

Consumer effects on ecosystem functioning in rock pools: roles of species richness and composition

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ABSTRACT: A key challenge in research linking biodiversity and ecosystem functioning is to incorporate the trophic interactions that characterise natural systems. There is a particular shortage of studies investigating consumer species richness and composition (identity) effects in the context of ecosystem development (or succession). We manipulated the richness and composition of an assemblage of molluscan grazers (*Patella ulyssiponensis*, *Gibbula umbilicalis* and *Littorina littorea*) added to rock pools denuded of existing biota. We created monocultures and all possible multispecies combinations in a substitutive design, and ran a field experiment for 13 mo. We used 2 separate nested analyses to isolate the roles of species richness, species composition nested within levels of species richness and the specific effect of the limpet *P. ulyssiponensis*, a putative key species. We found no evidence that the biomass or productivity of the developing macroalgal assemblage was affected by grazer richness or species composition nested within richness levels. Rather, the presence of *P. ulyssiponensis*, irrespective of the presence of other grazer species, acted to suppress mean values of these response variables. Biomass and productivity were not strongly related, showing that they provide unique information on ecosystem functioning in this system. Macroalgal species richness was also reduced by *P. ulyssiponensis*, and correlated positively with macroalgal biomass, indicating a link between these response variables. Macroalgal species composition was largely insensitive to either species richness or the presence of *P. ulyssiponensis*, but responded to particular combinations of species within levels of these factors. The key role of *P. ulyssiponensis* in determining ecosystem functioning is apparent from our results, but we note that consumer species richness may play an important role under more heterogeneous conditions.

KEY WORDS: Biodiversity · Ecosystem functioning · Grazing · Herbivory · Primary productivity · Succession · Species identity · Species richness

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INTRODUCTION

Over the last 2 decades understanding the effects of biodiversity on ecosystem functioning has emerged as a fundamental research theme (reviewed by Loreau et al. 2001, Hooper et al. 2005, Balvanera et al. 2006,

Benedetti-Cecchi 2006, Cardinale et al. 2006, Stachowicz et al. 2007). In light of rapid and pervasive human alterations to biodiversity (Pimm et al. 1995, Worm et al. 2006, Byrnes et al. 2007), this issue has important implications for the management of ecosystem services (Kremen 2005). Early seminal work

focused on the effect of plant richness on primary production in temperate grassland plots (e.g. Tilman 1996). Increasingly, however, both theoretical (Thébaud & Loreau 2003, Casula et al. 2006) and empirical work (reviewed by Duffy et al. 2007) has aimed to incorporate the trophic interactions that characterise natural systems, shifting emphasis towards the often complex effects of species diversity and composition in multi-trophic food webs.

Species richness can enhance ecosystem processes through complementarity — a class of mechanisms that includes resource partitioning and facilitation (Loreau 2000). The action of such mechanisms requires the presence of trait diversity, typically represented by multiple species, and increases on average with species richness (Petchey & Gaston 2002). Where inter-specific resource partitioning occurs, for example, increasing species richness will allow a greater proportion of the resource spectrum to be used, potentially enhancing the associated ecosystem process above that of the single best-performing species (e.g. Råberg & Kautsky 2007, Griffin et al. 2008).

While species richness may generally enhance ecosystem processes, there can be considerable, and even greater, variation in rates of ecosystem functioning within levels of species richness (Wojdak 2005). This variability can result from the inclusion or exclusion of particular species or combinations of species (Tilman 1996). Such composition (or identity) effects can predominate if one or several species are particularly well adapted to performing the process of interest, or where a combination of particular species results in an especially high level of resource partitioning or facilitation (e.g. Griffin et al. 2009a). Variation in ecosystem processes attributable to species composition may appear idiosyncratic and unpredictable (Naeem et al. 2002). However, in some cases, apparently idiosyncratic composition effects may be largely explained by the presence or absence of a single dominant species (Poley et al. 2007, O'Connor et al. 2008). Such species may exert a dominant influence on ecosystem functioning by virtue of their functional traits and high abundance (Grime 1998), such that they procure a large proportion of available resources and cannot be compensated for by other species (Schiel 2006). If one species is predicted *a priori* to be a key species, targeted comparisons of treatments with and without this species can test for its dominant effect on ecosystem functioning (O'Connor & Crowe 2005, O'Connor et al. 2008).

Primary consumers (herbivores) play a critical role in many ecosystems, particularly in the marine environment, strongly affecting primary producer biomass, diversity and composition, with potentially large impacts on ecosystem functioning (e.g. McNaughton 1985,

Hughes 1994, Paine 2002, Worm et al. 2002). Theory predicts that consumer species richness will enhance the rate and breadth of resource uptake, reducing the biomass of primary producers (Holt & Loreau 2001, Duffy 2002). Numerous studies have demonstrated effects of grazer richness and composition on the final and accumulated biomass of primary producers (upon termination of experiments) (e.g. Naeem & Li 1997, Duffy et al. 2001, Gamfeldt et al. 2005). However, biomass accumulation measures the net balance of production and consumption and thus may be a poor measure of the rate of primary productivity when losses to consumers are high (Raffaelli & Hawkins 1999). The potential mismatch between consumer effects on producer biomass and productivity may be further compounded by shifts in producer species composition (Duffy 2003) and/or stimulated mass-specific rates of primary production resulting from compensatory responses to grazing (Carpenter 1986) and/or reduced density dependence (Altieri et al. 2009). To our knowledge, however, no previous studies have quantified the effects of consumer species richness and composition on both primary producer biomass and productivity.

Herbivores are expected to have particularly marked effects on the recruitment and initial growth of primary producers, as the early life history stages of primary producers lack the mechanisms that protect them from predation as adults (Santelices 1990, Carson & Root 1999). Disturbances are typically patchy (Dethier 1984), allowing mobile herbivores to migrate into a recently disturbed area from surrounding unaffected habitat (Hartnoll & Hawkins 1985, Burrows & Hawkins 1998). During the early stages of community development, following the loss of a pre-existing community or the creation of new habitat, herbivores may thus have strong effects on community composition (Hawkins 1981, Lubchenco 1983, Lotze et al. 2001, Belliveau & Paul 2002), diversity (Lubchenco 1978), biomass (e.g. Hixon & Brostoff 1996) and productivity (Masterson et al. 2008).

We present the findings of a field experiment designed to determine the independent effects of — and distinguish between — consumer species richness, species composition and the presence of a putative key species on the development and functioning of macroalgal assemblages in rock pools. We used relatively homogeneous artificial intertidal pools located on a breakwater in the UK, naturally dominated by diverse erect assemblages of macroalgae (Griffin 2008). Pioneering (Jones 1946) and recent (Paine 2002, Jenkins et al. 2005, Moore et al. 2007) field research has shown that consumers as a group can play an important role in controlling macroalgal communities on rocky shores (see Jenkins et al. 2008 for review).

O'Connor & Crowe (2005) tested the effect of consumer identity and richness on mature macroalgal assemblages in intertidal pools in Ireland, but the study presented here represents the first test on the recruitment phase in this system. Patellid limpets typically reach larger body sizes and maintain larger standing stocks than do other molluscan grazers on exposed rocky shores in northwestern Europe (Jenkins et al. 2001). Coupled with their powerful rasping foraging technique, these traits produce a strong impact on the standing stock of macroalgal assemblages (Moore et al. 2007). Based on previous research (Hawkins 1981, Hawkins & Hartnoll 1983), and consistent with O'Connor & Crowe (2005), we put forward the orange-footed limpet *Patella ulyssiponensis* as a key species in this system.

We manipulated the richness and composition of 3 locally abundant grazers (*Gibbula umbilicalis*, *Littorina littorea* and *Patella ulyssiponensis*, as in O'Connor & Crowe 2005) and quantified treatment-specific effects on the structure and functioning of developing rock pool communities. Specifically, we quantified effects on the structure (species composition and diversity) and functioning (biomass and productivity) of developing macroalgal assemblages. We first posited that community structure and functioning will be determined by richness, not the composition of grazer species (Hypothesis 1). We also tested the hypothesis that the presence of *P. ulyssiponensis* affects community structure and functioning regardless of the presence or absence of other grazer species (Hypothesis 2). Subsets of treatments were compared to address these distinct hypotheses.

MATERIALS AND METHODS

Study site. We conducted this experiment using relatively homogeneous intertidal rock pools situated on the seaward side of a large coastal defence structure, the Plymouth breakwater (completed in 1841, approximately 1.5 km long and 0.1 km wide), on the English Channel coast, southern UK. Two pools, separated by approximately 1.5 m, are located on the upper surfaces of each of numerous large concrete blocks (2.5 m high, and 2.4 × 4.8 m on their upper surface). Compared with natural rock pools, the dimensions of the pools vary minimally (mean ± SD: depth = 0.31 ± 0.04 m; total rock surface area = 0.806 ± 0.088 m²; volume = 54.48 ± 7.63 l). They have vertical sides, making area and volume calculations simple. The pools are subject to natural colonisation and hosted communities that resemble those of natural rock pools in the region, with macroalgal assemblages being dominant. The orientation and positioning of the blocks subject the pools to

similar wave exposure (moderate to high) and tidal height (ca. 3 m above chart datum). Additionally, the physical homogeneity of the pools themselves (size, rugosity and substrate material) created an opportunity to isolate the role of consumers in a relatively controlled setting whilst maintaining exposure of assemblages to the natural marine environment.

Experimental design and establishment. The total area of substrate ([perimeter × depth] + pool surface area) and volume (pool surface area × depth) of each pool were calculated from digital images (Image JTM). With entire pools forming the replicate units, we manipulated both the richness and composition of 3 consumer species added to the pools: the orange-footed limpet *Patella ulyssiponensis*, the topshell *Gibbula umbilicalis* and the periwinkle *Littorina littorea* (as in O'Connor & Crowe 2005); hereafter, these species are referred to by their generic names only in full or as an initial (i.e. P, G or L, respectively). We selected these species because they are the most abundant primary consumers in midshore rock pools at local sites (J. Griffin unpubl. data) and, thus, most likely to have strong influences on ecosystem processes (Grime 1998). We incorporated a range of sizes within each species (maximum shell length): *Littorina*, 14 to 18 mm; *Gibbula*, 12 to 14 mm; *Patella*, 25 to 40 mm.

We included all species in monocultures (G, L, P), all 3 possible 2-species combinations (GL, GP, LP) and a treatment containing all 3 species (GLP). Additionally, grazer-free caged (CC) and uncaged controls (UC) allowed us to test for the effect of cages on response variables. Subsets of treatments were compared to test our 2 hypotheses.

We employed a substitutive design such that initial total consumer density (~14 g shell-free dry mass m⁻²) was equalised across treatments varying in richness, requiring a reduction in the density of component species with increasing richness. The substitutive design makes the assumption that after local extinction of species, those remaining compensate for their loss by increasing in numbers or biomass, i.e. show density compensation (e.g. Griffin et al. 2008). Since 'extinct' species are replaced by individuals of those remaining, this design tests whether functional compensation would be possible given biomass compensation and reveals the net effect of intraspecific and interspecific interactions (Jolliffe 2000, Griffen 2006).

Initial biomass of grazers was always equally divided among species present (i.e. 14 g m⁻² per number of species). Previous work on nearby rocky shores (Noël 2007, Noël et al. 2009) showed that this biomass density was well within the natural range of variability of total biomass of these 3 species (6.2 to 25.7 g shell-free dry biomass m⁻²) and also close to their mean (±1 SD) summed biomass (13.31 ± 4.91 g shell-free dry biomass

m^{-2}). Before the addition of grazers, pools were emptied of water and all organisms (including existing grazers) were manually removed. Using a large propane burner, we subsequently cleared all remaining macrobiota from the pools, ensuring that all remnants of the pre-existing communities (including highly resistant coralline forms) were visibly removed. Cages (8 mm stainless steel welded wire mesh, chosen to also allow passage of light and propagules) were then constructed over pools to maintain experimental treatments by preventing grazer dispersal and immigration of large-bodied grazers.

Grazers were collected from local shores, carefully transplanted to a Perspex substrate and maintained in flowing seawater for no more than 3 d before transplantation to the study pools. Two weeks after the initial establishment of treatments, we checked the abundance of grazers and added individuals to maintain equal densities to compensate for transplant-induced mortality (primarily of *Patella*). Secondary additions were largely successful. Visual estimates of density at the midpoint in the experiment (6 mo) showed that all grazers had suffered considerable, but variable, rates of mortality. This could have been caused by resource limitation early in the experiment. *Patella* was able to maintain a higher biomass than the other 2 species. In line with a standard substitutive experiment, we aimed to re-equilibrate interspecific densities. We thus added appropriate numbers of *Gibbula* and *Littorina* to reach a biomass equal to the mean biomass of *Patella* (in treatments with an equal number of species) after 6 mo. To avoid promoting possible negative density-dependent effects, we did not keep 'topping-up' treatments throughout the remainder of the experiment (7 to 12 mo). Instead, we allowed grazer densities to change through the second half of the experiment and interpreted results in light of these final densities. Specifically, final grazer biomass varied among species (Fig. 1); thus, species-specific effects were a combination of functional traits and biomass effects (see 'Discussion'). Importantly, species-specific biomasses in multispecies treatments conformed to a substitutive design with unequal monoculture densities (single species biomass/number of species, Griffin et al. 2009b), and each species was proportionally represented in multispecies treatments according to their monoculture densities. Mean total grazer biomass in multispecies treatments thus closely approximated that expected from species-specific final biomasses in single-species treatments (dotted lines in Fig. 1; 1-sample *t*-tests against expected: GL, $p = 0.36$; GP, $p = 0.40$; LP, $p = 0.77$; GLP, $p = 0.226$). With the caveat that species-specific effects included species-specific biomass effects, our hypotheses could be tested with confidence.

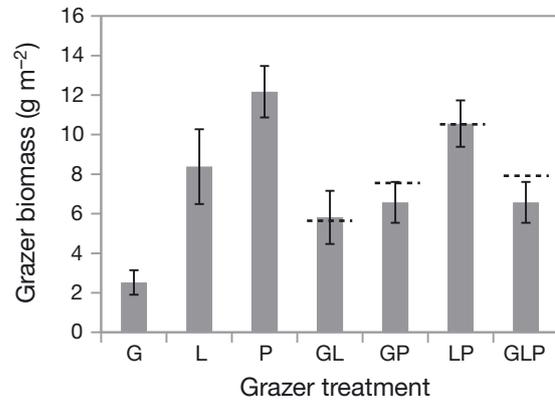


Fig. 1. Mean (\pm SE) final biomass (shell-free) of manipulated grazers according to treatment. Single-species treatments are G: *Gibbula*, L: *Littorina*, P: *Patella*. Two-species treatments are GL: *Gibbula* + *Littorina*; GP: *Gibbula* + *Patella*; LP: *Littorina* + *Patella*. Three-species treatment is GLP: *Gibbula*, *Littorina* and *Patella*. Starting biomass was $\sim 14 \text{ g m}^{-2}$ in each treatment; the biomass of grazers thus fell in all treatments. Dashed lines indicate the biomass expected in multiple species treatments based on the final mean of component monocultures

Each treatment had 4 replicates, giving a total of 36 pools studied. Treatments were randomly assigned to pools, resulting in interspersed replicates. The manipulations were fully established in July 2006 and ran for a total of 13 mo until late August 2007. The cages were thoroughly cleaned every 3 to 4 mo throughout the experiment to prevent the excessive build-up of ephemeral algae, which could shade the underlying pools.

Measurement and calculation of response variables. All response variables were measured upon termination of the experiment. We estimated instantaneous gross primary productivity by measuring rates of oxygen flux between biota and the discrete body of water (the pool) in both light and artificially darkened conditions (see Nielsen 2001, Martins et al. 2007, Noël et al. 2010 for detailed descriptions of this technique applied to rock pools). We measured the concentration of oxygen in each rock pool (HQ20 Hach Portable LDOTM) before and after an hour-long dark period (community respiration) and finally after a period of re-exposure to natural light (including both photosynthesis and community respiration). Gross primary productivity was calculated by simply compensating net oxygen flux under light conditions with oxygen consumption under darkened conditions (Nielsen 2001). Measurements were made in each pool on 3 replicate days under consistently bright, sunny conditions (23 to 25 August 2007), before averaging the values for each pool. We corrected rates of oxygen exchange for diffusion at the water–air interface by applying a diffusion constant ($K = 0.32 \text{ g m}^{-2} \text{ h}^{-1}$) calculated for shallow (<1 m) shel-

tered water with very limited wave action (see Kinsey 1985 for correction methodology). We standardised measures of gross primary productivity (GPP) to both the total surface area of the pool (area-specific GPP; e.g. Martins et al. 2007) and the mass of macroalgae (biomass-specific GPP; e.g. Littler & Littler 1980). Our approach, which focuses on benthic algal productivity, has been verified by Martins et al. (2007) who showed that the rate of primary productivity in rock pools typical of UK rocky shores is almost totally (>98%) driven by macroalgae, with <2% attributable to phytoplankton.

Following measurement of oxygen flux rates, the abundances of all macroalgal taxa within each pool was ascertained. Firstly, we estimated the percentage cover of encrusting coralline algae and bare rock within 4 replicate 400 cm² quadrats (Dethier 1984). Secondly, we collected all erect macroalgae from all pools. We then sorted these in the laboratory to the lowest taxonomic level possible (mostly to species), dried all these taxa in the oven at 60°C for 3 d and reweighed them (De Wreede 1985). Approximately 80% of the biomass of *Corallina officinalis* consists of its heavy calcite skeleton; thus, raw dry mass measures of macroalgal assemblages in rock pools can largely reflect the abundance of this one species (Griffin 2008). We thus converted dry biomass measures of *Corallina officinalis* to calcium carbonate-free measures using a conversion factor of 0.2 estimated from laboratory dissolution of calcite in weak acid (Carpenter 1986, Griffin 2008).

As an additional measure of ecosystem-level grazer treatment effects we calculated the total mass of macroalgae by summing the masses of component species and normalised to per m² of pool substrate. Richness (number), evenness (Pielou's J') and diversity (Shannon's H') (see e.g. Magurran 2004) of macroalgae were also calculated.

The relative tolerance of macroalgal taxa to consumption is probably related to their functional morphology (Steneck & Dethier 1994). Effects of consumption are thus likely to be most evident when macroalgal taxa are grouped according to morphology and/or functional traits. Macroalgal taxa were therefore further divided into morpho-functional groups (i.e. crustose coralline, foliose, canopy, sheet-like and turf-forming) according to known functional attributes of the species (categories adapted from Littler & Littler 1980, Arenas et al. 2006).

Analysis. All measures of functioning and diversity were considered in separate univariate analyses. Treatment effects on the composition of macroalgal (morpho-functional groups and taxa) assemblages were assessed through multivariate analyses. However, crustose coralline algae and bare rock were both

measured as proportions of total substrate coverage (%), thus were not comparable to biomass measures of morpho-functional groups. We therefore analysed treatment effects on these variables through separate univariate analyses.

To test both of our hypotheses we used ANOVA for univariate response variables and a permuted multivariate ANOVA (PERMANOVA) (Anderson 2001) for multivariate responses. To test Hypothesis 1 we used a 2-factor nested model with 3 levels of species composition nested within both single (P, L, G) and 2 species (GL, GP, LP) levels of species richness (Model 1), a model similar to that used in several previous biodiversity–ecosystem functioning experiments (Jonsson & Malmqvist 2000, O'Connor & Crowe 2005, Wojdak 2005). As a complementary test of Hypothesis 1, and to test for an effect of consumer species richness at the 3-species level, we calculated the expected value of each univariate response variable at the 3-species level as the average of single-species effects on this response. We then compared the observed values with expected mean values using 2-tailed 1-sample t -tests (Barton & Schmitz 2009). To test Hypothesis 2, we conducted planned comparisons to directly compare treatments with *Patella* (P, GP, LP, GLP) to those without *Patella* (CC, L, G, GL). This was also a 2-way nested analysis with species composition nested within treatments with or without *Patella* (Model 2; see O'Connor & Crowe 2005 and O'Connor et al. 2008 for a comparable approach).

Univariate analyses were validated through Cochran's test for heterogeneous variances, multivariate analysis through the PERMDISP2 (Anderson 2006) procedure, which tests for heterogeneity in multivariate dispersion between treatments. Under Model 2 (Hypothesis 2) area-specific GPP was log transformed to achieve homogeneous variances.

Where PERMANOVA with pairwise comparisons identified significant between-group differences in composition (of macroalgal taxa, morpho-functional groups or animal taxa), the 'Similarity Percentages' (SIMPER) procedure was used to identify those taxa or groups underlying the difference (Clarke & Warwick 2001). Multivariate analyses were performed on Bray-Curtis dissimilarity measures and permuted 999 times.

To check whether the cages used to contain the manipulated grazers significantly affected response variables, we conducted both univariate and multivariate comparisons detailed above between caged (CC) and uncaged (UC) control treatments. Univariate analyses were performed in GMAV (Institute of Marine Ecology, University of Sydney), multivariate analyses in PRIMER (Clarke & Warwick 2001).

Finally, to explore relationships between univariate response variables across the entire data set, we per-

formed correlation analyses. Specifically, we tested the correlations between macroalgal diversity (richness, H' and J') and measures of ecosystem functioning (area-specific productivity, mass-specific productivity and biomass). Additionally, given the effects of grazing by *Patella* on both area-specific productivity and biomass, we explored the link between these 2 responses through correlation.

RESULTS

A single replicate from each of the treatments, L, G and CC, was excluded from the experiment owing to damage to cages after winter storms. Analyses were performed by using the average of the 3 remaining replicates in each of the relevant treatments to balance our design and reduce the degrees of freedom appropriately (Underwood 1997). Comparisons between caged and uncaged grazer-free controls indicated that cages did not have a significant effect on any of the univariate or multivariate responses ($p > 0.1$ in all cases).

Neither grazer richness nor composition within levels of species richness affected macroalgal biomass (Fig. 2) or either of the measures of GPP (Fig. 3, Table 1, Model 1). All 3 grazers in combination suppressed macroalgal biomass 44% below the expected level (Fig. 2) (based on monoculture performance), although this was not statistically significant (1-sample t -test, $p = 0.08$). The presence of *Patella*, on the other hand, significantly reduced both macroalgal biomass and the rate of area-specific productivity (Fig. 2, Table 1, Model 2).

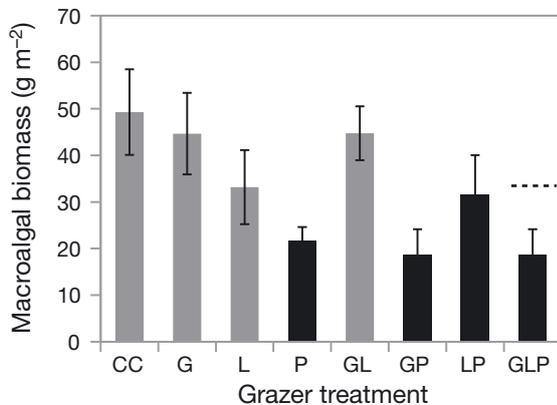


Fig. 2. Treatment means (\pm SE) of accumulated macroalgal biomass. CC: grazer-free (caged) control; all other treatment codes as in Fig. 1. The dashed line indicates the expected level of macroalgal biomass in the 3-species treatment (GLP) based on the mean of component monocultures. Black bars: treatments with *Patella*; grey bars: treatments without *Patella*. See Table 1 for ANOVA

Multivariate analyses showed the relative abundances and composition of macroalgal taxa were not significantly affected by species richness, composition within levels of richness (Table 2, Model 1) or the presence of *Patella* (Table 2, Model 2). At the level of morpho-functional group, however, effects of species composition within richness levels (Table 2, Model 1, $GL \neq GP$), in addition to composition within levels of *Patella* (Table 2, Model 2, $CC \neq GL$), were detected. Specifically, within the 2-species level (Model 1) GL resulted in a greater abundance of turf-forming algae (32.3% of difference, SIMPER) but less canopy algae (24.9% of difference) than did GP. GL also had more turf-forming algae (33.7% of difference), although it had less sheet-like algae than CC (16.6% of difference) (*Patella* absent, Model 2).

Neither species richness nor composition within species richness levels affected the cover of bare rock or crustose coralline algae (Table 3, Model 1). The presence of *Patella* did, however, result in a significantly greater coverage of bare rock (Table 3, Model 2), while *Patella* had no effect on the cover of crustose coralline algae.

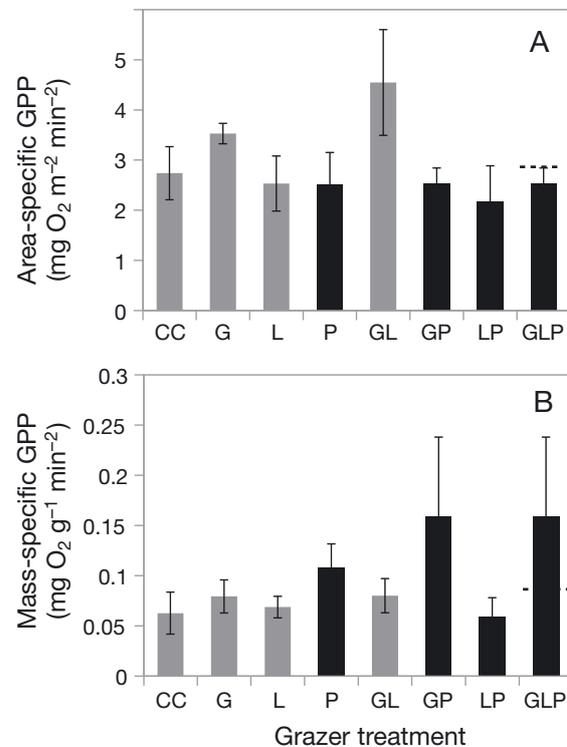


Fig. 3. Treatment means (\pm SE) of (A) area-specific gross primary productivity (GPP) and (B) mass-specific GPP. See Table 1 for ANOVA and post-hoc tests. Treatment codes are as in Figs. 1 & 2. The dashed line indicates the expected level of macroalgal biomass in the 3-species treatment (GLP) based on the mean of component monocultures. Black bars: treatments with *Patella*; grey bars: treatments without *Patella*. See Table 1 for ANOVA

Macroalgal species richness was not affected by grazer richness or composition within richness levels; however, macroalgal diversity (H') was significantly lower at the 2-species level compared with the 1-species level (Fig. 4, Table 4, Model 1). This reduction in diversity can be attributed to a lower level of macroalgal species evenness in 2 species mixtures (Table 4, Model 1). The effect of grazer richness did not extend to the highest level of grazer richness; the observed levels of macroalgal richness ($p = 0.16$), diversity ($p = 0.27$) and evenness ($p = 0.58$) did not differ from expected (1-sample t -tests; Fig. 4). The pres-

ence of *Patella* significantly reduced the richness of macroalgae but had no effect on macroalgal diversity (H') or evenness (J') (Fig. 4, Table 4, Model 2).

Across all caged study pools, macroalgal species richness was positively correlated with macroalgal biomass (Table 5), while macroalgal species evenness displayed the opposite (negative) relationship with macroalgal biomass (Table 5). No measure of macroalgal diversity was related to either measure of productivity. Notably, the 2 measures of ecosystem functioning that were affected by *Patella* (biomass and area-specific productivity) were not correlated ($r = 0.20$, $p = 0.30$, $n = 29$).

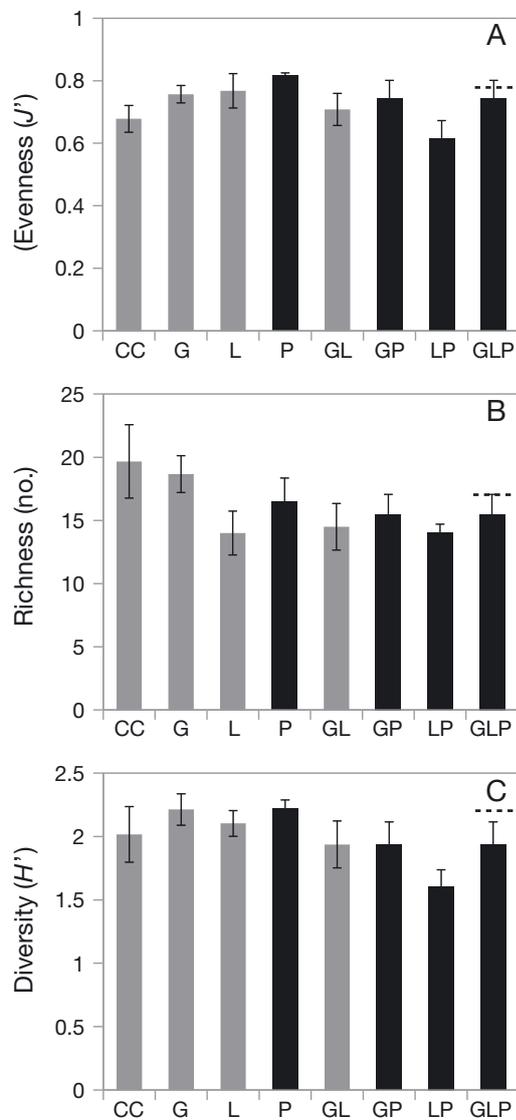


Fig. 4. Treatment means (\pm SE) of macroalgal species (A) evenness (J'), (B) richness (number [no.]) and (C) diversity (H'). Treatment codes are as in Figs. 1 & 2. The dashed line indicates the expected level of macroalgal biomass in the 3-species treatment (GLP) based on the mean of component monocultures. Black bars: treatments with *Patella*; grey bars: treatments without *Patella*. See Table 4 for ANOVA

DISCUSSION

Our results show that the effects of consumers on the structure and functioning of developing macroalgal assemblages were largely determined by the inclusion of the limpet *Patella ulyssiponensis*. Specifically, *Patella* reduced the richness and biomass of macroalgae, increased the cover of bare substrate and suppressed the rate of gross primary productivity.

Our findings must be interpreted in light of changes in grazer biomass that occurred during the experiment (given the equalising of species' biomass densities at the start and midpoint of the experiment, see 'Materials and methods'). Total grazer biomass fell during the experiment in all treatments, indicating that grazer mortality exceeded growth. The reduction in grazer biomass varied among species, which can be most clearly seen at the single species level. *Gibbula* suffered a far higher level of biomass reduction compared with the other 2 species (Fig. 1). This is unlikely to be a result of the stress of transplantation; in a previous laboratory experiment (Griffin et al. 2009b) we found no transplant-induced mortality in this species. Although previous work shows that *Gibbula* can reach the high biomass densities established in single-species treatments at the start of the experiment (Noël et al. 2009), the physical (e.g. wave exposure) and biological (e.g. algal habitat provision) conditions at the study site evidently did not suit *Gibbula* as much as it did the other 2 species. Food limitation of *Gibbula* may also help to explain this species' relatively high mortality rate, given that *Gibbula* has the smallest mean body size of all the grazers used here and relative metabolic demand is greater in smaller-bodied organisms (West et al. 1997).

Consistent with the idea that species impacts on ecosystem functioning will be related to their biomass (Grime 1998), in this experiment, as in natural pools (Manley 2008), species-specific grazing effects cannot be separated from biomass effects. This should not be considered as a confounding effect; rather, biomass acts

Table 1. Analysis of treatment effects on accumulated macroalgal biomass and productivity response (GPP) variables. Model 1 shows results of nested ANOVA to test Hypothesis 1. Model 2 shows results of nested ANOVA used to test Hypothesis 2. p-values in **bold** text denote significant effects (at alpha level = 0.05). NB: residual df reduced from 18 to 16 (Model 1) and from 24 to 21 (Model 2) owing to missing replicates

Source of variation	df	Macroalgal biomass			Area-specific GPP			Mass-specific GPP		
		MS	F	p	MS	F	p	MS	F	p
Model 1										
Richness	1	188.66	0.54	0.51	0.02	<0.01	0.95	<0.01	2.19	0.21
Composition (Richness)	4	352.53	2.02	0.14	4.68	3.19	0.06	<0.01	1.03	0.42
Residual	16	174.49			1.69			<0.01		
Model 2										
± <i>Patella</i>	1	1795.6	6.28	0.05	0.59	6.68	0.04	<0.01	0.79	0.41
Composition (± <i>Patella</i>)	6	286.06	1.64	0.19a	0.09	0.96	0.47	<0.01	1.1	0.4
Residual	21	174.98			0.09			<0.01		

in combination with species' functional traits to determine their effects (Grime 1998, Garnier et al. 2004, Vile et al. 2006). We suggest that future experiments should not necessarily aim to equalise biomass or numbers across all treatments as in a traditional substitutive de-

sign (as we did), but ensure that interspecific differences in standing stock are represented from the beginning of the experiment (see Griffin et al. 2009b for an example of this approach). This may be no simple task, however, given that species' biomasses and effects on ecosystem functioning can be highly

context-dependent, and this is especially true in heterogeneous environments such as rocky shores (Griffin et al. 2009b). This argues for site replication in future studies, as well as an explicit consideration of the effect of environmental variables on species' abundances and contributions to ecosystem functioning.

To our knowledge this experiment is the first to examine how consumer composition and diversity affect both producer standing stock and the gross rate of primary productivity. Our results show that the dominant negative effect of *Patella* on macroalgal biomass was also apparent in reduced rates of area-specific GPP, demonstrating an impact by this species on both stock and flux elements of ecosystem functioning (Chapin et al. 2000). These effects also suggest that the reduction in area-specific GPP may have been mediated by *Patella's* effect on algal biomass, although this is not supported by the weak correlation between macroalgal biomass and area-specific GPP (Table 5). Subtle and possibly interacting effects of grazers on the relative abundances of macroalgal taxa, macroalgal diversity and density-dependent competition or facilitation could all help to explain the lack of correspondence between macroalgal biomass and GPP overall. It is beyond the scope of the present study

Table 2. Results of PERMANOVA testing for treatment effects on the composition of macroalgal species and morpho-functional group. Model 1 shows results of multivariate nested ANOVA to test Hypothesis 1; Model 2 shows results of multivariate nested ANOVA used to test Hypothesis 2. p-values in **bold** text denote significant effects (at alpha level = 0.05). This analysis excludes crustose coralline algae

Source of variation	df	Macroalgal species			Macroalgal morpho-functional groups		
		MS	F	p	MS	F	p
Model 1							
Richness	1	1333.9	1.1268	0.37	442.72	0.71	0.76
Composition (richness)	4	4752.8	1.3777	0.09	623.79	1.95	0.04
Residual	16	13799			319.94		
Model 2							
± <i>Patella</i>	1	1929	1.78	0.13	962.92	1.62	0.2
Composition (± <i>Patella</i>)	6	1087	1.24	0.14	596.79	1.68	0.02
Residual	21	878.07			355.94		

Table 3. Analysis of treatment effects on the percentage covers of bare rock and crustose coralline algae. p-values in **bold** text denote significant effects (at alpha level = 0.05). NB: residual df reduced from 18 to 16 (Model 1) and from 24 to 21 (Model 2) owing to missing replicates

Source of variation	df	% bare rock			% crustose coralline algae		
		MS	F	p	MS	F	p
Model 1							
Richness	1	1180.67	0.55	0.50	86.89	0.49	0.52
Identity (richness)	4	2156.82	2.84	0.06	177.48	0.59	0.68
Residual	16	758.18			300.68		
Model 2							
± <i>Patella</i>	1	8911.13	7.76	0.03	12.29	0.06	0.81
Composition (± <i>Patella</i>)	6	1148.24	1.62	0.19	201.34	0.82	0.57
Residual	21	707.92			246.43		

Table 4. Nested ANOVA on aspects of macroalgal species diversity. p-values in **bold** text denote significant effects (at alpha level = 0.05). NB: residual df reduced from 18 to 16 (Model 1) and from 24 to 21 (Model 2) owing to missing replicates

Source of variation	df	Richness (no.)			Diversity (H')			Evenness (J')		
		MS	F	p	MS	F	p	MS	F	p
Model 1										
Richness	1	18.37	2.56	0.19	0.71	8.31	0.04	0.062	7.47	0.05
Composition (richness)	4	7.18	0.71	0.59	0.09	1.34	0.30	<0.01	1.39	0.28
Residual	16	10.13			0.06			<0.01		
Model 2										
\pm <i>Patella</i>	1	68.06	7.79	0.03	0.15	0.99	0.36	0.15	0.99	0.30
Composition (\pm <i>Patella</i>)	6	8.73	0.75	0.62	0.15	1.88	0.13	0.15	1.88	0.13
Residual	21	11.69			0.08			0.08		

to elucidate these possible effects, but we note that the noisy and possibly nonlinear relationship between these 2 related response variables (biomass and productivity) underlines that biomass accumulation should be used only with caution as a proxy of productivity in studies of consumer impacts (Masterson et al. 2008), and that these 2 response variables provide unique information on the effects of consumer richness and composition on ecosystem functioning.

Patella grazing did not cause any consistent changes in the composition of macroalgae, at the level of taxa or even morpho-functional group (Table 2), indicating that macroalgal taxa were similarly affected by *Patella* regardless of their morpho-functional traits. *Patella* did not reduce the species diversity (H') or evenness (J') of macroalgae, providing a further indication that the presence of *Patella* affected macroalgal taxa indiscriminately. Therefore, the observed reduction of macroalgal species richness in the presence of *Patella* (Fig. 4b) cannot be attributed to the vulnerability of particular species (or a morpho-functional group) to *Patella* grazing. The positive correlation between macroalgal biomass and species richness (Table 5) shows that a greater number of species are represented with an increasing abundance (biomass) of macroalgae, which may be purely a result of increasing 'sampling' of individuals, analogous to the well-documented species-accumulation curves produced when sampling for species richness estimation (e.g. Gotelli & Colwell 2001). Additional possible explana-

tions for this correlation include an increase in associational defences (e.g. Pfister & Hay 1988, Noël 2007) with macroalgal biomass and/or a positive effect of macroalgal richness on biomass accumulation through resource complementarity (Bruno et al. 2006). The fact that species evenness decreases with biomass (Table 5) indicates that the species that accumulate with increasing biomass remain rare, suggesting that they are probably epiphytic species gaining an associational defense on better-defended high biomass species (Noël 2007).

In contrast to the strong effects of grazing by *Patella*, grazer species richness did not affect the biomass or functioning of macroalgae. This is at odds with patterns emerging from a large number of empirical studies (reviewed by Hooper et al. 2005, Cardinale et al. 2006, Stachowicz et al. 2007) that show rates of resource consumption to be generally enhanced by increasing species richness. While our results imply that species richness does not affect resource consumption in this system, greater consideration of this apparent departure from theory is required. Firstly, our gradient of species richness was very limited (1 to 3 species), including only the most abundant grazers found on local rocky shores. This may have limited the strength of a species complementarity effect by offering limited functional diversity. Grazers from other phyla, such as the crustacean amphipods and isopods, may, for example, offer a greater potential for resource complementarity due to larger differences in feeding mode (Parker et al. 1993, Råberg & Kautsky 2007). Secondly, the relatively homogeneous conditions afforded by these artificial pools (e.g. substrate type and rugosity, tidal height and exposure) may have prevented interspecific complementarity from being realised in terms of resource use partitioning (Cardinale et al. 2004, Griffin et al. 2009b). Finally, while species richness effects on ecosystem functioning were not de-

Table 5. Pearson's correlations between aspects of macroalgal diversity and measures of ecosystem functioning recorded across all pools studied (excluding uncaged controls). Significant correlations are shown in **bold** text. n = 29

	Biomass		Area-specific productivity		Mass-specific productivity	
	r	p	r	p	r	p
Species richness (no.)	0.455	0.013	0.312	0.100	-0.297	0.118
Species diversity (H')	-0.099	0.609	0.159	0.410	-0.029	0.882
Species evenness (J')	-0.418	0.024	-0.004	0.985	0.187	0.33

tected here, we note that our results do suggest that grazer richness is important in this system, despite the dominant effects of grazing by *Patella*. Macroalgal biomass was reduced to a greater degree than expected in the 3-species mixture (Fig. 2). Although this was not statistically significant ($p = 0.08$), greater replication may have allowed detection of this possible diversity effect. Given the marginal significance of the richness effect, as well as the limited replication in our study, we feel it is premature to conclude that richness does not increase the strength of consumer control of macroalgae in this system.

A further suggestion that grazer richness affected macroalgae was apparent in macroalgal diversity (H') and evenness (J'), which were both lower when 2 species of grazers were present compared with when a single grazer was present (Table 4, Fig. 4). At the 3-species level there was no effect of grazer richness on macroalgal diversity or evenness (Fig. 4), which calls for a cautious interpretation of the effect of 1 versus 2 species on macroalgal diversity and evenness. Further empirical work is required to elucidate the effects of consumer diversity on resource diversity in this system and more generally.

Strong effects of species identity, as documented here, have been a common feature of biodiversity–ecosystem functioning research in studies ranging through primary producers (e.g. Bruno et al. 2005), consumers (e.g. Duffy et al. 2001) and predators (e.g. Straub & Snyder 2006). The obvious implication is that to understand and predict ecosystem functioning, we need to consider the identity of species lost or gained. Understanding effects of species based on their functional traits may allow functionally important species to be identified based on the biomass-weighted value of their functional traits (Garnier et al. 2004, Vile et al. 2006). However, over larger temporal and spatial scales species complementarity, and thus diversity, may become important (Cardinale et al. 2004, 2007). In relation to our study, experiments including the full range of habitat types and environmental contexts over which the focal species coexist, and over multi-generational time periods, would be required before one could conclude that the ecosystem functions measured here could be maintained by the single dominant species, *Patella ulysiponensis*.

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