

ASYMMETRIC COMPETITION VIA INDUCED RESISTANCE: SPECIALIST HERBIVORES INDIRECTLY SUPPRESS GENERALIST PREFERENCE AND POPULATIONS

JEREMY D. LONG,¹ REBECCA S. HAMILTON, AND JOCELYN L. MITCHELL

Marine Science Center, Northeastern University, 430 Nahant Road, Nahant, Massachusetts 01908 USA

Abstract. Species may compete indirectly by altering the traits of a shared resource. For example, herbivore-induced responses in plants may make plants more resistant or susceptible to additional herbivorous insect species. Herbivore-induced plant responses can significantly affect interspecific competition and herbivore population dynamics. These herbivore–herbivore indirect interactions have been overlooked in aquatic ecosystems where previous studies used the same herbivore species to induce changes and to assess the effects of these changes.

We asked whether seaweed grazing by one of two herbivorous, congeneric snail species (*Littorina obtusata* or *Littorina littorea*) with different feeding strategies and preferences would affect subsequent feeding preferences of three herbivore species (both snails and the isopod *Idotea baltica*) and population densities of three herbivore species (both snails and a third periwinkle snail, *Lacuna vincta*). In addition, we measured phlorotannin concentrations to test the hypothesis that these metabolites function as induced defenses in the Phaeophyceae.

Snail herbivory induced cue-specific responses in apical tissues of the seaweed *Fucus vesiculosus* that affected the three herbivore species similarly. When compared to ungrazed controls, direct grazing by *Littorina obtusata* reduced seaweed palatability by at least 52% for both snail species and the isopod species. In contrast, direct grazing by *L. littorea* did not decrease seaweed palatability for any herbivore, indicating herbivore-specific responses. Previous grazing by *L. obtusata* reduced populations of *L. littorea* on outplanted seaweeds by 46% but had no effect on *L. obtusata* populations. Phlorotannins, a potential class of inducible chemicals in brown algae, were not more concentrated in grazed seaweed tissues, suggesting that some other trait was responsible for the induced resistance. Our results indicate that marine herbivores may compete via inducible responses in shared seaweeds. These plant-mediated interactions were asymmetric with a specialist (*L. obtusata*) competitively superior to a generalist (*L. littorea*).

Key words: competition; consumer–prey interaction; inducible defense; macroalgae; plant–herbivore interaction; rocky intertidal; snails (*Littorina* spp.); trait-mediated indirect interactions.

INTRODUCTION

Competition between consumer species can fundamentally shape terrestrial and aquatic communities (Connell 1961, Strauss 1988, Denno and Kaplan 2007). Connell's (1961) classic work demonstrated that interspecific competition between barnacles was an important structuring force in rocky intertidal communities. Despite the accepted importance of competition on rocky shores, few studies have examined competitive interactions between intertidal herbivore species (but see Petraitis 1989). As in terrestrial systems (Hairston et al. 1960), intertidal herbivores living in dense plant cover rarely seem resource limited, leading to the assumption that competition does not occur between intertidal herbivores. However, recent studies of plant–insect

interactions suggest that competition between herbivores is frequently mediated by induced changes in plant traits (reviewed in Denno et al. 1995, Denno and Kaplan 2007). Such interactions have been ignored in the sea, despite the growing body of evidence that inducible responses are common in marine organisms (Lively et al. 2000, Toth and Pavia 2000, Trussell et al. 2002).

Terrestrial herbivores can strongly affect the performance, survival, and distribution of other herbivore species simply by grazing shared plants and inducing responses in those plants (Faeth 1986, Denno et al. 2000). These interactions may regulate insect populations (Haukioja 1990, Denno et al. 1995, Stout et al. 1998, Viswanathan et al. 2005) and may contribute to the dramatic population cycles of some herbivores (Barbosa and Schultz 1987).

Similarly, marine herbivores can alter numerous traits of marine algae including morphology and defensive chemistry (Cronin and Hay 1996). Direct contact with herbivores (Cronin and Hay 1996, Pavia and Toth 2000, Taylor et al. 2002) or just the chemical cues from grazing

Manuscript received 20 September 2006; revised 26 October 2006; accepted 1 November 2006. Corresponding Editor: J. J. Stachowicz.

¹ E-mail: j.long@neu.edu

(Toth and Pavia 2000, Rohde et al. 2004) can reduce the amount of herbivory a seaweed experiences by decreasing its palatability. However, the indirect effects of seaweed herbivory on other herbivore species remain unknown. For example, grazing by one herbivore species might increase, decrease, or have no effect on the palatability of a seaweed to another herbivore species. In the two studies that looked at how grazing by multiple species affected seaweed palatability, the same species of herbivore was used to induce changes in the seaweeds and to assess whether these changes were present (Pavia and Toth 2000, Rohde et al. 2004): cross-resistance was not investigated. The lack of studies examining the effects of seaweed's induced responses on multiple herbivores is surprising given that seaweeds encounter multiple natural enemies (Duffy and Hay 1990), and herbivores indirectly affect competitors via induced responses in some terrestrial plant communities (Denno and Kaplan 2007).

We tested whether grazing by one of two herbivorous, congeneric snail species (*Littorina littorea* or *Littorina obtusata*) with different feeding strategies and preferences would affect subsequent grazing by both snail species and an herbivorous isopod, *Idotea baltica*. We assessed induced responses by comparing the relative palatability of control seaweeds and seaweeds that were directly grazed. We also measured total phlorotannin concentrations of seaweeds to test the hypothesis that these metabolites function as induced defenses in the Phaeophyceae (Van Alstyne 1988, Pavia and Toth 2000, Lüder and Clayton 2004; but see Deal et al. 2003, Kubanek et al. 2004). To examine population-level effects of induction, we examined the number of herbivores moving onto induced and non-induced seaweeds in the field.

METHODS

Study system

On sheltered to moderately exposed rocky intertidal shores in the Gulf of Maine, fucoid algae (*Fucus* spp., *Ascophyllum nodosum*) often dominate the community. These species provide essential invertebrate habitat and ameliorate thermal/desiccation stress during low tide. Although fucoids are grazed by a variety of mollusks and crustaceans, Littorinid snails are the dominant grazers of fucoids and are strong controllers of community structure (Lubchenco 1978, Trussell et al. 2002). *Littorina obtusata* is a fucoid specialist that is typically found on either *Fucus vesiculosus* or *Ascophyllum nodosum* (see Plate 1). *Littorina littorea* is a feeding generalist with a wider diet breadth (McQuaid 1996). Both *Littorina* spp. co-occur in mid-intertidal emergent substrata dominated by *Fucus* spp.

Although *Fucus vesiculosus* is generally believed to be a low-preference food for *Littorina littorea* (Lubchenco 1978, Geiselman 1980), this snail will graze *F. vesiculosus* at high rates in no-choice experiments (J. D. Long, personal observation). Furthermore, emergent intertidal

substrata containing high densities of *L. littorea* are dominated by fucoid algae and often lack high-preference ephemeral algae such as *Ulva* and *Enteromorpha* (Lubchenco 1980). To quantify the importance of *Fucus* as habitat in mid-intertidal emergent communities for *L. littorea*, we surveyed the density of *L. littorea* on different substrata in an area with high *L. littorea* densities. We recorded the location of *L. littorea* in 50 23 × 23 cm quadrats randomly placed in the mid-intertidal zone at Canoe Beach, Nahant, Massachusetts, USA (42°25.21' N, 70°54.36' W). Substrata included *Fucus* spp., bare rock, algal crusts, *Semibalanus balanoides*, *Ascophyllum nodosum*, *Chondrus crispus*, shell hash, *Mastocarpus stellatus*, *Mytilus edulis*, and ephemeral algae. In addition, we determined the percentage cover of each of these substrata in 15 23 × 23 cm quadrats. Quadrats for percentage cover contained a grid with 36 evenly spaced points, and we recorded the first substrate encountered underneath these points after randomly placing the quadrats at Canoe Beach.

Our induction experiments were divided into two sequential phases: the induction phase and the bioassay phase. During the induction phase, we grew the seaweed *Fucus vesiculosus* (bladder wrack, class Phaeophyceae) in the presence or absence of herbivores for 21 days in outdoor tanks. The mesocosm experiment with *Littorina obtusata* as the inducing grazer started 8 June 2005, the mesocosm experiment with *Littorina littorea* as the inducing grazer started 10 July 2005, and the field experiment with *L. obtusata* as the inducing grazer started 16 August 2006. Seaweeds were collected at the end of the induction phase and were either offered to another set of herbivores in two-choice assays (mesocosm experiments) or transplanted into intertidal habitats to monitor herbivore populations (field experiment) during the bioassay phase. During the bioassay phase, seaweeds displaying induced resistance while growing in the presence of grazers should be less palatable (mesocosm experiments) and should contain fewer herbivores (field experiment) than seaweeds that grew in the absence of grazers. We also measured differences in phlorotannin levels of these seaweeds at the end of the induction phase of the mesocosm experiments.

Mesocosm assessments of previous grazing by *Littorina* spp. on herbivore feeding preferences

Induction phase.—Co-occurring herbivores and whole *Fucus vesiculosus* without severe grazing damage were collected from the intertidal zone in Acadia National Park near Ship Harbor, Mount Desert Island, Maine, USA (44°13.49' N, 68°19.46' W) and transported in coolers to the Mount Desert Island Biological Laboratory, Salisbury Cove, Maine (44°25.97' N, 68°17.51' W). All seaweeds were immediately rinsed with seawater and blotted dry to remove epiphytes and herbivores. Next, seaweeds were attached to anchored clothespins and added individually to tanks (length × width × height =



PLATE 1. Smooth periwinkle (*Littorina obtusata*) on *Fucus vesiculosus*. Photo credit: J. D. Long.

28 × 17 × 12 cm; water height = 8 cm). The starting seaweed masses were 20 ± 1 g and 25 ± 1 g in the experiments with *Littorina obtusata* and *Littorina littorea* as the inducing herbivores, respectively. Seawater entered these tanks at a rate of 0.7 ± 0.2 L/min. Paint-mesh bags (openings <500 microns) filtered out other macroalgae and herbivores before flow-through seawater entered tanks.

We added 10 large *Littorina obtusata* (shell length >7 mm) or four large *Littorina littorea* (shell length >20 mm) to grazer treatments. These densities represent high densities of snails observed on individual *Fucus vesiculosus* in the field (J. D. Long, *personal observation*). Preliminary results suggested that these relative densities would match the total grazing rates of these two snail species. Thus, grazer-specific effects would be independent of the total grazing damage seaweeds experienced. No grazers were added to grazer-free control tanks. Galvanized steel mesh (6-mm opening) covered all tanks, including grazer-free controls, and prevented snails in grazer treatments from escaping. Since sunlight exposure varied with position in our wet tables, treatment and control tanks were paired next to each other. Seaweeds experienced direct sunlight during most of the day, except during mid-day when they were shaded. Each pair of tanks was replicated 10 times. All tanks were checked daily to confirm that snails were not entering or escaping tanks. To reduce the buildup of detritus on seaweeds, each tank was stirred daily and

tanks were scrubbed and seaweeds were rinsed with seawater every 4–7 days.

Bioassay phase.—After the induction phase, seaweeds were rinsed and blotted with a paper towel. We examined induction in the apical, meristematic tissues because meristematic tissues are known to be the most responsive to grazing in other seaweeds (Sotka et al. 2002, Taylor et al. 2002), including *Fucus vesiculosus* (Hemmi et al. 2004, Rohde et al. 2004). Furthermore, we found no evidence of induced responses in other nonapical tissues in *F. vesiculosus* (J. D. Long and R. S. Hamilton, *unpublished data*). No tissues with reproductive vesicles or air bladders were offered to grazers.

We used three co-occurring grazer species, *Idotea baltica*, *Littorina littorea*, and *Littorina obtusata* to measure the relative palatability of apical tissues of directly grazed plants compared to equivalent control tissues. All three grazers consume *Fucus vesiculosus* (Salemaa 1987, Watson and Norton 1987; J. D. Long, *personal observation*). Single male *I. baltica* were offered a choice of a ~60 mg (blotted wet mass) piece of tissue from seaweeds directly attacked or from controls. The procedure used for the isopod was repeated for both snail species except that five snails were used per replicate and algal pieces weighed ~300 mg. The two seaweed choices were differentiated with colored thread (isopod assays) or labeled clothespins (snail assays). During the bioassay phase, each grazer or group of grazers was matched with one of the 10 replicates from

the induction phase to achieve true replication ($N = 10$). Grazing was allowed for 3–5 days, after which we measured the final wet masses of seaweeds. Grazing rates were corrected for autogenic growth in equivalent grazer-free controls using the formula $T_i(C_f/C_i) - T_f$, where T_i and T_f represent the initial and final masses, respectively, of tissue subjected to grazing, and C_i and C_f represent, respectively, the initial and final masses of control tissue (equation from Sotka et al. 2002).

Phlorotannin analysis followed the Folin-Ciocalteu method of Van Alstyne (1995). Tissue samples were homogenized and extracted in 80% methanol at 4°C for 24 h. Fifty microliters of extract were diluted with 1 mL deionized water and 1 mL 40% Folin-Ciocalteu reagent (Sigma, St. Louis, Missouri, USA). After 5 min, 1 mL of a saturated sodium carbonate solution was added. Samples were vortexed and then heated in a 50°C water bath for 30 min. Absorbance was read at 760 nm and compared to a standard curve generated with phloroglucinol (Sigma) samples. Phlorotannin concentration was corrected by a seaweed dry:wet mass ratio, and these data are reported as percentage of dry mass.

We analyzed grazing choice and phlorotannin concentrations using one-tailed, paired t tests because choices were paired in the bioassay phase, as were treatment and control tanks in the induction phase. We asked whether previous attack decreased palatability or increased phlorotannin concentrations. We used a sequential Bonferroni adjustment to account for the number of comparisons in the grazing choice experiment ($k = 3$ for both experiments, where k refers to the number of comparisons made during analysis; Rice 1989).

Field assessment of previous grazing by Littorina obtusata on herbivore populations

Induction phase.—Our mesocosm results suggested that grazing by *Littorina obtusata* reduced the palatability of *Fucus vesiculosus* to *Littorina littorea* (see Results). In order to assess whether this effect could alter snail densities in the field, we outplanted grazed (by *L. obtusata*) and ungrazed *F. vesiculosus* into the field. We followed the same protocol as described previously, with the following exceptions: (1) seaweeds and *Littorina obtusata* were collected from Nahant, Massachusetts, USA (42°25.76' N, 70°55.64' W) and transported to Northeastern University's Marine Science Center, Nahant, Massachusetts (42°25.09' N, 70°54.44' W); (2) because only grazing by *L. obtusata* reduced palatability in the mesocosm experiments, we used this herbivore to induce the seaweeds; (3) at the start of the induction phase, wet masses of control (mean $\pm$ SE; 35.7 $\pm$ 2.6 g) and treatment seaweeds (36.9 $\pm$ 2.3 g) were not significantly different ($P = 0.73$; ANOVA); (4) we replicated each treatment 33 times; (5) control and treatment tanks were randomly positioned in seawater tables; (6) to mimic low tides, we drained each tank at 08:00 hours daily for two hours: a conservative estimate

of emergence during a single low tide; and (7) *L. obtusata* densities in tanks were monitored, and lost individuals were replaced every four days.

Bioassay phase.—After the induction phase, seaweeds were rinsed, blotted dry, and weighed. Seaweeds were transplanted into the field following a modified approach initially described by Van Alstyne (1988). We created a single attachment point on each seaweed by cable tying stainless steel washers (9-mm diameter) to the basal region near the holdfast. A small piece of Tygon tubing was inserted between the seaweed and cable tie to prevent abrasion. Seaweeds were then attached to fishing swivels that had been anchored in marine epoxy (Z-spar, Los Angeles, California, USA) two days prior to field deployment. Because *Littorina* densities are patchy on small spatial scales (Vadas and Elner 1992; J. D. Long *personal observation*), we paired treatment and control plants 30 cm apart. Pairs were placed 1 m apart along a mid-intertidal transect at Canoe Beach, Nahant, Massachusetts (42°25.21' N, 70°54.36' W). *Fucus* spp., primarily *F. vesiculosus*, were the most abundant seaweeds at this site (Fig. 1B). Periwinkle snails dominated the herbivore community at this site and included *Littorina littorea*, *L. obtusata*, and *Lacuna vineta*.

To examine the effects of induction on herbivore populations, we monitored the number of snails on all transplanted seaweeds daily for four days. No non-snail herbivores were observed on seaweeds during the transplant period. Snail counts commenced 17–104 min prior to the minimum low tide. Because the mesocosm experiment suggested that induction occurred in apical tissues, we also recorded snail location on each seaweed (either apical half or basal half). However, very few snails were ever observed on basal portions, so we report the total snail densities on each plant. Snails were removed during each daily count. The final masses of seaweeds at the end of the induction phase were not significantly different (mean $\pm$ SE; 60.9 $\pm$ 2.7 g and 56.0 $\pm$ 3.2 g for ungrazed and grazed seaweeds, respectively; $P = 0.377$, ANOVA). Thus, we report the mean densities of snails found on each seaweed. Most of our transplants were lost to waves generated by the remnants of Hurricane Florence on 12 September 2006 (five days after transplant), so we stopped recording snail densities beyond four days after transplanting seaweeds into the field. We analyzed corrected snail densities using a two-tailed Wilcoxon signed-ranks test because the data were not normally distributed (e.g., many seaweeds had 0 snails).

RESULTS

Fucus represents an important substrate for *Littorina littorea*. Twenty percent of the *L. littorea* observed in our quadrats were found on *Fucus* spp. (Fig. 1A). Individuals of this algal genus represented >50% of substrate coverage at our site (Fig. 1B).

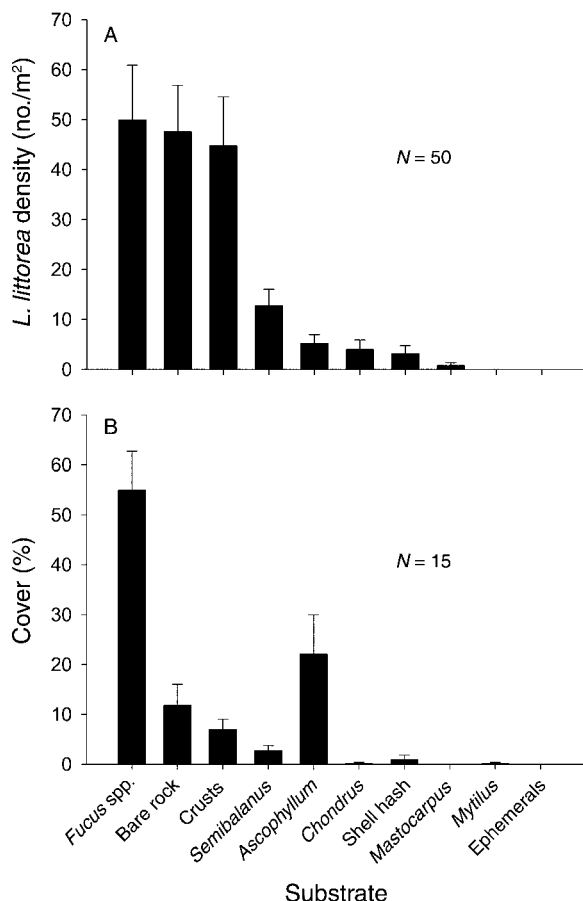


FIG. 1. (A) Densities of *Littorina littorea* on intertidal substrata and (B) percent cover of substrata in mid-intertidal quadrats at Canoe Beach, Nahant, Massachusetts, USA. *N* represents the number of quadrats (23 × 23 cm) used to record densities and substrata percent cover. Error bars indicate +SE.

During the 21-d induction phase for mesocosm experiments, seaweeds experienced similar grazing intensities in both experiments with *Littorina obtusata*, removing $3\% \pm 6\%$ and *Littorina littorea* removing $6\% \pm 2\%$ (mean $\pm$ SE) of seaweed mass. No herbivores escaped or entered tanks.

Mesocosm assessments of previous grazing by *Littorina* spp. on herbivore feeding preferences

Direct grazing by *Littorina littorea* did not induce a response in *Fucus vesiculosus* as measured by grazer-choice assays of three herbivores (Fig. 2A–C) and phlorotannin concentrations (Fig. 3A). Although feeding rates of all three herbivores were lower on *F. vesiculosus* tissue previously grazed by *L. littorea* or control *F. vesiculosus*, these differences were not statistically significant. In stark contrast, grazing by *Littorina obtusata* induced resistance in *Fucus vesiculosus* (Fig. 2D–F). All three herbivores preferred control tissues compared to those previously grazed by *L. obtusata*. Grazing by *L. obtusata* reduced the palatability

of *F. vesiculosus* tissues by 52%, 64%, and 55% compared to controls (for *Idotea baltica*, *L. littorea*, and *L. obtusata*, respectively).

Despite the significant differences we observed during choice bioassays, we never measured significant differences in the phlorotannin concentrations of treatment and control tissues (Fig. 3). Furthermore, equivalent treatment and control tissues never differed in phlorotannin concentration by more than 13%.

Field assessment of previous grazing by *Littorina obtusata* on herbivore populations

The number of *Littorina obtusata* moving onto control vs. directly grazed field transplants never differed significantly (Fig. 4A). We never observed significant differences in *Lacuna vincta* densities on grazed and ungrazed plants (Fig. 4B). However, we observed very few *Lacuna vincta* on our seaweeds and recommend further studies of *L. obtusata*–*Lacuna vincta* interactions. Significantly fewer *Littorina littorea* chose seaweeds that were previously grazed by *L. obtusata* compared to controls on the first day (46% less than controls) and second day (53% less than controls) after being transplanted into the field (Fig. 4C). Although *L. littorea* densities continued to be lower on grazed plants for two additional days, these differences were not significant. Interestingly, the trend of decreasing *L. littorea* densities on control seaweeds during the first three days was stronger than the trend on grazed seaweeds, suggesting that control plants were becoming less attractive (perhaps because they were also being induced).

DISCUSSION

The study of inducible defenses in seaweeds has focused on how grazing by a single herbivore species influences feeding preferences of conspecifics. Population-level effects, especially those examining interactions between herbivore species mediated by inducible defenses in seaweeds, are unknown. Here we show that previous grazing by a specialist herbivore, but not a generalist, altered traits of the seaweed *Fucus vesiculosus*, leading to similar effects on the feeding preferences of three herbivores and leading to a population-level effect for one of these generalist herbivores in the field. Grazing by *Littorina littorea* (a generalist) did not change *F. vesiculosus* palatability for any of the three herbivores. However, grazing by *Littorina obtusata* (a specialist) decreased the palatability of apical tissues for all three herbivores. Thus, the asymmetric, herbivore-induced resistance of *F. vesiculosus* displayed a high cue specificity (*L. obtusata* induced resistance, but *L. littorea* did not) but a low specificity of effect (induced resistance affected the feeding preferences of all three herbivores similarly). Previous grazing by *L. obtusata* reduced *L. littorea* densities on *F. vesiculosus* transplanted into the field.

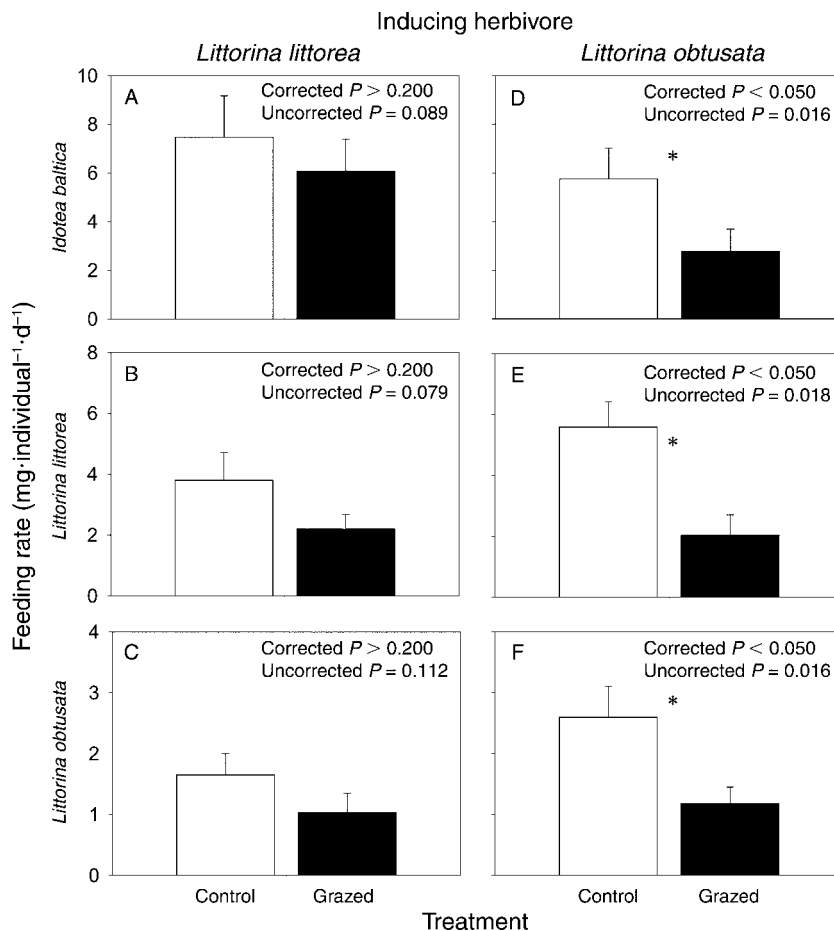


FIG. 2. Feeding rates of three herbivores that were offered a choice between *Fucus vesiculosus* apical tissues from algae previously grazed (solid bars; A–C, previously grazed by *Littorina littorea*; D–F, previously grazed by *Littorina obtusata*) or from grazer-free controls (open bars). Corrected *P* values were calculated using sequential Bonferroni adjustments (following Rice [1989]) of uncorrected *P* values (based on one-tailed, paired *t* tests). Significant differences ($P < 0.05$) between the palatability of treatment and control tissues after corrections are indicated by asterisks (*). Error bars indicate $\pm$ SE.

Competition via plant-mediated interactions is an important, yet often overlooked, structuring force for herbivore populations. For example, Denno et al. (2000) demonstrated that previous attack by the planthopper species *Prokelisia dolus* reduces the quality of *Spartina alterniflora* for a second planthopper species, *P. marginata*, and that these interactions may induce emigrations of *P. marginata* away from certain areas in salt marshes. In a review of interspecific interactions between herbivorous insects, Denno et al. (1995) found that competition between mandibulate insects was mediated by herbivore-induced changes in plants in over half of the cases examined. We observed a reduction in *Littorina littorea* densities on *Fucus vesiculosus* after being grazed by *Littorina obtusata*. Given that *F. vesiculosus* can represent over half of available substrate and that 20% of mid-intertidal *L. littorea* can be found on this seaweed, such interactions could profoundly influence *L. littorea* populations. The lack of studies examining interspecific competition in marine herbivores mediated

by changes in seaweeds suggests that the role of competition between herbivores may be underestimated in marine systems.

Most plant-mediated interactions between herbivorous insects are asymmetric (Denno and Kaplan 2007). Consistent with this finding, we observed asymmetry in plant-mediated interactions between two marine herbivorous snails. *Littorina obtusata* was a superior competitor to *Littorina littorea* for two reasons. First, previous grazing by *L. obtusata* suppressed grazing by *L. littorea* but not vice versa. Second, previous grazing by *L. obtusata* reduced *L. littorea* populations on *Fucus vesiculosus*, but *L. obtusata* populations were unaffected on these same seaweeds. Additionally, *L. littorea* is reported to have no effect on *L. obtusata* mortality, growth, or habitat selection (Seeley 1982, 1983). Presently, the traits responsible for this asymmetry are unknown. However, such asymmetry could arise because *L. obtusata* (a fucoid specialist) has a narrower diet breadth compared to *L. littorea* (a feeding

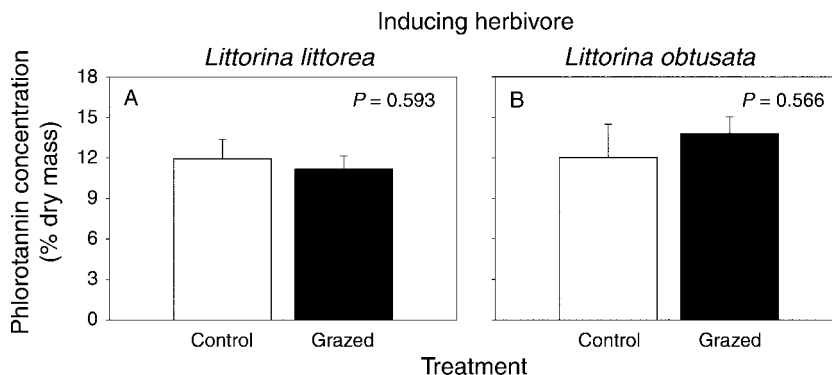


FIG. 3. Phlorotannin concentration of *Fucus vesiculosus* apical tissues from algae previously grazed by snails (solid bars; A, previously grazed by *Littorina littorea*; B, previously grazed by *Littorina obtusata*) or from grazer-free controls (open bars). Error bars indicate +SE.

generalist), and therefore, *L. obtusata* may be affected less by induced plant responses. Unfortunately, the hypothesis that specialists will be superior competitors to generalists because of their greater tolerance for induced plant responses has not been adequately tested in any system (Karban and Baldwin 1997, Denno and Kaplan 2007).

Several plants, seaweeds, and phytoplankton display herbivore-specific induced responses (Karban and Baldwin 1997, Toth and Pavia 2000; J. D. Long, *unpublished manuscript*). For example, colony formation in the phytoplankton *Phaeocystis globosa* was enhanced in response to ciliate cues but suppressed in response to copepod cues (J. D. Long, *unpublished manuscript*). The induced responses of *Fucus vesiculosus* were specific to the identity of the inducing herbivore since *Littorina obtusata* grazing induced responses but *Littorina littorea* grazing did not. This grazer-specific effect was independent of total grazing damage since both species removed similar amounts of tissue. Our cue-specific results are consistent with the finding that active grazing induced a response in *F. vesiculosus*, but artificial clippings did not (Rohde et al. 2004; but see Hemmi et al. [2004] for an alternative view). Presently, the underlying mechanism of this specificity is unknown. However, the feeding strategies and preferences differ remarkably between these two congeneric snail species (Steneck and Watling 1982), and these traits could affect *F. vesiculosus* responses differently. *L. obtusata* excavates seaweed tissue while *L. littorea* removes entire portions of seaweed tissue. When feeding on *F. vesiculosus*, *L. littorea* strongly prefers apical tissues, while *L. obtusata* feeds more readily on other tissues (e.g., mid-fronds; J. D. Long, *unpublished data*). Therefore, grazing by *L. littorea* should remove those tissues most likely to respond to herbivory, while grazing by *L. obtusata* may leave behind inducible tissues. Alternatively, *L. obtusata* may represent a greater threat to *F. vesiculosus* since *F. vesiculosus* is a preferred food for *L. obtusata* (Watson and Norton 1987) but a low preference food for *L. littorea* (Lubchenco 1978). Inducible defense

theory (Karban and Baldwin 1997) predicts that induced responses will be activated when the threat of herbivory is high (e.g., when the grazer is *L. obtusata* but not *L. littorea*). Given that herbivores in the sea, like those on land, differ markedly in their feeding strategies and preferences, consumer-specific responses could be common in seaweeds.

Inducible responses are hypothesized to occur primarily in apical tissues (Hemmi et al. 2004, Rohde et al. 2004; J. D. Long, *unpublished data*), which may help explain the discrepancies between the results from the mesocosm and the field experiments for *Littorina obtusata*. The strong reduction of *Littorina* feeding preferences after induction (Fig. 2) translated into reduced *L. littorea* densities but had no effect on *L. obtusata* densities in the field (Fig. 4). Thus, other factors regulate habitat selection in *L. obtusata*. The contrasting feeding preferences of these two species (*L. littorea* prefers apical tissues, and *L. obtusata* prefers mid-fronds and apical tissues equally) may affect the impact of inducible responses on their populations. Because inducible responses are hypothesized to occur primarily within the preferred tissues of *L. littorea*, this species may be more susceptible to inducible responses in *F. vesiculosus*. Additionally, there is anecdotal evidence that *L. obtusata* benefits from *F. vesiculosus* via decreased losses to predation when living on fucoid fronds compared to individuals living on nonfucoid substrata, perhaps because of its more cryptic coloration and morphology (Seeley 1983), especially in comparison to *L. littorea*.

Intertidal algae and their herbivores in the Gulf of Maine are typically exposed during low tide twice daily. Such exposure could affect herbivores, algae, and their interactions (Renaud et al. 1990). By submerging algae for 21 days during our initial mesocosm experiment, we exposed algae to conditions rarely encountered in the field. However, we also observed induced responses after mimicking tidal conditions during the transplant experiment, suggesting that exposure did not affect induction in *Fucus vesiculosus*.

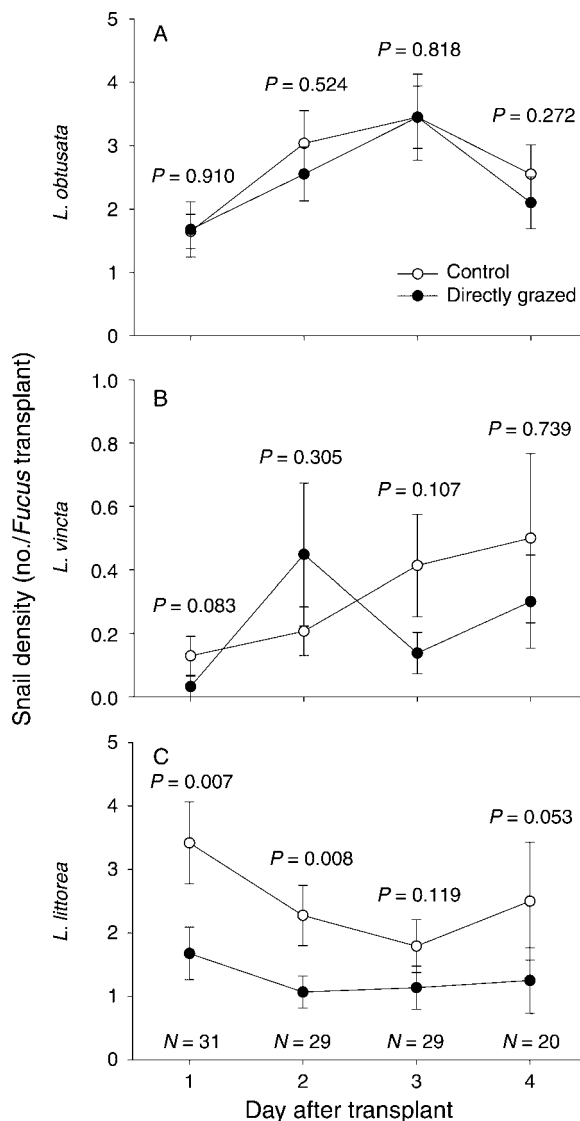


FIG. 4. Herbivorous snail densities on *Fucus vesiculosus* transplants in the field. Prior to transplantation, *F. vesiculosus* was grazed by *Littorina obtusata* (solid circles) or was ungrazed in controls (open circles). We observed (A) *L. obtusata*, (B) *L. littorea*, and (C) *Lacuna vineta* on transplanted seaweeds in the field. Differences between densities on directly grazed and control seaweeds were calculated using a two-tailed Wilcoxon signed-ranks test. N represents the number of outplanted seaweeds of each treatment. Error bars indicate $\pm$ SE.

Despite significant herbivore-induced resistance in *Fucus vesiculosus* that decreased its palatability to other herbivores, we never observed differences in phlorotannin concentrations of seaweeds in treatments and controls. Thus, we can reject the hypothesis that enhancement of total phlorotannin levels was the mechanism behind reduced seaweed palatability. Our results suggest that some other seaweed trait, perhaps the concentration of other metabolites (e.g., galactolipids; Deal et al. 2003), account for induced resistance in *F. vesiculosus*. This

contrasts with studies of *Ascophyllum nodosum* where grazing increased total phlorotannin concentrations and decreased seaweed palatability (Pavia and Toth 2000, Toth and Pavia 2000). Therefore, induction of total phlorotannin production is not the only mechanism of induced resistance in the Phaeophyceae.

This study provides evidence that previous grazing by *Littorina obtusata* altered *Fucus vesiculosus* traits that decreased the seaweed's palatability by over 50% for multiple grazer species. This, in turn, translated into a reduction in population densities of a competing snail species, *Littorina littorea*. In terrestrial systems, similar trait-mediated indirect interactions can significantly affect interspecific competition between herbivores and herbivore population densities (Faeth 1986, Denno et al. 1995, Viswanathan et al. 2005, Denno and Kaplan 2007). Presently, the paucity of studies on seaweed-induced responses and their ecological consequences constrains our ability to predict how induced responses will affect marine herbivore population dynamics. Future studies of seaweed-mediated competitive interactions between marine herbivores and how these interactions scale up to affect communities will improve our understanding of marine ecosystems and how they compare to their terrestrial counterparts.

ACKNOWLEDGMENTS

This research was made possible through the National Parks Ecological Research Fellowship Program, a partnership between the National Park Service, the Ecological Society of America, and the National Park Foundation. It is funded through a generous grant from the Andrew W. Mellon Foundation. Additional support was provided by NSF OCE-0240265 (G. Trussell), the Marine Science Center, and a Maren Fellowship from the Mount Desert Island Biological Laboratory to J. Long. D. Manski facilitated research in Acadia National Park. The shop crews at the Mount Desert Island Biological Laboratory, especially M. Hanscome and G. Gorczyca, and the MSC, especially J. McDonough and T. Maney, kept the seawater flowing and offered mechanical tips. E. Blume, E. Bryson, C. Matassa assisted with the Nahant experiments. Comments by T. Dwyer, C. Kicklighter, H. Long, C. Matassa, and two anonymous reviewers significantly improved the manuscript.

LITERATURE CITED

- Barbosa, P., and J. C. Schultz. 1987. Insect outbreaks. Academic Press, San Diego, California, USA.
- Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology 42:710–723.
- Cronin, G., and M. E. Hay. 1996. Induction of seaweed chemical defenses by amphipod grazing. Ecology 77:2287–2301.
- Deal, M. S., M. E. Hay, D. Wilson, and W. Fenical. 2003. Galactolipids rather than phlorotannins as herbivore deterrents in the brown seaweed *Fucus vesiculosus*. Oecologia 136: 107–114.
- Denno, R. F., and I. Kaplan. 2007. Plant-mediated interactions in herbivorous insects: mechanisms, symmetry, and challenging the paradigms of competition past. Pages 19–50 in T. Ohgushi, T. P. Craig, and P. W. Price, editors. Ecological communities: plant mediation in indirect interaction webs. Cambridge University Press, Cambridge, UK.

- Denno, R. F., M. S. McClure, and J. R. Ott. 1995. Interspecific interactions in phytophagous insects: competition reexamined and resurrected. *Annual Review of Entomology* 40:297–331.
- Denno, R. F., M. A. Peterson, C. Gratton, J. Cheng, G. A. Langellotto, A. F. Huberty, and D. L. Finke. 2000. Feeding-induced changes in plant quality mediate interspecific competition between sap-feeding herbivores. *Ecology* 81:1814–1827.
- Duffy, J. E., and M. E. Hay. 1990. Seaweed adaptations to herbivory. *BioScience* 40:368–375.
- Faeth, S. H. 1986. Indirect interactions between temporally separated herbivores mediated by the host plant. *Ecology* 67:479–494.
- Geiselman, J. L. 1980. Ecology of chemical defenses of algae against the herbivorous snail, *Littorina littorea*, in the New England rock intertidal community. Dissertation. Massachusetts Institute of Technology/Woods Hole Oceanographic Institution Joint Program. Massachusetts Institute of Technology, Cambridge, Massachusetts, USA.
- Hairton, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* 44:421–425.
- Haukioja, E. 1990. Induction of defenses in trees. *Annual Review of Entomology* 36:25–42.
- Hemmi, A., T. Honkanen, and V. Jormalainen. 2004. Inducible resistance to herbivory in *Fucus vesiculosus*—duration, spreading and variation with nutrient availability. *Marine Ecology Progress Series* 273:109–120.
- Karban, R., and I. T. Baldwin. 1997. Induced responses to herbivory. University of Chicago Press, Chicago, Illinois, USA.
- Kubaneck, J., S. E. Lester, W. Fenical, and M. E. Hay. 2004. Ambiguous role of phlorotannins as chemical defenses in the brown alga *Fucus vesiculosus*. *Marine Ecology Progress Series* 277:79–93.
- Lively, C. M., W. N. Hazel, M. J. Schellenberger, and K. S. Michelson. 2000. Predator-induced defense: variation for inducibility in an intertidal barnacle. *Ecology* 81:1240–1247.
- Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *American Naturalist* 112:23–39.
- Lubchenco, J. 1980. Algal zonation in New England rocky intertidal community: an experimental analysis. *Ecology* 61:333–344.
- Lüder, U. H., and M. N. Clayton. 2004. Induction of phlorotannins in the brown macroalga *Ecklonia radiata* (Laminariales, Phaeophyta) in response to simulated herbivory—the first microscopic study. *Planta* 218:928–937.
- McQuaid, C. D. 1996. Biology of the gastropod family Littorinidae. II. Role in the ecology of intertidal and shallow marine ecosystems. *Oceanography and Marine Biology: an Annual Review* 34:263–302.
- Pavia, H., and G. B. Toth. 2000. Inducible chemical resistance to herbivory in the brown seaweed *Ascophyllum nodosum*. *Ecology* 81:3212–3225.
- Petraitis, P. S. 1989. Effects of the periwinkle *Littorina littorea* (L.) and of intraspecific competition on growth and survivorship of the limpet *Notoacmea testudinalis* (Müller). *Journal of Experimental Marine Biology and Ecology* 125:99–115.
- Renaud, P. E., M. E. Hay, and T. M. Schmitt. 1990. Interactions of plant stress and herbivory: intraspecific variation in the susceptibility of a palatable versus an unpalatable seaweed to sea urchin grazing. *Oecologia* 82:217–226.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- Rohde, S., M. Molus, and M. Wahl. 2004. Regulation of anti-herbivore defence by *Fucus vesiculosus* in response to various cues. *Journal of Ecology* 92:1011–1018.
- Salemaa, H. 1987. Herbivory and microhabitat preferences of *Idotea* spp. (Isopoda) in the Northern Baltic Sea. *Ophelia* 27:1–15.
- Seeley, R. H. 1982. Association of *Littorina obtusata* and fucoid algae: effects of competition with *Littorina littorea*. *Malacological Review* 15:150.
- Seeley, R. H. 1983. A periwinkle/seaweed association: effects of competition, feeding specialization, and predation. *American Malacological Bulletin* 1:92.
- Sotka, E. E., R. B. Taylor, and M. E. Hay. 2002. Tissue-specific induction of resistance to herbivores in a brown seaweed: the importance of direct grazing versus waterborne signals from grazed neighbors. *Journal of Experimental Marine Biology and Ecology* 277:1–12.
- Steneck, R. S., and L. Watling. 1982. Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. *Marine Biology* 68:299–319.
- Stout, M. J., K. V. Workman, R. M. Bostock, and S. S. Duffey. 1998. Specificity of induced resistance in the tomato, *Lycopersicon esculentum*. *Oecologia* 113:74–81.
- Strauss, S. Y. 1988. The Chrysomelidae: a useful group for investigating herbivore–herbivore interactions. Pages 91–105 in P. Jolivet, E. Petitpierre, and T. H. Hsiao, editors. *The biology of Chrysomelidae*. Kluwer Academic, Boston, Massachusetts, USA.
- Taylor, R. B., E. Sotka, and M. E. Hay. 2002. Tissue-specific induction of herbivore resistance: seaweed response to amphipod grazing. *Oecologia* 132:68–76.
- Toth, G. B., and H. Pavia. 2000. Water-borne cues induce chemical defense in a marine alga (*Ascophyllum nodosum*). *Proceedings of the National Academy of Sciences (USA)* 97:14418–14420.
- Trussell, G. C., P. J. Ewanchuk, and M. D. Bertness. 2002. Field evidence of trait-mediated indirect interactions in a rocky intertidal food web. *Ecology Letters* 5:241–245.
- Vadas, R. L., and R. W. Elner. 1992. Plant–animal interactions in the north-west Atlantic. Pages 33–60 in D. M. John et al., editors. *Plant–animal interactions in the marine benthos*. Clarendon Press, Oxford, UK.
- Van Alstyne, K. L. 1988. Herbivore grazing increases polyphenolic defenses in the intertidal brown alga *Fucus distichus*. *Ecology* 69:655–663.
- Van Alstyne, K. L. 1995. Comparison of three methods for quantifying brown algal polyphenolic compounds. *Journal of Chemical Ecology* 21:45–58.
- Viswanathan, D. V., A. J. T. Narwani, and J. S. Thaler. 2005. Specificity in induced plant responses shape patterns of herbivore occurrence on *Solanum dulcamara*. *Ecology* 86:886–896.
- Watson, D. C., and T. A. Norton. 1987. The habitat and feeding preferences of *Littorina obtusata* (L.) and *L. mariae* Sacchi et Rastelli. *Journal of Experimental Marine Biology and Ecology* 112:61–72.