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Grain sizes retained by diatom biofilms during erosion on tidal flats linked to bed sediment texture

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ABSTRACT

Size-specific sediment retention by diatom biofilms was measured by eroding intertidal muds at increasing shear stresses (0.01–0.60 Pa) using a Gust microcosm. The grain sizes eroded from biofilm-covered sediment were compared to those from control cores from which the biofilms were destroyed using bleach. Biofilms were quantified using carbohydrate measurements. Cores from an intertidal mud flat in the Minas Basin of the Bay of Fundy (Canada) showed biofilms preferentially retained clays and very fine silts relative to fine and medium silts. In contrast, prior field observations on an intertidal sand flat indicated that fine and medium silts were preferentially retained by biofilms relative to clays and very fine silts. These contrasting results suggest a link between size-specific sediment retention and sediment texture, where sand biofilms retain coarser, non-cohesive sediment grains, while mud biofilms retain finer, cohesive sediment grains. This relationship implies that biofilms could contribute to a positive feedback that would preserve existing sediment texture.

1. Introduction

Diatoms and other benthic microbes secrete extracellular polymeric substances (EPS) that form a sticky web among sediment grains (Grant et al., 1986). These molecular networks of EPS are known as sediment biofilms. Previous studies (Holland et al., 1974; van De Koppel et al., 2001) have linked biofilms and sediment texture, noting that biofilm-covered sediment was associated with increased clay (<4 μm) and silt content ($\sim$4–63 μm). This association is due, in part, to the redistribution of EPS in the water column, which enhances flocculation, a process that increases the settling velocities of clays and silts, and thus their depositional fluxes to the seafloor (Bender et al., 1994; Decho, 2000; Stal, 2010). More importantly, because EPS increase the cohesion between sediment grains, they increase sediment erosion thresholds. Cohesion affects the erosion thresholds of finer sediment sizes more than coarser sizes because smaller particles have larger surface-area-to-mass ratios. As a result, biofilms reduce winnowing of fine sediment (Sutherland et al., 1998; van De Koppel et al., 2001).

A better understanding of the interactions between biofilms and fine sediment in coastal areas is crucial to assess and predict water quality. Focusing on fine sediment is a priority because contaminants, such as trace metals, adsorb preferentially to fine particles (Milligan and Loring, 1997) and bind to biofilms (Sutherland, 1990). Recently, both biofilms and suspended particles have been shown to increase contaminant retention by the seabed, notably with DDT (Guo et al., 2012). Other studies have shown an increased survival of pathogenic bacteria in the sediment when biofilms were present (Decho, 2000; Piggot et al., 2012). Fine sediment retention by biofilms may affect sensitive benthic communities. For instance, a reduction in silt content can decrease organic matter availability (e.g., Thrush and Dayton, 2002). The link between organic matter and grain size can forge complex links between grain size and the abundance of important species in intertidal ecosystems. In the Bay of Fundy, the abundance of *Corophium volutator*, which is considered a keystone species in the area, has been linked to the grain size of mudflats (Trites et al., 2005). A vulnerable population of semi-palmated sandpipers (*Calidris pusilla*) rely on *Corophium* as their main food source during migration (Shepherd et al., 1995). Biofilms in the area are dominated by diatoms (Daborn, 1991; Amos et al., 1992) and an association between local biofilms, *Corophium*, semipalmated sandpipers and sediment stability has been reported (Daborn et al., 1993). More specifically, it was observed that biofilm grazing by *Corophium* can destabilize the sediment. When sandpipers started feeding on the amphipods, a trophic cascade allowed biofilms to recover and stabilized the sediment (Daborn et al.,

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1993). Although the trophic cascade hypothesis has been questioned, the interdependence of biofilms, *Corophium*, sandpipers and sediment texture is clear (Hamilton et al., 2006).

Studies of the role of biofilms on size-specific sediment retention generally have considered broad size classifications, and they have not distinguished the behaviors of cohesive versus non-cohesive fractions (Holland et al., 1974; van De Koppel et al., 2001). McCave et al. (1995) argued that aggregates smaller than ~10 μm are not broken up by shear in the viscous bottom boundary layer and, as such, their constituent grains are not subject to hydrodynamic sorting, while grains larger than 10 μm can be sorted hydrodynamically. Increasing abundance of constituent sediment grains smaller than 10 μm may be associated with reduced erodibility (van Ledden et al., 2004) and reduced erosional sorting (Law et al., 2008) of sediment. An accurate understanding of erosion and sorting of a sediment bed, therefore, relies on an accurate understanding of the processes that control the abundance of fine sediment in the seabed. The goal of this work is to resolve the effect of biofilms on detailed, size-specific retention of sediment in the seabed, focusing particularly on the fine sediment fractions.

Previous research on size-selective erosion from sandy sediment with biofilms showed that clay-sized (< 4 μm) particles are not preferentially retained in the seabed during erosion. In one experiment, biofilms grown on sand were shown to preferentially retain 5-μm very-fine-silt-sized microspheres relative to the 1-μm clay-sized microspheres that were simultaneously released into a recirculating flume (Arnon et al., 2010). The authors argued that biofilm pore sizes allowed both particle sizes to deposit within the biofilm, but they reduced the resuspension of the larger particles more effectively than that of the finer particles. In another study, Garwood et al. (2013) used a Gust microcosm to apply a sequence of shear stresses to sediment cores from a sandy intertidal flat. They demonstrated that biofilms preferentially retained fine and medium silts (8–16 μm) relative to clays and very fine silts (< 8 μm). These two studies are inconsistent with the hypothesis that diatom biofilms always retain the finest grain sizes (Holland et al., 1974; van De Koppel et al., 2001). Garwood et al. (2013) speculated that the biofilms at their site did not retain the finest grain sizes because the biofilms were formed by cyanobacteria, whereas previous research had examined sorting associated with diatom biofilms. Alternatively, differences in sorting may have been reinforced by the substrates themselves, with mud biofilms preferentially retaining the finest, most cohesive grain sizes and sand biofilms preferentially retaining coarser, non-cohesive grain sizes.

Because previous studies reporting an association between biofilm and mud (clay and silt) content of the sediment focused on diatom biofilms (Holland et al., 1974; van De Koppel et al., 2001), and because none of the studies addressing size-specific sediment retention explicitly involved muddy substrates and diatom biofilms (Arnon et al., 2010; Garwood et al., 2013), a field study was conducted to quantify the effect of diatom biofilms on size-specific sediment retention in muds. Cores were collected and eroded biweekly over an 8-month period from an intertidal mudflat in the Minas Basin of the Bay of Fundy, Canada. This site was selected because previous research showed that diatom biofilms dominated the muddy sediment at the site (e.g., Daborn, 1991).

2. Methods

2.1. Field site

Natural sediment was eroded to test whether the effects of diatom biofilms on size-specific sediment retention in mud differed from that observed in sand. Sediment cores were collected from a macrotidal flat near Kingsport, Nova Scotia, in the Minas Basin of the Bay of Fundy (45.15°N, 64.37°W, Fig. 1). The landward edge of the site was located one meter (in horizontal distance) beyond the lower edge of a salt marsh, where the high marsh was dominated by *Spartina patens*, and the low marsh by *Spartina alterniflora*. The surface sediment at the site was composed of mud (see Section 3.2). The intertidal flats in this region of the basin experience slightly asymmetric semi-diurnal tides, with a stronger flood than ebb, and an average tidal range of 11.5 m (Faas et al., 1993).

2.2. Sample collection

Sediment cores were collected biweekly from April through November, 2012. To minimize diurnal and tidal influence on biofilm properties caused by migration of microorganisms in the

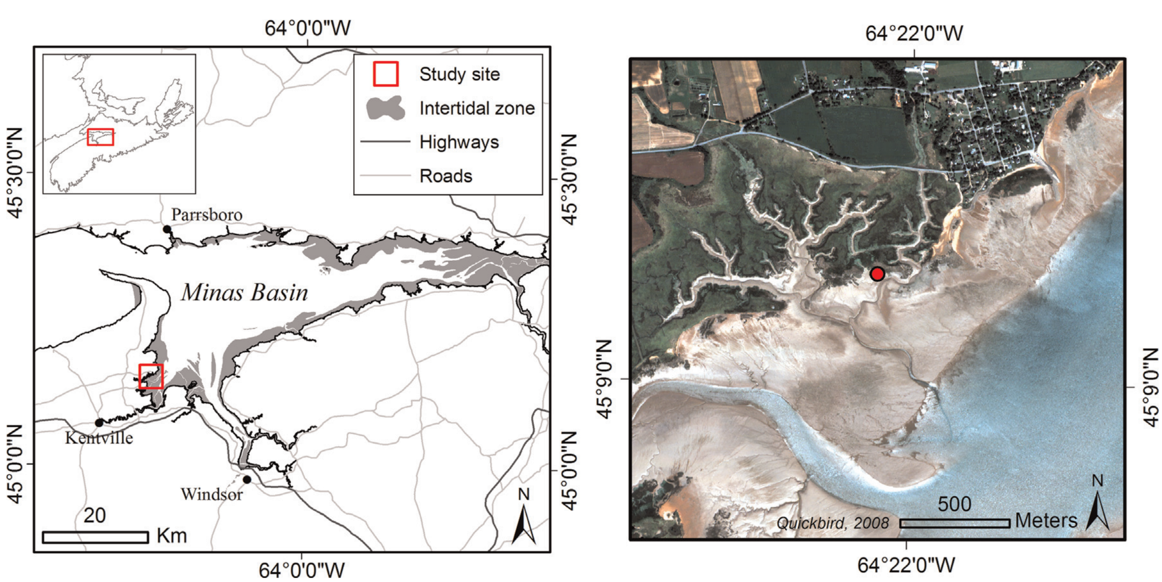

Fig. 1. Maps of the Minas Basin and intertidal flats. The field site is indicated by the red box and red dot, while the intertidal zones are shown in gray. The left panel is based on data from the Atlantic Climate Adaptation Solutions Association published in van Proosdij and Pietersma-Perrott (2012). For additional characterization of the site, including a LIDAR survey, see Law et al. (in preparation).