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Benthic-pelagic coupling in eutrophic estuaries from the temperate and sub-tropical zones: The contrasting roles of benthic suspension feeding and nutrient loading

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Charles C. Wall III

We, the dissertation committee for the above candidate for the

Doctor of Philosophy degree, hereby recommend

acceptance of this dissertation

Dr. Christopher J. Gobler – Dissertation Co-Advisor
Associate Professor, School of Marine and Atmospheric Sciences

Dr. Bradley J. Peterson – Dissertation Co-Advisor
Assistant Professor, School of Marine and Atmospheric Sciences

Dr. Robert C. Aller – Chairperson of Defense
Distinguished Professor, School of Marine and Atmospheric Sciences

Dr. Glenn R. Lopez
Professor, School of Marine and Atmospheric Sciences

Dr. J. Evan Ward
Professor, Department of Marine Sciences
University of Connecticut

This dissertation is accepted by the Graduate School

Lawrence Martin
Dean of the Graduate School

Abstract of the Dissertation

Benthic-pelagic coupling in eutrophic estuaries from the temperate and sub-tropical zones: The contrasting roles of benthic suspension feeding and nutrient loading

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Coastal waters have suffered from multiple stressors that have diminished habitat value and living marine resources in estuaries. Excess nutrient loading, leading to eutrophication, has been identified as a primary driver of these changes. Some level of nutrient loading is necessary to sustain production in marine systems, but the level of appropriate nutrient loading for a given estuary or resource species is unknown. Benthic

suspension feeders, such as bivalves and sponges, have the potential to buffer or mediate eutrophication through their filtration activities. Many eutrophic systems have lost suspension feeders due to overharvesting, disease, and harmful algal blooms. In a mesocosm study, the presence of bivalve suspension feeders was found to ameliorate algal blooms and increase light penetration to the benefit of seagrass, a critical habitat-forming organism. In a second mesocosm experiment, a high density of adult bivalve suspension feeders facilitated the growth of eelgrass while reducing the growth of juvenile bivalves, suggesting that high ecosystem filtration rates could have both positive and negative feedbacks on different estuarine resources. In the same experiment, nutrient loading had a positive effect on the growth of juvenile bivalves, suggesting that high nutrient loading could have a positive effect on some shellfish. In a field study in a sub-tropical estuary, the survival of sponges (*Spechiospongia vesparium*) was suppressed by harmful cyanobacterial blooms in some regions, while sponges in other regions had fast filtration rates sufficient to control algal blooms. In a second field study, a naturally-occurring eutrophication gradient was used to evaluate the effects of this process on multiple resource species, including juvenile bivalves and seagrass. The growth rates of eelgrass (*Zostera marina*) and bay scallops (*Argopecten irradians*) were impaired by eutrophication; hard clams (*Mercenaria mercenaria*) were tolerant of eutrophic conditions, and eastern oysters (*Crassostrea virginica*) benefited from eutrophic conditions. Managers have long sought to reduce nutrient loading to coastal waters, but ecosystem based management will need to simultaneously account for nutrient loading, habitat conservation, fisheries, and aquaculture. Managers can target species into specific areas of an estuary for restoration and to buffer eutrophication, or manage nutrient-loading regimes to favor the growth of key species.

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Publications

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Introduction

Benthic-pelagic coupling and living marine resources in estuaries

Estuaries and other coastal ecosystems have suffered multiple anthropogenic insults during the past century, including pollution, eutrophication, overfishing of fish and shellfish, introduction of invasive species, and loss of key habitats, such as seagrass beds, salt marshes, mangroves, and oyster reefs (Valiela *et al.* 1992, Nixon 1995, Cloern 2001, Jackson 2001, Kemp *et al.* 2005, Lotze *et al.* 2006, Valiela 2006). At the same time, resource value of estuaries and their various habitats has increased, as measured by monetary value (Costanza *et al.* 1997) or by ecosystem services provided to marine and terrestrial species, including humans (Irlandi and Peterson 1991, Beck *et al.* 2001, Bruno *et al.* 2003, Johnson and Heck 2006, 2007). In response to the ongoing degradation of coastal ecosystems, the current challenge to scientists and managers is to implement management schemes for our estuaries and coastal waters that balance preservation, conservation, and restored ecosystem function with ever-growing human populations and human demands as well as climate change in the coastal zone (Nixon *et al.* 2009). Anthropogenic nutrient loading is a major threat to coastal systems; it has increased world-wide and led to eutrophication in many systems (Nixon 1995, Cloern 2001, de Jonge *et al.* 2002). Eutrophication can have severe bottom-up effects on estuaries and estuarine resources, such as hypoxia/anoxia leading to loss of benthic habitat (Breitburg 2002, Altieri and Witman 2006), harmful algal blooms (Sunda *et al.* 2006), shading of seagrass beds (Dennison *et al.* 1989), and "regime changes" from a high-biomass benthos to a pelagic, microbially-dominated system (Jackson 2001, MacIntyre *et al.* 2004).

Concurrently, human overharvesting of fish and shellfish has removed species that may have once provided top-down control on the effects of estuarine eutrophication (Newell 1988, Jackson 2001). Benthic suspension feeders, such as bivalves and sponges, have the potential to control eutrophication by filtering phytoplankton (Officer et al 1982), transferring carbon and nutrients to the benthos (Smaal and Prins 1993), and increasing light penetration in the water column (Newell and Koch 2004, Wall *et al.*

2008). Beyond filtration, many suspension feeders also provide physical habitat structure (Butler et al 1995, Jackson 2001) or facilitate the growth of other biogenic habitat, i.e. seagrass (Peterson and Heck 1999, 2001; Bruno *et al.* 2003; Newell and Koch 2004; Wall *et al.* 2008). Finally, an estuary that has lost much of its benthic biomass and filtration capacity may channel nutrient loading into nuisance blooms of algae and jellies (Jackson 2001, Purcell *et al.* 2007).

Lotze *et al.* (2006) surveyed ecological changes in 12 major estuaries over historical time. They found that overharvesting of key species and habitat destruction preceded eutrophication in almost every case of degradation or loss, suggesting that eutrophication could be a symptom, rather than a cause, of estuarine degradation. This also suggests that protection and restoration of key species, especially benthic suspension feeders, could be one of the major solutions to estuarine degradation (Newell and Koch 2004, Cerco and Noel 2007, Newell *et al.* 2007). Beyond the question of nutrient loading *vs.* top-down control as drivers of estuarine dynamics (Heck and Valentine 2007), another pressing question in estuarine ecology is "how much nutrient loading is excessive?" Obviously severe cases are harmful and result in the symptoms described previously such as algal blooms and hypoxia (Nixon 1995, de Jonge *et al.* 2002, Cloern 2001). However, moderate levels of nutrient loading may enhance the growth and production of finfish and shellfish populations through increased quantity and quality of food particles (Nixon and Buckley 2002, Weiss *et al.* 2002, Carmichael *et al.* 2004). The 'tipping point' in estuarine nutrient loading, when fisheries yield is maximal but negative effects are minima,l is unknown. In addition, the relative importance of nutrient loading compared to the loss of filtration in the structuring of estuarine ecosystems has not been well-studied.

Benthic-pelagic coupling, defined as interactions between the water column and benthos, is a class of interactions that will be of importance to successful estuarine management. The benthos and the water column are often tightly coupled in shallow ecosystems. Benthic-pelagic coupling can take many forms, and can yield both positive and negative effects on estuarine resources. These forms include, but are not limited to, filtration by benthic suspension feeders (Officer *et al.* 1982, Smaal and Prins 1993,

Peterson et al 2006), sedimentation of phytoplankton leading to bottom anoxia (Breitburg 2002, Kemp *et al.* 2005), release or uptake of dissolved nutrients by micro- and macro-benthos (Boynton and Kemp 1985, Newell *et al.* 2002), or harm to benthic plants and animals by algal blooms (Gobler *et al.* 2005). Many shallow marine systems undergo complicated regime shifts from benthic to pelagic productivity that might be seasonal (MacIntyre *et al.* 2004) or the result of long-term anthropogenic changes (Valiela *et al.* 1992, Kemp *et al.* 2005). These regime shifts are often mediated by disruptions in normal benthic-pelagic couplings, such as human removal of suspension feeders (Newell 1988), harmful algal blooms that shut down normal filtration and nutrient cycling processes in the estuary (Gobler *et al.* 2005, Sunda *et al.* 2006), or extreme eutrophication which leads to anoxia and mortality in the benthos due to increased carbon deposition and respiration (Breitburg 2002, Altieri and Witman 2006).

In the coming years, scientists and managers will need to examine the dynamics of benthic-pelagic coupling to better understand the mechanisms leading to degradation of coastal marine ecosystems, and to devise ecosystem-based management schemes for these waters. For my dissertation, I will investigate several aspects of benthic-pelagic interactions in estuaries, and will demonstrate how an understanding of these interactions may help ecosystem managers address the problems of estuarine degradation.

Eutrophication and loss of estuarine resources:

It is well-established that eutrophication of coastal waters can have a multitude of adverse impacts on affected ecosystems, including nuisance algal blooms, hypoxia, and the subsequent loss of marine life and habitats (Nixon, 1995, de Jonge *et al.* 2002). One key group of autotrophs impacted by eutrophication is seagrasses. Seagrass beds are a valuable habitat in many temperate and tropical estuaries, providing structural habitat complexity (Heck and Wetstone 1977, Irlandi and Peterson 1991), damping waves and trapping sediment (Newell and Koch, 2004), modifying the sedimentary environment (Reise, 2002), providing a settlement site for juvenile bivalves (Bologna *et al.* 2005), and furnishing benthic primary production. Due to the array of ecological services provided

by seagrass beds, they are considered "ecosystem engineers" (Reise, 2002, Bruno *et al.* 2003). World-wide, seagrass populations have experienced significant declines in recent decades (Orth *et al.* 2006). Dense phytoplankton blooms or macroalgal growth resulting from nutrient loading can reduce light penetration to the benthos and shade seagrass beds (Valiela *et al.* 1992; Duarte 1995, Hauxwell *et al.* 2001, Gobler *et al.* 2005). Anthropogenic nutrient loading can also increase seagrass epiphyte loads which in turn decrease the quantity and quality of light at leaf surfaces and subsequently decrease seagrass productivity (Duarte 1995). Newell and Koch (2004), through a combination of modeling and field studies in Chesapeake Bay, have shown that the seagrass *Ruppia maritima*, which does not grow deeper than 3 m under optimal conditions, is very sensitive to decreases in light penetration due to algal blooms or resuspended sediment. Other experimental studies have demonstrated the decline of *Zostera marina* in response to nutrients (Taylor *et al.* 1999, Bintz *et al.* 2003), light reduction (Bintz and Nixon 2001), and epiphyte load (Brush and Nixon 2002). The degree to which suspension-feeding bivalves can alleviate these negative impacts on seagrass has not been well studied but will be discussed in subsequent sections.

While the effects of nutrient loading and eutrophication on seagrass populations in temperate ecosystems are clearly negative, the effects of eutrophication on suspension-feeding bivalves are more complex. Long Island, NY, estuaries, such as Great South Bay on the south shore and Peconic Bay on the east end, previously supported greater abundances of estuarine resources than they do today (Bricelj and Kuenster 1989, McHugh 1991, Gobler *et al.* 2005). These resources include shellfish such as the hard clam (*Mercenaria mercenaria*, McHugh 1991), the bay scallop (*Argopecten irradians*, Bricelj and Kuenster 1989), various finfish (NMFS 2006) and eelgrass beds (*Zostera marina*, Dennison *et al.* 1989). Shellfish and finfish are harvested directly in commercial and recreational fisheries, while seagrass beds are considered of paramount importance as structural habitat for shellfish and finfish in many coastal habitats (Heck and Wetstone 1977, Irlandi and Peterson 1991, Reise 2002, Bruno *et al.* 2003).

Overfishing (McHugh 1991, Lotze *et al.* 2006), habitat loss, eutrophication (Nixon 1995), and harmful algal blooms (Gobler *et al.* 2005) have all impacted estuarine

resources. Federal, state, and local managers, and non-profit organizations are all concerned with promoting the re-growth of these estuarine resources. Current management efforts have focused primarily on the impacts of anthropogenic nutrient loading in an attempt to limit eutrophication (Peconic Estuary Plan, 2004). Inorganic nutrient levels and chlorophyll *a* concentrations have declined in both Great South Bay (Gobler *et al.* 2005) and Peconic Bay (SCDHS 1976-2005) on a 10 – 20 year time scale, perhaps due to changes in land use and improved sewage treatment. Despite these decreases in inorganic nutrient concentrations and phytoplankton biomass, clam and scallop fisheries have not recovered, and low inorganic nutrients may have played a role in precipitating the harmful brown tide blooms (*Aureococcus anophagefferens*, Gobler *et al.* 2005, Sunda *et al.* 2006). This hysteresis between loss and recovery of resources with changing levels of eutrophication suggests that eutrophication is not the primary driver of changes in bivalve abundance (Lotze *et al.* 2006). An alternate explanation is that coastal ecosystems have undergone a regime-shift (Scheffer and Carpenter 2003) whereby plankton communities, sedimentary environments, and predation pressures are fundamentally different from historic conditions, and these new conditions are preventing recovery of bivalve populations. In either case, further reduction of nutrient loads and chlorophyll *a* concentrations are not likely to facilitate bivalve recovery in these systems.

There are multiple examples of coastal ecosystems around the world where the production of fisheries is proportional to nutrient loads and/or primary production (Ryther 1969, Houde and Rutherford 1993, Pauly and Christensen 1995, Nixon and Buckley 2002). As such, a plausible hypothesis regarding nutrients and shellfish populations in some Long Island estuaries is that nutrient loading rates are currently not high enough to support maximal growth of shellfish. High levels of inorganic nutrients favor larger phytoplankton cells (Malone 1980, Raven and Kubler 2002), and many larger cells, such as diatoms and prymnesiophytes, provide better nutrition to bivalves than smaller algal cells (Wikfors *et al.* 1992). In Great South Bay there is also evidence of a historical shift from larger cells (> 10-20 μm) in the 1970's (Weaver and Hirshfield 1976, Cassin 1978) to very small cells (< 5 μm) in today's waters (Lonsdale *et al.* 1996, Sieracki *et al.* 2004, Gobler *et al.* 2005). Cells smaller than 5 μm are retained with a

lower efficiency by bivalves compared to larger cells (Mohlenberg and Riisgard 1975), and these cells may consist of actively harmful algae like *Aureococcus anophagefferens* (Gobler *et al.* 2005).

Beyond the size of suspended phytoplankton cells, total suspended phytoplankton biomass may also effect the growth of shellfish populations. Studies in other northeastern estuaries have shown that northern quahogs (a.k.a "hard clams," *Mercenaria mercenaria*) and softshell clams (*Mya arenaria*) respond positively to nitrogen loading and high chlorophyll *a* levels (> 15 $\mu g\ l^{-1}$) in their habitats (Weiss *et al.* 2002, Carmichael *et al.* 2004). Weiss *et al.* (2002) and Carmichael *et al.* (2004) found that shell growth, soft tissue growth, and survival of these shellfish increased along a naturally-occurring gradient of nitrogen loading in Waquoit Bay, Massachusetts. They attributed these changes to increased quantity and quality of food particles due to nitrogen enrichment (Carmichael and Valiela 2005), but a similar response was not found for bay scallops in the same estuary (*Argopecten irradians*, Shriver *et al.* 2002). However, at very high nitrogen loadings, the production and subsequent decomposition of high levels of phytoplankton biomass can lead to hypoxia and anoxia, which may impair growth and survival of hard clams and softshell clams (Carmichael *et al.* 2004). Hypoxia and anoxia do not generally occur in Great South Bay and Peconic Bay, since both are shallow and well-mixed (Wilson *et al.* 1991, Hardy 1976).

There is evidence that quantity and quality of suspended particles in Long Island estuaries affect shellfish populations. Weiss *et al.* (2007) measured growth and survival of juvenile hard clams along gradients from the ocean inlet to the inner bay of Shinnecock Bay and Great South Bay on Long Island's south shore. They found that clam growth and survival were maximal at mid-points in the estuaries. The inner bays had high temperatures (> 24°C) and poor food sources (dinoflagellates and cells < 5μm) which reduced clam growth and survival. Sites near the ocean inlets also had reduced growth and survival under conditions of lower temperatures, low nutrients, and low phytoplankton biomass. Excluding the effects of temperature, the results of Weiss *et al.*

(2007) suggest that some degree of nutrient enrichment is required to produce the size and type of phytoplankton that bivalves require for maximal growth.

Florida Bay, FL, is a shallow, sub-tropical estuary between mainland Florida and the Florida Keys which has displayed numerous symptoms of estuarine eutrophication. Florida Bay is the largest estuary in Florida, being valuable for recreation and fisheries, and adjacent to the sensitive coral reef habitats of the Florida Keys National Marine Sanctuary (Phlips *et al.* 1999, Glibert *et al.* 2004, Peterson *et al.* 2006). Much of Florida Bay lies within the boundaries of Everglades National Park, and the bay is affected by freshwater runoff from the Everglades (Phlips *et al.* 1999). Beginning in the 1990's, Florida Bay has been affected by a series of ecological disruptions, including mass sponge die-offs (Butler *et al.* 1995), blooms of the cyanobacteria *Synechococcus* spp. (Phlips *et al.* 1999), and seagrass mortality (Robblee *et al.* 1991). The loss of seagrass beds is especially worrisome because of the variety of ecosystem services that seagrasses provide in temperate and tropical estuaries (Irlandi and Peterson 1991, Reise 2002, Newell and Koch 2004, Orth *et al.* 2006). Seagrass mortality was likely caused by multiple stressors (Robblee *et al.* 1991), including sulfide toxicity (Borum *et al.* 2005) and light attenuation due to dense cyanobacterial blooms (Peterson *et al.* 2006). The loss of sponges may have indirectly contributed to seagrass mortality through loss of filtration pressure in the bay, which could lead to increases in particle loads and decreases in light penetration harmful to seagrasses (Newell and Koch, 2004).

The cyanobacteria blooming in Florida Bay are *Synechococcus spp.*, which have previously been considered an oligotrophic, open-ocean species rather than a coastal bloom-forming species (Phlips *et al.* 1999). Other cyanobacteria, especially in freshwater, have been found to be toxic (Sivonen, 1990), and sponge mortality in other areas has been attributed to the detrimental effects of *Synechococcus* blooms and associated muco-polysaccharide production (Lynch and Phlips, 2000). Persistent, dense algal blooms have the potential for disrupting the ecology of the bay through associated anoxia, production of a harmful substances and/or the reduction of light availability for benthic plant communities (Phlips and Badylak 1996, Phlips *et al.* 1999, Sunda *et al.* 2006). In other systems, harmful algae have inhibited both benthic (Bricelj *et al.* 2001)

and pelagic (Gobler *et al.* 2002) grazers on the algae. This initiates a feedback loop where inhibited suspension feeding enables more algae growth, which in turn impairs more suspension feeders (Sunda *et al.* 2006). The precise impact of *Synechococcus* blooms in Florida Bay on benthic suspension feeding sponge populations in this ecosystem have yet to be described.

Anthropogenic nutrient loading has been a problem in several areas of south Florida (Lapointe *et al.* 2004), but so far a clear pattern of nutrient-loading leading to a *Synechococcus* blooms has yet to emerge (Glibert *et al.* 2004; Phlips *et al.* 1999). Phlips *et al.* (1999) describe Florida Bay as phosphorus-limited, with strong nutrient inputs from terrestrial run-off and groundwater, which is likely derived from the Everglades region (Lynch and Phlips, 2000). But Phlips *et al.* (1999) also note that the bloom-free eastern basin of Florida Bay receives the same nutrient inputs as the *Synechococcus*-plagued north-central basin, implying that nutrient inputs are not the direct or only cause of cyanobacterial blooms. Glibert *et al.* (2004) described a complex pattern of inorganic and organic nitrogen and phosphorus use by blooms which demonstrated that *Synechococcus* blooms could absorb dissolved organic nitrogen in the form of urea. To date, clear evidence does not exist to support nutrient loading as a cause for *Synechococcus* blooms in Florida Bay.

Filtration by benthic suspension-feeders and estuarine resources:

Benthic suspension feeders, such as bivalves and sponges, are among the most important estuarine resources. Bivalves are used for human food (Newell 1988, McHugh 1991) while some sponges are harvested for commercial use (Pronzato 1999). In addition to direct human consumption or harvest, benthic suspension feeders provide a variety of ecosystem services through their filtration, burrowing, and reef-building activities. These activities "control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials" (Jones *et al.* 1997), and as such should be considered "ecosystem engineers" (Reise 2002, Bruno *et al.* 2003). The filtration provided by bivalves has the potential to control eutrophication or to mediate its effects

(Officer *et al.* 1982) and significantly affect carbon cycling (Doering *et al.* 1986). By depositing solid, nutrient rich fecal material and pseudofeces, bivalves mediate a flux of organic matter and nutrients out of the water column and into the sediments (Smaal and Prins, 1993). Similarly, sponges filter significant amounts of phytoplankton and other particles in marine (Reiswig 1971, Yahel *et al.* 2003, Peterson *et al.* 2006) and freshwater (Pile *et al.* 1997) systems. In addition to their filtration functions, sponges and bivalves also provide biogenic habitat structure for other biota. Large aggregations of bivalves such as oyster reefs and mussel beds provide hard substrate for a variety of fish and invertebrates (Coen *et al.* 2007). Sponges also provide structural habitats that are utilized by other organisms as predation refuges and nursery grounds (Butler *et al.* 1995).

The loss of benthic suspension feeders is the loss of a critical estuarine resource, whether it occurs, through over-harvesting (Newell 1988, McHugh 1991), disease (Rothschild *et al.* 1994, Dahl and Allam 2007), hypoxia/anoxia (Breitburg 2002), or harmful algal blooms (Butler *et al.* 1995, Gobler *et al.* 2005). Jackson (2001) outlined a progression of disruption: over-harvesting leads to loss of biogenic structure, eventually ending in the dominance of microbes and gelatinous zooplankton. Such a disruption has occurred in many coastal ecosystems (Pauly *et al.* 2002, Purcell *et al.* 2007). Lotze *et al.* (2006) surveyed the history of degraded estuaries world-wide and found that overharvesting of suspension feeders and large vertebrates preceded eutrophication in most cases, suggesting that eutrophication is a symptom rather than a cause of degradation. They found that efforts to limit overharvesting and/or to protect critical habitats led to partial recovery of some systems. When suspension feeders are restored, a benthic-pelagic link is re-established that facilitates a trophic transfer from the pelagic zone to the benthos (Smaal and Prins 1993). As such, management efforts for our estuaries which simultaneously address protecting critical habitats (seagrass beds and coral reefs), conserving large vertebrates (fish, sharks, turtles), limiting nutrient inputs, and restoring benthic suspension feeders (bivalves and sponges) are most likely to successfully reverse Jackson's (2001) progression of ecological degradation.

Infaunal bivalves, like the hard clam (*Mercenaria mercenaria*) do not directly provide biogenic structure, but can facilitate another ecosystem engineer in shallow

coastal waters: seagrass (Reise 2002, Bruno *et al.* 2003, Wall *et al.* 2008). Various species of bivalves live in, on, or near seagrass beds, and the biodeposition of solid, nutrient rich fecal material and pseudofeces, creates a flux of organic matter and nutrients out of the water column and into the sediments (Smaal and Prins, 1993). This nutrient enrichment of sediments can increase the growth of seagrass, since seagrasses absorb most of their nutrients from the sediment through their roots and not from the water column (Peterson and Heck, 1999). Reusch *et al.* (1994) and Peterson and Heck (1999, 2001) showed that *Mytilus edulis* and *Modiolus americanus*, respectively, could increase seagrass productivity through sediment nutrient enrichment. By clearing algal populations and other suspended particles from the water column, bivalves may serve as a control on marine (Cerrato *et al.* 2004) and freshwater (Heath *et al.* 1995) algal blooms. While the work of Cerrato *et al.* (2004) and the modeling efforts of Newell and Koch (2004) suggest that bivalve filtration could increase ambient light and perhaps enhance seagrass productivity, no previous study has directly examined this relationship.

During the past century, many estuarine bivalve populations have suffered from overharvesting and habitat loss (Jackson, 2001; Lotze *et al.* 2006), an occurrence which could have secondary negative impacts on seagrass beds. Since bivalves may serve as a natural control on eutrophication (Officer *et al.* 1982), the loss of these populations could result in decreases in light reaching the benthos, a factor which often limits eelgrass productivity in estuaries (Dennison and Alberte, 1985; Bintz and Nixon, 2001). Great South Bay, a shallow estuary on Long Island, NY's south shore, has experienced an increase in eutrophication and frequent algal blooms, including harmful "brown tides" (*Aureococcus anophagefferens*; Gobler *et al.* 2005). These changes were concurrent with the loss of seagrass beds (*Zostera marina*; Dennison *et al.* 1989) and the removal of the dominant suspension feeding bivalve (*Mercenaria mercenaria*; Cerrato *et al.* 2004). Similarly, in Chesapeake Bay, MD the loss of oyster populations, *Crassostrea virginica*, has been hypothesized to have contributed to the demise of *Z. marina* in this system (Jackson, 2001; Newell and Koch, 2004; Kemp *et al.* 2005; Lotze *et al.* 2006).

In temperate estuaries the suspension feeding community is often composed of bivalves (Dame 1996), along with gastropod suspension feeders and ascidians, while the

dominant benthic suspension feeders in many tropical estuaries are sponges (Bell 2008). In Florida Bay, FL the sponge community is dominated by the species *Spechiospongia vesparium* (loggerhead sponge), *Tedania ignis* (fire sponge), and *Ircinia campana* (vase sponge) (Butler *et al.* 1995; Lynch and Phlips, 2000). Sponges, along with octocorals and solitary hard corals, are a key component of the Florida Bay benthic community, providing structural habitat for juvenile octopus, stone crabs, and spiny lobster *Panulirus argus* (Butler *et al.* 1995). In the early 1990's, there was a series of wide-spread sponge die-offs in Florida Bay that affected >40% of the loggerhead sponges and >70% of other sponge species (Butler *et al.* 1995). The loss of suspension feeders from this system was also concurrent with the loss of seagrass (*Thalassia testudinum*; Robblee *et al.* 1991) and the rise of algal blooms (Butler *et al.* 1995, Phlips *et al.* 1999). Cyanobacterial blooms (*Synechococcus* sp.) are a potential cause of sponge mortality (Butler *et al.* 1995), but subsequent laboratory experiments have failed to show a toxic effect by *Synechococcus* on sponges (Lynch and Phlips, 2000; Peterson *et al.* 2006). To date, the ultimate causes of the algal blooms and sponge mortality have not been resolved through studies of nutrient loading (Glibert *et al.* 2004), but studies of benthic and pelagic grazing on algal populations may provide new insights.

Synechococcus is not a "typical" bloom-forming phytoplankton due to its small size and its affinity for dissolved organic nutrients (Phlips *et al.* 1999; Glibert et al 2004). Smaller cells have a high surface area to volume ratio to maximize nutrient-absorption, and are generally thought to be adapted to oligotrophic conditions. Small phytoplankton that absorb dissolved organic nutrients, such as the brown tide species *Aureococcus anophagefferens*, are often "K-selected" or slow-growing organisms (Gobler *et al.* 2005). Moreover, small phytoplankton cells are typically under much tighter top-down control by grazers (Calbet and Landry, 2004; Sherr and Sherr, 2002), and are therefore less likely to form dense blooms. As such, blooms caused by picoplankton such as *Synechococcus* suggest an absence of top-down control by grazers.

Sponges represent a potential top-down control on algal populations. Dense bivalve suspension feeders serve as a control on phytoplankton blooms and carbon cycling in other estuarine ecosystems (Officer *et al.* 1982; Doering *et al.* 1986; Smaal and

Prins, 1993; Cerrato *et al.* 2004), and suspension feeders have the potential to facilitate other components of an ecosystem through increases in light penetration, like seagrasses (Newell and Koch, 2004, Wall *et al.* 2008). A dense sponge community can have filtration rates comparable to bivalves (Reiswig, 1971) and therefore may exert similar top-down control on algal populations, particle load, and light penetration in the water column. Sponges are able to retain picoplanktonic particles in the size range of *Synechococcus* (Reiswig, 1971; Lynch and Phlips, 2000), and field studies in other systems have shown that sponges are capable of depleting near-bottom waters of picoplankton (Pile *et al.* 1997; Yahel *et al.* 2003). If sponges are killed or impaired by very dense blooms, this might represent a positive feedback loop for the cyanobacteria as the blooms "escape" top-down control (Peterson *et al.* 2006; Sunda *et al.* 2006) and further proliferate.

It has been hypothesized that the cyanobacterial blooms in Florida Bay may result from the removal of top-down control by benthic suspension feeders rather than increased nutrient inputs. Peterson *et al.* (2006) surveyed sponge biomass following the major die-offs and conducted laboratory grazing experiments with native sponges. Extrapolating sponge biomass and filtration rates across several basins of Florida Bay, and combining sponge data with Nuttle *et al.*'s (2000) hydrological model, they concluded that the time required for sponges to filter the water column had increased (from an average baseline of 3 days) by as much as 12 days in some areas. The north central area with the densest *Synechococcus* blooms is also the area that has experienced the highest sponge mortality and has lost the most grazing capacity (Peterson *et al.* 2006; Phlips *et al.* 1999).

Persistent algal blooms and the loss of benthos have damaged the critical habitat of Florida Bay, and threaten adjacent reef habitats in the Florida Keys. Many questions remain unanswered about environmental disturbances in Florida Bay, such as characterization of the phytoplankton community, sponge-specific grazing rates on various components of the phytoplankton community, the role of zooplankton grazing, and the effect of salinity and other physiological stressors on grazing dynamics. Although anthropogenic nutrient loading contributes to harmful algal blooms in south Florida (Lapointe *et al.* 2004), knowledge of the coupling between sponge suspension

feeders and phytoplankton blooms will be essential to understand the ecological dynamics of algal blooms within Florida Bay. Some managers have suggested re-seeding of sponges in select basins of Florida Bay to restore benthic suspension feeding (B. Peterson, pers. comm.). Hopefully, the answers to these questions can inform future ecosystem-based management of Florida Bay and the connected regions of Everglades National Park and the Florida Keys National Marine Sanctuary.

As restoration programs proceed in Florida Bay, Great South Bay, or the Peconic Estuary, the filtration pressure of adult suspension feeders will begin to affect these estuarine systems. As mentioned before, suspension feeders can have a variety of positive effects on estuaries, such as reduced phytoplankton biomass (Officer *et al.* 1982, Doering *et al.* 1986), transfer of nutrients and biomass to the benthos (Smaal and Prins 1993, Jackson 2001), control of harmful algae (Cerrato *et al.* 2004), increased light penetration (Newell and Koch 2004), and facilitation of benthic plants (Newell *et al.* 2002, Lotze *et al.* 2006, Wall *et al.* 2008). However, it is not known how increased filtration pressure from restored adult shellfish will affect the growth and survival of juvenile shellfish or planktivorous fish. Juveniles of many benthic invertebrates settle on, or near, adults of the same species (Morse 1991), since the presence of adults indicates a favorable habitat. But the prodigious filtering capacity of many adult bivalves could deplete food particles from the water column and lead to food-limitation in growing juveniles (Frechette *et al.* 1992, Rheault and Rice 1996). Historically, estuaries supported high densities of adult suspension feeders and juvenile fish and shellfish simultaneously (Jackson *et al.* 2001), but modern restoration and aquaculture programs may face an eventual trade-off between locally high water filtration rates and the growth of juvenile fish and shellfish. Given this context of anthropogenic changes in benthic-pelagic coupling processes, this dissertation has the following specific objectives:

Dissertation Objectives:

1. To establish the potential for suspension-feeding bivalves to alleviate light-limitation of seagrass in eutrophic waters in an experimental setting.

2. To establish the individual and combined effects of nutrient loading and bivalve filtration on water quality (light, phytoplankton biomass) and the growth of estuarine resources (seagrass, juvenile bivalves, and juvenile fish) in an experimental setting.

3. To establish the interactions between cyanobacterial blooms and suspension-feeding sponges in a sub-tropical estuary by examining the effects of blooms on sponges and the potential for natural sponge populations to filter cyanobacterial blooms.

4. To establish the effect of nutrient loading on the growth of estuarine resources (seagrass, juvenile bivalves, and juvenile fish) along a temperate estuarine eutrophication gradient in a temperate estuary.

I. The facilitation of seagrass (*Zostera marina*) productivity by suspension-feeding bivalves in an experimental setting

Abstract:

Seagrasses and suspension feeders are both critical ecosystem engineers in estuaries. Seagrass beds are important structural habitats and suspension feeders, when abundant, can regulate phytoplankton densities. Furthermore, there may be mutual facilitation of growth and recruitment between seagrasses and suspension-feeding bivalves. In a series of mesocosm experiments, the effects of environmentally realistic densities of three different suspension-feeding bivalves (*Mercenaria mercenaria*, *Crassostrea virginica*, *Mytilus edulis*) on the growth of eelgrass (*Zostera marina*) in a eutrophied environment were examined. Experimental treatments with bivalves consistently yielded significantly lower chlorophyll *a* concentrations ($p < 0.05$), and most bivalve treatments also showed significant increases in light penetration ($p < 0.05$). Eelgrass productivity was measured by leaf area growth, and varied from 0.318 ± 0.018 cm^2 $shoot^{-1}$ d^{-1} to 0.832 ± 0.036 cm^2 $shoot^{-1}$ d^{-1} (mean ± SE); leaf area productivity was always significantly higher (on average, 48 ± 9.3% higher) in the treatments with the highest density of bivalves compared to a control without bivalves ($p < 0.05$). The data indicate that clearance of the water column and the subsequent increase in light penetration was the primary mechanism by which suspension-feeding bivalves facilitated the growth of eelgrass. These findings suggest that healthy populations of suspension-feeding bivalves can mitigate the effects of estuarine eutrophication and can facilitate the growth of seagrass in degraded, light-limited habitats.

Introduction:

Estuaries and other coastal ecosystems have suffered multiple anthropogenic insults during the past century including pollution, eutrophication, overfishing of fish and shellfish, introduction of invasive species, and loss of key habitats, such as seagrass beds (Valiela *et al.*, 1992; Nixon, 1995; Newell and Koch, 2004; Jackson et al 2001; Lotze *et al.*, 2006; Valiela, 2006). Seagrass beds are a valuable habitat in many temperate and tropical estuaries, providing structural habitat complexity (Heck and Wetstone, 1977), damping waves and trapping sediment (Newell and Koch, 2004), modifying the sedimentary environment (Reise, 2002), providing a settlement site for juvenile bivalves (Bologna *et al.*, 2005), and furnishing benthic primary production. Due to the array of ecological services provided by seagrass beds, they should be considered "ecosystem engineers" (Reise, 2002; Bruno *et al.*, 2003).

Eutrophication of coastal waters can have many adverse impacts on affected ecosystems, including nuisance algal blooms, hypoxia, and the subsequent loss of marine life and habitats (Nixon, 1995; de Jonge *et al.*, 2002). Dense phytoplankton blooms or macroalgal growth resulting from eutrophication can reduce light penetration to the benthos and shade seagrass beds (Valiela *et al.*, 1992; Duarte, 1995; Hauxwell *et al.*, 2001; Gobler et al 2005). Anthropogenic nutrient loading can also increase seagrass epiphyte loads which in turn decrease the quantity and quality of light at leaf surfaces and subsequently decrease seagrass productivity (Duarte, 1995). Newell and Koch (2004), through a combination of modeling and field studies in Chesapeake Bay, have shown that the seagrass *Ruppia maritima*, which does not grow deeper than 3 m under optimal conditions, is very sensitive to decreases in light penetration due to algal blooms or resuspended sediment. Other experimental studies have demonstrated the decline of *Zostera marina* growth in response to nutrients (Taylor *et al.*, 1999; Bintz *et al.*, 2003), light reduction (Bintz and Nixon, 2001), and epiphyte load (Brush and Nixon, 2002).

One guild of species that might facilitate the growth of seagrass is suspension feeding bivalves. Various species of bivalves live in, on, or near seagrass beds, and their suspension feeding activities have the potential to control eutrophication (Officer *et al.*,

1982) and significantly affect carbon cycling (Doering *et al.*, 1986). By depositing solid, nutrient rich fecal material and pseudo-feces, bivalves mediate a flux of organic matter and nutrients out of the water column and into the sediments (Smaal and Prins, 1993). This nutrient enrichment of sediments can increase the growth of seagrass, since seagrasses absorb most of their nutrients from the sediment through their roots and not from the water column (Peterson and Heck, 1999). Reusch *et al.* (1994) and Peterson and Heck (1999, 2001) showed that *Mytilus edulis* and *Modiolus americanus*, respectively, could increase seagrass productivity through sediment nutrient enrichment. By clearing micro-algal populations and other suspended particles from the water column, bivalves may serve as a control on marine (Cerrato *et al.*, 2004) and freshwater (Heath *et al.*, 1995) algal blooms. While the work of Cerrato *et al.* (2004) and the modeling efforts of Newell and Koch (2004) suggest that bivalve filtration could increase ambient light and perhaps enhance seagrass productivity, no previous study has directly examined this relationship.

During the past century, many estuarine bivalve populations have suffered from overharvesting and habitat loss (Jackson, 2001; Lotze *et al.*, 2006), an occurrence which could have secondary negative impacts on seagrass beds. Since bivalves may serve as a natural control on the effects of eutrophication (Officer *et al.*, 1982), the loss of these populations could result in decreases in light reaching the benthos, a factor which often limits eelgrass productivity in estuaries (Dennison and Alberte, 1985; Bintz and Nixon, 2001). Great South Bay, a shallow estuary on Long Island's south shore, has experienced an increase in eutrophication and frequent algal blooms, including harmful "brown tides" (*Aureococcus anophagefferens*; Gobler *et al.*, 2005). These changes were concurrent with the loss of seagrass beds (*Zostera marina*; Dennison *et al.*, 1989) and the removal of the dominant suspension feeding bivalve (*Mercenaria mercenaria*; Cerrato *et al.*, 2004). Similarly, in Chesapeake Bay the loss of oyster populations, *Crassostrea virginica*, has been hypothesized to have contributed to the demise of *Z. marina* in this system (Jackson, 2001; Newell and Koch, 2004; Kemp *et al.*, 2005; Lotze *et al.*, 2006).

For this study, the effects of various suspension feeding bivalves on the growth of the seagrass, *Zostera marina*, were examined. A eutrophied system was simulated by

loading nutrients to mesocosms containing various combinations of seagrass and bivalves. These experiments were designed to test the hypothesis that, in a eutrophied estuary, algal biomass would decrease and light penetration and seagrass productivity would increase as a function of bivalve filtration pressure.

Methods:

Five mesocosm experiments were carried out at the Stony Brook - Southampton Marine Science Center on Old Fort Pond in Southampton, New York from 18 May 2006 to 10 October 2006. Old Fort Pond exchanges tidally with Shinnecock Bay, one of the major Long Island south shore estuaries. The experiments were carried out in a series of 300 L polyethylene tanks (Nalgene©; depth 122 cm, inside diameter 60 cm), which have been used successfully in the past to examine the impacts of suspension-feeding bivalves on phytoplankton communities (Cerrato *et al.*, 2004). Prior to each experiment, all tanks were scrubbed, rinsed with fresh water, and then filled with seawater from Old Fort Pond. The mesocosms were ~90% immersed in Old Fort Pond to maintain a uniform ambient temperature. Small aquarium pumps (Rio® 180 Mini, pumping rate: 456 L h^{-1}) were added to mix the water column of each mesocosm, but were suspended only a few centimeters below the surface to minimize re-suspension of sediments or biodeposits. Measurements taken at the start of each experiment and every 1 -2 days during experiments included temperature, salinity, dissolved oxygen, chlorophyll *a*, and light attenuation. Surface and bottom readings of temperature and salinity during experiments confirmed that aquarium pumps kept the mesocoms well-mixed during experiments. Chlorophyll *a* (chl *a*) was measured by filtering mesocosm samples onto replicated GF/F filters and 5 μm polycarbonate filters, freezing and extracting in acetone, and measuring fluorescence with a Turner Trilogy fluorometer (Parsons *et al.*, 1984). Light was measured using a Li Cor LI-193 spherical underwater quantum sensor, and the light attenuation coefficient, K_d, was calculated from incoming irradiance and light at the bottom of the mesocosm using the following formula:

$$K_d = -\ln(\text{irradiance at depth}/\text{incoming irradiance})/z$$

To stimulate anthropogenic nutrient loading, all mesocosms received daily additions of ammonium (10 μM final concentration) and orthophosphate (0.625 μM final concentration), a nutrient loading rate which mimics rates found in more eutrophic regions of Long Island (Gobler and Boneillo, 2003).

Each mesocosm in all of the experiments contained a weighted plastic planter with clean sand and 12 shoots of the seagrass *Zostera marina*. *Zostera* shoots, 20-30 cm long, were harvested from eastern Shinnecock Bay on the day that each experiment commenced. Eelgrass was sorted to remove reproductive shoots, rinsed in seawater, separated into individual shoots with a segment of the attached rhizome, and marked with a small pinhole at the top of the sheath using an 18 gauge needle, according to the method of Zieman (1974). Twelve marked shoots were randomly assigned to each mesocosm. Shoots were gently buried in the planter, making sure the roots were intact and covered with sand, and the planters were carefully lowered to the bottom of the mesocosm.

Northern quahogs (*M. mercenaria*) and oysters (*C. virginica*) were locally harvested, and obtained from seafood markets while blue mussels (*M. edulis*) were collected by hand from Shinnecock Bay. Northern quahogs measured 52 ± 0.5 mm shell length, eastern oysters measured 85 ± 1 mm shell height, and blue mussels measured 39 ± 0.7 mm shell height (Table 1). Prior to each experiment, all bivalves were placed in a flowing seawater table for approximately 24 hr to acclimate to the temperature and salinity of Old Fort Pond. To eliminate any impact that the biodeposits might have on elevating productivity, bivalves and eelgrass shoots were separated by plastic dividers within the planter trays. Hard clams were partially buried with the siphon facing up, while mussels and oysters were simply placed on top of the planter.

At the end of each experiment, the planters with their seagrass shoots and bivalves were carefully removed from each mesocosm. Seagrass shoots that detached from the planter during the course of the experiment were not collected for further analysis. In the laboratory, the daily aboveground production and leaf epibiont biomass ($shoot^{-1}$) were determined. Seagrass shoots were collected and their growth was determined. Seagrass productivity was measured using a pin-hole marking technique (Zieman 1974) and

calculated for each experiment as leaf area productivity (cm^2 $shoot^{-1}$ d^{-1}) based on the growth of new leaf material from the shoots in each mesocosm. Epibiont mass was determined by scraping fouling organisms and algae form each leaf then drying them to a constant mass (± 0.01 mg) in an oven at 70°C.

Bivalves were retained after each experiment for the determination of lengths, widths, heights, and ash free dry weights. Twelve individuals were randomly selected for a clearance rate measurement using one of the methods outlined by Riisgard (2001). The 12 bivalves were placed individually in 1 L containers filled with water from one of the control mesocosm tanks which typically had high levels of chlorophyll a (> 20 μg L^{-1}). Experiments commenced when individuals were open and appeared to be feeding. Chl *a* samples taken before filtration and after a known length of time yielded a clearance rate for each individual according to the formula:

Clearance rate = (volume / time) * ln (initial chl *a* / final chl *a*)

The twelve individuals that were used for clearance rate measurements were then shucked, dried at 70°C, weighed, combusted at 450°C, and weighed again to determine ash-free dry weights of their tissues. These weights were used to normalize the clearance rates to tissue weight rather than to individual.

A "community" clearance rate for each mesocosm was estimated from these data using the average individual clearance rate multiplied by the number of individuals in the tank. This method assumed constant and continuous filtration from the bivalves in each tank. An estimated turnover time for the entire tank volume to pass through the bivalves was calculated for each tank by dividing the tank volume by this community clearance rate.

Experiment 1:

Experiment 1 was carried out for 18 days, from 18 May to 5 June, using the northern quahog *Mercenaria mercenaria*. There were two experimental treatments with 16 *M. mercenaria* per tank for a density of 57 individ. m^{-2} and a control treatment with no bivalves added (n = 4 for each treatment). This density is comparable to historical

densities of 53-105 clams m^{-2} for Great South Bay (Cerrato *et al.*, 2004). Modern densities of *M. mercenaria* in Great South Bay are two magnitudes of order lower ranging from 0.5 to 2 individuals m^{-2} (B. Peterson, pers obs). For all experiments, replicates for each treatment were placed among the array of mesocosms using a randomized blocks design (Sokal & Rohlfe, 1995) to minimize any effects due to placement of the mesocosm tank.

Experiment 2:

Experiment 2 was carried out for 12 days, from 7 June to 19 June, also with hard clams. There were two experimental treatments with 4 and 8 *M. mercenaria* added for densities of 14 and 29 individ. m^{-2}, respectively, and one control treatment (n = 4 for each treatment).

Experiment 3:

Experiment 3 was carried out for 8 days, from 20 June to 28 June, this time with the oyster *Crassostrea virginica*. The control treatment had no oysters while the two experimental treatments had 2 and 4 oysters added for densities of 7 and 14 individ. m^{-2}, respectively (n = 4 for each treatment). These densities are much higher than modern densities of oysters in Chesapeake Bay, estimated by Newell & Koch (2004) to be 0.43 individ. m^{-2}, but lower than historical densities which are estimated to have been as low as 43 individ. m^{-2} or as high as 150 individ. m^{-2} in a dense oyster reef habitat (Newell & Koch, 2004).

Experiment 4:

Experiment 4 was carried out for 8 days from 6 July to 14 July. Only one experimental treatment of 1 oyster per mesocosm (4 individ. m^{-2}) was contrasted with the control (n = 4 for each treatment).

Experiment 5:

Experiment 5 was the only experiment using blue mussels, *Mytilus edulis*, and was carried out for 14 days from 26 September to 10 October. The control treatment was

contrasted with two experimental treatments of 16 and 64 mussels per mesocosm for densities of 57 and 229 individ. m^{-2}, respectively (n = 4 for each treatment). These densities are commonly found in some areas of Long Island, but are much lower than those found in dense mussel beds in nearby Narragansett Bay, Rhode Island (814 – 9943 individ. m^{-2}; Altieri and Witman, 2006).

Statistical analysis:

To compare differences in seagrass productivity between treatments, one-way analysis of variance (ANOVA) and Tukey multiple comparison tests were carried out using the program SigmaStat 3.0. The dry weight of epiphytes on the seagrass was normalized by the area of the seagrass leaves, and also analyzed by treatment for each experiment using a one-way ANOVA. Since experiments 1 and 4 had only two treatments, *t*-tests were used in place of one-way ANOVAs. Chlorophyll *a* concentrations and light attenuation were analyzed for each experiment using a two-way repeated measures analysis of variance (ANOVAR), with treatment and day as factors. A linear regression was used to examine correlations between leaf area production and light attenuation. All values in text are reported as mean ± standard error (mean ± SE).

Results:

Experiment 1:

The temperature for all mesocosms in experiment 1 was 19.1°C ± 0.6 and the salinity was 21.96 ± 0.09. There was a remarkable difference in chl *a* concentrations over the course of the experiment between the control, which was 34.08 ± 9.54 μg L^{-1}, and the clam treatment, which was 3.04 ± 0.38 μg L^{-1} (Fig 1.1A). Through the experiment, the percentage of phytoplankton biomass in the >5 μm size fraction, as measured by chl *a*, was 33.4 ± 4.0% in the control treatment and 38.3 ± 6.7% in the "clams" treatment. The control treatment had greater light attenuation (1.101 ± 0.139 m^{-1}) than the clam treatment (0.814 ± 0.190 m^{-1}; Fig 1.1B). For this experiment, chl *a* concentrations and light attenuation varied significantly by treatment (Two-way

ANOVAR, $p<0.001$ for chl *a* and $p<0.01$ for light attenuation) and by day ($p<0.001$ for both). Concurrently, the leaf area productivity of the eelgrass in the control treatment (0.318 ± 0.02 cm^2 shoot^{-1} d^{-1}) was significantly lower than eelgrass productivity in the the "clams" treatment (0.462 ± 0.04 cm^2 shoot^{-1} d^{-1}; *t*-test, $p<0.05$; Fig 1.1C). The estimated turnover time due to bivalve filtration of the water in the "clams" treatment was 1.1 days (Table 1.1).

Experiment 2:

The average temperature for all mesocosms in experiment 2 was 20.3°C ± 0.6 and the average salinity was 26.29 ± 0.05. From day 2 to day 9, chl *a* values were consistently lowest in the high density clam treatment (24.31 ± 7.67 µg L^{-1}), intermediate in the low density clam treatment (33.85 ± 9.85 µg L^{-1}), and highest in the control (45.22 ± 14.33 µg L^{-1}; Fig 1.2A). The percentage of phytoplankton biomass in the >5 µm size fraction, as measured by chl *a*, was 32.2 ± 2.8% in the control treatment, 35.2 ± 3.5% in the low density treatment, and 37.6 ± 4.0% in the high density treatment. Light attenuation showed a similar pattern through day 8, with K_d being lowest in the high density treatment (0.648 ± 0.158 m^{-1}), intermediate in the low density treatment (0.813 ± 0.160 m^{-1}), and highest in the control (0.960 ± 0.203 m^{-1}; Fig 1.2B). Accordingly, chl *a* concentrations and light attenuation varied significantly by treatment and by day (Two-way ANOVAR, $p<0.001$ in all cases). The low clam density (14 individ. m^{-2}) treatment produced a leaf area productivity (0.832 ± 0.04 cm^2 shoot^{-1} d^{-1}), similar to that of the high density (29 individ. m^{-2}) treatment (0.806 ± 0.04 cm^2 shoot^{-1} d^{-1}). Eelgrass shoots in both clam treatments were significantly more productive than the control treatment (0.642 ± 0.07 cm^2 shoot^{-1} d^{-1} (Fig 1.2C; Tukey test, $p<0.05$). The estimated turnover time was 2.2 days for the high density treatment and 4.5 days for the low density treatment (Table 1.1).

Experiment 3:

The average temperature for all mesocosms in experiment 3 was 23.2°C ± 0.5 and the average salinity was 24.23 ± 0.56. As in experiment 2, a clear gradation in chl *a* levels was observed between the high density (11.05 ± 4.18 µg L^{-1}) oyster treatment, the low density (15.75 ± 7.40 µg L^{-1}) oyster treatment, and the control (25.64 ± 9.78 µg L^{-1};

Fig 1.3A). The percentage of phytoplankton biomass in the >5 μm size fraction, as measured by chl *a*, was 38.0 ± 1.7% in the control treatment, 35.2 ± 3.5% in the low density treatment, and 34.0 ± 2.5% in the high density treatment. Light attenuation had similarly consistent pattern over days 1-5; K_d was lowest in the high density treatment (1.502 ± 0.268 m^{-1}), intermediate in the low density treatment (1.586 ± 0.229 m^{-1}), and highest in the control (1.726 ± 0.224 m^{-1}; Fig 1.3B). Chlorophyll *a* concentrations varied significantly by treatment and by day (Two-way ANOVAR, $p<0.001$ in both cases); light attenuation varied significantly by treatment over days 1-5 (Two-way ANOVAR, $p<0.05$) and significantly by day (Two-way ANOVAR, $p<0.001$). Leaf area productivity was significantly higher in both the low density (0.495 ± 0.03 cm^2 $shoot^{-1}$ d^{-1}) and high density (0.548 ± 0.02 cm^2 $shoot^{-1}$ d^{-1}) treatments than in the control treatment (0.371 ± 0.03 cm^2 $shoot^{-1}$ d^{-1}; Tukey test, $p<0.05$ and $p<0.01$, respectively; Fig 1.3C). The estimated turnover times were 0.6 for the high density of oysters and 1.3 days for the low density treatment (Table 1.1).

Experiment 4:

The average temperature for all mesocosms in experiment 4 was 24.6°C ± 0.2 and the average salinity was 21.37 ± 0.09. Experiment 4 produced a clear difference in chl *a* concentrations between the control and oyster treatment that was mirrored by changes in algal biomass and light levels. The chl *a* levels in the control (49.16 ± 7.36 μg L^{-1}) were higher than in the oyster treatment (31.82 ± 4.57 μg L^{-1}; Fig 1.4A) while light attenuation was also higher in the control (1.688 ± 0.094 m^{-1}) than in the oyster treatment (1.239 ± 0.131 m^{-1}; Fig 1.4B). The percentage of phytoplankton biomass in the >5 μm size fraction, as measured by chl *a*, was 34.3 ± 4.7% in the control treatment and 28.4 ± 4.4% in the oyster treatment. Chlorophyll *a* concentrations varied significantly by treatment and by day (Two-way ANOVAR, $p<0.05$ and $p<0.01$, respectively). Light attenuation also varied between treatments and by day (Two-way ANOVAR, $p<0.05$ and $p<0.001$, respectively). Leaf area productivity was significantly higher in the experimental treatments with 4 oysters m^{-2} (0.560 ± 0.02 cm^2 $shoot^{-1}$ d^{-1}) than in the control treatments (0.355 ± 0.04 cm^2 $shoot^{-1}$ d^{-1}; two-tailed *t*-test, $p<0.01$; Fig 1.4C). The turnover time for the oyster treatment was 2.5 days (Table 1.1).

Experiment 5:

The average temperature for all mesocosms in experiment 5 was 19.3°C ± 0.7 and the average salinity was 28.88 ± 0.09. Unlike experiments 2 and 3, there was not a consistent relationship between mussel density and chl *a* levels; chl *a* was actually higher in the low density treatment than in the control treatment on day 7. The high density mussel treatment, however, had consistently lower chl *a* (15.45 ± 5.40 μg L^{-1}) than the low density treatment (40.11 ± 8.16 μg L^{-1}) and the control (40.37 ± 7.43 μg L^{-1}; Fig 1.5A). The percentage of phytoplankton biomass in the >5 μm size fraction, as measured by chl *a*, was 24.8 ± 5.2% in the control treatment, 29.2 ± 2.5% in the low density treatment, and 14.2 ± 5.4% in the high density treatment. Chlorophyll *a* levels varied significantly by treatment and by day (Two-way ANOVAR, $p<0.05$ and $p<0.001$, respectively). Unfortunately, we were not able to obtain light data for experiment 5, although the water in the high density mussel treatment was visibly clearer than the low density treatment and the control. Leaf area productivity was 0.790 ± 0.11 cm^2 $shoot^{-1}$ d^{-1} in the treatments with a high density (229 individ. m^{-2}) of mussels, 0.435 ± 0.02 cm^2 $shoot^{-1}$ d^{-1} in the low density (57 individ. m^{-2}) treatment, and 0.399 ± 0.08 cm^2 $shoot^{-1}$ d^{-1} in the control treatment (Fig 1.5B). The productivity was significantly higher in the high density treatment but did not significantly differ between the low density and the control treatments (1-way ANOVA and Tukey multiple comparison, $p<0.05$). The estimated turnover times were 3.6 days for the high density of mussels and 14.5 days for the low density of mussels (Table 1.1).

Bivalve filtration rates, turnover times, and facilitation of eelgrass productivity:

Length, weight, and clearance rate measurements were recorded for each group of bivalves (Table 1.1). In all cases, the bivalves cleared water taken from one of the control tanks at a significant rate (Table 1.1). *Crassostrea virginica*, which had the highest individual and weight-specific clearance rates (1.91 ± 0.97 L hr^{-1} g^{-1} AFDW), produced the shortest estimates for mesocosm turnover time (0.6 – 2.5 d; Table 1), followed by *M. mercenaria* (clearance rate = 0.41 ± 0.24 L hr^{-1} g^{-1} AFDW; turnover time = 1.1 – 4.5 d), and *M. edulis* (clearance rate = 0.29 ± 0.29 L hr^{-1} g^{-1} AFDW; turnover time

= 3.6 – 14.5 d). Epibiont biomass, as measured by mg AFDW of epibionts cm $^{-2}$ leaf area, did not differ significantly among treatments in any experiment (data not shown).

During our experiments, higher densities of bivalves produced dramatic decreases in water column chl *a* over the course of each experiment (Fig 1.1A,1.2A,1.3A,1.4A,1.5A). Experiments 1 through 4 also had significant decreases in light attenuation in the treatments with bivalves (Fig 1.1B,1.2B,1.3B,1.4B). There was a significant inverse correlation (Fig 6; $r^2 = 0.400$, $p<0.001$) between leaf area productivity and mean light attenuation coefficient for experiments 1 through 4 (light attenuation data was not available for experiment 5). There was also a significant inverse correlation between mesocosm turnover time (Table 1.1) and leaf area productivity among all experiments ($y = -0.015x + 0.647$, $r^2 = 0.21$, $p<0.05$; regression not shown).

Discussion:

This study has demonstrated, through a series of mesocosm experiments, that suspension-feeding bivalves can facilitate the growth of eelgrass. Over the course of five experiments, the effects of three densities of *Mercenaria mercenaria*, three densities of *Crassostrea virginica*, and two densities of *Mytilus edulis* were examined. In all cases, the highest density of bivalves produced significant decreases in chl *a*, increases in light penetration, and significant increases in leaf area productivity of *Zostera marina*. On average, eelgrass growth increased by 48 ± 9.3% in the presence of moderate densities of bivalves relative to control treatments. For *M. mercenaria* and *C. virginica*, intermediate or even low densities of these species filtered sufficiently to alter light and chl *a* levels to the benefit of eelgrass productivity. The results of these experiments help to refine our understanding of the function of suspension-feeding bivalves in estuarine ecosystems.

Some studies have suggested that suspension-feeding bivalves can control algal blooms and mediate the effects of eutrophication (Officer *et al.*, 1982; Cerrato *et al.*, 2004; Cloern, 1982) or significantly alter carbon-cycling (Doering *et al.*, 1986). Newell and Koch's (2004) modeling study predicted that filtration by bivalves could benefit

seagrass. To our knowledge, this is the first study that demonstrates the facilitation of eelgrass growth by the suspension feeding of bivalves in an experimental setting. The mechanism of facilitation is an increase in light penetration (Fig 1.1B,1.2B,1.3B,1.4B), paired with dramatic reductions in the standing stocks of phytoplankton (Fig 1.1A,1.2A,1.3A,1.4A,1.5A), due to clearance of the water column by the bivalves. Resuspended sediment or detrital particles can attenuate light and shade benthic plants just as easily as phytoplankton. Newell and Koch (2004) found that a sufficient density of suspension-feeding bivalves would remove both phytoplankton and resuspended sediment to the benefit of seagrasses. Other studies (Reusch *et al.*, 1994; Peterson and Heck, 2001) have demonstrated that nutrient fertilization by bivalves through biodeposition can enhance growth of seagrass. Peterson and Heck's (2001) study was carried out in St. Joseph Bay, Florida, an oligotrophic environment where light was plentiful and nutrients were scarce. Because of the eutrophic nature of a great number of estuaries (Nixon, 1995; de Jonge *et al.*, 2002; Kemp *et al.*, 2005; Valiela, 2006), mitigation of light limitation may be an even more common mechanism by which bivalve filtration benefits seagrass populations. This study was not designed to separate the relative contributions of nutrient fertilization and water transparency effects on seagrasses by bivalves in eutrophic estuaries.

During our experiments, higher densities of bivalves produced dramatic decreases in water column chl *a* and light attenuation (Fig 1.1,1.2,1.3,1.4,1.5), and there was a significant inverse correlation (Fig 6; $r^2 = 0.400$, $p<0.001$) between leaf area productivity and mean light attenuation coefficient. The decreases in chl *a*, increases in light penetration, and correlation between leaf area productivity and light levels suggest that the principal effect of the bivalves on eelgrass growth was mediated by clearing of the water column leading to increased light penetration. During our experiments, chlorophyll *a* levels tended to decrease in all the mesocosms ($\leq$20 µg chl *a* L^{-1}) toward the end of each experiment (Fig 1.1A,1.2A,1.3A,1.4A,2.5A), likely due to the development of high levels of phytoplankton biomass (> 60 µg chl *a* L^{-1}) which created a nutrient demand that greatly exceeded our nutrient loading rate (10 µM ammonium and 0.625 µM orthophosphate daily). Had our nutrient loading rate increased concurrently with increasing phytoplankton biomass to sustain the high biomass levels throughout the

experiment, the significant differences in seagrass productivity between control and shellfish treatments would have likely been even larger than observed (Fig 1.1C,1.2C,1.3C,1.4C,1.5B).

The depth of the water column in our experiments was 1.2 m, a depth comparable to some northeast US lagoons such as Great South Bay, Waquoit Bay (Valiela *et al.*, 1992), and Barnegat Bay (Bologna *et al.*, 2005) or European estuaries such as the Wadden Sea (Smaal and Prins, 1993), but shallower than systems such as Chesapeake Bay (Kemp *et al.*, 2005), San Francisco Bay (Officer *et al.*, 1982), or the Baltic Sea (Smaal and Prins, 1993). Smaal and Prins (1993) surveyed bivalve suspension feeding in several European estuaries and defined "filtration pressure" as the ratio of bivalve consumption to phytoplankton production in the overlying water column. Obviously, as the water column depth increases, the density of benthic suspension feeders required to balance the production in the overlying water column also increases. Smaal and Prins (1993) suggested that a density of 2 to 8 g AFDW bivalve tissue m^{-3} of water column was enough for bivalve suspension feeders to exert a strong influence on the overlying water column. Our experimental bivalve densities (7.5 – 79.1 g AFDW m^{-3}) met or exceeded this range of biomass, indicating that all of our experimental bivalve densities should have been able to clear the volume of the mesocosms. The lowest density of mussels, which did not exert a significant influence on chl *a*, light, or eelgrass growth, had a biomass of 9.1 g AFDW m^{-3}, above Smaal and Prins' (1993) mass requirement. This suggests that the individual or weight-specific clearance rate of a given suspension feeder may be more important than the total biomass or that lower temperatures present during this final experiment contributed to lower clearance rates.

Some recent studies have focused on the turnover time, or clearance time, for suspension feeders to filter the volume of a body of water (Cerrato *et al.*, 2004; Newell and Koch, 2004; Bologna *et al.*, 2005). In a previous mesocosm experiment with *Mercenaria mercenaria*, Cerrato *et al.* (2004) found that clearance times of 0.51 to 2.4 days were sufficient to prevent the development of dense brown tide blooms, while blooms proliferated at clearance times of 3.7 days or longer. In the present study,

clearance times based upon the measured clearance rates of bivalves used in our experiments, ranged from 0.64 days for our highest density of oysters to 14.5 days for our lowest density of mussels (Table 1.1). Interestingly, at the longest clearance time of 14.5 days, chl *a* levels and eelgrass growth in the low-density mussel treatment were not significantly different from the control. The clearance time (4.5 days) for the lowest density of hard clams, while longer than the critical values in Cerrato *et al.*'s (2004) study, did produce a significant decrease in chl *a* and a significant increase in eelgrass growth. All other clearance times were ≤ 3.6 days and also produced significant increases in eelgrass growth. Since these clearance times are based on clearance measurements for bivalves placed in water with high algal biomass (>20 μg l^{-1} chl *a*), clearance rates for bivalves feeding at lower concentrations of chl *a* may have been higher (Clausen and Riisgard, 1996).

The results of these mesocosm experiments, combined with the work of Officer *et al.* (1982), Cloern (1982), Cerrato *et al.* (2004), Newell and Koch (2004), and many others, suggest that dense communities of benthic suspension feeders can serve as a control on the negative effects of eutrophication. Clearly, this process benefits seagrass productivity through increased light penetration (Fig 1.1C,1.2C,1.3C,1.4C,1.5B). There are likely many other synergistic interactions between bivalves and seagrasses that facilitate growth and recruitment of both clades, perhaps to the benefit of entire ecosystems. Bivalves clear the water column and increase light penetration for seagrasses and benthic diatoms (Lotze *et al.*, 2006), while seagrasses provide habitat, predation refuges, and a benthic source of oxygen for bivalves and other organisms (Valiela *et al.*, 1992; Reise, 2002; Bruno *et al.*, 2003; Bologna *et al.*, 2005). Bivalves also fertilize seagrass roots through biodeposition (Peterson and Heck, 1999, 2001). Seagrasses can minimize benthic nutrient fluxes to the water column by stabilizing sediments and absorbing sediment pore-water nutrients (Reise, 2002; Bruno *et al.*, 2003). Together with bivalve filtration, these effects can reduce suspended sediment load and minimize pelagic phytoplankton abundances (Newell and Koch, 2004; Lotze *et al.*, 2006). The presence of dense bivalve and seagrass beds may both exert longer-term controls on eutrophication through the removal of nitrogen. Bivalve biodeposits facilitate

removal of nitrogen as N_2 gas through denitrification (Newell *et al.* 2002, Seitzinger *et al.* 2006) while seagrasses remove nitrogen through direct uptake (Welsh *et al.* 2000).

Recently, Pomeroy et al (2006) have suggested that oyster restoration would be unlikely to counter the effects of eutrophication in Chesapeake Bay, MD, USA, due to temporal and spatial decoupling of bivalve filtration pressure and algal blooms in this system. While these authors present several valid arguments, their points do not apply to the current study for the following reasons. Our mesocosms were meant to mimic a shallow, lagoon-type estuary, such as Long Island's (NY, USA) south shore estuaries, which have a mean depth of 1.2 m (Wilson *et al.* 1991). In these systems, the water column is chronically well-mixed (Wilson *et al.* 1991) and bivalves are evenly distributed (Weiss *et al.* 2007), suggesting bivalves, algal blooms, and seagrasses should be more spatially coupled than in Chesapeake Bay. In addition, eelgrass growth and maximum filtration rates of bivalves coincide during late spring through fall months (Grizzle *et al.* 2001, Hemminga and Duarte 2001), providing a close temporal link between bivalves and eelgrass in temperate lagoonal systems.

A productive, high-biomass benthic community seems to be one of the hallmarks of a healthy estuary, and many anthropogenic insults drive estuaries into phytoplankton- and microbial-dominated systems at the expense of the benthic community (Jackson, 2001; Kemp *et al.*, 2005; Lotze *et al.*, 2006). These experiments indicate that a healthy benthos (robust bivalves and seagrass populations) is more resistant to eutrophication than seagrass alone. Estuaries become more vulnerable to eutrophication, algal blooms, hypoxia, and degradation of benthic habitats when overharvesting or habitat loss removes the filtration pressure of bivalves. For example, Cerco and Noel's (2007) modeling study predicted a ten-fold increase in oyster biomass in Chesapeake Bay would lead to decreases in phytoplankton biomass and benthic nutrient fluxes, and increases in dissolved oxygen and submerged aquatic vegetation (SAV).

The bivalve densities used in our mesocosms (14-57 clams m^{-2} and 4-14 oysters m^{-2}) were higher than current densities in many US estuaries such as Great South Bay or Chesapeake Bay, but were lower than historical densities found in these same systems

(53-105 clams m^{-2}, mid-20^{th} century, Cerrato *et al.* 2004; 43-150 oysters m^{-2}, late 19^{th} century, Newell and Koch 2004). Jackson (2001) and Lotze *et al.* (2006) surveyed historical declines across a broad suite of organisms and habitats, and found that overharvesting and habitat destruction preceded eutrophication in most estuaries. As such, it would seem successful management efforts will need to take an 'ecosystem-based' approach which incorporates habitat conservation, shellfish restoration, and restrictions on nutrient loading to restore healthy estuarine function. In light of the results from this study, it appears that even a partial recovery of shellfish populations could help combat eutrophication and have a beneficial impact on seagrass habitats in shallow, eutrophied estuaries.

Bivalve species	Size (longest shell dimension, mm)	Ash-free dry tissue weight (g AFDW)	Clearance rate measured (L h^{-1} g^{-1} AFDW)	Estimated Turnover Time (days)
Hard Clam, (Quahog) *Mercenaria mercenaria*	52.2 ± 0.5	1.688 ± 0.158	0.41 ± 0.03	14 Clams m^{-2}: 4.5d 29 Clams m^{-2}: 2.2 d 57 Clams m^{-2}: 1.1 d
Eastern Oyster, *Crassostrea virginica*	84.5 ± 1.1	2.564 ± 0.149	1.91 ± 0.28	4 Oysters m^{-2}: 2.5 d 7 Oysters m^{-2}: 1.3 d 14 Oysters m^{-2}: 0.6 d
Blue Mussel, *Mytilus edulis*	39.0 ± 0.7	0.195 ± 0.020	0.289 ± 0.097	57 Mussels m^{-2}: 14.5 d 229 Mussels m^{-2}: 3.6 d

Table 1.1. Mean sizes, weights, and AFDW-normalized clearance rates for the three bivalve species. Measurements were taken once per species, and mean individual clearance rates were used to estimate turnover times. All measures are mean ± SE.

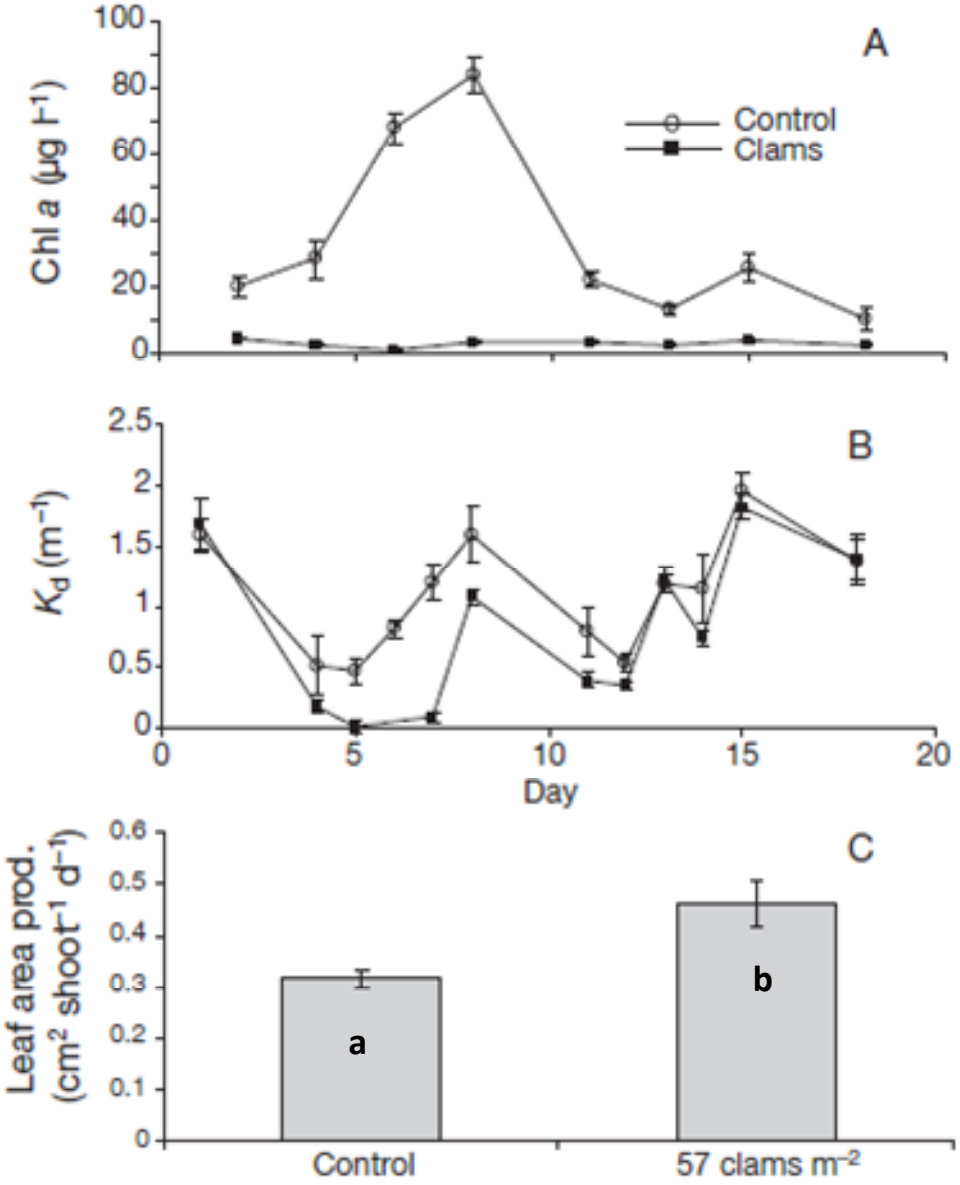

Figure 1.1. Temporal changes in (A) chlorophyll *a* (chl a µg L^{-1}) and (B) extinction coefficient (K_d m^{-1}) for experiment 1. C) Differences in eelgrass leaf area production, different letters indicate significance. Clams are *Mercenaria mercenaria*. All error bars are ± SE.

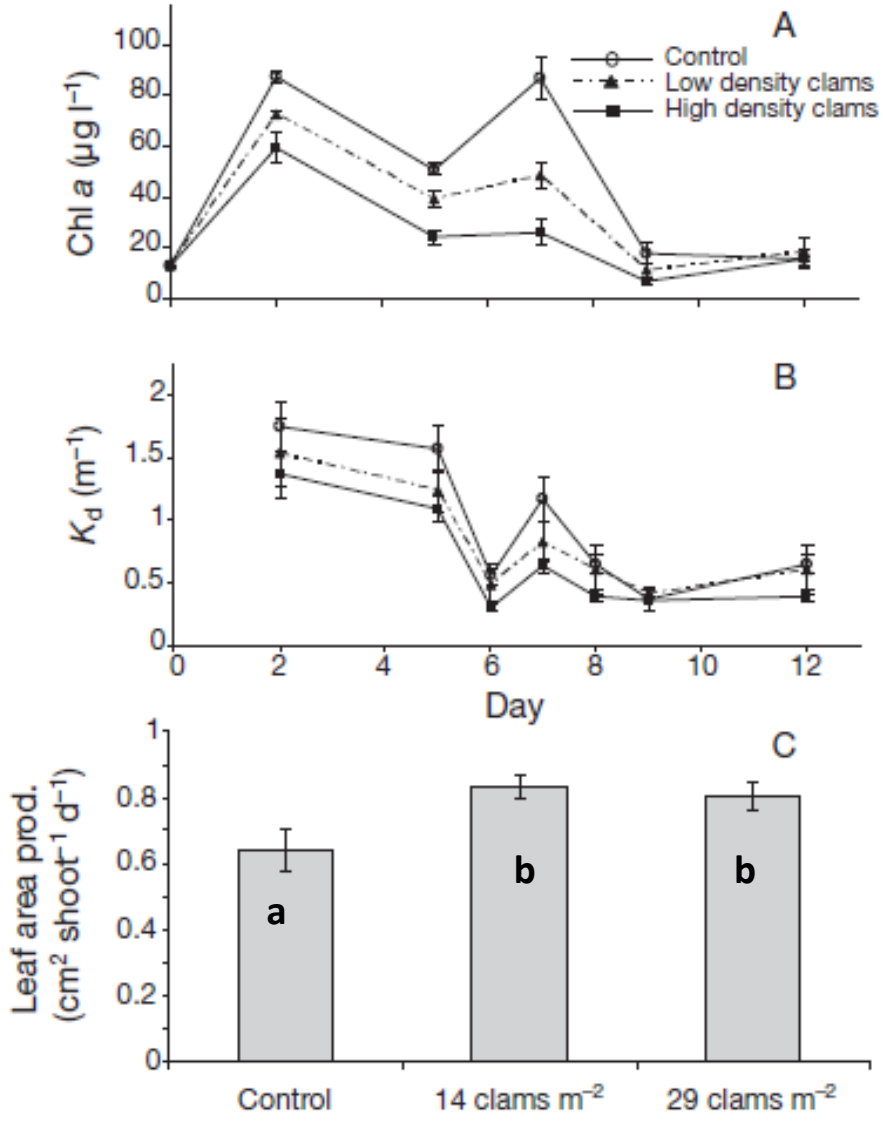

Figure 1.2. Temporal changes in (A) chlorophyll *a* (chl a µg L^{-1}) and (B) extinction coefficient (K_d m^{-1}) for experiment 2. C) Differences in eelgrass leaf area production, different letters indicate significance. Clams are *Mercenaria mercenaria*. All error bars are ± SE.

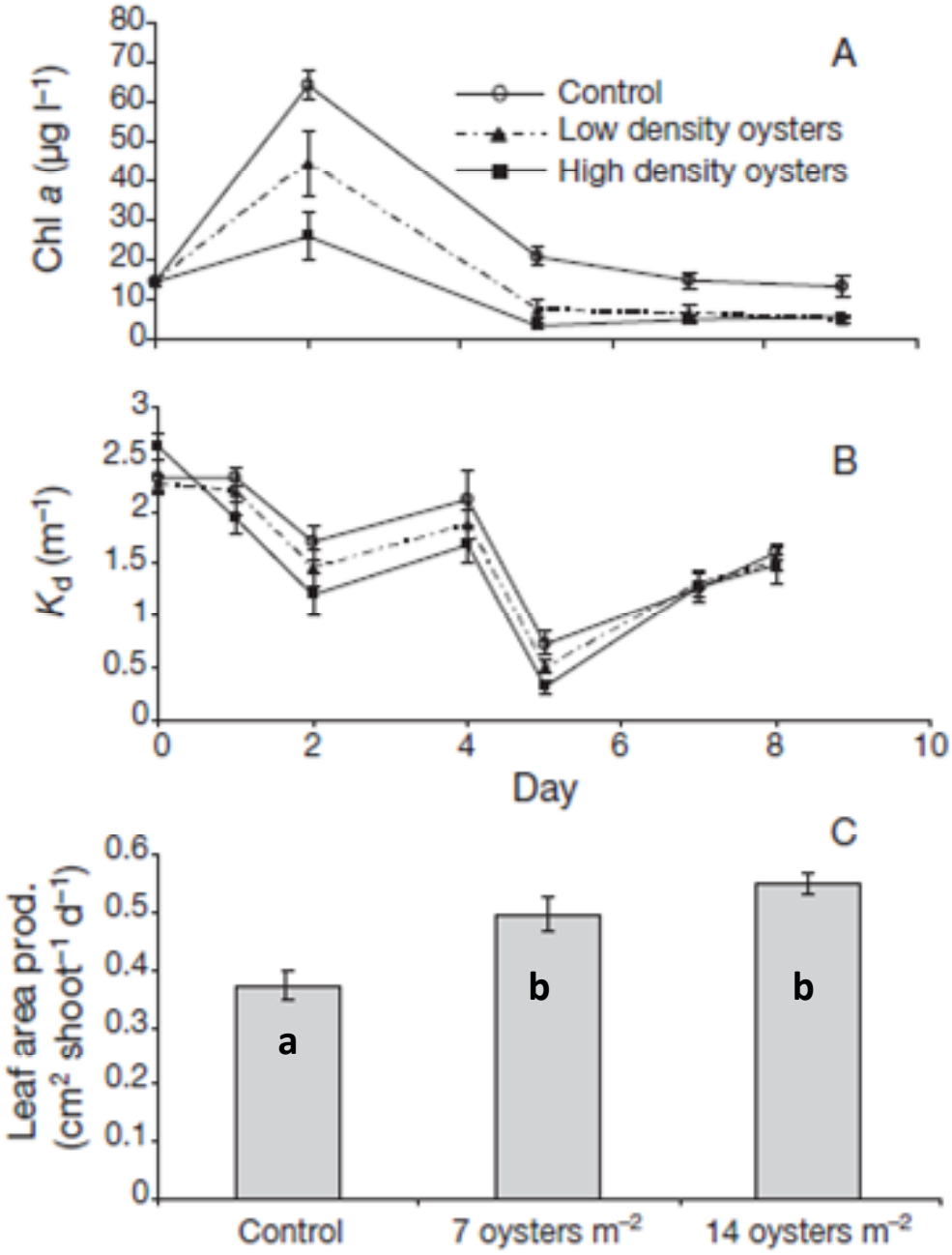

Figure 1.3. Temporal changes in (A) chlorophyll *a* (chl a µg L^{-1}) and (B) extinction coefficient (K_d m^{-1}) for experiment 3. C) Differences in eelgrass leaf area production, different letters indicate significance. Oysters are *Crassostrea virginica*. All error bars are ± SE.

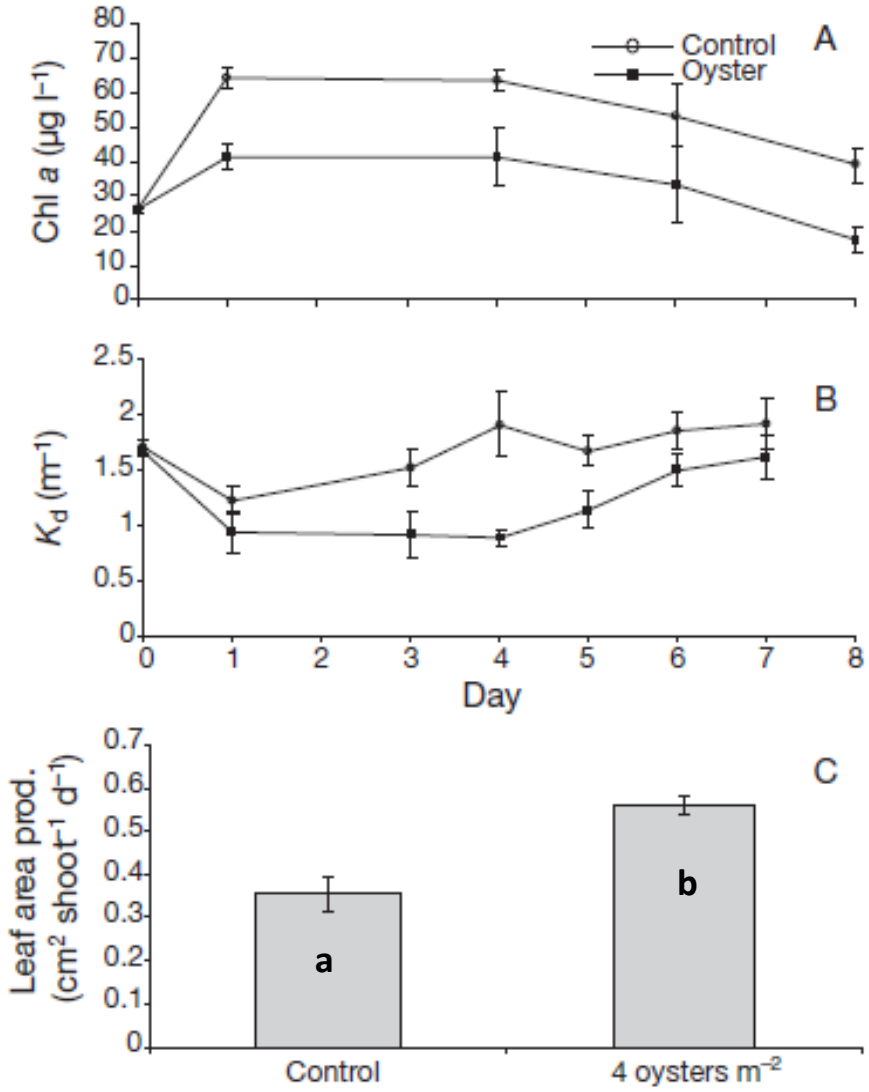

Figure 1.4. Temporal changes in (A) chlorophyll *a* (chl a µg L^{-1}) and (B) extinction coefficient (K_d m^{-1}) for experiment 4. C) Differences in eelgrass leaf area production, different letters indicate significance. Oysters are *Crassostrea virginica*. All error bars are ± SE.

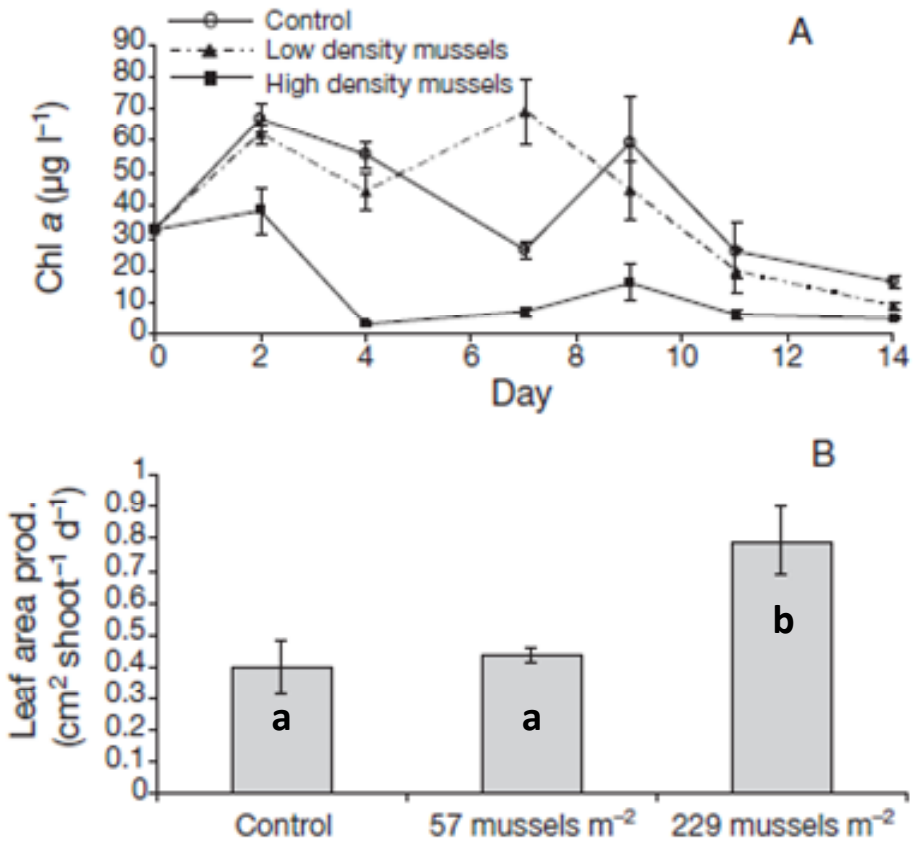

Figure 1.5. Temporal changes in (A) chlorophyll *a* (chl a µg L^{-1}) for experiment 5. B) Differences in eelgrass leaf area production, different letters indicate significance. Mussels are *Mytilus edulis*. All error bars are ± SE.

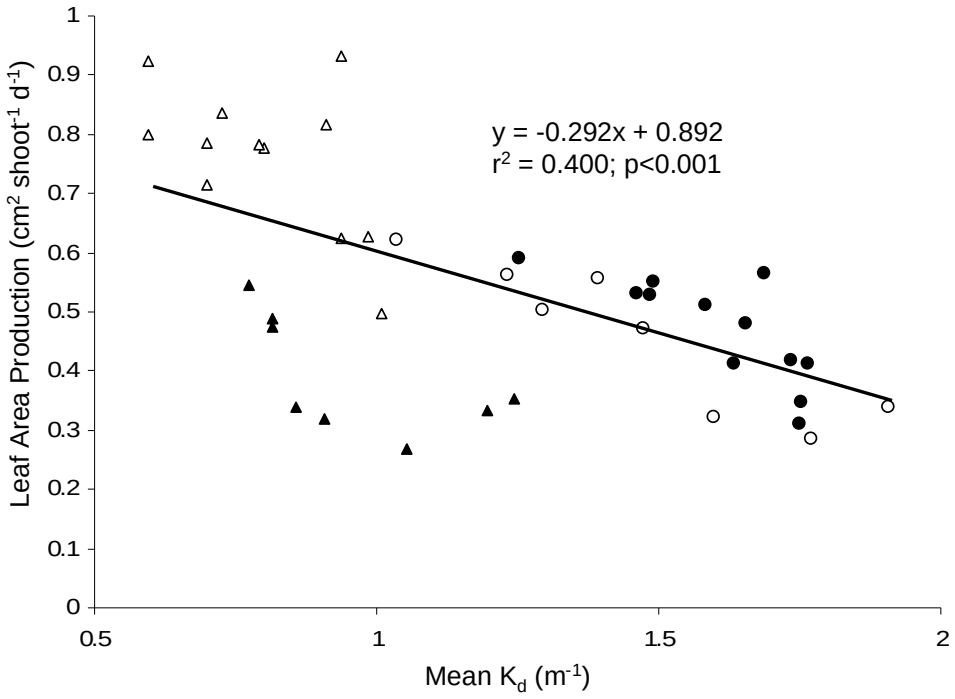

Figure 6

Figure 1.6. Changes in leaf area productivity as a function of mean K_d for all tanks from experiments 1-4. Symbols are as follows: ▲, experiment 1; Δ, experiment 2; ●, experiment 3; ○, experiment 4.

II. The growth of estuarine resources (*Zostera marina, Mercenaria mercenaria, Crassostrea virginica, Argopecten irradians, Cyprinodon variegatus*) in response to nutrient loading and enhanced suspension feeding by adult shellfish

Abstract:

While many coastal ecosystems previously supported high densities of seagrass and abundant bivalves, the impacts of overfishing, eutrophication, harmful algal blooms, and habitat loss have contributed to the decline of these important resources. Despite improvements in wastewater treatment in some watersheds and subsequent reduced nutrient loading to neighboring estuaries, seagrass and bivalve populations in these locations have generally not recovered. We performed three mesocosm experiments to simultaneously examine the effects of nutrient loading and historic suspension-feeder densities on the growth of eelgrass (*Zostera marina*), juvenile bivalves (hard clams, *Mercenaria mercenaria*, eastern oysters, *Crassostrea virginica*, and bay scallops, *Argopecten irradians*), and juvenile fish (sheepshead minnow, *Cyprinodon variegatus*). High nutrient loading rates led to significantly higher phytoplankton (chlorophyll *a*) levels in all experiments, significantly increased growth of juvenile bivalves relative to controls with lower nutrient loading rates in two experiments, and significantly reduced the growth of eelgrass in one experiment. The filtration provided by adult suspension-feeders (*M. mercenaria* and *C. virginica*) significantly decreased phytoplankton levels in all experiments, significantly increased light penetration and the growth of eelgrass in one experiment, and significantly decreased the growth of juvenile bivalves and fish in two experiments, all relative to controls with no filtration from adult suspension-feeders. These results suggest that an appropriate level of nutrient loading can have a positive effect on some estuarine resources, and that bivalve filtration can mediate the effects of nutrient loading to the benefit or detriment of different estuarine resources. Future ecosystem-based approaches will need to simultaneously account for anthropogenic nutrient-loading and bivalve restoration to successfully manage estuarine resources.

Introduction:

Estuaries are home to a variety of valuable living resources. Finfish and shellfish are harvested directly in commercial and recreational fisheries, while seagrass beds are considered of paramount importance as structural habitat for shellfish and finfish in many coastal areas (Heck and Wetstone 1977, Irlandi and Peterson 1991, Beck *et al.* 2001). Many of the world's estuaries currently support lower abundances of finfish, shellfish, and seagrasses than they did historically due to overfishing (Jackson *et al.* 2001, Lotze *et al.* 2006), habitat loss (Orth *et al.* 2006), eutrophication (Nixon 1995, de Jonge *et al.* 2002), and harmful algal blooms (Hallegraeff 1993, Gobler *et al.* 2005, Sunda *et al.* 2006). As such, estuarine management plans are typically focused on combating these harmful processes and restoring living resources (Cloern 2001, Newell 2004, Lotze *et al.* 2006).

Changes in inorganic nutrient loading to estuaries can indirectly influence the growth of marine resource species. High rates of nutrient loading have been associated with increases in pelagic productivity, decreased water clarity, hypoxia, and declines in seagrass growth and abundances (Short *et al.* 1995, Diaz and Rosenberg 2008, Wall *et al.* 2008). In response, estuarine management efforts often focus primarily on reducing anthropogenic nutrient loading in an effort to curb the negative effects of eutrophication (Cloern 2001, de Jonge *et al.* 2002). However, some level of nutrient loading must be necessary to sustain primary and secondary production (Nixon and Buckley 2002). Higher levels of inorganic nutrients can enhance primary production rates and can favor larger phytoplankton cells (Malone 1980, Raven and Kubler 2002), such as diatoms and prymnesiophytes, which are generally considered a good source of nutrition for bivalves (Beukema and Cadee 1991, Wikfors *et al.* 1992, Weiss *et al.* 2007). Studies in several estuaries have shown that blue mussels (*Mytilus edulis*), hard clams (*Mercenaria mercenaria*), and softshell clams (*Mya arenaria*) can respond positively to increased nitrogen loading and high chlorophyll *a* levels in their habitats (van Stralen and Dijkema 1994, Weiss *et al.* 2002, Carmichael *et al.* 2004, Weiss *et al.* 2007). Weiss *et al.* (2002) and Carmichael *et al.* (2004) found that shell growth, soft tissue growth, and survival of *M. mercenaria* and *M. arenaria* increased along a naturally-occurring gradient of

nitrogen loading in Waquoit Bay, Massachusetts, USA. They attribute these changes to increased quantity and quality of food particles due to nitrogen enrichment (Carmichael and Valiela 2005), although a similar response has not been found for bay scallops (*Argopecten irradians*, Shriver *et al.* 2002). While nutrient over-loading in estuaries has a well-known set of negative consequences (Valiela *et al.* 1992, Nixon 1995, Kemp *et al.* 2005), the stimulation of secondary production in bivalves could be an overlooked positive effect of nutrient loading (Nixon and Buckley 2002, Carmichael *et al.* 2004, Carmichael and Valiela 2005), especially in shallow ecosystems with well-mixed water columns that rarely experience hypoxia.

As described in many studies and reviews, suspension-feeding bivalves are both a fisheries resource and a provider of key ecosystem services (Dame 1996). These animals can have a variety of effects on estuaries through their suspension feeding activities, such as reducing phytoplankton biomass and other suspended particles (Officer *et al.* 1982, Hawkins *et al.* 1996, Barille *et al.* 1997), cycling nutrients and biomass between the benthos and the water column (Kautsky and Evans 1987, Smaal and Prins 1993), control of harmful algae (Cerrato *et al.* 2004), increased light penetration (Newell and Koch 2004), and facilitating the growth of benthic plants (Peterson and Heck 2001, Wall *et al.* 2008).

As bivalve populations have declined through overfishing, habitat loss, and disease, these ecosystem services have been lost and there are currently few estuaries with natural densities of bivalves sufficient to exert ecosystem-wide effects (Newell 1988, Lotze *et al.* 2006). In the absence of dense natural bivalve populations, bivalve aquaculture may achieve similar levels of ecosystem-wide impact (Souchu *et al.* 2001, Dumbauld *et al.* 2009). Some managers have considered aquaculture as a means to restore ecosystem functions previously provided by natural populations (Newell 2004, Ruesink *et al.* 2005), to combat eutrophication (Gifford *et al.* 2004, Cerco and Noel 2007), or to ease harvest pressures on wild populations (Dolmer and Frandsen 2002). Aquaculture is on the rise world-wide, and bivalve aquaculture may avoid some of the pitfalls of finfish aquaculture (Naylor *et al.* 2000) while controlling phytoplankton

blooms and affecting carbon and nutrient cycling in ways that are comparable to natural shellfish populations (Smaal *et al.* 2001, Newell 2004, Huang *et al.* 2008).

Commercial bivalve aquaculture operations strive to grow a maximum number of shellfish in a minimum of space (Frechette *et al.* 1992), with locally high filtration rates sometimes leading to "self-thinning" through density-dependent food limitation (Rheault and Rice 1996, Zhou *et al.* 2006). It is not well-known how these locally high filtration rates interact with adjacent natural bivalve populations (Ferreira *et al.* 2008), but locally high biodeposition rates from aquaculture have produced negative effects in some systems (Tenore *et al.* 1982, Feng *et al.* 2004), and intense aquaculture can exceed the ecological carrying capacity of some estuaries (Nunes *et al.* 2003, Duarte *et al.* 2003). As aquaculture develops for both commercial and restoration purposes, an improved understanding of these effects will help managers use bivalves to achieve healthy ecosystem functions (Dumbauld *et al.* 2009).

This study was designed to examine the combined effects of nutrient loading and adult bivalve filtration on the growth and survival of estuarine resource species (Fig 2.1): juvenile hard clams (*M. mercenaria*), bay scallops (*A. irradians*), and oysters (*Crassostrea virginica*), a juvenile planktivorous fish (sheepshead minnow, *Cyprinodon variegatus*), and eelgrass (*Zostera marina*). Juvenile sheepshead minnows are known to feed on both zooplankton and large phytoplankton (Samson *et al.* 2008). These five species were placed into an array of mesocosms with treatments of high or low nutrient loading and presence or absence of adult bivalves arranged in a 2 x 2 factorial design. The growth of all populations along with levels of light and size-fractionated chlorophyll *a* were monitored during three experiments which demonstrated that both nutrient loading and adult bivalve filtration can strongly influence the growth of multiple estuarine resources.

Methods:

We conducted three experiments with mesocosms placed in eastern Shinnecock Bay at the Stony Brook-Southampton Marine Science Center from June 5th, 2007, to September 6th, 2007. Shinnecock Bay is part of Long Island's south shore estuary lagoons (NY, USA) which have followed a trajectory in the decline of resources common to many estuaries around the world (Bricelj and Kuenster 1989, McHugh 1991, Gobler *et al.* 2005). Specifically, these lagoons have seen declines in shellfish such as the hard clam (McHugh 1991), the bay scallop (Bricelj and Kuenster 1989), various finfish, and eelgrass beds (Dennison *et al.* 1989). The 300-L mesocoms used in this study have been utilized previously to yield realistic growth rates and conditions for seagrass and shellfish (Cerrato *et al.* 2004, Wall *et al.* 2008). The depth of the mesocosms (1.2 m) is within the range of the mean depths found among Long Island's south shore estuary lagoons (Wilson *et al.* 1991). Moreover, the placement of the tanks in eastern Shinnecock Bay allowed for ambient light and temperature to be maintained during experiments. Replicate experimental mesocosms (n = 4 for each treatment) were stocked with juvenile northern quahogs (a.k.a. hard clams; ~10 mm shell length), bay scallops (~10 mm shell height), and/or eastern oysters (~10 mm shell height) at stocking densities (10 – 20 tank^{-1} or 36 – 72 m^{-2}; Table 1) more than an order of magnitude lower than standard commercial aquaculture stocking densities (~500 individ. m^{-2}; Barber and Davis 1997, Kraeuter and Castagna 2001) to avoid inter- and intraspecific competition for food (Rheault and Rice 1996, Kraeuter and Castagna 2001) among juvenile shellfish. Indeed, our estimated community clearance rates of juvenile bivalves indicated they filtered 0.4-1.5% d^{-1} of the total mesocosm volumes. All juvenile bivalves were placed in mesh cages (2 mm mesh size) near the bottom of the mesocosms. Juvenile shellfish were obtained from the Cornell Cooperative Extension shellfish hatchery in Southold, NY. Three-week-old sheepshead minnows (10-15 mm) were obtained from Cosper Environmental Services in Bohemia, NY. These planktivorous fish (Samson *et al.* 2008) were held in mesh baskets suspended near the tops of the experimental tanks (n = 10). A laminar circulating pump (Rio 180) was utilized to ensure mesocosms were well-mixed. In addition to the suspension feeders, individual shoots of eelgrass (n = 16) were

transplanted into planters containing low-organic sand and placed in each mesocosm (Wall *et al.* 2008).

Mesocosms were filled with eastern Shinnecock Bay water during high tide. Water from this region is fairly mesotrophic with mean total N (dissolved + particulate) concentrations of 0.2 ± 0.1 mg N L^{-1} or 16 ± 8 µM N measured from 2000 to 2005 (n = 50 measurements; SCDHS 2000-2005). For each experiment, we established a low nutrient loading rate for half of the experimental tanks (DIN loading of 0.065-0.255 mmoles N m^{-2} d^{-1}) using a 1-2% d^{-1} exchange with Shinnecock Bay water. The other half of the tanks received a high nutrient loading rate (5.49-10.70 mmoles N m^{-2} d^{-1}) that reflected ambient exchange plus nutrient additions of ammonium and the Redfieldian equivalent (16:1) of orthophosphate. These nutrient loading rates were within the range found in more eutrophic Northeast US estuaries such as the Childs River, MA, and Moriches Bay, NY (Taylor *et al.* 1999). Nutrient stocks were filter-sterilized (0.2 µm) and stored frozen. Experiments were run in semi-continuous mode, with 1-2% of the water volume being replaced daily mimicking the natural slow tidal exchange which occurs in the back-bay regions of the Peconic Estuary and Great South Bay, Long Island, NY, USA, resulting in residence times on the order of two-to-three months (Hardy 1976, Wilson *et al.* 1991). For each experiment, half of the experimental tanks contained adult suspension feeders (northern quahog or eastern oyster) and half of the tanks contained no adult suspension feeders. Stocking densities of adult bivalves in the experimental tanks (21 – 43 individuals m^{-2}) were comparable to historic densities of shellfish in Long Island South Shore Estuaries (Cerrato *et al.* 2004) but much higher than current densities (Weiss *et al.* 2007). Shellfish densities in the experiment treatments are orders of magnitude lower than stocking densities in modern aquaculture operations (Rheault and Rice 1996). Adult hard clams measured 56.70 ± 1.18 mm shell length and weighed 1.64 ± 0.11 g AFDW. Adult oysters measured 59.17 ± 0.79 mm shell height and weighed 0.66 ± 0.05 g AFDW. Adult shellfish were locally caught and obtained from seafood markets. The feeding activity of adult shellfish was estimated with a clearance rate method (Riisgard 2001) using water (>15 µg L^{-1} chlorophyll *a*) from the experimental tanks. Clearance rates were calculated according to the equation:

clearance rate = V/t x [ln(chl a_0 / chl a_t)]

where V is the volume of the container, t is the time, and chl a_0 and chl a_t are the chl *a* levels at the initial reading and at time t, respectively. This measurement was performed once per species. A 'community' clearance rate was estimated from these data using the average individual clearance rate and the number of individuals in the tank. An estimated clearance rate for the entire tank volume to be processed by the adult shellfish was calculated for each tank by dividing this community clearance rate by the tank volume. A summary of experimental conditions for all three experiments is presented in Table 1.

Experiments were conducted for ~two weeks, and shellfish growth was assessed via the changes in ash-free dry weight (AFDW) of tissue or by changes in shell lengths between initial and final individuals within each mesocosm (Weiss *et al.* 2007). The length of juvenile clams was measured by shell length (anterior-posterior; Kraeuter and Castagna 2001) and the size of juvenile oysters and scallops was measured by shell height (hinge-ventral margin; Rheault and Rice 1996). Bivalve tissue was dried at 70º C for at least 24 h and then ashed at 450º C for an additional 4 h (Gabbott and Walker 1971, Bass *et al.* 1990). One hundred bivalves of each species were selected from the initial set to provide a mean initial tissue AFDW. When fewer than 100 individuals were available for a mean initial AFDW, initial AFDW's were hind-casted based on initial lengths using length-weight regressions from 100+ individuals of the same species and size class. Juvenile fish growth was measured by total length only. Mean growth rates for all species based on length or weight were calculated by the change in length or tissue AFDW divided by the number of days between initial and final measurements. The quality and quantity of phytoplankton food particles available for bivalves was assessed by measuring whole and size-fractionated chlorophyll *a* (>5 µm) using polycarbonate filters and standard fluorometric techniques (Parsons *et al.* 1984). Chlorophyll in the <5 µm size fraction was calculated as the difference between whole and >5 µm chl *a*. Additional whole water samples were collected on pre-combusted glass fiber filters for the analysis of particulate organic carbon and nitrogen (POC, PON) on a CE Instruments Flash 1112 elemental analyzer (Sharp 1974).

The treatment effects on eelgrass productivity and epiphyte biomass were assessed by marking then harvesting eelgrass shoots from each replicate mesocosm. Leaf production during the experiment was measured using a modified leaf marking technique (Ibarra-Obando and Boudouresque 1994). Sixteen eelgrass shoots were marked at the base of the leaves by driving an 18-gauge hypodermic needle through all of the leaves on the shoot. The marked shoots were allowed to grow for the length of the experiment (13-15 d), after which all above-ground leaf material was harvested. In the laboratory, daily gross above-ground productivity, and leaf epibiont biomass (mg AFDW cm^{-2} leaf area) was determined. Productivity was determined by both mass (mg $shoot^{-1}$ d^{-1}) and leaf area growth (cm^2 $shoot^{-1}$ d^{-1}). Epiphyte biomass was scraped from each leaf, dried for at least 24 h at 70° C and then ashed at 450° C for an additional 4 h to determine AFDW.

Bottom light levels in each mesocosm were measured every 15 minutes by HOBO© Pendant-style data loggers with light sensors. A data logger was placed in each experimental tank near the bottom at a depth of approximately 1 m, a height just above eelgrass and shellfish cages preventing the obstruction of incoming light. A mean daily light level for each experimental tank was calculated by averaging values between 1000 and 1400 hrs, when the sun was most directly overhead. Since the HOBO© data loggers measure visible light levels in Lux instead of photosynthetically active radiation (PAR) in μmol m^{-2} s^{-1}, we compared measurement of light with the HOBO© loggers to those obtained with a LiCor© LI-192 underwater quantum sensor of PAR. There was a highly significant linear relationship between visible light in Lux as measured by the HOBO© data logger and PAR as measured by the LiCor© sensor over depths of 0.5-2.0 m (Visible light in LUX = 41.407 * PAR – 408.67, $r^2 = 0.98$, $p < 0.001$). Based on this finding, we believe that experimental light readings from HOBO© data loggers within our mesocosms were representative of the general trends in PAR.

Seawater dilution experiments were conducted to quantify the rates of microzooplankton grazing of micro-algal biomass within the mesocosm tanks (Landry *et al.* 1995). During each experiment, five liters of water from each replicate mesocosm within a treatment were pooled into a 20 L carboy for that treatment. Triplicate samples of 100, 70, 40 and 15% experimental dilutions of whole seawater with filtered seawater

(0.2 μm) from each carboy were established in 1 L polycarbonate bottles. To ensure nutrient-replete growth during these experiments, nitrate (20μM) and orthophosphate (1.25μM) was added to all of the bottles. A set of triplicate controls of whole seawater without nutrients were also established for each grazing experiments (Landry *et al.* 1995). Micro-algal growth rates (μ) within experimental bottles were quantified using the formula: $\mu = [\ln(B_t / B_o)] / t$, where μ is the net growth rate, B_t is the amount of biomass (chl *a*) present at the end of the experiments, B_o represents the amount of biomass at the beginning of experiments, and t is the duration of the experiment in days. The slope of first order linear regressions of dilution of seawater (x-axis) and the net growth rates (y-axis) were used to establish grazing mortality rates (Landry *et al.* 1995).

Statistical Analysis:

Differences in the growth of each animal species and eelgrass was assessed by means of 2-way analysis of variance (ANOVA), with nutrient loading level and presence/absence of adult bivalves as the two treatment factors using the software SigmaStat 3.5. When a significant effect on the response variables was detected, multiple comparison tests (Tukey's Studentized range) were used to test for significant differences between levels within the treatment. Mortality of juvenile bivalves was analyzed using a G-test of independence (Sokal and Rohlf 1995). Chlorophyll *a* and light level trends were analyzed with 3-way repeated-measures ANOVAs (ANOVARs) where level of nutrient loading and presence/absence of adult bivalves were the between-subject effects and day was the repeated within-subject effect. Each mesocosm tank was considered a subject for this analysis, which was conducted using the software Systat 13. In the case of significant interaction effects in the 3-way ANOVAR, the variance was decomposed by means of 2-way ANOVARs (day x bivalves and day x nutrients) Data that did not meet ANOVA assumptions were log-transformed to achieve normality. All statistical results were considered against a significance level of $\alpha = 0.05$.

Results:

Experiment 1:

Three separate mesocosm experiments were carried out using the above methods (Table 2.1). Experiment 1 ran from June 5th to June 18th, 2007. The average temperature in the experimental tanks was 20.30 ± 0.15 °C, the average salinity was 26.42 ± 0.04, and the average dissolved oxygen was 6.65 ± 0.14 mg L^{-1}. The "low nutrient loading" treatment received an average of 0.065 mmoles N m^{-2} d^{-1} and 0.006 mmoles P m^{-2} d^{-1} through a 1% d^{-1} exchange with Shinnecock Bay water whereas the "high nutrient loading" treatment received 10.70 mmoles N m^{-2} d^{-1} and 0.671 mmoles P m^{-2} d^{-1}. The densities of adult suspension feeders were 29 or 0 hard clams m^{-2} (8 or 0 individ. $tank^{-1}$). The estimated clearance time from bivalve filtration for the experimental tanks with hard clams was 42% d^{-1}. All tanks in this experiment were stocked with juvenile clams, juvenile oysters, and eelgrass (Table 2.1).

In this experiment, the higher nutrient loading rate (10.70 mmoles N m^{-2} d^{-1}) and the absence of adult hard clams produced significant increases in chlorophyll *a* compared to the low nutrient loading rate (0.065 mmoles N m^{-2} d^{-1}) and the presence of adult clams (29 individ. m^{-2}) over the course of a 13-day experiment (Fig. 2.2A-B; $p<0.01$ and $p<0.001$ for nutrient and bivalve treatments, respectively, 3-way ANOVAR). The level of whole chl *a* within each mesocosm varied significantly by day ($p<0.001$, Fig 2.2A, 3-way ANOVAR) and there was also a significant day x bivalve treatment interaction ($p<0.01$). When variance in whole chl *a* levels was decomposed with 2-way ANOVARs, the addition of bivalves consistently decreased whole chl *a* across both nutrient treatments ($p<0.05$), while nutrient loading significantly increased whole chl *a* only within the bivalves added treatment ($p<0.05$). Despite consistent directional effects from the nutrient and bivalve treatments (Fig 2.2B), chl *a* in the >5 µm size fraction varied significantly only by day ($p<0.001$, 3-way ANOVAR) and not by treatment. Chlorophyll *a* in the <5 µm size fraction was significantly increased by high nutrient loading and decreased by adult clam filtration ($p<0.01$ in both cases, 3-way ANOVAR, data not shown). Levels of chl *a* <5 µm also varied significantly by day ($p<0.001$) and

day x bivalve treatment interaction ($p<0.05$). When this variance was decomposed with 2-way ANOVARs, the addition of bivalves produced a significant drop in <5 µm chl *a* only within the high nutrient loading treatment ($p<0.01$), while nutrient loading produced a significant increase in <5 µm chl *a* only within the bivalves added treatment ($p<0.05$). The molar ratio of POC:PON was significantly higher under low nutrient loading (9.70 ± 0.61) and the absence of adult clams (10.51 ± 0.45) compared to high nutrient loading (9.22 ± 0.26) and the presence of adult clams (8.83 ± 0.24; $p<0.05$ for nutrient treatment, $p<0.01$ for clam filtration treatment, 2-way ANOVA).

The highest juvenile clam growth was in the presence of high nutrient loading and in the absence of adult hard clams, while the lowest was without nutrient loading but with adult hard clams present (Fig. 2.3A) However, only the nutrient loading treatment had a statistically significant effect: juvenile clam shell growth (Fig. 2.3A) and juvenile oyster soft tissue growth (Fig. 2.3B) were both significantly higher in the high nutrient loading treatment (0.032 ± 0.009 mm d^{-1} and 0.078 ± 0.016 mg AFDW d^{-1}, respectively) compared with treatments without experimental nutrient addition (0.00 ± 0.01 mm d^{-1} and 0.034 ± 0.015 mg AFDW d^{-1} respectively; $p<0.05$ for each, 2-way ANOVA). Despite the changes in chlorophyll *a*, light levels were not significantly different among treatments and subsequently eelgrass growth was not affected by the experimental treatments. Microzooplankton grazing rate data were not available for this experiment.

Experiment 2:

Experiment 2 ran from July 12th to July 27th, 2007. The average temperature in the experimental tanks was 24.27 ± 0.16 °C, the average salinity was 28.02 ± 0.16, and the average dissolved oxygen was 5.83 ± 0.12 mg L^{-1}. The "low nutrient loading" treatment received an average of 0.255 mmoles N m^{-2} d^{-1} and 0.072 mmoles P m^{-2} d^{-1} through a 2% d^{-1} exchange with Shinnecock Bay water. The "high nutrient loading" treatment received ambient exchange plus a daily experimental nutrient addition for a total of 5.75 mmoles N m^{-2} d^{-1} and 0.416 mmoles P m^{-2} d^{-1}. The densities of adult suspension feeders were 21 or 0 eastern oysters m^{-2} (6 or 0 individ. $tank^{-1}$). The

estimated turnover from bivalve filtration for the experimental tanks with oysters was 67% d^{-1}. All tanks in this experiment were stocked with juvenile clams, juvenile oysters, and eelgrass (Table 2.1).

Even though both treatments produced consistent directional effects on the levels of whole chlorophyll *a* (Fig 2.4A-B); whole chl *a* was not significantly altered by the treatments ($p>0.05$, 3-way ANOVAR). Whole chl *a* within each mesocosm tank varied significantly by day (Fig 2.4A, $p<0.01$, 3-way ANOVAR) and there was also a significant day x bivalve treatment interaction ($p<0.05$). When this variance was decomposed using 2-way ANOVARs, this interaction effect was removed and day was the only significant source of variation in whole chl *a*. Similarly, chl *a* in the >5 µm size class displayed consistent directional effects according to the treatments (Fig 2.4B) but the only significant variation was by day ($p<0.001$, 3-way ANOVAR). In contrast, chl *a* in the <5 µm size fraction was significantly enhanced by nutrient loading ($p<0.01$), significantly reduced by the addition of bivalves ($p<0.01$), and displayed a nutrient treatment x bivalve treatment interaction ($p<0.01$, 3-way ANOVAR, data not shown). When this variance was decomposed using 2-way ANOVARs, the decrease of <5 µm chl *a* by bivalves occurred only within the high nutrient loading treatment ($p<0.05$), and the increase in <5µm chl *a* by nutrient loading occurred only within the no bivalves treatment ($p<0.01$). Juvenile clam growth was significantly higher in the high nutrient loading treatment (0.039 ± 0.003 mm d^{-1} and 0.058 ± 0.005 mg AFDW d^{-1}) compared to the low nutrient loading treatment (0.030 ± 0.003 mm d^{-1} and 0.033 ± 0.005 mg AFDW d^{-1}) when measured by shell length (data not shown; $p<0.05$, 2-way ANOVA) or by dry tissue weight (Fig. 2.5A; $p<0.001$, 2-way ANOVA). Juvenile clam growth was not affected by the adult oyster filtration treatment. In contrast, the juvenile oysters responded to the adult bivalve treatment; juvenile oyster growth was significantly decreased in the presence of adult oyster filtration (Fig. 2.5B; $p<0.01$; 2-way ANOVA) but was not affected by the nutrient loading treatments. Juvenile oyster growth was 0.131 ± 0.022 mg AFDW d^{-1} in the absence of adult oysters and was 0.033 ± 0.017 mg AFDW d^{-1} in the presence of adult oysters. Light levels and eelgrass growth were not significantly affected by the experimental treatments (2-way ANOVA), although epiphyte biomass on eelgrass leaves was significantly higher under high nutrient loading (0.164 ± 0.013 mg

AFDW cm^{-2}) and adult oyster filtration (0.179 ± 0.011 mg AFDW cm^{-2}) compared to low nutrient loading (0.140 ± 0.012 mg AFDW cm^{-2}) and no adult oyster filtration (0.126 ± 0.006 mg AFDW cm^{-2}; $p<0.05$ by nutrient treatment, $p<0.001$ by oyster treatment, 2-way ANOVA). Microzooplankton grazing rates were not significantly different between treatments, and ranged from 2.31 to 2.39 d^{-1} (Table 2.2). POC/PON data were not available for this experiment.

Experiment 3:

Experiment 3 ran from August 22nd to September 6th, 2007. The average temperature in the experimental tanks was 24.56 ± 0.15 °C, the average salinity was 29.73 ± 0.09, and the average dissolved oxygen was 6.16 ± 0.16 mg L^{-1}. The "low nutrient loading" treatment received an average of 0.134 mmoles N m^{-2} d^{-1} and 0.099 mmoles P m^{-2} d^{-1} through a 2% d^{-1} exchange with Shinnecock Bay water. The "high nutrient loading" treatment received ambient exchange plus a daily experimental nutrient addition for a total of 5.49 mmoles N m^{-2} d^{-1} and 0.434 mmoles P m^{-2} d^{-1}. The densities of adult suspension feeders were 43 or 0 clams m^{-2} (12 or 0 individ. $Tank^{-1}$). The estimated turnover rate from bivalve filtration for the experimental tanks with hard clams was 63% d^{-1}. All tanks in this experiment were stocked with juvenile scallops, juvenile clams, juvenile oysters, juvenile sheepshead minnows, and eelgrass (Table 2.1).

In this experiment, and the presence of adult hard clams (43 individ. m^{-2}) produced significant decreases in total chlorophyll *a* compared to the absence of adult hard clams over the course of a 15-day experiment ($p<0.001$, 3-way ANOVAR, Fig. 2.6A-B), and whole chl *a* also varied significantly over time within each mesocosm tank ($p<0.001$). The significant decrease of whole chl *a* by the bivalves-added treatment was consistent across both levels of nutrient loading and over time during the experiment (Fig. 2.6A-B). Even though the high nutrient loading rate (5.49 mmoles N m^{-2} d^{-1}) produced a consistent directional effect on whole chl *a* compared to the low nutrient loading rate (0.134 mmoles N m^{-2} d^{-1}, Fig 2.6B), this effect was not statistically significant ($p>0.05$, 3-way ANOVAR). Trends in whole chl *a* were paralleled by the >5 μm size fraction of chl *a*, which was decreased by the addition of adult bivalves

($p<0.001$, 3-way ANOVAR, Fig. 2.6B) and also varied within each mesocosm tank by day ($p<0.05$). There was also a significant day x bivalve treatment interactive effect on levels on >5 µm chl*a* ($p<0.05$, 3-way ANOVAR). When this variance was decomposed using 2-way ANOVARs, the interactive effect was removed. Although >5 µm chl *a* was consistently increased by nutrient loading (Fig. 2.6B), this effect was not statistically significant ($p>0.05$). In contrast to Experiments 1 & 2, chl *a* in the <5 µm size fraction varied only by day ($p<0.001$, 3-way ANOVAR, data not shown) and was not affected by either treatment ($p>0.05$)..

Particulate organic nitrogen (PON) was significantly lower in the presence of adult clams (16.1 ± 1.24 µM) compared to the absence of adult clams (38.4 ± 3.37 µM; Table 2.2; $p<0.05$, 2-way ANOVA). Particulate organic carbon (POC) was affected by both experimental treatments. The levels of POC were higher in the high nutrient loading treatment (249.76 ± 52.82 µM) compared to the low nutrient loading treatment (215.14 ± 35.57 µM; $p<0.05$, 2-way ANOVA), and POC was lower in the presence of adult clams (116.88 ± 8.62 µM) compared to the absence of adult clams (310.35 ± 18.92 µM; Table 2.2; $p<0.001$, 2-way ANOVA). The molar ratio of POC:PON was not significantly affected by any of the treatments in Experiment 3 (Table 2.2). Microzooplankton grazing rates were not significantly different between treatments, and ranged from 0.45 to 0.73 d^{-1} (Table 2.2).

Light penetration to the bottom of the mesocosms was higher in the adult bivalve treatment (7,430 ± 437 Lux, $p<0.05$, 3-way ANOVAR) compared to the absence of adult bivalves (4,620 ± 182 Lux), was not significantly affected by the nutrient treatments ($p>0.05$), and varied significantly by day within each mesocosm tank ($p<0.001$, 3-way ANOVAR, data not shown). Eelgrass leaf area productivity was significantly enhanced by the presence of adult clams (0.549 ± 0.030 cm^2 $shoot^{-1}$ d^{-1}) compared to the treatments with no adult clams (0.421 ± 0.024 cm^2 $shoot^{-1}$ d^{-1}; Fig. 2.7C; $p < 0.001$, 2-way ANOVA). Eelgrass was also affected by the nutrient loading treatment; leaf area productivity was significantly decreased by the high nutrient loading treatment (0.431 ± 0.024 cm^2 $shoot^{-1}$ d^{-1}) compared to the low nutrient loading treatment (0.519 ± 0.029 cm^2 $shoot^{-1}$ d^{-1}; Fig. 2.7C; $p < 0.01$, 2-way ANOVA). There was a significant interaction ($p <$

0.01) of the treatment effects on eelgrass: the decline in leaf area productivity from the low to the high nutrient loading treatments occurred entirely within the presence of adult clams, while eelgrass growth was not significantly affected by nutrient loading in the absence of adult clams. When eelgrass productivity was measured by dry weight instead of leaf area, there was a significant increase in mass productivity in the presence of adult clams (1.87 ± 0.17 mg shoot^{-1} d^{-1}; Fig. 2.7C) compared to the absence of adult clams (1.27 ± 0.23 mg shoot^{-1} d^{-1} mass productivity, $p<0.05$, 2-way ANOVA). There were no detectable effects of nutrient loading on eelgrass mass productivity. Epiphyte growth on the eelgrass blades was also significantly denser in the presence of adult clams (0.186 ± 0.017 mg AFDW cm^{-2}) compared to the absence of adult clams (0.146 ± 0.009 mg AFDW cm^{-2}; $p<0.01$, 2-way ANOVA).

Juvenile clams were not significantly affected by any of the treatment factors in the third experiment. Juvenile oysters grew significantly faster in the absence of adult clams (0.257 ± 0.064 mg AFDW d^{-1}) compared to when adult clams were present (0.034 ± 0.067 mg AFDW d^{-1}; Fig. 2.7A $p<0.05$, 2-way ANOVA). Juvenile sheepshead minnows also grew significantly faster in the absence of adult clams (0.228 ± 0.017 mm d^{-1} $p<0.05$, 2-way ANOVA) compared to treatments with adult clams (0.177 ± 0.022 mm d^{-1}; Fig 2.7B). The fish growth rates showed an interesting interaction: the presence/absence of adult clams made more of a difference to the juvenile sheepshead minnows within the high nutrient loading treatment than within the low nutrient treatment (Fig. 2.7B; $p<0.05$, Tukey test). There were no differences in juvenile scallop growth rates, but juvenile scallop mortality was significantly higher in the presence of adult hard clams than in the absence of adult clams (96% with adult clams, 71% without adult clams; $p<0.001$; G-test of independence, data not shown). Juvenile fish and shellfish were not significantly affected by the nutrient loading treatments in this experiment (2-way ANOVA).

Discussion:

Over the course of three mesocosm experiments both enhanced nutrient loading and filtration by adult bivalves significantly affected the growth of juvenile shellfish, juvenile fish, and eelgrass, as well as phytoplankton and light levels in mesocosms. Adult bivalve filtration and nutrient loading were expected to affect eelgrass growth through changes in the density of phytoplankton, which in turn affects the benthic light regime (Newell and Koch 2004, Wall *et al.* 2008). Only Experiment 3 produced results consistent with this hypothesis, where a high density of adult clams decreased chlorophyll *a* levels (Fig 2.6A-B) and increased light penetration leading to an increase in eelgrass productivity (Fig 2.7C). The high nutrient loading treatment in Experiment 3 decreased eelgrass growth relative to the low nutrient loading treatment, and the effects of nutrient loading on eelgrass were most evident when adult clams were present (Fig 2.7C). Adult clams and adult oysters decreased chlorophyll *a* in Experiments 1 & 2 similarly to Experiment 3, (Figs 2.2A-B, 2.4A-B), but these changes in chl *a* did not produce significant effects on light or eelgrass. The density of epiphytes on eelgrass blades was increased by adult bivalve filtration in Expts 2 and 3, and by nutrient loading in Expt 2. Although thick epiphyte growth has been found to have a negative impact on seagrass in some cases (Duarte 1995), the densities of epiphytes measured in our experiments (0.13-0.19 mg AFDW cm^{-2}) were likely too low to block light at the blade surface (Brush and Nixon 2002). Although pore-water N and P concentrations in the seagrass planters were not measured, the planters were filled with low-organic sand from a dune area so eelgrass shoots were most likely not responding to sedimentary nutrient inputs. On a time-scale longer than these experiments (weeks – months), nutrient enrichment (or lack thereof) to the sediments will also affect seagrass growth and reproduction (Dennison *et al.* 1987, Peterson and Heck 2001, Carroll *et al.* 2008).

Growth rates of juvenile planktivorous fish and juvenile bivalves may be decreased by filtration pressure from adult bivalves, which clear food particles from the water column (Rheault and Rice 1996, Zhou *et al.* 2006), or may be increased by high nutrient loading, which may increase the quantity and quality of suspended food particles (Carmichael *et al.* 2004, Carmichael and Valiela 2005). All three experiments had some results consistent with this hypothesis: juvenile clam growth was increased by high nutrient loading in Experiments 1 and 2 (Fig 2.3A, 2.5A), juvenile oyster growth was also

increased by high nutrient loading in Experiment 1 (Fig 2.3B), while juvenile oyster growth was decreased by adult bivalve filtration in Experiments 2 and 3 (Fig 2.5B, 2.7A), and juvenile fish growth was also decreased by adult bivalve filtration in Experiment 3 (Fig 2.7B). Although there were no significant growth responses for scallops, juvenile scallop mortality was increased by adult bivalve filtration in Experiment 3.

The results of these experiments demonstrate the strong reliance of juvenile shellfish and finfish growth rates and survival on the short-term dynamics (days to weeks) of food availability as reflected by concentrations of chlorophyll *a*, POC, and PON. In Experiment 1, where nutrient loading had a strong effect on juvenile growth, the molar ratio of POC:PON was significantly reduced by the high nutrient loading treatment (Table 2.2), suggesting an enrichment of nitrogen in food particles could have contributed to enhanced shellfish growth (Fig 2.3A-B). Carmichael *et al.* (2004) and Carmichael and Valiela (2005) have interpreted nitrogen-enriched seston as an increase in the quality of food particles available to juvenile bivalves. Although the molar ratio of POC:PON did not change in Experiment 3, the quantities of POC and PON were both decreased by adult clam filtration (Table 2.2), with corresponding decreases in the growth rates of juvenile oysters and sheepshead minnows (Fig 2.7A-B) and a decrease in the survival of juvenile scallops. In all cases, increased growth rates of shellfish occurred in parallel with increases in whole or size-fractionated chlorophyll *a*. While there was a statistically significant change in chl *a* due to treatment factors in each experiment, the magnitude of these changes in Experiments 1 and 2 were relatively low (+/- 2 – 4 μg L^{-1}, Fig. 2.2A, 2.4A). It is possible that the availability of food particles to the juvenile shellfish was changed by the treatment factors in these experiments without large changes in the standing stock of chlorophyll *a* between treatments. Phytoplankton mortality rates due to microzooplankton grazing of 0.5 d^{-1} or greater are common in estuarine environments, and often result in >70% daily turnover of standing chl *a* (Calbet and Landry 2004). Microzooplankton grazing rates, as measured by dilution experiments (Landry *et al.* 1995), ranged from 2.3-2.4 d^{-1} in Experiment 2; these were faster than the estimated clearance rate from adult oyster filtration of 67% d^{-1}. Such rapid rates of phytoplankton community turnover could mask true food availability to juvenile bivalves and would account for enhanced bivalve growth responses in Experiment 2 in the absence of large

changes in chl *a*. In Experiment 3, microzooplankton grazing rates were slower (0.4-0.7 d^{-1}), and comparable to the adult clam clearance rate of 63% d^{-1}. In contrast to Experiments 1 and 2, this experiment had large treatment-driven changes in chl *a* (+/- 20 - 40 μg L^{-1}, Fig 2.6A) and growth differences in response to adult clam filtration (Fig 2.7A-C). Lonsdale *et al.* (2009) found that natural populations of bivalves could exert grazing pressure on phytoplankton that was comparable to grazing by microzooplankton, and noted that bivalves also fed upon microzooplankton and copepod nauplii. Future work will need to examine the extent to which benthic suspension feeding alters both phytoplankton growth and microzooplankton grazing, and how turnover in the plankton community affects the growth and recruitment of juvenile bivalves.

During these experiments, the treatment factor driving the growth responses changed from nutrient loading in the first experiment, to combined factors in the second experiment, and finally to exclusively adult bivalve filtration in the third experiment. These differences may partly reflect differences in treatment administered: Experiment 1 had a larger difference in nutrient loading rate between the high nutrient treatment and the control than the other experiments, while Experiment 3 had a larger difference in clam density between adult clam treatments than Experiment 1 (Table 2.1). These results may have also been influenced by seasonal trends: Lower temperatures during the first experiment (17-23° C) may have yielded lower nutrient regeneration rates (Nagata and Kirchman 1992, Miller *et al.* 1995) and low bivalve filtration rate (Kraeuter and Castagna 2001), making external nutrient loading a more important process. Conversely, higher temperatures (23-25° C) for the second and third experiments likely promoted faster bivalve filtration (Kraeuter and Castagna 2001, Weiss *et al.* 2007) and pelagic nutrient regeneration (Nagata and Kirchman 1992, Miller *et al.* 1995). There is also evidence of seasonal succession in the phytoplankton community, since the <5 μm size fraction of chl *a* responded more strongly to the treatment factors in Expts 1 & 2 (Jun & Jul) while the >5 μm size fraction responded more strongly in Expt 3 (Aug). As such, it seems that bivalve filtration can mediate the eutrophication of estuarine food webs, and the relative importance of this mediating role can change seasonally or with changing rates of nutrient loading or densities of bivalves.

The densities of adult hard clams used in our Experiments 1 and 3 (8-12 individ. $tank^{-1}$, or 29-43 individ. m^{-2}) are comparable to historic densities of northern quahogs (hard clams) in Great South Bay (50-100 individ. m^{-2}, Cerrato *et al.* 2004) but are much higher than current densities in NY estuaries (0.4 - 5 individ. m^{-2}, Weiss *et al.* 2007). Similarly, the density of adult oysters used in Experiment 2 (6 individ. $tank^{-1}$, or 21 individ. m^{-2}) are comparable to historic densities of Eastern oysters in reefs in Chesapeake Bay (43-150 individ. m^{-2}), but are much higher than current densities (0.43 individ. m^{-2}; Newell and Koch 2004). However, all of the densities used in experiments are several orders of magnitude less than levels used for bivalve aquaculture (Rheault and Rice 1996; K. Rivara, Aeros Cultured Oyster Co., pers. comm.). The estimated water column clearance rates from these densities of adult bivalves were 42 – 67% d^{-1}, within the range reported to control algal bloom formation (Cerrato *et al.* 2004, Wall *et al.* 2008). Consistent with this idea, the presence of adult bivalves yielded lower phytoplankton biomass in all three experiments (Figs 2.2B, 2.4B, 2.6B). Such ecosystem-wide filtration pressure may have been typical of historic (19^{th} century) natural bivalve populations in Chesapeake Bay (Newell 1988, Newell and Koch 2004) or Great South Bay (mid-20^{th} century, McHugh 1991, Cerrato *et al.* 2004). Similarly, modern high-density bivalve aquaculture may also achieve these ecosystem filtration rates (Dumbauld *et al.* 2009), especially in coastal lagoons with slow flushing times (Souchu *et al.* 2001), and in one case the loss of filtration due to the removal of bivalve aquaculture led to symptoms of eutrophication (Huang *et al.* 2008). Estuarine management programs may consider bivalve restoration as a management tool to control pelagic algal blooms (Cerrato *et al.* 2004), combat eutrophication (Cerco and Noel 2007), facilitate the growth of eelgrass (Fig 2.7C; Peterson and Heck, 2001, Newell and Koch, 2004, Wall *et al.* 2008), or even to effect "regime change" of eutrophic estuaries (Petersen *et al.* 2008), although the potential impacts on juvenile shellfish must also be considered.

While enhanced bivalve filtration was beneficial to eelgrass and to some extent epiphytes on eelgrass, they exerted a significantly negative effect on the growth of juvenile fish and shellfish in two out of three experiments (Fig 2.5B, 2.7A-B) and in one case even led to a significant increase in juvenile scallop mortality (Expt 3). Rheault and Rice (1996) placed juvenile eastern oysters (*C. virginica*) and bay scallops (*A. irradians*)

in a compartmented flume and found decreased growth and condition index in the shellfish that were downstream compared to the upstream dense populations. From an initial ambient chlorophyll *a* concentration of 4 to 8 μg L^{-1}, each batch of shellfish decreased chl *a* by 27-35% compared to the upstream compartment (Rheault and Rice 1996). In Experiment 3 of our study, the high density of adult hard clams produced a large average daily drop in mean chl *a* levels (Fig 2.6B, -73%) and a decrease of 36% in experiment-long chl *a* means compared to the control, and also led to decreased growth of juvenile oysters (Fig 2.7A) and decreased survival of juvenile scallops. The concentrations of chl *a* in Experiment 3 were relatively high (25.09 ± 2.56 μg L^{-1} with no adult clams; 15.90 ± 2.20 μg L^{-1} with adult clams; Table 2.2); this drop in chlorophyll *a* produced a significant decrease in juvenile oyster growth but not juvenile clam growth. It is likely that juvenile clam food requirements were saturated at a lower chlorophyll *a* concentration than juvenile oyster food requirements (Tenore and Dunstan 1973). These impacts illustrate an eventual trade-off between the benefits and costs of higher ecosystem filtration rates: Despite the benefits to seagrass, high rates of water column turnover by adult shellfish could serve as a negative feedback on juvenile fish and shellfish populations (Fig 2.5B, 2.7A-B) by decreasing food availability (Fig 2.6A-B) or even by direct consumption of larval bivalves by adults (Andre and Rosenberg 1991, Andre *et al.* 1993). Such density-dependent limitation is a common phenomenon within bivalve aquaculture (Rheault and Rice 1996, Zhou *et al.* 2006), and over-stocking of aquaculture operations may exceed the carrying capacity of some estuaries (Guo *et al.* 1999, Duarte *et al.* 2003). The extent to which juvenile suspension feeders may be food-limited within estuarine ecosystems is not well known, but will certainly depend on the species involved and the particular physics and biology of each ecosystem (Newell 2004, Ferreira *et al.* 2008).

These experiments were not designed to investigate the effects of re-suspension on either eelgrass or bivalves. While our experimental tanks were well-mixed, there was likely not sufficient water motion to re-suspend sediment or detritus from bottoms of the mesocosms. Re-suspended particles have a negative impact on eelgrass through turbidity and decreased light penetration (Newell and Koch 2004). The effects of re-suspension on bivalves are more complicated, as water motion can deliver organic food particles in the

forms of detritus, fecal pellets, and benthic microalgae to bivalves, and at the same time dilute food concentrations with inorganic sediment (Hawkins *et al.* 1996, Barille *et al.* 1997). Newell and Koch (2004) have suggested that a sufficient density of bivalves would reduce both total suspended particles and phytoplankton to the benefit of benthic plants.

Many estuarine management plans have focused on the need to reduce nutrient loads to mitigate the effects of eutrophication (Nixon 1995, Cloern 2001, de Jonge *et al.* 2002). Partly through changes in land use and better sewage treatment, inorganic nutrient levels and/or chlorophyll *a* concentrations have declined in many coastal waters,, such as the North Sea (Nunnieri *et al.* 2007, Artioli *et al.* 2008), the Dutch Wadden Sea (Philippart *et al.* 2007), Narragansett Bay, RI, USA (Fulweiler *et al.* 2007), Long Island Sound, USA (CTDEP 1991 – 2007), and the Peconic Estuary, NY, USA (SCDHS, 1976-2005). Despite this "oligotrophication" of some coastal waters (Nixon *et al.* 2009), the recovery of estuarine resources in these systems has not been reported. The high nutrient loading rates in our experimental tanks are comparable to measured nutrient loading rates in eutrophic northeast U.S. estuaries (Taylor *et al.* 1999), from which valuable estuarine resources have been lost (Ryther 1989, McHugh *et al.* 1991, Valiela *et al.* 1992). However, positive effects on bivalves under enhanced levels of nutrient loading have been reported (Reitan *et al.* 2002, Weiss *et al.* 2002, Carmichael *et al.* 2004). Eutrophic systems with high levels of nutrient loading often have hypoxia/anoxia (Nixon 1995, Diaz and Rosenberg 2008), which can decrease bivalve survival (Carmichael *et al.* 2004), but our well-mixed mesocosms remained normoxic (>4 mg L^{-1} DO) during experiments. Considering this information, our findings suggest that nutrient loading could be allowed to increase in some relatively oligo- or mesotrophic and well-mixed coastal systems with increased secondary production of eastern oysters and northern quahogs as a positive benefit (Nixon and Buckley 2002). Of course, such potential benefits would need to be considered in light of potentially negative effects of higher nutrient loads in an ecosystem such as hypoxia (Diaz and Rosenberg 2008), loss of seagrass beds (Valiela *et al.* 1992, Dennison *et al.* 1989), and harmful algal blooms (Anderson *et al.* 2008).

Future ecosystem-based management of estuaries will need to simultaneously administer bivalve restoration, control of nutrient loading, conservation of key fishery species, the burgeoning aquaculture industry, and protection of critical habitats such as seagrass meadows and salt marshes. Bivalve filtration can have significant and complex impacts on estuarine food webs (Prins *et al.* 1998, Petersen *et al.* 2008), and bivalve filtration can mediate the effects of nutrient loading on the growth of estuarine resources, including eelgrass, finfish, and shellfish. These two-week mesocosm experiments were short-term perturbation experiments, representing how resource species might respond to a pulse of nutrient-loading. Many coastal systems receive long-term "press disturbance" additions of nutrients (Valiela *et al.* 1992, de Jonge *et al.* 2002) and it is difficult to extrapolate from two-week experiments to longer-term trends. Enhanced biodeposition by bivalves that leads to denitrification (Newell *et al.* 2002, Seitzinger *et al.* 2006) or enhanced nitrogen uptake by seagrass beds (Welsh *et al.* 2000) may be the most important long-term sinks for nitrogen, although of course these longer-term processes are linked to the short-term growth and survival of bivalves and seagrasses.

Quantitative modeling of bivalve filtration, phytoplankton dynamics, and hydrology of estuaries will aid in the aforementioned management goals (Dame and Prins 1998, Duarte *et al.* 2003, Ferreira *et al.* 2008). Based on the results of these experiments and other findings, some general conclusions can be drawn. The first is that eelgrass is light-limited in many eutrophic estuaries (Dennison and Alberte 1985, Duarte 1995) and will benefit from proximity to the enhanced filtration of bivalve beds (Wall *et al.* 2008). Additionally, bivalves can benefit seagrasses through enhanced biodeposition (Peterson and Heck 2001, Carroll *et al.* 2008). As such, re-planting of eelgrass beds should focus on areas that have high light penetration and/or are adjacent to existing dense bivalve populations. The second conclusion is based on our finding that juvenile resource bivalves respond to enhanced inorganic nutrient loading with increased growth, and respond with decreased growth to high densities of adult bivalves. This is likely mediated by food limitation: inorganic nutrients encourage the growth of larger and more nutritious phytoplankton (Wikfors *et al.* 1992, Raven and Kubler 2002) while dense collections of adult bivalves can limit juvenile growth by clearing too many of these food particles (Rheault and Rice 1996, Zhou *et al.* 2006). This issue of food limitation

between juvenile and adult bivalves may be best seen through the lens of intensifying aquaculture operations: As aquaculture becomes more prevalent and shellfish stocking densities increase, aquaculture operations may limit each other or adjacent natural populations (Nunes *et al.* 2003, Ferreira *et al.* 2008). Clearly, predators (Gosselin and Qian 1997, Polyakov *et al.* 2007) and hypoxia/anoxia (Altieri and Witman 2006, Diaz and Rosenberg 2008) also exert significant mortalities on juvenile bivalves in the field. However, in absence of hypoxia and differential predation, restoration, re-seeding, and aquaculture of clams, oysters, and scallops are more likely to succeed in areas that have moderate nutrient loading rates, and managers must carefully consider the spacing between aquaculture operations as well as between aquaculture operations and natural bivalve populations.

			Experiment 1	Experiment 2	Experiment 3
Stocking densities of response organisms (n = # per tank)	**Juvenile bivalves**	***M. mercenaria***	10	20	10
		C. virginica	15	10	10
		A. irradians	0	0	10
	Juvenile fish	***C. variegatus***	0	0	10
	Eelgrass shoots	***Z. marina***	16	16	16
Experimental conditions	**Adult bivalve species**		*M.mercenaria*	*C. virginica*	*M. mercenaria*
	Density of adult bivalves	**+ Bivalves**	29 m^{-2}	21 m^{-2}	43 m^{-2}
		- Bivalves	0	0	0
	Estimated clearance rate from + Bivalves treatment		42% d^{-1}	67% d^{-1}	63% d^{-1}
	Exchange with ambient water		1% d^{-1}	2% d^{-1}	2% d^{-1}
	Nutrient loading rate (mmoles N m^{-2} d^{-1})	**high N**	10.70	5.75	5.49
		low N	0.065	0.255	0.134

Table 2.1. Stocking densities of response organisms and summary of experimental conditions. Treatments were "+ Bivalves" or "- Bivalves" for presence or absence of adult bivalves and "high N" or "low N" for high or low nutrient loading. Nutrients were added as 16:1 inorganic N:P. A total of 16 tanks were used for each 2 x 2 factorial experiment with n = 4 tanks per treatment combination.

		whole chl *a* µg L^{-1}	>5 µm chl *a* µg L^{-1}	POC µM	PON µM	POC:PON	Microzooplankton grazing rate d^{-1}
Expt 1	**low N/+Bivalves**	6.60 ± 0.91	4.92 ± 0.75	244.00 ± 44.06	27.21 ± 3.83	8.85 ± 0.33	no data
	low N/-Bivalves	8.39 ± 1.18	5.58 ± 0.80	150.46 ± 13.55	13.34 ± 2.09	11.40 ± 0.77	available
	high N/+Bivalves	7.72 ± 0.95	5.44 ± 0.83	200.40 ± 26.71	23.13 ± 3.66	8.81 ± 0.39	
	high N/-Bivalves	9.38 ± 1.19	6.21 ± 0.84	184.90 ± 15.63	19.25 ± 1.62	9.62 ± 0.23	
Expt 2	**low N/+Bivalves**	3.57 ± 0.29	2.12 ± 0.27	no data	no data	no data	2.36 ± 0.52
	low N/-Bivalves	3.89 ± 0.42	2.83 ± 0.41	available	available	available	2.39 ± 0.63
	high N/+Bivalves	4.64 ± 0.68	2.62 ± 0.43				2.36 ± 0.45
	high N/-Bivalves	6.51 ± 0.46	3.68 ± 0.41				2.31 ± 0.53
Expt 3	**low N/+Bivalves**	14.15 ± 2.61	8.96 ± 2.30	120.53 ± 18.73	16.05 ± 2.55	7.65 ± 0.89	0.55 ± 0.32
	low N/-Bivalves	21.76 ± 3.25	22.58 ± 4.23	272.08 ± 15.24	32.77 ± 3.72	8.42 ± 0.54	0.45 ± 0.07
	high N/+Bivalves	19.92 ± 3.64	12.40 ± 3.69	113.24 ± 2.66	16.31 ± 1.07	7.00 ± 0.46	0.73 ± 0.19
	high N/-Bivalves	29.00 ± 3.77	31.95 ± 5.76	348.62 ± 9.64	43.95 ± 3.42	8.00 ± 0.47	0.63 ± 0.17

Table 2.2. Levels of chlorophyll *a*, POC, PON, and microzooplankton grazing rates. Values are mean ± SE of experimental tanks for each treatment combination averaged over the course of each experiment. Treatments were "+ Bivalves" or "- Bivalves" for presence or absence of adult bivalves and "high N" or "low N" for high or low nutrient loading. Nutrients were added as 16:1 inorganic N:P. A total of 16 tanks were used for each 2 x 2 factorial experiment with n = 4 tanks per treatment combination. Values of >5 µm chl *a* that are greater than whole chl *a* for Expt 3 reflect plankton communities where virtually all chl *a* is in the >5 µm size-fraction.

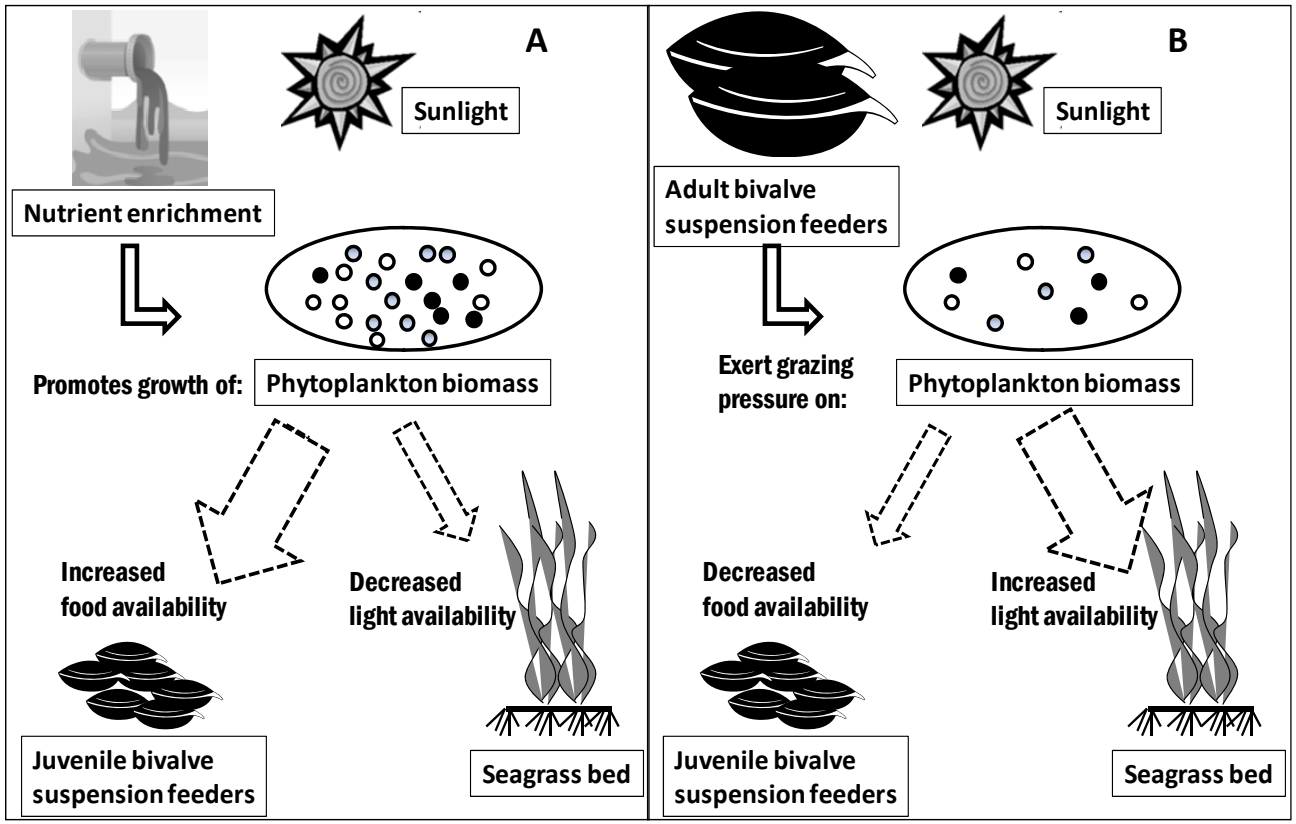

Figure 2.1. Conceptual model of experiments. Conceptual model of the effects of nutrient loading (A) and adult bivalve filtration (B). Solid arrows represent treatment factors that are expected to act on phytoplankton biomass, and dashed arrows represent hypothesized responses of juvenile bivalves and seagrass shoots to changes in phytoplankton biomass.

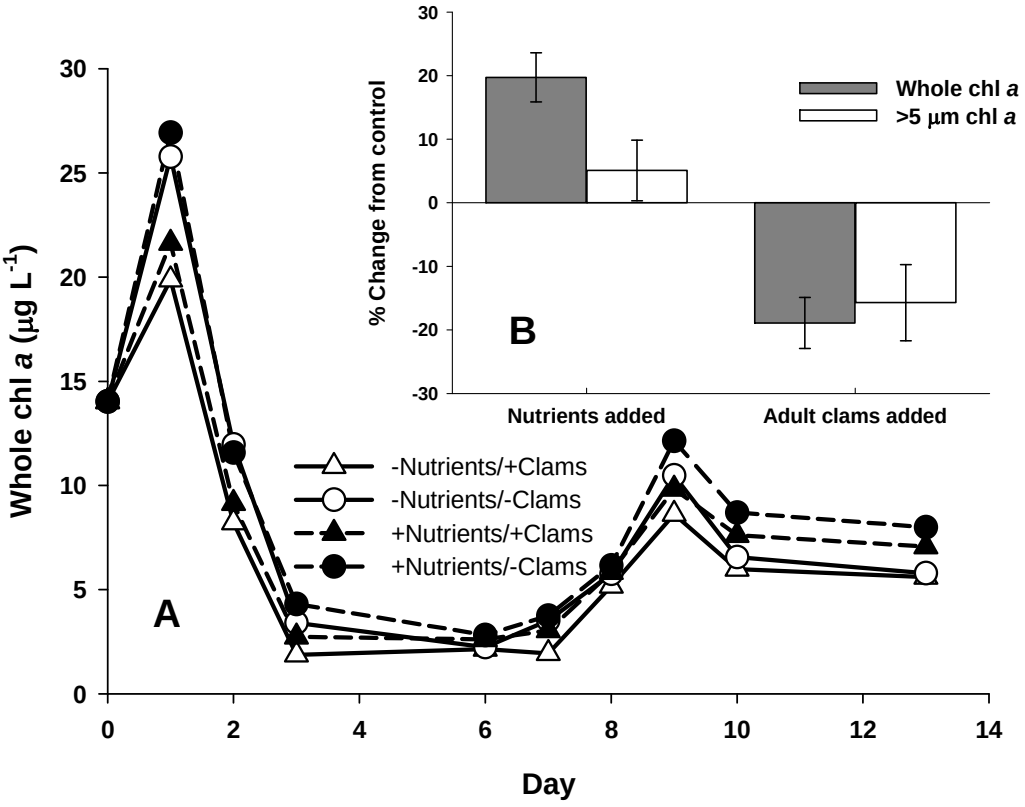

Figure 2.2. Chlorophyll *a* dynamics in Experiment 1. Time series data points (A) represent the mean (n=4) for each of the treatment combinations. Error bars are not presented for the sake of visual clarity. The mean relative standard deviation of measurements for whole chl *a* was 19.8% during the experiment. Inset (B) shows mean (± SE) daily percent increase or decrease from nutrient addition over both bivalve treatments and from bivalve addition over both nutrient treatments. See text for magnitudes of nutrient loading and densities of adult bivalves.

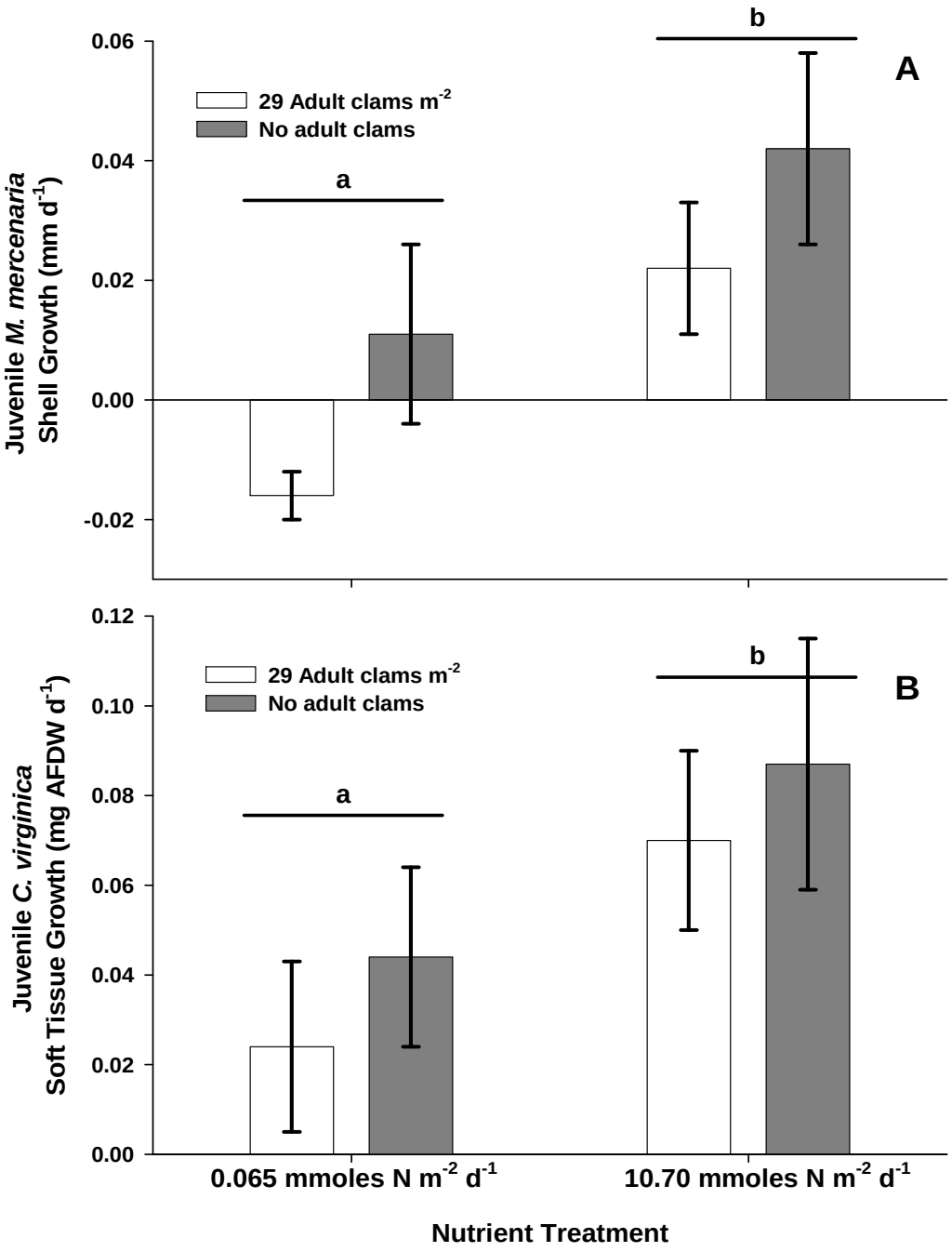

Figure 2.3. Growth responses from Experiment 1 for (A) juvenile *Mercenaria mercenaria* and (B) juvenile *Crassostrea virginica*. Bars are means ± SE. Slightly negative shell growth for juvenile *M. mercenaria* is within measurement errors of zero. Letters above bars indicate significant difference. Nutrients were added as 16:1 inorganic N:P.

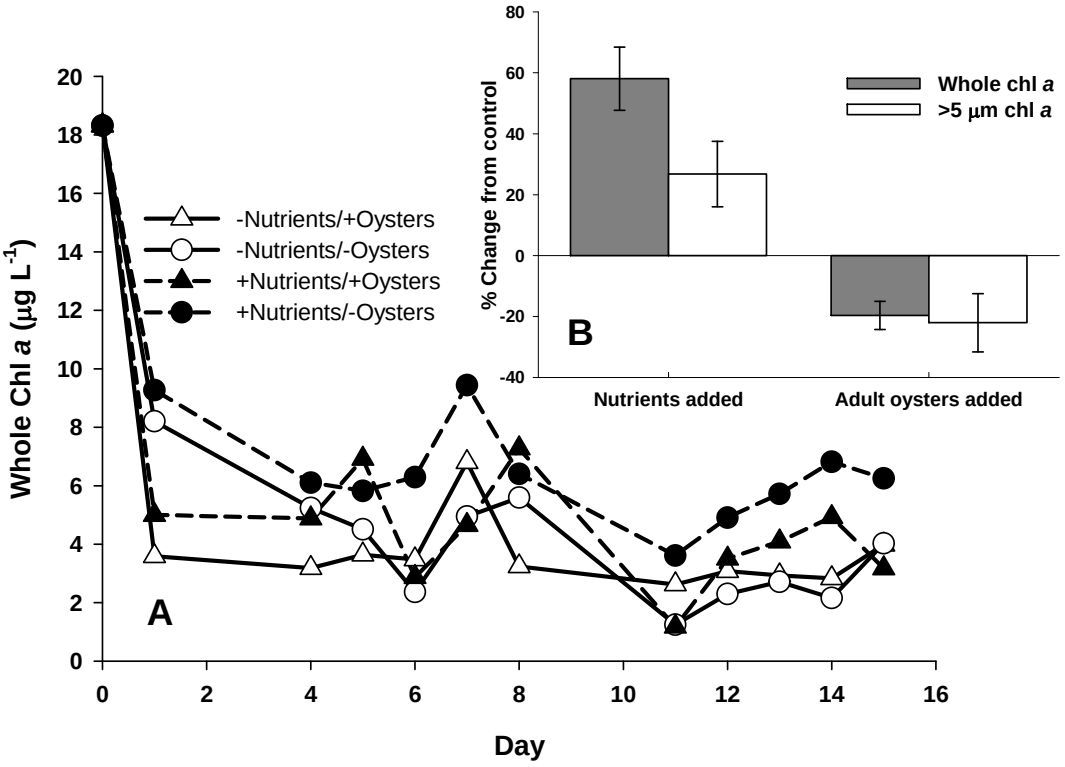

Figure 2.4. Chlorophyll *a* dynamics in Experiment 2. Time series data points (A) represent the mean (n=4) for each of the treatment combinations. Error bars are not presented for the sake of visual clarity. The mean relative standard deviation of measurements for whole chl *a* was 46.0% during the experiment. Inset (B) shows mean (± SE) daily percent increase or decrease from nutrient addition over both bivalve treatments and from bivalve addition over both nutrient treatments. See text for magnitudes of nutrient loading and densities of adult bivalves.

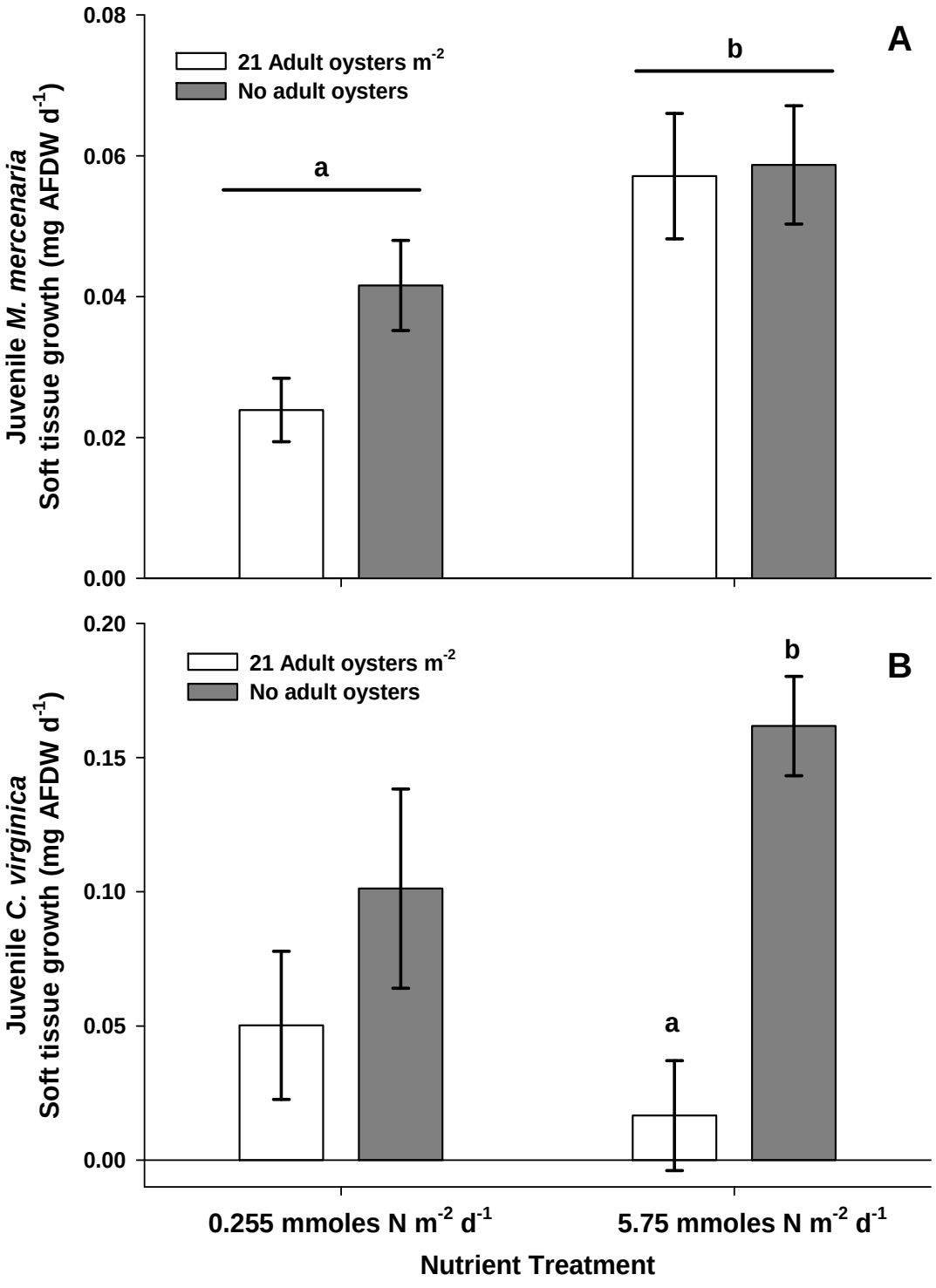

Figure 2.5. Growth responses from Experiment 2 for (A) juvenile *Mercenaria mercenaria* and (B) juvenile *Crassostrea virginica*. Bars are means ± SE. Letters above bars indicate significant difference. Nutrients were added as 16:1 inorganic N:P.

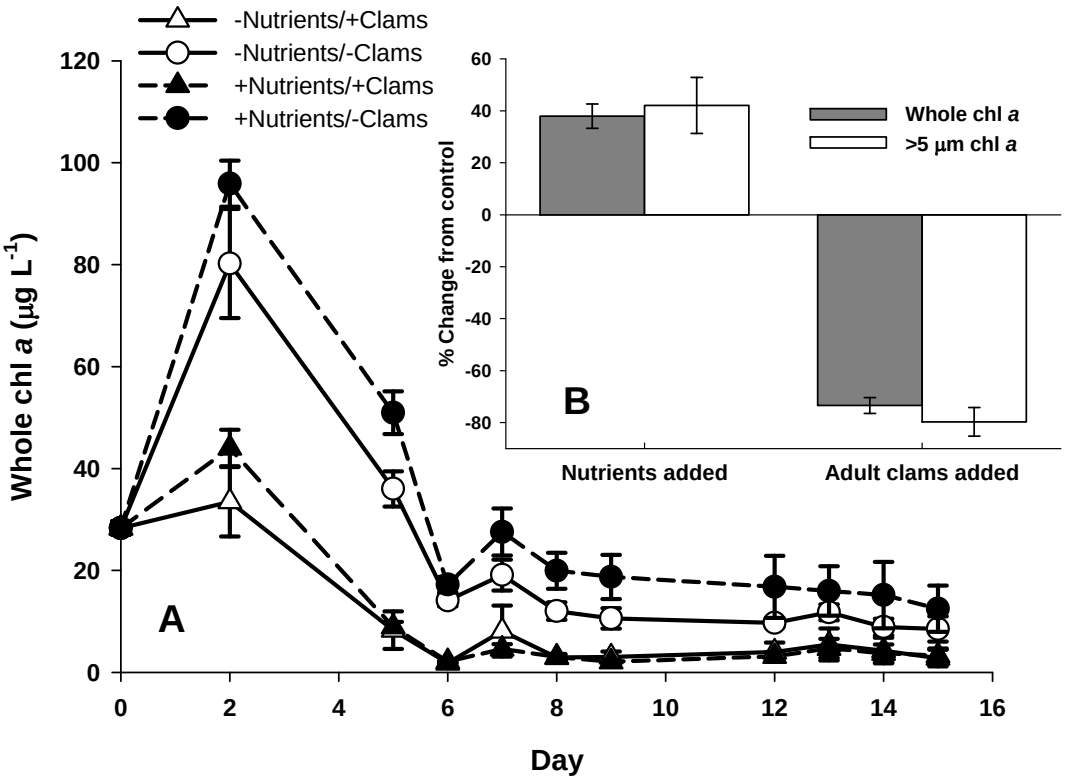

Figure 2.6. Chlorophyll *a* dynamics in Experiment 3. Time series data points (A) represent the mean (± SE, n=4) for each of the treatment combinations. Inset (B) shows mean (± SE) daily percent increase or decrease from nutrient addition over both bivalve treatments and from bivalve addition over both nutrient treatments. See text for magnitudes of nutrient loading and densities of adult bivalves.

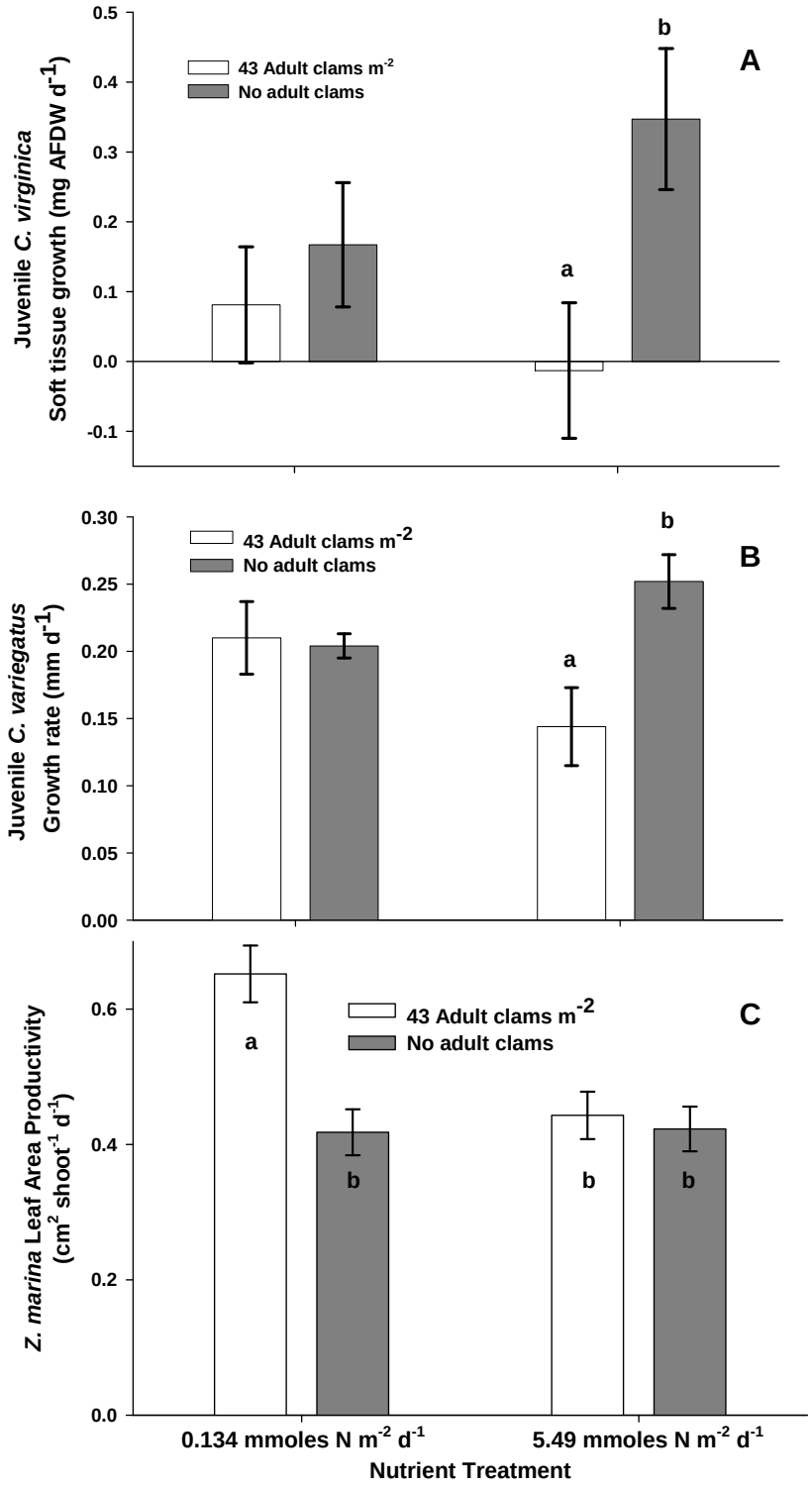

Figure 2.7. Growth responses from Experiment 3 for (A) juvenile *Crassostrea virginica*, (B) juvenile *Cyprinodon variegatus*, and (C) *Zostera marina.* Bars are means ± SE. Letters above bars indicate significant difference. Nutrients were added as 16:1 inorganic N:P.

III. Survival and suspension feeding by loggerhead sponges (*Spechiospongia vesparium*) during harmful cyanobacterial blooms in a shallow sub-tropical lagoon, Florida Bay, FL, USA

Abstract:

Shallow, coastal lagoons are vulnerable to eutrophication and harmful algal blooms, often due to the loss of benthic suspension feeders. Florida Bay, FL, USA, is a sub-tropical lagoon that has suffered from a series of ecological disturbances, including cyanobacterial blooms, loss of seagrass habitat, and widespread sponge mortality. A field study was executed at sites across Florida Bay to investigate effects of cyanobacterial blooms of the genus *Synechococcus* on the suspension-feeding loggerhead sponge (*Spechiospongia vesparium*). *In situ* measurements of loggerhead sponge survival, water pumping rates, and particle retention were made seasonally under bloom and non-bloom conditions for naturally-occurring and transplanted sponges. The mortality of transplanted loggerhead sponges significantly increased following cyanobacterial blooms. Cyanobacteria blooms depressed sponge water pumping rates, particle retention, and chl*a* filtration rates. When loggerhead sponge community filtration rates were compared with cyanobacteria growth rates, sites with low abundances of sponges had persistent, dense blooms and harbored positive net growth rates for cyanobacteria (0.77 – 1.42 d^{-1}). In contrast, sites with high abundances of sponges had few or no blooms and net growth rates for cyanobacteria that were slow or negative (-0.21 – 0.20 d^{-1}). This suggests that the loss of filtration from sponge mortality in Florida Bay has contributed to the persistence of algal blooms. Restoration of benthic suspension feeders such as sponges could be an important management tool to mitigate algal blooms in shallow coastal lagoons, although survival of transplanted populations will likely require concurrent improvement of water quality by other means since blooms inhibited sponge pumping, particle retention, and chlorophyll a removal.

Introduction:

Harmful algal blooms are increasing world-wide (Hallegraeff 1993, Lotze *et al.* 2006) and have led to human health concerns, loss of benthic habitats, and damage to estuarine resources (Gobler *et al.* 2005; Sunda et al 2006). Many of these algal blooms can be linked to eutrophication (Anderson et al 2008; Heisler et al 2008) or loss of benthic filtration (Newell 1988, Lotze *et al.* 2006). Benthic suspension feeders can filter the water column quickly enough to suppress blooms of phytoplankton in some systems (Officer *et al.* 1982, Cerrato *et al.* 2004; Wall et al 2008), and such top-down control should be more prevalent in ecosystems that are shallow and have a high density of consumers (Smaal and Prins 1993, Heck and Valentine 2007), such as shallow coastal lagoons. Since coastal lagoon systems often have extended physical turnover times, which makes them more vulnerable to harmful micro-algal blooms (Cloern 2001), the loss of benthic suspension feeders from such a system likely represents a more significant loss of top-down control than for a deeper, well-flushed ecosystem.

Florida Bay, FL, USA, is a shallow, sub-tropical lagoon between mainland Florida and the Florida Keys; it is the largest estuary in Florida, valuable for recreation and fisheries, and adjacent to the sensitive habitats of the Florida Keys National Marine Sanctuary and Everglades National Park. Since the late 1980's, Florida Bay has been affected by a series of ecological disruptions, including sponge die-offs (Butler *et al.* 1995), blooms of the cyanobacteria *Synechococcus* spp. (Phlips *et al.* 1999), and seagrass mortality (Robblee *et al.* 1991). The root cause of these disturbances may be linked to human alterations of the freshwater flow in the Everglades, which is upstream of Florida Bay (Phlips *et al.* 1999, Nuttle *et al.* 2000). These ecological disruptions have resulted in widespread loss of benthic habitat for juvenile fish and spiny lobster (Robblee *et al.* 1991, Butler *et al.* 1995) and a loss of benthic filtration from suspension-feeding sponges (Peterson *et al.* 2006). These changes may eventually result in a "regime shift" from a benthic-dominated system to a pelagic-dominated system in some regions of Florida Bay (Chasar *et al.* 2005), which is remarkable considering this system has an average depth of only 1 m (Nuttle *et al.* 2000). As such, Florida Bay could be considered an ideal case study in the eutrophication and loss of benthic filtration in a shallow coastal lagoon.

The dominant benthic suspension feeders in Florida Bay are sponges, especially *Spechiospongia vesparium*, the loggerhead sponge; Butler *et al.* 1995; Lynch and Phlips, 2000). Loggerhead sponges are fully heterotrophic, with a high abundance of microbial endosymbionts (Weisz *et al.* 2008). Sponges, along with octocorals and solitary hard corals, are a key component of the Florida Bay benthic community, providing structural habitat for juvenile octopus, stone crabs, and spiny lobster *Panulirus argus* (Butler *et al.* 1995). In the early 1990's, there were a series of widespread sponge die-offs in Florida Bay that affected >40% of the loggerhead sponges and >70% of other sponge species (Butler *et al.* 1995). Cyanobacterial blooms which occurred during sponge mortality are a putative cause (Butler *et al.* 1995), although subsequent laboratory-based experiments have failed to show a direct toxic effect by *Synechococcus* on sponges (Lynch and Phlips, 2000; Peterson *et al.* 2006). The precise causes of micro-algal blooms and sponge mortality in Florida Bay have yet to be resolved.

Persistent, dense blooms of cyanobacteria ($> 10^6$ cells mL^{-1}) have the potential for disrupting the ecology of estuaries through associated hypoxia, toxin production and/or the reduction of light availability for benthic plant communities (Phlips and Badylak 1996; Phlips *et al.* 1999; Sunda *et al.* 2006). An understanding of the bottom-up and top-down controls on *Synechococcus* blooms in Florida Bay will be crucial to successful ecosystem management and may provide clues to aid management of other coastal lagoons. Anthropogenic nutrient loading has been a problem in several areas of south Florida (Lapointe *et al.* 2004), but a clear pattern of nutrient loading that promotes *Synechococcus* blooms in Florida Bay has not emerged (Phlips *et al.* 1999, Glibert *et al.* 2004, Goleski et al 2010). In shallow, well-mixed systems such as Florida Bay, benthic suspension feeders such as bivalves or sponges can exert top-down control on phytoplankton (Officer *et al.* 1982). Dense sponge communities can pump water at rates sufficient to rapidly turn over entire water column volumes (Reiswig 1974) and can deplete near-bottom waters of picoplankton (Reiswig 1971a, Pile *et al.* 1997, Yahel *et al.* 2003). Cyanobacterial blooms in Florida Bay, perhaps combined with other environmental factors, seem to have disrupted pelagic (Goleski *et al.* 2010) and possibly benthic (Peterson *et al.* 2006) grazing in Florida Bay. Peterson *et al.* (2006) found that sponge mortality in the north-central region of Florida Bay increased water column

turnover time by sponge filtration from 3 d to 15 d and this region of Florida Bay has experienced the most dense and persistent cyanobacterial blooms (Phlips *et al.* 1999, Goleski *et al.* in press). To date, no study has considered how *in situ* changes in cyanobacteria blooms affect sponge populations in Florida Bay.

In this study, we sought to measure the effect of cyanobacterial blooms on the filtration and survival of loggerhead sponges (*S. vesparium*) in Florida Bay. We measured the survival of *S. vesparium* in regions of Florida Bay with and without cyanobacterial blooms. Through the InEx technique, we were able to separately measure water pumping rates and particle retention (Yahel *et al.* 2005) of suspension feeding sponges. The second objective was to use measured *in situ* filtration rates of loggerhead sponges under both bloom and non-bloom conditions to determine whether sponges exert significant top-down control on cyanobacterial blooms in this shallow, sub-tropical lagoon.

Methods:

Six study sites were sampled across Florida Bay to cover a range of bloom densities and geographic areas (Fig 3.1). These sites were Man O' War Key (N 25° 01.562', W 080° 55.764'), Barnes Key (N 24° 58.442', W 080° 48.279'), Samphire Keys (N 25° 06.478', W 080° 43.341'), Twin Key (N 24° 57.086', W 080° 43.865'), Park Key (N 25° 06.993', W 080° 32.178'), and Duck Key (N 25° 10.501', W 080° 29.270'). These study sites were visited each season over a one year period: 17-30 July 2006, 6-11 November 2006, 8-15 January 2007, 31 March - 6 April 2007, and 1-7 June 2007. Study sites were re-visited to survey water pumping rates from 7-15 December 2007. Additional study sites, Whipray Basin (N 25° 06.370', W 080° 45.020') and Blackwater Sound (N 25° 11.288', W 080° 25.945'), were used to investigate sponge water pumping rates, growth, and survival during the July and November 2006 sampling periods only.

Sponge Survival:

Loggerhead sponges were the focus of this study as they are the largest and most abundant sponge in Florida Bay (Peterson *et al.* 2006; C.C. Wall, pers. obs). Loggerhead sponges (1 – 3 L biovolume) were collected from sites in and around Lignumvitae Basin (N 24° 54.8', W 080° 44.5'), which hosted bloom-free water and abundant sponges at the beginning of the study. Sponges were removed from the bottom and grown onto marked bricks for ~5 days following the methods of Peterson *et al.* (2006). After attachment, sponges were rapidly transported in opaque vessels filled with seawater and transplanted (n = 4) to each study site and survival of transplanted sponges at each sampling time was recorded. Transplanted sponges were replaced as needed to maintain a sample size of four individuals at each site. Survival time was calculated in months for the transplanted sponges. Dead sponges were assumed to have survived half of the interval since the previous time-point.

Filtration and Particle Retention:

To measure *in situ* filtration rates of naturally occurring sponges and on transplanted sponges, the "InEx" method of Yahel *et al.* (2003, 2005) was employed. This method has been used to successfully measure filtration rates of several suspension feeders that have discrete siphons or oscula, such as sponges, bivalves, and solitary tunicates (Yahel *et al.* 2005). The InEx method consists of two techniques that separately measure pumping rate and particle retention. To measure pumping rates, small diameter plastic tubes (0.8-1.2 cm) loaded with a small amount of fluorescein dye were placed just above an osculum of an actively pumping sponge. Using an underwater video camera and/or stopwatch, the time for the pumping action of the sponge to eject dye from the tube was measured, yielding the "dye front speed." Dye front speed multiplied by the cross-sectional area of the tube provides a water pumping rate in mL s^{-1} $osculum^{-1}$, which was then scaled to L s^{-1} $individual^{-1}$ by multiplying by the number of oscula; rates were further normalized to sponge volume using direct measurements or estimates based on dimensions (L s^{-1} L^{-1} sponge biovolume). Pumping rate measurements were also made over bricks as a control for ambient water motion. Extreme light extinction during some micro-algal blooms prohibited measurement of pumping rates on some occasions and for

sites with very high bloom densities (Fig 2, Man O'War Key and Samphire Keys) only transplanted sponges were available.

Particle retention by sponges was measured by obtaining small volumes of inhaled and exhaled water (Yahel *et al.* 2003, 2005) in small plastic tubes (approx. 10 mL) with re-sealable caps. The "inhaled" sample was obtained from the ambient water around the sponge using a syringe to draw water into the "In" tube, while the exhaled sample was captured by placing the "Ex" tube just above the sponge's osculum. The "Ex" tube was held in place for a time that was 2x the dye-flushing time, usually 10-20 s. Both tubes were immediately capped underwater after obtaining the sample. Paired inhaled-exhaled samples were replicated three times per sponge, and at least three sponges were sampled per site per time point. The inhaled and exhaled samples were fixed in the field with a 1% formalin solution, and kept refrigerated until they could be flash-frozen in liquid N_2, always within three days after sampling. Abundance of heterotrophic bacteria (stained with SYBR Green I; Jochem 2001), picocyanobacteria, and photosynthetic picoeukaryotes were determined on a FACSort (Becton-Dickinson) flow cytometer using fluorescence patterns and particle size from side angle light scatter (Olson *et al.* 1991).

Inhaled and exhaled samples of chlorophyll *a* were also obtained, using a modified InEx method to obtain larger sample volumes (≥ 60 mL). Inhaled chl *a* samples were taken from ambient water with a syringe, while exhaled chl *a* samples were taken from pumping sponges using intravenous drip bags. These flexible, plastic bags were fitted with 1-cm Tygon tubing that was placed over the osculum of the pumping sponge and the tubing was held in place for 1 – 2 minutes typically ensuring ≥ 60 mL of water was collected. The bags and syringes were sealed underwater, and then kept refrigerated until the water could be filtered through GF/F filters, always within 2 hours. The filters were frozen and analyzed for chl *a* using standard fluorometric procedures (Parsons *et al.* 1984). Chlorophyll *a* samples were replicated as with the InEx samples, and chl *a* samples of exhaled water < 60 mL were discarded as insufficient samples.

Paired "In" and "Ex" samples were used to calculate retention efficiencies for chl *a* and the various cell populations using the equation:

Retention efficiency = 100 x ([In] – [Ex]) / [In]

Where "[In]" is the inhaled concentration and "[Ex]" is the exhaled concentration. The means of the "In" samples were used for total ambient cell concentrations at each site and each time point. Sponge filtration of cells or chl *a* by sponges was calculated using as

Filtration rate = water pumping rate x ([In] – [Ex])

Filtration rates calculated as above have the units of material removed per unit time per unit sponge biovolume. Water pumping rates and InEx samples were paired for individual sponges. On occasions where InEx samples but no water pumping rates had been obtained, a water pumping rate for that site and time point was hindcasted using a multiple regression of water pumping rate on cyanobacteria density, temperature, and salinity (see *statistical analyses* section). These hindcasted values for pumping rate were then combined with cell or chl *a* retention to calculate the filtration rate. Cyanobacterial cell densities, sponge water pumping rates, sponge retention efficiencies, and sponge survival were measured for 3 or more individual sponges per site per seasonal time-point. While we did not capture variation on a shorter (hours to weeks) time scale, our measurements provide "seasonal snapshots" that reflect longer-term variation in cyanobacteria blooms and sponge activity.

Estimating the impact of sponge grazing on cyanobacteria blooms in Florida Bay:

Biovolume-specific filtration rates of sponges (cells consumed $time^{-1}$ sponge $biovolume^{-1}$) were scaled to basin-wide filtration rates (cells consumed $time^{-1}$ m^{-2}) using the natural abundances (biomass m^{-2}) of loggerhead sponges in Florida Bay and the relationship between biomass and biovolume of loggerhead sponges in Florida Bay (Peterson *et al.* 2006). These basin-wide filtration rates were divided by the mean number of cells present in the water column for each basin to produce an instantaneous grazing rate (d^{-1}), akin to a zooplankton grazing rate (Calbet and Landry 2004). Sponges were assumed to be evenly distributed, have access to the whole, well-mixed water

column (Nuttle *et al.* 2000, pers. obs.), and to pump continuously at measured rates. These sponge grazing rates were then compared to the cyanobacteria growth rates as measured by Goleski *et al.* (2010) concurrently during this study to estimate net cyanobacterial growth or decline per basin and per time point as a function of sponge grazing and cyanobacterial cellular growth.

Statistical Analyses:

A "bloom threshold" of 350 x 10^3 cyanobacterial cells mL^{-1} (Phlips et al 1999; Goleski *et al.* 2010) was used to classify each site at each time point as "bloom" or "non-bloom" and a mean of the cyanobacterial densities for each site for two time points was used to classify the interim between those time points. The survival of transplanted sponges during each sampling period and at each site was tallied as a frequency of live/dead and analyzed using a G-test of independence to compare frequencies of live/dead after bloom and non-bloom periods. Water pumping rates, retention efficiencies, and filtration rates were analyzed using t-tests and 2-way analysis of variance (ANOVA) to compare values for sites, dates, bloom *vs.* non-bloom conditions, and transplanted *vs.* naturally-occurring sponges. Further analysis of water pumping rates, retention efficiencies, and cell removal rates was carried out by Spearman Rank Order correlations with ambient cyanobacteria densities, ambient chlorophyll *a*, temperature, and salinity. Water pumping rates were regressed on cyanobacteria density, temperature, and salinity using a forward step-wise multiple linear regression. Since the mortality of sponges in bloom-prone regions limited sample sizes during some time points for some locations, this regression equation was then used to hindcast water pumping rates for sites and dates where no water pumping rates were available. If data did not meet ANOVA assumptions, non-parametric tests or ln-transformed data were used. Statistical analyses were executed using SigmaStat 3.5.

Results:

Bloom dynamics:

Cyanobacterial densities (Fig 3.2) varied significantly across sites ($p < 0.01$) and dates ($p < 0.001$, 2-way ANOVA). Of the six sites visited, four had cyanobacteria blooms with cell densities above 350 x 10^3 cells mL^{-1} (Fig 3.2). Three of those sites in the north-central and southwestern regions of Florida Bay, Samphire Keys, Barnes Key, and Man O' War Key had blooms >10^6 cells mL^{-1} (Fig 3.2). The cyanobacteria densities at the Samphire Keys measured 590 x 10^3 cells mL^{-1} in Jul 2006, increased to 1,200 x 10^3 cells mL^{-1} in Nov 2006, and then decreased from Jan through Jun 2007. The cyanobacteria at Barnes Key were 3,200 x 10^3 cells mL^{-1} in Nov 2006, declined to 620 x 10^3 cells mL^{-1} in Jan 2007, and subsequently declined further to non-bloom levels from Apr-Jun 2007. The cyanobacteria at Man O' War Key reached 4,400 x 10^3 cells mL^{-1} in Jan 2007, which was the highest density of cyanobacteria recorded in this study. The density at this site decreased to 500 x 10^3 cells mL^{-1} in Apr of 2007, and declined to non-bloom levels in Jun 2007 (Fig 3.2). These three sites lie along the "north-central to southwestern axis" of Florida Bay (Fig 3.1) and bloom dynamics at these sites were consistent with those described by Phlips *et al.* (1999) and Glibert *et al.* (2004). The fourth site which experienced cyanobacterial blooms was Duck Key in the northeast region of the bay (Fig 3.1). This site was not found to have cyanobacteria blooms in previous studies (Phlips *et al.* 1999, Glibert *et al.* 2004). Cyanobacterial densities at Duck Key were 610 x 10^3 cells mL^{-1} at this site in Nov 2006 and 410 x 10^3 cells mL^{-1} in Jun 2007 (Fig 3.2). The two remaining sites, Twin Keys (southern region) and Park Key (northeastern region) had low densities of cyanobacteria throughout the study, ranging from 4.5 x 10^3 – 160 x 10^3 cells mL^{-1} at Twin Keys and 21 x 10^3 – 280 x 10^3 cells mL^{-1} at Park Key (Fig 3.2). Levels of chl *a* were strongly positively correlated with cyanobacteria densities across all sites and dates ($r = 0.619$, $p < 0.001$, Spearman correlation). Cyanobacteria densities were not correlated with temperature or salinity.

Temperatures were maximal in Jul 2006, ranging from 28.6 – 30.9°C, declined from Nov 2006 (23.1 – 25.1°C) through Jan 2007 (18.2 – 20.8°C), and began to rise

again from Apr (22.8 – 25.4°C) through Jun 2007 (27.5 – 29.1°C; Table 3.1). Salinities were variable (30.0 – 39.7) across sites and dates (Table 3.1). Although salinity was not significantly different by site, salinities across all sites in Jun 2007 (37.9 ± 0.5, mean ± SE) were greater than salinities in Nov 2006 (33.9 ± 1.4, Tukey test, $p < 0.05$; Table 3.1). Salinity was not significantly correlated with temperature, chl *a*, or cyanobacteria densities.

Sponge survival:

The survival of transplanted loggerheads ranged from 38% at Samphire Keys to 100% at Duck Key, but was not significantly different by site (data not shown). Survival of transplanted sponges differed by date and bloom *vs.* non-bloom conditions (Fig 3.3A; G-test of independence, $p < 0.05$). Survival was low (50%) from Jul-Nov 2006, increased to 91% from Nov 2006 – Jan 2007, decreased to 65% from Jan-Apr 2007, and increased again to 100% from Apr-Jun 2007. Sponge survival was significantly higher following non-bloom conditions (86%) than following bloom conditions (53%) across all sites and dates (Fig 3A, G-test of independence, $p < 0.001$). Sponge survival did not discernibly vary as a function of salinity or temperature. The survival time of transplanted loggerhead sponges varied from 10 months (length of entire study) at Duck Key to 1.5 months at Whipray Basin and Samphire Keys, both in the the north-central region. The $\log_{10}$ of survival time at each site was significantly negatively correlated with mean annual levels of chl *a* (Fig 3.3B, $r = -0.826$, $p < 0.05$, Pearson correlation).

Water pumping rates:

The water pumping rates of sponges under non-bloom conditions were significantly higher (0.114 ± 0.019 L s^{-1} L^{-1}) than sponges under bloom conditions (0.007 ± 0.003 L s^{-1} L^{-1}, $p < 0.001$, 2-way ANOVA) and there was a strong negative correlation between sponge water pumping rates and cyanobacteria densities (Fig 3.4, $r = -0.794$, $p < 0.001$, Spearman correlation). The water pumping rates of natural sponges were significantly higher (0.139 ± 0.024 L s^{-1} L^{-1}) than those of transplanted sponges (0.016 ± 0.004 L s^{-1} L^{-1}, $p < 0.001$, 2-way ANOVA). Water pumping rates were measured for both natural and transplanted sponges at Barnes Key and Twin Keys, and under non-

bloom conditions pumping rates of transplanted and natural sponges were similar ($p > 0.05$, Mann-Whitney rank sum test). The $\log_{10}$ of water pumping rates was explained by a multiple linear regression on cyanobacterial densities and salinity according to the following equation:

$$\text{Log}_{10}(\text{Pumping rate}) = -0.746*\log_{10}(\text{Cyano. density}) + 0.0479*S + 0.461$$

This regression explained 68% of the variance in $\log_{10}$(pumping rates) where pumping rate is expressed in "L s^{-1} L^{-1}" and cyanobacteria density is expressed in "cells mL^{-1}" ($r^2 = 0.68$, $n = 54$, $p < 0.001$). Temperature was rejected from the forward step-wise model as a significant predictor of pumping rate.

Retention efficiencies:

The retention efficiency of particles by loggerhead sponges varied by cyanobacterial cell abundance, site, and date (Table 3.2). The mean (± SE) retention of cyanobacteria by loggerhead sponges across all sites and dates (46 ± 2.2%) was significantly higher than the sponges' retention of chl *a* (35 ± 1.9%) or eukaryotic phytoplankton (36 ± 1.8%; Table 3.2; $p < 0.001$, ANOVA-on-ranks). The mean retention of bacteria (40 ± 1.7%) was not significantly different from the retentions of other cell populations. Retention efficiencies of loggerhead sponges for cyanobacteria were significantly different by site and date ($p < 0.001$ for both, 2-way ANOVA). Sponges at Duck Key had the highest average retention of cyanobacteria (51 ± 4.8%) while sponges at Barnes Key had the lowest (34 ± 4.9%). Retention of cyanobacteria at all sites was highest in Jun 2007 (69 ± 2.5%) and lowest in Jul 2006 (30 ± 4.9%). The retention efficiencies of natural sponges were not significantly different from retention efficiencies of transplanted sponges for any cell population ($p > 0.05$, 2-way ANOVA). The retention of eukaryotic phytoplankton by sponges across all sites and dates was significantly lower under bloom conditions (29 ± 3.5%) compared to non-bloom conditions (39 ± 2.1%; $p < 0.05$, 2-way ANOVA). Moreover, the retention of cyanobacteria and eukaryotic phytoplankton by sponges were both negatively correlated with ambient densities of cyanobacteria (Fig 3.5; $r = -0.247$, $p < 0.01$ for cyanobacteria retention; $r = -0.389$, $p < 0.001$ for eukaryotic cell retention; Spearman correlation). The retention of chl *a* by

sponges was not correlated with any of the other variables measured. The retention of bacteria and cyanobacteria by sponges was weakly correlated with salinity ($r = 0.186$ and 0.183, $p < 0.05$, Spearman correlation), but was not correlated with any of the other variables.

Chlorophyll *a* filtration rates:

Chlorophyll *a* filtration rates were not significantly different by site but did differ by date ($p < 0.001$, 2-way ANOVA on ln-transformed data, Table 3.3). The mean biovolume-specific chl *a* filtration ranged from 0.18 ± 0.04 µg ch l*a* d^{-1} mL^{-1} in Nov 2006 to 5.15 ± 1.05 µg chl *a* d^{-1} mL^{-1} in Jun 2007 (Table 3.3). Chlorophyll *a* filtration rates (Fig 3.6) were significantly lower (0.74 ± 0.20 µg chl *a* d^{-1} mL^{-1}) under bloom conditions than under non-bloom conditions (2.68 ± 0.45 µg chl *a* d^{-1} mL^{-1}, $p < 0.05$, 2-way ANOVA on log(x+1)-transformed data, Fig 3.6). The mean value of chl *a* filtration was higher for natural sponges than for transplanted sponges but this difference was non-significant (Fig 3.6). Chlorophyll *a* filtration rates were negatively correlated with cyanobacteria density ($r = -0.463$, $p < 0.001$, Spearman correlation) and were positively correlated with ambient chl *a* ($r = 0.279$, $p < 0.01$) and salinity ($r = 0.341$, $p < 0.001$).

Net growth rates of cyanobacteria as a function of sponge filtration:

Since there was a difference in measured pumping rates of natural *vs.* transplanted sponges, and this difference may have been biased by the lack of naturally-occurring sponges in bloom areas, a second multiple linear regression of water pumping rate on environmental conditions was conducted using only data from naturally-occurring sponges. This regression ($r^2 = 0.55$, $n = 25$, $p < 0.001$) was used as a better predictor of the pumping rates of natural sponges:

$$\text{Log}_{10}(\text{Pumping rate}) = -0.446*\log_{10}(\text{Cyano. density}) + 0.0435*S + 0.724$$

For this analysis, biovolume-based pumping rates were converted to biomass-based rates using a biovolume-dry weight linear regression (Peterson *et al.* 2006). In this case, pumping rate is expressed as "L hr^{-1} g DW^{-1}" to enable comparisons using Peterson *et al.*'s (2006) surveys of sponge biomass in Florida Bay.

Estimated net growth rates of cyanobacteria (Goleski *et al.* 2010) varied from positive to negative across Florida Bay during this study (Fig 3.7). The mean of cyanobacterial cellular growth across all sites and dates was 1.08 ± 0.21 d^{-1}, and ranged from 0.45 ± 0.15 d^{-1} at Duck Key to 1.81 ± 1.27 d^{-1} at Barnes Key (Fig 3.7). Since no growth rate data were available for Man O' War Key, the universal mean (1.08 ± 0.21 d^{-1}) was used for that site. These cellular growth rates are consistent with those previously reported for laboratory cultures of *Synechococcus* sp (Kana and Glibert 1987), the species of cyanobacteria which blooms in Florida Bay (Philips et al 1999). The mean grazing or removal rate of cyanobacteria by loggerhead sponges across all sites was 0.45 ± 0.10 d^{-1}, and ranged from 0.16 ± 0.10 d^{-1} at Samphire Keys to 0.83 ± 0.23 d^{-1} at Park Key (Fig 3.7). Cyanobacterial net growth rates were strongly positive ($0.77 – 1.42$ d^{-1}) at ManOWar Key, Samphire Keys, and Barnes Key, low ($0.02 – 0.20$ d^{-1}) for Twin Keys and Park Key, and were negative (-0.21 d^{-1}) for Duck Key (Fig 3.7).

Discussion:

Over the course of a one-year field study (Jul 2006-Jun 2007), we documented a cyanobacterial bloom of the genus *Synechococcus* in north-central and western Florida Bay, with bloom densities ranging from $10^5 – 10^6$ cells mL^{-1}. Survival of transplanted loggerhead sponges decreased following bloom periods and was negatively correlated with mean annual phytoplankton biomass. *In situ* measurements of loggerhead sponge water pumping rates and retention efficiency of particles revealed that both measures declined in the presence of dense cyanobacterial blooms. The sponges' chl*a*-based filtration rates decreased nearly four-fold under bloom conditions. Finally, study sites with blooms $> 10^6$ cells mL^{-1} had net positive cyanobacteria growth rates averaged over the year, while the other sites had loggerhead grazing rates sufficient to limit or exceed cyanobacteria growth rates when averaged over the year. Together, these findings demonstrate the key role sponges can play in preventing blooms, and the role cyanobacterial blooms can play in depressing sponge populations.

The results of the present study suggest cyanobacterial blooms have a negative impact on Florida Bay's sponge community and likely contributed to prior widespread sponge mortality (Butler *et al.* 1995, Stevely and Sweat 1998). Extracellular polysaccharides or toxins associated with *Synechococcus* cells in Florida Bay (Phlips *et al.* 1989; Lynch and Phlips 2000; Carmichael and Li 2006) may have disrupted sponge filtration and retention by affecting the choanocyte cells which are responsible for feeding in sponges. These compounds have impaired the filtration of other suspension feeders (Rohrlack *et al.* 1999; Gainey and Shumway 1991; Liu and Buskey 2000) and thus may have contributed toward sponge mortality. Lynch and Phlips (2000) did not find significant mortality of sponges exposed to natural and cultured *Synechococcus* (~5 x 10^6 cells mL^{-1}) over a time scale of 5 d, so it is reasonable to assume damage to sponges occurs over a longer time scale. In this study, the survival of transplanted loggerhead sponges after bloom periods declined significantly compared to survival after non-bloom periods on a time scale of ~two months (Fig 3.3A-B).

When the mortality of transplanted sponges was examined on a site-by-site basis, the picture becomes more complicated. The significant impact of cyanobacteria on sponge survival in this study was entirely due to mortality of sponges following bloom events at Samphire Keys, Whipray Basin, and Man O' War Key (Fig 3.1). Monthly water quality records for the region around the Samphire Keys indicate that chlorophyll *a* levels were elevated (4 to 7 $\mu g\ L^{-1}$) for 5 months during the fall-winter 2006-2007 period compared to a spring-summer baseline of 1 to 2 $\mu g\ L^{-1}$ (Table 3.4, SERC-FIU 2007). Given the strong correlation between chlorophyll *a* and cyanobacteria densities in this estuary found during this ($p<0.001$) and other studies (Phlips et al 1999; Glibert et al 2004; Goleski et al 2010) and the historical occurrence of cyanobacteria blooms in these regions of the bay, these trends suggests that the 2006-2007 cyanobacteria bloom in the north-central area persisted for several months, leading to damage to natural and transplanted sponges. Sponges at Barnes Key, which also experienced blooms along the "north-central to southwestern axis" (Figs 3.1 & 3.2), did not have mortality following bloom periods. Water quality records for the region near Barnes Key show that levels of chlorophyll *a* increased to 2.5 – 3.0 $\mu g\ L^{-1}$ for short periods in Oct 2006 and Jan 2007,

but in both cases decreased to 0.5 – 1.5 μg L^{-1} within a month (Table 3.4, SERC-FIU 2007). Transplanted sponges at Duck Key, which experienced blooms in the northeastern region in Nov 2006 and Jun 2007 (Figs 3.1 & 3.2), did not exhibit any mortality. Monthly water quality readings from the region around Duck Key confirm that chlorophyll *a* levels were only briefly above 2.0 μg L^{-1} in Oct to Nov of 2006, and then returned to a baseline of < 0.5 μg L^{-1} for the remainder of the study (Table 3.4, SERC-FIU). Collectively, these data suggest that cyanobacteria blooms were substantially shorter in duration and lesser in intensity at Duck Key and Barnes Key than at the Samphire Keys, so it is reasonable to assume these shorter blooms had a lesser impact on sponges.

Physical conditions (temperature, salinity, suspended sediment load) can be the underlying drivers of sponge mortality and several authors have suggested high or variable salinity as contributing to both sponge mortality and cyanobacteria blooms (Butler *et al.* 1995, Phlips *et al.* 1999, Peterson *et al.* 2006). During this study, the period with the highest salinities (Apr-Jun 2007, Table 3.1) corresponded to low cyanobacteria densities at most sites (Fig 3.2) and with 100% survival of transplanted loggerhead sponges at all sites. Moreover, sponge pumping rates generally increased, rather than decreased with increasing salinity and temperature.

The presence of cyanobacteria blooms clearly depressed sponge pumping rates in Florida Bay (Fig 3.4). Water pumping rates were significantly lower under bloom conditions, and there was a strong negative relationship between water pumping rates and cyanobacteria cell density (Fig 3.4). Sponge water pumping rates had a weak positive relationship with salinity over the range of salinities observed (30-39), and no detectable relationship with temperature. Temperature and salinity are obvious criteria that structure the physiology of all marine organisms, but they seemingly play a small role relative to cyanobacteria densities in affecting the responses of sponges over the range of values that we measured in Florida Bay. Many sponge species undergo periodic cessations of pumping activity on the scale of hours to days (Reiswig 1971b), and the sponges may pump less water to satisfy their food requirements when phytoplankton are dense. The

phenomenon is well known from bivalves, which slow pumping and/or retain proportionately fewer particles at high particle loads (Winter 1973, Navarro and Winter 1982, Clausen and Riisgard 1996), although there is considerable inter-specific diversity among bivalves in response to natural seston loads (Hawkins *et al.* 1996, Urrutia *et al.* 1996). But if the high particle load of cyanobacteria blooms clogs the canal systems of sponges and/or forces sponges to shut down their water pumping for extended periods of time, these effects could be a potential mechanism for the damage caused by blooms to sponge communities (Lynch and Phlips 2000) as reflected in the higher sponge mortality observed during some blooms in Florida Bay (Fig 3.3). High particle concentrations have been shown to decrease the growth of the sponge *Axinella corrugata* in a laboratory experiment (Duckworth *et al.* 2003). Little is known about the particle selection ability of sponges; although bivalve suspension feeders are known to pre-ingestively reject particles as a way of dealing with high particle loads (Hawkins *et al.* 1996, Ward *et al.* 1998). Harmful algal blooms in temperate environments have been known to suppress the water pumping activity of many bivalve suspension feeders (Shumway 1990, Sunda *et al.* 2006), through a combination of high particle load, poor nutritive quality of particles, and active toxic effects of the algae.

Most measurements of sponge pumping rates have been conducted in reef environments with clear water and relatively low particle loads (Reiswig 1974, Yahel *et al.* 2003, Weisz *et al.* 2008). Far fewer studies have been designed to understand how phytoplankton blooms affect sponge pumping within shallow coastal lagoons such as Florida Bay. The mean loggerhead sponge pumping rates in this study was 0.090 ± 0.016 L s^{-1} L sponge biovolume^{-1}, which is comparable to values for the same species of 0.069 mL s^{-1} mL^{-1} reported by Lynch and Phlips (2000), but lower than the values reported by Weisz *et al.* (2008) and Peterson *et al.* (2006) (0.176 L s^{-1} L^{-1} and 0.230 L s^{-1} L^{-1} respectively). The mean of pumping rates for loggerhead sponges under non-bloom conditions, was 0.113 ± 0.014 L s^{-1} L^{-1}, which is closer to the value of 0.176 L s^{-1} L^{-1} reported by Weisz *et al.* (2008) for the same species in a reef environment, suggesting cyanobacterial abundance may account for observed differences.

Weisz *et al.* (2008) characterize loggerhead sponges as having a "high microbial abundance" within their tissues relative to other sponges; this abundance largely consists of heterotrophic bacteria. Such a high microbial abundance would lead to a high respiratory demand for oxygen, possibly creating anoxic micro-environments within the sponge tissue (Hoffmann *et al.* 2005). Sponges that are subjected to high loads of particulate organic matter ($10^5 – 10^6$ cyanobacterial cells mL^{-1}) and dissolved organic matter (EPS secretion, Phlips *et al.* 1999) may not be able to pump water fast enough to satisfy the oxygen demand of microbes within their tissues. Although data is not available for *S. vesparium*, oxygen consumption rates of other tropical sponges range from 6 to 27 μmol O_2 h^{-1} g DW^{-1} (Yahel *et al.* 2003, Koopmans *et al.* 2010). Combining loggerhead sponge water pumping rates during bloom periods (0.007 L s^{-1} L^{-1} or 0.114 L h^{-1} g DW^{-1}) with mean dissolved oxygen levels during bloom periods (5 to 7 mg L^{-1}; SERC-FIU 2007) yields sufficient oxygen delivery only if the sponge is absorbing greater than 25% of the dissolved oxygen. Measured O_2 removal efficiencies for other sponges range from 1.1 to 5.6% (Yahel *et al.* 2003); at these low O_2 removal efficiencies loggerhead sponges under bloom conditions would not receive enough oxygen, making localized hypoxia/anoxia within the sponges' tissues is another possible mechanism of damage by cyanobacteria blooms.

Loggerhead sponges in Florida Bay were able to retain substantial proportions of cyanobacteria and other picoplankton that passed through their canal systems. The mean retention of cyanobacteria by loggerhead sponges was 46 ± 2.2% across all sites and dates, which was significantly higher than retention by sponges of eukaryotic cells (36 ± 1.8%) or chl *a* (35 ± 1.9%), and cyanobacteria retention was comparable to retention of heterotrophic bacteria (40 ± 1.7%, Table 3.2). There was a significant negative correlation between retention efficiency and cyanobacteria density in Florida Bay (Fig 3.5), and overall retention efficiencies were much lower than those reported for other sponge species and in other environments. Reiswig (1971a) reports retention efficiency by reef sponges of ~95% for bacteria and ~85% for unarmored flagellates, and 39-66% for diatoms and dinoflagellates. Pile *et al.* (1997) found sponges to retain 58-66% of *Synechococcus* cells in a lake environment, and Yahel *et al.* (2003) found sponges to retain 85-95% of all cells in a reef environment. Given that none of these studies

measured particle retention in loggerhead sponges (*S. vesparium*), some of these differences may be due to innate differences between species (Turon *et al.* 1997). Another explanation for the discrepancy between low retention efficiencies measured for loggerhead sponges in Florida Bay (46% of cyanobacteria, 40% of bacteria) and the high retention measured in other environments could result from the ambient particle load as reef environments tend to have low particle loads and Florida Bay had turbid waters and blooms of 10^5-10^6 cyanobacteria cells mL^{-1} (Table 3.1). Yahel *et al.* (2003) measured ambient *Synechococcus* concentrations several orders of magnitude lower, ranging from 10^3-10^4 cells mL^{-1}, which were retained at 85-95% by the reef sponge *Theonella swinhoei*. The feeding requirements of loggerhead sponges in Florida Bay may have been saturated by dense ambient cell concentrations, which would not be observed in most reef environments. This may be similar to food saturation in bivalves, which have been observed to retain a lower percentage of particles and/or decrease their filtration rates at very high food concentrations (Tenore and Dunstan 1973, Clausen and Riisgard 1996). Alternatively, this could be due to substances produced by cyanobacteria cells inhibiting sponges as described above. Studies of sponge metabolism and assimilation (Riisgard *et al.* 1993, Koopmans *et al.* 2010) may indicate how many of these retained particles are actually ingested by sponges and gauge the contribution of endosymbiotic microbial communities to sponge metabolism (Yahel *et al.* 2003). If sponges are retaining large numbers of cells in their canal systems without being able to ingest or process those particles, then the mechanism of damage to sponges may be clogging of the canal system by cyanobacteria (Duckworth *et al.* 2003).

Independent measurements of water pumping rates and particle retention provide true filtration rates (Yahel *et al.* 2005). When chl *a* filtration rates were normalized to sponge biovolume (Table 3.3, Fig 3.6), loggerhead sponges filtered 3.6 x less chl *a* per unit time under bloom conditions than under non-bloom conditions. Although sponges feed on bacteria and detrital particles in addition to phytoplankton (Reiswig 1971a), this depression of chl *a* filtration rates by cyanobacteria blooms indicates that sponges are receiving less food during blooms. Bass *et al.* (1990) demonstrated that a phytoplankton community dominated by picoplanktonic cyanobacteria was nutritionally deficient for bivalve suspension feeders, and the same may hold true for sponge suspension feeders in

Florida Bay. Consistent with this hypothesis, Duckworth and Pomponi (2005) found that a diet of eukaryotic microalgae provided better nutrition and supported faster growth in the sponge *Halichondria melanadocia* compared to sponges fed a diet of bacterial cells.

While there was no difference between the retention efficiencies of natural and transplanted sponges, there was a strong decrease in the water pumping rates of transplanted sponges compared to natural sponges, and this difference was present, but marginally non-significant ($p < 0.10$) for chl*a*-based filtration rates. This suggests that transplanted sponges may have a lower filtration capacity in areas of Florida Bay affected by cyanobacteria blooms. Some bivalve suspension feeders have been known to adapt or acclimate to harmful algal blooms (Bricelj *et al.* 2005; Hegaret *et al.* 2007). The water pumping rates of natural and transplanted sponges were both negatively correlated with cyanobacteria density (Fig 3.4), but this negative correlation was much stronger for transplanted sponges (slope = -0.66; $r = -0.816$, $p < 0.001$, Spearman correlation) than for naturally-occurring sponges (slope = -0.32; $r = -0.587$, $p < 0.01$). The regressions of $\log_{10}$(pumping rate) *vs.* $\log_{10}$(cyano. density) have significantly different slopes for transplanted and natural sponges ($p < 0.05$, ANCOVA). Since the water pumping rates of natural sponges were less negatively affected by cyanobacteria densities, this may reflect an acclimation or adaptation on the part of the loggerhead sponge community that previously had been exposed to blooms, especially since transplanted sponges were harvested from a bloom-free area (Fig 3.1, 3.2) and were therefore "naïve" with respect to cyanobacterial blooms. Another hypothesis is that the transplanted sponges were stressed or damaged by the transplantation process and were not able to fully recover their water pumping functions. There are very few studies of the long-term responses of sponges to high particle loads or harmful algal blooms, so the degree to which sponges in affected regions of Florida Bay can adapt to and recover from persistent cyanobacterial blooms remains an open question.

The loss of sponge community in Florida Bay could explain the persistence of cyanobacteria blooms (Peterson *et al.* 2006) in the absence of clear trends in nutrients that would promote blooms (Glibert *et al.* 2004; Goleski *et al.* 2010). Peterson *et al.* (2006) calculated that the sponge filtration time of the north-central region's water

column was 3 d before the mortality event, and increased to 15 d afterwards, which corresponds to a turnover of 0.07 d^{-1}. This is consistent with our study, where we found that cyanobacteria intrinsic growth rates were ~ 1 d^{-1}, and loggerhead sponge grazing rates on cyanobacteria ranged from 0.16 d^{-1} at Samphire Keys in the north-central region to 0.84 d^{-1} at Park Key in the northeastern region (Fig 3.1, Fig 3.7). The three sites in our study that lie along the bloom-prone "north-central to southwestern axis" identified by Phlips *et al.* (1999) all had blooms > 10^6 cells mL^{-1}, and all had loggerhead sponge community grazing rates insufficient to keep pace with cyanobacteria growth rates (Fig 3.1, Fig 3.7). The other three study sites, which either had no blooms or intermittent blooms < 10^6 cells mL^{-1} (Fig 3.2), all had loggerhead sponge community grazing rates sufficient to limit or outpace cyanobacteria growth rates when averaged over the year (Fig 3.7), and the sponge community grazing rate would be even higher if other sponge species were included (Peterson *et al.* 2006). This suggests that the lack of benthic suspension feeding contributes to the development and persistence of harmful cyanobacteria blooms in Florida Bay. The loss of benthic grazing represents a positive feedback for the cyanobacteria, where harmful blooms impair grazers, and the loss of grazing enables further growth of cyanobacteria (Sunda *et al.* 2006). Unfortunately, this positive feedback for the cyanobacteria is a "death spiral" for sponges (Butler *et al.* 1995; this study), with resulting loss of ecosystem services provided by sponges (Bell 2008), and could eventually affect the entire benthic community (Chasar *et al.* 2005). This represents a "chicken or egg" management dilemma: more ecosystem filtration from suspension feeders is required to control algal blooms and improve water quality (Officer *et al.* 1982, Cerco and Noel 2007, Wall *et al.* 2008), but water quality must first be improved before successful restoration of sponges can be attempted (Johnston and Clark 2007).

While the ultimate cause of ecological disturbances in Florida Bay remains unresolved (Fourqurean and Robblee 1999), much of the focus in research and management has been on the altered hydrology in the upstream Everglades (Nuttle *et al.* 2000, Marshall *et al.* 2009) and subsequent changes in nutrient loading (Glibert *et al.* 2004). Cyanobacterial blooms have been a persistent (Phlips *et al.* 1999) and damaging disturbance to the Florida Bay benthic community (Butler *et al.* 1995), and loss of

benthic communities has been linked to estuarine decline world-wide (Lotze *et al.* 2006). While many studies of bottom-up factors (e.g. nutrient loading) have provided valuable information (Fourqurean *et al.* 1993, Phlips and Badylak 1996, Rudnick *et al.* 1999, Glibert *et al.* 2004), this study demonstrates that successful control of cyanobacteria blooms in Florida Bay can be achieved with adequate top-down, benthic grazing.

		Man O'War Key	Barnes Key	Samphires	Twin Keys	Park Key	Duck Key	Seasonal trends mean (range)
July 2006	T	30.9	30.7	28.6	29.3	29.7	30.7	30.0 (28.6 - 30.9)
	S	31.0	33.4	37.4	36.7	36.7	34.6	35.0 (31.0 - 37.4)
mean ± SE (n)	Chl *a*	0.76 ± 0.09 (9)	1.14 ± 0.08 (9)	1.65 ± 0.17 (8)	0.61 ± 0.03 (9)	0.53 ± 0.09 (12)	0.48 ± 0.04 (26)	0.86 (0.48 - 1.65)
	Cyanobacteria	115 ± 59 (12)	62.2 ± 3.5 (9)	587 ± 110 (9)	164 ± 2.2 (9)	278 ± 26 (9)	252 ± 32 (9)	243 (62.2 - 587)
Nov 2006	T	25.1	25.0	24.8	24.9	23.10	23.2	24.3 (23.1 - 25.1)
	S	37.6	36.6	31.2	36.8	31.40	30.0	33.9 (30.0 - 37.6)
mean ± SE (n)	Chl *a*	0.81	4.37 ± 0.39 (3)	1.39	0.29 ± 0.03 (20)	0.21 ± 0.02 (11)	1.63 ± 0.10 (15)	1.45 (0.21 - 4.37)
	Cyanobacteria	55.7 ± 20.0 (9)	3210 ± 323 (27)	1240 ± 124 (12)	54.6 ± 13.0 (30)	62.2 ± 5.5 (15)	607 ± 21 (18)	870 (54.6 - 3210)
Jan 2007	T	18.2*	18.5*	20.8	20.0	19.9	18.5	19.8 (18.2 - 20.8)
	S	37.3	37.10	32.9	35.7	31.8	31.8	34.4 (31.8 - 37.3)
mean ± SE (n)	Chl *a*	10.37	6.18 ± 0.23 (4)	1.06 ± 0.00 (3)	0.49 ± 0.06 (15)	0.38 ± 0.16 (3)	2.12 (1)	3.43 (0.38 - 10.37)
	Cyanobacteria	4370 ± 118 (6)	616 ± 30.0 (14)	137 ± 18.0 (6)	17.7 ± 3.4 (17)	28.3 ± 12.7 (12)	75.8 ± 8.4 (9)	875 (17.7 - 4370)
Apr 2007	T	23.6	23.5	25.4	23.6	23.3	22.8	23.7 (22.8 - 25.4)
	S	37.5	38.0	37.1	38.8	35.4	36.2	37.2 (35.4 - 38.8)
mean ± SE (n)	Chl *a*	0.63 ± 0.15 (7)	0.69 ± 0.05 (12)	0.61	0.11 ± 0.03 (12)	0.54 ± 0.05 (9)	0.37 ± 0.04 (20)	0.49 (0.11 - 0.69)
	Cyanobacteria	503 ± 5 (9)	28.9 ± 4.0 (12)	19.8 ± 1.5 (15)	4.48 ± 0.33 (9)	20.9 ± 0.7 (9)	8.09 ± 0.35 (9)	97.5 (4.5 - 503)
June 2007	T	28.4	29.1	28.6*	28.3*	27.9*	27.5*	28.3 (27.5 - 29.1)
	S	36.5	38.8	39.7*	37.7*	37.8*	37.0*	37.9 (36.5 - 39.7)
mean ± SE (n)	Chl *a*	0.76 ± 0.04 (11)	0.75 ± 0.04 (18)	0.53 ± 0.04 (15)	1.13 ± 0.13 (12)	1.46 ± 0.18 (15)	2.71 ± 0.08 (11)	1.22 (0.53 - 2.71)
	Cyanobacteria	36.6 ± 1.5 (12)	13.0 ± 3.3 (12)	11.4 ± 0.3 (9)	13.3 ± 0.5 (12)	21.3 ± 1.4 (12)	408 ± 9 (12)	83.9 (11.4 - 408)
Annual trends	T*	26.2 (18.1 - 31.7)	26.3 (18.4 - 32.4)	26.1 (18.5 - 31.9)	26.1 (19.0 - 33.1)	26.2 (18.8 - 31.5)	26.1 (19.6 - 31.6)	
mean (range)	S*	37.9 (34.0 - 42.4)	37.7 (35.1 - 42.2)	36.6 (29.9 - 43.9)	37.9 (35.1 - 42.7)	33.2 (29.4 - 37.8)	32.4 (25.9 - 37.0)	
	Chl *a*	2.67 (0.63 - 10.37)	2.63 (0.69 - 6.18)	1.05 (0.53 - 1.65)	0.53 (0.11 - 1.13)	0.62 (0.21 - 1.46)	1.46 (0.37 - 2.71)	
	Cyanobacteria	1020 (36.6 - 4370)	785 (13.0 - 3210)	399 (11.4 - 1240)	50.9 (4.5 - 164)	82.1 (20.9 - 278)	270 (8.1 - 607)	

Table 3.1: Summary of temperature (T, °C), salinity (S), chl *a* (µg L^{-1}), and cyanobacteria density (10^3 cells mL^{-1}) at all sites and sampling dates. *****T and S values marked with asterisk, including T and S values for annual trends, are taken from the South Florida Water Management District, who conducted monthly sampling at nearby sites from Oct 2006 – Sept 2007.

		Man O'War Key	Amb. density	**Barnes Key**	Amb. density	**Samphires**	Amb. density	**Twin Keys**	Amb. density	**Park Key**	Amb. density	**Duck Key**	Amb. density
Cyanobacteria	**Jul 2006**	33.2 ± 17.3 (3)	115	9.8 ± 7.2 (3)	62.2	26.5 ± 6.9 (3)	587	28.6 ± 12.0 (3)	164	49.1 ± 13.5 (3)	278	30.0 ± 8.8 (3)	252
	Nov 2006	13.3 ± 6.8 (3)	55.7	22.8 ± 3.8 (9)	3210	27.9 ± 8.0 (4)	1240	47.4 ± 5.0 (10)	54.6	64.0 ± 4.2 (5)	62.2	56.5 ± 4.5 (6)	607
% Retention	**Jan 2007**	0.79 (1)	4370	62.5 ± 6.0 (5)	616	41.6 (1)	137	49.3 ± 7.3 (6)	17.7	21.9 ± 6.4 (4)	28.3	32.2 ± 6.9 (7)	75.8
mean ± SE (n)	**Apr 2007**	80.9 ± 5.7 (3)	503	17.3 ± 8.8 (4)	28.9	39.3 ± 9.5 (5)	19.8	59.2 ± 12.6 (3)	4.48	63.6 ± 4.2 (3)	20.9	62.7 ± 6.2 (4)	8.09
	Jun 2007	79.1 ± 5.4 (4)	36.6	58.8 ± 7.5 (4)	13.0	81.4 ± 3.8 (3)	11.4	68.4 ± 1.7 (4)	13.3	66.8 ± 3.8 (4)	21.3	79.1 ± 5.4 (4)	408
Euk. Phyto.	**Jul 2006**	32.4 ± 10.3 (3)	0.205	64.0 ± 6.5 (3)	0.266	14.6 ± 7.3 (3)	0.336	34.4 ± 16.1 (3)	0.912	24.1 ± 2.9 (3)	0.128	16.2 ± 8.7 (3)	0.148
	Nov 2006	nd	nd	16.9 ± 4.2 (9)	2.46	15.6 ± 3.3 (4)	2.58	42.0 ± 7.6 (10)	2.17	39.5 ± 9.7 (5)	0.165	29.6 ± 3.9 (6)	2.19
% Retention	**Jan 2007**	15.7 (1)	2.47	27.0 ± 8.5 (5)	2.58	17.6 (1)	0.674	35.3 ± 5.1 (6)	0.278	32.7 ± 8.2 (4)	0.365	32.0 ± 5.8 (7)	1.13
mean ± SE (n)	**Apr 2007**	73.4 ± 3.0 (3)	0.558	25.3 ± 7.9 (4)	0.180	42.4 ± 11.0 (5)	0.460	39.9 ± 9.5 (3)	0.070	48.9 ± 9.3 (3)	0.139	65.0 ± 5.1 (3)	0.574
	Jun 2007	54.8 ± 11.4 (4)	0.351	36.1 ± 4.7 (4)	0.284	54.3 ± 6.0 (3)	0.257	26.1 ± 8.7 (4)	0.124	42.4 ± 5.0 (4)	0.364	49.0 ± 6.9 (4)	2.28
Bacteria	**Jul 2006**	36.9 ± 5.0 (3)	547	44.8 ± 1.1 (3)	448	62.9 ± 2.9 (3)	487	38.8 ± 9.2 (3)	1130	40.7 ± 1.1 (3)	659	15.7 ± 3.8 (3)	558
	Nov 2006	34.7 ± 7.4 (3)	197	18.7 ± 5.7 (9)	1840	27.6 ± 9.9 (4)	1790	40.6 ± 1.9 (10)	337	42.3 ± 0.8 (5)	415	53.6 ± 3.4 (6)	1250
% Retention	**Jan 2007**	0.0 (1)	2740	59.9 ± 4.8 (5)	515	62.9 (1)	491	39.5 ± 5.6 (6)	293	20.8 ± 1.8 (4)	301	18.3 ± 3.9 (7)	380
mean ± SE (n)	**Apr 2007**	74.7 ± 4.1 (3)	788	42.2 ± 4.0 (4)	260	43.1 ± 11.1 (5)	186	23.4 ± 2.6 (3)	224	34.2 ± 3.3 (3)	377	63.3 ± 0.9 (3)	535
	Jun 2007	49.2 ± 3.8 (4)	382	28.9 ± 2.8 (4)	243	65.7 ± 2.4 (3)	285	38.6 ± 0.7 (4)	368	42.9 ± 4.1 (4)	492	69.9 ± 1.0 (4)	536
Chlorophyll *a*	**Jul 2006**	35.6 ± 9.7 (3)	0.76	50.2 ± 5.4 (3)	1.14	34.8 ± 12.0 (3)	1.65	41.3 ± 7.1 (3)	0.61	33.9 ± 12.3 (4)	0.53	46.5 ± 8.1 (8)	0.48
	Nov 2006	nd	0.81	2.4 (1)	4.37	nd	1.39	28.9 ± 8.3 (6)	0.29	39.0 ± 6.1 (4)	0.21	12.4 ± 4.2 (5)	1.63
% Retention	**Jan 2007**	nd	10.37	51.7 ± 3.2 (2)	6.18	50.8 (1)	1.06	37.9 ± 13.4 (5)	0.51	22.2 (1)	0.38	82.3 (1)	2.12
mean ± SE (n)	**Apr 2007**	25.2 ± 18.3 (3)	0.63	31.3 ± 11.2 (4)	0.69	nd	0.61	28.2 ± 6.7 (4)	0.11	49.1 ± 3.2 (3)	0.54	25.1 ± 6.4 (7)	0.37
	Jun 2007	22.3 ± 5.3 (4)	0.76	31.9 ± 3.3 (6)	0.75	32.4 ± 9.0 (5)	0.53	33.6 ± 4.9 (6)	1.13	47.3 ± 4.6 (5)	1.46	46.0 ± 2.0 (4)	2.71

Table 3.2. Retention efficiencies (% retention). Shown are retention efficiencies of loggerhead sponges feeding on cyanobacteria, eukaryotic phytoplankton, bacteria, and chl *a*, along with ambient densities of cells (10^3 cells mL^{-1}) or chl *a* ($\mu g\ L^{-1}$) for all stations and timepoints. Values are given as mean ± SE (n). No data indicated by "nd."

	Man O'War Key	Barnes Key	Samphires	Twin Keys	Park Key	Duck Key	Seasonal trends mean ± SE (n)
July 2006	1.04 ± 0.65 (3)	4.01 ± 3.10 (3)	1.17 ± 0.44 (3)	0.46 ± 0.09 (3)	0.28 ± 0.13 (4)	1.34 ± 0.25 (8)	1.33 ± 0.41 (24)
Nov 2006	nd	0.03 (1)	nd	0.30 ± 0.10 (5)	0.18 ± 0.04 (4)	0.08 ± 0.03 (5)	0.18 ± 0.04 (15)
Jan 2007	nd	2.26 ± 0.21 (2)	0.75 (1)	1.81 ± 0.83 (6)	0.61 (1)	3.32 (1)	1.82 ± 0.49 (11)
Apr 2007	0.01 ± 0.01 (3)	1.14 ± 0.50 (4)	nd	0.58 ± 0.26 (4)	1.98 ± 0.20 (3)	1.93 ± 0.64 (7)	1.26 ± 0.28 (21)
June 2007	0.96 ± 0.22 (4)	3.98 ± 0.49 (6)	3.01 ± 0.83 (5)	12.34 ± 3.72 (6)	6.56 ± 1.41 (5)	1.22 ± 0.08 (4)	5.15 ± 1.05 (30)
Annual trends	0.70 ± 0.24 (10)	2.86 ± 0.65 (16)	2.15 ± 0.57 (9)	3.75 ± 1.37 (24)	2.42 ± 0.79 (17)	1.31 ± 0.24 (25)	2.33 ± 0.38 (101)

Table 3.3. Filtration rates of loggerhead sponges feeding on chl *a* (µg d^{-1} mL^{-1} sponge biovolume) for all sites and timepoints. Filtration rates are normalized to sponge biovolumes. Values are given as mean ± SE (n). No data indicated by "nd."

	2006						2007					
	Jul	**Aug**	**Sept**	**Oct**	**Nov**	**Dec**	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**
Rabbit Key Basin (near Man O'War Key)	0.71	0.76	0.64	0.58	2.63	0.27	11.61	2.77	0.21	0.19	0.28	0.70
Twin Key Basin (near Barnes Key)	1.40	0.90	0.81	2.72	0.42	1.54	2.73	1.16	1.77	0.14	1.43	3.04
Whipray Basin (near Samphire Keys)	0.88	1.82	6.55	4.08	2.71	7.09	4.09	3.93	3.48	1.18	1.36	1.94
Peterson Keys (near Twin Keys)	0.73	0.98	0.70	1.06	0.54	4.19	1.39	1.69	0.80	0.12	0.28	0.13
Butternut Key (near Park Key)	0.35	0.26	0.42	0.22	0.48	0.13	0.63	0.25	0.35	0.54	0.19	0.18
Duck Key	0.44	0.66	0.50	2.12	1.41	0.20	0.24	0.29	0.45	0.37	0.17	0.25

Table 3.4. Monthly chlorophyll *a* levels (μg L^{-1}) at SERC-FIU monitoring sites located near sponge study sites. Southeast Environmental Research Center – Florida International University "Data were provided by the SERC-FIU Water Quality Monitoring Network which is supported by SFWMD/SERC Cooperative Agreement #4600000352 as well as EPA Agreement #X7-96410603-3."

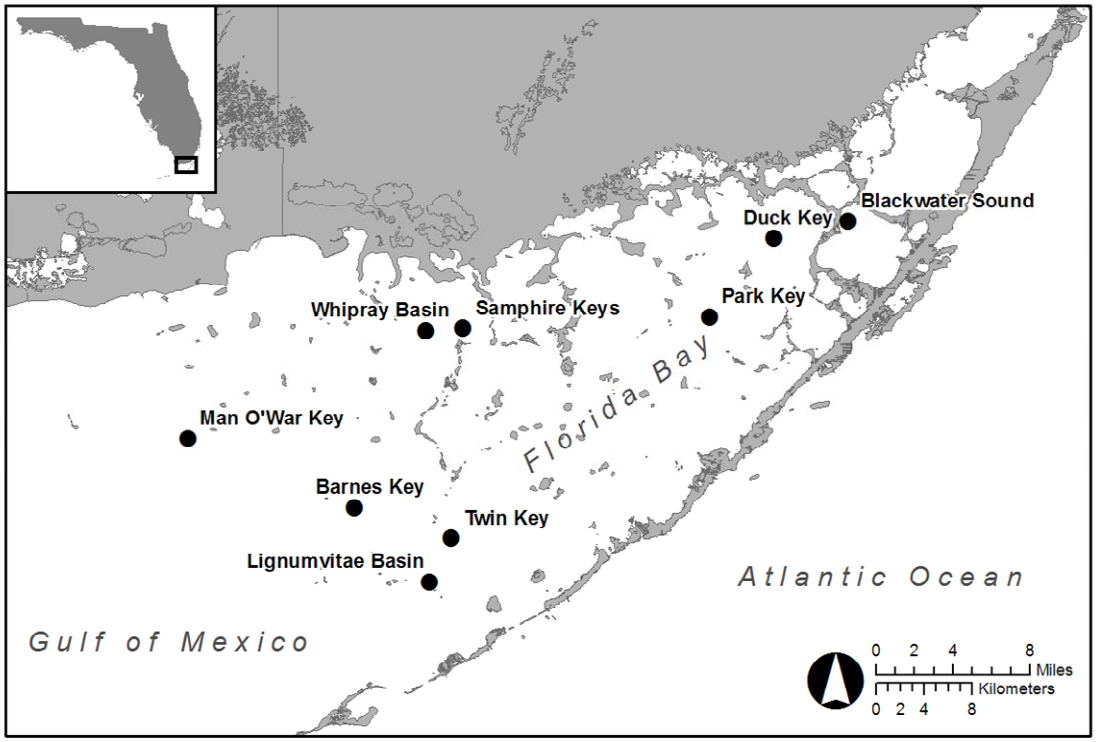

Figure 3.1. Locations of study sites in Florida Bay, FL, USA. Study sites are named by the nearest mangrove key.

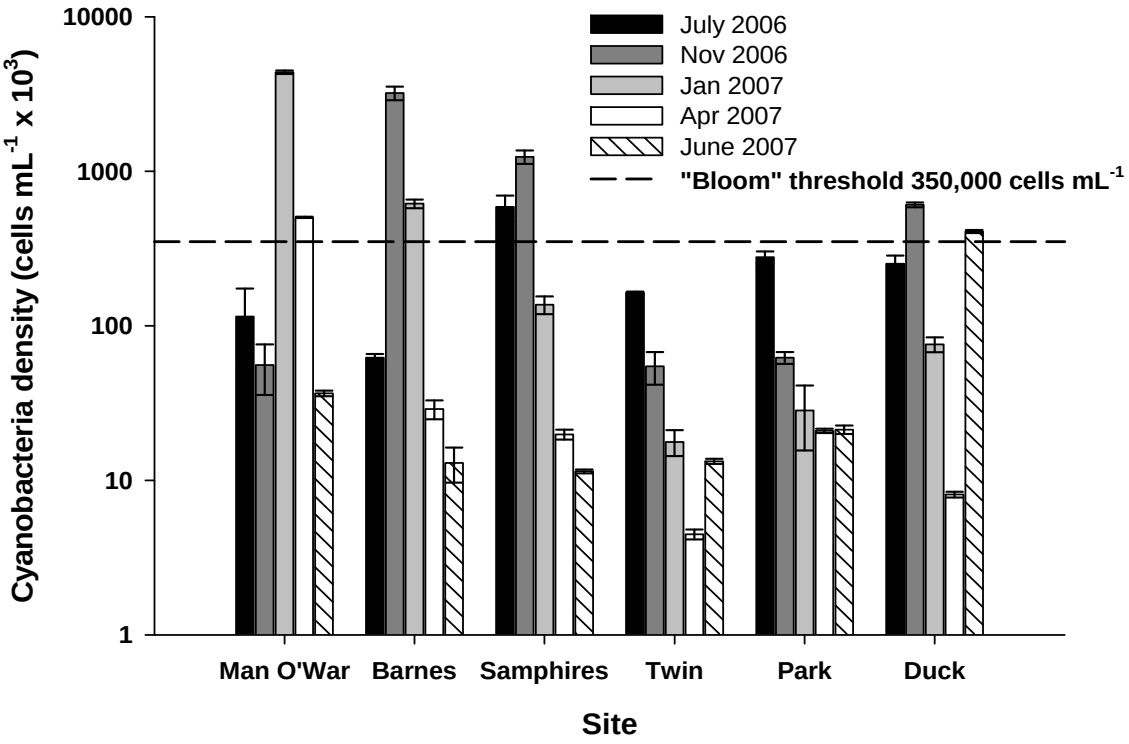

Figure 3.2: Cyanobacteria densities at Florida Bay study sites, 2006 - 2007. Values are mean ± SE.

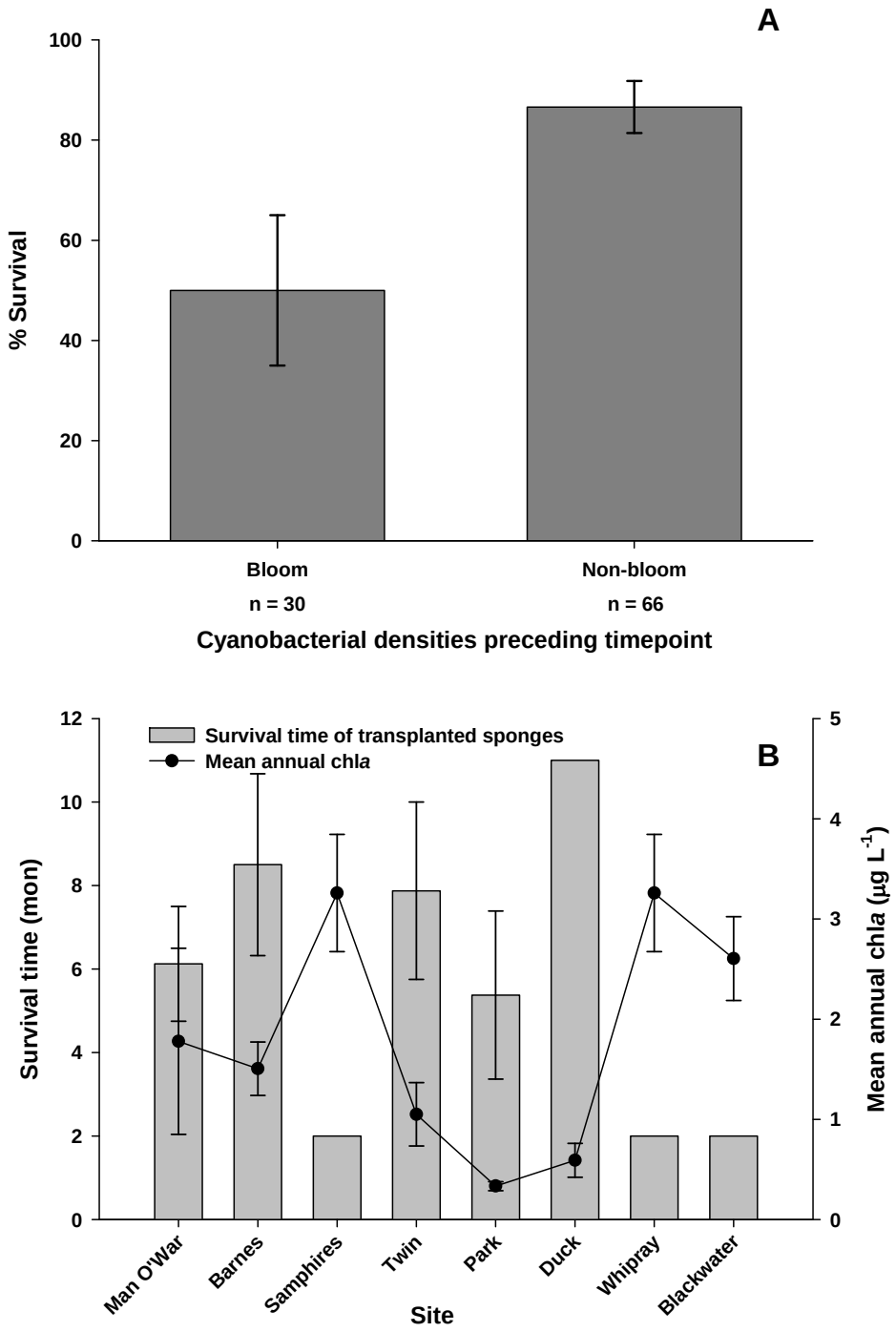

Figure 3.3. Survival (%) of transplanted loggerhead sponges. Shown are survival following bloom *vs.* non-bloom conditions (A), and survival time in months at each study site (mean ± SE) plotted alongside mean annual chl *a* for nearby SERC-FIU monitoring sites. A cyanobacteria density of 350 x 10^3 cells mL^{-1} was used as the bloom *vs.* non-bloom threshold.

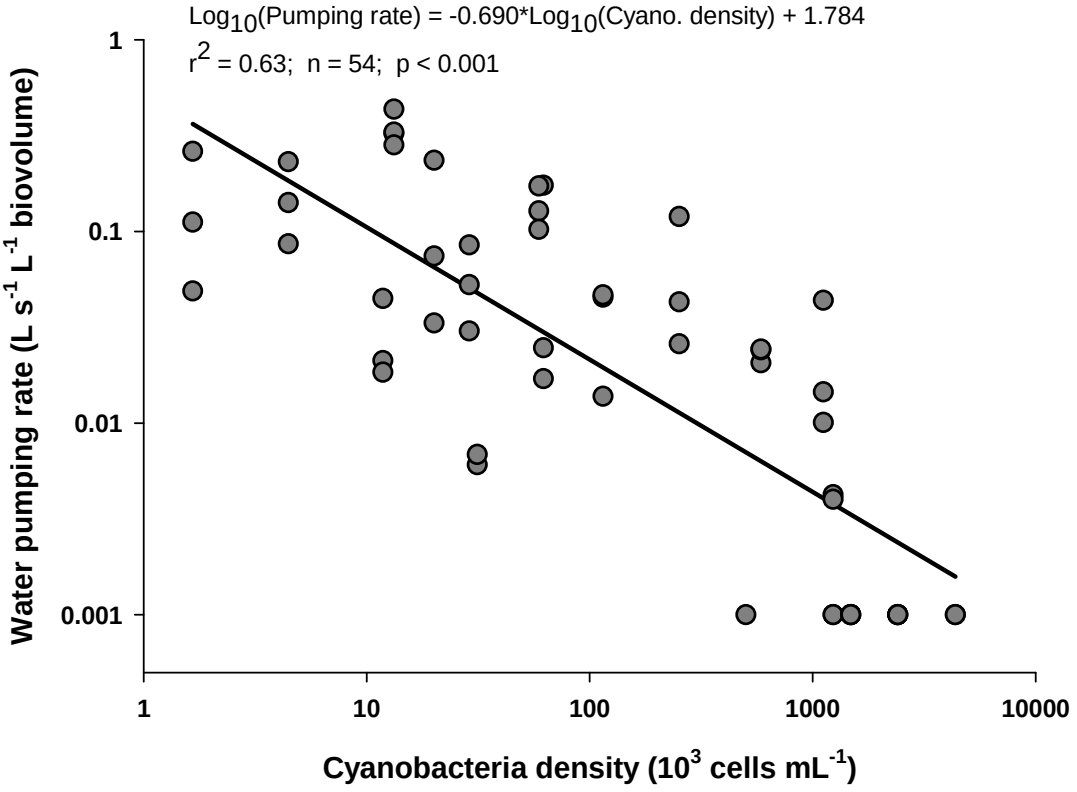

Figure 3.4. Measured water pumping rates. Water pumping rates (n = 54) of loggerhead sponges normalized to sponge biovolume (L s^{-1} L^{-1} sponge tissue) across the range of observed cyanobacteria densities. Regression is shown for just cyanobacteria density; r^2 increases to 0.68 if salinity and cyanobacteria are both included as predictor variables (see text for full equation).

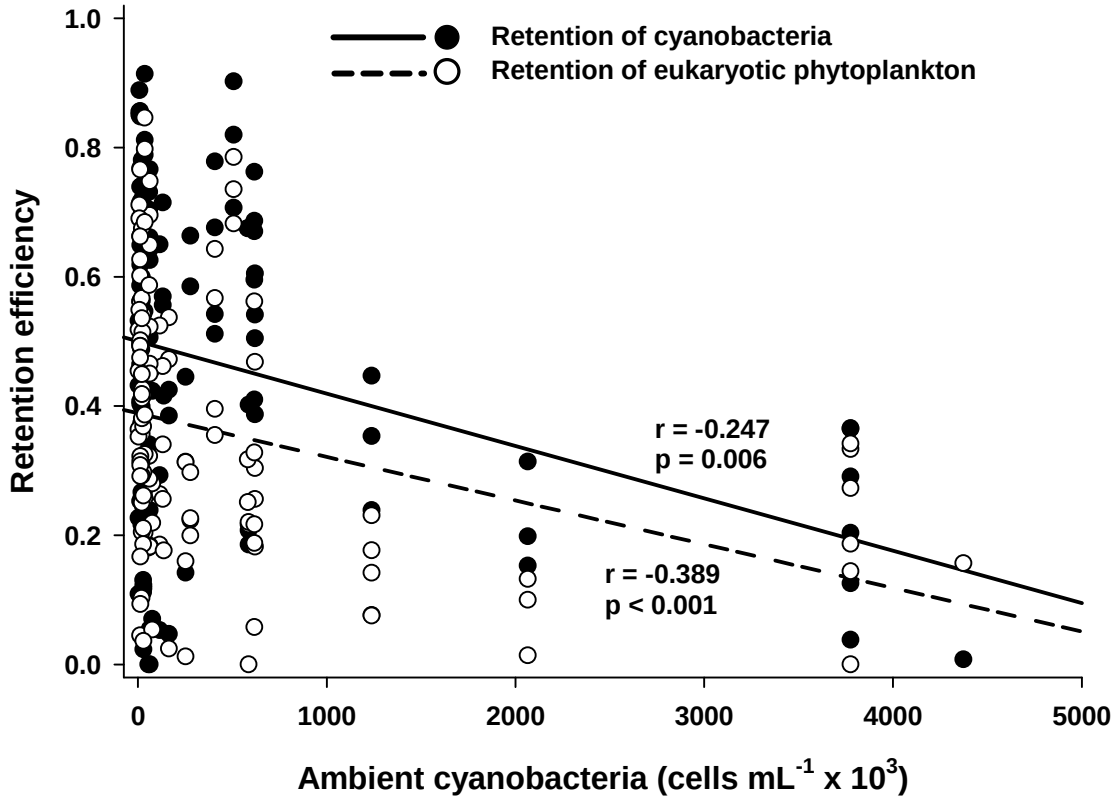

Figure 3.5. Retention efficiencies. Retention of cyanobacteria and eukaryotic phytoplankton by loggerhead sponges *vs.* ambient cyanobacteria density (n = 123 for cyanobacteria retention, n = 120 for eukaryotic phytoplankton retention).

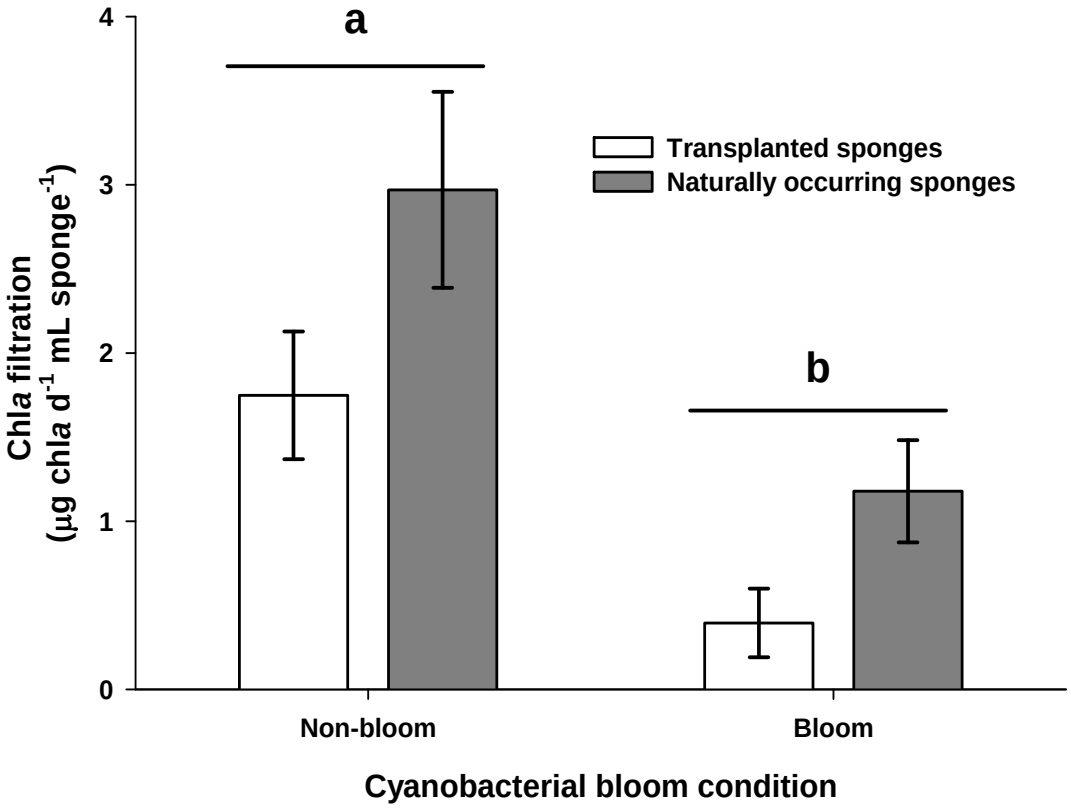

Figure 3.6. Chlorophyll *a* filtration. Comparison of chlorophyll *a* filtration rates under bloom and non-bloom conditions by transplanted and naturally occurring loggerhead sponges (n = 101). A cyanobacteria density of 350 x 10^3 cells mL^{-1} was used as the threshold for bloom *vs.* non-bloom conditions. Different letters above bars indicate significant difference. Values are mean ± SE.

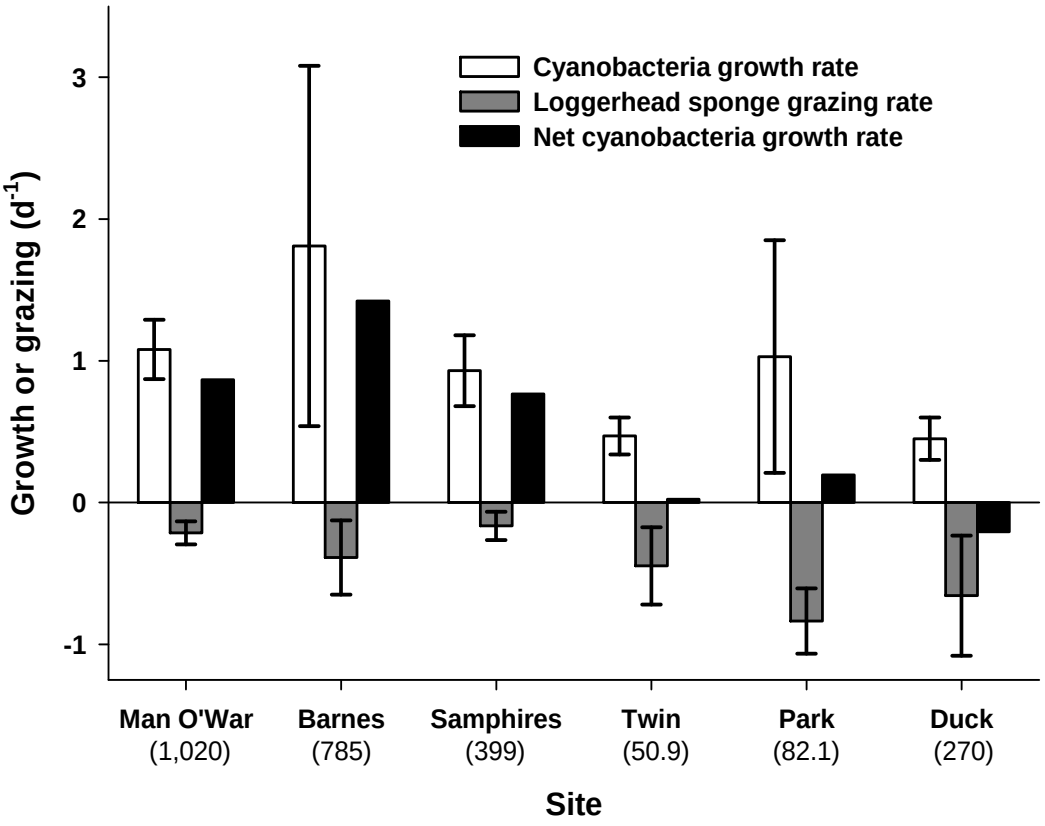

Figure 3.7. Growth and grazing. Cyanobacteria growth rates (n = 18), loggerhead sponge grazing rates (n = 5 per site), and net cyanobacteria growth (growth – grazing) averaged over all time-points for each site. Values of bars are mean ± SE. Numbers below each site name are the mean annual cyanobacteria density for that site in cells mL^{-1} x 10^3.

IV. The growth of estuarine resources (*Zostera marina, Mercenaria mercenaria, Crassostrea virginica, Argopecten irradians,Crepidula fornicata*) across a naturally-occurring eutrophication gradient in the Peconic Estuary, NY, USA

Abstract:

While many coastal ecosystems previously supported dense meadows of seagrass and dense stocks of bivalves, the impacts of overfishing, eutrophication, harmful algal blooms, and habitat loss have contributed to the decline of these important resources. Anthropogenic nutrient loading that leads to eutrophication has been identified by some researchers as a primary driver of these losses, but others have described potential positive effects of eutrophication on estuarine resources. The Peconic Estuary, Long Island, NY, USA, offers a naturally occurring nutrient loading gradient from eutrophic tidal creeks in its western reaches to mesotrophic bays in the eastern region. I conducted a two year field grow-out experiment at four stations across this gradient to examine the effects of eutrophication on the growth of estuarine resources: eelgrass (*Zostera marina*), juvenile bivalves (northern quahogs, *Mercenaria mercenaria*, eastern oysters, *Crassostrea virginica*, and bay scallops, *Argopecten irradians*), and the non-resource suspension feeder, the slipper limpet (*Crepidula fornicata*). Water quality parameters including phytoplankton community biomass and composition were also monitored at each site, and effects of water quality on estuarine resources was analyzed with multiple regression models. Northern quahogs and eastern oysters grew maximally within eutrophic locales and their growth was positively correlated with high densities of autotrophic nanoflagellates and centric diatoms in these regions ($p < 0.001$). The growth rates of northern quahogs were positively correlated with relative water motion, suggesting an important role for tidal currents in delivering seston to suspension feeders. Bay scallops and slipper limpets were negatively impacted by eutrophication, growing at the slowest rate at the most eutrophic sites. Bay scallop growth was negatively correlated with densities of dinoflagellates, which were more abundant at the most eutrophic site (p

< 0.001). Eutrophication seemed to primarily impact shellfish in the Peconic Estuary through changes in the quality of food and not the quantity since the growth rates of shellfish were more often correlated with densities of specific cell-types or quality of seston than bulk measures of phytoplankton and organic seston. Eelgrass growth was negatively impacted by eutrophication due to decreased light levels and increased epibiont loads. These results suggest that nutrient loading can have significant and complex effects on estuarine resource species, and that select species (e.g. oysters, clams) may benefit from eutrophication under some conditions while other species will perform poorly (e.g. scallops, seagrass). Future ecosystem-based approaches that seek to restore estuarine resources will need to account for the differential effects of nutrient loading as managers target species and regions to be restored.

Introduction:

Estuaries are home to a variety of valuable living resources. Finfish and shellfish are harvested directly in commercial and recreational fisheries, while seagrass beds are considered of paramount importance as structural habitat for shellfish and finfish in many coastal areas (Heck and Wetstone 1977, Irlandi and Peterson 1991, Beck *et al.* 2001). Many of the world's estuaries currently support lower abundances of finfish, shellfish, and seagrasses than they did historically due to overfishing (Jackson *et al.* 2001, Lotze *et al.* 2006), habitat loss (Short and Neckles 1999, Orth *et al.* 2006), eutrophication (Nixon 1995, de Jonge *et al.* 2002), and harmful algal blooms (Gobler *et al.* 2005, Sunda *et al.* 2006, Anderson *et al.* 2008). As such, estuarine management plans are typically focused on combating these harmful processes and restoring living resources (Lotze *et al.* 2006, Cerco and Noel 2007).

Changes in inorganic nutrient loading to estuaries can directly and indirectly influence the growth of marine resource species. High rates of nutrient loading have been associated with increases in pelagic productivity, commonly referred to as the process of eutrophication (Nixon 1995, de Jonge *et al.* 2002). Eutrophication has a well-known set of negative consequences, such as decreased water clarity, hypoxia, harmful algal blooms, and declines in seagrass growth and abundances (Duarte 1995, Diaz and Rosenberg 2008, Anderson *et al.* 2008). In response, estuarine management efforts often focus primarily on reducing anthropogenic nutrient loading in an effort to slow or reverse eutrophication (Cloern 2001, de Jonge *et al.* 2002).

However, not all estuaries and not all estuarine species are equal, and there is not a single "stimulus-response" relationship between nutrient enrichment and eutrophication (Borum *et al.* 1996, Cloern 2001). The susceptibility of estuarine systems to eutrophication will vary according to the particular hydrology, biology, and human activity in each system (Cloern 2001, Bricker *et al.* 2008). Some level of nutrient loading must be necessary to sustain primary and secondary production (Nixon and Buckley 2002), given that all systems have some loss of nutrients through burial or export. High levels of inorganic nutrients favor larger phytoplankton cells (Malone 1980, Raven and

Kubler 2002), such as diatoms and prymnesiophytes, which are generally considered a good source of nutrition for bivalves (Beukema and Cadee 1991, Wikfors *et al.* 1992, Weiss *et al.* 2007). Studies in several estuaries have shown blue mussels (*Mytilus edulis*), hard clams (*Mercenaria mercenaria*), softshell clams (*Mya arenaria*), and king scallops (*Pecten maximus*) can respond positively to increased nitrogen loading and high chlorophyll *a* levels in their habitats (van Stralen and Dijkema 1994, Weiss *et al.* 2002, Reitan *et al.* 2002, Carmichael *et al.* 2004, Weiss *et al.* 2007). Weiss *et al.* (2002) and Carmichael *et al.* (2004) found that shell growth, soft tissue growth, and survival of *M. mercenaria* and *M. arenaria* increased along a naturally-occurring gradient of nitrogen loading in Waquoit Bay, Massachusetts, USA. They attribute these changes to increased quantity and quality of food particles due to nitrogen enrichment (Carmichael *et al.* 2004), although a similar response was not found for bay scallops in the Waquoit Bay system (*Argopecten irradians*, Shriver *et al.* 2002). While nutrient over-loading in estuaries has a well-known set of negative consequences (Valiela *et al.* 1992, Nixon 1995, Kemp *et al.* 2005), the stimulation of secondary production in bivalves could be an overlooked positive effect of nutrient loading (Nixon and Buckley 2002, Carmichael *et al.* 2004), especially in shallow ecosystems with well-mixed water columns that rarely experience hypoxia.

The precise distinction between nutrient loading and nutrient **over**-loading remains an open question, and has clear ecological and financial implications for the management of estuaries. Systems that are well-flushed will be able to absorb and export more anthropogenic nutrients without experiencing negative effects than systems that are poorly-flushed, stratified, or otherwise vulnerable to eutrophication (Cloern 2001, de Jonge *et al.* 2002). The biota of an estuary also influences how the system reacts to nutrient loading. The filtration capacity of an intact benthos, with bivalve suspension feeders, can buffer the negative effects of eutrophication (Officer *et al.* 1982, Cerco and Noel 2007, Wall *et al.* 2008). Some authors have suggested that aquacultured bivalves could provide levels of water column filtration comparable to wild populations (Souchu *et al.* 2001, Newell 2004, Huang *et al.* 2008).

The level at which nutrient loading and its effects become harmful to a particular living resource will also vary between species and with the overall health of the estuary, and it is likely that decreases in nutrient loading leading to decreases in organic matter (oligotrophication) could likewise benefit some living resources and harm others (Nixon *et al.* 2009). Seagrasses are sensitive to eutrophication and to subsequent declines in light levels (Dennison *et al.* 1989, Duarte 1995), but could be recovered or facilitated by the presence of suspension-feeding bivalves which ameliorate turbidity (Newell and Koch 2004, Wall *et al.* 2008) or enhance nitrogen within sediments Carroll *et al.* 2008). Mobile fauna can avoid (at least temporarily) regions of low dissolved oxygen or poor water quality (Breitburg 2002), but most benthic organisms must simply endure the effects of eutrophication. Some species of bivalves, such as hard clams, soft-shell clams, and eastern oysters (*Mercenaria mercenaria, Mya arenaria, Crassostrea virginica*) can endure short periods of hypoxia (Kraeuter and Castagna 2001, Carmichael *et al.* 2004, Kennedy *et al.* 1996) and may even benefit from nutrient-derived increases in quantity and quality of food particles (Weiss *et al.* 2002, Carmichael *et al.* 2004). Other bivalve species, such as bay scallops (*Argopecten irradians*) and blue mussels (*Mytilus edulis*) are more sensitive to declines in water quality, and may not survive the effects of high nutrient loads (Shriver *et al.* 2002, Altieri and Witman 2006). As plans for aquaculture and restoration of living resources proceed, it will be vital for managers to know how various levels of nutrient loading will affect the growth and survival of resource species (Cloern 2001, Newell 2004, Lotze *et al.* 2006). Ecosystem based-management (Slocombe 1993, Lotze *et al.* 2006) will also require a careful examination of where nutrient loads need to be reduced, where they can remain at current levels, and even where they might be allowed to increase somewhat (Nixon and Buckley 2002).

Eutrophication leads to shifts in distribution and abundance, and many potential nuisance organisms have increased their ranges and abundances in eutrophic systems, concurrent with the removal of previously dominant organisms and the increase of nutrient loading (Mills 2001, Sunda *et al.* 2006, Lotze *et al.* 2006). The slipper limpet *Crepidula fornicata* is a gastropod suspension feeder, is not currently a resource species, and is proliferating in areas formerly dominated by bivalve suspension feeders (Lewis *et al.* 1997, Lewis and Rivara 1998, Harke *et al.* in progress). While slipper shells may

provide some of the filtration services formerly provided by bivalves (Barille *et al.* 2006, Harke *et al.* in progress), they are generally not considered a commercially important shellfish, and are invasive in areas of the northeast Atlantic (Barille *et al.* 2006). However, comprehensive estuarine management plans should incorporate the potential response of all species to changing levels of nutrient loading.

This study was designed to examine the effects of nutrient loading across a naturally-occurring estuarine gradient on water quality and the growth and survival of estuarine resource species: juvenile hard clams (*M. mercenaria*), bay scallops (*A. irradians*), oysters (*C. virginica*), and eelgrass (*Z. marina*). Juvenile slipper shells (*C. fornicata*) were also included as a non-resource suspension feeder. These five species were placed at four field sites spaced across a naturally occurring nutrient-loading gradient within the Peconic Estuary. The growth of all populations along with levels of light, nutrients, size-fractionated chlorophyll *a*, particulate organic matter, and phytoplankton community composition and abundances were monitored during two growing seasons (2008 – 2009) to assess the effects of different water quality characteristics on the growth of these living marine resources.

Methods:

Study site:

The Peconic Estuary, Long Island, NY, USA, is a system that provides a unique opportunity to study the effects of nutrient loading on several marine resource species simultaneously. The Peconic Estuary is a chain of interconnected bays totaling 218 km^2 with an average depth of 4.7 m and an average tidal range of 0.76 m (Hardy 1976). There is a gradient of nutrient and chlorophyll *a* concentrations from high in the western regions (more concentrated human activities, less tidal mixing) to low in the eastern parts of the estuary (less concentrated human activities, more tidal mixing; Hardy 1976, SCDHS 1976-2005). Mean annual total nitrogen in the Peconic River is 0.70 mg L^{-1}, decreases to 0.48 mg L^{-1} in Flanders Bay, and decreases further to 0.38 to 0.37 mg L^{-1} in

Great and Little Peconic Bays (SCDHS 1976-2005). Hypoxia/anoxia is generally not present in the Peconic Estuary, due to wind and tidal mixing, and a lack of salinity-based stratification (Hardy 1976), so differences observed in the growth of estuarine resources should be due primarily to nutrient-enrichment of algal biomass, and not to hypoxia. The Peconic Estuary was formerly the site of productive fisheries for scallops, oysters, hard clams, soft-shell clams, eels, and menhaden (Hardy 1976), but these resources have been greatly diminished due to over-harvesting and the effects of the harmful brown tide algae (Cosper *et al.* 1987, Gobler *et al.* 2005). There have been concurrent losses of eelgrass habitat throughout the Peconic Estuary (Pickerell and Schott 2006). There are very few measures of productivity in this system. Bruno *et al.* (1983) conducted seasonal sampling of the phytoplankton community in Little Peconic Bay. They describe the phytoplankton community as dominated by chain-forming diatoms *Skeletonema costatum* and *Thalassiosira* sp., constituting chains > 20 µm from December to March and single cells or chains < 20 µm during the rest of the year. Productivity was minimal at this site from Nov to Jan (0.072 g C m^{-2} d^{-1}) and increased to a maximum of 2.60 g C m^{-2} d^{-1} in Sept (Bruno *et al.* 1983).

Four study sites were established in the Peconic Estuary across the estuarine gradient from a eutrophic tidal creek in western Flanders Bay to more mesotrophic conditions in Great and Little Peconic Bay (Fig 4.1). In order of west to east, and in order of most eutrophic to least eutrophic, the sites were Meetinghouse Creek (MHC), Flanders Bay (FB), Great Peconic Bay (GPB), and Little Peconic Bay (LPB), and cover a total distance of approximately 20 km. Sites were approximately the same depth (1.8 – 2.5 m), and comparable in salinity and temperature, such that the gradient of nutrient loading / eutrophication should have been a primary factor driving differences in growth responses between the sites. All sites were sampled bi-weekly from 30 Jun to 5 Nov 2008. Since near hypoxic conditions were observed at MHC in 2008 during summer months, the three western sites (MHC, FB, GPB; Fig 4.1) were sampled tri-weekly from 9 Sept – 10 Nov 2009 when mid-day dissolved oxygen levels rose beyond 3 mg L^{-1} in MHC. The sites were similar in depth (2 m), and all experimental organisms were kept off of the bottom. The sediment type ranged from mud at MHC to sand at the eastern sites.

The estuarine species transplanted to each site were eelgrass (*Zostera marina*), northern quahgos (*Mercenaria mercenaria*), eastern oysters (*Crassostrea virginica*), and bay scallops (*Argopecten irradians* v. *irradians*). The growth of slipper limpets (*Crepidula fornicata*) was measured as a non-commercial molluscan suspension feeder which has recently proliferated in areas formerly dominated by resource bivalves (Lewis *et al.* 1997, Lewis and Rivara 1998). Eelgrass shoots were placed in planters and lowered to the bottom (Wall et al 2008). Each eelgrass planter was stocked with 32 separated shoots that had been hand-collected the previous day in Shinnecock Bay, and kept in flowing seawater until use in the field. Initial lengths of shoots were 20 to 30 cm, and reproductive shoots or shoots with less than 5 cm rhizome material were not used. Eelgrass was harvested and replaced every two weeks, and eelgrass productivity was quantified by leaf area growth and above-ground biomass production according to the methods of Ibarra-Obando and Boudouresque (1994). Epiphytes were scraped from eelgrass leaves at each time-point for measurement of epiphyte loading. Light levels at the depths of eelgrass trays (2m) were measured every 20 min by HOBO data loggers, and daily averages were taken between 9:20am and 2:40pm, when the sun was most directly overhead. Eelgrass growth was not measured in 2009.

Shellfish, obtained from the hatchery at Cornell Cooperative Extension, Southold, NY, were placed in mesh cages (~2 mm mesh size) and bags kept in wire cages as described in Weiss et al (2007). The initial sizes of hard clams, Eastern oysters, bay scallops, and slipper limpets in 2008 were 14.9 ± 0.2 mm, 7.5 ± 0.2 mm, 12.3 ± 0.2 mm, and 14.1 ± 0.2 mm, respectively. The initial sizes of northern quahogs, eastern oysters, bay scallops, and slipper limpets in 2009 were 13.4 ± 0.1 mm, 9.8 ± 0.2 mm, 15.7 ± 0.3 mm, and 16.6 ± 0.5 mm, respectively. For each resource bivalve species, 50 individual bivalves were stocked at each field site. Slipper limpets were stocked at a density of 40 individuals per site in 2008 and 25 individuals per site in 2009. All individuals were marked with bee-tags ("Queen Marking Kits," The Bee Works, www.beeworks.com) attached with Super Glue Gel™ so individual growth rates by shell length or by shell height could be measured. Shellfish were placed at the field sites in 2 mm mesh ADPI™ bags held in standard aquaculture cages (91 x 53 x 46 cm, Weiss *et al.* 2007). Clams and slipper limpets were measured by shell length (anterior-posterior), while oysters and

scallops were measured by shell height (hinge-ventral margin). Shell size was measured to the nearest 0.1 mm using hand-held calipers. Shell growth measurements were made every two weeks and at the end of the experiment and expressed as mean growth in mm week^{-1}. At the beginning of the experiment, 50 individuals of each species, which were not deployed in the field, were sacrificed to obtain initial ash-free dry tissue weights (AFDW), lengths, and heights. Ash-free dry weights were measured by drying whole shellfish to a constant weight at 70° C, and then combustion at 450° C for 4 h. Ash-free dry tissue weights and condition indices were measured on all surviving individuals at the end of the experiment, and mean growth rates by weight were calculated in mg AFDW week^{-1}. Shellfish and cages were cleaned of fouling material at every sampling point. The growth of organisms at each study site was monitored at each time point in 2008 and 2009.

Water quality parameters were measured bi-weekly at each site including chlorophyll *a*, dissolved oxygen, salinity, light attenuation, dissolved nutrient concentrations, POC/PON concentrations, and phytoplankton community composition and abundances. Temperature and ambient light levels were monitored continuously by HOBO© pendant-style data loggers. Light at the surface and at depth was also measured using a Li-Cor LI-192 Quantum Sensor™. Relative differences in bulk water motion (tidal mixing + wind mixing) between sites were measured using a plaster block dissolution method (Doty 1971, block dimensions 5 x 3.5 x 3cm) averaged over a 24 hour period. Chlorophyll *a* was measured in the whole and >5 µm size fractions using polycarbonate filters and standard fluorometric techniques (Parsons *et al.* 1984) and the detection limit was determined to be 0.2 µg chl *a* L^{-1} based on replicated blank measurements. Temperature, salinity and dissolved oxygen were measured using a YSI-556® probe with a thermistor, conductivity sensor, and polarographic oxygen sensor (Clark cell). Particulate organic carbon and particulate organic nitrogen were collected on pre-combusted glass fiber filters and processed using a CE Instruments Flash 1112 elemental analyzer (Sharp 1974), and the detection limits were determined to be 3.2 µM for POC and 0.3 µM for PON based on replicated blank filters and 200 mL sample volumes. Whole water samples for enumeration of nano- and micro-plankton were preserved using a Lugol's iodine solution and enumerated on an inverted microscope

after settling (Hasle 1978). The detection limit for this method of plankton enumeration is 1 cell mL^{-1}; replicated counts revealed that the coefficient of variation for dinoflagellate densities was 16% among replicate samples and the coefficient of variation for densities of all other cell types was 8.4%.

Sediment samples were taken in triplicate at each site July 2008 using modified 60 mL syringes as cores. Each 10cm-deep core was thoroughly mixed and then half was aliquotted for grain size analysis using a 63 μm sieve to separate sand from silt+clay. The other aliquot was used to determine porosity using wet and dry weights corrected for salt according to the calculation provided by Burdige (2006). After porosity measurements, dry sediments were combusted at 450° C for 4 h and organic content was calculated as % loss-on-ignition. This method can overestimate organic content for clay sediments due to the loss of hydrated mineral forms at 450° C (R. Aller, pers. comm.).

Water quality parameters were analyzed using two-way analysis of variance (ANOVA), repeated measures analysis of variance (ANOVAR), and Spearman correlations. Growth of eelgrass was analyzed using two-way ANOVAs to assess significant differences between sites and dates. Two-way ANOVARs were used to analyze measurements of tagged individual shellfish over several time points. When data did not meet the ANOVA assumptions, a non-parametric test was used (ANOVA on ranks or Friedman's repeated measures test). Chlorophyll *a* and light level trends were analyzed using two-way ANOVAs with site and time-point. When a significant effect on the response variables was detected, post-hoc tests (Tukey's Studentized range or Dunn's method) were used to test for significant differences between levels within the treatment. Correlation and regression analyses were used to account for growth responses in terms of water quality parameters. The significance of all statistical results was considered against the level of $\alpha = 0.05$. Basic statistical analyses were carried out on the software SigmaStat 3.0.

For regression analysis, data from both years were pooled and cell densities were transformed by $\log_{10}(x + 1)$ to achieve normality. Mean water quality parameters for each site during each sampling interval were aligned with week-by-week specific shell

growth rates. Prior to each regression analysis, all available predictor variables were screened for auto-correlation using Pearson correlation coefficients and Bonferroni-adjusted p-values; in the case of auto-correlation, only one variable from the correlated set or pair was used for the regression analyses. Shellfish growth rates were converted into specific growth rates using the equation:

$$\text{Specific growth} = [\ln(\text{size}_2) - \ln(\text{size}_1)]/(\Delta\text{time}).$$

These growth rates were calculated using shell size for the week-by-week time-points. A repeated measures multiple regression analysis was performed on these data according to the methods of MacDonald and Ward (2009). For this analysis, the group of shellfish at each site in each year was treated as a subject, using a mean specific growth rate (n = 50 individ. per site per year). For the seasonal mean growth rates, specific growth was calculated using shell sizes and ash-free dry weights for each individual of each species. Mean water quality parameters for each site for the whole season were aligned with seasonal shell-based and weight-based specific growth rates. Shellfish growth rates were then analyzed using a multiple linear regression with water quality parameters using a forward stepwise selection (F to enter $p < 0.05$; F to remove $p > 0.10$; Sokal and Rolhf 1995). Growth rates of individual shellfish were removed as outliers if the predicted value differed from the actual value by more than three standard deviations. Multiple regression analyses were carried out using the software Systat 13.

Results:

Physical characteristics:

Temperatures in 2008 started at 25 – 27° C in Jul and declined to 10 -11° C by early Nov (Table 4.1). While there was a statistical difference in temperature between sites ($p<0.001$, Friedman RM test), this difference was of small magnitude: the median temperature at Meetinghouse Creek was 24.9° C while the median temperature at the other sites ranged from 24.0 – 24.1° C. Salinities in 2008 were lowest in Meetinghouse Creek (26.3 ± 0.1) and increased from west to east to a maximum at Little Peconic Bay

(28.4 ± 0.1; Table 4.1). Salinity was very stable at each site and did not vary by date. Dissolved oxygen at the level of the shellfish cages (1.5 – 2 m) was lower in Meetinghouse Creek (seasonal mean of 4.18 ± 0.47 mg L^{-1}) compared to the other three sites (seasonal means of 6.60 to 7.23 mg L^{-1}; $p < 0.001$, ANOVAR; Table 4.1). Dissolved oxygen (DO) at all sites in 2008 was negatively correlated with temperature ($r = -0.415$, $p < 0.01$, Spearman correlation). The percent saturation of dissolved oxygen was calculated from DO concentrations and expected saturation at given temperatures and salinities. The percent saturation of dissolved oxygen was lower in Meetinghouse Cr in both years (Table 4.1), and dissolved oxygen saturation was positively correlated with salinity ($r = 0.508$, $p < 0.001$) and negatively correlated with chl *a* ($r = -0.287$, $p < 0.05$, Spearman correlation).

Three sites were sampled in 2009: Meetinghouse Creek, Flanders Bay, and Great Peconic Bay (Fig 4.1). In 2009, temperatures ranged from 23 to 24° C in early Sept and declined to between 10 and 11° C by early Nov (Table 4.1). There was no difference in temperatures between sites ($p > 0.05$, ANOVAR). Salinities in 2009 were lowest in Meetinghouse Creek (24.9 ± 0.6) and increased from west to east to a maximum at Great Peconic Bay (26.4 ± 0.4) and did not vary by date. Dissolved oxygen at 2 m depth was significantly lower in Meetinghouse Creek (4.29 ± 0.46 mg L^{-1}) compared to the other sites (5.66 ± 0.38 mg L^{-1}; $p < 0.001$, ANOVAR; Table 4.1).

Relative water motion as measured by plaster dissolution increased from west to east in a stepwise manner ($p < 0.001$, ANOVA on ln-transformed data; Fig 4.2), and the slowest field plaster dissolution (2.108 ± 0.023 g d^{-1}, Meetinghouse Creek) was significantly faster than the no-flow control ($p < 0.05$, Tukey test; 1.321 ± 0.024 g d^{-1}). Plaster dissolution was positively correlated with salinity ($r = 0.790$, $p < 0.001$) and dissolved oxygen ($r = 0.491$, $p < 0.001$, Spearman correlation). Additionally, salinity and dissolved oxygen were correlated ($r = 0.428$, $p < 0.01$), providing an overall trend in physical conditions of increased salinity, dissolved oxygen, and tidal flushing from west to east. Sediment in Meetinghouse Creek consisted of sulfidic mud with a very high organic content (Table 4.2), a high porosity, and a high percentage of fine-grained

particles. The other three sites had sandy sediment with a lower organic content, lower porosity, and more coarse-grained particles (Table 4.2).

Phytoplankton and organic seston:

Measures of food availability were tracked in three major ways: chlorophyll *a*, particulate organic carbon and nitrogen (POC and PON), and cell counts of nano- and microplankton. Chlorophyll *a* varied over time in 2008 (Fig 4.3A) but was consistently high in Meetinghouse Creek (26.30 ± 1.36 μg L^{-1}), lower in Flanders Bay (7.01 ± 0.79 μg L^{-1}), and declined further to the east in Great and Little Peconic Bays (3.77 ± 0.41 and 3.23 ± 0.20 μg L^{-1}, respectively; $p < 0.001$, 2-way ANOVA; Fig 4.3B). Virtually all chl*a* was in the >5 μm size fraction in Meetinghouse Creek (~100%), and this percentage declined in the eastern sites but never dropped below 76% based on seasonal averages (Fig 4.3B).

Levels of POC paralleled chl*a* (Fig 4.3A,C), and over the whole season there were strong positive correlations between whole chl*a* and POC ($r = 0.888$, $p < 0.001$) and PON ($r = 0.858$, $p < 0.001$). Levels of POC were highest in Meetinghouse Creek (301.10 ± 46.39 μM) and declined from west to east to 53.91 ± 4.39 μM in Little Peconic Bay ($p < 0.001$, 2-way ANOVA; Fig 4.3D). The molar ratio C:N in the organic seston was lowest in Meetinghouse Creek (7.06 ± 0.33) and increased in the eastern sites (9.23 – 10.01; $p < 0.001$, 2-way ANOVA), but did not have a consistent east-west pattern (Fig 4.3D). Over the whole season, there was a strong negative correlation between C:N molar ratios and whole chl*a* ($r = -0.579$, $p < 0.001$) and between C:N and POC ($r = -0.575$, $p < 0.001$; Fig 4.3D).

Cell densities of diatoms and dinoflagellates varied widely by site and date in 2008 (Figs 4.3E-H). Total diatom abundances in Meetinghouse Creek were 3.4×10^4 cells mL^{-1} in July of 2008, subsequently declined to < 1 cell mL^{-1} in Oct, and rebounded to 440 cells mL^{-1} in Nov of 2008. Diatoms at this site were mostly centrics of the genera *Thalassiosira*, *Chaetoceros,* and *Skeletonema*. Diatom densities were lower at Flanders Bay and Great and Little Peconic Bays (30 – 4,800 cells mL^{-1}) and pennate diatoms of the genera *Nitzschia* and *Asterionellopsis* were more prevalent (Fig 4.3F). Dinoflagellate

cell densities were higher in Meetinghouse Creek (3,190 ± 1,170 cells mL^{-1}) than the other sites (means of 60 – 310 cells mL^{-1}; $p < 0.001$, Friedman's RM test, Figs 4.3G-H), and consisted of the genera *Cochlodinium* and *Gymnodinium*, and the species *Prorocentrum micans*. Dinoflagellate densities increased in Meetinghouse Creek throughout the fall of 2008 (Fig 4.3G) as the bloom of centric diatoms disappeared (Fig 4.3E), while dinoflagellate densities declined to < 1 cell mL^{-1} at the other three sites by Oct-Nov of 2008. Other autotrophic nanoflagellates, consisting of cryptophytes and prymnesiophytes, were also significantly higher in Meetinghouse Creek (1,060 ± 270 cells mL^{-1}) than in Little Peconic Bay (330 ± 60 cells mL^{-1}; $p < 0.05$, ANOVAR; Fig 4.3H).

In 2009, patterns of chlorophyll *a*, POC, and PON were similar to 2008 (Fig 4.4). Chlorophyll *a* varied over time (Fig 4.4A) but was significantly higher in Meetinghouse Creek (15.02 ± 2.33 μg L^{-1}) than the other sites (1.86 – 2.06 μg L^{-1}; $p < 0.001$, 2-way ANOVA; Fig 4.4B) and virtually all of the chl*a* at all three sites was in the >5 μm size fraction (Fig 4B). Particulate organic carbon varied by site and date (Fig 4.4C); POC was significantly higher in Meetinghouse Creek (170.40 ± 15.48 μM) than Flanders Bay (50.59 ± 6.36 μM), which was also significantly higher than Great Peconic Bay (35.23 ± 1.35 μM; $p < 0.001$, 2-way ANOVA; Fig 4.4D). The molar ratio of C:N was significantly lower in Meetinghouse Creek (6.57 ± 0.33) than at the other two sites (7.99 – 8.27; $p < 0.05$, 2-way ANOVA; Fig 4.4D). Similarly to 2008, levels of POC in 2009 over the whole season were strongly positively correlated with whole chl*a* ($r = 0.783$, $p < 0.001$), and levels of PON were also positively correlated with whole chl*a* ($r = 0.867$, $p < 0.001$, Spearman correlation). Whole chlorophyll *a* and POC both had negative correlations with the C:N molar ratio in 2009 ($r = -0.830$, $p < 0.01$ and $r = -0.767$, $p < 0.05$, respectively).

Cell densities of diatoms varied by site and by date in 2009 (Fig 4.4E-H), and there were some similarities to plankton dynamics in 2008. Meetinghouse Creek had a bloom of predominantly centric diatoms (*Thalassiosira, Skeletonema,* and *Chaetoceros* spp.) that was first measured at 18,860 cells mL^{-1} in Sept and declined to 240 cells mL^{-1} by Nov (Fig 4.4E). Densities of diatoms were generally lower at the other two sites, and

pennate diatoms were more prevalent in Flanders and Great Peconic Bays (Fig 4.4E-F). While the fall diatom bloom in Meetinghouse Creek was declining, the numbers of dinoflagellates steadily increased (Fig 4.4G), which were mostly of the species *Prorocentrum minimum*. Dinoflagellate densities in Meetinghouse Creek (240 – 4,760 cells mL^{-1}) were significantly higher than at the other two sites in 2009 (25 – 140 cells mL^{-1}; $p < 0.05$, ANOVAR on ln-transformed data; Fig 4.4H). Due to large variation between dates, densities of other autotrophic nanoflagellates and diatoms were not significantly different between sites in 2009.

Over the course of both years, whole chl*a*, >5 µm chl*a*, POC, and PON were all strongly positively correlated (r-values of 0.79 to 0.95, Spearman correlation). Additionally, these values were all significantly negatively correlated with C:N of organic seston (r-values of -0.29 to -0.51, Spearman correlation) suggesting that the organic seston in the Peconic Estuary was mostly phytoplankton and not detritus, and that sites with high phytoplankton biomass tended to have nitrogen-enriched organic seston. Levels of chl*a* were positively correlated with centric diatoms ($r = 0.311$, $p < 0.05$), dinoflagellates ($r = 0.773$, $p < 0.001$), and autotrophic microflagellates ($r = 0.492$, $p < 0.001$) but not with pennate diatoms or autotrophic nanoflagellates. Centric diatoms were positively correlated with temperature ($r = 0.410$, $p < 0.01$) while pennate diatoms were negatively correlated with temperature ($r = -0.324$, $p < 0.05$), suggesting that there was a seasonal succession within the diatom community. Dinoflagellates were more prevalent at the western sites and their abundances were negatively correlated with salinity ($r = -0.582$, $p < 0.001$) and relative water motion ($r = -0.723$, $p < 0.001$, Spearman correlation).

Light penetration:

Mid-day light levels varied considerably between sites ($p < 0.01$) and dates ($p < 0.01$, 2-way ANOVA; Fig 4.5A). When averaged over the whole season, mid-day light levels were significantly higher at Little Peconic Bay (8.73 ± 1.52 kiloLux) compared to Meetinghouse Creek (3.54 ± 1.04 kiloLux; $p < 0.05$, ANOVA), and seasonal mean light levels increased consistently from west to east (Fig 4.5B). Bi-weekly measurements of PAR taken with a LiCor sensor confirmed the general trends of visible light measured in

kiloLux by the HOBO loggers. The percentage of surface PAR reaching the eelgrass trays at 2m was very low in Meetinghouse Creek (seasonal mean of 6.2 ± 0.8%) and increased towards the eastern sites to a seasonal mean of 18.7 ±1.3% at Little Peconic Bay (data not shown). Light levels as measured by the HOBO loggers were positively correlated with temperature ($r = 0.453$, $p < 0.01$) and with salinity ($r = 0.501$, $p < 0.01$, Spearman correlation), likely reflecting increased insolation in the summer months compared to the fall and increased light levels at the eastern sites which received more tidal flushing. Light levels were negatively correlated with whole chl*a* ($r = -0.371$, $p < 0.05$) and >5 μm chl*a* ($r = -0.500$, $p < 0.01$), as well as with total diatoms ($r = -0.394$, $p < 0.05$, Spearman correlation), indicating that light attenuation at the western sites may be due to elevated phytoplankton densities.

Eelgrass growth:

The leaf area production of eelgrass shoots (*Z. marina*) varied significantly by site ($p < 0.01$) and by date in 2008 ($p < 0.01$, 2-way ANOVA; Fig 4.6A). Leaf area production was slow and variable from Jul to Aug (0.38 – 0.65 cm^2 $shoot^{-1}$ d^{-1}), increased at most sites from Sept to Oct, and then declined to very low levels from late Oct to early Nov (Fig 6A). The maximum leaf area production was at Flanders Bay in mid-Sept (0.91 ± 0.09 cm^2 $shoot^{-1}$ d^{-1}; Fig 4.6A). When averaged over the whole season, leaf area production was significantly higher in the three eastern sites (means of 0.48 – 0.56 cm^2 $shoot^{-1}$ d^{-1}) compared to Meetinghouse Creek (0.40 ± 0.02 cm^2 $shoot^{-1}$ d^{-1}; $p < 0.001$, ANOVA on ranks; Fig 4.6B), representing a 20 – 40% increase from Meetinghouse Creek to the three eastern sites. Eelgrass shoots were frequently found uprooted or damaged, and large spider crabs (*Libinia emarginata*) were frequently observed crawling over or burrowing in the eelgrass trays (pers. obs.). This disturbance was quantified at each time point as "the percent of eelgrass shoots uprooted," which increased significantly by site from west to east ($p < 0.01$, 2-way ANOVA; Fig 4.6C). Over the course of the whole season, 79.2 ± 7.8% of all planted eelgrass shoots were uprooted at Little Peconic Bay, compared to 43.8 ± 6.4% at Flanders Bay and 36.5 ± 10.5% at Meetinghouse Creek (Fig 4.6C). Although productivity of above-ground eelgrass

biomass followed similar trends to leaf area production, there were no significant differences in biomass productivity between sites (data not shown).

The growth of epibionts on eelgrass blades was highest in Meetinghouse Creek, reaching a maximum of 14.8 mg AFDW cm^{-2} leaf area in Aug and averaging 4.0 ± 1.5 mg AFDW cm^{-2} leaf area over the whole season. The seasonal mean epibiont load in Meetinghouse Creek was significantly higher than epibiont densities at the other three sites ($p < 0.01$, ANOVA on ranks, data not shown). These epibionts in Meetinghouse Creek consisted of brown filamentous algae, solitary tunicates *Molgula* sp., and organic detritus (pers. obs.). In contrast, epibionts at the other three sites were never > 1.5 mg AFDW cm^{-2} leaf area, and averaged from 0.48 to 0.75 mg AFDW cm^{-2} leaf area over the whole season. The epibionts at the three eastern sites consisted mostly of brown and green filamentous algae, and epiphyte-grazing grass shrimp (*Palaemonetes pugio*) were frequently observed at the Flanders Bay site (pers. obs.), which had the lowest mean epibiont load on eelgrass blades (0.48 ± 0.06 mg AFDW cm^{-2}).

Shellfish growth (*M. mercenaria*):

The growth rates of the four species of shellfish were measured by shell growth and by soft tissue growth for the growing season in both years. Shellfish growth rates were generally faster in the Jul to Sept period of 2008 and the Sept period of 2009, and then slowed or stopped altogether with the cooler temperatures in Oct to Nov of both years. Juvenile clams (*Mercenaria mercenaria*) had an initial mean shell length of 14.9 ± 0.2 mm and reached lengths of 24 to 28 mm by the end of the 2008 season (Fig 4.7A). There was significant variation in bi-weekly growth rates by site ($p < 0.001$), date ($p < 0.001$), and site x date interaction ($p < 0.001$, 2-way ANOVAR). This interaction can be seen in Fig 4.7A, where clams at Meetinghouse Creek were smaller than clams at the other sites, and then eventually surpassed the growth of clams at the Great Peconic Bay site. When rates were calculated as whole season mean growth rates, the maximal shell and soft tissue growth rates were found at Little Peconic Bay (0.66 ± 0.02 mm wk^{-1} and 20.5 ± 1.2 mg AFDW wk^{-1}, respectively, Fig 4.7B). This shell growth was not significantly different from the shell growth at Meetinghouse Creek (0.59 ± 0.02 mm wk^{-}

^{1}) or Flanders Bay (0.58 ± 0.02 mm wk^{-1}), but was significantly higher than the shell growth at Great Peconic Bay (0.50 ± 0.02 mm wk^{-1}; $p < 0.001$, ANOVA; Fig #B). Soft tissue growth rates followed a similar pattern, ranging from 20.5 ± 1.2 mg AFDW wk^{-1} at Little Peconic Bay to 11.7 ± 0.9 mg AFDW wk^{-1} at Great Peconic Bay, with significant comparisons noted in Fig 4.7B (between site differences $p < 0.001$, ANOVA on ranks).

The growth rates of clams were generally slower in 2009 (Figs 4.7C-D), due to a shorter season and colder average temperatures over the Sept to Nov season of 2009 (16.0° C) compared to the Jul to Nov season of 2008 (21.9° C), and tri-weekly growth rates also varied significantly by site ($p < 0.001$), date ($p < 0.001$), and site x date interaction ($p < 0.001$, 2-way ANOVAR; Fig 4.7C). Juvenile clams had an initial mean shell length of 13.4 ± 0.1 mm in Sept and reached lengths of 16 to 18 mm by Nov (Fig 4.7C). Seasonal mean shell growth rates were higher at Meetinghouse Creek (0.51 ± 0.02 mm wk^{-1}) and Flanders Bay (0.46 ± 0.01 mm wk^{-1}) compared to Great Peconic Bay (0.34 ± 0.01 mm wk^{-1}; $p < 0.001$, ANOVA on ranks; Fig 4.7D). Soft tissue growth rates were also higher at Meetinghouse Creek in 2009 (7.8 ± 0.4 mg AFDW wk^{-1}) than at Flanders Bay (6.3 ± 0.3 mg AFDW wk^{-1}), which was higher than the soft tissue growth at Great Peconic Bay (5.0 ± 0.3 mg AFDW wk^{-1}; $p < 0.001$, ANOVA on ranks; Fig 4.7D). The trend of faster growth at the western site (Meetinghouse Creek) and slower growth in one of the eastern sites (Great Peconic Bay) was consistent in both years, although the significance of particular site contrasts differs by year and by measure of growth (Fig 4.7B,D).

Shellfish growth (*Crassostrea virginica*):

Juvenile oysters (*C. virginica*) had an initial mean shell height of 7.5 ± 0.2 mm in Jul of 2008 and rapidly attained shell heights of 48 to 56 mm by Nov (Fig 4.8A); these growth rates were much faster than those of juvenile clams (Fig 4.7). The bi-weekly shell growth rates of oysters in 2008 varied significantly by date ($p < 0.001$), and site x date interaction ($p < 0.001$, 2-way ANOVAR) but not by site. However, replication for the repeated measures test was reduced due to the loss of tags from individual oysters, and seasonal mean growth rates were highly significantly different between sites. The

site x date interaction can be seen in Fig 4.8A, where oysters at the Meetinghouse Creek site are smaller than oysters at the other sites from Jul to Aug, and then eventually surpassed the oysters at Flanders Bay and Great Peconic Bay. Similarly to the juvenile clams in 2008, the seasonal mean growth of juvenile oysters was fastest at the westernmost (Meetinghouse Creek) and easternmost (Little Peconic Bay) sites, and slower at Flanders Bay and Great Peconic Bay in the middle of the estuary (Fig 4.7, 4.8B). The seasonal mean growth of oysters was maximal at Meetinghouse Creek in 2008 as measured by shell growth (2.57 ± 0.08 mm wk^{-1}) or soft tissue growth (44.0 ± 3.0 mg AFDW wk^{-1}), and this was the fastest seasonal shell growth measured for any group of shellfish in this study. The shell growth at Meetinghouse Creek was not significantly different from shell growth at Little Peconic Bay (2.45 ± 0.08 mm wk^{-1}), but was significantly higher than shell growth at Flanders Bay (2.08 ± 0.05 mm wk^{-1}) and Great Peconic Bay (2.20 ± 0.07 mm wk^{-1}; $p < 0.001$, ANOVA on ranks; Fig 4.8B). The soft tissue growth at Meetinghouse Creek was significantly higher than the soft tissue growth at the other three sites in 2008; additionally the soft tissue growth at Little Peconic Bay (29.9 ± 2.3 mg AFDW wk^{-1}) was higher than the soft tissue growth at Great Peconic Bay (18.3 ± 1.5 mg AFDW wk^{-1}; $p < 0.001$, ANOVA on ranks; Fig 4.8B).

The growth rates of juvenile oysters were generally slower in 2009 due to a shorter season and colder temperatures; these oysters had an initial mean shell height of 9.8 ± 0.2 mm in Sept and reached sizes of 17 to 24 mm by Nov 2009 (Fig 4.8C). The tri-weekly growth rates of juvenile oysters varied significantly by site ($p < 0.001$), date ($p < 0.001$), and site x date interaction ($p < 0.001$, 2-way ANOVAR). Season mean shell growth was significantly faster in Meetinghouse Creek (1.32 ± 0.07 mm wk^{-1}) compared to Flanders Bay (0.82 ± 0.10 mm wk^{-1}), which was also significantly faster than shell growth in Great Peconic Bay (0.44 ± 0.08 mm wk^{-1}; $p < 0.001$, ANOVA; Fig 4.8D). Soft tissue growth followed a similar pattern with highest growth at Meetinghouse Creek (6.1 ± 0.5 mg AFDW wk^{-1}), although there was no difference between soft tissue growth at Flanders Bay (2.4 ± 0.4 mg AFDW wk^{-1}) and Great Peconic Bay (1.8 ± 0.3 mg AFDW wk^{-1}; ANOVA on ranks; Fig 4.8D). Seasonal growth trends of fast growth in the western site (Meetinghouse Creek) and slower growth in the intermediate sites (Flanders Bay and Great Peconic Bay) were observed both years (Fig 4.8B,D).

Shellfish growth (*Argopecten irradians*):

Juvenile bay scallops (*A. irradians*) had an initial mean shell height of 12.3 ± 0.2 mm in Jul of 2008 and rapidly reached shell heights of 38 to 48 mm by Nov 2008 (Fig 4.9A). Scallop shell growth rates were comparable to those of juvenile oysters (Fig 4.8), but scallop soft tissue growth was much faster than oyster soft tissue growth. The bi-weekly shell growth rates of juvenile scallops varied significantly by site ($p < 0.001$), date ($p < 0.001$), and site x date interaction ($p < 0.001$, 2-way ANOVAR; Fig 4.9A). Seasonal mean shell growth of juvenile scallops in 2008 was maximal at the westernmost site Little Peconic Bay (2.10 ± 0.05 mm wk^{-1}), and declined to the west to a minimum of 1.51 ± 0.08 mm wk^{-1} in Meetinghouse Creek (Fig 4.9B). Seasonal scallop shell growth at Meetinghouse Creek was significantly lower than at the other three sites ($p < 0.001$, ANOVA; Fig 4.9B). Soft tissue growth of scallops in 2008 followed a similar pattern, with a minimum of 48.7 ± 4.6 mg AFDW wk^{-1} in Meetinghouse Creek and a maximum of 95.5 ± 5.3 mg AFDW wk^{-1} in Little Peconic Bay, with significant differences noted on Fig 4.9B ($p < 0.001$, ANOVA). The soft tissue growth rates of scallops in 2008 were the maximum soft tissue growth rates recorded in this study, and even the minimum soft tissue growth of scallops was faster than the maximum soft tissue growth of juvenile oysters (Figs 4.8B, 4.9B).

The growth rates of juvenile scallops in 2009 were generally slower than 2008 due to a shorter season and colder temperatures; juvenile scallops had an initial mean shell height of 15.7 ± 0.3 mm in Sept 2009 and attained sizes of 29 to 33 mm by Nov 2009 (Fig 4.9C). Tri-weekly shell growth rates varied significantly by site ($p < 0.001$), date ($p < 0.001$), and site x date interaction ($p < 0.001$, 2-way ANOVAR). This site x date interaction can be seen in Fig 4.9C, where scallops at the Flanders Bay site were the smallest in late Sept, they eventually surpassed the growth of scallops at the other two sites by Nov. Seasonal mean growth rates of juvenile scallops in 2009 were significantly higher at the mid-estuary site Flanders Bay compared to the other sites, whether measured by shell growth (1.90 ± 0.04 mm wk^{-1}) or soft tissue growth (37.7 ± 1.6 mg AFDW wk^{-1}; $p < 0.001$, ANOVA; Fig 4.9D).

Shellfish growth (*Crepidula fornicata*):

Juvenile slipper limpets (*C. fornicata*) had an initial mean shell length of 14.1 ± 0.2 mm in Jul of 2008, and reached lengths of 26 to 30 mm by Nov 2008 (Fig 4.10A). Slipper limpet growth rates were comparable to juvenile clam growth rates (Fig 4.7) and much slower than oyster or scallop growth (Figs 4.8-9). Slipper limpet initial sizes and growth rates were generally more variable than those of the other shellfish (Fig 4.10), especially in 2009, and this is likely due to the fact that slipper limpets were collected from the wild while other shellfish were raised in a hatchery from common brood-stock and kept under uniform conditions before use in this study. The bi-weekly shell growth of slipper limpets in 2008 varied significantly by date ($p < 0.001$), and site x date interaction ($p < 0.05$, 2-way ANOVAR) but not by site. As with the juvenile oysters, replication in the repeated measures test was reduced due to the loss of tags from individual slipper limpets. Mean seasonal shell growth rates were significantly higher in Great Peconic Bay (0.85 ± 0.05 mm wk^{-1}) and Little Peconic Bay (0.84 ± 0.04 mm wk^{-1}) compared Meetinghouse Creek (0.59 ± 0.04 mm wk^{-1}; $p < 0.001$, ANOVA; Fig 4.10B). Seasonal slipper limpet soft tissue growth rates were marginally non-significant between sites ($p = 0.06$, ANOVA on ranks) and ranged from 10.5 ± 0.9 mg AFDW wk^{-1} at Meetinghouse Creek to 14.3 ± 1.2 mg AFDW wk^{-1} at Little Peconic Bay (Fig 4.10B).

The growth rates of juvenile slipper limpets were generally slower in 2009 than in 2008 due a shorter season and colder temperatures (Fig 4.10C-D). Juvenile slipper limpets had an initial mean shell length of 16.6 ± 0.5 mm and grew slowly to final lenghts of 20 to 22 mm (Fig 4.10C). Tri-weekly growth rates of slipper limpets were not significantly different by site or date ($p > 0.05$, 2-way ANOVAR) in 2009. Seasonal mean growth rates were also not significantly different by site ($p > 0.05$, ANOVA); shell growth ranged from 0.38 ± 0.13 mm wk^{-1} at Meetinghouse Creek to 0.54 ± 0.12 mm wk^{-1} at Great Peconic Bay while soft tissue growth ranged from 6.0 ± 1.8 mg AFDW wk^{-1} at Flanders Bay to 6.9 ± 1.9 mg AFDW wk^{-1} at Great Peconic Bay (Fig 4.10D).

Multiple regression analysis:

Specific growth rates of shellfish at each time point were analyzed using a repeated measures multiple regression approach (MacDonald and Ward 2009). Over the course of both growing seasons, temperature was the most significant predictor variable for shellfish growth on a week-by-week basis (Table 4.3). Temperature was the only significant predictor of scallop shell growth on a week-by-week basis. Juvenile clam growth rates had a positive relationship with densities of centric diatoms, while slipper limpets had a negative correlation with centric diatoms (Table 4.3). Juvenile oyster growth rates were negatively correlated with densities of dinoflagellates on a week-by-week basis, although this relationship was not present when the data were examined on a mean annual basis (Tables 4.3-4).

When shellfish growth was averaged over the entire growing season for each site and year, the effect of temperature largely disappeared as sites tended to have very similar mean seasonal temperatures. Variables associated with food availability and phytoplankton community dynamics were strongly different by site (Figs 4.3-4) and appear to have strongly influenced shellfish growth on a whole season basis. Measures of phytoplankton biomass and organic matter (chl *a*, chl *a* >5 μm, POC, and PON) were all autocorrelated in the mean annual data set, so only whole chl *a* was included in the regression models. Mean specific growth was calculated from shell growth and from soft tissue growth for each species. The model of seasonal shell growth for juvenile clams was positively dependent on densities of autotrophic nanoflagellates, relative water motion, % of chl *a* >5 μm, and salinity (Table 4.4). The model for seasonal soft tissue growth of clams was positively dependent on levels of centric diatoms, relative water motion, % of chl *a* >5 μm, and the C:N of organic seston (Table 4.4). Despite the overall significance of these models, they were relatively poor predictors of clam growth, with r^2 values of only 0.28 and 0.23 for shell growth and soft tissue growth, respectively.

The seasonal shell and soft tissue growth of oysters was strongly positively dependent on temperature (Tables 4.3-4). Juvenile oyster growth was also negatively dependent on densities of pennate diatoms for both metrics of growth. Oyster shell growth was also positively dependent on densities of centric diatioms. Oyster soft tissue growth was positively dependent on whole chl *a* (Table 4.4). These models were

generally good predictors of oyster growth with r^2 values of 0.81 and 0.84 for shell growth and soft tissue growth, respectively.

On a seasonal basis, scallop shell growth was negatively dependent on dinoflagellate densities and positively dependent on autotrophic nanoflagellates (<20 μm) and autotrophic microflagellates (>20 μm, Table 4.4). Scallop soft tissue growth was also negatively dependent on dinoflagellate densities as well as salinity, while positively dependent on (Table 4.4). The scallop growth models had an r^2 of 0.31 for shell growth and 0.34 for soft tissue growth. The seasonal growth models for slipper limpets had generally low r^2 values of 0.22 and 0.25 for shell growth and soft tissue growth, respectively. These low values reflect the considerable within-site variability in the growth rates of this species (Fig 4.10). Slipper limpet shell growth was negatively dependent on microflagellate densities and % of chl *a* >5 μm, while positively correlated with dinoflagellate densities. Slipper limpet soft tissue growth was positively dependent on temperature and negatively dependent on microflagellate densities (Table 4.4).

Discussion:

Over the course of a two-year field study, we demonstrated that the growth of eelgrass and four species of juvenile shellfish differed significantly at sites along a eutrophication gradient in the Peconic Estuary, NY, USA. The growth of eelgrass was inhibited by eutrophication due to lowered light levels and increased epiphyte growth on eelgrass blades. The growth of shellfish was more complicated, both between species and between sites within each species. Juvenile northern quahogs and eastern oysters appeared tolerant of eutrophic conditions, and their growth rates were positively dependent on some variables associated with eutrophication or increased food availability. Juvenile bay scallops and slipper limpets were negatively affected by eutrophication, and their growth rates were more often negatively dependent on variables associated with eutrophication. Finally, there was some evidence of compensatory growth in clams and oysters following changes in water quality at the most eutrophic site.

Eutrophication gradient:

The hypothetical existence of an eutrophication gradient was confirmed in both years by data on phytoplankton biomass, phytoplankton community dynamics, and levels of organic seston. Levels of chlorophyll *a*, POC, and PON were highest in Meetinghouse Creek and decreased consistently from west to east (Figs 4.3A-D, 4.4A-D) in both years, suggesting that there was more phytoplankton and more organic matter present in the water column at the western sites. The C:N molar ratio of organic seston increased from west to east, suggesting that high levels of organic matter in Meetinghouse Creek were also nitrogen-enriched. Nitrogen enrichment is considered one of the hallmarks of eutrophication (Nixon 1995, de Jonge *et al.* 2002) and has multiple direct and indirect effects on plankton communities and estuarine resources (Cloern 2001, Carmichael *et al.* 2004). Finally, total phytoplankton cell abundances were greatest in Meetinghouse Creek, and displayed different community structure and dynamics than the other sites (Fig 4.3E-H, 4.4E-H). Meetinghouse Creek displayed a distinct "bloom-and-crash" dynamic that was not present at the other sites, where cell densities tended to be more stable over time. Additionally, dinoflagellates and autotrophic nanoflagellates were more numerous at Meetinghouse Creek, while the other sites tended to have communities dominated by diatoms with an increased prevalence of pennate diatoms, especially in 2008. Shifts in phytoplankton composition and abundance, especially increased abundance of dinoflagellates, has been associated with eutrophication in other estuarine systems (Anderson et al 2008, Heisler et al 2008). Although there undoubtedly was re-suspension of sediment and organic detritus, extremely strong correlations between POC, PON, and chl *a* confirm previous conclusions regarding this estuary that most organic seston in this estuary consists of phytoplankton (Gobler and Sañudo-Wilhelmy 2001).

Physical characteristics:

While temperature did not differ considerably between field sites, there were consistent differences in salinity, dissolved oxygen, and tidal flushing. Hardy (1976) found tidal flushing times from Flanders Bay, Great Peconic Bay, and Little Peconic Bay of 55, 48, and 32 d, respectively. Even though plaster dissolution is marker of bulk water

motion and not tidal flushing specifically, our plaster dissolution measurements increased from west to east in a step-wise fashion consistent with increased tidal flushing (Fig 4.2). Salinity increased with tidal flushing towards the mouth of the estuary (Table 4.1), although salinities in this study ranged from 24 – 28, which falls within the optimal growth conditions for the five species in question (Galtsoff 1964, Hemminga and Duarte 2000, Kraueter and Castagna 2001, Brand 2006). While dissolved oxygen was high (66 – 95% saturation, 5 – 7 mg L^{-1}) at Flanders Bay, Great Peconic Bay, and Little Peconic Bay, dissolved oxygen saturation was consistently lower at the level of the shellfish cages in Meetinghouse Creek (53± 4% saturation and minimum of 2.0 mg L^{-1} in 2008, 50 ± 3% saturation and minimum of 3.2 mg L^{-1} in 2009; Table 4.1). These oxygen levels are at or approaching hypoxia, and could have negative consequences for estuarine resource species (Breitburg 2002, Diaz and Rosenberg 2008). Furthermore, these oxygen levels were based on day-time readings, and oxygen levels were undboutedly lower at night (Valiela *et al.* 1992).

Eelgrass growth and light availability:

Eelgrass (*Z. marina*) was expected to be strongly light-limited in this estuary, which was found to be the case in many other studies of eelgrass and eutrophication (Dennison *et al.* 1989, Duarte 1995). In previous mesocosm studies, an increase of mid-day light levels from 15% surface irradiance to 55% surface irradiance increased eelgrass leaf area productivity 0.33 to 0.72 cm^2 $shoot^{-1}$ d^{-1} (Wall *et al.* 2008), and an increase from 4.6 kLux to 7.4 kLux increased eelgrass growth from 0.42 to 0.55 cm^2 $shoot^{-1}$ d^{-1} (Wall, unpub. data), which is similar to the increase in light and eelgrass growth from Meetinghouse Creek to Flanders Bay in this study (Fig 4.5B, 4.6B). Light levels increased consistently from west to east with decreasing levels of chl*a* and organic seston in the water column (Figs 4.3-4, 4.5B), and at the same time, epibiont loads on eelgrass leaves were highest in the most eutrophic site with the lowest light penetration. Brush and Nixon (2002) found that dense epibionts could block light at the leaf surface and inhibit growth of eelgrass. However, the growth of transplanted eelgrass shoots was considerably variable in space and time (Fig 4.6A), and the only significant increase in leaf area production along this gradient was from Meetinghouse Creek to Flanders Bay

(Fig 4.6B), even though light levels continued to increase to the east. The increased light levels at 2 m depth at the eastern sites (Fig 4.5B), though higher than the western sites, were not more 20% of surface PAR on a seasonal mean basis which Dennison et al (1993) proposed as being the effective lower limit on eelgrass growth. Light levels at the depth of the eelgrass trays may not have been enough to support substantial growth of eelgrass, suggesting that the effective range of eelgrass in this estuary is now in areas less than 2 m depth; additionally, there is no naturally-occurring eelgrass in the western Peconic Estuary (Pickerell and Schott 2006). Carroll *et al.* (2008) did find eelgrass at a depth of 2 m in adjacent Shinnecock Bay, and these plants achieved similar leaf area productivities (0.20 to 0.91 cm^2 $shoot^{-1}$ d^{-1} this study; 0.18 to 0.61 cm^2 $shoot^{-1}$ d^{-1} in Carroll *et al.* 2008). Eelgrass in Shinnecock Bay also displayed a much stronger correlation with light levels than was found in this study.

The disturbance of planted eelgrass shoots increased considerably from west to east (Fig 4.6C), and the most likely candidate is the spider crab (*L. emarginata*). These crabs are abundant, have been observed eating eelgrass and burrowing in eelgrass beds, and may pose a significant barrier to eelgrass restoration in this estuary (C. Pickerell, pers. comm.). Eelgrass shoots that are recovering from disturbance or are consumed outright will obviously have slower growth than undisturbed plants, and this persistent disturbance could also explain the non-linear reliance of eelgrass growth on increasing light levels among the eastern study sites (Figs 4.5-6).

Shellfish growth:

The growth of juvenile shellfish was expected to increase with increasing food availability, given acceptable physical conditions of temperature, salinity, and dissolved oxygen. The specific growth (shell-based) of all juvenile shellfish was strongly positively dependent on temperature on a "week-to-week" basis in both years (Table 4.3). This is not surprising, considering the temperature variations observed during this study (10 - 26° C). The summer and early fall temperatures in this estuary (19° - 26° C) are within what should be an optimal growth range for hard clams (Grizzle *et al.* 2001), oysters (Shumway. 1996), scallops (MacDonald *et al.* 2006), and slipper limpets (Newell

and Kofoed 1977). There were multiple characteristics of eutrophication (increased food availability, nitrogen-enrichment, plankton composition) which seemed to influence bivalve growth during this study. Nitrogen-enriched organic matter is a symptom of N loading (Valiela et al 1992) and more rapid growth in the presence of high levels of PON likely reflects the importance of N-enriched organic matter as an important food source (Carmichael *et al.* 2004, Carmichael and Valiela 2005). Juvenile northern quahog growth rates were positively dependent on densities of autotrophic nanoflagellates and centric diatoms, as well as % of chl *a* >5 μm. Bivalves should be able to retain particles >5 μm with near 100% efficiency (Riisgard 1988), and phytoplankton blooms consisting of cells <5 μm are harmful to most bivalves.

Weekly growth rates of juvenile bay scallops and juvenile slipper most strongly to temperature (Table 4.3). Bay scallops are not known to be food-limited in most estuaries and can respond negatively to eutrophic conditions in many cases (Valiela *et al.* 1992, Shriver *et al.* 2002) although a related species (*Pecten maximus*) showed increased growth and survival in response to enhanced nutrient loading (Reitan *et al.* 2002). Slipper limpets can survive in very turbid waters, but are thought to be less efficient than oysters and clams at particle selection under high seston loads (Beninger *et al.* 2007). A reduced particle selection ability may explain their negative response to high levels of organic seston in this estuary.

Seasonal growth of shellfish:

The mean seasonal growth for each species was strongly different by site (Figs 4.7-10). The sites differed by salinity, tidal flushing, phytoplankton composition, and level of organic matter (Table 4.1, Figs 4.3-4), but not by temperature within each year. When mean seasonal shellfish growth rates were regressed onto mean seasonal water quality variables for each site, the effects of temperature on growth are diminished or removed (Table 4.4). The seasonal growth of juvenile northern quahogs was positively dependent on densities of autotrophic nanoflagellates and centric diatoms, as well as % of chl *a* >5 μm. Bivalves should be able retain particles >5 μm with near 100% efficiency (Riisgard 1988), and phytoplankton blooms consisting of cells <5 μm are harmful to most

bivalves (Gobler *et al.* 2005). Autotrophic nanoflagellates and centric diatoms are known to be nutritious food sources for suspension feeders (Wikfors *et al.* 1992, Greenfield *et al.* 2005), and juvenile hard clams have been observed to grow faster with greater concentrations of PON in the Waquoit Bay system (Weiss *et al.* 2002, Carmichael *et al.* 2004). Larger phytoplankton such as nanoflagellates, microflagellates, and centric diatoms, greater abundances of these phytoplankton, and N-enriched organic matter are all more likely to be found within the most eutrophic regions of the estuary, such as Meetinghouse Creek.

Juvenile oysters also showed a positive dependence on food availability on a whole season basis. Oyster shell growth was positively correlated with densities of centric diatoms, while soft tissue growth was positively dependent levels of chl *a* (Table 4.4). Pacific oysters (*Crassostrea gigas*) are known to grow and survive well in turbid waters with high levels of organic seston (Barille *et al.* 1997), and there is some evidence for historical increases of Eastern oyster growth (*C. virginica*) in response to eutrophication (Kirby and Miller 2005). Seasonal growth of oysters was negatively dependent on pennate diatoms (Table 4.4), possibly reflecting a poor nutritive value of this cell type (Greenfield *et al.* 2005, Weiss *et al.* 2007).

The seasonal growth of juvenile bay scallops was most strongly predicted by a negatively correlation with dinoflagellate densities for both shell and soft tissue growth (Table 4.4), even though there was some evidence for positive food dependence of shell growth on nanoflagellates and microflagellates. Dinoflagellates are thought to be a poor nutritive source for many suspension feeders (Greenfield *et al.* 2005, Weiss *et al.* 2007), and some species of the dinoflagellate community in the Peconic Estuary are known to be actively toxic to bay scallops in particular (*Cochlodinium polykrikoides*, Gobler *et al.* 2008; Tang and Gobler 2009). Even though densities of potentially beneficial cell types were high in Meetinghouse Creek, this effect was likely outweighed for the scallops by the prevalence of dinoflagellates, resulting in poor scallop growth in Meetinghouse Creek and faster scallop growth in the eastern parts of the estuary (Fig 4.9). Scallop soft tissue growth was negatively dependent on salinity in the multiple regression model. The optimal salinity for growth of larval and juvenile bay scallops has been reported as 24 –

26 (Brand 2006), which falls within the range of salinities measured in this study (24 – 28). Shriver *et al.* (2002) found a positive correlation with bay scallop growth and salinity over a much wider salinity range of 18 – 30. Meetinghouse Creek always had the lowest salinity, lowest dissolved oxygen, and greatest abundances of dinoflagellates during this study and hence the negative correlation with salinity could have been driven largely by poor growth at this location.

Juvenile slipper limpets showed no positive relationship with food availability on a "week-by-week" or on a whole season basis except for a slight positive correlation of shell growth with dinoflagellates (Tables 4.3-4). Slipper limpet shell growth had a negatively relationship with % of chl*a* >5 µm and microflagellates on a whole season basis (Table 4.4). Slipper limpets are known to feed more efficiently on <5 µm particles than bivalves (Kach and Ward 2008, Harke *et al.* unpub. data) so slipper limpets may be at a competitive advantage when the phytoplankton community consists of a greater proportion of <5 µm cells. However, juvenile shellfish were stocked at a very low density (200 ~15 mm individuals in a 91 x 53 x 46 cm cage) to prevent inter- and intra-specific competition within cages, and there was always sufficient chl *a* in the > 5 µm size fraction (Figs 4.3B, 4.4B) to support the growth of bivalves. While slipper limpets can capture smaller particles than bivalves, their qualitative particle selection may be less efficient than some bivalves (*C. gigas*, Beninger *et al.* 2007), so slipper limpets may be stressed by very high organic seston loads or by poor nutritive quality of seston. Despite this reduced qualitative particle selection efficiency, slipper limpets are found in some environments containing high portions of re-suspended sediment in the seston (Barille *et al.* 2006).

The whole season regression models had an overall better fit for oyster growth (r^2 = 0.81 – 0.84) and scallop growth (r^2 = 0.31 – 0.34) than they did for clam growth (r^2 = 0.28 – 0.23, Table 4.4). Hard clams are slow-growing, have slower clearance rates than Eastern oysters, and may saturate their food requirements at lower levels than oysters (Tenore and Dunstan 1973, Newell and Koch 2004). Hard clams are also more broadly tolerant of variable environmental conditions than bay scallops (Kraueter and Castagna 2001, Shumway and Parsons 2006). It is likely that the slow-growing, slow-feeding,

broadly tolerant species (hard clam) will have a smaller range of response to eutrophication than the fast-growing, fast-feeding species (eastern oyster) or the fast-growing, water quality-sensitive species (bay scallop).

Inter-specific differences:

During this study, there were marked spatial differences in the growth of the four suspension-feeding shellfish, with clams and oysters growing maximally in the western extent of the Peconic Estuary and scallops and slipper limpets growing fastest in the eastern region. These four species differ in their tolerances to environmental conditions; however temperature (10 to 27° C) and salinity ranges (24 to 28) for this study were well within the acceptable ranges for growth and survival for all four species (Grizzle *et al.* 2001, Shumway 1996, MacDonald *et al.* 2006, Newell and Kofoed 1977). The four species differ in their particle-capture efficiencies, especially for particles < 10 μm. Most suspension feeders have a minimum size of particle that can be retained on their feeding apparatus, then the retention efficiency increases over some size range, and particles are retained near 100% efficiency above that size range. For bay scallops, this size range is 5 to 7 μm (MacDonald *et al.* 2006), while this size range is lower for the other species in this study (3 to 4 μm for quahogs, Grizzle *et al.* 2001; 1 to 6 μm for oysters, Newell and Langdon 1996; 2 to 4 μm for slipper limpets, Barille *et al.* 2006). These particle-retaining differences have been linked to the gill structure of each species, with very small particle retention correlated with the presence of eulatero-frontal cirri on the gills of bivalves (Riisgard 1988) and mucous-net secretion in the gills of gastropods (Barille *et al.* 2006). However, chl *a* in the >5 μm size fraction made up the majority of available chl *a* at all sites in both years (Table 4.1, Figs 4.2-3), so the growth of any species was probably not strongly limited by the size of food particles.

The four species differ in their weight-specific metabolisms, clearance rates, methods of regulating ingestion, and tolerance of high seston loads. Of the four species studied, bay scallops have the highest clearance rates (3 to 10 L hr^{-1} g DW^{-1}; MacDonald *et al.* 2006), which is comparable to clearance rates of eastern oysters (5 to 6 L hr^{-1} g DW^{-1}; Newell and Langdon 1996), but higher than those of northern quahogs (2.6 to 3.4

L hr^{-1} g DW^{-1}; Grizzle *et al.* 2001) or slipper limpets (0.76 L hr^{-1} g DW^{-1}; Barille *et al.* 2006). Similarly, respiration rates of bay scallops were higher at 20° C (1.7 mL O_2 hr^{-1} g DW^{-1}; MacDonald *et al.* 2006) than respiration rates of eastern oysters (0.3 mL O_2 hr^{-1} g DW^{-1}; Shumway 1996), northern quahogs (0.8 mL O_2 hr^{-1} g DW^{-1}; Grizzle *et al.* 2001) or slipper limpets (1.25 mL O_2 hr^{-1} g DW^{-1}; Newell and Kofoed 1977). However, it should be noted that eastern oysters increased their respiration rates to 1.0 to 1.5 mL O_2 hr^{-1} g DW^{-1} at salinities < 20 (Shumway and Koehn 1982), which are common in mesohaline regions of Chesapeake Bay but not encountered during this study.

The combination of high clearance rate and high respiration rate in bay scallops enables this species to grow very quickly (Fig 4.9) and to take advantage of relatively low food concentrations with high growth efficiency under suitable environmental conditions, such as the Great Peconic and Little Peconic Bay sites (Table 4.1, Fig 4.1, 4.9). A related species, *Placopecten magellanicus*, exhibited reduced clearance rates at total seston concentrations of 6 mg L^{-1} and reduced growth and survival at 10 mg L^{-1} (MacDonald *et al.* 2006). In contrast, eastern oysters and northern quahogs were able to maintain high clearance rates at seston concentrations up to 25 and 30 mg L^{-1} in laboratory experiments (Newell and Langdon 1996, Grizzle *et al.* 2001) and the slipper limpet maintained a constant clearance rate on > 15 μm particles under total seston concentrations up to 200 mg L^{-1} (Barille *et al.* 2006). Additionally, eastern oysters can still feed at reduced clearance rates in seston up to 500 mg L^{-1} (Shumway 1996). Slipper limpets seem able to regulate their ingestion under high seston loads by reducing their retention efficiency of small (< 15 μm) particles. Eastern oysters and northern quahogs regulate their ingestion under high seston loads through a combination of shell closure, pseudo-feces production, and reduction in clearance rate (Newell and Langdon 1996, Grizzle *et al.* 2001). In contrast, the only method available to scallops is reduction in clearance rate, as scallops do not seem to be able to close their shells for extended periods and have lower rates of pseudo-feces production (MacDonald *et al.* 2006). Northern quahogs and eastern oysters have more physiological mechanisms for regulating ingestion under high particle loads than bay scallops; consequently, quahogs and oysters performed much better than bay scallops at the western sites, which had high levels of organic seston compared to the eastern sites were bay scallops grew fastest (Fig 4.7-9). It is not clear why slipper limpets

were not able to take advantage of the high food availability at the western sites of the Peconic Estuary, despite their tolerance for high seston loads in other systems (Barille *et al.* 2006). Although they possess the mechanisms to tolerate high particle loads, this suggests that slipper limpets perform maximally under lower food concentrations.

Effects of water motion:

On a whole season basis, the soft tissue growth of northern quahogs, bay scallops, and slipper limpets were all positively correlated with relative water motion, although this effect was non-significant for bay scallops and slipper limpets after the effects of other variables were added to the regression model (Table 4.4). Many studies and reviews have noted the importance of water motion to disrupt benthic boundary layers and to deliver food to suspension feeders (Wildish and Kristmanson 1984, Dame 1996). Grizzle and Morin (1989) advanced the "horizontal seston flux" hypothesis, where they found that horizontal seston flux was a better predictor of hard clam (northern quahog) shell growth rates than either seston concentration or flow speeds alone. We did not measure tidal current speed in absolute terms, but relative water motion (Fig 4.2) and tidal mixing (Hardy 1976) clearly increased from west to east, counter to the eutrophication gradient in the Peconic Estuary. The dependence on water motion to deliver food may explain the growth patterns for hard clams and eastern oysters in 2008, where growth was maximal at the Meetinghouse Creek (maximum food) and Little Peconic Bay (maximum flow), and minimal at the mid-estuary sites.

The food flux delivered to a suspension feeder is the product of water flow speed and seston concentration (Wildish and Kristmanson 1984, Grizzle and Morin 1989), and this parameter seems most important to northern quahogs (Table 4.4). As chl *a* and POC concentrations decreased to the eastern Peconic Estuary, tidal flushing and relative water motion increased, so the total delivery of seston may have stayed the same, explaining why there were no strong dependencies on bulk food measures. Measurements of actual tidal current speeds as well as continued monitoring of seston quantity and quality will be needed to confirm this. For the range of sites studied in the Peconic Estuary, it may be

that total food delivery was adequate for all species and growth differences were due to physical conditions or changes in the quality of phytoplankton composition.

Hypoxia and compensatory growth:

The shell growth trajectories for hard clams and eastern oysters displayed evidence of compensatory growth in 2008. Compensatory growth is any period of improvement of growth conditions following suppression of growth and has been identified in both vertebrates and invertebrates (Wilson and Osbourn 1960, Bayne 2002). The shell growth of hard clams and eastern oysters in Meetinghouse Creek was slow during Jul – Aug and then accelerated in the early fall of 2008 (Fig 4.7A, 4.8A). Mid-day dissolved oxygen at the levels of the shellfish cages were 2 – 4 mg L^{-1} in Jul – Aug of 2008, began climbing in mid Sept, and recovered to >5 mg L^{-1} by early Oct of 2008. However, since dissolved oxygen was not measured continuously, the severity or duration of any hypoxia at this site is unknown, although oxygen levels were likely lower at night. Hard clams are known to be especially tolerant of hypoxia (Winn and Knott 1992), and eastern oysters can also tolerate short (< 2 weeks) periods of hypoxia (Lenihan and Peterson 1998). Hard clams and eastern oysters tolerated summer hypoxia in Meetinghouse Creek (no significant mortality, data not shown) and were able to take advantage of increased food availability when dissolved oxygen levels increased in the early fall. While adult northern quahogs and eastern oysters are broadly tolerant of short periods (hours to days, Kennedy *et al.* 1996, Grizzle *et al.* 2001) of hypoxia/anoxia, exposure to hypoxia does decrease their growth, metabolism, and filtration rates (Widdows *et al.* 1989, Grizzle *et al.* 2001), and prolonged or repeated exposure (> 2 weeks) will result in mortality (Lenihan and Peterson 1998). In contrast, bay scallops (*A. irradians* v. *concentricus*) displayed significant mortality after only 6 h exposure to DO concentrations of 4 mg L^{-1} at a temperature of 31° C (Peterson *et al.* 1996), and bay scallops in this study did not show signs of accelerated or compensatory growth at the Meetinghouse Creek site (Fig 4.9A).

Conclusions:

The Peconic Estuary displays a spatial gradient of eutrophication from high levels organic seston in the west to low levels in the eastern regions, and these levels of eutrophication could be a proxy for a temporal gradient as anthropogenic nutrient loading increases or decreases in the future. This gradient has multiple simultaneous effects on living marine resources. Eelgrass (*Z. marina*) was negatively impacted by reduced light levels due to high phytoplankton biomass and high epibiont loads in the western site (Fig 4.5, 4.6B) and also negatively impacted by disturbance from benthic macro-fauna (Fig 4.6C) in the eastern sites. Hard clams (*M. mercenaria*) and Eastern oysters (*C. virginica*) were tolerant of eutrophic conditions and low dissolved oxygen in the western region, and were able to take advantage of food availability at this site with compensatory growth as water quality improved. When physical parameters like temperature and salinity are controlled for, food quality and quantity may interact to determine growth rates of juvenile bivalves. On a seasonal basis, the growth of clams and oysters between sites was most often positively dependent on measures of food quality, such as densities of autotrophic nanoflagellates, centric diatoms, and % of chl *a* > 5 μm (Table 4.3) all of which were maximal at the eutrophic end of the eutrophication gradient (Figs 4.3-4). The soft tissue growth of eastern oysters was the only shellfish metric observed to be positively dependent on a variable that describes bulk plankton or carbon availability (whole chl *a*, Table 4.4). Juvenile bay scallop (*A. irradians*) growth rates were lowest at the eutrophic end of the gradient, which also featured summer hypoxia and high densities of dinoflagellates, which are known to be a poor and/or toxic food source (Greenfield *et al.* 2005, Gobler *et al.* 2008, Tang and Gobler 2009). Similarly to bay scallops, juvenile slipper limpets (*C. fornicata*) grew counter to the eutrophication gradient with fastest growth at the mesotrophic end, suggesting that there may be some niche-overlap with bay scallops in this estuary.

Many anthropogenic insults have led to the degradation of estuaries, with the concurrent loss of estuarine resources (Lotze *et al.* 2006) such as clams, oysters, scallops, and eelgrass. Increases in anthropogenic nutrient loading, leading to eutrophication, have been identified as a primary driver of estuarine degradation (Nixon 1995, de Jonge *et al.* 2002), but recent research and reviews have raised the possibility of beneficial nutrient loading under some conditions and for some species (Nixon and Buckley 2002,

Carmichael *et al.* 2004). Undoubtedly, eutrophication is a complex problem that continues to challenge our scientific understanding, and will require a variety of management approaches (Cloern 2001).

Managers seeking to control nutrient loading and to restore living marine resources will need to consider these complex effects of eutrophication on multiple resources, and the interactions of nutrient loading with physical parameters (e.g., tidal flushing). Certainly, trade-offs exist between the cost of nutrient reduction *vs.* the benefits to estuarine habitats, and some species are tolerant of and may even benefit from eutrophic conditions (e.g., quahogs and eastern oysters). Excessive nutrient reduction may even disrupt food supplies to the benthos (Nixon *et al.* 2009). Given the findings of this study, restoration or aquaculture efforts for clams and oysters are likely to be successful in areas with high nutrient loading and high levels of organic seston. In contrast, since bay scallops and eelgrass will require the clearest water with lower levels of suspended organic matter for maximal growth, restoration or aquaculture efforts for these organisms should target well-flushed regions with low nutrient loads and low levels of organic seston. Any plan to re-seed or restore seagrasses or bivalve populations into a eutrophic system will need to take into account the species in question and its unique responses to varying levels of nutrient loading. The simultaneous restoration and management of seagrass beds and bivalve populations will likely have synergistic effects (Newell and Koch 2004, Wall *et al.* 2008, Carroll *et al.* 2008), as each group of organisms provides multiple benefits for the other. Successful ecosystem-based management will need to balance multiple uses of estuaries, multiple estuarine species, and perhaps multiple levels of nutrient loading within the same estuary.

	Site	Temp. (° C)	Salinity (psu)	D.O. (mg L^{-1})	Whole Chl*a* (µg L^{-1})	>5 µm Chl*a* (µg L^{-1})	POC (µM)	PON (µM)	C:N
2008	Meetinghouse Cr.	10.5 - 26.7	25.72 ± 0.25	4.18 ± 0.47	26.30 ± 2.40	26.04 ± 2.30	301.1 ± 46.4	42.48 ± 5.71	7.06 ± 0.33
	Flanders B.	10.8 - 26.5	27.34 ± 0.24	7.23 ± 0.52	7.01 ± 1.42	6.46 ± 1.51	121.6 ± 23.5	12.51 ± 2.20	10.01 ± 0.81
	Great Peconic B.	10.9 - 26.3	28.26 ± 0.18	6.93 ± 0.34	3.77 ± 0.73	2.80 ± 0.49	57.75 ± 5.61	6.61 ± 0.76	9.23 ± 0.51
	Little Peconic B.	11.1 - 25.9	28.45 ± 0.14	6.60 ± 0.36	3.23 ± 0.33	2.44 ± 0.31	53.91 ± 4.39	5.96 ± 0.57	9.55 ± 0.37
2009	Meetinghouse Cr.	9.9 - 23.2	24.45 ± 0.72	4.29 ± 0.46	15.02 ± 4.39	16.19 ± 3.87	177.8 ± 26.5	26.49 ± 3.06	6.67 ± 0.59
	Flanders B.	10.6 - 22.6	25.97 ± 0.61	5.59 ± 0.58	2.06 ± 0.44	2.16 ± 0.60	51.43 ± 12.03	6.32 ± 1.18	8.10 ± 0.41
	Great Peconic B.	11.4 - 22.7	26.67 ± 0.63	5.73 ± 0.58	1.86 ± 0.38	1.84 ± 0.45	35.70 ± 2.10	4.44 ± 0.41	8.20 ± 0.34

Table 4.1. Summary of environmental conditions. Values are given as annual mean ± SE for each site in 2008 and 2009, except for temperature, which is given as a range. Measurements in 2008 are from 30 Jun to 5 Nov; measurements in 2009 are from 9 Sept to 10 Nov. Values of >5 µm chl *a* that are greater than whole chl *a* reflect phytoplankton communities where virtually all cells are in the >5 µm size class.

	Sediment Properties	Porosity ϕ	Org. Content (% LOI)	Silt+Clay (% dw)
2008	Meetinghouse Cr.	0.86 ± 0.01	12.38 ± 1.64	53.00 ± 1.20
	Flanders B.	0.42 ± 0.01	0.44 ± 0.02	2.67 ± 0.74
	Great Peconic B.	0.42 ± 0.01	0.57 ± 0.26	2.31 ± 0.07
	Little Peconic B.	0.45 ± 0.02	0.39 ± 0.01	2.65 ± 0.46

Table 4.2. Summary of sediment properties at field sites. Values are given as mean ± SE for samples taken at the beginning of the study in July 2008. Organic content at Meetinghouse Creek site is likely an over-estimate due to loss of hydrated mineral forms in clays at the temperature of combustion (450° C, R. Aller pers. comm.).

Species	Significant Predictor Variables	Direction of Effect	F-ratio	P-value	Adj. R^2
Mercenaria mercenaria	temperature	+	121.36	< 0.001	0.772
	centric diatoms	+	7.17	0.037	
Crassostrea virginica	temperature	+	11.23	0.015	0.750
	dinoflagellates	−	41.55	0.001	
Argopecten irradians	temperature	+	142.16	< 0.001	0.642
Crepidula fornicata	temperature	+	34.18	0.001	0.605
	centric diatoms	−	11.54	0.015	

Table 4.3. Repeated measures multiple regression of weekly shellfish growth rates on environmental variables. Growth rates were entered as mean specific growth (wk^{-1}) at each time point (2008-2009, n = 50 per site) based on shell sizes. For the purposes of repeated measures analysis, the group of shellfish at each site was treated as a subject (n = 4 in 2008, n = 3 in 2009). Adjusted r^2 is not valid in repeated measures context but is shown for sake of comparison (MacDonald and Ward 2009).

Species	Shell Growth: Significant Predictor Variables	Standardized Coefficient	F-ratio	P-value		Soft Tissue Growth: Significant Predictor Variables	Standardized Coefficient	F-ratio	P-value	
Mercenaria mercenaria	nanoflagellates	1.600	64.82	< 0.001	**N**	centric diatoms	0.866	69.49	< 0.001	**N**
	relative water motion	1.138	51.91	< 0.001	252	relative water motion	0.633	38.20	< 0.001	315
	% of chl*a* >5 µm	1.470	27.37	< 0.001	**Adj. R^2**	% of chl*a* >5 µm	0.516	21.75	< 0.001	**Adj. R^2**
	salinity	1.332	18.29	< 0.001	0.277	C:N organic seston	0.385	10.93	0.001	0.228
Crassostrea virginica	temperature	1.587	401.26	< 0.001	**N**	temperature	1.628	477.17	< 0.001	**N**
	pennate diatoms	-0.842	112.80	< 0.001	202	pennate diatoms	-1.003	174.74	< 0.001	204
	centric diatoms	0.235	59.16	< 0.001	**Adj. R^2**	chlorophyll *a*	0.377	159.09	< 0.001	**Adj. R^2**
					0.812					0.836
Argopecten irradians	dinoflagellates	-0.904	63.18	< 0.001	**N**	dinoflagellates	-1.265	35.04	< 0.001	**N**
	nanoflagellates	0.407	13.29	< 0.001	203	temperature	1.150	27.81	< 0.001	203
	microflagellates	0.201	10.73	0.001	**Adj. R^2**	salinity	-1.175	15.65	< 0.001	**Adj. R^2**
					0.314					0.339
Crepidula fornicata	microflagellates	-0.565	20.08	< 0.001	**N**	temperature	0.550	69.09	< 0.001	**N**
	% of chl*a* >5 µm	-0.340	16.98	< 0.001	189	microflagellates	-0.224	11.46	< 0.001	206
	dinoflagellates	0.477	13.70	< 0.001	**Adj. R^2**					**Adj. R^2**
					0.216					0.247

Table 4.4. Multiple regression of seasonal shellfish growth rates on environmental variables. Growth rates were entered as specific growth (wk^{-1}) based on shell sizes and soft tissue weights (AFDW). Shown are standardized beta-coefficient (slope), F-ratio, p-value, and adjusted r^2 of each model.

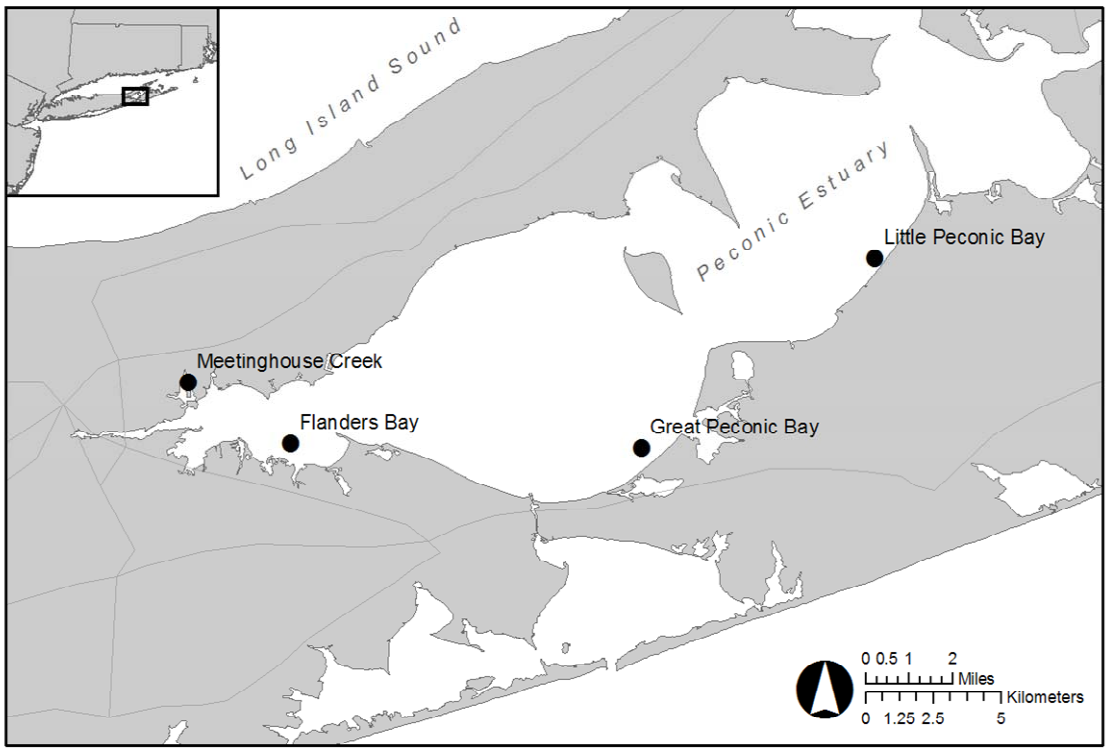

Figure 4.1. Location of study sites. Abbreviations are as follows: Meetinghouse Creek (MHC), Flanders Bay (FB), Great Peconic Bay (GPB), and Little Peconic Bay (LPB). All sites were visited bi-weekly from 30 Jun to 5 Nov 2008. MHC, FB, and GPB were visited tri-weekly from 9 Sept to 10 Nov 2009. All sites are approximately 2m depth.

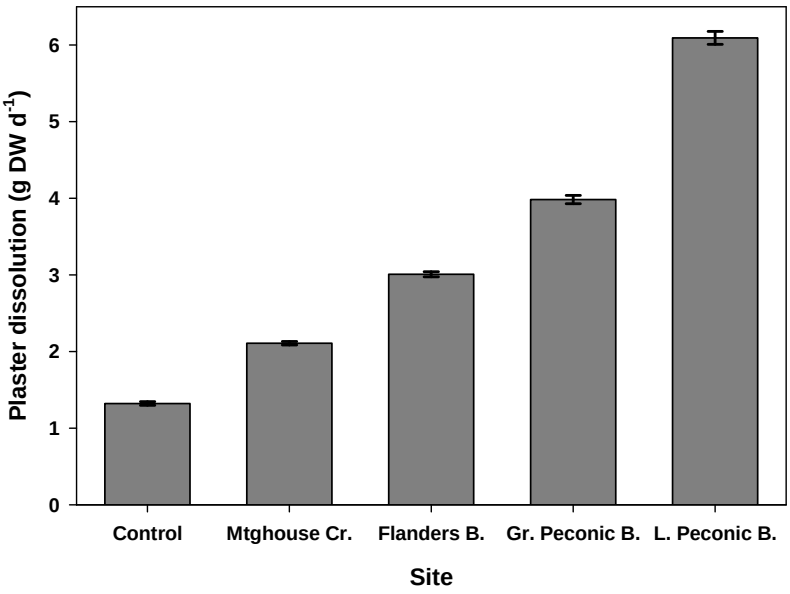

Figure 4.2. Relative water motion at study sites. Bars represent mean ± SE of plaster dissolution at the four study sites and a "no-flow" control (n = 8 per treatment). Plaster blocks were placed inside shellfish cages approximately 30 cm above the bottom. All treatments are significantly different from each other ($p < 0.001$, Tukey post-hoc test).

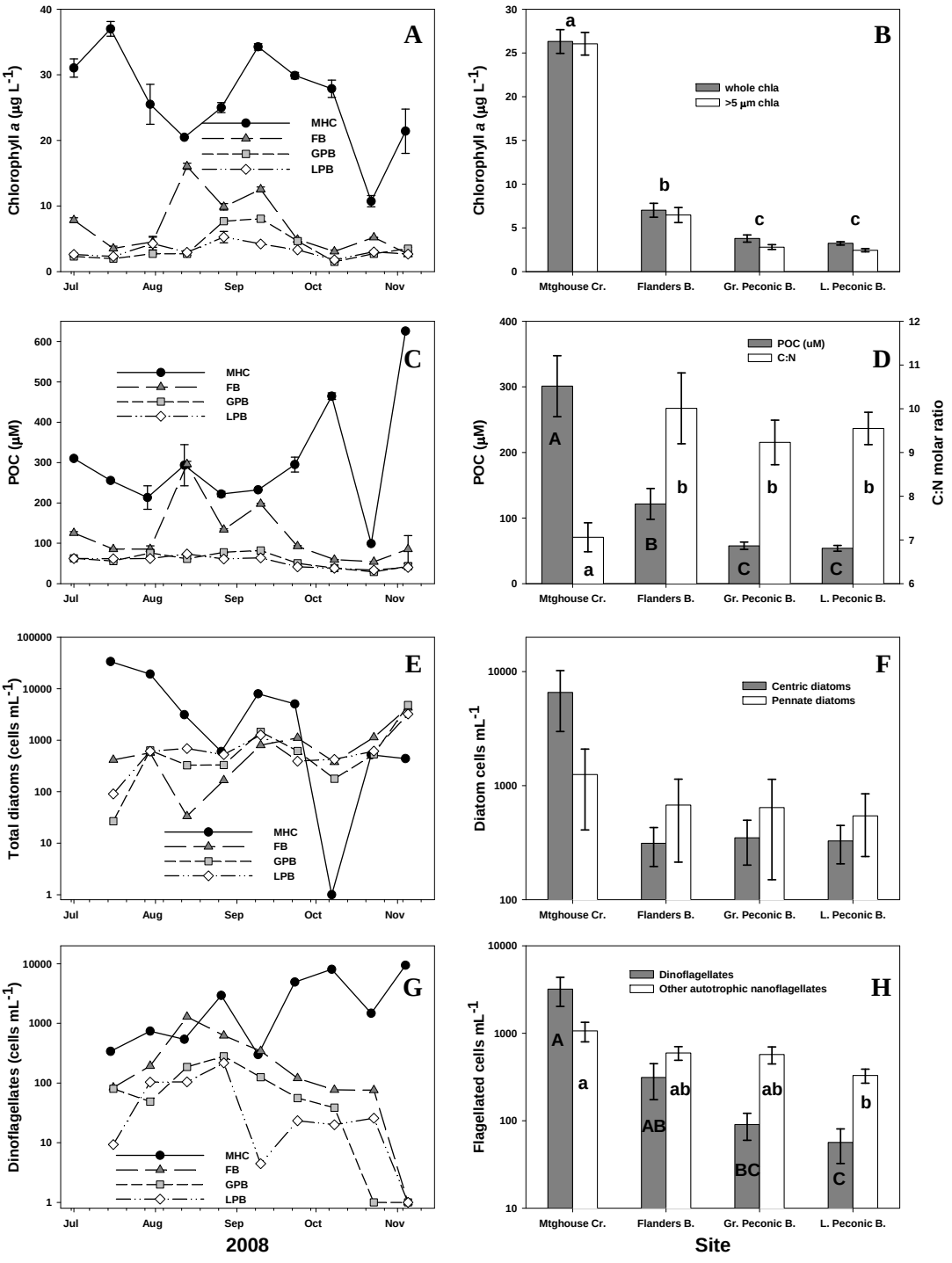

Figure 4.3. Phytoplankton dynamics at field sites in 2008. Shown are time series (mean or mean ± SE) and seasonal averages (mean ± SE) for each site for chlorophyll *a* (A-B); POC and C:N of organic seston (C-D); cell densities of diatoms (E-F); and densities of flagellated cells (G-H). Letters indicate significant differences between site means.

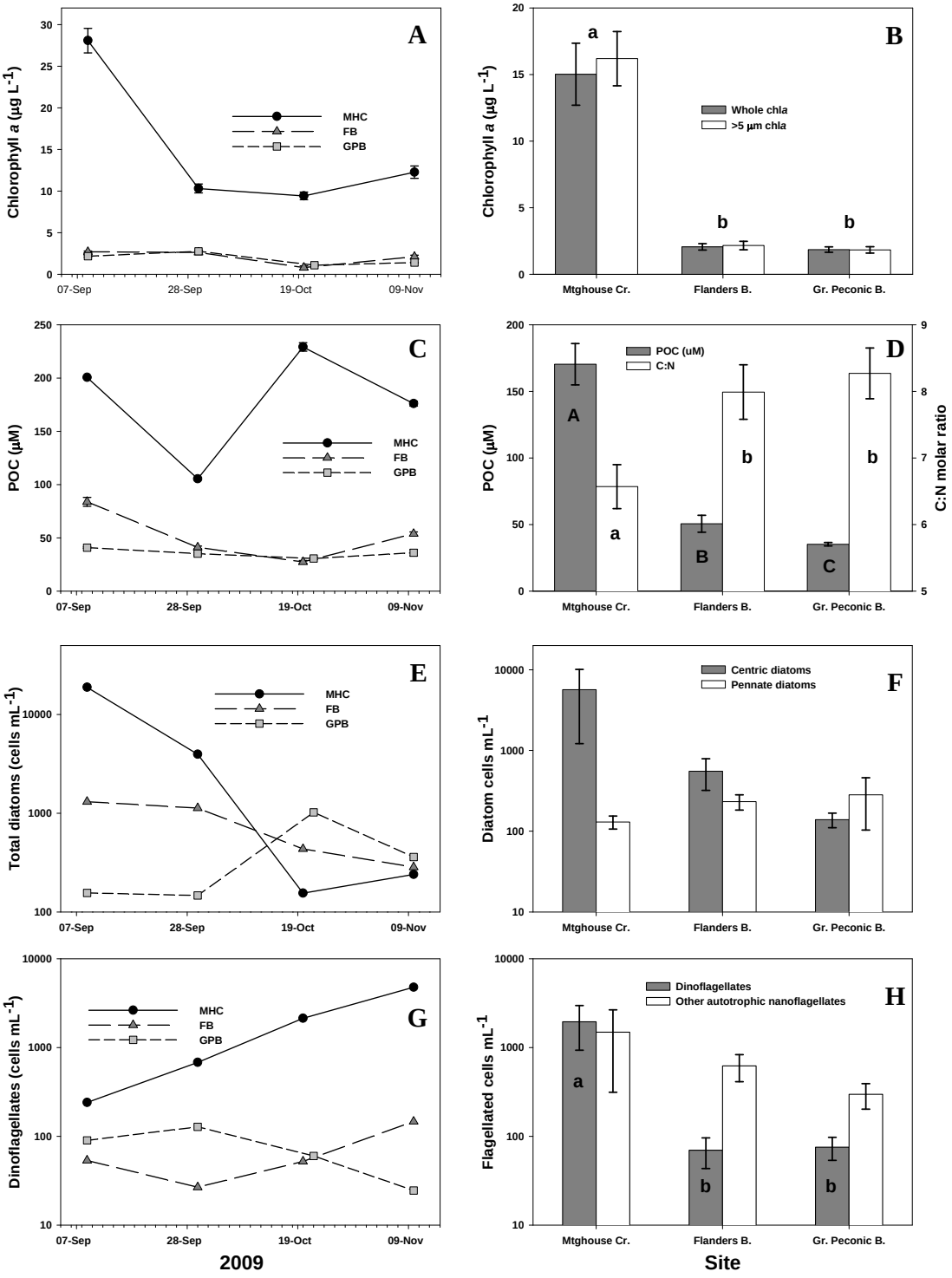

Figure 4.4. Phytoplankton dynamics at field sites in 2009. Shown are time series (mean or mean ± SE) and seasonal averages (mean ± SE) for each site for chlorophyll *a* (A-B); POC and C:N of organic seston (C-D); cell densities of diatoms (E-F); and densities of flagellated cells (G-H). Letters indicate significant differences between site means.

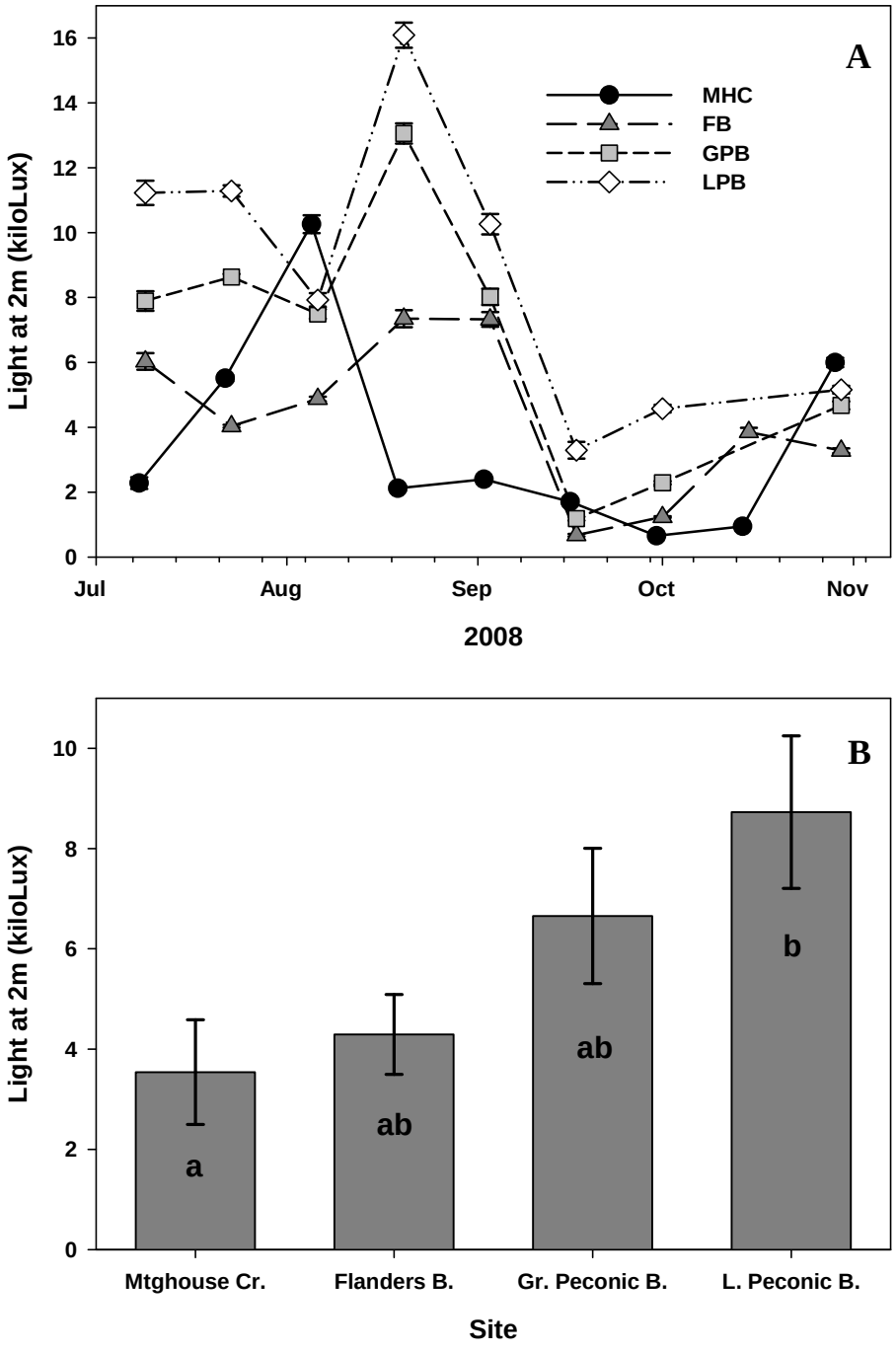

Figure 4.5. Light levels at study sites in 2008. Time series (A) and seasonal means (B) of mid-day visible light in kiloLux reaching eelgrass trays at 2 m depth. Values are mean ± SE; letters indicate significant differences between seasonal means (B).

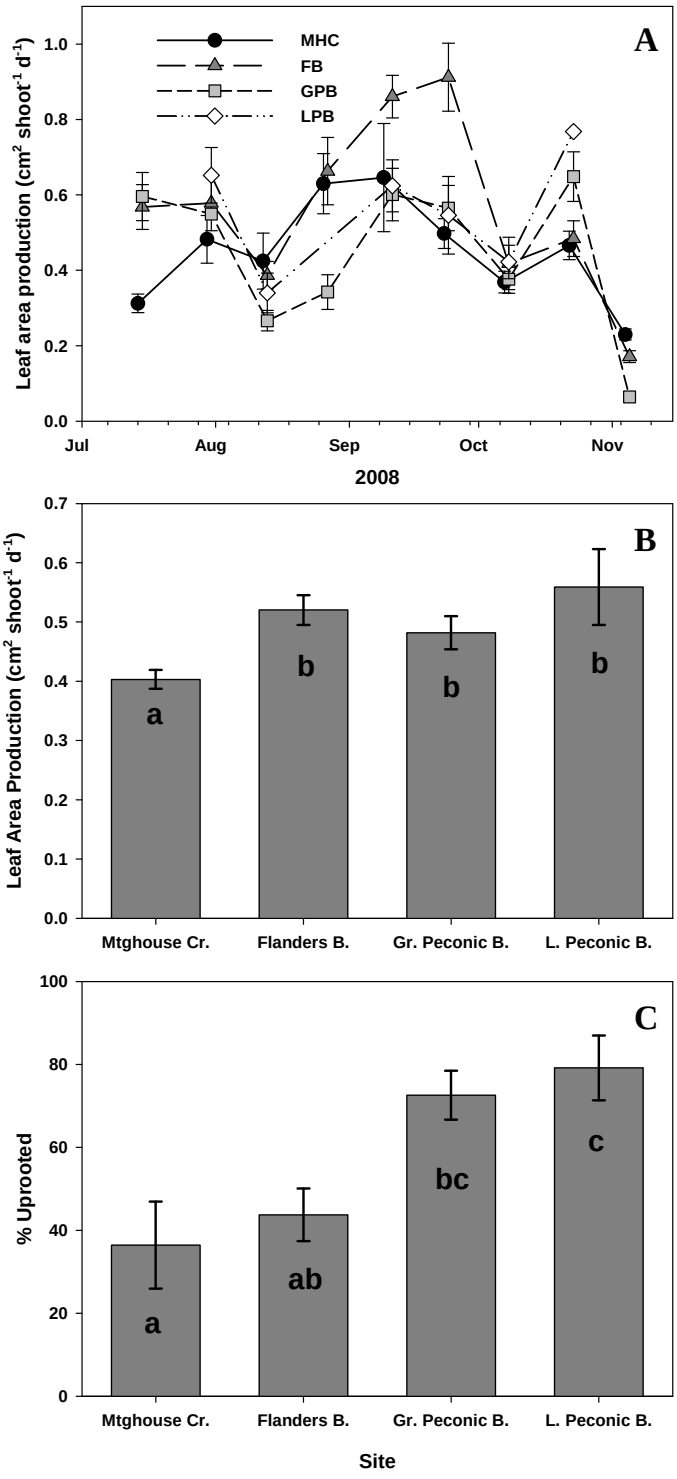

Figure 4.6. Eelgrass growth at study sites. Shown are time series of eelgrass (*Z. marina*) leaf area production (A), seasonal means of leaf area production (B), and seasonal means of uprooting disturbance (C). Values are mean ± SE; letters indicate significant difference.

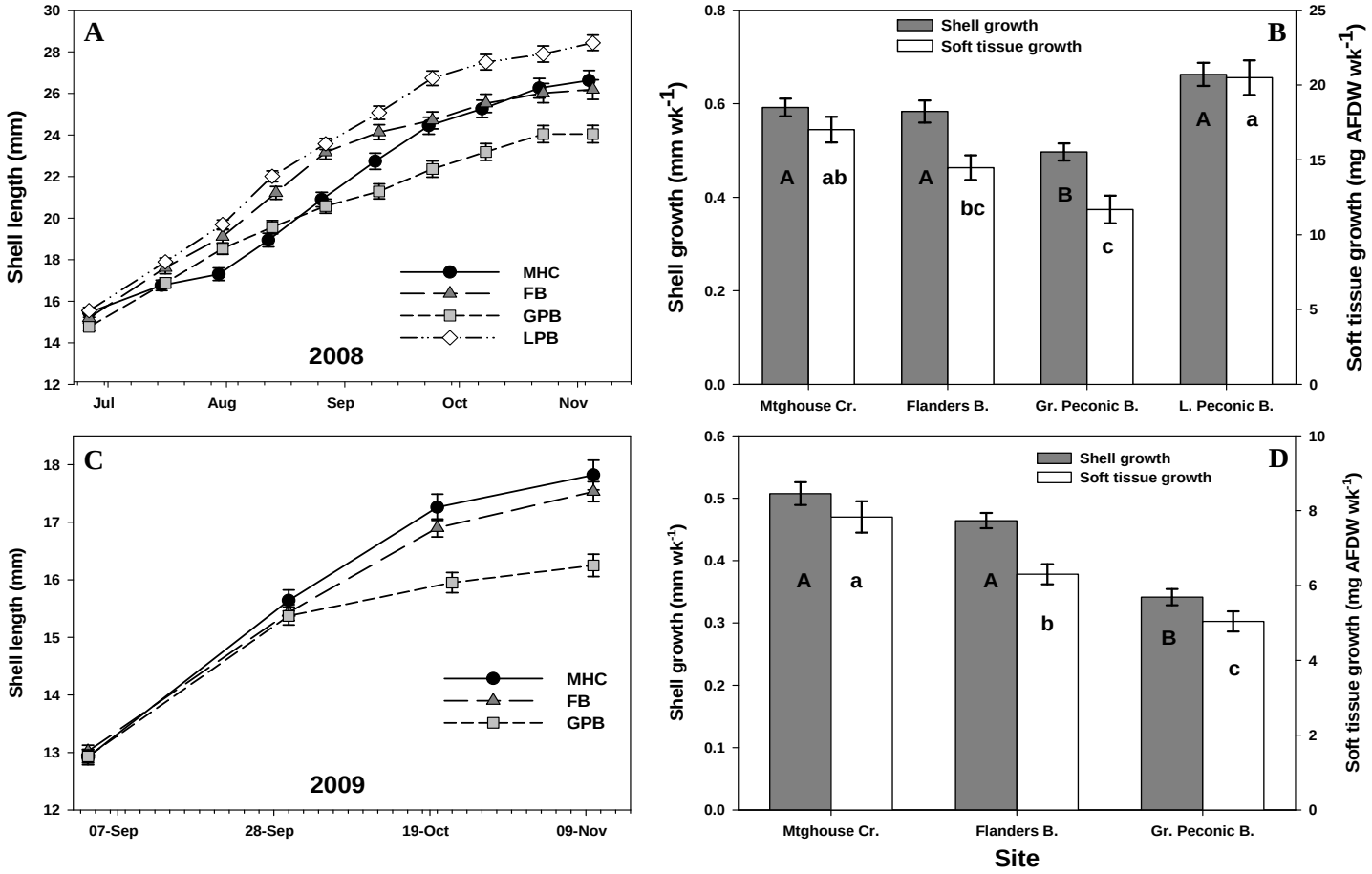

Figure 4.7. Growth of northern quahogs (*M. mercenaria*). Shown are time series of shell length (A) and seasonal mean growth rates (B) for 2008 and the same data for 2009 (C-D). Values are mean ± SE; capital letters indicate significant differences between seasonal means of shell growth, while lower-case letters indicate significant differences for soft tissue growth. N = 50 individuals per site for both years.

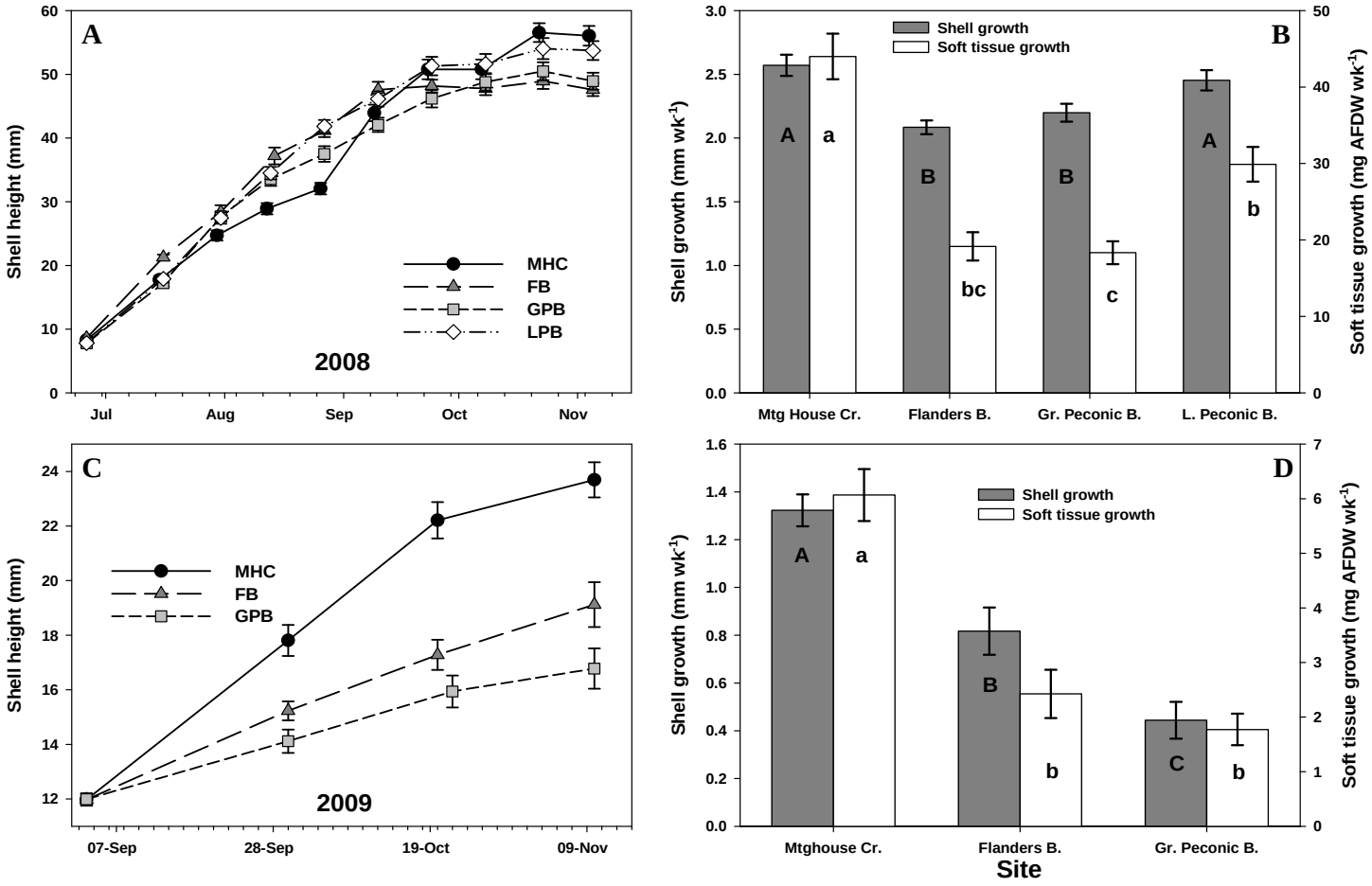

Figure 4.8. Growth of eastern oysters (*C. virginica*). Shown are time series of shell height (A) and seasonal mean growth rates (B) for 2008 and the same data for 2009 (C-D). Values are mean ± SE; capital letters indicate significant differences between seasonal means of shell growth, while lower-case letters indicate significant differences for soft tissue growth. N = 50 individuals per site for both years.

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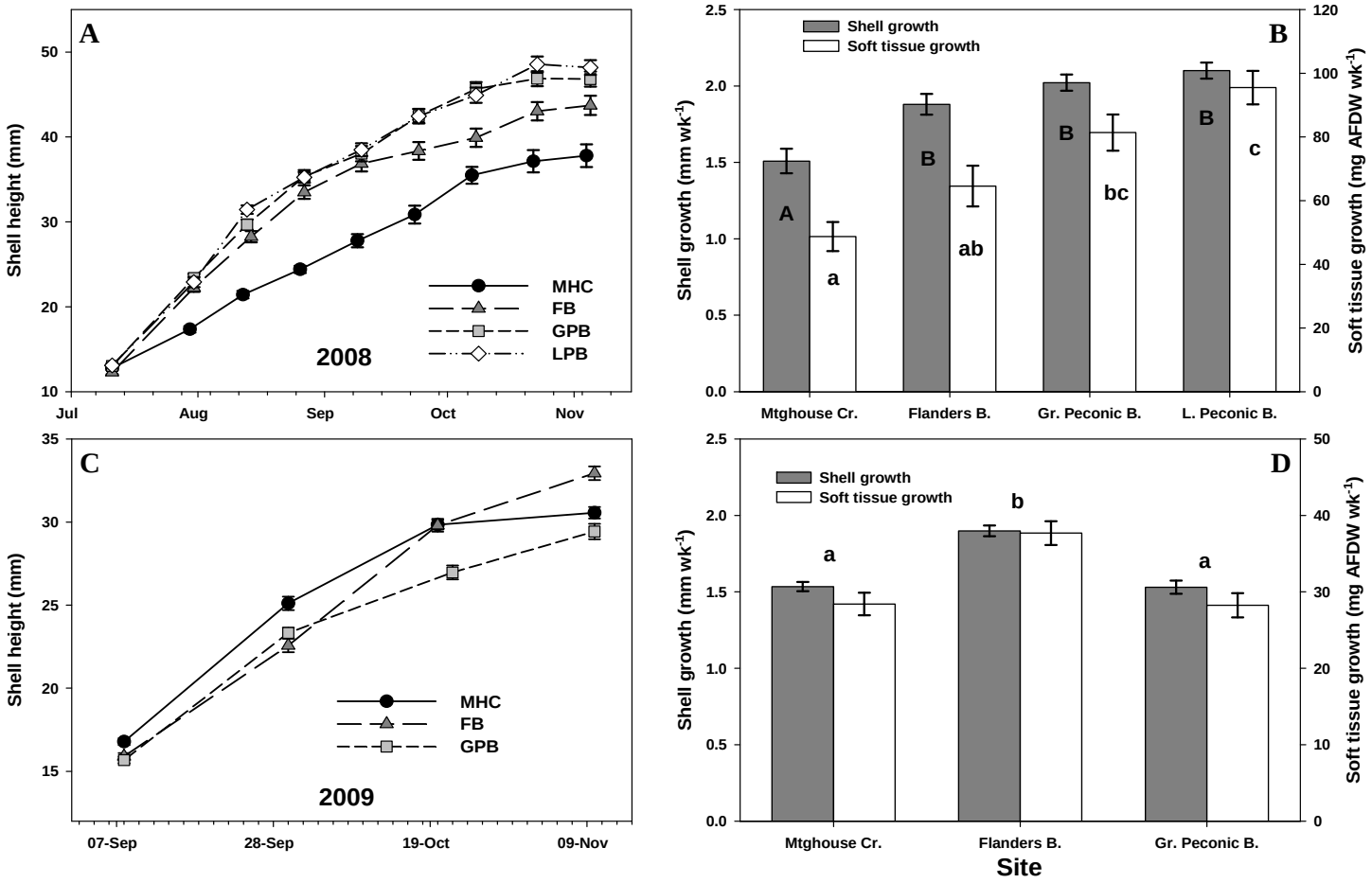

Figure 4.9. Growth of bay scallops (*A. irradians*). Shown are time series of shell height (A) and seasonal mean growth rates (B) for 2008 and the same data for 2009 (C-D). Values are mean ± SE; capital letters indicate significant differences between seasonal means for shell growth, while lower-case letters indicate significant differences for soft tissue growth. In panel D, multiple comparisons tests were the same for both growth measures, so one set of letters was used. N = 50 individuals per site for both years.

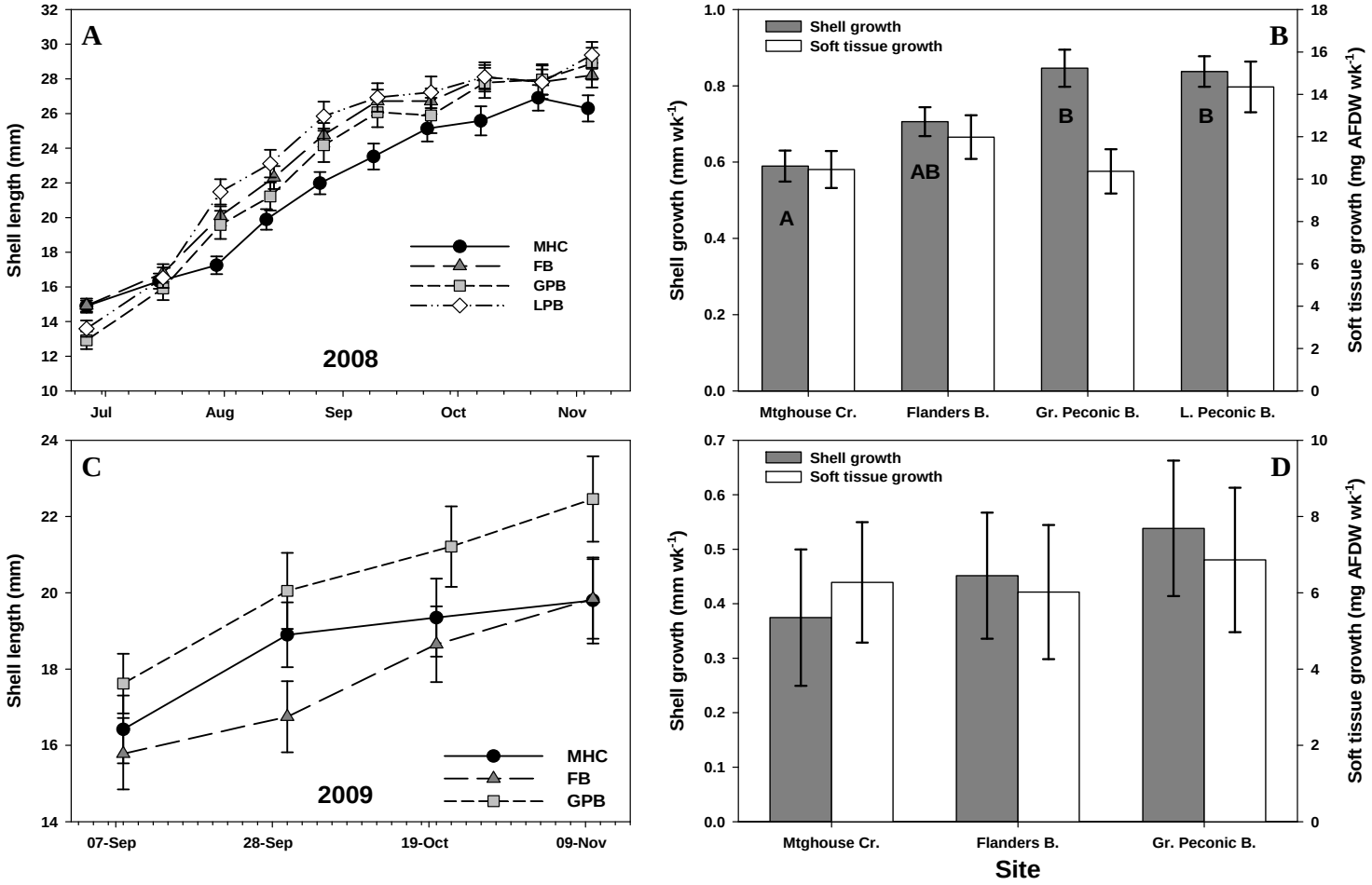

Figure 4.10. Growth of slipper limpets (*C. fornicata*). Shown are time series of shell length (A) and seasonal mean growth rates (B) for 2008 and the same data for 2009 (C-D). Values are mean ± SE; letters indicate significant differences between seasonal means. N = 40 individuals per site in 2008 and 25 individuals per site in 2009.

V. Conclusions

It is well-established that anthropogenic nutrient loading has fundamentally altered the structure and function of coastal ecosystems (Nixon 1995, de Jonge *et al.* 2002) and these effects have led to habitat degradation and loss of living marine resources through associated effects of eutrophication. Coastal eutrophication frequently leads to phenomena such as harmful algal blooms (Butler *et al.* 1995, Sunda *et al.* 2006, Anderson *et al.* 2008), shading of seagrass beds (Duarte 1995), and hypoxia/anoxia (Breitburg 2002, Diaz & Rosenberg 2008). However, since estuaries are complex ecosystems which are subjected to multiple stressors (Breitburg *et al.* 1999, Lotze *et al.* 2006), simple "stimulus-response" signals between nutrient loading and eutrophication are rarely forthcoming (Borum 1996, Cloern 2001). Cloern (2001) describes a set of features and processes that act as a "filter" between nutrient loading and eutrophication, such as hydrology, sediment load, and degree of top-down, food web control. To robustly understand and manage estuaries as whole ecosystems, we must account for the multiple stressors acting on multiple time-scales which impinge on these systems as conceptual and quantitative models of eutrophication are developed (Cloern 2001, Lotze *et al.* 2006).

One of the most important buffers between nutrient-loading the subsequent effects of eutrophication is top-down control provided by estuarine food webs. Predation is a basic ecological process that can have far-reaching effects on marine and terrestrial ecosystems (Steneck *et al.* 2002) and top-down control should be especially prevalent in shallow marine ecosystems (Heck & Valentine 2007). Importantly, many benthic habitats (seagrass beds, kelp forests) are recognized as valuable structural habitats precisely because they provide a predation refuge for marine animals (Summerson and Peterson 1984, Beck *et al.* 2001, Bruno *et al.* 2003). Since virtually all coastal marine ecosystems have been depleted of large (and small) predators by human activities (Jackson *et al.* 2001), most ecological studies of marine systems take place in a context of

vastly reduced predation pressure and may have underestimated the importance of top-down control (Heck & Valentine 2007).

Benthic suspension feeders, such as bivalves and sponges, have the potential to exert profound top-down control on shallow coastal ecosystems through benthic-pelagic coupling processes (Newell 1988, Dame 1996). Benthic suspension feeders, such as bivalves and sponges, can process large volumes of water (Haven & Morales-Alamo 1970, Winter 1973, Reiswig 1974) while selectively removing plankton and organic detritus particles (Hawkins *et al.* 1996, Ward *et al.* 1998). Benthic suspension feeders also have significant and complex effects on nutrient cycling (Kautsky & Evans 1987, Prins *et al.* 1998, Southwell *et al.* 2008), phytoplankton community dynamics (Smaal *et al.* 2001, Souchu *et al.* 2001, Peterson *et al.* 2006), and sediment characteristics (Tenore *et al.* 1982, Reise 2002). Moreover, the suspension feeders themselves can sometimes serve as critical benthic habitat structure in the form of oyster reefs (Coen *et al.* 2007) or large sponges (Butler *et al.* 1995). Suspension-feeding bivalves and sponges have been shown to control or even reverse eutrophication in some estuaries (Officer *et al.* 1982, Peterson *et al.* 2006, Petersen *et al.* 2008). At the same time, efforts to restore bivalves and their ecosystem services have been frustratingly elusive in other eutrophic systems (Mann & Powell 2007, Doall *et al.* 2008). When abundant, benthic suspension feeders may act as a keystone or foundation species in estuarine ecosystems by exerting top-down control on phytoplankton communities as well as through their habitat-forming and nutrient cycling activities (Dame 1996, Bruno *et al.* 2003). Successful restoration of estuarine habitats, estuarine species, and their associated ecosystem services will depend on many factors, including our knowledge of how these species respond to eutrophication.

Seagrasses are a critical habitat for finfish and shellfish (Summerson and Peterson 1984, Beck *et al.* 2001) that are threatened by eutrophication (Duarte 1995) and climate change (Short and Neckles 1999). In Chapter 1, I demonstrated that suspension-feeding bivalves (northern quahog, *Mercenaria mercenaria*; Eastern oyster, *Crassostrea viginica*; blue mussel, *Mytilus edulis*) could facilitate the growth of eelgrass (*Zostera marina*) through increased light penetration in mesocosms designed to simulate eutrophic lagoons.

To my knowledge, this is the first demonstration of facilitation of seagrass through water column clearance by bivalves as previous studies on the relationship between bivalves and seagrasses have focused on facilitation through biodeposition (Reusch *et al.* 1994, Peterson and Heck 2001). A broader conclusion from this study is that under eutrophic conditions, the density of one functional group (suspension feeders) can mediate the effects of eutrophication on another functional group (seagrasses), and that nutrient enrichment interacts with other stressors (fisheries loss of bivalve populations, Cloern 2001) to impact estuarine habitats.

Living marine resources (e.g., seagrasses and bivalves) are the central component of most coastal restoration strategies (Lotze *et al.* 2006), and an understanding of how living marine resources interact with each other as well as with multiple stressors is required for comprehensive, ecosystem-based management of estuaries (Christensen *et al.* 1996). Eutrophication due to anthropogenic nutrient loading is one stressor (Nixon 1995), and the growing aquaculture industry will have another set of impacts on estuarine ecosystems (Naylor *et al.* 2000, Feng *et al.* 2004) which may or may not be stressors on these systems (Dumbauld *et al.* 2009). Shellfish aquaculture creates a high density of suspension feeders (Frechette *et al.* 1996), and this activity has the potential to create positive and negative effects. High density shellfish aquaculture has created negative effects on the benthos through increased biodeposition (Tenore *et al.* 1982, Newell 2004), while at the same time aquaculture cages can serve as functional habitat for finfish and crustaceans (Hosack *et al.* 2006, Powers *et al.* 2007), and bivalve aquaculture can buffer eutrophication through increased filtration rates (Smaal *et al.* 2001, Huang *et al.* 2008). It is not well-known how bivalve aquaculture operations will influence each other or natural populations, and how these effects will interact with nutrient loading (Duarte *et al.* 2003, Ferreira *et al.* 2008). In the mesocosm experiments presented in Chapter 2, I demonstrated that high levels of water column filtration from adult bivalves could slow the growth of juvenile bivalves, and that enhanced nutrient loading could accelerate the growth of juvenile bivalves (northern quahogs, *M. mercenaria*; eastern oysters, *C.virginica*). In contrast, filtration from adult bivalves enhanced the growth of eelgrass (*Z. marina*), while nutrient loading slowed eelgrass growth. To my knowledge, this is the first demonstration of simultaneous effects of filtration and nutrient loading on multiple

estuarine resource species in an experimental setting. These findings suggest that despite its broad negative impacts on some aspects of estuarine ecosystems, some estuarine resources may benefit from nutrient loading that increases food availability, e.g. "eutrophication" in the broadest sense (Carmichael *et al.* 2004). While enhanced filtration is typically considered a positive effect on estuaries (Officer *et al.* 1982, Cerco and Noel 2007), an overstocking of bivalve aquaculture operations could have a negative feedback on adjacent aquacultured or native shellfish populations through excessive filtration. These findings demonstrate how nutrient enrichment and aquaculture may interactively affect estuaries, and also points toward differential responses to eutrophication by different marine resources (e.g., seagrasses and bivalves).

Harmful algal blooms are a growing threat to marine habitats and species (Gobler *et al.* 2005, Anderson *et al.* 2008). These blooms are linked to nutrient loading (Heisler *et al.* 2008), but as with eutrophication, simple "stimulus-response" signals between nutrient loading and harmful algal blooms have been somewhat elusive (Smayda 2008). Harmful algal blooms may proliferate through feedback loops that suppress grazing and lead to further algal growth (Sunda *et al.* 2006). In an experimental setting, sufficient densities of suspension feeders have been shown to slow or reverse development of harmful algal blooms (Cerrato *et al.* 2004), and loss of suspension feeders has been implicated in the persistence of harmful algal blooms (Newell 1988, Peterson *et al.* 2006). In Chapter 3, I demonstrated that a sponge (*Spechiospongia vesparium*) in a sub-tropical lagoon functioned similarly to bivalves in temperate estuaries through filtration of phytoplankton in the water column. In regions with abundant sponges, *in situ* measurements of filtration rates revealed that these suspension feeders were able to graze the cyanobacteria population at rates equal to or greater harmful cyanobacterial intrinsic growth rates. In regions with few remaining sponges, cyanobacteria blooms proliferated due to a suppression of benthic and pelagic (Goleski *et al.* 2010, in press) grazing. To my knowledge, these are the first *in situ* measurements of sponge filtration rates during a harmful algal bloom. These findings indicate the importance of top-down control in general and benthic filtration specifically in controlling harmful algal blooms in lagoonal estuaries. However, managers striving to reduce such events may face a "chicken or egg" dilemma as restoration of suspension feeders may control algal blooms, but water quality

may first have to be improved by other means to ensure survival of re-stocked suspension feeders as my research demonstrated that transplanted sponges were unable to survive persistent harmful algal blooms.

Eutrophication has multiple and complex effects on estuaries; some effects can be generalized (Nixon 1995) and others will be estuary- and species-specific (Cloern 2001). The traditional view has been that enhanced nutrient loading will always lead to negative consequences for estuarine habitats (de Jonge *et al.* 2002, Kemp *et al.* 2005), and this is certainly true for many systems, species, and levels of nutrient loading (Valiela *et al.* 1992, Duarte 1995, Anderson *et al.* 2008). This view, however, does not consider the potential positive effects of nutrient loading and eutrophication on some organisms (Nixon and Buckley 2002). Whereas the definition of eutrophication includes increased and enriched organic matter (Nixon 1995), suspension feeders are a functional group that could benefit from eutrophication (Smaal and van Stralen 1990, Beukema and Cadee 1991, Carmichael *et al.* 2004). Not all suspension feeders are equal, and eutrophication will change both the amount of organic seston in an estuary and the composition of the phytoplankton community (Cloern 2001, Smayda 2008). In Chapter 4, I found that these changes in the quantity and quality of organic seston had differential effects on multiple species of suspension feeders (northern quahogs, *M. mercenaria*; eastern oysters, *C. virginica*; bay scallops, *Argopecten irradians*; slipper limpets, *Crepidula fornicata*), as well as on eelgrass (*Z. marina*), a critical habitat-forming organism. Northern quahogs and eastern oysters were were tolerant of eutrophic changes in phytoplankton composition and may have benefited from increased food availability. These species are well-adapted to high concentrations of organic seston, and regulate their activity under eutrophic conditions through a combination of shell closure, reduced clearance rate, particle selectivity, and pseudo-feces production (Newell and Langdon 1996, Grizzle *et al.* 2001). Bay scallops and eelgrass were negatively impacted by eutrophication. Bay scallops can achieve fast growth under mesotrophic conditions by maintaining high clearance rates and high respiration rates (MacDonald *et al.* 2006), but these organisms are poorly adapted to high seston concentrations and relatively intolerant of harmful algae and hypoxia that may accompany eutrophication (Peterson *et al.* 1996, Gobler *et al.* 2005). Although eelgrass can benefit from nutrient deposition to the sediments (Peterson

and Heck 2001, Carroll *et al.* 2008), eelgrass growth and survival is suppressed when nutrient loading leads to micro- and macro-algal blooms that shade eelgrass beds (Duarte 1995, Hauxwell *et al.* 2003). To my knowledge, this is the largest number of resource species that have been simultaneously monitored in a controlled study of eutrophication in the same estuary. These findings indicate that there are potential positive effects of eutrophication on some resource species, and at the same time negative effects on other resource species. This evidences the trade-offs in the management of nutrient loading in estuaries, and indicates that different levels of nutrient loading might be permitted in different embayments of an estuary. "Nutrient loading zones" could be incorporated into management schemes alongside multiple-use marine zoning (Halpern *et al.* 2008) and marine protected areas (Pauly *et al.* 2002).

We now know more about the interactions between functional groups in estuaries (bivalves and seagrasses), and about the responses of resource species to eutrophication. In addition, this work has shed light on the functional role of sponges in a sub-tropical lagoon in response to harmful algal blooms. Sponges play an important role in elemental cycling on coral reefs (Weisz *et al.* 2007, Southwell *et al.* 2008) but little is known about their biogeochemical role in shallow lagoonal systems like Florida Bay. What we still do not know are the most successful strategies for restoring estuarine resources. Wide-ranging measurement of estuarine conditions, which already exists for many systems, could be used in conjunction with data on responses of multiple resource species to create spatial models of the most suitable sites for restoration. Benthic suspension feeders and seagrasses are not just resource species, but are also biogeochemical engines (Smaal and Prins 1993, Reise 2002) that cycle nutrients, carbon, and trace metals through benthic-pelagic coupling. As abundances of suspension feeders and seagrasses change through restoration, aquaculture, or eutrophication, these elemental cycles will be altered proportionately to the changes in biomass or areal coverage of the benthos (Orth *et al.* 2006, Sandwell *et al.* 2009). Future research should describe and quantify how biogeochemical cycles will change with the restoration of resource species and the development of aquaculture using mass-balance models for nitrogen or other elements of interest.

In this dissertation I have described multiple interactions between nutrient loading, suspension feeders, and seagrasses that are mediated through benthic-pelagic coupling, and it is my hope that these findings will inform successful ecosystem-based management in the future. In the big picture, estuaries and other coastal waters once supported much higher abundances of vertebrates, invertebrates, and submerged aquatic vegetation (Jackson *et al.* 2001, Lotze *et al.* 2006), and these waters were characterized by strong benthic-pelagic coupling that channeled productivity and biomass towards the benthos (Jackson 2001, Kemp *et al.* 2005, Lotze *et al.* 2006). Presumably this abundance of consumers exerted much greater top-down control (Myers *et al.* 2007, Heck and Valentine 2007) than exists in present-day estuaries. On a historic time-scale, the signs and symptoms of eutrophication co-occur with removal of consumers and increased nutrient loading (Lotze *et al.* 2006), so alteration of food webs may be equally to blame as nutrient loading for the degradation of coastal habitats (Newell 1988, Steneck *et al.* 2002). Successful ecosystem-based management of estuaries will account for multiple stressors, multiple species, and species-specific responses to environmental conditions. There has been a scientific consensus about the basic need for ecosystem-based management for over a decade (Christensen *et al.* 1996, Costanza *et al.* 1997), but a comprehensive understanding in marine systems has lagged behind terrestrial systems (Hooper *et al.* 2005) and implementation in real-world management plans has been slow and inherently difficult due to the multiple factors that need to be addressed in each system (Halpern *et al.* 2008). Management goals that aim to restore benthic-pelagic coupling pathways through top-down control by suspension feeders and facilitation of seagrass habitat will help us achieve vibrant, productive estuaries.

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