## AN OVERVIEW OF MICROBIAL INTERACTIONS WITH SEDIMENT DYNAMICS

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#### ABSTRACT

In aquatic environment, microorganisms such as bacteria and microalgae usually secrete a matrix of mucilaginous extracellular polymeric substances (EPS) to form a "microbial biofilm" when they are associated with solid surfaces (e.g., sediment particles, plant surfaces). Biofilms and the associated mucilaginous secretions form a cohesive matrix surrounding sediment particles, modifying the sediment properties, changing the sediment stability, and influencing the sediment dynamics. The purpose of this overview is to examine recent information concerning the roles of microbial interactions with sediment dynamics. The microbial biofilm affects a number of changes on the physico-chemical and biological properties of sediment particles. Also microbial biofilms are associated with considerable variability in the properties of natural sediments. Sedimentological factors and biological factors interact in a complex manner within the hydrodynamic regime both on a temporal as well as on a spatial scale.

Keywords: sediment; biofilm; biostabilization; biological and sedimentological factors; bioflocculation

### **1. INTRODUCTION**

Sedimentary systems are governed by a series of dynamic processes such as erosion, transport, deposition and deformation, which create numerous sedimentary structures, including ripple marks of different morphologies and dimensions, current laminations, ball and pillow structures, convolute bedding, bubble sand, and so on (Noffke N & Paterson D, 2008). Physical sediment dynamics, usually accompanied by the associated release and relocation of contaminants in aquatic environment, is an important element that must be considered in the plans development of modern integrated management of rivers and coastal areas (Paterson et al., 2000; Foerstner et al., 2004). The possibility of sediment erosion occurrence and the degree in terms of erosion rates and depth are determined by the interplay of two kinds of forces imposed on sediments with different effects, one is the hydrodynamic forcing (e.g. river flow, tidal flow, density driven circulation and wind waves) and the other is the resisting forces (e.g. sediment cohesion, gravity, biogenic stabilization) (Gerbersdorf et al.,

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2008). The physico-chemical sediment properties, such as bulk density, particle size, mineralogy and organic carbon content, have become the main considerations in most studies aiming to elucidate the mechanisms governing the stability of cohesive sediments (Jepsen et al., 1997; McNeil & Lick, 2004). However, sediment is not composed of mineral particles alone. Great varieties of microorganisms colonize the sediment and exert influences on the sedimentary dynamics. The microbiota that colonize the sediments come into play, interacting with physical and chemical Whereas the interaction parameters. of microorganisms with sediment dynamics has become a main focus of many studies (Noffke N & Paterson D, 2008). In recent years, the importance of biogenic influence on sediment dynamics, the mucilaginous matrix especially by of extracellular polymeric substances (EPS) produced by bacteria, microalgae and macrofauna, has received a more and more increasing attention (Paterson, 1997; de Brouwer et al., 2000; Decho, 2000; de Deckere et al., 2001). Studies showed that biological processes even seem to be the major impact factor of sediment cohesiveness in some intertidal areas (Black et al., 2002). Therefore, with respect to the physico-chemical sediment properties, many detailed field-studies have also been carried out in order to evaluate and sometimes quantify the effect of biological factors on sediment dynamics. These studies have all shown that biological factors, such as the microbial activities and their metabolic products, may have a significant influence on the sediment dynamics. Sediment dynamics has been well-documented by microorganisms (Yallop et al., 1994; Riethmüller et al., 2000) which secrete EPS during their metabolic activities.

### 2. MICROBIAL BIOFILM IN AQUATIC ENVIRONMENT

When microorganisms such as bacteria and microalgae are associated with solid surfaces (e.g., sediment particles, plant surfaces), they secrete a matrix of mucilaginous extracellular polymeric substances (EPS) to form a "microbial biofilm" (Fig. 1). EPS are the primary structuring agent for microbial microenvironments, which control the physical properties of biofilms. In aquatic environment, biofilm and the associated mucilaginous secretions form a cohesive matrix surrounding the sediment particles and produce a significant impact on the sediment dynamics, which make microbial biofilm become a focus studied solely of its influence on sediment dynamics in recent years.



**Fig. 1** Conceptual diagram of a microbial biofilm within a solid surface. The biofilm consists of microbial cells such as diatoms, cyanobacteria, heterotrophic bacteria embedded within a matrix of extracellular polymeric secretions (EPS) which closely surround the solid.

Biofilm exists in aquatic environments, especially with more obvious performance in the polluted waters. Biofilm not only plays an important role on the absorption and degradation of the pollutants in water system, but also strongly changes the characteristics of sediment particles, such as the morphology, bulk density, water content, plasticity, mechanical properties, and so on. Because of the frequent exchange of materials, rich nutrients and severe life events in the border zones of brackish/fresh water and the junctions of land and sea, the effect of biofilm in these areas is particularly significant. So nowadays most related studies are focused on marine-related systems and only a few on freshwater systems. As the effect of biofilm on the bed stability is mostly concentrated in the junctions of land and sea or the estuary areas, the study object is mainly fine sediment. It is generally believed that why biofilm could strengthen the stability of bed sediment especially the fine sediment, on one hand is because the biofilm growth can form a relatively smooth and stable surface, and on the other is because the EPS secreted by the microorganisms can adhesion the sediment particles together. So the flow shear stress should overcome not only the cohesion between the particles but also the adhesive force between the particles established by the biofilm. Andersen (2001) examined the erodibility of two microtidal mudflats and found that the seasonal variation of the erodibility at the two sites is actually opposite to each other with high erodibility in the summer period at the site dominated by macrofauna and low erodibility at the site with a scarce macrofaunal population. This shows that complex interactions exist between benthic diatoms (which stabilizes the surface) and macrofauna (which often destabilizes the surface). Such interactions will have to be further evaluated and included in modeling tools when predictions of the sediment dynamics at fine-grained deposits are needed. Tolhurst (2008)investigated the development of a microphytobenthic biofilm and associated changes in the sediment over 45 days and found that biofilm developed rapidly and gradually formed a multi-level structure with a certain thickness. But there is also some researches (Stal, 2003) believe that the correlation between bed anti erodibility and biofilm is not so significant. So there are still controversies about the mechanism of bed stability enhanced by the microbial biofilm, which needs further study. It is noteworthy that the water environments of freshwater and seawater as well as their biocoenosis are completely different. Therefore the formed biofilms are unequal. The effect of biofilm on the sediment particles in the marine

environment is different from that in the freshwater system. It is generally believed that the microorganisms in the water stick the sediment particles together through biofilm, inducing the changes of sediment characteristics (Vignag, 2009). Biofilm packs sediment, fills the gap between the particles and provides more ion adsorption sites. It is found that the critical drag force of surface particles is related with the biomass and biofilm. Under the biofilm influence, the critical drag force fluctuated over time. Although the biofilm could still enhance the particle stability with time after the emergence of the largest critical drag forces, the degree of enhancement declines. With the deep study on various characteristics of biofilm, the knowledge of biofilm formation, composition, structure and function has made considerable However, in many researches progress. the alternative substrates are used to culture biofilm under some specific conditions in the laboratory, so the understanding about the role of biofilm in the natural water environment and its effect on sediment dynamics also subject to a certain degree of restriction. In the study subjects, the research of biofilm in water environment present a tendency from that in sea water to that in fresh water. The key research questions, including the difference of effect on biofilm between the seawater and freshwater environment, the mechanism of biofilm on the sediment dynamics, etc., need to be further explored. Further study on biofilm would be of broad and important significance for the development of sediment dynamics.

# **3. EFFECT OF MICROORGANISMS ON SEDIMENT STABILIZATION**

Sediment stability is very important for cohesive sediment dynamics. In the traditional study, researchers regarded the physico-chemical conditions as the most important drivers of sediment stability. However, the sediment stabilization mainly induced by biological activities, especially the influence of highly hydrated matrices of biofim, has gradually been given an increasing attention in the last decades. With an increasing amount of reports of biological effects on erodibility of fine-grained sediments, 'biostabilization' (Paterson, 1994), which refers to the fixation of sediment by the influence of microorganisms, has become a focus of many studies. Yet the effect of microorganisms on sediment (de)stabilization is complex. On the whole, the influence can be categorized into two groups: the stabilization/deposition of sediment by binding and destabilization/erosion the of sediment bv

bioturbation (Rhoads et al., 1978). When coming to the sediment stabilizing effect of biofilm, the EPS adhesive mucilaginous secreted bv microorganisms is well understood. Some researches demonstrated that EPS plays an important role in the stabilization and deposition of sediment. EPS probably exerts its effect by binding sediment grains (Paterson, 1997; Wustman et al., 1998), decreasing drag (Paterson, 1999; Deckere et al., 2001), or by inclusion of particles in reinforced EPS networks such as tube-like structures (de Brouwer et al., 2005). Therefore EPS would increase the sediment stability, especially on the surface of intertidal muddy sediments (Underwood & Paterson, 1993; Kornman et al., 1998) and enhance the deposition of sediment particles (de Brouwer et al., 2000; Herman et al., 2001). And although frequent resuspension of intensively bioturbated sediment by wind-driven waves and tidal currents may be resulted because microorganisms change the characteristics and placement of individual sediment particles as well as the bulk characteristics and the boundary properties of the sediment surface (Nowell & Jumars, 1984), the excretion of EPS especially by microorganisms binds sediment particles thereby reducing sediment resuspension (Grant et al., 1986; Paterson, 1989). The growth of biofilms, referring to cells within a matrix of extracellular polymeric substances secreted by microorganism, has been shown to be important in mediating the properties of and the processes in muddy sediments (Paterson, 1997; Black et al., 2002). The net effect of biofilm growth is usually considered to be stabilising, however, microorganisms such as diatoms can destabilise sediments (de Jonge&van der Bergs, 1987; Sutherland, 1998) and natural biofilms exhibit a wide range of erosion thresholds (Defew et al., 2002). The stabilising effect of biota is usually attributed to the secretion of EPS; however, recent work indicates that the relationship may be more complex, with the microorganisms themselves being important in structuring or stabilising the EPS and sediment (de Brouwer et al., 2002; Tolhurst et al., 2003; de Brouwer et al., 2005). On the other hand, a lot of laboratory flume studies indicated that the net effect of microorganisms appeared to be destabilizing (Luckenbach, 1986; Grant & Daborn, 1994). Result of the experiment in situ flume studies at Skeffling mudflat in Humber estuary combined with laboratory studies showed an increasing erodibility when bioturbation activity by Macoma balthica increased (Widdows et al., 1998ab). Similar results were found for Cerastoderma edule, but there was also a positive correlation between the Cerastoderma density and biodeposition. In some

cases, both stabilization and destabilization of the sediment by a single species was observed. For instance, Gerdol and Hughes (1994) found that the amphipod Corophium volutator caused destabilization of the sediment bed due to grazing on microphytobenthos and reworking of the sediment by burrowing and tube formation. In contrast, Mouritsen et al. (1998) attributed the stabilization of well-defined bed structures to the presence of Corophium volutator. They suggested that the coating of the walls of burrowing holes by EPS was responsible for the observed stabilization (see also Meadows et al., 1990).

### 4. INTERPLAY BETWEEN BIOLOGICAL AND SEDIMENTOLOGICAL FACTORS

There are many key-parameters for the transport of cohesive sediment, including the critical bed shear stress for erosion (the erosion threshold), the erosion rate, the settling velocity of the material, and so on (Andersen, 2005). These parameters mainly depend on the physical and chemical characteristics of the sediment, such as water content, bulk density, mineralogy, plasticity, salinity, and the adsorption and cation exchange capacity (de Deckere et al., 2001). None of these parameters could easily be predicted based on the distributions of grain sizes. both due to the cohesive nature of the sediment and the generally strong biological interaction in the important processes (Widdows and Brinsley, 2002). The physical and chemical characteristics of the sediment are modified by the microbial activities (Paterson et al., 1999). Researchers (Yallop et al., 2000; de Brouwer et al., 2005) found that sediment stability correlated with a range of biological variables, including the concentration of chlorophyll a, the extracellular carbohydrate and EPS fractions. water content, bacterial biomass, and so on. Over the last decades, biological factors of sediment stabilisation have been given increasing attention in many studies. Meanwhile microbial biofilms are believed to be associated with considerable variability in the properties of natural sediments. EPS binding capacity is clearly affected not only by the local physico-chemical environment, but also by the characteristics of sediments in aquatic systems (Shin et al., 2001). Many biological factors, such as the taxonomic composition of benthic communities, their physiological state and bacterial action, which in turn depend on the abiotic conditions, would exert significant influence on the biofilm nature (de Brouwer & Stal, 2001). Therefore, some studies have addressed the reciprocal influence of biology and sedimentology, especially with regard to sediment stabilization (de Brouwer et al., 2000;

Gerbersdorf et al., 2005, 2008). It has been well known that biological and sedimentological variables sometimes show patterns of covariance (de Brouwer et al., 2003). Referred researches (Brouwer, 2000; Sabine et al., 2008) usually study the mutual interrelations between biological activity physico-chemical properties from and the macroscopic view, and nowadays most are limited to field sampling, data extracting, and then building the attachment of corresponding factors by some direct correlation analysis. By using multiple regression analysis researchers discovered that sediment stability in their laboratory mesocosms was best predicted by using a combination of biogeochemical properties of sediment particles, including many biological and sedimentological factors, such as bulk density, water content, mineralogy, plasticity, cation exchange capacity, the concentration of chlorophyll a, the concentration of pheophytin, the concentration of colloidal carbohydrate, and so on (de Brouwer et al., 2005; Gerbersdorf et al., 2005; Tolhurst et al., 2008; Gerbersdorf et al., 2008). The studies indicated that sedimentological factors and biological factors interact in a complex manner within the hydrodynamic regime both on a temporal as well as on a spatial scale. Nowadays it is believed that microorganisms and their metabolic activities would interact with the sedimentological factors to influence sediment dynamics. There are many affecting ways, such as binding fine-grained sediment, changing the water content, enhancing the organic content through the secretion products, and so on. Furthert studies should be undertaken addressing on both a biological and a physical perspective, which could better assess the optimal predictors of sediment stability and make contribution on the risk assessment improvement of contaminated riverine sites along with a focus on biofilm production and distribution.

# 5. BIOLOGICAL FLOCCULATION OF SUSPENDED PARTICLES

Sediment flocculation is a critical component for the understanding of cohesive sediment dynamics. It is a non-negligible phenomenon in nature, which has been paid much attention in many fields (Rojas-Reyna et al., 2010; Son and Hsu 2011). From the macroscopic view, it is classified into the two classes of organic-flocculation and inorganic-flocculation. **Biological-flocculation** could be regarded as one form of organic-flocculation. Traditionally, the referred study has largely been devoted to the inorganic-flocculation. However, over the last

decades, the bioflocculation of sediment by biological activity has been given increasing Bioflocculation is different attention. from conventional inorganic-flocculation, in which microorganisms plays a key role. As a living organism, it has a great difference with the general inert material because of the association of life activities. There have been many mechanisms of charge-neutralization bioflocculation, such as theory, capsula theory, cellulose fibrils outside the cell theory, EPS bridging theory, and so on (Smith et al, 1992). Nowadays the most generally accepted theory is EPS bridging theory, which believes that the material basis of bioflocculation is EPS and EPS acts in the manner of "bridge" on the particle surfaces resulting in the generation of flocculation. The process of biological flocculation alters the hydrodynamic characteristics of sediment by changing the density, porosity, settling velocity and surface area of flocs (Droppo, 2001). Natural bioflocculation sediment comprises many different substances with concentrations that are generally site specific and time varying. Although an accurate taxonomy is currently lacking, the biological-flocs of sediment can generally be divided by inorganic and organic fractions. The inorganic fraction mainly consists of various fine cohesive minerals, such as kaolinite, illite, montmorillonite, carbonate, and so on (Van Leussen, 1994; McAnally, 1999). The organic fraction is prevalently made of numerous microorganisms, their metabolic products (EPS), and residuals from dead organisms (Crump and Baross, 2000; Simon et al., 2002; Bhaskar et al., 2005). These two fractions are intimately related by physical, chemical and biological processes, making the biological-flocs of sediment a complex, reactive biomaterial distributed in the aquatic environment. Flocculation of biological forms aggregates that increase in size by collecting suspended sediment, organic particles, and microorganisms (Federico Maggi, 2009). There is a general consensus that the interaction between suspended sediment particles and microorganisms may exert manifold impacts on chemical and mechanical floc responses. Experiments in controlled conditions and field observations have given evidence that the organic matter (especially the EPS) had substantial effects on flocculation time, floc size, density, and settling velocity (Guenther and Bozelli, 2004; Passow and De La Rocha, 2006; Bowers et al., 2007). Furthermore, it is generally accepted that EPS increase the aggregation efficiency (Kiorboe et al., 1990), while relatively little is known about the effect on floc breakup (Alldredge et al., 1990). Researches have demonstrated that bioflocculation sediment was composed of complex networks of biofilm and appeared to be of complicated physical floc structures. The EPS was found to embed particles and permeate the void space, representing the dominant physical bridging mechanism of the flocs and contributed to the extensive surface area, architecture characteristics and mechanical properties of bioflocculation sediment (Steven N. Liss, 1996; Huiming Zhao, 2011). But nowadays referred conclusions are most qualitative illustrations. Mechanistic models to describe the between interaction mineral particles and microorganisms are an instrumental aid to interpreting biofloccultion sediment dynamics. Yet, nowadays little work (Federico Maggi, 2009) explicitly coupled mineral and biomass dynamics at length scales comparable to the floc size, thus leaving a serious gap in our understanding of the feedback between mineral particles and Coupling microorganisms. mineral and microorganism dynamics represents therefore the best target to understand the implication and fate of biomass-affected suspended sediment that commonly occur in natural conditions.

### 6. SUMMARY

Microbial factors play critical roles in the sediment dynamics. Many of the geochemical and biological processes which are mediated by microorganisms as well as their secretions biofilm occur in a complex manner within the hydrodynamic regime. The microbial biofilm represents an important element for consideration during the investigation and the interpretation of biological, chemical, and sedimentological data in aquatic systems. While the biofilm is a common microbial adaptation in aquatic systems, the complexity of biofilms and the resulting effects on sediment dynamics are still not well understood. Nowadays most relevant researches are qualitative illustrations, as not much work has been done on the quantitative researches and mathematical modeling of influence from biofilm on sediment dynamics. Researchers are yet to carry out much intensive theoretical studies of influence of biofilm on physico-chemical properties of sediments with special focus on sediment dynamics.

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#### REFERENCES

- Alan W. Decho: Microbial biofilms in intertidal systems: an overview, *Continental Shelf Research*, 20, 1257–1273, 2000.
- Alldredge, A.L., Granata, T.C., Gotschalk, C.C., Dickey, T.D.: The physical strength of marine snow and its implications for particle disaggregation in the ocean, *Limnology and Oceanography*, 35 (7), 1415–1428, 1990.
- Andersen T.J.: Seasonal variation in erodibility of two temperate, microtidal mudflats, *Estuarine, Coastal and Shelf Science*, 53 (1): 1-12, 2001.
- Andersen, T.J., Lund-Hansen, L.C., Pejrup, M., Jensen, K.T., Mouritsen, K.N.: Biologically induced differences in erodibility and aggregation of subtidal and intertidal sediments: a possible cause for seasonal changes in sediment deposition, *Journal of Marine Systems*, 55, 123– 138, 2005.
- Bhaskar, P.V., Grossart, H.P., Bhosle, N.B., Simon, M.: Production of macroaggregates from dissolved exopolymeric substances (EPS) of bacterial and diatom origin, *FEMS Microbiology Ecology*, 53 (2), 255–264, 2005.
- Black, K.S., Tolhurst, T.J., Paterson, D.M., Hagerthey, S.E.: Working with natural cohesive sediments, *Journal of Hydraulic Engineering*, 1, 1–8, 2002.
- Bowers, D.G., Binding, C.E., Ellis, K.M.: Satellite remote sensing of the geographical distribution of suspended particle size in an energetic shelf sea, *Estuarine. Coastal* and Shelf Science, 73, 457–466, 2007.
- Chambless J.D., Hunt S.M., Stewart P.S.: A three-dimensional computer model of four hypothetical mechanisms protecting biofilms from antimicrobials, *Applied and Environmental Microbiology*, 72(3):2005-2013, 2006.
- Crump, B.C., Baross, J.A.: Characterization of the bacterially-active particle fraction in the Columbia River estuary, *Marine Ecology – Progress Series*, 206, 13–22, 2000.
- de Brouwer, J.F.C, Bjelic, S., de Deckere, E.M.G.T., Stal, L.J.: Interplay between biology and sedimentology in an intertidal mudflat (Biezelingse Ham, Westerschelde, The Netherlands), *Continental Shelf Research*, 20, 1159–1177, 2000.
- de Brouwer J.F.C., Stal L.J.: Short-term dynamics in microphytobenthos distribution and associated extracellular carbohydrates in surface sediments of and intertidal mudflat, *Marine Ecology Progress Series*, 218, 33–44, 2001.
- de Brouwer, J.F.C., Ruddy G.K., Jones T.E.R., Stal L.J.: Sorption of EPS to sediment particles and the effect on the rheology of sediment slurries, *Biogeochemistry*, 61, 57–71, 2002.
- de Brouwer J.F.C., De Deckere E.M.G.T., Stal L.J.: Distribution of extracellular carbohydrates in three intertidal mudflats in Western Europe. Estuarine, *Coastal and Shelf Science*, 56, 313–324, 2003.
- de Brouwer J.F.C., Wolfstein K., Ruddy G.K., Jones T.E.R., Stal L.J.: Biogenic stabilization of intertidal sediments: the importance of extracellular polymeric substances produced by benthic diatoms, *Microbial Ecology*, 4, 501–512, 2005.

- de Deckere E., Tolhurst T.J., de Brouwer J.F.C.: Destabilization of cohesive intertidal sediments by infauna. Estuarine, *Coastal and Shelf Science*, 53, 665–669, 2001.
- Defew E.C., Tolhurst T.J., Paterson D.M.: Sitespecific features influence sediment stability of intertidal flats, *Hydrology* and Earth System Science, 6(5), 971–981, 2002.
- de Jonge, V.N., J. van den Bergs: Experiments on the resuspension of estuarine sediments containing benthic diatoms, *Estuarine and Coastal Marine Science*, 24, 725–740, 1987.
- Droppo I.G.: Rethinking what constitutes suspended sediment, *Hydol Process*, 15, 1551–64, 2001.
- Federico Maggi: Biological flocculation of suspended particles in nutrient-rich aqueous ecosystems, *Journal of Hydrology*, 376, 116–125, 2009.
- Foerstner U., Heise S., Schwartz R., Westrich B., Ahlf W.: Historical contaminated sediments and soils at the river basin scale, *Journal of Soils and Sediments*, 4, 247–260, 2004.
- Gerbersdorf S.U., Jancke T., Westrich B.: Physico-chemical and biological sediment properties determining erosion resistance of contaminated riverine sediments – temporal and vertical pattern at the Lauffen reservoir/River Neckar, Germany, *Limnologica*, 35, 132–144, 2005.
- Gerbersdorf S.U., Jancke T., Westrich B., Paterson D.M.: Microbial stabilization of riverine sediments by extracellular polymeric substances, *Geobiology*, 6, 57-69, 2008.
- Gerdol V., Hughes R.G.: Effect of Corophium volutator on the abundance of benthic diatoms, bacteria and sediment stability in two estuaries in southeastern England, *Marine Ecology Progress Series*, 114, 109-115, 1994.
- Grant J., Bathmann U.V., Mills E.L.: The interaction between benthic diatom films and sediment transport. Estuarine, *Coastal and Shelf Science*, 23, 225–238, 1986.
- Grant J., Daborn G.: The effects of bioturbation on sediment transport on an intertidal mudflat, *Netherlands Journal of Sea Research*, 32, 63–72, 1994.
- Guenther M., Bozelli R.: Factors influencing algae-clay aggregation, *Hydrobiologia*, 523 (1-3), 217-223, 2004.
- Herman M.J., Middelburg J., Heip H.R.: Benthic community structure and sediment processes on an intertidal flat: results from the ECOFLAT project, *Continental Shelf Research*, 21, 2055–2071, 2001.
- Jepsen R., Roberts J., Lick W., 1997. Effects of bulk density on sediment erosion rates. Water Air and Soil Pollution 99, 21–31.
- Kiorboe T., Andersen K.P., Dam H.G.: Coagulation efficiency and aggregate formation in marine-phytoplankton, *Marine Biology*, 107 (2), 235–245, 1990.
- Kornman B., de Deckere E.M.G.T.: Temporal variation in sediment erodibility and suspended sediment dynamics in the Dollard estuary. In: Black, KS, Paterson, DM, Cramp, A (Eds.), Sedimentary Processes in the Intertidal Zone, Vol 139, The Geological Society, London, pp 231–241, 1998.
- Luckenbach M.W.: Sediment stability around animal tubes: The roles of hydrodynamic processes and biotic activity, *Limnology and Oceanography*, 31, 779–787, 1986.
- McAnally W.: Aggregation and deposition of estuarial fine sediment. Ph.D. Thesis, University of Florida, USA, 1999.

- McNeil J., Lick W.: Erosion rates and bulk properties of sediments from the Kalamazoo River, *Journal of Great Lakes Research*, 30, 407–418, 2004.
- Meadows P.S., Tait J, Hussain S.A.: Effects of estuarine infauna on sediment stability and paricle sediment, *Hydrobiologia*, 190, 263-266, 1990.
- Minwoo Son, Tian Jian Hsu: The effects of flocculation and bed erodibility on modeling cohesive sediment resuspension, *Journal of Geophysical research-oceans*, 116: C03021, 1-18, 2011.
- Mouritsen K.M., Mouritsen L.T., Jensen K.T.: Change of topography and sediment characteristics on an intertidal mudflat following mass mortality of the Amphipod Corophium volutator, *Journal of the Marine Biological Association of the United Kingdom*, 78, 1167-1180, 1998.
- Noffke N., Paterson D.: Microbial interactions with physical sediment dynamics, and their significance for the interpretation of Earth's biological history, *Geobiology*, 6, 1–4, 2008.
- Nowell, A.R.M., Jumars, P.A.: Flow environments of aquatic benthos, *Annual Review of Ecology and Systematics*, 15, 303–328, 1984.
- Passow, U., De La Rocha, C.: Accumulation of mineral ballast on organic aggregates, *Global Biogeochemical Cycles*, 20, GB1013. doi:10.1029/2005GB002579, 2006.
- Paterson D.M.: Microbiological mediation of sediment structure and behaviour. In Microbial Mats (eds Stal LJ, Caumette P). Springer, Berlin, Germany, pp. 97–109, 1994.
- Paterson D.M.: Biological mediation of sediment erosibility: ecology and physical dynamics. In Cohesive Sediments (eds Burt N, Parker R, Watts J). Wiley and Sons, Chichester, UK, pp. 215–229, 1997.
- Paterson D.M., Black K.S.: Water flow, sediment dynamics and benthic ecology, Adv Ecol Res 29, 155–193, 1999.
- Rhoads D.C., Yingst J.Y., Ullman W.J.: Seafloor stability in central long Island sound: Part I. Temporal changes in erodibility of fine-grained sediment. In Estuarine Interactions Academic Press, New York, pp. 221–244, 1978.
- Riethmüller R., Heineke M., Kuhl H., Keuker-Rudiger R.: Chlorophyll a concentration as an index of sediment surface stabilisation by microphytobenthos, *Continental Shelf Resesrch.* 20 (10–11), 1351–1372, 2000.
- Rojas-Reyna R., Schwarz S., Heinrich G., Petzold G., Schütze S., Bohrisch J.: Flocculation efficiency of modified water soluble chitosan versus commonly used commercial polyelectrolytes, *Carbohydrate Polymers*, 81(2), 317-322, 2010.
- Sabine U.G., Thomas J., Westrich B., Paterson D.M.: Microbial stabilization of riverine sediments by extracellular polymeric substances, *Geobiology*, 6(13):57-69, 2008.
- Shin H.S., Kang S.T., Nam S.Y.: Effect of carbohydrate and protein in the EPS on sludge settling characteristics, *Water Science and Technology*, 43, 193–196, 2001.
- Simon M., Grossart H.P., Schweitzer B., Ploug H.: Microbial ecology of organic aggregates in aquatic ecosystems, *Aquatic Microbial Ecology*, 28, 175–211, 2002.
- Smith G., Straver M.H., Lugtenberg B.J., Kijne J.W.: Flocculence of Saccharomyces cerevisiae cells is induced by

nutrient limitation, with cell surface hydrophobicity as a major determinant, *Applied and Environmental Microbiology*, 53(11), 3709-3714, 1992.

- Stal L.J.: Microphytobenthos, their extracellular polymeric substances, and the morphogenesis of intertidal sediments, *Geomicrobiology Journal*, 20: 463-478, 2003.
- Steven N.L., Ian G.D., Derrick T.F., and Gary G.L.: Floc Architecture in Wastewater and Natural Riverine Systems, *Environmental Science & Technology*, 30, 680-686, 1996.
- Sutherland T.F., Amos C.L., Grant J.: The Erosion Threshold of Biotic Sediments: A Comparison of Methods. In Black, K. S., D. M. Paterson & A. Cramp (eds), Sedimentary Processes in the Intertidal Zone. Geological Society, Special Publications 139, London: 135–148, 1998.
- Tolhurst T.J., Jesus B., Brotas V., Paterson D.M.: Diatom migration and sediment armouring an example from the Tagus Estuary, Portugal, *Hydrobiologia*, 503, 183–193, 2003.
- Tollhurst T.J., Consalvey M., Paterson D.M.: Changes in cohesive sediment properties associated with the growth of a diatom biofilm, *Hydrobiologia*, 596, 225–239, 2008.
- Underwood, G.J.C., Paterson, D.M., Seasonal changes in diatom biomass, sediment stability and biogenic stabilization in the Severn estuary, *J Mar Biol Assoc UK*, 73, 71–887, 1993.
- Van Leussen, W.: Estuarine Macroflocs. Ph.D. Thesis, University of Utrecht, The Netherlands, 1994.
- Vignag E., Sloan W.T., Haynes H.: Entrainment of biostabilized non-cohesive sediments modelling biofilm adhesion as an elastic force. 33rd IAHR congress: Water Engineering for a Sustainable Enviroment, Vancouver Canada 51-58, 2009.
- Widdows J., Brinsley M.D., Elliott M.: Use of in situ flume to quantify particle flux (biodeposition rates and sediment erosion) for an intertidal mudflat in relation to changes in current velocity and benthic macrofauna. In Sedimentary processes in the intertidal zone (Black, K. S., Paterson, D. M. & Cramp, A., eds). Geological Society, London, Special Publications, 139, pp. 85–98, 1998a.
- Widdows J., Brinsley M.D., Salkeld P.N., Elliott M.: Use of annular flumes to determine the influence of current velocity and bivalves on material flux at the sediment-water interface, *Estuaries*, 21, 552–559, 1998b.
- Widdows J., Brinsley M.: Impact of biotic and abiotic processes on sediment dynamics and the consequences to the structure and functioning of the intertidal zone, *J. Sea Res*, 48 (2), 143–156, 2002.
- Yallop M.L., de Winder B., Paterson D.M,. Stal L.J.: Comparative structure, primary production and biogenic stabilization of cohesive and non-cohesive marine sediments inhabited by microphytobenthos, *Estuar. Coastal and Shelf Science*, 39, 565–582, 1994.
- Yallop M.L., Paterson D.M., Wellsbury P.: Interrelationships between rates of microbial production, exopolymer production, microbial biomass, and sediment stability in biofilms of intertidal sediments, *Microb Ecol*, 39, 116–127, 2000.
- ZHAO H.M., FANG H.W., CHEN M.H.: Floc Architecture of Bioflocculation Sediment by ESEM and CLSM, SCANNING, 2011, 33, 1–9, 2011.