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Spatial scale mediates the effects of biodiversity on marine primary producers

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Abstract. Most studies evaluating the effects of biodiversity on ecosystem functioning are conducted at a single location, limiting our understanding of how diversity–function relationships may change when measured across different spatial scales. We conducted a species-removal experiment at three sites nested in each of three regions along the rocky intertidal coastline of the Gulf of Maine, USA, to evaluate the potential for scale-dependent effects of species loss on the biomass of intertidal seaweed assemblages. We randomly assigned 50 plots in the mid-intertidal zone at each site to one of five treatments (n = 10 plots each): an unmanipulated control, a polyculture plot that contained our three target seaweed species, and three monoculture plots. We manipulated diversity by removing all non-target species from monoculture and polyculture plots, then removing additional biomass from polyculture plots, proportionate to species' relative abundances, so that the average amount removed from monoculture and polyculture plots was equivalent at each site. At the largest spatial scale, all sites considered together, after accounting for region and site nested within region seaweed diversity had consistent, positive effects on seaweed cover. Diverse polyculture plots always had higher cover than was predicted by the average performance of the component seaweed species and usually had higher cover than even the best-performing component species. Diversity effects weakened and became less consistent at smaller spatial scales, so that at the scale of individual sites, diverse polycultures only performed better than the average of monocultures ~40% of the time. Hence, our results indicate that weak and/or inconsistent biodiversity effects at the level of individual sites may scale up to stronger, more consistent effects at larger spatial scales. Quantitative summaries of biodiversity experiments conducted at the scale of individual sites do not capture this spatial aspect of biodiversity effects and may therefore underestimate the functional consequences of biodiversity loss.

Key words: Ascophyllum; *biodiversity; ecosystem functioning;* Fucus; *Gulf of Maine; macroalgae;* Mastocarpus; *resilience; rocky intertidal; seaweeds; spatial scale.*

Introduction

Motivated by global declines in biodiversity (Barnosky et al. 2011), a large and growing body of research, summarized in recent meta-analyses (Cardinale et al. 2011, Hooper et al. 2012), has documented the importance of biodiversity in mediating a variety of community- and ecosystem-level processes. However, critical gaps remain in our understanding of the functional consequences of biodiversity declines. In particular, most studies are conducted at only one location, so we have a limited understanding of how diversity–function relationships may change when measured across different spatial scales. Scaling-up of biodiversity effects and relationships remains one of the greatest challenges in the field (Cardinale et al. 2012, Naeem et al. 2012).

This knowledge gap is surprising given the fact that the relationship between productivity (as an independent variable) and diversity (as a dependent variable) can change depending on the scale over which the relationship is evaluated (Rosenzweig 1995, Chase and Leibold 2002). For example, Chase and Leibold (2002) found that producer richness was unimodally related to in situ primary productivity across 30 ponds in 10 watersheds, but when the relationship was evaluated at the scale of watersheds (three ponds per watershed), richness increased linearly with increasing productivity. However, whereas observational approaches like this one can hint at potential relationships between biodiversity and productivity across spatial scales, the relationships may not be causal (Tilman et al. 1997), and experimental approaches are necessary to evaluate the functional consequences of biodiversity change (Loreau et al. 2001).

To date, one of the best approaches to replicated biodiversity experiments across multiple sites has been the BIODEPTH program, which involved coordinated manipulations of grassland plant diversity at eight

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locations in Europe. This program provided key insights into the generality of functional consequences of biodiversity change on producer abundance (Hector et al. 1999, Spehn et al. 2005). Here, we take a similar approach to evaluate how spatial scale mediates the effects of species loss from a marine ecosystem. However, in contrast to these previous experiments examining biodiversity effects across multiple sites, where sites were characterized by different species (e.g., Hector et al. 1999, Spehn et al. 2005), our experiments manipulated the same set of three species, which collectively comprised ~80% of seaweed cover at all of our study locations (see *Materials and methods*).

Our experiments were deliberately set up to evaluate the effects of spatial scaling on the functional consequences of biodiversity declines. Our study sites spanned the coast of the Gulf of Maine in the western North Atlantic Ocean, where intertidal algal diversity is relatively low and a consistent assemblage of species extends for >500 km from Cape Cod in the south to the Bay of Fundy in the north (Taylor 1957, Humm 1969). We set up nine study sites along the coastline of the Gulf of Maine: three sites in each of three regions (Fig. 1). We removed seaweed species from experimental plots, taking equivalent total seaweed biomasses from monoculture and polyculture plots, to evaluate whether more diverse plots would ultimately be characterized by higher seaweed biomass. We hypothesized that the relationship between biodiversity and ecosystem functioning would depend on the scale over which effects were considered. We specifically predicted that the magnitude and consistency of biodiversity effects would differ for sites, regions, and the Gulf of Maine coastline. Our experimental design, which consisted of a press manipulation maintained for >2 yr at sites nested within regions and regions nested within a coastline, was used to evaluate how biodiversity effects operated at these different scales (coast-wide, regional, and local) and changed over time.

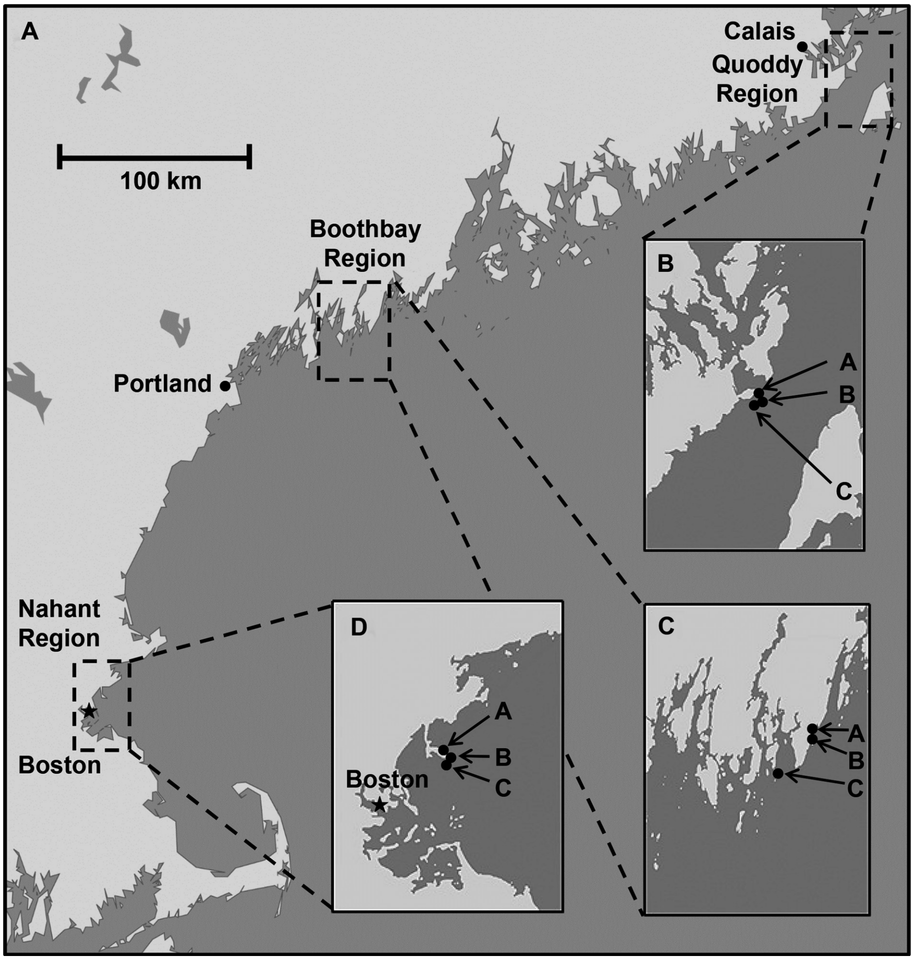

Fig. 1. (A) Study locations along the Gulf of Maine, USA, coast. We conducted our experiments in three regions along the coast, spanning 500 km of coastline. Identical experiments were conducted at three sites in each of the three regions: (B) Quoddy, (C) Boothbay, and (D) Nahant.

MATERIALS AND METHODS

Study sites and species

Experiments were conducted on intertidal rocky reefs in three regions along the coast of the Gulf of Maine (Fig. 1A). These included three sites on Quoddy Head in Lubec, Maine (44°48.4′ N, 66°58.2′ W; Fig. 1B), three sites in the Boothbay region of Maine (43°50.4′ N, 69°34.0′ W; Fig. 1C), and three sites in Nahant, Massachusetts (42°25.3′ N, 70°54.5′ W; Fig. 1D). These sites span a gradient in temperature and oceanographic conditions (Bryson et al. 2014). TidbiT temperature dataloggers (Onset Computer Corporation, Bourne, Massachusetts, USA), deployed at our study sites from May to November 2011 and recording every 15 min, revealed a gradient in mean air temperatures of 5.6°C (Quoddy, 14.7° ± 0.2°C [mean ± SE]; Boothbay, 18.2° ± 0.4°C; Nahant, 20.3° ± 0.9°C), a gradient in maximum air temperatures of 11.3°C (Quoddy, 26.1° ± 1.1°C; Boothbay, 33.1° ± 1.3°C; Nahant, 37.4° ± 3.2°C; Appendix S1: Fig. S1), and a gradient in mean water temperatures of 5.1°C (Quoddy, 10.4° ± 0.1°C; Boothbay, 14.3° ± 0.1°C; Nahant, 15.6° ± 0.1°C). Dataloggers were not deployed during winter months due to the potential for damage due to ice scour.

Grazing pressure and nutrient availability also differ along the coastline of the Gulf of Maine. Harvesting of the snail *Littorina littorea*, an important mediator of seaweed diversity and abundance (Lubchenco 1978), is especially prevalent in the Quoddy region (Watts 2016), creating a gradient in grazer abundances, with highest grazer densities in the Nahant region and lowest densities in the Quoddy region (Bryson et al. 2014). Nitrate concentrations are typically higher in the Quoddy region than in either the Boothbay or Nahant region due to tidally driven upwelling of nutrients in the Grand Manan Channel (Benes and Bracken 2016).

The mid-intertidal zone at our study locations was characterized by abundant cover of three seaweed species: *Fucus vesiculosus* L. (Ochrophyta, Phaeophyceae; hereafter, *Fucus*), *Ascophyllum nodosum* (L.) Le Jolis (Ochrophyta, Phaeophyceae; hereafter, *Ascophyllum*), and *Mastocarpus stellatus* (Stackhouse) Guiry (Rhodophyta, Florideophyceae; hereafter, *Mastocarpus*). Our initial surveys indicated that these three species collectively comprised 80% of upright macroalgal cover across all sites.

Experimental design

To evaluate the consequences of species loss, we conducted a seaweed species-removal experiment and measured the effects of those removals on algal cover in experimental plots (Stachowicz et al. 2008*b*). At each site, we marked and surveyed 50 circular plots, 0.5 m in diameter, in the mid-intertidal zone. Plot elevations were 1.37 ± 0.02 m (mean ± SE) above mean low water (MLW) in the Nahant region, 1.32 ± 0.02 m above MLW in the Boothbay region, and 1.65 ± 0.04 m above MLW in the Quoddy region. Plot elevations were higher in the Quoddy region due to greater tidal amplitudes adjacent to the Bay of Fundy. Each plot was separated by at least 1 m from the nearest plot. Plots were established and initially surveyed in July 2010.

Plots were randomly assigned to five treatments: (1) a *Fucus* monoculture, (2) an *Ascophyllum* monoculture, (3) a *Mastocarpus* monoculture, (4) a three-species polyculture consisting of only the target seaweed species (i.e., *Fucus*, *Ascophyllum*, and *Mastocarpus*), and (5) an unmanipulated control. Two-species assemblages were not included in our design due to logistical constraints; with 5 treatments × 10 plots per treatment × 3 sites × 3 regions, our experiment already included 450 plots. Due to regional and local-scale variation in the elevation of experimental plots and changes in tidal amplitude along the coast, there were regional differences in the proportion of time that plots were exposed to air (general linear model; region $F_{2,435} = 794.8$, $P < 0.001$; and site(region) $F_{6,435}$, $P < 0.001$; note that site was nested within region for all analyses). However, after accounting for region and site(region), there were no differences in emersion time between experimental treatments (treatment $F_{4,435} = 1.3$, $P = 0.288$). Similarly, there were regional differences in initial algal cover (region $F_{2,433} = 237.3$, $P < 0.001$) and site (site[region] $F_{6,433} = 14.4$, $P < 0.001$). However, after accounting for region and site (region), there were no differences in initial macroalgal percent cover between experimental treatments (treatment $F_{4,433} = 1.0$, $P = 0.427$). Cover was a good surrogate for macroalgal biomass based on removals associated with plot maintenance ($F_{1,257} = 56.7$, $P < 0.001$). Note that cover values could exceed 100% due to canopy layers overlaying understory species.

We used a substitutive design to manipulate diversity in our experimental plots. Specifically, we manually removed all species that were not our three target species from all monoculture and polyculture plots, then removed all non-target species from monoculture plots (e.g., we removed *Ascophyllum* and *Mastocarpus* from *Fucus* plots), and finally removed additional biomass from polyculture plots, proportionate to species' relative abundances, so that the average amount removed from monoculture and polyculture plots was equivalent at each site (contrast, polyculture vs. monocultures $F_{1,348} = 0.1$, $P = 0.736$). The wet mass of material removed from each plot was recorded, and additional "compensatory weeding" of polyculture plots was performed as necessary to ensure that polyculture biomass removals were equivalent to the mean of monoculture biomass removals for that site. Initial removals were performed in August and September 2010, and the first post-removal survey was conducted in October 2010. Additional removals and surveys were conducted three times each year (surveys in April, July, and October) until October 2012. Initial removals of seaweed species to establish our experimental treatments resulted in substantial disturbances to plots associated with the removal of macroalgal biomass. Subsequent removals of non-target species to maintain the treatments did not require the removal of nearly as much biomass. We evaluated recovery from the initial disturbance to assess the relationship between seaweed diversity and resilience in algal cover.

Statistical analyses

All statistical analyses were conducted using general linear models (PROC GLM in SAS v. 9.4 [SAS Institute 2012]; see Appendix S2) and *t* tests, after verifying that the data met the assumptions of normality and homogeneity of variances. We used the general linear model framework to evaluate responses as a function of both continuous (e.g., initial algal richness) and categorical (e.g., experimental treatments) variables. Region and site(region) were included in all models to account for site and regional differences. Because algal cover could be non-destructively sampled throughout the experiment and because there was a strong relationship between algal cover and biomass (see *Materials and methods: Experimental design*), we used percent cover as our response variable in all analyses.

We evaluated the relationship between the initial algal species richness, surveyed in the plots during July 2010, and the initial algal cover using a general linear model after accounting for region and site(region). We examined effects of experimental treatments (treatment) on algal cover in plots from October 2010 (month 3) to October 2012 (month 27) using repeated-measures ANOVA, after accounting for region and site(region). Note that control plots were not included in this analysis because we wanted to account for disturbance associated with establishment and maintenance of our experimental treatments. We also included treatment × region and treatment × site(region) interactions in the model (Appendix S2: Table S1). Within-subjects effects were evaluated using Greenhouse-Geisser adjusted *P* values. Similar general linear model analyses were also conducted separately for each region (Appendix S2: Tables S2–S4) and site (Appendix S2: Tables S5–S13) to assess whether the response of algal cover to biodiversity manipulations differed at regional and local scales.

To evaluate whether diverse polyculture plots exhibited higher cover than the average of the component monocultures maintained separately (i.e., non-transgressive overyielding; Hector et al. 2002), we included a contrast between monoculture and polyculture treatments in all generalized linear models. Statistical comparisons between best-performing monocultures and polycultures (i.e., transgressive overyielding) were conducted post-hoc using *t* tests. We assessed the magnitude of these overyielding effects by calculating mean log-response ratios ($\mathrm{LR}_{\mathrm{mean}}$) and maximum log-response ratios ($\mathrm{LR}_{\mathrm{max}}$; Cardinale et al. 2011):

$$\mathrm{LR}_{\mathrm{mean}} = \ln\left(\frac{P}{M_{\mathrm{mean}}}\right), \tag{1}$$

$$\mathrm{LR}_{\mathrm{max}} = \ln\left(\frac{P}{M_{\mathrm{max}}}\right) \tag{2}$$

where P was the mean percent cover in the polyculture plots, M_{mean} was the mean percent cover in the corresponding monoculture plots, and M_{max} was the percent cover of the component species with the highest cover in monoculture. Values of $\mathrm{LR}_{\mathrm{mean}} > 0$ indicate non-transgressive overyielding; the diverse polyculture assemblage performs better, in this case has higher percent cover, than the average performance of the species in that assemblage. Values of $\mathrm{LR}_{\mathrm{max}} > 0$ indicate transgressive overyielding; the diverse polyculture assemblage performs better than even the best-performing species in that assemblage. Log ratios are more effective at comparing monoculture and polyculture assemblages than simple ratios are (e.g., D_{max}; Loreau 1998) because the natural log linearizes the ratio so that deviations in the numerator are equivalent to deviations in the denominator (Hedges et al. 1999).

To quantify effects of our biodiversity manipulations on resilience in algal cover, the return of a disturbed plot to its previous undisturbed state (Allison and Martiny 2008), we compared the cover of control and experimental plots to evaluate recovery following the substantial disturbance associated with initial removal of algal biomass. We defined recovery time as the number of months required for the average cover of the monoculture or polyculture plots at a particular site to be statistically indistinguishable ($P > 0.05$) from the average cover of the un-manipulated control plots at that site. We considered an experimental treatment at a site "recovered" if cover was equivalent to that in the corresponding control for two or more consecutive surveys. If a particular treatment at a site had not recovered by the final survey in October 2012, we assigned it a value of 36 months, based on an earliest potential recovery date two surveys following the final survey (i.e., in July 2013). Our estimate of recovery was therefore conservative, as it is possible that treatment-by-site combinations that had not recovered by the final survey would not have been equivalent to the corresponding control during the two subsequent surveys in April and July 2013. Because recovery was based on comparisons of manipulated and control treatments at each site, it could only be calculated at the level of site. To account for this, Site was treated as the experimental unit, with recovery quantified four times for each Site, once for each Treatment. We then compared the differences between monoculture and polyculture means for each site, which were evaluated using sequential corrected Bonferroni tests (Drezner and Drezner 2016).

RESULTS

Coast scale: comparisons across all sites

After accounting for effects of region ($F_{2,436} = 82.5$, $P < 0.001$) and site(region) ($F_{6,436} = 6.9$, $P < 0.001$), we found a positive relationship between initial seaweed richness, the number of seaweed species present in plots in July 2010, prior to our experimental manipulations, and initial seaweed cover ($F_{1,436} = 18.2$, $P < 0.001$; Fig. 2; Appendix S2: Table S14). Initial macroalgal cover and richness were highest on Quoddy Head, intermediate in the Boothbay region of Maine, and lowest in Nahant ($P < 0.05$ after Tukey adjustment for all comparisons).

Our experiment was designed to test whether this observed relationship between algal richness and algal cover was a causal one and to evaluate how the effect of biodiversity on cover changed over space and time. Whereas values for control treatments are included in our presentation of changes in seaweed cover over time (Fig. 3A), we did not include the controls in these analyses, instead focusing on comparisons between monocultures and polycultures across all sites, nested within regions. Our analyses of treatment effects only included time points after experimental manipulations were conducted, though we show pre-manipulation values (0 months) to illustrate that there were no initial differences between treatments (see *Materials and Methods*). After accounting for region ($F_{2,299} = 152.2$, $P < 0.001$) and site(region) ($F_{6,299} = 22.5$, $P < 0.001$), differences in seaweed percent cover between our experimental treatments were striking (treatment $F_{3,299} = 43.0$, $P < 0.001$), emerged rapidly, and intensified with time (time × treatment $F_{18,1794} = 5.9$, $P < 0.001$; Fig. 3A; Appendix S2: Table S1), despite the fact that an equivalent amount of biomass was removed, on average, from monoculture and polyculture plots (see *Materials and methods*).

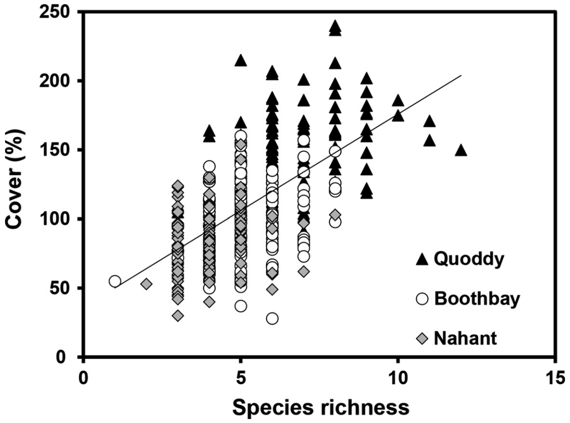

FIG. 2. Seaweed cover increases with seaweed species richness. Initial surveys prior to experimental manipulation indicated a positive relationship between richness and seaweed cover ($P < 0.001$) after accounting for region (Quoddy, Boothbay, and Nahant; $P < 0.001$) and site nested within region ($P < 0.001$).

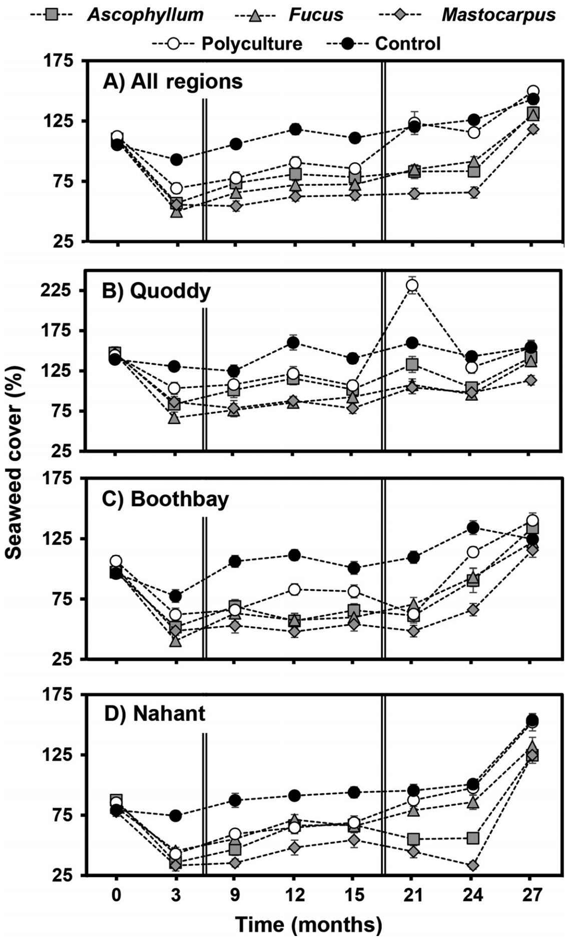

FIG. 3. Changes in seaweed cover associated with experimental manipulations of diversity. Values are means ± SE of monocultures (*Ascophyllum*, *Fucus*, and *Mastocarpus*; gray symbols), polycultures (open circles), and controls (filled circles) over the course of our 27-month experiment (A) across all regions and within each region: (B) Quoddy, (C) Boothbay, and (D) Nahant. Month "0" corresponds to July 2010. Double vertical lines indicate winter months during which sampling did not occur. Seaweed cover can be greater than 100% due to canopy layers overlaying understory species. Note that the *y*-axes differ in the different panels to accommodate higher average cover in the Quoddy region.

Overall effects of biodiversity on algal cover emerged rapidly and increased over the course of the experiment (Fig. 4A). Diverse polyculture assemblages always had higher cover than the average of the single-species monocultures (i.e., non-transgressive overyielding; $P < 0.003$ in all cases for contrasts between monoculture and polyculture treatments; Fig. 5, Table 1), and polyculture cover exceeded the cover of the most abundant monoculture species most (57%) of the time (i.e., transgressive overyielding; Fig. 5, Table 2). More diverse plots were also more resilient, recovering more rapidly following the substantial removal of biomass at the start of the experiment. On average, cover in polyculture plots became equivalent to that in unmanipulated controls 9.1 ± 2.4 (mean ± SE) months earlier than in monocultures

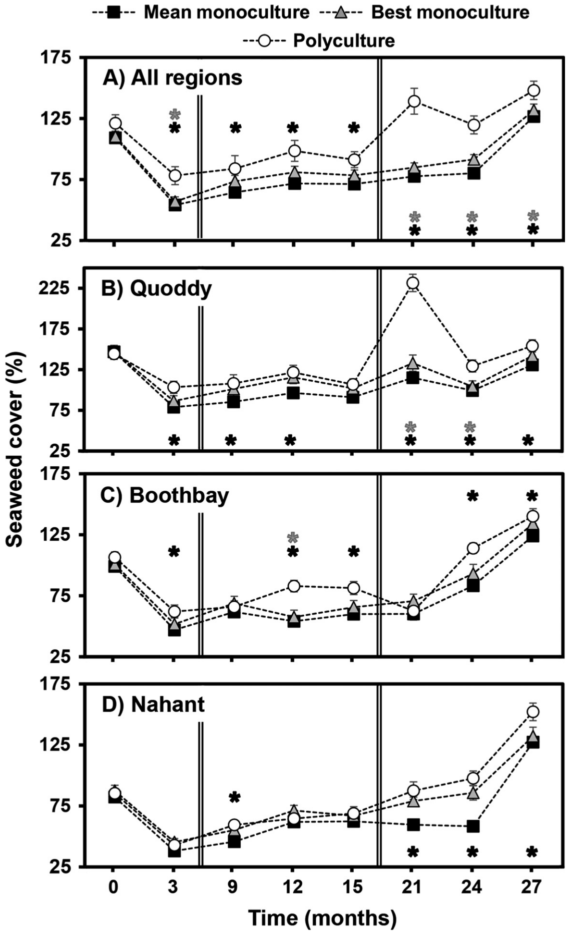

FIG. 4. Effects of diversity on seaweed cover change with time and region. Values are means ± SE of the mean monoculture (black squares), the best-performing monoculture (gray triangles), and the polyculture (open circles) (A) across all regions and within each region: (B) Quoddy, (C) Boothbay, and (D) Nahant. Gray asterisks indicate statistically significant differences ($P < 0.05$) between the polyculture and the best-performing monoculture for a particular date, and black asterisks indicate statistically significant differences between the polyculture and the mean of the monocultures. Month "0" corresponds to July 2010. Double vertical lines indicate winter months during which sampling did not occur. Seaweed cover can be greater than 100% due to canopy layers overlaying understory species. Note that the y-axes differ in the different panels to accommodate higher average cover in the Quoddy region.

($t = 3.8$, df = 8, $P = 0.005$) despite subsequent, less substantial removals of biomass to maintain experimental treatments. Cover in polyculture plots recovered, becoming equivalent to unmanipulated control plots, more rapidly than cover in *Ascophyllum* ($P = 0.015$), *Fucus* ($P = 0.029$), or *Mastocarpus* ($P = 0.003$) plots (Fig. 3).

The magnitudes of overyielding effects were strongest at the scale of the coast and declined at smaller scales (Fig. 5). This was especially evident for transgressive overyielding; on average, LR_{max} was lower at the scale of sites than at the scale of the coastline (one-sample t test, $t = 3.1$, df = 8, $P = 0.015$).

Regional scale: comparisons between regions

Effects of our experimental manipulations differed between regions (treatment × region $F_{6,299} = 5.9$, $P < 0.001$; Appendix S2: Table S2). Treatment effects were strong ($P < 0.001$ in all cases; Appendix S2: Tables S2–S4) and biodiversity effects occurred (Fig. 4B–D, Tables 1, 2) in all regions. However, the three regions differed in some important ways. First, *Ascophyllum* was the most abundant seaweed species in monoculture in the Quoddy region (Fig. 3B), whereas *Fucus* was the most abundant in the Nahant region (Fig. 3D); *Ascophyllum* and *Fucus* were equivalent in the Boothbay region (Fig. 3C). Second, the different regions differed from each other with respect to biodiversity effects. Averaged across all sites, overyielding was most evident in the Quoddy region (non-transgressive, 86% of census dates, average $LR_{mean} = 0.290$, Table 1; transgressive, 29% of dates, average $LR_{max} = 0.171$, Table 2, Fig. 4B) and least evident in the Nahant region (non-transgressive, 57%, average $LR_{mean} = 0.228$, Table 1; transgressive, 0%, average $LR_{max} = 0.045$, Table 2, Fig. 4D); the Boothbay region was intermediate between the two other regions (non-transgressive, 71%, average $LR_{mean} = 0.222$, Table 1; transgressive, 14%, average $LR_{max} = 0.120$, Table 2, Fig. 4C).

However, regions also complemented each other with respect to biodiversity effects (Fig. 4B–D, Table 1); when overyielding did not occur in the Quoddy region (15 months), it occurred in the Boothbay region. Similarly, when overyielding did not occur in the Boothbay region (9 and 21 months), it occurred in the Quoddy and Nahant regions. And when overyielding did not

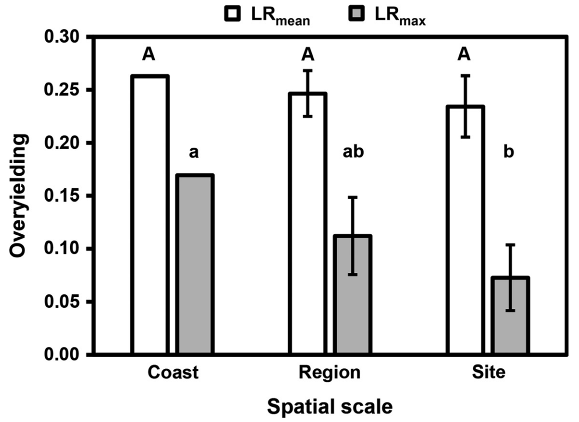

FIG. 5. Effects of spatial scale on overyielding. Values are overall average (± SE) mean log-response ratios (LR_{mean}; white bars) and maximum log-response ratios (LR_{max}; gray bars) at the coast, region, and site scales. Letters indicate statistically significant differences between scales ($P < 0.05$), with capital letters indicating comparisons between LR_{mean} values and lowercase letters indicating comparisons between LR_{max} values. Whereas there were no differences in LR_{mean} values at the different scales ($P > 0.35$ in all cases), LR_{max} values were lower at the scale of sites than at the scale of the coast ($P = 0.015$).

TABLE 1. Non-transgressive overyielding (LR_{mean}) in experimental plots at different spatial scales across time.

	Time (months since start of experiment)						
Location	3	9	12	15	21	24	27
All sites	**0.246**	**0.184**	**0.232**	**0.182**	**0.464**	**0.364**	**0.167**
Quoddy	**0.270**	**0.235**	**0.233**	0.162	**0.700**	**0.265**	**0.163**
A	**0.373**	**0.500**	**0.166**	−0.058	**0.478**	0.130	0.116
B	0.050	0.030	**0.321**	**0.276**	**0.723**	**0.359**	0.153
C	**0.378**	0.114	0.204	**0.364**	**0.987**	0.350	0.233
Boothbay	**0.278**	0.067	**0.426**	**0.305**	0.039	**0.315**	**0.123**
A	0.235	0.164	**0.388**	0.187	0.219	0.195	0.147
B	0.359	0.300	**0.514**	**0.367**	−1.680	**0.406**	0.106
C	0.233	−0.253	0.395	**0.367**	**0.440**	**0.388**	0.109
Nahant	0.115	**0.261**	0.042	0.097	**0.384**	**0.515**	**0.179**
A	0.258	0.149	0.152	0.047	0.285	**0.464**	**0.205**
B	0.035	0.244	−0.078	0.038	**0.526**	**0.474**	0.077
C	0.021	**0.397**	0.120	0.328	0.273	**0.645**	**0.263**

Notes: Values are mean log-response ratios (LR_{mean}) comparing the cover in polyculture plots to the average cover in the corresponding monoculture plots. Entries in boldface type indicate statistically significant overyielding ($P < 0.05$).

TABLE 2. Transgressive overyielding (LR_{max}) in experimental plots at different spatial scales across time.

	Time (months since start of experiment)						
Location	3	9	12	15	21	24	27
All sites	**0.196**	0.054	0.112	0.088	**0.375**	**0.233**	**0.127**
Quoddy	0.178	0.064	0.051	0.048	**0.554**	**0.219**	0.083
A	0.257	0.219	0.072	−0.185	**0.359**	0.097	−0.003
B	−0.026	−0.181	0.084	0.147	**0.517**	**0.283**	0.076
C	0.300	0.067	−0.033	0.097	**0.874**	0.188	0.198
Boothbay	0.180	−0.043	**0.364**	0.213	−0.123	0.203	0.045
A	0.099	0.146	0.245	0.051	0.143	0.092	0.058
B	0.279	0.150	0.333	0.293	−1.879	0.163	0.049
C	0.104	−0.398	0.189	0.225	**0.173**	0.170	0.012
Nahant	−0.059	0.073	−0.097	0.028	0.103	0.129	0.141
A	0.105	0.063	−0.127	−0.085	0.068	0.095	**0.177**
B	−0.085	0.050	−0.104	−0.030	0.264	0.080	−0.012
C	−0.237	0.090	−0.084	0.021	−0.093	0.239	0.081

Notes: Values are log-response ratios (LR_{max}) comparing the cover in polyculture plots to the best-performing component species grown in monoculture. Entries in boldface type indicate statistically significant overyielding ($P < 0.05$).

occur in the Nahant region (3, 12, and 15 months), it occurred in the Boothbay region.

Site-scale comparisons

Treatment effects remained relatively strong at the level of individual sites, with the exception of two sites in the Boothbay region (Boothbay A $F_{3,35} = 2.2$, $P = 0.107$; Boothbay B $F_{3,36} = 2.7$, $P = 0.062$; Appendix S2: Tables S5–S13). However, these treatment effects did not translate into strong effects of diversity on algal cover; overyielding was least evident at the scale of individual sites, and underyielding was even evident in a few instances (Tables 1, 2). For example, at the regional scale, the diverse polyculture plots had higher cover than the average single-species plots during approximately 71% of sampled time intervals. In contrast, at the site scale, polyculture cover exceeded the average of the monocultures during only about 40% of sampled time intervals. Furthermore, overyielding seldom occurred at all three sites within a region simultaneously. Of 21 time intervals sampled (3 regions × 7 census periods), all three sites within a region only exhibited non-transgressive overyielding on three occasions. And transgressive overyielding was even less common at the site scale. It only occurred on 6 of 63 (3 sites × 3 regions × 7 census periods) occasions, and only once simultaneously at all sites within a region.

Sites within a region often complemented each other with respect to diversity effects (Table 1). For example, non-transgressive overyielding in the Nahant region was driven by site C at 9 months and by site B at 21 months.

Similarly, non-transgressive overyielding in the Quoddy region was driven by site A at 9 months and by site B at 24 months.

Discussion

As predicted, the functional consequences of species loss differed between sites within regions and between regions along the coastline, highlighting the role of spatial scale in mediating the effects of biodiversity on producer biomass. Most of the variation in the effects of biodiversity on seaweed cover occurred at the site scale. On average, each site was only characterized by non-transgressive overyielding, which occurred when three-species polyculture plots had higher cover than the average cover of the component species growing alone, during two to three (~40%) of the seven censuses conducted over our 27-month experiment (Table 1). Underyielding also occasionally occurred at the site scale, especially during the spring (i.e., months 9 and 21) when *Fucus* and *Ascophyllum* individuals recruited into newly cleared bare space in their respective monoculture plots. As results were averaged over larger spatial scales, overyielding occurred more often (Tables 1, 2) and was greater in magnitude (Fig. 5). Non-transgressive overyielding occurred, on average, during five of seven (71%) censuses at the regional scale, and during all censuses at the coastline scale. Transgressive overyielding, which occurred when three-species polyculture plots had higher cover than even the best-performing seaweed species growing by itself, was, not surprisingly, less common than non-transgressive overyielding (Cardinale et al. 2011). However, it was similarly affected by scale, occurring during 10% of censuses at the site scale, 14% of censuses at the regional scale, and 57% of censuses at the coastline scale (Table 2).

It is important to note that scaling, as we discuss it here, does not involve evaluation of diversity effects in plots of different sizes (e.g., Roscher et al. 2005). All experimental plots were identical in size, but we averaged effects of diversity on seaweed cover at different scales—site, region, and coast—and found substantial differences in effects at those different scales. This pattern may have emerged because of complementarity in space and time (Hillebrand and Matthiessen 2009). Increasing spatial heterogeneity tends to enhance complementarity effects in biodiversity experiments. For example, Wacker et al. (2008) showed that plant assemblages growing on plots characterized by heterogeneous nutrient availability (no nutrients, nitrogen [N] addition, phosphorus [P] addition, and N + P addition) were characterized by stronger complementarity effects than those receiving a uniform application of the same average N and P concentrations. Thus, for example, heterogeneity in nutrient availability along the Gulf of Maine coastline (Benes and Bracken 2016) could contribute to stronger and more prevalent overyielding effects when multiple regions are considered together. Similarly, Stachowicz et al. (2008*a*) compared the performance of monocultures and diverse assemblages of intertidal seaweeds growing under uniform, laboratory conditions to the same assemblages in the field and found that complementarity effects occurred under spatially heterogeneous field conditions but not under uniform laboratory conditions.

Biodiversity effects are also mediated by the degree of connectivity between sites. For example, France and Duffy (2006) showed that increasing the dispersal potential of interacting organisms reduced the effect of diversity on productivity, and Matthiessen et al. (2007) showed that biodiversity effects were stronger in closed systems than in open systems. It is possible that biodiversity effects were not as prevalent at the site scale because plots within sites were connected via dispersal. However, dispersal would be limited between sites within regions dispersal distances of these species are typically on the order of meters (Dudgeon et al. 2001) and even more limited between regions separated by hundreds of kilometers along the Gulf of Maine coastline.

The size of experimental plots may also affect the potential for spatial heterogeneity at the site scale. Stachowicz et al. (2008*b*) conducted a similar manipulation of seaweed diversity at a single site on the coast of California, USA, and found that consistent transgressive overyielding emerged after 24 months and continued through the duration of the 3-yr experiment. In contrast, consistent transgressive overyielding never occurred at any of our sites, even after 27 months. One difference between the Stachowicz et al. (2008*b*) experiment and ours is that their experimental plots (1.5 m in diameter = 1.8 m^2) were nine times larger than ours (0.5 m in diameter = 0.2 m^2) in area. Of course, other differences between the coastlines of northern California and the Gulf of Maine, including more pronounced seasonality in temperature in New England, especially in the Nahant region (Appendix S1: Fig. S1; Harley 2008), and higher nutrient availability in California (Bracken et al. 2011, Benes and Bracken 2016), could have contributed to these differences, as well.

When multiple subgroups collectively contribute to a larger combined group, such as sites within regions or regions along a coastline, complementarity in space can result in more sustained production of the larger group despite variation in the subgroups comprising it. This is the case with sockeye salmon in Bristol Bay, Alaska, USA, where fish from multiple river systems contribute to a single fishery. Production of individual populations can be highly variable, but climatic conditions detrimental to fish in one river system can favor fish in another, nearby system, allowing relatively consistent production of the fishery (Hilborn et al. 2003). In our experiment, overyielding at the regional scale was seldom associated with overyielding at all three sites within that region; typically only one or two sites exhibited overyielding. Sites within regions differed with respect to temperature, wave exposure, tidal elevation, and nutrient availability (M. Bracken, *unpublished data*), and this heterogeneity may have contributed to emergent effects of biodiversity at the regional scale (Wacker et al. 2008).

The scaling of biodiversity effects from site to region to coastline has important implications for marine conservation and the ecosystem-based management of marine resources. Given links between biodiversity, ecosystem functioning, and ecosystem services, "managing for biodiversity" (sensu Palumbi et al. 2009) has been proposed as an approach to ecosystem-based management. Our results suggest that the maintenance of consistent biodiversity effects at larger spatial scales requires conservation efforts targeted at multiple locations within a region. This is similar in practice to arguments for networks of marine reserves based on propagule dispersal (e.g., Shanks et al. 2003), suggesting that networks of marine reserves may achieve multiple conservation goals simultaneously, i.e., protection of both populations and ecosystem functions at a regional scale.

In conclusion, we have shown that the scale over which the relationship between biodiversity and marine ecosystem functioning is evaluated mediates the strength of the relationship. Biodiversity effects were weakest and most inconsistent at the scale of individual sites and strongest and most consistent at the scale of the entire coastline. Results from a single site or region are not necessarily generalizable to other sites or regions due to differences in biotic and abiotic conditions. Spatial and temporal complementarity of sites nested within regions and regions nested within the Gulf of Maine coastline resulted in emergent biodiversity effects at larger scales. Thus, weak and/or inconsistent biodiversity effects at individual sites may scale up to stronger, more consistent effects at larger spatial scales. Quantitative summaries of biodiversity experiments conducted at the scale of individual sites (e.g., Cardinale et al. 2011) do not capture this aspect of scale and may therefore underestimate the effect of biodiversity on ecosystem functioning.

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