
4-1-2017

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DIFFERENTIAL TOXIC EFFECTS OF *ULVA LACTUCA* (CHLOROPHYTA) ON THE HERBIVOROUS GASTROPODS, *LITTORINA LITTOREA* AND *L. OBTUSATA* (MOLLUSCA)¹

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Members of the genus *Ulva* are widespread and abundant in intertidal and shallow subtidal areas but there are conflicting data regarding susceptibility to herbivory. While some studies have documented that *Ulva* spp. were favored by a diversity of marine herbivores, other work has revealed herbivore deterrence. We investigated grazing and growth rates of the littorinid species, *Littorina littorea* and *L. obtusata*, when offered *Fucus vesiculosus*, *Ascophyllum nodosum*, *Ulva lactuca*, and *Chondrus crispus*, highlighting distinctive vulnerabilities to toxic effects of *U. lactuca*. *Ulva lactuca* was the preferred food of *L. littorea*, while *L. obtusata* showed no grazing on this ephemeral algal species. In contrast, *F. vesiculosus* was highly preferred by *L. obtusata*. Although *L. littorea* demonstrated a grazing preference for *U. lactuca*, growth rate of this gastropod species was nearly 3× greater when fed *F. vesiculosus*, suggesting a non-lethal, negative effect of *U. lactuca* on *L. littorea* with long-term exposure. Mortality of *L. obtusata* ranged from 0% to 100% when held in the presence of various *Ulva* densities for 1 week, and *Ulva* exudate depressed herbivory of this gastropod. We conclude that the water-soluble, toxic exudate produced by *U. lactuca* in response to herbivory had allelochemical properties, and may contain a cleavage product (acrylic acid) of dimethylsulfoniopropionate or reactive oxygen species (i.e., H₂O₂). Observed differences in susceptibility to *Ulva* toxicity by the littorinid species may be related to generalist versus specialist feeding and habitat strategies.

Key index words: allelochemicals; grazer preferences; herbivorous snails; *Littorina* spp.; marine algae; rocky intertidal; *Ulva lactuca*

Abbreviations: DMSP, dimethylsulfoniopropionate; FM, fresh mass; ROS, reactive oxygen species

macroalgal abundance and distribution patterns. Herbivores do not always consume the most common macroalgae in their habitat (Hay 1986, Duffy and Hay 1991, 1994); rather, morphological and biochemical differences may affect grazer preferences (Paine and Vadas 1969a, Littler and Littler 1980, Granado and Caballero 2001).

Members of the genus *Ulva* are widespread and abundant in intertidal and shallow subtidal areas of rocky and soft sediment shores, sometimes accumulating in thick mats (Rivers and Peckol 1995, Valiela et al. 1997, Nelson et al. 2003a, Van Alstyne et al. 2015), but there are conflicting data regarding susceptibility to herbivory. Studies have documented that *Ulva* spp. were favored by a diversity of marine herbivores (Lubchenco 1978, Sousa 1979, Littler et al. 1983, Watson and Norton 1985, Duffy and Hay 1994, Granado and Caballero 2001, Souza et al. 2008, Van Alstyne et al. 2009), while other research reported herbivore deterrence (Van Alstyne and Houser 2003, Erickson et al. 2006) in choice experiments. Some *Ulva* species, including *Ulva lactuca*, release a toxic substance into water, detrimentally affecting development (Nelson et al. 2003b, Nelson and Gregg 2013), and sometimes resulting in high mortality rates (Magre 1974, Johnson and Welsh 1985) of invertebrate populations. Notably, Van Alstyne et al. (2001) isolated relatively high concentrations of dimethylsulfoniopropionate (DMSP) from several *Ulva* species; cleavage products of this compound were associated with herbivore deterrence of several sea urchin species but not of the isopod *Idotea (Pentidotea) wosnesenskii* Brandt.

Littorina spp. are abundant herbivorous gastropods along North Atlantic shorelines. *Littorina littorea* Linnaeus is a habitat and feeding generalist (Brenchley and Carlton 1983, Watson and Norton 1985, Long et al. 2007) whose intertidal distribution includes the upper intertidal zone downward into subtidal areas. Success of this gastropod species in estuarine and marine habitats is related to its tolerance of widely ranging environmental conditions (Newell et al. 1971, Murphy 1979, Sokolova et al. 2000, Davenport and Davenport 2005). *Littorina littorea* consume a diversity of algae (Hylleberg and Christensen 1978, Lubchenco 1978, Petraitis 1989)

Food preferences of marine herbivores are complex and poorly understood, yet they shape

¹Received 8 April 2016. Accepted 13 November 2016.

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Editorial Responsibility: C. Harley (Associate Editor)

and even small invertebrate eggs and barnacle cyprids (Brenchley 1982). Generalist herbivores have been shown to prefer macroalgae with sheet-like morphologies like *U. lactuca* (Littler and Littler 1980, Littler et al. 1983, Vadas 1992).

Unlike *L. littorea*, *L. obtusata* Linnaeus is a habitat and feeding specialist with a more limited distribution (Reid 1996), relying on *Fucus vesiculosus* and *Ascophyllum nodosum* for both food and habitat (Watson and Norton 1987). This gastropod species was unable to tolerate high heat or freezing temperatures, and used dense fucoid canopies to prevent desiccation on warm and sunny days (Hammerson 2004). Furthermore, in contrast to *L. littorea*, a broadcast spawner, *L. obtusata* are ovipositors, directly laying egg cases on fucoid algae (Reid 1996).

Here, we investigate grazing and growth rates of the littorinid species, *L. littorea* and *L. obtusata*, when offered *F. vesiculosus* Linnaeus, *A. nodosum* (Linnaeus) Le Jolis, *U. lactuca* and *Chondrus crispus* Stackhouse. We characterize species differences in response to these food resources, highlighting distinctive vulnerabilities to toxic effects of *U. lactuca*.

MATERIALS AND METHODS

All macroalgae, snails, and seawater used in laboratory experiments were freshly collected from Ft. Wetherill, Jamestown, RI (41°28.5' N, 71°21.3' W). We surveyed intertidal regions (including tidepools) to determine the distribution of *L. littorea* and *L. obtusata* on the various macroalgal species used in this study (Putnam 2016). Both gastropod species occurred among fronds of fucoid algae and *C. crispus*. While *L. littorea* occurred in tidepools and lower intertidal regions with ulvoid algae, we never found *L. obtusata* associated with these ephemeral green algae. Specimens were transported in coolers and held aerated at ambient water temperatures (temporal range = 14°C–18°C) until the initiation of experiments (within 2 d). Organisms were used only once in experiments to avoid any residual effects. For grazing and growth rate experiments, we used similarly sized (*t*-tests, $P > 0.05$) *L. littorea* (~6.8–11.5 mm) and *L. obtusata* (~6.5–12.0 mm).

We conducted paired-choice experiments to determine the dietary preferences of *L. littorea* and *L. obtusata* for *F. vesiculosus*, *A. nodosum*, *U. lactuca*, and *C. crispus*. Both control (no grazers) and experimental containers ($n = 12$, both treatments) held ~1.5 g fresh mass (FM) of each algal species, 300 mL seawater, and four snails (either *L. littorea* or *L. obtusata*). Seawater was changed daily and experiments were run for 4 d at ambient temperatures in Percival growth chambers on Innova platform shakers for aeration. Irradiance level was 100 $\mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ on a 12:12 L:D schedule. Only epiphyte-free, ungrazed adult fronds were selected, and apical regions (~5–6 cm length) were cut the day prior to initiation of experiments and allowed to wound heal overnight under aeration at ambient temperatures.

We measured grazing rates of *L. obtusata* on *F. vesiculosus* in ambient seawater (control) and water that had held *U. lactuca* for 24 h prior to use. Each replicate container ($n = 10$) received ambient seawater or *Ulva*-exudate water and ~2 g FM of *F. vesiculosus*. To prepare the exudate, we added ~80 g FM of *U. lactuca* to 8,000 mL seawater, aerated at ambient temperature and a 12L:12D schedule for 24 h; the water was

then filtered to remove any fragments of algae prior to use. We used the “*Ulva*” water at full strength and diluted to 50% with ambient seawater. We generated “fresh” altered water daily over the 4-d experimental period.

In all grazing experiments, initial and final algal masses were determined following removal of gravitational water with a lettuce spinner. Grazer-free algal controls (paired with experimental treatments) were run to correct for autogenic growth. Grazing rates were calculated using the formula $T_i (C_f/C_i) - T_f$, where T_i and T_f represent the initial and final algal weights, respectively, of tissue subjected to grazing, and C_i and C_f were, respectively, the initial and final weights of control algal fronds (equation from Sotka et al. 2002).

We measured growth rates of *L. littorea* and *L. obtusata* when offered *F. vesiculosus*, *A. nodosum*, *U. lactuca*, or *C. crispus* as a food source. Each experiment was run for 25–30 d (water changed every other day) and snails (4 snails in each container) were provided ad libitum food supply (~6 g FM of fresh algae weekly). Experimental conditions were as described above, except for growth rate (and mortality rate, described below) determinations using *U. lactuca*. Because of its high metabolic rates, we maintained irradiance at 16L:8D as a precaution against occurrence of low oxygen within the containers. Dissolved oxygen concentrations and pH levels ranged from ~6.5 to 9.3 $\text{mg} \cdot \text{L}^{-1}$ and 7.9–9.5, respectively, under all treatment conditions. We measured initial shell length of each snail with digital calipers (Control Company Traceable 3,415 \pm 0.01 mm) and marked shells with colored nail varnish to identify individuals. For analyses, we first determined mean snail growth rate for each container and used containers as replicates ($n = 5$).

We documented mortality rates of *L. obtusata* in the presence of various quantities of *U. lactuca* (0, 1, 3 or 6 g FM \cdot 300 mL^{-1}). The highest treatment density was comparable to a dense ulvoid tidepool population (personal observations) or heavy bloom (Nelson and Gregg 2013). Replicate ($n = 10$) containers held four snails and water was changed daily.

We analyzed grazer choice experiments using two-tailed, paired *t*-tests. We applied one-factor analysis of variance (ANOVA) for growth rate comparisons. Tukey's multiple range test was used to make comparisons among means from significant ANOVA tests. Homogeneity of variance was determined using the F_{max} test (Sokal and Rohlf 2012).

RESULTS

Littorina littorea and *L. obtusata* demonstrated contrasting preferences in paired-choice experiments (Table 1). *Ulva lactuca* was the preferred food of *L. littorea* (*t*-test: $t_{11} = 5.1$, $P < 0.0003$, *Fucus* vs. *Ulva*), while *L. obtusata* showed little or no grazing on this species. In contrast, *F. vesiculosus* was highly preferred by *L. obtusata* in all paired-choice experiments (*t*-tests: *Fucus* vs. *Ulva*, $t_{11} = 13.3$, $P < 0.0001$; *Fucus* vs. *Ascophyllum*, $t_{11} = 10.0$, $P < 0.0001$; *Fucus* vs. *Chondrus*, $t_{11} = 5.6$, $P < 0.0001$). Notably, neither gastropod species demonstrated high grazing rates on *A. nodosum*, though both species occurred near and within *A. nodosum* canopies in their natural habitat.

Growth rates of the two gastropod species when fed common intertidal macroalgae revealed a pattern distinctive from short term, paired-choice grazing preferences (Tables 1 and 2). Although

TABLE 1. Mean (\pm SE) grazing rate ($\text{mg FM} \cdot \text{d}^{-1}$) of *Littorina littorea* and *L. obtusata* comparing choice of *Fucus vesiculosus* with other algal species, *Ulva lactuca*, *Ascophyllum nodosum*, and *Chondrus crispus*. The left column under each snail species is grazing rate on *Fucus* and the right column is grazing rate on the algal species with which *Fucus* was paired in each choice experiment.

Paired algal species	<i>L. littorea</i>		<i>P</i> -value	<i>L. obtusata</i>		<i>P</i> -value
<i>Fucus</i> versus <i>Ulva</i>	20.0 \pm 4.8	70.0 \pm 6.7	0.0003	70.0 \pm 5.6	-20.0 \pm 4.6	<0.0001
<i>Fucus</i> versus <i>Ascophyllum</i>	98.0 \pm 10.0	14.3 \pm 2.0	<0.0001	83.9 \pm 5.8	12.2 \pm 5.8	<0.0001
<i>Fucus</i> versus <i>Chondrus</i>	13.1 \pm 3.6	18.9 \pm 5.2	>0.05	46.8 \pm 4.7	25.4 \pm 2.5	<0.0001

P-values were generated from two-tailed, paired *t*-tests, *df* = 11.

TABLE 2. Mean (\pm SE) growth rates (mm per 30 d) of *Littorina littorea* and *L. obtusata* when fed *Fucus vesiculosus*, *Ascophyllum nodosum*, *Ulva lactuca*, and *Chondrus crispus*.

	<i>L. littorea</i>	<i>L. obtusata</i>
<i>F. vesiculosus</i>	0.48 \pm 0.03	0.40 \pm 0.06
<i>A. nodosum</i>	0.06 \pm 0.01	0.36 \pm 0.06
<i>U. lactuca</i>	0.18 \pm 0.06	ND
<i>C. crispus</i>	0.09 \pm 0.03	0.06 \pm 0.03

ND = no data because of high mortality of *L. obtusata*.

L. littorea demonstrated clear grazing preference for the green alga, growth rate of this gastropod species was nearly 3 \times greater when fed *F. vesiculosus* compared with *U. lactuca* (ANOVA: $F_{3,16} = 15.9$, $P < 0.0001$, Tukey: $P < 0.05$). Growth rates when fed *A. nodosum* or *C. crispus* were similar (Tukey: $P > 0.05$) and low, thus reflecting grazing choices. *L. obtusata* had high growth rates when fed either furoid species compared with *C. crispus* (ANOVA: $F_{2,12} = 7.9$, $P = 0.007$; Tukey: $P < 0.05$). We were unable to document growth of *L. obtusata* on *U. lactuca* because of high snail mortality (>75%) within 1 week (we repeated the growth rate experiment twice). These treatments had been part of a larger design (Putnam 2016), and nearly 100 *L. obtusata* died in each experiment; however, most surviving individuals (~25) lived when transferred to seawater without algae.

Littorina obtusata demonstrated a clear depression in herbivory when held in *Ulva* exudate (ANOVA: $F_{2,27} = 60.0$, $P < 0.0001$). Grazing rate (mean \pm SE) of *L. obtusata* on *F. vesiculosus* when held in 100% (10 g FM \cdot L $^{-1}$) *Ulva*-water (10.0 \pm 8.2 mg FM \cdot d $^{-1}$) was a magnitude lower than herbivory in ambient seawater (128.6 \pm 6.6 mg FM \cdot d $^{-1}$). Grazing was reduced to 43.0 \pm 8.6 mg FM \cdot d $^{-1}$ in 50% *Ulva*-water, indicating a dosage effect (Tukey: $P < 0.05$).

We documented mortality of *L. obtusata* when held in the presence of *U. lactuca* (Fig. 1) of varying densities. In the absence of this green alga, and under low *Ulva* density (1 g FM \cdot 300 mL $^{-1}$), no snails died during the 7 d period. In contrast, at highest *Ulva* density, we recorded 70% mortality by day 2, and all individuals were dead by day 5. Mean snail survival remained at 25% after day 5 in the 3 g FM treatment.

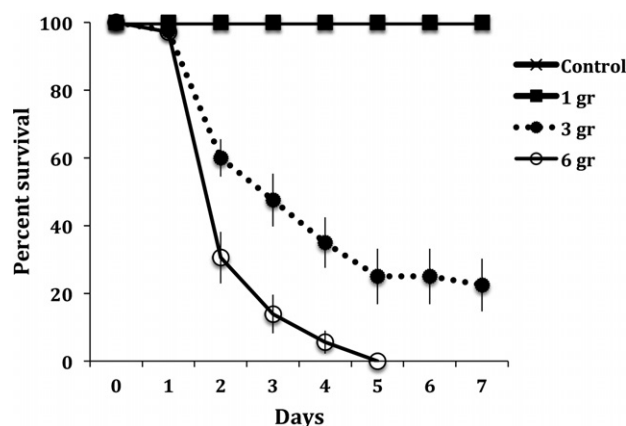


FIG. 1. Mean (\pm SE) percent survival of *Littorina obtusata* held in the presence of various densities (0, 1, 3, or 6 g FM \cdot 300 mL $^{-1}$) of *Ulva lactuca*.

DISCUSSION

This study found disparate sensitivities of the congeners, *L. littorea* and *L. obtusata*, to toxic effects of *U. lactuca*. *L. littorea* demonstrated a clear preference for *U. lactuca* in a paired-choice grazing experiments. In contrast, this green algal species deterred grazing by *L. obtusata*, and in experiments measuring growth and mortality rates, *L. obtusata* suffered high mortality in the presence of *U. lactuca*. Such species differences in susceptibility to *Ulva* toxicity may be related to generalist versus specialist feeding and habitat strategies of these herbivorous gastropods.

The allelochemical effects of exudates produced by ulvoid species have been documented. Related members of the Ulvophyceae, *U. fenestrata* Postels et Ruprecht and *Ulvaria obscura* (Kützting) Gayral, produced water-soluble exudates that were toxic to larval development of the oyster, *Crassostrea gigas* Thunberg (Nelson et al. 2003b, Nelson and Gregg 2013). The presence of *U. lactuca* in simulated tide-pools resulted in high mortality of the crustacean, *Balanus balanoides* Linnaeus (Magre 1974), and *Ulva* spp. inhibited growth of microalgae in laboratory cultures (Jin and Dong 2003, Nan et al. 2004, Jin et al. 2005). Similarly, we found significant growth reduction in *F. vesiculosus* and *C. crispus* when grown

with *U. lactuca* (unpublished data). Interestingly, Jin and Dong (2003) found that continuous release of allelochemicals from fresh fronds of *U. pertusa* was essential to inhibit growth; the filtrate produced no negative effect on microalgae. In this study, neither consumption nor presence of *U. lactuca* fronds was necessary to produce a toxic effect in *L. obtusata*; instead, grazing rate on *F. vesiculosus* was significantly depressed when gastropods were held in “*Ulva*” exudate. However, *L. obtusata* experienced massive mortality only when held in higher *Ulva* density treatments. Furthermore, most snails surviving the growth experiment using *U. lactuca* as food lived when transferred to seawater without *Ulva*. Thus, the observed toxic effect may be reversible when a grazer is no longer exposed, as observed in other research (Dacey et al. 1994).

Several toxic exudates produced by *U. lactuca* may have caused the negative effects in *L. obtusata*. DMSP (and its cleavage products) and reactive oxygen species (ROS) serve a variety of purposes in algae, yet these compounds can be toxic to herbivores and competitors (Ross and Van Alstyne 2007, Potin 2008, Van Alstyne 2008, Van Alstyne et al. 2015). Dimethyl sulfide and acrylate function as an activated chemical defense in microalgae (Wolfe et al. 1997, Archer et al. 2003, Fredrickson and Strom 2008). Van Alstyne et al. (2001) documented a similar defense system in *Ulva* spp. that acted as a grazer deterrent for the sea urchins, *Strongylocentrotus droebachiensis* O.F. Müller and *S. purpuratus* Stimpson, and the gastropod *Littorina sitkana* Philippi (Van Alstyne et al. 2009). However, herbivory by the isopod *I. wosnesenskii* was stimulated by acrylate, indicating specificity of the DMSP-activated defense (Van Alstyne et al. 2001).

Comparable to the role of DMSP as a grazer deterrent, ROS released by plants and algae under certain environmental conditions may negatively affect herbivores. For example, increased oxidative damage in the midgut of insects feeding on previously wounded plants (Bi and Felton 1995), and decreased metabolic rate of the mud shrimp *Crangon crangon* Linnaeus held under conditions of elevated H_2O_2 (Abele-Oechger et al. 1997) suggested that ROS were important components of induced resistance. Ramputh et al. (2002) documented reduced herbivory by the insect *Ostrinia nubilalis* Hübner on *Zea mays* Linnaeus genetically transformed to produce elevated ROS. Ulvoid species released ROS such as H_2O_2 under increasing irradiance (Collén and Pedersen 1996) and environmental stressors, i.e., temperature change and desiccation (Ross and Van Alstyne 2007, Van Hees and Van Alstyne 2013). In this study, *U. lactuca* remained submerged at stable, ambient water temperatures and irradiance levels below those that resulted in high H_2O_2 release by another ulvoid species (Collén and Pedersen 1996), making environmental stress an unlikely trigger of ROS. The brown

alga *Ascoseira mirabilis* Skottsberg, which released a burst of non- H_2O_2 ROS after wounding, inhibited grazing by the amphipod *Gondogeneia antarctica* Chevreux (McDowell et al. 2014). Thus, grazing by *L. obtusata* may have triggered a wound response and subsequent release of ROS by *U. lactuca* that resulted in its toxic effect.

Although *L. littorea* demonstrated a preference for *U. lactuca* over the fucoid species, *F. vesiculosus* and *A. nodosum*, in grazing experiments, growth rates when fed *U. lactuca* were relatively low. *Ulva* spp. has higher calorific values compared with other macroalgae (Paine and Vadas 1969b, Littler and Littler 1980); Yaich et al. (2011) and Van Alstyne et al. (2009) reported high (8.4% DM) protein content and percent nitrogen, respectively, in *U. lactuca*. These biochemical characteristics suggest high nutritive value of *Ulva*, and Van Alstyne et al. (2009) argued that grazing preference by the generalist herbivore, *L. sitkana*, for ulvoid green algae containing high concentrations of DMSP might be due to high nitrogen content of the algae. However, our results revealed that *F. vesiculosus* supported substantially higher growth rates of *L. littorea*. This inconsistency between grazing preferences and growth rates suggests a non-lethal, negative effect of *U. lactuca* on *L. littorea* with long-term exposure.

Species differences in detoxification abilities might enable *L. littorea* to better tolerate exudate released by *U. lactuca* following damage from herbivory. Sotka and Whalen (2008) detailed approaches used by herbivores to detoxify and/or metabolize secondary compounds, including cytochrome P450 enzymes and glutathione S-transferases. Production of these enzymes by insects was induced following exposure to plant metabolites, and such induction was correlated with diet choice (Karban and Agrawal 2002). Berenbaum et al. (1996) argued that the P450-system was a “key innovation” in detoxification by insect herbivores (genus *Papilio*). Li et al. (2004, 2007) suggested that generalist herbivores required a diversity of detoxification genes to manage the range of dietary allelochemicals to which they are exposed. The use of these detoxification methods by marine herbivores has not been documented; however, genome sequencing of the sea urchin *S. purpuratus* (Sodergren et al. 2006) revealed a diversity of detoxification genes, suggesting that this generalist herbivore has the capacity to metabolize a variety of compounds (Sotka and Whalen 2008). As a feeding generalist, *L. littorea* may have a greater ability than specialist *L. obtusata* to detoxify compounds released by *U. lactuca*.

Both gastropod species exhibited low preference for *A. nodosum* in choice experiments. This fucoid species has high constitutive levels of phlorotannins (Long and Trussell 2007, Putnam 2016), and polyphenolics can serve as a grazer deterrent (e.g., Van Alstyne 1988, Peckol et al. 1996, Pavia and Toth

2000, Amsler 2001, Jormalainen and Honkanen 2008, Koivikko et al. 2008). Putnam (2016) found that induced *Ascophyllum* fronds deterred herbivory by *L. littorea*, while grazing by *L. obtusata* was not reduced, even when fronds had been induced 5× above constitutive levels. In this study, *L. obtusata* exhibited high growth rates when fed either fucoid species. Kubanek et al. (2004) reported enhanced survivorship and growth of the amphipod *Ampithoe valida* Smith raised on an artificial diet containing high levels of phlorotannins extracted from *F. vesiculosus*. They suggested that polyphenolics served other purposes for the amphipods, such as a carbon source (Bernays and Chamberlain 1980), medicinal aid (Schultz et al. 1990) and nutritional enhancement (Bernays et al. 1989). *Littorina obtusata* use fucoid algae such as *F. vesiculosus* and *A. nodosum* for food and habitat, directly depositing egg cases on algal fronds. Thus, this gastropod species is in contact with phlorotannins throughout its life. Specialized insect herbivores, with limited ability to use many species for food, gain the ability to tolerate plant defenses of their host species (Ali and Agrawal 2012).

Specialist mesoherbivores are relatively uncommon in marine communities (Hay 1991, 1992, Paul et al. 2001); however, if the ability to live among and feed on seaweed fronds reduces predation risk, then these grazers may be under strong selective pressure to tolerate chemical defenses (Hay 1992). Predation risk is greater for *L. obtusata* than *L. littorea* due to its smaller size and thinner shell wall. Seeley (1986) compared museum-retained *L. obtusata* shells from 1871 and 1893 with living specimens from 1982 to 1984, and found that the contemporary population had significantly thicker shells and little or no spire. This rapid change corresponded to the introduction of the crab *Carcinus maenas* Linnaeus and its movement up the New England coast (Reid 1996). A more recently introduced crab, *Hemigrapsus sanguineus* De Haan, also preys on *L. obtusata* (Griffen and Byers 2009). Notably, fucoid algae serve as a refuge for this gastropod from predators. Wilbur and Steneck (1999) found that *L. obtusata* chromatically conform to fronds of *A. nodosum* on which they live and feed, providing protection from visual predators like *C. maenas*.

Differing tolerances of environmental conditions may contribute to the dissimilar responses of these littorinid species to the toxic effects of *U. lactuca*. Widespread success of *L. littorea* in estuarine and marine habitats is related to its ability to withstand large temperature, salinity and oxygen fluctuations (Newell et al. 1971, Murphy 1979, Sokolova et al. 2000). Davenport and Davenport (2005) concluded that *L. littorea* was more tolerant of environmental stressors than *L. obtusata*. Some research has suggested that mechanisms enabling species to endure widely varying environmental conditions may provide them with the ability to

withstand other stressors, including pollutants such as heavy metals and oil spills (Redpath and Davenport 1988, Barreiro et al. 1993, Castilla 1996, Crowe et al. 2000, Hrs-Brenko 2006). Thus, it might be predicted that *L. littorea* would be better adapted than *L. obtusata* to cope with a toxic exudate from *U. lactuca*.

In summary, herbivore generalist *L. littorea* and specialist *L. obtusata* demonstrated distinctive grazing preferences that revealed differing susceptibilities to a toxic exudate released by *U. lactuca* in response to herbivory. Although the identity of the toxin is unknown, its disparate effects have clear implications for the distribution and impact of these important intertidal mesoherbivores. Strong preference by *L. littorea* for this green algal species can greatly affect species diversity and abundances in tidepools (Magre 1974, Lubchenco 1978) and lower intertidal areas (Vadas 1992). In contrast, by relying predominantly on fucoid algae for food and habitat, *L. obtusata* likely have minimal impact on their host seaweed species (Hay 1992). However, such specialization is a successful strategy for *L. obtusata*, allowing it to maintain modest (Pavia and Toth 2000) and relatively stable abundances on the perennial fucoid algae.

We appreciate the field and laboratory assistance of Noemi Collazo. The manuscript was greatly improved by suggestions of three anonymous reviewers. This research was funded by Smith College endowed funds of the Department of Biological Sciences (PP) and the B. Elizabeth Horner Fund (AP).

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