LETTER

Effects of macroalgal species identity and richness on primary production in benthic marine communities

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Abstract

Plant biodiversity can enhance primary production in terrestrial ecosystems, but biodiversity effects are largely unstudied in the ocean. We conducted a series of field and mesocosm experiments to measure the relative effects of macroalgal identity and richness on primary productivity (net photosynthetic rate) and biomass accumulation in hard substratum subtidal communities in North Carolina, USA. Algal identity consistently and strongly affected production; species richness effects, although often significant, were subtle. Partitioning of the net biodiversity effect indicated that complementarity effects were always positive and species were usually more productive in mixtures than in monoculture. Surprisingly, slow growing species performed relatively better in the most diverse treatments than the most productive species, thus selection effects were consistently negative. Our results suggest that several basic mechanisms underlying terrestrial plant biodiversity effects also operate in algal-based marine ecosystems, and thus may be general.

INTRODUCTION

Dramatic, ongoing changes in the earth's biodiversity have generated great interest in the influence of genetic, species and functional group diversity on ecosystem properties and services (Hooper *et al.* 2005). Habitat degradation and fragmentation, overexploitation and other factors have reduced species richness at large spatial scales (Pimm *et al.* 1995; Rosenzweig 2001). Yet in some systems regional and local species richness has increased significantly because of recent colonizations by exotic plants, animals and microbes (Gido & Brown 1999; Rosenzweig 2001; Sax & Gaines 2003). Such changes in biological communities are expected to have profound impacts on ecosystems and the services they provide to human societies (Hooper *et al.* 2005). To date, nearly all empirical research linking biodiversity and ecosystem functioning has focused on terrestrial plant communities (primarily grasslands) and model freshwater microbial systems (Hooper *et al.* 2005). Therefore, our ability to make any generalizations about biodiversity effects is quite limited (Giller *et al.* 2004). Research in this field in marine ecosystems is especially sparse (Emmerson &

Huxham 2002; Hooper *et al.* 2005); only a single study of the effects of intertidal macroalgal diversity has been published (Allison 2004) and the many potential linkages between subtidal marine plant diversity and ecosystem properties have not been investigated directly. Furthermore, currently we know little about the relative importance of species composition and diversity and the magnitude and direction of the selection and complementarity effects through which biodiversity can influence ecosystem properties (Hooper *et al.* 2005).

Here, we report the results of a series of experiments designed to measure the relative effects of macroalgal identity and richness on primary productivity measured as net photosynthetic rate and net biomass accumulation in shallow, subtidal marine habitats in coastal North Carolina. We conducted similar experimental manipulations in outdoor mesocosms and in the field during three seasons and at two sites. To explore the mechanisms mediating community-level primary production, we partitioned the net effect of biodiversity into components reflecting complementarity among species and the selection effect using the 'additive partitioning equation' of Loreau & Hector (2001). Selection

effects are more general than sampling effects and can be either positive or negative. In contrast, the 'sampling effect hypothesis' is restricted to positive effects on production and other ecosystem functions and assumes that the most productive species dominate species mixtures (Hector *et al.* 2002). Negative selection effects occur when slow growing species (as measured in monoculture) perform relatively better in polycultures than expected and are not competitively inferior (Hector *et al.* 2002). For example, negative selection effects could be driven by an inherent trade off between fast growth or palatability and competitive ability or reproductive output (Grime 2001; Hooper & Dukes 2004). Complementarity results from among-species differences in traits such as resource use, morphology or stress tolerance and is manifested as niche partitioning or facilitation that can enhance production (Loreau & Hector 2001; Petchey 2003). Our overall results contradict established paradigms based on earlier grassland experiments, but are remarkably similar to those from a number of more recent studies in terrestrial, freshwater wetland and salt marsh plant communities and could reflect a general relationship between plant biodiversity and ecosystem functioning.

METHODS

We conducted six independent experiments between May 2003 and August 2004. In three outdoor mesocosm experiments and two field experiments we measured algal biomass accumulation in the absence of herbivores as a proxy for primary production (Tilman *et al.* 2001). In the sixth experiment productivity was measured as net daytime photosynthetic rate using an oxygen sensor. Standing plant biomass can be a poor indicator of primary production, especially in aquatic algal-based systems. This is because grazing is generally intense in marine communities (Cyr & Face 1993), which can remove most algal biomass yet maximize primary production by reducing resource limitation (Carpenter 1986). Post-production tissue loss from senescence and physical disturbance can also complicate the relationship between plant biomass and primary production, especially in high-energy aquatic systems. Our experiments minimized problems associated with tissue loss from herbivory, senescence and disturbance by confining algae within mesocosms or within mesh enclosures in the field. Standing macroalgal biomass is also a measure of habitat provision and quality: like plants in terrestrial ecosystems, macroalgae fill the role of foundation species (Dayton 1972; Bruno *et al.* 2003) in many benthic marine habitats, providing the physical framework that hundreds of other species inhabit (Edgar 1990; Hacker & Steneck 1990; Taylor & Cole 1994). The size and complexity of plant-generated habitats are usually positively and causally related to the density and diversity of associated species (Heck & Orth 1980; Bruno & Bertness 2001).

Each of the six experiments included four to nine algal species in monoculture and a complete mixture of all species (*n* = 10 replicates/treatment). Four of the six experiments also included intermediate levels of species richness achieved by randomly selecting a subset of the experimental species pool (i.e. the composition of each replicate of an intermediate diversity treatment was randomly and independently determined; *n* = 10 for each richness level). This design enabled us to: (i) partition the relative effects of species identity and richness (Loreau 1998); (ii) partition the net effect of biodiversity into component complementarity and selection effects (Loreau & Hector 2001); (iii) rigorously detect both transgressive and non-transgressive over-yielding (Fridley 2001); and (iv) estimate the shape of detected relationships between richness and production. We included macroalgae from each of the three major divisions (Rhodophyta, Phaeophyta and Chlorophyta) in all experiments and used species that were most abundant in shallow subtidal hard substratum environments near Morehead City and Beaufort, North Carolina at the time of each experiment. We created experimental macroalgal assemblages by attaching thalli to 25 × 25 cm Vexar plastic mesh screens (5-mm openings). Algae were attached by the base of the stipe (or at the holdfast) using a cable tie such that the thalli floated upward in a natural orientation. Polyculture screens included two or three thalli of each species, the positions of which were determined haphazardly. Unlike most similar terrestrial plant experiments, our experiments started with adult plants at natural densities rather than with seedlings or sparsely planted juveniles. We measured the percent change in algal wet mass in the absence of herbivores to assess net algal biomass production. Wet weights were determined after removing excess water from the algae using a salad spinner (60 revolutions). Initial algal wet mass on each replicate screen in the six experiments ranged from 36 to 120 g, but was the same for all treatments within a given experiment (i.e. a replacement design) and for each species within a given polyculture treatment. Final biomass measurements included algal fragments that had broken off from the screen or parent plant yet remained in the mesocosm. Mesograzers (e.g. amphipods and isopods) were removed by placing the screens and attached algae in a bath of dilute pesticide (1-napthyl *n*-methyl-carbamate, Sevin) with several rinses to remove pesticide residue (as in Carpenter 1986; Duffy & Hay 2000).

The field and mesocosm experiments were terminated when significant growth was observable for at least half the species. If a species was lost entirely from an experiment within the first few days, we omitted from analysis the monoculture treatment for that species and also subtracted its mass from the initial mass of the mixture treatment(s). In

Table 1 Results of the macroalgal surveys at four sites in 2004

Site (month)	Richness	Biomass (g)	Dominant species
BFD (May)	2.2 (1, 3)	33.3 (0.1, 66.6)	*Hypnea musciformis, Polysiphonia harveyi*
MCFD (May)	2.5 (2, 4)	49.0 (23.4, 98.3)	*P. harveyi, H. musciformis*
CL (May)	4.4 (3, 6)	54.4 (8.1, 108.8)	*Sargassum filipendula, Gracilaria tikvahiae*
RIJ (May)	4.0 (2, 7)	160.75 (60.5, 806.3)	*Codium fragile, S. filipendula*
BFD (June)	2.8 (1, 4)	72.4 (4.9, 261.9)	*C. fragile, G. tikvahiae*
MCFD (June)	2.5 (1, 3)	20.3 (5.2, 40.7)	*H. musciformis, P. harveyi*
CL (June)	1.5 (0, 4)	106.4 (0, 387.4)	*S. filipendula*
RIJ (June)	3.4 (1, 6)	165. 2 (28.0, 545.2)	*C. fragile, S. filipendula*

Values are means ($n = 15$) with the minimum and maximum recorded values in parentheses. BFD, the Beaufort floating docks; MCFD, Morehead City floating docks; CL, Cape Lookout; RIJ, Radio Island Jetty.

the two experiments in which this occurred, losses were largely due to methodological constraints; i.e. *Polysiphonia harveyi* in mesocosm experiment I was very fragile and quickly disintegrated after handling, and *Hypnea* and *Dictyota* in field experiment II could not be attached tightly enough with cable ties to avoid losses due to currents and boat wakes without causing tissue damage or self-shading. Although these experiments were of relatively short duration (2.5–5 weeks) compared with similar experiments in terrestrial plant systems, the duration was appropriate for these macroalgal assemblages, in which maturation, senescence and compositional turnover often occur over weeks (Table 1). Furthermore, accurately measuring algal biomass production over longer periods (i.e. months to years) in the field is exceedingly difficult because of natural senescence, herbivory and physical disturbances that remove algal tissue. A compensating advantage of the rapid succession in this system is that it allowed us to conduct multiple experiments with similar suites of algae under different conditions, and thus assess the generality of biodiversity effects.

Mesocosm experiments

Experimental algal assemblages were maintained in outdoor, flow-through seawater mesocosms at The University of North Carolina's Institute of Marine Sciences in Morehead City, North Carolina, USA. The mesocosms were clear plastic aquaria (60 L in mesocosm experiment I and 30 L in mesocosm experiments II and III) that were placed in shallow tables (6 per table in mesocosm experiment I and 20 per table in mesocosm experiments II and III). Dump buckets placed above the mesocosms gradually filled with seawater, periodically emptying into the mesocosms below (*c.* 1 dump per min). The dumping action aerated the water and approximated the turbulence of local rocky substratum environments (Duffy & Hay 2000). Light, temperature and salinity in the mesocosms were very similar to field conditions (unpublished data). Seawater was pumped continuously from the adjacent Bogue Sound and filtered through a gravel filter and 100-μm mesh nylon filter bags to prevent herbivore colonization. The experimental screens with attached algae were placed in the mesocosms (one screen each) 30 cm below the water's surface. The mesocosms were originally randomly assigned to tables and positions, and were then rearranged every 5 days to reduce position effects. Mesocosm experiments were performed in the spring, summer and fall so that we could test the generality of the results across seasons and a temporal gradient of environmental conditions (light, temperature and nutrient concentrations all vary seasonally) and to determine whether species relative yields varied throughout the year (timing and initial algal wet mass of each experiment: I, 7 May 2003 to 10 June 2003 and 60 g; II, 1 July 2003 to 28 July 2003 and 90 g; III, 5 October 2003 to 22 October 2003 and 36 g).

Field experiments

We performed one field experiment at each of two sites: (I) on the floating docks at Duke University's Marine Laboratory on Pivers Island, North Carolina (16 July 2003 to 6 August 2003, initial algal wet mass = 42 g) and (II) 1 km to the SW, adjacent to Radio Island Jetty (RIJ), Radio Island, North Carolina (14 August 2003 to 4 September 2003, initial algal wet mass is 48 g). Both are estuarine sites with low wave energy and high current velocity, < 1 km from Beaufort Inlet. A majority of the algae for all six experiments were collected from these sites. Screens in the field experiments were fastened to the bottoms of polyvinyl chloride (PVC) enclosures covered with a double layer of transparent monofilament mesh (1-cm openings) to limit access by herbivores and tissue loss while minimizing reductions of light and flow. Each enclosure was $60 \times 30 \times 25$ cm (l, w, h), with a mesh divider at the midpoint of the longest dimension, so that two experimental units could be inserted per enclosure. For field experiment I, enclosures were attached to floating docks, 1 m below the

water's surface regardless of tidal elevation. In field experiment II at Radio Island, enclosures were attached to PVC racks in a randomized complete block design and anchored with concrete blocks on sandy substrata adjacent to a rock jetty. At Radio Island the depth of the algal screens ranged from 1 to 3 m during a tidal cycle. To limit the immigration of mesograzers, pesticide applications were repeated every 2–3 days by removing whole enclosures from the water and dipping them into the pesticide bath.

Photosynthesis measurements

We measured net photosynthesis as the rate of daytime oxygen production in outdoor 34 L sealed glass aquaria using a Foxy fibre optic oxygen sensor (Ocean Optics). Photosynthesis measurements were made in filtered seawater 24 h after the algae were collected using macroalgae attached to screens as in the field and mesocosm experiments. We ran one replicate of each treatment (eight monocultures and polycultures of four and eight species; total algal biomass per replicate was always 120 g and was the same for each species in polycultures) and one control with no algae in the aquarium on each of 10 relatively cloudless days in August 2004 and continued each run until oxygen concentration increased by 10% (usually 15–25 min). We monitored light and temperature inside the aquaria with a Li-Cor underwater quantum sensor and StowAway Tidbit waterproof temperature loggers. Water movement inside the aquaria was generated with two 120 GPH powerheads. Horizontal free stream flow averaged 5.5 ± 0.4 cm s^{-1} (range: 0.1–26.7 cm s^{-1}; measured with a SonTek Acoustic Doppler Velocimeter).

Statistical analysis

We tested the relationship between algal diversity and biomass production in two ways. First, for each experiment we conducted a separate one-factor ANOVA on the log-transformed change in mass (and change in oxygen concentration in the photosynthesis experiment), including all monocultures and the most diverse polyculture (which contained all the species grown in monoculture). The treatment sum of squares was partitioned into an *a priori* contrast (richness effect) between the highest-diversity mixture and the monoculture treatments (d.f. = 1) as in Duffy *et al.* (2005). The residual SS is then attributable to variance among the monocultures and constitutes a test of the effect of species identity (identity effect). Both effects were tested using the error MS from the ANOVA as the denominator in the *F*-test. We calculated the magnitude of effects (ω^2, the relative contribution expressed as the percentage of the total variance) for the algal identity and richness effects (Kirk 1995; Graham & Edwards 2001). The

second test of algal diversity effects on production incorporated data from the five experiments that measured algal biomass growth into a single comparison using a meta-analysis. For each experiment, we calculated the mean and SD of percent change in biomass for the pooled monoculture treatments and for the highest richness mixture. We then calculated the effect size as Hedges' *d* to compare the mixture and monoculture mean values for a given experiment. The mean and 95% CI of the effect size across the five experiments was calculated, with values from individual experiments weighted by their SD and sample size, using Meta-Win 2.0.

For each growth experiment we calculated 'relative yield totals' (RYT) (Fridley 2001) and D_{max} (Loreau 1998) as conservative tests of non-transgressive and transgressive over-yielding respectively. In a replacement design such as ours, where initial biomass or density is held constant across treatments, non-transgressive overyielding occurs when the mixture performance is greater than that of the average monoculture, i.e. RYT > 1 (Fridley 2001). In contrast, transgressive over-yielding occurs when the mixture yield is greater than that of any monoculture ($D_{max} > 0$).

## Algal biomass and diversity field surveys

We quantified natural patterns of macroalgal richness and biomass at four sites during the summer of 2004. One site was a subtidal artificial jetty at Cape Lookout, North Carolina, on the ocean side of Core Banks (a barrier island). The other three sites were in the Bogue Sound estuary: (i) RIJ; (ii) the Morehead City floating docks; and (iii) the Beaufort floating docks. Using SCUBA all four sites were sampled in May and June 2004. At each site we placed a 25×25-cm quadrat (0.0625 m^2, the size of the algal communities in the field and mesocosm experiments) at 15 random positions along a transect at 1-m depth. All macroalgae was removed from each quadrat and identified and weighed later the same day in the laboratory.

RESULTS

We found 24 species of macroalgae in the eight combined surveys (Table 1). In general the two rocky subtidal sites were dominated by one brown (*Sargassum filipendula*) and one green (*Codium fragile*) alga and the two floating dock sites were dominated by three red (*Hypnea musciformis*, *P. harveyi* and *Gracilaria tikvahiae*) and one green species (*C. fragile*). Overall wet macroalgal biomass averaged 87 g per 0.0625 m^2 (pooled across all eight site/month combinations) and varied significantly among sites but not months (ANOVA results on log transformed data: site $F = 11.94$, d.f. = 3, 100, $P < 0.0001$; month $F = 0.02$, d.f. = 1, 100,

$P = 0.88$; site × month $F = 2.96$, d.f. = 3, 100, $P = 0.035$). Species richness ranged from 1 to 7, averaged three species/quadrat and varied among both sites and months (ANOVA results: site $F = 8.59$, d.f. = 3, 100, $P < 0.0001$; month $F = 13.57$, d.f. = 1, 100, $P = 0.0004$; site × month $F = 15.49$, d.f. = 3, 100, $P < 0.0001$).

When experiments were analysed separately, algal species richness significantly enhanced biomass accumulation in three of the five growth experiments (Figs 1 and 2, Table 2). When all five growth experiments were considered together in a meta-analysis, species richness again significantly enhanced algal biomass (mean effect size = 0.4799, 95% CI = 0.032–0.93). Thus, our experiments revealed an overall positive effect of species richness on algal community biomass production. Nevertheless, in four of the five growth
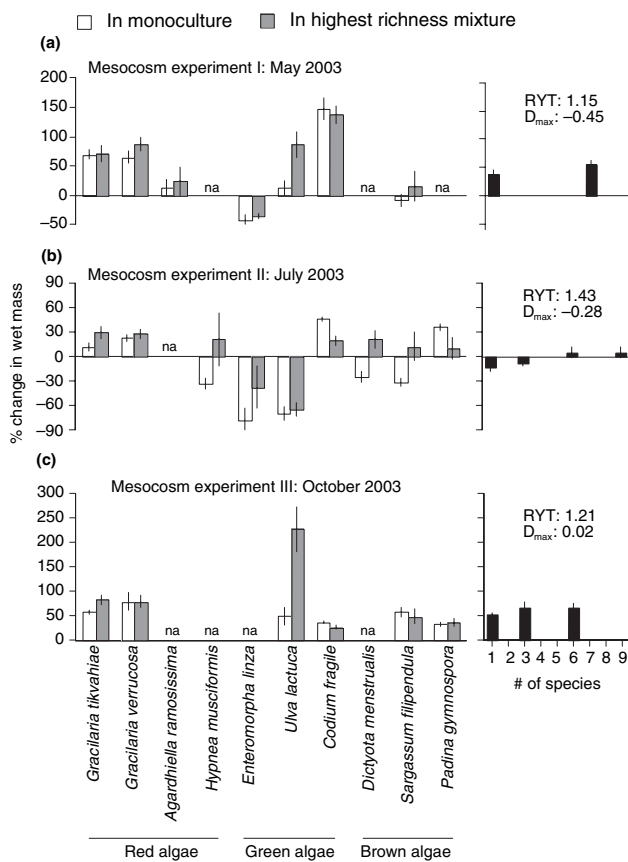
Figure 1 Effects of algal species identity and richness on macroalgal growth rates (i.e. net primary production) in the three mesocosm experiments. Species not used in an experiment are indicated by 'na'. Values are mean ± 1 SE. Sample size is 10 for all treatments and the average monoculture (the one-species treatment in right-hand panels) was calculated as the pooled mean of all monoculture replicates. Note that scales on the y-axis differ. RYT, relative yield total. See Table 2 for statistical analyses.
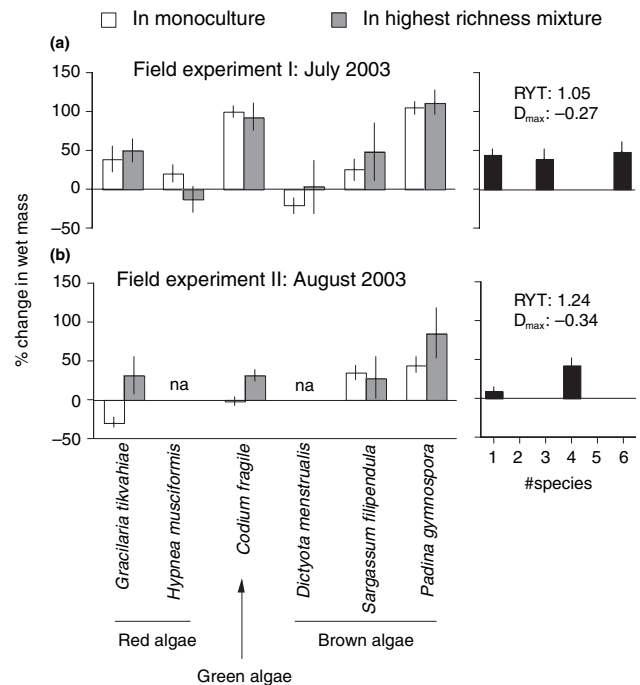
Figure 2 Effects of algal species identity and richness on macroalgal growth rates (i.e. net primary production) in the two field experiments. Species not used in an experiment are indicated by 'na'. Values are mean ± 1 SE. Sample size is 10 for all treatments and the average monoculture (the one-species treatment with black bars) was calculated as the pooled mean of all monoculture replicates. RYT, relative yield total. See Table 2 for statistical analyses.

experiments algal identity influenced biomass accumulation much more strongly than species richness (Figs 1 and 2). Algal identity explained 7–76% of the variation in biomass accumulation across the six experiments, whereas algal richness never explained more than 9% (Table 2). Thus, we found that the effect of algal species richness on biomass accumulation was statistically significant but usually considerably weaker than the dominant influence of species identity. Algal community productivity measured as O_2 production also varied considerably with species identity but was not affected by algal species richness (Fig. 3, Table 2). During the experiment, light averaged 856.2 ± 14.7 μE and temperature averaged 29.0 ± 0.16 °C and neither significantly affected photosynthesis (linear regression: light $P = 0.06$; temperature $P = 0.80$) or varied among treatments (ANOVA: light $P = 0.52$, temperature $P = 0.98$).

Partitioning of the net biodiversity effect (Loreau & Hector 2001) revealed that both complementarity and selection effects influenced biomass production in diverse algal mixtures (Fig. 4a). Surprisingly, selection effects (Loreau & Hector 2001) were negative in four of five

Table 2 Results of statistical analyses of the six algal diversity experiments

	SS	d.f.	*F*	*P*	ω^2
Mesocosm experiment I					
Identity effect	235 572	6	29.0	< 0.001	0.68
Richness effect	2973	1	2.2	0.140	0.00
Mesocosm experiment II					
Identity effect	157 509	8	43.0	< 0.001	0.76
Richness effect	2906	1	6.3	0.014	0.01
Mesocosm experiment III					
Identity effect	13 982	5	2.2	< 0.100	0.07
Richness effect	8374	1	6.5	0.014	0.07
Field experiment I					
Identity effect	117 294	5	17.0	< 0.001	0.55
Richness effect	119	1	0.1	0.770	0.00
Field experiment II					
Identity effect	32 869	3	20.8	< 0.001	0.53
Richness effect	5987	1	11.3	0.002	0.09
Photosynthesis experiment					
Identity effect	80	7	4.9	< 0.001	0.28
Richness effect	0	1	0.1	0.780	0.00

Richness and identity effects were tested with orthogonal planned contrasts. The block factor in field experiment II was not significant, $P = 0.82$, and was not included in the final analyses. Effect sizes were estimated as ω^2 (Kirk 1995), with negative estimates reported as zero.

experiments (and zero in the other). In contrast, complementarity effects were positive in all experiments, and were usually larger than selection effects. These positive complementarity effects reflect a strong trend towards comparable or better performance in mixture than in monoculture
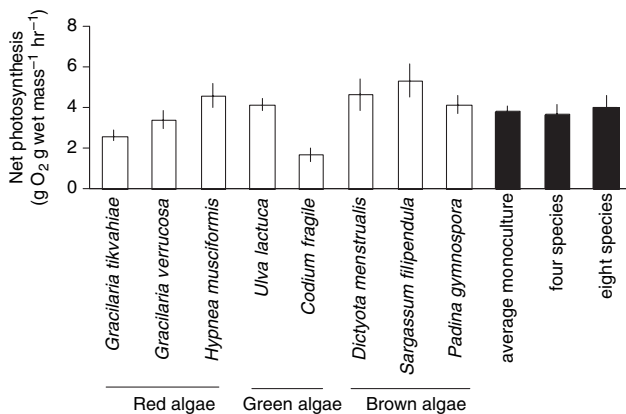
Figure 3 Effects of algal species identity and richness on net photosynthesis (primary productivity). Values are mean ± 1 SE. Sample size is 10 for all monoculture and mixture treatments and 80 for the average monoculture, calculated as the mean of all monoculture replicates. See Table 2 for statistical analyses.

for most species across all experiments (Figs 1, 2 and 4). While both slow and fast growing species were generally more productive in polycultures, the performance enhancement was significantly greater for the slower growing species (Fig. 4b). As a consequence – and despite the very strong positive relationship between the performance of a species in monoculture and its performance in the most diverse mixtures (Fig. 4c) – the most productive species constituted only 14–32% of the final mixture biomass, failing to outcompete the lowest yielding species (Fig. 4d).

DISCUSSION

There are a number of obvious and fundamental differences between benthic marine algal communities and terrestrial plant communities (Carr *et al.* 2003; Giller *et al.* 2004). For example, macroalgae, unlike plants, do not have roots and usually live on hard substratum thereby removing the potential for belowground interspecific interactions that are known to be important in driving some terrestrial plant diversity effects (Tilman *et al.* 2001; Hooper *et al.* 2005). Furthermore, in most benthic marine communities, the physical forcing of resource delivery via currents and the high resource flux compared with terrestrial habitats reduces the potential for the partitioning of nutrients and other limiting resources. Despite these and many other differences our results are largely concordant with recent work in terrestrial ecosystems (Fridley 2002; Hector *et al.* 2002; Hooper & Dukes 2004), possibly reflecting a general relationship between plant biodiversity and ecosystem functioning.

Species identity had a striking effect on macroalgal production, explaining up to 76% of the variance within experiments. This pattern and specific algal growth rates were concordant between the mesocosm and field experiments. Production also varied among species in the short-term photosynthesis experiment, although growth and photosynthesis rankings differed as some fast-growing species (e.g. *C. fragile*) had relatively low net photosynthetic rates. But overall, species identity appears to be much more important than species richness in controlling primary biomass production in this benthic marine community. These results were the same for the intermediate and highest richness treatments. The dominance of species identity reflects the large variance in growth rate among species, which in some experiments varied fivefold. Additionally, some of the fastest growing species were significantly more productive than polycultures of up to nine species (e.g. *Gracilaria* and *Padina*). Most previous experimental tests of the plant biodiversity–productivity hypothesis in grassland and wetland communities show, as our experiment do, that species and functional group composition play a much larger role in controlling ecosystem processes than diversity (Hector *et al.* 1999; Loreau 2000; Downing & Leibold 2002;

Figure 4 (a) The net biodiversity effect and its component complementarity and selection effects for each experiment [based on the additive partitioning equation of Loreau & Hector (2001)]. (b–d) Relationships between the performance (% change in wet biomass) of a species in monoculture and; (b) relative performance in polyculture (polyculture per cent growth − monoculture per cent growth), (c) performance in polyculture, and (d) proportion of the total final polyculture biomass (i.e. dominance). The dashed line in (b) and (c) is the 1 : 1 growth function; points above this line are cases where species grew faster in mixture. Data in (b–d) are pooled from the five growth experiments ($n = 32$) and included only the most diverse polycultures; each point represents mean ($n = 10$) performance of a given species in a given experiment. Statistical values are from linear regression analysis. The polyculture growth of *Ulva* in mesocosm experiment 3 (Fig. 1c) was a statistical outlier (Grubb's outlier test $P < 0.005$) and was removed from the analyses in (b) and (c).
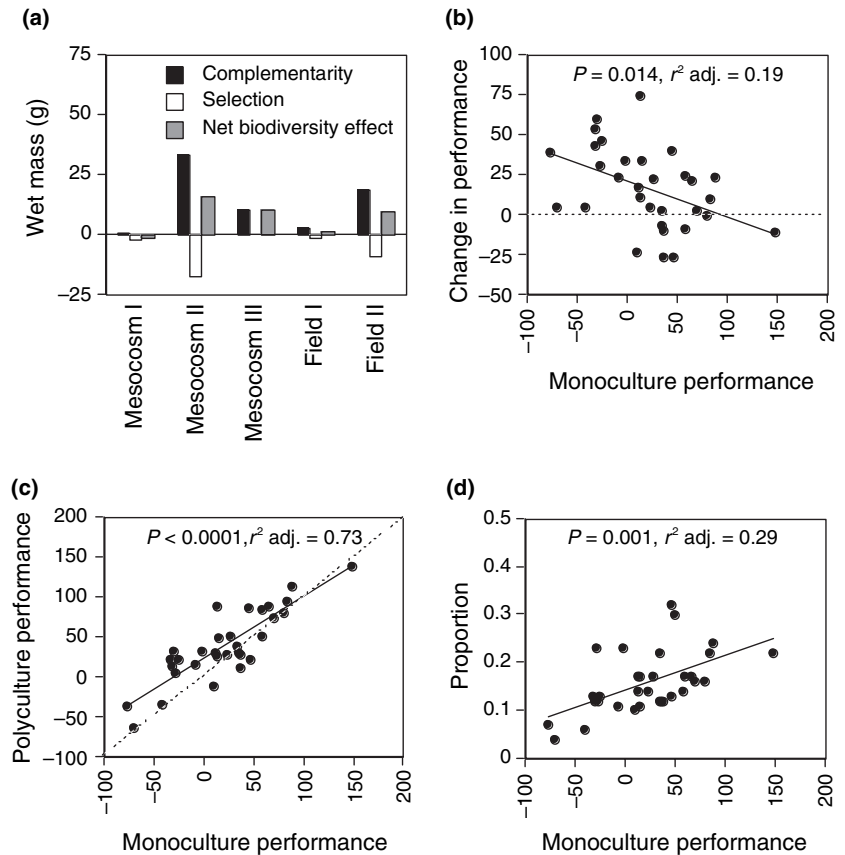
Fridley 2002; Callaway *et al*. 2003). In fact, many recent experiments have failed to find strong or consistent plant diversity effects on productivity (Engelhardt & Ritchie 2002; Hector *et al*. 2002; Hooper & Dukes 2004; Downing 2005; Hooper *et al*. 2005) and transgressive over-yielding appears to be fairly uncommon and usually relatively weak (Fridley 2002; Hector *et al*. 2002; Hooper & Dukes 2004; Hooper *et al*. 2005). In our experiments it is possible that richness effects could have been greater if herbivores were included as consumers (e.g. fishes, urchins and amphipods) strongly influence algal biomass and community composition in this system (Duffy & Hay 2000). The facilitation of neighbours by chemically defended species could also enhance the biomass of polycultures in comparison with monocultures of palatable species, e.g. *Enteromorpha*, in the presence of herbivores (Hay 1986; Pfister & Hay 1988).

Although the effect size of richness was always small and transgressive over-yielding occurred in only one experiment, several lines of evidence indicate that species richness did enhance production in the five growth experiments. First, a meta-analysis indicated a significant overall effect of species richness on macroalgal biomass production. Second, in 24 of the 32 species/experiment combinations, biomass production was greater in mixture than in monoculture, by an average of 34% (SE = 7.4). Additionally, the RYT averaged 1.21 and was > 1 in all five growth experiments (and was 1.43 in mesocosm experiment II) indicating that, on average, species performed better in mixtures of four to nine species than in monocultures. Third, complementarity effects and net biodiversity effects were always positive (Fig. 4a), reflecting the generally enhanced performance of most species in polycultures (Loreau & Hector 2001). We suspect that these richness effects were caused by facilitation. For example, neighbouring species could provide structural support (Harley and Bertness 1996). Increased algal richness and complexity could also increase turbulent flow and reduce the diffusive boundary layer, thereby maximizing metabolite delivery and photosynthesis (Carpenter & Williams 1993; Cardinale *et al*. 2002). Additionally, the presence of species that readily uptake nutrient pulses (e.g. *Enteromorpha* spp.) could enhance nutrient pools in species mixtures by releasing nitrogen (Fong *et al*. 2003; Tyler *et al*. 2003), potentially augmenting the supply to neighbouring species.

Production may be related to species diversity not only because of resource partitioning and facilitation (i.e.

complementarity), but also because diverse assemblages are more likely to contain a high-performing species (selection). Selection effects were weaker than complementarity effects and were also negative in four of the growth experiments and zero in the fifth experiment (Fig. 4a). The consistently negative selection effects we found are somewhat surprising and were caused by the relatively higher yield of slow growing species in polycultures. The slower growing species are clearly not competitively inferior and were more productive in the presence of the faster growing species. These results may reflect intrinsic tradeoffs between fast growth and competitive ability, reproductive output or other life history features in marine algal communities, complicating generalizations about the role of the selection effect (Steneck & Dethier 1994; Grime 2001; Hector *et al.* 2002).

Our results are very similar to those of the large-scale Biodepth experiment in European grasslands (Hector *et al.* 2002), in which plant species that were most productive in monoculture did not dominate polycultures (usually constituting < 50% of mixture biomass) and selection effects were generally weak and often negative (Loreau & Hector 2001), averaging 0.2 (across sites and treatments). Likewise, Hooper & Dukes (2004) found that plant functional group selection effects were strongly negative (the mean across years and richness treatments was − 44.7). In our experiments, and in both of these terrestrial plant experiments, negative selection effects reduced the net positive effect of richness, supporting the idea that different mechanistic effects of biodiversity can counteract each other, sometimes leading to weak net effects (Loreau & Hector 2001; Hooper & Dukes 2004). The concordance of these results from both terrestrial and aquatic systems is somewhat surprising given the common view that the selection effect is one of the dominant mechanisms driving *positive* plant diversity–production relationships (Huston 1997; Tilman 1999; Huston *et al.* 2000; Hector *et al.* 2002). Such positive selection effects, often called the 'sampling effect', occur when the most productive species (i.e. those that grow fastest in monoculture) also dominate diverse communities, excluding slower growing species and monopolizing resources (Loreau 2000). Apparently, in many plant communities, the most productive species do not dominate polycultures and are outcompeted by slow growing species that often perform as well or better, on average, in mixtures than they do alone (Hector *et al.* 2002; Hooper & Dukes 2004). These results contradict the argument that diversity effects are driven mainly by a simple statistical sampling phenomenon (Huston 1997). They also have important implications not only for how biodiversity influences productivity, but also for the maintenance of plant diversity, as the relatively superior performance of slow growing species in mixtures should facilitate coexistence.

In conclusion, evidence from a series of field and mesocosm experiments indicates that the mechanisms and effects of biodiversity in benthic marine macroalgal communities show strong similarities to those found in terrestrial and wetland vascular plant systems. Our results and those from most other recent experimental tests of plant biodiversity effects (Fridley 2001; Engelhardt & Ritchie 2002; Hector *et al.* 2002; Hooper & Dukes 2004; Downing 2005; Hooper *et al.* 2005) contradict earlier conclusions and suggest that: (i) plant richness effects are often relatively weak and frequently undetectable; (ii) compositional effects are much stronger than richness effects; (iii) transgressive over-yielding is rare; (iv) the most productive species rarely dominate polycultures; and (v) selection effects are often negative and can substantially reduce net biodiversity effects. These and other similarities suggest that several basic mechanisms through which plant diversity influences ecosystem functioning are general and operate in very different communities and taxa.

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