

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

3 *Hope, J. A¹, Paterson, D.M² and Thrush, S.F¹*

4 ¹ *Institute of Marine Science, University of Auckland, Private Bag 92019, Auckland, New Zealand*

5 ² *Sediment Ecology Research Group, School of Biology, University of St Andrews, Scotland*

6 Corresponding author; Julie.hope@auckland.ac.nz

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.

30 **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.

47 **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.

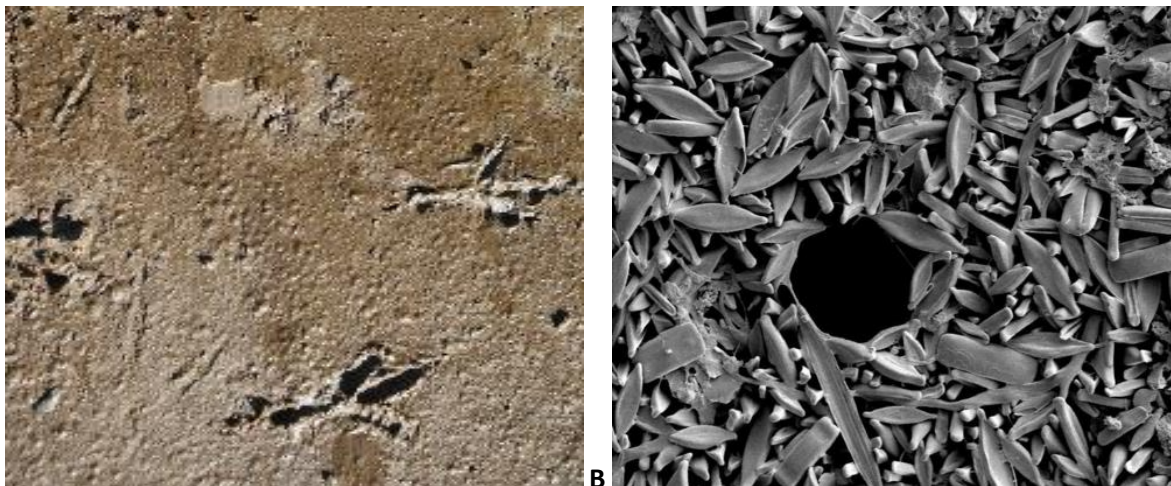
63 The contribution of MPB to the delivery of multiple ES stems from their central role as primary
64 producers at the base of benthic foodwebs, their rapid transfer of organic matter, and mediation of
65 energy and nutrients (Christianen et al., 2017). For example, MPB primary production is often closely
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**

74 MPB communities are dominated by unicellular eukaryotic algae, cyanobacteria and euglenoids that
75 inhibit the surface layers sediments within the photic zone (MacIntyre et al., 1996). Their colonisation
76 of the seafloor extends from shallow intertidal areas to the edge of the continental shelf (Cahoon,
77 1999; Pinckney, 2018) and their presence can appear as a subtle brown or green shading on the
78 sediment surface or they can be invisible to the naked eye. MPB are well adapted to the harsh
79 conditions of estuaries, where temperature, light, nutrient and hydrodynamic conditions regularly
80 fluctuate. Their productivity is regulated by the availability of these abiotic resources (Kromkamp et
81 al., 1995; Perkins et al., 2001), but they respond rapidly and efficiently to prevailing environmental
82 conditions (Falkowski and Raven, 2013; Hopes and Mock, 2015). MPB have colonised habits from
83 freshwater to extremely saline environments (Forster et al., 2006; Potapova, 2011) and in intertidal
84 environments, productivity and biomass can shift with the tidal cycle (Serôdio and Catarino, 1999). In
85 many turbid estuaries of Europe, the productivity of MPB is restricted during immersion periods
86 (Migne et al., 2009) but they are highly adapted to maximise their photosynthetic efficiency at
87 extremely low ($2.8 \mu\text{M photons m}^{-2} \text{ s}^{-1}$; Gattuso et al., 2006) and high ($>2000 \mu\text{M photons m}^{-2} \text{ s}^{-1}$;
88 Cahoon, 1999) light conditions. Even in the high Antarctic with less than 0.1% of the summer sunlight
89 penetrates the ice, MPB contribute significantly to marine primary production (Dayton et al., 1986;
90 Lohrer et al., 2013). In the 19th century the naturalist Ernst Haeckel, presented some of the first
91 amazing images of microscopic algae but suggested these organisms, although beautiful, played no
92 significant role within the ecosystem. Perspectives have changed considerably over recent years and
93 it is well recognised that MPB and biofilms contribute substantially to the functioning of coastal soft-
94 sediments (Miller et al., 1996; O'Meara et al., 2017; Paterson et al., 2018; Pinckney, 2018). The
95 functionally important roles of MPB were addressed in two key articles by MacIntyre et al. (1996) and
96 Miller et al. (1996) who appropriately called MPB biofilms in soft-sediments "The secret garden".
97 These organisms are microscopic, and often form only a thin layer on the sediment surface (Fig 1A),
98 but diatoms and cyanobacteria can mediate both small and large-scale processes (Chapman et al.,
99 2010). For instance, MPB influence biogeochemical gradients within the sediment (MacIntyre et al.,

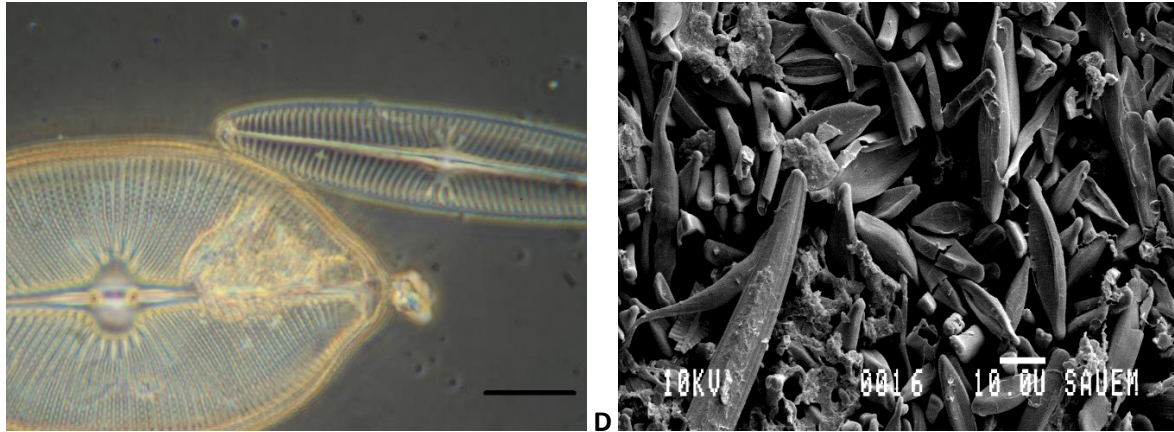
100 1996) where many ecologically significant processes take place, they influence sediment stability by
101 altering sediment properties and processes (Fagherazzi et al., 2014) and trap particles from overlying
102 water (Kornman and de Deckere, 1998). Despite the clear emphasis on the importance of 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, benthic-pelagic exchange of sediment, the cycling of nutrients and oxygen
114 production (Chen et al., 2017; Jones et al., 2017; Longphuir 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

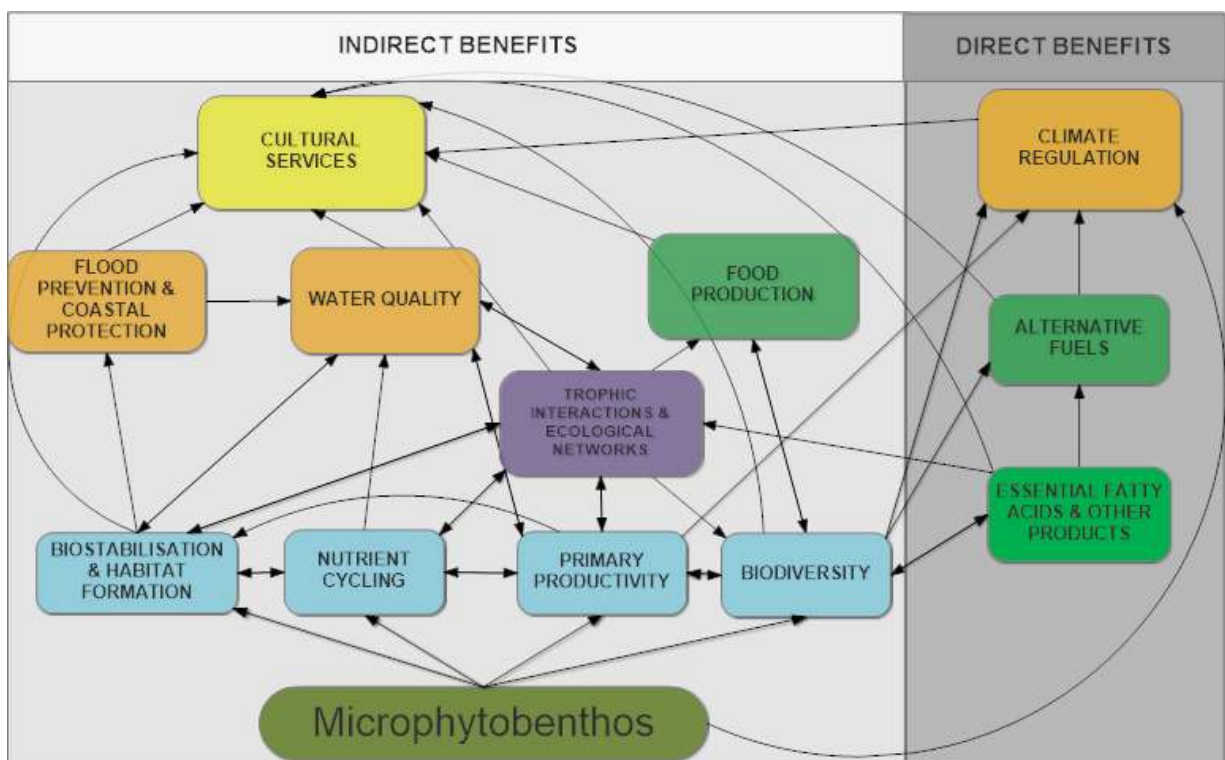
B



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

125
 126 The widespread distribution, rapid turnover rates and adaptability of MPB (Hopes and Mock, 2015;
 127 Oakes et al., 2012) supports their evolutionary success and has allowed MPB to occupy many aquatic
 128 habitats. Unlike their planktonic cousins, many benthic diatoms are motile and capable of moving
 129 through the sediment (Cartaxana et al., 2016; Consalvey et al., 2004) allowing them to optimise light
 130 and nutrient conditions. Their mechanism of locomotion is unusual and facilitated by the production
 131 and release of extracellular polymeric material (EPS) that can change the cohesive properties of the
 132 seabed (Paterson, 1989; Tolhurst et al., 2002) and provides a rich source of organic material to bacteria
 133 (Tobias et al., 2003). There is evidence that seasonal changes in diatom-EPS production influences
 134 bacteria assemblages (Moerdijk-poortvliet et al., 2018) and that there is a strong mutual dependency
 135 between diatoms and bacteria assemblages (Koedooder et al., 2019). Locomotion and EPS secretion
 136 also provide ecological resilience to stressors such as hypoxia, heavy metal toxicity and organic
 137 pollutants (Decho, 2000; Larson and Sundbäck, 2008; Sundbäck et al., 2010). These characteristics of
 138 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.

152

153 4. INDIVIDUAL ECOSYSTEM FUNCTIONS & SERVICES

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

155 While the role of biodiversity in ecosystem function and ES delivery is widely accepted, it is difficult to
156 establish simple cause and effect relationships due to the non-linear and complex interactions
157 between stressors, biodiversity, functionality and ES delivery (Harrison et al., 2014; Thrush et al.,
158 2013). Productivity–biodiversity relationships are far from clear in any system, but especially in less
159 well-studied marine systems. Despite this, diversity in primary producers has been positively related
160 to increases in grazer diversity (Balvanera et al., 2006) and this can increase overall ecosystem
161 productivity (Jones et al., 2017; Worm et al., 2006). In turn, there are feedbacks between trophic levels
162 with the activity of macrofauna modulating microbial (Foshtomi et al., 2015) and macrobenthic
163 (Widdicombe and Austen, 1999) diversity. Furthermore, the interactions between MPB, N-cycling
164 bacteria and benthic invertebrates can significantly affect N retention and N removal processes, which
165 creates a more inhabitable environment for benthic organisms (Douglas et al., 2018). The presence of
166 fauna can also alter flow dynamics which stimulates the MPB (Christensen et al., 2003). These
167 ecological interactions are critical for nutrient cycling and overall productivity (Hicks et al., 2018;
168 Thrush et al., 2006).

169 **4.2. Productivity (S) & carbon sequestration (R)**

170 MPB capture and fix up to one third of atmospheric CO₂ with estimates of 30 to 230 g Carbon fixation
171 m² y⁻¹ on intertidal flats (Heip et al., 1995). ‘Unvegetated’ coastal sediments have been estimated to
172 cover a global area of 23.9 x 10¹² m² (Duarte et al., 2004), a much greater expanse than vegetated
173 sediments, while others estimate the continental shelf area as covering 28 x 10⁶ km² (MacKenzie and
174 Lerman, 2006). A recent study of productivity in the South Atlantic Bight (Pinckney, 2018) suggests
175 that over 90% of the habitat could support benthic production and switch the benthos from net
176 heterotrophic to net autotrophic. These authors propose that benthic productivity in continental shelf
177 regions is a neglected area in biogeochemical and trophodynamic studies. The South Atlantic Bight
178 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 CO₂ 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 CO₂ respired as
202 much as 1 mol of carbon is bound in the shell of resident bivalves (Fodrie et al., 2017).

203 MPB primary productivity fuels secondary production in estuarine systems and first order consumers,
204 such as grazing bivalves and worms, provide an important link in the transfer of energy to higher
205 organisms (Como et al., 2014). Through stable isotopes and fatty acid biomarkers, basal food sources
206 such as MPB can be traced back from higher trophic consumers (Como et al., 2014; Moens et al., 2002)
207 and MPB provide a higher quality carbon to consumers than marine angiosperms such as mangroves
208 or seagrasses (Kang et al., 2007; Miller et al., 1996). The ratio of carbon to nitrogen (C:N ratio) has also
209 been used to determine the response of MPB to stressors, indicating changes to this basal food source.
210 The C:N ratio, along with the labile nature of MPB-carbon, perhaps explains the preference for MPB
211 as a dietary source. For example, C:N in crustaceans residing in mangrove systems emphasise the role
212 of MPB production over that of mangroves (Guest et al., 2008; Mazumder and Saintilan, 2010). As a
213 high quality, labile food source for many meio- and macro-fauna species, the majority of carbon
214 produced by MPB is often remineralised and transformed within the ecosystem (Bauer et al., 2013).
215 Nonetheless, respired carbon in sediments can also be recaptured and recycled by MPB repeatedly
216 within the sediment (Oakes and Eyre, 2014) and bivalves can use substantial amounts of MPB-derived
217 carbon to CO₂ which is then calcified into calcium carbonate shells (producing up to 1000g CaCO₃ m²
218 y⁻¹, Gutiérrez et al., 2003). Shells slowly dissolved in the ocean, taking up to 30 years for a 4 year old
219 oyster (Suykens et al., 2011). The presence of shell hash also influences benthic metabolism (Dolmer
220 and Frandsen, 2002) by adding complexity and increasing habitat heterogeneity (Thrush et al., 2004).
221 It provides new habitat for other species (Gutiérrez et al., 2003), and can mitigate against pollutants
222 (Casado-Coy et al., 2017). These benefits support incentives to conserve and restore shellfish beds as
223 potential carbon sinks (Fodrie et al., 2017). The transfer of carbon offshore via the migration of
224 juvenile fish and invertebrates (Dahlgren et al., 2006; Vasconcelos et al., 2011) and through the
225 metazoan foodweb is also critical for the survival of many fish and bird species. While MPB do not play
226 the same obvious habitat forming or carbon sink roles as some of the less palatable estuarine and
227 coastal plants (mangroves, seagrass and saltmarsh), the MPB mediate the quantity and form of carbon
228 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

280
281 In sandy, oligotrophic systems the standing stock of organic
282 matter (OM), MPB biomass and nutrients may be low (Piemer
283 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
284 productivity *per se* (Billerbeck et al., 2007). Lower nutrient
285 inputs, does not always limit MPB as nutrients are efficiently
286 recycled and retained within the sediment (Heip et al., 1995).
The relative effect of MPB on N-retention and recycling can
287 fluctuate both seasonally due to growth (Banta et al., 2004;
288 Nielsen et al., 2017), and daily due to nutrient uptake and
289 transfer to other organisms (Tobias et al., 2003). MPB
productivity can also be enhanced by advective flushing in
290 permeable sediments (Cook and Røy, 2006). Pressure
291 differences around bedforms and mounds induce flow, allowing
292 MPB to intercept nutrients at the sediment-water interface
with flushing (from deeper sediment) proposed to explain MPB
293 growth in low nutrient systems (Marinelli et al., 1998). The
294 interception of nutrients by MPB promotes efficient N-retention
and recycling within the bed and limits nutrient efflux
295 (Ehrenhauss and Huettel, 2004; Huettel et al., 2014) anywhere
296 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

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

353 the sediment, primarily through nutrient excretion (Murray et al., 2014; Passarelli et al., 2012a), which
354 stimulates the growth of MPB (Lohrer et al., 2004a; Stock et al., 2014). These positive effects can often
355 counteract grazing pressure on MPB and suggest that the complex interactions between MPB, fauna
356 and environmental conditions must also be considered when assessing biostabilisation.

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

370 These relationships highlight the diverse and complex roles of MPB on services such as erosional
371 protection and habitat formation in soft-sediment ecosystems. Changes to hydrodynamic regimes
372 may place a selective pressure on MPB, removing particular functional groups (Dupuy et al., 2014)
373 with cascading effects on first order consumers. Conversely, habitat homogenisation can result in the
374 loss of food and shelter, negatively affecting faunal diversity (Thrush et al., 2006) and in turn influence
375 the trophic status of coastal systems (Hicks et al., 2011). Habitat (from the patch to whole system) and
376 species diversity, (microbial to macrofauna), are therefore intricately linked and cannot be considered
377 in isolation due to complex feedbacks within the ecological network.

378 **4.5. The provision of fuels, foods & nutraceuticals (P)**

379 MPB provide consumers with essential fatty acids (EFAs), the omega-3s, which are a vital component
380 for growth and development in fish (Emata et al., 2004; Sprague et al., 2016), molluscs (Knauer and
381 Southgate, 1999) and humans (Calder, 2014; Lenihan-Geels et al., 2013). As many EFAs cannot be
382 efficiently synthesised by higher organisms, microalgae are the main source of EFAs in the biosphere
383 (Behrens and Kyle, 1996). While humans typically consume omega-3s from oily fish such as salmon,
384 herring and mackerel, these compounds are synthesised by microalgae at the base of the foodweb
385 with the benthic foodweb often underpinning the productivity of these higher organisms. MPB are a
386 significant food source for many shellfish and their high EFA content ensures they are underpinning
387 marine food production services. The MPB can contribute up to 70% of the diet of harvested and
388 farmed mussels, oysters and cockles (Dubois et al., 2007; Morioka et al., 2017; Sauriau and Kang,
389 2000)). Additionally, recent studies have demonstrated that MPB can be both a direct and indirect
390 food resource for shore birds (Elnor et al., 2005; Schnurr et al., 2019) and economically important fish
391 species (França et al., 2011; Melville and Connolly, 2003).

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

401 In addition to naturally removing substantial amounts of CO₂ from our atmosphere, a transition from
402 fossil fuels to the use of MPB derived biofuel would reduce current CO₂ emissions and this has the

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

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.

477 **Acknowledgements**

478 JAH received funding from The Oceans of Change Project. DMP received funding from the MASTS
479 pooling initiative (The Marine Alliance for Science and Technology for Scotland) and their support is
480 gratefully acknowledged. MASTS is funded by the Scottish Funding Council (grant reference HR09011)
481 and contributing institutions". The authors would like to thank two anonymous reviewers and the
482 editors for their constructive comments and feedback, which significantly improved this manuscript.
483 Further thanks to Ewa Siwicka and Amanda Vieillard for helpful discussions surrounding network
484 construction and ecological functions and services and to Samantha Ladewig for helpful comments.

485 **Author Contribution Statement**

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

488 **References**

- 489 Alongi, D.M., 2014. Carbon cycling and storage in mangrove forests. *Ann. Rev. Mar. Sci.* 6, 195–219.
490 doi:10.1146/annurev-marine-010213-135020
- 491 An, S., Joye, S.B., 2001. Enhancement of coupled nitrification-denitrification by benthic
492 photosynthesis in shallow estuarine sediments. *Limnol. Ocean.* 46, 62–74.
- 493 Annis, G.M., Pearsall, D.R., Kahl, K.J., Washburn, E.L., May, C.A., Franks, R., Cole, J.B., Ewert, D.N.,
494 Game, T., Doran, P.J., 2017. Designing coastal conservation to deliver ecosystem and human
495 well-being benefits 1–21. doi:10.1371/journal.pone.0172458
- 496 Auta, H.S., Emenike, C.U., Fauziah, S.H., 2017. Distribution and importance of microplastics in the
497 marine environment: A review of the sources, fate, effects, and potential solutions. *Environ.*
498 *Int.* 102, 165–176. doi:10.1016/j.envint.2017.02.013
- 499 Baas, J.H., Baker, M.L., Malarkey, J., Bass, S.J., Manning, A.J., Hope, Julie, A., Peakall, J., Lichtman, Ian,
500 D., Ye, L., Davies, Alan, G., Parsons, Daniel, R., Paterson, David, M., Thorne, Peter, D., 2019.
501 Integrating field and laboratory approaches for ripple development in mixed sand–clay –EPS.
502 *Sedimentology* accepted m. doi:10.1111/sed.12611
- 503 Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D., Schmid, B., 2006.
504 Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol.*
505 *Lett.* 9, 1146–1156. doi:10.1111/j.1461-0248.2006.00963.x
- 506 Balvanera, P., Siddique, I., Dee, L., Paquette, A., Isbell, F., Gonzalez, A., Byrnes, J., Connor, M.I.O.,
507 Hungate, B.A., Griffin, J.N., 2014. Linking Biodiversity and Ecosystem Services: Current
508 Uncertainties and the Necessary Next Steps. *Bioscience* 64, 49–57. doi:10.1093/biosci/bit003
- 509 Banta, Gary T., Pedersen, Morten Foldager, Nielsen, S.L., 2004. Decomposition of marine primary
510 producers: Consequences for nutrient recycling and retention in coastal ecosystems, in:
511 Nielsen, Søren Laurentius, Banta, G T, Pedersen, M F (Eds.), *Estuarine Nutrient Cycling: The*
512 *Influence of Primary Producers*. pp. 187–216. doi:10.1007/978-1-4020-3021-5_7
- 513 Barbier, E.B., 2017. Marine Ecosystem services. *Curr. Biol.* 27, R507–R510.
514 doi:10.1016/j.cub.2017.03.020
- 515 Barlow, J., Sims, R.C., Quinn, J.C., 2016. Bioresource technology techno-economic and life-cycle
516 assessment of an attached growth algal biorefinery. *Bioresour. Technol.* 220, 360–368.
517 doi:10.1016/j.biortech.2016.08.091

- 518 Barranguet, C., Kromkamp, J.C., Peene, J., 1998. Factors controlling primary production and
519 photosynthetic characteristics of intertidal microphytobenthos. *Mar. Ecol. Prog. Ser.* 173, 117–
520 126.
- 521 Basu, S., Mackey, K.R.M., 2018. Phytoplankton as key mediators of the biological carbon pump: Their
522 responses to a changing climate. *Sustain.* 10. doi:10.3390/su10030869
- 523 Bauer, J.E., Cai, W., Raymond, P.A., Bianchi, T.S., Hopkinson, C.S., Regnier, P.A.G., 2013. The changing
524 carbon cycle of the coastal ocean. doi:10.1038/nature12857
- 525 Behrenfeld, M.J., Boss, E., Siegel, D.A., Shea, D.M., 2005. Carbon-based ocean productivity and
526 phytoplankton physiology from space 19, 1–14. doi:10.1029/2004GB002299
- 527 Behrens, P.W., Kyle, D.J., 1996. Microalgae as a source of fatty acids. *J. food lipids* 3, 259–272.
- 528 Bennett, A., Bianchi, T.S., Means, J.C., 2000. The Effects of PAH Contamination and Grazing on the
529 Abundance and Composition of Microphytobenthos in Salt Marsh Sediments (Pass Fourchon,
530 LA, U.S.A.): II: The Use of Plant Pigments as Biomarkers. *Estuar. Coast. Shelf Sci.* 50, 425–439.
531 doi:10.1006/ecss.1999.0572
- 532 Bennett, E.M., Cramer, W., Begossi, A., Cundill, G., Díaz, S., Egoh, B.N., Geijzendorffer, I.R., Krug, C.B.,
533 Lavorel, S., Lazos, E., Lebel, L., Martín-López, B., Meyfroidt, P., Mooney, H.A., Nel, J.L., Pascual,
534 U., Payet, K., Harguindeguy, N.P., Peterson, G.D., Prieur-Richard, A.H., Reyers, B., Roebeling, P.,
535 Seppelt, R., Solan, M., Tschakert, P., Tschardtke, T., Turner, B.L., Verburg, P.H., Viglizzo, E.F.,
536 White, P.C.L., Woodward, G., 2015. Linking biodiversity, ecosystem services, and human well-
537 being: three challenges for designing research for sustainability. *Curr. Opin. Environ. Sustain.*
538 14, 76–85. doi:10.1016/j.cosust.2015.03.007
- 539 Biggs, R., Peterson, G.D., Rocha, J.C., 2018. The Regime Shifts Database: a framework for analyzing
540 regime shifts in social-ecological systems. *Ecol. Soc.* 23, 9.
- 541 Billerbeck, M., Røy, H., Bosselmann, K., Huettel, M., 2007. Benthic photosynthesis in submerged
542 Wadden Sea intertidal flats 71, 704–716. doi:10.1016/j.ecss.2006.09.019
- 543 Black, K.S., Tolhurst, T.J., Paterson, D.M., Hagerthey, S.E., 2002. Working with Natural cohesive
544 sediment. *J. Hydraul. Eng.* 128, 2–8. doi:10.1061/(ASCE)0733-9429(2002)128:1(2)
- 545 Blake, W.H., Walsh, R.P.D., Barnsley, M.J., Palmer, G., Dyrinda, P., James, J.G., 2003. Heavy metal
546 concentrations during storm events in a rehabilitated industrialized catchment 1939, 1923–
547 1939. doi:10.1002/hyp.1218

- 548 Blanchard, F., Guarini, J., Orvain, F., Sauriau, P., 2001. Dynamic behaviour of benthic microalgal
549 biomass in intertidal mudflats 85–100.
- 550 Borsje, B.W., de Vries, M.B., Hulscher, S.J.M.H., de Boer, G.J., 2008. Modeling large-scale cohesive
551 sediment transport affected by small-scale biological activity. *Estuar. Coast. Shelf Sci.* 78, 468–
552 480. doi:10.1016/j.ecss.2008.01.009
- 553 Boudreau, B.P., Huettel, M., Forster, S., Jahnke, R.A., McLachlan, A., Middelburg, J.J., Nielsen, P.,
554 Sansone, F., Taghon, G., van Raaphorst, W., Webster, I., Weslawski, J.M., Wiberg, P., Sundby,
555 B., 2001. Permeable marine sediments: Overturning an old paradigm. *EOS Trans.* 82, 133–140.
- 556 Brennan, L., Owende, P., 2010. Biofuels from microalgae-A review of technologies for production,
557 processing, and extractions of biofuels and co-products. *Renew. Sustain. Energy Rev.* 14, 557–
558 577. doi:10.1016/j.rser.2009.10.009
- 559 Cahoon, L., 1999. The role of benthic microalgae in neritic ecosystems. *Oceanogr. Mar. Biol.* 37, 47–
560 86.
- 561 Cai, W., 2011. Estuarine and coastal ocean carbon paradox: CO₂ sinks or sites of terrestrial carbon
562 incineration? *Ann. Rev. Mar. Sci.* 3, 123–145. doi:10.1146/annurev-marine-120709-142723
- 563 Calder, P.C., 2014. Very long chain omega-3 (n-3) fatty acids and human health. *Eur. J. Lipid Sci.*
564 *Technol.* 116, 1280–1300. doi:10.1002/ejlt.201400025
- 565 Carpenter, S.R., Mooney, H.A., Agard, J., Capistrano, D., DeFries, R.S., Diaz, S., Dietz, T., Duraiappah,
566 A.K., Oteng-Yeboah, A., Pereira, H.M., Perrings, C., Reid, W. V., Sarukhan, J., Scholes, R.J.,
567 Whyte, A., 2009. Science for managing ecosystem services: Beyond the Millennium Ecosystem
568 Assessment. *Proc. Natl. Acad. Sci.* 106, 1305–1312. doi:10.1073/pnas.0808772106
- 569 Cartaxana, P., Cruz, S., Gameiro, C., Kuhl, M., 2016. Regulation of intertidal microphytobenthos
570 photosynthesis over a diel emersion period is strongly affected by diatom migration patterns.
571 *Front. Microbiol.* 7, 1–11. doi:10.3389/fmicb.2016.00872
- 572 Casado-Coy, N., Martinez-Garcia, E., Sanchez-Jerez, P., Sanz-Lazaro, C., 2017. Mollusc-shell debris
573 can mitigate the deleterious effects of organic pollution on marine sediments. *J. Appl. Ecol.* 54,
574 547–556. doi:10.1111/1365-2664.12748
- 575 Chapman, M.G., Tolhurst, T.J., Murphy, R.J., Underwood, A.J., 2010. Complex and inconsistent
576 patterns of variation in benthos, micro-algae and sediment over multiple spatial scales. *Mar.*
577 *Ecol. Prog. Ser.* 398, 33–47. doi:10.3354/meps08328

- 578 Charpy-Roubaud, C., Sournia, A., 1990. The comparative estimation of phytoplanktonic,
579 microphytobenthic and macrophytobenthic primary production in the oceans. *Mar. Microb.*
580 *Food Webs* 4, 31–57.
- 581 Chen, X.D., Zhang, C.K., Paterson, D.M., Thompson, C.E.L., Townend, I.H., 2017. Hindered erosion:
582 The biological mediation of noncohesive sediment behavior. *Water Resour. Res.* 53, 4787–
583 4801. doi:10.1002/2016WR020105
- 584 Chisti, Y., 2008. Biodiesel from microalgae beats bioethanol. *Trends Biotechnol.* 26, 126–131.
585 doi:10.1016/j.tibtech.2007.12.002
- 586 Christensen, P.B., Glud, R.N., Dalsgaard, T., Gillespie, P., 2003. Impacts of longline mussel farming on
587 oxygen and nitrogen dynamics and biological communities of coastal sediments. *Aquaculture*
588 218, 567–588. doi:10.1016/S0044-8486(02)00587-2
- 589 Christianen, M.J.A., Middelburg, J.J., Holthuijsen, S., Compton, T., 2017. Benthic primary producers
590 are key to sustain the Wadden Sea food web: stable carbon isotope analysis at landscape scale.
591 *Ecology* 98, 1498–1512. doi:10.1002/ecy.1837
- 592 Cole, M., Lindeque, P., Halsband, C., Galloway, T.S., 2011. Microplastics as contaminants in the
593 marine environment: A review. *Mar. Pollut. Bull.* 62, 2588–2597.
594 doi:10.1016/j.marpolbul.2011.09.025
- 595 Como, S., Lefrancois, C., Maggi, E., Antognarelli, F., Dupuy, C., 2014. Behavioral responses of juvenile
596 golden gray mullet *Liza aurata* to changes in coastal temperatures and consequences for
597 benthic food resources. *J. Sea Res.* 92, 66–73. doi:10.1016/j.seares.2013.10.004
- 598 Consalvey, M., Jesus, B., Perkins, R.G., Brotas, V., Underwood, G.J., Paterson, D.M., 2004.
599 Monitoring migration and measuring biomass in benthic biofilms: the effect of dark/far-red
600 adaptation and vertical migration on fluorescence measurements. *Photosynth. Res.* 81, 91–
601 101. doi:10.1080/0269249X.2004.9705870
- 602 Cook, P.L.M., Revill, A.T., Butler, E.C. V, Eyre, B.D., 2004. Carbon and nitrogen cycling on intertidal
603 mudflats of a temperate Australian estuary. II. Nitrogen cycling. *Mar. Ecol. Prog. Ser.* 280, 39–
604 54. doi:10.3354/meps08270
- 605 Cook, P.L.M., Røy, H., 2006. Advective relief of CO₂ limitation in microphytobenthos in highly
606 productive sandy sediments. *Limnol. Oceanogr.* 51, 1594–1601. doi:10.4319/lo.2006.51.4.1594
- 607 Costanza, R., de Groot, R., Sutton, P., van der Ploeg, S., Anderson, S.J., Kubiszewski, I., Farber, S.,
608 Turner, R.K., 2014. Changes in the global value of ecosystem services. *Glob. Environ. Chang.* 26,

609 152–158. doi:10.1016/j.gloenvcha.2014.04.002

610 Dahlgren, C.P., Kellison, G.T., Adams, A.J., Gillanders, B.M., Kendall, M.S., Layman, C.A., Ley, J.A.,
611 Nagelkerken, I., Serafy, J.E., 2006. Marine nurseries and effective juvenile habitats : concepts
612 and applications. *Mar. Ecol. Prog. Ser.* 312, 291–295.

613 Davies, K.K., Fisher, K.T., Dickson, M.E., Thrush, S.F., Le Heron, R., 2015. Improving ecosystem service
614 frameworks to address wicked problems. *Ecol. Soc.* 20. doi:10.5751/ES-07581-200237

615 Dayton, P.K., Watson, D., Palmisano, A., Barry, J.P., Oliver, J.S., I, D.R., 1986. Distribution patterns of
616 benthic microalgal standing stock at McMurdo Sound, Antarctica 207–213.

617 de Deckere, E.M.G.T., Tolhurst, T.J., de Brouwer, J.F.C., 2001. Destabilisation of cohesive intertidal
618 sediments by infauna. *Estuar. Coast. Shelf Sci.* 53, 665–669.

619 de Jonge, V.N., van Beusekom, J.E.E., 1995. Wind- and tide-induced resuspension of sediment and
620 microphytobenthos from tidal flats in the Ems estuary 40, 766–778.

621 Decho, A.W., 2000. Microbial biofilms in intertidal systems: an overview. *Cont. Shelf Res.* 20, 1257–
622 1273.

623 Dolmer, P., Frandsen, R.P., 2002. Evaluation of the Danish mussel fishery: suggestions for an
624 ecosystem management approach 13–20. doi:10.1007/s10152-001-0095-6

625 Douglas, E.J., Pilditch, C.A., Kraan, C., Schipper, L.A., Lohrer, A.M., Thrush, S.F., 2017. Macrofaunal
626 functional diversity provides resilience to nutrient enrichment in coastal sediments. *Ecosystems*
627 1–13. doi:10.1007/s10021-017-0113-4

628 Douglas, E.J., Pilditch, C.A., Lohrer, A.M., Savage, C., Schipper, L.A., Thrush, S.F., 2018. Sedimentary
629 environment influences ecosystem response to nutrient enrichment. *Estuaries and Coasts* 41,
630 1994–2008. doi:10.1007/s12237-018-0416-5

631 Drylie, T.P., Lohrer, A.M., Needham, H.R., Bulmer, R.H., Pilditch, C.A., 2018. Benthic primary
632 production in emerged intertidal habitats provides resilience to high water column turbidity. *J.*
633 *Sea Res.* 142, 101–112. doi:10.1016/J.SEARES.2018.09.015

634 Duarte, C.M., Krause-jensen, D., 2018. Intervention options to accelerate ecosystem recovery from
635 coastal eutrophication. *Front. Mar. Sci.* 5, 1–8. doi:10.3389/fmars.2018.00470

636 Duarte, C.M., Middelburg, J.J., Caraco, N., 2004. Major role of marine vegetation on the oceanic
637 carbon cycle. *Biogeosciences Discuss.* 1, 659–679. doi:10.5194/bgd-1-659-2004

- 638 Dubois, S., Orvain, F., Marin-léal, J.C., Ropert, M., Lefebvre, S., 2007. Small-scale spatial variability of
639 food partitioning between cultivated oysters and associated suspension- feeding species , as
640 revealed by stable isotopes 336, 151–160.
- 641 Dupuy, C., Mallet, C., Guizien, K., Montanie, H., Breret, M., Mornet, F., Fontaine, C., Nerot, C.,
642 Orvain, F., 2014. Sequential resuspension of biofilm components (viruses, prokaryotes and
643 protists) as measured by erodimetry experiments in the Brouage mudflat (French Atlantic
644 coast). J. Sea Res. 92, 56–65. doi:10.1016/j.seares.2013.12.002
- 645 Ehrenhauss, S., Huettel, M., 2004. Advective transport and decomposition of chain-forming
646 planktonic diatoms in permeable sediments. J. Sea Res. 52, 179–197.
647 doi:10.1016/j.seares.2004.01.004
- 648 Elner, R.W., Beninger, Æ.P.G., Jackson, D.L., Potter, Æ.T.M., 2005. Evidence of a new feeding mode in
649 western sandpiper (*Calidris mauri*) and dunlin (*Calidris alpina*) based on bill and tongue
650 morphology and ultrastructure. doi:10.1007/s00227-004-1521-5
- 651 Emata, A.C., Ogata, H.Y., Garibay, E.S., Furuita, H., 2004. Advanced broodstock diets for the
652 mangrove red snapper and a potential importance of arachidonic acid in eggs and fry. Fish
653 Physiol. Biochem. 28, 489–491.
- 654 Fagherazzi, S., Mariotti, G., Banks, a. T., Morgan, E.J., Fulweiler, R.W., 2014. The relationships among
655 hydrodynamics, sediment distribution, and chlorophyll in a mesotidal estuary. Estuar. Coast.
656 Shelf Sci. 144, 54–64. doi:10.1016/j.ecss.2014.04.003
- 657 Falkowski, P.G., Raven, J.A., 2013. Aquatic photosynthesis. Princeton University press.
- 658 Fernandes, S., Sobral, P., Costa, M.H., 2006. *Nereis diversicolor* effect on the stability of cohesive
659 intertidal sediments. Aquat. Ecol. 40, 567–579. doi:10.1007/s10452-005-8000-z
- 660 Fodrie, F.J., Rodriguez, A.B., Gittman, R.K., Grabowski, J.H., Lindquist, N.L., Peterson, C.H., Piehler,
661 M.F., Ridge, J.T., 2017. Oyster reefs as carbon sources and sinks. Proc. R. Soc. B 284.
662 doi:10.1098/rspb.2017.0891
- 663 Forster, R.M., Créach, V., Sabbe, K., Vyverman, W., Stal, L.J., 2006. Biodiversity-ecosystem function
664 relationship in microphytobenthic diatoms of the Westerschelde estuary. Mar. Ecol. Prog. Ser.
665 311, 191–201. doi:10.3354/meps311191
- 666 Foshtomi, M.Y., Braeckman, U., Derycke, S., Sapp, M., Van Gansbeke, D., Sabbe, K., Willems, A.,
667 Vincx, M., Vanaverbeke, J., 2015. The link between microbial diversity and nitrogen cycling in
668 marine sediments is modulated by macrofaunal bioturbation. PLoS One.

669 doi:10.1371/journal.pone.0130116

670 França, S., Vasconcelos, R.P., Tanner, S., Máguas, C., José, M., Cabral, H.N., 2011. Assessing food web
671 dynamics and relative importance of organic matter sources for fish species in two Portuguese
672 estuaries: A stable isotope approach 72, 204–215. doi:10.1016/j.marenvres.2011.09.001

673 Franz, S., Altenburger, R., Heilmeyer, H., Schmitt-jansen, M., 2008. What contributes to the sensitivity
674 of microalgae to triclosan? 90, 102–108. doi:10.1016/j.aquatox.2008.08.003

675 Galloway, J.N., Dentener, F.J., Capone, D.G., Boyer, E.W., Howarth, R.W., Seitzinger, S.P., Asner, G.P.,
676 Cleveland, C.C., Green, P.A., Holland, E.A., Karl, D.M., Michaels, A.F., Porter, J.H., Townsend,
677 A.R., Vöosmarty, C.J., 2004. Nitrogen cycles: Past, present, and future. *Biogeochemistry* 70,
678 153–226. doi:10.1007/s10533-004-0370-0

679 Gattuso, J.-P., Gentili, B., Duarte, C.M. et al, Kleypas, J.A., Middelburg, J.J., Antoine, D., 2006. Light
680 availability in the coastal ocean: impact on the distribution of benthic photosynthetic organisms
681 and their contribution to primary production. *Biogeosciences* 3, 489–513. doi:10.5194/bgd-3-
682 895-2006

683 Geange, S., Townsend, M., Clark, D., Ellis, J.I., Lohrer, A.M., 2019. Communicating the value of
684 marine conservation using an ecosystem service matrix approach. *Ecosyst. Serv.* 35, 150–163.
685 doi:10.1016/j.ecoser.2018.12.004

686 Gilbert, F., Stora, G., Bonin, P., 1998. Influence of bioturbation on denitrification activity in
687 Mediterranean coastal sediments: An in situ experimental approach. *Mar. Ecol. Prog. Ser.* 163,
688 99–107.

689 Guest, M.A., Nichols, D.P., Frusher, S.D., Hirst, A.J., 2008. Evidence of abalone (*Haliotis rubra*) diet
690 from combined fatty acid and stable isotope analyses. *Mar. Biol.* 153. doi:10.1007/s00227-007-
691 0831-9

692 Gutiérrez, J.L., Jones, C.G., Strayer, D.L., Iribarne, O., 2003. Mollusks as ecosystem engineers: The
693 role of shell production in aquatic habitats. *Nord. Soc. Oikos* 101, 79–90.

694 Hale, A.R., Jacques, R.O., Tolhurst, T.J., Hale, R., Jacques, R.O., Tolhurst, T.J., 2019. Determining how
695 functionally diverse intertidal sediment species preserve mudflat ecosystem properties after
696 abrupt biodiversity loss. *J. Coast. Res.* 35, 389–396. doi:10.2112/JCOASTRES-D-17-00197.1

697 Hale, R., Godbold, J.A., Sciberras, M., Dwight, J., Wood, C., Hiddink, J.G., Solan, M., 2017. Mediation
698 of macronutrients and carbon by post-disturbance shelf sea sediment communities.
699 *Biogeochemistry* 135, 121–133. doi:10.1007/s10533-017-0350-9

- 700 Harris, R.J., Pilditch, C.A., Greenfield, B.L., Moon, V., Kröncke, I., 2016. The influence of benthic
701 macrofauna on the erodibility of intertidal sediments with varying mud content in three New
702 Zealand Estuaries. *Estuaries and Coasts* 39, 815–828. doi:10.1007/s12237-015-0036-2
- 703 Harrison, J.P., Schratzberger, M., Sapp, M., Osborn, A.M., 2014. Rapid bacterial colonization of low-
704 density polyethylene microplastics in coastal sediment microcosms. *BMC Microbiol.* 14, 232.
705 doi:10.1186/s12866-014-0232-4
- 706 Harrison, P.A., Berry, P.M., Simpson, G., Haslett, J.R., Blicharska, M., Bucur, M., Dunford, R., Egoh, B.,
707 Garcia-Llorente, M., Geamănă, N., Geertsema, W., Lommelen, E., Meiresonne, L., Turkelboom,
708 F., 2014. Linkages between biodiversity attributes and ecosystem services: A systematic review.
709 *Ecosyst. Serv.* 9, 191–203. doi:10.1016/j.ecoser.2014.05.006
- 710 Heip, C.H.R., Goosen, N.K., Herman, P.M.J., Kromkamp, J., Middelburg, J.J., Soetaert, K., 1995.
711 Production and consumption of biological particles in temperate tidal estuaries, *Oceano. and*
712 *Mar. Bio.* doi:10.1007/s00228-010-0816-3
- 713 Hewitt, J., De Juan, S., Lohrer, D., Townsend, M., Archino, R.D., 2014. Functional traits as indicators
714 of ecological integrity. NIWA client report No: HAM2014-001.
- 715 Hicks, N., Bulling, M.T., Solan, M., Raffaelli, D., White, P.C.L., Paterson, D.M., 2011. Impact of
716 biodiversity-climate futures on primary production and metabolism in a model benthic
717 estuarine system. *BMC Ecol.* 11.
- 718 Hicks, N., Liu, X., Gregory, R., Kenny, J., Lucaci, A., Lenzi, L., Paterson, D.M., Duncan, K.R., 2018.
719 Temperature driven changes in benthic bacterial diversity influences biogeochemical cycling in
720 coastal sediments. *Front. Microbiol.* 9. doi:10.3389/fmicb.2018.01730
- 721 Hochard, S., Pinazo, C., Grenz, C., Evans, J.L.B., Pringault, O., 2010. Impact of microphytobenthos on
722 the sediment biogeochemical cycles: A modeling approach. *Ecol. Modell.* 221, 1687–1701.
723 doi:10.1016/j.ecolmodel.2010.04.002
- 724 Hopes, A., Mock, T., 2015. Evolution of microalgae and their adaptations in different marine
725 ecosystems. *eLS.* doi:10.1002/9780470015902.a0023744
- 726 Hou, D., He, J., Lü, C., Sun, Y., Zhang, F., Otgonbayar, K., 2013. Effects of environmental factors on
727 nutrients release at sediment-water interface and assessment of trophic status for a typical
728 shallow lake, northwest china. *Sci. World J.* 2013. doi:10.1155/2013/716342
- 729 Howarth, R.W., Billen, G., Swaney, D.P., Townsend, A., Jaworski, N., Lajtha, K., Downing, J.A.,
730 Elmgren, R., Caraco, N., Jordan, T., Berendse, F., Freney, J., Kudeyarov, V., Murdoch, P., Zhao-

731 Liang, Z., 1996. Regional nitrogen budgets and riverine N & P fluxes for the drainages to the
732 North Atlantic Ocean: Natural and human influences. *Biogeochemistry* 35, 75–139.

733 Howe, R.L., Rees, A.P., Widdicombe, S., 2004. The impact of two species of bioturbating shrimp
734 (*Callinassa subterranea* and *Upogebia deltaura*) on sediment denitrification. *J. Mar. Biol.*
735 *Assoc. UK.* 84, 629–632. doi:10.1017/S002531540400966Xh

736 Huettel, M., Berg, P., Kostka, J.E., 2014. Benthic exchange and biogeochemical cycling in permeable
737 sediments. *Ann. Rev. Mar. Sci.* 6, 23–51. doi:10.1146/annurev-marine-051413-012706

738 Jahnke, R.A., Nelson, J.R., Marinelli, R.L., Eckman, J.E., 2000. Benthic flux of biogenic elements on the
739 Southeastern US continental shelf: Influence of pore water advective transport and benthic
740 microalgae. *Cont. Shelf Res.* 20, 109–127. doi:10.1016/S0278-4343(99)00063-1

741 Jesus, B., Brotas, V., Marani, M., Paterson, D.M., 2005. Spatial dynamics of microphytobenthos
742 determined by PAM fluorescence. *Estuar. Coast. Shelf Sci.* 65, 30–42.
743 doi:10.1016/j.ecss.2005.05.005

744 Jickells, T.D., Andrews, J.E., Parkes, D.J., 2016. Direct and Indirect effects of estuarine reclamation on
745 nutrient and metal fluxes in the global coastal zone. *Aquat. Geochemistry* 22, 337–348.
746 doi:10.1007/s10498-015-9278-7

747 Joensuu, M., Pilditch, C.A., Harris, R., Hietanen, S., Pettersson, H., Norkko, A., 2018. Sediment
748 properties, biota, and local habitat structure explain variation in the erodibility of coastal
749 sediments. *Limnol. Ocean.* 63, 173–186. doi:10.1002/lno.10622

750 Johnson, M.B., Wen, Z., 2010. Development of an attached microalgal growth system for biofuel
751 production. *Appl. Microbiol. Biotechnol.* 85, 525–534. doi:10.1007/s00253-009-2133-2

752 Jones, H.F.E., Pilditch, C.A., Hamilton, D.P., Bryan, K.R., Jones, H.F.E., Pilditch, C.A., Hamilton, D.P.,
753 Karin, R., 2017. Impacts of a bivalve mass mortality event on an estuarine food web and bivalve
754 grazing pressure. *New Zeal. J. Mar. Freshw. Res.* 51, 370–392.
755 doi:10.1080/00288330.2016.1245200

756 Kang, C.K., Eun, J.C., Paik, S.K., Hyun, J.P., Lee, K.S., An, S., 2007. Contributions of primary organic
757 matter sources to macroinvertebrate production in an intertidal salt marsh (*Scirpus triquetra*)
758 ecosystem. *Mar. Ecol. Prog. Ser.* 334, 131–143. doi:10.3354/meps334131

759 Kebede-Westhead, E., Pizarro, C., Mulbry, W., 2004. Treatment of Dairy Manure Effluent Using
760 Freshwater Algae: Elemental composition of algal biomass at different manure loading rates. *J.*
761 *Agric. Food Chem.* 52, 7293–7296.

- 762 Kemp, W., Boynton, W.R., Adolf, J., Boesch, D.F., Boicourt, W.C., Brush, G., Cornwall, J., Fisher, T.,
763 Glibert, P., Hagy, J., Harding, L., Houde, E., Kimmel, D., Miller, W., Newell, R.I.E., Roman, M.R.,
764 Smith, E.M., Stevenson, J., 2005. Eutrophication of Chesapeake Bay: Historical trends and
765 ecological interactions. *Mar. Ecol. Prog. Ser.* 303, 1–29. doi:10.3354/meps303001
- 766 Kenworthy, J., Paterson, D., Bishop, M., 2016. Response of benthic assemblages to multiple
767 stressors: Comparative effects of nutrient enrichment and physical disturbance. *Mar. Ecol.*
768 *Prog. Ser.* 562, 37–51. doi:10.3354/meps11935
- 769 Kingston, M.B., Gough, J.S., 2009. Vertical migration of a mixed-species *Euglena* (*Euglenophyta*)
770 assemblage inhabiting the high-intertidal sands of NYW beach, Oregon. *J. Phycol.* 45, 1021–1029.
771 doi:10.1111/j.1529-8817.2009.00748.x
- 772 Knauer, J., Southgate, P.C., 1999. A review of the nutritional requirements of bivalves and the
773 development of alternative and artificial diets for bivalve aquaculture. *Rev. Fish. Sci.* 7, 241–
774 280. doi:10.1080/10641269908951362
- 775 Koch, E.W., Barbier, E.B., Silliman, B.R., Reed, D.J., Perillo, G.M.E., Hacker, S.D., Granek, E.,
776 Primavera, J., Muthiga, N., Polasky, S., Halpern, B.S., Kennedy, C.J., Kappel, C. V., Wolanski, E.,
777 2009. Non-linearity in ecosystem services: Temporal and spatial variability in coastal
778 protection. *Front. Ecol. Environ.* 7, 29–37. doi:10.1890/080126
- 779 Koedooder, C., Stock, W., Willems, A., Mangelinckx, S., Marzinelli, E.M., Campbell, A.H., 2019.
780 Diatom-bacteria interactions modulate the composition and productivity of benthic diatom
781 biofilms. *Front. Microbiol.* 10, 1–11. doi:10.3389/fmicb.2019.01255
- 782 Koppel, J. Van De, Herman, P.M.J., Thoolen, P., Heip, C.H.R., 2001. Do alternate stable states occur in
783 natural ecosystems? Evidence from a tidal flat. *Ecology* 82, 3449–3461. doi:10.1890/0012-
784 9658(2001)082[3449:DASSOI]2.0.CO;2
- 785 Kornman, B.A., de Deckere, E.M.G.T., 1998. Temporal variation in sediment erodibility and
786 suspended sediment dynamics in the Dollard estuary. *Geol. Soc. London, Spec. Publ.* 139, 231–
787 241. doi:10.1144/GSL.SP.1998.139.01.19
- 788 Kowalski, N., Dellwig, O., Beck, M., Grunwald, M., Fischer, S., Piepho, M., Riedel, T., Freund, H.,
789 Brumsack, H.-J., Böttcher, M.E., 2009. Trace metal dynamics in the water column and pore
790 waters in a temperate tidal system: Response to the fate of algae-derived organic matter.
791 *Ocean Dyn.* 59, 333–350. doi:10.1007/s10236-009-0192-7
- 792 Kritzer, J.P., DeLucia, M.B., Greene, E., Shumway, C., Topolski, M.F., Thomas-Blate, J., Chiarella, L.A.,

- 793 Davy, K.B., Smith, K., 2016. The importance of benthic habitats for coastal fisheries. *Bioscience*
794 66, 274–284. doi:10.1093/biosci/biw014
- 795 Kromkamp, J., Peene, J., van Rijswijk, P., Sandee, A., Goosen, N., 1995. Nutrients, light and primary
796 production by phytoplankton and microphytobenthos in the eutrophic, turbid Westerschelde
797 estuary (The Netherlands). *Hydrobiologia* 311, 9–19. doi:10.1007/BF00008567
- 798 Larson, F., Sundbäck, K., 2008. Role of microphytobenthos in recovery of functions in a shallow-
799 water sediment system after hypoxic events. *Mar. Ecol. Prog. Ser.* 357, 1–16.
800 doi:10.3354/meps07426
- 801 Laverock, B., Gilbert, J.A., Tait, K., Osborn, A.M., Widdicombe, S., 2011. Bioturbation: Impact on the
802 marine nitrogen cycle. *Biochem. Soc. Trans.* 39, 315–320. doi:10.1042/BST0390315
- 803 Legrand, H., Herlory, O., Guarini, J., Blanchard, G.F., Richard, P., 2006. Inhibition of
804 microphytobenthic photosynthesis by the herbicides atrazine and diuron 39–45.
- 805 Lenihan-Geels, G., Bishop, K.S., Ferguson, L.R., 2013. Alternative sources of omega-3 fats: Can we
806 find a sustainable substitute for fish? *Nutrients* 5, 1301–1315. doi:10.3390/nu5041301
- 807 Lichtman, I.D., Baas, J.H., Amoudry, L.O., Thorne, P.D., Malarkey, J., Hope, J.A., Peakall, J., Paterson,
808 D.M., Bass, S.J., Cooke, R.D., Manning, A.J., Davies, A.G., Parsons, D.R., Ye, L., 2018. Bedform
809 migration in a mixed sand and cohesive clay intertidal environment and implications for bed
810 material transport predictions. *Geomorphology* 315, 17–32.
811 doi:10.1016/j.geomorph.2018.04.016
- 812 Lohrer, A.M., Cummings, V.J., Thrush, S.F., 2013. Altered sea ice thickness and permanence affects
813 benthic ecosystem functioning in coastal Antarctica 224–236. doi:10.1007/s10021-012-9610-7
- 814 Lohrer, A.M., Thrush, S.F., Gibbs, M.M., 2004a. Bioturbators enhance ecosystem function through
815 complex biogeochemical interactions. *Nature* 431, 1092–1095. doi:10.1038/nature03042
- 816 Lohrer, A.M., Thrush, S.F., Hewitt, J.E., Berkenbusch, K., Ahrens, M., Cummings, V.J., 2004b.
817 Terrestrially derived sediment: Response of marine macrobenthic communities to thin
818 terrigenous deposits. *Mar. Ecol. Prog. Ser.* 273, 121–138. doi:10.3354/meps273121
- 819 Longphuir, S.N., Lim, J.H., Leynaert, A., Claquin, P., Choy, E.J., Kang, C.K., An, S., 2009. Dissolved
820 inorganic nitrogen uptake by intertidal microphytobenthos: Nutrient concentrations, light
821 availability and migration. *Mar. Ecol. Prog. Ser.* 379, 33–44. doi:10.3354/meps07852
- 822 MacIntyre, H.L., Geider, R.J., Miller, D.C., 1996. Microphytobenthos: The ecological role of the

823 "Secret Garden" of unvegetated, shallow- water marine habitats. I. Distribution, Abundance
824 and Primary Production. *Estuaries and Coasts* 19, 186–201. doi:10.2307/1352224

825 MacKenzie, F., Lerman, A., 2006. Carbon in the oceanic coastal margin, in: *Carbon in the*
826 *Geobiosphere - Earth's Outer Shell - TOPICS IN GEOBIOLOGY*. Vol. 25. Springer, Dordrecht, pp.
827 255–287.

828 Maher, D., Eyre, B.D., 2011. Insights into estuarine benthic dissolved organic carbon (DOC) dynamics
829 using ¹³C-DOC values, phospholipid fatty acids and dissolved organic nutrient fluxes. *Geochim.*
830 *Cosmochim. Acta* 75, 1889–1902. doi:10.1016/j.gca.2011.01.007

831 Malarkey, J., Baas, J.H., Hope, J.A., Aspden, R.J., Parsons, D.R., Peakall, J., Paterson, D.M., Schindler,
832 R.J., Ye, L., Lichtman, I.D., Bass, S.J., Davies, A.G., Manning, A.J., Thorne, P.D., 2015. The
833 pervasive role of biological cohesion in bedform development. *Nat. Commun.* 6, 1–6.
834 doi:10.1038/ncomms7257

835 Martin, C.L., Momtaz, S., Gaston, T., Moltschaniwskyj, N.A., 2016. A systematic quantitative review
836 of coastal and marine cultural ecosystem services: Current status and future research. *Mar.*
837 *Policy* 74, 25–32. doi:10.1016/j.marpol.2016.09.004

838 Mazumder, D., Saintilan, N., 2010. Mangrove leaves are not an important source of dietary carbon
839 and nitrogen for crabs in temperate Australian mangroves. *Wetlands* 30, 375–380.
840 doi:10.1007/s13157-010-0021-2

841 MEA, 2005. *Millenium Ecosystem Assessment, ecosystems and human well-being*. World Resources
842 Institute. Washington DC.

843 Melville, A.J., Connolly, R.M., 2003. Spatial analysis of stable isotope data to determine primary
844 sources of nutrition for fish. *Oecologia* 136, 499–507. doi:10.1007/s00442-003-1302-8

845 Michels, J., Stippkugel, A., Lenz, M., Wirtz, K., Engel, A., 2018. Rapid aggregation of biofilm-covered
846 microplastics with marine biogenic particles. *Proc. R. Soc. B* 285, 20181203.

847 Middelburg, J.J., Soetaert, K., Herman, P.M.J., Heip, C.H.R., 1996. Denitrification in marine
848 sediments: A model study. *Global Biogeochem. Cycles* 10, 661–673.

849 Migne, A., Spilmont, N., Boucher, G., Denis, L., Hubas, C., Janquin, M., Rauch, M., Davoult, D., 2009.
850 Annual budget of benthic production in Mont Saint-Michel Bay considering cloudiness,
851 microphytobenthos migration, and variability of respiration rates with tidal conditions. *Cont.*
852 *Shelf Res.* 29, 2280–2285. doi:10.1016/j.csr.2009.09.004

853 Miller, D.C., Geider, R.J., MacIntyre, H.L., 1996. Microphytobenthos: The ecological role of the
854 “Secret Garden” of unvegetated, shallow-water marine habitats. II . Role in sediment stability
855 and shallow-water food webs. *Estuaries and coasts* 19, 202–212. doi:10.2307/1352224

856 Moens, T., Luyten, C., Middelburg, J., Herman, P., Vincx, M., 2002. Tracing organic matter sources of
857 estuarine tidal flat nematodes with stable carbon isotopes. *Mar. Ecol. Prog. Ser.* 234, 127–137.
858 doi:10.3354/meps234127

859 Moerdijk-poortvliet, T.C.W., Breugel, P. Van, Sabbe, K., Beauchard, O., Stal, L.J., Boschker, H.T.S.,
860 2018. Seasonal changes in the biochemical fate of carbon fixed by benthic diatoms in intertidal
861 sediments. *Limnol. Oceanogr.* 63, 550–569. doi:10.1002/lno.10648

862 Morioka, H., Kasai, A., Miyake, Y., Kitagawa, T., Kimura, S., 2017. Food Composition for blue mussels
863 (*Mytilus edulis*) in the Menai Strait, UK, based on physical and biochemical analyses. *J. Shellfish*
864 *Res.* 36, 659–668. doi:10.2983/35.036.0315

865 Mouchet, M.A., Lamarque, P., Martín-López, B., Crouzat, E., Gos, P., Byczek, C., Lavorel, S., 2014. An
866 interdisciplinary methodological guide for quantifying associations between ecosystem
867 services. *Glob. Environ. Chang.* 28, 298–308. doi:10.1016/j.gloenvcha.2014.07.012

868 Murphy, R.J., Tolhurst, T.J., 2009. Effects of experimental manipulation of algae and fauna on the
869 properties of intertidal soft sediments. *J. Exp. Mar. Bio. Ecol.* 379, 77–84.
870 doi:10.1016/j.jembe.2009.08.005

871 Murphy, R.J., Tolhurst, T.J., Chapman, M.G., Underwood, A.J., 2004. Estimation of surface
872 chlorophyll on an exposed mudflat using digital colour-infrared (CIR) photography. *Estuar.*
873 *Coast. Shelf Sci.* 59, 625–638. doi:10.1016/j.ecss.2003.11.006

874 Murray, F., Douglas, A., Solan, M., 2014. Species that share traits do not necessarily form distinct and
875 universally applicable functional effect groups. *Mar. Ecol. Prog. Ser.* 516, 23–34.
876 doi:10.3354/meps11020

877 Nielsen, S.L., Risgaard-petersen, N., Banta, G.T., 2017. Nitrogen retention in coastal marine
878 sediments — a field study of the relative importance of biological and physical removal in a
879 Danish Estuary. *Estuaries and Coasts* 40, 1276–1287. doi:10.1007/s12237-017-0216-3

880 O’Meara, T.A., Hillman, J.R., Thrush, S.F., 2017. Rising tides, cumulative impacts and cascading
881 changes to estuarine ecosystem functions. *Sci. Rep.* 7, 1–7. doi:10.1038/s41598-017-11058-7

882 Oakes, J.M., Eyre, B.D., 2014. Transformation and fate of microphytobenthos carbon in subtropical,
883 intertidal sediments: potential for long-term carbon retention revealed 13C-labeling.

- 884 Biogeosciences 11, 1927–1940. doi:10.5194/bg-11-1927-2014
- 885 Oakes, J.M., Eyre, B.D., Middelburg, J.J., 2012. Transformation and fate of microphytobenthos
886 carbon in subtropical shallow subtidal sands: A ¹³C-labeling study. Limnol. Oceanogr. 57, 1846–
887 1856. doi:10.4319/lo.2012.57.6.1846
- 888 Oguz, T., Gilbert, D., 2007. Abrupt transitions of the top-down controlled Black Sea pelagic
889 ecosystem during 1960 – 2000: Evidence for regime-shifts under strong fishery exploitation and
890 nutrient enrichment modulated by climate-induced variations 54, 220–242.
891 doi:10.1016/j.dsr.2006.09.010
- 892 Paerl, H.W., Fitzpatrick, M., Bebout, B.A.I., 1996. Seasonal nitrogen fixation dynamics in a marine
893 microbial mat : Potential roles of cyanobacteria and microheterotrophs 41, 419–427.
- 894 Parsons, D.R., Schindler, R.J., Hope, J.A., Malarkey, J., Baas, J.H., Peakall, J., Manning, A.J., Ye, L.,
895 Simmons, S., Paterson, D.M., Aspden, R.J., Bass, S.J., Davies, A.G., Lichtman, I.D., Thorne, P.D.,
896 2016. The role of biophysical cohesion on subaqueous bed form size. Geophys. Res. Lett. 43,
897 1566–1573. doi:10.1002/2016GL067667
- 898 Passarelli, C., Hubas, C., Nicolas Segui, A., Grange, J., Meziane, T., 2012a. Surface adhesion of
899 microphytobenthic biofilms is enhanced under *Hediste diversicolor* (O.F. Müller) trophic
900 pressure. J. Exp. Mar. Bio. Ecol. 438, 52–60. doi:10.1016/j.jembe.2012.10.005
- 901 Passarelli, C., Olivier, F., Paterson, D., Hubas, C., 2012b. Impacts of biogenic structures on benthic
902 assemblages: microbes, meiofauna, macrofauna and related ecosystem functions. Mar. Ecol.
903 Prog. Ser. 465, 85–97. doi:10.3354/meps09915
- 904 Passarelli, C., Hubas, C., Paterson, D.M., 2018. Mudflat Ecosystem Engineers and Services, in:
905 Beninger, P.G. (Ed.), Mudflat Ecology. Aquatic Ecology Series, Vol. 7. Springer, Cham, pp. 243–
906 269.
- 907 Paterson, D.M., 1989. Short-term changes in the erodibility of intertidal cohesive sediments related
908 to the migratory behavior of epipellic diatoms. Limnol. Oceanogr. 34, 223–234.
909 doi:10.4319/lo.1989.34.1.0223
- 910 Paterson, D.M., Black, K.S., 1999. Water flow, sediment dynamics and benthic biology. Adv. Ecol.
911 Res. 29, 155–193. doi:10.1016/S0065-2504(08)60193-2
- 912 Paterson, D.M., Hope, J.A., Kenworthy, J., Biles, C.L., Gerbersdorf, S.U., 2018. Form, function and
913 physics: the ecology of biogenic stabilisation. J. Soils Sediments 18, 3044–3054.
914 doi:10.1007/s11368-018-2005-4

- 915 Patil, V., Tran, K., Giselrød, H.R., 2008. Towards sustainable production of biofuels from microalgae.
916 Int. J. Mol. Sci. 9, 1188–1195. doi:10.3390/ijms9071188
- 917 Penny, G., 2007. Environmental values and observations of change: A survey with Ngati Whanaunga
918 of Manaia. NIWA report prepared by Aranovus Research, AQCC042.
- 919 Perkins, R., Underwood, G., Brotas, V., Snow, G., Jesus, B., Ribeiro, L., 2001. Responses of
920 microphytobenthos to light: primary production and carbohydrate allocation over an emersion
921 period. Mar. Ecol. Prog. Ser. 223, 101–112. doi:10.3354/meps223101
- 922 Piehler, M.F., Smyth, A.R., 2011. Habitat-specific distinctions in estuarine denitrification affect both
923 ecosystem function and services. Ecosphere 2, 1–17. doi:10.1890/ES10-00082.1
- 924 Pinckney, J.L., 2018. A mini-review of the contribution of benthic microalgae to the ecology of the
925 continental shelf in the South Atlantic Bight 2070–2078.
- 926 Potapova, M., 2011. Patterns of diatom distribution in relation to salinity, in: The diatom world.
927 Springer, Dordrecht, pp. 313–332. doi:10.1007/978-94-007-1327-7
- 928 Prata, J.C., Lavorante, B.R.B.O., Montenegro, C.B.S.M., 2018. Influence of microplastics on the
929 toxicity of the pharmaceuticals procainamide and doxycycline on the marine microalgae
930 *Tetraselmis chuii*. Aquat. Toxicol. 197, 143–152. doi:10.1016/j.aquatox.2018.02.015
- 931 Pratt, D.R., Pilditch, C.A., Lohrer, A.M., Thrush, S.F., 2014. The effects of short-term increases in
932 turbidity on sandflat microphytobenthic productivity and nutrient fluxes. J. Sea Res. 92, 170–
933 177. doi:10.1016/j.seares.2013.07.009
- 934 Pratt, D.R., Pilditch, C.A., Lohrer, A.M., Thrush, S.F., Kraan, C., 2015. Spatial distributions of grazing
935 activity and microphytobenthos reveal scale-dependent relationships across a sedimentary
936 gradient. Estuaries and Coasts 38, 722–734. doi:10.1007/s12237-014-9857-7
- 937 Rabalais, N.N., Turner, R.E., Wiseman, W.J., 2002. Gulf of Mexico hypoxia, A.K.A. “The Dead Zone.”
938 Annu. Rev. Ecol. Syst. 33, 235–263. doi:10.1146/annurev.ecolsys.33.010802.150513
- 939 Risgaard-Petersen, N., Nicolaisen, M.H., Revsbech, N.P., Lomstein, B.A., 2004. Competition between
940 ammonia-oxidizing bacteria and benthic microalgae. Appl. Environ. Microbiol. 70, 5528–5537.
941 doi:10.1128/AEM.70.9.5528
- 942 Risgaard-Petersen, N., Rysgaard, S., Nielsen, L.P., Revsbech, N.P., 1994. Diurnal variation of
943 denitrification and nitrification in sediments colonized by benthic microphytes. Limnol. Ocean.
944 39, 573–579.

- 945 Rivero, S., Villasante, S., 2016. What are the research priorities for marine ecosystem services? Mar.
946 Policy 66, 104–113. doi:10.1016/j.marpol.2016.01.020
- 947 Sauriau, P., Kang, C., 2000. Stable isotope evidence of benthic microalgae-based growth and
948 secondary production in the suspension feeder *Cerastoderma edule* (Mollusca, Bivalvia) in the
949 Marennes-Oléron Bay. doi:10.1023/A
- 950 Schnurr, P.J., Drever, M.C., Kling, H.J., Elner, R.W., Arts, M.T., 2019. Seasonal changes in fatty acid
951 composition of estuarine intertidal biofilm: Implications for western sandpiper migration.
952 Estuar. Coast. Shelf Sci. doi:10.1016/j.ecss.2019.04.047
- 953 Serôdio, J., Catarino, F., 1999. Fortnightly light and temperature variability in estuarine intertidal
954 sediments and implications for microphytobenthos primary productivity 2, 235–241.
- 955 Shuba, E.S., Kifle, D., 2018. Microalgae to biofuels: ‘Promising’ alternative and renewable energy,
956 review. Renew. Sustain. Energy Rev. 81, 743–755. doi:10.1016/j.rser.2017.08.042
- 957 Small, N., Munday, M., Durance, I., 2017. The challenge of valuing ecosystem services that have no
958 material benefits. Glob. Environ. Chang. 44, 57–67. doi:10.1016/j.gloenvcha.2017.03.005
- 959 Snelgrove, P.V.R., Soetaert, K., Solan, M., Thrush, S., Wei, C., Danovaro, R., Fulweiler, R.W., Kitazato,
960 H., Ingole, B., Norkko, A., Parkes, R.J., Volkenborn, N., 2018. Global carbon cycling on a
961 heterogeneous seafloor. Trends Ecol. Evol. 33. doi:10.1016/j.tree.2017.11.004
- 962 Spears, B.M., Saunders, J.E., Davidson, I., Paterson, D.M., 2008. Microalgal sediment biostabilisation
963 along a salinity gradient in the Eden Estuary, Scotland: Unravelling a paradox. Mar. Freshw. Res.
964 59, 313. doi:10.1071/MF07164
- 965 Spilmont, N., Seuront, L., Meziane, T., Welsh, D.T., 2011. There’s more to the picture than meets the
966 eye: Sampling microphytobenthos in a heterogeneous environment. Estuar. Coast. Shelf Sci. 95,
967 470–476. doi:10.1016/j.ecss.2011.10.021
- 968 Sprague, M., Dick, J.R., Tocher, D.R., 2016. Impact of sustainable feeds on omega-3 long-chain fatty
969 acid levels in farmed Atlantic salmon, 2006-2015. Sci. Rep. 6, 1–9. doi:10.1038/srep21892
- 970 Stal, L.J., 2012. Cyanobacterial mats and stromatolites. doi:10.1007/978-94-007-3855-3
- 971 Stock, W., Heylen, K., Sabbe, K., Willems, A., Troch, M. De, 2014. Interactions between benthic
972 copepods, bacteria and diatoms promote nitrogen retention in intertidal marine sediments 9,
973 1–7. doi:10.1371/journal.pone.0111001
- 974 Sundbäck, K., Alsterberg, C., Larson, F., 2010. Effects of multiple stressors on marine shallow-water

- 975 sediments: Response of microalgae and meiofauna to nutrient-toxicant exposure. *J. Exp. Mar.*
 976 *Bio. Ecol.* 388, 39–50. doi:10.1016/j.jembe.2010.03.007
- 977 Sundbäck, K., Linares, F., Larson, F., Wulff, A., Engelsen, A., 2004. Benthic nitrogen fluxes along a
 978 depth gradient in a microtidal fjord: The role of denitrification and microphytobenthos. *Limnol.*
 979 *Oceanogr.* 49, 1095–1107. doi:10.4319/lo.2004.49.4.1095
- 980 Sundbäck, K., Mcglathery, K., 2005. Interactions between benthic macroalgal and microalgal mats,
 981 in: *Interactions between macro-and microorganisms in marine sediments*. pp. 7–29.
- 982 Sundbäck, K., Miles, A., 2002. Role of microphytobenthos and denitrification for nutrient turnover in
 983 embayments with floating macroalgal mats: A spring situation. *Aquat. Microb. Ecol.* 30, 91–
 984 101.
- 985 Sundbäck, K., Miles, A., Linares, F., 2006. Nitrogen dynamics in nontidal littoral sediments: Role of
 986 microphytobenthos and denitrification. *Estuaries and Coasts* 29, 1196–1211.
- 987 Sundbäck, K., Snoeijs, P., 1991. Effects of nutrient enrichment on microalgal community composition
 988 in a coastal shallow-water sediment system: An Experimental Study. *Bot. Mar.* 34, 341–358.
- 989 Suykens, K., Schmidt, S., Delille, B., Harlay, J., Chou, L., Bodt, C. De, Fagel, N., Borges, A. V., 2011.
 990 Benthic remineralization in the northeast European continental margin (northern Bay of Biscay
 991) Continental Shelf Research Benthic remineralization in the northwest European continental
 992 margin (northern Bay of Biscay). *Cont. Shelf Res.* 31, 644–658. doi:10.1016/j.csr.2010.12.017
- 993 TEEB, 2010. The Economics of Valuing Ecosystem Services and Biodiversity, in: *The Economics of*
 994 *Ecosystems and Biodiversity. Ecological and economic foundations*, Routledge Abingdon, UK, p.
 995 410p.
- 996 Thrush, S.F., Halliday, J., Hewitt, J.E., Lohrer, A.M., 2008. The effects of habitat loss, fragmentation,
 997 and community homogenization on resilience in estuaries. *Ecol. Appl.* 18, 12–21.
 998 doi:doi:10.1890/07-0436.1
- 999 Thrush, S.F., Hewitt, J.E., Cummings, V.J., Ellis, J.I., Hatton, C., Lohrer, A., Norkko, A., 2004. Muddy
 1000 waters: Elevating sediment input to coastal and estuarine habitats. *Front. Ecol. Environ.* 2, 299–
 1001 306. doi:10.1890/1540-9295(2004)002[0299:MWESIT]2.0.CO;2
- 1002 Thrush, S.F., Hewitt, J.E., Gibbs, M., Lundquist, C., Norkko, A., 2006. Functional role of large
 1003 organisms in intertidal communities: Community effects and ecosystem function. *Ecosystems*
 1004 9, 1029–1040. doi:10.1007/s10021-005-0068-8

- 1005 Thrush, S.F., Hewitt, J.E., Kraan, C., Lohrer, A.M., Pilditch, C.A., Douglas, E., 2017. Changes in the
1006 location of biodiversity– ecosystem function hot spots across the seafloor landscape with
1007 increasing sediment nutrient loading. *Proc. R. Soc. B Biol. Sci.* 284. doi:10.1098/rspb.2016.2861
- 1008 Thrush, S.F., Hewitt, J.E., Lohrer, A.M., 2012. Interaction networks in coastal soft-sediments highlight
1009 the potential for change in ecological resilience. *Ecol. Appl.* 22, 1213–1223. doi:10.1890/11-
1010 1403.1
- 1011 Thrush, S.F., Hewitt, J.E., Parkes, S., Lohrer, A.M., Pilditch, C., Woodin, S.A., Wethey, D.S., Chiantore,
1012 M., De Juan, S., Kraan, C., Rodil, I., Savage, C., Van Colen, C., 2014. Experimenting with
1013 ecosystem interaction networks in search of threshold potentials in real-world marine
1014 ecosystems. *Ecology* 95, 1451–1457. doi:10.1890/13-1879.1
- 1015 Thrush, S.F., Townsend, M., Hewitt, J.E., Davies, K., Lohrer, A.M., Lundquist, C., Cartner, K., 2013. The
1016 many uses and values of estuarine ecosystems, in: Dymond, J. (Ed.), *Ecosystem Services in New
1017 Zealand – conditions and trends*. Manaaki Whenua Press, pp. 226–237.
- 1018 Tobias, C., Giblin, A., McClelland, J., Tucker, J., Peterson, B., 2003. Sediment DIN fluxes and
1019 preferential recycling of benthic microalgal nitrogen in a shallow macrotidal estuary. *Mar. Ecol.*
1020 *Prog. Ser.* 257, 25–36. doi:10.3354/meps257025
- 1021 Tolhurst, T.J., Black, K.S., Shayler, S.A., Mather, S., Black, I., Baker, K., Paterson, D.M., 1999.
1022 Measuring the in situ erosion shear stress of intertidal sediments with the Cohesive Strength
1023 Meter (CSM). *Estuar. Coast. Shelf Sci.* 49, 281–294. doi:10.1006/ecss.1999.0512
- 1024 Tolhurst, T.J., Defew, E.C., Perkins, R.G., Sharples, A., Paterson, D.M., 2006. The effects of tidally-
1025 driven temporal variation on measuring intertidal cohesive sediment erosion threshold. *Aquat.*
1026 *Ecol.* 40, 521–531. doi:10.1007/s10452-005-9001-7
- 1027 Tolhurst, T.J., Gust, G., Paterson, D.M., 2002. The influence of an extracellular polymeric substance
1028 (EPS) on cohesive sediment stability, in: Winterwerp, J.C., Kranenburg, C. (Eds.), *Fine sediment
1029 dynamics in the marine environment*. Elsevier, pp. 409–425.
- 1030 Tolhurst, T. J., Gust, G., Paterson, D.M., 2002. The influence of an extracellular polymeric substance
1031 (EPS) on cohesive sediment stability . *Proc. Mar. Sci.* 5, 409–425. doi:10.1016/S1568-
1032 2692(02)80030-4
- 1033 Townsend, M., Davies, K., Hanley, N., Hewitt, J.E., Lundquist, C.J., Lohrer, A.M., 2018. The challenge
1034 of implementing the marine Ecosystem Service concept. *Front. Mar. Sci.* 5, 1–13.
1035 doi:10.3389/fmars.2018.00359

- 1036 Tuominen, L., Mäkelä, K., Lehtonen, K., Haahti, H., Hietanen, S., Kuparinen, J., 1999. Nutrient fluxes,
1037 porewater profiles and denitrification in sediment influenced by algal sedimentation and
1038 bioturbation by *Monoporeia affinis*. *Estuar. Coast. Shelf Sci.* 49, 83–97.
1039 doi:10.1006/ecss.1999.0492
- 1040 Turkelboom, F., Thoonen, M., Jacobs, S., 2015. Ecosystem Service trade-offs and synergies. *Ecol. Soc.*
1041 21, 43. doi:10.13140/RG.2.1.4882.9529
- 1042 Underwood, G.J.C., Hanlon, A.R.M., Oxborough, K., Baker, N.R., 2005. Patterns in microphytobenthic
1043 primary productivity: Species-specific variation in migratory rhythms and photosynthetic
1044 efficiency in mixed-species biofilms. *Limnol. Ocean.* 50, 755–767.
- 1045 Underwood, G.J.C., Paterson, D.M., 2003. The importance of extracellular carbohydrate production
1046 by marine epipelagic diatoms. *Adv. Bot. Res.* 40, 183–240.
- 1047 Vasconcelos, R.P., Reis-santos, P., Costa, M.J., Cabral, H.N., 2011. Connectivity between estuaries
1048 and marine environment: Integrating metrics to assess estuarine nursery function. *Ecol. Indic.*
1049 11, 1123–1133. doi:10.1016/j.ecolind.2010.12.012
- 1050 Villbrandt, M., Stal, L.J., Krumbein, W.E., 1990. Interactions between nitrogen fixation and oxygenic
1051 photosynthesis in a marine cyanobacterial mat. *FEMS Microbiol. Ecol.* 74, 59–71.
- 1052 Walsh, M.J., Doren, L.G. Van, Sills, D.L., Archibald, I., Beal, C.M., Lei, X.G., Huntly, M.E., Johnson, Z.,
1053 Greene, C.H., 2016. Algal food and fuel coproduction can mitigate greenhouse gas emissions
1054 while improving land and water-use efficiency public policies. *Environ. Res. Lett.* 11.
1055 doi:10.1088/1748-9326/11/11/114006
- 1056 Watermann, F., Hillebrand, H., Gerdes, G., Krumbein, W.E., Sommer, U., 1999. Competition between
1057 benthic cyanobacteria and diatoms as influenced by different grain sizes and temperatures.
1058 *Mar. Ecol. Prog. Ser.* 187, 77–87. doi:10.3354/meps187077
- 1059 Watson, S.C.L., Beaumont, N.J., Widdicombe, S., Paterson, D.M., 2019. Comparing the network
1060 structure and resilience of two benthic estuarine systems following the implementation of
1061 nutrient mitigation actions. *Estuar. Coast. Shelf Sci.* 0–1. doi:10.1016/j.ecss.2018.12.016
- 1062 Webb, A.P., Eyre, B.D., Bay, P., Victoria, T., 2004. Effect of natural populations of burrowing
1063 thalassinidean shrimp on sediment irrigation, benthic metabolism, nutrient fluxes and
1064 denitrification 268, 205–220.
- 1065 Weerman, E., Herman, P., van de Koppel, J., 2011. Macrobenthos abundance and distribution on a
1066 spatially patterned intertidal flat. *Mar. Ecol. Prog. Ser.* 440, 95–103. doi:10.3354/meps09332

- 1067 Weerman, E.J., Belzen, J. Van, Rietkerk, M., Temmerman, S., Kefi, S., Herman, P.M.J., Koppel, J. Van
1068 De, 2012. Changes in diatom patch-size distribution and degradation in a spatially self-
1069 organized intertidal mudflat ecosystem. *Ecology* 93, 608–618.
- 1070 Weerman, E.J., van de Koppel, J., Eppinga, M.B., Montserrat, F., Liu, Q., Herman, P.M.J., 2010. Spatial
1071 self-organization on intertidal mudflats through biophysical stress divergence. *Am. Nat.* 176,
1072 E15–E32. doi:10.1086/652991
- 1073 Widdicombe, S., Austen, M.C., 2001. The interaction between physical disturbance and organic
1074 enrichment: An important element in structuring benthic communities 46, 1720–1733.
- 1075 Widdicombe, S., Austen, M.C., 1999. Mesocosm investigation into the effects of bioturbation on the
1076 diversity and structure of a subtidal macrobenthic community. *Mar. Ecol. Prog. Ser.* 189, 181–
1077 193.
- 1078 Widdows, J., Brinsley, M., 2002. Impact of biotic and abiotic processes on sediment dynamics and
1079 the consequences to the structure and functioning of the intertidal zone. *J. Sea Res.* 48, 143–
1080 156. doi:10.1016/S1385-1101(02)00148-X
- 1081 Wiegner, T.W., Sitzinger, S.P., Breitburg, D.L., Sanders, J.G., 2003. The effects of multiple stressors on
1082 the balance between autotrophic and heterotrophic processes in an estuarine system.
1083 *Estuaries* 26, 352–364.
- 1084 Wood, R.J., Mitrovic, S.M., Lim, R.P., St, M., Warne, J., Dunlop, J., Ke, B.J., 2019. Benthic diatoms as
1085 indicators of herbicide toxicity in rivers – A new SPEcies At Risk (SPEAR herbicides) index 99,
1086 203–213. doi:10.1016/j.ecolind.2018.12.035
- 1087 Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K.,
1088 Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J., Watson, R., 2006. Impacts of
1089 biodiversity loss on ocean ecosystem services. *Science* (80-). 314, 787–790.
1090 doi:10.1126/science.1132294
- 1091 Wulff, A.A., Sundbäck, K., Nilsson, C., Carlson, L., Jönsson, B., 1997. Effect of Sediment Load on the
1092 Microbenthic Community of a Shallow-Water Sandy Sediment. *Estuaries* 20, 547–558.
- 1093 Wyness, A.J., Paterson, D.M., Mendo, T., Defew, E.C., Stutter, M.I., Avery, L.M., 2019. Factors
1094 affecting the spatial and temporal distribution of *E.coli* in intertidal estuarine sediments. *Sci.*
1095 *Total Environ.* 661, 155–167. doi:10.1016/j.scitotenv.2019.01.061
- 1096 Yletyinen, J., Brown, P., Pech, R., Hodges, D., Hulme, P.E., Malcolm, T.F., Maseyk, F.J.F., Peltzer, D.A.,
1097 Perry, G.L.W., Richardson, S.J., Smaill, S.J., Stanley, M.C., Todd, J.H., Walsh, P.J., Wright, W.,

- 1098 Tylianakis, J.M., 2019. Understanding and managing social–ecological tipping points in primary
1099 industries 69, 335–347. doi:10.1093/biosci/biz031
- 1100 Zhou, W., Min, M., Li, Y., Hu, B., Ma, X., Cheng, Y., Liu, Y., Chen, P., Ruan, R., 2012. A hetero-
1101 photoautotrophic two-stage cultivation process to improve wastewater nutrient removal and
1102 enhance algal lipid accumulation. *Bioresource Technology* 110, 448–455.
1103 doi:10.1016/j.biortech.2012.01.063
- 1104