Impact of Eastern Oyster, *Crassostrea virginica,* Biodeposit Resuspension on Phytoplankton Community Structure in Estuarine Systems with Tidal Resuspension

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Running page head: Oyster biodeposit resuspension and plankton responses

ABSTRACT

Anthropogenic disturbances in the Chesapeake Bay have depleted Eastern oyster (*Crassostrea virginica*) abundance and altered the estuary's environment and water quality. Efforts to rehabilitate oyster populations are underway, however, the effect of oyster biodeposits on water quality and plankton community structure are not clear. In July 2017, six shear turbulence resuspension mesocosms (STURM) were used to determine differences in plankton composition with and without the daily addition of oyster biodeposits to a muddy sediment bottom. STURM systems had a volume-weighted RMS turbulent velocity of 1.08 cm s^{-1}, energy dissipation rate ~0.08 cm^2 s^{-3} and bottom shear stress ~0.36 - 0.51 Pa during mixing-on periods during four weeks of tidal resuspension. Phytoplankton increased their Chl *a* content in their cells in response to low light in tanks with biodeposits. The diatom *Skeletonema costatum* bloomed and had significantly longer chains in tanks without biodeposits. These tanks also had significantly lower total suspended solids concentrations, zooplankton carbon concentrations, nitrite+nitrate concentrations, and higher phytoplankton carbon concentrations. Results suggest that the absence of biodeposit resuspension initiates nitrogen uptake for diatom reproduction, increasing the cell densities of *S. costatum*. The low abundance of the zooplankton population in non-biodeposit tanks suggests an inability of zooplankton to graze on *S. costatum* and negative effects of *S. costatum* on zooplankton. A high abundance of the copepod *Acartia tonsa* in biodeposit tanks may have reduced *S. costatum* chain length. Oyster biodeposit addition and resuspension efficiently transferred phytoplankton carbon to zooplankton carbon, thus supporting the food web in the estuary.

Keywords: Biodeposit resuspension, phytoplankton, zooplankton, oyster, STURM, mesocosm, *Crassostrea virginica,* plankton, *Skeletonema costatum, Acartia tonsa*

1. INTRODUCTION

Anthropogenic disturbances in the Chesapeake Bay, the largest estuary on the US Atlantic coast, have depleted the abundance of the eastern oyster *Crassostrea virginica* (Newell 1988) and increased nutrient loading and phytoplankton abundance (Kemp et al. 2005, Ator et al. 2019, Harding et al. 2019, Murphy et al. 2019). Although efforts to rehabilitate the oyster population through restoration (Schulte & Burke 2014) and aquaculture (Williamson et al. 2015; Ray et al. 2015) are underway, the impacts of the production and deposition of biodeposits on water quality and plankton community structure have not been evaluated. The euryhaline, epibenthic, bivalve filter feeder *C. virginica* filters large volumes of water and efficiently filters particles larger than 3 μm from the water column (Haven & Morales-Alamo 1970). Large amounts of faeces and pseudofaeces produced by oysters as biodeposits reflect a transport of particulate organic matter from the water column to the sediments (Jordan 1987). While it is generally assumed that oyster biodeposits remain in oyster reefs (Newell et al. 2005, Kellogg et al. 2013), recent studies suggest that biodeposits can be resuspended (Colden et al. 2016, Porter et al. 2018a) and transported by currents (Lund 1957, Widdows et al. 1998, Testa et al. 2015). Studies suggest that nutrient regeneration from bivalve biodeposits may outweigh the presumed beneficial removal of phytoplankton biomass by stimulating new phytoplankton blooms (Doering et al. 1986, Asmus and Asmus 1991, Souchu et al. 2001) - at least in oligotrophic waters (Cranford et al. 2007) – and that bivalve feeding can skew phytoplankton demography

toward smaller species that are no longer eaten by bivalves (Souchu et al. 2001, Cranford et al. 2007, Jiang et al. 2019).

Historically, three factors have been used to explain the size structure of phytoplankton communities: turbulence (Petersen et al. 1998, Iversen et al. 2010, Fouilland et al. 2016), nutrient supply (Van Meersche & Pinckney 2019), and grazing by herbivores (Lebour 1922, Harvey et al. 1935). Overall, small algae are better competitors for light and nutrients than larger algae (Riegman et al. 1993). The effects of increased mixing on phytoplankton biomass results from complex interactions between the nutrient dynamics, light environment, and organismal physiology and behavior (Petersen et al. 1998). Phytoplankton growth rates decrease with turbulence while grazing rates increase, especially at low and intermediate turbulence levels (Peters & Marrasé 2000). Previous experimental studies of mixing observed a variety of contradictory responses by phytoplankton (Estrada et al. 1987, Kiørboe 1993, Estrada & Berdalet 1997, Thomas et al. 1997, Fouilland et at 2016) and zooplankton (Davis et al. 1991, Dower et al. 1997). Iversen et al. (2010) showed that chlorophyll *a*, primary production rates, and diatom and dinoflagellate abundance were positively correlated to turbulence, regardless of nutrient conditions, and that abundance of autotrophic flagellates and total phytoplankton were positively correlated to turbulence only when nutrients were added. Slow mixing times stimulated the development of a mixed community of flagellates and small diatoms while fast mixing conditions developed a large diatom-dominated community, which stayed suspended only with high rates of mixing (Fouilland et al. 2016). Theoretical and experimental evidence suggests that sinking rates increase with cell volume (Smayda and Boleyn1965, 1966a,b, Smayda 1970, 1974, Smayda & Bienfang 1983, Kiørboe 1993). Large non-motile cells have higher sinking rates, when mixing rates are low, resulting in loss from the mixed zone, while mixing allows these

large species to remain in the water column (Kiørboe 1993). Other factors such as shape and geometry also affect settling (Durante et al. 2019). Nutrient additions enhanced the biomass of the algal < 20 μm fraction and increased the proportion of diatoms at the expense of cyanobacteria and cryptophytes (Van Meersche and Pinckney 2019). Diatoms were previously thought to be passive prey for copepods, the dominant mesozooplankton (Lebour 1922, Harvey et al. 1935). However, recent investigations reveal that phytoplankton exhibit defense mechanisms that negatively affect zooplankton (Pančić & Kiørboe 2018) and these can include physiological characteristics (*e.g*. toxicity, bioluminescence), morphological characteristics (*e.g*. silica shell, colony formation), and behavioral defenses (*e.g*., escape response) (Pančić & Kiørboe 2018).

This study examines effects of oyster biodeposits and benthic boundary-layer flow on benthic-pelagic coupling processes as well as phytoplankton and mesozooplankton community in a controllable whole-ecosystem context. The specific questions addressed were: (1) How do resuspended biodeposits and their nutrients affect phytoplankton abundance and composition in mesocosm experiments with high bottom shear and realistic water column turbulence? (2) How does oyster biodeposit resuspension affect ecosystem processes such as the mesozooplankton community? These experiments were designed to determine if the combined effect of high bottom shear stress with tidal resuspension of sediments and oyster biodeposits directly, indirectly, or non-linearly impact ecological interactions and water quality. Particular emphasis was placed on understanding the effect of biodeposit addition and resuspension on changes in the phytoplankton and mesozooplankton community structure and biomass in the ecosystem.

2. MATERIALS & METHODS

2.1. Mecocosm Setup and Mixing

In June and July 2017, six cylindrical Shear TUrbulence Resuspension Mesocosm (STURM, Porter et al. 2018b) tanks were set up at the Patuxent Environmental and Aquatic Research Laboratory (PEARL), Morgan State University, in St. Leonard, Maryland, with a ~10 cm deep muddy sediment bottom, covered by pre-screened, unfiltered Chesapeake Bay water from the Patuxent estuary. STURM systems contain a single paddle that produces high instantaneous bottom shear stress to resuspend biodeposits and sediment, with realistic water column turbulence levels without overmixing the water column (Porter et al. 2018b). The STURM tanks are the successor design of large linked mesocosms reported by Porter et al. (2004a, b). The tanks have a water volume of 1000 L, a water column depth of one meter, and a sediment surface area of 1 m^2. Paddle speed was set to 12.5 RPM and a single paddle slowly moved in a forward-stop-backward-stop motion (9 s - 1.5 s – 8 s - 1.5 s) to avoid plug flow during the mixing-on phase. Mixing followed a 4 h on : 2 h off cycle in all systems to simulate tidal cycles throughout a four-week experiment.

Direct flow and turbulence measurements were made using an Acoustic Doppler Velocimeter (ADV) to determine water column root mean square (RMS) turbulent velocities and energy dissipation rates at predefined locations throughout the tank, and at different mixing speeds. RMS turbulent velocity (cm s^{-1}) is defined in Tennekes and Lumley (1972) as

$$q = \sqrt{\frac{1}{3}(< u^2 > + < v^2 > + < w^2 >)} \quad (1)$$

where $<u^2>$, $<v^2>$, and $<w^2>$ are the variances of their respective velocity components. Energy dissipation rates (cm^2 s^{-3}) were determined following Sanford (1997). Volume-weighted RMS

turbulent velocities as determined using Surfer (Golden Software) were approximately 1.08 cm s^{-1} (Fig. 1a), and volume weighted energy dissipation rates were approximately 0.0772 cm^2 s^{-3} during mixing-on (Fig. 1b); this is similar to the intermediate mixing treatment of Petersen et al. (1998). These turbulence levels are comparable to ones used in resuspension tanks in previous experiments comparing resuspension vs non-resuspension systems (Porter et al. 2010), and in linked mesocosms (Porter et al. 2004a, b), lower than used in Porter et al. (2018a), and are in a realistic range (Porter et al. 2018b, Table 1 in Sanford 1997). In addition, this mixing setting kept energy dissipation rates at realistic Chesapeake Bay levels.

Shear stress at the bottom was determined directly using hot-film anemometry (Gust 1988). Shear (or 'friction') velocity (u_* in cm s^{-1}), defined by

$$u_* = \sqrt{\frac{\tau_b}{\rho}} \tag{2}$$

where τ_b is bottom shear stress in dynes cm^{-2} and ρ is the density of water in g cm^{-3}, was measured at five locations across the tank radius. Bottom shear stress [Pa] was calculated as $\tau_b = \frac{u_*^2 \rho}{10}$. At the chosen mixing setting of 12.5 RPM, maximum instantaneous bottom shear stress reached 0.36 - 0.51 Pa in all tanks (Fig. 1c, Porter et al. 2018b) and produced resuspension of biodeposits and sediments in the tanks during the mixing-on phases.

The mesocosms were prepared with muddy sediment, collected on 7 June, 2017, from the mesohaline Patuxent estuary (38^0 22 min. 0.856 N, 76^0 30 min. 0.731 W), a tributary of the Chesapeake Bay. Sediment was transported to PEARL where it was placed in outdoor mesocosms on June 12 after anaerobic defaunation (Porter et al. 2006). The sediment was equilibrated to realistic biogeochemical pore water gradients in the dark over a two week period

with a 30 cm water column of 0.5 µm filtered Patuxent estuary water (PEW) as described by Porter et al. (2006, there Treatment HG-m; Porter et al. 2010, 2013). During the sediment equilibration phase in the dark, the partial water column was oxygenated and 50 % of the 0.5 µm filtered PEW in the tanks replaced daily with 0.5 µm filtered PEW for two weeks. At the end of the sediment equilibration period, tanks were emptied and filled to one meter water column height with unfiltered ambient PEW. Each day, 10 % of the water in each tank was exchanged during the mixing-off phase and replaced with 0.5 μm absolute filtered PEW to mimic tidal exchange and without introducing a new plankton community.

During mixing-on, three tanks each received a daily addition of oyster biodeposits starting after the first water column sampling. Thus, day one of sampling, *i.e*., time 0, is excluded in all data analyses except where the initial phytoplankton biomass is compared to the experimental phytoplankton biomass. During the day-one afternoon mixing-on phase, each tank received 62 g of biodeposits in addition to the ambient resuspended TSS in the tanks to get started. On all subsequent days 4.76 g (SD ± 2.93 g) total suspended solids from biodeposits were added daily to each tank. Biodeposits from oysters feeding on natural plankton from the Patuxent estuary were generated in an indoor raceway in continuous flow conditions. Total suspended solids (TSS), particulate inorganic matter (PIM), particulate organic matter (POM), and quality (ratio POM/PIM) of the added biodeposits were determined daily while particulate carbon (PC), particulate nitrogen (PN), chlorophyll *a* (chl *a*) and phaeophytin concentrations were determined in biodeposis every other day.

The STURM tanks were wrapped in reflective bubble wrap (Shelter Institute) to reduce overheating of the tank water during high outdoors summer temperatures (≤ 38 ^{0}C). In addition, two layers of window screen mesh were placed over the superstructure to reduce insolation, ca

1.5 m above the tanks. Light levels of ~ 356 µmol photons m^{-2} s^{-1} were measured at the water surface of the R (Resuspension) tanks and R_BD (Resuspension with biodeposit addition) tanks, using a LI-192 Underwater Quantum sensor (LI-COR Biosciences) attached to a model LI-250 readout. Previous experiments indicate that light levels of about 160 µmol photons m^{-2} s^{-1} are required at the water surface to prevent light limitation (Porter et al. 2004a). Therefore, any light limitation within the tanks was due to the impact of sediment and biodeposit resuspension and the density of phytoplankton that resulted.

The tanks were slowly and evenly filled with pre-screened, unfiltered 12.0 PSU salinity water containing the resident plankton community from the Patuxent estuary. Only megazooplankton > 3 cm were excluded. Mixing began with the programmed tidal cycles and all tanks were synchronized. The experiment took place from 26 June to July 26, 2017 (30d). Rainstorms added freshwater to the tanks on experiment days 10, 14, 18, and 27, each time reducing salinity from 12 to 10 PSU. On day 25 the seams of the walls of one R_BD tank burst open and the tank was lost. The experiment continued with the five remaining tanks until day 30, and the results from days 25 through 30 were averaged from the remaining two R_BD tanks. During the evening of day 10, a data acquisition failure in the mixing system caused the mixing in all systems to be off for two mixing-on phases. After fixing the issue (cable unplugged), the systems continued without any further problems until the end of the experiment. Following this event, researchers began constant remote monitoring of the systems using a remotely accessible status webpage (Porter et al. 2018b). Using a separate cleaning stick for each tank to prevent tank cross-contamination, tank walls were cleaned of periphyton every day to minimize wall growth (Chen et al. 1997) and the wall material was left in the tank.

2.2. Sampling regime and variables sampled

Biological and geochemical variables measured included water column chl *a*, phaeophytin, TSS concentrations, phytoplankton identification and cell counts, phytoplankton pigment composition using high performance liquid chromatography (HPLC), water column nutrient concentrations (ammonium, nitrate plus nitrite, dissolved inorganic nitrogen [DIN], phosphate, total dissolved nitrogen [TDN], total dissolved phosphorus [TDP]), with samples taken at mid depth. In addition, light profiles, Secchi depth, and sediment chlorophyll *a* were determined. Finally, particle bulk settling speeds were measured during mid-day mixing-off phases in the R_BD and the R tanks using optical backscatter turbidity data.

In each tank, turbidity was continuously measured at 1 second intervals with optical backscatter turbidity sensors (OBS-3, D&A Instrument Company) located at mid-depth. Turbidity was calibrated with concurrently collected mid-depth TSS samples, analyzed by filtration and weighing as described in Porter et al. (2018a). Water temperatures were taken at 10 minute intervals in all tanks using Campbell T107 temperature probes as in Porter et al. (2010, 2013, 2018a). A heat wave occurred during days 18 – 19, and 26 – 28, however, water temperatures in the tanks were similar to water temperatures measured in a shallow local Patuxent estuary cove (31.2 ^{0}C), making tank cooling intervention unnecessary. Silver bubble wrap and two layers of window screen above the tanks were sufficient to shield the tanks from excessive heat.

Twice a week light profiles were measured during mixing-on and -off phases as described in Porter et al (2018a) to determine irradiance levels at the bottom, and mean geometric irradiance in the water column was calculated as $\exp[0.5 \times \{\ln(E_0)+\ln(E_{Sed})\}]$, where E_0 and E_{Sed}

are irradiances at the surface of the water column and the bottom, respectively. The values obtained for mean geometric irradiance were similar to irradiance values measured at 50 cm depth. Secchi depth was measured daily during the mixing-on and –off phases as in Porter et al. (2018a).

Four-l water samples were taken from mid depth of each tank twice a week during mixing-on for measurements of particulates and solutes and on days 15, 22, and 29, and at the end of the mixing-off phases. Water was filtered through 47 mm Whatman GFF filters (0.7 μm nominal pore size) and filters were analyzed for TSS, PIM and POM as described in Porter et al. (2018a), following Berg and Newell (1986). Known volumes of water were filtered through 47 mm Whatman GFF filters and filters were analyzed for particulate phosphorus (PP) concentrations, and chl *a* and phaeophytin concentrations. Water column chl *a* concentrations were analyzed using fluorometric techniques after extraction with 90 % acetone (EPA Method 445.0) to provide estimates of phytoplankton biomass, where phaeophytin was measured fluorometrically following acidification. In addition, water was filtered through pre-washed 25 mm Whatman GFF filters to measure PN and PC concentrations. The solute was captured and frozen in individual vials until it was analyzed for dissolved nutrients including ammonium (NH_4^+), nitrate + nitrite ($NO_3^- + NO_2^-$), dissolved phosphate (PO_4^{3-}), dissolved silicate (Si), total dissolved nitrogen (TDN) concentrations, and total dissolved phosphorus (TDP) concentrations using analytical procedures outlined in Porter et al. (2018a). Dissolved organic nitrogen (DON) was calculated by subtracting NH_4^+ and $NO_3^- + NO_2^-$ from TDN, and dissolved organic phosphorus was calculated by subtracting PO_4^{3-} from TDP. Exchange water was also sampled for dissolved nutrients to track any nutrient inputs through a 10 % daily water exchange. In addition, the fill water was sampled for particulates to confirm that their abundance in the 0.5 μm filtered

fill water was low. The same techniques were used to analyze particulates in the biodeposits. For quality control of all variables, every sixth sample was analyzed in duplicate. Nutrients and water column chl *a* and phaeophytin were analyzed by the Analytical Services Laboratory of the Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, UMCES, (water column chemistry methods and particulates methods https://www.umces.edu/nasl/methods).

Samples for pigment analysis were collected from the mid depth of each tank and stored in a -80 ^{0}C freezer until analysis using high performance liquid chromatography (HPLC, Van Heukelem & Thomas 2001). Following Jeffrey & Vesk (1997), Marshall (1994) and Marshall et al. (2005), some pigments characteristic of phytoplankton in the Chesapeake Bay area, our source water, were defined as: alloxanthin (Cryptophyceae), fucoxanthin (Chrysophyceae and Bacillariophyceae), lutein (Chlorophyceae and Prasinophyceae), perdidinin (Dinophyceae, and zeaxanthin (cyanobacteria, prochlorophytes, rhodophyta and some Chlorophyceae), neoxanthin (Chlorophyceae and Prasinophyceae), and prasinoxanthin (Prasinophyceae). The ratio of chlorophyll *b* to chlorophyll *a* was taken to indicate chlorophytes (Van Meersche & Pinckney 2019). HPLC samples were analyzed by Analytical Services of the Horn Point Laboratory, UMCES.

Moreover, water subsamples were preserved biweekly in Lugol's iodine solution for later microscopic phytoplankton identification and cell counts. Phytoplankton cells were counted using Utermöhl procedures (Utermöhl 1958, Marshall & Alden 1990, Lacouture 2001) and 20 random fields were counted at 500X for most cells smaller than 10 µm. A minimum of ten random fields and 200 individual cells were counted at 12.5 x 25 = 312.5X. A scan of the entire settling chamber was performed at 125X. The sample volume was 125 ml and the subsample

volume in the counting chamber was 2.5 ml. Phytoplankton biomass was determined by converting mean cell volumes of individual taxa to cell carbon according to Strathmann (1967) and Smayda (1978).

Phytoplankton biomass was estimated for three phytoplankton cell size ranges (cell volume 3-240 μm^3, 241-6,200 μm^3, 6,201-65,300 μm^3) to determine if phytoplankton size of the community changed over the experiment and in response to the treatments. Fluorescence microscopy (MacIssac & Stockner 1993), and flow cytometry (Veldhuis & Kraay, 2000) was not applied. Dissolved organic carbon (DOC) concentrations were similar in R tanks with 194.99 (SD ± 56.09) µmol carbon l^{-1} and 205.58 (SD ± 36.55) µmol carbon l^{-1} in R_BD tanks (p = 0.6628). To determine if the light regime in the R and R_BD tanks affected phytoplankton, the ratio of chl *a* to carbon was determined from the chl *a* concentration and total phytoplankton carbon determined from direct counts. Phytoplankton abundance at time zero (morning after the fill, before biodeposits were added) was compared to average phytoplankton abundance during the experiment (day 2-29) to determine any change in the phytoplankton community from initial conditions. While counting *Skeletonema costatum* cells in the phytoplankton samples, *Skeletonema* chain length appeared to be longer in the R tanks than in the R_BD tanks, thus *Skeletonema costatum* chain length was determined across all tanks between days 10 and 30.

During each water sampling, the exact times of sampling for each OBS-3 turbidity meter was recorded to establish linear calibration curves of TSS versus OBS volts (Table 1, $p <$ 0.0001). The linear calibrations for each OBS-3 turbidity meter (Table 1) were used to determine TSS concentrations in the tanks from continuous OBS turbidity measurements. Bulk particle settling speed (mm s^{-1}) was measured in all tanks using the settling profiles generated by the OBS-3 turbidity meters during mixing-off phases. The distance from the surface to the turbidity

sensor (0.5 m depth) was divided by the time to reduce the initial TSS concentration by 50 % of the range to its steady state value. Bivalves repackage organic and inorganic matter into biodeposits, likely increasing the average size structure and settling of the particles in the R_BD tanks compared to R tanks. More frequent samples of TSS, PIM, POM, POM:PIM, PN, PP, PC, chl *a* were also collected during three mixing-off periods on days 15, 22 and 29 to examine changes in the particulate properties over time during settling.

Sediment chl *a*, and sediment phaeophytin concentrations were measured at the end of the experiment and the samples analyzed fluorometrically (Parsons et al. 1984). At time zero, no microphytobenthos was expected to be present, as the sediments had been kept in the dark during the sediment re-equilibration process after defaunation before STURM experiment start. Sediment cores were taken at the end of the experiment, the contents washed through a 0.5 mm diameter mesh, and the sample preserved with buffered formaldehyde, however, no macrofauna was found in any of the tanks.

2.3. Zooplankton

Mesozooplankton was sampled twice a week during mixing-off by pumping 40 l $tank^{-1}$ at 27 l min^{-1} through a 63 µm Nitex screen using a diaphragm pump, and these samples were washed into bottles and preserved with buffered formaldehyde. Dominant taxa and age groups of the mesozooplankton were determined on a dissecting microscope using direct counts. To estimate the dry weights of the individuals of the different taxa, the number of individuals was multiplied by their taxa's respective weight characteristic (Table 2). Dry weight for polychaetes was determined from measured polychaete length (White & Roman 1992). The dominant taxa were copepod nauplii, *Acartia tonsa* adults, polychaete larvae, and copepodites. Zooplankton

densities (#/L) were converted to carbon (μg l^{-1}) for each taxon following White and Roman (1992, table 1: "Carbon [µg C ind^{-1}] = 0.32 W"), and the taxa were combined for an estimate of combined mesozooplankton biomass to compare their relative biomass to phytoplankton biomass (in a common carbon unit).

2.4. Statistical analyses

The same statistical analyses were used as in Porter et al. (2010, 2013, 2018a). Chl *a*, phaeophytin, total suspended solids, the dissolved inorganic and organic nutrients and particulate nitrogen, phosphorus, and carbon were each averaged from day 2 – 29 of the experiment for each tank (8 measurements over a 4-week period). An additional measurement on day 1, while graphed, was not included in the statistical analysis as no biodeposits had yet been added to the R_BD tanks. For some variables, statistical analysis was performed only on data from day 15 to the end of the experiment. A split plot design in SAS 8.2 was used for mixing-on–off particulate concentrations (PC, PN), on-off geometric mean irradiance, on–off irradiance at the sediment surface as well as on-off water column chl *a* concentrations, phaeophytin concentrations, and ratio of chl *a* to phaeophytin. In addition, split plot in time in SAS 8.2 was used to compare the initial phytoplankton biomass to average biomass during day 2-29. Post-hoc tests for the split plot design were the Student Newman Keuls test and least squares means analyses in SAS 8.2. Statistical t-tests were used to determine if there was a shift towards smaller phytoplankton cells (cell volume 3-240 μm^3) versus larger cells (241-65,300 μm^3) in the R and R_BD tanks, respectively.

Mesozooplankton abundance was averaged for each tank from day 3 – 28. Only data from the mixing-on phases were included in statistical comparisons. Statistical t-tests were used

for on-phase water column Chl *a*, phaeophytin, PN, PC, the dissolved nutrient data, the dissolved oxygen, zooplankton abundance, and the sediment chl *a* data, water column accessory pigment to chl *a* ratios, and direct counts of phytoplankton abundance.

Linear regression of mesozooplankton biomass and phytoplankton biomass (estimated from direct cell counts) were used to determine the relationship between the mesozooplankton community and phytoplankton. Statistical *t*-tests and regression analyses were done using the Microsoft Excel Analysis tool pak (Microsoft Corp.). Significance of all analyses was defined at the $p \leq 0.05$ level.

3. RESULTS

3.1. Biodeposits added

On average, 4.8 (SD ± 2.9) g TSS, 478 (SD ± 220) mg PC, 64.1 (SD ± 33.4) mg PN, and 14.2 (SD ± 8.6) mg PP in the biodeposits were added to each tank daily (Table 3h) with a ratio of POM to PIM of 0.6 (SD ± 0.3). With 2.73 (SD ± 1.9) mg Chl *a*, 6.63 (SD ± 4.76) mg phaeophytin, small amounts of chl *a* were found in biodeposits and added to the tanks with the biodeposits daily. On the first day, in the afternoon mixing-on phase after sampling, 62.1 g TSS, 3 g PC, 398 mg PN and 123.6 mg PP were added to each tank (Table 3h).

3.2. Water column processes

Water temperatures ranged from 22.61 to 30.46 ^{0}C in the experiment (R tanks: 27.24 [SD ± 1.63] ^{0}C; R_BD tanks: 27.21 [SD ± 1.67] ^{0}C), and temperature in the six tanks tracked each other closely ($p = 0.7498$, Fig. 2). Water temperatures were about 2.4 ^{o}C cooler over the first part

of the experiment from day 0 to 15 than in the second part of the experiment (day 15 to the end) during which the experiment experienced two heat waves.

Total suspended solid (TSS) concentrations were significantly higher in the tanks with oyster biodeposits (R_BD; 222.46 [SD ± 58.71] mg l^{-1}; Fig. 3, Table 3a) than in the resuspension tanks without added biodeposits (137.4 [SD ± 72.05], p = 0.0225, days 2-29 mg l^{-1}; Fig. 3, Table 3a). TSS in R tanks came from resuspended bottom sediment, TSS in R_BD tanks came from resuspended bottom sediment plus resuspended oyster biodeposits. TSS was resuspended during mixing-on of the tidal cycle due to high bottom shear stress. Later in the experiment, TSS was mediated by bottom shear stress and stabilizing effects of microphytobenthos. Throughout the experiment, TSS concentrations increased from ~ 150 mg l^{-1} in day 0 – 15 of the experiment in the R_BD tanks to ~ 275 mg l^{-1} in the second half of the experiment (days 15 – 30). Throughout the experiment, TSS concentrations increased from ~ 80 mg l^{-1} held from day 0 – 15 of the experiment in the R tanks to ~ 200 mg l^{-1} held during the second half of the experiment (days 21 – 30).

Water column chl *a* levels continuously increased from ~ 5 µg l^{-1} at the beginning of the experiment to ~ 80 µg l^{-1} at the end of the experiment in the R tanks and increased from ~ 5 µg l^{-1} at the beginning of the experiment to ~ 40 µg l^{-1} held from day 10 - 25 to ~ 80 µg l^{-1} towards the end of the experiment in the R_BD tanks (Fig. 4a). Chlorophyll *a* concentrations were similar between the R and the R_BD tanks (Fig. 4a, $p = 0.9085$).

Chl *a* did not substantially resuspend and settle in the R_BD tanks as chl *a* concentrations were the same during the mixing-on and -off phases, however, chl *a* concentrations were significantly reduced in the R tanks during mixing-off compared to R_BD tanks during mixing off (Fig. 4a, d). Phaeophytin concentrations were significantly higher in R_BD tanks than in R

tanks, and phaeophytin concentrations differed significantly between the mixing-on and the mixing-off' phases as degraded material was resuspended and deposited in R_BD tanks but were similar during the mixing-on and –off phases for R tanks (Fig. 4b, e). The ratio of chl *a* to phaeophytin linearly increased within the first eight days of the experiment in R tanks (Fig. 4c, f) and was about four times higher in R with ~ 2 compared to R_BD tanks with ~ 0.5 from day 10 to the end of the experiment. It was significantly higher during the mixing-off phase of R_BD systems than during the mixing-on phase, however, the ratios were the same during mixing-on and mixing-off for R tanks (Fig. 4f). Finally, during mixing-off, the particulate carbon (PC), particulate nitrogen (PN) and particulate phosphorus (PP) concentrations were significantly lower in the R tanks than in R_BD tanks.

PC, PN, and PP concentrations were linearly related to TSS concentrations (Table 4, $p < 0.0001$), and PC and PN concentrations were significantly enhanced in R_BD tanks (Fig. 3, Table 3c). With 8.39 (SD ± 0.88) in R tanks, the C to N ratio was similar as in R_BD tanks with 8.23 (SD ± 0.13) (Table 3c, $p = 0.6214$). Much of the PN, PC, and PP settled out during mixing-off phases in all tanks.

While chl *a* concentration was similar between R tanks and R_BD tanks (Fig. 4a, Table 3b), significant differences in the phytoplankton community were observed through use of high performance liquid chromatography (HPLC, Fig. 5) and taxonomic enumerations of phytoplankton biomass (Fig. 6). In addition, the ratio of chl *a* : carbon was significantly higher in R_BD tanks than in R tanks (Fig. 6g, $p = 0.0002$, Table 3b).

Nitrate plus nitrite concentrations ($NO_2^- + NO_3^-$, Fig. 7b, $p = 0.0433$, Table 3d) and dissolved inorganic nitrogen concentrations (DIN, Fig. 7c, $p = 0.0395$, Table 3d) were significantly higher in tanks that received biodeposits than in R tanks. Total dissolved nitrogen

(TDN, Fig. 7e) and total dissolved phosphorus (TDP, Fig. 7h) were significantly higher in R_BD tanks than in R tanks over the second half of the experiment (d15 to the end, $p = 0.0015$ and $p = 0.0049$, respectively).

Dissolved phosphate (PO_4^{3-}) concentrations (Fig. 7f) decreased in all tanks from ~ 1.5 µmol l^{-1} at the start of the experiment to ~ 0.2 µmol l^{-1} at day 15. After day 15 it increased again to ~ 0.3 µmol l^{-1} in the R_BD tanks but remained at ~ 1 µmol l^{-1} in R systems that experienced a bloom of *S. costatum* (> 2,000 µg carbon l^{-1}). While nutrient concentrations were related to the phytoplankton cell counts in R and R_BD tanks, they did not relate to the chl *a* concentrations. Ammonium (NH_4^+) concentrations were similar between R and R_BD tanks ($p = 0.3316$, Fig. 7a, Table 3d). Dissolved organic phosphorus (DOP) concentrations (Fig. 7g, Table 3d) and dissolved organic nitrogen (DON) concentrations (Fig. 7d, Table 3d) were similar in all tanks. Dissolved silicate concentrations ranged from about 100 µmol l^{-1} to 20 µmol l^{-1} over the experiment and silicate was at no time limiting, *i.e.*, less than 5 µmol l^{-1}, in any of the systems (Fig. 7i).

3.3. Light penetration

Light, as measured by a modified secchi disk, penetrated 25 cm into R_BD tanks during resuspension (Fig. 8a) and 20 - 50 cm into R tanks during mixing-on. During the mixing-off phases, secchi depth reached between 30 - 50 cm in R_BD tanks and ~ 80 cm in tanks that had not received oyster biodeposits (Fig. 8a). Measured bottom irradiance levels during the resuspension phase were low in R_BD and R tanks due to high turbidities as a result of high TSS concentrations (Fig. 3). Irradiance at the sediment surface during mixing-on was similar in the R (~2.03 [SD ± 1.89] µmol m^{-2} s^{-1}) and in the R_BD systems (0.57 [SD ± 1.4], $p = 0.1126$). Geometric mean irradiance in the water column during mixing-on was higher in R tanks with ~

16.24 (SD ± 3.11) µmol m^{-2} s^{-1} to R_BD tanks than in R_BD tanks with 6.43 (SD ± 7.05) µmol m^{-2} s^{-1} (p = 0.0489) that had higher TSS concentrations. During the mixing-off phase, significantly more light reached into all tanks than during mixing-on, and, light levels were higher in R tanks than in R_BD tanks during mixing-off (p = 0.0014, Fig. 8b). Significantly more light reached into R tanks than R_BD tanks with mixing-on and –off combined as determined with a Student Newman Keuls test in SAS 8.2 ($p \leq 0.05$).

Microphytobenthos grew on the sediment bottoms of tanks despite high bottom shear stress (~ 0.36-0.51 Pa during mixing-on phases (Fig. 1c). Light limitation (Fig. 8b), and sediment chl *a* concentrations were similar with 42.75 (SD ± 3.05) mg m^{-2} in R tanks and 38.77 (SD ± 6.20) mg m^{-2} in R_BD tanks (p = 0.5541). Sediment phaeophytin concentrations with 206.53 (SD ± 17.25) mg m^{-2} in R tanks and 212.44 (SD ± 21.57) mg m^{-2} in R_BD tanks were not significantly different (p = 0.7767).

3.4. Particle Settling

Defining an estimate of the bulk settling velocity as the distance from the surface to the turbidity sensor (0.5 m depth) divided by the time to reduce the initial TSS concentration by 50 % of the range to its steady state value, bulk settling speeds changed in R_BD tanks over the course of the experiment while they hardly changed in R tanks (Fig. 9). While particles settled slowly on day 2 (bulk settling speed 0.5 to 0.7 mm s^{-1} in all systems), bulk settling speeds increased continuously to about 2 mm s^{-1} until day 14 in R_BD tanks, and after day 15 increased dramatically to 4 to 8 mm s^{-1} in the R_BD tanks over the second half of the experiment. The switch to increased bulk settling speeds coincided with the start of an increase in TSS (Fig. 3), phosphate (Fig. 7f), DIN (Fig. 7c), nitrate + nitrite (Fig. 7b) concentrations that lasted for the

remainder of the experiment (Fig. 7). The ratio of POM : PIM was similar in the R (0.24 [SD ± 0.07]) and R_BD tanks (0.23 [SD ± 0.04], $p = 0.8908$). In addition, this increase in nutrient concentrations overcame nutrient limitation in R_BD systems while the R systems became nutrient limited (DIN < 2 µmol l^{-1}, PO_4^{3-} < 1 µmol l^{-1}, Fig. 7c, f, Fisher et al. 1992, 1999, Poikane et al 2019).

3.5. Phytoplankton

Diatoms, phytoflagellates, dinoflagellates, chlorophytes and cyanobacteria were found in the tanks using direct counts (Table 5). While direct counts of dinoflagellate (Fig. 6d) abundances and HPLC (peridinin, Fig. 5g) were similar in all tanks, diatom abundance was significantly higher in R tanks than in R_BD tanks (Fig. 6b, f), likely indicated by the fucoxanthin signal in the HPLC results (Fig. 5a). *Skeletonema costatum* was the dominant diatom in R tanks, and was significantly more abundant there than in R_BD tanks (Fig. 10a, $p = 0.0141$). In addition, average *S. costatum* chain length was significantly longer with 11.2 (SD ± 0.2) cells per chain in R tanks than in R_BD tanks with 9.8 (SD ± 0.6) cells per chain ($p = 0.0036$, Fig. 10b) as determined from 360 individuals in the R tanks and 190 individuals in the R_BD tanks. The ratio of alloxanthin to chl *a* (indicative of Cryptophyceae) was significantly higher in R_BD tanks in the second half of the experiment (Fig. 5d) and direct counts detected *Cryptomonas sp*. in the tanks.

Chlorophytes were significantly more abundant in R_BD tanks as the ratio of chlorophyll b to chl *a* was significantly higher in R_BD tanks than in R tanks (Fig. 5b). Moreover, neoxanthin and lutein (both indicate chlorophyceae and prasinophyceae) were significantly higher in R_BD tanks (Fig. 5f, e), however there were no significant differences in

prasinoxanthin between treatment tanks (Fig. 5h) indicating prasinophyceae. Thus, it was chlorophytes that were significantly more abundant in biodeposit tanks than in the R tanks.

Direct counts of Cyanobacteria abundance were not significantly different (Fig. 6e), however, the ratio of zeaxanthin to chl *a*, often used to indicate cyanobacteria (e.g., Van Meersche & Pinckney 2019) but sometimes used to indicate prochlorophyte, rhodophyta and some chlorophyceae (Jeffrey & Vesk 1997), was significantly higher in biodeposit tanks (Fig. 5c). It is possible that very small prochlorophytes were in the samples that cannot be counted with the Utermöhl technique used in this study as picoplankton have to be counted with fluorescence microscopy (MacIssac & Stockner 1993) or analyzed by flow cytometry (Veldhuis & Kraay 2000).

Total phytoplankton biomass (Fig. 11a), total cell density (Fig. 11g), diatom biomass (Fig. 11b), and phytoflagellate biomass (Fig. 11c) were significantly lower at time zero than during the experiment (day 2 - 29) in all treatments, while dinoflagellate biomass was variable (Fig. 11d). Over the course of the experiment, biomass shifted towards a diatom-dominated phytoplankton community, especially in R tanks where the percentage of phytoplankton community composed of diatoms increased by 31 % (Fig. 12a, b). In addition, over the second half of the experiment most diatoms (84.4 %) in R tanks were *S. costatum* by cell density, contrasted with only 6.8 % of diatoms in biodeposit tanks.

Over the course of the experiment, the abundance of small phytoplankton cells (cell volume of 3 to 240 μm^3, Table 5) increased continuously in R tanks, and the biomass of small cells was significantly higher with 2,704.5 (SD ± 2,034.3) µg carbon l^{-1} than the biomass of larger cells (cell volume 241- 65,300 μm^3, Table 5) with 788.3 (SD ± 474.6) µg carbon l^{-1} (p = 0.0319, Fig. 13c). In contrast, with a biomass of 557.0 (SD ± 422.2) µg carbon l^{-1}, small cells did

not dominate the phytoplankton community in the biodeposit tanks where large cells had a biomass of 359.9 (SD ± 138.4) µg carbon l^{-1} (p = 0.2450, Fig. 13d). In the second half of the experiment, 85.6 % and 5.7 % of the small phytoplankton (cell volume of 3 to 240 μm^3, Table 5) were *S. costatum* in R tanks and R_BD tanks, respectively.

Some patterns of species abundance, in addition to *S. costatum*, emerged from direct phytoplankton counts. Small individuals of the diatom *Cyclotella sp.* (smaller than 10 µm, size 1, Table 5) were found in R_BD tanks throughout the experiment, *Cyclotella sp.* was only found during the first half of the experiment in R tanks and was completely absent during the second half of the experiment. Another small diatom *Cylindrotheca closterium* (size 1, Table 5) was found in all tanks throughout the experiment. However, *Cyclindrotheca closterium* larger than 40 µm (size 2, Table 5) was abundant in the R tanks during the second half of the experiment, and only appeared occasionally in R_BD tanks. The dinoflagellate *Gymnodinium sp.* (10 – 20 µm, size 2, Table 5) was abundant in the R_BD tanks during the second half of the experiment while they were mostly abundant in the R tanks during the first half of the experiment. The phytoflagellates *Cryptomonas sp*. and *Pyramimonas sp.* (size 2, Table 5) were abundant in all tanks during the first part of the experiment and disappeared entirely during the second half of the experiment. While the diatom *Thalassionema nitzschoides* (size 2, Table 5) was more abundant in the first half of the experiment in the R_BD tanks, it was mostly more abundant in the second half of the experiment in the R tanks. The diatom *Chaetoceros sp.* (size 2, Table 5) was present in the second half of the experiment in the R tanks and only very occasionally detected in R_BD tanks. *Scenedesmus quadricauda* were rare and encountered once in a single R tank.

3.6. Macrofauna and mesozooplankton

No macrofauna was observed in any tanks at the end of the experiment, however, mesozooplankton was abundant in biodeposit tanks. Dominant mesozooplankton taxa were adult *Acartia tonsa* copepods (Fig. 14d), copepodites (Fig. 14e), copepod nauplii (Fig. 14c), and polychaete larvae (Fig. 14b) (Table 3f). It took nearly a week for adult copepods and 10 days until polychaete larvae were detected (Fig. 14d, b). Pumps likely destroyed the adult mesozooplankton stages (Adey & Loveland 1998) during the initial raw water fill of the tanks at the start of the experiment. The R_BD tanks contained 52.32 (SD ± 27.17) adult *Acartia tonsa* l^{-1} throughout the experiment ($p = 0.0018$, Fig. 14d, Table 3f), while R tanks contained 4.99 (SD ± 3.45) adult *Acartia tonsa* l^{-1}. On days during the heat wave (days 13 – 17), *Acartia tonsa* abundance in the water column decreased to about 42 to 47 individuals l^{-1} in R_BD systems (Fig. 14d) when copepods potentially migrated towards the bottom of the tank; however, they increased again on day 21. Polychaete larvae continuously increased in all systems up to 80 to 99 individuals l^{-1} in both systems at the end of the experiment and polychaete concentrations were not significantly different between all tanks ($p = 0.3559$, Fig. 14b). Polychaete larvae were grouped by size (large = ~ 0.536 mm; small = ~ 0.152 mm) for carbon determinations. Occasionally, veliger larvae, harpacticoid copepods, flatworms, nematodes, cyclopoid copepods, and other calanoid copepods were found, but abundances were similar between treatments (Table 1f). In addition, rotifers (> 63 μm) were caught in our zooplankton net. Mesozooplankton community was positively correlated with phytoplankton biomass (from counts, converted to carbon) in R tanks (Fig. 14f) but not in R_BD tanks (Fig. 14g).

4. DISCUSSION

4.1 Suspended solids, water clarity and biogeochemistry

TSS concentrations increased due to added resuspended oyster biodeposits (e.g. Hildreth 1980) and particle settling rates likely increased because of particles adhering to each other. While the effect of suspended sediment concentration on particle size is not understood (Berhane 1997, Walker et al. 2005), both the mass and size of particles is dependent on the energy dissipation rate. The floc settling rate is influenced by floc composition and the ratio of POM : PIM, which was similar in R and R_BD tanks, shape, porosity and water content (Droppo et al. 1997). Measured particle sinking velocities of ~ 1 - 8 mm s^{-1} in oyster biodeposit tanks (Fig. 9) were consistent with biodeposit settling rates of 0.19 - 16.25 mm s^{-1} for zebra mussels, *Dreissena polymorpha* (McLean et al. 2018), 3 - 18 mm s^{-1} for *Mytilus edulis* biodeposits (Callier et al. 2006), 1 - 18 mm s^{-1} in *M. edulis'* biodeposits (Chamberlain 2002, as cited in Weise et al. 2009), and 1 - 45 mm s^{-1} with green lipped mussel *Perna canaliculus* biodeposits (Giles & Pilditch 2004).

TSS concentrations in the second half of the experiment were more variable, probably due to microphytobenthos formation, stabilizing some tanks more than others (Yallop et al., 1994, Widdows & Brinsley, 2002). Despite some variability in TSS concentration, clear differences in ecological responses were detectable in R and R_BD tanks (e.g., see phytoplankton in section 3.5 and zooplankton in section 3.6).

Oyster biodeposit additions decreased water clarity and light availability and increased water column nitrate + nitrite concentrations. Nitrate + nitrite and phosphate concentrations during the second part of the experiment were significantly higher in tanks with biodeposits.

Biogeochemical sediment nutrient and gas fluxes, also measured in this experiment, were similar between the R and R_BD tanks (unpublished data).

4.2 Algal biomass and composition

Tanks with sediment resuspension had increased chl *a* concentrations (Porter et al. 2010) beyond the management threshold of 40 µg chlorophyll *a* (chl *a*) l^{-1} (https://www.epa.gov). Such sediment resuspension may enhance sediment nutrient release (Morin and Morse 1999) or conversely dampen the effect of nutrient inputs on the phytoplankton community (Kang et al. 2013). To examine the role of resuspended biodeposits and associated nutrients on phytoplankton abundance with high bottom shear and realistic water column turbulence, our initial hypothesis was that biodeposit additions and resuspension enhances nutrient concentrations (Porter et al. 2018a). Increased chl *a* concentrations (Browning et al. 2019, Gerhard et al. 2019), and community structure (Medina-Gómez et al. 2019, Villamaña et al. 2019) are a likely result.

The non-significant differences in chl *a* concentration between treatments (Fig. 4a) were inconsistent with significantly higher direct counts of phytoplankton biomass in R tanks relative to R_BD tanks. These observations refute our original hypothesis. Phytoplankton direct cell counts and HPLC pigments show significant effects of tidal sediment and biodeposit resuspension on the phytoplankton abundance and community structure. The effects of differential mixing on phytoplankton abundance and community structure (Iversen et al 2010, Fouilland et at 2016) is controlled for in this experiment that ensured similar turbulence intensity, volume-weighted energy dissipation rate, and bottom shear stress. Biodeposition may alleviate phytoplankton growth limitation during periods of N limitation (Cranford et al. 2007). While in R_BD tanks nutrients were never limiting, nutrient limitation is inferred in R tanks after week 15

(Fig. 7c, f) if published nutrient limitation thresholds for dissolved silicate of < 5 µmol l^{-1}, DIN < 2 µmol l^{-1} (Mediterranean threshold Poikane et al. 2019), and phosphate < 0.1 µmol l^{-1} (Fisher et al. 1992; Fisher et al. 1999, T. Fisher, Horn Point Laboratory, University of Maryland Center for Environmental Science, pers. comm.) are applied.

Skeletonema costatum blooms after day 15 significantly reduced nitrate + nitrite and phosphate concentrations in R tanks and potentially suppressed cryptophytes and cyanobacteria as diatoms can rapidly take up and store nitrate, which outcompete cryptophytes and cyanobacteria (Lomas & Glibert 2000, Clark et al. 2002, Sarthou et al. 2005, Kamp et al. 2015). In contrast, chlorophytes became significantly more abundant in biodeposit tanks after day 15 where no nutrient limitation was experienced.

The R_BD tanks with less *S. costatum* and shorter chain length had significantly higher nitrate + nitrite levels than R tanks, with both higher nutrient levels and increasing temperature associated with smaller chain length in phytoplankton (Takabayashi et al. 2006). Although chain lengths remained significantly longer in R tanks, chain length decreases in the second half of the experiment coincided with increased temperatures and decreased nutrient concentrations. Moreover, R_BD tanks with significantly shorter chain length had significantly higher abundances of *Acartia tonsa*. *Skeletonema marinoi (*one of six subspecies of *S. costatum,* Bergkvist et al. 2012)*,* changes morphology to single celled or shorter chain phenotype when exposed to *Acartia tonsa* (Bergkvist et al. 2012). Copepod chemical cues have been observed to trigger chain fragmentation in *S. marinoi* (Bergkvist et al. 2012), and the significantly higher abundance of *Acartia tonsa* in biodeposit tanks may have provided chemical cues for chain splitting so that chain length was significantly shorter in these tanks than in R tanks. Copepodamide chemical cues, released by marine zooplankton also triggered defenses such as

chain length shortening in a study by Grebner et al. (2019). Grazing activity increased chain length (Martin 1970, Deason 1980, O'Connors et al. 1980), however, Bjærke et al. (2015) suggested this could be due to the induced splitting of chains. *Skeletonema* chain length decreased with increasing abundance of mesozooplankton (Turner et al. 1983), which is also supported in this study. Other studies found certain algae (*Scenedesmaceae*) prevent predation by increasing their size (via added chain length) or develop armor spines (Hessen & Van Donk 1993) when exposed to copepods (Bjaerke et al. 2015), however, *S. costatum* has no spines as defenses.

Observations of chain length increases with experimental silicate limitation (Fouilland et al. 2016) may arise because diatom cells stop their cellular cycle in the G2 phase at their maximum size (Martin-Jéséquel et al. 2000). However, the absence of silicate limitation in our experiment (Fig. 7i) is not consistent with longer chain lengths. Since light absorption is higher for smaller cell fragments than for larger cell fragments (Agusti 1991, Finkel et al. 2000), less light in biodeposit tanks would have allowed the smaller *S. costatum* fragments found in biodeposit tanks to absorb more light. Moreover, the ratio of chl *a* : carbon was significantly higher in R_BD tanks that were more light limited than R tanks (Fig. 6g, $p = 0.0002$), which suggests an adaptation to the low light regime in R_BD tanks by increasing the chl *a* content per cell in the phytoplankton (Buchanan et al. 2005, Porter et al. 2018a). Phytoplankton acclimate to light limitation by changes in pigment concentration to maximize photosynthetic rate (Finkel et al. 2004). Following the phytoplankton size analysis above, there was no shift to smaller phytoplankton in the R_BD tanks ($p = 0.2450$) to potentially explain the shift to a higher chl *a* : carbon ratio in the R_BD tanks.

Oyster biodeposit resuspension affects ecosystem components such as the mesozooplankton community, with increased *Acartia tonsa* biomass in R_BD tanks relative to R tanks. While the mesozooplankton community was positively correlated with phytoplankton biomass in R tanks (Fig. 13f), zooplankton biomass was low in R tanks, considering that more than a third of carbon transitioned into phytoplankton biomass but subsequently did not translate into zooplankton biomass. Zooplankton grazing of phytoplankton biomass appeared minimal in R tanks with a large bloom of long-chain *S. costatum*. The mesozooplankton community was not correlated with phytoplankton biomass in R_BD tanks (Fig. 14 g), and mesozooplankton abundance was higher than expected from phytoplankton biomass.

Biodeposit tanks had a carbon deficiency of 2.54 g compared to R tanks. Phytoplankton carbon in R_BD was 2.54 g lower relative to R tanks. Estimates suggested that mesozooplankton may consume 5–15 % of primary production (Carlson 1978, Behrenfeld & Falkowski, 1997, Calbet, 2001, Anderson et al. 2019). Assuming a 10 % trophic transfer to higher level predators (mesozooplankton), 1.11 g phytoplankton carbon would be converted to 0.111 g mesozooplankton biomass in biodeposit tanks. The same conversion of phytoplankton to mesozooplankton in the R tanks converts 3.65 g of phytoplankton carbon to 0.365 g of mesozooplankton carbon. The difference in phytoplankton to mesozooplankton carbon weight conversions between the treatments shows that biodeposit tanks had only 30% of the biomass conversions (0.111 g) that non-biodeposit tanks (0.365 g) had, despite greatly enhanced zooplankton populations. R tanks had 0.1314 (SD ± 0.037) g carbon zooplankton per tank and thus R_BD tanks were expected to have 0.385 g carbon per tank, which was calculated by adding actual zooplankton carbon, 0.1314 g + established carbon deficiency of biodeposit tanks, 0.254 g; this estimate was similar to observed values (0.3193 [SD ± 0.044] g carbon per tank).

In biodeposit tanks the 'missing' phytoplankton must have been converted to zooplankton, though potential grazing effects of the microzooplankton community are not included in the analysis. The resuspension of protists may alter the microbial food web (Shimeta et al. 2003), all of which may have selectively affected microzooplankton grazing in tanks. However, decreased microzooplankton abundance has been associated with resuspension (Lawrence et al. 2004). While increased DOC concentrations can yield increased heterotrophic picoplankton concentrations (La Rosa et al. 2002), our DOC concentrations were similar between R and R_BD tanks ($p = 0.6628$), suggesting an expectation of similar heterotrophic picoplankton concentrations between treatments. Olson et al. (2006) also suggested higher abundance of smaller phytoplankton at times of intense mesozooplankton grazing, and increased chlorophyte abundance was detected in R_BD tanks with intense mesozooplankton grazing, which are consistent with these observations. However, phytoplankton size analysis revealed that R tanks shifted to smaller (cell volume 3-240 μm^3, including *S. costatum*) phytoplankton species over the experiment ($p = 0.0319$) while biodeposit tanks had no such shift ($p = 0.2450$), refuting this idea. In this experiment, nutrients decreased more in the R than in the R_BD tanks and became limiting in R tanks. The presence of smaller plankton sizes in R tanks (mostly *S. costatum*) is consistent with the available nutrients, because smaller size allows plankton to better compete for nutrients (Riegman et al. 1993).

The low presence of grazing of the long chains of the *S. costatum* bloom in the R tanks is unusual, as copepods generally feed more on longer chains (Bjærke et al. 2015). *S. costatum* took up nitrate + nitrite in R tanks, and more than a third of carbon was partitioned in the phytoplankton in the R tanks, without conversion to mesozooplankton. In R_BD tanks much of the carbon remained in added biodeposit particulate carbon and was transformed into

zooplankton tissue. A lower carbon content of total suspended solids resulted in poor food quality and low grazing rates by zooplankton despite abundance and quality of diatom-dominated algal food in a study by Wood et al. (2016). Food quality on a mass basis (e.g., POM : PIM ratio, C : N ratio) was poor in all tanks due to sediment resuspension.

Multiple studies show that *S. costatum* negatively affect copepods. *S. costatum* releases unsaturated C_7 and C_8 aldehydes that may affect the egg hatching success of copepods (Pohnert et al. 2002, d'Ippolito et al. 2002, Pohnert 2005) as found in experiments with diatom cultures, and *S. costatum* and other diatoms release aldehydes that have been found to arrest copepod embryo development (Miralto et al. 1999), either of which may have affected the copepod population in R tanks. *S. costatum* can have adverse effects on copepod reproduction, evidenced by Budge and Parrish (1999) and Pohnert (2005) findings that 65 % of the hatched nauplii *C. helgolandicus* had deformed limbs after feeding on *S. costatum. S. costatum* reduces both fecundity and egg hatching success in *Acartia clausi* and causes reduced fecundity but not a reduction in hatching success in *Temora stylifera* (Ban et al. 1997). Jónasdóttir et al. (1998) has suggested the potential for phytoplankton toxicity. Perhaps in R tanks the abundant *S. costatum* with long chains negatively affected copepod reproductive success; this would help to understand the lower abundance of copepod nauplii in R than in R_BD tanks during the second half of the experiment. Recent investigations reveal that phytoplankton exhibit defense mechanisms that negatively affect zooplankton (Pančić & Kiørboe 2018).

The > 40 µm diatom species with defenses such as spines (Van Donk 2011) included the *Chaetocerus subtilis* and *Chaetocerus sp.,* and *Cylindrotheca closterium* (= *Nitzschia closterium*) predominantly found in R tanks, with small *C. closterium* present in R_BD tanks. *Scenedesmus quadricauda* was observed only once in this study, in an R tank. Cyanobacteria were observed in

both treatments. *C. closterium,* an epizoic diatom species, can proliferate on the surface of copepods (Gárate and Lizárraga 2016). Cyanobacteria likely have poor nutritional quality for zooplankton due to inadequate fatty acid composition (Ahlgren et al. 1992), production of nonribosomal peptides, e.g., nodularin and spumigin (Mazur-Marzec et al. 2016) and low manageability of the filaments (Gliwicz and Siedlar 1980). Filamentous cyanobacteria have a negative effect on copepod egg production despite high concentrations of non-cyanobacterial food and alter the transfer of the essential micronutrient thiamin (i.e., vitamin B_1) to copepods (Fridolfsson et al. 2019). While cyanobacteria abundance was significantly higher in R_BD tanks ($p = 0.0056$) than R tanks when measured as the ratio of zeaxanthin : chl *a* using HPLC (cyanobacteria abundance was similar using direct counts, $p = 0.7260$), *Acartia tonsa* was abundant in the R_BD tanks and we found no negative effects of cyanobacteria on *Acartia tonsa*.

Less abundant and shorter-chained *S. costatum* were found in biodeposit tanks suggesting the potential for diatom settling. Longer *S. costatum* chains of live and unstressed (Smayda 1974, Waite et al. 1997) cells have greater buoyancy whereas shorter chains settle more easily (Smayda & Boleyn 1966b). Although the shorter-chained *S. costatum* may have settled out in R_BD tanks contributing to lower *S. costatum* abundance in these tanks, mixing should have countered this effect. *Skeletonema. costatum* aggregates may have formed during resuspension promoting faster sinking (Ziervogel & Forster 2005), although energy dissipation rate was similar in all systems. Chl *a* concentrations between mixing-on and mixing-off were not significantly different, suggesting a lack of settling of *S. costatum* in the R_BD tanks.

Although Chl *a* measurements are typically used to indicate phytoplankton biomass, using chl *a* alone as an indicator of phytoplankton biomass may be misleading. In this experiment, chl *a* abundance did not differ among treatments, whereas significant differences

were detected in phytoplankton biomass based on the count data and HPLC analysis. As suggested by Van Meersche and Pinckney (2019), chl *a* measurements should be supplemented with an additional measure of phytoplankton biomass. The significantly higher chl *a* : carbon ratio in biodeposit tanks than in R tanks suggests a low light adaptation of the phytoplankton in R_BD tanks (Buchanan et al. 2005, Porter et al. 2018a).

4.3 Temporal and experimental considerations

In this study, as in Porter et al. (2018a), multiple system effects had a lag time and became apparent only in the second half of the experiment and phytoplankton acclimated their physiology (and internal stoichiometry) to novel nutrient and light conditions (e.g. Wirtz & Pahlow 2010). Ecosystems are complex with positive and negative feedback loops, high connectivity, non-linear changes, and delays between cause and effect (Scholes & Kruger 2011). The response time for phytoplankton and zooplankton populations to increase after biodeposit addition is affected by the longevity and physiology of the organisms (Harley et al. 2017), transformation and fate of biodeposits, and by the phytoplankton-copepod feedback loops. Episodic meteorological and nutrient-load events can drive coastal planktonic ecosystem dynamics and Guadayol et al. (2009) observed that nutrient enrichments resulted in increased chl *a* concentrations a week after addition. Longer phytoplankton time lags have been observed such as two weeks following resuspension in the German Bight, Germany (Su et al. 2015), similar to the time lag in this research.

Short-duration experiments will not necessarily include all the direct and indirect interactions of nutrient, phytoplankton, and mesozooplankton dynamics. Indirect effects have often been identified by accident when experiments produced unanticipated results (Wootton

2002). In the present case, R tanks were light limited and any regenerated nitrate + nitrite through sediment resuspension was taken up by a bloom of *Skeletonema costatum*. While phytoplankton carbon was transferred to *Acartia tonsa* in the biodeposit treatment with less abundant and shorter-chained *S. costatum* than observed in R tanks, phytoplankton carbon transfered to the mesozooplankton community in R tanks potentially had negative effects on copepod reproduction. Copepods, preying on microzooplankton, have been found to allow an increase in phytoplankton in a trophic cascade (Stibor et al 2004a, b, Vadstein et al. 2004, Armengol et al. 2017). However, in R_BD tanks, the abundant *Acartia tonsa* decreased phytoplankton abundance and did not release phytoplankton from grazing pressure.

Field observations of the consequences of resuspended sediments and biodeposits are difficult to track (Testa et al 2015) and typical experimental ecosystem experiments with low bottom shear stress do not support resuspension (Doering et al. 1986, Porter et al. 2010). Though the STURM facility (Porter et al. 2018b) allows high bottom shear stress and realistic water column turbulence levels for benthic-pelagic coupling experiments (Porter et al. 2010, 2013, 2018), oysters were not directly included in this experiment, as the primary focus was on biodeposits. Bivalve filtration of phytoplankton (Cloern et al. 1982, Cohen et al. 1984, Porter et al. 2004a) would have resulted in competition between zooplankton and oysters for algae. The size distribution of phytoplankton might shift towards smaller species (Souchu et al. 2001, Cranford et al. 2007, Jiang et al. 2019) because oysters efficiently filter phytoplankton larger than 3 μm in size (Haven & Morales-Alamo 1970). While it is generally assumed that oysters reduce seston and phytoplankton concentrations, while ignoring biodeposits (Newell & Koch 2004), evidence that oyster reefs measurably reduce water column particulates or impact phytoplankton or microphytobenthic biomass or productivity (Plutschak et al. 2010) is generally

lacking. Oyster-related seston decreases (interpreted as depletion) can be spatially variable (Grizzle et al. 2018) and the interplay between bottom shear stress with sediment and biodeposit resuspension and oysters suggest observations should be interpreted with caution.

Phytoplankton did not shift to smaller cells in biodeposit tanks; however, this response did not include an assessment of picophytoplankton. Improved light penetration associated with oyster filtration (Porter et al. 2004a, Newell & Koch 2004) illuminates the surface of the sediment and alters sediment biogeochemical processes (Porter et al. 2004a). In this study, rather than promoting a phytoplankton bloom (Doering et al. 1986, Asmus and Asmus 1991, Souchu et al. 2001), particularly in oligotrophic systems (Cranford et al. 2007), oyster biodeposit addition and resuspension led to increased zooplankton populations, *Acartia tonsa*, and no phytoplankton bloom. Copepods play a key role in the food web as the main vector from the primary producers to higher trophic levels (Hansen et al. 1994, Verity & Smetacek 1996, Stibor et al. 2004a) while copepod chemical cues may have indirect cascading effects in plankton food webs (Grebner 2019). Several potential connections between biodeposit resuspension and both phytoplankton and zooplankton community structure are suggested from this study. Oyster biodeposits under these experimental conditions were funneled to higher trophic levels without negatively affecting water quality. In addition, diatoms with defenses may have important consequences on prey-predator relationships and on the biomass flux through marine food chains.

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Figure Legends

Fig. 1. (a) Turbulence intensity, (b) energy dissipation rate during a mixing-on phase in the R tanks and in the R_BD tanks. The R_BD tanks had daily additions of biodeposits over a 4-wk experiment. : measurement locations. Tidal cycles (4 h mixing-on, 2 h mixing-off) were generated in all tanks. (c) Bottom shear stress in the STURM tanks during a mixing-on phase.

Fig. 2. Temperature in R tanks (T1, T2, T6) and R_BD tanks (T3, T4, T5) over the experiment, measured in 10 min intervals. Statistical significance is indicated as $p \leq 0.05$. Minimum (Min) and maximum (max) temperature over the experiment. Average temperature in all tanks was 27.22 (SD ± 1.65) ^{0}C.

Fig. 3. Total suspended solids concentrations (TSS, mean ± SD, $n = 3$ for each system and mixing phase) over time tank types during the mixing-on phases and the mixing-off phases as measured using OBS3 sensors, calibrated with TSS samples. Samples on Day 1 were taken shortly after mixing was started and no biodeposits had been added to R_BD yet. R_BD received daily oyster biodeposit additions over the experiment. Difference between R and R_BD during mixing-on as well as during mixing-off statistically significant ($p \leq 0.05$).

Fig. 4. Left panels: time series of 3 variables; right panels: data from R and R_BD tanks for mixing-on and mixing-off phases averaged over the three days as indicated by ellipses in panel (a). (a) Chlorophyll *a* (Chl *a*), (b) phaeophytin (Phaeo), and (c) ratio of chl *a* and phaeophytin concentrations (means ± SD, $n = 3$ tanks for each system and mixing phase) over time in the R versus the R_BD tanks during the mixing-on and –off phases. Differences between on phases statistically significant at $p \leq 0.05$. (d) chlorophyll *a*, (e) phaeophytin, and (f) ratio of chlorophyll *a* to phaeophytin during mixing-on and mixing-off phases. Different letters indicate statistical differences ($p \leq 0.05$).

Fig. 5. (a - h) Ratios of phytoplankton accessory pigments to chlorophyll *a* (all measured by HPLC). $N = 3$ tanks for each system, means ± SD. *P*-values indicate statistical difference at $p \leq 0.05$. Fuco (= fucoxanthin): chl *a*, (b) Chl b: Chl a, (c) Zea (=Zeaxanthin): chl *a*, (d) Allo (=alloxanthin): chl *a*, (e) lutein: chl *a*, (f) Neo (= neoxanthin): chl *a*, (g) Perid (=Peridinin): chl *a*, (h) Prasino (= Prasinochanthin): chl *a*.

Fig. 6. Phytoplankton carbon (C) determined from direct cell counts) in the resuspension tanks (R) and in the resuspension tanks with daily biodeposit additions (R_BD). (a) Total phytoplankton C, (b) diatoms C, (c) phytofl. (phytoflagellates) C, (d) dino (dinoflagellates) C, (e) cyano (cyanobacteria) C. (f) Diatom cell density. (g) Ratio of chlorophyll *a* to total phytoplankton C. Means ± SD, $n = 3$.

Fig. 7. (a) Ammonium (NH_4^+), (b) nitrate + nitrite (NO_3^- + NO_2^-), (c) dissolved inorganic nitrogen (DIN), (d) dissolved organic nitrogen (DON), (e) total dissolved nitrogen (TDN), (f) phosphate (PO_4^{3-}), (g) dissolved organic phosphorus (DOP), (h) total dissolved phosphorus (TDP), (i) dissolved silica, (j) total nitrogen (TN), (k) total phosphorus (TP), (l) TN : TP ratio. The horizontal dashed lines in panels c, f and i indicate thresholds for nutrient limitation for the respective nutrients (see 'Results'). *P*-values indicate statistical difference at $p \leq 0.05$, d15-e indicates *p*-value of d15 to the end of the experiment. Means ± SD, $n = 3$.

Fig. 8. (a) Mean (± SD) irradiance (photosynthetically active radiation, downwelling attenuation, LiCor light meter) calculated at the sediment surface during mixing-on and mixing-off phases in treatments. (b) Mean (± SD) secchi depth measured in R and R_BD systems during the mixing-on and mixing-off phases over the experiment. (c) Mean (± SD) geometric mean irradiance during mixing-on and -off; different letters indicate statistical difference ($p \leq 0.05$). $n = 3$ for each system.

Fig. 9. Mean (± SD) bulk settling speeds over time in systems with tidal resuspension (R) and in systems with tidal resuspension and daily additions of oyster biodeposits (R_BD). Statistical significance at $p \leq 0.05$, $n = 3$ for each system.

Fig. 10. (a) Mean ± SD *Skeletonema costatum* carbon concentrations in R and in R_BD tanks over the experiment, $n = 3$. (b) Mean ± SD *Skeletonema costatum* chain length (# cells) in R and in R_BD tanks over the experiment. Average *Skeletonema costatum* chain length in R tanks was

11.2 (SD ± 0.2) cells per chain and chain length in R_BD tanks was 9.8 (SD ± 0.6) cells per chain, respectively. Statistical difference is indicated as $p \leq 0.05$.

Fig. 11. Initial average (± SD) phytoplankton biomass at time 0 (i.e., T0) and of day 2-29 during the experiment (i.e. Ex) in the resuspension tanks (R) and in the resuspension tanks with daily biodeposit additions (R_BD). (a) Total phytoplankton biomass (total carbon, µg l^{-1}), (b) diatom C, (c) phytoflagellate C (phytofl.), (d) dinoflagellate C (dino), (e) cyanoflagellate, (cyano), (f) ratio of Chl *a* to total phytoplankton C, (g) total cell density. Different capital letters in a – g indicate statistical differences ($p \leq 0.05$, $n = 3$ for each system).

Fig. 12. Percent composition by cell density of diatoms, phytoflagellates, dinoflagellates and cyanobacteria over the experiment in (a) resuspension tanks (R) and (b) in resuspension tanks with daily biodeposit additions (R_BD). Day 1 is T0.

Fig. 13. (a, b) Relationship of cell volume (µm^3) and carbon constant determined after Strathman (1967) and Smayda (1978). Mean (± SD) carbon content in three different phytoplankton cell volume ranges (µm^3) in the (c) R tanks and in the (d) R_BR tanks, respectively, $n = 3$ for each system. (e, f) Percent contribution of each size fraction to the phytoplankton biomass in the (e) R and in the (f) R_BD tanks.

Fig. 14. Zooplankton abundance of main taxa over the experiment. (a) Total zooplankton carbon (all taxa), (b) polychaete larvae, (c) *Acartia tonsa* nauplii, (d) *Acartia tonsa* adults, (e) *Acartia tonsa* copepodites. (f) Relationship of mesozooplankton biomass to phytoplankton biomass in the

R tanks, (g) relationship of mesozooplankton biomass and phytoplankton biomass in R_BD tanks (common carbon unit). $N = 3$, mean ± SD. Statistical difference is indicated as $p \leq 0.05$. For additional species see Table 3.

Table Legends

Table 1. Linear relationship of optical backscatter sensor (OBS3) volts and total suspended solid concentrations (TSS) in the 6 tanks. Linear relationship between OBS-Volts and TSS. T1, T2, T6 = resuspension tanks, R; T3, T4, T5 = resuspension tanks with daily biodeposit additions, R_BD.

Table 2. Weight characteristics of zooplankton used for conversions to zooplankton carbon. Small polychaetes in the experiment were ~0.152 mm and large polychaetes ~0.536 mm long.

Table 3. Summary of statistical results for the resuspension (R) and resuspension with biodeposit addition (R_BD) systems, mixing-on phases. All systems contain muddy sediments. Statistical *t*-tests used in all analyses. Significance was defined as the $p \leq 0.05$, and significant differences are **bolded**. Included in the analysis were all days of the experiment except for day 1 on which no biodeposits had been added yet to any systems. Sediment results are from the end of the experiment. Means ± SD, $n = 3$.

Table 4. Linear relationship of total suspended solids (TSS) and particulate carbon (PC), particulate nitrogen (PN) and particulate phosphorus (PP). Linear relationship between PN and PC.

Table 5. Phytoplankton species found in our samples and their cell volumes determined after Smayda (1978) and their carbon constants after Strathman (1967). Cyano = cyanobacteria, P = phytoflagellate, D = diatom, Dino = dinoflagellate. Also see Fig. 13 a - f.