

# Asymmetric interference competition between herbivorous gastropods, introduced *Littorina littorea* and indigenous *L. obtusata*

Alysha B. Putnam<sup>1,2</sup>, Paulette Peckol<sup>1,\*</sup>

<sup>1</sup>Department of Biological Sciences, Smith College, Northampton, MA 01063, USA

<sup>2</sup>Greenfield Community College, Greenfield, MA 01301, USA

**ABSTRACT:** Competitive interactions may affect distribution and abundance of mobile organisms, such as the intertidal herbivorous gastropods *Littorina littorea* and *L. obtusata*, in areas of resource overlap. We examined intra- and interspecific competition between US New England populations by measuring effects of snail density and food availability on growth rates and abundances. We investigated mechanisms of interference, including resistance (phlorotannin) induction of furoid algae, and impacts of snail presence, waterborne cues, and mucus on herbivory. *L. obtusata* density increased significantly within furoid canopies following repeated (every 12 h for 3 d) removal of *L. littorea* at both study sites. In the laboratory, *L. obtusata* growth rate was lower in the presence of *L. littorea*, but not in the presence of conspecifics. In contrast, *L. littorea* abundances were not strongly affected by its congener, and growth rates were similar under varying *L. obtusata* densities and food supply. Instead, *L. littorea* demonstrated intraspecific effects under limited food and higher snail densities. While herbivory by *L. littorea* was not diminished on *Fucus vesiculosus* grazed by *L. obtusata*, fronds of *F. vesiculosus* and *Ascophyllum nodosum* grazed by *L. littorea* were less palatable to *L. obtusata*, indicative of asymmetric competition. Reduced herbivory by *L. obtusata* in the presence of *L. littorea* or its waterborne cues indicate that these forms of interference negatively influence *L. obtusata*. Coexistence of these species may be due to renewability of resources and the ability to change location, allowing the competitively inferior *L. obtusata* to maintain modest abundances within perennial furoid canopies.

**KEY WORDS:** Asymmetric competition · Herbivorous gastropods · *Littorina* spp. · Interference · Algal-grazer interaction · Inducible resistance

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## INTRODUCTION

Competitive interactions play a critical role in shaping the abundance and distribution of organisms in marine systems, often influencing patterns of biodiversity. In exploitative competition, one species consumes scarce resources faster than their competitor(s), thus making the resource unavailable, while interference competition occurs when one user negatively hinders (or harms) another species, affecting its ability to access the resource (Underwood 2000). For exam-

ple, sessile invertebrate species may exploit limited attachment substrata and food, sometimes resulting in space monopolization by the dominant species (e.g. Connell 1961, 1983, Menge 1976, Wetthey 1983, 2002), while macroalgae often compete for space, irradiance, and nutrients (e.g. Lubchenco 1980, Carpenter 1990, Peckol & Rivers 1995, Worm & Karez 2002). Some species demonstrate interference competition by releasing toxic chemicals, making areas around them uninhabitable for other species (Magre 1974, Lubchenco 1980, Ridenour & Callaway 2001).

\*Corresponding author: ppeckol@smith.edu

Mobile organisms also compete for food and habitat (Underwood 1978, Schoener 1983, Robertson & Gaines 1986, Petraitis 1989, 2002, Navarrete & Castilla 1990, Wootton 1993, Moksnes 2004, Spitz et al. 2006), but these interactions may not result in species exclusion. For example, intraspecific competition for limited food has been shown to affect individual size and density of herbivore populations (Branch & Branch 1981, Fletcher & Creese 1985, Ortega 1985), and interspecific effects between sympatric congeners caused shifts in foraging characteristics, allowing for coexistence (Haven 1973, Schmitt 1996).

Along the North Atlantic coastline, *Littorina littorea* and *L. obtusata* are 2 abundant herbivorous gastropods with sometimes overlapping intertidal distributions. *L. littorea* commonly occurs in both rocky and soft sediment areas from the upper intertidal zone downward into subtidal areas (Brenchley & Carlton 1983, Watson & Norton 1985, Norton et al. 1990). The 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 & Davenport 2005). *L. littorea* consumes a diversity of algae (Lubchenco 1978, Petraitis 1989, Norton et al. 1990, Peckol & Putnam 2017) and even small invertebrate eggs and barnacle cyprids (Brenchley 1982). Controversy remains regarding its status as a native or introduced species to the western Atlantic coastline (Carlton 1982, 1992, Wares et al. 2002, Chapman et al. 2007, Cunningham 2008); however, molecular analyses by Blakeslee et al. (2008) confirmed a relatively recent (~500 yr ago) introduction from Europe.

In contrast to *L. littorea*, indigenous *L. obtusata* is a more selective grazer (Norton et al. 1990), commonly found on 2 furoid algae, *Fucus vesiculosus* and *Ascophyllum nodosum*, which it uses as food and habitat (Watson & Norton 1987, Norton et al. 1990, Trussell et al. 1993, Reid 1996). While *L. littorea* has wide tolerances of fluctuating environmental conditions, *L. obtusata* is less tolerant of high heat or freezing temperatures, relying on dense furoid canopies to prevent desiccation on warm and sunny days (Hammerston 2004). Unlike *L. littorea*, a broadcast spawner, *L. obtusata* is oviparous, directly laying egg masses on furoid algae (Reid 1996).

Several studies have identified *L. littorea* as a competitively superior intertidal herbivore. For example, *L. littorea* exerted competitive pressure, limiting distribution and growth of *L. saxatilis* (Behrens Yamada & Mansour 1987, Eastwood et al.

2007) and the limpet *Testudinalia testudinalis* (Petraitis 1989; note that this species has been previously placed in *Notoacmea*, *Tectura*, *Lottia* and *Acmaea*). Brenchley & Carlton (1983) found that addition of *L. littorea* resulted in emigration of the mud snail *Tritia obsoleta* (formerly *Ilyanassa*) in salt marsh habitats.

Competitive interactions involving *L. obtusata* have been less documented than those of its congener *L. littorea*. Kozminsky (2013) linked successful recruitment of *L. obtusata* with food availability, suggesting intraspecific competition between recruits and adult snails. Herbivory may result in induction of resistance in the Phaeophyceae (e.g. in *F. vesiculosus* and *A. nodosum*) that subsequently serves as a grazer deterrent (Van Alstyne 1988, Peckol et al. 1996, Toth & Pavia 2000, Amsler 2001, Hemmi et al. 2004, Flöthe et al. 2014, Haavisto et al. 2017). Long et al. (2007) explored interference competition among herbivores via grazer-induced resistance in *F. vesiculosus*, and concluded that *L. obtusata* exerted both inter- and intraspecific effects. However, they found no differences in phlorotannin levels between ungrazed and grazed fronds, and the mechanism of this interaction was left unresolved.

Because *L. littorea* and *L. obtusata* have overlapping spatial distributions and food resources in rocky intertidal areas, competition may be occurring between these species. Although *Ulva lactuca* is a preferred food of *L. littorea* (Lubchenco 1978, Watson & Norton 1985, Norton et al. 1990, Peckol & Putnam 2017), it is an ephemeral species and therefore an unstable resource. *L. littorea* was found to consume *F. vesiculosus* (Watson & Norton 1985, Barker & Chapman 1990, Norton et al. 1990) despite its preference for *U. lactuca*, while *L. obtusata* showed a strong preference for furoids over ephemeral green algae (Watson & Norton 1987, Peckol & Putnam 2017). We hypothesized that these herbivores might demonstrate some form of interference competition in their area of overlap. Using field and laboratory experiments, we explored intra- and interspecific competitive interactions between New England populations of *L. littorea* and *L. obtusata*. We manipulated snail density and food availability to determine effects on growth rates and abundances. We investigated potential mechanisms of interference competition by (1) determining grazing rates on ungrazed and grazed (induction of resistance) fronds of furoid algae, and (2) measuring the impact of snail presence, waterborne cues, and mucus on herbivory.

## MATERIALS AND METHODS

### Study sites

Two sites were selected for study: Ft. Wetherill State Park, Jamestown, Rhode Island, USA (41° 28' 43" N, 71° 21' 44" W) and Pemaquid Point, Bristol, Maine, USA (43° 49' 59" N, 69° 30' 53" W). The sites contained moderate densities of both *Littorina littorea* and *L. obtusata* and had similar habitat structure. The intertidal areas had semi-exposed and somewhat sheltered regions, and included vertical rock walls, grading into gentler slopes. Both sites had thick (~70 to 100% cover) algal canopies consisting of mixtures of *Fucus vesiculosus* and *Ascophyllum nodosum*. Mean ( $\pm$ SD) snail densities (number m<sup>-2</sup>) during summer (June and August surveys combined, n = 20) were as follows: Rhode Island: *L. obtusata* high-intertidal = 161.6  $\pm$  69.4, mid-intertidal = 66.4  $\pm$  68.3; *L. littorea* high-intertidal = 63.2  $\pm$  68.6, mid-intertidal = 47.2  $\pm$  47.9; Maine: *L. obtusata* high-intertidal = 109.7  $\pm$  84.6, mid-intertidal = 116.6  $\pm$  91.7; *L. littorea* high-intertidal = 50.9  $\pm$  68.5, mid-intertidal = 85.1  $\pm$  81.8.

### Field density manipulations

We investigated interspecific interactions between *L. littorea* and *L. obtusata* in Rhode Island (July) and Maine (August). Experimental sites in high- and mid-intertidal regions were selected in areas with steep vertical aspect where furoid canopies were consistent and dense (at least 75% cover). We conducted 4 separate experiments, manipulating *L. littorea* and *L. obtusata* densities in Rhode Island and Maine. Treatment conditions for each experiment included: control area (no manipulation), removal (density reduction of 1 congener), and addition (density increase of 1 congener). The snails taken from removal replicates were added to the addition replicates, thereby doubling unmanipulated densities. Removal, control, and addition treatment replicates were each established within 1 m wide areas in high- and mid-intertidal areas. There was an unmanipulated 1 m wide area between each treatment replicate within each set (for each experiment, n = 4 or 5 replicate sets; namely removal, control, and addition at both tidal levels). Initial and final densities of the species being monitored within each treatment area (high- and mid-intertidal zones) were taken using a 0.25 m<sup>2</sup> (0.5  $\times$  0.5 m) quadrat. Initial densities (mean  $\pm$  SD m<sup>-2</sup>) of the species to be monitored after density manipulation of its congener were as follows: for *L. obtu-*

*sata*—Rhode Island: high-intertidal removal = 48.1  $\pm$  27.6, control = 47.0  $\pm$  20.4, addition = 62.0  $\pm$  23.2 (ANOVA p = 0.69); mid-intertidal removal = 37.2  $\pm$  18.4, control = 24.8  $\pm$  11.2, addition = 30.0  $\pm$  7.6 (ANOVA p = 0.68); Maine: high-intertidal removal = 44.8  $\pm$  20.1, control = 39.2  $\pm$  21.6, addition = 35.2  $\pm$  20.8 (ANOVA p = 0.50); mid-intertidal removal = 22.4  $\pm$  12.4, control = 20.8  $\pm$  10.4, addition = 25.6  $\pm$  27.2 (ANOVA p = 0.92); for *L. littorea*—Rhode Island: high-intertidal removal = 45.2  $\pm$  16.8, control = 50.8  $\pm$  18.8, addition = 32.0  $\pm$  18.4 (ANOVA p = 0.47); mid-intertidal removal = 26.8  $\pm$  6.0, control = 30.8  $\pm$  20.0, addition = 28.0  $\pm$  14.4 (ANOVA p = 0.54); Maine: high-intertidal removal = 10.0  $\pm$  10.4, control = 18.0  $\pm$  8.4, addition = 21.0  $\pm$  14.4 (ANOVA p = 0.41); mid-intertidal removal = 17.0  $\pm$  5.2, control = 23.0  $\pm$  8.8, addition = 24.0  $\pm$  11.2 (ANOVA p = 0.50). At subsequent low tides (total of 6, at ~12 h intervals for 3 d), individuals of either *L. obtusata* or *L. littorea* were again removed from high- and mid-intertidal removal replicates. Initial snail removal densities were as follows: for *L. littorea* removal—Rhode Island: high-intertidal ~50 m<sup>-2</sup>, mid-intertidal ~35 m<sup>-2</sup>; Maine: high-intertidal ~25 m<sup>-2</sup>, mid-intertidal ~35 m<sup>-2</sup>; for *L. obtusata* removal—Rhode Island: high-intertidal ~55 m<sup>-2</sup>, mid-intertidal ~35 m<sup>-2</sup>; Maine: high-intertidal ~30 m<sup>-2</sup>, mid-intertidal ~25 m<sup>-2</sup>. Removal numbers declined with subsequent low tides, generally ranging from ~10 to 25 m<sup>-2</sup>, depending on species and tidal height. Removed snails were always added to the addition treatment of each set; control areas remained unmanipulated. After 3 d, we recorded final densities of the species being monitored.

### Laboratory experiments

All macroalgae, snails, and seawater used in laboratory experiments were freshly collected from Ft. Wetherill, Jamestown, Rhode Island. Specimens were transported in coolers and held aerated at ambient water temperatures (range = 13 to 18°C) until the initiation of experiments (within 2 d). Organisms were used only once in experiments to avoid any residual effects, and we used similarly sized *L. littorea* (~6.8 to 11.5 mm) and *L. obtusata* (~6.5 to 12.0 mm). Experiments were conducted in Percival growth chambers on Innova platform shakers for aeration, at ambient water temperatures and irradiance level of 100  $\mu$ mol photons m<sup>-2</sup> s<sup>-1</sup> on a 12 h light:12 h dark schedule. Experiments were conducted in lidded glass containers (500 ml) and seawater was changed daily in all experiments.

### Effects of snail density and food availability on growth rates

We investigated potential effects of inter- and intraspecific competition between *L. littorea* and *L. obtusata* on their growth rates under ad libitum and limiting food resources of either *F. vesiculosus* or *A. nodosum*. Each of 4 experiments were run for 25 to 30 d. The experimental design included treatment conditions ( $n = 5$ , each treatment) that manipulated snail species and densities on a specified food source, either in a high food (available 100% of time) or a low food (available 25% of time) regime. Snails held in high food treatments were provided ~6 g fresh mass (FM) of fresh algae weekly, while those held in the low food regime were provided algae for the first 7 d, then subsequently starved for the duration of the experiment. Water was changed daily in all containers. To examine density effects, we added 4 (low density, either *L. littorea* or *L. obtusata*) or 8 (high density) snails to containers. The high density treatments assessed intraspecific (8 ind. of same species) and interspecific (4 ind. of each species) effects. Thus, for each experiment, we had 2 food availabilities and 3 density/species treatment conditions. The inside surface area of the containers was 568 cm<sup>2</sup>. Thus, our low and high density treatments were 70 and 140 snails m<sup>-2</sup>, respectively, within the range of field abundances (see 'Study sites' above). We measured initial shell length of each snail with digital calipers (Control Company Traceable; 3415 ± 0.01 mm) and marked shells with colored nail varnish to identify individuals. For analyses, we determined mean snail growth rate for each container and used containers as replicates.

### Grazing rate determinations

Only epiphyte-free, non-reproductive, ungrazed algal fronds (unless otherwise noted) were selected for use in experiments, and apical (distal) regions (~6 to 7 cm length) of fronds were cut the day prior to initiation of experiments and allowed to wound heal overnight under aeration at ambient temperatures. Initial and final algal FM was determined following removal of gravitational water with a lettuce spinner. Grazer-free algal controls were run to correct for autogenic growth, and all experiments were run for 4 d. 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

masses, respectively, of tissue subjected to grazing, and  $C_i$  and  $C_f$  are, respectively, the initial and final masses of grazer-free control algal tissues (equation from Sotka et al. 2002).

### Induction of resistance

We evaluated potential effects from inter- and intraspecific interference competition by both gastropod species on herbivory of pre-grazed (grazed) fronds (induction of resistance) of *F. vesiculosus* and *A. nodosum* (8 experiments). During the induction phase, similarly sized (<12 mm) *L. littorea* or *L. obtusata* were allowed to graze on distal regions of *F. vesiculosus* or *A. nodosum* (~6 g FM of each species in 5 containers holding 4 snails each) for 1 wk. This length of time allowed induction (if any) of phlorotannins (Peckol et al. 1996) or of other changes to algal thalli (e.g. toughness, additional changes in chemistry). Ungrazed fronds were held under similar conditions without snails. We selected fronds that visually had a similar amount (area) of algal tissue removed by each snail species. Ungrazed fronds were paired with the grazed tissues in choice experiments to assess intra- and interspecific induction by each gastropod species. A thin thread was attached to each frond of grazed algae to differentiate algal fronds (ungrazed vs. grazed) in replicate containers. Grazer-free algal controls (both ungrazed and grazed fronds) were used to correct for autogenic growth. Both control (no grazers) and experimental treatments ( $n = 12$ , both treatments) held ~1.5 g FM of ungrazed and grazed tissues in 300 ml seawater; 4 snails (either *L. littorea* or *L. obtusata*) were included in experimental containers.

### Phlorotannin determination

Total phlorotannin concentrations (mg g<sup>-1</sup> dry mass, DM) of control (ungrazed) and grazed (by *L. littorea* and *L. obtusata*) fronds of *F. vesiculosus* and *A. nodosum* were determined using a modified version of the Folin-Denis method (Ragan & Glombitza 1986, Yates & Peckol 1993, Targett & Arnold 1998). Non-reproductive, distal regions were selected, and extractions were conducted using fresh (non-frozen) material ( $n = 8$ , all treatments). Phlorotannin levels were calculated from a standard curve of phloroglucinol and expressed on a DM basis using regression analysis.

### Presence of congener

We measured grazing rates of *L. littorea* and *L. obtusata* on *F. vesiculosus* in the presence of its congener. Grazer-free control containers held pre-weighed algae (~2 g FM). The 'grazer-only' treatment contained pre-weighed algae and 4 snails of either gastropod species, while the 'grazer with congener' treatment contained pre-weighed algae, 4 grazers, and 4 ind. of the other snail species held in submerged mesh bags unable to access the algae. Therefore, the included congener was present, but not in direct contact with the grazer (n = 13, all treatments).

### Effects of waterborne cues and mucus

To further identify any avoidance behavior by *L. obtusata* of *L. littorea*, we investigated the effect of waterborne cues of *L. littorea* on *L. obtusata* grazing rates. We did not conduct the reciprocal experiment, i.e. of waterborne cues of *L. obtusata* on *L. littorea*, because other experiments revealed limited effects of the former species on *L. littorea* (see 'Results'). Following collection, *L. littorea* were held aerated without food at ambient temperatures for 2 d to allow them to excrete any residual consumed food. This species then grazed on *F. vesiculosus* for 1 d to generate waterborne cues to be used in the experiment. To standardize the water, 100 *L. littorea* (<12 mm) were held in a volume of 10 l of seawater. The water was then filtered to remove any fragments of algae prior to use; we generated this experimental water daily over the 4 d period. Each replicate container received ambient seawater or water containing *L. littorea* cues and ~2 g FM of *F. vesiculosus*. This waterborne cue experiment had 4 treatments (n = 8). Two grazer-free controls were used: *F. vesiculosus* held in ambient seawater or water containing *L. littorea* cues, while 2 experimental groups contained 4 *L. obtusata* (plus algae) in ambient seawater or water containing *L. littorea* cues. Ammonium levels were undetectable in ambient and ~6  $\mu\text{M}$  in experimental treatments; nitrate concentrations showed the opposite pattern, i.e. ~6 and <5  $\mu\text{M}$  in ambient and experimental treatments, respectively.

We investigated the effect of mucus trails generated by *L. littorea* on grazing rate of *L. obtusata*. We placed 10 *L. littorea* in glass containers containing 300 ml of seawater for 24 h, allowing the snails to crawl around and leave mucus on the container walls to be used in the experimental treatment. 'Mucused'

containers were created each day to allow *L. obtusata* contact with fresh *L. littorea* mucus. Grazer-free controls contained algae with no grazers. We added 4 *L. obtusata* to containers with ~2 g FM *F. vesiculosus* and no *L. littorea* mucus and containers that had been 'mucused' by *L. littorea* (n = 9, each treatment). We also measured the effect that *L. littorea* mucus might have on the movement behavior of *L. obtusata*, recording the number of snails submerged, on algae (*F. vesiculosus*), or out of the water (emerged) during day and night (growth chamber, 12 h light:12 h dark) in all treatment conditions.

### Statistical analysis

Prior to statistical analyses, homogeneity of variance was determined using the  $F_{\text{max}}$  test (Sokal & Rohlf 2012) and normality was evaluated using the Kolmogorov-Smirnov test. We applied 2-tailed *t*-tests for all grazing experiments. For the 8 choice trials (grazed vs. ungrazed fronds), we employed 2-tailed, paired *t*-tests. We applied 1-factor ANOVA for analysis of phlorotannin concentrations (ungrazed and grazed fronds of *F. vesiculosus* and *A. nodosum* by *L. littorea* and *L. obtusata*) and 2-factor ANOVA for the 4 field density manipulation experiments (*L. obtusata* and *L. littorea* response to varying densities of their congener conducted at 2 tidal levels in Maine and Rhode Island, density  $\times$  tidal height) and 4 laboratory growth rate determinations (density  $\times$  food) under varying snail densities (inter- and intraspecific effects) and food availability. Tukey's multiple range test was used to make comparisons among means from significant ANOVA tests.

## RESULTS

### Field density manipulations

At both Maine and Rhode Island study sites, manipulation of densities of *Littorina littorea* (removal and addition for 6 low tides, 3 d) from high- and mid-intertidal areas resulted in a consistent response by *L. obtusata*. In Maine (Fig. 1a), we found tidal height (2-factor ANOVA,  $F_{1,24} = 5.73$ ,  $p = 0.025$ ) and density ( $F_{2,24} = 5.85$ ,  $p = 0.008$ ) effects, but no interaction (density  $\times$  height,  $p = 0.41$ ) between these variables. *L. obtusata* abundances increased significantly following *L. littorea* removal compared with control and addition treatments (Tukey's test,  $p < 0.05$ ). In Rhode Island (Fig. 1b), we did not document



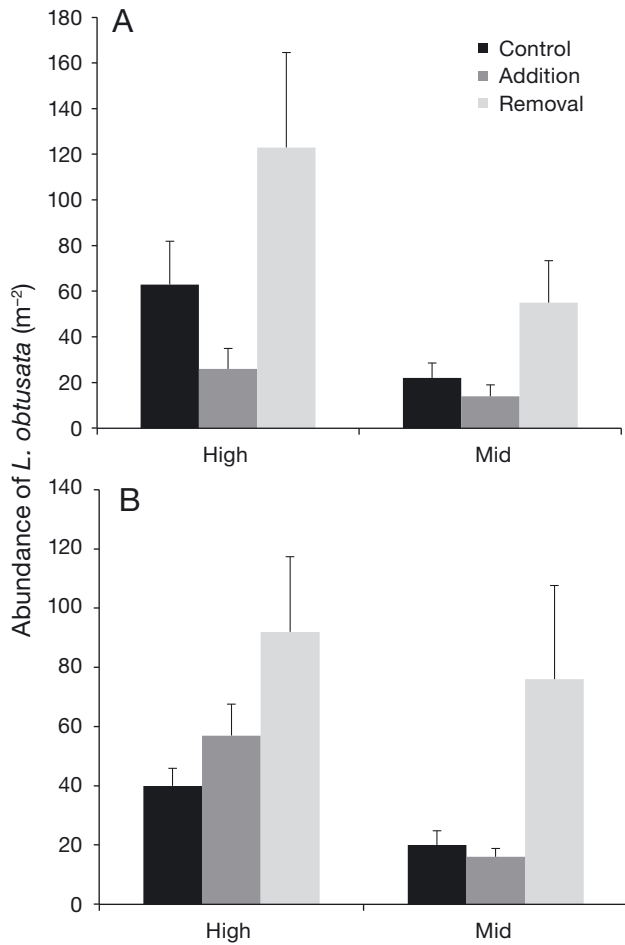


Fig. 1. Mean (+SE) abundances (number m<sup>-2</sup>) of *Littorina obtusata* in high- and mid-intertidal areas after the manipulation of *L. littorea* densities at (A) Pemaquid Point, Bristol, Maine and (B) Fort Wetherill, Jamestown, Rhode Island. Treatments included control, addition (*L. littorea* added from removal plots), and removal (*L. littorea* removed every 12 h for 3 d) (n = 4 [Rhode Island] or 5 [Maine] replicate sets, each tidal level)

a tidal height effect (2-factor ANOVA,  $p = 0.09$ ); however, removal of *L. littorea* resulted in higher densities of *L. obtusata* compared with control and addition treatments (2-factor ANOVA,  $F_{2,18} = 5.71$ ,  $p = 0.012$ ; Tukey's test,  $p < 0.05$ ). Although we observed declines in *L. obtusata* density with *L. littorea* addition in Maine, there was not sufficient statistical power to detect a significant effect.

Manipulation of *L. obtusata* densities had no clear effect on abundances of *L. littorea*. Final (mean  $\pm$  SD m<sup>-2</sup>) densities (pooled across tidal height) of *L. littorea* were as follows: for Maine, control =  $8.5 \pm 5.0$ , removal =  $17.0 \pm 13.1$ , addition =  $16.0 \pm 12.1$  (ANOVA,  $p = 0.52$ ); for Rhode Island, control =  $44.7 \pm 34.1$ , removal =  $38.7 \pm 13.1$ , addition =  $29.3 \pm 4.8$  (ANOVA,  $p = 0.21$ ).

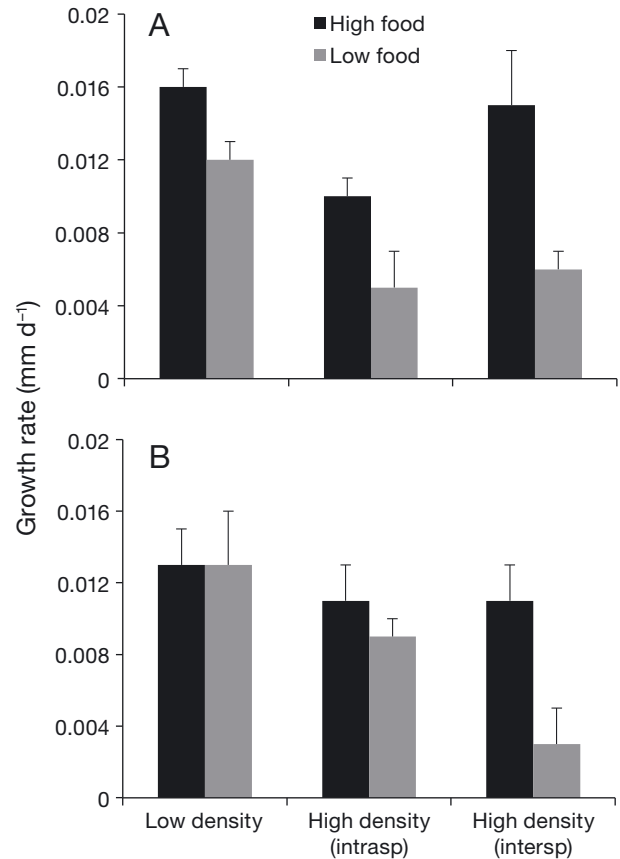


Fig. 2. Mean (+SE) growth rate (mm d<sup>-1</sup>) of (A) *Littorina littorea* and (B) *L. obtusata* on *Fucus vesiculosus* at low or high density of snails (intra- and interspecific effects) under high (100%) and low (25%) food availability

### Effects of density and food availability on snail growth rates

We measured effects of snail density (intra- and interspecific effects) and food availability (100 and 25% accessibility) on growth rates of *L. littorea* and *L. obtusata*. When offered *Fucus vesiculosus* as food (Fig. 2), 2-factor ANOVA revealed food and density effects for both *L. littorea* (food:  $F_{1,23} = 18.4$ ,  $p = 0.0003$ ; density:  $F_{2,23} = 6.4$ ,  $p = 0.006$ ; interaction:  $p = 0.90$ ) and *L. obtusata* (food:  $F_{1,23} = 4.5$ ,  $p = 0.04$ ; density:  $F_{2,23} = 4.1$ ,  $p = 0.04$ ; interaction:  $p = 0.29$ ). Under low food availability, *L. obtusata* showed reduced growth rate (Tukey's test,  $p = 0.03$ ) at high densities (compared with low density treatment) in the presence of *L. littorea*, indicating a negative interspecific effect, but not in the presence of its conspecific (Fig. 2b). *L. littorea* demonstrated the opposite pattern, namely, lower growth rate under high densities of its conspecific (intraspecific effect), but not congeneric (Tukey's test,  $p = 0.04$ ). However, perform-

ance under low food did not vary (Tukey's test,  $p = 0.81$ ) between the 2 high density treatments (Fig. 2a).

*L. littorea* demonstrated low growth rates when offered *Ascophyllum nodosum*, and performance was similar (mean growth = 0.002 to 0.003 mm d<sup>-1</sup>) across treatments. Statistical analysis did not detect an effect of density or food availability on growth (2-factor ANOVA, food:  $p = 0.48$ ; density:  $p = 0.34$ ).

In contrast with *L. littorea*, growth rates of *L. obtusata* when offered *A. nodosum* as a resource were relatively high under the low snail density/high food availability treatment (Fig. 3). *L. obtusata* demonstrated food and density effects (2-factor ANOVA, food:  $F_{1,23} = 42.8$ ,  $p < 0.0001$ ; density:  $F_{2,23} = 5.6$ ,  $p = 0.01$ ; interaction:  $p = 0.11$ ). Although growth rates were similar and low across treatments under limited *A. nodosum* availability, under high food availability, *L. obtusata* growth at high density was reduced compared with the low density treatment (Tukey's test,  $p = 0.002$ ) in the presence of *L. littorea* (interspecific effect), but not in the presence of higher density of members of its own species (Tukey's test,  $p = 0.29$ ).

#### Effects of grazed (induced) algae on grazing preferences

The littorinid species demonstrated distinctive responses to grazed (intra- and interspecific effects) and ungrazed furoid algae. When offered a choice of *F. vesiculosus* or *A. nodosum* that was ungrazed or had been grazed by its conspecific (intraspecific effect), neither *L. littorea* nor *L. obtusata* had a significant preference (paired *t*-tests, for *F. vesiculosus*: *L.*

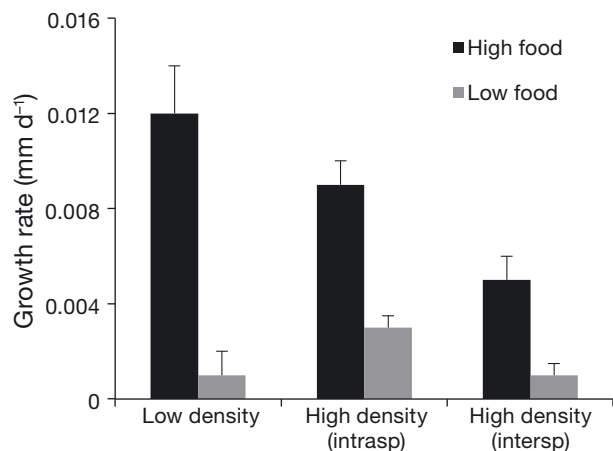


Fig. 3. Mean (+SE) growth rate (mm d<sup>-1</sup>) of *Littorina obtusata* on *Ascophyllum nodosum* at low or high density of snails (intra- and interspecific effects) under high (100%) and low (25%) food availability

*littorea*,  $p = 0.13$ ; *L. obtusata*,  $p = 0.48$ ; for *A. nodosum*: *L. littorea*,  $p = 0.50$ ; *L. obtusata*,  $p = 0.48$ ), though in each trial the grazed fronds were consumed at a lower rate than ungrazed tissues (Figs. 4 & 5). Further, statistical analysis (paired *t*-test,  $p = 0.19$ ) did not detect a difference in herbivory of *L. littorea* between ungrazed *F. vesiculosus* tissues and fronds had been grazed by its congener (interspecific effect). In contrast, *L. obtusata* showed lower consumption of *F. vesiculosus* grazed by *L. littorea* compared with ungrazed fronds ( $t_{11} = 7.6$ ,  $p < 0.0001$ ), indicating an interspecific deterrent effect. Both gastropod species demonstrated reduced herbivory on *A. nodosum* grazed by their congener (*L. littorea*:  $t_{11} = 2.4$ ,  $p = 0.03$ ; *L. obtusata*:  $t_{11} = 4.0$ ,  $p = 0.002$ ).

#### Phlorotannin concentrations

Constitutive (ungrazed) phlorotannin concentrations varied between the 2 furoid species, with *A. nodosum* showing nearly 2-fold higher levels ( $t_{12} = 4.6$ ,

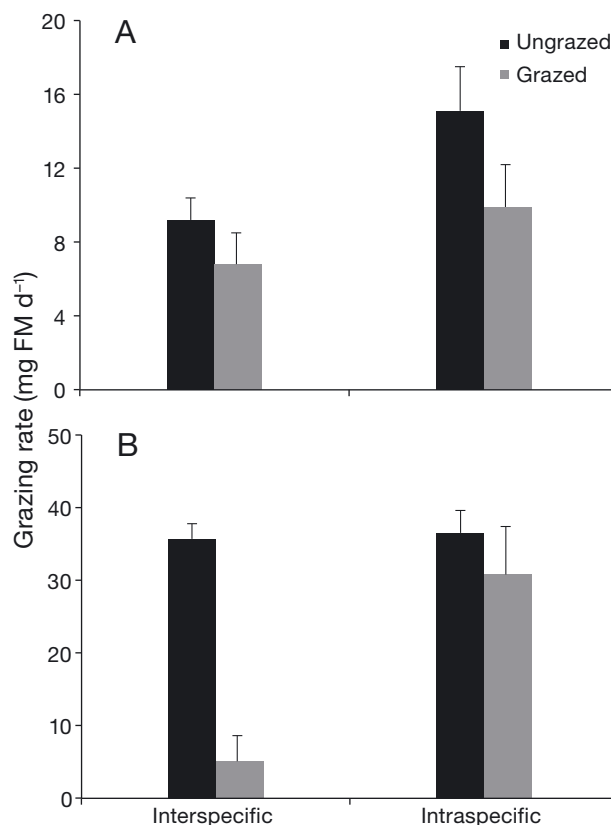


Fig. 4. Mean (+SE) grazing rate (mg fresh mass [FM] d<sup>-1</sup>) of (A) *Littorina littorea* and (B) *L. obtusata* when offered ungrazed *Fucus vesiculosus* and algae that had been grazed by congener (interspecific effect) or by its own species (intraspecific effect)

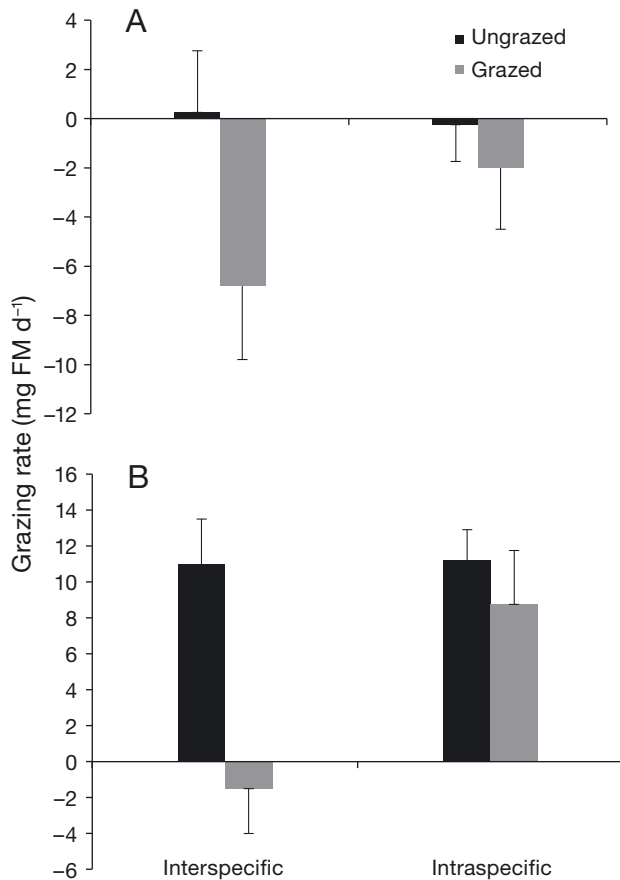


Fig. 5. Mean ( $\pm$ SE) grazing rate (mg fresh mass [FM] d<sup>-1</sup>) of (A) *Littorina littorea* and (B) *L. obtusata* when offered ungrazed *Ascophyllum nodosum* and algae that had been grazed by congener (interspecific effect) or by its own species (intraspecific effect)

$p = 0.0006$ ) than *F. vesiculosus* (Fig. 6). Grazing by *L. obtusata* induced *F. vesiculosus* fronds above ungrazed levels (1-factor ANOVA,  $F_{2,18} = 7.7$ ,  $p = 0.004$ , Tukey's test,  $p < 0.05$ ); however, we did not detect a significant induction of phlorotannins above constitutive levels by *L. littorea* (Tukey's test,  $p = 0.75$ ). Both littorinid species induced phlorotannins in *A. nodosum* above ungrazed levels (1-factor ANOVA,  $F_{2,21} = 7.1$ ,  $p = 0.005$ ); however, induced levels were similar between the 2 gastropod species (Tukey's test,  $p = 0.88$ ).

#### Effects of littorinid presence, waterborne cues, and mucus trails on herbivory

We measured herbivory of *L. obtusata* in the presence of *L. littorea* as well as its waterborne cues and mucus trails (Table 1). *L. obtusata* demonstrated a lower grazing rate on *F. vesiculosus* in the presence

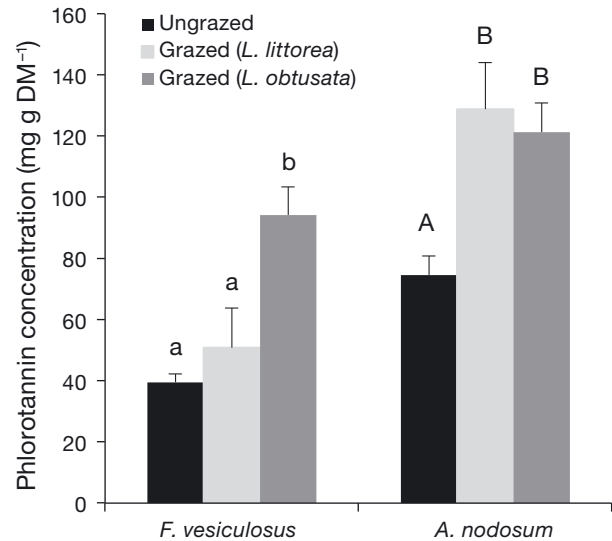


Fig. 6. Mean ( $\pm$ SE) phlorotannin concentrations (mg g<sup>-1</sup> dry mass [DM]) of *Fucus vesiculosus* and *Ascophyllum nodosum* comparing ungrazed and previously grazed fronds by *Littorina littorea* and *L. obtusata*. Treatments sharing lowercase (*F. vesiculosus* assays) or uppercase (*A. nodosum* assays) letters are not significantly different as tested with 1-factor ANOVA and Tukey's tests

Table 1. Mean ( $\pm$ SE) grazing rate (mg fresh mass d<sup>-1</sup>) of *Littorina obtusata* on *Fucus vesiculosus* under various treatment conditions. The '*L. littorea* presence' (n = 13) treatment placed *L. obtusata* in contact with *L. littorea* held in bags; the 'waterborne cue' treatment held *L. obtusata* in *L. littorea* water (n = 8); the '*L. littorea* mucus' (n = 9) treatment placed *L. obtusata* in contact with *L. littorea* mucus on surfaces of experimental containers. The control treatment lacked experimental manipulations. Grazer-free algal controls run in each experiment to correct for autogenic growth were used in the calculation of grazing rates

	<i>L. littorea</i> presence	Waterborne cue	<i>L. littorea</i> mucus
Control	44.3 $\pm$ 3.7	84.7 $\pm$ 4.3	70.7 $\pm$ 9.5
Experimental	29.2 $\pm$ 5.0	45.6 $\pm$ 3.9	68.5 $\pm$ 7.3
<i>t</i> -values	2.2	4.9	0.1
<i>p</i> -values	0.036	0.0002	0.94

(no contact) of *L. littorea* or its waterborne cues compared with the control treatments. In contrast, we did not detect a significant effect of the presence of mucus trails of *L. littorea* on *L. obtusata* grazing rates. Similarly, location (submerged vs. emerged) of *L. obtusata* in containers was not strongly influenced by the presence or absence of *L. littorea* mucus trails (data not shown). Herbivory of *L. littorea* was similar (*t*-test,  $p = 0.73$ ) in the presence ( $22.0 \pm 5.4$  mg FM d<sup>-1</sup>) and absence ( $25.1 \pm 6.7$  mg FM d<sup>-1</sup>) of *L. obtusata*.



## DISCUSSION

This study revealed negative interactions between *Littorina littorea* and *L. obtusata* in field and laboratory experiments, indicative of asymmetric competition. Interspecific, but not intraspecific, competition affected growth, herbivory, and distribution of *L. obtusata*. In contrast, *L. littorea* demonstrated intraspecific effects under limited food availability and higher densities when fed a diet of *Fucus vesiculosus*; however, its performance was not strongly affected by *L. obtusata*. Thus, coexistence of indigenous *L. obtusata* and introduced *L. littorea* in temperate rocky intertidal areas may be possible due to distinctive species characteristics and selective habitat and feeding preferences of the former species.

Results of field and laboratory density manipulations of the littorines provided evidence of interference competition by *L. littorea* on *L. obtusata*. In the field, abundances of *L. obtusata* increased 2- to 3-fold above unmanipulated controls following the removal of *L. littorea* at both study areas. In the laboratory, *L. obtusata* had reduced growth rate in the presence of *L. littorea*, but not in the presence of its conspecific, under limiting food resources (*F. vesiculosus*) and abundant food supply (*Ascophyllum nodosum*). This latter negative response of *L. obtusata* to some form of interference by *L. littorea* may be similar to that experienced in a field setting where food is rarely limiting. Other studies have established that *L. littorea* as a successful competitor for resources in intertidal habitats (Brenchley & Carlton 1983, Behrens Yamada & Mansour 1987, Petraitis 1989, Eastwood et al. 2007), and Frid & James (1988) suggested resource partitioning by the mud snail *Peringia (Hydrobia) ulvae* permitted coexistence with *L. littorea*. As noted by Brenchley & Carlton (1983), competitive interactions may be subtle, becoming evident through density manipulations rather than by comparing distribution patterns.

Our study revealed mechanisms of interference between these intertidal herbivores. Grazer-deterrent effects of constitutive and induced phlorotannin levels in brown algae often involve complex interactions between herbivores and the environment (Steinberg 1988, Steinberg & van Altena 1992, Peckol et al. 1996, Targett & Arnold 1998, Amsler 2001, Kubanek et al. 2004, Long & Trussell 2007, Koivikko et al. 2008, Haavisto et al. 2017). Several studies have reported herbivore avoidance following induction of resistance (phlorotannins) in *Fucus* spp., including *F. vesiculosus* (Van Alstyne 1988, Yates & Peckol 1993, Rohde et al. 2004) and *A. nodosum* (Pavia & Toth

2000, Toth & Pavia 2000, Borell et al. 2004). In contrast, other work reported that herbivores were tolerant of this form of chemical defense (Steinberg & van Altena 1992, Pavia et al. 1997, Jormalainen et al. 2001, Hemmi et al. 2004, Kubanek et al. 2004). We measured induction of resistance in *F. vesiculosus* by *L. obtusata* and in *A. nodosum* by both species. Notably, phlorotannins in *A. nodosum* were 2-fold higher than values measured in *F. vesiculosus*, and both herbivores showed low preference for *A. nodosum* in paired-choice grazing experiments (Peckol & Putnam 2017). While herbivory by *L. littorea* was not diminished on *F. vesiculosus* grazed by *L. obtusata*, fronds of both furoid algae grazed by *L. littorea* were less palatable to *L. obtusata*, indicating a strong interspecific effect. Similarly, Yun et al. (2010) found that *F. vesiculosus* grazed by *L. littorea* deterred grazing by the isopod *Idotea baltica*, while another *Littorina* species, *L. brevicula*, induced resistance in *Laminaria japonica* that decreased grazing of the abalone *Haliotis discus* (Molis et al. 2008). Recently, Jones & Long (2017) documented variation in the strength of herbivore-induced deterrence with grazer identity.

The lack of significant grazing deterrence among conspecifics under elevated phlorotannin levels coupled with strong avoidance by *L. obtusata* of both furoid species grazed by *L. littorea* indicates that herbivore-induced interference cannot be fully explained by phlorotannin induction. Instead, as suggested by some research (Hemmi et al. 2004, Kubanek et al. 2004, Sotka & Gantz 2013), compounds other than phlorotannins may be induced by *L. littorea* that result in reduced palatability to its congener. For example, Deal et al. (2003) characterized metabolites linked to reduced palatability, and concluded that galactolipids and other non-phenolic compounds produced the strongest deterrence. Notably, Flöthe et al. (2014) found that defensive responses by *F. vesiculosus* to herbivory were associated with induction of several genes, and grazing by snails and isopods elicited distinctive gene expression. Such differences in gene regulation may be caused by species differences in saliva (Coleman et al. 2007) or herbivore specialization (Ali & Agrawal 2012). Similarly, defensive responses caused by gene expression in terrestrial plants were species dependent (Walling 2000, Reymond et al. 2004).

The furoid species responded differently to herbivory by the littorines, suggesting specificity of induction. Pavia & Toth (2000) postulated that differences between *L. obtusata* and the isopod *Idotea granulosa* in their ability to induce resistance in *A. nodosum*

might be related to varying feeding capabilities and damage caused by the 2 herbivores, while Rohde et al. (2004) found a similar ability by *L. littorea* and *I. baltica* to induce defense in *F. vesiculosus*. Comparable to our findings, Molis et al. (2006) documented distinctive induction of the kelp *Ecklonia cava* by herbivores with the same grazing mode. Interestingly, we observed unique grazing marks on the furoid algae; *L. littorea* removed larger portions of tissue through all cell layers, while *L. obtusata* consumed surface layers. Although both littorines are taenioglossam grazers, *L. littorea* has pointed shaped cusps while *L. obtusata* has broad, blunt, and short cusps (Reid 1996). Molis et al. (2008) argued that a combination of mechanical and chemical cues might be necessary to induce anti-herbivory defenses in some algae. Thus, these patterns of herbivory, due to distinctive radular structures, may explain differences in induction of macroalgal defenses and in grazer response to these compounds.

We identified other mechanisms of interference competition by *L. littorea* on *L. obtusata*. Herbivory by *L. obtusata* was reduced in the presence (no contact) of *L. littorea* or its waterborne cues. Similarly, the ladybird *Propylea japonica* showed a reduced feeding rate on aphids when exposed to fecal matter left behind on a plant by *Harmonia axyridis* (Agarwala et al. 2003). Brenchley & Carlton (1983) suggested that contact with *L. littorea* interfered with foraging and locomotory activities of *Tritia obsoleta*. Thus, waterborne cues produced by *L. littorea* (or its presence) might negatively influence *L. obtusata* distribution and grazing in a field setting.

We documented negative interspecific effects between *L. littorea* and *L. obtusata* indicative of asymmetric competition, yet these species coexist in a natural field setting across a range of densities (<30 to sometimes >200 m<sup>-2</sup>). Further, we were unable to elucidate a clear effect of addition (>2-fold above unmanipulated controls) of *L. littorea* on abundances of *L. obtusata*, suggesting that the latter species is tolerant of its congener across a range of densities and tidal levels. Species exclusion might be unlikely due to renewability of resources and the ability to change location (Underwood 1978, Ritchie 2002). Because of its mobility, the competitively inferior *L. obtusata* may demonstrate behavioral avoidance, as detailed for other species (Thorp 1976, Race 1982, Jensen et al. 2002). With the exception of extremely exposed shores, there is an abundance of micro- and macroalgal species along temperate rocky coastlines (Lubchenco 1980, Goecker & Kåll 2003), so food is rarely limiting (Underwood 1978, Petraitis 1989, Pavia &

Toth 2000). Additionally, similar to our results, Petraitis (2002) demonstrated that increased *L. littorea* density resulted in a marked depression of its growth rate due to intraspecific competition. Chesson (2000) argued that strong intraspecific competition may dampen interspecific pressure, permitting stable species coexistence. Thus, more restricted food and habitat preferences may be successful strategies for *L. obtusata*, allowing it to maintain modest, relatively stable abundances (Pavia & Toth 2000) and gain refuge from predation (Hay et al. 1989, Duffy & Hay 1994) within the perennial furoid algal canopies.

While the mechanisms of interference being exerted by *L. littorea* on *L. obtusata* were not fully elucidated, our study revealed notable characteristics of this asymmetric competitive interaction. We documented several examples of interference by *L. littorea* that reduced grazing and growth rates of *L. obtusata*, and found that abundances of the latter species are clearly influenced by *L. littorea* in the field setting. However, their ability to coexist despite adverse interspecific effects highlights the dynamic and complex nature of the interactions between these herbivorous gastropods and their environment.

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#### LITERATURE CITED

- ✦ Agarwala BK, Yasuda H, Kajita Y (2003) Effect of conspecific and heterospecific feces on foraging and oviposition of two predatory ladybirds: role of fecal cues in predator avoidance. *J Chem Ecol* 29:357–376
- ✦ Ali JG, Agrawal AA (2012) Specialist versus generalist insect herbivores and plant defense. *Trends Plant Sci* 17: 293–302
- ✦ Amsler CD (2001) Induced defenses in macroalgae: the herbivore makes the difference. *J Phycol* 37:353–356
- ✦ Barker KM, Chapman ARO (1990) Feeding preference of periwinkles among four species of *Fucus*. *Mar Biol* 106: 113–118
- ✦ Behrens Yamada S, Mansour R (1987) Growth inhibition of native *Littorina saxatilis* (Olivier) by introduced *L. littorea* (L.). *J Exp Mar Biol Ecol* 105:187–196
- ✦ Blakeslee AMH, Byers JE, Lesser MP (2008) Solving cryptogenic histories using host and parasite molecular genetics: the resolution of *Littorina littorea*'s North American origin. *Mol Ecol* 17:3684–3696

- Borell EM, Foggo A, Coleman RA (2004) Induced resistance in intertidal macroalgae modifies feeding behaviour in herbivorous snails. *Oecologia* 140:328–334
- Branch GM, Branch ML (1981) Experimental analysis of intraspecific competition in an intertidal gastropod, *Littorina unifasciata*. *Aust J Mar Freshwater Res* 32:573–589
- Brenchley GA (1982) Predation on encapsulated larvae by adults: effects of introduced species on the gastropod *Ilyanassa obsoleta*. *Mar Ecol Prog Ser* 9:255–262
- Brenchley GA, Carlton JT (1983) Competitive displacement of native mud snails by introduced periwinkles in the New England intertidal zone. *Biol Bull (Woods Hole)* 165: 543–558
- Carlton JT (1982) The historical biogeography of *Littorina littorea* on the Atlantic coast of North America and implications for the interpretation of the structure of New England USA intertidal communities. *Malacol Rev* 15:146
- Carlton JT (1992) Introduced marine and estuarine mollusks of North America: an end-of-the-20th-century perspective. *J Shellfish Res* 11:489–505
- Carpenter RC (1990) Competition among marine macroalgae: a physiological perspective. *J Phycol* 26:6–12
- Chapman JW, Carlton JT, Bellinger MR, Blakeslee AMH (2007) Premature refutation of a human-mediated marine species introduction: the case history of the marine snail *Littorina littorea* in the Northwestern Atlantic. *Biol Invasions* 9:995–1008
- Chesson P (2000) Mechanisms of maintenance of species diversity. *Annu Rev Ecol Syst* 31:343–366
- Coleman RA, Ramchunder SJ, Moody AJ, Foggo A (2007) An enzyme in snail saliva induces herbivore-resistance in a marine alga. *Funct Ecol* 21:101–106
- Connell JH (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42:710–723
- Connell JH (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am Nat* 122:661–696
- Cunningham CW (2008) How to use genetic data to distinguish between natural and human-mediated introduction of *Littorina littorea* to North America. *Biol Invasions* 10:1–6
- Davenport J, Davenport JL (2005) Effects of shore height, wave exposure and geographical distance on thermal niche width of intertidal fauna. *Mar Ecol Prog Ser* 292: 41–50
- Deal MS, Hay ME, Wilson D, Fenical W (2003) Galactolipids rather than phlorotannins as herbivore deterrents in the brown seaweed *Fucus vesiculosus*. *Oecologia* 136: 107–114
- Duffy JE, Hay ME (1994) Herbivore resistance to seaweed chemical defense: the roles of mobility and predation risk. *Ecology* 75:1304–1319
- Eastwood MM, Donahue MJ, Fowler AE (2007) Reconstructing past biological invasions: niche shifts in response to invasive predators and competitors. *Biol Invasions* 9: 397–407
- Fletcher WJ, Creese RG (1985) Competitive interactions between co-occurring herbivorous gastropods. *Mar Biol* 86:183–191
- Flöthe CR, Molis M, John U (2014) Induced resistance to periwinkle grazing in the brown seaweed *Fucus vesiculosus* (Phaeophyceae): molecular insights and seaweed-mediated effects on herbivore interactions. *J Phycol* 50: 564–576
- Frid CLJ, James R (1988) Interactions between two species of saltmarsh gastropod, *Hydrobia ulvae* and *Littorina littorea*. *Mar Ecol Prog Ser* 43:173–179
- Goecker ME, Käll SE (2003) Grazing preferences of marine isopods and amphipods on three prominent algal species of the Baltic Sea. *J Sea Res* 50:309–314
- Haavisto F, Koivikko R, Jormalainen V (2017) Defensive role of macroalgal phlorotannins: benefits and trade-offs under natural herbivory. *Mar Ecol Prog Ser* 566:79–90
- Hammerson GA (2004) Connecticut wildlife: biodiversity, natural history, and conservation. University Press of New England, Hanover, NH
- Haven SB (1973) Competition for food between the intertidal gastropods *Acmaea scabra* and *Acmaea digitalis*. *Ecology* 54:143–151
- Hay ME, Pawlik JR, Duffy E, Fenical W (1989) Seaweed-herbivore-predator interactions: host-plant specialization reduces predation on small herbivores. *Oecologia* 81:418–427
- Hemmi A, Honkanen T, Jormalainen V (2004) Inducible resistance to herbivory in *Fucus vesiculosus*—duration, spreading and variation with nutrient availability. *Mar Ecol Prog Ser* 273:109–120
- Jensen GC, McDonald PS, Armstrong DA (2002) East meets west: competitive interactions between green crab *Carcinus maenas*, and native and introduced shore crab *Hemigrapsus* spp. *Mar Ecol Prog Ser* 225:251–262
- Jones E, Long J (2017) The relative strength of an herbivore-induced seaweed defense varies with herbivore species. *Mar Ecol Prog Ser* 581:33–44
- Jormalainen V, Honkanen T, Heikkilä N (2001) Feeding preferences and performance of a marine isopod on seaweed hosts: cost of habitat specialization. *Mar Ecol Prog Ser* 220:219–230
- Koivikko R, Eranen JK, Loponen J, Jormalainen V (2008) Variation of phlorotannins among three populations of *Fucus vesiculosus* as revealed by HPLC and colorimetric quantification. *J Chem Ecol* 34:57–64
- Kozminsky EV (2013) Effects of environmental and biotic factors on the fluctuations of abundance of *Littorina obtusata* (Gastropoda: Littorinidae). *Hydrobiologia* 706: 81–90
- Kubanek J, Lester SE, Fenical W, Hay ME (2004) Ambiguous role of phlorotannins as chemical defenses in the brown alga *Fucus vesiculosus*. *Mar Ecol Prog Ser* 277: 79–93
- Long JD, Trussell GC (2007) Geographic variation in seaweed induced responses to herbivory. *Mar Ecol Prog Ser* 333:75–80
- Long JD, Hamilton RS, Mitchell JL (2007) Asymmetric competition via induced resistance: specialist herbivores indirectly suppress generalist preference and populations. *Ecology* 88:1232–1240
- Lubchenco J (1978) Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *Am Nat* 112:23–39
- Lubchenco J (1980) Algal zonation in the New England rocky intertidal community: an experimental analysis. *Ecology* 61:333–344
- Magre EJ (1974) *Ulva lactuca* L. negatively affects *Balanus balanoides* (L.) (*Cirripedia Thoracica*) in tidepools. *Crustaceana* 27:231–234
- Menge BA (1976) Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecol Monogr* 46:355–393

- Moksnes PO (2004) Interference competition for space in nursery habitats: density-dependent effects on growth and dispersal in juvenile shore crabs *Carcinus maenas*. *Mar Ecol Prog Ser* 281:181–191
- Molis M, Körner J, Ko YW, Kim JH, Wahl M (2006) Inducible responses in the brown seaweed *Ecklonia cava*: the role of grazer identity and season. *J Ecol* 94:243–249
- Molis M, Körner J, Ko YW, Kim JH (2008) Specificity of inducible seaweed anti-herbivory defences depends on identity of macroalgae and herbivores. *Mar Ecol Prog Ser* 354:97–105
- Murphy DJ (1979) A comparative study of the freezing tolerances of the marine snails *Littorina littorea* (L.) and *Nassarius obsoletus* (Say). *Physiol Zool* 52:219–230
- Navarrete SA, Castilla JC (1990) Resource partitioning between intertidal predatory crabs: interference and refuge utilization. *J Exp Mar Biol Ecol* 143:101–129
- Newell RC, Pye VI, Ahsanullah M (1971) The effect of thermal acclimation on the heat tolerance of the intertidal prosobranchs *Littorina littorea* (L.) and *Monodonta lineata* (Da Costa). *J Exp Biol* 54:525–533
- Norton TA, Hawkins SJ, Manley NL, Williams GA, Watson DC (1990) Scraping a living: a review of littorinid grazing. *Hydrobiologia* 193:117–138
- Ortega S (1985) Competitive interactions among tropical intertidal limpets. *J Exp Mar Biol Ecol* 90:11–25
- Pavia H, Toth GB (2000) Inducible chemical resistance to herbivory in the brown seaweed *Ascophyllum nodosum*. *Ecology* 81:3212–3225
- Pavia H, Cervin G, Lindgren A, Aberg P (1997) Effects of UV-B radiation and simulated herbivory on phlorotannins in the brown alga *Ascophyllum nodosum*. *Mar Ecol Prog Ser* 157:139–146
- Peckol P, Putnam AB (2017) Differential toxic effects of *Ulva lactuca* (Chlorophyta) on the herbivorous gastropods, *Littorina littorea* and *L. obtusata* (Mollusca). *J Phycol* 53: 361–367
- Peckol P, Rivers JS (1995) Competitive interactions between the opportunistic macroalgae *Cladophora vagabunda* (Chlorophyta) and *Gracilaria tikvahiae* (Rhodophyta) under eutrophic conditions. *J Phycol* 31:229–232
- Peckol PS, Krane JM, Yates JL (1996) Interactive effects of inducible defense and resource availability on phlorotannins in the North Atlantic brown alga *Fucus vesiculosus*. *Mar Ecol Prog Ser* 138:209–217
- Petraitis PS (1989) Effects of the periwinkle *Littorina littorea* (L.) and of intraspecific competition on growth and survivorship of the limpet *Notoacmea testudinalis* (Müller). *J Exp Mar Biol Ecol* 125:99–115
- Petraitis PS (2002) Effects of intraspecific competition and scavenging on growth of the periwinkle *Littorina littorea*. *Mar Ecol Prog Ser* 236:179–187
- Race MS (1982) Competitive displacement and predation between introduced and native mud snails. *Oecologia* 54:337–347
- Ragan MA, Glombitza KW (1986) Phlorotannins, brown algal polyphenols. *Prog Phycol Res* 4:129–241
- Reid DG (1996) Systematics and evolution of *Littorina*. The Dorset Press, Dorchester
- Reymond P, Bodenhausen N, Van Poecke RMP, Krishnamurthy V, Dicke M, Farmer EE (2004) A conserved transcript pattern in response to a specialist and a generalist herbivore. *Plant Cell* 16:3132–3147
- Ridenour WM, Callaway RM (2001) The relative importance of allelopathy in interference: the effects of an invasive weed on a native bunchgrass. *Oecologia* 126:444–450
- Ritchie M (2002) Competition and coexistence of mobile animals. In: Sommer U, Worm B (eds) *Competition and coexistence*. Ecological studies, Vol 161. Springer-Verlag, Berlin, p 109–131
- Robertson DR, Gaines SD (1986) Interference competition structures habitat use in a local assemblage of coral reef surgeonfishes. *Ecology* 67:1372–1383
- Rohde S, Molis M, Wahl M (2004) Regulation of anti-herbivore defence by *Fucus vesiculosus* in response to various cues. *J Ecol* 92:1011–1018
- Schmitt RJ (1996) Exploitation competition in mobile grazers: trade-offs in use of a limited resource. *Ecology* 77: 408–425
- Schoener TW (1983) Field experiments on interspecific competition. *Am Nat* 122:240–285
- Sokal RR, Rohlf FJ (2012) *Biometry: the principles and practice of statistics in biological research*, 4th edn. WH Freeman and Company, New York, NY
- Sokolova IM, Bock C, Pörtner HO (2000) Resistance to freshwater exposure in White Sea *Littorina* spp. I: Anaerobic metabolism and energetics. *J Comp Physiol B* 170:91–103
- Sotka EE, Gantz J (2013) Preliminary evidence that the feeding rates of generalist marine herbivores are limited by detoxification rates. *Chemoeology* 23:233–240
- Sotka EE, Taylor RB, Hay ME (2002) Tissue-specific induction of resistance to herbivores in a brown seaweed: the importance of direct grazing versus waterborne signals from grazed neighbors. *J Exp Mar Biol Ecol* 277:1–12
- Spitz J, Rousseau Y, Ridoux V (2006) Diet overlap between harbor porpoise and bottlenose dolphin: An argument in favour of interference competition for food? *Estuar Coast Shelf Sci* 70:259–270
- Steinberg PD (1988) Effects of quantitative and qualitative variation in phenolic compounds on feeding in three species of marine invertebrate herbivores. *J Exp Mar Biol Ecol* 120:221–237
- Steinberg PD, van Altena I (1992) Tolerance of marine invertebrate herbivores to brown algal phlorotannins in temperate Australasia. *Ecol Monogr* 62:189–222
- Targett NM, Arnold TM (1998) Predicting the effects of brown algal phlorotannins on marine herbivores in tropical and temperate oceans. *J Phycol* 34:195–205
- Thorp JH (1976) Interference competition as a mechanism of coexistence between two sympatric species of the grass shrimp *Palaemonetes* (Decapoda: Palaemonidae). *J Exp Mar Biol Ecol* 25:19–35
- Toth GB, Pavia H (2000) Water-borne cues induce chemical defense in a marine alga (*Ascophyllum nodosum*). *Proc Natl Acad Sci USA* 97:14418–14420
- Trussell G, Johnson AS, Rudolph SG, Gilfillan ES (1993) Resistance to dislodgement: habitat and size-specific differences in morphology and tenacity in an intertidal snail. *Mar Ecol Prog Ser* 100:135–144
- Underwood AJ (1978) An experimental evaluation of competition between three species of intertidal prosobranch gastropods. *Oecologia* 33:185–202
- Underwood AJ (2000) Experimental ecology of rocky intertidal habitats: What are we learning? *J Exp Mar Biol Ecol* 250:51–76
- Van Alstyne KL (1988) Herbivore grazing increases polyphenolic defenses in the intertidal brown alga *Fucus distichus*. *Ecology* 69:655–663
- Walling LL (2000) The myriad plant responses to herbivores. *J Plant Growth Regul* 19:195–216



- Wares JP, Goldwater DS, Kong BY, Cunningham CW (2002) Refuting a controversial case of a human-mediated marine species introduction. *Ecol Lett* 5:577–584
- Watson DC, Norton TA (1985) Dietary preferences of the common periwinkle, *Littorina Littorea* (L.). *J Exp Mar Biol Ecol* 88:193–211
- Watson DC, Norton TA (1987) The habitat and feeding preferences of *Littorina obtusata* (L.) and *L. mariae* Sacchi et Rastelli. *J Exp Mar Biol Ecol* 112:61–72
- Wethey DS (1983) Geographic limits and local zonation: the barnacles *Semibalanus (Balanus)* and *Chthamalus* in New England. *Biol Bull (Woods Hole)* 165:330–341
- Wethey DS (2002) Biogeography, competition, and microclimate: the barnacle *Chthamalus fragilis* in New England. *Integr Comp Biol* 42:872–880
- Wootton JT (1993) Indirect effects and habitat use in an intertidal community: interaction chains and interaction modifications. *Am Nat* 141:71–89
- Worm B, Karez R (2002) Competition, coexistence and diversity on rocky shores. In: Sommer U, Worm B (eds) *Competition and coexistence*. Ecological studies, Vol 161. Springer-Verlag, Berlin, p 133–163
- Yates J, Peckol P (1993) Effects of nutrient availability and herbivory on polyphenolics in the seaweed *Fucus vesiculosus*. *Ecology* 74:1757–1766
- Yun HY, Rohde S, Linnane K, Wahl M, Molis M (2010) Seaweed-mediated indirect interaction between two species of meso-herbivores. *Mar Ecol Prog Ser* 408:47–53

Editorial responsibility: Inna Sokolova,  
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