# CONTROLS ON BENTHIC BIODIVERSITY AND TROPHIC INTERACTIONS IN A TEMPERATE COASTAL LAGOON

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**ABSTRACT**

Coastal lagoons are shallow land-margin ecosystems that are vulnerable to nutrient over-enrichment and macroalgal blooms. Dense macroalgal mats influence sediment chemistry, benthic community structure and trophic dynamics. Understanding the controls on macroalgal mat formation and how these mats influence the faunal community is key to managing nutrient enrichment in coastal systems. The objectives of this dissertation were to: (1) examine the effects of macroalgae on the density and community composition of benthic fauna in Hog Island Bay; and (2) examine top-down influence on algal biomass by examining grazer controls on algae.

The macroalgal biomass that created a discernible negative impact on the faunal community was much lower than reported previously, but the macroinvertebrate response was non-linear which may be indicative of shallow coastal systems. Macroalgae increased pore water $NH_4^+$ concentration and $NH_4^+$ flux from the upper sediment layers. Increasing total density of infauna resulted in a decreased flux, which may be the result of enhanced nitrification from increased oxygen availability associated with macroalgae and infauna. Invertebrate biodiversity was highest at medium macroalgal density. Increasing species richness appeared to positively influence $NH_4^+$ flux in the presence of macroalgae, but negatively in the absence of macroalgae. The summer peak in invertebrate density paralleled the peak in macroalgae so macroalgae are thought to be a strong benthic-structuring factor. The main difference between the lagoon and tidal-creek sites was species richness, where the tidal-creek supports high densities but only of a few generalist species.

Amphipods and snails were significant consumers of macroalgae, but reduced grazing rates and grazer abundance at high macroalgal density prevented these grazers from controlling macroalgal proliferation. Interpretation of top-down effects in shallow coastal systems will be skewed if macroalgal density is not considered in calculating per capita grazing rates, since there is potential to underestimate grazing impact at mid-densities and to overestimate grazing impact at high-densities. In these systems physical processes may be more important in advection of macroalgae and local bloom formation, with nutrient status and remineralization secondarily important in sustaining blooms.

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> Is a wild call and a clear call that may not be denied…..
> -John Masefield

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# 1. INTRODUCTION

## 1.1 Background

Coastal lagoons are important land margin ecosystems, especially along the Atlantic coast of the U.S. (Nixon 1982). Lagoons are shallow and well mixed; freshwater and nutrient inputs are mainly via groundwater and precipitation. The sea floor is in the photic zone and benthic primary producers are the dominant autotrophs. As land margin ecosystems, lagoons are vulnerable to nutrient over-enrichment primarily from agriculturally enriched groundwater (Boynton et al. 1996). Increased nutrient loads have lead to increased production of opportunistic macroalgae in coastal areas and, in some cases, the algae have formed high-density mats (Rosenberg 1985; Hull 1987; Raffaelli et al. 1991; Isaksson and Pihl 1992; Norkko and Bonsdorff 1996a, 1996b; Norkko 1998). The formation of macroalgal mats can affect sediment chemistry, community structure and trophic dynamics. Dense algal mats affect benthic community recruitment by reducing light and oxygen, by interfering with larval settlement (Ólafsson 1988) and by altering predator-prey relationships (Norkko and Bonsdorff 1996a, 1996b). Mass blooms of macroalgae are widespread in shallow coastal systems and are considered a nuisance, especially when they decompose (Raffaelli et al. 1998). Understanding the controls on algal mat formation and how these mats influence the faunal community is key to managing nutrient enrichment in coastal systems.

The purposes of this research were: (1) to examine the effects of algal mats on the density and community composition of the benthic infauna and epifauna in Hog Island Bay; and (2) to examine top-down influence on algal biomass in Hog Island Bay by

examining grazer controls on algae. While massive blooms of macroalgae have been found to have a negative impact on the macrofauna in shallow systems (Table 1.1), chronic low-level effects of macroalgal biomass should also be important in community structure, and negative impact may occur at much lower macroalgal densities than have been previously reported in the literature. Consequently, the effect of nutrient loading on benthic fauna is likely to have a much lower threshold than that associated with macroalgal blooms. Few studies examining grazer control on algae have been done at natural field algal densities where changes in physical and chemical factors are likely to influence per capita grazing rates. In addition, food quality and grazer size are factors related to grazer control of algal biomass. Studies have shown that nitrogen content of food is important in determining the quality of the food for the grazer and the grazing rate (Mann 1988; Buchsbaum et al. 1991; Hauxwell et al. 1998) and little is known about the impact of different size grazers.

### 1.2 Benthic Biodiversity and Community Structure

High macroalgal densities frequently lead to hypoxic or anoxic conditions at the sediment-macroalgal mat interface due to algal respiration and decay in the deeper layers of algal mats where light does not penetrate. The change in oxygen availability has been shown to increase the density and biomass of the epifauna while decreasing the density and biomass of the infauna. Increases in epifauna have resulted in large increases in total biomass in areas studied, but have also been associated with a change in dominant species (Nicholls et al. 1981; Isaksson and Pihl 1992; Pihl et al. 1995). The decline in infauna has been most severe where the algae are dense, long lasting and eventually

become incorporated into the sediments (Price and Hylleberg 1982; Everett 1991; Thiel and Watling 1998; Thiel et al. 1998).

The reduced oxygen availability at the sediment surface resulting from the formation of dense algal mats often leads to local extinction of the benthic fauna (Hull 1987; Isaksson and Pihl 1992). The feeding and burrowing activities of benthic animals ventilates the sediments as well as stimulates the decomposition of organic matter (Hansen and Kristensen 1997; 1998; Raffaelli et al. 1998). Bioturbators generate more oxidized sediment conditions by pulling oxygen down into the sediment, often up to several centimeters in depth (Raffaelli et al. 1998). This can enhance nitrification-denitrification and thus promote removal of sediment nitrogen pools (Seitzinger 1988; Hansen and Kristensen 1998). However, the bioturbating fauna enhance the decomposition of organic matter and increase nitrogen mineralization (Hansen and Kristensen 1997; 1998) and it is also thought that bioturbating activities lead to a release of nitrogen and increased macroalgal growth (Seitzinger 1988; Raffaelli et al. 1998). The loss of bioturbation when benthic animals become locally extinct can lead to accumulation of organic matter and nutrients in the sediment (Hansen and Kristensen 1997).

The effects of the macroalgae may reach beyond the benthic invertebrates to other organisms in the system. Fish assemblage structures have been altered by the persistence of algal mats (Isaksson and Pihl 1992; Pihl et al. 1994; 1995) and dense algal mats are avoided by shorebirds, possibly due to changes in abundance of invertebrates (Nicholls et al. 1981; Raffaelli et al. 1989). Even with these negative conditions, algal mats may still function as refugia for species that make the trade-off to a hazardous environment to

escape from predators (Norkko and Bonsdorff 1996a, 1996b; Norkko 1998). The macroalgal mats are also important in structuring the benthic community since they frequently coincide with summer production and recruitment (Ólafsson 1988; Norkko and Bonsdorff 1996a) as well as provide an annual organic input to the sediment (Hull 1987; Theil and Watling 1998).

Many studies have shown that the presence of dense macroalgal mats can have dramatic effects on the benthic faunal community (Nicholls et al. 1981; Soulsby et al. 1982; Raffaelli et al. 1989; Isaksson and Pihl 1992; Norkko and Bonsdorff 1996a; Norkko 1998; Bolam et al. 2000; Österling and Pihl 2001). Most of these studies have focused on moderate to high algal biomass but the negative impact on macrofauna probably occurs at much lower algal biomass. In addition, much of this work has been on mudflats and intertidal areas and has focused on the effect of a single filamentous algal species (Table 1.1). Algal mats, like those in Hog Island Bay, are often composed of numerous algal species. Overall, little is known about the range of algal densities that would produce negative effects on the benthic community in a subtidal system.

**1.3 Trophic Interactions**

Macroalgal biomass may be controlled by bottom-up processes such as nutrient enrichment (Valiela et al. 1997), but in some areas, grazing (top-down process) can mediate algal accumulation and control algal biomass (Duffy and Hay 1991; Geertz-Hansen et al. 1993; Valiela et al.1997; Hauxwell et al. 1998; Duffy and Hay 2000; Giannotti and McGlathery 2001). It has been shown that small invertebrate grazers (i.e., amphipods, isopods and small gastropods) may control macroalgal biomass accumulation

under low and moderate nutrient loading (Hauxwell et al. 1998; Giannotti and McGlathery 2001). Duffy and Hay (2000) found that selective amphipod grazing can alter the community structure of benthic macroalgae and that their impact was disproportionately greater than their biomass. Thus, factors influencing grazer abundance are important in determining the degree to which nutrient enrichment controls algal biomass. In addition, little is known about grazer size as a factor in grazing rate. Understanding these factors is important in evaluating the role of nutrient enrichment in the proliferation of macroalgae in shallow coastal systems (Heck et al. 2000). Factors that may influence grazers include food supply and food quality, predation from fish and the physico-chemical environment such as sedimentation and anoxia (Geertz-Hansen et al. 1993; Duffy and Hay 2000; Heck et al. 2000). Grazers decrease biomass of preferred macroalgal species and can, therefore, alter competitive interactions within the algal community. In addition to oxygen stress from dense macroalgal mats, sedimentation and water currents may alter the physico-chemical environment of coastal systems making the habitat unsuitable for grazer species or make the macroalgae less palatable. While it is known that algal mats baffle water currents and trap sediment, little is known about how increased sedimentation affects grazers.

Studies on grazer control of macroalgal biomass have used laboratory grazing rates to extrapolate to field grazing or grazing rates from the field with cages suspended in the water column (Hauxwell et al. 1998; Giannotti and McGlathery 2001). This approach may yield erroneous estimates of system-level grazing impact, as grazing under the favorable laboratory conditions is expected to be higher and less variable than under field conditions and suspended cages used in some experiments do not include physico-

chemical factors that are important in grazing rates. Per capita grazing rates should differ at different macroalgal densities because higher macroalgal density leads to greater canopy depth and self-shading of algae that can alter physico-chemical conditions. This will reduce grazing rates as well as grazer numbers. Thus, examining per capita grazing rates at various algal densities in the field is important for scaling up grazing measurements to the system.

High algal density is also related to increased sedimentation as large mats baffle water currents. This increased sedimentation can decrease the palatability of the algae for grazers as well as reduce suitable habitat. Increased sedimentation will reduce food quality for grazers and thus reduce grazing as well as make it difficult for the grazers to reach the algal surface and feed on the algae. Some amphipods live in tubes on the algal surface and graze the algae within close proximity to these tubes. The presence of sediment may deter these amphipods from building these tubes and grazing the algae. Indirectly, these factors will affect grazer numbers and per capita grazing rate.

Grazer size may also be an important factor in grazing rate and thus in grazer control on macroalgae (Duffy and Hay 2000). Mesograzers, especially crustaceans like amphipods, are abundant in near-shore habitats, have high rates of secondary production, and are thus critical in near-shore trophic transfer (Duffy and Hay 2000). Small amphipods, within a species, are usually younger and potentially more voracious than large amphipods of the same species and would likely have a higher grazing rate.

Food quality is a further component that may influence grazing rate. Epifaunal grazers feed on detritus and macroalgae (Duffy and Hay 1991, 2000) as well as microalgae and epiphytes. Detritus from algae has large amounts of nitrogen available

and little structural/fibrous material, which makes it potentially highly palatable (Mann 1988). Algae have a higher nutritive value than macrophytes like marsh grass and seagrass because of the proportion of fibrous material present and algae are thus more efficiently assimilated (Mann 1988; Buchsbaum et al. 1991; Enriquez et al. 1993). There are also significant differences in nutritive quality between algal species. Furthermore, algae decompose rapidly and this makes detritus from algae a potentially significant nutritional source to grazing amphipods.

**1.4 Site Description**

Hog Island Bay (HIB) is a lagoon within the Virginia Coast Reserve (VCR) on the Eastern Shore of Virginia (Figure 1.3). The VCR lagoons are dominated by benthic microalgae and macroalgae. Nutrient input to HIB is derived primarily from groundwater flow enriched by agricultural activities, which provides a low nutrient load to the lagoon. In algal-dominated lagoons like HIB, processes within the lagoon influence the fate of nutrients entering the lagoon and the degree to which those nutrients are exported to the coastal ocean (Figure 1.1). For instance, macroalgal mats reduce the flux of nutrients across the sediment-water column interface (McGlathery et al. 1997) and can limit the phytoplankton growth in the overlying water (Valiela et al. 1997). In this way, macroalgae act as a filter in some areas, temporarily retaining nutrients in the lagoon. Some of the macroalgal-bound nutrients are permanently buried in the sediments as recalcitrant detrital material. In addition, grazing on the macroalgae allows for transfer of nutrients throughout the food web, which can either lead to further retention time of algal-bound N in the lagoon or transport out of the lagoon with animals as vectors. This

has important implications for the fate and transport of nutrient inputs from the coastal watershed through HIB to the coastal ocean. This research complements ongoing studies of macroalgal mediation of nitrogen processing in the VCR lagoons by providing information on the macrofauna, the trophic transfers of nutrients, the grazers and top-down control of macroalgae in this system.

The VCR contains 14 barrier islands, shallow shoals, mudflats, marsh islands, mainland marshes, tidal creeks and deep channels. It is managed by The Nature Conservancy and is a Long-Term Ecological Research (LTER) site. Each year over 30 extratropical storms occur with magnitudes sufficient to elevate tides above the highest norms (Hayden et al. 1999) and to generate waves and storm surges that can transport large amounts of macroalgae and sediment.

Study locations in HIB include a barrier island tidal creek (Creek), a mid-lagoon shoal (Shoal) and a back barrier embayment (Hog). Macroalgal mats accumulate seasonally, particularly in the shallow shoal sites in the middle of the lagoon where nutrient levels are low and light levels are moderate (McGlathery et al. 2000). Macroalgal biomass is typically lowest at the Hog embayment site. Since the greatest macroalgal accumulation is at the Shoal site, this will be the main site for most experiments. Macroalgae at the Shoal site usually bloom in late June – early July and can form dense mats (up to 30-cm thick) over the sediment surface. The red macroalga *Gracilaria tikvahiae* composes approximately 90% of the total algal biomass and has reached densities over 4600-g ww $m^{-2}$ (over 1800 g dw $m^{-2}$), so that total biomass including all algal species is greater. In addition, drift macroalgae are washed into the mid-lagoon Shoal and can further increase the algal biomass. Thus the Shoal site

provides the best site for examining the impact of high algal density on community structure and the potential for grazing control of macroalgal proliferation.

### 1.5 Definitions

Palatability: Palatability to herbivores is a function of nutritional value, toughness, or feeding deterrents in the food source. Palatability is used throughout as an indicator of both nitrogen content, which has been shown to be a factor in grazing rate, and surface coatings, such as sediment, that may reduce or enhance grazing on macroalgae, and therefore influence palatability of algae.

Community structure: Community structure will refer mainly to the organisms. My main focus will be on the benthic macrofaunal community structure including infauna and epifauna.

Food quality: Food quality is a combination of both nitrogen content and structural materials that may be present in algae or detritus.

### 1.6 Objectives

In order to examine controls on macroalgal mat formation and the influence of macroalgae on macrofauna, I developed a conceptual model for this system to highlight the main regulators of macrofaunal and grazer densities and grazing rates (Figure 1.2).

The following objectives were considered:

- monitoring seasonal changes in the macrofauna present within the macroalgal mats and within the sediment immediately under the macroalgal mats to determine if the macrofauna differ among established sites in the lagoon and barrier-island tidal creek

- determining the value of algal density that creates a negative impact on the macrofauna.
- determining the influence of macroalgae and macroinvertebrates on $NH_4^+$ dynamics.
- estimating macroalgal biomass loss to the dominant grazers (amphipods and snails) and estimating grazing rates for different sizes of amphipods.
- determining what impact physico-chemical factors have on grazer abundance.
- examining grazing on live and detrital macroalgae and determining which has a higher nitrogen content (as a measure of palatability and nutritional quality).
- comparing grazing rates on the dominant macroalgae when combined at different densities.

**1.7 Dissertation Organization**

The body of this dissertation is divided into three main chapters. Chapter 2 deals with the impact that macroalgal density has on macroinvertebrate density and biodiversity as well as $NH_4^+$ pore water profiles and Chapter 3 deals with the interactions between macroalgal density and per capita grazing rates based on two field experiments and a series of laboratory experiments. Chapter 4 examines the seasonal and spatial variation in invertebrate density in three sites in Hog Island Bay including the mid-lagoon Shoal, the back-barrier embayment of Hog, and the barrier island tidal Creek on Hog Island. The final chapter (Chapter 5) links these chapters together with conclusions and consideration of the interactions.

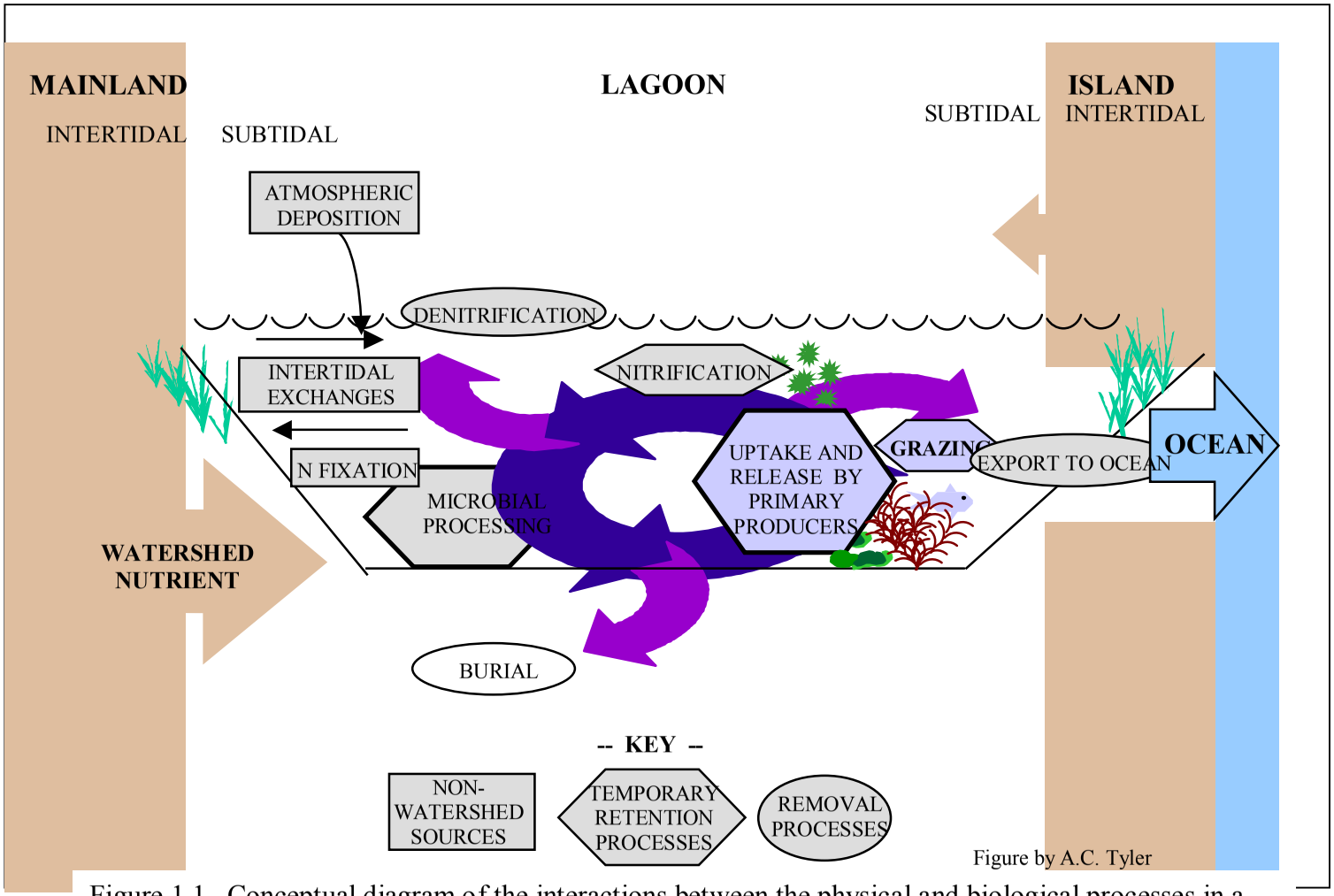



Figure 1.1. Conceptual diagram of the interactions between the physical and biological processes in a lagoonal system.

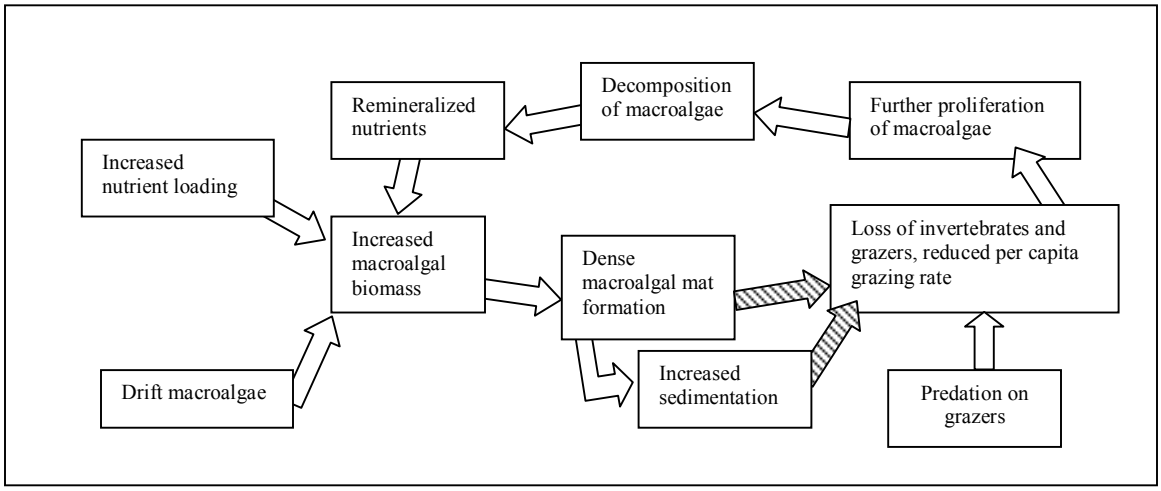



Figure 1.2. Model of the factors that may affect macroinvertebrate and grazer density and grazing rate at the Virginia Coast Reserve. Shaded arrows indicate the main factors to be tested with this research.

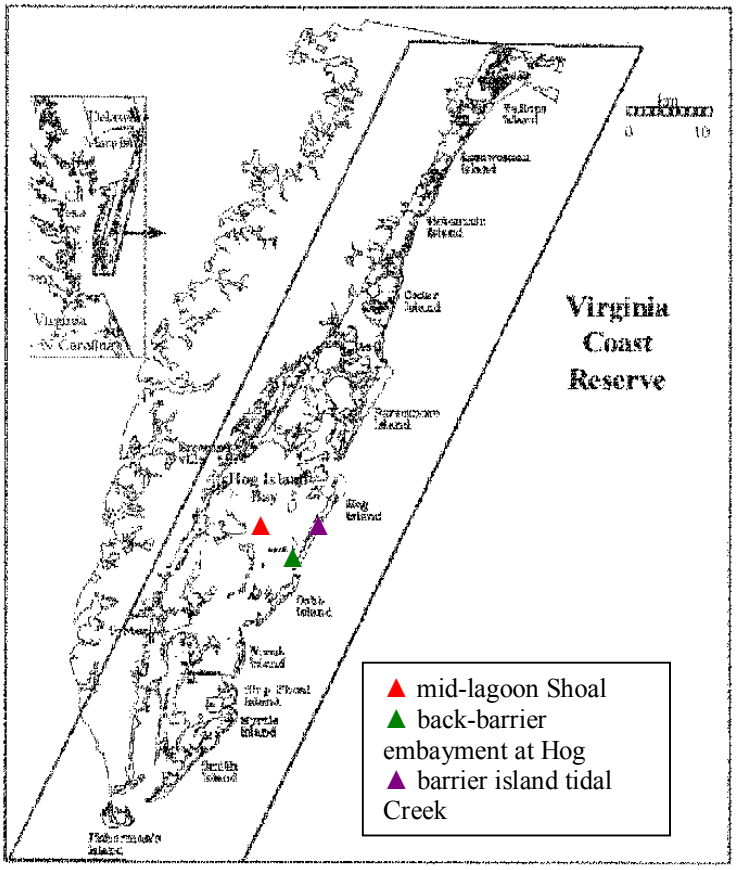



**Figure 1.3**. **Figure of the Virginia Coast Reserve including Hog Island Bay and Hog Island. The three main study locations are indicated.**

Table 1.1. Previous studies on the impact of macroalgal mats on benthic macrofauna.

| Location | Algal type | Algal biomass | Conclusion | Source |
|---|---|---|---|---|
| Intertidal, field experiment | Filamentous green algae | 2000-g ww $m^{-2}$ | Decreased diversity | Bolam et al. 2000 |
| Intertidal mudflat, field experiment | Filamentous green algae | 0 – 3000-g ww $m^{-2}$ | Increased infauna | Hull 1987 |
| Intertidal mudflat, field experiment | Filamentous green algae | >2000-g ww $m^{-2}$ | Decreased density of burrowing amphipod species | Raffaelli et al. 1989 |
| Intertidal mudflat, field experiment | Filamentous green algae (mainly) | No biomass, 10 – 12-cm depth coverage with algae | Increased faunal biomass, decrease infauna, increase epifauna | Nicholls et al. 1981 |
| Subtidal, field and laboratory experiment | Filamentous green algae | 1200-g ww $m^{-2}$ | Decreased epifauna and infauna | Österling and Pihl 2001 |
| Subtidal, laboratory experiment | Filamentous green and brown algae | 1000-g ww $m^{-2}$ 2000-g ww $m^{-2}$ | Decreased infauna | Norkko et al. 2000; Norkko 1998; Norkko and Bonsdorff 1996 |
| Subtidal, field experiment | Filamentous green and brown algae (epiphytic on seagrass) | No biomass, used % cover | Decreased epifauna | Isaksson and Pihl 1992 |

# 2. Impact of Macroalgal Blooms on Benthic Biodiversity and Ecosystem Functioning

## 2.1 Introduction

Lagoons are shallow, littoral zone systems in which sufficient light penetrates the water column to support considerable growth of benthic primary producers such as seagrasses, macroalgae and benthic microalgae. In coastal lagoons subject to moderate to high nutrient loading, fast-growing macroalgae often have a competitive advantage and dominate over slow-growing macroalgae and seagrasses (Sfriso et al. 1992; Valiela et al. 1997). As macroalgae accumulate, thick mats may form over the sediment surface and within the water column; this influences nutrient cycling at the sediment-water column interface as well as benthic faunal community composition and functioning (e.g. McGlathery et al. 1997; Trimmer et al. 2000; Rysgaard et al. 1995; Hansen and Kristensen 1997). There is much evidence for loss of numerous benthic faunal species with the accumulation of macroalgae; in particular, bioturbators frequently become locally extinct along with their utility in ventilating the sediments and promoting nutrient recycling (see, for example, Hull 1987; Bonsdorff 1992; Everett 1994; Rysgaard et al. 1995; Hansen and Kristensen 1997). This issue of changes in biodiversity and ecosystem functioning has become a principal concern in marine ecology, and in ecology in general, in recent years (Tilman 2000; Worm et al. 2002; Duffy 2003; Duffy et al. 2003; Emmerson and Huxham 2002). However, with few exceptions, studies have not focused on effects at more than one trophic level (Duffy 2003; Duffy et al. 2003; Emmerson and Huxham 2002). Systems like lagoons may be particularly vulnerable to loss of diversity

and associated ecosystem functioning since lagoons are shallow land-margin ecosystems, and as such, are more susceptible to human impacts that drive most biodiversity loss (Jenkins 2003).

Nutrient cycling within the sediments is enhanced by macroalgae, probably due to increased inputs of organic matter following senescence (Trimmer et al. 2000). Because macroalgae have little structural material and decompose rapidly (Mann 1988; Buchsbaum et al. 1991; Enriquez et al. 1993), there is increased potential for substantial and rapid contribution of nutrients to the sediments and the overlying water column. This is especially important in shallow systems like lagoons because there is high sediment surface-area to water volume ratio, which increases the relative significance of sediment-water column interactions in the system (Sand-Jensen and Borum 1991). Nutrient regeneration may provide an important source of nitrogen to sustain benthic macroalgal productivity and some systems may function as self-regenerating through this recycling of nitrogen (McGlathery et al. 1997; Stimson and Larned 2000; Trimmer et al. 2000; Sundbäck et al. 2003). Even with drifting macroalgal mats, the accumulation of $NH_4^+$ occurs quickly (within-24 hours) and can alter sediment-water column nutrient exchange (Astill and Lavery 2001).

Remineralization of organic matter in the sediments and within dense macroalgal mats typically causes a build-up of ammonium ($NH_4^+$) within and under macroalgal mats, primarily when mats are thick and light attenuates quickly. Light is attenuated in the top few cm of dense macroalgal mats (Peckol and Rivers 1996; Astill and Lavery 2001), which effectively leaves the bottom of mats in the dark and supports photosynthesis only in the upper layers of the mat. High respiration near the bottom of the mat results in

hypoxic and anoxic conditions (Krause-Jensen et al.1996; Astill and Lavery 2001). Ammonium builds up under low oxygen conditions in the bottom of the mat and in the underlying surface sediments in part because nitrification is inhibited and in part due to decomposition of macroalgae (McGlathery et al. 1997; Trimmer et al. 2000; Astill and Lavery 2001). There is little information on the effects of these processes in deeper sediment layers underlying macroalgal accumulations.

The build-up of $NH_4^+$ in sediments under macroalgal mats may also be a function of local extinction or reduced activity of macrofauna caused by anoxic or hypoxic conditions associated with dense macroalgal mats (Nicholls et al. 1981; Thrush 1986; Raffaelli et al. 1989; Isaksson and Pihl 1992; Everett 1994; Posey et al. 1995; Norkko and Bonsdorff 1996; Hansen and Kristensen 1997; Hansen and Kristensen 1998; Norkko 1998; Yamamuro and Koike 1998; Norkko et al. 2000; Österling and Pihl 2001; Posey et al. 2002). Benthic macrofauna, especially bioturbators and bio-irrigators, are important in nutrient exchange in marine sediments for several reasons. Activities such as burrowing rework sediments and may move organic matter to different depths within the sediment. Burrow dwellers ventilate their burrows and are important in oxygenation of deeper sediments and solute exchange at the sediment-water column interface. Thus, macrofauna directly enhance the release of $NH_4^+$ by stimulating mineralization and enhancing transport processes to greater depths in the sediment (Hansen and Kristensen 1997; Hansen and Kristensen 1998; Yamamuro and Koike 1998). By oxygenating the sediments, benthic fauna also stimulate nitrification and thus can be important in stimulating coupled nitrification-denitrification (Rysgaard et al. 1995; Gilbert et al. 1998; Hansen and Kristensen 1998).

While it is known that high-density macroalgal mats have a negative impact on macrofauna (see Table 1.1), chronic low-level effects of macroalgal biomass also may have an important influence on benthic community structure, and it is likely that negative impacts of macroalgal accumulations may occur at much lower macroalgal densities than have been reported previously in the literature. As noted for seagrass systems and terrestrial systems, changes in habitat structure can produce extreme shifts in abundance and distribution of species, with small patches often supporting higher densities of some species due to the greater edge area on small patches (Kolasa 1989; With and Crist 1995; Eggleston et al. 1998; Eggleston et al. 1999). If macroalgal density is used as a proxy for patch size, then increasing algal density would lead to reduction in invertebrate density. Specifically, low macroalgal biomass should have the highest invertebrate density followed by a decline as algal biomass increases, with more reductions in invertebrate density related to changes in physico-chemical parameters. Studies on the impact of macroalgal density on macrofaunal communities have largely been done in intertidal systems, with a few subtidal studies (Table 1.1). In the subtidal systems, a significant decrease in infauna and epifauna, as well as a loss of diversity, has been associated with moderate to high macroalgal densities (Table 1.1). The consequences of decreased macrofauna, even at low macroalgal density, may include accumulation of organic matter and nutrients in the sediment and reduced top-down control on macroalgal growth. To my knowledge, no study has examined directly the relationship among macroalgal density, macrofauna, and $NH_4^+$ pore water concentration and flux. If negative impacts on either macrofauna or on $NH_4^+$ cycling occur at lower macroalgal densities than have been previously reported, then these studies have underestimated the impact of macroalgal

accumulations on benthic biodiversity and ecosystem functioning. This study addressed this issue by focusing on the following objectives:

- to determine the value of algal density that creates a negative impact on the macrofauna.
- to determine the impact of macroalgal density on pore water $NH_4^+$ concentrations and calculated fluxes.
- to develop relationships among macroalgal density, macrofauna, and $NH_4^+$ pore water fluxes.

I hypothesized that (1) low densities of macroalgae would have a conspicuous effect on the benthic macrofauna by causing local extinction, shifting the dominant species present and increasing epifauna that can utilize algae for food or refuge but escape from the negative effects of algal mats and (2) increasing macroalgal biomass at the sediment surface will increase $NH_4^+$ concentration to greater depth in the sediments than has been previously reported.

## 2.2 METHODS

### *2.2.1 Macroalgal Density and Macroinvertebrates*

Algal density at the Shoal site was manipulated within cages to mimic the average algal density (control density) as well as to test the affect of near-zero algae (no-algae control), low and high algal densities on both infaunal and epifaunal abundances and community composition. Cages of 1-$m^2$ were constructed of rebar and plastic-coated wire mesh (mesh size ~8-$cm^2$) with a wire mesh lid to prevent algae from being removed from cages at high tide. In addition, there was a no-cage control consisting only of rebar.

There were three replicates of five algal densities (0-g ww $m^{-2}$, 1000-g ww $m^{-2}$, 2000-g ww $m^{-2}$, 3000-g ww $m^{-2}$, and ≥5000-g ww $m^{-2}$) to represent the range occurring naturally at this site. The algae were composed primarily of the dominant species, *Gracilaria tikvahiae* and *Ulva lactuca*. The mesh on the cages was large enough to allow most fauna to move freely between the cage and surrounding area while still maintaining the algae at the approximate prescribed density. Even with the lid on the cages, light was sufficient to saturate algal photosynthesis. Cages were cleaned regularly to minimize fouling. Sampling occurred bi-weekly for the 6-week experiment (June through July, 2000). Cores (9.5-cm inner diameter, taken through the algae to 20-cm depth into the sediment) were taken from random locations within the cages. Following sampling for sediment chemical and physical parameters ($NH_4^+$ pore water profiles and sediment characteristics), cores were sieved through a 1-mm mesh to collect algae and macrofauna. Macrofauna were sorted by species, and faunal abundance and diversity measures were related to the macroalgal treatment densities. Although a 0.5-mm mesh is typically recommended for macroinvertebrate studies, mesh sizes smaller than 1-mm clogged with sediment and I was unable to recover the macrofaunal specimens. Thus, a 1-mm mesh was used.

Macroalgal samples for organic C and N analysis were freeze dried and ground to homogeneity with a mortar and pestle. Sub-samples were placed in tin cups and analyzed for organic carbon (C) and nitrogen (N) content using a Carlo Erba NA 2500 Elemental analyzer. Organisms present in the sediments were removed prior to the determination of porosity, organic content, and C:N.

*2.2.2 $NH_4^+$ Profiles*

Initial and final sediment porosity and sediment organic content were measured. Because these sampling techniques were destructive, 5 additional cores were collected to determine the average sediment characteristics at the initiation of the experiment. Sediment porosity and organic content were measured at depth intervals of 1, 2, 3, 4, 5, 7, 9, 11, and 13 cm. A sediment plug of 1 or 2-$cm^3$, depending on the depth interval, was sampled using a 5-cc syringe core. For porosity, wet weight was recorded, the sediments were dried at 60 °C, and re-weighed. Porosity was determined to be the volume of water per volume of sediment (ml/ml). The sediments were then combusted at 550°C and re-weighed to determine the sediment organic content. Sediment organic content was calculated as the percent mass (g) lost on combustion.

Pore water $NH_4^+$ was sampled using a technique developed by Berg and McGlathery (2001). A small (2-mm diameter) stainless steel probe attached to a syringe was used to gently suction interstitial water while leaving the surrounding sediment relatively undisturbed. The probe can collect temporally and spatially discrete pore water samples to a depth resolution as fine at 1-cm (Berg and McGlathery 2001). Pore water was sampled with the high-resolution probe in the sediment cores at the bi-weekly sampling intervals. Using the probe, 1.5-ml of interstitial water was gently suctioned using a 10-cc syringe at depths of 1, 2, 3, 4, 5, 7, 9, 11, 13, and 15-cm. In addition, water column samples were taken immediately above each core in the field for a 0-cm (<1-cm above sediment surface) depth measurement. Pore water samples were filtered immediately (Supor, 0.45-μm), stored in sterile bags, and frozen for later analysis. $NH_4^+$ concentrations of the pore water were determined using a modification of Solórzano's

(1969) phenol-hypochlorite method. Frozen samples were analyzed within 2 months of collection. $NH_4^+$ concentrations were determined spectrophotometrically at 635-nm. Profiles of pore water $NH_4^+$ concentration with depth in the sediment cores were then constructed to determine the effect of algal density on pore water $NH_4^+$ concentration.

Diffusive $NH_4^+$ fluxes (nmol $cm^{-2}$ $s^{-1}$) were calculated using Fick's First Law,

$$\text{Flux} = -\varphi D_s \frac{dNH_4^+}{dz} \qquad (1)$$

where $\varphi$ is the average porosity of all experimental cores, $D_s$ is the diffusivity of the sediments and $dNH_4^+/dz$ is the change in $NH_4^+$ concentration with depth (z) from the sediment surface. In this experiment the $NH_4^+$ flux was calculated based on the change in $NH_4^+$ concentration from the top centimeter of sediment to the water column. Diffusivity was calculated using an equation from Iversen and Jorgensen's (1993) diffusivity table,

$$D_s = \frac{D}{1 + 2(1 - \varphi)} \qquad \text{for } D = (9.76 + 0.398T_c)\ 10^{-6} \qquad (2)$$

where D ($cm^2$ $s^{-1}$) is the diffusivity constant as a function of temperature ($T_c$) (°C). This flux calculation is an underestimation of the actual nutrient flux by 30-50% because bioturbation is not taken into account (Berg et al., 2001).

*2.2.3 Statistical Analyses*

2.2.3.1 Macroinvertebrate Analysis

SAS® software 8.2 was used for statistical analyses, unless otherwise stated. A one-way ANOVA was used to analyze the effects of algal density on macroinvertebrate

density. Macroinvertebrate data were rank transformed according to Potvin and Roff (1993). Rank transformation preserves the place of zero values in the data analysis and makes the data more likely to satisfy the assumptions of parametric models (Potvin and Roff 1993). In abundance data, the zeroes are important since the absence of species may indicate the effect of a treatment. Post hoc Tukey tests were used to determine the significance ($P \leq 0.05$) of algal treatments on the macroinvertebrate density. Diversity indices for the algal treatments were also calculated.

2.2.3.2 Nutrient Analyses

Pore water $NH_4^+$ profiles were analyzed using multivariate analysis of variance (MANOVA). Comparisons were made between the profile of the top 5-cm for each algal treatment and controls for the different sampling times, since invertebrate activity was expected to be highest in the upper 5-cm. Post hoc Tukey tests were used to determine significant changes among the algal treatments, depths and sampling times.

Depth integrated averages of $NH_4^+$ pore water concentration were analyzed with ANOVA and post hoc Tukey test to determine to influence of macroalgal density on the average pore water concentration. Flux measurements were calculated from the top 1-cm of sediment and analyzed with ANOVA and post hoc Tukey tests to determine the influence of macroalgal density on $NH_4^+$ flux. Regression of infaunal density on $NH_4^+$ flux was also examined to determine the significance of the interaction between the infauna and flux measurements.

C:N and %N of macroalgae at the end of the experiment were analyzed for the different algae treatments with ANOVA and post hoc Tukey tests.

2.2.3.3 Canonical Correspondence Analysis

CANOCO™ was used to perform canonical correspondence analysis (CCA) to examine how the benthic community responds to various densities of algae. CCA is a multivariate method to illustrate the relationships between biological assemblages of species and their environment (ter Braak and Verdonschot 1995). CCA is a weighted averaging method utilizing direct gradient analysis techniques to integrate community and environmental data by constraining the species ordination pattern to one that is most consistent with the environmental variables. The main advantage of such a technique is the simultaneous ordering of species and environmental variables. In addition, there is very good performance when the data are nonlinear and unimodal in relation to environmental gradients (Palmer 1993). The algorithm is an iteration of reciprocal averaging and multiple regression that stops on convergence of site scores from the previous iteration and those predicted by multiple regression (ter Braak 1986; Palmer 1993). The regression coefficients and correlation coefficients from the regression are a measure of how well the extracted variation in community composition is explained by the environmental variables (ter Braak 1986). CCA is a useful tool for resolving the influence of both natural and contaminant gradients on community structure and is especially well suited for use with estuarine data (ter Braak 1988; Rakocinski et al. 1997).

CCA was used to resolve the interaction of the environmental variables of macroalgal density, $NH_4^+$ pore water concentration and $NH_4^+$ flux on benthic community structure. Since $NH_4^+$ flux data were not available for T2 sampling period, the T0 flux values were substituted for the CCA to provide a complete data set. The T0 flux

measurements were used since there was no significant difference in the $NH_4^+$ pore water concentrations between the two sampling periods. Hill's scaling of inter-species distances was used in the analysis, which has the advantage of expressing scores as standard deviation units (ter Braak 1995). To de-emphasize rare species, abundances were downweighted. The significance of the ordination axes was evaluated with a Monte-Carlo permutation test.

## 2.3 RESULTS

### *2.3.1 Macroinvertebrates*

Because the prescribed macroalgal density changed largely due to growth during the 6-week treatment period, initial and final macroalgal biomass measures for each cage were averaged to determine the algal biomass treatment for that cage. The algae treatments resulting were: near-zero (no-algae control) <500-g ww $m^{-2}$, low 500 – 1200-g ww $m^{-2}$, medium (field density control) 1300 – 3000 g-ww $m^{-2}$, high >3000-g ww $m^{-2}$, and no-cage control. Statistical analyses were based on rank transformed data, but figures are presented with the raw data to give an idea of the actual abundances of invertebrates. While I had expected the no-cage control to be similar to the medium/field density algal treatment, the no-cage control was not significantly different from the high algae treatment (Tukey F = 4.51, $P < 0.05$). The most likely explanation is that the rebar posts used to mark the no-cage areas entangled the macroalgae as it drifted with water currents. Once entangled, the macroalgae continued to collect and grow, which resulted in a high density macroalgal accumulation. This same process occurs regardless of the material used for markers at the mid-lagoon Shoal site (*pers. obs.*).

The macroalgal treatments had significantly different invertebrate densities ($F_{4,12} = 44.4$, $P < 0.0001$) with the near-zero algal treatment having the highest invertebrate density (Figure 2.1). Snails were the dominant taxa, especially at the near-zero treatment (Figure 2.2), followed by amphipods. Snail density was significantly higher than all other taxa and amphipods were significantly more abundant than taxa other than snails ($F_{5,81} = 90.1$, $P < 0.0001$) (Figure 2.2). For all taxa, there was a significant difference in macroinvertebrate density at all algal treatments ($F_{3,81} = 61.0$, $P < 0.0001$). Infaunal and epifaunal densities were significantly different ($F_{7,142} = 8.1$, $P < 0.0001$) (Figure 2.3). Epifauna had significantly higher density at near-zero algal treatment ($F_{3,71} = 4.27$, $P < 0.008$). The infaunal density at the field average (medium) and high algal treatments were significantly higher than infaunal density at the near-zero and low algal treatments ($F_{3,71} = 7.37$, $P < 0.0002$). There were 31 species representing amphipods, clams, crabs, snails, shrimp, worms and other taxa (Table 2.1). Macroinvertebrates were most diverse, had the greatest species richness, and the highest evenness at the medium algal treatment (Table 2.2) but the total number of individuals was highest at the near-zero algae treatment (Table 2.2, Figure 2.1). Increasing invertebrate species richness tended to increase $NH_4^+$ flux when macroalgae were present ($R^2 = 0.0582$), but had a strong negative influence on $NH_4^+$ flux in the absence of macroalgae (<500-g ww $m^{-2}$) ($R^2 = 0.7656$) (Figure 2.4).

The %N of *G. tikvahiae* was significantly higher than that of *U. lactuca* ($F_{3,19} = 41.4$, $P < 0.0001$) but only the medium and high algal densities were significantly different ($F_{3,19} = 5.9$, $P < 0.005$) (Table 2.3).

### *2.3.2 Nutrients and Sediment Parameters*

At the T2 time point (week 2), there was an exceptionally low tide at the mid-lagoon Shoal site, which temporarily exposed the sediment at the experimental site. Because of this, there was no water column sampling and no flux measurement available for the T2 time point. There was no significant difference in $NH_4^+$ concentration between T0 and T2 time points and these were, therefore, combined in the analyses. Statistical analysis indicated that there was no significant difference among the pore water profiles for the different macroalgal density treatments (excluding the near-zero macroalgal treatment) during the entire treatment period ($F_{3,53} = 0.77$, $P < 0.51$). The low, medium and high algal treatments were therefore pooled into a single algae treatment class for comparison to the near-zero algal treatment (no-algae control).

At T0 (initial time point), there was no significant difference in $NH_4^+$ concentration with algal treatment or depth ($F_{9,45} = 0.89$, $P < 0.54$) (Figure 2.5a). At T4 (week 4) there was both a significant algal treatment effect ($F_{1,50} = 4.38$, $P < 0.018$) and a significant depth effect ($F_{4,50} = 2.83$, $P < 0.03$) (Figure 2.5b). Contrary to my expectation, the no-algae treatment had a significantly higher depth-integrated $NH_4^+$ pore water concentration than the algae treatment (Figure 2.6a). However, the $NH_4^+$ concentration in the top 1-cm of sediment was higher in the algae treatment (Figure 2.6b). The same pattern was evident at T6 (week 6) with the no-algae treatment having a significantly higher depth-integrated $NH_4^+$ pore water concentration than the algae treatment ($F_{1,50} = 8.63$, $P < 0.0006$) and a significant increase in $NH_4^+$ pore water concentration with depth ($F_{4,50} = 2.84$, $P < 0.03$) (Figure 2.5c, Figure 2.6a). The algae

treatment had a significantly higher concentration in the top 1-cm of sediment (Figure 2.6b) ($F_{1, 53} = 13.3$, $P < 0.0001$). The $NH_4^+$ pore water concentration was significantly different at T0, T4 and T6 time points for both the depth-integrated concentrations and the top 1-cm concentrations ($F_{2,250} = 117.0$, $P < 0.0001$) (Figure 2.6). Around 3-cm depth there was a shift from higher $NH_4^+$ concentration under the algae to higher concentration in the no-algae treatment (Figure 2.5). While both the no-algae and algae treatments showed an increase in NH4+ over time (relative to T0), the no-algae treatment increased to a greater extent than the algae treatment.

Diffusive flux of $NH_4^+$ at the sediment water interface did not significantly differ between the algae and no-algae treatments at T0, but flux was significantly higher in the algae treatment at T4 and T6 ($F_{1,40} = 17.6$, $P < 0.0001$) (Figure 2.7). Flux at T0 was significantly lower than T4 and T6 (Tukey $\alpha = 0.05$), but T4 and T6 fluxes did not significantly differ from each other even though the flux from the algae treatment increased at T6 (Figure 2.7). As total infaunal density increased, $NH_4^+$ flux decreased significantly resulting in a negative relationship ($R^2 = 0.18$, $F = 16.8$, $P < 0.0045$) (Figure 2.8). The algae treatment resulted in higher fluxes, but increased infaunal density was negatively related to $NH_4^+$ flux both with and without algae (Figure 2.9).

The organic matter (g) content of the sediment cores from the final sampling period indicated a significant influence of macroalgae and sediment depth ($F_{3,145} = 3.05$, $P < 0.030$). There was a trend for the no-algae treatment to have a higher organic matter content than the algae treatment at depths greater than 3-cm ($F_{1,145} = 3.45$, $P < 0.066$) (Table 2.4).

### *2.3.3 Canonical Correspondence Analysis*

In Figure 2.10, the arrows represent gradients in the environmental variables: macroalgal density, $NH_4^+$ flux, and $NH_4^+$ pore water concentration. The arrows point in the direction of maximum change in the variable and the arrow length is proportional to the maximum rate of change. Thus the longest arrow, in this case $NH_4^+$ flux, is the most important environmental variable in the ordination diagram. However, there is a strong relationship between $NH_4^+$ flux and macroalgal density as indicated by the acute angle between these environmental variables. All three environmental variables are strongly correlated with the canonical correspondence analysis (CCA) ordination axes. $NH_4^+$ concentration strongly correlated with CCA1 ($r = -0.99$), the horizontal axis; $NH_4^+$ flux strongly correlated with CCA2 ($r = 0.92$), the vertical axis; and macroalgal density strongly correlated with CCA3 ($r = -0.76$), an axis in 3-D space. There is also a significant relationship between species and environmental variables ($F = 2.02$, $P < 0.035$). CCA1 explains 62.7% of the variance in the species-environment relationship (eigenvalue = 0.63).

The species distributions (symbol points) on the ordination diagram indicate the environmental preference of each species. Preference is implied by location of the species point relative to the arrows of environmental variables. Those points closest to the arrowhead prefer higher than average conditions for that variable, while those opposite the arrowhead prefer lower than average conditions for that variable. Taxa in the upper left quadrant in CCA space were associated with higher $NH_4^+$ fluxes, taxa in the lower left quadrant were associated with high $NH_4^+$ pore water concentrations, and those

taxa in the upper right quadrant were associated with higher macroalgal density. For example, both dominant grazers *Astyris (Mitrella) lunata* and *Ampithoe rubricata* show a distribution in low macroalgal density and higher $NH_4^+$ pore water concentration (Figure 2.10). The majority of shrimp species, indicated by the dashed line in Figure 2.10, also have low macroalgal density preference but are associated with low $NH_4^+$ flux. Several worm species are associated with large $NH_4^+$ flux but other worm species are associated with lower $NH_4^+$ flux (solid lines in Figure 2.10).

## 2.4 DISCUSSION

### *2.4.1 Macroinvertebrates and macroalgal density*

The value of macroalgal biomass that caused a significant decline in macroinvertebrate density was lower than has been reported previously for subtidal systems (Figure 2.1) (see Isaksson and Pihl 1992; Ahern et al. 1995; Norkko and Bonsdorff 1996; Norkko 1998; Norkko et al. 2000; Österling and Pihl 2001). This indicates that the negative effect of nutrient enrichment occurs much sooner during the eutrophication process than is currently believed. Although Ahern et al. (1995) show a similar inverse relationship between macroalgae and invertebrates, it is not clear if the macroalgal biomass values used were wet weight or dry weight, so it is difficult to compare their macroalgal threshold for changes in invertebrate density to those in HIB. Theirs was also a comparative study among sites rather than experimental study at one site, like the current study (Ahern et al. 1995).

The loss of invertebrates at such low macroalgal density may have serious consequences in shallow coastal systems. First, the dominant species, which are also the

dominant grazers, were most affected by the accumulation of algal biomass (Figure 2.2). This will limit considerably the top-down control on macroalgal biomass accumulations. In particular, snails had high grazing rates and potential for controlling macroalgal biomass (Chapter 3); the decline of snail density at such low algal biomass will severely limit their ability to control algal blooms. Additionally, the loss of other invertebrates such as clams and worms (Figure 2.2) may affect nutrient cycling by limiting mineralization and bioturbation (Hansen and Kristensen 1997; Dauwe et al. 1998; Hansen and Kristensen 1998). This is also important because it provides evidence that low-density macroalgal accumulations are detrimental to benthic invertebrate community structure in shallow systems and it alters the current view that negative consequences only occur in high density mats. In this study, approximately 500-g ww $m^{-2}$ of macroalgal accumulation caused a significant decline in invertebrate density (Figures 2.1, 2.2). These losses can also strongly affect community organization with accompanying changes in ecosystem functions (Duffy 2002; Worm et al. 2002; Emmerson and Huxham 2002) such as greater ammonium accumulation in the upper sediment layers in the presence of macroalgae (Figure 2.5b).

The effects of algal biomass on invertebrates are complex, and individual species or groups of taxa may respond differently to increased macroalgal biomass (Figure 2.2). Amphipods, clams and snails appeared most sensitive to increased algal biomass. Hull (1987) also found a marked decline in amphipods in all but low algal biomass plots, but there was also a rapid recovery after the burial of senescing algal mats in the sediments. This is likely also the case in HIB because amphipods showed especially high grazing rates on macroalgal detritus (see Chapter 3), and the decomposition of the macroalgal

mats would provide a suitable food source for the amphipods. Increased sedimentation associated with increased macroalgal biomass may be responsible for the decline in clam populations, as clams may have siphons clogged with silt. The dramatic decline in snails from the near-zero algal biomass treatment is most likely a result of changes in the physical conditions, especially the macroalgae acting as a barrier to their access to the sediment surface. Norkko and Bonsdorff (1996) found a rapid recovery in gastropod populations following senescence of macroalgal mats.

The level of complexity of habitats is thought to play a major role in structuring benthic communities (Pihl et al. 1995; Dial and Roughgarden 1998). In the present study, near-zero algal biomass should provide a low level of complexity and high algal biomass should provide a high level of complexity but the greater extent of edge available with small patches (near-zero and low algal biomass) is also a factor influencing benthic community structure. However, with increasing algal densities, the likelihood of negative effects of changes in physico-chemical parameters are increased (Astill and Lavery 2001), and even though anoxia was unlikely at the Shoal site during this study period, it is generally important in systems where macroalgal mats are stable. Invertebrate density was highest at the near-zero treatment (Figure 2.1, Figure 2.2 for most taxa) but diversity, species richness and evenness were all highest at the medium/field algal treatment (Table 2.2). As the structural complexity increases from near-zero to medium algal biomass, there is a potential influence on food and shelter, which may explain the increase in the diversity parameters (Pihl et al. 1995). Worm et al. (2002) also found that consumers and resources interact to control diversity and ecosystem functioning for intertidal macroalgal communities. The peak in primary

producer diversity shifted depending on consumer pressure and system resources. In systems with low productivity, the diversity peaked when consumer pressure was lowest (Worm et al. 2002). This may apply to invertebrate community diversity as well, but with different controls such as macroalgal density (Figure 2.1, Table 2.2) and consumer pressure (not tested). The presence of macroalgae changes the habitat structure, perhaps by increasing patch size (Eggleston et al 1998; Eggleston et al 1999), which reduces abundance of the dominant species and promotes the coexistence of more species. This may be a result of competition among species, which would be consistent with the intermediate disturbance hypothesis (Dial and Roughgarden 1998; Widdicombe and Austen 1999) or, more simply, that the conditions at the medium/field algal treatment were beneficial to some species but displaced others (Widdecombe and Austen 1999).

In the present study, the response of the total invertebrate community to macroalgal biomass was not linear, and resulted in a steep decline from near-zero algae treatment to field average algae treatment, but then increased slightly at the high algae treatment (Figure 2.1). It is mostly likely that the increased invertebrate density associated with high macroalgal biomass is due to reduced predation and increased deposit feeders and not to the changes in physico-chemical conditions induced by the macroalgae. Increased supply of detritus provided by the macroalgal mats increases the abundance of deposit feeders (Hull 1987), and at high macroalgal biomass, this may account for the slightly greater abundance of invertebrates. Reduction of current velocity associated with dense macroalgal mats may also increase settlement of planktonic larvae and the macroalgae may act as a barrier to epibenthic predators (Hull 1987; Bonsdorff 1992; Bonsdorff et al. 1995; Norkko and Bonsdorff 1996a, 1996b). These mechanisms

would increase invertebrate density at high macroalgal biomass (Figure 2.1). However, high macroalgal biomass also has been shown to reduce oxygen availability and exchange with the sediment and cause increased sedimentation and silt accumulation, which would potentially decrease invertebrate density (Norkko and Bonsdorff 1996c). This was unlikely to occur during the study period since the Shoal site was physically dynamic, which may not allow establishment of anoxic conditions under algae except at the highest macroalgal densities and during low-wind periods when the mats become stable. Furthermore, soft-bodied invertebrates are able to take up amino acids through the body wall and leakage from rapidly growing or senescing macroalgae may provide enough dissolved organic matter to provide the energy needed for basal metabolism (Price and Hylleberg 1982). This may provide a direct link between the invertebrates and the macroalgal mats. In HIB, there is a large release of dissolved organic nitrogen (DON) that is potentially available for uptake (Tyler et al. 2001). While soft-bodied organisms like worms do not show an increase in density at the high macroalgal treatment (Figure 2.2), infauna in general do (Figure 2.3). Snails and crabs also show an increase in density at the high macroalgal treatment indicating that the connection between invertebrates and macroalgae may extend beyond soft-bodied species to those with exoskeletons as well.

It was hypothesized that higher macroalgal biomass would favor epibenthic fauna with the assumption that they are mobile and able to take advantage of the macroalgae and at the same time escape the negative conditions associated with the mats. There was an increase in the density of epibenthic fauna at the high algal treatment, though not statistically significant, indicating that the epibenthos benefited to some extent from high

biomass algal mats (Figure 2.3). This is in agreement with studies in subtidal systems (Isaksson and Pihl 1992; Österling and Pihl 2001), however, other studies have not tested the effects of such high density (>3000 gww $m^{-2}$) mats on epifaunal communities. While overall the epifaunal density declined, epibenthos maintained a higher density than infauna (Figure 2.3) which is in partial support of my hypothesis. However, implicit in the prediction that epifauna would increase in response to an increase in macroalgal biomass is the idea that infauna would decrease under the same conditions. The significant increase in infaunal density at the medium/field and high biomass algal treatments (Figure 2.3) contradicts that assumption and other studies that do show a decline in infauna with macroalgal mat formation (Norkko and Bonsdorff 1996b, 1996c). Our result may indicate that infauna have the ability to tolerate degraded conditions and that the algae create a barrier to predators (Hull 1987; Bonsdorff 1992; Bonsdorff et al. 1995; Pihl et al. 1995).

### *2.4.2 Relationships of macrofauna and macroalgal biomass with $NH_4^+$*

Studies have shown that macroalgae may act as a barrier to the flux of $NH_4^+$ to the overlying water column (Rysgaard et al. 1995; McGlathery et al. 1997) and that the presence of macroalgae enhances sediment nutrient cycling (mineralization) and causes a build-up of $NH_4^+$ in surface sediments underlying macroalgal mats (McGlathery et al. 1997; Trimmer 2000; Astill and Lavery 2001; Tyler et al. 2003). Our results indicate that macroalgae did induce a greater flux of $NH_4^+$ from the sediment into the macroalgal mat (Figure 2.7) and that this was most likely due to increased mineralization. However, there was not a build-up of $NH_4^+$ deeper than 3- to 4-cm under the macroalgal mats

(Figures 2.5, 2.6, 2.7). While this result is consistent with accumulation of $NH_4^+$ in the top 4-cm in a similar laboratory study (Burton et al., *in prep.*), there is a notable difference in the accumulation of $NH_4^+$ with depth between the laboratory and this field study. Burton et al. (*in prep*) found a significantly greater accumulation of $NH_4^+$ with depth up to 13-cm under algae, but the present field study had a "crossover" where below 3- to 4-cm depth the no-algae treatment had a greater accumulation of $NH_4^+$ (Figure 2.5). It is possible that algal uptake and stimulated growth is a factor driving the $NH_4^+$ concentration profile (Christensen et al. 2000). The recycling of nitrogen remineralized from algae is an important source to sustain macroalgal production (McGlathery et al. 1997; Trimmer et al. 2000). However, if uptake by macroalgae created a gradient that did not permit accumulation of $NH_4^+$ with depth then the gradient of $NH_4^+$ would be much steeper than is seen in this study and there would be a lower $NH_4^+$ concentration in the surface sediments. Studies have shown that very little of the nutrients released from the sediment pass through the algal layer to the water column (Rysgaard et al. 1995; McGlathery 1997; Tyler et al. 2001). Thus, algae can prevent the release of nutrients to the pelagic system though assimilation of the nutrients (McGlathery 1997). Support for this comes from the observations that there was substantial macroalgal growth in the field cages (see section *2.3.1*) and that there is low phytoplankton concentration when macroalgal density is high in HIB (McGlathery et al. 2001). Another factor driving the $NH_4^+$ concentration profile may be wave action and tidal pumping (Shum and Sundby 1995; Rocha 1998). Since algae slow water currents (Sfriso and Marcomini 1997), the no-algae treatment would be more exposed to wave action and bottom currents. The lack of wave action and tidal pumping in the Burton et al. (*in prep.*) laboratory experiment

may account for the differences in $NH_4^+$ pore water concentration with depth. In addition, the macroalgal mat in the laboratory experiment was very stable and this influenced the oxygen conditions deep in the sediment. Under field conditions, tidal pumping would likely deliver more oxygen to the sediment in the no-algae treatment (Shum and Sundby 1995) and more oxygen in the surface sediments would support nitrification and reduce accumulation of $NH_4^+$. The higher $NH_4^+$ concentration with depth in the no-algae treatment was likely related to higher organic matter content (Figure 2.5, Table 2.4) but it is unclear why there is more organic matter with depth in the no-algae treatment relative to the algal treatments.

While separately macroalgae and macroinvertebrates have been shown to strongly influence ecosystem process such as nutrient fluxes, there is also an important link among these factors (Worm et al. 2002; Duffy 2002; Duffy 2003; Duffy et al. 2003). Macroalgal density has dramatic effects on both the composition (diversity) and density of the macrofaunal community, which then has effects on nutrient cycling (see below). In order to fully understand the linkages between biodiversity and ecosystem functioning, animals, particularly consumers, need to be considered (Emmerson and Huxham 2002; Duffy 2002; Worm et al. 2002; Duffy et al 2003). The influence of macroinvertebrates on $NH_4^+$ flux has opposing effects depending on whether macroalgae is present or not (Figure 2.4). When macroalgae are present, increasing invertebrate species richness appears to increase $NH_4^+$ flux, which has important implications for N-retention within the ecosystem. Since macroalgal mats have been shown to function as self-regenerating through the recycling of nitrogen (McGlathery et al. 1997; Stimson and Larned 2000; Trimmer et al. 2000; Sundbäck et al. 2003), the increased flux with a diverse invertebrate

population may increase the N available to macroalgae and may lead to greater accumulation of macroalgal biomass. However, the influence of invertebrate diversity may vary with macroalgal biomass as well. Invertebrate diversity peaked at field average macroalgal density but declined with high algal density (Table 2.2) so the greatest influence of invertebrate diversity may occur up to field algal biomass but have an upper limit when algal biomass is high enough to reduce diversity.

Studies have shown that the presence of bioturbating infauna may increase oxygenation of the sediment and stimulate nitrification, thus reducing the build-up of $NH_4^+$ under macroalgal mats (Rysgaard et al. 1995; Hansen and Kristensen 1997). Most studies indicate that increased infaunal density leads to greater $NH_4^+$ fluxes (see Hansen and Kristensen 1997; Hansen and Kristensen 1998; Kristensen and Hansen 1999; Mortimer et al. 1999; Bartoli et al 2000; Pennifold and Davis 2001), but most studies have been based on the influence of one species on $NH_4^+$ flux. However, a study by Marinelli and Williams (2003) found that the highest $NH_4^+$ fluxes were associated with moderate infaunal density. The results of the present study are contrary to these (Figure 2.8 and Figure 2.9). With high densities of organisms and high rates of bioturbation in the no-algae treatment, oxygen will be more widespread, which will alter the balance of ammonification, nitrification and denitrification. In dense assemblages of infauna, bioturbation "zones" will overlap and the oxidizing conditions may predominate deep into the sediment column (Martinelli and Williams 2003). As long as anoxic zones were still proximate to these increasingly oxic zones, this would enhance nitrification/ denitrification which may be reflected in a lower $NH_4^+$ flux (Aller 1982). Thus, looking at the total infaunal community may give a different picture of nutrient fluxes than

examining one or few species. For example, *Nereis* spp. are often related to $NH_4^+$ fluxes (see Hansen and Kristensen 1997; Hansen and Kristensen 1998; Kristensen and Hansen 1999). In the present study, when *Nereis* sp. were present $NH_4^+$ flux was highest, which is in contrast to the relationship portrayed by total infaunal density. To my knowledge, there have been no studies relating total infaunal density to nutrient fluxes and this discrepancy in results between the types of studies should be investigated further.

The influence of individual species is further elucidated by cannonical correspondence analysis (CCA) (Figure 2.10). *Nereis* sp. and *Chaetopterus* sp. (parchment worm) showed the strongest influence on $NH_4^+$ flux (Figure 2.10). Both of these species form U-shaped tubes that are irrigated, but nereids may also be highly mobile and active worms. Another species that appears to be important in increasing $NH_4^+$ flux is *Tellina* sp. (bivalve). This is also a highly active, burrowing species. However, these few species occurred at low density and may not provide enough activity to substantially influence $NH_4^+$ flux. Even though many of the species associated with the low $NH_4^+$ flux (Figure 2.10, group enclosed in large solid line) also are active, burrowing, and tube-builders, none build U-tubes like *Nereis* sp. and *Chaetopterus* sp. and the tube structure may be an important variable in $NH_4^+$ flux. Also in CCA, $NH_4^+$ concentration explained 62.7% of the variance in the species-environment relationship indicating that $NH_4^+$ concentration was an important determinant of species distribution (Figure 2.10). Just a few species (*A. lunata*, *P. intermedius*, and *P. vulgaris*) were associated with high $NH_4^+$ concentration, so the majority of species occur associated with low $NH_4^+$ concentration. The association of many species, especially worms, with low $NH_4^+$

concentration may also explain the negative relationship between $NH_4^+$ flux and invertebrate density (Figure 2.8) since lower concentration would lead to lower flux.

Another factor relating macrofauna to nutrient fluxes is macrofaunal excretion. Pennifold and Davis (2001) measured excretion rates of benthic macrofauna and found that excretion could account for >200% of the $NH_4^+$ measured in the water column. Thus, the macrofauna play a considerable role in nutrient cycling. While excretion was not measured in the present study, it is potentially a large contributor to $NH_4^+$ cycling in HIB and may explain the higher pore water concentration in the no-algae treatment (Figure 2.6).

### *2.4.3 Summary*

This study shows that macroalgal mats do have an influence on macroinvertebrate density, pore water $NH_4^+$ concentration and $NH_4^+$ flux at the sediment-water interface. Macroalgal density is an important factor in determining abundance of macro-invertebrates, and low macroalgal biomass causes a significant decline in total invertebrate density affecting the dominant species to the greatest extent. Thus, the threshold of macroalgal biomass that creates a negative impact on the faunal community is much lower than reported previously in the literature, and is probably less than 500-g ww $m^{-2}$.

Regardless of what mechanisms structure the benthic faunal community, the presence of macroalgae has been linked to local extinction and reduced activity of bioturbating infauna. These responses by macrofauna have been associated with hypoxic and anoxic events in other systems (Aller 1982; Rysgaard et al. 1995; Hansen and

Kristensen 1997). While hypoxic and anoxic events have occurred in HIB, the dynamic nature of the Shoal likely prevented reduced oxygen conditions during the study period.. Non-linear responses, such as the oxygen dynamics and the macroinvertebrate response to macroalgal accumulation, may be indicative of shallow coastal systems like lagoons where the active nature of the system leads to more heterogeneous responses (Figures 2.1, 2.2, 2.3).

While specific macroalgal biomass was not a factor in $NH_4^+$ dynamics, the presence or absence of algae was an important factor. Macroalgae increased pore water $NH_4^+$ concentration in the upper sediment layers and increased $NH_4^+$ flux from the sediment. Invertebrates were also important in controlling $NH_4^+$ flux, but the pattern of influence varied depending on what portion of the invertebrate community was considered. Total infauna resulted in a decreased flux with increased infaunal density, but several individual species had the opposite effect. It is interesting to note that at medium and high macroalgal biomass, there was an increase in infauna and an increase in $NH_4^+$flux but still a negative relationship between invertebrate density and flux. This relationship may be the result of increased oxygen availability associated with the macroalgae and infaunal density which would enhance nitrification. This may also be an explanation for the lack of build-up of $NH_4^+$ in the sediment pore water to depth greater than 3- or 4-cm.

Biodiversity of invertebrates was highest at the medium/field average algal biomass, but there was overlap in species richness among the near-zero-algae and algal treatments (Figure 2.4). Increasing invertebrate species richness appears to have a positive influence on $NH_4^+$ flux in the presence of macroalgae, but a strong negative

impact on flux in the absence (<500-g ww $m^{-2}$) of macroalgae. This may have serious implications in systems subject to nutrient over-enrichment and subsequent algal blooms, since this provides further evidence that macroalgal mats can become self-sustaining. However, with the decline in species richness at high macroalgal density (Table 2.2), there may be an upper limit to the positive impact that the interaction of invertebrates and macroalgae has on nutrient flux.

**ACKNOWLEDGEMENTS**
I would like to thank Jessie Burton for her *huge* role in the sediment pore-water portion of these experiments. Also, thanks to the VCR-LTER support staff, especially Philip Smith.

Table 2.1 Species present and total density of each from density experiment, summer 2000, Shoal site.

| Species (common name) | Taxanomic grouping | Total N (# $m^{-2}$) |
|---|---|---|
| *Alpheus heterochelis* (big-claw snapping shrimp) | Decapod, Shrimp | 384.6 |
| Amphipods* | Amphipod | 3461.5 |
| *Ampithoe rubricata* (red-eyed amphipod) | Amphipod | 16923.1 |
| *Amphitrite ornata* † | Annelid (worm), polychaete | |
| *Anachis avara* (greedy dove shell) | Mollusk, Gastropod | 961.5 |
| *Arabella iricolor* (opal worm) | Annelid (worm), polychaete | 192.3 |
| *Astyris (Mitrella) lunata* (crescent mitrella) | Mollusk, Gastropod | 47692.3 |
| *Axius serratus* (lobster shrimp) | Decapod, Shrimp | 2115.4 |
| *Buccinum undatum* (waved whelk) | Mollusk, Gastropod | 192.3 |
| *Callinectes sapidus* (blue crab) | Decapod, Crab | 1538.5 |
| *Chaetopterus variopedatus* (parchment worm) | Annelid (worm), polychaete | 192.3 |
| *Clymenella torquata* (bambooworm) | Annelid (worm), polychaete | 961.5 |
| *Diopatra cuprea* (plumed worm) | Annelid (worm), polychaete | 192.3 |
| *Ensis directus* (common razor clam) | Mollusk, Bivalve | 6153.8 |
| *Erichsonella filiformis* | Isopod | 384.6 |
| *Eurypanopeus depressus* (mud crab) | Decapod, Crab | 11730.8 |
| *Glycera* sp. (bloodworm) | Annelid (worm), polychaete | 3269.2 |
| *Glycera americana* (bloodworm) | Annelid (worm), polychaete | 192.3 |
| *Goniada maculata* (chevronworm) | Annelid (worm), polychaete | 4423.1 |
| *Hippolyte* spp. (grass shrimps) | Decapod, Shrimp | 1153.8 |
| *Ilyanassa obsoleta* (mud dog whelk) | Mollusk, Gastropod | 192.3 |
| Isopods | Isopod | 3269.2 |
| juvenile mud crab | Decapod, Crab | 2500.0 |
| *Molgula* sp. (sea grape sea squirt) | Chordate | 384.6 |
| *Nereis* sp. (clam worm) | Annelid (worm), polychaete | 192.3 |
| *Nucula proxima* (near nut clam) | Mollusk, Bivalve | 192.3 |
| *Pagurus longicarpus* (long-clawed hermit crab) | Decapod, Crab | 192.3 |
| *Palaemonetes intermedius* (shore shrimp) | Decapod, Shrimp | 1153.8 |
| *Palaemonetes vulgaris* (shore shrimp) | Decapod, Shrimp | 384.6 |
| *Pinnixa* sp | Decapod, Crab | 192.3 |
| *Tellina* sp. | Mollusk, Bivalve | 192.3 |

* unidentified amphipods were not identified to the species level but represent the following families: Ampithoidae, Bataidae, Cheirocratidae, Gammaridae, Haustoriidae, Hyalidae, Ischyroceridae, Liljeborgiidae, Lysianassidae, Stenothoidae, and Unciola.
† represents rare species in this sampling regime.

Table 2.2 Diversity indices for algal density treatments.

| Algal treatment | S-W[1] | richness | J | Total n |
|---|---|---|---|---|
| Near-zero algae | 0.966 | 20 | 0.607 | 61346 |
| Low algae | 1.292 | 20 | 0.812 | 22307 |
| Medium algae | 1.568 | 25 | 0.986 | 35384 |
| High algae | 1.338 | 19 | 0.841 | 34615 |

[1] S-W is the Shannon-Weiner diversity index, richness is species richness, J is evenness, and Total n is the total number of individuals $m^{-2}$ of all species.

Table 2.3 Mean (standard deviation) of %N for the algal density treatments.

| Algal treatment | Gracilaria tikvahiae | Ulva lactuca |
|---|---|---|
| Near-zero algae | 3.04 (0.11) | 2.63 (0.09) |
| Low algae | 2.95 (0.00) | 2.30 (0.00) |
| Medium algae | 3.02 (0.23) | 2.67 (0.07) |
| High algae | 2.93 (0.24) | 2.71 (0.16) |

Table 2.4 Mean organic matter (± standard deviation) for final sediment cores with the algae or no-algae treatment from summer 2000.

| | Whole core | Top of core* | Bottom of core* |
|---|---|---|---|
| No-algae | 0.0744 (0.189) | 0.0245 (0.009) | 0.0958 (0.225) |
| Algae | 0.0410 (0.020) | 0.0289 (0.023) | 0.0463 (0.016) |

* Top of core refers to the top 3-cm of sediment and bottom of core refers to sediment below 3-cm depth.

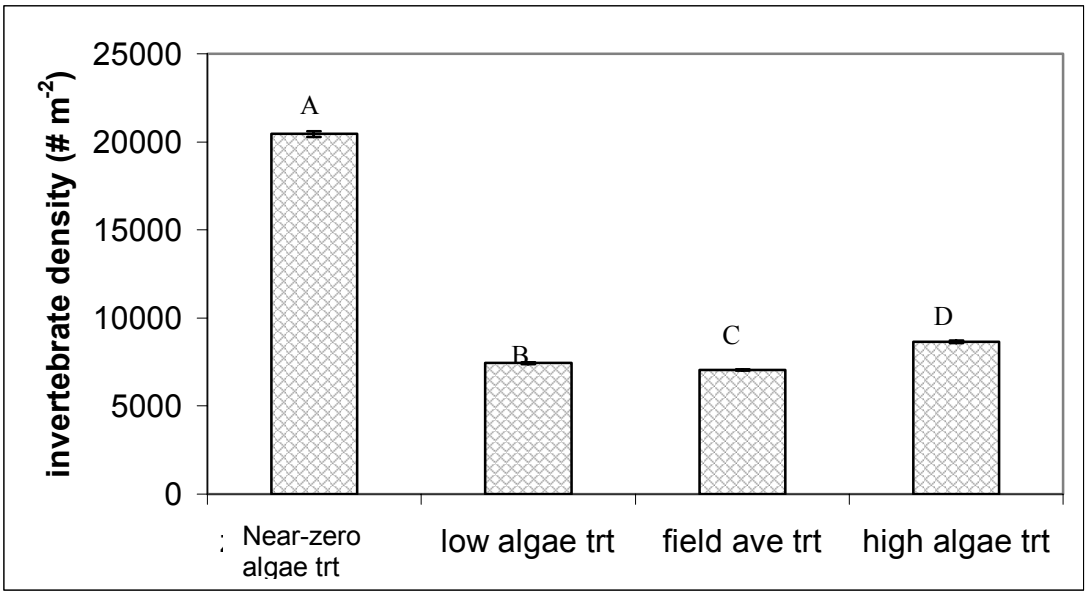



Figure 2.1 Mean (± standard error) for invertebrate density (from non-transformed data). Treatments with different letters are significantly different. The high algal treatment was not significantly different from the no-cage control.

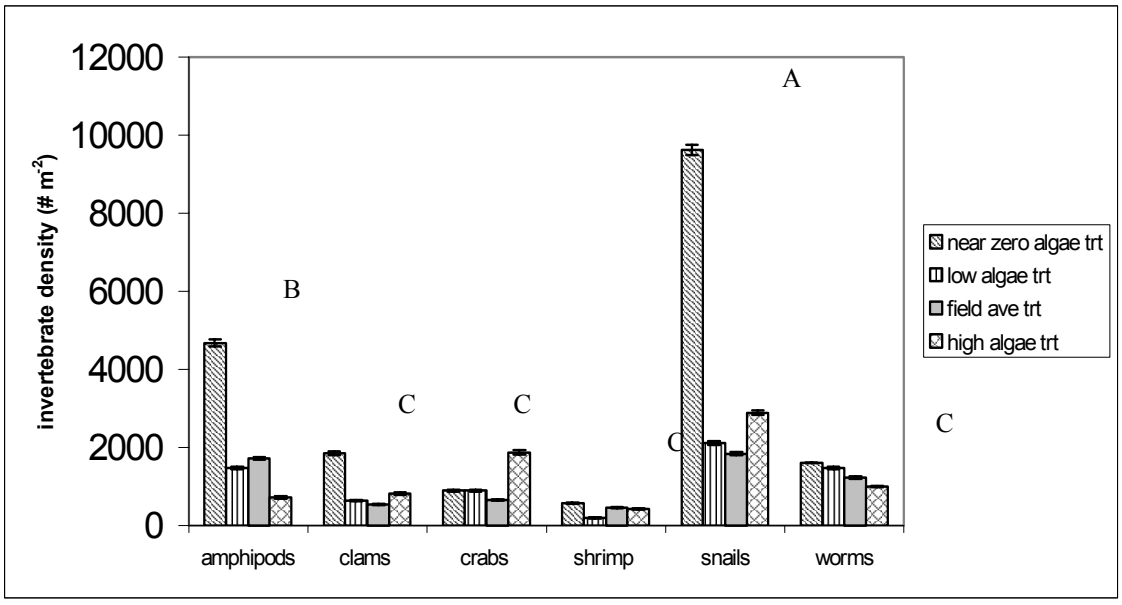



Figure 2.2 Mean (± standard error) for major taxa (from non-transformed data) at four macroalgal density treatments. Treatments with different letters are significantly different. Invertebrate density is significantly different at all algal treatments for all major taxa.

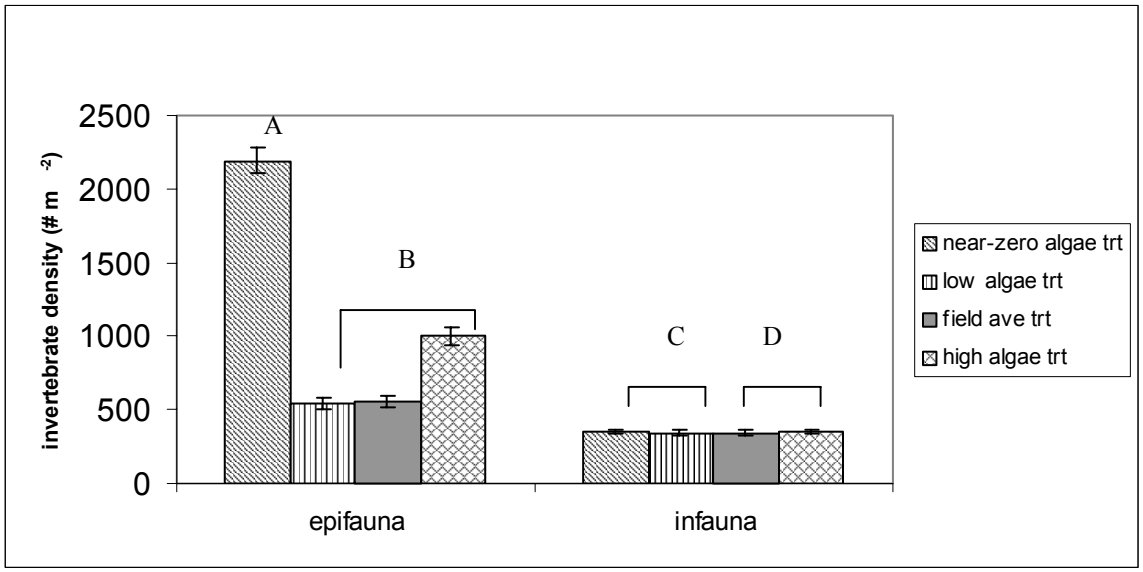



Figure 2.3 Mean (± standard error) for epifauna and infauna (from non-transformed data) at four macroalgal density treatments. Epifauna and infauna density were significantly different ($F_{7,142} = 8.1$, $P < 0.0001$). Treatments with different letters are significantly different.

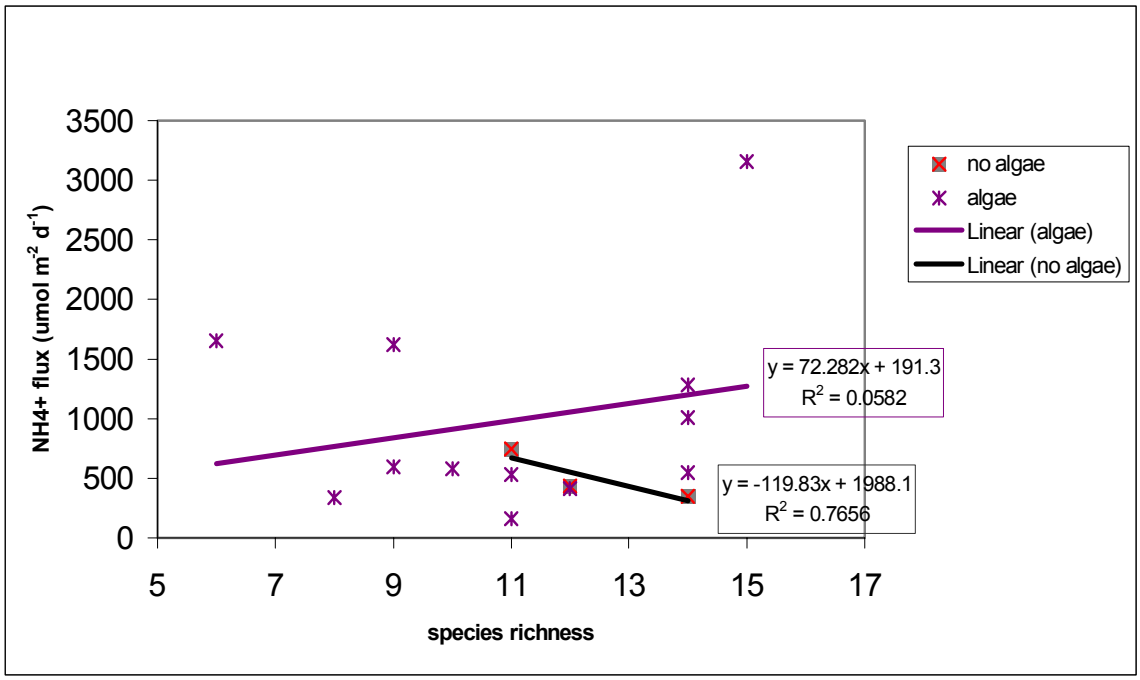



Figure 2.4 Relationship between invertebrate species richness and $NH_4^+$ flux in the presence and absence of macroalgae.

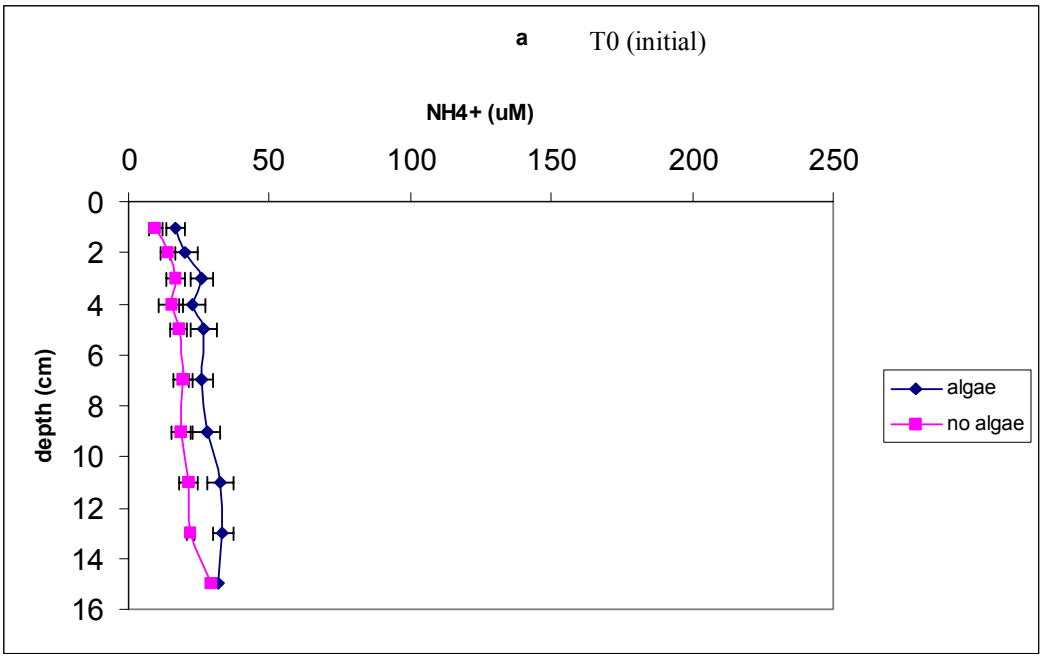



Figure 2.5a

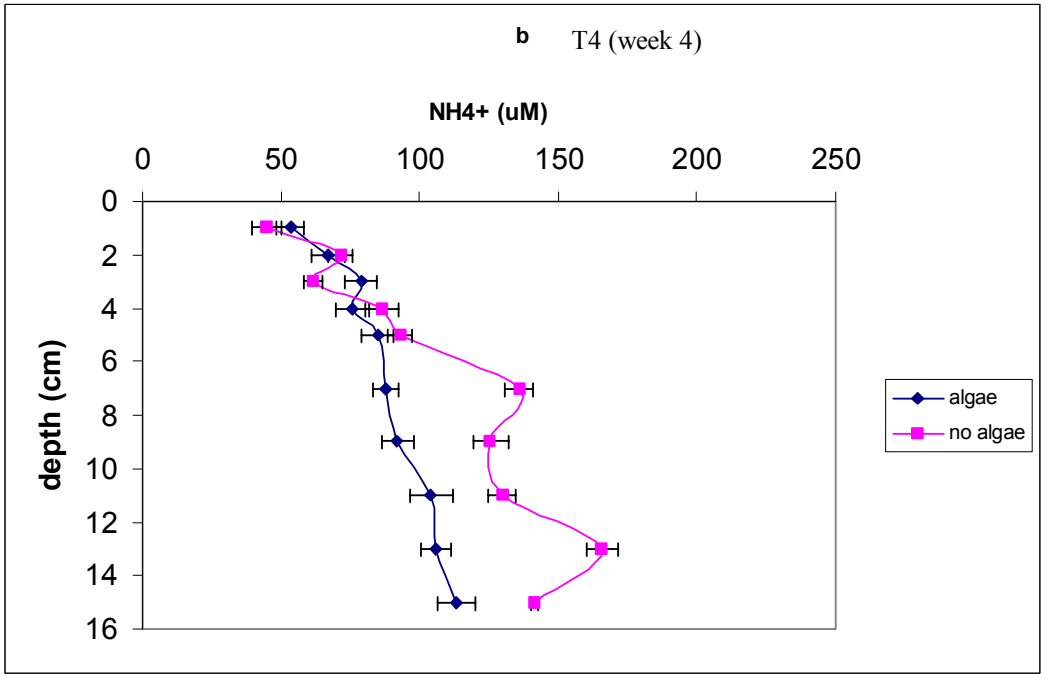



Figure 2.5b

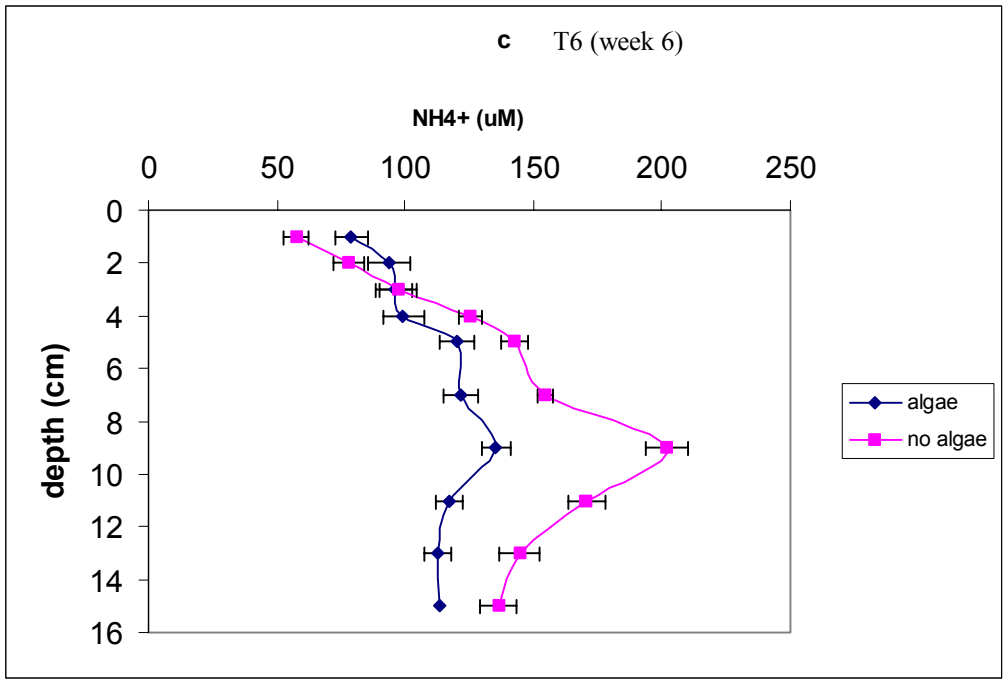



Figure 2.5 Pore water $NH_4^+$ concentration profiles for **(a)** T0 (initial weeks), **(b)** T4 (week 4), and **(c)** T6 (week 6). Points represent mean concentration and bars are standard error.

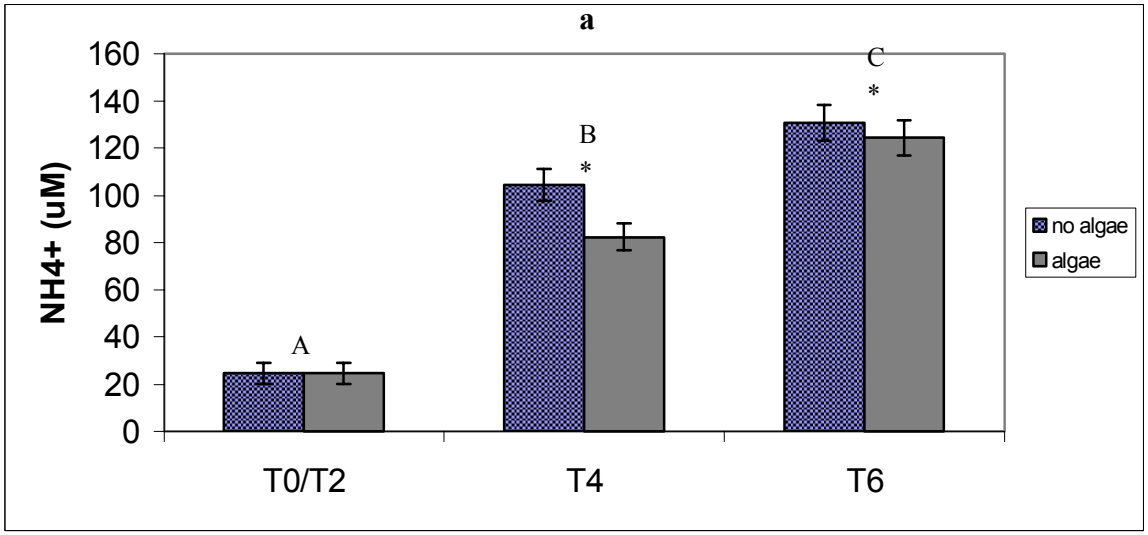



Figure 2.6 **(a)** Depth integrated mean (± standard error) pore water concentration for all time points and algal treatments. Letters indicate significantly different concentrations with time point and * indicates significantly different concentrations with algal treatment.

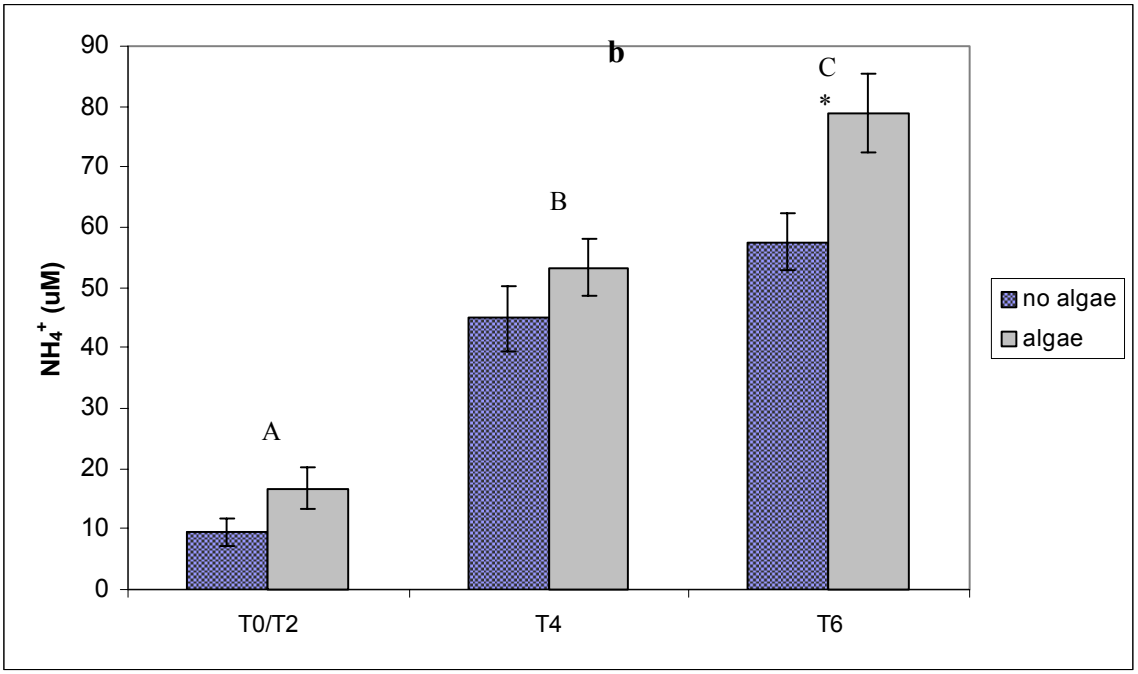



Figure 2.6 **(b)** Mean (± standard error) pore water concentration for top 1-cm of sediment core, for all time points and algal treatments. Letters indicate significantly different concentrations with time point and * indicates significantly different concentrations with algal treatment.

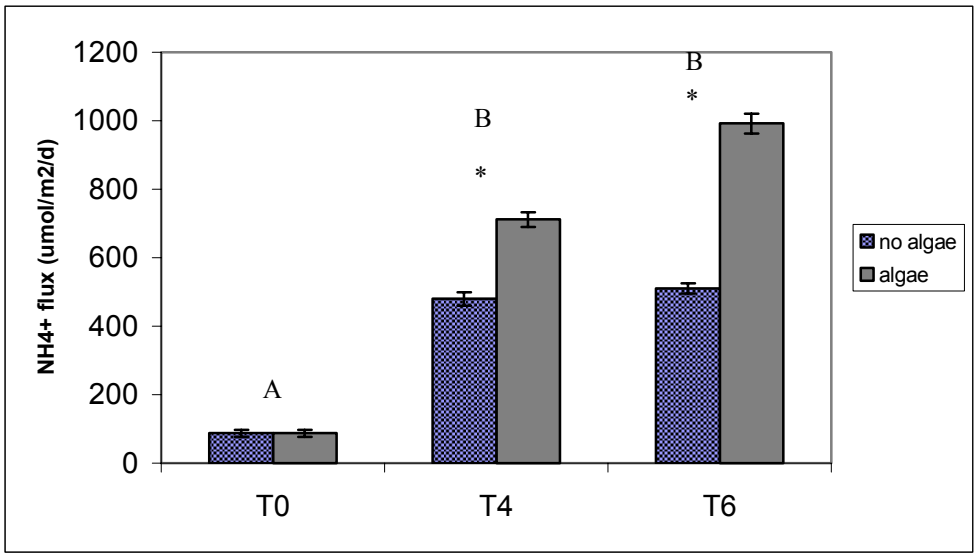



Figure 2.7 Mean (± standard error) pore water flux for all time points and algal treatments. Letters indicate significantly different concentrations with time point and * indicates significantly different concentrations with algal treatment.

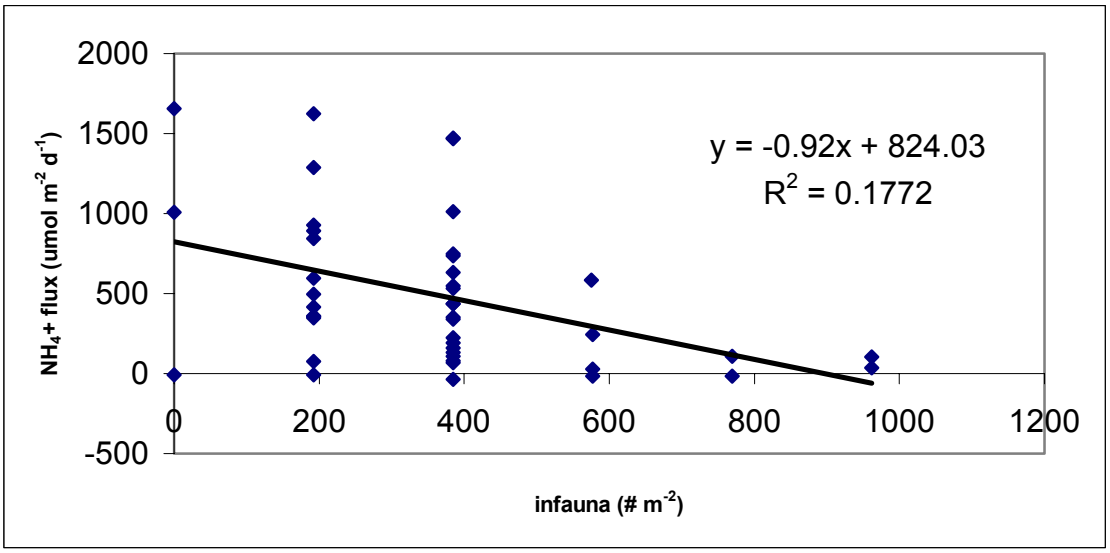



Figure 2.8 Regression of infaunal density and $NH_4^+$ diffusive flux for all infauna and time points.

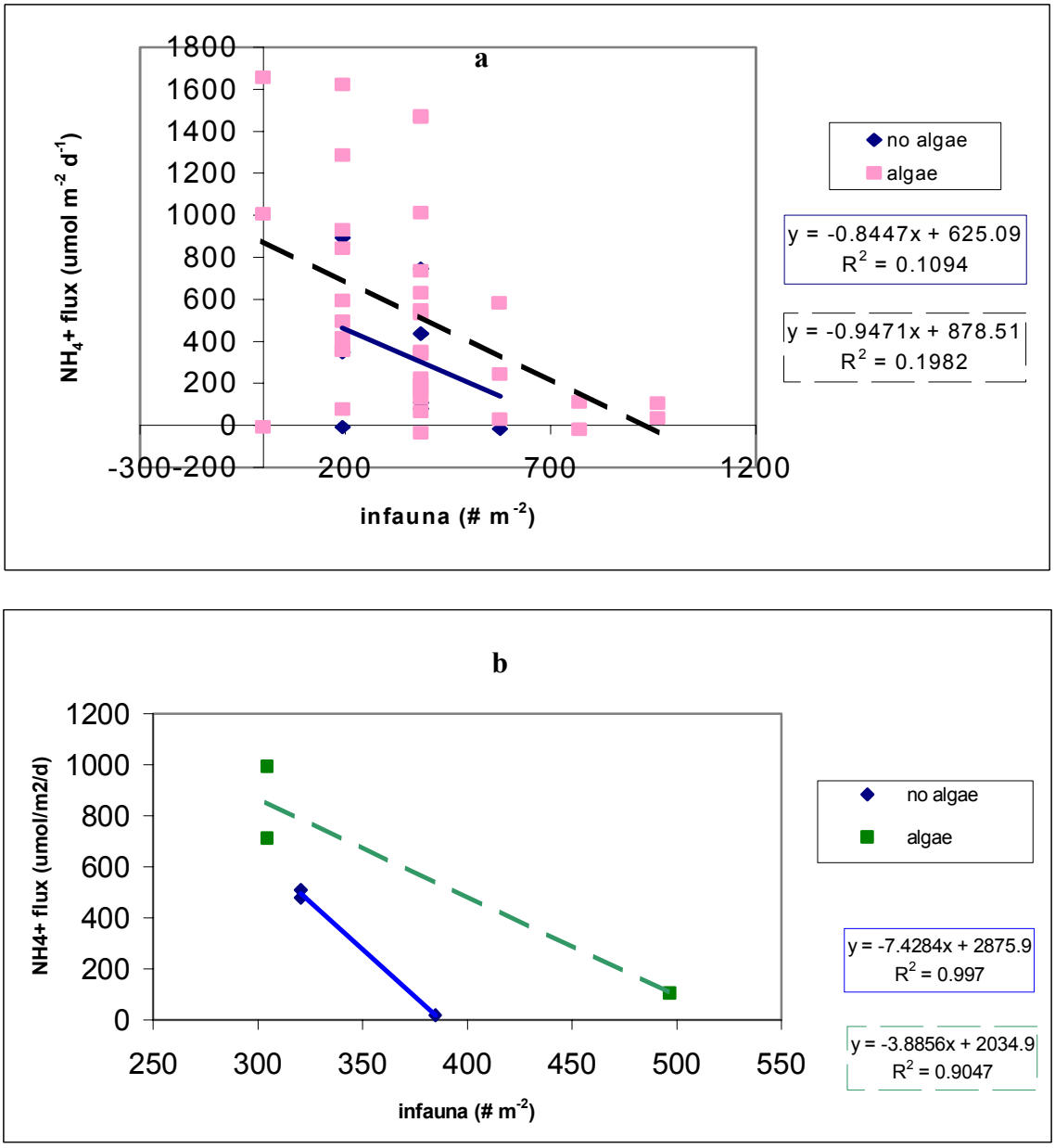
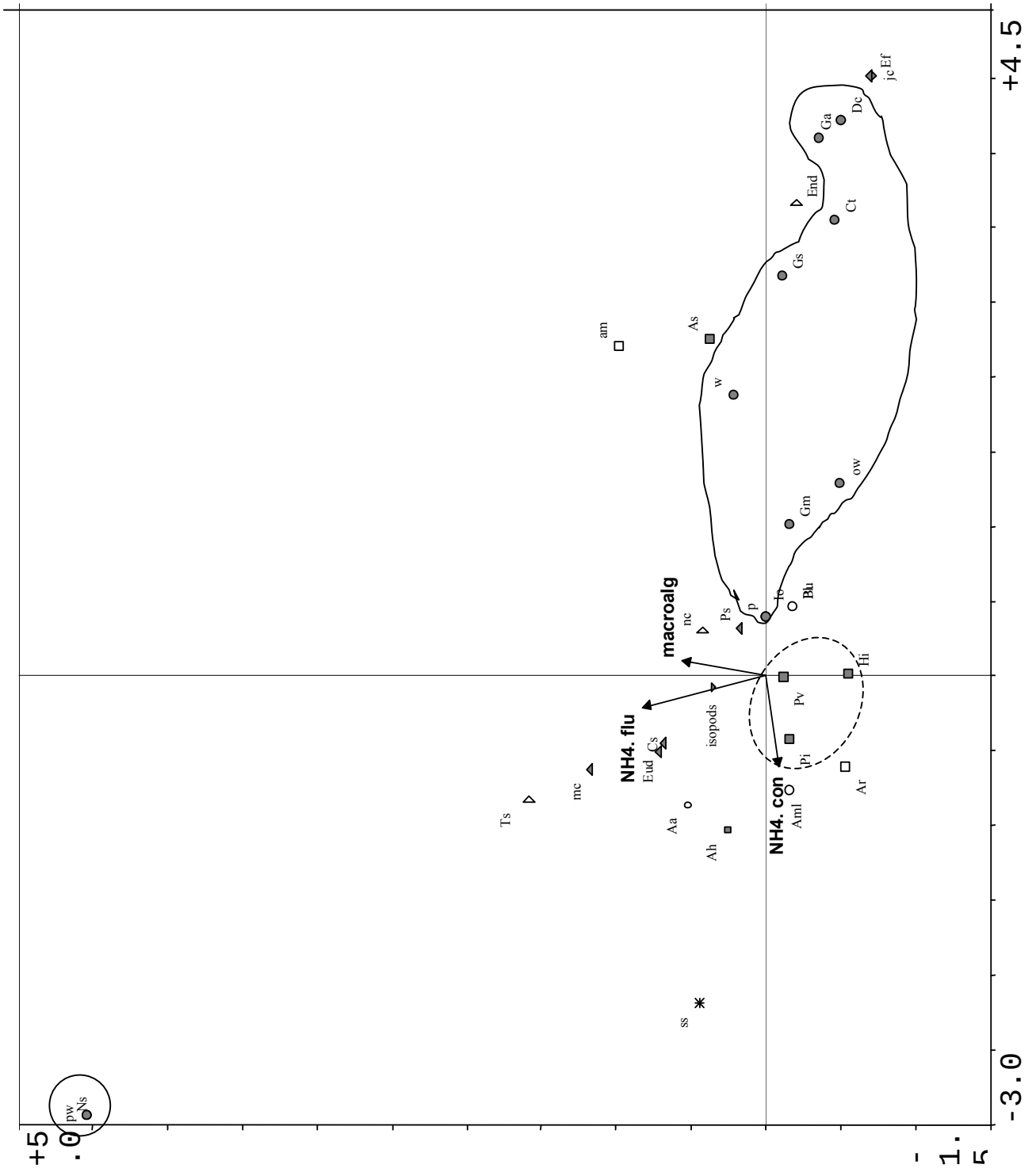



Figure 2.9 (a) Regression of infaunal density and $NH_4^+$ diffusive flux for the algae and no-algae treatments over all time points. Dashed line and box represent the algae treatment and solid line and box represent no-algae treatment. (b)Regression of infaunal density and mean $NH_4^+$ diffusive flux for the algae and no-algae treatments over all time points. Dashed line and box represent the algae treatment and solid line and box represent no-algae treatment.

Figure 2.10 (*below*). Canonical correspondence analysis (CCA) ordination diagram of the distribution of species (symbols) and environmental variables (arrows). The symbols represent classes of species: ○ snails, ● worms, □ shrimp, □ amphipods, △ crabs, ▷ clams, ▽ isopods, and * other. The species are: **Ah** *Alpheus heterochelis*, **am** amphipods unidentified, **Ar** *Ampithoe rubricata*, **Ao** *Amphitrite ornata*, **Aa** *Anachis avara*, **As** *Axius serratus*, **Bu** *Buccinum undatum*, **Cs** *Callinectes sapidus*, **Gm** *Goniada maculata*, **Ct** *Clymenella torquata*, ***End*** *Ensis directus*, **Eud** *Eurypanopeus depressus*, **Ef** *Erichsonella filiformis*, **isopods** isopods unidentified, **Dc** *Diopatra cuprea*, **Gs** *Glycera* sp., **Ga** *Glycera americana*, **Hi** *Hippolyte* sp., **Io** *Ilyanassa obsoleta*, **jc** juvenile crab, **Ps** *Pinnixa* sp, **Aml** *Astyris (Mitrella) lunata*, **Ns** *Nereis* sp., **nc** nut clam, **ow** opal worm, **Pl** *Pagurus longicarpus*, **Pi** *Palaemonetes intermedius*, ***Pv*** *Palaemonetes vulgaris*, **pw** parchment worm, **ss** sea squirts, **mc** mud crabs, **Ts** *Tellina* sp, **p** unidentified polychaetes, **w** worm unidentified. The dashed line encloses several species of shrimp while the solid lines enclose worm groups.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# 3. Interactions between Macroalgal Density and Grazing

## 3.1 Introduction

Macroalgal biomass may be controlled directly through both bottom-up and top-down processes in coastal ecosystems (e.g., Sand-Jensen and Borum 1991; Valiela et al. 1997; Lubchenco 1978; Duffy and Hay 1991; Hauxwell et al. 1998; Giannotti and McGlathery 2001). Nutrients have been considered the main control on macroalgal bloom formation since increases in macroalgal blooms have coincided with anthropogenic nutrient loading to coastal systems (Nixon 1995). Herbivores have a natural role in controlling macroalgal biomass in estuarine systems. But, this top-down control has been linked to nutrient status of the system, where herbivore control is lessened as nutrient input to a system increases (Hauxwell et al. 1998; Lotze et al. 2000; Giannotti and McGlathery 2001; Lotze et al. 2001). Thus, oligotrophic systems are more strongly top-down controlled than eutrophic systems. However, the effects of nutrient enrichment interact with consumer pressure resulting in a dynamic balance of consumer and resource control (Worm et al. 2002). Typically, when grazers are present the stimulatory effects of increased nutrient loading on macroalgal and epiphyte growth are diminished, but both low-productivity systems and high-productivity systems can experience a rapid change in species composition and system functioning when the balance of consumers and resources is skewed (Worm et al. 2002). Similar to macroalgal dominated systems, small grazers also have a role in top-down control of seagrass systems (Valiela et al. 1997; Gacia et al. 1999; Heck et al. 2000). Seagrasses themselves are less likely to be grazed than macroalgae or phytoplankton because seagrasses tend to have a higher C:N and are thus poor food quality (Valiela et al. 1997). However, grazers

offer potential control of macroalgae (especially epiphytes) (Heck et al. 2000) and there is evidence that invertebrate density does not change markedly with changes in seagrass biomass (Ahern et al. 1995). In contrast to subtidal systems, rocky intertidal systems respond to increased nutrient loading with increased macrophyte diversity dominated by slow-growing algae (Nielsen 2003). Also, herbivore effectiveness is not reduced with higher nutrient loading in rocky intertidal areas and physical factors may be more important in herbivore effectiveness (Nielsen 2001).

Regulation of macroalgal bloom species may begin at early life stages where grazers intercept the propagules of bloom-forming species (Lotze and Worm 2000; Lotze et al. 2000; Lotze et al. 2001). The most grazer-susceptible species tend to be fast-growing and those with a high growth response to nutrient enrichment so that grazer control of early life stages become less efficient as nutrient loads to a system increase (Lotze et al. 2001). Herbivore effects are also strong on adult life stages and grazing pressure should prevent overabundance of macroalgae (Valiela et al. 1997). However, growth responses of macroalgae relative to nutrient status of the system is also important and macroalgal growth rates can be high enough to overcome grazing pressure. Both Hauxwell et al. (1998) and Giannotti and McGlathery (2001) found that grazers could control macroalgal biomass accumulation, but only at low to moderate nutrient loading. At higher rates of nutrient loading, fast-growing macroalgal species overcome grazing pressure due to increased macroalgal growth rates, and the system becomes dominated by macroalgae (Valiela et al. 1997; Hauxwell et al. 1998). Reduced grazing pressure is also a factor in macroalgal proliferation (Geertz-Hansen et al. 1993; Valiela et al. 1997; Hauxwell et al. 1998). Macroalgal growth and decomposition change the physico-

chemical conditions rapidly (within 24 hr, Astill and Lavery 2001), which creates conditions that can be unsuitable for macrofauna when macroalgae accumulate in dense mats. Macroalgal accumulations can alter sediment-water column nutrient exchange, increase ammonium levels within macroalgal mats and in the underlying sediments, and create hypoxic conditions, especially at night (Krause-Jensen et al. 1996; McGlathery et al. 1997; Astill and Lavery 2001). Frequent hypoxic and anoxic periods associated with dense macroalgal mats have been responsible for benthic macrofauna and fish kills (Norkko and Bonsdorff 1996b, 1996c; Hauxwell et al. 1998; Balducci et al. 2001). Predation by fish also lowers densities of herbivorous amphipods and other mesograzers, which may provide an indirect release of grazer control on macroalgae (Warwick et al. 1982; Heck et al. 2000). Mesograzers are important for controlling algal biomass and factors that affect grazers and grazing rates are important in understanding the effects of nutrient enrichment on shallow ecosystems (Heck et al. 2000).

While intense herbivore pressure may reduce macroalgal bloom formation, selective herbivory on both recruits and adult stages may alter species composition and favor dominance of certain macroalgal species. Food selection by herbivores is correlated with nitrogen content (Mattson 1980; McGlathery 1995; Galán Jiménez et al. 1996; Hauxwell et al. 1998), with some amphipods exhibiting a preference even with small differences in %N (Galán Jiménez et al. 1996). Higher grazing rates and more intense grazing pressure have been linked to increased nitrogen content of macrophytes (Mattson 1980; McGlathery 1995; Hauxwell et al. 1998) but high grazing rates have also been linked to reduced food quality (high C:N) where grazers consume more, up to a point, to meet their nutritional requirements (Mattson 1980; Hauxwell et al. 1998). In

this way, grazers are important in structuring the macroalgal community (Duffy and Hay 2000; Lotze et al. 2000; Lotze et al. 2001). In amphipod dominated systems, it has been found that red seaweeds prevail (Duffy and Hay 2000). Specifically, when ampithoids are the dominant amphipods, their preference for green and brown macroalgae leads to a dominance of red macroalgal species. Brown macroalgae predominate in some systems, which may be the result of dominance of other grazer species or the presence of omnivorous fish (Duffy and Hay 2000; Lotze et al. 2000; Lotze and Worm 2000). The presence of fish can both reduce the abundance of grazing amphipods and remove fast-growing algal competitors like green algal species resulting in the dominance of brown species (Duffy and Hay 2000). Thus, strong and selective herbivory favors the less palatable red and brown seaweed species (Duffy and Hay 2000; Lotze et al. 2000).

Macroalgae have been found to significantly impact nutrient cycles, oxygen dynamics and sediment processes (Sfriso and Marcomini 1997; Balducci et al. 2001). Macroalgae may act as filters and reduce the flux of nutrients across the sediment-water column interface (McGlathery et al. 1997). Macroalgae enhance sediment nutrient cycling, likely due to the increased input of organic matter (Trimmer et al. 2000; Tyler et al. 2003; McGlathery et al. 2004). The increased mineralization rates cause a build-up of ammonium and may provide a nitrogen source to sustain macroalgal production (McGlathery et al. 1997; Trimmer et al. 2000; Astill and Lavery 2001). Furthermore, dense macroalgal accumulations have been linked to anoxic and hypoxic conditions at the sediment surface, which influences invertebrate populations by causing local extinction and reduced activity (Hull 1987; Isaksson and Pihl 1992;Valiela et al. 1997; Giannotti

and McGlathery 2001). In addition to oxygen stress from dense macroalgal mats, sedimentation may make the habitat unsuitable for grazer species or make the macroalgae less palatable. While it is known that algal mats baffle water currents and trap sediment, little is known about how increased sedimentation affects grazers or per capita grazing rate (see Figure 1.2).

Hog Island Bay (HIB) is characterized by distinct seasonal patterns in macroalgal biomass, with a peak in the summer and a crash or decline by late summer and fall (McGlathery et al. 2001). Macroalgal biomass accumulates in localized mats and the collapse of these high-density mats has led to periods of anoxia and significant release of algal bound nutrients (McGlathery et al. 2001; Tyler et al. 2001). It is interesting to note that Hog Island Bay (HIB), especially the mid-lagoon Shoal site, is a snail and amphipod-dominated system (Chapter 2) and has macroalgal blooms dominated by the red seaweed *Gracilaria tikvahiae*, which agrees with the work of Duffy and Hay (2000). HIB receives relatively low nutrient loads, which implies that grazers should be able to control macroalgal biomass accumulations (Hauxwell et al. 1998; Lotze et al. 2000; Giannotti and McGlathery 2001; Lotze et al. 2001). However, the mid-lagoon Shoal site consistently has macroalgal densities greater than 3000g-ww $m^{-2}$ (classified as high macroalgal density) in the summer biomass peak. Since recent studies have found grazer control of macroalgal biomass at low to moderate nutrient loads (Hauxwell et al. 1998; Giannotti and McGlathery 2001), it is interesting that similar grazer control is not found at the mid-lagoon Shoal site.

Most studies examining grazer control of macroalgae have tested the interaction of nutrients and grazing on macroalgal biomass and have not been done at natural field

macroalgal densities where changes in physical and chemical factors are likely to influence per capita grazing rates. For example, Hauxwell et al. (1998) examined field grazing rates on algae under a range of nutrient loading regimes, but algal density was not considered in determining grazing rates nor when scaling-up to system-wide impacts of grazing on macroalgal biomass control. Specifically, per capita grazing rates were measured outside of algal mats and then scaled to the number of grazers found in each system (Hauxwell et al. 1998). Giannotti and McGlathery (2001) used laboratory per capita grazing rates to scale-up grazer impact to the system, which may over-estimate grazer impact by providing less variable conditions than in the field. To accurately scale up per capita grazing rates to estimates of grazing impact under natural field conditions, the effects of differing macroalgal densities on per capita grazing rates need to be considered. Macroalgae will influence both numbers of grazers (as Hauxwell et al. (1998) considered), and their per capita grazing rates (as influenced by changing physico-chemical conditions). I focused on macroalgal density and the associated physico-chemical factors as the important mechanisms affecting per capita grazing rates at the mid-lagoon Shoal site in HIB. My hypothesis was that per capita grazing rates would increase up to a moderate macroalgal density, after which point, rates would decrease. Other important parameters that may affect per capita grazing rates included (1) the presence of detrital algae as an alternative food source for grazers; (2) amphipod size since grazers of different sizes may consume macroalgae at different rates; (3) how the presence of more than one macroalgal species and how different macroalgal ratios affect grazing rates; (4) increased sedimentation associated with dense macroalgae as a possible

deterrent to grazing. I designed a series of field and laboratory experiments to address the following objectives:

- Estimate macroalgal biomass loss to the dominant grazers (amphipods and snails) and estimate grazing rates for different sizes of amphipods
- Examine grazing on live and detrital macroalgae and determine which has a higher nitrogen content (as a measure of palatability and nutritional quality).
- Estimate macroalgal biomass loss to different size-classes of amphipods.
- Compare grazing rates on the dominant macroalgae when combined at different densities
- Determine what impact sedimentation has on per capita grazing rates.

I examined grazer impact on various macroalgal densities in field experiments to see how per capita grazing rates were influenced by macroalgal biomass under low nutrient loading. In addition, I applied this information to understanding grazer control of macroalgal blooms and the system-wide implications of macroalgal biomass loss to the dominant grazers in a model estimating macroalgal growth and grazer impact at various macroalgal densities. This model also incorporates self-shading within the mat to accurately reflect macroalgal growth rates.

## 3.2 METHODS

### *3.2.1 Field Experiments*

Grazing rates (mg ww $ind^{-1}$ $d^{-1}$) were determined in two field experiments on *Ulva lactuca* and *Gracilaria tikvahiae* by the amphipod *Ampithoe rubricata* and the snail *Astyris (Mitrella) lunata.* In the first field experiment in August 2001, organisms were

enclosed in cages made from 10-cm diameter polycarbonate tubes cut length-wise with open sides covered with plastic mesh (0.5-mm). The cages were 30-cm in length and rested on rebar platforms approximately 2-cm above the sediment surface to prevent small cages from filling with sediment; the small polycarbonate cages were placed within larger cages to prevent the small cages from being covered with algae. The polycarbonate tubing allowed maximum light penetration to the algae within the cages. The small mesh size was necessary for containing the amphipods and snails within the cages and excluding other grazers. The mesh allowed for chemical exchange with the sediment. Placement near the sediment surface where current flows are lower did not diminish water flow through the cages; early experiments showed that placing cages directly on the sediment surface caused cages to fill with sediment. Cages were cleaned regularly to prevent fouling.

Cages were arranged in a randomized block design with 6 treatments and 5 replicates. The treatments were 3 algal densities (low (100-g ww·$m^{-2}$), medium (1500-g ww·$m^{-2}$), and high (5000-g ww·$m^{-2}$)) of *U. lactuca* and *G. tikvahiae*. Amphipods were used as the grazer in one series of experiments and snails as the grazer in a second series of experiments. Control cages, with macroalgae only, for each density were used to correct for growth of macroalgae in determining loss to grazers. Each experiment was one week in duration. The macroalgal densities chosen for the field experiments were based on field surveys of HIB (McGlathery et al. 2001 and *unpublished data*). This experiment tested the effect of algal density on grazers by using field experiments without extrapolating from laboratory grazing rates. This experimental design should minimize the effects of shading and alteration of water flow due to small mesh sizes.

This design also minimized the amount of mesh used and placing the cages near the sediment surface where water flow is slower minimized the alteration of water flow attributed to small mesh sizes.

In the second field experiment in September 2002, grazing rates (mg ww $ind^{-1}$ $d^{-1}$) were, again, determined on *U. lactuca* and *G. tikvahiae* by the amphipod *A. rubricata* and the snail *A. lunata.* Different from the first field experiment, organisms were enclosed in mesh (0.5-mm) bags, approximately 10-$cm^2$, that were held open with a plastic ring to prevent compression. The bags were filled with *G. tikvahiae* at low density (corresponding to 100-g ww $m^{-2}$) and placed inside of larger cages made from rebar and plastic coated wire mesh. The larger cages were filled with macroalgae (three densities: low (100-g ww $m^{-2}$); medium (3000-g ww $m^{-2}$); high (6000-g ww $m^{-2}$)) as well as an algae-free control. Experimental bags contained either amphipod or snail grazers corresponding to field averages (17 amphipods per bag ≈ 1740 $m^{-2}$; 6 snails per bag ≈ 600 $m^{-2}$), and no-grazer controls to correct for algal growth. Bags with amphipods were suspended within the larger cages in the macroalgae since amphipods naturally occur higher in algal mats; bags with snails were placed near the sediment surface since the snails naturally occur lower in the algal mats. Bags were arranged in a randomized block design with 6 treatments (algal density of two algal species) and 5 replicates. Bags without grazers were also placed in the larger cages to correct for growth of the algae at the various densities. The experiment was one week in duration. C:N of the algae was measured at the end of the experiment.

These different experimental designs were used to examine the effect of macroalgal density in two ways: (1) The direct effect of the algae on grazing rate was

determined by placing grazers in cages with varied algal density and minimizing other confounding factors like light and nutrient exchange. In addition, there were different amounts of algae available to the grazers in the different treatments, which is more like field conditions when macroalgae accumulate. (2) The indirect effects of the algal density on grazing rates was determined by placing grazers in mesh bags with set macroalgal biomass within bags and with macroalgal density manipulated outside the bags. This second experimental design examined the effects of physico-chemical factors on grazing rate without providing additional algae for grazing at higher macroalgal density.

Grazing rate was calculated as algal mass (ww) loss in the grazer + algae treatments corrected for the average algal growth rate for each treatment during the same time period. Change in biomass of the algae was measured as change in wet weight on day 6 or day 7 of the field grazing experiments. Specific growth rates were calculated as the increase in algal wet weight assuming exponential growth:

$$\mu = (\ln B_t - B_0) \bullet t^{-1}$$

where $B_0$ and $B_t$ are the algal biomass before and after t days of growth.

*3.2.2 Laboratory Experiments*

3.2.2.1 Amphipod size experiments

Laboratory grazing experiments were conducted using different size classes of the amphipod *A. rubricata*. Amphipods were considered large if they were greater than 0.5-mm in length and small if they were less than 0.5-mm. Small plexiglas cylinders (10-cm length, 5-cm diameter, 196-ml volume) closed at the ends with 0.5-mm mesh contained a

single amphipod and ~1.0-g ww algae (either *U. lactuca* or *G. tikvahiae*) or algae alone (control). There were 5 replicates placed inside an aerated aquarium with water from the mid-lagoon Shoal site. Algal wet weight was measured at experiment initiation (time 0) and on days 2, 4, 6 and 8. Grazing rate was calculated as described above and related to amphipod size class. Grazing rate was corrected for algal growth by subtracting growth in controls.

3.2.2.2 Sedimentation experiments

Small plexiglas cylinders (10-cm length, 5-cm diameter, 196-ml volume) closed at the ends with 0.5-mm mesh contained either a single amphipod or snail and ~1.0-g ww of algae (either *U. lactuca* or *G.tikvahiae*) or algae alone (control). Half of the treatments were coated with 2-cc of sediments from surface sediments at the Shoal site while the other half of the treatments were cleaned of all sediment. There were 4 replicates of sediment coated, not coated, and control cylinders placed inside an aerated aquarium with water from the mid-lagoon Shoal site. Algal wet weight was measured at experiment initiation (time 0) and on days 2, 4, 6 and 8. Grazing rate was calculated for grazers on each algal species and related to sediment coating. Grazing rate was corrected for algal growth by measuring growth in controls. Dry weights and C:N of the sediments were determined as described below.

3.2.2.3 Detrital and live macroalgal grazing experiments

Detritus was prepared in the growth chamber by placing a large amount of macroalgae (*U. lactuca* and *G. tikvahiae*) from the Shoal site in the dark without aeration until the macroalgae began to die. The macroalgal detritus was then placed in small plexiglas cylinders (10-cm length, 5-cm diameter, 196-ml volume) closed at the ends with 0.5-mm mesh. The cylinders contained either a single amphipod or snail and ~1.0-g ww algae (either live *U. lactuca* or *G. tikvahiae*) or detritus, or algae or detritus alone (controls). There were 4 replicates of each treatment and controls. Wet weight of algae or detritus was measured at experiment initiation (time 0) and on days 2, 4, 6 and 8. Since the detrital algae were fragile, the detritus was drained on towels rather than patted dry for wet weight measurements. Grazing rate was calculated for grazers on each algal species and detritus. Grazing rate was corrected for algal growth or detrital decomposition by measuring growth or decomposition (as changes in wet weight), respectively, in controls. Dry weights and C:N of the algae and detritus were determined.

3.2.2.4 Macroalgal density ratios experiments

Small plexiglas cylinders (10-cm length, 5-cm diameter, 196-ml volume) closed at the ends with 0.5-mm mesh contained either two amphipods or two snails and both *U. lactuca (Ul)* and *G. tikvahiae (Gt)* in three ratios. Three total grams of algae were placed in the cylinders at densities of 1 *Ul*: 1 *Gt*, 1 *Ul*: 5 *Gt*, or 1 *Ul*: 10 *Gt*. No grazer controls contained the same ratios of algae and were used to correct for growth. There were three replicates. The cylinders were placed in water from the Shoal site and aerated. Algal wet

weights were measured at experiment initiation and on days 2, 4, and 6. Grazing rates were calculated for the different grazers and related to algal density ratios.

### *3.2.3 C:N Content*

At the end of each experiment, all algae were collected, briefly washed in deionized water, patted dry, weighed, and freeze-dried for 72-hours for tissue %C and %N analysis. Dried tissue was ground using a coffee grinder and mortar and pestle, and C and N content were determined on a Carlo-Erba Elemental Analyzer (NA 2500, Rodano, Italy).

### *3.2.4 Model Parameters*

To estimate the effect grazers may have on macroalgal biomass accumulation at the Shoal site, I modeled the amount of growth of *U. lactuca* and *G. tikvahiae* and the amount grazed by either the amphipod, *A. rubricata*, or the snail, *A.lunata* for each macroalgal density treatment. Macroalgal growth on an aerial basis (g dw $m^{-2}$ $d^{-1}$) was estimated based on algal biomass from field surveys and growth changes due to self-shading as biomass increases (McGlathery et al. 2003a). Per capita grazing rates (g dw $ind^{-1}$ $m^{-2}$ $d^{-1}$) were calculated from field experiments in the summer and were assumed not to change between seasons. These grazing rates are expected to give conservative estimates because macroalgal C:N is higher in the summer than in other seasons (McGlathery et al. 2001), which would provide a lower quality food source and potentially higher grazing rates (Mattson 1980; Hauxwell et al. 1998). Overall grazing loss on an aerial basis was calculated by multiplying per capita grazing rates by grazer

numbers (ind) from field surveys and field experiments (Chapter 2, Chapter 4). Conversions from wet weights (ww) to dry weights (dw) were 7.4 for *G. tikvahiae* and 4.4 for *U. lactuca* based on macroalgal monitoring data.

3.2.4.1 Macroalgal growth estimates

To model macroalgal growth in the field under different macroalgal densities, potential (% $d^{-1}$) macroalgal growth rates for the two algal species were calculated based on Tyler (2003). The potential growth rate was then used to calculate actual growth rate based on algal biomass and a shading function from Krause-Jensen et al. (1996), which accounts for self-shading and different light regimes within macroalgal canopies.

3.2.4.2 Grazing losses

The amount of each macroalgal species consumed by the grazers was calculated from the per capita field grazing rates for each macroalgal density treatment (Figures 3.1 and 3.2). The overall change in macroalgal biomass takes into account macroalgal growth under the density treatments, whereas Hauxwell et al. (1998) calculated grazing rates in absence of macroalgal growth. Since maximal grazing rates occurred at medium algal density (Figures 3.1 and 3.2), polynomial equations were used to calculate grazing rates for different algal densities (Figure 3.4) by the two grazer species. Mean per capita grazing rates were used in the polynomial model estimates; this accounted for changes in per capita grazing rates with changes in macroalgal biomass in a smooth way with a peak in grazing rates close to medium macroalgal densities. Linear relationships had low $R^2$ values that lead me to question the validity of such a relationship. The use of a fixed per capita grazing rate would not account for actual changes in macroalgal biomass. Once the

overall grazing rates were determined (g-dw $m^{-2}$ $d^{-1}$), they were applied to survey data of macroalgal biomass to determine the modeled grazing rates and the impact these grazers may have on macroalgal biomass at different densities in the field. To determine the potential for grazing to control macroalgal growth, the modeled grazing rates were plotted against actual growth rates of each macroalgal species for macroalgal survey data. The macroalgal survey data were grouped into density categories based on the field experiments to determine the relationship between grazing and macroalgal density.

### *3.2.5 Statistical Analysis*

Analysis of variance models for randomized block design were used to assess the effect of algal density, algal species, and grazer on per capita grazing rates. Analysis of variance using general linear models was used to assess differences in %N and C:N between algal densities, algal species and grazers. Differences were accepted as significant at $P < 0.05$. SAS® 8.2 software was used for statistical analyses.

## 3.3 RESULTS

### *3.3.1 Field grazing experiments*

Both *Ampithoe rubricata* and *Astyris lunata* had significantly higher grazing rates ($F_{2,48} = 4.67$, $P = 0.015$) at the medium macroalgal density in August 2001 (Figures 3.1 and 3.2). *A. rubricata* did not graze *Ulva lactuca* or *Gracilaria tikvahiae* at the highest macroalgal density (Figure 3.1) while only *U. lactuca* was not grazed by *A. lunata* at high density (Figure 3.2). A similar, though not significant, trend was seen in September 2002 where both *A. rubricata* and *A. lunata* had higher grazing rates at the low and medium *G. tikvahiae* densities (Figure 3.3). In both years, *A. lunata* had higher grazing

rates than *A. rubricata,* and they were significantly higher in 2002 ($F_{1,48} = 3.36$, $P = 0.074$ for 2001; $F_{1,24} = 5.64$, $P = 0.028$ for 2002). Based on the per capita grazing rates, the average macroalgal growth rates, and range in numbers of grazers at each site, I was able to predict the ability of these dominant grazers to control macroalgal biomass at different macroalgal densities. *A. rubricata* was able to control up to 100% of new and standing macroalgal biomass (Table 3.1 and Table 3.2) at low to medium macroalgal densities in 2001 and at all densities in 2002. *A. lunata* was able to control up to 100% of new and standing macroalgal biomass at low densities in 2001 and at all densities in 2002 (Table 3.1 and Table 3.2).

In August 2001, the highest density macroalgae had significantly higher C:N in both *U. lactuca* and *G. tikvahiae* ($F_{2,85} = 15.52$, $P < 0.0001$). *U. lactuca* had significantly lower C:N at all densities than *G. tikvahiae* ($F_{2,85} = 43.81$, $P < 0.0001$) (Figure 3.14).

There were no significant differences in C:N of the macroalgae among densities in 2002. However, the presence of grazers seemed to lower the C:N of *G. tikvahiae* in the 2002 experiment ($F_{2,123} = 2.66$, $P = 0.075$) (Figure 3.15).

There was a significant decrease in %N as macroalgal density increased ($F_{2,79} = 23.7$, $P < 0.0001$) (Figure 3.16). While the %N was not significantly different between the algal species, there was a shift toward *G. tikvahiae* having a higher %N than *U. lactuca* with increasing macroalgal density.

### *3.3.2 Laboratory grazing experiments*

In the laboratory experiments, small *A. rubricata* had significantly higher grazing rates than large *A. rubricata* ($F_{1,16} = 14.45$, $P < 0.0005$) (Figure 3.5). In addition, both

sizes of *A. rubricata* had a significantly higher grazing rate on *U. lactuca* than *G. tikvahiae* ($F_{1,16} = 26.73$, $P < 0.0002$). While there was no significant difference in grazing rates on algae with and without sediment coating, sediment seems to enhance grazing on *G. tikvahiae*, while it deters grazing on *U. lactuca* (Figure 3.6 and Figure 3.7). *A. lunata* did not graze *U. lactuca* with the sediment coating (Figure 3.7). There was no significant difference in grazing rates by the two grazers on either algal species or detritus. However, snails evidently preferred *U. lactuca*, while amphipods preferred detritus (Figure 3.8, Figure 3.9).

Per capita grazing rates were significantly higher with the highest proportion of *G. tikvahiae* ($F_{2, 31} = 16.24$, $P<0.0001$) (Figure 3.10 and Figure 3.11). Amphipods did not graze *G. tikvahiae* except when it was present at the highest proportion (Figure 3.10). When *G. tikvahiae* was present in the highest proportion, snails had a higher per capita grazing rate; at the mid-proportion, snails had higher per capita grazing rates on *U. lactuca* (Figure 3.11). There was no perceptible grazing by snails at the 1 *U. lactuca*:1 *G. tikvahiae* treatment (Figure 3.11).

Macroalgal detritus had a significantly lower C:N ($F_{2, 24} = 63.2$, $P<0.0001$) than live *U. lactuca* and *G. tikvahiae* (Table 3.4). The C:N of *G. tikvahiae* was also significantly lower than *U. lactuca*. The same significance pattern held true for %N as well ($F_{2, 24} = 54.5$, $P<0.0001$) (Table 3.4) where detritus had the highest %N followed by *G. tikvahiae* and *U. lactuca*. *G. tikvahiae* had a significantly higher C:N ($F_{5, 48} = 6.8$, $P<0.0001$) at all ratios of *U. lactuca* to *G. tikvahiae* (Table 3.5). C:N was also significantly higher at the 1 *U. lactuca*:10 *G. tikvahiae* treatment than at the 1 *U.*

*lactuca*:1 *G. tikvahiae* treatment, but neither the 1:10 nor the 1:1 were significantly different from the 1 *U. lactuca*:5 *G. tikvahiae* (Table 3.5).

*3.3.3 Model results*

The calculated growth increases of *G. tikvahiae* and *U. lactuca* were highest at the high-density treatment (Table 3.3), due both to higher potential growth rates and a higher initial biomass at the high-density treatment. Possible loss of macroalgal biomass to grazers was lowest at the high-density treatment and in the spring due to low grazer abundance (Table 3.6).

To emphasize the potential for grazers to control macroalgal accumulations under field conditions, the modeled grazing and growth rates for each algal species at field macroalgal densities were plotted for each grazer (Figure 3.12 and Figure 3.13). If loss of macroalgal biomass due to consumption by grazers equaled the gain of biomass due to growth, then biomass of the algae would not change and points would fall on the 1:1 line. Grazing by amphipods on either macroalgal species shows that grazing and growth are of similar magnitude (fall near or to the left of the 1:1 line) at both low and medium density categories, but many points indicate that grazing is higher than macroalgal growth; at high macroalgal density, grazing begins to be outstripped by growth (Figure 3.12a and Figure 3.13a). Also, at very low *U. lactuca* density there are negative grazing rates that fall to the right of the 1:1 line, indicating lack of amphipod control over growth under some low density conditions (Figure 3.13a). With snails as the grazer, all points scatter to the left of the 1:1 line suggesting that growth and grazing are of similar magnitude and

that snails should be able to control macroalgal biomass accumulation (Figure 3.12b and Figure 3.13b).

## 3.4 DISCUSSION

### *3.4.1 Controls on Macroalgal Biomass and Community Composition*

Mesograzers such as amphipods and snails clearly can control macroalgal biomass in systems with low to moderate nutrient loads (Hauxwell et al 1998; Giannotti and McGlathery 2001; this study at low and mid-macroalgal density) and thus can mitigate the negative effects of macroalgal blooms. However, even in a system with low nutrient loads and high per capita grazing rates, such as HIB, grazers do not control algal proliferation. Shallow coastal systems like lagoons may have blooms independent of the nutrient status of the system (Thomsen 2004, *in prep*). Physical factors like wind may be more important in the development of macroalgal blooms in shallow systems since the advection of macroalgae can cause large accumulations locally (Lawson 2003), with the nutrients to support growth likely coming from nutrient regeneration in the sediments (McGlathery et al. 1997; Trimmer et al. 2000; Astill and Lavery 2001). This physical transport of macroalgae may reduce the importance of new recruits and nutrient status that are generally regarded as being important in macroalgal bloom formation (e.g., Lotze et al. 2000; Worm et al. 2001;Valiela et al. 1997; Hauxwell et al. 1998).

In developing an understanding of the regulation of macroalgal biomass and trophic interactions in shallow systems, the control by mesograzers may not be a linear response to increased resources. Factors that are important in determining grazer density, grazing rate, and macroalgal proliferation at the mid-lagoon Shoal site (Figure 1.2) are

macroalgal density (Figures 3.1-3.3) and sedimentation. Many studies have linked increased nutrients to increased macroalgal biomass (see Valiela et al. 1997 for example), but in HIB, recycling of nutrients within the mats may be more important for maintaining macroalgal biomass once it accumulates and this system may become self-sustaining (Table 3.3) (McGlathery et al. 1997; Trimmer et al. 2000; Astill and Lavery 2001). The formation of macroalgal mats leads to increased sedimentation as water currents slow (Rhoades and Boyer 1982; Sfriso and Marcomini 1997), which inhibits grazing on *U. lactuca* by snails (Figure 3.7) and may be a factor in determining community composition. Snails do not graze *U. lactuca* at high density in the field (Figure 3.2) nor when it has a sediment coating (Figure 3.7); in the field, *U. lactuca* consistently has a sediment coating at high density. However, these factors would not lead to the dominance of *G. tikvahiae* like at the Shoal site. In the field experiments without the sediment coating (Figure 3.2) snails had a higher grazing rate on *U. lactuca* than *G. tikvahiae*, which may be due to the lower C:N of *U. lactuca* and thus a higher nutritional quality for the grazer (Hauxwell et al. 1998). In addition, amphipods had high grazing rates on *U. lactuca* in the laboratory (Figure 3.5). This may be important in benthic community structure since a preference for *U. lactuca* would cause the dominance of *G. tikvahiae*.

The per capita grazing rates reported here are high compared to other literature values (Table 3.7) (see Nicotri 1977; Hauxwell et al. 1998; Giannotti and McGlathery 2001). Based on the laboratory experiment where small *A. rubricata* had a significantly higher grazing rate than large *A. rubricata* (Figure 3.5), our data show that grazer size may be an important variable in calculating grazing rates. As Duffy and Hay (2000) found, grazing

amphipods have both a strong and disproportionate impact on the benthic macroalgal community relative to their biomass; this can be extended to include amphipod size as an important factor since smaller amphipods may have an even greater impact on the benthic macroalgal community. The high grazing rates may also be a factor of breakage and loss of macroalgae, although it is likely only a minor factor given the small mesh size used. Another factor that influences per capita grazing rates is the macroalgal biomass available to the grazers. Our grazing rates were consistently higher in the mid-algal densities (Table 3.7) so that algal density may be an important factor for appreciable grazing and per capita grazing rates. The medium algal biomass is similar to field conditions so may provide the best balance of food and refuge for the grazers and therefore maximizes grazing rates (Figures 3.1, 3.2, 3.3). The decrease at the high macroalgal densities may be due to changes in the physico-chemical parameters associated with very dense algal mats, particularly a change in oxygen dynamics. The low grazing rates at the lower macroalgal densities may be related to lower encounter frequency or to a greater impact of physical factors. Studies have shown that grazering activity can potentially damage more of the plant than is actually consumed resulting in gretaer changes in plant biomass and suprression of plant growth (e.g. Silliman and Zieman 2001). The overall high grazing rates seen in this study may also be a result of this type of biomass loss as well and may also account for the higher grazing rates by snails.

Snails (*A. lunata*) in both experiments had significantly higher per capita grazing rates than amphipods (*A. rubricata*) (Figures 3.1, 3.2, 3.3), which is consistent with previous work showing that snails tend to be more efficient grazers with higher biomass control (Lein 1980; Jernakoff and Nielson 1997; Lotze and Worm 2000). In addition,

snails have higher density than amphipods in the field (Table 3.6) (chapters 2 and 4) and thus can impact macroalgal biomass considerably. Amphipods have also been shown to be more selective feeders and influence algal community composition to a greater extent than snails (Lein 1980; Jernakoff and Nielson 1997; Lotze and Worm 2000) and red seaweeds such as *G. tikvahiae* have been shown to prevail in amphipod-dominated treatments (Duffy and Hay 2000). If *A. rubricata* has a preference for softer food types (Jernakoff and Nielson 1997) like *U. lactuca* (Figures 3.5, 3.10) and a greater selectivity and influence on community composition, this may be an explanation for the dominance of *G. tikvahiae* in Hog Island Bay (HIB). In addition, early life stages of macroalgae are more susceptible to herbivore control than adult life stages (Lotze et al. 2000). The macroalgal community at the mid-lagoon Shoal site in HIB is supported in large part by drift algae, which would allow the algae to "escape" the more vulnerable early life stages and make the algal biomass more difficult for the herbivores to control, thus highlighting the importance of physical forces in macroalgal accumulations (Lawson 2003).

Another factor in effective macroalgal bloom control is linked to high herbivore density and species richness (Lotze and Worm 2000). My previous work showed that as macroalgal biomass and density increased, even at fairly low macroalgal biomass, herbivore density was reduced at the Shoal site (Chapter 2). The decline in both density and species richness of the macroinvertebrate community occurs rapidly (Norkko and Bonsdorff 1996c), and thus the ability of macroinvertebrates to effectively control macroalgae is reduced. This would also be true when macroalgae accumulate at the Shoal site due to drift and advection driven by the wind and would be independent of the nutrient status of the system. Further evidence for reduced control by mesograzers in this

system is that the ability to control new growth is outstripped at and above average field macroalgal density (mid-density) (Tables 3.1, 3.2) and the high initial biomass in the high-density treatment may allow the algae to "escape" the grazing pressure (Geertz-Hansen et al. 1993).

In the second field experiment, the grazers had access to a small amount of algae that was surrounded by the varied algal densities so that the effects of the density are indirect and may be more physico-chemical in nature. Since *A. rubricata* were able to graze >100% of new and standing macroalgal biomass regardless of the macroalgal density treatment and *A. lunata* were able to graze up to 100% of new and standing biomass in all but the high algal density treatments (Tables 3.1, 3.2), there was essentially no "escape" for the algae from the grazing pressure. The physico-chemical effects were expected to be greatest at high density where light transmission, redox potential, pH, and water column oxygen concentration are all reduced (Norkko and Bonsdorff 1996a; Balducci et al. 2001) and this is reflected in the lack of biomass control by snails (*A. lunata*) at high macroalgal density (Tables 3.1, 3.2).

Based on laboratory experiments, snails prefer *U. lactuca* as a food source to *G. tikvahiae* or detritus and amphipods preferred detritus (Figure 3.9). Given that detritus had the lowest C:N and highest %N (Table 3.4), it was surprising that both grazers studied did not consume it at the highest rate. Crossman et al. (2001) suggest that detritus, although shown to be higher in N, is not appropriate as a food source for all grazers because the C and N may not be in forms available to all grazers. In the laboratory setting, both grazers had higher per capita grazing rates on *U. lactuca* than on *G. tikvahiae* when it was present alone (Figures 3.5, 3.6, 3.7, 3.8, 3.9), or when *G.*

*tikvahiae* was present in lower proportions such as the 1:1 and 1:5 treatments (Figures 3.10 and 3.11). What this indicates is that while these grazers do consume both *U. lactuca* and *G. tikvahiae*, there is a preference for *U. lactuca* that may lead to the dominance of *G. tikvahiae*. Once *G. tikvahiae* is the dominant macroalgae, as in the laboratory 1:10 treatment, it may be consumed more simply because it is encountered more frequently (Figures 3.10 and 3.11). If this same pattern holds true in the field setting, then this is a good example of how small grazers in a system can control the benthic community structure.

### *3.4.2 Grazer Impact Estimates Predicted from Model*

With wind as a dominant driver of physical processes in HIB (Lawson 2003) and the high probability of reduced grazing pressure as macroalgae accumulate, there is potential for large accumulations of macroalgae. The model indicates that macroalgal growth increase is greatest at high density (Table 3.3) and potential loss to grazers is lowest at high density (Table 3.6). These directionally opposite trends coupled with wind as a driving force indicate that this is a system where macroalgae can clearly escape control by grazers, similar to the inner estuary of the Geertz-Hansen et al. (1993) study. While other studies have shown a link between increased nutrient loading and reduced grazer pressure (McGlathery 1995; Hauxwell et al. 1998), this study indicates that macroalgal density is a large driving force in determining grazer impact.

The model results indicate that amphipods cannot maintain the high grazing rates necessary to control macroalgal biomass in this system (Figures 3.12, 3.13), which is a combination of both reduced amphipod density with increasing macroalgal biomass

(Chapter 2) and the amphipod preference for detritus as a food source (Figure 3.8) (Duffy and Hay 2000). Since more detritus is expected to be produced at higher macroalgal density (Trimmer et al. 2000; Tyler et al. 2003)—due to senescence and decomposition of macroalgae in the lower layers of the mat—then this would further reduce the impact that amphipods have on the live macroalgae. Previous studies have shown that different mesograzers can have different feeding preferences and thus different effects on the community organization (Cruz-Rivera and Hay 2000; Duffy and Hay 2000). The fact that the model results indicate snails should be able to control macroalgal biomass at all densities while amphipods can not (Figures 3.12, 3.13) provides additional support for species specific impacts (Duffy and Hay 2000).

It was interesting that the model indicated lack of control over *U. lactuca* under some low density conditions as well (Figure 3.13a). Many ampithoids are tubiculous and use fine debris to build tubes and nests (Gosner 1971). The lack of refuge and lack of debris when *U. lactuca* density is very low would lead to unsuitable habitat conditions for these amphipods and thus negatively impact grazing rate.

### *3.4.3 Summary*

In conclusion, this study shows that both *A. rubricata* and *A. lunata* are significant consumers of both *U. lactuca* and *G. tikvahiae* and should have the ability to control macroalgal biomass at low and mid densities, but low grazing rates and reduced grazer abundance at high macroalgal density prevent these grazers from controlling macroalgal proliferation. It is also important to consider that in shallow coastal systems like lagoons, nutrient status may not be the main control on macroalgal proliferation. Physical

processes may be more important in advection of macroalgae and local bloom formation. Nutrient remineralization in the sediments is then important in sustaining blooms (McGlathery et al. 1997; Trimmer et al. 2000; Astill and Lavery 2001; Tyler et al. 2003; McGlathery et al. 2004).

These grazers play an important role in the transfer and recycling of nutrients bound in macroalgal tissue. This has important implications for the fate and transport of nutrient inputs from the coastal watershed through HIB to the coastal ocean. And while this system is not currently nutrient over-enriched, the areas surrounding HIB are heavily influenced by agriculture and may eventually lead to over-enrichment of this system. Understanding the top-down influence of grazers remains an important aspect of nutrient over-enrichment and macroalgal biomass control. A key factor in understanding top-down controls in HIB is the effect of macroalgal density on per capita grazing rates. If macroalgal density is not considered, which it has not been in previous studies, there is potential to underestimate grazing impact at mid-densities by 26-36% and to overestimate grazing impact at high-densities by more than 60% and up to 89%. Clearly, there can be dramatic impacts on interpretation of top-down effects in shallow coastal systems.

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**Table 3.1**. Impact of grazing on new biomass (% removal based on average growth rates and the range of grazer densities measured at Shoal site)

| Summer 2001 | | | | |
|---|---|---|---|---|
| | *Ulva* | | *Gracilaria* | |
| Algal density within cages | Snail | Amphipod | Snail | Amphipod |
| Low (100-g ww) | 76 - >100% | >100% | >100% | >100% |
| Medium (1500 g) | 15 – 30% | >100% | 22– 44% | >100% |
| High (5000 g) | 0% | 0% | 1 - 3% | 0% |
| Fall 2002 | | | | |
| | *Gracilaria* | | | |
| Algal density outside of cages | Snail | | Amphipod | |
| None (0-g ww) | 66 - >100% | | >100% | |
| Low (100-g) | >100% | | >100% | |
| Medium (3000-g) | 66 - >100% | | >100% | |
| High (6000-g) | 43 - 86% | | >100% | |

**Table 3.2**. Impact of grazing on standing biomass (% removal based on range of grazer field densities and initial algal biomass and specific growth rate)

| Summer 2001 | | | | |
|---|---|---|---|---|
| | *Ulva* | | *Gracilaria* | |
| Algal density within cages | Snail | Amphipod | Snail | Amphipod |
| Low (100-g ww) | 73.8 - >100% | >100% | 71.4 - >100% | >100% |
| Medium (1500 g) | 49.4 – 98.7% | 0% | 18.3 – 36.5% | >100% |
| High (5000 g) | 0% | 0% | 0.7 – 1.4% | 0% |
| Fall 2002 | | | | |
| | *Gracilaria* | | | |
| Algal density outside of cages | Snail | | Amphipod | |
| None (0-g ww) | >100% | | >100% | |
| Low (100-g) | >100% | | >100% | |
| Medium (3000-g) | >100% | | >100% | |
| High (6000-g) | 69.8 - >100% | | >100% | |

**Table 3.3**. Mean (standard deviation) of macroalgal growth rates.

| | *Gracilaria tikvahiae* | | | *Ulva lactuca* | | |
|---|---|---|---|---|---|---|
| | Summer | Fall | Spring | Summer | Fall | Spring |
| High density | 4.06 (0.08) | na[1] | na[1] | 4.12 (0.02) | na[1] | na[1] |
| Medium density | 3.30 (0.35) | 2.87 ( 0) | 2.30 (0.31) | 3.70 (0.33) | 2.87 (0) | 2.78 (0.13) |
| Low density | 0.88 (0.70) | 0.77 (0.63) | 0.88 (0.51) | 1.26 (0.99) | 0.77 (0.63) | 1.38 (0.78) |

[1] na = no algae at that density

**Table 3.4**. Mean (standard error) of C:N and %N of macroalgae and detritus from laboratory grazing experiments.

| C:N | | | %N | | |
|---|---|---|---|---|---|
| *Ulva lactuca* | *Gracilaria tikvahiae* | Macroalgal detritus | *Ulva lactuca* | *Gracilaria tikvahiae* | Macroalgal detritus |
| 38.65 (2.42) | 23.31 (1.82) | 15.72 (1.90) | 0.82 (0.34) | 1.39 (0.45) | 1.98 (0.58) |

**Table 3.5**. Mean (standard error) of C:N and %N of *Ulva lactuca* and *Gracilaria tikvahiae* combined in different ratios from laboratory grazing experiments.

| | 1 *U. lactuca*: 1 *G. tikvahiae* | | 1 *U. lactuca*: 5 *G. tikvahiae* | | 1 *U. lactuca*: 10 *G. tikvahiae* | |
|---|---|---|---|---|---|---|
| | *U. lactuca* | *G. tikvahiae* | *U. lactuca* | *G. tikvahiae* | *U. lactuca* | *G. tikvahiae* |
| C:N | 5.76 (0.39) | 5.78 (0.70) | 5.75 (0.52) | 6.38 (0.84) | 6.15 (0.41) | 6.51 (0.53) |
| %N | 5.22 (0.52) | 5.47 (0.72) | 5.39 (0.52) | 4.88 (0.73) | 5.14 (0.39) | 4.75 (0.50) |

**Table 3.6**. Mean (standard error) number of *Ampithoe rubricata* or *Astyris (Mitrella) lunata* from summer 2000 (see also Chapter 2).

| Macroalgal treatment | *Ampithoe rubricata* | *Astyris (Mitrella) lunata* |
|---|---|---|
| Low density | 2576.9 (75.2) | 6115.4 (106.9) |
| Medium density | 929.5 (38.0) | 2179.5 (42.5) |
| High density | 144.2 (17.0) | 2740.4 (54.4) |

**Table 3.7** Comparison of per capita grazing rates from this study and those reported previously.

| Algal species | Grazer species | Grazing rate (mg ww $ind^{-1}$ $d^{-1}$) | Study |
|---|---|---|---|
| *Ulva lactuca*<br>low density<br>medium density<br>high density | *Astyris lunata,*<br>*Ampithoe rubricata* | <br>41.6, 2.7<br>81.6, 36.8<br>0.0, 0.0 | Present study |
| *Gracilaria tikvahiae*<br>low density<br>medium density<br>high density | *Astyris lunata,*<br>*Ampithoe rubricata* | <br>30.7, 6.7<br>75.9, 37.3<br>15.9, 0.0 | Present study |
| *Ulva lactuca* | *Ilyanassa obsoleta* | 9.32 – 10.83 | Giannotti and McGlathery 2001 |
| *Cladophora vagabunda* | *Idotea baltica*<br>various amphipods | 7.3<br>0.75 - 2.0 | Hauxwell et al. 1998 |
| *Gracilaria foliifera* | *Idotea baltica*<br>*Ampithoe valida* | 4.29<br>4.29 | Nicotri 1977 |

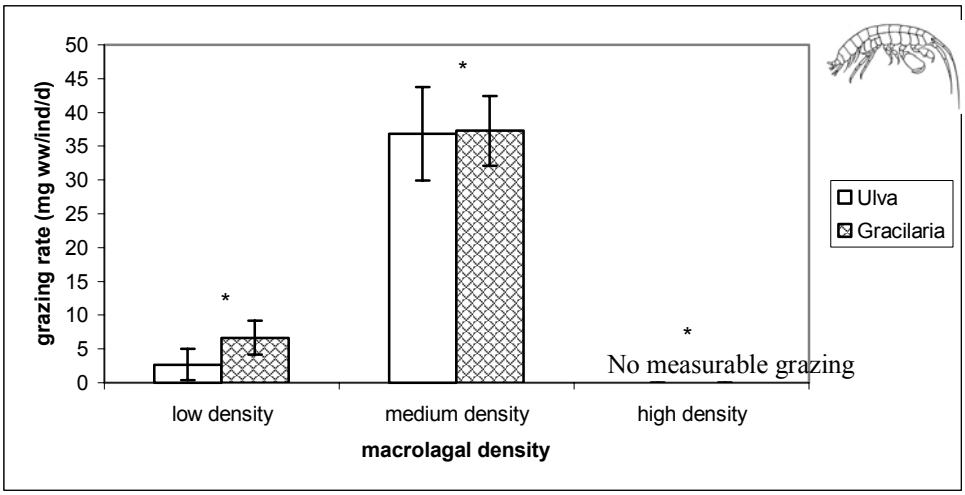



Figure 3.1. *Ampithoe rubricata* per capita grazing rate ± standard error for grazing on *Ulva lactuca* and *Gracilaria tikvahiae*, August 2001. * indicates significant difference among algal densities. There was no significant difference in grazing rates on *U. lactuca* and *G. tikvahiae*.

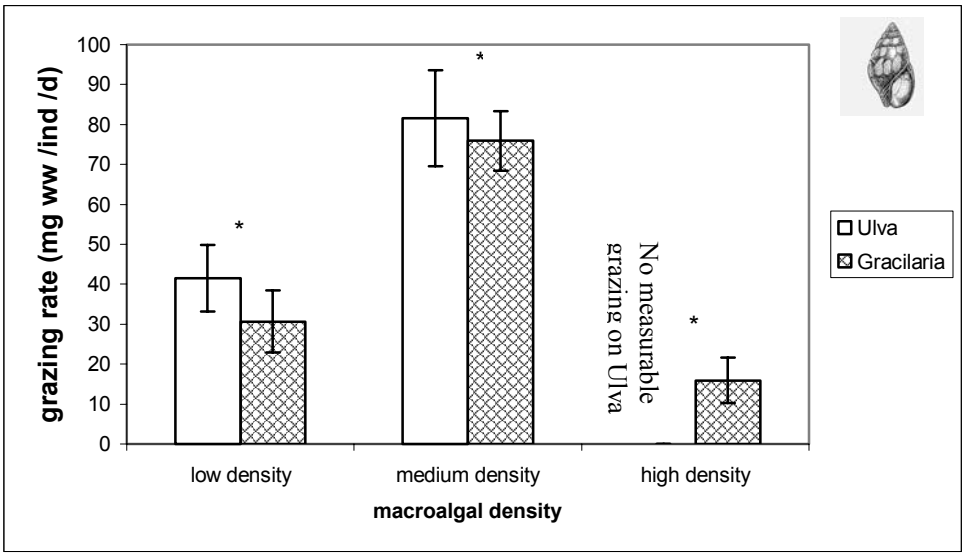



Figure 3.2. *Astyris (Mitrella) lunata* per capita grazing rate ± standard error for grazing on *Ulva lactuca* and *Gracilaria tikvahiae*, August 2001. * indicates significant difference among algal densities. There was no significant difference in grazing rates on *U. lactuca* and *G. tikvahiae*.

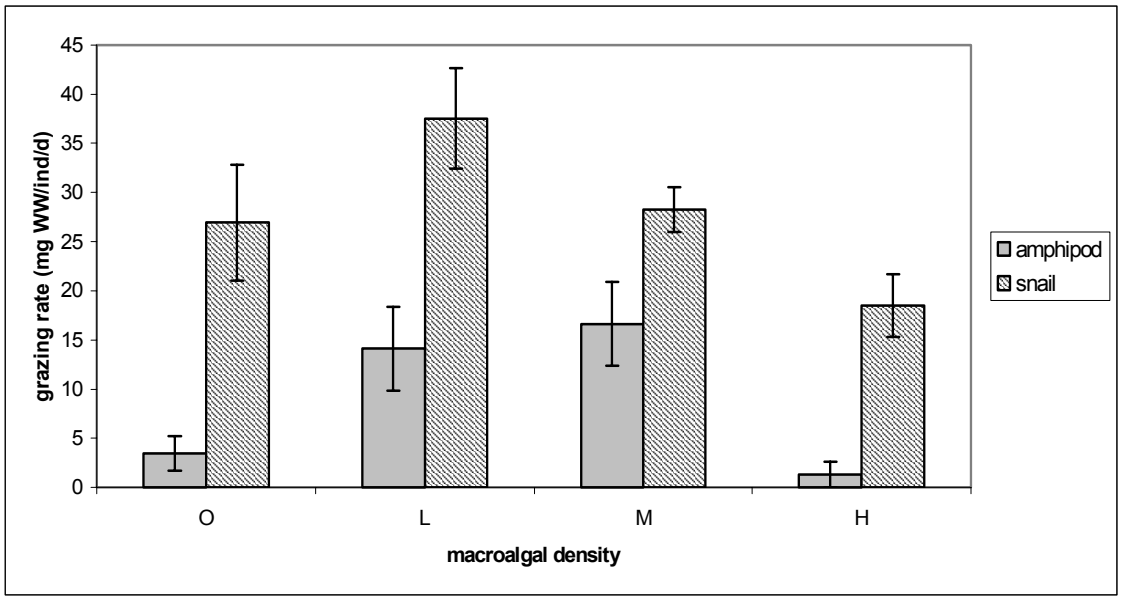



Figure 3.3. Per capita grazing rates ± standard error for *Ampithoe rubricata* (amphipod) and *Astyris (Mitrella) lunata* (snail) on *Gracilaria tikvahiae*, September 2002. * indicates significant difference among algal densities. Amphipods and snails had significantly different grazing rates (see text).

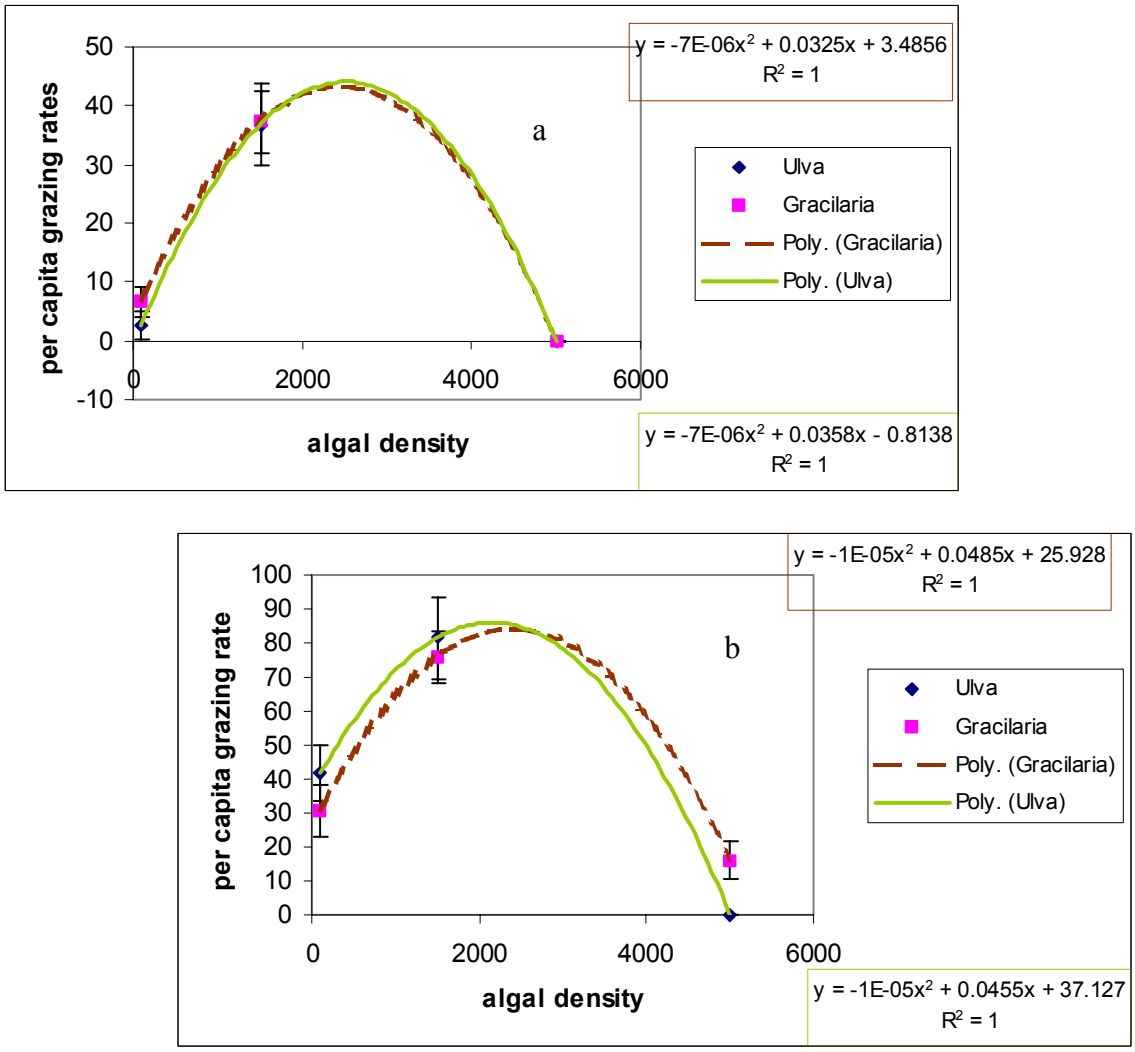



Figure 3.4. Model of the effect of algal density on per capita grazing rates. (a). *Ampithoe rubricata* per capita grazing rates on *Ulva lactuca* and *Gracilaria tikvahiae*, August 2001, for macroalgal density manipulations within small cages. (b). *Astyris (Mitrella) lunata* per capita grazing rate on *Ulva lactuca* and *Gracilaria tikvahiae*, August 2001, for macroalgal density manipulations within small cages.

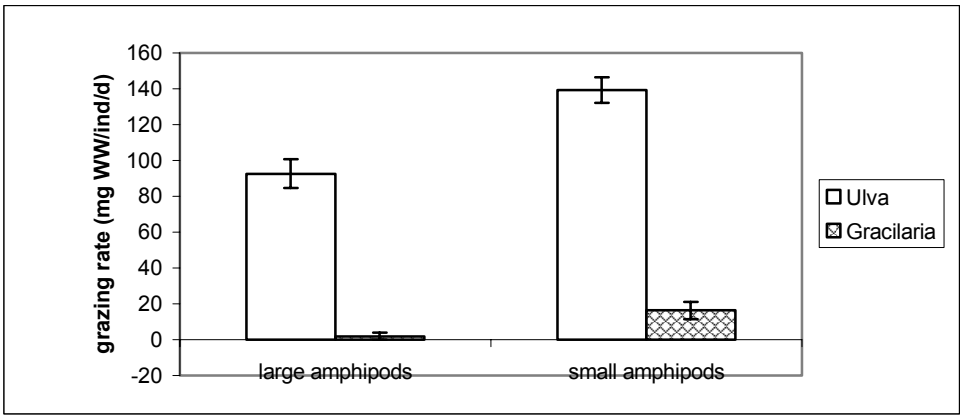



Figure 3.5. *Ampithoe rubricata* per capita grazing rate ± standard error for grazing on *Ulva lactuca* and *Gracilaria tikvahiae*, laboratory grazing experiment, 2002. * indicates significant difference between amphipods of different size classes.

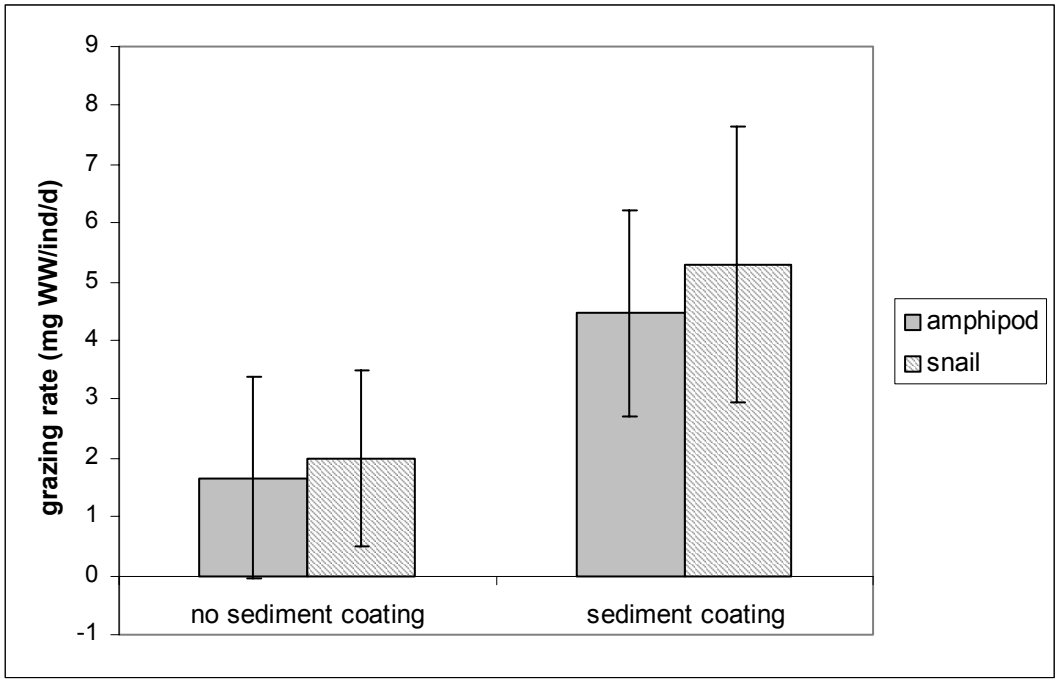



Figure 3.6. Mean per capita grazing rates on *Gracilaria tikvahiae* (+/- standard error) with and without sediment coating. Laboratory 2002.

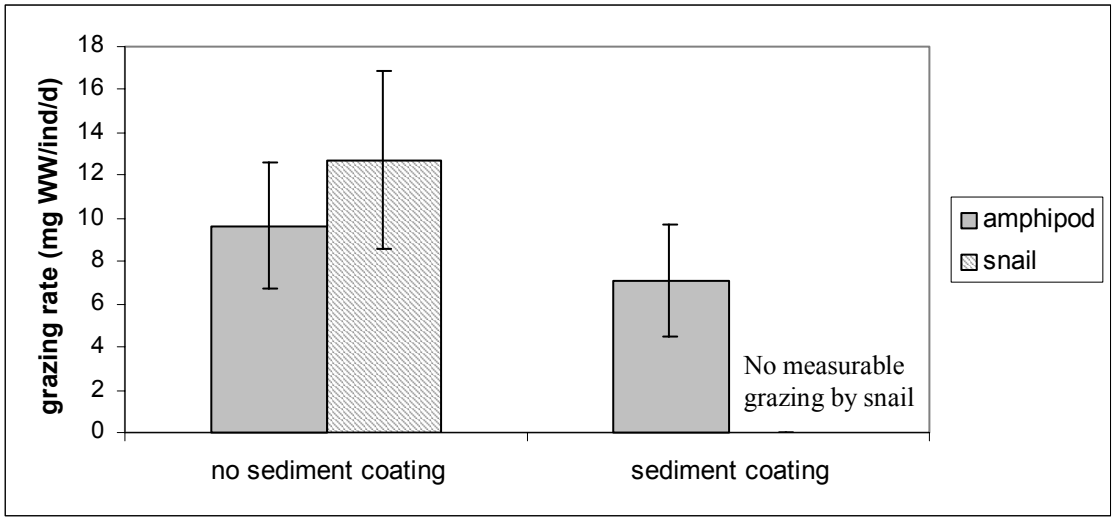



Figure 3.7. Mean per capita grazing rates on *Ulva lactuca* (+/- standard error) with and without sediment coating. Laboratory 2002.

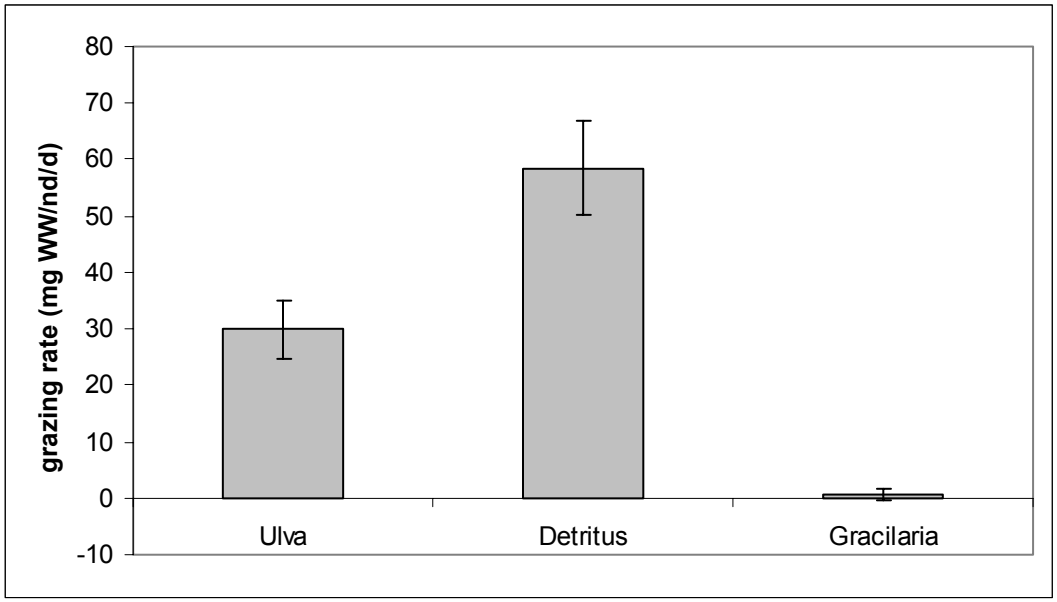



Figure 3.8. Mean amphipod per capita grazing rates (+/- standard error). Laboratory 2002.

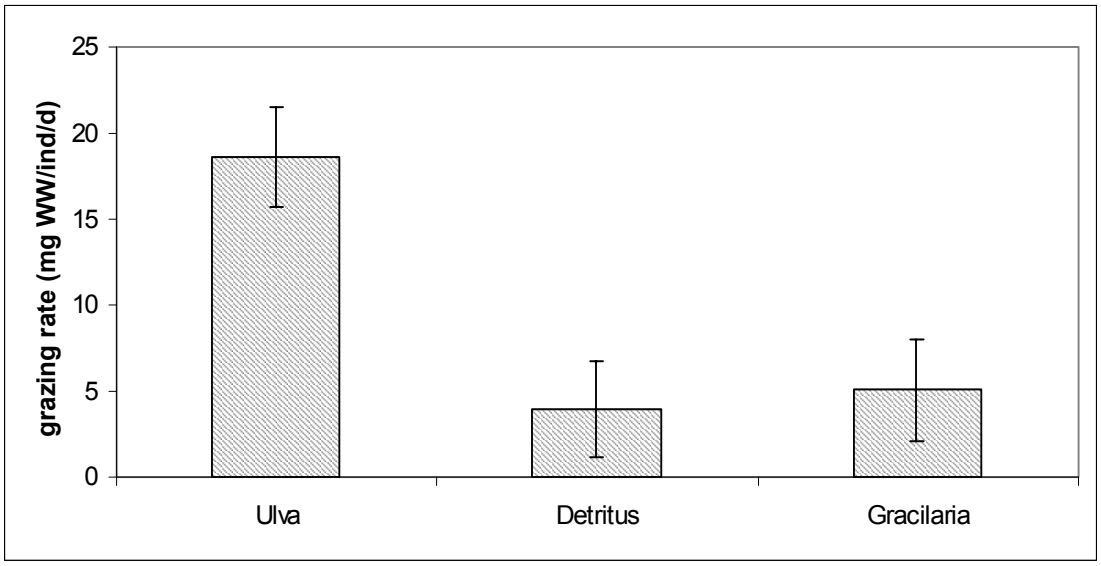



Figure 3.9. Mean snail per capita grazing rates (+/- standard error). Laboratory 2002.

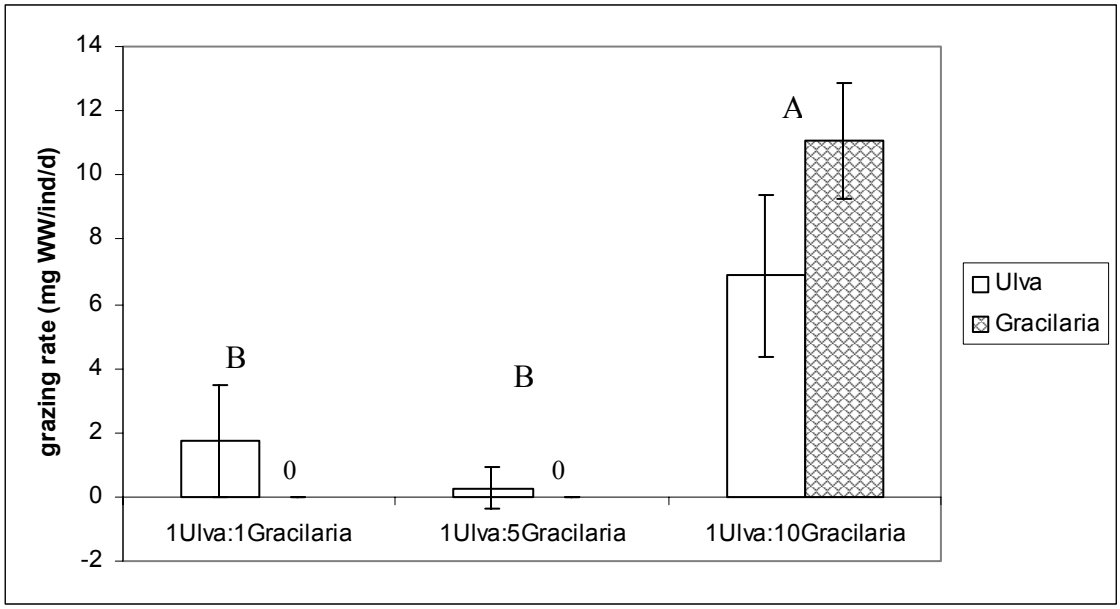



Figure 3.10. Mean amphipod per capita grazing rates (+/- standard error) on *U. lactuca* and *G. tikvahiae* present in different proportions. Laboratory 2002. Treatments with the same letter are not significantly different.

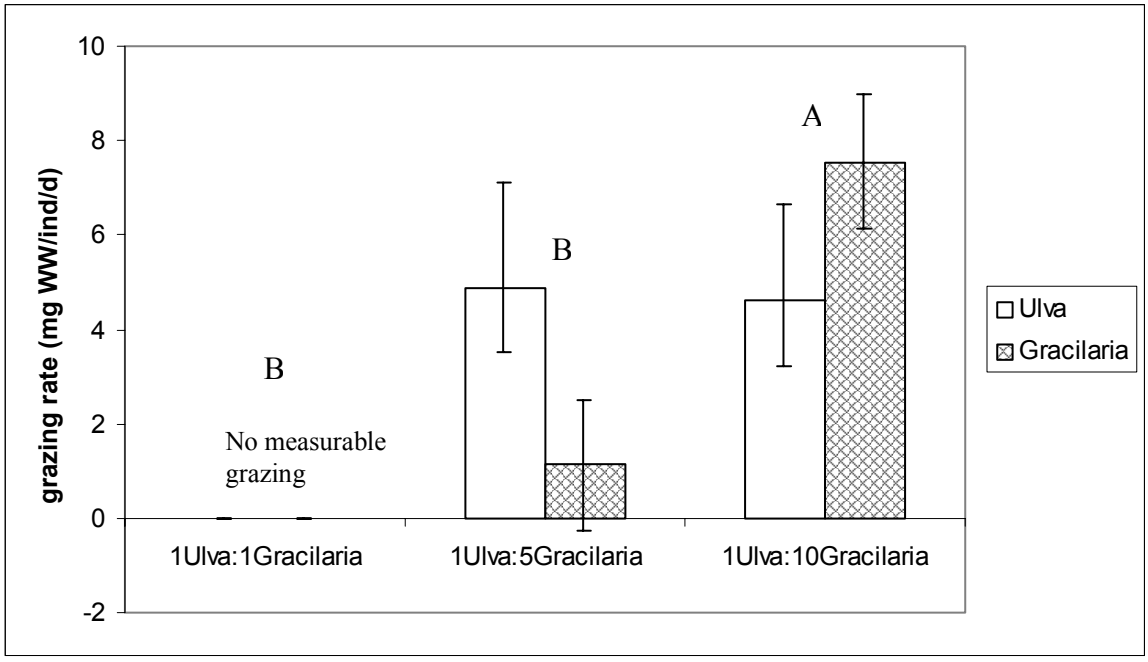



Figure 3.11. Mean snail per capita grazing rates (+/- standard error) on *U. lactuca* and *G. tikvahiae* present in different proportions. Laboratory 2002. Treatments with the same letter are not significantly different.

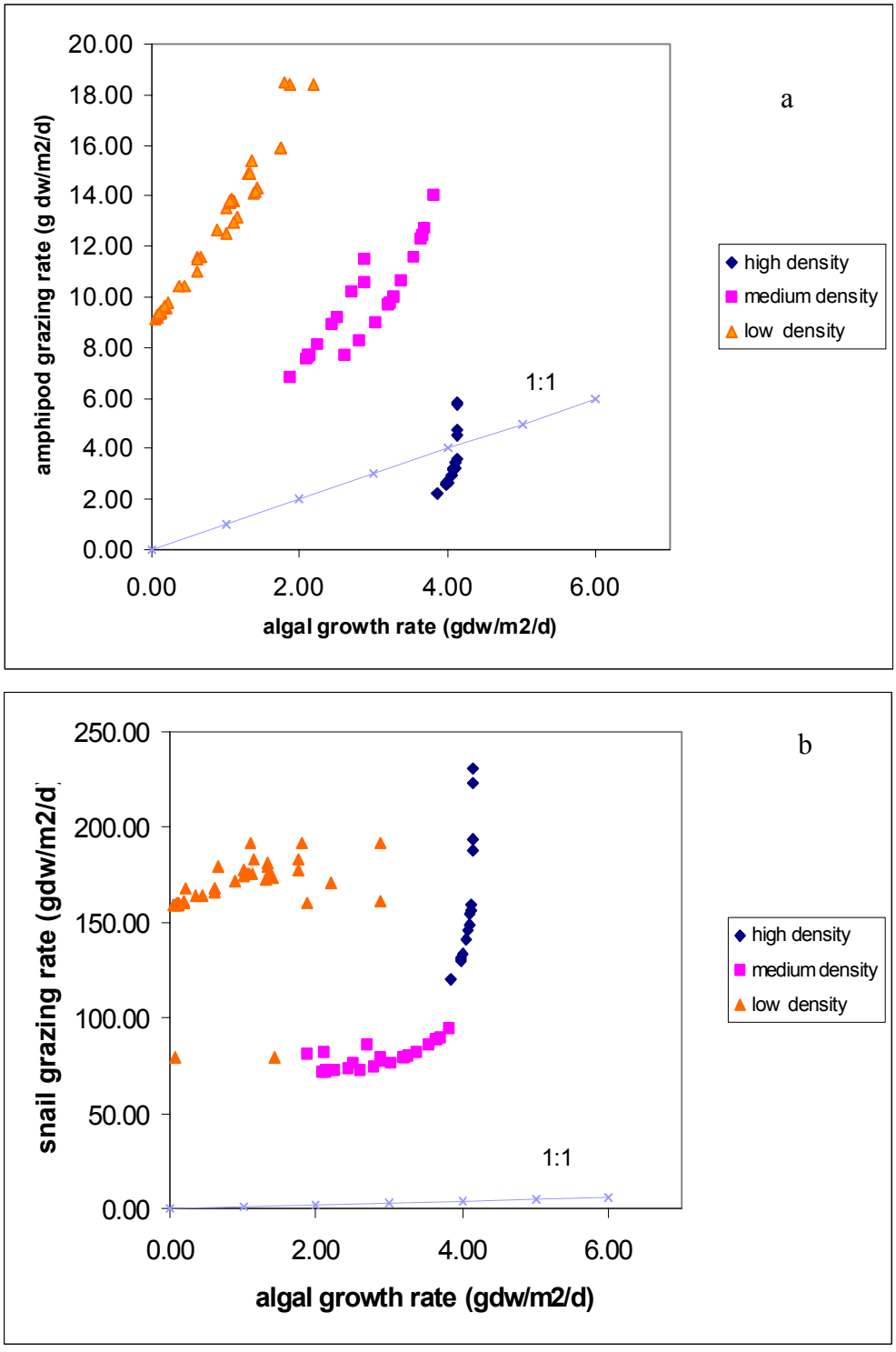



Figure 3.12. Modeled grazing rates on *Gracilaria tikvahiae* by (a) amphipods and (b) snails versus *G. tikvahiae* growth rate for three macroalgal density regimes. A 1:1 line is also shown.

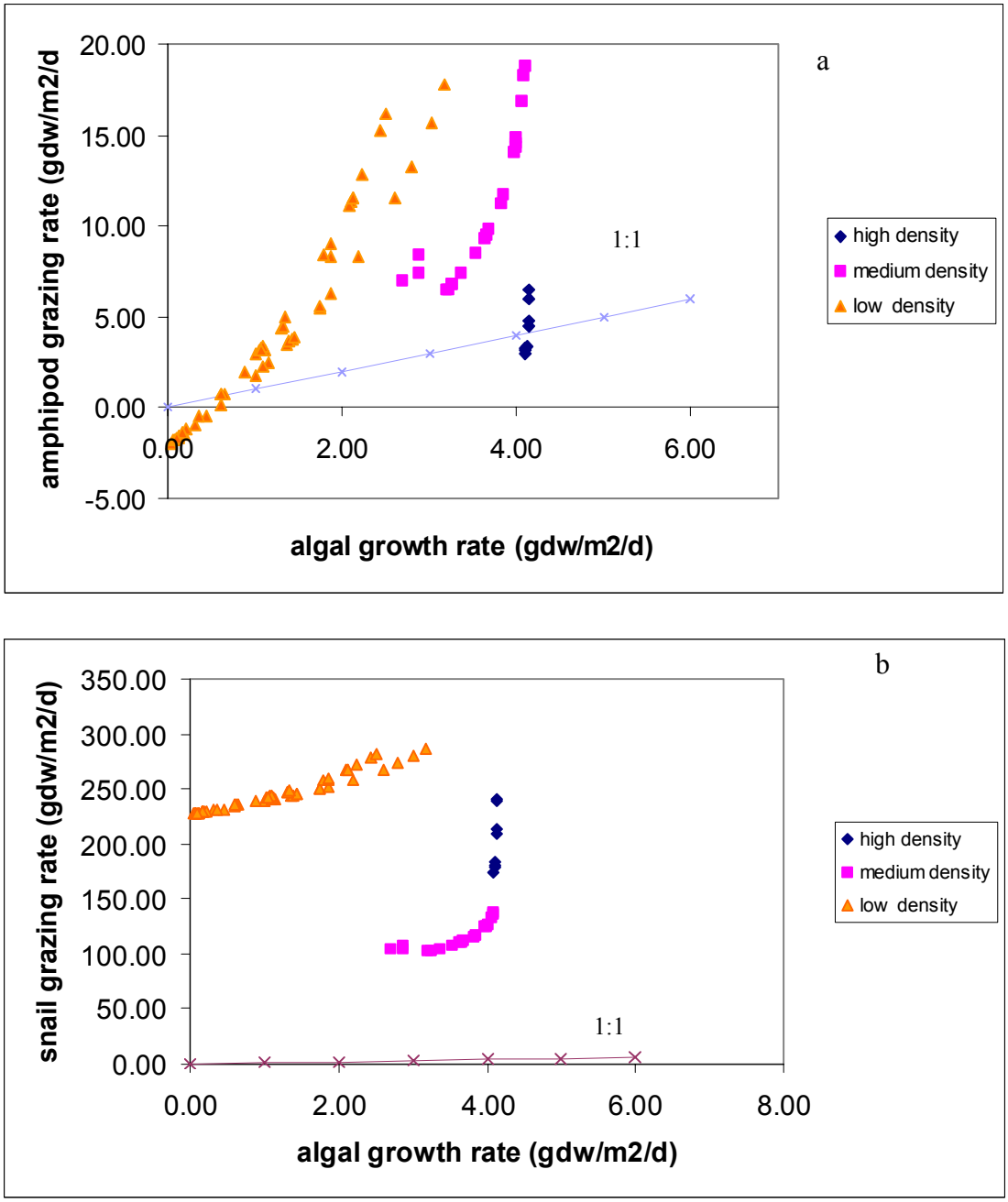



Figure 3.13. Modeled grazing rates on *Ulva lactuca* by (a) amphipods and (b) snails versus *U. lactuca* growth rate for three macroalgal density regimes. A 1:1 line is also shown.

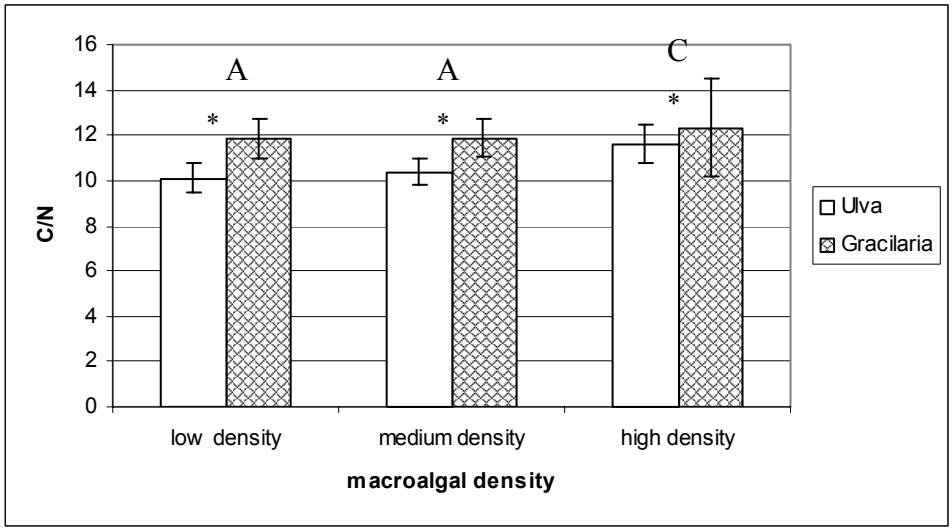



Figure 3.14. Mean (+/- standard error) C:N of *Ulva lactuca* and *Gracilaria tikvahiae* from 2001 field grazing experiments. * represents significant difference in C:N between the macroalgal species. Treatments with the same letter are not significantly different.

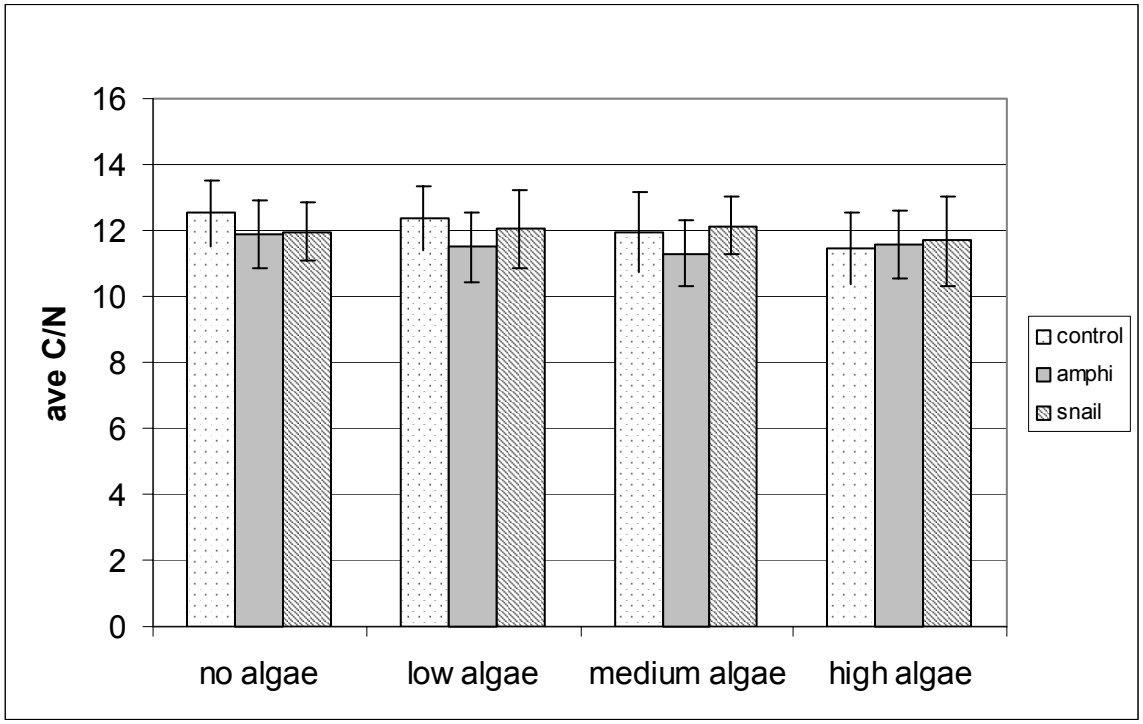



Figure 3.15. Mean (+/- standard error) C:N of *Gracilaria tikvahiae* from 2002 field grazing experiments.

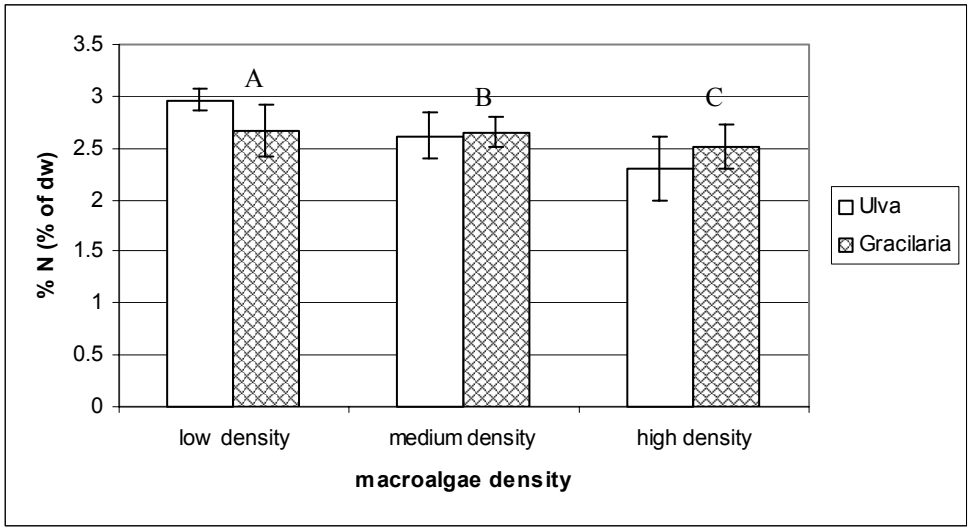



Figure 3.16 Mean (+/- standard error) %N (% of dry weight) of *Ulva lactuca* and *Gracilaria tikvahiae* from 2001 field grazing experiments. * represents significant difference in %N between the macroalgal species. Treatments with the same letter are not significantly different.

# 4. Seasonal and Spatial Variation in Invertebrate Density in Hog Island Bay

## 4.1 Introduction

In shallow systems like lagoons, benthic primary production is often more important than pelagic production and in many coastal lagoons macroalgae have become a dominant feature (Sfriso et al. 1992; Valiela et al. 1997). It is widely accepted that nutrient enrichment leads to a shift from seagrasses and perennial macroalgae to fast-growing macroalgae and phytoplankton (Sand-Jensen and Borum 1991; Valiela et al. 1997). Increases in the frequency of hypoxic and anoxic events in enriched coastal waters have been associated with the loss of diversity in benthic communities and subtidal macroalgal beds (Howarth 1991; Vitousek et al. 1997). Lagoons are especially vulnerable to nutrient enrichment (Nixon 1982; Taylor et al. 1995; Boynton et al. 1996), and this represents one of the greatest threats to the integrity of these coastal ecosystems (Nixon 1990; Nixon 1995; Vitousek et al. 1997 and references therein). Macroalgae can have both positive and negative effects on associated fauna. They can provide a food source through direct assimilation or through detritus-based food chains (Lubchenco 1978; Soulsby et al. 1982; Warwick et al. 1982; Hull 1987; Sogard and Able 1991) as well as a protective refuge from predators (Norkko and Bonsdorff 1996a, 1996b; Norkko 1998). Negative effects of macroalgae include harmful exudates that are toxic to some organisms (Sogard and Able 1991) and low dissolved oxygen within and under dense macroalgal mats (Hull 1987; Isaksson and Pihl 1992). Both the positive and negative effects of the macroalgae are important in structuring the benthic community.

Marine benthic invertebrates also play a key role in the structure and functioning of benthic communities (for example, Lubchenco 1978; Kristensen et al. 1985;

Widdicombe and Austen 1998; Duffy and Hay 2000; Lotze and Worm 2000; Kelaher et al. 2003). In particular, it is thought that small, mobile herbivores (mesograzers) are especially important (Duffy and Hay 2000) since they are ubiquitous in vegetated habitats and can occur at high densities. Mesograzers have also been found to be important in the structure and biomass of macroalgal communities mainly through selective grazing (see Chapter 3; Hauxwell et al. 1998; Duffy and Hay 2000; Giannotti and McGlathery 2001). In addition, benthic animal activities, especially bioturbation and bio-irrigation through burrowing, feeding and respiration, can influence sediment nutrient cycling processes (Aller 1982; Aller and Aller 1998).

It is clear that macroalgal biomass and benthic fauna interact to structure the benthic community. When macroalgae accumulate, there is a significant decline in the density of benthic fauna (Table 1.1) (see Chapter 2). This decline can affect grazer control of macroalgal biomass, accumulation of organic matter, and nutrient cycling at the sediment-water column interface (Aller 1982; Geertz-Hansen et al. 1993; Rysgaard et al. 1995; Hansen and Kristensen 1997; Hansen and Kristensen 1998; Hauxwell et al. 1998; Kristensen 2000; Lotze and Worm 2000; Chapter 2; Chapter 3), which may further enhance macroalgal growth. Macroalgae also influence larval settlement and predator-prey interactions (Ólafsson 1988; Norkko 1998; Norkko and Bonsdorff 1996a). Many studies have investigated the impact of high-density macroalgal bloom effects, but little is known about chronic low-density macroalgal accumulations and monitoring of the benthic faunal community may provide insight into the potential for chronic low-level effects of the presence of macroalgae.

Studies on stable isotope composition provide a tool for investigating spatial and trophic relationships by providing indications of the origins and transformations of organic matter (Peterson et al. 1985; Jennings et al. 1997). Primary producers have distinct N stable isotope signatures that reflect inorganic N-sources as well as some fractionation during uptake (Lajtha and Marshall 1994). Consumers typically show a 2-4‰ increase in $\delta^{15}N$ relative to their food source due to fractionation of light and heavy isotopes during metabolism (Jennings et al. 1997; McClelland et al. 1997). However, some animals have exhibited $\delta^{15}N$ lower than producers and there is a strong species-specific variation in fractionation (Macko et al. 19982). The C stable isotope is typically not enriched with increasing trophic level or only slightly enriched (≤1‰), but may act as a good indicator of the source of production (Peterson et al. 1985; Jennings et al. 1997). The $^{15}N$ and $^{13}C$ composition of macroalgae and invertebrate grazers can be used to determine trophic links in shallow coastal systems (Michener and Schell 1994; Jennings et al. 1997; McClelland et al. 1997). In addition, consumers tend to utilize organic matter produced within the same region of the system in which they reside (Deegan and Garritt 1997; Wainright et al. 2000). Temperature is one of many factors that may contribute to variation in $\delta^{13}C$ of algae since the $CO_2$ pool changes with changes in temperature (Fry et al. 1985; Michener and Schell 1994).

The study lagoon, Hog Island Bay (HIB), is subject to relatively low levels of nutrient loading. However, since the wasting disease of the 1930's decimated seagrass beds, benthic macroalgae and microalgae have dominated HIB (McGlathery et al. 2001). Currently, the lagoon is in a state of change from algal-domination to seagrass-domination, which is likely to occur in the next decade or so. Monitoring of the current

state will provide important background information and a database against which future changes may be compared. With the increased structure provided by seagrasses, there will likely be an increase in animal species as well as in numbers of individuals (Williams and Heck 2001). Estuaries and lagoons are spatially complex with variations in water and organic matter exchange that may influence invertebrate distributions, especially as different species may move throughout the system (Day et al. 1989; Thrush et a. 1994; Deegan and Garritt 1997). Movement through or location within the system may have a seasonal pattern or may be related to a species tolerance for certain conditions. In addition, macroalgal biomass changes seasonally which may influence faunal distribution. Because the invertebrates found in the lagoon may not be representative of a spatially heterogeneous system, a barrier island tidal creek was chosen for comparison. Salt marsh creeks are another shallow water habitat affected by the presence of macroalgae and may be subject to similar structuring factors on the benthic community as the lagoon. Additional factors such as lower wave action and those associated with anoxic events when the creeks become discontinuous with the lagoon at low tide are also important (Sogard and Able 1991; Harlin and Rines 1993).

To investigate the interaction of macroalgae and macroinvertebrates at three sites, this study had the following objectives:

- monitor seasonal changes in the macrofauna present within the macroalgal mats and within the sediment immediately under the macroalgal mats to determine if the macrofauna differed among sites in the lagoon and barrier-island tidal creek.

- monitor seasonal differences in amphipod size classes to determine when smaller amphipods are present in the lagoon and what impact this may have on top-down control of macroalgal biomass.
- examine $^{15}N$ and $^{13}C$ stable isotope composition of dominant macroalgae and grazers to establish potential trophic links and differences on seasonal and spatial scales.

My hypotheses were (1) that macroinvertebrate density will increase from spring through summer, after which it will decline likely due to changes in macroalgal bloom dynamics; (2) that small amphipods will dominate in spring and summer, while large amphipods will dominate in fall as eggs hatch in spring and summer but brood rearing declines in fall; and (3) that the $^{15}N$ and $^{13}C$ signatures of macroalgae and invertebrate consumers from the different sites will differ relative to different seasonal patterns of macroalgal growth and consumers relying on locally produced organic matter.

## 4.2 METHODS

### *4.2.1 Site Characteristics*

Study locations in Hog Island Bay (HIB) include a barrier island tidal creek (Creek site), a back-barrier embayment (Hog site), and a mid-lagoon shoal (Shoal site). The creek chosen for comparison to the lagoonal sites is a barrier-island tidal creek that opens at the back-barrier embayment site (Hog site) and is frequently discontinuous with the lagoon at low tide. Preliminary observations of the lagoon sites and barrier-island tidal creek indicated that they would be interesting comparative sites for invertebrate studies for several reasons. The Creek site was dominated by the macroalga *Ulva lactuca*, a green seaweed with laminar sheet morphology. The lagoonal sites were

dominated by *Gracilaria tikvahiae*, a red filamentous seaweed. Algal mats that formed in the lagoon were composed of numerous algal species with many different morphologies, while those in the barrier island tidal creeks tended to be of only one or two algal species, mainly *U. lactuca* and sometimes *G. tikvahiae*. Perhaps the most interesting difference between the lagoon and tidal creeks was the different fauna present in each. The lagoon had a variety of amphipods that were observed to feed on the algae, while the tidal creeks had noticeably few amphipods but an abundance of gastropods. In addition, the tidal creek tended to have more persistent algal mats than the lagoon. The majority of creeks became discontinuous with the lagoon during tidal cycles, which meant that at low tide the water draining from the creeks became trapped within the creek bottom.

The Shoal site is bordered by a relict oyster shoal on the south side, which traps macroalgae and typically has the greatest macroalgal density of sites surveyed in HIB (McGlathery et al. 2001). The Shoal site sediments have approximately 2% dry weight (dw) sediment organic content (McGlathery et al. 2001). The Hog site is adjacent to *Spartina alterniflora* marsh and has moderate accumulations of macroalgae, and less than 0.5% dw sediment organic content (McGlathery et al. 2001). The Creek site drains a *S. alterniflora* marsh and typically maintains some standing water at low tide. Both the Hog and Creek sites have a diurnal fluctuation of dissolved oxygen (DO) when algae are present, but maintain relatively constant DO concentrations when algae are absent and when snails are present at the Creek site (Giannotti and McGlathery 2001). While a similar pattern may be present at the Shoal site, it has never been quantified. The highly

dynamic nature of the currents at the Shoal site may prevent hypoxic conditions except with very dense macroalgal accumulations.

*4.2.2 Monitoring*

To monitor changes in benthic community structure, plastic traps, 34-cm x 38-cm, lined with 1-mm mesh were partially buried in the sediment and left open to algal settlement and algal mat formation at the Shoal, Creek and Hog sites. Sampling was done monthly in the summer and bi-monthly in the spring and fall. No sampling was conducted in winter. Algae and the associated macrofauna were collected and sorted by species. Sediment within the traps was sieved through a 1-mm mesh and animals sorted by species. In addition, sediment cores (9.5-cm inner diameter, 20-cm depth) were sieved through 1-mm mesh to monitor infauna. Monitoring with traps and cores was implemented in summer 1999 and was completed in fall 2001. Monitoring of amphipod size classes was implemented in summer 2002 until summer 2003 to examine the density of amphipods in different size ranges. Amphipods were sieved through 0.5-mm mesh. Amphipods were classified as large if they were greater than 0.5-mm in length and small if they were less than 0.5-mm.

Traps of similar design have been used on and around oyster reefs by Eggleston et al. (1998) and Harding and Mann (1999). The main advantages of these traps is that they require minimal habitat disturbance, they have a known sample area, are inexpensive and simple to construct, and catch efficiency is less variable than tow nets (Rozas and Minello 1997). This design appears to work well in complex, shallow estuarine habitats, especially those with vegetation. There is potential bias in the use of such traps because

they themselves are a structure and will attract some organisms over others. However, they mimic the low vertical profile of subtidal oyster reefs (Eggleston et al. 1998) and given that oyster reefs and other structures entrap macroalgae at the lagoon sites, the relationship between the invertebrates and macroalgae in the traps is still realistic.

### *4.2.3 Isotope Methods*

The stable isotopes $^{13}C$ and $^{15}N$ were used to trace the nutrient sources in primary producers and grazers. Samples included macroalgae and invertebrate grazers from the monitoring. Species samples were pooled by season and by site resulting in summer, fall and spring samples for 2000-2001 from the lagoonal sites and the creek site. There were 44 macroalgal samples chiefly of *U. lactuca* and *G. tikvahiae*, but *Agardhiella* sp. was also included. There were 36 invertebrate samples representing the most abundant invertebrates: various amphipods; the gastropods *Ilyanassa obsoleta* and *Astyris (Mitrella) lunata*; and shore shrimp *Palaemonetes pugio* and *P. vulgaris*. Macroalgae were cleaned of epiphytes, rinsed with deionized water and freeze dried. Animals were held in filtered seawater or artificial seawater for 24h to clear their guts. They were rinsed with deionized water and freeze dried. Once dry, samples were ground into a homogeneous powder and combined with other samples of the same species, location and sampling date to make a composite sample and to reduce variations between samples. Shells were removed from fauna (where relevant); animal samples were acidified in 10% HCl, re-dried and ground for isotope analysis.

All isotope analyses were performed at the Stable Isotope Facility at University of California at Davis, Department of Agronomy on the Europa Hydra 20/20, a continuous flow IRMS used for high precision analysis of combusted solid samples at natural

abundance. Samples were weighed into tin capsules and combusted. The resulting gases were introduced into the mass spectrometer for analysis. Data were reported relative to international standards: (1) $N_2$ in air for stable nitrogen isotope analysis, (2) Pee Dee Belemnite (PDB) for stable carbon isotope analysis. Analytical precision was ± 0.2. Stable isotope ratios were expressed as: $\delta X = [(R_{sample} / R_{standard})-1] \cdot 10^3$ where X represents the isotope being examined. Temperature (C) data were obtained for nearby sites from the LTER database.

*4.2.4 Statistical Analysis*

Analysis of variance (ANOVA) was used to test for significant differences in invertebrate density among sites and seasons using SAS® 8.2 software. When differences were detected, a post-hoc Tukey test was used to clarify the variation. Macroinvertebrate data were rank transformed according to Potvin and Roff (1993). Rank transformation preserves the place of zero values in the data analysis and makes the data more likely to satisfy the assumptions of parametric models (Potvin and Roff 1993). In abundance data, the zeroes are important since the absence of species may indicate the effect of a treatment. A Shannon-Weiner diversity index (*H'*) was calculated for each site. Canonical correspondence analysis (CCA) in CANOCO™ was used to examine how the benthic community responds to various densities of algae and algal species.

Multivariate analysis of variance (MANOVA) was used to test for differences in isotopic composition of individual species within macroalgal and invertebrate grazer groupings at each site and among seasons. ANOVA with a post-hoc Tukey test was used to elucidate the differences in $^{15}N$ or $^{13}C$ composition of each species.

## 4.3 RESULTS

### *4.3.1 Invertebrate density*

Invertebrate density was significantly different in spring, summer, and fall ($F_{2,8665}$ = 77.99, $P < 0.0001$), with the highest invertebrate density occurring in the summer at all three sites (Figure 4.1). Spring and summer samplings occurred before macroalgal blooms crashed, but fall samplings occurred post-crash. The Hog site had significantly higher invertebrate density than Creek and Shoal sites (fall ($F_{2,8665} = 34.06$, $P < 0.0001$) (Figure 4.1). The invertebrate diversity index was highest at the Shoal site, but the highest species richness occurred at the Hog site (Table 4.1). A list of invertebrates is presented in Table 4.3.

Amphipod, snail and shrimp densities showed similar trends to the total invertebrate density. Amphipod density was significantly higher in the summer at both Hog and Shoal ($F_{2,243} = 5.28$, $P < 0.0057$) and, overall, Creek had very few amphipods and was significantly different from Hog and Shoal sites ($F_{2,243} = 3.41$, $P < 0.0347$) (Figure 4.2a). There was no significant difference in amphipod size class among seasons and no amphipods were found in the spring monitoring ($F_{5,17} = 0.31$, $P < 0.899$) (Figure 4.2b). However, the density of large amphipods increased from summer to fall while the density of small amphipods decreased (Figure 4.2b). Snail density did not differ significantly among the three sites, but did show a trend for higher snail density in the summer (Figure 4.3). *Astyris (Mitrella) lunata* and *Ilyanassa obsoleta* were the two dominant snail species and in most cases made-up close to 90% or more of the snail density. There is a noticeable transition from dominance of *I. obsoleta* at the Creek site to dominance of *A. lunata* at the Shoal site (Table 4.2). Shrimp density was significantly

higher in the summer at all three sites ($F_{2,201} = 11.58$, $P < 0.0001$) (Figure 4.4). While not significantly different among the three sites, Shoal site had the highest worm density. Worm density was significantly higher in the spring ($F_{2,411} = 3.45$, $P < 0.0328$) and decreased in summer and again in fall (Figure 4.5).

### *4.3.2 Invertebrate-macroalgal relationships*

Both snail and amphipod densities were positively related to macroalgal biomass ($F_{1,19} = 29.88$ for snails and $F_{1,19} = 58.47$ for amphipods, $P < 0.0001$) (Figure 4.6, Figure 4.7, respectively). The range of macroalgal biomass (g dw $m^{-2}$) at each site was: Creek 1.3 – 70.4; Hog 0.97 – 223.7; Shoal 0.26 – 77.8, all of which are considered low macroalgal biomass (McGlathery et al. 2001). The strongest relationship between snail density and macroalgal biomass occurred at Hog site ($R^2 = 0.903$) (Figure 4.6), while the strongest relationship between amphipod density and macroalgal biomass occurred at Shoal site ($R^2 = 0.884$) (Figure 4.7). There was a weak relationship between amphipod density and macroalgal biomass at Creek site ($R^2 = 0.067$) (Figure 4.7), but amphipods rarely occurred at the Creek site.

In canonical correspondence analysis (CCA) biplots, the arrows represent gradients in the environmental variables, which were macroalgal biomass of all macroalgal species recorded in the monitoring effort (Figure 4.8). *Hypnea* sp. and *Polysiphonia* sp. have the longest arrows, which indicate that they are the most important environmental variables in the ordination diagram, which indicates that these species have a strong influence on the invertebrate community when they occur in HIB. There are also strong relationships between several groups of macroalgae, as indicated by the

acute angle between these environmental variables. *Gracilaria tikvahiae*, *Ulva lactuca* and *Fucus* sp. are grouped together on the ordination diagram and are also the dominant macroalgal species in terms of biomass.

Four environmental variables are strongly correlated with CCA ordination axes. *Gracilaria tikvahiae* strongly correlated with CCA1 (r = 0.69); *Ulva lactuca* correlated with CCA2 (r = 0.48); *Polysiphonia* sp. correlated with CCA3 (r = 0.35); and *Grinnelia americana* correlated strongly with CCA4 (r = 0.67). All four CCA axes explain 47.9% of the variance.

The species distributions (symbol points) on the ordination diagram indicate the environmental preference of each species. Preference is implied by location of the species point relative to the arrows of environmental variables. Those points closest to the arrowhead prefer higher than average conditions for that variable, while those opposite the arrowhead prefer lower than average conditions for that variable. For example, a group of amphipods is strongly associated with *G. tikvahiae* while ampithoid amphipods are strongly associated with *Bryopsis* sp. (Figure 4.8). Both *Ilyanassa obsoleta* and *Astyris (Mitrella) lunata*, the numerically dominant snail species, have no macroalgal preference as is indicated by their location opposite all macroalgae. A similar pattern was evident for *Palaemonetes* spp. of shrimp (Figure 4.8).

### *4.3.3 Stable isotope composition*

<u>*Spatial variation*</u>: The macroalgae at Hog and Shoal sites were enriched in both $^{13}C$ and $^{15}N$ relative to the Creek site ($F_{N,2,43} = 12.92$, $P < 0.0001$; $F_{C,2,43} = 7.14$, $P < 0.0031$) (Figure 4.9). Even though both *U. lactuca* and *G. tikvahiae* became more enriched in $^{15}N$

along the gradient from Creek to Hog to Shoal, there was no significant difference in isotope values between Hog and Shoal sites. Thus, Hog and Shoal site isotope data were combined into a single representation of the lagoon for comparison to Creek isotope data.

*Seasonal variation*: Spring (May) macroalgal isotope values were significantly different from the summer (August) and fall (October) values ($F_{N,2,43} = 4.19$, $P < 0.026$; $F_{C,2,43} = 3.79$, $P < 0.035$) (Figure 4.10). At the lagoonal sites, *U. lactuca* was significantly more enriched in both $^{15}N$ and $^{13}C$ in the spring while *G. tikvahiae* was depleted in both isotopes in the spring (Figure 4.10). At the Creek site, *U. lactuca* was significantly more depleted in both isotopes in the spring and *G. tikvahiae* did not show a clear pattern (Figure 4.11). There was no significant effect of temperature on the macroalgal $^{15}N$ or $^{13}C$ ($F_{C,3,23} = 0.95$, $P < 0.43$; $F_{N,3,23} = 1.48$, $P < 0.25$).

*Food-web relationships*: At the lagoonal sites, the shrimp and amphipods surveyed appeared to utilize mainly *U. lactuca* as a food source and, to a lesser extent, *G. tikvahiae* (Figure 4.12; Table 4.4) as was indicated by $^{13}C$ similar to the food source and enrichment in $^{15}N$ by 2 to 4‰ over the macroalgae (Table 4.4). The snails at the lagoonal sites and the invertebrates from the Creek site likely had food sources other than the macroalgae, or additional to the macroalgae. The $^{13}C$ of these invertebrates was enriched greater than 2‰ over the macroalgae and the $^{15}N$ was variable (Figure 4.12; Table 4.4).

## 4.4 Discussion

### *4.4.1 Seasonal relationships*

At all three sites, there was a peak in total invertebrate density in the summer (Figure 4.1), which is consistent with other studies (Sogard and Able 1991; Rysgaard et

al. 1995; Hauxwell et al. 1998). Rysgaard et al. (1995) found a peak in benthic infauna in the summer months, but it was a broader seasonal pattern with invertebrate density increases beginning in May and declining in November. Hauxwell et al. (1998) also noted a seasonal peak in grazing amphipods and isopods in July and August with declines occurring in early fall. Densities of all species in the present study also declined in the fall (Figure 4.1). The summer peak in invertebrates is likely related to macroalgal growth dynamics and the positive influence macroalgae may have on invertebrate communities at low algal biomass (Figures 4.6, 4.7). In winter, densities of most species decline to near zero and over-winter survival is probably due to successful use of resources in the summer (Sogard and Able 1991). However, when looking at the major taxonomic groups separately, there are some different patterns. The decline in amphipods at the Creek site during the summer (Figure 4.2a) may be due to physico-chemical factors at the site as well as biological factors. Since the Creek site becomes discontinuous with the lagoon at low tide there are more severe or frequent hypoxic and anoxic events (Giannotti and McGlathery 2001), which in turn may lead to more sulfide present in the Creek. Additionally, marsh creeks have been shown to have high predation rates and probably do not provide a protective refuge from predation even with macroalgal cover (Sogard and Able 1991). Thus, the amphipods may be preyed upon more heavily. In addition, the Creek site is dominated by the snail *Ilyanassa obsoleta*, which has been found to limit the recruitment of other invertebrates like amphipods by consuming settling larvae (DeWitt and Levinton 1985; Hunt et al. 1987).

There is a non-significant trend showing a transition from more small amphipods in the summer to more large amphipods in the fall (Figure 4.2b), probably based on life

history characteristics of the amphipods. Amphipods that survive over winter would begin brooding eggs as soon as water temperatures were suitable for growth of eggs and juveniles. The seasonal trend may simply represent the growing and maturing of juveniles over time (Gosner 1971). It is also possible that the decline in macroalgae in the fall does not provide sufficient host plants for amphipods to brood their eggs and juveniles (Poore and Steinberg 1999).

Although herbivorous amphipods are generally not specialized, some species have displayed strong preferences among host plant species (Hay et al. 1987, 1990; Poore and Steinberg 1999). Other factors, such as predators and host plant structure, have also been shown to be important in selection of plants used by amphipods (Hacker and Steneck 1990; Duffy and Hay 1994). Poore and Steinberg (1999) have also found that amphipods avoided host plants that did not support feeding and had a strong preference for those supporting the highest survival and growth. While amphipods other than ampithoids did not show a strong preference for a particular macroalgal species, the numerically dominant ampithoid amphipods had a preference for *Bryopsis* sp., a filamentous green macroalgae (Figure 4.8). Most ampithoids are tubiculous and build their tubes directly on macroalgae (Gosner 1971) so the preference for *Bryopsis* sp. is most likely related to host plant structure (Duffy and Hay 1994). Presumably, *Bryopsis* sp. supports highest survival and growth through its structure and as a food source (Poore and Steinberg 1999).

Many decapod species studied, including most of the shrimp species common to HIB, have a higher density associated with vegetation, including macroalgae and especially *Ulva* spp. (Sogard and Able 1991; Deegan 2002; Lazzari and Tupper 2002;

Raposa et al. 2003). The pattern in HIB for significantly higher shrimp density in the summer (Figure 4.4) coincides with macroalgal peak biomass and this may be because the macroalgae provide a preferred quality of habitat for the shrimp. However, CCA did not reveal a preference for a certain macroalgal species (Figure 4.8), indicating that it was the total macroalgal biomass, and not the biomass of a particular species that likely drives these density patterns. Eggleston et al. (1998) also found that grass shrimp density was linked to vegetation patch size and that smaller patches (those with greater perimeter: area ratios) contained higher densities of shrimp. They proposed that the shrimp were responding to edge effects of the smaller patches and utilizing the patch edge as a refuge from predators then periodically foraging in the surrounding habitat. In this way, small patches provide a larger edge and would benefit the shrimp by providing both a refuge edge and foraging edge. Since the macroalgae in the present study were of low density, it is likely that the "patch" size was also small and contributed to the peak shrimp density (Figure 4.4). This is further supported by the overall decline in shrimp density with increasing macroalgal density (Chapter 2) where it can be argued that patch size increases with algal density and the larger patch size would not support the same high density of shrimp with less edge available (Eggleston et al. 1998).

An important factor influencing worm density may be that with the peak in macroalgal biomass, there may be interference with worm recruitment so that as macroalgal biomass increases, the worm density decreases (Figure 4.5) (Ólafsson 1988; Norkko and Bonsdorff. 1996b). In addition, high densities of *I. obsoleta* have negatively affected worm abundances (Kelaher et al. 2003). Foraging activities of *I. obsoleta* interfere with recruitment and feeding by worms (DeWitt and Levinton 1985; Hunt et al.

1987; Kelaher et al. 2003). While no direct links between *A. lunata* and worms have been made previously, it has been demonstrated that *A. lunata* effectively reduces newly settled juvenile invertebrates (Osman and Whitlatch 1996) and may therefore have a similar effect on worms. There may also be increased predation in summer especially with nursery fish present and/or peak in total invertebrates. In particular, shrimp forage on infauna and may reduce worm density (Eggleston et al. 1998); with the summer peak in shrimp density there may be a direct link to decreased worm density (Figure 4.4, 4.5).

Isotopic fractionations have been shown to occur both with seasonal variations and as a function of water temperature, resulting in isotopic depletions in the winter months and associated with low temperatures (Fry et al. 1985; Goericke et al. 1994). The seasonal variation in the present study suggests a similar pattern (Figures 4.10, 4.11) with enrichment in both isotopes at the Creek site typically peaking in the warmer months, and a lesser trend at the lagoon sites. Since there is no winter data, it is not possible to compare cold months to previous studies. However, there was not a significant effect of temperature on the isotopic composition of the macroalgae and it is likely that the effect of temperature on isotopic composition is complex (Fry et al. 1985).

### *4.4.2 Spatial relationships*

Since the Creek site has more stable and persistent algal mats, it is surprising that the Creek site had lower density and diversity than the lagoonal sites (Figure 4.1; Table 4.1). However, previous work has found that saltmarsh creeks typically support only a few generalist species (Sogard and Able 1991). The "stress" of intertidal patterns that lead to anoxia and high sulfide levels at the Creek site may drive this pattern. Persistent

anoxic events have been shown to occur at the Creek, especially in the presence of dense macroalgal mats (Giannotti and McGlathery 2001). These periods of anoxia along with high organic matter input to the Creek would also lead to high sulfide production. These chemical factors may actually be stronger structuring factors on the community at the Creek site than the macroalgae itself since only the fauna that could tolerate such harsh conditions would persist there.

The Hog site is more protected than the Shoal site, and typically supports lower macroalgal biomass accumulations than the Shoal site (McGlathery et al. 2001). Since anoxia is less likely to occur at these sites due to their physically dynamic nature, macroalgal biomass may be the dominant structuring factor at the lagoonal sites, with the higher macroalgal density at the Shoal site leading to lower invertebrate density than at Hog (Figure 4.1)(see also Chapter 2). Local extinction and loss of diversity have been associated with moderate to high density macroalgal accumulations (Table 1.1) so it is presumably the driving force in these dynamic lagoonal sites as well. However, macroalgal biomass from this monitoring is considered low biomass relative to the biomass classifications outlined in the density experiments (Chapter 2) and relative to other subtidal studies (Table 1.1). Thus, the positive relationship between algal biomass and invertebrate density observed (Figure 4.6, 4.7) was only representative of low algal biomass and it is not possible to determine what the relationship would be at higher algal biomass from this study method.

There is an interesting transition in dominant snail species from the Creek site to the Hog and Shoal sites (Table 4.2). *I. obsoleta* dominates the Creek site but *Astyris (Mitrella) lunata* dominates the Shoal site with Hog as the transitional site for these snail

species. However, all sites show a peak in density in the summer (Figure 4.3) coinciding with a peak in macroalgal biomass. *I. obsoleta* has been shown to prefer low flow sites, even preferring creek banks to the middle of creeks (Levinton et al. 1995), and to be attracted to sites enriched with *Ulva* sp. detritus (Kelaher et al. 2003). Both of these preferences are met at the Creek site. Since both snail species have been shown to limit recruitment of other invertebrates (DeWitt and Levinton 1985; Hunt et al. 1987; Osman and Whitlatch 1995, 1996), it may be an issue of each species being the superior competitor at its site of respective dominance. Specifically, *A. lunata* may be the superior competitor in areas with high flow and rapid currents, like the Shoal site, while *I. obsoleta* is the superior competitor at low flow sites. Hog may function as an intermediate site in terms of flow characterisitics and thus has both species in moderate abundance (Table 4.2). CCA showed no preference by these snails for a macroalgal species (Figure 4.8) so the dominance of different macroalgal species at the different sites probably did not play a role in the snail distribution.

Within coastal systems, carbon isotope ratios are altered by seasonal and environmental factors including temperature and irradiance as well as growth rate and respiratory demands of primary producers (Michener and Schell 1994; Hemminga and Mateo 1996; Jennings et al. 1997). Depletion of $^{13}C$ may be due to increased respiratory demands or reduced growth rates while fast growth rates can produce $^{13}C$-enriched tissues (Michener and Schell 1994). While irradiance data were not recorded in this study, changes in light regimes may be reflected in the greater depletion of $^{13}C$ in macroalgae at the Creek site compared to the macroalgae in the lagoon (Hog and Shoal sites), with greater respiratory demand on primary producers at the Creek much more

likely than in the lagoon (Figures 4.9, 4.10, 4.11). Macroalgae at the Creek site were also depleted in $^{15}N$ relative to the lagoon sites (Figures 4.9, 4.10, 4.11), which may indicate that a relatively large amount of ammonium was available for uptake which could result in a propensity for the utilization of the lighter isotope and lead to a lower $^{15}N$ signature.

### *4.4.3 Food web relationships*

In determining trophic relationships among primary producers and consumers, it is generally accepted that the consumer will reflect the carbon source within 2‰ (usually <1‰) with larger changes indicating an alternate food source or higher trophic level for the consumers (Macko et al. 1982; Michener and Schell 1994; Jennings et al. 1997). Most studies also indicate an enrichment in $^{15}N$ of 2 to 4‰ for each trophic level (Michener and Schell 1994; Jennings et al. 1997; McClelland et al. 1997), but $^{15}N$ may also be depleted in some grazers, especially micrograzers, and has been shown to be variable with species (Macko et al. 1982). Invertebrate species in the present study were enriched in $^{15}N$ relative to all macroalgae, with the exception of the snails relative to *G. tikvahiae* in the lagoon (ranging from approximately –0.8 to 5.3‰) (Table 4.4). *Palaemonetes* spp. in the lagoon showed approximately 3 to 4‰ enrichment in $^{15}N$ over the macroalgae, but with a $^{13}C$ signature most similar to *U. lactuca* indicating that *U. lactuca* was an important food source (Figure 4.12; Table 4.4). However, *Palaemonetes* spp. have also been shown to feed on microalgae and epiphytic macroalgae (Fleeger et al. 1999) as well as infauna (Eggleston et al. 1998) and these different food sources may be responsible for some of the variation in the $^{13}C$ signatures, especially at the Creek site.

*Ilyanassa obsoleta* is an omnivore that feeds at different trophic levels (Curtis and Hurd 1979, 1981), which is also important to consider in determining the relationship to source material. $C_4$ marsh plants and benthic algae have been found to be more enriched in $^{13}C$ than the macroalgae in this study (e.g. Peterson and Fry 1987; Michener and Schell 1994) and would be important to consider in future studies, especially at the Creek site where *Spartina alterniflora* and its detritus are more available locally. Little is known about the feeding habits of the gastropod *Astyris (Mitrella) lunata*, but it is likely an omnivore (Osman and Whitlatch 1995; Moore and Wetzel 2000), as is reflected in the lack of relationship to the macroalgal isotope signatures and which may also be a factor in the lack of control over macroalgal bloom formation (Chapter 3). From the available data and with the existing understanding of the fractionation of C and N isotopes between grazers and their food, it appears that amphipods graze both species of macroalgae in the lagoon (Figure 4.12; Table 4.4). However, the mixing of amphipod species in this analysis causes a "loss" of information in interpreting the food web at these sites. Since *Ampithoe rubricata* is the dominant amphipod at these lagoon sites (see Chapter 2 for Shoal site), it is likely that the isotope signatures reported here reflect mainly *A. rubricata*, but in future studies the amphipods should be sorted by species since different species have different feeding habits.

As this study was not designed entirely to sample for food web analysis, several items were not included that would also shed some understanding on the trophic dynamics of this system. For example, fungi, bacteria and microalgae are likely important to the mesograzers studied, especially since microalgae dominate HIB. Other

organisms, such as worms, that may be prey to the shrimp and snails may also be important to consider in future studies to complete the picture of the food web.

### *4.4.4 Conclusions*

There are clear seasonal differences in the density of invertebrates, but the three sites monitored show similar patterns. The summer peak in invertebrate density parallels the peak in macroalgal biomass so macroalgae are thought to be a strong benthic structuring factor even at low density, especially in the lagoonal sites where hypoxia is less likely than in the Creek site. The main difference between the lagoon and Creek sites was the species richness, where the Creek supports only a few generalist species.

The greater $^{13}C$ depletion of macroalgae at the Creek site compared to the macroalgae in the lagoon may be the result of a different respiratory demands by primary producers at the Creek than that in the lagoon. The summer depletion in $^{13}C$ in *U. lactuca* may be related to shading within macroalgal mats and resultant changes in *U. lactuca* growth rate. Thus, both irradiance and respiratory demand could affect the variability in isotope signatures between the Creek and lagoonal sites. *Palaemonetes* spp. and amphipods in the lagoon appear to consume macroalgae while the isotope signature of snails indicates a preference for other food sources, probably detritus, carrion, or settling larvae.

*Acknowledgements*
This work was supported by the VCR-LTER. Invaluable field help and logistical support were given by Liz Skane, Tracie Mastronicola, Christy Tyler, Sarah Lawson, Jessie Burton, Mads Thomsen, J. Devin Herod, Brian Silliman, M. Miller, C. Jiron-Murphy and the VCR-LTER Staff especially Jimmy Spitler, Kathleen Overman, Jason Restein, and Philip Smith.

**Table 4.1.** Species richness and Shannon-Weiner diversity index for invertebrates at each site.

| | Creek site | Hog site | Shoal site |
|---|---|---|---|
| Species richness | 19 | 57 | 47 |
| S-W diversity index | 0.217 | 0.822 | 0.926 |

**Table 4.2.** Percentage of each snail species present at each site.

| | Creek site | Hog site | Shoal site |
|---|---|---|---|
| *Astyris (Mitrella) lunata* | 10.7% | 58.1% | 87.1% |
| *Ilyanassa obsoleta* | 82.1% | 29.0% | 3.2% |

**Table 4.3** Species found at the three sites monitored with density over entire monitoring period.

| **Species** | Taxanomic grouping | Site(s)‡ | Total N (# $m^{-2}$) |
|---|---|---|---|
| *Alpheus heterochelis* | Shrimp | H, S | 235.3 |
| *Amphithoe rubricata* | Amphipod | H, S | 47.1 |
| Unidentified amphipods | Amphipod* | C, H, S | 321.4 |
| *Amphitrite* sp. | Worm | H, S | 39.2 |
| *Anachis avara* | Snail | H | 23.5 |
| *Anadara ovalis* | Bivalve | H, S | 141.2 |
| *Anomia simplex* | Bivalve | S | 7.8 |
| *Arabella iricolor* | Worm | S | 62.7 |
| *Astyris (Mitrella) lunata* | Snail | C, H, S | 549.0 |
| *Axius serratus* | Shrimp | H | 7.8 |
| *Bittium* sp. † | Snail | | |
| Bryozoan | Bryozoa | H | 1 colony $m^{-2}$ |
| *Callianassa* sp. † | Shrimp | | |
| *Callinectes sapidus* | Crab | C, H | 62.7 |
| *Caprella* sp. | Caprellid amphipod | H, S | 31.4 |
| *Clymenella torquata* † | Worm | | |
| *Crangon septemspinosa* | Shrimp | H, S | 23.5 |
| *Crepidula fornicata* † | Gastropod | | |
| *Crucibulum striatum* | Snail | S | 7.8 |
| crab megalops | Crab | H, S | 15.7 |
| *Cyathura polita* | Isopod | H, S | 31.4 |
| *Drilonereis* sp. † | Worm | | |
| *Ensis directis* | Bivalve | H | 7.8 |
| *Erichsonella attenuata* | Isopod | S | 15.7 |
| *Eteone heteropoda* | Worm | C, S | 15.7 |
| *Eurypanopeus depressus* | Crab | C, H, S | 251.0 |
| *Glycera* spp. | Worm | H, S | 23.5 |
| *Goniada* sp. | Worm | H | 7.8 |
| *Hippolyte* sp. | Shrimp | H, S | 141.2 |
| *Hippolyte pleuracantha*† | Shrimp | | |
| *Hippolyte zostericola* | Shrimp | S | 15.7 |
| hermit crabs-unidentified | Crab | H | 7.8 |
| *Sclerodactyla* sp.(hairy sea cucumber) | Echinoderm | S | 15.7 |
| *Idotea* sp. † | Isopod | | |
| *Ilyanassa obsoleta* | Snail | C, H, S | 509.8 |
| *Jassa falcata* | Amphipod | H | 7.8 |
| juvenile mud crabs | Crab | C, H, S | 431.4 |
| *Lepidonotus squamatus* † | Worm | | |
| *Leucophytia (Melampus) bidentatus* | Snail | C | 7.8 |
| *Libinia emarginata* | Crab | S | 7.8 |
| *Libinia dubia* | Crab | S | 7.8 |

| | | | |
|---|---|---|---|
| *Littorina* sp. | Snail | C | 7.8 |
| *Littorina littorea* † | Snail | C | |
| *Littorina irrorata* | Snail | C | 7.8 |
| *Littorina saxatilis* | Snail | C, S | 15.7 |
| Lumbrenerid thread worms | Worm | H, S | 15.7 |
| *Malacobdella grossa* | Worm | S | 7.8 |
| *Modiolus dimiss*us | Bivalve | C | 7.8 |
| *Molgula* sp. (sea squirt) | Ascidian | H, S | 70.6 |
| *Mytilus edulis* | Bivalve | H, S | 47.1 |
| *Neopanopeus sayi* | Crab | H | 39.2 |
| *Nereis* sp. | Worm | C, S | 39.2 |
| *Nereis pelagica* | Worm | C | 7.8 |
| *Nereis succinea* | Worm | C, H, S | 149.0 |
| *Nereis virens* | Worm | H | 7.8 |
| *Nucula* sp. (near nut shell) | Bivalve | H | 23.5 |
| *Ovatella myosotis* | Snail | S | 7.8 |
| *Pagurus acadianus* | Crab | H | 7.8 |
| *Pagurus longicarpus* | Crab | H, S | 70.6 |
| *Palaemonetes intermedius* | Shrimp | H, S | 15.7 |
| *Palaemonetes pugio* | Shrimp | C, H, S | 337.3 |
| *Palaemonetes vulgaris* | Shrimp | H, S | 368.6 |
| *Pandalus propinquus* | Shrimp | C, S | 15.7 |
| *Panopeus herbstii* | Crab | C, H, S | 164.7 |
| Paraonidae (worm) | Worm | H, S | 15.7 |
| *Pectinaria gouldii* | Worm | H | 7.8 |
| *Penaeus aztecus* | Shrimp | S | 7.8 |
| *Pinnixa chaetopterana* (crab) | Crab | S | 7.8 |
| *Pista maculata* | Worm | S | 7.8 |
| *Platynereis* sp. | Worm | H | 7.8 |
| *Rhithropanopeus harrisii* | Bivalve | C | 15.7 |
| *Sabella* sp. † | Worm | | |
| *Scoloplos* sp. † (Orbiniidae worm) | Worm | | |
| *Sthenelais boa* | Worm | H, S | 15.7 |
| *Syllis* sp. (worm) † | Worm | | |
| *Tellina* sp. | Bivalve | H | 7.8 |
| *Uca* sp | Crab | C | 31.4 |
| *Upogebia affinus* † | Shrimp | | |
| *Urosalpinx cinerea* | Snail | H, S | 15.7 |

‡ sites were C for Creek, H for Hog embayment, and S for mid-lagoon Shoal. See text for additional site descriptions.

* unidentified amphipods were not identified to the species level but represent the following families: Ampithoidae, Bataidae, Cheirocratidae, Gammaridae, Haustoriidae, Hyalidae, Ischyroceridae, Liljeborgiidae, Lysianassidae, Stenothoidae, and Unciola.

† indicates rare species within this sampling regime.

**Table 4.4** Potential fractionation (Δ) of macroalgae by invertebrates.

| | Species | Δ *U. lactuca* | | | | Δ *G. tikvahiae* | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Lagoon | | Creek | | Lagoon | | Creek | |
| | | $^{15}N$ | $^{13}C$ | $^{15}N$ | $^{13}C$ | $^{15}N$ | $^{13}C$ | $^{15}N$ | $^{13}C$ |
| Shrimp | *Palaemonetes vulgaris* | 3.66 | 1.76 | 5.32 | 5.31 | 2.54 | 3.74 | 4.58 | 9.17 |
| | *Palaemonetes pugio* | 4.79 | 1.61 | 0.45 | 5.19 | 3.67 | 3.59 | -0.29 | 9.05 |
| Snails | *Ilyanassa obsoleta* | 0.38† | 9.90† | 1.47 | 3.48 | -0.75† | 11.9† | 0.74 | 7.35 |
| | *Astyris (Mitrella) lunata* | 0.71 | 2.35 | ‡ | ‡ | -0.41 | 4.33 | ‡ | ‡ |
| Amphipods | Mixed amphipods | 3.21 | -0.37 | ‡ | ‡ | 2.09 | 1.61 | ‡ | ‡ |

† Based on one value only.

‡ Not present at the Creek site during the survey period.

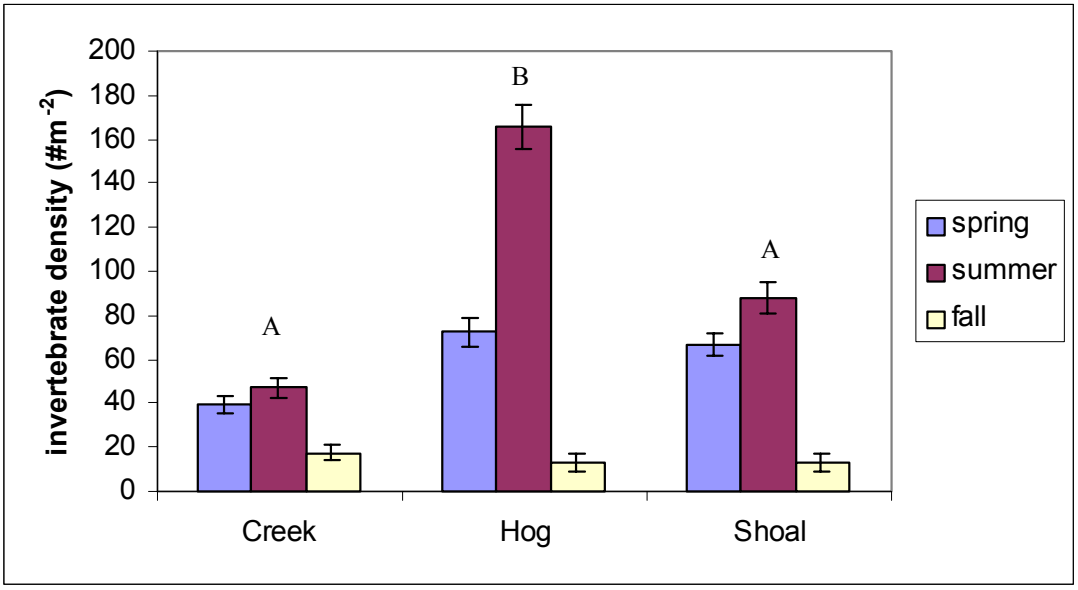
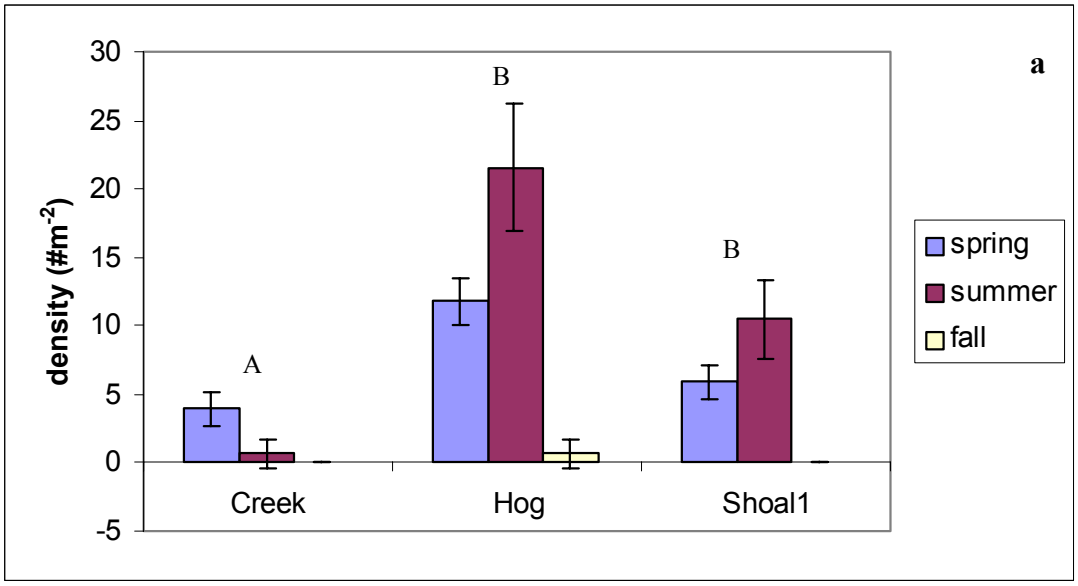



Figure 4.1. Mean (± SE) invertebrate density for the 3 study locations over 3 seasons. Different letters indicate significant difference between sites. All seasons were significantly different.



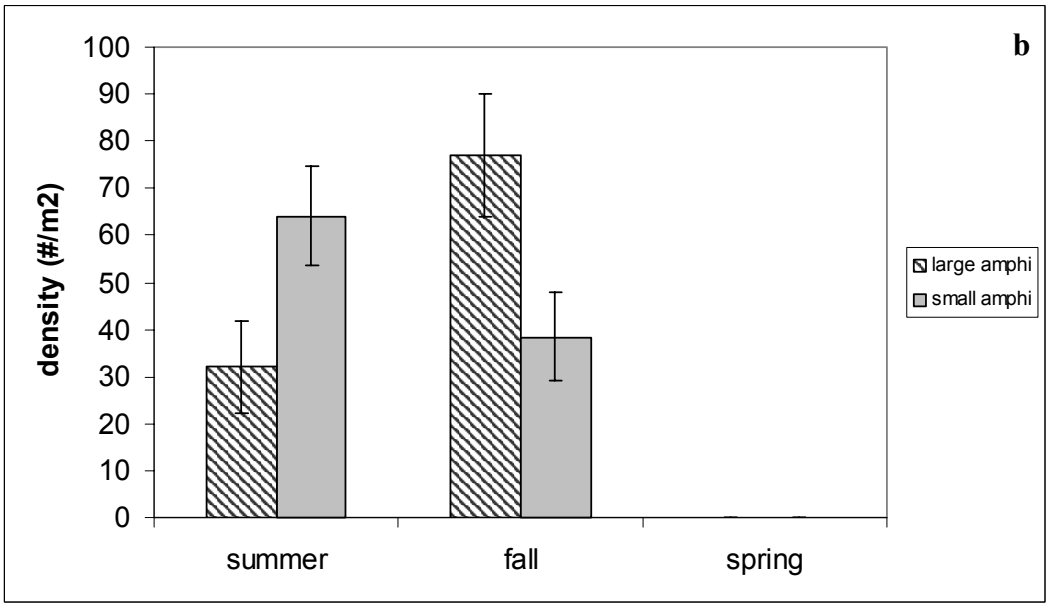




Figure 4.2. (a) Mean (± SE) amphipod density for the 3 study locations over 3 seasons. Different letters indicate significant difference between sites. Summer and fall were significantly different. (b) Mean (± SE) amphipod density by size from Shoal monitoring.

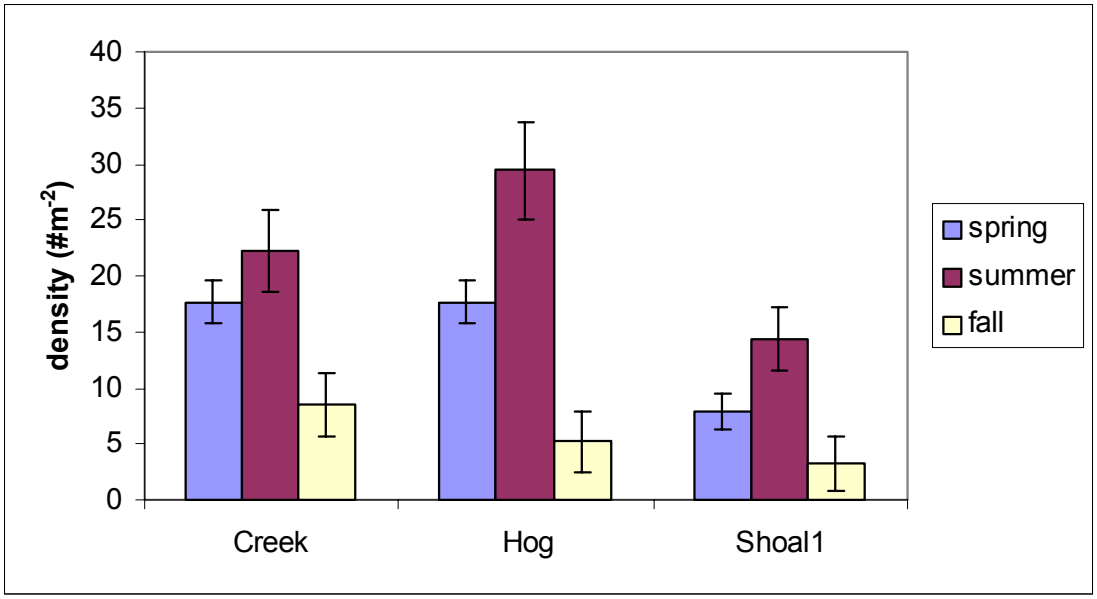



Figure 4.3. Mean (± SE) snail density for the 3 study locations over 3 seasons. There was no significant difference among sites or seasons.

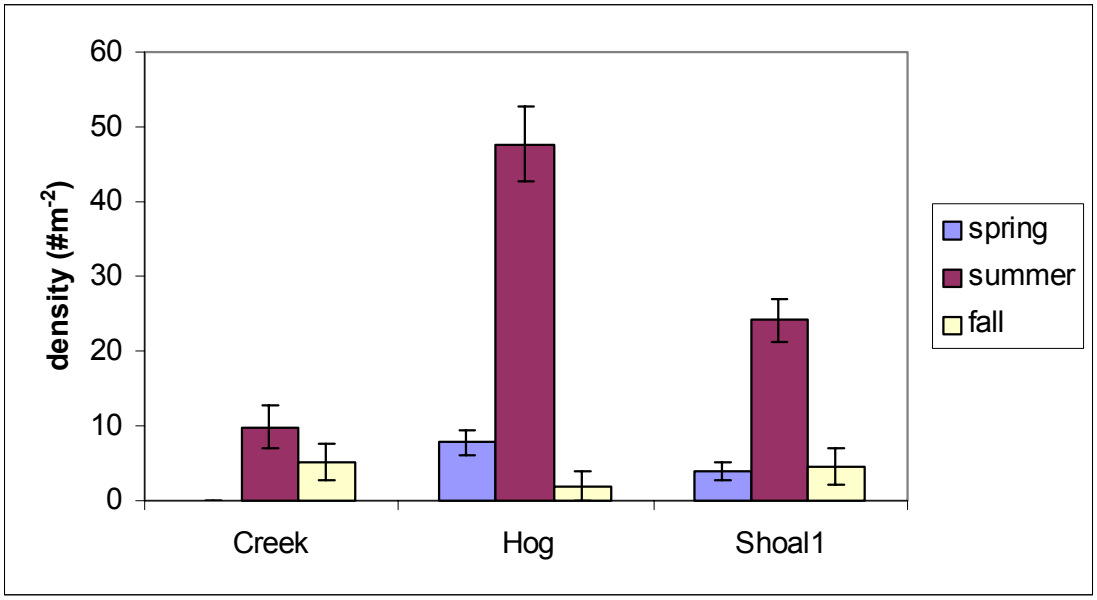



Figure 4.4. Mean (± SE) shrimp density for the 3 study locations over 3 seasons. There was no significant difference among sites. Fall and spring were not significantly different.

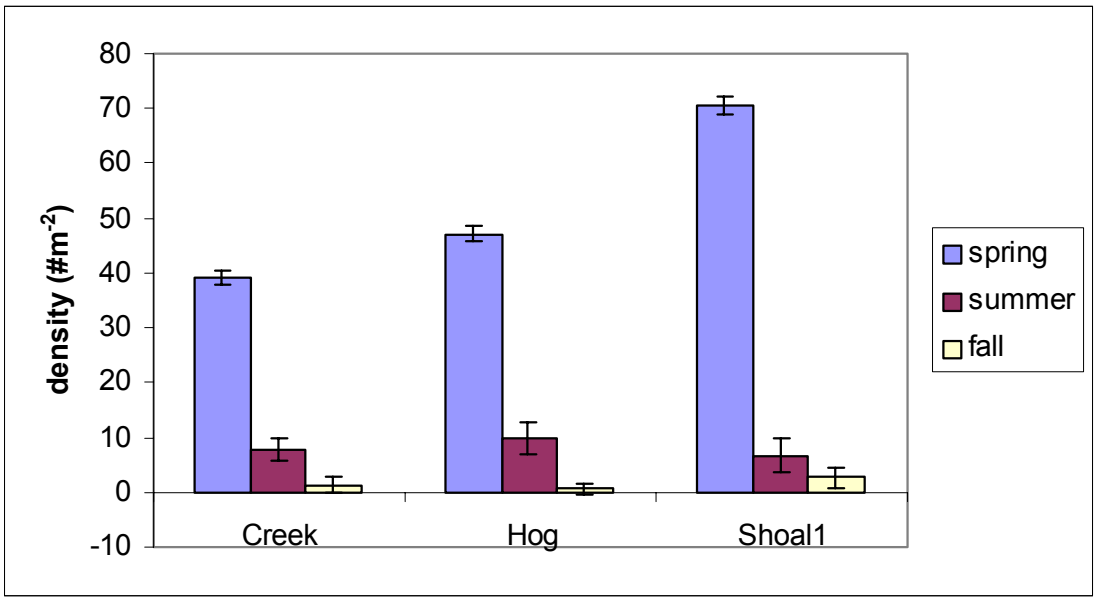



Figure 4.5. Mean (± SE) worm density for the 3 study locations over 3 seasons. There was no significant difference among sites. Worm density in spring was significantly higher than other seasons.

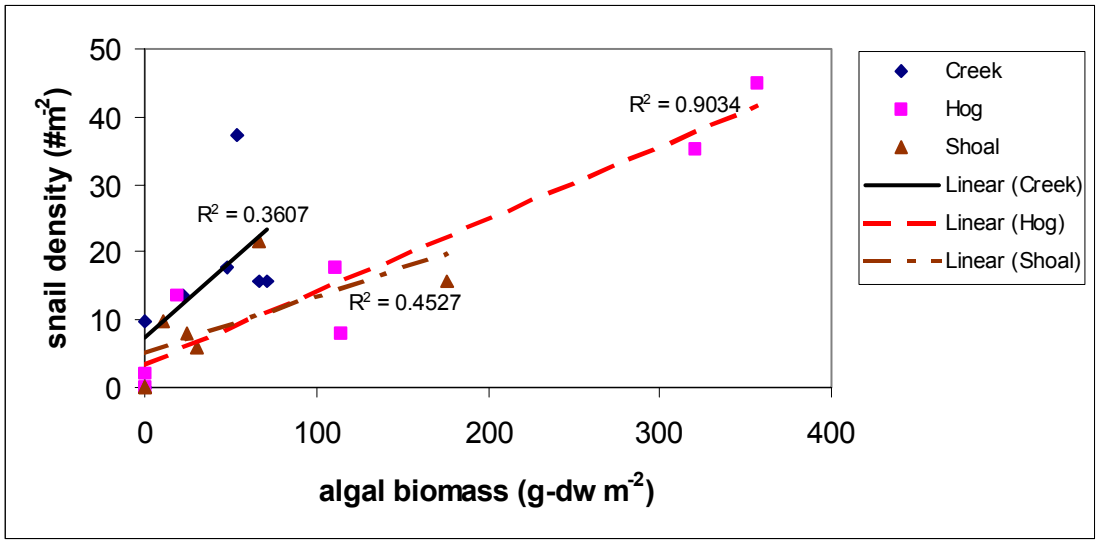



Figure 4.6. Snail density and macroalgal biomass relationships for the 3 study locations. $R^2$ values for each site are located adjacent to the trend line for the site.

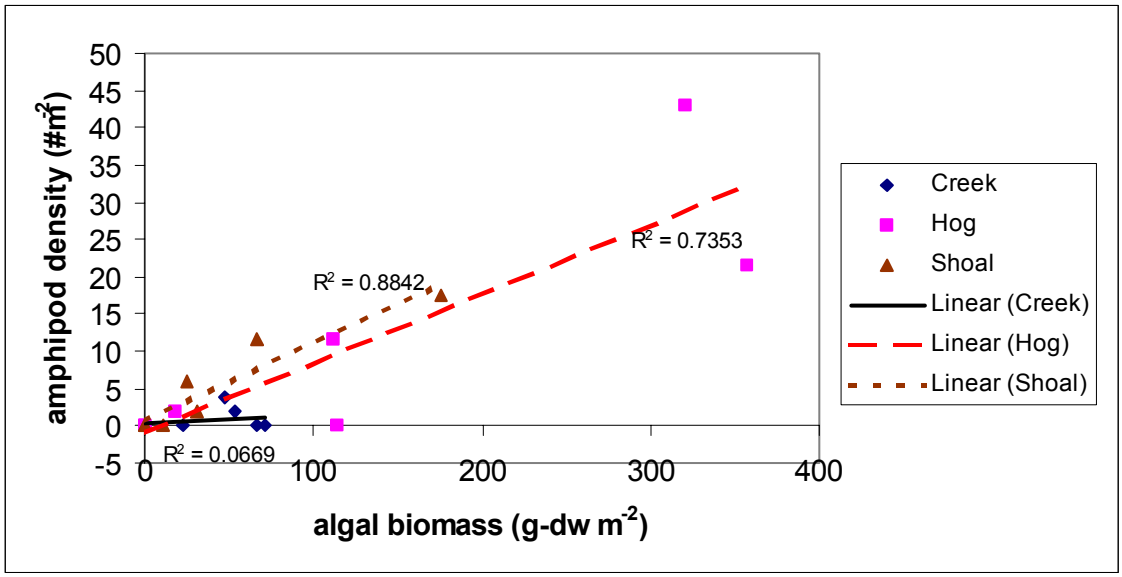
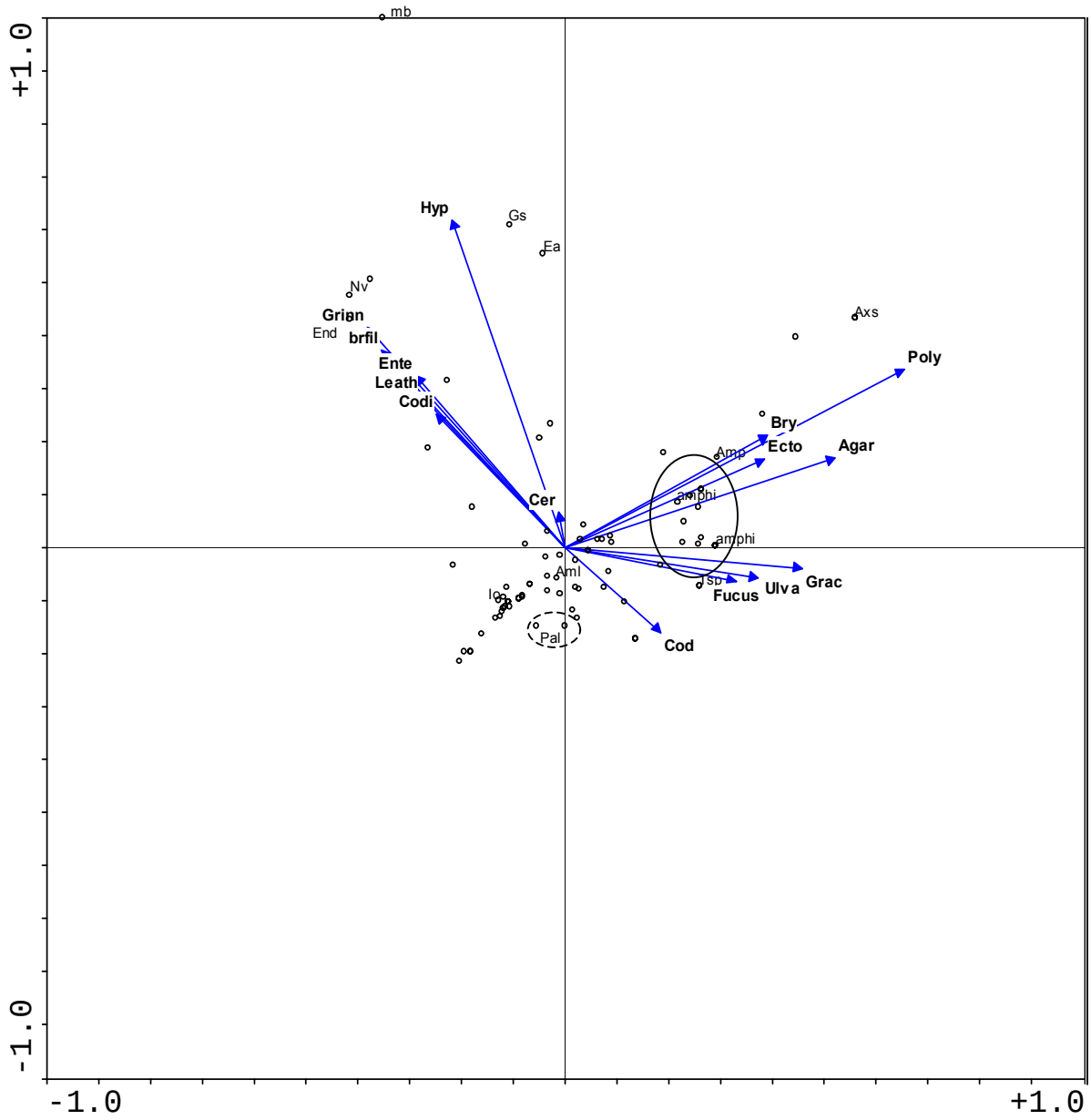



Figure 4.7. Amphipod density and macroalgal biomass relationships for the 3 study locations. $R^2$ values for each site are located adjacent to the trend line for the site.

Figure 4.8 (*below*). Canonical correspondence analysis (CCA) ordination diagram of the distribution of species (○) and environmental variables (arrows). The species are: **amphi** amphipods unidentified, **Amp** ampithoid amphipods, **Axs** *Axius serratus*, **End** *Ensis directus*, **Ea** *Erichsonella attenuata*, **Gs** *Glycera* sp., **Io** *Ilyanassa obsoleta,* **Aml** *Astyris (Mitrella) lunata*, **Nv** *Nereis virens*, **Pal** *Palaemonetes* spp., **Tsp** *Tellina* sp., **mb** muscles. The solid line encloses the majority of amphipod taxa, and the dashed line encloses 2 of 3 *Palaemonetes* spp. The environmental variables are macroalgal species: **Hyp** *Hypnea* sp., **Grinn** *Grinnellia americana*, **brfil** unidentified brown filamentous alga, **Ente** *Enteromorpha* sp., **Leath** *Leathesia difformis*, **Codi** *Codium fragile* spp. *tometosoides*, **Cod** *Codium* sp., **Fucus** *Fucus* sp., **Ulva** *Ulva lactuca*, **Grac** *Gracilaria tikvahiae*, **Agar** *Agardhiella* sp., **Ecto** *Ectocarpus* sp., **Bry** *Bryopsis* sp., **Poly** *Polysiphonia* sp.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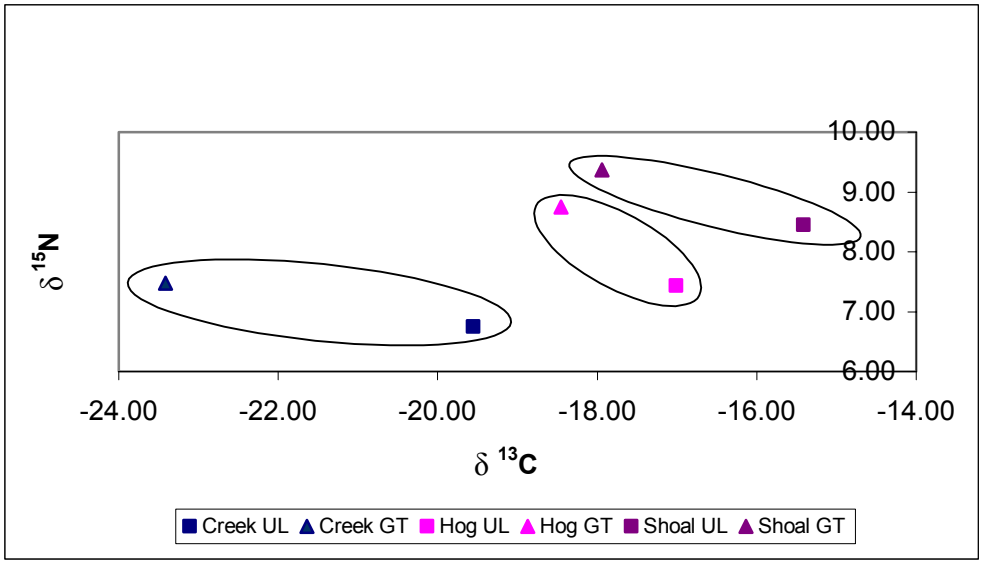


Figure 4.9 Dual isotope plot for the three sites monitored from August 2000 to August 2001. ▲ represent *Gracilaria tikvahiae* and ■ represents *Ulva lactuca*.

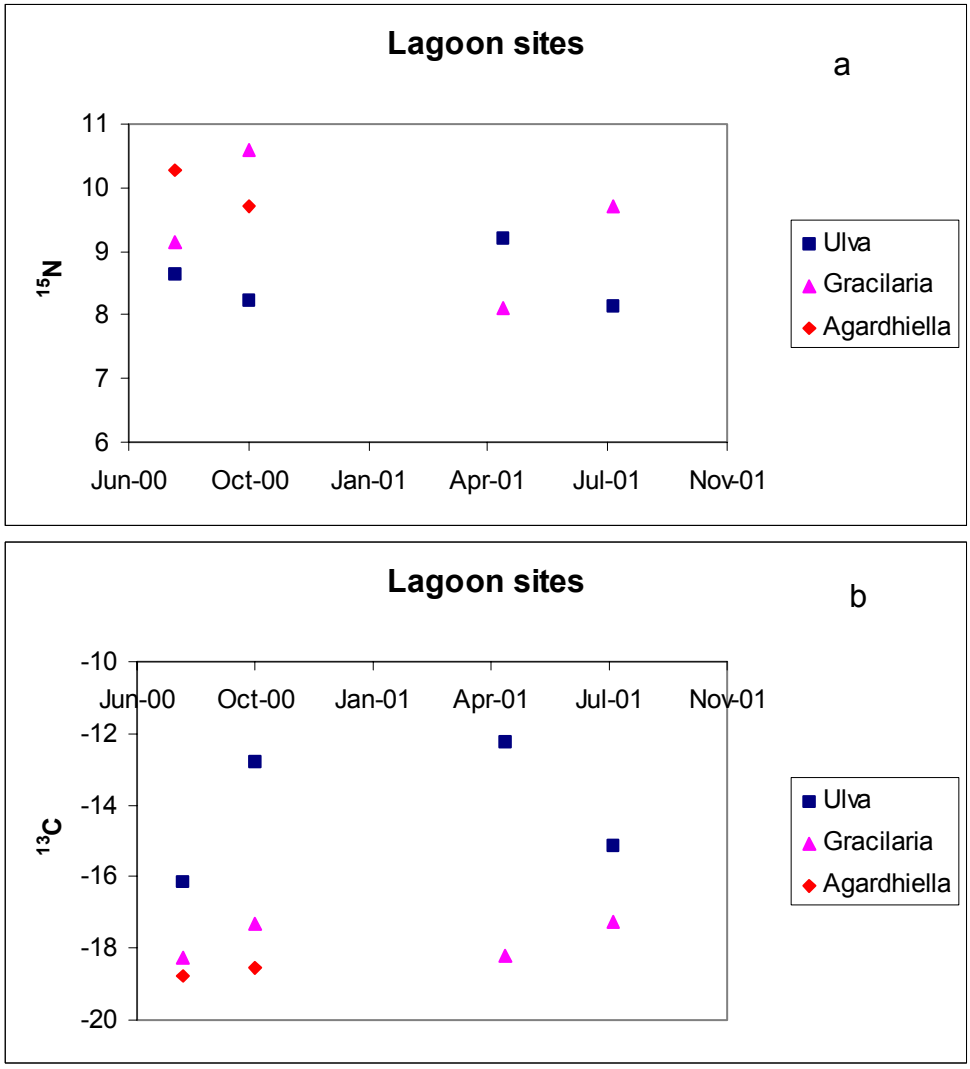


Figure 4.10 Seasonal trends for (a) $\delta^{15}N$ (b) $\delta^{13}C$ of macroalgae at the lagoon sites.

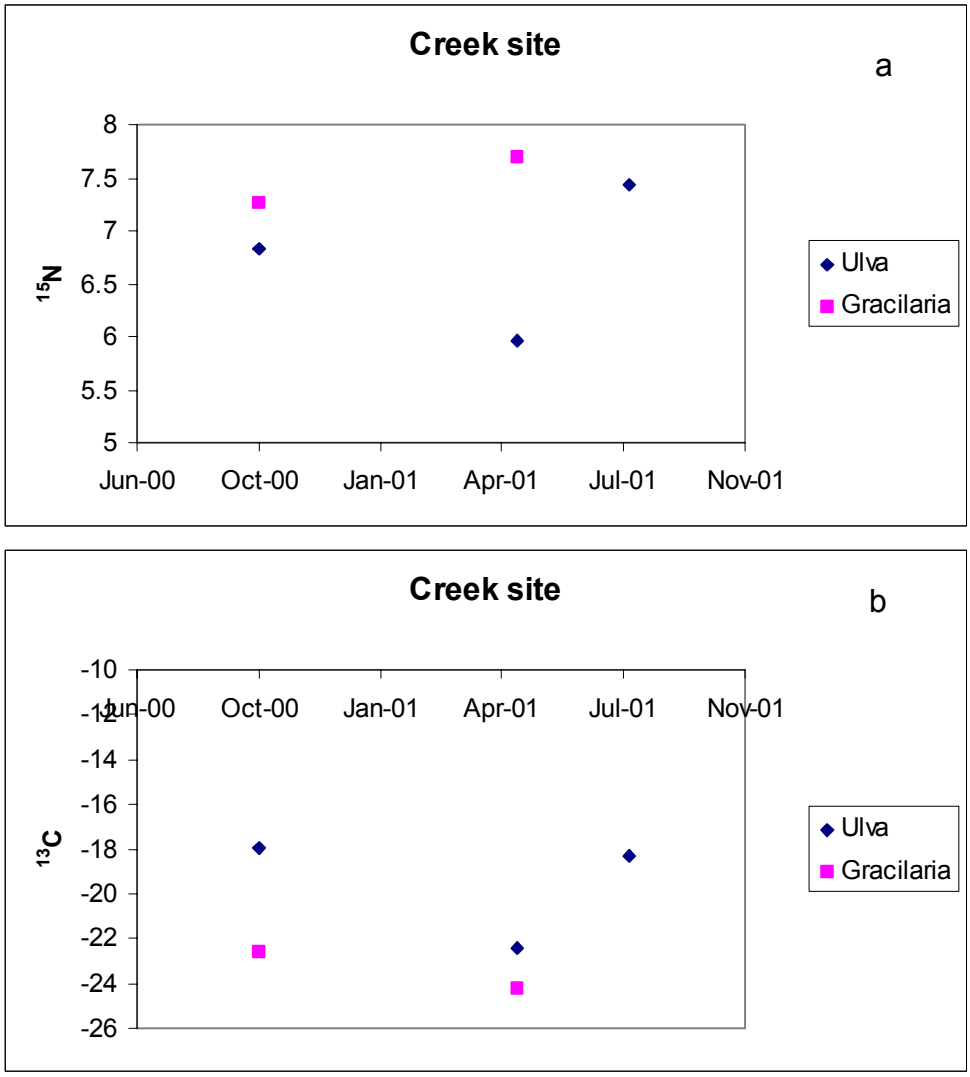


Figure 4.11 Seasonal trends for (a) $\delta^{15}N$ (b) $\delta^{13}C$ of macroalgae at the Creek site.

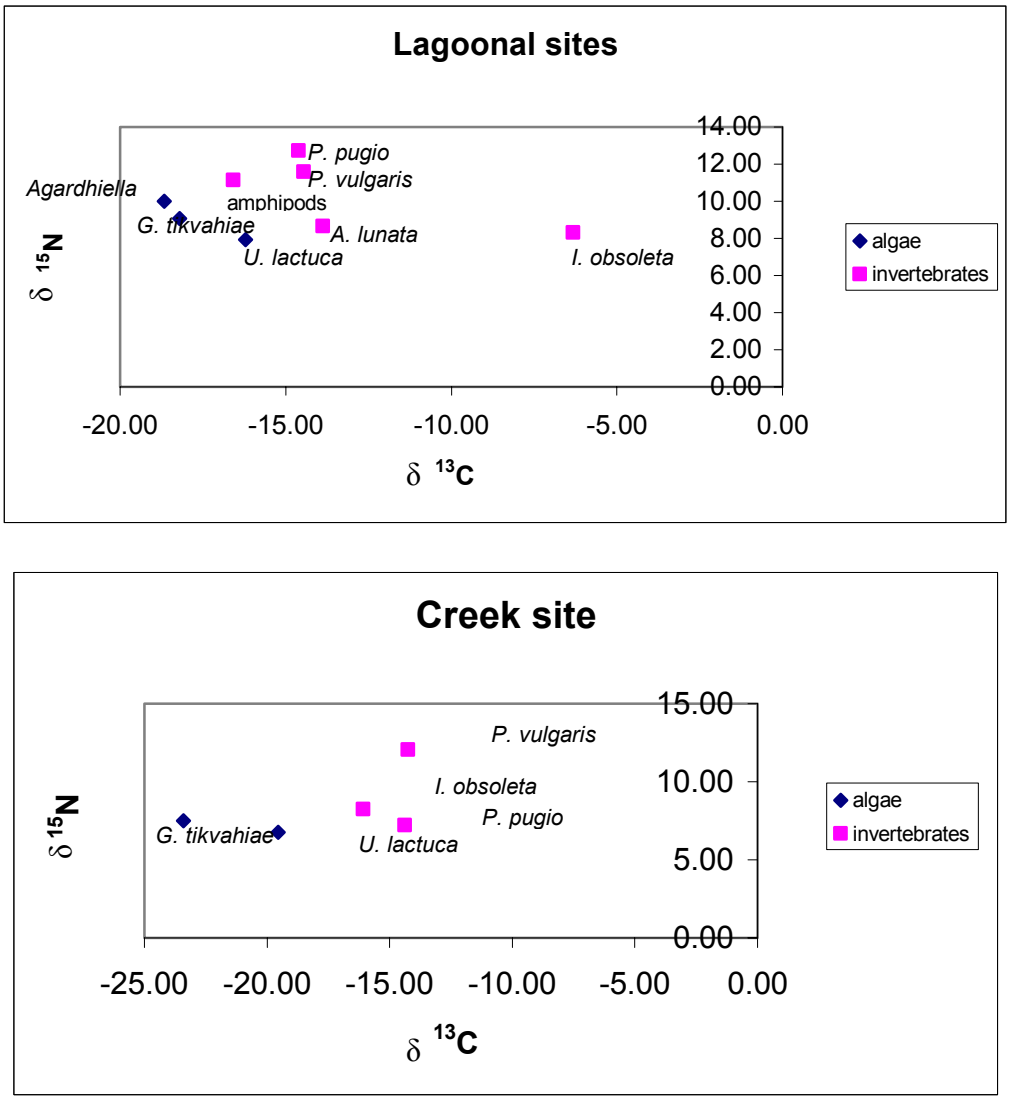


Figure 4.12 Dual isotope plots of macroalgae (♦) and invertebrates (■) at the (a) lagoon sites and (b) the Creek site.

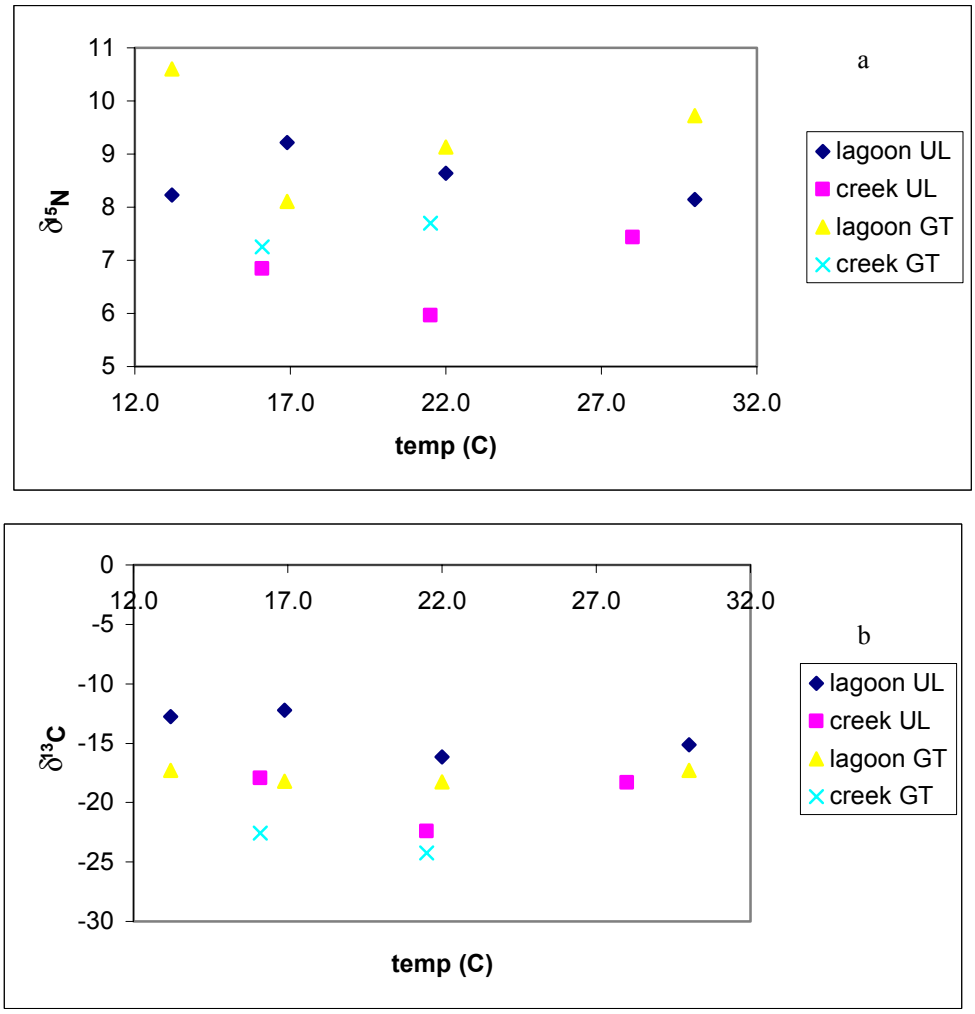


Figure 4.13 Relationship of (a) $\delta^{15}N$ and (b) $\delta^{13}C$ of macroalgae to temperature (C). UL is *Ulva lactuca* and GT is *Gracilaria tikvahiae*.

## 5. CONCLUSIONS

The interactions between bloom-forming macroalgae and benthic fauna play a key role in the response of shallow coastal systems to external nutrient loading. In Hog Island Bay macroalgal accumulations clearly influence benthic faunal community composition, sediment chemistry and trophic dynamics. The seasonal variation in both the abundance and diversity of macroinvertebrates appeared to be driven largely by macroalgal biomass in both open-lagoon and creek sites in the bay, with a summertime peak in both invertebrate density and macroalgal biomass. However, the peak in invertebrate density occurred at low macroalgal biomass, and an increase in macroalgal density caused a significant decline in invertebrate density, particularly of the dominant species. Previous work on the effects of macroalgae on benthic macrofauna has focused only on bloom conditions where macroalgal densities are extremely high. This study showed that the negative effects of macroalgal accumulation on benthic invertebrates occur at a significantly lower density than previously believed. This implies that the consequences of nutrient enrichment on benthic fauna, namely the loss of biodiversity and associated functions (i.e., bioturbation), occur earlier in the eutrophication process before macroalgal blooms form. Future research should be directed at understanding these biodiversity losses and the associated impact on system functioning. It is apparent from studies in rocky intertidal systems (e.g., Worm et al. 2002) that the biodiversity of consumers and macroalgae interact to control nutrient dynamics, but the direction of those interactions is not entirely clear, especially in soft-bottomed systems.

The loss of bioturbators as macroalgae accumulate influences the biogeochemistry of the sediments underlying the macroalgal mats, and this has important

feedbacks for the persistence of macroalgal populations. This study showed that the presence of macroalgae resulted in an increase in pore water $NH_4^+$ concentrations in the upper sediment layers and that this caused a higher flux of $NH_4^+$ across the sediment-water interface. This work agrees with other studies that have suggested that the higher sediment $NH_4^+$ concentrations underlying macroalgal mats results from increased mineralization from the input of macroalgal organic matter. However, this study also showed that the increased sediment $NH_4^+$ concentrations and fluxes are also likely the result of the loss of a number of key species (especially *Nereis* spp. and *Chaetoptera* sp.) that have a positive influence on $NH_4^+$ fluxes. The positive feedback of increased nutrient regeneration and fluxes from sediments underlying macroalgal mats is important in sustaining macroalgal populations. This is especially important in systems such as Hog Island Bay that receive relatively low external nutrient loads where macroalgae rely primarily on sediment nutrient sources to meet their growth demand.

Since grazing rates can exceed macroalgal growth rates in systems that receive low to moderate external nutrient loading, it was expected that the dominant grazers (*Astyris (Mitrella) lunata* and *Ampithoe rubricata*) would be able to control macroalgal proliferation in Hog Island Bay. However, even though per capita grazing rates were high, and the model results indicated that grazers could consume new growth at low to moderate macroalgal densities, dense macroalgal accumulations did still occur in localized areas in the bay. We believe that physical factors such as wind are important in the development of macroalgal blooms in shallow systems such as Hog Island Bay, and that this can counteract the effects of consumer control on macroalgal proliferation. Advection may cause macroalgae to accumulate to a high enough biomass that grazers

cannot keep pace with new growth because both per capita grazing rates and grazer numbers decrease dramatically at high macroalgal densities. These results emphasize the important coupling of biological and physical processes in shallow coastal ecosystems. More work needs to be done on determining the relative importance of advection, grazing and nutrients in controlling macroalgal blooms in these systems. Another important factor in understanding the top-down control on macroalgal bloom formation that should be addressed in future studies is the impact predators have on grazer density. Cascading effects of overfishing on top predators may result in increases in small fishes that consume mesograzers, and the resulting decline in grazing pressure may be an alternate explanation for macroalgal proliferation in some shallow coastal ecosystems. While this has been studied in seagrass communities, there has been little work done in macroalgal-dominated systems such as Hog Island Bay. The work presented here demonstrates that the importance of top-down processes in controlling primary producers varies as a function of nutrient status of the system as well as physical factors and that macrofauna and their associated functioning are impacted at much lower macroalgal density than has been previously thought.

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