

# Snail grazing facilitates growth of a bloom-forming alga

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**ABSTRACT:** Herbivory often has a negative effect on plants. However, there is a growing number of examples, primarily in terrestrial ecosystems, where herbivory causes an increase in plant size, growth rate, and/or reproductive output. In marine ecosystems, the positive effects of herbivores on macroalgae are not as well studied, although limited evidence exists for herbivore-induced increases in macroalgal growth rates via 2 mechanisms: nutrient addition via grazer defecation, and epiphyte removal. In this study, we examined the effects of grazing by the mud snail *Ilyanassa obsoleta* on *Ulva lactuca*, the dominant bloom-forming macroalga in many New England estuaries. We found that the presence of *I. obsoleta* had a significant positive, rather than negative, effect on *U. lactuca*. Through caging experiments, we established that this positive effect was not due to fecal nutrient inputs from the snail. Similarly, snail contact in the absence of grazing did not affect *U. lactuca* growth rates. In contrast, grazing by *I. obsoleta* significantly reduced the microalgal cover on heavily fouled *U. lactuca* blades, indicating that snail herbivory of microalgal films likely facilitates *U. lactuca* growth. Our study demonstrates the surprising, positive effect that an abundant herbivore can have on the growth of a macroalgal bloom species.

**KEY WORDS:** Facilitation · Compensation · Herbivory · Algal bloom · *Ulva lactuca* · *Ilyanassa obsoleta*

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## INTRODUCTION

The negative effects of herbivores on primary producers are well known. However, research in terrestrial, aquatic, and marine systems is increasingly revealing instances where herbivory can positively influence plants and algae via a variety of mechanisms. Overcompensation, a phenomenon where plants experiencing light to moderate herbivory have a higher growth rate and/or reproductive output than related, undamaged plants (Agrawal 2000), has been observed in a wide range of plant–herbivore interactions, including multiple species of grasses and unguates (McNaughton 1979, Lennartsson et al. 1997), scarlet gilia and unguates (Gronemeyer et al. 1997, Paige 1999), pondweed and swans (Nolet 2004), and turtlegrass and sea urchins (Valentine et al. 1997). Herbivory can also positively impact plants through indirect pathways, such as fertilization via herbivore

nitrogenous wastes (McNaughton 1983, 1997, Bazely & Jefferies 1985) or the preferential grazing of neighboring or epiphytic competitors (Dudley 1992, Littler et al. 1995, Stachowicz & Hay 1996, Jernakoff & Nielson 1997, Kamermans et al. 2002, Hughes et al. 2004).

One trophic relationship that has recently attracted attention is the effect of herbivores on bloom-forming macroalgae in coastal ecosystems throughout the world. Macroalgal blooms result from a variety of environmental cues, including anthropogenic nitrogen inputs (Nixon 1995, Fletcher 1996), and pose serious threats to coastal ecosystems and economies. The large floating mats of algae that form during bloom events can decrease coastal biodiversity by outcompeting perennial algal species and seagrasses for light, space, or nutrients (Valiela et al. 1997, Hauxwell et al. 1998, 2001, Worm & Lotze 2006). Decomposition of bloom macroalgae also contributes to the occurrence of hypoxic events (Valiela et al. 1997, Raffaelli et al. 1998),

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which can result in mass fish kills (Deacutis & Oviatt 2004). Moreover, several bloom-forming macroalgal species produce toxic chemicals (Nelson et al. 2003), which may have negative ecological and/or economic consequences.

Determining the effects of herbivores on macroalgal blooms is an important step towards understanding bloom severity and persistence. Several studies have observed herbivores exerting significant top-down control on macroalgal bloom species (Geertz-Hansen et al. 1993, Korpinen et al. 2007), though this effect has been shown to decrease with increasing nutrients (Horne et al. 1994, Worm & Lotze 2006). In addition, grazer preferences can differentially influence which algal species are present in blooms, with less palatable species becoming dominant (Lotze & Worm 2000, Lotze et al. 2001, Nelson et al. 2008). Further complicating our understanding of herbivore-bloom relationships, herbivores can have a positive effect on bloom species by increasing the amount of nitrogen available (Fong et al. 1997) or consuming epiphytes (Kamermans et al. 2002).

In this study, we explored the relationship between herbivores and bloom-forming algae by examining the effect of the mud snail *Ilyanassa obsoleta* on the growth of *Ulva lactuca*. *I. obsoleta* is a common inhabitant of sheltered intertidal and subtidal soft sediment communities in eastern North America (Crisp 1969, Curtis & Hurd 1981), where it can occur in densities of over 1400 m<sup>-2</sup> (C. S. Thornber unpubl. data). *I. obsoleta* often co-occurs with *U. lactuca*, which can exceed densities of 1600 g wet mass m<sup>-2</sup> during bloom events. While *I. obsoleta* is primarily a deposit feeder, it is also an opportunistic consumer of carrion and possesses a crystalline style for the digestion of plant materials (Curtis 1980). Macroalgae form a regular component of the mud snails' diet (Scheltema 1964, Curtis & Hurd 1981, Edwards & Welsh 1982) and mud snails have been found to decrease *U. lactuca* biomass in the laboratory (Giannotti & McGlathery 2001). However, our preliminary laboratory experiments conducted in 2006 showed no negative effect of mud snail grazing on *U. lactuca* growth (C. S. Thornber unpubl. data). Therefore, our study first addressed whether *I. obsoleta* grazing decreases *U. lactuca* biomass or facilitates increased growth. Through a series of feeding assays that paired various densities of mud snails with *U. lactuca*, we demonstrated that *I. obsoleta* positively influences *U. lactuca* growth rates. Next, we investigated the mechanism underlying this facilitation, by examining *U. lactuca* performance when exposed to *I. obsoleta* nitrogenous excretions, physical contact (implying a reaction to *I. obsoleta* chemical cues as observed in a terrestrial plant-herbivore interaction; Dyer et al. 1995), and grazing of microalgal films. We discuss our

results in the context of herbivore effects on macroalgal blooms and the potential implications this has for bloom severity and persistence.

## MATERIALS AND METHODS

**Study species and locale.** Narragansett Bay, Rhode Island, USA, is a well-mixed estuarine system of ~370 km<sup>2</sup>. During the summer in the shallow, protected areas of Narragansett Bay, macroalgal blooms composed of *Ulva lactuca* and tubular *Ulva* species (Chlorophyta) are a regular occurrence (Granger et al. 2000, C. S. Thornber unpubl. data). *U. lactuca* blades are distromatic, typically growing attached to hard substrates, but blades can detach and continue growing in the water column. Currently, *U. lactuca* is the only recorded species of blade-forming *Ulva* in Rhode Island waters. However, *Ulva* species are notoriously difficult to identify based on morphology alone and the genus is under taxonomic revision in this area.

*Ilyanassa obsoleta* is the most abundant invertebrate epibenthic species found in intertidal and shallow subtidal estuarine habitats of Narragansett Bay (M. Guidone & C. S. Thornber unpubl. data). During bloom events, floating and washed up *U. lactuca* are found covered with these mud snails, which appear to be grazing across the blades (M. Guidone pers. obs.).

We conducted all feeding experiments at the University of Rhode Island's Bay Campus (Narragansett, RI, USA) in outdoor flow-through seawater tables during the summers of 2006, 2007, and 2008. The tables were supplied with filtered, ambient temperature seawater from Narragansett Bay. Replicates were held within the seawater tables in 2.5 l semi-transparent plastic buckets (we used 5 l buckets for nitrogen input experiments only); several mesh-covered holes in the sides of each bucket allowed for sufficient seawater flow. Buckets were covered with clear Plexiglas to prevent the input of outside nutrient sources and rainwater.

**Feeding assays.** Unless otherwise noted, we used juvenile *Ilyanassa obsoleta* (10 to 14 mm in length) in all experiments, since they have a lower incidence of parasitic infection that can affect feeding rates (Curtis & Hurd 1983). In addition, all pieces of *Ulva lactuca* were between 0.65 and 1.25 g wet mass.

Our initial feeding assay was conducted using 4 *Ilyanassa obsoleta* in each of 20 experimental buckets. An equal number of non-herbivore controls were run concurrently; to maintain consistency, control algae were taken from the same thalli as their experimental counterparts in a paired design. We measured wet algal biomass at the beginning and the conclusion of the experiment. We spun each algal piece in a salad

spinner 20 times to remove excess water prior to measuring its wet mass. Experiments ran for 2 wk, as algal tissue begins to degrade after ~2.5 wk. Replicates (with matched controls) were removed from the experiment prior to its conclusion in the rare case that more than one-third of the initial algal wet mass was lost. In the few instances where replicates were removed before Day 5 of the experiment, they were excluded from the final data analysis, as these blades were assumed to be in a state of decline prior to the start of the experiment. We repeated this experiment in 2007 with identical methods. To determine if higher densities or different size classes of *I. obsoleta* have a different effect on *U. lactuca* biomass, we conducted 4 additional experiments using the following numbers and sizes of *I. obsoleta*: 6 juveniles 10–14 mm in length, 12 juveniles 10–14 mm, 5 adults >14 mm, and 12 recruits <10 mm. Each combination had 10 replicates with an equal number of non-herbivore controls; all other methods were the same as those used in the initial non-choice assay. Following the conclusion of these experiments, 29 of the snails (25 juveniles and 4 adults) were haphazardly chosen for gut content analysis. These snails were placed in ethanol and transferred to the laboratory, where we extracted their gut contents and determined their composition using light microscopy.

In addition, due to our field observations that *Ilyanassa obsoleta* is present on washed up algae during low tide, we also assessed whether *I. obsoleta* would consume *Ulva lactuca* under low tide conditions. Low tide was simulated every other day for 4 h by lowering the water level in the tanks from 10 to 1 cm. We used 3 *I. obsoleta* in each of 10 replicates, with an equal number of controls; initial and final wet mass for each replicate was measured as previously described. Additionally, we measured the initial and final organic content, calculated as percent ash-free dry mass, of the *U. lactuca* by combusting a portion of each replicate thallus (with a known dry mass) in a muffle furnace for 2 h at 500°C and weighing the resulting mass (Thornber et al. 2006).

As all experiments resulted in increased growth of *Ulva lactuca* in the presence of *Ilyanassa obsoleta* (see 'Results'), we conducted 3 additional manipulative experiments to determine the likely cause(s) of this growth. (1) We tested whether nutrient input via *I. obsoleta* defecation could be the cause of the increased growth in the presence of *I. obsoleta*. We used the same methods described for our initial feeding assays, except that we used 5 l buckets and prevented snail grazing by sequestering the 3 *I. obsoleta* within a small plastic cage with mesh holes in the side, allowing water and nutrient exchange to occur while preventing direct contact between the snails and algae. Caged snails were not provided with an additional food

source. However, feces were present throughout the experiment, indicating that microalgal fouling inside the cages was a sufficient food source. We measured the initial and final wet mass and organic content of each algal piece as described above, as well as the initial and final percentage of nitrogen of algal tissues using a continuous flow, isotope mass spectrometer located at the US EPA Atlantic Ecology Division in Narragansett, Rhode Island.

(2) We tested whether *Ilyanassa obsoleta* contact with the *Ulva lactuca* was responsible for facilitating *U. lactuca* growth, which would indicate a potential influence from *I. obsoleta* saliva or other chemical cues. In this experiment, *U. lactuca* in the herbivore treatment were exposed to snails without grazing by dragging a deshelled *I. obsoleta* body across the length of each blade 20 consecutive times every other day. To ensure that this contact was not damaging the blades or having an effect by removing epiphytic microalgae, we included a contact control treatment where a finger was dragged across each blade 20 consecutive times, replicating the contact from the herbivore treatment. An equal number of unmanipulated controls were run concurrently. Each of the 3 treatments had 15 replicates; initial and final wet mass and organic content were measured as described above.

(3) We conducted 2 experiments to determine if *Ilyanassa obsoleta* were primarily grazing the microalgal films on the *Ulva lactuca* blades, rather than grazing the blades themselves. For the first experiment, forty 100 cm<sup>2</sup> pieces of fiberglass window screening (1 mm<sup>2</sup> mesh) were weighed and placed in seawater tables for 2 wk, to ensure sufficient fouling with microalgae (primarily benthic diatoms). Window screens were then removed from the seawater tables, blotted dry, and weighed to determine the microalgal mass. We then placed 1 screen and 3 *I. obsoleta* into each of 20 replicate buckets, with an equal number of non-herbivore controls. After 2 wk, all screens were removed and again blotted dry and weighed. For the second experiment, to determine if *I. obsoleta* graze microalgae off of *U. lactuca*, we first placed *U. lactuca* in a flow-through seawater tank prior to the start of the experiment to ensure sufficient fouling (transporting blades from the field to the laboratory typically results in the accidental removal of benthic diatoms). We placed a fouled *U. lactuca* thallus with 3 *I. obsoleta* in each of 10 replicate buckets, with an equal number of non-herbivore controls. We calculated the average microalgal wet mass at the start of the experiment by taking 5 additional 10 cm<sup>2</sup> pieces of *U. lactuca* and rinsing them in distilled water to remove the microalgae; microalgal mass was measured by filtering this water through a Whatman 2 filter (8 µm particle retention) with a known mass. After 2 wk, all *U. lactuca*

pieces were removed and the final microalgal wet mass was calculated by rinsing a 10 cm<sup>2</sup> piece of each *U. lactuca* thallus and filtering through a Whatman 2 filter.

We analyzed the results of all paired designed feeding assays using paired *t*-tests or the Wilcoxon paired-sample tests, where appropriate. The experiment for snail contact was analyzed using one-way ANOVA. Organic content and % nitrogen were analyzed using repeated measures ANOVAs. When we performed multiple tests, we adjusted *p*-values using the multi-stage procedure (Rice 1990). All statistical analyses were conducted with JMP v.7.0.2 (SAS Institute).

## RESULTS

In our Expts 1 and 2 using 4 juvenile *Ilyanassa obsoleta*, algae in the herbivore treatments grew twice as much as algae in the control treatments (Fig. 1; Expt 1,  $t_{15} = 5.564$ ,  $p < 0.0001$ ; Expt 2 not shown). We obtained similar results when we manipulated snail density and size (Fig. 1; 6 juveniles 10–14 mm in length,  $t_9 = 4.157$ ,  $p = 0.0025$ ; 12 juveniles 10–14 mm,  $t_9 = 6.115$ ,  $p = 0.0002$ ; 5 adults >14 mm,  $t_9 = 3.395$ ,  $p = 0.0079$ ; 12 recruits <10 mm,  $t_9 = 2.641$ ,  $p = 0.0269$ ). Of the 29 mud snails that had their gut contents examined, only 4 contained *U. lactuca* tissue, while 20 of the mud snail guts contained diatoms.

When we simulated low tide, *Ulva lactuca* again grew significantly more in the herbivore treatment than in the control (Fig. 1;  $t_{19} = 3.381$ ,  $p = 0.003$ ). The mean initial organic content of the *U. lactuca* tissue

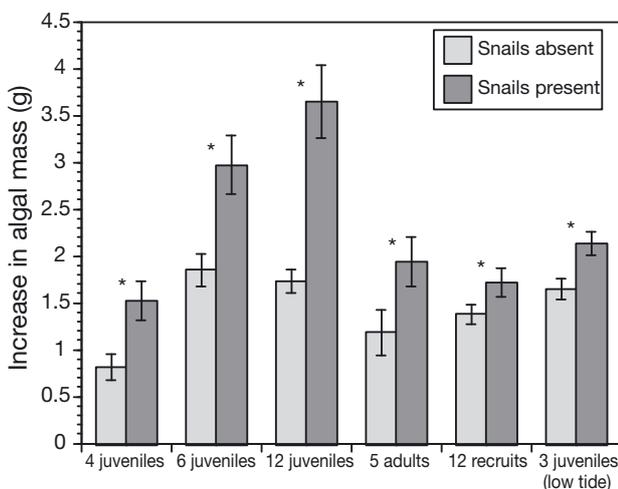


Fig. 1. *Ulva lactuca*. Changes of algal wet mass (means  $\pm$  1 SE) in 6 feeding assays and various densities and size classes of *Ilyanassa obsoleta* (juveniles = 10–14 mm in length, adults >14 mm, recruits <10 mm). All experiments ran for 2 wk.

\*Significant ( $p < 0.05$ ) difference between treatments

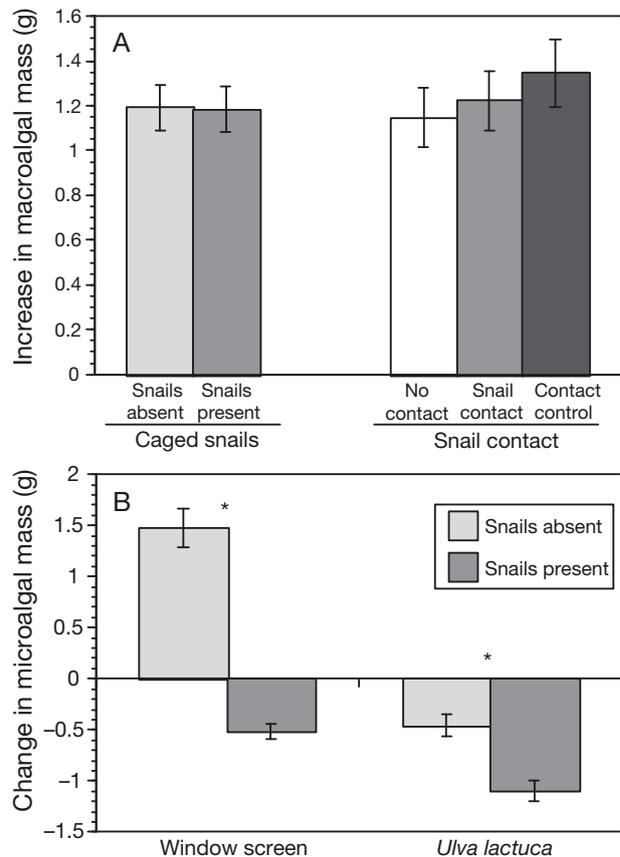


Fig. 2. *Ulva lactuca*. Experiments examining the potential cause(s) of facilitated growth. (A) Changes in macroalgal mass (means  $\pm$  1 SE) in the presence or absence of caged *Ilyanassa obsoleta* and after contact with deshelled *I. obsoleta* bodies or controls. (B) Changes in microalgal wet mass (means  $\pm$  1 SE) in experiments examining *I. obsoleta* consumption of microalgae grown on window screen and *U. lactuca*. \*Significant ( $p < 0.05$ ) difference between treatments

was 73.34%; it did not change significantly over the course of the experiment ( $F_{1,38} = 0.00002$ ,  $p = 0.98$ ).

Increased growth rates of experimental thalli disappeared when we caged the snails within our buckets; we found no significant difference in *Ulva lactuca* growth between treatments with and without caged snails (Fig. 2A;  $W = 6.50$ ,  $p = 0.79$ ). While organic content of *U. lactuca* increased significantly from the start to the end of the experiment ( $F_{1,32} = 4.89$ ,  $p < 0.0001$ ; Table 1), there was no significant difference in the increase in organic content between treatments ( $F_{1,32} = 1.13$ ,  $p = 0.29$ ). Nitrogen content decreased significantly from the start to the end of the experiment ( $F_{1,32} = 1.44$ ,  $p < 0.0001$ ; Table 1); there was no significant difference in the decrease in % nitrogen between treatments ( $F_{1,32} = 0.45$ ,  $p = 0.5$ ), indicating the algae did not respond to nutrients released by snail feces.

Table 1. *Ulva lactuca*. Percent organic content and percent nitrogen for the experiment examining nitrogen inputs by caged *Ilyanassa obsoleta*. Values are means  $\pm$  1 SE

Snails	Organic content (%)			Nitrogen (%)		
	Initial	Final	$\Delta$	Initial	Final	$\Delta$
Absent	61.79 $\pm$ 1.30	73.65 $\pm$ 0.63	11.87 $\pm$ 1.94	1.59 $\pm$ 0.083	1.16 $\pm$ 0.032	-0.41 $\pm$ 0.091
Present	61.79 $\pm$ 1.30	71.09 $\pm$ 0.76	9.30 $\pm$ 1.22	1.59 $\pm$ 0.083	1.07 $\pm$ 0.020	-0.49 $\pm$ 0.096

We also found no significant difference in *Ulva lactuca* growth among treatments in the mud snail contact experiment (Fig. 2A;  $F_{2,42} = 0.68$ ,  $p = 0.51$ ), indicating that snail contact alone does not trigger increased algal tissue growth. Organic content in this experiment decreased significantly from the start to the end of the experiment by  $\sim 8\%$  ( $F_{1,42} = 2.06$ ,  $p < 0.0001$ ); this decrease did not differ significantly among the treatments ( $F_{2,42} = 2.54$ ,  $p = 0.09$ ).

By contrast, we found a 2-fold decrease in microalgal biomass in the presence of herbivores compared to non-herbivore controls. This was true for substrates of window screening (Fig. 2B;  $t_{19} = 8.73$ ,  $p < 0.0001$ ) as well as *Ulva lactuca* blades (Fig. 2B;  $t_9 = -5.54$ ,  $p = 0.0004$ ). The reduction of microalgal wet mass on *U. lactuca* in both treatments is likely the result of spinning the algae to remove excess water prior to obtaining the final *U. lactuca* wet mass, as diatom removal occurred following this step. However, microalgal wet mass had a significantly greater decrease in the treatment with herbivores.

## DISCUSSION

Increased plant growth resulting from light to moderate herbivory is a common phenomenon in terrestrial plants and occurs due to a wide variety of mechanisms including overcompensation in response to grazer damage, nutrient additions via grazer defecation, and the removal of neighboring competitors (McNaughton 1983, Agrawal 2000). Herbivores can also positively affect macroalgal growth through the addition of nutrients (Fong et al. 1997) and, in a situation similar to the removal of neighboring competitors, grazers can preferentially remove epiphytes that grow on algal blades (Dudley 1992, Littler et al. 1995, Kamermans et al. 2002, Jormalainen et al. 2003, Råberg & Kautsky 2008). In our study, *Ulva lactuca* growth was greatest when snails grazed directly on the blades; this was true for experiments that simulated subtidal and low tide conditions. We found no evidence for increased *U. lactuca* growth from snail contact alone. The facilitation we observed was neither due to the mud snails' nitrogenous wastes, since growth rate differences disap-

peared when mud snails were present but restricted from grazing on the blades. In addition, analyses showed no differences in tissue content between algae in the herbivore and control treatments, indicating that the algae were not storing the nitrogen for future growth. An alternative explanation for these results is that the rate of snail defecation was insufficient to raise nitrogen levels in the caged treatments. However, even though snail diets were not supplemented with additional food, we believe this is an unlikely possibility given that snail feces were present each time the buckets were removed from the seawater tanks to measure algal wet mass, which occurred every 3 to 4 d.

The observed algal growth is most likely caused by the removal of the microalgal films that are typically found growing on the *Ulva lactuca* blades. Our results clearly show that *Ilyanassa obsoleta* prefer to graze these microalgae rather than consume the *U. lactuca* blades directly; in both experiments where microalgal biomass was measured, it was significantly lower when the snails were present. Given that mud snails are primarily deposit feeders and have been observed to graze across *U. lactuca* blades in the field, their consumption of the fouling microalgae is not entirely surprising. What is unexpected is that, despite being capable of consuming *U. lactuca* tissue (Scheltema 1964, Curtis & Hurd 1981, Giannotti & McGlathery 2001, present study), *I. obsoleta* preferentially consume the microalgae on the *U. lactuca* blades to the extent that they have a positive effect on *U. lactuca* growth. Similarly, Kamermans et al. (2002) observed an increase in *U. lactuca* growth in the presence of amphipods that consumed diatom films. Increased growth of *U. expansa* was also observed in the presence of horn snail grazing by Fong et al. (1997), who attributed this to horn snail movement within the sediment layer releasing nitrogen to the water column. However, the researchers also observed that the snails were not consuming the *U. expansa*, but were grazing over the surface of the blade and the tank, assumingly consuming the microalgal and bacterial films growing on these surfaces. Positive grazer effects due to epiphyte removal have also been found for the freshwater green alga *Cladophora glomerata* (Dudley 1992), the brown alga *Fucus vesiculosus* (Jormalainen et al. 2003,

Råberg & Kautsky 2008), the red coralline algae *Porolithon pachydermum* (Littler et al. 1995) and *Neogoniolithon strictum* (Stachowicz & Hay 1996), and a variety of seagrass species (Hughes et al. 2004, Heck & Valentine 2006).

In our experiments, while gut contents indicated that *Ilyanassa obsoleta* occasionally consume *Ulva lactuca*, the presence of *I. obsoleta* still significantly increased *U. lactuca* growth. In contrast, Giannotti & McGlathery (2001) observed that *I. obsoleta* consumed significant amounts of *U. lactuca* biomass. Differences in experimental design may explain this discrepancy, as Giannotti & McGlathery (2001) placed sediment in the bottom of their replicates. We did not use sediment in our replicate buckets so that we could mimic the interaction of *I. obsoleta* grazing on floating and washed up algal mats, where the snails do not have direct access to the sediment surface (however, grazing experiments using these species with sediment present have yielded similar findings to ours; A. Tyler pers. comm.). The difference in our findings may also reflect population or species-level differences between Rhode Island and Virginia mud snails and/or *Ulva*. Regardless of the source of this discrepancy, since our results are consistent across 3 summers, different mud snail densities, and treatments simulating subtidal and intertidal conditions, we conclude our results demonstrate a real, positive effect of *I. obsoleta* grazing on *U. lactuca* blade growth.

Bottom-up forces have long been linked to macroalgal blooms (Nixon 1995, Fletcher 1996, Valiela et al. 1997). Our results suggest that the top-down effects of herbivores may also contribute to the excessive growth observed during macroalgal bloom events. While top-down effects are not traditionally thought of as having large positive effects in eutrophic areas, similar positive top-down effects have been observed in seagrass systems. Several seagrass studies that have simultaneously manipulated nutrient levels and mesograzer abundance have found that mesograzers can control epiphyte fouling, even at high nutrient levels (Neckles et al. 1993, Williams & Ruckelshaus 1993, Heck et al. 2000). Seagrass habitats also serve as a model system, highlighting the complexities of plant–epiphyte–grazer relationships that likely occur in other ecosystems, including algal bloom communities. Studies that have examined the effects of more than one mesograzer species on seagrass fouling have found that the impact of each individual species is not always the same as the impact of the species combined (Jernakoff & Nielson 1997, Duffy et al. 2001, Duffy & Harvilicz 2001). The outcomes of these interactions become even more complex as higher trophic levels are added (Heck et al. 2006). We conclude that the positive impact of *Ilyanassa obsoleta* grazing on *Ulva lactuca* growth, coupled with the high densities of mud snails

at sites where blooms occur, may act to exacerbate bloom severity and persistence. However, field studies are needed to determine the exact effects of *I. obsoleta* grazing within bloom communities.

**Acknowledgements.** Funding for this study was provided by Bay Window (NOAA), RI DEM, RI Sea Grant, and the University of Rhode Island. We thank J. Burkhardt and A. Viveiros for their help in the laboratory, R. McKinney with US EPA Atlantic Ecology Division for use of a mass spectrometer, and E. Preisser, N. Rohr, P. Steinberg and 3 anonymous reviewers for reviewing previous versions of this manuscript.

#### LITERATURE CITED

- Agrawal AA (2000) Overcompensation of plants in response to herbivory and the by-product benefits of mutualism. *Trends Plant Sci* 5:309–313
- Bazely DR, Jefferies RL (1985) Goose faeces: a source of nitrogen for plant growth in a grazed salt marsh. *J Appl Ecol* 22:693–703
- Crisp M (1969) Studies on the behavior of *Nassarius obsoleta* (Say) (Mollusca, Gastropoda). *Biol Bull (Woods Hole)* 136:355–373
- Curtis LA (1980) Daily cycling of the crystalline style in the omnivorous, deposit-feeding estuarine snail *Ilyanassa obsoleta*. *Mar Biol* 59:137–140
- Curtis LA, Hurd LE (1981) Nutrient procurement strategy of a deposit-feeding estuarine neogastropod, *Ilyanassa obsoleta*. *Estuar Coast Shelf Sci* 13:277–285
- Curtis LA, Hurd LE (1983) Age, sex, and parasites: spatial heterogeneity in a sandflat population of *Ilyanassa obsoleta*. *Ecology* 64:819–828
- Deacutis C, Oviatt CA (2004) Eutrophication in Narragansett Bay. 41°N 3:10–11
- Dudley TL (1992) Beneficial effects of herbivores on stream macroalgae via epiphyte removal. *Oikos* 65:121–127
- Duffy JE, Harvilicz AM (2001) Species-specific impacts of grazing amphipods in an eelgrass-bed community. *Mar Ecol Prog Ser* 223:201–211
- Duffy J, MacDonald KS, Rhode JM, Parker JD (2001) Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test. *Ecology* 82:2417–2434
- Dyer MI, Moon AM, Brown MR, Crossley DA (1995) Grasshopper crop and midgut extract effects on plants: an example of reward feedback. *Proc Natl Acad Sci USA* 92:5475–5478
- Edwards SF, Welsh BL (1982) Trophic dynamics of a mudsnail [*Ilyanassa obsoleta* (Say)] population on an intertidal mud flat. *Estuar Coast Shelf Sci* 14:663–686
- Fletcher RL (1996) The occurrence of green tides—a review. In: Schramm W, Niehuis PK (eds) *Marine benthic vegetation: recent changes and the effects of eutrophication*. Springer, Berlin, p 7–43
- Fong P, Desmond JS, Zedler JB (1997) The effect of a horn snail on *Ulva expansa* (Chlorophyta): consumer or facilitator of growth? *J Phycol* 33:353–359
- Geertz-Hansen O, Sand-Jensen K, Hansen DF, Christiansen A (1993) Growth and grazing control of abundance of the marine macroalga, *Ulva lactuca* L. in a eutrophic Danish estuary. *Aquat Bot* 46:101–109
- Giannotti A, McGlathery K (2001) Consumption of *Ulva lactuca* (Chlorophyta) by the omnivorous mud snail *Ilyanassa obsoleta* (Say). *J Phycol* 37:209–215

- Granger SL, Mark J, Buckley BA, Schwartz M (2000) An assessment of eutrophication in Greenwich Bay, Vol 1. Rhode Island Sea Grant, Narragansett, RI
- Gronemeyer PA, Dilger BJ, Bouzat JL, Paige KN (1997) The effects of herbivory on paternal fitness in scarlet gilia: better moms also make better pops. *Am Nat* 150:592–602
- Hauxwell J, McClelland J, Behr PJ, Valiela I (1998) Relative importance of grazing and nutrient controls of macroalgal biomass in 3 temperate shallow estuaries. *Estuaries* 21: 347–360
- Hauxwell J, Cebrian J, Furlong C, Valiela I (2001) Macroalgal canopies contribute to eelgrass (*Zostera marina*) decline in temperate estuarine ecosystems. *Ecology* 82:1007–1022
- Heck KL Jr, Valentine JF (2006) Plant–herbivore interactions in seagrass meadows. *J Exp Mar Biol Ecol* 330:420–436
- Heck KL, Pennock JR, Valentine JF, Coen LD, Sklenar SA (2000) Effects of nutrient enrichment and small predator density on seagrass ecosystems: an experimental assessment. *Limnol Oceanogr* 45:1041–1057
- Heck KL Jr, Valentine JF, Pennock JR, Chaplin G, Spitzer PM (2006) Effects of nutrient enrichment and grazing on shoalgrass *Halodule wrightii* and its epiphytes: results of a field experiment. *Mar Ecol Prog Ser* 326:145–156
- Horne A, McClelland J, Valiela I (1994) The growth and consumption of macroalgae in estuaries: the role of invertebrate grazers along a nutrient gradient in Waquoit Bay, Massachusetts. *Biol Bull (Woods Hole)* 187:279–280
- Hughes AR, Bando KJ, Rodriguez LF, Williams SL (2004) Relative effects of grazers and nutrients on seagrasses: a meta-analysis approach. *Mar Ecol Prog Ser* 282:87–99
- Jernakoff P, Nielson J (1997) The relative importance of amphipod and gastropod grazers in *Posidonia sinuosa* meadows. *Aquat Bot* 56:183–202
- Jormalainen V, Honkanen T, Koivikko R, Eränen J (2003) Induction of phlorotannin production in a brown alga: defense or resource dynamics? *Oikos* 103:640–650
- Kamermans P, Malta EJ, Verschuure JM, Schrijvers L, Lentz LF, Lien ATA (2002) Effect of grazing by isopods and amphipods on growth of *Ulva* spp. (Chlorophyta). *Aquat Ecol* 36:425–433
- Korpinen S, Jormalainen V, Honkanen T (2007) Effects of nutrients, herbivory, and depth on the macroalgal community in the rocky sublittoral. *Ecology* 88:839–852
- Lennartsson T, Tuomi J, Nilsson P (1997) Evidence for an evolutionary history of overcompensation in the grassland biennial *Gentianella campestris* (Gentianaceae). *Am Nat* 149:1147–1155
- Littler MM, Littler DS, Taylor PR (1995) Selective herbivory increases biomass of its prey: a chiton–coralline reef-building association. *Ecology* 76:1666–1681
- Lotze HK, Worm B (2000) Variable and complementary effects of herbivores on different life stages of bloom-forming macroalgae. *Mar Ecol Prog Ser* 200:167–175
- Lotze HK, Worm B, Sommer U (2001) Strong bottom-up and top-down control of early life stages of macroalgae. *Limnol Oceanogr* 46:749–757
- McNaughton SJ (1979) Grazing as an optimization process: grass-ungulate relationships in the Serengeti. *Am Nat* 113:691–703
- McNaughton SJ (1983) Compensatory plant growth as a response to herbivory. *Oikos* 40:329–336
- McNaughton SJ (1997) Promotion of the cycling of diet-enhancing nutrients by African grazers. *Science* 278: 1798–1800
- Neckles H, Wetzel R, Orth R (1993) Relative effects of nutrient enrichment and grazing on epiphyte-macrophyte (*Zostera marina* L.) dynamics. *Oecologia* 93:285–295
- Nelson TA, Lee DJ, Smith BC (2003) Are 'green tides' harmful algal blooms? Toxic properties of water-soluble extractions from two bloom-forming macroalgae, *Ulva fenestrata* and *Ulvaria obscura* (Ulvophyceae). *J Phycol* 39: 874–879
- Nelson TA, Haberlin K, Nelson AV, Ribarich H and others (2008) Ecological and physiological controls of species composition in green macroalgal blooms. *Ecology* 89: 1287–1298
- Nixon S (1995) Coastal marine eutrophication: a definition, social causes, and future concerns. *Ophelia* 41:199–219
- Nolet BA (2004) Overcompensation and grazing optimisation in a swan–pondweed system? *Freshw Biol* 49:1391–1399
- Paige KN (1999) Regrowth following ungulate herbivory in *Ipomopsis aggregata*: geographic evidence for overcompensation. *Oecologia* 118:316–323
- Råberg S, Kautsky L (2008) Grazer identity is crucial for facilitating growth of the perennial brown alga *Fucus vesiculosus*. *Mar Ecol Prog Ser* 361:111–118
- Raffaelli DG, Raven JA, Poole LA (1998) Ecological impact of green macroalgal blooms. *Oceanogr Mar Biol Annu Rev* 36:97–125
- Rice WR (1990) A consensus combined p-value test and the family-wide significance of component tests. *Biometrics* 46:303–308
- Scheltema RS (1964) Feeding habits and growth in the mud-snail *Nassarius obsoletus*. *Chesapeake Sci* 5:161–166
- Stachowicz JJ, Hay ME (1996) Facultative mutualism between an herbivorous crab and a coralline alga: advantages of eating noxious seaweeds. *Oecologia* 105:377–387
- Thornber C, Stachowicz JJ, Gaines S (2006) Tissue type matters: selective herbivory on different life history stages of an isomorphic alga. *Ecology* 87:2255–2263
- Valentine JF, Heck KL, Busby J Jr, Webb D (1997) Experimental evidence that herbivory increases shoot density and productivity in a subtropical turtlegrass (*Thalassia testudinum*) meadow. *Oecologia* 112:193–200
- Valiela I, McClelland J, Hauxwell J, Behr PJ, Hersh D, Foreman K (1997) Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. *Limnol Oceanogr* 42:1105–1118
- Williams SL, Ruckelshaus MH (1993) Effects of nitrogen availability and herbivory on eelgrass (*Zostera marina*) and epiphytes. *Ecology* 74:904–918
- Worm B, Lotze HK (2006) Effects of eutrophication, grazing, and algal blooms on rocky shores. *Limnol Oceanogr* 51:569–579

Editorial responsibility: Peter Steinberg,  
Sydney, New South Wales, Australia

Submitted: August 5, 2010; Accepted: October 25, 2010  
Proofs received from author(s): December 7, 2010