

# 1 The potential for mobile demersal fishing to reduce carbon 2 storage and sequestration in seabed sediments

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9

## 10 **Abstract**

11 Subtidal marine sediments are one of the planet's primary carbon stores and strongly influence  
12 the oceanic sink for atmospheric CO<sub>2</sub>. By far the most pervasive human activity occurring on  
13 the seabed is bottom trawling and dredging for fish and shellfish. A global first-order estimate  
14 suggested mobile demersal fishing activities may cause 160-400 Mt of organic carbon (OC)  
15 to be remineralised annually from seabed sediment carbon stores. There are, however, many  
16 uncertainties in this calculation. Here, we discuss the potential drivers of change in seabed  
17 OC stores due to mobile demersal fishing activities and conduct a systematic review,  
18 synthesising studies where this interaction has been directly investigated. Mobile demersal  
19 fishing would be expected to reduce OC in seabed stores, albeit with site-specific variability.  
20 Reductions would occur due to lower production of flora and fauna, the loss of fine flocculent  
21 material, increased sediment resuspension, mixing and transport, and increased oxygen  
22 exposure. This would be offset to some extent by reduced faunal bioturbation and respiration,  
23 increased off-shelf transport and increases in primary production from the resuspension of  
24 nutrients. Studies which directly investigated the impact of demersal fishing on OC stocks had  
25 mixed results. A finding of no significant effect was reported in 51% of 59 experimental  
26 contrasts; 41% reported lower OC due to fishing activities, with 8% reporting higher OC. In  
27 relation to remineralisation rates within the seabed, 14 experimental contrasts reported that  
28 demersal fishing activities decreased remineralisation, with four reporting higher  
29 remineralisation rates. The direction of effects was related to sediment type, impact duration,  
30 study design and local hydrography. More evidence is urgently needed to accurately quantify  
31 the impact of anthropogenic physical disturbance on seabed carbon in different environmental  
32 settings, and incorporate full evidence-based carbon considerations into global seabed  
33 management.

34

## 35 1. Introduction

36

37 Through a mixture of physical, chemical and biological processes, the ocean has absorbed  
38 ~40% of anthropogenic CO<sub>2</sub> emissions since the industrial revolution (Gruber et al. 2019,  
39 Watson et al. 2020). The term “blue carbon” describes the ability of marine ecosystems to  
40 absorb CO<sub>2</sub> from the atmosphere or water column, assimilate this inorganic carbon (IC) into  
41 organic compounds and isolate it from remineralisation for centennial to millennial time-scales  
42 (Nellemann et al. 2009). This process of carbon capture is key to maintaining the ecological  
43 functioning of the ocean (Bauer et al. 2013) and is beneficial as a sink for anthropogenic CO<sub>2</sub>  
44 (Khatriwala et al. 2009, Gruber et al. 2019).

45

46 Research on blue carbon initially focused on the coastal vegetated habitats of mangroves,  
47 seagrass and saltmarsh, due to their ability to fix CO<sub>2</sub> directly, store high concentrations of  
48 organic carbon (OC) *in-situ* within underlying sediments and to accrete this OC indefinitely  
49 over time (McLeod et al. 2011, Duarte et al. 2013). Although these habitats are some of the  
50 most intense OC sinks on the planet (Duarte et al. 2013), with sequestration rates considerably  
51 higher than forests on land (McLeod et al. 2011), their limited spatial scale of approximately 1  
52 million km<sup>2</sup> or ~0.2% of the ocean’s surface, means they only contain a small proportion of the  
53 ocean’s total OC stock (Nellemann et al. 2009, Duarte et al. 2013, Duarte 2017, Howard et al.  
54 2017, Atwood et al. 2020).

55

56 By far the largest mass of OC occurs in the pelagic zone (Nellemann et al. 2009), with much  
57 of this in flux between the oceanic IC pool and the atmosphere (Bauer et al. 2013). However,  
58 at depths below 1000 m, pelagic OC may become isolated from atmospheric exchange  
59 processes for centennial time scales (Caldeira et al. 2002, Nellemann et al. 2009, Krause-  
60 Jensen and Duarte 2016). How this should be accounted for remains a matter of debate, and  
61 so pelagic OC is rarely used in the quantification or classification of blue carbon (Lovelock and  
62 Duarte 2019). That withstanding, subtidal marine sediments contain the ocean’s biggest OC  
63 store, estimated to hold ~87 Gt of OC in the upper 5 cm (Lee et al. 2019) or ~2.3 Tt in the top  
64 1 m (Duarte et al. 2013, Atwood et al. 2020). Quantification of annual sequestration rates in  
65 these sediments is relatively poorly constrained, however they have been estimated globally  
66 at approximately 126 - 350 Mt OC yr<sup>-1</sup> (Berner 1982, Seiter et al. 2004, Burdige 2007, Keil  
67 2017, Lee et al. 2019, Smeaton et al. 2021).

68

69 Seabed sediments are subjected to a wide range of direct physical impacts from human  
70 pressures, namely: shipping, mineral extraction, fishing, energy developments, deployment of  
71 cables and pipelines, coastal development, dredging of shipping access channels and

72 disposal of dredge spoil (Halpern et al. 2019, O'Hara et al. 2021). By far the most widespread  
73 source of disturbance is bottom trawling and dredging for fish and shellfish (Oberle et al.  
74 2016a, Amoroso et al. 2018, Kroodsmas et al. 2018, O'Hara et al. 2021). These pressures are  
75 pervasive and long lasting, with improved technologies over the last two centuries increasing  
76 the spread of mobile fishing gears to deeper waters and much of the global ocean (Roberts  
77 2007, Watson and Morato 2013, Kroodsmas et al. 2018). Compared to many other types of  
78 stressors, in intensively fished areas, trawling and dredging can also occur on the same area  
79 of seabed numerous times in a year (Tillin et al. 2006, Hinz et al. 2009, Oberle et al. 2016a).

80

81 Globally, fishing pressure with mobile demersal gear is concentrated in subtidal areas at  
82 depths above 1000 m in coastal habitats and offshore on continental shelves and slopes  
83 (Amoroso et al. 2018, Kroodsmas et al. 2018). In total these areas cover around 9% of the  
84 global seabed, yet they store an estimated 360 Gt in their top 1 m of sediment (Atwood et al.  
85 2020). Continental shelf sediments are also highly productive, estimated to sequester up to  
86 86% of all OC that is buried annually in global subtidal sediments (Bernier 1982, Seiter et al.  
87 2004, Atwood et al. 2020, Smeaton et al. 2021).

88

89 Mobile demersal fishing activity significantly alters seabed faunal communities (Kaiser et al.  
90 2006, Sciberras et al. 2016, Hiddink et al. 2017), restructures the top layers of benthic  
91 sediments (Trimmer et al. 2005, Puig et al. 2012, Eigaard et al. 2016, Oberle et al. 2016b) and  
92 resuspends large volumes of sediment into the water column (Jones 1992, Ruffin 1998,  
93 Thrush and Dayton 2002, Durrieu de Madron et al. 2005, Martín et al. 2014b, Palanques et al.  
94 2014). However, the net effect of this disturbance on OC stores is poorly resolved. Through  
95 mixing, resuspension and oxidation of surface sediments, along with the disturbance of  
96 benthic communities, fishing likely generates a source of "underwater carbon emissions" via  
97 increased remineralisation of OC, and will also limit future OC sequestration by inhibiting long-  
98 term sediment settlement and consolidation (Martín et al. 2014b, Keil 2017, Luisetti et al. 2019,  
99 De Borger et al. 2021, Sala et al. 2021). This disturbance can be expected to increase IC  
100 concentrations in the ocean, and via this, slow the rate of CO<sub>2</sub> uptake from the atmosphere,  
101 while contributing to ocean acidification and potentially leading to increased release of oceanic  
102 CO<sub>2</sub> to the atmosphere (Khatiwala et al. 2009, Pendleton et al. 2012, Bauer et al. 2013, Keil  
103 2017, Lovelock et al. 2017, Luisetti et al. 2019, LaRowe et al. 2020, Sala et al. 2021). To place  
104 the effect of mobile demersal fishing in full context, it is important to better quantify the impacts  
105 of different pressures on OC storage and to understand how these compare with natural  
106 hydrological disturbances to seabed sediments in different environmental settings  
107 (Winterwerp and Kranenburg 2002, Pusceddu et al. 2005b, Arndt et al. 2013, Rühl et al. 2020).

108

109 The cycling and storage of OC at the seabed is highly complex and is influenced by: sediment  
110 fauna, flora and microbiome; its lithology and granulometry; and the chemistry, hydrology and  
111 biology of the surrounding water column (Burdige 2007, Bauer et al. 2013, Keil 2017,  
112 Middelburg 2018, Snelgrove et al. 2018, LaRowe et al. 2020, Rühl et al. 2020). With all of  
113 these factors affected by many positive and negative feedback mechanisms, it is challenging  
114 to definitively identify the impact of trawling and dredging on net OC storage (Keil 2017,  
115 Snelgrove et al. 2018, LaRowe et al. 2020, Rühl et al. 2020). In this review we discuss the  
116 potential drivers of change in sediment OC due to mobile demersal fishing activities, and  
117 summarise empirical evidence where their effects on sediment OC has been investigated. We  
118 also discuss recent peer reviewed publications which aim to quantify the impact of mobile  
119 demersal fishing at global, regional and national scales, and highlight why the results must be  
120 viewed with both concern and caution (Luisetti et al. 2019, Paradis et al. 2021, Sala et al.  
121 2021). If seabed sediments were to be recognised as a quantifiable and manageable blue  
122 carbon resource it could unlock huge climate change mitigation potential and carbon financing  
123 opportunities (Avelar et al. 2017, Seddon et al. 2019).

124

125

## 126 **2. Links between seabed sediment OC and mobile demersal fishing**

127

### 128 **2.1 Production of benthic micro- and macroalgae**

129 Seabed OC is mostly allochthonous, with much of it originating from terrestrial run-off and  
130 primary production in surface waters from phytoplankton, macroalgae and wetland vegetation  
131 (Bauer et al. 2013, Turner 2015, Krause-Jensen and Duarte 2016, LaRowe et al. 2020, Legge  
132 et al. 2020). Through the ocean's "biological pump" much of this OC will be consumed,  
133 repackaged, excreted or remineralised before a remaining proportion of OC reaches the  
134 seabed (Turner 2015, Keil 2017, Middelburg 2018). On sediments in the euphotic zone, some  
135 OC is autochthonous – i.e. produced *in-situ* by microphytobenthos, and by macroalgae found  
136 on more stable sediments, hard substrate or attached to biogenic material (MacIntyre et al.  
137 1996, Gattuso et al. 2006).

138

139 While the impact of mobile demersal fishing on benthic algae is little studied, it is known that  
140 benthic macroalgae are easily damaged by physical disturbance, and the structure and  
141 abundance of microphytobenthos is highly dependent on both natural and anthropogenic  
142 perturbation (MacIntyre et al. 1996, Fragkopoulou et al. 2021). In general, mobile demersal  
143 fishing is expected to lead to a reduction in algal cover and sediment surface chlorophyll a  
144 concentration (Fig. 1a) (Mayer et al. 1991, MacIntyre et al. 1996, Watling et al. 2001, Tiano et  
145 al. 2019, Fragkopoulou et al. 2021). For example, scallop dredging at depths of 8-15 m in the

146 Damariscotta River Estuary of the Northwest Atlantic led to clear visual disturbance of diatom  
147 mats and caused a significant reduction in chlorophyll a concentration (Mayer et al. 1991,  
148 Watling et al. 2001). Among algae, kelp and coralline algae can require years and decades  
149 respectively, to recover following disturbance (Dayton et al. 1992, Fragkopoulou et al. 2021).  
150 By contrast ephemeral macroalgae and microphytobenthos can recover quickly, especially  
151 from less chronic disturbance (MacIntyre et al. 1996, Ordines et al. 2017). For example, in the  
152 *Pesquera Rica* trawling grounds of the Balearic Islands, red algae beds of Peyssonneliaceae  
153 and Corallinophycidae persist within trawled areas, although their biomass is around 39-47%  
154 lower compared to untrawled areas (Ordines et al. 2017).

155

156 In some cases, especially in oligotrophic environments, disturbance from mobile demersal  
157 fishing may release nutrients from sub-surface sediments and promote primary production,  
158 increasing the density of microphytobenthos (Fig. 1a) (Fanning et al. 1982, Falcão et al. 2003,  
159 Dounas et al. 2007, Palanques et al. 2014). Counteracting this, sediment suspended by fishing  
160 increases turbidity (Ruffin 1998, Palanques et al. 2001) which reduces light penetration and  
161 thus photosynthetic rates (Fig. 1a) (MacIntyre et al. 1996). For example, there are contrasting  
162 results from fishing impact studies within the Northeast Atlantic. Experimental trawling activity  
163 in the Frisian Front significantly reduced chlorophyll a concentration at the sediment surface  
164 (Tiano et al. 2019), whereas investigations over a range of trawling intensities in muddy  
165 sediments of the Irish Sea found a positive correlation between chlorophyll a concentration  
166 and fishing frequency (Sciberras et al. 2016).

167

168 In most settings, high frequency mobile demersal fishing would be expected to reduce the  
169 abundance of benthic flora on euphotic sediments and to therefore limit the quantity of OC  
170 stored directly, and via secondary production (Fig. 1a) (Miller et al. 1996, Middelburg 2018,  
171 Mandal et al. 2021). Additionally, benthic micro- and macroalgae are known to increase the  
172 stability and accumulation rate of seabed sediments (Yallop et al. 1994, Miller et al. 1996), a  
173 primary driver of OC burial and storage (Middelburg 2018, LaRowe et al. 2020). This  
174 represents a further mechanism through which disturbance of benthic algae from mobile  
175 demersal fishing would limit the potential sequestration rate of OC within sedimentary seabed  
176 habitats (Fig. 1a).

177

## 178 **2.2 Benthic faunal production and processing of OC**

179 The impact of mobile demersal fishing gears on benthic fauna has been widely studied. Long-  
180 term effects on community structure and faunal biomass are site-specific and fishing gear  
181 dependent (Collie et al. 2000, Kaiser et al. 2002, Thrush and Dayton 2002, Kaiser et al. 2006,  
182 Hiddink et al. 2017, Sciberras et al. 2018). Gears which penetrate most deeply into sediment,

183 such as dredges and hydraulic gears, tend to have greater impact than gears with less  
184 penetration, such as demersal seines and otter trawls (Collie et al. 2000, Kaiser et al. 2006,  
185 Hiddink et al. 2017, Sciberras et al. 2018), although habitat type also has an influence  
186 (Rijnsdorp et al. 2020). The largest impacts follow initial experimental trawling events or are  
187 seen when comparisons are made to an area of long standing protection (Thrush and Dayton  
188 2002, Cook et al. 2013). Many studies may underestimate the damage done by mobile fishing  
189 gears and overestimate speed of recovery because they measure recovery of areas already  
190 impacted (Collie et al. 2000, Kaiser et al. 2002, Kaiser et al. 2006, Hinz et al. 2009, Cook et  
191 al. 2013, Hiddink et al. 2017, Sciberras et al. 2018).

192

193 To a greater or lesser extent, bottom trawling and dredging reduce total benthic biomass and  
194 production of benthic fauna and cause loss in abundance and diversity of sessile epifauna and  
195 long-lived shallow burrowing infauna (Kaiser et al. 2002, Queirós et al. 2006, Tillin et al. 2006,  
196 Sciberras et al. 2018, Tiano et al. 2020). Long-term fishing with mobile gears leads to  
197 preponderance of small-bodied, opportunistic, motile infauna, and larger, highly vagrant,  
198 scavenging macrofauna (Kaiser et al. 2002, Thrush and Dayton 2002, Kaiser et al. 2006, Tillin  
199 et al. 2006). But even within the largely resistant opportunistic meiofauna, mobile demersal  
200 fishing still affects diversity and community structure (Schratzberger et al. 2009, Pusceddu et  
201 al. 2014).

202

203 Benthic fauna are primary drivers of carbon cycling in sediments (Middelburg 2018, Snelgrove  
204 et al. 2018, LaRowe et al. 2020, Rühl et al. 2020). For example, in a well-studied area off  
205 Vancouver Island, taxonomic and functional richness of benthic fauna explained a similar  
206 proportion of variance in pelagic-benthic nutrient flux (~20%) when compared to a suite of  
207 environmental variables (Belley and Snelgrove 2016, 2017). Much of the OC that reaches the  
208 seabed is directly consumed by deposit and suspension feeding fauna, and is thereafter  
209 incorporated into biomass, expelled as faeces and pseudofaeces, or metabolised and  
210 remineralised through respiration (Arndt et al. 2013, Keil 2017, Middelburg 2018, Snelgrove  
211 et al. 2018, Rühl et al. 2020). While respiration reduces the concentration of OC available for  
212 burial and storage, the consumption and processing of OC by benthic fauna may increase  
213 proportions of refractory compounds resistant to microbial decomposition, or form specific OC-  
214 mineral interactions which can isolate the OC from remineralisation processes, thus improving  
215 the potential for burial and long-term storage (Fig. 1b) (Arndt et al. 2013, Middelburg 2018,  
216 LaRowe et al. 2020).

217

218 Bioturbation and bio-irrigation activities generally increase OC remineralisation due to  
219 oxygenation of surface sediments and an increase in the concentration of other electron

220 acceptors, therefore promoting microbial degradation (Fig. 1b) (Hulthe et al. 1998, Arndt et al.  
221 2013, Keil 2017, Snelgrove et al. 2018, LaRowe et al. 2020). However, these activities also  
222 transport OC rich surface sediments to deeper sediment layers, potentially increasing their  
223 chance of burial and long-term storage (Fig. 1b) (van der Molen et al. 2012, Middelburg 2018,  
224 Snelgrove et al. 2018, Rühl et al. 2020, De Borger et al. 2021). For example, in the North Sea,  
225 bioturbation by infauna has been found to promote remineralisation by exposing buried  
226 material to oxygen (Hulthe et al. 1998) while also being significant in moving carbon from the  
227 surface to deeper sediment layers (van der Molen et al. 2012, Middelburg 2018).

228

229 The composition and abundance of benthic fauna can also influence the stability and  
230 accumulation rates of sediment, which are key drivers of OC burial and storage (Middelburg  
231 2018, LaRowe et al. 2020). While increased bioturbation activity generally has a destabilising  
232 effect, burrowing fauna can increase the stability and accumulation rate of sediment if there is  
233 an increase in biogenic material such as worm tubes or mucus production, or an increase in  
234 structural complexity at the sediment surface from the presence of sedentary and sessile  
235 epifauna and biogenic habitat (Fig. 1b) (Ekdale et al. 1984, Thrush and Dayton 2002, Roberts  
236 2007, Borsje et al. 2014, Rühl et al. 2020). For example, in fine sands and muds of the  
237 Northeast Atlantic the presence of the tube building polychaete *Lanice conchilega* can lead to  
238 increased sediment accretion rates due to changes in flow dynamics around the worm tubes,  
239 with impacts on sedimentation dynamics beyond the biogenic structure and over a longer  
240 duration than the lifetime of the individual worm (Borsje et al. 2014). In contrast, in the same  
241 habitat the density of the Manila clam (*Ruditapes philippinarum*) was positively correlated to  
242 sediment erosion rates due to enhanced bioturbation activities (Sgro et al. 2005).

243

244 Faunal biomass and production are some of the main contributors of OC in seabed sediments.  
245 Therefore, the expected overall impact of mobile demersal fishing on faunal mediated  
246 processes is a reduction in OC storage, with the effect somewhat offset by reduced  
247 bioturbation and respiration causing lower remineralisation rates. Where the balance lies  
248 depends on the many complex interactions discussed above, which are site-specific.

249

250

### 251 **2.3 Alteration to sediment composition**

252 Mobile demersal fishing gears can alter the granulometry, topography and vertical structuring  
253 of seabed sediments (Trimmer et al. 2005, Puig et al. 2012, Martín et al. 2014b, Oberle et al.  
254 2016a, Oberle et al. 2016b), with extent of change influenced by gear used, sediment type,  
255 local hydrology and frequency of fishing (Kaiser et al. 2002, Trimmer et al. 2005, Martín et al.  
256 2014b, Oberle et al. 2016b). Gears that penetrate more deeply into sediment and have a larger

257 footprint cause most impact (Kaiser et al. 2002, Martín et al. 2014b, Eigaard et al. 2016). In  
258 highly mobile habitats, the structure and composition of sediment may not be greatly altered  
259 by mobile demersal fishing due to strong natural forcing mechanisms, while those found in  
260 less hydrologically active environments could be highly affected (Kaiser et al. 2002, Trimmer  
261 et al. 2005, Martín et al. 2014b, Oberle et al. 2016b). However, greater sediment mobility may  
262 itself be a consequence of long-term use of mobile fishing gears, due to loss of fauna and flora  
263 that stabilise sediments (Roberts 2007).

264

265 Topographic alterations from mobile fishing gears can consist of visible trawl/dredge tracks  
266 and homogenisation in large-scale seabed topography (Kaiser et al. 2002, Martín et al. 2014b,  
267 Palanques et al. 2014, Eigaard et al. 2016, Oberle et al. 2016a, Oberle et al. 2016b, Tiano et  
268 al. 2020). For example, multibeam surveys have shown that chronic trawling on the continental  
269 slopes of the Palamós canyon in the Northwest Mediterranean has had drastic flattening  
270 effects on soft sediments (Puig et al. 2012). Mobile demersal fishing also mixes and overturns  
271 the top layer of seabed, generally causing a homogenisation of the sediment structure and an  
272 increase in density of surface sediments (Martín et al. 2014a, Pusceddu et al. 2014, Oberle et  
273 al. 2016b, Paradis et al. 2019). The sediment's vertical profile can also be altered, with an  
274 increase in coarse material towards the surface, caused by winnowing, resuspension and loss  
275 of fine material (Fig. 1c) (Martín et al. 2014a, Martín et al. 2014b, Palanques et al. 2014,  
276 Pusceddu et al. 2014, Mengual et al. 2016, Oberle et al. 2016b, Paradis et al. 2019). If the  
277 local hydrology is relatively depositional, the sediment may be overlain by a surface layer of  
278 fine material from the re-deposition of fine sediment which has been re-suspended from  
279 deeper layers (Palanques et al. 2014, Oberle et al. 2016b, Tiano et al. 2020). On the Northwest  
280 Iberian shelf, all these processes and impacts were identified within a study across different  
281 trawling intensities and environmental settings, highlighting the complexity in predicting fine-  
282 scale effects of mobile demersal fishing on sediment structure (Oberle et al. 2016b).

283

284 The loss of fine, flocculent material and OC-mineral interactions via mobile demersal fishing  
285 is another mechanism by which OC sequestration could be reduced (Fig. 1c) (Martín et al.  
286 2014b, Pusceddu et al. 2014, Oberle et al. 2016a). The physical mixing of surface sediments  
287 generally causes an increase in oxygen penetration (Martín et al. 2014a, Tiano et al. 2019,  
288 De Borger et al. 2021), resulting in reduced OC-mineral interactions (Arnarson and Keil 2007,  
289 Estes et al. 2019) and increased microbial respiration and remineralisation (Fig. 1c)  
290 (Kristensen et al. 1995, Dauwe et al. 2001, Keil 2017, van de Velde et al. 2018). The process  
291 of physical encapsulation of OC by sediment particles and the resultant protection from  
292 remineralisation, is seen as a key process in long term OC storage (Burdige 2007, Arndt et al.  
293 2013, Estes et al. 2019, LaRowe et al. 2020). For example, in sediment samples from the



294 Northeast Pacific coasts of Mexico and Washington state, 50% of the oldest OC stores were  
295 sorbed to mineral surfaces (Arnarson and Keil 2007).

296

297 Further, due to their often biological origin, fine grained sediments such as silts and clays  
298 typically have higher concentrations of OC compared to habitats dominated by sand and  
299 coarse sediment (Burdige 2007, Paradis et al. 2021, Smeaton et al. 2021). As mobile demersal  
300 fishing generally exposes or suspends fine material, this would tend to reduce overall OC  
301 storage through resuspension, oxidation and remineralisation (Fig. 1c). Finally, mobile  
302 demersal fishing can lead to “organic matter priming”, whereby more easily degraded “labile”  
303 OC at the surface is mixed with less easily degraded “recalcitrant” material. This can lead to  
304 significantly increased total OC remineralisation rates, although the process is known to vary  
305 between environmental settings (van Nugteren et al. 2009, Bengtsson et al. 2018, Riekenberg  
306 et al. 2020).

307

#### 308 **2.4 Sediment resuspension and transport**

309 Large volumes of seabed sediments are sufficiently dynamic to be moved laterally and  
310 vertically, and become resuspended in the water column by tides, waves and storms (Soulsby  
311 1997, Winterwerp and Kranenburg 2002, Ferré et al. 2008). Mobile demersal fishing activities  
312 have at times been shown to exceed, or be a large contributor to, the quantities of sediment  
313 displaced by natural forcing mechanisms (Jones 1992, Pusceddu et al. 2005b, Ferré et al.  
314 2008, Martín et al. 2014b, Pusceddu et al. 2015, Mengual et al. 2016, Oberle et al. 2016a,  
315 Paradis et al. 2018). Magnitudes involved are highly dependent on depth, gear and sediment  
316 type, with deeper penetrating gears and finer sediments causing larger dispersed volumes  
317 (Churchill 1989, Ruffin 1998, Durrieu de Madron et al. 2005, Pusceddu et al. 2005b, Ferré et  
318 al. 2008, O’Neill and Summerbell 2011, Martín et al. 2014b, Palanques et al. 2014, Mengual  
319 et al. 2016, Oberle et al. 2016a). Depending on local hydrographic conditions, sediment may  
320 remain in suspension for extended periods of time, and can be transported across large  
321 vertical and lateral distances (Durrieu de Madron et al. 2005, Martín et al. 2006, Palanques et  
322 al. 2006, Ferré et al. 2008, Martín et al. 2008, Martín et al. 2014b, Palanques et al. 2014,  
323 Pusceddu et al. 2015, Oberle et al. 2016a). In the Northern Mediterranean, otter trawling  
324 resulted in average suspended sediment concentrations ranging between 6 - 50 mg/l,  
325 depending on the study site (Palanques et al. 2001, Durrieu de Madron et al. 2005). The  
326 sediment within the water column was found to persist for up to five days (Palanques et al.  
327 2001), while off-shelf transport was 1.4 - 9 times higher when compared to sediment volumes  
328 without trawling (Ferré et al. 2008, Palanques et al. 2014). The loss of seabed topography, as  
329 discussed above (Puig et al. 2012, Martín et al. 2014b, Oberle et al. 2016b), may also alter

330 local-scale hydrographic conditions, increasing sediment boundary water flows and the  
331 magnitude of sediment resuspension (Smith and McLean 1977, Soulsby 1997).

332

333 Natural sediment disturbance during storms is known to stimulate increased water column  
334 microbial production (Cotner et al. 2000) and higher OC remineralisation rates (Wainright and  
335 Hopkinson Jr 1997, Pusceddu et al. 2005b). In general, the resuspension and transport of  
336 sediment from mobile demersal fishing will lead to a reduction in OC content (Pusceddu et al.  
337 2005b, Martín et al. 2006, Pusceddu et al. 2015), largely due to increased oxygen exposure  
338 times and shifts between anoxic and oxic states, which generally increase remineralisation  
339 rates (Fig. 1d) (Kristensen et al. 1995, Hulthe et al. 1998, Dauwe et al. 2001, Keil 2017).  
340 Aerobic remineralisation in marine sediments has been measured at between four and ten  
341 times faster than in anaerobic conditions, however this is known to vary depending on  
342 environmental settings (Kristensen et al. 1995, Hulthe et al. 1998). Fishing induced  
343 disturbance may further promote remineralisation, as sediment which is deposited under oxic  
344 conditions, buried under anoxia and re-exposed to oxygen can promote especially high OC  
345 degradation rates (Hulthe et al. 1998). This has been identified in the biochemical signature  
346 of suspended particulate OC within trawling grounds of the North Mediterranean, with a  
347 significant shift from labile to refractory OC compounds (Pusceddu et al. 2005a, Pusceddu et  
348 al. 2005b, Pusceddu et al. 2015).

349

350 Previous studies have shown that it is challenging to fully quantify the amount of OC that will  
351 be remineralised after disturbance, rather than simply being moved elsewhere (Wainright and  
352 Hopkinson Jr 1997, Pusceddu et al. 2005b, Martín et al. 2006, Martín et al. 2008, Lovelock et  
353 al. 2017). There is also the potential that sediment resuspension from mobile demersal fishing  
354 could increase OC storage in adjacent areas (Fig. 1d). This could occur from higher  
355 sedimentation rates near to fishing grounds leading to increased burial of OC which is already  
356 present within the seabed, or burial of benthic algae and sessile fauna (Churchill 1989, Jones  
357 1992, O'Neill and Summerbell 2011, Oberle et al. 2016a, Sciberras et al. 2016). It could also  
358 lead to transportation of OC-rich shelf and slope sediments (Atwood et al. 2020) to deeper  
359 waters below mixing depths (Fig. 1d) (Caldeira et al. 2002, Martín et al. 2006, Ferré et al.  
360 2008, Martín et al. 2008, Paradis et al. 2018, Legge et al. 2020). Such off-shelf induced  
361 transport of sediment and OC has been recorded as deep as 1750 m in continental slope  
362 trawling grounds of the Palamós canyon in the Northwest Mediterranean (Martín et al. 2006,  
363 Palanques et al. 2006, Martín et al. 2008).

364

365 Overall, increased sediment resuspension from mobile demersal fishing would be expected to  
366 reduce the current store of OC in seabed sediments due to disturbance of accumulations and

367 increased oxygen exposure times (Keil 2017, Luisetti et al. 2019, De Borger et al. 2021).  
368 Future sequestration would also be limited as newly settling organic material would be kept in  
369 suspension, precluding it from burial and storage (Churchill 1989, Ruffin 1998, Martín et al.  
370 2014b, Oberle et al. 2016a). The magnitude of impact, however, will be largely based on local  
371 hydrography, which primarily determines the fate of resuspended OC (Wainright and  
372 Hopkinson Jr 1997, Ferré et al. 2008).

373

## 374 **2.5 Alteration in pelagic primary production**

375 As most seabed OC is allochthonous, the total amount which reaches seabed sediments is  
376 strongly driven by the level of primary production in the overlying water column (Seiter et al.  
377 2004, Turner 2015, Atwood et al. 2020). As noted previously, sediment disturbance by mobile  
378 fishing gears, or natural forces, can release significant concentrations of nutrients into the  
379 water column (Fanning et al. 1982, Falcão et al. 2003, Polymenakou et al. 2005, Palanques  
380 et al. 2014). In shallower areas, released nutrients will likely enter into or remain in the euphotic  
381 zone, where their fertilisation effect can increase phytoplankton primary production (Fig. 1e),  
382 (Fanning et al. 1982, Dounas et al. 2007, Palanques et al. 2014). For example, modelling  
383 predictions from trawling experiments in the Eastern Mediterranean at Heraklion Bay, estimate  
384 that nutrient upwelling from bottom trawling could increase net annual primary production by  
385 15% (Dounas et al. 2007) with subsequent settlement raising OC in seabed sediments (Falcão  
386 et al. 2003, Polymenakou et al. 2005, Palanques et al. 2014, Turner 2015). Alongside this, as  
387 discussed for microphytobenthos, demersal fishing activity can also reduce rates of  
388 photosynthesis by increasing turbidity (Fig. 1e), (Ruffin 1998, Palanques et al. 2001, Adriano  
389 et al. 2005, Cloern et al. 2014).

390

## 391 **2.6 The contribution of vertebrate fauna to OC storage**

392 Although not a focus of this review, the removal of vertebrate species by benthic and pelagic  
393 fisheries could influence the mass of OC stored in seabed sediments (Pershing et al. 2010,  
394 Atwood et al. 2015, Mariani et al. 2020). The emerging field of “fish carbon” describes the  
395 contribution of vertebrate fauna to OC storage and sequestration within seabed sediments  
396 from defecation, pelagic mixing, bioturbation, trophic interactions and deadfall (Trueman et al.  
397 2014, Turner 2015, Saba et al. 2021). Although the magnitudes of effect are poorly resolved,  
398 the reduction in population size and average body size of marine vertebrates that results from  
399 over-harvest, is expected to reduce the amount of carbon exported to the seabed (Fig. 1f)  
400 (Pershing et al. 2010, Trueman et al. 2014, Atwood et al. 2015, Mariani et al. 2020). For  
401 example, since 1950, the combined catch of Tuna, Mackerel, Shark and Billfish is estimated  
402 to have prevented approximately 21.8 Mt of OC being stored in seabed sediments (Mariani et  
403 al. 2020). The removal of predatory vertebrates will also cause trophic cascades, potentially

404 leading to alterations in benthic faunal communities, triggering the feedback mechanisms on  
405 OC discussed above (Atwood et al. 2015).

406

## 407 **2.7 Interactions and feedback mechanisms**

408 All factors discussed here interact in a variety of positive and negative feedback loops. For  
409 example, alterations in sediment characteristics will influence the community structure of  
410 benthic flora and fauna, and vice versa. Additionally, pelagic primary production, trophic  
411 interactions, and the abundance and community composition of vertebrate fauna will all further  
412 alter benthic population changes induced by mobile demersal fishing. These factors are also  
413 influenced by chemical and physical oceanographic processes that are outside the scope of  
414 this review. The structure and diversity of the microbiome is also strongly influenced by the  
415 composition of benthic flora and fauna (Middelburg 2018, LaRowe et al. 2020, Rühl et al.  
416 2020). However, the microbiome itself can be impacted by mobile demersal fishing activities  
417 adding further complexity to the overall picture (Watling et al. 2001, Polymenakou et al. 2005).

418

## 419 **3. Experimental results**

420 From a systematic literature search (see Supplementary material), 40 peer-reviewed studies  
421 were identified which investigated the impact of mobile demersal fishing on the seabed, and  
422 directly measured OC or organic matter (OM) and/or remineralisation rates in seabed  
423 sediments (Table 1). The 40 studies covered 12 oceanic realms with greatest representation  
424 from the Northeast Atlantic (43%), Mediterranean (23%) and Northwest Atlantic (15%). The  
425 majority of studies (58%) investigated the impacts of commercial fishing activities. The  
426 remainder either used experimental trawling/dredging methods (33%), a mixture of  
427 experimental trawling and monitoring of commercial fishing (5%), or mathematical modelling  
428 of fishing impacts (5%). A variety of experimental setups were employed including impact-  
429 control site comparisons (43%), before-after fishing impact (23%), and low-high impact  
430 contrasts which lacked controls (20%). Additionally, 13% of studies used a before-after  
431 control-impact design either alone or in combination with an impact-control experiment; and  
432 one investigated the recovery of seabed sediment OC after a long-term closure to mobile  
433 demersal fishing (Table 1). It should be noted that for many of these studies, in areas  
434 considered “control sites” there is the potential for them to still be affected by mobile demersal  
435 fishing activities. This often occurs due to insufficient monitoring (e.g. no Vessel Monitoring  
436 System data on smaller vessels), lack of enforcement (i.e. within a supposed closed area) or  
437 lack of recovery time since cessation of fishing, particularly given the long timescales of  
438 recovery expected for many habitats (Roberts 2007).

439

440 Of the 40 studies identified, 11 investigated the effect of mobile demersal fishing across  
441 multiple sites, habitat types or gear-types, and made inferences for each investigation  
442 separately (Table 1); this produced a total of 62 experimental contrasts (Table S1). Of these,  
443 59 measured changes in OC/OM concentration. A finding of no significant effect was reported  
444 in 51% of contrasts; 41% reported lower OC in fished sites compared to unfished control sites  
445 (or in areas with higher fishing intensities), with 8% reporting higher OC (Table S1).

446

447 Studies which reported a negative impact from mobile demersal fishing on OC generally  
448 occurred in muddy sediments, while those which reported higher OC in response to this  
449 disturbance, or no effect, occurred in a mixture of sandy and muddy sediments (Table S1). On  
450 average, the duration of impact was higher for studies which reported a negative effect of  
451 demersal fishing on OC, when compared to those which reported a positive or non-significant  
452 effect, with estimated values of median impact duration at 36 months and 18 months  
453 respectively (Table S1). Most that reported a negative impact from demersal fishing were  
454 Impact-Control studies (75%) or Before-After fishing impact studies (13%). In contrast, those  
455 that reported no significant effects were predominantly Low-High impact studies lacking  
456 controls (43%) and Impact-Control studies (27%). The 5 studies which reported an increase  
457 in OC were relatively evenly spread between Impact-Control designs (60%) and Before-After  
458 designs (40%). The median depth at which the research was conducted was relatively similar  
459 between different experimental outcomes, with median depths of 22 m, 31 m and 20 m, for  
460 studies which reported a decrease, no significant effect, and an increase in OC respectively  
461 (Table S1).

462

463 Within the literature examined, there were 18 inferences about the impact of mobile demersal  
464 fishing pressure on sediment carbon remineralisation rate. Of these, 78% reported that  
465 demersal fishing activity decreased remineralisation rate in seabed sediments, with the rest  
466 concluding opposite (Table S1). Although no clear trend was identified between studies, it  
467 seems the result is highly dependent on local hydrographic conditions. For example, in more  
468 depositional environments, mobile demersal fishing may cause oxygenation of sediments and  
469 redeposition of recently expelled organic material back to the seabed, leading to an increase  
470 in remineralisation rate (Duplisea et al. 2001, Polymenakou et al. 2005, van de Velde et al.  
471 2018). In more hydrologically active environments, resuspension and lateral/vertical transport  
472 of sediments would be expected to reduce OC in surface sediments which, along with removal  
473 of fauna, could limit the rate of remineralisation (Pusceddu et al. 2014, Tiano et al. 2019, De  
474 Borger et al. 2021, Morys et al. 2021).

475

476 The evidence discussed earlier in Section 2 would suggest that removing or reducing  
477 demersal fishing pressure from the seabed would have net benefits to carbon sequestration  
478 and storage. However, the experimental results identified here indicate study-specific and site-  
479 specific outcomes. The majority of studies which identified no significant effect in sediment  
480 OC used an experimental design which compared sites with different magnitudes of fishing  
481 impact but lacked controls. There is a clear need for further identification and investigation of  
482 seabed sediment habitats that have had true long-term protection from demersal fishing.  
483 Those studies which reported an increase in OC, or no effect, also generally occurred in  
484 sandier sediments which may be subjected to higher levels of natural disturbance; however,  
485 as highlighted in this review, there will also be sandier areas where the impact of fishing activity  
486 outweighs natural forcing mechanisms. Finally, many of the studies identified in the systematic  
487 review were not primarily designed to investigate the impact of demersal fishing on carbon  
488 storage or remineralisation, although this may not affect the direction of their conclusions.

489

#### 490 **4. Future research**

491 As highlighted by the varied results, there is a clear need for further research into the potential  
492 impact of mobile demersal fishing on OC sequestration and storage in seabed sediments.  
493 Recent first order estimates have suggested that globally, mobile demersal fishing could  
494 remineralise between 160 - 400 Mt of OC from marine sediment stores annually (Sala et al.  
495 2021). It has also been suggested that historical trawling on global continental slopes could  
496 have removed ~6000 Mt of OC from the upper-most centimetre of sediment alone (Paradis et  
497 al. 2021). In addition, it has been estimated that ~2 Mt of OC is remineralised from UK shelf  
498 sediments each year by mobile demersal fishing (Luisetti et al. 2019). Although these  
499 estimates contain large generalisations, their scale reveals the massive potential for mobile  
500 demersal fishing to reduce carbon stores.

501

502 Following disturbance by mobile demersal fishing a proportion of OC will be remineralised in  
503 the benthos or in the water column, however some will simply remain in-situ and be re-buried,  
504 and a further proportion will be transported over a range of distances either being consumed  
505 or re-buried (Pendleton et al. 2012, Lovelock et al. 2017). A key research gap is the  
506 quantification of OC that follows each of these processes in different environmental settings  
507 and under different types of fishing impact. Sala et al. (2021) only account for remineralisation  
508 of disturbed OC which remains in-situ or resettles within 1 km<sup>2</sup>, as they consider the fate of  
509 sediment which stays in suspension as unknown. In their paper, Sala et al. (2021) consider  
510 that 87% of the OC disturbed remains in-situ or resettles uniformly across global fishing effort,  
511 and of this anything between 1-69.3% will be remineralised, with the magnitude dependent  
512 upon two relatively coarse metrics, namely: estimated proportion of OC which is labile, and

513 oceanic basin degradation rate. In contrast, Luisetti et al. (2019) use an upper estimate that  
514 100% of the OC resuspended by mobile demersal fishing will be remineralised, but they do  
515 not consider the fate of OC that is disturbed but remains in-situ. Although both studies give a  
516 representation to the scale of OC which may be lost, improved quantification of these metrics  
517 is clearly needed before accurate measures of OC lost, or inorganic carbon produced, can be  
518 quantified. OC in seabed sediments is not naturally inert, passing through a range of aerobic  
519 and anaerobic remineralisation pathways to varying sediment depths. Thus more  
520 consideration is needed to understand the influence of natural remineralisation rates within  
521 seabed sediments under different environmental settings, and therefore quantify the additional  
522 effect of mobile demersal fishing in each area. In seabed sediment habitats with high  
523 hydrodynamic activity, low deposition rates, and high oxygen penetration depths, the  
524 additional disturbance of demersal fishing on OC may be more limited.

525

526 We must also consider the cumulative or finite nature of disturbance by demersal mobile  
527 fishing on OC stores. It is not clear how much of the estimated 360 Gt of OC in the top 1 m of  
528 sediment is actually under threat (Atwood et al. 2020). While mobile demersal fishing can only  
529 penetrate between around 2 and 20 cm into the sediment (Hiddink et al. 2017), repeated  
530 chronic impacts may continue to disturb and displace sediment more deeply (Sala et al. 2021).  
531 It is possible, that in chronically fished areas significant further loss of OC stores will not occur  
532 due to historic depletion in OC stocks. However, in such areas carbon sequestration and  
533 accumulation of OC would be limited by the frequency of disturbance to newly settled material  
534 (Sala et al. 2021). By contrast, if new fishing grounds emerge, these could act as huge sources  
535 of carbon emissions as sediment becomes disturbed and OC is remineralised (Gogarty et al.  
536 2020).

537

538 There is also a need to identify a clear baseline from which changes in OC can be measured.  
539 Standing stock of OC in global seabed sediments is relatively well resolved at a number of  
540 spatial scales (e.g. Seiter et al. 2004, Lee et al. 2019, Luisetti et al. 2019, Atwood et al. 2020,  
541 Legge et al. 2020, Diesing et al. 2021, Smeaton et al. 2021). However, precise estimates of  
542 OC remineralisation, accumulation and burial rates are generally lacking (Berner 1982,  
543 Burdige 2007, Keil 2017, Wilkinson et al. 2018, Luisetti et al. 2019, Legge et al. 2020, Diesing  
544 et al. 2021). Any studies which aim to quantify the impact of demersal fishing on carbon  
545 storage and sequestration must therefore quantify both the before and after scenarios for  
546 robust conclusions to be drawn.

547

548 It is important that future research into the impact of mobile demersal fishing on carbon storage  
549 is focused in areas which are expected to contain significant stocks of OC or have large future

550 sequestration potential, based on their geographic projections (Atwood et al. 2020), sediment  
551 characteristics (Smeaton et al. 2021) and local hydrology (Lee et al. 2019). Research should  
552 also focus on areas that overlap with significant mobile demersal fishing pressure (Amoroso  
553 et al. 2018, Kroodsma et al. 2018, Sala et al. 2021), and where this can be compared to areas  
554 that could be considered truly “unfished”, either from well enforced protected areas or specific  
555 environmental settings.

556

557 On land, retrospective analyses of changes in human use and vegetation cover have been  
558 critical to estimating how people have altered the planetary carbon cycle. It is vital that this  
559 historical context is considered when further investigating the potential impact of mobile  
560 demersal fishing on global seabed OC sequestration and storage, and the opportunities for  
561 recovery if this pressure is removed. Due to the extended timeframes needed for some seabed  
562 habitats to fully recover, true long-term protection and monitoring of OC is needed to fully  
563 deduce carbon storage potential. Without considering areas of seabed that have experienced  
564 genuine long-term protection, it is not possible to gain a true baseline from which impacts can  
565 be compared (Pinnegar and Engelhard 2008). Within this review, only one study could be  
566 found which looked at the direct recovery of OC in seabed sediments following the medium-  
567 to-long term removal of fishing pressure (Wang et al. 2021). Gaining further evidence is vital  
568 to understand how much OC can accumulate when mobile demersal fishing is removed, and  
569 how this may change over the course of recovery.

570

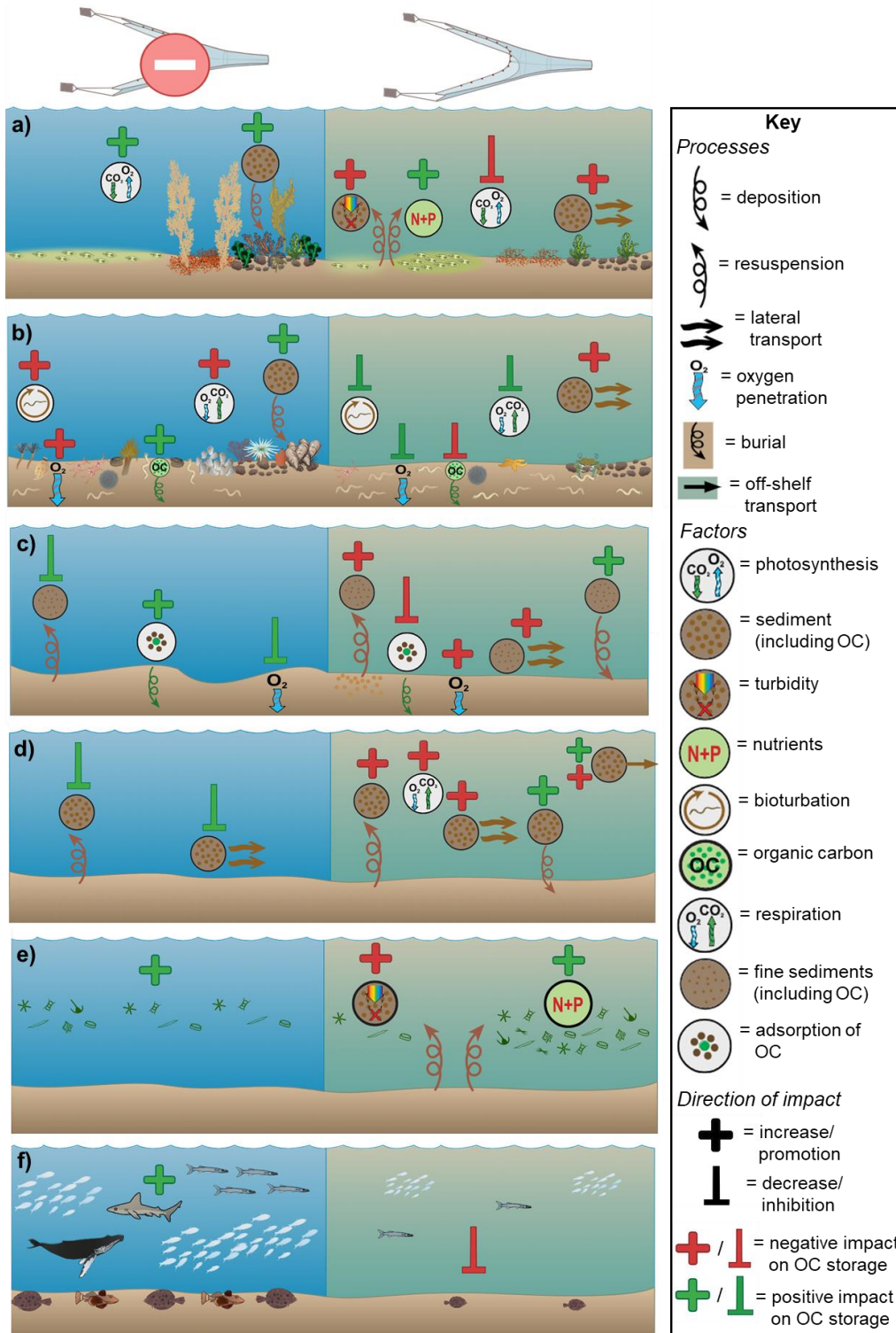
## 571 **5. Concluding remarks**

572 Seabed sediments are one of the planet’s primary OC stores and strongly influence the  
573 oceanic sink for atmospheric CO<sub>2</sub> (Gruber et al. 2019, Atwood et al. 2020, Watson et al. 2020,  
574 Sala et al. 2021). It is an urgent priority to better understand the effect of mobile fishing gear  
575 use on seabed OC sequestration and storage, and to incorporate clear blue carbon  
576 considerations into global seabed management. As only around 2-3% of the world’s seabed  
577 is currently closed to trawling and dredging (Roberts et al. 2017, Marine Conservation Institute  
578 2021), increasing the scale of protection could offer huge climate change mitigation potential  
579 and bring corresponding gains in biodiversity (Roberts et al. 2017, Seddon et al. 2019, Roberts  
580 et al. 2020, Sala et al. 2021). Across the world, mobile demersal fisheries are highly fuel  
581 inefficient and produce most of the fishing industry’s direct greenhouse gas emissions (Parker  
582 et al. 2018). A shift to less damaging fishing methods could provide major net benefits for  
583 increasing natural carbon sequestration and storage in the seabed, whilst significantly  
584 reducing emissions of CO<sub>2</sub>.

585



586 The results of recent regional and global scale publications which calculated first-order  
587 estimates of CO<sub>2</sub> produced from disturbance to seabed sediments by mobile demersal fishing  
588 must be taken with both concern and caution (Luisetti et al. 2019, Paradis et al. 2021, Sala et  
589 al. 2021). As identified in this review, demersal fishing by trawling and dredging is in many  
590 cases likely to limit the storage and sequestration of OC, but to draw firm conclusions more  
591 experimental studies covering a wide range of environmental settings, habitat types and  
592 fishing pressures is required to address the large number of unknowns and site-specific drivers  
593 associated with the status of OC on the seabed.  
594



595  
 596 **Figure 1.** The effects of mobile demersal fishing activity (right) and absence of demersal  
 597 fishing activity (left) on a) benthic algae, b) benthic infauna and epifauna, c) sediment  
 598 characteristics, d) sediment dynamics, e) pelagic primary production, f) vertebrate fauna, and  
 599 how each of these changes may impact seabed sediment organic carbon (OC) stores.  
 600 Addition symbols indicate when a factor/process would be expected to increase in the  
 601 presence/absence of fishing; inhibitory arrows indicate when a factor/process would be  
 602 expected to decrease. The colour of the addition/inhibition symbols indicates whether this  
 603 change is predicted to impact OC sequestration and storage either positively (green) or  
 604 negatively (red). Symbols courtesy of Integration and Application Network  
 605 ([ian.umces.edu/media-library](http://ian.umces.edu/media-library))

606 **Table 1.** Summary of studies which investigated the impact of mobile demersal fishing on the seabed  
 607 and directly measured organic carbon (OC) or organic matter (OM), and/or remineralisation rates of  
 608 OC/OM in the sediment. The last two columns indicate whether the presence or increase in demersal  
 609 fishing activity was reported to cause lower (red), higher (green), no significant effect (orange) or mixed  
 610 effects (grey) in the concentration or mass of OC/OM ("OC/OM"), or organic carbon remineralisation  
 611 rate ("Remin' rate"), within seabed sediments.

Reference	Oceanic region	Sediment	Depth (m BCD)	Gear	Study type	Impact type	Impact duration	Contrasts	OC/OM	Remin' rate
Adriano et al. (2005)	N Mediterranean	Sandy-mud	~1	Clam dredge	BA	Commercial fishing	5 yrs	1	Green	
Atkinson et al. (2011)	SE Atlantic	Muddy-sand	346-459	Otter-trawl	LH	Commercial fishing	1-4 yrs data	1	Yellow	
Bhagirathan et al. (2010)	N Indian	Mud	15-40	Otter-trawl	BA	Experimental	15 months	1	Red	
Brown et al. (2005)	NE Pacific	Muddy-sand	25-35	Otter-trawl	BACI IC	Experimental Commercial fishing	1 day 10 yrs	2	Yellow	
De Berger et al. (2021)	NE Atlantic	Mud & Sand	9-148	Mixed trawls	IC-LH	Modelled	15 yrs data	10	Red	Red
Dolmer et al. (2001)	NE Atlantic	Muddy-sand	7	Mussel dredge	IC	Experimental	< 1 month	1	Yellow	
Duplisea et al. (2001)	NE Atlantic	Muddy-sand	~50	Beam trawl	IC-LH	Modelled	n.d.	1		Green
Eleftheriou and Robertson (1992)	NE Atlantic	Sand	~7	Scallop dredge	BA	Experimental	9 days	1	Yellow	
Ferguson et al. (2020)	SW Pacific	Muddy-sand	4	Otter trawl	BACI	Experimental	3 months	1	Yellow	
Fiordelmondo et al. (2003)	N Mediterranean	Sand	~2	Clam dredge	IC	Experimental	1 day	1	Red	
Goldberg et al. (2014)	NW Atlantic	Fine sand	3-5	Hydraulic dredge	IC	Experimental	1 day	1	Yellow	
Hale et al. (2017)	NE Atlantic	Mud & Sand	19-29	Otter trawl & Scallop dredge	LH	Commercial fishing	2+ yrs data	2	Grey	
Lamarque et al. (2021)	NE Atlantic	Sandy-mud	33-78	Mixed trawls	LH	Commercial fishing	n.d.	1	*	
Lindeboom and de Groot (1998)	NE Atlantic	Mud & Sand	30-75	Mixed trawls	BACI IC	Experimental Commercial fishing	15 months 5-50 yrs	3	Yellow	
Liu et al. (2011)	W Pacific	Sandy-mud	20	Mixed trawls	IC	Commercial fishing	1-2 yrs	1	Green	
Martín et al. (2014a)	NW Mediterranean	Mud	453-591	Otter trawl	IC	Commercial fishing	3+ yrs data	1	Red	
Mayer et al. (1991)	NW Atlantic	Mud & Mixed	8-20	Otter trawl & Scallop dredge	IC	Experimental	1 day	2	Grey	
McLavery et al. (2020)	NE Atlantic	Sandy-mud	3-11	Mussel dredge	LH	Commercial fishing	1.5 yrs data	4	*	
Mercaldo-Allen et al. (2016)	NW Atlantic	Fine sand	3-5	Hydraulic dredge	IC	Experimental	1 day	1	Green	
Meseck et al. (2014)	NW Atlantic	Fine sand	5-6	Hydraulic dredge	BACI	Experimental	1 day	1	Yellow	
Morys et al. (2021)	Baltic	Muddy-sand	12	Benthic Dredge	IC	Experimental	1 day	1	Red	Red
Palanques et al. (2014)	NW Mediterranean	Mud	40-70	Otter trawl	IC	Commercial fishing	2 yrs data	1	Green	
Paradis et al. (2019)	SW Mediterranean	Mud	550	Otter trawl	IC	Commercial fishing	9 yrs data	1	Red	Green
Paradis et al. (2021)	NW Mediterranean	Mud	425-494	Otter trawl	IC	Commercial fishing	1+ yrs data	1	Red	
Polymenakou et al. (2005)	NE Mediterranean	Sandy-mud	30-51	Otter trawl	BA	Commercial fishing	8 months	1		Green
Pusceddu et al. (2005a)	NE Mediterranean	Sandy-mud	30-80	Otter trawl	BA	Commercial fishing	8 months	1	Green	
Pusceddu et al. (2014)	NW Mediterranean	Mud	454-556	Otter trawl	IC	Commercial fishing	3 yrs data	1	Red	Red
Rajesh et al. (2019)	N Indian	Sand	5-35	Beam trawl	BA	Experimental	4 days	2	Red	
Ramalho et al. (2018)	NE Atlantic	Muddy-sand	285-550	Otter trawl	IC	Commercial fishing	2+ yrs data	1	Red	
Ramalho et al. (2020)	NE Atlantic	Muddy-sand	285-550	Otter trawl	LH	Commercial fishing	2+ yrs data	1	Yellow	
Rosli et al. (2016)	SW Pacific	Sandy-mud	670-1561	Otter trawl	LH	Commercial fishing	31 yrs data	2	*	
Sciberras et al. (2016)	NE Atlantic	Mud & Sand	20-43	Otter trawl & Scallop dredge	LH	Commercial fishing	3 yrs data	2	Yellow	
Serpetti et al. (2013)	NE Atlantic	Muddy-sand	769-823	Mixed trawls	IC	Commercial fishing	~10 yrs	1	Yellow	
Sheridan and Doerr (2005)	NW Atlantic	Mud & Sand	5-20	Otter trawl	IC	Commercial fishing	7 months	1	Yellow	
Smith (2000)	NE Mediterranean	Sandy-mud	~200	Otter trawl	BACI	Commercial fishing	7 months data	1		
Tiano et al. (2019)	NE Atlantic	Muddy-sand	34	Mixed trawls	BA	Experimental	1 day	2	Yellow	Red
Trimmer et al. (2005)	NE Atlantic	Muddy-sand	~20-80	Beam trawl	LH	Commercial fishing	3 yrs data	2	*	
van de Velde et al. (2018)	NE Atlantic	Mud	~7	Unknown	BA	Commercial fishing	< 1 month	1		Green
Wang et al. (2021)	W Pacific	Mud & Sand	1-28	Mixed trawls	Recovery	Commercial fishing	2.5 yrs	1	Red	
Watling et al. (2001)	NW Atlantic	Muddy-sand	15	Scallop dredge	BA	Experimental	1 day	1	*	

612 For "Study type": BA = Before-after fishing impact, IC = Impact-control site comparison, LH = low to high impacted sites, BACI = before-after control-  
 613 impact, "Recovery" = change after removal of commercial fishing. For "Impact duration": those suffixed with "data" indicate where the exact duration  
 614 of impact is unknown and the stated time is the period for which data was available "Contrasts" = the number of experimental contrasts conducted  
 615 in each study. For "OC/OM" those with an asterisk (\*) indicate where further analysis was needed – see Supplementary material. The "OC/OM"  
 616 column is empty for Polymenakou et al. (2005) as the result was based on the same data which is reported in Pusceddu et al. (2005a). n.d. = no  
 617 data.

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