

Nutrient enrichment alters the consequences of species loss

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Summary

1. Loss of biodiversity and nutrient enrichment are two of the most pervasive drivers of change in ecosystems globally. However, little is known about how these disturbances interact to affect ecosystem functioning.

2. We established a field experiment to test for effects of loss of consumer species on algal assemblages (richness and assemblage structure) and ecosystem functioning (ecosystem productivity and algal biomass accumulation) on rocky shores. We manipulated the presence of three common molluscan grazer species in newly created rock pools over 13 months. Our grazer manipulation was based on a subtractive experimental design, and we also manipulated nutrient concentrations to evaluate explicitly how resource availability affected the consequences of species loss.

3. We found that the effects of loss of grazer species on algal assemblages and their functioning depended strongly on both the identity of the grazer species lost and of those remaining in the community. Moreover, the effects of loss of species depended on nutrient availability, making it extremely difficult to predict the effects of species loss generally without detailed knowledge of a system.

4. Our results demonstrate clearly that the effects of grazer species loss on primary producers and ecosystem functioning may not be generalisable based on grazer functional roles or traits.

5. Synthesis. Our findings highlight the need to include key physical drivers, such as nutrient availability, explicitly into biodiversity–ecosystem functioning models in order to move towards a predictive framework that incorporates the effects of both environmental heterogeneity and anthropogenic stressors.

Key-words: algae, benthic, biodiversity, ecosystem functioning, grazing, marine, nutrient enrichment, plant–herbivore interactions, rock pools

Introduction

Predicting the consequences of species loss remains an elusive goal of critical importance for the maintenance of ecosystem functioning and services (Cardinale *et al.* 2012; Hooper *et al.* 2012). This difficulty is compounded by the idiosyncratic effects of species loss on ecosystem functioning. Identity effects, which are associated with the loss of particular species, but not necessarily with a loss in diversity, are highly prevalent in marine systems and arguably more important than species diversity *per se* (Duffy *et al.* 2001; Emmerson *et al.* 2001; Stachowicz, Bruno & Duffy 2007; Hensel & Silliman 2013). For example, the loss of a key grazer species,

the limpet *Patella ulyssiponensis*, has been shown to enhance algal biomass in intertidal rock pools. However, its replacement by other grazing gastropods could not compensate for its loss, even at increased densities (O'Connor & Crowe 2005). In general, the magnitudes and directions of the effects of loss of consumer species are highly variable and often depend on physical drivers, such as nutrient regimes (Boyer, Kertesz & Bruno 2009; O'Connor & Donohue 2013). Thus, our understanding of the consequences of changes in diversity is complicated by effects of environmental context on biodiversity–ecosystem functioning (BEF) relationships. In fact, the effects of environmental variability (e.g. tidal elevation in intertidal ecosystems) can mask the effects of changes in biodiversity on resource use by species (Bracken, Jones & Williams 2011).

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Direct effects of consumers on primary producers are often mediated by environmental context. For example, the ability of grazers to regulate primary production in coastal systems can be modified by nutrient availability (Nielsen 2001; Worm *et al.* 2002; Bertness *et al.* 2008; Gruner *et al.* 2008; O'Connor & Donohue 2013). Here, we combine these perspectives to ask how environmental context – the supply of limiting nutrients – affects the functional consequences of a decline in consumer diversity on a rocky shore. We specifically examine grazer species richness effects throughout community development (succession) rather than restricting our focus to effects on established communities. This approach allows us to account for successional changes in algal traits that may influence the direction and/or magnitude of effects and the role of complementarity among grazer species (Farrell 1991), which has been overlooked in several previous studies (Griffin *et al.* 2010; Aguilera & Navarrete 2012).

Previous BEF experiments have been criticised for their lack of applicability to real-world contexts, and it has been argued that species loss experiments should be based on more realistic experimental scenarios (Bracken *et al.* 2008; Stachowicz *et al.* 2008a; Crowe, Bracken & O'Connor 2012). The importance of molluscan grazers controlling algal biomass on rocky shores is well known (e.g. Jones 1946; Southward 1964; Hawkins & Hartnoll 1983). However, the presence of several common grazer species is subject to considerable spatiotemporal variability, frequently as a consequence of human-induced pressures. For example, the topshells *Phorcus* sp. and *Gibbula* sp. are sensitive to particularly cold winters and their ranges in Ireland and Britain are expected to shift northward under predicted global warming conditions (Mieszkowska *et al.* 2007). Other gastropod grazers, such as littorinids and limpets, are frequently subject to significant human exploitation (Cummins *et al.* 2002; Martins *et al.* 2010), in addition to shifting species ranges as the climate warms (Moore, Thompson & Hawkins 2007; Firth *et al.* 2009). Concurrent with these changes, nutrient enrichment has been identified as one of the major threats to coastal ecosystems (Worm & Lotze 2006; Diaz & Rosenberg 2008). There is, for example, growing evidence that the Irish Sea is becoming increasingly enriched with anthropogenic nutrients (Allen *et al.* 1988; Hydes *et al.* 2004; Gowen *et al.* 2008).

We tested the context dependency of predicted effects of species loss on the establishment of new communities and ecosystem functioning by comparing the effects of loss of grazer species at ambient conditions with those in nutrient-enriched environments. Based on previous studies (e.g. Lubchenco 1978; Sousa 1984; Farrell 1991; O'Connor & Crowe 2005; Noel *et al.* 2009; Griffin *et al.* 2010), we tested the hypotheses that, in developing communities in rock pools, the loss of the assumed 'key' grazer species (*Patella ulyssiponensis*), but not the loss of other species considered functionally similar (*Littorina littorea*, *Gibbula umbilicalis*; i.e. species identity not richness), would lead to an increase in gross ecosystem productivity and total accumulated algal biomass. We also hypothesized that this increase in total algal biomass would not be driven by a shift in algal assemblage structure,

nor differences in algal species richness, which would indicate that grazing effects were homogenous across all algal species. Further, certain characteristic algal traits are often associated with nutrient-enriched environments (Hawkins *et al.* 1994), which may interact with the effects of different grazer species based on their different modes of feeding (Hawkins & Hartnoll 1983; Hawkins *et al.* 1989). We therefore manipulated nutrient concentrations to test explicitly whether potential species loss effects varied with nutrient enrichment.

Materials and methods

Our experiment was done on an exposed rocky shore at Carnsore Point, Co. Wexford, Ireland (52°10.3'N, 6°21.8'W). The site is composed largely of granite and is typical of exposed shores in this region (e.g. O'Connor & Crowe 2005; O'Connor *et al.* 2011). This shore contains a network of patches of rock, mussels, barnacles and algae (O'Connor & Crowe 2008). The mid-shore contains many shallow rock pools dominated by macroalgae (e.g. *Lithothamnion* spp., *Corallina officianalis*, *Chondrus crispus*, *Ulva* spp., *Scytosiphon lomentaria* and *Fucus vesiculosus*) and a suite of grazing gastropods (comprising primarily *Patella ulyssiponensis*, *Littorina littorea* and *Gibbula umbilicalis*).

Natural rock pools differ in shape, size, shore height and colonisation history, making it difficult to compare them without confounding other factors (Underwood & Skilleter 1996). To limit this variability, we constructed experimental pools by drilling with a diamond-tipped corer. All pools were 30 cm diameter, although their maximum depth varied between 9.5 and 14.5 cm due to variable topography of the surrounding bedrock (Gollety & Crowe 2013). Forty experimental pools were created, each at least 1 m apart within the mid-shore, along approximately 300 m of shoreline. Rock pools of a wide range of sizes are naturally present, and the experimental pools were similar in volume to many on the shore (Gollety & Crowe 2013).

We crossed grazer diversity manipulations with nutrient additions in our experimental intertidal rock pools. The presence of different grazer species was manipulated to create our experimental treatments. Our experiment used a subtractive design equivalent to the additive design that is commonly used in consumer biodiversity experiments (e.g. Cardinale *et al.* 2003, 2006). The relative advantages and disadvantages of different experimental designs used to test for effects of multiple consumer species are well documented (e.g. Underwood 1978; O'Connor & Crowe 2005; Byrnes & Stachowicz 2009). Our approach was chosen based on: (i) the logistical constraints of this experimental platform; (ii) our desire to avoid unsustainable and unrealistic experimental densities within the constructed pools (Harley 2006); and (iii) previous studies in rock pools which did not identify density-dependent effects (e.g. O'Connor & Crowe 2005). Pools contained either all three of the manipulated grazer species at realistic densities (i.e. *Patella*, *Littorina* and *Gibbula*), or one of the three species was not present (i.e. no *Patella*, no *Littorina* or no *Gibbula*), or none of the three species was present.

Manipulated grazer densities were based on mean densities in natural rock pools at the experimental site, as determined in a pilot study in which 20 quadrats in pools <10 cm in depth were sampled: *Patella* 28 ± 7 (SE) individuals per m², *Littorina* 22 ± 6 individuals per m² and *Gibbula* 38 ± 8 individuals per m². Thus, the numbers of manipulated consumers in each rock pool comprised: 4 *Patella* (≈ 48 g), 3 *Littorina* (≈ 18 g) and 6 *Gibbula* (≈ 18 g) and the density and biomass of each species present mimicked their actual abundances on this shore. Treatments were allocated randomly to each pool and each

grazer combination treatment was replicated four times. Owing to difficulties transplanting limpets (*Patella*), all grazers initially colonized the pools naturally and were removed from pools when required according to each treatment. *Littorina* and *Gibbula* were added to the pools at the appropriate densities where required to establish treatments. Natural colonisation dynamics of both algae and grazers were allowed to take place for 2 months prior to establishment of our experimental treatments.

To test for an interaction between effects of loss of grazer species and nutrient enrichment, another complete set of all the manipulation grazer treatments was established concurrently where nutrient concentrations were enhanced to compare the simultaneous effects of grazer treatments at ambient and enriched nutrient conditions. Nutrient enrichment was achieved by the addition of slow release fertilizer pellets (Osmocote®) in plastic mesh cases (10 cm × 10 cm; Worm, Reusch & Lotze 2000; Atalah & Crowe 2010; O'Connor & Donohue 2013). Mesh cases were added to every experimental pool to control for any experimental artefacts caused by the presence of the case rather than the nutrients. Initially, 160 g of fertilizer was added to each nutrient-enriched pool, and after 6 weeks water samples were taken during low tide to test whether this method was effective. Water samples from experimental pools with added nutrients had greater concentrations of both soluble molybdate-reactive phosphorus (MRP (mean ± SE): 472 ± 22 µM; MS = 257.86, $F_{1,24} = 9980.75$, $P < 0.001$) and dissolved inorganic nitrogen (DIN: 1520 ± 142 µM; MS = 237.77, $F_{1,24} = 1106.90$, $P < 0.001$) than treatments at ambient conditions (MRP: 0.86 ± 0.03 µM; DIN: 4 ± 0.6 µM). The ambient treatments reflect nutrient conditions that are typical for this region (Allen *et al.* 1988; McGovern *et al.* 2002; Hydes *et al.* 2004; Gowen *et al.* 2008). Our aim was to simulate pulses of nutrients into the system, for example similar to land-based run-off following precipitation (Sharp 1983). Thus, water samples were collected from each pool just before a flooding tide to ascertain the maximum nutrient concentrations experienced during a tidal cycle. As is common to all studies utilizing rock pools in this way (e.g. Nielsen 2001; Methratta 2004; Masterson *et al.* 2008; Atalah & Crowe 2010), the enriched nutrient concentrations were very high, although not high enough to be detrimental to algal growth (Gordillo, Dring & Savidge 2002), while the mean nutrient concentrations would be considerably lower (i.e. when pools were flooded concentrations would be much lower). The clear difference between ambient and enriched pools assured us that the enrichment treatment was effective. Following this, fertilizer pellets were replaced every 8–12 weeks to sustain enhanced concentrations of nutrients in enriched treatments for the duration of the experiment.

It was necessary to cover each pool with stainless steel mesh lids (0.9 mm wire diameter, 4.17 mm aperture, 67% open area) to maintain grazer manipulations. Previous studies have shown that this size mesh does not affect algal assemblage structure, biomass or stability (O'Connor & Crowe 2005; Donohue *et al.* 2013; O'Connor *et al.* 2013) and algal species composition in our experimental pools at ambient conditions without grazer removals did not differ from that in shallow rock pools ($n = 10$) on the shore (PERMANOVA; pseudo- $F_{1,12} = 1.34$, $P = 0.27$) at the end of the experiment. Experimental treatments were maintained monthly and the experiment ran for 13 months to allow for algal recruitment and community development (see Farrell 1991).

We measured gross ecosystem productivity (GEP; following Nielsen 2001) by quantifying dissolved oxygen concentrations in rock pool seawater using an optical probe (HQ20 Hach Lange portable LDO™, Loveland USA) after periods of artificially induced darkness

(for measurement of ecosystem respiration) and subsequent similar periods of sunlight (enabling quantification of net primary productivity). GEP is expressed as mg O₂ m⁻² min⁻¹, was standardised to account for slight variation among pool volumes and was calculated as the sum of ecosystem respiration and net productivity rates (Nielsen 2001). The latter showed a consistently similar pattern in response to treatments. Thus, only GEP is reported here for clarity and brevity. Our measurements were taken at estimated saturating irradiance (> 1000 µmol m⁻² s⁻¹) during sunny days and stable weather conditions and followed recommendations for the incubation method as a tool for examining ecosystem functioning relationships (Noël *et al.* 2010). To further increase accuracy, readings were taken each of three consecutive days at the end of the experiment and their means were used in the analyses (even though variability among days was negligible). Destructive samples were taken at the end of the experiment and the biomass (dry weight) of all algal species quantified.

We used factorial ANOVA (proc GLM in SAS v. 9.2; SAS 2008) to model each dependent variable (i.e. ecosystem productivity, total algal biomass and algal species richness) as a function of the main effects of loss of each of *Patella*, *Littorina* and *Gibbula*; the addition of nutrients; the interaction between loss of each grazer species and addition of nutrients (i.e. *Patella* × nutrients, *Littorina* × nutrients and *Gibbula* × nutrients); the interactive effect of all three grazers (*Patella* × *Littorina* × *Gibbula*); and the interaction between the combined effect of the three grazer species and the addition of nutrients (*Patella* × *Littorina* × *Gibbula* × nutrients). These interaction terms were designed to test for an overall effect of loss of all three grazer species that differed from the summed effect of individual grazer species (i.e. *Patella* × *Littorina* × *Gibbula*; as described by Cardinale *et al.* 2003) – an effect of consumer biodiversity – and whether that biodiversity effect changed with nutrient additions (*Patella* × *Littorina* × *Gibbula* × nutrients).

We used permutational multivariate analysis of variance (PERMANOVA; Anderson 2001; McArdle & Anderson 2001), using the same statistical model described above, to test for differences in algal assemblage structure among treatments. These analyses were based on Bray–Curtis similarity matrices with 9999 permutations of the residuals under a reduced model (using the Vegan package in R version 2.15.2; R Development Core Team 2013). Similarity of percentages (SIMPER) analysis (Clarke & Warwick 2001) was used to identify which algal taxa were important in discriminating among significant treatments.

Results

ECOSYSTEM PRODUCTIVITY AND ALGAL BIOMASS

Gross ecosystem productivity was enhanced by nutrient enrichment ($F_{1,30} = 9.6$, $P = 0.004$) and was greater in pools where *Littorina* was present ($F_{1,30} = 8.5$, $P = 0.007$; Fig. 1a; Table 1a). We found that the effect of consumer biodiversity on algal biomass depended on whether nutrients were added to the pools (*Patella* × *Littorina* × *Gibbula* × nutrients interaction: $F_{1,30} = 6.7$, $P = 0.015$; Table 1b). At ambient nutrient levels, algal biomass in rock pools containing a diverse grazer assemblage was lower than predicted based on the biomass in pools from which certain grazer species were not present (*Patella* × *Littorina* × *Gibbula* interaction: $F_{1,15} = 15.9$, $P = 0.001$; Fig. 1b; Table 2a). Specifically, at ambient

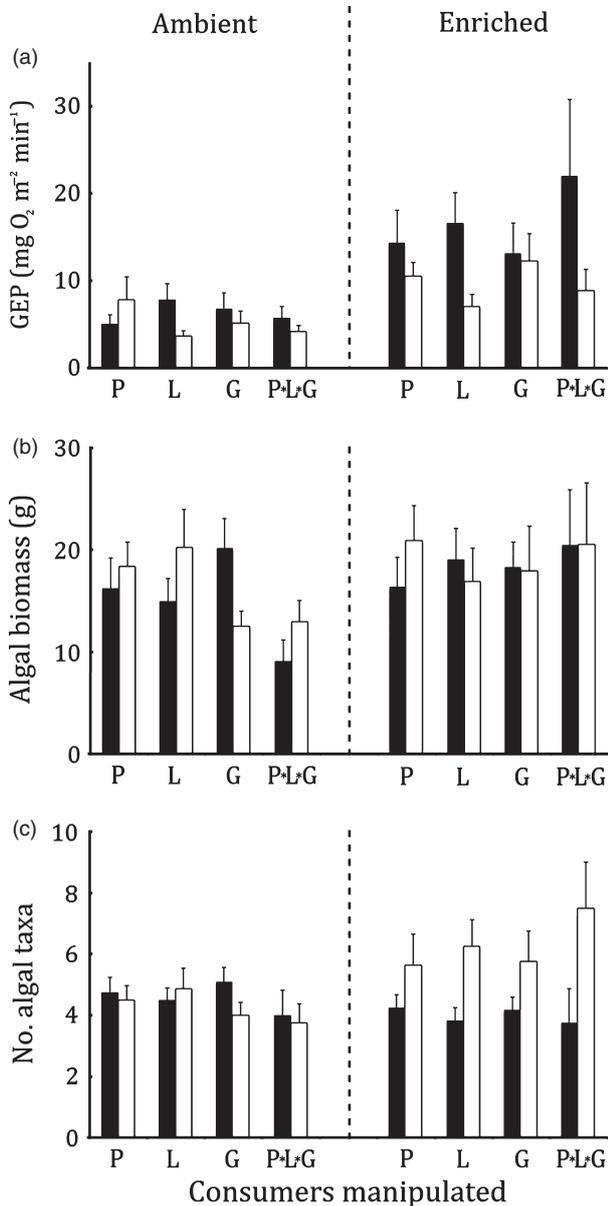


Fig. 1. Mean (\pm SE) (a) gross ecosystem productivity (GEP), (b) algal biomass and (c) number of algal taxa in rock pools with different grazer species present (closed bars) or absent (open bars), at ambient and nutrient-enriched conditions, after 13 months. P = *Patella*; L = *Littorina*; G = *Gibbula*. These results are presented consistent with our statistical model to illustrate how the loss of the three manipulated grazer species each affected algal assemblages and their functioning and how these effects compare to their summed effects (i.e., testing for a *Patella* \times *Littorina* \times *Gibbula* interaction; an effect of consumer biodiversity) and whether that additive or synergistic effect changed with nutrient enrichment (i.e., *Patella* \times *Littorina* \times *Gibbula* \times nutrients).

nutrient levels the loss of *Littorina* resulted in greater algal biomass while the loss of *Gibbula* resulted in lower algal biomass (Fig. 1b; Table 2a). In contrast, however, when nutrients were added, there was no effect of loss of grazer diversity on algal biomass (*Patella* \times *Littorina* \times *Gibbula* interaction: $F_{1,15} = 0.6$, $P = 0.45$; Table 2d), and there were

no effects of individual grazer species loss ($P > 0.31$ in all cases; Table 2d; Fig. 1b).

ALGAL SPECIES RICHNESS AND ASSEMBLAGE STRUCTURE

Algal species richness was greater when *Littorina* was removed ($F_{1,30} = 6.1$, $P = 0.019$; Fig. 1c; Table 1c), whereas the effect of *Gibbula* on algal richness depended on whether nutrients were added to pools (*Gibbula* \times nutrients interaction: $F_{1,30} = 4.3$, $P = 0.047$; Fig. 1c; Table 1c). This appears to be because at ambient conditions the loss of *Gibbula* tended to reduce species richness, whereas in enriched pools algal richness appeared to increase after the loss of *Gibbula* (Fig. 1c; Table 2). Similarly, while nutrient enrichment altered algal assemblage structure significantly ($F_{1,30} = 3.7$, $P = 0.004$; Table 1d), the effect of *Gibbula* on algal assemblage structure varied between enriched rock pools and those at ambient conditions (*Gibbula* \times nutrients interaction: $F_{1,30} = 2.5$, $P = 0.039$; Table 1d). Specifically, the loss of *Gibbula* had no effect at ambient conditions ($F_{1,15} = 1.3$, $P = 0.28$; Table 2c) but altered algal assemblage structure in enriched pools ($F_{1,15} = 2.6$, $P = 0.026$; Table 2f). SIMPER analyses showed that algal assemblages in enriched pools contained greater proportions of *Ulva* spp., *Fucus vesiculosus*, *Porphyra umbilicalis*, *Chondrus crispus*, *Palmaria palmata*, *Polysiphonia* spp. and *Osmunda osmunda* and less biomass of species such as *Scytosiphon lomentaria*, *Corallina officinalis*, *Punctaria latifolia*, *Ceramium rubrum* and *Gelidium sesquipedale* (Table 3). Moreover, in nutrient-enriched pools, the loss of *Gibbula* led to a reduction in *Ulva* spp., *F. vesiculosus* and *P. umbilicalis* and an increase in *S. lomentaria*, thus reducing the effect of nutrient enrichment (Table 4). In other words, the presence of *Gibbula* enhanced the effect of nutrients on algal assemblage structure.

Discussion

We found that the effects of loss of grazer species on ecosystem functioning depended upon both the diversity and identity of the species present and, moreover, that environmental context can modify or even negate these effects. Gross ecosystem productivity was greater in nutrient-enriched rock pools than in pools at ambient conditions, and the presence of the wrinkle *Littorina* (but not the presence of other grazer species) also led to an increase in productivity. The exact mechanism by which *Littorina* enhanced productivity is unclear but may be related indirectly to the associated reduction in algal species richness. The effects of grazer species loss on accumulated algal biomass were regulated by nutrient conditions, grazer identity and grazer diversity. Under ambient nutrient conditions, *Littorina* reduced algal biomass, whereas the topshell *Gibbula* enhanced algal biomass. In these ambient pools, the increase in biomass associated with removing a diverse grazer assemblage was less than predicted based on the removals of each grazer species separately. In contrast, there were no effects of grazer species loss on algal biomass in

Table 1. Effects of nutrient additions and consumer removals on aspects of rock pool ecosystem functioning after 13 months. All analyses are based on 30 denominator degrees of freedom using Type III Sums of Squares. Bold *P*-values indicate statistically significant sources of variation

Source of variation	d.f.	(a) Gross ecosystem productivity		(b) Total algal biomass		(c) Algal taxon richness		(d) Algal assemblage structure	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<i>Patella</i>	1	1.2	0.29	1.9	0.18	0.4	0.53	0.7	0.62
<i>Littorina</i>	1	8.5	0.007	0.4	0.54	6.1	0.019	0.8	0.55
<i>Gibbula</i>	1	<0.1	0.83	3.0	0.091	<0.1	0.96	1.8	0.12
Nutrients	1	9.6	0.004	0.2	0.67	0.9	0.34	3.7	0.004
<i>Patella</i> x Nutrients	1	0.8	0.37	0.2	0.65	0.9	0.36	0.7	0.6
<i>Littorina</i> x Nutrients	1	0.4	0.55	2.7	0.101	1.9	0.18	0.9	0.49
<i>Gibbula</i> x Nutrients	1	0.4	0.55	2.2	0.15	4.3	0.047	2.5	0.039
<i>Patella</i> x <i>Littorina</i>	1	0.8	0.39	1.5	0.24	0.2	0.65	0.9	0.48
x <i>Gibbula</i>									
<i>Patella</i> x <i>Littorina</i> x <i>Gibbula</i> x Nutrients	1	0.7	0.4	6.7	0.015	3.3	0.077	0.8	0.56

Table 2. Effects of consumer manipulations on aspects of rock pool ecosystem functioning (where there was an interactive effect with nutrient enrichment) at ambient and enriched nutrient levels after 13 months. All analyses are based on 15 denominator degrees of freedom using Type III Sums of Squares. Bold *P*-values indicate statistically significant sources of variation

Source of variation	d.f.	Ambient						Enriched					
		(a) Total algal biomass		(b) Algal taxon richness		(c) Algal assemblage structure		(d) Total algal biomass		(e) Algal taxon richness		(f) Algal assemblage structure	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<i>Patella</i>	1	0.9	0.35	0.1	0.82	0.4	0.8	1.1	0.31	0.9	0.34	0.9	0.5
<i>Littorina</i>	1	5.7	0.031	0.8	0.39	0.5	0.76	0.3	0.57	6.0	0.028	1.1	0.38
<i>Gibbula</i>	1	11.5	0.004	3.0	0.1	1.3	0.28	<0.1	0.89	1.6	0.22	2.6	0.026
<i>Patella</i> x <i>Littorina</i> x <i>Gibbula</i>	1	15.9	0.001	3.5	0.082	1.8	0.15	0.6	0.45	0.8	0.4	0.3	0.95

Table 3. SIMPER analysis of taxa contributing to dissimilarity in algal assemblages in response to nutrient enrichment in rock pools after 13 months. Mean Bray–Curtis dissimilarity = 44.02%

Taxon	Mean biomass (g)				
	Ambient	Enriched	Mean dissimilarity	Contribution (%)	Cumulative contribution (%)
<i>Ulva</i> spp.	13.39	15.92	14.04	31.9	31.9
<i>Scytosiphon lomentaria</i>	2.21	0.45	9.15	20.8	52.7
<i>Corallina officinalis</i>	0.83	0.5	5.3	12	64.7
<i>Fucus vesiculosus</i>	0.21	0.49	4.05	9.2	73.9
<i>Porphyra umbilicalis</i>	0.16	0.39	2.92	6.6	80.5
<i>Chondrus crispus</i>	0.07	0.12	1.94	4.4	85
<i>Punctaria latifolia</i>	0.1	0.07	1.63	3.7	88.7
<i>Ceramium rubrum</i>	0.06	0.03	1.44	3.3	91.9
<i>Palmaria palmata</i>	0.01	0.1	1.13	2.6	94.5
<i>Gelidium sesquipedale</i>	0.06	0.03	0.88	2	96.5
<i>Polysiphonia</i> spp.	0.01	0.6	0.87	2	98.5
<i>Ectocarpus</i> spp.	0.01	0.02	0.4	0.9	99.4
<i>Osmunda osmunda</i>	0.00	0.02	0.28	0.6	100

nutrient-enriched rock pools. Further, algal species richness was not affected by nutrient enrichment *per se*, but rather nutrient concentration determined some effects of loss of

grazer species on algal species richness. The presence of *Littorina* consistently led to a reduction in algal species richness, whereas *Gibbula* tended towards a positive effect on

Table 4. SIMPER analysis of taxa contributing to differences in algal assemblages with and without *Gibbula* present, in nutrient-enriched rock pools after 13 months. Mean Bray–Curtis dissimilarity = 55.82%

Taxon	Mean biomass (g)		Mean dissimilarity	Contribution (%)	Cumulative contribution (%)
	Absent	Present			
<i>Ulva</i> spp.	15.35	16.3	40.94	73.3	73.3
<i>Scytosiphon lomentaria</i>	1.03	0.07	3.84	6.9	80.2
<i>Fucus vesiculosus</i>	0.37	0.57	2.71	4.9	85.1
<i>Porphyra umbilicalis</i>	0.1	0.57	2.39	4.3	89.4
<i>Corallina officinalis</i>	0.27	0.67	2.15	3.9	93.2
<i>Palmaria palmata</i>	0.23	0.01	0.97	1.7	95.0
<i>Chondrus crispus</i>	0.17	0.09	0.95	1.7	96.7
<i>Punctaria latifolia</i>	0.14	0.02	0.5	0.9	97.6
<i>Polysiphonia</i> spp.	0.14	0	0.48	0.9	98.4
<i>Gelidium sesquipedale</i>	0.05	0.01	0.27	0.5	98.9
<i>Ceramium rubrum</i>	0.05	0.01	0.23	0.4	99.3
<i>Osmunda osmunda</i>	0.04	0	0.2	0.4	99.7
<i>Ectocarpus</i> spp.	0.04	0	0.18	0.3	100

species richness under ambient conditions and a negative effect in enriched pools. Algal assemblage structure was also affected by nutrient enrichment, which led to increases in ephemeral algae and fucoid species. However, contrary to what was expected, the presence of *Gibbula* enhanced the effects of nutrient enrichment by also increasing the biomass of algae, such as *Ulva* spp., *F. vesiculosus* and *P. umbilicalis*. It is possible that this may have been driven by the ability of *Gibbula*, with its fine brush-like radulae, to remove epiphytic diatoms (Hawkins & Hartnoll 1983; Hawkins *et al.* 1989) and enhance production of the macrophytes. This warrants further investigation to identify the exact mechanisms.

In contrast to our predictions, the loss of the limpet *Patella* did not lead to an increase in total algal biomass (O'Connor & Crowe 2005; Griffin *et al.* 2010) nor play a key role in any of the processes quantified. This is surprising given the established importance of limpets as key grazers on emergent rock (Jones 1946; Southward 1964; Hawkins & Hartnoll 1983; Sousa 1984; Farrell 1991; Jenkins *et al.* 2005; Coleman *et al.* 2006) and in rock pools in NW Europe (O'Connor & Crowe 2005; Noel *et al.* 2009; Griffin *et al.* 2010). Instead, the loss of *Littorina* and *Gibbula* often affected processes either at ambient or enriched conditions. Somewhat unexpectedly, algal biomass did not increase when none of the three grazer species were present. This indicates that the effect of the loss of *Littorina* was ameliorated by the presence of the remaining species. Alternatively, another mechanism other than grazing may control algal biomass in the absence of the three most abundant molluscan grazers. Our results therefore show that the effects of loss of species depend on both the identity and diversity of the species lost and of those present. This is a key point because previous studies based on the removal of all grazer species concluded that effects of their loss can be less important than nutrient enrichment (Worm *et al.* 2002; Worm & Lotze 2006; Masterson *et al.* 2008). However, the relative importance of total grazing pressure in comparison with nutrients varies among algal functional groups present and depends on background oceanic productiv-

ity conditions (Menge *et al.* 2003; Nielsen & Navarrete 2004; Burkepile & Hay 2006). Our results show for the first time that the effects of nutrient enrichment can determine the effects of grazer species loss (in terms of algal biomass and assemblage structure) and that, at ambient conditions, the loss of different species of grazer affects algal biomass in different ways (i.e. positively, negatively or neutral depending which grazer species are present). Importantly, we found that these effects differed from the effects of an overall reduction in grazing pressure (i.e. when none of the three grazer species were present). Thus, our findings indicate clearly that the effects of species loss are unlikely to be generalisable based on their functional role or predicted based on the effects of single-species removals (Emmerson *et al.* 2001; Bruno *et al.* 2005; O'Connor & Crowe 2005; Brandt, Witman & Chiriboga 2012).

Neither the reduction in algal biomass in the presence of *Littorina* nor the increased biomass in the presence of *Gibbula* under ambient conditions were driven by shifts in algal assemblage structure but rather by proportionally similar increases or decreases in all algal species. This is consistent with previous studies, which indicate that gastropod grazers may not exert a preference for certain algal species in rock pools (O'Connor & Crowe 2005; Griffin *et al.* 2010). It is also possible that effects of enclosure over time may have masked grazer food preferences. Algal assemblage structure was affected by nutrient enrichment, as expected, with enriched communities experiencing increases in ephemeral algae (e.g. *Ulva lactuca*, *Porphyra umbilicalis*; Worm *et al.* 2002; Worm & Lotze 2006). However, there were also increases in fucoids and red turf algae (e.g. *Chondrus crispus*) in enriched pools. Thus, although the effects of loss of grazer species on total algal biomass seem to have been negated by nutrient enrichment (an apparently antagonistic effect), these algal communities differed significantly in composition and structure. This difference in algal communities with nutrient enrichment has important implications for the interpretation of our findings. For example, by focussing on total algal

biomass it could be concluded that nutrient-enriched rock pools were resistant to grazer species loss, but these enriched communities comprised different algal assemblage structures from the ambient pools and may not be characterised by the same properties as the ambient assemblages in terms of key processes such as associated secondary production (Bruno *et al.* 2005; Stachowicz *et al.* 2008b; Bracken, Jones & Williams 2011). For example, nutrient-enriched rock pools were dominated by algae that are thought to be more palatable to grazers, such as *Ulva* spp. (Hawkins & Hartnoll 1983), potentially enhancing secondary production and leading to a resource-driven shift in trophic dynamics. Also, different algal species may contribute more to total primary productivity rates (Mann 1973; Bruno *et al.* 2005). Therefore, comparisons based on total algal biomass can conceal differences in the mechanisms driving individual algal taxa responses to biotic (grazing) and abiotic (nutrients) factors, which must be considered to understand how trophic (grazing) and non-trophic (competition among algal taxa) processes respond to changing environmental conditions (O'Connor & Donohue 2013; Williams, Bracken & Jones 2013; Mrowicki & O'Connor 2015).

Some unexpected results included the consistent negative effect of *Littorina* on algal species richness and the highly context-dependent effect that *Gibbula* had on algal assemblages. In contrast with classic theory, when none of the three grazer species were present, thus releasing dominant algae from grazing pressure (Connell 1978), and combined with nutrient enrichment (Worm *et al.* 2002; Hillebrand 2003), we recorded the greatest, rather than the lowest, algal taxon richness. A previous study (Griffin *et al.* 2010) found that algal taxon richness was correlated with total algal biomass and both were determined by the presence of *Patella*. Our results differed because both *Littorina* and *Gibbula* affected algal biomass, whereas *Patella* had no effect, and we did not observe a correlation between algal taxon richness and total algal biomass. Our findings highlight the difficulty applying general principles across different locations, even those with a similar suite of species and show that current ecological theories are inadequate to understand the mechanisms driving biodiversity patterns. Importantly, predictions based on current general models are unlikely to be useful for local effects, which is the scale usually most relevant for management decisions. Our results also highlight that care should be taken when exploitation strategies are focused on one species of grazer, such as the harvesting of winkles or limpets (e.g. Cummins *et al.* 2002; Martins *et al.* 2010), as we have shown that species-specific effects should be expected even within functional groups.

This study builds on earlier work, which examined the role of grazers on succession (Sousa 1984; Farrell 1991) and concluded that different consumer species may be important at different successional phases (Aguilera & Navarrete 2012). A key strength of our field study is that we incorporated several successional phases, which more accurately represents the impact of potential species loss on community development than removals from established communities (e.g. O'Connor

& Crowe 2005). We show that even within the guild, the presence of different grazer species alters the trajectory of algal communities and this interacts with environmental conditions (nutrients). We found no difference between algal communities in experimental pools at ambient conditions without any experimental treatments applied compared to other rock pools on the shore at the end of the experiment. Thus, we could infer that we had achieved a late successional phase in these 'control' pools and that the experimental treatments that differed from these represented a divergent assemblage.

Rocky shores are dynamic systems and only further longer-term studies will tell whether the observed responses to our experimental treatments will persist (Sousa 1984; Bertness *et al.* 2002). Previous studies identified how feeding rates and preferences may vary among grazing species in benthic systems (e.g. Lubchenco 1978; Duffy *et al.* 2001; Burkepille & Hay 2008). We have characterised how the loss of grazer species affects rock pool assemblages and their functioning. The next step is to integrate these findings to a whole food-web perspective by incorporating multiple trophic levels (Bruno & Cardinale 2008; O'Connor *et al.* 2013). It is unclear how the indirect effects of predation could alter community dynamics in rock pools and we should not assume that it would be similar to processes described for emergent rock because competitive interactions among benthic species can vary under different predatory regimes and environmental conditions (Lubchenco & Menge 1978; Poore *et al.* 2012; O'Connor & Donohue 2013; Mrowicki, Maggs & O'Connor in press).

Although our experimental design did not incorporate tests for density dependence, it was akin to simulated species loss experiments and is an essential first step required to unravel complicated processes. Further studies should include explicit tests for density effects of species loss and the remaining grazer species (Benedetti-Cecchi 2004; He *et al.* 2005; O'Connor & Crowe 2005; Hensel & Silliman 2013). Comparisons of rare and common species should also be considered where practical to fully investigate the potential for less common species to provide resistance or resilience to perturbations in highly dynamic systems (Walker 1992; Benedetti-Cecchi 2004; Matias *et al.* 2012).

In conclusion, this study has identified specific interactions between effects of species loss and environmental conditions in a marine benthic system and highlights the wide range of outcomes that can arise from interactions between algal communities and their grazers. The study also highlights the importance of context dependency when designing and interpreting BEF experiments. This is particularly important in the context of multiple human impacts and the relative importance of species loss compared to other drivers of environmental change such as nutrient enrichment (Crain 2008; Tilman, Reich & Isbell 2012). Much more empirical research is required to provide accurate data, which is essential to develop BEF models that incorporate interactions under different environmental conditions (Boyer, Kertesz & Bruno 2009; Godbold & Solan 2009; Cardinale *et al.* 2012). Future studies should, therefore, examine realistic species loss scenarios under predicted and current levels of anthropogenic

stresses at appropriate scales to yield findings that can be better incorporated into ecosystem management (Bracken *et al.* 2008; Naeem 2008; Crowe, Bracken & O'Connor 2012; O'Connor & Donohue 2013).

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Data accessibility

Data are available at <http://dx.doi.org/10.5061/dryad.r2c26>.

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