



Impacts of Bottom Fishing on Sediment Biogeochemical and Biological Parameters in Cohesive and Non-cohesive Sediments

Sciberras, Marija; Parker, Ruth; Powell, Claire; Robertson, Craig; Kroger, Silke; Bolam, Stefan; Hiddink, Jan

Limnology and Oceanography

DOI:

[10.1002/lno.10354](https://doi.org/10.1002/lno.10354)

Published: 01/11/2016

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):

Sciberras, M., Parker, R., Powell, C., Robertson, C., Kroger, S., Bolam, S., & Hiddink, J. (2016). Impacts of Bottom Fishing on Sediment Biogeochemical and Biological Parameters in Cohesive and Non-cohesive Sediments. *Limnology and Oceanography*, 61(6), 2076-2089. <https://doi.org/10.1002/lno.10354>

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1 **Impacts of bottom fishing on the sediment infaunal community and biogeochemistry of**
2 **cohesive and non-cohesive sediments**

3

4 Marija Sciberras¹, Ruth Parker², Claire Powell², Craig Robertson¹, Silke Kröger², Stefan Bolam²,
5 Jan Geert Hiddink¹

6

7 ¹School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey, LL59 5AB, United
8 Kingdom, +44 (0)1248 388150

9

10 ²Centre for Environment, Fisheries and Aquaculture Science, Pakefield Road, Lowestoft,
11 Suffolk, NR33 0HT, United Kingdom

12

13 Corresponding author

14 email: m.sciberras@bangor.ac.uk

15 T: (0044) 01248388150

16

17

18 **Keywords**

19 benthic infauna, bioturbation, ecosystem approach to fisheries management, ecosystem
20 functioning, nutrient cycling, trawling, dredging, biogeochemistry, fishing impact, soft
21 sediments, community bioturbation potential

22

23

24 **Abstract**

25

26 Bottom-trawl fisheries are wide-spread and have large effects on benthic ecosystems. We
27 investigate the effect of scallop dredging on sand and otter trawling on mud by measuring
28 changes in the infaunal community and the biogeochemical processes which they mediate. We
29 hypothesize that changes in biogeochemistry due to fishing will be larger in mud where
30 macrofauna-mediated processes are expected to play a greater role, than in sand where
31 hydrodynamics mediate the redox system. We sampled benthic infauna, sediment pore-water
32 nutrients, oxygen, chlorophyll-*a*, apparent redox potential discontinuity layer, organic carbon and
33 nitrogen content over a gradient of fishing intensity in sand and mud. The effects of fishing on
34 biogeochemistry were stronger on mud than on sand, where biogeochemistry appeared to be
35 more strongly influenced by tidal currents and waves. On mud, trawling increased sediment-
36 surface chlorophyll-*a* and ammonium concentration beyond 5 cm depth, but decreased
37 ammonium and silicate concentration in the upper sediment layers. The effects of fauna and
38 bioturbation potential on biogeochemistry were very limited in both mud and sand habitats. Our
39 results suggests that otter trawling may be affecting organic-matter remineralization and nutrient
40 cycling through sediment resuspension and burial of organic matter to depth rather than through
41 the loss of bioturbation potential of the benthic community. In conclusion, our hypothesis that
42 the effects of trawling on biogeochemistry are larger in mud is supported, but the hypothesis that
43 these effects are mediated by changes in the infauna is not supported. These results imply that
44 management of trawling on muddy sediments should have higher priority.

45

46 Introduction

47

48 Fishing with bottom towed fishing gear is a major source of physical disturbance for marine
49 benthic ecosystems. Large parts of most shelf and deep seas have been intensively exploited by
50 bottom fishing for decades (Halpern et al. 2008; Puig et al. 2012). As nets, beams, trawl doors,
51 chains and dredges pass over the seabed, the sediment surface is disturbed and 20 – 50 % of the
52 resident biota (e.g. bivalves, burrowing crustaceans, tube-building polychaetes and echinoderms)
53 is damaged or removed (Jennings and Kaiser 1998; Kaiser et al. 2006). Previous studies have
54 shown that bottom fishing results in a decrease in benthic secondary production, as well as
55 changes in the community structure and size composition of benthic invertebrate communities
56 (Hiddink et al. 2006; Hinz et al. 2009; Bolam et al. 2014a). Shifts towards higher abundances of
57 scavenging and deposit feeding organisms and small-bodied infaunal species have also been
58 reported due to trawling (Kaiser et al. 2000; Tillin et al. 2006).

59

60 In addition to changes to benthic faunal communities, bottom fishing can alter the
61 biogeochemical characteristics of the sediment and that of the overlying water column through a
62 combination of the removal of surficial sediments and the burial or mixing of organic matter
63 (Duplisea et al. 2001; Warnken et al. 2003; O'Neill and Summerbell 2011). The resuspended
64 sediment created by groundropes, chains and nets as bottom trawls are dragged along the seabed
65 increases the water turbidity and the concentration of particulate organic matter in the overlying
66 water and may enhance phytoplankton primary production due to higher nutrient loads (Riemann
67 and Hoffman 1991; Pilskaln et al. 1998; Palanques et al. 2001). Changes within the sediment
68 matrix, such as an increase in sediment sorting and porosity (Trimmer et al. 2005) can result in

69 changes to the oxygen regime (Warnken et al. 2003), which may influence key steps in the
70 nitrogen cycle, as oxygen regulates both nitrification and denitrification in benthic sediments
71 (Rysgaard et al. 1994). Because of their weight, otter trawl boards and dredges create large
72 furrows in the sea floor that range between 5 and 35 cm deep depending on the type of sediment
73 (Eigaard et al. 2015). The redistribution of organic matter that results from this ploughing action
74 may shift the balance between aerobic and anaerobic mineralization, as the organic matter is
75 buried beneath the narrow oxic zone before mineralization is complete (Mayer et al. 1991;
76 Pilskaln et al. 1998). Duplisea et al. (2001) and Trimmer et al. (2005) found higher rates of
77 organic matter remineralization via sulphate reduction at high trawling disturbance areas.

78

79 Indirectly, bottom fishing may affect the oxygen regime and biogeochemical processing of
80 carbon by altering the composition of the benthic fauna, which itself regulates oxygen and redox
81 structure through bioturbation and bioirrigation (Kristensen 2000; Duplisea et al. 2001;
82 Waldbusser et al. 2004). Mesocosm experiments by Olsgard et al. (2008) showed that the
83 reduction of large-bodied bioturbators such as the surficial modifiers *Brissopsis lyrifera* and
84 *Nuculana minuta*, resulted in a lower efflux of silicate (SiO_4^-) and nitrate/nitrite (NO_x) from the
85 sediment to the overlying water. Declines in the density of burrow- and tube-building organisms
86 may result in changes to benthic respiration and denitrification due to a reduction in oxygen
87 penetration and microbial metabolism (Aller and Aller 1998; Braeckman et al. 2010). It may
88 therefore be expected that trawling will affect sediment chemistry through a reduction in
89 community bioturbation potential, burrow density and functional diversity.

90

91 Habitat characteristics may be strong determinants of the relative impact of bottom fishing
92 activity on both the infauna and sediment biogeochemical processes. For example, the effects of
93 bottom fishing on benthic carbon mineralization and sediment characteristics (e.g. particle size
94 distribution, porosity) have been demonstrated to be smaller in highly natural disturbed areas
95 where wave and tidal actions lead to bulk sediment disturbance and transport (Osinga et al. 1996;
96 Trimmer et al. 2005). Similarly, several studies have shown that the effects of fishing on fauna
97 are smaller in coarse than fine sediment (Collie et al. 2000; Kaiser et al. 2006; references
98 therein), as the former are characterized by a higher fraction of small-sized, fast growing and
99 highly productive species that are more adapted to continual natural disturbance by tides and
100 waves (Kaiser and Spencer 1996). Experiments have shown that the influence of bioturbation on
101 nutrient regeneration and oxygen consumption is greater in diffusion dominated (low
102 disturbance, fine sediments and low rates of sediment pore water exchange) than in advection
103 dominated (high disturbance, coarse sediments and consequently high rates of sediment pore
104 water exchange) systems, as sediment processes in the former are more strongly influenced by
105 bioturbation (reviewed by Mermillod-Blondin and Rosenberg 2006). It may therefore be
106 expected that trawling disturbance will have stronger effects on the fauna and biogeochemical
107 processes in mud than on sand by altering diffusion of dissolved oxygen from the sediment-
108 overlying seawater into the pore water and oxygenation of the sediment pore water by sediment
109 resuspension.

110

111 Few empirical studies to date have investigated the combined effects of bottom fishing on both
112 the infaunal community and the biogeochemical processes which they mediate (Pilskaln et al.
113 1998; Duplisea et al. 2001; Waldbusser et al. 2004; Hiddink et al. 2006), and this is important for

114 understanding the impacts of fishing on ecosystem functioning. This study fills this knowledge
115 gap by assessing the large-scale impact of chronic bottom fishing on benthic community
116 structure and sediment biogeochemistry across different fishing pressure gradients and habitat
117 types (muddy vs. sandy habitats). The following hypotheses are tested; (i) fishing will negatively
118 affect benthic invertebrate abundance and reduce the bioturbation potential of the community as
119 large bioturbatory macrofaunal species are removed by trawling; (ii) fishing will result in
120 changes in the sediment redox and associated biogeochemistry as a result of sediment
121 resuspension (e.g. lower concentration of NH_4^+ in upper sediment layers) and sediment/carbon
122 mixing to depth (e.g. higher concentration of NH_4^+ in pore-water); (iii) changes in sediment
123 biogeochemistry due to fishing will be larger in mud where macrofauna-mediated processes are
124 expected to play a more significant role, than in sand where physical processes such as tides and
125 currents generally mediate the redox system.

126

127 **Methods**

128

129 The effects of chronic bottom fishing on benthic infauna and sediment biogeochemistry were
130 investigated over gradients of commercial bottom fishing intensity on muddy and sandy fishing
131 grounds in the north Irish Sea between the 28th June and 6th July 2014 (Fig.1). The sandy fishing
132 ground was located off the east coast of the Isle of Man where scallop dredging for *Pecten*
133 *maximus* and some otter trawling for *Aequipecten opercularis* occurs. Scallop dredging occurs
134 between May and November, whereas otter trawling occurs between June and October (Murray
135 et al. 2010; Dignan et al. 2014). Within the Isle of Man territorial waters trawling is traditionally
136 conducted by vessels fishing with single rig otter trawls with net openings of 18m to 32m

137 (Dignan et al. 2014). Scallop dredgers are allowed a maximum number of 8 dredges per side,
138 with a maximum number of 9 teeth per dredge each 110mm in length (Murray et al. 2010). The
139 muddy fishing ground was located off the coast of Cumbria, England, where otter trawling for
140 *Nephrops norvegicus* and gadoid fish occurs. The fishery operates throughout the year with a
141 peak activity from spring to early summer (Hinz et al. 2009). Vessels are limited to operate otter
142 trawls with a maximum headline length of 9m (NWIFCA 2013, pers. comm.). These areas were
143 selected because both of them showed a spatial gradient in fishing pressure within areas of
144 homogenous sediment types (Supplementary material, SM 1). Other habitat characteristics were
145 similar between the two areas (water depth, bottom temperature and tidal currents) (SM 1).

146

147 **Station selection**

148

149 Within each of the two areas, sixteen 1 x 2 km sites were selected along a gradient of fishing
150 pressure. Sampling site selection was based on existing knowledge of sediment type and water
151 depth (CEFAS, unpubl. data and information available in British Geological Survey maps) and
152 natural tidal and wave bed-stress to ensure comparability. The average (\pm SE) water depth at the
153 muddy study sites was 35.5 ± 3.8 m, whilst that at the sandy sites was 26.3 ± 4.0 m (SM 1). Bed
154 shear stress was used as a measure of natural disturbance to quantify tidally generated currents
155 and wave action that affect sediment transport by advection and hence the structure of the
156 invertebrate community. Estimates of the mean tidal- and wave-bed shear stress (Nm^{-2}) at the
157 study sites were derived from a two-dimensional hydrographical model of the Irish Sea (detailed
158 description on shear stress calculations in Hiddink et al. 2006), and ranged between 0.11 - 0.25
159 Nm^{-2} and 0.4 – 1.4 Nm^{-2} , respectively (SM 1).

160

161 The fishing pressure at each of the 32 stations was estimated by computing the accumulated
162 swept areas within a year from all the bottom-contact fishing gears (otter and bottom pair trawls,
163 scallop dredges) by vessels larger than 15 m registered to fish in UK waters. In order to obtain a
164 measure of the chronic disturbance experienced at the two study areas, fishing pressure estimates
165 were calculated from Vessel Monitoring System (VMS) data averaged over a three year period
166 before the study was conducted. At the time of site selection, VMS data for the period January
167 2009 to December 2011 were available for the sandy study area and for the period January 2010
168 to December 2012 for the muddy study area. VMS data were combined with logbook data (that
169 provide information on the number of hours of fishing and average vessel speed during fishing),
170 together with estimates of the dimensions of the different gear components to calculate the total
171 seabed area swept (km^2) by a fishing gear per annum (for details refer to Hintzen et al. 2012;
172 Eigaard et al. 2015). Fishing pressure is defined as the number of times an area is swept by
173 bottom gear in a year (km^2 swept km^{-2} seabed), and is hereafter referred to as fishing frequency.
174 Owing to the exemption of vessels smaller than 15 m from the VMS reporting process of
175 positional information, the estimates of fishing frequency may be underestimates of the actual
176 fishing intensity, however these are still useful indicators of the relative fishing pressure at the
177 sampled sites.

178

179 **Sampling of invertebrate populations and sediment biogeochemistry**

180

181 Three sediment cores with overlying water were collected at random locations within each
182 sampling site using a 0.1 m^2 NIOZ (Netherlands Institute for Sea Research, Texel) corer. The

183 corer (30 cm internal diameter) collected sediment to a maximum depth of 50 cm, depending on
184 sediment hardness. Only intact cores with overlying water were used, as drainage of water would
185 disturb biogeochemical profiles. Oxygen profile readings and pore-water nutrient samples were
186 collected from one of the three cores collected at each sampling site, chlorophyll-*a* and organic
187 carbon and nitrogen content were determined for two replicate cores and sediment particle size
188 analysis (PSA) and infauna composition from all three cores.

189

190 **Oxygen profiles**

191

192 To measure benthic oxygen status, a 10 cm wide by 30 cm long sediment Perspex sub-core was
193 sampled from the NIOZ core to collect sediment together with the overlying water. Sediment
194 oxygen concentration profiles were measured immediately after collection using Clarke-type
195 oxygen microelectrodes from Unisense (Revsbech 1989). Two profiles were taken for each sub-
196 core. The oxygen penetration depth (OPD), which is the depth to which free oxygen is present in
197 the sediment, was estimated as the deepest depth at which oxygen saturation above 0% was
198 observed using a method adapted from Rabouille et al. (2003).

199

200 **Particle size analysis (PSA), porosity, chlorophyll-*a* and organic carbon analysis**

201

202 5 cm diameter sediment sub-cores were collected for PSA and for porosity, chlorophyll-*a* and
203 organic carbon and nitrogen analysis. Sub-cores were frozen at -20 °C upon collection and
204 transported to the laboratory for analysis. A combination of dry sieving and laser diffraction
205 techniques were used to produce a complete particle size distribution for sediment particles

206 larger and smaller than 1 mm, respectively. Porosity was calculated following methods described
207 by Holme and McIntyre (1984). Sediment chlorophyll-*a* was extracted from the thawed sub-
208 cores using acetone and analysed using a fluorometer as described by Tett (1987). Samples for
209 the analysis of sediment organic carbon and nitrogen were thawed, freeze dried and acidified as
210 described in Hedges and Stern (1984). Organic carbon and nitrogen content was then determined
211 using a Thermo-Finnigan elemental analyser.

212

213 **Pore-water nutrient profile data**

214

215 Samples for pore-water nutrients were extracted using a sipping system from intact NIOZ cores
216 at the following sediment depths; 0, 1, 2, 3, 4, 5, 7.5, 10, 14, 17, 20 cm (D. B. Sivyer unpubl.).
217 The extracted water samples were filtered using 0.2 µm filters and analysed for nitrate, nitrite,
218 ammonium, silicate and phosphate using a scalar auto-analyser (Kirkwood et al. 1996). At the
219 sandy sites, the deepest pore-water sample was taken at 14 cm as the NIOZ corer generally
220 penetrated to about 15 cm in sand.

221

222 **Infauna**

223

224 Following removal of the sub-cores for the non-faunal sediment samples (above), the rest of the
225 core sample was sieved over a 1 mm sieve and the benthic invertebrates collected were fixed and
226 preserved in 4 % formaldehyde solution for subsequent identification. In the laboratory, all
227 invertebrates were identified to the highest practicable taxonomic resolution (mostly species) and
228 the wet weight of each individual organism was measured after blotting.

229

230 The sediment within the sub-core used for oxygen measurements (ca. 0.16 m³, equivalent to ca.
231 35 % of the total core sample) was also sieved over a 1mm sieve and the infauna preserved in 4
232 % formaldehyde solution. However, the volume of sediment removed for PSA, chlorophyll-*a*,
233 porosity and organic carbon and nitrogen was small (0.018 m³, equivalent to ca. 4 % of total core
234 sample) and was assumed to have negligible contribution to overall infauna abundance and
235 biomass. Furthermore, the freezing and thawing process damages animal tissue hence making the
236 process of species identification difficult. Therefore, sediment sub-samples collected for PSA,
237 chlorophyll-*a*, porosity and organic carbon and nitrogen were not processed for infauna.

238

239 **Sediment Profile Images**

240

241 A Sediment Profile Imagery (SPI) camera was deployed five times at each station to obtain
242 estimates of the depth of the apparent redox potential discontinuity (aRPD) layer, which is the
243 depth at which the sediment transitions from an oxidising to a reducing environment, as
244 determined by the Fe³⁺/Fe²⁺ colour boundary. Penetration depth (the depth that the SPI prism had
245 penetrated the sediment surface) and the depth of the aRPD layer were measured from the
246 images using the NIH software ImageJ as described in Teal et al. (2010).

247

248 **Analyses**

249 **Environmental conditions at the sampling sites**

250

251 Station characteristics were reviewed after the survey with the most up to date fishing frequency
252 estimates and actual sediment composition information collected during the survey (PSA and
253 water depth data). Multi-Dimensional Scaling (MDS) of normalized environmental variables (%
254 sand, % mud, water depth, tide stress and wave stress) was used to exclude outlier stations in
255 terms of the environmental variables examined. Further, we carried out correlation tests using
256 Pearson's coefficient to identify sites that contributed to a significant correlation between fishing
257 frequency and each of the environmental variables mentioned above. These sites were removed
258 to avoid confounding the effect of fishing with that of other environmental variables. Out of a
259 total of 32 sites that were sampled during the survey, 19 sites were retained for statistical
260 analyses; 11 sites from the muddy study area and 8 sites from the sandy area. The environmental
261 parameters (water depth, tide and wave bed stress, % sediment grain size composition) at these
262 19 stations were not significantly correlated to fishing frequency (see SM 2).

263

264 **Effect of fishing on faunal parameters**

265

266 Analyses exploring the relationship between different faunal parameters (total infaunal density
267 and biomass, species trait-specific biomass) and fishing frequency (yr^{-1}) were performed using
268 General Linear Models (glm package) in R v.3.0.3. A Gaussian error distribution was used for
269 each model. Homogeneity of residuals was established through visual examination of plotted
270 standardized residuals versus fitted values. Data was log-transformed whenever homogeneity of
271 variance was violated. Mean and standard error value (Mean \pm SE) are provided throughout the
272 text.

273

274 The community bioturbation potential (BP_C), first described by Solan et al. (2004), was used to
275 estimate how the potential of the benthic assemblages to regulate ecosystem processes through
276 their sediment reworking activities is influenced by fishing. This metric combines abundance
277 (A_i) and biomass (B_i) with information about the behavioural traits of individual species that are
278 known to regulate biological sediment mixing; R_i describes modes of sediment reworking and M_i
279 describes levels of motility of the taxa in the assemblage (Solan et al. 2004). Values for R_i and M_i
280 were obtained from Queiros et al. (2013). The community bioturbation potential, BP_C , was
281 calculated as follows (Queiros et al. 2013):

282

$$BP_C = \sum_{i=1}^n \sqrt{\frac{B_i}{A_i}} \times A_i \times M_i \times R_i$$

283

284 Additionally, the influence of fishing on species with different biological traits was examined.
285 Three traits that may influence the vulnerability of species to fishing or influence sediment
286 processes (e.g. nutrient cycling) through changes in macrofauna composition and/or abundance
287 were selected, namely feeding mode, mobility and mode of bioturbation. ‘Modalities’ within
288 each trait were chosen to encompass the range of possible attributes of all the taxa; for example,
289 modalities for mobility were ‘swimming’, ‘burrowing’, ‘crawling’ and ‘sessile’. A full
290 description of the modalities within each trait category is given in SM 3. Traits information was
291 obtained from the biological traits database generated from the BENTHIS project (Bolam et al.
292 2014b, <http://www.benthis.eu/en/benthis/Results.htm>, accessed 25 September 2015). The
293 biomass of species within each trait and modality class was summed to obtain the total biomass
294 of organisms within the different modalities (e.g. total biomass of sessile species). A GLM

295 model with interaction [$\log(\text{biomass}) \sim \text{fishing} * \text{modality}$] was fitted for each of these traits to
296 assess how the response to fishing disturbance changes among species with different trait
297 characteristics.

298

299 **Effect of fishing on biogeochemical parameters**

300

301 The effect of fishing on the bulk biogeochemical properties of the upper 5 cm of the sediment
302 (chlorophyll-*a*, organic carbon and nitrogen content, porosity, OPD and aRPD) was examined
303 using General Linear Models (GLMs). Pore-water nutrient profile concentrations were integrated
304 into three depth categories that represent the observed general zonation in sediment chemistry
305 due to natural (i.e. macrofauna) and anthropogenic (i.e. bottom fishing) factors. Whilst we
306 acknowledge that oxidation zones will be shallower in mud and potentially deeper in sand, we
307 use similar zone intervals across the two sediment types for comparability across the regions and
308 sediment types. We use a generic conceptual zonation pattern (rather than site-specific zonation)
309 to illustrate broad differences in the effect of fishing on different depth zone-related processes in
310 the two sediment types. We believe that findings from this approach have wider generalizability
311 and applicability than a site-specific approach. The depth categories examined were as follows:

312 (i) *0 – 2 cm*: according to the OPD and aRPD measurements at the study sites this is

313 predominantly the *oxic* zone where there is still free oxygen which acts as the electron acceptor
314 and where oxidation of ammonium (NH_4^+) to nitrate (NO_3^-) leads to low concentration of NH_4^+
315 in this layer. Changes in this zone may be driven by faunal respiration (as seen in OPD data),

316 organic matter input or sediment resuspension or mixing due to fishing; (ii) *2 – 5 cm*:

317 *anoxic/suboxic* zone where free oxygen is no longer available and organic matter breakdown is

318 through NO_3^- , manganese (Mn) and iron (Fe) cycles. Denitrification processes result in low
319 concentration of TOxN (Total Oxidised Nitrogen – NO_3^- and NO_2^-) but organic matter
320 breakdown can induce higher NH_4^+ in this layer. Fishing is likely to affect the biogeochemistry
321 of the sediment at this depth by removing and/or reducing macrofauna that play a critical role in
322 sediment mixing and often linked to the aRPD or Biological Mixing Depth (BMD); (iii) 5 – 20
323 cm: *fully anoxic* zone where oxygen is depleted and sulphate (SO_4^{2-}) is mainly used as the
324 electron acceptor. NO_3^- concentration in pore-water is low at these depths but NH_4^+ increases as a
325 result of organic matter degradation in a reducing environment. Bottom fishing may have an
326 effect on the biogeochemistry in this zone by increasing organic matter supply by sediment and
327 carbon burial to depth. Macrofaunal influences are expected to be minimal at this zone because
328 the sediment is too anoxic for most macrofauna to survive, unless they are deep sediment
329 burrowers. GLM models with interaction [$\log(\text{nutrient concentration}) \sim \text{fishing} * \text{depth zone}$]
330 were examined for each of the nutrients to assess how the response to fishing disturbance
331 changes with sediment depth.

332

333 Direct statistical comparisons of the relationship between response and predictor variable in mud
334 and sand was not attempted as the overlap in the range of fishing frequencies between the two
335 study areas was only limited. All analyses were based on the mean values for each variable at
336 each sampling site.

337

338 **Results**

339

340 The muddy sites were composed of more than 60% mud ($< 63 \mu\text{m}$) and the sediment was poorly
341 sorted, whereas the sandy sites were composed of more than 95% sand ($> 63 \mu\text{m}$ and < 2000
342 μm) and the sediment was moderately well sorted (SM 1). The fishing frequencies between the
343 two study areas did not overlap; the fishing frequency ranged from 2.95 to 8.51 yr^{-1} at the muddy
344 sites and from 0 to 1.63 yr^{-1} at the sandy sites (SM 1).

345

346 **Effect of fishing on faunal parameters**

347

348 There was no significant effect of fishing on total infaunal abundance or biomass in either mud
349 (abundance: $t = 0.39$, $df = 9$, $p = 0.71$, $r^2 = 0.02$; biomass: $t = 0.27$, $df = 9$, $p = 0.79$, $r^2 = 0.01$) or
350 sand (abundance: $t < 0.001$, $df = 6$, $p = 0.99$, $r^2 < 0.001$; biomass: $t = 1.73$, $df = 6$, $p = 0.13$, $r^2 =$
351 0.33) (Fig.2a, b). The infaunal community in mud was dominated by fewer species but larger
352 individuals, whereas the sand community was characterized by a more diverse assemblage of
353 smaller individuals. The average total infaunal density and biomass in sand were 198.14 ± 27.14
354 individuals m^{-2} and $1.54 \pm 0.29 \text{ g WW m}^{-2}$, respectively (Fig.2a, b). In mud, the average infaunal
355 density and biomass were 34.69 ± 2.46 individuals m^{-2} and $5.29 \pm 0.99 \text{ g WW m}^{-2}$, respectively
356 (Fig.2a, b). The community bioturbation potential index (BP_C) was similar between the two
357 sediment types and did not change significantly with fishing frequency in mud ($t = 0.12$, $df = 9$, p
358 $= 0.90$, $r^2 = 0.01$) and sand ($t = 0.88$, $df = 6$, $p = 0.41$, $r^2 = 0.11$) (Fig.2c). However, different
359 sediment reworking functional groups dominated the community in sand and mud; regenerator
360 and biodiffusor species such as the polychaetes *Maxmuelleria lankesteri* and *Nephtys incisa*, and
361 the malacostracan *Callianassa subterranea* dominated the total community biomass at the
362 muddy sites, whereas surficial modifiers such as the bivalves *Lucinoma borealis* and *Ensis ensis*,

363 the echinoderms *Astropecten irregularis* and *Labidoplax* sp. and the phoronid *Phoronis* sp.
364 dominated the total community biomass at the sandy sites (SM 4). An assessment of the effect of
365 fishing frequency on infaunal community composition using either species density or biomass
366 data did not reveal any significant relationships between fishing and the biotic community in
367 either mud or sand (Mud: $F_{[1,10]} = 1.05$, $p = 0.38$, $r^2 = 0.10$; Sand: $F_{[1,7]} = 1.58$, $p = 0.11$, $r^2 =$
368 0.20).

369

370 Sessile species ($3.96 \pm 0.80 \text{ g m}^{-2}$) and deposit feeding organisms ($3.32 \pm 0.77 \text{ g m}^{-2}$) had
371 significantly higher biomass than species with other motilities and feeding strategies in mud
372 (Fig.2d, e; significant ‘Modality term’ in Table 1a, b). However, none of the motility, feeding or
373 bioturbation modalities examined at the muddy sites showed a significant relationship with
374 fishing frequency (non-significant ‘fishing term’ in Table 1). In contrast, fishing resulted in a
375 significant increase in the biomass of surface deposit feeders and suspension feeders relative to
376 predators and scavengers at the sandy sites (Fig.2g; significant ‘interaction term’ in Table 2a).
377 There was no significant effect of fishing on species with different mobilities or bioturbation
378 modes in sand (Table 2b, c).

379

380 **Fishing impact on biogeochemical parameters**

381

382 The sediment at the muddy sites had significantly higher organic carbon and nitrogen content
383 than the sandy sites (organic carbon: $0.87 \pm 0.04 \text{ \%m/m}$ in mud vs. $0.06 \pm 0.01 \text{ \%m/m}$ in sand;
384 organic nitrogen: $0.1 \pm 0.004 \text{ \%m/m}$ in mud vs. $0.02 \pm 0.001 \text{ \%m/m}$ in sand) (Fig.3b, c). The
385 average chlorophyll-*a* content of the muddy substratum was $1.8 \pm 0.18 \text{ }\mu\text{g/g}$ (Fig.3a), whereas

386 that in sand was $< 1 \mu\text{g/g}$, which was lower than the minimum detection limit of the fluorometer
387 hence why no data is plotted for sand in Fig. 3a. At the muddy sites, sediment chlorophyll-*a*
388 content and porosity increased significantly with fishing frequency indicating that the sediment
389 matrix contained more water and phytodetritus at sites exposed to higher fishing disturbance
390 (Fig.3a, d; Table 3a). There was a slight but significant increase in organic nitrogen content with
391 fishing frequency at the sandy sites, but no significant effects of fishing on organic carbon
392 content (Table 3b).

393

394 The oxygen penetration depth (OPD) and the depth of the apparent redox discontinuity layer
395 (aRPD) were shallower than 2 cm across the sites sampled in the muddy substratum. The OPD
396 ranged between 0.30 and 1.20 cm and the aRPD between 0.85 and 1.90 cm in mud (Fig.3e, f).
397 Most of the oxygen profiles showed a smooth decreasing trend in the concentration of free
398 oxygen with sediment depth, indicating that the oxygen distribution in mud was governed by
399 molecular diffusion between the oxic seawater and the oxygen-consuming sediment (SM 5A).
400 Neither the OPD nor the aRPD showed a significant relationship with fishing frequency in mud
401 (Table 3a). The coarse sand mixed with shell fragments at the sandy sites only allowed oxygen
402 profiling of the top 2 cm of the sediment core. High concentrations of oxygen were still present
403 at 2 cm (SM 5B), thus suggesting that the OPD in sand was deeper than 2 cm. In sand, the SPI-
404 camera penetrated to a maximum depth of 6.26 cm (compared to 21.36 cm in mud) and no aRPD
405 layer was visible, thus suggesting that the aRPD in sand was deeper than 6 cm. A subset of SPI-
406 images is presented in SM 6 to illustrate the different nature of the sediments at the two study
407 sites. The lack of an obvious colour stratification together with a visible fluff layer in most of the

408 SPI-images obtained from the muddy sites indicate that the sediment is highly disturbed at these
409 sites (SM 6).

410

411 The concentrations of ammonium (NH_4^+) and silicate (SiO_4^-) in pore-water were an order of
412 magnitude higher in mud than in sand (Fig.4, SM 5), reflecting the higher organic carbon and
413 chlorophyll-*a* (and associated diatom) levels in mud, which are the source of these inorganic
414 nutrients. The integrated-depth profiles for NH_4^+ in mud (Fig.4a) shows significantly higher
415 concentrations of NH_4^+ in sediment deeper than 2 cm ($48.13 \pm 17.72 \mu\text{mols/l}$) than in the upper 2
416 cm of the sediment ($24.43 \pm 19.04 \mu\text{mols/l}$) (significant 'Depth zone' term in Table 4a). The
417 concentration of NH_4^+ and SiO_4^- decreased significantly with fishing frequency within the top 2
418 cms of the muddy sediment, but increased significantly with fishing between 5 and 20 cm
419 (Fig.4a, c; significant interaction term in Table 4a, c). Phosphate (PO_4^{3-}) concentrations were
420 similar across all depth zones in mud, and did not show any significant effect of fishing (Fig.4b,
421 Table 4b). The concentration of NH_4^+ , SiO_4^- and PO_4^{3-} in the upper 5 cms were consistently low
422 at the sandy sites, indicating higher pore-water flow between the sediment and water column and
423 an upper mobile well-oxygenated sediment layer that is typical of sand but not of mud (Fig.4d -
424 f). NH_4^+ and PO_4^{3-} showed an overall small but significant increase in concentration with fishing
425 frequency. However we found no significant interaction effect of fishing and depth zone
426 suggesting a homogeneous effect of fishing with depth (Table 4a, b).

427

428 Discussion

429

430 Our assessment of the effects of bottom fishing disturbance on the infauna and biogeochemical
431 properties of soft sediments revealed some effects of bottom fishing on benthic biogeochemical
432 processes, but these effects differed between mud and sand. Scallop dredging on sand had little
433 effect on the infauna and sediment biogeochemistry; other factors such as tidal currents and
434 waves might play a role in regulating the biogeochemical processes in this hydrodynamic
435 environment. Several studies have shown that bottom currents generated by tides and waves play
436 an important role in transporting interstitial water into and out of highly permeable sediments
437 such as sands (Huettel et al. 1996; Huettel and Webster 2001; Ehrenhaus et al. 2004). In contrast,
438 otter trawling on mud increased sediment chlorophyll-*a*, porosity, the concentration of NH_4^+ in
439 the pore-water deeper than 5 cm and decreased the concentration of NH_4^+ in the top 2 cm. These
440 observations point towards a number of possible mechanisms through which trawling may be
441 impacting organic matter remineralization and nutrient cycling in mud. First, otter trawling may
442 be resuspending sediment in the upper (0 – 2 cm) sediment layers, which acts to decrease the
443 pore-water concentrations of nutrients typically generated at depth (e.g. NH_4^+) as these are lost to
444 the overlying water column. Bobbins and chains scrape off surface sediment layers, causing the
445 redistribution of both sediment particles and nutrients as they are dragged along the seabed
446 (Jones 1992). Second, otter trawling may be burying organic matter to deeper sediment, which
447 acts to increase NH_4^+ production at depth (beyond 5 cm) as organic matter is broken down under
448 anaerobic conditions. Otter boards leave distinct tracks on the seafloor, ploughing grooves which
449 can vary from a few cms down to 35 cm in muds (Eigaard et al. 2015). Therefore, it is likely that
450 the increase in NH_4^+ production at the depths observed at the muddy sites is due to organic
451 matter burial or mixing to depth by otter board action. Furthermore, the presence of significant
452 pore-water TOxN concentrations below 5 cms at some sites illustrates that there must be

453 significant pore-water relocation caused by trawling, which is the only process which could act
454 to these depths at the sites. The injection of carbon to depth is also likely to stimulate localized
455 Fe reduction which mediates increased phosphate release at depth. Future analysis of total
456 organic carbon and C:N ratios in profiles would enable age determination and source of carbon,
457 hence allowing the mechanism of impact to be identified better.

458

459 The elevated concentration of dissolved nutrients released from the sediment could account for
460 the increase in sediment chlorophyll-*a* observed at the higher trawling frequency muddy areas
461 (e.g. Sparks-McConkey and Watling 2001). However, this is unlikely as the main source of
462 chlorophyll-*a* at the muddy area is deposition of phytoplankton rather than generation at source
463 as the amount of light reaching the seabed at the studied sites is negligible (Foden et al. 2008).
464 Furthermore, tidal currents are likely to move any released nutrients over distances larger than
465 the distance between our sampling sites. Benthic macrofauna are known to play an important
466 role in controlling the levels of total organic carbon (TOC) and chlorophyll-*a* in the sediment by
467 controlling rates of TOC remineralization (via redox) and phytodetritus incorporation within the
468 sediment via bioturbation processes. For example, in an extensive survey of the North Sea soft
469 sediments, Solan et al. (2012) and R. Parker (unpubl.) found that a decrease in community
470 complexity and bioturbation capacity led to a decrease in sediment oxygenation and carbon
471 cycling which resulted in higher sediment TOC, and a decrease in sediment reworking rates that
472 led to lower chlorophyll-*a* concentrations due to lower phytodetritus incorporation within the
473 sediment. We found no significant effect of trawling on infaunal abundance and BP_C at either of
474 the study areas and therefore have no evidence that trawling is affecting the sediment
475 biogeochemistry through changes in macrofaunal composition and/or loss of bioturbation

476 potential. Alternatively, trawling may lead to a substantial reduction in bacterial biomass as the
477 sediment is resuspended in the water column, hence slowing down the remineralization of the
478 labile portion of organic matter within the sediment. Watling et al. (2001) observed a 50%
479 reduction in microbial biomass after dredging an undisturbed area by commercial scallop
480 dredgers. This reduction is expected to be higher in heavily trawled areas than in lightly trawled
481 areas, hence the higher concentration of chlorophyll-*a* observed at higher trawling frequency
482 areas. It is well acknowledged that a lot of the nutrient cycling and flux is linked to the microbial
483 activity within the sediment (Snelgrove 1997; Friedrich et al. 2002; Tait et al. 2014). Future
484 examination of the microbial sediment community in areas with different fishing pressure would
485 improve our understanding in this regard.

486
487 Previous surveys from 2003 and 2004 at sites within the muddy area found significant decreases
488 in both infaunal abundance and biomass with increasing trawling frequencies (Queiros et al.
489 2006; Hinz et al. 2009). Particularly striking between these older surveys and the present survey
490 is the absence of *Amphiura filiformis* from the latter. *A. filiformis* dominated the community
491 biomass (64.13%) in surveys from 10 years ago, whereas burrowing shrimps such as *Callinassa*
492 *subterranea*, *Upogebia deltaura* and *Jaxea nocturna* were among the species that dominated the
493 biomass in the present study. Large quantities of suspended sediments (such as those generated
494 by trawling) are known to inhibit the growth of *A. filiformis* but not that of the burrowing mud
495 shrimps (Amaro 2005). The sustained high trawling frequencies over the years at this area may
496 thus be having long-term changes in community composition. The lack of detection of an effect
497 of trawling on infaunal biomass (and any associated changes in biogeochemistry) in this study is
498 more likely to be due to the lack of a true zero (lowest fishing frequency was 3 yr⁻¹) rather than

499 of no effect of trawling. Queiros et al. (2006) recorded a change in body size spectrum at the
500 muddy area; from lots of large and small size classes in lightly trawled area (0.1 yr^{-1}) to a
501 decrease in biomass across the entire size range for more heavily trawled areas (3.5 yr^{-1}). We
502 recognize that our study at the muddy area would have benefitted from having a true control (i.e.
503 areas of no fishing). However, these sites were hard to find as sites with very low or no fishing
504 were characterized by different habitat conditions (sediment composition, tide and wave stress)
505 from sites where fishing occurred.

506

507 A number of limitations associated with the use of fishing pressure indices estimated from VMS
508 data records should be borne in mind for the interpretation of the effects of fishing on the
509 sediment properties and the infauna obtained in this study. First, is the mismatch of spatial scales
510 between the VMS data (km^2) and the sampling gear (m^2), which creates difficulty in determining
511 the exact magnitude of disturbance experienced by the community at the sampled sites. Second,
512 is the temporal variability in the spatial distribution of the fishing fleet from year to year such
513 that the frequency of disturbance at the areas surveyed may differ between years and between
514 sampling sites. Third, is the difficulty of obtaining high resolution VMS data (often withheld
515 from the scientific community for confidentiality reasons, Hinz et al. 2013), which may be used
516 to determine the last fishing disturbance event relative to the benthic sampling event and
517 recovery times of the infauna and biogeochemical processes. The infauna are expected to recover
518 over longer time-scales than the sediment biogeochemical properties, as the former depends on
519 recolonization processes such as larval dispersal and post-larval growth and immigration, which
520 take longer to occur. These discrepancies in spatial and temporal scale between fishing pressure
521 estimates and that truly experienced by the community at the time of sampling might have

522 reduced our ability to detect small-scale or subtle changes in the biota and biogeochemistry at the
523 sampled sites. Future controlled BACI studies with multiple sampling times after the disturbance
524 event would help to address these limitations.

525

526 In conclusion, this study has found some effects of bottom trawling on biogeochemistry and
527 infauna on mud but not on sand, where the biogeochemistry appeared to be more strongly
528 influenced by tidal currents and waves. Our first hypothesis that fishing will negatively affect
529 benthic invertebrate abundance and reduce the bioturbation potential was therefore not
530 supported. Our second hypothesis that fishing results in changes in the sediment redox and
531 associated biogeochemistry as a result of sediment resuspension and sediment/carbon mixing to
532 depth as was only partly supported as we did not find an increase in the oxygen penetration depth
533 and higher NO_x in pore-water with increasing fishing, but did find a lower concentration of NH_4^+
534 and SiO_4^- with increasing fishing frequency within the top 2 cm of the sediment and a higher
535 concentration at > 5 cm depth on mud. Our third hypothesis that changes in sediment
536 biogeochemistry due to fishing are larger in mud where macrofauna-mediated processes are
537 expected to play a more significant role than in sand where physical processes such as tides and
538 currents generally mediate the redox system, was partly supported, as we did find larger changes
539 in mud than in sand, but only little evidence that this was mediated by macrofauna. This suggests
540 that otter trawling may be affecting organic-matter remineralization and nutrient cycling through
541 sediment resuspension and burial of organic matter to depth rather than through the loss of
542 bioturbation potential of the benthic community. Under the Marine Strategy Framework
543 Directive (MSFD), European countries are committed to achieve good environmental status
544 (GES) by 2020 (Anon 2008, <http://eur-lex.europa.eu/legal->

545 [content/EN/TXT/?uri=CELEX%3A32008L0056](#), accessed 11 November 2015). GES requires
546 that both benthic communities and ecosystem processes and functions are not adversely affected
547 by anthropogenic activities (descriptor 6, seafloor integrity) (Rice et al. 2012). These results
548 imply that management of otter trawling activities on muddy sediments may be more important
549 for maintaining GES of the seabed than management of scallop dredging on sand.

550 **Acknowledgements**

551 The work undertaken herein, including the collection of the benthic data, the numerical analyses,
552 interpretation and reporting was funded under the EU FP7 BENTHIS (Benthic Ecosystem
553 Fisheries Impact Studies) project (312088) and the NERC funded SSB (Shelf Sea
554 Biogeochemistry) programme (NE/K001639/1). The article does not necessarily reflect the
555 views of the European Commission / NERC and does not anticipate the Commission's / NERC's
556 future policy in this area. All those who have contributed to any aspects of the work undertaken
557 herein are gratefully acknowledged. The authors declare that they have no conflict of interest.

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693 **Fig.1** Map of the sampling sites at the sandy sediment location (Isle of Man fishing ground, S1 –
694 S8) and the muddy sediment location (*Nephrops* fishing ground, M1 – M11)

695

696 **Fig.2** The effect of bottom fishing on (a) total infaunal abundance, (b) total infaunal biomass
697 (grams wet weight, g WW), (c) community bioturbation potential (BP_C) and on the biomass of
698 species with different feeding modes, mobility and modes of bioturbation in mud (d – f) and sand
699 (g – i). The dotted lines represent GLM models for significant effects of fishing on different trait
700 modalities. [Feeding modes: Susp = suspension feeder, Dep = deposit feeder, SubD = subsurface
701 deposit feeder, Scav = scavenger, Pred = predator. Mobility: sessile, burrower, crawler,
702 swimmer. Bioturbation mode: None = non-bioturbating organism, Diff = diffusor, Sdep =
703 surface deposition, DC = downwards conveyor, UC = upwards conveyor]

704

705 **Fig.3** The effect of bottom fishing on biogeochemical parameters in mud (black symbols) and
706 sand (grey symbols): (a) sediment chlorophyll-*a* content, (b) organic carbon content, (c) organic
707 nitrogen content, (d) sediment porosity, (e) maximum oxygen penetration depth (OPD) in cm, (f)
708 apparent redox discontinuity layer (aRPD) in cm. The dotted line represents the GLM model for
709 significant effect of fishing (see results text for data on sediment chlorophyll-*a*, aRPD and OPD
710 in sand)

711

712 **Fig.4** Depth-integrated ammonium, phosphate and silicate concentration (log₁₀-transformed)
713 profiles recorded at increasing fishing frequency in mud (a – c) and sand (d – f). The solid line
714 represents the GLM model for significant effect of fishing*depth zone, dotted line represents the
715 GLM model for significant effect of fishing

716 **Table 1** Statistical outputs of the general linear models (GLMs) examining the relationship
 717 between the biomass of species with different biological traits (Modality) and fishing frequency
 718 (yr^{-1}) (Fishing) in mud. ‘Fishing x Modality’ refers to the interaction term of the GLM.
 719 Significant relationships are shown in bold. df (x,y) indicates model and residual degrees of
 720 freedom, F is the F-statistic for the GLM model
 721

| Mud: <i>Nephrops</i> fishing ground | | | |
|--------------------------------------------|-----------|----------|--------------------|
| a. Feeding mode | df | F | <i>p</i> |
| Fishing | 1,45 | 0.16 | 0.69 |
| Modality | 4,45 | 11.76 | < 0.0001 |
| Fishing x Modality | 445 | 0.34 | 0.85 |
| b. Mobility | df | F | <i>p</i> |
| Fishing | 1,36 | 0.16 | 0.69 |
| Modality | 3,36 | 17.90 | < 0.0001 |
| Fishing x Modality | 3,36 | 0.44 | 0.72 |
| c. Bioturbation mode | df | F | <i>p</i> |
| Fishing | 1,45 | 0.31 | 0.58 |
| Modality | 4,45 | 14.08 | < 0.0001 |
| Fishing x Modality | 4,45 | 0.37 | 0.83 |

722

723

724 **Table 2** Statistical outputs of the general linear models (GLMs) examining the relationship
 725 between the biomass of species with different biological traits (Modality) and fishing frequency
 726 (yr^{-1}) (Fishing) in sand. ‘Fishing x Modality’ refers to the interaction term of the GLM.
 727 Significant relationships are shown in bold

728

| Sand: Isle of Man fishing ground | | | |
|-----------------------------------------|-----------|----------|--------------------|
| a. Feeding mode | df | F | <i>p</i> |
| Fishing | 1,30 | 2.39 | 0.13 |
| Modality | 4,30 | 5.13 | 0.003 |
| Fishing x Modality | 4,30 | 2.93 | 0.04 |
| b. Mobility | df | F | <i>p</i> |
| Fishing | 1,24 | 1.22 | 0.28 |
| Modality | 3,24 | 10.03 | 0.0002 |
| Fishing x Modality | 3,24 | 2.62 | 0.07 |
| c. Bioturbation mode | df | F | <i>p</i> |
| Fishing | 1,30 | 1.78 | 0.19 |
| Modality | 4,30 | 11.32 | < 0.0001 |
| Fishing x Modality | 4,30 | 1.60 | 0.20 |

729

730

731 **Table 3** Statistical outputs of the GLM models examining the relationship of different
 732 biogeochemical parameter to fishing frequency (yr^{-1}) in (a) mud and (b) sand. Significant
 733 relationships are shown in bold. t and SE indicate the t-statistic and the standard error for the
 734 GLM model, aRPD is the apparent redox discontinuity layer, OPD is the oxygen penetration
 735 depth
 736

(a) Mud: *Nephrops* fishing ground

| Biogeochemical parameter | slope | SE | t | p | adj-r ² |
|-------------------------------------------|-------------|-------------|-------------|-------------|--------------------|
| Organic carbon (%m/m) | 0.01 | 0.03 | 0.09 | 0.93 | 0.001 |
| Organic nitrogen (%m/m) | 0.01 | 0.01 | 0.73 | 0.49 | 0.001 |
| chlorophyll- <i>a</i> ($\mu\text{g/g}$) | 0.23 | 0.08 | 2.80 | 0.02 | 0.43 |
| Porosity | 0.01 | 0.01 | 2.35 | 0.04 | 0.31 |
| aRPD (cm) | -0.16 | 0.08 | -2.08 | 0.08 | 0.29 |
| OPD (cm) | 0.04 | 0.05 | 0.85 | 0.42 | 0.001 |

(b) Sand: Isle of Man fishing ground

| | | | | | |
|-------------------------|--------------|--------------|-------------|-------------|-------------|
| Organic carbon (%m/m) | 0.02 | 0.01 | 2.15 | 0.07 | 0.34 |
| Organic nitrogen (%m/m) | 0.005 | 0.002 | 2.98 | 0.02 | 0.53 |
| Porosity | 0.02 | 0.01 | 1.71 | 0.14 | 0.22 |

737

738

739 **Table 4** Statistical output of the GLM models examining the relationship of pore-water nutrient
 740 concentrations (\log_{10} -transformed) to fishing frequency (yr^{-1}) and sediment depth in mud and
 741 sand; Significant model terms are shown in bold. F is the F-statistic for the GLM model
 742

| | Mud | | Sand | |
|----------------------------------------------------|------------|-------------------|-------------|-------------------|
| a. $\log_{10}(\text{NH}_4^+)$ | F | <i>p</i> | F | <i>p</i> |
| Fishing | 4.24 | 0.04 | 9.75 | 0.01 |
| Depth zone | 26.11 | < 0.001 | 9.06 | 0.01 |
| Fishing x Depth zone | 3.45 | 0.04 | 0.25 | 0.78 |
| b. $\log_{10}(\text{PO}_4^{3-})$ | | | | |
| Fishing | 0.10 | 0.75 | 11.45 | 0.01 |
| Depth zone | 1.37 | 0.27 | 27.91 | < 0.001 |
| Fishing x Depth zone | 0.74 | 0.49 | 0.62 | 0.56 |
| c. $\log_{10}(\text{SiO}_4^-)$ | | | | |
| Fishing | 10.89 | 0.003 | 1.81 | 0.21 |
| Depth zone | 35.26 | < 0.001 | 6.58 | 0.02 |
| Fishing x Depth zone | 12.03 | < 0.001 | 0.16 | 0.86 |

743

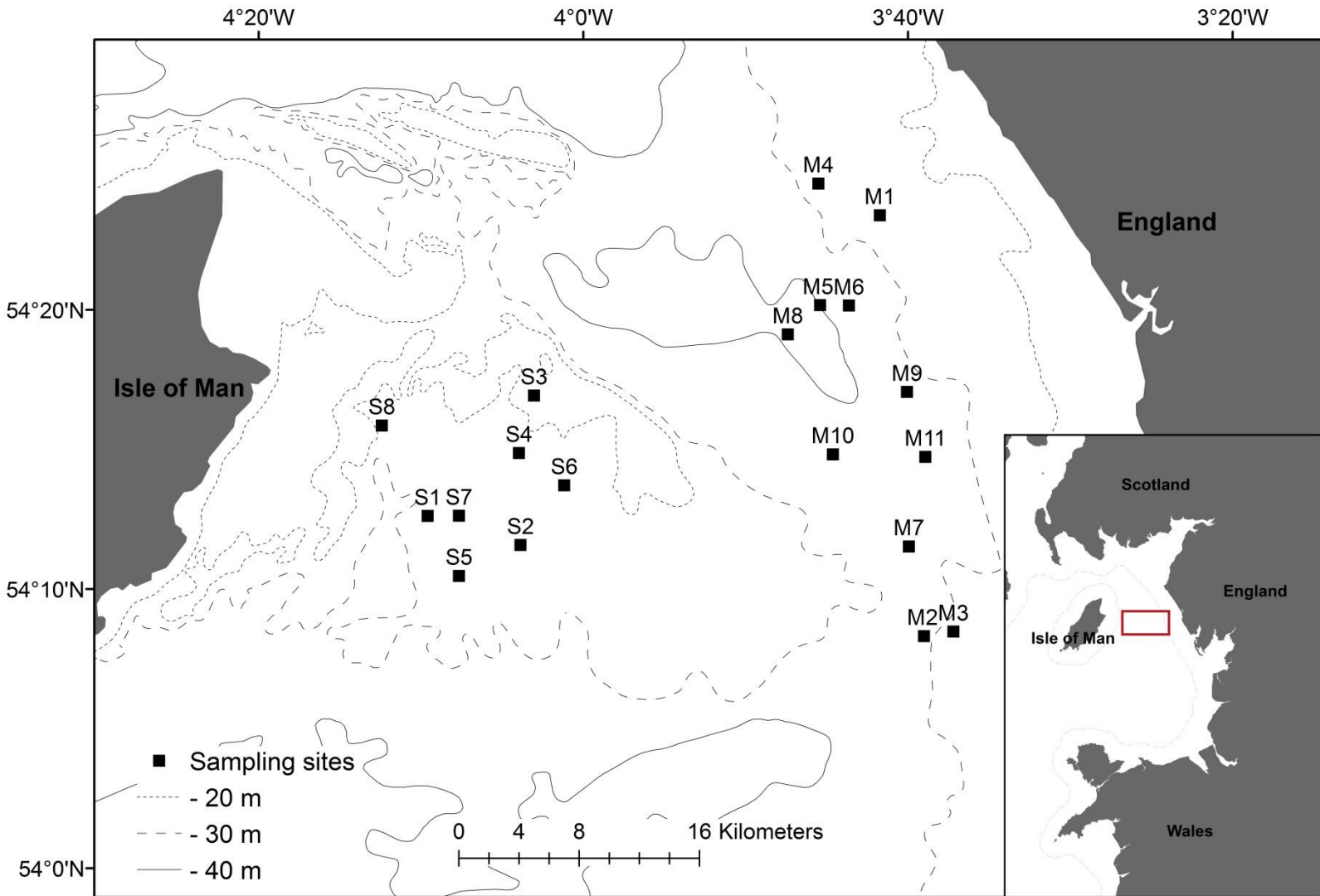


Fig.1 Map of the sampling sites at the sandy sediment location (Isle of Man fishing ground, S1 – S8) and the muddy sediment location (*Nephrops* fishing ground, M1 – M11)

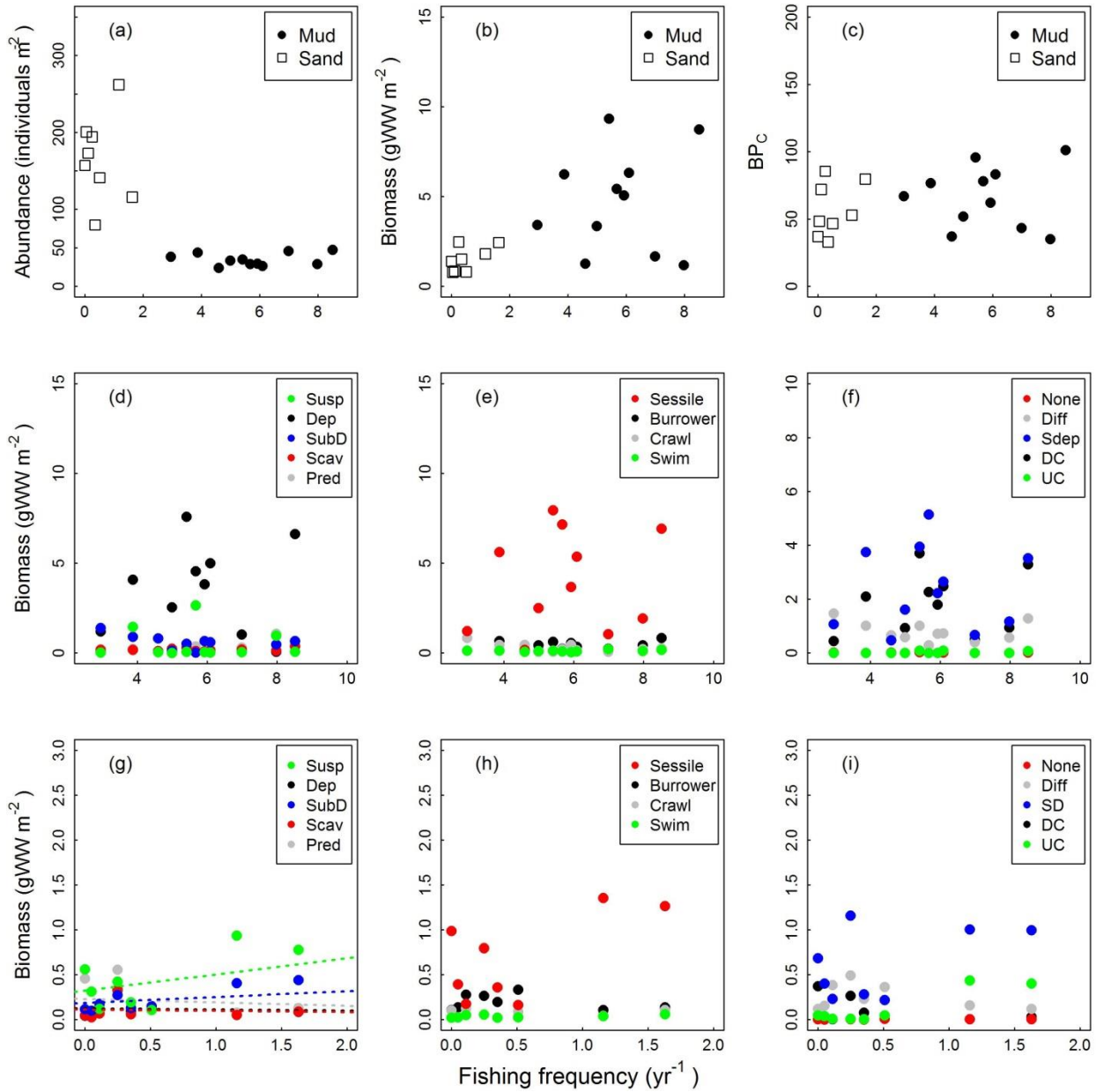


Fig.2 The effect of bottom fishing on (a) total infaunal abundance, (b) total infaunal biomass (grams wet weight, g WW), (c) community bioturbation potential (BPC_C) and on the biomass of species with different feeding modes, mobility and modes of bioturbation in mud (d – f) and sand (g – i)

(g – i). The dotted lines represent GLM models for significant effects of fishing on different trait modalities.¹

¹ Feeding strategies: Susp = suspension feeder, Dep = deposit feeder, SubD = subsurface deposit feeder, Scav = scavenger, Pred = predator. Mobility: sessile, burrower, crawler, swimmer. Bioturbation mode: None = non-bioturbating organism, Diff = diffusor, Sdep = surface deposition, DC = downwards conveyor, UC = upwards conveyor.

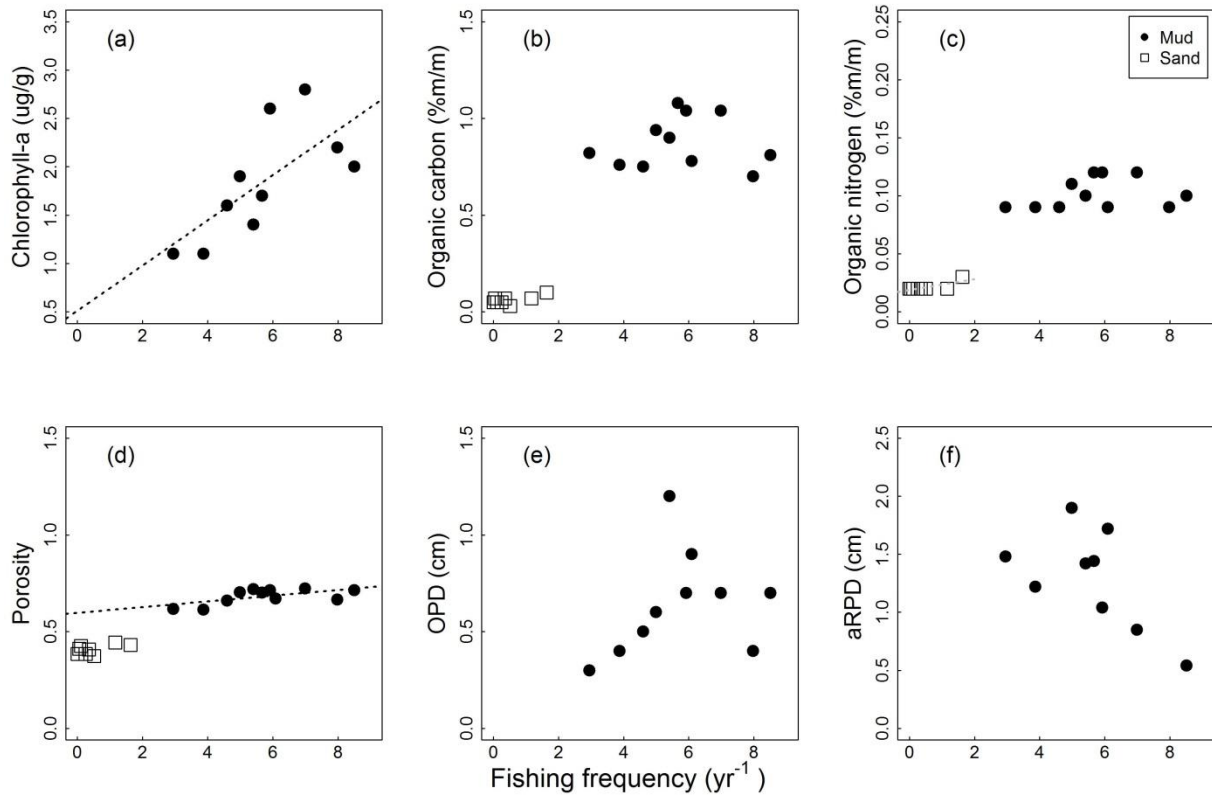


Fig.3 The effect of bottom fishing on biogeochemical parameters in mud (black dots) and sand (open squares): (a) sediment chlorophyll-*a* content, (b) organic carbon content, (c) organic nitrogen content, (d) sediment porosity, (e) maximum oxygen penetration depth (OPD) in cm, (f) apparent redox discontinuity layer (aRPD) in cm. The dotted line represents the GLM model for significant effect of fishing (see results text for data on sediment chlorophyll-*a*, aRPD and OPD in sand)

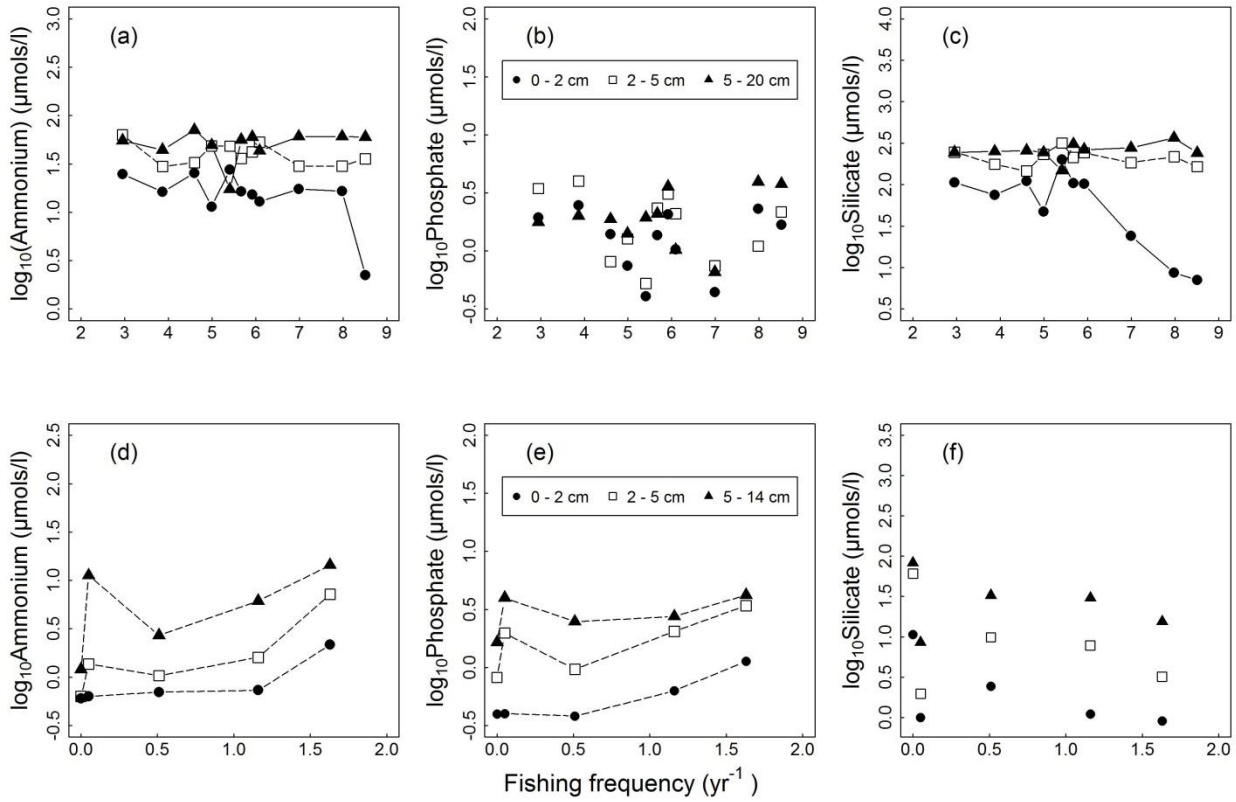


Fig.4 Depth-integrated ammonium, phosphate and silicate concentration (log₁₀-transformed) profiles recorded at increasing fishing frequency in mud (a – c) and sand (d – f). The solid line represents the GLM model for significant effect of fishing*depth zone, dotted line represents the GLM model for significant effect of fishing