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Additive effects of physical stress and herbivores on intertidal seaweed biodiversity

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Abstract. Patterns in rocky intertidal seaweed biodiversity influence the resilience and functioning of these important primary producer communities. In turn, seaweed biodiversity patterns are the result of many ecological factors. We determined the influences of thermal and desiccation stress, herbivory, and nutrients on seaweed biodiversity on a northern California rocky shoreline. In a fully crossed design at two tidal heights at wave-protected and exposed sites, we deployed screens to reduce stress, removed herbivores, and added nutrients for 18 months. The treatments reduced temperature, increased relative humidity, decreased herbivore abundances, and increased nitrogen in both seawater and seaweeds. Seaweed abundance and biodiversity (cover, biomass, species richness, diversity, evenness, and community composition) were influenced by tidal height, physical stress, and herbivores. Wave exposure affected all response variables except biomass and evenness. Stress and herbivores had independent additive effects on seaweed abundance and diversity. Physical stress did not make the community as a whole more susceptible to herbivores, and screens had overarching positive effects on seaweed biodiversity even though they also had positive effects on herbivore abundance. Nutrients had virtually no effect on seaweed biodiversity, and we observed no bottom-up effects of nutrient addition on herbivore density or biomass. Small green algae and diatoms were important contributors to overall algal cover and to changes in composition across treatments, but larger macroalgae dominated the species richness response. The striking absence of interactions between stress and herbivory highlights how seaweed communities can respond independently to important drivers of biodiversity. Thus, nonadditive, potentially synergistic effects do not necessarily complicate the understanding of how seaweed biodiversity responds to environmental change.

Key words: biodiversity; Bodega Marine Reserve, California; herbivores; nutrients; physical stress; rocky intertidal zone; seaweed; tidal height; wave exposure.

INTRODUCTION

Globally, biodiversity is changing at unprecedented rates, primarily due to anthropogenic effects including overexploitation of natural resources, species introductions, agriculture, habitat destruction, eutrophication, and climate change (Vitousek et al. 1997). Changes in species diversity can alter ecosystem functioning because organisms differ in their effects on biogeochemical processes (Loreau et al. 2002, Hooper et al. 2005, Worm et al. 2006), and changing biodiversity therefore ranks high among factors that influence ecosystem functioning (Hooper et al. 2012). Changes in biodiversity have been documented best on land, but are also evident in marine ecosystems (Southward et al. 1995, Beaugrand et al. 2002, Dulvy et al. 2003, Kappel 2005, Lotze et al. 2006,

Hawkins et al. 2009). Biodiversity is strongly shaped by ecological (including anthropogenic) and evolutionary processes, resulting in patterns that are anything but random (Paine 1966, Petraitis et al. 1989, Worm et al. 2005).

Temperate rocky intertidal ecosystems long have been used as model systems for experimental studies of species composition and diversity (Connell 1972). Here, we focus on biodiversity patterns in the intertidal seaweed community, exclusive of other sessile organisms, to facilitate understanding of the drivers of natural patterns in biodiversity and the functional role of seaweeds as key marine primary producers and foundation species. There is often, but not always, a positive relationship between seaweed ecosystem function and biodiversity (Allison 2004, Arenas et al. 2009, Boyer et al. 2009, Bracken et al. 2011, Aquilino and Stachowicz 2012). In prior work, we found that both biomass and nitrogen acquisition increase with seaweed richness (Bracken and Stachowicz 2006, Bracken et al. 2008, Stachowicz et al. 2008). Importantly, we also found that the biodiversity–ecosystem function relationship depended on natural, nonrandom patterns in seaweed

biodiversity (Bracken et al. 2008), highlighting the growing recognition that realistic nonrandom changes in biodiversity, such as the ones we consider here, can have profound influences on ecosystem function that are not predicted from studies of random assemblages (Ostfeld and LoGiudice 2003, Zavaleta and Hulvey 2004, Selmants et al. 2012). Understanding the functional consequences of realistic changes in biodiversity needs to be based on elucidation of the factors underlying diversity patterns in the field.

Rocky intertidal seaweed diversity is influenced at the local scale by a variety of factors, including abiotic stress (Seapy and Littler 1982), physical disturbance (Sousa 1979), herbivory (Hawkins and Hartnoll 1983, Nielsen 2003, Altieri et al. 2009), nutrient availability (Bracken and Nielsen 2004, Kraufvelin et al. 2010), and pollution (Littler and Murray 1975). Seaweed species richness is a unimodal function of each of these factors, with few exceptions. For example, at low levels of herbivory, susceptible, fast-growing ephemeral species dominate the seaweed assemblage, but as herbivory increases, slow-growing, herbivore-resistant taxa eventually replace ephemeral species and diversity declines (Lubchenco 1978). Similarly, under low nitrogen availability, slow-growing species dominate, but as nitrogen availability increases, fast-growing species with higher nitrogen requirements can overgrow the assemblage, and diversity declines (Worm et al. 2002, Bokn et al. 2003). A similar pattern in seaweed diversity can result from physical disturbances such as from waves (Denny 1995, Jonsson et al. 2006) or floating logs that remove patches of organisms and initiate a succession in which diversity often, but not always, peaks at intermediate levels of disturbance (Sousa 1979, MacQuaid and Branch 1984, Svensson et al. 2007 for subtidal seaweeds).

Seaweed biodiversity is also influenced by the strong gradients in aerial exposure and physical stress (defined here as thermal and desiccation stress) that characterize intertidal habitats, in addition to the obviously important site factors of wave exposure (Menge and Branch 2001). Much research has been devoted to explaining intertidal zonation patterns based on the physiological responses of seaweeds to physical stress (Schonbeck and Norton 1978, Dring and Brown 1982, Skene 2004). A complementary body of research has addressed how intertidal communities of sessile organisms, including seaweeds, vary across other intertidal gradients such as wave action (Coleman et al. 2006, Viejo 2009, Scrosati et al. 2011). Tidal height is a good proxy for physical stress, but other factors, including herbivory, co-vary across tidal height and can confound interpretation of biodiversity patterns, thus necessitating direct manipulations of stress and other factors to determine their effects (for seaweeds, Kaehler and Williams 1998, Allison 2004, Thompson et al. 2004, Morelissen and Harley 2007, Bertocci et al. 2010).

Given the extensive literature on intertidal seaweeds, surprisingly few studies have involved experimental manipulations of more than two factors to test their effects on biodiversity, typically expressed as algal abundance (cover, density, biomass). Notable exceptions are Thompson et al. (2004), who addressed insolation stress, herbivores, and desiccation/nutrient effects on microalgae and macrophyte recruits, and Atalah and Crowe (2010), who addressed sediments, herbivores, and nutrients in tide pools (but not all factors simultaneously). Thompson et al. (2004) emphasized that physical stress is rarely manipulated in intertidal studies, and presented a conceptual model including stress as an important modifier of herbivory and bottom-up effects on the intertidal "biofilm" community. Both studies quantified algal abundance and community composition but not richness, diversity, or evenness. On the other hand, Bertocci et al. (2010) focused more broadly on diversity (abundance, richness, community composition) in response to physical disturbance and removal of the canopy seaweed. In general, there is a paucity of multifactorial marine studies (Hillebrand et al. 2007, Crain et al. 2008), particularly ones that address diversity sensu lato, despite its importance for ecosystem functioning.

Stress, herbivory, and nutrients each can influence the effects of the others on seaweed biodiversity. For example, nutrient inputs might affect diversity only when herbivory is reduced (Nielsen 2003), and the effect of herbivory can depend on nutrient availability, particularly in eutrophic systems (Worm et al. 2002, Masterson et al. 2008). Yet, herbivore–nutrient interactions are not always evident (Thompson et al. 2004, Guerry et al. 2009) or are limited to specific taxa (Atalah and Crowe 2010). Both seaweeds and herbivores respond negatively to stress, but desiccation can render seaweeds disproportionately susceptible to herbivory if deterrent chemicals are reduced, a result not always observed (Renaud et al. 1990, Dethier et al. 2005). Desiccation also affects acquisition of carbon and nitrogen by seaweeds (Thomas et al. 1987, Davison and Pearson 1996, Williams and Dethier 2005) and thus also seaweed growth and abundance.

Much of the intertidal seaweed literature is devoted to single-species responses to ecological factors, primarily top-down herbivory and bottom-up nutrients. A closer examination of this literature reveals, somewhat surprisingly, that interactions among experimental factors are often few or weak, a research result of fundamental importance, yet rarely highlighted (e.g., Worm et al. 1999, 2000, Lotze et al. 2000, Nielsen 2001, Thompson et al. 2004, reviewed in Dethier et al. 2005, Edwards et al. 2006, Morelissen and Harley 2007, Atalah and Crowe 2010). To our knowledge, no study has addressed how intertidal seaweed biodiversity sensu lato responds to stress, herbivory, and nutrients, and it remains unclear whether these major factors act additively, synergistically, or antagonistically (Atalah and Crowe 2010).

Our goal was to understand the combined influence of thermal and desiccation stress (hereafter "stress"), herbivory, and nutrients on intertidal seaweed biodiversity sensu lato (i.e., cover, biomass, richness, diversity, evenness, and composition) in the field, to complement our prior research on seaweed biodiversity and ecosystem functioning and to address the gap in knowledge about how multiple factors shape biodiversity patterns beyond mere abundance, as summarized previously. Our study site was situated on an exposed rocky coastline of the Bodega Marine Reserve in northern California, within the California Current upwelling ecosystem, which has the highest seaweed and herbivore richness of the world's four coastal upwelling ecosystems (Blanchette et al. 2009).

MATERIALS AND METHODS

Effects of stress, herbivory, and nutrients on algal abundance and diversity

We conducted an 18-month-long field experiment beginning in March 2007 to determine the effects of stress (thermal and desiccation), herbivory, and nutrient availability on intertidal algal diversity within the Bodega Marine Reserve (see Plate 1). The Reserve is far from major anthropogenic disturbances, including eutrophication, and has been a marine life refuge or protected area since 1965.

We randomly assigned all possible combinations of stress (ambient, reduced), herbivores (natural abundances, removed), and nutrients (ambient, fertilized) for a total of eight treatments to plots ($n = 5$ per treatment) at two tidal heights and two wave exposure regimes (for a total of 160 plots in a fully crossed design). Plots were circular (50 cm diameter), and most were spaced 2 m apart on the emergent rocks that cover ~80% of the substratum. The wave-protected sites were the opposite sides of Horseshoe Cove (UTM NAD83 38.31672, −123.0711; 38.31587, −123.0691) and the two open ocean-exposed environments (hereafter "exposed") were Mussel Point (38.32342, −123.0782) and Lessoniopsis Point (38.31412, −123.0706) (see Appendix A for treatment details and efficacy, and Appendix A: Fig. A1 for plot map). The average water velocity measured at plot level with a ruggedized field acoustic velocimeter (Vectrino, Nortek AS, Vangkroken, Norway) was 30% lower in the protected vs. exposed sites (Appendix A). The tidal heights "high" and "mid" corresponded to "effective shore levels" (sensu Harley and Helmuth 2003) based on the upper and lower limits of the rockweed *Pelvetiopsis limitata* (Setchell) N. L. Gardner in the upper- to mid-intertidal zone at each exposure regime (1.58 to 4.33 m above mean lower low water; Appendix A).

Before initiating treatments, we carefully scraped algae and removed sessile invertebrates from the plots and quantified algal dry mass. We ameliorated stress by covering plots with Vexar mesh screens strapped to vinyl-coated galvanized steel welded cloth that was raised ~10 cm above the algal canopy and open to non-avian predators (Morelissen and Harley 2007). Screens effectively reduced temperature (by 6°C maximum) and increased relative humidity (by >40%) at the canopy level, while still transmitting photosynthesis-saturating light levels, determined by comparing irradiances measured in plots to photosynthesis–irradiance curves for the seaweed community (Appendix A discussion and Fig. A2). Although screens could have changed water flow regimes, sediments did not accumulate in any plots due to considerable flow at even the wave-protected sites (40 cm/s under calm conditions). To control grazers, we painted all plot circumferences with copper antifouling hull paint and manually removed the dominant herbivores (primarily mollusks; Appendix B) every two weeks in herbivore removal plots (Bracken et al. 2011). Manual removals were a necessary complement to copper-paint borders because littorine and turban snails, collectively the most abundant herbivores in our experimental plots, are not deterred by copper paint (Aquilino and Stachowicz 2012). Removal was 75% effective, and herbivore densities were significantly lower in removal plots (Appendix A: Fig. A3; Appendix C: Table C6). Dispensers (5 cm diameter polyvinyl chloride cylinders drilled with four orthogonal 2-mm holes and lined with nylon sacks) in the middle of each plot discharged ammonium, nitrate, and phosphorus fertilizer (Osmocote, Scott-Sierra Agricultural Products, Marysville, Ohio, USA) or served as controls with no fertlizer. The fertilizer was replaced every two weeks. Concentrations of each nutrient were elevated above ambient levels in fertilized plots, nutrient spillover into unfertilized plots was not significant, and tissue nitrogen levels were significantly elevated in two of the three dominant seaweed species in fertilized compared to unfertilized plots (Appendix A: Table A1 and Fig. A4).

We placed hoops divided into sectors over plots to visually census the percentage of algal cover by species, and to count mobile invertebrates quarterly through September 2008. At the end of the experiment (October 2008), we cleared species from plots to determine dry biomass, and related biomass to percentage of cover for each species to predict plot biomass based on percentage cover data from censused plots. Although removal was not perfect for taxa such as diatoms, percentage cover was highly related to initially cleared ($r^2 = 0.68$, $P < 0.001$) and final biomass ($r^2 = 0.81$, $P < 0.001$). Herbivores collected from natural abundance plots and nutrient treatment plots were processed for ash-free mass to assess a potential bottom-up nutrient enrichment effect.

Statistical analyses

Data were analyzed with fully crossed, fixed-factor ANOVAs for algal percent cover, species richness, dry biomass (in grams), diversity (Shannon index H'), evenness (Pielou's J), and herbivore density (number
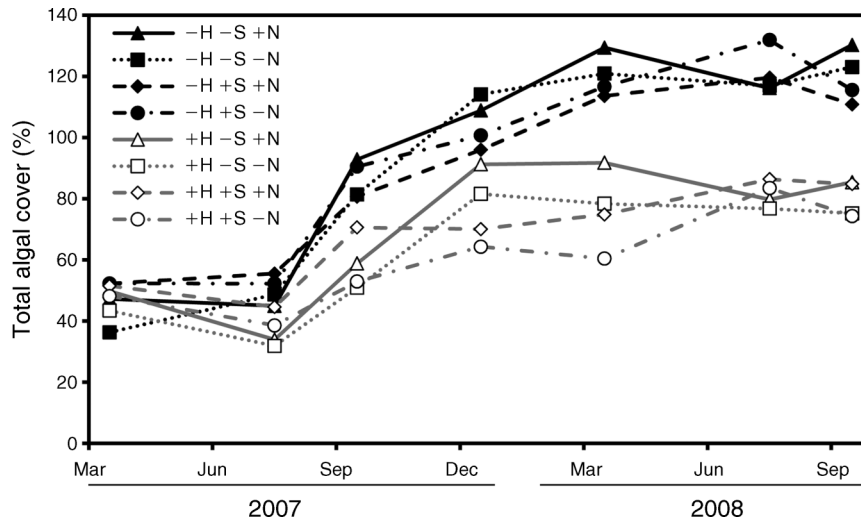
Fig. 1. Mean changes in algal cover on a northern California rocky shore over the course of the experiment by treatment replicate, averaged across exposure regimes and tidal heights ($n = 20$ plots). Solid black symbols indicate herbivore removal treatments (−H), open gray symbols are unmanipulated herbivore treatments (+H), circles and diamonds indicate screens (+S), squares and triangles indicate no screens (−S), solid and dashed lines are fertilizer additions (+N), and dotted and dot-dashed lines are ambient nutrient controls (−N). The cover exceeded 100% where the algal canopy was layered.

per plot) and final mass. Factors included wave exposure regime (protected, exposed), tidal height (high, mid), screens to reduce temperature and increase humidity (+/− screens), herbivore removals (natural abundance vs. removals), and nutrient additions (ambient vs. added nutrients), with site (Horseshoe Cove North, Horseshoe Cove South, Mussel Point, Lessoniopsis Point) nested within wave exposure. Plot response variables were averaged across the final three censuses (March, July, September 2008) (SAS version 9.2. [SAS 2008]). Residuals were examined before and after data transformation; transformations were effective where applied. We calculated the magnitude of effect (ω^2) for each factor tested (Graham and Edwards 2001). Because results based on biomass at the end of the experiment did not change qualitatively from percentage cover results, we report only percentage cover results for diversity, evenness, and species composition. Differences among treatments in algal species composition were tested using permutational multivariate analysis of variance (PERMANOVA [Anderson 2001]) on a Bray-Curtis similarity matrix. Pairwise a posteriori comparisons were performed on factors for which $P \leq 0.05$. The similarity percentage analysis SIMPER (Primer v. 6.0, Primer-E Ltd., Plymouth, UK [Clarke 1993]) was used to estimate the percentage contribution of each species to the within-group similarity and among-group dissimilarity.

RESULTS

Algal abundance and diversity responses

Algal cover in the plots increased rapidly through December 2007, after which biomass recovered from the initial clearing (Fig. 1; paired two-tailed t test of initial vs. final cleared biomass averaged across plots within a treatment, $P = 0.150$, df $= 30$). However, species richness and diversity were higher prior to initial plot clearings than at the end of the study (paired two-tailed t tests of initial vs. final plot values averaged over the final three census dates [March, July, September 2008] to account for seasonal differences between initial [March 2007] and final [September 2008] census dates, $P < 0.001$, df $= 318$).

As is typical for intertidal habitats in the northeastern Pacific, algal cover was greater at more wave-exposed sites ($F_{1, 126} = 11.1$, $P = 0.001$) and lower on the shore ("mid" tidal height; $F_{1, 126} = 14.6$, $P < 0.001$), compared to the more wave-protected and higher shore plots (Fig. 2; Appendix C: Table C1) where seaweeds are exposed longer to hotter, drier conditions (Appendix A). Across stress, herbivory, and nutrient manipulations, herbivore removal resulted in 30–40% greater algal cover ($F_{1, 126} = 151$, $P < 0.001$). Algal biomass cleared from plots at the end of the experiment varied with tidal height ($F_{1, 126} = 158$, $P < 0.001$), protective screens ($F_{1, 126} = 9.09$, $P = 0.003$), and herbivores ($F_{1, 126} = 13.0$, $P < 0.001$) (Fig. 2; Appendix C: Table C2). Despite successfully increasing nutrient concentrations in the seawater and algal tissues in fertilized plots (Appendix A: Table A1, Fig. A3), nutrients had no effect on algal cover or biomass. There was a height × herbivore interaction ($F_{1, 126} = 24.1$, $P < 0.001$) in which cover increased dramatically at the mid-height in the absence of herbivores and a height × screen × herbivore interaction ($F_{1, 126} = 4.20$, $P = 0.043$) in which herbivores reduced cover only under screens higher on the shore; lower down, herbivore removal enhanced cover regardless of screens. For biomass, there
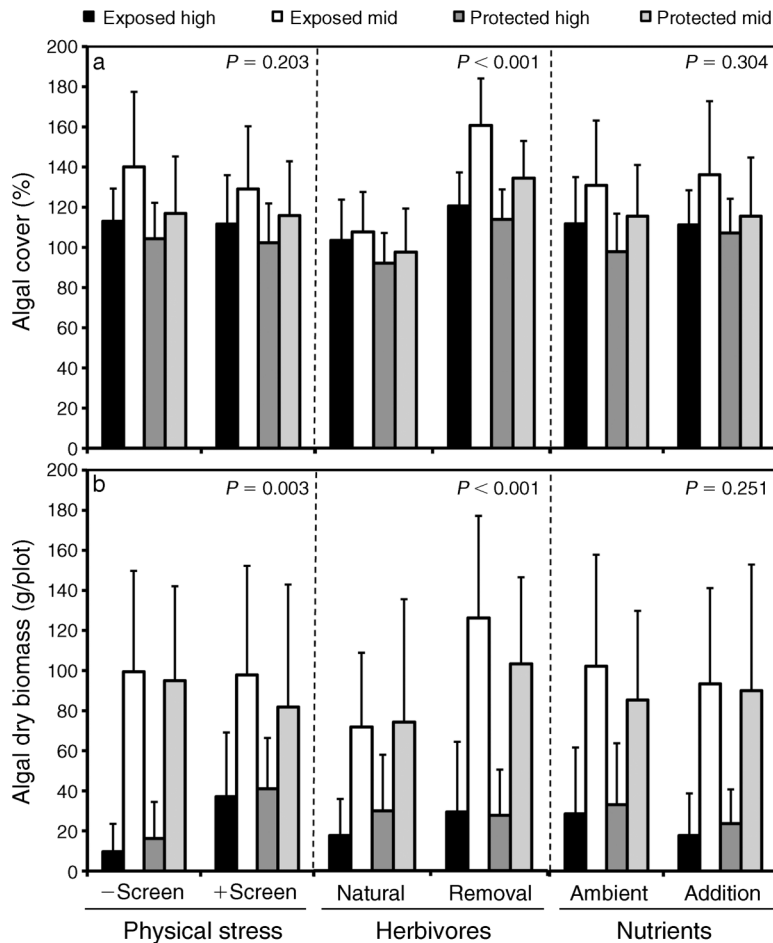
Fig. 2. Main treatment effects on algal cover and biomass. (a) Algal cover averaged over the final three census dates (March, July, and September 2008) and (b) biomass at the end of the experiment. Treatments were physical stress (screened and unscreened plots), herbivores (natural herbivore abundances, herbivore removals), and nutrients (ambient nutrients, fertilizer additions), by wave exposure and tidal height (high vs. mid). P values indicate statistical comparisons of main effects in each panel. Values are mean + SD of $n = 20$ plots each.

was a height × screen interaction ($F_{1, 126} = 18.8$, $P < 0.001$) in which screens enhanced biomass higher on the shore but not lower down, and a height × herbivore interaction ($F_{1, 126} = 6.77$, $P = 0.010$) in which herbivores influenced biomass only lower on the shore. There was an exposure × screen × herbivore interaction ($F_{1, 126} = 4.20$, $P = 0.042$) in which herbivores did not affect biomass in wave-protected plots regardless of screening, but at exposed sites biomass was higher where herbivores were removed in screened but not unscreened plots. An important point is that the magnitude of the effect (ω^2) of each interaction term was low (Appendix C).

Algal richness was high in our plots. We observed 59 algal taxa in our field censuses, half of which were observed in every census (Appendix D: Table D1). The highest number of algal taxa identified was 41 in a single census and 20 in a single plot. Algal richness was higher at wave-exposed sites ($F_{1, 126} = 30.2$, $P < 0.001$; Appendix C: Table C3; Fig. 3) and in plots lower on

the shore ($F_{1, 126} = 86.0$, $P < 0.001$). Algal richness increased slightly under the protection of screens, particularly at the exposed sites ($F_{1, 126} = 3.39$, $P = 0.068$). Herbivore removal increased algal richness ($F_{1, 126} = 10.6$, $P = 0.001$). Nutrients had no effects on algal richness. No interactions were found among the manipulated factors of screens, herbivores, and nutrients. There was an exposure × height interaction ($F_{1, 126} = 4.28$, $P = 0.041$) in which richness varied with tidal height only in wave-exposed plots. Notably, the effects of stress and herbivores were evident even though a series of heat waves beginning in March 2008 caused seaweed mortality in the unscreened plots (i.e., reductions observed in the June census) and therefore increased the overall variance (Fig. 1).

Algal diversity (Shannon index H') and evenness (J) were higher under screens (diversity, $F_{1, 126} = 4.90$, $P = 0.028$; Appendix C: Table C4; Fig. 3; evenness, $F_{1, 126} = 4.08$, $P = 0.046$; Appendix C: Table C5; Fig. 3).
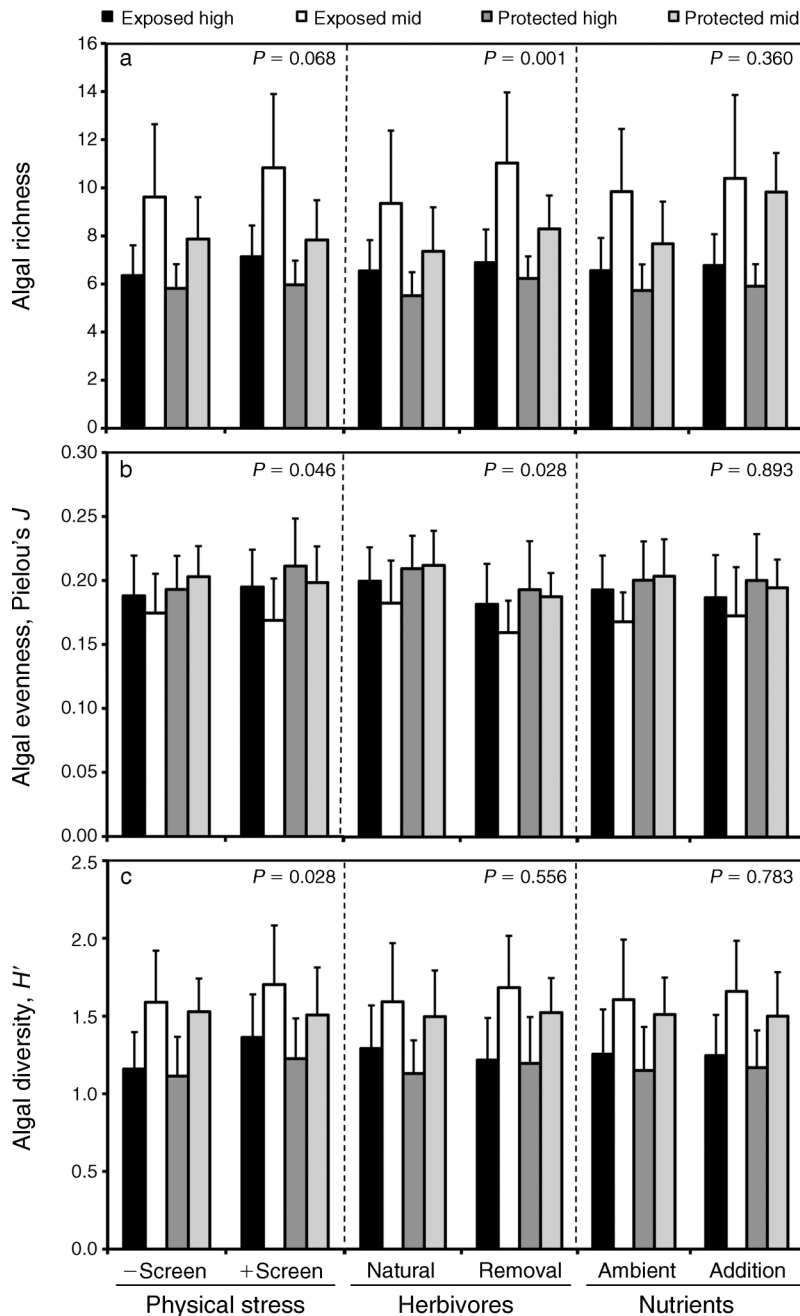
Fig. 3. Main treatment effects on algal diversity. (a) richness (as number of algal taxa), (b) evenness (calculated as J), and (c) diversity (calculated as H') averaged across March, July, and September 2008. Treatments were physical stress (screened and unscreened plots), herbivores (natural herbivore abundances, herbivore removals), and nutrients (ambient nutrients, fertilizer additions), by wave exposure and tidal height. H' and J were based on percentage cover values. P values indicate statistical comparisons of main effects illustrated in each panel. Values are mean + SD of $n = 20$ plots each.

Herbivores strongly reduced species richness but enhanced evenness ($F_{1, 126} = 4.92$, $P = 0.028$), resulting in no effect on diversity ($F_{1, 126} = 0.40$, $P = 0.556$). Diversity was higher in wave-exposed plots ($F_{1, 126} = 7.1$, $P = 0.008$) and lower on the shore ($F_{1, 126} = 64$, $P < 0.00$). Evenness differed with tidal height ($F_{1, 126} = 19.6$, $P < 0.001$). Wave exposure influenced diversity ($F_{1, 126} = 7.10$, $P = 0.008$) but not evenness. Nutrients influenced diversity and evenness only in interaction with screens (H', $F_{1, 126} = 4.20$, $P = 0.042$; J, $F_{1, 126} = 5.80$, $P = 0.018$). Diversity and evenness were higher in screened plots at ambient levels but nutrient additions muted this effect. The magnitude of the effect of this interaction, however, was low, as indicated by ω^2 values.

Algal species composition

The small-bladed green seaweed *Blidingia minima* var. *minima* (Nägeli ex Kützing) Kylin, diatoms, and the larger seaweeds, *Mastocarpus papillatus* (C. Agardh) Kützing and *Pelvetiopsis limitata*, accounted for at least 50% of the algal cover, depending on conditions (Appendix D). For example, the cover of *M. papillatus* and *P. limitata* increased to nearly 25% each at the mid vs. high tidal height. Changes in community composition were associated with wave exposure (pseudo-$F_{1,126}$ = 13.12, $P < 0.001$), tidal height (pseudo-$F_{1,126}$ = 60.34, $P < 0.001$), screens (pseudo-$F_{1,126}$ = 12.39, $P < 0.001$), and herbivores (pseudo-$F_{1,126}$ = 5.81, $P < 0.001$) (Appendix D: Table D2). There were no interactions among the manipulated factors of screens, herbivores, and nutrients, but interactions occurred with exposure and tidal height. There were interactions between exposure and height (pseudo-$F_{1,126}$ = 9.40, $P < 0.001$), exposure and screens (pseudo-$F_{1,126}$ = 2.17, $P = 0.026$), height and screens (pseudo-$F_{1,126}$ = 3.06, $P = 0.003$), and height and herbivores (pseudo-$F_{1,126}$ = 2.03, $P = 0.039$), but all had low ω^2 values.

Differences in algal composition among stress, herbivory, and nutrient treatments were driven primarily by changes in the most abundant species: *Blidingia minima* var. *minima*, diatoms, *Pelvetiopsis limitata*, and *Mastocarpus papillatus* (Fig. 4), followed by cyanobacteria. A SIMPER analysis (Appendix D: Table D3) revealed that *B. minima* var. *minima* was the most important contributor to changes in algal cover across all factors, contributing 18–45% to the average dissimilarity, depending on the factor. For example, *B. minima* var. *minima*'s contribution was 18% at natural herbivore abundances and 31% when herbivores were removed. Diatoms accounted for 6–40% of the differences in community structure. The contribution of diatoms to the average dissimilarity of the community structure increased under increased physical stress such as at higher elevations (from 7% cover at mid to 31% at high tidal heights) and when unprotected by screens (from 12% to 22%), but decreased with herbivory (18% herbivore removal vs. 15% in natural abundance plots). Diatoms also responded positively to nutrient additions, but this factor was not significant in the PERMANOVA analysis. *P. limitata* and *M. papillatus* were the only large seaweeds that contributed >10% each to differences in community structure. The cover of these two species increased from 21% to 36% when protected from grazing, from 24% to 34% when protected from physical stress, and from 16% to 41% when lower in the intertidal zone.

Herbivore responses

We identified at least 18 invertebrate herbivore species, primarily limpets, chitons, and snails (Appendix B). Littorinid snails were the most abundant herbivores; densities typically exceeded 50 and often 100 individuals in natural abundance plots. Herbivore abundance varied with exposure ($F_{1,126}$ = 4.58, $P = 0.034$), tidal height ($F_{1,126}$ = 19.0, $P < 0.001$), herbivore removal ($F_{1,126}$ = 259, $P < 0.001$), and screens ($F_{1,126}$ = 23.4, $P < 0.001$) (Appendix A: Fig. A2; Appendix C: Table C6). Herbivores were more abundant in cooler, moister conditions, e.g., lower in the intertidal zone and under screens, particularly higher on the shore (height × screen interaction, $F_{1,126}$ = 4.61, $P = 0.034$). Screens likely provided refuge from shorebird predation, but predatory crabs, whelks, and seastars were observed in screened plots.

We found no bottom-up effects of nutrients on the herbivores. The abundance and ash-free biomass of the combined limpets, chitons, and herbivorous snails in the fertilized vs. unfertilized natural abundance plots did not differ with exposure, screens, or nutrients, although the biomass was higher at the mid tide height ($F_{1,38}$ = 7.564, $P = 0.009$, Appendix C: Table C7), corresponding to higher densities.

Screens resulted in higher abundances of both algae (Figs. 2 and 3) and herbivores (Appendix A: Fig. A2), particularly high on the shore. Because herbivores reduced algal abundance and richness, they could have cancelled positive effects of physical stress on algal biodiversity. To separate physical stress from herbivore effects, we compared the least squares means (LSMs) for cover, biomass, richness, diversity, and evenness in the physical stress treatments at unmanipulated "natural" levels of herbivore abundance (Table 1). Herbivores clearly congregated under screens; untransformed LSMs were nearly double in screened vs. unscreened "natural abundance" plots. Nevertheless, the increased abundance did not cancel the positive effects of screens on the seaweed community; LSMs were higher for the screened treatments vs. the unscreened treatments, except for cover, for which values were very close. This result is evidence for an overarching positive effect of ameliorating harsh physical conditions on seaweed abundance and diversity, even in the face of increased herbivore abundance.

DISCUSSION

Our experimental manipulations revealed that thermal and desiccation stress and herbivory combine to influence intertidal seaweed biodiversity in largely nonrandom and additive ways (Figs. 3 and 4; Appendix C). Before addressing this main result further, we point out that richness, diversity, and evenness were higher at the end of our 18-month experiment than initially, although biomass and cover were not different. Higher richness and diversity potentially indicate that the community was at a midsuccessional stage after the initial clearing, and that diversity would be likely to decline later if superior competitors dominated in the absence of disturbance, as found for tide pools (Lubchenco 1978) but not emergent rocks (Sousa 1979). Marine succession following disturbances is highly context specific (Dudgeon and Petraitis 2001,

▦ *Cumagloia andersonii*　　　　▥ *Endocladia muricata*

◼ *Mazzaella flaccida*　　　　◼ Cyanobacteria

◨ *Cladophora columbiana*　　　　◻ *Pelvetiopsis limitata*

▩ *Mastocarpus* crust ("*Petrocelis*")　　　▤ *Mastocarpus papillatus*

◼ *Hildenbrandia* spp.　　　　▦ Diatoms

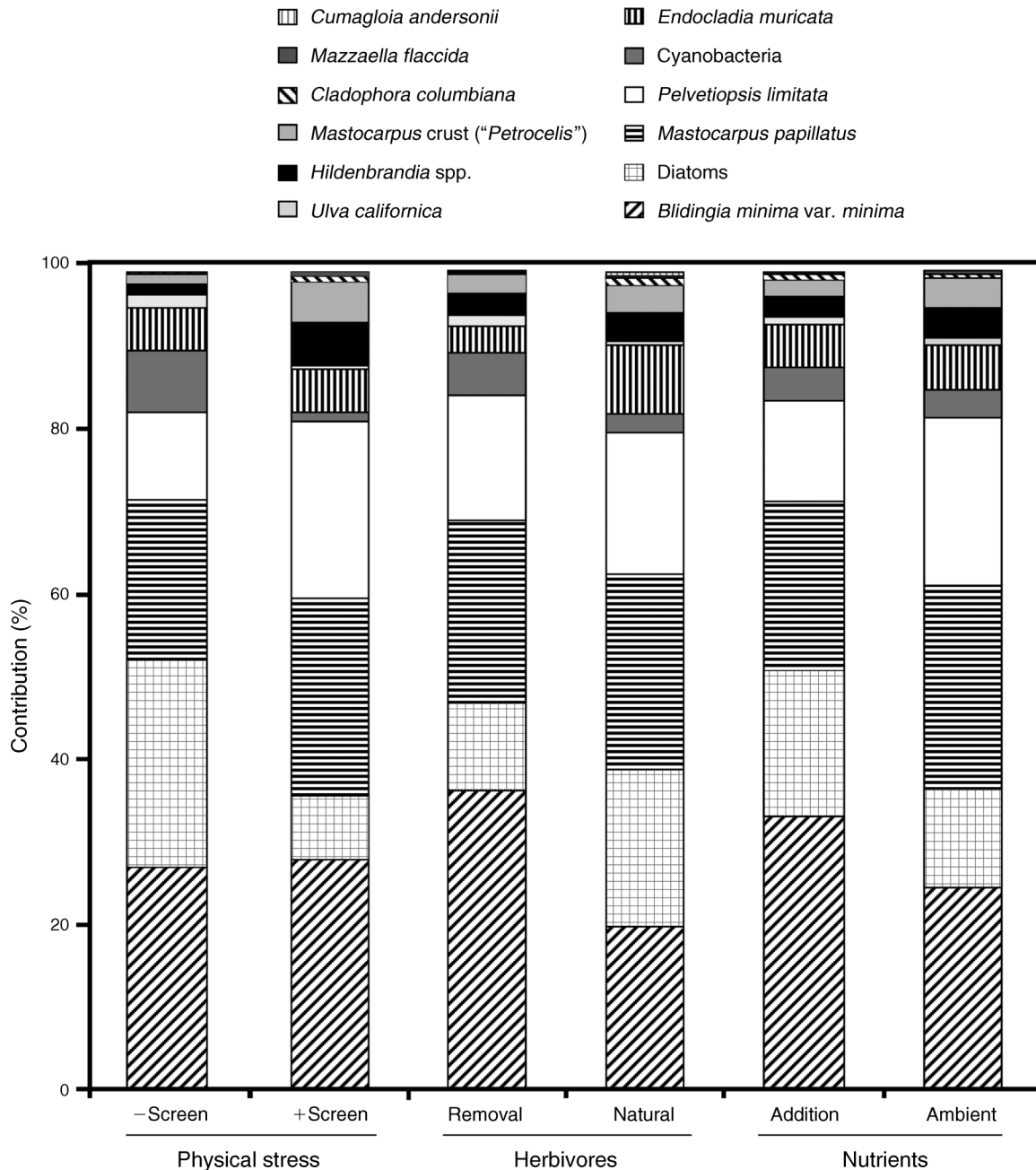▨ *Ulva californica*　　　　◪ *Blidingia minima* var. *minima*

Fig. 4. Contributions to community composition of algal taxa collectively comprising 99% of the factor similarity in experimental plots based on a SIMPER analysis. Comparisons are between shaded (+screens) and unshaded (−screens) plots; plots with natural herbivore abundances (Natural) and herbivores removed (Removal); and plots receiving ambient nutrients (Ambient) and fertilizer additions (Addition). Data were derived from estimates of cover averaged over the final three census dates ($n = 20$ plots each, averaged across March, July, and September 2008).

Svensson et al. 2007), and there is no evidence that treatment differences were maximized because the community was at a midsuccessional stage of higher diversity. For example, our initially cleared but subsequently unmanipulated control plots were visually indistinguishable from the adjacent community, and the final diversity ($H' = 1.2$–1.4) was similar to that

reported in undisturbed plots in another study at the exposed areas of the Bodega Marine Reserve conducted over 27 months (Aquilino and Stachowicz 2012).

Many of the biodiversity responses in our study were governed by changes in relative abundances and not species richness, the focal metric of interest in most seaweed biodiversity–ecosystem function studies, includ-

TABLE 1. Least-squares means (LSMs, $n = 40$ per treatment, untransformed values) for responses of seaweeds on a northern California rocky shore to physical stress treatments in plots with natural herbivore abundances.

Physical stress	Herbivore abundance (no./plot)	Cover (%)	Biomass (g/plot)	Richness, S	Diversity, H'	Evenness, Pielou's J
−Screen	75.1	82.0	45.4	6.87	1.30	0.69
+Screen	131	78.2	53.5	7.61	1.46	0.75

Notes: The "+Screen" row indicates plots covered by screens that reduced temperature and increased humidity relative to unscreened ("−Screen" row) plots under ambient conditions. Values are based on analyses of variance in herbivore abundance and seaweed cover, biomass, richness, diversity, and evenness after accounting for other model factors. See Appendix C for model details.

ing our previous work (e.g., Bruno et al. 2006, Stachowicz et al. 2008; but see Altieri et al. 2009, Arenas et al. 2009). In particular, small stress-tolerant species (cyanobacteria, diatoms) were reduced under more benign conditions where larger seaweeds flourished, which together resulted in increased biomass at the expense of algal cover, diversity, and evenness. Abundant, responsive, but small taxa in the community likely have been overlooked in the field (e.g., *B. minima* is easily misidentified as *Ulva* recruits); few studies have addressed them (but see Thompson et al. 2004). Such species are generally underappreciated in terms of ecosystem functioning, which is likely disproportionate to their biomass (Bracken and Low 2012). Their high turnover and palatability (with some exceptions) contribute to food web support (Nicotri 1977, Underwood 1984, Nagarkar et al. 2004), and cyanobacteria might be important in fixing nitrogen on rocky shores (Stewart 1967, Magalhäes et al. 2005). Under conditions of increased physical stress, such taxa will become relatively more important in the community, with largely unstudied consequences for ecosystem functioning.

Predictably, wave exposure and tidal height influenced algal diversity. More importantly, the effects of screens and herbivores were strong enough to be discernible within the variation attributable to tidal height, wave exposure, and seasons (spring, summer, fall; Figs. 1, 2, and 3). Both ambient physical stress and herbivory reduced algal abundance (cover, biomass) and richness, but their effects on diversity, evenness, and species composition were largely in opposite directions. Stress reduction increased seaweed richness, evenness, and diversity, which in turn could create positive feedbacks in the community because higher richness is associated with reduced desiccation (Aquilino and Stachowicz 2012).

The independent effects of physical stress and herbivores were striking. For example, despite higher herbivore abundance under screens, we found few interactive effects of stress and herbivores on algal cover, biomass, species richness, diversity, evenness, or community structure. The interactions found were associated primarily with tidal height and exposure, and they contributed little to the overall effects (low ω^2 values). Screen effects were strongest higher on the shore, not surprisingly, and herbivore effects were stronger lower in the intertidal. Herbivores did not

disproportionately affect seaweed biodiversity when the environment was more stressful (Table 1). This result supports the points made in the *Introduction* that nonadditive effects of multiple environmental factors might not be as common as assumed. In any case, more attention should be paid to assessing possible synergisms and antagonisms (Burkepile and Hay 2006, Crain et al. 2008, Atalah and Crowe 2010).

Unlike screens and herbivores, nutrients had no effect on seaweed biodiversity. The lack of an overall nutrient effect is not surprising, as our site is within a strong upwelling region with high nutrient availability (but see Fujita et al. 1989, Nielsen 2001). The effect of nutrients on seaweeds in the Bodega Marine Reserve seems confined to a smaller spatial scale, such as mussel beds, where local-scale nutrient inputs enhance the growth of *Pyropia* spp. (Aquilino et al. 2009), or high on the shore, where access to seawater nutrients is limited (Bracken et al. 2011) and physical stress is more severe (e.g., nutrients × stress interaction for diversity and evenness; Appendix C: Tables C4 and C5).

The absence of interactive effects between screens and herbivores on seaweed biodiversity highlights a need to understand both the response of herbivory to intertidal stress and any cascading effects on benthic primary producers (Thompson et al. 2004, Helmuth et al. 2006, Morelissen and Harley 2007). Seaweeds and herbivores both responded positively to screens, and thus, herbivores hypothetically could cancel any gain afforded to seaweeds when stress is reduced. In contrast, we found that screens had an overwhelmingly positive effect on seaweed abundance and diversity, even in the face of increased herbivore abundance (Table 1). Although our screens demonstrably reduced thermal and desiccation stress, they might have changed other factors that could have influenced seaweed biodiversity, such as propagule supply if water flow was altered. If screens influenced herbivores in some manner independent of their effect on stress, a stress–herbivore interaction might have been masked. Functional relationships describing both seaweed biodiversity and herbivory responses to stress are needed, but we had only two levels of manipulated factors. For now, we assume the screen effects on seaweeds and herbivores were primarily in response to stress reduction, and offer testable hypotheses for seaweed–stress–herbivore relationships.
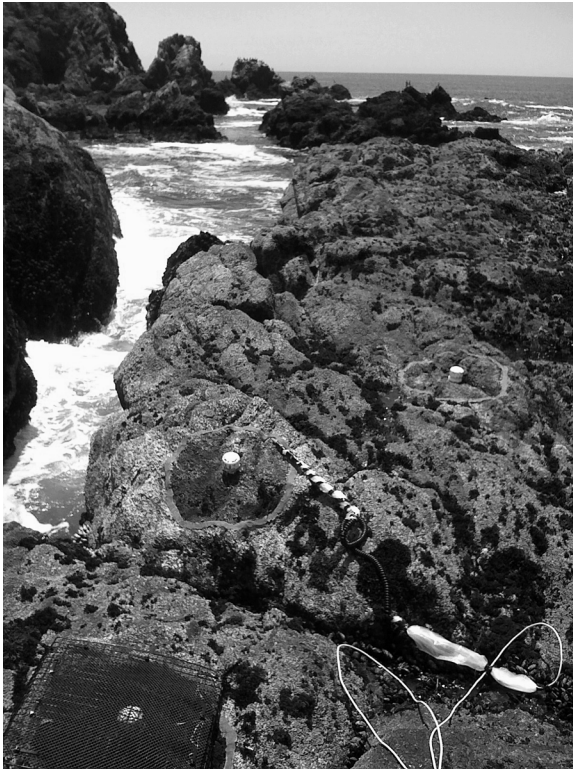
PLATE 1. Experimental plots in the Bodega Marine Reserve, northern California, USA, including a +Screen plot (lower left) and two −Screen plots (center). White cylinders in the center of each plot are nutrient dispensers. Also shown is the temperature–humidity probe used to evaluate the effectiveness of screens. Photo credit: S. L. Williams.

One explanation for the apparent absence of a stress–herbivore interaction could lie in stress effects on grazing intensity per se, which have rarely been addressed in intertidal studies (but see Underwood 1984, Thompson et al. 1997). For example, herbivores might have fed more slowly when cooler (Menge et al. 2002). Alternatively, the screens could have simply offered refuges after foraging bouts in the open, or epiphytes could have provided an unaccounted food source. In contrast to our finding that herbivore abundance decreased under hotter, drier conditions, studies on similar communities in southern California (where conditions are hotter and drier than at our site) demonstrated a positive warming effect on some of the same herbivores we studied. In one study, higher temperatures stimulated grazing by the turban snail *Chlorostoma funebralis* A. Adams (Yee and Murray 2004). In another study, over a long-term increase in water temperature, intertidal invertebrates became more abundant and seaweeds declined (Schiel et al. 2004). Herbivore effects in this study, however, could not be separated from other potential effects, including direct effects of temperature, or perhaps latitudinal variation in grazing intensity (Jenkins et al. 2001). Another hypothesis for our finding that seaweed

biodiversity responded positively to stress reduction despite increased herbivore abundance is that reduced desiccation can result in higher levels of herbivore-deterrent chemicals, rendering seaweeds less susceptible to grazing (Renaud et al. 1990, Dethier et al. 2005). Although these two studies were devoted to a few individual species, as opposed to seaweed communities, the hypothesis follows that the effects of desiccation-altered palatability on herbivory, and in turn seaweed biodiversity, should be most evident in low-diversity communities dominated by unpalatable seaweeds. Clearly, much remains to be learned about the relationships among stress, herbivores, and their grazing on seaweeds.

With respect to temperature and desiccation, Bodega Bay is one of the least stressful intertidal sites along the Pacific coast of North America (Helmuth et al. 2002), due to its open exposure to swells and intense upwelling, thick fog in summer, and relatively short cumulative tidal exposures. The site is also more benign compared to the North Atlantic (Jenkins et al. 2008). Interestingly, the Bodega Bay region is likely to experience even cooler sea temperatures and climate associated with increased upwelling in the future (Snyder et al. 2003, García-Reyes and Largier 2010), which should reduce stress. Local seaweed biodiversity is thus likely to increase, even if herbivores become more abundant. It follows that the important roles these seaweeds play in biomass accumulation, community stability, and nitrogen acquisition could remain relatively unchanged in the future (Bracken et al. 2008, Stachowicz et al. 2008, Bracken et al. 2011). Predictions for our study site contrast with those for the northeastern Atlantic Ocean, where canopy-forming fucoids (that are more common at higher latitudes and on more protected shores) and their production are predicted to decline in the future (Hawkins et al. 2009). Clearly, forecasting changes in seaweed biodiversity and corresponding effects on the ecological roles of seaweeds hinges upon poorly understood responses of the herbivore community and grazing intensity to thermal and desiccation stress. At the very least, our results reveal that physical stress and herbivory can have independent, additive effects on seaweed biodiversity.

Understanding the drivers of changing seaweed biodiversity allows informed predictions to be made about how ecosystem functions might respond to specific changes in the environment, particularly when the relationship between biodiversity and ecosystem function is known. If factors combine additively to influence biodiversity, as in our study, then predicting how biodiversity will respond to a changing environment will be less complicated than if factors interact synergistically.

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SUPPLEMENTAL MATERIAL

Appendix A

Experimental treatments and efficacy: intertidal physical stress, herbivores, and nutrients (*Ecological Archives* E094-097-A1).

Appendix B

Invertebrate taxa and abundance in experimental plots (*Ecological Archives* E094-097-A2).

Appendix C

Statistical analyses for cover, biomass, richness, diversity, evenness, herbivore abundance, and herbivore biomass (*Ecological Archives* E094-097-A3).

Appendix D

Algal taxa identified in experimental plots and multivariate analyses of species composition (*Ecological Archives* E094-097-A4).