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Impacts of Oyster Aquaculture on Subaqueous Soils and Infauna

Chelsea E. Duball,* Jose A. Amador, Lauren E. Salisbury, and Mark H. Stolt

Abstract

Oyster aquaculture maintains water quality via filter-feeding processes; however, few studies have investigated the impacts of resulting biodeposits on the underlying soils. In this study, we investigated the impacts of oyster aquaculture by comparing biodeposition rates, physical and chemical properties of subaqueous soils, and infaunal communities among aquaculture and control sites in three coastal lagoons in Rhode Island. Aquaculture study sites ranged in age of use from 0 (control) to 21 yr. We applied biodeposits at an equivalent amount generated by as high as 2000 oysters m^{-2} wk^{-1} to control soils and did not observe significant enrichment, suggesting that soils and infauna can process considerable amounts of biodeposit-derived N (5.4 g m^{-2} d^{-1}) and C (44.3 g m^{-2} d^{-1}) quickly. Although soils under aquaculture sites received significant biodeposits (67.8–346.47 g dry wt. m^{-2} d^{-1}), soil N and C levels were only significantly higher at the 12-yr site and at deeper depths (5–20 cm) in 50% of sites, suggesting considerable soil processing and/or mixing. Signs of detrimental impacts on the soil environment in aquaculture sites included elevated soil pore-water sulfide levels, independent of time in aquaculture, and a shift in infaunal community structure, favoring higher populations of deposit feeders and opportunistic species indicative of environmental disturbance. Although our results suggest that biodeposit-derived N and C additions are offset by infaunal processing, the changes in infaunal community structure and elevated pore-water sulfides indicate that coastal managers should consider the possibility of a decrease in soil quality as a function of aquaculture-related site disturbance.

Core Ideas

- Oyster filter feeding expels N- and C-rich biodeposits onto soils beneath aquaculture racks.
- Soils and infauna are capable of processing considerable amounts of oyster-derived N and C inputs.
- Oyster aquaculture primarily affects infaunal communities and soil and pore-water sulfide levels.

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*Corresponding author (cduball@uwyo.edu).

Lagoons are one of the more common types of estuaries along the coast of most continents (Kjerfve and Magill, 1989). Although these ecosystems are highly productive, in many populated regions, they have become exceedingly stressed by excess nitrogen (N) inputs from sources such as stormwater, septic systems, and agricultural runoff (Kjerfve, 1994; RISMP, 2014). For example, N inputs to coastal lagoons from urban and suburban development and expansion in southern New England have doubled since preindustrial times, causing eutrophication (Nixon and Buckley, 2007). One way to address the effects of eutrophication in coastal waters is to increase filter-feeding bivalve populations through expansion of shellfish aquaculture (Rice et al., 2000; Ulanowicz and Tuttle, 1992). Shellfish can improve water quality by removing phytoplankton from the water column during filter feeding and incorporating N into their tissue (Cloern, 1982; Officer et al., 1982).

Although oyster aquaculture can have a significant role in maintaining water quality and nutrient cycling, there is also the potential for negative environmental effects (Black, 2001; Magill et al., 2006; Rice et al., 2000). As oysters feed on naturally suspended particulate matter within the water column, they consolidate and excrete the undigested portion as feces or pseudofeces, collectively known as biodeposits. Biodeposition is important in the transfer of N and carbon (C) from phytoplankton and particulates in the water column to the underlying soil, a process known as benthic–pelagic coupling (Dame, 2012; Doering et al., 1987). The N and C in biodeposits can be consumed by benthic infauna, accumulate in the soil, or be transformed to dissolved organic forms, followed by mineralization and/or denitrification (Dame, 2012; Giles and Pilditch, 2006; Newell et al., 2002). However, in areas where oyster stocking densities are high, fast-sinking biodeposits can cause excess accumulation of organic material in the benthic environment (Black, 2001; Magill et al., 2006), that can result in anoxia and alteration to nutrient cycling in soils (i.e., nitrification; Rice et al., 2000).

In the United States, the total value of aquaculture products (fish and shellfish) has increased 26% in the last decade (USDA, 2013). Over that same time, total oyster production has increased by 75%. Even greater increases in oyster aquaculture have occurred in southern New England (Still, 2016). In

C. Duball, Ecosystem Science and Management Dep., Univ. of Wyoming, 1000 E. University Ave., Laramie, WY 82071, USA; J. Amador and M. Stolt, Natural Resources Science Dep., Univ. of Rhode Island, 1 Greenhouse Rd., Kingston, RI 02881, USA; L. Salisbury, Marine Biology Dep., Univ. of Saint Andrews, North Haugh, St. Andrews, KY16 9ST, UK. Assigned to Associate Editor John Brooks.

Abbreviations: DW, dry weight; IRIS, Indicator of Reduction in Soils; NP, Ninigret Pond; PP, Potter Pond; SWDI, Shannon–Weiner diversity index; WP, Winnapaug Pond.

Rhode Island, nearly all of that expansion has occurred in the coastal lagoons (RISMP, 2014). As oyster aquaculture continues to expand in these critical ecosystems, a better understanding of the positive and negative environmental impacts of aquaculture is necessary.

We examined the environmental impacts of oyster aquaculture on soils and infauna across aquaculture and control sites in three coastal lagoons in southern Rhode Island. This study consisted of two components: (i) characterization of biodeposits and short-term effects on soils, and (ii) effects of time in aquaculture on soils and infauna. We hypothesized that as a result of filter-feeding processes, oyster biodepositional loads would increase with higher stocking densities and production and larger oysters, and that those loads would be enriched in N and C. Thus, we expected the natural loading of N- and C-rich biodeposits to cause the soils under oyster aquaculture to have lower bulk density values and higher levels of sulfides, N, and C, and that the infaunal community structure would shift to favor a larger abundance of deposit-feeding, opportunistic infauna. In addition, we expected the physical, chemical, and biological changes to the soil to be greater the longer a site had been used for aquaculture.

Materials and Methods

Study Area

We examined the environmental impacts of oyster aquaculture in three coastal lagoons in Rhode Island: Ninigret (NP), Winnapaug (WP), and Potter (PP) Ponds (Supplemental Fig. S1). These lagoons, locally referred to as coastal ponds, are permanently breached by narrow inlets that exchange seawater with Block Island Sound. Average water depth is <2 m (Boothroyd et al., 1985), average flushing time is <5 d (Supplemental Table S1), and N inputs average 30 kg N ha^{-1} yr^{-1} (Pfeiffer-Herbert, 2007). The subaqueous soils in all three lagoons were mapped as part of the USDA Natural Resources Conservation Service MapCoast Partnership (Payne and Turenne, 2009). Nearly all of the oyster aquaculture in these lagoons occurs on shallow washover fans (water depths < 1.5 m) mapped as the Nagunt soil series (mixed, mesic Sulfic Psammowassents).

To examine impacts as a function of time in aquaculture, we selected sites from preexisting oyster farms, representing a range of ages (i.e., time an area was used for oyster aquaculture) to monitor and sample. We used the time function tool in Google Earth to view archived aerial photos to establish when specific sections of each farm were first established with active oyster racks, and the dates were confirmed with farm owners. Seven aquaculture study sites were established: one in NP (5 yr), three in WP (6, 13, and 21 yr), and three in PP (6, 8, and 12 yr). Two sites were in aquaculture for 6 yr, thereby each were designated as 6(PP) and 6(WP) based on their lagoon location. Sites 6(PP) and 6(WP) allowed us to conduct additional age–site comparisons, because they were in aquaculture for the same duration of time, but in different lagoons. A control site (in aquaculture for 0 yr) was established in each lagoon in areas that were never used for aquaculture and at least 300 m away from any aquaculture activity. Both aquaculture and control sites in all three lagoons were located on the same soil type (Nagunt series). Established control sites were also used to assess the effects of biodeposits on soils in the short term.

Characterization of Biodeposits and Short-term Effects on Soils

We measured rates of biodeposition from a range of different-sized oysters (6, 10, and 13 cm) representing stocking densities of 540 to 870 oysters m^{-2} per unit of time during August of both years of the study, following modified methods outlined in Higgins et al. (2011). Two metal pans (2645 cm^3) were attached to the bottom of actively farmed oyster racks at aquaculture sites, and to a rack containing no oysters placed within a control site at the three study lagoons. Pans were left in place for 3 d to collect biodeposits, after which samples were carefully collected to ensure minimal loss of material. Samples were dried (60°C) and total dry weight (DW) was determined. The weight of material collected in the control site pans was minimal to none (clearly not biodeposit material). Material collected in aquaculture sites was clearly biodeposits, with the exception of few macroalgae or macrofauna, which were excluded from the final weight measurements. Thus, we assumed that oyster biodeposits accounted for all the mass in the trays below the active oyster racks, representing the bulk of the particulate matter that naturally settles beneath aquaculture racks (Newell et al., 2005). Total biodeposit DW was used to calculate biodeposit rates per area (g DW m^{-2} d^{-1}) and per oyster (g DW $oyster^{-1}$ d^{-1}). A subsample of the biodeposits was dried at 60°C and analyzed for total N and C as described below for soil samples.

In August 2016, we established three subplots within control areas of NP to simulate biodeposit inputs to the soil produced from no oysters (control), an average stocking density (500 oysters m^{-2}), and a high stocking density (2000 oysters m^{-2}). Biodeposits were collected from an upwelling system, also located in NP, Rhode Island, to ensure a sufficient supply of biodeposits from oysters grown in high densities and within a confined environment. Collected biodeposits were allowed to settle at 4°C for 1 d, after which the water was decanted. Concentrated biodeposits were transferred to six pans (530 cm^2) at concentrations according to treatment type, and frozen at −15°C. Subsamples were collected from each individual pan and analyzed for total N and C. We applied one premeasured pan of frozen biodeposits to each subplot area, and a pan of ice to represent a control input. To allow the biodeposits to settle onto the soil surface and minimize losses to the water column, the pans were carefully placed face-down on the soil surface, and a weight was placed on top of the pan to keep it in place. To diminish the impact of water flow on the biodeposit inputs, a plastic frame was inserted around each subplot and covered with a 1-mm mesh. The pans were removed after 1 d. Soils were sampled before application (0 ds), and 1, 3, and 7 d after application using a 2-cm diameter plastic syringe, inserted into the upper 2 cm of the soil. Triplicate soil samples were collected and composited by each subplot and analyzed for total N and C as described below.

Effects of Time in Aquaculture on Soils and Infauna

Soil samples were collected from areas directly adjacent to racks of the aquaculture sites and from control sites located on washover fans. Oysters were grown on racks elevated ~15 to 20 cm above the soil surface. Soils were sampled to 20 cm at each aquaculture age site with a 10-cm-diam. aluminum core (1570 cm^3) (Payne, 2007). Four cores were collected down to a depth of 20 cm within

three plots per age site, in early summer 2016. Three of the cores were composited by depth increment (0–2.5, 2.5–5, 5–10, and 10–20 cm) and frozen at −15°C until analyzed. The full volume of soil in the fourth core was sieved (0.5-mm mesh) in the field for resident benthic infauna analysis. Infauna that remained in the sieve were preserved in 70% ethanol, dyed with rose bengal to aid identification, and stored at room temperature for later identification and sorting (Dye, 2006).

Samples for bulk density analysis were collected separately using a known-volume 5.5-cm-diam. (475-cm^3) core and divided into the same depth increments as the larger soil cores. To determine soil bulk density, the oven-dry (105°C) soil weight was divided by the original soil volume and corrected for coarse (>2-mm) fragment content (Soil Survey Staff, 2014).

To determine soil sulfide content, soil materials were mixed in a 1:1 (v/v) ratio of soil to deionized water slurry and incubated at room temperature for 16 wk (Soil Survey Staff, 2014). Each week pH was measured (Payne and Stolt, 2017). A decrease in pH was assumed to result from oxidation of soil sulfides to sulfuric acid during long-term incubation of soil (Schoeneberger et al., 2012). We used the resulting change in pH (ΔpH) as a proxy for soil sulfide levels, assuming all soils had similar buffering capacity.

Total organic N and C content were measured with a CE Instruments Model NC2100 elemental analyzer. Soil samples were pretreated with 1.0 M hydrochloric acid to remove calcium carbonate, rinsed three times with deionized water, dried at 60°C, ground with a mortar and pestle, and passed through a 0.25-mm mesh sieve before analysis (Midwood and Boutton, 1998; Payne, 2007).

To assess soil pore-water sulfide levels, we used Indicator of Reduction in Soils (IRIS) tubes made from polyvinyl chloride (PVC) tubing and coated with iron oxide (Fe^{3+}) paint (Rabenhorst, 2008). Under anaerobic soil conditions, the Fe^{3+} paint will be reduced to Fe^{2+} and can react with sulfides in the soil solution, thus changing the color on the tubes from orange (Fe^{3+}) to black as insoluble iron monosulfides (FeS) and pyrite (FeS_2) are formed (Fanning et al., 2010; Rabenhorst et al., 2010; Stolt, 2005). Three tubes, placed roughly 20 cm apart, were inserted into the soil at both aquaculture and control sites and left in place for 2 d in August 2016. Each tube was photographed to estimate sulfide levels, assessed by the percentage of black color change (Rabenhorst et al., 2010).

Benthic infauna were identified to the species level. Each preserved sample was observed under a dissecting microscope to identify organisms on the basis of anatomical features, and subsequently sorted into functional feeding groups (e.g., deposit, suspension, scavenger, interface, predator, grazer, or parasite) using Bousfield (1973), Weiss (1995), Pollock (1998), and WoRMS Editorial Board (2017) for guidance.

Using infaunal population data, we also calculated the functional diversity (H) of each site using the Shannon–Weiner diversity index (SWDI):

$$H = -\Sigma[p_i \times \ln(p_i)]$$

where H is the SWDI index value and p_i is the number of individuals within each functional feeding group divided by the total number of infauna for that sample.

Functional evenness (E_H) was also calculated as follows:

$$E_H = H/\ln(S)$$

where E_H is the evenness value and S is the total number of functional feeding groups in the community.

Statistical Analyses

Soil and infaunal data were analyzed using SigmaPlot 11.2 (Systat Software). Data that failed tests of normality and equal variance were log-transformed. For all statistical tests, we used $\alpha = 0.05$ as the level of significance, and thus all analyses resulting in a p value of ≤ 0.05 were considered significant in this study. Oyster biodeposition rates were compared as a function of oyster size using a linear regression analysis. Soil properties were compared across all sites, ranging from 0-(control) to 21 yr of aquaculture, and depth increments (0–2.5, 2.5–5, 5–10, and 10–20 cm), using two-way ANOVA. We conducted multiple comparisons versus a control group using the Holm–Sidak method, to compare control site values to aquaculture age site values. Total abundance, functional feeding group abundance, and diversity of infauna were compared across all sites (0–21 yr of aquaculture) using a Kruskal–Wallis one-way ANOVA based on ranks. Multiple comparisons versus a control group were conducted using Dunn's method, to compare control site median values to median values at each aquaculture age site. We used Spearman rank order correlations to assess the relationships between total abundance of infauna and soil properties (bulk density, total N, total C, and ΔpH). Soil parameters, species, and functional feeding group data were subjected to multivariate analyses and for species diversity, abundance, and evenness using PRIMER 7 environmental statistical software (Clarke and Gorley, 2015). A comparison of species composition between sites was analyzed using a Bray Curtis similarity index.

Results

Characterization of Biodeposits and Short-term Effects on Soils

Rates of biodeposition per oyster were significantly and positively correlated with oyster size ($r^2 = 0.9028$) (Supplemental Fig. S2). Biodeposition rates per oyster varied from 0.47 to 0.88 g DW $oyster^{-1}$ d^{-1} for the largest oysters (13-cm), to 0.15 to 0.28 g DW $oyster^{-1}$ d^{-1} for moderate size (10-cm) oysters, and 0.05 to 0.18 g DW $oyster^{-1}$ d^{-1} for the smallest (6-cm) oysters (data from 2015 and 2016, Supplemental Table S2). Biodeposition rates per unit area also varied as a function of oyster size and stocking density, varying from 323.08 to 479.08 g DW m^{-2} d^{-1} for 13-cm oysters, to 126.19 to 242.75 g DW m^{-2} d^{-1} for 10-cm oysters, and 35.17 to 101.75 g DW m^{-2} d^{-1} for 6-cm oysters (Supplemental Table S2). Biodeposits averaged across all oyster sizes and sampling years had a mean (SD) total N and C concentration (g kg^{-1}) of 10.4 (2.6) and 82.5 (12.6), respectively.

To assess the short-term (1-wk) effects of biodeposits on soil, concentrated biodeposits were placed on the soil at concentrations representing a control (no oysters), average, and high oyster stocking densities. One day after application, levels of C and N in the upper 2 cm of soil varied across all treatment subplots, regardless of biodeposit application rate (Supplemental Fig. S3). The levels of soil N and C returned to initial conditions (0 d) just 3.5 and 7 d after application of biodeposits.

Effects of Time in Aquaculture on Soils and Infauna

We examined the effects of time in aquaculture on soils using metrics of N and C levels, bulk density, soil and pore-water sulfides, and the resident infaunal community. The highest level of N (0.37 g kg^{-1}) was observed at 10 to 20 cm in the 12-yr aquaculture site, with the lowest N level (0.04 g kg^{-1}) observed at 0 to 2.5 cm in the 13-yr site, indicating soil N levels are independent of age of aquaculture use (Fig. 1). However, levels of N at control sites were significantly different ($p \leq 0.05$) from the 12-yr (10–20 cm) and 13-yr (2.5–5 cm) aquaculture sites. There were also significant differences ($p \leq 0.05$) in N levels among soil depths across aquaculture and control sites; specifically, N levels were considerably lower in the surface soils (0–2.5 and 2.5–5 cm) compared with greater soil depths (5–10 and 10–20 cm) for five out of eight sites.

The data suggest that soil C levels are independent of age of aquaculture use (Fig. 1). The highest level of C was observed at 10 to 20 cm in the 12-yr aquaculture site, whereas the lowest level of C was observed at 0 to 2.5 cm in the 13-yr site. Soil C levels in control sites were significantly different from levels in the 6(PP) (at 0–5 cm), 6(WP) (at 2.5–5 cm), and 12-yr (at 0–5 and 10–20 cm) sites. There were also significant differences in C levels among different depth increments, across all sites; specifically, C levels were lower in the surface soils (0–2.5 and 2.5–5 cm) compared with greater soil depths (5–10 and 10–20 cm) for six out of eight sites.

Soils at both aquaculture and control sites contained enough sulfides to cause a change in pH (ΔpH) after incubation (Supplemental Fig. S4). Aquaculture sites used for 5 and 8 yr had the lowest ΔpH (all depths), with the highest values observed at the aquaculture sites used for 13 and 21 yr (all depths). However, there were no significant differences in ΔpH between aquaculture and control sites once the effects of depth were considered. Pore-water sulfide concentrations were noticeably higher in all aquaculture sites compared with control sites, as indicated by the magnitude of the black color change on the IRIS tubes (Fig. 2). The highest sulfide concentrations were evident in the upper 10 cm of the soil profile across all aquaculture sites, regardless of age.

The 6(PP), 8-, and 12-yr aquaculture sites had the lowest average bulk density (<1.2 g cm^{-3}) in the surface soils (0–2.5 cm) (Supplemental Table S3). Bulk density values of the control sites were only significantly different from the 13-yr aquaculture site. Bulk density was significantly different among all depth increments, across all sites. However, 50% of all sites had lower bulk density values in the surface of the soils (0–2.5 cm) compared with soils at greater depths (2.5–5, 5–10, and 10–20 cm).

A total of 64 species of infauna were identified, belonging to seven different functional feeding groups (Supplemental Table S4). The five most abundant species at each site comprised between 67 and 74% of the total infauna (Supplemental Table S5). There was noticeable overlap among the five most abundant species found across aquaculture and control sites; these included the species *Diploydora commensalis*, *Prionospio dubia*, and *Capitella capitata*. Aquaculture sites had nearly double the abundance of the deposit-feeding opportunistic species *C. capitata* compared with control sites, and the majority (23%) of infauna at aquaculture sites was composed of *Corophium*

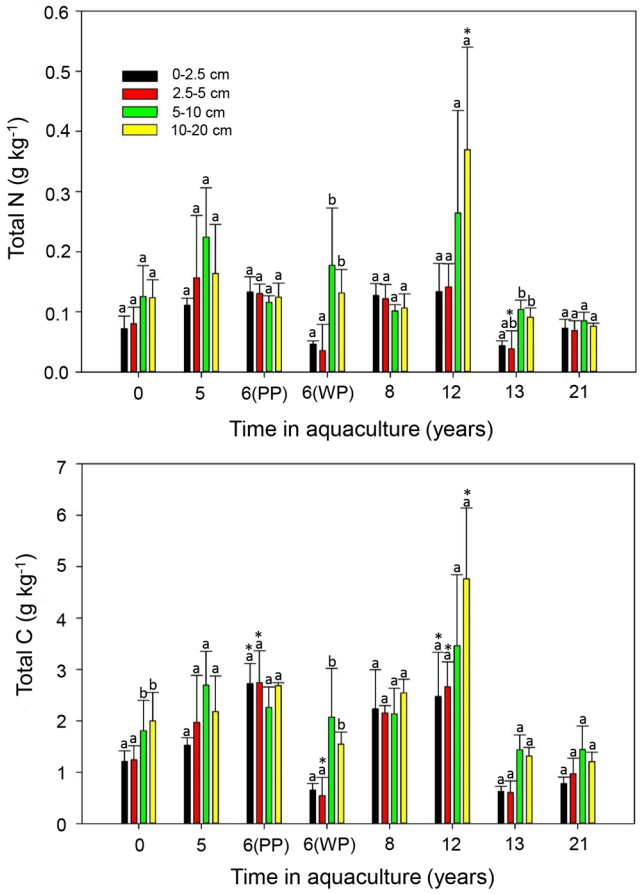

Fig. 1. Mean (n = 3) levels of total N (top) and total C (bottom) at different soil depths as a function of years in aquaculture. Error bars represent 1 SD from the mean. Significant differences ($p \leq 0.05$) from the control site (0 yr) are indicated with an asterisk (*). Bars with the same letter indicate no significant differences among depths within a site. PP, Potter Pond; WP, Winnapaug Pond.

volutator, another opportunistic species. There was also a higher relative abundance of deposit feeders across all aquaculture sites >5 yr compared with control sites (Fig. 3).

Total abundance of infauna was significantly different among all sites, regardless of age (Fig. 3). Control sites had significantly lower total abundance, compared with the 6(PP) and 8-yr aquaculture sites. Additionally, functional feeding group analyses showed populations of deposit feeders, interface feeders, and parasites were significantly different across all sites (Fig. 3). Deposit feeder populations were significantly larger or more abundant at the 6(PP), 6(WP), and 8-yr aquaculture sites compared with control sites. Interface feeder populations were significantly larger or more abundant at the 6(PP) and 8-yr aquaculture sites compared with control sites.

The SWDI values for functional diversity ranged from 1.4 to 1.8, and functional evenness values ranged from 0.7 to 0.9, with no significant difference in species diversity between aquaculture and control sites, or among differently aged sites. Comparison of the species composition of aquaculture sites of different ages showed that aquaculture sites within a particular lagoon are more closely related to each other than they are to the control site within that lagoon (Supplemental Fig. S5). The species composition was also more similar among younger-age sites than among older-age sites.

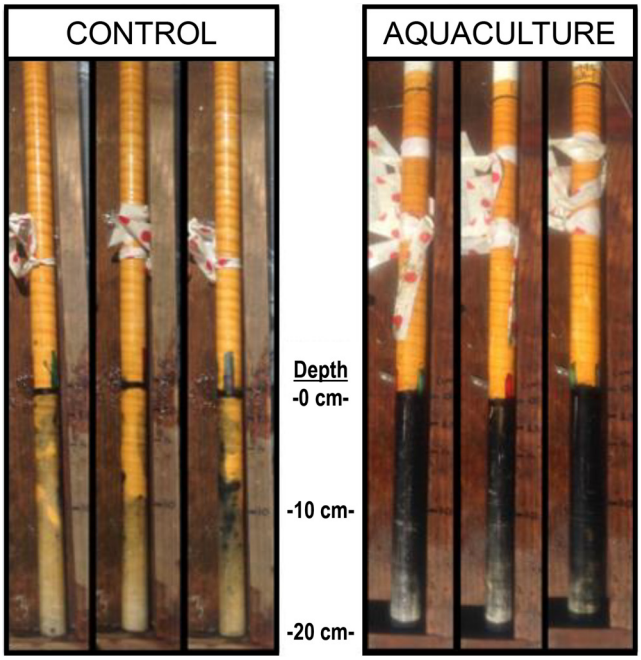

Fig. 2. Example of Indicator of Reduction in Soils (IRIS) tube reactions from soils at control and aquaculture sites. Minimal black color indicates low sulfide presence within the soil-pore water at control sites. Greater magnitude of black color indicates higher soil pore-water sulfide levels at aquaculture sites. Note that aquaculture site tubes are completely black, compared with control sites, which only have few patches black from of Fe monosulfide (FeS) formation. Depth increments are provided to indicate the full range of the soil profile from 0 to 20 cm.

Discussion

Characterization of Biodeposits and Short-term Effects on Soils

On average, 1 to 2 g N and 6 to 17 g C is deposited on the soil surface from each 1-m^{-2} rack per day, as the oysters likely remove the N and C from the water column via filter feeding. Our results show that larger oysters produce more biodeposits than the smaller ones, as expected. Our rates are representative of biodeposition values reported for oysters in general (Supplemental Table S2). A study conducted by Haven and Morales-Alamo (1966) reported similar ranges for biodeposition rates of *C. virginica*, and Mitchell (2006) reported similar rates for near-market-size (6-cm) oysters. These results could strongly support the role of oysters in maintaining water quality, as they remove N and C from the water column and consolidate it into biodeposits. However, it should be noted that N and C are also incorporated into the oyster tissue during growth, although those parameters were not measured in this study.

Contrary to our original hypothesis, even at high stocking densities, no accumulation of N or C was observed in the upper 2-cm of the soil, at any treatment plot or time period after application of biodeposits (Supplemental Fig. S3). If the N and C in biodeposits had behaved conservatively (i.e., no losses), we would have expected the concentration of N and C to increase by 0.8 g N kg^{-1} soil and 6.6 g C kg^{-1} soil for the high stocking density addition rate, and by 0.2 g N kg^{-1} soil and 1.6 g C kg^{-1} soil for the average stocking density addition rate. These changes would

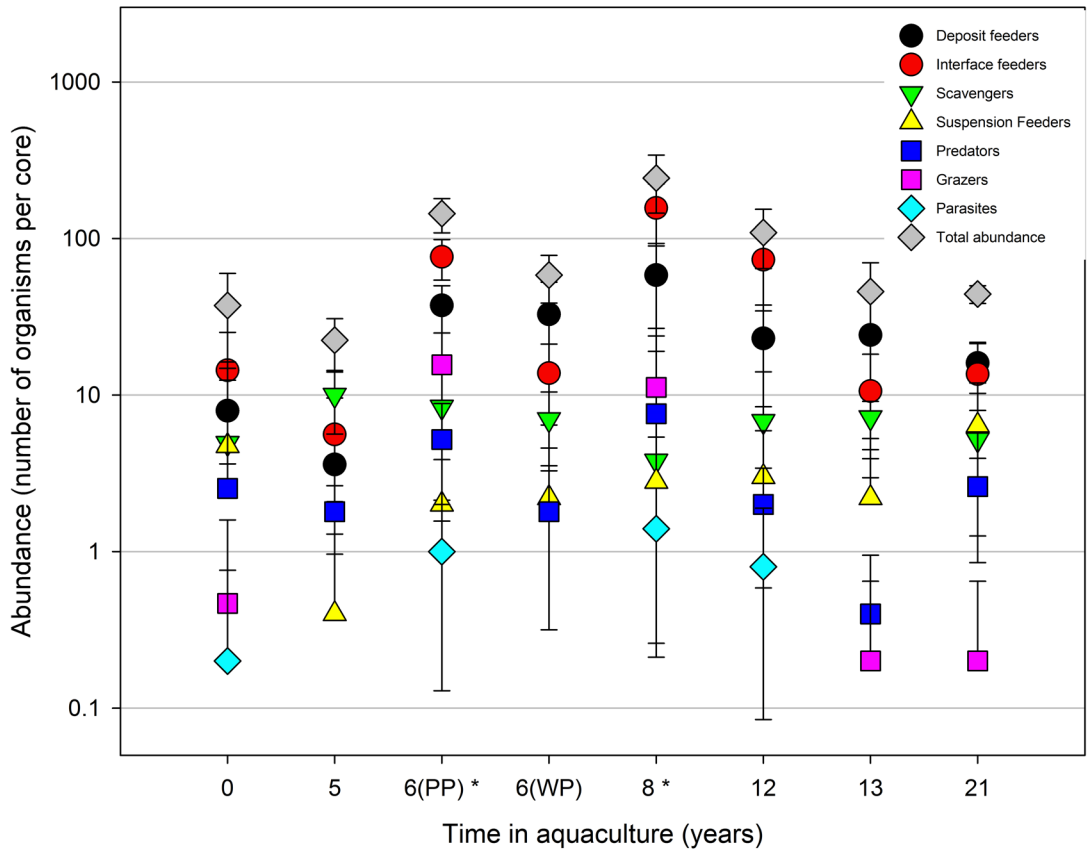

Fig. 3. Mean (n = 3) abundance of infauna within each functional feeding group, and total abundance, as a function of years in aquaculture. Each mean represents the average number of infauna from a 1570-cm^3 soil core. Error bars represent 1 SD from the mean. Significant differences ($p \leq 0.05$) in total abundance from the control site (0 yr) are indicated with an asterisk (*). PP, Potter Pond; WP, Winnapaug Pond.

be readily detected with our analytical methods. A similar study conducted in New Brunswick, Canada, found there was no indication of organic enrichment in the soil from oyster biodeposits (Mallet et al., 2006). We assumed that processing of the N and C occurred in the upper 2 cm of the soils that we sampled, representing losses of 5.4 g N m^{-2} d^{-1} and 44.3 g C m^{-2} d^{-1} at the average application rate, and 21.6 g N m^{-2} d^{-1} and 177.1 g C m^{-2} d^{-1} at high application rate. Other studies have quantified gaseous N losses in shallow coastal substrates, similar to the soils observed in our study. Lamontagne and Valiela (1995) reported rates of denitrification for soils in shallow estuaries as high as 0.24 g N m^{-2} d^{-1}. In NP, Humphries et al. (2016) reported denitrification rates under oyster reefs and oyster aquaculture as high as 0.20 g N m^{-2} d^{-1}. Our estimates of N loss, however, are one order of magnitude higher than those accounted for by denitrification rates reported in the literature. However, we observed evidence of burrowing infauna at the soil surface of all plots receiving biodeposits when we sampled 1 d after application, indicating that additional losses of N and C could be due to infaunal processing, and translocation deeper into the soil profile, or by assimilation into infaunal tissues.

Effects of Time in Aquaculture on Soils and Infauna

Neither soil N nor C levels increased proportionally with time in aquaculture use (Fig. 1), suggesting that N and C enrichment is likely controlled in part by factors other than biodeposition rates. Kellogg et al. (2014) suggested that long-term accumulation rates for N and C in benthic environments are likely site specific, depending on aquaculture practices such as stocking density, position within the water column, maintenance protocols, and harvest techniques. Specific aquaculture practices may also influence deposition rates, biogeochemical processes, and soil resuspension (Kellogg et al., 2014).

Physical disturbances may explain the dynamics of N and C within the surface soils. Although bulk density varied among all sites and depth increments (Supplemental Table S3), value were lower in surface soils (0–2.5 cm) compared to soils than at greater depths (2.5–5, 5–10, and 10–20 cm) at 50% of all sites, suggesting effects of physical disturbance at the soil surface. Because recreational users and oyster farmers use shallow areas of the lagoons preferentially, the soil surface at these sites experience haphazard physical disturbances from foot traffic and recreational activities (e.g., wild shellfish harvesting, dropping of boat anchors). Additionally, soil disturbances are likely more frequent and sustained at aquaculture sites, from routine maintenance of heavy aquaculture gear and foot traffic from farm workers (De Grave et al., 1998; Forrest and Creese, 2006). Monitoring all aquaculture sites to understand the effects of site-specific practices was beyond the scope of this study, although these effects of disturbance are worth evaluating in future studies. We speculate, however, that over time, disturbance causes resuspension of the surface soils and compaction of the underlying soil causing the potential for organic N and C to accumulate at greater depths. Thus, aquaculture practices may facilitate sequestration of greater amounts of N and C deeper into the soil.

Infaunal bioturbation and translocation, specifically at aquaculture sites, may also explain lower concentrations of N and C in the surface soil. We observed significantly higher abundance of infauna, particularly deposit feeding worms, in aquaculture sites (>5 yr) compared with control sites, which could enhance N mineralization and denitrification within the surface soils. This process is common in marine systems, where bioturbation helps to stimulate remineralization by introducing oxygen into subsurface soils, and it has been documented to increase the decay of organic matter by a factor of 10 (Kristensen and Kostka, 2005). Bioturbation activity also increases denitrification by up to 400%, resulting from environmental alterations that affect biogeochemical processes (Laverock et al., 2011). We also found lower concentrations of N (at 4 of 7 sites) and C (at 5 of 7 sites) in the upper 5 cm, compared with the lower 15 cm of the soil (Fig. 1). These results provide further evidence of infaunal bioturbation in these systems and the translocation of N and C from the surface to greater depths in the soil.

Time in aquaculture did not significantly affect the species diversity of infaunal communities. However, the abundance of some functional feeding groups, such as deposit feeders, was higher at aquaculture sites. Mallet et al. (2006) also found larger populations of deposit feeders at aquaculture sites compared with the control sites and suggested that the difference could be due to higher levels of aquaculture-derived organic sedimentation or organic inputs. We found *C. capitata* (Supplemental Table S5), an opportunistic polychaete species associated with highly disturbed areas (Mallet et al., 2006), in aquaculture and control sites, but aquaculture sites had nearly double the abundance of this species. *Capitella capitata* represents a complex of six species with minor morphological differences and is used as an indicator of pollution, particularly in aquaculture areas (Grassle and Grassle, 1976; Dean, 2008). Additionally, *Corophium volutator*, an opportunistic tube-dwelling amphipod commonly found in Europe and northeastern North America (Flach, 1992; Meadows and Reid, 1966; Möller and Rosenberg, 1982; Raffaelli et al., 1991), accounted for most of the infauna at aquaculture sites but was rarely found at control sites. These opportunistic species have life-history traits (e.g., small size, fast growth, high reproductive capacity, and good dispersal ability) that facilitate rapid environmental responses and large increases in abundance in recently disturbed areas. This trend of higher opportunistic species is indicative of habitat disturbance, which results in dominance by trophic groups that live near the sediment–water interface, a process known as early benthic-community succession (Gaston and Nasci, 1988). The structure and maintenance routines of oyster aquaculture farms likely facilitates establishment of resilient, opportunistic benthic invertebrates. For example, routine farm maintenance results in frequent disturbance of the soil surface, because the cages that hold the oysters are often moved in and out of the water, and farmers consistently walk between oyster racks. In addition, the high density of oysters in these areas results in a large input of biodeposits, rich in N and C, under the cages, providing a viable food source for infauna. These activities and impacts likely help drive shifts in species composition, favoring lower-order trophic groups that can survive and thrive under environmental conditions enriched in N and C.

Another mechanism driving aquaculture-associated shifts in infaunal community composition may be changes in soil and pore-water sulfide levels. Our analysis found that soil sulfide levels were highest in the top 5 cm of the soil at all aquaculture sites, and soil sulfide levels were especially high within the 13- and 21-yr aquaculture sites, coincident with greater numbers of

opportunistic species. Substantial formation of black FeS on the IRIS tubes (Fig. 2) in the aquaculture sites indicated that soil pore-water sulfide levels were much higher at all aquaculture sites—regardless of duration of aquaculture use—than at control sites, especially in the upper 10 cm. Sulfide influences the benthos directly through its toxicity to fauna, and/or indirectly by reducing the toxicity of metals by forming insoluble metal sulfides (Wang and Chapman, 1999). The precipitation of metal sulfides is well understood (Brennan and Lindsay, 1996; Rickard and Morse, 2005), with substantial work examining the reduction in metal toxicity to the benthos (Di Toro et al., 1992; Hare et al., 1994; Lee et al., 2000). The biological implication of elevated sulfides and toxicity to the resident populations, however, is poorly understood (Wang and Chapman, 1999). Matisson and Lindén (1983) suggested the high sulfide levels and associated anoxia resulted in transitions toward communities dominated by opportunistic polychetes, such as *C. capitata*. Therefore, the trophic shift we observed may be partly associated with elevated sulfide levels in the soils.

Infauna abundance at sites used for oyster aquaculture for 13 and 21 yr was similar to infauna abundance values at control sites. This shift may be caused by trophic interactions or environmental responses not measured in this study. According to Snelgrove and Butman (1994), the processes that influence community composition and diversity of benthic infauna include those that operate pre- and post-colonization. Post-colonization processes include abiotic disturbance (Sanders, 1969), predation (Peterson, 1979), and competition (Wilson, 1991). In our study, post-colonization impacts could have included early-colonizing species switching feeding modes as they became accustomed to environmental changes, organisms migrating elsewhere as food became limited, and/or other predator–prey interactions and competition (Gaston and Nasci, 1988; Grabowski, 2004; Snelgrove et al., 2001). These trophic interactions could help to explain specific shifts in diversity and abundance for all sites, and especially those trends observed at the 13- and 21-yr sites.

Two of the aquaculture sites we investigated were in use for 6 yr [6(PP) and 6(WP)], offering a chance to investigate site-specific effects. These two sites responded differently to aquaculture than the control sites. The 6(PP) site had significantly higher total C levels, total infauna, number of deposit feeders, and number of interface feeders compared with the control site. In contrast, site 6(WP) only had significantly lower total C levels and greater number of deposit feeders than control sites. These differences suggest that site-specific factors are important in evaluating the impacts of aquaculture. It is important to consider how site-specific management factors, such as placement of aquaculture gear and frequency of rack movement, may influence particular locations within a site.

Conclusions

In this study, we examined soil physical and chemical properties and benthic infaunal communities among sites used for oyster aquaculture and adjacent control areas to test the relative environmental benefits and impacts of oyster aquaculture. We found that oyster aquaculture had no net negative impacts on soils and infauna in the short or long term. Although, high levels of N and C were stored in oyster biodeposits, higher levels of soil N and C were not evident at aquaculture sites compared with controls, even over long periods of oyster aquaculture (i.e., 21 yr), or with high oyster density or production rates. However, caution needs to be exercised, since we did not identify the exact mechanisms associated with the processing of N and C from short-term or long-term biodepositional loading to the soil. We suspect that denitrification and bioturbation are the leading mechanisms, but significant uncertainty exists due to site-specific factors. Our studies did show that oyster aquaculture resulted in an accumulation of sulfides in the soils and pore-waters. Elevated pore-water sulfide levels can be toxic to aquatic plants and animals and should be considered an environmental concern. Aquaculture shifted infaunal communities toward higher abundances of deposit feeders and opportunistic species, indicative of environmental disturbance or an accumulation of pore-water sulfides. Although our results suggest that oyster aquaculture causes variable effects on the subaqueous soil environment and biology, these signs could indicate a decrease in soil quality as a function of aquaculture-related site disturbance. Nevertheless, disturbance and biodeposition on the soil should be investigated further, particularly relative to sulfide accumulation and associated effects on infaunal communities, with particular consideration to materials assimilated into oyster tissues being taken into account.

Supplemental Material

Supplemental figures and tables include the following information: a map of the study sites (Supplemental Fig. S1); the relationship between oyster size and biodeposition rate (Supplemental Fig. S2); total N and C measured in the soil after short-term application of oyster biodeposits (Supplemental Fig. S3); mean ΔpH data for aquaculture and control sites (Supplemental Fig. S4); Bray Curtis similarity index for infaunal species (Supplemental Fig. S5); pond site characteristics (Supplemental Table S1); rates of oyster biodeposition measured in this study and other published studies (Supplemental Table S2); mean bulk density data for aquaculture and control sites (Supplemental Table S3); a key to all infaunal species identified in this study (Supplemental Table S4); and the top five species of infauna identified at control and aquaculture sites (Supplemental Table S5).

Conflict of Interest

We acknowledge there are no conflicts of interest to disclose for this paper.

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