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**The Interaction Between an Omnivorous Mud Snail and Bloom-Forming
Macroalgae is Context-Dependent in Shallow Estuaries**

by:

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A thesis submitted in partial fulfillment of
the requirement for the degree of
Master of Science

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TABLE OF CONTENTS

Acknowledgements.....	ii
List of Tables & Figures.....	iii
Abstract.....	iv
1. Introduction.....	1
2. Materials & Methods.....	5
2.1. Site Description.....	5
2.2. Macroalgal benefits to <i>Ilyanassa obsoleta</i>	6
2.3. Controls of nutrient availability by <i>Ilyanassa obsoleta</i>	8
2.4. Snail facilitation of macroalgal growth.....	10
3. Results.....	14
3.1. Macroalgal benefits to <i>Ilyanassa obsoleta</i>	14
3.2. Controls of nutrient availability by <i>Ilyanassa obsoleta</i>	15
3.3. Snail facilitation of macroalgal growth.....	16
4. Discussion.....	17
5. Conclusions.....	24
Literature Cited.....	37

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TABLES AND FIGURES

Table 1. Hourly nutrient flux values.....	25
Table 2. Results from three-way ANOVA for hourly fluxes.....	25
Table 3. Results from a two-way ANOVA for daily fluxes.....	26
Figure 1. Diagram of study area and surroundings.....	27
Figure 2. Field survey results in the Inner Harbor and South Harbor in summer 2010	28
Figure 3. Recovery rates for tethered snails and snail density, algal biomass, and number of eggs laid.....	29
Figure 4. Nitrogen excretion by <i>I. obsoleta</i>	30
Figure 5. Daily nitrogen fluxes in sediment microcosms	31
Figure 6. Gross Primary Production and Net Ecosystem Metabolism in sediment microcosms.	32
Figure 7. Algal growth rate in response to nutrient additions.....	33
Figure 8. Algal biomass measurements in response to snail and sediment presence.....	33
Figure 9. Algal growth rates in the Inner Harbor and South Harbor.....	34
Figure 10. Conceptual diagram illustrating different feedback mechanisms in the Inner Harbor and South Harbor.....	35

ABSTRACT

Eutrophication due to anthropogenic nutrient enrichment is the greatest factor leading to estuarine degradation. Even after external nutrient loading has been reduced, internal nutrient recycling has the potential to keep the system in a eutrophic state. In field studies, an association between the Eastern Mud Snail, *Ilyanassa obsoleta* (Say), and the opportunistic green macroalgae *Ulva* sp., has been observed and attributed to the detrital food source associated with the algal mat. In this study, we sought to determine the spatial and temporal context-dependence of this relationship, the reciprocal benefits of the association, and the potential feedbacks to macroalgal bloom formation in shallow coastal systems. In West Falmouth Harbor (WFH), MA, we confirmed the association in the more eutrophic Inner Harbor (IH) during the reproductive period when the macroalgae likely provides valuable oviposition substrate for *I. obsoleta*, but saw no trend in the less-impacted South Harbor (SH) or later in the summer when macroalgal biomass was lower and snails were not reproductive. In a microcosm study using sediments from two sites in WFH, *I. obsoleta* increased NH_4^+ flux to the water column likely due to direct excretion of NH_4^+ and dissolved organic nitrogen and grazing of benthic microalgae that cap the sediment surface and prevent the release of NH_4^+ to the water column. Gross primary production and net ecosystem metabolism were both decreased in the presence of snails, but only for the relatively sandy, low organic matter site (SH). *Ulva* sp. grew better when fertilized with snail excreta than with other individual inorganic and organic nitrogen sources. We observed differences in algal growth in the lab in the presence of sediment, and in the field across site and season, but could not confirm enhanced growth of macroalgae in the presence of snails in spite of the clear effect of snails on the release of nutrients from the benthos to the water column. The interaction between *I. obsoleta* and *Ulva* sp. is context dependent, with a stronger relationship in muddy eutrophic environments and early in the summer. Overall, our study uncovered new information regarding the complex relationship between *I. obsoleta* and *Ulva* sp. that is useful in understanding how internal nitrogen cycling may be controlled by biotic feedbacks and act to maintain macroalgal blooms in shallow estuaries.

1. Introduction

Coastal estuaries are among the most productive ecosystems in the world and not only serve as breeding grounds and nurseries for many different species of fish and macroinvertebrates (Berbier et al. 2011), but are also of great value economically for commercial fisheries and recreation (Costanza et al. 1997). Despite these benefits, estuaries are among the most threatened of all marine habitats due to a combination of eutrophication, overfishing, and habitat destruction (Lotze et al. 2006, Breitburg et al. 2009, Waycott et al. 2009), with eutrophication arising as the biggest problem currently facing our estuaries (Valiela et al. 1992, Nixon 1995, Cloern 2001, Bricker et al. 2007, McGlathery et al. 2007, Paerl 2009). Between 1961 and 1997, nitrogen (N) inputs to the US from human activity doubled (Howarth et al. 2002). In shallow estuaries where N is typically the limiting nutrient (Howarth & Marino 2006), excess N loading leads to macroalgal blooms (Valiela et al. 1997) that in turn create a variety of detrimental ecosystem-level changes (Valiela et al. 1997, McGlathery et al. 2001, Nixon et al. 2001). As eutrophication proceeds, macroalgae replace rooted plants, such as seagrasses, that obtain nutrients from the sediment (McGlathery 2001, Nixon et al. 2001, Hauxwell et al. 2001). When the macroalgae senesce, they are soon consumed by benthic microorganisms – an aerobic process. This in turn can lead to increased dissolved oxygen consumption which could have negative environmental consequences, including hypoxia (D'Avanzo et al. 1996).

The negative effects of eutrophication on macroinvertebrate communities have been thoroughly investigated (Pearson & Rosenberg 1978, Gray 1989, Cardoso et al. 2004, Wildsmith et al. 2011). Nonetheless, some tolerant species of macroinvertebrates persist in areas experiencing eutrophication (Fox et al. 2009, McLenaghan et al. 2011). In fact, Fox et al. (2009) found a significant *increase* in the abundance of the omnivorous gastropod *Ilyanassa obsoleta*

(Say), the Eastern Mud Snail, in the more eutrophied of two estuaries in Cape Cod, MA. 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).

I. obsoleta is an abundant neogastropod inhabiting many estuarine communities along the Atlantic coast. *I. obsoleta* can be described as an ecological “vacuum cleaner” that opportunistically consumes a wide variety of materials by surface deposit feeding using a crystalline style, depending much more on frequency of encounter than on actual nutritional requirements (Curtis & Hurd 1981). Most of *I. obsoleta*’s nutrition comes from micro-flora and fauna (Curtis & Hurd 1981). Even though some studies have indicated consumption of macroalgae by *I. obsoleta* (Curtis & Hurd 1981, Gianotti and McGlathery 2001), Curtis and Hurd (1981) found that snails kept on a diet of macroalgae alone did not increase in biomass or outlive starved control individuals. Kelaher et al. (2003) determined that even though *I. obsoleta* may not consume live macroalgae, the presence of macroalgal detritus in certain plots caused an associated increase in *I. obsoleta* abundance likely due to an increase in benthic bacteria and diatoms. Furthermore, similar macroalgal detritus has been observed in association with the bottom of living macroalgal mats (Krause-Jensen et al. 1999). These bacteria are an important food source for *I. obsoleta*, which suggests that algal mats may be associated with a viable food source.

Surface deposit feeding gastropods can have a strong impact on nutrient cycling, benthic microalgae (Pillay et al. 2009, McLenaghan et al. 2011, Weerman et al. 2011), and oxygenation of surface sediment (Premo 2011). The effects of invertebrates on sediment biogeochemistry may be context-dependent, varying in both space and time (Needham et al. 2011). Furthermore,

certain macroinvertebrate species, including *I. obsoleta*, have been observed in close proximity to bloom forming macroalgae (Fong & Desmond 1997, Guidone et al. 2010, McLenaghan et al. 2011) where the snail may promote macroalgal growth through enhancement of the N flux to the water column (McLenaghan et al. 2011) or removal of competing epiphytes (Guidone et al. 2010). While uptake of dissolved inorganic nitrogen (DIN) by macroalgae has been extensively studied (e.g. McGlathery et al. 1997, Teichberg et al. 2010, Ale et al. 2011), evidence exists that dissolved organic nitrogen (DON) may also be an important component of macroalgal N demand (Tyler et al. 2001, 2003, 2005). Thus, identifying the sources and availability of both DIN and DON under varying environmental conditions is important. 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 (Sundback et al. 2003, Tyler et al. 2003, Kamer et al. 2004). *I. obsoleta* therefore has the potential to influence the recycling of N in shallow systems. Thus, understanding the complex relationship between *I. obsoleta* and bloom-forming macroalgae, especially the snail-induced facilitation of nutrient release from the sediment to the water column where it may be available to fuel macroalgal growth, is important for the effective prediction and management of eutrophication in coastal estuaries.

While deposit-feeding snails may positively influence macroalgal growth, there is also the possibility for a reciprocal benefit of macroalgal for the snails. Indeed, there is evidence that the detritus associated with living mats of macroalgae may offer a viable food source for *I. obsoleta*, which, in return, may further facilitate the growth of these macroalgal blooms by increasing DIN and DON availability. In addition, in soft-bottomed environments where

substrate often limits (e.g. Kuhlmann 1997, Swanson 2004), macroalgae may provide an important oviposition site or predation refuge for *I. obsoleta*. We have observed numerous eggs deposited on the macroalgal thalli (C. Yarrington, pers. obs.). Furthermore, *I. obsoleta* is a prey item in the diets of several predatory species (e.g. Anderson 1970, Stenzler & Atema 1977, Ashkenas & Atema 1978) and it follows that the predatory pressure exerted by these organisms could cause a refuge driven association between the snail and macroalgae.

In this study we investigated the reciprocal benefits of the association between *I. obsoleta* and the bloom-forming Chlorophyte *Ulva* sp., most likely *Ulva lactuca* (L.), but hereafter referred to as *Ulva*. Our study site, West Falmouth Harbor, MA (WFH), is an ideal site for this project as it is representative of other shallow temperate systems, but also provides two different embayments that are in close proximity to one another but are subject to differing degrees of N loading. Our three primary objectives were: (1) to determine if snails utilize macroalgae as a predation refuge and/or oviposition substrate, (2) to measure the direct and indirect effects of *I. obsoleta* on water column DIN and DON in two different environmental settings, and (3) to assess the growth response of *Ulva* to different N species and determine the temporal and spatial variability in the effects of snail and sediment presence on algal growth in the laboratory and in two different embayments in West Falmouth Harbor, MA. Ultimately our findings were interpreted through the lens of understanding complex biotic feedbacks with eutrophication in shallow coastal systems.

2. Materials and Methods

2.1. Site Description

WFH is a 197 acre polyhaline estuary (salinity 20-30 ppt), with a tidal range of 1.5 m and an average depth of 0.6 m at mean low water (Howes et al. 2006). The structure of the harbor is a result of a combination of a drowned-river valley and a bar-built estuary (Howes et al. 2006). Due to groundwater input from a localized wastewater plume entering the innermost embayment of the harbor, the N load has doubled compared to background levels (Howes et al. 2006). There are three primary embayments in WFH (Figure 1). The Inner Harbor (IH), which is experiencing symptoms of moderate to severe eutrophication, has relatively high organic matter (OM) levels (7.0%) and an average sediment grain size of 1.7 mm (Scheiner 2011). In the IH, macroalgal blooms commonly occur during the summer and seagrass cover is lower than in the Outer Harbor (OH) (McGlathery et al. unpub. data, Tyler et al. unpub. data). The South Harbor (SH) has lower OM levels (mean 3.2%), similar sediment grain size (mean 1.6 mm, Scheiner 2011), low macroalgal biomass and is devoid of seagrass (Tyler et al. unpub. data). Finally, the OH, which was not used in this study sustains an intact seagrass community (McGlathery et al. unpub. data, Tyler et al. unpub. data). Due to rapid eutrophication and the associated macroalgal blooms in one embayment, WFH affords us the unique opportunity to investigate ecological feedbacks in different environmental contexts within a small geographic area.

2.2. Benefits of macroalgae to *I. obsoleta*

- a. The co-occurrence of *I. obsoleta* and *Ulva* was investigated in both the IH and SH on June 22-23 and August 2-3, 2010. A 0.25 m² quadrat was haphazardly placed 30 times in both harbors at a similar tidal height and distance from the *Spartina alterniflora* zone. We counted all snails, and macroalgae was collected for biomass measurement. Macroalgal biomass was measured by gently patting algal thalli dry with paper towels prior to wet weight measurement. Thalli were then rinsed in deionized water, blotted, frozen, and placed in a drying oven (60°C) to obtain dry weights (McLenaghan 2009). The relationship between macroalgal biomass and snail density was assessed in the IH using linear regression.

- b. In early (June 19-25) and late (July 30 – August 6) summer 2010 we investigated the possibility that *Ulva* mats in the IH are a predation refuge for *I. obsoleta* using the tethering method described in Silliman and Bertness (2002). Braided fishing line was attached to clean, dry snails using cyanoacrylate gel. Loops were tied in the end of each line and the tether was attached to a 1.27 cm diameter polyvinyl chloride (PVC) pipe with a zip-tie. Five snails were tethered to each pole that was then placed in the center of each 0.25 m² plot. A linear transect of 8 plots spaced one meter apart was established within a dense macroalgal mat and paired with an identical transect adjacent to but outside of the macroalgal mat. After seven days, each tether was scored as (1) snail present/alive, (2) snail dead/damaged, (3) snail missing, tether present or (4) tether and snail missing. The percentage of snails present/alive was calculated for each plot and the resulting data analyzed using a two-way ANOVA with season and within/outside of the mat as fixed factors. For these, and all following ANOVA tests, data were checked for normality (Ryan-Joiner test) and homogeneity of variance (Levene's test). When significant effects were

observed, we used Tukey's HSD test to determine treatment differences. All statistical analyses was conducted using Minitab 16 version 16.1.0.

c. In order to investigate the role of *Ulva* as a possible oviposition site for *I. obsoleta* and determine the potential for a reproductively driven attraction of *I. obsoleta* to *Ulva*, we measured oviposition on artificial algal substrate in the IH during two 7 d intervals beginning on June 18 and July 29, 2010. Artificial algal thalli were constructed from black plastic sheets to act as a morphological mimic of *Ulva*, without replicating other properties, such as a food source. Minimal fouling by organisms other than *I. obsoleta* eggs was observed on the plastic over this time period so snail attraction to microalgae on the plastic was unlikely. Artificial thalli were roughly hourglass shaped, 25 cm long and 12.5 cm wide, with a surface area of 290 cm² on each side. Five "fronds" with a total (back and front) surface area of 2,900 cm² per plot were attached to each PVC pole using a zip-tie. Three parallel linear transects of five 0.25 m² plots spaced one meter apart were established and PVC poles were inserted in the center of each plot. Transects one and two were outside of the mat and transect three was within the mat. Transect one was outside of the mat but without thalli attached to the poles, to ensure that the pole wasn't forcing accumulation of snails or *Ulva*. Transects two and three were artificial thalli treatments. After 7 d, all snails within the plots were counted, living macroalgae was collected for biomass measurements as above, and all *I. obsoleta* eggs deposited on the artificial thalli were counted. Data were analyzed using a one-way ANOVA with within/outside of the mat as the fixed factor.

2.3. Control of nutrient availability by *I. obsoleta*

a. In June 2010, urea, nitrate, ammonium and total dissolved nitrogen (TDN) excretion rates were determined for *I. obsoleta* 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 were much larger than snails from the SH and may have slightly different diets, the experiment was conducted separately with snails from each basin. Treatments of 0 and 2 snails (n=5) 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. 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.

Initial samples for ammonium, urea, nitrate, and TN 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. Because the bottle-to-bottle variation was extremely low (SE of the mean 0.001 $\mu\text{g NH}_4^+/\text{L}$, 0.005 $\mu\text{g urea}/\text{L}$, 0.120 $\mu\text{g NO}_3^-/\text{L}$, 0.958 $\mu\text{g TN}/\text{L}$, 0.005 $\text{mg O}_2/\text{L}$) these values were used for the initial time point for all bottles. Final DO readings and nutrient samples were taken from each bottle after 4 hours. All water samples were immediately filtered into Whirlpak bags and frozen. 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 the 2 treatments, divided by the number of snails, yielded the excretion rate per snail, which was summed over a 24 hr period (assuming 14 h light and 10 h dark) to obtain a daily excretion rate. Ammonium was analyzed according to Solorzano (1969) using the phenol-hypochlorite method. Nitrate and TN were measured using a Lachat Quikchem 8500 autoanalyzer with cadmium reduction and in-

line digestion methods, respectively (Lachat 2003). Urea was analyzed using the Goeyens et al. (1998) room temperature modification of the method described by Mulvenna and Savidge (1992). Because there were no significant differences between sites (one-way ANOVA), all results were pooled for presentation.

b. We used microcosm incubations with sediment and *I. obsoleta* followed by measurement of sediment-water column fluxes of N and O₂ 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 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 which could 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 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 ppt; temperature = 16-18 °C; light 150-200 μmol photons m⁻² s⁻¹; light:dark = 14h:10h). 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 recreate 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-hr intervals (0, 2, 4, 6, 8 hr). The transition from light to dark occurred at 4 hours, 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 ammonium, nitrate+nitrite and urea analysis using the methods described above. Hourly fluxes were analyzed by a 3-way ANOVA with site, snails, and light/dark as fixed factors. Daily fluxes were analyzed by a 2-way ANOVA with site and snails as fixed factors. IH and SH Gross Primary Production (GPP) and Net Ecosystem Metabolism (NEM) values were analyzed by a 1-way ANOVA with snails as the fixed factor.

2.4. The growth response of *Ulva* to nutrient additions

a. In order to test the effect of different N sources on *Ulva* growth, the growth rate of *Ulva* with a variety of N sources, including snail excreta, was measured in the laboratory. The five N

fertilization treatments were: Control (no addition), Ammonium addition, Nitrate addition, Urea addition, and Snail excreta addition (n = 5). Stock solutions of 10 mM-N for ammonium, nitrate, and urea were created using ammonium chloride, potassium nitrate, and urea, respectively, and a 1.25 mM for sodium phosphate tribasic dodecahydrate. All treatments started with a macroalgal frond weighing 0.099 +/- 0.003 g and contained 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 & Neori 1991). For all treatments an 8:1 N:P ratio was used in order to prevent P limitation. For the snail excreta treatment, a single snail was placed in a 473 mL polyethylene plastic, cup filled with 100 mL of growth media for 24 hr. After 24 hr the snail was removed and the macroalgal thallus from the Snail treatment was transferred from the old cup into the new 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). The experiment was conducted in a Caron Diurnal Incubator set at 20.0 °C with a 14:10 hr light to dark ratio. Macroalgal wet weight was measured on days 0, 2, 4, 7, and 10 using the method described above, and thalli were returned to their original cups. Data were analyzed using a one way ANOVA with N source as the fixed factor.

b. In an attempt to examine the interactive effects of snails and sediment on algal growth, a factorial microcosm study was conducting using different combinations of *I. obsoleta* (n = 2) and sediment. In microcosms consisting of clear polyethylene microcosms (14 cm tall x 11.6 cm I.D.) we imposed four fully crossed treatments (5 replicates), all containing *Ulva* (4.5 g ww): with snails, without snails, with sediment, and without sediment. Surface sediment (0-5 cm) was

collected on August 6, 2010 from both the IH and SH in WFH, homogenized and sieved (1 mm) to remove undesirable macrofauna. Half of the microcosms were filled with 4 cm of prepared sediment and 10 cm artificial seawater seeded with natural filtered water from WFH. *I. obsoleta* and *Ulva* were collected on August 6, 2010, acclimated in the laboratory for 3 d before adding to microcosms. Microcosms were covered with a mesh screen to prevent snail escape and containers were set under full spectrum lights ($150\text{-}200 \mu\text{mol photons m}^{-2} \text{s}^{-1}$). Throughout the experiment, chambers were mechanically bubbled with air for oxygenation and to prevent the build up of diffusion gradients at the sediment surface. All containers were then randomly placed in their incubation location. Macroalgal biomass was measured on days 0, 7, 14, and 21 as described above. Data were analyzed using a two-way ANOVA with snail and sediment as fixed factors.

c. To determine the potential effects of *I. obsoleta* on *Ulva* growth in the field, and capture the potential for context-dependence of the snail-macroalgae relationship, we set up an 8 d caging experiment to measure the impact of snail presence on macroalgal growth in both harbors in June and July 2010. Two parallel, linear transects, two meters apart, of 8 cages (one every meter) were established in each harbor. Cages were constructed from 0.64 cm mesh galvanized hardware cloth. The cages were cubic in shape (30 cm on each side) with a top made from the same material. Cages were worked into the sediment by hand so that approximately 15 cm was below the sediment surface and 15 cm was above the sediment surface. PVC stakes were driven into the sediment at opposite corners of the cages, outside of the perimeter of the cage, and attached with cable ties to secure the cage in location. These parameters replicate natural settings by using snail densities based on field survey data and by using a mesh that did not substantially reduce light levels in the cage (14.8% reduction \pm 2.5% SE). The mesh size was

small enough to keep all snails and macroalgae inside the cage. Macroalgae collected from the IH was placed in each cage (100 g wet weight [gww] in the IH; 50 gww in the SH), and within each transect, half of the cages were randomly selected for snail addition of 30 snails. Different amounts of macroalgae were used to reflect ambient macroalgal abundance at each site.

Macroalgal biomass was collected and wet weight was obtained at the end of the experiment and data were analyzed using a two-way ANOVA with site and presence of snails as fixed factors.

3. Results

3.1. Benefits of macroalgae to *I. obsoleta*

Our field measurements of snail density and macroalgal biomass in the IH confirmed the association between *I. obsoleta* and *Ulva* in June (Fig. 2A; $p < 0.001$), but suggest that this phenomenon is temporally variable as no association was observed in July (Fig. 2B; $p = 0.464$). However, average algal biomass was higher in June ($p = 0.001$) with a maximum single observation of $4,249 \text{ g m}^{-2}$ which is roughly 6.5 times higher than July (maximum = 650 g m^{-2}). Also, while we did observe snails in the SH, we observed a more even distribution, and algae was absent in both June and July (Fig. 2A and 2B). We did not observe a significant difference in predation rates inside or outside of the mat and predation was similar between times, although slightly higher in June (Fig. 3A; $\text{df} = 1, F = 0.12, p = 0.736$; $\text{df} = 1, F = 4.17, p = 0.051$, for within/outside mat and between months, respectively).

When artificial macroalgal thalli were supplied as an oviposition substrate within and outside of the algal mat in June, snail abundance and macroalgal biomass were both significantly higher within the macroalgal mat (Fig. 3B; $\text{df} = 1, F = 87.95, p < 0.001$; $\text{df} = 1, F = 39.62, p < 0.001$, for snail abundance and macroalgal biomass respectively). However, there was no difference between the number of eggs laid on artificial thalli within or outside of the mat (Fig. 3B; $\text{df} = 1, F = 0.01, p = 0.945$). Data from July is not shown because snails were not reproductive and we found no eggs on living or artificial substrate.

3.2. Control of nutrient availability by *I. obsoleta*

When nitrogen excretion by *I. obsoleta* was measured, of the 15.4 +/- 1.8 $\mu\text{mol N indiv}^{-1} \text{d}^{-1}$ that snails excreted (Fig. 4.), urea and NO_3^- accounted for relatively small proportions (-0.1 +/- 0.3 and 0.7 +/- 0.4 $\mu\text{mol N indiv}^{-1} \text{d}^{-1}$ respectively) while NH_4^+ and DON accounted for much higher proportions of the TN excreted (9.1 +/- 0.6 $\mu\text{mol N indiv}^{-1} \text{d}^{-1}$ and 6.2 +/- 1.4 $\mu\text{mol N indiv}^{-1} \text{d}^{-1}$, respectively).

In the microcosm experiments where sediment-water column flux rates were measured, hourly flux rates of N and DO were not significantly affected by snail presence in IH or SH sediment, but hourly NH_4^+ flux rates were higher in the IH than SH (df = 1, $F = 8.49$, $p = 0.008$; Table 1) and sediment uptake of NH_4^+ in the light was greater than the dark (df = 1, $F = 35.54$, $p < 0.001$) (Table 2). Hourly NO_3^- fluxes exhibited greater uptake in the light (df = 1, $F = 6.20$, $p = 0.020$). On a daily basis, however, the NH_4^+ flux in the presence of snails was greater than with no snails (df = 1, $F = 9.92$, $p = 0.049$) and was again greater in the IH than in the SH (df = 1, $F = 4.78$, $p = 0.008$). All other comparisons among hourly rates were not significant. After determining GPP (Fig. 6A) and NEM (Fig. 6B) using O_2 flux rates, we found no significant effect of snails, but consistently higher benthic O_2 production in the SH (df = 1, $F = 12.55$, $p = 0.004$; df = 1, $F = 12.36$, $p = 0.004$, respectively) (Table 3). Also, when daily N flux rates were determined (Fig. 5), NH_4^+ flux was significantly higher in the IH compared to the SH, and in the presence of snails (1466.7 $\mu\text{mol N m}^{-2} \text{d}^{-1}$, 794.8 $\mu\text{mol N m}^{-2} \text{d}^{-1}$, respectively) in both sites (df = 1, $F = 9.9$, $p = 0.008$; df = 1, $F = 4.8$, $p = 0.049$, respectively) (Table 3).

We scaled the per snail excretion rates (from part 2.3) to the equivalent of m^{-2} and compared the potential excretion $\text{m}^{-2} \text{d}^{-1}$ to the measured daily flux rates in order to determine

how much of the difference between the snail and no snail treatments could be explained by snail excretion. NH_4^+ from excretion was 175% to 284% of the difference between NH_4^+ flux rates in the presence and absence of snails.

3.3. *The growth response of Ulva to nutrient additions*

When 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 at a daily rate of $0.13 \pm 0.01 \text{ g d}^{-1}$ which was significantly higher than the growth rates in the control, NH_4^+ , urea, and NO_3^- treatments ($\text{df} = 4$, $F = 4.59$, $p = 0.009$) (Fig. 7). For all the treatments besides the excreta treatment, $17.1 \mu\text{mol N}$ was added on day 1 of the experiment, and was increased incrementally to $40.4 \mu\text{mol N}$ on the final day. The amount of N added in the excreta treatment was controlled, albeit unknown, at the time of additions, but using the data shown in Fig. 4 we found that approximately $9.2 \mu\text{mol NH}_4^+$, $-0.1 \mu\text{mol urea}$, $0.8 \mu\text{mol NO}_3^-$, and $6.4 \mu\text{mol DON}$ were added to excreta treatments each day. Because of the discrepancy in the amount of N added to the different treatments, we calculated daily macroalgal growth rate per $\mu\text{mol N}$ added and found that macroalgal growth was still significantly higher in the snail excreta treatment ($1.5 \pm 0.1 \text{ mg } \mu\text{mol N}^{-1}$) even when compared to the next highest treatment which was NH_4^+ ($0.7 \pm 0.1 \text{ mg } \mu\text{mol N}^{-1}$) ($\text{df} = 4$, $F = 15.64$, $p < 0.001$).

In the laboratory, when we measured macroalgal growth rate in the presence and absence of snails and sediment in a second, separate, microcosm experiment, snails had no net effect on macroalgal growth (Fig. 8; $\text{df} = 1$, $F = 0.13$, $p = 0.730$). However, in that same study, macroalgae in the presence of sediment decomposed at a significantly higher rate as indicated by

significantly lower biomass on days 14 and 21 ($df = 1, F = 9.29, p = 0.008$; $df = 1, F = 8.29, p = 0.011$, respectively). Likewise, in the field, there were no differences in macroalgal growth between cages with and without snails in June or July (Fig. 9A/B; $df = 1, F = 1.66, p = 0.203$). However, macroalgal growth was consistently higher in the IH ($df = 1, F = 39.22, p < 0.001$) in both June and July, but highest overall in June ($df = 1, F = 44.95, p < 0.001$).

4. Discussion

In our study, after confirming the association between *I. obsoleta* and *Ulva* in WFH, we found that there are reciprocal benefits to both organisms. Snails provide an additional N source to the macroalgae, which has the potential to facilitate macroalgal growth, although this mechanism was somewhat substrate dependent. In return, macroalgae likely provide dietary and reproductive benefits to snails. Understanding these interactions is essential to fully understand eutrophication in shallow coastal systems.

The very high *I. obsoleta* densities we observed (up to 1,465 ind. m⁻²) were greater than had been observed in other studies. For example, Fox et al. (2009) found 600 +/- 143 ind. m⁻², and Kelaher et al. (2003) observed only roughly 500 ind. m⁻². We also observed very high macroalgal biomass (up to 4,250 g ww m⁻²) compared to Hauxwell et al. (1998) who observed an average of about 360 g dry weight m⁻², at a nearby estuary. In the IH, the diminished relationship observed in our July field survey measurements is likely due in part to the diminished health, and increased scarcity of *Ulva*. Because the macroalgal mat was less intact, there was likely less of a detrital food source to attract *I. obsoleta*. Furthermore, snails were not reproductive in July as evidenced by a lack of snail eggs on living or artificial oviposition substrate, which would again preclude the snails from associating with the macroalgae.

In soft-bottomed communities, substrate is a known limiting factor for oviposition sites in several gastropod species (Pechenik 1978, Brenchly 1981, D'Asara 1986, DeMartini 1991, Kuhlmann 1997, Swanson 2004). We did observe large numbers of snail eggs on living algae (C. Yarrington, pers. obs.), and indirectly confirmed the use of *Ulva* as an oviposition site for *I. obsoleta* through the use of artificial algae. Even though there was a significantly greater number of snails in the treatments within the algal mat, the number of eggs laid on artificial algae was equivalent regardless of location. This suggests that while *I. obsoleta* clearly used the artificial macroalgae as an oviposition site, the detrital food source associated with the bottom of a real macroalgal mat was absent and it is thus likely that the snails moved on in search of a viable food source after depositing their eggs. The potential oviposition substrate attracts snails, but the associated detrital food source (Kelaher et al. 2003) maintains clumped snail distributions during periods of high macroalgal biomass.

Previous work has found that while *I. obsoleta* is not a major prey species, they do experience predation by the green crab *Carcinus maenas* (Stenzler & Atema 1977, Ashkenas & Atema 1978), the moonsnails *Polinices duplicatus* and *Lunatia heros* (Atema & Burd 1975, Stenzler & Atema 1977), and some migratory birds (Recher 1966, Anderson 1970). The method used in our study to estimate predation rates has been successfully implemented in past studies with other snail species, and when predation pressure was high, 98% of those tethered snails were consumed (Silliman & Bertness 2002), suggesting that predation is less important in our system where only 15-40% of snails were consumed. The equivalent loss of tethered snails inside and outside of mats indicates that macroalgal mats were not an effective refuge from predation for the snails, and we observed many *C. maenas* both inside and outside the macroalgal mat (C. Yarrington, pers. obs.).

The effects that macroinvertebrates have on sediment biogeochemistry can sometimes be context dependent (Needham et al. 2011). This was the case in our study, as illustrated by the variation in the effect of snails in the different harbors. Furthermore, while a two way ANOVA did not show any snail driven differences for GPP or NEM, a one way ANOVA revealed a significant reduction in both GPP and NEM in the SH in the presence of snails ($df = 7$; $F = 7.27$, $p = 0.036$; $df = 7$, $F = 8.08$, $p = 0.029$, respectively) but not in the IH. In the low-OM SH sediment (Scheiner 2011), snails had a significantly greater reductive effect on GPP and NEM by reducing the ability of the benthic microalgae to produce (and consume) oxygen. The IH, on the other hand has more OM (Scheiner 2011) and detritus available for grazing, so the snails' diet may be more mixed and the grazing pressure on microalgae in the IH may be lower. Furthermore, by reducing the amount of detritus in the IH through grazing, *I. obsoleta* has the potential to reduce NEM.

The N fluxes were likewise context dependent. The higher observed NH_4^+ flux rates in the IH could potentially be explained by varying sediment characteristics between the two harbors such as higher organic matter (OM) content and higher porewater NH_4^+ in the IH (Scheiner 2011). The observed hourly N flux values in this study exhibit similar patterns to past studies (McLenaghan 2011), but we observed much lower NH_4^+ flux rates in both harbors and a larger difference between light and dark. The variation in hourly nutrient flux rates of NH_4^+ and NO_3^- between the light and dark was likely caused by enhanced microalgal uptake of both NH_4^+ and NO_3^- in the light. The increase in *daily* ammonium release from sediment to water column in the presence of snails, especially in the IH, is likely a combination of direct release by excretion and indirect release by removal of microalgae. With reduced microalgal cover on the sediment surface, more nitrogen released to the porewaters through organic matter mineralization in the

sediments will reach the water column rather than being intercepted by the microalgae (McLenaghan et al. 2011). However, we did not observe a significantly greater reduction in N flux in the light in snail treatments, suggesting that excretion may be the more important of these two factors.

The excretion rates we found are consistent with prior studies that showed little urea and NO_3^- , and high NH_4^+ excretion (Duerr 1968). However, we also found that DON represents a large fraction of the N released in *I. obsoleta* excreta. McGlathery et al. (1997) measured NH_4^+ demand in a macroalgal mat that was 15 cm deep, a similar depth to the mat in our study site (C. Yarrington, pers. obs.) and found that NH_4^+ was assimilated at a rate of about $0.9 \text{ mmol m}^{-2} \text{ d}^{-1}$. Using our measured NH_4^+ excretion rate and the average snail density (405 ind. m^{-2}) from our June field measurements, we calculated that snails, through excretion alone, can release $3.7 \text{ mmol NH}_4^+ \text{ m}^{-2} \text{ d}^{-1}$. This is clearly higher than the assimilation rate measured by McGlathery et al. (1997) and suggests that snails have the potential to provide a substantial amount of NH_4^+ through excretion alone. When excretion rates were compared to flux rates, ammonium excretion rates were 175 - 284% of the difference in daily NH_4^+ release from the benthos to the water column as a result of snail presence. The additional snail excretion that wasn't measured in the change in fluxes in the presence of snails could be explained by NH_4^+ uptake by microalgae (Tyler et al. 2003) or bacteria responsible for denitrification and/or anaerobic ammonium oxidation (Dalsgaard et al. 2005).

When we measured macroalgal growth response to additions of different N species, the high macroalgal growth rate in the presence of snail excreta was likely due to the fact that the excreta treatment alone contained an additional DON source on top of a DIN source. Throughout the nutrient additions, a consistently *lower* total amount of N was added in the forms

of NH_4^+ , urea, NO_3^- , and DON through the excretion treatment when compared to the dedicated treatments for NH_4^+ , urea, and NO_3^- . Furthermore, when the daily macroalgal growth rate per $\mu\text{mol N}$ was calculated, macroalgae in the excreta treatment grew at a significantly higher rate suggesting that the DON compounds promote substantial growth. It therefore appears that the additional DON pool in snail excreta is an available and potentially important N source to fuel macroalgal growth.

Other studies have also observed the effects that specific macroinvertebrates can have on nutrient dynamics. Fong & Desmond (1997) found that the horn snail *Cerithidea californica* increased macroalgal growth and N content of *Ulva expansa* tissue, most likely by increasing water column nutrient concentration through excretion and transfer of nutrients from the sediment. McLenaghan et al. (2011) also attributed the growth of *Ulva* to an increase in nutrient transfer from the benthos and observed a reduction of benthic microalgae due to *I. obsoleta*. While in our study, direct snail contact with macroalgal fronds was never observed, Guidone et al. (2010) found a positive growth response of *Ulva lactuca* due to a reduction in epiphytic growth by grazing pressure from *I. obsoleta* on the surface of the fronds. When we measured the potential effect of snails on macroalgal growth in the field, our results were heavily context dependent. The two embayments in which these experiments took place are vastly different (Scheiner 2011), as were the conditions of the macroalgae in the two seasons. This was reflected in the observed macroalgal growth rates, with significantly higher growth rates observed in June, for both the IH and SH, and higher growth rates in the IH overall. While we did observe these differences based on season, and site, we did not observe any snail-driven effects on macroalgal growth. Also, because the number of snails used in the field experiment was based on average

field densities (McLenaghan 2009), not the high densities observed at our site, it is possible that a snail driven growth effect was precluded by an insufficient number of snails.

It is clear that *I. obsoleta* has the *potential* to promote algal growth, but the rapid rate of algal decomposition in the presence of sediment that we observed was probably due largely to the timing of the experiment in late summer when the *Ulva* had begun senesce. When this already unhealthy macroalgal tissue came into contact with the sediment and associated benthic microbes, decomposition may have been accelerated (Lomstein et al. 2006). While the presence of snails may have had a positive effect on macroalgal growth if fully healthy macroalgae had been used (McLenaghan et al. 2011), the condition of the macroalgae we used likely overpowered any growth related effects the snails may have had.

The resilient nature of *I. obsoleta*, coupled with the persistent macroalgal blooms in the IH that have replaced seagrass, create the possibility of a positive feedback between *I. obsoleta* and *Ulva* in the IH (Fig. 10). The potential for similar relationships have been found in other estuaries as well. For example, one study found that when plots were enriched with *Enteromorpha intestinalis* in the Mondego estuary, Portugal, three of the most abundant macroinvertebrates in the area, *Hydrobia ulvae*, a detritus feeding gastropod, *Hediste diversicolor*, and *Capitella capitata*, both polychaete worms, showed significant increases in abundance (Cardoso et al. 2004). Due to the fact that, much like *I. obsoleta*, *H. ulvae* also consumes detritus (Newell 1965), it is possible that it could have a similar effect to *I. obsoleta* with regard to creating positive feedbacks in certain shallow coastal systems. Conversely, past studies demonstrate the potential for the stimulation of microbial denitrification by bioturbating polychaete worms such as *H. diversicolor* and *C. capitata* (Mermillod-Blondin et al. 2004, Ieno et al. 2006) which could act to buffer nutrient additions and slow eutrophication. These past

studies, combined with this study show that these feedbacks are both present and important in eutrophic coastal systems.

5. Conclusions

The observed association between *I. obsoleta* and *Ulva* is complex, with potential benefits for both organisms involved. When dense mats are present, the snails gain valuable oviposition sites in a substrate-limited soft-bottomed environment and a food source associated with the bottom of the macroalgal mat. The macroalgae, on the other hand, gains an additional nutrient source made available by snails through excretion (this study), increased N release from the benthos (Fong & Desmond 1997, McLenaghan 2011, this study), reduction in competing benthic microalgae (McLanaghan 2011), and a reduction in epiphytes that compete for nutrients and light (Guidone et al. 2010). These mutual benefits create the possibility for a positive feedback that could potentially exacerbate the problem of excessive macroalgal growth in some shallow coastal estuaries. In the absence of macroalgal blooms, such as in the SH, we see a different feedback take place, with microalgae as the key primary producer (Fig. 10). Understanding these complex interactions and how they can affect nuisance bloom-forming macroalgae is essential in creating effective and comprehensive management strategies for shallow coastal systems threatened by eutrophication. Furthermore, it appears that the initial macroalgal bloom is what may catalyze the co-occurrence of the snail and the macroalgae. It follows that in an already eutrophic system, the most effective management strategy to control the associated macroalgal blooms could be manual removal of macroalgae, and in turn, snail eggs. This study demonstrates the complex context dependent nature of feedbacks in shallow coastal systems, and their potential to influence ecosystem processes and eutrophication.

TABLES AND FIGURES

Table 1.

Hourly nutrient flux values as $\mu\text{mol N m}^{-2} \text{hr}^{-1}$ +/- SE of the mean.

Site	Snails	Light/Dark	NH_4^+	Urea	NO_3^-
IH	No snails	Dark	113.5 +/- 28.6	8.6 +/- 8.1	-40.2 +/- 7.3
		Light	-26.7 +/- 6.9	-2.4 +/- 13.8	-65.2 +/- 19.4
	Snails	Dark	203.7 +/- 40.6	14.0 +/- 26.7	61.8 +/- 47.6
		Light	13.7 +/- 46.1	18.1 +/- 12.0	-98.1 +/- 27.4
SH	No snails	Dark	75.7 +/- 46.1	-56.1 +/- 50.3	65.9 +/- 36.9
		Light	-92.0 +/- 17.8	13.9 +/- 16.5	-30.2 +/- 67.3
	Snails	Dark	60.1 +/- 47.3	-9.5 +/- 21.6	-41.7 +/- 43.4
		Light	-24.1 +/- 14.9	1.1 +/- 7.5	-27.8 +/- 16.8

Table 2.

Results of a three-way ANOVA of NH_4^+ , urea, and NO_3^- , hourly flux rates with site, snails, and light or dark as fixed factors.

Source of variation	Factor(s)	df	F	P
NH_4^+	Site	1,15	8.5	0.008
	Snails	1,15	3.5	0.073
	Light/Dark	1,15	35.5	<0.001
	Site X Snails	1,15	0.6	0.431
	Site X Light/Dark	1,15	0.6	0.430
	Light/Dark X Snails	1,15	0.1	0.733
	Site X Snails X Light/Dark	1,15	1.9	0.184
Urea	Site	1,15	1.8	0.195
	Snails	1,15	0.8	0.378
	Light/Dark	1,15	1.2	0.280
	Site X Snails	1,15	0.0	0.906
	Site X Light/Dark	1,15	1.7	0.202
	Light/Dark X Snails	1,15	0.4	0.512
	Site X Snails X Light/Dark	1,15	1.3	0.275
NO_3^-	Site	1,15	1.0	0.325
	Snails	1,15	0.1	0.739
	Light/Dark	1,15	6.2	0.020
	Site X Snails	1,15	2.6	0.117
	Site X Light/Dark	1,15	0.9	0.348
	Light/Dark X Snails	1,15	0.1	0.810
	Site X Snails X Light/Dark	1,15	5.2	0.032

Table 3.

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

Source of variation	Factor(s)	df	<i>F</i>	<i>P</i>
NH_4^+	Site	1,15	9.9	0.008
	Snails	1,15	4.8	0.049
	Site X Snails	1,15	0.4	0.528
Urea	Site	1,15	1.4	0.253
	Snails	1,15	0.7	0.414
	Site X Snails	1,15	0.0	0.944
NO_3^-	Site	1,15	0.3	0.121
	Snails	1,15	0.3	0.600
	Site X Snails	1,15	3.2	0.100
GPP	Site	1,15	10.6	0.007
	Snails	1,15	0.9	0.352
	Site X Snails	1,15	2.8	0.119
NEM	Site	1,15	12.6	0.004
	Snails	1,15	2.0	0.179
	Site X Snails	1,15	1.5	0.239



Fig. 1. Aerial image of study area and surroundings (Image from MassGIS). Study sites indicated by stars.

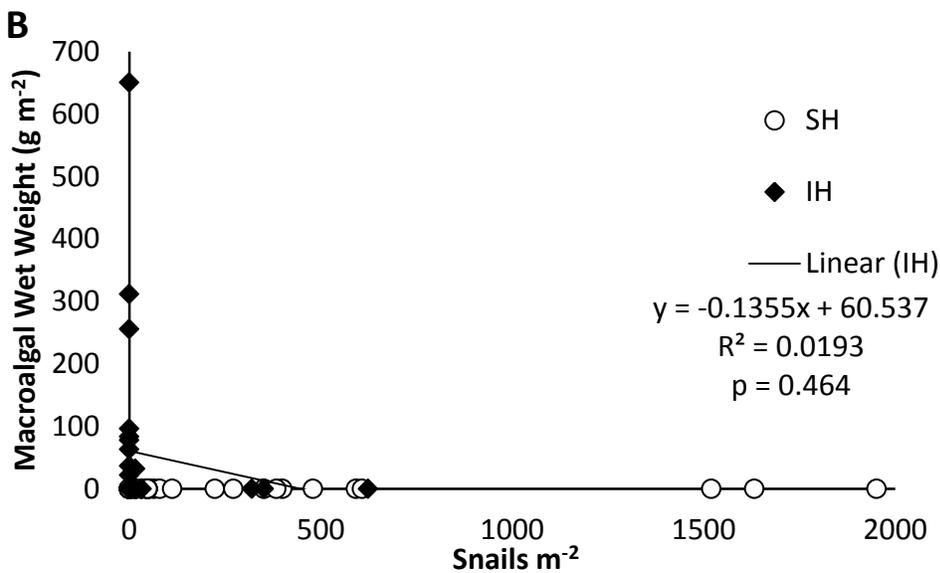
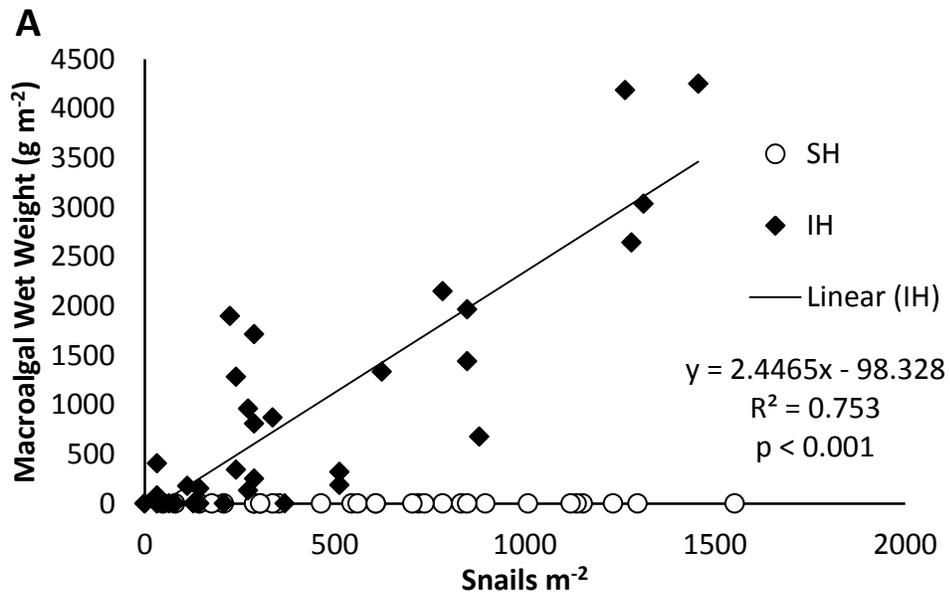


Fig. 2. Snail abundance vs. macroalgal biomass in early June (A) and late July (B) in the Inner Harbor (IH) and South Harbor (SH). Difference scales were used on both axes as values varied between months.

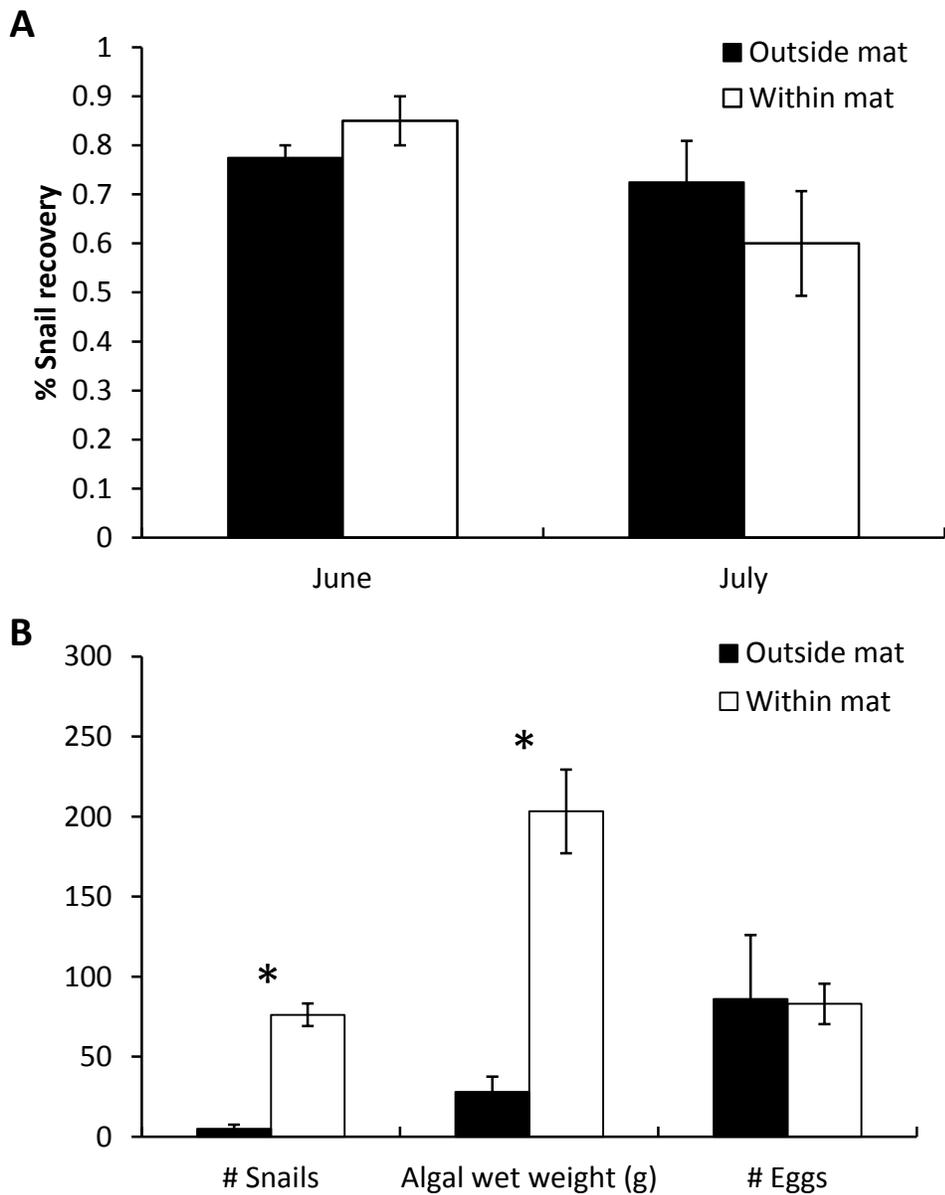


Fig. 3. (A) Recovery rates for tethered snails in June and July within and outside of a macroalgal mat. (B) Snail density, macroalgal biomass, and number of eggs deposited on artificial substrate per plot both outside of and within a macroalgal mat in June. Data from July not pictured as snails were not reproductive. Significant differences between treatments are denoted by an “*” ($p < 0.05$). Error bars represent standard error of the mean.

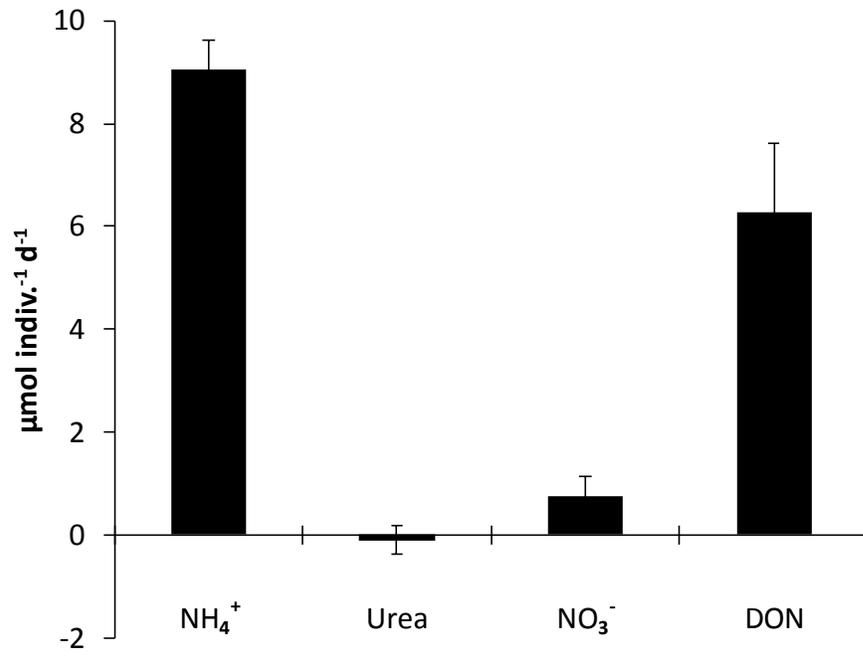


Fig. 4. N excretion rates per snail per day for NH₄⁺, urea, NO₃⁻, and DON. Values are a total of excretion measured in the light and dark. Error bars represent standard error of the mean.

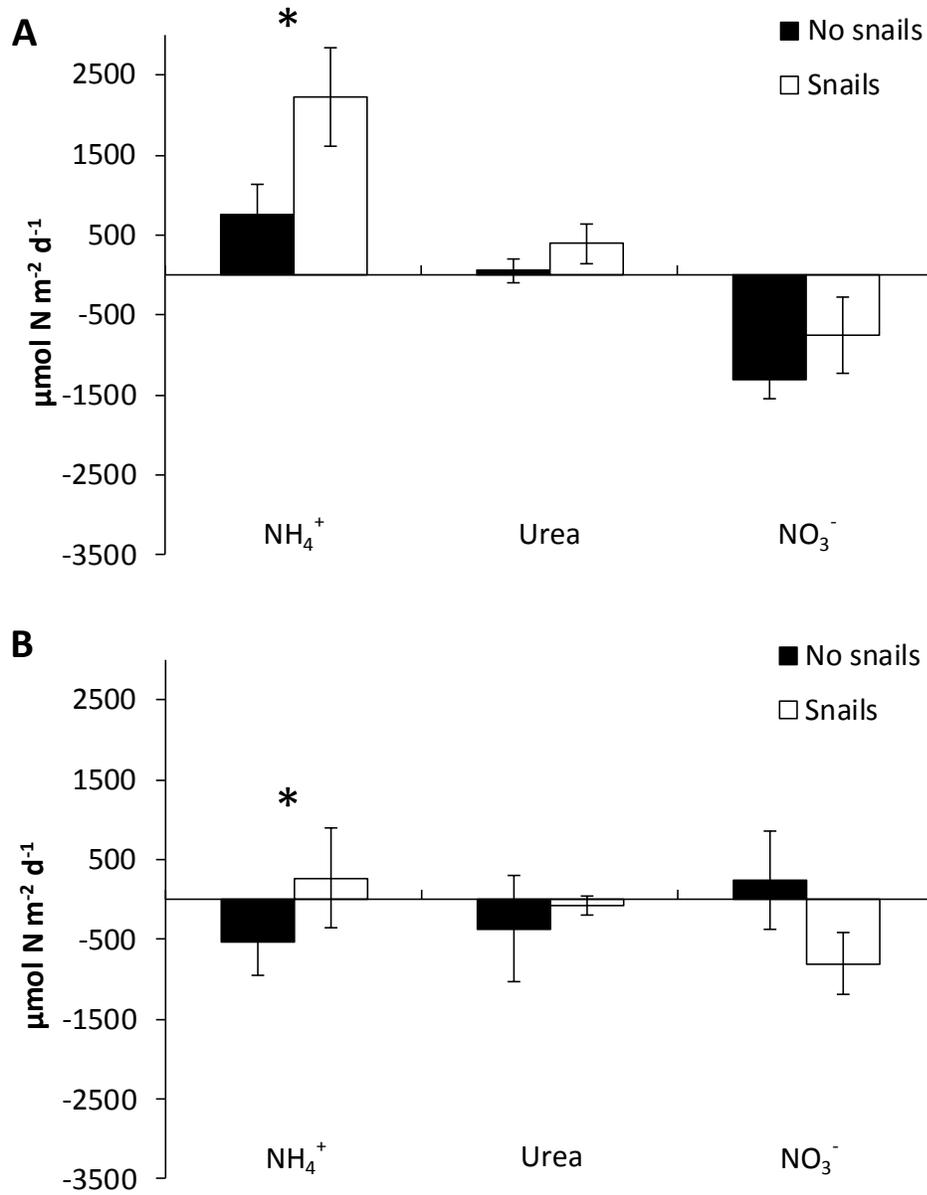


Fig. 5. Daily nitrogen fluxes for NH_4^+ , urea, and NO_3^- , with and without snails in Inner Harbor (A) and South Harbor (B) sediments. Significant differences attributed to snails presence are denoted by an “*” ($p < 0.05$). Error bars represent standard error of the mean.

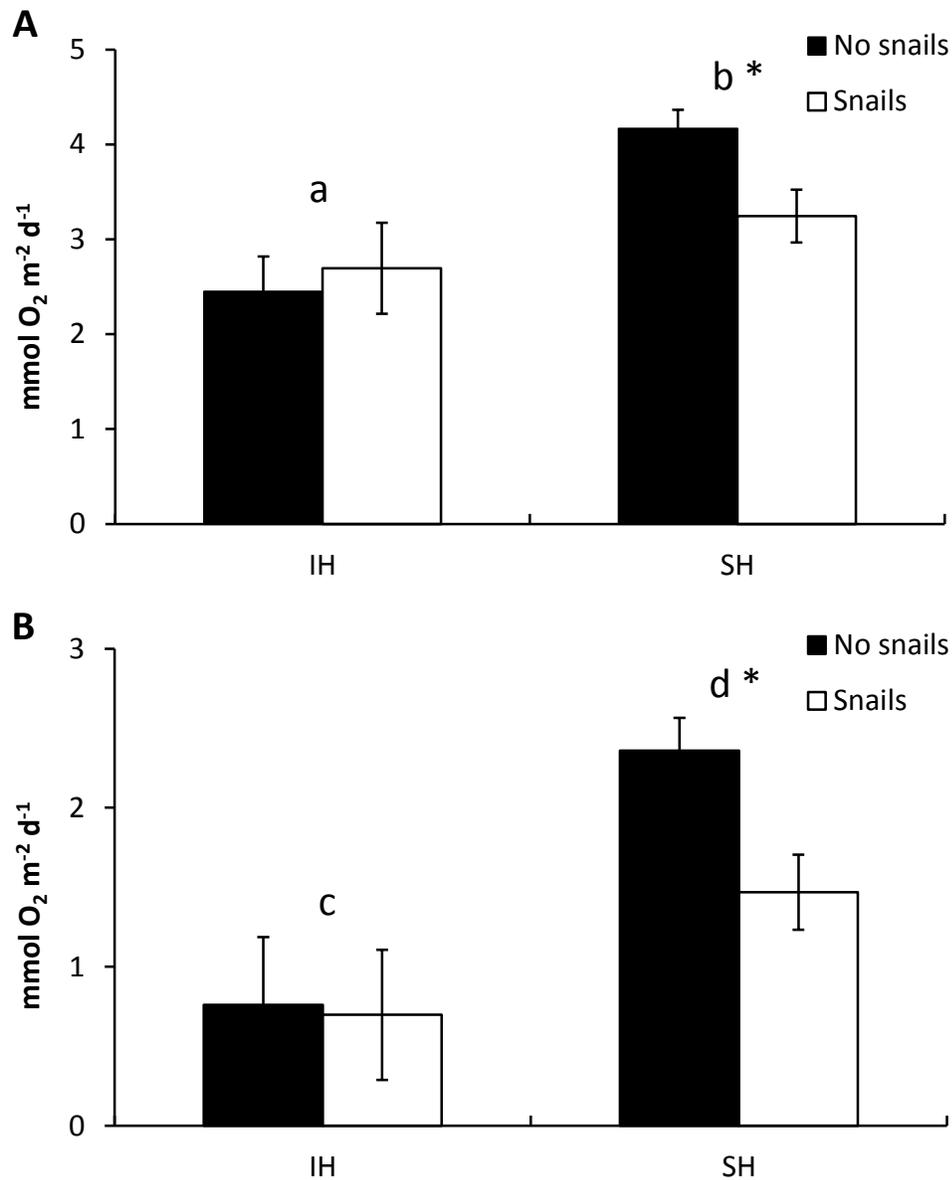


Fig. 6. (A) Gross Primary Production (GPP), and (B) Net Ecosystem Metabolism (NEM) in the Inner Harbor (IH) and South Harbor (SH) for treatments with and without snails. There were no differences caused by snails for either GPP or NEM. Dissimilar lowercase letters denote significant differences between site and an “*” indicates significant difference due to treatment ($p < 0.05$). Error bars represent standard error of the mean.

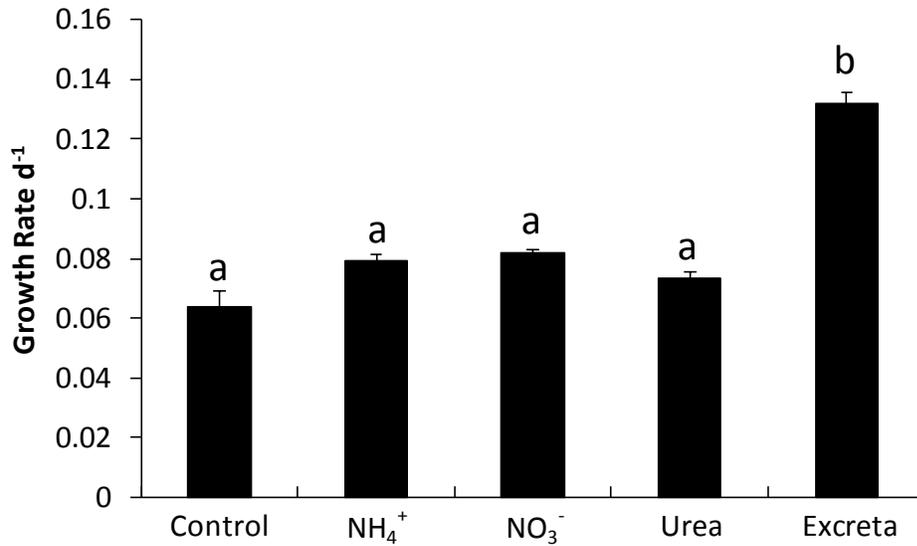


Fig. 7. Macroalgal growth rate in grams per day in response to control, NH₄⁺, NO₃⁻, urea, and excreta treatments. Dissimilar lowercase letters denote significant differences between treatments ($p < 0.05$). Error bars represent standard error of the mean.

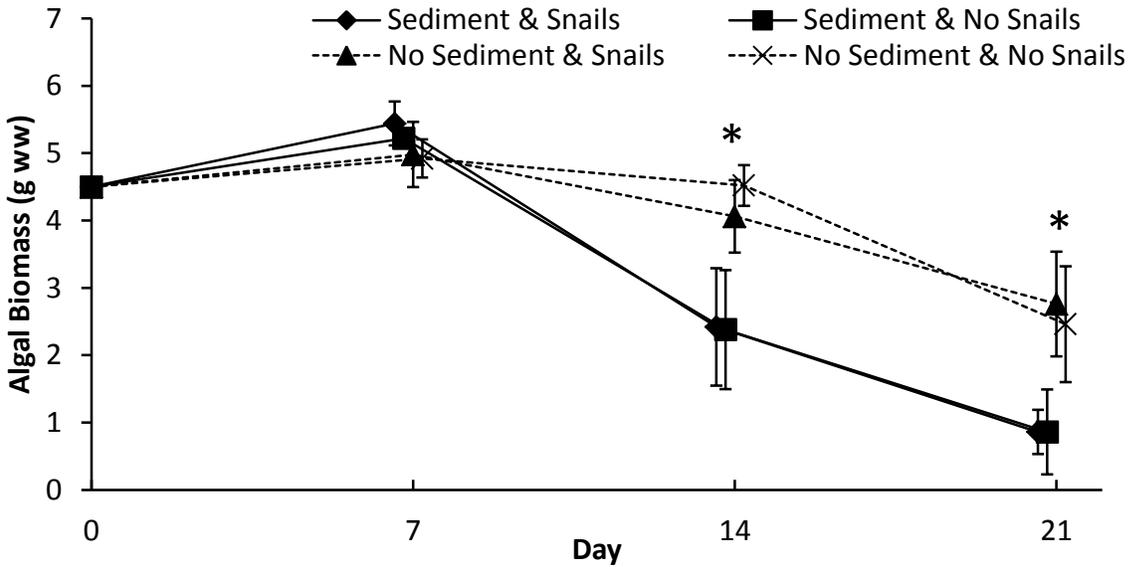


Fig. 8. Macroalgal biomass measurements for treatments with and without snails and sediment. Significant differences attributed to the presence of sediment, regardless of snail treatment, is denoted by an “*” ($p < 0.05$). Error bars represent standard error of the mean.

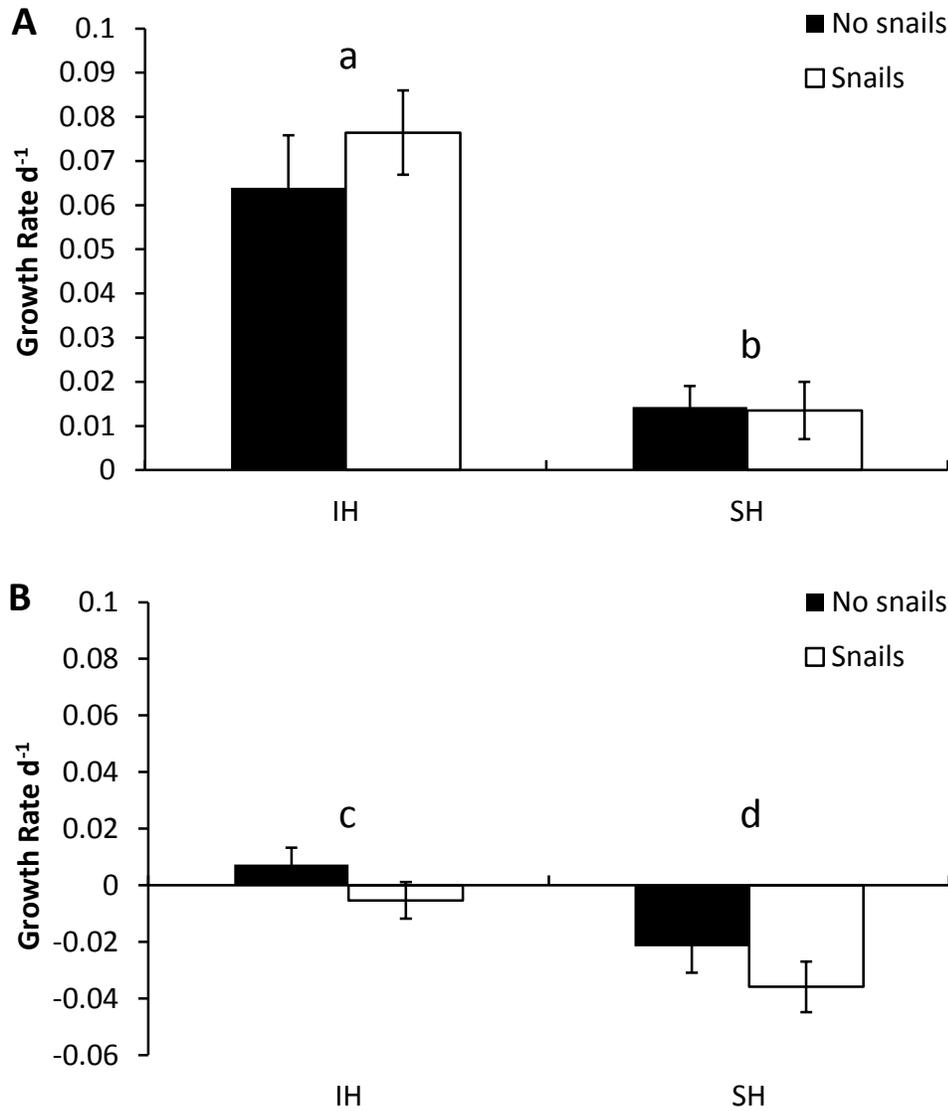


Fig. 9. Macroalgal growth rate in grams per day for (A) June and (B) July for the Inner Harbor (IH) and South Harbor (SH) with and without snails. Dissimilar lowercase letters denote significant differences between site ($p < 0.05$). There were no snail driven effects. Error bars represent standard error of the mean.

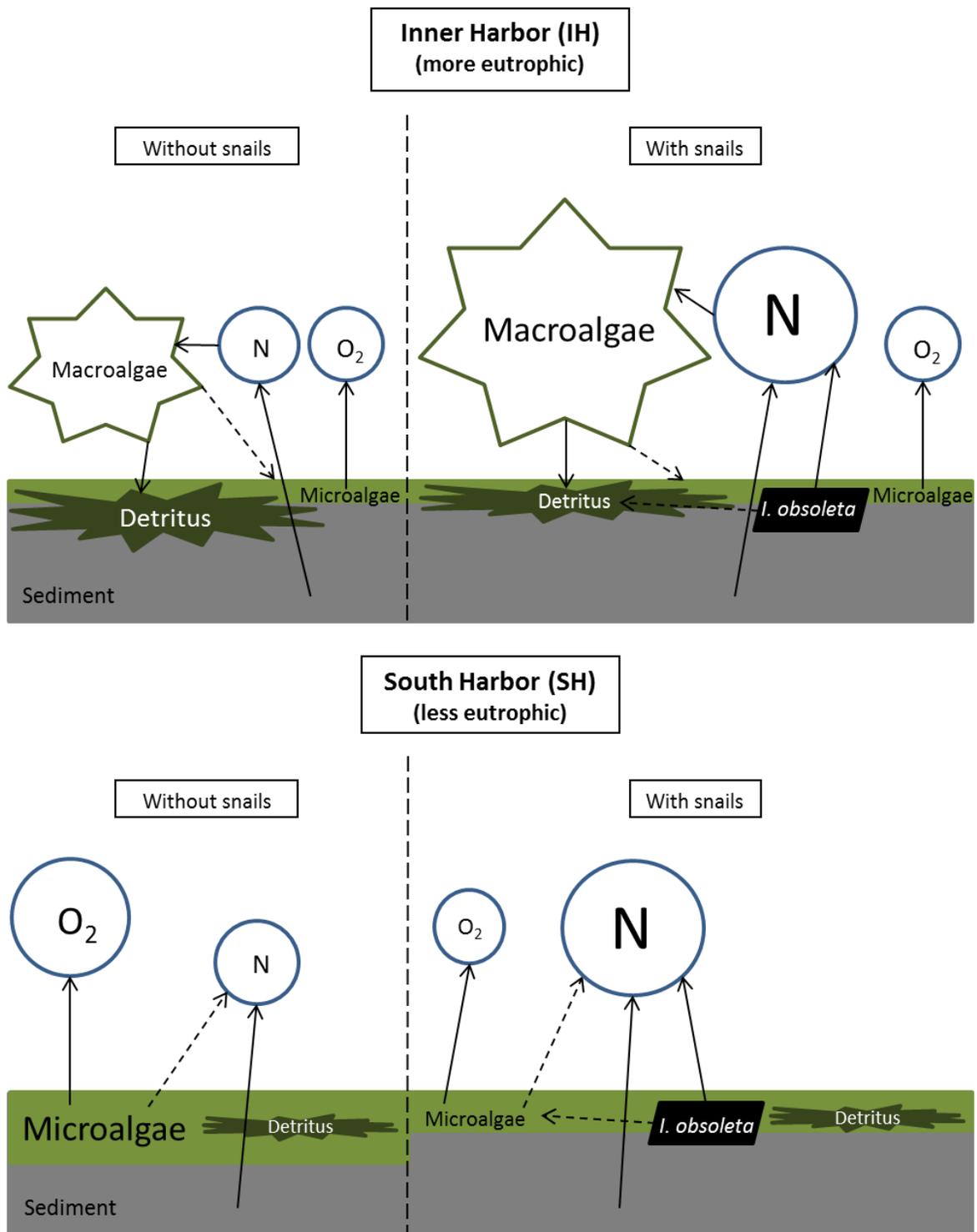


Fig. 10. General conceptual diagram of *I. obsoleta* effects on feedbacks in the Inner and South Harbors. Solid lines indicate positive interactions, dotted lines indicate negative interactions. Element and font size indicates relative magnitude. Nitrogen and Oxygen pools indicated by circled "N" and "O₂", respectively.

Literature Cited

- Ale, M. T., Mikkelsen, J. D., Meyer, A. S. (2011) Differential growth response of *Ulva lactuca* to ammonium and nitrate assimilation. *Journal of Applied Phycology* 23(3), 345-351.
- Anderson, W. (1970). A preliminary study of the relationship of salt ponds and wildlife South San Francisco Bay. *California Fish and Game* 56, 240-252.
- Ashkenas, L. R., Atema, J. (1978). A salt marsh predator-prey relationship: attack behavior of *Carcinus maenas* (L) and defenses of *Ilyanassa obsoleta* (Say). *Biol. Bull. Mar. Biol. Lab., Woods Hole* 155, 426.
- Atema, J., Burd, G. D. (1975). A field study of chemotactic responses of the mud snail *Nassarius obsoletus*. *J. chem. Ecol.* 1, 243-251.
- Barbier, E. B., Hacker, S. D., Kennedy, C., Koch, E. W., Stier, A. C., Silliman, B. R. (2011). The value of estuarine and coastal ecosystem services. *Ecological Monographs* 81(2), 169-193.
- Breitburg, D. L., Craig, J. K., Fulford, R. S., Rose, K. A., Boynton, W. R., Brady, D. C., Ciotti, B. J., Diaz, R. J., Friedland, K. D., Hagy III, J. D., Hart, D. R., Hines, A. H., Houde, E. D., Kolesar, S. E., Nixon, S. W., Rice, J. A., Secor, D. H., Targett, T. E. (2009). Nutrient enrichment and fisheries exploitation: interactive effect on estuarine living resources and their management. *Hydrobiologia* 629, 31-47.
- Brenchley, G. A. (1981). "Limiting resources and the limits to reproduction in the mud snails *Ilyanassa obsoleta* in Barnstable Harbor, Massachusetts." *Biol Bull* 161, 323.
- Bricker, S. B., Longstaff, B., Dennison, W., Jones, A., Boicourt, K., Wicks, C., Woerner, J. (2007). Effects of nutrient enrichment in the nation's estuaries: A decade of change. *Harmful Algae* 8(1), 21-32.
- Cloern, J. E. (2001). Our evolving conceptual model of the coastal eutrophication problem. *Marine Ecology Progress Series* 210, 223-253.
- Cohen, I., Neori A. (1991). *Ulva lactuca* biofilters for marine fishpond effluents: ammonia uptake kinetics and nitrogen content. *Botanica Marina* 34, 475-482.
- Connor, M. S. (1980). Snail Grazing Effects on the Composition and Metabolism of Benthic Diatom Communities and Subsequent Effects on Fish Growth. Massachusetts Institute of Technology and Woods Hole Oceanographic Institution, Woods Hole MA.
- Costanza, R., d'Arge, R., Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R., Paruelo, J., Raskin, R., Sutton, P., van den Belt, M. (1997). The value of the world's ecosystem services and natural capital. *Nature* 387, 253-260.

- Curtis, L. A., Hurd, L. E. (1981). Nutrient Procurement Strategy of a Deposit-feeding Estuarine Neogastropod, *Ilyanassa obsoleta*. Estuarine, Coastal and Shelf Science 13, 277-285.
- D'Asaro CN (1986). Egg capsules of eleven marine prosobranchs from northwest Florida. Bull Mar Sci 39, 76-91.
- D'Avanzo, C., Kremer, J. N., & Wainright, S. C. (1996). Ecosystem production and respiration in response to eutrophication in shallow temperate estuaries Marine Ecology Progress Series 141, 263-274.
- Dalsgaard, T., Thamdrup B., & Canfield, D. E. (2005). Anaerobic ammonium oxidation (anammox) in the marine environment. Research in microbiology 156, 457-64.
- DeMartini EE (1991). Spawning success of the male plainfin midshipman: Substratum as a limiting spatial resource. J Exp Mar Biol Ecol 146, 235-251.
- Dortch, Q. (1990). The interaction between ammonium and nitrate uptake in phytoplankton. Marine Ecology Progress Series 61, 183-201.
- Cardoso, P. G., Pardal, M. A., Raffaelli, D., Baeta, A., Marques, J. C. (2004). Macroinvertebrate response to difference species of macroalgal mats and the role of disturbance history. Journal of Experimental Marine Biology and Ecology 308, 207-220.
- Fong, P., Desmond, J.S. (1997). The effect of a horn snail on *Ulva expansa* (Chlorophyta): Consumer or facilitator of growth? J Phycol 33, 353-359.
- Fox, S. E., Teichberg, M., Olsen, Y. S., Heffner, L., Valiela, I. (2009). Restructuring of benthic communities in eutrophic estuaries: lower abundance of prey leads to trophic shifts from omnivory to grazing. Marine Ecology Progress Series 380, 43-57.
- Giannotti, A. L., & McGlathery, K. J. (2001). Consumption of *Ulva lactuca* (Chlorophyta) by the omnivorous mud snail *Ilyanassa obsoleta*. Journal of Phycology 37, 209-215.
- Goeyens, L., N. Kindermans, M. A. Yusuf, and M. Elskens. (1998). A room temperature procedure for the manual determination of urea in seawater. Estuarine Coastal and Shelf Science 47,415-418.
- Gray, J. S. (1989). Effects of environmental stress on species rich assemblages. Biol. J. Linn. Soc. 37,19-32.
- Guidone, M., Thornber, C. S., Field, E. (2010). Snail grazing facilitates growth of a bloom-forming alga. Marine Ecology Progress Series 420, 83-89.
- Hauxwell, J., Cebrian, J., Furlong, C., Valiela, I. (2001). Macroalgal canopies contribute to eelgrass (*Zostera marina*) decline in temperate estuarine ecosystems. Ecology 82(4), 1007-1022.

- Howarth, R. W., Boyer, E. W., Pabich, W. J., Galloway, J. N. (2002). Nitrogen Use in the United States from 1961–2000 and Potential Future Trends. *Ambio* 31(2), 1-9.
- Hauxwell, J., McClelland, J., Beir, P., Valiela, I. (1998). Relative importance of grazing and nutrient controls of macroalgal biomass in three temperate shallow estuaries. *Estuaries* 21(2), 347-360.
- Howarth, R. W., Marino, R. (2006). Nitrogen as the limiting nutrient for eutrophication in coastal marine ecosystems: Evolving views over three decades. *Limnology and Oceanography* 51, 364-376.
- Howes, B.L., Kelley S.W., Ramsey J., Samimy R.I., Schlezinger D.R., Eichner E.M. (2006) Linked watershed-embayment model to determine critical nitrogen loading thresholds for West Falmouth Harbor, MA. SMAST/DEP Massachusetts Estuaries Project, Massachusetts Department of Environmental Protection, Boston.
- Ieno, E. N., Solan, M., Batty P., Pierce, G. J. (2006). How biodiversity affects ecosystem functioning: roles of infaunal species richness, identity, and density in the marine benthos. *Marine Ecology Progress Series* 311, 263-271.
- Kelaher, B. P., Levinton, J. S., & Hoch, J. M. (2003). Foraging by the mud snail, *Ilyanassa obsoleta* (Say), modulates spatial variation in benthic community structure. *Experimental Marine Biology and Ecology* 292, 139-157.
- Krause-Jensen, D., Christensen, P. B., Rysgaard, S. (1999). Oxygen and nutrient dynamics within mats of the filamentous macroalga *Chaetomorpha linum*. *Estuaries* 22(1), 31-38.
- Kuhlmann, M.L. (1997). Regulation of fish reproduction by a predatory gastropod: an experimental investigation of indirect effects in a seagrass community. *J Exp Mar Biol Ecol* 218, 199–214.
- Lachat Instruments. (2003). Determination of Ammonium, Nitrate, Ortho-phosphate and Total Phosphorus. Loveland, CO.
- Lomstein, B. A., Guldborg, L. B., Neubauer, A.-T. A., Hanson, J., Andrew, D., Herbert, R., Viaroli, P., Giordani, G., Azzoni, R., de Wit R., Finster K. (2006). Benthic decomposition of *Ulva lactuca*: A controlled laboratory experiment. *Aquatic Botany* 85, 271-281.
- Lotze, H., Lenihan, H., Bourque, B., Bradbury, R., Cooke, R., Kay, M., Kidwell, S., Kirby, M., Peterson, C., Jackson, J. (2006). Depletion, degradation, and recover potential of estuaries and coastal seas. *Science* 312, 1806-1809.
- McGlathery, K. J., Krause-Jensen, D., Rysgaard, S., & Christensen, P. B. (1997). Patterns of ammonium uptake within dense mats of the filamentous macroalga *Chaetomorpha linum*. *Aquatic Botany* 59(1-2), 99-115.

- McGlathery, K. J., I. C. Anderson, and A. C. Tyler. (2001). Magnitude and variability of benthic and pelagic metabolism in a temperate coastal lagoon. *Marine Ecology Progress Series* 216, 1-15.
- McGlathery, K. J., Sundback, K., Anderson, I. C. (2007). Eutrophication in shallow coastal bays and lagoons: the role of plants in the coastal filter. *Marine Ecology Progress Series* 348, 1-18.
- McLenaghan, N. A. (2009). *Benthic macroinvertebrate diversity in a shallow estuary: controls on nutrient and algal dynamics*. Rochester Institute of Technology.
- McLenaghan, N.A., A.C. Tyler, U.H. Mahl, R. W. Howarth, R. M. Marino. (2011). Benthic macroinvertebrate functional diversity regulates nutrient and algal dynamics in a shallow estuary. *Marine Ecology Progress Series* 426, 171-184.
- Mermillod-Blondin, F., R. Rosenberg, F. Francois-Carcaillet, K. Norling, L. Mauclair. (2004). Influence of bioturbation by three benthic infaunal species on microbial communities and biogeochemical processes in marine sediment. *Aquat Microb Ecol* 36, 271-284.
- Mulvenna, P. F., Savidge, G. (1992). A modified manual method for the determination of urea in seawater using diacetylmonoxime reagent. *Estuarine, Coastal and Shelf Science* 34, 429-438.
- Needham, H., Pilditch, C., Lohrer, A., Thrush, S. (2011). Context-specific bioturbation mediates changes to ecosystem functioning. *Ecosystems* 14(7), 1096-1109.
- Newell, R. (1965). The role of detritus in the nutrition of two marine deposit feeders, the prosobranch *Hydrobia ulvae* and the bivalve *Macoma balthica*. *Proceedings of the Zoological Society of London* 144(1), 25-45.
- Nixon, S., Buckley, B., Granger, S., Bintz, J. (2001). Responses of very shallow marine ecosystems to nutrient enrichment. *Human and Ecological Risk Assessment* 7(5), 1457 – 1481.
- Nixon, S., Granger, S.L., Nowicki, B.L. (1995). Coastal marine eutrophication: a definition, social causes, and future concerns. *Ophelia* 41, 199-219.
- Paerl, H. (2009). Controlling eutrophication along the freshwater-marine continuum: dual nutrient (N and P) reductions are essential. *Estuaries and Coasts* 32, 593-601.
- Pearson, T. H., and R. Rosenberg. (1978). Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr. Mar. Biol. Ann. Rev.* 163, 229-311.
- Pechenik, J.A. (1978). Adaptations to intertidal development: studies on *Nassarius obsoletus*. *Biol Bull* 154, 282-291.

- Pillay, D., Branch, G., Steyn, A. (2009). Complex effects of the gastropod *Assimineia globulus* on benthic community structure in a marine-dominated lagoon. *Journal of Experimental Marine Biology and Ecology* 380, 47-52.
- Premo, K. (2011). *Invertebrate effects on sediment biogeochemistry and microphytobenthos following estuarine macroalgal blooms*. MS Thesis. Rochester Institute of Technology.
- Recher, H. F. (1966). Some aspects of the ecology of migrant shorebirds. *Ecology* 47, 393-407.
- Scheiner, C. (2011). *Scaling-up in Estuaries: The Feasibility of Using Small Scale Results to Draw Large Scale Conclusions*. MS Thesis. Rochester Institute of Technology.
- Silliman, B. R., & Bertness, M. D. (2002). A trophic cascade regulates salt marsh primary production. *Proceedings of the National Academy of Sciences* 99(16).
- Solorzano, L. (1969). Determination of ammonia in natural waters by the phenylhypochlorite method. *Limnology and Oceanography* 14, 799-801.
- Stenzler, D., Atema, J. (1977). Alarm response of the marine mud snail *Nassarius obsoletus*: specificity and behavioral priority. *J. chem. Ecol.* 3, 159-171.
- Swanson, C. (2004). Effect of substrate availability and conspecific cues on communal oviposition in the apple murex snail *Phyllonotus pomum*. *Marine Ecology Progress Series* 275, 175-184.
- Teichberg, M., Fox, S. E., Olsen, Y S., Valiela, I., Mertinetto, P., et al. (2010). Eutrophication and macroalgal blooms in temperate and tropical coastal waters: nutrient enrichment experiments with *Ulva* spp. *Global Change Biology* 16(9), 2624-2637.
- Thrush, S.F., Dayton, P.K. (2002). Disturbance to marine benthic habitats by trawling and dredging: implications for marine biodiversity. *Annual Review of Ecology and Systematics* 33, 449-473.
- Tyler, A. C., McGlathery, K. J., & Anderson, I. C. (2001). Macroalgae mediation of dissolved organic nitrogen fluxes in a temperate coastal lagoon. *Estuarine, Coastal and Shelf Science* 53, 155-168.
- Tyler, A.C., McGlathery, K.J. & Anderson I. C. (2003). Benthic algae control sediment-water column fluxes of nitrogen in a temperate lagoon. *Limnology and Oceanography*. 48, 2125-2137.
- Tyler, A. C., McGlathery, K. J., & Macko, S. A. (2005). Uptake of urea and amino acids by the macroalgae *Ulva lactuca* (Chlorophyta) and *Gracilaria vermiculophylla* (Rhodophyta). *Marine Ecology Progress Series* 294, 161-172.

- Tyler, A. C., & McGlathery, K. J. (2006). Uptake and release of nitrogen by the macroalgae *Gracilaria vermiculophylla* (Rhodophyta). *Phycological Society of America* 42, 515-525.
- USEPA. (2002). Short-term methods for estimating the chronic toxicity of effluents and receiving water to freshwater organisms. USEPA, 197-224.
- Valiela, I., Foreman K., LaMontagne, M., Hersh, D., Costa, J., D'Avanzo, C., Babione, M., Peckol, P., DeMeo-Adreson, B., Sham, C., Brawley, J., Lajtha, K. (1992). Couplings of Watersheds and Coastal Waters: Sources and Consequences of Nutrient Enrichment in Waquoit Bay, Massachusetts. *Estuaries* 15(4), 443-457.
- Valiela, I., McClelland, J., Hauxwell, J., Behr, P. J., Hersh, D., & Foreman, K. (1997). Macroalgal blooms in shallow estuaries: Controls and ecophysiological and ecosystem consequences. *Limnology and Oceanography* 42(5), 1105-1118.
- Waycott, M., Duarte, C., Carruthers, T., Orth, R., Dennison, W., Olyarnik, S., Calladine, A., Fourqurean, F., Heck, K., Hughes, A., Kendrick, G., Kenworthy, W., Short, F., Williams, S. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Science* 106(30), 12377-12381.
- Weerman, E. J., Herman, P. M. J., Koppel, J. (2011). Macroinvertebrate abundance and distribution on a spatially patterned intertidal flat. *Marine Ecology Progress Series* 440, 95-103.
- Wildsmith, M. D., Rose, T. H., Potter, I. C., Warwick, R. M., Clarke, K. R. (2011). Benthic macroinvertebrates as indicators of environmental deterioration in a large microtidal estuary. *Marine Pollution Bulletin* 62, 525-538.