

**The effects of trawling and primary production on size structured food webs in seabed ecosystems**

Howarth, Leigh; Somerfield, Paul J.; Blanchard, Julia; Waggitt, James; Allender, Susan; Hiddink, Jan Geert

Canadian Journal of Fisheries and Aquatic Sciences

DOI:

<https://doi.org/10.1139/cjfas-2020-0025>

Published: 01/10/2020

Peer reviewed version

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

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

Howarth, L., Somerfield, P. J., Blanchard, J., Waggitt, J., Allender, S., & Hiddink, J. G. (2020). The effects of trawling and primary production on size structured food webs in seabed ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences*, 77(10), 1659-1665. <https://doi.org/10.1139/cjfas-2020-0025>

Hawliau Cyffredinol / General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

1 The effects of trawling and primary production on size-structured food webs in
2 seabed ecosystems

3

4 Leigh M. Howarth¹, Paul J. Somerfield², Julia Blanchard³, James J. Waggitt¹, Susan Allender¹,
5 Jan G. Hiddink^{1*}

6

7 ¹ Bangor University, School of Ocean Sciences, Menai Bridge, UK, LL59 5AB

8

9 ² Plymouth Marine Laboratory, Prospect Place, Plymouth, UK, PL1 3DH

10

11 ³ Institute for Marine and Antarctic Studies and Marine Sociology, University of Tasmania,
12 Hobart, Australia, TAS 7001

13

14 * Corresponding author

15

16 **Abstract**

17 Understanding how different drivers shape relationships between abundance and body
18 mass (size-spectra) is important for understanding trophic and competitive interactions in
19 food webs, and for predicting the effects of human pressures. Here, we sample seabed
20 communities from small polychaetes (< 0.001g) to large fish (> 1kg) in the Celtic Sea to
21 examine how bottom trawling and primary production affect their size spectra, and to
22 compare these to predictions from a model that couples predator and detritivore
23 communities. Size spectra were not well approximated by linear fits because of truncation of
24 the size spectra of detritivores. Low primary production resulted in lower abundance of
25 benthic fauna. Bottom trawling reduced the abundance of predators and large detritivores,
26 but allowed small detritivores to increase in abundance. These empirical size spectra were
27 partly consistent with predictions from the size spectra model, showing that understanding
28 the structuring of benthic communities requires a consideration of both size and functional
29 group. The findings highlight the need for an ecosystem approach to understanding the
30 effects of exploitation and climate change on marine ecosystems.

31

32

33 **Key words:** Body size; bottom-up; top-down; bottom trawls; macroecology; size
34 distribution; climate change

35

36

37 Introduction

38 Marine ecosystems are subject to a range of anthropogenic pressures, many of which are
39 increasing in intensity and occurrence (Lotze et al. 2006; Poloczanska et al. 2013). Two
40 important pressures on marine ecosystems are fishing and changes in primary production
41 due to climate change and eutrophication. High levels of fishing pressure can truncate age
42 and size distributions of target and non-target species, drive shifts in maturation to earlier
43 ages and sizes, and remove large predators, which can cause communities to exhibit steeper
44 size spectrum slopes than those exposed to lower fishing intensities (e.g. Daan et al. 2005;
45 Queirós et al. 2006). Changes in primary production can result from eutrophication and
46 might result from climate change (Behrenfeld et al. 2015; Behrenfeld et al. 2006). High levels
47 of primary production can increase rates of growth and biomass accumulation, raising size
48 spectral intercepts (Jennings and Blanchard 2004; e.g. Macpherson et al. 2002). These
49 drivers rarely operate in isolation, and their interactions can generate unexpected ecological
50 responses (Crain et al. 2008). For example, a recent study found that higher levels of primary
51 production make benthic ecosystems more resilient to bottom trawling impacts (Hiddink et
52 al. 2017), and that the effects of bottom trawling on the trait composition of benthos are
53 greater in areas of high primary production (Howarth et al. 2018b). Hence, there is a need to
54 better understand how marine ecosystems react to multiple drivers (Fu et al. 2018).

55

56 The body-size distributions of aquatic communities are governed by fundamental ecological
57 principles. In aquatic ecosystems, most predators are larger than their prey because they are
58 unable to consume organisms larger than themselves (Jennings et al. 2002b; Law et al.
59 2009). This, in combination with higher population growth rates at the base of food webs
60 and inefficient energy transfer between trophic levels, is why large organisms are much
61 rarer within the aquatic environment than small ones (Sprules et al. 2016). A size spectrum
62 characterises the size distribution of all individuals in an ecosystem according to biomass
63 across size classes. When plotted as a frequency distribution of log abundance vs. log body
64 size, these 'size spectra' typically have negative slopes close to -1 which emerge from the
65 predatory, competitive and feeding interactions within ecosystems (Blanchard et al. 2009).
66 This negative slope is a macro-ecological phenomenon that exhibits remarkable regularity
67 among different types of organisms and habitats (Gómez-Canchong et al. 2013; Macpherson
68 et al. 2002). Various models describe how community size spectra arise from individual-level
69 size-based processes (Blanchard et al. 2017). The simplest of these aggregate all individuals
70 within a single size spectrum regardless of their feeding strategy. However, recent evidence

71 suggests this is too simplistic, as organisms with different trophic positions (e.g. detritivores
72 and predators) are expected to exhibit different size spectra and different responses to
73 pressures. Theory predicts that when food availability falls with body size (as in most aquatic
74 food webs where larger predators eat smaller prey), the size spectrum slope is steeper than
75 when organisms of different sizes compete for a shared unstructured resource (e.g.
76 autotrophs, herbivores and detritivores; hereafter dubbed 'detritivores') (Blanchard et al.
77 2009).

78

79 Blanchard et al. (2009) constructed a size spectrum model that described the feeding
80 interactions between predators and benthic detritivores. Their simplest models were
81 'uncoupled' and assumed that neither feeding group affected another. In contrast, 'coupled'
82 models were more complex and assumed that predators fed on a range of smaller-sized prey
83 which included detritivores, while detritivores fed on a non-size-structured food pool of
84 detritus. This model predicted that detritivores have shallower, but truncated (with a
85 steeper slope at larger body sizes), size spectral slopes compared to predators, and that
86 predator slopes steepen in response to fishing pressure. Detritivore truncation started at 1g
87 when coupled with predation and at 100g without coupling due to senescence of
88 detritivores. In contrast, fishing was predicted to release detritivores from their predators,
89 resulting in greater abundances of large detritivores and a shallowing of their size spectral
90 slopes. Even though there is clear evidence that bottom trawling affects benthic
91 invertebrates (Sciberras et al. 2018), there is debate about how important this effect is
92 relative to predation release (van Denderen et al. 2013). The Blanchard et al. (2009) model
93 assumed fishing has no direct effect on predators <10g and no direct effect on detritivores.
94 Hence, fishing could only affect detritivores through competition release. High levels of
95 primary production were predicted to provide more energy to the ecosystem, supporting
96 faster growth rates and larger body sizes in both groups, resulting in higher size spectra
97 intercepts and shallower slopes. Conversely, low levels of primary production provided less
98 energy, reducing the abundance of large body sizes and steepening slopes. To date, no
99 rigorous empirical test of these predictions has been carried out.

100

101 To improve our understanding of how multiple drivers and predator-prey interactions shape
102 size spectra and affect food web dynamics we test the prediction of the 'coupled' model in
103 Blanchard et al. (2009) with empirical observations. By sampling benthic predators and

104 detritivores in the Irish and Celtic Seas and the western English Channel across gradients of
105 bottom trawling pressure and primary production, we test the following hypotheses:

106 H1: The size spectrum slope of detritivores is shallower than that of predators, because
107 detritivores share a common unstructured food source while predators eat prey smaller
108 than themselves and food availability falls with body size because of energy loss in trophic
109 transfers. The detritivore size spectrum will be truncated at larger sizes (>1 g) because
110 detritivores experience predation pressure (Figure 1A sketches the hypothesis).

111 H2: Higher levels of primary production will provide more energy to the ecosystem,
112 supporting faster growth rates and larger body sizes in both groups, resulting in higher
113 intercepts and shallower slopes. Low levels of primary production will not provide enough
114 energy to support a full range of sizes, so size spectra in the predator communities will be
115 truncated, with relatively steep slopes (Figure 1B).

116 H3: Bottom trawling will result in steeper size spectral slopes in predators because larger
117 predators are caught and removed (e.g. Nilssen et al. 1986). This will release detritivores
118 from their predators, resulting in greater abundance of large detritivores and therefore a
119 shallowing of detritivores' size spectral slopes (Figure 1C).

120

121 **Methods**

122 Here we examine normalized size-spectra. A normalized size spectrum converts the
123 biomasses or abundances to densities by dividing them by the width of the size classes
124 (Blanchard et al. 2017). The intercept and the slope of the size spectrum characterise the
125 total abundance in the community and its rate of decrease with body size. We use the terms
126 'slope', 'intercept' and 'abundance' to describe patterns in the size spectra in this paper. The
127 'slope' is the slope of the fit through the data of a particular section of the size spectrum.
128 The 'intercept' is defined here as the point where the size spectrum starts, at \log_{10} body
129 mass = -3.

130

131 **Sampling**

132 This study analyses a dataset described by Howarth et al. (2018b) and available from
133 (Howarth et al. 2018a). In brief, trawling intensity (quantified as the swept-area-ratio, SAR
134 (yr^{-1}), from Vessel Monitoring Systems data) and primary production (PP, $\text{mg C m}^{-2} \text{ yr}^{-1}$,
135 estimated by the MODIS satellite sensor) for the United Kingdom were divided into four
136 categories (divided at equal intervals on a log scale for trawling intensities, and equal
137 intervals on a natural scale for PP, Table 1). Sampling stations were then chosen in the Irish

138 Sea, Celtic Sea and western English Channel to cover all combinations of the four levels of
139 trawling intensity and primary production on areas of seabed with similar sediments and
140 depths (sand and muddy sand with moderate shear bed stress between 40 and 100m depth,
141 <http://jncc.defra.gov.uk/ukseamap>). Twenty stations were sampled in September 2015 and
142 again in April 2016 (Figure 2). A retrospective multivariate analysis of the environmental
143 variables at the sampling stations indicated that the environmental conditions at two
144 stations were dissimilar to the others based on their sediment particle size distribution (with
145 very low and very high mean sediment particle sizes respectively). These were excluded
146 from further analyses (details in Howarth et al. 2018b). Hence, data are missing for the
147 combination of low trawling and moderately high primary production. Three different
148 sampling gears were deployed at each station to ensure a large size range of the benthic
149 community (small invertebrates to demersal fish) was captured. Day grabs primarily sampled
150 infauna and very small epifauna, 2m beam trawls primarily sampled large infauna and
151 epifaunal organisms, and 4m beam trawls primarily sampled larger epifauna and fish. All
152 organisms caught were identified to at least family level (often to species), counted, and
153 wet-weighed.

154

155 The scaled abundance and biomass were used to create \log_{10} normalised biomass size
156 spectraby aggregating individual body masses into \log_{10} bins. A normalized size spectrum
157 converts the biomasses to densities by dividing them by the width of the body mass classes
158 (Sprules et al. 2016). Abundance and biomass values for the 2m and 4m beam trawls were
159 scaled to account for differences in sampling area and efficiency compared to the Day grab
160 (for which we assumed 100% of the fauna from 0.1 m² was collected) as described in
161 Howarth et al. (2018b). The scaling was based on the assumption that \log_{10} normalised
162 biomass in the body mass categories that overlap between the sampling gears are
163 continuous. Biomasses from the 2m beam trawl were scaled so that the \log_{10} normalised
164 biomass per body mass category in the overlapping body mass categories matched the Day
165 grab \log_{10} normalised biomass per body mass category. Subsequently, biomasses from the
166 4m beam trawl were scaled so that the \log_{10} normalised biomass per body mass category in
167 the overlapping body mass categories matched the (previously scaled) 2m beam trawl \log_{10}
168 normalised biomass per body mass category. For a more detailed description of these
169 methods see the "Gear calibrations" section and Supplementary Material of Howarth et al.
170 (2018b).

171

172 Predators are defined here as animals that obtain most of their food by eating and killing
173 whole living organisms. Detritivores are defined as animals that obtain most of their food
174 from plants or detritus (dead organic material) and the group therefore includes herbivores
175 and detritivores (SM, Table S1 lists all the classification for all taxa encountered). Our
176 definition of detritivores and predators is more refined than that of Blanchard et al. (2009),
177 where all grab-collected animals were defined as detritivores and all trawl-caught animals as
178 predators.

179

180 Analysis

181 Because our hypotheses assume non-linear patterns in size spectra (e.g. truncation), linear
182 models were not considered a suitable approximation, especially because non-linearity
183 makes the range of body sizes over which the slope and intercept are fitted very important .
184 We therefore fitted a Generalized Additive Mixed Model (GAMM) using the *gamm* function
185 in the package *mgcv* in R (Wood 2015) to examine the effects of trawling, primary
186 production and feeding strategy on benthic size spectra. Sampling station was included as a
187 random effect because the measurements for the different size-classes are not independent.
188 The response variable is the \log_{10} normalised biomass per body mass category. We fitted
189 and compared GAMMs to test the different hypotheses (Table 2). Interactions were
190 specified using the *te* function in *mgcv* that produces a full tensor product smooth. To make
191 the interpretation of the results easier, H1 and H2 predictions were plotted using only low
192 fishing effort stations ($SAR < 1.4 \text{ y}^{-1}$), while H3 predictions were plotted for intermediate PP
193 stations ($550\text{-}1000 \text{ mg C m}^{-2} \text{ yr}^{-1}$).

194

195 Because the normalised biomass is \log_{10} transformed, size classes without biota resulted in
196 undefined data, which can result in an underestimation of the steepness of size spectra. To
197 avoid this, the normalised biomass for size classes without biota was replaced by a very
198 small value, calculated as 0.5 times the lowest non-zero value in that size class. A sensitivity
199 analysis showed that the results and conclusion were not affected by the replacement value
200 chosen.

201

202 Although the survey design used categorisations of bottom trawling intensity and primary
203 production levels, statistical analyses used them as continuous variables for greater power
204 and more accurate estimation of effects. For ease of plotting, however, the fitted values
205 generated by the statistical models were plotted against \log_{10} size class and plotted between

206 the categorical levels of fishing pressure and primary production (even though the model
207 fitted them as continuous variables).

208

209 Results

210 Combining samples from three different sampling gears resulted in continuous size spectra
211 with \log_{10} body mass classes spanning 6 orders of magnitude from small worms <1mg to
212 large fish >1kg. The recorded size spectra had some distinct deviations from a straight line,
213 in particular for detritivores, and would have therefore been poorly described by simply
214 estimating their intercepts and slopes from linear fits.

215

216 The AIC of the GAMM that used PP, bottom trawling intensity and feeding strategy as
217 explanatory variables was lower than that of models that omitted one or more of these
218 variables (Model 6 in Table 2, $R^2 = 0.931$, $n = 464$, Figure S2), indicating that each of these
219 variables increased the explanatory power of the model. This full model is therefore used to
220 infer and plot relationships below.

221

222 Detritivores were more abundant than predators at body masses <3g and predators were
223 more abundant than detritivores at sizes >10g (H1, Figure 3, Table 2). The detritivore size
224 spectrum slope became steeper (more negative) at \log_{10} body mass > 0 (1 g), while the slope
225 for predators was more constant, suggesting that predation depresses and truncates the
226 abundance of large detritivores. The size spectrum slope for detritivores is therefore similar
227 to that of predators at small body sizes, and steeper at large body sizes. The AIC of the
228 model including feeding strategy was much lower than a model that did not include it (Δ AIC
229 of model 6 vs. model 5 = 331.4 Table 2).

230

231 The size spectral intercepts were higher at higher PP for small detritivores, but detritivore
232 size spectra converged at large body sizes, making the size spectral slopes somewhat steeper
233 at high PP (H2, Figure 3, Table 2). For predators, the size spectra had the lowest intercept at
234 the lowest PP, but there was no clear differentiation between the other levels of PP. No
235 truncation of the predator size spectrum was evident at low PP. The AIC of the model that
236 included PP was lower than a model that did not include it (Δ AIC of model 6 vs. model 3 =
237 59.4, Table 2).

238

239 Bottom trawling effort did not affect predator slopes, but the size spectrum was lower over
240 most of the range of body sizes for predators at higher fishing effort (H3, Figure 4, Table 2).
241 Small detritivores were more abundant, while large detritivores were less abundant, at high
242 trawling effort. The AIC of the model that included trawling effort was lower than a model
243 that did not include it (Δ AIC of model 6 vs. model 4 = 49.2, Table 2).

244

245 Discussion

246 This study investigated the effects of bottom trawling and primary production on the size
247 spectra of temperate seabed communities, over six orders of magnitude of body mass. Ours
248 is one of the first studies to empirically compare size spectra between functional groups
249 (Blanchard et al. 2017; Blanchard et al. 2009; Robinson et al. 2016), and it shows that
250 distinguishing between the two feeding strategies improves our ability to understand how
251 food web dynamics translate into size spectra. Our results show that normalised benthic size
252 spectra are not well approximated by linear fits because of truncation in the size spectra of
253 detritivores.

254

255 H1, that the slopes of detritivores size spectra would be shallower than those of predators
256 because detritivores share common food sources while predation is size-structured, was not
257 supported by the results. We discuss possible reasons for this further below. The 2nd part of
258 H1, that the detritivores size spectrum is truncated at large sizes because detritivores
259 experience predation pressure, was supported. The comparison of coupled (where
260 predators eat detritivores) and uncoupled (where they do not) models in Blanchard et al.
261 (2009) showed that the body mass at which the truncation begins is driven by the existence
262 of predation on detritivores, beginning at 1g with predation in coupled models and at 100g
263 in uncoupled models due to senescence of detritivores. Our results based on empirical data
264 show that the truncation starts around 1g, indicating that top-down effects of predation on
265 detritivores strongly affect their size spectra. That predatory feeding strategies can support
266 larger body sizes than detritivory is supported by fundamental ecological theory (Elton 1927;
267 Sheldon and Kerr 1972) and empirical studies (Jennings and Mackinson 2003; Jennings and
268 Blanchard 2004; Jennings et al. 2001), both of which suggest that trophic level generally
269 increases with body size. This is because predators tend to ingest prey smaller than
270 themselves and that large organisms feeding at low trophic levels (e.g. baleen whales) are
271 rare (Blanchard et al. 2017; Cohen et al. 1993). Overall, the coupled model predictions were
272 largely consistent with our empirical data, highlighting the importance of predator-

273 detritivore coupling in food web dynamics. These results therefore show that an
274 understanding of the structuring of benthic communities requires a consideration of both
275 size and functionality.

276

277 Higher levels of primary production should equate to greater quantities of phytoplankton,
278 detritus and other organic matter sinking towards the seafloor (Blanchard et al. 2009). In
279 turn, this should result in greater abundances of detritivores and provide more prey to the
280 predator community, and may be why predator size spectra were higher in areas with higher
281 primary production. Conversely, areas with less available energy should be less able to
282 support large body sizes, making the slopes of size spectra more negative as predicted by
283 models (Blanchard et al. 2009). H2, that high levels of primary production would result in
284 higher size spectral intercepts and shallower slopes by providing more energy to the
285 ecosystem, which should support faster growth rates and larger body sizes, was only partly
286 supported. The intercepts of the size spectra were lower at lower PP for both detritivores
287 and predators, but no shallowing of the slopes was evident. In fact, the slope for detritivores
288 was steeper at high PP. The 2nd part of H2, that the predator size spectrum is truncated at
289 large sizes because at low levels of primary production there is not enough energy to
290 support a full range of sizes, was not supported by the results. These findings suggest that
291 although higher PP can support a higher standing stock of benthic invertebrates, the lack of
292 shallower size spectra slopes shows that it does not result in a faster growth of benthic
293 biota, contrary to expectations (Sprules and Munawar 1986). Our understanding of the
294 strength of competition over resources in soft-sediment benthic invertebrates is very limited
295 (Branch 1984; Wilson 1990), but these results suggest that the increase in standing stock
296 (represented by the higher intercept) has increased competition over resources among the
297 benthos, to a level where the same amount of resources are available per unit benthic
298 biomass as at lower PP.

299

300 H3 was that bottom trawling will result in steeper size spectral slopes in predators because
301 they are caught at larger sizes, and that this will release detritivores from predation resulting
302 in greater abundance of large detritivores and therefore a shallowing of their size spectral
303 slopes. Although H3 was not supported by the results, we did find a lowering of the size
304 spectra of predators at higher trawling effort, suggesting that the abundance of all predators
305 regardless of size is reduced by trawling. There was no evidence of release of predation
306 pressure on large detritivores, as these also decreased in abundance with trawling effort.

307 There was, however, an increase in the abundance of small detritivores, which can be
308 indicative of a decrease in predation or a decrease in competition with large detritivores.
309 The coupled model of Blanchard et al. (2009) predicted that fishing causes strongest declines
310 in large predators, in turn releasing detritivores from predation pressure. The model did not
311 include the direct and well-documented effect of bottom trawling on benthic invertebrates,
312 which removes around 10% of fauna in a trawl pass depending on the gear and habitat
313 (Sciberras et al. 2018), decreasing abundance of long-lived biota by 37% on a typical fishing
314 ground (Hiddink et al. 2019). An obvious reason for the lack of an increase in the abundance
315 of large detritivores is, therefore, that the direct negative effect of bottom trawling is larger
316 than the positive effect of predator release. Smaller detritivores did increase in abundance
317 in response to bottom trawling, and this can be explained by a combination of several
318 factors: a release of predation pressure due to removal of predators by trawling (van
319 Denderen et al. 2013); a release from competition with large detritivores due to removal by
320 trawling; and a higher population growth rate which results in a smaller effect of a similar
321 level of fishing mortality (Hiddink et al. 2019). An increase in abundance of small and short-
322 lived fauna in response to trawling is often assumed in modelling studies (Hiddink et al.
323 2008; van Denderen et al. 2013), but so far empirical evidence for such an increase has been
324 sparse (Hiddink et al. 2019; Jennings et al. 2002c). The conclusion that predation reduces the
325 abundance of large detritivores (H1) may seem to contradict the conclusion that removing
326 predators through trawling does not result in an increase in the abundance of large
327 detritivores (H3). This is not a contradiction though, as explained above. The direct effect of
328 bottom trawling on detritivores outweighs the indirect effect through removal of their
329 predators.

330

331 In summary, this is the first study to compare the size spectra of different functional groups
332 across interacting gradients of trawling pressure and primary production. Our results
333 highlight the importance of predator-detritivore interactions for the dynamics of benthic
334 food webs. Overall, some of our results agree with the coupled model predictions of
335 Blanchard et al. (2009), while some results do not match those predictions. Some of these
336 discrepancies seem to be because the direct effects of trawling on detritivores were not
337 included in the coupled model, and this can easily be modified. The reasons for other
338 differences between the empirical data and model predictions (the lack of slope difference
339 between detritivores and predators of small sizes, and the lack of effect of PP on slopes) are
340 less obvious and more fundamental, as they relate to how the processes of growth and

341 mortality were modelled by Blanchard et al. (2009). These discrepancies suggest that the use
342 of a shared resource by detritivores, rather than a size-structured resource by predators,
343 does not necessarily result in different size spectral slopes. Mechanisms that could explain
344 such deviations are less efficient feeding by large detritivores compared to smaller ones, or a
345 larger predator/prey body mass ratio than expected for predators (Jennings et al. 2002a).
346 Performing separate analyses for detritivores that are commonly preyed upon and for
347 detritivores that are largely inedible may also provide further insights (van Denderen et al.
348 2013). The findings highlight the interactive effects different stressors have on marine
349 ecosystems, which need to be understood if an ecosystem approach to managing the effects
350 of exploitation and climate change on marine ecosystems is to be effective.

351

352 Data accessibility

353 Data used in this paper are archived in the British Oceanographic Data Centre under
354 doi:10.5285/674d4224-7cc5-4080-e053-6c86abc0626e (Howarth et al. 2018a).

355

356 Acknowledgements

357 This work was supported by the Natural Environment Research Council and Department for
358 Environment, Food and Rural Affairs [grant number NE/L003279/1, Marine Ecosystems
359 Research Programme]. PJS acknowledges support from Natural Environment Research
360 Council through its National Capability Long-term Single Centre Science Programme, Climate
361 Linked Atlantic Sector Science, grant number NE/R015953/1. We would like to thank Ian
362 Pritchard, Wendy Robertson, Tanya Riley, Maria Giulia Moretti-Bushin, Jack Buckingham,
363 Hannah Herson, Charlotte Mathews, Claude Eric-Marquet, Craig Robertson, Marija
364 Sciberras, Kathryn Hughes, Sowmiya Shivaji, Tom Perkins, Michael Spence, James Pilkington,
365 Julia Rulent, Anna Canning, Gillian Peacock, Pascal Dubois, Anna Krystali, Nikki Lacey,
366 Federico Ghiazza, Lucy Hawkesworth, Sarah Holmes, Sarah Dashfield, Christine Pascoe
367 Natalie Welden, Marine Cendrier and Camille Govoue-Maurin for their assistance with
368 sampling and laboratory work.

369

370 References

- 371 Behrenfeld, M.J., O'Malley, R.T., Boss, E.S., Westberry, T.K., Graff, J.R., Halsey, K.H., Milligan,
372 A.J., Siegel, D.A., and Brown, M.B. 2015. Reevaluating ocean warming impacts on
373 global phytoplankton. *Nature Climate Change* **6**(3): 323-330.
- 374 Behrenfeld, M.J., O'Malley, R.T., Siegel, D.A., McClain, C.R., Sarmiento, J.L., Feldman, G.C.,
375 Milligan, A.J., Falkowski, P.G., Letelier, R.M., and Boss, E.S. 2006. Climate-driven
376 trends in contemporary ocean productivity. *Nature* **444**: 752-755.

377 Blanchard, J.L., Heneghan, R.F., Everett, J.D., Trebilco, R., and Richardson, A.J. 2017. From
378 Bacteria to Whales: Using Functional Size Spectra to Model Marine Ecosystems.
379 Trends Ecol Evol **32**(3): 174-186.

380 Blanchard, J.L., Jennings, S., Law, R., Castle, M.D., McCloghrie, P., Rochet, M.J., and Benoît, E.
381 2009. How does abundance scale with body size in coupled size-structured food
382 webs? J. Anim. Ecol. **78**(1): 270-280.

383 Branch, G.M. 1984. Competition between marine organisms: Ecological and evolutionary
384 implications. Oceanography and Marine Biology, an annual review **22**: 429-593.

385 Cohen, J.E., Pimm, S.L., Yodzis, P., and Saldaña, J. 1993. Body sizes of animal predators and
386 animal prey in food webs. J. Anim. Ecol.: 67-78.

387 Crain, C.M., Kroeker, K., and Halpern, B.S. 2008. Interactive and cumulative effects of
388 multiple human stressors in marine systems. Ecology Letters **11**: 1304–1315.

389 Daan, N., Gislason, H., G. Pope, J., and C. Rice, J. 2005. Changes in the North Sea fish
390 community: evidence of indirect effects of fishing? ICES J. Mar. Sci. **62**(2): 177-188.

391 Elton, C. 1927. Chapter VII: Time and animal communities. Animal Ecology. The Macmillan
392 Company, New York, NY: 83-100.

393 Fu, C., Travers-Trolet, M., Velez, L., Grüss, A., Bundy, A., Shannon, L.J., Fulton, E.A., Akoglu,
394 E., Houle, J.E., and Coll, M. 2018. Risky business: the combined effects of fishing and
395 changes in primary productivity on fish communities. Ecol. Model. **368**: 265-276.

396 Gómez-Canchong, P., Blanco, J.M., and Quiñones, R.A. 2013. On the use of biomass size
397 spectra linear adjustments to design ecosystem indicators. Scientia Marina **77**(2):
398 257-268.

399 Hiddink, J.G., Rijnsdorp, A.D., and Piet, G. 2008. Can bottom trawling disturbance increase
400 food production for a commercial fish species? Canadian Journal of Fisheries and
401 Aquatic Science **65**: 1393-1401.

402 Hiddink, J.G., Jennings, S., Sciberras, M., Bolam, S.G., Cambiè, G., McConnaughey, R.A.,
403 Mazor, T., Hilborn, R., Collie, J.S., Pitcher, R., Parma, A.M., Suuronen, P., Kaiser, M.J.,
404 and Rijnsdorp, A.D. 2019. Assessing bottom-trawling impacts based on the longevity
405 of benthic invertebrates. Journal of Applied Ecology **56**(5): 1075-1083.

406 Hiddink, J.G., Jennings, S., Sciberras, M., Szostek, C.L., Hughes, K.M., Ellis, N., Rijnsdorp, A.D.,
407 McConnaughey, R.A., Mazor, T., Hilborn, R., Collie, J.S., Pitcher, R., Amoroso, R.O.,
408 Parma, A.M., Suuronen, P., and Kaiser, M.J. 2017. Global analysis of depletion and
409 recovery of seabed biota following bottom trawling disturbance. Proceedings of the
410 National Academy of Sciences **114**: 8301–8306.

411 Howarth, L.M., Somerfield, P., Blanchard, J., and Hiddink, J.G. 2018a. Celtic and Irish Sea
412 benthic biomass size spectra data, September 2015 and April 2016. *Edited by U.*
413 *British Oceanographic Data Centre - Natural Environment Research Council.*

414 Howarth, L.M., Waggitt, J.J., Bolam, S.G., Eggleton, J., Somerfield, P.J., and Hiddink, J.G.
415 2018b. The effects of bottom trawling and primary production on the biological
416 traits composition of benthic assemblages. Mar. Ecol.-Prog. Ser. **602**: 31-48.

417 Jennings, S., and Mackinson, S. 2003. Abundance-body mass relationships in size-structured
418 food webs. Ecology Letters **6**(11): 971-974.

419 Jennings, S., and Blanchard, J.L. 2004. Fish abundance with no fishing: predictions based on
420 macroecological theory. J Anim Ecology **73**(4): 632-642.

421 Jennings, S., Warr, K.J., and Mackinson, S. 2002a. Use of size-based production and stable
422 isotope analyses to predict trophic transfer efficiencies and predator-prey body
423 mass ratios in food webs. Marine Ecology Progress Series **240**: 11–20.

424 Jennings, S., Pinnegar, J.K., Polunin, N.V.C., and Warr, K.J. 2001. Impacts of trawling
425 disturbance on the trophic structure of benthic invertebrate communities. Marine
426 Ecology Progress Series **213**: 127-142.

427 Jennings, S., Pinnegar, J.K., Polunin, N.V.C., and Warr, K.J. 2002b. Linking size-based and
428 trophic analyses of benthic community structure. *Marine Ecology Progress Series*
429 **226**: 77-85.

430 Jennings, S., Nicholson, M.D., Dinmore, T.A., and Lancaster, J. 2002c. The effect of chronic
431 trawling disturbance on the production of infaunal communities. *Marine Ecology*
432 *Progress Series* **243**: 251-260.

433 Law, R., Plank, M.J., James, A., and Blanchard, J.L. 2009. Size-spectra dynamics from
434 stochastic predation and growth of individuals. *Ecology* **90**(3): 802-811.

435 Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C., Kidwell, S.M.,
436 Kirby, M.X., Peterson, C.H., and Jackson, J.B. 2006. Depletion, degradation, and
437 recovery potential of estuaries and coastal seas. *Science* **312**(5781): 1806-1809.

438 Macpherson, E., Gordo, A., and Garcia-Rubies, A. 2002. Biomass size spectra in littoral
439 fishes in protected and unprotected areas in the NW Mediterranean. *Estuarine,*
440 *Coastal and Shelf Science* **55**(5): 777-788.

441 Nilssen, E.M., Larsen, R.B., and Hopkins, C.C.E. 1986. Catch and size-selection of *Pandalus*
442 *borealis* in a bottom trawl and implications for population dynamics analyses. *ICES*
443 *CM* **4**: 12.

444 Poloczanska, E.S., Brown, C.J., Sydeman, W.J., Kiessling, W., Schoeman, D.S., Moore, P.J.,
445 Brander, K., Bruno, J.F., Buckley, L.B., Burrows, M.T., Duarte, C.M., Halpern, B.S.,
446 Holding, J., Kappel, C.V., O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Schwing, F.,
447 Thompson, S.A., and Richardson, A.J. 2013. Global imprint of climate change on
448 marine life. *Nature Climate Change* **3**: 919–925.

449 Queirós, A.M., Hiddink, J.G., Hinz, H., and Kaiser, M.J. 2006. The effects of chronic bottom
450 trawling disturbance on biomass, production and size spectra of invertebrate
451 infauna communities from different habitats. *Journal of Experimental Marine*
452 *Biology and Ecology* **335**: 91-103.

453 Robinson, J.P.W., Baum, J.K., and Giacomini, H. 2016. Trophic roles determine coral reef fish
454 community size structure. *Canadian Journal of Fisheries and Aquatic Sciences* **73**(4):
455 496-505.

456 Sciberras, M., Hiddink, J.G., Jennings, S., Szostek, C.L., Hughes, K.M., Kneafsey, B., Clarke, L.J.,
457 Ellis, N., Rijnsdorp, A.D., McConnaughey, R.A., Hilborn, R., Collie, J.S., Pitcher, C.R.,
458 Amoroso, R.O., Parma, A.M., Suuronen, P., and Kaiser, M.J. 2018. Response of
459 benthic fauna to experimental bottom fishing: a global meta-analysis. *Fish and*
460 *Fisheries* **19**: 698-715.

461 Sheldon, R.W., and Kerr, S.R. 1972. The population density of monsters in Loch Ness.
462 *Limnology and Oceanography* **17**: 796-797.

463 Sprules, W.G., and Munawar, M. 1986. Plankton size spectra in relation to ecosystem
464 productivity, size, and perturbation. *Canadian Journal of Fisheries and Aquatic*
465 *Sciences* **43**(9): 1789-1794.

466 Sprules, W.G., Barth, L.E., and Giacomini, H. 2016. Surfing the biomass size spectrum: some
467 remarks on history, theory, and application. *Canadian Journal of Fisheries and*
468 *Aquatic Sciences* **73**(4): 477-495.

469 van Denderen, P.D., van Kooten, T., and Rijnsdorp, A.D. 2013. When does fishing lead to
470 more fish? Community consequences of bottom trawl fisheries in demersal food
471 webs. *Proceedings of the Royal Society B: Biological Sciences* **280**(1769): 20131883.

472 Wilson, W.H. 1990. Competition and Predation in Marine Soft-Sediment Communities. *Annu.*
473 *Rev. Ecol. Syst.* **21**: 221-241.

474 Wood, S. 2015. Package 'mgcv'. Mixed GAM Computation Vehicle with GCV/AIC/REML
475 Smoothness Estimation. Version 1.8-6.

476

477 Tables

478

479 **Table 1.** The range of values that defined the four experimental treatments of trawling
480 intensity and primary productivity sampled in this study, and that were used for plotting
481 intensity levels in Figures 2-4.

| Treatment | Trawling intensity, BT, swept area ratio (yr ⁻¹) | Primary production, PP, (mg C m ⁻² yr ⁻¹) |
|-----------------|---|---|
| 1 – Low | $\geq 0 \leq 0.4$ | $\geq 0 \leq 550$ |
| 2 - Medium low | $> 0.4 \leq 1.4$ | $> 550 \leq 775$ |
| 3 - Medium high | $> 1.4 \leq 5$ | $> 775 \leq 1000$ |
| 4 - High | $> 5 \leq 15$ | $> 1000 \leq 1500$ |

482

Table 2. GAMM outputs for statistical comparison of different models. Response variable = \log_{10} Normalized biomass. PP = primary production: $\text{mg C m}^{-2} \text{yr}^{-1}$, BT = bottom trawling: swept-area-ratio, yr^{-1} , FS = Feeding strategy: predators PD or detritivores DV. The *te* function in *mgcv* package in R produces a full tensor product smooth. Comparison of the AIC in the column 'Test of' with model 6 provides a test of the hypothesis in that column. Δ_i is differences in AIC values between each model and the most parsimonious model (model 6). w_i are Akaike weights and represent weight of evidence (out of 1.00) that each model is the best model in the set.

| | Model | AIC | Δ_i | w_i | Test of: |
|---|---|--------|------------|-------|----------|
| 1 | <code>te(log₁₀class)</code> | 1054.9 | 321.6 | 0 | |
| 2 | <code>te(log₁₀class, by = FS)</code> | 786.6 | 53.2 | 0 | |
| 3 | <code>te(log₁₀class, BT, by = FS)</code> | 766.1 | 32.8 | 0 | H2 |
| 4 | <code>te(log₁₀class, PP, by = FS)</code> | 770.6 | 37.3 | 0 | H3 |
| 5 | <code>te(log₁₀class, BT, PP)</code> | 1053.5 | 320.1 | 0 | H1 |
| 6 | <code>te(log₁₀class, BT, PP, by = FS)</code> | 733.4 | 0.0 | 1 | |

Figures

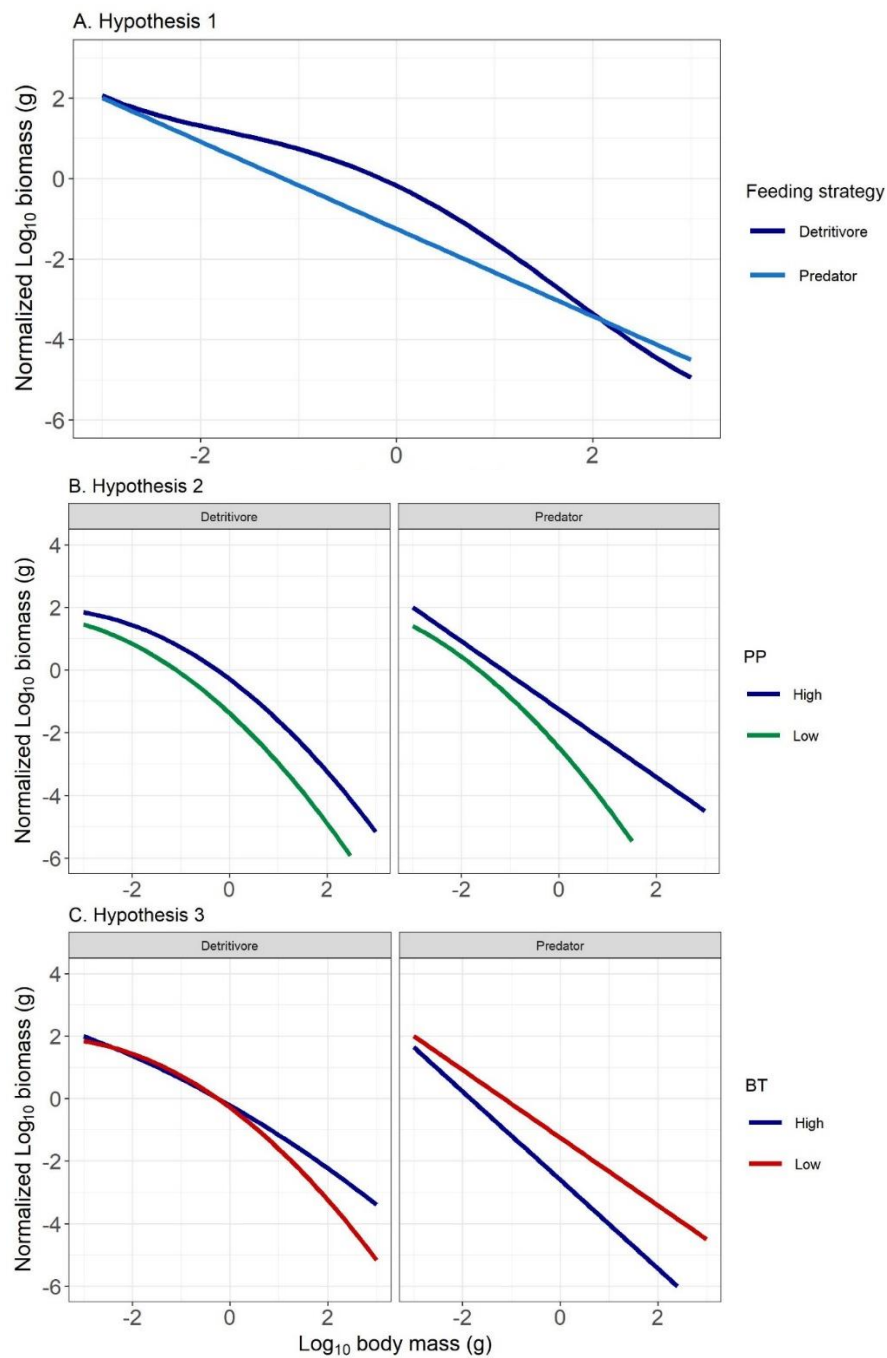


Figure 1. Hypothesized size-spectra for hypotheses 1, 2 and 3. A) Log_{10} normalised size spectra of the benthic community for the two feeding strategies. B) Log_{10} normalised size spectra of the benthic community for the two feeding strategies for different levels of primary production (PP). C) Log_{10} normalised size spectra of the benthic community for the two feeding strategies for different levels of bottom trawling effort (BT).

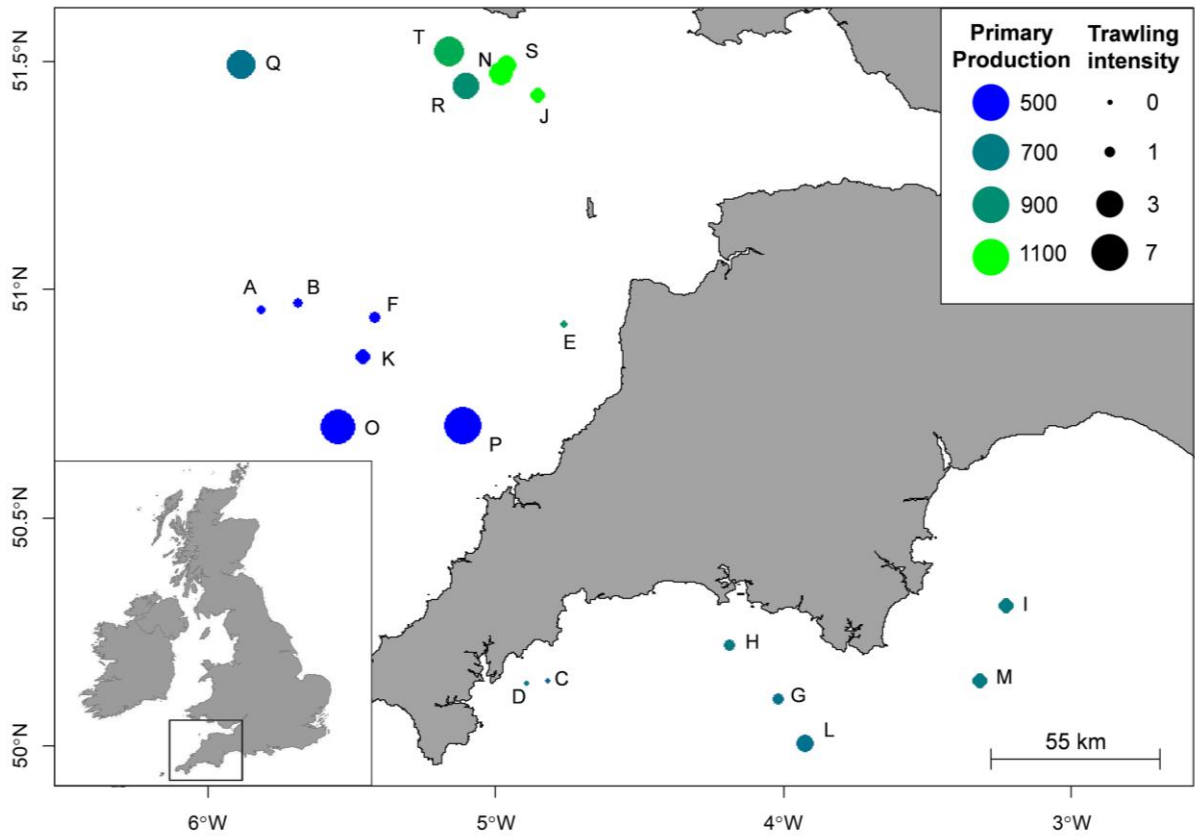


Figure 2. Sampling stations in the study area in southwest of the United Kingdom. Each point represents a 1 x 0.6 nautical mile box, the shade and size of which signifies the level of primary production ($\text{mg C m}^{-2} \text{ yr}^{-1}$) and trawling intensity (yr^{-1}).

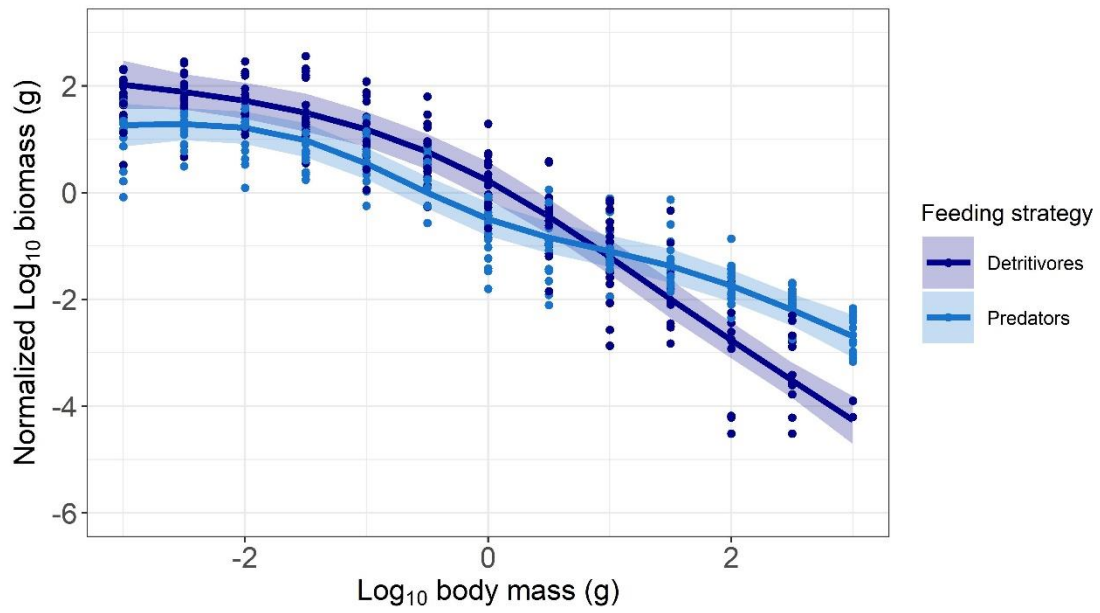


Figure 3. Log₁₀ normalised size spectra of the benthic community for the two feeding strategies, for stations with low bottom trawling effort (testing H1). Points show log₁₀ normalised biomass per 0.5 m² for each size class for each station, and lines and shaded areas represent the fitted GAMM and their 95% confidence intervals.

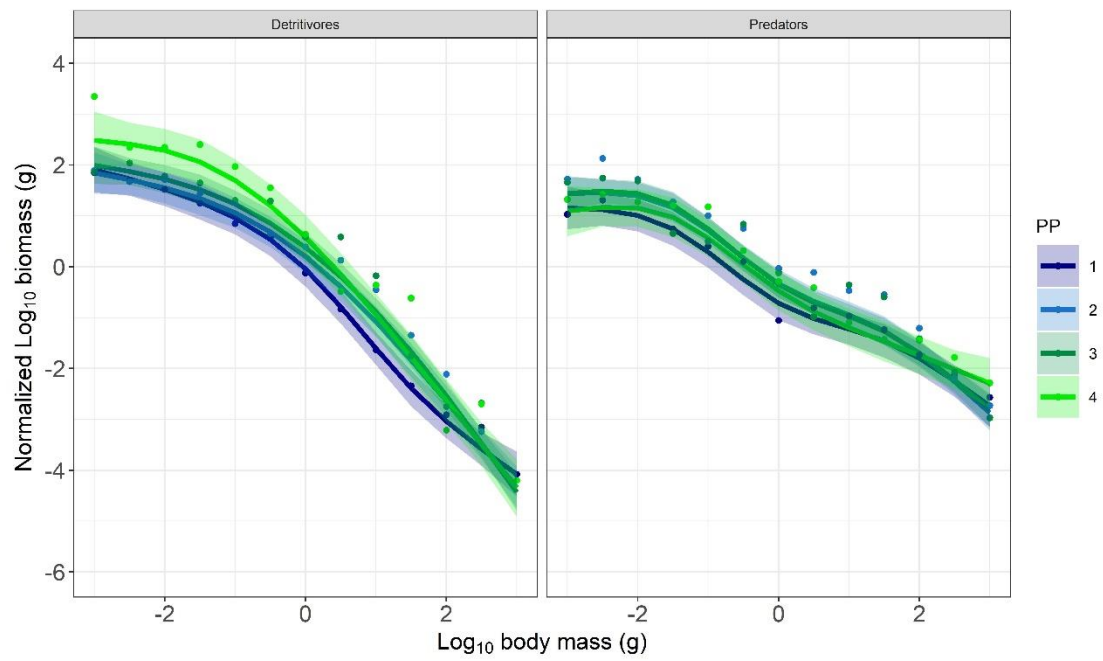


Figure 4. Log₁₀ normalised size spectra of the benthic community for the two feeding strategies for different levels of primary production (PP, see Table 1 for category levels), for areas with low bottom trawling effort (testing H2). Points show the mean log₁₀ normalised biomass per 0.5 m² for each size class over all stations, and lines and shaded areas represent the fitted GAMM and their 95% confidence intervals.

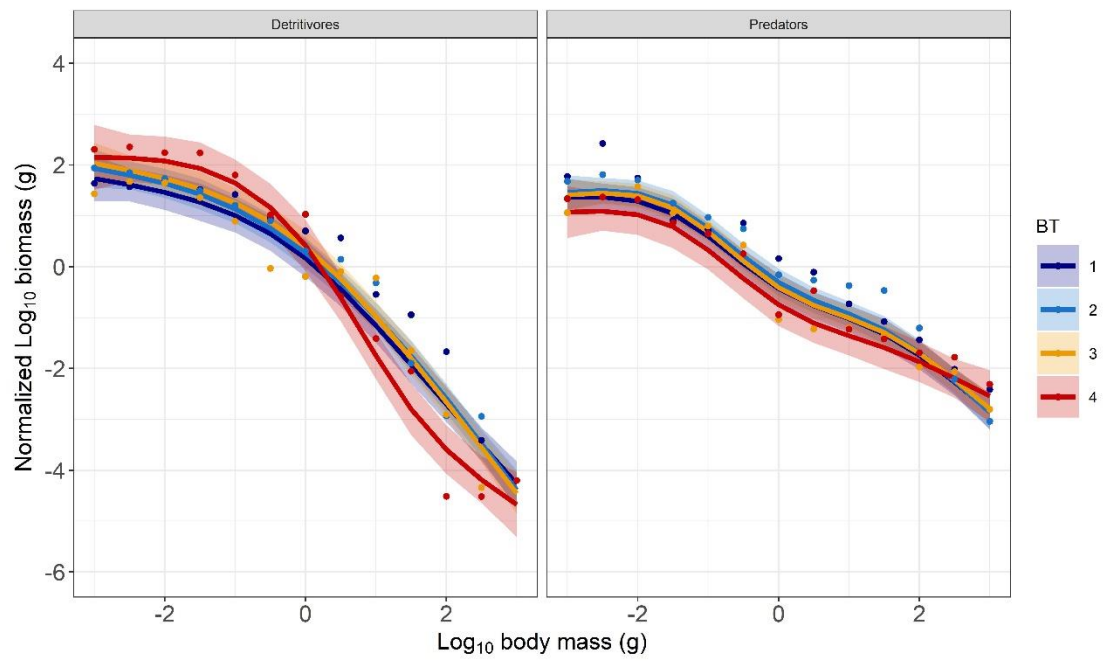


Figure 5. Log₁₀ normalised size spectra of the benthic community for the two feeding strategies for different levels of bottom trawling effort (BT, see Table 1 for category levels), for areas with intermediate primary production (testing H3). Points show the mean over all stations log₁₀ normalised biomass per 0.5 m² for each size class, and lines and shaded areas represent the fitted GAMM and their confidence intervals.