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# The Growth of Estuarine Resources (*Zostera marina*, *Mercenaria mercenaria*, *Crassostrea virginica*, *Argopecten irradians*, *Cyprinodon variegatus*) in Response to Nutrient Loading and Enhanced Suspension Feeding by Adult Shellfish

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

**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

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## Introduction

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

estuarine management plans are typically focused on combating these harmful processes and restoring living resources (Cloern 2001; Newell 2004; Lotze et al. 2006).

Changes in nutrient loading to estuaries can indirectly influence the growth of marine resource species. High rates of nutrient loading have been associated with increases in pelagic productivity, decreased water clarity, hypoxia, and declines in seagrass growth and abundances (Short et al. 1995; Diaz and Rosenberg 2008; Wall et al. 2008). In response, estuarine management efforts often focus primarily on reducing anthropogenic nutrient loading in an effort to curb the negative effects of eutrophication (Cloern 2001; de Jonge et al. 2002). However, some level of nutrient loading must be necessary to sustain primary and secondary production (Nixon and Buckley 2002). Higher levels of inorganic nutrients can enhance primary production rates and can favor larger phytoplankton cells (Malone 1980; Raven and Kubler 2002), such as diatoms and prymnesiophytes, which are generally considered a good source of nutrition for bivalves (Beukema and Cadee 1991; Wikfors et al. 1992; Weiss et al. 2007). Studies in several estuaries have shown that blue mussels (*Mytilus edulis*), northern quahogs (*Mercenaria mercenaria*), and softshell clams (*Mya arenaria*) can respond positively to increased nitrogen loading and high chlorophyll *a* levels in their habitats (Vanstralen and Dijkema 1994; Weiss et al. 2002, 2007; Carmichael et al. 2004). Weiss et al. (2002) and Carmichael et al. (2004) found that shell growth, soft tissue growth, and survival of *M. mercenaria* and *M. arenaria* increased with nitrogen loading rates along a naturally occurring gradient in Waquoit Bay, MA, USA. They attribute these changes to increased quantity and quality of food particles due to nitrogen enrichment (Carmichael and Valiela 2005), although a similar response has not been found for bay scallops (*Argopecten irradians*, Shriver et al. 2002). While nutrient overloading in estuaries has a well-known set of negative consequences (Valiela et al. 1992; Nixon 1995; Kemp et al. 2005), the stimulation of secondary production in bivalves could be an overlooked positive effect of nutrient loading (Nixon and Buckley 2002; Carmichael et al. 2004; Carmichael and Valiela 2005), especially in shallow ecosystems with well-mixed water columns that rarely experience hypoxia.

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

As bivalve populations have declined through overfishing, habitat loss, and disease, these ecosystem services have been lost and there are currently few estuaries with natural densities of bivalves sufficient to exert ecosystem-wide effects (Newell 1988; Lotze et al. 2006). In the absence of dense natural bivalve populations, bivalve aquaculture may achieve similar levels of ecosystem-wide impact (Souchu et al. 2001; Dumbauld et al. 2009). Some managers have considered aquaculture as a means to restore ecosystem functions previously provided by natural populations (Newell 2004; Ruesink et al. 2005), to combat eutrophication (Gifford et al. 2004; Cerco and Noel 2007), or to ease harvest pressures on wild populations (Dolmer and Frandsen 2002). Aquaculture is on the rise worldwide, and bivalve aquaculture may avoid some of the pitfalls of finfish aquaculture (Naylor et al. 2000) while controlling phytoplankton blooms and affecting carbon and nutrient cycling in ways that are comparable to natural shellfish populations (Smaal et al. 2001; Newell 2004; Huang et al. 2008).

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

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

nutrient loading and adult bivalve filtration can strongly influence the growth of multiple estuarine resources.

## Methods

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

Mesocosms were filled with eastern Shinnecock Bay water during high tide. Water from this region is fairly mesotrophic with mean total N (dissolved+particulate) concentrations of 0.2±0.1 mg N L$^{-1}$ or 16±8 μM N measured from 2000 to 2005 ($n$=50 measurements; SCDHS 2000–2005). For each experiment, we established a low nutrient loading rate for half of the experimental tanks (DIN loading of 0.065–0.255 mmol N m$^{-2}$ day$^{-1}$) using a 1–2% day$^{-1}$ exchange with Shinnecock Bay water. The other half of the tanks received a high nutrient loading rate (5.49–10.70 mmol N m$^{-2}$ day$^{-1}$) that reflected ambient exchange plus nutrient additions of ammonium and the Redfieldian equivalent (16:1) of orthophosphate. These nutrient loading rates were within the range found in more eutrophic Northeast US estuaries such as the Childs River, MA and Moriches Bay, NY (Taylor et al. 1999). Nutrient stocks were filter-sterilized (0.2 μm) and stored frozen. Experiments were run in semi-continuous mode, with 1–2% of the water volume being replaced daily mimicking the natural slow tidal exchange which occurs in the back-bay regions of the Peconic Estuary and Great South Bay, Long Island, NY, USA, resulting in residence times on the order of 2 to 3 months (Hardy 1976; Wilson et al. 1991). For each experiment, half of the experimental tanks contained adult suspension feeders (northern quahog or eastern oyster) and half of the tanks contained no adult suspension feeders. Stocking densities of adult bivalves in the experimental tanks (21–43 individuals m$^{-2}$) were comparable to historic densities of shellfish in Long Island South Shore Estuaries (Kassner 1993) but higher than current densities (0–5 individuals m$^{-2}$; Weiss et al. 2007). Shellfish densities in the experiment treatments were also orders of magnitude lower than stocking densities in modern aquaculture operations (Rheault and Rice 1996). Adult clams measured 56.70±1.18 mm shell length and weighed 1.64±0.11 g ash-free dry weight (AFDW). Adult oysters measured 59.17±0.79 mm shell height and weighed 0.66±0.05 g AFDW. Adult shellfish were locally caught and obtained from seafood markets. The feeding activity of adult shellfish was estimated with a clearance rate method (Riisgard 2001) using water (>15 μg L$^{-1}$ chlorophyll $a$) from the experimental tanks. Clearance rates were calculated according to the equation:

$$\text{clearance rate} = V/t \times [\ln(\text{chla}_0/\text{chla}_t)]$$

where $V$ is the volume of the container, $t$ is the time, and chl $a_0$ and chl $a_t$ are the chl $a$ levels at the initial reading and at time $t$, respectively. This measurement was performed once per species. A "community" clearance rate was estimated from these data using the average individual clearance rate and the number of individuals in the tank. An estimated clearance rate for the entire tank volume to be processed by the adult shellfish was calculated for each tank by dividing

**Table 1** Stocking densities of response organisms and summary of experimental conditions

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

Treatments were "+ bivalves" or "− bivalves" for presence or absence of adult bivalves and "high N" or "low N" for high or low nutrient loading. Nutrients were added as 16:1 inorganic N/P. A total of 16 tanks were used for each 2×2 factorial experiment with $n$=4 tanks per treatment combination

this community clearance rate by the tank volume. A summary of experimental conditions for all three experiments is presented in Table 1.

Experiments were conducted for ~2 weeks, and shellfish growth was assessed via the changes in AFDW of tissue or by changes in shell lengths between initial and final individuals within each mesocosm (Weiss et al. 2007). The length of juvenile clams was measured by shell length (anterior-posterior; Kraueter and Castagna 2001), and the size of juvenile oysters and scallops was measured by shell height (hinge-ventral margin; Rheault and Rice 1996). Bivalve tissue was dried at 70°C for at least 24 h and then ashed at 450°C for an additional 4 h (Gabbott and Walker 1971; Bass et al. 1990). One hundred bivalves of each species were selected from the initial set to provide a mean initial tissue AFDW. When fewer than 100 individuals were available for a mean initial AFDW, initial AFDW's were hind-casted based on initial lengths using length-weight regressions from 100+ individuals of the same species and size class. Juvenile fish growth was measured by total length only. Mean growth rates for all species based on length or weight were calculated by the change in length or tissue AFDW divided by the number of days between initial and final measurements. The quality and quantity of phytoplankton food particles available for bivalves was assessed by measuring whole and size-fractionated chlorophyll *a* (>5 μm) using polycarbonate filters and standard fluorometric techniques (Parsons et al. 1984). Chlorophyll in the <5-μm-size fraction was calculated as the difference between whole and >5 μm chl *a*. Additional whole water samples were collected on pre-combusted glass fiber filters for the analysis of particulate organic carbon (POC) and nitrogen (PON) on a CE Instruments Flash 1112 elemental analyzer (Sharp 1974).

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

Bottom light levels in each mesocosm were measured every 15 min by HOBO© Pendant-style data loggers with light sensors. A data logger was placed in each experimental tank near the bottom at a depth of approximately 1 m, a height just above eelgrass and shellfish cages preventing the obstruction of incoming light. A mean daily light level for each experimental tank was calculated by averaging values between 10:00 and 14:00 h, when the sun was most directly overhead. Since the HOBO© data loggers measure

visible light levels in lux instead of photosynthetically active radiation (PAR) in micromoles per square meter per second, we compared measurement of light with the HOBO© loggers to those obtained with a LiCor© LI-192 underwater quantum sensor of PAR. There was a highly significant linear relationship between visible light in lux as measured by the HOBO© data logger and PAR as measured by the LiCor© sensor over depths of 0.5–2.0 m (visible light in LUX=41.407×PAR−408.67, $r^2$=0.98, $p<$ 0.001). Based on this finding, we believe that experimental light readings from HOBO© data loggers within our mesocosms were representative of the general trends in PAR.

Seawater dilution experiments were conducted to quantify the rates of microzooplankton grazing of micro-algal biomass within the mesocosm tanks (Landry et al. 1995). During each experiment, 5 L of water from each replicate mesocosm within a treatment were pooled into a 20-L carboy for that treatment. Triplicate samples of 100%, 70%, 40%, and 15% experimental dilutions of whole seawater with filtered seawater (0.2 μm) from each carboy were established in 1 L polycarbonate bottles. To ensure nutrient-replete growth during these experiments, nitrate (20 μM) and orthophosphate (1.25 μM) were added to all of the bottles. A set of triplicate controls of whole seawater without nutrients were also established for each grazing experiments (Landry et al. 1995). Micro-algal growth rates ($\mu$) within experimental bottles were quantified using the formula: $\mu=[\ln(B_t/B_o)]/t$, where $\mu$ is the net growth rate, $B_t$ is the amount of biomass (chl *a*) present at the end of the experiments, $B_o$ represents the amount of biomass at the beginning of experiments, and $t$ is the duration of the experiment in days. The slope of first-order linear regressions of dilution of seawater ($x$-axis) and the net growth rates ($y$-axis) were used to establish grazing mortality rates (Landry et al. 1995).

### Statistical Analysis

Differences in the growth of each animal species and eelgrass were assessed by means of two-way analysis of variance (ANOVA), with nutrient loading level and presence/absence of adult bivalves as the two treatment factors using the software SigmaStat 3.5. When a significant effect on the response variables was detected, multiple comparison tests (Tukey's studentized range) were used to test for significant differences between levels within the treatment. Mortality of juvenile bivalves was analyzed using a $G$ test of independence (Sokal and Rohlf 1995). Chlorophyll *a* and light level trends were analyzed with three-way repeated-measures ANOVAs (ANOVARs) where level of nutrient loading and presence/absence of adult bivalves were the between-subjects effects and day was the repeated within-subjects effect. Each mesocosm tank was considered a subject for this analysis, which was conducted using the software Systat 13. In the case of significant interaction effects in the three-way ANOVAR, the variance was decomposed by means of two-way ANOVARs (day×bivalves and day×nutrients). Data that did not meet ANOVA assumptions were $\log(x+1)$-transformed to achieve normality. All statistical results were considered against a significance level of $\alpha$=0.05.

## Results

### Experiment 1

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

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

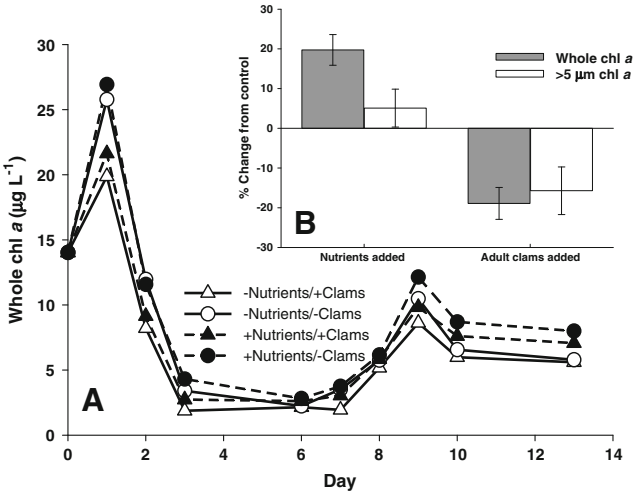


**Fig. 1** Chlorophyll *a* dynamics in experiment 1. Time series data points (**a**) represent the mean ($n$=4) for each of the treatment combinations. *Error bars* are not presented for the sake of visual clarity. The mean relative standard deviation of measurements for whole chl *a* was 19.8% during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

and decreased by adult clam filtration ($p$<0.01 in both cases, three-way ANOVAR, data not shown). Levels of chl *a* <5 µm also varied significantly by day ($p$<0.001) and day×bivalve treatment interaction ($p$<0.05). When this variance was decomposed with two-way ANOVARs, the addition of bivalves produced a significant drop in <5 µm chl *a* only within the high nutrient loading treatment ($p$< 0.01), while nutrient loading produced a significant increase in <5 µm chl *a* only within the bivalve-added treatment ($p$< 0.05). The molar ratio of POC/PON was significantly higher under low nutrient loading (9.70±0.61; Table 2) and the absence of adult clams (10.51±0.45) compared to high nutrient loading (9.22±0.26) and the presence of adult clams (8.83±0.24; $p$<0.05 for nutrient treatment, $p$<0.01 for clam filtration treatment, two-way ANOVA).

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

## Experiment 2

Experiment 2 ran from July 12 to July 27, 2007. The average temperature in the experimental tanks was 24.27±0.16°C, the average salinity was 28.02±0.16, and the average dissolved oxygen was 5.83±0.12 mg L$^{-1}$. The "low nutrient loading" treatment received an average of 0.255 mmol N m$^{-2}$ day$^{-1}$ and 0.072 mmol P m$^{-2}$ day$^{-1}$ through a ~2% day$^{-1}$ exchange with Shinnecock Bay water. The "high nutrient loading" treatment received ambient exchange plus a daily experimental nutrient addition for a total of 5.75 mmol N m$^{-2}$ day$^{-1}$ and 0.416 mmol P m$^{-2}$ day$^{-1}$. The densities of adult suspension feeders were 21 or 0 eastern oysters m$^{-2}$ (6 or 0 individual tank$^{-1}$). The estimated turnover from bivalve filtration for the experimental tanks with oysters was 67% day$^{-1}$. All tanks in this experiment were stocked with juvenile clams, juvenile oysters, and eelgrass (Table 1).

Although both treatments produced consistent directional effects on the levels of whole chlorophyll *a* (Fig. 3a, b), whole chl *a* was not significantly altered by the treatments ($p$>0.05, three-way ANOVAR). Whole chl *a* within each mesocosm tank varied significantly by day (Fig. 3a, $p$<0.01, three-way ANOVAR), and there was also a significant day×bivalve treatment interaction ($p$<0.05). When this variance was decomposed using two-way ANOVARs, this interaction effect was removed and day was the only significant source of variation in whole chl *a*. Similarly, chl *a* in the >5-µm-size class displayed consistent directional effects according to the treatments (Fig. 3b), but the only significant variation was by day ($p$<0.001, three-way ANOVAR). In contrast, chl *a* in the <5-µm-size fraction was significantly enhanced by nutrient loading ($p$<0.01), significantly reduced by the addition of bivalves ($p$<0.01), and displayed a nutrient treatment×bivalve treatment interaction ($p$<0.01, three-way ANOVAR, data not shown). When this variance was decomposed using two-way ANOVARs, the decrease of <5 µm chl *a* by bivalves occurred only within the high nutrient loading treatment ($p$<0.05) and the increase in <5 µm chl *a* by nutrient loading occurred only within the no bivalves treatment ($p$<0.01).

Juvenile clam growth was significantly higher in the high nutrient loading treatment (0.039±0.003 mm day$^{-1}$ and 0.058±0.005 mg AFDW day$^{-1}$) compared to the low nutrient loading treatment (0.030±0.003 mm day$^{-1}$ and 0.033±0.005 mg AFDW day$^{-1}$) when measured by shell length (data not shown; $p$<0.05, two-way ANOVA) or by dry tissue weight (Fig. 4a; $p$<0.001, two-way ANOVA). Juvenile clam growth was not affected by the adult oyster filtration treatment. In contrast, the juvenile oysters

**Table 2** Levels of chlorophyll *a*, POC, PON, and microzooplankton grazing rates

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

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

responded to the adult bivalve treatment; juvenile oyster growth was significantly decreased in the presence of adult oyster filtration (Fig. 4b; $p<0.01$; two-way ANOVA) but was not affected by the nutrient loading treatments. Juvenile oyster growth was 0.131±0.022 mg AFDW $day^{-1}$ in the absence of adult oysters and was 0.033±0.017 mg AFDW $day^{-1}$ in the presence of adult oysters. Light levels and eelgrass growth were not significantly affected by the experimental treatments (two-way ANOVA), although epiphyte biomass on eelgrass leaves was significantly higher under high nutrient loading (0.164±0.013 mg AFDW $cm^{-2}$) and adult oyster filtration (0.179±0.011 mg AFDW $cm^{-2}$) compared to low nutrient loading (0.140±0.012 mg AFDW $cm^{-2}$) and no adult oyster filtration (0.126±0.006 mg AFDW $cm^{-2}$; $p<0.05$ by nutrient treatment, $p<0.001$ by oyster treatment, two-way ANOVA). Microzooplankton grazing rates were not significantly different between treatments and ranged from 2.31 to 2.39 $day^{-1}$ (Table 2). POC/PON data were not available for this experiment.

## Experiment 3

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

In this experiment, the presence of adult northern quahogs (43 individuals $m^{-2}$) produced significant decreases in total chlorophyll *a* compared to the absence of adult clams over the course of a 15-day experiment ($p<0.001$, three-way ANOVAR, Fig. 5a, b), and whole chl *a* also varied significantly over time within each mesocosm tank ($p<0.001$). The significant decrease of whole chl *a* by the bivalve-added treatment was consistent across both levels of nutrient loading and over time during the experiment (Fig. 5a, b). Even though the high nutrient loading rate (5.49 mmol N $m^{-2}$ $day^{-1}$) produced a consistent directional effect on whole chl *a* compared to the low nutrient loading rate (0.134 mmol N $m^{-2}$ $day^{-1}$, Fig. 5b), this effect was not statistically significant ($p>0.05$, three-way ANOVAR). Trends in whole chl *a* were paralleled by the >5-μm-size fraction of chl *a*, which was decreased by the addition of adult bivalves ($p<0.001$, three-way ANOVAR, Fig. 5b) and also varied within each mesocosm tank by day ($p<0.05$). There was also a significant day×bivalve treatment interactive effect on levels on >5 μm chl *a* ($p<0.05$, three-way ANOVAR). When this variance was decomposed using two-way ANOVARs, the interactive effect was removed. Although >5 μm chl *a* was consistently increased by nutrient loading (Fig. 5b), this effect was not statistically significant ($p>0.05$). In contrast to experiments 1 and 2, chl

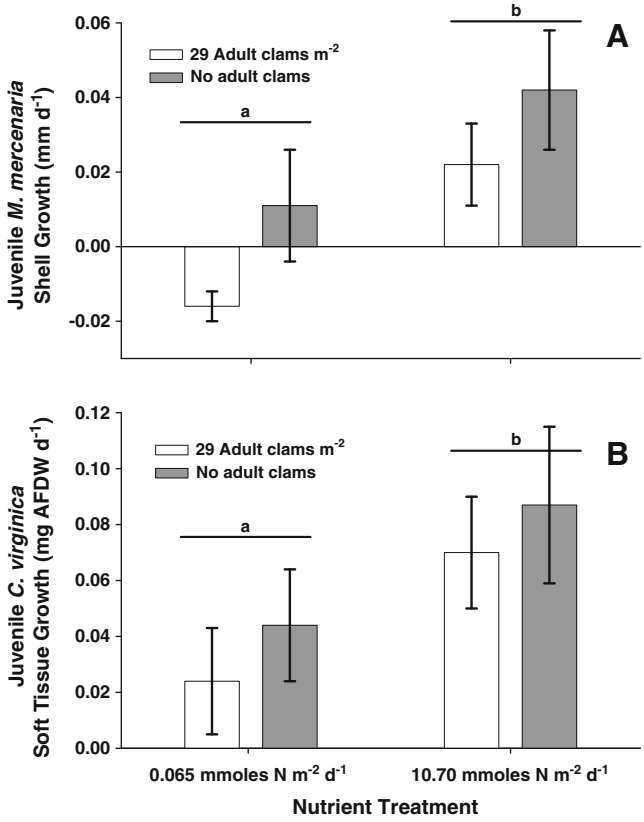


**Fig. 2** Growth responses from experiment 1 for **a** juvenile *M. mercenaria* and **b** juvenile *C. virginica*. *Bars* are means ± SE. Slightly negative shell growth for juvenile *M. mercenaria* is within measurement errors of zero. *Letters above bars* indicate significant difference. Nutrients were added as 16:1 inorganic N/P

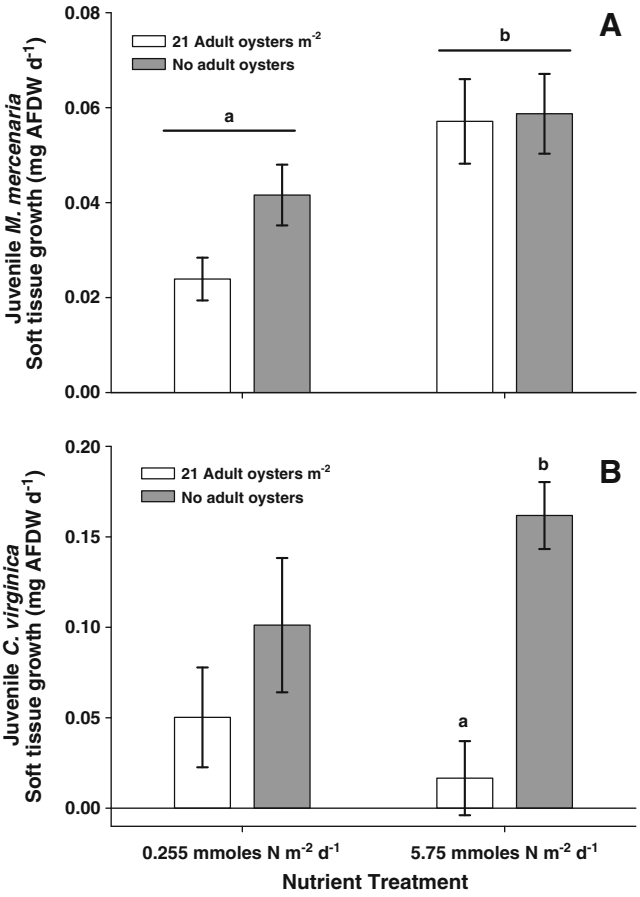


**Fig. 4** Growth responses from experiment 2 for **a** juvenile *M. mercenaria* and **b** juvenile *C. virginica*. *Bars* are means ± SE. *Letters above bars* indicate significant difference. Nutrients were added as 16:1 inorganic N/P

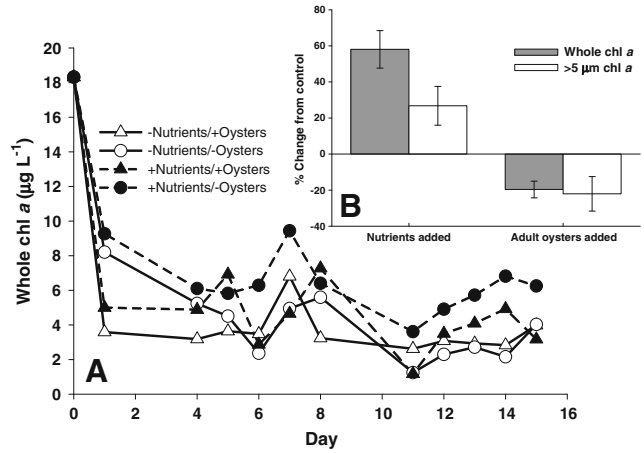


**Fig. 3** Chlorophyll *a* dynamics in experiment 2. Time series data points (**a**) represent the mean ($n$=4) for each of the treatment combinations. *Error bars* are not presented for the sake of visual clarity. The mean relative standard deviation of measurements for whole chl *a* was 46.0% during the experiment. *Inset* (**b**) shows mean (± SE) daily percent increase or decrease from nutrient addition over both bivalve treatments and from bivalve addition over both nutrient treatments. See text for magnitudes of nutrient loading and densities of adult bivalves

*a* in the <5-µm-size fraction varied only by day ($p$<0.001, three-way ANOVAR, data not shown) and was not affected by either treatment ($p$>0.05).

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

Light penetration to the bottom of the mesocosms was higher in the adult bivalve treatment (7,430±437 lux, $p$<0.05, three-way ANOVAR) compared to the absence of adult

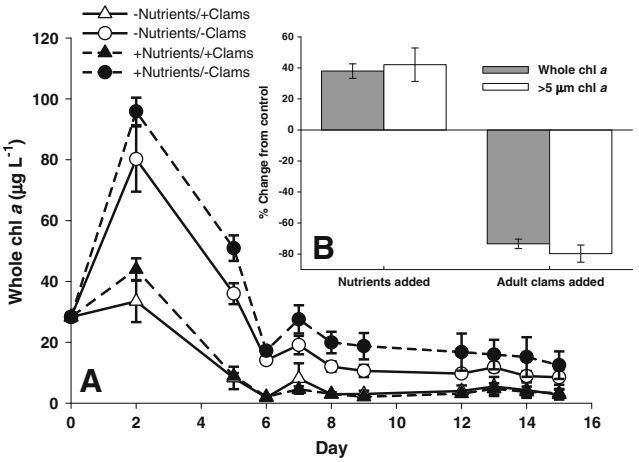


**Fig. 5** Chlorophyll *a* dynamics in experiment 3. Time series data points (**a**) represent the mean (± SE, $n$=4) for each of the treatment combinations. *Inset* (**b**) shows mean (± SE) daily percent increase or decrease from nutrient addition over both bivalve treatments and from bivalve addition over both nutrient treatments. See text for magnitudes of nutrient loading and densities of adult bivalves

bivalves (4,620±182 lux), was not significantly affected by the nutrient treatments ($p$>0.05), and varied significantly by day within each mesocosm tank ($p$<0.001, three-way ANOVAR, data not shown). Eelgrass leaf area productivity was significantly enhanced by the presence of adult clams (0.549±0.030 cm$^2$ shoot$^{-1}$ day$^{-1}$) compared to the treatments with no adult clams (0.421±0.024 cm$^2$ shoot$^{-1}$ day$^{-1}$; Fig. 6a; $p$<0.001, two-way ANOVA). Eelgrass was also affected by the nutrient loading treatment; leaf area productivity was significantly decreased by the high nutrient loading treatment (0.431±0.024 cm$^2$ shoot$^{-1}$ day$^{-1}$) compared to the low nutrient loading treatment (0.519± 0.029 cm$^2$ shoot$^{-1}$ day$^{-1}$; Fig. 6a; $p$<0.01, two-way ANOVA). There was a significant interaction ($p$<0.01) of the treatment effects on eelgrass: The decline in leaf area productivity from the low to the high nutrient loading treatments occurred entirely within the presence of adult clams, while eelgrass growth was not significantly affected by nutrient loading in the absence of adult clams. When eelgrass productivity was measured by dry weight instead of leaf area, there was a significant increase in mass productivity in the presence of adult clams (1.87± 0.17 mg shoot$^{-1}$ day$^{-1}$; Fig. 6a) compared to the absence of adult clams (1.27±0.23 mg shoot$^{-1}$ day$^{-1}$ mass productivity, $p$<0.05, two-way ANOVA). There were no detectable effects of nutrient loading on eelgrass mass productivity. Epiphyte growth on the eelgrass blades was also significantly denser in the presence of adult clams (0.186±0.017 mg AFDW cm$^{-2}$) compared to the absence of adult clams (0.146±0.009 mg AFDW cm$^{-2}$; $p$<0.01, two-way ANOVA).

Juvenile clams were not significantly affected by any of the treatment factors in the third experiment. Juvenile

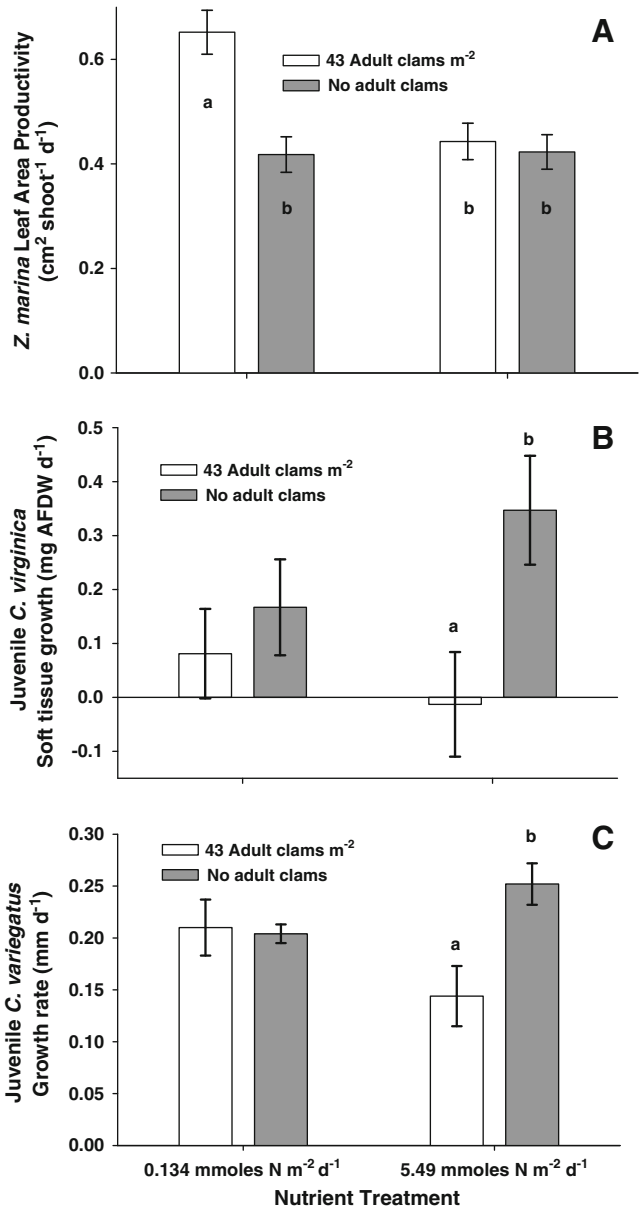


**Fig. 6** Growth responses from experiment 3 for **a** *Z. marina*, **b** juvenile *C. virginica*, and **c** juvenile *C. variegatus*. *Bars* are means± SE. *Letters above bars* indicate significant difference. Nutrients were added as 16:1 inorganic N/P

oysters grew significantly faster in the absence of adult clams (0.257±0.064 mg AFDW day$^{-1}$) compared to when adult clams were present (0.034±0.067 mg AFDW day$^{-1}$; Fig. 6b; $p$<0.05, two-way ANOVA). Juvenile sheepshead minnows also grew significantly faster in the absence of adult clams (0.228±0.017 mm day$^{-1}$, $p$<0.05, two-way ANOVA) compared to treatments with adult clams (0.177± 0.022 mm day$^{-1}$; Fig. 6c). The fish growth rates showed an interesting interaction: The presence/absence of adult clams made more of a difference to the juvenile sheepshead minnows within the high nutrient loading treatment than within the low nutrient treatment (Fig. 6c; $p$<0.05, Tukey

test). There were no differences in juvenile scallop growth rates, but juvenile scallop mortality was significantly higher in the presence of adult clams than in the absence of adult clams (96% with adult clams, 71% without adult clams; $p < 0.001$; $G$ test of independence, data not shown). Juvenile fish and shellfish were not significantly affected by the nutrient loading treatments in this experiment (two-way ANOVA).

## Discussion

Over the course of three mesocosm experiments, both enhanced nutrient loading and filtration by adult bivalves significantly affected the growth of juvenile shellfish, juvenile fish, and eelgrass, as well as phytoplankton and light levels in mesocosms. The growth of juvenile eastern oysters was the most responsive to the treatment factors; oyster growth was enhanced by high nutrient loading in experiment 1 and decreased by the presence of adult bivalves in experiments 2 and 3. Juvenile northern quahog growth was enhanced by nutrient loading in experiments 1 and 2. The growth of juvenile sheepshead minnows was decreased by the presence of adult bivalves in experiment 3, while the growth of eelgrass shoots was simultaneously increased by adult bivalves and decreased by high nutrient loading in experiment 3. These findings support a conceptual model (Fig. 7), whereby increased nutrient loading acts to increase algal biomass, while increased densities of adult suspension-feeding bivalves decrease phytoplankton abundance. In turn, these changes in phytoplankton biomass affect the growth responses of juvenile bivalves and planktivorous fish through changes in available food particles and affect the growth response of eelgrass through changes in light penetration (Fig. 7). Collectively, these results provide new insight into the manner in which nutrients, and filter feeding bivalves may structure estuarine food webs.

Adult bivalve filtration and nutrient loading were expected to affect eelgrass growth through changes in the density of phytoplankton, which in turn affects the benthic light regime (Newell and Koch 2004; Wall et al. 2008; Fig. 7). Experiment 3 produced results consistent with this hypothesis, where a high density of adult clams decreased chlorophyll *a* levels (Fig. 5a, b) and increased light penetration leading to an increase in eelgrass productivity (Fig. 6a). The high nutrient loading treatment in experiment 3 decreased eelgrass growth relative to the low nutrient loading treatment, and the effects of nutrient loading on eelgrass were most evident when adult clams were present (Fig. 6a). Adult clams and adult oysters decreased chlorophyll *a* in experiments 1 and 2 similarly to experiment 3 (Figs. 1a, b and 3a, b), but these changes in chl *a* did not produce significant effects on light or eelgrass. The density of epiphytes on eelgrass blades was increased by adult bivalve filtration in experiments 2 and 3 and by nutrient loading in experiment 2. Although thick epiphyte growth has been found to have a negative impact on seagrass in some cases (Duarte 1995), the densities of epiphytes measured in our experiments (0.13–0.19 mg AFDW $cm^{-2}$) were likely too low to significantly block light at the blade surface (Brush and Nixon 2002). On a time-scale longer than these experiments (weeks–months), nutrient enrichment (or lack thereof) to the sediments will also affect seagrass growth and reproduction (Dennison et al. 1987; Peterson and Heck 2001; Carroll et al. 2008).

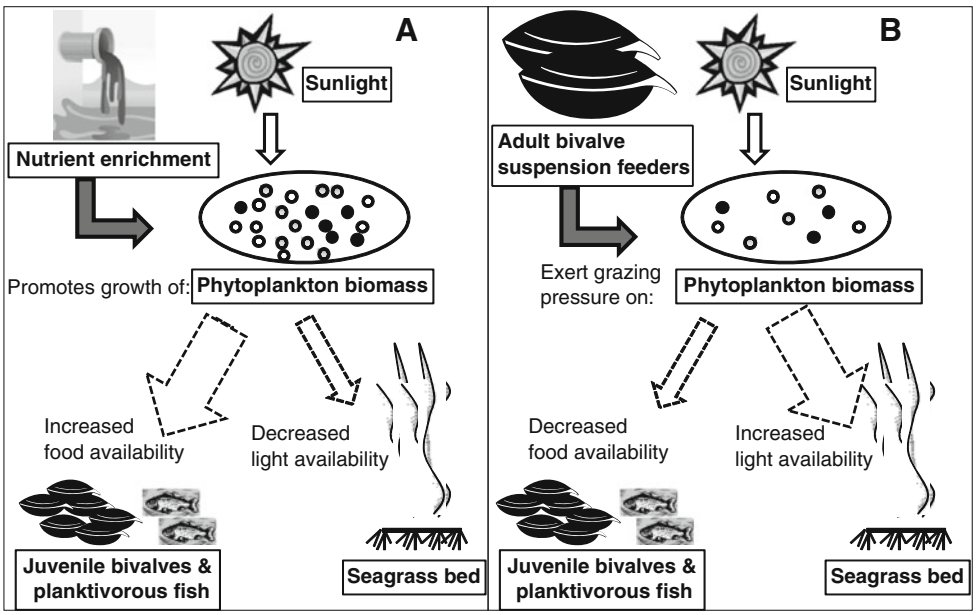


**Fig. 7** Conceptual model of the effects of nutrient loading (**a**) and adult bivalve filtration (**b**) in mesocosm experiments. *Solid gray arrows* represent treatment factors that are expected to act on phytoplankton biomass, and *dashed arrows* represent hypothesized responses of juvenile bivalves, juvenile planktivorous fish, and seagrass shoots to changes in phytoplankton biomass

Growth rates of juvenile planktivorous fish and juvenile bivalves may be decreased by filtration pressure from adult bivalves, which clear food particles from the water column (Rheault and Rice 1996; Zhou et al. 2006), or may be increased by high nutrient loading, which may increase the quantity and quality of suspended food particles (Carmichael et al. 2004; Carmichael and Valiela 2005; Fig. 7). All three experiments had some results consistent with this hypothesis: Juvenile clam growth was increased by high nutrient loading in experiments 1 and 2 (Figs. 2a and 4a), juvenile oyster growth was also increased by high nutrient loading in experiment 1 (Fig. 2b), while juvenile oyster growth was decreased by adult bivalve filtration in experiments 2 and 3 (Figs. 4b and 6b), and juvenile fish growth was also decreased by adult bivalve filtration in experiment 3 (Fig. 6c). Although there were no significant growth responses for scallops, juvenile scallop mortality was increased by adult bivalve filtration in experiment 3.

The results of these experiments demonstrate the strong reliance of juvenile shellfish and planktivorous finfish growth rates and survival on the short-term dynamics (days to weeks) of food availability as reflected by concentrations of chlorophyll *a*, POC, and PON (Fig. 7). In experiment 1, where nutrient loading had a strong effect on juvenile growth, the molar ratio of POC/PON was significantly reduced by the high nutrient loading treatment (Table 2), suggesting an enrichment of nitrogen in food particles could have contributed to enhanced shellfish growth (Fig. 2a, b). Carmichael et al. (2004) and Carmichael and Valiela (2005) have interpreted nitrogen-enriched seston as an increase in the quality of food particles available to juvenile bivalves. Although the molar ratio of POC/PON did not change in experiment 3, the quantities of POC and PON were both decreased by adult clam filtration (Table 2), with corresponding decreases in the growth rates of juvenile oysters and sheepshead minnows (Fig. 6b, c) and a decrease in the survival of juvenile scallops. In all cases, increased growth rates of shellfish occurred in parallel with increases in whole or size-fractionated chlorophyll *a*. While there was a statistically significant change in chl *a* due to treatment factors in each experiment, the magnitude of these changes in experiments 1 and 2 were relatively low (±2–4 μg $L^{-1}$; Figs. 1a and 3a). It is possible that the availability of food particles to the juvenile shellfish was changed by the treatment factors in these experiments without large changes in the standing stock of chlorophyll *a* between treatments. Phytoplankton mortality rates due to microzooplankton grazing of 0.5 $day^{-1}$ or greater are common in estuarine environments and often result in >70% daily turnover of standing chl *a* (Calbet and Landry 2004). Microzooplankton grazing rates ranged from 2.3 to 2.4 $day^{-1}$ in experiment 2; these were faster than the estimated clearance rate from adult oyster filtration of 67% tank volume $day^{-1}$. Such rapid rates of phytoplankton community turnover could mask true food availability to juvenile bivalves and would account for enhanced bivalve growth responses in experiment 2 in the absence of large changes in chl *a*. In experiment 3, microzooplankton grazing rates were slower (0.4–0.7 $day^{-1}$) and comparable to the adult clam clearance rate of 63% tank volume $day^{-1}$. In contrast to experiments 1 and 2, this experiment had large treatment-driven changes in chl *a* (±20–40 μg $L^{-1}$; Fig. 5a) and growth differences in response to adult clam filtration (Fig. 6a–c). Lonsdale et al. (2009) found that natural populations of bivalves in a shallow embayment could exert grazing pressure on phytoplankton that was comparable to grazing by microzooplankton and noted that bivalves also fed upon microzooplankton and copepod nauplii. Future work will need to examine the extent to which benthic suspension feeding alters both phytoplankton growth and microzooplankton grazing and how turnover in the plankton community affects the growth and recruitment of juvenile bivalves.

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

The densities of adult northern quahogs used in our experiments 1 and 3 (8–12 individuals $tank^{-1}$, or 29–43 individuals $m^{-2}$) are comparable to historic densities of

northern quahogs (hard clams) in Great South Bay (50–100 individuals $m^{-2}$, Kassner 1993, cf. Cerrato et al. 2004) but are much higher than current densities in NY estuaries (0–5 individuals $m^{-2}$, Weiss et al. 2007). Similarly, the density of adult oysters used in experiment 2 (6 individuals $tank^{-1}$, or 21 individuals $m^{-2}$) is comparable to historic densities of Eastern oysters in reefs in Chesapeake Bay (43–150 individuals $m^{-2}$) but is much higher than current densities (0.43 individuals $m^{-2}$; Newell 1988; MacKenzie 1996). However, all of the densities used in experiments are several orders of magnitude less than levels used for bivalve aquaculture (Rheault and Rice 1996; K. Rivara, Aeros Cultured Oyster Co., personal communication). The estimated water column clearance rates from these densities of adult bivalves were 42–67% tank volume $day^{-1}$, within the range reported to control algal bloom formation (Cerrato et al. 2004; Wall et al. 2008). Consistent with this idea, the presence of adult bivalves yielded lower phytoplankton biomass in all three experiments (Figs. 1b, 3b, and 5b). Such ecosystem-wide filtration pressure may have been typical of historic (nineteenth century) natural bivalve populations in Chesapeake Bay (Newell 1988; MacKenzie 1996) or Great South Bay (mid-twentieth century, McHugh 1991; Kassner 1993). Similarly, modern high-density bivalve aquaculture may also achieve these ecosystem filtration rates (Dumbauld et al. 2009), especially in coastal lagoons with slow flushing times (Souchu et al. 2001) and in some cases the loss of filtration due to the removal of bivalve aquaculture can lead to symptoms of eutrophication (Huang et al. 2008). Estuarine management programs may consider bivalve restoration as a management tool to control pelagic algal blooms (Cerrato et al. 2004), combat eutrophication (Cerco and Noel 2007), facilitate the growth of eelgrass (Fig. 6a; Peterson and Heck 2001; Newell and Koch 2004; Wall et al. 2008), or even to effect "regime change" of eutrophic estuaries (Petersen et al. 2008), although the potential impacts on juvenile shellfish must also be considered.

While enhanced bivalve filtration was beneficial to eelgrass and to some extent epiphytes on eelgrass, they exerted a significantly negative effect on the growth of juvenile fish and shellfish in two out of three experiments (Figs. 4b and 6b, c) and in one case even led to a significant increase in juvenile scallop mortality (experiment 3). Rheault and Rice (1996) placed juvenile eastern oysters (*C. virginica*) and bay scallops (*A. irradians*) in a compartmented flume and found decreased growth and condition index in the shellfish that were downstream compared to the upstream dense populations. In experiment 3 of our study, the high density of adult clams produced a large average daily drop in chl *a* levels (Fig. 5b, −73%) and a decrease of 36% in experiment-long chl *a* means compared to the control and also led to decreased growth of juvenile oysters (Fig. 6b) and decreased survival of juvenile scallops. The concentrations of chl *a* in experiment 3 were relatively high (25.09±2.56 μg $L^{-1}$ with no adult clams; 15.90±2.20 μg $L^{-1}$ with adult clams; Table 2); this drop in chlorophyll *a* produced a significant decrease in juvenile oyster growth but not juvenile clam growth. It is likely that juvenile clam food requirements were saturated at a lower chlorophyll *a* concentration than juvenile oyster food requirements (Tenore and Dunstan 1973). These impacts illustrate an eventual trade-off between the benefits and costs of higher ecosystem filtration rates: Despite the benefits to seagrass, high rates of water column turnover by adult shellfish could serve as a negative feedback on juvenile fish and shellfish populations (Figs. 4b and 6b, c) by decreasing food availability (Fig. 5a, b) or even by direct consumption of larval bivalves by adults (Andre and Rosenberg 1991; Andre et al. 1993). Such density-dependent limitation is a common phenomenon within bivalve aquaculture (Rheault and Rice 1996; Zhou et al. 2006), and overstocking of aquaculture operations may exceed the carrying capacity of some estuaries (Guo et al. 1999; Duarte et al. 2003). The extent to which juvenile suspension feeders may be food-limited within estuarine ecosystems is not well-known but will certainly depend on the species involved and the particular physics and biology of each ecosystem (Newell 2004; Ferreira et al. 2008).

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

in some relatively oligo- or mesotrophic and well-mixed coastal systems with increased secondary production of eastern oysters and northern quahogs as a positive benefit (Nixon and Buckley 2002). Of course, such potential benefits would need to be considered in light of potentially negative effects of higher nutrient loads in an ecosystem such as hypoxia (Diaz and Rosenberg 2008), loss of seagrass beds (Valiela et al. 1992; Dennison et al. 1989), and harmful algal blooms (Anderson et al. 2008).

Future ecosystem-based management of estuaries will need to simultaneously administer bivalve restoration, control of nutrient loading, conservation of key fishery species, the burgeoning aquaculture industry, and protection of critical habitats such as seagrass meadows and salt marshes. Quantitative modeling of bivalve filtration, phytoplankton dynamics, and hydrology of estuaries will aid in the aforementioned management goals (Dame and Prins 1998; Duarte et al. 2003; Ferreira et al. 2008). Based on the results of these experiments and other findings, some general conclusions can be drawn. First, eelgrass is light-limited in many eutrophic estuaries (Dennison and Alberte 1985; Duarte 1995) and will benefit from proximity to the enhanced filtration of bivalve beds (Fig. 7; Wall et al. 2008). Additionally, bivalves can benefit seagrasses through enhanced biodeposition (Peterson and Heck 2001; Carroll et al. 2008). As such, re-planting of eelgrass beds should focus on areas that have high light penetration and/or are adjacent to existing dense bivalve populations. The second conclusion is that juvenile resource bivalves can respond positively to enhanced nutrient loading but may experience decreased growth in the presence of high densities of adult bivalves (Fig. 7). This is likely mediated by food limitation: Nutrients encourage the growth of larger and more nutritious phytoplankton (Wikfors et al. 1992; Raven and Kubler 2002) while dense collections of adult bivalves can limit juvenile growth by clearing too many of these food particles (Rheault and Rice 1996; Zhou et al. 2006). This issue of food limitation between juvenile and adult bivalves may be best seen through the lens of intensifying aquaculture operations: As aquaculture becomes more prevalent and shellfish stocking densities increase, aquaculture operations may limit each other or adjacent natural populations (Nunes et al. 2003; Ferreira et al. 2008). Clearly, predators (Gosselin and Qian 1997; Polyakov et al. 2007) and hypoxia/anoxia (Altieri and Witman 2006; Diaz and Rosenberg 2008) also exert significant mortalities on juvenile bivalves in the estuarine ecosystems. However, in absence of hypoxia and differential predation, restoration, re-seeding, and aquaculture of bivalves are more likely to succeed in areas that have moderate nutrient loading rates, although managers must carefully consider the spacing between both natural and aquacultured bivalve populations.

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