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The role of microphytobenthos in soft-sediment ecological networks and their contribution to the delivery of multiple ecosystem services.

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Abstract

1. Sediment dwelling, microscopic primary producers, that occupy sediments in the photic zone, are commonly referred to as microphytobenthos (MPB). The MPB are essential components of soft-sediment systems, but are often overlooked when assessing coastal ecosystem functionality and service delivery.
2. The MPB are involved in several complex interactions and feedbacks that underpin the delivery of vital ecosystem services. MPB profoundly influence the flow and cycling of carbon and nutrients, such as nitrogen, directly and indirectly underpinning highly productive shallow water marine foodwebs. The MPB can also stabilise sediments through the formation of biofilms, and significantly improve water quality by mediating the benthic-pelagic coupling of nutrients, sediment and pollutants.
3. The functional role of the MPB is compromised by increasing anthropogenic pressures such as nutrient enrichment, sedimentation, herbicides and emerging contaminants such as microplastic

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pollution. However, MPB are extremely good at buffering the effects of these land sourced stressors at the interface between land and sea.

4. *Synthesis:* Society often appreciates the final provisioning of goods and services from our coastal marine environments. However, provisioning services are only possible due to the multitude of supporting and regulating services that underpin them. MPB are central to benthic ecological networks, and contribute to ecosystem service delivery through various pathways. Understanding the critical role of MPB in complex networks is therefore essential to appreciate their importance in ecosystem function and service delivery into the future.

Key words: Benthic microalgae, ecosystem services, estuarine systems, microphytobenthos, MPB, service delivery, soft-sediment ecology.

1. INTRODUCTION

Except under extreme environmental forcing, it is often challenging to connect the effects of anthropogenic stressors to changes in ecosystem function, particularly in coastal soft-sediment ecosystems. It is especially difficult to envisage Ecosystem Services (ES), which are supported by small sediment-dwelling organisms. The microphytobenthos (MPB) are particularly overlooked when assessing coastal ecosystem service delivery, yet they are important microbial primary producers that photosynthesise on the sediment surface in intertidal and photic subtidal zones. To rectify this problem, we first need to better understand the dynamics of these small but vital organisms, the processes and functions that underpin ES delivery (Geange et al., 2019) and the influence of multiple stressors on the flow of ES from soft-sediment ecosystems. We also need to understand the complex feedbacks and networks that connect different organisms, processes and functions that support ES delivery in these ecosystems.

This paper seeks to draw attention to the importance of MPB for soft-sediment ecosystem function and the delivery of vital ecosystem services. Evidence has been drawn primarily from coastal and estuarine studies to highlight the context-dependent role of MPB in ecosystems. Anthropogenic pressures that may alter the role of MPB in ecological networks is considered and future requirements in this area of research are suggested.

2. ECOSYSTEM SERVICES

Ecosystem services (ES) have been discussed widely (Carpenter et al., 2009; Costanza et al., 2014; MEA, 2005; TEEB, 2010) and an important justification for ES research is in ensuring that the hidden

infrastructure that nature provides society and supports human wellbeing is recognised and protected (TEEB, 2010). ES delivery is deteriorating at an alarming rate with over 60% loss globally over the past 50 years (MEA, 2005). Despite the wide array of ES provided by soft-sediment ecosystems (Thrush et al., 2013) the majority of ES investigations to-date have focussed on charismatic organisms (e.g. whales and dolphins) and habitats (e.g. coral reefs, seagrasses, mangroves) (Alongi, 2014; Barbier, 2017; Koch et al., 2009). These species and habitats are easier to value due to their contributions to carbon sequestration, coastal protection and charisma in the eyes of society. However, we must not take for granted the life-sustaining, regulating and supporting ES provided by estuaries and other less charismatic coastal soft-sediment dominated habitats (Passarelli et al., 2018). These ecosystems play an integral and disproportional role in carbon sequestration, as well as keeping our waters clean and healthy (Thrush et al., 2013). Excluding the delivery of ES from coastal ecosystems in decision frameworks promotes short-term gains that will compromise the long-term delivery of multiple ES across different ecosystems.

The contribution of MPB to the delivery of multiple ES stems from their central role as primary producers at the base of benthic foodwebs, their rapid transfer of organic matter, and mediation of energy and nutrients (Christianen et al., 2017). For example, MPB primary production is often closely linked to coastal fish and shellfish production (Kritzer et al., 2016; Morioka et al., 2017). MPB also play a central role in water purification, by influencing the removal, transformation, and retention of pollutants (Kowalski et al., 2009; Snelgrove et al., 2018; Tolhurst et al., 2002). MPB mediate sediment dynamics by providing protection against erosion (Paterson et al., 2018), which in turn reduces the resuspension of fine sediments (Tolhurst et al., 1999) and enhances water clarity. Coastal soft-sediments also provide important recreational and cultural services, attracting bird watchers, tourists, and supporting culturally significant species and habitats that rely on the benthic foodweb.

3. MICROPHYTOBENTHOS

MPB communities are dominated by unicellular eukaryotic algae, cyanobacteria and euglenoids that inhabit the surface layers sediments within the photic zone (MacIntyre et al., 1996). Their colonisation of the seafloor extends from shallow intertidal areas to the edge of the continental shelf (Cahoon, 1999; Pinckney, 2018) and their presence can appear as a subtle brown or green shading on the sediment surface or they can be invisible to the naked eye. MPB are well adapted to the harsh conditions of estuaries, where temperature, light, nutrient and hydrodynamic conditions regularly fluctuate. Their productivity is regulated by the availability of these abiotic resources (Kromkamp et al., 1995; Perkins et al., 2001), but they respond rapidly and efficiently to prevailing environmental conditions (Falkowski and Raven, 2013; Hopes and Mock, 2015). MPB have colonised habitats from freshwater to extremely saline

environments (Forster et al., 2006; Potapova, 2011) and in intertidal environments, productivity and biomass can shift with the tidal cycle (Serôdio and Catarino, 1999). In many turbid estuaries of Europe, the productivity of MPB is restricted during immersion periods (Migne et al., 2009) but they are highly adapted to maximise their photosynthetic efficiency at extremely low ($2.8 \mu\text{M photons m}^{-2} \text{ s}^{-1}$; Gattuso et al., 2006) and high ($>2000 \mu\text{M photons m}^{-2} \text{ s}^{-1}$; Cahoon, 1999) light conditions. Even in the high Antarctic with less than 0.1% of the summer sunlight penetrates the ice, MPB contribute significantly to marine primary production (Dayton et al., 1986; Lohrer et al., 2013). In the 19th century the naturalist Ernst Haeckel, presented some of the first amazing images of microscopic algae but suggested these organisms, although beautiful, played no significant role within the ecosystem. Perspectives have changed considerably over recent years and it is well recognised that MPB and biofilms contribute substantially to the functioning of coastal soft-sediments (Miller et al., 1996; O'Meara et al., 2017; Paterson et al., 2018; Pinckney, 2018). The functionally important roles of MPB were addressed in two key articles by MacIntyre et al. (1996) and Miller et al. (1996) who appropriately called MPB biofilms in soft-sediments "The secret garden". These organisms are microscopic, and often form only a thin layer on the sediment surface (Fig 1A), but diatoms and cyanobacteria can mediate both small and large-scale processes (Chapman et al., 2010). For instance, MPB influence biogeochemical gradients within the sediment (MacIntyre et al., 1996) where many ecologically significant processes take place, they influence sediment stability by altering sediment properties and processes (Fagherazzi et al., 2014) and trap particles from overlying water (Kornman and de Deckere, 1998). Despite the clear emphasis on the importance of MPB in the 'secret garden' papers, and recent studies confirming the role of MPB in the above processes, their contribution is still often disregarded. MPB communities are often influenced by sediment type, nutrient concentrations and temperature (Sundbäck and Snoeijs, 1991; Watermann et al., 1999). While diatoms (Fig 1B-D), often dominate the MPB in mid-latitude temperate systems, this can shift seasonally to cyanobacteria and chlorophytes (Barranguet et al., 1998) or spatially to euglena on high intertidal sediments (Kingston and Gough, 2009). In the mudflats around Sydney, green filamentous algae are the dominant primary producers, replacing the MPB altogether (Murphy et al., 2004), while cyanobacteria dominate other sandy systems throughout the year (Cook et al., 2004; Paerl et al., 1996; Stal, 2012).

Single celled, photosynthesising organisms are quantitatively important for estuarine and shelf primary productivity, benthic-pelagic exchange of sediment, the cycling of nutrients and oxygen production (Chen et al., 2017; Jones et al., 2017; Longphuir et al., 2009; Pinckney, 2018). MPB productivity also supports energy transfer to higher organisms (MacIntyre et al., 1996) with compositional changes in the MPB taxa altering the nutritional quality of this primary food source (Muller-Navarra et al., 2000).

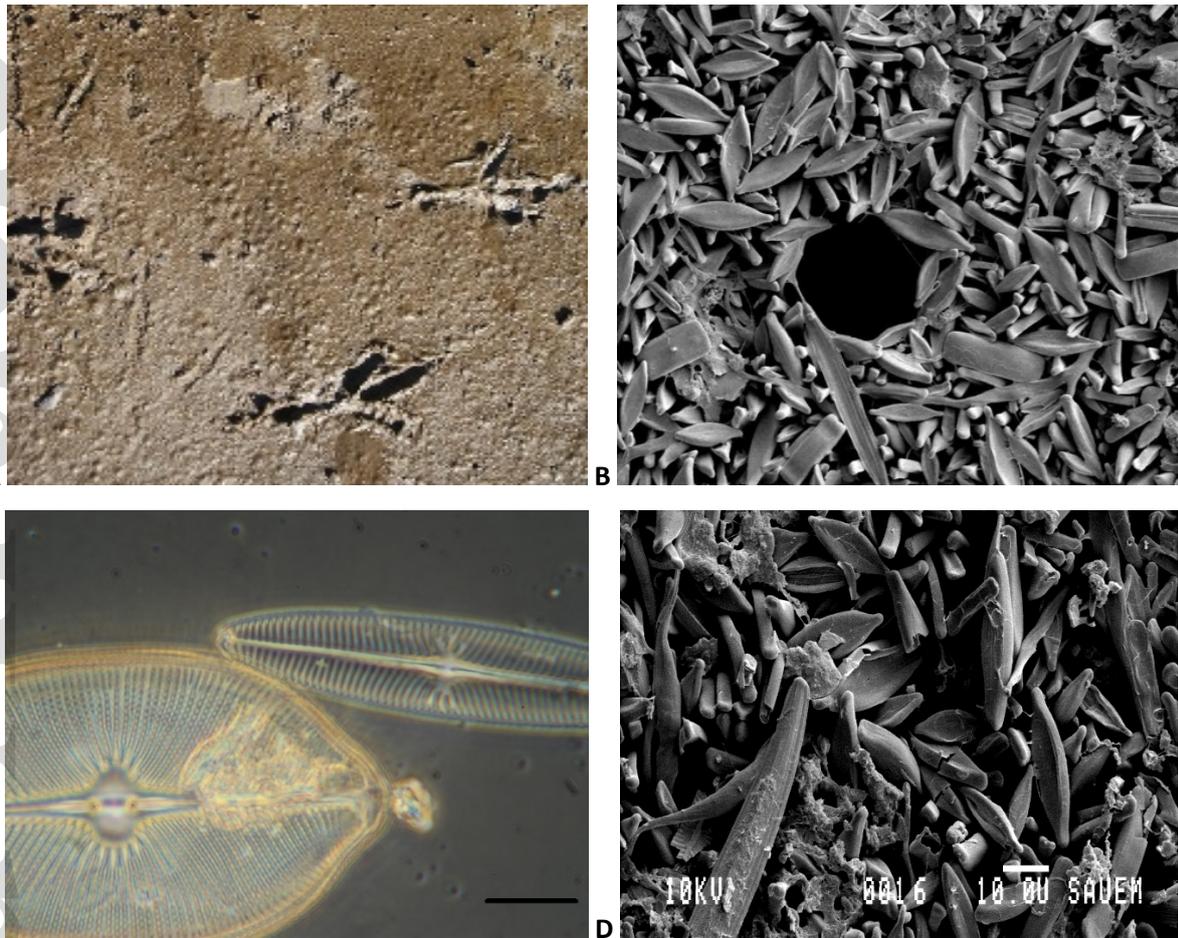


Fig 1: A) A light golden biofilm on the surface of sandy sediment of the Eden estuary, UK B) Low temperature scanning electron micrograph of a natural diatom biofilm: Dee Estuary UK. Scale bar - 10 μ m. C) Light micrograph of two cosmopolitan diatom species that often dominate MPB in intertidal sediments. Left - *Navicula humerosa*. Right - *Navicula digitoradiata*. Scale bar - 10 μ m. D) Low temperature scanning electron micrograph of a mixed MPB community. Scale bar - 10 μ m.

The widespread distribution, rapid turnover rates and adaptability of MPB (Hopes and Mock, 2015; Oakes et al., 2012) supports their evolutionary success and has allowed MPB to occupy many aquatic habitats. Unlike their planktonic cousins, many benthic diatoms are motile and capable of moving through the sediment (Cartaxana et al., 2016; Consalvey et al., 2004) allowing them to optimise light and nutrient conditions. Their mechanism of locomotion is unusual and facilitated by the production and release of extracellular polymeric material (EPS) that can change the cohesive properties of the seabed (Paterson, 1989; Tolhurst et al., 2002) and provides a rich source of organic material to bacteria (Tobias et al., 2003). There is evidence that seasonal changes in diatom-EPS production influences bacteria assemblages (Moerdijk-poortvliet et al., 2018) and that there is a strong mutual dependency between diatoms and

bacteria assemblages (Koedooder et al., 2019). Locomotion and EPS secretion also provide ecological resilience to stressors such as hypoxia, heavy metal toxicity and organic pollutants (Decho, 2000; Larson and Sundbäck, 2008; Sundbäck et al., 2010). These characteristics of the MPB as well as hydrodynamic stress (Hope, 2016). Many MPB-mediated ES are thus likely to continue except under extreme environmental degradation, but their resilience should not be taken for granted. ES result from complex interactions between biophysical processes and human behaviour (Mouchet et al., 2014) and are underpinned by multiple ecosystem functions, processes and complex feedbacks (Thrush et al., 2012). MPB play a central role in several complex interactions (Fig 2), that define these functions but the indirect roles of MPB and their interactions with other organisms are vulnerable to environmental change (Pratt et al., 2014; Thrush et al., 2013).

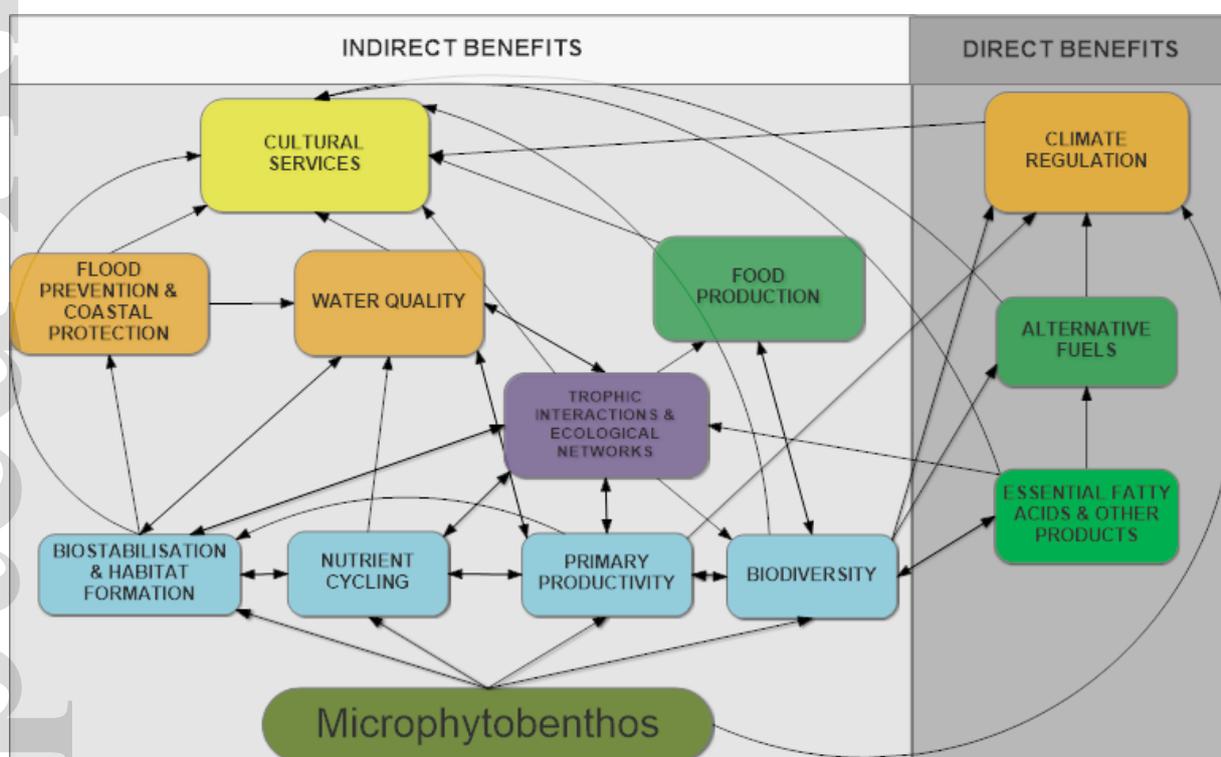


Fig 2: Contribution of microphytobenthos (MPB) to Ecosystem Services (ES) delivery. Blue-supporting services (S), Green-provisional services (P), Orange-regulating services (R), and Yellow-cultural services (bundled, C). The network illustrates that cultural services are underpinned by several ES in the network and that MPB are at the base of the network. Purple - trophic interactions and the importance of the ecological network in soft-sediments. These factors are all essential when considering functioning of these ecosystems and the provision of ES.

4. INDIVIDUAL ECOSYSTEM FUNCTIONS & SERVICES

4.1. Biodiversity (S) & habitat services (S)

While the role of biodiversity in ecosystem function and ES delivery is widely accepted, it is difficult to establish simple cause and effect relationships due to the non-linear and complex interactions between stressors, biodiversity, functionality and ES delivery (Harrison et al., 2014; Thrush et al., 2013). Productivity–biodiversity relationships are far from clear in any system, but especially in less well-studied marine systems. Despite this, diversity in primary producers has been positively related to increases in grazer diversity (Balvanera et al., 2006) and this can increase overall ecosystem productivity (Jones et al., 2017; Worm et al., 2006). In turn, there are feedbacks between trophic levels with the activity of macrofauna modulating microbial (Foshtomi et al., 2015) and macrobenthic (Widdicombe and Austen, 1999) diversity. Furthermore, the interactions between MPB, N-cycling bacteria and benthic invertebrates can significantly affect N retention and N removal processes, which creates a more inhabitable environment for benthic organisms (Douglas et al., 2018). The presence of fauna can also alter flow dynamics which stimulates the MPB (Christensen et al., 2003). These ecological interactions are critical for nutrient cycling and overall productivity (Hicks et al., 2018; Thrush et al., 2006).

4.2. Productivity (S) & carbon sequestration (R)

MPB capture and fix up to one third of atmospheric CO₂ with estimates of 30 to 230 g Carbon fixation m² y⁻¹ on intertidal flats (Heip et al., 1995). ‘Unvegetated’ coastal sediments have been estimated to cover a global area of 23.9 x 10¹² m² (Duarte et al., 2004), a much greater expanse than vegetated sediments, while others estimate the continental shelf area as covering 28 x 10⁶ km² (MacKenzie and Lerman, 2006). A recent study of productivity in the South Atlantic Bight (Pinckney, 2018) suggests that over 90% of the habitat could support benthic production and switch the benthos from net heterotrophic to net autotrophic. These authors propose that benthic productivity in continental shelf regions is a neglected area in biogeochemical and trophodynamic studies. The South Atlantic Bight may be representative of over 70% of global continental shelves, but global estimates of benthic primary productivity remain poor (Charpy-Roubaud and Sournia, 1990) and widely debated (Cai, 2011; Pinckney, 2018) as the benthic productivity in these areas is rarely considered.

The overall productivity of coastal soft-sediment depends on the daily light levels, temperature, tidal elevation, salinity, exposure period, as well as local hydrodynamics. The latter can resuspend and transport the MPB offshore (de Jonge and van Beusekom, 1995; T. J. Tolhurst et al., 2002). Despite estimates that the MPB are responsible for the production of around 500 million tons of organic carbon annually (Cahoon, 1999), their contribution to the carbon cycle in ecosystem and global biogeochemical

models is often overlooked. Benthic productivity can exceed phytoplankton productivity in nearshore waters and continental shelf regions (Jahnke et al., 2000; Jones et al., 2017; Pinckney, 2018). Although coastal waters account for just 10% of the ocean's surface area, these areas are rich in nutrients. These nutrients fuel photosynthesis, with upwelling and outflow from land, linking these systems to the open ocean (MacKenzie and Lerman, 2006). Coastal waters are hot spots of productivity and often visible on the edge of satellite images, yet coastal waters are excluded from remote sensing estimates of phytoplankton productivity due to the added complexity of elevated turbidity (Behrenfeld et al., 2005). As the interface between land and sea, intertidal sediments should be considered a significant component of a land to sea continuum rather than an isolated ecosystem. It seems counterintuitive to exclude benthic primary productivity from oceanic productivity models or to disregard them as insignificant when they are sources of primary producers to the open ocean.

MPBs efficiently convert solar energy into biomass at a rate around 10 times greater than that of terrestrial plants. Up to 1.83 kg of CO₂ can be fixed for 1kg of microalgae biomass (Chisti, 2008) with much of this energy channelled into metazoan and microbial foodwebs (Maher and Eyre, 2011; Moerdijk-poortvliet et al., 2018). While the high productivity of these ecosystems often results in fixed carbon being consumed and respired back to the atmosphere, for every 0.6 mol of CO₂ respired as much as 1 mol of carbon is bound in the shell of resident bivalves (Fodrie et al., 2017).

MPB primary productivity fuels secondary production in estuarine systems and first order consumers, such as grazing bivalves and worms, provide an important link in the transfer of energy to higher organisms (Como et al., 2014). Through stable isotopes and fatty acid biomarkers, basal food sources such as MPB can be traced back from higher trophic consumers (Como et al., 2014; Moens et al., 2002) and MPB provide a higher quality carbon to consumers than marine angiosperms such as mangroves or seagrasses (Kang et al., 2007; Miller et al., 1996). The ratio of carbon to nitrogen (C:N ratio) has also been used to determine the response of MPB to stressors, indicating changes to this basal food source. The C:N ratio, along with the labile nature of MPB-carbon, perhaps explains the preference for MPB as a dietary source. For example, C:N in crustaceans residing in mangrove systems emphasise the role of MPB production over that of mangroves (Guest et al., 2008; Mazumder and Saintilan, 2010). As a high quality, labile food source for many meio- and macro-fauna species, the majority of carbon produced by MPB is often remineralised and transformed within the ecosystem (Bauer et al., 2013). Nonetheless, respired carbon in sediments can also be recaptured and recycled by MPB repeatedly within the sediment (Oakes and Eyre, 2014) and bivalves can use substantial amounts of MPB-derived carbon to CO₂ which is then calcified into calcium carbonate shells (producing up to 1000g CaCO₃ m² y⁻¹, Gutiérrez et al., 2003). Shells

slowly dissolved in the ocean, taking up to 30 years for a 4 year old oyster (Suykens et al., 2011). The presence of shell hash also influences benthic metabolism (Dolmer and Frandsen, 2002) by adding complexity and increasing habitat heterogeneity (Thrush et al., 2004). It provides new habitat for other species (Gutiérrez et al., 2003), and can mitigate against pollutants (Casado-Coy et al., 2017). These benefits support incentives to conserve and restore shellfish beds as potential carbon sinks (Fodrie et al., 2017). The transfer of carbon offshore via the migration of juvenile fish and invertebrates (Dahlgren et al., 2006; Vasconcelos et al., 2011) and through the metazoan foodweb is also critical for the survival of many fish and bird species. While MPB do not play the same obvious habitat forming or carbon sink roles as some of the less palatable estuarine and coastal plants (mangroves, seagrass and saltmarsh), the MPB mediate the quantity and form of carbon available to other organisms. MPB are important players in the global carbon cycle, much like phytoplankton (Basu and Mackey, 2018) and we must understand and quantify their contribution to the delivery of ES and how they interact with other organisms in these complex ecological networks.

4.3. Water quality (R) & nutrient cycling (S)

Increasing loads of nutrients, sediment and pollutants from land are significant stressors affecting coastal water quality (Auta et al., 2017; Hou et al., 2013), biodiversity (Thrush et al., 2017) and ecosystem functioning (Douglas et al., 2018; Wulff et al., 1997). Heavy metals, organic pollutants and polycyclic aromatic hydrocarbons, pathogens and microplastics accumulate in coastal soft-sediments (Bennett et al., 2000; Cole et al., 2011; Kowalski et al., 2009; Wiegner et al., 2003; Wyness et al., 2019), and these can bind to MPB and the EPS they secrete. Despite recent reductions in heavy metal and PAH inputs, buried substances can be remobilised by changing environmental conditions such as climate change, and storm events (Bennett et al., 2000; Blake et al., 2003; Wyness et al., 2019). Due to their position at the sediment-water interface, the MPB can influence the release and transformation of redox-sensitive metals (Kowalski et al., 2009) and form different communities on the surface of plastic particles (Michels et al., 2018) compared to surrounding sediment particles (Harrison et al., 2014).

While the MPB often mediate and influence the accumulation, breakdown and sequestration of nutrients, sediment and contaminants, their role in the delivery of multiple ES is also at risk from the input of other pollutants such as herbicides and pharmaceuticals. Recently the structure of benthic diatom assemblages has been used to indicate environmental contamination by herbicides and other substances (Wood et al., 2019). The herbicides diuron and atrazine (Legrand et al., 2006), the antibiotic doxycycline, the local

anaesthetic procainamide (Prata et al., 2018) and the biocide triclosan (Franz et al., 2008) are all known to affect both growth and photosynthesis and therefore the functional role of primary producers.

Reducing the clarity of overlying waters with increased sediment or phytoplankton biomass, together with excess nutrients can break down key processes and functions mediated by MPB on the seafloor and force the system into an alternative state (Van de Koppel et al., 2001) dominated by planktonic communities. These types of regime shifts have been observed in several systems (Biggs et al., 2018) including the Chesapeake Bay (Kemp et al., 2005), the Black Sea (Oguz and Gilbert, 2007) and other European estuaries (Jickells et al., 2016). In the Chesapeake Bay, the system shifted from clear waters largely dominated by seagrass and oysters to a system dominated by planktonic communities in the 1950s. This was driven by excess nutrient inputs and the over-harvesting of oysters (Kemp et al., 2005). The ensuing lower light availability on the seafloor (Pratt et al., 2014), and hypoxia associated with the decomposing bloom algae (Rabalais et al., 2002) can drastically shift ecosystem functionality resulting in positive feedback mechanisms that prevent these systems from returning to former states (Biggs et al., 2018). MPB can no longer photosynthesise as effectively during inundation (Drylie et al., 2018; Kromkamp et al., 1995; O'Meara et al., 2017), which reduces their ability to mediate nutrient fluxes to the water column, further exacerbating the issue (Sundbäck et al., 2006). When functionally important fauna such as deep-dwelling bivalves are reduced, this further undermines the capacity of the system to respond to increasing nutrient or sediment loads and highlights the need to understand the complex interactions between organisms.

In clear estuaries, MPB can assimilate up to 96% of the daily dissolved inorganic nitrogen (DIN) supplied to estuaries (Hochard et al., 2010), but these processes are altered as the water clarity changes. MPB nutrient uptake can often exceed denitrification by 1-2 orders of magnitude (Sundbäck et al., 2004; Sundbäck and McGlathery, 2005), especially in oligotrophic systems (Cook et al., 2004), but their competitive edge is dependent on environmental conditions such as light levels. Through tight N-recycling, MPB uptake can ensure the system remains productive whilst limiting the efflux of DIN into overlying water (Box 1). This efficient remineralisation of nutrients is often reflected in a greater photosynthetic efficiency (net primary productivity (NPP) normalised by MPB biomass) in sandy sediments compared to mud (Billerbeck et al., 2007). This results in a close association between the MPB and bacteria that preferentially utilise decomposing MPB (Banta et al., 2004) and labile EPS as a carbon substrate for biochemical processes such as denitrification (Tobias et al., 2003).

Box 1: Nutrient cycling and MPB

In sandy, oligotrophic systems the standing stock of organic matter (OM), MPB biomass and nutrients may be low (Piehler and Smyth, 2011), but this is often due to higher turnover rates (Boudreau et al., 2001; Huettel et al., 2014) rather than a lack of productivity *per se* (Billerbeck et al., 2007). Lower nutrient inputs, does not always limit MPB as nutrients are efficiently recycled and retained within the sediment (Heip et al., 1995). The relative effect of MPB on N-retention and recycling can fluctuate both seasonally due to growth (Banta et al., 2004; Nielsen et al., 2017), and daily due to nutrient uptake and transfer to other organisms (Tobias et al., 2003). MPB productivity can also be enhanced by advective flushing in permeable sediments (Cook and Røy, 2006). Pressure differences around bedforms and mounds induce flow, allowing MPB to intercept nutrients at the sediment-water interface, with flushing (from deeper sediment) proposed to explain MPB growth in low nutrient systems (Marinelli et al., 1998). The interception of nutrients by MPB promotes efficient N-retention and recycling within the bed and limits nutrient efflux (Ehrenhauss and Huettel, 2004; Huettel et al., 2014) anywhere between 30-100% (Sundbäck and Miles, 2002).

As an ecosystem becomes more eutrophic, the permanent removal of nitrogen by denitrification becomes an increasingly fundamental ES provided by coastal sediments (Duarte and Krause-Jensen, 2018). This step in the natural nitrogen cycle can at times remove up to 50% of reactive nitrogen in estuarine systems (Galloway et al., 2004). Despite MPB competing with denitrifying bacteria for DIN in low nutrient systems (Sundbäck and Miles, 2002) the MPB play a critical role in the conversion of reactive N to N₂ gas and thus denitrification processes, even stimulating denitrification (An and Joye, 2001). The alternation between oxygenation and deoxygenation of the sediment can significantly influence biogeochemical cycling of nitrogen. At night, when nitrogen limitation and deoxygenation may occur, the drawdown of dissolved oxygen can facilitate denitrification processes with MPB

contributing to community respiration and reduced sediment oxygen concentrations (An and Joye, 2001). Moreover, cyanobacterial mats can turn sediments anaerobic within minutes (Villbrandt et al., 1990) allowing aerobic non-heterocystous species to fix nitrogen in the absence of oxygen (Stal, 2012).

When light is sufficient, MPB photosynthesis oxygenates the upper sediment layers, and provides a labile carbon substrate for N-cycling bacteria (Middelburg et al., 1996). This supports elevated aerobic respiration, and enhances nitrification (the conversion of NH₄⁺ to NO₂⁻ and NO₃⁻, Risgaard-Petersen et al., 2004, 1994), which is often the most important source of NO₃⁻ for denitrification (Middelburg et al., 1996). This, of course, depends on the degree of competition between MPB and bacteria for DIN, N availability in

the sediment (An and Joye, 2001), local environmental conditions as well as resident benthic communities (Foshtomi et al., 2015).

Bioturbators that typically feed on MPB enhance sediment oxygenation and the transport of labile carbon to greater depths in the sediment, while also increasing the surface area of oxic-anoxic interfaces that are essential for coupled processes (Gilbert et al., 1998; Laverock et al., 2011; Tuominen et al., 1999). Sediment reworking has been demonstrated to increase denitrification and coupled nitrification-denitrification by up to 300% (Tuominen et al., 1999; Webb et al., 2004). Bioturbation also alters the efflux of O₂, CO₂ and DIN across the sediment-water interface (Howarth et al., 1996; Howe et al., 2004). The complex interactions and individual effects of MPB and infauna, can therefore alter sediment properties (Murphy and Tolhurst, 2009) that stimulate or inhibit biogeochemical processes in soft-sediments.

4.4. Erosional protection (R) & habitat formation (S)

MPB such as diatoms and cyanobacteria secrete carbon-rich EPS, which binds sediment particles together at the sediment-water interface creating a 'biofilm' (Underwood and Paterson, 2003). Biofilm formation can increase the resistance of the sea bed to hydrodynamic stress and raise sediment erosion thresholds through the cohesion between particles (Black et al., 2002; Joensuu et al., 2018). Biofilm formation can also smooth the surface and reduce bed roughness. This forms a protective 'skin' which again increases the resistance to flow (Consalvey et al., 2004; Underwood et al., 2005). Often biofilms can be visible to the eye, yet even when invisible or just a subtle hint of brown or green is detectable on the sediment surface (MacIntyre et al., 1996) sediment properties can be significantly (Tolhurst et al., 2006). Biostabilisation can positively affect ecosystem functioning and ES delivery, however excessive deposition of fine material can also act as a stressor on benthic communities (Lohrer et al., 2004b; Thrush et al., 2004). Various disturbances can interact with organic enrichment resulting in complex effects on benthic communities (Widdicombe and Austen, 2001), which are detectable across small and large environmental gradients (Pratt et al., 2015; Spears et al., 2008; Spilmont et al., 2011). The diversity of the benthos can be important for maintaining the stabilisation of coastal sediments and the delivery of this key ES (Hale et al., 2019).

As sediment loads increase, MPB may also accumulate more sediment and pollutants in the bed (Paterson and Black, 1999), which improves light availability and water quality. Improving water quality is in itself an important ES but the biological stabilisation of the bed also contributes to other ES such as erosional protection and habitat formation (Malarkey et al., 2015; Passarelli et al., 2018). In cold temperate

systems, the influence of MPB on suspended sediment loads can often be restricted to warmer periods when irradiances are high and physical disturbances are low (Borsje et al., 2008; Widdows and Brinsley, 2002). Conversely, in warmer climates where other taxa such as green filamentous algae dominate, MPB biomass can be higher during cooler months (Murphy and Tolhurst, 2009). Thus, the seasonal effects of MPB on ecosystem function and ES delivery will vary across different systems.

In seasonal systems, the increase in MPB and EPS can be limited by the appearance of grazers (Fernandes et al., 2006; Weerman et al., 2012). In addition to abundance, grazer size (Harris et al., 2016) and other infaunal traits (Hewitt et al., 2014) can influence MPB biomass. As such, biostabilisation of the sediment-water interface by MPB can be affected by ecological links in a variety of ways. For example, surface dwellers that bulldoze surface layers can destabilise the sediment (de Deckere et al., 2001) and resuspend MPB (Dupuy et al., 2014). Conversely, infauna can also stabilise the sediment, primarily through nutrient excretion (Murray et al., 2014; Passarelli et al., 2012a), which stimulates the growth of MPB (Lohrer et al., 2004a; Stock et al., 2014). These positive effects can often counteract grazing pressure on MPB and suggest that the complex interactions between MPB, fauna and environmental conditions must also be considered when assessing biostabilisation.

The cohesive nature of EPS reduces both bedload transport and bedform development such as ripple formation and size (Baas et al., 2019; Lichtman et al., 2018; Parsons et al., 2016), which can significantly affect large-scale geomorphological features of sediment. Biostabilisation, by altering sedimentary properties and processes, can lead to the formation of large ridge and runnel systems (Weerman et al., 2010) and state changes in sedimentary habitats (Koppel et al., 2001). The protrusion of burrows, mounds and tube mats influence sediment stability by increasing the thickness of the benthic boundary layer, lowering bed roughness and increase the surface area available for MPB (Passarelli et al., 2012b; Paterson and Black, 1999). These modifications to sediment microtopography increase the surface area of sediment, the patchy distribution of porewater nutrients and influence physical disturbance (Blanchard et al., 2001). Collectively these features contribute and lead to a complex spatial mosaic of MPB across the sediment (Jesus et al., 2005; Weerman et al., 2011). These changes can lead to new habitat formation where MPB facilitate the recruitment of larger organisms, which further facilitates habitat complexity (Thrush et al., 2008).

These relationships highlight the diverse and complex roles of MPB on services such as erosional protection and habitat formation in soft-sediment ecosystems. Changes to hydrodynamic regimes may place a selective pressure on MPB, removing particular functional groups (Dupuy et al., 2014) with cascading effects on first order consumers. Conversely, habitat homogenisation can result in the loss of

food and shelter, negatively affecting faunal diversity (Thrush et al., 2006) and in turn influence the trophic status of coastal systems (Hicks et al., 2011). Habitat (from the patch to whole system) and species diversity, (microbial to macrofauna), are therefore intricately linked and cannot be considered in isolation due to complex feedbacks within the ecological network.

4.5. The provision of fuels, foods & nutraceuticals (P)

MPB provide consumers with essential fatty acids (EFAs), the omega-3s, which are a vital component for growth and development in fish (Emata et al., 2004; Sprague et al., 2016), molluscs (Knauer and Southgate, 1999) and humans (Calder, 2014; Lenihan-Geels et al., 2013). As many EFAs cannot be efficiently synthesised by higher organisms, microalgae are the main source of EFAs in the biosphere (Behrens and Kyle, 1996). While humans typically consume omega-3s from oily fish such as salmon, herring and mackerel, these compounds are synthesised by microalgae at the base of the foodweb with the benthic foodweb often underpinning the productivity of these higher organisms. MPB are a significant food source for many shellfish and their high EFA content ensures they are underpinning marine food production services. The MPB can contribute up to 70% of the diet of harvested and farmed mussels, oysters and cockles (Dubois et al., 2007; Morioka et al., 2017; Sauriau and Kang, 2000)). Additionally, recent studies have demonstrated that MPB can be both a direct and indirect food resource for shore birds (Elner et al., 2005; Schnurr et al., 2019) and economically important fish species (França et al., 2011; Melville and Connolly, 2003).

Oil production from microalgae not only produces 30 times more oil per unit area than oilseed crops (Johnson and Wen, 2010) but the use of microalgae instead of land crop oils means that this energy production does not have to compete with food production or other forms of land use (Brennan and Owende, 2010; Patil et al., 2008). While typically, planktonic algae are the focus of many biofuel industries, the high production costs associated with the collection and sedimentation of planktonic algae, is driving the industry towards the use of MPB that attach to hard substrata (Barlow et al., 2016; Johnson and Wen, 2010). Attached microalgae are both easier and cheaper to harvest, and biofuel can be coupled with wastewater treatment to maximise economic gains whilst limiting environmental impacts (Barlow et al., 2016; Zhou et al., 2012).

In addition to naturally removing substantial amounts of CO₂ from our atmosphere, a transition from fossil fuels to the use of MPB derived biofuel would reduce current CO₂ emissions and this has the potential to be highly productive, reaching 115,200 L ha⁻¹ yr⁻¹ (Shuba and Kifle, 2018). The powerful nutrient filtering capacity of the MPB means that they can be used to reduce the nutrient content of

disposed manure (Kebede-Westhead et al., 2004). Their use as an intermediary step could also help mitigate against the leaching of nutrients from agricultural run-off before it reaches the marine environment. These options would involve fewer trade-offs with other ES such as food production on land, as well as utilise nutrients from waste products like manure to generate biofuel. This could result in a win-win situation and sustainable ES delivery but industrial scaling of these processes would require significant economic investment (Walsh et al., 2016).

4.6. Cultural services

Through the provision of non-material benefits, society gains immensely from natural environments (Small et al., 2017) but cultural ES are often excluded from assessments as they are difficult to quantify and can vary across time, space and culture (Geange et al., 2019). There are a number of indirect links between the supporting role of MPB in ecosystem function and the provision of cultural benefits, making it difficult to quantify the direct contribution of MPB to cultural ES. For example, the MPB support harvested shellfish and fish species (Morioka et al., 2017; Melville & Connolly, 2003; Franca et al., 2011), improve the quality and clarity of our waters and underpin marine foodwebs. These links are the foundation of cultural ES provision, and increase our recreational use, and appreciation of the marine environment, as well as non-use benefits such as 'existence' value (Martin et al., 2016). It is often our association with the natural environment that drives our desire to protect it, and these connections improve our health and wellbeing (Annis et al., 2017). The loss of provisioning or regulating ES that underpin healthy and productive ecosystems can result in a spiritual or cultural disconnection (Penny, 2007).

5. THE IMPORTANCE OF INTERACTIONS & FEEDBACKS

The complex interactions and feedbacks between organisms and the sedimentary environment have recently been documented through manipulative experiments in both the laboratory (Hale et al., 2017; Harris et al., 2016) in the field (Douglas et al., 2017; Hale et al., 2019; Kenworthy et al., 2016; Thrush et al., 2014) and in modelling studies (Watson et al., 2019). These studies help to disentangle the underlying processes and functions that lead to ES delivery, but the examination of feedback processes or a breakdown of interactions are particularly important (O'Meara et al., 2017; Yletyinen et al., 2019). The loss of ES cannot easily be predicted from the resilience of individual species or functional groups (Watson et al., 2019). We must take an ecosystem-based approach and attempt to unravel the interactions, trade-offs and synergies between various ES. This should include the role of inconspicuous, but well-connected, organisms within the system such as MPB.

This review has described the essential and multiple roles of MPB in ecosystem function and we have argued that their fast growth rates and adaptability make MPB resilient and flexible to change. Their role in ecosystem interactions is critical and their interactions with other organisms are likely to change as we continue to put pressures on soft-sediment ecosystems. Through the use and management of estuarine ecosystems for specific 'requirements' and our demand for particular ES, we create feedbacks which ultimately alter the underlying processes and functions that influence the potential for future ES delivery (Balvanera et al., 2014). The breakdown of tightly coupled processes and functions due to human pressure can drive the ecosystem towards a regime shift (Thrush et al., 2014). Subsequently key functions are lost and the capacity of the ecosystem to deliver ES is diminished, with feedbacks and drivers operating differently across habitats, spatial and temporal scales (Rivero and Villasante, 2016).

6. FUTURE INVESTIGATIONS FOR MPB AND ES DELIVERY

Negative effects on carbon and nutrient cycling in the marine environment will influence the global climate regulation and this can feedback to the productivity of both marine and terrestrial systems. The close coupling of productivity and nutrient cycling in soft-sediments, means that the effects of anthropogenic stressors on different aspects of coastal soft-sediment ecosystem, will likely lead to the loss of multiple ecosystem services. Each step in this complex socio-ecological network is affected by the decisions we make (Yletyinen et al., 2019) and the multiple stresses we put on the system. Moving beyond simple cause and effect relationships is an important element of improved prediction and management decisions. Soft-sediment systems are inherently complex and many ES studies only focus on the delivery of specific ES. However, in all ecological systems, complex processes and functions deliver multiple ES simultaneously (Turkelboom et al., 2015). The complex interactions between humans and ecosystems lead to 'wicked problems' in terms of trade-offs in ES delivery (Davies et al., 2015). Wicked problems are social or cultural problems complicated by the need for a change in mindset or behaviour of society, economic issues and problems where there is no single solution and resolution of one issue may lead to another problem. An example of a 'wicked' socio-ecological problem involves our increasing population and the demand for food production on land. Unfortunately, this increase in food production leads to elevated nutrient loads and eutrophication downstream in estuaries (Bennett et al., 2015). Society cannot be ignorant of the interactions and connectivity between habitats when management decisions are made for ES delivery, as the assessment and management of services in isolation leads to benefits being limited or compromised in adjacent habitats. Favouring short-term gains over long-term sustainable ES delivery does not promote sustainability for the future (Townsend et al., 2018). Rather than avoid the complexity of ecological networks, future studies supporting ES need to address the

interdependency of services (Fig 2) and the scaling effects on service provision. While Productivity in estuaries, coasts and the continental shelf is not place-based but nevertheless an essential global service.

We recognise that the role of MPB and related ecosystem interactions and functions are often taken for granted. Due to their inconspicuous nature, these single-celled algae can be overlooked as an integral part of a complex ecosystem of interactions and feedbacks that are critical for the delivery of life-sustaining ES. The “secret garden” discussed in Macintyre et al. (1996) and Miller et al. (1996) should no longer remain a secret.

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Author Contribution Statement

JAH conceived the paper and lead the manuscript production. All authors contributed to the ideas presented in this paper, drafting of the manuscript and gave final approval for publication.

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