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Benthic Ecology of Northern Quahog Beds with Different Hydraulic Dredging Histories in Long Island Sound

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ABSTRACT

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This paper evaluates benthic community composition of four shellfish beds in Long Island Sound near Milford, Connecticut, where northern quahog or hard clams, *Mercenaria mercenaria* (Linnaeus 1758), were harvested by hydraulic dredge. These leased beds reflect a variety of dredging histories; 0 year (dredged just before sampling began), 1 year postharvest, 2 years postharvest, and an inactive clam bed left fallow for at least 10 years. Benthic sediment was sampled at 1- to 2-week intervals from June to October 2011 using a Smith–McIntyre grab. Benthic community composition was significantly influenced by dredging history and sampling month. Abundance of benthic organisms (number of individuals and biovolume) and total organic matter concentrations were significantly greater at the 0-year site than at the 1-, 2-, and 10+-year sites, and significantly greater at the 1- and 2-year sites than at the 10+-site. Newly settled bivalves, primarily *Nucula* spp. and *Yoldia limulata*, were significantly more prevalent on the recently harvested 0-, 1-, and 2-year sites *vs*. the 10+-year site and highest at the 0-year site. A significantly greater number of species was observed on the 1- and 2-year sites *vs*. the 0- and 10+-year locations. Species richness at the 0-year site was significantly lower than at the 1-, 2-, and 10+-year sites, whereas diversity and evenness at the 0-year site was significantly lower than at the 10+-year site. This study observed successional changes in community structure of inshore clam beds related to the length of time elapsed after harvest dredging.

ADDITIONAL INDEX WORDS: *Bivalves, shellfish beds, aquaculture, seabed harvesting, total organic matter*.

INTRODUCTION

Marine benthic communities in the inshore coastal zone are subject to both natural and anthropogenic sources of disturbance. Shallow-water habitats in Long Island Sound (LIS) regularly experience periodic disruption of seafloor sediments that result from seasonal storm and wind events and from the action of tidal currents and waves. Aquaculture activities, such as shellfish harvesting, represent intermittent sources of anthropogenic seafloor disturbance. Hydraulic dredging uses pressurized seawater to loosen clams from surface sediments for collection by a dragged metal cage (Getchis, 2006; MacKenzie *et al.,* 2002). Disruption of the seafloor, whether an outcome of natural or man-made processes, can physically displace surface sediments and dislodge resident organisms from the seabed, altering sediment characteristics and benthic community structure. Impacts on inshore habitat and recovery of benthic assemblages relate closely to the intensity, duration, spatial scale, and frequency of the disturbance (Dumbauld, Ruesink, and Rumrill, 2009).

Hydraulic shellfish dredging to harvest northern quahog or hard clam, *Mercenaria mercenaria* (Linnaeus 1758), has been conducted in Connecticut waters since the 1950s. Nearly 168 square miles (43,511 ha) of LIS seafloor is currently leased to harvesters for shellfish aquaculture (Getchis, 2005). Clams are collected from leased beds over a period of hours or days and effort varies with type of harvest activity, crop cycle, and size of cultivated beds (Dumbauld, Ruesink, and Rumrill, 2009). Postharvest, beds remain undisturbed for 2 to 5 years while small clams left behind by the dredge grow to market size. Reseeding of beds occurs naturally through seasonal settlement and recruitment or by transfer of clams from other locations. Commercial aquaculture produces more than 450,000 bushels of clams annually and contributes maritime jobs, revenue, and a source of sustainable, locally grown, high-quality seafood to Connecticut's economy (Connecticut Department of Agriculture, 2014). Shellfish harvest activities in LIS have been a factor shaping benthic community composition in the inshore coastal zone for more than half a century.

Successional processes related to natural disturbance of benthic communities have been well studied in LIS (*e.g*., McCall, 1977; Rhoads, McCall, and Yingst, 1978; Sanders, 1958). Abundance and distribution of organisms vary according to the stage of postdisturbance recovery, with species typically exhibiting either an opportunistic or equilibrium life-history strategy (McCall, 1977). Recolonization of benthic fauna in disturbed areas is shaped by a variety of synergistic factors including environmental conditions (*e.g*., sediment type, hydrodynamics), life-history characteristics (*e.g*., feeding mode, adult motility), population processes (*e.g*., life span, generation

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time), seasonal cycles (*e.g.*, reproductive cycles, settlement), and biotic interactions (*e.g.*, predation, competition) (Rosenberg, 2001; Zajac, Whitlatch, and Thrush, 1998; Zajac and Whitlach, 1982). The variable nature of the inshore environment contributes to the potential for more than one pattern of postdisturbance recovery (Probert, 1984). Long-term biological recovery, then, indicates re-establishment of an equilibrium community, rather than a wholesale return to the pre-existing assemblage, since even in the absence of disturbance, a community may not remain stable (Seiderer and Newell, 1999). Adaptive strategies displayed by infauna in response to seafloor disruption may account for spatial and temporal variability in population abundances (McCall, 1977).

Compositions of infaunal communities in LIS are closely tied to sediment texture and grain size (Zajac *et al.*, 2000). Patterns of community structure and abundance are influenced by the relative proportions of silt and clay making up sediments, as deposit feeders show a preference for finer, organically rich sediments, whereas suspension feeders are generally more numerous in slightly coarser sediments (Sanders, 1956). A study of soft-sediment communities by Sanders (1956) identified 119 species of benthic fauna and a dominant "*Nephtys incisa–Yoldia limulata*" community type in LIS's central basin. Another study, conducted south of New Haven Harbor, identified three successional LIS communities: opportunists found in high numbers during initial recolonization, *e.g., Streblospio benedicti, Capitella capitata, Ampelisca abdita*; species at peak abundance during the mid-stage of succession, *e.g.*, the bivalves *Nucula proxima* and *Tellina agilis*; and climax community species with low population densities, *e.g.*, polychaete *Nephthys incisa* and bivalve *Ensis directus* (McCall, 1977; Rhoads, McCall, and Yingst, 1978). Observations from these studies suggest that although the species composition of LIS has remained generally consistent over time, changes in species abundance and dominance may occur (Zajac *et al.,* 2000).

Recent studies in LIS have examined short-term effects of shellfish harvesting on benthic communities and sediment biogeochemistry by comparing newly harvested clam beds to sites dredged 1 to 2 years ago (Goldberg *et al.,* 2012, 2014; Meseck *et al.*, 2014). These studies, which showed little difference in species composition or abundance between dredged and adjacent uncultivated beds over weeks to months, suggest that dynamic inshore coastal areas favor establishment of communities resilient to disturbance. The present study examines longer-term ecological changes in benthic community structure on clam beds allowed to remain uncultivated over a broader time frame: 0 year (harvested just before sampling), 1 year postharvest, 2 years postharvest, and an inactive, not-dredged bed, undisturbed by harvesting for at least 10 years (10+).

METHODS

A field experiment was conducted on four leased shellfish beds where hard clams were periodically harvested. Study sites, distributed within a 60-ha area, reflect a range of dredging histories: 0 year (dredged just before sampling), 1 year postharvest, 2 years postharvest, and an inactive bed, not dredged for 10+ years. Sites were located within the same embayment, west of Charles Island, near Milford, Connecticut, within 1200 m of a midpoint 41°11.206′ N and –73°4.341′ W (Figure 1). Seawater depth in the study area varied with tidal cycle from 3.1 m to 4.9 m.

Hydraulic Harvesting

Hydraulic dredging at the 0-year site was conducted 17–30 June 2011 by the commercial clam vessel F/V *Raging Bull*, operated by the Jesse D. Shellfish Company. Clams were placed on this transplant bed during the previous year. The hydraulic dredge measured 61 cm wide, weighed 204 kg, and produced 1.97 kg/cm^2 of water pressure passing through 30.5 m of 10.2-cm hose to a 1-cm-diam manifold pipe. The manifold was positioned 35.6 cm from the teeth, which were set at a 12° angle, resulting in sediment penetration to a depth of 25–76 mm. The dredge was towed at speeds of 1.2 to 1.6 knots. The same commercial clammer also harvested the 1-year site during 2010 (see Goldberg *et al.*, 2014) and the 2-year site during 2009, using a similar dredge (Goldberg *et al.,* 2012). The 10+-year bed was held by the State of Connecticut Department of Agriculture, Bureau of Aquaculture, and so remained uncultivated for an extended period (Thomas Barrell pers. commun.).

Sediment Sampling, Grain Size, and Total Organic Matter (TOM)

Each study site was divided into two replicate plots, designated A and B. Plots measured 0.7 to 1 ha in size and were further subdivided into nine sampling boxes. Benthic sampling was conducted at 1- to 2-week intervals from June to October 2011 aboard the National Oceanic and Atmospheric Administration Fisheries R/V *Victor Loosanoff*. Sediment was collected from three randomly selected boxes within each replicate (A and B) at all four study sites (10+ years, 2 years, 1 year, and 0 year) using a Smith–McIntyre grab. This provided a total of 24 sediment samples, six per study site. Sediment grab samples had an approximate surface area of 0.1 m^2. Sediment depth (mm) was measured for each grab sample and a subsample of 50 g of sediment was removed for grain size and TOM analysis. GPS coordinates were recorded for each individual grab.

For grain size determination, sediment samples were dried at 60°C, acid washed with 1 M hydrochloric acid to remove shell matter, wet sieved to remove fine sediment (<63 μm), and dried again at 60°C. Next, sediment was dry sieved for 20 minutes using a Meinzer II sieve shaker into the following size fractions: 1 mm, 500 μm, 250 μm, 125 μm, 63 μm, and <63 μm (from wet sieving) for classification according to Wentworth (1922).

Sediment samples were dried at 60°C and TOM was determined by the loss-on-ignition method (Nelson and Sommers, 1996). Briefly, a weighed sample was placed in a ceramic crucible and heated at 440°C overnight. The organic matter content represents the difference between the initial and final sample weight.

Sediment collected in the grab was immediately washed through 4-mm and 1-mm sieves while aboard the boat. Live animals on the 4-mm screen were identified and released, whereas all the material retained on the 1-mm screen was transferred to storage jars and held on ice for sorting at the laboratory. Samples were sorted using 10× lighted magnifiers;

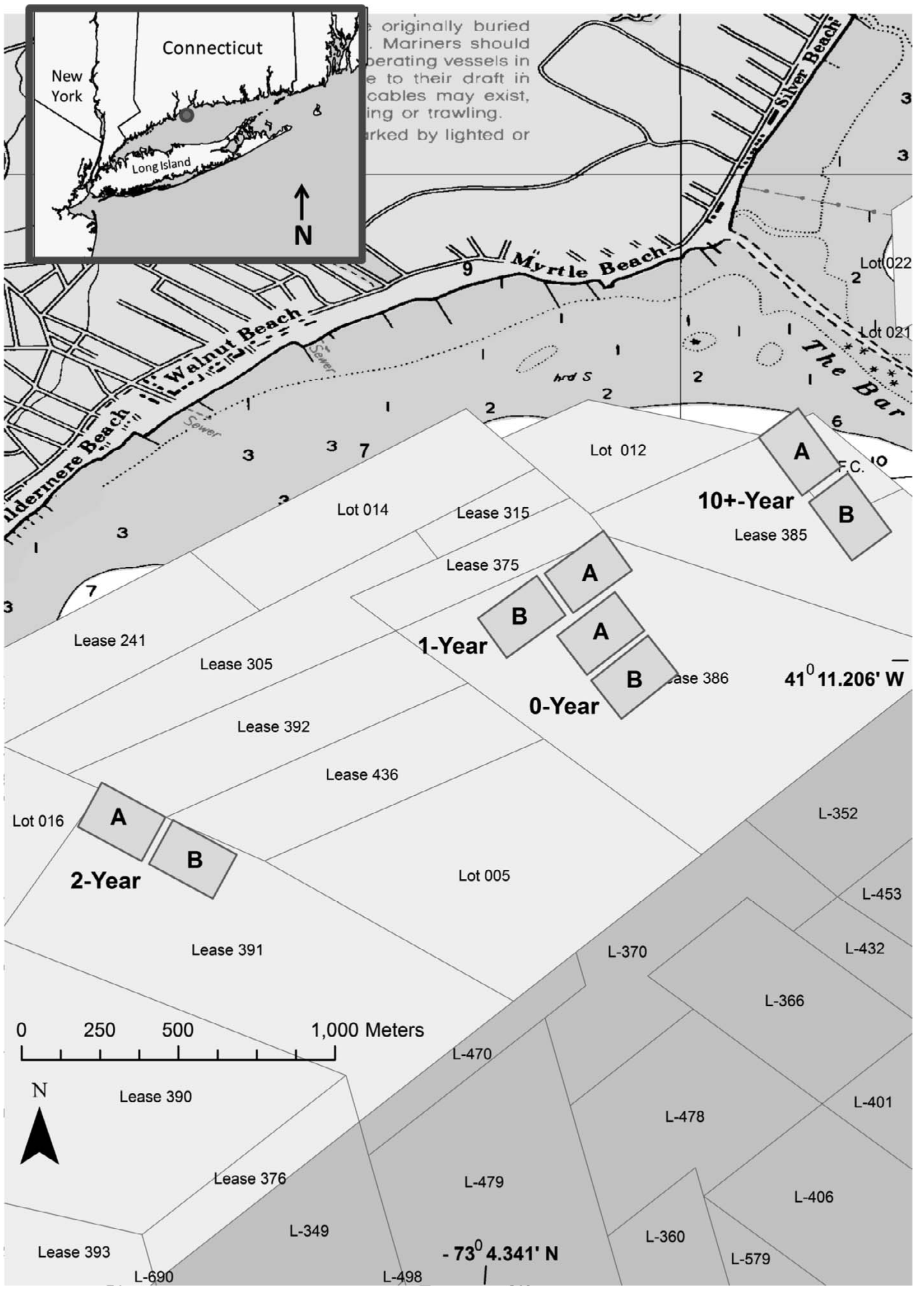

Figure 1. Study site in Long Island Sound (inset) off the coast of Milford, Connecticut, U.S.A. Four leased beds were sampled, each with different harvesting histories: 0 year, 1 year, 2 years, and 10+ years postharvest. Boxes show replicated plots for each treatment.

live organisms were removed and held in a refrigerator for 24–48 hours. Organisms were then counted and identified to the lowest taxon possible (Gosner, 1978; Morris, 1947; Pollock, 1943; Smith, 1964; Weiss, 1995). Biovolume was determined by volume displacement in seawater of all organisms in a grab sample using a graduated cylinder.

Environmental data (temperature, salinity, and dissolved oxygen) were measured near the sediment–water interface at the beginning and end of each sampling trip by a handheld Yellow Springs Instrument Co. ProDO optical dissolved oxygen and temperature meter, and a Yellow Springs Instrument Co. salinity, conductivity, and temperature meter.

Statistical Analysis

Benthic assemblage data were analyzed using the statistical software program PRIMER version 6 (Clarke and Gorley, 2006) with the PERMANOVA (permutational multivariate ANOVA [MANOVA]) add-on (Anderson, Gorley, and Clarke, 2008). A square-root transformation was applied and the Bray–Curtis

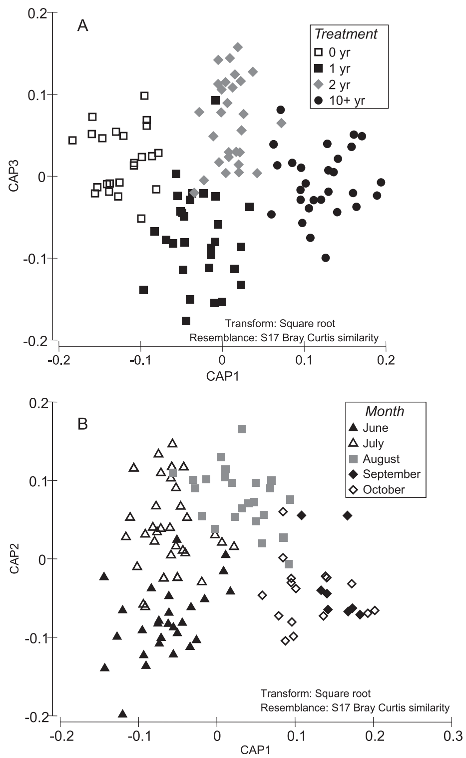

Figure 2. Canonical analysis of principal components identifying organisms associated with (a) dredging treatment and (b) sampling month.

resemblance measure was used to generate the similarity matrix. Nonmetric multidimensional scaling (MDS) plots were used to visualize sample relationships in the benthic assemblage data. The PERMANOVA routine was used to test for differences between treatments (time after dredging), sampling interval (weeks), and plot (nested in treatment) with grain size as a covariate. The canonical analysis of principal coordinates (CAP) routine was used to identify organisms in the benthic assemblage that were associated with treatment (time after dredging) and season (sampling month). Analysis of similarity (ANOSIM) tests were used to look for effects of dredging treatment and season on benthic assemblage composition. The PERMDISP (homogeneity of dispersions) routine (Anderson, Gorely, and Clarke, 2008) was used to test the homogeneity of multivariate dispersions or the patterns of distribution of individual organisms within the four dredging treatments. A bootstrap-based modified t test was used to test for differences in grain size between treatments, and grain size between plots within individual treatments (Wilcox, 2003). A bootstrap-based repeated-measures analysis, using difference scores and a 20% trimmed mean as the location estimator, was used to compare postdredging treatments over time for ecological parameters (number of species, number of individuals), Margalef richness (total number of different organisms present, not taking into account the proportion and distribution of each species), Shannon diversity (an index that accounts for both the richness and the percentage of each species within a benthic community sample), Pielou evenness (an estimate of how evenly individuals are distributed among the different species present), biovolume, and molluscan phyla, as well as a chemical parameter, TOM.

Individual plots were averaged to generate a single time series per dredging treatment for comparison.

RESULTS

Environmental parameters were measured during each sampling event. Seawater temperatures ranged from 14.4 to 23.6°C over the study period. Mean salinity measured 25.8 ± 0.09 SE, and mean dissolved oxygen values were above saturation at 6.59 ± 0.37 SE parts per million.

PERMANOVA detected a significant effect of sediment grain size ($p = 0.0001$), dredging treatment ($p = 0.0014$), sampling week ($p = 0.0001$), plot (nested in treatment; $p = 0.0001$), and the interaction between treatment and week ($p = 0.0001$) on benthic assemblages. A pairwise comparison of treatments for individual weeks was performed to check this interaction, but the number of permutations was limited because of small sample size (24), and none of the pairwise comparisons was significant.

Mean grain size (Φ) measured 3.12 for 0 year, 2.76 for 1 year, 2.51 for 2 years, and 2.51 for 10+ years. Sites were characterized as fine (1, 2, 10+ years) to very fine (0-year) sand sediments. Sediment Φ size differed significantly among the dredging treatments (all $p \leq 0.013$), except for the 10+- and 2-year site comparison ($p = 0.41$); therefore grain size was incorporated as a covariate into the PERMANOVA routine.

The ANOSIM test detected significant differences in benthic assemblages among all of the treatments (all $p = 0.001$), with the greatest difference between the 0-year and 10+-year sites ($R = 0.872$). Differences between the 1- and 2-year sites, although significant, were less pronounced, and had the lowest R value of all paired comparisons ($R = 0.163$). All other paired treatments had intermediate R values (0.381–0.544). These differences were apparent in both the MDS plot (not shown) and the CAP plot (Figure 2a). CAP analysis was used to identify which species were correlated with each dredging treatment. Species that increased or decreased in abundance in association with the 0-year or 10+-year sites are listed in Table 1. Presence of the bivalves *M. mercenaria, Mulinia lateralis*, *Mya arenaria, Nucula* spp., *Yoldia limatula,* gastropods, *Haminoea solitaria, Illyanassa trivittata, Turbonilla* spp. polychaetes *Nepthys* spp., *and Pectinaria gouldii* was correlated (>0.25) with the 0-year site. Organisms associated with the 10+-year treatment included the amphipods *Ampelisca* spp., *Leptocheirus pinquis*, bivalves *Crassostrea virginica, E. directus*, crustacean *Xanthidae* spp., echinoderm *Leptosynapta* spp., gastropod *Crepidula fornicata*, nemertean *Lineus* spp., and polychaetes *Clymenella torguata, Drilonereis* spp., *Melinna cristata,* and *Phylodoce* spp. Several species associated with the 1- and 2-year communities also overlapped with the 10+-year site, suggesting a transition in species composition with time after harvest. The gastropod *Crepidula fornicata* was correlated with both the 10+-year and 1-year sites. Species dominating the 2-year treatment included several species also associated with the 10+- year (*H. solitaria, Mya arenaria, P. gouldii*) and 1-year sites (*Melinna cristata*). The bivalve *Anadara transverse*

Table 1. *Dominant species associated with 0-year and 10+-year postharvest treatments, as determined by canonical analysis of principal coordinates (Spearman correlations >25%).*

	Correlation Coefficient
Species Associated w/ 0 Years	
Yoldia limatula	−0.76
Nucula spp.	−0.72
Turbonilla spp.	−0.66
Nephtys spp.	−0.63
Haminoea solitaria	−0.59
Mercenaria mercenaria	−0.55
Illyanassa trivittata	−0.39
Mya arenaria	−0.29
Mulinia lateralis	−0.26
Pectinaria gouldii	−0.25
Species associated w/ 10+ Years	
Lineus spp.	0.60
Ampelisca spp.	0.53
Phylodoce spp.	0.47
Clymenella torquata	0.47
Crassostrea virginica	0.40
Crepidula fornicata	0.40
Xanthidae spp.	0.39
Ensis directus	0.32
Leptocheirus pinquis	0.29
Drilonereis spp.	0.29
Melinna cristata	0.26
Leptosynapta spp.	0.25

and the isopod *Edotea* spp. were correlated with 2-year site only.

Sampling month influenced the composition of the benthic assemblages, as shown in the CAP plot (Figure 2b). ANOSIM results based on sampling month indicate that benthic assemblages for all months differed significantly ($p \leq 0.027$) except for comparisons between August and September and September and October. Seasonal differences in benthic assemblages were most pronounced between the months of July and October ($p = 0.001$; $R = 0.312$).

PERMDISP found that dispersion in benthic communities within treatments across the sampling period was greatest in the 10+-year treatment, whereas the 0-year assemblages showed the lowest dispersion. The 1- and 2-year treatments showed an intermediate level of within-treatment variability.

Repeated-measures analysis detected significant differences between dredging treatments for number of species, number of individuals, Margalef richness, Shannon diversity, Pielou evenness, biovolume, mollucan phyla, and also for TOM (Table 2). The number of individuals at the 10+-year site was significantly lower than at the other treatments (Figure 3a). The 1- and 2-year sites contained significantly more species than the 0-year and 10+-year sites (Figure 3b). Significantly more mollusks were found on the 0-year bed *vs*. the other locations, and the lowest number of mollusks was observed at the 10+-year site (Figure 3c). Margalef indicated significantly lower species richness at the 0-year site compared with the 10+-, 2-, and 1-year sites, which did not differ. The Shannon and Pielou indices indicated lower diversity and evenness at the 0-year compared with the 10+-year site. Biovolume of organisms was significantly higher at the 0-year site *vs*. the 10+-, 2-, and 1-year sites, whereas biovolumes at the 1- and 2-year sites were significantly greater than at the 10+-year location. TOM (mg/g) was significantly greater at the 0-year site as compared with the 1-, 2-, and 10+- year sites (Figure 4), whereas TOM concentrations were significantly lower at the 10+-year site compared with the 0-, 1-, and 2-year sites. TOM at the 1- and 2-year postharvest sites did not differ.

DISCUSSION

This study observed significant differences in benthic community structure related to the hydraulic dredge harvesting history of clam beds. Some differences in benthic assemblages were apparent immediately after dredging disturbance (*e.g.*, the newly harvested 0-year site), whereas other differences were related to the time interval since dredging. The recently harvested 0-year site was very similar to the predominant central basin, LIS benthic community described by Sanders (1956) over 50 years ago, typically composed of suspension (*P. gouldii* [*Cistenoides* old name], *Mulinia lateralis)* and deposit feeders *(Nephtys incisa*, *Nucula proxima, Y. limatula*).

Natural or anthropogenic changes in seafloor conditions and sediment characteristics after disturbance may reduce habitat suitability for certain organisms while offering a more favorable environment for others (Sparks-McConkey and Watling, 2001). Recently disturbed environments are typically recolonized by pioneer species with rapid reproductive cycles, brief life spans, and high dispersal rates (Rhoads, McCall, and Yingst, 1978; Thistle, 1981). Periodic disruption of the seafloor is necessary for some species to persist in marine soft-bottom communities (Thistle, 1981). In a South Carolina study, organisms were more abundant in mechanically harvested tidal creeks *vs*. unharvested reference creeks within a few weeks of harvest (Maier *et al.,* 1998). In LIS studies examining short-term effects of hydraulic shellfish dredging, few significant differences were observed in direct comparisons between adjacent dredged and not-dredged clam beds in the first few weeks and months immediately after harvest (Goldberg *et al.,* 2012, 2014). The present study observed higher biomass and quantity of individual organisms during the first few years after harvest, followed by a reduction in biovolume and overall abundance within 10+ years postdredging.

Bivalve mollusks comprised the largest proportion of species associated with the 0-year site, and were significantly more abundant on this newly dredged bottom. Suspension-feeding clams are considered early colonizers in LIS, known to settle in nearshore, high-current, disturbance-prone areas (Rhoads, McCall, and Yingst, 1978). A previous study on a Connecticut shellfish lease found greater numbers of newly settled hard clams on recently dredged seabed compared with nearby not-dredged bottom (Goldberg *et al.,* 2014). Increased numbers of settling bivalves have been observed after harvest at other locations along the eastern seaboard (*e.g.,* Kyte, Averill, and Hendershott, 1976; Pfitzenmeyer, 1972a,b; Rice, Hickox, and Zehra, 1989). A pulse of bivalve settlement was observed, primarily *Nucula* spp., at the newly harvested site during mid-July, 3 weeks after dredging, which may indicate a localized settling event related to recent bottom cultivation. A spike in young-of-the-year *Y. limatula* was similarly observed during late July. In a study of sediment texture and molluscan abundance in LIS, Franz (1976) observed low evenness and high dominance in the *Nucula*/*Nepthys*/*Yoldia* infaunal

Table 2. *Results of repeated-measures tests for ecological indices and total organic matter comparing clam beds with different dredging histories. Number indicates which year was consistently greater in the pairwise comparison;* p*-values indicated by * ≤ 0.05, ** ≤ 0.01, *** ≤ 0.001, ns = not significant.*

	Number of Species	Number of Individuals	Margalef Richness	Shannon Diversity	Pielou Evenness	Biovolume	Mollusks	Total Organic Matter
0 *vs.* 1	1***	ns	1***	ns	ns	0***	0**	0*
0 *vs.* 2	2***	ns	2**	ns	ns	0**	0***	0***
0 *vs.* 10	ns	0***	10***	10*	10*	0***	0***	0***
1 *vs.* 2	ns	ns	ns	ns	ns	ns	ns	ns
1 *vs.* 10	1**	1***	ns	ns	ns	1***	1***	1***
2 *vs.* 10	2**	2***	ns	ns	ns	2***	2***	2***

community. The presence of very fine sediments (3.12 Φ) at the 0-year site may account for the high abundance of newly settled bivalves observed in this study, as both *Nucula* spp. and *Y. limatula* are highly associated with very fine sand bottom (Franz, 1976; McCall, 1977; Sanders 1956).

Cultivation of sediments by hydraulic dredging may alter the physical and chemical properties of bottom sediments in such a way that settlement, recruitment, or survival of young shellfish is enhanced. Slightly smaller sediments at the 0-year site, compared with the other locations, may reflect a geographic gradient of decreasing particle size, or may indicate resuspension of sediments into the water column by recent dredging activity and subsequent size grading as material resettled on the seafloor (Sparsis, DeAlteris, and Rice, 1993). Tilling of the seafloor by harvesting may resuspend, disperse, and redistribute finer sediment components (Maier *et al.*, 1998), potentially increasing TOM and food availability for bivalves. Higher TOM concentrations at the 0-year site *vs.* the other locations may be attributed to a variety of factors including (1) generally higher deposition of TOM at the 0-year site, (2) remixing of not-yet-decomposed organic matter back into sediments during dredging, (3) less bioturbation activity resulting in a slower rate of degradation, or (4) a combination of these factors. Conversely, greater biodiversity at the 10+-year site suggests more bioturbation, greater reworking, and a higher rate of degradation of organic matter in the sediments, which would account for consistently lower TOM than found at the other sites. In a study in Italy, Fiordelmondo *et al.* (2003) observed increased nutritional availability of sediment organic matter after clam harvesting. Deposit-feeding mollusks, such as *Nucula* spp. and *Y. limatula*, obtain nourishment from processing organically rich surface sediments (Sanders, 1956). Higher numbers of newly settled mollusks on recently harvested bottom may reflect a habitat preference for slightly finer sediments, increased survival due to the presence of greater food availability via elevated TOM, or reflect short-

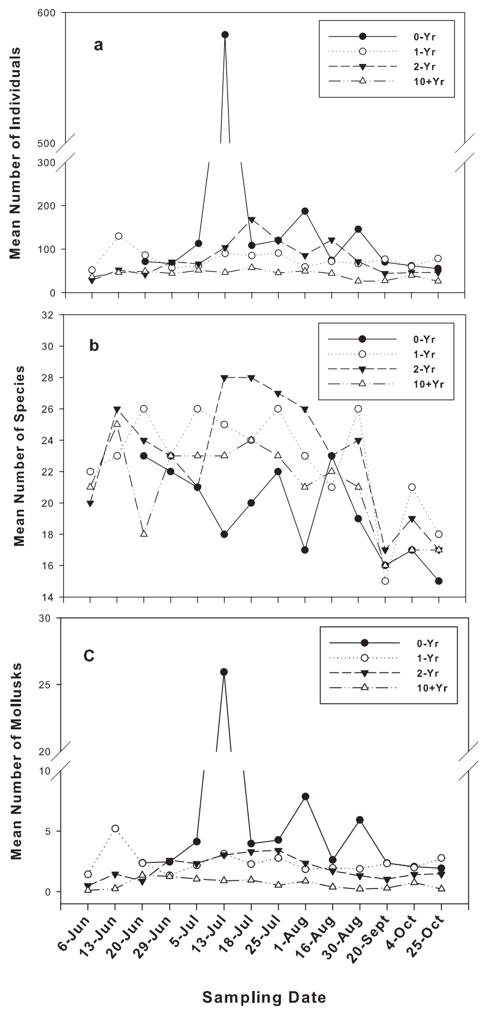

Figure 3. Mean number of individuals (a), mean number of species (b), and mean number of mollusks (c) on clam beds with different dredging histories from June to October 2011.

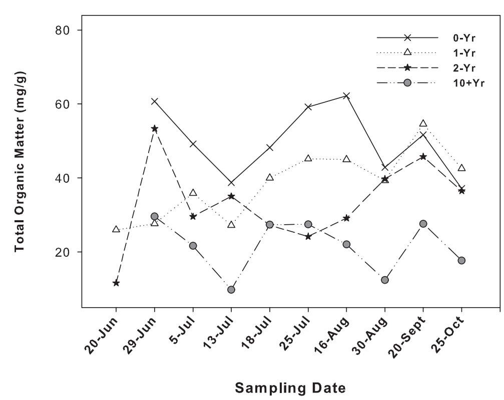

Figure 4. Mean total organic matter (mg/g) for clam beds with different dredging histories from June to October 2011.

term changes to sediment chemistry, texture, or particle size mediated by harvesting activities.

The 1- and 2-year postharvest sites contained a significantly greater number of species than found at the newly harvested 0-year and fallow 10+-year locations, suggesting ongoing recolonization during the first few years postharvest. When disturbance occurs at regular intervals, recruitment and productivity may remain high (Rhoads, McCall, and Yingst, 1978). Although recolonization of disturbed bottom generally occurs rapidly in the inshore coastal zone (Sparks-McConkey and Watling, 2001), recovery of benthic communities can continue for months (Thistle, 1981). In a study of hydraulic clam dredging in Canada, an increase in abundance of nontarget species, a decline in taxonomic distinctness, and continued recolonization of the seafloor was observed up to 2 years postharvest (Gilkinson *et al*., 2005). Species richness, diversity, and evenness indices did not differ among the 1-, 2-, and 10+-year beds, indicating a greater similarity between these communities, *vs*. the recently harvested bed. Our study suggests that 1 to 2 years after harvest represents a transition period between colonization by early pioneer communities and establishment of longer-term equilibrium assemblages, when species representing both life-history strategies may co-occur.

The community of species correlated with the 10+-year site reflected a broader range of phyla and functional ecological roles than those associated with the 0-year site. Ecological indices (species richness, diversity, evenness) were higher at the fallow 10+-year site than the newly harvested location. Environments that remain uncultivated for an extended period would be expected to surpass initial stages of recolonization and include species that require a longer time frame to establish and more constant conditions to be sustained. When harvesting occurs intermittently, a wider variety of organisms may accumulate over time, reflective of natural variations in annual year class strength and seasonal abundance cycles. Other LIS studies of successional processes have also noted reduced diversity on newly recolonized seafloor and more varied and longer-term communities in less frequently disturbed locations (McCall, 1977). Gradual migration of adults into disturbed patches may also contribute to more complex community composition over time (Zajac and Whitlach, 1991). The assemblage of species found at the 10+-year site indicates progression toward establishment of an equilibrium community. Molluscan species like *Crassostrea virginica* and *Crepidula fornicata*, which attach and adhere to substrate, were closely associated with the fallow 10+-year site, where the bottom remained more stable. Polychaetes represented a greater proportion of the most common species at the 10+-year site, suggesting a proliferation of these species in undisturbed sediments. Older, established communities typically support a greater diversity of organisms, but at a lower carrying capacity than opportunistic pioneer communities. However, the presence of regular disturbance events in LIS habitats suggests that few communities consistently achieve or sustain mature successional composition (Rhoads, McCall, and Yingst, 1978).

Benthic community composition was significantly influenced by month of sampling, independent of dredging history. Species assemblages showed distinct patterns associated with sampling month that were apparent regardless of harvest year. Rising spring and summer seawater temperatures trigger spawning events, larval settlement, and recruitment that increase benthic population size, whereas declining autumn temperatures signal a slowdown in overall productivity and abundance. Previous short-term studies of early summer hydraulic dredging in LIS found sampling month to have a greater influence on seafloor community composition than one-time harvesting when followed over a single growing season (Goldberg *et al.,* 2012, 2014). Natural shifts in dominant taxa and benthic community structure related to season are generally apparent regardless of the stage of postharvest recovery (Maier *et al*., 1998).

CONCLUSIONS

Successional changes in benthic community composition related to hydraulic harvesting history were observed on LIS clam beds. The present study suggests that biomass of organisms on clam beds is greatest in the first few years after harvest. Greater numbers of newly settled bivalves on recently dredged bottom may be related to the higher levels of TOM observed there. Benthic assemblages on sites undisturbed for 1 and 2 years postharvest contained the highest number of species and represented a transition in composition between the 0-year and 10+-year postharvest communities. Recently dredged bottom (0 to 2 years) contained more individuals and higher biomass than the fallow (10+ years) location. Left uncultivated for 10+ years, benthic assemblages will revert gradually through succession to communities with fewer individuals per species but generally greater species diversity and evenness as compared to newly harvested bottom. Cultivation of sediments may bring about short-term changes to the consistency of sediments that influence species composition. Frequent natural disturbance and intermittent dredge harvesting on LIS clam beds in the inshore coastal zone may result in a patchwork of ecological communities with differing composition and at varying stages of succession.

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