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Do snails facilitate bloom-forming macroalgae in a eutrophic estuary?

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ABSTRACT

Blooms of macroalgae are one of the most visible and problematic results of eutrophication-driven estuarine degradation because they can smother seagrass, obstruct fishing, and close beaches to tourism. Not surprisingly, high densities of herbivores are commonly associated with these blooms. Invertebrates in other systems can facilitate macrophyte growth under equilibrium conditions by releasing nutrients or reducing competitors. Based on laboratory experiments it has been suggested that the omnivorous snail *Ilyanassa obsoleta* likewise facilitates bloom-forming macroalgae in estuaries of the Northeastern US. If snails enhance macroalgal blooms as suggested, it would have broad implications for nutrient retention and cycling in estuaries. We tested whether snails actually do facilitate macroalgal blooms in a natural setting through community surveys, laboratory incubations, and field experiments. We confirmed in our surveys that snail densities were positively correlated with macroalgal biomass, and in laboratory incubations that snail excreta enhanced macroalgal growth and that snail activity mobilized sediment nutrients and enhanced sediment–water column coupling. Snails thus have the potential to influence nutrient recycling and retention. However, snails did not facilitate macroalgal growth in our field manipulations of snails and bloom-forming macroalgae along an estuarine eutrophication gradient. Macroalgal growth in our experiment was highly variable across the estuarine gradient and through the growing season, suggesting that large-scale variation in physical factors such as nutrients, light, or temperature plays the dominant role in limiting macroalgal blooms. The departure of our field results from predictions of laboratory studies reinforces previous warnings that laboratory experiments can be useful tools for elucidating mechanisms that drive field patterns, but are not a substitute for field experiments where they are possible. While snails do not appear to directly influence macroalgal growth, we suggest that the potential influence of snails on benthic metabolism and nutrient cycling demands further investigation in the field.

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1. Introduction

Estuaries are among the most valuable ecosystems in the world, supporting productive fisheries, providing tourist revenue, and acting as filters of terrestrial run-off (Barbier et al., 2011). Despite these benefits, estuaries are among the most threatened of all marine habitats due to a combination of human impacts (Breitburg et al., 2009; Halpern et al., 2008; Lotze et al., 2006). Eutrophication is arguably the greatest problem currently facing estuaries (Bricker et al., 2007; Cloern, 2001), with a doubling of anthropogenic nitrogen (N) inputs from 1961 to 1997 (Howarth et al., 2002). In shallow estuaries where N is typically the limiting nutrient (Howarth and Marino, 2006), excess N loading often leads to macroalgal blooms that in turn create a variety of detrimental changes to community composition and ecosystem processes (McGlathery et al., 2001; Nixon et al., 2001; Valiela et al., 1997). For example, macroalgae can smother and replace rooted plants, such as seagrasses, that obtain nutrients from the sediment (Hauxwell et al., 2001; McGlathery, 2001; Thomsen et al., 2012). When the macroalgal blooms crash, decomposition by aerobic microorganisms depletes dissolved oxygen leading to the creation of dead zones and associated fish kills (Raffaelli et al., 1998; Soulsby et al., 1982). Macroalgal blooms also cause economic damage by inhibiting fishing and aquaculture activities, prompting beach closures and impacting other recreational activities (Raffaelli et al., 1998; Valiela et al., 1997). These negative consequences have made understanding the factors that trigger and maintain macroalgal blooms an urgent priority for conservation and management of coastal ecosystems. While strategies to reduce external nutrient sources are essential, further investigation of internal nutrient sources is needed to gain a deeper understanding of N dynamics in shallow coastal systems, as internal nutrient recycling may be sufficient to fuel macroalgal growth in the absence of external loading (Kamer et al., 2004; Sundback et al., 2003; Tyler et al., 2003).

Can herbivores facilitate the formation or maintenance of macroalgal blooms? High densities of some macroinvertebrates have been observed in association with bloom forming macroalgae (Fong et al., 1997; Guidone et al., 2010), and it has been recently suggested that

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these numerous herbivores may be facilitating blooms rather than simply opportunistically grazing on the abundant macroalgal biomass (Guidone et al., 2010, 2012; McLenaghan et al., 2011). There is a body of research that suggests herbivore facilitation of macroalgal blooms might be possible since grazers can have the paradoxical effect of enhancing growth of macroalgae under equilibrium (non-bloom) conditions by three possible mechanisms. First, herbivores can fertilize algae by recycling nutrients through consumption and excretion (Bracken, 2004; Hurd et al., 1994; Pfister, 2007; Taylor and Rees, 1998; Williamson and Rees, 1994). Although these findings come primarily from studies of isolated tidepools where herbivores and algae would be expected to be tightly coupled, there is recent evidence that the fertilizer effect can be important on emergent rock surfaces in wave exposed areas (Aquilino et al., 2009). Second, herbivores may facilitate macroalgae by selectively grazing on the epiphytes that would otherwise compete with macroalgae for nutrients and light (Duffy, 1990; Guidone et al., 2010; Raberg and Kautsky, 2008). Finally, in soft-bottomed environments, surface deposit-feeding gastropods can impact nutrient cycling, benthic microalgae, and oxygenation of surface sediment (Ieno et al., 2006; McLenaghan et al., 2011; Pillay et al., 2009; Premo, 2011; Weerman et al., 2011). By removing benthic microalgae, "bull-dozing" sediments, or otherwise altering the redox status at the sediment surface, snails can promote benthic–pelagic coupling by increasing the efflux of N mineralized in the sediments to the water column where it is presumably available for uptake by macroalgae (Ieno et al., 2006; McLenaghan et al., 2011; Raffaelli, 2006). If snails did enhance macroalgal blooms by one of these mechanisms, as suggested, it would have broad implications for nutrient retention and cycling in estuaries.

Working with one of the worst offending bloom-forming macroalgae of the Northern Atlantic (*Ulva spp.*) and one of the dominant benthic invertebrates associated with those blooms (the snail *Ilyanassa obsoleta*), Guidone et al. (2010) found that snails facilitated growth of macroalgae under laboratory conditions. Through a clever set of experiments, they further deduced that snails facilitated *Ulva* growth in the laboratory by both fertilizing with nitrogenous waste and removing epiphytic competitors, and that the dominant mechanism differed between the recently differentiated *Ulva* species *Ulva compressa* and *Ulva lactuca* (Guidone et al., 2012). Their assertion that snails could facilitate macroalgal blooms seemed bolstered by contemporary laboratory work with the same species which similarly found that *Ulva* fared better in the presence of the snails associated with increased N flux to the water column (McLenaghan et al., 2011). Likewise, earlier work by Fong and Desmond (1997) found that a Pacific species of bloom-forming *Ulva* could derive significant nutrient resources from co-occurring snails. Regardless of the facilitation pathways, the prediction of these laboratory studies is that co-occurring snails will exacerbate blooms of nuisance macroalgae.

However, evidence for actual facilitation of *Ulva* growth in the field has been inconclusive at best. A study in an eastern North Atlantic estuary found that *Ulva* grew better in large-mesh cages than in small-mesh cages (Kamermans et al., 2002). This effect was attributed to grazing of epiphytes by amphipods and isopods which could enter the large-mesh cages but not small-mesh cages, however the abundance of grazers was not directly manipulated nor quantified in the cages, and the potential artifacts associated with different mesh sizes cannot be ruled out. On the other side of the Atlantic, Thomsen and McGlathery (2005) found higher abundance of *Ulva* in association with tube-building worms, but attributed this positive association to anchoring of *Ulva* thalli against tidal movement, and although they hypothesized growth could be enhanced, they did not quantify growth. Guidone et al. (2012) directly tested the predictions of their laboratory facilitation results in the field, but they found no effect of snails on *Ulva* growth. Perhaps the lack of effect was due to the small size of their experimental units (just 3 snails and one *Ulva* blade in a 0.67 L cage), but they largely attributed the lack of effect to the direct or indirect consequences of lack of nutrient limitation at their eutrophic Narragansett Bay field site.

To test the general hypothesis that invertebrates can facilitate the growth of bloom-forming algae in a natural setting, we conducted experiments using *Ulva* spp. and the snail *Ilyanassa* since the best evidence for facilitation comes from laboratory work with these species. We used a multifaceted approach to test the following specific hypotheses. First, we conducted community surveys to test the hypothesis that there is a positive association between macroalgal biomass and snail abundance under bloom conditions. Second, we conducted laboratory experiments to test the hypothesis that snails can increase the availability of nutrients and macroalgal growth under laboratory conditions. Third, we conducted manipulations of snails along a eutrophication gradient to test the complimentary hypotheses that snails enhance growth of *Ulva* in the natural estuary setting, and that their facilitation is contingent on background nutrient concentrations.

2. Materials and methods

2.1. Site description

We conducted our study in West Falmouth Harbor, Cape Cod, USA (WFH; 41° 36′ N, 70° 38′ W) which is an 80 hectare enclosed polyhaline estuary (salinity range 20–30 psu), with a tidal range of 1.5 m and an average depth of 0.6 m at mean low water (Howes et al., 2006). There are three primary basins in WFH: Inner Harbor (also known as Snug Harbor), South Harbor, and Outer Harbor (Fig. 1). A localized plume of wastewater-contaminated groundwater entering the innermost embayment of the harbor has created a gradient of eutrophication across WFH (Howes et al., 2006). As a result of this contamination, the N loading to the Inner Harbor is roughly four times that to the Outer Harbor (Howarth et al., in press). We established study sites at opposite ends of this gradient in the Inner Harbor (IH) and South Harbor (SH) because they differ in severity of eutrophication but are similar in other physical aspects including distance from the mouth of the estuary and sediment composition (6% gravel, 67% sand, 27% mud IH versus 3% gravel, 76% sand, 21% mud SH; Scheiner, 2011). The Inner Harbor has more severe symptoms of eutrophication including opportunistic macroalgal growth (McGlathery et al. unpub. data, Tyler et al. unpub. data) and higher sediment organic matter (OM, 7.0%; Scheiner, 2011) than the South Harbor, which has lower macroalgal biomass and half the sediment OM (3.2%; Scheiner, 2011).

2.2. Community survey of algae and snail abundance

We quantified the co-occurrence of *I. obsoleta* and *Ulva* in the IH and SH in June, during the peak bloom period, and again in July following the peak. We counted all snails and collected all macroalgae within 30 replicate 0.25 m^2 quadrats haphazardly placed at a similar depth and distance from shore at each study site during each period. Macroalgal wet biomass from each quadrat was determined after patting each frond dry with a paper towel. The relationship between macroalgal biomass and snail density was assessed with linear regression and the effect of month and site on snail density was assessed using two-way ANOVA. All data were analyzed with JMP version 10.0.

2.3. Control of nutrient availability by snails in the laboratory

To examine the effect of *I. obsoleta* on nutrient availability, we conducted two experiments: the first to quantify nutrient released directly by snail through their excreta, and the second to examine the indirect effect of snails on the release of nutrients from sediments.

We conducted the first experiment in June 2010 to determine urea, nitrate (NO_3^-), ammonium (NH_4^+) and total dissolved nitrogen (TDN) excretion rates using a modification of Connor (1980) that involves placing snails in sealed containers and measuring the change in solute concentration over time. Because snails from the IH tended to be larger than snails from the SH and potentially had different diets, we conducted

Fig. 1. Aerial image of West Falmouth Harbor study area and surroundings. Image courtesy of the Office of Geographic Information (MassGIS), Commonwealth of Massachusetts, Information Technology Division. The harbor is comprised of three subembayments: the Outer Harbor (OH) which connects to adjacent Buzzards Bay and the South Harbor (SH) and the Inner Harbor (IH), where we conducted our experiments. Experimental sites are noted with stars.

the experiment separately with snails from each basin. Many of the snail shells were coated with a thick layer of microalgae, which was scraped off to prevent microalgal nutrient uptake from confounding excretion rates. Treatments of 0 and 2 snails ($n = 5$ replicates/treatment) were placed in 300 mL BOD bottles that were either left clear or wrapped in aluminum foil to block light and then filled with filtered (0.2 μm) seawater collected from the mouth of WFH.

Initial nutrient samples were taken from the stock filtered seawater and dissolved oxygen (DO) readings (Hach HQ40d® with a LBOD101 probe) were taken from one set of replicates. Final DO readings and nutrient samples were taken from each bottle after 4 h. All water samples were immediately filtered (Gelman Supor® 0.45 μm) into Whirlpak® bags and frozen at −20 °C. NH_4^+ was analyzed according to Solorzano (1969) using the phenol-hypochlorite method. $NO_3^- + NO_2^-$ (hereafter noted as just NO_3^-) and total dissolved nitrogen (TDN) were measured using a Lachat Quikchem 8500® autoanalyzer with cadmium reduction and in-line digestion methods, respectively (Lachat Instruments, 2003). Urea was analyzed using the Goeyens et al. (1998) room temperature modification of the method described by Mulvenna and Savidge (1992). DON was calculated based on the difference between TDN and $NH_4^+ + NO_3^-$. The compound-specific production rate was calculated based on the change in N-species concentration over time for each treatment (0 and 2 snails) in the light and dark. The difference between the change in N concentration between treatments with and without snails, divided by the number of snails, yielded the excretion rate per individual, which was summed over a 24 h period (assuming 14 h light and 10 h dark) to obtain a daily excretion rate. Because there was not a significant difference between sites, or light and dark (one-way ANOVA), all results were pooled for presentation.

In the second experiment, we used microcosm incubations with sediment and *I. obsoleta* followed by measurement of sediment–water column fluxes of N and O_2 to determine the net effect of *I. obsoleta* on water column nutrient availability through direct excretion and indirect stimulation of sediment–water column fluxes. Sediment was collected on June 24, 2010 from both the IH and SH of WFH using a 9.5 cm inner diameter core tube. Sediment stratification was preserved by

sectioning the sediment (0–2, 2–5, 5–10 cm) prior to sieving (1 mm mesh) to remove macrofauna that may vary between cores and have a confounding effect on experimental results. Sections were homogenized separately prior to reconstruction of 8 microcosms from each Harbor in clear polycarbonate core-tubes (ID = 9.5 cm; height = 30 cm). Core bottoms were sealed with rubber stoppers, and microcosms were wrapped in opaque material from the top of the sediment surface to the bottom of the core-tube in order to prevent light penetration along the sides. Microcosms acclimated for 24 days in an indoor flowing seawater table under ambient conditions (salinity = 28–32; temperature = 16–18 °C; light 150–200 μmol photons m^{-2} s^{-1}; light: dark = 14 h:10 h). Unfiltered artificial seawater seeded with natural water was constantly circulated and each microcosm was mechanically bubbled in order to oxygenate the water and prevent the buildup of diffusion gradients at the sediment surface. Previous experiments showed that this method of sediment reconstruction and acclimation recreates natural field conditions with the minimum disturbance to sediment porewater and organic matter concentrations while homogenizing across microcosms and removing unwanted organisms (Tyler unpub. data). Following the acclimation period, 0.7 g of organic matter (as oven dried [60 °C] finely ground macroalgal thalli) was added to simulate deposition of a moderate macroalgal bloom (Hauxwell et al., 1998). The following day, two *I. obsoleta* were added to half of the microcosms from each site and the 31 d incubation period began.

After 31 d, flux measurements were performed according to methods described by Tyler et al. (2001). Microcosms were carefully drained and re-filled with ambient seawater prior to sealing with a clear lid to prevent exchange of gases with the atmosphere. Sampling was performed at 5 time points, spaced at 2-h intervals (0, 2, 4, 6, 8 h). The transition from light to dark occurred at 4 h, after the sample was collected. At each sampling, DO was measured using a Hach LDO-BOD1 oxygen probe. A water sample (50–60 mL) was then removed using a syringe fitted with a 5 cm silicone tube and an equal volume of water with known nutrient concentrations was returned to the microcosm prior to recapping. Nutrient samples were filtered immediately (Gelman Supor®, 0.45 μm) and frozen for later NH_4^+, NO_3^- and urea analyses using the methods described above. Flux rates were calculated based on the change in concentration over time, with a correction for the volume of water removed during sampling (Tyler et al., 2001). Daily flux rates were calculated from the light and dark rates assuming a 14 h light:10 h dark day. Gross primary production (GPP) was calculated based on the difference between the light and dark hourly flux rates. All fluxes were analyzed using a 2-way ANOVA with site and snails as fixed factors, following tests for normality and homogeneity of variance to meet the assumptions of the test. We scaled the per snail excretion rates measured as described above to the equivalent density of snails used in these flux experiments and compared the potential excretion m^{-2} d^{-1} to the difference in measured daily flux rates with and without snails in order to determine the contribution of snail excreta to the measured enhancement of flux rates by snails.

2.4. The growth response of Ulva to nutrient additions in the laboratory

We examined the response of *Ulva* to differing snail mediated nutrient conditions in the lab using two experiments: the first examined the effect of different nitrogen species, including snail excreta, on macroalgal growth, and the second examined the separate and interactive effect of snails and sediment since previous discrepancies between lab and field studies have been attributed to lack of sediment in laboratory studies.

In the first experiment, we used five N fertilization treatments: control (no addition), NH_4^+ addition, NO_3^- addition, urea addition, and snail excreta addition (n = 5 replicates/treatment). Stock solutions for NH_4^+, NO_3^-, urea and phosphate (PO_4^{3-}) were created using ammonium chloride, potassium nitrate, urea, and sodium phosphate tribasic dodecahydrate, respectively. Individual macroalgal fronds (initial weight 0.099 +/− 0.003 g) were grown in 473 mL polyethylene plastic cups containing 100 mL of growth media (USEPA, 2002), substituting artificial seawater for freshwater. The rate of N fertilization for nitrate, ammonium and urea treatments was increased daily assuming a 10% growth rate per day with 4% tissue N content (Cohen and Neori, 1991) and phosphate was added to all treatments in an 8:1 N:P ratio to prevent P limitation. For the snail excreta treatment, a single snail was placed in a cup with 100 mL of growth media for 24 h, after which the snail was removed and a macroalgal thallus from a snail treatment cup was transferred into the cup that had held the snail. This ratio of snail:macroalgae was higher than we observed in the field, but allowed for the evaluation of the growth rate of macroalgae with a quantity of excreta that is consistent across replicates and did not exceed the amount of N added to other treatments (see Results). A control treatment, with no addition of N, was also used. The experiment was conducted in a Caron® Diurnal Incubator set at 20.0 °C with a 14 h:10 h light to dark ratio. Macroalgal wet weight was measured on days 0, 2, 4, 7, and 10 by gently removing thalli from cups, patting drying and returning to original cups after weighing. The specific growth rate was calculated assuming exponential growth based on Pedersen and Borum (1996) and significant treatment differences analyzed using a one-way ANOVA with N source as the fixed factor, differences between treatments were assessed with the Tukey LSD post-hoc test.

In the second experiment, we examined the interactive effects of snails and sediment on macroalgal growth in a microcosm study that crossed presence of *I. obsoleta* and sediment. In microcosms consisting of clear polyethylene microcosms (14 cm tall × 11.6 cm I.D.) containing *Ulva* (4.5 gww), we crossed two levels of snail treatment (with and without snails) with two levels of sediment treatment (with and without sediment) in a fully factorial design (n = 5 replicates per treatment). Surface sediment (0–5 cm) was collected on August 6, 2010 from both the IH and SH in WFH, homogenized and sieved (1 mm). Microcosms for the with-sediment treatments were filled to 4 cm with prepared sediment and to 14 cm with artificial seawater seeded with natural filtered water from WFH. Microcosms for the with-snail treatments received 2 snails. *I. obsoleta* and *Ulva* were collected on August 6, 2010, acclimated in the laboratory for 3 d before adding to microcosms. The shorter acclimation time here was designed for the smaller amount of sediment. Microcosms were covered with a mesh screen to prevent snail escape, randomized and set under full spectrum lights (150–200 μmol photons m^{-2} s^{-1}). Throughout the experiment, each unit was gently bubbled with air for oxygenation and to prevent the build up of diffusion gradients at the sediment surface. Macroalgal biomass was measured on days 0, 7, 14, and 21 and the specific growth rate calculated as described above. Data were analyzed using a two-way repeated measures ANOVA with snails and sediment as fixed factors.

2.5. Test of snail facilitation of Ulva growth in a natural setting

To determine the potential effects of *I. obsoleta* on *Ulva* growth in the field, and to capture the potential for context-dependence of the snail-macroalgae relationship, we conducted an 8 d caging experiment to measure the impact of snail presence on macroalgal growth in both harbors in June and again in July 2010. We installed sixteen cages (>1 m apart) in each harbor that were cubic in shape (30 cm on each side) with tops and sides constructed from 7 mm mesh galvanized hardware cloth. Cages were worked into the sediment by hand so that approximately 15 cm was below the sediment surface (to prevent escape of snails) and 15 cm was above the sediment surface. PVC stakes were driven into the sediment and secured to the outside of two opposing corners of the cages to anchor the cages in place. Macroalgae collected from the IH was placed in each cage (100 g wet weight [gww] in the IH; 50 gww in the SH), and half of the cages were randomly selected for addition of 30 snails for an effective density of 333 snails m^{-2}. Different amounts of macroalgae were used at each

site to reflect ambient macroalgal abundances. Snail densities, based on field abundances (McLenaghan, 2009), were equivalent to those used in laboratory microcosm experiments. The mesh size was small enough to prevent escape of snails, but coarse enough that it did not substantially reduce light levels in the cage (14.8% reduction ± 2.5% SE measured with a LI-COR® LI-192 underwater quantum sensor). At the end of the experiment, all macroalgae were collected from each cage and the growth weight was calculated based on wet weight as decribed above. Results were analyzed using a three-way ANOVA with date, site and presence of snails as fixed factors.

3. Results

3.1. Community survey of algae and snail abundance

Our field measurements of snail density and macroalgal biomass revealed a strong association between the abundance of *I. obsoleta* and biomass of *Ulva* during June bloom conditions in the Inner Harbor (Fig. 2; $R^2 = 0.75$, $p < 0.001$). There was no association between snail abundance and macroalgal biomass after the bloom in the Inner Harbor, or at any time in the South Harbor ($R^2 < 0.02$, $p > 0.46$ all cases). Our surveys also revealed high variability in *Ulva* abundance, with average biomass in the Inner Harbor of 500.5 ± 116.3 (SE) g wet weight m^{-2} (gww m^{-2}) and 54.3 ± 24.6 (SE) gww m^{-2} in June and July, respectively. The maximum Inner Harbor biomass in June of 4249 gww m^{-2} was over 6 times greater than the maximum in July (650 gww m^{-2}). While we did observe *Ulva* in our South Harbor study area in both June and July, it was sufficiently scarce that it was not found within our quadrats. Snail densities were also variable, with a mean density of 270 ± 47 (SE) snails m^{-2} (range = 0–880 snails m^{-2}) in June and 46 ± 25 (SE) snails m^{-2} (range = 0–624 snails m^{-2}) in July after the bloom had dissipated in the Inner Harbor. In the South Harbor, mean snail density in June (644 ± 73 (SE) snails m^{-2}; range = 48–1552 snails m^{-2}) was greater than in July (299 ± 94 (SE) snails m^{-2}; range = 0–1952 snails m^{-2}) and was consistently higher than in the Inner Harbor ($F = 23.19$, df = 1, $p < 0.0001$).

3.2. Control of nutrient availability by snails in the laboratory

In our first laboratory experiment we measured a TDN excretion rate of 15.4 ± 0.9 (SE) μmol N $indiv^{-1}$ d^{-1}, and found that urea and NO_3^- accounted for relatively small proportions (−0.1 ± 0.2 (SE) and 0.7 ± 0.3 (SE) μmol N $indiv^{-1}$ d^{-1} respectively) while NH_4^+ and DON accounted for larger proportions of the TDN excreted (9.0 ± 0.5 (SE) μmol N $indiv^{-1}$ d^{-1} and 6.3 ± 0.8 (SE) μmol N $indiv^{-1}$ d^{-1}, respectively). In the second microcosm experiment to quantify the effect of snails on sediment–water column nutrient flux rates, we found that snails had a positive effect on daily NH_4^+ release from the sediment (df = 1, $F = 9.92$, $p = 0.049$) and that the NH_4^+ flux was greater in the IH than in the SH (df = 1, $F = 4.78$, $p = 0.008$) (Fig. 3, Table 1).

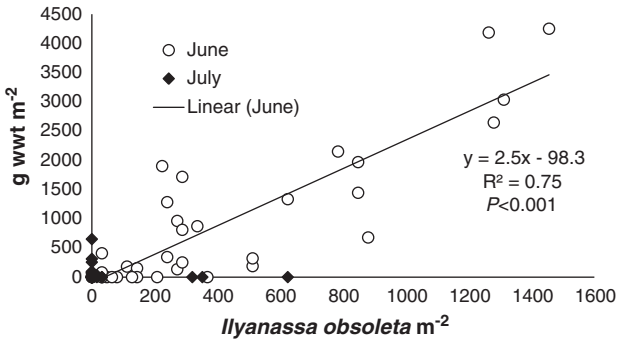

Fig. 2. Snail abundance versus macroalgal biomass in early June and late July 2010 in the Inner Harbor.

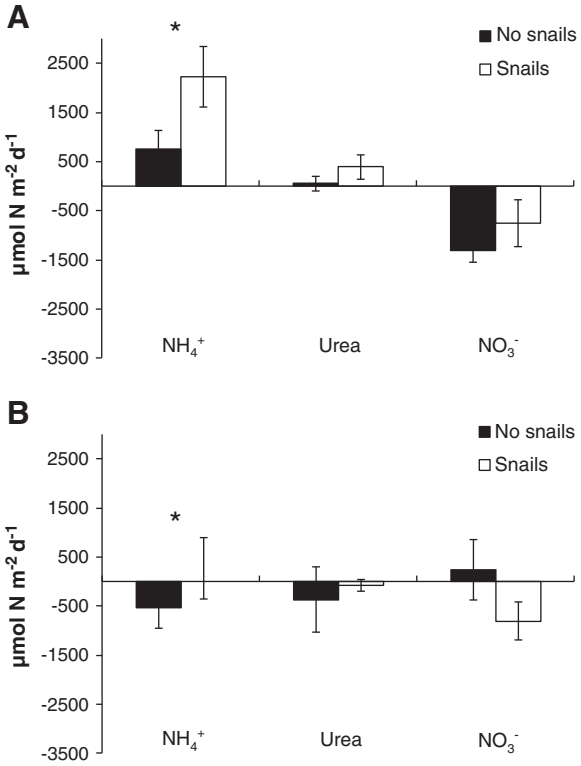

Fig. 3. Daily nitrogen fluxes for NH_4^+, urea, and NO_3^-, with and without snails in Inner Harbor (A) and South Harbor (B) sediments. Positive values indicate a net flux from the sediment to the water column. Significant differences attributed to snail presence are denoted by an "*" ($p < 0.05$). Error bars represent standard error of the mean.

The measured rate of NH_4^+ released in snail excreta (2551 ± 129 (SE) μmol N m^{-2} d^{-1}) was 1.7 times greater than the difference between the snail and no snail treatments for the IH (difference = 1466 μmol N m^{-2} d^{-1}), and 3.2 times greater in the SH (difference = 795 μmol N m^{-2} d^{-1}). None of the comparisons in flux of other N species were significant ($F < 3.2$, $p > 0.100$ all cases).

Net ecosystem metabolism (NEM), based on the daily oxygen flux rate, indicated that the IH was net heterotrophic and that the SH was net autotrophic (Fig. 4) (df = 1, $F = 12.55$, $p = 0.004$). Snails did not have a significant effect on NEM overall, but in the SH reduced the net oxygen production by 80%. GPP was significantly greater in the IH (df = 1, $F = 12.36$, $p = 0.004$), but there was no significant effect of snails (Table 1).

Table 1
Results of a two-way ANOVA of NH_4^+, urea, NO_3^-, GPP, and NEM daily sediment–water column flux rates with site and snails as fixed factors.

	Factor	df	*F*	*P*
NH_4^+	Site	1,15	9.9	0.008
	Snails	1,15	4.8	0.049
	Site × snails	1,15	0.4	0.528
Urea	Site	1,15	1.4	0.253
	Snails	1,15	0.7	0.414
	Site × snails	1,15	0.0	0.944
NO_3^-	Site	1,15	0.3	0.121
	Snails	1,15	0.3	0.600
	Site × snails	1,15	3.2	0.100
GPP	Site	1,15	10.6	0.007
	Snails	1,15	0.9	0.352
	Site × snails	1,15	2.8	0.119
NEM	Site	1,15	12.6	0.004
	Snails	1,15	2.0	0.179
	Site × snails	1,15	1.5	0.239

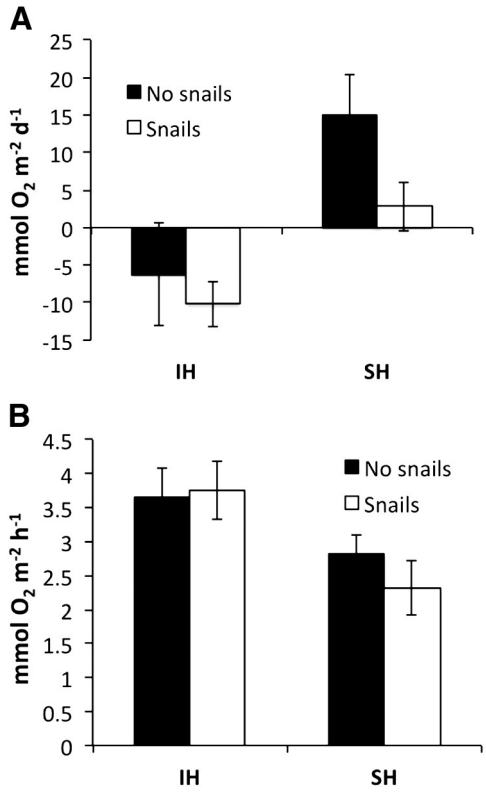

Fig. 4. Net ecosystem metabolism (A) and gross primary production (B) estimated based on measured dissolved oxygen fluxes. Positive values indicate a net flux from the sediment to the water column. Error bars represent standard error of the mean.

3.3. The growth response of Ulva to nutrient additions in the laboratory

In the first nutrient addition experiment in which we tested the ability of *Ulva* to effectively utilize snail excreta relative to other N sources, we found that macroalgae fertilized with snail excreta grew faster than control and NH_4^+, urea, and NO_3^- addition treatments (df = 4, $F = 3.69$, $p = 0.02$) (Fig. 5). For NH_4^+, urea, and NO_3^- addition treatments, 17.1 μmol N was added on day 1 of the experiment, and was increased incrementally to 40.4 μmol N on the final day. Since the amount of N added in the excreta treatment was controlled, but unknown at the time of additions, we standardized our *Ulva* growth measurements in each treatment to a per μmol N added basis using the subsequently determined N concentration in excreta (approximately 9.2 μmol N as NH_4^+, 0 μmol N as urea, 0.8 μmol N as NO_3^-, and 6.4 μmol N as DON were added to the excreta treatments each day). We found that macroalgal growth was still significantly higher in the snail excreta treatment (1.5 ± 0.1 (SE) mg μmol N^{-1}) even when compared to the next highest treatment, which was NH_4^+ (0.7 ± 0.1 (SE) mg μmol N^{-1}) (df = 4, $F = 15.64$, $p < 0.001$).

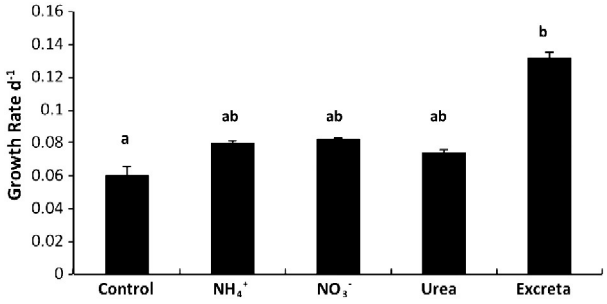

Fig. 5. Specific growth rate of *Ulva* in grams per day in response to control, NH_4^+, NO_3^-, urea, and excreta fertilization treatments. Dissimilar lowercase letters denote significant differences between treatments ($p < 0.05$). Error bars represent standard error of the mean.

In the second experiment in which we measured macroalgal growth rate in the presence and absence of snails and sediment, macroalgal biomass declined in all treatments, and we found that snails had no effect on macroalgal growth (Fig. 6; df = 1, $F = 0.017$, $p = 0.983$). However, macroalgae in the presence of sediment senesced at a significantly higher rate with sediment than without as indicated by significantly lower biomass in treatments with sediment (df = 1, $F = 9.200$, $p = 0.003$).

3.4. Test of snail facilitation of Ulva growth in a natural setting

There was no effect of snails on the specific growth rate of macroalgae in the field (Fig. 7; df = 1, $F = 0.433$, $p = 0.513$). However, there was a significant site × date interaction (df = 1, $F = 5.235$, $p < 0.026$) and post-hoc analysis revealed that growth rate was always higher in the Inner Harbor than South Harbor, and higher in June than July within the Inner Harbor (Fig. 7).

4. Discussion

Despite previous laboratory studies that suggest snails may exacerbate macroalgal blooms by facilitating macroalgal growth, and our own laboratory experiments that found snails could enhance macroalgal growth by excreting nutrients and possibly by releasing sediment nutrients, we found no evidence that snails enhance macroalgal growth in a natural estuary setting. However, we did find large variation in macroalgal growth through time and across sites, indicating that macroalgal growth was sensitive to environmental conditions, and controlled by other large-scale factors. Moreover, the lack of snail effects at the less eutrophic site where macroalgal growth was lower indicates that a lack of snail effects in our study cannot be attributed to an absence of nutrient limitation.

We found that high densities of snails (up to 1465 per m^2) were associated with macroalgal bloom conditions in the eutrophic sub-basin of West Falmouth Harbor, but that densities were even higher in the South Harbor, where *Ulva* was present, but sparse. Because *Ulva* was absent from all samples in the South Harbor, we were unable to adequately test our initial hypothesis of an association between snails and macroalgae in this basin, but have demonstrated that snails may be present in very high densities in the absence of macroalgal mats. These densities rival those observed in other systems such as 1600 per m^2 in Narragansett Bay (Guidone et al., 2012) and exceed observations of Fox et al. (2009) (600 +/− 143 ind. m^{-2}) in nearby Waquoit Bay, Johnson and Short (2013) (748 ind. m^{-2}) in enriched creeks of Plum Island Sound, and Kelaher et al. (2003) (roughly 500 ind. m^{-2}) on Long Island. At these densities, we found that snails have the *potential* to provide limiting nutrients, especially NH_4^+ and DON compounds that enhance macroalgal growth, most likely through a combination of excretion and disturbance of the sediment surface. In

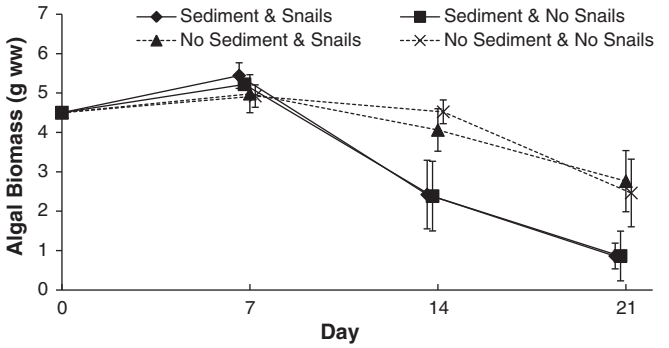

Fig. 6. Macroalgal biomass measurements for treatments with and without snails and sediments. Error bars represent standard error of the mean.

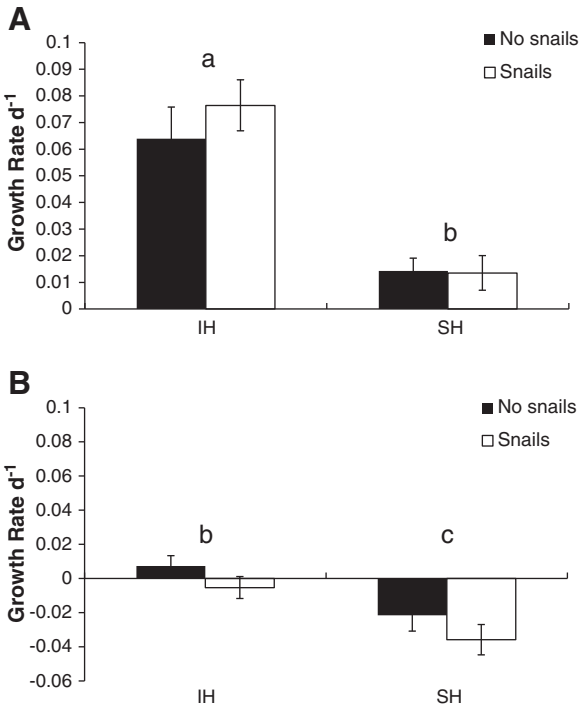

Fig. 7. Specific growth rate (d^{-1}) for caged macroalgae in (A) June and (B) July for the Inner Harbor (IH) and South Harbor (SH) with and without snails. Dissimilar lowercase letters denote significant differences between site*date ($p < 0.05$). There were no snail-driven effects. Error bars represent standard error of the mean.

our laboratory experiments, snails were most frequently observed in and on the sediments, but occasionally on the walls of the chambers. As such, the effects of bioturbation on sediment biogeochemistry may actually be underestimated here relative to the field situation where snails were never observed on the walls of the cages. However, the absence of a snail effect on macroalgal growth in our field experiment suggests that the strong correlation between snail abundance and macroalgal biomass is because macroalgae attracts snails rather than snails boosting macroalgal growth. This is not surprising as there are a number of reasons that snails could be attracted to macroalgae. First, *Ulva* can provide a valuable food resource as living thalli (Giannotti and McGlathery, 2001), epiphytes on thalli (Guidone et al., 2012), or as detritus (Kelaher et al., 2003). Indeed, Premo (2011) found that *I. obsoleta* enhanced the removal of *Ulva* detritus. Further, *I. obsoleta* is consumed by a number of predators, including crabs (Ashkenas and Atema, 1978), predatory moonsnails (Stenzler and Atema, 1977), and some migratory birds (Recher, 1966) and thus macroalgae may provide a predation refuge as it does for other snails (Lubchenco, 1978). However, this doesn't appear to be the case in this instance, as Yarrington (2012) demonstrated no difference in predation losses between the inside and outside of the macroalgal mat. It is also likely that snails are attracted to *Ulva* because it provides a substrate for egg attachment. Eggs were attached to macroalgal thalli and never directly on sediment, and the association between snails and algae in June (but not July) in the Inner Harbor coincides with the peak period of egg laying (Yarrington, 2012).

Why did we find no snail effect in our field experiment despite predictions from laboratory experiments suggesting that it could be important? In the other instance where a study tested *I. obsoleta* facilitation of *Ulva* growth in the field, the lack of facilitation was subsequently attributed to lack of nutrient limitation either because the field experiment was placed at a bloom site where an excess of nutrients swamped any snail-derived nutrients or because the experimental enclosures were not located within a mat of blooming algae where there might be localized nutrient depletion (Guidone et al., 2012). We conducted our experiment to address these potential swamping effects and maximize the potential to detect a facilitation effect in two ways. First, we conducted our experiment across an eutrophication gradient where one site was established within a mat of blooming algae, and second, we repeated the experiment during peak bloom conditions and again post-peak. Although we found large differences between sites and through time, we failed to detect any effect of snails, suggesting that seasonal factors limit growth overall, and that some factor other than nutrients ultimately limits *Ulva* growth. Our field experiments were conducted over a short time period (8 d), and it is possible that the short duration of our experiments limited observation of an effect. But we were able to observe a significant effect of excreta on growth relative to the control in our laboratory experiments after 7 d in our 10 d laboratory fertilization experiment, suggesting that we should have seen the hint of a trend in our field experiments if one were to occur over a longer time scale. We also suggest that the lack of sediments in previous laboratory experiments may have lead to overestimation of the potential importance of snail facilitation. When we crossed sediment with snail presence in mesocosm incubations, we found a consistent negative effect of sediment on macroalgal growth suggesting that the presence of sediment can actually increase the rate of senescence either by facilitating microbial access to senescent tissue, or by competing with *Ulva* for nutrients. This experiment was conducted later in the summer when the macroalgae was in a slower growth phase, but we still observed only an effect of sediment, with no interaction with or main effect of snail presence. Where facilitation was initially observed in the lab, sediment was not included in the mesocosms (Guidone et al., 2010), and when sediment was crossed with snails in the lab (similar to the laboratory portion of our study) sediment had a positive effect on growth of two species of *Ulva* but snails a facilitative effect on just one species (Guidone et al., 2012). However, in the latter study, snails were not given access to the sediment so the interactive effect of snails on sediment biogeochemistry and benthic microalgal growth, observed in McLenaghan et al. (2011) and in our microcosm studies (Fig. 3) was not captured. The high potential contribution of snails to the total N flux through excretion relative to the observed enhancement of the flux in microcosms with snails and sediments, suggests that excreta is rapidly immobilized by the sediment microbial community (bacteria and benthic microalgae). This idea is further developed by the enhancement of benthic microalgae in the presence of low densities of snails, i.e. densities high enough to stimulate growth through fertilization, but low enough not to decimate microbial populations by grazing (Connor, 1980; Premo and Tyler, submitted for publication). Where we observed senescence of macroalgae, rather than growth, both in the laboratory and in the South Harbor in July, nutrients released from decomposing tissue would also have been available to support new growth. As such, nutrients supplied directly by snails would be less important. It should also be noted that other laboratory studies cited as evidence for snail facilitation of bloom-forming *Ulva* found increased uptake of nutrients by the algae (Fong et al., 1997) or slowed decomposition rates (McLenaghan et al., 2011) but failed to detect positive effects on macroalgal *growth*.

Our study and previous publications have focused on the *net* effect of snails on algae. It is entirely possible that snails facilitate growth of macroalgae by providing needed nutrients, or some other mechanisms such as removing epiphytes, but that the facilitative effect is canceled out by a negative effect of snails such as direct grazing or egg-laying on macroalgal thalli. Bruno et al. (2003) remarked on such instances as potentially complicating the search for facilitative interactions but promoting species co-existence. If positive and negative effects of snails on *Ulva* operate in parallel, it could explain why lab and field experiments disagree. Where laboratory experiments have best mimicked field conditions by including both sediment and snails, either facilitation was documented but the snails were kept isolated from the macroalgae and sediments by mesh (Guidone et al., 2012) such that a negative effect of grazing could not have occurred allowing only

facilitation to affect the net outcome of the interactions, or snails were allowed to roam freely but there was no net effect of snails on macroalgal growth (this study). Further, in the nearby Waquoit Bay system, grazers such as amphipods are capable of controlling *Ulv*a growth under low to moderate nutrient loading conditions (Fox et al., 2012). These grazers had free access to the macroalgae in our field experiments and had the potential to compensate for any increase in growth associated with snail-induced fertilization. Thus biological and physical factors that vary in the field, such as the macrofaunal community or temperature fluctuations, but were controlled in the lab, may limit the net effect of snails on macroalgae and lead to the lower growth rates observed in the field relative to the laboratory. Regardless of whether snails do not facilitate macroalgal growth at all, or their facilitative effect is simply neutralized by negative interactions, the lack of a net positive effect in the field suggests that snails are not responsible for exacerbating macroalgal blooms.

Although laboratory experiments can offer a unique avenue for elucidating the mechanisms underlying patterns in nature, we are not the first to argue that field experiments should take precedent over lab experiments (Carpenter, 1996; Skelly, 2002). We suggest that where a given interaction can be examined in the field or laboratory, that the priority should be field observation and experimentation over time periods sufficient to fully characterize the mechanisms within a heterogeneous environment. If facilitation of *Ulva* by *I. obsoleta* occurs only under controlled laboratory conditions, is it ecologically relevant? The association between *I. obsoleta* and blooming *Ulva* is a real and apparently wide-spread pattern worthy of exploring. However, if the field experiments had been conducted first and the lack of facilitation identified, it seems unlikely that the laboratory experiments would ever seem warranted. We suggest that future efforts should be spent understanding what ecological effects snails do have in the field since they clearly have the potential to affect sediment chemistry and mediate water-column nutrients and so likely affect other ecologically relevant variables such as benthic metabolism, decomposition rates and benthic microalgal growth (McLenaghan et al., 2011; Premo and Tyler, submitted for publication). These effects may accelerate system-wide nutrient recycling and impact overall nutrient retention.

The negative effects of eutrophication on macroinvertebrate communities have been thoroughly investigated (Cardoso et al., 2004; Gray, 1989; Pearson and Rosenberg, 1978; Wildsmith et al., 2011). However there are some tolerant species of macroinvertebrates that persist, and potentially thrive in areas experiencing eutrophication (Altieri, 2008; Fox et al., 2009; Johnson and Short, 2013; McLenaghan et al., 2011). *I. obsoleta* is one of these species that appears to increase in abundance under eutrophic conditions (Fox et al., 2009; Johnson and Short, 2013). It is important to understand the ecological role of these remaining, tolerant species in systems undergoing eutrophication as they have the potential to affect N dynamics (McLenaghan et al., 2011) and have a disproportionate effect on sustaining ecosystem services in degraded ecosystems (Altieri, 2008).

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