



FEATURE ARTICLE

Facilitation cascade maintains a kelp community

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ABSTRACT: There is increasing interest in how facilitation cascades — nested positive indirect interactions involving at least 3 species — maintain community structure. Here we investigated whether the positive relationship between the kelp *Ecklonia radiata* and the gastropod *Phasianotrochus eximius* is mediated by a third species, the sea urchin *Holopneustes purpurascens*, via a facilitation cascade. Both the urchin and the gastropod are found enmeshed within the lamina of the common kelp *E. radiata*, which the urchin is known to consume. Sampling of urchin and gastropod abundances at 4 sites in Sydney, Australia, over 2 yr revealed that both *H. purpurascens* and *P. eximius* were more abundant on kelp than on other algal substrates and that the gastropod was more abundant on kelp with than without the urchin. Large *P. eximius* were found only on plants inhabited by *H. purpurascens*, suggesting that either *P. eximius* is able to survive longer when it is part of this association or that adults actively move onto this substrate. When the presence/absence of *H. purpurascens* on kelp plants was manipulated experimentally in the field, greater recolonisation by *P. eximius* of kelp with than without urchins was observed. Urchins, by contrast, did not differentially respond to kelp with and without the gastropod, indicating that the association between the kelp and the urchin is maintained by a unidirectional facilitation cascade. Our study adds to growing evidence that facilitation cascades are a common mechanism by which community structure is maintained. Studies are now needed to assess their sensitivity to environmental change.

KEY WORDS: Indirect effect · Plant · Herbivore · Positive interaction · Marine

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The urchin *Holopneustes purpurascens* and the gastropod *Phasianotrochus eximius* enmeshed within the common kelp *Ecklonia radiata*.

Image: Vivian Ward

INTRODUCTION

Indirect effects, where the effect of one species on another is mediated by one or more additional species, are pervasive in ecological systems (Menge 1995, Abrams & Matsuda 1996, Stachowicz 2001, Wootton 2002, Werner & Peacor 2003, Ohgushi 2008). Consequently, our ability to predict the responses of ecosystems to perturbations is dependent on understanding indirect effects (Paine 1980, Dambacher et al. 2002, Bolker et al. 2003, Borer et al. 2005, Borrett et al. 2010).

There is growing interest in when and where indirect effects lead to facilitation cascades (Bruno & Bertness 2001, Bruno et al. 2003, Altieri et al. 2010, Angelini et al. 2011). In a facilitation cascade, a basal species facilitates an intermediary species, which in

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turn facilitates the focal species or community (Altieri et al. 2007, Thomsen et al. 2010). In many instances, these cascades arise through the provision of structured habitat by the basal and intermediary facilitators, which are in turn utilised by secondary inhabitants for protection from natural enemies and/or adverse micro-climates (Thomsen et al. 2010). Among these habitat cascades are those underpinned by shelter building. In this case, a plant facilitates a herbivore by providing food and/or structural habitat, and the herbivore in turn facilitates other organisms by modifying the physical architecture of the plant to provide shelter (Bruno & Bertness 2001, Ohgushi 2005, Thomsen et al. 2010).

Shelter building occurs when a species provides habitat that is subsequently utilised by secondary inhabitants for protection from natural enemies and/or adverse micro-climates when the builder vacates. In terrestrial systems, leaf-rolling and stem-boring invertebrates protect themselves from predators and abiotically stressful conditions by creating shelters that are used not only by their own populations but also by whole communities of associated invertebrates (Strauss 1991, Martinsen et al. 2000). By contrast, there are few examples of shelter building in the sea (Ohgushi 2005). This may be because in many marine ecosystems, such as coral reefs, herbivory is substantially greater than terrestrial herbivory and often exceeds the amount of primary production of macrophytes (Cyr & Pace 1993). In addition, abiotic factors such as wave action, tides and currents in shallow coastal habitats where marine herbivory is concentrated may make shelters more difficult to build and maintain.

This paper examines how shelter building by the sea urchin *Holopneustes purpurascens* mediates the relationship between the gastropod *Phasianotrochus eximius* and the common kelp *Ecklonia radiata*. *H. purpurascens* is unusual among sea urchins in that it is arboreal, inhabiting the canopy of the living alga that it uses as both habitat and food (Fig. 1; Steinberg 1995, Rogers et al. 1998). *H. purpurascens* spawn predominantly in the Australian summer (Williamson & Steinberg 2002), and larvae settle onto a range of red foliose and crustose algae such as the coralline turfing alga *Corallina officinalis* and the foliose red alga *Delisea pulchra* (Swanson et al. 2006). Juveniles later move to the kelp *E. radiata*, where they wrap themselves within the algal thallus (Steinberg 1995, Williamson et al. 2000, 2004, Marzinelli et al. 2011). This shift increases the sea urchin's rate of survival, growth and reproductive output (Williamson & Steinberg 2012). The gastropod *P. eximius* occurs on the same host plants as the urchin, and the two are



Fig. 1. Urchin *Holopneustes purpurascens* and gastropod *Phasianotrochus eximius* (top) enmeshed within the common kelp *Ecklonia radiata*

usually found together, enmeshed within the fronds of *E. radiata* (Steinberg 1995, Rogers et al. 1998).

Here we test the hypothesis that the association between *Ecklonia radiata* and *Phasianotrochus eximius* is maintained by a facilitation cascade, whereby the kelp *E. radiata* facilitates the intermediary, *Holopneustes purpurascens*, and *H. purpurascens* in turn facilitates *P. eximius* by building shelters from kelp blades. First, we tested (1) whether *H. purpurascens* and *P. eximius* were each more abundant on the kelp *E. radiata* than on other algal species and (2) whether *P. eximius* was more abundant on *E. radiata* with than without *H. purpurascens*. Second, we tested the longevity of the shelter provided by *H. purpurascens* for *P. eximius* by assessing changes in the abundance of *H. purpurascens* on *E. radiata* over time. Third, the size distribution of *P. eximius* on all host plants was compared to that on *E. radiata* plants containing *H. purpurascens* to assess whether *P. eximius* are likely to recruit directly to, or immigrate post-recruitment to, the *E. radiata*/*H. purpurascens* association. As the majority of *P. eximius* were larger in the association than on other species of algae (including *E. radiata* without *H. purpurascens*), it was hypothesised that the gastropods must be actively seeking the sheltered association post-recruitment. Hence, fourth, a field experiment tested the hypothesis that there would be greater recolonisation of *P. eximius* to *E. radiata* plants with *H. purpurascens* compared to those without the urchin. This experiment allowed us to distinguish the effects of the sea urchin per se from plant properties that might have made individual *E. radiata* attractive to both *H. purpurascens* and *P. eximius* in the absence of any interaction between

the latter 2 species. Finally, laboratory experiments were conducted to determine if urchins, by contrast, responded to kelp with and without the gastropod.

MATERIALS AND METHODS

Study site

Field experiments were done in rocky subtidal habitats (between 1 and 5 m depth) at Bare Island (33° 59' 38" S, 151° 12' 00" E), Balmoral (33° 83' 02" S, 151° 24' 88" E), Long Bay (33° 96' 50" S, 151° 25' 37" E) and Fairlight (33° 80' 00" S, 151° 27' 54" E) in Sydney, New South Wales, Australia. These sites were sheltered from large waves and comprised irregular patches of barrens and macroalgal habitat in which both *Holopneustes purpurascens* and *Phasianotrochus eximius* occurred. Forests of the kelp *Ecklonia radiata* were common at all sites surveyed, with other spatially dominant macroalgal species including the brown algae *Sargassum vestitum* and *S. linearifolium*, the coralline turfing red alga *Corallina officinalis* and the foliose red alga *Delisea pulchra* and a mosaic of crustose algae encrusting understory rock (*Sporolithon durum* and *Lithamnion* spp.; Wright et al. 2005). Other canopy-forming algae, such as *Phyllospora comosa*, were notably absent from the study region (Coleman et al. 2008). A more comprehensive discussion of the habitat type is found in Wright et al. (2005).

Spatial variation in abundance of snails and urchins

The 4 Sydney study sites were sampled over 2 yr to test the hypotheses that (1) both *Phasianotrochus eximius* and *Holopneustes purpurascens* would be more abundant on *Ecklonia radiata* than on the common species of macroalgae, *Sargassum vestitum*, *S. linearifolium* and *Corallina officinalis*; (2) *P. eximius* would be more abundant on *E. radiata* with than without *H. purpurascens*; and (3) these patterns would persist across seasons and years. Fairlight and Bare Island were sampled once every season, in October, February, April and June, between October 2009 and June 2011. Balmoral was sampled on the first 4 dates but was replaced by sampling at Long Bay from October 2010 to June 2011 because by June 2010, both *P. eximius* and *H. purpurascens* had virtually disappeared from the Balmoral site.

During each sampling period, 10 haphazardly selected replicate plants of the algal species *Ecklonia radiata* (mean wet weight, patted dry \pm SE: 900 \pm 14 g), *Sargassum vestitum* (250 \pm 2 g), and *S. linearifolium*

(270 \pm 2 g) and a small amount of *Corallina officinalis* (66 \pm 1 g), a turfing species that does not exist as discrete plants, were collected. Plants were collected from 2 to 7 m depth at each site using SCUBA, sealed in plastic bags *in situ*, and then transported back to the laboratory at Macquarie University, where animals were removed for enumeration by twice immersing the plants in fresh water for 30 s. A pilot study in which the abundances of mobile fauna on plants were compared between plants with and without immersion confirmed that this method was 100% efficient in removing all animals greater than 0.5 mm (J. E. Bell unpubl. data). Within each sample, the numbers of *P. eximius* and *H. purpurascens* were counted.

Separate univariate permutational analyses of variance (PERMANOVAs; Anderson 2001a) compared the abundances of *Phasianotrochus eximius* and *Holopneustes purpurascens* among algal substrates and sampling times at each study site. PERMANOVAs apply the traditional ANOVA partitioning procedure to a distance matrix but use permutations to obtain p-values (Anderson 2001b). Unlike ANOVAs, PERMANOVAs do not have explicit assumptions about the underlying distributions of data. The PERMANOVAs, run in PRIMER v6 (PRIMER-E), used 4999 permutations of Euclidean distances among samples. To partition any differences among algal substrates into effects of algal identity and algal biomass, 2 sets of PERMANOVAs were run. The first used raw species counts, while the second included algal biomass as a covariate. PERMANOVAs for Bare Island and Fairlight had 3 orthogonal factors: year (random), season (fixed) and algal species (fixed). PERMANOVAs for Balmoral and Long Bay each had 2 factors: season and algal species (each fixed). Where significant treatment effects were seen at $\alpha = 0.05$, PERMANOVAs were followed by pairwise *a posteriori* tests.

A 1-way univariate PERMANOVA of Euclidean distances among samples tested for any significant difference in the abundances of *Phasianotrochus eximius* on plants with *Holopneustes purpurascens* compared to plants without *H. purpurascens*. This analysis used data pooled across all algal species at all seasons and sites and was chosen over a correlation because gastropod abundance was not necessarily expected to increase with urchin abundance on kelp with urchins. In addition, to assess the degree to which the presence of *H. purpurascens* increases the abundance of *P. eximius* on *Ecklonia radiata*, we calculated a 'magnification ratio' (sensu Thomsen et al. 2010). This was simply the ratio of the number of *P. eximius* on *E. radiata* with *H. purpurascens* to the number of *P. eximius* on *E. radiata* without *H. purpurascens*.

Persistence of urchins

For *Phasianotrochus eximius* to benefit from shelter building by *Holopneustes purpurascens*, presumably there would need to be some temporal persistence of shelters and, hence, urchins on individual *Ecklonia radiata*. The temporal stability of urchin numbers on individual *E. radiata* was assessed through a study at Fairlight. In December 2009, 15 *E. radiata* plants were randomly selected, 5 initially with no *H. purpurascens*, 5 with a low density of *H. purpurascens* (1 to 2 per plant) and 5 with a high density of snails (3 or more snails per plant). Plants were tagged with flagging tape and surveyed at the same time (mid-morning) every day for 7 consecutive days. The number of *H. purpurascens* on tagged plants was recorded over time. A PERMANOVA on Euclidean distances among samples, with the factors (1) initial urchin density (zero, low, high); (2) plant nested within density; and (3) time as a repeated measure, was used to assess whether differences in numbers of urchins among plants were maintained through time.

Size-frequency distribution of snails

To assess whether *Phasianotrochus eximius* are likely to recruit directly to, or immigrate post-recruitment to, the *Ecklonia radiata*/*Holopneustes purpurascens* association, we determined the size distribution of *P. eximius* on host plants with and without *H. purpurascens*. A length-frequency plot was generated from the individuals collected at Fairlight during seasonal algal collections between October 2009 and June 2011. Whole plants were bagged and taken to the laboratory, where the numbers of *H. purpurascens* and *P. eximius* were counted, and *P. eximius* were then measured (described above). Individuals were pooled into 1 mm size classes. A Kolmogorov-Smirnov test was used to test for a difference in the size class frequency distributions of *P. eximius* on *E. radiata* with versus without *H. purpurascens*.

Post-recruitment movement

Snails

To test the hypothesis that the positive relationship between the gastropod and urchin is, in part, maintained by juvenile and adult *Phasianotrochus eximius* immigrating more rapidly to *Ecklonia radiata* with than without *Holopneustes purpurascens*, we con-

ducted a recolonisation experiment at Fairlight in December 2010. All mobile fauna >10 mm in diameter were removed from 20 haphazardly selected *E. radiata* by hand using SCUBA. Two *H. purpurascens* (determined from the average number of urchins per *E. radiata*, see 'Results') were added to 10 of the defaunated plants that had been randomly assigned to this treatment, with the other 10 plants left free of urchins. Each of the treatments contained a mix of *E. radiata* plants that immediately prior to the experiment housed urchins and those that did not. To maintain assigned urchin densities, all experimental plants were caged using flexible plastic garden fencing (mesh size 20 mm). The mesh was fine enough to prevent urchins from passing through but coarse enough to allow free movement of *P. eximius*. Cages covering the head of the plant were attached to eyebolts in the rocky substratum using bungee cords. This allowed for the natural movement of the cages with the water currents. After 24 h, plants were harvested and sealed in plastic bags (as described above) before being taken back to the laboratory, where plants were immersed in fresh water (as described above) and the number of recolonising *P. eximius* on each plant counted.

The process of caging can impact the number of epifauna (Kennelly 1991, Taylor 1998). To test how complete the recolonisation was on caged plants after 24 h, we compared numbers of gastropods recolonising cages with and without urchins to numbers on 10 replicate unmanipulated plants with *Holopneustes purpurascens* and 10 replicate unmanipulated plants without the urchin.

To test the hypotheses that (1) there was a difference in the number of gastropods recolonising kelp with urchins and without and (2) this difference matched the natural difference in gastropod density between uncaged kelp with urchins and without, a 2-factor, fully orthogonal PERMANOVA was conducted. The test used Euclidean distances, with statistical procedures as described above.

Urchins

The field experiment tested whether colonisation of kelp by *Phasianotrochus eximius* is influenced by the presence of *Holopneustes purpurascens*. To test the converse, that *H. purpurascens* actively select *Ecklonia radiata* with *P. eximius* over kelp without the gastropods, a laboratory experiment was run. Similar-sized pieces and weights (30 to 60 g) of *E. radiata* were placed at opposite ends (separated by

14 cm) of a 40 l plastic bin filled with filtered seawater (0.22 μm). The pieces of kelp were chosen to contain minor grazing scars from *H. purpurascens*, as this presumably indicates that they are palatable to the urchins. First, no-choice controls, in which urchins were offered pieces of gastropod-free *E. radiata* at either end of the tank, determined whether in the absence of choice gastropods displayed a consistent pattern of movement towards a particular end of the tank. Second, choice treatments where 6 *P. eximius* (average number of *P. eximius* per *E. radiata* in the field, see 'Results') were added to one but not the other piece of kelp assessed selection of one treatment over the other. At the start of each test, 1 adult *H. purpurascens* (32 to 58 mm oral-aboral length) was placed in the centre of the plastic bin (7 cm from either treatment) and given 30 min to make a choice between *E. radiata* pieces. An urchin was deemed to have made a choice if it touched one of the pieces of kelp. Positions of the treatments (with or without *P. eximius*) were swapped after 15 replicates to account for any bias between sides, and the seawater was changed between replicates (30 replicates in total). New urchins and kelp and fresh seawater were used for each replicate. The experiment, initially conducted during the day, was repeated at night, when *H. purpurascens* may be more active (J. E. Williamson unpubl. data).

Separate chi-squared tests for differences in the proportion of urchins moving towards one treatment over the other were done for trials run during the day and the night. These analyses only used urchins that made a choice and had the null hypothesis that the proportion of urchins moving towards each treatment would not statistically differ from a 50:50 ratio.

RESULTS

Spatial variation in abundance of snails and urchins

Across all sites and sampling times, the mean (\pm SE) abundance of *Phasianotrochus eximius* was 1.8 ± 0.3 ind. per plant on *Ecklonia radiata*, 0.2 ± 0.1 ind. per plant on *Sargassum vestitum*, 0.3 ± 0.1 ind. per plant on *S. linearifolium* and 0.2 ± 0.1 ind. per plant on *Corallina officinalis*. The magnitude of this difference among algal substrates, however, varied according to season and site (significant Se \times S interactions, Table 1). The pattern of greater abundance of *P. eximius* on *E. radiata* than on any of the 3 other algal substrates was strongest in summer, the season of peak gastropod abundance (post hoc tests,

Table S1 in the Supplement, available at www.int-res.com/articles/suppl/m501p001supp.pdf). At 3 of the 4 sites, this pattern, although weaker, also persisted at other times of the year (Table 1). At the fourth site, Balmoral, no significant difference in gastropod abundance was evident among algal substrates in autumn. Among the 3 other algal species, few differences in gastropod abundance were seen (Table S1 in the Supplement). Where differences were apparent, *C. officinalis* generally supported fewer gastropods than *S. vestitum* and *S. linearifolium*. The difference in gastropod abundance between *E. radiata* and other algal substrates was largely independent of differences in algal biomass among treatments (Table S2 in the Supplement).

Holopneustes purpurascens displayed similar differences in abundance among algal substrates as the gastropod. Across all sites and sampling times, the mean (\pm SE) abundance of *H. purpurascens* was $0.5 \pm$

Table 1. Permutational analyses of variance testing for sources of spatial variation in the abundance of *Phasianotrochus eximius* among potential host plant species (S: *Ecklonia radiata*, *Sargassum vestitum*, *S. linearifolium*, *Corallina officinalis*), seasons (Se: spring, summer, autumn, winter) and years (Y: 2009/2010, 2010/2011). Balmoral and Long Bay were sampled only in 1 yr each. Numbers in **bold** indicate a significant difference at $p < 0.05$. $n = 10$

	df	MS	Pseudo- <i>F</i>	p
Bare Island				
Y	1	28.8	14.8	0.001
Se	3	1.5	0.8	0.513
S	3	18.2	9.4	0.001
Y \times Se	3	1.2	0.6	0.613
Y \times S	3	11.9	6.1	0.001
Se \times S	9	1.3	0.7	0.732
Y \times Se \times S	9	2.2	1.1	0.345
Residual	288	1.9		
Fairlight				
Y	1	26.5	5.1	0.021
Se	3	49.9	9.7	0.001
S	3	59	11.4	0.001
Y \times Se	3	11.5	2.2	0.084
Y \times S	3	14.4	2.8	0.036
Se \times S	9	20.3	3.9	0.001
Y \times Se \times S	9	8.6	1.6	0.098
Residual	288	5.2		
Balmoral				
Se	3	107.7	12.1	0.001
S	3	137.6	15.4	0.001
Se \times S	9	49.4	5.6	0.001
Residual	144	8.9		
Long Bay				
Se	3	1.6	2.7	0.055
S	3	3.6	6.3	0.001
Se \times S	9	0.6	1	0.433
Residual	144	0.6		

0.1 ind. per plant on *Ecklonia radiata*, 0.02 ± 0.01 ind. per plant on *Sargassum vestitum*, 0.01 ± 0.01 ind. per plant on *S. linearifolium* and 0.01 ± 0.01 ind. per plant on *Corallina officinalis*. Like *Phasianotrochus eximius*, *H. purpurascens* displayed variation in abundance among algal substrates in at least some seasons and years at each of the 4 sites sampled (Table 2, Table S1 in the Supplement). During all seasons and at all sites where differences among algal substrates were detected, the urchin was more abundant on *E. radiata* than on the other 3 algal species (Table 2, Table S1). Like the gastropod, the urchin displayed stronger patterns of difference among algal substrates in summer, when its abundance was greatest, than in other seasons (Table S1). Significant differences in urchin abundance between *E. radiata* and the other algal substrates were in most instances still apparent in analyses where algal biomass was included as a covariate (Table S3 in the Supplement).

Phasianotrochus eximius not only was more abundant on *Ecklonia radiata* than on any of the other algal species sampled but was also significantly more abundant on *E. radiata* plants that contained *Holopneustes purpurascens* (mean \pm SE: 4.6 ± 0.8 ind. per plant) compared to those that did not (mean \pm SE: 0.7 ± 0.2 ind. per plant; PERMANOVA: pseudo- $F_{1,958} = 5.6$, $p = 0.024$). On *E. radiata*, *H. purpurascens* magnified the abundance of *P. eximius* 6.6-fold.

Persistence of urchins

During the tagging study, up to 11 urchins were recorded on 1 *Ecklonia radiata* host (Fig. 2). Abundances of urchins on individual plants displayed considerable temporal variation at the scale of days, with abundances changing by as much as 6 individuals in the space of 24 h (Fig. 2). There was no consistent direction to this change (i.e. increase or decrease in numbers), with both emigration and immigration occurring. However, plants that started with higher numbers of urchins maintained higher numbers of urchins than plants starting with few or no urchins throughout the experiment (*a posteriori* tests, significant urchin density effect, repeated measures PERMANOVA: $F_{6,84} = 35.83$, $p = 0.001$, Fig. 2).

Size-frequency distribution of snails

There was a significant difference in the size-frequency distribution of *Phasianotrochus eximius* between kelp plants with and without *Holopneustes pur-*

Table 2. Permutational analyses of variance testing for sources of spatial variation in the abundance of *Holopneustes purpurascens* among potential host plant species (S: *Ecklonia radiata*, *Sargassum vestitum*, *S. linearifolium*, *Corallina officinalis*), seasons (Se: spring, summer, autumn, winter) and years (Y: 2009/2010, 2010/2011). Balmoral and Long Bay were sampled only in 1 yr each. Numbers in **bold** indicate a significant difference at $p < 0.05$. $n = 10$

	df	MS	Pseudo- <i>F</i>	p
Bare Island				
Y	1	1.13	6.4	0.004
Se	3	0.64	3.6	0.012
S	3	4.02	22.7	0.001
Y \times Se	3	0.08	0.4	0.687
Y \times S	3	0.84	4.8	0.001
Se \times S	9	0.43	2.4	0.008
Y \times Se \times S	9	0.13	0.7	0.693
Residual	288	0.18		
Fairlight				
Y	1	0.25	0.9	0.353
Se	3	0.7	2.5	0.049
S	3	6.14	22.3	0.001
Y \times Se	3	0.26	0.9	0.443
Y \times S	3	0.54	1.9	0.123
Se \times S	9	0.89	3.2	0.002
Y \times Se \times S	9	0.24	0.9	0.543
Residual	288	0.28		
Balmoral				
Se	3	0.04	0.7	0.572
S	3	0.23	3.8	0.01
Se \times S	9	0.04	0.7	0.718
Residual	144	0.06		
Long Bay				
Se	3	0.36	2.2	0.091
S	3	2.03	12.4	0.001
Se \times S	9	0.36	2.2	0.027
Residual	144	0.16		

purascens (Kolmogrov-Smirnov test: $p < 0.01$, Fig. 3). *P. eximius* greater than 9 mm in length were only observed on *Ecklonia radiata* with *H. purpurascens*; however, smaller *P. eximius* were found across habitats both with and without *H. purpurascens* (Fig. 3).

Post-recruitment movement

Snails

Following removal of *Phasianotrochus eximius* from *Ecklonia radiata*, an average of $7.2 (\pm 1.9, 1 \text{ SE})$ gastropods recolonised each kelp plant with *Holopneustes purpurascens*, while $2.8 (\pm 1.2, 1 \text{ SE})$ recolonised kelp plants without urchins (Fig. 4). By contrast, on uncaged kelp, the average gastropod density was 8.7 per plant ($\pm 2.2, 1 \text{ SE}$) where urchins were present and $1.6 (\pm 1.2, 1 \text{ SE})$ per plant where they were absent

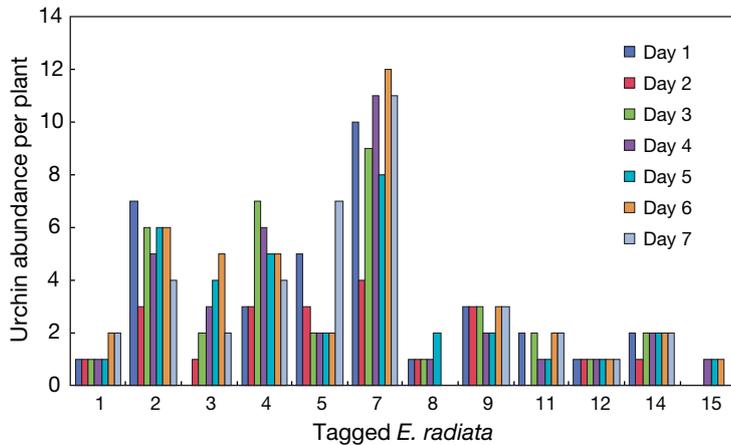


Fig. 2. Abundance of *Holopneustes purpurascens* on individually tagged *Ecklonia radiata* over a period of 7 d. For plants 6, 10, 13, no. of urchins = 0 over all 7 d

(Fig. 4). Hence, in the recolonization experiment, the effect of urchins on gastropod abundance matched natural differences in gastropod numbers between kelp plants with and without urchins (PERMANOVA, main effect of urchins: pseudo- $F_{1,1} = 12.0$, $p = 0.004$; non-significant caging \times urchin interaction: pseudo- $F_{1,31} = 0.70$, $p = 0.393$).

Urchins

In daytime no-choice controls, in which urchins were offered *Ecklonia radiata* without gastropods at

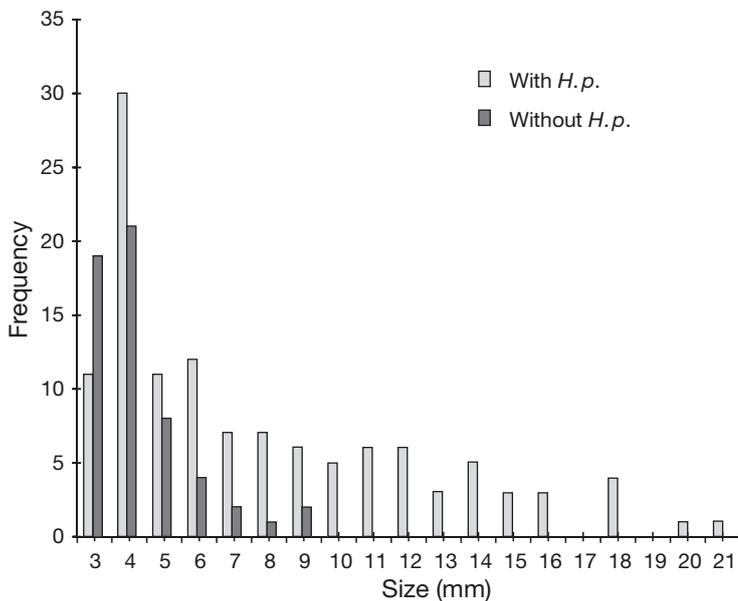


Fig. 3. Size-frequency distribution of *Phasianotrochus eximius* on kelp with *Holopneustes purpurascens* (with *H. p.*; $n = 21$ plants) and without *H. purpurascens* (without *H. p.*; $n = 8$ plants)

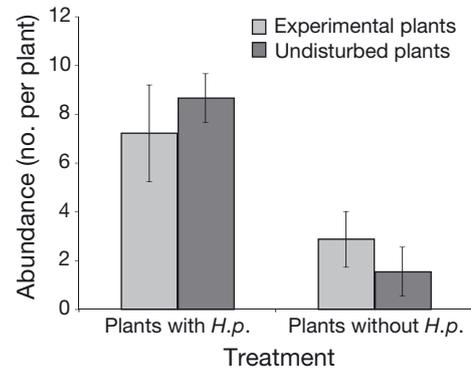


Fig. 4. Mean \pm SE natural abundance (undisturbed plants; dark grey bars) and post-recruitment recolonisation following removal (experimental plants; light grey bars) of *Phasianotrochus eximius* on *Ecklonia radiata* with and without *Holopneustes purpurascens* (*H.p.*). $n = 10$ plants

either end of the tank, only 2 individuals out of the 30 tested selected a piece of kelp. The 2 urchins differed from one another in the direction they moved, such that there was no evidence for selection in the absence of choice ($\chi^2 = 0$, $df = 1$, $p = 1$). When *Holopneustes purpurascens* were offered *E. radiata* versus *E. radiata* with *Phasianotrochus eximius* during the day, no urchins out of the 30 individuals tested made a choice. When *H. purpurascens* was given a choice between *E. radiata* with versus without *P. eximius* at night, 12 out of 30 urchins made a choice, but there was no significant difference in the choice made ($\chi^2 = 1.2$, $df = 1$, $p = 0.273$).

DISCUSSION

The objective of this study was to determine the nature of the relationship between the kelp *Ecklonia radiata*, the canopy-dwelling sea urchin *Holopneustes purpurascens* and the gastropod *Phasianotrochus eximius*. Through a combination of field and laboratory experiments and surveys, it was demonstrated that the relationship between *E. radiata* and *P. eximius* was the net outcome of a positive indirect effect, whereby *E. radiata* facilitates *H. purpurascens*, and the urchin in turn facilitates *P. eximius*. This relationship appeared to be hierarchical, as the urchin did not respond to the abundance of the gastropods. Hence, the relationship fitted the definition of a facilitation cascade (see Altieri et al. 2007, Bishop et al. 2012).

Following recruitment to the coralline turfing alga *Corallina officinalis* or foliose red algae

Delisea pulchra (Swanson et al. 2004, 2006), *Holopneustes purpurascens* displays a chemically mediated ontogenetic shift in diet and moves to *Ecklonia radiata* (Williamson et al. 2004). Consequently, at each of the 4 field sites surveyed, *H. purpurascens* was more abundant on the kelp *E. radiata* than on the other representative habitat-forming algae examined (*Sargassum vestitum*, *S. linearifolium*, *C. officinalis*). *Phasianotrochus eximius* abundances followed those of the urchin, with more *P. eximius* on *E. radiata* than on the other 3 algal substrates, and over 6 times more *P. eximius* on *E. radiata* with the urchin than without. Although *E. radiata* had a larger surface area than the other algal species, differences in the abundance of gastropods and urchins among algal substrates persisted even when differences in algal biomass were controlled. The relatively high magnification ratio for the association between the gastropod and urchin (cf. Thomsen et al. 2010) highlights the strength of this relationship.

Greater numbers of *Phasianotrochus eximius* recolonised kelp with than without *Holopneustes purpurascens*, irrespective of whether the kelp had recently housed urchins or not, but in laboratory experiments, the urchin did not respond to the presence of the gastropod. Hence, it appears that the urchin and gastropod were not simply responding independently to the same sort of kelp and that the relationship between the kelp, urchin and gastropod was, instead, a hierarchical facilitation cascade (sensu Thomsen et al. 2010, Angelini et al. 2011). Although we did not quantify the position on the kelp at which the gastropod was found, our field observations and previous research (Steinberg 1995) suggest that the majority of gastropods are enmeshed in the kelp-blade nests formed by urchins. Hence, the urchin facilitates the gastropod. Nevertheless, during winter, when urchin densities decreased, *P. eximius* was sometimes found away from urchins, nestled in the centre of *Ecklonia radiata* plants (J. E. Bell pers. obs.). Hence, the relationship was facultative, not obligate, and varied in strength over time. Our study did not determine the mechanism by which *H. purpurascens* facilitated *P. eximius*.

By providing shelter and increasing the heterogeneity of the kelp substrate, *Holopneustes purpurascens* may reduce *Phasianotrochus eximius* dislodgement during wave action and/or protect the gastropod from predation by large crustaceans or predatory fish (Steinberg 1995, Rogers et al. 1998, Williamson et al. 2004). Alternatively or additionally, *P. eximius* may eat the excrement of *H. purpurascens*. Coprophagy is often exhibited by animals that

have simple digestive systems (such as isopods and some gastropods; Wieser 1978) and are less able to assimilate the necessary levels of nutrients from plants alone (Mattson 1980). *P. eximius* may employ this strategy by consuming the readily available and relatively large fecal pellets produced by *H. purpurascens*, with which it is closely associated.

Larger *Phasianotrochus eximius* were only found on host plants with *Holopneustes purpurascens*, whereas smaller gastropods were found on *Ecklonia radiata* both with and without the urchin. This suggests that small *P. eximius* recruit to the kelp, irrespective of whether it houses an urchin, but that subsequent processes restrict larger gastropods to kelps with urchins. This pattern was at least in part because of post-settlement movement of large *P. eximius* onto kelp with the urchin. When we removed all *P. eximius* from *E. radiata*, there was greater recolonisation of plants with the urchin than of plants from which it had been excluded. This movement may be in response to a cue produced by the urchin or, alternatively, *P. eximius* may move around randomly until they find a plant with the urchin. It is possible, however, that greater rates of growth and/or survivorship of *P. eximius* on *E. radiata* with the urchin than without may also contribute to the pattern.

The abundance of *Holopneustes purpurascens* on individual *Ecklonia radiata* displayed considerable temporal variation at the scale of days, indicative of their movement within and between plants. As sampling of urchins was only conducted every 24 h, it is possible that the urchins displayed movement at even shorter temporal scales, and indeed, from the laboratory experiment, it appeared that most of this movement might occur overnight. Despite this movement of urchins, certain plants tended to maintain higher densities of urchins, and gastropods were able to rapidly respond to their presence. In recolonisation experiments, differences in gastropod abundance between kelp with and without urchins were established in less than 24 h. Previous studies on facilitation cascades have primarily focused on relationships established over much longer periods of time (Thomsen et al. 2010, Bishop et al. 2013).

Our study has shown that facilitation cascades can be maintained even where distributions of intermediary facilitators are spatially and temporally dynamic.

Although early evidence for facilitation cascades has primarily come from marine intertidal (e.g. Altieri et al. 2007) and terrestrial (e.g. Angelini et al. 2011) environments, our study adds to growing evidence that these interactions might also be common in the

marine subtidal (see Thomsen et al. 2010) environment. Subtidal seagrass can, by trapping drift macroalgae, facilitate invertebrates (Thomsen 2010). In the lagoons of French Polynesia, gammarid amphipods and chaetopteric polychaetes induce the growth of branch-like 'fingers' on corals through nutrient provisioning, which in turn facilitates the abundance and diversity of fishes (Bergsma 2012). In subtidal environments, where predation is often intense and waves and currents produce abiotically stressful conditions, positive interactions among species may be expected to play a particularly important role in the organisation of ecological communities (Bertness & Callaway 1994, Jones et al. 1994, 1997, Hacker & Gaines 1997, Stachowicz 2001). Further studies are now needed to address those factors that influence the incidence and strength of facilitation cascades in subtidal environments.

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