Influence of a dominant consumer species reverses at increased diversity

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Abstract. Theory and experiments indicate that changes in consumer diversity affect benthic community structure and ecosystem functioning. Although the effects of consumer diversity have been tested in the laboratory and the field, little is known about effects of consumer diversity in the subtidal zone, one of the largest marine habitats. We investigated the grazing effects of sea urchins on algal abundance and benthic community structure in a natural subtidal habitat of the Galápagos Islands. Three species of urchins (*Eucidaris*, *Lytechinus*, and *Tripneustes*) were manipulated in inclusion cages following a replacement design with three levels of species richness (one, two, and three species) with all possible two-species urchin combinations. Identity was the main factor accounting for changes in the percentage of substrate grazed and benthic community structure. Two out of the three two-species assemblages grazed more than expected, suggesting a richness effect, but analyses revealed that this increased grazing was due to a sampling effect of the largest and commercially valued urchin species, *Tripneustes*. Benthic community structure in treatments with *Eucidaris*, *Lytechinus*, and *Tripneustes* alone was significantly different at the end of the experiment, suggesting that resource use differentiation occurred. Communities in *Tripneustes* enclosures were characterized by abundant crustose coralline algae and grazed substrate, while those without it contained abundant green foliose algae (*Ulva* sp.). An unexpected emergent property of the system was that the most species-rich urchin assemblage underyielded, grazing less than any other assemblage with *Tripneustes*, effectively reversing its dominant influence observed in the two-species treatments. While further experiments are needed to discern the mechanisms of underyielding, it may be related to changing interspecific interactions as richness increases from two to three species or to density-dependent *Tripneustes* grazing. This study highlights the general importance of evaluating consumer richness effects across the entire range of species richness considered, as the performance of the most species-rich consumer assemblage could not be predicted by manipulations of intermediate levels of consumer species richness.

Key words: benthic community; biodiversity and ecosystem functioning; consumer richness; Eucidaris; *Galápagos Islands; grazing; identity;* Lytechinus; *sea urchins; subtidal;* Tripneustes; *underyielding.*

INTRODUCTION

Understanding the significance of biodiversity for ecosystem functioning is one of the key challenges of ecology in an era of global change (Sala 2001). Ecosystem functioning includes community- and ecosystem-level processes, such as production, standing biomass, invasion resistance, food web dynamics, element cycling, resource use, and trophic transfer (Stachowicz et al. 2007). After initial experiments performed in plant terrestrial systems (e.g., Hooper and Vitousek 1997, Tilman et al. 1997), biodiversity and ecosystem functioning (BEF) studies expanded to include microbial (e.g., Naeem and Li 1997), freshwater

(e.g., Covich et al. 2004), and marine (e.g., Duffy et al. 2001) systems. Synthetic reviews and meta-analyses performed across different ecosystem types have consistently found that biodiversity has profound influences on many processes and properties at both community and ecosystem levels (Cardinale et al. 2006, Stachowicz et al. 2007). A general trend is that, as species richness increases, biomass production of the focal group also increases, and in turn, causes an increase in resource use by this group (Cardinale et al. 2006, Duffy 2009).

Understanding the relationship between consumer richness and ecosystem functioning is important in marine ecosystems because most marine extinctions have occurred at high trophic levels due to the widespread harvest of consumers (Duffy 2002, Byrnes et al. 2007), and because the removal of large predatory fish, sea urchins, and other key consumers have provoked dramatic shifts in community structure (Strong 1992, Witman and Sebens 1992, Jackson et al.

2001, Byrnes et al. 2006). Focusing on consumer diversity effects is thus particularly relevant for addressing conservation concerns (Srivastava and Vellend 2005); moreover, it is crucial for understanding how top-down consumption may dampen or change diversity effects in lower trophic levels (Duffy et al. 2007, Bruno et al. 2008). Motivated by these issues, the number of investigations of marine consumer richness effects has increased during the last decade (studies cited in O'Connor and Bruno 2007, Stachowicz et al. 2007, Bruno et al. 2008); however, with the exception of a few recent studies (Burkepile and Hay 2008, 2010, Byrnes and Stachowicz 2009), subtidal experiments performed entirely in the field are rare. Since richness effects may be more readily discerned in field than in laboratory experiments (Stachowicz et al. 2008), there is a need to conduct BEF experimental research under field conditions in order to be able to uncover the actual significance of biodiversity effects on any process of interest (Stachowicz et al. 2008, Duffy 2009).

Here, we address this need by investigating the effects of consumer richness on the abundance of organisms at lower trophic levels (as a proxy of resource use) in a natural subtidal habitat of the Galápagos Marine Reserve (GMR). Our hypothesis was that, as consumer richness increases from one to three species, the abundance of prey species decreases (Duffy 2002, Cardinale et al. 2006). To test this, we conducted experiments with the three most common urchin species in the central archipelago (Appendix A): the slate pencil urchin, Eucidaris galapagensis, the green sea urchin, Lytechinus semituberculatus, and the white sea urchin, Tripneustes depressus. These species represent the most significant invertebrate meso-grazer guild in the system (Brandt and Guarderas 2002, Irving and Witman 2009) and will be hereafter referred to by genus. Tripneustes is harvested for local consumption in the GMR (Luna 2000), and there is interest in developing an organized fishery for this particular urchin species (Luna 2000; M. Brandt, unpublished data). Therefore, in addition to the main objective of testing BEF theory in natural subtidal systems, this study is relevant for understanding the potential consequences of overharvesting sea urchins.

Given that identity effects are more common than richness effects in marine BEF studies (Stachowicz et al. 2007), we first asked whether urchin species richness or identity had an effect on (1) the percentage of the substrate grazed by the urchins, and (2) benthic community structure. Since pilot experiments identified the largest species Tripneustes as a key grazer (M. Brandt and J. Witman, unpublished data), we also asked whether Tripneustes was solely responsible for any significant effect (O'Connor and Crowe 2005).

Methods

Study site

The experiment was conducted from December 2007 to the end of January 2008 at Caamaño Island (00°76′71″ S, 90°28′24″ W) in the central Galápagos archipelago. The substrate extending underwater on the south west side of the island is dominated by large (~6 m²) rocky platforms down to 12 m depth, which are separated by narrow cracks. The experiment was conducted on nearly flat, large bedrock platforms at 10 m depth. The sessile benthic community living on the rocky substrate consists of mainly algae, of which Ceramium, Dictyota, Gelidium, Hildenbrandia, Jania, Lithothamnium, Polysiphonia, and Ulva are the most conspicuous genera (Appendices B–E). Although underrepresented, encrusting invertebrates were present, with sea anemones (Bunodosoma sp.), mollusks (Hipponix sp., Serpulorbis margaritaceus), barnacles (Megabalanus peninsularis), tube-building polychaete worms (Spirobranchius giganteus), and tunicates (Pyura haustor) being the most common. Of the 19 urchin species reported for the Galápagos (Hickman 1998), Eucidaris, Lytechinus, and Tripneustes comprise 91% of the total urchin biomass (Brandt and Guarderas 2002). Qualitative feeding observations indicate that Lytechinus browses on algae and remnants of other organisms, while Tripneustes apparently prefers to feed on algal tufts and encrusting algae (Hickman 1998). Eucidaris is known as an omnivore and bioeroder, which grazes on encrusting algae, but also feeds on Pocillopora and Pavona corals (Glynn et al. 1979).

Experimental design

The richness and identity of urchin species (Eucidaris, Lytechinus, and Tripneustes) was manipulated in inclusion cages bolted to the rock substrate by drilling. The experimental unit consisted of a circular cage (0.5 m² area) made of plastic-coated steel mesh (3.5 cm openings; Aquamesh, Northbridge, Massachusetts, USA). There were three levels of species richness: one species (hereafter termed "mono-assemblages," as an equivalent to monocultures in plant BEF studies); two species, with all three possible two-factor pairwise urchin species combinations; and three species. These latter two levels are referred to as "multi-assemblages," an equivalent to plant polycultures. To avoid confounding richness with density, we used a replacement (substitutive) experimental design (Stachowicz et al. 2007, Byrnes and Stachowicz 2009). This was achieved by holding total urchin density constant at six individuals per 0.5 m², which is well within the range of natural densities for these species in the Galápagos (Irving and Witman 2009, Witman et al. 2010).

Control cages lacking urchins were employed to ensure that the reduction in the percent cover of algae and encrusting invertebrates within treatments was due to urchin grazing. The percent cover of substrate grazed was measured and used as one of the response variables. The percent cover of substrate grazed in the controls did not increase over the course of the experiment ($F_{1,8} = 2.47$, $P = 0.16$), indicating that all grazing generated in treatments was due to urchin grazing. Each urchin
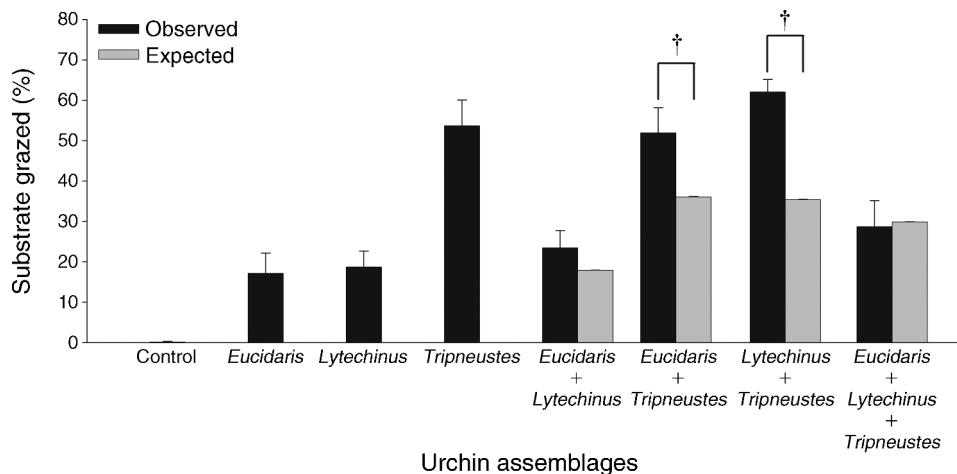
FIG. 1. Effects of sea urchin assemblages (seven treatments with different numbers of species and combinations and control cages) on the percentage of substrate grazed (mean + SE; sample size $N = 5$) in a natural subtidal habitat of the Galápagos Islands. Daggers (†) denote where the 95% confidence intervals did not overlap between observed and expected values (data from Table 4).

assemblage (seven treatments; Fig. 1) and control cage was replicated five times, yielding a total of 40 cages deployed. To reduce potential caging artifacts related to reduced light and food supply, the experiment was maintained every other day by scuba divers who brushed algae and epifaunal invertebrates off the cages. The experiment ran for five weeks.

The rocky substrate inside the cages was photographed with a Canon G7 digital camera (Canon, Lake Success, New York, USA) in an underwater housing once before and after the conclusion of the experiment. The camera and two strobes were mounted on a quadrapod frame (Witman 1985) to standardize the distance to the substrate. Five images were taken of each treatment and control to ensure complete coverage of the substrate within the cages. Overlapping areas of the 10-megapixel resolution images were cropped and merged in Adobe Photoshop (version 10.0.1) to construct a single image that corresponded to the total area of the substrate within each cage (0.5 m²). The percent cover of algae and encrusting invertebrates in the photos was estimated by the random dot method by superimposing a transparent layer with 1000 random dots on each image. Organisms were identified to the lowest possible taxonomic level. Where species identifications could not be made, a descriptive name was assigned to the organism and then photo-referenced to ensure consistent identification.

Statistical analyses

The average percent cover of algae, the percentage of substrate grazed and encrusting invertebrates attached to the rock substrate in the cages did not differ between treatments and controls prior to the start of the experiment (one-factor ANOVA; algae, $F_{7,32} = 0.61$, $P = 0.75$; substrate grazed, $F_{7,32} = 1.01$, $P = 0.44$; encrusting invertebrates, $F_{7,32} = 0.92$, $P = 0.50$).

Consequently, the percent cover at the end of the experiment was used to evaluate the effects of urchins. The response variables for testing the effects of urchins were (1) percentage of the substrate grazed and (2) benthic community structure. To separate the effect of urchin richness from identity (Schmid et al. 2002, O'Connor and Bruno 2007), two-factor nested models were applied to all mono- and two-species assemblages. This was done separately by a two-factor nested ANOVA for the response variable percentage of the substrate grazed and by a two-factor nested PERMANOVA (permutational multivariate analysis of variance; Anderson 2001) for benthic community structure. In both cases, factor 1, richness, was considered fixed, as we were specifically interested in determining the grazing impact of the three most conspicuous and abundant urchin species in the GMR, namely *Eucidaris*, *Lytechinus*, and *Tripneustes* (Brandt and Guarderas 2002), while factor 2, identity, was nested in factor 1 and treated as random, following the convention of similar experimental designs (O'Connor and Crowe 2005, O'Connor and Bruno 2007, O'Connor et al. 2008). In order to analyze the grazing effects of the three-species assemblages, we performed the following: (1) LR_{mean} and LR_{max} calculations, (2) comparisons of the 95% confidence intervals of the observed vs. expected grazing means, and (3) comparisons of the percentage of substrate grazed in the three-species assemblage with that of its best-performing component species when in mono-assemblage (LR_{mean} and LR_{max} stand for the logarithmic response ratios between the percentage grazed of a multi-assemblage and the average percentage grazed by the component mono-assemblages and between the percentage grazed of a multi-assemblage and the percentage grazed by the mono-assemblage that grazed the most, respectively.) All these tests helped us reveal if the three-species assemblage grazed less, equal

to, or more than expected, and than the best-performing urchin species when alone.

A richness effect occurs when a multi-assemblage performs differently than the average performance of its component species in mono-assemblages, which is known as non-transgressive overyielding (Fridley 2001, Stachowicz et al. 2007). One way to measure it is by estimating LR_{mean} (Cardinale et al. 2006), which we calculated as: $LR_{mean} = \ln$ (percentage grazed in multi-assemblage/average percentage grazed by the component mono-assemblages) for all two-species and three-species multi-assemblages. LR_{mean} values greater than zero indicate a richness effect and can be explained by the significant influence of dominant species (sampling effect; Huston 1997), and/or by resource use complementarity or positive interactions between species (Loreau 1998, Stachowicz et al. 2007). In order to separate complementarity from the sampling effect (Loreau 1998, Cardinale et al. 2006), transgressive overyielding (LR_{max}) was calculated for all two-species and three-species multi-assemblages as: $LR_{max} = \ln$ (percentage grazed in multi-assemblage/average percentage grazed by the mono-assemblage that grazed the most). Transgressive overyielding occurs when the response of the multi-assemblages is greater than the highest performing mono-assemblage (Stachowicz et al. 2007). Values greater than zero unambiguously indicate complementarity (Loreau 1998). To take into account the variability in the data, we ran one-factor ANOVA tests between all multi-assemblages and their highest performing mono-assemblage. In addition, and to evaluate how general transgressive and non-transgressive overyielding was in our system, we performed one-sample t tests of mean LR_{mean} and LR_{max} values to evaluate whether they were different from zero. Finally, we estimated the expected grazing of all multi-assemblages by resampling the observed mono-assemblage data matrix 10 000 times with replacement (Duffy et al. 2003), and then compared the 95% confidence intervals between observed and expected values for all multi-assemblages.

The potential effects of *Tripneustes* as a key species in this system (O'Connor and Crowe 2005) were tested by comparing treatments with *Tripneustes* to those without it. This was done separately by a two-factor nested ANOVA for the response variable percentage of the substrate grazed and by a two-factor nested PERMA-NOVA for benthic community structure. Factor 1 was the presence or absence of *Tripneustes* and fixed, and factor 2 (nested in factor 1) was the composition of the assemblage and random. PRIMER 5 (Clarke 1993) was used to generate nonmetric multidimensional scaling (NMDS) ordinations to compare benthic community structure among urchin treatments. SIMPER (similarity of percentages) was run in PRIMER 5 to identify which taxa or substrate type, such as substrate grazed, sediment, dead barnacles, and so forth, was important in discriminating among treatments. All multivariate analyses were performed using Bray-Curtis similarity coefficients (Clarke and Warwick 2001) on range-standardized data.

A one-factor ANOVA test was conducted to examine whether the percent cover of algae differed among the three urchin mono-assemblages and thus explore if resource use partitioning among urchin species occurred. For this particular test, the percent cover of algae was pooled by functional groups according to Steneck and Dethier (1994). Since algal abundance increased in some urchin treatments but decreased in others, the change (final – initial percent cover) was calculated and then range-standardized in order to be able to run the ANOVAs. Range standardization involved converting the change in the percent cover of algal functional groups, so they ranged from 0 to 200 (maximum 100% increase or a 100% decrease) by subtracting the minimum from each observed value and then dividing by the range (Legendre and Legendre 1998). All other univariate ANOVA tests performed on the cover of substrate grazed were run on arcsine-transformed data. PERMANOVA tests were also applied on range-standardized data and further fourth-root transformed to reduce the influence of dominant taxa or substrate type (Clarke and Warwick 2001), such as substrate grazed, sediment, dead barnacles, and so forth. All ANOVA and PERMANOVA tests were fully balanced. Post hoc Tukey's HSD tests were run for all significant ANOVAs and PERMANOVAs. The magnitude of effects (ω^2) in tests of urchin richness and identity, and the influence of the presence/absence of *Tripneustes* were calculated only on the significant factors as recommended by Graham and Edwards (2001).

RESULTS

Consumer identity effects on the amount of substrate grazed

Urchin identity significantly affected the percentage of substrate grazed, but urchin richness did not (nested ANOVA; Table 1a). For example, urchin identity explained 73% of the variance in the percentage of the substrate grazed (Table 1a). The *Tripneustes* mono-assemblages grazed at least two times more of the rocky substrate than the *Eucidaris* and the *Lytechinus* mono-assemblages (Table 1, Fig. 1), and the multi-assemblage lacking *Tripneustes* (*Eucidaris*+*Lytechinus*) grazed significantly less than the other two-species assemblages, as indicated by post hoc tests following the significant main effect of urchin identity (Table 1, Fig. 1). The presence of *Tripneustes* also had a significant effect on the percentage of the substrate grazed (Table 1b). There was a clear pattern of a greater percentage of the substrate grazed in all treatments containing *Tripneustes* compared to treatments lacking it (Fig. 1), which explained 64% of the variation. Finally, the assemblage composition had a highly significant effect and explained 24% of the variance in the percentage grazed

TABLE 1. ANOVA tests on the percentage of substrate grazed by sea urchins (*Eucidaris*, *Lytechinus*, and *Tripneustes*) in a natural subtidal habitat of the Galápagos Islands.

Source of variation	df	MS	F	P	ω^2
a) Test to determine the effect of urchin richness vs. urchin identity					
Richness, R	1	0.247	0.997	0.375	0
Identity, $I[R]$†	4	0.248	14.943	<0.001	0.731
Residual	24	0.017			0.269
b) Test to determine the influence of the presence/absence of *Tripneustes*					
Presence/absence *Tripneustes*, P/A‡	1	1.874	10.616	0.017	0.639
Assemblage composition, $C[P/A]$§	6	0.176	11.235	<0.001	0.241
Residual	32	0.016			0.120

Note: Analyses were performed on arcsine-transformed data; nested factors are displayed in brackets; $N = 5$; magnitude of effect (ω^2) estimates were calculated only for significant factors (Graham and Edwards 2001).

† Post hoc tests indicated that the percentage of substrate grazed was significantly higher in *Tripneustes* than in *Eucidaris* and *Lytechinus* mono-assemblages, and that it was lower in *Eucidaris*+*Lytechinus* than in the other two-species assemblages (df = 24, Tukey's HSD post hoc $Q = 3.09$, $P = 0.05$).

‡ The percentage of substrate grazed was higher in assemblages where *Tripneustes* was present (df = 32, $Q = 3.024$, $P = 0.05$).

§ Post hoc tests indicated that the percentage of substrate grazed in the multi-assemblage *Eucidaris*+*Lytechinus*+*Tripneustes* was significantly lower than in any other urchin assemblage containing *Tripneustes*, and that it was significantly lower in the controls relative to any other urchin assemblage without *Tripneustes* (df = 32, $Q = 2.04$, $P = 0.05$).

(Table 1b). The most diverse multi-assemblage, *Eucidaris*+*Lytechinus*+*Tripneustes,* grazed less than any other assemblage containing *Tripneustes* (Table 1, Fig. 1).

Consumer identity effects on benthic community structure

Urchin species identity had a highly significant effect on the magnitude of the changes in the percent cover of algae and sessile invertebrates comprising the response variable benthic community structure (Table 2a). Identity explained 33% of the variation in benthic community structure. Results of NMDS ordinations depicted relatively large distances between communities of all mono-assemblages (Fig. 2). Suggesting the occurrence of resource use partitioning among urchin species, benthic communities subjected to grazing and predation by *Eucidaris*, *Lytechinus*, and *Tripneustes* in the mono-assemblage treatments were significantly different (post hoc tests following the significant main effect of identity in PERMANOVA; Table 2). In addition, benthic communities were significantly different among all two-species assemblages, with the exception of *Eucidaris*+*Tripneustes* and *Lytechinus*+*Tripneustes*, where benthic communities were similar (Table 2). The average dissimilarities in community structure among mono-assemblages (Appendix B) and among the two-species assemblages (Appendix C) were relatively low. The encrusting coralline alga *Lithothamnium* sp. was the best discriminator of benthic community structure for the mono-assemblages, as it contributed 24% to the similarity of the *Tripneustes* replicates compared to ~8% in both *Eucidaris* and in *Lytechinus* mono-assemblages (Appendix D).

The singular influence of *Tripneustes* significantly affected benthic community structure in the treatments (Table 2b). It is evident from Fig. 2 that all urchin assemblages containing *Tripneustes* form a separate group from those without it. More than 60% of the cumulative similarity in assemblages containing *Trip-*

TABLE 2. PERMANOVA tests of the grazing effects of sea urchins on benthic community structure (change in percent cover) in a natural subtidal habitat of the Galápagos Islands.

Source of variation	df	MS	F	P	ω^2
a) Test to determine the effect of urchin richness vs. urchin identity					
Richness, R	1	0.285	0.472	0.899	0
Identity, $I[R]$†	4	0.604	3.613	<0.001	0.329
Residual	24	0.167			0.671
b) Test to determine the influence of the presence/absence of *Tripneustes*					
Presence/absence *Tripneustes*, P/A	1	1.409	3.703	0.013	0.197
Assemblage composition, $C[P/A]$‡	6	0.380	2.283	0.002	0.164
Residual	32	0.167			0.639

Note: Analyses were performed on range-standardized and fourth-root transformed data; nested factors are displayed in brackets; $N = 5$; magnitude of effect (ω^2) estimates were calculated only for significant factors (Graham and Edwards 2001).

† Post hoc tests indicated that the benthic communities were significantly different among all mono-assemblages, and that they were significantly different among all two-species assemblages with the exception of *Eucidaris*+*Tripneustes* and *Lytechinus*+*Tripneustes* (df = 24, Tukey's HSD post hoc $Q = 3.53$, $P = 0.05$).

‡ Post hoc tests indicated that benthic communities within the *Eucidaris*+*Lytechinus*+*Tripneustes* assemblage were significantly different than those in *Tripneustes* mono-assemblages; and that the benthic communities of all assemblages without *Tripneustes* were significantly different among each other (df = 32, $Q = 3.84$, $P = 0.05$).
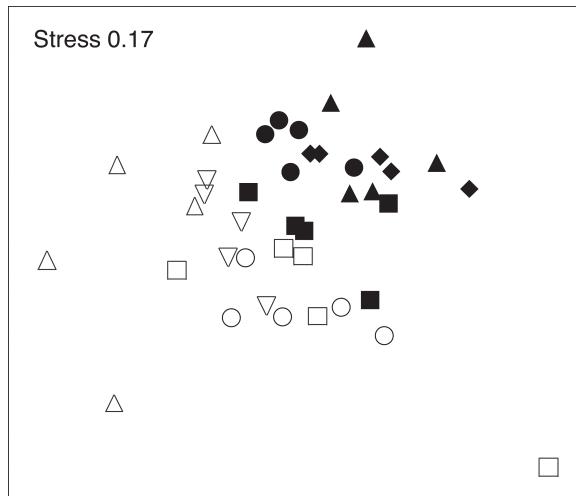
FIG. 2. Nonmetric multidimensional scaling plot (NMDS) of assemblages of benthic organisms (range-standardized and fourth-root transformed change of percent cover of algae and sessile invertebrates) under seven treatments (urchin species combinations) and the control cages lacking urchins. Solid symbols represent treatments with *Tripneustes*. Symbols are: solid triangles, *Tripneustes*; solid circles, *Eucidaris+Tripneustes*; solid diamonds, *Lytechinus+Tripneustes*; solid squares, *Eucidaris+Lytechinus+Tripneustes*; open up-pointing triangles, controls; open circles, *Lytechinus*; open down-pointing triangles, *Eucidaris*; and open squares, *Eucidaris+Lytechinus*.

neustes was characterized by the amount of substrate grazed (26.9%), diatoms (18.7%), and *Lithothamnium* sp. (18.5%), while 50% of the cumulative similarity in assemblages without *Tripneustes* was characterized by sediment (19.2%), *Ulva* sp. (17.5%), and diatoms (12.9%) (Appendix E).

There was also a highly significant effect of the species composition of the urchin assemblages on benthic community structure (Table 2b). Most benthic communities exposed to grazing by urchin assemblages containing *Tripneustes* (*Tripneustes*; *Eucidaris+Tripneustes*; *Lytechinus+Tripneustes*) clustered relatively close to each other; however, the benthic communities exposed to grazing by *Eucidaris+Lytechinus+Tripneustes* clustered in a distinctly different axis space that was closer to the treatments without *Tripneustes* (Fig. 2). Benthic communities of the most species-rich urchin assemblage were significantly different than those in the *Tripneustes* mono-assemblages, and all benthic communities without *Tripneustes* were significantly different from each other (post hoc tests following the significant main effect of assemblage composition in PERMANOVA; Table 2).

Consumer richness effects

Overyielding.—Although the main effect of species richness was nonsignificant in the nested ANOVA, overyielding statistics revealed a significant pattern related to species richness and a nonsignificant trend related to complementarity. For example, non-trans-

TABLE 3. Calculations of non-transgressive (LR_{mean}) and transgressive (LR_{max}) overyielding for all multi-assemblages.

Urchin assemblages	LR_{mean}	LR_{max}
Eucidaris+Lytechinus	0.268	0.226
Eucidaris+Tripneustes	0.382	−0.034
Lytechinus+Tripneustes	0.540	0.145
Eucidaris+Lytechinus+Tripneustes	−0.040	−0.627

Note: LR_{mean} and LR_{max} values greater than zero indicate that urchin multi-assemblages grazed differently than the average performance of their component species in mono-assemblages, and that multi-assemblages grazed more than their highest performing component species in mono-assemblages, respectively.

gressive overyielding occurred as LR_{mean} values were greater than 0 for all of the two-species assemblages (Table 3). In addition, one-sample *t* tests indicated that the average LR_{mean} values were significantly different than zero ($N = 3$, $P = 0.037$), which means that the magnitude of the grazing/predation of the two-urchin species assemblages exceeded that of the average performance of each component urchin species alone. In this case, the effect of two species together enhanced resource consumption.

Comparing the mean percentage of the substrate grazed in the experiments (observed) to the mean expected percentage grazed calculated by resampling indicated nonoverlapping 95% confidence intervals for the assemblages *Eucidaris+Tripneustes* and *Lytechinus+Tripneustes*. Thus, these particular two-species assemblages grazed more than expected, based on their average performance when alone (Fig. 1, Table 4).

Transgressive overyielding ($LR_{max} > 0$) occurred for two of the three two-species assemblages: *Eucidaris+Lytechinus* and *Lytechinus+Tripneustes* (Table 3). Thus, when together, complementarity or some other form of positive interactions occurred among these particular species combinations not only to enhance their overall grazing impact, but to exceed that of the highest urchin performer as mono-assemblages. However, one-factor ANOVAs revealed that no two-species assemblage grazed more than their most effective grazer as a mono-assemblage (Table 5), relegating the pattern

TABLE 4. Comparisons of observed vs. expected values of percentage (95% confidence intervals) of substrate grazed.

	Substrate grazed	
Urchin assemblage	Observed (%)	Expected (%)
Eucidaris+Lytechinus	14.98–31.91	17.79–18.04
Eucidaris+Tripneustes	**39.71–64.13**	**35.23–35.55**
Lytechinus+Tripneustes	**55.97–68.15**	**35.94–36.23**
Eucidaris+Lytechinus+Tripneustes	15.99–41.40	29.75–29.99

Notes: Estimation of expected percentage of substrate grazed was calculated by resampling the observed mono-assemblages data matrix 10 000 times with replacement (Duffy et al. 2003). Urchin assemblages in boldface correspond to nonoverlapping 95% confidence intervals between observed and expected percentage grazed and are represented in Fig. 1.

TABLE 5. ANOVA results for comparisons between the percentage of substrate grazed by the urchin multi-assemblages vs. their highest-performing urchin species when in mono-assemblage.

Source of variation	df	SS	F	P
Eucidaris+Lytechinus vs. *Lytechinus*	1	0.009	0.737	0.416
Error	8	0.097		
Eucidaris+Tripneustes vs. *Tripneustes*	1	0.001	0.042	0.843
Error	8	0.166		
Lytechinus+Tripneustes vs. *Tripneustes*	1	0.018	1.344	0.280
Error	8	0.107		
Eucidaris+Lytechinus+Tripneustes vs. *Tripneustes*†	1	0.177	7.689	0.024
Error	8	0.184		

Note: Analyses were performed on arcsine-transformed data; $N = 5$.

† Post hoc tests indicated that the percentage of substrate grazed in the multi-assemblage *Eucidaris+Lytechinus+Tripneustes* was significantly lower than in the *Tripneustes* mono-assemblages (df = 8, Tukey's HSD post hoc $Q = 2.31$, $P = 0.05$).

of transgressive overyielding to a nonsignificant trend. Similarly, when evaluating how general transgressive overyielding was in this study, we found that LR_{max} values were not significantly different than zero ($N = 3$, $P = 0.280$).

Underyielding.—The most species-rich urchin assemblage, *Eucidaris+Lytechinus+Tripneustes*, grazed as expected (Table 4, Fig. 1). Interestingly, this multi-assemblage grazed significantly less than its best-performing species (*Tripneustes*) when in the mono-assemblages ($LR_{max} = -0.627$; Tables 3 and 5, Fig. 1). In a similar way, LR_{max} for the two-species assemblage of *Eucidaris+Tripneustes* was slightly negative (−0.034), suggesting that together these species cannot exceed the grazing achieved by the best-performing species (*Tripneustes*) when in mono-assemblage. Nevertheless, the grazing achieved by this two-species assemblage was not significantly different than that of *Tripneustes* (Table 5), which indicates a nonsignificant trend of underyielding.

Richness and benthic community structure.—In contrast to the striking effects of consumer identity on benthic community structure, consumer richness did not have an effect on benthic community structure (Fig. 2, Table 2a). Nonmetric multidimensional scaling (NMDS) ordinations located benthic communities within *Eucidaris* and *Lytechinus* mono-assemblages close to those of the *Eucidaris+Lytechinus* assemblages (Fig. 2). Similarly, communities within the *Tripneustes* mono-assemblages were not substantially separated in ordination space, and were not significantly different from the other two-species multi-assemblages containing *Tripneustes* (post hoc tests following the significant main effect of assemblage composition in PERMANOVA; Table 2). Consequently, there was no consistent pattern of difference in benthic community structure as urchin richness increased (Fig. 2).

DISCUSSION

The results of this study show that the identity of sea urchins strongly affected both the percentage of substrate grazed and the benthic community structure

in a natural subtidal habitat of the Galápagos Islands (Tables 1 and 2). Identity explained most of the variability in the percentage of substrate grazed, while post hoc tests further revealed that *Tripneustes* drove this identity effect (Table 1, Fig. 1). In addition, there were some important signs of richness effects for the two-species multi-assemblages "*Eucidaris+Tripneustes*" and "*Lytechinus+Tripneustes*," as the 95% confidence intervals of observed and expected percentage of substrate grazed did not overlap (Table 4). Given that none of these urchin multi-assemblages grazed significantly more than the best-performing urchin species (*Tripneustes*) when alone, the mechanism behind these richness effects most probably corresponds to a sampling effect due to the presence of the dominant species, *Tripneustes* (Table 5, Fig. 1; Cardinale et al. 2006). This is further supported by the significant influence of the presence of *Tripneustes* on the amount of substrate grazed in comparisons of urchin assemblages with and without this species (Table 1b). The metabolic theory of ecology (Brown et al. 2004), and empirical data (Hillebrand et al. 2009) indicate that consumer body mass predicts per-capita rates of metabolism, respiration, growth, and consumption. Consequently, one potential explanation for the dominant identity effect of *Tripneustes* on the amount of the substrate grazed is that it is a function of its larger body size compared to the other two urchin species. This is reasonable, as there is some evidence that species with large body sizes generally have disproportionate effects in BEF studies (Solan et al. 2004).

The composition of the urchin assemblages (with or without *Tripneustes*) also had an effect on the percentage of substrate grazed and explained roughly one-quarter of the variability in the data (Table 1b). This was mainly due to underyielding in the form of reduced grazing within the three-species assemblage *Eucidaris+Lytechinus+Tripneustes* compared to that of any assemblage containing *Tripneustes* (Table 1, Fig. 1). It is possible that this most diverse urchin assemblage underyielded because it had fewer *Tripneustes* individ-

uals than the other urchin assemblages. By the same reasoning, we would expect that the two-species assemblages containing three *Tripneustes* would have grazed significantly less than the mono-assemblages with six *Tripneustes*. This was not the case, however, as the amount grazed in these two treatments with different *Tripneustes* densities was equivalent (Table 5). Another potential explanation is related to the fact that the foraging behavior of some urchin species can change at high densities. For example, Ayling (1981) demonstrated higher per-capita grazing of urchin species in high density feeding "fronts." In the present study, it is possible that the grazing intensity of *Tripneustes* may have decreased at a lower density of two urchins in the three-species multi-assemblage. Similar to the green urchin *Evechinus chloroticus*, which has a grazing threshold between five and six individuals per 1.0 m^2 (Ayling 1981), *Tripneustes* may have a grazing threshold between two and three individuals per 0.5 m^2. In addition, it seems that *Tripneustes*' foraging behavior does not change when together with just one other urchin species, as its grazing effect is the same when alone as with *Eucidaris* or as with *Lytechinus*, but it does in combination with two other urchin species (Fig. 1, Table 5). However, videotaped observations of a single *Tripneustes* in a fenced enclosure with two *Eucidaris* at another similar Galápagos subtidal site revealed aggressive behavior of *Eucidaris* toward *Tripneustes* as individual *Eucidaris* "chased" *Tripneustes* around the enclosure (J. Witman, *unpublished video data*). *Eucidaris* aggression toward *Tripneustes* would reduce its foraging time and this could explain the negative value of LR$_{max}$ for the *Eucidaris*+*Tripneustes* assemblage (Table 3). In addition, this behavior could explain the significant underyielding of the three-species multiassemblage (Tables 3 and 5, Fig. 1). Further research is needed to evaluate the role of density-dependent grazing in these urchin assemblages and to investigate changing intra and interspecific interactions (Byrnes and Stachowicz 2009) in order to elucidate the actual mechanism(s) causing the underyielding observed in the most species-rich assemblage.

Consumer identity in the broadest sense, the singular presence of *Tripneustes*, and combinations of particular species within assemblages with or without *Tripneustes* had a significant effect on benthic community structure (Table 2). In general terms, the differences in community structure across all assemblages was driven mainly by the high percent cover of substrate grazed in assemblages containing *Tripneustes* (Fig. 2, Appendices B–E), even though data were fourth-root transformed in order to reduce the influence of dominant taxa or substrate type (Clarke and Warwick 2001). Nevertheless, there were some interesting differences in community structure among the urchin treatments. Benthic communities in the assemblages with *Tripneustes* were characterized by the encrusting coralline algae *Lithothamnium* sp. and diatoms, while those without *Tripneustes* were typified

by the green foliose algae *Ulva* sp. and sediment (Appendix E).

We also found signs of transgressive overyielding (LR$_{max}$), which is a stringent way of determining complementarity in BEF studies (Cardinale et al. 2006); it occurred in two of the three pairwise two-species assemblages (Table 3). It has been shown that sufficient environmental heterogeneity can facilitate the expression of niche differences (Stachowicz et al. 2008). In our study, the probability of niche differences being expressed may be due to the availability of several food types (algal functional groups), which allowed for greater niche complementarity in resource use by the different urchin species (Byrnes et al. 2006, Griffin et al. 2008). Our data suggest that this might be the case, as articulated calcareous algae decreased in the *Lytechinus* mono-assemblages, while encrusting coralline algae increased in *Tripneustes* mono-assemblages (Appendix F). In addition, we found that *Tripneustes* preferentially grazed diatoms or erect algae off encrusting coralline algae, facilitating the persistence of the corallines and making them more apparent in the photos (Appendix G). This was not observed with the other two urchin species, as their grazing seems to remove all algae attached to the substrate by boring deeper into the rock (Appendix H). The relatively high abundance of sediment in assemblages containing *Eucidaris* and *Lytechinus* and low amounts in those containing *Tripneustes* further support the idea of more penetrating grazing by *Eucidaris* and *Lytechinus* (Appendices B–D). Taken together, these data imply resource use partitioning (Griffin et al. 2008), as each urchin species had different effects on particular algal functional groups. In another field manipulation of subtidal grazer diversity, Burkepile and Hay (2008) similarly found species-specific effects of herbivorous fish on algal community structure and a disproportionately strong effect of a single species, the redband parrotfish. Complementarity occurred among parrotfish and surgeonfish in their most species-rich treatment, containing two of the three species considered, with positive indirect effects documented for corals via the reduction of macroalgae (Burkepile and Hay 2008). The results of our study showed that the effects of the most species-rich consumer assemblages could not be predicted from pairwise two-species assemblages, underscoring the importance of manipulating all levels of species richness in the total range of species richness considered.

It is well known that consumer inclusion experiments can accentuate the effects of consumers (Hairston 1989, Englund 1997, Burkepile and Hay 2008), potentially leading to hyper consumption. There are several lines of evidence suggesting that this was not an issue in our study. For instance, the urchin densities used in the cages are representative of natural urchin densities in the Galápagos (Brandt and Guarderas 2002, Witman et al. 2010). In fact, Irving and Witman (2009) reported average densities of multi-species assemblages (*Eucida-*

ris+*Lytechinus*) of approximately eight and 15 individuals per 0.25 m^2 in subtidal algal turf and barrens habitats, respectively. An equivalent number of urchins scaled for the area of our inclusion cages (0.5 m^2) would be between 16 and 30; thus, in this respect, the densities of six urchins per 0.5 m^2 that we used in the treatments was very conservative. Secondly, the grazing levels occurring in the cages were similar to those previously observed in the field. In a study conducted off the same island in 2002, M. Brandt and L. Vinueza (*unpublished data*) found that *Eucidaris* grazing levels (measured as percentage of substrate grazed) increased significantly in 10 × 10 m control plots after 46 days ($F_{1,18} = 28.197$, $P < 0.001$). The mean percent cover of the substrate grazed, which was ~18% at the beginning of the study, increased to ~61% after six weeks. Consequently, the levels of urchin grazing observed within the cages of the present experiment are comparable to that previously documented outside of any cage structure, both in extent (net increase of 42% of substrate grazed in previous study vs. ~40% of mean substrate grazed in this study among all urchin assemblages; Fig. 1) and also in the speed of the grazing responses (6 weeks previously vs. 5 weeks during this experiment). Although we examined the effects of biodiversity across two trophic levels, our cages prevented potential grazing and top-down effects from fish, which are poorly known for this system, from being expressed. Experiments are being conducted to evaluate the effects of top-down predation and compensatory grazing by fish on the strength of urchin-mediated trophic cascades in the Galápagos subtidal (J. Witman, *unpublished data*).

Effect sizes quantifying the strength of richness and identity effects are seldom reported for consumer richness studies; however, when they are, identity effects seem to be stronger (Stachowicz et al. 2007), explaining up to 76% of the variance in some experiments (Bruno et al. 2008). Results from this subtidal experiment coincide with this pattern, as identity effects explained the vast majority (73%) of the variance. On the other hand, the probability of finding a richness effect is likely related to the duration of the experiments (Cardinale et al. 2007, Stachowicz et al. 2008). The length of our study was relatively short (five weeks), consequently, it is possible that a stronger richness effect might have been expressed if our experiment ran longer. However, the species manipulated in this study are strong interactors (sensu Paine 1980), and the experiment could have only been extended a week or so more before all algae and invertebrates on the substrate in the *Tripneustes* cages were completely consumed (M. Brandt and J. D. Witman, *personal observations*).

Conclusions and implications

This study demonstrated that strong effects of sea urchin diversity occurred principally as consumer identity effects, yet subtle richness effects were also present. Surprisingly, the dominant influence of *Trip-neustes* at the one- and two-species levels reversed at the three-species level, resulting in lower amounts of substrate grazed by the most species-rich urchin assemblage (underyielding) and negating our original hypothesis that prey abundance decreases with increasing consumer richness from one to three species. Had we chosen to examine consumption effects across only two levels of urchin diversity (one to two species), the emergent property of underyielding of the most diverse urchin assemblage would not have been detected. Our study thus highlights the importance of evaluating consumer richness effects across all possible diversity levels of the manipulated species. Furthermore, it suggests that nonlinear effects of increasing consumer species richness (Bruno and Cardinale 2008) deserve greater attention when trying to understand consumer diversity effects and the consequences of predator species extinctions. The finding that *Tripneustes* grazed significantly more and differently than the other urchin species indicates that population reductions of this species will result in dramatic changes in benthic community structure. The inference that *Tripneustes* enhances the persistence of encrusting coralline algae by consuming diatoms or erect algae covering it, suggests there may be a positive feedback between *Tripneustes* and corals, since encrusting coralline algae facilitate coral recruitment (Heyward and Negri 1999), and can enhance their recovery from disturbance (Birrell et al. 2008) or reduce their mortality (Burkepile and Hay 2008). Consequently, managers of the GMR are cautioned to consider the potential effects of a local extirpation of *Tripneustes*, given interest in opening a fishery for it in the near future (Luna 2000).

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SUPPLEMENTAL MATERIAL

Appendix A

A photograph depicting the sea urchin species in this study (*Ecological Archives* E093-077-A1).

Appendix B

A table listing SIMPER (similarity of percentages) analyses of taxa and other substrate types contributing to the differences in benthic community structure between urchin mono-assemblages (*Ecological Archives* E093-077-A2).

Appendix C

A table listing SIMPER analyses of taxa and other substrate types contributing to the differences in benthic community structure between two-species urchin multi-assemblages (*Ecological Archives* E093-077-A3).

Appendix D

A table listing SIMPER analyses of taxa and other substrate types contributing to the similarities in benthic community structure among replicates of urchin mono-assemblages (*Ecological Archives* E093-077-A4).

Appendix E

A table listing SIMPER analyses of taxa and other substrate types contributing to the similarities in benthic community structure among replicates of assemblages with and without *Tripneustes* (*Ecological Archives* E093-077-A5).

Appendix F

A table showing one-factor ANOVAs testing whether the net change of the percent cover of algal functional groups differed among the three urchin mono-assemblages (*Ecological Archives* E093-077-A6).

Appendix G

A photograph showing a fragment of the substrate grazed within a *Tripneustes* mono-assemblage (*Ecological Archives* E093-077-A7).

Appendix H

A photograph showing a fragment of the substrate grazed within a *Eucidaris+Lytechinus* multi-assemblage (*Ecological Archives* E093-077-A8).