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3

4 **Title:** Mediation of nitrogen by post-disturbance shelf communities experiencing organic matter
5 enrichment

6

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21 **Abstract**

22 Microbes and benthic macro-invertebrates interact in sediments to play a major role in the
23 biogeochemical cycling of organic matter, but the extent to which their contributions are modified
24 following natural and anthropogenic changes has received little attention. Here, we investigate how
25 nitrogen transformations, ascertained from changes in archaeal and bacterial N-cycling microbes
26 and water macronutrient concentrations ($[\text{NH}_4\text{-N}]$, $[\text{NO}_2\text{-N}]$, $[\text{NO}_3\text{-N}]$), in sand and sandy mud
27 sediments differ when macrofaunal communities that have previously experienced contrasting
28 levels of chronic fishing disturbance are exposed to organic matter enrichment. We find that
29 differences in macrofaunal community structure related to differences in fishing activity affect the
30 capacity of the macrofauna to mediate microbial nitrogen cycling in sand, but not in sandy mud
31 environments where the range of disturbance frequency was higher than that in the sandy area.
32 Whilst we found no evidence for a change in ammonia oxidiser community structure, we did find
33 an increase in archaeal and bacterial denitrifier (*AnirKa*, *nirS*) and anammox (*hzs*) transcripts in
34 macrofaunal communities characterized by higher ratios of suspension to deposit feeders, and a
35 lower density but higher biomass of sediment-reworking fauna. Our findings suggest that nitrogen
36 transformation in shelf sandy sediments is dependent on the stimulation of specific nitrogen cycling
37 pathways that are associated with differences in the composition and context-dependent expression
38 of the functional traits that belong to the resident bioturbating macrofauna community.

39

40

41 **Keywords:** ammonia-oxidisers, bioturbation, bottom fishing, denitrification, ecosystem
42 functioning, microbial-invertebrate interactions, nitrogen cycling.

43

44 **Introduction**

45

46 Marine soft-sediments cover almost 70% of the earth's surface and play a fundamental role in the
47 remineralization of organic carbon and nutrient cycling (Olsgard et al. 2008). According to current
48 nitrogen budgets, it is estimated that up to 80% of the nitrogen needed by primary producers in
49 shallow shelf seas is provided by benthic remineralization processes, primarily driven by microbial
50 organisms that occur across the oxic/anoxic interface near the sediment surface (Dale & Prego
51 2002; Zehr & Kudela 2011). With 23% of the global human population concentrated in coastal
52 areas, at an average density nearly 3 times higher than the global average (Small & Nicholls 2003)
53 and an increase in demand in food production, coastal and shelf sea benthic systems are
54 increasingly vulnerable to anthropogenic activities such as fishing and are at higher risk of
55 eutrophication following excessive nutrient input. Any change in the balance and distribution of
56 reactive nitrogen (e.g. ammonium NH_4^+ , nitrite NO_2^- and nitrate NO_3^-), oxygen, and organic
57 substrates are likely to have profound consequences for nitrification, denitrification and anaerobic
58 ammonium oxidation (anammox) that regulate coastal nitrogen budgets (Laverock et al. 2011).

59

60 Bottom fishing that uses demersal gear such as trawls and dredges to catch fish, crustaceans and
61 bivalves living in, on or in association with the seabed, exerts a number of pressures on benthic
62 systems that might influence sedimentary nutrient generation and budgets (Pilskaln et al. 1998;
63 Olsgard et al. 2008). Physical processes such as sediment resuspension and sediment mixing caused
64 by trawling alter grain size distribution, sediment sorting and porosity (Trimmer et al. 2005) that
65 may in turn disrupt nitrification and denitrification processes (Rysgaard et al. 1994; Kitidis et al.
66 2017) through changes in oxygen penetration depth within the sediment (Warnken et al. 2003) and
67 burial of organic matter to anoxic layers before aerobic remineralisation can take place (Mayer et al.
68 1991; Pilskaln et al. 1998). The combination of removal of surficial sediments and mixing or burial
69 of organic matter to depth (Duplisea et al. 2001; Warnken et al. 2003) occurs on different time-

70 scales to those of alterations in community structure; changes in pore-water and bottom water
71 nutrient levels due to sediment resuspension return to pre-trawling levels within minutes to hours
72 (e.g. Falcao et al. 2003; Trimmer et al. 2005; Goldberg et al. 2014), whilst microbial assemblage
73 structure and biomass in the surficial sediment layers (upper 1 cm) return to pre-disturbance levels
74 within days (Fiordelmondo et al. 2003) to 4 - 6 months (Watling et al. 2001). In contrast,
75 macrofaunal communities can take up to 4 – 5 years to recover (Kaiser et al. 2006; Lambert et al.
76 2014). Over extended and repeated periods of fishing activity, changes in the functional
77 composition of invertebrate communities can have a disproportionate influence on nutrient cycling
78 through changes in the bioturbation potential of the benthic community (Duplisea et al. 2001;
79 Widdicombe et al. 2004). The active redistribution of particles (bioturbation) and fluids
80 (bioirrigation) by infaunal macro-invertebrates, such as bivalves, polychaetes and crustaceans,
81 directly contributes to the spatial and temporal heterogeneity of oxic and anoxic zones (Bertics &
82 Ziebis 2009), organic matter availability (Levin et al. 1997) and the distribution of metabolic
83 electron acceptors (Fanjul et al. 2007) that are important in controlling microbial process rates
84 (Gilbertson et al. 2012; Laverock et al. 2014). The close association between the macrobenthic
85 invertebrate community composition and microbial activity suggests that a reduction in bioturbation
86 potential of the benthic community ensuing from the loss or change in relative composition of
87 invertebrate species associated with bottom fishing will lead to changes in microbial-mediated
88 processes such as nitrification, denitrification and anammox. Relative to the direct physical effects
89 of fishing gear on sediment and faunal structure, however, the extent to which microbial-
90 invertebrate coupling is modified and affects nutrient budgets in post-disturbance communities has
91 received little attention.

92

93 Fluctuations in organic matter input following events such as algal blooms or run-off associated
94 with high intensity precipitation, also have a prominent influence on benthic invertebrate fauna (van
95 Oevelen et al. 2009; Zhang et al. 2015) and microbial community composition (Franco et al. 2007;

96 Mayor et al. 2012; Tait et al. 2015). Benthic communities may be affected positively as food
97 becomes available to both invertebrate grazers and bacteria and archaea, or negatively because an
98 excess of organic matter may result in deoxygenation of the sediment (Quijon et al. 2008; Mayor et
99 al. 2012). Zhang et al. (2015) observed a doubling effect on macrofaunal production and biomass
100 during a spring algal bloom relative to the end of the bloom in the Western English Channel.
101 Increases in organic matter have also been related to increases in bacterial biomass (Tait et al.
102 2015), in bacterial growth efficiency and carbon mineralization (Mayor et al. 2012), leading to
103 subsequent increases in NH_4^+ sediment flux, oxygen consumption and denitrification (Caffrey et al.
104 1993; Conley & Johnstone 1995). Whether post-disturbance benthic communities retain the
105 assimilative capacity to 'process' system-level nutrient inputs has not been adequately evaluated.

106

107 Here, we investigate how post-disturbance macro-invertebrate communities affect archaeal and
108 bacterial N-cycling community activity and composition and associated nutrient concentrations. We
109 compare communities (macro-invertebrate and microbial) from sites that have been exposed to
110 different levels of chronic fishing activity, on the *a priori* assumption that benthic macro-
111 invertebrate communities would be restructured by chronic physical disturbance and that the
112 adjusted post-disturbance community would persist long after the perturbation event (Kaiser et al.
113 2006). Further, we examine whether the effect of organic matter enrichment is sufficient to alter
114 nitrogen dynamics by activating the microbial community. Our motivation was that the addition of
115 organic matter would likely result in an increase in microbial activity, leading to increases in NH_4^+
116 sediment flux, oxygen consumption and denitrification that might be sufficient to offset any
117 negative biogeochemical effects related to faunal change associated with prior fishing activity. To
118 widen the generalizability of our conclusions, we examine the effects of chronic fishing disturbance
119 and organic matter enrichment on nitrogen cycling in different sediment types; a diffusion
120 dominated community (sandy mud) and an advection dominated community (sand). We assume
121 that the level of biogeochemical performance that is realized in either sediment type will depend at

122 least in part on the structure and composition of the post-disturbance macro-invertebrate
123 community, as the active redistribution of particles and fluids by the macrofauna disproportionately
124 influences benthic fluxes and total benthic metabolism (Mermillod-Blondin et al. 2004; Mermillod-
125 Blondin & Rosenberg 2006).

126

127 **Methods**

128

129 **Sediment collection and experimental set-up**

130 In order to investigate how the effects of organic matter enrichment (levels: Non-enriched and
131 Enriched) and previous exposure to bottom fishing (levels: Low and High) affect macro-
132 invertebrate activity and microbial transformations of nitrogen in sand (S) and in sandy mud (sM)
133 communities, we collected and maintained intact sediment cores (n = 40, 5 cores per treatment;
134 LWH, 20 × 20 × 12 cm) with their associated fauna using a 0.1 m² NIOZ (Netherlands Institute for
135 Sea Research, Texel) corer from two fishing grounds in the Irish Sea. Sandy (S) sites were located
136 off the east coast of the Isle of Man where scallop dredging for *Pecten maximus* and some otter
137 trawling for *Aequipecten opercularis* occurs, whereas sand muddy (sM) sites were located off the
138 coast of Cumbria, England, where otter trawling for *Nephrops norvegicus* and gadoid fish occurs
139 (Table 1). Logistics such as available ship time for collecting and storage space in constant-
140 temperature rooms for housing the mesocosms posed limitations on the number of within-treatment
141 replicates for this study. We acknowledge that we used a relatively small number of replicates and
142 caution that p-values close to a probability value of 0.05 should be interpreted with care;
143 nonetheless we adopt a conservative approach and present marginal (p<0.075) findings that indicate
144 possible trends. Within each fishing ground, sediment cores were collected from two sites of
145 contrasting exposure to chronic fishing disturbance (Table 1). We categorized fishing activity at
146 each site by calculating the number of times the site is swept by bottom fishing gear in a year (km²
147 swept km⁻² seabed yr⁻¹) using Vessel Monitoring System (VMS) records for UK registered vessel >

148 15 m over the 3 year period prior to our survey (further details in Sciberras et al. 2016). Since VMS
149 is only mandatory for vessels over 15 m (EC 2003), the activity of vessels smaller than 15 m,
150 particularly those between 8 and 15 m is not represented. Therefore, estimates of fishing frequency
151 may be underestimates of the actual fishing intensity, but as the spatial distribution of large and
152 small trawlers are correlated, our measure of fishing frequency is a useful indicator of the relative
153 fishing disturbance experienced by benthic communities at the sampled sites. Variation in habitat
154 characteristics (e.g. sediment grain size composition, organic matter content, water depth, bottom
155 temperature and tidal shear stress) among replicate cores collected from within each of the two
156 sediment types was minimized to ensure that any observed differences reflected differences
157 associated with changes in species composition due to fishing rather than environmental variability
158 (Table 1, Electronic Supplementary Material (ESM) 1). Sediment grain size and organic matter
159 content were determined for a separate sediment sample ($\phi = 5$ cm, 5 cm deep) taken from each
160 NIOZ core sample collected on-site. A combination of dry sieving (1 – 9.5 mm at 0.25 ϕ intervals)
161 and laser diffraction techniques (Malvern 2000 particle sizer, range: 0.21 – 1003.44 μm) were used
162 to produce a complete particle size distribution. Organic matter content was estimated by mass loss
163 on ignition of ~ 5 g of dried sediment at 550 °C for 6 hours (Holme & McIntyre 1984).

164

165 Each intact sediment core was transferred to a Perspex aquarium, overlaid by ~20 cm (8 L) of
166 ambient seawater and incubated in the laboratory in the dark at constant temperature (13°C,
167 approximating mean sea bottom temperature during the sampling period, 22-28th June 2015) for 1
168 month. The experimental period incorporated a 15 day acclimatization period prior to the addition
169 of organic matter and a 15 day experimental period following the addition of organic matter.
170 Enriched treatments (n = 20) received 50 mL of the microalga *Isochrysis galbana* on day 16
171 (concentration of ~ 22 cells μL^{-1} ; based on field observations of chlorophyll-*a* levels at ~ 10 m
172 depth for the central Celtic Sea during a typical spring algal bloom, pers. comm. Dr. Alex Poulton,

173 National Oceanography Centre, Southampton). All aquaria were aerated by bubbling with filtered
174 air for the duration of both the acclimatization and experimental periods.

175

176 **Water nutrient, microbial and macro-invertebrate community analysis**

177 A pre-filtered (0.45 μm , NALGENE) water sample was collected from approximately mid-point of
178 the overlying water column of each aquarium at the end of the experiment. Absolute concentrations
179 of ammonium ($[\text{NH}_4\text{-N}]$), nitrite ($[\text{NO}_2\text{-N}]$) and nitrate ($[\text{NO}_3\text{-N}]$) were quantified using
180 colorimetric techniques and a segmented flow nutrient autoanalyser (Bran and Luebbe, Model
181 AAIII).

182

183 To quantify abundance and activity of N-cycling associated microbes, sediment samples (1 mL)
184 were collected from the top 1 cm of the sediment from each core at the end of the experiment and
185 added to a LifeGuard Soil Preservation Solution (MoBio Laboratories, Inc., Carlsbad, California,
186 USA) and stored at -20°C until further analysis. RNA and DNA were extracted from 0.4g sediment
187 samples using the RNA PowerSoil[®] Total RNA Isolation Kit with the RNA PowerSoil[®] DNA
188 Elution Accessory Kit (MoBio Laboratories, Inc., Carlsbad, California, USA). Changes in the
189 abundance of transcripts for key nitrogen cycling processes, nitrification (archaeal and bacterial
190 ammonia monooxygenase, *amoA* that convert NH_4^+ into NO_2^- and NO_3^-), denitrification (archaeal
191 and bacterial nitrite reductase, *nirK* and *nirS* that convert NO_3^- into N_2) and anammox (hydrazine
192 oxidoreductase, *hzor* that converts NO_2^- and NH_4^+ into N_2) were analysed *via* quantitative PCR
193 (qPCR). In addition, as proxies for bacterial and archaeal abundance and activity, archaeal and
194 bacterial 16S rRNA genes and 16S RNA were also quantified. Terminal Restriction Fragment
195 Length Polymorphism (T-RFLP) was used to compare the impact of fishing frequency and organic
196 matter addition on the composition of total and active bacterial and archaeal communities. A
197 detailed methodology for RNA, DNA and gene extraction, qPCR and associated primers and T-
198 RFLP is provided in ESM2.

199

200 All invertebrates were recovered (500 μm sieve), fixed and preserved in 4 % formaldehyde solution
201 for subsequent identification to the highest practicable taxonomic resolution (mostly species) and
202 the abundance and wet weight of each taxon was measured after blotting. Tube worms were
203 weighed excluding tubes. The values of total biomass include fragments of organisms that could not
204 be assigned to specific taxa.

205

206 **Statistical analysis**

207 Statistical analyses to examine the effects of fishing frequency and organic matter enrichment on
208 benthic communities (macrofauna, microbial) and water nutrients were kept separate for sand and
209 sandy mud, primarily because the fisheries under study at the two sediment types use different
210 fishing gears and operate in distinct habitat types with taxonomically different communities and
211 because the range of fishing frequency was not comparable between the two study locations (Table
212 1). At the sandy mud fishing ground, very low or no fishing sites were characterized by different
213 habitat conditions (sediment composition, tide and wave stress) from sites where fishing occurred.
214 Therefore, sampling from sites with fishing frequency comparable to that in sand for the low fishing
215 frequency treatment would have biased our conclusions about the effects of fishing and enrichment
216 in sandy mud. The terms 'low' and 'high' are therefore used in a relative sense.

217

218 Linear regression models (full factorial, independent nominal variables: fishing frequency F,
219 organic matter enrichment E) were fitted for the response variables for the invertebrate community
220 (total invertebrate density, biomass and species richness, the ratio of suspension to deposit feeders),
221 microbial community (abundance of bacterial and archaeal nitrifiers (AOB *amoA*, AOA *amoA*),
222 denitrifiers (*AnirKa*, *nirS*), and anammox (*hzo*)) and associated concentrations of dissolved
223 inorganic nitrogen ($[\text{NH}_4\text{-N}]$, $[\text{NO}_2\text{-N}]$ and $[\text{NO}_3\text{-N}]$). The ratio of suspension to deposit feeders
224 was examined as an indicator of compositional and functional change, as high levels of suspension

225 feeder mortality (relative to deposit feeders) in fished areas have been shown to reduce the benthic
226 oxygen demand and result in higher rates of nitrification (Allen & Clarke 2007). Information on
227 species feeding mode was obtained from the biological traits database generated from the
228 BENTHIS project (Bolam et al. 2014, <http://www.benthis.eu/en/benthis/Results.htm>, accessed 16
229 July 2016). Further, to assess whether the sediment reworking potential of the macro-invertebrate
230 community differed among treatments, species were classified as epifauna (E), surficial modifiers
231 (SM), biodiffusors (B), upwards/downwards conveyors (C) and regenerator (R) following Solan et
232 al. (2004) and updated by Queiros et al. (2013). Epifaunal organisms include species that occur
233 predominantly above the sediment-water interface whose activities are limited to the near-surface
234 sediment. Surficial modifiers are organisms whose activities are mostly restricted to the uppermost
235 few centimetres of the sediment, rarely venturing above the sediment-water interface. Biodiffusors
236 include organisms with activities that usually result in a constant and random local sediment
237 biomixing over short distances (ca. 5 cm). Conveyors include burrow-building species that are
238 vertically oriented in the sediment typically feeding head-down (upward conveyors) or head-up
239 (downward conveyors) at depth in the sediment. Regenerators are excavators that dig and
240 continuously maintain burrows in the sediment and by doing so they mechanically transfer sediment
241 from depth to the surface (Solan et al. 2004; Kristensen et al. 2012). Density and biomass was
242 summed to obtain the total of each reworking mode. A linear regression model incorporating the
243 independent terms mode of sediment reworking (R_i), fishing frequency (F), organic matter
244 enrichment (E), and their interactions, was fitted for total density and total biomass. A significant
245 interaction term (F : R_i , E : R_i or F : E : R_i) would indicate that changes in total density or total
246 biomass reflect differences in response across bioturbation groups that depend on fishing frequency
247 and/or organic matter enrichment.

248

249 Where there was evidence of violation of homogeneity of variance, the data were analyzed using a
250 generalised least squares (GLS) estimation procedure to allow the residual spread to vary with

251 individual independent variables (Zuur et al. 2009). To determine the optimal variance structure, we
252 compared the full linear regression models to the equivalent GLS models incorporating specific
253 variance structures using Akaike information criteria (AIC) and by inspection of model residual
254 patterns. The optimal fixed-effects structure was then obtained by applying a backward selection
255 using the likelihood ratio test obtained by maximum-likelihood (ML) estimation. Following Zuur et
256 al. (2009), the optimal model was estimated using REML estimation. Homogeneity of residuals was
257 established through visual examination of plotted standardized residuals versus fitted values. All
258 analyses were performed using the *nlme* package (v. 3.1, Bates et al. 2013) in the R statistical and
259 programming environment (R Development Core Team 2005). A summary of the linear regression
260 models output is presented in Table 2 and 3, coefficient tables that indicate the direction and
261 magnitude of differences among treatments are presented in supplementary material, ESM 3. Unless
262 indicated differently, univariate results are expressed as mean \pm standard error.

263

264 Differences in macrofaunal and microbial community composition associated with different fishing
265 frequency and organic matter enrichment treatments were examined using PERMANOVA
266 (Permutational analysis of variance). The relative contribution of species to significant effects was
267 identified using SIMPER (Similarity percentages). All PERMANOVA and SIMPER analyses were
268 conducted in PRIMER-E (Version 7, <http://www.primer-e.com/>).

269

270 **Results**

271

272 **Sandy sediments**

273 Macro-invertebrate density ranged from 100 to 3700 ind. m⁻², total biomass from 1 to 853.25 gWW
274 m⁻² and species richness from 3 to 22, but were not affected by fishing frequency or organic matter
275 enrichment (Models 1 – 3, Table 2a). However, the ratio of suspension to deposit feeders (Model
276 4, Table 2a, Figure 1a) and overall macro-invertebrate composition (PERMANOVA, density:

277 Pseudo-F = 6.79, p = 0.001; biomass: Pseudo-F = 2.56, p = 0.009; nMDS Figure 1b) were
278 dependent on the frequency of fishing. The nMDS ordination for density and biomass data was very
279 similar, therefore only that for density is presented in Figure 1b. Deposit feeders such as the
280 polychaete *Lagis koreni* and the echinoderms *Leptosynapta inhaerens*, *Echinocardium cordatum*
281 and *Echinocyamus pusillus* were more abundant than suspension feeders in communities that had
282 previously experienced a low frequency of bottom fishing (density: deposit feeders = 635 ± 155 ind.
283 m^{-2} , suspension feeders = 92.5 ± 20 ind. m^{-2}), whereas suspension feeders such as *Phoronis* sp.,
284 *Owenia fusiformis* and *Abra alba* were more abundant in communities that had previously
285 experienced a high frequency of bottom fishing (density: deposit feeders = 262.5 ± 70 ind. m^{-2} ,
286 suspension feeders = 357.5 ± 47.5 ind. m^{-2}) (Table 3a). Compositional differences were largely
287 associated with a higher density of echinoderms (in particular *L. inhaerens*, *E. cordatum*, juvenile
288 asteroids and *E. pusillus*) at lower fishing frequency, and a higher density of polychaetes (*O.*
289 *fusiformis*, *Magelona* spp., *Sthenelais limicola*, *Ophelina acuminata* and *Chaetozone* sp.) (SIMPER,
290 Table 3a) and larger individuals of *E. cordatum* (34g) and the bivalves *Acanthocardia echinata*
291 (6g), *Chamelea striatula* (3g) and *Thracia phaseolina* (1.4 g) at the higher fishing frequency sites
292 (SIMPER, Table 3b).

293

294 Sediment reworking group density depended on the interactive effects of sediment reworking group
295 identity and the frequency of fishing (Model 5, Table 2a); biodiffusor (e.g. *E. cordatum*, *Glycera*
296 *oxycephala*) and conveyor species (e.g. *L. koreni*, *T. phaseolina*, *Spiophanes bombyx*) were more
297 abundant after a low frequency of fishing (density: 492.5 ± 133.28 ind. m^{-2} and 430 ± 172.92 ind. m^{-2} ,
298 respectively) than they were after a high frequency of fishing (density: 180 ± 80.78 ind. m^{-2} and
299 197.5 ± 42.89 ind. m^{-2} , respectively) (Figure 2a). Sediment reworking group biomass, however, was
300 dependent on the independent effects (Model 6, Table 2a) of organic matter enrichment (Figure 2b)
301 and sediment reworking group identity (Figure 2c), with a greater biomass attributed to biodiffusors

302 (e.g. *E. cordatum*, *Sigalion mathilde*, *Lumbrineris* sp.) and when sediments were enriched with
303 organic matter.

304

305 T-RFLP profiling for archaeal and bacterial 16S rRNA genes revealed significant differences in the
306 total microbial community structure between communities that experienced low and high frequency
307 of fishing activity (PERMANOVA: Archaea, Pseudo-F = 2.22, $p = 0.05$; Bacteria, Pseudo-F = 4.03,
308 $p = 0.03$), but not among enriched and non-enriched treatments (Archaea, Pseudo-F = 0.66, $p =$
309 0.61; Bacteria, Pseudo-F = 0.92, $p = 0.42$; ESM4 Figure S2). The density of the metabolically
310 active bacterial denitrifier (*nirS*) was dependent on the independent effects of fishing frequency
311 (Figure 3a) and organic matter enrichment (Figure 3b), whilst both archaeal (*AnirKa*) denitrifiers
312 (Figure 3c) and anammox (*hzo*) hydrazine oxidoreductase transcripts (Figure 3d) were dependent
313 solely on the effect of fishing frequency (Models 7 – 9, Table 2a). We found no evidence that the
314 density of bacterial (AOB *amoA*) or archaeal (AOA *amoA*) ammonia oxidisers, or ammonia
315 oxidiser community structure (AOB:AOA *amoA* ratio) were affected by the frequency of fishing or
316 the level of organic matter enrichment (Models 10 – 12, Table 2a).

317

318 For nutrients, we found that $[\text{NO}_2\text{-N}]$ and $[\text{NO}_3\text{-N}]$ were dependent on an independent effect of
319 fishing frequency (Models 13–14, Table 2a, Figure 4), whilst $[\text{NH}_4\text{-N}]$ was not affected by fishing
320 frequency or organic matter enrichment (Model 15, Table 2a).

321

322 **Sandy Mud sediments**

323 Relative to sandy sediments, total density (25 to 450 ind. m^{-2}), total biomass (0.8 to 119.8 gWW m^{-2})
324 and species richness (1 to 9) were lower in sandy mud macro-invertebrate communities. Total
325 macro-invertebrate density (Model 16, Table 2b, Figure 5a, b) and species richness (Model 17,
326 Table 2b, Figure 5c,d) were dependent on the independent effects of fishing frequency and organic
327 matter enrichment. Mean total density and species richness were highest for communities that had

328 experienced a greater frequency of fishing (density: $227.5 \pm 40.5 \text{ m}^{-2}$; species richness: 5.00 ± 0.89
329 core^{-1}) or organic matter enrichment (density: $200.00 \pm 30.51 \text{ m}^{-2}$, species richness: 4.70 ± 0.68
330 core^{-1}). In contrast, we found no evidence of any macro-faunal response in terms of biomass (Model
331 18, Table 2b). Similarly, the ratio of suspension to deposit feeders did not differ between any of our
332 treatments (Model 19, Table 2b). Sediment reworking group density (Model 20, Table 2b),
333 however, reflected the independent effects of fishing frequency (Figure 5e), organic matter
334 enrichment (Figure 5f) and sediment reworking group identity (Figure 5g), whilst sediment
335 reworking group biomass was influenced solely by sediment reworking group identity (Model 21,
336 Table 2b with a greater biomass attributed to biodiffusors (e.g. *Goneplax rhomboides*, *Nephtys* sp.)
337 (Figure 5h). Nevertheless, community composition did not differ between sites of low and high
338 fishing frequency (PERMANOVA, density: Pseudo-F = 1.30, $p = 0.25$; biomass, Pseudo-F = 1.37,
339 $p = 0.22$, ESM 5) or between enriched and non-enriched treatments (density: Pseudo-F = 0.82, $p =$
340 0.55 ; biomass: Pseudo-F = 0.74, $p = 0.63$) (Figure 6).

341

342 T-RFLP profiling for archaeal and bacterial 16S rRNA genes did not reveal any differences in total
343 microbial community structure that related to either fishing frequency (PERMANOVA, Archaea:
344 Pseudo-F = 1.07, $p = 0.37$; Bacteria: Pseudo-F = 1.47, $p = 0.15$), or organic matter enrichment
345 (Archaea: Pseudo-F = 0.23, $p = 0.95$; Bacteria: Pseudo-F = 1.29, $p = 0.24$) (ESM4 Figure S3).
346 Indeed, we were unable to find any evidence supporting the view that bacterial denitrifiers (*nirS*
347 transcripts, range: 903 – 6330 copies g^{-1} sediment), anammox (*hzs* transcripts, range: 3160 –
348 165000 copies g^{-1} sediment) or bacterial (AOB *amoA* transcripts, range: 1270 – 251000 copies g^{-1}
349 sediment) or archaeal ammonia oxidisers (AOA *amoA* transcripts, range: 2700 – 83900 copies g^{-1}
350 sediment) respond to differences in fishing frequency or organic matter enrichment (Models 22, 24–
351 26, Table 2b). In contrast, however, archaeal (*AnirKa*) denitrifiers did respond (Model 23, Table
352 2b) positively to the effects of increasing fishing frequency (Figure 7a) and negatively to increasing
353 organic matter enrichment (Figure 7b), although these effects were independent of one another. We

354 also found evidence that the mean ratio of bacterial to archaeal ammonia oxidisers (AOB : AOA
355 *amoA*) increased with organic matter enrichment (Model 27, Table 2b, Figure 7c).

356

357 Despite changes in the microbial and macrofaunal attributes of our sandy mud communities, [NH₄-
358 N], [NO₂-N] and [NO₃-N] were not affected by fishing frequency or organic matter enrichment
359 (Models 28 – 30, Table 2b).

360

361 **Discussion**

362

363 Our findings suggest that nitrogen transformation in shelf sea sediments is dependent on whether
364 specific microbial transcripts are influenced by differences in the composition of the bioturbating
365 macrofauna, environmental context (here, nutrient enrichment and sediment type), and recent
366 history of anthropogenic disturbance (here, frequency of bottom fishing), although these effects are
367 not necessarily interactive and their relative importance is context dependent (Wohlgemuth et al.
368 2017). We find that the modification of invertebrate community structure following bottom fishing
369 is particularly important for the mediation of biogeochemical processes and is not necessarily offset
370 by the effects of organic matter enrichment on microbial composition and activity. These effects
371 were observed in sand but not in sandy mud (where the range of fishing frequency from bottom-
372 towed fishing gear was higher than that in the sandy area). In sand, we found that sediment
373 characterized by higher ratios of suspension to deposit feeders and a lower density but higher
374 biomass of bioturbating fauna, was associated with increased activity of denitrifying archaea and
375 bacteria (*AnirKa*, *nirS*) and anammox (*hzs*) and higher levels of bottom water [NO₂-N] and [NO₃-
376 N]. The higher biomass of bioturbating species, in particular *Echinocardium cordatum*,
377 *Acanthocardia echinata* and *Chamelea striatula* and the higher density of bioirrigating tube-
378 building species such as *Phoronis* sp. and *Owenia fusiformis*, offers an explanation for the enhanced
379 denitrifier activity. *E. cordatum* is known to displace large volumes of sediment (20 000 cm³ m⁻² d⁻¹

380 by 40 individuals m⁻², Lohrer et al. 2005) and although the shallow-burying bivalves *A. echinata*
381 and *C. striatula* and the tube-building polychaetes do not build extensive burrow systems deep
382 within the sediment, their active mixing of the uppermost sediment layers and their dominating
383 biomass, means that their bioturbation activities are likely to have stimulated microbial
384 denitrification and anammox, possibly by increasing the flux of [NO₂-N] and [NO₃-N] across the
385 water-sediment interface, which constitutes the substrate for nitrite reductase and anammox (Howe
386 et al. 2004; Dang et al. 2010). Measured sediment particle reworking rates using fluorescent
387 sediment profile imaging techniques at the same study sites confirm more intense particle
388 reworking activity in communities that have previously experienced a higher frequency of bottom
389 fishing, substantially extending the maximum depth of sediment reworking (low frequency fishing,
390 1.99 ± 0.19 cm; high frequency fishing, 4.64 ± 0.5 cm) and increasing the volume of sediment
391 available for nitrification (Hale et al. 2017). It is interesting to note that, although some bioturbation
392 groups - such as biodiffusors and upwards/downwards conveyors – were, on average, twice as
393 abundant at sites with a history of low frequency of fishing, the biomass of biodiffusors and
394 surficial modifiers was substantively higher (24 times and 60 times higher, respectively) at sites
395 with a history of high frequency of fishing. It appears that biomass had an overriding effect over
396 density; larger individuals with a greater *per capita* effect on sediment mixing have a
397 disproportionate effect on microbial activity and composition and, in turn, nutrient concentrations
398 (Osinga et al. 1995; Bird et al. 1999). The increased abundance of active suspension feeders
399 (relative to deposit feeders) is also likely to have stimulated microbial denitrification and anammox,
400 through an increase in the provision of [NO₂-N] and [NO₃-N] as water is actively moved into the
401 sediment during feeding (Howe et al. 2004; Dang et al. 2010). Although we may conclude that
402 macrofaunal bioturbation and bioirrigation activities had a stimulatory effect on microbial
403 denitrification, it remains unclear why we did not detect any change in archaeal or bacterial nitrifier
404 (*amoA* gene) abundance in either sand or sandy mud sediments.

405

406 Given the findings elsewhere that report higher mortality of suspension feeders at locations that are
407 subject to fishing activity (e.g. Tillin et al. 2006; van Denderen et al. 2015), it is surprising that we
408 found a higher ratio of suspension to deposit feeders in sand communities that experienced a higher
409 frequency of chronic fishing. However, a clear trend that emerges from previous studies is that the
410 degree of natural disturbance in which a community develops determines the degree to which it is
411 affected by bottom fishing (Kaiser & Spencer 1996; Hiddink et al. 2006; Sciberras et al. 2013). The
412 macro-invertebrate communities at our sandy study sites are adapted to living in physically dynamic
413 areas that are characterized by relatively high near-bed current flows (Hiddink et al. 2009) and
414 infrequent fishing activity (1.63 times yr⁻¹), so community recruitment and growth is unlikely to be
415 significantly affected by fishing. In contrast, the macro-invertebrate communities of our sandy mud
416 sites show substantive compositional changes that relate to a fishing frequency of 3.8 times yr⁻¹,
417 such that further increases in fishing activity (8.4 times yr⁻¹) have proportionally less effect on
418 microbial and/or macrofaunal community composition and structure. We recognize that our study
419 would benefit from additional locations where bottom fishing is absent, but such areas were not
420 comparable as they were characterized by very different habitat conditions (sediment composition,
421 tide and wave stress). In agreement with Braeckman et al. (2014), however, we find that that
422 benthic functional diversity (expressed as community bioturbation potential, BP_C) had a strong
423 influence on biogeochemical cycling (sediment community oxygen consumption, denitrification
424 rates, alkalinity and NH₄ fluxes) in sandy sediments with high BP_C but not in muddy sediments,
425 where the BP_C was found to be significantly lower than in sand.

426
427 We hypothesized that the addition of organic matter would increase microbial activity (measured
428 here as the gene transcript abundance). Thus, the correlation between enrichment and macrofaunal
429 density and species richness in sandy mud and the relative biomass of different functional groups in
430 sand was unexpected (given the short time scale of the experiment) and most likely the result of
431 stochastic variation in the abundance of infauna and unrelated to the enrichment treatment.

432 However, in sandy sediments, organic matter enrichment correlated with a reduction in the variation
433 and mean activity of bacterial denitrifiers (*nirS*), and in sandy mud sediments with a reduction in
434 mean activity of archaeal denitrifiers (*AnirKa*), and a change in ammonia oxidiser community
435 structure, altering the ratio of ammonia oxidising bacteria to ammonia oxidising archaea (as in
436 Gilbertson et al. 2012). An effect, however, was not found for all microbes measured, for example
437 for the nitrifiers (AOB *amoA*, AOA *amoA*) and anammox (*hzs*) in either sand or sandy mud. A
438 number of studies have reported increases in bacterial biomass and activity upon addition of organic
439 material within days or even hours (e.g. Luna et al. 2002; Gihring et al. 2009). However, others
440 have reported a delayed microbial response (~ 1 - 2 weeks) (Tait et al. 2015) as instead of feeding
441 directly on sinking phytodetrital material, benthic microbes may consume the organic matter
442 released via the grazing activity of deposit and suspension feeders, thus explaining the lack of
443 response for some microbes in our study. The lesser importance of organic matter enrichment
444 relative to fishing frequency related changes in macrofaunal composition documented here, may be
445 emphasising habitat-specific differences in organic matter incorporation rate and/or differences in
446 the response time of different components of the benthic community. Our study highlights the
447 importance of understanding the response of multiple ecosystem components over the longer term if
448 we are to provide ecosystem-relevant evidence to underpin decisions that aim to secure the
449 protection of natural capital (Pittman & Armitage, 2016), and ensure the sustainable management of
450 coastal and shelf sea ecosystem services (Voss et al. 2013).

451

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462 [6c86abc0d02c/](https://www.bodc.ac.uk/data/published_data_library/catalogue/10.5285/46ecc183-c08d-2211-e053-6c86abc0d02c/) (doi:10.5285/46ecc183-c08d-2211-e053-6c86abc0d02c).

463 **References**

464

465 Allen JI, Clarke KR (2007) Effects of demersal trawling on ecosystem functioning in the North Sea:
466 a modelling study. *Mar Ecol Prog Ser* 336:63-75

467

468 Bates S, Deepayan S and the R Development Core Team (2013) nlme: Linear and Nonlinear
469 Mixed Effects Models. R package version 3.1-113

470

471 Bertics VJ, Ziebis W (2009) Biodiversity of benthic microbial communities in bioturbated coastal
472 sediments is controlled by geochemical microniches. *ISME J* 3:1269-1285

473

474 Bird FL, Ford PW, Hancock GJ (1999) Effect of burrowing macrobenthos on the flux of dissolved
475 substances across the water-sediment interface. *Mar Freshwater Res* 50:523-532

476

477 Bolam SG, Coggan RC, Eggleton J, Diesing M, Stephens D (2014) Sensitivity of macrobenthic
478 secondary production to trawling in the English sector of the Greater North Sea: A biological trait
479 approach. *J Sea Res* 85:162–177

480

481 Braeckman U, Yazdani Foshtoni M, Van Gansbeke D, Meysman F, Soetaert K, Vincx M,
482 Vanaverbeke J (2014) Variable importance of macrofaunal functional biodiversity for
483 biogeochemical cycling in temperate coastal sediments. *Ecosystems* 17:720-737

484

485 Caffrey JM, Sloth NP, Kaspar HF, Blackburn TH (1993) Effect of organic loading on nitrification
486 and denitrification in a marine sediment microcosm. *FEMS Microbiol Ecol* 12:159-167

487

488 Conley DJ, Johnstone RW (1995) Biogeochemistry of N, P and Si in Baltic Sea sediments: response
489 to a simulated deposition of a spring diatom bloom. *Mar Ecol Prog Ser* 122:265-276
490

491 Dale AW, Prego R (2002) Physico-biogeochemical controls on benthic-pelagic coupling of nutrient
492 fluxes and recycling in a coastal upwelling system. *Mar Ecol Prog Ser* 235:15–28
493

494 Dang H, Chen R, Wang L, Guo L, Chen P, Tang Z, Tian F, Li S, Klotz MG (2010) Environmental
495 factors shape sediment anammox bacterial communities in hypereutrophic Jiaozhou Bay, China.
496 *Appl Environ Microb* 76:7036-7047
497

498 Duplisa DE, Jennings S, Malcolm SJ, Parker R, Sivyer DB (2001) Modelling potential impacts of
499 bottom trawl fisheries on soft sediment biogeochemistry in the North Sea. *Geochem Trans* 2:112-
500 117
501

502 Falcão M, Gaspar MB, Caetano M, Santos MN, Vale C (2003) Short-term environmental impact of
503 clam dredging in coastal waters (south of Portugal): chemical disturbance and subsequent recovery
504 of seabed. *Mar Environ Res* 56: 649–664
505

506 Fanjul E, Grela MA, Iribarne O (2007) Effects of the dominant SW Atlantic intertidal burrowing
507 crab *Chasmagnathus granulatus* on sediment chemistry and nutrient distribution. *Mar Ecol Prog Ser*
508 341:177–190
509

510 Fiordelmondo C, Manini E, Gambi C, Pusceddu A (2003) Short-term impact of clam harvesting on
511 sediment chemistry, benthic microbes and meiofauna in the Goro Lagoon (Italy). *Chem Ecol*
512 19:173-187
513

514 Franco MA, Mesel I, Demba Diallo M, Gucht VDK, Gansbeke VD, Van Rijswijk P, Costa MJ,
515 Vincx M, Vanaverbeke J (2007) Effect of phytoplankton bloom deposition on benthic bacterial
516 communities in two contrasting sediments in the southern North Sea. *Aquat Microb Ecol* 48:241–
517 254
518

519 Gihring TM, Humphrys M, Mills HJ, Huettel M, Kostka JE (2009) Identification of phytodetritus-
520 degrading microbial communities in sublittoral Gulf of Mexico sands. *Limnol Oceanogr* 54:1073–
521 1083
522

523 Gilbertson WW, Solan M, Prosser JI (2012) Differential effects of microorganism-invertebrate
524 interactions on benthic nitrogen cycling. *FEMS Microb Ecol* 82:11-22
525

526 Goldberg R, Rose JM, Mercaldo-Allen R, Meseck SL, Clark P, Kuropat C, Pereira JJ (2014) Effects
527 of hydraulic dredging on the benthic ecology and sediment chemistry on a cultivated bed of the
528 Northern quahog, *Mercenaria mercenaria*. *Aquaculture* 428:150-157
529

530 Hale R, Godbold JA, Sciberras M, Dwight J, Wood C, Hiddink JG, Solan M (2017) Mediation of
531 macronutrients and carbon by post-disturbance shelf sea sediment communities. *Biogeochemistry*.
532 DOI 10.1007/s10533-017-0350-9
533

534 Hiddink JG, Davies TW, Perkins M, Machairopoulou M, Neill SP (2009) Context dependency of
535 relationships between biodiversity and ecosystem functioning is different for multiple ecosystem
536 functions. *Oikos* 118:1892-1900
537

538 Hiddink JG, Jennings S, Kaiser MJ, Queiros AM, Duplisea DE, Piet GJ (2006) Cumulative impacts
539 of seabed trawl disturbance on benthic biomass, production, and species richness in different
540 habitats. *Can J Fish Aquat Sci* 63:721-736
541

542 Holme NA, McIntyre AD (1984) *Methods for the study of marine benthos*. Blackwell Scientific
543 Publications, London
544

545 Howe RL, Rees AP, Widdicombe S (2004) The impact of two species of bioturbating shrimp
546 (*Callianassa subterranea* and *Upogebia deltaura*) on sediment denitrification. *J Mar Biol Assoc*
547 UK 84:629–632
548

549 Kaiser MJ, Clarke KR, Hinz H, Austen MCV, Somerfield PJ, Karakassis I (2006) Global analysis
550 of response and recovery of benthic biota to fishing. *Mar Ecol Prog Ser* 311:1–14
551

552 Kaiser MJ, Spencer BE (1996) The effects of beam trawl disturbance on infaunal communities in
553 different habitats. *J Anim Ecol* 65:348–358
554

555 Kitidis V, Tait K, Nunes J, Brown I, Woodward EMS, Harris C, Sabadel AJM, Sivyer DB, Silburn
556 B, Kröger S (accepted) Seasonal Benthic Nitrogen Cycling in a temperate Shelf Sea: the Celtic Sea.
557 *Biogeochemistry*: DOI: 10.1007/s10533-017-0311-3
558

559 Kristensen E, Penha-Lopes G, Delefosse M, Valdemarsen T, Quintana CO, Banta GT (2012) What
560 is bioturbation? The need for a precise definition for fauna in aquatic sciences. *Mar Ecol Prog Ser*
561 446:285-302
562

563 Lambert GI, Jennings S, Kaiser MJ, Davies TW, Hiddink JG (2014) Quantifying recovery rates and
564 resilience of seabed habitats impacted by bottom fishing. *J Appl Ecol* 51:1326-1336
565

566 Laverock B, Gilbert JA, Tait K, Osborn AM, Widdicombe S (2011) Bioturbation: impact on the
567 marine nitrogen cycle. *Biochem Soc Trans* 39:315-320
568

569 Laverock B, Tait K, Gilbert JA, Osborn AM, Widdicombe S (2014) Impacts of bioturbation on
570 temporal variation in bacterial and archaeal nitrogen-cycling gene abundance in coastal sediments.
571 *Environ Microb Rep* 6:113-121
572

573 Levin L, Blair N, DeMaster D, Plaia G, Fornes W, Martin C, Thomas C (1997) Rapid subduction of
574 organic matter by maldanid polychaetes on the North Carolina slope. *J Mar Res* 55:595-611
575

576 Lohrer AM, Thrush SF, Hunt L, Hancock N, Lundquist C (2005) Rapid reworking of subtidal
577 sediments by burrowing spatangoid urchins. *J Exp Mar Biol Ecol* 321:155-169
578

579 Luna GM, Manini E, Danovaro R (2002) Large fraction of dead and inactive bacteria in coastal
580 marine sediments: Comparison of protocols for determination and ecological significance. *Appl*
581 *Environ Microb* 68:3509-3513
582

583 Mayer LM, Schick DF, Findlay R, Rice DL (1991) Effects of commercial dragging on sedimentary
584 organic matter. *Mar Environ Res* 31:249-261
585

586 Mayor DJ, Thornton B, Zuur AF (2012) Resource quantity affects benthic microbial community
587 structure and growth efficiency in a temperate intertidal mudflat. *PLoS One* 7:1-6
588

589 Mermillod-Blondin F, Rosenberg R, Francois-Carcaillet F, Norling K, Mauclair L (2004)
590 Influence of bioturbation by three benthic infaunal species on microbial communities and
591 biogeochemical processes in marine sediment. *Aquat Microb Ecol* 36:271-284
592

593 Mermillod-Blondin F, Rosenberg R (2006) Ecosystem engineering: The impact of bioturbation on
594 biogeochemical processes in marine and freshwater benthic habitats. *Aquat Sci* 68:434–442
595

596 Olsgard F, Schaanning MT, Widdicombe S, Kendall MA, Austen MC (2008) Effects of bottom
597 trawling on ecosystem Functioning. *J Exp Mar Biol Ecol* 366:123-133
598

599 Osinga R, Lewis WE, Wopereis JLM, Vriezen C, van Duyl FC (1995) Effects of the sea urchin
600 *Echinocardium cordatum* on oxygen uptake and sulfate reduction in experimental benthic systems
601 under increasing organic loading. *Ophelia* 41:221-236
602

603 Pilskaln CH, Churchill JH, Mayer LM (1998) Resuspension of sediment by bottom trawling in the
604 Gulf of Maine and potential geochemical consequences. *Conserv Biol* 12:1223-1229
605

606 Pittman J, Armitage D (2016) Governance across the land-sea interface: A systematic review.
607 *Environ Sci Pol* 64:9-17
608

609 Quijón PA, Kelly MC, Snelgrove PVR (2008) The role of sinking phytodetritus in structuring
610 shallow-water benthic communities. *J Exp Mar Biol Ecol* 366:134–145
611

612 Queiros AM, Birchenough SNR, Bremner J, et al (2013) A bioturbation classification of European
613 marine infaunal invertebrates. *Ecol Evol* 3: 3958-3985
614

615 Rysgaard S, Risgaard-Petersen N, Sloth NP, Jensen K, Nielsen LP (1994) Oxygen regulation of
616 nitrification and denitrification in sediments. *Limnol Oceanogr* 39:1643–1652
617

618 Small C, Nicholls RJ (2003) A global analysis of human settlement in coastal zones. *J Coast Res*
619 19:584-599
620

621 Sciberras M, Hinz h, Bennell JD, Jenkins SR, Hawkins SJ, Kaiser MJ (2013) Benthic community
622 response to a scallop dredging closure within a dynamic seabed habitat. *Mar Ecol Prog Ser* 480:83-
623 98
624

625 Sciberras M, Parker R, Powell C, Robertson C, Kroeger S, Bolam S, Hiddink JG (2016) Impacts of
626 bottom fishing on the sediment infaunal community and biogeochemistry of cohesive and non-
627 cohesive sediments. *Limnol Oceanogr* (doi: 10.1002/lno.10354)
628

629 Solan M, Cardinale B, Downing AL, Engelhardt KAM, Ruesink JL, Srivastava DS (2004)
630 Extinction and ecosystem function in the marine benthos. *Science* 12:1177-1180
631

632 Tait K, Airs RL, Widdicombe CE, Tarran GA, Jones MR, Wddicombe S (2015) Dynamic responses
633 of the benthic bacterial community at the Western English Channel observatory site L4 are driven
634 by deposition of fresh phytodetritus. *Prog Oceanogr* 137:546-558
635

636 Tillin HM, Hiddink JG, Jennings S, Kaiser MJ (2006) Chronic bottom trawling alters the functional
637 composition of benthic invertebrate communities on a sea-basin scale. *Mar Ecol Prog Ser* 318:31-45
638

639 Trimmer M, Petersen J, Sivyer DB, Mills C, Young E, Parker ER (2005) Impact of long-term
640 benthic trawl disturbance on sediment sorting and biogeochemistry in the southern North Sea. *Mar*
641 *Ecol Prog Ser* 298:79–94
642
643 van Denderen PD, Bolam SG, Hiddink JG, Jennings S, Kenny A, Rijnsdorp AD, van Kooten T
644 (2015) Similar effects of bottom trawling and natural disturbance on composition and function of
645 benthic communities across habitats. *Mar Ecol Prog Ser* 541:31–43
646
647 van Oevelen D, Soetaert K, Franco MA, Moodley L, van Ijzerloo L, Vincx M, Vanaverbeke J
648 (2009) Organic matter input and processing in two contrasting North Sea sediments: insights from
649 stable isotope and biomass data. *Mar Ecol Prog Ser* 380:19–32
650
651 Voss M, Bange HW, Dippner JW, Middelburg JJ, Montoya JP, Ward B (2013) The marine nitrogen
652 cycle: recent discoveries, uncertainties and the potential relevance of climate change. *Philos T Roy*
653 *Soc B* 368:1-11
654
655 Warnken, KW, Gill GA, Dellapenna TM, Lehman RD, Harper DE, Allison MA (2003) The effects
656 of shrimp trawling on sediment oxygen consumption and the fluxes of trace metals and nutrients
657 from estuarine sediments. *Estuar Coast Shelf Sci* 57:25–42
658
659 Watling L, Findlay RH, Mayer LM, Schick DF (2001) Impact of a scallop drag on the sediment
660 chemistry, microbiota and faunal assemblages of a shallow subtidal marine benthic community. *J*
661 *Sea Res* 46:309-324
662

663 Widdicombe S, Austen MC, Kendall MA, Olsgard F, Schaanning MT, Dashfield SL, Needham HR
664 (2004) The importance of bioturbators for biodiversity maintenance: the indirect effect of fishing
665 disturbance. *Mar Ecol Prog Ser* 275:1–10

666

667 Wohlgemuth D, Solan M, Godbold JA (2017) Species contributions to ecosystem process and
668 function can be population dependent and modified by biotic and abiotic setting. *Proc R Soc B*
669 284:20162805

670

671 Zehr JP, Kudela RM (2011) Nitrogen Cycle of the Open Ocean: From Genes to Ecosystems. *Annu*
672 *Rev Mar Sci* 3:197-22

673

674 Zhang Q, Warwick RM, McNeill CL, Widdicombe CE, Sheehan A, Widdicombe S (2015) An
675 unusually large phytoplankton spring bloom drives rapid changes in benthic diversity and
676 ecosystem function. *Prog Oceanogr* 137:533-545

677

678 Zuur AF, Iena EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions
679 in ecology with R. Springer, New York, USA

680

681 **Table 1.** Summary of environmental characteristics and bottom fishing frequency of our study sites. The mean \pm SE (n = 10) values for percentage
682 sand, percentage mud and organic matter content (mg) for areas that have experienced low and high fishing frequency in sandy Mud (sM-low and sM-
683 high) and sandy sediments (S-low and S-high) are listed.

684

Site code	Geographical location (latitude, longitude)	Fishing frequency (times fished per annum)	Depth (m)	Tide stress (Nm ⁻²)	Wave stress (Nm ⁻²)	Sand (%)	Mud (%)	Organic matter (mg)
sM - low	54.15 N, -3.63 W	3.8	26.00	0.17	0.69	33.48 \pm 2.62	66.48 \pm 2.62	70 \pm 6.33
sM - high	54.26 N, -3.73 W	8.4	28.54	0.22	0.68	36.43 \pm 1.98	63.55 \pm 1.99	90 \pm 12.65
S - low	54.20 N, -4.05 W	0.25	19.80	0.17	1.00	99.51 \pm 0.38	0.02 \pm 0.02	40 \pm 6.33
S - high	54.26 N, -4.19 W	1.63	18.79	0.11	0.73	94.2 \pm 0.68	4.7 \pm 0.53	70 \pm 9.49

685

686

687 **Table 2a.** Linear regression models to examine the effects of fishing frequency and enrichment (full factorial, $F \times E$) **in sand (S)**, for macro-
688 invertebrate community (Models 1-4: invertebrate density, biomass and species richness, the ratio of suspension to deposit feeders), sediment
689 reworking groups (Ri, reworking group density and biomass, Models 5-6), microbial community (Models 7-12: abundance of bacterial and archaeal
690 denitrifiers (*AnirKa*, *nirS*), anammox (*hzo*), bacterial and archaeal nitrifiers (AOB *amoA*, AOA *amoA*) and ratio of bacterial and archaeal *amoA*
691 transcripts) and associated levels of dissolved inorganic nitrogen (Models 13 -15: [NO₂-N], [NO₃-N], [NH₄-N]). The test statistic (L-ratio or F value),
692 degrees of freedom (df) and probability value (p) are listed for marginal ($p < 0.075$) or significant ($p < 0.05$) terms. Where all independent variables
693 were found insignificant, we present the intercept only model. The class of variance-covariate used to specify different variances for each level of
694 stratification within-group are also provided.

695

Sediment type: SAND (S)									
Macro-invertebrate community (Initial linear model: Response variable ~ F × E)									
Model ID	Model	Response variable	Fishing frequency (F)	Enrichment (E)	Interaction (F : E)	Intercept only	Variance-covariate		
1	GLS	Macro-invertebrate density				L = 2.54, df = 1, p = 0.11	E		
2	GLS	Macro-invertebrate biomass				L = 3.37, df = 1, p = 0.07	E × F		
3	GLS	Species richness				L = 1.32, df = 1, p = 0.25	E		
4	GLS	suspension: deposit feeders ratio	L = 17.07, df = 1, p < 0.001				F		
Sediment reworking groups (Initial linear model: Response variable ~ F × E × Ri)									
Model ID	Model	Response variable	Fishing frequency (F)	Enrichment (E)	Reworking mode (Ri)	F : E	F : Ri	Intercept only	Variance-covariate
5	GLS	Ri density					L = 15.92, df = 4, p = 0.003		Ri × F
6	GLS	Ri biomass		L = 4.09, df = 1, p = 0.04	L = 27.05, df = 4, p <				Ri × F

				0.0001			
Abundance of active N-cycling associated microbes (Initial linear model: Response variable ~ F × E)							
Model ID	Model	Response variable	Fishing frequency (F)	Enrichment (E)	Interaction (F : E)	Intercept only	Variance-covariate
7	GLS	<i>nirS</i>	L = 3.63, df = 1, p = 0.05	L = 11.26, df = 1, p < 0.001			F
8	GLS	<i>AnirKa</i>	L = 6.41, df = 1, p = 0.01				E × F
9	GLS	<i>hzo</i>	L = 6.59, df = 1, p = 0.01				F
10	GLS	AOA <i>amoA</i>				L = 1.25, df = 1, p = 0.26	E
11	GLS	AOB <i>amoA</i>				L = 2.50, df = 1, p = 0.11	F
12	GLS	AOB : AOA <i>amoA</i> ratio				L = 3.28, df = 1, p = 0.07	E
Water nutrient concentration (Initial linear model: Response variable ~ F × E)							
Model ID	Model	Response variable	Fishing frequency (F)	Enrichment (E)	Interaction (F : E)	Intercept only	Variance-covariate
13	GLS	[NO ₂ -N]	L = 5.99, df = 1, p = 0.01				F
14	GLS	[NO ₃ -N]	L = 19.47, df = 1, p < 0.0001				F × E
15	GLS	[NH ₄ -N]				L = 1.12, df = 1, p = 0.29	E × F

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699 **Table 2b.** Linear regression models to examine the effects of fishing frequency and enrichment (full factorial, $F \times E$) in sandy mud (sM), for macro-
700 invertebrate community (Models 16-19: invertebrate density, biomass and species richness, the ratio of suspension to deposit feeders), sediment
701 reworking groups (R_i , reworking group density and biomass, Models 20-21), microbial community (Models 22-27: abundance of bacterial and archaeal
702 denitrifiers (*nirS*, *AnirKa*), anammox (*hzo*), bacterial and archaeal nitrifiers (AOB *amoA*, AOA *amoA*) and ratio of bacterial and archaeal *amoA*
703 transcripts) and associated levels of dissolved inorganic nitrogen (Models 28-30: $[NO_2-N]$, $[NO_3-N]$, $[NH_4-N]$). The test statistic (L-ratio or F value),
704 degrees of freedom (df) and probability value (p) are listed for marginal ($p < 0.075$) or significant ($p < 0.05$) terms. Where all independent variables
705 were found insignificant, we present the intercept only model. The class of variance-covariate used to specify different variances for each level of
706 stratification within-group are also provided.

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Sediment type: sandy Mud (sM)									
Macro-invertebrate community (Initial linear model: Response variable ~ $F \times E$)									
Model ID	Model	Response variable	Fishing frequency (F)	Enrichment (E)	Interaction (F : E)	Intercept only	Variance-covariate		
16	GLS	Macro-invertebrate density	L = 5.27, df = 1, p = 0.02	L = 4.31, df = 1, p = 0.04			F		
17	GLS	Species richness	L = 3.83, df = 1, p = 0.05	L = 7.75, df = 1, p = 0.005			F		
18	GLS	Macro-invertebrate biomass				L = 1.29, df = 1, p = 0.26	F × E		
19	LM	suspension: deposit feeders ratio				F = 12.33, df = 16, p = 0.77	-		
Sediment reworking groups (Initial linear model: Response variable ~ $F \times E \times R_i$)									
Model ID	Model	Response variable	Fishing frequency (F)	Enrichment (E)	Reworking mode (R_i)	F : E	F : R_i	Intercept only	Variance-covariate
20	GLS	R_i density	L = 8.51, df = 1, p = 0.004	L = 5.59, df = 1, p = 0.02	L = 54.17, df = 1, p < 0.0001				F × E
21	GLS	R_i biomass			L = 8.23, df = 1, p = 0.02				F × R_i

Abundance of active N-cycling associated microbes (Initial linear model: Response variable ~ F × E)							
Model ID	Model	Response variable	Fishing frequency (F)	Enrichment (E)	Interaction (F : E)	Intercept only	Variance-covariate
22	LM	<i>nirS</i>				F = 0.005, df = 17, p = 0.94	-
23	LM	<i>AnirKa</i>	F = 3.86, df = 1, p = 0.07	F = 3.97, df = 1, p = 0.06			-
24	LM	<i>hzo</i>				F = 0.33 , df = 17, p = 0.57	-
25	LM	AOA <i>amoA</i>				F = 0.46 df = 17, p = 0.51	-
26	LM	AOB <i>amoA</i>				F = 0.17 , df = 17, p = 0.68	-
27	LM	AOB : AOA <i>amoA</i> ratio		F = 13.33, df = 1, p = 0.002			-
Water nutrient concentration (Initial linear model: Response variable ~ F × E)							
Model ID	Model	Response variable	Fishing frequency (F)	Enrichment (E)	Interaction (F : E)	Intercept only	Variance-covariate
28	GLS	[NO ₂ -N]				L = 1.37, df = 1, p = 0.24	F × E
29	LM	[NO ₃ -N]				F = 0.49 , df = 19, p = 0.49	-
30	GLS	[NH ₄ -N]				L = 1.73, df = 1, p = 0.19	F × E

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711 **Table 3.** The similarity percentage (SIMPER) dissimilarity tables (up to 90% of cumulative
712 differences) of taxa (a) density and (b) biomass in **sandy sites** that experienced contrasting levels of
713 fishing frequency (Levels: low and high fishing frequency). Information on species feeding mode/s
714 (SDF for surface deposit feeder; SubDF for subsurface deposit feeder; ASF for active suspension
715 feeder; PSF for passive suspension feeder; Pred for predator; Scav for scavenger; Det for
716 detritivore; feeding mode was not allocated to taxon level higher than genus and are denoted by “-
717 ”), sediment reworking functional type (E for epifauna; SM for surficial modifiers; UC/DC for
718 upward and downward conveyors; B for biodiffusors; and R for regenerators) and mobility (1 for
719 organisms that live in fixed tubes; 2 indicates limited movement; 3 indicates slow, free movement
720 through the sediment matrix; 4 indicates free movement via burrow system) are provided.
721

a. Groups tested: Taxon density between low and high fishing activity in sandy sediment						
Species	Feeding mode	³Sediment reworking functional type	³Mobility	Low fishing frequency	High fishing frequency	Contr. Diss. (%)
<i>Lagis koreni</i>	¹ SubDF	UC/DC	1	3.59	1.56	8.81
<i>Phoronis sp.</i>	¹ PSF, ASF	SM	1	0.34	3.00	8.74
<i>Leptosynapta inhaerens</i>	¹ SubDF, Det	SM	3	2.88	0.00	8.39
<i>Echinocardium cordatum</i>	¹ SDF, SubDF	B	3	2.57	0.85	6.93
Asteroid juvenile	-	E	3	1.46	0.00	4.29
<i>Owenia fusiformis</i>	¹ PSF, ASF, SDF, SubDF	SM	1	0.20	1.11	3.36
<i>Magelona sp.</i>	² SDF	SM	2	0.14	0.73	2.64
<i>Glycera oxycephala</i>	¹ Pred, Scav	B	3	0.94	0.20	2.60
<i>Echinocyamus pusillus</i>	¹ SDF, SubDF	SM	3	0.84	0.00	2.43
<i>Sthenelais limicola</i>	² Pred, Scav	B	3	0.10	0.71	2.28
<i>Ophelina acuminata</i>	² SubDF	B	3	0.20	0.76	2.27
<i>Chaetozone sp.</i>	² SDF	SM	2	0.00	0.64	2.07
<i>Magelona johnstoni</i>	² SDF	SM	2	0.20	0.66	2.03
<i>Dosinia lupinus</i>	² ASF, PSF	SM	2	0.54	0.00	1.94
<i>Poecilochaetus serpens</i>	¹ SDF, SubDF, PSF, ASF	SM	2	0.54	0.41	1.91
<i>Thracia phaseolina</i>	¹ PSF, ASF, SDF,	UC/DC	2	0.47	0.34	1.79

	SubDF					
<i>Aricidea sp.</i>	² SDF, SubDF	SM	3	0.58	0.10	1.75
<i>Spiophanes bombyx</i>	¹ PSF, ASF, SDF, SubDF	UC/DC	1	0.61	0.10	1.70
<i>Corystes crassivelanus</i>	¹ Pred, Scav	R	4	0.40	0.60	1.67
<i>Venus casina</i>	² ASF, PSF	SM	2	0.44	0.30	1.62
<i>Ophiuroid juvenile</i>	-	SM	2	0.54	0.10	1.61
<i>Scalibregma inflatum</i>	¹ SDF, SubDF	B	4	0.14	0.50	1.58
<i>Abra alba</i>	¹ PSF, ASF, SDF, SubDF	SM	2	0.00	0.56	1.57
<i>Nephtys caeca</i>	¹ Pred, Scav	B	3	0.44	0.00	1.53
<i>Goniada sp.</i>	¹ Pred, Scav	B	3	0.34	0.24	1.51
<i>Ensis juvenile</i>	¹ ASF	SM	2	0.34	0.20	1.22
<i>Sthenelais sp.</i>	² Pred, Scav	B	3	0.00	0.38	1.20
<i>Nephtys sp.</i>	¹ Pred, Scav	B	3	0.10	0.34	1.15
<i>Spio sp.</i>	¹ SDF, SubDF	UC/DC	2	0.30	0.20	1.14
Terebellidae	-	UC/DC	1	0.20	0.24	1.09
Syllidae	-	B	3	0.00	0.30	1.05
<i>Abra prismatica</i>	¹ PSF, ASF, SDF, SubDF	SM	2	0.24	0.00	0.79
<i>Gattyana cirrhosa</i>	¹ Pred, Scav	B	3	0.10	0.20	0.76
Nematoda	-	SM	2	0.00	0.24	0.75
<i>Scolecipis squamata</i>	² SDF	UC/DC	2	0.24	0.00	0.70
<i>Scoloplos armiger</i>	² SubDF	B	3	0.24	0.00	0.70
Sabellidae	-	SM	1	0.10	0.20	0.64
<i>Bathyporeia gracilis</i>	² SDF, SubDF	SM	3	0.20	0.00	0.57
<i>Orbinia sp.</i>	² SubDF	B	3	0.10	0.10	0.57
<i>Pagurus sp.</i>	¹ SDF, Pred, ASF	E	4	0.00	0.20	0.53
<i>Cerebratulus sp.</i>	² Pred, Scav	B	3	0.20	0.00	0.52
b. Groups tested: Taxon biomass between low and high fishing activity in sandy sediment						
Species	Feeding mode	³Sediment reworking functional type	³Mobility	Low fishing frequency	High fishing frequency	Contr. Diss. (%)
<i>Echinocardium</i>	¹ SDF,	B	3	0.28	1.06	19.76

<i>cordatum</i>	SubDF					
<i>Corystes crassivelanus</i>	¹ Pred, Scav	R	4	0.30	0.29	11.17
<i>Thracia phaseolina</i>	¹ PSF, ASF, SDF, SubDF	UC/DC	2	0.05	0.25	6.19
<i>Lagis koreni</i>	¹ SubDF	UC/DC	1	0.23	0.12	6.06
<i>Acanthocardia echinata</i>	¹ PSF, ASF	SM	2	0.00	0.24	4.94
<i>Chamelea striatula</i>	¹ PSF, ASF	SM	2	0.00	0.17	4.41
<i>Nephtys incisa</i>	¹ SDF, SubDF	B	3	0.09	0.03	3.06
<i>Glycera oxycephala</i>	¹ Pred, Scav	B	3	0.11	0.01	2.94
<i>Phoronis sp.</i>	¹ PSF, ASF	SM	1	0.01	0.1	2.56
<i>Sigalion mathilde</i>	² Pred, Scav	B	3	0.00	0.06	2.13
<i>Lumbrineris sp.</i>	¹ Pred, Scav	B	3	0.00	0.07	1.96
<i>Ophelina acuminata</i>	² SubDF	B	3	0.01	0.06	1.92
<i>Owenia fusiformis</i>	¹ PSF, ASF, SDF, SubDF	SM	1	0.01	0.07	1.91
<i>Sthenelais limicola</i>	² Pred, Scav	B	3	0.01	0.05	1.88
<i>Venus casina</i>	² ASF, PSF	SM	2	0.03	0.07	1.85
<i>Scolelepis squamata</i>	² SDF	UC/DC	2	0.06	0.00	1.38
<i>Pagurus sp.</i>	¹ SDF, Pred, ASF	E	4	0.00	0.04	1.36
<i>Abra alba</i>	¹ PSF, ASF, SDF, SubDF	SM	2	0.00	0.07	1.26
<i>Abra prismatica</i>	¹ PSF, ASF, SDF, SubDF	SM	2	0.04	0.00	1.26
Asteroid juvenile	-	E	3	0.04	0.00	1.22
<i>Cerianthus sp.</i>	¹ PSF, Pred	SM	1	0.00	0.05	1.18
<i>Nucula hanleyi</i>	¹ SubDF, Det	SM	3	0.00	0.05	1.01
<i>Dosinia lupinus</i>	² ASF, PSF	SM	2	0.03	0.00	0.95
<i>Glycera alba</i>	¹ Pred, Scav	B	3	0.02	0.01	0.88
<i>Travisia forbesi</i>	¹ SDF, SubDF	B	3	0.03	0.00	0.87
<i>Ensis juvenile</i>	¹ ASF	SM	2	0.00	0.03	0.82
<i>Scalibregma inflatum</i>	¹ SDF, SubDF	B	4	0.01	0.02	0.80
<i>Gattyana cirrhosa</i>	¹ Pred, Scav	B	3	0.02	0.02	0.77

<i>Sthenelais</i> sp.	² Pred, Scav	B	3	0.00	0.05	0.77
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Data sources

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¹ MarLIN, 2006. *BIOTIC - Biological Traits Information Catalogue*. Marine Life Information Network.

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Plymouth: Marine Biological Association of the United Kingdom. [03/07/2017] Available from

726

<www.marlin.ac.uk/biotic>

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² Biological traits database developed under the BENTHIS (Benthic Ecosystem Fisheries Impact Studies)

728

project. [16/07/2016]. <http://www.benthis.eu/en/benthis/Results.htm>

729

³ Queiros AM, Birchenough SNR, Bremner J, et al (2013) A bioturbation classification of European marine

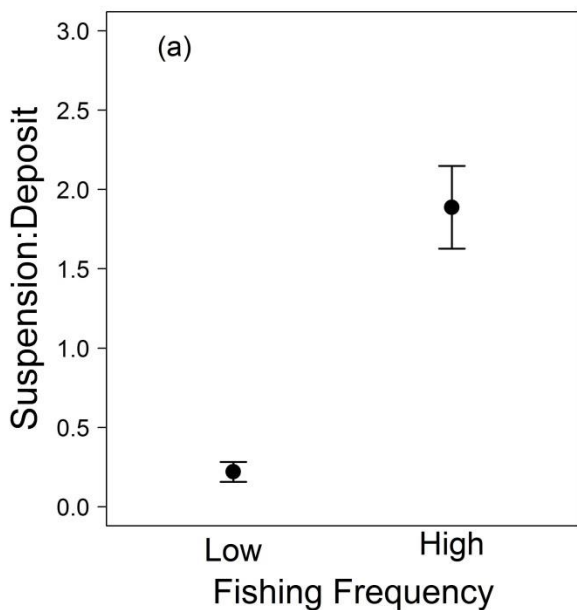
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infaunal invertebrates. *Ecol Evol* 3: 3958-3985

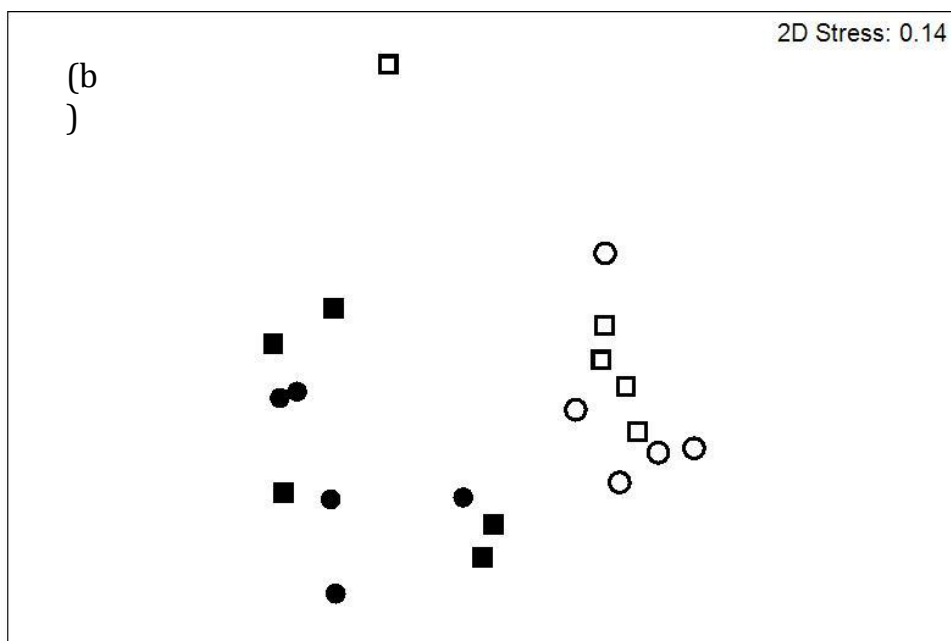
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732 **Figure 1.** The (a) independent effect of fishing frequency on the ratio of suspension:deposit feeders
733 (mean \pm SE) and (b) a non-metric multidimensional scaling (nMDS) ordination of square-root
734 transformed Bray-Curtis resemblance matrix of macro-invertebrate density for communities in
735 sand. In (b) contrasting levels of bottom fishing frequency (open symbol low, closed symbol high)
736 and organic matter enrichment (circle non-enriched, square enriched) are presented, and the MDS
737 dimensionality representation stress value is indicated.

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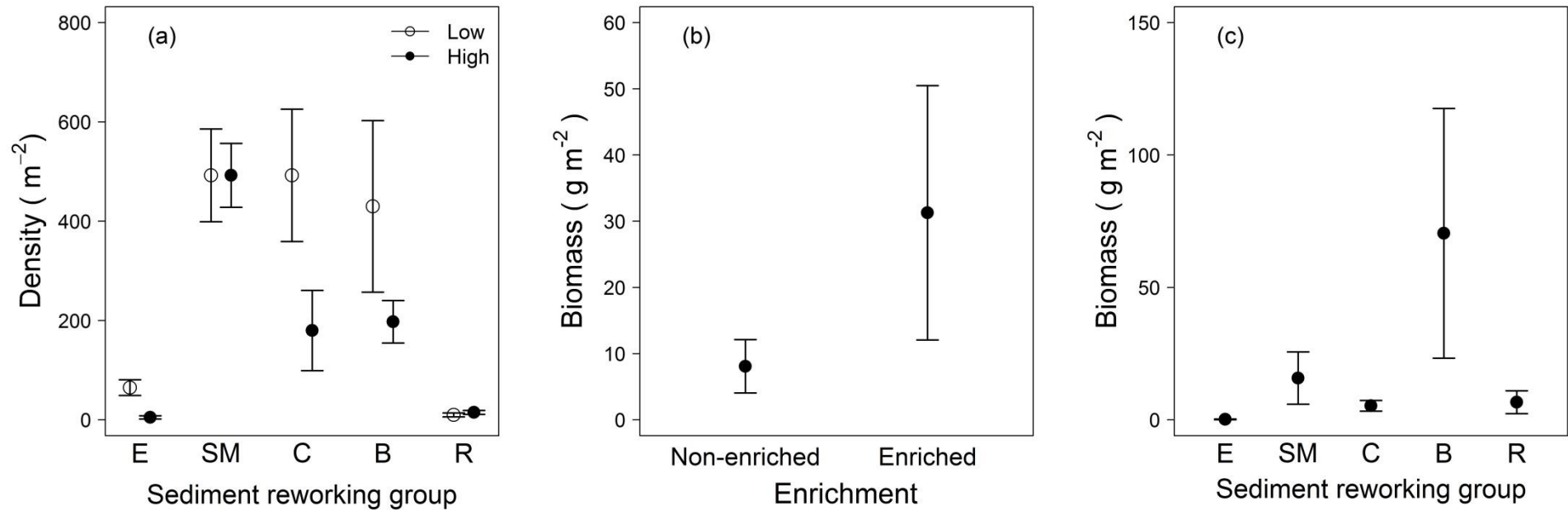


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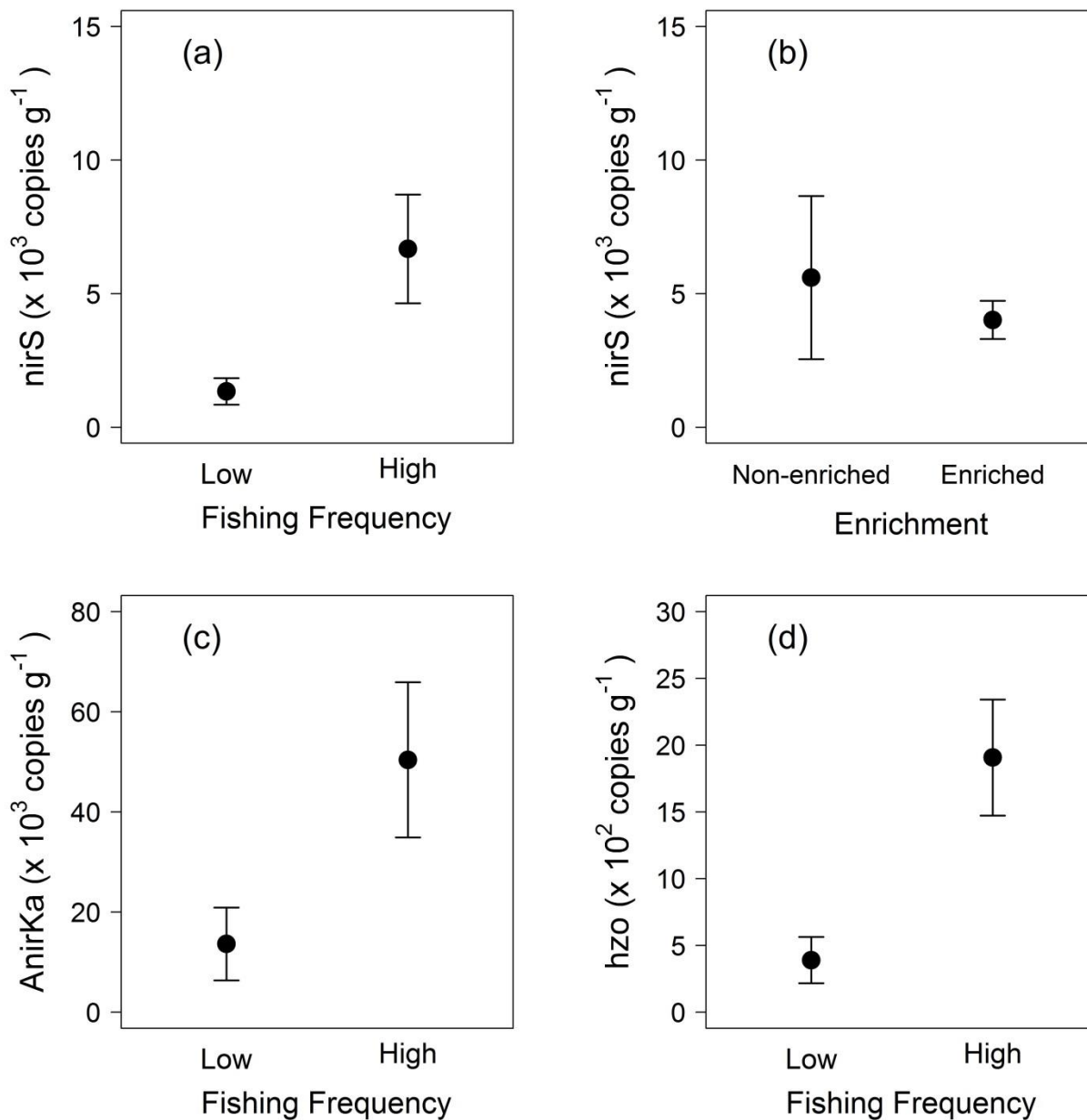
744

745 **Figure 2.** The (a) interactive effects of sediment reworking group identity and the frequency of fishing on sediment reworking group density, and (b-c)
 746 the independent effects of organic matter enrichment and sediment reworking group identity on sediment reworking group biomass in sandy sediments
 747 (mean \pm SE). In (a) contrasting levels of bottom fishing frequency (open symbol low, closed symbol high) are presented. In (a) and (c) sediment
 748 reworking groups include epifauna (E), surficial modifiers (SM), conveyors (C), biodiffusors (B) and regenerators (R).
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751 **Figure 3.** The independent effects of (a) fishing frequency and (b) organic matter enrichment on
752 abundance of the metabolically active bacterial denitrifier (*nirS*) and the independent effect of
753 fishing frequency on (c) archaeal (*AnirKa*) denitrifiers and (d) anammox (*hzo*) hydrazine
754 oxidoreductase transcripts in sandy sediments. Values plotted are mean \pm SE.
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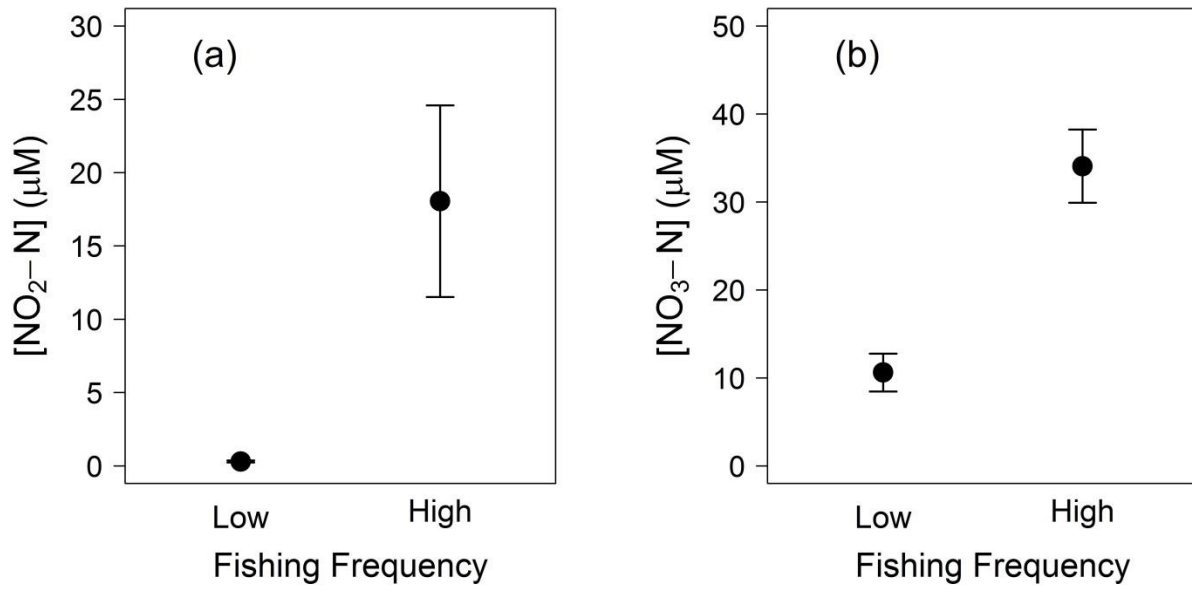


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760 **Figure 4.** The independent effect of fishing frequency on (a) [NO₂-N] and (b) [NO₃-N] in sandy
761 sediments. Values plotted are mean ± SE.

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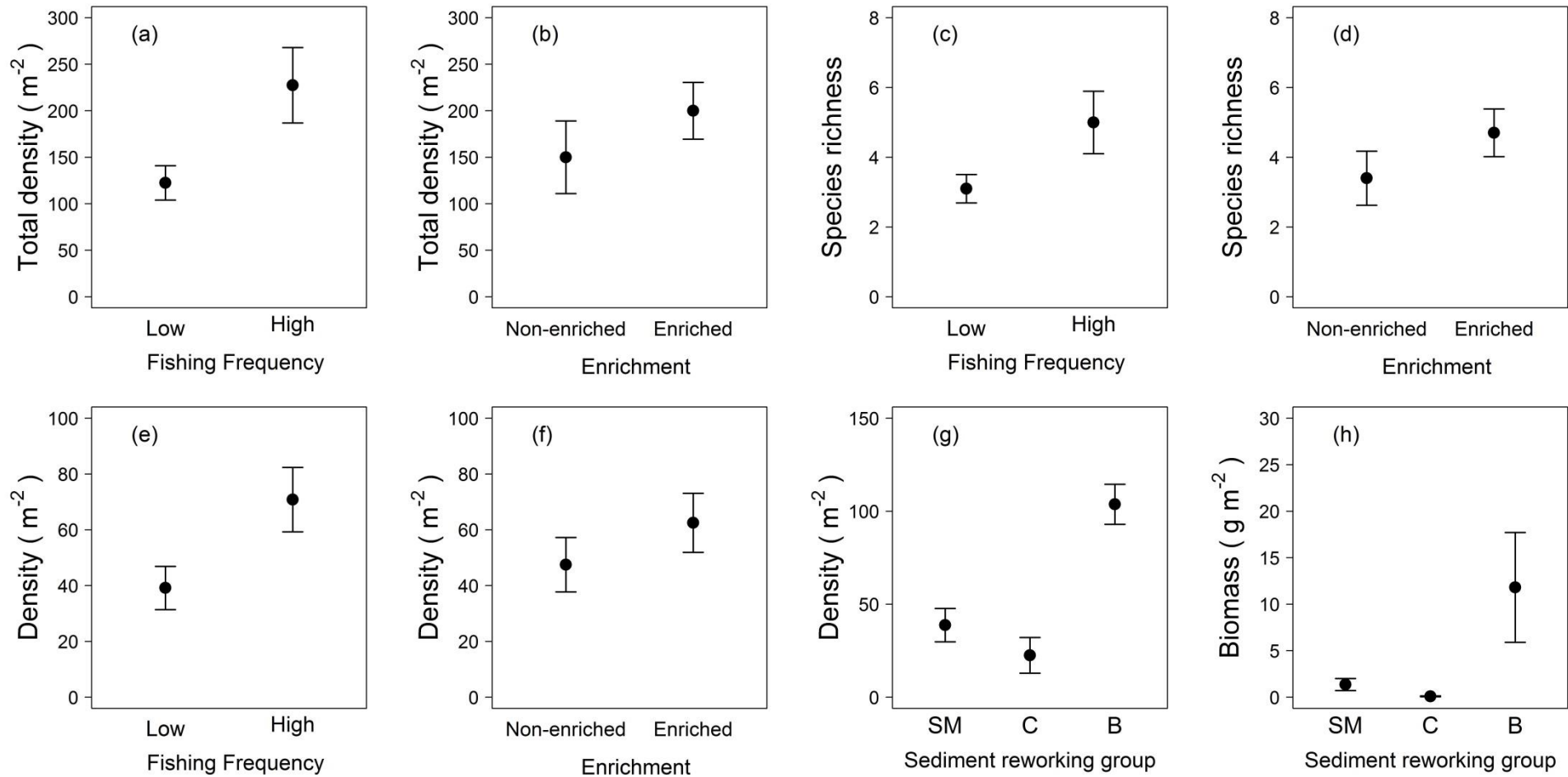


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765 **Figure 5.** The independent effects of fishing frequency and organic matter enrichment on (a,b) total macrofaunal density, (c,d) species richness and
 766 (e,f) sediment reworking group density. Sediment reworking group density (g) and biomass (h) were dependent on sediment reworking group identity
 767 (SM: surficial modifiers, C: conveyors, B: biodiffusors). There were no species for sediment reworking groups E (epifauna) and R (regenerators) in
 768 sandy mud. Values plotted are mean \pm SE.

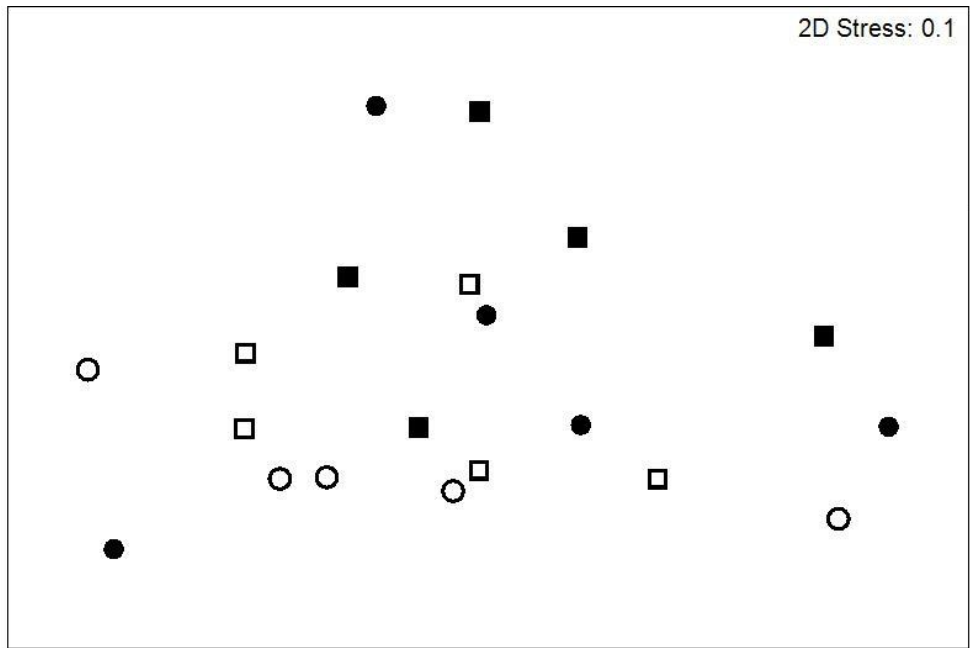
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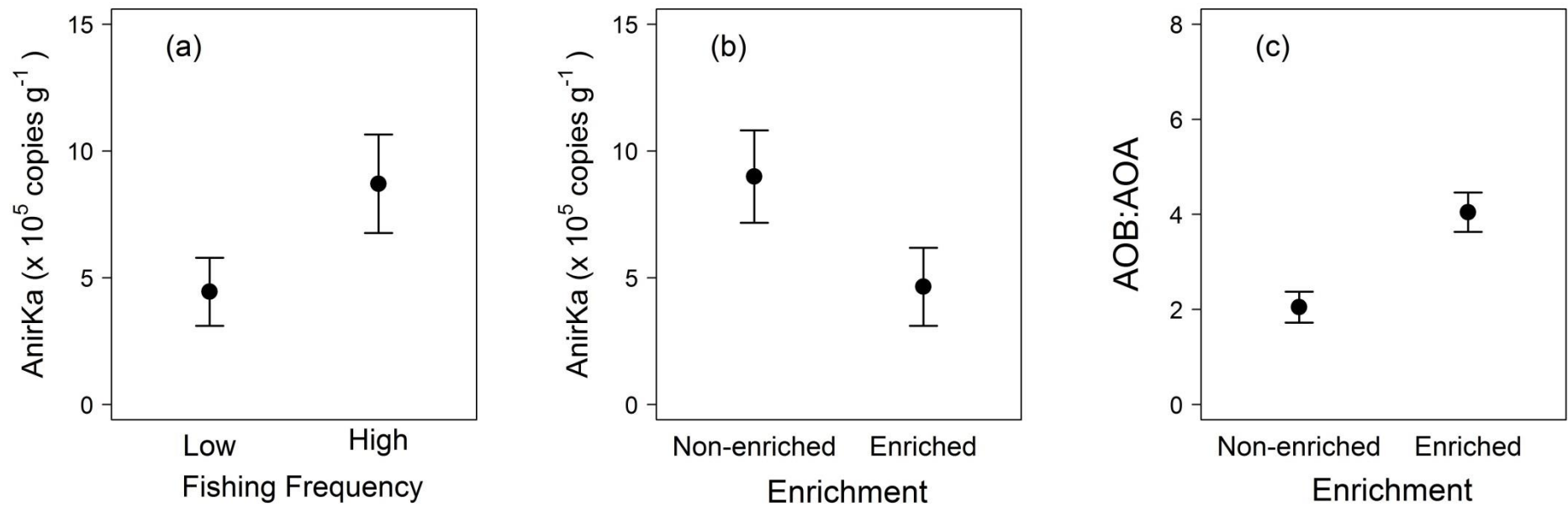
771 **Figure 6.** Non-metric multidimensional scaling (nMDS) ordination of square-root transformed
772 Bray-Curtis resemblance matrix of macro-invertebrate density for communities in sandy mud that
773 experienced contrasting levels of bottom fishing frequency (open symbol low, closed symbol high)
774 and of organic enrichment (circle non-enriched, square enriched). MDS dimensionality
775 representation stress value = 0.1.

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779 **Figure 7.** The independent effects of (a) fishing frequency and (b) organic matter enrichment on archaeal (*AnirKa*) denitrifiers, and of (c) organic
780 matter enrichment on the ratio of bacterial to archaeal ammonia oxidisers (AOB : AOA *amoA*). Values plotted are mean \pm SE.



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