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Review Article

Biostabilization: Parameterizing the interactions between microorganisms and siliciclastic marine sediments

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ARTICLE INFO	A B S T R A C T		
Keywords: Biostabilization Great Oxidation Event Microbial mats Microbially induced sedimentary structures	Microbial mats have existed for much of Earth's history. They represent some of the earliest evidence of life, are essential in biogeochemical cycles, and played a pivotal role in oxygenating the atmosphere. In addition, benthic microbiota impact sediment properties by enhancing the cohesion and stability of the substratum, a process known as 'biostabilization', which affects sediment dynamics and rheology. A substantial body of research has focused on experimentally quantifying biostabilization in siliciclastic sediments. This review compiles and synthesizes these studies in order to facilitate comparison of results. They, in turn, are compared with; (1) the Shields' diagram, (2) shear stress values in shallow marine environments, and (3) occurrences of microbially induced sedimentary structures in the marine stratigraphic record. The findings reveal significant variability in outcomes, with increases in the Shields' Parameter ranging from 0.1 to 4 orders of magnitude. They also demonstrate that high-energy hydrodynamic conditions, such as those above fairweather wave base, inhibit microbial colonization. Additionally, the review briefly discusses two applications of the data: (1) refining models of the Great Oxidation Event, and (2) evaluating microbial biostabilization as a response to increased coastal erosion driven by climate change.		

1. Introduction

Biostabilization occurs when biological activity directly or indirectly results in an increased threshold of the stress required to initiate the erosion of sediment (Paterson, 1994). This shear stress can be due to the force exerted by currents, mechanical stress, or intraparticle stress from gas pressure (Noffke et al., 2022). In most cases, the term refers to the process whereby microorganisms colonize the substratum and increase the shear strength of the sediment. Those colonizing species initially form biofilms consisting of cells and extracellular polymeric substance (EPS) that physically binds the cells to the mineral grains of the sediment (Stal, 2010). With time, biofilms thicken into microbial mats comprising a community of co-existing microorganisms, often dominated by a filamentous species, living in an organized, often stratified structure (Konhauser, 2007; Prieto-Barajas et al., 2018).

Aside from biostabilization, microbial mats interact with loose sediment by baffling, trapping and binding sediment grains in EPS (Droppo et al., 2007). Benthic cyanobacteria, in particular, influence fluid flow dynamics at the sediment water interface. This interaction between bacteria, sediment, and fluid flow may be preserved in the form of microbially induced sedimentary structures (MISS), which have been observed in both modern environments and the rock record (Noffke et al., 1996; Hagadorn and Bottjer, 1997; Noffke et al., 2003a; Porada and Bouougri, 2007; Davies et al., 2016). Wrinkle structures are the most commonly reported example of MISS preserved in siliciclastic environments, though many morphologies have been described. Initially, the origin of wrinkle structures was thought to be primarily physical, produced by current waning, shear stress from wind, or sediment loading (Dżułyński and Simpson, 1966; Allen, 1984). Subsequent work showed that, when compared to modern examples, they may represent in situ preserved microbial mats and often represent the preserved evidence of microbial mats, though they may also be produced abiotically (Hagadorn and Bottjer, 1997; Noffke et al., 2002; Davies et al., 2016; Pratt, 2021). Examples of wrinkle structures, and other MISS are recorded as early as the Archean (with the oldest reported MISS dated at 3.48 Ga) (Noffke et al., 2006, 2008, 2013; Westall et al., 2006; Tice, 2009; Gamper et al., 2012; Duda et al., 2016). These structures represent evidence of some of the earliest forms of life on Earth. In certain cases,

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trapping and binding may result in the formation of a biolaminite or siliciclastic stromatolites or siliciclastic agglutinated microbialites (Martin et al., 1993; Gerdes et al., 2000; Reid et al., 2000; Suarez-Gonzalez et al., 2019). It should also be noted that these terms are also sometimes used to describe stromatolites in carbonate or mixed carbonate-siliciclastic settings in cases where sand is agglutinated by stromatolites. In other cases, EPS is mineralized via microbiallymediated mineralization processes, often producing carbonate cements in organosedimentary structures like stromatolites (Reid et al., 2000; Dupraz et al., 2009; Petrash et al., 2012; Noffke and Awramik, 2013).

Biostabilization is thought to be an important process, particularly in marginal marine environments, where it can increase the yield strength of the substratum against the stress produced by the combination of waves, tides, and currents (Paterson, 1994; Noffke, 2010). It is important to understand the role of biological activity in sedimentation for several reasons: First, microbial mats are now understood as ubiquitous, affecting a wide variety of processes including the formation and preservation of physical sedimentary structures in the rock record. Second, understanding the role of biostabilization in erosion resistance may aid in protections against coastal erosion, a threat to important ecological and economical resources. Recent studies have found that microbial mats can have an impact of the long-term geomorphological evolution of coastal settings (Fisher et al., 2023). Third, cyanobacteria have played an important role in Earth's history as their evolution, and more specifically their ability to perform oxygenic photosynthesis has often been cited as the driver for the Great Oxygenation Event (GOE) at 2.45 Ga (Schirrmeister et al., 2015; Hamilton, 2019), the time when oxygen first accumulated into the atmosphere (Farquhar et al., 2000). As such, the environments and processes associated hold great significance in the coevolution of Earth's atmosphere, hydrosphere and biosphere. It is therefore necessary to better determine the range of shear stress thresholds characteristic of biostabilized sediment.

There are many studies pertaining to biostabilization, however varying methods make it difficult to synthesize the data and provide a general overview. The methods employed are both qualitative and quantitative, with almost no two studies being alike. The studies originate from a range of disciplines (e.g. sedimentology, microbiology, engineering) and are consequently presented from distinct disciplinary perspectives, influencing both the formulation of the research questions and the interpretation of the scientific results.

In this review, we synthesize the published findings on the biostabilization of siliciclastic sediment in marginal marine and shallow marine environments with the aim of establishing a framework of the critical erosion thresholds produced by benthic microorganisms. We achieve this goal by conducting a review of existing experimental data and comparing these results to (1) the Shields' curve, (2) values of shear stress produced by the hydrodynamic regime of shallow marine environments, and (3) rock-record occurrences of MISS in siliciclastic marginal- and shallow-marine environments. These findings can be applied towards future endeavours in understanding the distribution of microbial mats in the rock record to better understand the importance of microbial mats and biostabilization from the Proterozoic onwards.

2. Methods

The data included in this study are assembled from all available literature. First, all publications that parameterize the effects of biostabilization are included ranging from quantitative measurements to qualitative assessments. From this collection, any available quantitative data were extracted and organized. Numerical results have been reported in the literature primarily as critical erosion velocities (ν) or as critical shear stresses (τ_c). To compare these data, velocities are converted to critical shear stresses using the following equation: Where ρ_w is the density of seawater. Shields' parameter datapoints (θ_{cr}) are calculated from the data and plotted on a Shields' curve using the following formula:

$\theta_{cr} = \tau_c / [(\rho_s - \rho_w)gd]$

Where ρ_s is the density of the sediment (approximated by the density of quartz, 2650 kg/m³), ρ is the density of the fluid (in this case the density of seawater, 1020 kg/m³), g is the acceleration due to gravity, and d is the particle diameter (Beheshti and Ataie-Ashtiani, 2008). The Shields parameter is plotted as a function of grain size diameter, which is compiled from the above studies. In cases where grain size was originally described nonspecifically (e.g. such as 'sand'), the data are plotted as upper fine sand (250 µm). This grain size was chosen due to the affinity of photosynthethic cyanobacteria with fine sand as their preferred substratum as documented in modern studies (Watermann et al., 1999; Noffke et al., 2002; Noffke, 2010; Stal, 2010). In cases where a wide range of grain sizes is reported, the average is used.

Six studies are included that used qualitative methods to assess the effects of biostabilization in sediments. These included no quantitative measure of biostabilization, but instead used visual criteria such as, for example, recording the shape and distribution of ripples. As a result, these studies are not included in the quantitative data (Fig. 1, Fig. 2), but are included in Table 1 to provide a complete overview of the previous research.

Publications that provide measured or modelled assessments of shear stress in modern marginal- and shallow-marine environments are used to constrain preservation thresholds of microbial mats in these settings. For the purposes of this paper, we consider any hydraulic energy capable of moving 250 μ m (upper fine) sand grains as 'energetic': i.e., current energies that exceed the Shields' curve.

The inclusion criteria for fossil examples are: (1) reference to MISS, (2) data derived from a primarily clastic or mixed carbonate-clastic succession, and (3) data support deposition in a shallow marine setting. Occurrences of stromatolites are not included here as they represent specific environments where minerals precipitate (Noffke, 2010). Each study is reviewed for evidence of mat occurence and interpreted sedimentary environment. Where possible, the environmental interpretation is refined on the basis of the photographic data, strip logs or the written description in their respective studies. Environments are refined because in many cases, the broad term of "shallow marine" is applied with a general definition of "where the seafloor is within the photic zone". From a sedimentological perspective, more specific terminology is typically applied for the following reasons: (1) The depth of light penetration can vary significantly depending on the turbidity of water, meaning the depth of water is not the limiting parameter, (2) light penetration does not account physical characteristics in shallow marine environments like wave energy, tidal influence, or sediment dynamics, (3) ecologically speaking, there are different zones within the photic zone, including the intertidal, subtidal and neritic zones, and (4) geomorphologically speaking, this definition does not distinguish between features like the shoreface, delta front, shelf, or slope, for example, which are all very different environments.

In terms of classification scheme and depositional environment, here we are using the following definitions: (1) Wave base is defined as the depth that is less than or equal to half of the wavelength of a surface gravity wave and is the depth to which a surface gravity wave will entrain sediment (Reading, 2002); (2) Fairweather wave base (FWWB) is the mean depth of wave base during fairweather, or normal, wave energies (Reading, 2002; Peters and Loss, 2012); (3) Storm weather wave base (SWWB) is the mean depth of wave base during storm conditions; (4) The shoreface is defined here as the zone between mean low tide and mean FWWB (Reading, 2002; Dashtgard et al., 2021); (5) Between mean FWWB and mean SWWB encompasses the offshore and/or offshore transition.



Fig. 1. A summary of the literature results showing erosion threshold measured in BI (upper), velocity (middle), and stress (lower) separated into values for abiotic control sediment (X) and biotic sediment (+). (a) (Amos et al., 2004) (b) (Cady and Noffke, 2009) (c) (Chen et al., 2017) (d) (Dade et al., 1990) (e) (de Brouwer et al., 2005) (f) (Defew et al., 2002) (g) (Droppo et al., 2007) (h) (Droppo, 2009) (i) (Fang et al., 2014) (j) (Friend et al., 2003a) (k) (Friend et al., 2005) (l) (Friend et al., 2008) (m) (Gerbersdorf et al., 2007) (h) (Droppo, 2009) (i) (Grant and Gust, 1987) (p) (Hagadorn and Mcdowell, 2012) (q) (Lundkvist et al., 2007) (r) (Malarkey et al., 2015) (s) (Neumann et al., 1970) (t) (Neumeier et al., 2006) (u) (Noffke, 1998) (v) (Paterson et al., 2000) (w) (Thom et al., 2015) (x) (Tolhurst et al., 2006) (y) (Tolhurst et al., 2008) (z) (Tolhurst et al., 2010) (A) (Underwood and Paterson, 2003) (B) (Vignaga et al., 2013) (C) (Waqas et al., 2020) (D) (Watts et al., 2003) (E) (Widdows et al., 2007) (G) (Yallop et al., 1994) (H) (Zhang et al., 2023).

3. Mechanisms of biostabilization

The process of biostabilization begins with the microbial colonization of a substratum. Microorganisms, like bacteria, cyanobacteria, green algae, and diatoms, settle onto a submerged substratum in a variety of ways including via gravity, molecular diffusion, or selfpropulsion (Characklis and Cooksey, 1983; Gerbersdorf and Wieprecht, 2015). At this stage, microorganisms adhere to the substratum through London dispersion forces, a type of weak intermolecular force that occurs between all atoms and molecules that arises from temporary fluctuations in the electron density of an atom or molecule, creating a temporary dipole (Nichols and Mancuso Nichols, 2008). Microorganisms can adhere to the substratum when they are sufficiently close enough (< 1.5 nm) for short-range polar forces (e.g., hydrogen bonds, hydrophobic interaction) and for EPS to be secreted (Busscher and Weerkamp, 1987; Thom et al., 2015). Rough substrata are more likely to result in successful adhesion because of increased surface area and some protection offered from shear forces (Ferris et al., 1989; Characklis et al., 1990; Donlan, 2002). Microorganisms often exhibit specific preferences for the particle sizes of the substrates they colonize. For instance, cyanobacteria tend to favor fine sand, but can also thrive in sand particles ranging between 0.06 and 2 mm (Watermann et al., 1999; Stal, 2003; Noffke, 2010; Stal, 2010). Fine-grained sediments (<0.0004 mm)

present more challenges for colonization due to their cohesive nature, which can limit the movement of mobile microorganisms through the sediment (Stal, 2003; Noffke, 2021). Furthermore, fine-grained material suspended in the water column can be detrimental to photoautotrophs that require light for energy, as increased turbidity impedes light penetration (Noffke, 2021). Conversely, gravel (>2 mm) is generally less favoured, likely due to the high hydrodynamic conditions associated with its transport (Noffke, 2021). Nevertheless, gravel deposited in areas where hydrodynamic conditions have eased may eventually be colonized by biofilms and microbial mats. Microorganisms have also been observed to broadcast chemically after successful adhesion and in doing so promote further colonization by similar or other microorganisms (Gerbersdorf and Wieprecht, 2015). This step may lead to the transition from a monospecific biofilm to the development of complex microbial mats composed of a wide variety of microorganisms that compete for space with one another over light, nutrients, and electron donors/acceptors (Costerton et al., 1995; Gerdes, 2010; Prieto-Barajas et al., 2018).

Microorganisms also adapt to changing sedimentation rates. During periods of latency, microbial mats may develop through processes like growth and/or binding, creating a network within the sediment (Noffke, 2021). In contrast, during periods of increased sedimentation rates, some microorganisms adjust by orienting their filaments perpendicular





Fig. 2. Examples from the literature where both grain size and either shear velocity or shear stress values were given of biostabilization experiments plotted relative to the Shields' curve as a representation of expected incipient motion for a given grain size. The values for grain size were rounded to the upper limit of the Wentworth grain size given, and in the case of more general terms like "sand" the upper limit for fine sand (250 µm) was used. "Combined Flow Stress Data" refers to literature data both measured and modelled for the stress in shallow marine environments as a result of combined flow.

to the mat surface, extending into the overlying water column. This orientation helps to reduce the water's velocity (Black, 1932; Noffke, 2010; Frantz et al., 2015; Noffke, 2021; Noffke et al., 2021). Ultimately, the reduced water velocity leads to the deposition of suspended particles.

In general, at least three conditions need to be met for a microbial mat to form; (1) the growth rate of the mat must outpace consumption by grazing fauna, (2) sedimentation rates cannot exceed the time required to colonize the sediment surface, and (3) biogenic, chemical and mechanical erosion must be low enough that the microbial mat growth rate exceeds the pace of mat deterioration (Walter, 1976; Gerdes et al., 1991; Stal, 2012). While physicochemical factors such as nutrient availability, salinity, and light availability are significant, it is the hydrodynamic regime that plays a critical role in determining the distribution of microbial mats. In addition, adsorbed ions assist in binding sediment and other microorganisms to an existing biofilm by reducing electrostatic repulsions between like charges (de Brouwer et al., 2002; Gerbersdorf and Wieprecht, 2015). As with substratum preference, different microorganisms have distinct nutrient requirements. Cyanobacteria, for example, are adapted to lower nutrient levels than other microalgae or diatoms (Gerbersdorf and Wieprecht, 2015; Stal, 2010). For photoautotrophic organisms, light is also a necessity that can be hampered by events like algal blooms or environmental conditions such as settling silt or clay under low energy conditions, whereas too much or too strong of light can induce photo-oxidative stress (Gerbersdorf and Wieprecht, 2015; Stal, 2010). Cyanobacteria are also well adapted to cope with environmental fluctuations in light, temperature, salinity, and water availability (Stal, 2010). In general, microbial colonization is optimized by fine-grained sand, composed of translucent quartz, where hydrodynamic conditions are high enough to sweep away mud, but low enough that mats are not eroded, and sufficient light penetrates to support photosynthesis (Noffke et al., 2002). Under ideal conditions, microbial mats can grow to be centimetres thick (e. g. Lalonde et al., 2007).

Biostabilization is one of the four microbial processes that contribute to the formation of MISS; the other three are growth, baffling/trapping, and binding (Noffke, 2010; Noffke et al., 2022). Under this classification scheme, biostabilization directly contributes to the development of MISS features such as roll-ups or mat curls, petees, shrinkage cracks, sponge pore fabric or fenestrae, gas domes, and mat chips (Noffke et al., 2022). Additionally, certain MISS (e.g., microsequences, multidirected ripple marks, erosional remnants and pockets, wrinkle structures, and oscillation cracks) result from the interactions of all four microbial processes. Examples illustrating the role of biostabilization in MISS formation are presented in Figs. 4 and 5. Studies documenting the conditions leading to the formation of MISS in modern environments are ongoing, but frequently limited to intertidal environments. For instance, research has demonstrated that large roll-ups and mat chips can form during severe storms with winds exceeding 50 km h^{-1} , when the intertidal zone is inundated with storm waters (Maisano et al., 2019, 2022).

The stabilizing effect of biofilms also changes the preservation potential of seafloor sediments (Gehling, 1999). While early work focused on the taphonomic implications to fossil preservation, it has since become clear that microbial biostabilization also affects physical sedimentary structures like ripples or heterolithic bedding (Cuadrado, 2020). Biostabilization alters these structures, which typically reflect the hydrodynamic conditions of the depositional environment, by increasing substrate resistance to erosion, reducing friction, or increasing substrate adhesiveness due to the presence of EPS. This suggests that both the preservation of physical sedimentary structures and the energy required to produce them is affected by microbial colonization of the sediment. As an example, in modern intertidal environments, microbial colonization has been demonstrated to stabilize 3D ripples, creating sinoidal structures over rippled laminae that may be misinterpreted as fine-grained sediment (Cuadrado, 2020).

Biostabilization has been classified into three types based on flume experiments and field studies (Noffke, 2010; Noffke et al., 2022). Type I involves epibenthic microbial mats, Type II involves endobenthic

Table 1

A compilation of literature experiments of biostabilization providing study area, sedimentary environment, grain size, the criteria for erosion threshold, and the measured erosion threshold.

Publication	Study Area	Environment	Sediment Grain Size	Erosion Threshold Criteria	Erosion Threshold
Amos et al., 2004	Venice, Italy	Intertidal to sublittoral lagoon, marshes and mudflats	Clay to sand	For cohesive fraction: "the value of bed stress at which S [suspended mass] reaches ambient values in a regression plot S and shear stress" (Sutherland et al., 1998; Amos et al., 2000, pg. 10)	1.90 Pa
Cady and Noffke, 2009	Portsmouth Island, USA	Tidal flat	Sand	"A digital system analyzes the first release of sand grains from the flume chamber, an event that marks the start of erosion of the microbial mat." (Cady and Noffke, 2009, pg. 6)	0.0009–1.6 m/s
Chen et al., 2017	Yancheng, Jiansu Province, China	Lower intertidal flat Lab conditions	Very fine sand	"An optical backscatter sensor (OBS-3+) located 7 cm above the bed surface was used to measure the real-time suspended sediment concentration the maximum concentration was 60 kg/m ³ (3.5 % by volume)." (Chen et al., 2017, pg. 4791)	0.258 Pa
Cuadrado et al., 2011	Bahia Blanca estuary, Argentina	Tidal flat	Fine silt to medium	N/A	Not measured
Dade et al., 1990	Flume	Laboratory	Fine sand	"samples were monitored visually through a dissecting microscope with low-angle lighting. Flow velocity in the flume was increased until one of the test sampels was observed to erode; this flow environment constituted a 'critical erosion' condition for the particular treatment." (Dade	0.0146–0.0149 m/s without bacteria 0.0174–0.0329 m/s with bacteria
De Backer et al., 2010	Ijzermondding tidal flat, Belgium	Tidal Flat	Not reported	et al., 1990, pg 8) "The point of incipient erosion was determined as the pressure at which the light transmission in the measuring cell decreased below 90 %." (De Backer et al., 2010, pg 1168)	Up to approximately 170 kPa Typically 20–70 kPa
de Boer, 1981	Netherlands	Intertidal shoal	Sand	Observation	CuSO4 resulted in erosion
de Brouwer et al., 2005	Flume	Laboratory	Fine sand	"Viscosity changes under increasing shear stress were monitored in order to identify the point of incipient motion of the sediment, which indicated structural breakdown of the sediment and hence the critical erosion shear stress." (de Brouwer et al., 2005, pg. 502) "Sediment stability is expressed as a threshold for	Control = 2–3 Pa Maximum of 5–11 Pa
2002	Eden estuary, Netherlands	Tidal flat	Mud to silty sand	sediment oralised as the termined when the light transmission across the test chamber dropped below 90 % (approximately equal to an erosion rate of 0.01 kg m ⁻²) as the bed fails." (Defew et al., 2002, pg 973)	2.0–2.9 Pa
Droppo et al., 2001 Droppo et al.,	Flume	Laboratory	Silt and clay	By observing bed movement or by monitoring the suspended solid concentration through a calibrated OBS probe (not used for all experiments due to malfunctions "The bottom shear stress was computed from the	0.325 Pa
2007	Flume	Laboratory	Clay	observed wave conditions and using the applet provided by Sherwood at http://woodshole.er.us gs.gov/staffpages/csherwood/sedx_equations/Ru nWCCalcs.html, and it was based on the unstratified, three-layer eddy viscosity formulation of Madsen et al. (1993)." (Droppo et al., 2007, pg 578)	0.01–0.07 Pa BI≥ 30
Droppo, 2009	Flume	Laboratory	Clay to sand	"The τ_{crit} was defined as the point where there was a significant increase in SS [suspended sediment] concentration above the ambient level (Type 1b erosion, Amos et al., 2003) as observed by the OBS [optiacl backscatter] probe and via visual observations with the above techniques." (Droppo, 2009, ps 692)	0.23 Pa
Fang et al., 2014	Flume	Lab conditions	Silt and sand	"when 'weak transport' commenced; that is when 20 or more particles were simultaneously in motion across the surface of a box." (Fang et al., 2014, pg 651)	Silt 0.0174 m/s Sand 0.0153 m/s
Friend et al., 2003a Friend et al.,	Ria Formosa, Portugal	Tidal lagoon	Silty sand to sand	" the first incremental pressure-step with a mean transmission value of less than 90 %" (Friend et al., 2003a, 2003b, pg 1903) " $\tau_{\rm C}$ was used as a measure for sediment stability	0.5–0.9 to >9.1 Pa (exceeded maximum of cohesion strength meter)
2005	Southampton Water, England	Mudflat	Coarse silt	and was defined as the point at which the measured light transmission fell below 90 % of the starting light transmission in the CSM [cohesive strength meter] chamber." (Friend et al., 2005, pg 410)	0.3–0.6 Pa

Publication	Study Area	Environment	Sediment Grain Size	Erosion Threshold Criteria	Erosion Threshold
Friend et al., 2008	Pilsey Sands, Chichester Harbour, England	Estuary	Fine sand	N/A	1.7 Pa
Gerbersdorf et al., 2008 a	Lauffen reservoir, River Neckar, Germany	River	Clay to mud	N/A	1–5 Pa
Gerbersdorf et al., 2008	Eden estuary, Scotland	Mudflat Laboratory	150 um glass beads	Cohesive strength meter; "A sequence of water jets are fired onto the substratum with gradually increasing force/stagnation pressure and sediment resuspension is determined." (Gerbersdorf et al., 2008, pg. 284)	107 Pa
Gerbersdorf	Flume	Laboratory	Sand	N/A	12 Pa 0.3 Pa with bare cand
Grant and Gust, 1987	Flume	Laboratory	Fine sand	"For minor microbial binding, for instance in the clear sediment cores, u _{*crit} was defined as the movement of 10 or more mucus-sand aggregates (see also below) similar to the definition for erosion of sterile sand in control cores (movement of 10 or more sand grains). In sediment cores with well-developed mats of purple or cyanobacteria, no single grain movements occured; instead, large pieces of laminae and embedded sand were torn up in carpet-like fashion." (Grant and Gust, 1987, pg. 245)	0.0406 m/s 0.0104 m/s sterile contro
Hagadorn and Mcdowell, 2012	Flume	Laboratory	Medium sand	"Using a suite of pilot sediment trays, the minimum flow velocities capable of mobilizing sediment were determined. Experiments were then repeated using at least two sets of inoculated sediment, in which experimental trays were allowed to equilibrate I nthe flume in stepwise 7 min increments; this equilibration time facilitated usage of the same mat community through a continuum of flow velocities, before it was completely eroded." (Hagadorn and Mcdowell, 2012, pg. 800)	0.25–0.32 m/s caused flip overs 0.30–0.40 m/s caused roll ups
Holland et al., 1974	Lab conditions	Laboratory	Clay to sand	"The velocity of the stirrer (in rpm) at which the sediment began to resuspend was noted. In flasks where the surface sediments did not resuspend during the intial stirring period, the stirring speed was increased on a replicate culture until the sediments did resuspend. The velocity of the stirrer (in rpm) was recorded at this point." (Holland et al., 1974, pg. 192)	Up to 350 rpm
Lundkvist et al., 2007	Miniflume	Laboratory	Sand	"The critical erosion threshold (U _{crit}) was defined as the current velocity at which a significant rise in turbidity above ambient was observed for the first time during stepwise velocity increments." (Lundkvist et al., 2007, pg. 1146)	0.4 m/s Increased 150 % compared to abiotic conditions
Madsen et al., 1993	Flume	Laboratory	Medium sand	" the shear velocity at which mineral grains and attached organic material at the sediment surface were moved." (Madsen et al., 1993, pg. 163)	0.028 m/s
Malarkey et al., 2015	Flume	Laboratory	Fine sand	"Bed morphology was quantified from time-lapse photography, permitting calculation of bedform dimensions and migration rates." (Malarkey et al., 2015, pg. 2)	0.439 m/s
Neumann et al., 1970	Rock Harbour Cays, Abaco, Bahamas	Peritidal	Silt to sand	"Observations were taken of the initial configuration of the substrate before artificial currents were applied and of the manner in which the mats and inbound sediment were eroded." (Neumann et al., 1970, pg. 277)	0.40–1.1 m/s
Neumeier et al., 2006	Hythe, Southampton Water, England Flume	Mudflat Lab conditions	Fine silt	The erosion inreshold (τ_{crit}) was determined by undertaking a linear regression of the SSC [suspended sediment concentration] (measured by the OBS [optical backscatter sensor]) and τ_0 from the data following the initial significant increase of SSC. τ_{crit} was defined when the regression line intersects the value of the background SSC (SSC in still water)." (Neumeier et al., 2006, pg. 546)	5–10 times higher than abiotic sediment
Noffke, 1998	Mellum, Germany	Lower supratidal	Very fine sand	N/A	5–100 % increase in sediment stability
Paterson et al., 2000				"Bed erosion is manifested by the decrease in the transmision of light across the chamber aused by the suspension of sediment."	connent stability
	Humber Estuary, England	Mudflat	Not reported	"The CSM [cohesive strength meter] jet was calibrated using the literature values for the suspension of sorted sand fraction to convert velocity data to Nm^{-2} (Tolhurst et al. 1999)"	1.5–2.8 Pa

Publication	Study Area	Environment	Sediment Grain Size	Erosion Threshold Criteria	Erosion Threshold
Sutherland et al., 1998				"Stability was expressed as a threshold for sediment erosion, the point at which the transmission above the bed was decreased against background level by a set % (usually 10 %)." (Paterson et al., 2000, pg. 1377 "The critical shear stress (U _{*crit}) for erosion in the Sea Carousel was determined as the x-intercept of a	
	Upper South Cove and Lunenburg Bay, Canada	Shallow coastal embayment	Unconsolidated mud	regression analysis of SPM [suspended particulate matter] vs logU _* [shear velocity] fitted with a logarithmic function." (Sutherland et al., 1998, pg. 228)	Erosion rates varied by a factor of 2 and 4
Thom et al., 2015	Flume	Laboratory	0.1–0.2 mm glass beads	"In this study, the critical bed shear stress is defined as the point of incipient particle/aggregate motion where the detachment exposes the underlying abiotic sediment." (Thom et al., 2015, pg. 276)	BI = 4.8-10
Tolhurst et al., 2006	Westerschelde Estuary, Netherlands	Mudflat	Not reported	"A drop in transmission below 90 % is taken as the critical threshold, and is approximately equal to the erosion of 0.01 kg m ^{-2} of cohesive sediment (Tolhurst et al., 1999, 2000; Vardy et al., 2007)." (Tolhurst et al., 2006, pg. 353)	6.3 Pa 3.7 Pa without biofilm
Tolhurst et al., 2008	Eden estuary, Scotland	Laboratory	Clay to sand	"Bed erosion is inferred from the drop in the transmission of infrared light aross the chamber caused by the suspension of sediment. A drop in transmission below 90 % is taken as a critical drop (Tolhurst et al., 1999), and is approximately equal to erosion of 0.01 kg m ⁻² of cohesive sediment." (Tolhurst et al. 2008, ng. 227)	Approximately 3.4 Pa
Tolhurst et al., 2010	Tambourine Bay, Australia	Mudflat	Not reported	"The Cohesive Strength Meter (CSM) was used to measure the relative erosion rate (S _i) and erosion threshold (Tolhurst et al., 1999; Vardy et al., 2007)." (Tolhurst et al., 2010, pg. 2)	3.0–4.5 Pa with mangrove canopy 1.0–4.0 Pa without mangrove canopy
Underwood and Paterson, 2003	Severn Estuary, England	Mudflat	Not reported	N/A	2.7 Pa upper mudflat 2.0 Pa middle mudflat
Vignaga et al., 2013	Flume	Laboratory	Sand, gravel, and 1.1 mm glass beads	"However, it rapidly became apparent that long- established methods based on the frequesncy of movement of individual grains are poor predictors of entrainment in biostabilized sediments. The biofilm-sediment composite membrane began to oscilalte in the flow until it eventually ripped and a chunk of biofilm and grains was washed away." (Vignaga et al., 2013, pg 770)	43 % increase for glass beads 35 % increase for gravel 30 % increase for sand 2.90 Pa (maximum)
Waqas et al., 2020	St Lawrence Estuary, Canada	Subarctic intertidal	Silt to medium sand	"The motion of the biolfilm and subsequent erosion patterns were observed using a high- resolution digital camera (Sony HDR-SR5E 4 megapixel)." (Vignaga et al., 2013, pg. 773) "The erosion threshold (τ_{crit}) was defined when the transmission decreased to 70 % of intial transmission, considering the first 30 % transmission drop due mainly to surface 'fluff' (unconsolidated particles and organic material) resupension, which is not so significant for the sediment dynamics in intertidal areas." (Waqas et al., 2020, pg. 4)	0.8–1.1 Pa low marsh 5–7.5 Pa high marsh 0.6–0.9 Pa mudflat 0.6–1.2 Pa sandflat
Watts et al., 2003	Blackwater River, England	River	Not reported	Erosion threshold were calculated using methods established by Tolhurst et al. (1999) using a Cohesize Strength Meter.	2.5 Pa high marsh 2.7 Pa low marsh 1.7 Pa mudflat
Widdows et al., 2000	Molenplaat tidal flat, Westerschelde, Netherlands	Tidal flat	Silt to sand	"critical erosion velocity (\bar{U}_{crit} .cm/s) defined as the current velocity (x) required to increase suspended particulate matter (SPM) concentration (y) above a threshold of 50 mg l ⁻¹	0.27–0.35 m/s May–June
Widdows et al., 2007	Fall Estuary, Tavy Estuary, Tamar Estuary, St John Lake, England	Mudflats	Not reported	"The erosion threshold is defined as the bed shear stress required to resuspend sediment particles from the bed." (Widdows et al., 2007, pg. 1178)	1.4 Pa Fall Estuary 0.10 Pa Tavy Estuary 0.07 PaTamar Estuary 0.14 Pa <i>St Jo</i> hn Lake
Yallop et al., 1994	Texel, Netherlands Severn Estuary, Portishead, England	Intertidal beach and mudflat	Sand (Texel) Silt (Portishead)	Used a cohesive strength meter and followed methods as outlined by Paterson (1989).	26 Pa Texel 71 Pa Portishead
Zhang et al., 2023	Flume	Laboratory	Silt and sand	Resuspension threshold determined by cross-plot of shear stresses and suspended sediment concentrations (Amos et al., 2004; Sutherland et al., 1998).	0.85 Pa Abiotic sand control 0.94 Pa Sand mat 0.74 Pa Sand "fluff"

microbial mats, and Type III involves biofilms (Fig. 3). In epibenthic stabilization (Type I), the microbial mat forms on top of the sediment. Frictional forces are reduced by the EPS in the mat producing a smoother surface (Paterson, 1994). Studies suggest that epibenthic microbial mats can withstand 9–12 times greater flow velocities than their abiotic counterparts (Noffke, 2010).

Type I mats are associated with larger erosional remnants and pockets produced in reaction to storm conditions, where part of the mat is eroded leaving an area of the substratum unprotected from stress, which may then become deformed by a current (Noffke, 1999). These features are also present in Type II mats (see below), although often smaller due to the differences in stabilizing effect. Type I mats preserved in the rock record are also associated with sponge pore fabrics produced by trapped gas bubbles beneath the surface of the mat, which, in turn, produces a high porosity texture (Noffke, 2010).

Type II biostabilization occurs when organisms form an organic network between the grains of the substratum (Noffke, 2010). The surface of this type of mat is not smooth as in Type I because sediment grains present topographic irregularities in the microbial mat. Because of this, endobenthic mats are associated with turbulent flow in the overlying water column, whereas epibenthic mats induce laminar flows



Fig. 3. Schematic showing the types of biostabilization in sediment: Type I is epibenthic biostabilization where sediment is fixed primarily via EPS and a network of microbial filaments and the surface is smooth, Type II is endobenthic biostabilization, where an organic network forms within the sediment and the surface remains rougher than Type I, Type III is a product of biofilms coating the surface of sediment grains forming aggregates. This figure has been modified from Noffke, 2010. Sediment is sand-sized, but diagram is not to scale.

(Noffke, 2010). Type II mats are associated with wrinkling of the sediment, producing what is known as transparent wrinkle structures where epibenthic mats are associated with non-transparent wrinkle structures (Noffke, 2010). Some workers have posited that endobenthic mats often lead to the formation of smaller ripples (i.e. microripples) compared to abiotic sediment under the same flow conditions (Noffke, 2010). This has been ascribed to the endobenthic mat increasing the shear strength of the sediment, however little research has been reported that supports this: an exception is the erosion diagram for *endo*- and epi-benthic organisms provided by Noffke, 2010, p.46, Fig. 11.17). In general, endobenthic mats increase erosion thresholds by 3–5 times that of abiotic counterparts (Noffke, 2010).

Type III biostabilization occurs when a grain, or an aggregate of grains, is coated in a biofilm (Noffke, 2010). These grains have a lower density than non-coated grains and consequently they stay in suspension longer or they are deposited at the substratum surface. Type III mats are not associated with the formation of MISS or microbial mats. Not all studies presented herein used the above framework to distinguish mat types as this is a relatively new classification scheme (Noffke, 2010; Noffke et al., 2022).

4. Results

The process of biostabilization has been observed, reported, and tested experimentally in modern environments and laboratory conditions. Table 1 provides a summary of the literature included in this review meeting the criteria outlined in the above Methods. Studies were included that described the effect of biostabilization in siliciclastic environments either quantitatively or qualitatively, including sedimentary environments beyond shallow marine sedimentary environments. Forty studies met our criteria. The studies are compared in Fig. 1, which provides a summary of the quantitative data obtained from each. Six qualitative studies are not included in Fig. 1.

Results for reported critical erosion velocities range from 0.0153 ms⁻¹ to 1.6 ms⁻¹ and for reported critical shear stresses, results range from 0.258 to 107 Pa (Table 1). Studies using BI report up to 30 times higher erosion thresholds for biostabilized sediments, and as low as 1.05 times higher. Qualitative results universally report some level of increased stabilization, most commonly based on the preservation of sedimentary structures otherwise destroyed. Studies are conducted in environments ranging from controlled laboratory conditions, intertidal flats, lagoons, marshes, estuaries, and rivers. Studies also employ an assortment of criteria to determine erosion threshold. Published measured values of shallow marine shear stress and modelled values are included in Fig. 2. These values range from 0.01 to 414.1 Pa. These values are measured in various conditions (i.e., fairweather or storm conditions) and various shallow marine environments (i.e., shoreface, shelfal, etc.). These variations are all discussed at length below.

The included examples of microbial structures from literature are presented in Table 2. Fifty-nine instances are presented ranging from Archean- to Quaternary-aged materials. Examples have been included from every continent except Antarctica. The shallow marine environments include deltaic, shoreface, shelfal, intertidal, ramp, and epeiric examples. Trends in the associated sedimentological descriptions and the implications for hydraulic energy regime are discussed below.

5. Discussion

5.1. Rheological studies of microbial mats

Methodological approaches vary considerably: some simply observing this effect in natural environments (de Boer, 1981); some measuring in situ with equipment such as cohesive strength meters (Friend et al., 2003a; Cady and Noffke, 2009); while other efforts include the removal of sediment and microbial communities from natural environments to laboratory settings (Tolhurst et al., 2008). Other



Fig. 4. Examples of MISS formed either via the process of biostabilization or through a combination of microbial processes including biostabilization. (A) Mat chips and curls, also known as roll ups, from modern microbial mat located in Las Rocas, Argentina. Photo is plan-view of mat, scale is visible in top-middle of photo and is 30 cm. (B) Mat curls and mat chips in cross section view of sample from Purcell Supergroup, Montana, USA. Scale is 3 cm. (C) Petees forming in modern microbial mat located in Abu Dhabi, United Arab Emirates. (D) Petees in rock sample from the Purcell Supergroup, Montana, USA. (E) Shrinkage cracks in modern microbial mat located in Abu Dhabi, United Arab Emirates. (F) Shrinkage cracks from the Purcell Supergroup, Montana, USA. (G) Sponge pore fabric, or fenestrae, from a modern microbial mat in Las Rocas, Argentina. (H) Cemented fenestrae from the Shunda Formation, Jasper, Alberta, Canada. (I) Gas domes from a modern microbial mat located in Abu Dhabi, United Arab Emirates. (J) Rock record gas domes and mat chips viewed from the top down on a bedding plane from the Purcell Supergroup, Montana, USA.

studies are carried out solely under laboratory conditions, in flumes, using glass beads or sediments (Gerbersdorf et al., 2008; Vignaga et al., 2013; Thom et al., 2015). Many previous studies have reported a measurement of the critical threshold of erosion, a parameter which is defined within the scope of that research. Some definitions include: the critical shear velocity when ten or more mineral grains move at the same time (Heinzelmann and Wallisch, 1991); the velocity for which mineral grains and attached organic material at the sediment surface moved (Madsen et al., 1993); or when resuspended sediment substantially reduces light transmission (> 30 %) (Paterson, 1989). This threshold is typically reported as a velocity of the flow or as a unit of pressure or

stress (Pa or N m⁻²). Studies may also refer to erosion types (after Amos et al., 2003). Type I erosion decreases asymptotically over time and is characterized by the release of flocs and pellets due to surface erosion. Type II erosion is constant and results in rip-up clasts and larger aggregates moving as bedload. Further examples of erosion threshold criteria that have been used are included in Table 1. Less commonly, some studies offer stabilization coefficients which are expressed as ratios of the erosion threshold of biotic sediments to control-sediment (i.e., abiotic sediments) (Holland et al., 1974; Grant and Gust, 1987; Paterson, 1994). This is sometimes referred to as the Biostabilization Index (BI) (Heinzelmann and Wallisch, 1991; Amos et al., 2004; Droppo et al.,



Fig. 5. Examples of MISS formed either via the process of biostabilization or through a combination of microbial processes including biostabilization. (A) Multidirectional ripple marks from Coos Bay, Oregon, USA (B) Multidirectional ripple marks on a bedding plane surface of sandstone unit 12 from the Sinqueni Formation, Pongola Supergroup, South Africa located in the Wit Mfolozi River Gorge. Photo courtesy of Nora Noffke. For a full description of the site, please see Noffke et al. (2008). (C) Cracking modern mat and erosional remnants and pockets from a modern microbial mat in Abu Dhabi, United Arab Emirates. (D) Rock record example of erosional remnants and pockets from the Purcell Supergroup, Montana, USA. (E) Wrinkle structures from a modern microbial mat formed on the Petitcodiac River, New Brunswick, Canada. (F) Wrinkle marks in the rock record from the Purcell Supergroup, Montana, USA. (G) Oscillation cracks recorded in modern microbial mats situated in Abu Dhabi, United Arab Emirates. (H) Possible oscillation cracks viewed one a bedding plane recorded in the rock record in samples collected from the Purcell Supergroup, Montana, USA.

2007), which may be reported in conjunction with measurements of the threshold of erosion. Regardless of methodology, it should be explicitly stated that the measurement of interest in this review is the shear strength of the biostabilized sediment, a property that is intrinsic to the sediment and microbial mat, regardless of how it is ascertained. The range observed in the degree of biostabilized sediments is due to a wide variety of factors, discussed at length below, including species of microorganism, grain size, and physicochemical conditions.

The consensus of these studies is that mechanical properties of microbial mats are variable and dependent on several factors including particle size, water salinity, species of microorganism, the age of the mat, the season, and the time of day (irradiance) (Friend et al., 2005; De Backer et al., 2010; Thom et al., 2015; Schmidt et al., 2016; Cardoso et al., 2019; Waqas et al., 2020). Mat failure has been recorded between flow velocities of 0.0009–1.6 m/s and between 0.07 and 71 N m⁻² shear stress measurements (Yallop et al., 1994; Droppo et al., 2007; Cady and Noffke, 2009). The results reported in BI range from a 5 % increase in stability to over 30 times greater (Droppo et al., 2007; Noffke, 1998). It has also been shown that higher bed stress because of turbulent flow conditions as compared to laminar flow conditions during mat colonization and growth inhibits biofilm growth (Pereira et al., 2002). Laminar flow produced a greater number of cells, but turbulent flow resulted in a denser biofilm, with a greater number of cells per measure of volume. It has been hypothesized that this may be due to reduced attachment, resulting in thinner, but denser biofilms (Pereira et al., 2002; Thom et al., 2015). It was also found that biofilms kept in the dark did not

Table 2

A compilation of examples from literature of microbial mats or MISS reported in clastic marine successions. Environmental settings have been refined in some cases using geological descriptions and photos from the original publications.

Publication	Location	Age	Environment	Sedimentological Description
Aubineau et al., 2018	Republic of Gabon	Paleoproterozoic	Channels near fair-weather wave base (reintepreted as lower shoreface)	 Moulende quarry FB2 Member Massive sandstone beds, thinly laminated shale, interbedded siltstone
Bailey et al., 2006	USA	Neoproterozoic- Cambrian	Subtidal storm deposits (reinterpreted as upper offshore to lower shoreface)	 Harkless Formation Finely laminated sandstone Symmetrical ripples, trough cross-bedding, hummocky cross-stratification, wavy laminae Horizontal trace fossils like <i>Planolites</i>, <i>Diplichnites</i>, <i>Taphrhelmonthopsis</i> associated with wrinkle structures Vertical trace fossils like <i>Bergauria</i> and <i>Skolithos</i> occur in beds
Buatois et al., 2013	Argentina	Carboniferous- Permian	Lower to middle shoreface	 Santa Elena Formation Matgrounds occur with hummocky cross-stratified to wave-ripple cross-laminated very fine-grained sandstone, abundant mica Arenicolites, Diplocraterion, Gordia, Helminthoidichnites, Lockeia, Palaeophycus, Skolithos
Buatois et al., 2013	Canada	Cambrian	Shallow marine and deltaic under storm influence	 Chapel Island Formation Symmetrical to quasi-symmetrical ripples, hummocky cross- stratification, graded tempestites, pot and gutter casts, soft-sediment deformation structures, mass-flow deposits Bedding plane bioturbation associated with MISS including Cochlichnus, Helminthopsis, Helminthoidichnites, Allocotichnus, Diplichnites, Rusophycus, and Treptichnus
Callow and Brasier,	Russia	Neoproterozoic	Shallow marine	 Pyrite, shrinkage cracks
Calner and Eriksson, 2012	Sweden	Cambrian	Shoreface and lower shoreface (reintepreted as lower shoreface)	 Norretorp Member, Mickwitzia Member, Aleklinta Member Fine-grained sandstone interbedded with mudstone Current and wave ripples, tool marks Cruziana ichnofacies
Calner and Eriksson, 2012	Sweden	Silurian	Shoreface and lower shoreface (reintepreted as lower shoreface)	 Frojel Formation, Burgskvik Formation Wrinkle structures occur on the bedding plane or medium- to thickly-bedded, massive to hummocky cross-stratified, mica-rich quartz arenites
Calner, n.d.	Sweden	Silurian	Shallow marine	 Burgsvik Formation Wrinkle structures occur on the bedding plane or laminated, fine-grained, mica-rich quartz sandstone beds ranging from 0.1 to 1.0 m. MISS have patchy distribution Thickly bedded, massive to hummocky cross-stratifiedd, fine-grained quartz sandstone Bioturbation is rare
Chakraborty et al., 2012 Csonka and Brandt,	India	Mesoproterozoic	Lower with upper shoreface showing rafted mats.	 Rippled bed tops Bhalukona Formation, Kansapathat Formation, Lower Sandstone Formation Tabular bedded (dm-m scale) fine to medium-grained moderate to porly sorted sandstones sometimes separated by mud partings Interally structureless of trough cross-stratified or low-angle planar curved cross-stratified or planar laminated Rip-up clasts, oscillation ripples, and soft-sediment deformation at basal part present Troughts capped by wave-rippled sheets Tabular cross-stratified bedding in a chevron pattern with shallow concave-upwards erosional surfaces, rare planar laminae, low-angle truncation surfaces and reactivation surfaces Gros Ventre Formation
2012	USA	Cambrian	Shallow marine	 Green-grey calcareous shales with grey striped conglomeratic and oolitic limestones with overlying limetsone and underlying quartzite Mud damage flexage helding cillstance and mudtrying quartzite
Davis, 1968 El Kabouri et al	USA	Ordovician	Shallow marine	Mud-arapes, Haser bedding, siltstones and mudstones New Richmond Sandstone Saharo Group
2023	Morocco	Paleoproterozoic- Neoproterozoic	Shallow marine	• Interbedded sandstone and claystone with cm-thick alternating ripples and cross-bedding
Eoff, 2014 Feng et al., 2019	USA	Cambrian	Shallow marine	 Lone Rock Formation Glauconitic and micaceous, fossiliferous, thinly bedded sadnstone, thin wavy laminae Flat-pebbled conglomerate near the top of a condensed section Xiahuancang Formation
	China	Triassic	Lower shoreface to offshore transition	 Finely laminated siltstone and fine-grained, thinly bedded sandstone with abundant bivalves Few limestone interbeds in upper part Laminated siltstone (5–60 cm) Rare trace fossils in siltstone, abundant in sandstone Symmetrical ripples, vertical burrows, cross-bedding, hummocky cross-stratification, fining-upwards trend

Publication	Location	Age	Environment	Sedimentological Description
				• Wrinkle structures common in the bedding surface between
				underlying sandstone and overlying siltstone
Gaillard and				Santa Rosa Formation
Racheboeuf, 2006				Medium- to coarse-grained sandstone fining upwards to
				Flot hodding, gross lomination, horizontal stratification, ways and
				flaser bedding, very well preserved symmetrical ripples locally
				scoured hedding planes
	Bolivia	Devonian	Near shore	• Lockeia, rare Rusophycus, rare Isopodichnus, very rare
				Protovirgularia, abundant Paleohelcura, rare Diplichnites, very rare
				Nereites, common Psammichnites, common Gordia associated with
				microbial films, very rare Torrowangea, common Skolithos, common
				Altichnus, rare?Catenichnus, common Paleophycus, common
0.111				Diplocraterion, common Phycosiphon, and other tracks and trails
2009	Australia	Neoproterozoic	Shallow marine	Rawiisley Quarizite Fossils present bioturbation present
Harazim et al 2013				Beach Formation
1111121111 et ul., 2010				Heterolithic succession of thinly bedded hummocky cross-stratified
	Canada	Ordovician	Storm-dominated lower shoreface to	and planar-stratified sandstone and mudstone
			offshore transition	 Oscillation ripples, syneresis or shrinkage cracks
				 Cruziana, Monomorphichnus, Trichophycus, Planolites
Hickman-Lewis				 Hooggenoeg Formation
et al., 2018				 Grey-black chert to fine- to coarse-grained volcaniclastics,
			Shallow water volcanic-hydrothermal	conglomerate
	South Africa	Archean	shelf	Ripples, flaser bedding, hugh-angle cross-bedding, soft sediment deformation lanticular load structures acceptionary lanilli trough
				cross hedding, tabular cross stratification, wave ripple cross
				lamination rin-un clasts
Hillier and				Grev Sandstone Formation
Morrissery, 2010				Sandstone and mudstone
				• Planar and low angle laminae, hummocky cross-stratification,
				wave ripples, soft sediment deformation, rare massive beds, rare
			Storm-influenced distal delta front to	trough cross-stratification with mud drapes, common syneresis
	Wales	Silurian	intertidal	cracks, flaser and lenticular bedding, "planed-off current ripples",
				desiccation cracks, convolute laminae
				• Wrinkle marks associated with bed tops
				Chondrites, Palaeophycus, Planolites, rare Scolicia, Macaronichnus,
				Gyrounus, Snaubcyunarichnus, Chonarues, Skounos, Arenicoues,
Kilias 2012				Cape Vani Sedimentary Basin
				• "Ferruginous and white volcaniclastic sandy tuff/sandstones"
	Greece	Quaternary	Shallow water to tidal flat	 Planar and herringbone cross-bedding, small-scale, fining upwards
				sequences, flaser, wavy, and lenticular bedding, marine trace fossils,
				beveled ripples, desiccated silicified mudstone beds
Kumar and Ahmas,				 Jodhpur Sandstone
2014			Shallow marine (reintepreted as	• Fine- to coarse-grained red, light yellowish brown to light grey
	India	Neoproterozoic	intertidal)	sandstone, pebbly sandstone, siltstone, and shale
				• Irough cross bedding, planar cross bedding, wave and current
Lan and Chen 2012				• Yurabi Formation
Lan and Chen, 2012				 Sandstone, mudstone, minor interbeds of dolomicrite and
	Australia	Neoproterozoic	Shallow subtidal to intertidal	dolostone
				 Oriented grains, sand cracks
Liu et al., 2013	Russia	Neoproterozoic	Shallow marine	• Taseeva Group
Loughlin and Hillier,	United		Challow maring (reinterreted as lower	 Caerfai Group
2010	Kingdom	Cambrian	shoreface to upper offshore)	 Sandstone and shale
	Rungdom		shoreface to upper ofishore)	Bioturbated
Luo et al., 2019				Kockatea Formation
	Australia	Triassic	Fair-weather wave base to shallow sub-	Bioturbated or cross-laminated alternating ferruginous mudstone,
			tidal	suitstone, and nne-grained sandstone
Manning-Berg et al				Angenerat Formation
2019	Canada	Mesoproterozoic	Subtidal to lower intertidal	Chert
Marenco and				 Campito Formation, Poleta Formation, Harkless Formation
Bottjer, 2008				 Alternating terrigenous clastic and carbonate units
	LICA	Combrian	Challow subtidal shalf	 Interbedded greenish micaceous siltstone and cross-bedded
	UBA	Gailipilail	Sitatiow Subtidat Sileli	quartzites
				 Pyrite, MISS, and bioturbation on bedding planes
				Microfossils present
Mata and Bottjer,			Below fair-weather wave base, above	Beduh Shale
2009	Iraq	Triassic	storm-weather wave base	 Interbedded shale, marl, sandstone, and limestone with sandy
Mate on I Daw				tempestites and scour marks
mata and Bottjer,			Provimal temperation on a silicial action	Campil Member Hummoolay aroos stratification - ways simples and data - and
2009	Italy	Triassic	inner ramp	 nummocky cross-stratification, wave ripples sandstone and siltstone
			mici tamp	Rare highlighting Asteriacites Cochlichnus and Diplocraterion

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Publication	Location	Age	Environment	Sedimentological Description
Mata and Bottjer, 2009	USA	Triassic	Below fair-weather wave base to lower shoreface	 Virgin Limestone Member Hummocky cross-stratification, interbedded with shale
Mata and Bottjer,				 Thaynes Formation Hummody gross stratification, trough gross stratification, gualax
2009				• Fullimocky cross-stratification, trough cross-stratification, swaley cross-stratification
	USA	Triassic	Between fair-weather wave base and	 Interbedded siliciclastic and carbonate lithologies
			storm weather wave base	• Wrinkle structures are commonly found on the bedding planes of
				hummocky cross-stratified beds with overlying interbedded very fine
Manan at al. 2017				sandstone and shale
Menon et al., 2017				 Intrites-like structures discoidal impressions interpreted as fluid
	United	N		escape structures
	Kingdom	Neoproterozoic	Shallow marine deltaic	 Thinly interlaminated mudstone, siltstone, and fine-grained
				sandstone
Nofflee and Nitesh				 Silicified microbial matgrounds Mauroria Formation, Cluss de l'Ord Formation, Foulan Formation
1994				Maurerie Formation, Cluse de l'Ord Formation, Foulon Formation, Landevran Formation
1991				 Thin cross-bedded sandstone interbedded with shale, hummocky
	France	Ordovician	Shallow marine to intertidal	cross-stratified sandstone interbedded with shale, rippled sandstone
			(reintepreted as lower shoreface)	with shale drapes, flaser bedding, interbedded shale and siltstone,
				gutter casts
Nofflin et al. 2002				Cruziana, Daedalus, Phycodes, Planolites Nucleus Formation
Nolike et al., 2002				 Planar laminae, current and wave rinnles, hummocky cross-
				stratification and amalgamated hummocky cros-stratification
	Namibia	Neoproterozoic	Storm-influenced shelf	 Wrinkle structures occur with quartz-rich fine sandstone beds
				(2–20 cm thick) interbedded with sandy mudstone or siltstone with
				planar laminae, ripple marks, and abundant mud clasts
Noffke et al., 2003b	South Africa	Archeon	Shallow marine storm dominated shelf	 Ntombe Formation Siltetone and shale alternating with rippled fine grained quartzites
	South Allica	Archean	Shanow marine, storm-dominated shen	 Oscillation ripples
Noffke et al., 2006				Brixton Formation
				 Sandy shale and silty sandstone units at the base, to sandstone beds
So	South Africa	Archean	Shelf, proximal shelf, shoreface	in the middle, and orthoquartzite bars at the top
			·····, -····, ·····	 Planar lamination, hummocky cross-stratification, ripple marks
				• wrinkle structures become more prevenant in middle to upper part of sections
Parizot et al., 2005				Magaliesberg Formation
				 Medium- to coarse-grained and fine- to medium-grained sandstone
				with horizontal laminae, planar cross-bedding, trough cross-
	Courth A Color	D-1	Post data in a state or a state of the state	stratification, channel fills, wave, current and wind ripple marks,
	South Africa	Paleoproterozoic	Braid-deitaic épéiric marine coastine	minor desiccated mudrock partings, double crested and flat-topped
				 Mudstone, siltstone, and very fine-grained sandstone with soft
				sediment deformation, minor flaser structures, ripple cross-
				lamination, wave ripples, mudcracks, and channel-fills
Pfluger, 1999				• Tanezzuft Shale
				 Interbedded sandstone, siltstone, and shale Fresive based candstone with gutter casts
	Libya	Silurian	Above storm wave base	 Wrinkle structures occur on the bedding planes of sandstone beds
				associated with trace fossils like Gyrochorte and Skolithos, with low
				biotubation levels
Porada et al., 2008	Germany	Jurassic	Subtidal to Intertidal	• Schwarzen Jura
Druce et el 2004				 "Event beds laterally grading into tidal flats" Virgin Limestone Member
Pruss et al., 2004				 Virgili Linestone Member Mixed carbonate-siliciclastic succession ranging from 150 to 200 m
			Subtidal (reintepreted as lower	thick
	USA	Triassic	shoreface)	 Wrinkle structures present in dark red siltstone talus and
				calcareous siltstone
				Hummocky cross-stratification
Pruss et al., 2004			Low operate open marine, below fair	 Thaynes Formation Interheddod earborate and cilicial actio reaks
	USA	Triassic	weather wave base, periodically storm-	Wrinkle structures occur on the bedding plane of laminated
	Obri	THUSSIC	influenced	siltstone (1.5 m thick) between two beds of dm-scale bivalve-crinoid
				shell beds
Pruss et al., 2004				Campil Member
				Red siltstone
				• Wrinkle structures on the bedding planes of sandstone and siltetone, and on the bedding planes of an scale hummooly gross
	Italy	Triassic	Inner ramp	stratified sandstone
				 Mica is concentrated on the troughs of wrinkle structures
				• Asteriacites, Cochlichnus, Diplocraterion, Palaeophycus, and Planolites
				present
Rule and Pratt, 2019	LICA	Macoprotessesia	Subtidal low approved at ditions	Appekunny Formation Thinky hadded are illustrated with warishing sites to be a set of the
	UJA	mesoproterozoic	Subtual, low energy conditions	■ mining between argumateous sinstone with variably sing claystone, and rare very fine-grained sandstone laminae

Publication	Location	Age	Environment	Sedimentological Description
				 Planar laminae, small-scale hummocky cross-stratification, unidirectional cross-lamination, symmetrical ripples, interference ripples, scour surfaces, intraclasts
Sadlok, 2013	Poland	Cambrian	Shelf	 Wisniowka Sandstone Formation Quartz-rich sandstone, mudstone, and heterolithic units
Samanta et al., 2011				 Flaser, wavy, lenticular bedding, MISS on bedding planes <i>Rusophycus</i> adundant Sonia Sandstone Formation
				• Well sorted, well rounded quartz arenite medium sandstone (60 m
	India	Neoproterozoic	Supralittoral to neritic	 thick) Planar and cross laminae, washed out dunes, wave ripples, interference ripples rill marks trough cosets
Sarkar et al., 2005				 Sonia Sandstone Formation
	India	Neoproterozoic	Supralittoral to neritic	 Well sorted medium to coarse-grained sandstone Adhesion laminae, low amplitude impact ripples, wave ripples, washed out dunes, herringbone cross-bedding
Sarkar et al., 2006				 Chorhat Sandstone Formation Siltstone to medium-grained sandstone
	India	Paleoproterozoic	Shallow shelf to coastal margin (we interpret MISS to occur in lower shoreface and upper offshore)	 Adhesion laminae, cross-set with inverse grading, massive or quasiplanar and wavy laminated beds, often amalgamated, wave ripples, divergent parting lineation, rill marks, mudclasts, wart marks, erosional bases, gutters, humocky cross-stratification
Sarkar et al., 2008				 MISS are associated with bedding planes of storm beds Sonia Sandstone Formation
	India	Neoproterozoic	Supralittoral to neritic	 Well sorted medium to coarse-grained sandstone Adhesion laminae, low amplitude impact ripples, wave ripples, washed out dunes, herringbone cross-bedding
Sarkar et al., 2014	India	Mesoproterozoic	Inner shelf, shoreface, coastal	 Vindhyan Supergroup Carbonate, sandstone, shale, and volcaniclastics Newland Formation, Revett Formation, Mount Shields Formation
beilieber, 1990				McNamara Formation
	USA	Mesoproterozoic	Shallow marine to offshore	 Sandstone and shale Rippled patches on otherwise smooth surfaces, wavy-undulose horizontal laminae mine
Stimson et al., 2017	Canada	Cambrian	Inner to middle shelf above storm weather wave base	 King Square Formation Interbedded grey, fine-grained sandstone (20–70 cm thick) and dark grey to light grey mica-rich siltstone and shale (1–5 cm thick) coarsening upward Locally bioturbated, planar and sharp bedding planes, symmetrica straight to sinuous ripples, bifurcated ripples, asymmetric and climbing ripples, interference ripples, wavy, flaser, and lenticular bedding common, synsedimentary deformation, rare marine invertebrate body fossils Arenicolites, Arthraria, Cocluchnus, Cruziana, Didymaulichnus, Gordia, Helminthopsis, Monocraterion, Paleophycus, Paleodictyon, Planolites, Psammichnites, Rusophycos, Skolithos, and Taenidium reported
Tarhan et al., 2017	Australia	Neoproterozoic	Between fair-weather wave base and storm-wave base deposited under oscillatory and combined flow	 Ediacara Member of the Rawnsley Quartzite Thinly bedded, well sorted, fine- to coarse-grained feldspathic quartz sandstone with symmetrical ripples Helminthoidichnites present
Tice, 2009	South Africa	Archean	Between fair-weather wave base and storm weather wave base	 Buck Reef Chert Black and white banded chert and finely laminated iron-rich chert (5 m thick) with no soft sediment deformation or current activity
Warren et al., 2022	Brazil	Mesoproterozoic	Shoreface to foreshore	 Tiradentes Formation Flat or rippled bed surfaces, metasandstone and metaconglomerate, trough cross-bedding, horizontal stratification, rare swaley and hummocky cross-stratification, oriented quartz
Webb and Spence, 2008	Australia	Permian	Shallow, protected, low energy embayment	grains • Bacchus Marsh Formation • Interbedded dolomitic sandstone and siltstone, diamictite • Climbing ripples, planar, trough, and ripple cross-lamination, plani impressions, soft sediment deformation, abundant organic matter.
Wignall et al., 2020	Canada	Triassic	Middle shelf to offshore	 Planolites, Muensteria Blind Fiord Formation Heterolithic sandstone, silstone, and shale Thinly laminated, bioturbated, amminoid and bivalve fossils, ripples, flaser and lenticular bedding, sinuous ripples Phycosiphon, Planolites, Catenichnus, Planolites, and Thalassinoides present in beds without MISS
Xing et al., 2010	China	Mesoproterozoic	Foreshore to nearshore	 Yunmengshan Formation Thickly bedded, fine- to medium-grained quartz sandstone interbedded with thin mudstones Oriented grains

Table 2 (continued)

Publication	Location	Age	Environment	Sedimentological Description
Yang et al., 2019	China	Paleoproterozoic	Relatively restricted shallow marine from fair-weather wave base to below storm weather wave base	 Chuanlinggou Formation Thinly bedded fine-grained sadnstone, siltstone, shale Wrinkled layers are dark coloured, laminated, with floating, aligned quartz grains, and abundant aligned mica Sand veins, cross-bedding, asymmetric wave ripples, straight to slightly catenary crests separated by flat troughs

exhibit a stabilizing effect (Thom et al., 2015). In freshwater, water velocity has also been shown to affect the structure and composition of biofilms, with certain species more prevalent under different flow regimes (Besemer et al., 2007; Graba et al., 2013). Assemblage plays an important role in marine stabilization as well, with different species exhibiting variable tolerance for conditions such as light and grain size (Gerbersdorf and Wieprecht, 2015).

There have been several studies surrounding the effect of seasons on microbial mat communities and the subsequent variability in stabilizing effect. Seasonal effects vary immensely between case studies, seemingly due to factors like latitude and environment. In a tidal flat and barrier island environment along the North Sea, microbial mats were noted to develop in early spring with filamentous cyanobacteria adapted to cold environments (Cardoso et al., 2019). Microbial mats diversified into the summer and fully matured in late summer, finally decomposing over the winter. Studies conducted using fluvial samples have shown that the greatest biostabilization effect occurs in the spring, with the lowest degree of biostabilization happening in late autumn and early winter as mats begin to degrade (Noffke and Krumbein, 1999; Thom et al., 2015; Schmidt et al., 2016). In particular, erosion thresholds were found to be six times higher in the spring than in the autumn, and measurements also suggested that EPS production was highest in the spring months (Schmidt et al., 2016). Similar results were reported from a tidal environment, with the highest stabilizing effect observed in June versus the least effect in September (Widdows et al., 2000). Similarly, another study of the Venice Lagoon, Italy established that biostabilization was five times higher in summer as compared to winter months (Amos et al., 2004). By contrast, a study of a subarctic lower intertidal environment in Canada showed that the highest erosion threshold occurred in the autumn months during the storm season, and that the lowest threshold occurred in winter when the area was under sea-ice cover (Waqas et al., 2020)

The influence of microorganisms can also be observed within the scale of a single day. While not entirely analogous to the effect of microorganisms such as cyanobacteria, it was observed that diatom biomass bound to fine-grained sediment, leading to temporary diatomaceous mud accumulation in the spring and summer; the lack of this effect resulted in erosion in the winter (De Backer et al., 2010). However, it was also found that physical forces like wave energy and storms were still more important factors in determining sediment dynamics over longer time frames. Another study showed that sediments were more stable during the day than at night on an upper intertidal mudflat as a result of diatom migration (Friend et al., 2005). In an earlier daynight study of non-cohesive intertidal sediments, a higher degree of stabilization was recorded at night in areas with high biomass, while the lowest degree of stabilization was recorded during both day and night in areas of much lower biomass (Friend et al., 2003b). Ultimately, it has been suggested that temporal variations in sediment stability simply relate to the cycle of biofilm development and decay (Droppo et al., 2007)

Links have been made between biogeochemical parameters of microbial mats and the degree of biostabilization. Correlations have been reported between sediment EPS content and sediment stability in laboratory studies (Holland et al., 1974; Defew et al., 2002). One study in a subarctic environment explored factors that may be correlated with biostabilization using Spearman's rank correlation and demonstrated that the three greatest predictors of erosion threshold were elevation (rs = 0.59), organic matter content ($r_s = 0.56$), and chlorophyll *a* content $(r_s = 0.47)$, but EPS content was not a good indicator $(r_s = 0.5 \text{ and } 0.32)$ (Waqas et al., 2020). Despite this finding, recent studies have sought to look at the effect of EPS additives in sand substrates as a mitigation technique against erosion, finding linear correlation between EPS content and stability (Schindler et al., 2023). Others have found a stronger relationship using regression analysis between chlorophyll a (r^2 = 0.875), colloidal carbohydrates ($r^2 = 0.774$) and erosion rates (Sutherland et al., 1998). Using multivariate statistics, Friend et al. (2005) established no significant relationship between the critical erosion shear stress and chlorophyll *a*, or carbohydrate content. Results are again variable between studies, suggesting that the variables controlling the degree of biostabilization may be complex and also sitespecific, meaning there may not be one single dictating parameter (e. g. Defew et al., 2002).

Research has also focused on the mechanics of biostabilization failure, finding, for example, that incipient motion (i.e., initiation of mat failure) happens in "chunks or aggregates" (e. g. Thom et al., 2015). Several studies discuss gas bubbles produced within the mat as a failure mechanism; this may occur when the mat is exposed to too much light, leading to oxygen oversaturation as a result of photosynthesis (Sutherland et al., 1998; Gerbersdorf and Wieprecht, 2015). Additionally, other gases like methane produced by bacterially mediated organic matter decomposition might contribute to reduced stability from the buoyancy produced (Thom et al., 2015).

Researchers have previously incorporated the Shields' diagram into a model that shows the impact biofilms have on sediment remobilization (Righetti and Lucarelli, 2007). The Shields' diagram describes the critical threshold of shear stress at which the individual particles of a sedimentary surface comprising approximately spherical and uniform sediments are entrained (Shields, 1936; Beheshti and Ataie-Ashtiani, 2008). The diagram represents the relationship between grain size (or a representation of grain size) or Reynolds number against the Shields' parameter, which is a dimensionless ratio of bottom shear stress to the immersed weight of the grains. Noffke (2010) quantified the critical shear stress for erosion of epibenthic (TI) and endobenthic (TII) microbial mats using in situ measurements obtained via a portable erosion meter. These values were subsequently plotted on a modified Shields diagram to contextualize the erosion thresholds within established sediment transport theory. In epibenthic (TI) mats, initial erosion is reported between 0.9 and 1.6 m/s in 3-5 cm of water depth, a shear strength nine times greater than abiotic comparisons (Noffke, 2010). In the case of endobenthic (TII) mats, initial erosion is reported between 0.3 and 60 cm/s in 3-5 cm of water depth, a shear strength 3-5 times greater than abiotic sediments (Noffke, 2010). In both cases, measurements show that the shear strengths of biotic sediments are enhanced in comparison to the expected shear strength for abiotic sediment of similar properties.

Thirty-five quantitative data points were obtained from published studies included in this review. Of these, 33 data points plot above the Shields' diagram (Fig. 2), suggesting that microbial presence measurably increases the predicted threshold of particle motion. The microbial mat-enhanced Shield Parameters range from 0.01 to more than a 3800-fold increase over modelled abiotic sediment (Fig. 2). For fine sand, the velocity associated with the abiotic threshold of erosion is

approximately 0.02 m/s, and we find that vast majority of biostabilized fine sand sediments withstand velocities exceeding this velocity. These findings suggest further variables exert considerable influence on the degree of stability introduced by the microbial mat, such as chlorophyll or carbohydrate composition (Sutherland et al., 1998; Friend et al., 2005; Waqas et al., 2020).

The reported rheological research is decidedly influenced by several factors. One factor is simply the definitions of certain parameters or thresholds. For example, the critical bed shear stress value often stems from incipient motion of sediment grains (Dey, 1999; Noffke, 2010). Some studies define this as when 20+ particles move simultaneously (Fang et al., 2014), whereas others focus on observable erosion (Dade et al., 1990). Another is when the microbial mats flip or roll at certain velocities (Hagadorn and Mcdowell, 2012). Cohesive strength meters and turbidity sensors measure erosion by monitoring light transmission reduction due to suspended sediment, and require calibration (Paterson et al., 2000; Lundkvist et al., 2007).

Results are variably reported in pascals, newton per square metre, current velocity, or BI. An early study used stirrer speed in revolutions per minute to report when sediment resuspended (Holland et al., 1974). A few experiments were strictly observational and focused on bedform migration or erosion following microbial mat removal using CuSO₄ solution (de Boer, 1981), tracking MISS formation and erosion using successive photographs (Cuadrado et al., 2011) or observing bedform steepness (Fang et al., 2017). Similarly, a recent study used aerial and satellite imagery to assess geomorphological changes in back barrier environments and found microbial mats were acting as stabilizers, affecting the geomorphological dynamics of the back barrier system (Fisher et al., 2023). Finally, experiments have been conducted both in situ and under laboratory conditions. Laboratory conditions (e.g., sorting and packing) impact sediment erodibility (Paterson, 1997), while in situ measurements bias towards intertidal settings for practical reasons.

The above variances produce diverse results for the strength properties of microbially colonized sediment. Clearly, more research regarding the rheology of microbial mats is merited. Future research should focus on documenting the shear stress involved with microbial mat failure and fully establishing the underlying sediment and biogeochemical properties.

Wave generated shear stress $\underline{\mathrm{versus}}$ the shear strength of biostabilized sediments.

With the above in mind, there remains the question of what magnitude of energy is potentially present in shallow marine sedimentary environments that a microbial mat might need to withstand in order to proliferate.

Sediment dynamics in relation to current energy have been explained by models like Hjulström's curve and Shields' diagram, which investigate grain motion thresholds under conditions of unidirectional hydraulic currents (Shields, 1936; Hjulström, 1939). A great deal of work has also revised Shields' original model to account for complications such as the presence of cohesive sediments (Righetti and Lucarelli, 2007; Miedema, 2013). Furthermore, shallow marine environments exhibit the added complication of wave-associated currents contributing to bed shear stress. Where possible, based on what parameters were reported in the study, literature examples are shown in relation to a general Shields' diagram in Fig. 2. Thirty-five data points from the literature included in this review provided enough data to compare to the Shields' diagram and they confirm the wide variability observed in this dataset.

There are few published studies that measure the shear stress associated with wave induced (combined flow) conditions in shallow water, with more examples utilizing models. Some examples are as follows. Measurements and models of wave-induced bed shear in shallow marine environments include results exceeding 5 Pa in water depths ranging from 10 to 20 m on the southwest coast of England (Valiente et al., 2019). Another study measured velocity 1 m above the seafloor in water depths ranging from 3.4 to 5.0 m on the fine sand shoreface of Tibjak

Beach, northern Canada, and reported a mean current velocity of up to 0.49 m/s, with fairweather conditions of less than 0.08 m/s (Héquette and Hill, 1993). Measurements from the San Francisco Bay, USA measured combined-flow bed shear stress values up to 2.75 Pa 5 and 15 cm above the seabed and reported a mean value of 0.13 Pa (Chang et al., 2022). Values were modelled for the French-Spanish shelf to show bottom shear stress ranging from 0.01 to more than 1 Pa in less than 30 m of water on the inner shelf (Dufois et al., 2008). Similarly, modelled numbers for the combined-flow shear stress for Australian shelves reported a range of 0.057-0.4 Pa in water depths of 10-27 m (Hemer, 2006). A study based on measurements 0.65 m above the seabed from northern France, along a macrotidal middle to upper shoreface in approximately 5 m water depth, found the combined flow shear velocity ranged from less than 0.012 m/s to 0.12 m/s at Dunkirk and exceeded 0.015 m/s at Calais during the duration of the experiment (Héquette et al., 2008). Values modelled for Canadian continental shelves found mean combined-flow bed shear velocity of more than 0.05 m/s (Li et al., 2021).

Studies have also reconstructed the conditions required to form sedimentary structures like hummocky cross-stratification, which are classically associated with shoreface environments in clastic shallow marine settings (Dumas and Arnott, 2006). The study reported that hummocks formed in a wave tunnel with oscillatory velocities of 0.5–0.9 m/s, unidirectional currents of 0.05–0.01 m/s, and long wave periods of 8–10 s. Raising the unidirectional current above 0.1 m/s produced dunes. Studies also show that cyanobacteria may double the fluid velocities required to produce physical sedimentary structures like ripples and dunes (Hagadorn and Mcdowell, 2012).

Under the admittedly flawed assumption that variably oriented unidirectional currents produced by waves are analogous to unidirectional currents produced by gravity in fluvial settings, these data for combined flow conditions are included in Fig. 2. Of the above values, 8 plot above the threshold of incipient motion on a general Shields' curve (Héquette and Hill, 1993; Dumas and Arnott, 2006; Dufois et al., 2008; Valiente et al., 2019; Li et al., 2021; Chang et al., 2022), while 6 plot below the threshold for expected incipient motion (Héquette and Hill, 1993; Hemer, 2006; Dufois et al., 2008; Héquette et al., 2008; Chang et al., 2022) (Fig. 2). This suggests that the range of hydraulic energies in shallow marine settings are not entirely antagonistic to the development of microbial mats. The strongest recorded microbial mat may be able to withstand the highest shear stresses reported, but the range of shear stresses that microbial mats can withstand is similar in range to that of shear stresses measured in shallow marine wave-influenced sedimentary environments (Fig. 2). Based on these considerations it seems likely that some microbial mats were vulnerable to erosion in such energetic (i.e., wave-influenced) settings.

Distribution of siliciclastic microbial mats in the rock record.

Microbial mats were common in shallow marine depositional systems since at least 3.5 billion years ago (Tice and Lowe, 2004; Reitner et al., 2011; Noffke et al., 2013; Duda et al., 2016), but they then became restricted to extreme environments following the evolution of grazing and burrowing animals (i.e. the Agronomic Revolution and Cambrian Substrate Revolution) (Mángano and Buatois, 2017; Seilacher, 1999). The ranges of paralic, clastic sedimentary environments that include marine microbial mats as fossils in the geological record is broad and includes the outer through inner shelf and ramps, shoreface, intertidal and lagoon (Table 2). Several studies also report inexact depositional settings, in particular 'shallow marine'. It should be noted that there are few examples of evidence of microbial mats in the middle and upper shoreface (Chakraborty et al., 2012; Buatois et al., 2013).

Table 2 is a compilation of the literature that reports both microbial mats and their sedimentological occurrence – at least for marine clastic settings. The table summarizes the age and marine depositional environment of 57 microbial mat occurrences in the rock record. These span much of Earth's geological record from the Archean to the Miocene. Their depositional settings include deep through shallow-water

occurrences. Of these, 32 are definitively below fair-weather wave base including shelf, ramp, offshore, lower shoreface (sporadically reworked), lagoon and estuary. Five occurrences are within the middle or upper shoreface. Eight occurrences are sub- to inter-tidal flat. The remaining 13 are "shallow marine" and the information to refine these interpretations was not available.

The preservation potential of MISS should also be considered. As with other biogenic sedimentary structures, conditions must facilitate their preservation. In the case of microbial mats, the intersection of their ecological and taphonomic windows determines their preservation (Noffke et al., 2002). As discussed above, the ecological window demands adequate water, light, and nutrients, as well as conducive hydrodynamic conditions: the shear stress of the water present must not exceed the stabilizing properties of the mat, but should be high enough to inhibit sediment accumulation on the mat surface (Noffke et al., 2002). Sedimentary events must bury the microbial mat without completely destroying MISS (Noffke et al., 2002). Importantly, the EPS present in sandy substrates lowers vertical permability (Ref kinneyia structures) lowering the migration of water and gases from the substrate to the seafloor. This can lead to in situ mineralization of the organic matter (e.g. pyritization; Gehling, 1999), even in oxygenated environments with the nature of the organic matter dictating the type of mineral (Kah and Knoll, 1996; Tice et al., 2011; Alleon et al., 2016; Hickman-Lewis et al., 2020; Noffke, 2021). Noffke (2021) asserts that MISS are primarily associated with transgressive systems tracts (TST sensu Catuneanu, 2006) (Noffke, 2021; Noffke et al., 2002). Given that TST are associated with increasing accommodation space, this maybe a reasonable conclusion, however, the prior statement is admittedly based on few studies (Noffke, 2021).

Despite the stabilizing effects of microbial mats, they are predominantly preserved in quiescent settings. The very occurrence of hummocky cross-stratification in rock measures attests to this fact as it is an aggrading oscillation energy-formed sedimentary structure that represents a response to high wave energies often associated with storms, and thus preclude microbial stabilization. That said, 5 of the cited examples do occur within persistently wave-agitated parts of the shoreface, suggesting that microbial mats have limited viability in wave-influenced settings, at least during fairweather intervals between storm events. Interestingly, there is some evidence that "biostabilization is disturbance-stimulated, rather than disturbance-limited". This is because recently disturbed sand beds stimulate microbial EPS production, suggesting that newly disturbed sand beds, such as those in high energy settings, favor microbial colonization (Chen et al., 2022). This is supported by earlier works that found that sediments under flowing conditions exhibited greater resistance to erosion than those formed under quiescent conditions (Droppo et al., 2001). In a more recent study, this idea was further explored by observing biofilms that were cultivated for 5 or 10 days and episodically "eroded" by increasing the shear stress applied in a flume (Chen et al., 2022). These samples were then compared to biofilms cultivated under a low, constant bottom shear stress. The biofilms exposed to higher and more frequent shear stress events exhibited greater shear strength. The authors suggest that this may be because of remnants of the original biofilm in the sediment after an erosional event that stimulate and accelerate the process of recolonization (Chen et al., 2022). Based on this synthesis, the threshold of sediment entrainment still dictates the upper limit of pervasive microbial mat colonization, and so there is a hydraulic limit to where microorganisms can permanently colonize, but the above findings may partially explain the wide range of hydraulic energies observed. Accordingly, in the rock record, we observe MISS in lower energy settings (e.g., below fair-weather wave base). In short, we conclude that microbial mat distributions were largely limited to locales that were sheltered from wave energies or were below fair-weather wave base, as the rheological dataset above indicates.

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during the Archean, it is generally accepted that the volumes of tidal prisms were notably larger (Crawford et al., 2022).

Although it is difficult to parameterize the magnitude of tidal currents in ancient environments, greater tidal volumes logarithmically increase tidal current velocities. Although the magnitude of tides varies substantially with latitude, shelf, and coastline geomorphology, there would have been large portions of the world coastlines that would have precluded microbial colonization of sediment. For example, tidal currents in (mesotidal) Puget Sound, USA (in this case, near Puffin Island) routinely have flood and ebb currents in excess of 40 cm/s (Pentcheff, 2024). In macrotidal settings, such as the Minas Basin in the Bay of Fundy, currents exceeding 350 cm/s are common (Cornett et al., 2010). Noffke (2010) proposed that tidal environments favor different types of mats in different intertidal zones. The lower intertidal is associated with Type III biostabilization, the biofilm type; the upper intertidal is associated with Type II biostabilization, endobenthic mats; the lower supratidal zone is associated with Type I biostabilization, the epibenthic mat for the study areas investigated (Noffke, 2010). Noffke (2010) further speculated that micro-, meso-, and macrotidal settings exhibited characteristic microbial mat distributions, however more data are needed to fully establish a tide / microbial mat landscape.

These findings set the stage for a broader conversation. Microbial mat distributions are thought to be more widespread before the evolution of (microbial mat-feeding) animals (Seilacher, 1999). However, as discussed above, factors beyond mat-feeding metazoans also dictate the presence or absence of microbial mats (e.g. ultraviolet radiation intensity on the microbial mat surface, potential for desiccation, and nutrient limitations) (Stal, 2012; Gerbersdorf and Wieprecht, 2015). Hydraulic energies present an additional factor to consider and despite the understanding that microbial mats stabilize sediment, that effect has, as demonstrated, been considered primarily as a function of growth conditions rather than the context of characteristic sedimentary environments. Importantly, some recent research indicates that cyanobacteria may have become established in continental settings as early as the Paleoproterozoic (Sánchez-Baracaldo, 2015). However, it is important to recognize the preliminary nature of such findings. More critically the spatial significance of fresh-water biomes, even today, does not rival the areal extent of marginal- and shallow-marine environments. Estimates vary, but freshwater settings rarely exceed 3 % of Earth's areal extent, whereas 71 % of the area of the planet is covered by oceans (Shiklomanov and Rodda, 2004; Downing et al., 2012). Using the ETOPO1 relief dataset, the total area of oceans covered by water of a depth of less than 50 m, well within the photic zone, is approximately 3.74 % of Earth's total surface area (NOAA National Geophysical Data Center, 2009).

However, establishing reasonable constraints on microbial mat distribution is important. Firstly, microbial mats influence sedimentary environments not only by stabilizing the sediment-water interface, but by greatly limiting solute exchange between porewater and bottom water with consequences to the geochemical conditions below the sediment-water interface and in bottom waters (Aller, 1982). Secondly, if microbial mats in subaqueous settings become limited owing to the evolution of animals, how do the above considerations impact our understanding of the Agronomic Revolution, the Cambrian Substrate Revolution, and Lower Paleozoic biomes? Finally, if microbial mats were an important contributor to oxygenation of the oceans, then having a firm understanding of their distributions in the rock record is critical to establishing the extent of their presence in the photosynthetically important shallow-water marine settings. Addressing any of these three research topics requires as refined an understanding as possible of microbial mat distributions. This synthesis adds the dimension of hydraulic energy.

6. The importance of parameterizing biostabilization

The erosion of microbial mats in paralic settings is not limited to wave erosion. As a result of the Earth's moon being closer to the Earth

There are numerous applications of parameterizing the effect of

biostabilization including coastal management (Bone et al., 2022), problems of taphonomy (Janssen et al., 2022), and the refinement of modelling inputs. Prediction of benthic microorganism distributions and their productivities are limited by many factors: however, although chemical limitations are often considered, physical limitations, such as those imposed by hydraulic energies, are less often included in these models (Planavsky et al., 2021). The usage of biostabilization in coastal geomorphology and increased stability of coastal infrastructure is also discussed below. In both cases, the spatial restrictions of these benthic microorganisms should be considered. Here we present an application of note focused on the relationship between cyanobacteria and early Earth history: the role of physical constraints in modelling the rates of atmospheric oxygenation during the GOE, and the applications to coastal protection.

6.1. The Great Oxidation Event

Filamentous benthic cyanobacteria are considered important early contributors to the oxygenation of Earth's atmosphere, having evolved prior to planktonic species (Schirrmeister et al., 2015; Hamilton, 2019). There is some debate as to whether these filamentous species originated in marine or freshwater settings, as well as conflicting evidence regarding timing of photosynthetic evolution from different methods such as lipid biomarkers or fossils (e.g. Blank, 2008). At the time of the GOE, there is evidence of mat-forming microorganisms in both shallow marine and intertidal settings (Noffke et al., 2003b, 2008; Tice, 2009; Davies et al., 2016; Homann et al., 2018). The occurrence of benthic cyanobacterial mats is limited by several environmental factors: the depth of the photic zone, particle size, magnitude of irradiance, availability of nutrients, water salinity, seasons, species of microorganism, life-stage of microorganisms, and the hydraulic energy of the depositional setting to name a few (Stal and Caumette, 1994; Friend et al., 2005; De Backer et al., 2010; Thom et al., 2015; Schmidt et al., 2016; Cardoso et al., 2019; Waqas et al., 2020).

There have been several approaches to modelling the rates and mechanisms of atmospheric oxygenation during the GOE (Towe, 1990; Ward et al., 2016; Planavsky et al., 2021; Jaziri et al., 2022; Wogan et al., 2022). In general, these models use various percentages of modern productivity levels to predict the equivalent amount of oxygen produced in the time frame considered in the model (e.g., Towe, 1990; Ward et al., 2016). This amount of oxygen is then used to balance various sinks (e.g. Fe concentrations). Spatial limitations are typically not considered in these models, with only a few studies accounting for possible areal constraints (e.g., Planavsky et al., 2021). In one other study, the spatial dimension taken into account is altitude (Wogan et al., 2022). There is also, as previously discussed, molecular evidence suggesting that marine planktonic cyanobacteria were derived from older benthic, freshwater cyanobacteria (Rye and Holland, 2000; Sánchez-Baracaldo, 2015) further confounding our understanding of photosynthetic sources at this time. In short, areal constraints, and in particular, physical limitations such as the depth of the photic zone, the turbidity of water, and hydraulic energy are typically unaccounted for. In this sense, mat distribution is as much a matter of physical limitations as are the metabolic pathways heavily favoured in models of oxygenation rates. To produce accurate models, the total possible area populated by benthic microbial mats should be accurately assessed in the calculation of possible rates of oxygen production. This is particularly important in terms of understanding how cyanobacterial evolution relates to the GOE.

There is a significant body of evidence that supports the timing of the GOE; Briefly, this includes the disappearance of detrital pyrite, uraninite and siderite from fluvial and deltaic deposits, an increase in the retention of iron in paleosols, an enrichment of chromium and uranium in iron formations, and perhaps most importantly, the disappearance of sedimentary sulfur isotope mass-independent anomalies indicative of atmospheric SO₂ processing in the absence of appreciable ozone (e.g. Mills et al., 2023 for review). However, several geochemical proxies (e.

g. Planavsky et al., 2014) and molecular clock estimates (Sánchez-Baracaldo et al., 2022) have suggested that cyanobacteria evolved by at least 3.0 Ga, and perhaps even earlier (Boden et al., 2021). A remaining question that follows from this hypothesis is what happened in the hundreds of million years between the first production of O2 and the GOE? While the exact confluence of factors controlling the success of Earth's earliest oxygenic phototrophs remains an open question (Planavsky et al., 2021) several hypotheses have been put forth to account for depressed cyanobacterial efficiency, including rapid rates of clastic and pyroclastic influx (Knoll, 1979) nutrient limitation (Bjerrum and Canfield, 2002) a lack of emergent continents and thus limited areal extent for mat formation (Lalonde and Konhauser, 2015), iron toxicity (Swanner et al., 2015), and/or exposure to unfiltered ultraviolet irradiation (Mloszewska et al., 2018). What has not yet been considered is the inability of cyanobacterial mats to colonize shallow, wave agitated marine environments.

6.2. Coastal protection

Coastal erosion is a growing concern due to the impacts of climate change and rapid coastal development, which have led to accelerated erosion rates (Perricone et al., 2023). Traditional infrastructure for coastal protection such as seawalls, jetties, breakwaters, or rock groynes are associated with a range of negative ecological consequences like ecosystem degradation and a loss of biodiversity (Moosavi, 2017; van Slobbe et al., 2013). In the search for solutions to this growing issue, some researchers have turned to nature for inspiration, utilizing ecosystem engineers like coral or oyster reefs, mangroves, saltmarsh vegetation, seagrasses, or polychaete reefs as natural barriers to increasingly destructive hydrodynamic activity (Perricone et al., 2023). This concept is often called 'bioprotection' in the literature (Carter and Viles, 2005; Coombes et al., 2013; Gowell et al., 2015). The process of biostabilization has also been considered as a potential mitigation tool to protect coastal developments from waves, tides, and currents utilizing mat-forming microorganisms (Noffke, 2010).

The footprint of marine infrastructure is predicted to be $39,400 \text{ km}^2$ by 2028: this includes structures for aquaculture, commercial shipping, recreation, energy production, transportation, cables, and coastal protection (Bugnot et al., 2020). Already, it's estimated that approximately 14 % of the shorelines in the U.S.A. and over half of urban shorelines have undergone "shoreline hardening", defined as the installation of engineered structures to stabilize sediment, prevent erosion, and provide flood protection (Gittman et al., 2015, 2016). These include concrete, positioned boulders, gabions, plastic matting, or rock mattresses, which can be expensive, logistically impractical, carbon intensive, or disruptive to natural geomorphological processes and ecological communities (Schindler et al., 2023).

Biofilms have been proposed to protect coastal infrastructure (Bone et al., 2022) by facilitating mineral precipitation making anthropogenic structures 'harder' or 'self-healing'. Also, the idea of using biostabilized sediments to prevent scour and erosion has recently become of interest to the engineering and coastal management communities (e.g. Schindler et al., 2023). As discussed above, a recent study showed that the addition of EPS to cohesionless sediments reduced scour depth and the volume of material eroded (Schindler et al., 2023). The study found a strong linear relationship between EPS content and sediment resistance to scouring.

A recent study sought to distinguish between the effects of added EPS to sediment alone and that of a biofilm (Ge et al., 2024). The authors found that in the first 17 days, added EPS and developing biofilms exhibited similar shear strengths, but after the 17-day mark, biofilms surpassed the EPS-sediment mixture (Ge et al., 2024). The increase in shear strength is attributed to the "larger-size aggregates" produced by the biofilm (Ge et al., 2024). This study also concluded that more research is merited to understand the effect produced by various microbiota under different physicochemical conditions to practically apply this research (Ge et al., 2024).

While these studies are indeed promising, our results, if viewed from a sedimentological perspective, suggest the solution may be more complex. The range of shear strengths documented here provide a framework for the degree of shear stress where this application might be suitable. One might be able to stabilize the backshore, or other quiescent or sheltered settings with inoculated sediments, however, based on our synthesis, it seems unlikely that the upper shoreface, or any hydrodynamically energetic setting, can be effectively colonized by microbial mats. During storm events, for example, it is the retreat of the shoreface and foreshore setting that functionally results in shoreline erosion. During large storms with deepening waters associated with coastal setup, the foreshore is exposed to wave energies similar to the upper shoreface (Stockdon et al., 2006; Billson et al., 2019; Lobeto et al., 2024). Our results would suggest that few to none of the studies presented here would suggest that microbial mats can withstand such energies. As stated by Schindler et al. (2023) we agree that more research is required as to the types of biopolymers used in this application of biostabilization and other engineering and environmental considerations.

7. Conclusions

In this review, we summarized the current literature pertaining to biostabilized siliciclastic sediments, as well as their distribution in the rock record of clastic, paralic settings. A diverse set of methods and results is presented here from the existing literature. Studies range from observational, to in situ measurements, to controlled laboratory experiments, with varying definitions of incipient motion or mat failure. This diversity leads to a wide range of results dependent on a suite of variables including the assemblage of microorganisms and environmental conditions such as substratum grain size, light intensity and timing, and nutrient availability. Hydrodynamic conditions also undoubtedly play a role in the establishment and proliferation of microorganisms in these sediments. Despite wide variability, the overwhelming result is some level of increased resistance to erosion in microbially fixed sediments. As such, we conclude the following:

- The current literature represents studies conducted using a variety of methods due in part to the multidisciplinary nature of this subject. While these various approaches can be positively viewed as contributing to understanding microbial mat rheology, the resulting datasets are variably presented and not entirely comparable. We have tried here to address these inconsistencies in order to provide an overview of the currently available data on this topic. Challenges in comparing these data include factors such as determining thresholds for microbial mat failure or the onset of grain movement, as examples.
- 2. Factors such as the specific organisms stabilizing the sediment and various environmental conditions contribute to a wide range of biostabilization outcomes.
- 3. Although microbial mats are shown to stabilize sediment, the context of that stabilization regarding characteristic hydraulic energies of sedimentary environments remains unresolved, especially in comparison to the rock record. The similarities between measured microbial mat shear strength and the shear force applied by measured and modelled currents indicate that some microbial mats are susceptible to erosion in wave-influenced settings. This is generally supported by the rock record, in which we observe that MISS are typically preserved in more quiescent settings such as below fairweather wave base (FWWB) or in intertidal settings. The distribution of microbial mats in the rock record supports the interpretation that wave-influenced settings, at least above FWWB, have sustained limited microbial colonization throughout geological time. Highenergy events and even particularly strong tidal currents would likely preclude widespread microbial colonization.
- 4. Finally, future rheological studies of biostabilized sediments are warranted as many aspects as possible of the complex interplay

between microbial mats and sediment dynamics are unresolved. Particular attention should focus on the interaction of organism specific- and environmental-variables. These studies have applications to our understanding of deep time such as the GOE, which is often modelled without considering the limitations of the hydrodynamic regime. An additional application in its infancy of research is the use of biostabilization in the protection of coastal infrastructure through the addition of EPS to coastal sediments.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

All data used in this review are included in the manuscript tables.

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