

The effect of buoyant biofilms on the erodibility of sublittoral sediments of a temperate microtidal estuary

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Abstract

An in situ benthic flume (Sea Carousel) was deployed at eight stations along a transect (Upper South Cove, Nova Scotia) to examine the influence of biofilms on sediment erodibility. Subsamples of the material eroded within the Sea Carousel were collected by pumping and were analyzed for suspended particulate matter (SPM). Undisturbed syringe cores of the seabed were also collected and analyzed for major physical properties (bulk density, mineralogy, grain size) and organic character (chlorophyll, pheopigment, colloidal carbohydrate, organic content). Strong relationships between erosion thresholds and rates and sediment chlorophyll ($r^2 = 0.948$, $r^2 = 0.875$) and colloidal carbohydrate ($r^2 = 0.854$, $r^2 = 0.774$) content were observed, suggesting that both pigment and mucilage biofilm variables serve as good indicators of sediment stability. Erosion rates varied by a factor of 7 along the station transect, while erosion thresholds varied only by a factor of 2. Thus, erosion rate was a more sensitive indicator of trends in sediment stability than was erosion threshold. X-ray computed tomography revealed the presence of a buoyant chlorophyll-containing gel mud in the uppermost millimeters of the sediment column. The sectioning of undisturbed syringe cores revealed that the buoyant layer was associated with the surface chlorophyll layer. The reduction of sediment weight (geostatic load) in the surface biogenic layer may have a significant effect on sediment erodibility and explain the low erosion thresholds observed in this estuary.

Diatoms play a significant role in the stabilization of marine sediments (Holland et al. 1974; Grant et al. 1986a,b; Paterson et al. 1990; Madsen et al. 1993). Mucopolysaccharides, which are secreted by benthic diatoms for purposes of attachment and locomotion (Harper 1977; Edgar and Pickett-Heaps 1984), form connective strands between sediment grains and therefore contribute to intergrain binding (Frankel and Mead 1973; Grant et al. 1986b; Paterson 1989). Sediment cohesion increases as mucopolysaccharides, laid down by actively migrating diatoms, eventually fill interstitial voids and form a complex matrix in the diatom-inhabited surficial layer (Paterson 1989). These extensive mucilage networks or “biofilms” reduce bottom roughness and surface frictional drag (Lindahl 1972), thereby reducing the susceptibility for erosion.

Population explosions of benthic diatoms that occur in both intertidal and subtidal settings of cohesive and noncohesive sediments (Round 1971; Baillie and Welsh 1980; Anderson 1983; Paterson and Underwood 1990) will alter erosion of sediments and reduce both the magnitude and frequency of resuspension events (Neumann et al. 1970;

Scoffin 1970; Holland et al. 1974; Grant et al. 1986b). This reduction in resuspension rates will have a great impact on diatom-related processes at the sediment–water interface, the advection of pore-water nutrients from the sediment to the overlying water column (Grant and Bathmann 1987; Floderus and Hakanson 1989), the availability of particulates as food for suspension feeders (Baillie and Welsh 1980; Grant et al. 1990; Shaffer and Sullivan 1988; Frechette and Grant 1991), and the sedimentary processes affecting coastal engineering projects (Amos et al. 1992b).

Mucopolysaccharide secretions have a broader functional significance than that of locomotion. An increase in sediment stability associated with the formation of a mucilage matrix will create a more stable habitat for diatoms and allow certain physiological requirements to be met. A stabilized sediment column may be exploited by diatoms as they migrate to the water-sediment interface to capture light for photosynthesis and then to the underlying nutrient-rich sediment to undergo heterotrophy (Lewin and Lewin 1960). Downward migration will also prevent seaward drift of resuspended cells during ebb tide (Heckman 1985).

In the past, estimates of sediment erodibility have been largely based on erosion coefficients derived from laboratory studies of abiotic sediment. These laboratory results, obtained from artificially settled abiotic sediment, did not include the complexities arising from biochemical and geophysical influences that occur in nature subsequent to

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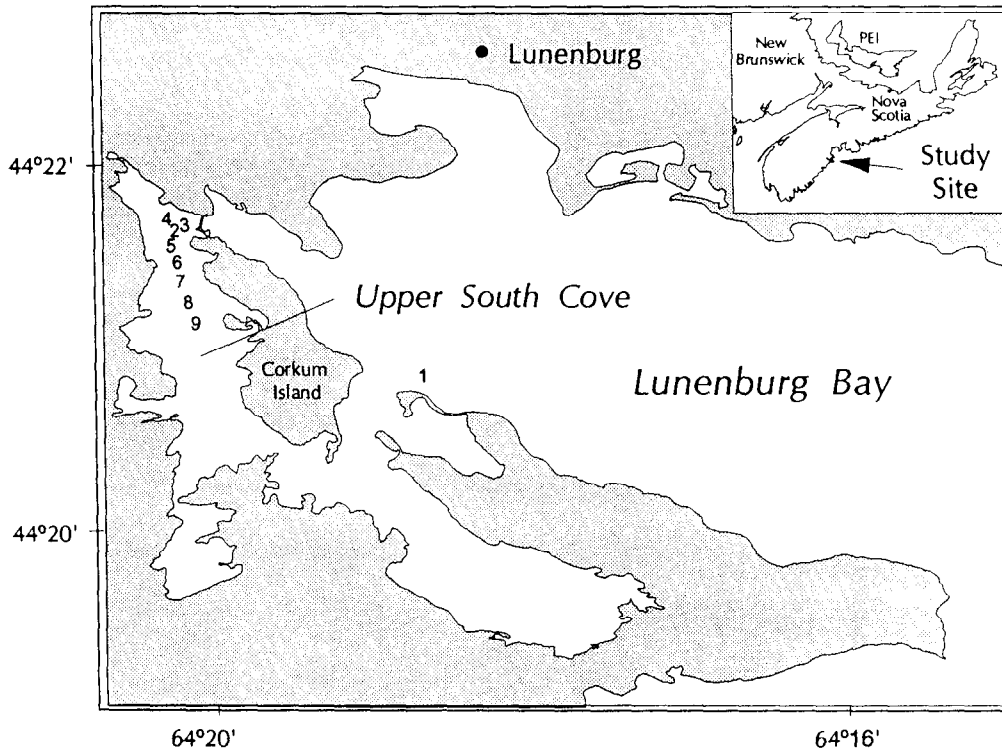


Fig. 1. Location of stations in Upper South Cove and Lunenburg Bay, Nova Scotia.

sediment deposition (Amos et al. 1992a). The properties of natural sediment are a result of recent and historical events integrating oceanographic, sedimentological, and biological conditions. These factors are highly interactive and not easily predicted. Because the application of results based on laboratory studies may not be realistic (Nowell and Jumars 1987), it is important to carry out sediment stability measurements in situ or on sediments that retain their natural properties during laboratory measurements.

Erosion of undisturbed subtidal sediments and subsequent sampling of resuspended matter was carried out with the use of an in situ benthic annular flume (Sea Carousel; Amos et al. 1992b). Several studies have assessed the effect of diatom biofilms on the stabilization of intertidal sediments (Grant et al. 1986a,b; Paterson 1989; Paterson et al. 1990); however, little is known of the effect of diatom biofilms on the erosion thresholds of permanently submerged sediments. Diatoms concentrate in the upper 2 mm of sediment and form mucilage biofilms that alter the biochemical and geophysical properties of sediment and may stabilize the seabed (Paterson 1989). This paper examines the relationship between biofilms and the erosion thresholds, erosion rates, and erosion type of subtidal sediment in Upper South Cove, Lunenburg Bay, Nova Scotia.

Study site

Upper South Cove is a shallow coastal embayment situated within Lunenburg Bay, Nova Scotia, located 63 km southwest of Halifax (Fig. 1). It is a region of particular interest since it contains a commercial mussel farm and is

presently being assessed as a site for suspended and bottom scallop culture. The cove has a length of 3.5 km, an average width of 0.5 km, an average depth of 1–2 m (max. depth of 8.5 m). The inner termination of the cove was created in 1968 due to the construction of a causeway between Corkum's Island and the mainland. The narrow constriction located at the mouth of the cove causes water to enter and leave this region as a tidal jet. A long ebb tide and a short flood tide result in marked differences in tides between the cove and Lunenburg Bay (Dowd 1991).

Upper South Cove can be divided into two regions based on tidal excursion (Dowd 1991). Water in the inner half of the cove will not be flushed out on a single tidal cycle; however, water in the outer cove region, defined by a midpoint ~1.4 km from the cove mouth, is renewed with each tide. Sediment deposition in the inner cove is likely controlled by the velocity distribution and by the asymmetry of the tide, which together cause a headward residual motion of sediment. As a result, the inner cove is a region of net deposition of fine sediments, while sediment near the tidally scoured entrance contains higher proportions of sand.

In situ testing of sediment stability may result in realistic measures of the erodibility of sediment; however, difficulties arise in the establishment of dominant factors involved. In order to delineate the effect of biofilms on the erodibility of sediment, the inner half of the cove was chosen since little variation in physical properties, such as sediment grain size and porosity, exists in the sediment. Sediment chlorophyll is generally high in this shallow region as light penetrates to the sediment–water interface (Grant et al. 1995).

Sediment in the inner cove is characterized by unconso-

lidated muds composed of 20–30% silt and clay (Grant et al. 1995). The sediment is highly pelletized with an organic content of ~22% and surface porosities of up to 87%. The average current in the cove is 0.12 m s^{-1} . Resuspension of fine material occurs at peak flows of $0.3\text{--}0.6 \text{ m}^{-1} \text{ s}$ during flood tide (Emerson et al. 1994). Observations made by Scuba in the cove and other poorly flushed embayments along the southeastern shore of Nova Scotia (northwest arm) reveal the occurrence of similar gel muds. Sea Carousel deployments performed on dredge material dumpsites in Miramichi Bay, New Brunswick, and under fish pens in Deep Cove, Maine, also reveal the presence of chlorophyll-containing gel muds. Therefore, the results of this study may be applied to environmental issues concerning the stability and transport of gel muds at dumpsites and aquaculture sites.

Methods

Seven stations were chosen along a transect extending over the inner half of Upper South Cove, as well as an additional station located outside the cove in Lunenburg Bay, Nova Scotia (Fig. 1). The erodibility of the sediment at these stations was determined by use of the Sea Carousel, an in situ benthic annular flume (Amos et al. 1992a), from 16 to 19 October 1993. Duplicate deployments of the Sea Carousel were performed at Sta. 3.

The Sea Carousel—Sea Carousel has a radius of 1.0 m, an annulus width of 0.15 m and a height of 0.30 m. A 0.35-hp motor, powered from the surface, drives a movable lid. Eight small paddles, attached below the movable lid, induce flow in the annulus at the onset of lid rotation. A skirt is situated on the outer wall of the annulus and standardizes penetration of the flume into the seabed.

Optical backscatter sensors (Downing and Beach 1989) were located inside (0.03 and 0.18 m above the skirt) and outside the annulus to measure ambient and resuspended solids. A window was situated in the inner flume wall, through which an underwater videocamera recorded erosion of the seabed. Azimuthal and vertical components of flow within the annulus were recorded with a Marsh-McBirney electromagnetic current meter. Data were stored on an underwater storage module and intermittently downloaded to a surface computer. The speed of the rotating lid was increased stepwise at 10-min intervals to increase near-bed flow and, thus, shear velocities. Shear velocity values were derived from lid speed as outlined in Amos et al. (1992a). These calculations were based on previous measurements made using an omnidirectional, flush-mounted, hot-film probe and on particle velocity profiles obtained through video observations.

A sampling port was situated 0.2 m above the flume skirt at a height similar to the upper optical backscatter sensor. During the deployment, water samples were collected from this port with the aid of a foot pump, attached to a 0.25-inch (i.d.) tygon hose. The volume of the hose was flushed before each water sample was collected.

Water samples—Water samples containing eroded material were collected at each speed increment, 2 min after the flow was increased, and analyzed for suspended particulate

matter (SPM), chlorophyll, and pheopigment. SPM was determined gravimetrically through filtration. Whatman glass-fiber filters (GF/C) were dried at 55°C for 48 h and subsequently desiccated for 2 h. An isotonic solution of ammonium formate was used to rinse the filters to remove salts. Chlorophyll was measured by fluorescence in acetone extraction using a Turner Designs model 10 fluorometer (Parsons et al. 1984).

Sediment cores—Replicate 60-ml syringe cores (i.d. 2.6 cm, length of 6 cm) were taken from a Van Veen Grab sample collected at each station located inside the cove. One core from each station was analyzed for bulk density by X-ray computed tomography using a GE Hilite Advantage CT scanner (Amos et al. 1996b). Tomogram-averaged bulk density measurements were made every 1.5 mm (min. thickness of tomogram slice) in the upper centimeters of the sediment column. Below this depth, 1.5-mm tomograms were made at depth intervals of 5 mm. Bulk density values were derived by converting Hounsfield units to CT scanner values and then transforming the CT values to sediment bulk densities. The correlation coefficient for a calibration between CT values and sediment bulk density was 0.992. The spatial resolution of this technique is 0.06 mm^3 , yielding results applicable to the scale of the biofilm present in this study.

The topmost 1 and 2 mm of a second core collected from each station were analyzed for both chlorophyll and pheopigment concentrations, since the chlorophyll maximum was generally above a depth of 2 mm in the sediment. Slices of each sediment layer were cut in 1-mm depth intervals. Each layer was placed in 10 ml of 90% acetone:water solution, contained in centrifuge tubes, and stored for 24 h in a cold and dark refrigerator. These samples were then centrifuged at 2,000 rpm for 5 min. Chlorophyll and pheopigment concentrations of the supernatant were determined fluorometrically according to Parsons et al. (1984). The values for the 1- and 2-mm sediment slices of each core were averaged. The surface topography of the sediment cores may have influenced the sediment component concentration of the 1-mm surface interval, limiting its use as an indicator of sediment erodibility. The remaining core was sectioned in 1-mm slices to a depth of 15 mm, then in 1-mm slices every 5 mm, and finally in 1-mm slices every 10 mm thereafter.

Each 1-mm slice of a third core collected from each station was split and analyzed for particulate organic matter and carbohydrate concentrations. One-half of each slice was dried at 55°C for 48 h and processed with a Perkin-Elmer CHN 2400 elemental analyzer to determine particulate organic carbon (POC) and particulate nitrogen (PN). The other half of each sediment layer was analyzed for colloidal and bulk carbohydrate using a phenol-sulphuric acid method (Dubois et al. 1956) modified for sediments (Lui et al. 1973). The half-slices were placed in test tubes acid washed with 10% HCl and rinsed 7 times with SuperQ water. The extraction process was modified for analysis of carbohydrates in marine sediments by using a 30 ppt saline solution instead of distilled water (Underwood et al. 1995). The test tubes were shaken thoroughly. The samples were centrifuged for 10 min at 2,000 rpm after an extraction period of one hour. The supernatant (colloidal carbohydrate fraction) from each

Table 1. Sediment biofilm measurements of the topmost 2 mm of single cores collected at Sta. 3, 5, 6, 7, 8, and 9 in upper South Cove (station locations indicated by number in Fig. 1).

Sediment component	Sta.					
	3	5	6	7	8	9
Station depth (m)	3.5	5.2	6.5	3.3	8.5	6.1
Station distance along cove (km)	0.13	0.23	0.46	0.67	0.9	1.3
Chlorophyll ($\mu\text{g ml}^{-1}$)	5.12	3.64	2.32	4.47	1.97	2.63
Pheopigment ($\mu\text{g ml}^{-1}$)	12.2	12.7	11.5	12.4	11.8	9.94
Chlorophyll:pheopigment	0.42	0.29	0.21	0.36	0.17	0.27
Colloidal carbohydrate (mg ml^{-1})	0.14	0.07	0.04	0.1	0.06	0.07
Bulk carbohydrate (mg ml^{-1})	1.93	2.45	1.84	1.51	2.01	2.66
POC (mg ml^{-1})	1.8	2.59	1.97	2.14	2.08	2.06
PN (mg ml^{-1})	0.18	0.25	0.21	0.23	0.22	0.21
POC:PN	10	10.2	9.5	9.4	9.7	10
C:Chl	352	711	849	479	1,054	783
Bulk density (kg m^{-3})	950	895	812	954	1,006	1,150
Inorganic content (%)	77.3	73.9	75.7	82.2	77.2	79.3

sample was transferred to a set of clean test tubes. One milliliter of 5% phenol and 5 ml of concentrated sulphuric acid were added to each supernatant and sediment pellet (bulk carbohydrate fraction). Each sample was shaken, allowed to stand for 1 hr, analyzed using a spectrophotometer at 485 nm, and standardized against a calibration curve of glucose equivalents. The values for the 1-mm and 2-mm sediment slices of each core were also averaged.

A Siemens diffractometer 500 was used to determine the mineralogy of the clay fraction ($<2 \mu\text{m}$) collected from surface bulk samples of the grab cores. Talc was the standard against which kaolinite, chlorite, and mica were determined, and corundum was the standard for quartz and plagioclase.

Erosion measurements—The critical shear stress (U_{*crit}) for erosion in the Sea Carousel was determined as the x -intercept of a regression analysis of SPM vs. $\log U_*$ fitted with a logarithmic function. Peak erosion rates were obtained from a plot of a 10-s time-averaged time-series of erosion rates. The optical backscatter data collected at each station were calibrated with the corresponding SPM concentration of the water samples. Instantaneous erosion rates were calculated by standardizing the SPM concentration by the volume and area of the flume and then dividing by the time difference between optical backscatter readings. This continuous dataset was then time-averaged at a 10-s interval. The peaks of the erosion rates were obtained from the time-series plot. They occurred at the onset of each speed increment (see Fig. 4). Net erosion rates were calculated as the differential concentrations of the eroded sediment variables of the water samples divided by the elapsed time and normalized to unit bed area. Regressions were used to correlate the sediment biofilm components to erosion thresholds, peak erosion rates, and net erosion rates.

Results

Biological and physical sediment predictors—The sedimentary column of the cores collected from stations in the cove consisted of an oxidized layer of golden brown, loosely

bound, silty clay overlying black, reduced sediment occurring at a depth of ~ 2 mm. Table 1 shows the concentrations of chlorophyll, pheopigment, colloidal carbohydrate, bulk carbohydrate, POC, and PN measured within the topmost 2 mm of Sta. 2–9 located in the inner half of the cove (Fig. 1). Sediment characteristics of Sta. 1, located outside the cove are discussed in a later section.

A negative relationship was observed between sediment chlorophyll concentration and the depth of station ($r^2 = 0.891$, $P = 0.005$), whereas a positive relationship was observed between sediment colloidal carbohydrate and chlorophyll content ($r^2 = 0.826$, $P = 0.012$). No significant relationships were found between chlorophyll or colloidal carbohydrate and any other sediment properties listed in Table 1. Pheopigment, bulk carbohydrate, POC, and PN showed little variation in concentration in the surface sediment across stations.

Relationship between sediment erodibility and sediment biofilm predictors—Regressions of U_{*crit} (determined from Sea Carousel deployments) vs. the sediment biofilm constituents revealed that chlorophyll content ($r^2 = 0.948$, $P = 0.001$; Fig. 2A), colloidal carbohydrate content ($r^2 = 0.854$, $P = 0.008$; Fig. 2B), and depth of station ($r^2 = 0.843$, $P = 0.01$; Fig. 2C) were significantly related with U_{*crit} . Duplicate deployments of the Sea Carousel at Sta. 3 revealed that the coefficient of variation for the mean U_{*crit} value was 5.42%.

Figure 3 is a time-series plot of current speed, SPM, and peak erosion rates measured at Sta. 9. The continuous dataset of SPM and peak erosion rates were derived from the calibrated optical backscatter sensors. The peak erosion rates were negatively related with sediment chlorophyll ($r^2 = 0.778$, $P = 0.02$), colloidal carbohydrate content ($r^2 = 0.778$, $P = 0.02$), and U_{*crit} ($r^2 = 0.691$, $P = 0.04$).

Net erosion rates showed a negative relationship with sediment chlorophyll concentrations ($r^2 = 0.875$, $P = 0.006$; Fig. 4A), sediment colloidal carbohydrate concentrations ($r^2 = 0.774$, $P = 0.021$; Fig. 4B), and U_{*crit} ($r^2 = 0.786$; $P = 0.019$; Fig. 4D) and showed a positive relationship with the

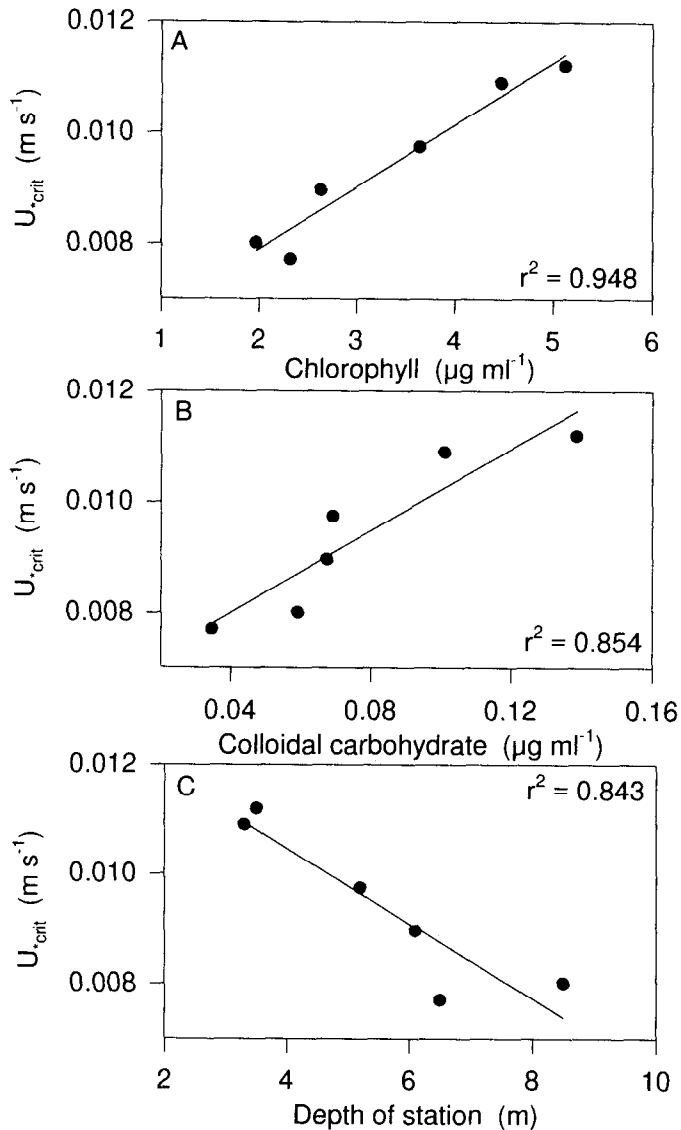


Fig. 2. Regressions showing the relationship between U_{*crit} and sediment chlorophyll concentration (A), sediment colloidal carbohydrate concentration (B), and depth of station (C).

depth of the station ($r^2 = 0.982$, $P < 0.001$; Fig. 4C). The coefficient of variation determined for the mean erosion rate measured from duplicate deployments of the Sea Carousel at Sta. 3 was 9.2%.

Vertical profiles of bulk density and chlorophyll—The vertical gradients in bulk density measurements of stations in the cove became more structured toward the inner termination of the cove (Fig. 5). These profiles were divided into three distinct sediment layers: a biogenic layer, a consolidating layer, and an underlying uniform layer. The biogenic layer was characterized by bulk densities $< 1,000 kg m^{-3}$ (positively buoyant). This buoyant layer became thinner seaward through the estuary. The consolidating layer ranged between 1,000 to 1,100 $kg m^{-3}$ and extended to depths of 15 mm at the inner station. The consolidating layer of Sta.

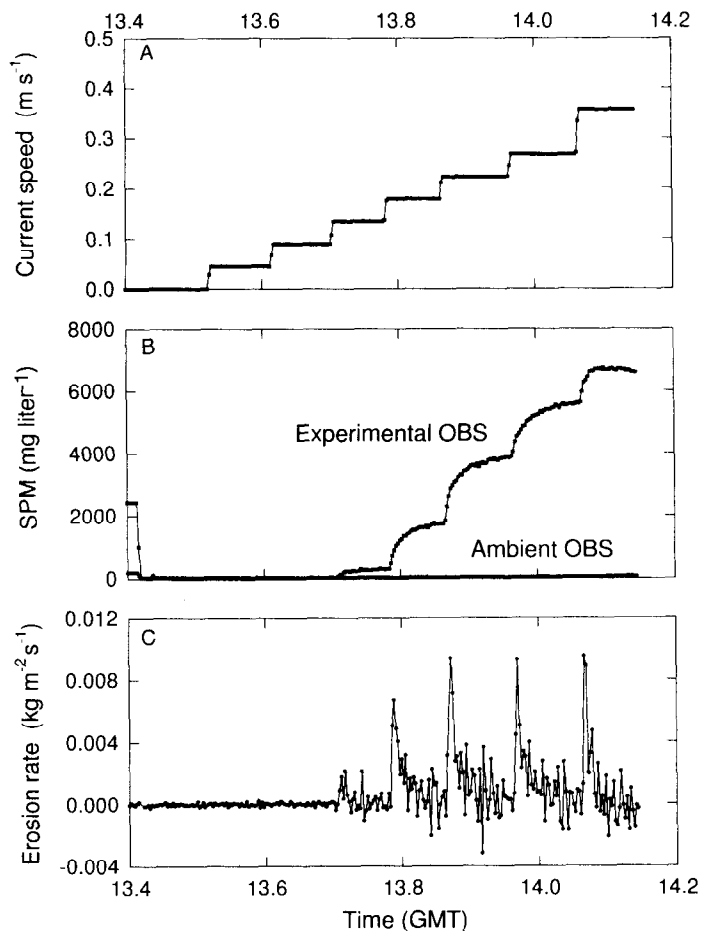


Fig. 3. Time-series plots of current speed (A), SPM (B), and peak erosion rates (C) obtained from a Sea Carousel deployment at Sta. 9 in Upper South Cove.

9 reached a maximum bulk density value of 1,300 $kg m^{-3}$ at a shallow depth of 11 mm. This station is located in the cove center or the transition zone defined by tidal excursion.

Histograms of the bulk density distributions of the surface 15 mm of Sta. 3 (derived from the catscan analysis) show the replacement of this positively buoyant material by a more homogeneous material of higher bulk density (Fig. 6). The absence of peaks at densities approaching zero (gas) may be due to the integration of gas and biofilm material. The gas voids (necessary to cause positive buoyancy) were probably smaller than the voxel height (1.5 mm). Dark spheres observed in the tomogram images may be gas bubbles, but were typically $< 1 mm$ in diameter. A core of a sediment wedge and air was used to calibrate the CT values to bulk density (Amos et al. 1996b). A histogram of the bulk density distribution of the sediment wedge taken midcore showed two strong peaks representing the air and sediment components.

The bulk density profiles show that there is a general increase in surface bulk density from the inner to the central region of the cove. The positively buoyant zone corresponds to the zone of high chlorophyll gradients near the sediment surface (Fig. 7), indicating an association between buoyancy and biofilm production. The high surface chlorophyll concen-

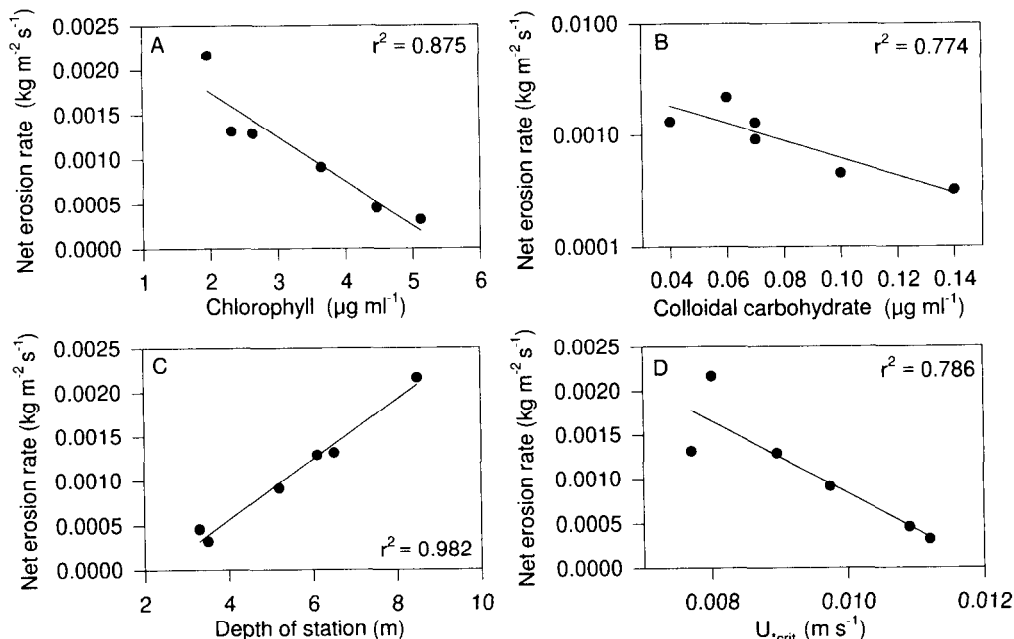


Fig. 4. Regressions showing the relationship between net erosion rate and sediment chlorophyll (A), sediment colloidal carbohydrate (B), depth of station (C), and U_{*crit} (D).

trations and high ratios of chlorophyll to pheopigment observed at shallow Sta. 3 and 7 (Table 1) suggest greater growth activity at these stations relative to the remaining stations.

Although U_{*crit} was not significantly correlated with bulk density, bulk density in general is positively related to erosion threshold. Fig. 8 shows this positive relationship of combined results from six seabed stability studies using the Sea Carousel in widely varying environments (Amos et al. 1996a; Sutherland 1996). The erosion thresholds reported in this study lie at the lower end of the threshold and bulk density values of

this combined dataset. Although the sediment chlorophyll and carbohydrate contents may explain the variation in U_{*crit} , the low bulk density values or buoyant properties may be responsible for the generally low erosion thresholds.

Discussion

Biological and physical properties of the sediment—Several physical and biological properties of the sediment surface were measured in order to determine a suitable quantitative predictor of the erodibility of sediment of the cove.

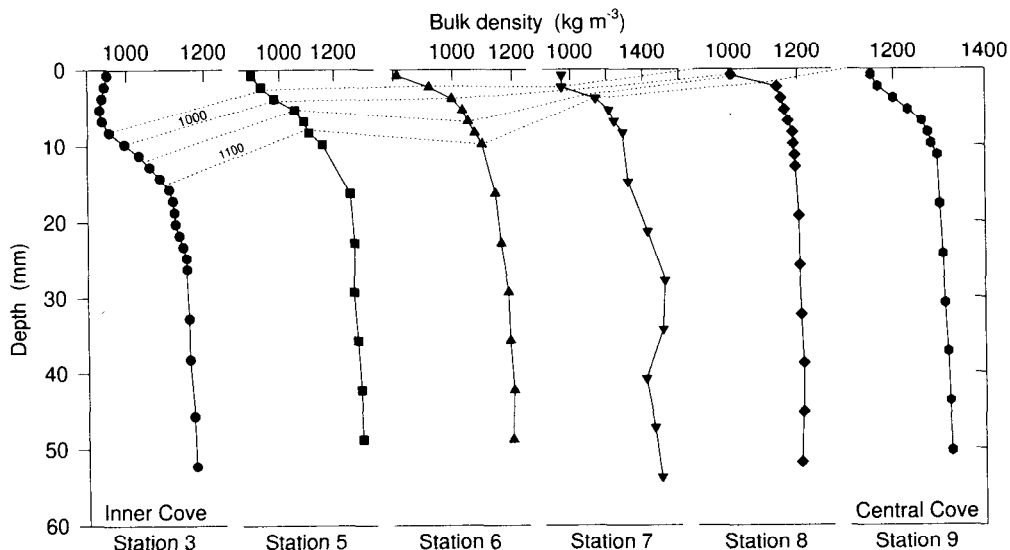


Fig. 5. Bulk density profiles of Sta. 3, 5, 6, 7, 8, and 9 located along a transect in Upper South Cove. Dotted lines represent isopycnals. Station locations are indicated in Fig. 1.

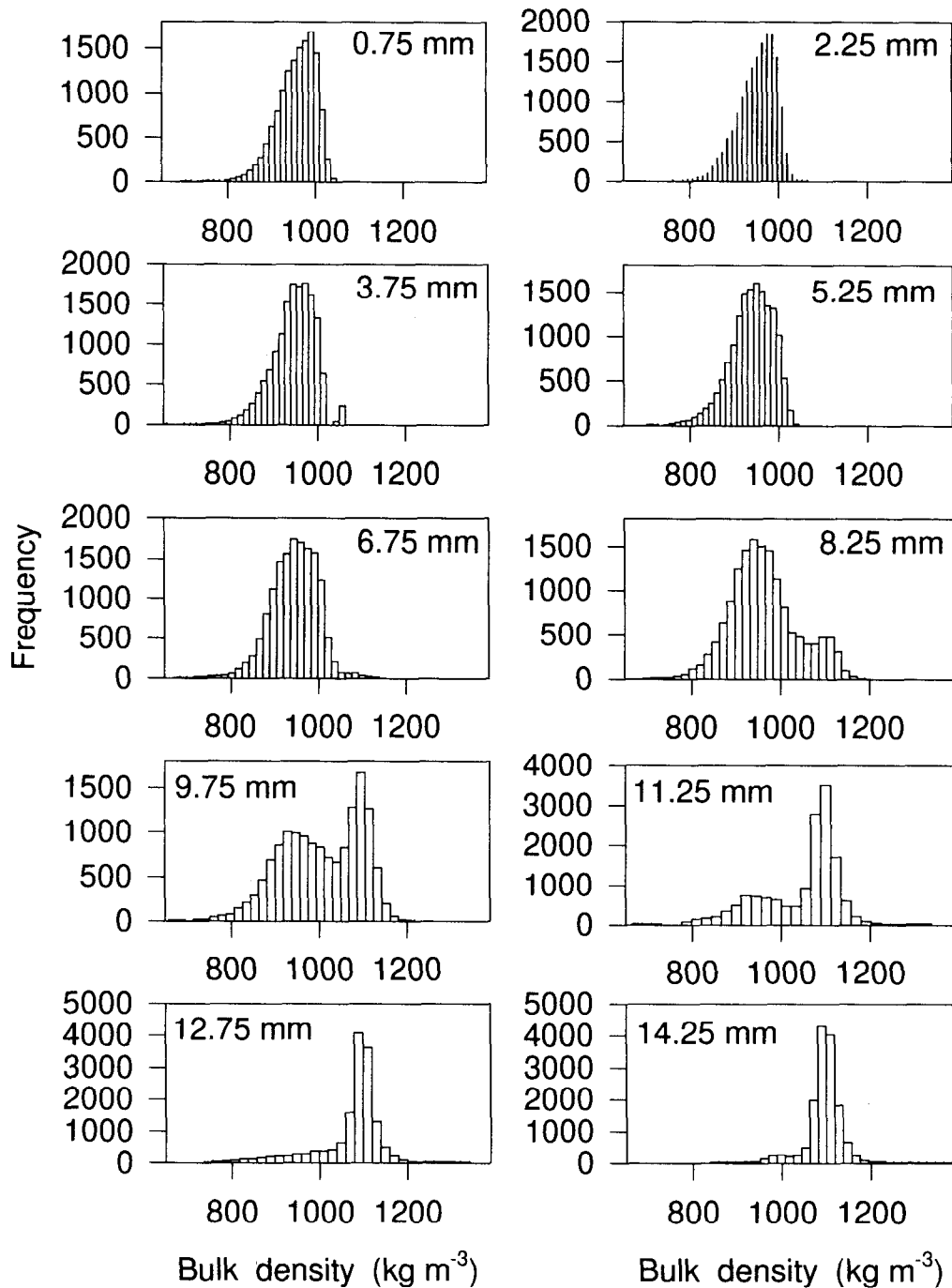


Fig. 6. Bulk density histograms of the uppermost 15 mm of a sediment core collected at Sta. 3 in Upper South Cove. Bulk density measurements were obtained through catscan analysis.

Little variation in the physical properties of the surface sediment layer, such as bulk density, mineralogy, and grain size, was observed for the stations located in the inner half of the cove (Fig. 1). Diver observations revealed that a gel-like material formed a blanket over this region consisting of unconsolidated muds.

The accumulation of fine particles in the sediment of the inner half of the cove may be influenced by limited tidal excursion (Dowd 1991), removal and biodeposition of the

clay material by bivalves (Haven and Morales-Alamo 1966; Kautsky and Evans 1987), scavenging of fine particles by a hydrodynamically active fluff layer (Stolzenbach et al. 1992), and subsequent biostabilization of the fine fraction at the sediment-water interface by benthic diatoms (Mayer et al. 1985). Approximately 90% of the inner half of the cove is flushed every 2–4 d (Dowd 1991), permitting the retention of fine particles relative to the outer half of the cove, which is flushed tidally with less turbid oceanic water. In addition,

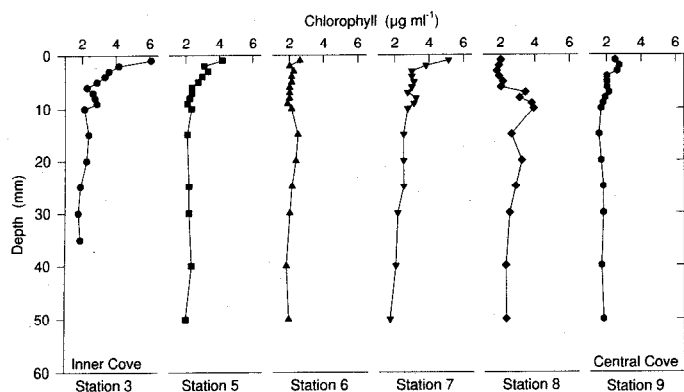


Fig. 7. Sediment chlorophyll profiles of Sta. 3, 5, 6, 7, 8, and 9 located along a transect in Upper South Cove. Station locations are indicated in Fig. 1.

the sedimentation of fine particles between 1 and 3 μm has been reported to be enhanced by bivalve suspension feeders (Haven and Morales-Alamo 1966). This small-sized inorganic fraction would normally settle very slowly in surrounding areas (Simpson 1982). The colonization and stabilization of the organic-mineral aggregates supplied to the sediment-water interface could occur through diatom migration.

The sediment colloidal carbohydrate and chlorophyll content exhibited the largest variation of the sediment biological properties measured in the cove (Table 1). The variation in sediment chlorophyll was probably due to light availability at the varying depths. The transect of stations in the cove ran from the shallow inner termination (3.5 m) to a depositional basin (8.5 m). The colloidal carbohydrate fraction is a measure of extracellular polymeric substances (EPS) or mucopolysaccharides secreted by diatoms for locomotion. It is not surprising that the sediment colloidal carbohydrate concentration showed a positive relationship with sediment chlorophyll concentration, as found in other biostabilization studies (Underwood and Paterson 1993). Little variation in the biological properties, such as pheopigment, bulk carbohydrate, POC, and PN, was also observed for the surface sediment in this region, suggesting limited usefulness of such properties as indicators of sediment erodibility (Table 1). However, variations in sediment chlorophyll and carbohydrate showed strong trends in sediment erodibility.

Relationship between U_{*crit} and sediment biofilm predictors—Both chlorophyll and colloidal carbohydrate content exhibited a positive relationship with U_{*crit} at stations in the cove (Fig. 2A,B). Grant and Gust (1987) stressed that photopigments are only an indication of the microbial biomass responsible for increasing intergrain binding and suggested that extracellular polymeric substances may serve as a more predictive assay of sediment stability. Underwood and Paterson (1993) demonstrated that colloidal carbohydrate and sediment water content were the best biochemical predictors for incipient erosion of intertidal sediment. In this study, a stronger relationship was observed between U_{*crit} of subtidal sediment and chlorophyll relative to that with colloidal carbohydrate, and may be due to the fact that carbohydrates are

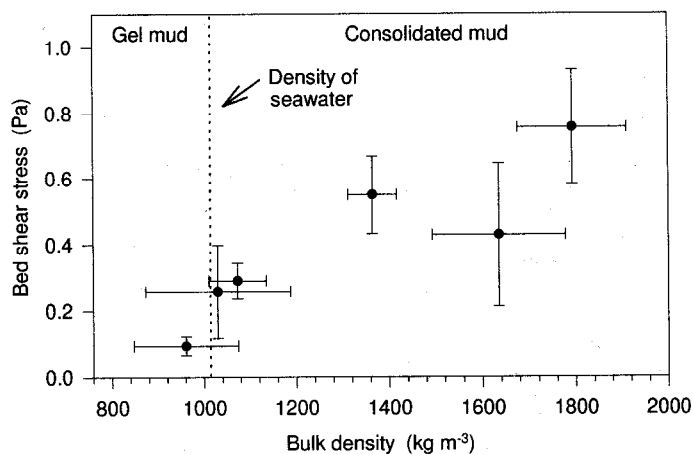


Fig. 8. The relationship between critical bed shear stress (Pa) and bulk density (kg m^{-3}). This combined dataset was collected in six different regions using the Sea Carousel. MS, Manitoounuk Sound; HE, Humber Estuary; MB, Miramichi Bay; HH, Hamilton Harbour; FR, Fraser River; LB, Lunenburg Bay.

also produced by nonpigmented organisms. Other investigators have found that pigment concentrations are useful predictors of U_{*crit} (Grant and Gust 1987; Madsen et al. 1993). Madsen et al. (1993) found that the pigment-derived biovolume of motile diatoms, responsible for laying down mucous trails through active migration, was the only measured variable in their study that correlated significantly with U_{*crit} .

The sampling depth of biofilm components in the sediment column could affect the sensitivity of the biofilm measurements used as predictors of sediment erodibility. Madsen et al. (1993) remarked that the total chlorophyll and colloidal carbohydrate contents may have been diluted by sampling the uppermost 5 mm of the sediment column. Diatom biofilms have been reported to be limited to the topmost 2 mm of sediment (Paterson 1989). In this study, the sediment chlorophyll maximum was often limited to the upper millimeters of the sediment column. A depth of 2 mm was sampled for chlorophyll and carbohydrate content to avoid the dilution of a near-surface signal by the diatom-free underlying sediment.

The erosion of larger flake-shaped organic-mineral aggregates or laminae associated with well-developed biofilms at the shallower stations suggests a biogenic modification of the effective particle size and shape. Low-temperature scanning electron micrograph (Underwood and Paterson 1993; Paterson 1995) and thin-section (Frankel and Meade 1973; Wachendorfer et al. 1994) techniques have shown that established biofilms consist of a continuous fabric of mineral particles embedded in EPS. The extent to which EPS pervades the sediment column would influence the degree to which the size, shape, and density of aggregates or physical properties become altered. However, conventional methods of sediment size analysis result in the destruction of these biomediated aggregates and, according to Johnson (1974), create artifacts. Results of standard sedimentological methods, such as grain size analysis, do not incorporate the glueing effect of EPS and the associated changes in sediment

characteristics and may not correlate well with sediment erodibility. Therefore, conventional sedimentological methods measuring sediment geotechnical properties may not be useful in determining factors responsible for sediment erodibility in situations of well-established biofilms.

Relationship between erosion rate and sediment biofilm predictors—Although net erosion rates were correlated with the surface-sediment colloidal carbohydrate and chlorophyll content in the cove (Fig. 4A,B), the calculation of net erosion rates incorporated the erosion of the sediment column to a depth well below the 2-mm biostabilized surface layer. The initial stages of the erosion process would therefore be controlled by surface biomediated binding, but the net erosion rate would also be a function of the microfabric of the underlying sediment. This microfabric would depend collectively on the history of bed deposition, preservation of biofilm at depth, and consolidation processes.

In this study, the values of net erosion rates varied across stations by a factor of 7, while the values of U_{*crit} and peak erosion rates varied by a factor of 2 and 4, respectively. The large variations in erosion rates may have been influenced more by the sediment properties of the underlying sediment than by the shallow chlorophyll gradients (Fig. 7). A quiescent environment should favor a steep chlorophyll gradient within the sediment column (de Jonge and de Jonge 1995). Paterson et al. (1994) found that the sediment underlying the biofilm was more easily eroded than was the surficial biostabilized layer. Although erosion threshold is a critical measurement of erodibility, erosion rate may serve as a more suitable indicator of biophysical controls on erosion (Grant and Daborn 1994).

Vertical profiles of bulk density and chlorophyll in the sediment—The thickening of the buoyant surface biogenic layer landward through the cove could be due to an increase in sedimentation rates in this direction (Fig. 5). The station transect along the central axis of the cove (Fig. 1) is located in an area of particle retention (Dowd 1991). However, the classical extinction of chlorophyll with depth in sediment at Sta. 3, 5, and 7 suggests that this low-density surface layer was an established structure and not a recently deposited fluff layer (Fig. 7). Video observation of the erosion trials confirms that an established biofilm was present at Sta. 3. Biofilm growth may have succeeded the sedimentation rates of fluff material following active migration of diatoms to the illuminated accreting fluff-water interface. In this case, the accreting surficial sediment would then be considered to be a biogenic growth structure, not a sedimentary unit (Wachendorfer et al. 1994). The low bulk density layer may persist since the macrostructure or "open card house" arrangement of unconsolidated muds is easily influenced and managed by the larger motile diatoms (Paterson 1994).

Trapped oxygen bubbles generated by actively photosynthesizing benthic diatoms in the surficial sediment layer appear to be responsible for positively buoyant bulk density values. The colonization of diatoms and associated production of EPS within the aggregates would increase adhesion and prevent this low bulk density fluff layer from floating. The CTs revealed numerous tiny dark spheres (0.5–1 mm in

diam) in the upper centimeter of Sta. 3 that could represent minute oxygen bubbles. During the incubation of *Nitzschia curvilineata* on sediment, oxygen bubbles of up to 1 mm in diameter were trapped within the biofilm (Sutherland et al. 1998). Flat oxygen bubbles 2–10 mm in diameter have also been observed to occur 1 mm below the surface of "blister" mats (Jorgensen et al. 1983). The consumption of oxygen by diatoms during dark periods in these mats caused a rapid depletion of the oxygen pools. Infauna and bacteria may also contribute to the rapid depletion of oxygen bubbles trapped in biofilms. Alterations in bulk density could take place on the timescales as short as seconds if millimeter-size bubbles were liberated from the biofilm sediment through disturbance events, such as finning of groundfish or clapping of scallops. Therefore, the bulk density of biofilms containing trapped oxygen bubbles may fluctuate with the diel photosynthetic cycle of diatoms and with the occasional release of bubbles from the mat, and may consequently impact the erodibility of sediment.

All submerged objects are subject to buoyancy in a fashion defined by the Archimedes principle. In terms of seabed stability, it is the apparent (buoyant) weight of sediment that balances the drag force at the point of erosion. Adhesion and biostabilization add to this apparent weight (by increasing resisting forces of the bed), whereas gas bubbles reduce it through positive buoyancy. At the limit, the bed should be able to sustain a positive buoyancy equal to, but not greater than, the drag force for erosion; otherwise, the bed would fail simply through the action of the buoyant force. Buoyant forces below this limit may be perceived as reducing the drag force required for bed erosion and hence the apparent strength of the bed. Thus, unless the buoyant force for sediments of low bulk density is known, errors in determining U_{*crit} due to bubble formation may be large.

Significant trends in erosion threshold and rate were found that were strongly biofilm dependent. Biological sediment constituents, such as chlorophyll and colloidal carbohydrate, were useful predictors of surface-erosion measurements, such as U_{*crit} and peak and net erosion rates. Net erosion rate appeared to be the most important indicator of sediment erodibility. Although the variations in sediment erodibility were explained by the variations in sediment chlorophyll and carbohydrate contents, the low bulk density layer may be responsible for the low range of U_{*crit} values reported here. The positively buoyant properties of this surface layer may reduce U_{*crit} through the lift forces (elimination of sediment weight) of oxygen bubbles produced through biofilm photosynthesis. Because the low bulk density gradient was inversely related to the chlorophyll gradient, the existence of a positively buoyant layer in the topmost millimeters of the sediment column may have been held in place by the biofilm fabric. Adhesive (chlorophyll and carbohydrate) and cohesive (particle-to-particle attractions) properties tend to dominate in sediments with low bulk densities. Finally, future studies should examine the effect of oxygen bubble production, depletion, and liberation within biofilms on the physical properties of surficial sediments and the consequent influence on sediment erodibility.

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