



Biodiversity effects on productivity and stability of marine macroalgal communities: the role of environmental context

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The influence of biodiversity on ecosystem functioning has been the focus of much recent research, but the role of environmental context and the mechanisms by which it may influence diversity effects on production and stability remain poorly understood. We assembled marine macroalgal communities in two mesocosm experiments that varied nutrient supply, and at four field sites that differed naturally in environmental conditions. Concordant with theory, nutrient addition promoted positive species richness effects on algal growth in the first mesocosm experiment; however, it tended to weaken the positive diversity relationship found under ambient conditions in a second experiment the next year. In the field experiments, species richness increased algal biomass production at two of four sites. Together, these experiments indicate that diversity effects on algal biomass production are strongly influenced by environmental conditions that vary over space and time. In decomposing the net biodiversity effect into its component mechanisms, seven of the eight experimental settings showed positive complementarity effects (suggesting facilitation or complementary resource use) countered by negative selection effects (i.e. enhanced growth in mixture of otherwise slow growing species) to varying degrees. Under no conditions, including nutrient enrichment, did we find evidence of positive selection effects commonly thought to drive positive diversity effects. Species richness enhanced stability of algal community biomass across a range of environmental settings in our field experiments. Hence, while species richness can increase production, enhanced stability is also an important functional outcome of maintaining diverse marine macroalgal communities.

Concerns over losses of native species worldwide have motivated over a decade of intensive study of biodiversity effects on community properties and ecosystem processes (Tilman et al. 1997, Hooper et al. 2005). The importance of species richness in driving primary production has been the main focus, and synthesis is now possible across more than one hundred experimental tests of richness effects (Balvanera et al. 2006, Cardinale et al. 2006, Worm et al. 2006). Recent meta-analyses suggest that species richness commonly has a positive effect on biomass of plant communities, although the mechanisms responsible for these effects have not been assessed in most studies (Cardinale et al. 2006). Increasingly, researchers are decomposing net biodiversity effects into additive components of complementarity (e.g. resource partitioning or positive interactions that can lead to enhanced production) and selection (dominance of productive species or enhanced performance of slow-growing species in mixtures) as a means to interpret effects of species richness on primary production (Loreau and Hector 2001, Fridley 2002, Hooper and Dukes 2004, Hooper et al. 2005).

While theory predicts that richness effects will vary with environmental context (Cardinale et al. 2000, Fridley 2001), relatively few manipulative studies have evaluated

species richness effects on biomass production for the same species assemblage over a range of settings. In studies of terrestrial grasslands, experimentally enhanced resources (CO₂ and nutrients) can increase the strength of the relationship between species richness and production (Reich et al. 2001, Fridley 2002, 2003). Theory predicts that elevated resources will increase dominance of highly productive species, leading to greater yield of mixed assemblages through positive selection effects as evenness declines (Fridley 2001, Grime 2001, Aarssen et al. 2003). On the other hand, facilitation or partitioning of resources among species might be more common where resources are limited (Brooker and Callaghan 1998, Hooper et al. 2005), increasing complementarity effects. Studies that have crossed resource supply with species richness have so far provided sparse quantitative evidence either way (Fridley 2002, Zhang and Zhang 2006a) and there is a need for better understanding of the role of resources in richness–production relationships, including the manner in which complementarity and selection effects influence net responses. In addition to resources, other forms of environmental context may influence the strength of richness effects on plant production, such as drought or temperature (Pfisterer and Schmid 2002, Zhang and Zhang 2006b)

and herbivore richness and composition (Bruno et al. 2008). To date, we know little of the role of environmental context on richness–production relationships outside of terrestrial plant and microbial communities, and marine systems have received almost no attention on this topic (Worm et al. 2006, Stachowicz et al. 2007).

Environmental variability is central to studies evaluating another potential outcome of species richness: community stability. Theory and experimental evidence indicate that species richness can lead to decreased variability (increased stability) of aggregate community properties such as biomass over time (Cottingham et al. 2001, Steiner et al. 2005) and space (Loreau et al. 2003, Weigelt et al. 2008). Species richness could stabilize production through insurance effects; i.e. higher species richness leads to a diversity of functional responses and increased probability of community persistence (Naem 1998, Yachi and Loreau 1999). In addition, other mechanisms such as increased stability of component populations (Ives et al. 1999, Valone and Hoffman 2003) or overyielding (Tilman 1999) could lead to reduced variability in diverse assemblages. Theory still exceeds empirical tests of plant diversity–stability relationships, and whether and how they act in many systems remain to be explored in depth (Stachowicz et al. 2007).

We tested the influence of environmental context on species richness effects in benthic macroalgal communities of North Carolina by: 1) conducting two mesocosm experiments in two years to evaluate the diversity–production relationship under conditions of ambient and enriched nutrients, 2) examining the effects of species richness under a range of conditions that occur within estuarine environments through an experiment replicated at four field sites, and 3) assessing whether species richness has a stabilizing effect on community biomass over space within and across the range of field settings. We measured multiple response variables in our mesocosm experiments to test the hypothesis that the metric measured can influence interpretation of diversity–function studies (Hector and Bagchi 2007, Gamfeldt et al. 2008), and quantified the contributions of complementarity and selection effects to net biodiversity effects (Loreau and Hector 2001).

Methods

We varied nutrient supply in two mesocosm experiments (July 2004 and August 2005) and chose four sites to represent a range of conditions under which to conduct our field experiment (July 2005). Macroalgae were collected for each experiment from docks and jetties near Morehead City and Beaufort, North Carolina, USA, and assembled in monocultures or six-species mixtures in a replacement design (60 g wet mass for all treatments, similar to field densities: Bruno et al. 2005). Algal thalli were attached to 25 × 25 cm plastic mesh screens (5 mm openings) with small cable ties, and mesograzers (e.g. amphipods and isopods) were removed by placing screens in dilute pesticide (Sevin: 1-naphthyl n-methyl-carbamate) (Bruno et al. 2005).

The mesocosms were 30-l clear plastic tanks each containing one algal screen, placed in outdoor water tables (at the Univ. of North Carolina Inst. of Marine Science, Morehead City), with positions re-randomized every five

days. Filtered water from Bogue Sound was supplied by dump buckets, simulating turbulent flow of local hard substratum habitats (Bruno et al. 2005). Species used in the mesocosms were those most common in the field in both years: the greens *Codium fragile* and *Ulva lactuca*, reds *Gracilaria tikvahiae* and *Hypnea musciformis*, and browns *Sargassum flipendula* and *Padina gymnospora*. The first experiment ($n = 7$) ran for 18 days and the second ($n = 10$) for 20 days; otherwise, experimental design was the same in both years. To half of the mesocosms, we added 15 g of slow-release fertilizer, an amount found to substantially elevate NO_3^- ($26.1 \pm 6.7 \mu\text{M}$, ambient = $5.3 \pm 0.6 \mu\text{M}$), NH_4^+ ($27.0 \pm 4.1 \mu\text{M}$, ambient = $2.1 \pm 0.4 \mu\text{M}$) and PO_4^- ($1.2 \pm 0.4 \mu\text{M}$, ambient = $0.2 \pm 0.0 \mu\text{M}$) in a pilot experiment. Fertilizer was divided into two centrifuge tubes drilled with small holes and placed in floating rings; empty tubes were floated in the ambient-nutrient mesocosms to control for shading. We changed the fertilizer three times per week to insure constant elevation of nutrients.

We evaluated several response variables important to community and ecosystem level processes. Change in wet algal biomass was measured as a proxy for primary production; algae were spun in a salad spinner for 20 s, and wet weight was recorded for each species. Tissue nitrogen (N) content can indicate growth potential, and carbon (C) to N ratios can indicate food quality for herbivores (Hall et al. 2007). Tissue C and N were determined using a CHN analyzer. Epiphytic algal growth provides an additional measure of primary production that can vary with macrophyte species richness (Engelhardt and Ritchie 2001), and can influence light and nutrient availability. We quantified epiphyte biomass in 2005 by measuring chlorophyll-a on a 2.5 × 2.5 cm sanded PVC tile placed into each mesocosm for seven days then frozen until later fluorometric analysis.

In the field experiment, the same species were used except that the brown *Dictyota menstrualis* was substituted for the green *Ulva lactuca* due to a shift in field abundances. The field experiment included a mixture of three randomly selected species in addition to the monocultures and six-species mixture ($n = 5$). Plastic screens holding the algae were attached with cable ties to a rebar rack in random order, with 10 cm between screens. This design was repeated at four sites spanning a 20 km distance near Morehead City and Beaufort, NC (Fig. 1). At each site, in mid-July 2005, we quantified light with a LI-COR spherical PAR sensor, temperature, and salinity (refractometer) at the benthos at 1 m depth, as well as flow (mass loss from Plaster of Paris cubes over 24 h). We estimated fish abundance by seining three haphazardly selected locations at each site, and mesograzers by placing two algal mimics (frayed polypropylene ropes) at each site for five days. Mesograzers were rinsed into a 0.42 mm mesh sieve and preserved in ethanol for later identification. The experiment ran for 13 days, after which we measured wet mass of algae.

For the mesocosm experiments, we used three-factor ANOVA (algal treatment, nutrient treatment, year) to test for effects on wet mass (change from initial), tissue N, and C:N; we first adjusted n to 7 (randomly dropping three points) in the second experiment. Two-factor ANOVA was used to evaluate epiphyte biomass (chlorophyll-a on tiles),

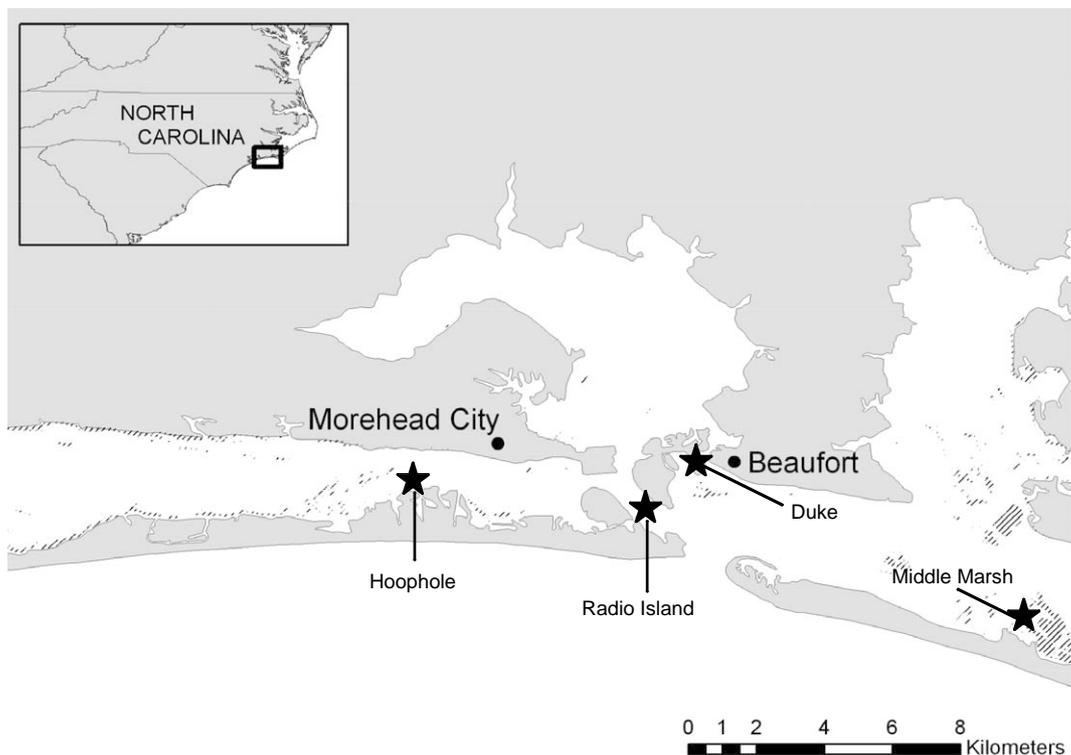


Figure 1. Map showing field experiment sites near Morehead City and Beaufort, North Carolina, USA.

measured only in 2005. To assess diversity effects within a nutrient treatment in a given year, we followed one-factor ANOVA on algal treatment with least square mean planned contrasts comparing performance of all monocultures to the six species mixture (Bruno et al. 2005).

For the field experiment, one-factor ANOVA was used to compare abiotic conditions and faunal abundance among sites. We used two-factor ANOVA (algal treatment, site) to test for differences in algal growth. Within sites, we followed one-factor ANOVA with planned contrasts of algal monocultures versus the mixtures to evaluate richness effects as above. For all experiments, log transformations were used as needed to meet statistical assumptions. JMP (ver. 7, SAS, USA) was used for all analyses.

To further explore richness effects, we calculated relative yield totals (RYT) as a conservative test of non-transgressive overyielding; i.e. when the mixture outperforms the average monoculture ($RYT > 1$) (Loreau 1998). We calculated D_{max} to test for transgressive overyielding; i.e. when the mixture yield is greater than that of any monoculture ($D_{max} > 0$) (Loreau 1998). We also evaluated diversity effects on each species' performance by calculating D_i , the deviation of a species' yield in mixture relative to expected yield (monoculture performance). $D_i > 0$ indicates overyielding and < 0 underyielding due to interactions with other species in the mixture (Loreau 1998, Hooper and Dukes 2004). Finally, we used the additive partitioning equation of Loreau and Hector (2001) to calculate the net biodiversity effect and its component complementarity and selection effects for each environmental setting.

The coefficient of variation (CV), calculated as the standard deviation of biomass divided by the mean, can be used to assess whether species richness enhances stability

(as evidenced by reduced CV in mixture) of community biomass across time or space (Cottingham et al. 2001, Romanuk et al. 2006, Weigelt et al. 2008). We evaluated spatial community stability by calculating CV of final algal biomass across replicates of each composition ($n = 5$) within a given site in our field experiment. We used a paired t-test to assess overall patterns of CV of the one versus six-species compositions ($n = 4$ sites). We also calculated CV for each composition across all its replicate positions within and among sites ($n = 20$) to evaluate spatial variability on a landscape scale. We compared CV of each species' mass alone versus in the six-species mixture, as decreased population variability could be one mechanism by which species richness stabilizes aggregate community biomass (Ives et al. 1999). We calculated summed covariance of species masses within the six-species mixtures, as negative covariance resulting from asynchronous species responses can be evidence of insurance effects (Lehman and Tilman 2000).

Results

Mesocosm experiments

Growth and other responses to ambient and enriched nutrients

In the two mesocosm experiments, algal growth varied significantly among species compositions (Fig. 2a–b; three-factor ANOVA, $F_{6,168} = 2.41$, $p = 0.0293$). Growth of algae was much greater overall in the 2004 experiment than in 2005 ($F_{1,168} = 19.49$, $p < 0.0001$). There was a significant interaction between algal treatment and year ($F_{6,168} = 11.27$, $p < 0.0001$), as some species grew exceptionally well in 2004

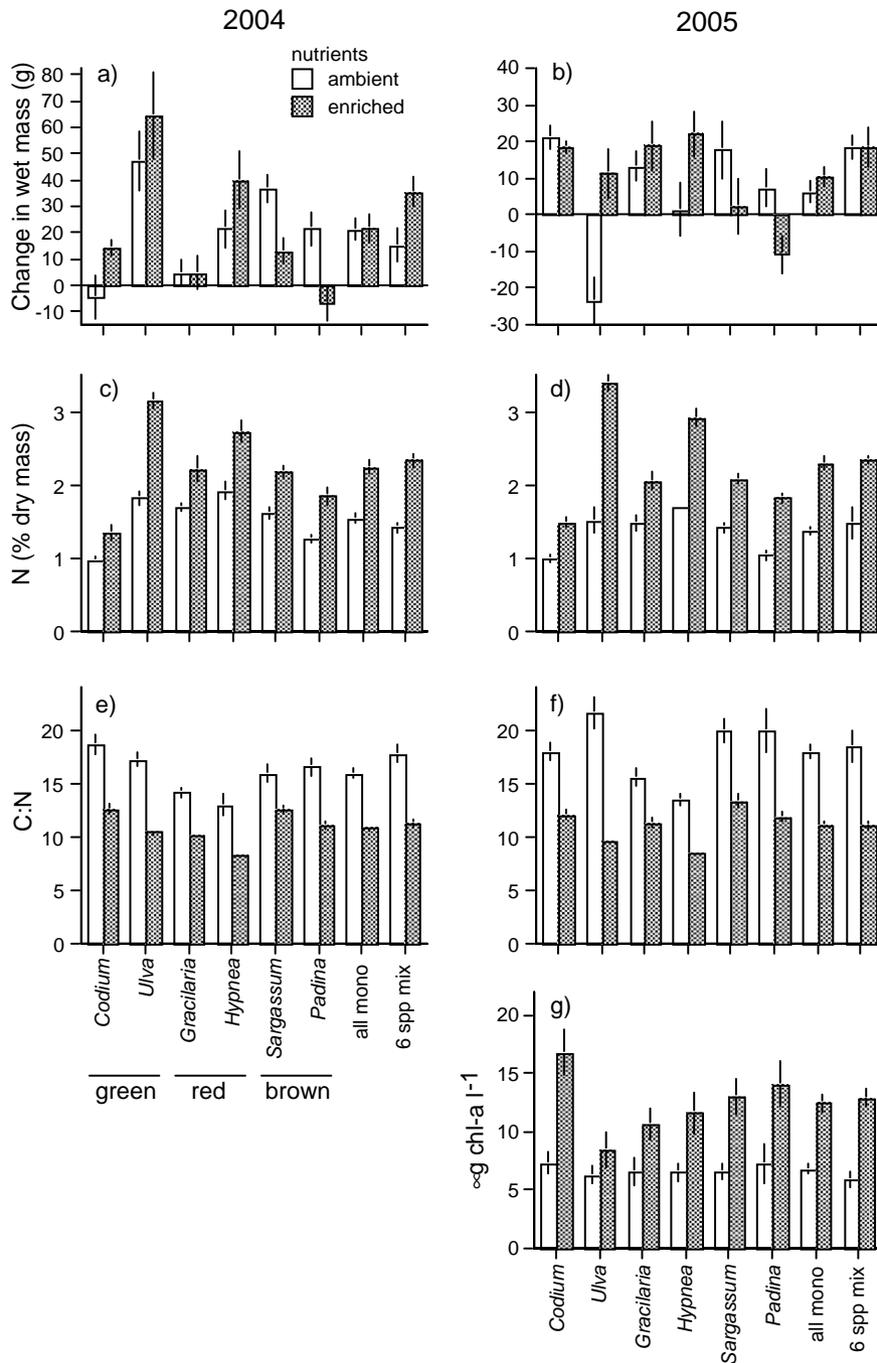


Figure 2. Change in algal wet mass, percent nitrogen (N) of dry algal tissue, and carbon to nitrogen ratios (C:N) in 2004 and 2005 mesocosm experiments, and chlorophyll-a concentration of epiphytes on tiles in the 2005 experiment. Note the difference in scale on the y-axis in the top panels. Values are means \pm 1 SE. Sample size was seven in 2004 and 10 in 2005 for all monoculture treatments and the six-species mixture. The average across all monoculture replicates is shown for comparison ($n=42$ in 2004 and 60 in 2005).

and poorly in 2005 (e.g. *Ulva*), while others performed better in 2005 (e.g. *Codium*, *Gracilaria*).

Nutrients had no significant effect on macroalgal growth overall, as species responded differently to increased nutrients (Fig. 2a–b; nutrient \times algal treatment interaction, $F_{6,168} = 7.12$, $p < 0.0001$). In 2004, *Sargassum* and *Padina* biomass declined with nutrients relative to ambient conditions (t-tests, $p = 0.0065$ and 0.0102 , respectively), whereas the mixture and *Codium* grew better with added nutrients

($p = 0.0306$ and 0.0650 , respectively; Fig. 2a). In 2005, *Ulva* and *Hypnea* gained significant biomass with nutrient addition ($p = 0.0023$ and 0.0276 , respectively), while the growth of *Padina* declined ($p = 0.0114$) and *Sargassum* showed a similar tendency (Fig. 2b).

Algal treatments varied significantly in N concentration (three-factor ANOVA, $F_{6,166} = 59.82$, $p < 0.0001$), ranging from $\sim 1\%$ (*Codium*) to 2.5% (*Ulva*) of dry mass (Fig. 2c–d). Nutrient addition produced large increases in tissue

N concentration (three-factor ANOVA, $F_{1,166} = 360.12$, $p < 0.0001$), although species differed in the magnitude of their responses (algal treatment \times nutrient interaction, $F_{6,166} = 6.28$, $p < 0.0001$), with *Ulva* increasing most and *Codium* and *Gracilaria* least (Fig. 2c–d).

Algal treatments differed significantly in C:N (three-factor ANOVA, $F_{6,166} = 20.51$, $p < 0.0001$) and this ratio declined with nutrient enrichment ($F_{1,166} = 452.45$, $p < 0.0001$; Fig. 2e–f) in both years. Algal treatments differed in their responses to nutrient addition (algal treatment \times nutrient interaction, $F_{6,166} = 3.46$, $p = 0.0030$), with *Ulva* dropping more in C:N and *Gracilaria* less than other treatments (Fig. 2e–f).

Epiphyte biomass on tiles (as chlorophyll-a) in 2005 varied significantly with algal treatment (two-factor ANOVA, $F_{6,126} = 2.52$, $p = 0.0246$); tiles in the *Codium* treatment had the highest epiphyte biomass overall and those in the *Ulva* treatment the lowest (Fig. 2g). Nutrient addition led to significant increases in epiphyte biomass on tiles ($F_{1,126} = 66.89$, $p < 0.0001$). Epiphytes responded most to nutrients where macroalgae did not; e.g. in the *Codium* treatment.

Richness effects

There were positive richness effects on algal growth in both years; however, nutrients appeared to drive the positive response in one year but not in the other. In 2004, species richness had no effect on growth under ambient conditions (Fig. 2a; planned contrast of mixture versus monocultures, $F_{1,47} = 0.28$, $p = 0.5999$), and although two species (*Codium* and *Gracilaria*) performed better in mixture than predicted by monoculture yields ($D_i > 0$), most species underyielded ($RYT < 1$) (Fig. 3a). Nutrient enrichment altered this relationship, with growth of the mixture exceeding that of the average monoculture (Fig. 2a; planned contrast, $F_{1,47} = 3.49$, $p = 0.0687$), five of six species performing better in mixture than predicted, strong complementarity effects driving the positive net biodiversity effect, and $RYT = 1.22$ (Fig. 3a).

In 2005, ambient nutrient conditions produced strong positive richness effects: the mixture exceeded growth of the average monoculture (Fig. 2b; planned contrast, $F_{1,68} = 4.95$, $p = 0.0296$), five of six species performed better in mixture than predicted, complementarity effects were very important, and $RYT = 1.23$ (Fig. 2b). With nutrient

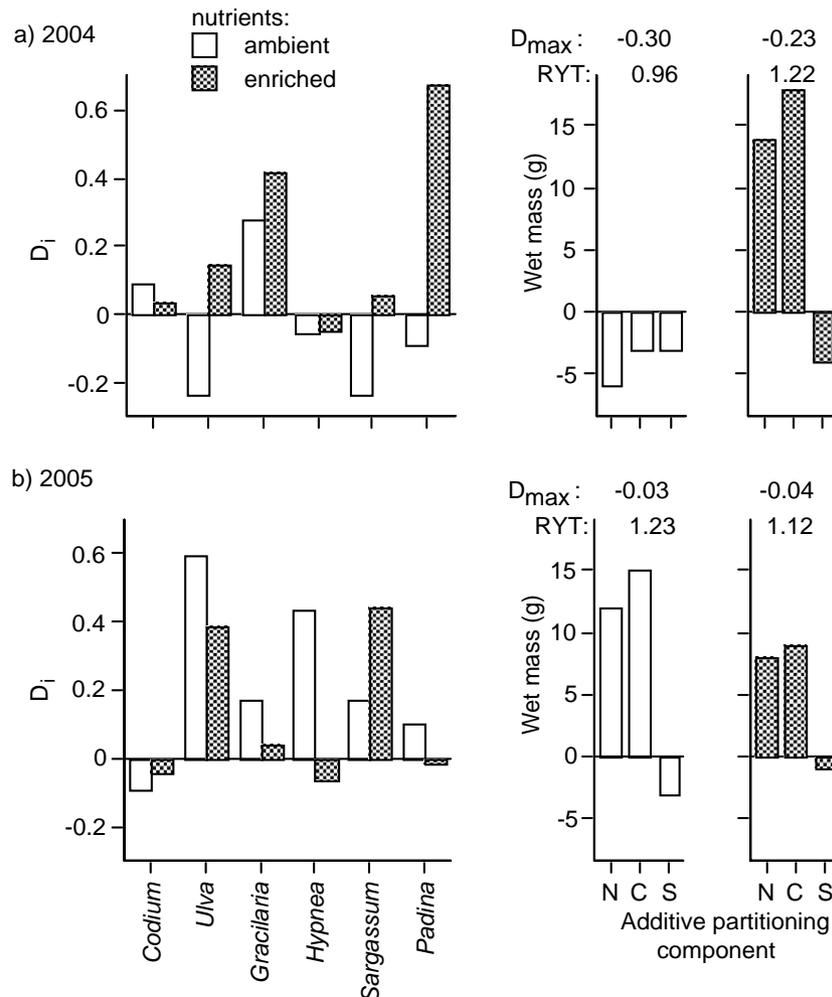


Figure 3. Left: D_i , the deviation of each species yield (as wet mass) in mixture relative to its yield in monoculture under ambient and enriched conditions in the 2004 and 2005 mesocosm experiments. Right: the net biodiversity effect (N) and its component complementarity (C) and selection (S) effects, D_{max} , and RYT (Methods) for algal wet mass under ambient and enriched conditions in the two experiments.

enrichment, there was a non-significant trend of species richness enhancing growth (Fig. 2b; planned contrast, $F_{1,68} = 1.71$, $p = 0.1956$), three species had $D_i > 0$, a positive net biodiversity effect resulted from strong complementarity, and $RYT = 1.12$ (Fig. 3b). Hence, nutrient addition somewhat dampened the effects of richness on production in 2005. In both years, selection effects were negative, relatively small, and comparable regardless of nutrient treatment.

Although species richness enhanced growth under some conditions, there was no evidence of transgressive overyielding under any circumstances (D_{max} always < 0). In addition, for the response variables of macroalgal %N and C:N, and epiphyte biomass, there were no effects of species richness (Fig. 2c–g, no significant planned contrasts).

Field experiments

Environmental context

The four field experiment locations provided a range of conditions in which to test the importance of environment on richness effects (Table 1). Light at one-meter depth was 2–3 times greater at Radio Island Jetty (RIJ) than at the other sites. Water temperature was significantly higher and flow nearly two times lower at Duke than at Hoophole (HH). Salinity was significantly greater at Duke than at the other three sites, which had similar salinities (Table 1).

Of all fish captured, 73% were the omnivorous sparid *Lagodon rhomboides* (pinfish), which is known to consume the red algae *Gracilaria tikvahiae* and *Hypnea musciformis*, but to avoid the introduced green *Codium fragile* as well as chemically defended brown species (Stoner 1980, Bruno et al. 2008). Both total fish abundance and pinfish abundance (Table 1) were significantly lower at RIJ than at the other sites, which did not differ. Similarly, total epifaunal abundance (primarily copepods, gastropods, and gammarid and caprellid amphipods) on algal mimics was significantly lower at RIJ than at the other sites (Table 1). The gammarid *Ampithoe longimana*, an important consumer of brown macroalgae in this system (Duffy and Hay 1994, Bruno et al. 2008), was rare at all sites (≤ 4 per mimic).

Growth responses to site conditions

Algal performance in the field experiment varied by site (two-factor ANOVA, $F_{3,125} = 9.21$, $p < 0.0001$), with growth greatest at Middle Marsh (MM) and lowest at HH (Fig. 4). Growth differed by algal treatment ($F_{7,125} =$

43.18, $p < 0.0001$); *Codium* and *Padina* grew best overall, while *Hypnea* and *Sargassum* lost substantial biomass. There were different patterns of algal composition performance across sites (site \times algal treatment interaction, $F_{21,125} = 6.13$, $p < 0.0001$); e.g. *Padina* performed best at Duke (one-factor ANOVA by site, $F_{3,16} = 5.32$, $p = 0.0453$), *Sargassum* at RIJ ($F_{3,16} = 3.94$, $p = 0.0273$), and both *Dictyota* ($F_{3,16} = 16.54$, $p < 0.0001$) and *Hypnea* ($F_{3,16} = 18.24$, $p < 0.0001$) at MM.

Richness effects

According to planned contrasts, species richness and macroalgal growth were positively related at two of the four sites, RIJ and HH (Fig. 4). At RIJ, the three-species and six-species mixtures both exceeded production of the monocultures (planned contrasts, three-species mix, $F_{1,33} = 9.03$, $p = 0.0053$; six-species mix, $F_{1,33} = 7.11$, $p = 0.0122$; Fig. 4d). At HH, the three-species mixture exceeded growth of the monocultures ($F_{1,32} = 18.33$, $p = 0.0002$), but the six-species mixture did not (Fig. 4a). At all sites, positive complementarity effects were nearly balanced by negative selection effects, and summed to small but positive net biodiversity effects in all but one case (Duke). Performance of species in mixtures frequently exceeded that predicted from monocultures (D_i , Fig. 4), especially *Hypnea* at HH and Duke, *Sargassum* at Duke, and *Dictyota* at RIJ. Calculations of RYT exceeded one at all sites but MM. Despite several indications of positive richness effects, transgressive overyielding was not detected at any site ($D_{max} < 0$).

Stability of algal community biomass

At the landscape scale, i.e. across all replicates of a composition at all field sites, stability of community biomass increased with species richness, as indicated by a 46% reduction in CV between one and six-species mixtures (Fig. 5a). Within sites, six-species assemblages were significantly less variable than the average monoculture (paired t-test, $n = 4$ sites, $p = 0.0138$; Fig. 5a), with three-species mixtures intermediate and also significantly less variable than monocultures (paired t-test, $p = 0.0403$). Negative covariance among species biomass responses in the six-species mixtures was evident at three of four sites (Fig. 5a). Population variability did not decline with species richness (CV of species in monoculture versus six-species mix; Fig. 5b).

Table 1. Light, temperature, flow, salinity, number of pinfish captured in seines, and total number of epifauna on algal mimics at each of the field experiment sites (HH = Hoophole, Duke = Duke Marine Laboratory dock, MM = Middle Marsh, RIJ = Radio Island Jetty) in mid-July 2005. Values are means (SE). Results of one-factor ANOVA by site are listed, with Tukey test results indicated by letters (means with the same letter do not differ).

Site	Light ($\mu\text{M E m}^{-2} \text{s}^{-1}$)	Temperature ($^{\circ}\text{C}$)	Flow (g lost 24 h^{-1})	Salinity (no units)	Pinfish (no. seine $^{-1}$)	Epifauna (no. mimic $^{-1}$)
HH	367 (141) ^a	28.3 (0.2) ^a	20.2 (0.2) ^b	31 (0) ^a	72 (39) ^b	129 (0) ^b
Duke	518 (153) ^a	29.7 (0.2) ^b	12.3 (1.7) ^a	35 (1) ^b	20 (14) ^{ab}	103 (8) ^b
MM	675 (97) ^a	28.8 (0.2) ^{ab}	14.4 (0.8) ^{ab}	32 (0) ^a	39 (17) ^{ab}	154 (38) ^b
RIJ	1531 (137) ^b	28.8 (0.2) ^{ab}	19.8 (3.0) ^{ab}	31 (0) ^a	1 (1) ^a	40 (1) ^a
DF	3, 8	3, 8	3, 12	3, 8	3, 8	3, 4
F	15.21	6.29	4.81	11.85	4.41	20.00
p	0.0011	0.0169	0.0201	0.0026	0.0415	0.0072

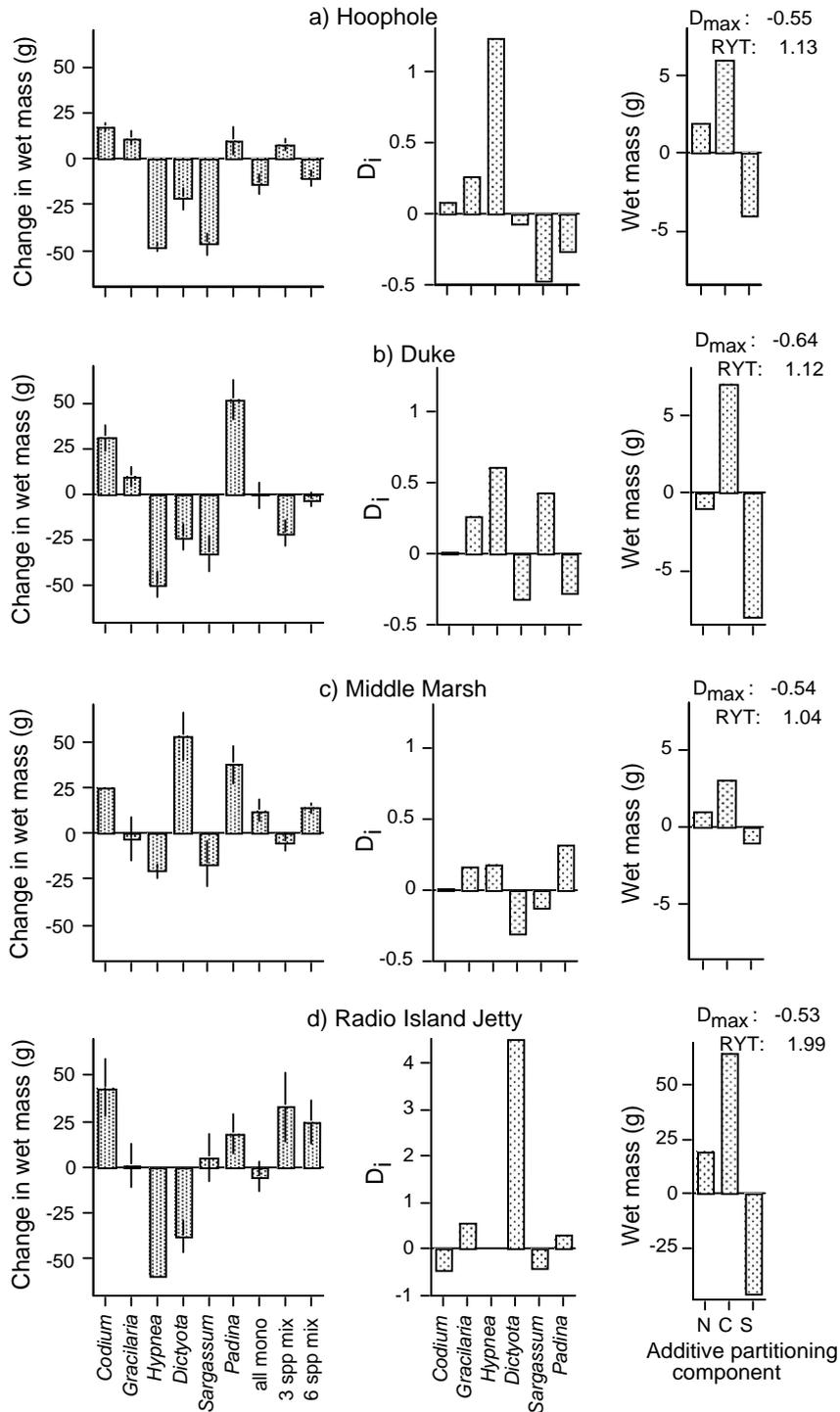


Figure 4. Left: change in algal wet mass at (a) Hoophole, (b) Duke, (c) Middle Marsh and (d) Radio Island Jetty. Values are means \pm 1 SE. Center: D_i , the deviation of each species' yield (as wet mass) in mixture relative to its yield in monoculture at each field site. Right: the net biodiversity effect (N) and its component complementarity (C) and selection (S) effects, D_{max} , and RYT (Methods) for algal wet mass in experiments at each field site. Note that *Hypnea* lost all biomass at Radio Island Jetty and is not included in center or right figures.

Discussion

To expand inferences possible from studies focused primarily on terrestrial grasslands and aquatic microbes, we used marine macroalgal communities to explore 1) the role

of environmental setting in the relationship between species richness and ecosystem function, and 2) the effects of species richness and environmental context on community stability.

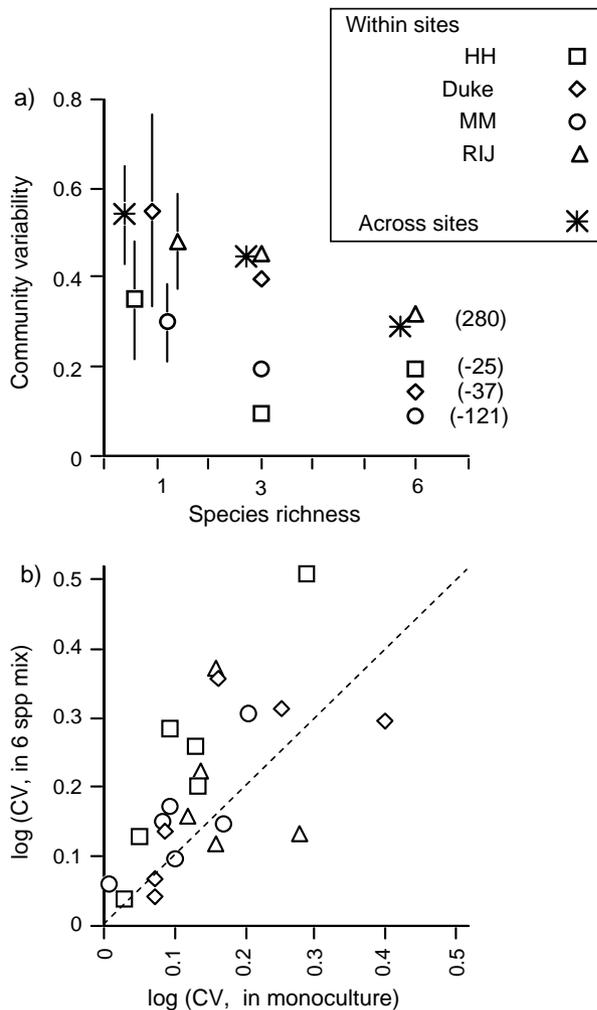


Figure 5. (a) Species richness effects on spatial community variability (as coefficient of variation, CV) of algal wet mass within the four field experiment sites (abbreviations as in Table 1), and across sites. Mean CV is shown for monocultures at each site and across sites ($n=6$). Summed covariances of species masses in the 6 species mixtures at each site are given in parentheses. (b) Population variability in one versus six-species compositions at the four field sites, with dotted line indicating 1:1 relationship.

Diversity–production relationships

Overall, our mesocosm and field experiments demonstrate that environmental context is very important to the relationship between species richness and biomass production in marine benthic macroalgal communities of North Carolina. Experiments using identical species assembled in different years and resource conditions, and across four field sites, found significant richness effects on biomass in four of eight experimental settings (2/4 in mesocosms and 2/4 in the field), according to planned contrasts. Theory and modeling predict such variation in patterns with environmental context (Cardinale et al. 2000, Fridley 2001), but few empirical studies have provided explicit tests that also explore the additive components of net biodiversity effects (Loreau and Hector 2001) under a range of environmental conditions (but see Fridley 2002, Zhang and Zhang 2006a). In our experiments, despite the range in responses to species richness

overall, decomposing diversity into its component effects yielded surprisingly consistent results. In seven out of eight experimental settings, complementarity effects were positive, and in all eight settings, selection effects were negative. The extent to which we found positive net biodiversity effects (six out of eight settings) depended on the degree to which negative selection effects balanced positive complementarity effects. Negative selection effects, resulting from slow-growing species performing better in mixture than in monoculture, were also common in our previous studies in this system (Bruno et al. 2005), and have now been found in a number of studies on terrestrial plants and freshwater microbes (Hector et al. 1999, 2002, Fridley 2002, Hooper and Dukes 2004, Cardinale et al. 2005, Zhang and Zhang 2006a). The accumulating evidence that negative selection effects are present or even common supports the need for quantitative evaluation of the components of biodiversity effects on production in future richness–production studies.

In our experimental system, complementarity could arise through facilitation by neighbors that increase structural support (Harley and Bertness 1996; also see Engelhardt and Ritchie 2001), leak nitrogen (Fong et al. 2003, Tyler et al. 2003), or increase turbulent flow, thereby increasing metabolite delivery and photosynthesis (Carpenter and Williams 1993, Cardinale et al. 2002), or perhaps complementary use of different forms of N (Bracken and Stachowicz 2006). In field settings, highly palatable species could gain protection from herbivory through close proximity to unpalatable or chemically defended species (Hay 1986, Pfister and Hay 1988), and buffering against high flows by neighbors could promote persistence of more delicate species. Several of these mechanisms could potentially lead to increased negative selection effects if the species benefited grew poorly in monoculture. For example, *Hypnea*, a very palatable species (Bruno et al. 2008), performed poorly in monocultures in all field settings but relatively better in mixture at three sites where herbivore density was high (HH, Duke and MM), and relatively delicate species had greatly improved performance in mixture at the two sites with highest flow velocities; i.e. *Hypnea* at HH and *Dictyota* at RIJ.

Environmental heterogeneity is predicted to enhance opportunity for complementary resource use, increasing richness effects over time (Pacala and Tilman 2002). This pattern has been supported by a number of studies (Tilman et al. 2001, Hooper and Dukes 2004, Cardinale et al. 2007, Stachowicz et al. 2008), although a recent experiment that explicitly tested this idea found that heterogeneity per se was not sufficient to generate richness effects (Weis et al. 2008). Marine macroalgae experience high degrees of environmental variation on daily and weekly cycles and with storms, upwelling, and pollution events; large fluctuations in species' biomass are common over short time periods (Hay and Sutherland 1988, Bruno et al. 2005). We found positive complementarity effects in seven out of eight experimental settings in just 2–3 weeks. It is certainly possible that complementarity effects would further increase over time in this system; however, we would be especially interested in how longer experimental periods influence the balance of positive complementarity versus negative selection effects.

As in several studies in grassland assemblages (Reich et al. 2001), increased resources enhanced the diversity–productivity relationship in our marine macroalgal assemblages; however, this effect was inconsistent across our two mesocosm experiments. Nutrient enrichment led to a positive effect of species richness on macroalgal growth in the first experiment, when ambient conditions did not. In the second experiment, despite a positive trend in richness effects with nutrient addition, enrichment somewhat weakened the strongly positive relationship found under ambient conditions. In fact, ambient nutrient conditions yielded very similar richness effects on algal growth in 2005 to those produced under nutrient-enriched conditions in 2004, including nearly identical RYT and contributions of complementarity and selection to net effects. Hence, while nutrients can be very important in driving positive diversity effects, these effects were also context specific, perhaps influenced by higher maximum temperatures in 2005 (12 days of water temperatures $\geq 30^{\circ}\text{C}$ for the period of 1 week before plus the experimental period) compared to 2004 (2 days = 30°C) (NOAA Beaufort monitoring station, <<http://tidesandcurrents.noaa.gov>>). High temperatures in 2005 could have led to decomposition of algal tissues and release of N (Hanisak 1993). Both *Ulva* and *Hypnea* followed the same general pattern of poor performance in ambient nutrient monocultures in 2005 (Fig. 2b), and much improved relative growth in mixtures (Fig. 3b, left); it is possible that greater biomass of these species in monocultures exacerbated negative effects of temperature, perhaps by trapping heated or poorly oxygenated waters (due to oxygen demand of decomposition) in layers of tissue. For both of these species, adding N seemed to ameliorate the stressful conditions experienced in monoculture, and both made relatively lower biomass contributions to mixtures than they did under ambient conditions.

Notably, our results do not support theoretical predictions that enhanced resources lead to dominance in mixture of high-yielding species in monoculture and thus increased positive selection effects (Grime 2001, Aarssen et al. 2003). In our experiments, complementarity was strongly positive and selection effects were negative in both years regardless of nutrient enrichment. In a test of three levels of soil nutrients on experimental plantings in an old field, Fridley (2002) found increased positive selection effects in intermediate compared to low nutrient conditions but no clear evidence that fertility promoted positive selection effects across all three levels. In microbial mesocosms, Zhang and Zhang (2006a) found that negative selection effects became more negative with nutrient enrichment. Thus experiments that quantitatively assessed components of diversity effects in three very different systems did not confirm theory and caution that where resources enhance richness effects, positive selection effects should not be assumed.

Biomass accumulation as a proxy for primary production commonly serves as the ecosystem ‘function’ in tests of plant diversity effects, with the assumption that other important processes are correlated; however, few studies have tested this idea by assessing multiple response variables. In our mesocosm experiments, we measured several alternate response variables, which were highly sensitive to changes in nutrient supply but, unlike growth, were not sensitive to species richness. However, species

varied in the magnitude and sign of responses across the range of measures in our mesocosm experiments (Fig. 2), suggesting that a ‘multi-functionality’ of ecosystem services could result from enhanced species richness (Duffy et al. 2003, Bracken and Stachowicz 2006, Hector and Bagchi 2007, Gamfeldt et al. 2008).

Diversity/stability relationships

Species richness led to enhanced spatial stability of community biomass at a landscape scale, i.e. across the 20 km spanned by our four field experiment sites. Different functional responses to environmental conditions among species, as were evident in our experiments, could promote stabilization of aggregate community biomass over space due to the increased probability that some species will contribute biomass regardless of the conditions at a particular location, an idea that is usually applied in the context of temporal variability (the insurance hypothesis; Yachi and Loreau 1999). Within a particular environmental setting, effects of species richness on spatial stability of community biomass were overall positive, with several possible mechanisms at work. Negative covariance of species’ biomasses in the six-species mixtures in some settings was suggestive of insurance effects (Lehman and Tilman 2000), while overyielding may have also led to declines in variation (Tilman 1999) in settings where it was found. It is also possible that averaging of fluctuations in species abundances over space reduced variability in community biomass of more diverse assemblages (‘portfolio effect’; Doak et al. 1998, Tilman et al. 1998); however, final biomass in our species mixtures lacked the evenness needed to test this model (Cottingham et al. 2001). While community stability was enhanced by species richness, stability of component populations did not increase with increased species richness (Fig. 5b), in concert with theory and most other studies with primary producers (Cottingham et al. 2001, van Ruijven and Berendse 2007, but see Valone and Hoffman 2003).

Studies that have explicitly evaluated spatial stability of aggregate community properties have found support for positive relationships with species richness in freshwater microbial microcosms (Fukami et al. 2001, Morin and McGrady-Steed 2004), although less so in terrestrial grasslands (positive relationship with functional diversity but not species richness; Weigelt et al. 2008). In marine systems, we know of two other studies that have examined species richness effects on stability of marine producers, both focused on temporal stability. Allison (2004) found decreased temporal stability, as resistance to heat stress, in more diverse rocky shore algal communities, due to greater biomass before heat treatments; however, diverse assemblages were more resilient to heat stress (recovered faster). In another study, microalgal biomass accumulation was more stable over time in high than low richness treatments regardless of sediment type or temperature (Watermann et al. 1999 as reanalyzed by Worm et al. 2006). The role of species richness in spatial community stability deserves further study in marine systems (Stachowicz et al. 2007) as well as others.

Conclusions

Our experimental manipulations of benthic macroalgal communities in North Carolina showed that 1) environmental context strongly influences the relationship between species richness and production, resulting in positive richness effects (according to planned contrasts) in half (four of eight) of our tests in mesocosm and field experiments, 2) negative selection effects were pervasive and frequently balanced positive complementarity effects, 3) nutrients can strengthen richness effects on algal growth, but these effects also appear to be context specific, and 4) spatial stability of algal communities increased with species richness within and across the variation in our four field experiment locations. Our results are in agreement with a recent review finding transgressive overyielding to be uncommon across many ecosystem types, but do not support the assertion that positive selection effects may commonly drive species richness effects (Cardinale et al. 2006); in fact, in the thirteen separate experimental tests in this system for which we have decomposed net biodiversity effects, we have yet to find positive selection effects (this study, Bruno et al. 2005). As a number of recent studies have found similar results (Hector et al. 2002, Hooper and Dukes 2004), there is a need for additional study to quantify the components of the net biodiversity effect (Loreau and Hector 2001) before consensus is possible.

Studies to date in marine systems suggest that species richness effects on aggregate producer biomass are present but subtle and inconsistent over time and space; approximately half (9/17) of the richness contrasts possible from studies in North Carolina and Jamaica exhibited positive richness effects (this study, Bruno et al. 2005, 2006, 2008). While experiments in marine producer communities in other regions are needed, studies so far suggest that diversity may have less influence on primary production in marine systems compared with terrestrial and freshwater systems (Cardinale et al. 2006). However, the stabilizing effect of species richness on community biomass across the field sites in our study suggests that stability may be more strongly influenced by species richness than is production, at least over short time scales. Whether this is a distinction relative to other ecosystem types (Balvanera et al. 2006) will require additional work in other marine settings. We conclude that overall values of biodiversity are considerable when more functions of the ecosystem are considered (Duffy et al. 2003, Hector and Bagchi 2007, Gamfeldt et al. 2008); e.g. both productivity and spatial stability.

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