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Effects of bioturbation on the erodibility of cohesive *versus* non-cohesive sediments along a current-velocity gradient: A case study on cockles

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ABSTRACT

Soft-bottom bioturbators are ecosystem engineers in the sense that they can have considerable effects on sediment erodibility and resuspension. The common cockle *Cerastoderma edule* is a bioturbating filter feeder that is widespread along the European Atlantic coastline. Its presence and activity can decrease sediment erosion thresholds in cohesive sediments but little is known about its effect on non-cohesive sediments. Using controlled annular flume experiments, we investigated the relative effects of different cockle densities on sediment resuspension in cohesive *vs.* non-cohesive sediments by assessing the following: (i) the mud and sand burrowing behavior of cockles, (ii) critical erosion thresholds, (iii) the mass of eroded sediment and (iv) erosion rates. Our results show that cockles were more active in non-cohesive sediment compared with cohesive sediment. Despite their lower activity, the presence of cockles in cohesive sediment increased sediment erodibility by reducing the critical erosion threshold (U_{crit}) and increasing both the mass of eroded sediment and erosion rate. In contrast, cockles had no effect on erodibility in non-cohesive sediment, especially on the eroded sediment mass and erosion rate. The mass eroded was not significantly different between cohesive and non-cohesive sediments when cockles were present. Our experiments show that the increased erodibility of cohesive sediment due to the bioturbation by cockles is density dependent: higher cockle density results in stronger effects on erodibility. Moreover, this increase in cohesive sediment erosion due to cockle bioturbation was positively correlated with current velocity. In contrast, the erosion of non-cohesive sediment only depended on the current stress and was unaffected by cockle density. Considering the high abundance of *C. edule*, its widespread distribution and its extensive activities, the results of this study could be widely applicable to intertidal mud flats around the world.

1. Introduction

The morphology and ecology of intertidal mudflats are determined by the dynamics between sediment stability and erosion (Kristensen et al., 2013). Intertidal mudflats can have strong seasonal dynamics, with periods of accretion and erosion alternating over a season (Yang et al., 2008). Sediment dynamics can also be event driven, with erosion levels on the order of 100 mm occurring during a single storm (Hu et al., 2015). Such short-term sediment dynamics on intertidal mudflats are important for understanding the long-term dynamics of ecosystems like seagrass meadows (Suykerbuyk et al., 2016) and salt marshes (Bouma et al., 2016). Thus, understanding the processes controlling sediment dynamics of intertidal flats is of key importance. However, sediment dynamics are complex as they involve interactions between physical, geochemical and biological processes influencing sediment erodibility (Grabowski et al., 2011).

Benthic organisms can act as ecosystem engineers in the sense that their presence or activity may alter erosional processes in the surface sediment layer by modifying both the critical erosion threshold and erosion rate of soft-bottom substrates (Paterson, 1989; Willows et al., 1998; Passarelli et al., 2014). They can be divided into two main functional groups: bio-stabilizers and bio-destabilizers (Widdows and Brinsley, 2002). Bio-stabilizers make the sediment surface more resistant to erosion. For instance, diatoms produce extracellular polymeric substances (EPS), a mucus that creates bonds between particles and thus increases erosion thresholds (Meadows et al., 2012; Paterson, 1997). Additionally, aggregates of tube-building macroinvertebrates stabilize the particles against resuspension and erosion, in concert with

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the activities of bacteria and microalgae (Krasnow and Taghon, 1997; Borsje et al., 2014). In contrast, bio-destabilizers or bioturbators (*e.g.* macrobenthic shellfish or lugworms) destabilize the sediment surface and make it sandier, by continuously bioturbating the sediment, hence resuspending fine particles into the water column (Volkenborn et al., 2007; Volkenborn and Reise, 2006).

In general, sediments can be divided into cohesive and non-cohesive sediments, which strongly differ in erodibility because of their differences in physical and chemical properties (Flemming, 2000; Grabowski et al., 2011). Cohesive sediments contain a significant proportion of silt (*i.e.*, < 63 μm diameter), which binds the sediment particles together and makes the sediment harder to erode. Apart from altering erodibility, the grain size distribution of the sediment also influences the structure of the invertebrate community living within the sediment (Flemer et al., 2002; Cozzoli et al., 2013). Although macrobenthic organisms typically have a clear preference for a specific sediment grain-size, many species can occur across a broad range of habitats (Ellingsen, 2002; Cozzoli et al., 2013).

Previous studies on the biological effects of macrobenthos have mostly focused on the destabilization and resuspension of cohesive sediments (*e.g.* Widdows et al., 1998; Andersen, 2001; Dickhudt et al., 2009; Briggs et al., 2015; Van Colen et al., 2013), even though macrobenthic organisms can also be abundant and hence potentially influence sediment erosion in non-cohesive sediments (Van Colen et al., 2013). For instance, the common cockle *C. edule*, while showing a preference for muddy bottoms, can inhabit sediments with a median grain size ranging from 50 μm (fully cohesive) to 250 μm (fully non-cohesive) (Cozzoli et al., 2013). The biogenic effects of bioturbators may be expected to vary with sediment type and population density. How this subsequently translates into erosion characteristics may, moreover, depend on the physical setting, with cohesive sediments being more typical for low-energy areas and non-cohesive sediments being more typical for high-energy environments. Hence, there is a need for an in-depth study addressing the combined effects of bioturbating behavior, bioturbator density and physical setting on the sediment erosion characteristics of both cohesive and non-cohesive sediments.

The aims of the present study are to compare the bioturbation effects of the cockle *C. edule* on the erosion of both cohesive and non-cohesive sediments subject to tidal currents. More specifically, we aimed to (i) provide a visual description of the mud and sand burrowing behavior of cockles, (ii) quantify critical sediment erosion thresholds (i.e., current velocity when erosion starts), (iii) quantify the mass of the eroded sediment and (iv) calculate the net erosion rates. The common cockle *C. edule* is an ideal model species as it inhabits both cohesive and non-cohesive sediments along the European Atlantic coastline and is a well-recognized ecosystem engineer. By its burrowing behavior, *C. edule* has been shown to lower sediment erosion thresholds and change the erosional dynamics of cohesive sediments (Montserrat et al., 2009), but little is known about its effects on non-cohesive sediments. Our experimental study was conducted by gradually increasing current velocities in an annular flume and testing their effects on both cohesive and non-cohesive sediments in the absence and presence of two densities of cockles. We hypothesized that the magnitude of the bioturbation effect of the cockle *C. edule* on sediment resuspension will be dependent on both current velocity and sediment cohesiveness.

2. Materials and methods

2.1. Target organism

The common cockle *C. edule* is a widespread and dominant suspension-feeding bivalve that lives and burrows in the top few centimeters of sediments along the European Atlantic coastline (Tebble, 1966). Malham et al. (2012) reviewed the biology of *C. edule*, including its genetics, immunology, production, development, feeding energetics, growth, predators, and extrinsic environmental drivers. Cockles are defined as bioturbators as they disturb the sediment and increase turbidity levels by their vertical and horizontal activity and by excreting fecal pellets into the water column (Richardson et al., 1993; Widdows et al., 1998). Cockles may occur in very high densities in some areas, up to 5000 individuals m^{-2}; conditions favoring high density are found in the intermediate to high intertidal zone (between 20 and 60% of emersion time for tidal cycle) with oceanic salinity levels (35 g L^{-1}), intermediate levels of mud content (grain size between100 and 200 μm) and moderate levels of hydrodynamic stress (between 30 and 70 cm s^{-1} of maximal tidal current velocity) (Coosen et al., 1994; Cozzoli et al., 2014). A moderate density of 500 cockles/m^2 has been estimated to occupy about 16% and disturb about 29% of the sediment surface in one week (Flach, 1966). Earlier studies have shown that increasing the presence of cockles can increase sediment erodibility (Ciutat et al., 2006, 2007) and significantly lower the sediment erosion threshold (Neumeier et al., 2006), making it an ideal model species to study the effects of bioturbation.

2.2. Sediment and animal collection

Sediment samples were collected from two tidal flats located in the tidal basin of the Oosterschelde estuary in the Netherlands: Zandkreek (cohesive, 51°23′15.5″N 3°49′48.6″E) and Oesterdam (non-cohesive, 51°27′51.5″N 4°13′16.3″E). These locations are characterized by a low to moderate peak in tidal current (*ca.* 35 cm s^{-1}) and low wave exposure (Cozzoli et al., 2017), with the average tidal amplitude measured as 290.652 cm in Zandkreek and 333.182 cm in Oesterdam. *C. edule* can occur with an average biomass of *ca.* 15 g AFDW m^{-2} with peaks up to 100 g AFDW m^{-2} at Zandkreek and an average biomass of 30 g AFDW m^{-2} with peaks up to 200 g AFDW m^{-2} at Oesterdam (Cozzoli et al., 2014). Considering its high abundance, widespread distribution and extensive activities, *C. edule* is expected to affect sediment erosion at these locations and, indeed, on tidal flats throughout the Oosterschelde basin.

At each of the two sites, the top 15 cm of sediment was collected and transported to the laboratory, and fauna were removed by wet-sieving through a 1 mm mesh. Sieving also removed shell debris and other larger particles or sediment aggregates that may influence sediment erodibility. Particle Size Distribution D50 is the median diameter or the medium value of the particle size distribution and is considered an important parameter characterizing particle size. The mud content (fraction of sediment particles < 63 μm; Montserrat et al., 2009) and the median grain size data of both sediment types were measured using a Mastersizer 2000 (Malvern Instruments Ltd., Malvern, UK). Non-cohesive sediments (median grain-size D50 = 273.92 μm) were defined as sandy sediments containing 0% silt (Fig. 1A), and cohesive sediments were defined as muddy sediments with ≥32% silt content (median grain-size D50 = 101.43 μm) (Fig. 1B).

Specimens of the cockle *C. edule* were collected from the Oesterdam, located in Zeeland, the Netherlands, and transported to the laboratory. After collection, the cockles were left to acclimate in buckets filled with aerated seawater for 24 h in a temperature-controlled room at 15 °C. After this period, active cockles were transferred to flumes, which had been previously filled with sediment, and left for another 48 h before starting the experiment. The average shell length of the selected cockles was 36.0 ± 1.2 mm (n = 96) with a range from 31.7 mm to 38.2 mm. The majority of the cockles dug into the sediment and buried themselves in < 10 min after they were introduced to the sediment surface. When individuals were inactive and remained on the sediment surface for one day, they were replaced with new individuals. Two different densities of cockles were used in the experiments, which were set according to the relevant densities at the sites where sediments were collected (Cozzoli et al., 2014): a low density (LD) of 228 ind. m^{-2} with a biomass of 14.1 g ash-free dry weight (AFDW) m^{-2} (n = 3), and a high density (HD) of 686 ind. m^{-2} with the biomass of

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