COMMUNITY ECOLOGY - ORIGINAL PAPER

Grazing intensity influences the strength of an associational refuge on temperate reefs

Stuart Levenbach

Abstract Recent studies have emphasized the role of positive interactions in ecological communities, but few have addressed how positive interactions are mediated by abiotic stress and biotic interactions. Here, I investigate the effect of a facilitator species on the abundance of macroalgae over a gradient of herbivory. Grazing by sea urchins can be intense on temperate reefs along the California coast, with benthic macroalgae growing exclusively in physical refuges and interspersed within colonies of the strawberry anemone, *Corynactis californica*. Field experiments indicated that the net effect of *C. californica* on turf algae was strongly nonlinear over a gradient in density of sea urchins. At low intensities of urchin grazing, the anemone and macroalgae competed for space, with algae capable of overgrowing *C. californica*. At intermediate grazing intensities, *C. californica* provided a refuge for turf algae but not for juvenile kelp. Neither turf algae nor kelp benefited from the presence of *C. californica* at the highest levels of grazing intensity, as sea urchins consumed nearly all macroalgae. The hump-shaped effect observed for *C. californica* contrasts with the prevailing view in ecological theory that positive interactions are more common in harsh environmental conditions. The results reported here qualify this view and underscore the need to evaluate positive interactions over a range of abiotic stress and consumer pressure.

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Introduction

Herbivory is a fundamental process that structures ecological communities (Hairston et al. 1960), and many primary producers have evolved morphological and chemical adaptations that enable them to tolerate, escape, or defend against herbivory (Hay and Steinberg 1992; Coley and Barone 1996; Mauricio 2000). Heavily defended plant species sometimes ameliorate consumer pressure on neighboring primary producers lacking these adaptations. For example, thorny terrestrial plants create a physical refuge for neighboring plants by impeding herbivore access (Rebollo et al. 2002). In the marine environment, chemically defended algae can protect undefended algae from grazing by herbivorous fish (Hay 1986; Pfister and Hay 1988). Associational refuges, where consumption of the target species is reduced when growing in the presence of a neighboring species, are common in both terrestrial (Atsatt and O'Dowd 1976; Olff et al. 1999) and marine environments (Hay and Steinberg 1992; Rosenthal and Kotanen 1994). Factors that allow primary producers to persist in heavily grazed ecosystems may be important in maintaining plant diversity (Callaway et al. 2005) and supporting higher trophic levels (Hacker and Gaines 1996).

A unique aspect of associational refuges is that they are a combination of two simultaneous interactions—competition and facilitation—that together produce a net effect. For example, Levine (2000) reported that sedge depressed reproductive performance in neighboring macrophytes by 60%, but this negative effect was offset by a 75% reduction in herbivory on neighboring macrophytes. This tradeoff

between competition and protection from herbivory has led some ecologists to predict that associational refuges specifically, and positive interactions in general, should be more common in areas of intense abiotic stress and/or consumer pressure (Bertness and Callaway 1994).

Conceptual models offer disparate views regarding the effect of facilitators in extremely harsh environments. When the facilitator benefits neighboring species, its effect has typically been modeled as a linear (Brooker and Callaghan 1998) or an exponential function (Bertness and Callaway 1994). When the positive effects of a facilitator species wane because the benefactor no longer mitigates environmental conditions, or it competes with neighbors for extremely limited resources, it has been modeled as a unimodal function (Hacker and Gaines 1997; Bruno et al. 2003).

The research presented here is among the first to quantify the net effect of a facilitator over a gradient of consumer pressure while controlling for spatial variability in environmental conditions. Many empirical studies have compared the effect of a facilitator between one or two "harsh" and "benign" environments and thus are unable to capture a wide range of environmental conditions (Bertness and Shumway 1993; Greenlee and Callaway 1996; Callaway 1998; Bertness et al. 1999). While some have examined facilitation along a gradient of abiotic stress (Callaway et al. 2002; Maestre and Cortina 2004) and consumer pressure (Brooker et al. 2006), these investigations have relied on existing spatial variability in the abiotic and/or biotic conditions. Controlling for spatial variability is critical, as species-specific adaptations can confound patterns between facilitation and environmental stress (Pennings et al. 2003).

Temperate reef ecosystems are well suited to the study of associational refuges. Grazing pressure from sea urchins can be extremely high, and urchin barrens are frequent phenomena in kelp-dominated regions (Lawrence 1975; Harrold and Pearse 1987). Foliose algae (e.g., kelp) are typically rare on barren reefs, and hard substrata are dominated by encrusting coralline algae and bare space. However, patches of edible, turf-forming algae may persist when grown in association with organisms that deter grazing. In the Santa Barbara Channel (USA), turf-forming algae are common on intensively grazed reefs that have high abundances of the small colonial anemone, *Corynactis californica* (hereafter: *Corynactis*). *Corynactis* has particularly powerful nematocysts (Skaer and Picken 1965), aggressively uses its mesenterial filaments to kill neighboring sessile organisms (Chadwick 1987), and can impede the movement of benthic invertebrates (Patton et al. 1991; Levenbach 2008a, b).

Here I manipulated the abundance of *Corynactis*, benthic macroalgae, and sea urchins to estimate the effect of the facilitator (i.e., *Corynactis*) over a gradient of consumer pressure (i.e., sea urchin density). My conceptual model is that the net effect of *Corynactis* on macroalgae should be a hump-shaped function of grazing intensity if (a) *Corynactis* and macroalgae compete for attachment space in the absence of sea urchin grazing, and (b) *Corynactis* does not entirely deter grazing by sea urchins. If so, I hypothesize that in these circumstances *Corynactis* should: (1) provide the greatest benefit to algae at intermediate grazing intensities, and (2) indirectly benefit from sea urchins grazing on macroalgal competitors. I test whether the underlying assumptions are valid for (a) and (b) and subsequently explore the shape of the relationship that describes the effect of *Corynactis* on turf algae (Fig. 1).

Materials and methods

Study system

I conducted field work at Naples Reef (34°25′N, 119°57′W) and Coal Oil Point (34°23′N, 119°52′W) in the Santa Barbara Channel, CA, USA. Naples Reef is a 2-ha outcrop of shale located 1.6 km offshore and 23 km west of Santa Barbara (Ebeling et al. 1985). Water depth on the reef ranges from 7.5 to 17 m. Coal Oil Point is similar in size, consists of bedrock ranging in depth from 2 to 8 m, and is situated 15 km west of Santa Barbara. The purple sea urchin, *Strongylocentrotus purpuratus*, and the red sea urchin, *Strongylocentrotus franscicanus*, are common, and total urchin density on both reefs can exceed 85 individuals per m^2 (Levenbach, unpublished data). At these densities, grazing intensity is extreme and kelp (e.g., *Macrocystis pyrifera*) is rare. The corallimorpharian (commonly called strawberry anemone), *Corynactis*, forms clonal aggregates that can exceed 500 polyps per 0.25 m^2 at both study sites (Levenbach, unpublished data). Multi-species algal turf (<3 cm in height), consisting of filamentous algae (*Ceramium* sp., *Ectocarpus* sp., *Pterosiphonia* sp.) and foliose red algae (*Polyneura latissima, Laurencia crispa,*
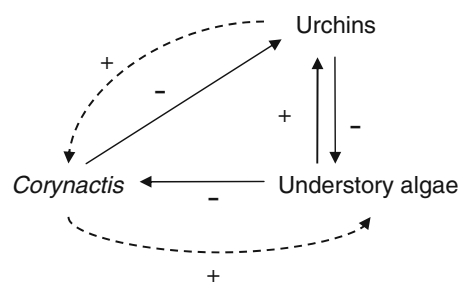
Fig. 1 An interaction web of sea urchins, turf algae, and strawberry anemones (*Corynactis californica*) showing direct (*dashed line*) and indirect (*dotted line*) effects and positive (+) and negative (−) interactions

Rhodymenia spp.) is often interspersed among *Corynactis* colonies.

Interaction between *Corynactis* and macroalgae in the absence of herbivory

I manipulated *Corynactis* and benthic macroalgae to test whether they compete for attachment space in the absence of sea urchins, and if so, to determine which species was the superior competitor. I established plots of 50×50 cm haphazardly along a 300 m^2 section of Naples Reef at an approximate depth of 11 m. I spaced plots at least 1 m apart and randomly assigned each plot to a treatment. To measure the effect of *Corynactis* on macroalgae, I removed anemones from randomly chosen plots and measured the subsequent change in cover of turf algae and density of kelp in these removal plots ($N = 10$) relative to the unmanipulated control plots ($N = 9$). To measure the effect of algae on *Corynactis*, I removed macroalgae from other randomly chosen plots and measured the subsequent change in cover and density of *Corynactis* in removal plots ($N = 10$) relative to the unmanipulated control plots ($N = 9$). Both response variables of cover and density of *Corynactis* were measured because the anemone can persist for months in a starved state, shrinking in size in response to diminished resources (Levenbach, unpublished data), and so competition from algae could have changed the body size but not density of *Corynactis* over a 12-month field experiment.

I estimated the percentage cover of benthic macroalgae and sessile invertebrates in experimental plots in June 2003. I placed a 50×50 cm aluminum frame, threaded with a grid of monofilament line, over each plot and recorded the primary space holder at each intersection ($N = 81$), if one was present. When it was not possible to identify taxa to species, they were categorized based on genus or general morphology (e.g., red algal turf, encrusting bryozoans). I counted the number of *Corynactis* polyps and kelp in addition to all other attached organisms and mobile grazers. To establish the treatments, I removed *Corynactis* and algal turf from designated plots using forceps, while urchins were collected and relocated far from the experimental area. I maintained removals every three weeks for 12 months, although *Corynactis* recruited poorly once removed. Initial cover of *Corynactis* averaged $17 \pm 2\%$ (mean $\pm$ 1 SE) and less than 1% after removal. Initial cover of turf algae averaged $60 \pm 13\%$, and $6 \pm 1\%$ after removal. The experiment continued for 12 months to allow *Corynactis* to undergo several cycles of asexual reproduction and one season of sexual reproduction (Chadwick and Adams 1991; Holts and Beauchamp 1993). In June 2004, I counted the percentage cover of benthic macroalgae and estimated sessile invertebrates and mobile grazers, kelp, and *Corynactis* in each plot.

In the *Corynactis* removal and unmanipulated control plots, I compared the proportional change in the percentage cover of algal turf [ln(final cover/initial cover)] and the proportional change in the density of kelp sporophytes [ln(final density/initial density)] by a one-tailed Student's *t* test. In the algae-removed and unmanipulated control plots, I compared the proportional change in cover [ln(final cover/initial cover)] and density [ln(final density/initial density)] of *Corynactis* by one-tailed Student's *t* test. I used JMP 6.0.0 for all statistical analyses.

The manipulation of algae to examine the response of *Corynactis* provided two opportunities to explore the nature of the relationship between these species in the absence of grazing. The first was the press manipulation itself, and the second was the subsequent relaxation period (beginning after I ended the year-long press), when algae were allowed to naturally recolonize the plots. In a separate experiment, I removed algae from ten experimental plots for one year (June 2003–2004), and these were then allowed to re-establish for the subsequent year (June 2004–2005). Algae were left unmanipulated in an additional eight control plots for this two-year period. Plots were 50×50 cm and placed at least 1 m apart at a depth of 11 m at Naples Reef. I removed algae with hand tools, and benthic cover and abundance of *Corynactis* were estimated using the same methods described above. Ambient sea urchin densities were unmanipulated in this experiment, but extremely low (mean $\pm$ 1 SE: 0.15 ± 0.8 individuals/0.25 m^2 in June 2004 and zero in June 2005).

I evaluated the effects of removing benthic macroalgae on the proportional change in cover [ln(final cover/initial cover)] and density [ln(final density/initial density)] of *Corynactis* in experimental plots after 12 months of removing algae and again after 12 months of algal re-establishment using ANOVA.

Estimating the effect of *Corynactis* on macroalgae along a gradient of herbivory

To assess how facilitation interacted with consumer pressure, I experimentally manipulated urchin densities surrounding transplanted assemblages of *Corynactis* and benthic macroalgae. I expedited transplanting the anemone by collecting mussels (*Mytilus californianus*) covered with *Corynactis* from an offshore oil production platform in the Santa Barbara Channel (Platform Gilda; 34°10′56″N, 119°25′07″W). I removed the living mussel and I retained the shell for the experiment. I thinned *Corynactis* on the shells to 50% cover of the shell surface, with the remaining area scraped bare. In August 2004, I attached the experimental shells with *Corynactis* to Naples Reef, where the density of sea urchins was extremely low, to obtain a lush growth of algae on the shells prior to initiating the

experiment. By November 2005, the previously bare space on mussel shell substrates had been colonized by several species of turf-forming algae (e.g., *Pterosiphonia* sp., *Rhodymenia* spp.) and juvenile kelp (*Macrocystis pyrifera* and *Pterygophora californica*). During this pre-experimental phase, the mean (±1 SE) cover of *Corynactis* on the shells declined from 50 to 8% (±1%), representing 4.1 (±0.47) g aggregate wet weight.

To initiate the experiment, I transplanted 44 shells with *Corynactis* and macroalgae from Naples Reef to Coal Oil Point, an urchin barren reef, where they were attached to the bottom at a depth of 8 m in 22 pairs. I removed all *Corynactis* polyps from one mussel shell in each pair using hand tools, leaving algae in place, and I left the other shell unmanipulated. Pairs of shells were spaced 4 m apart over a 500 m² section of the reef where urchin densities were high. I photographed shells when first attached to Coal Oil Point for use in subsequent estimates of initial biomass. Eight days later, I collected all the mussel shells and transferred them into the lab, where *Corynactis* and macroalgae were removed from the shells. I counted *Corynactis* polyps and recorded aggregate wet weight on a Mettler AE100 analytical balance. I categorized algae into major taxonomic groups, blotted them with a paper towel, and weighed them. I weighed kelp blades separately from stipes and holdfasts because urchins did not consume stipes and holdfasts during the field experiment.

Calculating proportional change in algal biomass required the initial biomass to be estimated for each shell. To do this, ten of the shells placed at Naples Reef to obtain algae were sacrificed at the end of the pre-experimental phase and used to establish the relationship between algal cover and wet weight at the start of the experiment. I photographed the shells prior to being collected to estimate cover, and returned to the lab, where the turf algae and kelp blade wet weights were recorded. The best-fit regression models to the data were: kelp blade wet weight $= 0.78e^{4.43(\text{initial cover})}$, ($r^2 = 0.79$) and red algal wet weight $= 5.52(\text{initial cover})$; ($r^2 = 0.69$).

I photographed all of the shells in the experiment using an Olympus C-4000 digital camera attached to a 23 cm tall aluminum frame. Using Adobe Photoshop 7.0, a grid of approximately 50 points was overlaid on each photograph and, at each point, I recorded the primary space holder and any kelp blades. Where kelp blades extended beyond the shell periphery, I recorded the number of points overlaying them. I calculated turf algal cover as the number of points on turf algae divided by the total number of points on the shell. I calculated kelp cover as the number of points on kelp blades divided by the total number of points on the shell plus any additional points beyond the shell periphery that overlay kelp blades.

To create a gradient of grazing intensity, I counted urchins, manipulated, and then recounted at Coal Oil Point immediately prior to attaching mussel shell transplants to the bottom. Initial urchin density was 51 ± 3 individuals/m², consisting of 96% purple urchins (*S. purpuratus*) and 4% red urchins (*S. fransciscanus*). I demarcated a 2-m radius around each pair of shells and assigned one of three urchin treatments: low grazing intensity (all urchins removed; $N = 7$), intermediate grazing intensity (half of urchins removed; $N = 10$), and high grazing intensity (unmanipulated; $N = 5$). I recounted urchins three days after attaching the mussel shells and again at the end of the experiment (eight days). I used the mean of the three counts to estimate average urchin density during the experiment. I converted the density of urchins into biomass using the regression equation: wet weight (g) $= 0.6492(\text{test diameter in cm})^{2.76}$ (Russell 1987); purple urchin test diameter at Coal Oil Point was normally distributed with a mean of 2.34 cm ($N = 880$).

My operational measure for the net benefit of *Corynactis* to algae was the difference between the logged ratios of algal wet weight (g wet weight) consumed on shells with or without *Corynactis*:

$$f = \ln(A_{\text{fp}}/A_{\text{ip}}) - \ln(A_{\text{fo}}/A_{\text{io}}) \tag{1}$$

$f =$	net benefit
$A_{\text{fp}} =$	final algal biomass, *Corynactis* present
$A_{\text{ip}} =$	initial algal biomass, *Corynactis* present
$A_{\text{fo}} =$	final algal biomass, *Corynactis* absent
$A_{\text{io}} =$	initial algal biomass, *Corynactis* absent

Because of the short duration of the experiment (eight days), and the calm conditions under which it was performed, algal loss due to senescence and breakage was assumed to be minimal and the proportional change in algae during the experiment was used as an estimate of the amount of algae consumed by grazers.

To validate my conceptual model of a hump-shaped distribution, I initially fitted the data with fourth-order regression models in a stepwise approach, and tested each fit by ANOVA:

$$f = y_0 + aU \tag{2}$$

$$f = y_0 + aU + bU^2 \tag{3}$$

$$f = a \exp(-0.5(\ln(U/U_0)/b)^2) \tag{4}$$

$$f = y_0 + a \exp(-0.5(\ln(U/U_0)/b)^2) \tag{5}$$

$U =$ Sea urchin biomass (g wet weight)

After I determined that a hump-shaped distribution served as the best fit, I estimated the shape of the function by plotting the proportion of turf algae consumed on shells

with or without *Corynactis* against the respective biomass of urchins. I selected a simple harvest model to fit each dataset:

$$dA/dt = -q(C)UA \tag{6}$$

where $q(C)$ is the grazing rate by urchins (U) on algae (A) when the level of *Corynactis* is C. Or, after rearranging,

$$\ln(A_f/A_i) = -(q_0 - q_1 C)TU \tag{7}$$

where T is the length of the observation period (eight - days). The difference between these fitted relationships for a given biomass of urchins is the estimate of the net effect function. In this case, it represents the amount of turf algae protected by the presence of *Corynactis*. I only calculated this function for turf algae because no positive effects of *Corynactis* on juvenile kelp were detected at any urchin density. The parameters q_0 and q_1 were estimated separately for shells with or without *Corynactis*, and the two best fit functions were tested for significance by ANOVA.

Results

Interaction between *Corynactis* and macroalgae in the absence of herbivory

After 12 months of continuously removing *Corynactis*, algal turf cover declined from 63.7 ± 4.1 to $53.6 \pm 4.2\%$ (mean $\pm$ 1 SE) in removal plots and from 56.2 ± 4.3 to $38.2 \pm 4.7\%$ in unmanipulated control plots. Although the cover of turf algae at the end of the experiment was 15% higher in removal plots relative to controls, the difference was not statistically significant ($t = 1.16$, $df = 17$, $P = 0.13$). The density of juvenile kelps increased from 1.4 ± 0.5 to 7.0 ± 1.3 individuals/0.25 m^2 (mean $\pm$ 1 SE) in removal plots and from 0.8 ± 0.3 to 4.7 ± 1.5 individuals/0.25 m^2 in control plots. The difference between removal and control plots with respect to the proportional change in juvenile kelp density was not statistically significant ($t = 0.61$, $df = 17$, $P < 0.28$).

The effect of *Corynactis* on turf algae was weak and highly variable at best. By contrast, turf algae had strong effects on *Corynactis*. Population growth of *Corynactis*, as measured either by relative changes in cover (Fig. 2a) or density (Fig. 2b), was strongly negative in the presence of algae, and positive (but indistinguishable from 0 for the period of this experiment) in the case where algae were removed (cover $t = 3.12$, $df = 17$, $P < 0.01$; density $t = 2.35$, $df = 17$, $P < 0.02$).

Following the end of the press experiment, algae were allowed to re-establish for one year as a second test of the competitive effect of algae on *Corynactis*. From June 2003 to 2004, I reduced algal cover from 60 to 14%, but
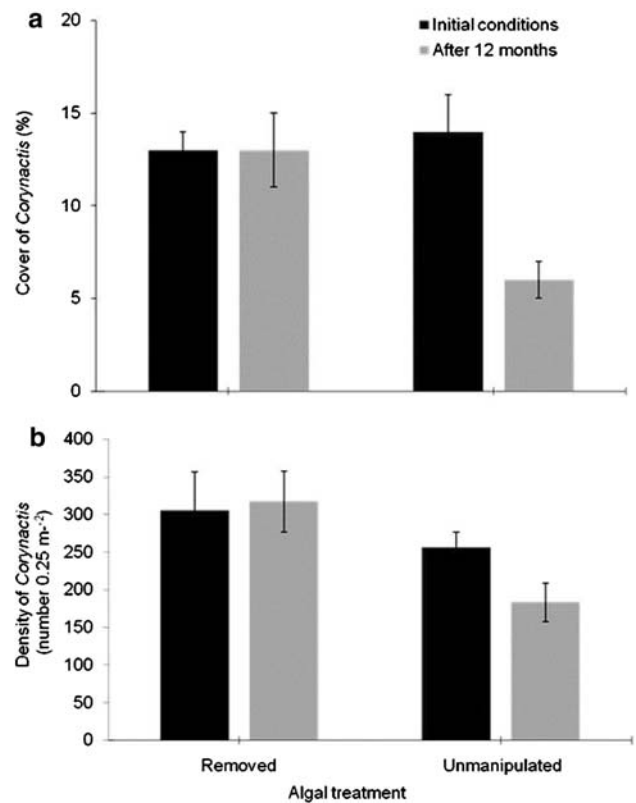

Fig. 2 a Percentage cover and **b** density of *Corynactis* (mean $\pm$ 1 SE) before (*black bars*) and after (*gray bars*) 12 months of removing algae from treatment (removed, $n = 10$) versus control (unmanipulated, $n = 9$) plots

one year after I stopped the manipulation (June 2005), algae had returned to >50% cover (Fig. 3). Throughout the two-year period covering both the press and relaxation portions of the experiment, algal cover remained high (>50% cover) on the unmanipulated control plots (Fig. 3).
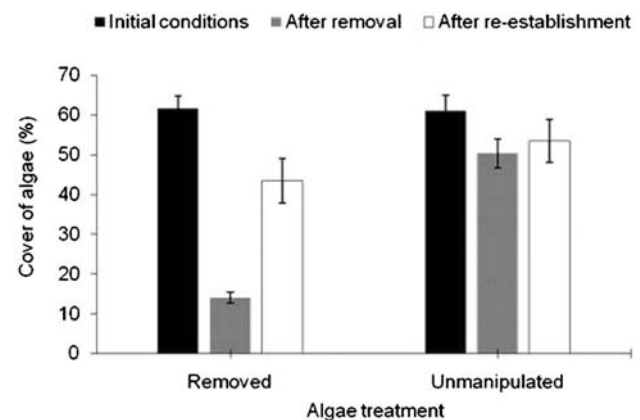

Fig. 3 Percentage cover of algae (mean $\pm$ 1 SE) in treatment (removed, $n = 10$) versus control (unmanipulated, $n = 8$) plots at initial conditions in June 2003 (*black bars*), after 12 months removal (*gray bars*, June 2004), and following 12 months re-establishment (*open bars*, June 2005)
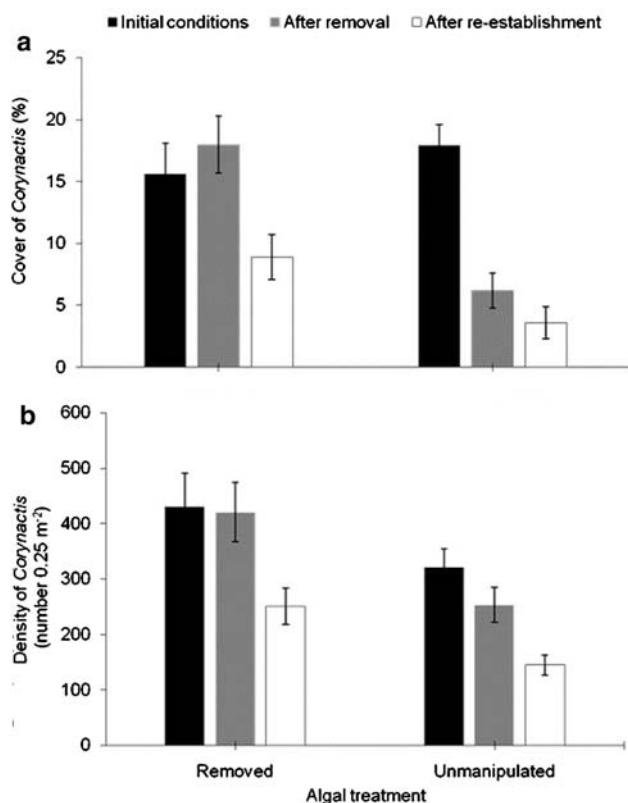
Fig. 4 **a** Percentage cover and **b** density of *Corynactis* (mean ± 1 SE) in treatment (removed, *n* = 10) versus control (unmanipulated, *n* = 8) plots at initial conditions in June 2003 (*black bars*), after 12 months removal (*gray bars*, June 2004), and following 12 months re-establishment (*open bars*, June 2005)

Whereas the cover of *Corynactis* increased (relative to controls) when algae were experimentally removed, it declined sharply (relative to controls) when algae naturally recolonized the manipulated plots (ANOVA, $F_{(1,32)}$ = 11.12, $P < 0.01$). The density of *Corynactis* responded in a similar, marginally significant trend (ANOVA, $F_{(1,32)}$ = 3.25, $P = 0.08$). The patterns of responses in cover (Fig. 4a) and density (Fig. 4b) of *Corynactis* suggest that, at least for the period of the experiment, competition from algae had a stronger effect on body size than number of anemones, as the relative decline in cover was nearly twice that of density.

Estimating the effect of *Corynactis* on macroalgae along a gradient of herbivory

There was no benefit to juvenile kelp (∼30 cm in height) from neighboring *Corynactis* colonies. Significantly more kelp was eaten at intermediate and high urchin densities compared to low densities (Table 1; ANOVA, $F_{(2,41)}$ = 9.09, $P < 0.001$); however, there was no difference in juvenile kelp density between substrates with or without *Corynactis* (ANOVA, $F_{(2,19)}$ = 1.93, $P = 0.17$).

Table 1 Percentage (mean ± 1 SE) of turf algae and kelp consumed (g wet weight) on shell substrates with or without *Corynactis* at three levels of grazing intensity

Grazing intensity	*N*	Turf algae consumed (%)		Kelp consumed (%)	
		With *Corynactis*	Without *Corynactis*	With *Corynactis*	Without *Corynactis*
Low	7	55 ± 6	52 ± 8	18 ± 18	8 ± 6
Intermediate	10	70 ± 6	93 ± 2	84 ± 16	100 ± 0
High	5	92 ± 4	99 ± 1	100 ± 0	100 ± 0

In contrast to kelp, *Corynactis* lessened grazing on turf algae, but the extent to which the anemone provided protection depended upon consumer pressure. Relative to the shells without *Corynactis*, there was more algal biomass when associated with *Corynactis* under a moderate grazing regime than there was under low and high grazing intensities. I evaluated successively more complex model representations and evaluated goodness of fit to experimental data on algal biomass as a function of urchin biomass. A linear regression model was nonsignificant ($P = 0.88$). A two-parameter quadratic model was significant but with a low coefficient of determination ($P = 0.02$, $r^2 = 0.35$). The three-parameter lognormal model had a relatively high coefficient of determination ($P < 0.001$, $r^2 = 0.57$), all three parameters were highly significant, and the residuals were normally distributed. A four-parameter lognormal model had the highest coefficient of determination, but the fourth parameter was not significant ($P < 0.001$, $r^2 = 0.63$, fourth parameter: $P = 0.07$). Thus, a three-parameter lognormal model best represented the data, indicating a hump in the relationship between consumer pressure and the net benefit of *Corynactis* to turf algae (Fig. 5).

The regression models fitted to shells with or without *Corynactis* were both significant (with *Corynactis* q_0 = 1.27×10^{-3}, $q_1 = 5.15 \times 10^{-5}$, $r^2 = 0.52$, $P < 0.001$; without *Corynactis* $q_0 = 1.68 \times 10^{-3}$, $q_1 = -1.69 \times 10^{-3}$, $r^2 = 0.51$, $P < 0.001$). The difference between the predicted values for these two models, otherwise defined as the net effect function, was strongly nonlinear over the gradient of grazing pressure (Fig. 6). The benefit to turf algae from associating with *Corynactis* rose sharply with initial increases in grazing pressure, peaked at a moderately low value (equivalent to a density of ∼10 purple sea urchins/m²), then gradually declined as grazing intensity increased further (Fig. 6). At Coal Oil Point, a site of intense grazer pressure, the associational benefit of *Corynactis* to turf algae was ∼20% of the peak benefit at the average density of purple sea urchins (∼50/m²; equivalent to ∼340 g urchin biomass), and ∼3% of peak benefit at the maximum density of purple urchins observed in a m² (∼85/m²).
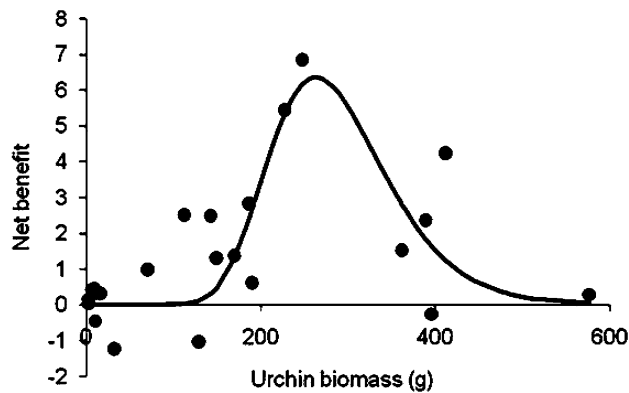
Fig. 5 Net benefit of *Corynactis* to macroalgae along a gradient of sea urchin grazing pressure, with a fitted lognormal three-parameter model (see Eq. 4; $P < 0.001$, $r^2 = 0.57$). The operational measure for net benefit is the difference between the logged ratios of algal wet weight consumed on shells with *Corynactis* minus the proportion consumed on the paired shell without *Corynactis* (see Eq. 1). Urchin grazing pressure is expressed as the estimated biomass of purple urchins (g wet weight)
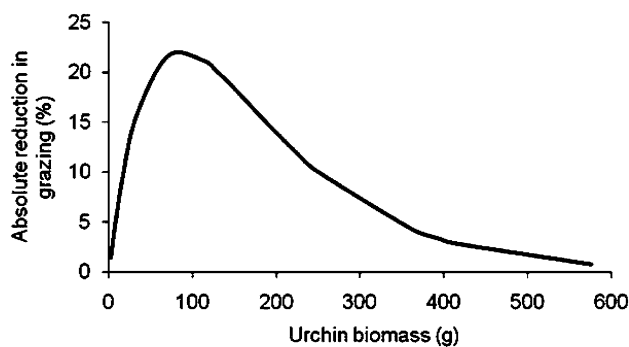

Fig. 6 Net benefit of *Corynactis* to macroalgae along a gradient of sea urchin grazing pressure. The *line* represents the percentage of turf algae biomass protected by *Corynactis*, plotted as the difference between functions fit separately to consumption of algae on shells with or without *Corynactis*. Urchin grazing pressure is expressed as the estimated biomass of purple urchins (g wet weight)

Discussion

Competition and consumer-resource interactions are fundamental ecological processes, and a goal of ecology has been to identify factors that mediate these interactions. In this regard, indirect effects play an important role, and the scientific literature is replete with examples of consumers that maintain diversity by preying upon superior competitors (Paine 1974; Olff and Ritchie 1998), and to a much lesser extent, examples of facilitators that protect vulnerable species by hindering consumers (Hay 1986; Stachowicz and Hay 1999; Callaway et al. 2005). This study demonstrates the interesting scenario whereby the facilitator that mediates a consumer-resource interaction is also an inferior competitor to the species that it indirectly

benefits (e.g., Dungan 1986). Since the consumer preys upon the superior competitor, the consumer indirectly benefits the same facilitator that impinges upon the consumer's own behavior. In this respect, indirect effects have an important, stabilizing role on the interactions among sea urchins, turf algae, and *Corynactis*.

My field manipulations revealed that benthic macroalgae was the superior space competitor to *Corynactis* in the absence of sea urchin grazers. Both the cover and density of *Corynactis* declined in response to competition from algae, although cover declined more than density. However, as grazing intensity from sea urchins increased from zero, turf algae gained a substantial benefit from associating with its inferior competitor, *Corynactis*. The net benefit function was sharply skewed left, indicating a rapidly rising benefit of the associational refuge with initial increases in grazer pressure then gradually declined to zero at extremely high densities of sea urchins. These results underscore that the amount of consumer pressure is important to positive interactions, and, in extremely harsh conditions, the species of interest may no longer benefit neighboring organisms.

Foraging urchins are most likely deterred by *Corynactis* nematocysts, which are particularly powerful (Skaer and Picken 1965). This mechanism was proposed by Patton et al. (1991) to explain slow *Pisaster* predation rates on clams (*Chama arcana*) within patches of *Corynactis*. When sea urchins touch *Corynactis*, they withdraw their tube feet and exhibit other signs of stress (Levenbach 2008a). However, as shown by the current study, the positive indirect benefit to macroalgae is contingent upon the density of sea urchins. While the exact mechanism remains to be explored, it is possible that high contact rates of urchins with *Corynactis* overwhelm the ability of the anemone to deter the grazer. Urchins also engage in riskier behavior when starving, such as actively foraging for macroalgae in close proximity to predators (Vadas et al. 1986).

My field experiment failed to yield conclusive evidence that *Corynactis* harms algae in a competitive interaction, despite the fact both occupy primary space. This may be a result of strong background variability in algal cover and the small amount of surface area covered by *Corynactis* relative to benthic macroalgae in my experiment. Although *Corynactis* aggressively defends territory against other sessile invertebrates, its mesenterial filaments do not affect algae (Chadwick 1987). As a result, algae are able to overgrow *Corynactis* polyps and otherwise interfere with the capture of food (Coyer et al. 1993). The lack of recolonization by *Corynactis* once it was removed from experimental plots suggests that algae recruit to open space faster, and would competitively exclude *Corynactis* were it not for factors that influence the biomass of understory algae, such as fluctuations in urchin grazing.

This study explored the net effect function over a narrow range in cover of *Corynactis*. Ideally, it would be helpful to know the shape of the response *surface* with the variables of grazing intensity and a broad range in cover (i.e., a three-dimensional depiction of how the net effect changes over all combinations of herbivore and facilitator abundance). Naturally occurring *Corynactis* is often much more extensive than the roughly 8% cover used on transplanted mussel shells. In 2000 and 2001, over 30% of the bottom of Naples Reef was covered by *Corynactis* (Santa Barbara Coastal LTER, unpublished data), and similar patterns have been observed at the Santa Barbara Channel Islands (Kushner et al. 2001). When *Corynactis* forms such an extensive cover, it is a strong deterrent to sea urchin movement (Levenbach 2008a), and therefore may elicit a stronger positive effect on algal biomass than was observed in this study.

Much of the literature driving conceptual models of positive interactions is based on terrestrial plant interactions, where facilitators compete with their neighbors in benign conditions and benefit their neighbors in harsh conditions (e.g., high salinity or low rainfall). This has led to predictions that positive interactions increase in number or importance as "environmental stress" (i.e., abiotic stress or consumer pressure) increases (Bertness and Callaway 1994; Brooker and Callaghan 1998). However, this and similar studies suggest that there are physiological and biological limits to facilitation. For example, tussock grass benefited nearby shrubs by increasing soil moisture, but competed with neighbors at sites with either high or extremely low rainfall (Maestre and Cortina 2004). This generates a quadratic net effect function, where under certain environmental conditions the benefits of a facilitator are outweighed by its own resource uptake. When individual performance, relative to conspecifics lacking facilitators, is no greater under extreme environmental stress than more moderate conditions, it generates an asymptotic net benefit function. For example, Callaway et al. (2002) found that alpine plants competed with neighbors in regions where conditions were benign, and benefited neighboring regions where conditions were harsh (i.e., cold). However, the benefit to neighbors in terms of plant biomass or leaf number was no greater in harsh than in intermediate levels of stress. Both quadratic and asymptotic relationships between facilitators and environmental stress have found support in spatially explicit theoretical models of positive interactions (Travis et al. 2006).

Neither of these two models is appropriate for the interaction between *Corynactis* and turf algae. *Corynactis* is an inferior competitor to macroalgae and its positive effect asymptotes to zero at very high levels of grazing pressure, producing a hump-shaped net effect function

(Fig. 6). Studies of deer herbivory on pine saplings concealed in heather provide some evidence that the hump-shaped function derived in this study can be generalized to associational refuges in terrestrial systems (Brooker et al. 2006). The conditions necessary to produce this response are that the benefactor must be (a) a weak competitor and (b) unable to ameliorate extreme environmental stress.

Positive effects depend on the life history of interacting organisms (Callaway and Walker 1997). In this study, kelp plants ($\sim$30 cm in height) were not protected by *Corynactis*, because their fronds swept beyond the periphery of *Corynactis* and were quickly consumed by nearby urchins. However, other studies suggest that small kelp recruits (<3 cm) are protected within *Corynactis* colonies (Levenbach 2008b). Kelp plants most likely lose protection as they grow and become accessible to urchins, in much the same manner that tree saplings lose protection when they emerge from neighboring plants and become apparent to herbivores (Brooker et al. 2006). As canopy-forming kelp plants continue to grow, they may indirectly benefit *Corynactis* by shading understory algal competitors (Reed and Foster 1984) or by altering flow regimes which in turn increase food supply (Gaylord et al. 2004). In this respect, *Corynactis* may enhance the recruitment and growth of juvenile kelp, have no effect on subadults, and indirectly benefit from large adult plants.

In this study, the unimodal relationship between protection and grazing pressure might have been dependent upon the duration of the experiment, if the percent of turf algae that was consumed varied nonlinearly over time with an asymptote near 100%. Previous studies have found that transplanted *Corynactis* colonies facilitate the recruitment and persistence of turf algae within an urchin barren for as long as two years, using an amount of *Corynactis* cover approximately double that used in the present study (Levenbach 2008b). This implies that the final result depends upon the amount of cover, and that a cover of 8% may be too low to sustain turf algae under a moderate grazing intensity.

The existence of a unimodal or nonlinear underlying function teaches an important lesson: that efforts to quantify positive interactions need to consider the underlying relationships with environmental factors. The shapes of such functions or surfaces cannot be revealed by studies that use only two levels of stress, which has been a common approach. As a result, simplistic assumptions concerning "benign" and "harsh" environments may lead to a failure to detect positive interactions (Pennings et al. 2003; Maestre et al. 2005). Consequently, direct tests of the interplay between competition and facilitation should be conducted across a range of abiotic stress or consumer pressure.

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