RESEARCH ARTICLE

Soft Shell Clams (*Mya arenaria*) Contribute to Macroalgal Blooms in a Partially-restored Gulf of Maine Back-barrier Lagoon

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ABSTRACT

Like many Eastern US salt marshes, East Harbor salt marsh lagoon on Cape Cod was isolated from tidal flow in the 1800s, resulting in near-freshwater conditions and loss of native salt marsh species. After partial restoration in 2002, salt marsh species recolonized East Harbor, and soft shell clam (*Mya arenaria*) recolonization was prolific, with peak densities reaching 3,200 individuals m^{-2} in 2005. However, severe macroalgal blooms in 2006–2007 resulted in anoxia and mortality of benthic organisms (including clams), and macroalgae still dominate primary productivity at the site. The causes of algal blooms at East Harbor are not understood. We conducted a mesocosm study (2009–2011) to evaluate whether soft shell clams contributed to macroalgal blooms by altering nutrient cycling and increasing water clarity. In 2011, we added periwinkles (*Littorina littorea*) to evaluate whether grazers reduced algal productivity. In all three years of our study, macroalgal biomass and percent cover, benthic and water column nutrients, and water clarity were significantly higher in treatments with clams than controls. In 2011, periwinkles significantly reduced algal growth even when clams were present. These findings suggest that soft shell clam recolonization of East Harbor played an important role in algal blooms by increasing nutrient availability and water clarity, and that the absence of gastropod grazers allowed macroalgae to proliferate. Full tidal flushing may mitigate macroalgal blooms at East Harbor and in other, similar systems by reducing nutrient loading that increases algal productivity, and by maintaining water temperatures within a range that allows algal grazers to establish.

Keywords: estuary, macroalgae, mollusk, New England, tidal restoration

Beginning in the late 1800s, the construction of roads, impoundments, and dikes throughout the eastern United States isolated estuaries, lagoons, and salt mashes from tidal exchange, resulting in eutrophication, fish kills, invasion by aggressive freshwater plants and exotic species, and algal blooms (Roman et al. 2002, Portnoy et al. 2007). Today, many of these systems are being tidally-restored so they can again function as biogeochemical filters, buffers against coastal erosion, and habitat for a wide variety of flora and fauna (Redington 1994, Roman et al. 2002). Although many of these projects have resulted in successful outcomes, optimal functioning is often not achieved immediately. In fact, restoration of salt marshes can take several years to equilibrate to baseline or target conditions (Zedler 2000, Smith and Warren 2012).

East Harbor (Truro, MA, USA; Figure 1) is a back-barrier salt marsh lagoon within Cape Cod National Seashore (CCNS) that underwent partial tidal restoration in 2002 after almost 150 years of tidal restriction. Since tidal flow was partially restored, numerous species of fish and benthic invertebrates have successfully colonized the marsh (Portnoy et al. 2007, Thelen and Thiet 2009). Nekton recolonization was dominated by soft shell clams (*Mya arenaria*), which reached peak densities of 3,200 individuals m^{-2} in 2005 (Thelen and Thiet 2009). Clams continue to dominate the benthic fauna, although in much lower densities (12–46 individuals m^{-2} in 2007 and 2008 and 1–8 individuals m^{-2} in 2011; Thiet et al. in press). Despite these successful restoration outcomes, nuisance macroalgal blooms of gutweed (*Enteromorpha intestinalis*) and the green alga (*Cladophora* spp.) occurred in the lagoon in 2006–2007, resulting in severe anoxia and fish and shellfish mortality (Portnoy et al. 2007). Today, macroalgae remain the dominant form of plant life in the lagoon and continue to threaten the establishment of widgeon grass (*Ruppia maritima*), eelgrass (*Zostera marina*), and various benthic fauna (Smith et al. 2011). External inputs of organic and inorganic N into the system are minimal, and organic N export from the system

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Figure 1. Map of East Harbor, Cape Cod National Seashore, MA, depicting three distinct sections: the tide creek (Moon Pond), lagoon, and northwest cove. Culverts are indicated; the 1.22-m diameter clapper valve culvert opened in 2002 is connected directly with Cape Cod Bay, and the culvert under High Head Road is the constriction that limits tidal range in the lagoon. Map Credit: Erica Kidd, Antioch University New England.

is high (Portnoy et al. 2007); thus, nutrient loading from external sources is not implicated in algal blooms at the site.

Herbivore grazers such as common periwinkle (*Littorina littorea*) and mud snails (*Ilyanassa obsoleta*) regulate macroalgal growth in most eastern hard- and soft-bottom ecosystems (Lubchenco 1983, Petraitis 1983, Bertness 1984). Since their introduction to the eastern US from Europe approximately 150 years ago, periwinkles have become the most abundant gastropod and dominant herbivore in New England hard- and soft-bottom habitats (Petraitis 1983), where they can reach densities as high as 400–800 snails m^{-2} in wave-protected areas (Bertness 1984). While periwinkles are prevalent in many salt marshes of CCNS, they have been absent from or extremely rare in the East Harbor lagoon (Thelen and Thiet 2009, Smith et al. 2011). In 2005, periwinkles were relatively common in Moon Pond and were present but uncommon in the lagoon (Thelen and Thiet 2009). Periwinkles were observed in Moon Pond (not the lagoon) in 2007 but not in 2008 and were absent from all areas of East Harbor in 2011 (Thiet et al. in press). Smith et al. (2011) recently showed that periwinkle survival in experimental mesocosms dropped precipitously at water temperatures between 28–30°C. This suggests that periwinkle colonization of East Harbor is, in part, limited by high water temperatures in the lagoon, which regularly reach 28°C and can be 30–35°C during summer months (Portnoy et al. 2007, Smith et al. 2011).

Mud snails also consume macroalgae, but to a lesser extent; their diet is much more varied than that of periwinkles and includes detritus, bacteria, sediment microalgae (diatoms), and carrion as well as macroalgae (Kelaher et al. 2003). They have also been very rare in the lagoon since restoration began, although they are becoming more abundant after intentional introductions during 2008–2010 (Smith et al. 2010). Mud snails were not detected in 2005 (Thelen and Thiet 2009), and were observed in very low densities (0.1–0.3 individuals m^{-2}) in Moon Pond in 2007, 2008, and 2011 (Thiet et al. in press). Thiet et al. (in press) detected mud snails in very low densities (0.5 individuals m^{-2}), and only in the lagoon, in 2011. Regardless, the absence of these and other important consumers in the past and present translates to greatly reduced grazing pressure on macroalgal growth.

Water residency time, sediment chemistry, water clarity, salinity, and nutrients also influence macroalgae biomass (Smith 1984, Taylor et al. 1995). With respect to the latter, macroalgae may be nitrogen (N) or phosphorus (P) limited in coastal marine

environments (Fong et al. 2004, Valiela et al. 1997); N in particular limits macroalgal growth in temperate and marine environments (Pedersen and Borum 1997, Valiela et al. 1997) and in systems with brief water residency times (Smith 1984). Nutrients tend to accumulate in East Harbor due in part to its long water residency times (~130 d; Portnoy et al. 2007).

In the Great Lakes, the population explosion of zebra mussels (*Dreissena polymorpha*) has been implicated in facilitating algal blooms by increasing water clarity (Lowe and Pillsbury 1995) and enhancing benthic P levels through the deposition of feces and pseudo-feces (Stankovich 2005). Mollusk feces and pseudo-feces are also high in ammonium (NH_4^+) and therefore add to the total system nitrogen load (Dame 1996, Sprent, 1987). Soft shell clams, which are often abundant in soft-bottom saltwater habitats, increase NO_3 levels in an oxidized zone varying between 0.5–5 mm around their burrows (Henriksen et al. 1983) and increase denitrification in estuarine sediments (Pelegri and Blackburn 1995). Soft shell clams can achieve population densities of 200–10,000 individuals m^{-2} depending on clam size and water quality conditions (Pelegri and Blackburn 1995, Zettler and Forster 2004, Thelen and Thiet 2009).

Given the relationship between zebra mussels and Great Lakes macroalgal blooms, we asked whether soft shell clams might facilitate macroalgal blooms at East Harbor, CCNS, via similar mechanisms. Previous work on macroalgal blooms in eastern US estuaries has focused on nutrient loading from surrounding terrestrial landscapes (Valiela et al. 1997), but nutrient inputs to East Harbor from external sources are negligible (Portnoy et al. 2007). We conducted a series of laboratory studies with experimental mesocosms to evaluate: (1) whether macroalgal cover and biomass differed in experimental mesocosms containing soft shell clams versus mesocosms without clams; (2) whether soft shell clams increased water clarity, benthic N and P, and water column N and P; and (3) whether periwinkle snails could significantly reduce macroalgal growth through grazing.

Methods

Site Description

East Harbor is a 291-ha back-barrier salt marsh lagoon in Truro, MA, USA, managed by Cape Cod National Seashore (Figure 1). The site is made up of three sections: the main tidal creek (Moon Pond), a small sub-embayment known as the northwest cove, and a large 140-ha shallow (≤2 m) open-water lagoon. East Harbor was isolated from Cape Cod Bay in 1868 by a 305-m dike through the original inlet, which greatly reduced salinity levels and created an artificial freshwater ecosystem (Smith et al. 2008). In 2002, CCNS opened two clapper valves (total 1.22 m d) in a drainage pipe connecting Moon Pond to Cape Cod Bay. Today, tide ranges in Moon Pond approach ~46 cm, but daily tides in the lagoon only reach 2–3 cm (Portnoy et al. 2007).

Experimental Design

During the summers of 2009–2011, we used experimental mesocosms to evaluate the effects of soft shell clams (and, in 2011, periwinkles) on macroalgal percent cover and biomass, water clarity (indicated by phytoplankton levels, quantified as chlorophyll *a*), and sediment and water column N and P levels. We constructed mesocosms using 10-gallon aquaria to which we added beach sand (average depth 15 cm) and water collected from East Harbor (average depth 13 cm) (total depth ~26–30 cm). The water was unfiltered, all floating macroalgae and nekton were removed, and no artificial substrate was added to the aquaria. Clams were added to the sediment in each aquarium (except control and periwinkle-only treatments) by manually seeding them into sediment so their siphons were flush with the sediment surface, and fed a highly concentrated formula of phytoplankton (Phyto Feast®, Campbell, CA) every other day. To avoid potential bias in chlorophyll *a* measurements introduced by feeding, an equal volume of phytoplankton was added to control mesocosms at each feeding, and chlorophyll *a* samples were collected on days between feedings. Clams were collected by hand from Moon Pond and the lagoon at East Harbor. Previous researchers keeping laboratory clams have run fresh saltwater through experimental mesocosms to simulate natural tidal flow (Auffrey et al. 2004); instead, we maintained closed systems to accurately measure fluctuating nutrient levels throughout our experiment. Mesocosms were maintained in a greenhouse in Eastham, MA, for all experimental runs in 2009 and 2010 and a shade cloth was used to mitigate solar heating. In 2011 we moved to a grow room on site at CCNS and used overhead lights to mimic field light conditions. Mesocosms were kept in a cool water bath (2.4 m × 0.8 m) to prevent overheating. We maintained mesocosms at field water temperatures (average: 24–25°C), and salinity was maintained near East Harbor levels (21–25 ppt) by adding fresh water as necessary. Air bubblers (Hagen Elite 800–1, 1.5"l × 0.75"w, 3/16" d) were used to oxygenate mesocosms.

Our 2009 experiment was conducted in two consecutive four-week runs (Aug 2–Oct 8, 2009), for which we established eight total mesocosms: four with soft shell clams (12–14 clams per aquaria, average length ~5.75 cm) and four controls without clams. In 2010, we expanded our replication to 16 total mesocosms, eight with clams (12–14 clams per aquaria, average length ~5.75 cm) and eight clam-free controls. In 2010 we conducted two consecutive three-week runs (June 4–July 22, 2010); run length was shortened that year to ensure clam survival in hot greenhouse temperatures (2009 was an unusually cloudy summer and thus greenhouse temperatures were not a concern that year).

In 2011, we expanded the study to include treatments with periwinkle grazers. That year, we designed a 2×2 full-factorial experiment in which 8 total mesocosms were established in the following treatment combinations: clams only (n = 2 mesocosms; 12 clams per mesocosm, average length ~7 cm), clams + periwinkles (n = 2 mesocosms; 12 clams and 10 periwinkles per mesocosm), periwinkles only (n = 2 mesocosms; 10 periwinkles per mesocosm), and clam- and periwinkle-free controls (n = 2 mesocosms). We had fewer mesocosms in 2011 due to high clam mortality in some mesocosms, so we ran three consecutive experimental runs of three weeks each (May 23–Aug 8, 2011) to maximize experimental replication. Fresh clams and periwinkles were used for each experimental run, and mesocosms were topped with 2-cm wire hardware cloth to prevent periwinkles from escaping. At the start of each experimental run in 2010 and 2011, we inoculated each mesocosm (including controls) with a baseline of 0.5 g gutweed.

In each experimental run, we quantified macroalgal percent cover weekly in each mesocosm by holding a grid over the water surface and counting the number of 1-cm squares occupied by algae. Macroalgal biomass (g) in each mesocosm was quantified at the end of each run by harvesting, drying, and weighing. Due to lower light levels in the grow room in 2011 than the greenhouse in 2009 and 2010, macroalgal growth was too low to form large clumps that floated to the water surface. Thus, we quantified biomass differently that year by using a sterile syringe to siphon algae that colonized the sediment surface and mesocosms walls and running chlorophyll *a* analyses on those samples as a proxy for algal biomass.

Once weekly during each experimental run in 2010 and 2011, we measured water column phytoplankton levels as an indicator of water clarity by quantifying chlorophyll *a* content in a 200 mL water column sample from each mesocosm. We used the non-acidification technique for extracted chl *a* (Welschmeyer 1994), which minimizes bias caused by fluorescence from interfering compounds such as chl *b* and *c* and organic matter.

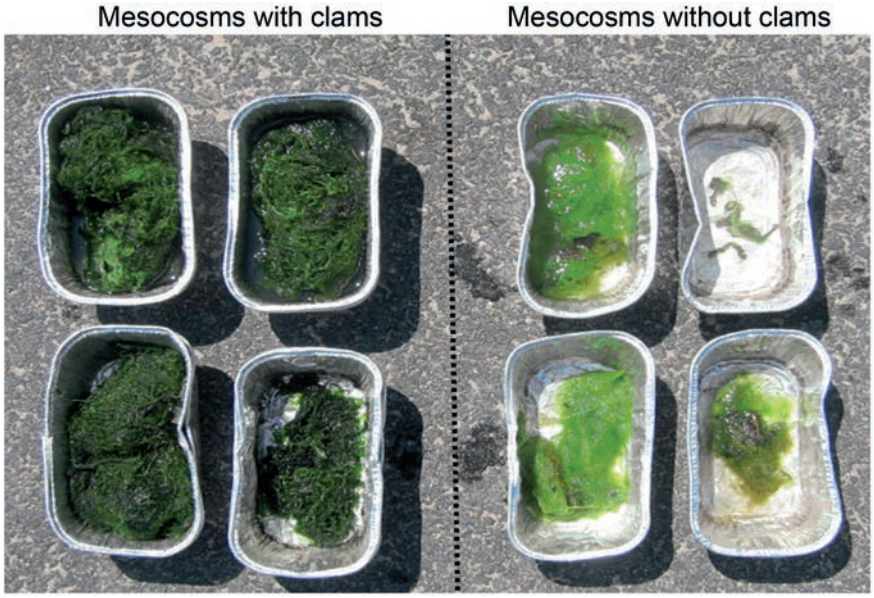

Figure 2. Photos showing the different biomass of macroalgae collected from mesocosms with and without soft shell clams in 2010 experiments. Clam mesocosms were colonized by only gutweed (*Enteromorpha intestinalis*), and controls were colonized by only the green alga *Cladophora* spp. Photo credit: R. Clark.

We quantified sediment porewater PO_4, NH_4^+, and NO_3 by sampling sediment porewater (45 mL to 3–5 cm depth) weekly during each run (in 2009 two sediment porewater samples were collected per week) using 0.4 cm wide hollow Teflon coated stainless steel tubing connected to a 50 mL sterile syringe with a Millex-HA (Ireland) 0.45 µM fine filtration unit. New filtration units were used for each sample. A sterile syringe was used on each sample date and syringes were triple rinsed between samples with a 1:4 HCl:water solution. We also collected weekly (except 2009 run 1) water column samples (45 mL) for nutrient assays using the same syringe and filtration unit. Porewater and water column samples were frozen at -20°C immediately after sampling and thawed at room temperature prior to analysis. A SmartChem™ Discrete Analyzer (Unity Scientific, Brookfield, CT, USA) was used for orthophosphate analysis, NH_4^+ was analyzed by flow injection analysis colorimetry (Knepel and Bogren 2001), and NO_3 was analyzed using the copper-cadmium reduction method (Diamond 2003).

Data Analysis

We compared macroalgal percent cover, macroalgal biomass, sediment porewater N and P, water column N and P, and chl *a* (2010–11 only) in clam versus control mesocosms (2009 and 2010), and among the four treatments in our 2011 experiments. We ran discrete statistical tests for each experimental run. Our data did not meet the assumptions necessary for use of parametric analyses, transformation did not improve data distributions, and sample sizes were small; thus, for clam versus control data (2009 and 2010) we used non-parametric Wilcoxon rank sum analyses with repeated measures to compare response variables. For comparison among our four treatments in 2011, we used repeated measures ANOVA on log-transformed data, except for algal percent cover and sediment chlorophyll *a* data, for which we used standard ANOVA because data were

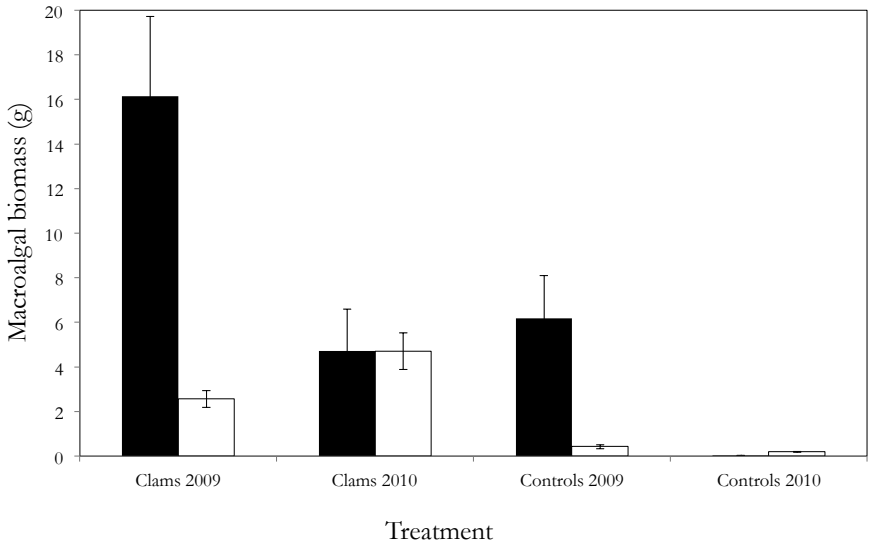

Figure 3. Mean (±SE) macroalgal biomass (g) in clam and control mesocosms in 2009 and 2010. Solid bars are Run 1, open bars are Run 2. Due to high algal biomass and risk of anoxia in clam mesocosms in 2009, we harvested macroalgae from all mesocosms in weeks two and four in run 1 that year; in all other runs in 2009 and 2010, we harvested macroalgae only at the end of each run. Test statistics are given in Supplemental Table 1.

collected only once at the end of each run that year. Tukey's HSD tests were used to compare specific treatment means. JMP 8 statistical software (SAS v.9, SAS Institute, Cary, NC) and XLSTAT (v. 5.01) were used for statistical analyses, and significance was determined at $\alpha \leq 0.05$ unless otherwise noted.

Results

Macroalgal Biomass and Percent Cover

Three macroalgal species grew in our experimental mesocosms: gutweed, the green alga *Cladophora* spp., and an unidentifiable brown algae species (Figure 2). In 2009 and 2010 when light levels were good, gutweed growth began on the sediment surface and clam siphons within one week, and spread to mesocosm walls and floated to the water surface within two weeks. In 2009, gutweed grew only in clam mesocosms and *Cladophora* grew only in controls. In both runs that year, *Cladophora* colonized the sediment surface and walls of control mesocosms, and grew more slowly than the gutweed in clam mesocosms. In 2010, gutweed was the only species that grew in experimental mesocosms, and in 2011 mesocosms were colonized by gutweed and a brown algal species; however, brown algal growth was too minimal to identify it to species. Algal growth was slower in 2011 than in 2009 and 2010 due to lower light levels in the laboratory than in the greenhouse used in prior years. Mesocosms with clams had significantly higher macroalgal biomass (Figures 2, 3) and percent cover (Figures 4, 5) than control mesocosms in all but one of our seven experimental runs over the three study years (Table 1, Supplementary Table 1). In 2009, macroalgal biomass did not differ significantly between clam and control mesocosms in run 1, but clam mesocosms had significantly higher macroalgal biomass than controls in run 2 (Figure 3, Supplementary Table 1). That year, algal percent cover was significantly higher in clam mesocosms than controls in both runs 1 and 2 (Figure 4, Supplementary Table 1). In 2010, clam mesocosms had significantly higher algal biomass and percent cover than controls in both runs 1 and 2 (Figures 3 and 4, Supplementary Table 1). In our 2011 study with periwinkles, percent cover in clam-only treatments was significantly higher than controls in runs 1 and 2, but neither clam-periwinkle nor periwinkle-only treatments were different from controls (Figure 5, Table 1).

In 2011, we used sediment chl *a* as a proxy for algal biomass. That year sediment chl *a* in the first run was higher in clam-only, clam-periwinkle, and periwinkle-only treatments than the periwinkle-only and control

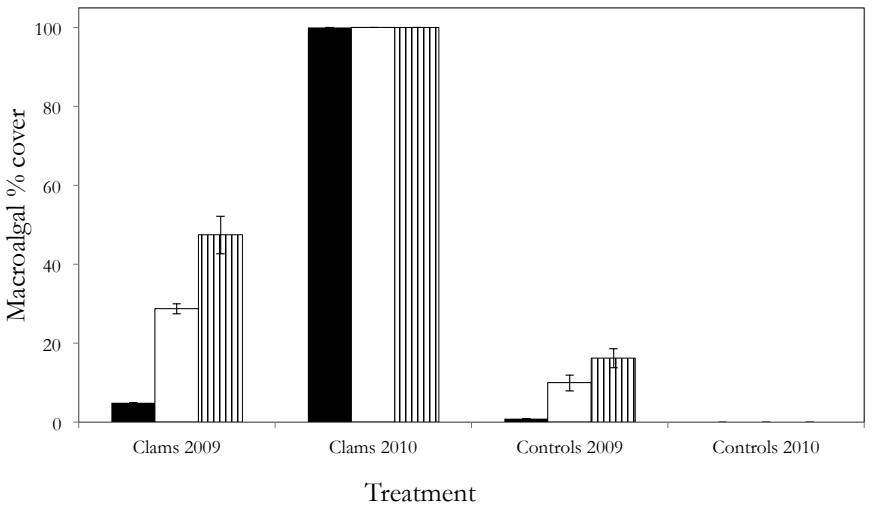

Figure 4. Mean (±SE) macroalgal percent cover in clam and control mesocosms by week in 2009 and 2010. These data are Run 2 only; test statistics and Run 1 data are in Supplemental Table 1. Solid bars are week 1 of the run, open bars are week 2, and striped bars are week 3.

Table 1. Results from Tukey's HSD tests on 2011 data for water column chlorophyll a, macroalgal percent cover, and macroalgal biomass (as sediment chl *a*). All F- and *p*-values are results of ANOVA tests, and ANOVA tests for water column chl *a* were run with repeated measures. Significance was determined at $p \leq 0.05$.

	Water column chl *a*	Macroalgal percent cover	Sediment chl *a*
Run 1	F = 23.7, $p < 0.001$	F = 7.9, $p = 0.004$	F = 8.2, $p = 0.035$
Run 2	F = 129.5, $p < 0.001$	F=11.9, $p = 0.001$	F = 482.6, $p < 0.001$
Run 3	F = 43.8, $p < 0.001$	F=1.0, $p = 0.412$	F = 8.9, $p = 0.03$

Week	**1**	**2**	**3**	**4**		
Run 1						
Clams+periwinkles vs controls	Y	N	Y	N	N	Y
Clams+periwinkles vs periwinkles only	Y	N	Y	Y	N	Y
Clams+periwinkles vs clams only	N	N	N	N	Y	N
Clams only vs controls	Y	N	Y	N	Y	Y
Clams only vs periwinkles only	Y	N	Y	Y	Y	Y
Periwinkles only vs controls	N	N	N	N	N	Y
Run 2						
Clams+periwinkles vs controls	Y	Y	N		N	Y
Clams+periwinkles vs periwinkles only	Y	Y	Y		N	Y
Clams+periwinkles vs clams only	N	N	Y		Y	N
Clams only vs controls	Y	Y	Y		Y	Y
Clams only vs periwinkles only	Y	Y	Y		Y	Y
Periwinkles only vs controls	Y	N	Y		N	N
Run 3						
Clams+periwinkles vs controls	Y	Y	Y		N/A	N
Clams+periwinkles vs periwinkles only	Y	Y	N		N/A	N
Clams+periwinkles vs clams only	N	N	N		N/A	N
Clams only vs controls	Y	Y	N		N/A	Y
Clams only vs periwinkles only	Y	Y	N		N/A	Y
Periwinkles only vs controls	N	N	N		N/A	Y

treatments. Furthermore, clam-periwinkle had significantly higher chl *a* concentrations than periwinkle-only treatments, and we observed the same trends in runs 2 and 3 (Supplementary Figure 1, Table 1).

Water Column Chlorophyll a

To evaluate the effect of clams on water clarity, we measured phytoplankton levels as indicated by water column chl *a* in 2010 and 2011. Water column chl *a* was highly variable among treatments but tended to be highest in controls. In 2010, water column chl *a* did not differ significantly between clam-only and control mesocosms in either run (Figure 6, Supplementary Figure 2, Supplementary Table 1). In 2011, chl *a* levels decreased over time in run 1 and increased significantly over time in run 3 (treatment*time interaction, run 1: F = 11262.4; $p = 0.01$; run 2: F

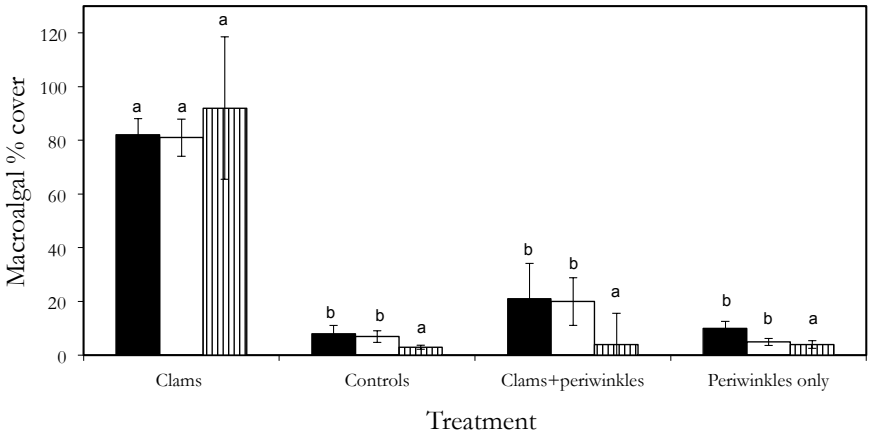

Figure 5. Mean (±SE) macroalgal percent cover in clam, clams+periwinkles, periwinkles only, and control mesocosms by run in 2011. Macroalgal percent cover was quantified once in each mesocosm at the end of each run. Solid bars are Run 1, open bars are Run 2, and striped bars are Run 3. Different letters above bars within each run denote statistically significant differences at determined by Tukey's HSD tests ($p < 0.05$); test statistics are given in Table 1.

Table 2. Results from Tukey's HSD tests on 2011 data for sediment porewater PO_4, NH_4^+, and NO_3. "Y" denotes a significant difference between the treatment groups indicated. All F- and *p*-values are from ANOVA tests with repeated measures, and significance was determined at $p \leq 0.05$.

	PO_4 (µM)	NH_4^+ (µm)	NO_3 (µm)
Run 1	F = 22.65, $p < 0.0001$	F = 64.21, $p < 0.0001$	F = 31.56, $p < 0.0001$
Run 2	F = 8.32, $p = 0.003$	F = 5.29, $p = 0.015$	F = 4.65, $p = 0.022$
Run 3	F = 37.46, $p = 0.002$	F = 48.14, $p = 0.001$	F = 54.08, $p = 0.001$

Week	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**
Run 1												
Clams+periwinkles vs controls	Y	N	Y	Y	Y	Y	Y	Y	N	N	Y	Y
Clams+periwinkles vs periwinkles only	N	N	Y	Y	Y	Y	Y	Y	N	N	Y	Y
Clams+periwinkles vs clams only	N	N	N	N	N	N	Y	N	N	N	N	N
Clams only vs controls	N	N	Y	Y	Y	Y	Y	Y	N	N	Y	Y
Clams only vs periwinkles only	N	N	Y	Y	Y	Y	Y	Y	N	N	Y	Y
Periwinkles only vs controls	N	N	N	N	Y	Y	Y	Y	N	N	Y	Y
Run 2												
Clams+periwinkles vs controls	Y	Y	Y		Y	Y	N		N	Y	Y	
Clams+periwinkles vs periwinkles only	Y	N	N		Y	Y	N		N	N	N	
Clams+periwinkles vs clams only	N	N	N		N	N	N		N	N	N	
Clams only vs controls	Y	N	N		Y	Y	N		N	N	Y	
Clams only vs periwinkles only	Y	N	N		Y	N	N		N	N	N	
Periwinkles only vs controls	N	N	N		N	N	N		N	N	Y	
Run 3												
Clams+periwinkles vs controls	Y	Y	Y		Y	N	N		Y	Y	Y	
Clams+periwinkles vs periwinkles only	Y	Y	N		Y	N	N		Y	N	Y	
Clams+periwinkles vs clams only	N	N	N		Y	N	N		N	N	N	
Clams only vs controls	Y	Y	N		Y	N	N		Y	Y	Y	
Clams only vs periwinkles only	Y	Y	N		Y	N	N		Y	N	N	
Periwinkles only vs controls	N	N	N		Y	N	N		Y	Y	Y	

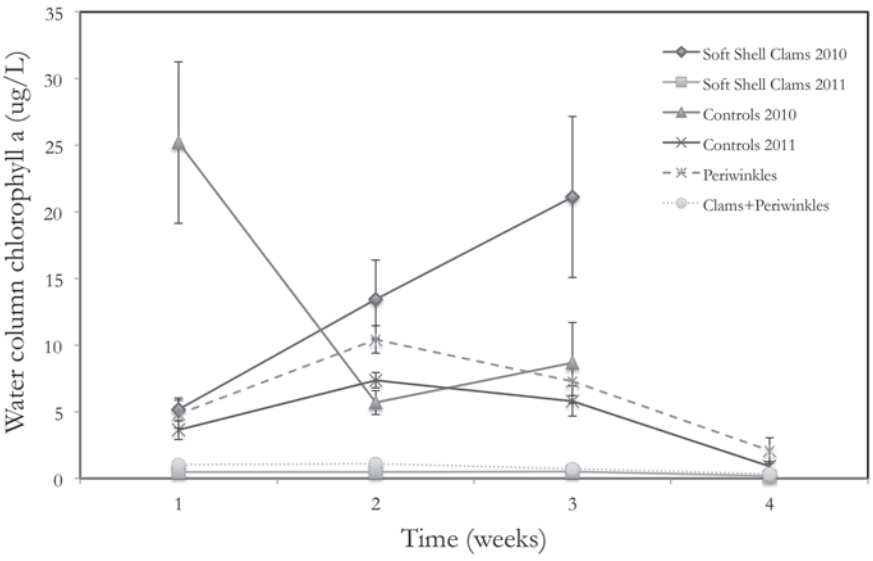

Figure 6. Mean (±SE) water column chlorophyll *a* (µg/L) in mesocosms by week in 2010 and 2011. These data are for Run 1 only in each year; water column chlorophyll *a* data for Run 2, 2010, and Runs 2 and 3, 2011, are shown in Supplemental Figures 2 and 3, respectively. Test statistics for Run 2, 2010, are given in Supplemental Table 1, and test statistics for 2011 runs are given in Table 1.

= 5.03, $p = 0.16$; run 3: F = 12.40, $p = 0.0001$). More specifically, in the first run chl *a* in clam-only and clam-periwinkle mesocosms was significantly lower than in controls except in week 2. In run 2, chl *a* in clam-periwinkle mesocosms was statistically lower than in controls, except in week 3, but the clam-only treatment was lower than controls throughout the experiment (Supplementary Figure 3, Table 1). In weeks 1 and 2 of run 3, clam-only chl *a* was significantly lower than in periwinkle-only and controls, and clam-periwinkle was lower than periwinkle-only. Chl *a* in clam-periwinkle was significantly lower than in controls all three weeks of run 3 (Table 1).

Sediment Porewater Chemistry

Sediment porewater PO_4 was consistently higher in clam mesocosms than controls in 2010 and 2011. In

Table 3. Results from Tukey's HSD tests on 2011 data for water column PO_4, NH_4^+, and NO_3. "Y" denotes a significance difference between the treatment groups indicated. All F- and *p*-values are from ANOVA tests with repeated measures, and significance was determined at $p \leq 0.05$.

	PO_4 (µM)				NH_4^+ (µm)				NO_3 (µm)			
Run 1	F = 28.38, $p < 0.0001$				F = 45.14, $p < 0.0001$				F = 19.91, $p < 0.0001$			
Run 2	F = 14.93, $p = 0.0003$				F = 10.44, $p = 0.001$				F = 7.64, $p = 0.004$			
Run 3	F = 339.05, $p < 0.0001$				F = 29.68, $p = 0.003$				F = 15.02, $p = 0.012$			
Week	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**
Run 1												
Clams+periwinkles vs controls	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
Clams+periwinkles vs periwinkles only	N	Y	Y	Y	Y	Y	Y	Y	N	Y	N	Y
Clams+periwinkles vs clams only	N	N	N	N	N	N	Y	N	N	Y	N	Y
Clams only vs controls	N	Y	Y	Y	Y	Y	Y	Y	N	N	Y	N
Clams only vs periwinkles only	N	Y	Y	Y	Y	Y	N	N	N	N	N	Y
Periwinkles only vs controls	N	N	N	N	Y	Y	N	Y	N	N	N	Y
Run 2												
Clams+periwinkles vs controls	Y	Y	Y		Y	Y	Y		N	Y	Y	
Clams+periwinkles vs periwinkles only	Y	Y	Y		Y	N	N		N	N	N	
Clams+periwinkles vs clams only	N	N	N		N	N	N		N	N	N	
Clams only vs controls	Y	Y	Y		Y	Y	Y		N	N	Y	
Clams only vs periwinkles only	Y	Y	N		Y	N	N		N	N	N	
Periwinkles only vs controls	N	N	N		N	Y	N		N	N	Y	
Run 3												
Clams+periwinkles vs controls	Y	Y	Y		Y	Y	N		Y	Y	Y	
Clams+periwinkles vs periwinkles only	Y	Y	Y		Y	N	N		N	N	Y	
Clams+periwinkles vs clams only	N	Y	N		Y	N	N		N	N	N	
Clams only vs controls	Y	Y	Y		Y	N	N		Y	N	Y	
Clams only vs periwinkles only	Y	Y	N		N	N	N		N	N	N	
Periwinkles only vs controls	N	Y	N		N	N	N		N	N	Y	

2009, sediment porewater PO_4 was significantly lower in clam mesocosms than controls in run 1, but differences in porewater PO_4 in clam and control mesocosms in run 2 were not significant (Supplementary Figure 4, Supplementary Table 1). In 2010, porewater PO_4 was higher in clam mesocosms than controls in both runs 1 and 2 (run 1: significant at $\alpha \leq 0.10$; run 2, significant at $\alpha \leq 0.05$) (Supplementary Figure 4, Supplementary Table 1). In 2011, porewater PO_4 differed significantly among treatments in all three runs, and porewater PO_4 levels were typically significantly higher in clam-only and clam-periwinkle mesocosms than in periwinkle-only and control mesocosms (Figure 7, Supplementary Figure 5, Table 2). That year, sediment porewater PO_4 levels increased significantly as time progressed in runs 1 and 3, but not run 2 (treatment*time interaction, run 1: F = 7.90; $p < 0.0001$; run 2: F = 0.30, $p = 0.94$; run 3: 3.51, $p = 0.03$).

Porewater NH_4^+ was often higher in mesocosms with clams during the three years of our experiment. In 2009, sediment porewater NH_4^+ in clam mesocosms was significantly higher than controls in both runs 1 and 2 (Supplementary Figure 6, Supplementary Table 1). In 2010, clam mesocosms had significantly higher porewater NH_4^+ than control mesocosms in both runs 1 and 2 (Supplementary Figure 6, Supplementary Table 1). In 2011, porewater NH_4^+ levels differed significantly among treatments in all three runs (Figure 7, Supplementary Figure 7, Table 2), and sediment porewater NH_4^+ levels were regularly significantly higher in clam-only and clam-periwinkle mesocosms than in periwinkle-only and control mesocosms (Table 2). That year, sediment porewater NH_4^+ levels increased significantly as time progressed in each of the three experimental runs (treatment*time interaction, run 1: F = 3.10; $p < 0.01$; run 2: F = 5.93; $p < 0.000$; run 3: F = 3.22; $p < 0.04$).

Porewater NO_3 was regularly higher in mesocosms with clams throughout our experiment. In 2009, porewater NO_3 did not differ significantly between clam and control mesocosms in either run at $\alpha \leq 0.05$, but mesocosms with clams had significantly higher NO_3 than controls at $\alpha \leq 0.10$ in run 2 (Supplementary Figure 8, Supplementary Table 1). In 2010, sediment porewater NO_3 was not significantly higher in clam than control mesocosms in run 1, but differences were significant in run 2 at $\alpha \leq 0.10$ (Supplementary Figure 8, Supplementary Table 1). In 2011, sediment

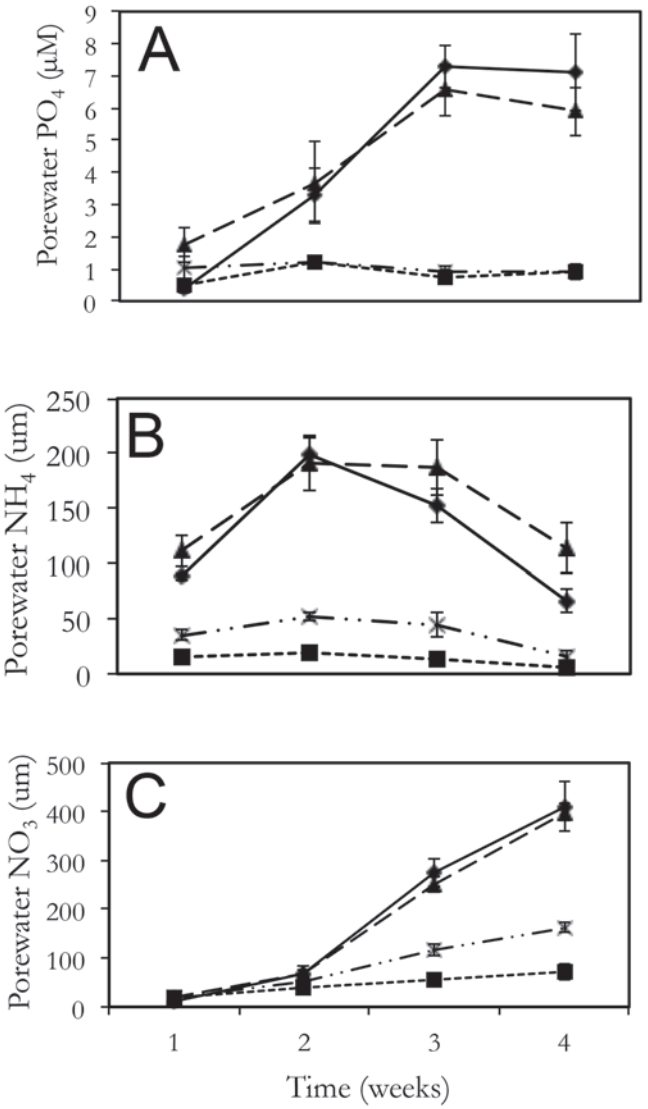

Figure 7. Mean (±SE) sediment porewater PO_4 (µM) (A), NH_4^+ (µm) (B), and NO_3 (µm) (C) in mesocosms by week in 2011. These data are for Run 1 only; sediment porewater PO_4, NH_4^+, and NO_3 in Runs 2 and 3, 2011, are given in Supplemental Figures 5, 7, and 9, respectively. Test statistics for all runs are given in Table 1. Diamond shapes represent the clams-only treatment, triangles represent clams + perwinkles, exes represent periwinkles-only, and squares represent controls.

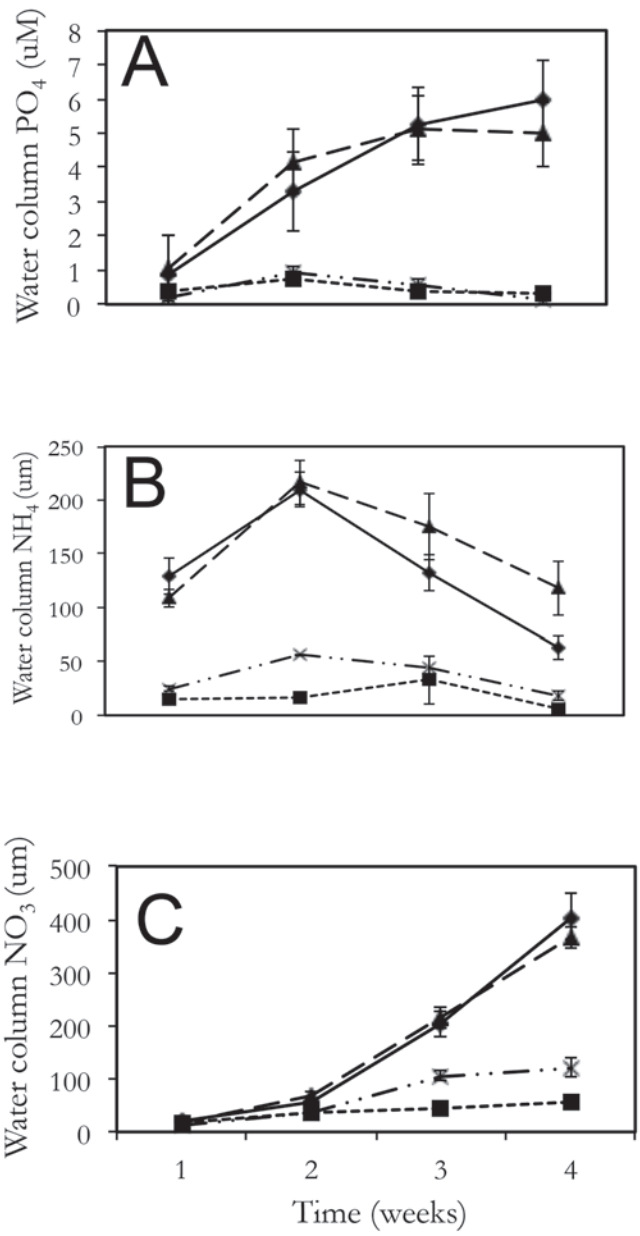

Figure 8. Mean (±SE) water column PO_4 (µM) (A), NH_4^+ (µm) (B), and NO_3 (µm) (C) in mesocosms by week in 2011. These data are for Run 1 only; water column PO_4, NH_4^+, and NO_3 in Runs 2 and 3, 2011, are given in Supplemental Figures 11, 13, and 15, respectively. Test statistics for all runs are given in Table 1. Diamond shapes represent the clams-only treatment, triangles represent clams+perwinkles, exes represent periwinkles-only, and squares represent controls.

porewater NO_3 levels differed significantly among treatments in all three runs (Figure 7, Supplementary Figure 9, Table 2), and sediment porewater NO_3 levels were regularly significantly higher in clam-only and clam-periwinkle mesocosms than in periwinkle-only and control mesocosms (Table 2). That year, sediment porewater NO_3 levels increased significantly as time progressed in runs 1 and 2, but not in run 3 (treatment*time interaction, run 1: F = 14.89; $p < 0.0001$; run 2: F = 12.79; $p < 0.0001$; run 3: F= 1.91; $p < 0.16$).

Water Column Chemistry

Water column PO_4 was regularly higher in mesocosms with clams. In 2009, water column PO_4 in clam mesocosms was significantly higher than in controls (Supplementary Figure 10, Supplementary Table 1).

In 2010, water column PO_4 in clam mesocosms was significantly higher than controls in both runs 1 and 2 (Supplementary Figure 10, Supplementary Table 1). In 2011, water column PO_4 levels differed significantly among treatments in all three runs (Figure 8, Supplementary Figure 11, Table 3) and clam-only and clam-periwinkle mesocosms had significantly higher PO_4 than periwinkle-only and control mesocosms in all three runs that year, often for the entire duration of each run (Table 3). That year, water column PO_4 increased significantly over time in all three runs (treatment*time interaction, run 1: $F = 6.53$; $p < 0.0001$; run 2: $F = 4.73$; $p = 0.001$; run 3: $F = 4.56$; $p = 0.01$).

As with PO_4, water column NH_4^+ was regularly higher in mesocosms with clams. In 2009, water column NH_4^+ was significantly higher in clam mesocosms than in control mesocosms (Supplementary Figure 12, Supplementary Table 1). In 2010, water column NH_4^+ was significantly higher in clam mesocosms than in controls in both runs 1 and 2 (Supplementary Figure 12, Supplementary Table 1). In 2011, water column NH_4^+ differed significantly among treatments in all three runs (Figure 8, Supplementary Figure 13, Table 3), and clam-only and clam + periwinkle mesocosms had significantly higher NH_4^+ than periwinkle-only and control mesocosms in run 1 (Table 3). That year, water column NH_4^+ decreased significantly as time progressed in run 2 (treatment*time interaction, run 1: $F = 0.69$; $p = 0.719$; run 2: $F = 8.50$; $p < 0.0001$; run 3: $F = 2.25$; $p = 0.11$).

Water column NO_3 was usually higher in mesocosms with clams. In 2009, water column NO_3 did not differ significantly between clam and control mesocosms at $\alpha \leq 0.05$, but a strong trend towards higher NO_3 in clam mesocosms was significant at $\alpha \leq 0.10$ (Supplementary Figure 14, Supplementary Table 1). In 2010, clam mesocosms had significantly higher water column NO_3 than control mesocosms in both runs 1 and 2 (Supplementary Figure 14, Supplementary Table 1). In 2011, water column NO_3 levels differed significantly among treatments in all three runs (Figure 8, Supplementary Figure 15, Table 3), and clam-only and clam-periwinkle mesocosms had significantly higher NO_3 than periwinkle-only and control mesocosms in runs 1 and 2, but differences were inconsistent across weeks in both runs (Table 3). That year, water column NO_3 increased significantly over time in runs 1 and 2, but not run 3 (treatment*time interaction, run 1: $F = 251.84$; $p < 0.0001$; run 2: $F = 10.33$, $p < 0.0001$; run 3: $F = 1.81$, $p = 0.18$).

Discussion

Prior research suggests that the effects of nutrient enrichment on algal growth do not vary significantly across spatial scales, and thus small-scale mesocosm studies of the response of algae to nutrient enrichment may be scaled up to more natural aquatic systems (Elser et al. 2007, Spivak et al. 2011). This, combined with the high replication in our experiment and our multi-year observations of clam and periwinkle population cycles and macroalgal blooms at East Harbor, gives us confidence that trends we observed in our mesocosms may be scaled up to East Harbor as a whole.

In all three years of our experiment, we observed a strong trend toward significantly greater macroalgal percent cover and biomass and significantly higher nutrient levels in experimental treatments with clams than in treatments without clams. Macroalgal growth was likely enhanced in treatments with clams due to their ability to increase benthic and water column nutrient levels (Michaud et al. 2006) and, secondarily, to reduce water column chlorophyll *a* and improve light penetration into the water column.

Macroalgal biomass and percent cover in our 2011 experiments with periwinkles were significantly lower in treatments to which we added periwinkle grazers, even when clams were present (i.e., the clam + periwinkle treatments). Together, these findings suggest that rapid and dense soft shell clam colonization (3,200 individuals m^{-2} in 2005; Thelen and Thiet 2009) of East Harbor three years after its restoration contributed to the 2006–2007 algal blooms by clarifying the water column and increasing benthic and water column N and P, and that the absence of gastropod grazers allowed macroalgae to proliferate.

Bivalve filtration rates and nutrient deposition rates are directly linked (Hawkins and Bayne 1992, Zettler and Forster 2004), and therefore bivalve abundance directly affects nutrient deposition levels. Our findings concur with previous studies that document bivalve deposition of N and P into the benthos and water column via their feces and pseudo-feces, and by excretion of other waste (Allen and Garrett 1971, Bootsma et al. 2006, Lowe and Pillsbury 1995, Stankovich 2005). Over all three years of our study, both sediment porewater and water column NH_4^+ were higher in treatments with clams than treatments without clams in all but one experimental run (2011, run 2, week 3), suggesting that clams either excreted excess NH_4^+ into both the benthos and water column, or that excess NH_4^+ excreted into the benthos diffused into the water column (Fong et al. 2004). While decomposition and remineralization of macroalgae may have also added inorganic N to the benthos and water column in clam mesocosms, we observed an inverse relationship between increasing macroalgal growth in clam treatments and decreasing NH_4^+ levels. For instance, water column NH_4^+ in 2009 was significantly higher in clam mesocosms than controls and declined sharply after week one; at the same time, macroalgal growth commenced immediately in clam mesocosms and spiked during week two. In subsequent years, sediment and water column NH_4^+ peaked in clam treatments during weeks 1 and 2 and

declined rapidly as algal growth began in earnest. This suggests that clams excreted and deposited excess NH_4^+ through siphon excretion and shell gape diffusion (Zettler and Forster 2004), which N-limited macroalgae assimilated as it became more available (Fong et al. 2004).

Sediment porewater and water column NO_3 levels were much lower overall than NH_4^+ in both clam and control treatments each year of our study. Nitrification can be up to three times higher in soft shell clam burrows than in surrounding sediment due to a pronounced oxidized zone around clam siphons (Henriksen et al. 1983, Kristensen et al. 1985, Pelegri and Blackburn 1995). Notwithstanding, since soft shell clam burrows lie between the nitrification and denitrification zones, most of the NO_3 produced may be denitrified to N_2O before being released into the water column (Pelegri and Blackburn 1995), or the NO_3 may be rapidly consumed by other benthic organisms (Michaud et al. 2006). If this is the case at East Harbor, which contains anoxic sediments that likely facilitate denitrification, clams may not be contributing sufficient NO_3 to the system to enhance algal growth. Nonetheless, as with NH_4^+, NO_3 was consistently higher in our clam treatments and there was a slight inverse correlation between NO_3 and macroalgal growth. Differences in NO_3 between treatments with and without clams were especially pronounced in 2011, in which clam-only and clam-periwinkle treatments had consistently higher sediment and water column NO_3 than treatments without clams.

Sediment porewater and water column PO_4 were generally higher in clam treatments than treatments without clams, particularly in 2010 and 2011, suggesting that clams are contributing excess PO_4 to this system. However, unlike with NH_4^+, PO_4 did not decrease as algal growth increased, which supports prior observations that primary productivity at East Harbor is N-limited (Lee 2008, Portnoy et al. 2007). Pedersen and Borum (1997) observed that neither sea lettuce (*Enteromorpha lactuca*) nor green hair algae (*Cladophora sericea*) responded appreciably to P enrichment, and other studies have shown that macroalgae are N-limited in northeastern US coastal lagoons (Taylor et al. 1995) and temperate marine bays (Oviatt et al. 1995). Fong et al. (2004) observed that gutweed increased both N and P uptake during high nutrient pulses; in turn decreasing available N and P in the water column, but gutweed retained more N (73–98%) than P (79–88%) in tissues.

The effects of soft shell clams on nutrient cycling in East Harbor may be further influenced by the long water residency time in the lagoon, which prevents excess nutrients from being flushed out of the system (Portnoy et al. 2007). The high water residency time also causes elevated summer water temperatures (up to 35°C) (Portnoy et al. 2007, Smith et al. 2011), which reduce the survival of some gastropod grazers like periwinkles that typically regulate macroalgal growth in functioning salt marshes (Smith et al. 2011). The 2006–2007 macroalgal bloom at East Harbor caused very high clam mortality, and today clam densities remain much lower than they were in 2005 (Thiet et al. in press); thus, the cycle of heavy clam colonization, subsequent macroalgal blooms, and resultant clam dieback may signify this system's process of equilibrating to greater stability in population densities and physical properties following restoration. Nonetheless, although severe macroalgal blooms have not occurred in East Harbor since 2007, macroalgae continue to dominate the aquatic plant community at the site and threaten the productivity of widgeon grass, eelgrass, and benthic fauna (Smith 2011). Seeding the system with certain gastropod grazers may keep algal growth in check, but some gastropods, such as periwinkles, will likely only survive if summer water temperatures at the site are lower (Smith et al. 2011). This can be achieved by increasing the daily tide range in the main lagoon and northwest cove, thereby reducing water temperatures and creating a more hospitable environment for periwinkles. Improving tidal range would also flush out excess nutrients that enhance macroalgal growth by virtue of the fact that water residency time would be substantially reduced (Portnoy et al. 2007). Such alterations would move East Harbor closer to its original, pre-restricted condition. Managers of salt marshes similar to East Harbor that remain partially restricted should prioritize regular, sufficient tidal flushing to reduce nutrient loading and maintain relatively low summer water temperatures; such emphasis may ensure more rapid equilibration toward the desired restoration outcomes.

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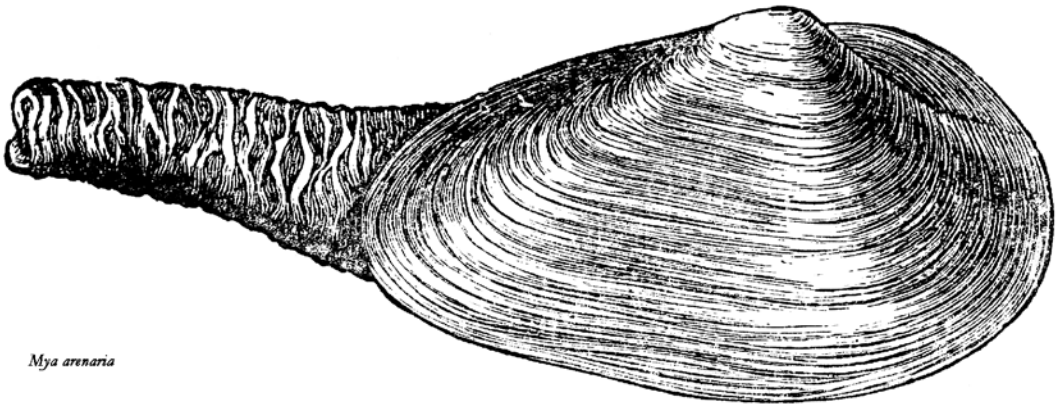

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