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MACROFAUNAL COMMUNITY STRUCTURE FOLLOWING THE RESTOCKING OF NORTHERN QUAHOG (*MERCENARIA MERCENARIA*) TO GREAT SOUTH BAY, LONG ISLAND, NY

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ABSTRACT Overharvest of the once highly abundant northern quahog, or hard clam [*Mercenaria mercenaria* (Linnaeus, 1758)], has decimated local populations on Long Island, NY, and the ecosystem services they provide. Among the potential ecological consequences of the loss of hard clams, impacts on benthic community structure and function have not been well documented. This study took advantage of a large-scale hard clam restoration effort by The Nature Conservancy in Great South Bay, NY, to investigate these parameters. The benthic communities between areas planted with high densities of adult clams (i.e., spawner sanctuaries) and adjacent sites with no transplants were compared. In clam-stocked areas, there were greater trophic and taxonomic group densities, especially for some environmentally sensitive groups such as crustaceans, and increased species richness, which in turn altered community structure of the resident infauna. Differences between paired sites for macrofaunal diversity and community structure were also observed, likely reflecting larger scale differences in invertebrate communities. Minimal differences were observed in sediment porosity, carbon and nitrogen content, and total organic matter between adjacent areas with and without clams, although all of these parameters were significantly associated with community structure. Although shell density was significantly higher in clam-stocked plots, it explained little of the variation in macrofaunal composition on its own or in combination with other environmental parameters, but in combination with the living clams may have added enough environmental complexity to enhance densities of different trophic groups. Within the short period of 3 y, differences in the benthic community with the presence versus the absence of clams were already detectable. More long-term data incorporating the effect of processes at multiple scales are needed to gain insight into the complexity of rehabilitating coastal benthic environments following the removal of important species such as clams. The results of this work support the notion that *M. mercenaria* acts as an ecosystem engineer, modifying the environment by creating habitat and enhancing the abundance of other species.

KEY WORDS: northern quahog, hard clam, *Mercenaria mercenaria*, restoration, macrofauna, Great South Bay, Long Island

INTRODUCTION

For shallow water ecosystems such as estuaries, suspension-feeding bivalve molluscs can drive the dynamics of the entire system. They can serve as food for vertebrate and invertebrate predators such as finfish, large gastropods, crabs, and horseshoe crabs (MacKenzie Jr. 1977, Lowery et al. 2007, Polyakov et al. 2007, LoBue & Bortman 2011, see Shumway 2011 and chapters therein). Shells from bivalves can persist in the marine environment long after the individual has perished (Kidwell 1985, 1991, Powell et al. 1989, Alexander & Dietl 2001). They can accumulate in sufficient density to provide habitat for epibionts and refugia for small mobile fauna (Gutiérrez et al. 2000, Gutiérrez et al. 2003, Hewitt et al. 2005, Commito et al. 2008), which then alter community structure (Lejart & Hily 2011). As infauna, their bioirrigation and bioturbation activities can structure the sediment environment for other organisms, boosting larval recruitment and enhancing primary and secondary production (Aller 1982, Maurer 1983, Norkko & Shumway 2011).

Most bivalves are obligate suspension feeders whose filtering activity can structure the dynamics of entire shallow water ecosystems in numerous ways (Cloern 1982, Kremer & Nixon

2012). Bivalves have been hypothesized to alter benthic communities by reducing infaunal recruitment (Woodin 1976). Alternatively, they have been suggested to enhance benthic community diversity by producing and modifying the environment in ways that provide new habitat and resources for benthic species (Aller 1982). Bivalves can increase pelagic–benthic coupling and exert top–down grazing control of algal populations, thereby reducing turbidity (Loo & Rosenberg 1989, Norkko et al. 2001, Newell 2004, Porter et al. 2004, Cranford et al. 2011, Wikfors et al. 2011, Cranford 2019, Strand & Ferreira 2019). Increased water clarity, greater light penetration, and nutrient availability from bivalve excretion can result in increased growth and expansion of submerged aquatic vegetation, including sea grasses, which can further increase habitat for other organisms (Phelps 1994, Prins et al. 1997, McCay et al. 2003, Newell & Koch 2004, Wall et al. 2008, Carroll et al. 2008, Filgueira et al. 2019). Bivalve filtration can also reduce eutrophication by promoting rates of denitrification (Newell et al. 2002, Cerco & Noel 2007, Petersen et al. 2019).

In addition to their ecosystem roles, bivalves are a source of recreational and commercial harvest (Smaal et al. 2019 and references therein). Overharvest of estuarine bivalves has been strongly linked to the collapse of many coastal ecosystems (Jackson et al. 2001), including overharvest of the northern quahog, or hard clam [*Mercenaria mercenaria* (Linnaeus, 1758)], shellfishery of Great South Bay (GSB), Long Island, NY (Bricelj 2009). Located along the southern edge of Long Island,

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GSB is a well-mixed, shallow, productive lagoonal ecosystem (Carpenter et al. 1991) that sustains a wide variety of finfish (Gabriel 1921, Neville et al. 1939) and shellfish (Gabriel 1921, Greene 1981). Before the mid-1970s, densities of hard clams were high enough to filter a volume equal to the entire GSB in 2.6 days (Kassner 1993). They served as common prey for whelks, crabs, and horseshoe crabs (MacKenzie Jr. 1977, Lowery et al. 2007, LoBue & Bortman 2011), and induced substantial top-down control of pelagic algae (Lonsdale et al. 2009). Great South Bay provided over half of the hard clams consumed in the United States (McHugh 1991, McHugh 2001) until overharvest in the mid-to-late 1970s caused fishery collapse (Buckner 1984, Kraeuter et al. 2005). Densities of clams are now too low to promote successful reproduction for these free-spawning animals (Kraeuter et al. 2005), even though harvest has been dramatically curtailed. It has also been suggested that recovery has been hampered by sporadic blooms of the toxic alga *Aureococcus anophagefferens* (Hargraves & Sieburth, 1988), a brown tide species, since the late 1980s (Bricelj & Lonsdale 1997, Gobler et al. 2005). This toxic alga can impact the cilia of many species of bivalves (Draper et al. 1990), including juvenile *M. mercenaria* (Greenfield & Lonsdale 2002). Although the survivorship of hard clam larvae is not impacted by *A. anophagefferens*, larvae fed this alga have slower growth rates (Padilla et al. 2006) and brown tide appears to be a low-quality diet for larvae (Przeslawski et al. 2008).

Efforts by The Nature Conservancy (TNC) to restore hard clams to the GSB (Doall et al. 2008, LoBue et al. 2008, LoBue & Udelhoven 2013) provided the opportunity to examine the macroinvertebrate composition, community structure, and trophic

function in a protected habitat where clams had been stocked versus nearby benthic environments in the protected bottomlands where clams are still rare. Specifically, this study tested whether the replanting of hard clams affected densities, species richness, and trophic structure of local benthic invertebrates by comparing communities in areas stocked with clams and paired nearby areas where clams had not been stocked.

MATERIALS AND METHODS

In 2004, TNC began seeding 54 km² of privately owned bottomlands in central GSB where previous fishing had removed the vast majority of clams. Adult clams ranging from approximately 4.7 to 11 cm in size were transplanted in 50 evenly spread sites, ranging from 0.5 to 3.5 ha, to create a network of populations of clams at high densities to enhance fertilization success and, hopefully, reduce recruitment limitation. Planted clams were dropped from boats at the surface and allowed to dig into the sediment naturally. Typically, 95% of clams burrowed in the sediment within 24 h. Clams that were harvested the day before planting were found to burrow greater than 99% of the time. In June and September of 2007, three subtidal sites of paired stocked and adjacent nonstocked plots (Fig. 1) were assessed.

Infaunal Organisms

Sampling at each nonstocked area took place 25 m from the edge of the paired stocked area (Fig. 2) to control for differences in local environmental conditions, including salinity, temperature, dissolved oxygen, and sediment type. Macrofauna were sampled in June 2007 along three 25-m transects laid down by

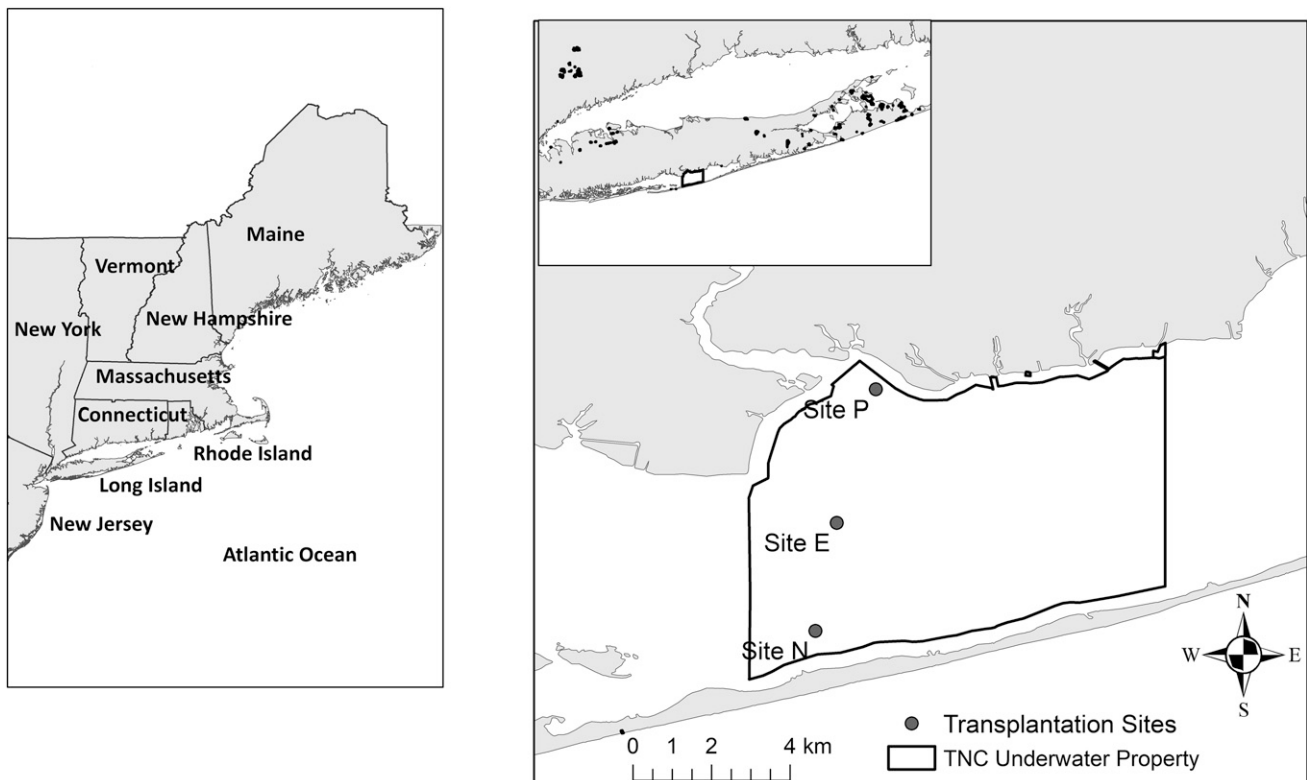


Figure 1. The TNC reserve is located in Great South Bay on the South Shore of Long Island, NY, and is 54 km² in area. The three study sites for this work were approximately equally spaced, spanning from the northern to the southern extent of the TNC reserve.

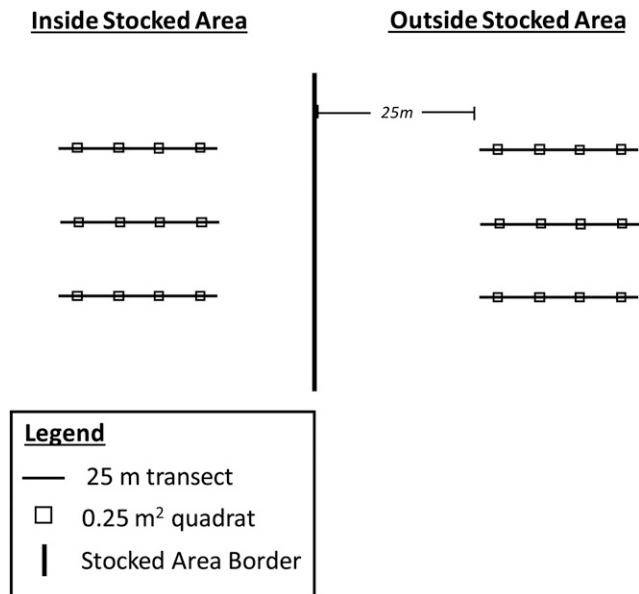


Figure 2. Macrofauna were sampled along three 25-m transects laid down by divers within the stocked areas and at least 25 m from the edge of the stocked area for the paired samples outside of the stocked area. Four 0.25 m² quadrats, spaced evenly along each transect, were sampled.

divers at sites E and P, and in September for site N. Four 0.25-m² quadrats were spaced evenly along each transect, totaling 12 quadrats at each site except for site P where SCUBA malfunctions only allowed for nine quadrats to be sampled. In the center of each quadrat, one 15-cm diameter, 15-cm deep core (sampling area 0.0177 m²) was collected for infaunal organisms. Each core was rinsed through a 1-mm sieve and preserved in 10% buffered formalin. Divers also manually extracted all living hard clams in each quadrat to compare clam and shell densities inside and outside stocked areas. All specimens were identified to the lowest possible taxon, and in many cases to genus and species, and then enumerated. Lower taxonomic groups were aggregated into major taxa, including polychaetes, bivalves, gastropods, amphipods, and other crustaceans to facilitate pairwise comparisons when densities were low. Even after aggregation, taxa classified as “miscellaneous” occurred too infrequently for analysis and were excluded.

Taxa were assigned to feeding guilds based on Ranasinghe et al. (1994), Macdonald et al. (2010), and personal knowledge. Polychaete assignments were made using the comprehensive diet compendiums of Fauchald and Jumars (1979) and Jumars et al. (2015). If a trophic assignment could not be made based on these studies, other sources were consulted. If no data were available for a species, the trophic group of the closest relative with available data was used. Organisms were placed into general trophic groups based on what food material they consume: carnivores, herbivores, and omnivores, as well as where they collect their food: suspension feeders, interface feeders, deposit feeders, and deep deposit feeders. Carnivores exclusively consume living prey items. Herbivores only derive nutrition from photosynthetic biomass. Omnivores subsist on a variety of living and nonliving material. Suspension feeders draw plankton from the overlying water column. Interface feeders consume biodeposits above and below the sediment surface. Deposit feeders consume settled material at and below

the sediment surface. Deep deposit feeders feed on biodeposits just below the surface.

Environmental Variables

Separate cores, 4 cm in diameter and 10 cm deep, were collected within each quadrat for organic matter content (OMC), and 2 cc of surface sediment was collected with syringes for carbon and nitrogen content and sediment porosity. Once returned to the laboratory, all environmental samples were frozen until processed. Each sediment core was cut into 2-cm depth fractions. Total OMC was measured via the loss-on-ignition method (Heiri et al. 2001). Each 2-cm fraction was dried at 60°C and then further subdivided into two subsamples, approximately 5–6 g each. Each subsample was weighed, placed into a crucible, and combusted at 550°C for 4 h and then weighed again. The percent mass lost via combustion was taken as percent OMC. Mean OMC was computed by averaging five equal subsamples of the 10-cm-depth cores. Porosity was quantified from the 2-mL surface sediment sample. The sample was weighed wet immediately after collection, dried at 60°C, and then weighed again. The difference between wet and dry mass was used to quantify porosity. For each syringe sample, triplicate subsamples were weighed and carbon and nitrogen content were then measured with a Flash EA1113 Elemental Analyzer (CE Elantech) and averaged. Hard clam shell and shell fragments were also removed from surface sediment in each plot. Densities of complete hard clam shells (left and right valves) and broken shells with the hinge intact were the only parts of the shell hash used in the analyses.

Statistical Comparisons: Univariate Environmental Parameters, Biodiversity, Taxonomic and Trophic Density, Community Structure, and Relation to Environmental Variables

The data did not meet the assumptions of analysis of variance, even after multiple attempts to transform the data. Differences between treatments for environmental parameters, univariate diversity metrics, and community structure were, therefore, determined by two-way mixed model permutational analysis of variance (PERMANOVA, Anderson et al. 2008) with the following factors: (1) site (site E, N, and P; random factor) and (2) treatment (stocked, nonstocked; fixed factor). Permutational analysis of variance requires independent samples and homogeneous dispersions (Anderson et al. 2006, Anderson et al. 2008), the latter determined by performing PERMDISP tests (Anderson et al. 2008). On occasions where the data failed to meet the assumption of homogenic dispersion, PERMANOVA is still considered to be robust enough to detect differences reliably given the largely balanced design of this study (Anderson & Walsh 2013). If tests for main effects indicated the presence of differences, pairwise PERMANOVA tests were conducted to identify the nature of the significant effect between each pair of factor levels or for the interaction in the case of the two-way crossed test. For comparing environmental parameters, log-transformed univariate parameters were decomposed into Euclidean resemblance measures. For densities of major taxa, trophic group, along with community structure, comparisons were done with the Bray–Curtis resemblance of root-transformed densities. Comparisons of univariate measures of species richness and the Shannon–Wiener index were done with Euclidean distance, with no

transformation applied. In several instances, pairwise computation of distance measures for major taxa and trophic group densities resulted in undefined computations because of all zero samples. All zero samples indicated no occurrence for a particular taxon or trophic group, was deemed uninformative for community composition, and thus removed. A small number of parameters did not meet the homogeneity of dispersion requirement; however, PERMANOVA is considered robust enough to detect differences (Anderson et al. 2008).

Multivariate analyses were conducted in PRIMER v 6.13 (Clarke & Gorley 2006). Interpolation of abiotic factors was conducted using the maximum expectation algorithm in PRIMER to replace missing replicates and to run correlation analyses. Abiotic factors were then normalized and biological data standardized to compensate for unequal replication between sites. Significance of the differences in community structure between sites was tested by PERMANOVA with concomitant contributing taxa identified by similarity percentage (SIMPER) up to a 70% cutoff. Nonmetric multidimensional scaling was conducted to depict community structure of root-transformed densities using Bray–Curtis similarities. The PRIMER routine DistLM was run to find the best combination of abiotic factors that significantly matched with the biotic data. DistLM performs step-wise, distance-based linear modeling using the adjusted R^2 selection criterion to estimate the relative proportion in the biological data explained by each singular and combination of abiotic factors. For all statistical tests, a critical α of less than 0.05 was considered significant.

RESULTS

Faunal Comparisons: Species Richness, Major Taxa, and Trophic Density, Community Structure

Species richness was higher in areas stocked with hard clams at two sites, the northernmost site, P, and the central site, E (Table 1). Shannon–Wiener index (Table 1) was significantly higher in the stocked plot for site E. Adult hard clams were exclusively found in the stocked areas (Fig. 3); none were found in paired sites where clams were not stocked, preventing statistical analyses. There were significant differences in the densities of non-amphipod crustaceans (PERMANOVA, Pseudo- $F = 12.11$, $P = 0.001$), just amphipods (Pseudo- $F = 3.5656$, $P = 0.035$), and all polychaetes (Pseudo- $F = 15.871$, $P = 0.001$) between areas stocked with clams and those not stocked. Pairwise comparisons for amphipods were only

significantly different for site P ($t = 2.9065$, $P = 0.017$). Amphipod densities were significantly different in the stocked plot of site P only ($t = 2.9065$, $P = 0.017$; Fig. 4A). All non-amphipod crustaceans had higher densities in the stocked plots for sites E and P (site E, $t = 3.087$, $P = 0.022$; site P, $t = 3.9684$, $P = 0.001$; Fig. 4B), but for site N, densities were higher in the nonstocked plots ($t = 2.2715$, $P = 0.041$; Fig. 4B). Differences among sites for the polychaetes were mixed. Higher densities were found in the nonstocked plot for site E ($t = 2.4138$, $P = 0.026$) and higher densities were found in the stocked plot for site P ($t = 4.9461$, $P = 0.001$; Fig. 4E). For the remaining major taxonomic groups, no differences were found in densities across pairwise comparisons of sites.

Significant differences were found among sites for densities of most feeding guilds. Carnivores had a higher density in the stocked plot for site P ($t = 2.7058$, $P = 0.015$; Fig. 5A). Herbivores had greater densities in the nonstocked plot at site E ($t = 2.4979$, $P = 0.007$) but were higher in the stocked plot at site P ($t = 2.5486$, $P = 0.002$; Fig. 5B). Site P exhibited the most elevated densities of all trophic groups in the stocked plots. Omnivores ($t = 5.2126$, $P = 0.001$), suspension feeders ($t = 3.0265$, $P = 0.005$), and interface feeders ($t = 5.0337$, $P = 0.001$) had significantly higher densities for most trophic groups (Fig. 5C–E).

Macrofaunal community structure was marginally non-significant as a function of site ($P = 0.052$) but was significant for treatment ($P = 0.003$), and there was a significant site by treatment interaction ($P = 0.001$; Table 2). Furthermore, pairwise comparisons were significant for all sites (Table 2). Ordination of Bray–Curtis similarities illustrated a distinct separation of the community structure inside and outside of stocked sites (Fig. 6). Average dissimilarity calculated by SIMPER ranged from 42.77 to 60.12 and identified six taxa as contributing to differences in community structure in all three sites (Table 3). Presence of polychaetes was the most responsible for differences in community structure between treatments across sites, but the gastropod *Acteocina canaliculata* and unidentified Crustacea also contributed to dissimilarity between treatments among sites. The taxonomic groups identified by SIMPER belonged to the carnivore, herbivore, and omnivore feeding guilds, primarily feeding at and below the sediment surface.

Environmental Variables and Correlations with Faunal Patterns

No significant differences were detected in porosity (Pseudo- $F = 8.7537$, $P = 0.16$) OMC (Pseudo- $F = 6.4558$, $P = 0.162$),

TABLE 1.
Species richness and Shannon's diversity index (H') for each of the three-paired stocked and nonstocked sites.

Species richness	Site	Stocked Mean	Nonstocked Mean	Resem	Den. df	t	P	Perms
	Site E	10.92 ± 0.72	7.5 ± 0.51	ED	22	3.8508	0.002	21
	Site N	18 ± 0.90	18.83 ± 0.93	ED	22	0.64599	0.557	24
	Site P	17.33 ± 0.93	9.83 ± 0.93	ED	19	5.5937	0.001	63
Shannon–Wiener	Site E	2.16 ± 0.07	1.45 ± 0.08	ED	22	6.5969	0.001	991
	Site N	2.51 ± 0.046	2.60 ± 0.06	ED	22	1.08	0.283	998
	Site P	2.03 ± 0.16	1.98 ± 0.10	ED	19	0.28522	0.75	995

Comparisons were conducted with pairwise PERMANOVA of univariate diversity metrics with significant main PERMANOVA test outcomes. Errors are SEM. Bold values indicate $P < 0.05$. Resem, resemblance measure; ED, Euclidean distance; Den df, denominator degrees of freedom; t , t -statistic; Perms, unique permutations.

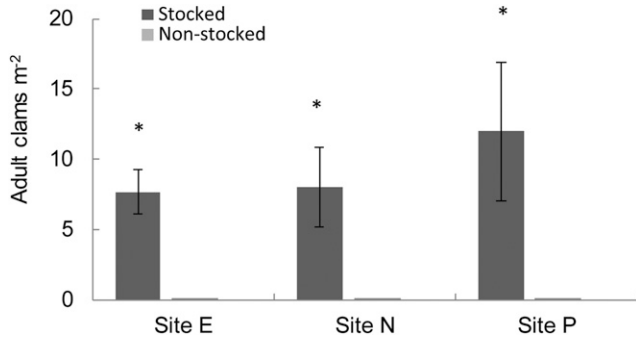


Figure 3. Live adult hard clam densities for each of the transplant areas. No live hard clams were found in adjacent nontransplant areas. Black and gray bars represent stocked and nonstocked treatments, respectively. * Indicates significantly different densities ($P < 0.05$).

carbon (Pseudo- $F = 6.379$, $P = 0.163$), and nitrogen (Pseudo- $F = 0.0502$, $P = 0.921$) content between stocked and nonstocked sites (Fig. 7A–D). Shell and shell fragments were almost

exclusively found in the stocked areas. Shell density was significantly different between paired sites, site E ($t = 5.8977$, $P = 0.001$), N ($t = 3.8084$, $P = 0.002$), and P ($t = 3.7282$, $P = 0.004$) (Fig. 7E).

Of all of the environmental parameters measured, DistLM indicated that OMC in the top 10 cm of the sediment explained 8.96% of the variation in community structure. The only environmental model that was significantly correlated with community structure was the combination of OMC in the top 10 cm, organic carbon and nitrogen, and porosity (Table 4). The full environmental model only explained 22.12% of macrofaunal community structure and was not significant ($P = 0.1613$) (Table 4).

DISCUSSION

The role and nature of ecosystem engineering suspension-feeding bivalves varies among species and traits of species such as reef-forming oysters and mussels to more infaunal species such as pinnids and hard clams. In a large meta-analysis of

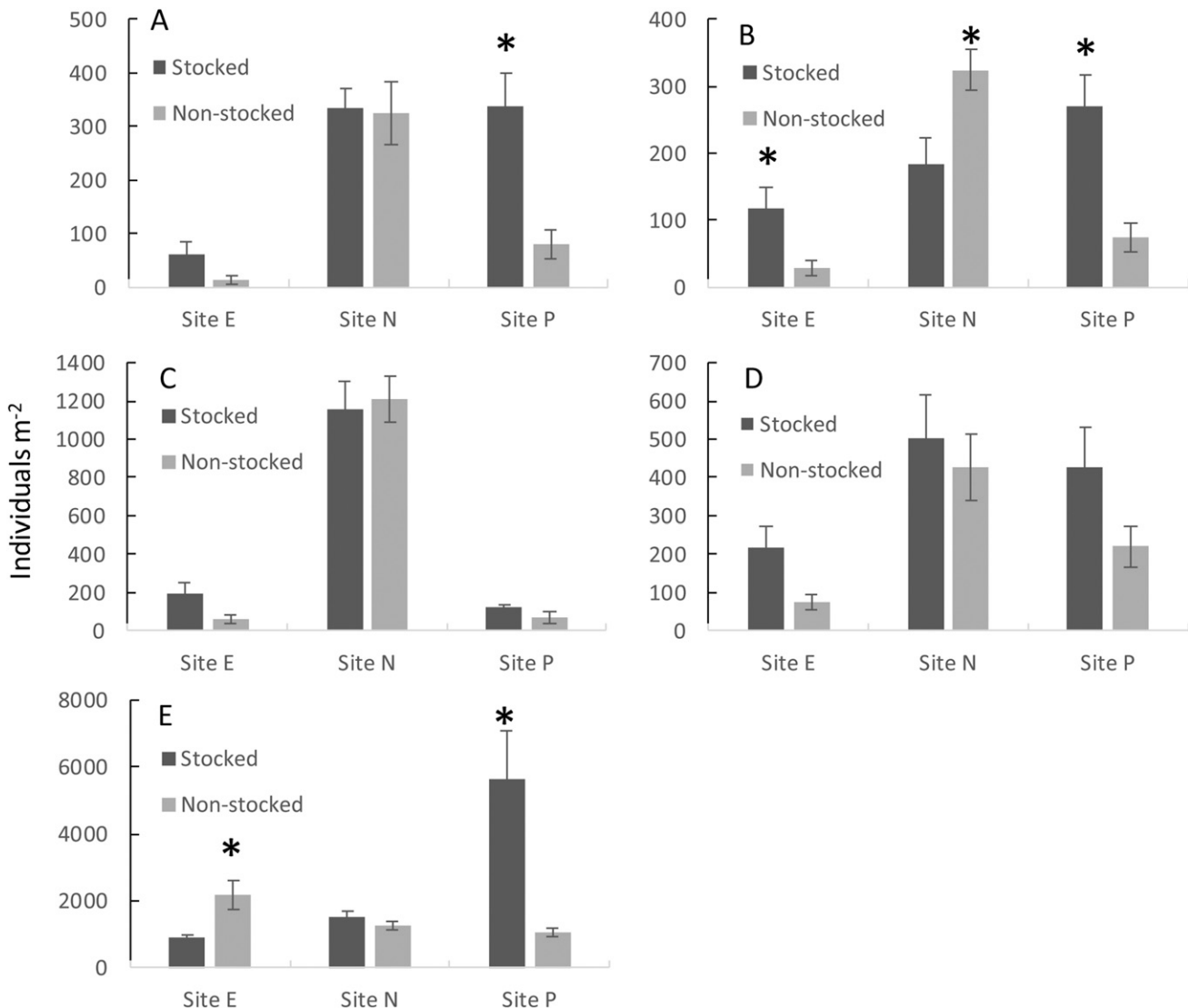


Figure 4. Mean density for major taxa in stocked and nonstocked sites. Error bars represent SEM. (A) Amphipoda. (B) Other Crustacea. (C) Bivalvia (*Mercenaria mercenaria* excluded). (D) Gastropoda. (E) Polychaeta. Black and gray bars represent stocked and nonstocked treatments, respectively. * Indicates significantly different densities ($P < 0.05$).

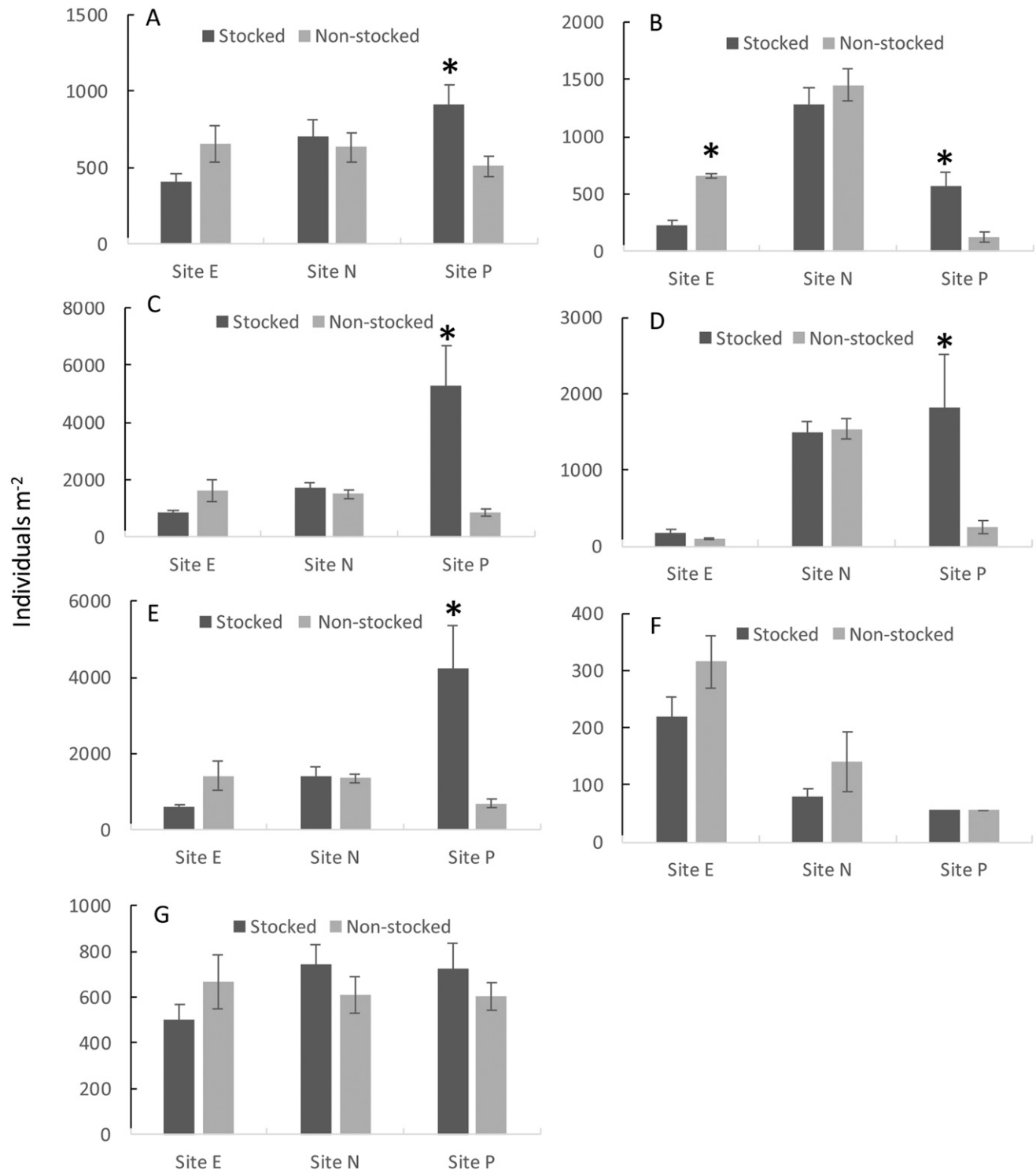


Figure 5. Mean density of feeding guilds in stocked and nonstocked sites. (A) Carnivore. (B) Herbivore. (C) Omnivore. (D) Suspension. (E) Interface. (F) Deposit. (G) Deep deposit. Black and gray bars represent stocked and nonstocked treatments respectively. * Indicates a significant difference ($P < 0.05$). Error bars represent SEM.

engineering bivalve studies, Bateman and Bishop (2017) found that irrespective of trait, all types of foundational bivalves enhanced community species abundance and densities, but the effect size of the response depended on the nature of habitat modification. Reef-building species are epifaunal and their

exposed shell provides more habitat complexity than buried bivalve shell of infaunal species (Gutierrez et al. 2003, Summerhayes et al. 2009). Gregarious species, such as some oysters and mussels, can exert considerable water entrainment when filtering, impacting the survivorship of settling larvae

TABLE 2.
Pairwise PERMANOVA of community structure between stocked and nonstocked hard clam beds in Great South Bay.

Source	Resem	df	SS	MS	Pseudo-F	P(perm)	Perms
Site	BC	2	56,885	28,442	5.0282	0.052	180
Treatment	BC	1	4,586.9	4,586.9	4.5108	0.003	996
Site X treatment	BC	2	11,313	5,656.6	5.5628	0.001	997
Residuals	BC	63	64,063	1,016.9			
Pairwise comparisons	Resem	Den. df			t	P	Perms
Site E	BC	22	–	–	2.1927	0.001	997
Site N	BC	22	–	–	1.8274	0.001	997
Site P	BC	19	–	–	2.5419	0.001	997

Resem, resemblance measure; BC, Bray–Curtis; Den df, denominator degrees of freedom; t, t-statistic; Perms, unique permutations.

(Wilkie et al. 2013), and ostensibly alter community composition of neighboring infauna, a long-held hypothesis regarding the impacts of dense aggregations of suspension feeders (Woodin 1976). Infaunal species, including *Mercenaria mercenaria*, do not appear to have similar impacts. Rather, the impact of high densities of *M. mercenaria*, through burrowing, feces production, and shell accumulation, can enhance larval settlement and colonization, generating an abundant resident infauna (Maurer 1977), and do not reduce the successful recruitment of settling larvae (Maurer 1983).

As an infaunal species, the burrowing, filtering, and metabolic activity of *Mercenaria mercenaria* can alter the surrounding environment, changing sediment characteristics, enhancing pelagic–benthic transfer of organic matter, adding shell to the sediment matrix, and creating habitat resources for other organisms (Aller 1982, Maurer 1983, Gutierrez et al. 2003, McCay et al. 2003, Summerhayes et al. 2009). Like other suspension feeders, *M. mercenaria* can filter large amounts of seawater (15.2–136.6 mL ind⁻¹ h⁻¹; Grizzle et al. 2001 and

references therein, Cerrato et al. 2004, Lonsdale et al. 2009), excrete ammonia and amino acids (large individuals: 35.3×10^6 M/g over a 24-h period, Sma & Baggaley 1976), and release organic carbon (Doering & Oviatt 1986, Doering et al. 1986, 1987). Similar to Maurer (1977), this study found that the density, species richness, and taxonomic density of benthic infauna was enhanced with the presence of hard clams. Especially notable was an augmented abundance of non-amphipod crustaceans. Crustaceans as a group are noted for their sensitivity to ecological change (Phillips 1977, Rinderhagen et al. 2000). Enhanced species richness and taxonomic density bolstered community-level change in areas stocked with hard clams compared with nonstocked areas. These results support the notion that *M. mercenaria* acts as an ecosystem engineer, modifying the environment by creating habitat and enhancing the abundance of other species.

Like other dominant suspension-feeding bivalves (Cummings et al. 1998, Cummings et al. 2001, Norkko et al. 2001, Hewitt et al. 2002, Beadman et al. 2004, Borthagaray & Carranza 2007, Commito et al. 2008), the presence of *Mercenaria mercenaria* resulted in significantly different benthic communities. Communities stocked with hard clams contained different functional structure, as has been seen elsewhere when dominant bivalves are restored (Rodney & Paynter 2006), in bivalve ecosystem engineer stocking experiments (van der Zee et al. 2015), and studies of bivalve engineered/nonengineered habitats (Christianen et al. 2017). Although communities were different between stocked and unstocked sites, identification of possible drivers of change had mixed evidence. The taxa responsible for community differences among sites were few and spanned the gamut of feeding guilds. Multivariate community analyses showed that certain sediment characteristics were individually correlated with community structure: organic matter, carbon, nitrogen, and porosity. There were, however, no significant patterns among sites for differences in these variables. Based on analyses of communities, these sediment variables explained little of the observed variation (from 9% to 20%) in benthic community structure. These results suggest these abiotic parameters are important to community structure, but differences between sites may not have been detected because of processes not measured in this study. Benthic sediment nutrient fluxes from dominant bivalves can be highly density dependent (Sandwell et al. 2009, Jones et al. 2011), and the presence of hard clams can elevate organic loads in the

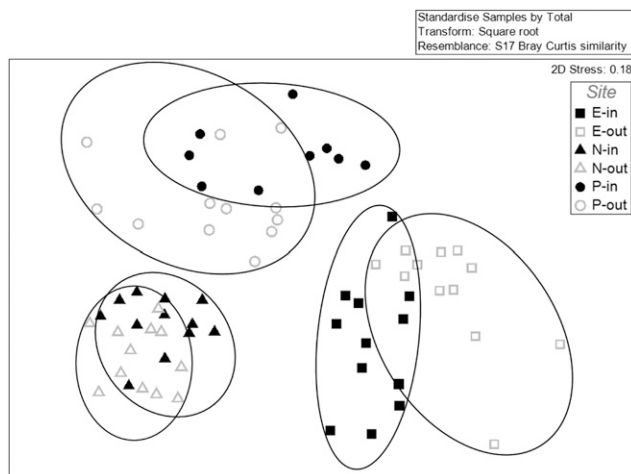


Figure 6. Nonmetric multidimensional scaling of macrofauna Bray–Curtis similarities of root-transformed densities. Symbols indicate paired sites (E = square, N = triangles, and P = circles). Closed symbols represent where clams were stocked (in) and open symbols indicate an adjacent area where clams were not stocked (out). Contours added to help visualize data for each site and treatment.

TABLE 3.
Average and pairwise SIMPER results for each stocked and nonstocked site, at the 70% cutoff.

Taxon	Food location trophic group	Average dissimilarity	Site E	Site N	Site P
		Feeding mode	52.11	42.77	60.12
Mollusca					
<i>Acteocina canaliculata</i>	Deep deposit	Carnivore	5.71	3.56	6.87
<i>Astyris lunata</i>	Interface	Carnivore	–	2.17	–
<i>Ensis directus</i>	Suspension	Herbivore	3.58	–	–
<i>Gemma gemma</i>	Suspension	Herbivore	4.95	–	–
<i>Mya arenaria</i>	Suspension	Herbivore	5.34	2.49	–
Mactridae	Suspension	Herbivore	–	3.64	3.7
<i>Crepidula</i> spp.	Suspension	Herbivore	–	2.31	4
<i>Nucula</i> spp.	Deep deposit	Omnivore	3.88	–	–
Unknown Bivalvia	Suspension	Herbivore	–	4.45	–
Polychaeta					
<i>Polygordius</i> spp.	Interface	Omnivore	11.42	5.17	7.83
<i>Glycera</i> spp.	Deep Deposit	Carnivore	4.47	3.02	5.72
Unknown Polychaeta	Interface	Omnivore	8.71	2.64	4.52
Maldanidae	Deep deposit	Omnivore	3.22	2.8	3.83
Goniadidae	Deep deposit	Carnivore	–	–	2.47
<i>Nephtys</i> spp.	Deep deposit	Carnivore	5.58	–	4.15
<i>Paraonis fulgens</i>	Deposit	Omnivore	6.49	–	–
Paraonidae	Interface	Omnivore	–	3.02	–
<i>Nereis</i> spp.	Interface	Omnivore	–	3.68	5.26
<i>Nereis succinea</i>	Deposit	Omnivore	–	2.41	–
Ampharetidae	Interface	Omnivore	–	3.41	–
<i>Pectinaria gouldii</i>	Deep deposit	Omnivore	–	3.75	–
<i>Pista palmata</i>	Interface	Omnivore	–	5.01	–
Terebellidae	Interface	Omnivore	–	2.72	–
<i>Sabellaria vulgaris</i>	Suspension	Omnivore	–	–	7.05
<i>Lepidonotus</i> spp.	Interface	Carnivore	–	–	3.69
Crustacea					
Ampeliscidae	Suspension	Omnivore	–	4.06	3.69
Ostracoda	Interface	Omnivore	–	2.6	–
Mysidae	Interface	Omnivore	–	–	2.63
<i>Ovalipes ocellatus</i>	Interface	Carnivore	2.41	–	–
<i>Oxyurostylis smithi</i>	Interface	Herbivore	–	3.19	–
Unknown Crustacea	Interface	Omnivore	5.15	2.79	3.75

Cell values are the percent contribution of each species to the observed dissimilarity. Bolded values indicate taxa that contributed to differences across all three sites.

surrounding sediment (Doering et al. 1986, Mojica Jr. & Nelson 1993, Carroll et al. 2008). Research previously reporting the positive association of hard clams and elevated nutrient levels had higher clam densities higher than the current study (Doering et al. 1986, Mojica Jr. & Nelson 1993, Carroll et al. 2008). In this study, clams were stocked at a density of 7.7–12 m⁻², whereas Doering et al. (1986) performed mesocosm experiments with densities greater than 16 m⁻². Mojica Jr. and Nelson (1993) did not report clam densities, but examined hard clams in high aggregation grow-out bags typically used in shellfish mariculture, which can reach into the thousands of seed-sized (10 mm) individuals (Mojica Jr. & Nelson 1993). Indeed, Carroll et al. (2008) recommend establishing hard clams at 16 individuals m⁻² in Long Island estuaries for nutrient levels to effect surrounding habitat during the restoration process.

The density of shell debris was significantly different between clam-stocked and nonstocked sites but was not significantly correlated with community structure. The aggregation of shell debris and living bivalves may have stabilized the benthos,

preventing sediment resuspension, and producing conditions favorable to enhance the benthic community (Gutierrez et al. 2003, Hewitt et al. 2005, Coco et al. 2006, Jones et al. 2011) in a manner that was not captured. In addition, bivalve shell hash can have an effect on sediment pH, enhancing survivorship of juvenile bivalves (Green et al. 2009, Green et al. 2013, Waldbusser et al. 2013).

Historically, GSB had two major shellfisheries, the eastern oyster [*Crassostrea virginica* (Gmelin, 1791)] and *Mercenaria mercenaria*. When co-occurring, shell hash from *C. virginica* can provide predation protection for hard clams (Castagna & Kraeuter 1977, Peterson et al. 1995). Hence, these previously abundant species would have provided habitat and environmental complexity through their physical presence and the postmortem shell added to the sediment matrix. Such complexity is now absent since the extirpation of *C. virginica* a century ago (LoBue & Udelhoven 2013) and the relatively depauperate densities of hard clams throughout the bay since the 1970s. With anthropogenic fishing pressure, which started in the

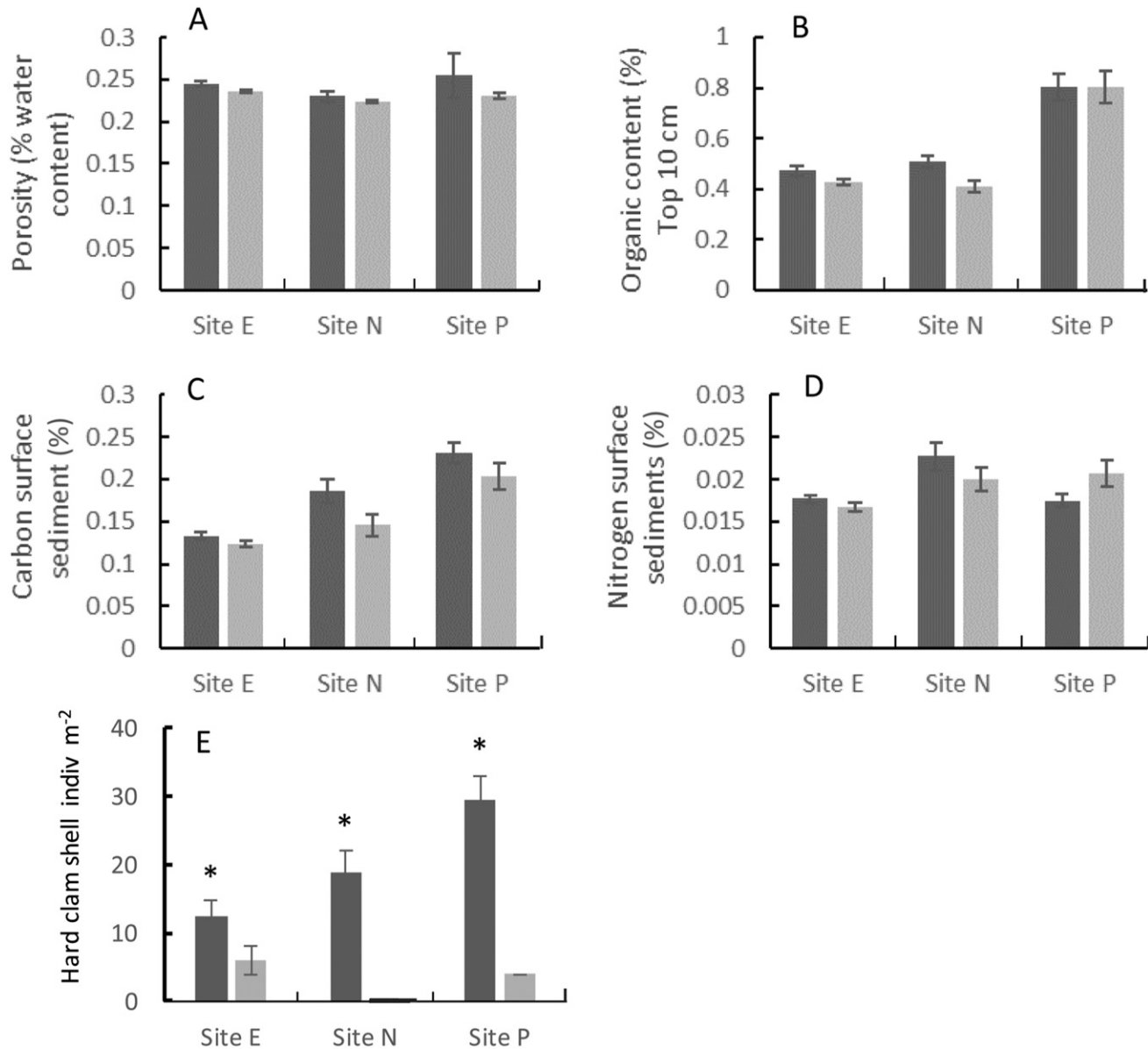


Figure 7. Environmental parameters from Great South Bay sampled simultaneously with benthic infauna (black = stocked, gray = nonstocked). (A) Porosity of the top 2 cm of the sediment. (B) Organic content of the top 10 cm of the sediment surface. (C) Carbon content of 2 cm of sediment surface. (D) Nitrogen content of 2 cm of sediment surface. (E) Density of hard clam shell in each stocked and nonstocked clam bed. Error bars are SEM ($n = 12$ for each site except for P-in, in which only nine quadrats were sampled). Black and gray bars represent stocked and nonstocked treatments, respectively. * Indicates significantly different densities ($P < 0.05$). Error bars are SEM.

1880s, GSB has seen a regime change, switching from a high diversity and trophically complex system to a simpler one lacking key species and connectivity to the ocean (Nuttall et al. 2011). Given the large biological and environmental change seen in GSB over more than 100 y and the relatively short duration (3 y) of this study, recovery for the benthic community in GSB will likely require much more time. Recovery of coastal marine environments from the loss of dominant species may require 15–25 y or more, and recovery may never be to the original state, but rather to an alternative one (Borja et al. 2010).

Over the relatively short period of time of this study, replanted clams increased benthic functional diversity, species

densities and richness, and community structure; however, further study is required to parse out the net impact *Mercenaria mercenaria* has on the abiotic environment, and how that, in turn, impacts benthic infauna, whether the emerging trends found here continue through time. Future experiments should consider the impacts of different densities of hard clams and shell debris at different spatial scales through time and the possible interactions between them. Hewitt et al. (2005) demonstrated that shell debris in mussel beds affects beta diversity of benthic species between patches and that impact was dependent on shell patch size, density, and debris particle size. Indeed, bivalve and shell hash density have been shown to hold a wide range of scale-dependent relationships that strongly

TABLE 4.

Sequential combinations of environmental variables that were significant ($P < 0.05$) for macrofauna community structure in hard clam beds in Great South Bay as indicated by the DistLM function run for 9,999 simulations.

Variables	Adjusted R^2	SS (trace)	Pseudo- F	P -value	Proportion of variation explained	Cumulative proportion of variation explained	Residual df
Organic matter 10 cm	7.60E-02	12,232	6.5933	0.0001	8.96E-02	8.96E-02	67
Organic matter 10 cm and total nitrogen	0.11826	7,454.5	4.2108	0.0010	5.46E-02	0.14419	66
Organic matter 10 cm, total carbon, and total nitrogen	0.13633	4,128.6	2.3809	0.0237	3.02E-02	0.17443	65
Organic matter 10 cm, total carbon, total nitrogen, and porosity	0.15376	3,973.7	2.3388	0.0283	2.91E-02	0.20354	64
Organic matter 10 cm, total carbon, total nitrogen, porosity, and shell density	0.15935	2,406	1.4255	0.1613	1.76E-02	0.22116	63

regulate sediment grain size distribution, macrofaunal diversity, and community structure. This is especially important because the relative distribution and abundance of macrofauna organize along gradients of habitat complexity regulated by dominant bivalve ecosystem engineers (Commito et al. 2008, Sueiro et al. 2011). Additional parameters worth considering are grain size, chlorophyll concentration, and sediment pH. Thus, for managers seeking to rehabilitate coastal benthic environments, restoration of habitat complexity in addition to restoration of important ecosystem engineers may be a goal worth incorporating.

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