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Seaweed richness and herbivory increase rate of community recovery from disturbance

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Abstract. The importance of herbivores and of plant diversity for community succession and recovery from disturbance is well documented. However, few studies have assessed the relative magnitude of, or potential interactions between, these factors. To determine the combined effect of herbivory and surrounding algal species richness on the recovery of a rocky intertidal community, we conducted a 27-month field experiment assessing algal recruitment and succession in cleared patches that mimic naturally forming gaps in the ambient community. We crossed two herbivore treatments, ambient and reduced abundance, with monocultures and polycultures of the four most common algal species in a mid–high rocky intertidal zone of northern California. We found that both the presence of herbivores and high surrounding algal richness increased recovery rates, and the effect of algal richness was twice the magnitude of that of herbivores. The increased recovery rate of patches containing herbivores was due to the consumption of fast-growing, early colonist species that preempt space from perennial, late-successional species. Mechanisms linking algal richness and recovery are more numerous. In polycultures, herbivore abundance and species composition is altered, desiccation rates are lower, and propagule recruitment, survival, and growth are higher compared to monocultures, all of which could contribute the observed effect of surrounding species richness. Herbivory and species richness should jointly accelerate recovery wherever palatable species inhibit late-successional, herbivore-resistant species and recruitment and survival of new colonists is promoted by local species richness. These appear to be common features of rocky-shore seaweed, and perhaps other, communities.

Key words: algae; biodiversity; Bodega Marine Reserve; California, USA; disturbance; field experiment; herbivores; resilience; rocky shore; seaweed.

INTRODUCTION

Understanding the mechanisms that determine rates of community recovery from disturbance has received renewed interest, given increasing influence of human-caused disturbances on natural ecosystems (Vitousek et al. 1997, Moorcroft 2009). In addition to extrinsic factors, such as resource supply and environmental stress (Sousa 1979a, Worm et al. 2002), a variety of biotic community characteristics can influence recovery rates. For example, a number of studies have independently examined how consumers, ambient species diversity or composition, and timing or rate of recruitment change recovery rates (Sousa 1979b, 1984, McCook and Chapman 1993, Allison 2004, MacDougall 2005, Bertness and Silliman 2008). However, few studies have simultaneously investigated the effect of multiple biotic factors. This complicates comparisons among studies and precludes an understanding of the relative importance of these factors and their interactions on community recovery. Ultimately, this lack of a

synthetic understanding of the most important factors driving recovery makes prioritization among management and restoration targets difficult. Here we investigate the relative and interactive effects two factors known to affect the rate of recovery of primary-producer communities from controlled disturbance: producer species richness and herbivory.

The effects of producer species richness on community response to disturbance suggest that greater resilience (rate of recovery) of more species-rich assemblages can be due to complementarity (Mulder et al. 2001), sampling effects (i.e., the insurance hypothesis; Tilman 1996), or facilitation (Allison 2004). This work remains isolated from a largely separate body of work on how postdisturbance recovery of producer communities can be accelerated or inhibited by herbivory, depending on herbivore preferences and mode of succession (Menge and Sutherland 1976, Lubchenco 1978, Farrell 1991, Olf and Ritchie 1998). Interactions between these factors could alter their impacts on recovery. Such interactions could take several forms. For example, primary-producer richness could alter herbivore abundance and species composition (e.g., Knops et al. 1999) or decrease the impact of existing consumers (Hillebrand and Cardinale 2004, Edwards et al. 2010). In either case, these effects could accelerate or slow succession,

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depending on the intensity of the shift in grazing pressure (Lubchenco 1978) or the particular herbivore species affected (Burkepile and Hay 2010). Alternatively, consumer effects may be sufficiently strong to overwhelm the effects of species richness at the producer level (Paine 2002, Schmitz 2003). Studies that simultaneously manipulate grazers and ambient community composition are needed to develop a synthetic understanding of these across- and within-trophic-level influences on community recovery.

Here we investigate the combined influence of herbivory and ambient macroalgal species richness on recovery of intertidal algal communities. Removal of herbivores in rocky intertidal systems exerts a strong influence on algal biomass, diversity, composition, and succession (Lubchenco and Gaines 1981, Underwood et al. 1983, Benedetti-Cecchi 2000, Worm et al. 2002). Separate studies show that high algal species richness increases biomass, reduces temporal variation in cover, and enhances community recovery from disturbance due to facilitation and complementarity (Allison 2004, Stachowicz et al. 2008*a, b*). In addition, recovery of disturbed areas can be affected by the species identity of the surrounding community (e.g., Sousa 1984, Kim and DeWreede 1996, Dudgeon and Petraitis 2001, Bulleri and Benedetti-Cecchi 2006). However, no studies have experimentally assessed the relative importance of producer richness (or composition) and herbivory, or their interaction on community recovery.

We conducted a field experiment to assess how herbivore presence and abundance interacts with existing macroalgal species richness to influence community recovery after severe, small-scale disturbance events. We report the effects of surrounding algal species richness and herbivory on the rate and degree of recovery in terms of cover, dry mass, density, and species diversity and evenness of the disturbed algal community. We use these data to assemble a general picture of the combined effects of herbivores and surrounding algal species richness on community recovery.

METHODS

Study system

This study was conducted at the Bodega Marine Reserve on the northern coast of California, USA (38°19'12" N, 123°4'24" W). The four most common perennial macroalgal species compose >85% of total algal cover on emergent substrate in the mid- to high intertidal zone on the reserve (Stachowicz et al. 2008*b*). These species are the canopy-forming brown alga *Pelvetiopsis limitata*, the foliose red alga *Mastocarpus papillatus*, the turf-forming red alga *Endocladia muricata*, and the turf-forming green alga *Cladophora columbiana*. The ephemeral species *Ulva* spp. and *Porphyra* spp. comprise much of the remaining algal cover. From field surveys, the most abundant herbivores are the periwinkle snails *Littorina plena* and *L. scutulata* and the limpets *Lottia digitalis* and *L. scabra* (J. Stachowicz,

unpublished data). Common sessile invertebrates include the mussel *Mytilus californianus* and acorn barnacles *Chthamalus dalli* and *Balanus glandula*.

Plot establishment, maintenance, and surveying

We used 72 previously established 1.5 m diameter plots in the mid-high intertidal zone (~1 m above mean lower low water) containing one of six algal treatments: monocultures of *Cladophora*, *Endocladia*, *Mastocarpus*, and *Pelvetiopsis*, a polyculture of all four species, and an unmanipulated control. Algal treatments were established in March 2004 and maintained by weeding nontarget species (see Stachowicz et al. [2008*b*] for more details). Due to loss of three plots prior to the establishment of this experiment, there were 10 replicates of the polyculture, 11 of the *Endocladia* monoculture, and 12 of each of the other monocultures and the control plots.

In May 2008 we established two 10 × 10 cm cleared patches within each algal monoculture and polyculture (control plots were left unmanipulated). Natural disturbances on the scale of 100-cm² occurred in the 12 algal control plots at a mean rate of about two times per plot per year over the four years prior to the start of our experiment (K. Aquilino and J. Stachowicz, *unpublished data*), whereas larger disturbances were rare. These small disturbances can occur due to dislodgement of a few individuals by waves and/or desiccation (Haring et al. 2002).

After scraping the rock surface within the patches bare of all visible algae, we randomly assigned one of the two patches within each algal plot to an herbivore-reduction treatment. We applied a 2-cm wide border of marine epoxy (Z-spar A-788 Splash-Zone compound, Pettit Paints, Rockaway, New Jersey, USA) around each herbivore-reduction patch, and removed all mobile invertebrates. We covered the dry epoxy with a thin layer of Tree Tanglefoot (Tanglefoot Company, Grand Rapids, Michigan, USA), a highly adhesive vegetable gum resin, to prohibit mobile herbivores from invading. The resin inhibits entry by gastropods and lacks toxic effects that can confound experimental results (Geller 1991, Benedetti-Cecchi and Cinelli 1997; K. Aquilino, *unpublished data*). The Tanglefoot barrier reduced the presence of limpets by a mean of 91% and snails by 66% (see *Results: Potential mechanisms underlying herbivore and diversity effects on recovery*). Patches allowing access to herbivores had epoxy and Tanglefoot at the corners to control for any unintended effects of the materials. We reapplied Tanglefoot every two weeks, at which time any mobile invertebrates that breached the barrier were removed. Any algal frond that was long enough to foul the Tanglefoot barrier from within or outside the patch was trimmed with scissors to prevent the formation of bridges on which mobile herbivores could enter herbivore-exclusion plots. Algae were also trimmed in and near patches allowing herbivores.

We surveyed patches monthly, quantifying the abundance of mobile herbivores and visually estimating the cover of all algal and sessile invertebrate species. Visual estimation yields an accurate representation of relative algal cover and better quantifies cover of rare species than estimates using the random point-count method (Dethier et al. 1993). We verified visual estimates for a subset of the plots by digitally measuring percent cover in photographs using ImageJ (*available online*).² For 200 independent measurements of percent cover of individual algal species within experimental patches, our visual estimates deviated from our digital analysis by $2.7\% \pm 0.2\%$ (mean \pm SE). Starting five months into the experiment, we also counted the number of discrete macroscopic individuals of each algal species to assess recruitment.

At each sampling period we haphazardly selected and surveyed one 10×10 cm location within each of the 12 algal control plots to estimate when algal cover in experimental patches recovered to ambient levels. However, because these unmanipulated areas sampled within algal control plots were not clipped at the edges like the experimental patches within manipulated algal plots, they could only be taken as a rough estimate of expected final cover in experimental plots. After 27 months, when cover in most treatments had recovered to ambient cover, we destructively sampled the algae in each patch to quantify dry mass.

Statistical analysis

To analyze recovery rates, we compared the slope of perennial algal cover over time among treatments. We analyzed perennial cover instead of total algal cover to assess recovery rates because there was very little cover of ephemeral algae in the ambient community. Because some treatments recovered to ambient levels of cover during the course of the experiment, to assess recovery speed we analyzed only the time interval between the start of the experiment and when the mean cover in one treatment group reached ambient cover (at 18 months). During this recovery interval we expected a slow, monotonic (i.e., directional) increase in cover for all treatments. We therefore used mixed models, regarding algal richness treatment, herbivore treatment, and time as fixed effects, and algal richness plot and herbivore patch as random effects. Treating time as a fixed effect accounted for our expected monotonic increase in cover over the 18-month recovery interval, where duration since the initial clearing overwhelmingly drove the effect of time on perennial algal cover, to slow recovery rates of these species. We examined the interaction between time and treatments (i.e., the effect of treatments on the “slope” of perennial cover over time) to assess the effect of treatments on recovery rates. We tested the assumptions of this model and subsequent models by plotting the residuals vs. the fitted values and with quantile–

quantile plots. We performed natural log transformations on perennial cover to correct for nonnormal distributions of residuals for this analysis and subsequent models involving the analysis of algal cover over time.

Unlike perennial algal cover, we expected a much faster rate of recovery from the initial cleared condition for ephemeral algal cover, algal richness, evenness, or Shannon diversity, which rapidly increased and then plateaued in all treatments, or algal density, which we did not begin to measure until five months into the experiment (but which may have increased monotonically prior to our measurements). Thus to assess the effect of treatments on these variables, where changes over time reflected mostly random processes rather than the directional response to the initial clearing, we treated time as a random effect in our models.

To understand the relative importance of treatments at particular time points, we used ANOVA to compare recovery of perennial algal cover, density, richness, evenness, and Shannon diversity among treatments at discrete points during the experiment. We also compared the dry mass of algae among treatments at the end of the experiment. For these models, we treated plot as a random factor to account for spatial arrangement of herbivore treatments within algal richness treatments.

We assessed the relative importance of algal richness and identity by first performing one-way ANOVAs testing the effect of all five algal treatments on cover separately for patches with and without herbivores at the date when the first treatment had recovered. We then performed a priori contrasts between the polyculture and monoculture treatments (richness effect, $df = 1$) on the results of these ANOVAs. We used the residual treatment sums of squares, attributable to variation among the monocultures ($df = 3$), to evaluate the effect of species identity (Bruno et al. 2005). We also compared the strongest performing monoculture to the polyculture, where appropriate, using the models described here. Many studies of diversity effects attempt to assess the underlying mechanism of a diversity effect by using other statistical partitions (e.g., Loreau and Hector 2001) based on comparing the yield of a species in monoculture with its yield in polyculture, weighted by the species relative abundance at the beginning of the experiment (planting density). In our experiments, initial cover of all species was, by definition, zero, and algal spores recruited from the surrounding plot and beyond at unknown rates; thus we could not estimate “planting density” to calculate relative yields.

Finally, to assess evidence for several potential mechanisms for herbivore and algal richness or identity effects on recovery, we used mixed models to evaluate treatment effects on the cover of each individual perennial species and the abundance of herbivores. In these mixed models we regarded algal richness treatment and herbivore treatment as fixed effects, and time, algal plot, and herbivore patch as random effects.

² <http://rsb.info.nih.gov/ij/>

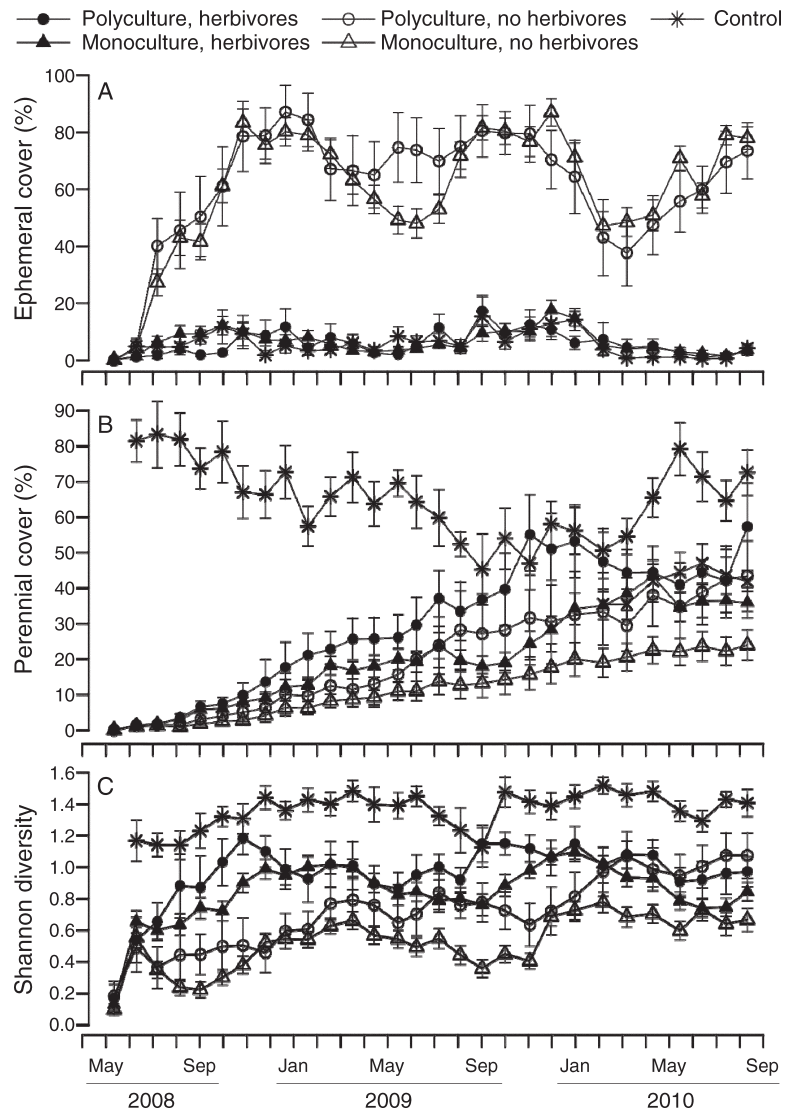


FIG. 1. Time series of (A) ephemeral species cover, (B) perennial species cover, and (C) Shannon diversity (mean \pm SE) of all algae in patches with and without herbivores in monocultures and polycultures, and surveys of cover in unmanipulated control plots. Note that ephemeral cover was consistently high in herbivore-exclusion patches, with some seasonal variation, and that perennial cover increased in all treatments over time, leveling off in patches with herbivores within polycultures at 18 months.

All analyses were performed in R 2.11.1, using the lme4 package (Bates and Maechler 2010, R Development Core Team 2010) with REML (restricted log-likelihood) method for model fitting for mixed models. We ran Markov Chain Monte Carlo (MCMC) for 10 000 iterations using the function “pvals.fnc” from the “languageR” package (Baayen 2010) to generate P values for mixed models with repeated measures.

RESULTS

Patterns of community recovery

The cover of ephemeral species (mostly *Ulva* spp. and diatoms) was largely controlled by herbivores. Unmanipulated control plots and experimental patches with

herbivores had an order of magnitude lower of ephemeral cover than those without ($t = -21.8$, $P_{\text{MCMC}} < 0.0001$, Fig. 1A; Markov Chain Monte Carlo [MCMC]). There was no difference in ephemeral cover in experimental patches among algal richness treatments ($t = 0.35$, $P_{\text{MCMC}} = 0.68$). The low cover of ephemeral species in unmanipulated algal control plots indicated that these species were not a major component of undisturbed communities. Thus we focused on the most common late-successional perennial algal species to assess recovery.

Perennial cover in experimental patches increased in all treatments throughout the experiment until reaching a plateau at about 50% cover (Fig. 1B). This was lower than ambient cover due to the clipping required to

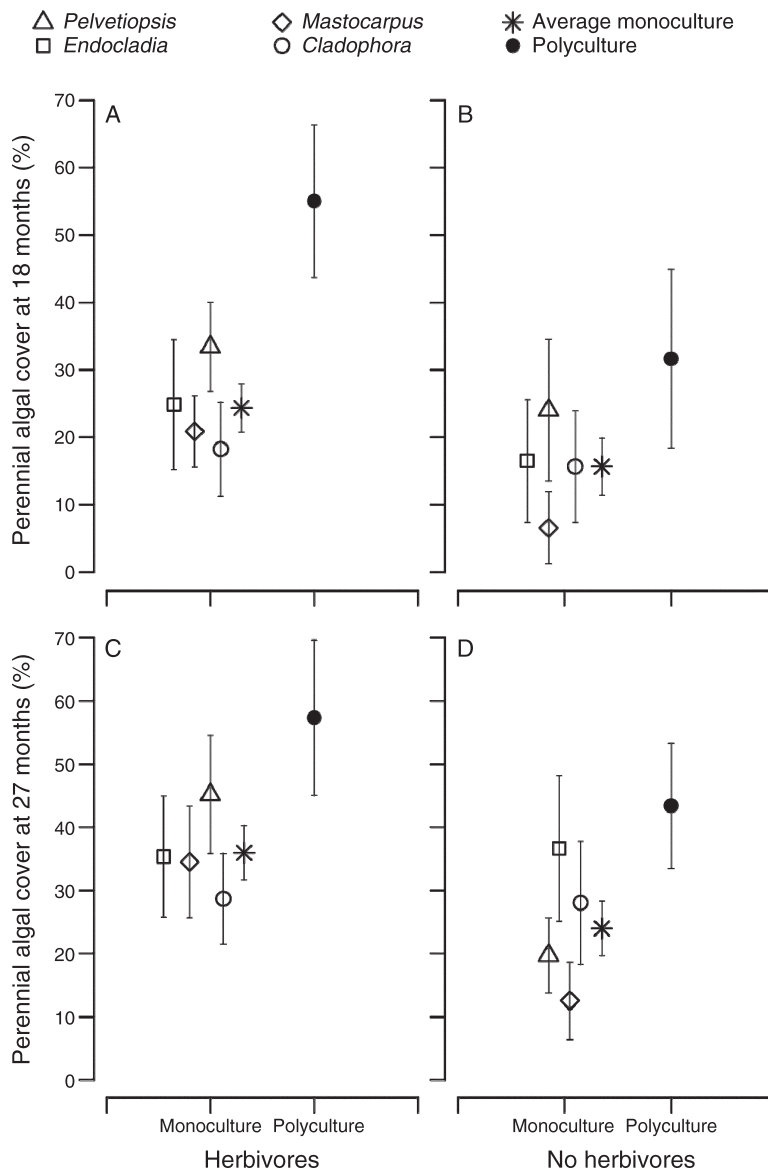


FIG. 2. (A, B) Cover (mean \pm SE) of perennial algae in patches within monoculture and polyculture plots, with and without herbivores, at 18 months, when cover in patches in polycultures with herbivores had reached ambient levels; and (C, D) at 27 months, when recovery rate in most treatments had leveled off. Monoculture points are scattered for clarity.

maintain herbivore treatments. The recovery phase of perennial algae, when all experimental patches were still responding to the initial cleared condition, ended after 18 months (in November 2009), when mean perennial algal cover in the patches with herbivores within polycultures reached the perennial cover in algal control plots (Fig. 1B). The slope of this increase in cover over time was augmented by both the presence of herbivores and the richness of the surrounding algal community, and thus the patches within polycultures that allowed herbivore access were the first to fully recover. The rate of recovery of perennial cover was nearly 1.5 times faster in patches with herbivores than without (Appendix 1; time \times herbivore interaction, $t = 2.24$, $P_{MCMC} = 0.027$)

and almost two times faster in cleared patches within polycultures than within monocultures (time \times algal richness interaction, $t = 2.3$, $P_{MCMC} = 0.022$). There was no interactive effect of algal richness and herbivore treatments on the rate of perennial cover recovery ($t = 0.10$, $P_{MCMC} = 0.93$). Correspondingly, at 18 months, herbivores and algal richness both resulted in higher perennial cover (Fig. 2A, B; $F_{1,55} = 17.2$, $P < 0.0001$; $F_{1,55} = 7.9$, $P = 0.0068$, respectively), with cover in the polyculture treatment with herbivores having nearly double the cover of the next highest cover treatment (polyculture without herbivores).

Partitioning the effects of algal treatment between species richness and species identity at this time point,

we found strong effects of richness ($F_{1,52} = 7.9$, $P = 0.0071$) and no effects of identity ($F_{3,52} = 1.1$, $P = 0.34$) when herbivores were present, and weaker effects of richness ($F_{1,52} = 3.9$, $P = 0.052$) and no effect of identity ($F_{3,52} = 0.85$, $P = 0.47$) when herbivores were absent (Fig. 2A, B). The lack of variation among monocultures suggests that the elevated cover in polyculture was likely not the result of the inclusion of any one high-cover species; however, we lacked power to detect significant differences in perennial cover at 18 months between specific monocultures and the polyculture (Ryan's Q; $P > 0.05$ for all pairwise comparisons when herbivores were removed; $P < 0.05$ only for polyculture–*Mastocarpus* and polyculture–*Cladophora* treatment comparisons when herbivores were present). Although we were unable formally to partition effects of richness into sampling and complementarity (see *Methods: Statistical analysis*), these results suggest that both sampling and complementarity contributed to the observed effects of species richness on recovery.

After 27 months, when we terminated the experiment, the effects of herbivores ($F_{1,55} = 5.8$, $P = 0.019$) and algal richness ($F_{1,55} = 6.2$, $P = 0.016$) on perennial cover remained (Fig. 2C, D) but were reduced in magnitude because many plots had fully recovered sometime between 18 and 27 months (Fig. 1B). Although there was no significant interaction term ($F_{1,55} = 0.55$, $P = 0.52$), polyculture patches had similar cover at this point, regardless of herbivore presence, whereas monocultures tended to achieve higher perennial cover in the presence of herbivores than in their absence (32% vs. 20% cover). Dry mass of perennial algae collected at the end of the experiment showed similar trends to cover, though neither the effect of herbivore presence ($F_{1,55} = 1.3$, $P = 0.25$) nor algal richness ($F_{1,55} = 2.2$, $P = 0.14$) was statistically significant. Still, the highest perennial dry mass was in patches with herbivores in polycultures (3.9 ± 1.0 g), and the lowest was in patches without herbivores in monocultures (2.2 ± 0.45 g) (mean \pm SE). There was no difference among perennial species in the ratio of dry mass (g) to percent cover among treatments, indicating that the difference in the effect of treatment on biomass vs. cover was likely due to high variance in the ratio of mass per unit cover within algal species rather than among treatments.

There was an herbivore \times algal richness interaction on dry mass of ephemeral algae ($F_{1,55} = 6.5$, $P = 0.013$), which was always very low in patches with herbivores (~ 0.1 g per plot) but was more than double the mass in patches within polycultures (1.92 ± 0.78 g) than monocultures (0.62 ± 0.16 g) (mean \pm SE). The lack of a similar interactive effect on ephemeral cover was due to variation in turf height of ephemeral algae among plots where its cover was high. Turf height of ephemeral algae tended to be taller in polycultures than monocultures, possibly due to reduced desiccation in these plots (Stachowicz et al. 2008b). Thus unlike perennial algae, which had consistent dry mass per unit cover across

treatments, ephemeral algae in monocultures had lower dry mass per unit area than in polycultures, explaining differences in treatment effects between dry mass and cover. Total dry mass of all algal species (ephemeral plus perennial algae) was greater in patches within polycultures than monocultures ($F_{1,55} = 4.8$, $P = 0.033$), but as with cover, this trend was mostly driven by ephemeral algae.

Shannon diversity, richness, and evenness of algal cover was greater in patches with herbivores over the entire experiment (Shannon diversity [Fig. 1C], $t = 7.3$, $P_{\text{MCMC}} < 0.0001$; richness, $t = 2.3$, $P_{\text{MCMC}} = 0.0042$; evenness, $t = 10.1$, $P_{\text{MCMC}} < 0.0001$) due to the large reduction in dominance by ephemeral species in these patches compared to those without herbivores. Some rare species more commonly or exclusively occurred in patches with herbivores (Appendix C: Table C1), possibly due to reduced competition with ephemeral species in these patches. Richness and Shannon diversity were also higher in patches within polycultures than monocultures (richness, $t = 2.4$, $P_{\text{MCMC}} = 0.0042$; Shannon diversity [Fig. 1C], $t = 2.1$, $P_{\text{MCMC}} = 0.016$), but evenness did not differ among algal richness treatments ($t = 1.34$, $P_{\text{MCMC}} = 0.18$). At 27 months, there was no longer an effect of herbivores on richness or Shannon diversity in recovered patches (richness, $F_{1,55} = 0.92$, $P = 0.34$; Shannon diversity, $F_{1,55} = 0.16$, $P = 0.69$); however the effect of surrounding algal richness persisted (richness, $F_{1,55} = 4.9$, $P = 0.030$; Shannon diversity, $F_{1,55} = 4.9$, $P = 0.031$). Thus while herbivores tended to increase algal diversity by removing early successional species such as *Ulva* and diatoms that can inhibit perennial species, the importance of herbivores for the diversity of the recovering community diminished over time as a greater diversity of species recruited to polycultures than monocultures, even when herbivores were absent. In contrast, the effects of surrounding algal richness treatment persisted.

Potential mechanisms underlying herbivore and diversity effects on recovery

The density of perennial algae was increased both by herbivores (Fig. 3; $t = 3.4$, $P_{\text{MCMC}} < 0.0001$) and algal richness ($t = 1.6$, $P_{\text{MCMC}} = 0.021$). The dominant influence on perennial density in patches shifted from herbivory at the beginning of the experiment to surrounding algal richness at the end. At five months, when patches still had relatively more bare space open to recruitment, there was greater density of perennial algae in patches with herbivores than without ($F_{1,55} = 23.9$, $P < 0.0001$), but no difference in density among algal treatments ($F_{1,55} = 0.14$, $P = 0.71$). In contrast, at the end of the experiment (27 months), there was no significant difference in perennial density among herbivore treatments ($F_{1,55} = 0.35$, $P = 0.56$), but polycultures had higher perennial density than monocultures ($F_{1,55} = 7.0$, $P = 0.011$). Thus while herbivores clearly affect perennial recruitment by maintaining bare space, recruitment is

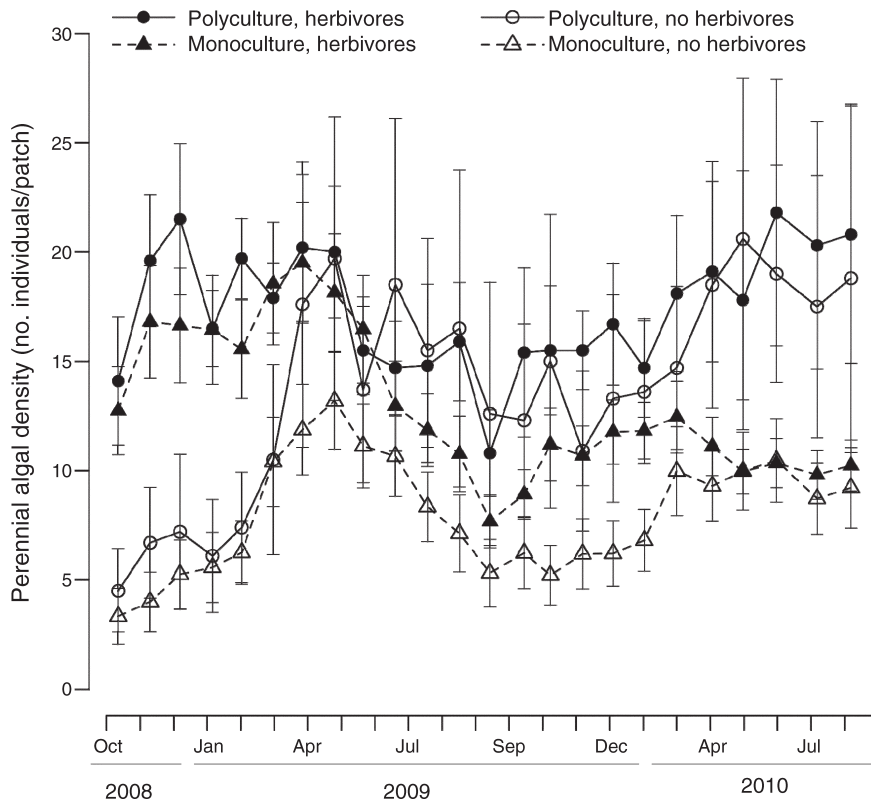


FIG. 3. Density (number of discrete individuals per patch; mean \pm SE) of perennial algae across algal richness and herbivore treatments. Patch size is 10×10 cm.

also greater in polyculture patches than monocultures, even in the absence of herbivores, suggesting that settlement, postsettlement survival, or both are greater in polycultures.

As further evidence that the local presence of adults affected recovery of each algal species, we found that cover and density of a given species tended to be higher in patches within algal treatments containing conspecifics. This was true for *Pelvetiopsis* and *Endocladia* (Fig. 4A, C; cover, $t = 5.9$, $P_{\text{MCMC}} < 0.0001$ and $t = 1.70$, $P_{\text{MCMC}} = 0.0028$ for each species, respectively; density, $t = 5.2$, $P_{\text{MCMC}} < 0.0001$ and $t = 2.2$, $P_{\text{MCMC}} = 0.0024$). Though there was a similar effect for *Cladophora* (cover, $t = 2.3$, $P_{\text{MCMC}} = 0.0012$; density, $t = 2.6$, $P_{\text{MCMC}} = 0.0030$), it was driven mostly by very high *Cladophora* cover in one *Cladophora* monoculture plot. Total *Cladophora* cover was very low overall in nearly all other experimental patches (Fig. 4D). However, *Mastocarpus* had neither higher cover ($t = 0.84$, $P_{\text{MCMC}} = 0.22$) nor density ($t = 0.18$, $P_{\text{MCMC}} = 0.81$) in patches within plots where it was present (Fig. 4B), possibly due to an alternative life stage present in most algal treatments (see *Discussion*). The polyculture and the *Pelvetiopsis* and *Endocladia* monocultures had the three fastest rates of recovery (in declining order; see Appendix B: Table B1) and all contained locally recruiting species, suggest-

ing that increased propagule arrival from local conspecifics (within 0.5 m) enhanced recovery.

Most mobile invertebrates were equally abundant among algal treatments in patches allowing herbivores (see Appendix C: Table C4 for full list); however, the grazing limpet *Lottia scabra* was more abundant in polycultures than in monocultures (Fig. 5A; $t = 3.5$, $P_{\text{MCMC}} < 0.0001$). Juvenile limpets were also more abundant in polycultures, not only in patches allowing herbivores (Fig. 5B; $t = 6.1$, $P_{\text{MCMC}} < 0.0001$), but also in herbivore-reduction patches ($t = 4.8$, $P_{\text{MCMC}} < 0.0001$). Given their size (< 2 mm), they likely recruited directly to herbivore-reduction patches rather than crawling over Tanglefoot barriers.

DISCUSSION

Our field experiment demonstrated that both herbivores and surrounding algal richness independently affect the rate of recovery from disturbance. The effect of algal richness was twice the magnitude of the effect of herbivores. Herbivores commonly accelerate algal succession in intertidal systems (Lubchenco 1983, Sousa 1979b, 1984, Farrell 1991, Branch et al. 1992, Benedetti-Cecchi 2000), and in this study, as in many others, herbivory likely promoted recovery by releasing perennial algae from competition with fast-growing ephemeral species. The strong effect of surrounding species

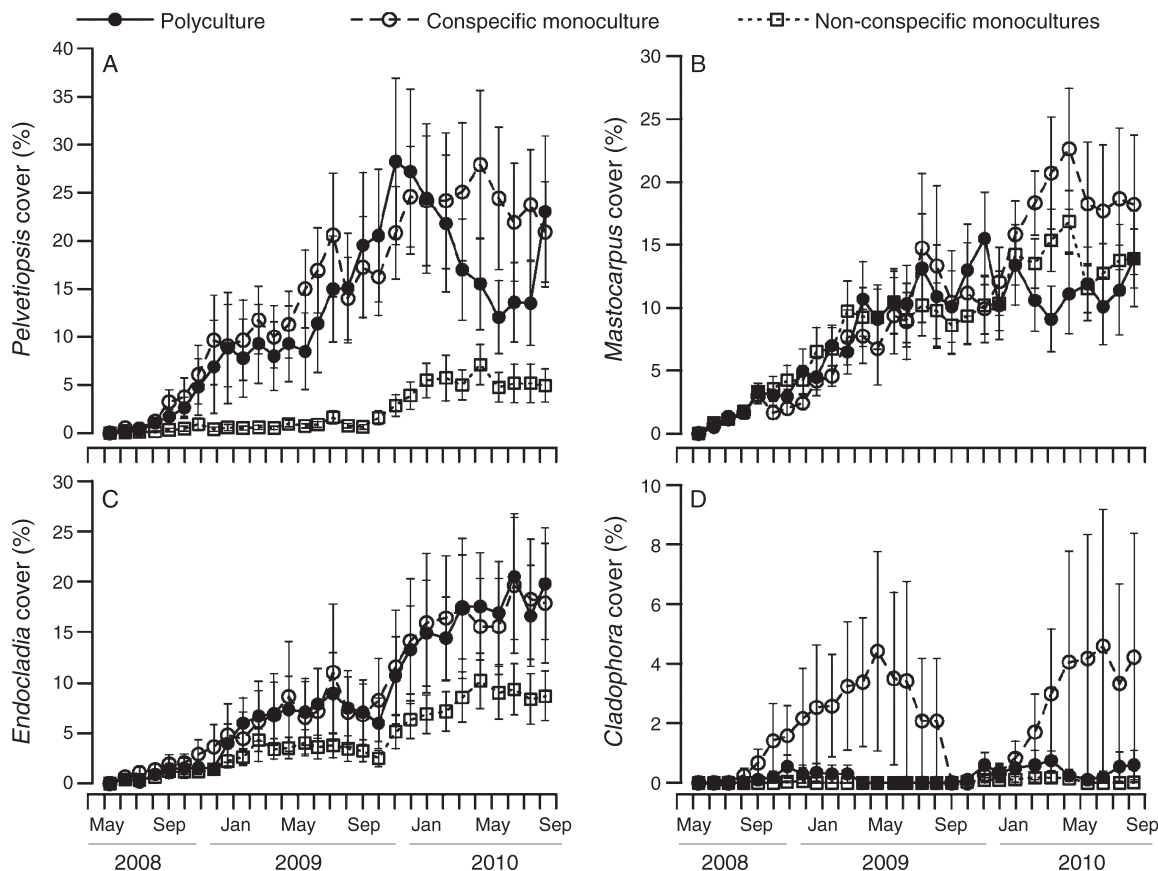


FIG. 4. Cover (mean \pm SE) of perennial algal species (A) *Pelvetiopsis*, (B) *Mastocarpus*, (C) *Endocladia*, and (D) *Cladophora* in patches within polycultures, conspecific monocultures (i.e., the monoculture of that species), and non-conspecific monocultures (i.e., the mean of all other monocultures).

richness on patch recovery seems to be driven by a combination of increased recruitment due to the proximity of conspecifics (Sousa 1984, Menge et al. 1993), increased survival caused by reduced desiccation (Stachowicz et al. 2008b), and perhaps increased abundance of certain grazers. We found surprisingly few interactions between algal richness and herbivore presence on recovery, perhaps due to the lack of direct grazing on adults of the perennial species we manipulated. Here we discuss the mechanisms driving the main effects of herbivores and surrounding algal richness on recovery and the implications of our findings for understanding the role of resident diversity in community recovery.

Our results are consistent with those from previous studies on rocky shores in that herbivores accelerated recovery by shifting algal species composition from fast-growing, opportunistic species to slower-growing, but herbivore-resistant, perennial species (Fig. 1A, B). Herbivores tend to prefer early successional, ephemeral species, such as *Ulva* and diatoms, which can inhibit the recovery of later successional, perennial species by preemption of space (Farrell 1991, Benedetti-Cecchi 2000). In our experimental patches with herbivores, the

consumption of ephemeral species maintained bare space for perennial species to colonize and grow, and allowed these patches to recover more quickly to predisturbance cover and diversity. By the end of the experiment, *Endocladia* benefitted most from the presence of herbivores (Appendix C: Table C2), perhaps because its recumbent morphology is very susceptible to competition from fast-growing algae, like *Ulva*. *Mastocarpus* and *Pelvetiopsis* were less affected by the presence of herbivores by the end of the experiment (see also Sousa [1984]), probably because the erect morphologies of these species allow them eventually to grow above *Ulva*. Greater cover of perennial species such as *Endocladia* and *Cladophora* and more frequent occurrence of rare species in patches with herbivores (Appendix C: Table C1) contributed to greater Shannon diversity (Fig. 1C) and richness in these patches.

The strong effects of both herbivores and algal richness can be partially attributed to herbivore feeding preferences. In laboratory feeding trials, limpets demonstrated no appreciable consumption of adult perennial algae in this system (K. Aquilino and J. Stachowicz, *unpublished data*), suggesting that these algae rapidly escaped herbivory by achieving large size. Furthermore,

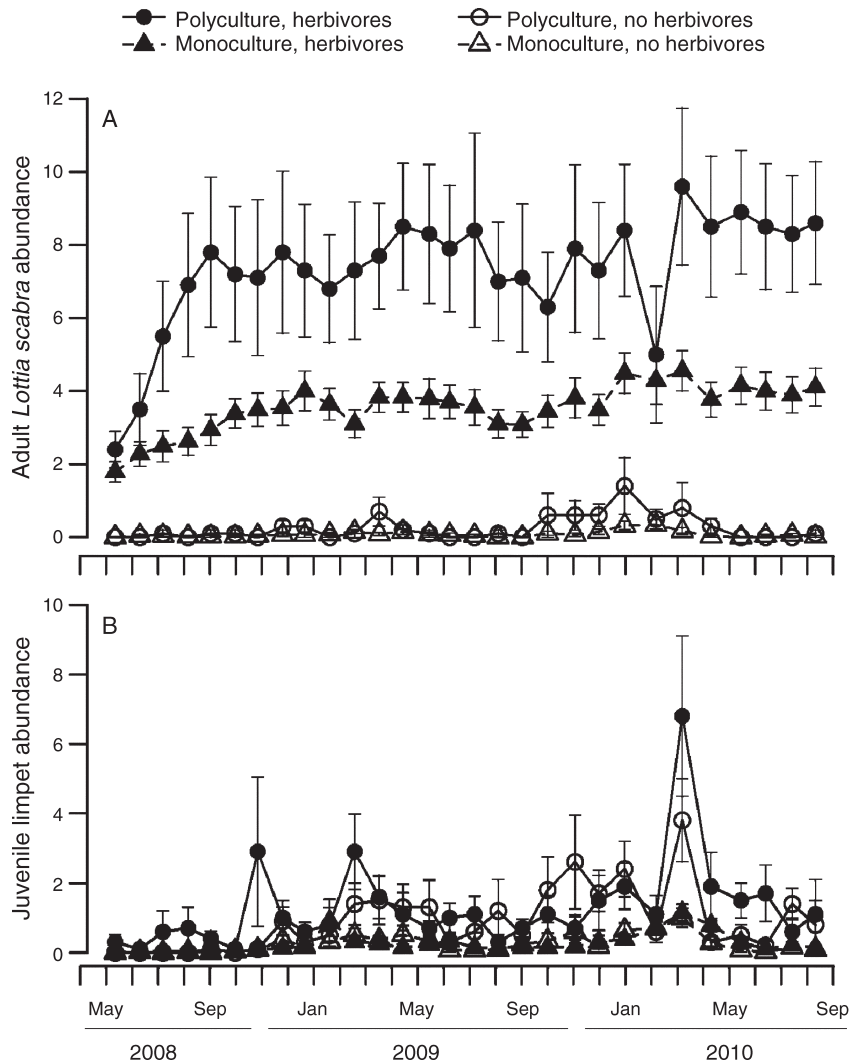


FIG. 5. Abundance (mean \pm SE) of (A) the adult limpet *Lottia scabra* and (B) juvenile limpets across algal richness and herbivore treatments.

limpets, littorine snails, and perennial algae coexist in unmanipulated plots, indicating that these herbivores do not restrict perennial algal distribution via direct grazing, despite consuming perennial species at early life history stages (Sousa 1979b, Hawkins and Hartnoll 1983, Jernakoff 1983, Jenkins et al. 2005). In contrast, most herbivores showed strong preferences for fast-growing, early colonists like *Ulva* in the field and lab (Lubchenco 1983, Sousa 1984; K. Aquilino and J. Stachowicz, unpublished data).

The strength of the effect of algal richness on recovery, compared to herbivore effects, increased throughout the experiment (Fig. 1B). At the end of the recovery period (18 months) the effect of richness was also greater than that of species identity, consistent with previous findings on the effect of richness on algal cover in this system (Stachowicz et al. 2008a, b). This suggests that there may be complementarity among species,

resulting in faster recovery of polycultures. However, we did not find statistical support for differences between the polyculture and the best-performing monoculture(s) for any recovery metric (Appendix B). Still, the lack of strong identity effects suggests that sampling effects are not primarily responsible. We suspect that a combination of complementarity and sampling effects act in this system, and here we explore potential biological mechanisms of these effects.

Local recruitment is likely one mechanism that contributed to enhanced recovery in polycultures. For two of four species, *Pelvetiopsis* and *Endocladia*, there was higher cover in recovering patches in polycultures and conspecific monocultures than in other monocultures (Fig. 4). There is evidence from other studies in this system for local recruitment of a variety of species (Sousa 1984, Allison 2004), potentially due to very locally restricted dispersal (Menge et al. 1993, Pearson

and Brawley 1996, Williams and Di Fiori 1996). The lack of a local recruitment signal for *Mastocarpus* may have been because its encrusting, tetrasporophyte phase, *Petrocelis*, was not manipulated, and its cover was similar among algal treatments. *Cladophora* cover was too low in recovered patches to test for such a signal. The increased total recruitment and recruit diversity in patches within high ambient algal richness suggests there may be strong, stabilizing feedbacks of diversity in this system. Primary-producer species richness is commonly associated with stability of total abundance in experiments (e.g., Tilman et al. 2006, Stachowicz et al. 2008b), but here we show that species richness may also be stabilized in species-rich assemblages.

Reduced environmental stress in polycultures also likely contributed to richness effects on recovery. Bare patches within polycultures experience reduced desiccation compared to those within monocultures of any of the four species we investigated (Stachowicz et al. 2008b), perhaps because higher algal biomass in polyculture (which is the result of complementarity; see Stachowicz et al. [2008b]) reduces airflow over the substrate, decreasing evaporative moisture loss. Greater canopy cover in polycultures could also increase shading in disturbed patches, reducing irradiance that can kill germinating spores (Jones 1959, Burns and Mathieson 1972). Indeed, juveniles of perennial species grow and survive better in polyculture (Stachowicz et al. 2008a), which likely contributed to accelerated recovery.

Though some grazers were more abundant in polyculture than monoculture (Fig. 5), we do not suspect that this affected perennial recovery, because ephemeral cover was equally low in monoculture and polycultures with herbivores. Thus the main mechanism by which herbivores affect recovery, removal of ephemeral algae, was equally effective in monoculture and polyculture.

The potential mechanisms for faster recovery rates within polycultures (i.e., increased recruitment of nearby species and decreased abiotic stress) suggest that richness, in this case, may affect recovery only when patch size is within dispersal distance of most individuals (Sousa 1984, Farrell 1989) or small enough that abiotic effects of the surrounding community permeate the patch. The composition of species recruiting to a small 100-cm² bare patch on a rocky shore or a small 100-m² treefall gap in a forest can depend strongly on the composition of species in the surrounding community (Hubbell et al. 1999). In larger patches created by catastrophic events, such as massive ice scour on rocky shores (McCook and Chapman 1993) or large fires in terrestrial habitats (McDougall 2005), the effects of the surrounding community on recovery may diminish with distance from the edge of the patch (Dudgeon and Petraitis 2001). Yet disturbance events from the deaths of a few individuals often result in small disturbed areas within large areas of intact communities, so the strong effect of surrounding richness on this type of patch-level recovery may be widespread.

Predicting the consequences of projected increased frequency and intensity of disturbance events requires understanding how variation at adjacent trophic levels interacts with primary-producer diversity to affect recovery. While the importance of the frequency and intensity of small-scale disturbances in rocky-shore communities (Sousa 1979a, b, 1984), temperate and tropical forests (Schaetzl et al. 1988, McCarthy 2001), and elsewhere (Pickett and White 1985) is well appreciated, this study is the first to our knowledge to explicitly test how the species richness or composition of the surrounding community acts in concert with variation in consumers to impact recovery. Although the effect of consumers on recovery rates is well documented, our results suggest that the effect surrounding species richness can be twice as strong. We would expect qualitatively similar findings in any system in which (1) herbivores facilitate late-successional species either by preferentially consuming early-successional species that inhibit later successional species or by other means; and (2) ambient species richness promotes recruitment and/or survival of colonists. In rocky-shore communities, there is strong evidence for the first characteristic (Lubchenco 1983, Sousa 1979b, 1984, Farrell 1991, Benedetti-Cecchi and Cinelli 1993; but see Benedetti-Cecchi [2000], Maggi et al. [2011]). In other ecosystems, herbivores can accelerate, decelerate, or have little effect on succession, depending on variation in community attributes such as preference among grazer species, site fertility, and primary-producer defenses (Gibson and Brown 1991, Davidson 1993, Olf et al. 1997). The few available tests of the second characteristic suggest this also may be common in rocky-shore communities (Allison 2004, White and Shurin 2007, Stachowicz et al. 2008b). Facilitation in diverse communities through buffering of harsh environmental conditions has been shown in other communities (Mulder et al. 2001), though the effect on recruitment of new species is only rarely tested explicitly. The joint effects of herbivory and algal richness on recovery should thus be similar across many rocky-shore algal communities. Our work provides a framework for predicting whether similar effects are likely in other systems, subject to future testing.

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LITERATURE CITED

Allison, G. 2004. The influence of species diversity and stress intensity on community resistance and resilience. *Ecological Monographs* 74:117–134.

- Baayen, R. H. 2010. languageR: Data sets and functions with "Analyzing linguistic data: a practical guide to statistics." R package version 1.0. <http://cran.r-project.org/web/packages/languageR/index.html>
- Bates, D., and M. Maechler. 2010. lme4: linear mixed-effects models using Eigen and Eigen. R package version 0.777375-36. <http://cran.r-project.org/web/packages/lme4/index.html>
- Benedetti-Cecchi, L. 2000. Predicting direct and indirect interactions during succession in a mid-littoral rocky shore assemblage. *Ecological Monographs* 70:45–72.
- Benedetti-Cecchi, L., and F. Cinelli. 1993. Early patterns of algal succession in a midlittoral community of the Mediterranean Sea: a multifactorial experiment. *Journal of Experimental Marine Biology and Ecology* 169:15–31.
- Benedetti-Cecchi, L., and F. Cinelli. 1997. Confounding in field experiments: direct and indirect effects of artifacts due to the manipulation of limpets and macroalgae. *Journal of Experimental Marine Biology and Ecology* 209:171–184.
- Bertness, M. D., and B. R. Silliman. 2008. Consumer control of salt marshes driven by human disturbance. *Conservation Biology* 22:618–623.
- Branch, G. M., J. M. Harris, C. Parkins, R. H. Bustamante, and S. Eekhout. 1992. Algal "gardening" by marine grazers: effects of territorial fish and limpets. Pages 405–423 *in* D. M. John, S. J. Hawkins, and J. H. Price, editors. *Plant–animal interactions in the marine benthos*. Clarendon Press, Oxford, UK.
- Bruno, J. F., K. E. Boyer, J. E. Duffy, S. C. Lee, and J. S. Kertesz. 2005. Effects of macroalgal species identity and richness on primary production in benthic marine communities. *Ecology Letters* 8:1165–1174.
- Bulleri, F., and L. Benedetti-Cecchi. 2006. Mechanisms of recovery and resilience of different components of mosaics of habitats on shallow rocky reefs. *Oecologia* 149:482–492.
- Burkpile, D. E., and M. E. Hay. 2010. Impact of herbivore identity on algal succession and coral growth on a Caribbean reef. *PLoS ONE* 5:e8963.
- Burns, R. L., and A. C. Mathieson. 1972. Ecological studies of economic red algae. III. Growth and reproduction of natural and harvested populations of *Gigartina stellata* (Stackhouse) batters in New Hampshire. *Journal of Experimental Marine Biology and Ecology* 9:77–95.
- Davidson, D. W. 1993. The effects of herbivory and granivory on terrestrial plant succession. *Oikos* 68:23–35.
- Dethier, M. N., E. S. Graham, S. Cohen, and L. M. Tear. 1993. Visual versus random-point percent cover estimations: objective is not always better. *Marine Ecology Progress Series* 96:93–100.
- Dudgeon, S., and P. S. Petraitis. 2001. Scale-dependent recruitment and divergence of intertidal communities. *Ecology* 82:991–1006.
- Edwards, K. F., K. M. Aquilino, R. J. Best, K. L. Sellheim, and J. J. Stachowicz. 2010. Prey diversity is associated with weaker consumer effects in a meta-analysis of benthic marine experiments. *Ecology Letters* 13:194–201.
- Farrell, T. M. 1989. Succession in a rocky intertidal community: the importance of disturbance size and position within a disturbed patch. *Journal of Experimental Marine Biology and Ecology* 128:57–73.
- Farrell, T. M. 1991. Models and mechanisms of succession: an example from a rocky intertidal community. *Ecological Monographs* 61:95–113.
- Geller, J. B. 1991. Gastropod grazers and algal colonization on a rocky shore in Northern California: the importance of the body size of grazers. *Journal of Experimental Marine Biology and Ecology* 150:1–17.
- Gibson, C. W. D., and V. K. Brown. 1991. The effects of grazing on local colonisation and extinction during early succession. *Journal of Vegetation Science* 2:291–300.
- Haring, R. N., M. N. Dethier, and S. L. Williams. 2002. Desiccation facilitates wave-induced mortality of the intertidal alga *Fucus gardneri*. *Marine Ecology Progress Series* 232:75–82.
- Hawkins, S. J., and R. G. Hartnoll. 1983. Grazing of intertidal algae by marine invertebrates. *Oceanography and Marine Biology Annual Review* 21:195–282.
- Hillebrand, H., and B. J. Cardinale. 2004. Consumer effects decline with prey diversity. *Ecology Letters* 7:192–201.
- Hubbell, S. P., R. B. Foster, S. T. O'Brien, K. E. Harms, R. Condit, B. Wechsler, S. J. Wright, and S. Loo de Lao. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* 283:554–557.
- Jenkins, S. R., R. A. Coleman, P. Della Santina, S. J. Hawkins, M. T. Burrows, and R. G. Hartnoll. 2005. Regional scale differences in the determinism of grazing effects in the rocky intertidal. *Marine Ecology Progress Series* 287:77–86.
- Jernakoff, P. 1983. Factors affecting the recruitment of algae in a midshore region dominated by barnacles. *Journal of Experimental Marine Biology and Ecology* 67:17–31.
- Jones, E. W. 1959. Experiments on some effects of certain environmental factors on *Gracilaria verrucosa* (Hudson) Papenfuss. *Journal of the Marine Biological Association of the United Kingdom* 38:153–167.
- Kim, J. H., and R. E. DeWreede. 1996. Effects of size and season of disturbance on algal patch recovery in a rocky intertidal community. *Marine Ecology Progress Series* 133:217–228.
- Knops, J. M. H., D. Tilman, N. M. Haddad, S. Naeem, C. E. Mitchell, J. Haarstad, M. E. Ritchie, K. M. Howe, P. B. Reich, E. Siemann, and J. Groth. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters* 2:286–293.
- Loreau, M., and A. Hector. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72–76.
- Lubchenco, J. 1978. Plant species-diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *American Naturalist* 112:23–39.
- Lubchenco, J. 1983. *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity, and plant escapes during succession. *Ecology* 64:1116–1123.
- Lubchenco, J., and S. D. Gaines. 1981. A unified approach to marine plant–herbivore interactions. I. Populations and communities. *Annual Review of Ecology and Systematics* 12:405–437.
- MacDougall, A. S. 2005. Responses of diversity and invasibility to burning in a northern oak savanna. *Ecology* 86:3354–3363.
- Maggi, E., I. Bertocci, S. Vaselli, and L. Benedetti-Cecchi. 2011. Connell and Slatyer's models of succession in the biodiversity era. *Ecology* 92:1399–1406.
- McCarthy, J. 2001. Gap dynamics of forest trees: a review with particular attention to boreal forests. *Environmental Reviews* 9:1–59.
- McCook, L. J., and A. R. O. Chapman. 1993. Community succession following massive ice-scour on a rocky intertidal shore: recruitment, competition and predation during early, primary succession. *Marine Biology* 115:565–575.
- Menge, B. A., T. M. Farrell, A. M. Olson, P. Van Tamelen, and T. Turner. 1993. Algal recruitment and the maintenance of a plant mosaic in the low intertidal region on the Oregon coast. *Journal of Experimental Marine Biology and Ecology* 170:91–116.
- Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *American Naturalist* 110:351–369.
- Moorcroft, P. R. 2009. Biodiversity patterns in managed and natural landscapes. Pages 445–457 *in* S. A. Levin, editor. *The Princeton guide to ecology*. Princeton University Press, Princeton, New Jersey, USA.

- Mulder, C. P. H., D. D. Uliassi, and D. F. Doak. 2001. Physical stress and diversity–productivity relationships: the role of positive interactions. *Proceedings of the National Academy of Sciences USA* 98:6704–6708.
- Olf, H., J. D. Leeuw, J. P. Bakker, R. J. Platerink, and H. J. v. Wijnen. 1997. Vegetation succession and herbivory in a salt marsh: changes induced by sea level rise and silt deposition along an elevational gradient. *Journal of Ecology* 85:799–814.
- Olf, H., and M. E. Ritchie. 1998. Effects of herbivores on grassland plant diversity. *Trends in Ecology and Evolution* 13:261–265.
- Paine, R. T. 2002. Trophic control of production in a rocky intertidal community. *Science* 296:736–739.
- Pearson, G. A., and S. H. Brawley. 1996. Reproductive ecology of *Fucus distichus* (Phaeophyceae): an intertidal alga with successful external fertilization. *Marine Ecology Progress Series* 143:211–223.
- Pickett, S. T. A., and P. S. White. 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando, Florida, USA.
- R Development Core Team. 2010. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Schaetzl, R. J., S. F. Burns, D. L. Johnson, and T. W. Small. 1988. Tree uprooting: review of impacts on forest ecology. *Plant Ecology* 79:165–176.
- Schmitz, O. J. 2003. Top predator control of plant biodiversity and productivity in an old-field ecosystem. *Ecology Letters* 6:156–163.
- Sousa, W. P. 1979a. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* 60:1225–1239.
- Sousa, W. P. 1979b. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecological Monographs* 49:227–254.
- Sousa, W. P. 1984. Intertidal mosaics: patch size, propagule availability, and spatially variable patterns of succession. *Ecology* 65:1918–1935.
- Stachowicz, J. J., R. J. Best, M. E. S. Bracken, and M. H. Graham. 2008a. Complementarity in marine biodiversity manipulations: reconciling divergent evidence from field and mesocosm experiments. *Proceedings of the National Academy of Sciences USA* 105:18842–18847.
- Stachowicz, J. J., M. Graham, M. E. S. Bracken, and A. I. Szoboszlai. 2008b. Diversity enhances cover and stability of seaweed assemblages: the role of heterogeneity and time. *Ecology* 89:3008–3019.
- Tilman, D. 1996. Biodiversity: population versus ecosystem stability. *Ecology* 77:350–363.
- Tilman, D., P. B. Reich, and J. M. H. Knops. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* 441:629–632.
- Underwood, A. J., E. J. Denley, and M. J. Moran. 1983. Experimental analysis of the structure and dynamics of mid-shore rocky intertidal communities in New South Wales. *Oecologia* 56:202–219.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. *Science* 277:494–499.
- White, L. F., and J. B. Shurin. 2007. Diversity effects on invasion vary with life history stage in marine macroalgae. *Oikos* 116:1193–1203.
- Williams, S. L., and R. E. Di Fiori. 1996. Genetic diversity and structure in *Pelvetia fastigiata* (Phaeophyta: Fucales): Does a small effective neighborhood size explain fine-scale genetic structure? *Marine Biology* 126:371–382.
- Worm, B., H. K. Lotze, H. Hillebrand, and U. Sommer. 2002. Consumer versus resource control of species diversity and ecosystem functioning. *Nature* 417:848–851.

SUPPLEMENTAL MATERIAL

Appendix A

A table showing the results of a mixed model assessing the rate of recovery of algal cover over the first 18 months of the experiment, before any one treatment had reached ambient cover (*Ecological Archives* E093-078-A1).

Appendix B

A figure showing percent cover of perennial algae, Shannon diversity, and density of perennial algae by algal species treatment; and a table of the estimated slopes and standard errors of percent cover of perennial algal species during the recovery period in the presence and absence of herbivores (*Ecological Archives* E093-078-A2).

Appendix C

Tables showing the occurrence and abundance of algal and mobile invertebrate species across treatments (*Ecological Archives* E093-078-A3).