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Plant–animal diversity relationships in a rocky intertidal system depend on invertebrate body size and algal cover

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Abstract. Considerable research has examined the influence of herbivores on the maintenance of plant diversity, but fewer studies have examined the reciprocal effect of plant diversity on the animals that use the plant community for food and shelter, particularly in marine systems. Several mechanisms could underlie such effects. Animal diversity and abundance could be increased by complementary use of different plants by different animals, or by an indirect effect of plant diversity on plant production that results in more total plant biomass in high plant-diversity communities. Alternatively, plant species identity could play a dominant role leading to sampling effects or no effect of diversity at all. We conducted a six-year field manipulation of the richness of rocky shore seaweeds in northern California and measured the effects of algal richness and identity on the invertebrate community, from meiofauna to macrofauna. We found that diverse algal communities hosted more species of both large and small invertebrates than the average algal monoculture but that the mechanisms underlying this pattern differed substantially for organisms of different size. More species of macrofauna occurred in the polycultures than in any of the monocultures, likely due to the greater total cover of algae produced in polycultures. Rare and common macrofaunal taxa responded to host plant species richness in opposite ways, with more occurrences of rare taxa and lower abundance of very common taxa in the polycultures. In contrast, meiofaunal richness in polycultures was no different than that of monocultures of finely branched species, leading to strong effects of algal identity. Our findings are similar to those from terrestrial systems in that the effects of plant diversity we observed were most related to the greater amount of habitat in polycultures as a result of overyielding in algal biomass. However, our findings differ from those in terrestrial systems in that the primary mechanisms for both richness and identity effects appear related to the value of plants as shelter from harsh abiotic conditions or predation rather than food, and in that animal body size altered the mechanisms underlying diversity effects.

Key words: *Bodega Marine Reserve, California, USA; complementarity; gastropod; habitat; herbivore; limpet; littorine; macroalgae; meiofauna; productivity; seaweed; shelter.*

Introduction

In the face of global species loss, understanding the mechanisms linking biodiversity and ecosystem function has been a major priority for community ecology. Early efforts focused on primary producers, seeking to understand the effect of plant diversity on productivity at the base of the food web. Results from this work showed that higher productivity in diverse communities can be driven by the response of a few dominant species and/or by the complementary use of resources by functionally diverse species (Cardinale et al. 2006, Stachowicz et al. 2007). Similarly, when later studies examined the propagation of these effects to higher trophic levels, they showed that animal diversity and abundance can also be influenced by the characteristics of particular primary-producer species and/or by producer diversity (e.g., Haddad et al. 2001, Parker et al. 2001, Cardinale et al. 2006, Stachowicz et al. 2007).

More recently, reviews of this literature have sought to further understand the mechanisms linking plant and animal diversity and to predict when different mechanisms are expected to be strongest (Borer et al. 2012, Castagneyrol and Jactel 2012). For example, the majority of reported effects of plant diversity on the abundance and diversity of terrestrial arthropods appear to arise from the higher total productivity achieved by more diverse plant communities, rather than from differences in the effects of each plant species on

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particular animal species (Borer et al. 2012). In addition, correlations between plant and animal diversity are stronger for terrestrial arthropods that are primary consumers, including both herbivores and pollinators (Castagneyrol and Jactel 2012). Including species that are omnivorous or from higher trophic levels, i.e., not directly dependent on the manipulated plants for food, can weaken these relationships (Scherber et al. 2010, Castagneyrol and Jactel 2012, Rzanny and Voigt 2012).

So far, these reviews have focused on terrestrial systems due to a relative dearth of studies from marine systems (Castagneyrol and Jactel 2012). However, there are some key differences between plant–animal relationships in marine vs. terrestrial systems that might alter expectations regarding the relationship between plant and animal diversity. First, in comparison to terrestrial insects, marine herbivores generally tend to be less specialized in their host plant use (Hay and Steinberg 1992, Poore et al. 2008). Second, several studies suggest that many marine consumers respond more to the value of a habitat as refuge from predators or abiotic stresses rather than its food value (e.g., Duffy and Hay 1991; reviewed in Hay and Steinberg [1992]). Third, marine plants and macroalgae are frequently colonized by epiphytic microalgae and other microorganisms, which provide a food source independent of macrophyte identity and can therefore decouple preferences for food and habitat (Hay and Fenical 1988, Heck and Valentine 2006, Poore et al. 2008). The relative importance of macrophytes as food vs. habitat is also partly determined by grazer body size, which varies substantially over the high phylogenetic diversity of herbivorous marine invertebrates (Hay and Steinberg 1992). For smaller organisms, body size also directly affects habitat selection, as aquatic invertebrates often select habitats with internal spaces that match their body size (Hacker and Steneck 1990, Warfe et al. 2008). This suggests that a diversity of microhabitat dimensions, or a greater total amount of habitat, may be more important than a diversity or abundance of food resources in driving invertebrate composition.

Despite an abundance of literature detailing variation among marine algae in the composition of their associated fauna (e.g., Holmlund et al. 1990, Taylor and Cole 1994, Bates 2009) and evidence for distinct microhabitat preferences among co-occurring species (e.g., Hicks 1986, Hacker and Steneck 1990, Wieters et al. 2009, Aguilera and Navarrete 2012), there have been relatively few explicit tests of the effects of marine producer diversity on animal diversity or abundance (Parker et al. 2001, Bates and DeWreede 2007, Gustafsson and Bostrom 2009, 2011, Moran et al. 2010). Unlike terrestrial plant studies, marine studies rarely find that epifaunal abundance or diversity increases with the number of plant or algal species. Some confirm strong identity effects, finding that plant species vary in the animal communities they support (e.g., Parker et al. 2001, Bates and DeWreede 2007, Gustafsson and Bostrom 2009). One study found that a diverse macroalgal community offered a superior predation refuge relative to the average monoculture but was no better at reducing predation than a community comprised of a single, highly folded macroalga (Moran et al. 2010). In such cases, richness effects may be attributable to a sampling effect, the increased likelihood that diverse communities will contain producer species that are particularly attractive to animals due to food or refuge value. Most of these experiments consist of assembled communities in which total algal biomass or cover is controlled to separate the effect of habitat diversity from habitat quantity. Thus these studies provide rigorous tests of whether producer diversity affects animal communities through mechanisms such as microhabitat niche complementarity or complexity, but they do not test indirect mechanisms such as an increase in overall producer biomass in diverse communities, which appears to be the dominant connection between plant diversity and arthropod community diversity in terrestrial systems (Borer et al. 2012).

To better understand the effects of primary-producer diversity on marine invertebrate communities, we manipulated the richness of common macroalgal species that vary in their habitat characteristics and measured the effects on invertebrates with a substantial range of body sizes. We used a long-term experiment initiated in 2004 in the rocky intertidal zone of northern California, which established monoculture plots of each of four dominant species of macroalgae as well as polyculture plots with all four species. This design is analogous to the grassland experiments that have consistently found effects of plant species richness on arthropod diversity (e.g., Borer et al. 2012). Two of these seaweed species form short, dense turfs, and two form taller, branching canopies. In addition, as previously reported, polycultures of these species produced higher overall algal cover than any of the monocultures after the first two years of the experiment (Stachowicz et al. 2008). Thus effects of algal species richness on the invertebrate community could emerge if invertebrates respond differently to the morphology or palatability of different species of algae and/or if they respond to differences in the total amount of algal cover.

Using surveys for both meiofauna (e.g., foraminifera, ostracods, copepods, nematodes) and larger macrofauna (e.g., limpets, littorines, chitons, and crabs) within these experimental plots, we tested the effects of algal identity, richness, and total cover on invertebrate richness, abundance, and composition (see Plate 1 for photos of a range of invertebrates included in this study). Comparing across and within the range of body sizes represented by the meiofauna and the macrofauna, we found evidence for multiple mechanisms linking invertebrate and macroalgal diversity within the same community. We link these differences to variation in body size and in food and habitat requirements, and show that invertebrate size and habitat requirements are

likely more important than trophic status for predicting response to marine primary-producer diversity.

Methods

Study system

This study was conducted in the Bodega Marine Reserve, California, USA (38°19′12″ N 123°04′24″ W), in the mid-high intertidal zone, where the dominant algal species are the turf-forming green alga *Cladophora columbiana*, the turf-forming red alga *Endocladia muricata*, the canopy-forming red alga *Mastocarpus papillatus*, and the canopy-forming brown alga *Pelvetiopsis limitata*. These species collectively represent >85% of seaweed cover and occur in an intermixed patchwork rather than in discrete zones (Stachowicz et al. 2008). Beginning in 2004, the species richness of the community was manipulated via species removal in 72 1.5 m diameter circular plots. Plot size was chosen to be large enough to allow for many individual algae to become established (up to hundreds of individuals per plot) and to provide sufficient area of treated habitat to allow animals to perceive and respond to the treatment. For example, plots were much larger than our observations of movements of tagged individual limpets over periods of weeks to months. We established 12 monocultures of each of the four algal species separately (48 total plots), 12 polycultures with the four main species in combination, and 12 unmanipulated controls. Plots were set up in 12 blocks selected to group one plot of each treatment by similar exposure and initial cover composition. Removal of nontarget species was continued four times per year throughout the experiment to maintain the experimental treatments. Because of this continued weeding, the target perennial species were abundant only in their respective monocultures, the polycultures, and the controls (see Appendix A for cover of each species in each treatment). Also, the average cover of fast-growing ephemeral species (*Ulva* spp. and *Pyropia* [formerly *Porphyra*] spp.) was maintained at <6% in winter and <13% in summer and fall. Ephemeral abundance was lowest in polycultures and unmanipulated controls, where there was less available bare rock.

Surveys of the invertebrate community and associated algae

We surveyed plots for macrofauna in winter (January), spring (April), summer (July), and fall (October) of each year between summer 2006 and summer 2011 (excepting spring 2011) for a total of 20 sampling periods. All invertebrate data were thus obtained after the positive effect of algal polyculture on total algal cover had emerged (Stachowicz et al. 2008; see also *Results: Richness, abundance, and diversity of macrofauna*). Because two experimental plots were lost to disturbance by harbor seals early in the experiment, we carried out these surveys for a total of 70 plots (11 each of the *Endocladia* and polyculture treatments, 12 each for all other treatments and controls). For each sampling period, we used a 1 m diameter hoop divided into quadrants to identify the central portion of the plot (excluding the outer 0.25 m radius as a buffer) and then haphazardly placed a 0.2 × 0.2 m quadrat in each quarter of the plot. Within each quadrat, we visually estimated cover for each species of algae and calculated total percent canopy cover in a plot as the summed cover of all algal species, excluding prostrate forms (crusts and films), averaged over the four quadrats. We also identified and counted all mobile invertebrates that could be observed on and under the algal cover without destructive sampling of algal turfs or mussel beds. For analysis, we combined the data from all four quadrats in a plot as our measure of total abundance of each species of mobile invertebrate in each plot. We used this plot-level estimate to calculate macrofaunal species richness and species diversity using Shannon's diversity index ($H' = -\Sigma\, p_i \ln p_i$ where p_i is the proportional abundance of species i). We note that the majority of the individuals surveyed were adults or larger juveniles, rather than new recruits, which we were less likely to detect in the field.

In addition to these surveys of macrofauna, we also performed a single intensive survey of smaller species (meiofauna) that live within the algae and require destructive sampling and microscopy to identify and enumerate. To survey these species we removed 3 cm diameter cores of each algal species over two days in the summer (August) of 2007. We removed four cores of the same algal species from each monoculture plot, and one of each species (again for a total of four cores) from the polyculture plots. Because *Cladophora* turfs had a very large number of smaller taxa (ostracods, nematodes, harpacticoid copepods, foraminifera, and mites), we limited enumeration of these taxa to 1 cm diameter subsamples from each larger sample. To avoid disturbing plots that were being used as reference plots for another study, we did not destructively sample from the control plots. Additionally, to avoid substantially decreasing the total amount of algae present in a plot, we were not able to survey two of the *Cladophora* plots, and we were able to collect only one out of four cores in one plot and only two out of four cores in another. We therefore had a total of 56 plots surveyed for meiofauna (12 *Pelvetiopsis*, 12 *Mastocarpus*, 11 *Endocladia*, 11 polycultures, and 10 *Cladophora*). We transported these samples to the lab and examined each one under the microscope to isolate all invertebrates and record abundance by species. To compare richness and abundance at the plot level, we combined all samples from each plot to calculate plot-level abundance of each species. For the two *Cladophora* plots with only one and two cores, our best estimates of the corresponding plot-level data were obtained by multiplying the core-level data by four and two, respectively.

Statistical analyses

Macrofauna.—We tested for effects of algal species richness and identity on the richness and abundance of

macrofauna over the six years of the experiment using general linear mixed models. We included treatment, season, a treatment × season interaction, and year as the fixed effects, and to account for spatial and temporal nonindependence, we included sampling period (20 levels), block (12 levels), and plot (70 levels) as the random effects.

We did not include year × season interactions because some years (2006 and 2011) were not sampled in all four seasons. However, we did examine treatment effects by season within each year of the study and found that effects varied in magnitude but not direction. Therefore we are confident that this model accurately accounts for the major temporal variation and tests for overall effects of treatment that hold despite that variation. Additionally, we treated year as an unordered, discrete variable rather than a continuous variable because our data collection began at the point when total algal cover had stabilized following initial removals, and there was no longer any consistent increase in algal cover over time (see *Results: Richness, abundance, and diversity of macrofauna* and also Stachowicz et al. 2008). We also examined models using an autoregressive structure for the covariance among repeated measurements of the same plot to account for decreasing similarity with increasing time between sampling periods. However, these models did not achieve higher likelihood than the simpler case of symmetrical clustering between all observations of the same plot.

Finally, we used a modified version of this model framework to test how total canopy cover, known to be higher in algal polycultures (Stachowicz et al. 2008), affected the richness and abundance of macrofauna. We included canopy cover (ranging from 0% to >100% for multilayered canopies) as a continuous fixed effect, along with season, species richness (monoculture vs. polyculture), and all possible interactions between these effects. We simplified the treatment variable to monoculture vs. polyculture to clarify the presentation of slopes and focus on the primary contrast of interest, after ensuring that all slopes were in the same direction (i.e., all individual monoculture treatment slopes were in the same direction).

We conducted these analyses in SAS (SAS Institute 2008) using the MIXED procedure with the Kenward-Roger method for estimating denominator degrees of freedom (Littell et al. 1996) and likelihood ratio tests to assess the significance of random effects. All residuals were checked for adherence to assumptions of normality and equal variance, and response variables (specifically abundance) were log-transformed where necessary to meet these assumptions.

Meiofauna.—To test for plot-level differences in richness and abundance of the meiofauna, sampled at a single time point, we again used a mixed model with treatment as the fixed effect and block as the random effect, but this reduced to a fixed-effects model as block had no effect ($P = 1.0$). Additionally, to compare the community of meiofauna found in a single algal species collected in monoculture vs. polyculture, we used the data at the level of individual samples and randomly selected a single sample from each monoculture to compare to the samples of the same algal species from the polycultures. We used a fixed-effects ANOVA with algal species, species richness (monoculture vs. polyculture), and their interaction as the effects, and repeated this over 100 independent random selections of the single samples from the monoculture plots. These analyses were conducted in R (R Development Core Team 2012). We note that there was no equivalent to this analysis for the macrofauna because in the polycultures, all species of algae were intermixed at both the scale of individual quadrats (0.04 m^2) and the scale of whole plots (0.785 m^2).

To further test for differences in meiofauna community composition among treatments, we used multivariate analyses to compare both the plot-level abundance data (i.e., the summed abundance of each taxon over all four samples taken from a single plot), as well as the individual samples of the same algal species in monoculture and polyculture. First, for the plot-level meiofauna data, we transformed the taxon × plot abundance matrix using three different transformations with increasing down-weighting of the most abundant species: square-root, fourth-root, and presence/absence. From these transformed matrices we then calculated Bray-Curtis similarity matrices and used these in analysis of similarities (ANOSIM) and nonmetric multidimensional scaling (MDS) analyses to test for differences in community composition among treatments and to display these differences in two dimensions, respectively. Second, to test for differences in community composition between monoculture and polyculture samples of the same algal species, we again selected a single sample from each of the monoculture plots and grouped these with the polyculture samples of the same species, creating four separate data sets. Although the multivariate analysis was not sufficiently automated to allow replication over multiple random selections of the monoculture samples, the univariate analyses showed that this source of variation should have little effect. We analyzed each of these data sets using ANOSIM and MDS, using the transformations and metrics described for the plot-level data. All multivariate analyses were carried out in PRIMER v6 (Clarke 1993, Clarke and Gorley 2006). We used multivariate approaches primarily for the meiofauna because composition in the macrofauna was dominated by a few very common species. However, we did perform ANOSIM and MDS analyses on a presence/absence transformed matrix of summer macrofaunal composition for comparison.

Individual taxa and groups of taxa.—Beyond summarizing richness, abundance, diversity, and composition, we also examined individual taxa and groups of taxa for differential abundance across algal treatments. For both

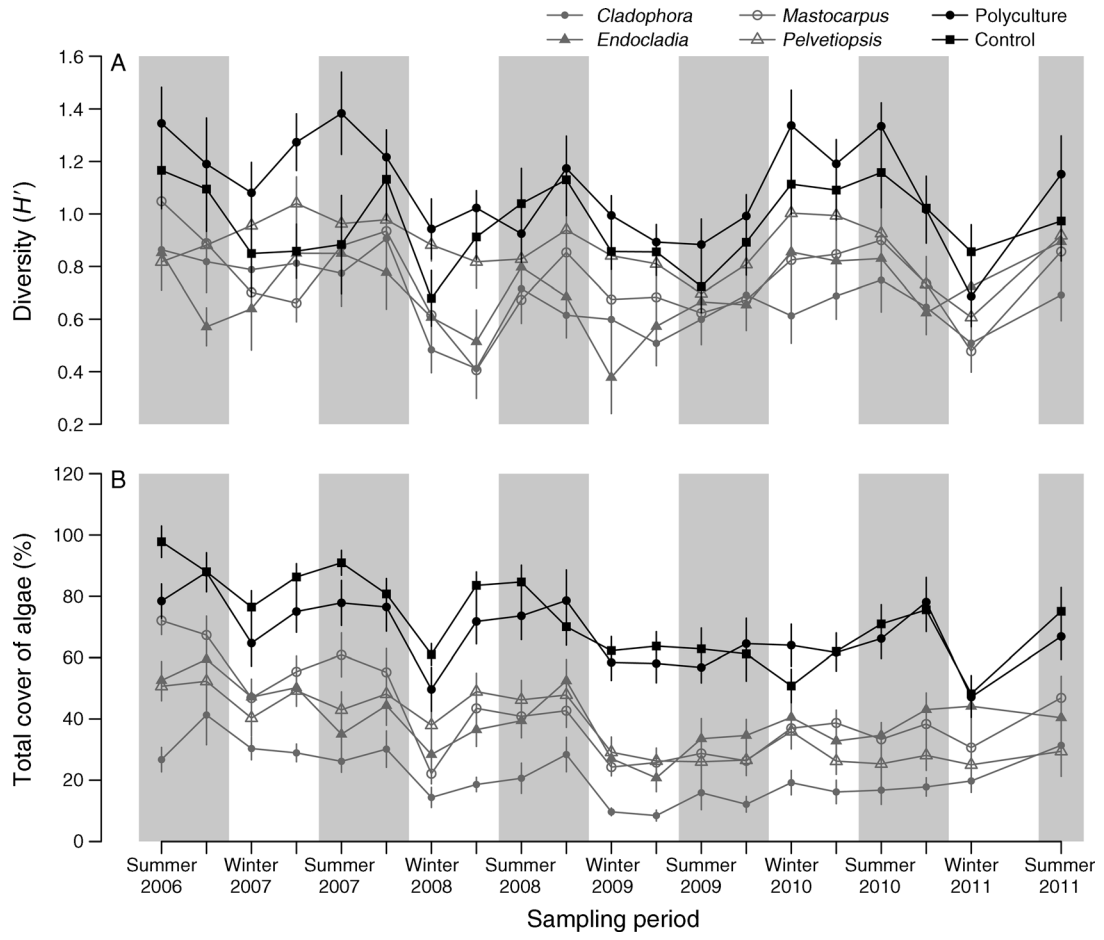

FIG. 1. Time series of (A) macrofaunal diversity (Shannon's diversity index, H'), and (B) total algal cover in monoculture, polyculture, and control treatments over the course of the species diversity experiment in the intertidal zone at Bodega Marine Reserve, California, USA. Summer and fall seasons are shaded gray. Error bars are ±SE.

macro- and meiofauna, we treated the most common species separately and grouped less common species based on taxonomy and/or body form (see Appendix B for lists of these groups). However, even at the level of group, many types of macrofauna were absent from large numbers of plots at any individual sampling period, resulting in a high number of zero values in their abundance distributions. To address this, for these groups we summed total abundance in each plot over the 20 sampling periods to obtain a normal distribution of total occurrences over the course of the experiment. We note that this should be viewed as a measure of the number of observations or occurrences of these groups rather than total abundance, because some individuals may have been counted in multiple sampling periods.

RESULTS

Richness, abundance, and diversity of macrofauna

Over the six years of the experiment, macrofaunal diversity was consistently higher in polycultures and controls than in monocultures, as was the total cover of algae (Fig. 1). The higher macrofaunal diversity (Shannon's diversity index) was driven by opposite effects of algal species richness on macrofaunal richness and abundance, especially of the most common species. Species richness per plot was consistently higher in polycultures and controls than in monocultures (Fig. 2A), although the magnitude of this effect was stronger in summer and fall (significant treatment × season effect and significant richness contrasts for each season separately as shown in Table 1). Depending on the season, polyculture plots had one to two additional species, which equated to 25–40% higher richness. This higher species richness was not driven by total abundance, which was lower in polycultures and controls across all seasons, with no treatment × season interaction (Fig. 2B, Table 1). Because we found that polycultures were very similar to controls in their richness and abundance (Fig. 2), we excluded the controls from additional analyses to simplify presentation. The similar effects of polycultures and controls are not surprising given that the total cover (Fig. 1B) and

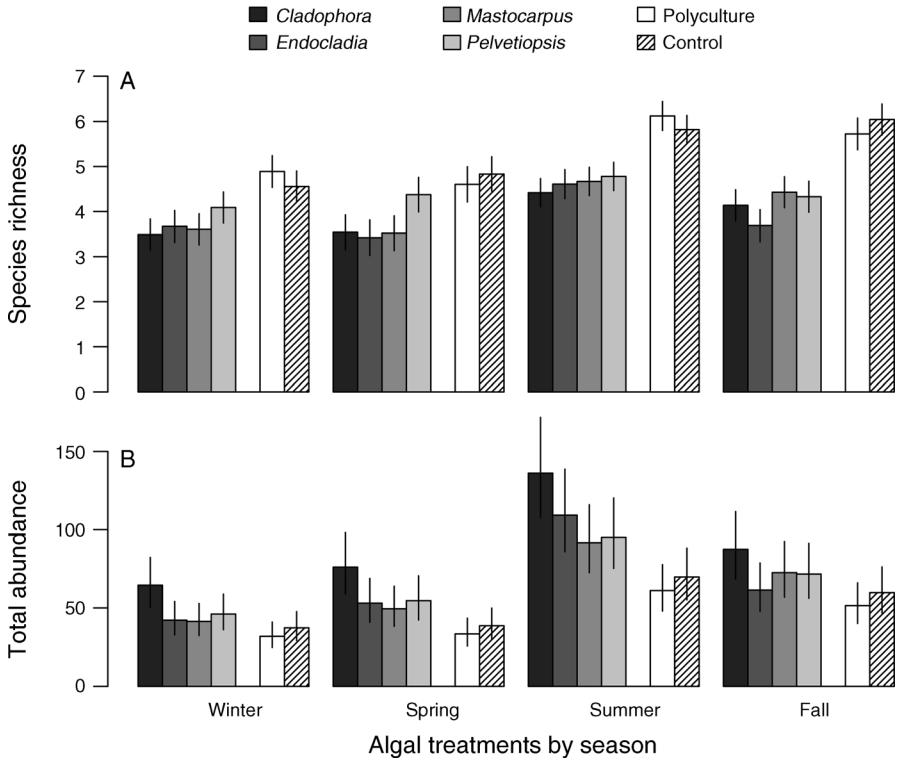

FIG. 2. (A) Species richness and (B) total abundance of macrofauna per plot. In (B), abundance was log-transformed for analysis, and means were back-transformed for presentation. Error bars are ±SE.

species composition (Appendix A) of algae were largely equivalent in the two treatments throughout the experiment.

In contrast to the effects of algal species richness, there were no consistent differences in richness or abundance of macrofauna among monocultures. Comparing species richness between monocultures within each season, there were only five significant comparisons ($P < 0.05$) out of 24 (six comparisons in each of four seasons). Against an adjusted P value of $0.05/24 = 0.0021$, the only significant difference was that richness was higher in *Pelvetiopsis* than in the other monocul-

TABLE 1. Statistical results for effects of algal treatment, season, and year on macrofauna richness and abundance in a species diversity experiment in the intertidal zone at Bodega Marine Reserve, California, USA.

Fixed effect	df	F	P	Random effect	$P > \chi^2$
Macrofauna species richness					
Treatment	5, 54.3	15.9	<0.0001	Plot	<0.0001
Season	3, 11	4.16	0.0337	Block	0.069
Treatment × season	15, 1295	1.92	0.0177	Sampling period	<0.0001
Year	5, 11	3.59	0.0359		
Algal richness contrast, winter	1, 53.3	37.42	<0.0001		
Algal richness contrast, spring	1, 261	35.68	<0.0001		
Algal richness contrast, summer	1, 53	31.4	<0.0001		
Algal richness contrast, fall	1, 53.4	64.75	<0.0001		
Macrofauna total abundance					
Treatment	5, 53.2	2.75	0.0278	Plot	<0.0001
Season	3, 11	8.71	0.003	Block	<0.0001
Treatment × season	15, 1295	1.01	0.4372	Sampling period	<0.0001
Year	5, 11	7.97	0.0021		
Algal richness contrast	1, 53	9.33	0.0035		

Notes: Algal richness contrasts test for a significant difference between the combined monocultures and the combined polyculture and control treatments. Where there was a significant treatment × season interaction individual models were fit for each season; the contrasts from those season-specific models are given here. Random effects were tested using likelihood ratio tests.

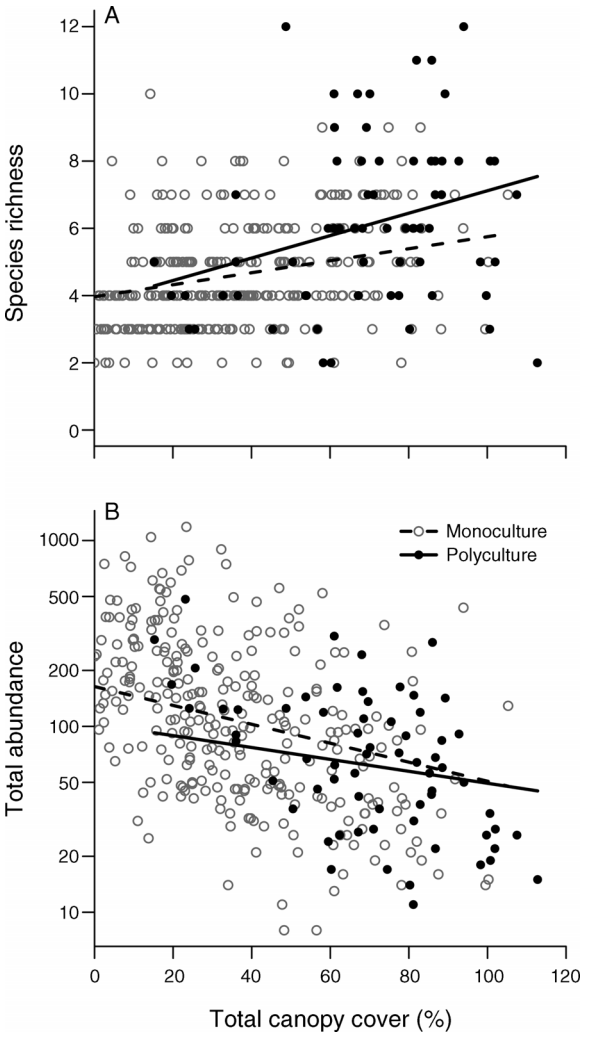

FIG. 3. Effect of total canopy cover (%) on total macrofauna (A) richness and (B) abundance. Data are shown for the summer season, but the relationship was the same for other seasons (no interaction between canopy cover and season). In panel (A), the difference in slopes for monocultures vs. polycultures was marginally significant, but both slopes were positive. This was confirmed by analyzing the two diversity levels separately; both fit a non-zero slope ($P \leq 0.05$). In panel (B) the two slopes were not significantly different. For both panels (A) and (B) the intercepts were not significantly different. Abundance was log-transformed for analysis and is presented on a log scale. See Table 2 for statistical results.

tures in spring (Fig. 2A). As with species richness, multivariate community composition also differed between algal polycultures and monocultures, but not among monocultures (see Appendix C: Fig. C1 for detailed results). Finally, there were no differences in abundance between monocultures (all $P > 0.05$). Both richness and abundance varied by year and were significantly clustered by random effects of plot and sampling period, and abundance also varied by block (Table 1).

The higher richness and lower abundance of macrofauna in polycultures was also associated with the difference in total canopy cover of algae (Fig. 3), which was higher in polycultures than monocultures (Fig. 1B). We found that species richness increased with canopy cover in both polycultures and monocultures and did so at a slightly higher rate in polycultures (Fig. 3A; see significant canopy cover × species richness interaction in Table 2). The lack of a seasonal effect on richness in this analysis (Table 2) also suggests that seasonal differences in mean species richness (Fig. 2A) were at least partly driven by seasonal differences in algal cover. In contrast to richness, total macrofaunal abundance decreased with increasing canopy cover in both monocultures and polycultures, with no difference in slope (Fig. 3B, Table 2). Season did not affect this relationship but did have a significant effect on overall abundance (Table 2), suggesting that seasonal changes in mean abundance (Fig. 2B) were not completely explained by algal cover. Random effects were the same as in the previous analysis of mean richness and abundance (Table 2).

Richness, abundance, and composition of the meiofauna

In our one-time sampling of the meiofauna, both richness and abundance were higher in polycultures than in the average monoculture (Fig. 4A, B; $P < 0.0001$ for contrast of polyculture vs. monocultures). However, the polyculture richness was not significantly different from the species richness in *Cladophora* and *Endocladia* monocultures, and abundance was higher in *Cladophora* than in polyculture (significant treatment differences in Fig. 4A and 4B are from pairwise comparisons based on an adjusted α of 0.005 [0.05/10 comparisons]).

The two orders of magnitude difference in total abundance between treatments likely played a large role in the difference in richness. In addition, the four orders of magnitude difference in abundance between individual taxa (from <1 to >1000 individuals per plot) meant that rarefaction did not provide a meaningful way of separating this effect. However, multivariate analyses did allow us to jointly test for differences in composition and abundance in a different way. Based on the abundances of all taxa in each plot, we found significant differences in composition among treatments (ANOSIM treatment effect $P = 0.001$; Fig. 5A). Further, these results largely held with increasing down-weighting of abundant species. Using the square-root transformation of abundances in the ANOSIM analysis, we found that all pairwise comparisons of treatments were significant (all $P <$ an adjusted α of 0.005 [0.05/10]). Using a fourth-root transformation, all comparisons remained significant ($P < 0.004$) except for the difference between the two frondose algae species, *Pelvetiopsis* vs. *Mastocarpus* ($P = 0.10$). Finally, when we removed all abundance data via the presence/absence transformation, all differences remained significant except for *Pelvetiopsis* vs. *Mastocarpus* ($P = 0.62$), and polyculture vs. *Cladophora* ($P = 0.47$) and vs. *Endocladia* ($P = 0.01$).

TABLE 2. Statistical results for effects of total canopy cover on macrofauna richness and abundance (along with interactions between canopy cover, algal richness treatment [monocultures vs. polyculture], and season).

Fixed effect	df	F	P	Random effect	$P > \chi^2$
Macrofauna species richness					
Algal richness	1, 263	0.12	0.7259	Plot	<0.0001
Season	3, 75.8	1.14	0.3402	Block	0.069
Season × algal richness	3, 1085	0.83	0.4796	Sampling period	<0.0001
Cover	1, 577	26.24	<0.0001		
Cover × algal richness	1, 588	3.8	0.0517		
Cover × season	3, 1098	2.1	0.0992		
Cover × season × algal richness	3, 1090	0.52	0.6675		
Year	5, 11.1	3.91	0.0272		
Macrofauna total abundance					
Algal richness	1, 197	3.2	0.0752	Plot	<0.0001
Season	3, 54.4	8.11	0.0001	Block	<0.0001
Season × algal richness	3, 1075	0.27	0.8476	Sampling period	<0.0001
Cover	1, 1072	24.73	<0.0001		
Cover × algal richness	1, 1062	2.12	0.1453		
Cover × season	3, 1087	2.24	0.0823		
Cover × season × algal richness	3, 1077	0.01	0.9986		
Year	5, 11.1	6.42	0.0049		

Thus, after equalizing the abundance of rare and common species within a sample, there was still clear compositional differentiation between *Cladophora*, *Endocladia*, and the larger, less branched algae.

Whereas the species of algae sampled had a large effect on meiofauna richness, abundance, and composition (Figs. 4A, B and 5A), there was no effect of the species richness treatment in which an alga was growing (i.e., monoculture vs. polyculture) on any of these community metrics. Comparing the samples of each algal species taken from polyculture to single samples from the corresponding monocultures, there was a strong effect of algal species ($P < 0.0001$), but no effect of algal species richness and no interaction between the two (Fig. 4C, D). This held across the 100 random selections of the single samples from each monoculture plot (mean $P > 0.5$ for both species richness and species richness × algae species effects across all trials). There were also no multivariate differences in composition between the monoculture and polyculture samples of a single algal species (Fig. 5B). Results of individual ANOSIM analyses for the effect of algal species richness are as follows: for *Cladophora*, $P = 0.24$; for *Endocladia*, $P = 0.41$; for *Mastocarpus*, $P = 0.38$; and for *Pelvetiopsis*, $P = 0.088$. These results were not affected by the use of different transformations.

Effects of algal identity and species richness on individual species of invertebrates

Over the 30 taxa of macrofauna we identified (see Appendix B: Table B1 for a complete list), we found opposite effects of algal species richness on rare and common species. Most of the rarer groups and species, which we summed over all sampling periods to obtain normally distributed total occurrence data, were present more often in polycultures (Fig. 6A). Using an ANOVA for the effect of treatment on log-transformed total occurrences for each of these groups, polyculture occurrence was greater than that of monocultures for arthropods ($P = 0.0012$), chitons ($P = 0.0013$), worms ($P = 0.0006$), and *Lottia pelta* ($P = 0.0003$), and marginally so for bivalves ($P = 0.0089$) using an adjusted α of 0.008 (0.05/6 taxa). *Chlorostoma* (formerly *Tegula*) *funebralis* ($P = 0.59$) abundance did not vary between monocultures and polycultures. For the three most abundant macrofaunal species, however, effects of algal species richness on average plot abundance at a single sampling period were either neutral or negative (Fig. 6B). *Littorina* spp. ($P = 0.014$) and *Lottia scabra* ($P = 0.012$) were less abundant in polycultures compared to monocultures, while *Lottia digitalis* was unaffected ($P = 0.27$). In combination, these results for macrofauna taxa clearly underlie the overall finding of higher species richness but lower abundance in polycultures (Fig. 2). Polycultures had more occurrences of rare species, but lower abundances of the most common species.

Whereas macrofaunal species differed in their distribution between monocultures and polycultures, the 31 taxa of meiofauna (Appendix B: Table B2) were strongly affected by the species of algae in the monoculture (Fig. 6C) rather than its presence in a monoculture vs. polyculture plot (Figs. 4C, D and 5B). Comparing the monocultures, for most taxa there was a highly significant effect of algal treatment (Fig. 6C; for all but three taxa, $P < 0.0001$). Additionally, for almost all taxa with significant effects of algal identity, abundance was highest in the most densely branched turf algae (*Cladophora*), followed by the slightly less dense turf algae (*Endocladia*), and finally by the much more coarsely branched canopy algae (*Mastocarpus* and *Pelvetiopsis*). Exceptions to this pattern were the bivalves ($P < 0.0001$ for effect of algal species, but *Cladophora* and *Endocladia* were similar) and three taxa with no effect of algal species: fly larvae ($P = 0.043$),

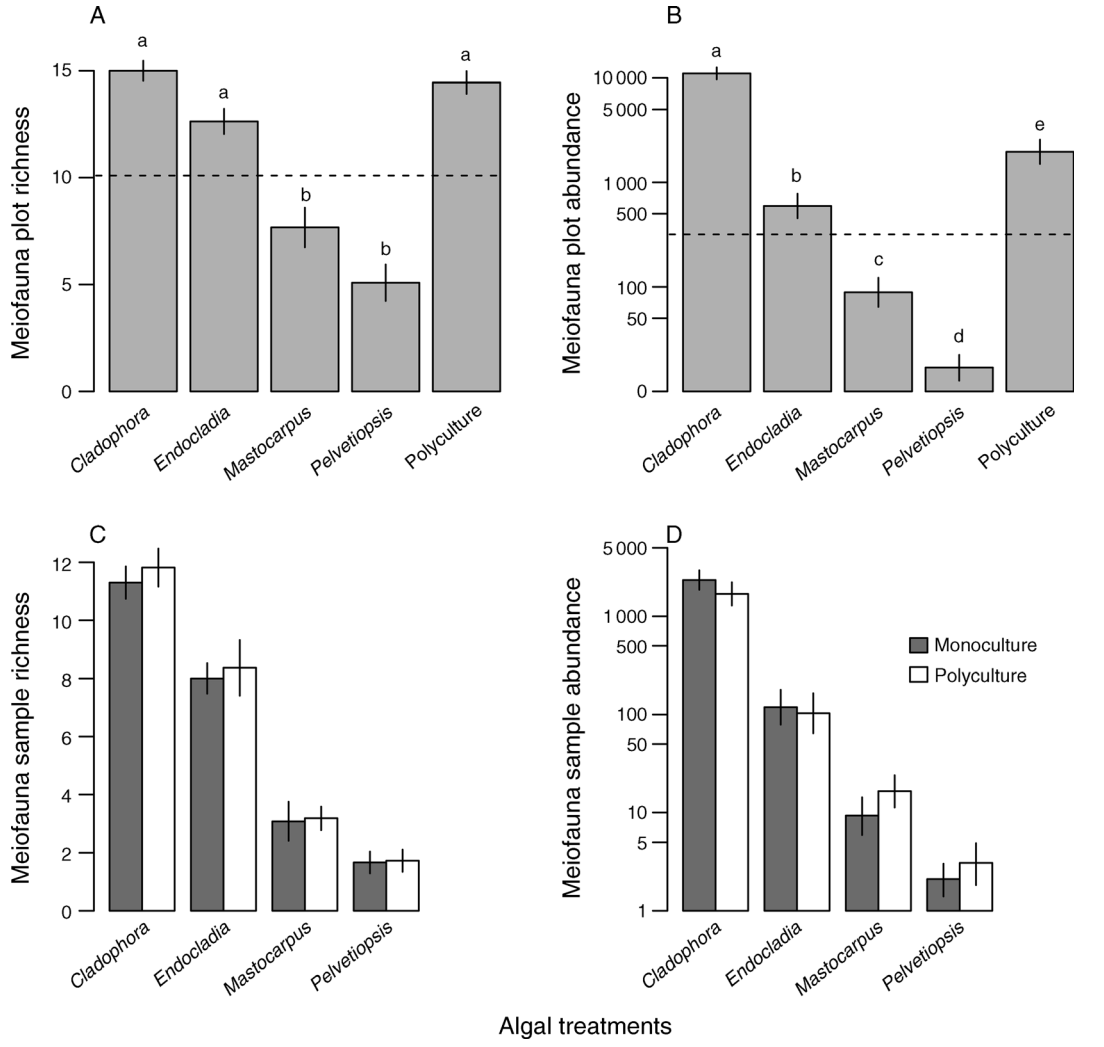

FIG. 4. Average richness and abundance of meiofauna by treatment, at the level of (A, B) plots, and (C, D) individual samples of algae. In panels (A) and (B), different letters indicate significant treatment differences from pairwise comparisons based on an adjusted α of 0.005 [0.05/10 comparisons], and dashed horizontal lines indicate the mean response of the four monoculture treatments. In panels (C) and (D), richness and abundance, respectively, are compared between individual samples of the same algae taken from polycultures and monocultures. Abundance was log-transformed for analysis and is presented on a log scale. Error bars are ±SE.

gammarid amphipods ($P = 0.21$), and gastropods ($P = 0.066$), each tested against an adjusted α of 0.004 (0.05/12 taxa).

DISCUSSION

We found that diverse algal communities hosted more species of both large and small invertebrates than the average algal monoculture. However, we also found that the mechanisms underlying this pattern differed substantially between the meiofauna and macrofauna. More species of macrofauna occurred in the polycultures than any of the monocultures (Fig. 2A), indicating some emergent effect of algal richness on macrofaunal richness. On the other hand, algal identity effects were the best predictor of meiofaunal richness, and any species richness effects were purely the effect of including turf species in polycultures (Fig. 4A). In fact, the meiofauna in each component algal species within polycultures were indistinguishable from those found in the corresponding monocultures (Fig. 5B).

We also found substantial variation within the meiofauna and macrofauna. Within the macrofauna, rare and common taxa responded to host plant species richness in opposite ways, leading to more occurrences of rare taxa and lower abundance of very common taxa in the polycultures (Fig. 6A, B). Within the meiofauna, we found that most small species reached greatest abundance within a particular alga, *Cladophora*, but that some of the larger meiofauna showed no such variation among algal species. In this discussion, we

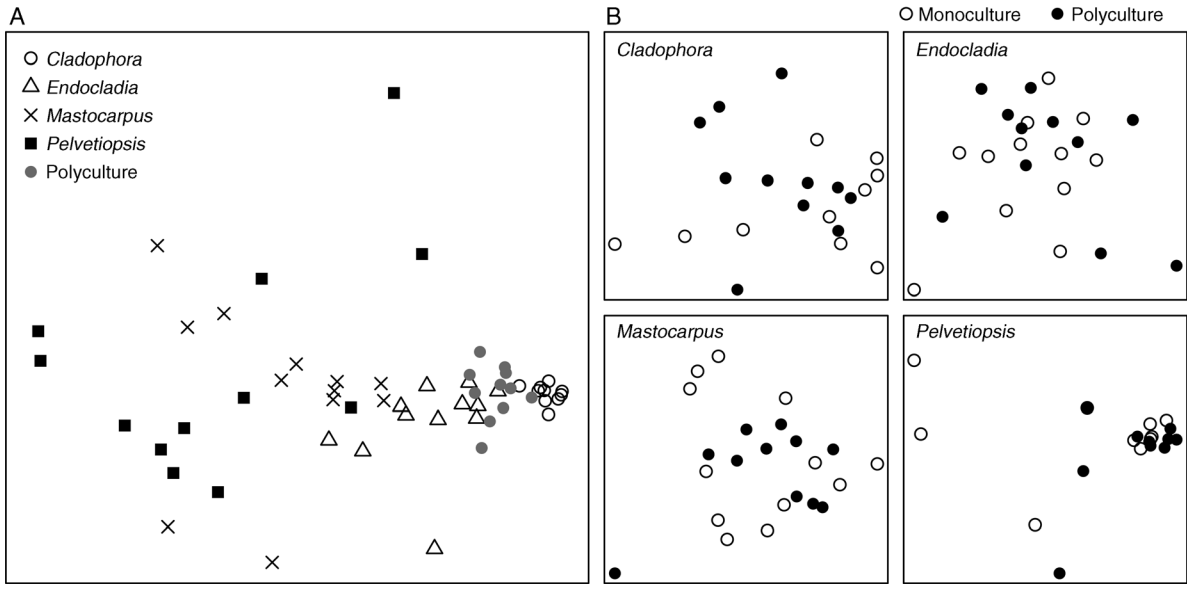

FIG. 5. Meiofaunal community composition (A) across all treatment plots and (B) from samples of each individual algal species growing in monoculture vs. polyculture. All plots are nonmetric multidimensional scaling plots based on Bray-Curtis similarities among samples, where abundance has been fourth-root transformed. Minimum stress values were (A) 0.13 and (B) 0.20 (*Cladophora*), 0.17 (*Endocladia*), 0.13 (*Mastocarpus*), and 0.01 (*Pelvetiopsis*).

interpret the variation between and within these groups of invertebrates, focusing on the effects of invertebrate body size in determining the role of producer identity vs. species richness vs. abundance, and the importance of producers as food vs. habitat. We also compare our findings with previous marine and terrestrial studies on the effects of plant and macroalgal diversity on animal communities.

Effects of producer identity, composition, and productivity

Animal diversity and abundance can be increased by plant identity effects (if a particular plant species is a superior food or habitat), by complementary use of different plants (either by different animals with different requirements or by the same animals requiring a mixed diet or habitat), or by an indirect effect of plant diversity on plant production that results in greater total plant biomass (Srivastava and Lawton 1998, Stachowicz et al. 2007, Borer et al. 2012). In marine systems, several studies have found strong effects of plant identity on the diversity and abundance of invertebrates when macrophytes vary in their morphology (Parker et al. 2001, Bates and DeWreede 2007, Gustafsson and Bostrom 2009), while other studies have found redundancy among different macroalgae in the animal communities they support (Gibbons 1991, Kelaher et al. 2007).

In this study, we found strong effects of seaweed identity on meiofauna but not macrofauna. Most of the meiofauna taxa reached their highest abundance in the most densely branched of the four algae species in this system (*Cladophora*; Fig. 6C), which is consistent with a number of other studies of producer complexity–invertebrate diversity relationships (Dean and Connell 1987, Jeffries 1993, Gee and Warwick 1994, Kostylev et al. 2005, Hauser et al. 2006, Hooper and Davenport 2006, Thomaz et al. 2008). In contrast, most of the macrofauna showed no association with any particular algal species (Fig. 6A, B). Their increased richness in polycultures therefore did not result from the additive accumulation of invertebrates specialized to use different algal species (i.e., the "resource specialization hypothesis" [Hutchinson 1959, Strong et al. 1984]). Instead, we found that macrofaunal richness and abundance were largely driven by the indirect effects of algal species richness on total algal biomass. Interestingly, in experiments that found no effect of marine producer richness on epifaunal communities, plant biomass or cover was often equalized across treatments to isolate the direct effects of species richness. In one study that did find greater infaunal richness in seagrass polycultures, plant species richness led to greater belowground biomass and thus greater total habitat availability (Gustafsson and Bostrom 2011). The association between increased plant biomass or cover in polycultures and increased effects of plant richness on faunal richness argues that an important mechanism underlying plant diversity effects on faunal communities is greater total food or habitat availability, as has been reported for terrestrial systems (Borer et al. 2012). Similarly, weaker richness and stronger identity effects in studies that equalize biomass across treatments (e.g., Parker et al. 2001) suggest that direct complementary effects of marine macrophytes on the invertebrate community may be weak.

This difference between meiofaunal and macrofaunal responses demonstrates that species that vary in size also

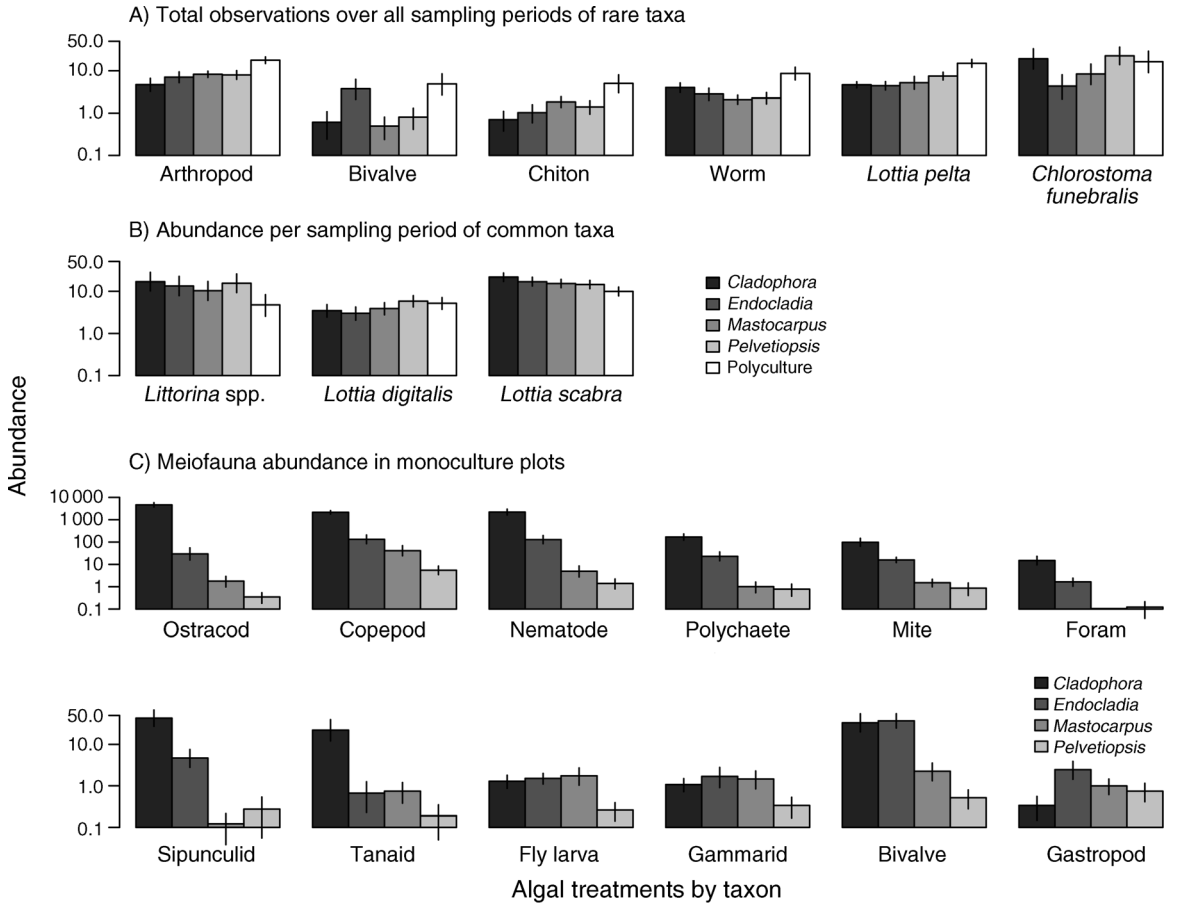

FIG. 6. Abundances of major species and taxonomic groups. In (A), macrofaunal groups or species that were highly variable in their presence/absence in a plot at any one sampling period (and therefore have poorly distributed abundances) are presented as the average total occurrences per plot over the entire six years of the experiment (which is normally distributed). In (B), the three common macrofaunal species with well-distributed abundance data at the level of a single survey are presented using the average abundance per sampling period. In (C), the average abundance of the major species and taxonomic groups of meiofauna are given for the monoculture plots. Abundance was log-transformed for analysis and is presented on a log scale; note that the scale of the *y*-axis differs between lines of plots. Error bars are ±SE.

likely vary in their instantaneous perception of producer identity and diversity. Whereas smaller species may have a daily range of movement no larger than an individual plant (Hay and Steinberg 1992), larger species will constantly be in contact with multiple species of algae when they are found together in polyculture. In addition, species that are larger than individual algal thalli and move along the substrate between rather than within the algae should be less likely to be influenced by the fine-scale differences in structure among algal species. For these two reasons, we suggest that animals that are small relative to the size of an algal thallus should be more likely to respond to algal species identity, whereas species that are large or have high mobility relative to the size or area occupied by a single alga should be more likely to respond to algal species richness or emergent effects of that richness, such as higher biomass. This held both between the meiofauna and the macrofauna and within the meiofauna, where the smallest species (ostracods, copepods, mites, and foraminifera) responded strongly to algal identity but the larger species (bivalves and gammarids) did not (Fig. 6C).

Producers as food vs. habitat

In addition to the effect of body size on the perception of plant identity and diversity, the differential responses we observed between and within the meiofauna and macrofauna may also be due to variation in the way species balance the acquisition of food and habitat. In this system, the most abundant macrofaunal herbivores (limpets and littorines) preferentially graze ephemeral algae such as diatoms and thin foliose forms such as *Ulva* spp. and *Pyropia* (formerly *Porphyra*) spp. rather than perennial algae. In small, cleared patches within the plots studied here, removing perennial algae greatly increased the abundance of these ephemerals, and limpets and littorines quickly removed ephemerals from patches to

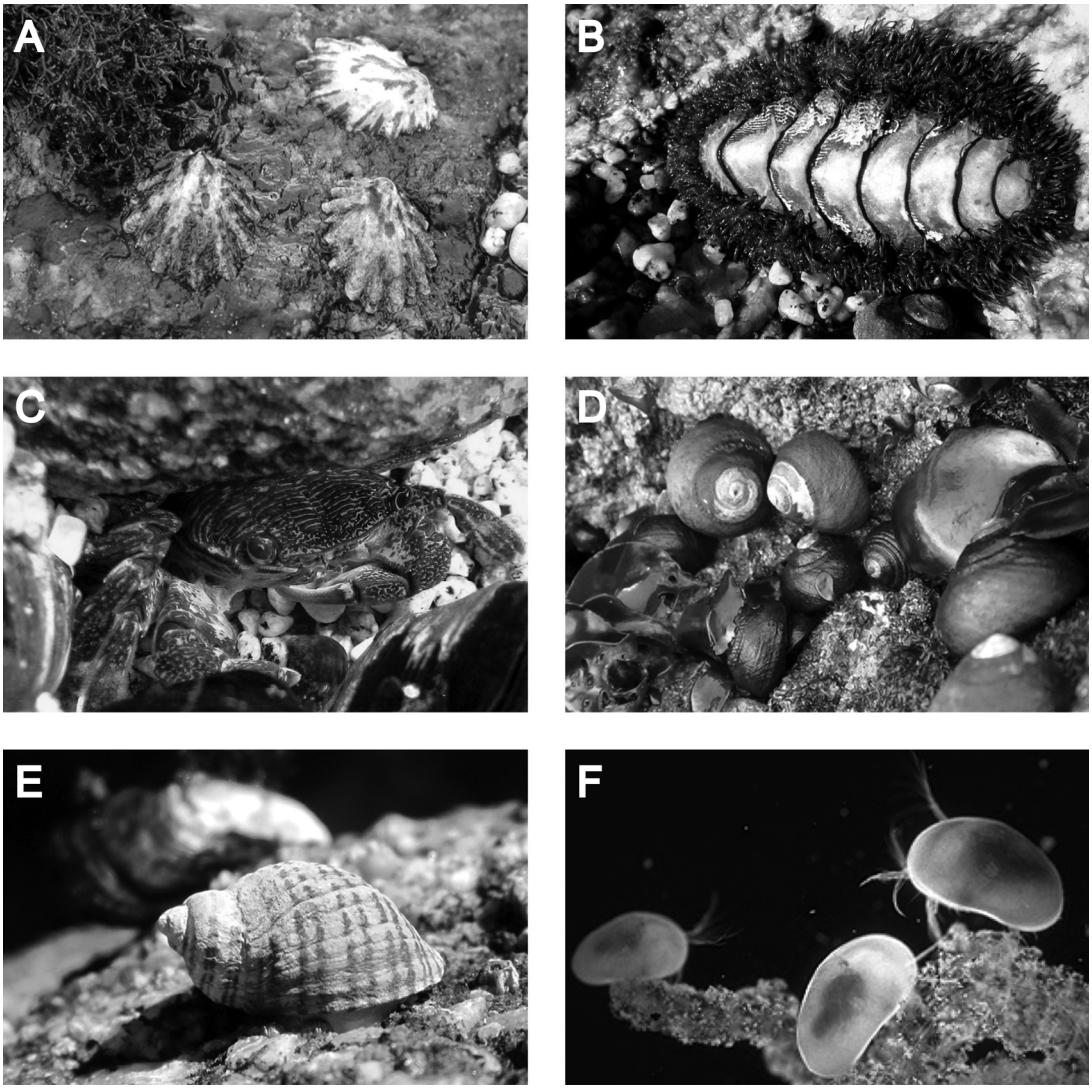

PLATE 1. Some common mobile invertebrates from the mid-high intertidal zone considered in this study: (A) the limpet *Lottia scabra*; (B) the chilton *Mopalia mucosa*; (C) the shore crab *Pachygrapsus crassipes*; (D) the black turban snail *Chlorostoma* (*Tegula*) *funebralis*; (E) the predaceous whelk *Nucella ostrina*; (F) ostracods found within the fine branches of Cladophora turfs. Photo credits: (A, D, E) Grace Ha, (B, C) Kristin Aquilino, and (F) Stachowicz Lab.

which they had access (Aquilino and Stachowicz 2012). Thus these grazers are likely more abundant in algal monocultures than polycultures (Figs. 2B, 6B) because monocultures have less perennial algal cover and therefore more bare rock available for their preferred food to colonize (Fig. 1B; Stachowicz et al. 2008). This is analogous to previous findings of reduced abundance of insects in polycultures that included fewer palatable species (C_4 grasses; Haddad et al. 2001), although in this case the more palatable options include none of the manipulated species but instead increase in availability with the lower canopy cover in monocultures.

Macrofaunal species that are more often found in polyculture (Figs. 2A, 6A) must either be eating something other than ephemeral algae or responding to the habitat rather than the food value of a patch. These include arthropods such as crabs, amphipods, and isopods; chitons; the rarest limpet species (*Lottia pelta*); and soft bodied "worm" taxa (Fig. 6a; Appendix B: Table B1). For herbivorous taxa, the benefits of the polyculture over each monoculture could be because multiple algal species are required for food or shelter or because of the higher total abundance of algae in polycultures. For the former option, a mixed algal diet did enhance growth of turban snails (*Chlorostoma funebralis*) and shore crabs (*Pachygrapsus crassipes*), although the increase over a diet of ephemeral algae alone was modest (~15%; Aquilino et al. 2012). Further, this effect was strongest for *Chlorostoma funebralis*, and this species was one of the few taxa not found at higher

frequency in polycultures (Fig. 6A). Many other small grazers are more likely to feed on microalgae or thin, ephemeral, foliose forms than on erect perennial forms (Steneck and Watling 1982, Steneck and Dethier 1994, Aquilino et al. 2012), so it seems unlikely that these grazers are choosing host plant communities with more perennial and less ephemeral algae based on feeding.

Instead, these species are likely benefiting from the higher canopy cover of algae because it ameliorates the abiotic stress associated with the high intertidal zone, reducing desiccation rates in the understory (Stachowicz et al. 2008). The slightly steeper increase of species richness with cover in polyculture plots (Fig. 3A) also suggests that a multilayer canopy, which is not as likely in a monoculture with a single growth form, may be beneficial in this regard. Such dense canopies can enhance settlement rates and buffer both recruits and adults from thermal stress (e.g., Bertness et al. 1999), and any of these mechanisms could underlie the habitat value of polycultures over monocultures. Habitat associations in marine systems can also be due to predator avoidance (e.g., Duffy and Hay 1991), and one study did find that algal identity and richness affected predation rates on amphipods in mesocosms as well as their abundance in the field (Moran et al. 2010). Higher cover of macroalgae in diverse plots could protect animals from avian predators in systems such as this one (Farrell 1991), but at the upper tidal limit, abiotic stress is generally more limiting than predation (Menge and Sutherland 1987). Consistent with this, the limpets and littorines that are more abundant in plots with low algal cover are particularly well adapted at sealing in moisture and preventing desiccation and as a result are frequently the highest species in the intertidal zone (Gowanloch and Hayes 1926, Connell 1972, Wolcott 1973, Farrell 1991). If they are better adapted to resist desiccation and do not need a refuge from predators, then they would gain no benefit from high algal cover in polyculture and instead choose habitat based on food availability rather than environmental conditions.

Finally, whereas species of macrofauna appear to vary in their use of food vs. habitat to determine location at low tide, the smaller meiofauna form a food web within the structure provided by *Cladophora* (Jansson 1967). Amelioration of desiccation and/or wave stress may also be important for these species (Hicks 1986), and previous work has shown that invertebrates are less likely to migrate away from algae exposed to air during low tide if those algae are densely branched and moisture retaining, such as in species of *Cladophora* (Hooper and Davenport 2006). Only a few (if any) of these species are likely to feed directly on the *Cladophora* itself, with most feeding on epiphytic microbiota. These species may include both generalists and specialists feeding on particular microalgae, bacteria, fungi, flagellates, ciliates, detritus, or other species in the meiofauna (Jansson 1967, Fenchel 1978, Hicks 1986, Bracken et al. 2007). The fact that we found similar responses to algal identity across these diverse groups suggests again that the habitat value of the macroalgae is likely more important than direct trophic links (i.e., consumption of the macroalgae itself), in contrast with findings for terrestrial systems (Scherber et al. 2010, Castagneyrol and Jactel 2012). However, part of the habitat value of the densely branched algae may lie in their ability to trap microalgae and a diversity of other food (Hicks 1986). This feature of aquatic macrophytes as a substrate for the widely used food resource of epiphytic microalgae is a key difference between marine and terrestrial animal–plant relationships, and it is part of what allows many marine invertebrates to choose macrophytes for their habitat value regardless of their value as food (Hay and Fenical 1988, Heck and Valentine 2006, Poore et al. 2008).

Implications for ecosystem functioning

We found variation in the response of invertebrates to algal species richness, both within and between the macrofauna and meiofauna we surveyed. In addition, that variation appeared to be related to invertebrate size, increased biomass in algal polycultures, and the relative importance of food vs. habitat. Importantly, this variation also means that our conclusions about the value of algal diversity as a driver of animal diversity are strongly dependent on the type of invertebrates under study and whether we consider only the direct or indirect effects of plant diversity. If we had considered only macrofauna, we would conclude that all species of algae are equally important and that more than one species is required to maximize animal diversity. If we had considered only meiofauna, we would conclude that only one species of algae (*Cladophora*) is required for the maintenance of invertebrate diversity. By including a range of invertebrates, however, we found that some invertebrates benefit from the food available in bare space, some from the habitat characteristics and greater total cover of a multilayer canopy of perennials, and some from the dense branching of an algal turf. Other marine studies that have identified effects of producer species richness on faunal species richness suggest habitat complexity and reduced susceptibility to predation or abiotic stress, rather than food availability, as the primary mechanisms underlying these effects (Moran et al. 2010, Gustafsson and Bostrom 2011). Furthermore, across the available marine studies, faunal communities in diverse mixtures tend to differ from monocultures more strongly when indirect effects mediated through the effects of plant diversity on plant biomass are also considered.

Beyond these patterns, understanding how plant diversity shapes animal communities may also be important to our understanding of stability and resilience. This is especially true in systems where herbivory alters plant diversity and species composition (e.g., Lubchenco 1978, Lubchenco and Gaines 1981, Hay 1985, Williams et al. 2013). In this system, by removing ephemeral algae, limpets and littorine snails

facilitate succession of perennial species (Sousa 1984, Geller 1991, Aquilino and Stachowicz 2012, Williams et al. 2013), which should then increase the diversity of other invertebrates but decrease the abundance of these important herbivores. Given that grazer abundance is well known to affect algal diversity (e.g., Lubchenco 1978), there is potential for feedback between plant and animal diversity. As we continue to study the recovery of the algal community in this system following eight years of localized species removal, both plant and animal diversity are likely to play important and interacting roles, offering an opportunity to understand these feedbacks in greater detail.

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Supplemental Material

Appendix A

Consistency of algal treatments over the course of the experiment (*Ecological Archives* E095-112-A1).

Appendix B

Summary of occurrences by taxonomic group for macro- and meiofauna (*Ecological Archives* E095-112-A2).

Appendix C

Multivariate composition of the macrofaunal community (*Ecological Archives* E095-112-A3).