). Thus, barnacle removals in the −*Asco*−*Sbal* treatment were a "press" experiment (Bender et al. 1984) through the first three years (1974–76), then a "pulse" for the rest of the experiment, while the initial fucoid removals were a pulse treatment.

Because of variation in the inclination of the shore, the number of quadrat subsamples in each cross-shore transect varied. In the first survey, we "oversampled" by making estimates in quadrat pairs at each meter along a transect tape. Community composition proved consistent within upper and lower shore levels, so thereafter we sampled a single quadrat at each meter. Upper and lower sectors were defined largely by the greater abundance of the herbivorous littorine snail, *Littorina littorea,* on the low shore. The initial number of plots surveyed was 14 (control transect: five upper and nine lower), 18 (canopy-only removal transect: nine upper and nine lower), and 18 (canopy and barnacle removal transect: nine upper and nine lower; numbers were double these for the pre-removal survey).

Recruitment

In New England, recruitment of barnacles is strongly pulsed, occurring only for 1–2 months in spring (e.g., Menge 1976, Lubchenco and Menge 1978, Menge 1991, Bertness et al. 2002, Bryson et al. 2014, Petraitis and Dudgeon 2015). Similarly, recruitment of mussels and fucoids is also temporally limited (summer for mussels, spring and fall for fucoids). Further, recent recruits of all these groups are sufficiently large to be detected by eye, so we also counted them in the field during surveys.

Sampling frequency

To capture short-term responses to the removals, sampling was conducted frequently after initiation (nine surveys in 1974) but with diminishing frequency thereafter (seven in 1975, three in 1976, and one each in 1977 and 1979). In 1977, BAM and JL relocated to the U.S. west coast, and monitoring lapsed after the last survey in 1979. On a visit in 2009, BAM was astonished to observe that the patterns that had been established by 1979 were still evident (e.g., Fig. 1), which prompted resampling by MESB and HL in 2011 and 2013.

Data analysis

In part to comply with constraints on how much fucoid-covered space could be cleared on the property of Northeastern University's Marine Science Institute, and the lack of nearby sites protected from human intervention, this study was pseudo-replicated. That is, it had only one transect associated with each type of treatment (areas of 24, 36, and 36 m^2), thereby constraining the generality of inferences possible from statistical analysis (Hurlbert 1984, 2004). Despite this flaw, such experiments can still contribute importantly to ecological understanding (Oksanen 2001, 2004), and even be iconic (e.g., Paine 1966, 1974). In this case, we believe that this limitation is offset by the unprecedented time-series that these experiments provide for evaluating the potential for alternative states on rocky shores.

In our experiment, plots (subsamples) were sampled repeatedly through time, so we considered each sample date as a temporal replicate (i.e., we substituted space with time). The experiment was surveyed 21 times in the 1970s and four times in the 2010s, so to be conservative in assessing changes in abundance, in most analyses we used data only from the last four surveys conducted in the 1970s. Further, because sampling for algal recruits was not initiated until fall 1974, we limited analysis of recruitment to data from 1975 to 1979. Counts of recruits were not done in the 2010s.

To analyze community-level responses to decade, shore level and treatment, and thereby test for alternative community states, we used PERMANOVA followed by MDS (non-metric multidimensional scaling), using percent cover of algae and sessile invertebrates and density of mobile invertebrates as response variables. To determine the extent of the change in community structure from the 1970s to the 2010s, we evaluated which species contributed most to abundance in each treatment, and to dissimilarity between treatments using SIMPER.

We used three-way analysis of variance (ANOVA) to test effects of decade (1970s, 2010s), shore level (upper and lower), and treatment (+Asco+Sbal, −Asco+Sbal, and −Asco−Sbal) on percent cover of fucoids, mussels, and barnacles, and on density of littorine snails. We also used three-way ANOVA to test effects of year, treatment, and shore level on recruitment of algae and invertebrates in the 1970s. Post hoc comparisons were made using linear contrasts.

Analyses were conducted with JMP v. 12.0.1 (SAS Institute, Cary, North Carolina, USA) and PRIMER v. 6.1.13 (Clarke and Gorley 2006) with PERMANOVA 1.0.3 (Anderson and Gorley 2008). Data were normalized with arcsine (percent cover; sine[square root $x \times 0.01$]) and log transformations (density; ln $[x + 1]$). For PERMANOVA and SIMPER, data were fourth-root-transformed ($x^{0.25}$), and analyses were based on a Bray–Curtis resemblance matrix. Examination of plots of residuals (actual vs. predicted) indicated that transformed data were normally distributed.

RESULTS

Initial community surveys

Our primary goal in selecting the three swaths for the experiment was to have similar covers of *Ascophyllum* in each, and in this, we succeeded (Fig. 3; Appendix S1: Table S1). In the lower zone, where *Ascophyllum* abundance was highest, covers ranged from ~85 to 95% and did not differ among treatments (Fig. 3F). In the upper zone, *Ascophyllum* cover was initially higher in the −Asco+Sbal treatment, but total fucoid cover (*Ascophyllum* + *Fucus* spp.) did not differ among treatments (+Asco+Sbal = 54% ± 10%, −Asco+Sbal = 67.1% ± 8.2%, −Asco−Sbal = 63.3% ± 14.0%; $P = 0.73$, $n = 3$; Fig. 3A). Some differences did occur among other taxa or groups, but these were not systematically associated with particular treatments (Fig. 3; Appendix S1: Table S1). For example, crustose algae were less abundant in the lower zone −Asco+Sbal treatment, *S. balanoides* was more abundant in the upper zone −Asco−Sbal treatment, and *Littorina obtusata* was more abundant in the upper zone −Asco+Sbal and scarcer in the lower zone +Asco+Sbal treatment. Other minor differences occurred with densities of *L. littorea*, *L. saxatilis*, and *Nucella lapillus*, but in no consistent pattern (Fig. 3).

Removal of the *Ascophyllum* canopy had almost immediate negative consequences for several understory species in the lower zone. This was particularly evident for encrusting coralline algae, which was nearly eliminated within days of canopy removal in the −Asco+Sbal treatment and sharply reduced in the −Asco−Sbal treatment (Fig. 4). Some recovery of encrusting corallines
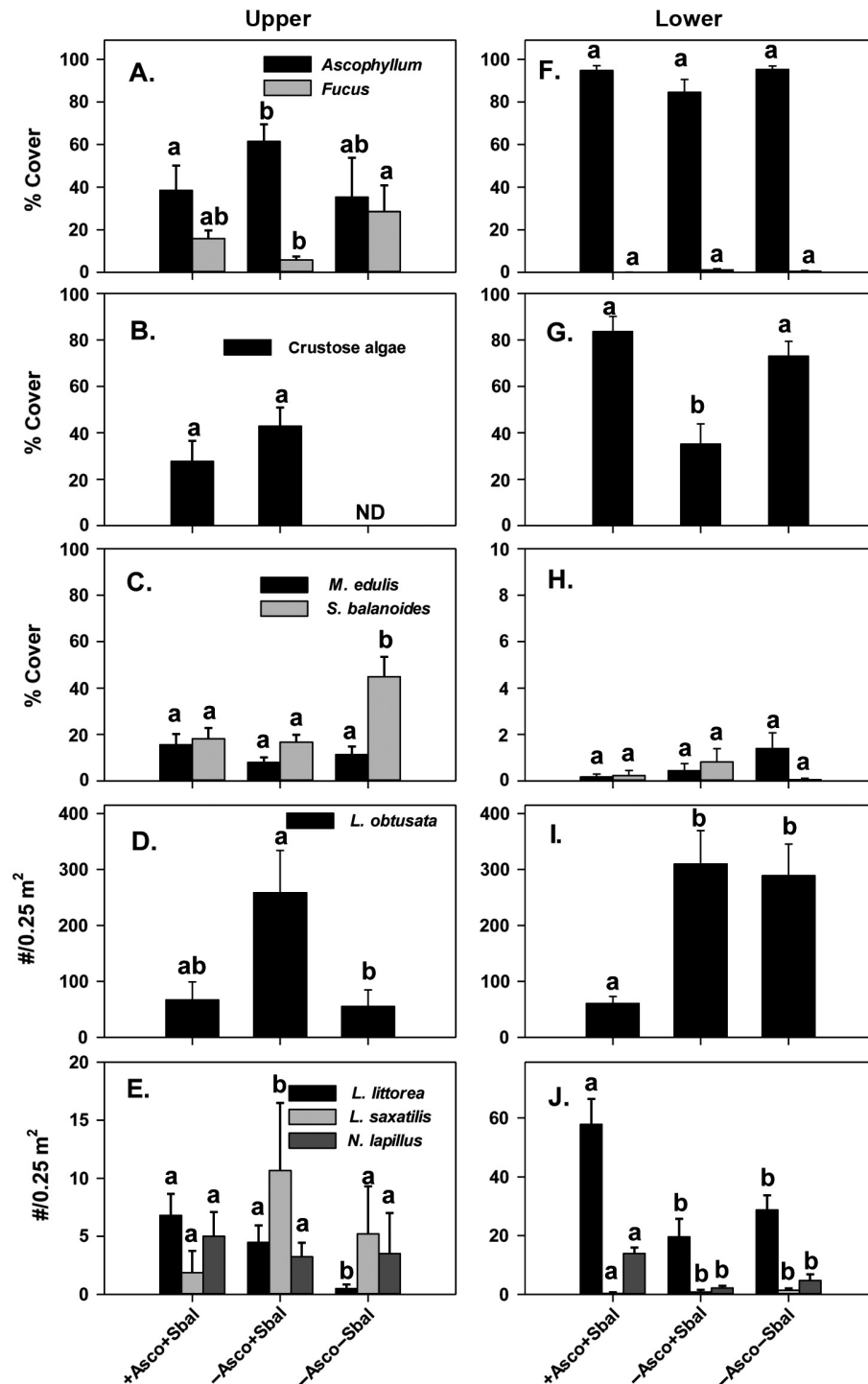
Fig. 3. Initial abundance of major taxa or functional groups. Control (+*Asco*+*Sbal*) data were taken 28 March 1974 and pre-removal experimental (−*Asco*+*Sbal* and −*Asco*−*Sbal*) data were taken 17 March 1974. Bars with the same letter are not different at $P < 0.0167$ (Bonferroni-corrected P for multiple comparisons; linear contrasts) for each taxon or functional group. Bar codes are shown in the left panel (A–E) of each pair of figures.
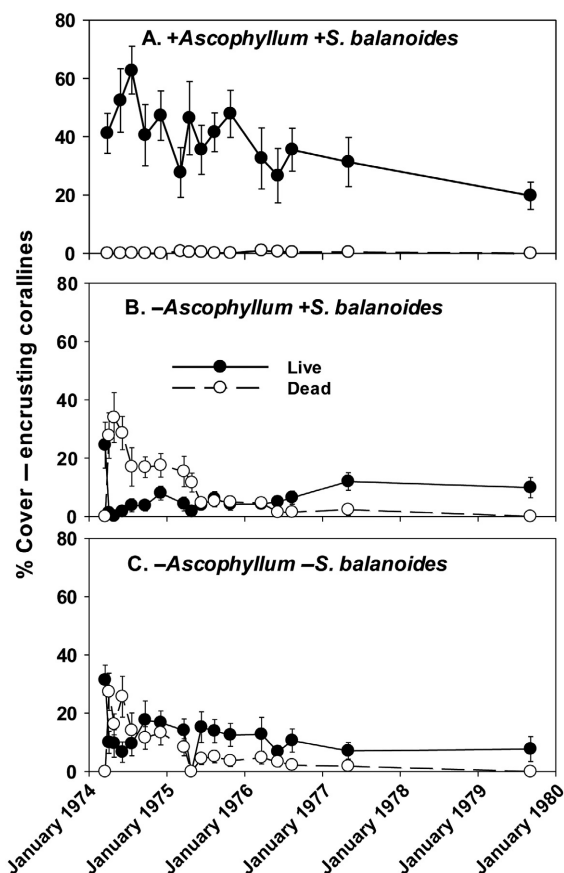
Fig. 4. Changes in the abundance (percent cover) of encrusting coralline algae in the 1970s in three lower shore treatments: A. +*Ascophyllum*+*Semibalanus balanoides*, B. −*Ascophyllum*+*S. balanoides*, and C. −*Ascophyllum*−*S. balanoides.* Data are means ± 1 SE. Encrusting coralline algae were essentially absent from the higher shore.

occurred beginning late 1974, but full recovery to predisturbance cover (~25–40%) had not occurred by 1979 (Fig. 4), or even by the 2010s (cover in −*Asco*+*Sbal* = 2 ± 0.8 to 20 ± 7.1; in −*Asco*−*Sbal* = 0 ± 0 to 8.6% ± 4.1%). As suggested by the steady declines in controls in the 1970s (Fig. 4A) and the persistently low values in controls in the 2010s (2.3% ± 1.5% to 10.1% ± 7.8%), encrusting coralline cover in the understory evidently began a long-term decline in the 1970s if not earlier.

Although mortality of several other taxa (*C. crispus,* several species of bryozoans and hydrozoans) was severe, percent covers were too low (<2%) to analyze. Most of these were upward

extensions into the *Ascophyllum* understory of species that live lower on the shore or in the subtidal.

Community changes—Sessile species

Post-manipulation community structure varied with all factors (Fig. 5; Appendix S1: Table S2, three-way PERMANOVA; treatment × decade $P = 0.026$, treatment × level $P = 0.004$, decade × level $P = 0.001$). The MDS plots (Fig. 5) illustrate these results. Community structure in the 2010s differed strongly by decade but primarily in the lower shore, as shown by the non-overlap of inter-decadal envelopes in Fig. 5C and the inclusion of the 1970s envelope in the 2010s envelope in Fig. 5A. Similarly, treatment effects were most evident in the lower shore than in the upper shore (Fig. 5B, D). Upper shore community structure varied much more widely than did lower shore community structure (Fig. 5). Hence, the inter-decadal comparisons (Fig. 5A, C) suggest that in the lower shore in particular, community structure was in a different state in the 2010s than in the 1970s, and the between-treatment comparisons demonstrate the persistent effect of *Ascophyllum* removal on sessile community structure (Fig. 5B, D).

Rank order of species contributions to structure across all samples varied by treatment (Appendix S1: Table S3; SIMPER analysis). The order of the top five contributors to sessile organism community structure differed sharply between the control and the two treatment transects (Fig. 6). *Ascophyllum* was the lead contributor in the control, but contributed the least in the two treatments (8.96% in −*Asco*+*Sbal* and 6.37% in −*Asco*−*Sbal*). As summarized in Fig. 6 and Appendix S1: Table S3, *Ascophyllum* and *Fucus* spp. were leading contributors to dissimilarities in community structure between control and −*Asco*+*Sbal* treatments (10.71% and 7.48%, respectively; Appendix S1: Table S4). Leading contributors to dissimilarities between control and −*Asco*−*Sbal* treatments included *Ascophyllum* (11.86%) and *Fucus* spp. (5.8%), but algal crusts also contributed to differences between these treatments (*Verrucaria*, 8.06%; crustose corallines, 7.05%; and *Hildenbrandia*, 6.51%). These algal crusts and *Fucus* spp. and *Ascophyllum* contributed similar amounts (~8%) to dissimilarity between the two experimental treatments (Appendix S1: Table S4). Thus, although
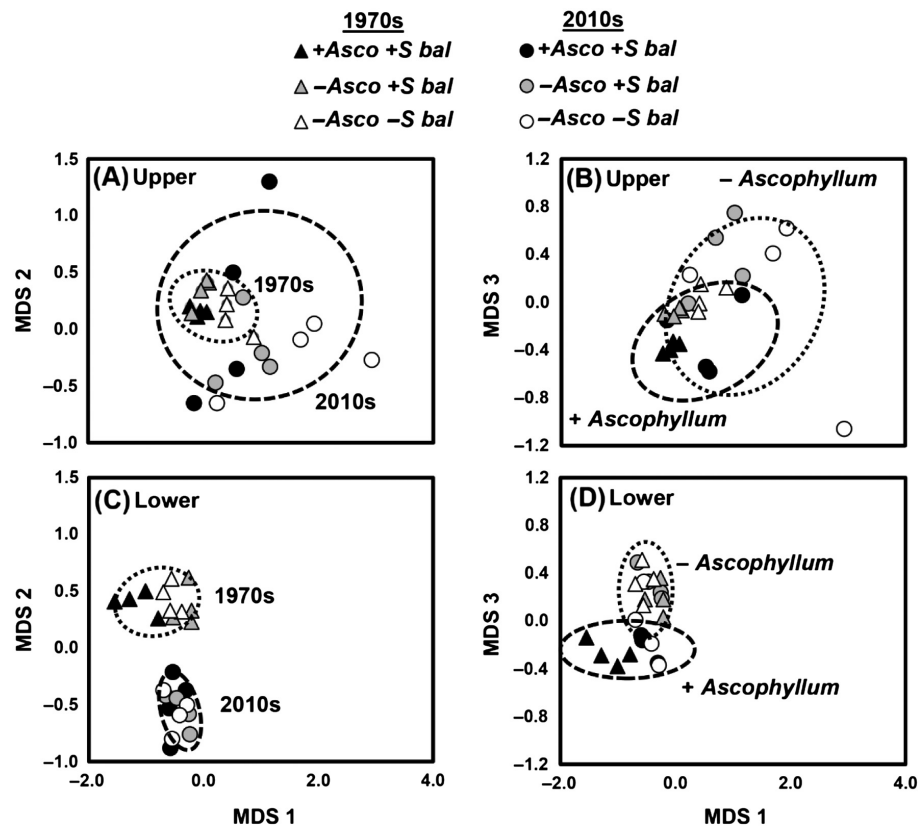
Fig. 5. Non-metric multidimensional scaling (MDS) plots of differences in composition of sessile species associated with tidal elevation, time, and experimental treatment. Upper panels (A, B) depict communities higher on the shore, whereas lower panels (C, D) show communities lower on the shore. Left-hand plots (A, C) show MDS axes 1 and 2, whereas right-hand plots (B, C) show MDS axes 1 and 3. Decadal differences between sessile species assemblages were less apparent higher on the shore (A) than lower on the shore (C; PERMANOVA: decade × level, $P = 0.001$). Treatment differences were also less apparent higher on the shore (B) than lower on the shore (D; PERMANOVA: treatment × level, $P = 0.004$). Shapes of symbols indicate decade (triangles = 1970s, circles = 2010s), whereas shading of symbols indicates experimental treatment (black = +Asco+Sbal, gray = −Asco+Sbal, white = −Asco−Sbal). Ellipsoids delineate 95% CIs surrounding identified groupings. 3-d stress = 0.09 based on fourth root transformation and a Bray–Curtis resemblance matrix.

community compositions remained similar through time, the relative abundance in the treatments contrasted strongly to those in the controls, particularly those of the dominant space occupiers.

Community changes—Mobile species

Mobile species composition varied by treatment and decade (three-way PERMANOVA, $P = 0.034$) and by decade and level ($P = 0.001$), although the treatment effect ($P = 0.020$) was weaker than decade ($P = 0.001$) and level ($P = 0.001$) effects (Appendix S1: Table S5). As with sessile

invertebrates, upper and lower shore and the 1970s and 2010s cluster distinctly in ordination space (Fig. 7). Mobile assemblage structure on the upper shore differed from lower shore structure, and assemblage structure in the 2010s differed from that in the 1970s (Fig. 7A, B). Mobile species varied in abundance weakly with experimental treatment, suggesting that changes in composition were relatively independent of our 1970s manipulations (Appendix S1: Table S5).

Consistent with this conclusion, mobile assemblages in the 1970s were similar to those in the 2010s, with the same rank order in both decades
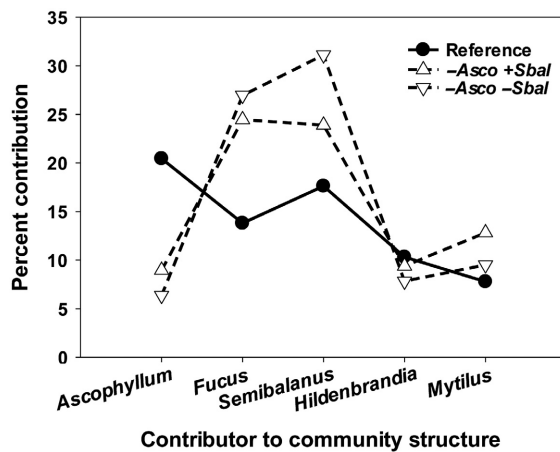
Fig. 6. SIMPER analysis of the percent contribution to sessile community structure of five dominant species. Reference = +*Asco*+*Sbal* treatment. See Appendix S1: Table S3 for details of analysis.

(Appendix S1: Table S6). The littorines *L. obtusata* and *L. littorea* were the main contributors to similarity in the 1970s and 2010s, while the tiny (~3 mm shell length) *L. saxatilis* was the main contributor to inter-decade dissimilarity (Appendix S1: Table S6A–C). The pattern for similarities and dissimilarities in zones was identical (Appendix S1: Table S6D–F). Thus, clearance of *Ascophyllum* had minimal effects on the composition and relative abundance of consumers, but abundance of all common mobile species (*L. littorea, L. obtusata, L. saxatilis, N. lapillus*) decreased through time.

Changes in fucoid abundance

To identify which of the dominant taxa were responsible for most of the changes by decade, zone, and treatment, we used univariate methods. Abundance of *Ascophyllum* varied with decade, treatment, and shore level (Appendix S1: Table S7; three-way ANOVA, three-way interaction, $P = 0.0014$, 2, 36 df, model-adjusted $R^2 = 0.929$). Abundance of *Fucus* spp. also varied with each factor (Appendix S1: Table S7; three-way ANOVA, two-way interactions: decade × treatment interaction, $P = 0.0005$, 2, 36 df; decade × shore level interaction, $P = 0.0083$, 1, 36 df; model-adjusted $R^2 = 0.5799$). In controls in the 1970s, *Ascophyllum* was the dominant canopy space occupier at both shore levels, but occupied only about 50% of space

on the upper shore while occupying 80–100% of canopy space on the lower shore (Fig. 8A, C). *Fucus* spp. was virtually absent on the lower shore but was subdominant on the upper shore, occupying 5–25% of canopy space. In the 2010s, abundance of *Ascophyllum* in controls had declined at both shore levels, from about 50% to about 10% on the upper shore and from about 80% to about 40% on the lower shore (Fig. 8B, D; 70s > 10s,
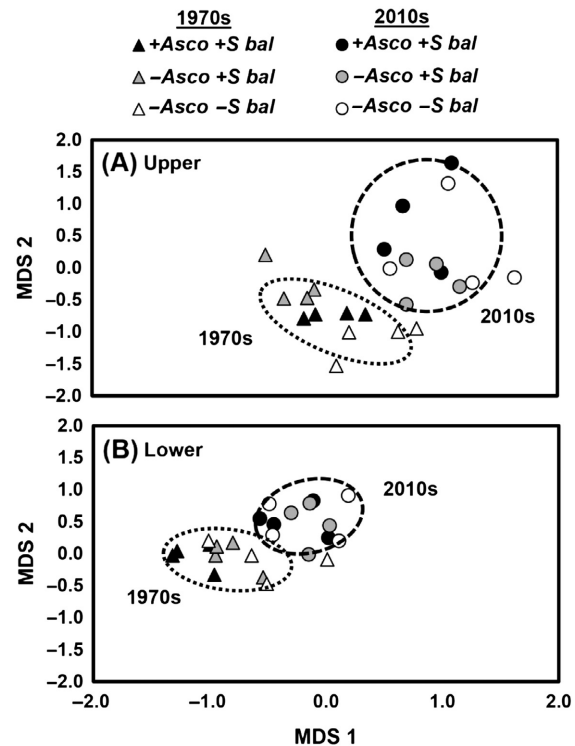

Fig. 7. Non-metric multidimensional scaling (MDS) plots of differences in composition of mobile species associated with tidal elevation, time, and experimental treatment. Panels indicate elevation on the shore: (A) upper intertidal zone and (B) lower intertidal zone. Decadal differences between mobile species assemblages were more apparent higher on the shore (A) than lower on the shore (B; PERMANOVA: decade × level, $P = 0.001$). Shapes of symbols indicate decade (triangles = 1970s, circles = 2010s), whereas shading of symbols indicates experimental treatment (black = +*Asco*+*Sbal*, gray = −*Asco*+*Sbal*, white = −*Asco*−*Sbal*). Ellipsoids delineate 95% CIs surrounding identified groupings. 3-d stress = 0.08 based on fourth root transformation and a Bray–Curtis resemblance matrix.
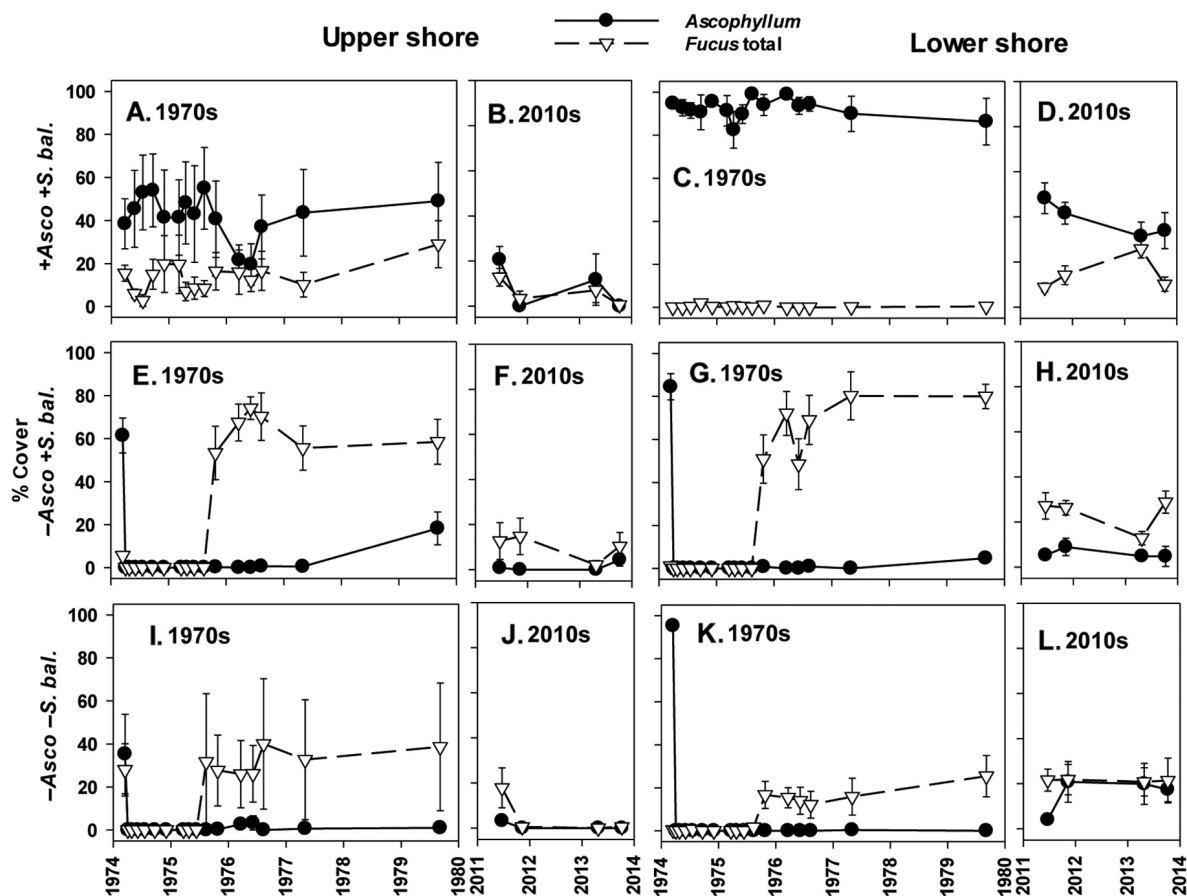
Fig. 8. Percent cover of *Ascophyllum nodosum* and *Fucus* spp. (mostly *F. vesiculosus* but with small amounts of *F. distichus* and *F. spiralis* [latter on upper shore]) on upper and lower shores in the 1970s and 2010s in three treatments: +*Ascophyllum*+*Semibalanus* (+*Asco*+*Sbal*), −*Ascophyllum*+*Semibalanus* (−*Asco*+*Sbal*), and −*Ascophyllum* −*Semibalanus* (−*Asco*−*Sbal*). Data are means ± 1 SE. Symbols and lines for each species are shown above the figures.

linear contrasts in both cases, $P < 0.0001$). On the upper shore, however, *Fucus* spp. abundance did not change from the 1970s to the 2010s (linear contrasts, $P = 0.23$), and actually increased on the lower shore (linear contrasts, $P = 0.029$).

By summer 1975, removal of *Ascophyllum* led to a dominance reversal in the −*Asco*+*Sbal* treatment, with *Fucus* spp. (mostly *F. vesiculosus*) occupying 60% (upper) to 80% (lower) of canopy space, levels that persisted to the 1979 sample (Fig. 8E, G). Removal of barnacles as well as rockweed (−*Asco*−*Sbal*) had no effect on *Ascophyllum* cover (linear contrasts, $P = 0.5$ or greater), but *Fucus* spp. abundance increased less in the absence of barnacles than in their presence in both zones (Fig. 8E vs. I, G vs. K; linear contrasts, upper $P = 0.001$, lower $P = 0.0001$).

Abundance in the experimental treatments in the 2010s revealed four striking patterns (Fig. 8B, D, F, H, J, L). First, in experimental treatments, *Ascophyllum* still had not recovered dominance under any set of conditions, with its highest abundance being 14% (Fig. 9, −*Asco*−*Sbal* treatment; compared to initial abundance of 95% in 1974; Fig. 8K). Second, *Fucus* spp. was still the dominant canopy species in the lower shore in the −*Asco*+*Sbal* treatment (Figs. 8H and 9), and was co-dominant with *Ascophyllum* in the −*Asco*−*Sbal* treatment (Figs. 8L and 9), occupying 9–23.9% of canopy space. Third, in controls, abundance of *Ascophyllum* was dramatically lower in the 2010s than it had been in the 1970s (Fig. 8A–D; linear contrasts upper and lower $P < 0.0001$), declining to about half its original
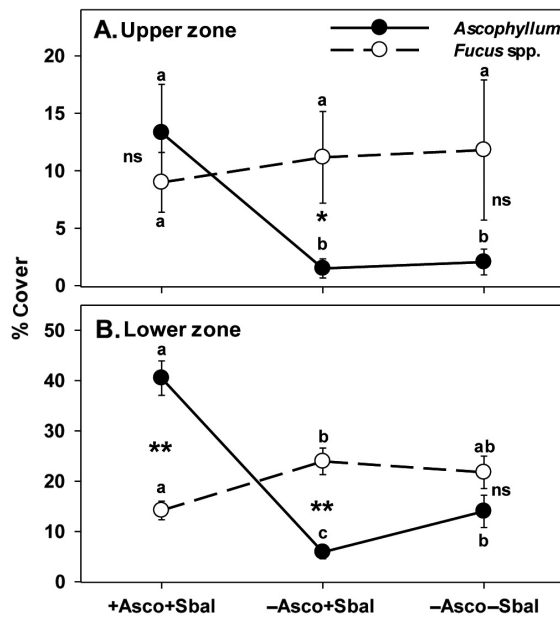
Fig. 9. Mean abundance (±1 SE) of *Ascophyllum nodosum* and *Fucus* spp. in the 2010s in upper and lower zones. Lowercase letters indicate among-treatment differences for each fucoid in each zone (means sharing the same letter are not different in linear contrasts; two-way ANOVA testing effect of zone and treatment: *Ascophyllum*, zone × treatment, $F = 6.14$, 2, 177 df, $P = 0.0026$, adjusted $R^2 = 0.478$; *Fucus* spp., zone main effect, $F = 20.02$, df = 2, 177, $P < 0.0001$, adjusted $R^2 = 0.109$). ** ($P < 0.01$), * ($P < 0.05$), and ns (not significant; $P > 0.05$) indicate significance of differences between species within each treatment. Probabilities were Bonferroni-corrected for multiple *t*-tests. Codes shown in panel A apply to panel B as well.

cover. In contrast, control abundance of *Fucus* spp. had stayed at similar levels in the upper zone (Fig. 8A, B; linear contrasts, $P = 0.23$), but had increased in the low zone (Fig. 8C, D; linear contrasts, $P = 0.029$). Fourth, in the −*Asco*+*Sbal* treatment, abundance of *Fucus* spp. had also declined sharply from the 1970s to the 2010s (Fig. 8E–H; linear contrasts upper $P = 0.036$, lower $P = 0.004$). *Fucus* spp. abundance in the −*Asco*−*Sbal* treatments, already relatively low and/or highly variable in the 1970s, did not change by the 2010s (Fig. 8I–L; linear contrasts upper and lower $P = 0.22$). Since barnacles facilitate recruitment of *Fucus* spp., this pattern was related to the barnacle removal component of this treatment.

Changes in sessile invertebrate abundance

Abundance of spatially dominant sessile invertebrates, mussels (*M. edulis*), and barnacles (*S. balanoides*) also varied with decade, treatment, and shore levels (Appendix S1: Table S7; three-way ANOVA; *Mytilus*: three-way interaction, $P = 0.007$, adjusted $R^2 = 0.653$; *Semibalanus*: three-way interaction, $P = 0.0008$, adjusted $R^2 = 0.515$). In both zones, barnacles tended to be more abundant than mussels (Fig. 10). In the 1970s in controls, both mussels and barnacles were more abundant on the upper shore, but less abundant on the lower shore (Fig. 10A–D; linear contrasts, upper mussels $P < 0.0001$, barnacles $P = 0.0005$, lower mussels $P = 0.03$, barnacles $P = 0.005$). Similar declines in abundance across decades were observed for mussels in the −*Asco*+*Sbal* treatment (Fig. 10E vs. F; linear contrasts $P = 0.0001$), but mussels were generally scarce in the other treatments in the 1970s and 2010s so no temporal changes were detected (Fig. 10, linear contrasts for each treatment × zone × decade combination $P > 0.19$ or more). Barnacle abundance did not differ between decades on the upper shore (linear contrasts $P = 0.32$), but because of dense annual spring recruitment pulses (followed by sharp winter declines) in the 1970s were greater than in the 2010s (Fig. 10G, H; linear contrasts $P = 0.34$). In the −*Asco*−*Sbal* treatment, decadal decline in barnacle abundance occurred on the upper, but not the lower shore (Fig. 10I–L; linear contrasts upper shore $P = 0.0002$, lower shore $P = 0.55$). As noted earlier (and in contrast to the lower shore), control of barnacle abundance on the upper shore ceased after 1976, allowing abundance to follow natural patterns.

Changes in herbivore abundance

Although prior studies indicate that littorines have no direct effect on adult fucoids in this system (Lubchenco 1983, Bryson et al. 2014), *L. littorea* can inhibit recruitment of *Fucus* spp., and both *L. littorea* and *L. obtusata* can facilitate adult fucoid persistence by grazing epiphytes from the adults (Lubchenco 1983). Further, by providing micro-refuges from grazing snails, barnacles serve the important role of fucoid recruitment facilitators (Lubchenco 1983). Since these interactions suggest that our manipulations might have important indirect effects on herbivores, we tested their responses to the pulse/press perturbations.
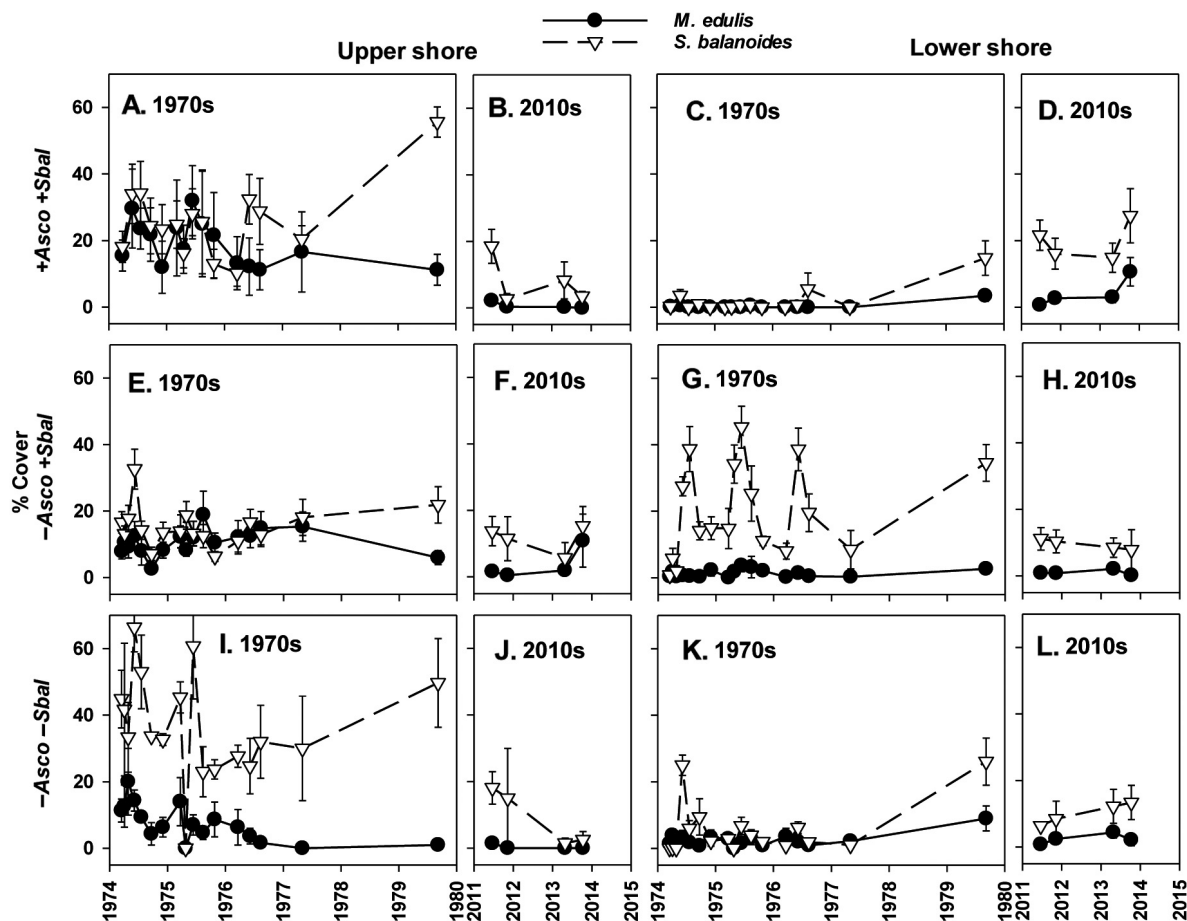
Fig. 10. Percent cover of mussels *Mytilus edulis* and barnacles *Semibalanus balanoides* on upper and lower shores in the 1970s and 2010s in three treatments: +Ascophyllum+Semibalanus (+*Asco*+*Sbal*), top row of panels; −Ascophyllum+Semibalanus (−*Asco*+*Sbal*), middle row; and −Ascophyllum−Semibalanus (−*Asco*−*Sbal*), bottom row. Data are means ± 1 SE. Codes for symbols and lines are shown above the figure.

Littorina littorea abundance varied by all three factors (Fig. 11; Appendix S1: Table S7; two-way interactions: decade × zone and treatment × zone, $P < 0.0001$ and $P = 0.21$, respectively; adjusted $R^2 = 0.724$). Abundance of *L. littorea* did not change through time in the upper zones in any of the treatments (linear contrasts, $P = 0.15$ or higher) or in the lower −*Asco*+*Sbal* treatment (linear contrasts, $P = 0.32$), but was less abundant in the 2010s than in the 1970s in +*Asco*+*Sbal* and −*Asco*−*Sbal* treatments (linear contrasts, $P = 0.0032$ and 0.0011, respectively). In the upper zones in the 1970s, *L. littorea* was least abundant in the −*Asco*−*Sbal* treatment (linear contrasts, $P = 0.03$ and 0.004 for comparisons to the other two treatments, which did not differ, $P = 0.42$). In the 2010s, densities in

the +*Asco*+*Sbal* treatment were greater than in the −*Asco*−*Sbal* treatment (linear contrasts, $P = 0.042$), but no differences were observed in other among-treatment comparisons. In the lower zones in both the 1970s and 2010s, *L. littorea* abundance did not vary among treatments (linear contrasts, $P = 0.16$ or higher).

Littorina obtusata abundance also varied across all three factors (Fig. 11; Appendix S1: Table S7; two-way interactions: decade × zone and decade × treatment, $P = 0.017$ and 0.019, respectively; adjusted $R^2 = 0.681$). With the exception of the lower shore −*Asco*−*Sbal* treatment (linear contrast, $P = 0.5$), abundance of *L. obtusata* was less in the 2010s than in the 1970s in all zones and treatments. Within decades,
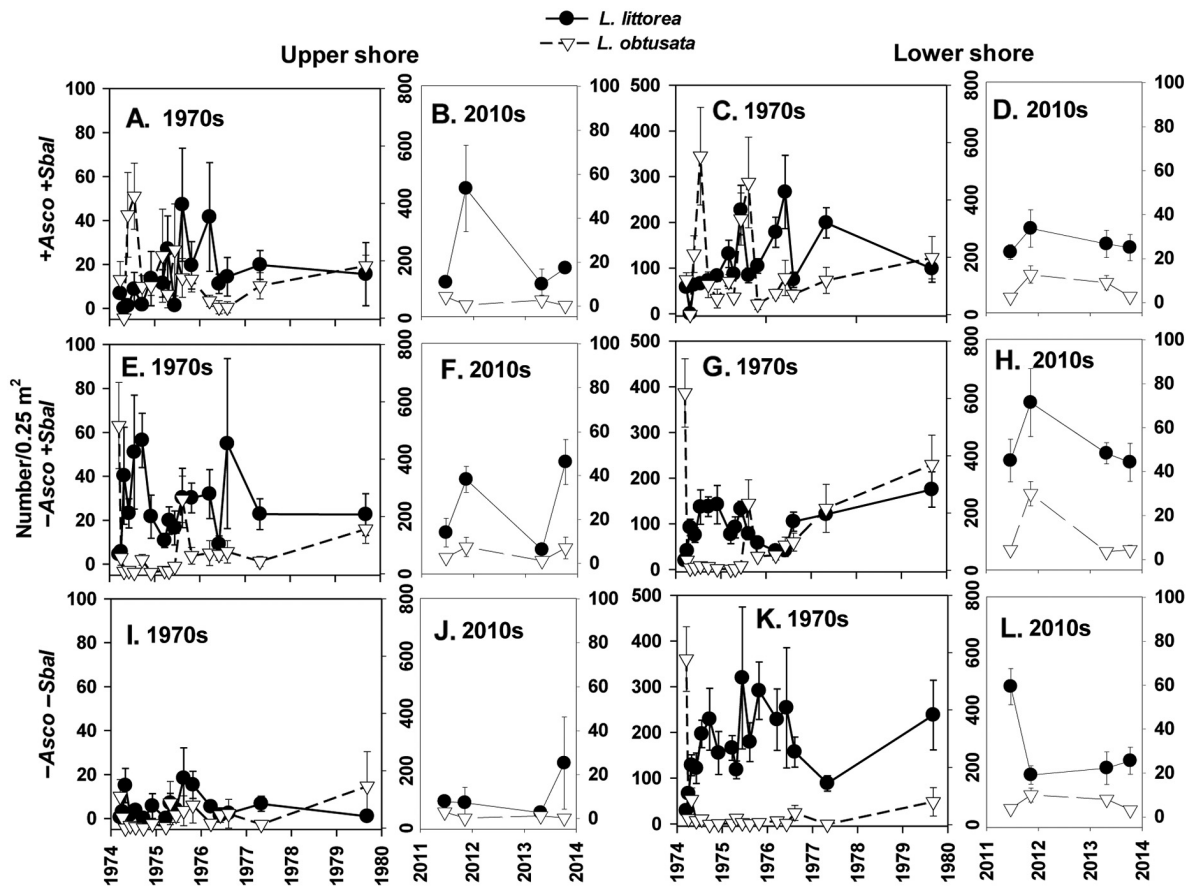
Fig. 11. Density (number/0.25 m^2) of the snails *Littorina littorea* and *L. obtusata* on upper and lower shores in the 1970s and 2010s in three treatments: +*Ascophyllum*+*Semibalanus* (+*Asco*+*Sbal*), top row of panels; −*Ascophyllum*+*Semibalanus* (−*Asco*+*Sbal*), middle row; and −*Ascophyllum*−*Semibalanus* (−*Asco*−*Sbal*), bottom row. Data are means ± 1 SE. Note that *y*-axis scales vary: 1970s panels (A, C, E, G, I, and K) show *L. littorea* density on the left axis and *L. obtusata* density on the right axis (range for all 0–800), and the scales for *L. littorea* differ between upper (0–100) and lower (0–500) shores. Scales in 2010s panels (B, D, F, H, J, L) are all on the right *y*-axis and are all the same, 0–100.

abundance did not differ in either the 1970s or 2010s in either upper or lower zones (linear contrasts, *P* = 0.14 or higher).

Recruitment

Ascophyllum recruitment was always low relative to that of *Fucus* spp. (Fig. 12; Appendix S1: Table S8). For both *Ascophyllum* and *Fucus* spp., recruitment varied with all factors (Fig. 13; Appendix S1: Table S9; *Ascophyllum* – two-way interactions: year × treatment and year × zone; *P* < 0.0001 and 0.016, respectively, adjusted *R*^{2} = 0.602; *Fucus* spp. – three-way interaction;

P = 0.011, adjusted *R*^{2} = 0.333). Averaging across time (using only periods when recruitment occurred: spring months for barnacles, spring and fall for fucoids, summer for mussels; Figs. 13 and 14), both fucoids recruited at much higher densities on the lower shore in the absence than in the presence of a canopy (Fig. 12A, B; two-way ANOVAs: *Ascophyllum* *P* = 0.007, adjusted *R*^{2} = 0.118; *Fucus* spp. *P* = 0.001, adjusted *R*^{2} = 0.157). On the upper shore, *Ascophyllum* also recruited at higher densities in the absence of a canopy (Fig. 12A). In addition, *Ascophyllum* also recruited at higher densities in the presence
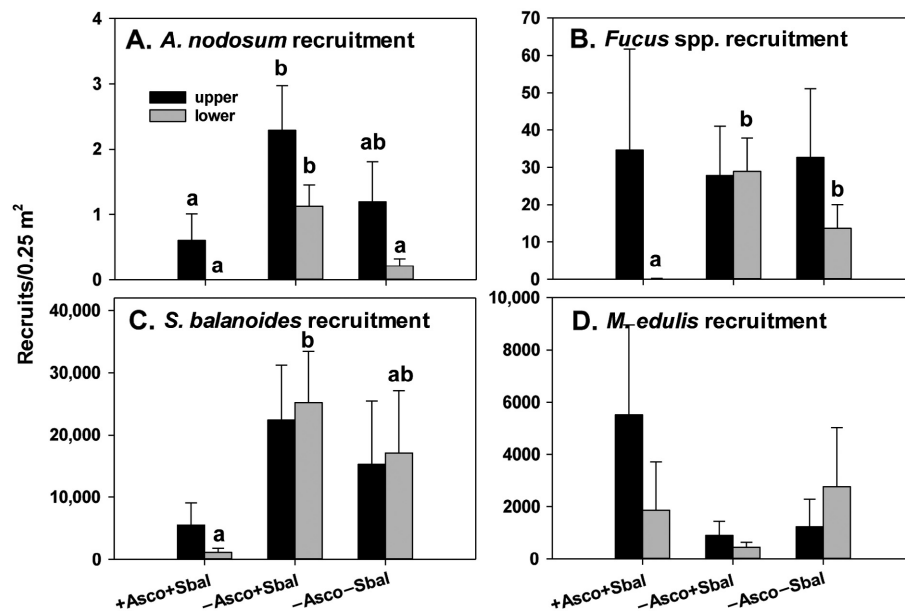
Fig. 12. Recruitment (number/0.25 m²) of A. *Ascophyllum nodosum,* B. *Fucus* spp., C. *Semibalanus balanoides,* and D. *Mytilus edulis* on upper and lower shores in the 1970s in three treatments: +*Ascophyllum*+*Semibalanus* (+*Asco*+*Sbal*), −*Ascophyllum*+*Semibalanus* (−*Asco*+*Sbal*), and −*Ascophyllum*−*Semibalanus* (−*Asco*−*Sbal*). Data are means ± 1 SE. Note that y-axis scales vary among treatments and shore levels.

of *Semibalanus* (Fig. 12A), especially on the lower shore. *Fucus* spp. recruitment was not affected by canopy cover on the upper shore (Fig. 12B).

Barnacles settled at vastly greater densities than did the fucoids, and on the lower shore, barnacle recruitment was greatly reduced in the presence of a canopy (Fig. 12C; two-way ANOVA, treatment effect P 0.023, adjusted R^2 = 0.108; linear contrasts). A similar but non-significant trend was observed in the upper zone (Fig. 12C). Although mussel recruitment was also far greater than that of fucoids, no differences were detected among treatments or zones (Fig. 12D; two-way ANOVA, P = 0.56 or higher), although potential differences in the +*Asco*+*Sbal* treatment may have been obscured by high spatial and temporal variance.

Discussion

Two results of this experiment stand out: (1) The alternate, *Fucus* spp.-dominated state induced by the removal of the *Ascophyllum* canopy persisted for 38 yr without reverting back to an *Ascophyllum*-dominated state and (2) the abundance of five of the six dominant species in this system (fucoids, mussels, littorines) all declined during

these nearly four decades. Below, we explore the likely reasons underlying these results and their ecological implications.

Do these results demonstrate an alternative state?

Ascophyllum nodosum is a classic example of a long-lived, iteroparous organism. Age estimates of individuals range from decades (50–60 yr) to centuries (>100 yr), depending on whether or not a location is subject to ice scour (Aberg 1992). *Ascophyllum* reproduces annually, producing (on Swedish shores) ~2.5 × 10⁹ eggs/m² per year, and with annual reproductive effort ranging from 33 to 74%, where reproductive effort = reproductive biomass/ (reproductive biomass + net annual growth) (Aberg 1996, Aberg and Pavia 1997). Similar to our results in Massachusetts, recruitment in Maine was low despite an enormous annual investment in reproductive output, likely a result of low tenacity of the sporelings (Vadas et al. 1990). In laboratory experiments, even modest flow can remove most or all *Ascophyllum* recruits (Vadas et al. 1990). Similar results have been observed elsewhere for other fucoid species (Taylor and Schiel 2003, Taylor et al. 2010). Our field observations in the 1970s indicated
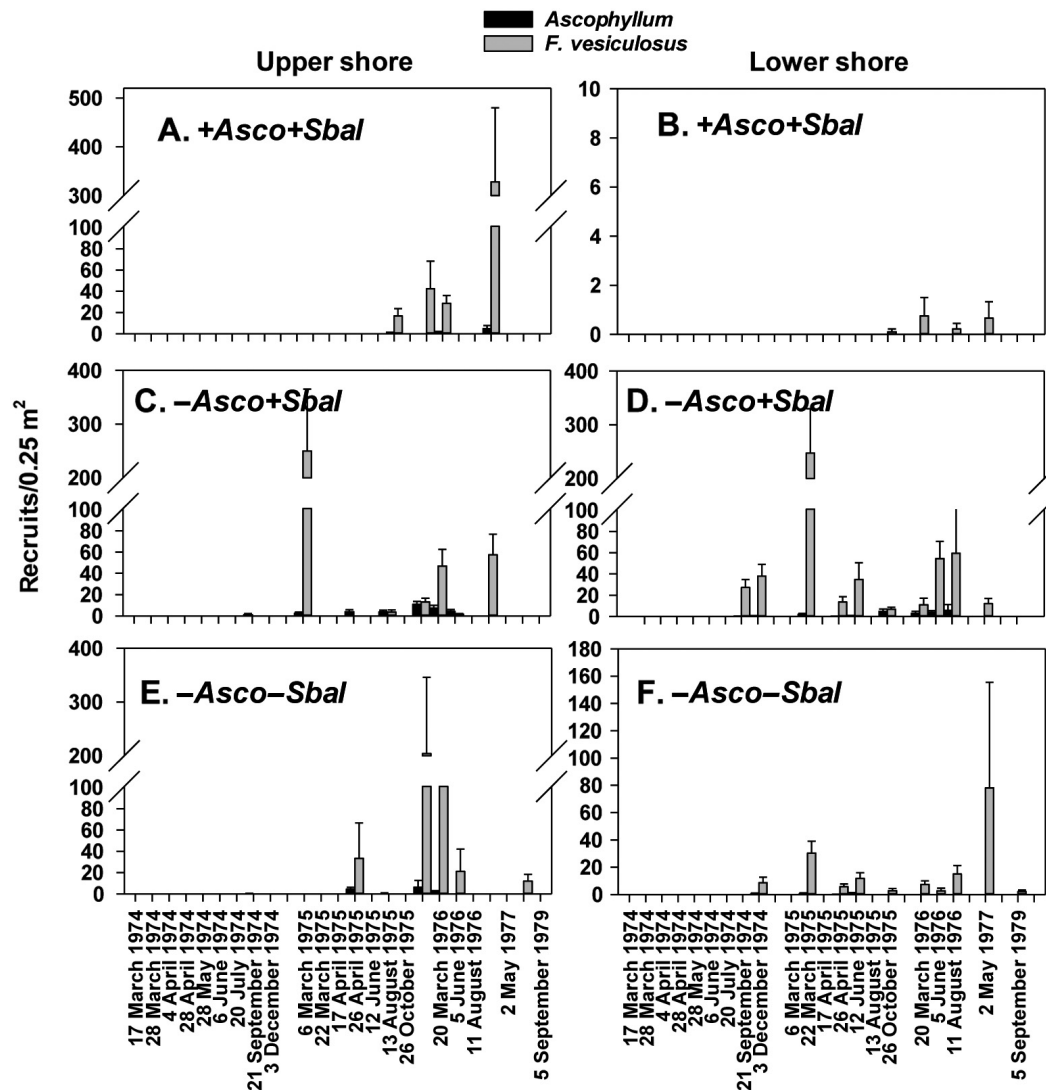
Fig. 13. Recruitment (number/0.25 m^2) of *Ascophyllum nodosum* and *Fucus* spp. on upper and lower shores in the 1970s in three treatments: A, B, +*Ascophyllum*+*Semibalanus* (+*Asco*+*Sbal*); C, D, −*Ascophyllum*+*Semibalanus* (−*Asco*+*Sbal*); and E, F, −*Ascophyllum*−*Semibalanus* (−*Asco*−*Sbal*), bottom row. Data are means ± 1 SE. Note that *y*-axis scales vary among treatments and shore levels.

that even gentle finger touches were sufficient to knock sporelings off the rock (B. A. Menge, *personal observations*).

Slow recovery by *Ascophyllum* after clearance to the rock surface has been reported previously (Keser and Larson 1984, Jenkins et al. 2004, Ingolfsson and Hawkins 2008, Bryson et al. 2014), with recovery periods reported to take 20 yr or longer. *Ascophyllum* recovery rates tend to be long relative to other fucoids. For example,

recovery of the fucoid *Hormosira banksii* in New Zealand occurred within three to eight years depending on site (Schiel and Lilley 2007, 2011).

Some evidence suggests that *Ascophyllum* recovery rate is dependent on the size of the clearance. For example, Petraitis (2013; see also Petraitis and Dudgeon 2004*a, b*) noted that *Ascophyllum* recovery in small (1 m^2) clearances occurred within three years, while in plots >2 m^2 *Ascophyllum* had not recovered after nine years of monitoring. If
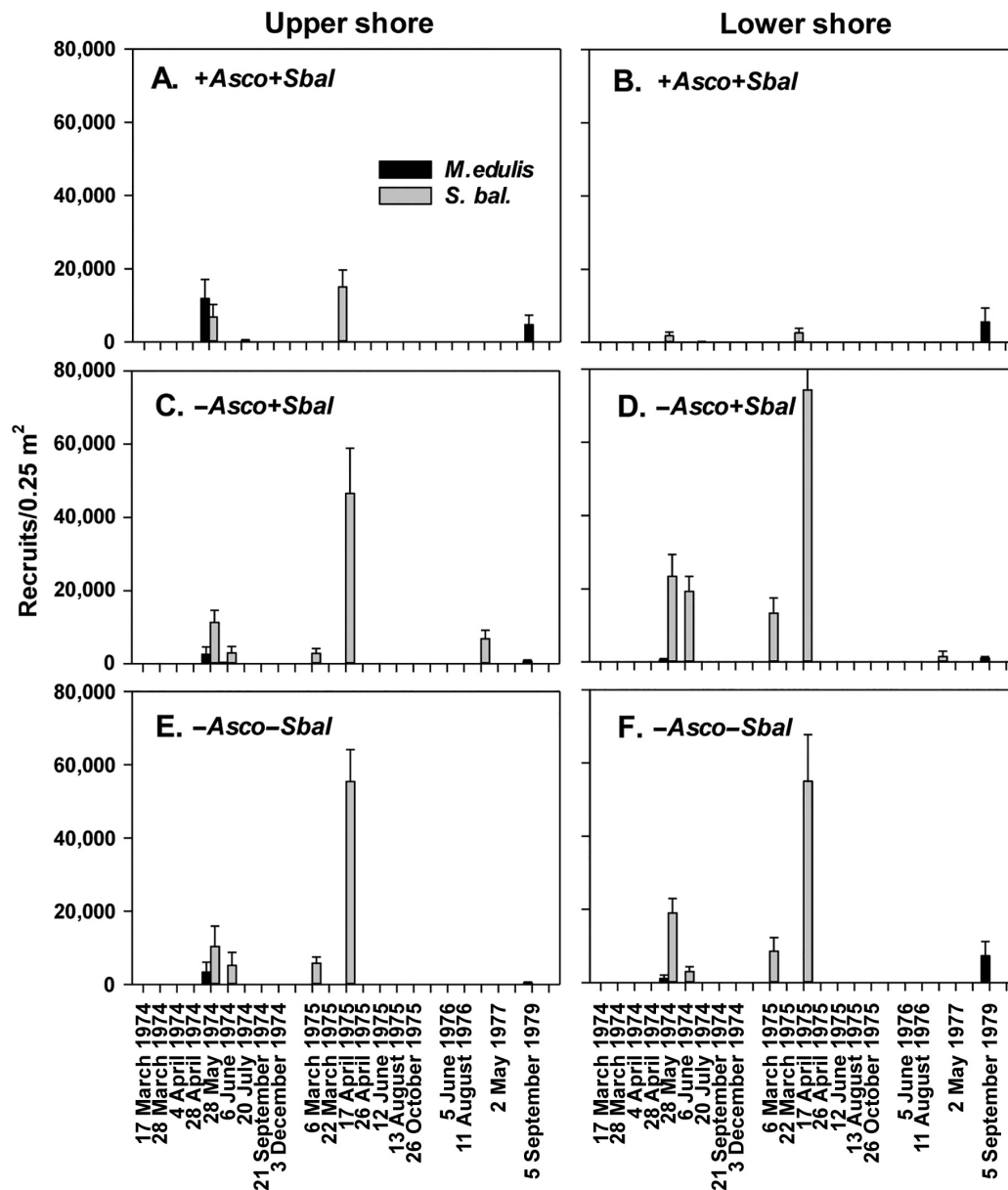
Fig. 14. Recruitment (number/0.25 m^2) of *Mytilus edulis* and *Semibalanus balanoides* on upper and lower shores in the 1970s in three treatments: A, B, +*Ascophyllum*+*Semibalanus* (+*Asco*+*Sbal*); C, D, −*Ascophyllum*+*Semibalanus* (−*Asco*+*Sbal*); and E, F, −*Ascophyllum*−*Semibalanus* (−*Asco*−*Sbal*), bottom row. Data are means ± 1 SE.

removal of *Ascophyllum* leaves the holdfast and parts of the stipe, however, as in harvesting efforts, recovery also can be fast, within two to three years (Keser et al. 1981, Ang et al. 1996, Ugarte et al. 2006). Bryson et al. (2014) observed that recovery of *Ascophyllum* varied geographically along the New England coast. Over seven to eight years,

recovery at Nahant, MA, was slow (15% cover) to absent (0% cover) at wave-protected and wave-exposed sites, respectively, and faster (43% cover) to slow (~6% cover) at wave-protected and wave-exposed sites near Lubec, ME.

Our discovery of little to no recovery after 38 yr appears to be the slowest measurement of

resilience of *Ascophyllum* on record. The lack of recovery was particularly surprising to us since we observed annual recruitment of *Ascophyllum* in both cleared plots during our surveys in the 1970s, suggesting that recovery might occur within 10–15 yr. These patterns contrast with the changes observed in *Fucus* spp. (mostly *F. vesiculosus*), which had become the dominant canopy in the removal swaths by summer of the second year of the experiment (Fig. 8). This dominance continued through 1979, five years after the clearances, and *Fucus* spp. was still the dominant (or co-dominant) canopy in the 2010s. At the community level, the assemblages differed at the levels of shore, decade, and importantly, treatment (Fig. 5). That is, by the 2010s, community states differed both across decades and among treatments begun in 1974.

Does *Fucus* spp. qualify as an alternative stable state? It is debatable that an alternative stable state could ever be documented, given that most systems studied to date vary considerably, require long-term observation to document persistence, and in recent decades have been impacted by a changing environment. As noted in the *Introduction*, several criteria must be met for a community state to be considered a true stable state (Connell and Sousa 1983, Peterson 1984, Paine and Trimble 2004, Schroder et al. 2005). States must persist for a long time, spanning multiple generations of the dominant (or all) species, be resistant to subsequent perturbations, occur in the same location with the same environment, be the result of a pulse experiment, and not be artificially maintained by repeated, press-type manipulations. They must also be "stable" in the sense of persisting at about the same levels of abundance and the same species composition through time. It seems more likely, and less controversial, that "alternative states" whether stable or not are more likely to be demonstrable.

Although we did not observe the experiment between 1979 and 2009, we believe it is unlikely that the dominance of *Fucus* spp. changed during this time. As noted above, the main alternative dominant, *Ascophyllum*, has an extremely slow turnover, with poor abilities to colonize and replace existing stands of *Fucus* (or any other potential dominant). Thus, we suggest that, at least, our results document an alternative state. *Fucus* spp. dominated removal treatments for about 35 yr, and since they reproduce annually

for about 2/3 of the year and live for 2–4 yr (Keser and Larson 1984), multiple generations were clearly spanned. *Ascophyllum* reaches reproductive maturity at 3–5 yr, and has a generation time of 6–10 yr (Sundene 1973), so during our study four to six generations had occurred. Recent observations suggest that *Ascophyllum* remains reproductive; after three months in clearances *Ascophyllum* recruits covered an average of 1.7% + 0.6%, and up to 30% in some plots (M. E. S. Bracken, *unpublished data*). Over the long term, however, as indicated by our study, most such recruits fail to establish. Multiple perturbations such as "Nor'easters" (major storms occurring 20–40 times per year; Zielinski 2002) and the formation of coastal sea ice (Wethey 1985, McCook and Chapman 1997, Petraitis et al. 2009, Muhlin et al. 2011) occurred during this 35-yr period. The experimental plots were clearly in the same place and experienced the same environment, being separated from one another by only 1–2 m. With the exception of barnacle removal in one treatment during the first few years of the experiment, the experiment was a pulse, with *Ascophyllum* being removed once, in spring 1974. No subsequent manipulations were performed to maintain the different community states. Finally, the community states that existed in 2013 were clearly different from one another, with different abundance of dominants and subdominants in control vs. removal plots (Figs. 5 and 9).

However, abundance of either or both fucoids has clearly not persisted at the same abundance in either the upper or lower shore during the 35-yr period (Fig. 5). In this sense, the *Fucus* spp. "state" is not "stable." Nonetheless, we conclude that the persistent dominance of *Fucus* spp. and its associated species in the experimental removals represent an alternative state to the usual *Ascophyllum* dominance.

Mechanisms maintaining the alternative state

In New England, *F. vesiculosus* and other *Fucus* spp. tend to recruit regularly, densely, and for a long portion of the year (May–December, Keser and Larson 1984, September–December, Muhlin et al. 2011). Our data were consistent with trends seen in Maine (Keser and Larson 1984), with relatively high recruitment within stands of *Fucus* spp. (Fig. 12), suggesting that the alternate state was self-maintained. We also note that virtually

no *Fucus* spp. recruitment occurred under a canopy of *Ascophyllum* (Fig. 12) and that *Ascophyllum* recruitment was rarely successful under any fucoid canopy. Although the herbivorous snail *L. littorea* can have direct negative effects on fucoid recruitment (Lubchenco 1983), historically they had no direct effect on abundance of larger (>3 cm length) fucoids. In caging exclusion experiments, abundance of existing fucoid recruits larger than 3–5 cm did not differ in the presence and absence of *L. littorea* (Lubchenco 1983). Similarly, in recent studies in this system (Bryson et al. 2014), fucoids were somewhat more abundant in the presence than in the absence of grazers (but potentially due to caging effects).

In our experiment, we observed decadal decreases in low zone abundance of *L. littorea* (Fig. 11; Appendix S1: Table S6), while *Fucus* spp. abundance remained similar (−*Asco*−*Sbal*), became lower (−*Asco*+ *Sbal*) or higher (+*Asco*+*Sbal*). If grazing was involved in maintenance of the alternate state, littorine and fucoid abundance would be either positively (if grazers kept *Fucus* spp. thalli free of epiphytes; Lubchenco 1983) or negatively correlated (but see Bryson et al. 2014). A second influence could be the indirect enhancement of fucoid recruitment by barnacles, which were initially more abundant in the −*Asco*+*Sbal* treatment and which provide fucoid recruits a refuge from littorine and limpet grazing (Lubchenco 1983, Farrell 1988). The inconsistent relationship between littorine and fucoid abundance in our experiment, and the lack of grazer effects on large fucoids in historical and recent experiments suggest that littorine grazers were unlikely to affect long-term abundance of either fucoid.

Predation on mussels was suggested to be an important mechanism in facilitating persistence of fucoids in studies in the 1970s (Menge 1976, 1978*b*). Recent studies (Bryson et al. 2014) indicate that this effect was still important at Nahant, but found that mussel cover never reached the high abundance seen in the 1970s. If whelk predation was an important mechanism during our experiment, we would have expected to see increases, not decreases, in fucoid abundance. The sharp decline in both whelk and mussel abundance documented since the 1970s (Sorte et al. 2016) and the decreases in fucoid abundance we observed suggest that facilitation by whelks was unimportant. Finally, the possibility

that human traffic at the Canoe Beach Cove site has increased and negatively influenced *Ascophyllum* recovery also seems unlikely. Access to the site requires a relatively long walk across slippery, *Ascophyllum*-covered rocks. Furthermore, there is very limited parking (for local residents only) outside the gate to the Marine Science Center property, so the location of this study is relatively free of collecting or trampling.

Climate change impacts?

Although the treatments remained dominated (or co-dominated with *Ascophyllum* in −*Asco*−*Sbal* treatments) by *Fucus* spp. after 35 yr, our data also indicate that abundance of other important species, including *M. edulis*, *L. littorea*, and *L. obtusata*, had all declined, in some cases dramatically, by the 2010s. Other evidence has shown that the biogeographic range (Jones et al. 2010) and abundance (Sorte et al. 2016) of *M. edulis* have retracted northward and declined sharply, respectively, and Jones et al. (2010) have linked these changes to rising temperatures. Rapid climate change in the Gulf of Maine is associated with negative effects on other marine biota including cod (Pershing et al. 2015) and with shifts in subtidal community composition (Dijkstra et al. 2011). Climate impacts have been widespread, affecting species biogeographic ranges or abundance or both in Western Europe, California, Chile, and New Zealand as well as the Northwest Atlantic (see Table 1 in Helmuth et al. 2006, and Southward et al. 1995, Harley et al. 2012, Yesson et al. 2015, Schiel et al. 2016 for a few examples). Effects are usually negative, but in some cases positive effects of temperature have been documented (Yesson et al. 2015, Schiel et al. 2016). Temperature stress is a major factor underlying actual or expected shifts in distribution, but other aspects of climate change such as pH and salinity changes are also likely to influence algal species including fucoids (Harley et al. 2012, Jueterbock et al. 2013, Ferreira et al. 2014). Thus, we hypothesize that the consistent decreases in abundance seen in our study likely are due to climate change impacts, most probably warmer temperatures.

Multiple community states in the New England rocky intertidal

Petraitis and colleagues (Petraitis and Dudgeon 1999, 2004*a*, *b*, 2015, Petraitis and Latham 1999,

Petraitis et al. 2009, Petraitis 2013) have reported extensively on an experimental study of alternate states in wave-protected shores on the coast of Maine. Specifically, they tested the hypothesis that the mussel *M. edulis* is a MSS to the usual dominance of *Ascophyllum*. This hypothesis was prompted by observations of "co-occurrence of mussels and rockweeds in bays that are sheltered from wave surge…" and of beds of mussels occurring in mud flats near stands of *Ascophyllum* (Petraitis 2013). This suggested that predation control of mussels observed in prior research in wave-sheltered coves (Menge and Sutherland 1976, Lubchenco and Menge 1978) was not occurring in the bays observed by Petraitis. The experiment involved cleared plots in *Ascophyllum* stands ranging in size from 1 to 8 m². The well-replicated experiment was begun in 1996–1997, with 60 plots spread over several different islands along the central Maine coast.

After clearance, *F. vesiculosus* colonized and dominated cover in large clearings in south- and some north-facing bays, although in north-facing bays the outcome was highly variable (as indicated by large confidence intervals; Figure 2 in Petraitis et al. 2009). In other north-facing bays, *M. edulis, Fucus,* and *Ascophyllum* all remained sparse for the first eight years of the experiment, but in the last year reported, *Fucus* and *M. edulis* abundance increased to average covers of about 13% and 18%, respectively, with mussel cover in several plots ranging from about 40% to nearly 80% (Petraitis et al. 2009, Petraitis 2013). Based on these results, Petraitis concluded that mussels were a MSS in his system and that stochastic processes led unpredictably to either the mussel state or the fucoid state.

This conclusion was controversial. Bertness et al. (2002) criticized Petraitis and colleagues' claims (Petraitis and Dudgeon 1999, Petraitis and Latham 1999), suggesting that mussel or fucoid dominance was deterministic and driven by water flow characteristics of the particular habitat. Under high flow, predators of mussels were inhibited from foraging, leading to a mussel state, while with low flow, predators were free to roam and controlled mussels, indirectly allowing fucoids to dominate. Exchanges ensued with arguments by Petraitis and Dudgeon (2004a, b) that the experiments of Bertness et al. (2002) were done in different locations, not the same place. Bertness

et al. (2004) responded that despite searching, they had never found mussel-dominated patches in fucoid-dominated areas and concluded that such situations likely were very rare on the Maine coast. Bertness et al. (2004) also argued that long-term experiments were necessary to test Petraitis and Dudgeon (1999, 2004a, b) claims of discovering an alternative stable state.

Addressing this latter criticism, a long-term report on their experiment done in similar environments was later published by Petraitis et al. (2009) as summarized earlier. Questions still remain, however. First, Petraitis and colleagues did all their research on Swan's Island, Maine. As noted by Bertness et al. (2004), it would be very interesting to know whether similar patterns of mussel patches within fucoid stands occur in other sheltered bays along the New England coast. Second, although mussels were slightly more abundant than *F. vesiculosus* in some of the north-facing bays, average cover of both was relatively low (but perhaps increasing) in 2005. Given these low abundances, referring to these still-changing stands as alternative stable states seems questionable. It would be interesting to learn what the fate of mussel patches in north-facing bays was in the intervening decade (2005–2016). Third, *F. vesiculosus* quickly dominated space in south-facing bays, with abundance plateauing by 2002 and persisting at this level through 2005 (Petraitis et al. 2009). One might argue that, as in our study, *F. vesiculosus* was more of an alternative state than were mussels. Although maintaining an experiment for the nine-year time frame of the Petraitis study is admirable, the study still was short relative to the generation times of *Ascophyllum* and *F. vesiculosus*.

Control of mussels: Predation, recruitment, facilitation, or climate?

A number of researchers have investigated the factors responsible for determining mussel abundance in the northwest Atlantic seaboard, with most studies occurring in New England and Nova Scotia. Based on experiments ranging across sites in Massachusetts and Maine, and wave exposures from high to low, BAM and JL concluded that predation, mostly by whelks, was strong in relatively wave-protected sites and held mussels in check, allowing fucoids (mid-zone) and foliose red algae (low zone) to dominate space (Menge

1976, 1978a, b, Lubchenco and Menge 1978). Similar results were obtained near Damariscotta, Maine, where consumers controlled prey (barnacles and mussels) in fucoid-dominated, but not in mussel-dominated habitats (Bertness et al. 2002, Silliman et al. 2013). More recently, Bryson et al. (2014) found results consistent with those of Menge and Lubchenco in southern New England. Consumers controlled abundance of sessile invertebrates on wave-protected shores, but not on wave-exposed shores. On northern Maine shores, in contrast, consumers had no effect, and both wave-exposed and wave-protected sites were dominated by *Ascophyllum*.

In contrast, in Nova Scotia, McCook and Chapman (McCook and Chapman 1991, 1993, 1997) found that predation had minimal to no effects on community recovery after ice scour had removed algae and mobile and sessile invertebrates near Halifax in 1987. They concluded that community recovery was primarily driven by characteristics of *Fucus* spp., including recruitment, self-thinning, and growth and that mussel recovery was minimal and independent of predation. They also argued that the large scale of the ice scour, which affected ~50 km of exposed coast, and the intensity of the disturbance—rock surfaces "were left virtually bare of plants or animals"—contrasted with the small-scale experiments conducted by Menge and Lubchenco. The research was conducted from 1987 to 1992, and succession over that period of time resulted in fucoid dominance of space at all locations studied, with sparse and patchy mussel cover.

Similarly, across several embayments on Swan's Island, Maine, Petraitis (1987, 1990) reported minimal direct effects of whelk predation on mussel abundance, arguing that indirect effects of littorine grazing and whelk predation on barnacles had greater influences on mussel recruitment. Recently, Petraitis and Dudgeon (2015) also argued that recruitment of all dominants, including mussels, barnacles, and fucoids, was the primary factor underlying patterns of abundance of each of these taxa in their studies of multiple community states.

Most recently, Sorte et al. (2016) reported the results of surveys of mussel abundance ranging from 1972 to 2015 along 450 km of the New England coast. The primary result was that mussel abundance had declined dramatically along this entire coast, and the authors suggested that this was most likely driven primarily by climate warming. This result complemented those of Jones et al. (2009, 2010), who found that the southern range limit of *M. edulis* had retreated northward by ~350 km, from North Carolina to Delaware. Other changes detected by Sorte et al. (2016) were an increase in barnacle abundance and a drastic decrease in whelk (*N. lapillus*) abundance. Consistent with these results, Petraitis et al. (2015) found that mussel recruitment rates had decreased strikingly between samples taken in 2000 and 2012, declining by 15% per year.

Synthesizing across these results, we suggest that differences among the various studies are explainable by several factors. One factor is wave exposure and/or flow rates. As has been noted repeatedly over the years, wave exposure is difficult to quantify (Bell and Denny 1994, O'Donnell and Denny 2008), especially at high spatial and temporal resolution, making comparisons among studies difficult. However, based on our observations and gleaning information from the literature, we suggest that some of the differences between our research, that of Bertness et al. (2002, 2004), Silliman et al. 2013), and Petraitis' work are due to differences in wave exposure. Our New England sites ranged from very wave-exposed (Pemaquid Point, East Point at Nahant, Little Brewster Point) to moderately wave-protected shores (Canoe Beach Cove, a site that during severe storms can be swept by large waves), while Petraitis' Swan Island sites are in wave-sheltered bays, with minimal waves even during severe storms), and are near very wave-sheltered mud flats where *M. edulis* can form beds (Petraitis et al. 2009, Petraitis 2013). If predator activity or survival is influenced by conditions such as high sedimentation, low salinity, or low oxygen level in bays, it is possible that interaction strength between predators and prey along a wave exposure gradient is unimodal, with maximal levels at areas of moderate water motion and low at areas of high or low water motion. Another possibility is that the susceptibility of whelks to higher-level predators such as crabs or fish is highest in sheltered bays, where activity of these highly mobile consumers is minimally impeded by water motion, thereby reducing whelk effects through reductions in abundance, size, and/or activity level.

A second factor is the relative size and abundance of mussels and fucoid algae. In contrast to

the experiments of Menge (1976) and Lubchenco and Menge (1978), McCook and Chapman (1997) and Petraitis (2013) note that they did not observe mussels outcompeting fucoids. In our 1970s experiments, which mostly involved following recolonization of cleared areas in the presence and absence of consumers, we observed that any fucoid recruits that colonized in exclusion cages were trapped by mussel byssal threads and pulled beneath the mussels. Although we also observed adult plants of *Fucus* spp. suffering this fate, many adult fucoids with mussels beneath them were not entrapped. Thus, we were not surprised to learn that fucoids were not outcompeted by mussels where mussels were either present in a layer under a fucoid canopy or sparse.

In the Nova Scotia example, the system was basically reset to bare rock during ice scour events, with both consumers and prey being scoured off the rock. *Nucella lapillus* reproduces by attaching capsules with fertilized eggs to the rock yielding crawl-away non-dispersive hatchlings. In contrast, fucoids, barnacles, and mussels produce planktonic spores or larvae. Hence, given the difference in dispersal capacity, the lack of a predation effect during early succession is also unsurprising. It would be interesting to know the current state of this system since it has now had almost 30 yr to recover.

Observations made during BAM's visit to his Massachusetts sites in 2009 were stunning: Mussels were nearly absent from both former wave-exposed study sites where they had been abundant (East Point, Little Brewster Point) and the more wave-protected sites (Canoe Beach Cove, Little Brewster Island). In their place at the exposed sites was a variety of algae, with *Fucus* spp. as a dominant. These observations, those of Jones et al. (2010), and the more spatially and temporally extensive surveys reported in Bryson et al. (2014) and Sorte et al. (2016) associated with warming in the Gulf of Maine suggest that large-scale changes in this system have been largely due to climate warming. Although human harvest and predation by invasive crabs (*Carcinus maenas*, *Hemigrapsus sanguineus*) have been suggested as additional or alternative mechanisms of mussel reduction (Tyrrell et al. 2006, Sorte et al. 2016), neither is a factor at our study site. Mussel harvest is disallowed and neither

crab species is abundant at Canoe Beach Cove (M. E. S. Bracken, *personal observations*).

Comparisons to other ecosystems

Large brown algae (mostly kelps and fucoids) are dominant habitat-forming species in most temperate regions of the world, often occupying most of the canopy space in intertidal and subtidal communities. By the 1990s, our understanding of most such systems, especially kelp beds, was that they usually were resilient to abiotic and biotic perturbations and could recover relatively quickly from even large perturbations such as El Niños or regional extirpation of herbivore-controlling top predators (e.g., Estes and Palmisano 1974, Dayton and Tegner 1984, Dayton et al. 1984, 1992, Estes et al. 1998). Recent trends, however, make it clear that massive shifts are underway in many if not most temperate regions where such organisms dominate the landscape (Connell and Russell 2010, Johnson et al. 2011, Harley et al. 2012, Yesson et al. 2015, Schiel et al. 2016, Wernberg et al. 2016). The most dramatic examples have occurred in the Southern Hemisphere, where thermally driven shifts in macrophyte abundance have occurred in western Australia (Wernberg et al. 2016: shift from kelp to seaweed turfs), eastern Tasmania (Johnson et al. 2011: decline in kelp abundance, increase in sea urchin barrens), and New Zealand (Schiel et al. 2016: increases in fucoid cover with warmer temperature, local decreases in fucoid cover with La Niña). In the British Isles and Ireland, many brown algal species have decreased in abundance with increased temperature, although others have increased or not changed (Simkanin et al. 2005, Yesson et al. 2015). Our data showing decreases in both fucoids are consistent with the general trends toward generally decreasing abundance of brown algae. These apparent consequences of climate change suggest that even more dramatic changes in coastal ecosystem productivity, composition, and diversity are inevitable and should be of major scientific and societal concern.

Contributions to theory

Investigations of the "stability" of populations, communities, and ecosystems have a long history in ecology (e.g., MacArthur 1955, Lewontin 1969, May 1973, Sutherland 1974, 1981, 1990, Pimm 1982, 1991, Connell and Sousa 1983,

Peterson 1984, Scheffer et al. 1993, 2001, Grimm and Wissel 1997, Schroder et al. 2005, Petraitis 2013). Apart from semantic issues, a major hindrance to progress has been the difficulty in conducting long-term experimental studies that meet the stringent criteria necessary for testing the resilience, persistence, and resistance of ecological systems. Although our study has its limitations, we believe that it does exemplify each of these standards. With results of others from a variety of North Atlantic locations, we have shown that the dominant fucoid in wave-protected regions, *Ascophyllum*, is highly persistent (decades to centuries), resistant to all but the most intense perturbations, and has very low resilience (little to no recovery decades after disturbance). In contrast, *Fucus* spp., dominant at some sites of intermediate wave exposure (e.g., Grindstone Neck in Maine; Menge 1976, Bryson et al. 2014, Sorte et al. 2016), was highly resilient (recolonizing cleared space within a year of disturbance), highly persistent, and highly resistant in our experiment. It appears to satisfy the criteria needed for an alternative stable state: (1) Its 38 yr of persistence after removal would have encompassed multiple generations, (2) the location of the experiment was one which had previously been occupied by *Ascophyllum*, (3) multiple perturbations (e.g., tropical storms, Nor'easters, ice abrasion) occurred over the decades, and (4) its takeover of space was the result of a pulse perturbation. We suggest that, unless perturbed by a major and/or chronic disturbance (e.g., ice scour, continued warming), the *Fucus* spp. state will persist indefinitely.

How might the *Fucus* spp. state revert back to *Ascophyllum*? We can only speculate, but it seems that reestablishment would require a scenario where *Ascophyllum* recruits would survive. This would most likely result from co-occurrence of several events: (1) severe disturbance from (e.g.,) ice scour clearing the site down to bare rock coinciding with (2) *Ascophyllum* reproduction and (3) successful recruitment during (4) exceptionally calm flow conditions. Since even a few successful recruits can grow to create a dense and thick canopy, just moderate recruit survival would likely facilitate *Ascophyllum* recovery. Recovery might also require unusually poor reproductive output by *Fucus* spp., or non-overlap in *Fucus* spp. and *Ascophyllum* propagule release.

Conclusions

We conclude that *Fucus* spp. can form a self-maintaining alternative state. The generality of this result remains unclear. The experiment was done once, at a single wave-protected site. However, Petraitis' observation that *Fucus* spp. was a persistent dominant in many of his replicates, particularly south-facing bays, is consistent with our result, and suggests the alternative hypothesis that *Fucus* spp., not mussels, were an alternative state in his study. As noted above, published reports of his study covered only nine years and the mussel increases he observed were mostly in the last year reported (2005). Better resolution of this issue could be obtained by knowing how the Swan's Island system has changed in the intervening time.

The likely influence of climate change in our system complicates interpretations. Although the evidence for a negative effect of climate change on mussels appears strong, the timing and causes of the changes in the fucoid cover cannot be pinpointed. During BAM's visit in 2009, *Fucus* spp. cover in the $-Asco+Sbal$ treatment appeared higher than it did when surveyed in 2011 and 2013 (compare Fig. 1 to Figs. 8 and 9). Thus, it is possible that relatively sharp declines in fucoid abundance have been relatively recent, although the mechanism remains unknown.

Integrating across the broader range of research undertaken in the past 40 yr along the New England coast highlights several points. For example, when viewed in larger and longer spatial and temporal contexts, including a broader wave exposure gradient, a larger geographic extent, and the dynamic changes occurring over several decades, results sometimes reported as inconsistent with other results actually seem mostly complementary. Consumer pressure may vary unimodally along a wave exposure gradient, with peak rates occurring at wave-protected sites and low rates occurring at wave-exposed and very sheltered bays. At large spatial scales, the influence of more factors including climate-induced warming and oceanographic variability likely comes into play. Warming has had an impact on mussel abundance in southern New England, where this species was once very common on wave-exposed shores (Menge 1976, Sorte et al. 2016). In contrast, Bryson et al. (2014) suggest that

mussels (and barnacles) were likely historically scarce in northern New England as a result of unfavorable oceanographic conditions. These conclusions are consistent with results from large marine ecosystems in the eastern Pacific Ocean (Menge et al. 2003, 2015, Navarrete et al. 2005, Menge and Menge 2013), and point toward the need for the development of a global model of coastal ecosystem structure and dynamics.

ACKNOWLEDGMENTS

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SUPPORTING INFORMATION

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