1   **The role of microphytobenthos in soft-sediment ecological networks and their contribution**

2   **to the delivery of multiple ecosystem services.**

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7   **Abstract**

8   1.   Sediment dwelling, microscopic primary producers, that occupy sediments in the photic zone, are

9   commonly referred to as microphytobenthos (MPB). The MPB are essential components of soft-

10   sediment systems, but are often overlooked when assessing coastal ecosystem functionality and

11   service delivery.

12   2.   The MPB are involved in several complex interactions and feedbacks that underpin the delivery of

13   vital ecosystem services. MPB profoundly influence the flow and cycling of carbon and nutrients,

14   such as nitrogen, directly and indirectly underpinning highly productive shallow water marine

15   foodwebs. The MPB can also stabilise sediments through the formation of biofilms, and

16   significantly improve water quality by mediating the benthic-pelagic coupling of nutrients,

17   sediment and pollutants.

18   3.   The functional role of the MPB is compromised by increasing anthropogenic pressures such as

19   nutrient enrichment, sedimentation, herbicides and emerging contaminants such as microplastic

20   pollution, yet MPB are extremely good at buffering the effects of these land sourced stressors at

21   the interface between land and sea.

22   4.   *Synthesis:* Society often appreciate the final steps in the provisioning of goods and services from

23   our coastal marine environments. However, provisioning services are only possible due to the

24   multitude of supporting and regulating services that underpin them. MPB are central to many

25   benthic ecological networks, and contribute to ecosystem service delivery through various

26   pathways. Understanding the critical role of MPB in complex networks is therefore essential to

27   appreciate their importance in ecosystem function and service delivery into the future.

28   Key words: Benthic microalgae, ecosystem services, estuarine systems, microphytobenthos, MPB,

29   service delivery, soft-sediment ecology.

1. INTRODUCTION

31   Except under extreme environmental forcing, it is often challenging to connect the effects of

32   anthropogenic stressors to changes in ecosystem function, particularly in coastal soft-sediment

33   ecosystems. It is especially difficult to envisage Ecosystem Services (ES), which are supported by small

34   sediment-dwelling organisms. The microphytobenthos (MPB) are particularly overlooked when

35   assessing coastal ecosystem service delivery, yet they are important microbial primary producers that

36   photosynthesise on the sediment surface in intertidal and photic subtidal zones. To rectify this

37   problem, we first need to better understand the dynamics of these small but vital organisms, the

38   processes and functions that underpin ES delivery (Geange et al., 2019) and the influence of multiple

39   stressors on the flow of ES from soft-sediment ecosystems. We also need to understand the complex

40   feedbacks and networks that connect different organisms, processes and functions that support ES

41   delivery in these ecosystems.

42   This paper seeks to draw attention to the importance of MPB for soft-sediment ecosystem function

43   and the delivery of vital ecosystem services. Evidence has been drawn primarily from coastal and

44   estuarine studies to highlight the context-dependent role of MPB in ecosystems. Anthropogenic

45   pressures that may alter the role of MPB in ecological networks is considered and future requirements

46   in this area of research are suggested.

2. ECOSYSTEM SERVICES

48   Ecosystem services (ES) have been discussed widely (Carpenter et al., 2009; Costanza et al., 2014;

49   MEA, 2005; TEEB, 2010) and an important justification for ES research is in ensuring that the hidden

50   infrastructure that nature provides society and supports human wellbeing is recognised and protected

51   (TEEB, 2010). ES delivery is deteriorating at an alarming rate with over 60% loss globally over the past

52   50 years (MEA, 2005). Despite the wide array of ES provided by soft-sediment ecosystems (Thrush et

53   al., 2013) the majority of ES investigations to-date have focussed on charismatic organisms (e.g.

54   whales and dolphins) and habitats (e.g. coral reefs, seagrasses, mangroves) (Alongi, 2014; Barbier,

55   2017; Koch et al., 2009). These species and habitats are easier to value due to their contributions to

56   carbon sequestration, coastal protection and charisma in the eyes of society. However, we must not

57   take for granted the life-sustaining, regulating and supporting ES provided by estuaries and other less

58   charismatic coastal soft-sediment dominated habitats (Passarelli et al., 2018). These ecosystems play

59   an integral and disproportional role in carbon sequestration, as well as keeping our waters clean and

60   healthy (Thrush et al., 2013). Excluding the delivery of ES from coastal ecosystems in decision

61   frameworks promotes short-term gains that will compromise the long-term delivery of multiple ES

62   across different ecosystems.

63   The contribution of MPB to the delivery of multiple ES stems from their central role as primary

64   producers at the base of benthic foodwebs, their rapid transfer of organic matter, and mediation of

65   energy and nutrients (Christianen et al., 2017). For example, MPB primary production is often closely

66   linked to coastal fish and shellfish production (Kritzer et al., 2016; Morioka et al., 2017). MPB also play

67   a central role in water purification, by influencing the removal, transformation, and retention of

68   pollutants (Kowalski et al., 2009; Snelgrove et al., 2018; Tolhurst et al., 2002). MPB mediate sediment

69   dynamics by providing protection against erosion (Paterson et al., 2018), which in turn reduces the

70   resuspension of fine sediments (Tolhurst et al., 1999) and enhances water clarity. Coastal soft-

71   sediments also provide important recreational and cultural services, attracting bird watchers, tourists,

72   and supporting culturally significant species and habitats that rely on the benthic foodweb.

73   **3.   MICROPHYTOBENTHOS**

MPB communities are dominated by unicellular eukaryotic algae, cyanobacteria and euglenoids that inhibit 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 habits 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 µM photons m^{-2} s^{-1}; Gattuso et al., 2006) and high (>2000 µM photons m^{-2} 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.,

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100 1996) where many ecologically significant processes take place, they influence sediment stability by

101 altering sediment properties and processes (Fagherazzi et al., 2014) and trap particles from overlying

102 water (Kornman and de Deckere, 1998). Despite the clear emphasis on the importance of MPB in the

103 'secret garden' papers, and recent studies confirming the role of MPB in the above processes, their

104 contribution is still often disregarded. MPB communities are often influenced by sediment type,

105 nutrient concentrations and temperature (Sundback and Snoeijs, 1991; Watermann et al., 1999).

106 While diatoms (Fig 1B-D), often dominate the MPB in mid-latitude temperate systems, this can shift

107 seasonally to cyanobacteria and chlorophytes (Barranguet et al., 1998) or spatially to euglena on high

108 intertidal sediments (Kingston and Gough, 2009). In the mudflats around Sydney, green filamentous

109 algae are the dominant primary producers, replacing the MPB altogether (Murphy et al., 2004), while

110 cyanobacteria dominate other sandy systems throughout the year (Cook et al., 2004; Paerl et al., 1996;

111 Stal, 2012).

112 Single celled, photosynthesising organisms are quantitatively important for estuarine and shelf

113 primary productivity, bentho-pelagic exchange of sediment, the cycling of nutrients and oxygen

114 production (Chen et al., 2017; Jones et al., 2017; Longphuirt et al., 2009; Pinckney, 2018). MPB

115 productivity also supports energy transfer to higher organisms (MacIntyre et al., 1996) with

116 compositional changes in the MPB taxa altering the nutritional quality of this primary food source

117 (Muller-Navarra et al., 2000).

118 **A**   **B**

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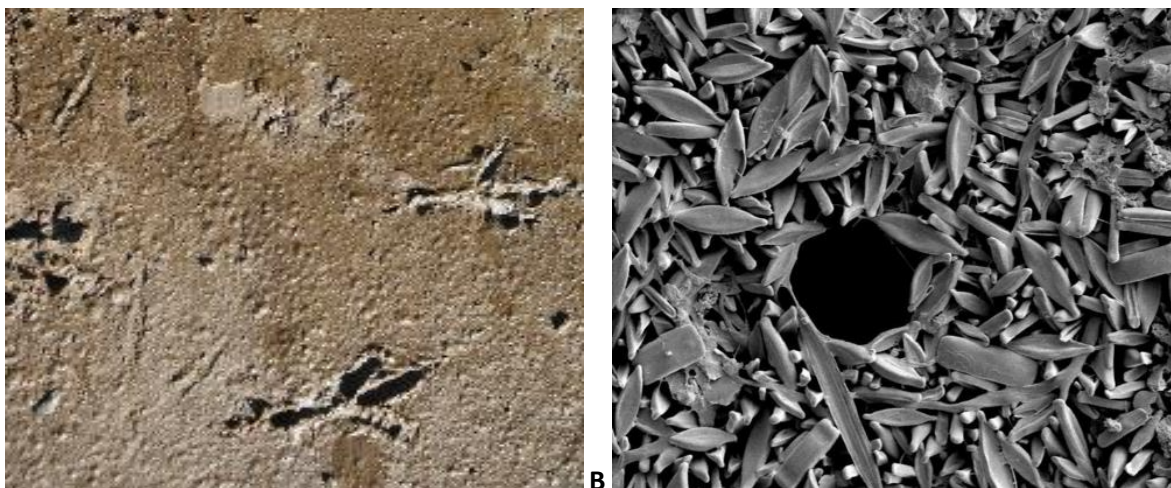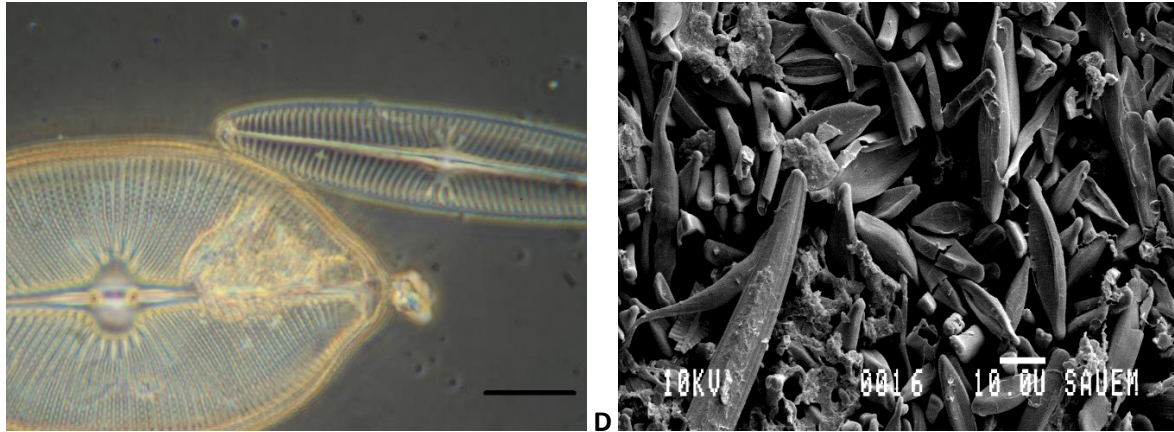
Fig 1: A) A light golden biofilm on the surface of sandy sediment of the Eden estuary, UK B) Low temperature scanning electron micrograph of a natural diatom biofilm: Dee Estuary UK. Scale bar - 10 µm. C) Light micrograph of two cosmopolitan diatom species that often dominate MPB in intertidal sediments.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

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

139 continue except under extreme environmental degradation, but their resilience should not be taken

140 for granted. ES result from complex interactions between biophysical processes and human behaviour

141 (Mouchet et al., 2014) and are underpinned by multiple ecosystem functions, processes and complex

142 feedbacks (Thrush et al., 2012). MPB play a central role in several complex interactions (Fig 2), that

143 define these functions but the indirect roles of MPB and their interactions with other organisms are

144 vulnerable to environmental change (Pratt et al., 2014; Thrush et al., 2013).
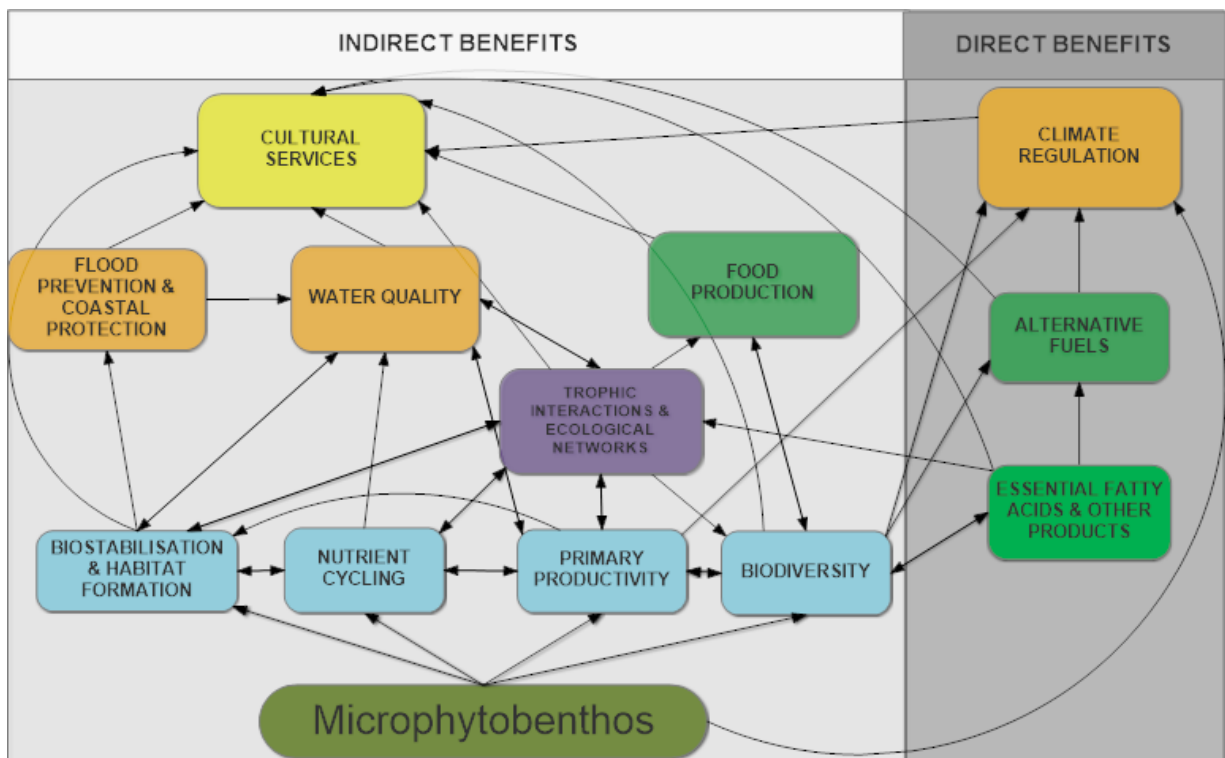
145

146 Fig 2: Contribution of microphytobenthos (MPB) to Ecosystem Services (ES) delivery. Blue-supporting

147 services (S), Green-provisional services (P), Orange-regulating services (R), Yellow-cultural services

148 (bundled, C). The network illustrates that cultural services are underpinned by several ES in the

149 network and that MPB are at the base of the network. Purple - trophic interactions and the importance

150 of the ecological network in soft-sediments. These factors are all essential when considering

151 functioning of these ecosystems and the provision of ES.

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153 **4. INDIVIDUAL ECOSYSTEM FUNCTIONS & SERVICES**

154   **4.1. Biodiversity (S) & habitat services (S)**

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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 CO_2 with estimates of 30 to 230 g Carbon fixation $m^2\ y^{-1}$ on intertidal flats (Heip et al., 1995). 'Unvegetated' coastal sediments have been estimated to cover a global area of $23.9 \times 10^{12}\ m^2$ (Duarte et al., 2004), a much greater expanse than vegetated sediments, while others estimate the continental shelf area as covering $28 \times 10^6\ km^2$ (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

179   primary productivity remain poor (Charpy-Roubaud and Sournia, 1990) and widely debated (Cai, 2011;

180   Pinckney, 2018) as the benthic productivity in these areas is rarely considered.

181   The overall productivity of coastal soft-sediment depends on the daily light levels, temperature, tidal

182   elevation, salinity, exposure period, as well as local hydrodynamics. The latter can resuspend and

183   transport the MPB offshore (de Jonge and van Beusekom, 1995; T. J. Tolhurst et al., 2002). Despite

184   estimates that the MPB are responsible for the production of around 500 million tons of organic

185   carbon annually (Cahoon, 1999), their contribution to the carbon cycle in ecosystem and global

186   biogeochemical models is often overlooked. Benthic productivity can exceed phytoplankton

187   productivity in nearshore waters and continental shelf regions (Jahnke et al., 2000; Jones et al., 2017;

188   Pinckney, 2018). Although coastal waters account for just 10% of the ocean's surface area, these areas

189   are rich in nutrients. These nutrients fuel photosynthesis, with upwelling and outflow from land,

190   linking these systems to the open ocean (MacKenzie and Lerman, 2006). Coastal waters are hot spots

191   of productivity and often visible on the edge of satellite images, yet coastal waters are excluded from

192   remote sensing estimates of phytoplankton productivity due to the added complexity of elevated

193   turbidity (Behrenfeld et al., 2005). As the interface between land and sea, intertidal sediments should

194   be considered a significant component of a land to sea continuum rather than an isolated ecosystem.

195   It seems counterintuitive to exclude benthic primary productivity from oceanic productivity models or

196   to disregard them as insignificant when they are sources of primary producers to the open ocean.

197   MPBs efficiently convert solar energy into biomass at a rate around 10 times greater than that of

198   terrestrial plants. Up to 1.83 kg of CO_2 can be fixed for 1kg of microalgae biomass (Chisti, 2008) with

199   much of this energy channelled into metazoan and microbial foodwebs (Maher and Eyre, 2011;

200   Moerdijk-poortvliet et al., 2018). While the high productivity of these ecosystems often results in fixed

201   carbon being consumed and respired back to the atmosphere, for every 0.6 mol of CO_2 respired as

202   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 CO_2 which is then calcified into calcium carbonate shells (producing up to 1000g $CaCO_3$ m^2 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

229   phytoplankton (Basu and Mackey, 2018) and we must understand and quantify their contribution to

230   the delivery of ES and how they interact with other organisms in these complex ecological networks.

231   **4.3. Water quality (R) & nutrient cycling (S)**

232   Increasing loads of nutrients, sediment and pollutants from land are significant stressors affecting

233   coastal water quality (Auta et al., 2017; Hou et al., 2013), biodiversity (Thrush et al., 2017) and

234   ecosystem functioning (Douglas et al., 2018; Wulff et al., 1997). Heavy metals, organic pollutants and

235   polycyclic aromatic hydrocarbons, pathogens and microplastics accumulate in coastal soft-sediments

236   (Bennett et al., 2000; Cole et al., 2011; Kowalski et al., 2009; Wiegner et al., 2003; Wyness et al., 2019)**,**

237   and these can bind to MPB and the EPS they secrete. Despite recent reductions in heavy metal and

238   PAH inputs, buried substances can be remobilised by changing environmental conditions such as

239   climate change, and storm events (Bennett et al., 2000; Blake et al., 2003; Wyness et al., 2019). Due

240   to their position at the sediment-water interface, the MPB can influence the release and

241   transformation of redox-sensitive metals (Kowalski et al., 2009) and form different communities on

242   the surface of plastic particles (Michels et al., 2018) compared to surrounding sediment particles

243   (Harrison et al., 2014).

244   While the MPB often mediate and influence the accumulation, breakdown and sequestration of

245   nutrients, sediment and contaminants, their role in the delivery of multiple ES is also at risk from the

246   input of other pollutants such as herbicides and pharmaceuticals. Recently the structure of benthic

247   diatom assemblages has been used to indicate environmental contamination by herbicides and other

248   substances (Wood et al., 2019). The herbicides diuron and atrazine (Legrand et al., 2006), the antibiotic

249   doxycycline, the local anaesthetic procainamide (Prata et al., 2018) and the biocide triclosan (Franz et

250   al., 2008) are all known to affect both growth and photosynthesis and therefore the functional role of

251   primary producers.

252   Reducing the clarity of overlying waters with sediment or phytoplankton biomass together with excess

253   nutrients can break down key processes and functions mediated by MPB on the seafloor and force the

254   system into an alternative state (Koppel et al., 2001) dominated by planktonic communities. These

255   types of regime shifts have been observed in several systems (Biggs et al., 2018) including the

256   Chesapeake Bay (Kemp et al., 2005), the Black Sea (Oguz and Gilbert, 2007) and other European

257   estuaries (Jickells et al., 2016). In the Chesapeake Bay, the system shifted from clear waters largely

258   dominated by seagrass and oysters to a system dominated by planktonic communities in the 1950s.

259   This was driven by excess nutrient inputs and the over-harvesting of oysters (Kemp et al., 2005). The

260   ensuing lower light availability on the seafloor (Pratt et al., 2014), and hypoxia associated with the

261   decomposing bloom algae (Rabalais et al., 2002) can drastically shift ecosystem functionality resulting

262   in positive feedback mechanisms that prevent these systems from returning to former states (Biggs et

263   al., 2018). MPB can no longer photosynthesise as effectively during inundation (Drylie et al., 2018;

264   Kromkamp et al., 1995; O'Meara et al., 2017), which reduces their ability to mediate nutrient fluxes

265   to the water column, further exacerbating the issue (Sundbäck et al., 2006). When functionally

266   important fauna such as deep-dwelling bivalves are reduced, this further undermines the capacity of

267   the system to respond to increasing nutrient or sediment loads and highlights the need to understand

268   the complex interactions between organisms.

269   In clear estuaries, MPB can assimilate up to 96% of the daily dissolved inorganic nitrogen (DIN)

270   supplied to estuaries (Hochard et al., 2010), but these processes are altered as the water clarity

271   changes. MPB nutrient uptake can often exceed denitrification by 1-2 orders of magnitude (Sundbäck

272   et al., 2004; Sundbäck and McGlathery, 2005), especially in oligotrophic systems (Cook et al., 2004),

273   but their competitive edge is dependent on environmental conditions such as light levels. Through

274   tight N-recycling, MPB uptake can ensure the system remains productive whilst limiting the efflux of

275   DIN into overlying water (Box 1). This efficient remineralisation of nutrients is often reflected in a

276   greater photosynthetic efficiency (net primary productivity (NPP) normalised by MPB biomass) in

277   sandy sediments compared to mud (Billerbeck et al., 2007). This results in a close association between

278 the MPB and bacteria that preferentially utilise decomposing MPB (Banta et al., 2004) and labile EPS

279 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).

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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 N_2 gas and thus denitrification processes, even stimulating denitrification (An and

298 Joye, 2001). The alternation between oxygenation and deoxygenation of the sediment can

299 significantly influence biogeochemical cycling of nitrogen. At night, when nitrogen limitation and

300 deoxygenation may occur, the drawdown of dissolved oxygen can facilitate denitrification processes

301 with MPB contributing to community respiration and reduced sediment oxygen concentrations (An

302 and Joye, 2001). Moreover, cyanobacterial mats can turn sediments anaerobic within minutes

303 (Villbrandt et al., 1990) allowing aerobic non-heterocystous species to fix nitrogen in the absence of

304 oxygen (Stal, 2012).

305 When light is sufficient, MPB photosynthesis oxygenates the upper sediment layers, and provides a

306 labile carbon substrate for N-cycling bacteria (Middelburg et al., 1996). This supports elevated aerobic

307 respiration, and enhances nitrification (the conversion of NH_4^+ to NO_2^- and NO_3^-, Risgaard-Petersen et

308 al., 2004, 1994), which is often the most important source of NO_3^- for denitrification (Middelburg et

309 al., 1996). This, of course, depends on the degree of competition between MPB and bacteria for DIN,

310 N availability in the sediment (An and Joye, 2001), local environmental conditions as well as resident

311 benthic communities (Foshtomi et al., 2015).

312 Bioturbators that typically feed on MPB enhance sediment oxygenation and the transport of labile

313 carbon to greater depths in the sediment, while also increasing the surface area of oxic-anoxic

314 interfaces that are essential for coupled processes (Gilbert et al., 1998; Laverock et al., 2011;

315 Tuominen et al., 1999). Sediment reworking has been demonstrated to increase denitrification and

316 coupled nitrification-denitrification by up to 300% (Tuominen et al., 1999; Webb et al., 2004). B

317 ioturbation also alters the efflux of O_2, CO_2 and DIN across the sediment-water interface (Howarth et

318 al., 1996; Howe et al., 2004). The complex interactions and individual effects of MPB and infauna, can

319 therefore alter sediment properties (Murphy and Tolhurst, 2009) that stimulate or inhibit

320 biogeochemical processes in soft-sediments.

321 **4.4. Erosional protection (R) & habitat formation (S)**

322 MPB such as diatoms and cyanobacteria secrete carbon-rich EPS, which binds sediment particles

323 together at the sediment-water interface creating a 'biofilm' (Underwood and Paterson, 2003). Biofilm

324 formation can increase the resistance of the sea bed to hydrodynamic stress and raise sediment

325 erosion thresholds through the cohesion between particles (Black et al., 2002; Joensuu et al., 2018).

326 Biofilm formation can also smooth the surface and reduce bed roughness. This forms a protective

327 'skin' which again increases the resistance to flow (Consalvey et al., 2004; Underwood et al., 2005).

328   Often biofilms can be visible to the eye, yet even when invisible or just a subtle hint of brown or green

329   is detectable on the sediment surface (MacIntyre et al., 1996) sediment properties can be significantly

330   (Tolhurst et al., 2006). Biostabilisation can positively affect ecosystem functioning and ES delivery,

331   however excessive deposition of fine material can also act as a stressor on benthic communities

332   (Lohrer et al., 2004b; Thrush et al., 2004). Various disturbances can interact with organic enrichment

333   resulting in complex effects on benthic communities (Widdicombe and Austen, 2001), which are

334   detectable across small and large environmental gradients (Pratt et al., 2015; Spears et al., 2008;

335   Spilmont et al., 2011). The diversity of the benthos can be important for maintaining the stabilisation

336   of coastal sediments and the delivery of this key ES (Hale et al., 2019).

337   As sediment loads increase, MPB may also accumulate more sediment and pollutants in the bed

338   (Paterson and Black, 1999), which improves light availability and water quality. Improving water

339   quality is in itself an important ES but the biological stabilisation of the bed also contributes to other

340   ES such as erosional protection and habitat formation (Malarkey et al., 2015; Passarelli et al., 2018).

341   In cold temperate systems, the influence of MPB on suspended sediment loads can often be restricted

342   to warmer periods when irradiances are high and physical disturbances are low (Borsje et al., 2008;

343   Widdows and Brinsley, 2002). Conversely, in warmer climates where other taxa such as green

344   filamentous algae dominate, MPB biomass can be higher during cooler months (Murphy and Tolhurst,

345   2009). Thus, the seasonal effects of MPB on ecosystem function and ES delivery will vary across

346   different systems.

347   In seasonal systems, the increase in MPB and EPS can be limited by of the appearance of grazers

348   (Fernandes et al., 2006; Weerman et al., 2012). In addition to abundance, grazer size (Harris et al.,

349   2016) and other infaunal traits (Hewitt et al., 2014) can influence MPB biomass. As such,

350   biostabilisation of the sediment-water interface by MPB can be affected by ecological links in a variety

351   of ways. For example, surface dwellers that bulldoze surface layers can destabilising the sediment (de

352   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 CO_2 from our atmosphere, a transition from fossil fuels to the use of MPB derived biofuel would reduce current CO_2 emissions and this has the

17

403   potential to be highly productive, reaching 115,200 L ha^{-1} yr^{-1} (Shuba and Kifle, 2018). The powerful

404   nutrient filtering capacity of the MPB means that they can be used to reduce the nutrient content of

405   disposed manure (Kebede-Westhead et al., 2004). Their use as an intermediary step could also help

406   mitigate against the leaching of nutrients from agricultural run-off before it reaches the marine

407   environment. These options would involve fewer trade-offs with other ES such as food production on

408   land, as well as utilise nutrients from waste products like manure to generate biofuel. This could result

409   in a win-win situation and sustainable ES delivery but industrial scaling of these processes would

410   require significant economic investment (Walsh et al., 2016).

411   **4.6. Cultural services**

412   Through the provision of non-material benefits, society gains immensely from natural environments

413   (Small et al., 2017) but cultural ES are often excluded from assessments as they are difficult to quantify

414   and can vary across time, space and culture (Geange et al., 2019). There are a number of indirect links

415   between the supporting role of MPB in ecosystem function and the provision of cultural benefits,

416   making it difficult to quantify the direct contribution of MPB to cultural ES. For example, the MPB

417   support harvested shellfish and fish species (Morioka et al., 2017; Melville & Connolly, 2003; Franca

418   et al., 2011), improve the quality and clarity of our waters and underpin marine foodwebs. These links

419   are the foundation of cultural ES provision, and increase our recreational use, and appreciation of the

420   marine environment, as well as non-use benefits such as 'existence' value (Martin et al., 2016). It is

421   often our association with the natural environment that drives our desire to protect it, and these

422   connections improve our health and wellbeing (Annis et al., 2017). The loss of provisioning or

423   regulating ES that underpin healthy and productive ecosystems can result in a spiritual or cultural

424   disconnection (Penny, 2007).

425   **5. THE IMPORTANCE OF INTERACTIONS & FEEDBACKS**

426   The complex interactions and feedbacks between organisms and the sedimentary environment have

427   recently been documented through manipulative experiments in both the laboratory (Hale et al.,

428 2017; Harris et al., 2016) in the field (Douglas et al., 2017; Hale et al., 2019; Kenworthy et al., 2016;

429 Thrush et al., 2014) and in modelling studies (Watson et al., 2019). These studies help to disentangle

430 the underlying processes and functions that lead to ES delivery, but the examination of feedback

431 processes or a breakdown of interactions are particularly important (O'Meara et al., 2017; Yletyinen

432 et al., 2019). The loss of ES cannot easily be predicted from the resilience of individual species or

433 functional groups (Watson et al., 2019). We must take an ecosystem-based approach and attempt to

434 unravel the interactions, trade-offs and synergies between various ES. This should include the role of

435 inconspicuous, but well-connected, organisms within the system such as MPB.

436 This review has described the essential and multiple roles of MPB in ecosystem function and we have

437 argued that their fast growth rates and adaptability make MPB resilient and flexible to change. Their

438 role in ecosystem interactions is critical and their interactions with other organisms are likely to

439 change as we continue to put pressures on soft-sediment ecosystems. Through the use and

440 management of estuarine ecosystems for specific 'requirements' and our demand for particular ES,

441 we create feedbacks which ultimately alter the underlying processes and functions that influence the

442 potential for future ES delivery (Balvanera et al., 2014). The breakdown of tightly coupled processes

443 and functions due to human pressure can drive the ecosystem towards a regime shift (Thrush et al.,

444 2014). Subsequently key functions are lost and the capacity of the ecosystem to deliver ES is

445 diminished, with feedbacks and drivers operating differently across habitats, spatial and temporal

446 scales (Rivero and Villasante, 2016).

447 **6.   FUTURE INVESTIGATIONS FOR MPB AND ES DELIVERY**

448 Negative effects on carbon and nutrient cycling in the marine environment will influence the global

449 climate regulation and this can feedback to the productivity of both marine and terrestrial systems.

450 The close coupling of productivity and nutrient cycling in soft-sediments, means that the effects of

451 anthropogenic stressors on different aspects of coastal soft-sediment ecosystem, will likely lead to the

452 loss of multiple ecosystem services. Each step in this complex socio-ecological network is affected by

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453 the decisions we make (Yletyinen et al., 2019) and the multiple stresses we put on the system. Moving

454 beyond simple cause and effect relationships is an important element of improved prediction and

455 management decisions. Soft-sediment systems are inherently complex and many ES studies only focus

456 on the delivery of specific ES. However, in all ecological systems, complex processes and functions

457 deliver multiple ES simultaneously (Turkelboom et al., 2015). The complex interactions between

458 humans and ecosystems lead to 'wicked problems' in terms of trade-offs in ES delivery (Davies et al.,

459 2015). Wicked problems are social or cultural problems complicated by the need for a change in

460 mindset or behaviour of society, economic issues and problems where there is no single solution and

461 resolution of one issue may lead to another problem. An example of a 'wicked' socio-ecological

462 problem involves our increasing population and the demand for food production on land.

463 Unfortunately, this increase in food production leads to elevated nutrient loads and eutrophication

464 downstream in estuaries (Bennett et al., 2015). Society cannot be ignorant of the interactions and

465 connectivity between habitats when management decisions are made for ES delivery, as the

466 assessment and management of services in isolation leads to benefits being limited or compromised

467 in adjacent habitats. Favouring short-term gains over long-term sustainable ES delivery does not

468 promote sustainability for the future (Townsend et al., 2018). Rather than avoid the complexity of

469 ecological networks, future studies supporting ES need to address the interdependency of services

470 (Fig 2) and the scaling effects on service provision. While Productivity in estuaries, coasts and the

471 continental shelf is not place-based but nevertheless an essential global service.

472 We recognise that the role of MPB and related ecosystem interactions and functions are often taken

473 for granted. Due to their inconspicuous nature, these single-celled algae can be overlooked as an

474 integral part of a complex ecosystem of interactions and feedbacks that are critical for the delivery of

475 life-sustaining ES. The "secret garden" discussed in Macintyre et al. (1996) and Miller et al. (1996)

476 should no longer remain a secret.

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486   JAH conceived the paper and lead the manuscript production. All authors contributed to the ideas

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