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2 **FINAL REPORT TO THE NATURE CONSERVANCY, JUNE 2009**

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5 **AN ASSESSMENT OF THE IMPACT OF NUTRIENT LOADING, BIVALVE**  
6 **FILTRATION AND PHYTOPLANKTON COMMUNITIES ON ESTUARINE**  
7 **RESOURCES**

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**Chapter I:**

**The effects of eutrophication within Peconic Estuary on the growth and survival of estuarine shellfish and seagrass (*Zostera marina*, *Mercenaria mercenaria*, *Crassostrea virginica*, *Argopecten irradians*)**

*This was a field study conducted during the summer of 2008 and will be submitted as a manuscript to an international peer-reviewed journal this year.*

**Keywords:** *Zostera marina*, *Crassostrea virginica*, *Mercenaria mercenaria*, *Argopecten irradians*, *Crepidula fornicata*, *Cyprinodon variegatus*, eelgrass, seagrass, clams, oysters, scallops eutrophication, nutrients, nutrient-loading, bivalves, suspension feeders, ecosystem-based management, estuarine restoration, Peconic Bay, Peconic Estuary

1 **Abstract:** While many coastal ecosystems previously supported dense meadows of seagrass and  
2 dense stocks of resource bivalves, the impacts of overfishing, eutrophication, harmful algal  
3 blooms, and habitat loss have contributed to the decline of these important resources.  
4 Anthropogenic nutrient loading that leads to eutrophication has been identified by some  
5 researchers as a primary driver of these losses, but other researchers have described potential  
6 positive effects of eutrophication on estuarine resources. The Peconic Estuary, Long Island, NY,  
7 USA, offers a naturally occurring nutrient loading gradient from eutrophic tidal creeks in the  
8 western region to mesotrophic bays in the eastern region. We conducted a five-month field  
9 grow-out experiment at four stations across this gradient to examine the effects of eutrophication  
10 on estuarine resources: eelgrass (*Zostera marina*), juvenile bivalves (hard clams, *Mercenaria*  
11 *mercenaria*, Eastern oysters, *Crassostrea virginica*, and bay scallops, *Argopecten irradians*), and  
12 the non-resource suspension feeder, the slipper snail (*Crepidula fornicata*). Water quality  
13 parameters were also monitored at the field stations. Hard clams grew maximally at the least  
14 eutrophic site, but did not display a consistent east-west pattern along the eutrophication  
15 gradient. Eastern oysters grew maximally at the most eutrophic tidal creek, but also did not have  
16 a consistent east-west pattern. Bay scallops and slipper snails displayed consistent east-west  
17 patterns: growth was always maximal at the least eutrophic sites and minimal at the more  
18 eutrophic sites, although this pattern was more distinct for bay scallops. Eelgrass growth was  
19 depressed in the eutrophic tidal creek by low light levels and high epiphyte loading, maximal at a  
20 mid-estuary site, and depressed again at the less eutrophic site due to intense macro-benthic  
21 grazing. These results suggest that nutrient loading can have significant and complex effects on  
22 estuarine resource species, and that select species (e.g. oysters) may benefit from eutrophication  
23 under some conditions. Future ecosystem-based approaches that seek to restore estuarine

1 resources will need to account for the differential effects of nutrient loading as managers target  
2 species and regions to be restored.

3

1 **Introduction:**

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

12 Changes in inorganic nutrient loading to estuaries can indirectly influence the growth of  
13 marine resource species. High rates of nutrient loading have been associated with increases in  
14 pelagic productivity, decreased water clarity, hypoxia, and declines in seagrass growth and  
15 abundances (Duarte 1995, Diaz and Rosenberg 2008, Wall *et al.* 2008), commonly referred to as  
16 the process of eutrophication (Nixon 1995, de Jonge *et al.* 2002). In response, estuarine  
17 management efforts often focus primarily on reducing anthropogenic nutrient loading in an effort  
18 to curb the negative effects of eutrophication (Cloern 2001, de Jonge *et al.* 2002). However,  
19 some level of nutrient loading must be necessary to sustain primary and secondary production  
20 (Nixon and Buckley 2002). High levels of inorganic nutrients favor larger phytoplankton cells  
21 (Malone 1980, Raven and Kubler 2002), such as diatoms and prymnesiophytes, which are  
22 generally considered a good source of nutrition for bivalves (Beukema and Cadee 1991, Wikfors  
23 *et al.* 1992, Weiss *et al.* 2007). Studies in several estuaries have shown blue mussels (*Mytilus*

1 *edulis*), hard clams (*Mercenaria mercenaria*), and softshell clams (*Mya arenaria*) can respond  
2 positively to increased nitrogen loading and high chlorophyll *a* levels in their habitats (van  
3 Stralen and Dijkema 1994, Weiss *et al.* 2002, Carmichael *et al.* 2004, Weiss *et al.* 2007). Weiss  
4 *et al.* (2002) and Carmichael *et al.* (2004) found that shell growth, soft tissue growth, and  
5 survival of *M. mercenaria* and *M. arenaria* increased along a naturally-occurring gradient of  
6 nitrogen loading in Waquoit Bay, Massachusetts, USA. They attribute these changes to  
7 increased quantity and quality of food particles due to nitrogen enrichment (Carmichael and  
8 Valiela 2005), although a similar response has not been found for bay scallops (*Argopecten*  
9 *irradians*, Shriver *et al.* 2002). While nutrient over-loading in estuaries has a well-known set of  
10 negative consequences (Valiela *et al.* 1992, Nixon 1995, Kemp *et al.* 2005), the stimulation of  
11 secondary production in bivalves could be an overlooked positive effect of nutrient loading  
12 (Nixon and Buckley 2002, Carmichael *et al.* 2004, Carmichael and Valiela 2005), especially in  
13 shallow ecosystems with well-mixed water columns that rarely experience hypoxia.

14         Where to locate the line between nutrient loading and nutrient **over**-loading remains an  
15 open question, and has clear ecological and financial implications for the management of  
16 estuaries (PEP-CCMP 2003). Clearly, the answer will be different for each estuary. Systems  
17 that are well-flushed will be able to absorb more anthropogenic nutrients without experiencing  
18 negative effects than systems that are poorly-flushed, stratified, or otherwise vulnerable to  
19 eutrophication (Cloern 2001, de Jonge *et al.* 2002). The biota of an estuary also influences how  
20 the system reacts to nutrient loading. The filtration capacity of an intact benthos, with bivalve  
21 suspension feeders, can buffer the negative effects of eutrophication (Officer *et al.* 1982, Smaal  
22 and Prins 1993, Cerco and Noel 2007). Some authors have suggested that aquacultured bivalves

1 could provide levels of ecosystem filtration comparable to wild populations (Newell 2004, Zhou  
2 et al. 2006, Huang et al. 2008).

3           The level at which nutrient loading and its effects becomes harmful to a particular living  
4 resource will also vary between species and with the overall health of the estuary. Seagrasses are  
5 sensitive to eutrophication and subsequent declines in light levels (Dennison et al. 1989, Duarte  
6 1995), but could be recovered or facilitated by the presence of bivalves (Newell and Koch 2004,  
7 Wall et al. 2008, Carroll et al. 2008). Mobile fauna can avoid (at least temporarily) regions of  
8 low dissolved oxygen or poor water quality (Breitburg 2002), but most benthic organisms must  
9 simply endure the effects of eutrophication. Some species of bivalves, such as hard clams, soft-  
10 shell clams, and Eastern oysters (*Mercenaria mercenaria*, *Mya arenaria*, *Crassostrea virginica*)  
11 can endure short periods of hypoxia (Kraeuter and Castagna 2001, Carmichael et al. 2004,  
12 Kennedy et al. 1996) and may even benefit from nutrient-derived increases in quantity and  
13 quality of food particles (Weiss et al. 2002, Carmichael et al. 2004). Other bivalve species, such  
14 as bay scallops (*Argopecten irradians*) and blue mussels (*Mytilus edulis*) are more sensitive to  
15 declines in water quality, and may not survive the effects of high nutrient loads (Shriver et al.  
16 2002, Altieri and Witman 2006). As plans for aquaculture and restoration of living resources  
17 proceed, it will be vital for managers to know how various levels of nutrient loading will affect  
18 the growth and survival of resource species (Cloern 2001, Newell 2004, Lotze et al. 2006).  
19 Ecosystem based-management (Slocombe 1993, Lotze et al. 2006) will also require a careful  
20 examination of where nutrient loads need to be reduced, where they can remain at current levels,  
21 and even where they might be allowed to increase somewhat (Nixon and Buckley 2002).

22           Eutrophication leads to shifts in distribution and abundance, and many potential nuisance  
23 organisms have increased their ranges and abundances in eutrophic systems, concurrent with the

1 removal of previously dominant organisms and the increase of nutrient loading (Mills 2001,  
2 Sunda et al. 2006, Lotze et al. 2006). The slipper shell *Crepidula fornicata* is a gastropod  
3 suspension feeder, is not currently a resource species, and is proliferating in areas formerly  
4 dominated by bivalve suspension feeders (Lewis et al. 1997, Lewis and Rivara 1998, Harke et al.  
5 in progress). While slipper shells may provide some of the filtration services formerly provided  
6 by bivalves (Barille et al. 2006, Harke et al. in progress), they are not likely to be viewed as a  
7 positive living resource in the same vein as clams, oysters, or scallops, and estuarine  
8 management plans should incorporate the response of potential nuisance species to changing  
9 levels of nutrient loading.

10         The Peconic Estuary, Long Island, NY, USA, is a system that may provide a unique  
11 opportunity to study the effects of nutrient loading on several marine resource species  
12 simultaneously. The Peconic Estuary is a chain of interconnected bays totaling 218 km<sup>2</sup> with an  
13 average depth of 4.7 m and an average tidal range of 0.76 m (Hardy 1976). There is a gradient  
14 of nutrient loading and chlorophyll *a* concentrations from high in the western regions (more  
15 concentrated human activities, less tidal mixing) to low in the eastern parts of the estuary (less  
16 concentrated human activities, more tidal mixing, Fig. 1, Hardy 1976). Hypoxia/anoxia is  
17 generally not present in the Peconic Estuary, due to wind and tidal mixing, and a lack of salinity-  
18 based stratification (Hardy 1976), so differences observed in the growth of estuarine resources  
19 should be due primarily to nutrient-loading, and not to hypoxia. The Peconic Estuary was  
20 formerly the site of productive fisheries for scallops, oysters, hard clams, soft-shell clams, eels,  
21 and menhaden (Hardy 1976), but these resources have been greatly diminished due to over-  
22 harvesting and the effects of the harmful brown tide algae (Cosper *et al.* 1987, Gobler *et al.*

1 2005). There have been concurrent losses of eelgrass habitat throughout the Peconic Estuary  
2 (Pickerell and Schott 2006).

3 This study was designed to examine the effects of nutrient loading across a naturally-  
4 occurring estuarine gradient on the growth and survival of estuarine resource species: juvenile  
5 hard clams (*M. mercenaria*), bay scallops (*A. irradians*), oysters (*C. virginica*), a juvenile  
6 planktivorous fish (sheepshead minnow, *Cyprinodon variegatus*), and eelgrass (*Z. marina*).  
7 Juvenile slipper shells (*C. fornicata*) were also included as a non-resource suspension feeder.  
8 These six species were placed at four field sites spaced across the nutrient-loading gradient. The  
9 growth of all populations along with levels of light, nutrients, size-fractionated chlorophyll *a*,  
10 and particulate organic matter were monitored during a growing season (Jun – Nov) to determine  
11 the effects of different levels of nutrient loading on the growth of estuarine resources.

12

### 13 **Methods:**

14 Four study sites were established in the Peconic Estuary across the estuarine gradient  
15 from a eutrophic tidal creek in western Flanders Bay to more oligotrophic conditions in Great  
16 and Little Peconic Bay (Fig 2). In order of west to east, and in order of most eutrophic to least  
17 eutrophic, the sites are named Meetinghouse Creek (MHC), Flanders Bay (FB), Great Peconic  
18 Bay (GPB), and Little Peconic Bay (LPB). Sites were approximately the same depth (1.8 – 2.5  
19 m), and comparable in salinity and temperature, so the gradient of nutrient loading should be the  
20 primary factor driving differences in growth responses between the sites. The estuarine  
21 resources monitored at each site were eelgrass (*Zostera marina*), hard clams (*Mercenaria*  
22 *mercenaria*), eastern oysters (*Crassostrea virginica*), bay scallops (*Argopecten irradians*), and  
23 juvenile fish (sheepshead minnows, *Cyprinodon variegatus*). The growth of slipper shells

1 (*Crepidula fornicata*) was measured as a non-resource molluscan suspension feeder which has  
2 recently proliferated in areas formerly dominated by resource bivalves (Lewis et al. 1997, Lewis  
3 and Rivara 1998). Eelgrass shoots were placed in planters and lowered to the bottom, while  
4 juvenile fish and shellfish, obtained from a local hatchery, were placed in mesh cages (~2 mm  
5 mesh size) and bags kept in wire cages. Eelgrass planters and shellfish cages were anchored to  
6 the bottom, and a surface buoy marked each location. The growth of organisms at each study  
7 site was monitored bi-weekly over the course of the summer growing season from June to  
8 November 2008. Water quality parameters were also sampled bi-weekly such as chlorophyll *a*,  
9 dissolved oxygen, salinity, light attenuation, dissolved nutrient concentrations, and POC/PON  
10 concentrations. Temperature and ambient light levels were monitored continuously by HOBOb  
11 pendant-style data loggers. Differences in bulk water motion (tidal mixing + wind mixing)  
12 between sites were measured once using a plaster dissolution method (Doty 1971) averaged over  
13 a 24 hour period.

14 Chlorophyll *a* was measured in the whole and >5  $\mu\text{m}$  size fractions using polycarbonate  
15 filters and standard fluorometric techniques (Parsons et al. 1984). Salinity and dissolved oxygen  
16 were measured using a YSI-### probe. Particulate organic carbon and particulate organic  
17 nitrogen were collected on pre-combusted glass fiber filters and processed using a CE  
18 Instruments Flash 1112 elemental analyzer (Sharp 1974, Gobler and Sañudo-Wilhelmy 2001).

19 Eelgrass was harvested and replaced every two weeks, and eelgrass productivity was  
20 measured by leaf area growth and above-ground biomass production (Ibarra-Obando and  
21 Boudouresque 1994). Epiphytes were scraped from eelgrass leaves for measurement of epiphyte  
22 loading. For each shellfish species, 50 individuals were stocked at each field site. These  
23 individuals were marked with bee-tags (“Queen Marking Kits,” The Bee Works,

1 www.beeworks.com) attached with marine epoxy so individual growth rates by shell length  
2 could be measured. Clams and slipper shells were measured by shell length (anterior-posterior),  
3 while oysters and scallops were measured by shell height (hinge-ventral margin). Shell growth  
4 measurements were made every two weeks and at the end of the experiment and expressed as  
5 mean growth in  $\text{mm week}^{-1}$ . At the beginning of the experiment, 50 individuals of each species  
6 were sacrificed to obtain initial ash-free dry tissue weights (AFDW) and condition indices. Ash-  
7 free dry tissue weights and condition indices were measured on all surviving individuals at the  
8 end of the experiment, and mean growth rates by weight were calculated in  $\text{mg AFDW week}^{-1}$ .  
9 Condition indices were calculated according to the methods of Rheault and Rice (1996).  
10 Juvenile sheepshead minnows were collected and replaced every two weeks. Sheepshead  
11 minnow growth was measured in  $\text{mm week}^{-1}$  and  $\text{mg dry wt week}^{-1}$ . Length-weight regressions  
12 were used to estimate initial weights for sheepshead minnows. Shellfish and cages were cleaned  
13 of fouling material every two weeks, while fish cages were replaced every two weeks.

14 Growth of fish, shellfish, and eelgrass was analyzed using one- and two-way ANOVAs to  
15 check for significant differences between sites and time. A two-way repeated measures ANOVA  
16 was used to analyze measurements of tagged individuals over several time points. When data  
17 did not fit the ANOVA assumptions, a non-parametric test was used (Kruskal-Wallis test).  
18 Correlation and regression analyses were used to account for growth responses in terms of water  
19 quality parameters. Chlorophyll *a* and light level trends were analyzed using two-way ANOVAs  
20 with site and time-point. When a significant effect on the response variables was detected,  
21 multiple comparison tests (Tukey's Studentized range) was used to test for significant  
22 differences between levels within the treatment. Mortality of juvenile bivalves was analyzed

1 using a G-test of independence (Sokal and Rohlf 1995). All statistical results were considered  
2 significant if  $p < 0.05$ . Statistical analyses were carried out on the software SigmaStat 3.0.

3

#### 4 **Results:**

5 Field sampling was carried out bi-weekly from June 30<sup>th</sup>, 2008, to November 5<sup>th</sup>, 2008.

6 Physical trends of temperature, salinity, and dissolved oxygen for bottom waters (depth of ~ 2 m)  
7 are shown in Fig 3A-C. Temperatures of bottom waters started off at 25 – 27° C in July and  
8 declined to 10 – 11° C by early November, with only small difference between sites (Fig 3 A).  
9 Salinities of bottom waters were consistent over the course of the season, but did differ slightly  
10 between sites, ranging from 26 – 27 psu at Meetinghouse Creek, the most inland site, to 28 – 29  
11 psu at Great and Little Peconic Bays, the sites closest to the ocean exchange (Fig 3 B).

12 Dissolved oxygen in bottom waters differed more dramatically by both date and site, with  
13 bottom waters of Meetinghouse Creek often hypoxic or nearly anoxic during July – September  
14 (Fig 3 C). Dissolved oxygen varied at the other three sites but remained normoxic throughout  
15 the study (Fig 3 C). Since we anticipated hypoxia in the bottom waters of Meetinghouse Creek,  
16 the shellfish cages were placed at a depth of ~ 1 m, which should have avoided the hypoxia at 2  
17 m.

18 Chlorophyll *a* in the whole and >5 µm size differed significantly by site, by date, and by  
19 site x date interaction ( $p < 0.001$ , 2-way ANOVA, Fig 4 A). Meetinghouse Creek consistently  
20 had high chl *a*, 20 - 40 µg L<sup>-1</sup>, while Flanders Bay had intermediate chl *a*, 5 – 15 µg L<sup>-1</sup>, and  
21 Great and Little Peconic Bays had low chl *a*, <10 µg L<sup>-1</sup> all season. Even though there was  
22 temporal variation in chl *a* at all sites, this trend of high phytoplankton biomass in the west and  
23 lower phytoplankton biomass in the east is consistent when values for each site are averaged

1 across time points ( $p < 0.001$ , 1-way ANOVA, Fig 4 B). Virtually all of the chl *a* was in the  $>5$   
2  $\mu\text{m}$  size fraction at Meetinghouse Creek, and the proportion of phytoplankton in the larger size  
3 fraction decreased from west to east, but was, on average, never less than 76% of the total  
4 phytoplankton community (Fig 4 C).

5 The growth of all shellfish was generally high during the summer and declined with  
6 decreasing temperatures in October and November (Figs 5-7 C-D). The growth of hard clams  
7 (*Mercenaria mercenaria*) averaged over the whole growing season was significantly different  
8 between sites, when measured by shell growth ( $p < 0.001$ , ANOVA, Fig 5-A) or by soft-tissue  
9 growth ( $p < 0.001$ , ANOVA-on-ranks, Fig 5-B). By both measures, the clams at L. Peconic B.  
10 grew fastest, but there was not a consistent east-west pattern along the eutrophication gradient.  
11 Hard clams in Mtghouse Cr. had the second-fastest growth by shell length or AFDW, with clams  
12 at the mid-estuarine sites, Flanders B. and Gr. Peconic B., growing more slowly (Fig 5 A-B).  
13 There was also significant variation by date and a site x date interaction for hard clams ( $p < 0.001$ ,  
14 2-way repeated measures ANOVA, Fig 5 C-D). For example, shell growth of hard clams was  
15 slow at Mtghouse Cr. in the mid-summer and accelerated in the early fall (Fig 5 C-D).

16 The growth of eastern oysters (*Crassostrea virginica*) averaged over the whole growing  
17 season was also significantly different between sites, when measured by shell growth ( $p < 0.001$ ,  
18 ANOVA-on-ranks, Fig 6-A) or by soft-tissue growth ( $p < 0.001$ , ANOVA-on-ranks, Fig 6-B). By  
19 both measures, the oysters at Mtghouse Cr. grew fastest, but as with the hard clams, there was  
20 not a consistent east-west pattern along the eutrophication gradient. Eastern oysters in L.  
21 Peconic B. had the second fastest growth by shell length or AFDW, with oysters in the middle  
22 sites of Flanders B. and Gr. Peconic B. growing more slowly (Fig 6 A-B). The variation in shell  
23 growth rates of tagged individuals was significant by date and site x date interaction ( $p < 0.001$ , 2-

1 way repeated measures ANOVA, Fig 6 C-D), but there was not a significant difference by site.  
2 Nevertheless, the shell growth of oysters in Mtghouse Cr. had a similar pattern to clam growth at  
3 this site: oyster growth was slow in mid-summer and accelerated greatly in early fall (Fig 6 C-  
4 D).

5 The growth of bay scallops (*Argopecten irradians*) averaged over the whole growing  
6 season was significantly different by site when measured by shell growth ( $p < 0.001$ , ANOVA,  
7 Fig 7-A) or by soft-tissue growth ( $p < 0.001$ , ANOVA, Fig 7-B). In contrast to the hard clams and  
8 eastern oysters, bay scallops had a growth response with a consistent east-west pattern: scallop  
9 growth was highest in the east, at the least eutrophic site, and decreased stepwise to the west at  
10 the more eutrophic sites (Fig 7 A-B). Shell growth by date follows the same pattern, with a clear  
11 separation in mean shell height between the eastern sites (less eutrophic) and the western sites  
12 (more eutrophic) throughout the season (Fig 7 C-D). Shell growth was significantly different by  
13 site, date, and site x date interaction ( $p < 0.001$ , 2-way repeated measures ANOVA, Fig 7 C-D).

14 The mortality of shellfish was not significantly different by site for all three species (G-  
15 test of independence), however the percent survival by site tended to follow the growth trends by  
16 site, i.e. sites with the slowest growth had the highest mortality for that species and vice versa  
17 (data not shown). The growth of juvenile fish (sheepshead minnows, *Cyprinodon variegatus*)  
18 was not significantly different by site (1- and 2-way ANOVAs, data not shown).

19 Bulk water motion, as measured by rates of plaster dissolution, was significantly greater  
20 in the east, and decreased stepwise to the west, with water motion at all sites also significantly  
21 greater than a “no-flow” control ( $p < 0.001$ , ANOVA, Fig 8). There was no significant difference  
22 in bulk water motion between plaster blocks placed inside shellfish cages and outside shellfish  
23 cages (2-way ANOVA). However, we were not able to place plaster blocks inside the individual

1 shellfish bags, which were 2-mm mesh and may have reduced water motion relative to outside  
2 the mesh.

3         The growth of slipper snails (*Crepidula fornciata*) was significantly different between  
4 sites when averaged over the whole season for shell growth (Fig 9A) or soft tissue growth (Fig  
5 9B). The shell growth of slipper snails (Fig 9A) paralleled that of bay scallops (Fig 7A); slipper  
6 snail growth was significantly higher at the eastern sites compared to Flanders Bay and  
7 Meetinghouse Creek ( $p < 0.001$ , 1-way ANOVA). Oddly, the soft tissue growth and shell growth  
8 displayed differing patterns for slipper snails (Fig 9B). Individuals at Great Peconic Bay that had  
9 the fastest shell growth had relatively low soft tissue growth (Fig 9A-B,  $p < 0.05$ , 1-way  
10 ANOVA). Slipper snails in Meetinghouse Creek showed the slowest growth, by shell length or  
11 by soft tissue weight (Fig 9A-B).

12         The growth of eelgrass (*Zostera marina*) was measured on a per shoot basis by leaf area  
13 productivity (Fig 10A) and mass productivity (Fig 10B). For both measures, there was a  
14 depression in growth from July-early August when temperatures were warmest, a peak in growth  
15 from late August-September, and another depression in growth at the end of the season as  
16 temperatures cooled (Fig 10A-B). Leaf area productivity of eelgrass shoots was significantly  
17 higher at Flanders Bay, a mid-estuary site (Fig 10A,  $p < 0.01$ , 2-way ANOVA), and this effect  
18 was most pronounced from late August-September. Mass productivity of eelgrass shoots (Fig  
19 10B) followed a similar pattern, although the trend was not significant. The density of epiphytes  
20 on eelgrass blades was consistently higher at Meetinghouse Creek than the other sites from July-  
21 September (Fig 11,  $p < 0.01$ , ANOVA on ranks), and then declined at the end of the season. The  
22 eastern estuary sites (Great and Little Peconic Bays) had a strong and persistent disturbance of  
23 eelgrass shoots from macro-benthic animals, notably spider crabs *Libinia emarginata* (Fig 12,

1 pers. obs.). The number of eelgrass shoots uprooted by these animals was significantly higher at  
2 the eastern sites throughout the season (Fig 12,  $p < 0.01$ , 2-way ANOVA). In addition, many of  
3 the eelgrass shoots that remained rooted at these sites also showed evidence of grazing (data not  
4 shown).

## 6 **Discussion:**

7 Over the course of a growing season (Jun-Nov 2008), we demonstrated that the growth of  
8 eelgrass and four species of juvenile shellfish differed significantly at sites along an  
9 eutrophication gradient in the Peconic Estuary, NY, USA. The trend for three bivalve species  
10 was the same whether measured by shell growth or soft tissue growth, while the growth patterns  
11 of the gastropod *Crepidula fornicata* differed between shell growth and soft tissue growth. The  
12 growth responses for each species indicate that some estuarine resources had a consistent  
13 response to changing levels of nutrient loading and chlorophyll *a* (e.g. bay scallops), while other  
14 species had complex and possibly multi-modal response to a range of nutrient loading levels (e.g.  
15 hard clams, eastern oysters, eelgrass).

16 None of the shellfish species studied appeared to be solely food-limited, or at least not  
17 limited by food as measured by whole or  $> 5 \mu\text{m}$  chlorophyll *a*. The growth of juvenile hard  
18 clams (*M. mercenaria*) and eastern oysters (*C. virginica*) both displayed a “bi-modal” response  
19 to the eutrophication gradient of the Peconic Estuary. Both species had maximal growth at the  
20 two ends of the estuary, and minimal growth at the stations in between (Fig. 5 A-B, 6 A-B).  
21 High growth rates at the eutrophic end of the estuary (Mtghouse Cr.) could be due to an increase  
22 in the quantity and quality of seston under high-nutrient loading conditions (Carmichael et al.  
23 2004, Carmichael and Valiela 2005). High growth rates at the oligotrophic end of the estuary

1 could be due to increased flow from wind and tidal mixing (Fig 8), combined with more stable  
2 temperatures, salinities, and dissolved oxygen levels. It is difficult to explain the slower growth  
3 at the intermediate stations, especially Gr. Peconic B., where temperature, salinity, DO, and chl *a*  
4 (Fig 3 A-C, Fig 4 A-C) were indistinguishable from L. Peconic B., which promoted fast growth  
5 for all three species. Bulk water motion was significantly greater at L. Peconic B., and under  
6 oligotrophic conditions, this variable may have made the greatest difference to hard clams and  
7 scallops, and secondarily to oysters (Kennedy et al. 1996). Oysters are known to feed at faster  
8 rates than other shellfish (Tenore and Dunstan 1973) and may have been better able to take  
9 advantage of very dense phytoplankton communities in Mtghouse Cr. than the other shellfish  
10 species.

11 This study is consistent with the finding that bay scallops are generally not food-limited  
12 in most estuaries (Shriver et al. 2002). Scallops grew maximally at the lowest chl *a*, highest flow  
13 sites and minimally in the most eutrophic sites (Fig 7 A-B). This trend was maintained across  
14 the whole season, with less site x date variation than the other species (Fig 7 C-D). Although the  
15 trends in scallop mortality were not significant, the slowest-growing scallops in Mtghouse Cr.  
16 also had the highest mortality, while the faster growing scallops in Gr. and L. Peconic Bays had  
17 the lowest mortality.

18 The shell growth of slipper snails paralleled the growth of bay scallops (Fig 7A-B, Fig  
19 9A), although the geographic trend was more pronounced for bay scallops (Fig 7B). This  
20 suggests that both species would perform well in the relatively oligotrophic, high-flow, low  
21 chlorophyll eastern regions of the estuary, and that there may be competition or niche over-lap  
22 between bay scallops and slipper snails. Recent reports have suggested that slipper snails are  
23 proliferating in areas of the Peconic Estuary formerly dominated by bay scallops (Lewis et al.

1 1997, Lewis and Rivara 1998) and that slipper snails are able to filter phytoplankton  
2 communities containing very small or harmful algal cells more efficiently than bivalve  
3 suspension feeders (Kach and Ward 2008, Harke et al. in progress).

4         Due to previous findings on the effects of eutrophication on eelgrass (Dennison et al.  
5 1989, Duarte 1995, Wall et al. 2008), we expected the growth of eelgrass (*Z. marina*) to be  
6 maximal at the eastern end of the estuary, which has relatively high light levels and low  
7 phytoplankton biomass, and minimal in the dim light of the eutrophic tidal creek. Instead,  
8 eelgrass growth has a distinct “mid-estuary peak” at the Flanders Bay site (Fig 10A-B), and this  
9 effect is most prominent from late August through September. It is likely that low light levels  
10 (data not shown) and high epiphyte loading (Fig 11) slowed the growth of eelgrass in the most  
11 eutrophic site, Meetinghouse Cr. But even though light levels were higher at the eastern end of  
12 the estuary (data not shown), there was strong, persistent grazing disturbance at Great and Little  
13 Peconic Bays that approached 80% of all eelgrass shoots uprooted (Fig 12). The grazing and  
14 uprooting of eelgrass was mostly due to spider crabs, *Libinia emarginata* (pers. obs.). As such,  
15 the mid-estuary site, Flanders Bay, with intermediate light levels and relatively little grazing  
16 disturbance, seemed to represent the optimum site for eelgrass growth in this study. However, it  
17 is likely that eelgrass shoots that were adequately caged or shielded from grazers would perform  
18 well under the higher light levels at the eastern end of the estuary.

19         Our goal was to isolate the effects of nutrient-loading on bivalve growth. Although we  
20 tried to choose sites that were as similar as possible in physical characteristics, there were  
21 differences in this regard. Mtghouse Cr., the tidal creek with high nutrients and high chl *a*, was  
22 also more hypoxic, and somewhat warmer than the other three sites (Fig 3 A-C). This site also  
23 experienced a toxic algal bloom during late August and September (*Cochlodinium polykrikoides*;

1 data not shown). These variables, along with bulk water motion, represent possible confounding  
2 variables in our nutrient-loading study. Mid-summer temperatures at Mtghouse Cr. Were likely  
3 too warm (27-28° C, Fig 3 A) for maximal hard clam growth (Kraeuter and Castagna 2001;  
4 Weiss et al 2007); hard clam growth at this site later accelerated when temperatures dropped  
5 below 27° C (Fig 5 D). Interestingly, hard clams and oysters displayed their seasonal maximal  
6 and near-maximal growth rates, respectively, for all sites in Mtghouse Cr. during mid-September  
7 when bottom oxygen levels rose out of the hypoxic range and the *C. polykrikoides* bloom  
8 subsided. This finding suggests that while the food supply at this site was ideal for these two  
9 species, classic symptoms of eutrophication such as low bottom oxygen levels and harmful algal  
10 blooms prohibited these shellfish from benefiting from an abundant food supply. Such  
11 interactions of multiple physical and biological variables making growth rate comparisons based  
12 on nutrient loading and chlorophyll *a* difficult. Eventually a multi-variable regression model for  
13 the growth of juveniles of each species will be constructed and compared to growth models for  
14 eelgrass (*Zostera marina*), another critical restoration species. These models may help managers  
15 to target proposed restoration species to the areas of an estuary where they will have the greatest  
16 chance of success.

17 Many anthropogenic insults have led to the degradation of estuaries, with the concurrent  
18 loss of estuarine resources (Lotze et al. 2006) such as clams, oysters, scallops, and eelgrass.  
19 Increases in anthropogenic nutrient loading, leading to eutrophication, have been identified as a  
20 primary driver of estuarine degradation (Nixon 1995, de Jonge et al. 2002), but recent research  
21 and reviews have raised the possibility of beneficial nutrient loading under some conditions and  
22 for some species (Nixon and Buckley 2002, Carmichael et al. 2004). Undoubtedly,  
23 eutrophication is a complex problem that continues to challenge our scientific understanding, and

1 will require a variety of management approaches (Cloern 2001). Jackson (2001) and Lotze et al.  
2 (2006) have emphasized the need to restore upper trophic levels and suspension feeders as  
3 effective top-down controls on estuarine ecosystems. The re-seeding or restoration of  
4 suspension feeding bivalves in estuaries can have multiple benefits: the bivalves themselves are  
5 a resource for commercial and recreational fisheries, while simultaneously providing ecosystem  
6 services of filtration (Newell 1988, Dame 1996, Altieri and Witman 2006), top-down control of  
7 algal blooms (Officer et al. 1982, Cerrato et al. 2004), and transfer of nutrients and biomass to  
8 the benthos (Smaal and Prins 1993, Newell 2004). It is possible that bivalve aquaculture can  
9 achieve many of these goals simultaneously (Newell 2004, Huang et al. 2008), although over-  
10 stocking of aquaculture operations can have negative effects on adjacent wild and cultured  
11 bivalves (Newell 2004, Zhou et al. 2006).

12         Seagrass habitats are disappearing at an alarming rate worldwide (Orth et al. 2006), and  
13 restoration of seagrass beds could provide valuable habitat for fin fish and shellfish (Irlandi and  
14 Peterson 1991, Beck et al. 2001). The simultaneous restoration and management of seagrass  
15 beds and bivalve populations will likely have synergistic effects (Wall et al. 2008, Carroll et al.  
16 2008), as each group of organisms provides multiple benefits for the other.

17         Any plan to re-seed or restore seagrasses or bivalve populations into a eutrophic system  
18 will need to take into account the species in question and its responses to varying levels of  
19 nutrient loading. Based on our findings, we can recommend that restoration of scallops will have  
20 the greatest chance of success in high flow environments that are relatively oligotrophic,  
21 although inter-specific competition with *C. fornicata*, which also grew maximally in this region,  
22 could affect *A. irradians* growth. Restoration of clams and oysters could proceed over a wider  
23 variety of estuarine habitats, with oysters should being a prime candidate for restoration in the

1 most impacted, eutrophic estuarine waters. Finally, eelgrass restoration sites must balance light  
2 and nutrient regimes with the activity of benthic grazers which may disrupt eelgrass growth.

3

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13

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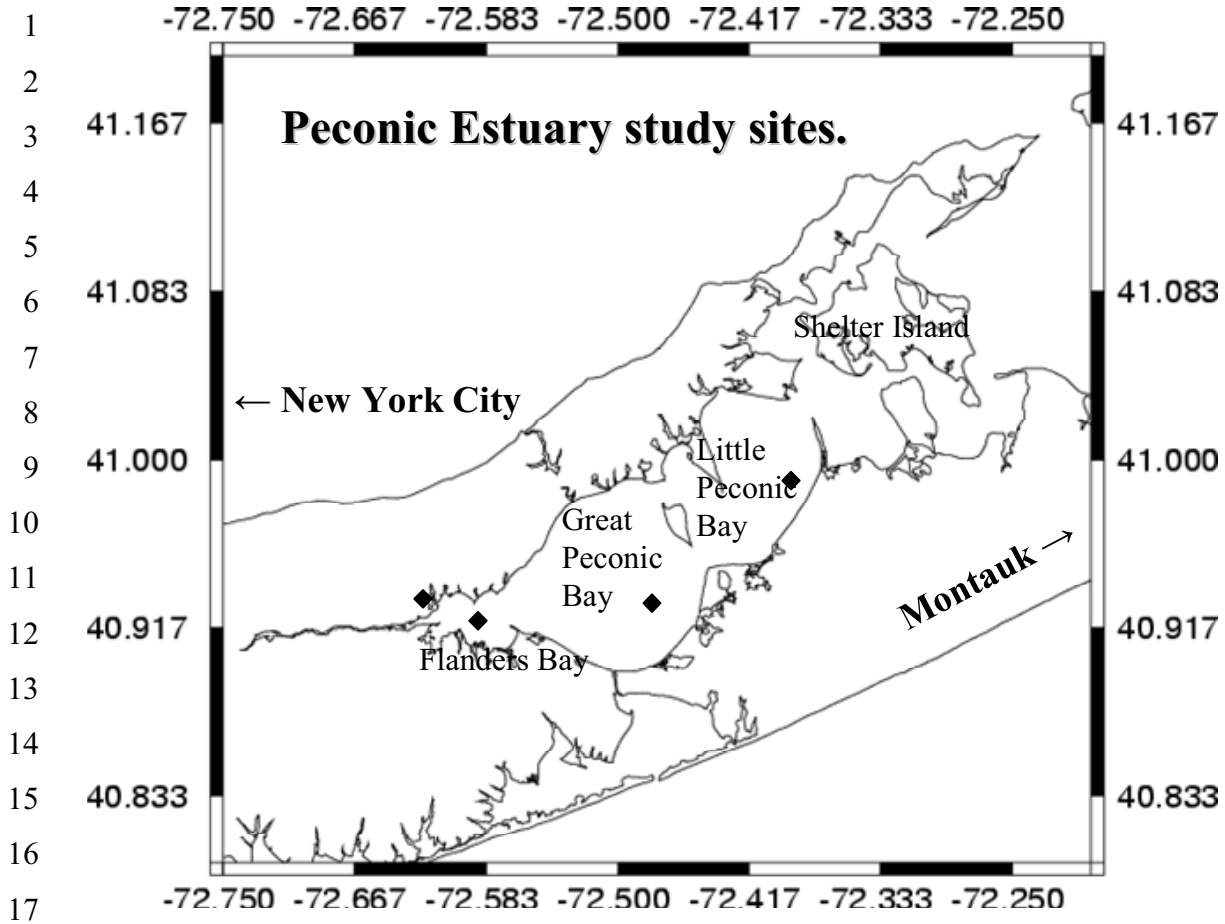
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18 Figure 1. Peconic Estuary study sites marked by: ◆

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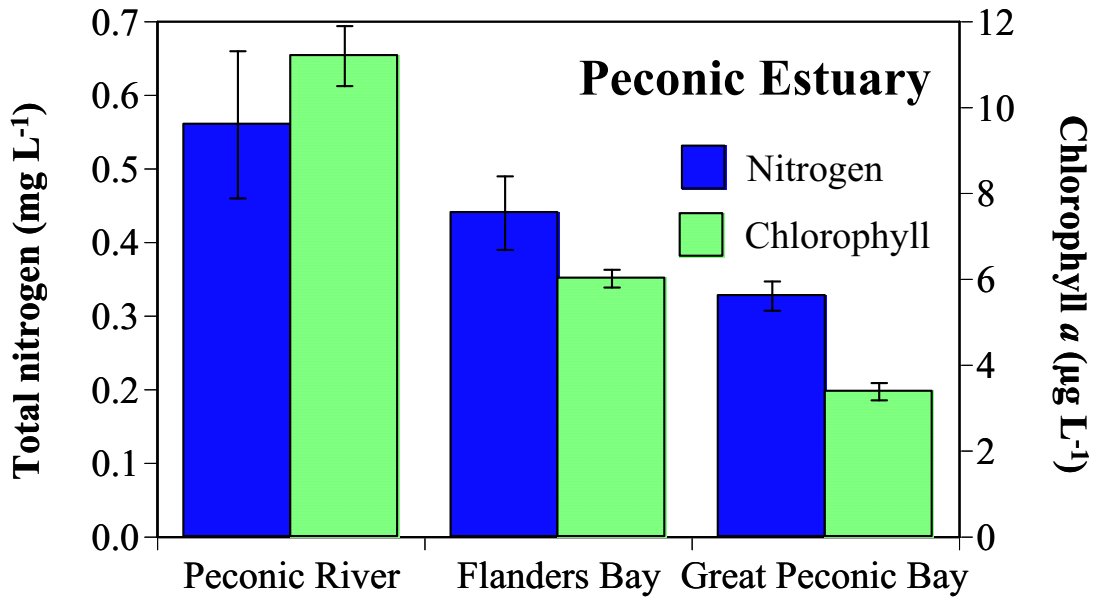
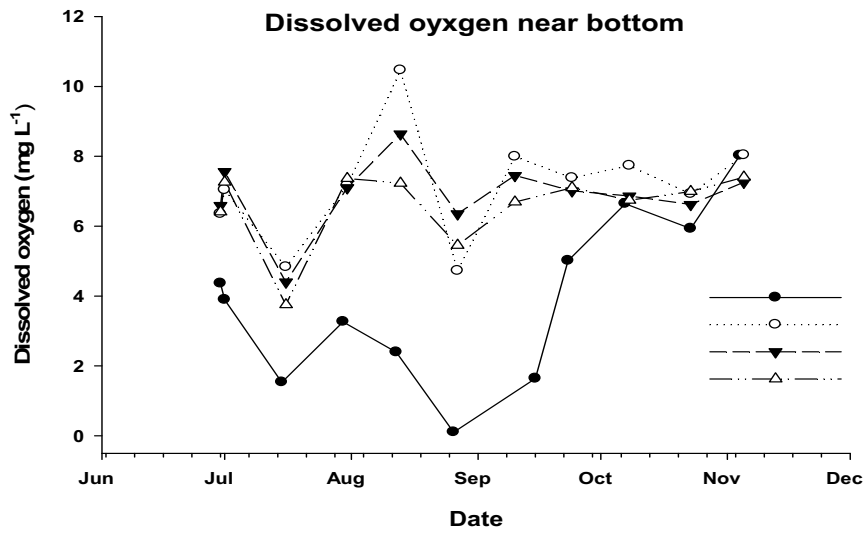
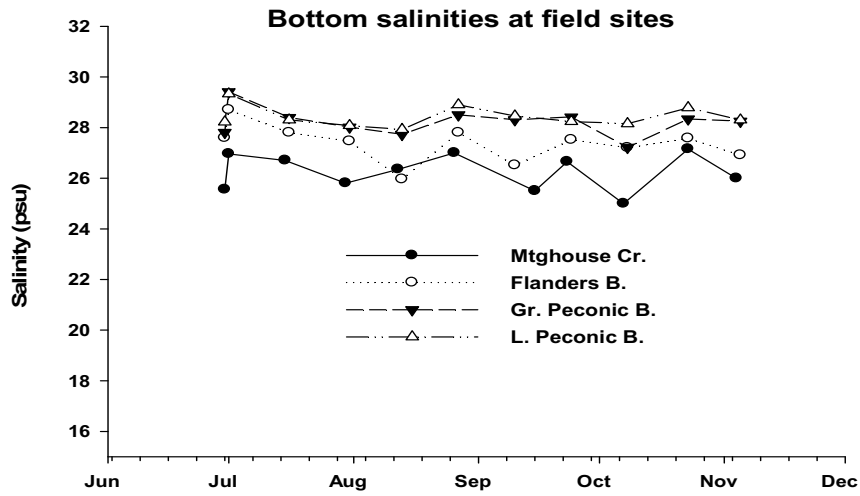
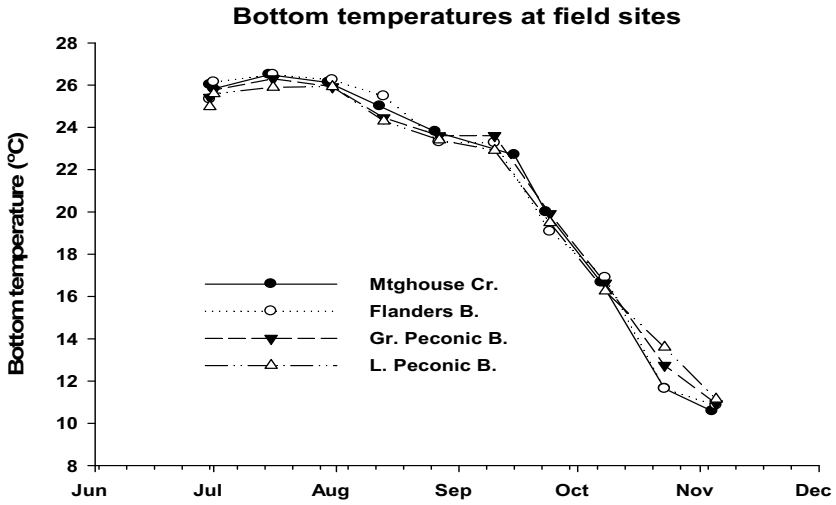


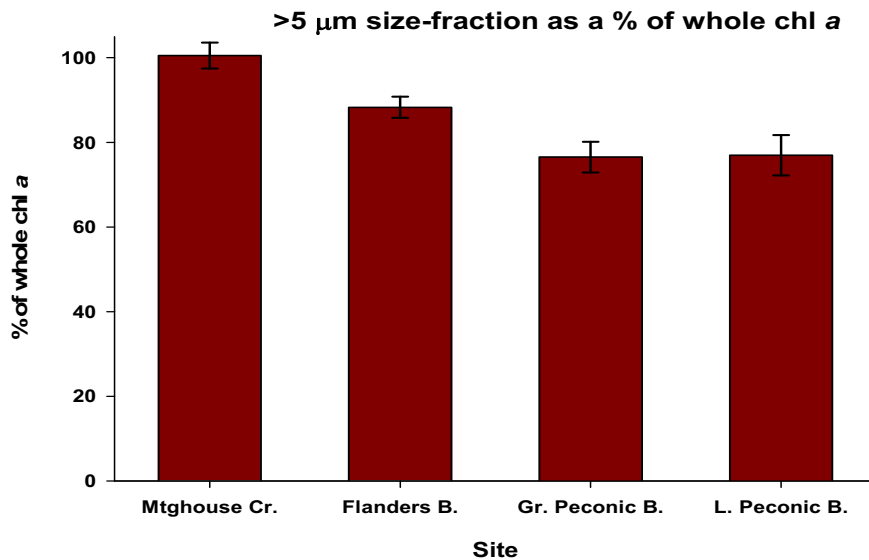
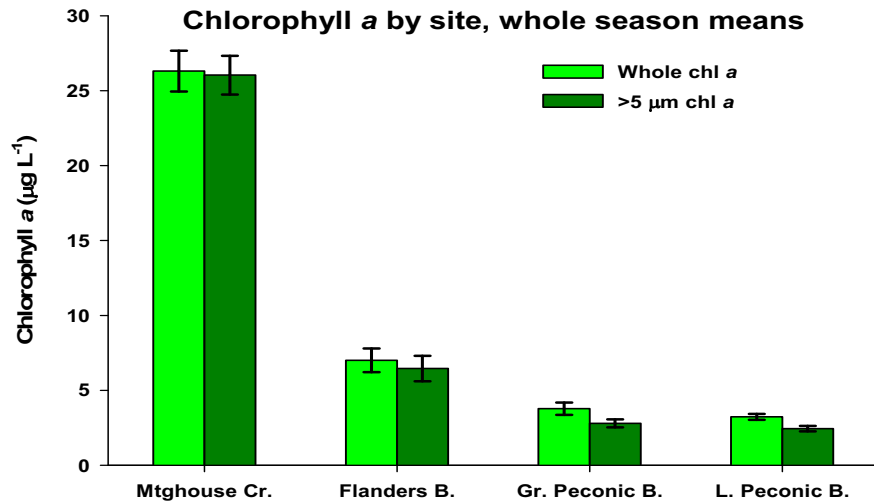
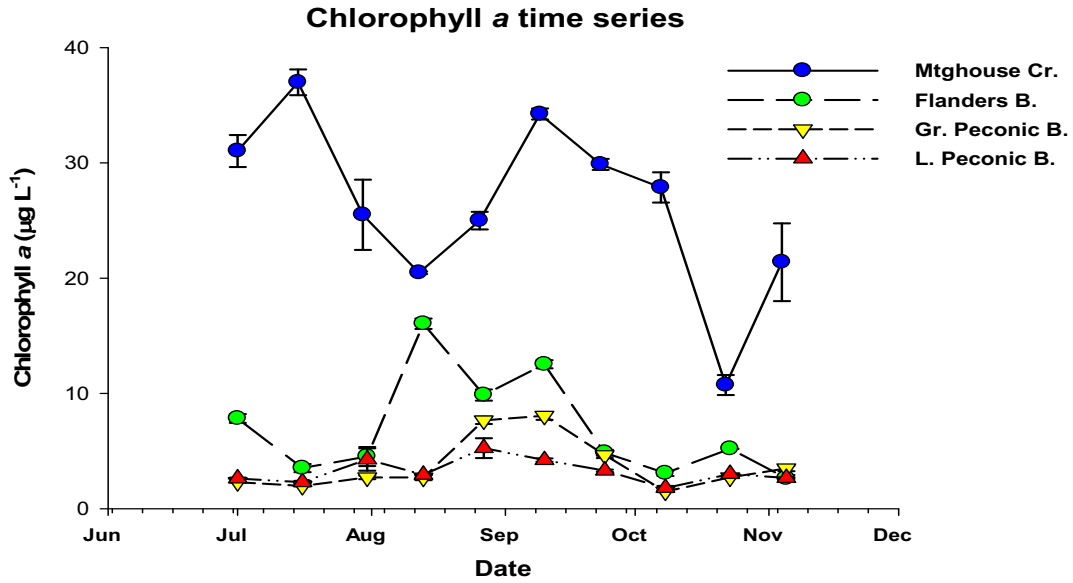
Figure 2. Concentrations of chlorophyll *a* and total nitrogen across the study area in the western Peconic estuary (stations 240, 110, 130; SCDHS 1976-2005).



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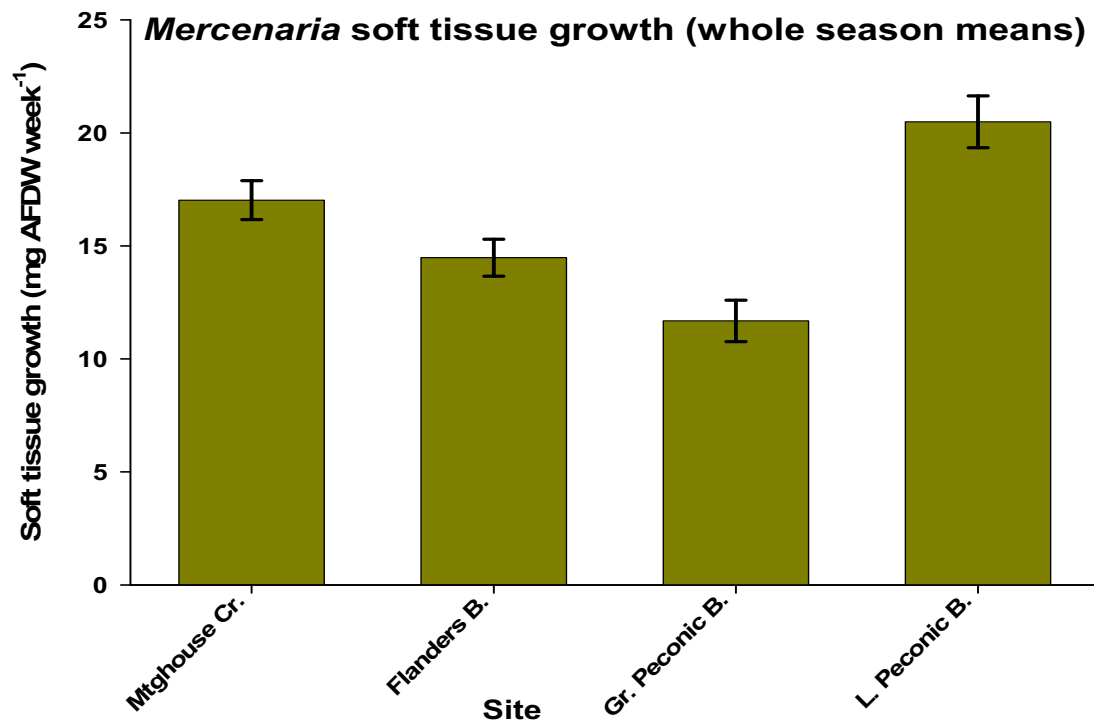
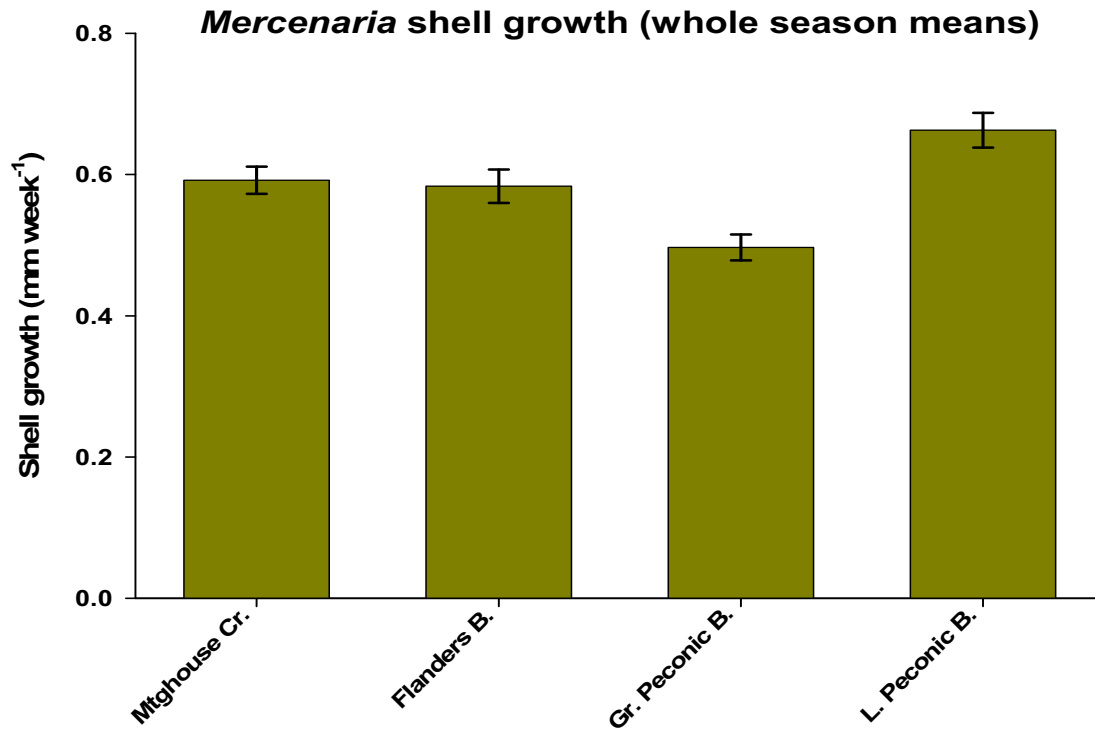
1 Figure 3 A-C. Temperature, salinity, and dissolved oxygen trends at 2 m depth, which is near  
2 the bottom at all field sites. The shellfish cage at Mtghouse Cr. was elevated to ~ 1 m, to avoid  
3 the hypoxia at 2 m.  
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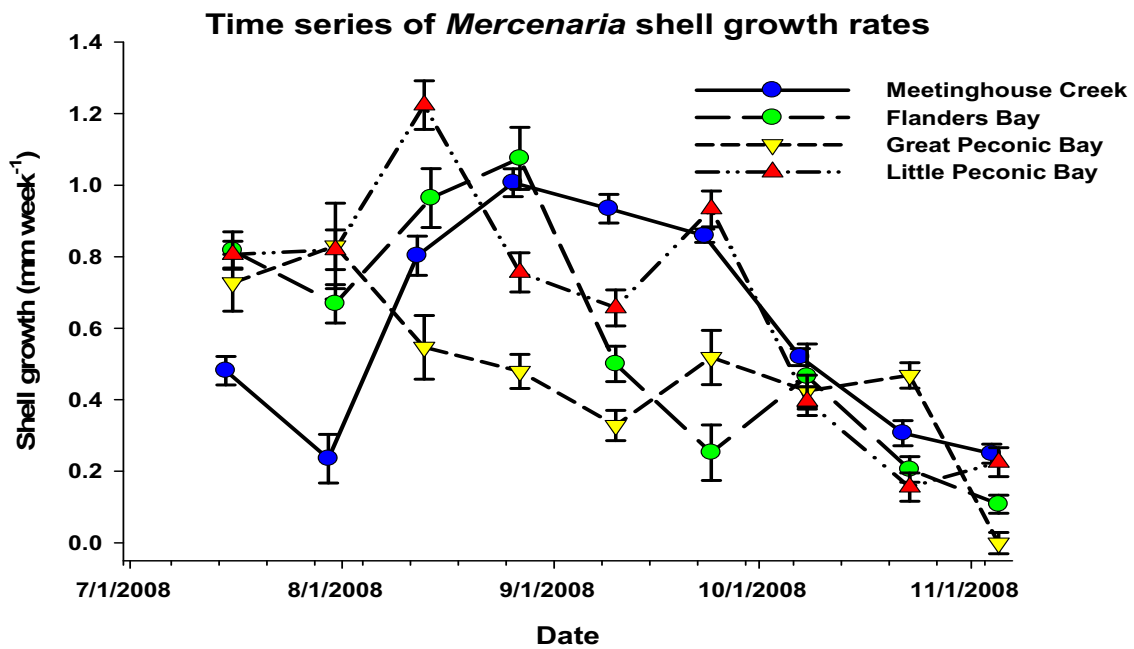
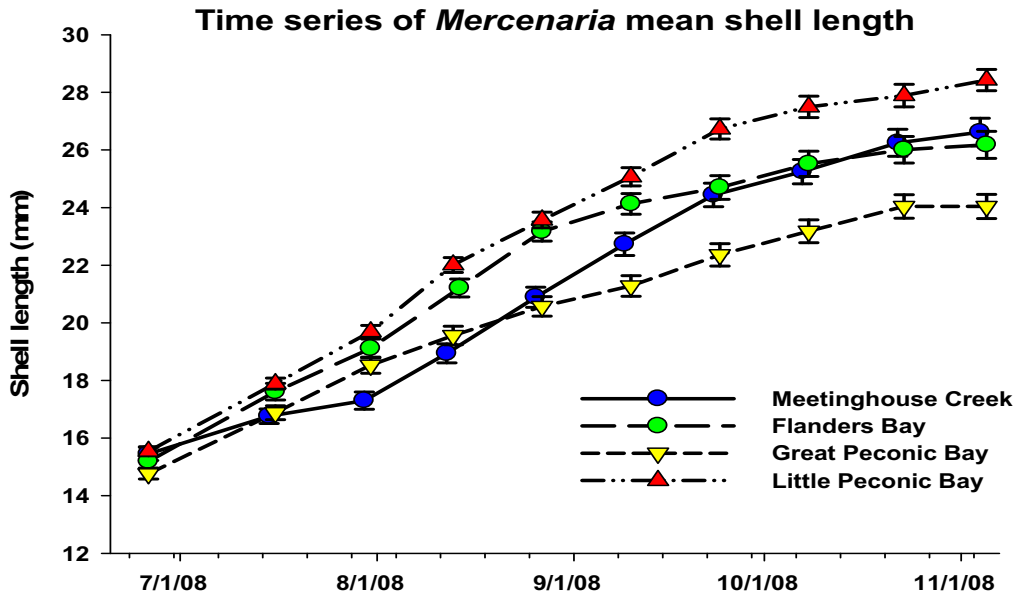
1 Figure 4 A-C. Chlorophyll *a* trends (mean  $\pm$  SE) by site and by time series (A), averaged by site  
2 (B), and % in  $> 5\mu\text{m}$  size fraction (C).

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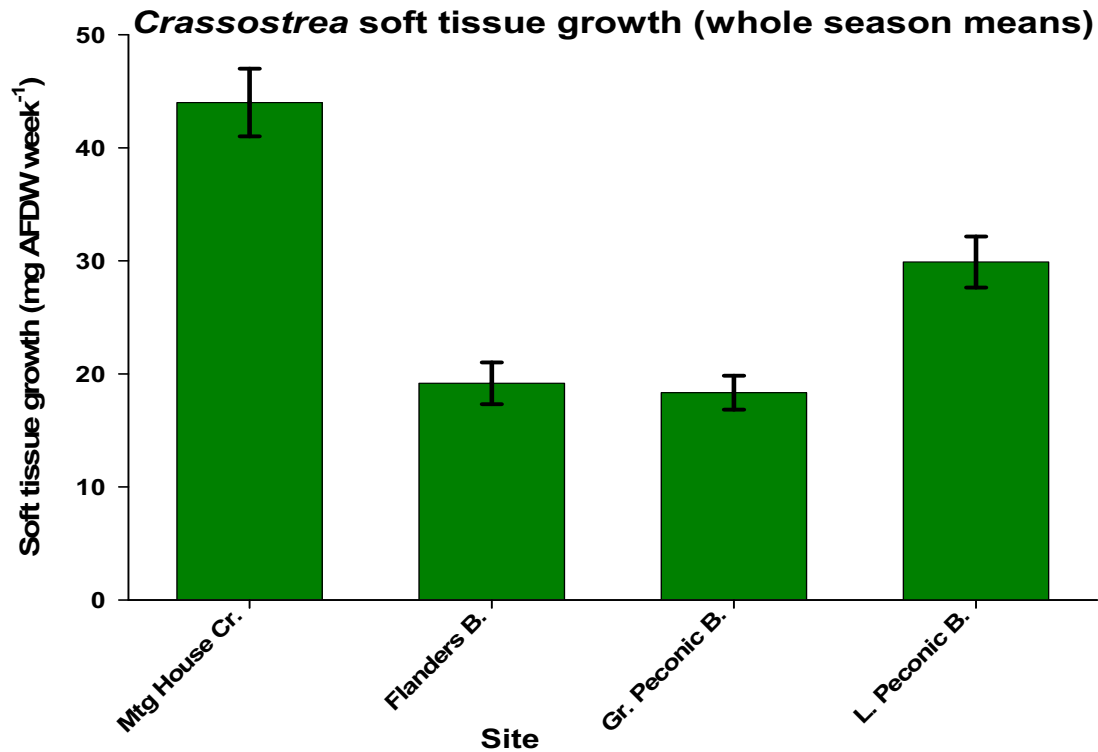
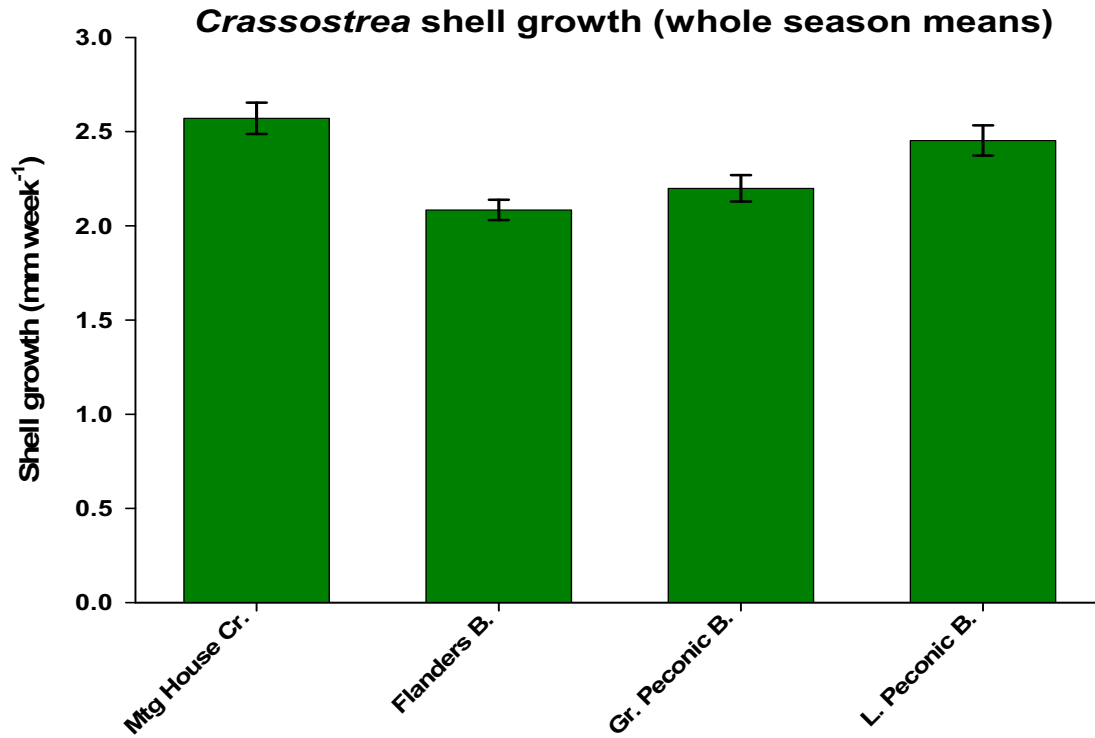
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3 Figure 5 A-B. Juvenile *M. mercenaria* shell growth (A) and soft tissue growth (B) averaged over  
4 the whole season (Jun-Nov).

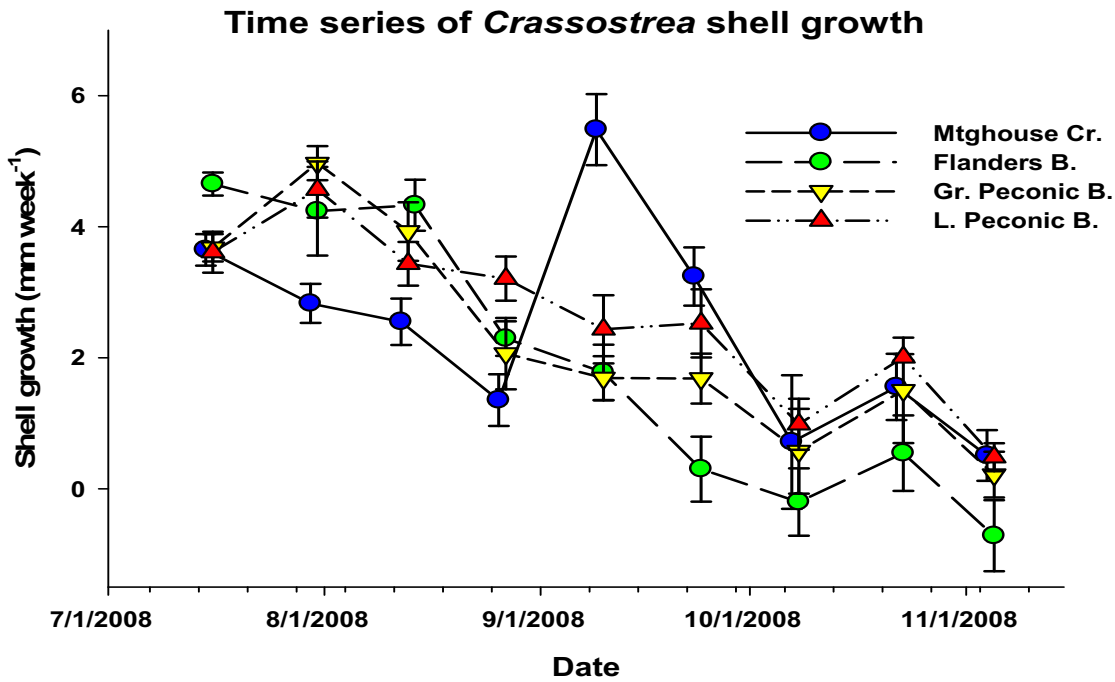
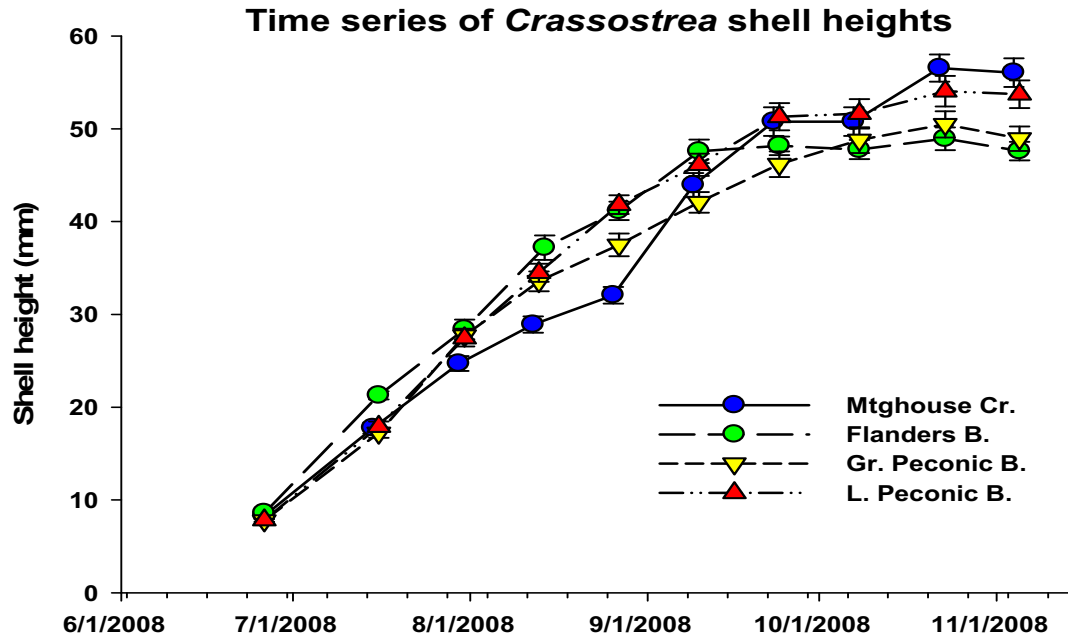


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Figure 5 C-D. Juvenile *M. mercenaria* mean shell length (C) and shell growth (D) at each timepoint.

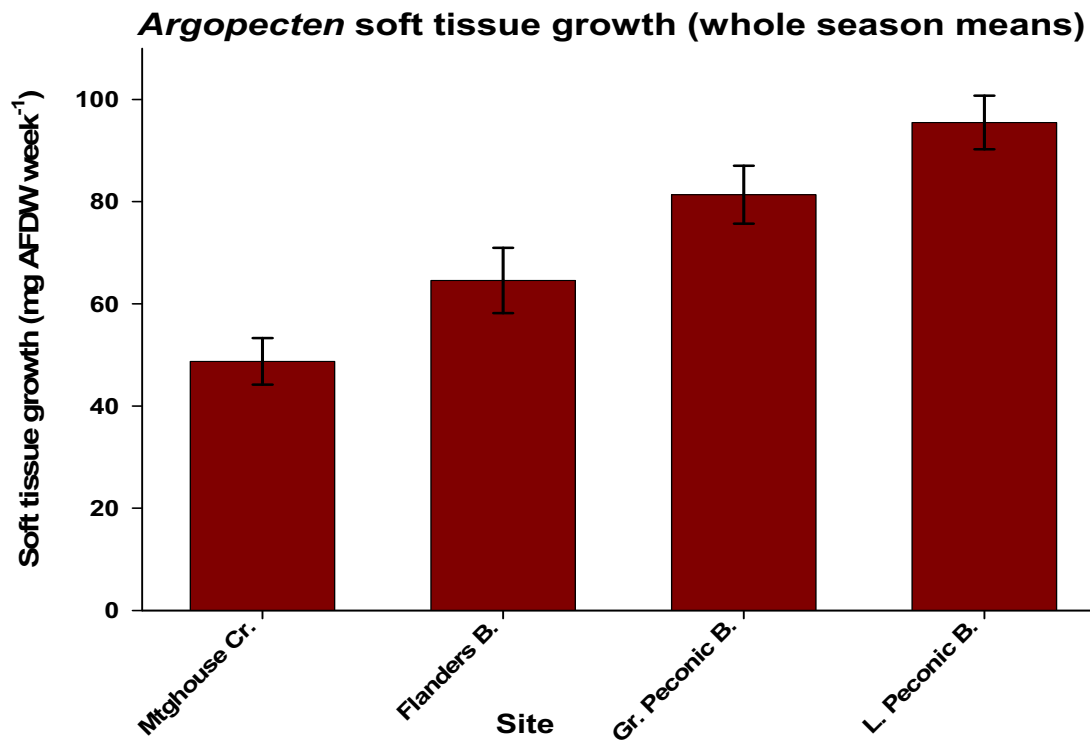
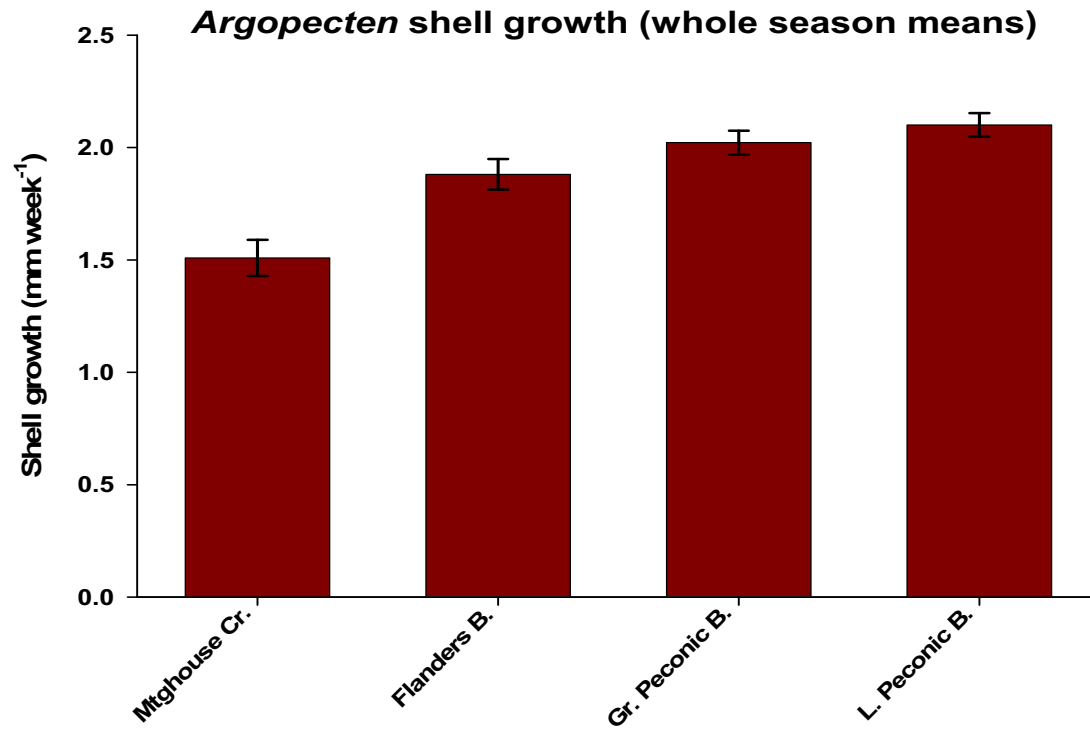


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 2 Figure 6 A-B. Juvenile *C. virginica* shell growth (A) and soft tissue growth (B) averaged over  
 3 the whole season (Jun-Nov).  
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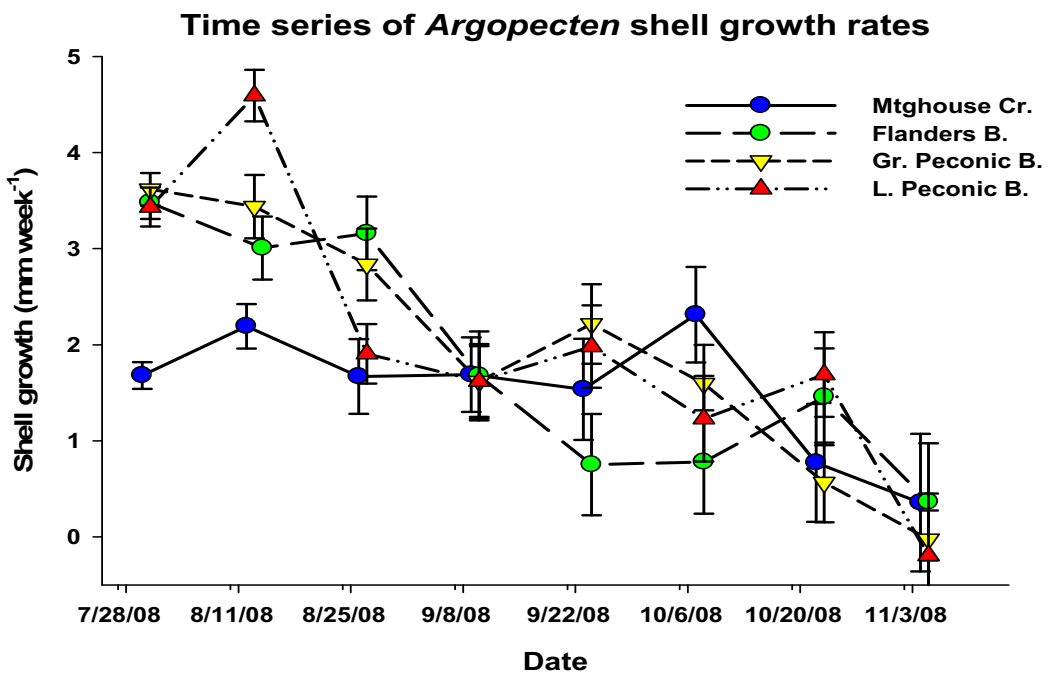
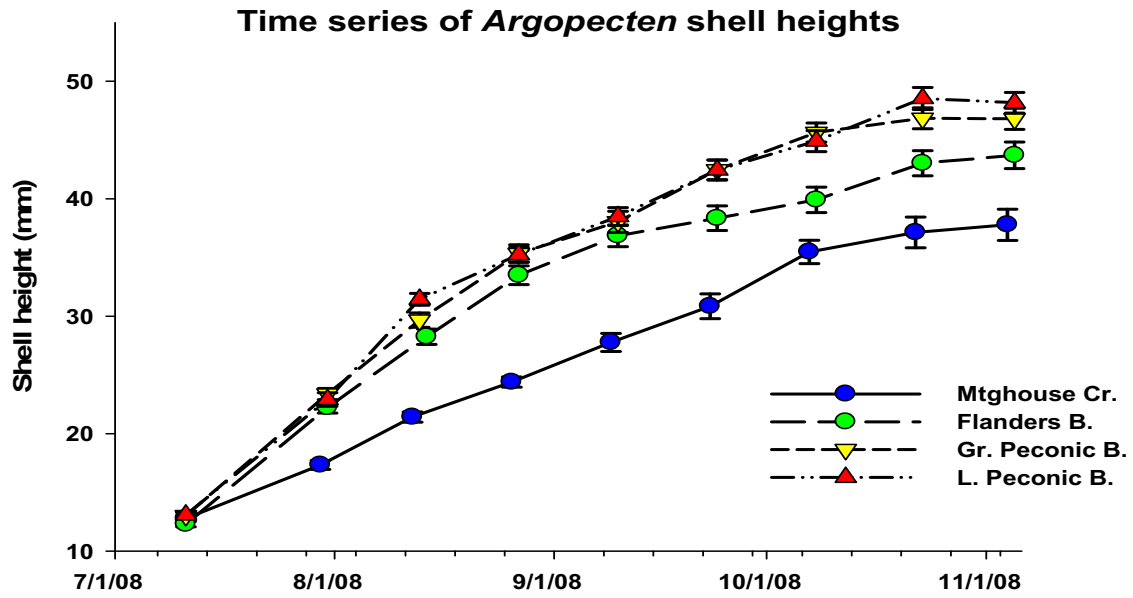


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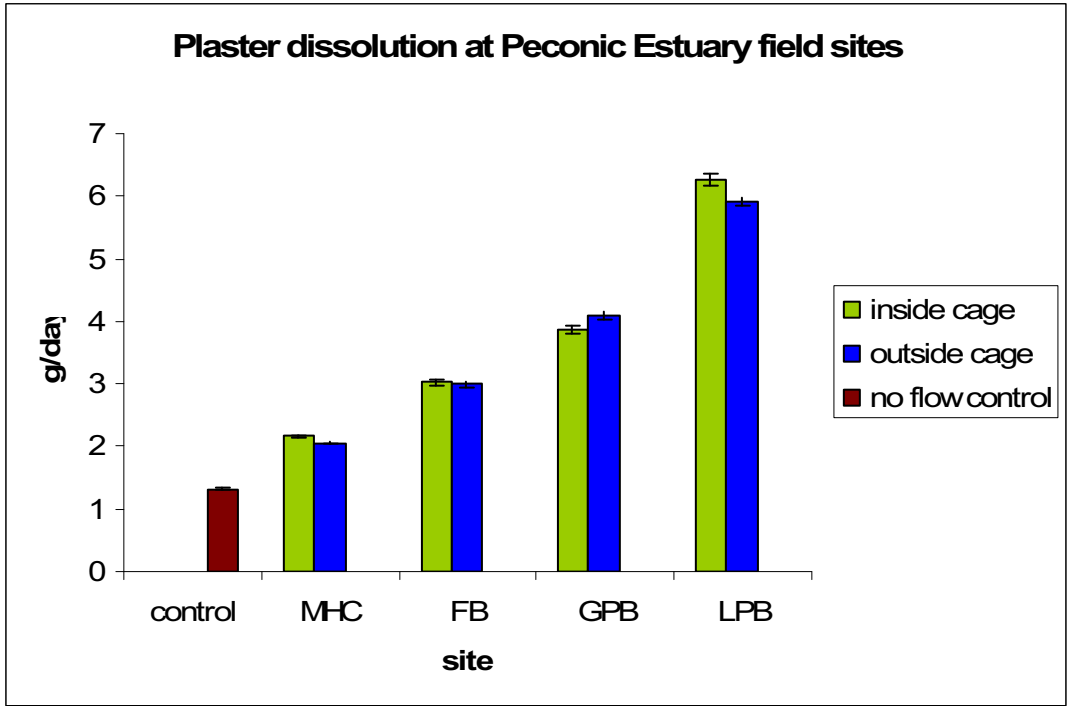
Figure 6 C-D. Juvenile *C. virginica* mean shell length (C) and shell growth (D) at each timepoint.



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 2 Figure 7 A-B. Juvenile *A. irradians* shell growth (A) and soft tissue growth (B) averaged over  
 3 the whole season (Jun-Nov).  
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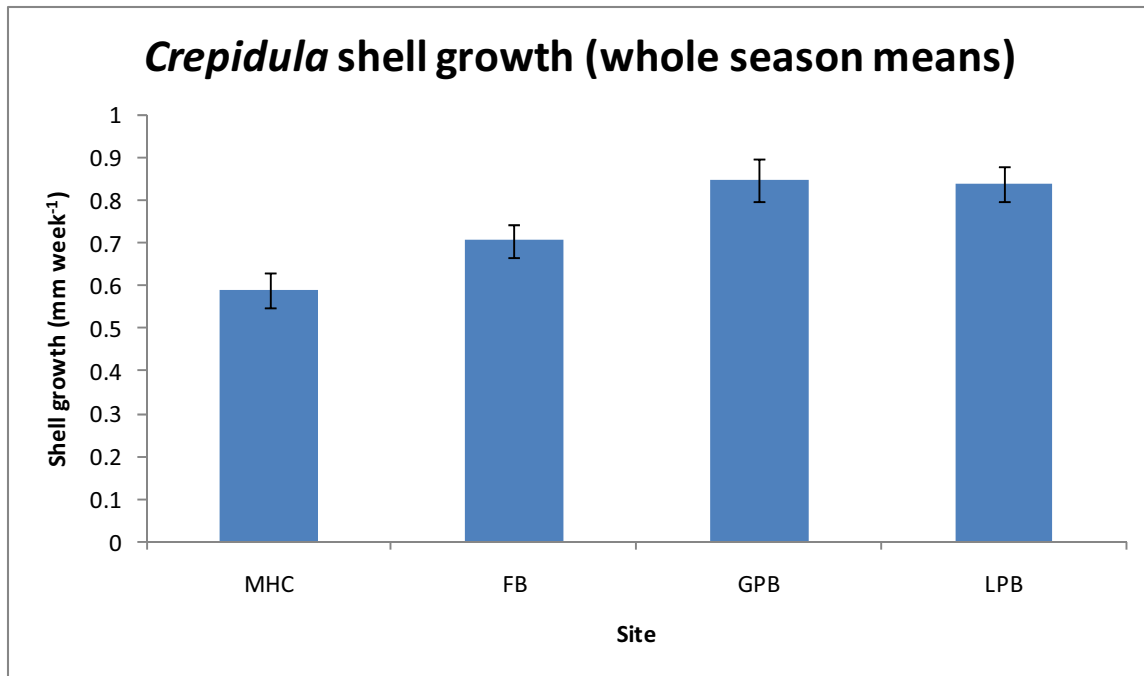


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 2 Figure 7 C-D. Juvenile *A. irradians* mean shell length (C) and shell growth (D) at each  
 3 timepoint.  
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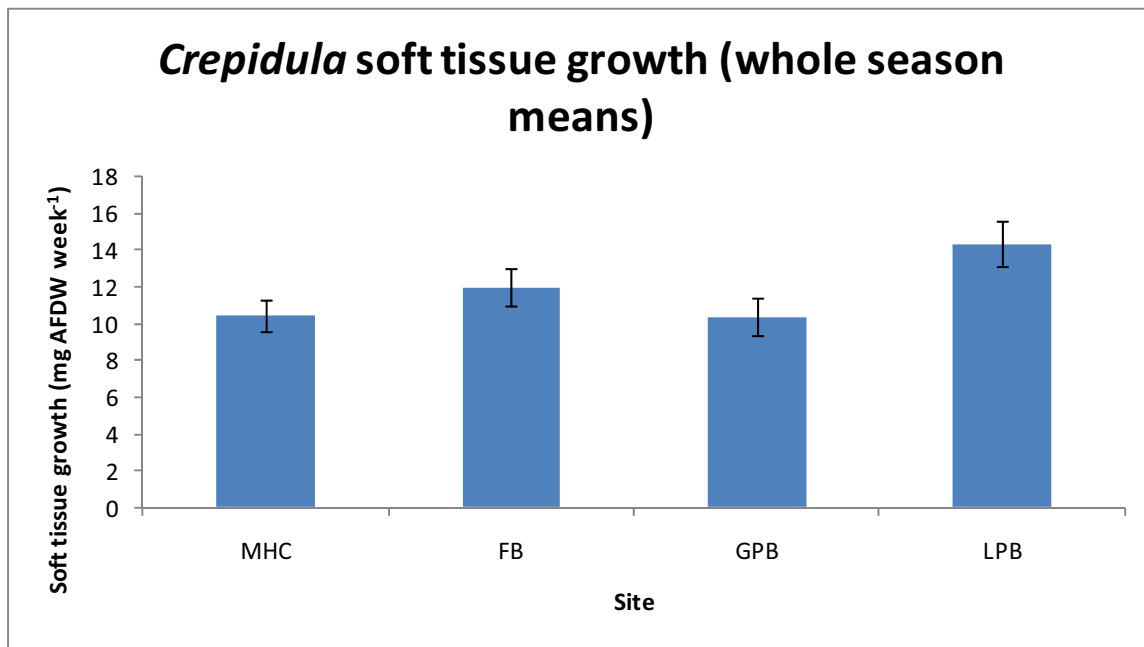


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 2 Figure 8. Dissolution of plaster blocks in  $\text{g d}^{-1}$  (mean  $\pm$  SE) placed at field stations and in a “no  
 3 flow” control tank. Dissolution measurements were averaged over 24 h from Oct 23<sup>rd</sup>-24<sup>th</sup>,  
 4 2008.

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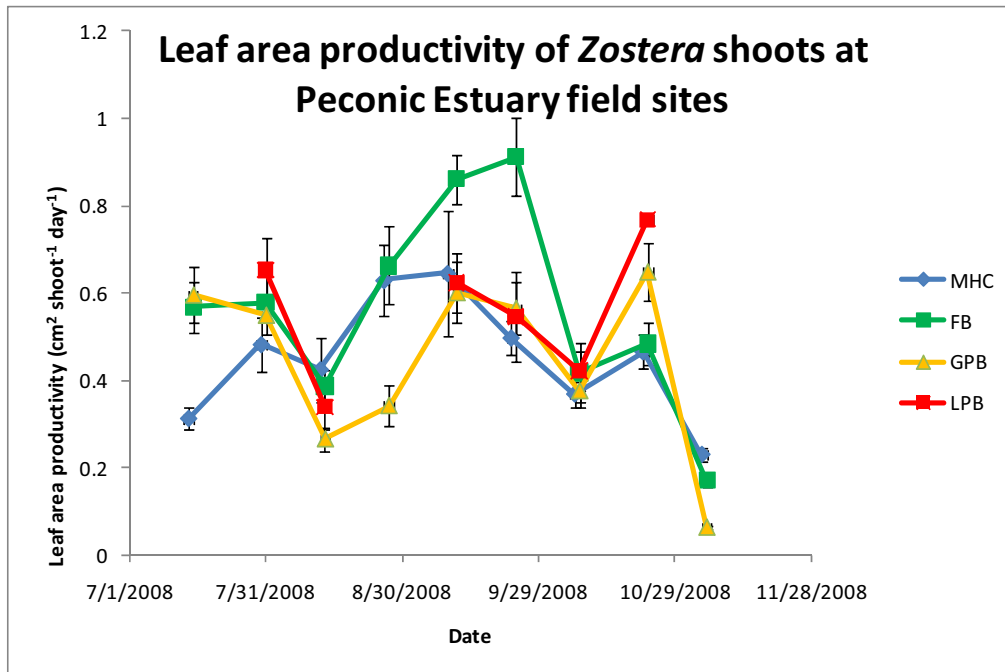
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4 Figure 9 A-B. Juvenile *C. fornicata* shell growth (A) and soft tissue growth (B) averaged over  
 5 the whole season (Jun-Nov).

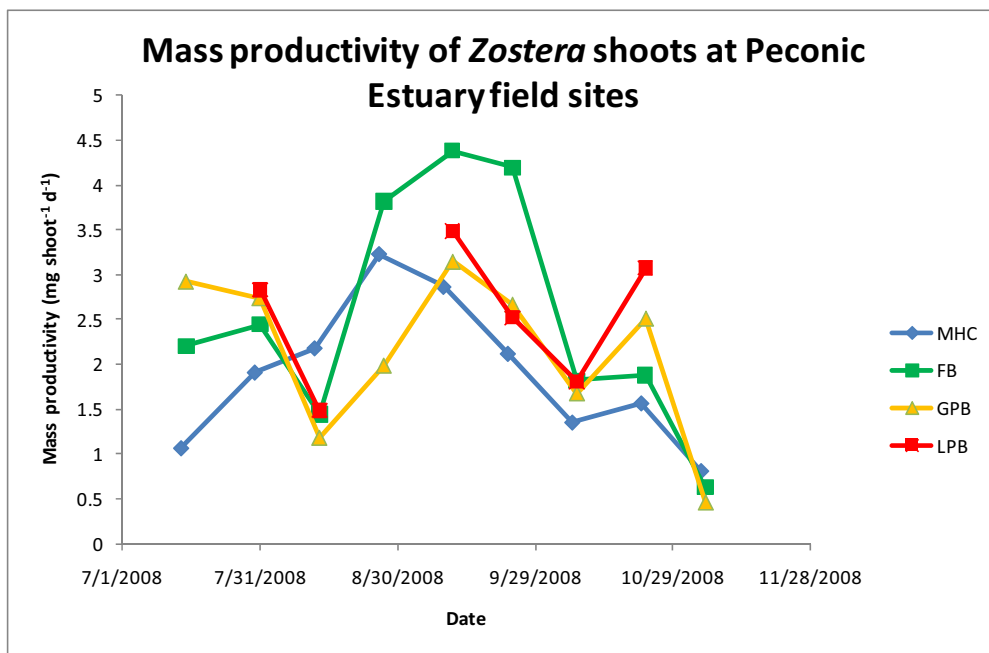
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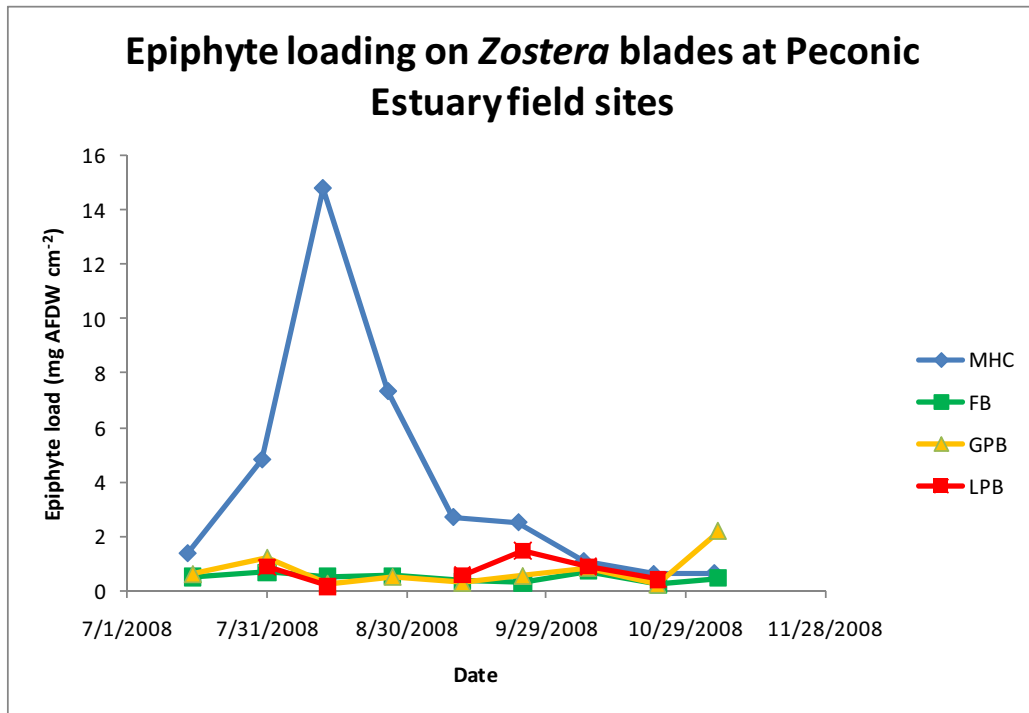


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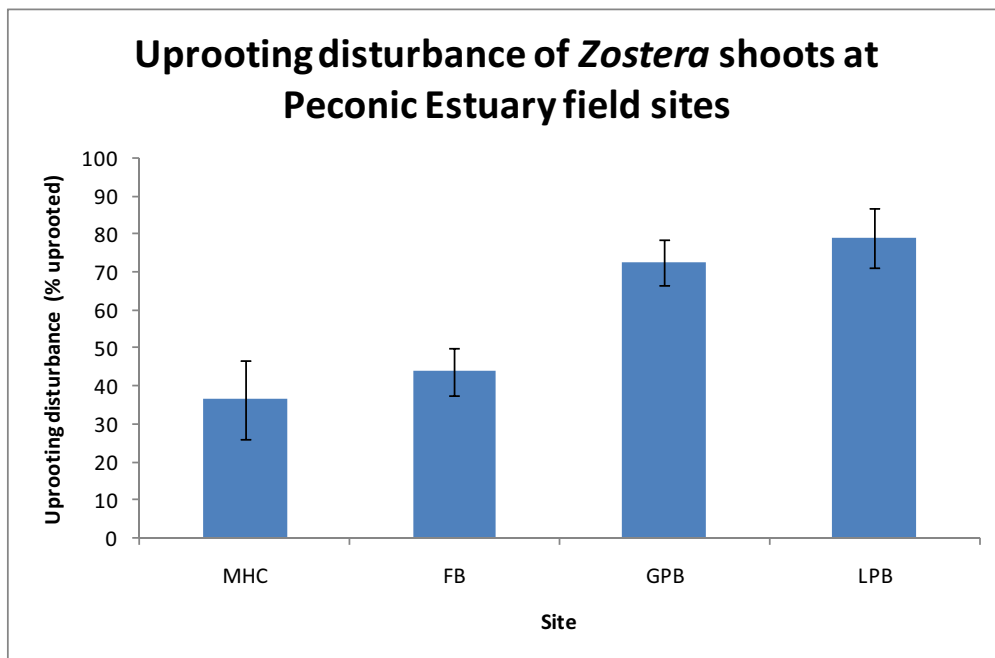


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4 Figure 10 A-B. Time series of eelgrass (*Z. marina*) growth rates at Peconic Estuary field sites  
5 measured by leaf area productivity (A, means  $\pm$  SE) and mass productivity (B, means).



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 2 Figure 11. Time series of epiphyte densities on eelgrass (*Z. marina*) blades at Peconic Estuary  
 3 field sites.



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 6 Figure 12. Uprooting disturbance of eelgrass shoots (*Z. marina*) at Peconic Estuary field sites.  
 7 Values are means  $\pm$  SE averaged over the whole season (Jun-Nov).

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**Chapter II:**

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

*This is manuscript based on field work conducted in 2007 for the TNC project. It was submitted to Aquatic Biology in April 2008.*

**Keywords:** *Zostera marina*, *Crassostrea virginica*, *Mercenaria mercenaria*, *Argopecten irradians*, *Cyprinodon variegatus*, eelgrass, seagrass, clams, oysters, eutrophication, nutrients, nutrient-loading, aquaculture, bivalves, suspension feeders, mesocosms, ecosystem-based management, estuarine restoration

1 **Abstract:** While many coastal ecosystems previously supported high densities of seagrass and  
2 resource bivalves, the impacts of overfishing, eutrophication, harmful algal blooms, and habitat  
3 loss have contributed to the decline of these important resources. Despite improvements in  
4 wastewater treatment in some watersheds and subsequent reduced nutrient loading to  
5 neighboring estuaries, seagrass and bivalve populations in these locations have generally not  
6 recovered. We conducted a series of mesocosm experiments to simultaneously examine the  
7 effects of nutrient loading and historic suspension-feeder densities on the growth of eelgrass  
8 (*Zostera marina*), juvenile bivalves (hard clams, *Mercenaria mercenaria*, Eastern oysters,  
9 *Crassostrea virginica*, and bay scallops, *Argopecten irradians*), and juvenile fish (sheepshead  
10 minnow, *Cyprinodon variegatus*). High nutrient loading rates led to significantly higher  
11 chlorophyll *a* levels and significantly increased growth of juvenile bivalves relative to controls  
12 with lower nutrient loading rates. The filtration provided by adult suspension-feeders (*M.*  
13 *mercenaria* and *C. virginica*) significantly decreased chlorophyll *a* levels, significantly increased  
14 light penetration and the growth of eelgrass, and significantly decreased the growth of juvenile  
15 bivalves and fish relative to controls with no filtration from adult suspension-feeders. These  
16 results suggest that either nutrient loading or bivalve filtration or both have the capacity to  
17 structure estuarine food webs and affect the recovery of estuarine resources. Future ecosystem-  
18 based approaches will need to account for both anthropogenic nutrient-loading and bivalve  
19 restoration to successfully manage estuarine resources.

20

1 **Introduction:**

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

12           Changes in inorganic nutrient loading to estuaries can indirectly influence the growth of  
13 marine resource species. High rates of nutrient loading have been associated with increases in  
14 pelagic productivity, decreased water clarity, hypoxia, and declines in seagrass growth and  
15 abundances (Duarte 1995, Diaz and Rosenberg 2008, Wall *et al.* 2008). In response, estuarine  
16 management efforts often focus primarily on reducing anthropogenic nutrient loading in an effort  
17 to curb the negative effects of eutrophication (Cloern 2001, de Jonge *et al.* 2002). However,  
18 some level of nutrient loading must be necessary to sustain primary and secondary production  
19 (Nixon and Buckley 2002). High levels of inorganic nutrients favor larger phytoplankton cells  
20 (Malone 1980, Raven and Kubler 2002), such as diatoms and prymnesiophytes, which are  
21 generally considered a good source of nutrition for bivalves (Beukema and Cadee 1991, Wikfors  
22 *et al.* 1992, Weiss *et al.* 2007). Studies in several estuaries have shown blue mussels (*Mytilus*  
23 *edulis*), hard clams (*Mercenaria mercenaria*), and softshell clams (*Mya arenaria*) can respond

1 positively to increased nitrogen loading and high chlorophyll *a* levels in their habitats (van  
2 Stralen and Dijkema 1994, Weiss *et al.* 2002, Carmichael *et al.* 2004, Weiss *et al.* 2007). Weiss  
3 *et al.* (2002) and Carmichael *et al.* (2004) found that shell growth, soft tissue growth, and  
4 survival of *M. mercenaria* and *M. arenaria* increased along a naturally-occurring gradient of  
5 nitrogen loading in Waquoit Bay, Massachusetts, USA. They attribute these changes to  
6 increased quantity and quality of food particles due to nitrogen enrichment (Carmichael and  
7 Valiela 2005), although a similar response has not been found for bay scallops (*Argopecten*  
8 *irradians*, Shriver *et al.* 2002). While nutrient over-loading in estuaries has a well-known set of  
9 negative consequences (Valiela *et al.* 1992, Nixon 1995, Kemp *et al.* 2005), the stimulation of  
10 secondary production in bivalves could be an overlooked positive effect of nutrient loading  
11 (Nixon and Buckley 2002, Carmichael *et al.* 2004, Carmichael and Valiela 2005), especially in  
12 shallow ecosystems with well-mixed water columns that rarely experience hypoxia.

13         As described in many studies and reviews, suspension feeding bivalves can have a variety  
14 of positive effects on estuaries, such as reducing phytoplankton biomass (Officer *et al.* 1982,  
15 Doering and Oviatt 1986), transferring nutrients and biomass to the benthos (Smaal and Prins  
16 1993, Jackson 2001), control of harmful algae (Cerrato *et al.* 2004), increased light penetration  
17 (Newell and Koch 2004), and facilitating the growth of benthic plants (Peterson and Heck 2001,  
18 Newell *et al.* 2002, Wall *et al.* 2008). As bivalve populations have declined through overfishing,  
19 habitat loss, and disease, these ecosystem services have been lost from estuaries (Newell 1988,  
20 Lotze *et al.* 2006). In the absence of dense natural bivalve populations, bivalve aquaculture may  
21 be a tool for managers to restore ecosystem functions previously provided by natural populations  
22 (Newell 2004, Ruesink *et al.* 2005), combat eutrophication (Gifford *et al.* 2004, Cerco and  
23 Seitzinger 2007), or ease harvest pressures on wild populations (Dolmer and Frandsen 2002).

1 Aquaculture is on the rise world-wide, and bivalve aquaculture may avoid some of the pitfalls of  
2 finfish aquaculture (Naylor *et al.* 2000) while controlling phytoplankton blooms and affecting  
3 carbon and nutrient cycling in ways that are comparable to natural shellfish populations (Newell  
4 2004, Zhou *et al.* 2006, Huang *et al.* 2008).

5 Commercial bivalve aquaculture operations strive to grow a maximum number of  
6 shellfish in a minimum of space (Frechette *et al.* 1992), with locally high filtration rates  
7 sometimes leading to “self-thinning” through density-dependent food limitation (Rheault and  
8 Rice 1996, Zhou *et al.* 2006). It is not well-known how these locally high filtration rates interact  
9 with adjacent natural bivalve populations (Ferreira *et al.* 2008), but locally high biodeposition  
10 rates from aquaculture have produced negative effects in some systems (Newell 2004 and  
11 references therein). As aquaculture develops for both commercial and restoration purposes, an  
12 improved understanding of these effects will help managers use bivalves to achieve healthy  
13 ecosystem functions.

14 This study was designed to examine the combined effects of nutrient loading and adult  
15 bivalve filtration on the growth and survival of estuarine resource species: juvenile hard clams  
16 (*M. mercenaria*), bay scallops (*A. irradians*), and oysters (*C. virginica*), a juvenile planktivorous  
17 fish (sheepshead minnow, *Cyprinodon variegatus*), and eelgrass (*Z. marina*). These five species  
18 were placed into an array of mesocosms with treatments of high or low nutrient loading and  
19 presence or absence of adult bivalves arranged in a 2 x 2 factorial design. The growth of all  
20 populations along with levels of light, nutrients, size-fractionated chlorophyll *a*, and particulate  
21 organic matter were monitored during three experiments which demonstrated that both nutrient  
22 loading and adult bivalve filtration can strongly influence the growth of multiple estuarine  
23 resources.

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**Methods:**

We conducted three mesocosm experiments placed within eastern Shinnecock Bay at the Stony Brook-Southampton Marine Science Center from June 5<sup>th</sup>, 2007, to September 6<sup>th</sup>, 2007. Shinnecock Bay is part of Long Island’s south shore estuary lagoons 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 (*Mercenaria mercenaria*, McHugh 1991), the bay scallop (*Argopecten irradians*, Bricelj and Kuenster 1989), various finfish (Beck *et al.* 2001), and eelgrass beds (*Zostera marina*, Dennison *et al.* 1989). The 300-L mesocosms 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 hard clams (~10 mm), scallops (~10 mm), and/or oysters (~10 mm) at stocking densities (10 – 20 tank<sup>-1</sup> or 36 – 72 m<sup>-2</sup>; Table 1) more than an order of magnitude lower than standard commercial aquaculture stocking densities (~500 individ. m<sup>-2</sup>; Barber and Davis 1997, Kraeuter and Castagna 2001) to avoid inter- and intraspecific competition for food (Rheault and Rice 1996, Kraeuter and Castagna 2001). Indeed, our estimated community clearance rates of juvenile bivalves indicated they filtered 0.4-1.5% d<sup>-1</sup> of the total mesocosm volumes. All juvenile bivalves were placed in mesh cages (~2mm mesh size) near the bottom of the mesocosms. Juvenile shellfish were obtained from the

1 Cornell Cooperative Extension shellfish hatchery in Southold, NY. Three-week-old sheepshead  
2 minnows (*Cyprinodon variegatus*, 10-15 mm) were obtained from Cosper Environmental  
3 Services in Bohemia, NY. These planktivorous fish (Samson *et al.* 2008) were held in mesh  
4 baskets suspended near the tops of the experimental tanks (n = 10). A laminar circulating pump  
5 (Rio 180) was utilized to ensure mesocosms were well-mixed. In addition to the suspension  
6 feeders, individual shoots of *Zostera marina* (n = 16) were transplanted into planters containing  
7 low-organic sand and placed in each mesocosm (Wall *et al.* 2008).

8         Mesocosms were filled with eastern Shinnecock Bay water during high tide. Water from  
9 this region is fairly mesotrophic with mean total N concentrations of  $0.2 \pm 0.1 \text{ mg N L}^{-1}$  or  $16 \pm 8$   
10  $\mu\text{M N}$  from 2000 to 2005 (n = 50 measurements; SCDHS 2000-2005). Actual measurements of  
11 each inorganic nitrogen, phosphorus and silicon species were made at the beginning of each  
12 experiment, in the middle of experiments, and on the final day using standard techniques  
13 (Valderrama 1981, Parsons *et al.* 1984). For each experiment, we established a low nutrient  
14 loading rate for half of the experimental tanks ( $0.065\text{-}0.255 \text{ mmol N m}^{-2} \text{ d}^{-1}$ ) using a 1-2%  $\text{d}^{-1}$   
15 exchange with Shinnecock Bay water. The other half of the tanks received a high nutrient  
16 loading rate ( $5.49\text{-}10.70 \text{ mmol N m}^{-2} \text{ d}^{-1}$ ) that reflected ambient exchange plus nutrient  
17 additions of ammonium and the Redfieldian equivalent of orthophosphate. These nutrient  
18 loading rates are within the range found in more eutrophic Northeast US estuaries such as the  
19 Childs River, MA, and Moriches Bay, NY (Taylor *et al.* 1999). Nutrient stocks were filter-  
20 sterilized ( $0.2 \mu\text{m}$ ) and stored frozen. Experiments were run in semi-continuous mode, with 1-  
21 2% of the water volume being replaced daily mimicking the natural tidal exchange which occurs  
22 in the back-bay regions of the Peconic Estuary and Great South Bay (Hardy 1976, Wilson *et al.*  
23 1991). For each experiment, half of the experimental tanks contained adult suspension feeders

1 (hard clam *M. mercenaria* or Eastern oyster *C. virginica*) and half of the tanks contained no adult  
2 suspension feeders. Adult hard clams measured  $56.70 \pm 1.18$  mm anterior-posterior and weighed  
3  $1.64 \pm 0.11$  g AFDW. Adult oysters measured  $59.17 \pm 0.79$  mm hinge-ventral margin and  
4 weighed  $0.66 \pm 0.05$  g AFDW. Adult shellfish were locally caught and obtained from seafood  
5 markets. The filtration of adult shellfish was estimated with a clearance rate method (Riisgard  
6 2001) using water ( $>15 \mu\text{g L}^{-1}$  chlorophyll *a*) from the experimental tanks. Clearance rates were  
7 calculated according to the equation:

$$8 \quad \text{clearance rate} = \ln(\text{initial chl } a / \text{final chl } a) * \text{volume} / \text{time}$$

9 This measurement was performed once per species. A ‘community’ clearance rate was estimated  
10 from these data using the average individual clearance rate and the number of individuals in the  
11 tank. An estimated turnover time for the entire tank volume to pass through the adult shellfish  
12 was calculated for each tank by dividing the tank volume by this community clearance rate. A  
13 summary of experimental conditions for all three experiments is presented in Table 1.

14 Experiments were conducted for ~two weeks, and shellfish growth was assessed via the  
15 changes in ash-free dry weight (AFDW) of tissue or by changes in lengths between initial and  
16 final individuals within each mesocosm (Weiss *et al.* 2007). The length of juvenile clams was  
17 measured by shell length (anterior-posterior; Kraeuter and Castagna 2001) and the size of  
18 juvenile oysters and scallops was measured by shell height (hinge-ventral margin; Rheault and  
19 Rice 1996). Bivalve tissue was dried at  $70^{\circ}\text{C}$  for at least 24 h and then ashed at  $450^{\circ}\text{C}$  for an  
20 additional 4 h (Gabbott and Walker 1971, Bass *et al.* 1990). One hundred bivalves of each  
21 species were selected from the initial set to provide a mean initial AFDW. When fewer than 100  
22 individuals were available for a mean initial AFDW, initial AFDW’s were hind-casted based on  
23 initial lengths using length-weight regressions from 100+ individuals of the same species and

1 size class. Juvenile fish growth was measured by total length only. Mean growth rates for all  
2 species based on length or weight were calculated by the change in length or AFDW divided by  
3 the number of days between initial and final measurements. In addition, treatment effects on  
4 eelgrass above-ground biomass, leaf morphometrics, leaf productivity and epiphyte biomass  
5 were assessed by marking then harvesting eelgrass shoots from each replicate mesocosm. Leaf  
6 production during the experiment was measured using a modified leaf marking technique  
7 (Ibarra-Obando and Boudouresque 1994). Sixteen eelgrass shoots were marked at the base of  
8 the leaves by driving an 18-gauge hypodermic needle through all of the leaves on the shoot. The  
9 marked shoots were allowed to grow for 14 d, after which all above-ground leaf material was  
10 harvested. In the laboratory, the number of leaves, leaf width, leaf length, daily gross above-  
11 ground production, and leaf epibiont biomass ( $\text{mg AFDW cm}^{-2}$  leaf area) was determined.  
12 Productivity was determined by both mass ( $\text{mg shoot}^{-1} \text{d}^{-1}$ ) and leaf area growth ( $\text{cm}^2 \text{shoot}^{-1} \text{d}^{-1}$ ).  
13 Epiphyte mass was determined by scraping fouling organisms and algae from each leaf, then  
14 drying them to a constant mass ( $\pm 0.01$  mg) in an oven at  $70^\circ\text{C}$ . Following dry weighing, the  
15 ash weight was determined by ashing the samples at  $450^\circ\text{C}$  for 4 h. Ash free dry weight  
16 (AFDW) was calculated as dry weight minus ash weight.

17 Bottom mesocosm light levels were measured every 15 minutes by HOBO© Pendant-  
18 style data loggers with light sensors. A data logger was placed in each experimental tank near  
19 the bottom at a depth of approximately 1 m, a height just above eelgrass and shellfish cages  
20 preventing the obstruction of incoming light. A mean daily light level for each experimental  
21 tank was calculated by averaging values between 1000 and 1400 hrs, when the sun was most  
22 directly overhead. Since the HOBO© data loggers measure visible light levels in Lux instead of  
23 photosynthetically active radiation (PAR) in  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , we compared measurement of light

1 with the HOBO© loggers to those obtained with a LiCor© LI-192 underwater quantum sensor of  
2 PAR. There was a highly significant linear relationship between visible light in Lux as measured  
3 by the HOBO© data logger and PAR as measured by the LiCor© sensor over depths of 0.5-2.0  
4 m (Visible light in LUX = 41.407 \* PAR – 408.67,  $r^2 = 0.98$ ,  $p < 0.001$ ). Based on this finding,  
5 we believe that experimental light readings from HOBO© data loggers within our mesocosms  
6 were representative of the general trends in PAR.

7         The quality and quantity of suspended food for bivalves was assessed in two ways. The  
8 distribution of phytoplankton biomass among size classes was estimated by the analysis of size  
9 fractionated chlorophyll *a* (whole and >5  $\mu\text{m}$ ) using polycarbonate filters and standard  
10 fluorometric techniques (Parsons *et al.* 1984). Whole water samples were collected on pre-  
11 combusted glass fiber filters for the analysis of particulate organic carbon and nitrogen (POC,  
12 PON) on a CE Instruments Flash 1112 elemental analyzer (Sharp 1974, Gobler and Sañudo-  
13 Wilhelmy 2001).

14         Seawater dilution experiments were conducted to quantify the rates of microzooplankton  
15 grazing of algal biomass within the mesocosm tanks (Landry *et al.* 1995). During each  
16 experiment, five liters of water from each replicate mesocosm within a treatment were pooled  
17 into a 20 L carboy for that treatment. Triplicate samples of 100, 70, 40 and 15% experimental  
18 dilutions of whole seawater with filtered seawater (0.2  $\mu\text{m}$ ) from each carboy were established in  
19 1 L polycarbonate bottles. To ensure nutrient-replete growth during these experiments, nitrate  
20 (20 $\mu\text{M}$ ) and orthophosphate (1.25 $\mu\text{M}$ ) was added to all of the bottles. A set of triplicate controls  
21 of whole seawater without nutrients were also established for each grazing experiments (Landry  
22 *et al.* 1995). Algal growth rates ( $\mu$ ) within experimental bottles were quantified using the  
23 formula:  $\mu = [\ln(B_t / B_0)] / t$ , where  $\mu$  is the net growth rate,  $B_t$  is the amount of biomass (chl *a*)

1 present at the end of the experiments,  $B_0$  represents the amount of biomass at the beginning of  
2 experiments, and  $t$  is the duration of the experiment in days. The slope of first order linear  
3 regressions of dilution of seawater (x-axis) and the net growth rates (y-axis) were used to  
4 establish grazing mortality rates (Landry *et al.* 1995).

## 5 Statistical Analysis

6 Differences in the growth of each animal species and eelgrass was assessed by means of  
7 Two-Way ANOVAs, with nutrient loading level and presence/absence of adult bivalves as the  
8 two treatment factors. Chlorophyll *a* and light level trends were analyzed using three-way  
9 ANOVAs with nutrient loading, presence/absence of adult bivalves, and day as factors. When a  
10 significant effect on the response variables was detected, multiple comparison tests (Tukey's  
11 Studentized range) was used to test for significant differences between levels within the  
12 treatment. Mortality of juvenile bivalves was analyzed using a G-test of independence (Sokal  
13 and Rohlf 1995). All statistical results were considered significant if  $p < 0.05$ .

14

## 15 **Results:**

### 16 Experiment 1

17 Three separate mesocosm experiments were carried out using the above methods (Table  
18 1). Experiment 1 ran from June 5<sup>th</sup> to June 18<sup>th</sup>, 2007. The average temperature in the  
19 experimental tanks was  $20.30 \pm 0.15$  °C, the average salinity was  $26.42 \pm 0.04$ , and the average  
20 dissolved oxygen was  $6.65 \pm 0.14$  mg L<sup>-1</sup>. The “low nutrient loading” treatment received an  
21 average of  $0.065$  mmol N m<sup>-2</sup> d<sup>-1</sup> through a 1% d<sup>-1</sup> exchange with Shinnecock Bay water  
22 whereas the “high nutrient loading” treatment received  $10.70$  mmol N m<sup>-2</sup> d<sup>-1</sup>. The densities of  
23 adult suspension feeders were 29 or 0 clams m<sup>-2</sup> (*M. mercenaria*). The estimated turnover time

1 from bivalve filtration for the experimental tanks with hard clams was 2.4 days. All tanks in this  
2 experiment were stocked with juvenile clams, juvenile oysters, and eelgrass (Table 1).

3 In this experiment, the higher nutrient loading rate ( $10.70 \text{ mmol N m}^{-2} \text{ d}^{-1}$ ) and the  
4 absence of adult hard clams produced significant increases in chlorophyll *a* compared to the low  
5 nutrient loading rate ( $0.065 \text{ mmol N m}^{-2} \text{ d}^{-1}$ ) and the presence of adult hard clams ( $29 \text{ individ.}$   
6  $\text{m}^{-2}$ ) over the course of a 13-day experiment (Fig. 1;  $p < 0.001$ , 3-way ANOVA). Chlorophyll *a* in  
7 the  $< 5 \mu\text{m}$  size fraction was significantly increased by high nutrient loading ( $p < 0.01$ ) and  
8 decreased by adult clam filtration ( $p < 0.001$ , 3-way ANOVA), while the  $> 5 \mu\text{m}$  size fraction was  
9 not significantly affected by the experimental treatments (3-way ANOVA). Particulate organic  
10 nitrogen (PON) was significantly higher in the presence of adult clams ( $25.17 \pm 2.57 \mu\text{M}$ )  
11 compared to the absence of adult clams ( $17.28 \pm 1.70 \mu\text{M}$ ;  $p < 0.05$ , 2-way ANOVA). Although  
12 particulate organic carbon (POC) did not change between treatments, the molar ratio of  
13 POC:PON was significantly higher under low nutrient loading ( $9.70 \pm 0.61$ ) and the absence of  
14 adult clams ( $10.51 \pm 0.45$ ) compared to high nutrient loading ( $9.22 \pm 0.26$ ) and the presence of  
15 adult clams ( $8.83 \pm 0.24$ ;  $p < 0.05$  for nutrient treatment,  $p < 0.01$  for clam filtration treatment, 2-  
16 way ANOVA). Mean chlorophyll *a* and POC/PON levels for all treatments are summarized in  
17 Table 3.

18 The highest juvenile hard clam growth was in the presence of high nutrient loading and in  
19 the absence of adult hard clams, while the lowest was without nutrient loading but with adult  
20 hard clams present (Fig. 2A) However, only the nutrient loading treatment had a statistically  
21 significant effect: juvenile clam growth (Fig. 2A) and juvenile oyster growth (Fig. 3B) were  
22 both significantly higher in the high nutrient loading treatment ( $0.032 \pm 0.009 \text{ mm d}^{-1}$  and  $0.078$   
23  $\pm 0.016 \text{ mg AFDW d}^{-1}$ , respectively) compared with treatments without experimental nutrient

1 addition ( $0.00 \pm 0.01 \text{ mm d}^{-1}$  and  $0.034 \pm 0.015 \text{ mg AFDW d}^{-1}$  respectively;  $p < 0.05$  for each, 2-  
2 way ANOVA). Juvenile bivalve growth for both species was marginally lower when adult clams  
3 were present, but not significantly so (Fig. 2A, 2B). Despite the changes in chlorophyll *a*, light  
4 levels were not significantly different among treatments (3-way ANOVA) and subsequently  
5 eelgrass growth was not affected by the experimental treatments (2-way ANOVA). Nitrate,  
6 ammonium, and phosphate accumulated within the nutrient enriched mesocosms and to a lesser  
7 extent in the adult clam only treatment during this experiment, while silicate levels were similar  
8 among treatments (Table 2). Microzooplankton grazing rate data were not available for this  
9 experiment.

10

## 11 Experiment 2

12 Experiment 2 ran from July 12<sup>th</sup> to July 27<sup>th</sup>, 2007. The average temperature in the  
13 experimental tanks was  $24.27 \pm 0.16 \text{ }^{\circ}\text{C}$ , the average salinity was  $28.02 \pm 0.16$ , and the average  
14 dissolved oxygen was  $5.83 \pm 0.12 \text{ mg L}^{-1}$ . The “low nutrient loading” treatment received an  
15 average of  $0.255 \text{ mmol N m}^{-2} \text{ d}^{-1}$  through a  $2\% \text{ d}^{-1}$  exchange with Shinnecock Bay water. The  
16 “high nutrient loading” treatment received ambient exchange plus a daily experimental nutrient  
17 addition for a total of  $5.75 \text{ mmol N m}^{-2} \text{ d}^{-1}$ . The densities of adult suspension feeders were 21  
18 or 0 oysters  $\text{m}^{-2}$  (*C. virginica*). The estimated turnover time from bivalve filtration for the  
19 experimental tanks with oysters was 1.5 days. All tanks in this experiment were stocked with  
20 juvenile clams, juvenile oysters, and eelgrass (Table 1).

21 Nitrate, phosphate, and silicate levels all increased during experiments, but did not differ  
22 among treatments, while ammonium levels were lowest in the no oyster, no nutrient treatment  
23 (Table 2). Treatments did not significantly affect total chl *a* levels or  $<5 \text{ } \mu\text{m chl } a$  (3-way

1 ANOVA), but did affect  $>5 \mu\text{m chl } a$ , which was higher in the absence of adult oysters ( $p < 0.05$ ,  
2 3-way ANOVA, Table 3). Juvenile clam growth was significantly higher in the high nutrient  
3 loading treatment ( $0.039 \pm 0.003 \text{ mm d}^{-1}$  and  $0.058 \pm 0.005 \text{ mg AFDW d}^{-1}$ ) compared to the low  
4 nutrient loading treatment ( $0.030 \pm 0.003 \text{ mm d}^{-1}$  and  $0.033 \pm 0.005 \text{ mg AFDW d}^{-1}$ ) when  
5 measured by shell length (data not shown;  $p < 0.05$ , 2-way ANOVA) or by dry tissue weight (Fig.  
6 3A;  $p < 0.001$ , 2-way ANOVA). Juvenile clam growth was not affected by the adult oyster  
7 filtration treatment. In contrast, the juvenile oysters responded to the adult bivalve treatment;  
8 juvenile oyster growth was significantly decreased in the presence of adult oyster filtration (Fig.  
9 3B;  $p < 0.01$ ; 2-way ANOVA) but was not affected by the nutrient loading treatments. Juvenile  
10 oyster growth was  $0.131 \pm 0.022 \text{ mg AFDW d}^{-1}$  in the absence of adult oysters and was  $0.033 \pm$   
11  $0.017 \text{ mg AFDW d}^{-1}$  in the presence of adult oysters. Light levels and eelgrass growth were not  
12 significantly affected by the experimental treatments (2-way ANOVA), although epiphyte  
13 biomass on eelgrass leaves was significantly higher under high nutrient loading ( $0.164 \pm 0.013$   
14  $\text{mg AFDW cm}^{-2}$ ) and adult oyster filtration ( $0.179 \pm 0.011 \text{ mg AFDW cm}^{-2}$ ) compared to low  
15 nutrient loading ( $0.140 \pm 0.012 \text{ mg AFDW cm}^{-2}$ ) and no adult oyster filtration ( $0.126 \pm 0.006 \text{ mg}$   
16  $\text{AFDW cm}^{-2}$ ;  $p < 0.05$  by nutrient treatment,  $p < 0.001$  by oyster treatment, 2-way ANOVA).  
17 Microzooplankton grazing rates were not significantly different between treatments, and ranged  
18 from 2.31 to 2.39  $\text{d}^{-1}$  (Table 3). POC/PON data were not available for this experiment.

19

### 20 Experiment 3

21 Experiment 3 ran from August 22<sup>nd</sup> to September 6<sup>th</sup>, 2007. The average temperature in  
22 the experimental tanks was  $24.56 \pm 0.15 \text{ }^\circ\text{C}$ , the average salinity was  $29.73 \pm 0.09$ , and the  
23 average dissolved oxygen was  $6.16 \pm 0.16 \text{ mg L}^{-1}$ . The “low nutrient loading” treatment

1 received an average of  $0.134 \text{ mmol N m}^{-2} \text{ d}^{-1}$  through a  $2\% \text{ d}^{-1}$  exchange with Shinnecock Bay  
2 water. The “high nutrient loading” treatment received ambient exchange plus a daily  
3 experimental nutrient addition for a total of  $5.49 \text{ mmol N m}^{-2} \text{ d}^{-1}$ . The densities of adult  
4 suspension feeders were 43 or 0 clams  $\text{m}^{-2}$  (*M. mercenaria*). The estimated turnover time from  
5 bivalve filtration for the experimental tanks with hard clams was 1.6 days. All tanks in this  
6 experiment were stocked with juvenile scallops, juvenile clams, juvenile oysters, juvenile  
7 sheepshead minnows, and eelgrass (Table 1).

8         In this experiment, the high nutrient loading rate ( $5.49 \text{ mmol N m}^{-2} \text{ d}^{-1}$ ) and the absence  
9 of adult hard clams again produced significant increases in total chlorophyll *a* compared to the  
10 low nutrient loading rate ( $0.134 \text{ mmol N m}^{-2} \text{ d}^{-1}$ ) and the presence of adult hard clams (43  
11 individ.  $\text{m}^{-2}$ ) over the course of a 15-day experiment (Fig. 4A;  $p < 0.01$ , 3-way ANOVA). Trends  
12 in total chl *a* were paralleled by the  $>5 \mu\text{m}$  size fraction of chl *a* which was higher under high  
13 nutrient loading ( $p < 0.01$ , 3-way ANOVA) and in the absence of adult clams ( $p < 0.001$ , 3-way  
14 ANOVA, Table 3). The  $<5 \mu\text{m}$  size fraction of chl *a* was significantly lower in the presence of  
15 adult clam filtration ( $p < 0.01$ , 3-way ANOVA, data not shown), but this smaller size fraction was  
16 not significantly altered by the nutrient treatments.

17         Particulate organic nitrogen (PON) was significantly lower in the presence of adult clams  
18 ( $16.1 \pm 1.24 \mu\text{M}$ ) compared to the absence of adult clams ( $38.4 \pm 3.37 \mu\text{M}$ ; Table 3;  $p < 0.05$ , 2-  
19 way ANOVA). Particulate organic carbon (POC) was affected by both experimental treatments.  
20 The levels of POC were higher in the high nutrient loading treatment ( $249.76 \pm 52.82 \mu\text{M}$ )  
21 compared to the low nutrient loading treatment ( $215.14 \pm 35.57 \mu\text{M}$ ;  $p < 0.05$ , 2-way ANOVA),  
22 and POC was lower in the presence of adult clams ( $116.88 \pm 8.62 \mu\text{M}$ ) compared to the absence  
23 of adult clams ( $310.35 \pm 18.92 \mu\text{M}$ ; Table 3;  $p < 0.001$ , 2-way ANOVA). The molar ratio of

1 POC:PON was not significantly affected by any of the treatments in Experiment 3 (Table 3).  
2 Silicate accumulated in high nutrient loading mesocosms, while a mid-experiment spike in  
3 phosphate and ammonium occurred in the mesocosms with high nutrient loading and adult clams  
4 (Table 2). Final levels of nitrate, ammonium, and phosphate did not differ among treatments.  
5 Microzooplankton grazing rates were not significantly different between treatments, and ranged  
6 from 0.45 to 0.73 d<sup>-1</sup> (Table 3).

7 Light penetration to the bottom of the mesocosms was higher in the adult bivalve  
8 treatment (Fig. 4B; p<0.001, 3-way ANOVA) but was not consistently affected by the nutrient  
9 treatments. Eelgrass growth was significantly higher in the presence of adult clams, as measured  
10 by leaf area productivity (0.569 ± 0.049 cm<sup>2</sup> shoot<sup>-1</sup> d<sup>-1</sup>) or mass productivity (1.87 ± 0.17 mg  
11 shoot<sup>-1</sup> d<sup>-1</sup>; Fig. 5C) compared to the treatments with no adult clams (0.422 ± 0.036 cm<sup>2</sup> shoot<sup>-1</sup> d<sup>-1</sup>  
12 leaf area productivity, 1.27 ± 0.23 mg shoot<sup>-1</sup> d<sup>-1</sup> mass productivity, p<0.05, 2-way ANOVA).  
13 Epiphyte growth on the eelgrass blades was also significantly denser in the presence of adult  
14 clams (0.186 ± 0.017 mg AFDW cm<sup>-2</sup>) compared to the absence of adult clams (0.146 ± 0.009  
15 mg AFDW cm<sup>-2</sup>; p<0.01, 2-way ANOVA).

16 Juvenile clams were not significantly affected by any of the treatment factors in the third  
17 experiment. However, juvenile oyster and fish growth were both highest in the absence of adult  
18 hard clams. Juvenile oysters grew significantly faster in the absence of adult clams (0.257 ±  
19 0.064 mg AFDW d<sup>-1</sup>) compared to when adult clams were present (0.034 ± 0.067 mg AFDW d<sup>-1</sup>;  
20 Fig. 5A p<0.05, 2-way ANOVA). Juvenile sheepshead minnows also grew significantly faster in  
21 the absence of adult clams (0.228 ± 0.017 mm d<sup>-1</sup> p<0.05, 2-way ANOVA) compared to  
22 treatments with adult clams (0.177 ± 0.022 mm d<sup>-1</sup>; Fig 5B). The fish growth rates showed an  
23 interesting interaction: the presence/absence of adult clams made more of a difference to the

1 juvenile sheepshead minnows within the high nutrient loading treatment than within the low  
2 nutrient treatment (Fig. 5B;  $p < 0.05$  interaction, 2-way ANOVA). This interaction was present  
3 but non-significant for juvenile oysters (Fig. 5A). Differences in juvenile scallop growth rates  
4 were not significant (2-way ANOVA), but juvenile scallop mortality was significantly higher in  
5 the presence of adult hard clams than in the absence of adult clams (96% with adult clams, 71%  
6 without adult clams;  $p < 0.001$ ; G-test of independence, data not shown). Juvenile fish and  
7 shellfish were not significantly affected by the nutrient loading treatments in this experiment (2-  
8 way ANOVA).

9

## 10 **Discussion:**

11 Over the course of three mesocosm experiments both enhanced nutrient loading and  
12 filtration by adult hard clams significantly affected the growth of juvenile shellfish, juvenile fish,  
13 and eelgrass, as well as phytoplankton and light levels in mesocosms. Adult bivalve filtration  
14 and nutrient loading were expected to affect eelgrass growth through changes in the density of  
15 phytoplankton, which in turn affects the benthic light regime (Newell and Koch 2004, Wall *et al.*  
16 2008). The results of Experiment 3 were consistent with this hypothesis, where a high density of  
17 adult hard clams decreased chlorophyll *a* levels and increased light penetration (Fig 4A-B)  
18 leading to an increase in eelgrass productivity (Fig 5C). In Experiment 1, adult hard clams  
19 decreased chlorophyll *a* (Fig 1) but did not have a significant effect on light or eelgrass, and  
20 there were no consistent effects on chl *a*, light, or eelgrass growth for Experiment 2. Eelgrass  
21 growth was not significantly affected by nutrient loading in any of the experiments. The density  
22 of epiphytes on eelgrass blades was increased by adult bivalve filtration in Expts 2 and 3, and by  
23 nutrient loading in Expt 2. Although thick epiphyte growth has been found to have a negative

1 impact on seagrass in some cases (Duarte 1995), the densities of epiphytes measured in our  
2 experiments (0.13-0.19 mg AFDW cm<sup>-2</sup>) were likely too low to block light at the blade surface  
3 (Brush and Nixon 2002).

4         Growth rates of juvenile fish and shellfish may be decreased by filtration pressure from  
5 adult bivalves, which clear food particles from the water column (Rheault and Rice 1996, Zhou  
6 *et al.* 2006), or may be increased by high nutrient loading, which may increase the quantity and  
7 quality of suspended food particles (Carmichael *et al.* 2004, Carmichael and Valiela 2005). All  
8 three experiments had some results consistent with this hypothesis: juvenile clam growth was  
9 increased by high nutrient loading in Experiments 1 and 2 (Fig 2A, 3A), juvenile oyster growth  
10 was also increased by high nutrient loading in Experiment 1 (Fig 2B), while juvenile oyster  
11 growth was decreased by adult bivalve filtration in Experiments 2 and 3 (Fig 3B, 5A), and  
12 juvenile fish growth was also decreased by adult bivalve filtration in Experiment 3 (Fig 5B).  
13 Although there were no significant growth responses for scallops, juvenile scallop mortality was  
14 increased by adult bivalve filtration in Experiment 3.

15         The results of these experiments demonstrate the strong reliance of juvenile shellfish and  
16 finfish growth rates and survival on the short-term dynamics (days to weeks) of food availability  
17 as reflected by concentrations of chlorophyll *a*, POC, and PON. In Experiment 1, where nutrient  
18 loading had a strong effect on juvenile growth, the molar ratio of POC:PON was significantly  
19 reduced by the high nutrient loading treatment (Table 3), suggesting an enrichment of nitrogen in  
20 food particles could have contributed to enhanced shellfish growth (Fig 2A-B). Carmichael *et al.*  
21 (2004) and Carmichael and Valiela (2005) have interpreted nitrogen-enriched seston as an  
22 increase in the quality of food particles available to juvenile bivalves. Although the molar ratio  
23 of POC:PON did not change in Experiment 3, the quantities of POC and PON were both

1 decreased by adult clam filtration (Table 3), with corresponding decreases in the growth rates of  
2 juvenile oysters and sheepshead minnows (Fig 5A-B). Although in most cases increased growth  
3 rates of shellfish occurred in parallel with increases in whole or size-fractionated chlorophyll *a*,  
4 there were also significant treatment-driven changes in chl *a* that did not produce growth  
5 responses in juvenile shellfish (Experiments 1 and 3, adult bivalve and nutrient loading  
6 treatments, respectively), and in one case, a shellfish growth response that was not mirrored by  
7 any changes in chl *a* (juvenile clams, Experiment 2). It is possible that the availability of food  
8 particles to the juvenile shellfish was changed by the treatment factors in this experiment despite  
9 static levels of chlorophyll *a* between treatments. Microzooplankton grazing rates, as measured  
10 by dilution experiments (Landry et al. 1995), ranged from 2.3-2.4 d<sup>-1</sup> in Experiment 2; these  
11 were faster than the estimated turnover time from adult oyster filtration of 1.5 d. Such rapid  
12 rates of phytoplankton community turnover could mask true food availability to juvenile bivalves  
13 and would account for enhanced bivalve growth responses in Experiment 2 in the absence of  
14 changes in chl *a*. In Experiment 3, microzooplankton grazing rates were slower (0.4-0.7 d<sup>-1</sup>), and  
15 comparable to the adult clam filtration time of 1.6 d. In contrast to Experiment 2, this  
16 experiment had a clear set of treatment-driven chl *a* differences (Fig 4A) and growth differences  
17 in response to adult clam filtration (Fig 5A-C).

18         During these experiments, the treatment factor driving the effects changed from nutrient  
19 loading in the first experiment, to combined factors in the second experiment, and finally to  
20 exclusively adult bivalve filtration in the third experiment. These differences may partly reflect  
21 differences in treatment administered: Experiment 1 had a larger difference in nutrient loading  
22 rate between the high nutrient treatment and the control than other experiments, while  
23 Experiment 3 had a larger clam density difference between adult clam treatments than

1 Experiment 1. These results may have also been influenced by seasonal trends: Lower  
2 temperatures during the first experiment (17-23° C) may have yielded lower nutrient  
3 regeneration rates (Nagata and Kirchman 1992, Miller *et al.* 1995) and low bivalve filtration rate  
4 (Kraeuter and Castagna 2001), making external nutrient loading a more important process.  
5 Conversely, higher temperatures (23-25° C) for the second and third experiments likely  
6 promoted faster bivalve filtration (Kraeuter and Castagna 2001, Weiss *et al.* 2007) and pelagic  
7 nutrient regeneration (Nagata and Kirchman 1992, Miller *et al.* 1995). As such, it seems that  
8 either nutrient loading or bivalve filtration can structure estuarine food webs, and the relative  
9 importance of these factors can switch seasonally or with changing rates of nutrient loading or  
10 bivalve filtration.

11         The densities of adult hard clams used in our Experiments 1 and 3 (8-12 individ. tank<sup>-1</sup>,  
12 or 29-43 individ. m<sup>-2</sup>) are comparable to historic densities of hard clams in Great South Bay (50-  
13 100 individ. m<sup>-2</sup>, Cerrato *et al.* 2004) but are much lower than current densities in NY estuaries  
14 (0.4 - 5 individ. m<sup>-2</sup>, Weiss *et al.* 2007). Similarly, the density of oysters used in Experiment 2 (6  
15 individ. tank<sup>-1</sup>, or 21 individ. m<sup>-2</sup>) are comparable to historic densities of Eastern oysters in  
16 Chesapeake Bay (43-150 individ. m<sup>-2</sup>), but are much lower than current densities (0.43 individ.  
17 m<sup>-2</sup>; Newell and Koch 2004). The estimated water column turnover times from these densities of  
18 adult bivalves were 1.5 - 2.4 days, within the range reported to control algal bloom formation  
19 (Cerrato *et al.* 2004, Wall *et al.* 2008). Consistent with this idea, the presence of adult bivalves  
20 yielded lower phytoplankton biomass in all three experiments, although the reduction in chl *a*  
21 was not significant for Expt 2. Such ecosystem-wide filtration pressure may have been typical of  
22 twentieth-century, unexploited natural bivalve populations in Chesapeake Bay (Newell 1988,  
23 Newell and Koch 2004) or Great South Bay (McHugh 1991, Cerrato *et al.* 2004). Similarly,

1 modern high-density bivalve aquaculture may also achieve these ecosystem filtration rates  
2 (Nunes *et al.* 2003, Zhou *et al.* 2006). Estuarine management programs may consider bivalve  
3 restoration as a management tool to control pelagic algal blooms (Cerrato *et al.* 2004), combat  
4 eutrophication (Cercio and Seitzinger 2007), and facilitate the growth of eelgrass (Fig 5C;  
5 Peterson and Heck, 2001, Newell and Koch, 2004, Wall *et al.* 2008), although the potential  
6 impacts on juvenile shellfish must also be considered.

7         While enhanced bivalve filtration was beneficial to eelgrass and to some extent epiphytes  
8 on eelgrass, they exerted a significantly negative effect on the growth of juvenile fish and  
9 shellfish (Fig 3B, 5A-B) and in one case even led to a significant increase in juvenile scallop  
10 mortality (Expt 3). Rheault and Rice (1996) placed juvenile Eastern oysters (*C. virginica*) and  
11 bay scallops (*A. irradians*) in a compartmented flume and found decreased growth and condition  
12 index in the shellfish that were downstream compared to the upstream dense populations. From  
13 an initial ambient chlorophyll *a* concentration of 4 to 8  $\mu\text{g L}^{-1}$ , each batch of shellfish decreased  
14 chl *a* by 27-35% compared to the upstream compartment (Rheault and Rice 1996). In  
15 Experiment 3 of our study, the high density of adult hard clams produced a comparable drop in  
16 mean chl *a* levels (Fig. 4A, -37%) compared to the control, and also led to decreased growth of  
17 juvenile oysters (Fig 5A) and survival of juvenile scallops. The concentrations of chl *a* in  
18 Experiment 3 were relatively high ( $25.09 \pm 2.56 \mu\text{g L}^{-1}$  with no adult clams;  $15.90 \pm 2.20 \mu\text{g L}^{-1}$   
19 with adult clams; Table 3); this drop in chlorophyll *a* produced a significant decrease in juvenile  
20 oyster growth but not juvenile clam growth. It is likely that juvenile clam food requirements  
21 were saturated at a lower chlorophyll *a* concentration than juvenile oyster food requirements  
22 (Tenore and Dunstan 1973). These impacts illustrate an eventual trade-off between the benefit  
23 and cost of higher ecosystem filtration rates: Despite the benefits to seagrass, high rates of water

1 column turnover by adult shellfish could serve as a negative feedback on juvenile fish and  
2 shellfish populations (Fig 3B, 5A-B) by decreasing food availability (Fig 4A). Such density-  
3 dependent food limitation is a common phenomenon within bivalve aquaculture (Rheault and  
4 Rice 1996, Zhou *et al.* 2006). The extent to which this may occur within estuarine ecosystems is  
5 not well known, but will certainly depend on the species involved and the particular physics and  
6 biology of each ecosystem (Newell 2004, Ferreira *et al.* 2008).

7 Many estuarine management plans have focused on the need to reduce nutrient loads to  
8 mitigate the effects of eutrophication (Nixon 1995, Cloern 2001, de Jonge *et al.* 2002). Partly  
9 through changes in land use and better sewage treatment, inorganic nutrient levels and/or  
10 chlorophyll *a* concentrations have declined in many formerly eutrophic systems, such as the  
11 North Sea (Nunniari *et al.* 2007, Artioli *et al.* 2008), the Dutch Wadden Sea (Philippart *et al.*  
12 2007), Narragansett Bay, RI, USA (Fulweiler *et al.* 2007), Long Island Sound, USA (CTDEP  
13 1991 – 2007), and the Peconic Estuary, NY, USA (SCDHS, 1976-2005). Despite this easing of  
14 eutrophication as measured by declines in inorganic nutrient and chlorophyll *a* concentrations,  
15 the recovery of estuarine resources in these systems has not been reported. The high nutrient  
16 loading rates in our experimental tanks are comparable to measured nutrient loading rates in  
17 eutrophic northeast U.S. estuaries (Taylor *et al.* 1999), from which valuable estuarine resources  
18 have been lost (Ryther 1989, McHugh *et al.* 1991, Valiela *et al.* 1992). However, there have  
19 been reported positive effects of moderate levels of nutrient loading. Weiss *et al.* (2002) and  
20 Carmichael *et al.* (2004) both saw increases in shell growth and soft tissue growth of quahogs  
21 (hard clams, *Mercenaria mercenaria*) and softshell clams (*Mya arenaria*) over the nutrient  
22 gradient from mesotrophic to eutrophic regions of the Waquoit Bay system, MA, USA. This  
23 parallels our increase in growth for juvenile hard clams and Eastern oysters from low to high

1 nutrient loading in Experiment 1 and juvenile clams in Experiment 2. Although Carmichael *et*  
2 *al.* (2004) also saw hypoxia in the systems with the highest nutrient loads, which decreased  
3 juvenile clam survival, our well-mixed mesocosms remained normoxic during experiments. In  
4 light of this information, our findings suggest that inorganic nutrient loading might be allowed to  
5 increase in some relatively oligotrophic and well-mixed coastal systems with increased  
6 secondary production of resource species as a positive benefit (Nixon and Buckley 2002). Of  
7 course, such potential benefits would need to be considered in light of potentially negative  
8 effects of higher nutrient loads in an ecosystem such as hypoxia (Diaz and Rosenberg 2008), loss  
9 of seagrass beds (Valiela *et al.* 1992, Dennison *et al.* 1989), and harmful algal blooms (Anderson  
10 *et al.* 2008).

11 Future ecosystem-based management of estuaries will need to simultaneously administer  
12 bivalve restoration, control of nutrient loading, conservation of key fishery species, the  
13 burgeoning aquaculture industry, and protection of critical habitats such as seagrass meadows  
14 and salt marshes. Bivalve filtration and nutrient loading can have significant and complex  
15 impacts on the growth of estuarine resources, including eelgrass, finfish, and shellfish. Based on  
16 the results of these experiments and other findings, some general conclusions can be drawn. The  
17 first is that eelgrass is light-limited in many eutrophic estuaries (Dennison and Alberte 1985,  
18 Duarte 1995) and will benefit from proximity to the enhanced filtration of bivalve beds (Wall *et*  
19 *al.* 2008). Additionally, bivalves can benefit seagrasses through enhanced biodeposition  
20 (Peterson and Heck 2001, Carroll *et al.* 2008). As such, re-planting of eelgrass beds should  
21 focus on areas that have high light penetration and/or are adjacent to existing dense bivalve  
22 populations. The second conclusion is based on our finding that juvenile resource bivalves  
23 respond to enhanced inorganic nutrient loading with increased growth, and respond with

1 decreased growth to high densities of adult bivalves. This is likely mediated by food limitation:  
2 inorganic nutrients encourage the growth of larger and more nutritious phytoplankton (Wikfors  
3 *et al.* 1992, Raven and Kubler 2002) while dense collections of adult bivalves can limit juvenile  
4 growth by clearing too many of these food particles (Rheault and Rice 1996, Zhou *et al.* 2006).  
5 Clearly, predators (Gosselin and Qian 1997, Polyakov *et al.* 2007) and hypoxia (Breitburg 2002,  
6 Altieri and Witman 2006) also exert significant mortalities on juvenile bivalves in the field.  
7 However, in absence of hypoxia and differential predation, restoration, re-seeding, and  
8 aquaculture of clams, oysters, and scallops are more likely to succeed in areas that have  
9 moderate nutrient loading rates. Managers must carefully consider the spacing between  
10 aquaculture operations as well as between aquaculture operations and natural bivalve  
11 populations.

12

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			Experiment 1	Experiment 2	Experiment 3
Stocking densities of response organisms (n = # per tank)	Juvenile bivalves	<i>M. mercenaria</i>	10	20	10
		<i>C. virginica</i>	15	10	10
		<i>A. irradians</i>	0	0	10
	Juvenile fish	<i>C. variegatus</i>	0	0	10
	Eelgrass shoots	<i>Z. marina</i>	16	16	16
Experimental conditions	Adult bivalve species		<i>M. mercenaria</i>	<i>C. virginica</i>	<i>M. mercenaria</i>
	Density of adult bivalves	+ B	29 m <sup>-2</sup>	21 m <sup>-2</sup>	43 m <sup>-2</sup>
		- B	0	0	0
	Estimated filtration time from + B treatment		2.4 d	1.5 d	1.6 d
	Exchange with ambient water		1% d <sup>-1</sup>	2% d <sup>-1</sup>	2% d <sup>-1</sup>
	Nutrient loading rate (mmoles N m <sup>-2</sup> d <sup>-1</sup> )	+ N	10.70	5.75	5.49
- N		0.065	0.255	0.134	

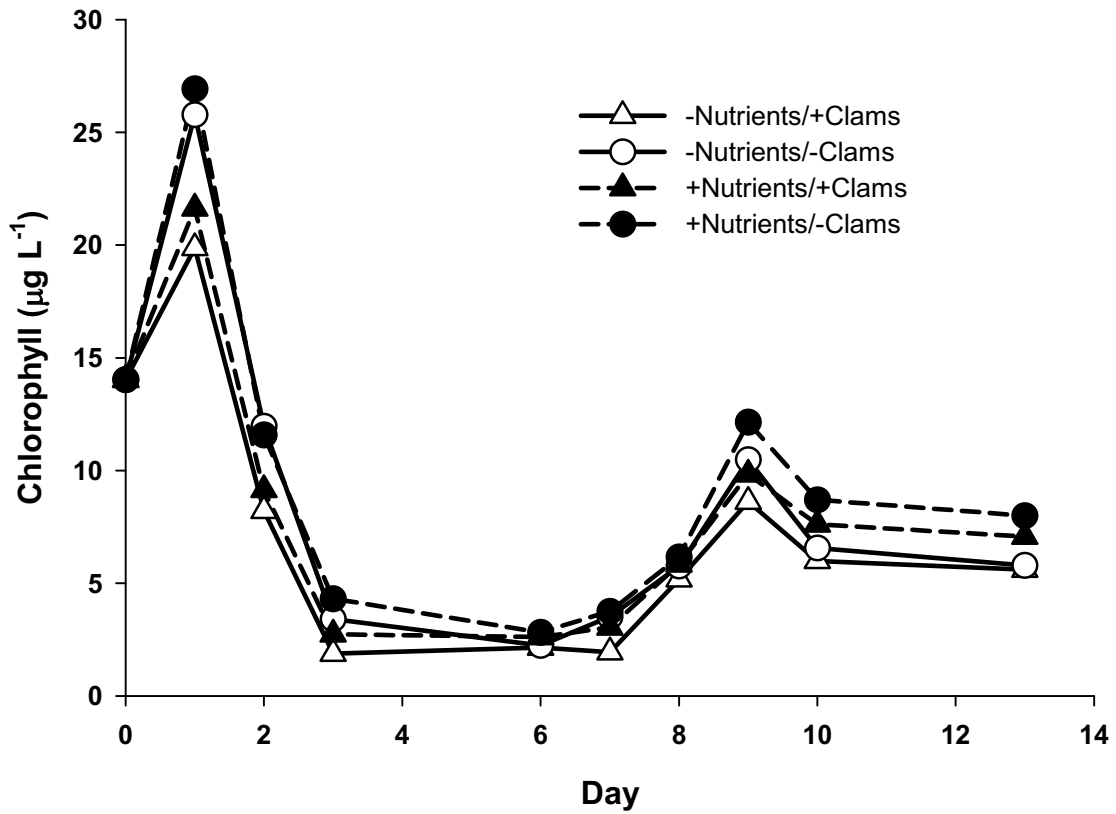
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2  
3 **Table 1. Stocking densities of response organisms and summary of experimental**  
4 **conditions.** Treatment abbreviations are “+N” or “-N” for high or low nutrient loading,  
5 and “+B” or “-B” for presence or absence of adult bivalves. A total of 16 tanks were  
6 used for each 2 x 2 factorial experiment with n = 4 tanks per treatment combination.  
7

day	Ammonium			Phosphate			
	-N/+B	-N/-B	+N/+B	-N/+B	-N/-B	+N/+B	
<b>Expt 1</b>	0	0.62 ± 0.45	0.62 ± 0.45	0.30 ± 0.07	0.30 ± 0.07	0.30 ± 0.07	
	7	9.16 ± 3.28	5.17 ± 0.66	58.85 ± 7.78	0.61 ± 0.14	0.28 ± 0.08	2.88 ± 0.33
	13	16.01 ± 6.92	5.43 ± 2.37	80.94 ± 11.71	0.96 ± 0.39	0.32 ± 0.05	2.96 ± 0.49
<b>Expt 2</b>	1	4.6 ± 2.02	0.32 ± 0.15	5.84 ± 1.66	1.47 ± 0.38	0.58 ± 0.07	1.36 ± 0.18
	8	2.34 ± 1.02	1.13 ± 0.74	10.87 ± 3.96	4.36 ± 0.60	3.34 ± 0.66	4.64 ± 0.41
	15	3.82 ± 1.46	2.10 ± 1.82	4.63 ± 1.55	4.33 ± 0.06	4.26 ± 0.23	4.34 ± 0.07
<b>Expt 3</b>	0	4.33 ± 0.19	4.33 ± 0.19	4.33 ± 0.19	1.87 ± 0.06	1.87 ± 0.06	1.87 ± 0.06
	7	2.52 ± 1.16	1.00 ± 0.11	15.46 ± 5.75	1.72 ± 0.41	0.71 ± 0.09	3.58 ± 0.7
	15	6.67 ± 0.44	6.37 ± 0.20	6.57 ± 0.39	4.71 ± 0.55	5.26 ± 0.66	4.32 ± 0.15
day	Nitrate			Silicate			
	-N/+B	-N/-B	+N/+B	-N/+B	-N/-B	+N/+B	
<b>Expt 1</b>	0	5.03 ± 0.39	5.03 ± 0.39	26.84 ± 3.25	26.84 ± 3.25	26.84 ± 3.25	
	7	8.35 ± 1.13	5.89 ± 0.16	7.02 ± 0.09	38.39 ± 1.17	34.45 ± 3.30	33.99 ± 2.85
	13	2.79 ± 0.37	2.11 ± 0.66	4.50 ± 0.83	49.92 ± 5.47	50.00 ± 6.90	50.73 ± 3.48
<b>Expt 2</b>	1	0.71 ± 0.49	0.49 ± 0.13	0.51 ± 0.20	20.92 ± 2.16	14.92 ± 1.24	19.63 ± 2.92
	8	0.68 ± 0.13	1.23 ± 0.44	3.36 ± 1.45	30.12 ± 5.17	42.29 ± 6.63	39.39 ± 8.70
	15	3.08 ± 0.07	3.76 ± 0.48	3.17 ± 0.22	27.63 ± 0.38	27.09 ± 0.11	28.48 ± 0.66
<b>Expt 3</b>	0	4.19 ± 0.55	4.19 ± 0.55	4.19 ± 0.55	32.68 ± 0.71	32.68 ± 0.71	32.68 ± 0.71
	7	1.83 ± 0.72	1.22 ± 0.24	1.32 ± 0.70	33.88 ± 1.75	32.43 ± 2.05	33.95 ± 2.37
	15	2.52 ± 0.14	4.07 ± 0.37	2.99 ± 0.41	47.01 ± 9.69	45.9 ± 5.10	37.27 ± 2.87

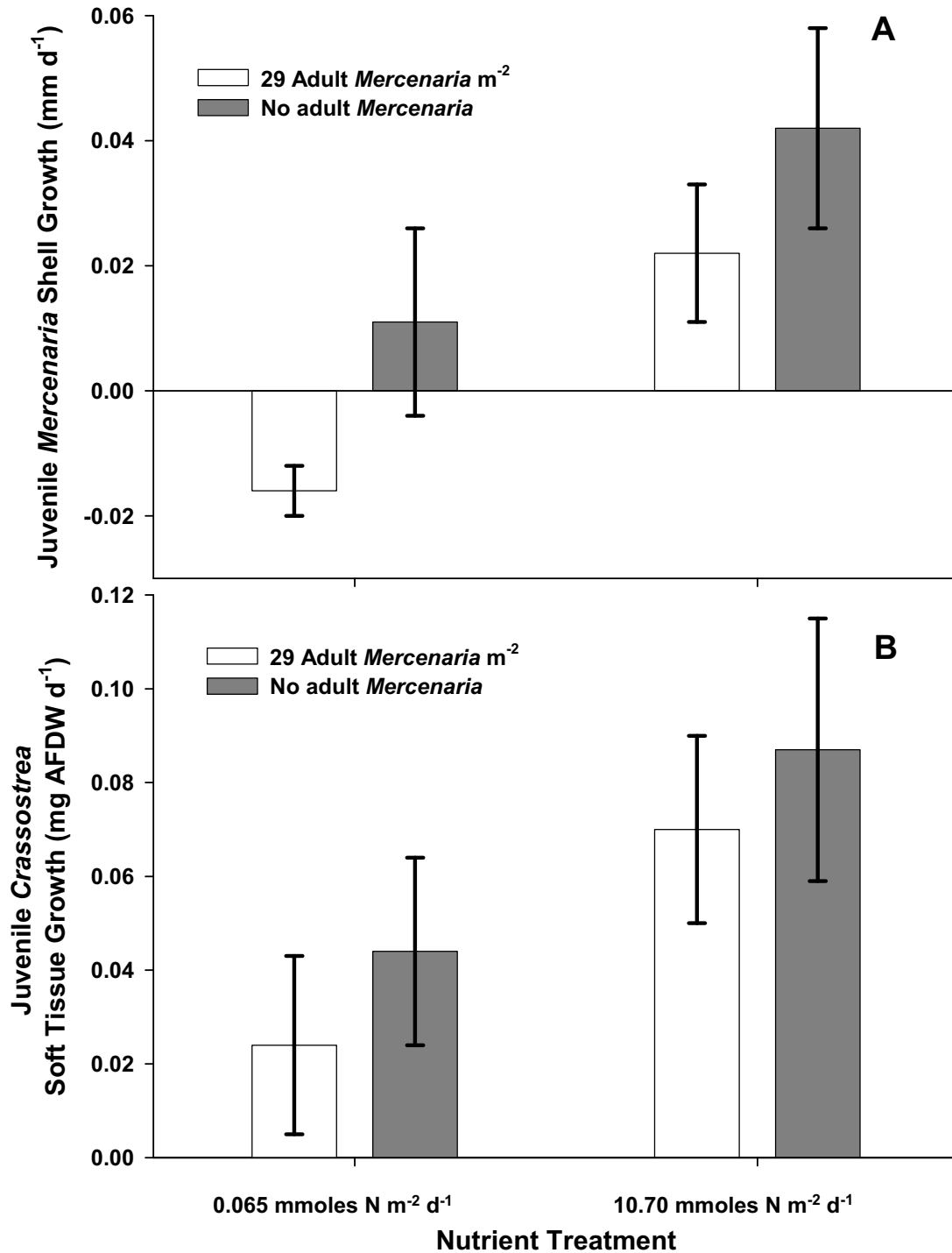
**Table 2. Levels of inorganic nutrients.** Inorganic nutrients ammonium ( $\text{NH}_4^+$ ), phosphate ( $\text{PO}_4^{3-}$ ), nitrate ( $\text{NO}_3^-$ ), and silicate ( $\text{Si}(\text{OH})_4$ ). Values in  $\mu\text{M}$  are mean  $\pm$  SE of  $n = 4$  experimental tanks for each treatment and timepoint. Treatment abbreviations are “+N” or “-N” for high or low nutrient loading, and “+B” or “-B” for presence or absence of adult bivalves. Identical values for day 0 of experiments 1 and 3 reflect single nutrient readings taken from source water for each experiment.

		whole chl <i>a</i> µg L <sup>-1</sup>	>5 µm chl <i>a</i> µg L <sup>-1</sup>	POC µM	PON µM	POC:PON	Microzooplankton grazing rate d <sup>-1</sup>
<b>Expt 1</b>	-N/+B	6.60 ± 0.91	4.92 ± 0.75	244.00 ± 44.06	27.21 ± 3.83	8.85 ± 0.33	no data
	-N/-B	8.39 ± 1.18	5.58 ± 0.80	150.46 ± 13.55	13.34 ± 2.09	11.40 ± 0.77	available
	+N/+B	7.72 ± 0.95	5.44 ± 0.83	200.40 ± 26.71	23.13 ± 3.66	8.81 ± 0.39	
	+N/-B	9.38 ± 1.19	6.21 ± 0.84	184.90 ± 15.63	19.25 ± 1.62	9.62 ± 0.23	
<b>Expt 2</b>	-N/+B	4.45 ± 0.72	2.63 ± 0.44	no data	no data	no data	2.36 ± 0.52
	-N/-B	4.59 ± 0.64	4.33 ± 1.00	available	available	available	2.39 ± 0.63
	+N/+B	5.71 ± 1.25	2.62 ± 0.43				2.36 ± 0.45
	+N/-B	7.52 ± 1.11	4.47 ± 0.88				2.31 ± 0.53
<b>Expt 3</b>	-N/+B	14.15 ± 2.61	8.96 ± 2.30	120.53 ± 18.73	16.05 ± 2.55	7.65 ± 0.89	0.55 ± 0.32
	-N/-B	21.76 ± 3.25	22.58 ± 4.23	272.08 ± 15.24	32.77 ± 3.72	8.42 ± 0.54	0.45 ± 0.07
	+N/+B	19.92 ± 3.64	12.40 ± 3.69	113.24 ± 2.66	16.31 ± 1.07	7.00 ± 0.46	0.73 ± 0.19
	+N/-B	29.00 ± 3.77	31.95 ± 5.76	348.62 ± 9.64	43.95 ± 3.42	8.00 ± 0.47	0.63 ± 0.17

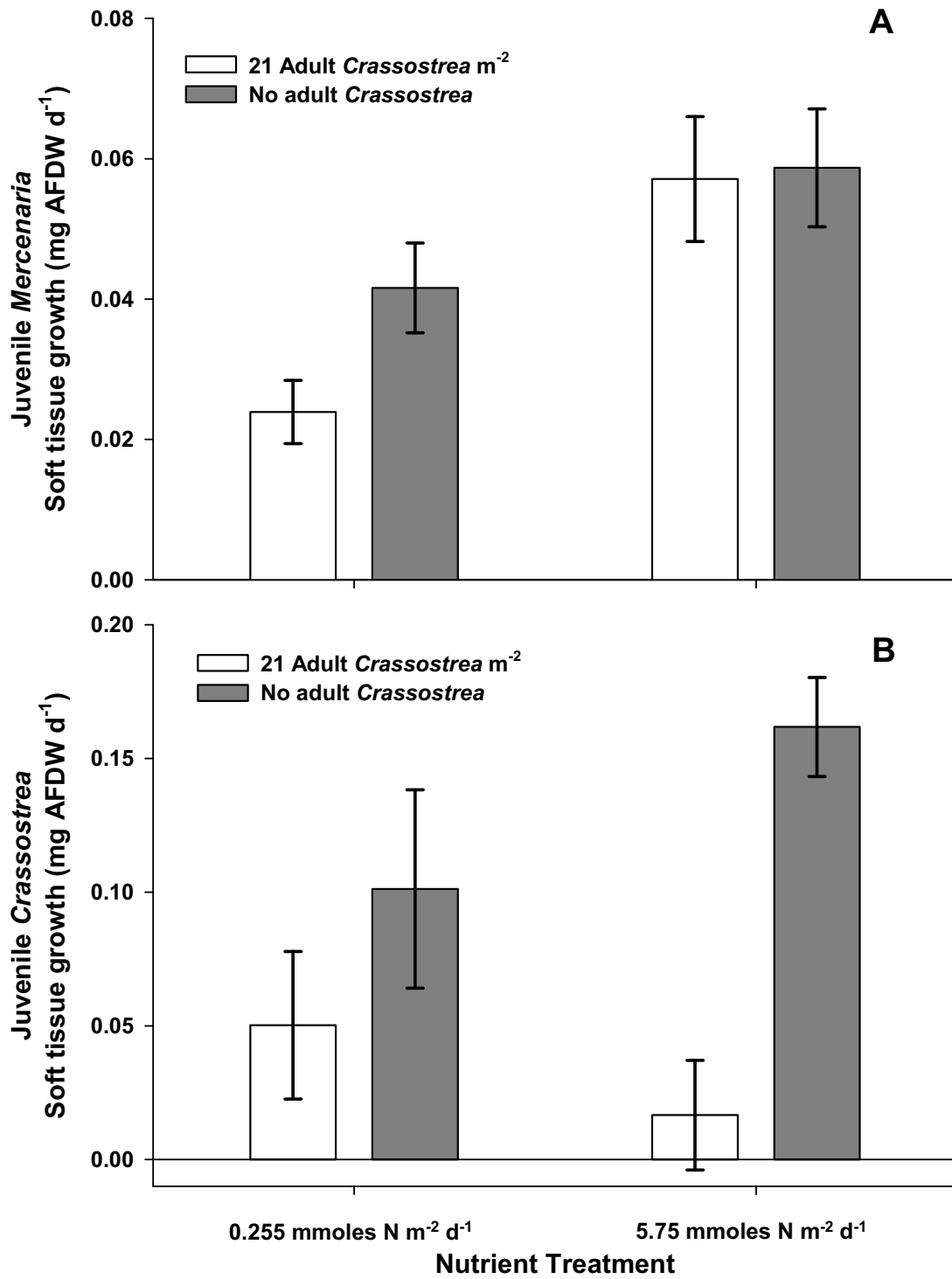
**Table 3. Levels of chlorophyll *a*, POC, PON, and microzooplankton grazing rates.** Values are mean ± SE of *n* = 4 experimental tanks for each treatment combination in each experiment. Treatment abbreviations are “+N” or “-N” for high or low nutrient loading, and “+B” or “-B” for presence or absence of adult bivalves. 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.



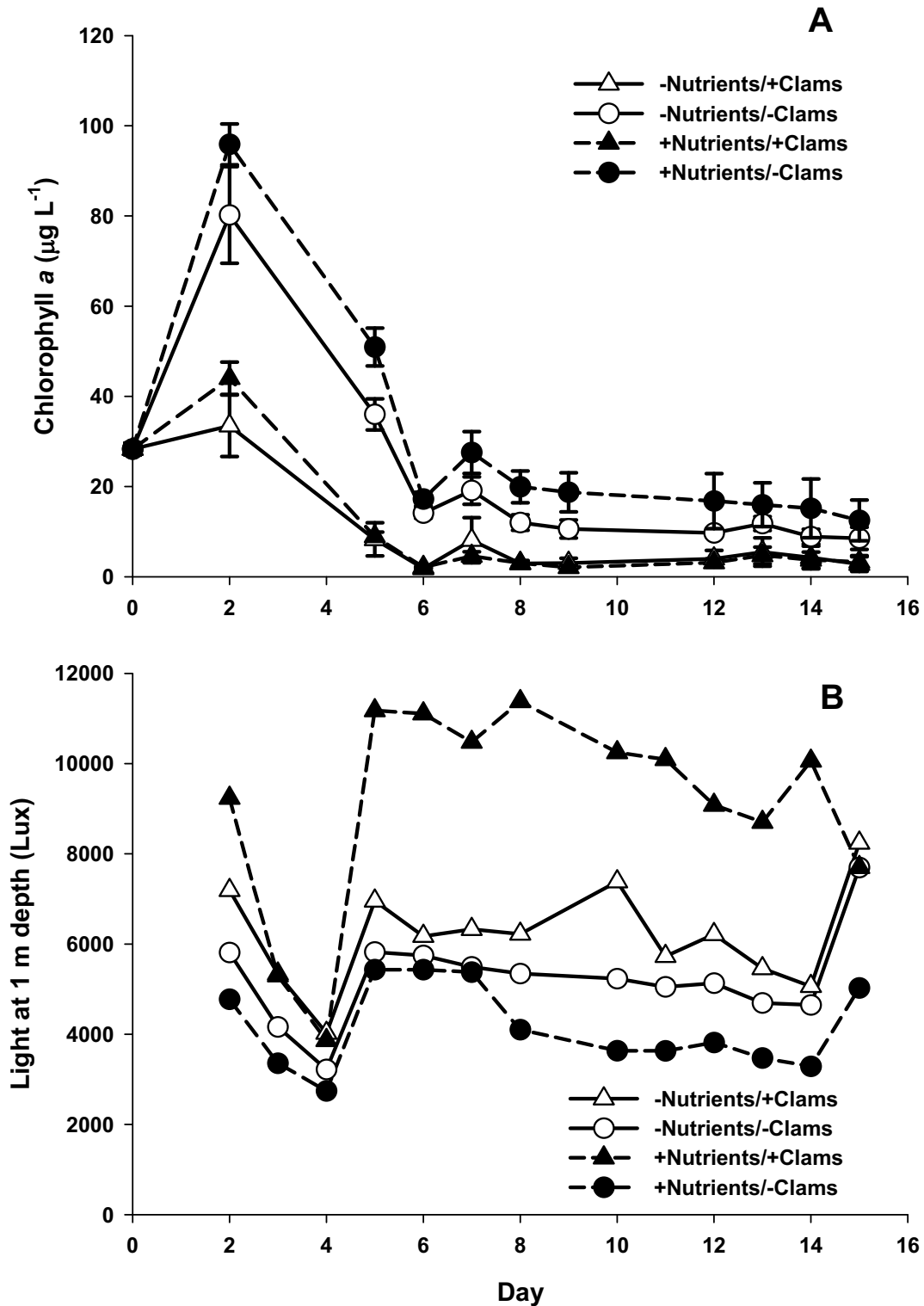
**Figure 1: Chlorophyll *a* dynamics in Experiment 1.** Data points represent the mean (n=4) for each of the treatment combinations. Error bars are not presented for the sake of visual clarity. The mean relative standard deviation of measurements was 19.8% during the experiment.



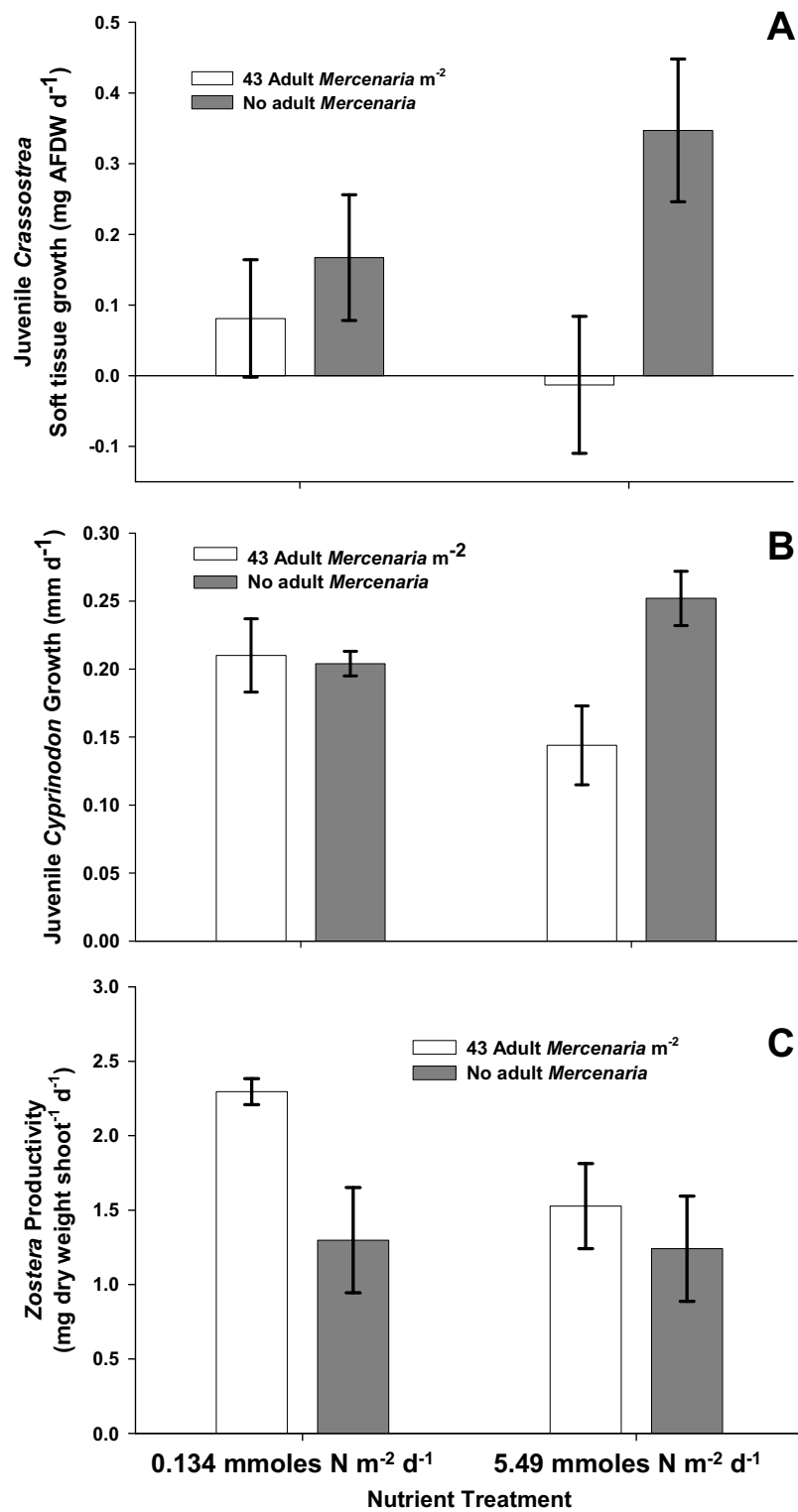
**Figure 2:** Growth responses from Experiment 1 for (A) juvenile *Mercenaria mercenaria* and (B) juvenile *Crassostrea virginica*. Bars are means  $\pm$  SE. Slightly negative shell growth for juvenile *M. mercenaria* is within measurement errors of zero.



**Figure 3:** Growth responses from Experiment 2 for (A) juvenile *Mercenaria mercenaria* and (B) juvenile *Crassostrea virginica*. Bars are means  $\pm$  SE.



**Figure 4: Chlorophyll *a* (A) and light dynamics (B) in Experiment 3.** Data points represent the mean ( $n=4$ ) for each of the treatment combinations. Error bars for light levels are not presented for the sake of visual clarity. The mean relative standard deviation of light measurements was 37.9% during the experiment.



**Figure 5:** Growth responses from Experiment 3 for (A) juvenile *Crassostrea virginica*, (B) juvenile *Cyprinodon variegatus*, and (C) *Zostera marina*. Bars are means  $\pm$  SE.

### **Chapter III:**

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

*This work was begun prior to support from The Nature Conservancy. However, support from the Nature Conservancy allowed the final data analyses and writing of this study to be completed. Additionally, the findings of this study informed the directions taken in chapters I and II of this report.*

**Key words:** *Zostera marina*, *Crassostrea virginica*, *Mercenaria mercenaria*, *Mytilus edulis*, seagrass, eelgrass, eutrophication, bivalves, suspension feeders, mesocosms

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  $0.318 \pm 0.018$   $\text{cm}^2 \text{ shoot}^{-1} \text{ d}^{-1}$  to  $0.832 \pm 0.036$   $\text{cm}^2 \text{ shoot}^{-1} \text{ d}^{-1}$  (mean  $\pm$  SE); leaf area productivity was always significantly higher (on average,  $48 \pm 9.3\%$  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 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). 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* 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 the filtration provided by bivalves has 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 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'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.

## **MATERIAL AND 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 filter-feeding bivalves on pelagic algal 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<sup>-1</sup>) 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 mesocosms 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 within 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, 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.

Hard clams (*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. 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 ( $\text{shoot}^{-1}$ ) were determined. Seagrass shoots were collected and their growth was determined. Seagrass productivity was calculated for each experiment as leaf area productivity ( $\text{cm}^2 \text{shoot}^{-1} \text{d}^{-1}$ )

based on the growth of new leaf material from the shoots in each mesocosm (Zieman, 1974). Epibiont mass was determined by scraping fouling organisms and algae from each leaf then drying them to a constant mass ( $\pm 0.01$  mg) in an oven at 70°C.

The bivalves were retained after each experiment for the determination of lengths, width, 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 in 1 L containers filled with water from one of the control mesocosm tanks which typically had high levels of chlorophyll *a* ( $> 20 \mu\text{g L}^{-1}$ ). Experiments commenced when individuals were open and filtering. Chl *a* samples taken before filtration and after a known length of time yielded a clearance rate for each individual according to the formula:

$$\text{Clearance rate} = (\text{volume} / \text{time}) * \ln (\text{initial chl } a / \text{final chl } a)$$

The twelve individuals that were used for the clearance rate measurement 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 and the number of individuals in the 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 hard clam *Mercenaria mercenaria*. There were two experimental treatments with 16 *M. mercenaria* per tank for a density of 57 individ. m<sup>-2</sup> 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<sup>-2</sup> 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<sup>-2</sup> (B. Peterson, pers obs). For all experiments, replicates for each treatment were placed among the array of mesocosms using a randomized blocks design (Sokal & Rohlf, 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<sup>-2</sup>, 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 *Crassostera 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<sup>-2</sup>, 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<sup>-2</sup>, but lower than historical densities which are estimated to have been as low

as 43 individ. m<sup>-2</sup> or as high as 150 individ. m<sup>-2</sup> 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<sup>-2</sup>) 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<sup>-2</sup>, 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<sup>-2</sup>; Altieri and Witman, 2006).

#### Statistical analysis

To compare differences in seagrass productivity between treatments, one-way ANOVA's 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 ANOVA, 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  $\pm$  SE.

## RESULTS

### Experiment 1

The temperature for all mesocosms in experiment 1 was  $19.1^{\circ}\text{C} \pm 0.6$  and the salinity was  $21.96 \pm 0.09$ . There was a remarkable difference in chl *a* concentrations over the course of the experiment between the control, which was  $34.08 \pm 9.54 \mu\text{g L}^{-1}$ , and the “clams” treatment, which was  $3.04 \pm 0.38 \mu\text{g L}^{-1}$  (Fig 1A). Through the experiment, the percentage of phytoplankton biomass in the  $>5 \mu\text{m}$  size fraction, as measured by chl *a*, was  $33.4 \pm 4.0\%$  in the control treatment and  $38.3 \pm 6.7\%$  in the “clams” treatment. The control treatment had greater light attenuation ( $1.101 \pm 0.139 \text{ m}^{-1}$ ) than the “clams” treatment ( $0.814 \pm 0.190 \text{ m}^{-1}$ ; Fig 1B). For this experiment, chl *a* concentrations and light attenuation varied significantly by treatment (Two-way RM ANOVA,  $p < 0.001$  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 ( $0.318 \pm 0.02 \text{ cm}^2 \text{ shoot}^{-1} \text{ d}^{-1}$ ) was significantly lower than eelgrass productivity in the “clams” treatment ( $0.462 \pm 0.04 \text{ cm}^2 \text{ shoot}^{-1} \text{ d}^{-1}$ ; *t*-test,  $p < 0.05$ ; Fig 1C). The estimated turnover time of the water in the “clams” treatment was 1.1 days (Table 1).

### Experiment 2

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

### Experiment 3

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

Fig 3A). The percentage of phytoplankton biomass in the  $>5 \mu\text{m}$  size fraction, as measured by chl  $a$ , was  $38.0 \pm 1.7\%$  in the control treatment,  $35.2 \pm 3.5\%$  in the low density treatment, and  $34.0 \pm 2.5\%$  in the high density treatment. Light attenuation had similarly consistent pattern over days 1-5;  $K_d$  was lowest in the high density treatment ( $1.502 \pm 0.268 \text{ m}^{-1}$ ), intermediate in the low density treatment ( $1.586 \pm 0.229 \text{ m}^{-1}$ ), and highest in the control ( $1.726 \pm 0.224 \text{ m}^{-1}$ ; Fig 3B). Chlorophyll  $a$  concentrations varied significantly by treatment and by day (Two-way RM ANOVA,  $p < 0.001$  in both cases); light attenuation varied significantly by treatment over days 1-5 (Two-way RM ANOVA,  $p < 0.05$ ) and significantly by day (Two-way RM ANOVA,  $p < 0.001$ ). Leaf area productivity was significantly higher in both the low density ( $0.495 \pm 0.03 \text{ cm}^2 \text{ shoot}^{-1} \text{ d}^{-1}$ ) and high density ( $0.548 \pm 0.02 \text{ cm}^2 \text{ shoot}^{-1} \text{ d}^{-1}$ ) treatments than in the control treatment ( $0.371 \pm 0.03 \text{ cm}^2 \text{ shoot}^{-1} \text{ d}^{-1}$ ; Tukey test,  $p < 0.05$  and  $p < 0.01$ , respectively; Fig 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).

#### Experiment 4

The average temperature for all mesocosms in experiment 4 was  $24.6^\circ\text{C} \pm 0.2$  and the average salinity was  $21.37 \pm 0.09$ . Experiment 4 produced a clear difference between the control and oyster treatment chl  $a$  concentrations that was mirrored by changes in algal biomass and light levels. The chl  $a$  in the control ( $49.16 \pm 7.36 \mu\text{g L}^{-1}$ ) was higher than in the oyster treatment ( $31.82 \pm 4.57 \mu\text{g L}^{-1}$ ; Fig 4A) while light attenuation was also higher in the control ( $1.688 \pm 0.094 \text{ m}^{-1}$ ) than in the oyster treatment ( $1.239 \pm 0.131 \text{ m}^{-1}$ ; Fig 4B). The percentage of phytoplankton biomass in the  $>5 \mu\text{m}$  size fraction, as measured by chl  $a$ , was  $34.3 \pm 4.7\%$  in the control treatment and  $28.4 \pm 4.4\%$  in the

oyster treatment. Chlorophyll *a* concentrations varied significantly by treatment and by day (Two-way RM ANOVA,  $p < 0.05$  and  $p < 0.01$ , respectively). Light attenuation also varied between treatments and by day (Two-way RM ANOVA,  $p < 0.05$  and  $p < 0.001$ , respectively). Leaf area productivity was significantly higher in the experimental treatments with one oyster ( $0.560 \pm 0.02 \text{ cm}^2 \text{ shoot}^{-1} \text{ d}^{-1}$ ) than in the control treatments ( $0.355 \pm 0.04 \text{ cm}^2 \text{ shoot}^{-1} \text{ d}^{-1}$ ; two-tailed *t*-test,  $p < 0.01$ ; Fig 4C). The turnover time for the oyster treatment was 2.5 days (Table 1).

### Experiment 5

The average temperature for all mesocosms in experiment 5 was  $19.3^\circ\text{C} \pm 0.7$  and the average salinity was  $28.88 \pm 0.09$ . 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* ( $15.45 \pm 5.40 \mu\text{g L}^{-1}$ ) than the low density ( $40.11 \pm 8.16 \mu\text{g L}^{-1}$ ) and the control ( $40.37 \pm 7.43 \mu\text{g L}^{-1}$ ; Fig 5A). The percentage of phytoplankton biomass in the  $>5 \mu\text{m}$  size fraction, as measured by chl *a*, was  $24.8 \pm 5.2\%$  in the control treatment,  $29.2 \pm 2.5\%$  in the low density treatment, and  $14.2 \pm 5.4\%$  in the high density treatment. Chlorophyll *a* levels varied significantly by treatment and by day (Two-way RM ANOVA,  $p < 0.05$  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  $0.790 \pm 0.11 \text{ cm}^2 \text{ shoot}^{-1} \text{ d}^{-1}$  in the treatments with a high density ( $229 \text{ individ. m}^{-2}$ ) of mussels,  $0.435 \pm 0.02 \text{ cm}^2 \text{ shoot}^{-1} \text{ d}^{-1}$  in the low density ( $57 \text{ individ. m}^{-2}$ ) treatment, and  $0.399 \pm 0.08 \text{ cm}^2 \text{ shoot}^{-1} \text{ d}^{-1}$  in the control

treatment (Fig 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).

#### 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). In all cases, the bivalves filtered from the control treatment mesocosms at a significant rate (Table 1). *Crassostrea virginica*, which had the highest individual and weight-specific clearance rates ( $1.91 \pm 0.97 \text{ L hr}^{-1} \text{ g}^{-1} \text{ AFDW}$ ), produced the shortest estimates for mesocosm turnover time (0.6 – 2.5 d; Table 1), followed by *M. mercenarina* (clearance rate =  $0.41 \pm 0.24 \text{ L hr}^{-1} \text{ g}^{-1} \text{ AFDW}$ ; turnover time = 1.1 – 4.5 d), and *M. edulis* (clearance rate =  $0.29 \pm 0.29 \text{ L hr}^{-1} \text{ g}^{-1} \text{ AFDW}$ ; turnover time = 3.6 – 14.5 d). Epibiont biomass, as measured by mg AFDW of epibionts  $\text{cm}^{-2}$  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 1A,2A,3A,4A,5A). Experiments 1-4 also had significant decreases in light attenuation in the treatments with bivalves (Fig 1B,2B,3B,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 1-4 (light attenuation data was not available for experiment 5). There was also a significant inverse correlation between mesocosm turnover time (Table 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 *Crassostera 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 of  $48 \pm 9.3\%$  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 filter-feeding bivalves in estuarine ecosystems.

Some studies have suggested that suspension-feeding bivalves control eutrophication and algal blooms (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 filtration of bivalves in an experimental setting. The mechanism of facilitation is an increase in light penetration (Fig 1B,2B,3B,4B), paired with dramatic reductions in the

standing stocks of phytoplankton (Fig 1A,2A,3A,4A,5A), due to the bivalves' clearance of the water column. 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 1,2,3,4,5) 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 principle 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 ( $\leq 20 \mu\text{g L}^{-1}$ ) toward the end of each experiment in all treatments (Fig 1A,2A,3A,4A,5A), likely due to the development of high levels of algal biomass ( $> 60 \mu\text{g L}^{-1}$ ) in control tanks whose nutrient demand greatly exceeded our nutrient loading rate ( $10 \mu\text{M}$  ammonium and  $0.625 \mu\text{M}$  orthophosphate daily). Had our nutrient loading rate increased concurrently with increasing algal 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 1C,2C,3C,4C,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 2-8 g AFDW bivalve tissue  $\text{m}^{-3}$  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  $\text{m}^{-3}$ ) 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  $\text{m}^{-3}$ , 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 lower filtration 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. Our 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). Interestingly, at the longest clearance time of 14.5 days, chl *a* levels and eelgrass growth in the low-density mussel treatment was 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  $\leq 3.6$  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 ( $>20 \mu\text{g l}^{-1}$  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 dense communities of benthic suspension feeders can serve as a control on the negative effects of eutrophication. Clearly, this benefits seagrass productivity through increased light penetration (Fig 1C,2C,3C,4C,5B). There are likely many other synergistic interactions between bivalves and seagrasses which 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 benthic nutrients (Reise, 2002; Bruno et al., 2003). These effects can work, together with bivalve filtration, to reduce suspended sediment load and minimize pelagic phytoplankton abundances (Newell and Koch, 2004; Lotze et al., 2006).

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 they present several valid arguments, these 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 bivalve filtration rates 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 tenfold increase in oyster biomass 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  $\text{m}^{-2}$  and 4-14 oysters  $\text{m}^{-2}$ ) 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  $\text{m}^{-2}$  and 43-150 oysters  $\text{m}^{-2}$ , respectively; Cerrato et al., 2004; 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 a '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 would seem that even a partial recovery of shellfish populations could help combat eutrophication and have a beneficial impact on seagrass habitats in shallow, eutrophied estuaries.



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**Table 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  $\pm$  SE.

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

## Figure Legends

**Figure 1.** Temporal changes in (A) chlorophyll *a* (chl *a*  $\mu\text{g L}^{-1}$ ) and (B) extinction coefficient ( $K_d \text{ m}^{-1}$ ) for experiment 1. C) Differences in eelgrass leaf area production. Clams are *Mercenaria mercenaria*. All error bars are  $\pm$  SE.

**Figure 2.** Temporal changes in (A) chlorophyll *a* (chl *a*  $\mu\text{g L}^{-1}$ ) and (B) extinction coefficient ( $K_d \text{ m}^{-1}$ ) for experiment 2. C) Differences in eelgrass leaf area production. Clams are *Mercenaria mercenaria*. All error bars are  $\pm$  SE.

**Figure 3.** Temporal changes in (A) chlorophyll *a* (chl *a*  $\mu\text{g L}^{-1}$ ) and (B) extinction coefficient ( $K_d \text{ m}^{-1}$ ) for experiment 3. C) Differences in eelgrass leaf area production. Oysters are *Crassostrea virginica*. All error bars are  $\pm$  SE.

**Figure 4.** Temporal changes in (A) chlorophyll *a* (chl *a*  $\mu\text{g L}^{-1}$ ) and (B) extinction coefficient ( $K_d \text{ m}^{-1}$ ) for experiment 4. C) Differences in eelgrass leaf area production. Oysters are *Crassostrea virginica*. All error bars are  $\pm$  SE.

**Figure 5.** Temporal changes in (A) chlorophyll *a* (chl *a*  $\mu\text{g L}^{-1}$ ) for experiment 5. B) Differences in eelgrass leaf area production. Mussels are *Mytilus edulis*. All error bars are  $\pm$  SE.

**Figure 6.** Changes in leaf area productivity as a function of mean  $K_d$  for all tanks from experiments 1-4. Symbols are as follows:  $\blacktriangle$ , experiment 1;  $\triangle$ , experiment 2;  $\bullet$ , experiment 3;  $\circ$ , experiment 4.

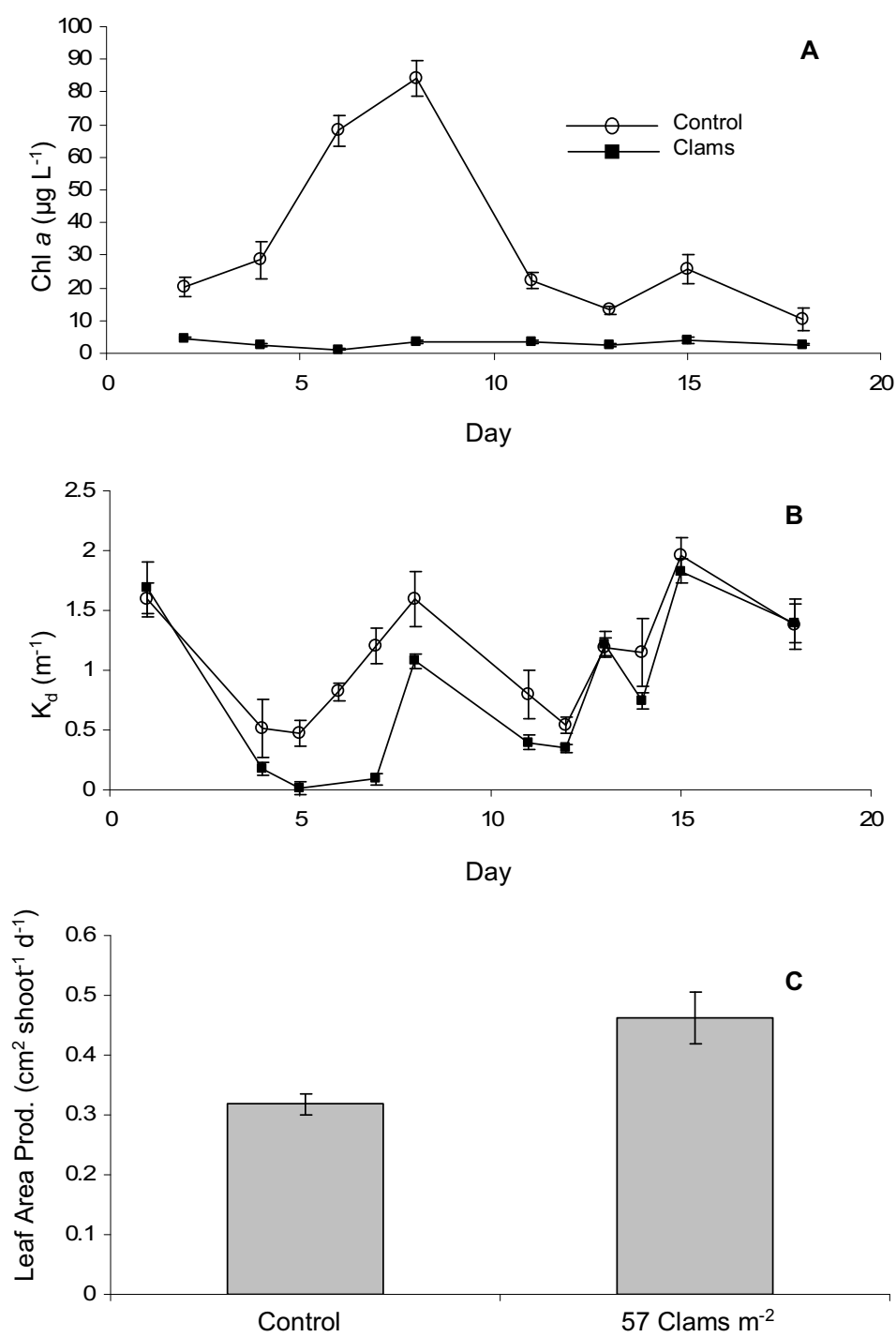
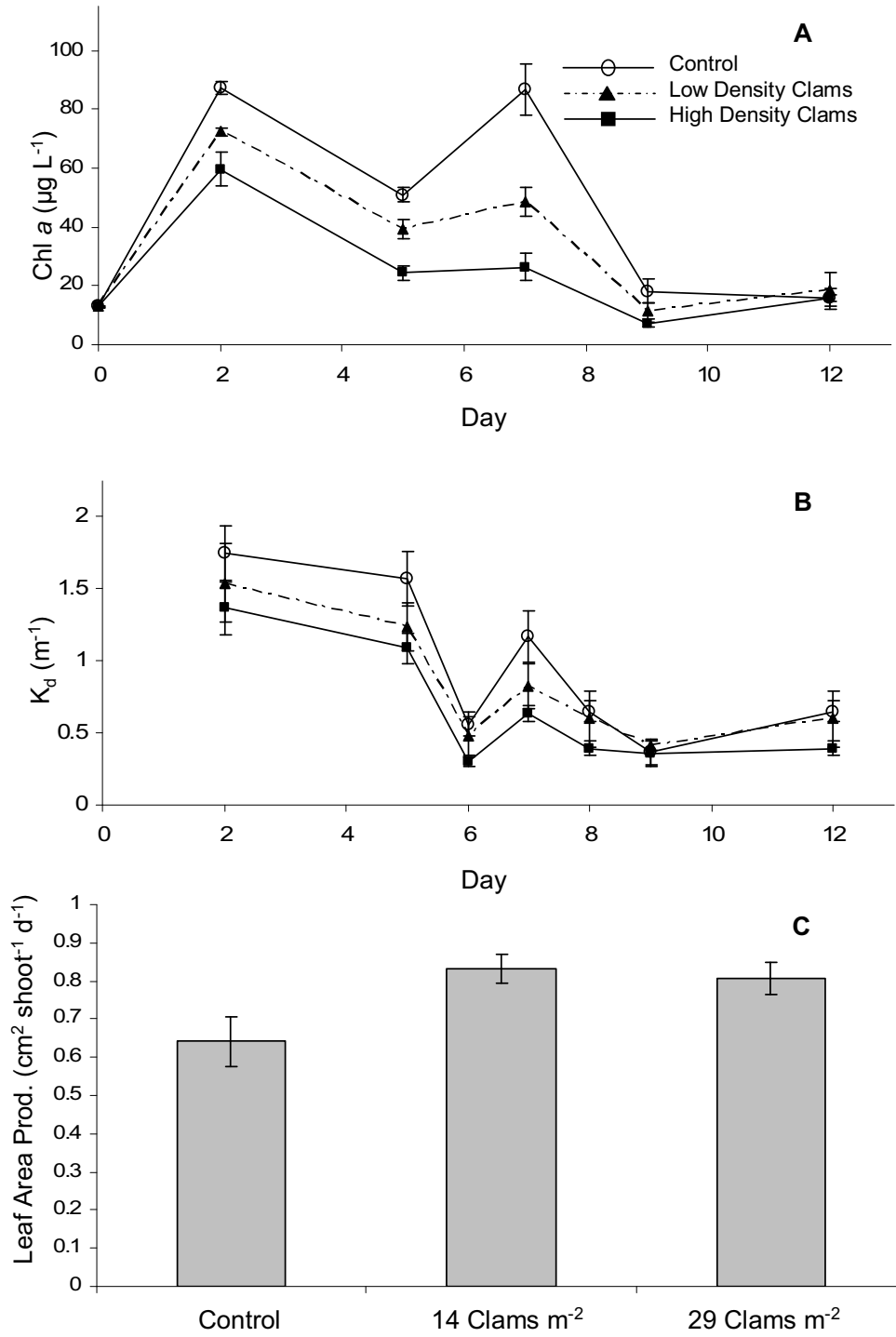
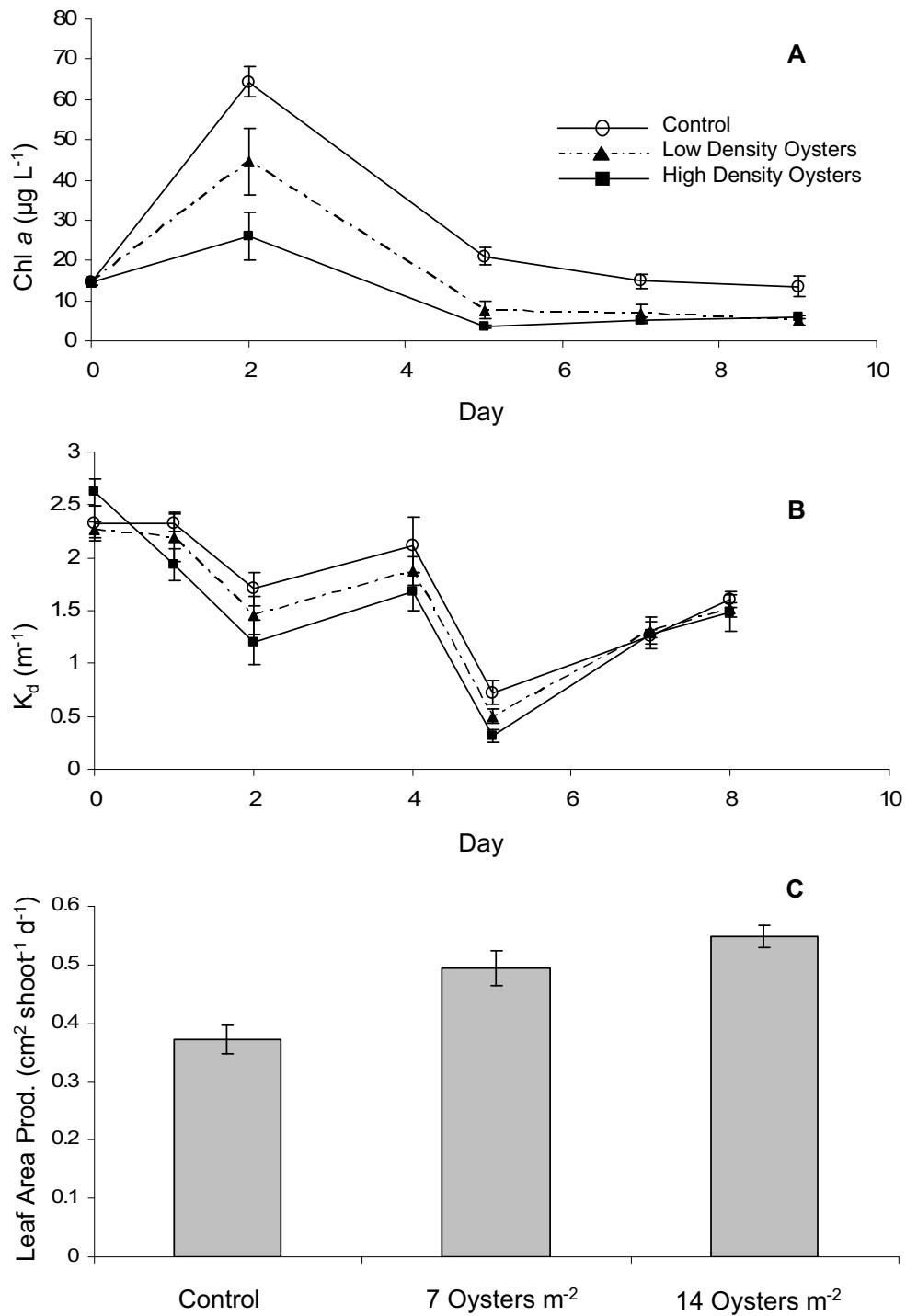


Figure 1



**Figure 2**



**Figure 3**

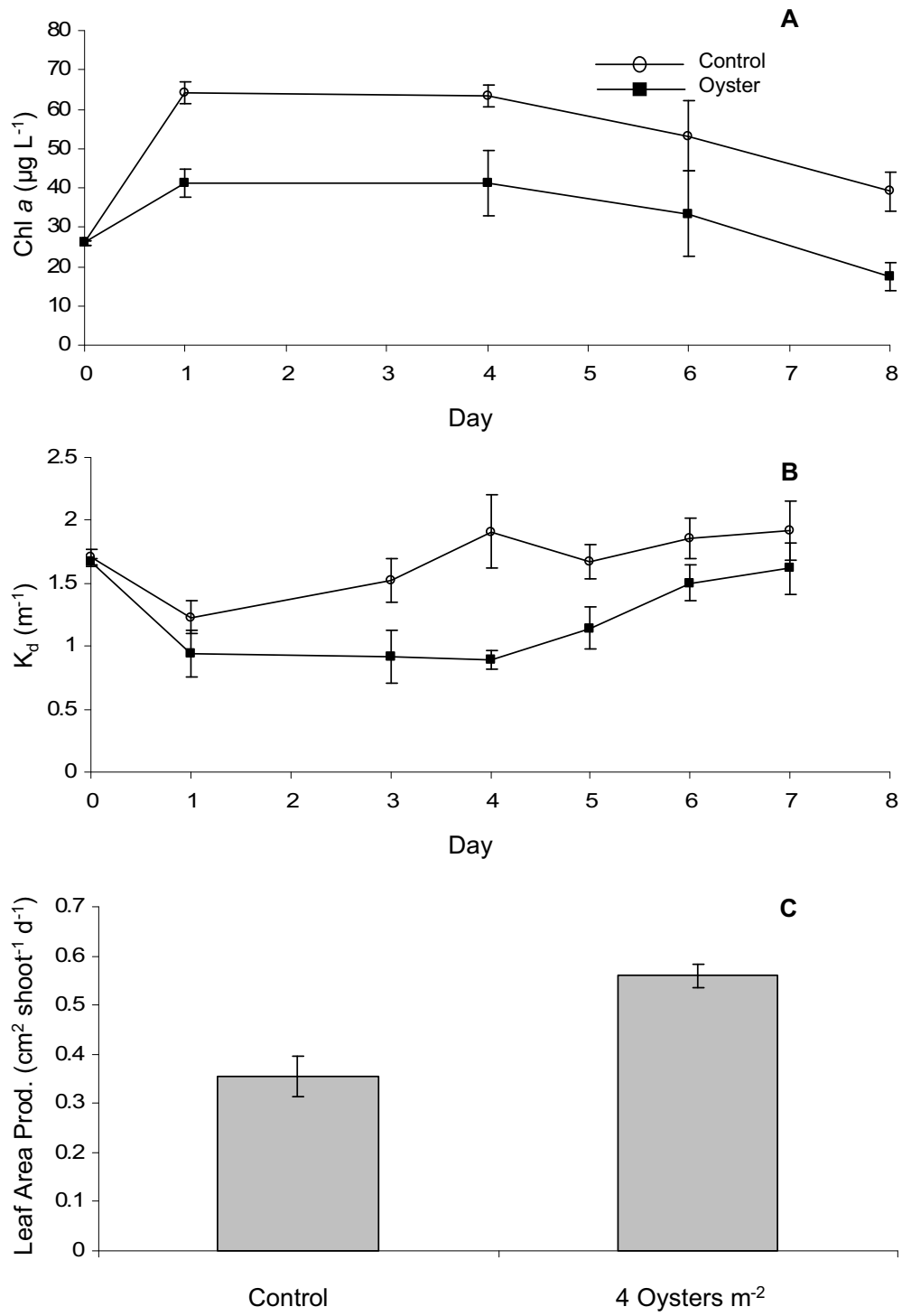
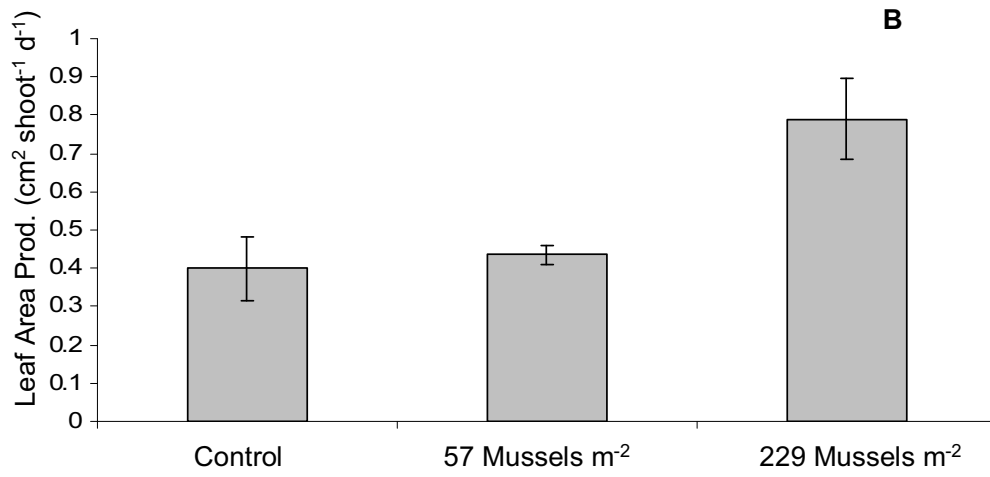
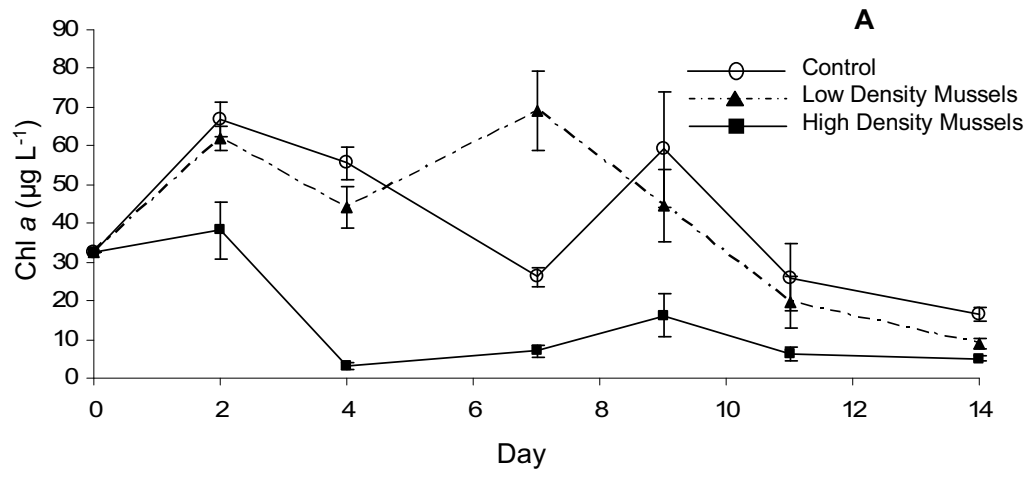
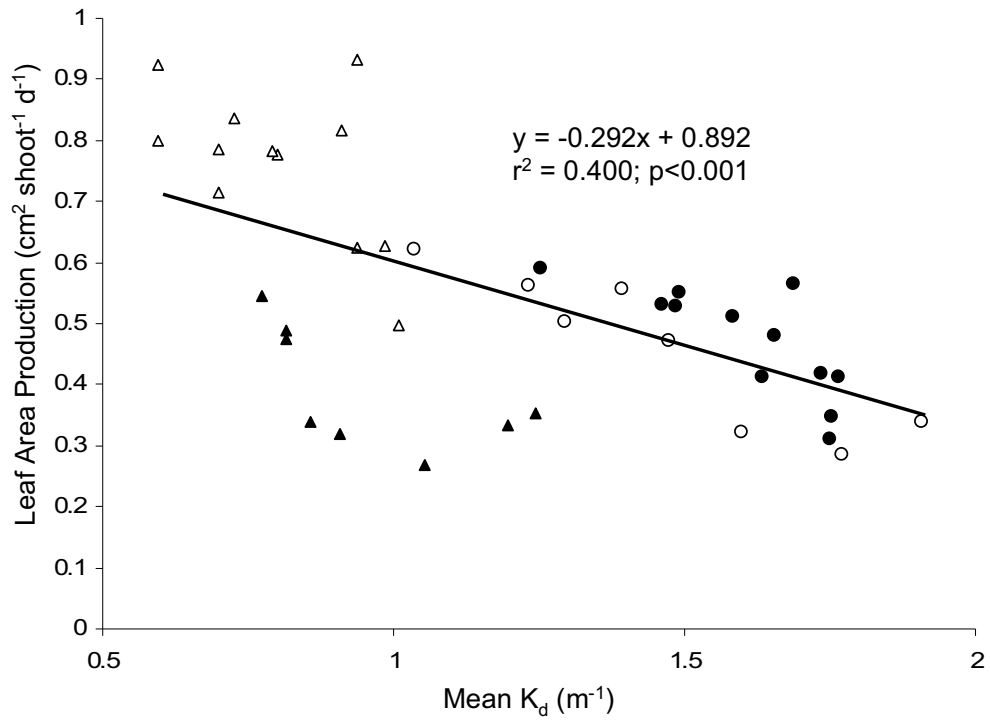


Figure 4



**Figure 5**



**Figure 6**

