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# Effects of hard clam (*Mercenaria mercenaria*) density and bottom shear stress on cohesive sediment erodibility and implications for benthic-pelagic coupling

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## ABSTRACT

The interacting effects of little neck hard clam (*Mercenaria mercenaria*) density and bottom shear stress on cohesive sediment erodibility were investigated. Short-term stepwise erosion experiments in 30 and 40 cm diameter Gust microcosms over a range of 0.0083 to 0.1932 Pa were performed using sequential 20-minute constant shear stress steps while sampling turbidity regularly. In addition, sediment erodibility was monitored in two one-month long ecosystem experiments with tidal resuspension and 0, 10, and 50 hard clams in 1 m<sup>3</sup> shear turbulence resuspension mesocosms (STURM) with an initial stepwise erosion experiment (0.313 to 0.444 Pa). In short-term erosion experiments, a low density of hard clams did not significantly affect sediment erodibility, but a high density of hard clams destabilized muddy sediments through significantly decreased critical shear stresses and higher erosion rates, resulting in higher cumulative suspended mass (CSM). In long-term erosion experiments, the sediment stabilized over time between treatments and decreased to a CSM of approximately 60 g m<sup>-2</sup> with different densities of hard clams. This was likely due to development of microphytobenthos, mediated by the filter-feeding clams, bottom shear stress and increased light. Bioturbation by a dense bed of hard clams in interaction with infrequent high bottom shear due to storms may increase CSM in the water column, with subsequent direct and indirect effects on the ecosystem. However, more controlled longer-term erosion studies to determine the interacting effects of long-term exposure to high bottom shear stress, benthos, and microphytobenthos on sediment erodibility and benthic-pelagic coupling are needed.

*Keywords:* bioturbation, shear stress, sediment erodibility, hard clam, *Mercenaria mercenaria*, microphytobenthos, short-term erosion, long-term erosion, critical shear stress, indirect effects

## 1. Introduction

### a. Sediment erodibility and macrofauna

Sediment erodibility is typically characterized by the critical shear stress  $\tau_c$ , the level of fluid shear stress at which sediment is first resuspended, and by the erosion rate  $E$ ,

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the rate at which resuspension occurs once the critical shear stress has been exceeded. Tides, waves, and storms produce benthic shear stress-induced sediment resuspension at variable time scales that can lead to high turbidity (Schoellhamer 2002). Sediment bed properties such as water content, grain size, and cohesion can be affected by the time history of resuspension and deposition (Sanford 2008) and/or by the composition of the benthos (Davis 1993; Wright, Friedrichs, and Hepworth 1997; Allen and Vaughn 2011). Sediments that are frequently disturbed by resuspension and subsequent deposition remain unconsolidated and relatively easy to erode (Sanford 2008). Macroinfauna change sediment erodibility by adhesive-cohesive bonding among particles (Blanchard et al. 1997) and by changing sediment water content (Aberle, Nikora, and Walters 2004). Polychaetes and amphipods alter the sediment water content and modify sediment stability through the type and composition of their burrow structures (Meadows and Tait 1989). Mucus secreted by organisms influences sediment cohesiveness (Blanchard et al. 1997) and thus sediment erodibility.

Bivalve suspension-feeders are widely known to reduce particulate concentrations in the water column through filtration (Cloern 1982; Officer, Smayda, and Mann 1982; Cohen et al. 1984; Newell 1988; Cerco and Noel 2007). However, in a few previous studies, dense aggregations of infaunal bivalves have been found to increase sediment erodibility (Willows, Widdows, and Wood 1998; Sgro, Mistri, and Widdows 2005; Ciutat, Widdows, and Pope 2007; see also Table 1) and thus potentially increase particulate concentrations in the water column with subsequent ecosystem effects, such as enhanced nutrient concentrations and reduced light penetration (Porter, Mason, and Sanford 2013).

It is difficult to functionally group benthos into stabilizers (enhance sediment deposition, inhibit erosion) or destabilizers (inhibit deposition, enhance erosion) (Jumars and Nowell 1984). François et al. (2002) and Gerino et al. (2003) grouped benthos into biodiffusers, upward/downward conveyors, gallery diffusers and regenerators. Conveyors (e.g. polychaetes) transport particles non-locally through the gut, gallery diffusers create tube systems and mix sediments while doing so, and regenerators dig tube systems and release large amounts of sediment into the overlaying water column. Most infaunal bivalve species, however, are biodiffusers (Norkko and Shumway 2011), or organisms which randomly move particles over short distances. This frequent, small scale particle movement results in diffusive mixing and transport in the sediment (Norkko and Shumway 2011) and interacts with bottom shear stress and bivalve density to affect sediment erodibility and transport.

Currently there is little consensus on the effect of infaunal bivalve density on sediment erodibility from short-term erosion studies. High densities of infaunal bivalves have been shown to increase sediment erodibility in short-term annular flume experiments (Willows, Widdows, and Wood 1998; Widdows and Brinsley 2002; Sgro, Mistri, and Widdows 2005; Ciutat, Widdows, and Pope 2007; see also Table 1). Sgro, Mistri, and Widdows (2005) found that increased bioturbation loosens surface sediments, causing enhanced sediment erosion in dense cockle (*Cerastoderma edule*) beds. Bed roughness also increased with increasing

Table 1. Studies examining the effect of epifaunal and infaunal bivalve density on sediment erodibility.

Epifaunal/infaunal	Increased/decreased erodibility with increasing density	Species	Densities used (No. m <sup>-2</sup> )/ sediment	Reference
Infaunal	Increased	<i>Macoma balthica</i>	250, 500, 1000, 1500 / Humber intertidal mudflat, U.K., 9–23% sand, 52–60% silt, 24–32% clay	Willows, Widdows, and Wood 1998
Infaunal	Increased	<i>Macoma balthica</i> , <i>Cerastoderma edule</i> , <i>Mya arenaria</i> , <i>Scrobicularia plana</i> , Microphytobenthos	In situ abundances on two Ecoflats / Westerschelde, Netherlands	Widdows, Brinsley, Salkeld, and Lucas 2000
Infaunal	Increased	<i>Ruditapes philippinarum</i>	0, 71, 129, 206 / Sediment from Northern Adriatic Sea, Italy, Alluvial mud, 10% sand, high silt and clay content	Sgro, Mistri, and Widdows 2005
Infaunal	Increased	<i>Cerastoderma edule</i>	0, 312 / muddy sediment, Tamar estuary, U.K., 72.3% silt and clay, 16.3% very fine sand, 10.6% fine to medium sand, 0.8% coarse sand	Ciutat, Widdows, and Pope 2007
Infaunal	Increased	<i>Mercenaria mercenaria</i>	0, 50 / muddy sediment, Baltimore Harbor, U.S.A., 3.27% sand, 38.7% silt, 58.03% clay	Porter, Mason, and Sanford 2013
Infaunal	Decreased	<i>Cerastoderma edule</i> , Microphytobenthos	0–100, plus 1000 added / Tidal flats, Wadden Sea, Netherlands	Eriksson et al. 2017

(continued)



Table 1. (Continued)

Epifaunal/infaunal	Increased/decreased erodibility with increasing density	Species	Densities used (No. m <sup>-2</sup> )/ sediment	Reference
Infaunal	No effect	<i>Cerastoderma edule</i> , <i>Macoma balthica</i> , <i>Hydrobia ulvae</i> , <i>Nereis diversicolor</i> , <i>Heteromastus filiformis</i>	<i>Cerastoderma edule</i> (184), <i>Macoma balthica</i> (88), <i>Hydrobia ulvae</i> (0–837), <i>Nereis diversicolor</i> (400), <i>Heteromastus filiformis</i> (400) / German Wadden Sea sediment, mixture of very fine grained sand and mud	Andersen et al. 2010
Infaunal	Increased, when less mud decreased	<i>Scrobularia plana</i> , <i>Nereis diversicolor</i> , <i>Cerastoderma edule</i>	<i>Scrobularia plana</i> 0, 57, 115, 229 / two sites at Tagus estuary, Portugal, 89.9/98.4% mud, rest sand	Soares and Sobral 2009b
Infaunal	No effect	<i>Ruditapes philippinarum</i>	34, 36, 37, 80, 115 / Jiaozhou Bay, East China, Four sites, 0–2% gravel, 62–90% sand, 6–28% silt, 3–8% clay	Jie et al. 2001
3/3 buried in soft sediment	Decreased	<i>Atrina zelandica</i>	Ratio of height to spacing according to field / Model, muddy sediment	Coco et al. 2006
Epifaunal	Increased, sandy decreased, some non-linear	<i>Macoma balthica</i> , <i>Hydrobia ulvae</i> , Microphytobenthos	Field cores used / Humber (U.K.), Westerschelde (Netherlands), sediment varied, 46% silt to sandy	Widdows and Brinsley 2002
Epifaunal	Decreased	<i>Mytilus edulis</i>	Clumps / Menai Strait, U.K., 21.8–65.1% silt and clay	Widdows, Pope, Brinsley, Gascoigne, and Kaiser 2009
Epifaunal	Non-additive, Non-linear	Species polyculture with three mussel species	55, 110 / Sand and gravel	Allen and Vaughn 2011

bioturbation (Sgro, Mistri, and Widdows 2005; Ciutat, Widdows, and Pope 2007). Others did not find enhanced sediment erodibility in similar cockle systems (Anderson et al. 2010; Eriksson et al. 2017), and Eriksson et al. (2017) has suggested that high abundances of sediment-living bivalves may stabilize the sediment by providing a network of physical structures with their shells and mucus production that immobilizes the sediment surface (Table 1). Other species such as the Manila clam (*Ruditapes philippinarum*) were found to have no density effect on sediment erodibility (Jie et al. 2001; Table 1). Of note is that a wide range of sediment grain sizes have been used in the experiments (Table 1) and that Soares and Sobral (2009b) found that sediment erodibility decreased with increasing sediment grain size. Thus, sediment grain size is a factor that must be considered. While it is clear then, that we do not have a good understanding of the effect of infaunal bivalve density on sediment erodibility from short-term (storms) erosion experiments with muddy sediment (Table 1), the effect of infaunal bivalve density on sediment erodibility when subjected to long-term (e.g., one-month) variable bottom shear stress is entirely unknown. Experiments to date have mainly focused on short-term erosion experiments, or on sediment cores including fauna and microphytobenthos taken in the field.

#### *b. Microphytobenthos and sediment erodibility*

Photosynthetic microbes inhabiting the surficial sediments, including diatoms and cyanobacteria, called microphytobenthos, affect benthic-pelagic coupling processes (Porter, Cornwell, Sanford, and Newell 2004; Porter, Sanford, Gust, and Porter 2004) and can stabilize or destabilize sediment. Extracellular polymeric substances secreted by microphytobenthos and cyanobacteria and the networks created by some filamentous cyanobacteria increase sediment stability and reduce resuspension (Yallop et al. 1994; Widdows and Brinsley 2002). However, under some circumstances microphytobenthos can also destabilize sediment as the mat ages due to bubble formation within the mat (Black et al. 2002; Porter, Cornwell, Sanford, and Newell 2004; Porter, Sanford, Gust, and Porter 2004), which leads to erosion even at moderate shear stress (Porter, Cornwell, Sanford, and Newell 2004; Porter, Sanford, Gust, and Porter 2004). Microphytobenthos biomass is affected by both the light that reaches the bottom and bottom shear (MacIntyre, Geider, and Miller 1996; Porter, Cornwell, Sanford, and Newell 2004; Porter, Sanford, Gust, and Porter 2004) as sediment resuspension alters the benthic light environment. Erosion of microphytobenthos can also start from weaker areas in the biofilm (Neumeier, Lucas, and Collins 2006). Microphytobenthos can also reduce nutrient regeneration from the sediments (Sundbäck, Miles, and Göransson 2000) and provide food for macrofaunal filter and deposit feeders (Muschenheim and Newell 1992; Herman et al. 2000; Widdows, Pope, Brinsley, Gascoigne, and Kaiser 2009; Porter, Mason, and Sanford 2013). The presence of cockles may affect conditions for microphytobenthos, as models have indicated that higher cockle (*Cerastoderma edule*) biomass increases microphytobenthos resuspension rates (Rakotomalala et al. 2015), and research from Van Colen et al. (2013) suggested that cockles may enhance

microphytobenthos biomass by decreasing other surface-dwelling grazing species. By disrupting and grazing the diatom film, benthic bioturbators were able to cause the resuspension of sediment otherwise stabilized by microphytobenthos (Montserrat et al. 2008). In addition, Eriksson et al. (2017) suggested that nutrients mediated by increased cockle densities led to enhanced microphytobenthos abundance that promoted sediment stabilization (Table 1). The effect of different densities of infaunal bivalves on sediment erodibility, including direct and indirect interactions affecting light and microphytobenthos in long-term experiments, is not well understood.

*c. Effects of hard clam, Mercenaria mercenaria, abundance*

The infaunal hard clam, *Mercenaria mercenaria*, is an abundant filter feeder, lives in muddy, sandy, and sandy mud sediments (Walker and Tenore 1984; Mann et al. 2005) similar to the studies listed in Table 1; however, little is known about its response to changing bottom shear stress. High densities (defined as  $> 25$  clams  $m^{-2}$  per Saila, Flowers, and Cannario 1967) of *M. mercenaria* have been found in California (400 individuals  $m^{-2}$ ; Murphy and Kremer 1985) and were found in grain sizes of 17% sand, 55% silt, 28% clay, that is, sandy mud according to the Folk (1954) classification, in the Providence River area (60 individuals  $m^{-2}$ ; Saila, Flowers, and Cannario 1967), and in Wassaw Island in Georgia ( $49 \pm 14$  clams  $m^{-2}$ ; Walker and Tenore 1984). Other locations such as Little Tybee Island ( $18 \pm 5$  clams  $m^{-2}$ ) and North Cabbage Island ( $12 \pm 6$  clams  $m^{-2}$ ) in Georgia support less dense populations (Walker and Tenore 1984) and Doering et al. (1986) used 16 clams  $m^{-2}$  in their mesocosm experiment. Mass plantings of hard clams have occurred in Cherrystone Inlet, Chesapeake Bay, in sandy sediments, at 700 to 800 individuals  $m^{-2}$  (Murphy, Anderson, and Luckenbach 2015) and at 347 individuals  $m^{-2}$  in North Carolina (Grabowski, Powers, and Hooper 2003). Reports by Peterson (2002) indicate that abundance varies from 0 to 112 hard clams  $m^{-2}$  in other locales with various sediments (Back Sound, North Carolina). No one has examined the effect of different densities of the hard clam, *M. mercenaria*, on sediment erodibility, short-term or long-term (but see Porter, Mason, and Sanford 2013).

In the experiments reported here, we examined the resuspension response of cohesive sediment containing zero, low, and high clam densities of *Mercenaria mercenaria*, (0 clams  $m^{-2}$ , 14–16 clams  $m^{-2}$ , and 40–57 clams  $m^{-2}$ ) to stepwise increases in bottom shear stress, as well as long-term exposure (one month) to tidally modulated high bottom shear stress. We hypothesized that: (1) A high density of hard clams decreases the critical erosional shear stress as compared with low density or control levels; (2) a high density of hard clams will reduce bed stability, as compared with control or low density systems, promoting higher erosion rates and cumulative suspended mass (CSM) when exposed to fluid stress; and (3) there is no difference in sediment erodibility during short-term (hours) and long-term (one-month tidal resuspension) erosion experiments. For all our experiments comparing short-term and long-term erosion experiments we used little neck hard clams, *M. mercenaria*, ( $\sim 2.5$  cm shell height,  $< 5$  cm shell length) and muddy sediments, and we used

erosion devices calibrated for shear stress using hot-film anemometry (Gust 1988; Gust and Müller 1997; Porter et al. 2018).

## 2. Materials and methods

### a. Benthic boundary-layer devices used for short-term and long-term erosion experiments

To determine the effect of two different densities of hard clams, *Mercenaria mercenaria*, (low, high) on cohesive sediment erodibility, short-term stepwise erosion experiments were performed in 30 and 40 cm diameter Gust microcosms (Gust and Müller 1997; see Table 2 and Fig. 1) against a control without clams. In addition, two long-term erosion experiments in a shear turbulence resuspension mesocosm (STURM) facility were performed with different clam densities (Porter et al. 2018; see Table 2 and Fig. 2).

Experiments in the interchangeable, portable, 30 and 40 cm diameter Gust microcosms, used as available, were carried out indoors. Both STURM mesocosm experiments were carried out outdoors, in the month of July of two different years (Table 2). All systems had a calibrated, programmable bottom shear stress, determined using hot film anemometry (Gust 1988; Gust and Müller 1997; Porter et al. 2018). The 40 cm and 30 cm diameter Gust microcosms used different experimental bottom shear stress step sequences over their erosion runs. The Gust microcosms did not have a sizable water column, whereas the STURM tanks had a 1 m deep water column with realistic root mean square (RMS) turbulent velocities (Fig. 2b) and energy dissipation rates (Fig. 2c), rendering long-term (here one month) benthic-pelagic coupling experiments with tidal resuspension or episodic sediment resuspension possible (Porter et al. 2018). Specific combinations of plate rotation speed and pumping rate produce defined, spatially uniform bottom shear velocities in Gust microcosms (Fig. 1b; Gust and Müller 1997). Shear (or “friction”) velocity ( $u_*$  in  $\text{cm s}^{-1}$ ) is defined by

$$u_* = \sqrt{\frac{10\tau_b}{\rho}}. \quad (1)$$

where  $\tau_b$  is bottom shear stress in Pa and  $\rho$  is the density of water in  $\text{g cm}^{-3}$ . Solving equation 1 for  $\tau_b$  in Pa yields

$$\tau_b = \frac{u_*^2 \rho}{10} \quad (2)$$

The  $1 \text{ m}^3$  tanks with  $1 \text{ m}^2$  sediment surface area STURM tanks create high instantaneous but homogeneous bottom shear stress (Fig. 2d) with low realistic water column mixing rates in a single system, by stirring of the water column with a single STURM paddle going forward 8 seconds stop 1.5 seconds going backward 9 seconds and stopping 1.5 seconds at pre-defined paddle rotations per minute (Fig. 2; Porter et al. 2018). The STURM tanks can be programmed to different magnitudes, frequencies, and extended periods (e.g., four weeks) of bottom shear stress (and thus resuspension) with proportional water column

Table 2. Experiments conducted comparing the erodibility of sediment of muddy sediments with three different densities of little neck *Mercenaria mercenaria* obtained from Cherrystone Aqua Farms, Cheriton, Virginia. The three different clam densities run were: 0 clams  $m^{-2}$ , a low density of 14–16 clams  $m^{-2}$  and a high density of 40–57 clams  $m^{-2}$ . Bottom shear stress in all devices was calibrated using hot-film anemometry. Temperatures in the mesocosm experiments were measured every 10 min. using Campbell temperature probes and a Campbell CR10X data logger. Surface Photosynthetically Active Radiation (PAR, in the 400–700 nm waveband) as measured with a LI-192 Underwater Quantum Sensor (LI-COR Biosciences) was similar in the summer 2003 and 2002 outdoor mesocosm experiments ( $p = 0.6173$ ).

Experiment	Year performed	Replication density (clams $m^{-2}$ )	Average PAR $\pm$ SD $\mu moles m^{-2} s^{-1}$ (N)	Average temperature ( $^{\circ}C$ ) (T range)	Folk (1954) sediment classification	Sediment origin
1 Stepwise erosion in 40 cm Gust microcosm	Spring 2011	n = 1 per density 0, 16, 40	indoors, no illumination added	room temperature, about 21	sandy clay	mesohaline Choptank River (Chesapeake Bay), USA
2 Stepwise erosion in 30 cm Gust microcosm	Spring 2015	n = 2 per density 0, 14, 42/57	indoors, no illumination added	room temperature, about 21	sandy clay	mesohaline Choptank River (Chesapeake Bay), USA
3 Stepwise erosion in STURM facility at the start of an ecosystem experiment in #5.	Summer 2003	n = 3 per density 10, 50	310.8 $\pm$ 108.6 (24)	25.6 $\pm$ 0.7 (25.56–26.18)	sandy mud	Baltimore Harbor, MD, USA
4 One month tidal resuspension in STURM facility, 0 vs. 50 clams $m^{-2}$ (2002 STURM experiment)	Summer 2002	n = 3 per density (Porter, Mason, and Sanford 2013) 0, 50	227.4 $\pm$ 78.6 (60)	26.3 (22.67–29.61)	sandy mud	Baltimore Harbor, MD, USA
5 One month tidal resuspension in STURM facility, 10 vs. 50 clams $m^{-2}$ (2003 STURM experiment)	Summer 2003	n = 3 per density 10, 50	237.6 $\pm$ 121.3 (48)	26.2 (23.72–29.03)	sandy mud	Baltimore Harbor, MD, USA

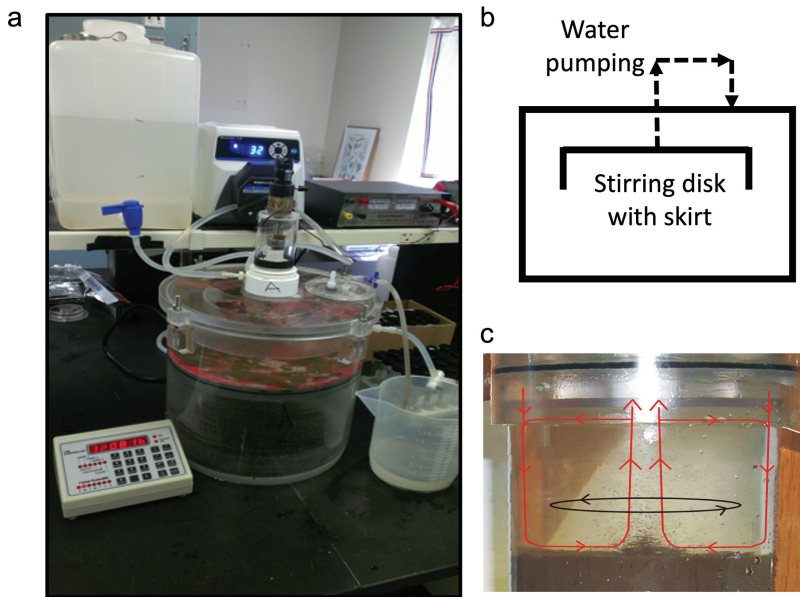


Figure 1. Set up for short-term stepwise erosion experiments performed in Gust microcosms according to Gust and Müller (1997). (a) 30 cm diameter Gust microcosm used for stepwise erosion experiments, here set up with an artificial bottom plate. (b) Schematic of Gust microcosm with stirring plate with skirt and water pumping to produce homogeneous bottom shear stress. (c) Flow field generated in Gust microcosms.

turbulence levels. A wide range of mixing settings allow long-term benthic-pelagic coupling resuspension experiments over muddy sediments with a variety of benthic organisms (Porter et al. 2018), here with the hard clam *Mercenaria mercenaria*. We used the mixing setting of 12.5 RPM to produce an instantaneous bottom shear stress of 0.444 Pa, a RMS turbulent velocity of  $1.08 \text{ cm s}^{-1}$ , and an energy dissipation rate of  $0.077 \text{ cm}^2 \text{ s}^{-3}$  during mixing-on (Porter, Mason, and Sanford 2013; Porter et al. 2018; see Fig. 2b and c). While the 2003 STURM experiment was started with a stepwise erosion experiment, in 2002 the experiment was started at the final target shear stress of 0.444 Pa without further intermediate shear stress steps.

*b. Clams, sediment samples, and sediment preparation and equilibration before experiments*

For all experiments (Table 2), 41 to 46 mm long hard clams, *Mercenaria mercenaria*, were obtained from Cherrystone Aqua Farms, Cheriton, Virginia, and held with 25 to 28 practical salinity units (PSUs) artificial seawater mixed with instant ocean sea salt to the same salinity as at the Cherrystone Aqua Farms site. Experiments in the Gust microcosm were run at 25 to 28 PSU while clams were run at 19 PSU in the mesocosm experiments

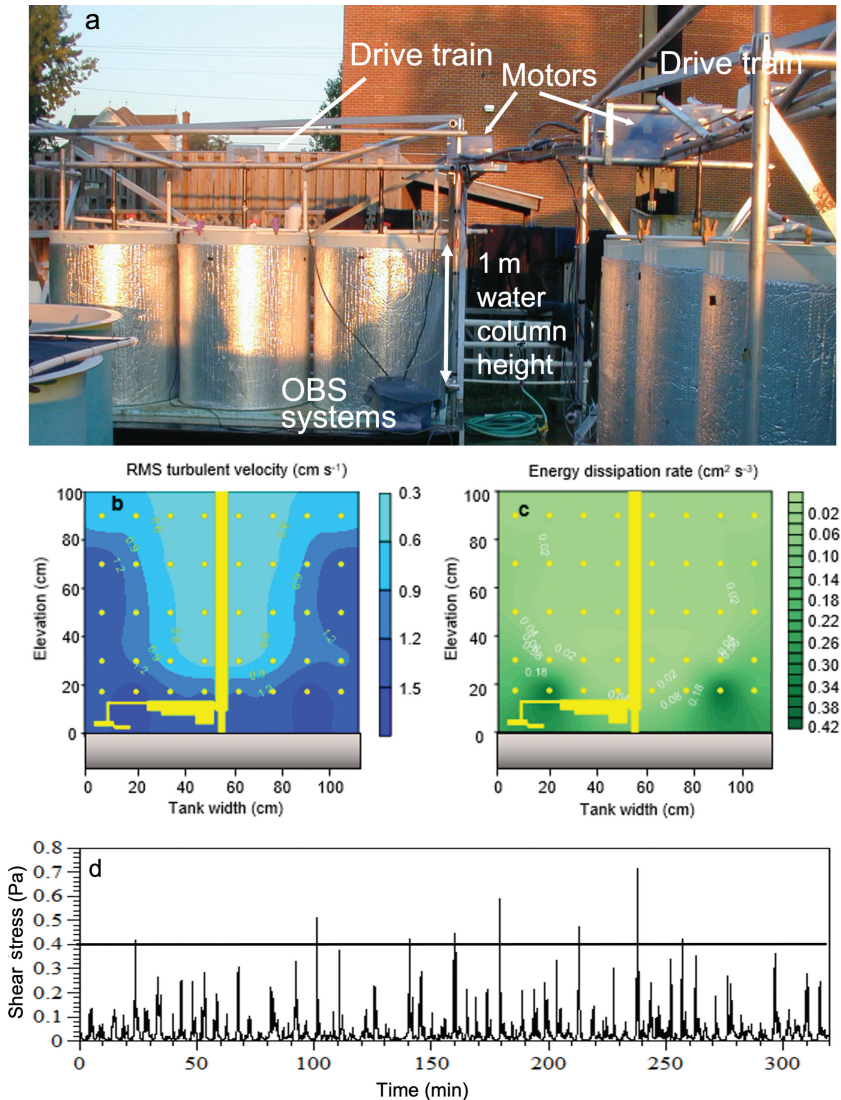


Figure 2. Shear TURbulence Resuspension Mesocosm (STURM) tanks with realistic root mean square (RMS) turbulent velocities, energy dissipation rates, and high instantaneous bottom shear stress. (a) STURM facility. (b) Volume-weighted RMS turbulent velocity and (c) energy dissipation rate in STURM tank with different densities of hard clams. (d) Shear stress during mesocosm experiments.

with the salinity gradually decreased and clams acclimated to 19 PSU before a mesocosm run. The Patuxent River water salinity was 15 PSU and thus had to be supplemented with 35 PSU salt water to achieve the desired salinity of 19 PSU in the STURM tanks. *M.*

*mercenaria* requires a minimum salinity of 18 PSU to avoid growth limitation (R. Grizzle personal communication). The seawater mixing tank was located indoors and water was always mixed one day before use to assure salts were dissolved completely. After sediment equilibration (described below), three densities of clams (Table 2) were distributed on the sediments of the experimental devices/tanks and allowed to bury and were replaced over two days if they did not bury, before the start of the experiment. Most hard clams buried quickly. In one replicate treatment with four clams in the 30 cm Gust microcosm, one clam did not bury and was removed, such that the erosion experiment was run with three clams.

Sediments for all Gust microcosm erosion experiments (Table 2) were collected from a shallow water site in the mesohaline Choptank River (Chesapeake Bay), USA. Grain sizes of two cores in the vicinity of our sediment collection site were 20% sand, 21% silt, and 59% clay (Cornwell, unpublished data, as cited in Porter, Owens, and Cornwell 2006) with sediment classified as sandy clay following Folk (1954).

For each STURM experiment (Table 2), sediment was collected with a Van Veen grab from Baltimore Harbor, USA (39 N 11'29", 76 W 31' 10.5"). Grain size at the collection site was 3.27% sand, 38.7% silt, 58.03% clay, measured as percent dry weight (Baker et al. 1997) and classified as sandy mud (Folk 1954). The sediment contained 0.33% particulate nitrogen and 4.57% particulate carbon. Collected sediment was kept in the dark to prevent microphytobenthos growth and kept anaerobic by placing plastic foil over the sediment surface for four days to defaunate it (Porter, Owens, and Cornwell 2006). Then the top 10 cm layer of sediment was removed and the underlying sediment distributed to the six STURM tanks or the Gust microcosm devices to form an approximately 10 cm layer of sediment in each device. Sediment was homogenized and then smoothed in each device with a smoothing paddle before the start of a two-week sediment consolidation period to equilibrate the sediments to natural pore-water gradients (Porter, Owens, and Cornwell 2006; Cornwell and Porter 2009).

For the STURM experiments, carefully, without resuspending sediments, a 20 cm layer of 0.5  $\mu\text{m}$  filtered Patuxent River water, amended to 19 PSU as described above, was added to each tank and oxygenated. To prevent microphytobenthos growth, tanks were kept in the dark during the 14-day sediment pre-equilibration period. About 10 cm of the overlying water column were replaced daily with 0.5  $\mu\text{m}$  absolute filtered 19 PSU Patuxent River water for 14 days to re-establish realistic sediment pore-water gradients (Porter, Owens, and Cornwell 2006, there treatment HD-m) before the start of the experiment. For the Gust microcosm experiments (Table 2) a 10 cm layer of 25 to 28 PSU water, made of distilled water and instant ocean sea salt, was added carefully to the microcosm by pouring instant ocean seawater on bubble wrap laid out on the sediments to not resuspend sediments, and then dissolved oxygen bubbling was initiated. The microcosms were kept in the dark to prevent microphytobenthos growth, with half the water replaced daily for 14 days to equilibrate the sediments to natural pore-water gradients (Porter, Owens, and Cornwell 2006; Cornwell and Porter 2009).



The start of each one-month STURM experiment was initiated by replacing and filling the six tanks (without resuspending any sediments) with unfiltered Patuxent River water, supplemented with higher levels of salt water to achieve the desired salinity of 19 PSU for the experiment.

*c. Stepwise erosion experiments in 30 and 40 cm Gust microcosms*

A stepwise erosion experiment with 0, 2, and 5 hard clams (i.e., 0, 16, 40 clams  $m^{-2}$ ) was performed in a 40 cm diameter Gust microcosm at Washington College, Chestertown, Maryland, in spring 2011 (Table 2). Shear stress was incrementally increased from 0.008 to 0.372 Pa with shear stress held constant at each step for 20 minutes. One water sample of  $1.1 \pm 0.4$  L was taken at the end of each step at 19 minutes and water was analyzed for total suspended solids (TSS) concentrations following Berg and Newell (1986). The water was replaced with premixed 25 PSU salinity water. The rotameter for the Gust microcosm clogged during the run with 16 hard clams  $m^{-2}$  at 0.233 Pa and with 0 hard clams at 0.276 Pa, so higher shear stress steps were abandoned.

Replicate stepwise erosion experiments with 0, 1, and 3 to 4 hard clams (i.e., 0, 14, and 42–57 clams  $m^{-2}$ ) were performed in a 30 cm Gust microcosm (Gust and Müller 1997; Table 2; Fig. 1) at room temperature ( $\sim 21$  °C) at The University of Baltimore, Baltimore, Maryland, in spring 2015. For the stepwise erosion experiments, bottom shear stress was incrementally increased from 0 to 0.1245 Pa with shear stress held constant at each step for 20 minutes. Every 2 minutes, a 20 mL water sample was taken by gravity flow from the Gust microcosm. Time of sampling and turbidity (in nephelometric turbidity units, or NTUs), measured on a 2100N Hach turbidity meter (Hach Company, Colorado), were noted at each step. After the last shear stress step, an approximately 2 L water sample was taken from the Gust microcosm to determine TSS concentration and establish a calibration curve of TSS concentration against NTU. We divided the sample into three concentrations using the sample concentration, plus two subsample concentrations where sample was diluted with deionized water, measured turbidity of the three concentrations and determined TSS concentrations by filtration. Samples were filtered through washed, pre-ashed and pre-weighed 47 mm glass fiber filters. During filtration, the sample column was rinsed with isotonic ammonium formate to remove salts. Samples were dried for at least 24 hours at 60 °C and then weighed on a Mettler XS105 analytical microbalance to 0.0000 digits. Total suspended solids were determined following techniques by Berg and Newell (1986).

A linear regression between NTU and TSS concentration ( $TSS = 3.95 \times NTU$ ,  $R^2 = 0.9794$ ,  $n = 3$ ) was used to estimate TSS concentration for each time point during the stepwise erosion experiment where NTU was measured. Occasionally, we observed hard clams digging as bottom shear stress was increased. Thus, at the end of the stepwise erosion experiment for the final three runs, burial depth of the clams was determined, measured from the sediment surface to the start of the buried clam using a plastic ruler (sediment was  $\sim 10$  cm deep).

*d. Stepwise erosion and long-term erosion experiments in the STURM systems*

A one-month experiment with muddy sediments with 0 and 50 little neck hard clams per  $\text{m}^2$ , *Mercenaria mercenaria*, and tidal resuspension in STURM tanks was performed in summer 2002 (Porter, Mason, and Sanford 2013; see also Table 2;  $n = 3$  tanks per treatment). A one-month experiment with muddy sediments with 10 and 50 hard clams per  $\text{m}^{-2}$  was performed in summer 2003 (Table 2;  $n = 3$  tanks per treatment). Both experiments were performed on the outdoor mesocosm pad at the Chesapeake Biological Laboratory, Solomons, Maryland.

The 2003 experiment (Table 2; Fig. 2) was started with a stepwise erosion experiment (no. 3 in Table 2). Over about 7 hours, bottom shear stress was increased in four steps from an area weighted instantaneous shear stress of 0 Pa for 8.8 minutes, 0.313 Pa for 125.5 minutes, 0.378 Pa for 98.7 minutes, and 0.444 Pa for 152.2 minutes, after which a 2-hour mixing-off phase at 0 Pa commenced. The final mixing setting for tidal resuspension of the ecosystem experiment was 0.444 Pa with 4-hour mixing-on and 2-hour mixing-off over a one-month period. Turbidity was measured at mid-depth of the tanks (50 cm) using optical backscatter sensors (OBS-3; D&A Instrument Company), calibrated with samples analyzed for TSS as described above. For the 2-hour mixing-off phase after the highest shear stress step (0.444 Pa) of the stepwise erosion experiment, particle mean bulk settling speed ( $\text{mm s}^{-1}$ ) was estimated, using the distance from the water surface to the OBS-3 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. The 2002 STURM experiment with 0 and 50 clams  $\text{m}^{-2}$  was set to 0.444 Pa at the start of the experiment, which we utilized as a single-step erosion experiment.

To mimic tidal exchange during one-month experiments, 10% of the tank water was replaced with 0.5  $\mu\text{m}$  absolute filtered 19 PSU water daily during mixing-off. We took 4 L water samples from mid-depth of each STURM tank biweekly during mixing-on over a 4-week period and three times during mixing-off and analyzed the samples for TSS concentrations following Berg and Newell (1986).

During the STURM ecosystem experiments and the initial stepwise erosion experiment in the STURM tanks, turbidity was measured continuously at one-second intervals in each tank with OBS-3 turbidity sensors located at mid-depth (50 cm above the bottom). They were calibrated against the mid-depth TSS samples. In post-processing, OBS data were averaged over 66-second intervals.

Twice a week during mixing-on and -off phases from day 7 to 23 in the 2003 experiment comparing 10 and 50 clams  $\text{m}^{-2}$ , light profiles were measured as described in Porter et al. (2018, 2020) during mixing-on and -off to determine irradiance levels at the sediments, whereas only on phase light was measured in the 2002 STURM experiment (Porter, Mason, and Sanford 2013). Secchi depth was measured most days over the 2002 and 2003 STURM experiments during mixing-on and twice a week at the end of the mid-day mixing-off phase.

For the 2002 experiment an additional 13.5 cm inside diameter cylindrical benthic chamber was used to equilibrate the sediments in an oxygenated water bath. Three 2.5 cm diameter sediment cores were taken from the benthic chamber after two weeks of equilibration in the dark to measure sediment chlorophyll *a* (chl *a*) and the percent water content so that the sediment surface in the tanks would not be disturbed at the beginning of the experiment. Mid-experiment and at the end 2.5 cm diameter sediment cores were taken from the tanks to determine microphytobenthos abundance, the percent water content, and sediment particulate organic matter content of the surface sediment. In the 2003 experiment, three 2.5 cm diameter sediment cores were taken per tank for the initial, mid-point, and end-point measurements of sediment chl *a* and percent water content. Sediment chl *a* samples were analyzed using high performance liquid chromatography (Van Heukelem and Thomas 2001).

To determine the occurrence of any resuspension of microphytobenthos in the STURM experiments, water column chl *a* samples were taken from mid-depth three times during mixing-on and the mixing-off phase that followed the -on phase. In the 2002 experiment, chl *a* was sampled on days 7, 17, 24 and in the 2003 experiment on days 6, 13, 20.

A split plot in time statistical analysis and a Student-Newman-Keuls test were performed in SAS 9.4 (SAS 2021) for on–off Secchi data, on–off light at the sediment surface in the 2003 mesocosm experiment, sediment chl *a* and chlorophyll on–off data for each STURM experiment ( $df = 11$ ) and for both experiments combined for Secchi depth ( $df = 23$ ). Days 5 to 25 were included in the analyses of the Secchi data for the 2002 experiment and days 4 to 26 for the 2003 experiment. For sediment chl *a* in the experiment comparing 10 and 50 hard clams  $m^{-2}$ , the Shapiro Wilks test for normality was accepted; however, the Levine's test showed heterogeneous variance and the data had to be log-transformed for the analysis. For Secchi depth and chlorophyll *a*, the Shapiro-Wilks and Levine's tests were both non-significant and no log transformations were necessary. Differences in chl *a* concentration between mixing-on and mixing-off were interpreted as resuspended microphytobenthos.

#### *e. Sediment Erosion and Critical Shear Stress Calculations*

While there are many different protocols available for estimating erosion rates and critical shear stresses from erosion tests (Sanford 2006), they all depend on measurements of suspended sediment mass as a function of applied stress. We measured suspended sediment mass using two different methods, one for the Gust microcosm experiments and one for the STURM experiments. In the Gust microcosm experiments samples were withdrawn from the microcosms at regular intervals during each stress step. These samples were used to calculate TSS concentration in the chamber in  $mg L^{-1}$ , which was multiplied by the remaining volume in the chamber to calculate the mass remaining in the chamber. This mass was added to the sum of all sediment masses sampled up to and including that sample to derive CSM at the time of sampling. "Cumulative" refers to the fact that TSS at any

time during an experiment represents the cumulative effects of all erosion, deposition, and sampling up to that time. In the STURM experiments turbidity data were converted to TSS concentration using a linear calibration as described in Section 2c above. Multiplying the TSS time series by the volume of the STURM tank (1,000 L) yielded time series of CSM. All CSM measurements were adjusted to common units of  $\text{g m}^{-2}$  by dividing by the bottom sediment area of each device and converting mg to g for clarity of presentation.

We chose a straightforward estimate of the average erosion rate  $E$  over the first approximately 20 minutes of each new applied shear stress. While there are other possible methods, this one allows direct comparison between all our experiments and is consistent with other examples from the literature (Tolhurst et al. 2000; Sanford 2006). We estimated  $E$  by taking the difference between  $CSM_{\text{end}}$  at the end of a step (or after 20 min, whichever came first) and  $CSM_{\text{beginning}}$  immediately before the beginning of that step, dividing by the step duration in seconds  $T_{\text{step}}$ , and converting g to mg for clarity of presentation; resulting erosion rate units are in  $\text{mg m}^{-2} \text{s}^{-1}$  (equation 3). Mathematically,

$$E = \frac{CSM_{\text{end}} - CSM_{\text{beginning}}}{T_{\text{step}}} \times 1,000 \frac{\text{mg}}{\text{g}}. \quad (3)$$

Note that any decrease in CSM during a step, which yields  $E < 0$  for that step, is interpreted as deposition.

Critical shear stresses,  $\tau_c$ , in the 30 cm and 40 cm Gust microcosm erosion tests were estimated by examining the time histories of CSM and reading off the shear stress at which CSM first sharply increased (Tolhurst et al. 2000; Sanford 2006). Critical shear stress data were pooled for each of the three clam densities in both the 30 cm and 40 cm Gust microcosms for further analysis with ANOVA in SAS 9.4 (SAS 2021) and a Student–Newman–Keuls test. The Shapiro Wilks test to check for normality, and Levene’s test for homogeneous variance were both non-significant, and no log transformations were necessary. All STURM erosion experiments employed an initial applied stress that was higher than any observed critical stress, so could not be used for critical stress estimation.

#### *f. Comparison between treatments (control, low, high clam density)*

We also performed a  $t$ -test comparing erosion rates in the 2003 STURM tanks with high and low density of hard clams for the 0.313 Pa erosion step, pooled with high density data for the 40 cm Gust microcosm 0.3222 Pa erosion step, using the Excel Analysis ToolPak (Microsoft 2021). Erosion results with a high density of clams at step 0.322 Pa in the 40 cm Gust microcosm were the only data available at very high shear stress in the Gust microcosms. The high shear stress steps used in the 2003 STURM tanks (0.313, 0.378, 0.444 Pa) were thus the primary means to examine erosion behavior at high bottom shear stresses, while the Gust microcosms were the primary means to examine erosion behavior at low bottom shear stresses, with the overlap at 0.31 to 0.32 Pa providing an opportunity for comparison between the two devices. We only used one erosion step, 0.444 Pa, for the

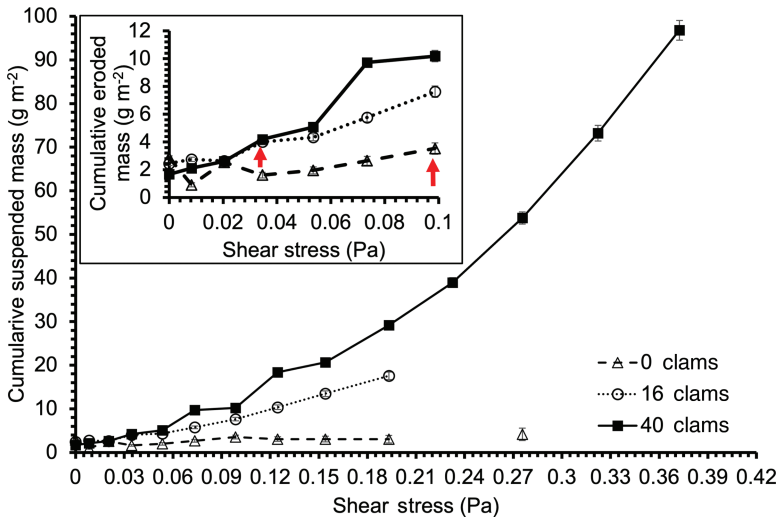


Figure 3. Cumulative suspended mass in 40 cm Gust microcosm as affected by hard clam density (0, 16, 40 clams  $\text{m}^{-2}$ ). Error bars indicate standard error of the mean (SE) determined from erosion experiments in the 30 cm Gust microcosm and the STURM tanks. Inset: Detail of cumulative eroded mass from 0 to 0.1 Pa to determine critical shear stress. Arrows in inset indicate critical erosional shear stress.

STURM experiment in 2002. We pooled the high-density STURM CSM of 2002 and 2003 and compared CSM for zero, low and high density clams at 0.444 Pa using ANOVA followed by a Student–Newman–Keuls test in SAS 9.4 (SAS 2021). The data were log transformed to satisfy normality (Shapiro Wilk’s test) and homogeneity (Levine’s test) of the data. To compare the effect of clam density on sediment erodibility across all experiments, we averaged CSM for each shear stress step for each clam density ( $\pm$  SE) using erosion data obtained in all devices STURM ( $n = 3$ ), 30 cm Gust microcosm ( $n = 2$ ), and 40 cm Gust microcosm ( $n = 1$ ).

### 3. Results

#### a. Stepwise erosion experiments in 30 and 40 cm Gust microcosms

In the 40 cm Gust microcosm, a high density of hard clams increased both the erosion rates and CSM, compared with a low density of clams or clam-free sediment (control) (Fig. 3 and 4). CSM increased most rapidly in the 40 cm Gust microcosm with 40 clams  $\text{m}^{-2}$ , followed by 16 clams  $\text{m}^{-2}$  and 0 clams  $\text{m}^{-2}$  (Fig. 3). Erosion rates were lowest in the treatment with 0 clams  $\text{m}^{-2}$ , slightly higher in the treatment with 16 clams  $\text{m}^{-2}$ , and highest in the treatment with 40 clams  $\text{m}^{-2}$  (Fig. 4).

Clam density affected critical erosional shear stress in stepwise erosion experiments in the 30 cm Gust microcosm, as well. In the treatment with 0 clams  $\text{m}^{-2}$ , CSM increased

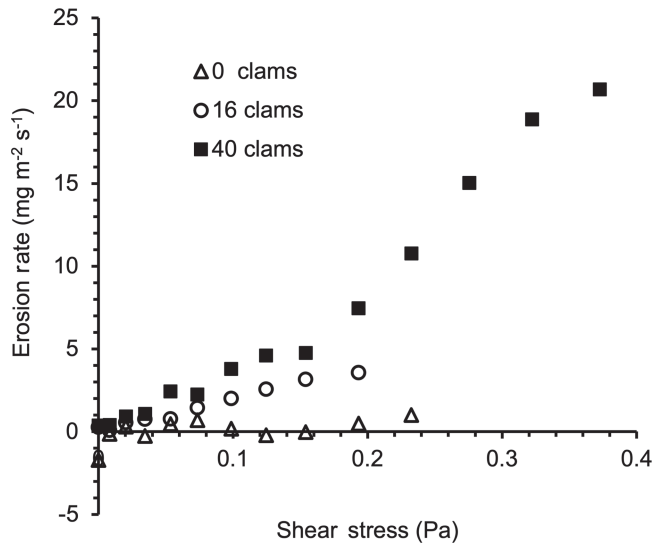


Figure 4. Erosion rates in 40 cm Gust microcosm as affected by hard clam density (0, 16, 40 clams  $\text{m}^{-2}$ ).

greatly starting at about 130 minutes (Fig. 5a) and 100 minutes (Fig. 5b; note that Fig. 5b has a different vertical axis scale) into the stepwise erosion experiment, corresponding to critical shear stress estimates of 0.099 and 0.073 Pa, respectively (Fig. 5a and b). In the treatment with 14 clams  $\text{m}^{-2}$ , CSM increased greatly starting at about 120 minutes into the stepwise erosion experiment in both trials and critical shear stress was 0.099 Pa in both runs (Fig. 5c and d). In the high-density treatment with 42 clams  $\text{m}^{-2}$  in the 30 cm Gust microcosm, CSM increased greatly starting at about 60 minutes into the experiment and critical shear stress was 0.035 Pa (Fig. 5e). In the high-density treatment with 57 clams  $\text{m}^{-2}$ , CSM increased greatly starting around 20 minutes into the experiment and critical shear stress was 0.008 Pa (Fig. 5f). The critical shear stresses for 0, 16, and 40 clams  $\text{m}^{-2}$  in the 40 cm Gust microcosm were of 0.1, 0.03, and 0.03 Pa, respectively. Combining the critical shear stress results measured in the 40 cm and 30 cm Gust microcosms, critical shear stress was  $0.091 \pm 0.015$  in the systems with 0 clams  $\text{m}^{-2}$ ,  $0.076 \pm 0.040$  in the systems with 14 to 16 hard clams  $\text{m}^{-2}$ , and  $0.024 \pm 0.014$  in the system with 40 to 57 clams  $\text{m}^{-2}$  (Fig. 6). A high density of clams significantly decreased critical erosional shear stress relative to the zero clams treatment while critical shear stress for the intermediate density case was intermediate between the high and low clam density treatments (Fig. 6).

Erosion rates under low applied stresses in the 30 cm Gust microcosm were highest in the treatment with the highest density of clams (42–57 clams  $\text{m}^{-2}$ ; Fig. 7). Erosion rates of the 0 clams  $\text{m}^{-2}$  and 14 clams  $\text{m}^{-2}$  treatments were low but variable below a shear stress of about 0.1 Pa (Fig. 7). Negative erosion at low applied shear stresses with 14 and 0 clams  $\text{m}^{-2}$  signifies net deposition over that interval and/or high inherent variability

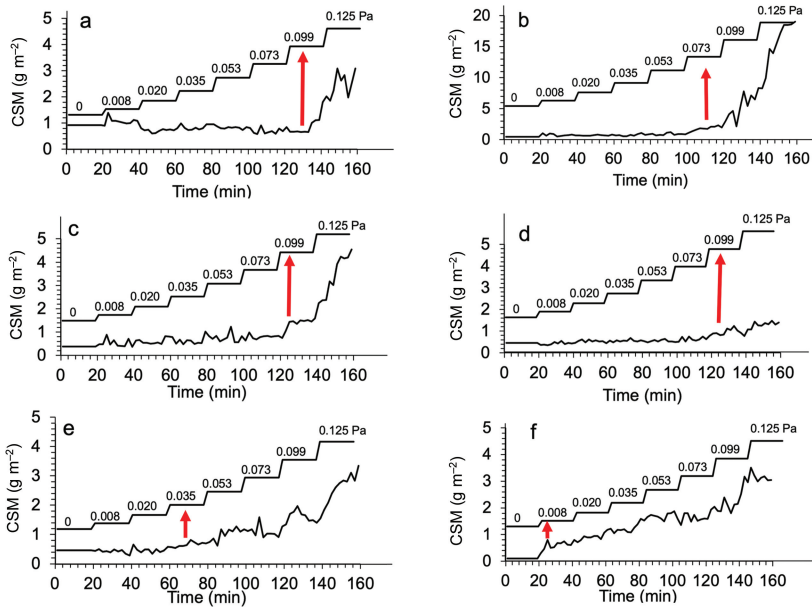


Figure 5. Cumulative suspended mass (CSM) in 30 cm microcosm with muddy sediment and hard clams under stepwise erosion (Pa). (a) and (b) 0 clams  $m^{-2}$ ; (c) and (d) low density of 14 clams  $m^{-2}$ ; (e) high density of 42 clams  $m^{-2}$ ; and (f) high density of 57 clams  $m^{-2}$ . Arrows indicate critical erosional shear stress. Note different vertical axis scale in (b).

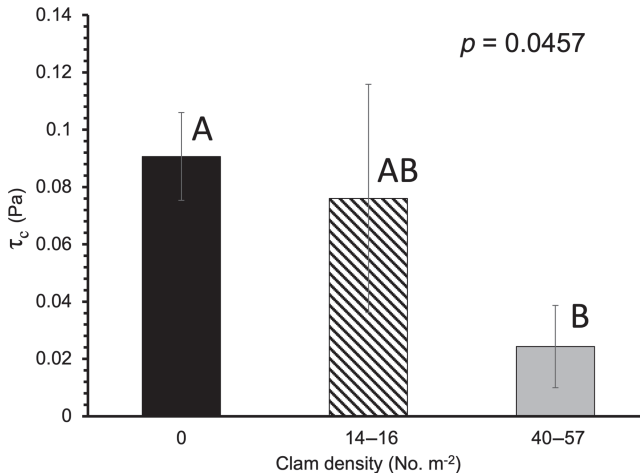


Figure 6. Critical erosional shear stress ( $\tau_c$ ) in the 30 and the 40 cm Gust microcosms with 0 clams, a low density of 14–16 clams  $m^{-2}$ , and a high density of 40–57 clams  $m^{-2}$ .  $N = 3$ . Means and standard deviations. Different letters indicate significant difference ( $p \leq 0.05$ ).

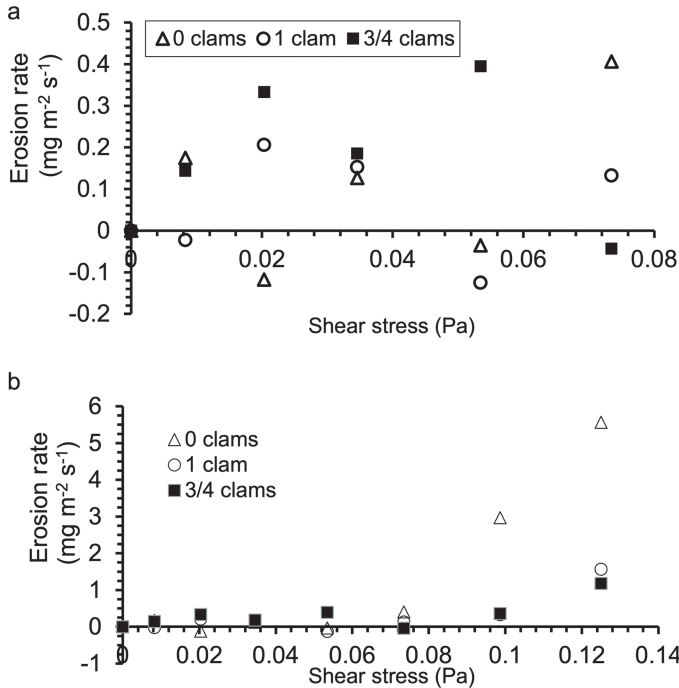


Figure 7. Erosion rates in a 30 cm Gust microcosm with three different hard clam densities and muddy sediment (0 clams m<sup>-2</sup>, low density of 1 clam = 14 clams m<sup>-2</sup>, high density of 3/4 clam = 42/57 clams m<sup>-2</sup>. (a) Detail of erosion rates at lower shear stress (0–0.08 Pa). (b) All data.

between successive intervals. Erosion rates increased rapidly in the zero clam treatments above 0.1 Pa (Fig. 7), that is, as soon as the critical stress was exceeded.

Several clams were observed digging deeper when shear stress increased and in one run one of three clams present began digging deeper after 9 minutes at a shear stress of 0.0203 Pa. In addition, one clam at the interface at the start of the experiment was completely buried by the end. In the setup with 57 clams m<sup>-2</sup> in the 30 cm Gust microcosm, at a shear stress step of 0.0346 Pa a clam started to burrow deeper. Average burial depth at the end of a stepwise erosion run, measured from the sediment surface to the start of the clam, was 3.3 ± 2.1 cm, ranging from 1 to 8 cm in the approximately 10 cm deep sediment. It is possible that this burrowing behavior led to some of the observed irregularities in erosion behavior.

*b. Stepwise erosion experiments in the STURM tanks*

A high density of 50 clams m<sup>-2</sup> increased CSM 2 to 3 times more compared with 10 clams m<sup>-2</sup> as demonstrated in the stepwise erosion experiment in the STURM facility at the beginning of the 2003 one-month experiment (Fig. 8). In all erosion steps, CSM increased more rapidly at the start of a new shear stress step but CSM quickly flattened out as time



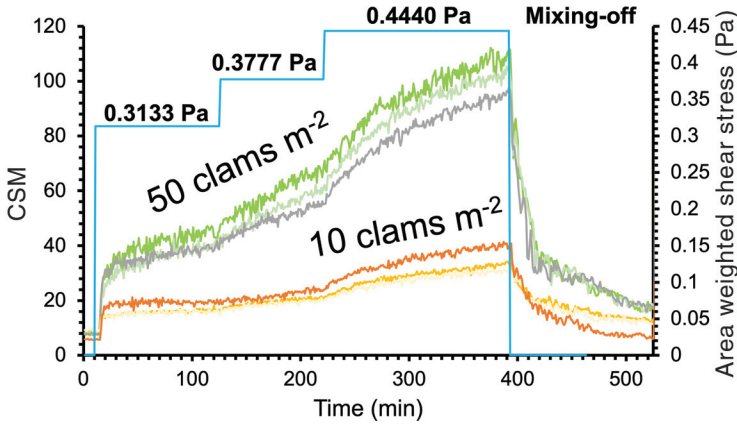


Figure 8. Stepwise erosion at the start of the 2003 ecosystem experiment using STURM tanks to compare muddy sediment with a high density of 50 clams  $m^{-2}$  against sediment with a low density of 10 clams  $m^{-2}$ . Different colors indicate cumulative suspended mass (CSM) in different tanks. Water volume of each STURM tank is 1,000 L and sediment surface area is  $1 m^{-2}$ .

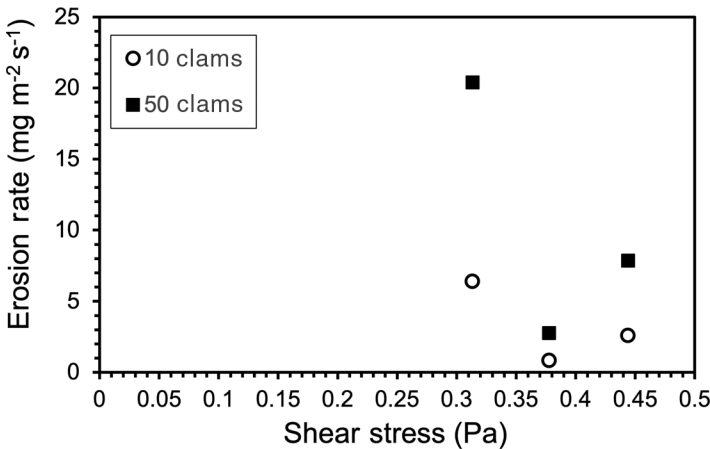


Figure 9. Shear stress steps and erosion rates, as seen in 2003 ecosystem experiment using STURM tanks to compare muddy sediment with a high density of 50 clams  $m^{-2}$  against sediment with a low density of 10 clams  $m^{-2}$ . See Figure 8 for cumulative suspended mass.  $N = 3$ .

progressed, likely due to limited sediment supply (Sanford and Maa 2001). At the start of the mixing-off phase after the highest shear stress step of 0.444 Pa, particles settled rapidly with a mean bulk settling speed of  $0.902 \pm 0.204 mm s^{-1}$ .

The first erosion step at 0.313 Pa in the 2003 STURM experiments, comparing a low and high density of clams, produced much higher erosion rates than the two shear stress steps of 0.378 and 0.444 Pa that followed (Fig. 9). This behavior is also broadly consistent with

a limited sediment supply as erodibility decreases with depth into the sediments. Erosion rates at the first 0.313 Pa erosion step were significantly higher at  $20.4 \pm 18.5 \text{ mg m}^{-2} \text{ s}^{-1}$  in the tanks with high density clams than  $6.4 \pm 3.8 \text{ mg m}^{-2} \text{ s}^{-1}$  in the tanks with low density clams ( $t$ -test,  $p = 0.01318$ ). Similarly, significantly higher erosion rates in the high compared with low-density treatments were also found at the next higher shear stress steps at 0.377 Pa. and 0.444 Pa (Fig. 9).

### c. Comparisons between the microcosms and STURM tanks

The erosion rate for 50 clams  $\text{m}^{-2}$  in the STURM tank at 0.313 Pa (Fig. 9) was similar to the erosion rate for 40 clams  $\text{m}^{-2}$  in the 40 cm Gust microcosm at a similar shear stress of 0.322 Pa ( $18.9 \text{ mg m}^{-2} \text{ s}^{-1}$ ,  $n = 1$ ; Fig. 4). These erosion rates are not significantly different, although the sequences of applied shear stresses leading up to these high values were quite different; the 0.313 Pa step was the first step in the STURM tanks, whereas the 0.322 Pa step was the 13th step in the 40 cm Gust microcosm. CSM at the end of the 0.322 Pa step in the Gust microcosm ( $73 \text{ g m}^{-2}$ ) was much higher than CSM at the end of the 0.313 Pa step in the STURM tanks ( $45 \text{ g m}^{-2}$ ), however. CSM at 0.444 Pa, the only step used in the 2002 STURM experiment, resulted in  $4.7 \pm 1.8 \text{ g m}^{-2}$  ( $n = 3$ ) in the zero clam treatment and  $87.8 \pm 21.5 \text{ g m}^{-2}$  ( $n = 3$ ) in the high density clam treatments. At 0.444 Pa, CSM in the high density clam treatments in 2002 and 2003 STURM experiments was similar at  $87.8 \pm 21.5 \text{ g m}^{-2}$  and  $103.7 \pm 5.7 \text{ g m}^{-2}$  (each  $n = 3$ ), respectively ( $t$ -test,  $p = 0.3358$ ).

### d. One-month tidal resuspension in STURM systems with different densities of hard clams

A high density of 50 hard clams  $\text{m}^{-2}$  initially destabilized the sediment leading to a CSM of ca  $200 \text{ g m}^{-2}$  in STURM experiments in Summer 2002 and summer 2003 (Fig. 10a and b). In contrast, initially only about  $50 \text{ g m}^{-2}$  of CSM were resuspended with 0 clams  $\text{m}^{-2}$  (Fig. 10a) and 10 clams  $\text{m}^{-2}$  (Fig. 10b). While CSM remained similar around  $50 \text{ g m}^{-2}$  over the course of the 4-week experiment for the 0 and 10 clams  $\text{m}^{-2}$  treatments (Fig. 10a and b), CSM decreased from the initially high destabilization down to about  $77 \text{ g m}^{-2}$  and  $20 \text{ g m}^{-2}$  in the treatments with 50 clams  $\text{m}^{-2}$  in 2002 and 2003, respectively (Fig. 10a and b). CSM became similar ( $\sim 43 \text{ g m}^{-2}$ ) between treatments with high and low densities of hard clams after about two weeks in 2003 (Fig. 10b;  $t$ -test,  $p = 0.4361$ ), after which CSM in the high density treatment became increasingly lower than CSM in the low density treatment. CSM in the high density treatment in 2002 decreased about 2.5 fold over three weeks to about  $76.5 \pm 2.1 \text{ g m}^{-2}$  but remained significantly higher than in the zero clam treatment at  $59.2 \pm 4.6 \text{ g m}^{-2}$  during days 21 through 25 (Fig. 10a;  $t$ -test,  $p = 0.0002$ ).

Initial Secchi depths were significantly greater in the tanks with 0 clams  $\text{m}^{-2}$  than in the tanks with 50 clams  $\text{m}^{-2}$ , with similar differences observed between the tanks with 10 and 50 clams  $\text{m}^{-2}$  (split plot in time, Student–Newman–Keuls test; Fig. 11a and b). Secchi depths and light at the bottom (from  $\sim 1$  to  $\sim 5 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) increased in the tanks with a high clam density in both experiments during mixing-on over the course of the STURM

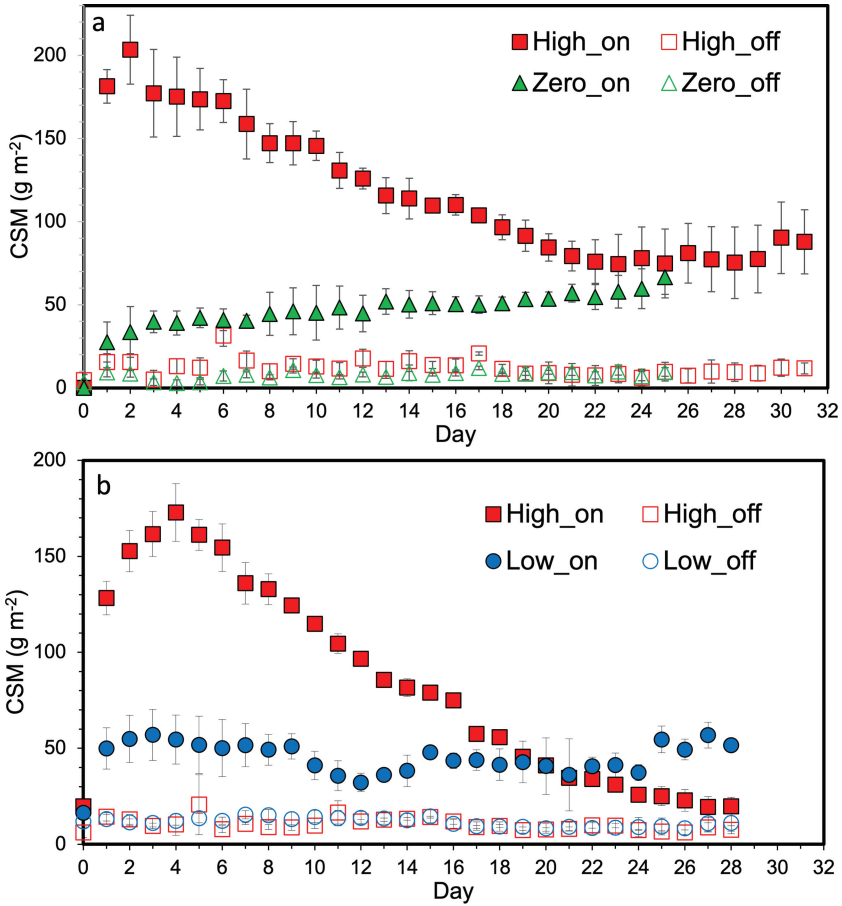


Figure 10. Average ( $\pm$  SD) of cumulative suspended mass (CSM) in four-week experiments in STURM systems with muddy sediments and different densities of hard clams. Zero = 0 clams  $m^{-2}$ , low = 10 clams  $m^{-2}$ , high = 50 clams  $m^{-2}$  (adapted from Porter, Mason, and Sanford 2013). (a) 2002 and (b) 2003 STURM experiments. Tidal resuspension is mimicked with 4-hour mixing-on “on” phases and 2-hour mixing-off “off” phases for four weeks.

ecosystem experiments (Fig. 11a and b) as CSM levels declined (Fig. 10a and b). In all tanks there was significantly more light at the sediments during mixing-off than during mixing-on as particles settled out rapidly during mixing-off (Fig. 11a–c and Fig. 10a and b). Secchi depths and irradiance at the sediments were similar among all treatments during the mixing-off phases (Fig. 11 a–c). Irradiance at the bottom in 2002 was only measured during mixing-on; it was similar between with  $0.9 \pm 1.2$  and  $2.0 \pm 0.4 \mu moles\ m^{-2}\ s^{-1}$  for the zero and high density clam treatments, respectively ( $p = 0.1305$ ).

Microphytobenthos abundance increased in all tanks over the course of the 2002 experiment, from  $5\ mg\ m^{-2}$  to  $30\ mg\ m^{-2}$  in the tanks without clams and from  $5\ mg\ m^{-2}$  to

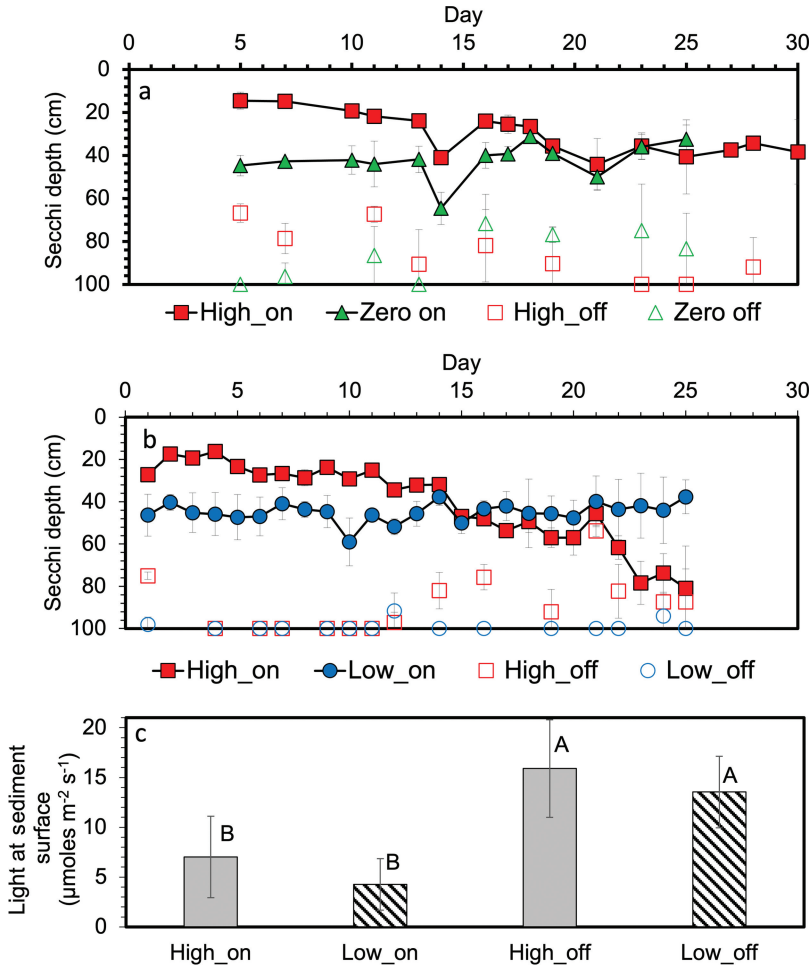


Figure 11. Light at the sediments during mixing-off and mixing-on in four-week experiments in STURM systems with muddy sediments and different densities of hard clams: Zero = 0 clams  $\text{m}^{-2}$ , low = 10 clams  $\text{m}^{-2}$ , high = 50 clams  $\text{m}^{-2}$ . Secchi depth in 2002 (a) and 2003 (b) and light at the sediment surface (c). Tidal resuspension is mimicked with 4-hour mixing-on “on” phases and 2-hour mixing-off “off” phases.

15  $\text{mg m}^{-2}$  in the tanks with 50 clams  $\text{m}^{-2}$  (Fig. 12a). In addition, microphytobenthos abundance was significantly higher (split plot in time, Student–Newman–Keuls test,  $p < 0.05$ ) in the tanks with 0 clams than in the tanks with 50 hard clams  $\text{m}^{-2}$  at mid-experiment and at the end (Fig. 12a). The tanks with 0 hard clams had lower CSM and allowed for more light to reach the bottom (Fig. 10a and Fig. 11a). In addition, water column chl *a* concentrations were significantly higher during mixing-on than mixing-off in the tanks with no clams;

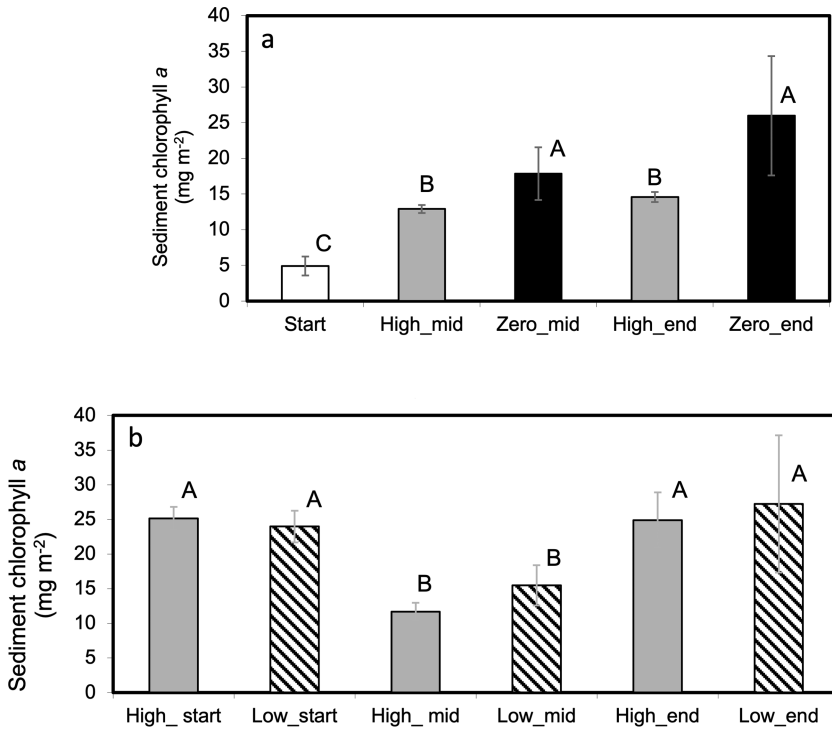


Figure 12. Microphytobenthos biomass in the top 1 cm of the sediment at the start of the experiment, mid-experiment, and at the end of four-week experiments in STURM systems with muddy sediment and different densities of hard clams. Zero = 0 clams  $m^{-2}$ , low = 10 clams  $m^{-2}$ , high = 50 clams  $m^{-2}$ . Different letters indicate statistical difference within a panel ( $p \leq 0.05$ ). (a) 2002 and (b) 2003 STURM experiments. Start cores in (a) taken from cores pre-equilibrated outside the tanks (see text).

however, they were similar during mixing-on and mixing-off, and significantly lower, in the tanks with 50 clams  $m^{-2}$  (Fig. 13a).

Microphytobenthos abundance in the initial sediment cores taken from all tanks in 2003 were about 25  $mg\ m^{-2}$  and not significantly different (Fig. 12b); some light may have reached the sediments during water exchanges during sediment equilibration. With mixing-on, mid-experiment microphytobenthos abundance decreased to about 15  $mg\ m^{-2}$  and was not significantly different between the tanks with 10 and 50 clams  $m^{-2}$  (Fig. 12b). At the end of the experiment, microphytobenthos abundance increased to about 30  $mg\ m^{-2}$  and was not significantly different between the tanks with 10 and 50 clams  $m^{-2}$  (Fig. 12b). While microphytobenthos biomass did not differ between the tanks with 10 and 50 hard clams  $m^{-2}$  each time it was measured over the experiment, in the treatment with 10 clams, microphytobenthos was resuspended, whereas it was not in the treatment with 50 clams

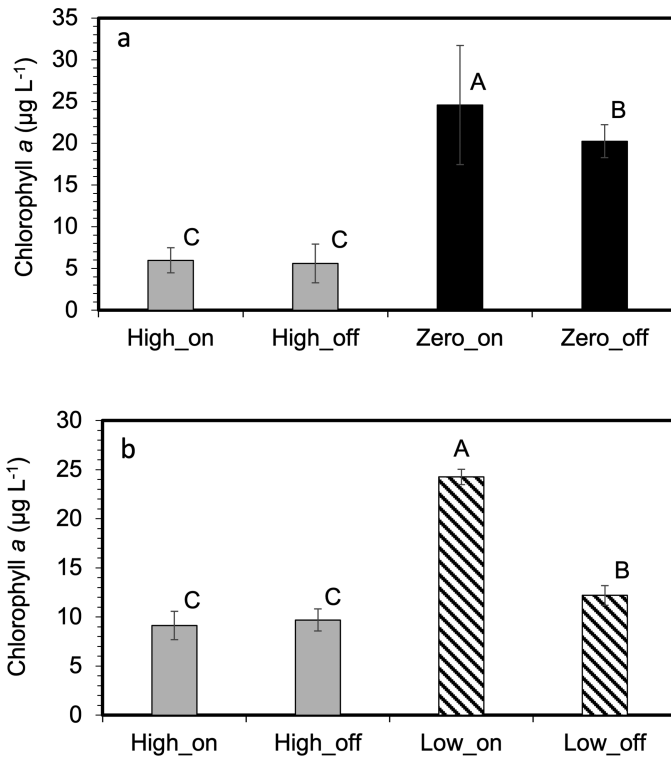


Figure 13. (a) Average  $\pm$  SD water column chlorophyll *a* concentrations measured during mixing-on and mixing-off on days 7, 17, and 24 in a 4-wk summer 2002 STURM experiment with muddy sediments and different densities of hard clams. (b) Average  $\pm$  SD water column chlorophyll *a* concentrations measured during mixing-on and mixing-off on days 6, 13, and 20 in a 4-wk summer 2003 STURM experiment. Zero = 0 clams  $\text{m}^{-2}$ , Low = 10 clams  $\text{m}^{-2}$ , High = 50 clams  $\text{m}^{-2}$ .

(Fig. 13b) as detected by the difference in water column chl *a* concentration during mixing-on compared with mixing-off. Water column chl *a* concentration was significantly higher during mixing-on than mixing-off in the tanks with 10 clams  $\text{m}^{-2}$  (Fig. 13b). There was significantly less chl *a* in the tanks with 50 clams  $\text{m}^{-2}$  than in the tanks with 10 clams  $\text{m}^{-2}$  and chl *a* concentrations during mixing-on and -off in the high clam treatment were similar (Fig. 13b). Percent water content in the top 0.5 cm of sediment was similar across tanks and time in all experiments.

*e. Erosion rates and cumulative suspended mass, respectively, as affected by clam density, all experiments combined*

CSM estimates for all experiments are compared in Figure 14, with CSM averaged ( $\pm$  SE) across erosion experiments for each clam density (zero, low, high) at each shear

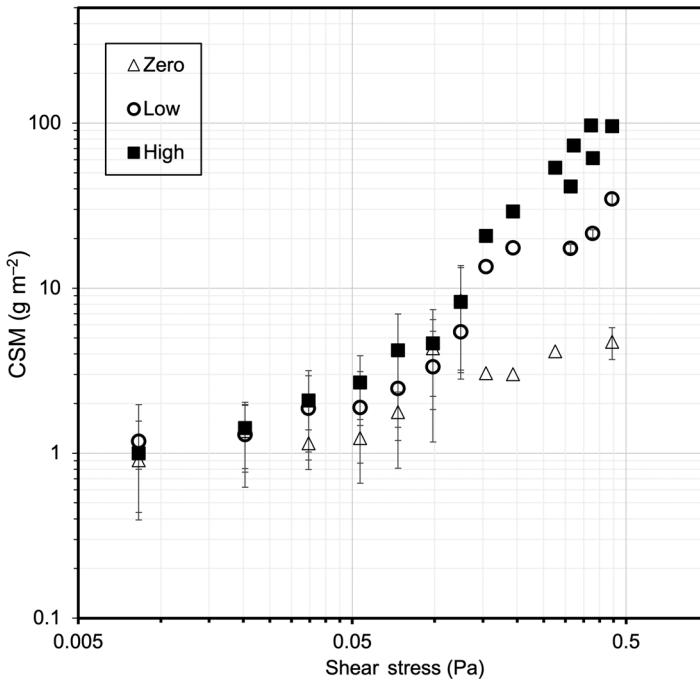


Figure 14. Cumulative suspended mass (CSM) for all clam density experiments. Mean ( $\pm$  SE) CSM ( $\text{g m}^{-2}$ ) as compared with shear stress (Pa) in stepwise erosion experiments for all clam density experiments in STURM tanks, a 30 cm Gust microcosm (30) and a 40 cm Gust microcosm (40). Zero = 0 clams  $\text{m}^{-2}$ , low = 10–16 clams  $\text{m}^{-2}$ , high = 40–57 clams  $\text{m}^{-2}$ . N = 3 for STURM, n = 2 for 30, n = 1 for 40.

stress step run. Despite some variability at the lower shear stress steps, trends emerge early on with a zero clam density having the lowest CSM over all shear stress steps (except 0.0986 Pa), followed by a low density of clams. Highest CSM across shear stress steps was found with a high density of clams. The treatments with more clams tended to erode faster and to start eroding sooner than the treatments with fewer clams in general. A prominent exception to this behavior was the zero clams treatment in the 30 cm Gust microcosms, which eroded very rapidly, though only after the critical stress was exceeded. CSM did not become consistent in the low clam treatments until a shear stress of  $\sim 0.032$  Pa or higher. On average, erosion rates were higher at high shear stresses, but increasing shear stress within a treatment did not always lead to increasing erosion rate. This was especially apparent for the STURM tank experiments, where the first shear stress step had the largest erosion rates in both treatments (Fig. 9). A deceleration or decline in erosion rate with increasing applied shear stress often indicates increasing resistance to erosion with depth into the sediment (Sanford and Maa 2001, Sanford 2006), also referred to as sediment supply limitation.

Erosion rates at the lowest 0.313 Pa erosion step used in the STURM tanks were significantly higher with  $20.4 \pm 18.5 \text{ mg m}^{-2} \text{ s}^{-1}$  in the tanks with high density clams than the  $6.4 \pm 3.8 \text{ mg m}^{-2} \text{ s}^{-1}$  in the tanks with low density (*t*-test,  $p = 0.01318$ ). Similarly, erosion rates were significantly higher in the high compared with the low density clam treatments at 0.377 Pa. and 0.444 Pa. The first erosion step in the STURM tanks started at high shear stress (0.313 Pa), thus, the results could not be compared with the erosion rates in the 30 cm Gust microcosm as the 30 cm Gust microcosm had been run only to a maximum of 0.1245 Pa.

However, the high shear stress steps used in the STURM tanks allowed us to examine what happens to the erosion rate when different densities of hard clams in cohesive sediments are subjected to very high bottom shear stress. Moreover, an erosion rate of  $18.9 \text{ mg m}^{-2} \text{ s}^{-1}$  in the 40 cm Gust microcosm with a high density of clams at step 0.322 Pa, that is, the only data available at a similar very high shear stress in the Gust microcosms as in the STURM tanks, fell within the range of the high clam density STURM tank treatment erosion rates of  $\text{mg m}^{-2} \text{ s}^{-1}$ .

CSM at 0.444 Pa of zero, low, and high density clams was significantly different (ANOVA, Student–Neuman–Keuls test,  $p < 0.01$ ) between treatments, combining CSM results from the 2003 and 2002 STURM experiments, with CSM highest in the high density treatment, followed by the low density and then the zero clam treatments.

#### 4. Discussion

Effects of bioturbation on the erodibility of cohesive sediments were investigated in short-term erosion experiments and in one-month long erosion experiments using the hard clam *Mercenaria mercenaria*, a bioturbator with shallow burrows (Doering 1982), which reworks the sediment through biodeposition, vertical and horizontal movements (Tettelbach et al. 2017), and valve adduction. Effects of different densities of little neck hard clams on sediment erodibility in short (on the order of hours) stepwise erosion experiments and one-month long erosion experiments with tidal resuspension were compared. Higher hard clam density decreased critical erosional shear stress,  $\tau_c$ , increased CSM and (usually) increased erosion rates. These effects were apparent in the short-term experiments, but not after repeated cycles of tidal resuspension and deposition.

Typical experiments examining bioturbator interactions with shear stress are carried out in short-term stepwise erosion experiments, often in annular flumes (Widdows et al. 1998; Jie et al. 2001; Sgro, Mistri, and Widdows 2005; Ciutat, Widdows, and Pope 2007). While dense beds of infaunal bivalves have led to sediment destabilization (Willows, Widdows, and Wood 1998; Widdows and Brinsley 2002; Sgro, Mistri, and Widdows 2005; Ciutat, Widdows, and Pope 2007), other researchers have not found any effects (Jie et al. 2001; Andersen et al. 2010; Eriksson et al. 2017; see Table 1) or decreased erodibility with increasing density and microphytobenthos (Eriksson et al. 2017; see Table 1). As outlined in Table 1, in short-term erosion experiments a dense population of infaunal bivalves in muddy sediment has been



found to increase, decrease, or not at all affect sediment erodibility, with little consensus. As can be reconciled from our experiments, bioturbation by a dense bed of little neck hard clams on muddy sediment destabilized bottom sediments in short-term erosion experiments (i.e., storm induced) and decreased the critical shear stress when microphytobenthos was excluded.

*a. Critical erosional shear stress,  $\tau_c$ , and cumulative suspended mass*

In our experiments, a high density of hard clams decreased the critical erosional shear stress while a low density did not. Hypothesis 1, that a high density of hard clams decreases the critical erosional shear stress as compared with low density or control levels, can be accepted. Hard clams significantly reduced the critical erosional threshold from  $0.091 \pm 0.015$  to  $0.024 \pm 0.014$  Pa, comparing zero densities with high densities. However, a low density of hard clams did not significantly reduce the critical erosional threshold ( $0.076 \pm 0.040$  Pa, ANOVA, Student–Neuman–Keuls test,  $p \leq 0.05$ ). As a result, CSM began increasing at much lower bottom shear stress in the high clam treatment than in the low and zero clam treatments where occasional deposition at lower shear stress ( $\sim 0$ – $0.1$  Pa) occurred. In contrast, in a study with different cockle densities, Ciutat, Widdows, and Pope (2007) found that the critical shear stress was relatively independent of cockle density (0.225 and 0.151 Pa for 0 and 312 animals  $m^{-2}$ , respectively). Sgro, Mistri, and Widdows (2005) found that an increasing density of the Manila clam, *Ruditapes philippinarum*, reduced critical erosion velocity; however, Jie et al. (2001) did not find any significant effect due to the abundance of the Manila clam. Grant and Daborn (1994) found no effect of *Corophium volutator* density on the critical shear velocity and suggested that amphipods seasonally reduce the sediment-erosion threshold by grazing on microphytobenthos, effectively decoupling the erosion rate and critical stress. Part of the differences between these studies may be the resolution of shear stress steps at low values or the definition of critical stress. The experiments reported here had very highly resolved applied shear stresses, and we defined critical stress as the lowest stress at which a noticeable increase in CSM occurred. However, differences between animal behavior probably also contributed.

Several hard clams were observed digging deeper as bottom shear stress increased. Allen and Vaughn (2009) studied the burrowing behavior of freshwater mussels in experimentally manipulated communities and suggested that the observed burrowing behavior was a mechanism by which mussels avoid dislodgement during high flows. Hard clams may be responding to high episodic shear stress (e.g., from storms) by vertical and horizontal movements and valve adduction. This is further supported by Sgro, Mistri, and Widdows's (2005) findings that natural densities of the Manila clam increased the erodibility of estuarine sediment because their vertical movements "loosened" the sediment. Horizontal movement of infaunal organisms near the bed surface (i.e., surface tracking) also increases sediment erodibility (Grabowski, Droppo, and Wharton 2011) and *Mercenaria mercenaria* has been observed to move horizontally (Tettelbach et al. 2017). *Cerastoderma edule* disturbed the

upper sediment layer through measurable movements due to its crawling and “shaking” behavior (Flach et al. 1996). For the Atlantic Razor clam, *Ensis directus*, a species burrowing to 70 cm depth, it has been suggested that the motions of its valves locally fluidize the surrounding soil and reduce burrowing drag (Winter, Deits, and Hosoi, 2012; Winter, Deits, Dorsch, and Hosoi 2014).

The depths to which clams burrowed in our experiment were likely dependent on siphon length, as shown in other studies (Zwarts and Wanink 1989). Average burial depth at the end of a stepwise erosion run, measured from the sediment surface to the start of the clam, was  $3.3 \pm 2.1$  cm, ranged from 1 to 8 cm and was thus highly variable. Doering (1982) found an average burial depth of 2.5 to 3 cm for *Mercenaria mercenaria* that increased to 4 to 4.5 cm in water containing predator *Asteria* effluent (Doering 1976). Hypoxic conditions are known to affect burial depth and can decrease the burial depth of clams (Marsden and Bressington 2009; Weissberger, Coiro, and Davey 2009); however, dissolved oxygen was not restricted in these experiments.

Hypothesis 2, that a high density of hard clams will reduce bed stability as compared with control or low density systems, promoting higher erosion rates and CSM when exposed to fluid stress, can also be accepted, though not after extended periods of time and not without exception. Erosion rates, CSM, and TSS concentrations were lowest in the control treatment, increased in the treatment with a low density of clams, and were highest in the treatment with a high density of hard clams. CSM increased much faster in the high density clam treatment than the low density clam treatment in the stepwise erosion experiment in the STURM tanks. The erosion rate during the stepwise erosion STURM tank experiments was significantly higher in the high density treatment ( $20.4 + 4.3 \text{ mg m}^{-2} \text{ s}^{-1}$ ) than in the low density treatment ( $6.4 + 3.8 \text{ mg m}^{-2} \text{ s}^{-1}$ ) at a shear stress of 0.313 Pa. The erosion rates at 0.313 Pa in the STURM tank corresponded well to erosion rates with a high density of clams at a similar shear stress in the 40 cm Gust microcosm. In the STURM tank, the 0.378 and 0.444 Pa steps that followed had lower erosion rates, likely indicating that erosion was limited by the amount of sediment available at the applied stresses. This may also have been the reason we did not see higher erosion rates in the 30 cm Gust microcosm. Reanalyzing data from Willows, Widdows, and Wood (1998) in a modeling study, van Prooijen, Montserrat, and Herman (2011) suggested the surface deposit feeder *Macoma balthica* increases the mass in the sediment fluff layer, and due to overlapping feeding areas, the erodibility is non-linear with density of the animals. The *Mercenaria mercenaria* used in our experiments, however, is a suspension-feeder and so may act differently. Nevertheless, our findings also are consistent with preferential loosening of the surface layer of sediments by feeding activity or movement, with deeper sediment layers remaining more resistant to erosion.

#### *b. Sediment consolidation*

Different investigators have utilized different sediment consolidation periods that may affect sediment erodibility (Grabowski, Droppo, and Wharton 2011). Widdows, Brinsley,

and Pope (2009) used a consolidation period of 24 hours and found no difference in erosion thresholds due to the presence of *Nereis diversicolor*, whereas Fernandes, Sobral, and Costa (2006) allowed the worms (and microbial community) to become established in the flume over 20 days and found significant differences in erosion thresholds. In our experiments we used a 14-day consolidation period over which we found pore-water gradients in muddy sediment become realistic (Porter, Owens, and Cornwell 2006), and thus microbial communities re-establish. A consolidation time of 24 hours is often used in engineering studies, but this time span may be insufficient for ecologically realistic sediment structures (Grabowski, Droppo, and Wharton 2011), and is too short to establish realistic pore-water gradients in muddy sediments (Porter, Owens, and Cornwell 2006). Sediment consolidation/equilibration time must be considered when designing short- or long-term erosion experiments.

*c. Short-term compared with long-term sediment erodibility*

Our prediction that sediment erodibility is the same during the commonly performed short-term (in the order of hours) compared with long-term (one-month tidal resuspension) erosion experiments was not supported. In 4-week long experiments, a high density of hard clams initially destabilized the sediment leading to a CSM of ca  $200 \text{ g m}^{-2}$ . However, the sediment stabilized over time and CSM became about similar between treatments with different densities of hard clams by the end of both sets of STURM experiments.

It is possible that the hard clams acclimated to high bottom shear stress and reduced their bioturbating behavior when exposed to long-term regularly recurring high shear stress. This may have led to sediment stabilization and facilitated microphytobenthos. Long-term behavioral responses to high bottom shear stress have not been studied. Eriksson et al. (2017) found that artificial cockle beds increased the nutrient uptake of microphytobenthos and promoted sediment accumulation, and suggested that the cockles facilitated the sediment-living algae by increasing sediment stability. The same study also suggested that high abundances of sediment-living bivalves may stabilize the sediment by providing a network of physical structures with their shells and through mucus production that binds the surface sediments, which possibly may have happened here.

Factors that mediate microphytobenthos biomass affect sediment erodibility (Yallop et al. 1994; Widdows and Brinsley 2002; Porter, Cornwell, Sanford, and Newell 2004; Porter, Sanford, Gust, and Porter 2004). Microphytobenthos biomass was significantly higher in the tanks with 0 clams during the mid and end points of the 2002 experiments, likely due to more light reaching the sediment surface in these tanks. Clams feeding on resuspended microphytobenthos likely reduced microphytobenthos biomass in the tanks with 50 hard clams  $\text{m}^{-2}$  in the 2002 experiments. Rakotomalala et al. (2015) found via modeling that an increased biomass of cockles increases microphytobenthos resuspension rates, and this could have aided microphytobenthos uptake by hard clams in these experiments. On the other hand, Van Colen et al. (2013) suggested that cockles may enhance microphytobenthos

biomass by decreasing other surface dwelling grazing species, but our sediments did not contain other macrofauna. Eriksson et al. (2017) suggested that nutrients produced by a dense bed of *Cerastoderma edule* led to microphytobenthos growth which then was responsible for the decreased sediment erodibility observed in the dense bed of cockles. In the 2003 STURM experiment comparing sediments with 50 and 10 hard clams  $\text{m}^{-2}$ , microphytobenthos increased over time perhaps mediated by enhanced nutrients produced by hard clams and light leading to a decreased sediment erodibility.

Microphytobenthos were resuspended in the treatment with 10 clams  $\text{m}^{-2}$  and the treatment without any clams, as determined by the difference in chl *a* concentration during mixing-on versus -off. However, in the high density treatment with 50 clams  $\text{m}^{-2}$  chlorophyll *a* concentrations were similar between the mixing-on and the mixing-off phase, and any resuspended microphytobenthos was likely consumed by the clams. Moreover, bivalve feeding and lower light at the sediment surface decreased microphytobenthos biomass in the high clam treatments compared to lower clam densities. More controlled longer term experiments with variable bottom shear stress should be undertaken to determine the interacting effects of long-term exposure to high bottom shear stress, benthos, and microphytobenthos on sediment erodibility.

The size of hard clams may affect the amount of initial sediments destabilization. We used similarly sized clams over all experiments. Other experiments have found smaller clams similar to those in this study (*Corbicula fluminea*) producing high net sediment reworking activity due to pedal feeding (Majdi, Bardon, and Gilbert 2014). While *Mercenaria mercenaria* does not pedal-feed, smaller clams are more metabolically active, and even smaller hard clams may cause more sediment erodibility while larger hard clams may cause less. Cozzoli et al. (2018, 2019) suggest a link of metabolic rate and sediment erodibility. More studies on the effect of infaunal clam size on bioturbation and sediment erodibility are needed.

Other factors such as sediment water content induced changes in  $\tau_c$  (Aberle, Nikora, and Walters 2004) can influence sediment erodibility over time. However, sediment water content in our experiments was similar over time and all treatments. The preponderance of the evidence in our long-term STURM experiments suggests that direct and indirect interactions leading to differential microphytobenthos abundance were the likely cause of observed erodibility changes.

#### *d. Indirect interactions*

Indirect interactions have been defined as interaction modifications that only become apparent when multiple species (or multiple environmental influences) are combined (Wootton 2002). Indirect interactions cannot be predicted by linear extrapolation from single or dual species experiments but require the complexity of a mesocosm or a field experiment (Wootton 2002; Porter, Cornwell, Sanford, and Newell 2004; Porter, Sanford, Gust, and Porter 2004). For example, Porter and colleagues (Porter, Cornwell, Sanford, and Newell

2004; Porter, Sanford, Gust, and Porter 2004) found that oyster feeding increased both light at the bottom and microphytobenthos biomass (direct effects). However, bottom shear eroded the microphytobenthos, thus reducing the microphytobenthos' positive effects on water quality (an indirect effect). The STURM experiments described here included direct (bivalve feeding, shear stress, and hard clams) and indirect interactions (water clarity, light, and microphytobenthos biomass) affecting particle concentrations and sediment stability. Bivalve feeding-reduced phytoplankton biomass, shear stress, and hard clams affected sediment erodibility, increasing turbidity and reducing light and affecting microphytobenthos biomass, which, in turn, contributed to sediment stability. Interactions by ecosystem engineering bivalves promoted microphytobenthos biomass (Donadi et al. 2013), thereby affecting sediment stabilization. As demonstrated by the 2002 and 2003 STURM experiments, direct and indirect interactions affected light and microphytobenthos, were important for sediment erodibility, and should be included in future studies.

Snapshots of sediment erodibility of an instantaneous composition of benthos and microphytobenthos in the field have been made by collecting sediment cores with associated fauna and microphytobenthos from the field and running short-term erosion experiments in annular flumes (Widdows, Brinsley, Salkeld and Lucas 2000; Widdows, Brown, Brinsley, Salkeld, and Elliott 2000; Widdows and Brinsley 2002) or Gust microcosms (Dickhudt et al. 2009). While these studies provide snapshots of the community, the precise interaction of stabilizing and destabilizing factors has been difficult to pinpoint in the field. Moreover, often multiple species and microphytobenthos are used together in the cores, which makes it difficult to assign causation to a particular species or factor (Table 1). In this study, we performed long-term laboratory studies on the effect of bioturbation of one bivalve species (similar size, with different densities) and bottom shear stress that included indirect effects. More controlled longer term experiments with variable bottom shear stress and desired species/combinations of species and direct and indirect factors measured, should be undertaken.

The interactions between sediment stabilizing and destabilizing processes in the STURM experiments were complex, dynamic, and continually at work. Physical variables (e.g., shear stress) and biological variables (e.g., benthos and microphytobenthos) interact over spatial and temporal scales. Temporal and spatial changes in the relationship between mean erosion rate and current velocity studied in stepwise erosion experiments in an annular flume were attributed to a varying abundance of *Macoma balthica* and the degree of algal biofilm that formed at two sites in the Humber estuary (Widdows, Brown, Brinsley, Salkeld and Elliott 2000). Models from Borsje et al. (2008) show small-scale biological activity by *Macoma balthica*, *Hydrobia ulvae*, and diatoms can affect large-scale cohesive sediment transport. Soares and Sobral (2009a) found that different densities of *Scrobularia plana* did not affect eroded mass at all sites and concluded microphytobenthos may have stabilized the sediment at some sites leading to a high spatial and temporal variability of sediment erodibility. Soares and Sobral (2009b) added that sediment cohesiveness also could have been a factor.

*Mercenaria mercenaria* is found on various grounds such as shell habitat, muddy sediment, sandy habitat, and sediments with sand–silt mixtures (Mann et al. 2005; Mackenzie, Pikanowski, and McGillan 2006). The present experiments were all done with cohesive muddy sediments (sandy clay/sandy mud, according to Folk, 1954, classification; see Table 2), which likely exhibited different inherent erodibility than sandy sediments (Li et al. 2017). More studies need to be performed to evaluate the effect of hard clam density and bottom shear stress across sediment types, including the development of any microphytobenthos. Other factors may contribute as well. For example, in aquaculture settings meshes are often placed over dense aggregations of bivalves to deter predators (Beal and Kraus 2002; Murphy, Anderson, and Luckenbach 2015; Munroe et al. 2015), which can cause reduced erosion and enhanced deposition rather than destabilization (Norkko and Shumway 2011).

Moreover, Allen and Vaughn (2011) found in flume experiments that certain polycultures had non-additive biodiversity effects on gravel erosion. Mussel species richness was associated with an increase in erosion at both low and high densities. Erosion in species mixtures was purely additive at low density, but at high density certain combinations of species showed non-additive effects on erosion. Thus, a polyculture affects sediment erodibility non-linearly, which then may translate into ecosystem effects. Lohrer, Thrush, and Gibbs (2004), while working with sea urchins, found that bioturbators enhanced ecosystem function through complex biogeochemical interactions. The degree of sediment and microphytobenthos stabilization and destabilization affected ecosystem functioning non-linearly in other STURM experiments (Porter, Cornwell, Sanford, and Newell 2004; Porter, Sanford, Gust, and Porter 2004), where microphytobenthos erosion due to moderate shear velocity ( $0.6 \text{ cm s}^{-1}$ ) led to increased nitrogen fluxes from the sediments in an ecosystem experiment. The initial sediment destabilization in STURM experiments with different densities of hard clams in this experiment led to increased nutrient concentrations (Porter, Mason, and Sanford 2013) in the water column and reduced light affecting microphytobenthos biomass. Thus, sediment destabilization can subsequently alter benthic–pelagic coupling processes such as the nutrient dynamics and light availability affecting the ecosystem. Our results show that interactions between species and bottom shear stress are key to understanding, managing, and restoring ecosystems under human influence.

## 5. Conclusions

Bioturbation by a dense bed of little neck hard clams on muddy sediment destabilized bottom sediments when first subjected to high bottom shear stresses (e.g., storm induced), leading to increased CSM in the water column, and decreased the critical shear stress when microphytobenthos were excluded. However, long-term differences between high and low density clam effects are not as clear, and direct and indirect interactions affecting light and microphytobenthos may be important. Experiments to date have mainly focused on short-term erosion experiments or on sediment cores including fauna and microphytobenthos taken in the field. More controlled longer-term experiments with variable bottom shear

stress should be undertaken to determine the interacting effects of long-term exposure to high bottom shear stress, benthos, and microphytobenthos on sediment erodibility. Sediment destabilization can subsequently alter benthic-pelagic coupling processes such as the nutrient dynamics and light availability affecting the ecosystem.

*Acknowledgments.* We thank Cherrystone Aqua Farms, Cheriton, Virginia, for providing hard clams, *Mercenaria mercenaria*, for all experiments. We thank G. Gust for a 40 cm microcosm and for his and V. Müller's help with extending the shear velocity calibration range. We thank the late Dr. Evamaria Koch for her 30 cm Gust microcosm. We thank the Chesapeake Biological Laboratory for space to set up the shear turbulence resuspension mesocosm (STURM) facility for the one-month experiments with different densities of hard clams, and Matthew Reardon and Heather Soulen for their technical assistance during the mesocosm runs. Elizabeth Combs helped run the erosion experiment in the 40 cm Gust microcosm. Our research was supported by the Hudson River Foundation (grant No. CBL-35236 to Robert P. Mason, E.T.P., and L.P.S.) and the University of Baltimore Foundation (grant No. 4200079 to E.T.P.); by a grant from the Yale Gordon College of Arts and Sciences at the University of Baltimore (to E.T.P.); a Washington College Faculty Enhancement grant (to E.T.P.); and by Maryland Sea Grant (Subaward No. SA75281870-R [R/P/AQ-65a] to E.T.P. and Subaward No. SA75281870-R [R/P/AQ-65b] to Jeffrey C. Cornwell and L.P.S.). We thank Robert P. Mason for supporting the mesocosm runs. This is University of Maryland Center for Environmental Science Contribution No. 6048.

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Received: 27 November 2019; revised: 4 May 2021.