



Increasing density of rare species of intertidal gastropods: tests of competitive ability compared with common species

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ABSTRACT: Many assemblages contain numerous rare species, which can show large increases in abundances. Common species can become rare. Recent calls for experimental tests of the causes and consequences of rarity prompted us to investigate competition between co-existing rare and common species of intertidal gastropods. In various combinations, we increased densities of rare gastropod species to match those of common species to evaluate effects of intra- and inter-specific competition on growth and survival of naturally rare or naturally common species at small and large densities. Rarity *per se* did not cause responses of rare species to differ from those of common species. Rare species did not respond to the abundances of other rare species, nor show consistently different responses from those of common species. Instead, individual species responded differently to different densities, regardless of whether they are naturally rare or abundant. This type of experimental evidence is important to be able to predict the effects of increased environmental variability on rare as opposed to abundant species and therefore, ultimately, on the structure of diverse assemblages.

KEY WORDS: Additive-design · Competition · Gastropods · Species-abundance · Rarity

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INTRODUCTION

The distributions and abundances of species are core topics of study in ecology (Andrewartha & Birch 1954). Generally, assemblages have relatively few common species and many relatively rare species (e.g. Rabinowitz et al. 1986, Gaston 1994). Common species often occupy many sites, whereas rare species can occur in only a few sites over a limited geographical range (Gaston 1994), or be widespread, but in small abundance everywhere (e.g. MacArthur & Wilson 1967).

Rare species, however defined, have been suggested to be more vulnerable to extinction, but many persist for long periods in small numbers or few places. Mechanisms for long-term maintenance of

rarity are not, however, well understood. Also, relatively few studies have attempted to understand the effects of increased abundance of naturally rare species on other species in an assemblage, especially in marine assemblages.

The competitive ability of rare species has been suggested as a mechanism to compensate for their small densities, by reducing the probability of extinction at local scales (Rabinowitz et al. 1986). Myers & Harms (2009), in contrast, suggested that individuals in small populations may not encounter other individuals frequently enough for intra-specific competition among different rare species to be important. No general relationship between abundance and competition exists, because many studies have contradictory conclusions (see review by Gaston & Kunin

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1997). There are clear patterns in competition between larger versus smaller organisms and for invertebrates versus vertebrates (reviews by Connell 1983, Schoener 1983), but there has been no comparable analysis of competitive ability of rare versus abundant species.

Rare species are often difficult to study and most studies have been mensurative, involving biotic characteristics (e.g. Rabinowitz 1978), abiotic variables (e.g. Virtanen & Oksanen 2007) or disturbance regimes (e.g. Clarke & Patterson 2007). Not all studies tested clear hypotheses (but see Gotelli & Simberloff 1987); many simply documented correlations. Exceptions are Fischer & Matthies (1998), who suggested a genetic basis for rarity of *Gentianella germanica*, Bruno (2002), who demonstrated that requirements for habitat limited the distributions of rare beach plants, and Boeken & Orenstein (2001) and Myers & Harms (2009), who each tested experimentally the role of rare species in recovery of plant communities. There have, however, been fewer manipulative studies of the role of rare species in assemblages of animals, although Angel et al. (2006) showed the effect of biotic disturbance in maintaining the rare limpet *Siphonaria compressa* in a sub-optimal habitat.

It is often simply accepted that abundant species are competitively dominant over rare species (e.g. Lin & Liu 2006), but it is always necessary to test such hypotheses. Competition can only occur when abundances of potential competitors are large relative to availability of necessary resources. Species that have small populations are less likely to have encounters with conspecifics than are species with large local abundances. Thus, competition within and among rare species may be unlikely to be important (Myers & Harms 2009).

Many intertidal assemblages have numerous species which: (1) are taxonomically related, (2) have similar requirements for habitat or food and (3) interact strongly through competition, predation and other biological interactions. Yet, these assemblages typically contain many species with very small abundances. Nevertheless, these species persist temporally and spatially, even when documented to be competitively inferior (Espinosa et al. 2006), or when they have very stringent requirements for habitat (e.g. Angel et al. 2006).

Rare gastropods can show greater small-scale variability and less large-scale variability than do common species (Chapman & Underwood 2008), although this is not consistent among assemblages (e.g. Chapman et al. 2005). Some rare species are

competitively dominant (Olabarria & Chapman 2001), although this may be modified by preferences for different microhabitats (Olabarria et al. 2002).

To investigate effects of changing densities on survival of naturally rare or naturally common gastropods, we manipulated the relative abundances of some common and rare species in pair-wise combinations to measure relative survival under conditions when abundances of rare species are increased to match the densities of common species. It has already been established that these species may exhibit interspecific competition (Olabarria & Chapman 2001). The models proposed to explain natural abundances of these common and rare species (and the tested hypotheses derived from them) were:

(1) Common and rare species have different natural abundances because rare species have more specific requirements for resources or individually need more resources than do common species. Therefore, rare species are more affected by intra-specific competition. Survival of rare species should be less than that of common species when densities of each type are at the natural densities of common species (Hypothesis 1). If densities of either type are increased to be greater than natural densities of common species, common species should have greater survival (Hypothesis 2);

(2) Rare species have smaller abundances because they are negatively influenced by competition from common species, but common species are less affected by other common, or by rare species. Rare species are therefore predicted to have decreased survival when kept with increased densities of common species (Hypothesis 3). In contrast, common species should not be as much affected when with enhanced densities of common or of rare species (Hypothesis 4);

(3) Alternatively, there is no general consequence of being rare that causes rare species to differ from common species when kept at similar enhanced densities or in the presence of other common or rare species. In this case, there will be no effects of being rare versus being common, or effects should be idiosyncratic (species respond differently, regardless of whether they are naturally rare or abundant; Hypothesis 5).

These predictions were tested by manipulating densities of combinations of common and rare intertidal gastropods in experimental assemblages. This design distinguished between asymmetrical intra- and interspecific effects of competition for common and rare species (e.g. Underwood 1986).

MATERIALS AND METHODS

Frequency and relative abundance of rare species

We used microgastropods, with an adult shell size of 0.7 to 3.0 mm. There are many species of microgastropods in coralline turfs on rocky shores all over the world, including southeast Australia (e.g. Kelaher et al. 2001). Data collected previously from assemblages colonizing coralline turfs (Matias et al. 2007) were used to determine the frequency of occurrence of different species of gastropods, so that they could be reliably defined as rare or common. A species was defined to be rare when its abundance was <1% of all individuals of all species of microgastropods over all samples. Densities of the rare species were consistently <4 per 225 cm² of turf. Common species were found in relatively large abundances (>15 per 225 cm² of turf); these also occurred in >90% of samples (with numbers of samples >20 in all cases). Using these definitions, 4 species of gastropods were chosen and their densities per 225 cm² (mean \pm SD) estimated (Fig. 1): (1) Common species 1, C1: *Eatoniella atropurpurea* (Frauenfeld, 1867); 21.2 \pm 17.6; (2) Common species 2, C2: *Amphithalamus incidatus* (Frauenfeld, 1867); 15.7 \pm 10.3; (3) Rare species 1, R1: *Alaba opiniosa* (Iredale, 1936); 1.2 \pm 2.6; (4) Rare species 2, R2: *Eatonina rubrilabiata* (Ponder & Yoo, 1980); 3.7 \pm 5.5. To collect snails for experiments, patches of coralline turfs were sampled from intertidal platforms at the Cape Banks Scientific Marine Research Area, Botany Bay, New South Wales, Australia. Artificial surrogates of coralline turfs (synthetic grass) were also deployed to collect extra specimens, minimizing the need to remove excessive amounts of natural turfs from the shore. Artificial turfs, deployed 6 wk prior to the experiment, were

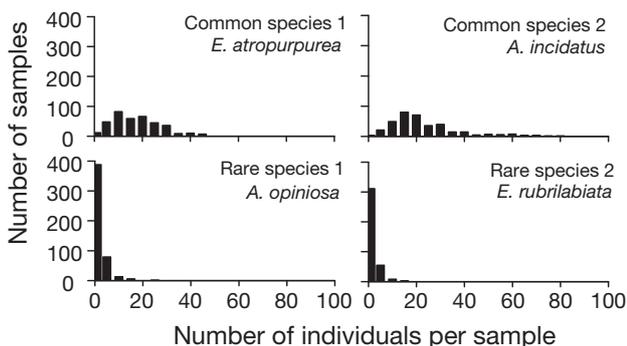


Fig. 1. Frequency of occurrence of common (*Eatoniella atropurpurea* and *Amphithalamus incidatus*) and rare species (*Alaba opiniosa* and *Eatonina rubrilabiata*)

rapidly colonized by gastropods in similar densities to those in natural turfs (Kelaher et al. 2001). All samples were washed under running water through a 500 μ m sieve. Strained gastropods were carefully sorted to species.

In total, ~10 000 gastropods were sorted to get the required numbers of each species. Twenty random sub-samples of ~100 individuals were identified and counted to provide estimates of relative abundances for each species. Abundant species were *Eatoniella atropurpurea* (55% of individuals) and *Amphithalamus incidatus* (42%); *Alaba opiniosa* (<1%) and *Eatonina rubrilabiata* (<1%) were amongst the least abundant species. These counts demonstrate that the species defined to be common or rare were consistently and correctly categorized in natural and in artificial habitats. Examination of data from extensive sampling and experiments over several years in other studies on similar assemblages including these species (Chapman & Underwood 2008 and their unpubl. data) showed that the rare species were always rare and common species always common.

Experimental set-up

In addition to turfs, the experimental species readily colonize bare rocky surfaces, where these are protected from desiccation. They also grow well on cores of rock in the laboratory (Olabarria & Chapman 2001). Therefore, cores (~1 to 2 cm deep, 3 cm diameter) were drilled out of 3 cm thick sandstone slabs previously attached to an intertidal platform at Cape Banks. These slabs had been in the field since November 2006 and were covered with algal biofilm. To check that similar amounts of biofilm were on the cores at the start of the experiment, algal biomass was estimated using Digital CIR quantitative imaging (see details in Murphy & Underwood 2006), which enabled rapid *in situ* measurements of chlorophyll *a* (as an index of biomass of micro-algae). This was repeated at the end of the experiment.

Five replicate cores were randomly assigned to each treatment (Table 1) and each core was enclosed in a mesh of 500 μ m to prevent snails from escaping. As a control test, 5 cores without snails were similarly enclosed with mesh. The experiment was left in running water in large aquaria, with plenty of space between cores, for 40 d (April to July 2008) under a 10 h light: 14 h dark cycle to mimic natural daylight and ambient water temperature (mean \pm SD = 18.8 \pm 1.3°C). This experimental set-up was previously used successfully to investigate survival of microgastro-

Table 1. Experimental treatments. Each treatment contained 4 individuals (standard density) of common species, *Eatoniella atropurpurea* (C1) or *Amphithalamus incidatus* (C2), or rare species, *Alaba opiniosa* (R1) or *Eatonina rubrilabiata* (R2), to which 12 individuals of C1, C2, R1 or R2 were added, except for the control; na: not available

Control + 0	Treatments			
	+ Common species +12C1	+ Common species +12C2	+ Rare species +12R1 +12R2	
4C1	16C1	4C1+12C2	4C1+12R1	4C1+12R2
4C2	4C2+12C1	16C2	4C2+12R1	4C2+12R2
4R1	4R1+12C1	4R1+12C2	16R1	na
4R2	4R2+12C1	4R2+12C2	na	16R2

Pods at different densities (Olabarria & Chapman 2001). Abundances of these small gastropods are dominated by small-scale (10s of cm) variation (Chapman & Underwood 2008), which also suggests that the size of these experimental units is entirely appropriate for examining competition among these species (see also Olabarria & Chapman 2001). Although there may be potential effects on the behaviour of gastropods due to handling and marking (see Chapman & Underwood 1992), the techniques used here have been used successfully in previous experiments (e.g. Olabarria & Chapman 2001).

Survival was defined by examining each individual gastropod under the dissecting microscope for signs of life, i.e. emergence or coherent movement of the foot. Four individuals of each species in each treatment were marked at the start of the experiment using enamel paint. Snails were submersed in seawater as soon as the paint was dry and any that did not emerge within 2 min were discarded and replaced by another marked individual (Olabarria & Chapman 2001). Each shell was measured from its apex to the lower lip of the opercular aperture, using an eyepiece micrometer (measurement error 0.001 mm). Growth was calculated as the size-specific rate of growth of each individual (final size/initial size) and transformed to natural logarithms.

Design of the experiment

Experimental treatments were sets of 1 or 2 species at different densities (Table 1). Based on previous experiments, standard density (4 individuals) was increased by adding 12 individuals, which was expected to be large enough to affect survival and/or growth (Olabarria & Chapman 2001). Treatments

allowed comparisons of inter- and intraspecific competitive interactions, but it was not possible to set up all possible combinations between rare species (Table 1), because not sufficient individuals of each rare species could be collected. All comparisons necessary to test the hypotheses described above were made using analyses of variance, which differed among the different tests; the details of the analyses are given in 'Results'.

RESULTS

Effects of density of conspecifics

Hypothesis 1 predicted that, at natural densities of common species, rarer species would survive less. There was, in fact, no difference among species at a density of 4 individuals per core (Fig. 2, Table 2). At increased densities, common species were predicted to survive better than rare species (Hypothesis 2), but survival of all species was similarly lower in treatments with increased densities, independently of whether species were common or rare (Fig. 2, Table 2; note that there was no interaction between Type of species and Density). These results do not support Hypotheses 1 or 2, that rare species would be more affected by intraspecific competition. Instead, the results support Hypothesis 5, that being rare or common makes no difference to intraspecific competition.

Mean growth differed between species. Density had no effect on growth of C1 (*Eatoniella atropurpurea*), C2 (*Amphithalamus incidatus*) or R1 (*Alaba opiniosa*), but, unusually, when averaged over all

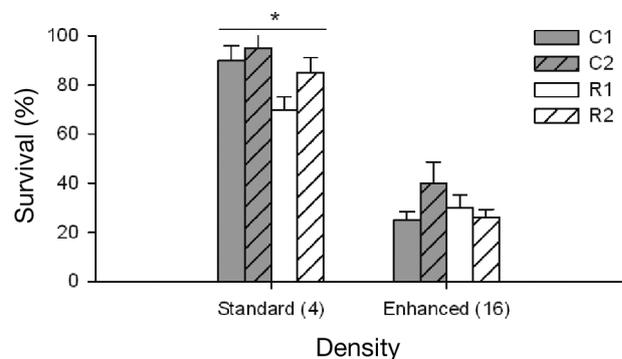


Fig. 2. Survival (mean + SE, n = 5) of common, *Eatoniella atropurpurea* (C1) and *Amphithalamus incidatus* (C2), and rare, *Alaba opiniosa* (R1) and *Eatonina rubrilabiata* (R2), species of gastropods at ambient and enhanced densities. Bars with different shading indicate different species. *: means differed significantly in Student-Newman-Keuls (SNK) tests at $p < 0.05$ (see Table 2)

Table 2. Mean percentage survival of common and rare species at different densities of conspecifics (n = 5); Type is a fixed factor with 2 levels (common vs. rare), Species is nested in Type (C1, *Eatoniella atropurpurea*, C2, *Amphithalamus incidatus* are common; R1, *Alaba opiniosa*, R2, *Eatonina rubrilabiata* are rare), Density is a fixed factor with 2 levels (4 vs. 16 snails per core). Main factors involved in significant interactions were not tested. Levels of significance: *p < 0.05; **p < 0.01; ***p < 0.001

Source	df	MS	F
Type = Ty	1	939	2.9
Species (Ty) = Sp(Ty)	2	330	2.1
Density = De	1	29908	105.1***
Ty × De	1	282	1.0
De × Sp(Ty)	2	282	1.8
Residual	32	158	
Pooled Residual, Sp(Ty) and De × Sp(Ty):			
Density (snails per core):	4	16	
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Survival (mean ± SE; n = 20)	85.0 ± 3.3	30.3 ± 2.9	

Table 3. Mean growth [ln(final size/initial size)] of common and rare species at different densities of conspecifics. Type is a fixed factor with 2 levels (common vs. rare), Species is nested in Type (*Eatoniella atropurpurea*, *Amphithalamus incidatus* are common; *Alaba opiniosa*, *Eatonina rubrilabiata* are rare). Density is a fixed factor with 2 levels (4 vs. 16 snails per core). Core is a random factor nested in the combinations of Species and Density. There were 2 replicate snails in each core. Data were transformed to ln(X) (Cochran's test: C = 0.6, p < 0.01). Levels of significance as in Table 2, SNK = Student-Newman-Keuls; '<' indicates p < 0.05

Source	df	MS	F
Type = Ty	1	0.003	0.1
Species (Ty) = Sp(Ty)	2	0.027	10.1***
Density = De	1	0.001	0.1
Ty × De	1	0.012	1.1
De × Sp(Ty)	2	0.011	4.1*
Core [De × Sp(Ty)]	32	0.003	1.0
Residual	40	0.003	
SNK test for Density × Species(Ty):			
Density (snails per core)	4		16
<hr/>			
<i>E. atropurpurea</i>	0.09 ± 0.02	=	0.07 ± 0.02
<i>A. incidatus</i>	0.08 ± 0.01	=	0.05 ± 0.01
<i>A. opiniosa</i>	0.09 ± 0.02	=	0.12 ± 0.01
<i>E. rubrilabiata</i>	0.08 ± 0.02	<	0.14 ± 0.02

treatments, mean growth of the rare species, R2 (*Eatonina rubrilabiata*) was significantly greater at the larger density (Student-Newman-Keuls [SNK] test in Table 3; note the significant Density × Species (Type) interaction).

Competition from common species

We hypothesized that rare species should have decreased survival when kept with large densities of common species (Hypothesis 3), but that common species should be less affected when kept with other common species or with large densities of rare species (Hypothesis 4).

There were, in fact, no general differences between survival of common and rare species when kept with larger densities of either of the 2 common species (Fig. 3). There were, however, significantly different patterns of survival for the individual species in each category [note the Treatment × Species (Type) interaction; Table 4]. There was significantly less survival of common species C1, *Eatoniella atropurpurea*, when with increased densities of either common species. Survival of the second common species, *Amphithalamus incidatus*, was, however, only significantly reduced by increased density of conspecifics. Both rare species (R1, *Alaba opiniosa* and R2, *Eatonina rubrilabiata*) survived significantly less when with increased densities of either of the common species, which did not differ in their effects (Table 4).

Eatoniella atropurpurea (C1) had a larger effect on itself and on the 2 rare species than on the other common species (Table 4). The increased density of the second common species C2 (*Amphithalamus incidatus*) caused greater interspecific and intraspecific reductions in density than was caused by C1.

Effects of increasing density of common or rare species

The effects on survival and growth of increased densities of common or rare species were examined in several analyses. As it was impossible to create all treatments involving increased densities of rare species (see Materials and methods), each of the rare species was examined in a separate analysis. First, the effect of enhanced density of R1 (*Alaba opiniosa*) was compared with the effects of increased density of the common species. The analysis was asymmetrical (Underwood 1992) because there were 2 species

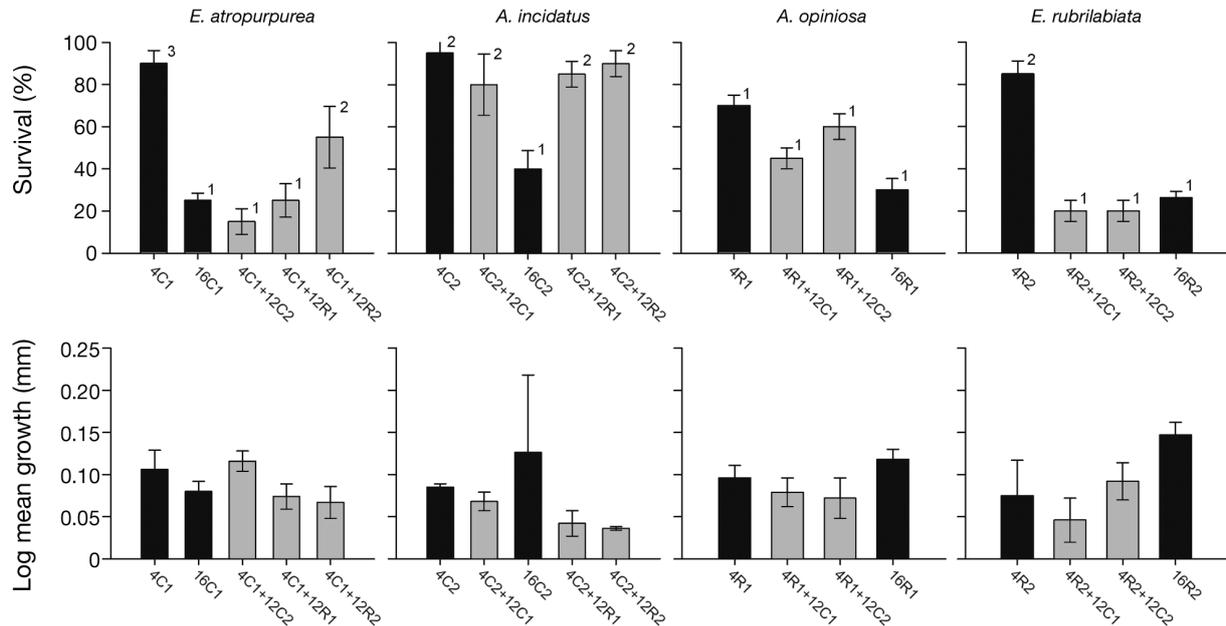


Fig. 3. Survival (mean ± SE, n = 5) and growth (mean ± SE, n = 3) of common, *Eatoniella atropurpurea* (C1), *Amphithalamus incidatus* (C2), and rare, *Alaba opiniosa* (R1) and *Eatonina rubrilabiata* (R2), species of gastropods in different experimental treatments. Black bars indicate intraspecific treatments. Different numbers on top of the bars = groups which differed significantly in Student-Newman-Keuls (SNK) tests at $p < 0.05$

Table 4. Variance of survival and growth of common and rare species in treatments with different densities of common species. Type is a fixed factor with 2 levels (common vs. rare). Species is 2 species of each type nested in Type. Treatment is a fixed comparison between treatments in which zero, 12 *Eatoniella atropurpurea* (C1) or 12 *Amphithalamus incidatus* (C2) were added. Analysis of survival uses data from 5 replicate cores (n = 5); growth data are means of 2 to 4 snails from each of 3 replicate cores (n = 3), transformed to $\ln(X)$. Main factors involved in significant interactions were not tested. Sources of variation were pooled if not significant at $p = 0.25$. Levels of significance as in Table 2, SNK = Student-Newman-Keuls; '<' indicates $p < 0.05$

Source	df	MS	F	df	MS	F
Type = Ty	1	844	2.2	1	0.004	1.2 ^a
Species (Ty) = Sp(Ty)	2	4052		2	0.000	0.1
Treatment = Tr	2	15031		2	0.003	1.2 ^a
Ty × Tr	2	1531	0.9	2	0.001	1.1
Tr × Sp(Ty)	4	1802	7.5***	4	0.001	0.2
Residual	48	240		24	0.003	

^aTested against pooled residual + Sp(Ty) + Tr × Sp(Ty)

SNK tests of Tr × Ty for mean survival:						
Treatment	+ 0		+ 12 C1		+ 12 C2	
4 C1	90	>	25	>	15	
			^		^	
4 C2	95	=	80	>	40	
			v			
4 R1	70	>	45	=	60	
					v	
4 R2	85	>	20	=	20	

nested in the type 'Common', but only 1 rare species. There was, in fact, no systematic difference due to being common or rare (analysis not shown; Type was not significant at $p > 0.25$). The interaction of Treatment (+C1, +C2, +R1) and Species (C1, C2) was significant ($F_{3, 48} = 6.54, p < 0.001$). Thus, particular species had different effects on other species,

When at enhanced density, the first common species (C1, *Eatoniella atropurpurea*) significantly reduced survival of itself (i.e. intraspecific competition) and of the second rare species (R2, *Eatonina rubrilabiata*) but had no effect on the other common species and the first rare species (R1, *Alaba opiniosa*; Table 5, Fig. 3). In contrast, the other common species (C2, *Amphithalamus incidatus*) caused significantly reduced survival of each of the common species, but had no significant influence on survival of the rare species R1 (Table 5). The first rare species (R1, *A. opiniosa*) showed the same pattern as C1—it reduced survival of C1 and of itself, but not of the other common species, C2 (Table 5).

The analysis of the second rare species (R2, *Eatonina rubrilabiata*) showed a similar pattern of competition from that shown by R1. It reduced survival of itself (i.e. intraspecific competition) and of the common species C1 (*Eatoniella atropurpurea*), but had no influence on survival of the other common species.

Table 5. Inter- and intraspecific effects of common species, *Eatoniella atropurpurea* (C1) and *Amphithalamus incidatus* (C2), and rare species, *Alaba opiniosa* (R1) and *Eatonina rubrilabiata* (R2). Data are mean survival when at a density of 4 snails per core (Control) or at enhanced density (+12 snails) of each of the other species. *: significantly different from Control (Student-Newman-Keuls, [SNK] tests, $p < 0.05$). na = not available

Mean survival in treatment	Control	+ 12			
		C1	C2	R1	R2
Effect on:					
C1 <i>E. atropurpurea</i>	90	25*(73%)	15*(84%)	25*(73%)	55*(39%)
C2 <i>A. incidatus</i>	95	80 (16%)	40*(58%)	85 (11%)	90 (5%)
R1 <i>A. opiniosa</i>	70	45 (36%)	60 (14%)	30 (57%)	na
R2 <i>E. rubrilabiata</i>	85	20*(76%)	20*(76%)	na	26*(70%)

Thus, all 4 species caused increased intraspecific reductions in survival and had various influences on other species. There was no general pattern that could be attributed to being rare or common and the same pattern was shown by 1 rare and 1 common species.

Similar analyses of growth showed no significant effects of enhanced density of any species on any other species (analyses not shown, but all tests not significant at $p > 0.25$).

Chlorophyll as an index of food

At the start of the experiment, biomass of chlorophyll *a* did not significantly differ among experimental treatments (smallest and largest means \pm SE of chlorophyll were 1.05 ± 0.14 and $1.69 \pm 0.04 \mu\text{g cm}^{-2}$; analysis of variance, not presented here, $p > 0.05$). Similarly, at the end of the experiment, there were again no differences (analysis of variance, $p > 0.05$, not presented; smallest and largest means were 0.86 ± 0.08 and $1.63 \pm 0.15 \mu\text{g cm}^{-2}$). Thus, amount of food at the start and at the end of the experiment did not differ for different species and densities. Changes in chlorophyll on each core were therefore uninformative.

DISCUSSION

To investigate how rare and common species might differ ecologically, we examined the effects of intra- and interspecific competition at normal and enhanced densities. Competitive interactions between the species examined were not generally determined by whether species were naturally common or rare. Common and rare species responded in the same

way to increased densities of conspecifics (rejecting Hypothesis 2) and to natural densities of common species (rejecting Hypothesis 3). Thus, changes in densities of either type of species were similarly influenced by intraspecific competition. Similarly, common and rare species showed similar responses to larger densities, regardless of whether the increased densities were due to common or rare species (clearly rejecting Hypothesis 4). There was no evidence that natural rarity *per se* caused rare species to differ from common species

in their responses to changes in densities of other species. Nor did rare, as opposed to common species have different effects on other species. The results strongly support the model that individual species respond differently, regardless of whether they are naturally rare or abundant (supporting Hypothesis 5) and, thus, that species showed idiosyncratic results (i.e. dependent on species identity; Emmerson et al. 2001).

Competitive interactions were expected (Olabarria & Chapman 2001) and, despite there being no pattern of change in abundance of microfloral food, intraspecific competition was found for all 4 of the species tested. All 4 were also involved in at least 1 interspecific competitive interaction. Thus, the experiment was sufficient to test for differences in competition between rare and common species.

Growth was generally not affected by competition from any species, regardless of their natural abundance. The only exception was 1 rare species, *Eatonina rubrilabiata*, which increased growth at larger densities of conspecifics. This is anomalous and is difficult to propose ecological processes that would allow greater growth when resources are under greater pressure. Possibly, more grazing associated with greater densities can enhance supplies of food (e.g. Branch 1984; Firth & Crowe 2010), although the measures of available food in the experimental treatments did not show greater standing stock of food for *E. rubrilabiata* at the large density. Standing stock is not, however, necessarily indicative of production. Overall, however, growth over the period of the experiment did not appear to be related to whether these grazers were naturally common or rare. As we used adult individuals only growth during the experiment was expected to be small.

Our results are contrary to the expectation that small natural abundances of rare species are a direct

result of competition (reviewed by Gaston & Kunin 1997), and that inferior competitive ability of rare species (e.g. rare grasses in American prairies, Rabenold et al. 1984) is a general explanation for rarity (see review by Lyons et al. 2005). In contrast, our results are consistent with those of Angel et al. (2006), who found no evidence that spatial distribution or abundance of the rare limpet *Siphonaria compressa* and the common gastropod *Assiminea globulus* were determined by interspecific competition. They also do not support previous suggestions that interspecific competition between individuals of the common limpet *Patella caerulea* and of the rare limpet *P. ferruginea* is the most likely explanation for the coexistence of these 2 species (Espinosa et al. 2006).

Most studies of competition between rare and common species have used experimental reductions of densities of the common species (e.g. Boeken & Shachak 2006, Myers & Harms 2009), or manipulated densities of rare species via propagules, e.g. seeds (Bruno 2002). This is possibly because of the work necessary to increase numbers of rare species, because of ethical constraints with manipulating densities of rare species, or because densities of rare species could not be maintained during experiments. This study overcame such difficulties, but, as with all laboratory experiments, any interpretation of results with respect to the real world must be made with care (e.g. Connell 1974). The limitations were reduced by minimizing disturbances and by making the size of the experimental units similar to that of many small patches of natural habitat in which these species live.

Although only 2 rare and 2 common species were studied here, the variation between the 2 species of each type was large. The individual rare species showed similar large amounts of difference in their competitive interactions, as did the 2 common species. Therefore, it is not likely that different conclusions could have been reached, if more species had been tested.

Our study presents the first experimental test of the effects of commonness and rarity on inter- and intraspecific competition between co-occurring species randomly selected from natural assemblages.

Idiosyncratic differences between different species within the common or rare category should not necessarily be surprising. Chapman & Underwood (2008) showed no general patterns of colonization across multiple spatial scales for common and rare species of similar microgastropods, but considerable variation among species within each of these cate-

gories. Neither of the 2 common species studied here showed the same patterns observed by Chapman & Underwood (2008), and 1 of the rare species (*Eatonina rubrilabiata*) showed no spatial variation in abundance. Many recent studies of the diversity-identity problem (e.g. Cardinale et al. 2006) have shown that different species have different effects on ecological processes, often with 1 species being responsible for a lot of the pattern perceived as an outcome of the assemblage (e.g. Bruno et al. 2006). We may, therefore, make more progress into understanding causes of rarity if we stop attempting to force species into either of these categories (Gaston 1994) and attempt more experiments with multiple species to identify the range of individual responses.

These findings thus expand our understanding of the role of rare species and are relevant to several branches of current ecological research. In order to support the argument that biological diversity must be conserved to maintain ecosystem functioning, research must be able to demonstrate that rare species — the great majority of species in assemblages — also make significant contributions (Lyons et al. 2005, Benedetti-Cecchi et al. 2008). These rare species have the potential to make significant contributions to ecological functions because they responded in the same way as common species. If persistence of rare species at small abundances can promote resistance or resilience to external stress or perturbations (Benedetti-Cecchi et al. 2008), their different environmental requirements and preferences could increase resilience in ecosystem functioning under perturbations that favour them over previously dominant species (Walker 1992).

It has also been suggested that reductions in density-dependent processes (e.g. competition) have a positive effect on rare species during adverse environmental conditions by reducing the risk of extinction and vulnerability to environmental instability (e.g. Benton et al. 2001, Benedetti-Cecchi et al. 2008). Recent studies showed that variability in assemblages depends on the relative contribution of rare and common species to spatial and temporal dynamics, suggesting that rare species may affect temporal changes in assemblages because of their susceptibility to fluctuations in environmental conditions (e.g. Easterling et al. 2000, Benedetti-Cecchi et al. 2006).

Understanding how species with small geographic ranges, specialized habitat requirements and small local abundances have persisted through time (e.g. Harrison et al. 2008), will advance our knowledge of species' responses to adversity.

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