Invasive bryozoan alters interaction between a native grazer and its algal food

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The epiphytic bryozoan Membranipora membranacea *encrusts the surface of kelp blades, causing recurrent large-scale defoliation events in kelp beds off the Atlantic coast of Nova Scotia, Canada. The gastropod* Lacuna vincta *grazes kelp, creating perforations that weaken blade tissues and increase the fragmentation rate. We assess the interaction between* M. membranacea *and* L. vincta *by measuring the grazing rate of snails on bryozoan-encrusted and non-encrusted kelp (*Saccharina latissima*) in no-choice and choice experiments in the laboratory conducted in November and December 2010. There was no effect of diet on grazing rate in no-choice experiments. In choice experiments, however,* L. vincta *grazed significantly more non-encrusted than encrusted kelp (7.1 versus 1.1 mg snail^{-1} d^{-1}), and grazing rate of non-encrusted kelp was almost twice that in the no-choice experiment (3.8 mg snail^{-1} d^{-1}), indicating that snails may avoid colonies of* M. membranacea *on partially encrusted kelp blades. We found no effect of diet on growth, reproduction and survival of snails maintained for four weeks on encrusted or non-encrusted kelp. By concentrating grazing damage on non-encrusted areas of blades,* L. vincta *may act synergistically with* M. membranacea *to increase the likelihood of blade breakage and canopy loss. This indirect effect of the invasive bryozoan could augment its direct effect on the standing biomass of native kelp beds and detrital export to adjacent communities.*

Keywords: *Lacuna vincta*, *Membranipora membranacea*, kelp, invasive species, growth, survival, reproduction, grazing, feeding preference, indirect effects

INTRODUCTION

Biological invasions represent one of the most significant threats to biodiversity on a global scale, resulting in drastic economic losses and ecological change (Vitousek *et al.*, 1996; Wilcove *et al.*, 1998; Bax *et al.*, 2003). The direct and indirect impacts of invasive species can alter ecosystem functions (Vitousek *et al.*, 1996; Chapin *et al.*, 2000), change community composition and diversity (Bangert & Huntly, 2010), displace or reduce the abundance of native species (Knick & Rotenberry, 1997), and alter food webs and energy flow (Geiger *et al.*, 2005). Biological invasions are becoming increasingly common in the marine realm through the transport of non-indigenous organisms in ballast water and by other vectors associated with human activity (Carlton & Geller, 1993; Bax *et al.*, 2003). Despite a growing recognition of this threat, community-level impacts have been quantitatively assessed for only a small proportion of marine invaders, and for fewer still have these impacts been experimentally demonstrated (Grosholz & Ruiz, 1996; Ruiz *et al.*, 1997; Parker *et al.*, 1999).

Non-native species often have direct negative effects on native species through processes such as competition and predation, resulting in reduced growth, survival and reproduction (Nichols *et al.*, 1990; Travis, 1993; Petren & Case, 1996; Parker *et al.*, 1999; Byers, 2000; Grosholz *et al.*, 2000). Non-native

species can also have positive effects on native species directly by introducing novel habitat or a new prey source (Rodriguez, 2006; Barber *et al.*, 2008; Tablado *et al.*, 2010) or indirectly through habitat modification (Posey, 1988). Alternatively, non-native species can indirectly intensify or weaken the interaction between native species, which can alter community dynamics (Brown *et al.*, 2002; Dohzono *et al.*, 2008; Martin *et al.*, 2010).

Membranipora membranacea Linnaeus, 1767 is an invasive bryozoan that was first reported in the Gulf of Maine in 1987 (Lambert *et al.*, 1992) and along the Atlantic coast of Nova Scotia in 1992 (Scheibling *et al.*, 1999). *Membranipora membranacea* encrusts kelps and other macroalgae (Saier & Chapman, 2004), peaking in cover (~100% on some kelp blades) in autumn (Scheibling & Gagnon, 2009; Krumhansl & Scheibling, 2011a). The impacts of *M. membranacea* on native communities have been explored largely in terms of the direct effects on the algal host, including large scale defoliation of kelp canopy (Dixon *et al.*, 1981; Lambert *et al.*, 1992; Scheibling *et al.*, 1999; Levin *et al.*, 2002; Scheibling & Gagnon, 2009) and increases in blade breakage and erosion (Krumhansl & Scheibling, 2011a) due to reductions in tissue strength following encrustation (Krumhansl *et al.*, 2011). *Membranipora membranacea* also reduces nutrient uptake and spore release from kelp blades (Hurd *et al.*, 2000; Saier & Chapman, 2004).

Encrustation by *M. membranacea* may also have direct effects on the native littorinid gastropod *Lacuna vincta* (Montagu, 1803), which encounters *M. membranacea* while grazing on the surface of kelp blades. These snails exploit brown algae for food and habitat, as well as a substrate on

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which to deposit egg masses (Smith, 1973; Chavanich & Harris, 2002; Toth & Pavia, 2002) and show a strong preference for the kelp *Saccharina latissima* (Linnaeus) (Johnson & Mann, 1986)—*S. latissima* is currently considered a synonym of *S. longicruris* (Bachelot de la Pylaie) Kuntze (McDevit & Saunders, 2010). Littorinid snails can be selective grazers and even generalists may have specific algal preferences (Norton *et al.*, 1990; McQuaid, 1996). *Lacuna vincta* has shown preference for tissue of reduced toughness (Johnson & Mann, 1986; Toth & Pavia, 2002; Chenelot & Konar, 2007). Therefore, the large calcareous colonies of *M. membranacea* may form a protective barrier that deters *L. vincta* from grazing the underlying kelp tissue, as has been shown for other mesograzer–epiphyte–host systems (Durante & Chia, 1991; Karez *et al.*, 2000).

Previous studies of the interaction between *M. membranacea* and *L. vincta* have been based on laboratory feeding experiments with individual snails as replicates. Choice experiments suggest that *L. vincta* are attracted to blades encrusted by the invasive bryozoan (Levin *et al.*, 2002), however snails fed a single diet of encrusted kelp showed reduced growth over six weeks (Chavanich & Harris, 2000). *Lacuna vincta* occurs naturally on kelp blades at high densities, at times exceeding 2000 snails m^{-2} (Johnson & Mann, 1986). If snails naturally feed in groups, feeding experiments that allow grazing in the presence of conspecifics may yield different and perhaps more realistic results than when food items are presented to individual snails. Just as initial grazing of kelps and fucoid algae by gastropods and other mesoherbivores facilitates grazing by subsequent herbivores (Viejo & Arrontes, 1992; Molis, 2010), the aggregate effect of multiple snails in breaching colonies of *M. membranacea* may increase the consumption rate of underlying kelp tissues.

We combined no-choice and choice experiments with a four-week feeding experiment in the laboratory, allowing grazing with conspecifics, to examine the effect of encrustation by *M. membranacea* on the grazing rate, growth, survival, and reproduction of *L. vincta*. Specifically, we predicted that the grazing rate of snails on kelp (*S. latissima*) encrusted by *M. membranacea* would be reduced compared to non-encrusted kelp when no choice was given. When given a choice, we predicted *L. vincta* would feed preferentially on non-encrusted tissue. We also predicted that snails maintained for a four-week period on an exclusive diet of kelp encrusted by the bryozoan would exhibit reduced growth and reproduction and increased mortality compared to a non-encrusted diet.

MATERIALS AND METHODS

Material collection

Lacuna vincta and kelp blades (*Saccharina latissima*) with or without *Membranipora membranacea* were collected by divers from a kelp bed at 5–7 m depth at The Lodge, St Margarets Bay, Nova Scotia, Canada (44°33.491′N 64°01.493′W). *Lacuna vincta* were haphazardly selected from kelp blades, and represent the demographic structure of populations present during the period of peak abundance of *M. membranacea* in this area. Materials were transported in closed bins and placed directly in flow-through seawater holding tanks. Blade material was used within 24 hours of collection for choice and no-choice feeding experiments, and within two

weeks of collection for the growth experiment. Collections took place on 7, 23 and 30 November 2010.

Feeding experiments

The effect of encrustation by *M. membranacea* on the grazing rate of *L. vincta* on *S. latissima* was examined in no-choice and choice feeding experiments. Two food treatments were applied in both these experiments: fully encrusted (100% bryozoan cover) and non-encrusted. In the no-choice experiment, 24 circular sections (4.9 cm diameter) were excised from blade tissue encrusted with healthy colonies of *M. membranacea* (with distinct growth bands around colony margins; Menon, 1972) and 24 from non-encrusted areas of the blades. The kelp discs were individually placed in 48 feeding arenas: cylindrical plastic containers (100 mm diameter, 80 mm high) with perforated sides (2 mm diameter holes) and 1 mm mesh tops. Twenty-four containers were randomly assigned as treatments and the other 24 as autogenic controls. Five snails, 4–9 mm in shell length, collected directly from kelp blades, were individually measured (0.1 mm precision) and placed in each of 12 replicate containers for each grazing treatment (encrusted and non-encrusted); autogenic controls received no snails. Average shell length did not differ between treatments at the start of the experiment ($t_{22} = 0.508$, $P = 0.618$). Discs were excised in the same manner for the choice experiment, and cut in half. Fully-encrusted and non-encrusted half-discs were paired by weight and thickness, and placed in 32 feeding arenas. Sixteen arenas were randomly assigned as treatments, and provided five snails of the same size-range from the same source population (but different individuals) as in the no-choice experiment; the remaining 16 arenas were used as autogenic controls. For both experiments, the distance (cm) of each disc from the meristem, where anti-grazing compounds are concentrated (Johnson & Mann, 1986), was measured as a correlate for polyphenol concentration to control for chemically-induced variations in palatability along the blade length if they existed.

All containers were randomly interspersed in the same flow-through seawater table, weighted so that the mesh-top faced upward, and maintained for six days at an average water temperature of 9°C for the no-choice experiment (24–30 November 2010) and 8.5°C for the choice experiment (1–7 December 2010). A combination of natural and overhead fluorescent (cool white) lighting mimicked the natural photoperiod (9L:15D). The mass of algal tissue grazed in each treatment container was measured as the difference in blotted fresh weight (0.001 g precision) of the kelp disc or half-disc between the beginning and end of the six-day experiment. Individual grazing rate is then the average change in algal biomass in treatment containers per day divided by the number of snails (mg snail^{-1} d^{-1}). Control containers represented autogenic changes in algal mass.

Grazing damage on *Membranipora membranacea* by *Lacuna vincta*

To characterize grazing damage by *L. vincta* on kelp blades encrusted by *M. membranacea*, 10 fully-encrusted discs were excised as described above. The discs were maintained for six days in separate feeding arenas along with five snails at

an average water temperature of 8.7°C. Photographs of grazing damage were taken at the end of the six-day period with a Nikon E995 3.35 megapixel digital camera mounted on a Nikon SMZ 1500 stereomicroscope at 0.75×, 1× and 2× magnification. There was no visual evidence of grazing damage on the discs at the start of the six-day period. For each disc, the area (mm²) of patches where zooids had been removed from the blade surface, and of full perforations of the blade was measured using image analysis software (ImageJ 1.45).

Growth, survival and egg production

The dietary effect of kelp encrusted by *M. membranacea* on the growth, reproduction, and survival of *L. vincta* was examined in a four-week laboratory experiment (8 November to 6 December 2010). Snails ranging from 5.5 to 7.5 mm in shell length were individually measured and placed in groups of five in each of 45 feeding arenas (as above) that were randomly assigned to one of three diet treatments (15 arenas per diet):

(1) non-encrusted kelp;
(2) fully-encrusted kelp;
(3) starved controls.

The containers were randomly interspersed in a flow-through seawater table. Arenas in fed treatments were each supplied with a disc (4.9 cm diameter) of the respective food type. Initial shell length did not differ between treatments (analysis of variance (ANOVA), $F_{2,162} = 0.04$, $P = 0.961$). Shell length of individual snails was re-measured and kelp discs in fed treatments were replaced at weekly intervals. Individuals within containers were distinguished based on initial size, and growth was measured as change in shell length from the initial value (mm). Egg production was highest between weeks three and four, and was measured by counting the number of egg masses in each container during this interval. The number of surviving snails in each container was also recorded at weekly intervals. Individuals that died during the course of the experiment were immediately removed and not replaced. Water temperature ranged from 8–12°C (average: 9.7°C) during the experiment.

Statistical analysis

Regression analysis revealed that grazing rate (pooled across encrusted and non-encrusted discs) was not influenced by the distance of excised discs from the meristem within the range used in the feeding experiments (no-choice: 8.5–111 cm, $r^2 = 0.12$, $P = 0.094$, choice: 11.5–106 cm, $r^2 = 0.095$, $P = 0.086$), and therefore this factor was not incorporated into subsequent analyses. Analyses of feeding experiments incorporated controls to account for autogenic changes in algal mass according to the methods described by Peterson & Renaud (1989). Mass changes (mg d^{-1}) of algal discs in the no-choice experiment were analysed by two-factor ANOVA with diet (encrusted and non-encrusted) and herbivore (presence and absence) as fixed factors. For the choice-experiment, the difference in mass change (mg d^{-1}) between encrusted and non-encrusted half-discs was calculated for each replicate container. The differences for treatments with snails and controls without snails were then compared using a two-tailed independent samples t-test. A log(x + 10) transformation was used for choice data to meet the assumption of homogeneity of variances (Levene's test,

$P > 0.05$) and to achieve normality of no-choice and choice data (Shapiro–Wilk test, $P > 0.05$).

In the growth experiment, paired t-tests were used to determine whether the shell length of individuals in each treatment at the end of week four differed from their initial shell length at the start of the experiment. A nested analysis of covariance (ANCOVA) was used to examine the effect of diet (fixed factor), container (random factor) nested within diet, and initial shell length as a covariate on individual growth at weeks three and four (after diet treatments began to diverge). At each interval, there was no effect of the covariate (week three, $F_{1,118} = 0.112$, $P = 0.738$; week four, $F_{1,118} = 0.009$, $P = 0.924$) and no interaction of the covariate with diet (week three, $F_{2,118} = 1.25$, $P = 0.289$; week four, $F_{2,118} = 2.39$, $P = 0.097$). Therefore, initial shell length was excluded as a covariate and the data were reanalysed using nested ANOVAs (one for each of weeks three and four). The data did not meet the assumptions of normality (Shapiro–Wilk test, $P < 0.05$) or homogeneity of variances (Levene's test, $P < 0.05$), even after transformation (square root- and log-transform), and untransformed data were used. ANOVA is generally considered robust to departures from normality. Heterogeneity of variances may inflate α leading to an increased Type I error rate and spurious rejection of the null hypothesis, which is of less concern when test results are non-significant (Underwood, 1997). Measures from individual snails that had not survived the full 4 weeks were excluded from analyses of growth so as not to confound the results with potential size-dependent mortality.

The effect of diet on egg mass production between weeks three and four, and on the proportion of snails surviving in each container by week four, was analysed using one-way ANOVA. Counts of egg masses were log(x + 0.1) transformed and proportional survival data were arcsine transformed to meet the assumption of homogeneity of variance (Levene's test, $P > 0.05$). Transformed data did not meet the assumption of normality (Shapiro–Wilk test, $P < 0.05$). Pairwise comparisons between diets were made with Tukey's honestly significant difference tests.

RESULTS

For the no-choice experiment, the interaction between diet and herbivore in a two-factor ANOVA comparing mass change of encrusted and non-encrusted kelp discs in treatment and control containers was not significant ($F_{1,44} = 0.065$, $P = 0.801$), but the effect of herbivore was highly significant ($F_{1,44} = 64.2$, $P < 0.001$), indicating that the grazing rates of *Lacuna vincta* on kelp encrusted by *Membranipora membranacea* and non-encrusted kelp were not different (Figure 1). However, in the choice-experiment, *L. vincta* consumed non-encrusted kelp at a rate 6.5 times greater than kelp encrusted by the bryozoan (Figure 1). The difference in mass change between encrusted and non-encrusted half-discs differed significantly between treatments with and without snails ($t_{30} = -5.17$, $P < 0.001$), indicating that snails fed preferentially on non-encrusted kelp when offered a choice. The grazing rate on non-encrusted kelp in the choice experiment was nearly double the rate in the no-choice experiment. The mass loss in autogenic controls was minimal in both experiments (Figure 1).

After six days of exposure to *L. vincta*, zooids from initially undamaged colonies of *M. membranacea* on fully-encrusted
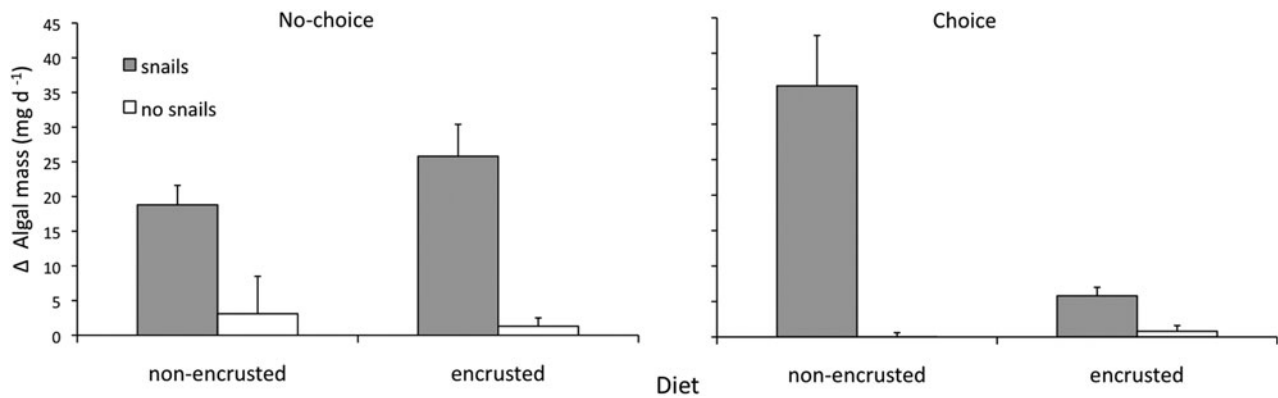
Fig. 1. Rates of algal mass loss due to grazing by *Lacuna vincta* on non-encrusted kelp (*Saccharina latissima*) or kelp encrusted by *Membranipora membranacea*, and autogenic changes in the absence of snails, in no-choice and choice feeding experiments. Data are mean (+ 1 standard error) daily loss of algal mass (no-choice: N = 12; choice: N = 16).

discs (Figure 2A) had been rasped (Figure 2B), leaving patches of bare blade (Figure 2C) with an average (± standard deviation) area of 21.2 ± 16.9 mm² (N = 13). Deeper excavations into kelp tissue also were evident, typically resulting in perforations (Figure 2D–F) with an average area of 17.9 ± 12.0 mm² (N = 10).

There was a significant increase in average shell length of *L. vincta* over the four-week experimental period in both fed treatments (non-encrusted: $t_{65} = 3.34$, $P < 0.001$, encrusted: $t_{61} = 3.04$, $P = 0.002$), but not in the starved control ($t_{36} = 0.799$, $P = 0.214$) (Figure 3). The average increase in shell length in the treatment fed encrusted kelp was about twice that in the treatment fed non-encrusted kelp, after three and four weeks. However, the difference between diets was not

statistically significant for either interval (Table 1). Significant variation among containers nested within treatments reduced the power of the test to detect a diet effect.

Snails in the fed treatments produced significantly more egg masses per individual between weeks three and four compared to the starved control ($F_{2,41} = 8.33$, $P < 0.001$) (Figure 4). The number of egg masses produced did not differ significantly between fed treatments (Tukey's test, $P > 0.05$). Although we did not record the number of females in each container, we assume that the random allocation of individuals to containers resulted in a similar distribution of female snails among treatments. It is unlikely therefore that differences in female number accounts for the strong treatment effect, although this may have increased variability among containers within diet treatments. The expected proportion of females in this experiment is 70% based on the sex-ratio of *L. vincta* measured in a previous study at the same time of year in St Margarets Bay (Johnson & Mann, 1986).

The proportion of snails surviving at the end of the experiment was significantly higher ($F_{2,42} = 15.0$, $P < 0.001$) in the fed treatments (>83%) compared to the starved control (50%) (Figure 5). There was no difference in the proportion of snails surviving between the fed treatments (Tukey's test, $P > 0.05$).
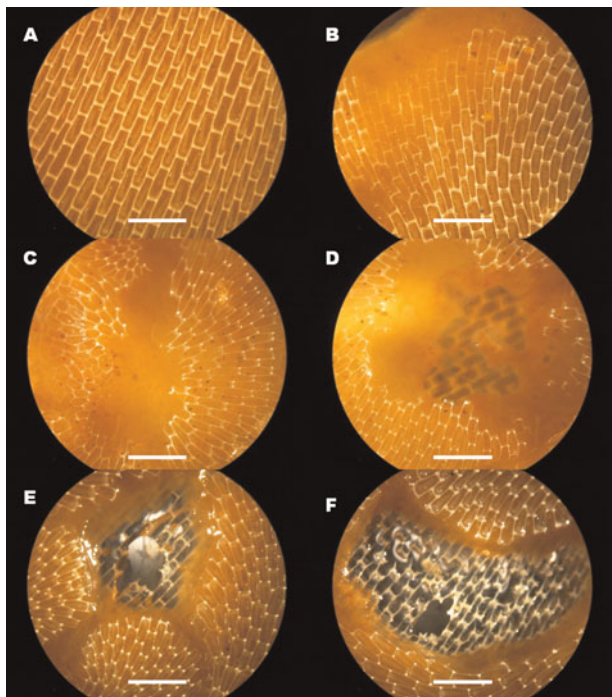
DISCUSSION

Contrary to our expectation, encrustation by *Membranipora membranacea* did not inhibit grazing by *Lacuna vincta* on blades of *Saccharina latissima*. When presented as the sole food item, blades encrusted by *M. membranacea* were grazed at a similar rate as non-encrusted blades (4–5 mg snail⁻¹ d⁻¹), which was comparable to previous estimates of grazing rate by multiple *L. vincta* on non-encrusted kelp blades in the laboratory (5.6–6.1 mg snail⁻¹ d⁻¹; Johnson & Mann, 1986). We found that *L. vincta* is capable of grazing colonies of *M. membranacea* to reach kelp tissue, which contradicts the previous assumption that *L. vincta* is strictly herbivorous and incapable of penetrating the calcareous colonies of bryozoa (McQuaid, 1996; Chavanich & Harris, 2000). This ability may be attributed to the taenioglossan radula of *L. vincta,* which is better suited to scraping and rasping the substratum with greater force than rhipidoglossan
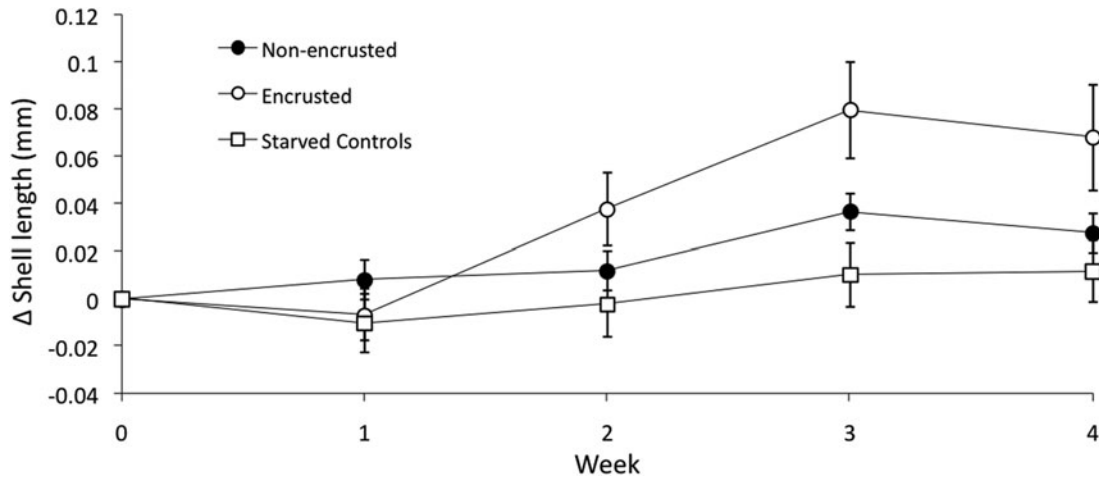

Fig. 2. Microphotographs of *Membranipora membranacea* after six-day exposure to *Lacuna vincta*: (A) healthy, ungrazed zooids; (B) rasped zooids in top left; (C) a swath of cleared zooids; (D–F) grazing perforation progressing from top layer of zooids through kelp tissue to bottom layer of zooids. Scale bar: 2 mm.

Fig. 3. Growth of *Lacuna vincta* (mm, shell length) on three diets: (1) non-encrusted kelp; (2) kelp encrusted with *Membranipora membranacea*; (3) starved. Data are mean ($\pm$ 1 standard error) change in shell length relative to initial shell length (non-encrusted: N = 66; encrusted: N = 62; starved: N = 37).

grazers, such as turbinids (Steneck & Watling, 1982). In similar single-diet feeding experiments, the turbinid gastropod *Tegula pulligo* (Gmelin, 1791) consumed significantly less kelp (*Agarum fimbriatum* Harvey, 1862) encrusted with the bryozoan *Lichenopora novae-zelandiae* (Busk, 1875) than kelp from which this bryozoan was removed (Durante & Chia, 1991). The ability of kelp-feeding *L. vincta* to effectively puncture structurally-fortified food such as bryozoan colonies is also enhanced by the pointed shape of the teeth, which concentrates stress at the tips (Padilla, 1985, 2001).

We found that a diet of kelp encrusted by *M. membranacea* did not inhibit growth relative to a diet of non-encrusted kelp over a four-week period, and may in fact enhance growth. In contrast, Chavanich & Harris (2000) observed lower growth when snails were fed encrusted kelp than when fed non-encrusted kelp in a six-week laboratory experiment with snails kept individually. The discrepancy between studies suggests that groups of snails graze encrusted blades more effectively than solitary snails, indicating that facilitation may be important for grazing in the presence of *M. membranacea*. The larger size of snails in our study (5.5–7.5 mm compared to 2 mm in the former study) also may have contributed to the disparity, as smaller mesoherbivores may be less capable of removing epibionts (Mancinelli & Rossi, 2001). Increasing the duration of growth studies would strengthen conclusions

about the effect of *M. membranacea* on the growth of snails feeding alone and in groups.

Contrary to our predictions, reproduction and survival were similar between snails fed kelp encrusted by *M. membranacea* and snails fed non-encrusted kelp over a four-week period. These findings along with the observed similarity in growth and grazing rates between treatments suggest that encrusted and non-encrusted kelp are of comparable nutritional value to *L. vincta*. Incidental ingestion of *M. membranacea* may be a source of additional nitrogen and calcium for grazers such as *L. vincta*. Increased somatic and gonadal growth has been observed in sea urchins fed kelp blades encrusted by *M. membranacea* in the laboratory (Nestler & Harris, 1994; Knip & Scheibling, 2007).

Although we found that *L. vincta* is capable of grazing blades that are fully-encrusted by *M. membranacea*, with no cost to growth, reproduction or survival over the observed period, snails showed a strong preference for non-encrusted kelp in choice experiments, as we predicted. Littorinids are selective grazers that have well-developed chemosensory capabilities for locating suitable algal foods (Imrie *et al.*, 1989; Norton *et al.*, 1990; McQuaid, 1996). *Membranipora membranacea* can limit the exchange of waterborne molecules and particles between kelp tissues and seawater (Hurd *et al.*, 2000; Saier & Chapman, 2004), and olfactory and gustatory stimulants that attract *L. vincta* to *S. latissima* may be stronger from non-encrusted blade tissues, leading snails to these areas more frequently than encrusted sections. Alternatively, the apparent preference for non-encrusted kelp blades may simply reflect habituation to this food source. *Membranipora membranacea* is a relatively novel food source for *L. vincta* and encounter rates with the native bryozoan, *Electra pilosa* Linnaeus, 1767, are expected to be infrequent due to its comparatively lower cover on kelp blades (Yorke & Metaxas, 2011).

The distribution and intensity of snail grazing on kelp blades has implications for the persistence of kelp beds. The natural erosion of kelp tissue from the distal end of the blade varies seasonally and is positively correlated with both the cover of *M. membranacea* and grazing damage by *L. vincta* (Krumhansl & Scheibling, 2011a). Intense grazing by *L. vincta* following rapid increases in abundance have been implicated in large reductions to kelp populations in

Table 1. Nested analysis of variance of the effect of diet (non-encrusted kelp, encrusted kelp and starved) and container within diet on change in shell length (mm) of *Lacuna vincta* after 3 and 4 weeks using untransformed data.

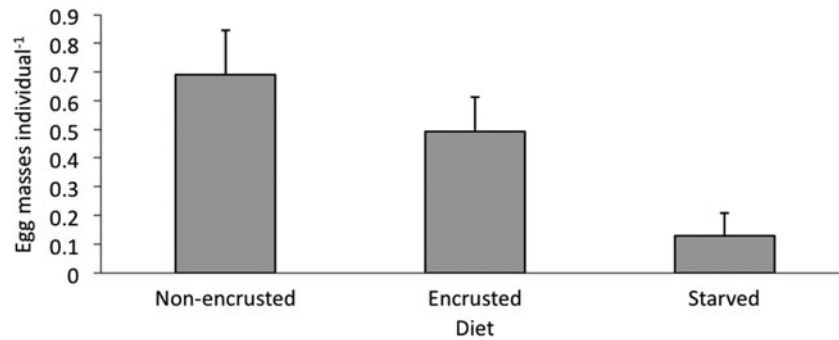| Factor	df	MS	F	P
Week three				
Diet	2	0.038	1.900	0.163
Container (diet)	40	0.020	2.000	0.002
Error	121	0.010		
Total	163			
Week four				
Diet	2	0.029	1.155	0.325
Container (diet)	40	0.025	2.111	0.001
Error	121	0.012		
Total	163			

Fig. 4. Egg mass production (egg masses individual^{-1}) of *Lacuna vincta* on three diets: (1) non-encrusted kelp; (2) kelp encrusted with *Membranipora membranacea*; (3) starved. Data are mean (+ 1 standard error) number of egg masses per individual in containers between weeks three and four (fed treatments: N = 15; starved: N = 14).
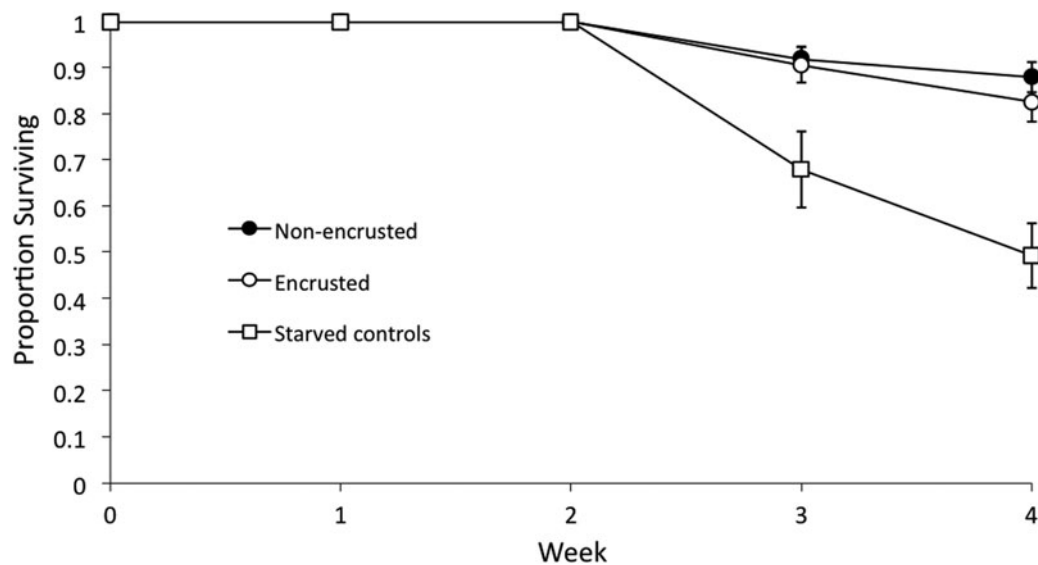

Fig. 5. Proportion of *Lacuna vincta* surviving on three diets: (1) non-encrusted kelp; (2) kelp encrusted with *Membranipora membranacea*; (3) starved. Data are mean ($\pm$1 standard error) proportion surviving in each container relative to initial number of individuals (N = 15).

the past (Fralick *et al.*, 1974). The effect of grazing damage on blade breakage is intensified during storms, resulting in large losses of kelp biomass (Krumhansl & Scheibling, 2011b). Our results suggest that *L. vincta* avoids colonies of *M. membranacea* and concentrates grazing on non-encrusted sections of kelp thalli. In the Gulf of Maine, *L. vincta* has been found at higher densities in non-encrusted areas of kelp blades colonized by *M. membranacea* (Chavanich & Harris, 2000). This suggests that grazing by *L. vincta* may augment the direct effects of encrustation by *M. membranacea* on blade breakage, if these damaging agents work synergistically to accelerate losses of kelp biomass and detrital export to adjacent communities. Our experimental results underscore the importance of assessing indirect effects of an invader on trophic interactions between native species, as these can have wide-ranging impacts on community dynamics.

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