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Running page head: Trawling and production on benthic functioning

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Abstract

Although many studies have investigated the effects of disturbance and environmental drivers on marine ecosystems, comparatively few have studied their interactions. Using fuzzy coded biological traits, we compared the functional composition, diversity and evenness of benthic communities in the English Channel, and Celtic and Irish Seas, across interacting gradients of bottom trawling and primary production. Fuzzy correspondence analysis indicated greater similarity in traits composition at sites of high trawling pressure than those of low trawling. In contrast, the analysis revealed no relationship between traits composition and primary production. Trawling and primary production had no effect on the traits "longevity", "sediment position" and "feeding mode". However, trawling had negative effects on all modalities within the trait "living habit", which were strongest for attached and epifaunal organisms, but weakest for burrow- and tube-dwelling species. Trawling also negatively affected most modalities within the trait "maximum weight", which were strongest for organisms weighing between < 0.1 g and 1 kg. Conversely, trawling positively affected organisms weighing > 10 kg. For the trait "bioturbation", upward conveyors were positively related with primary production, whilst other modalities exhibited no clear pattern. Because trawling affected some traits more than others, community biomass was less evenly distributed across traits in highly trawled areas, which resulted in lower levels of functional diversity and evenness. Overall, the effects of bottom trawling were greater in areas of high primary production.

Introduction

Marine ecosystems are subject to a range of anthropogenic stressors, many of which are increasing in intensity and occurrence (Lotze et al. 2006, Poloczanska et al. 2013). The use of bottom trawls has greatly increased over the last century (Watson et al. 2013, Howarth et al. 2014). In contacting the seafloor, bottom trawling can damage benthic habitats (Kaiser et al. 2000), reduce the abundance of target and non-target species (Hiddink et al. 2017), and truncate age and size distributions (Beamish et al. 2006, Jørgensen et al. 2007). In parallel, ocean acidification, eutrophication, and climate change are altering global levels of primary production (Frederiksen et al. 2006, Tait & Schiel 2013), which could significantly alter food web dynamics, fisheries production and ocean biogeochemistry (Gregg et al. 2003, Brander 2007, Blanchard et al. 2012). In areas where primary production increases, benthic communities should receive a greater input of energy, increasing their growth, reproduction and resilience to bottom trawling (Blanchard et al. 2009, Hiddink et al. 2017). Investigating the interactive effects of bottom trawling and primary production could therefore help to inform management and improve understanding of how multiple drivers affect marine ecosystems.

Most studies quantify the ecological effects of disturbance by measuring changes in species abundances (Mouillot et al. 2013, Stuart-Smith et al. 2013). However, species-based approaches convey little direct information on how disturbances affect ecosystem processes, such as nutrient cycling and habitat provisioning (Bremner & Frid 2005), which play a greater role in maintaining ecosystem integrity than the abundance of a particular species (Loreau et al. 2001). Hence, biological traits are increasingly being used to describe the physical, behavioural and life-history characteristics of species to evaluate their potential vulnerability to disturbance ('response traits') and contribution towards ecosystem function ('effect traits'– see Bolam *et al.* 2016). For example, bioturbation can be considered an 'effect trait' as the burrowing of benthic infauna can transport nutrients and oxygen from the sediment surface to deeper layers (Olsgard et al. 2008, Sciberras et al. 2016). In contrast, bottom trawls are more likely to damage sessile organisms than pelagic organisms (Kaiser et al. 2000, Tillin et al. 2006), meaning living habit can be considered a 'response trait'. Given that some

56   disturbances affect life histories and functions more than others, biological traits can help disentangle

57   the ecological effects of multiple stressors (Bremner et al. 2006)

58   Numerous studies show bottom trawling can change benthic traits composition. By reducing the

59   abundance of large predators, trawling can increase the abundance of small and fast-growing species,

60   which can recover quickly from disturbance and benefit from reduced predation (Bremner & Frid

61   2005, Tillin et al. 2006). Additionally, trawling can increase the availability of organic matter and dead

62   / injured animals, boosting the local abundance of mobile scavengers (Tillin et al. 2006, Kaiser &

63   Hiddink 2007, Craven et al. 2013). Trawling can also plough and re-suspend sediments which can

64   reduce the feeding efficiency of suspension feeders (Collie et al. 2000, Bradshaw et al. 2003).

65   Compared to bottom trawling, little is known about the effects of primary production on traits

66   composition. Nonetheless, areas of high primary production often support greater abundances of

67   small-bodied organisms that can quickly incorporate pulses of energy into growth and reproduction

68   (Macpherson et al. 2002, Jennings & Blanchard 2004, Gómez-Canchong et al. 2013). High levels of

69   primary production should also result in greater quantities of phytoplankton and other organic matter

70   sinking to the seafloor, which would benefit suspension and deposit feeders (Blanchard et al. 2009).

71   Given that trawling and primary production likely have contrasting consequences, their interaction

72   may produce different effects to them acting alone (Crain et al. 2008). These interactions could be

73   synergistic or additive, where the effects of one driver equal or exceed the sum of each in isolation

74   (see Gunderson *et al.* 2016). For example, the positive relationship between primary production and

75   small body size might be intensified by trawling, because fishing removes the largest individuals

76   (Beamish et al. 2006, Jørgensen et al. 2007, Fu et al. 2018). Alternatively, interactions may be

77   antagonistic, where the cumulative effect of several drivers is less than them acting alone. For

78   instance, the increased detritus and organic matter caused by high primary production levels may

79   increase population growth rates of suspension and deposit feeders, reducing recovery times and

80   their sensitivity to trawling effects.

81   Persistent and intense disturbances can reduce species abundances to levels that eliminate their

82   influence on ecosystem function (Howarth et al. 2014). Given that multiple species can perform the

83   same functional role (Fonseca & Ganade 2001), high species diversity presumably increases ecosystem

84   resilience because of the low probability of losing all species capable of performing a specific function

85   (Loreau et al. 2001, Cardinale et al. 2002). Biological traits can therefore measure the distribution

86   (functional evenness) and range (functional diversity) of functional roles present within an ecosystem

87   (Díaz & Cabido 2001, Mooney et al. 2009). Given the greater effects of bottom trawling on some

88   groups, trawling is expected to reduce the functional diversity and evenness of marine communities,

89   and reduce their resilience to further disturbance (Schleuter et al. 2010, Howarth et al. 2014).

90   In order to evaluate how primary production and fishing influence the functioning of benthic

91   ecosystems, we compare the functional composition, diversity and evenness of benthic communities

92   in the English Channel, and Celtic and Irish Sea, across interacting gradients of bottom trawling and

93   primary production. First, we hypothesize that bottom trawling will reduce the functional diversity

94   and evenness of benthic communities by reducing the abundance of long-lived predatory fish and

95   attached and suspension feeding invertebrates. Second, we hypothesize that both trawling and

96   primary production increase abundances of scavengers and small, short-lived species. Last, we

97   hypothesize reduced effects of trawling on suspension feeders in areas of high primary production,

98   but intensified effects of trawling on body size.

99   **Methods**

100   **Outline**

101   Benthic organisms were sampled over gradients of trawling intensity and primary production at

102   sampling stations with otherwise homogeneous environmental conditions. Their biological trait

103   composition, functional diversity and functional evenness were then related to trawling intensity and

104   primary production.

105

Study area

This work was carried out in the Irish Sea, Celtic Sea, and western English Channel. These areas are characterised by moderate levels of wave energy, depths of 20 – 100 m, and similar circalittoral sediments of muddy sand and gravel (Cooper et al. 2010). However, they also differ slightly in that sea surface temperatures are often lower, and primary production levels higher, within the Irish Sea. Between March and May, the Celtic Sea undergoes a distinct algal bloom that originates south of Ireland and temporarily increases chlorophyll a concentrations in the Celtic Sea, southern Irish Sea and western English Channel (Fasham et al. 1983, Garcia-Soto & Pingree 2009). This algal bloom can increase chlorophyll a levels to such an extent that it can homogenise any spatial differences that typically exist during the rest of the year. European beam and otter trawlers operate throughout these regions and target a wide range of species such as hake (*Merluccius merluccius*), plaice (*Pleuronectes platessa*), sole (*Solea solea*), monkfish (*Lophius piscatorius*) and whiting (*Merlangius merlangus*). However, the Irish Sea is characterised by a greater presence of otter trawlers targeting Nephrops prawns (*Nephrops norvegicus*), the Celtic Sea is characterised by a greater presence of beam trawlers targeting flat fish, and the western English Channel is the focus of a large king scallop (*Pecten maximus*) dredge fishery (Guénette & Gascuel 2012, Campbell et al. 2014, Howarth & Stewart 2014).

Data sources

Water column depths (m) were extracted from GEBCO (www.gebco.net) at a resolution of half-minute intervals. Information on seabed substrate type and bed shear stress was obtained from the UkSeaMap 2016 (http://jncc.defra.gov.uk/ukseamap). Annual levels of primary production (mg C m^{-2} yr^{-1}) between 2009 and 2013 (estimated by the MODIS satellite sensor) were provided by NEODAAS (www.neodaas.ac.uk) at a resolution of 1.1 x 1.1 km and averaged across all years. These data used Morel & Berthon's (1989) algorithm to convert depth, surface chlorophyll, and photosynthetically active radiation (PAR) into estimates of net primary production. However, like most satellite chlorophyll algorithms, it can over-estimate primary production in waters of high sediment loads or coloured dissolved organic matter. Fishing effort (hours spent bottom trawling and dredging) between

132   2011 and 2013 was provided by the MMO (www.gov.uk/government/organisations/marine-

133   management-organisation) at a resolution of 3.5 x 3.5 km, which was averaged by year. Trawling

134   intensity (swept area ratio yr^{-1}) averaged between the years 2010 and 2012 was supplied by Eigaard

135   *et al.* (2016) at a resolution of 1.8 x 1.8 km. Their data take into account differences in trawl size and

136   trawl type, which can strongly influence the level of disturbance trawling gears have on the benthos

137   (Hiddink et al. 2007). Swept area ratio can be interpreted as the mean number of times fishing gear

138   impacts an area in a year. A swept area ratio of one indicates that the swept area equals the cell area

139   (Gerritsen et al. 2013). Because swept area ratio is more informative than the number of hours spent

140   fishing, the MMO measures of fishing effort were converted to swept area ratio as described by

141   Gerritsen *et al.*, (2013). For this, we assumed that the average fishing vessel towed gears 24 m in width

142   at a speed of two knots. Our study solely used fishing effort provided by (Eigaard et al. 2017) except

143   for two stations (O and P) where we used MMO data instead. Beam trawlers in North Devon

144   intensively target this area (Campbell et al. 2014) which was not highlighted in the Eigaard dataset,

145   likely because of a lack of French and Spanish VMS data for their trawl fleets operating in the Celtic

146   Sea.

147   **Experimental design**

148   Trawling intensity and primary productivity were both divided into four categorical levels (Table 1)

149   and 1.8 x 1.1 km sampling stations were chosen to cover all combinations within the Irish Sea, Celtic

150   Sea and English Channel. To ensure comparability and to avoid confounding effects, stations were

151   restricted to "sand" and "muddy sand" substrates, between 40-100 m in depth, and of "moderate"

152   bed shear stress as defined by the UkSeaMap. Final sampling stations were selected based on their

153   proximity to one another, and their distance from restricted (military and fishing) zones and offshore

154   structures; greater distances were preferred in all cases. Stations were also selected based on their

155   similarity in depth and sediment composition. Some treatment combinations were rarer than others,

156   meaning there were instances where we had to sample stations coarser in substrate or located at

157   greater depth. Hence, there is some spatial clustering of sampling stations, and differences in

158 environmental characteristics may provide some scope for confounding effects which we test for in

159 our analyses.

160 **Sample collection**

161 A total of 20 stations were sampled both in September 2015 and April 2016 (Figure 1 and Table S1)

162 and data were pooled across both sampling events. Most benthic recovery processes are seasonal and

163 rely on distinct pulses in recruitment, which require time for larvae to settle and grow (Rodríguez et

164 al. 1993, Mann 2009). Hence, by sampling during and after the spring algal bloom, we aimed to

165 account for these seasonal differences.

166 At each station, seabed water samples were taken to quantify the chlorophyll a (Chl-a) content at time

167 of sampling, and to allow comparisons with the satellite-generated measures of primary production.

168 At each sampling station, a one-litre Niskin bottle fitted with a digital reversing thermometer was

169 deployed to one metre above the seafloor and triggered with a brass messenger three times. Upon

170 retrieval, the mean of 15 temperature measurements were recorded along with their standard

171 deviation (SD). For each station, we filtered between 900 and 1800 ml of seawater over 47 mm GF/F

172 filter papers in triplicate and stored these filters at -20˚C in the dark until further processing.

173 Five 0.1 m^2 Day grabs were taken within each sampling station. These samples were later used to

174 quantify sediment size, Chl-a, and infauna. To quantify sediment Chl-a, we subcored using a cut-off

175 syringe 14.5 mm in diameter to a depth of 8 mm which was preserved at -20˚C in the dark. To sample

176 meiofauna, we took two subcores 25 mm in diameter to a depth of 40 mm which were preserved in a

177 4% buffered formalin seawater solution. To sample infauna, we washed whatever sediment remained

178 of the Day grab samples over a 1-mm sieve before preserving the remaining material in 4% formalin.

179 Epifaunal organisms were sampled using two 2 m beam trawls (fitted with a 10 mm mesh and 2 mm

180 cod-end liner) which were towed for five minutes along the seafloor at a speed of 1.5 knots. Benthic

181 megafauna and demersal fish were sampled using two 4 m beam trawls (fitted with a chain matrix and

182 an 82 mm diamond cod-end) which were towed for 30 minutes at a speed of 3 knots. All organisms

7

183   caught by the trawls were identified to species level where possible, counted, and weighed using a

184   motion compensating balance. Subsampling was used for species comprising of more than 50

185   individuals. Small animals < 1 g were weighed in groups and their mean individual weight calculated.

186   **Particle size analysis (PSA)**

187   Sediment samples collected by the Day grab were analysed for particle size using both dry sieving and

188   a laser particle analyser. Both datasets were then combined as described in Mason (2011).

189   **Chl-a analysis**

190   Water samples were analysed for Chl-a content using the methods and equations described in

191   Lorenzen (1966) and JGOFS (1994). The same method was applied to the sediment cores, however,

192   these were centrifuged for 20 minutes at 2400 rpm before analysis in order to separate sediments

193   from the supernatant.

194   **Invertebrate sorting and identification**

195   Approximately 10 ml of 0.1% Rose Bengal was added to the formalin-preserved grab samples, gently

196   mixed, and left to stain for at least one hour before sorting. Samples were then washed over a 1-mm

197   sieve to remove all traces of formalin and moved to a white tray. All organisms were separated from

198   the sediment and preserved in 70% industrial methylated spirit (IMS). These organisms were sorted

199   into broad taxonomic groups using a dissection microscope and methyl blue dye. All individuals were

200   then identified to at least family level, counted, blotted dry, and weighed to the nearest 1 mg. Body

201   parts were reassembled to make whole organisms but were discarded if less than 20% of the individual

202   remained. Individuals were not counted if they did not possess a head. Mollusc shells were smashed

203   and discarded if empty. Tube-dwelling animals were separated from their tubes before weighing, and

204   hermit crabs were removed from their shells or epibionts and weighed separately.

205

206

207 **Data analysis**

208 **Comparisons of environmental characteristics**

209 Multivariate tests were used to test if differences in measured environmental characteristics existed

210 between sampling sites, and whether they could confound the effects trawling and primary

211 production. These environmental data were mean particle size, percentage gravel, percentage mud,

212 percentage sand, and water depth. A resemblance matrix using a Euclidean Distance measure was

213 created and visualised using non-Metric Dimensional Scaling (nMDS) with clusters generated from a

214 Similarity Profile (Simprof) routine. This analysis indicated two sampling stations (D and P) were

215 dissimilar to the others (S1). As station D had a very low outlying mean particle size (69 µm ± 2 SE) and

216 station P had a very high outlying mean particle size (937 µm ± 203 SE), these two stations were

217 excluded from further analysis.

218 **Verification of experimental treatments**

219 Trawling intensity, sediment and water Chl-a content were compared between the categorical levels

220 of fishing effort and primary productivity. Trawling intensity increased exponentially across levels of

221 fishing effort (S2a). The Chl-a content of the sediment samples displayed no relationship with levels

222 of primary production (S2b). In contrast, water Chl-a correlated tightly with levels of primary

223 production in September but not in April (S2c).

224 **Gear calibrations**

225 Because we used multiple types of sampling gears to capture several components of the benthic

226 ecosystem, each gear partly overlapped in the size of organisms they captured, but differed in

227 sampling area and catch efficiency. For each sampling gear, small animals were undersampled because

228 they passed through the sieves or nets of the gear, and large animals were rarely found because their

229 abundance was too low relative to the area sampled. This meant that the abundance and biomass

230 values obtained by the different sampling gears could not be combined until they were corrected to

231 represent the same sampling area and sampling efficiency, and were restricted to the size ranges that

9

232   were sampled effectively. Hence, we scaled the data from the different sampling gears based on the

233   assumption that the abundance of size ranges that were sampled by two sampling gears should be

234   the same after correction. We carried out the following correctional procedure on the whole dataset

235   for all stations combined to get the most robust correction factors.

236   Normalised biomass size spectra were created as described in Sprules & Barth (2015). The size

237   spectrum of each individual sampling gear showed an optimum relationship with different minimum

238   and maximum size ranges of organisms sampled (S3a). The size range of organisms sampled effectively

239   by each gear was identified as the range where the size spectrum exhibited a monotonic decline (S3b).

240   Abundance values from the Day grab samples were used as the base for the corrections because the

241   area sampled by the grab was known to be exactly 0.1 m^2. The abundance of organisms sampled by

242   the 2-m beam trawl were then corrected by performing a linear regression on the normalised biomass

243   per size class captured by the Day grab and 2-m beam trawl for the size ranges in which they

244   overlapped (S4a). This procedure was then repeated for the combination of the 2-m and the 4-m beam

245   trawl (S4b). To correct those size classes that were sampled by multiple gears, the total biomass within

246   each size class was then divided by the number of gears contributing to each size class.

247   **Constructing a fuzzy coded database**

248   Many traits-based studies assign species to discrete functional roles, such as 'predator' or 'detritivore'

249   (e.g. Friedlander & DeMartini 2002; Micheli & Halpern 2005; Williams *et al.* 2015). However, this

250   approach is overly simplistic because most aquatic species exhibit multiple traits (e.g. part-predator,

251   part-detritivore) and express ontogenetic shifts in their ecology as they develop (e.g. from

252   planktivorous larvae, to piscivorous adults). Hence, we used a method known as 'fuzzy coding' to help

253   overcome these issues. Fuzzy coding divides traits (e.g. maximum weight) into categories, or

254   'modalities,' that cover the full range of possible values for that trait (e.g. < 10 g; 10 – 100 g; > 100 g).

255   We then assigned scores to each trait indicating the affinity of species to those modalities; where low

256   scores represented no affinity, and high scores represented total and exclusive affinity (Chevenet *et*

257   *al.* 1994; Tillin *et al.* 2006). These scores were then converted to proportions totalling to one, and

258   multiplied by species biomass or abundance, effectively spreading out their abundance across

259   multiple traits.

260   We modified an existing fuzzy coded traits database of species, genus's and families compiled by

261   Bolam *et al.* (2017) to include maximum biomass and demersal fish (Table 2). These additional

262   information came from FishBase (www.fishbase.org), the BIOTIC database (www.marlin.ac.uk/biotic)

263   and Jennings *et al.* (2001). For taxa identified at a resolution higher than species (e.g. genus and

264   family), the database assigned scores based on their most closely-related taxa using the Best

265   Professional Judgement (BPJ) approach (Bolam et al. 2014). This strategy resulted in a reasonably

266   accurate completion of modalities wherever the entries across closely related taxa were fairly

267   consistent, but we were less confident where traits were variable across closely related taxa, making

268   it necessary to spread the fuzzy-scores across a wider number of modalities.

269   Overall, our functional traits database included information on six biological traits spanning across 32

270   modalities (Table 2). There is currently no accepted methodology for selecting the most appropriate

271   traits for a given study. However, the traits used in our study were intended to cover a combination

272   of response and effect traits with the potential to reflect an organism's life history (e.g. life span),

273   ecology (e.g. living habit), vulnerability (e.g. sediment position), and contribution towards ecosystem

274   processes (e.g. bioturbation). We also aimed to ensure our selected traits did not overlap in the

275   information they conveyed. For instance, both maximum weight (g) and maximum length (cm) can

276   describe an organism's size. However, maximum weight is more informative about how much energy

277   an organism has invested into its own growth (Brose et al. 2005, Gómez-Canchong et al. 2012), and

278   can more accurately reflect the size of an organism that does not exhibit bilateral symmetry. Hence,

279   we chose maximum weight over maximum length as a biological trait.

280

281

Relating functional indices to trawling and primary production

Functional diversity and evenness were estimated from the Shannon-Wiener Diversity Index and Pielou's Evenness using the biomass of each modality as described in Schleuter *et al.* (2010). To test whether functional diversity and evenness were significantly related to primary production and trawling intensity, two linear models were constructed as follows:

$$\text{Functional diversity} \sim \log_{10}(\text{trawling intensity}) * \log_{10}(\text{primary production})$$

$$\text{Functional evenness} \sim \log_{10}(\text{trawling intensity}) * \log_{10}(\text{primary production})$$

For visualisation purposes, fitted values were plotted against continuous levels of trawling and compared between categorical levels of primary production, and vice a versa. These visualisations therefore differed from the models, as the models fitted these as continuous variables. This was done using the *predict* function in R (Team 2017) across trawling gradients and the mean of each level of primary production, and vice a versa. Linear models are used throughout our analyses because previous studies show the log biomass of communities decrease linearly with the log of trawling pressure (Hiddink et al. 2006). This pattern occurs because a fixed fraction of benthic biomass is typically removed with every pass of a trawl.

Relating functional composition to trawling and primary production

To visualise the influence of trawling pressure and primary production on overall functional composition, a fuzzy correspondence analysis (FCA) was performed using the R package "ade4" (Dray et al. 2017). FCA is a type of correspondence analysis that can describe relationships among objects of interest (i.e. sampling stations) based on the abundances of fuzzy coded variables (i.e. modalities). To aid interpretation, the total biomass of each modality was summed across both survey periods. The scores generated by the first two FCA axes were then plotted for each station and modality. This meant each bubble represented an individual sampling station, the size of which was based on its trawling intensity or primary production. Stations that are plotted closer together in the ordination have similar patterns of biomass distributions across modalities. Hence, distances between the

307 stations reflect differences in the proportional biomass of modalities. For example, if the trawling

308 ordinations clearly separated the larger bubbles from the small, then trawling intensity could be

309 interpreted as having a strong influence on trait composition. In addition, modalities labelled closely

310 to the larger bubbles would be more associated with areas of high trawling pressure than areas of low

311 trawling pressure.

312 **Relating modality biomass to trawling and primary production**

313 To determine whether modality biomasses were significantly related with trawling pressure and

314 primary production, linear models were created as:

315 $\text{Log}_{10}(\text{biomass}) \sim \text{modality} * \text{log}_{10}(\text{trawling intensity}) * \text{log}_{10}(\text{primary production})$

316 and repeated for each trait, creating a total of six models. We based this approach assuming that a

317 significant interaction between modality and trawling and / or primary production would indicate

318 unequal response in the modalities within a trait to these pressures. Significant interactions were then

319 plotted using the visualisation methods described earlier.

320 **Results**

321 **Dataset description**

322 This study identified 332 different taxa, 52 (or 16%) of which were identified to species level, 221 were

323 to genus (63%) and 59 (21%) were to family. The modalities with the fewest taxa (< 20) were organisms

324 weighing > 10 kg, organisms buried > 10 cm deep within the sediment, and upward and downward

325 bioturbators (Table 2). In contrast, surface-depositors, free-living organisms and animals living on the

326 sediment surface contained the most taxa (> 200). The modalities with the lowest biomass (< 100 g

327 m^{-2}) were organisms with a life span of < 1 year, organisms weighing > 10 kg, crevice-dwelling

328 organisms, and pelagic species. In contrast, the most abundant modalities (> 3000 g m^{-2}) were free-

329 living animals, organisms with a life span between 3 – 10 years, and animals buried down to 5 cm in

330 the sediment.

13

Effect of trawling and primary production on functional indices

Functional diversity and functional evenness related positively to primary production and negatively to trawling (Table 3); the highest levels of functional evenness and diversity therefore coincided with low trawling and high primary production (Figure 2). The interaction between trawling and primary production was significantly negative, with the strongest trawling effect at high primary production. At low primary production, trawling did not affect functional evenness and diversity.

Effect of trawling and primary production on traits composition

FCA ordinations showed greater similarity in traits composition at stations subjected to high levels of trawling pressure than stations subjected to lower levels of trawling (Figure 3A). Intensively trawled stations were characterised by a greater biomass of organisms that weighed over 1 kg (g1001 and g10000), lived for over 10 years (l10), resided deep within the sediment (sp10) or were pelagic (spPelagic), did not contribute to bioturbation (bNone), and were predatory (fPred) and / or crevice-dwelling (lhCrev). In contrast, stations subjected to low levels of trawling were characterised by animals that attached to the seabed (lhAtt) or other animals (lhEpi), lived high up (sp0.5 and sp6.10) or on top of the sediment (spSurf), were diffusive (bDiff) bioturbators, weighed between 11 g – 1 kg (g11 and g101), lived < 1 year to 3 years (l1 and l1.3), and were suspension (fSusp) and / or surface-feeders (fSurf). Unlike these comparisons in trawling pressure, the FCA ordinations did not clearly separate stations of low and high primary production (Figure 3B).

Effect of trawling and primary production on modality biomass

Linear models relating modality biomass with primary production and trawling pressure for each biological trait showed significant interactions between modality and trawling and / or primary production, thus indicating different reactions by modalities to these two stressors (Table 4). Trawling and primary production did not interact significantly with modality biomass for the traits "longevity", "sediment position" and "feeding mode". For "living habit", we observed significant interactions between modality and primary production, and between modality and trawling pressure. Trawling

356   had negative effects on all modalities within this trait, and these effects were more pronounced under

357   high levels of primary production (Figure 4). This negative relationship was strongest for attached and

358   epifaunal organisms, and weakest for burrow- and tube-dwelling species. For "maximum weight", the

359   three-way interaction between modality, trawling, and primary production was significant. This meant

360   trawling had negative effects on most modalities within this trait, with the negative effect of trawling

361   strengthening under high levels of primary production (Figure 5). These negative relationships were

362   strongest in organisms weighing between < 0.1 g and 1000 g. In contrast, organisms weighing > 10 kg

363   exhibited a broadly positive relationship with trawling, which strengthened with increasing primary

364   production. Primary production had positive effects on the biomass of most modalities when plotting

365   primary production as a continuous variable (Figures S5 and S6), and that the positive effect of primary

366   production weakened under high levels of trawling. For "bioturbation", only the interaction between

367   modality and primary production was significant. Of the modalities within this trait, upward conveyors

368   related positively to primary production (Figure 6), whilst the other modalities exhibited no clear

369   pattern.

370   **Discussion**

371   Our study is the first to measure the joint effects of trawling and primary production on the functional

372   diversity and traits composition of benthic communities. Overall, bottom trawling had negative effects

373   on the functional diversity, evenness, and biomass of 12 of the 32 modalities investigated, whilst

374   primary production had positive effects. We also observed strong interactive effects between the two,

375   in that the degree to which one influenced the benthic community depended on the strength of the

376   other. This meant greater effects of bottom trawling on benthic communities in areas of high primary

377   production.

378   Community biomass was less evenly distributed across modalities in highly trawled areas, resulting in

379   lower levels of functional diversity and functional evenness. Whilst some studies suggest fishing can

380   reduce functional diversity and evenness (Worm et al. 2006, Martins et al. 2012), ours is the first to

381 directly relate reductions to incremental increases in trawling pressure. We also found stronger effects

382 of trawling on functional diversity and evenness in areas of high primary production. The cause of this

383 pattern remains unclear, especially considering recent evidence which suggests that high primary

384 production should buffer benthic communities from trawling impacts (Hiddink et al. 2017). Then again,

385 highly productive freshwater systems often coincide with high community biomass but low species

386 diversity (McQueen et al. 1989, Rudstam et al. 1993), and should therefore be less resilient

387 (Macpherson et al. 2002, Jennings & Blanchard 2004, Gómez-Canchong et al. 2013). Given the effects

388 of climate change, acidification, and eutrophication on global levels of primary production, such a

389 relationship could make marine ecosystems and the fisheries they support less resilient to the impacts

390 of fishing, particularly in areas where primary production increases (Blanchard et al. 2012, Tait & Schiel

391 2013).

392 Intensely trawled areas were characterised by lower biomasses of attached and epiphytic organisms

393 such as sea squirts (Tunicata), sponges (Porifera), bryozoans (e.g. *Flustra foliacea*, Crisiidae and

394 *Cellaria* spp), and soft (e.g. *Alcyonium digitatum*) and hard corals (e.g. *Caryophyllia smithii*). Many

395 studies document strong impacts on these organisms by mobile gears through physical disruption of

396 sediments (Kaiser et al. 2000, 2006, Bradshaw et al. 2003, Howarth, Pickup, et al. 2015) and associated

397 negative effects on suspension feeders (Collie et al. 2000, Bradshaw et al. 2003). However, these

398 organisms are functionally important to temperate marine ecosystems because they add three

399 dimensional structure to the seabed (Howarth, Roberts, et al. 2015). In doing so, they can provide

400 nursery habitats to a wide range of fish and invertebrates, supporting local levels of biodiversity and

401 the recruitment of commercially important species (Beck et al. 2001, Kamenos et al. 2004, Gibb et al.

402 2007, Howarth, Roberts, et al. 2015). Consequently, negative effects of bottom trawling could

403 potentially reduce their nursery habitat function (Kaiser et al. 2000, Bradshaw et al. 2001, Howarth et

404 al. 2011).

405 High levels of fishing pressure are expected to reduce the abundance of large predators, and favour

406 smaller competitor and prey species with shorter life histories (Bremner & Frid 2005, Tillin et al. 2006).

407 Alternatively, all body sizes could be affected given that bottom trawling is non-selective, causing

408 mortality in a wide range of non-target and target species ranging from nematodes to large sharks

409 (Fennessy 1994, Hiddink et al. 2006, Hinz et al. 2008, 2009). However, we found negative effects of

410 bottom trawling on a variety of body sizes (< 0.1 g to 10 kg) but no relationship with feeding mode.

411 Hence, our results indicate that bottom trawling removes biomass from most of the benthic

412 community, and not just large predators. Our results therefore suggest that fishing mortality is more

413 important for small-bodied organisms than the release from predation pressure caused by the

414 removal of targeted fish species.

415 Surprisingly, trawling had a broadly positive effect on the biomass of large organisms weighing > 10

416 kg such as rays (e.g. *Amblyraja radiata* and *Dipturus batis*), sharks (e.g. *Mustelus Asterias*), gadoids

417 (e.g. *Gadus morhua* and *Molva molva*) turbot (*Scophthalmus maximus*) and monkfish (*Lophius*

418 *piscatorius*). This unexpected result may reflect the low number of species (i.e. 11) represented in this

419 modality. Hence, any differences in the spatial distribution of these species across our sampling

420 stations would have had disproportionally strong effects on our results. Alternatively, this finding may

421 reflect the confounding effects of using fishing effort as an indicator of fishing disturbance. Logic

422 suggests fishing pressure should concentrate in areas with larger, more commercially viable species.

423 If true, this would reduce our ability to detect a negative relationship between fishing effort and the

424 abundance of large predatory fish.

425 The abundance of mobile scavengers can increase by up to 200 times in trawled areas as a result of

426 increased availability of carrion and other organic matter (Tillin et al. 2006, Kaiser & Hiddink 2007).

427 However, we detected no relationship between bottom trawling and the biomass of scavenging

428 organisms such as hermit crabs (e.g. *Pagurus* spp). Then again, given the dispersion of odour plumes,

429 resettlement of sediment and predation of damaged / injured organisms, high scavenger densities on

430 fishing grounds are likely to be relatively short-lived events (Howarth, Pickup, et al. 2015). Hence, our

431 approach, which was designed to detect long-term and large-scale changes, is unlikely to detect such

432 an event. However, our results support two other studies that suggest the benefits of an increased

433 food supply to scavengers cannot compensate for the direct mortality caused by bottom trawling

434 (Bolam 2014, Bolam et al. 2017). These two studies also observed recovery of bioturbating species in

435 3 – 5 months following bottom fishing. In our study, this modality was composed primarily of

436 burrowing polychaetes (e.g. Pectinariidae, Maldanidae and Eunicidae) which recover quickly from

437 disturbance (reviewed in Jennings, Kaiser, et al. 2001). This capacity may explain why we observed no

438 relationship between bottom trawling and the biomass of bioturbating organisms.

439 High levels of primary production should provide more energy to benthic deposit and suspension

440 feeders (Blanchard et al. 2009). However, we detected no relationship between primary production

441 and the biomass of deposit and suspension feeding organisms, such as bivalves (e.g. Cardiidae and

442 *Abra* spp), polychaetes (e.g. *Lagis koreni*), and anemones (Actiniaria). This may reflect the depth of

443 our sampling stations. Detritus is a poor energy resource, subject to degradation through microbial

444 action and consumption as it sinks through the water column towards the seabed (Gerlach et al. 1985).

445 Given that our sampling sites were located at depths between 40 and 90 m, the detritus reaching the

446 seabed may have been too low in energy to offer measurable benefit to deposit and suspension

447 feeders. We also expected a positive relationship between primary production and small body size,

448 and for this relationship to intensify under high trawling pressure. Whilst we found evidence of

449 primary production increasing the biomass of small-bodied organisms, in reality, this relationship

450 weakened with increasing trawling pressure. Hence, this pattern suggests the fishing mortality

451 inflicted on small organisms outweighs any benefits they receive from enhanced growth rates under

452 high primary production (Posey et al. 2002).

453 In summary, our evidence suggests that bottom trawling and primary production can cause functional

454 changes to benthic communities. Bottom trawling had negative effects on functional diversity,

455   functional evenness, and the maximum weight and living habit of the benthic community, and no

456   effects on their feeding mode, longevity, bioturbation, and sediment position. We also found greater

457   effects of trawling on benthic ecosystem functioning in areas of high primary production. Noting

458   changing levels of primary production globally, this interaction may reduce resiliency of ecosystems

459   and fish stocks to future fishing impacts. We therefore suggest further study of the interactions

460   between fishing disturbance and environmental perturbations, which could have strong implications

461   for conservation and fisheries management.

Data accessibility

463   Data used in this paper are archived in the British Oceanographic Data Centre (www.bodc.ac.uk)
464   under doi:10.5285/674d4224-7cc5-4080-e053-6c86abc0626e.

References

476   Aller RC (1982) The effects of macrobenthos on chemical properties of marine sediment and
477   overlying water. In: McCall PL, Tesz MJS (eds) Animal-Sediment Relations. Plenum Publishing
478   Company, New York, p 53–102

479   Beamish RJ, McFarlane GA, Benson A (2006) Longevity overfishing. Prog Oceanogr 68:289–302

480   Beck MW, Heck KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino
481   K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MP (2001) The Identification, Conservation, and
482   Management of Estuarine and Marine Nurseries for Fish and Invertebrates. Bioscience 51:633–
483   641

484   Bergmann M, Wieczorek SK, Moore PG, Atkinson RJA (2002) Discard composition of the *Nephrops*
485   fishery in the Clyde Sea area, Scotland. Fish Res 57:169–183

486   Blanchard JL, Jennings S, Holmes R, Harle J, Merino G, Allen JI, Holt J, Dulvy NK, Barange M (2012)
487   Potential consequences of climate change for primary production and fish production in large
488   marine ecosystems. Philos Trans R Soc B Biol Sci 367:2979–2989

489   Blanchard JL, Jennings S, Law R, Castle MD, McCloghrie P, Rochet MJ, Benoît E (2009) How does
490   abundance scale with body size in coupled size-structured food webs? J Anim Ecol 78:270–280

491   Bolam SG (2014) Predicting the effect of trawling based on biological traits of organisms and

492   functional correlates of these traits to predict which functions may be disproportionally
493   affected. BENTHIS Deliverable 4.3.

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

497 Bolam SG, Garcia C, Eggleton J, Kenny AJ, Buhl-Mortensen L, Gonzalez-Mirelis G, Kooten T van,
498   Dinesen G, Hansen J, Hiddink JG, Sciberras M, Smith C, Papadopoulou N, Gumus A, Hoey G Van,
499   Eigaard OR, Bastardie F, Rijnsdorp AD (2017) Differences in biological traits composition of
500   benthic assemblages between unimpacted habitats. Mar Environ Res 126:1–13

501 Bolam SG, McIlwaine PSO, Garcia C (2016) Application of biological traits to further our
502   understanding of the impacts of dredged material disposal on benthic assemblages. Mar Pollut
503   Bull 105:180–192

504 Borrvall C, Ebenman B, Tomas Jonsson TJ (2000) Biodiversity lessens the risk of cascading extinction
505   in model food webs. Ecol Lett 3:131–136

506 Bradshaw C, Collins P, Brand AR (2003) To what extent does upright sessile epifauna affect benthic
507   biodiversity and community composition? Mar Biol 143:783–791

508 Bradshaw C, Veale LO, Hill AS, Brand AR (2001) The effect of scallop dredging on Irish Sea benthos:
509   experiments using a closed area. Hydrobiologia 465:129–138

510 Brander KM (2007) Global fish production and climate change. Proc Natl Acad Sci USA 104:19709–
511   19714

512 Bremner J, Frid C. (2005) Biological traits of the North Sea benthos: does fishing affect ecosystem
513   function? Am Fish Soc Symp 41:477–489

514 Bremner J, Rogers SI, Frid CLJ (2006) Methods for describing ecological functioning of marine benthic
515   assemblages using biological traits analysis (BTA). Ecol Indic 6:609–622

516 Brose U, Cushing L, Berlow EL, Jonsson T, Banasek-Richter C, Bersier L-F, Blanchard J, Brey T,
517   Carpenter SR, Blandenier M-F, Cohen J, Dawah H, Dell T, Edwards F, Harper-Smith S, Jacob U,
518   Knapp R, Ledger M, Memmott J, Mintenbeck K, Pinnegar J, Rall B, Rayner T, Ruess L, Ulrich W,
519   Warren PH, Williams RJ, Woodward G, Yodzis P, Martinez N (2005) Body sizes of consumers
520   and their resources. Ecology 86:2545

521 Campbell MS, Stehfest KM, Votier SC, Hall-Spencer JM (2014) Mapping fisheries for marine spatial
522   planning: Gear-specific vessel monitoring system (VMS), marine conservation and offshore
523   renewable energy. Mar Policy 45:293–300

524 Cardinale BJ, Palmer MA, Collins SL (2002) Species diversity enhances ecosystem functioning through
525   interspecific facilitation. Nature 415:426–429

526 Chevenet Fran, Doleadec S, Chessell D (1994) A fuzzy coding approach for the analysis of long-term
527   ecological data. Freshw Biol 31:295–309

528 Collie JS, Hall SJ, Kaiser MJ, Poiner IR (2000) A quantitative analysis of fishing impacts on shelf-sea
529   benthos. J Anim Ecol 69:785–798

530 Cooper R, Long D, Doce D, Green S, Morando A (2010) Creating and assessing a sediment data layer
531   for UKSeaMap 2010. British Geological Survey Commercial Report, CR/09/168.

532 Crain CM, Kroeker K, Halpern BS (2008) Interactive and cumulative effects of multiple human
533   stressors in marine systems. Ecol Lett 11:1304–1315

534 Craven HR, Brand AR, Stewart BD (2013) Patterns and impacts of fish bycatch in a scallop dredge
535   fishery. Aquat Conserv Mar Freshw Ecosyst 23:152–170

536 Díaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem
537   processes. Trends Ecol Evol 16:646–655

538 Dray S, Bu-four A-B, Thiolouse J (2017) Package 'ade4'. Analysis of ecological Data: exploratory and
539   Euclidean methods in environmental sciences. Cran R Project.

540 Eigaard OR, Bastardie F, Hintzen NT, Buhl-Mortensen L, Buhl-Mortensen P, Catarino R, Dinesen GE,
541   Egekvist J, Fock H, Geitner K, Gerritsen H, González MM, Jonsson P, Kavadas S, Laffargue P,
542   Lundy M, Mirelis GG, Nielsen JR, Papadopoulou N, Posen PE, Pulcinella J, Russo T, Sala A, Silva
543   C, Smith C, Vanelslander B, Rijnsdorp AD (2017) The footprint of bottom trawling in European
544   waters: distribution, intensity and seabed integrity. ICES J Mar Sci 74:847–865

545 Fasham MJR, Holligan PM, Pugh PR (1983) The Spatial and Temporal Development of the Spring
546   Phytoplankton Bloom in the Celtic Sea , April 1979. Prog Oceanogr 12:87–145

547 Fennessy ST (1994) Incidental capture of elasmobranchs by commercial prawn trawlers on the
548   Tugela Bank, Natal, South Africa. South African J Mar Sci 14:287–296

549 Fonseca CR, Ganade G (2001) Species functional redundancy, random extinctions and the stability of
550   ecosystems. J Ecol 89:118–125

551 Frederiksen M, Edwards M, Richardson AJ, Halliday NC, Wanless S (2006) From plankton to top
552   predators: Bottom-up control of a marine food web across four trophic levels. J Anim Ecol
553   75:1259–1268

554 Friedlander AM, DeMartini EE (2002) Contrasts in density, size, and biomass of reef fishes between
555   the northwestern and the main Hawaiian islands: The effects of fishing down apex predators.
556   Mar Ecol Prog Ser 230:253–264

557 Fu C, Travers-Trolet M, Velez L, Grüss A, Bundy A, Shannon LJ, Fulton EA, Akoglu E, Houle JE, Coll M,
558   Verley P, Heymans JJ, John E, Shin Y-J (2018) Risky business: The combined effects of fishing
559   and changes in primary productivity on fish communities. Ecol Modell 368:265–276

560 Garcia-Soto C, Pingree RD (2009) Spring and summer blooms of phytoplankton (SeaWiFS/MODIS)
561   along a ferry line in the Bay of Biscay and western English Channel. Cont Shelf Res 29:1111–
562   1122

563 Gerlach SA, Hahn AE, Schrage M (1985) Size spectra of benthic biomass and metabolism. Mar Ecol
564   Prog Ser 26:161–173

565 Gerritsen HD, Minto C, Lordan C (2013) How much of the seabed is impacted by mobile fishing gear?
566   Absolute estimates from Vessel Monitoring System (VMS) point data. ICES J Mar Sci 70:523–
567   531

568 Gibb FM, Gibb IM, Wright PJ (2007) Isolation of Atlantic cod (Gadus morhua) nursery areas. Mar Biol
569   151:1185–1194

570 Gómez-Canchong P, Blanco JM, Quiñones RA (2013) On the use of biomass size spectra linear
571   adjustments to design ecosystem indicators. Sci Mar 77:257–268

572 Gómez-Canchong P, Quiñones RA, Brose U (2012) Robustness of size–structure across ecological
573   networks in pelagic systems. Theor Ecol 6:45–56

574 Gregg WW, Conkright ME, Ginoux P, O'Reilly JE, Casey NW (2003) Ocean primary production and
575   climate: global decadal changes. Geophys Res Lett 30

576 Guénette S, Gascuel D (2012) Shifting baselines in European fisheries: The case of the Celtic Sea and
577   Bay of Biscay. Ocean Coast Manag 70:10–21

578 Gunderson AR, Armstrong EJ, Stillman JH (2016) Multiple Stressors in a Changing World: The Need
579   for an Improved Perspective on Physiological Responses to the Dynamic Marine Environment.

580   Ann Rev Mar Sci 8

581   Hiddink JG, Jennings S, Kaiser MJ (2007) Assessing and predicting the relative ecological impacts of
582   disturbance on habitats with different sensitivities. J Appl Ecol 44:405–413

583   Hiddink JG, Jennings S, Kaiser MJ, Queiros AM, Duplisea DE, Piet GJ (2006) Cumulative impacts of
584   seabed trawl disturbance on benthic biomass, production and species richness in different
585   habitats. Can J Fish Aquac Sci 63:721–736

586   Hiddink JG, Jennings S, Sciberras M, Szostek C., Hughes KM, Ellis N, Rijnsdorp AD, McConnaughey RA,
587   Mazor T, Hilborn R, Collie JS, Pitcher R, Amoroso RO, Parma AM, Suuronen P, Kaiser MJ (2017)
588   Global analysis of depletion and recovery of seabed biota following bottom trawling
589   disturbance. Proc Natl Acad Sci In press

590   Hinz H, Hiddink JG, Forde J, Kaiser MJ (2008) Large-scale responses of nematode communities to
591   chronic otter-trawl disturbance. Can J Fish Aquat Sci 732:723–732

592   Hinz H, Prieto V, Kaiser MJ (2009) Trawl distrubance on benthic communities: chronic effects and
593   experimental predications. Ecol Appl 19:761–773

594   Howarth LM, Pickup SE, Evans LE, Cross TJ, Hawkins JP, Roberts CM, Stewart BD (2015) Sessile and
595   mobile components of a benthic ecosystem display mixed trends within a temperate marine
596   reserve. Mar Environ Res 107:8–23

597   Howarth LM, Roberts CM, Hawkins JP, Steadman DJ, Beukers-Stewart BD (2015) Effects of
598   ecosystem protection on scallop populations within a community-led temperate marine
599   reserve. Mar Biol 162:823–840

600   Howarth LM, Roberts CM, Thurstan RH, Stewart BD (2014) The unintended consequences of
601   simplifying the sea: Making the case for complexity. Fish Fish 15:690–711

602   Howarth LM, Stewart BD (2014) The dredge fishery for scallops in the United Kingdom (UK): effects
603   on marine ecosystems and proposals for future management. Marine Ecosystem Management
604   Report no. 5, University of York. York

605   Howarth LM, Wood HL, Turner AP, Beukers-Stewart BD (2011) Complex habitat boosts scallop
606   recruitment in a fully protected marine reserve. Mar Biol 158:1767–1780

607   Jennings S, Blanchard JL (2004) Fish abundance with no fishing: Predictions based on
608   macroecological theory. J Anim Ecol 73:632–642

609   Jennings S, Kaiser MJ, Reynolds JD (2001) Marine fisheries ecology. Blackwell, Oxford.

610   Jennings S, Pinnegar JK, Polunin NVC, Boon TW (2001) Weak cross-species relationships between
611   body size and trophic level belie powerful size-based trophic structuring in fish communities. J
612   Anim Ecol 70:934–944

613   Jennings S, Pinnegar JK, Polunin NVC, Warr KJ (2002) Linking size-based and trophic analyses of
614   benthic community structure. Mar Ecol Prog Ser 226:77–85

615   JGOFS (1994) Joint Global Ocean Flux Study (JGOFS) Protocols. Woods Hole Oceanographic
616   Institution, Massachusetts.

617   Jørgensen C, Enberg K, Dunlop ES, Arlinghaus R, Boukal DS, Brander K, Ernande B, Gårdmark AG,
618   Johnston F, Matsumura S, Pardoe H, Raab K, Silva A, Vainikka A, Dieckmann U, Heino M,
619   Rijnsdorp AD (2007) Ecology: Managing Evolving Fish Stocks. Science (80-) 318:1247–1248

620   Kaiser MJ, Clarke KR, Hinz H, Austen MC V, Somerfield PJ, Karakassis I (2006) Global analysis of
621   response and recovery of benthic biota to fishing. Mar Ecol Prog Ser 311:1–14

622   Kaiser M., Hiddink JG (2007) Food subsidies from fisheries to continental shelf benthic scavengers.

623   Mar Ecol Prog Ser 350:267–276

624 Kaiser MJ, Spence FE, Hart PJB (2000) Fishing-Gear Restrictions and Conservation of Benthic Habitat
625   Complexity. Conserv Biol 14:1512–1525

626 Kamenos N, G. Moore P, Hall-Spencer J (2004) Nursery-area function of maerl grounds for juvenile
627   queen scallops Aequipecten opercularis and other invertebrates. Mar Ecol Prog Ser 274:183–
628   189

629 Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli
630   D, Schmid B, Tilman D, Wardle DA (2001) Biodiversity and Ecosystem Functioning: Current
631   Knowledge and Future Challenges. Science (80-) 294:804 LP-808

632 Lorenzen CJ (1966) A method for the continuous measurement of the in vivo chlorophyll
633   concentration. Deep Sea Res 13:223–227

634 Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG, Kay MC, Kidwell SM, Kirby MX, Peterson
635   CH, Jackson JBC (2006) Depletion, Degradation, and Recovery Potential of Estuaries and Coastal
636   Seas. Science (80-) 312:1806 LP-1809

637 Macpherson E, Gordoa A, García-Rubies A (2002) Biomass Size Spectra in Littoral Fishes in Protected
638   and Unprotected Areas in the NW Mediterranean. Estuar Coast Shelf Sci 55:777–788

639 Mann KH (2009) Ecology of Coastal Waters. John Wiley & Sons, New York

640 Martins GM, Arenas F, Neto AI, Jenkins SR (2012) Effects of Fishing and Regional Species Pool on the
641   Functional Diversity of Fish Communities. PLoS One 7:e44297

642 Mason C (2011) NMBAQC's Best Practice Guidance. Particle Size Analysis (PSA) for Supporting
643   Biological Analysis. National Marine Biological AQC Coordinating Committee.

644 McGrady-Steed J, Harris PM, Morin PJ (1997) Biodiversity regulates ecosystem predictability. Nature
645   390:162

646 McQueen DJ, Johannes MRS, Post JR, Stewart TJ, Lean DRS (1989) Bottom-up and top-down impacts
647   on freshwater pelagic community structure. Ecol Monogr 59:289–309

648 Mermillod-Blondin F (2011) The functional significance of bioturbation and biodeposition on
649   biogeochemical processes at the water–sediment interface in freshwater and marine
650   ecosystems. J North Am Benthol Soc 30:770–778

651 Micheli F, Halpern BS (2005) Low functional redundancy in coastal marine assemblages. Ecol Lett
652   8:391–400

653 Mooney H, Larigauderie A, Cesario M, Elmquist T, Hoegh-Guldberg O, Lavorel S, Mace GM, Palmer
654   M, Scholes R, Yahara T (2009) Biodiversity, climate change, and ecosystem services. Curr Opin
655   Environ Sustain 1:46–54

656 Morel A, Berthon J-F (1989) Surface pigments, algal biomass profiles, and potential production of the
657   euphotic layer: Relationships reinvestigated in view of remote-sensing applications. Limnol
658   Oceanogr 34:1545–1562

659 Mouillot D, Graham NAJ, Villéger S, Mason NWH, Bellwood DR (2013) A functional approach reveals
660   community responses to disturbances. Trends Ecol Evol 28:167–177

661 Musick JA (1999) Ecology and conservation of long-lived marine animals. Am Fish Soc Symp 23:1–10

662 Olsgard F, Schaanning MT, Widdicombe S, Kendall MA, Austen MC (2008) Effects of bottom trawling
663   on ecosystem functioning. J Exp Mar Bio Ecol 366:123–133

664 Pearson TH, Rosenberg R (1978) Macrobenthic succession in relation to organic enrichment and
665   pollution of the marine environment. Oceanogr Mar Biol Annu Rev 16:229–311

666 Poloczanska ES, Brown CJ, Sydeman WJ, Kiessling W, Schoeman DS, Moore PJ, Brander K, Bruno JF,
667   Buckley LB, Burrows MT, Duarte CM, Halpern BS, Holding J, Kappel C V, O/'Connor MI, Pandolfi
668   JM, Parmesan C, Schwing F, Thompson SA, Richardson AJ (2013) Global imprint of climate
669   change on marine life. Nat Clim Chang 3:919–925

670 Rodríguez S, Ojeda F, Inestrosa N (1993) Settlement of benthic marine invertebrates. Mar Ecol Prog
671   Ser 97:193–207

672 Rosenberg R (1995) Benthic marine fauna structured by hydrodynamic processes and food
673   availability. Netherlands J Sea Res 34:303–317

674 Rudstam LG, Lathrop RC, Carpenter SR (1993) The Rise and Fall of a Dominant Planktivore: Direct and
675   Indirect Effects on Zooplankton. Ecology 74:303–319

676 Schleuter D, Daufresne M, Massol F, Argillier C (2010) A user's guide to functional diversity indices.
677   Ecol Monogr 80:469–484

678 Sciberras M, Parker R, Powell C, Robertson C, Kroger S, Bolam S, Geert Hiddink J (2016) Impacts of
679   bottom fishing on the sediment infaunal community and biogeochemistry of cohesive and non-
680   cohesive sediments. Limnol Oceanogr 61:2076–2089

681 Sprules WG, Barth LE (2015) Surfing the biomass size spectrum: some remarks on history, theory,
682   and application. Can J Fish Aquat Sci 73:477–495

683 Stuart-Smith RD, Bates AE, Lefcheck JS, Duffy JE, Baker SC, Thomson RJ, Stuart-Smith JF, Hill NA,
684   Kininmonth SJ, Airoldi L, Becerro MA, Campbell SJ, Dawson TP, Navarrete SA, Soler GA, Strain
685   EMA, Willis TJ, Edgar GJ (2013) Integrating abundance and functional traits reveals new global
686   hotspots of fish diversity. Nature 501:539–42

687 Tait LW, Schiel DR (2013) Impacts of Temperature on Primary Productivity and Respiration in
688   Naturally Structured Macroalgal Assemblages. PLoS One 8:e74413

689 Team RC (2017) R: A language and environment for statistical computing. R Foundation for Statistical
690   Computing, Vienna, Austria. URL https://www.R-project.org/.

691 Tillin HM, Hiddink JG, Jennings S, Kaiser MJ (2006) Chronic bottom trawling alters the functional
692   composition of benthic invertebrate communities on a sea-basin scale. Mar Ecol Prog Ser
693   318:31–45

694 Watson RA, Cheung WWL, Anticamara JA, Sumaila U, Zeller D, Pauly D (2013) Global marine yield
695   halved as fishing intensity redoubles. Fish Fish 14:493–503

696 Williams ID, Baum JK, Heenan A, Hanson KM, Nadon MO, Brainard RE (2015) Human, oceanographic
697   and habitat drivers of central and western pacific coral reef fish assemblages. PLoS One 10:1–
698   19

699 Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, Halpern BS, Jackson JBC, Lotze HK, Micheli F,
700   Palumbi SR, Sala E, Selkoe KA, Stachowicz JJ, Watson R (2006) Impacts of biodiversity loss on
701   ocean ecosystem services. Science (80-) 314:787–790

702

703

704

705

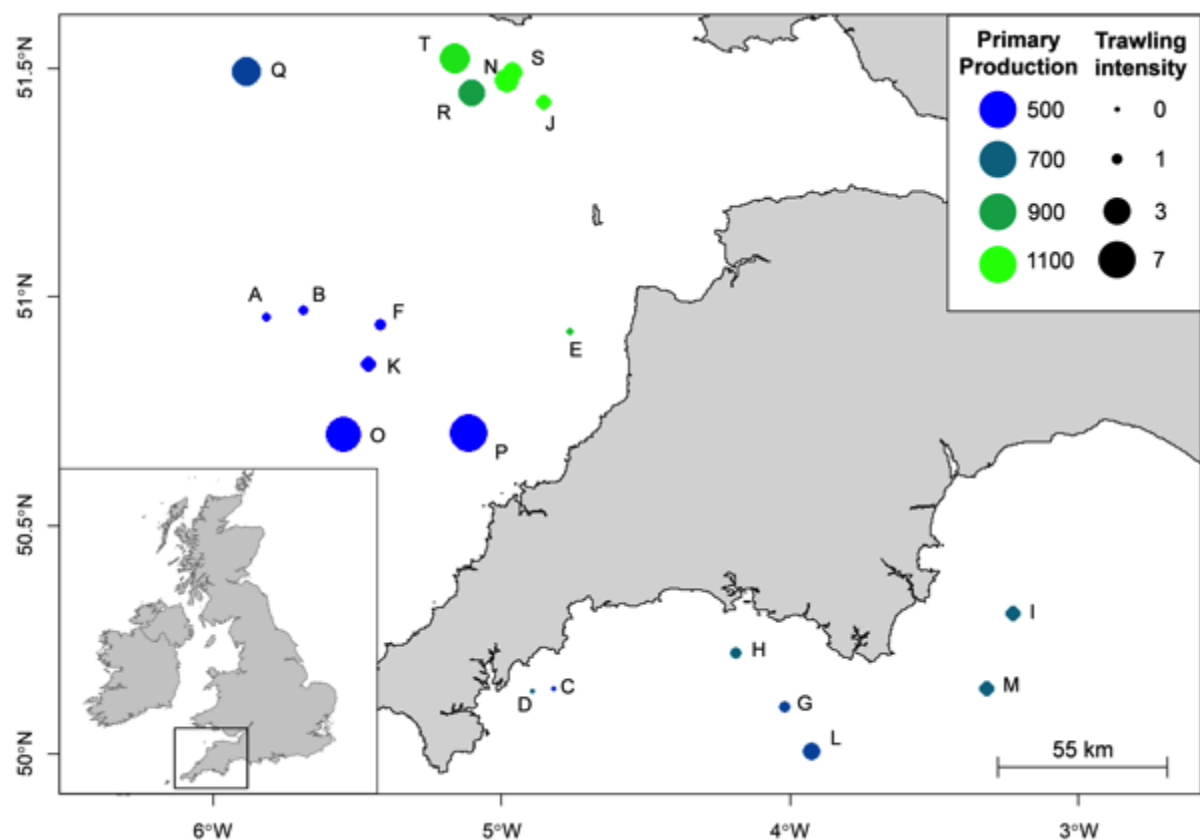706

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Figures

Figure 1. Sampling stations. Each point represents a 1 x 0.6 nautical mile box, the shade and size of which signifies the level of primary production (mg C m^{-2} yr^{-1}) and trawling intensity (yr^{-1}).
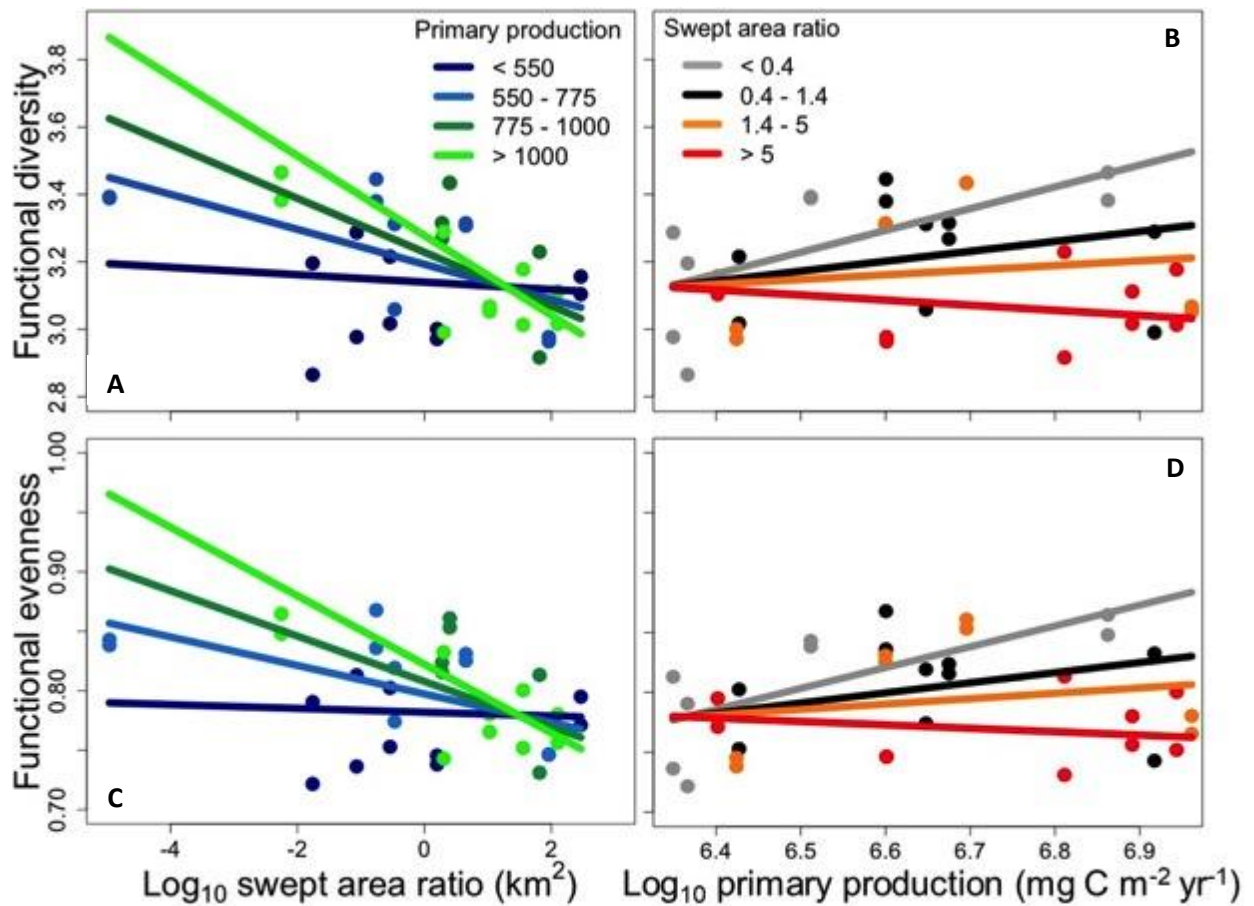
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Figure 2: Functional diversity (A) and functional evenness (B) plotted against trawling intensity and categorical levels of primary production. Functional diversity (C) and functional evenness (D) plotted against primary production and categorical levels of trawling intensity. Trend lines fitted by linear models.

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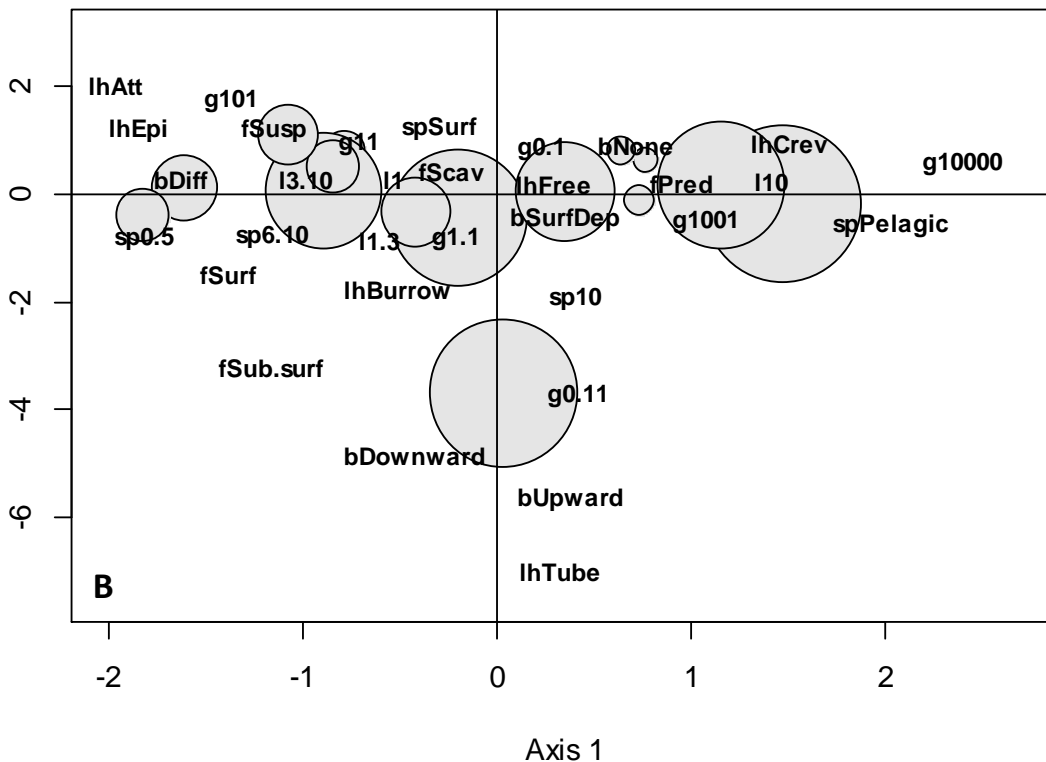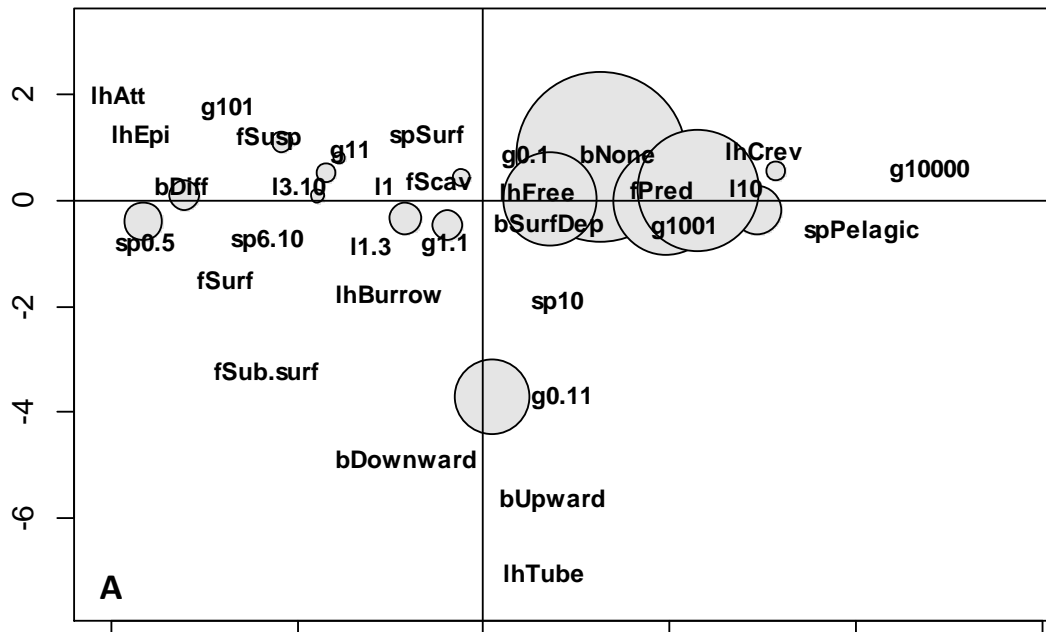720

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Figure 3. Plots of ordination scores from fuzzy correspondence analysis of modality biomass. Each bubble indicates a sampling station. Plots are identical except for the area of circles: (A) trawling intensity (yr–1); (B) primary production (mg C m-2 yr-1). The abbreviations give the names of the modalities. Stations that appear further apart have greater differences in overall trait composition. The location of the modalities indicates the types of stations with which they are associated.

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Figure 4. Biomass of modalities within the trait "living habit", plotted against trawling (swept area ratio) and categorical levels of primary production. Trend lines fitted by linear models.
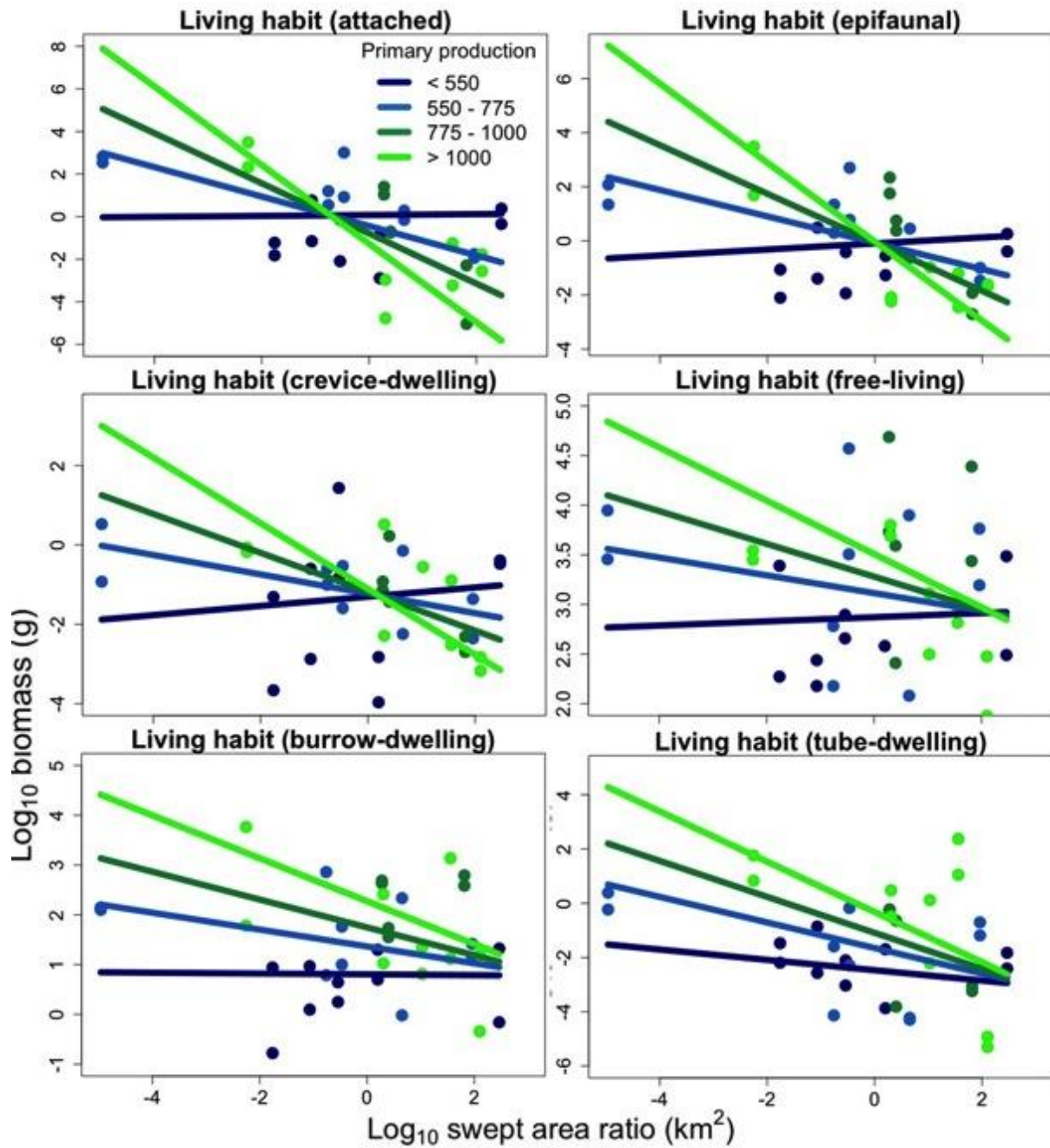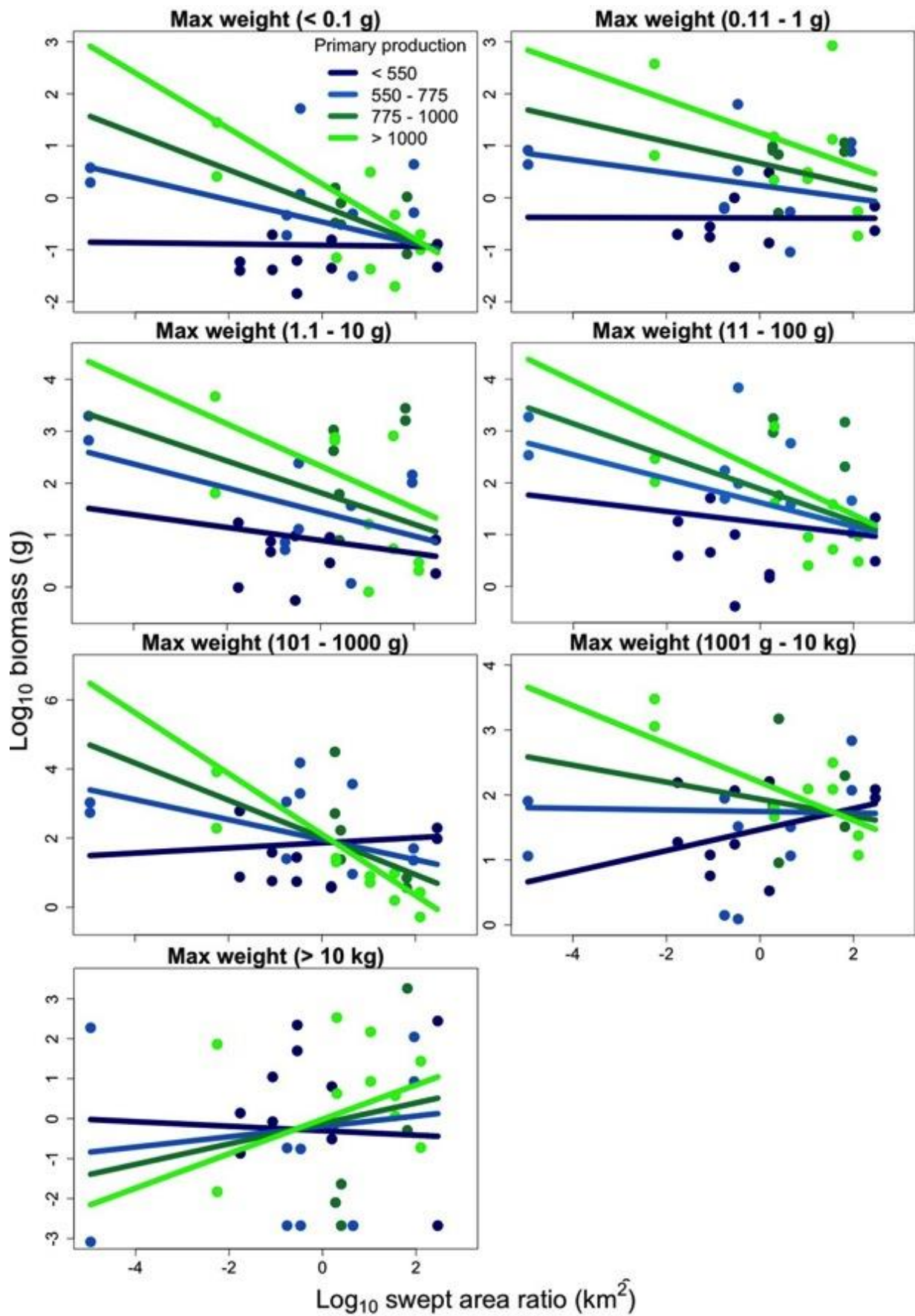
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Figure 5. Biomass of modalities within the trait "maximum weight", plotted against trawling intensity (swept area ratio) and categorical levels of primary production. Trend lines fitted by linear models.
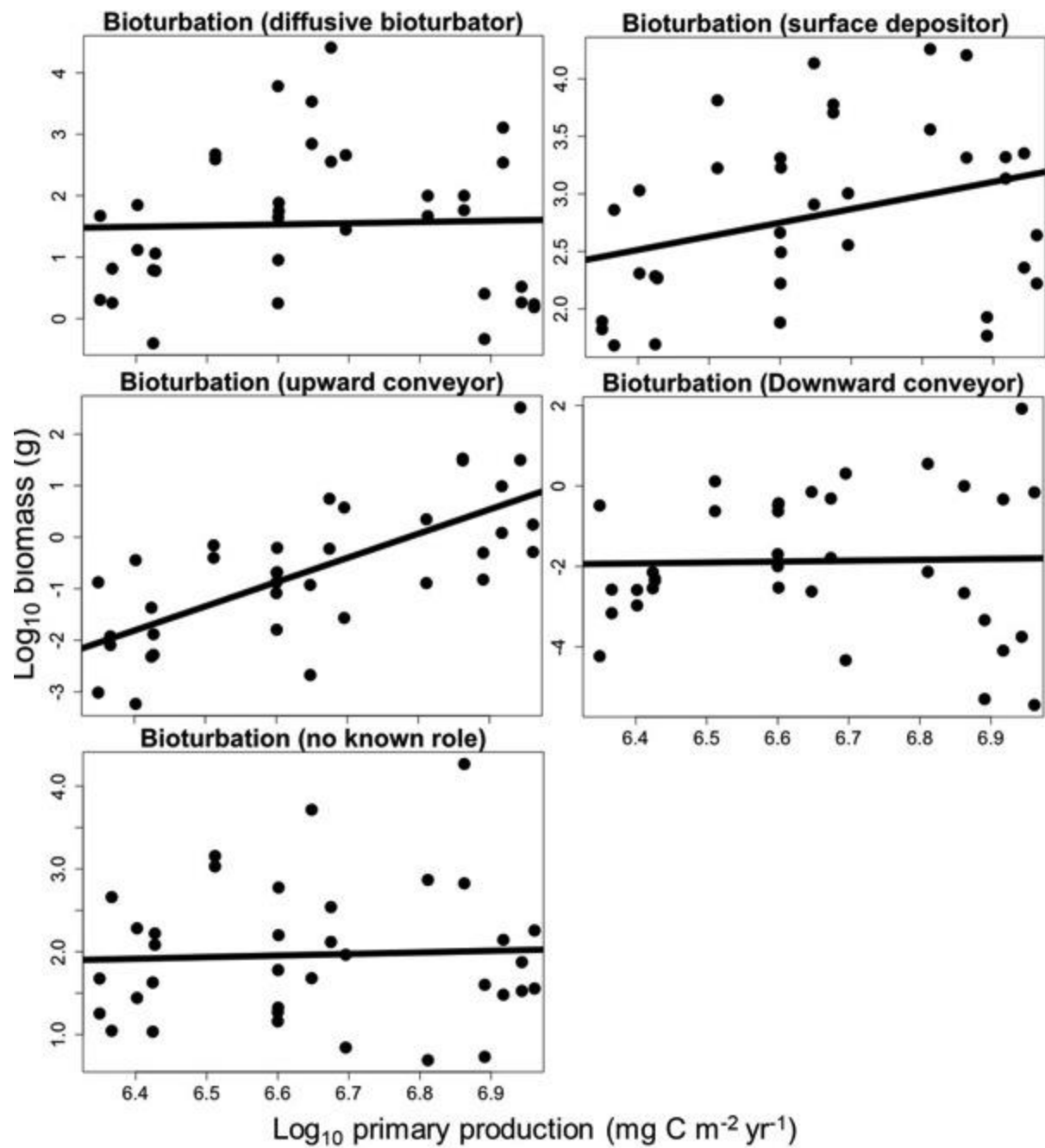
Figure 6. Biomass of modalities within the trait "bioturbation", plotted against primary production. Trend lines fitted by linear models.

754 **Table 1.** The range of values that defined the four experimental treatments of trawling intensity and
755 primary production sampled in this study.

Treatment	Swept area ratio (km^2)	Primary production (mg C m^{-2} yr^{-1})
1 - Low	≤ 0.4	≤ 550
2 - Medium low	$\geq 0.4 \leq 1.4$	$> 550 \leq 775$
3 - Medium high	$\geq 1.4 \leq 5$	$> 775 \leq 1000$
4 - High	> 5	> 1000

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Table 2. Description of biological traits used in this study, and the total biomass (pre-gear calibration) and number of taxa that fell within each modality.

| Trait	Code	Description	No. of taxa	Biomass (g m^{-2})	Relevance
Maximum weight	g0.1	< 0.1 g	108	298.1	Reflects trophic position, metabolic rate, energy requirements, generation time, commercial value, and catchability (Jennings et al. 2002, Brose et al. 2005, Sprules & Barth 2015).
	g0.11	0.11 - 1 g	71	801.8	
	g1.1	1.1 - 10 g	105	2305.8	
	g11	11 - 100 g	84	936.5	
	g101	101 - 1000 g	46	1421.8	
	g1001	1001 - 10000 g	33	256.5	
	g10000	> 10000 g	11	33	
Longevity	l1	< 1 yrs	45	15.3	Reflects age at maturity, somatic growth, and disturbance frequency / severity (Pearson & Rosenberg 1978, Musick 1999).
	l1-3	1 - 3 yrs	125	1152.2	
	l3-10	3 - 10 yrs	171	3557.9	
	l10	> 10 yrs	83	1328.1	
Living habit	lhTube	Tube-dwelling	31	329	Indicates potential to evade, or to be exposed to disturbance and predation pressure (Kaiser et al. 2000).
	lhBurrow	Burrow-dwelling	89	2015.8	
	lhFree	Free-living	222	3266.5	
	lhCrev	Crevice-dwelling	48	62.1	
	lhEpi	Epiphytic	34	140.6	
	lhAtt	Attached	29	239.5	
Location within sediment	spPelagic	Pelagic	63	79.9	Implications for sediment-water biogeochemistry and oxygen availability, and susceptibility to disturbance (Aller 1982, Collie et al. 2000).
	spSurf	Atop of sediment	233	1366.5	
	sp0-5	0 - 5 cm deep	124	3731.3	
	sp6-10	6 - 10 cm deep	53	729.2	
	sp10	> 10 cm deep	26	146.5	
Feeding mode	fSusp	Suspension feeder	127	1847.6	Implications for energy flow and susceptibility to disturbance (Rosenberg 1995, Bergmann et al. 2002, Craven et al. 2013).
	fSurf	Surface deposit feeder	107	1434	
	fSub-surf	Sub-surface deposit feeder	49	1559.7	
	fScav	Scavenger	60	355.8	
	fPred	Predator	163	854.9	
Bioturbation	bDiff	Diffusive bioturbator	112	2304.8	Implications for sediment-water biogeochemistry and oxygen availability (Mermillod-Blondin 2011).
	bSurfDep	Surface depositor	249	2897.3	
	bUpward	Upward conveyor	12	303.5	
	bDownward	Downward conveyor	17	186.4	
	bNone	None	88	361.4	

783 **Table 3.** Linear model outputs modelling functional diversity and functional evenness to trawling
784 intensity and primary production.

Model	Predictor	Value	SE	t	P	R^2
Functional diversity	Intercept	1.23	0.99	1.25	0.233	
	log(trawling)	1.6	0.61	2.61	0.020	
	log(primary production)	0.3	0.15	2.1	0.044	0.37
	log(trawling):log(primary production)	-0.25	0.09	-2.7	0.018	
Functional evenness	Intercept	0.26	0.24	1.07	0.305	
	log(trawling)	0.4	0.15	2.68	0.018	
	log(primary production)	0.08	0.04	2.25	0.041	0.38
	log(trawling): log(primary production)	-0.06	0.02	-2.77	0.015	

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Table 4. Linear model outputs modelling trait biomass to modality, trawling intensity, and primary
production.

| Trait	Predictor	df	MSE	F	P	R^2
	Modality	5	126.2	59.9	<0.001	
	log(trawling)	1	75.6	35.9	<0.001	
	log(production)	1	1.5	0.7	0.401	
Living habit	Modality : log(trawling)	5	9.1	4.3	<0.001	0.69
	Modality : log(production)	5	8.6	4.1	0.002	
	log(trawling) : log(production)	1	67.6	32.1	<0.001	
	Modality : log(trawling) : log(production)	5	4.6	2.2	0.057	
	Modality	6	52.3	17.4	<0.001	
	log(trawling)	1	7.9	2.7	0.104	
	log(production)	1	33.2	11.1	0.001	
Maximum weight	Modality : log(trawling)	6	1.4	0.5	0.822	0.39
	Modality : log(production)	6	1.7	0.6	0.734	
	log(trawling) : log(production)	1	2.7	0.9	0.339	
	Modality : log(trawling) : log(production)	6	8.1	2.7	0.015	
	Modality	3	351.7	274.9	<0.001	
	log(trawling)	1	13.6	10.6	0.001	
	log(production)	1	7	5.5	0.02	
Longevity	Modality : log(trawling)	3	0.8	0.6	0.605	0.87
	Modality : log(production)	3	0.6	0.5	0.711	
	log(trawling) : log(production)	1	16.2	12.7	<0.001	
	Modality : log(trawling) : log(production)	3	0.4	0.3	0.799	
	Modality	4	136.1	110.6	<0.001	
	log(trawling)	1	7.8	6.5	0.011	
	log(production)	1	22.1	18	<0.001	
Bioturbation	Modality : log(trawling)	4	1.2	1	0.432	0.39
	Modality : log(production)	4	4.7	3.8	0.005	
	log(trawling) : log(production)	1	10.5	8.6	0.004	
	Modality : log(trawling) : log(production)	4	0.4	0.3	0.863	
	Modality	4	101.4	89	<0.001	
	log(trawling)	1	5	4.4	0.037	
	log(production)	1	9.5	8.3	0.004	
Sediment position	Modality : log(trawling)	4	2.3	2	0.091	0.71
	Modality : log(production)	4	1.1	1.1	0.376	
	log(trawling) : log(production)	1	9.2	9.2	0.002	
	Modality : log(trawling) : log(production)	4	1.2	1.2	0.319	
	Modality	4	28.7	28.7	<0.001	
	log(trawling)	1	6.3	6.3	0.013	
	log(production)	1	16.2	16.2	<0.001	
Feeding mode	Modality : log(trawling)	4	1.21	1.2	0.305	0.51
	Modality : log(production)	4	0.45	0.4	0.769	
	log(trawling) : log(production)	1	19.2	19.2	<0.001	
	Modality : log(trawling) : log(production)	4	1.2	1.2	0.315	

Electronic supplementary material
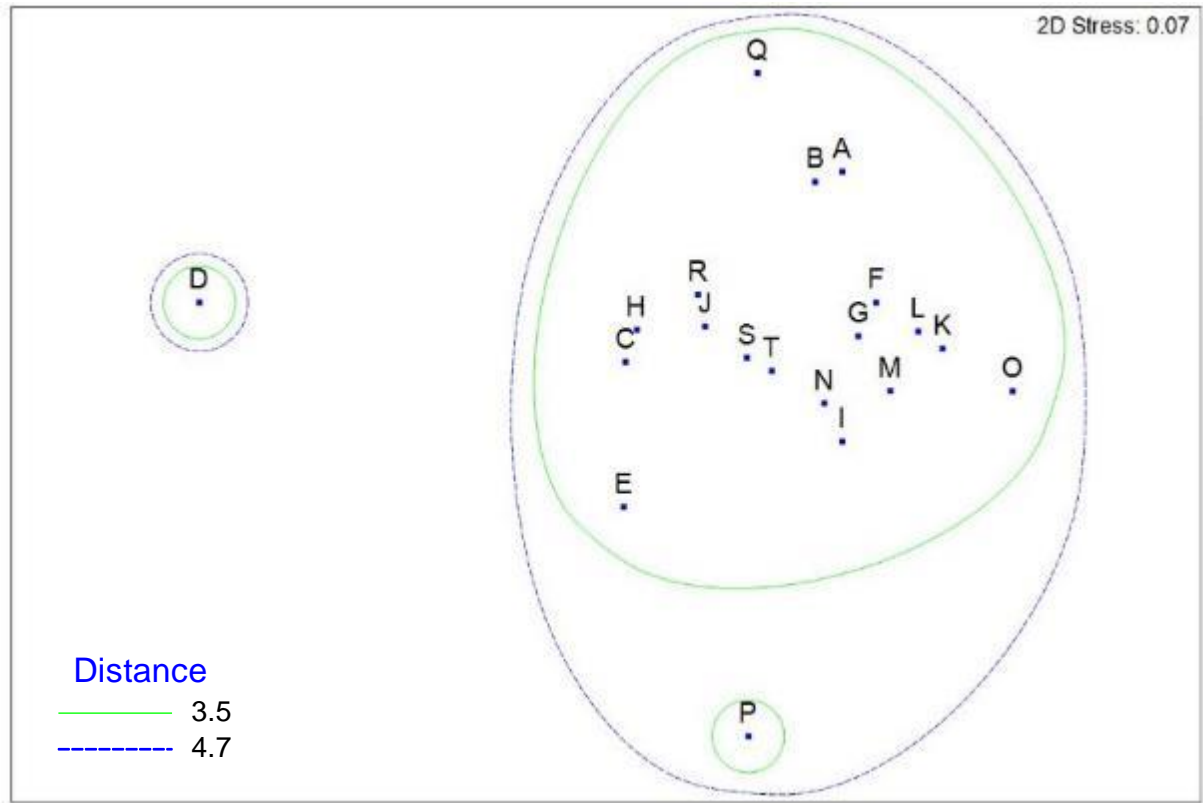
S1. nMDS plots of the different stations and their environmental characteristics before removing outliers.

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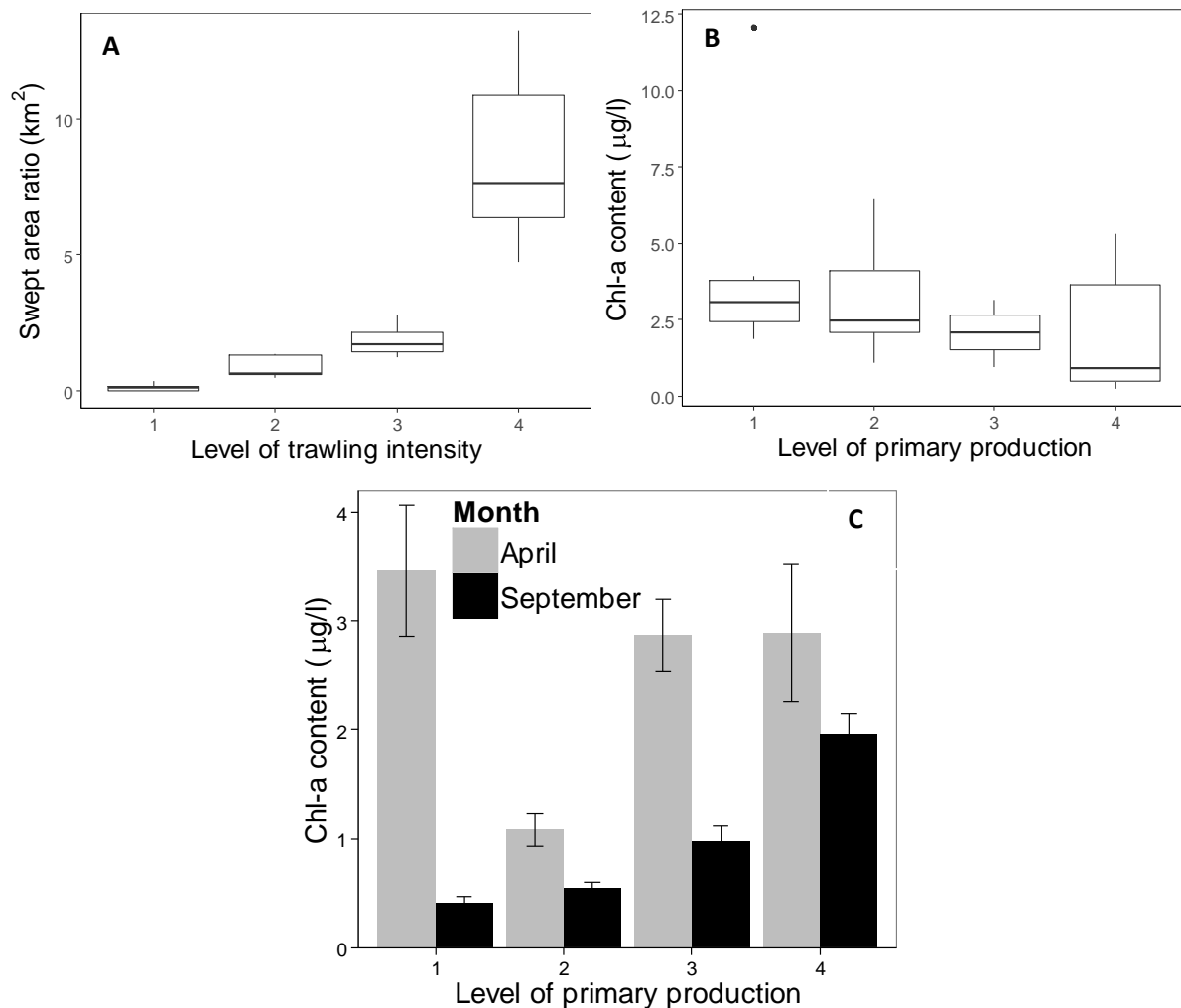
S2. The mean swept area ratio of the sampling stations plotted against their *a priori* experimental level of trawling intensity (A). The mean total Chl-a content of the sediment samples collected in April plotted against their *a priori* experimental level of primary production (B). The mean total Chl-a content of the water samples collected in September and April plotted against their *a priori* experimental level of primary production (C). Error bars represent ±1 SE.

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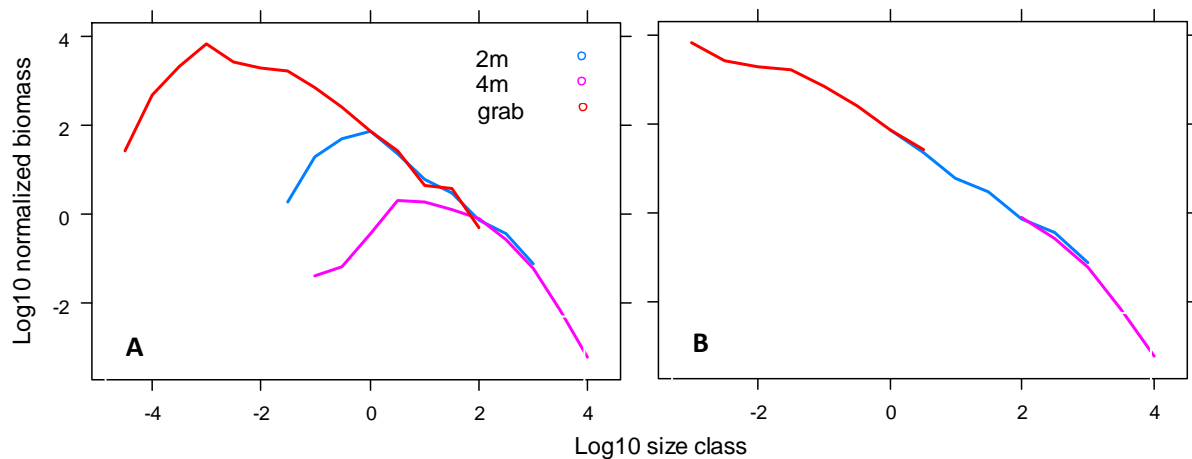
S3. The sampling gears captured organisms of markedly different size ranges (A). The amount of biomass each gear contributed was corrected to represent the same sampling area and were restricted to the size ranges that were sampled effectively. The extreme size classes inefficiently captured by each gear were then removed, resulting in a clear negative slope (B).

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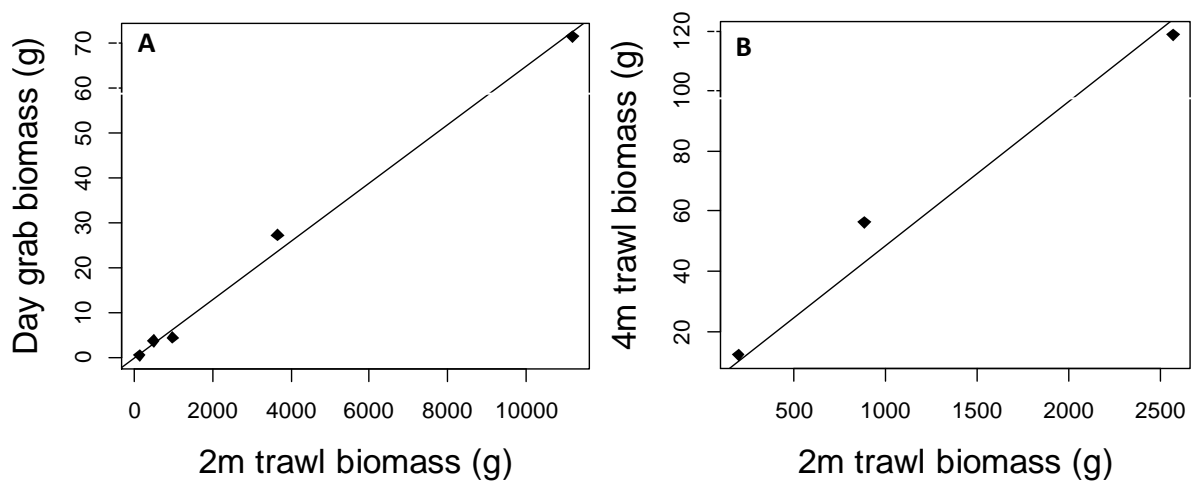
S4. Linear regressions models used to generate the catch coefficients. These were used to determine how much biomass the various gears contributed towards the final dataset. x and y axes represent normalised biomass.

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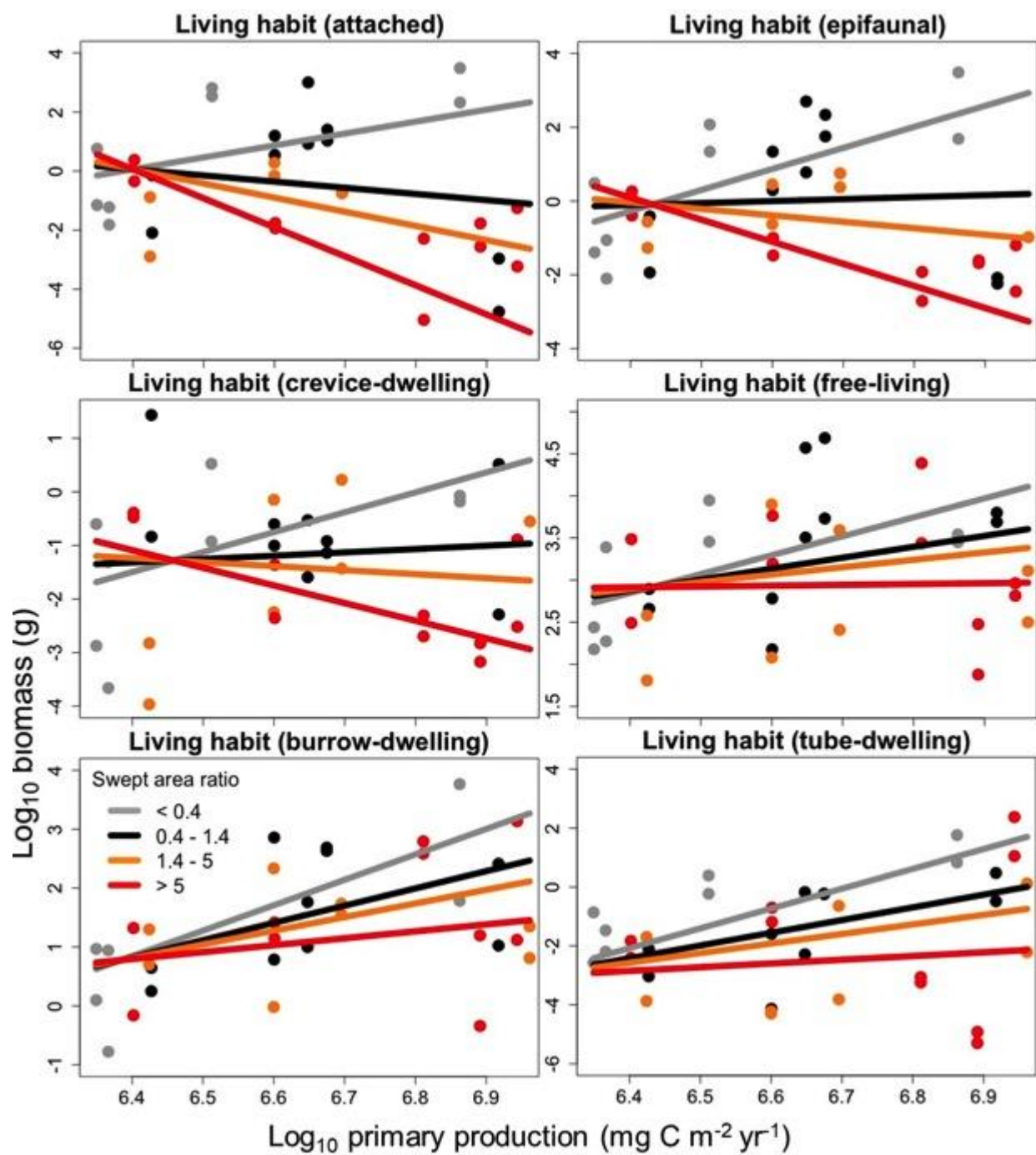
S5. Biomass of modalities within the trait "living habit", plotted against primary production and categorical levels of trawling intensity. Trend lines fitted by linear models.
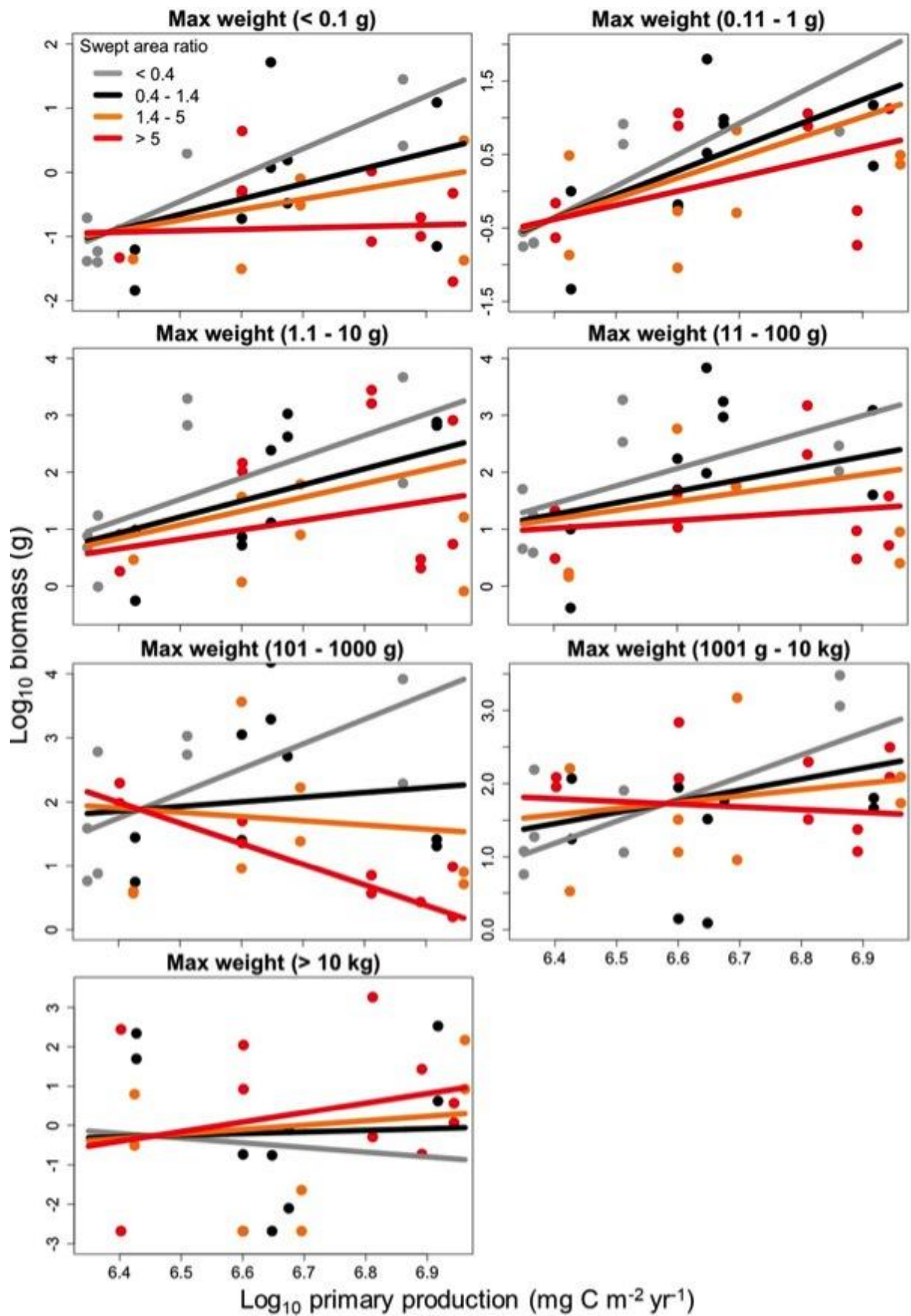
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864 **S6.** Biomass of modalities within the trait "maximum weight", plotted against primary production and
865 categorical levels of trawling intensity. Trend lines fitted by linear models.

866 **Table S1.** The latitude, longitude, mean annual primary productivity, mean annual trawling pressure,
867 depth and mean particle size of the 1 x 0.6 nautical mile stations sampled in this study.

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Station	Longitude	Latitude	Primary production (mg C m^{-2} yr^{-1})	Swept area ratio (yr^{-1})	Depth (m)
A	50.95762	-5.81468	581	0.17	86.5
B	50.96952	-5.68377	572	0.34	83.4
C	50.14108	-4.81793	672	0.01	62.0
D	50.13779	-4.89094	777	0.01	47.7
E	50.92419	-4.76168	955	0.11	41.6
F	50.94027	-5.42183	618	0.58	76.3
G	50.10285	-4.01841	735	0.47	64.0
H	50.2217	-4.19	770	0.63	41.3
I	50.3062	-3.22847	792	1.32	53.5
J	51.42451	-4.85315	1009	1.36	55.3
K	50.8516	-5.46147	616	1.22	77.0
L	50.00633	-3.9267	735	1.92	70.0
M	50.14212	-3.31622	808	1.49	62.0
N	51.49193	-4.96128	1054	2.80	51.4
O	50.69918	-5.5469	603	11.76	75.3
P	50.7029	-5.11145	613	13.23	59.4
Q	51.49384	-5.8869	735	7.10	96.0
R	51.44706	-5.10275	907	6.14	57.0
S	51.47474	-4.98225	1036	4.74	50.8
T	51.52256	-5.15893	983	8.18	43.7

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