BIODIVERSITY LOSS AND ECOSYSTEM FUNCTIONING: DISTINGUISHING BETWEEN NUMBER AND IDENTITY OF SPECIES

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Abstract. Given currently high rates of extinction, it is critical to be able to predict how ecosystems will respond to loss of species and consequent changes in community structure. Much previous research in this area has been based on terrestrial systems, using synthetically assembled communities. There has been much less research on inter-trophic effects in different systems, using in situ removal experiments. Problems with the design of early experiments have made it difficult to determine whether reductions in ecosystem functioning in low diversity treatments were due to the number of species present or merely to the reduced likelihood of including particular ("key") species or functional groups. We established a field experiment, using cage enclosures, to test whether the number or identity of grazing gastropods present would affect the diversity and productivity of intertidal algal communities. We found that there was no relationship between ecosystem functioning and diversity per se, but that different species had idiosyncratic effects. This appears to be a common feature of intertidal systems, which often contain strongly interacting species. In this case, the limpet *Patella ulyssiponensis* was the most influential primary consumer. Additional treatments enabled us to test the potential for other grazers to compensate for its loss. Early results (after four months) suggested that compensation was possible, implying potential redundancy of *P. ulyssiponensis*. This effect disappeared after 13 months, however, highlighting the context dependence of so-called redundancy and underlining the importance of long-term field-based experiments in this area.

Key words: algae; biodiversity; ecosystem functioning; gastropod; grazer; Ireland; Patella ulyssiponensis; *removal experiment; rocky shore; species identity; species loss.*

INTRODUCTION

Given currently high rates of extinction (Regan et al. 2001) and potential loss of ecosystem "goods and services" (Costanza et al. 1997), there is a clear need to understand the consequences of loss of biodiversity for the functioning of ecosystems (Daily et al. 1997, Heip et al. 1998, Chapin et al. 2000). Although the view that species richness is beneficial for ecosystem performance is widely endorsed (Tilman et al. 1996, Naeem et al. 1999), it is not accepted universally (Givinish 1994, Grime 1997, Wardle et al. 2000). Predicting the effects of species loss has proven complicated (Chapin et al. 1992), and the consequences for ecosystem functioning are hotly debated (Tilman 1999, Waide et al. 1999, Schwartz et al. 2000, Wardle et al. 2000, Mooney 2002, Naeem et al. 2002).

Research originally revolved around three main models to predict the relationship between diversity and ecosystem functioning: redundancy, rivet, and idiosyncratic (reviewed by Lawton 1994). More recently, Naeem et al. (2002) proposed a revised classification of models into three groups: "species are primarily redundant," "species are primarily singular," and "species impacts are context dependent." A key area

of debate in discriminating among these models is whether reductions in ecosystem functioning in low diversity treatments are due to the number of species present or merely to the reduced likelihood of including some particular ("key") species in those treatments (Grime 1997). In response to this, a wide range of experimental designs has emerged. Different designs, however, tend to have more power to detect either the effects of species number or the effects of species composition (Allison 1999). Only in low diversity situations can experiments discriminate between the two classes of model (Allison 1999).

The redundancy model was also controversial (Gitay et al. 1996) and has been recast in a more positive light as "biological insurance" (Lawton and Brown 1994, Yachi and Loreau 1999). Simulations provide clear support for the concept that other species may compensate for lost species and thus buffer ecosystem function against changing environmental conditions (Yachi and Loreau 1999). There have been few experimental tests, however, examining the potential for other species to fulfill the functional role of a removed species (Lawton and Brown 1994, Ruesink and Srivastava 2001, Bolam et al. 2002, Allison 2004).

Many experiments testing biodiversity-functioning models to date have been carried out in laboratory mesocosms of artificially created systems (e.g., Naeem et al. 1994), known as Synthetic Assemblage Experiments

(Diaz et al. 2003). Such laboratory-based experiments are useful for examining potential effects in nature, but are subject to a large number of experimental artifacts (Lamont 1995, Carpenter 1996, Kampichler et al. 2001). Most field experiments have also involved synthetically assembled communities in horticultural settings (e.g., Tilman 1997, Hector 1998). Recently, there have been calls for experiments specifically investigating the loss of species by their removal from a natural system, preferably in situ (Biles et al. 2003, Diaz et al. 2003). Field experiments based on the removal of species are more representative of the natural world and also allow for tests of compensation by other species (Schläpfer and Schmid 1999, Loreau 2000, Diaz and Cabido 2001). Long-term field experiments also allow tests of the effects of natural temporal variation in environmental conditions on the relationship between biodiversity and ecosystem function (Power et al. 1996, Wellnitz and Poff 2001). This is particularly important when testing redundancy or biological insurance hypotheses, as a wide range of contexts must be explored to even begin to determine whether a species is ecologically "redundant" (Yachi and Loreau 1999, Crowe, *in press*).

Research into the effects of loss of species on ecosystem functioning has been dominated by experiments within a single trophic level, usually primary producers (Petchey et al. 2004*a*). Diversity changes at one trophic level can have profound impacts on processes at other levels (McNaughton et al. 1988, Menge 1995, Power et al. 1996, Haddad et al. 2001, Hillebrand and Cardinale 2004). To date, there have been few studies examining the inter-trophic effects of species loss (Holt and Loreau 2002, Raffaelli et al. 2002, but see Stephan et al. 2000, Finke and Denno 2004, Hillebrand and Cardinale 2004). This lack of data means that trophic interactions are not incorporated into the current framework of biodiversity–ecosystem functioning theory (Duffy 2002, Raffaelli et al. 2002). The focus on primary producers has led to the neglect of potentially more complex effects of loss of animal diversity, whose impacts may be mediated through indirect interactions involving multiple trophic levels (Wootton 1994, Polis and Strong 1996, Downing and Leibold 2002, Holt and Loreau 2002).

Marine systems are potentially valuable for testing these issues because they have high levels of metazoan phylogenetic diversity (Steele 1991, May 1994, Vincent and Clarke 1995, Giller et al. 2004). To date, this potential has been underutilized (Schläpfer and Schmid 1999, Loreau et al. 2001, Emmerson and Huxham 2002). Marine ecosystems behave differently from terrestrial systems (Steele 1985, Cyr and Pace 1993, Giller et al. 2004), and it is important that we improve our knowledge of biodiversity–ecosystem functioning relationships in marine and other systems so that general and specific understanding can emerge (Chase 2000).

Random species loss has been assumed in many previous experiments (e.g., Naeem et al. 1994, McGrady-Steed et al. 1997). This may not reflect natural situations (Wardle 1999, Huston et al. 2000, Schwartz et al. 2000). Species loss is not random when the major drivers of this loss and the responses of individual species are known (Vitousek et al. 1997, Loreau et al. 2001, Grime 2002). Although documented global extinctions are rare in the marine environment, local extinctions and dramatic changes in abundance are widespread. To maximize the practical value of research into effects of loss of species, it should be targeted toward species vulnerable to local extinction and whose loss may affect provision of important ecosystem goods and services.

Rocky shores are highly productive and are significant providers of detrital material to other coastal ecosystems (Whittaker 1975, Raffaelli and Hawkins 1996). Such detrital material is largely derived from macroalgae; on shores that are dominated by microalgae, much of the primary production passes directly into a diverse assemblage of in situ grazers (Mann 1973, Miller and Mann 1973, Raffaelli and Hawkins 1996, Leguerrier et al. 2003). Changes in cover of macroalgae are therefore likely to affect significantly the flow of energy from the shore to the coastal system as a whole. On many shores, cover of macroalgae is controlled by the presence of grazing gastropods (Underwood 1980, Hawkins and Hartnoll 1983). Among the most influential species, are patellid limpets (Jones 1946, Southward 1964, Hawkins 1981, Underwood and Jernakoff 1981, Beovich and Quinn 1992, Boaventura et al. 2002, Hawkins et al. 1992) and littorinids (Lubchenco and Menge 1978, Bertness et al. 1983, Petraitis 1983). These species are threatened by harvesting in many parts of the world (Thompson et al. 2002) and are sensitive to pollution (Cummins et al. 2002, Féral et al. 2003). At a local scale, it is thus likely that one or more species of such gastropods may suffer periodic dramatic loss of abundance or extinction, with as yet unknown consequences for ecosystem functioning. They also provide a tractable model system for field-based in situ experiments.

In this study, we designed a field experiment to test whether loss of diversity of grazing gastropods would affect the diversity and cover of macroalgal communities in rock pools on an Irish shore. By examining the effects of loss of selected combinations of species, we examined the effect of reducing the number of species and distinguished it from the effect of losing particular species (Beovich and Quinn 1992, Schmitt 1996, Duffy 2002, Hooper et al. 2002).

Furthermore, treatments were incorporated to enable a direct test of the insurance hypothesis, involving the replacement of lost species with their equivalent biomass of other species and by allowing other non-manipulated species access to the experimental plots. From an assemblage of grazers, we simulated loss of

combinations of the three dominant species of gastropod: *Patella ulyssiponensis*, *Littorina littorea*, and *Gibbula umbilicalis*. Our target variables were: (1) total algal cover; (2) total accumulated algal biomass, and (3) algal assemblage structure. The first two variables are indicators of change in ecosystem functioning, in terms of potential detrital export, while the third measures community level effects among the primary producers. Algal cover and assemblage structure were measured several times during the experiment and destructive samples were taken at the end to measure accumulated algal biomass. Evidence from similar systems suggested that *P. ulyssiponensis* may emerge as a key species in this system (Jones 1946, 1948, Southward 1964, Hawkins 1981, Hawkins and Hartnoll 1983, Hawkins et al. 1992, Paine 2002). To test this hypothesis, planned comparisons were made among treatments with and without *P. ulyssiponensis* that each contained different combinations of grazers and different numbers of grazers. We tested the following models: (1) It is the identity not the number of dominant species of grazer that affects the structure and functioning of algal assemblages; (2) *P. ulyssiponensis* is a likely key species in this system, and (3) an increase in abundance of other grazers can compensate for the loss of certain species. The experiment ran for over a year to test the context dependency of the findings.

METHODS

Experimental model system

The experimental site was an exposed rocky shore on the southwestern coast of the island of Muighinis, near Carna, County Galway, Ireland. The shore comprised an outcrop of relatively flat undulating granite, which contained many shallow rock pools with similar assemblages of algae and grazing gastropods. Pilot surveys of the rock pools found a wide diversity of macroalgae and several species of grazer. Algal assemblages comprised several species of brown algae (e.g., *Fucus serratus* × *spiralis* hybrid), ephemeral and perennial green algae (e.g., *Enteromorpha* spp. and *Codium* sp.), and many species of encrusting and branching red algae (e.g., *Lithothamnion* spp. and *Gelidium* sp.). The algal assemblage is described more fully in the *Results* section. The most abundant species of grazing gastropods were *P. ulyssiponensis*, *L. littorea*, and *G. umbilicalis*, occurring at average densities of 10, 6, and 13 individuals/m², respectively. Although these species are all grazing gastropods and belong to the same "functional group" or "guild" (Simberloff and Dayan 1991, Wilson 1999), they each have different modes of feeding (Steneck and Watling 1982, Hawkins and Hartnoll 1983, Hawkins et al. 1989, Hill and Hawkins 1991) and different dietary preferences (Lubchenco 1978, Watson and Norton 1985, Imrie et al. 1989, Chapman and Johnson 1990) and might be expected to affect algal assemblages in different ways. Although

these are the only species we experimentally removed, other grazing gastropods were present. Four additional gastropod species were observed within the experimental plots during the experiment (*Patella pellucidum*, *Gibbula cineria*, *Littorina obtusata*, and *Littorina mariae*), as were the chiton *Leptochiton asellus*, and mesograzers such as amphipods. The other species, however, occurred at much lower densities. For example, the next most abundant species of gastropod was *Littorina obtusata*, approximately one individual of which was found in every 23 plots (equivalent to 0.36 individuals/m²) and one *Leptochiton asellus* was found in every 46 plots (equivalent to 0.18 individuals/m²). Mesograzers such as amphipods were present on the shore but were very rarely observed within the rock pools. We therefore manipulated all of the grazers likely to have a significant impact on macroalgal cover (Lubchenco 1978, Hawkins and Hartnoll 1983, Hawkins et al. 1989, Boaventura et al. 2002). The presence of other species of grazers was important, however, as it allowed us to test the redundancy (replaceability) of the manipulated species. The other species of grazer that were not manipulated were present at approximately natural densities.

Experimental design

The experiment was run for 13 months from July 2002. In total, 12 treatments were included in the experiment and subsets of these were analyzed to test the specific hypotheses. Six of these treatments were used to test hypotheses derived from models (1) and (2) that predict the effect of loss of biodiversity on ecosystem functioning and the role of *P. ulyssiponensis* (Table 1a). Each of these treatments had one, two, or three species of grazer removed. Two separate analyses were carried out. First, a nested design was used to assess contributions from species identity and richness by partitioning the variance between identity nested in richness (Schmid et al. 2002, Giller et al. 2004). Two pairs of treatments each had the same number, but different identities of species removed. Treatments B and C each had one species removed and treatments D and E each had two species removed. Two-factor nested analyses of treatments B, C, D, and E allowed us to separate the effects of overall species number from those of a particular species (i.e., "species identity"). The factors were "number of species lost," and "identity of species lost," the latter being nested in the former. This test does not, however, identify which species (if any) affected the variable being measured. Separate analyses of all six treatments tested for the effect of loss of a particular species, *P. ulyssiponensis*. Planned comparisons were made of six treatments, three of which involved the removal of *P. ulyssiponensis* (B, D, F) with three that did not (A, C, E), allowing a direct test of the key role of *P. ulyssiponensis*, in this system. Factor one was the presence or absence of *P. ulyssiponensis*,

TABLE 1. Subsets of experimental treatments that were compared to test different hypotheses.

Treatment and code	No. species removed	Species removed	Compensation	Cage present
a) Species number or identity				
A	0			
B	1	P		
C	1	L		
D	2	P, L		
E	2	L, G		
F	3	P, L, G		
b) Biomass compensation				
B	1	P	−	
G	1	P	+	
C	1	L	−	
H	1	L	+	
D	2	P, L	−	
I	2	P, L	+	
E	2	L, G	−	
J	2	L, G	+	
c) Cage effect				
A	0			−
K	0			+
B	1	P		−
L	1	P		+

Notes: (a) Treatments used to assess whether species number or identity affected algal cover, biomass, and assemblage structure, $n = 4$ plots. A subset of these treatments (B, C, D, E) was analyzed using nested ANOVA to differentiate between the effects of species diversity and species identity (see *Methods: Experimental design* for details). A second analysis compared treatments with *Patella ulyssiponensis* (A, C, E) and those without *P. ulyssiponensis* (B, D, F). (b) Treatments analyzed to test the effect of compensation for lost biomass of grazers, $n = 4$ plots. (c) Treatments analyzed to test for cage artifacts, $n = 3$ plots. For full explanations of each analysis refer to the *Methods: Experimental design*. P, *P. ulyssiponensis*; L, *Littorina littorea*; and G, *Gibbula umbilicalis*.

and factor two was the combination of species lost (nested in factor one).

When species were removed, the overall biomass of grazers present was also reduced. This may mimic effectively the situation in nature when a species has been driven locally extinct. Any subsequent changes in algal cover, biomass, and assemblage structure could, however, be due either to the lower number of species of grazers present or to the reduced biomass of grazers (Likens 1985, Lawton and Brown 1994, Ruesink and Srivastava 2001, Bolam et al. 2002). It is also possible that when one species goes extinct, other species would increase in number and compensate for the loss of species, as predicted by the redundancy (Walker 1992) and insurance models (Lawton and Brown 1993, Yachi and Loreau 1999). To test the potential confounding influence of biomass and the potential for compensation, we established a second set of treatments to control for the effect of the reduction in grazer biomass. For each of the treatments involving the removal of one or two species a comparable treatment was established in which additional individuals of the remaining species were added, equivalent to the loss of biomass of the

species removed (Table 1b). Analyses were done on eight of the treatments (B, C, D, E, G, H, I, J), in which the factors were ''number of species lost,'' ''identity of species lost'' (nested in number of species lost), and ''compensation for loss of biomass.''

The number of individuals added to compensate for loss of biomass was calculated by measuring the average biomass of each species. The relationship between shell length and dry mass was determined using samples of 30 individuals of each species. The average biomasses of the three manipulated grazers were: *P. ulyssiponensis*, 16 g; *L. littorea*, 6 g; and *G. umbilicalis*, 3 g. Appropriate numbers were added so that the overall total average biomass was maintained. The impacts of species loss on ecosystems were thus evaluated based on natural patterns of species abundances that reflect their contributions to ecosystem functioning (Schwartz et al. 2000, Grime 2002, Loreau et al. 2002). The average density in rock pools of the three manipulated grazers was calculated as 10 individuals/m² (mean ± 2 SE) for *P. ulyssiponensis*, 6 m⁻² (SE ± 1) for *L. littorea*, and 13 m⁻² (SE ± 3) for *G. umbilicalis*. When a species was included in a treatment, it was present at natural density, and individuals of different sizes were selected so that any effect the species may have at any stage in its adult life would be incorporated (Geller 1991, Keough et al. 1997, Boaventura et al. 2003).

Several methods of manipulating individual species of grazer with minimal experimental interference were tested, but the only effective method of controlling all three species was enclosure of experimental areas using cages with roofs. Cages can change the flow of water, moisture, shading, and other factors that may affect algae and grazers (Underwood 1980, Stocker 1986, Benedetti-Cecchi and Cinelli 1997). It was therefore possible that the cages may have introduced experimental artifacts (Underwood 1980, Menge and Lubchenco 1981, Vadas 1985). Control areas were, thus, marked on the shore and left open to ambient densities of all species, to allow us to detect any effect of the cage on algal assemblages. Comparison of unmanipulated plots only controls for the effect of the cage when no species have been removed. Potential artifacts may vary among treatments, confounding the results of the experiment (Johnson 1992, Peterson and Black 1994, Benedetti-Cecchi and Cinelli 1997). Another control for the effects of the cage was, therefore, added to control for the effect of the cage in treatment B, in which all *P. ulyssiponensis* were removed (Table 1c). This control area was also marked on the shore and all *P. ulyssiponensis* were manually removed from the immediate and surrounding area. Analyses were done on four of the treatments (A, K, B, L), in which the factors were ''number of species lost,'' ''identity of species lost'' (nested in number of species lost), and ''cage effect.'' In this way, variation in artifacts among treatments was assessed. Four replicate plots were assigned randomly

to each of the main treatments and three replicates were used for each of the two control treatments. The percentage cover of each algal species was sampled within each plot prior to establishing the treatments, and these baseline data were analyzed using NP-MANOVA (Anderson 2001). This analysis indicated that there were no initial systematic differences among algal assemblages in the experimental plots assigned to the different treatments.

Field and laboratory methods

Experimental plots were established along ~800 m of shore at about midtidal level. Cages were constructed within individual rock pools or on the edges of larger rock pools and all had a maximum water depth of ≤14 cm at low tide. Although pools on the shore ranged in size (approximately) from 0.5 to 25 m² and were up to 1 m deep, experimental plots were all established in pools from 0.5 to 10 m² in area and were generally 3–8 cm deep. None of the experimental pools was steep sided or contained significant crevices. The cages consisted of square fences, measuring 35 × 35 cm, made of stainless steel mesh (0.9-mm wire diameter, 4.17-mm aperture, 67% open area). They were 12 cm high, to allow for growth of algae. The fences were attached to the shore by drilling holes into the rock with a hammer action drill and securing the sides of the fences with stainless steel screws and washers. The roofs were also made from stainless steel mesh (0.6-mm wire diameter, 3.55-mm aperture, 73% open area). The roofs were attached to the tops of the fences and fixed with cable ties. This mesh size permitted access to the plot by many of the other grazers on the shore, many of which were smaller and/or more flexible than the manipulated species.

Cages were checked and maintained monthly. The number of grazers present in each plot was checked and maintained at the appropriate density for each treatment. The cages proved an efficient method of controlling the presence and abundance of all three species, with only occasional deviations from the assigned densities. Small juveniles of the manipulated species of grazer (<4.2 mm) occasionally entered all cages and were removed when necessary. Previous research has indicated that the presence of juvenile grazers such as these had no effect on algal assemblages (Benedetti-Cecchi 2000). The cages were scrubbed with a wire brush to remove any algae that built up on the roofs or fences.

After four and 13 months, percentage cover of the algal species present was sampled. To sample algal cover and assemblage structure, a 25 × 25 cm quadrat was placed in the center of each plot. The edge of the plot was not sampled to avoid sampling algae influenced strongly by the cage walls. Algal cover was estimated by identifying all species present under each of 64 intersections. Pilot trials had shown no loss of accuracy or precision by using 64 intersections rather

than 100. The quadrat was double-strung to prevent parallax error. Species within the quadrat that did not match any intersection point were also recorded and assigned a value of 1% cover. Algae were identified to species or as far as possible using Brennan (1950), Hiscock (1979, 1986), and advice from experts at the Martin Ryan Institute, National University of Ireland, Galway (particularly C. Loughnane).

The experiment was run for 13 months. Destructive samples were taken to measure accumulated algal biomass. At this time, all algae were removed from the 25 × 25 cm sampling area within each experimental plot. Algae were oven-dried at 70°C until they reached constant mass. Any sand that was mixed in with the algae was removed from the dried algae, although this was not possible in samples that contained a high proportion of *Corallina*. To correct the mass for sand that may have been accidentally included with the algae, five additional samples of *Corallina* (core of 10 × 10 cm) were taken from rock pools along the shore. These samples were then dried and weighed both before and after all the sand was carefully removed under a light microscope. By subtracting the difference, the average mass of sand contained per gram of *Corallina* was calculated and this correction factor was applied to the mass of *Corallina* occurring in each sample.

Statistical analyses

Analysis of variance (ANOVA) was used to test hypotheses involving total algal cover and total accumulated biomass. Analyses were done on data collected after four months (algal cover only) and 13 months (algal cover and accumulated biomass). GMAV version 5 for Windows was used for computations (Underwood and Chapman 1998). Cochran's test was used to test for homogeneity of variance. Variances were not heterogeneous and data were not transformed. Student-Newman-Keuls procedure was used to make post hoc comparisons among levels of significant terms. Where appropriate, post hoc pooling or elimination of terms was used to improve power of relevant tests (Winer et al. 1991, Underwood 1997). All nested factors are displayed in parentheses in the analysis tables.

Nonparametric multivariate analyses of variance (NP-MANOVA; Anderson 2003) were used to test hypotheses about algal assemblage structure. These data were square-root transformed to reduce the influence of the most abundant species on overall assemblage structure (Clarke and Warwick 2001). Nonmetric multidimensional scaling (nMDS) was used to produce two-dimensional ordinations to compare assemblage structure among treatments (Field et al. 1982, Clarke 1993). PRIMER-E (*Plymouth Routines in Multivariate Ecological Research*) version 5 was also used to run SIMPER (Similarity of Percentages) analyses to identify which species were important in discriminating among samples (Clarke and Gorley 2001). All multivariate analyses were done using Bray-Curtis similarity
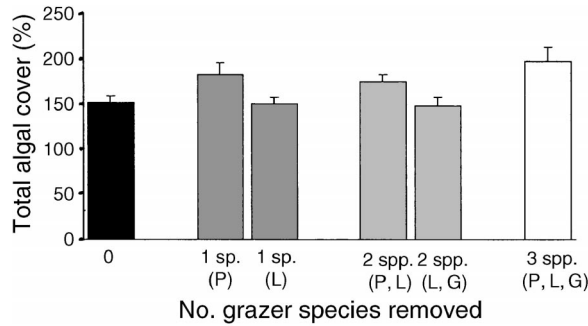
FIG. 1. Total algal cover (mean + SE; n = 4 plots) in treatments containing different numbers and identities of species after 13 months. The letters P, L, and G refer to the gastropod grazers removed in each treatment: *Patella ulyssiponensis*, *Littorina littorea*, and *Gibbula umbilicalis*, respectively.

coefficients (Bray and Curtis 1957, Clarke and Warwick 2001).

RESULTS

Distinguishing influence of identity vs. diversity of species and testing the importance of *P. ulyssiponensis*

When all species were present, the average total percentage of algal cover in the experimental plots was ~150% (Fig. 1). Algal cover did not increase progressively with increasing loss of diversity or grazers, but instead varied according to the identity of species lost (Fig. 1, Table 2). Comparisons of the three treatments with and without *P. ulyssiponensis* identified *P. ulyssiponensis* as a key species in this system, whose loss led to an increase in algal cover regardless of the presence or absence of other species (Fig. 1, Table 3). The total accumulated biomass showed a similar trend to algal cover, but no effect was found (Table 3). A significant increase in total accumulated biomass occurred, however, in treatments from which *P. ulyssiponensis* was removed (Table 3). These findings were similar to those after four months (Table 2).

There was no change in assemblage structure, therefore, this increase in total algal abundance resulted from an increase in nearly all the branching algae (Fig. 2, Table 4). The average differences in assemblages with *P. ulyssiponensis* present from those without *P. ulyssiponensis* were due to an increase in abundance

of most of the algal taxa, namely a *F. serratus × spiralis* hybrid, *Enteromorpha* sp., *Ulva* sp., *Ceramium* sp., *Corallina* sp., *Gelidium pulchellum*, *Ecotcarpus* agg., *Codium tomentosum*, and *Leathesia difformis*, and a decrease in abundance of the encrusting red algae "*Lithothamnia*" and *Hildenbrandia* spp. (Table 5). Seventeen algal taxa were counted in the plots with *P. ulyssiponensis* and 15 in those without (Table 5). The red alga *Osmunda pinnatifida* was recorded only once, in a plot that contained *P. ulyssiponensis*. Three species of compressed red alga *Osmunda osmunda*, *Chondrus crispus*, and *Palmaria palmata*, only occurred in plots from which *P. ulyssiponensis* had been removed.

Compensation by other species for the loss of extinct species

After four months it appeared that remaining species could compensate for the loss of *P. ulyssiponensis*, the species that most affected algal cover (Fig. 3a, Table 6). The treatments that contained increased biomass of *L. littorea* and *G. umbilicalis* appeared to fulfill the role of *P. ulyssiponensis* and algal cover levels remained around the average level of 150%. After 13 months, however, at increased densities, *L. littorea* and *G. umbilicalis* did not compensate for the loss of *P. ulyssiponensis*, and the levels of algal cover remained significantly higher than average (Fig. 3b, Table 6). No effect of compensation was detected on algal biomass.

Cage effects

The presence of cages did not have a significant effect on algal cover (Fig. 4, Table 7). After four months there was a nonsignificant trend (i.e., $P > 0.05$), for reduced cover of algae in cages without *P. ulyssiponensis* compared to open plots without *P. ulyssiponensis*. This was mainly attributable to a reduction in *Enteromorpha* spp. inside the cages. After 13 months, however, cages had no effect on algal cover. The cages had no effect on algal biomass or algal assemblages (Tables 4c and 7).

DISCUSSION

This experiment showed that in rock pools, the loss of species of grazer affected algal cover depending on the identity of the species lost. It was not a reduction in species diversity per se that affected algal cover or biomass; loss of *P. ulyssiponensis* caused increased

TABLE 2. ANOVA to test effects of removing different numbers of species of different identities on algal cover and total algal biomass accumulated at the end of the experiment; $n = 4$ plots.

| Source of variation | df | Algal cover | | | | | | Total algal biomass | | |
| | | After 4 mo | | | After 13 mo | | | | | |
		MS	F	P	MS	F	P	MS	F	P
Number, N	1	72.25	0.01	0.92	111.24	0.06	0.83	178.21	0.07	0.82
Identity, I(N)	2	5267.13	19.08	0.00	1792.14	4.54	0.03	2687.52	2.51	0.12
Residual	12	276.13			394.54			1068.93		

TABLE 3. ANOVA of planned comparisons of different combinations of grazers with and without *P. ulyssiponensis* on algal cover and total algal biomass accumulated at the end of the experiment; $n = 4$ plots.

| | | Algal cover | | | | | | Total algal biomass | | |
| | | After 4 mo | | | After 13 mo | | | | | |
Source of variation	df	MS	F	P	MS	F	P	MS	F	P
P. ulyssiponensis, P	1	7975.26	10.44	0.03	7360.94	29.39	0.01	6279.62	13.83	0.02
Combinations, C(P)	4	764.26	2.65	0.07	250.45	0.54	0.71	453.92	0.30	0.87
Residual	18	288.15			461.32			1489.81		

cover of macroalgae regardless of the presence or abundance of other species of grazer. Other studies have shown ecosystem functioning to differ dramatically depending on the identity of species lost (Hooper and Vitousek 1997, Mikola and Setälä 1998, Symstad et al. 1998, Emmerson et al. 2001, Ruesink and Srivastava 2001). Such idiosyncratic effects appear to be prevalent in intertidal systems (Scheibling 1994, Jernakoff and Nielsen 1997, Parker et al. 2001, Paine 2002) and removals of more than one species often result in complex interactive effects (Crowe, *in press*), suggesting that it will not be possible to make precise predictions about the functioning of ecosystems based purely on the numbers of species present. It is thought that idiosyncratic effects are more likely to occur in systems with key species than in systems with weak or diffuse effects on consumers (Allison et al. 1996, Crowe, *in press*).

Much of the previous research that also supported the ''idiosyncratic'' model involved Synthetic Assemblage Experiments (Naeem and Li 1998, Norberg 2000, Duffy et al. 2001, Diaz et al. 2003). The current experiment is one of the few designed specifically to test the effect of loss of species on ecosystem functioning that has been carried out in situ on a complete assemblage (other examples include Allison 2004, Finke and Denno 2004). Although the scale of manipulation was small, it was appropriate to the system under investigation. Analysis of control treatments indicated that the results from within our cages are applicable to natural pools at the study location. As long as such controls are incorporated, such in situ removal experiments generally yield results that are more applicable to the natural world than laboratory-based synthetic assemblage experiments (Biles et al. 2003, Diaz et al. 2003).

Field-based removal experiments also allow effective tests for compensation by other species present for the functions of those lost (Schläpfer and Schmid 1999, Loreau 2000, Diaz and Cabido 2001). In the current experiment, other species (including those we manipulated and those that were naturally present) were, in the end, unable to compensate for the loss of *Patella ulyssiponensis*. Biological insurance would not have been fully effective in this case. Had the experiment been stopped after four months, however, when compensation by increased abundance of *L. littorea* and *G. umbilicalis* was effective (see *Results*), we would have concluded falsely that *P. ulyssiponensis* was replaceable in this system. The effects of species loss are often context dependent (Paine 1995, Risser 1995, Chapin et al. 1998, Van der Heijden et al. 1998). The impact of grazers on intertidal assemblages, for example, depends on the timing and intensity of recruitment of

○ P, L, and G removed △ P removed □ P and L removed
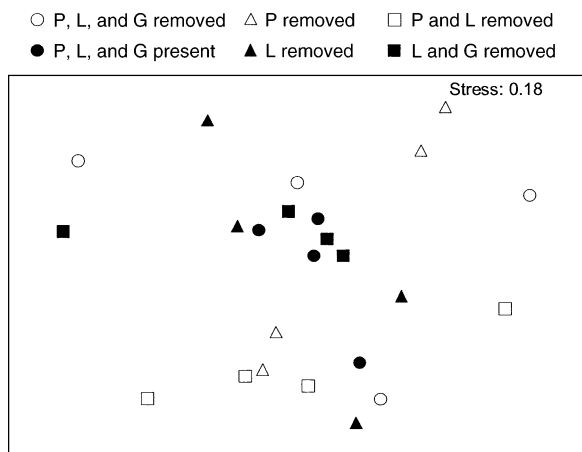● P, L, and G present ▲ L removed ■ L and G removed

FIG. 2. Nonmetric multidimensional scaling (nMDS) of algal assemblages under six different combinations of grazers, taken after 13 months (square-root transformed). Open symbols represent plots that had *P. ulyssiponensis* removed; filled symbols represent those in which *P. ulyssiponensis* remained. Species abbreviations (P, L, G) are as in Fig. 1.

TABLE 4. Nonparametric MANOVA comparisons of algal assemblage structure after 13 months in treatments with (a) different numbers of species lost and of different identities of species lost, $n = 4$ plots; (b) planned comparisons on different combinations of species with and without *P. ulyssiponensis*, $n = 4$ plots; and (c) with and without cages and with and without *P. ulyssiponensis*, $n = 3$ plots.

Source of variation	df	MS	F	P
a) Number, N	1	843.94	1.63	0.34
Identity, I(N)	2	518.38	0.76	0.71
Residual	2	679.88		
b) *P. ulyssiponensis*, P	1	1156.03	1.43	0.20
Combinations, C(P)	4	806.19	1.30	0.20
Residual	18	620.18		
c) *P. ulyssiponensis*, P	1	985.43	1.60	0.20
Cage = C	1	1539.55	2.49	0.05
P × C	1	423.24	0.69	0.63
Residual	8	616.96		

TABLE 5. SIMPER analyses of taxa contributing to differences in algal community structure in response to the loss of *P. ulyssiponensis* after 13 months; *n* = 4 plots.

Taxa	Avg. abundance		Avg. diss.	Diss. SD	Contrib. (%)	Cumulative (%)
	P present	P absent				
Fucus serratus × *spiralis* hybrid	2.75	14.42	4.92	1.23	13.62	13.62
"Lithothamnia"	33.75	24.33	3.87	1.28	10.71	24.32
Enteromorpha spp.	16.67	18.58	3.73	1.18	10.33	34.65
Ulva spp.	1.33	6.75	3.44	0.98	9.53	44.18
Ceramium rubrum	3.92	5.42	3.30	1.55	9.14	53.33
Corallina spp.	30.83	36.92	2.95	1.31	8.17	61.49
Gelidium pulchellum	2.08	2.33	2.50	1.95	6.93	68.42
Ectocarpus agg.	1.08	3.17	2.34	0.90	6.47	74.89
Codium tomentosum	0.25	2.75	1.68	0.65	4.65	79.54
Hildenbrandia spp.	0.92	0.42	1.53	1.14	4.24	83.78
Osmunda hybrida	0.58	0.92	1.39	1.15	3.84	87.62
Scytosiphon lomentaria	0.67	0.67	1.38	1.00	3.83	91.45
Leathesia difformis	0.17	0.92	1.19	0.78	3.29	94.73
Cladophora spp.	0.25	0.17	0.59	0.53	1.62	96.35
O. pinnatifida	0.00	0.58	0.58	0.41	1.61	97.96
O. osmunda	0.25	0.00	0.39	0.44	1.09	99.05
Palmaria palmata	0.08	0.00	0.18	0.30	0.49	99.54
Chondrus crispus	0.08	0.00	0.17	0.30	0.46	100.00

Notes: Average Bray-Curtis dissimilarity = 36.12. Key to abbreviations: Avg. abund., average abundance of each taxa under treatments with and without *P. ulyssiponensis* (P), Avg. diss., average dissimilarity contributed by each taxon; Diss. SD, measure of the variation in contribution to dissimilarity (Clarke 1993); Contrib. (%), percentage contributed to the overall Bray-Curtis dissimilarity between communities with and without *P. ulyssiponensis* present.

algae and other organisms that may themselves be temporally variable (Underwood et al. 1983, Farrell 1991, Benedetti-Cecchi 2000). Such context dependency must be considered to determine the value of the biological insurance provided by so-called redundant species (Hector et al. 2001, Crowe, *in press*). As it is not possible to manipulate or include all environmental circumstances within the design of any experiment, experiments must be run for a sufficient length of time that the environmental context can vary considerably (Allison et al. 1996, Cardinale et al. 2000, Crowe, *in press*). The influence of spatial variation in environmental circumstances at a range of scales should also be assessed where possible. Allison's (2004) recent

field experiment showed that the resilience of a rocky shore community to disturbance was consistent with the insurance hypothesis, but he also concluded that the effects of loss of diversity on community dynamics were complex and depended on the characteristics of the disturbance and of the species present.

Inter-trophic effects of loss of diversity on ecosystem functioning have rarely been examined using field-based removal experiments. Finke and Denno (2004) concluded recently that enhanced predator diversity reduced the overall effect of predation on herbivores and weakened cascading effects on basal resources. The design of their experiment did not, however, allow for differentiation between the effect of loss of species
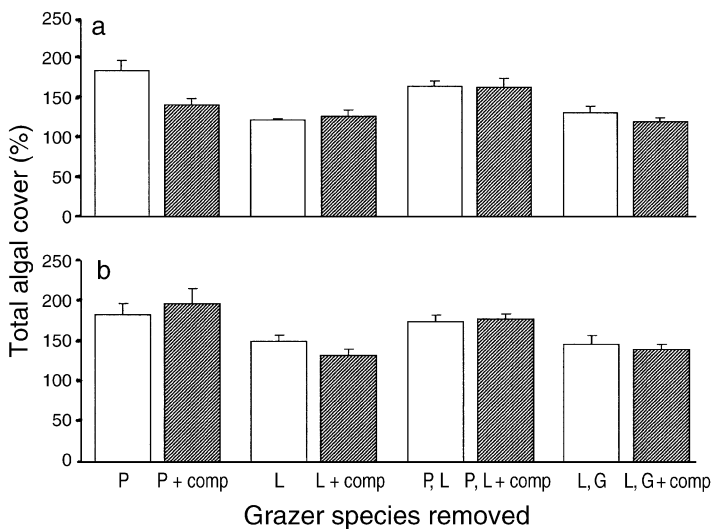

FIG. 3. Total algal cover (mean + 2 SE; *n* = 4 plots) in treatments with and without compensatory biomass of grazers after (a) four months and (b) 13 months. The letters P, L, and G refer to the grazers removed in each treatment, as in Fig. 1. Open bars represent treatments that do not include compensation for loss of biomass; hatched bars represent treatments that include compensation of biomass (+ comp) for the removed grazers.

TABLE 6. ANOVA to test effects of removing different combinations of species with and without compensation for the loss of biomass on algal cover and total algal biomass accumulated at the end of the experiment; $n = 4$ plots.

| | | Algal cover | | | | | | Total algal biomass | | |
| | | After 4 mo | | | After 13 mo | | | | | |
Source of variation	df	MS	F	P	MS	F	P	MS	F	P
Number, N	1	23.31	0.00	0.96	214.31	0.03	0.88	113.64	0.03	0.88
Identity, I(N)	2	5846.74	22.01	0.00	6732.86	14.6	0.00	3648.96	2.77	0.08
Compensation, C	1	1380.59	4.49	0.27	33.65	0.06	0.83	1015.91	1.36	0.45
N × C	1	288.36	0.22	0.69	0.08†	0	0.99	747.60	1.37	0.36
C × I(N)	2	1307.61	4.92	0.02	569.53	1.23	0.31	547.34	0.42	0.66
Residual	24	265.61			461.30			1315.81		

† Eliminated (Underwood 1997).

diversity and loss of particular species, a critical flaw identified in earlier research (Huston 1997). We have found that the loss of a specific primary consumer, *P. ulyssiponensis*, altered the mechanism of primary production in pools by causing an increase in macroalgal cover. This did not appear to be due to a dramatic change in algal community structure, but rather through increases in cover of nearly all of the non-encrusting species of algae. Detailed predictions about the nature of community level impacts can only be made if we understand the functional roles of the species involved (Bengtsson 1998, Diaz and Cabido 2001, Hooper et al. 2002, Schmid et al. 2002, Naeem and Wright 2003). On rocky shores, for example, different grazers are known to feed in different ways in accordance with their different radular structures (Steneck and Watling 1982, Hawkins and Hartnoll 1983, Hawkins et al. 1989, Hill and Hawkins 1991). Theoretical models have pre-

FIG. 4. Total algal cover (mean + SE; $n = 3$ plots) in treatments with all grazer species present with (+ cage) and without a cage and treatments from which *P. ulyssiponensis* (P) were removed with and without a cage after (a) four months and (b) 13 months. Open bars represent treatments with cages; hatched bars represent treatments without cages.

dicted that functional differences among species may form the basis of biodiversity effects on ecosystem functioning (Tilman et al. 1997, Loreau 1998). Our results together with other recently reanalyzed data (Petchey 2004, Petchey et al. 2004b) provide some experimental evidence that functional traits can explain effects of biodiversity on ecosystem functioning (Grime 2001).

The impacts of other patellid species such as *Patella vulgata* on algae on emergent rock are well documented (Conway 1946, Hawkins and Hartnoll 1983, Johnson et al. 1997), but there are few studies on the impacts of *P. ulyssiponensis* structuring rock pool algal assemblages (Myers and Delany 2002). Those that have been done suggest a high degree of context dependency. For example, studies in Mediterranean rock pools found that *P. ulyssiponensis* affected algal assemblages but these effects were highly variable (Benedetti-Cecchi and Cinelli 1992, Benedetti-Cecchi et al. 1996). Removal of all patellids from plots on British and Portuguese shores also showed that their effects varied among algal morphological groups and among shores (Boaventura et al. 2002).

Most previous research has measured biomass as a surrogate for standing stock and calculated primary productivity rates based on results from laboratory experiments. It would be extremely difficult to measure directly the rate of primary production by algae in the field, as it is difficult to evaluate the proportion of algal production consumed by grazers (Hawkins and Hartnoll 1983, Hawkins et al. 1992) or lost through wave action. It has been suggested that grazing rates are high in places where grazers have prevented the development of macroalgae, implying that algae are consumed at a small size (Sutherland 1972). It has also been shown that algae such as fucoids increase their primary productivity rates (in terms of grams of C per square meter per day) up to 100 times in response to heavy grazing (Kanwischer 1966). Grazed algal beds are in fact among the most productive systems in the world (Whittaker 1975, Gaines and Lubchenco 1982, Dethier and Duggins 1988). On rocky shores, the majority of microalgae are consumed by grazers while the majority of the macroalgae form detritus that underpins many
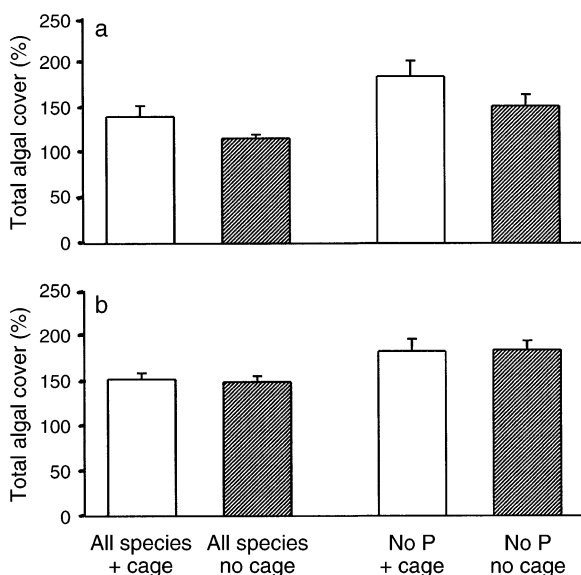
TABLE 7. ANOVA to test effect of the cage with and without *P. ulyssiponensis* on algal cover and on total algal biomass accumulated at the end of the experiment, $n = 4$ plots.

Source of variation	df	Algal cover						Total algal biomass		
		After 4 mo			After 13 mo					
		MS	F	P	MS	F	P	MS	F	P
P. ulyssiponensis, P	1	4760.08	10.54	0.01	2552.08	6.22	0.04	7.76	0.00	0.95
Cage, C	1	2380.08	5.27	0.05	0.81	0	0.97	376.55	0.22	0.65
P × C	1	60.75	0.13	0.72	117.19	0.29	0.61	2686.31	1.59	0.24
Residual	8	451.67			410.16			1689.30		

coastal food webs (Mann 1973, Miller and Mann 1973, Leguerrier et al. 2003). Changes in the abundance of macroalgae therefore indicate a change in the flow of energy from the rocky shore to the coastal ecosystem as a whole. We measured macroalgal cover and biomass to detect any changes in algal abundance that would indicate such a change in ecosystem functioning not as a direct measurement of standing stock or to be indicative of primary production rates (Hector 1998, Waide et al. 1999).

Vitousek and Hooper (1993) have suggested that systems with relatively few species (<10) may offer the best opportunity to explore relationships between biodiversity and ecosystem functioning because in those systems it should be possible to characterize the roles of each species in some detail. This was part of the rationale underlying the approach of Zedler et al. (2001), which is among the most comprehensive studies to date. Such systems also offer the opportunity to integrate manipulations of diversity and composition (Allison 1999) and resolve the sometimes heated debate about their relative contributions (Wardle et al. 2000, Naeem et al. 2002), as we have attempted to do here. It seems likely, however, that systems of differing diversity may exhibit different patterns of response to species loss. For example, Schläpfer and Schmid (1999) suggested that low diversity systems might be more likely to exhibit idiosyncratic effects, and high diversity treatments were more likely to contain redundant species. It should be possible to find intertidal systems with a range of degrees of diversity to test these ideas (Crowe, *in press*).

In common with most previous experiments we measured only one function of the system. Very few studies have considered more than one function at a time (but see Bolam et al. 2002). Zedler et al. (2001) measured recruitment and canopy cover as well as accumulation of biomass and nitrogen and found that different species were more important for different functions. Giller et al. (2004) suggest a range of functions of aquatic systems that may be amenable to experimental manipulation, including rates of decomposition (measured using litter bags), elemental cycling (such as movements of P, N, Si, or Fe), and sedimentation (using sediment traps). Similarly, although we have extended much of the previous research by considering two tro-

phic levels, it is likely that species may be lost from several trophic levels leading to an extremely complex set of possible consequences for a wide range of ecosystem functions (Raffaelli et al. 2002). Mathematical modeling is a necessary first step in getting to grips with such complexity (Petchey et al. 2004b). Key predictions must then be tested using a combination of mesocosm and field-based experiments, making use of the precision, control and replicability of mesocosms and the realism of field-based manipulations. No amount of experimental research, however, would be able to provide a basis to predict changes in all ecosystem functions in all environmental contexts as a consequence of the loss of a number of species (Crowe, *in press*). In conservation terms, it is then logical to take a precautionary approach and conserve whole assemblages of species regardless of their redundancy in relation to specified ecosystem processes. We agree with Hector et al. (2001), that importance for ecosystem functioning is by no means the only basis on which conservation of species is justified, but rather it can add extra weight to the case.

Marine systems remain underexploited as a tool for resolving the biodiversity–ecosystem functioning debate. We know that marine, terrestrial, and freshwater ecosystems behave differently (Giller et al. 2004). In order to develop general understanding of the effects of species loss (Chase 2000), this type of long-term, field-based removal experiment should be implemented in a wide variety of systems as part of an integrated approach combining theoretical and empirical research.

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