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1 **Impacts of bottom fishing on the sediment infaunal community and biogeochemistry of**

2 **cohesive and non-cohesive sediments**

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18 **Keywords**

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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 m^3, 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 m^3, 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 Fe^{3+}/Fe^{2+} 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 ± 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(biomass) ~ fishing * 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(nutrient concentration) ~ fishing * 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 µm) and the sediment was poorly

341   sorted, whereas the sandy sites were composed of more than 95% sand (> 63 µm 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 ± 0.29 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 ± 0.99 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 ± 0.80 g m^{-2}) and deposit feeding organisms (3.32 ± 0.77 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 ± 0.04 %m/m in mud vs. 0.06 ± 0.01 %m/m in sand;

384   organic nitrogen: 0.1 ± 0.004 %m/m in mud vs. 0.02 ± 0.001 %m/m in sand) (Fig.3b, c). The

385   average chlorophyll-*a* content of the muddy substratum was 1.8 ± 0.18 μg/g (Fig.3a), whereas

386   that in sand was < 1 µg/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 ± 17.72 µmols/l) than in the upper 2

416   cm of the sediment (24.43 ± 19.04 µmols/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 *Callianassa*

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**

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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 (log_{10}-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: *Nephrops* fishing ground			
a. Feeding mode	**df**	**F**	***p***
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**	***p***
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**	***p***
Fishing	1,45	0.31	0.58
Modality	4,45	14.08	**< 0.0001**
Fishing x Modality	4,45	0.37	0.83

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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**	***p***
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**	***p***
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**	***p***
Fishing	1,30	1.78	0.19
Modality	4,30	11.32	**< 0.0001**
Fishing x Modality	4,30	1.60	0.20

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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

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(a) Mud: *Nephrops* fishing ground

Biogeochemical parameter	slope	SE	t	*p*	*adj-r²*
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-*a* (µg/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

Biogeochemical parameter	slope	SE	t	*p*	*adj-r²*
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

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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

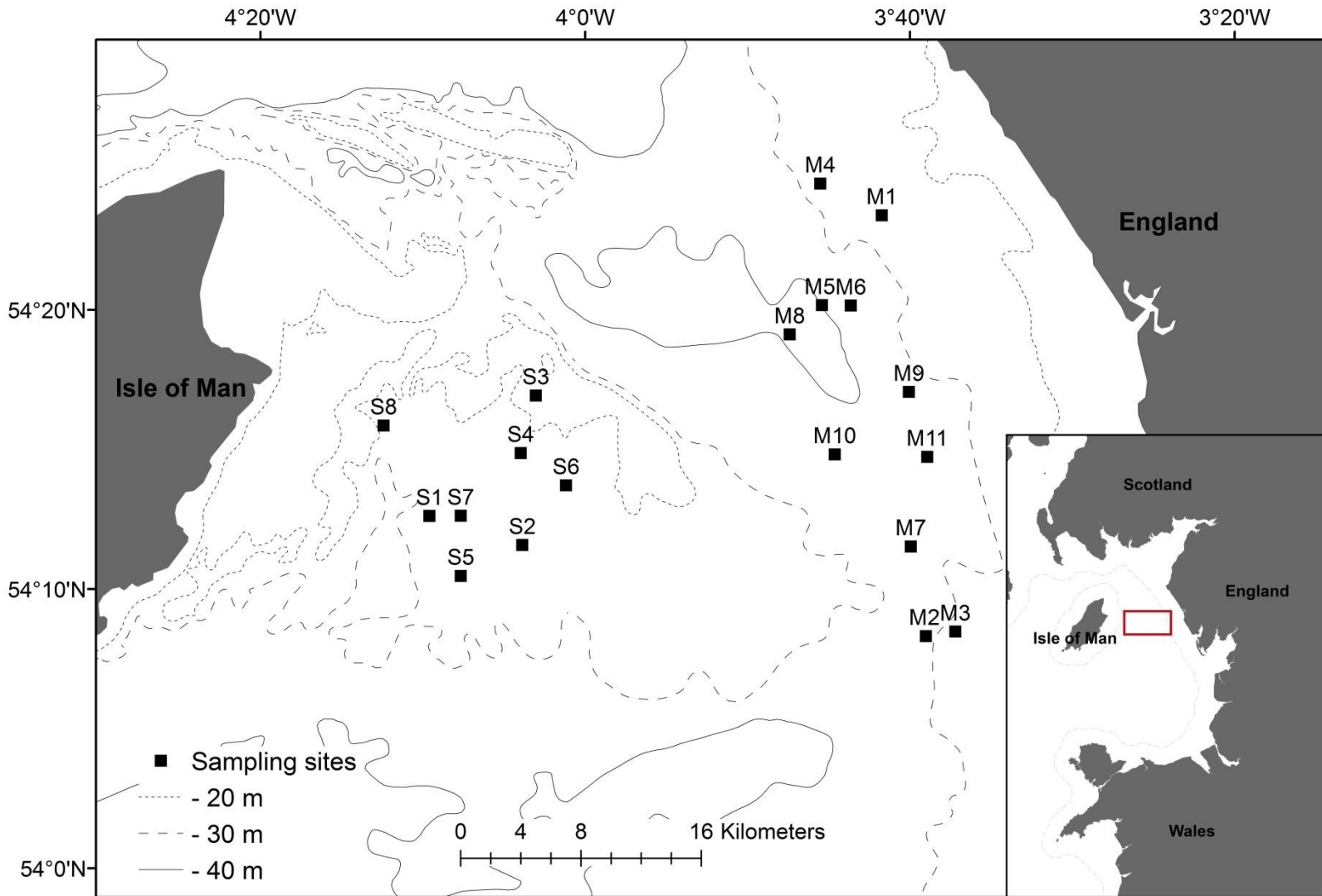|	Mud		Sand	
a. $\log_{10}(NH_4^+)$	**F**	*p*	**F**	*p*
Fishing	4.24	**0.04**	9.75	**0.01**
Depth zone	26.11	**< 0.001**	9.06	**0.01**
Fishing x Depth zone	3.45	**0.04**	0.25	0.78
b. $\log_{10}(PO_4^{3-})$				
Fishing	0.10	0.75	11.45	**0.01**
Depth zone	1.37	0.27	27.91	**< 0.001**
Fishing x Depth zone	0.74	0.49	0.62	0.56
c. $\log_{10}(SiO_4^-)$				
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 –

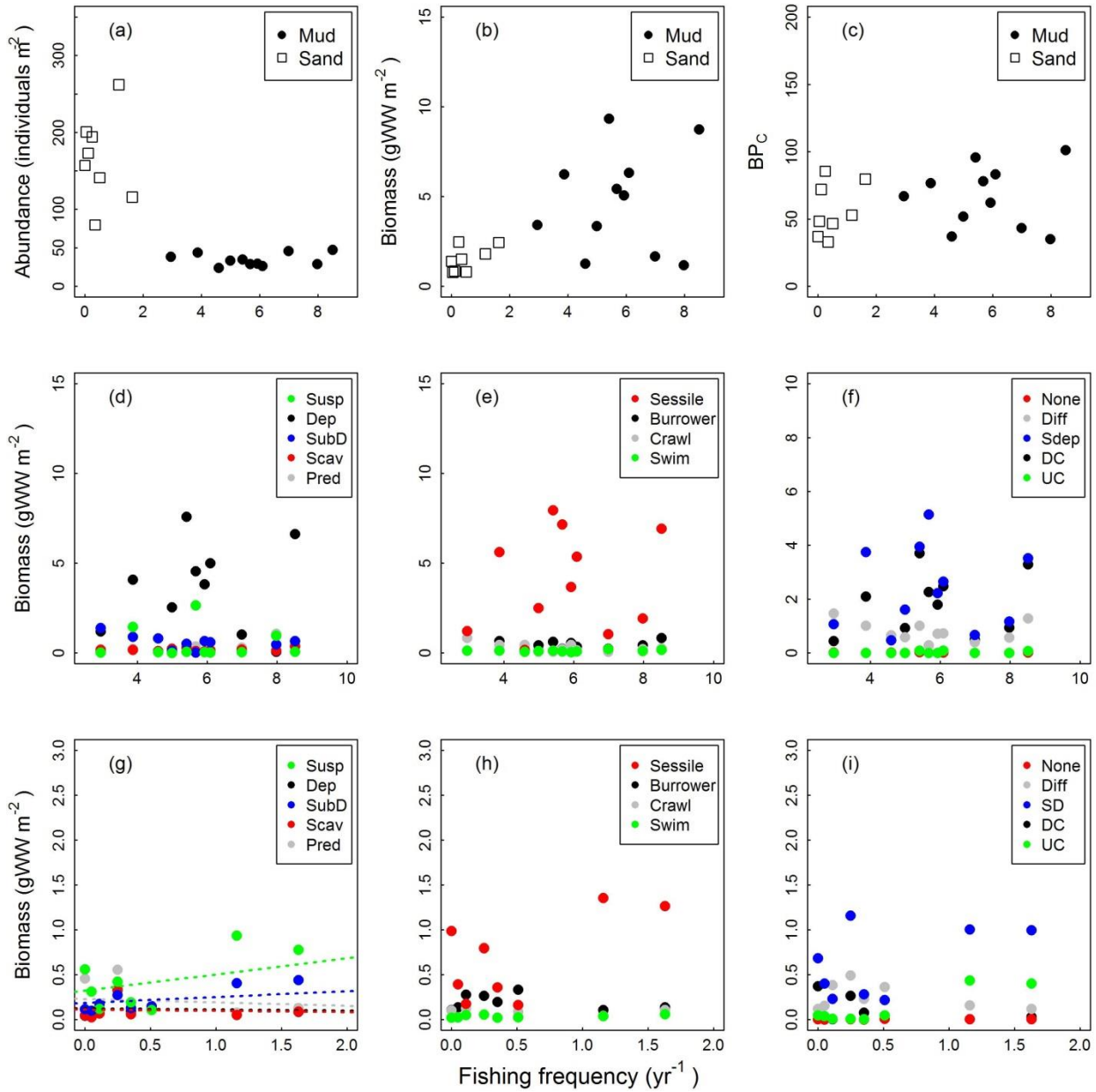S8) and the muddy sediment location (*Nephrops* fishing ground, M1 – M11)

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 (BP_C) and on the biomass of species with different feeding modes, mobility and modes of bioturbation in mud (d − f) and sand

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

modalities.[1]

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[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.
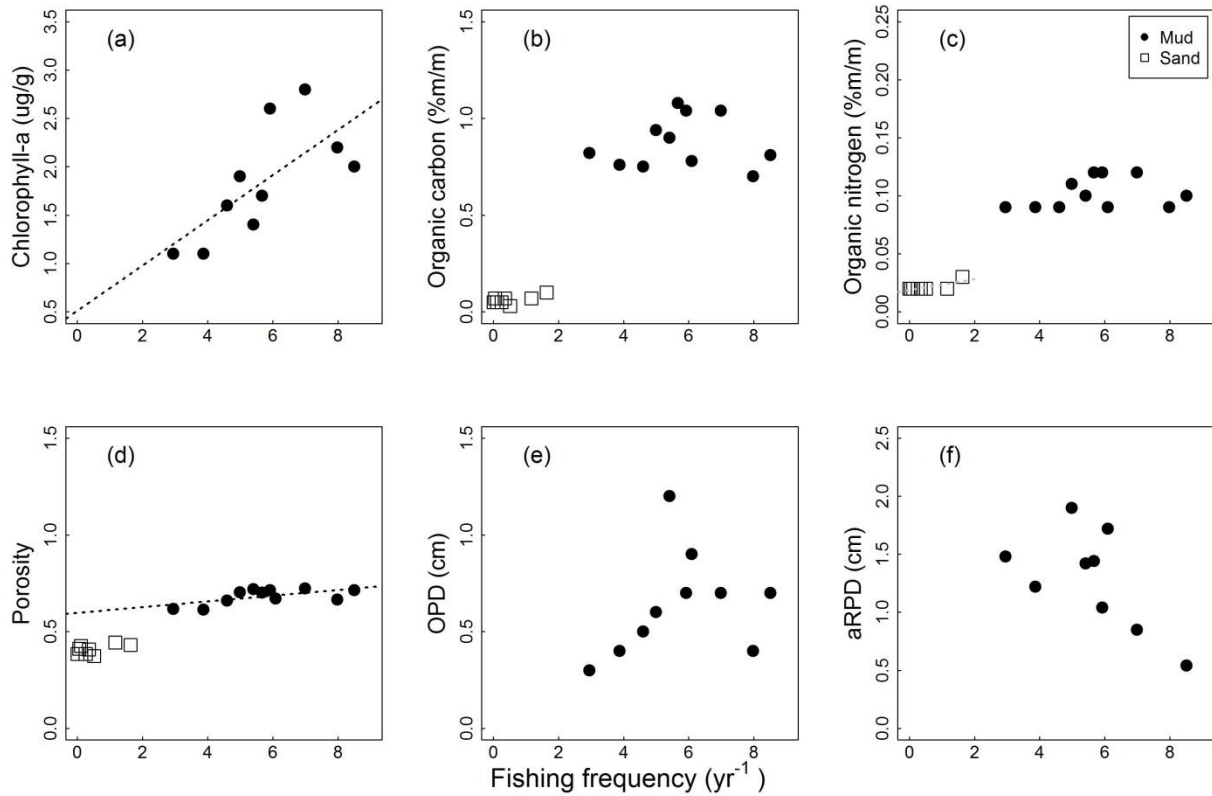
Fig.3 The effect of bottom fishing on biogeochemical parameters in mud (black dots) and sand (open squares): (a) sediment chlorophyll-*a* content, (b) organic carbon content, (c) organic nitrogen content, (d) sediment porosity, (e) maximum oxygen penetration depth (OPD) in cm, (f) apparent redox discontinuity 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)
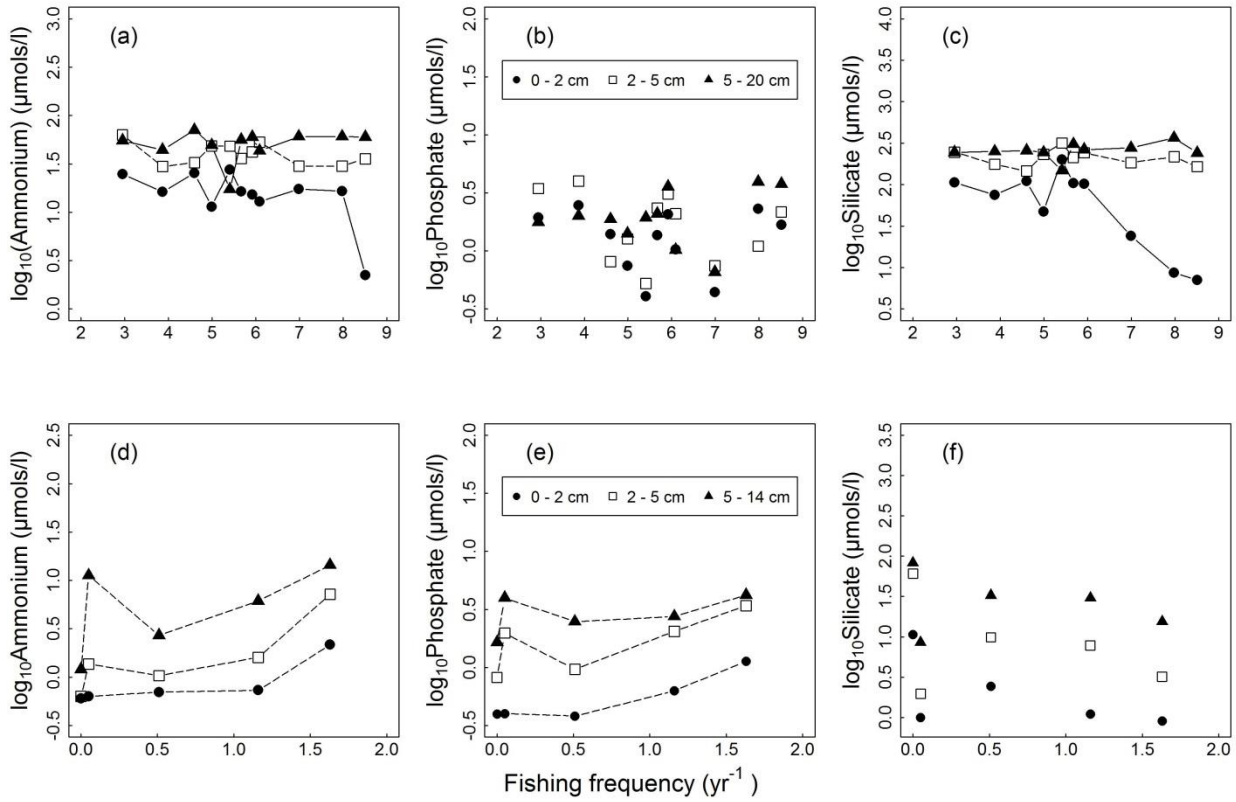
Fig.4 Depth-integrated ammonium, phosphate and silicate concentration ($\log_{10}$-transformed) profiles recorded at increasing fishing frequency in mud (a – c) and sand (d – f). The solid line represents the GLM model for significant effect of fishing*depth zone, dotted line represents the GLM model for significant effect of fishing