Biological Cohesion as the Architect of Bed Movement Under Wave Action

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Abstract    Cohesive extracellular polymeric substances (EPS) generated by microorganisms abundant on Earth are regarded as bed “stabilizers” increasing the erosion threshold in sedimentary systems. However, most observations of this phenomenon have been taken under steady flow conditions. In contrast, we present how EPS affect the bed movement under wave action, showing a destabilization of the system. We demonstrate a complex behavior of the biosedimentary deposits, which encompasses liquefaction, mass motion, varying bed formations and erosion, depending on the amount of EPS present. Small quantities of EPS induce higher mobility of the sediments, liquefying an otherwise stable bed. Bed with larger quantities of EPS undergoes a synchronized mechanical oscillation. Our analysis clarifies how biological cohesion can potentially put coastal wetlands at risk by increasing their vulnerability to waves. These findings lead to a revised understanding of the different roles played by microbial life, and their importance as mediators of seabed mobility.

Plain Language Summary The term “ecosystem engineering” emerged in the 1990s, which commonly refers to the activities of larger organisms like mangroves. However, while people think that bigger organisms generate bigger potential engineering effects, there may be microscale organisms who can result in significant impacts on the ecosystems through their number rather than their size. Currently, cohesive extracellular polymeric substances (EPS) generated by microorganisms have been widely reported to increase the threshold for sediment erosion by flowing water, which is known as “biostabilization.” However, we demonstrate that this is not the case under wave action. On the contrary, EPS show a destabilization effect of the system, turning an otherwise stable sedimentary bed into “soup.” Our analysis clarifies how neglecting even low content of EPS can result in inaccurate prediction of the bed stability and coastal safety under wave action. The risk of bed liquefaction is expected to pose potential threats to wetlands where microbial communities occupy habitats while the production of EPS is much higher. The misinterpretation of the vulnerability of wetlands when exposed to waves could put the existing ecosystems at risk, considering that these ecosystem services are valued at about US$10,000 per hectare.

1. Introduction

Microbial life and their secreted extracellular polymeric substances (EPS) serve as cooperative “ecosystem engineers,” which strongly influence sediment texture in both the earliest and modern sedimentary environments (Davis et al., 2006; Marani et al., 2007; Mariotti et al., 2014; Noffke et al., 2006). In fact, the stabilizing effect of EPS matrix in surficial biofilms has been widely reported over the last 20 years, and is known as “biostabilization” inhabiting depositional systems (Chen et al., 2017a; Gerbersdorf & Wieprecht, 2015; Packman, 2013; Paterson et al., 2018; Taylor & Paterson, 1998). Despite growing research interest, uncertainties and debates remain on some fundamental issues, such as the various behavior under different hydrodynamic systems and scales (Tolhurst et al., 2002). For instance, the studies which support the stabilizing effect rely almost completely on aquatic environments with steady flow conditions, where surficial erosion and bedforms are the primary concerns (~cm in upper layers) (Le Hir et al., 2007; Parsons et al., 2016; Van Colen et al., 2014; Vignaga et al., 2013). In the marine environment, however, wave action may induce liquefaction, where a certain depth of a sedimentary bed, ranging from tens of centimeters...
to meters below the bed surface, turns into a liquid state (Sumer et al., 2006). This can cause a powerful sediment flushing that moves downslope and across the shelf offshore (Craig et al., 2020; Mcanally et al., 2007; Mountjoy et al., 2018). Bed liquefaction describes quite a different process from surficial erosion, and is the cause of many catastrophic coastal disasters globally (Chung et al., 2006; Franco, 1994; Travis, 2005). What is less clear is whether microbiology acts as a stabilizer of the bed, helping to limit the potential for liquefaction, or not.

The literature on liquefaction in engineering is extensive, spanning more than 50 years (Lewis & Partridge, 1967; Nichols et al., 1994; Sumer, 2009). However, microbiological effects have not been widely recognized in liquefaction-related studies, despite the fact that the upper oceanic sediment, down to 50 cm depth, holds the majority of bacteria and archaea existing on Earth (5 × 10^28 cells; Danovaro et al., 2015; Flemming & Wuertz, 2019). A liquefaction zone was reported at a wetland restoration site, with abundant microalgae as primary productors supporting fish habitats, which caused severe damage to the ecosystem (Iwakuni, Japan, September 2016). The liquefaction had not been predicted based on experimental data using grains that were free from biological material. It seems that biological activities could possibly affect the risk of liquefaction, however the mechanism remains unknown. The unusually limited attention paid to biological cohesion and its effect in wave induced liquefaction probably reflects the multidisciplinary nature of the problem, but the role of EPS in geo-engineering systems is now being more widely recognized (Craig et al., 2020).

Experiments were conducted in a wave flume to examine the behavior of the bed as the EPS content in a well-sorted fine sand was progressively increased. Liquefaction was judged from the temporal variation of pore pressure, and linked to the deformation of the sediment-water interface determined using time-lapse photography. Sediment erosion and suspension was measured using an optical back-scatter turbidity sensor. This study provides the first systematic experiments to explore the effect of the pervasive ‘background’ EPS on the susceptibility of sandy bed to liquefaction, in contrast to the previous investigations that focused on the “biostabilization” of surficially accumulated EPS under steady flow conditions.

2. Materials and Methods

2.1. Experimental Setup

The present work describes laboratory experiments conducted in a 80 m-long, 0.5 m-wide, and 1.5 m-high laboratory wave flume, where a pit filled with a 0.25 m-thick sediment bed was created to examine the influence of pervasive biological cohesion on bed susceptibility to wave-induced liquefaction (see Figure S1a for information about the flume). The sediment bed was composed of a mixture of well-sorted fine sand (\(D_{50} = 0.165\) mm, see Figure S2 for the grain size distribution) and EPS with different quantities (0%–0.1% by weight, Table 1). Pore-water pressure and water surface elevation were measured by pressure sensors and wave gauges, respectively (Figure S1b). Xanthan gum, which is a bacterial polymer, shares chemical similarities with a wide variety of naturally occurring EPS, and is widely used as a substitute for EPS in marine ecology, soil science, and sediment stability research (Craig et al., 2020; Garci A-Ochoa et al., 2000; Van Colen et al., 2014; X. Zhang et al., 1996). Pretest bed samples were taken to determine the fraction of EPS (Table 1). The EPS extraction and measurements were based on the polysaccharide content. A sinusoidal input wave with a wave height of 0.12 m and period of 1.6 s was used for all test runs, in a water depth of 0.35 m. Video cameras were used to record the bed response, in addition to the pore-water pressure and water surface elevation measurements. Liquefaction was judged from the temporal variation of pore pressure, and linked to the deformation of the sediment-water interface determined using time-lapse photography. Sediment erosion and suspension was measured using an optical backscatter sensor (OBS 3+).

2.2. Preparation of the Bed

The sedimentary bed mixes are listed in Table 1 and range from 0% to 0.1% EPS (xanthan, see supporting information Text S1 for the EPS analysis). Sand-EPS mixtures used for experiments were made in the laboratory, by mixing natural dry sand and commercial xanthan with the determined content ratios. The xanthan (in a dry powder form) was first dissolved by agitation in water (one-part freshwater to four-parts sand/xanthan) for 10–20 min, after which any foam was removed from the surface of the solution. The liquid
xanthan was then added into the dry sand and stirred to form a uniform mixture. This resulted in a slurry, which was spread evenly, filling the pit to make a flat bed with a depth of 25 cm and length of 1 m (Figure S1b). The flume was then gradually filled with the required amount of freshwater (water depth of 0.45 m) and left for 20–22 h before the test was conducted. Here, note that since cohesion is enhanced by saline conditions, the effect may be greater in marine systems (Spears et al., 2008). Also note that the “abiotic” case is simply without added xanthan. It would be different if the situation without biofilms (which would require sterilization) would be compared to the one with biofilms.

2.3. Instrumentation

Three wave gauges (Yu Fan Technology Co, Chengdu) for recording water elevation were placed at the upstream edge of the pit to measure the incident wave height, the downstream edge to measure the wave height after passing the bed, and above the pore pressure sensors. The pressure transducers (HC-25, Rui-Heng Chang Tai Technology Co, Beijing) for measuring pore-water pressure were installed in the middle of the pit at three different depths (Figure S1b), z = 0.01, 0.09 and 0.23 m, where z was the vertical distance below the bed surface. An OBS 3+ (Campbell Scientific, Inc.) located 0.2 m downstream from the front edge of the pit and 0.035 m above the bed surface was used to measure the real-time suspended sediment concentration (the calibration of the OBS for the sand grains used in this study can be found in Figure S3). The monitoring range depends on sediment size, particle shape, and reflectivity. For the sediment used in this study, the maximum concentration was below 20 kg/m³, which was within the linear region of the OBS sensor (Figure S3). Pore-water pressure, water elevation and suspended sediment concentration (SSC) were measured simultaneously.

2.4. Time Development of EPP

The period-averaged excess-pore pressure, \( \bar{p} \) is calculated as:

\[
\bar{p} = \frac{1}{T} \int_{0}^{T} pdt
\]

where \( p \) is the excess-pore pressure at time \( t \) and \( T \) is the period for calculation. The value of the initial mean normal effective stress, \( \sigma_0 \) defined by:

<table>
<thead>
<tr>
<th>Test*</th>
<th>EPS (%)</th>
<th>Test duration (s)</th>
<th>Liquefaction (-)</th>
<th>( T_{bs}/T_{bb} ) (s/s)</th>
<th>( T_{es}/T_{eb} ) (s/s)</th>
<th>Final bed state (-)</th>
<th>Max SSC (g L(^{-1}))</th>
<th>Average SSC (g L(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0</td>
<td>1,580</td>
<td>No</td>
<td>—</td>
<td>—</td>
<td>R</td>
<td>6.51</td>
<td>3.59</td>
</tr>
<tr>
<td>2</td>
<td>0.005</td>
<td>1,500</td>
<td>Yes</td>
<td>23/58</td>
<td>1,303/523</td>
<td>R</td>
<td>7.94</td>
<td>2.17</td>
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<tr>
<td>3</td>
<td>0.01</td>
<td>1,800</td>
<td>Yes</td>
<td>11/23</td>
<td>1,772/469</td>
<td>R</td>
<td>10.61</td>
<td>2.58</td>
</tr>
<tr>
<td>4</td>
<td>0.02</td>
<td>1,550</td>
<td>Yes</td>
<td>13/28</td>
<td>—</td>
<td>F</td>
<td>19.17</td>
<td>7.03</td>
</tr>
<tr>
<td>5</td>
<td>0.05</td>
<td>1,470</td>
<td>Yes</td>
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<td>—</td>
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<td>3.19</td>
<td>1.71</td>
</tr>
<tr>
<td>6</td>
<td>0.1</td>
<td>1,550</td>
<td>Oscillation</td>
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<td>—</td>
<td>F</td>
<td>3.17</td>
<td>1.08</td>
</tr>
</tbody>
</table>

EPS, extracellular polymeric substances, represented by xanthan gum proxy. \( T \) is time and subscripts “bs” and “bb” refer to the bed surface and bed bottom, respectively. \( T_{bs}/T_{bb} \) is the ratio of the time to liquefaction in the two layers, reflecting how liquefaction first appears at the surface and progressively extends to the bed. Similarly, subscripts “es” and “eb” refer to the end of liquefaction at the surface and bed, respectively. The former is defined by the appearance of a rippled bed and the latter by the initiation of pore pressure dissipation at the bed bottom. The ratio \( T_{es}/T_{eb} \) indicates how the liquefaction gradually ends for bottom to top. In this study, only in the low EPS cases (Test 2 and 3), liquefaction stopped before the end of the test and ripples appeared. However, it should be noted that pore pressure dissipation can be reached for all liquefaction cases if time permitted. Final bed state is the state of the bed surface at the end of the test where F is a flat bottom and R is a rippled bed. SSC is the suspended sediment concentration measured using the optical backscatter sensor (OBS). All tests were run in a water depth = 0.35 m with a wave height = 0.12 m and wave period = 1.6 s.
Figure 1. Photographs of bed state during tests. (a) Test 1 (0% EPS), (b) Test 2 (0.005%), (c) Test 4 (0.02%), and (d) Test 6 (0.1%), looking in the side view of the flume and perpendicular to the direction of wave progression. Two bed states under a wave trough are given after 5 min (left column) and 25 min of wave action (right column). The length of the pit is 1 m. EPS, extracellular polymeric substances.

\[ \sigma_0 = \gamma' z \cdot \frac{1 + 2k_0}{3} \]

with, \( z \) is the depth from the bed surface/water-bed interface shown in Figure S1b. \( k_0 \) is the coefficient of lateral earth pressure at rest and the value is determined from Jaky’s equation, \( k_0 = 1 - \sin \phi \), where \( \phi \) is the friction angle (Lambe & Whitman, 1969). In this study, \( \phi \) of all sediment samples were measured by triaxial shear test, giving a mean value of 31°, which equates to a \( k_0 \) of 0.48. \( \gamma' \) was the submerged specific weigh of the sediment,

\[ \gamma' = \gamma_{\text{sat}} - \gamma \]

where \( \gamma_{\text{sat}} \) is the specific weight of the soil, and \( \gamma_{\text{sat}} = 19.8, 19.6, 19.0, 18.6, 18.3, 18.1 \text{ N/m}^3 \text{, for 0%, 0.005%, 0.01%, 0.02%, 0.05%, 0.1% EPS, respectively, and the value for } \gamma \text{ is 9.8. Therefore, } \sigma_0 \text{ for } z = 0.23 \text{ is 1.50, 1.47, 1.40, 1.33, 1.27, 1.25, for each EPS content, correspondingly. The bed is liquefied when } \rho \text{ exceeds } \sigma_0, \text{ and this criterion for the onset of liquefaction has been discussed in greater detail (Sumer et al., 2012).}

3. Results and Discussion

3.1. Abiotic Case

In the abiotic case, sediment moved as either bedload or as suspended load. Ripples developed and migrated (Figure 1a) while SSC increased to an averaged value of \( \sim 3.6 \text{ kg/m}^3 \) (Figure S4). Pore pressure rapidly increased to \( \sim 0.1 \text{ Pa} \) at the onset of wave load, and then dissipated and oscillated around zero (Figure S4). The susceptibility to liquefaction of the sandy bed under this set of wave condition was low. The result is in good agreement with other clean sand results, which involved sand with a similar grain diameter (Tzang & Ou, 2006).

3.2. Effect of EPS on Bed Mobility

The bed mobility increases and the bedform varies as the EPS increases from 0% to 0.1% (Figure 1). The upper range of 0.1% reflects the limit for a solid-liquid transition to occur (\( T_{\text{sw}}/T_{\text{sb}} \) column in Table 1). According to previous studies, higher critical shear stress is required to move sediment under currents when EPS
is present and this is considered as evidence of the bed stabilizing effect of EPS (Chen et al., 2017a, 2017b; Gerbersdorf & Wieprecht, 2015; Packman, 2013). However, results in the present study show that even at a comparatively low level of EPS (0.005%), liquefaction took place under the action of waves, that is, the bed was destabilized. In the low EPS cases, liquefaction stopped before the end of the test and ripples appeared (Figure 1b, $T_{eb}$ in Table 1). Hence, the bedforms (Figure 1b) were similar to the abiotic case (Figure 1a), albeit with different final dimension based on the final bed geometry. Critically, by considering only the final bedforms, the history of bed deformation and period of liquefaction was overlooked. Moreover, an increase of the EPS shortened the time at which the cycle of mass motion first appeared ($T_{bs}$ in Table 1) and also the development time of liquefaction throughout the depth profile ($T_{bb}$ in Table 1).

A liquefaction phase was again observed with a slightly higher concentration of EPS (Test 4 with 0.02% EPS), but the bed surface was flat after the waves stopped (Table 1), rather than rippled, and there was only a limited amount of mass motion in the last few minutes (Figure 1c).

In the 0.1% EPS case, the bed oscillated from the beginning of the test (Table 1). The bed surface rose as a wave trough passed and lowered under the wave crests. The undulation showed an almost invariant amplitude during the test. The bed acted as an elastic membrane under waves and there was no solid-liquid transition phase observed. This is quite different from the results observed in other cases with lower amounts of EPS present, where no sediment motion was observed until the onset of liquefaction ($T_{bs}$ in Table 1). This phenomenon echoes the early study recording a similar “oscillatory effect” from a local patch of biofilms observed in the field, where the surface reacted like the skin of a drum, vibrating slightly (Paterson, 1989). Nevertheless, the biological effect was far stronger than physical cohesion alone, where sand becomes prone to liquefaction for clay contents of up to 10%, beyond which the mixture is stabilized and no longer susceptible to liquefaction (Gratchev et al., 2006).

### 3.3. The Temporal Variation of EPP

The time variation of the excess-pore pressure (EPP) at the measured position, that is, pore water pressure in excess of the hydrostatic condition, is an established indicator for local liquefaction, used to explain the process in further detail (Gratchev et al., 2006; Sumer et al., 2006). Whilst the EPP inside the bed oscillated in phase with the waves (Figure 2a), the period-averaged EPP ($\bar{p}$ dash lines in Figure 2a, see 2.4 for the calculation) built up in all the biological cases. After several cycles, $\bar{p}$ reached a form of dynamic “equilibrium,” $\bar{p}_{max}$. When $\bar{p}_{max}$ exceeded the initial mean normal effective stress $\sigma_0$ (see Section 2.4 for the evaluation), the particles were then suspended and moved with the oscillatory motion generated by the waves. This has been commonly used to designate the onset of seabed liquefaction (Sumer et al., 2012). The behavior of the bed with an EPS range of 0.005%–0.02% in this study is in good agreement with this criterion (Figure 2a).

With further increases in EPS however, the value of $\bar{p}_{max}$ no longer exceeded $\sigma_0$. Liquefaction occurred with larger, but still small quantities of EPS, even though $\bar{p}_{max}$ was much lower than the threshold value of $\sigma_0$ (0.05% EPS, Figure 2a). When mixed with an even higher level of EPS (i.e., 0.1%), there was no accumulation but a drop of EPP, followed by a constant but negative value of period-averaged EPP (Figure 2a).

After an initial build-up of pore pressure, the beds with lower EPS content (in Test 2 and 3) lost stability. They transitioned through a liquefaction phase, before the onset of consolidation and the formation of a rippled bed (Figure 2b). In contrast, bed motion continued throughout the test duration in Tests 4–6 with higher EPS content, and showing consistent pore pressure (Figure 2d).

### 3.4. Effect of EPS on Sediment Erosion

Increasing quantities of EPS has a hysteresis effect on the erosion and suspension of sediment. Increasing EPS (Test 2–4) increased the maximum and average SSC level, while further increases of EPS (Test 5 and 6) showed a suppressing effect on erosion, despite of the high mobility of the beds (Table 1 and Figure 2c). The stimulating effect on erosion was particularly apparent in the 0.02% EPS case, where the SSC was highly variable in time and peaked at a value of 19.71 kg/m³, three times higher than that of the abiotic condition (6.51 kg/m³) (data shown in Table 1). In lower EPS cases (Test 2 and 3), the decline of SSC correlated with the rapid dissipation of EPP which began at around 800 s (Figure 2b). The increase in SSC was related with the
accumulation of EPP at bottom (Figure 2a), which caused an upward seepage flow, moving and suspending sand grains (Jia et al., 2014; Tzang & Ou, 2006). With increasing EPS however, the value of $p_{\text{max}}$ decreased (Figure 2a), meanwhile, the higher biological cohesion also hindered SSC by changing the mechanism of bed failure from local to nonlocal, involving many linked grains (Vignaga et al., 2013). Nevertheless, these results are quite different from previous ones obtained under steady flow conditions, where the presence of EPS act as a biological stabilizer, inhibiting erosion and decreasing sediment transport (Chen et al., 2017a; Fang et al., 2017).

3.5. Mechanism of Biological Cohesion Induced Mobility of Sediments

Under the wave crest, the wave pressure in excess of the hydrostatic pressure is positive and the bed tends to decrease in volume (Figure 3a and 3b center). In a well-sorted sand, grains stack up through contact and form a relatively stable structure (Figure 3c). Moderate wave force can only cause a finite displacement of the grains, and a relatively small variation of the pore pressure because of the high permeability of the bed. In contrast, biosedimentary beds are made up of an amorphous mixture of grains, organics, organisms and pore spaces, with EPS attaching to available surfaces or bridging between adjacent particles (Figures 3c, 3e–3g) (Chen et al., 2017b; Paterson et al., 2000; Van Colen et al., 2014; N. Zhang et al., 2018). The sand-EPS skeleton is rearranged at the expense of the pore volume, where the EPS bridges break and deform due to shear forces and torques (Figure 3c center). As a result, the waves compresses the sediment particles closer together, producing a plastic deformation as the original internal structure is changed. Such movement reduces the conveyance capacity of the interstices, and impedes the travel of the pressure wave through the sediment. The pore water pressure is therefore increased, which substantially lowers the effective stress of the bed and hence the bed resistance to shear stress.
Figure 3. Schematic of mechanism for EPS (low content) induced liquefaction of a sandy bed. Under load from the hydrostatic condition (left column) and wave forcing (crest, center column and trough, right column, respectively) (a), the bed responds differently for the biological condition (left) and abiotic condition (right) (b). The images in (b) are SEM images. The grain-EPS-grain contact and the excess-pore water response are represented at the µm scale (c). In the case with a high EPS content (i.e., 0.1%), a wave induces the composite elastic bed of sediment and EPS into synchronized mechanical oscillation (d). The elastic properties of the bed allow an immediate deformation of the bed, almost synchronous with the periodic pressure variation, whereby the water-bed interface is (nearly) 180° out of phase with the wave surface. Vertical profiles of EPS in flat beds were taken from the bare flat area, Jiangsu Coast, China (Sample 1, the median grain diameter, $D_{50}$, was 0.105 mm) and the natural salt marsh area, Eden Estuary, UK (Sample 2, $D_{50} = 0.180$ mm) (e). In bed with lower EPS content of 0.005–0.020% (e, sample 1), aggregates of biofilm and smaller grains are shown, while small patches of biofilm are attached to the surface of larger grains (f, scanning electron microscope image, sample freezing-dried). The biofilm-sedimentary matrixes are of greater integrity with higher EPS content (e, 0.040–0.150%, sample 2), shown by the nondestructive 3D image (sample hydrated) using x-ray microcomputed tomography (g). See supporting information Text S2 and S3 for information about the field sites. Such structures imply that the liquefaction susceptibility of a certain depth layer of natural sediments may be affected by the biological cohesion. EPS, extracellular polymeric substances; SEM, scanning electron microscopy.
Under the wave trough the bed rebounds, and the pore pressure reduces (Figure 3a and 3b, right). Seepage flow induces an upward drag on the grains due to the pressure gradient, passing through the pores where the hydraulic conveyance of the bed is reduced by EPS (Figure 3c, right) (Geng et al., 2017; Volk et al., 2016). EPS bridges would be further destroyed due to the relative displacement. Consequently, this cyclic process of collapse and rebound forces the grains closer together, and compresses the pore water between the particles. However, for the biological condition with 0.1% EPS, the response of the bed changes significantly. The bed deforms immediately from the onset of wave action without a solid-liquid transition, and behaves in a similar manner to fluid mud, which only fine cohesive sediment can form (Figure 3d, see Figure S5 for the rheological properties of the EPS 0.1%-sand mixture). The grain-grain skeleton is augmented by an EPS skeleton with grains embedded in an EPS matrix (Figure 3g). A Rayleigh-Taylor instability may also arise, where an upward drag force can increase locally due to a buoyancy effect, which causes channeling of EPS (lighter fluid) to push through denser sands (McLaren et al., 2019). Previous studies have shown the formation of volcano-like “water escape structures” (McLaren et al., 2019; Nichols et al., 1994), in which the upwelling pore EPS fluid can be squeezed out from the bottom sand structure, along with gas bubbles (Figure S6), creating a “vacuum effect” for the pore water, which explains the occurrence of negative pore pressure (Figure 2a). It should be noted that in this experiment xanthan gum was used as an EPS proxy to provide biological cohesion, which contains no protein, however the real EPS matrix may be more complex (Figures 3e–3g; Flemming & Wingender, 2010).

4. Implications and Conclusions

The experimental data in this study show that the pervasive distribution of microbial EPS with a mass concentration of 0.005%–0.1% throughout the sediment, can be a key factor in wave liquefaction dynamics. The analysis clarifies how neglecting the presence of even low content of EPS can result in inaccurate prediction of the bed stability. This is clearly important for the design of coastal structures and may also be relevant to the correct interpretation of the aleo environmental conditions of sedimentary successions formed by waves. Through sea-level rise, the risk of bed liquefaction is expected to impact more engineering structures and also poses potential threats to wetlands, where microbial communities occupy habitats such as salt marshes and submerged aquatic vegetation beds, where the production of EPS is much higher. The misinterpretation of the vulnerability of wetlands when exposed to waves could put the existing ecosystems at risk, considering that these ecosystem services are valued at about US$10,000 per hectare (Battin et al., 2008; Kirwan & Megonigal, 2013). These findings also expand the known diversity of behaviors from organic matter that moderate global biogeophysical cycles, and interface with the sediment dynamics that can potentially contribute to other major geological events.

Data Availability Statement

Data and the results presented in this study can be obtained through Mendeley Data online (http://dx.doi.org/10.17632/k74dnxrfcf.1).

References


