

**Bottom trawling affects fish condition through changes in the ratio of prey availability to density of competitors**

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1 **Bottom trawling affects fish condition through changes in the ratio of prey**  
2 **availability to density of competitors**

3

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26

27 **Abstract**

- 28 1. Bottom-trawl fisheries are wide-spread and cause mortality of benthic  
29 invertebrates, which in turn may lead to a decrease in the availability of prey for  
30 target fish species. Exploitation also reduces the abundance of the fish species  
31 themselves. Modelling studies have shown that bottom trawling could lead to  
32 both increases and decreases in fish production, but so far empirical evidence to  
33 test these ideas has been very limited. We hypothesize that the effect of bottom  
34 trawling on the food intake and condition of fish depends on how the ratio of  
35 prey to consumers changes with increasing fishing pressure.
- 36 2. We assessed the impact of bottom trawling on the food availability, condition  
37 and stomach contents of three flatfishes and Norway lobster in an area in the  
38 Kattegat that is characterized by a steep commercial bottom-trawling gradient  
39 due to the establishment of an area closed to all fisheries, but otherwise  
40 homogeneous environmental conditions.
- 41 3. For plaice, prey biomass initially decreased slower with trawling than the  
42 biomass of fish, and as a result the amount of food available per plaice increased  
43 before decreasing at trawling frequencies  $>5$  times  $y^{-1}$ . This pattern was  
44 mirrored in both the condition and stomach contents of plaice, and for Long-  
45 rough dab.
- 46 4. No effect of trawling on dab prey and condition was found. Conversely, the  
47 condition of the main target species Norway lobster increased as its biomass  
48 decreased with increased trawling intensities.
- 49 5. Together these results support the idea that when the abundance of the prey  
50 declines in response to exploitation, the ratio of the prey to consumer biomass  
51 will determine whether exploitation will result in an increase or a decrease of  
52 the food intake and condition of the predator.

53 *Synthesis and application.* Our study indicates that fish production may be maximized  
54 by keeping trawling intensities relatively low, although this may negatively affect the  
55 economically more important *Nephrops* fishery. The effects of bottom trawls may be  
56 mitigated by switching to gears that affect prey availability to a lesser extent, such  
57 pots/creels.

58

59 **Keywords:** Otter trawl, ecosystem effects of fishing, Kattegat, Marine protected area,  
60 density dependence

61 **Introduction**

62

63 Demersal fisheries using otter and beam trawls are widespread, and typically use heavy  
64 ground ropes and chains to drive fish and shellfish from the seabed into nets. Previous  
65 studies have found that physical disturbance by bottom trawling causes reductions in  
66 biomass, diversity and the body-size of benthic invertebrates (Hiddink *et al.* 2006;  
67 Kaiser *et al.* 2006). These effects differ according to the fishing gear used and the  
68 habitat in which it is deployed (Kaiser *et al.* 2006). The changes that arise from fishing  
69 disturbance in benthic ecosystems are conservation issues in themselves, but there is  
70 also ongoing concern that bottom fishing may impact the demersal fish species that  
71 depend on these habitats for food (e.g. cod, haddock and flatfish (Auster & Langton  
72 1999)). Consequently, trawling may cause changes in fish food intake, body condition  
73 and therefore yield in chronically trawled areas (Fogarty 2005).

74

75 Trawling may affect prey availability either negatively or positively depending on the  
76 diet of fish and the intensity of trawling. The biomass of benthic invertebrates and that  
77 of large benthic invertebrates in particular, decreases strongly with increasing trawling  
78 in most habitats (Hiddink *et al.* 2006). This decrease is therefore likely to result in a  
79 reduction in the amount of food available to many benthivorous fish species. However,  
80 modelling studies suggest that the removal of competition from large benthic fauna at  
81 low levels of bottom trawling may benefit small benthic invertebrates that are a  
82 preferred source of food source for some fish species (Hiddink, Rijnsdorp & Piet 2008;  
83 van Denderen, van Kooten & Rijnsdorp 2013). Very high intensities of trawling  
84 ultimately may also remove the smaller prey species (Hinz, Prieto & Kaiser 2009).  
85 Model outputs concluded that the effect of trawling on fish populations was dependent  
86 on the vulnerability of prey to trawling, the strength of competition among prey and  
87 non-prey organisms, and the extent to which the system was characterized by bottom-  
88 up or top-down control (van Denderen, van Kooten & Rijnsdorp 2013). Fishing resulted  
89 in higher yields and increased persistence when the preferred benthic prey species were  
90 more resistant to trawling than less preferred prey. These positive effects occurred in  
91 bottom-up controlled scenarios where fish feeding had only limited impact on benthic  
92 biomass. By contrast, fishing led to lower yields in all scenarios (top-down and bottom-  
93 up controlled systems) when high-quality prey were negatively affected by trawling.

94

95 Empirical support for such increases in food availability with trawling remains elusive.  
96 Jennings *et al.* (2002) found no change in the biomass of small infaunal polychaetes  
97 with chronic trawling. In fact, only one empirical study has recorded increases in food  
98 supply for fish: a comparison of fish diets between a high- and low-trawling area in  
99 Monterey Bay found that the abundance of an opportunistic worm species (a key prey  
100 item in the diet of some flatfish species) increased at high levels of trawling (Engel &  
101 Kvittek, 1998). Several studies show that commercial fish species such as dab *Limanda*  
102 *limanda* L. and Norway lobster *Nephrops norvegicus* L. scavenge on animals that were  
103 damaged by a trawl pass (Bergmann *et al.* 2002), but such short-term food subsidies by  
104 trawling are small relative to the long-term effects of trawling on prey availability  
105 (Kaiser & Hiddink 2007).

106

107 The indirect effects of trawling through changes in food availability occur at the same  
108 time as the direct removal of fish biomass that would occur with any fishing gear  
109 (Fogarty 2005), although the mobility of fish means that local changes in consumer  
110 abundance do not necessarily persist. Changes in prey abundance are more likely to  
111 have a negative effect on the food intake of fish if the amount of available prey per fish  
112 also declines. Figure 1 illustrates how different shapes of the relationship between prey  
113 and fish biomass and trawling frequency can cause different responses in the prey to  
114 fish biomass ratios (i.e. the amount of food available per fish). Subtle differences in the  
115 shape of the curve can result in the effect of trawling on the food/fish ratio changing  
116 from a declining relationship (e.g. Figure 1c, i and p) to an optimum curve (Figure 1a,  
117 e and f). If the fish decline more than their prey the food/fish ratio will go up with  
118 increasing levels of fishing.

119

120 Empirical studies that have examined the effect of trawling on both benthic prey and  
121 the fish simultaneously are scarce. Lloret *et al.* (2007) found that polychaete prey  
122 biomass and abundance was lowest in trawled areas and that red mullet, *Mullus*  
123 *barbatus* L., from these areas had lower lipid reserves. Similarly, the condition of the  
124 flatfish plaice *Pleuronectes platessa* L., was negatively related to trawling frequency in  
125 the Irish Sea. Plaice in this area were able to maintain their stomach fullness despite the  
126 reduction of prey biomass, and the reduced body condition was best explained by the  
127 additional energetic costs of searching at reduced prey densities (Hiddink *et al.* 2011;  
128 Johnson *et al.* 2015). Similarly Shephard, Brophy and Reid (2010) in the Celtic Sea

129 observed declines in the length-at-age of plaice with increasing trawling over gravel  
130 but not over sand.

131

132 Here we assessed the effect of bottom trawling on the food availability of fish by  
133 simultaneously measuring the abundance of prey, the food intake by fish, the resulting  
134 condition of fish and the abundance of fish in an area that had a steep gradient of  
135 commercial bottom trawling due to the presence of a permanently closed area, across  
136 an otherwise homogeneous environment in the Kattegat. This is one of the first studies  
137 that has measured all these parameters simultaneously (see Link *et al.* 2005), and is  
138 therefore able to explore how both changes in prey availability and fish abundance with  
139 trawling interact to cause changes in fish food intake and condition. Similar previous  
140 work often has not been able to detect the potential increases in prey abundance at low  
141 levels of trawling because too few areas with low trawling were available for sampling.  
142 The selected study area allowed us to overcome this limitation by sampling within and  
143 outside areas where trawling has been restricted while controlling for potential  
144 confounding variables.

145

146 The main objective of this study was to disentangle the effects of changes in prey  
147 availability that arise from trawling from the direct effects of trawling and from changes  
148 in competition over food sources that can be caused by concomitant changes in the fish  
149 population. Bottom trawling is likely to result in local and population level reductions  
150 in benthic prey availability, and population level reductions of fish. Because fish are  
151 mobile, the local removal of fish by trawling does not necessarily result in longer term  
152 reduction in abundance at a local scale because fish are mobile. We hypothesize that  
153 food intake and the resulting condition of benthivorous fish relates positively to the  
154 biomass of their prey and negatively to the biomass of competitors of benthivorous  
155 species (i.e. growth is density-dependent). As prey biomass is expected to decrease with  
156 increasing bottom trawling, but consumer biomass may show a variety of responses,  
157 the effect on the food availability per fish will depend on which the ratio of those  
158 variables. Fish condition could therefore either increase or decrease with increasing  
159 trawling intensity.

160

161 **Methods**

162 We studied three species of benthivorous flatfish (plaice *Pleuronectes platessa*, dab  
163 *Limanda limanda*, Long-rough dab *Hippoglossoides platessoides* (Fabricius, 1780))  
164 and Norway lobster *Nephrops norvegicus*. *Nephrops* was the main target species in the  
165 commercial fishery in the southern Kattegat and is fished at around MSY. Plaice are  
166 also targeted and the stock has been increasing. Dab and Long-rough dab are not  
167 commercially targeted in the area and usually discarded when caught. Plaice feed  
168 primarily on polychaetes and bivalves (Rijnsdorp & Vingerhoed 2001). Dab feeds on  
169 crustaceans, polychaetes, fish, mollusc siphons and (the arms of) brittle stars  
170 (Duineveld & Van Noort 1986). Long-rough dab feeds on shrimps, brittle stars and  
171 polychaetes (Amezcuca, Nash & Veale 2003). Norway lobster feed on a great diversity  
172 of prey, including crustaceans, molluscs, polychaetes, echinoderms and fish (Cristo &  
173 Cartes 1998).

174

#### 175 **Outline of sampling procedure**

176 The effects of chronic trawling on the weight-at-length of fish and Norway lobster  
177 (together called ‘fish’ in this paper) was investigated over a muddy fishing ground and  
178 associated closed areas in the southern Kattegat (Figure 2) in August 2013. Weight-at-  
179 length has been shown to be a proxy for fitness in plaice (Kennedy *et al.* 2008), and  
180 although such information is not available for the other species, it does not seem  
181 unreasonable to assume that such correlations also exist for these species. *Nephrops*  
182 condition is also likely to depend on their moult stage, with a newly moulted animals  
183 likely to be light (Eriksson 2006). Three different types of closed areas with different  
184 restrictions were created in the Kattegat in 2008 to protect the depleted cod stock, and  
185 these management measures resulted in a gradient in trawling effort (Vinther & Eero  
186 2013). The area was divided into a permanently closed area (No-take-zone), a  
187 seasonally selective closed area where gears that do not target cod are allowed after the  
188 first quarter, and a seasonally closed area (Figure 2). Outside these areas in the Kattegat  
189 fishing continues under regular TAC and effort management. The management regime  
190 had been in place for 5 years when we sampled the area. Infaunal benthic invertebrates  
191 were sampled using a grab while a trawl was used to sample fish and Norway lobsters.  
192 Permission to sample inside the closed areas was obtained from the Swedish Agency  
193 for Marine and Water Management.

194

#### 195 **Station selection**

196 We selected 19 sampling stations over muddy ground, between 25 and 40m depth and  
197 covering a large range of fishing pressure with stations in all different types of closed  
198 areas (No take zone: 6 stations, Seasonal selective closure: 7 stations, Seasonal closure:  
199 3 stations, Open area: 3 stations). Each station was defined as a box of 3x3 km. We  
200 reviewed station characteristics after the survey with the most up to date fishing  
201 pressure estimates and actual sediment composition information collected during the  
202 survey in order to exclude stations that were outliers in terms of sediment composition,  
203 depth and fishing pressure and thereby aimed to avoid any confounding effects due to  
204 strong deviation in these variables. To identify outliers we used Multi-Dimensional  
205 Scaling (MDS) after normalizing the different variables (see Results).

206

### 207 **Fishing pressure estimates**

208 Fishing pressure was estimated using European Community Satellite Vessel  
209 Monitoring System (VMS) data. The yearly area (km<sup>2</sup>) swept by a fishing gear was  
210 estimated for each station for a three and half year period, from January 2010 to August  
211 2013. These fishing pressures were estimated at each of the 19 stations by computing  
212 the accumulated swept areas within a year from all the bottom-contact fishing gears  
213 (otter and bottom pair trawls) by Danish and Swedish vessels larger than 15 m. We  
214 assume that the fishing effort of vessels <15m and other countries was small and has  
215 the same spatial distribution as that of vessels >15m. We used Danish and Swedish  
216 official catch and effort statistics to combine VMS data with logbook data, together  
217 with estimates regarding the dimensions of the different gears. The relationships  
218 between gear dimensions and vessel size (trawl door spread and vessel engine power)  
219 for different métiers (combinations of gear types and target species) were used to define  
220 the bottom contact to each logbook trip, and the extended logbook data were combined  
221 with interpolated vessel tracks based on VMS data (Hintzen *et al.* 2012). Vessel size  
222 information and gear specifications was collected in a pan-European industry-based  
223 questionnaire survey (Eigaard *et al.* 2015). This study enabled statistical modelling of  
224 the vessel size or vessel engine power ~ gear size relationships for different métiers to  
225 be conducted and deduce the width of the seabed swept for each of the (VMS  
226 interpolated) fishing events that occurred across the stations. Trawling intensity is  
227 expressed here as the swept area ratio ( $y^{-1}$ , the mean number of km<sup>2</sup> fished / the area of  
228 each station, 9km<sup>2</sup>).



229

### 230 **Sampling of fish and invertebrate populations**

231 Fish and invertebrates were sampled using RV Skagerrak. Two tows of 30 min were  
232 carried out at each station with an otter trawl (distance across mouth of the net 25 m,  
233 80 mm diamond mesh cod-end) at a speed of 3 knots between 07.45h and 17.00h. The  
234 total catch number and weight per species was measured. The length (to the nearest  
235 mm) and weight (to the nearest g) of the individual fish in the catch was recorded. If  
236 the catch of a species in a haul was large (>50 individuals), a subsample of  $\geq 50$  fish  
237 was measured and weighed. For *Nephrops*, the carapace length and the total weight was  
238 measured. Soft-shelled animals, males with missing limbs and all females (because of  
239 a smaller claw size) were excluded from further analysis to reduce variation in condition  
240 estimates. Benthic invertebrates were sampled by taking five 0.1 m<sup>2</sup> Smith-McIntyre  
241 grabs at haphazard locations within the station box. For each grab, a 50ml sediment  
242 sample was retained for grain size analysis and the rest of the sample was sorted over a  
243 1 mm sieve and preserved in 4% formalin for identification. All invertebrates were  
244 identified to the highest practicable taxonomic resolution (mostly genus or family) and  
245 the wet weight of each individual organism was estimated after blotting. Particle size  
246 distributions were determined using a Malvern laser diffraction particle sizer (Blott &  
247 Pye 2001).

248

### 249 **Fish condition**

250 The condition of individual fish was estimated as the weight-at-length of the fish. In  
251 the rest of this paper we will use 'condition' as a synonym of 'weight-at-length'. We  
252 used total fish weight for this condition proxy rather than eviscerated weight as higher  
253 numbers of fish could be processed that way. Using total weight implies that differences  
254 in gonad and stomach content weight between stations may have increased the variation  
255 in the condition. The 5% shortest and longest fish per species were excluded from all  
256 analyses to avoid biases that could be caused by particularly large or small fish. Only  
257 stations where more than 10 fish were caught were used for condition estimates to avoid  
258 biased condition estimates due to low numbers of fish; 2 stations were excluded for  
259 plaice.

260

### 261 **Stomach contents**

262 Plaice and dab of body length 182–299 mm and 168–274 mm, respectively, were  
263 selected for stomach-contents analysis. These size ranges minimized the likelihood of  
264 incorporating ontogenetic changes in diet. Stomachs of up to 20 individuals of each  
265 species per station were extracted and stored in 8% buffered formalin. Prey items were  
266 identified to the highest taxonomic resolution possible, counted, weighed and  
267 measured. In total, 200 plaice and 295 dab stomachs were analysed. The fraction of  
268 empty stomachs was reported separately; other analyses within this study only  
269 examined stomachs that had some contents to avoid including fish that had regurgitated  
270 their stomach contents. To investigate differences in energy content of the prey species  
271 consumed, the mean energy content per stomach was calculated using biomass  
272 conversion factors (Brey 2015). The level of stomach fullness of plaice and dab at each  
273 site was calculated as the mean stomach content weight as a percentage of body  
274 biomass. Stomach contents of Long-rough dab and Norway lobster were not examined.

275

## 276 **Analyses**

277 Because we were interested in understanding whether bottom trawling can result in  
278 decreases, increases or humped responses in prey availabilities, stomach contents and  
279 fish condition, we analysed most data using Generalized Additive Models (GAM) as  
280 these allow any shape of relationship to be fitted. To account for the non-independence  
281 of fish condition measurements within a station (because many individual fish were  
282 measured within a station), the effect of trawling or benthic production on the  
283  $\log_{10}(\text{weight})$  at  $\log_{10}(\text{length})$  of fish was estimated using GAMM from the package  
284 *mgcv* in R (Wood 2015; Zuur *et al.* 2009), using  $\log_{10}(\text{length})$  and trawling as fixed  
285 factors and using ‘Station’ as a grouping variable and a Gaussian error distribution. As  
286 the interaction between  $\log_{10}(\text{length})$  and trawling was not significant, this term was  
287 excluded from subsequent analyses. Homogeneity of residuals was established through  
288 visual examination of plotted standardized residuals versus fitted values.

289

## 290 **Results**

291

### 292 **Environmental conditions**

293

294 Particle size analysis and subsequent MDS indicated that four stations (K, O, Q and S)  
295 were less muddy than the other stations in combination with a high trawling intensity

296 (see Table S1 in Supporting Information, Figure 3). To avoid confounding of sediment  
297 composition with trawling intensity these stations were excluded from further analyses.  
298 The trawling intensity on the remaining stations ranged from 0.2 to 7.9  $y^{-1}$ . Some  
299 bottom trawling was recorded even in areas that were closed to all trawling.

300

### 301 **Infauna**

302 The community of infaunal invertebrates was dominated by brittlestars of the genus  
303 *Amphiura* (Forbes, 1843) in terms of abundance and by the ocean quahog *Arctica*  
304 *islandica* L. and heart urchins *Spatangoida* in terms of biomass. Together these three  
305 species comprised 92% of all invertebrate biomass. Mean total community biomass was  
306 not significantly related to trawling intensity (Figure 4a, Table 1a), but trawl intensity  
307 limited the total biomass that could be found at a station (90% quantile regression,  $P =$   
308 0.029). This pattern can be explained by the influence of the presence of low-density  
309 but high-biomass species such as *Arctica* and heart urchins. *Arctica* is long-lived with  
310 sporadic recruitment and particularly vulnerable to trawling activities (Witbaard &  
311 Bergman 2003). Heart urchins are a large but common species, however, their low  
312 density as adults in comparison to other macrofauna, means that that they may not be  
313 present in 5 x 0.1m<sup>2</sup> grabs even when they were present at station. As a result, both high  
314 and lower total biomasses may be encountered even in low trawling intensity stations  
315 while at high trawling stations high biomass were not found. Removing these two  
316 species considerably weakened the effect of trawling on overall benthic biomass (90%  
317 quantile regression,  $P = 0.26$ ).

318

319 The results of the stomach-contents analysis were used to identify the local prey size-  
320 spectrum and calculate from this prey availability for different predator species at  
321 different levels of trawling intensities. A comparison of the weight distribution of the  
322 infauna and the stomach contents indicated that plaice and dab preferentially selected  
323 small infauna as prey (Figure S1); 97.5% of plaice prey was <0.20g, while 97.5% of  
324 dab prey was <0.63g and these thresholds were therefore used to define the prey  
325 spectrum of these two predators (further stomach contents description are given in the  
326 'Stomach contents' section). When only the size classes that form the food for plaice  
327 and dab were considered, *Amphiura* was dominant; 76% of community biomass in the  
328 grabs <0.20 g (plaice prey) consisted of *Amphiura* and 84% of community biomass  
329 <0.63g (dab prey) consisted of *Amphiura*. Other species in the prey size classes were

330 mostly polychaetes and bivalves. The biomass of the infauna preyed upon by plaice  
331 declined slowly at low trawling frequencies, but faster at trawling frequencies above 5  
332  $y^{-1}$  (Figure 4b, Table 1a). There was no significant relationship between dab prey  
333 biomass and trawling intensity (Figure 4c, Table 1a). For Long-rough dab and  
334 *Nephrops*, prey availability could not be calculated as no stomach samples were taken  
335 for these two species.

336

### 337 **Fish and *Nephrops* biomass**

338 Most fish that were caught were c. 20 cm in length, while *Nephrops* was large and had  
339 a carapace length of c. 5 cm (Table S2). Dab and *Nephrops* biomass was about five  
340 times higher than those of plaice and Long-rough dab (Figure 5). There was a sharp  
341 decline in the biomass of dab and *Nephrops* as trawling intensity increased, but this  
342 decline levelled off at a trawling intensity of 5  $y^{-1}$  (Figure 5, Table 1b). The biomass of  
343 plaice and Long-rough dab did not change with trawling intensity (Figure 5, Table 1b).  
344 These four species comprised 89% of the catch biomass in the study area.

345

### 346 **Fish condition**

347 Weigh-at-length peaked at a trawling intensity of c. 5 times  $y^{-1}$  for both plaice and Long-  
348 rough dab (Figure 6, Table 1c). Weight-at-length for dab did not respond to trawling,  
349 while *Nephrops* weight-at-length increased with increasing fishing intensity (Figure 6,  
350 Table 1c). The difference between the highest and lowest condition recorded was  
351 approximately 4% for plaice, Long-rough dab and *Nephrops*.

352

353 Figure 6a and b also gives the ‘prey to consumer biomass ratio’ for plaice and dab for  
354 comparison with the fish condition. This ratio was calculated by fitting a GAM through  
355 the prey-biomass to fish-biomass ratios (Figure 4b and c divided by Figure 5e). We  
356 used total biomass of the three flatfish species plus *Nephrops* as the measure of the  
357 abundance of consumers because, in particular, plaice abundance was low in  
358 comparison with the abundance of competitors, and therefore the abundance of all  
359 species, including plaice, was considered a better proxy for the abundance of  
360 competitors than the abundance of plaice alone. The ‘plaice-prey to consumer-biomass  
361 ratio’ peaked at intermediate trawling intensities and showed a similar pattern to the  
362 weight-at-length for plaice. The ‘dab-prey to consumer-biomass ratio’ increased and  
363 also showed a similar pattern to (the non-significant) weight-at-length for dab. These

364 comparable patterns therefore suggest that the ratio of prey-availability to competitor-  
365 biomass affects the food intake by these fish and their resulting condition.

366

### 367 **Stomach contents**

368 Overall, dab stomachs were much fuller than plaice stomachs. The most common prey  
369 item in the stomach of both species was the brittlestar *Amphiura* spp., but the rest of the  
370 diet was comprised of mainly polychaetes and bivalves for plaice and crustaceans for  
371 dab (Figure S2). Even though *Amphiura* has a low energy density (Table S3), it still  
372 contributed most of the energy in the diet of both species at most stations. The  
373 percentage of empty stomachs did not respond to trawling in either of the two species  
374 (Figure 7a-b, Table 1d). Stomach fullness and the stomach energy content  
375 approximately doubled across the trawling gradient for plaice, but did not change with  
376 trawling for dab (Figure 7c-f, Table 1d).

377

### 378 **Discussion**

379 The results from this study support our hypothesis that food intake and the resulting  
380 condition of some benthivorous fish is affected by both competitor abundance and prey  
381 availability and relates positively to the biomass of their prey and negatively to the  
382 biomass of competitors. The effects of trawling on fish condition were modest (around  
383 a 4% increase across the trawling gradient for plaice, Long-rough dab and *Nephrops*  
384 relative to an untrawled situation). For plaice, prey biomass initially decreased more  
385 slowly than the biomass of consumers, and as a result the amount of food available per  
386 individual plaice increased initially before decreasing at higher trawling frequencies.  
387 This pattern was mirrored in both the condition and stomach contents of plaice, which  
388 both peaked at intermediate levels of trawling intensity. No significant effect of  
389 trawling on abundance of the preferred prey of dab was detected, and as fish biomass  
390 decline the prey/consumer ratio increased moderately for dab. Although not significant,  
391 again this pattern was mirrored in both the condition and stomach contents of dab,  
392 which both showed increases with increasing trawl intensity. No diet information was  
393 available for Long-rough dab, but body condition changed with trawling intensity in a  
394 similar way to plaice, which suggests that these two species may rely on a similar diet.  
395 *Nephrops* condition increased linearly with increasing trawling, suggesting that their  
396 food resources were not strongly affected by trawling, and that a release from  
397 competition was the overriding factor driving the increase in body condition for

398 *Nephrops*. In addition, scavenging on animals that were damaged by trawling  
399 (Bergmann *et al.* 2002) may provide more of a food source at higher fishing intensities.  
400 Together these results support the idea that when the abundance of both the prey and  
401 the target predator are affected by exploitation, it is important to know how the ratio of  
402 these changes as this will determine whether exploitation will result in an increase or a  
403 decrease of the food intake, condition and growth rates of the target species. Our results  
404 show that the assumption of Van Denderen *et al.* (2013) that prey abundance will  
405 increase with trawling was not supported, but our results do confirm that it is important  
406 to take into account the top-down effects of fish predation on benthic prey when trying  
407 to assess the effect of bottom trawling on fish productivity.

408

409 Foraging in areas where prey abundance is low is more energetically costly than  
410 foraging in areas where prey is more abundant due to the increased search time (Croy  
411 & Hughes 1991). If this increase in energy expenditure at low prey abundance is  
412 substantial, it could be expected that the effect of trawling on fish condition is stronger  
413 than the effect on stomach contents; fish may still fill their stomach at low prey  
414 abundance but need to expend more energy to do so. However, such a stronger effect  
415 of trawling on condition than on stomach contents was not evident from our results.

416

417 The results for plaice are different from the outcomes of a similar study in the Irish Sea,  
418 which found that trawling had a monotone negative effect on the condition of plaice  
419 (Hiddink *et al.* 2011), explained by dietary shifts in plaice towards energy-poor prey  
420 together with a potential decrease in foraging efficiency due to low prey densities  
421 (Johnson *et al.* 2015). However, the pattern in the condition of plaice seen in the Irish  
422 Sea (Hiddink *et al.* 2011) does follow the prey/predator ratio; both prey and fish  
423 abundance show a logarithmic decline with trawling but fish abundance declined more  
424 slowly and therefore the prey/predator ratio declined. Therefore, although a different  
425 response of plaice condition to trawling was recorded in this previous study, the  
426 mechanisms explaining the response are the same. This indicates that the response of  
427 fish food intake to bottom trawling may vary from one location to another according  
428 the conditions, and abundance of competitors.

429

430 An important assumption was that consumers compete for food and that growth was  
431 density-dependent. In a laboratory study the weight of a standard-length plaice of

432 247mm (Figure 6a) decreased from 157g after unlimited feeding to 143g after a month  
433 of starvation (Fonds *et al.* 1992). The best-condition plaice in our study had a similar  
434 weight to the well-fed laboratory fish, while the worst condition plaice in the Kattegat  
435 had a condition similar to starved fish (Figure 6). This suggests that the variation in  
436 plaice condition in the Kattegat indeed represents substantial differences in food  
437 availability. Another important assumption was that the different consumers at least  
438 partly share the same prey. Given the dominance of *Amphiura* in the environment, and  
439 in the stomachs of plaice and dab, this does not seem an unreasonable assumption.  
440 *Nephrops* was the most abundant species in the catch, and is likely to be undersampled  
441 because we fished during daylight hours when these animals tend to hide in their  
442 burrows. Because of the 80 mm mesh of the trawl, only 5% of *Nephrops* numbers were  
443 below the minimum landing size of 40 mm carapace length (Table S2), while it can be  
444 expected a large fraction of the population is too small to be retained in the net. It is  
445 therefore likely that *Nephrops* were considerably more abundant than all the flatfish  
446 species together. This means that even a limited prey overlap with flatfish may have  
447 made *Nephrops* an important competitor for the flatfish.

448

449 Any study using an observational approach has to consider the potential for  
450 confounding factors affecting conclusions. This study assumed that the condition of  
451 fish represented the local prey availability. Previous work suggests that flatfish forage  
452 within quite limited areas (de Castro *et al.* 2015). Contrary to the sessile *Nephrops*, the  
453 mobility of the fish in the study area is poorly known, and therefore, we cannot be sure  
454 that individuals captured at different stations had been feeding at that station in the time  
455 that they built up their condition (weeks) before sampling. This, however, does not  
456 affect the conclusions that trawling had an effect on the condition of three of the species,  
457 as mobility would break up any spatial pattern in condition; therefore, these analyses  
458 are likely to underestimate any effect of trawling on condition. This is confirmed by  
459 comparing the magnitude of the effect of trawling on condition with the effect on  
460 stomachs contents; the effect on condition was much smaller than the effect on the  
461 stomachs. As the stomach contents reflect the food intake in the previous 24h and the  
462 condition the previous weeks, this confirms that fish mobility weakens the observed  
463 effects.

464

465 A problem of using weight-at-length as an indicator of food intake is that as food intake  
466 increases, both length and weight may increase which means that a higher food intake  
467 will not be reflected in a straightforward increase in length-at-weight (Lloret, Shulman  
468 & Love 2014). The length ranges of fish in our samples included both juveniles and  
469 adults, and juvenile fish are likely to invest more energy into length growth than adults.  
470 This effect will therefore have decreased our ability to detect differences in food intake  
471 between stations.

472

### 473 **Implications**

474 A general assumption in fisheries management is that fish productivity increases with  
475 exploitation because of a reduction in competition over food and other resources. Here  
476 we show that fish productivity may decline with exploitation because of a decline in  
477 prey abundance. Our results show that the assumption of increasing fish productivity  
478 with exploitation is reasonable in the Kattegat fishery for *Nephrops* and dab, but not for  
479 plaice and Long-rough dab. Although body condition and food intake for these two  
480 species increased with trawling intensity up to a frequency of 3 to 5  $y^{-1}$ , there was no  
481 indication that bottom trawling had a positive effect on the prey availability for these  
482 species (which contradicts some scenarios in van Denderen, van Kooten & Rijnsdorp  
483 2013). Instead, in comparison to fishing gears that have no effects on prey abundance,  
484 intense bottom trawling appears to reduce the capacity of the Kattegat ecosystem to  
485 underpin the production of plaice and long-rough dab. In the Kattegat, no specific  
486 management for plaice and long-rough dab may be needed as both species are relatively  
487 low in abundance and long-rough dab is often discarded, especially as reducing trawling  
488 intensity may come at the expense of reducing production of the economically more  
489 important *Nephrops*. In areas where plaice is an important commercial species, the  
490 production of plaice may be maximized by avoiding trawling at high intensities, and  
491 keeping effort below the level at which plaice condition is starting to decline. This  
492 threshold was around 3-5 trawl passes  $y^{-1}$  in the Kattegat, but is fishing gear and system  
493 specific and is likely to change according to local factors such as substratum type and  
494 primary production. The effects of bottom trawls may be mitigated by switching to  
495 gears that affect prey availability to a lesser extent, such as gill nets, long-lines or pots  
496 and creels targeting *Nephrops* (Ziegler & Valentinsson 2008), but it seems unlikely that  
497 such gears can sustain the demersal fish market alone.

498



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503 942).

504

505 **Additional supporting information is found in the online version of this article.**

506 Table S1. Site characteristics.

507 Table S2. Size of the fish.

508 Table S3. Energy density of prey.

509 Table S3. Number of stomachs analysed.

510 Figure S1. Prey weight distribution.

511 Figure S2. Stomach energy content.

512

513 **Data Accessibility**

514 Infaunal biomass, fish abundance, lengths and weights are available on datadryad.org.

515 Stomach contents are available from DAPSTOM [https://www.cefas.co.uk/cefas-data-](https://www.cefas.co.uk/cefas-data-hub/fish-stomach-records/)  
516 [hub/fish-stomach-records/](https://www.cefas.co.uk/cefas-data-hub/fish-stomach-records/)

517

518 **References**

519

520 Amezcua, F., Nash, R.D.M. & Veale, L. (2003) Feeding habits of the order  
521 Pleuronectiformes and its relation to the sediment type in the North Irish Sea.  
522 *J Mar Biol Assoc UK*, **83**, 593–601.

523 Auster, P.J. & Langton, R.W. (1999). The effects of fishing on fish habitat. In *Fish*  
524 *habitat: essential fish habitat and rehabilitation* (ed L.R. Benaka), pp. 150-  
525 187. American Fisheries Society, Hartford, Connecticut.

526 Bergmann, M., Wiczorek, S., Atkinson, R. & Moore, P. (2002) Utilization of  
527 invertebrates discarded from the *Nephrops* fishery by variously selective  
528 benthic scavengers in the west of Scotland. *Marine Ecology-Progress Series*,  
529 **233**, 185-198.

530 Blott, S.J. & Pye, K. (2001) GRADISTAT: a grain size distribution and statistics  
531 package for the analysis of unconsolidated sediments. *Earth surface processes*  
532 *and Landforms*, **26**, 1237-1248.

533 Brey, T. (2015) *Population dynamics in benthic invertebrates. A virtual handbook.*  
534 *Version 01.2.* [http://www.thomas-](http://www.thomas-brey.de/science/virtualhandbook/navlog/index.html)  
535 [brey.de/science/virtualhandbook/navlog/index.html](http://www.thomas-brey.de/science/virtualhandbook/navlog/index.html) Alfred Wegener Institute  
536 for Polar and Marine Research, Germany.

537 Cristo, M. & Cartes, J.E. (1998) A comparative study of the feeding ecology of  
538 *Nephrops norvegicus* L.(Decapoda: Nephropidae) in the bathyal  
539 Mediterranean and the adjacent Atlantic. *Scientia Marina*, **62**, 81-90.

- 540 Croy, M.I. & Hughes, R.N. (1991) The role of learning and memory in the feeding  
541 behaviour of the fifteen-spined stickleback, *Spinachia spinachia* L. *Animal*  
542 *Behaviour*, **41**, 149-159.
- 543 de Castro, F., Shephard, S., Kraak, S.B., Reid, D.G. & Farnsworth, K.D. (2015)  
544 Footprints in the sand: a persistent spatial impression of fishing in a mobile  
545 groundfish assemblage. *Marine Biology*, **162**, 1239-1249.
- 546 Duineveld, G. & Van Noort, G. (1986) Observations on the population dynamics of  
547 *Amphiura filiformis* (Ophiuroidea: Echinodermata) in the southern North Sea  
548 and its exploitation by the dab, *Limanda limanda*. *Netherlands Journal of Sea*  
549 *Research*, **20**, 85-94.
- 550 Eigaard, O.R., Bastardie, F., Breen, M., Dinesen, G.E., Hintzen, N.T., Laffargue, P.,  
551 Mortensen, L.O., Nielsen, J.R., Nilsson, H.C., O'Neill, F.G., Polet, H., Reid,  
552 D.G., Sala, A., Sköld, M., Smith, C., Sørensen, T.K., Tully, O., Zengin, M. &  
553 Rijnsdorp, A.D. (2015) Estimating seabed pressure from demersal trawls,  
554 seines, and dredges based on gear design and dimensions. *ICES Journal of*  
555 *Marine Science*, **73 S1**, i27-i43.
- 556 Eriksson, S.P. (2006) Differences in the condition of Norway lobsters (*Nephrops*  
557 *norvegicus* (L.)) from trawled and creel-fishing areas. *Marine Biology*  
558 *Research*, **2**, 52-58.
- 559 Fogarty, M.J. (2005) Impacts of fishing activities on benthic habitat and carrying  
560 capacity: Approaches to assessing and managing risk. *Benthic Habitats and*  
561 *the Effects of Fishing*, **41**, 769-784.
- 562 Fonds, M., Cronie, R., Vethaak, A. & Van der Puyl, P. (1992) Metabolism, food  
563 consumption and growth of plaice (*Pleuronectes platessa*) and flounder  
564 (*Platichthys flesus*) in relation to fish size and temperature. *Netherlands*  
565 *Journal of Sea Research*, **29**, 127-143.
- 566 Hiddink, J.G., Jennings, S., Kaiser, M.J., Queirós, A.M., Duplisea, D.E. & Piet, G.J.  
567 (2006) Cumulative impacts of seabed trawl disturbance on benthic biomass,  
568 production and species richness in different habitats. *Canadian Journal of*  
569 *Fisheries and Aquatic Sciences*, **63**, 721-736.
- 570 Hiddink, J.G., Johnson, A.F., Kingham, R. & Hinz, H. (2011) Could our fisheries be  
571 more productive? Indirect negative effects of bottom trawl fisheries on fish  
572 condition. *Journal of Applied Ecology*.
- 573 Hiddink, J.G., Rijnsdorp, A.D. & Piet, G. (2008) Can bottom trawling disturbance  
574 increase food production for a commercial fish species? *Canadian Journal of*  
575 *Fisheries and Aquatic Science*, **65**, 1393-1401.
- 576 Hintzen, N.T., Bastardie, F., Beare, D., Piet, G.J., Ulrich, C., Deporte, N., Egekvist, J.  
577 & Degel, H. (2012) VMStools: open-source software for the processing,  
578 analysis and visualisation of fisheries logbook and VMS data. *Fisheries*  
579 *Research*, **115**, 31-43.
- 580 Hinz, H., Prieto, V. & Kaiser, M.J. (2009) Trawl disturbance on benthic communities:  
581 chronic effects and experimental predictions. *Ecological Applications*, **19**,  
582 761-773.
- 583 Jennings, S., Nicholson, M.D., Dinmore, T.A. & Lancaster, J. (2002) The effect of  
584 chronic trawling disturbance on the production of infaunal communities.  
585 *Marine Ecology Progress Series*, **243**, 251-260.
- 586 Johnson, A.F., Gorelli, G., Jenkins, S.R., Hiddink, J.G. & Hinz, H. (2015) Effects of  
587 bottom trawling on fish foraging and feeding. *Proceedings of the Royal*  
588 *Society B: Biological Sciences*, **282**, 20142336.

589 Kaiser, M.J., Clarke, K.R., Hinz, H., Austen, M.C.V., Somerfield, P.J. & Karakassis,  
590 I. (2006) Global analysis and prediction of the response of benthic biota to  
591 fishing. *Marine Ecology Progress Series*, **311**, 1-14.

592 Kaiser, M.J. & Hiddink, J.G. (2007) Food subsidies from fisheries to continental shelf  
593 benthic scavengers: are they important? *Marine Ecology Progress Series*, **318**,  
594 267-276.

595 Kennedy, J., Witthames, P.R., Nash, R.D.M. & Fox, C.J. (2008) Is fecundity in plaice  
596 (*Pleuronectes platessa* L.) down-regulated in response to reduced food intake  
597 during autumn? *Journal of Fish Biology*, **72**, 78-92.

598 Link, J., Almeida, F., Valentine, P., Auster, P., Reid & Vitaliano, J. (2005). The  
599 effects of area closures on Georges Bank. In *Fish Habitat: Essential Fish  
600 Habitat and Rehabilitation. American Fisheries Society Symposium 41* (ed  
601 L.R. Benaka), Vol. 41, pp. 345-369.

602 Lloret, J., Demestre, M. & Sánchez-Pardo, J. (2007) Lipid reserves of red mullet  
603 (*Mullus barbatus*) during pre-spawning in the northwestern Mediterranean.  
604 *Scientia Marina*, **71**, 269-277.

605 Lloret, J., Shulman, G. & Love, R.M. (2014) *Condition and Health Indicators of  
606 exploited marine fishes* Wiley Blackwell.

607 Rijnsdorp, A.D. & Vingerhoed, B. (2001) Feeding of plaice *Pleuronectes platessa* L.  
608 and sole *Solea solea* (L.) in relation to the effects of bottom trawling. *Journal  
609 of Sea Research*, **45**, 219-229.

610 Shephard, S., Brophy, D. & Reid, D. (2010) Can bottom trawling indirectly diminish  
611 carrying capacity in a marine ecosystem? *Marine Biology*, **157**, 2375-2381.

612 van Denderen, P.D., van Kooten, T. & Rijnsdorp, A.D. (2013) When does fishing lead  
613 to more fish? Community consequences of bottom trawl fisheries in demersal  
614 food webs. *Proceedings of the Royal Society B: Biological Sciences*, **280**,  
615 20131883.

616 Vinther, M. & Eero, M. (2013) Quantifying relative fishing impact on fish  
617 populations based on spatio-temporal overlap of fishing effort and stock  
618 density. *ICES Journal of Marine Science: Journal du Conseil*, **70**, 618-627.

619 Witbaard, R. & Bergman, M.J.N. (2003) The distribution and population structure of  
620 the bivalve *Arctica islandica* L. in the North Sea: what possible factors are  
621 involved? *Journal of Sea Research*, **50**, 11-25.

622 Wood, S. (2015). Package ‘mgcv’. Mixed GAM Computation Vehicle with  
623 GCV/AIC/REML Smoothness Estimation. Version 1.8-6. In.

624 Ziegler, F. & Valentinsson, D. (2008) Environmental life cycle assessment of Norway  
625 lobster (*Nephrops norvegicus*) caught along the Swedish west coast by creels  
626 and conventional trawls—LCA methodology with case study. *The  
627 International Journal of Life Cycle Assessment*, **13**, 487-497.

628 Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) *Mixed  
629 effects models and extensions in ecology with R* Springer Verlag.

630

631

632 **Tables**

633

634 Table 1. Statistical outputs of GAM and GAMM models. Relationship of response  
 635 variable to trawling frequency ( $y^{-1}$ ). Res.df are the residuals degrees of freedom. WW  
 636 = wet weight. A \* indicates that the fit of the GAM(M) curve is significantly better than  
 637 a straight line according to a Wald chi-square test.

a. Biomass of infauna, g WW per 0.1 m<sup>2</sup>. GAM

Parameter	n	res.df	F	P
Total infauna WW	15	13	1.176	0.298
Plaice infauna prey <0.20g WW	15	12.4	4.175	0.041*
Dab infauna prey <0.63 g WW	15	13	0.244	0.630

## b. Fish biomass per trawl. GAM

Species	n	res.df	F	P
<i>Pleuronectes platessa</i>	15	12.5	0.717	0.494
<i>Limanda limanda</i>	15	12.0	7.049	0.007*
<i>Hippoglossoides platessoides</i>	15	11.9	2.202	0.144
<i>Nephrops norvegicus</i>	15	12.3	7.301	0.007
Total	15	12.2	6.043	0.013

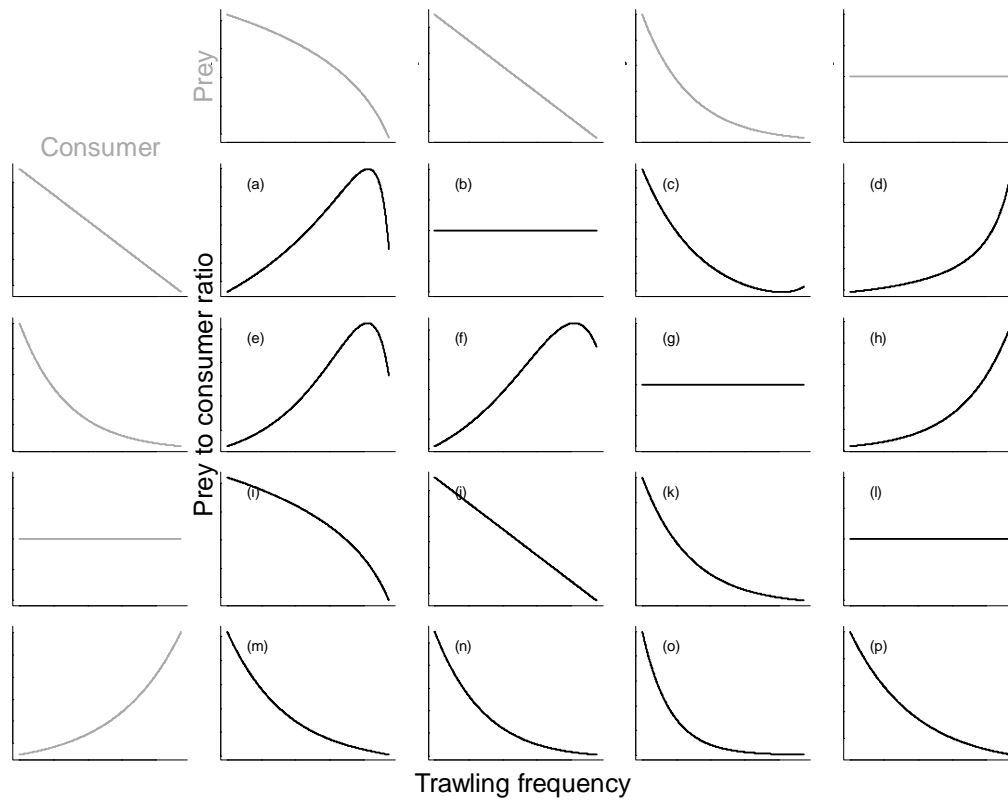
## c. Fish condition. GAMM

Species	n	res.df	F	P
<i>Pleuronectes platessa</i>	372	367.9	6.399	0.002*
<i>Limanda limanda</i>	915	912.0	1.201	0.273
<i>Hippoglossoides platessoides</i>	883	878.9	7.143	0.001*
<i>Nephrops norvegicus</i>	471	467.9	5.853	0.014

## d. Fish stomach contents. GAM

Species	n	res.df	F	P
<i>Pleuronectes platessa</i> % empty	13	11.0	0.803	0.389
<i>Limanda limanda</i> % empty	15	12.2	1.555	0.247
<i>Pleuronectes platessa</i> fullness	13	8.9	4.849	0.024
<i>Limanda limanda</i> fullness	15	13.0	2.750	0.121
<i>Pleuronectes platessa</i> energy	13	9.3	4.340	0.034
<i>Limanda limanda</i> energy	15	13.0	2.550	0.134

638

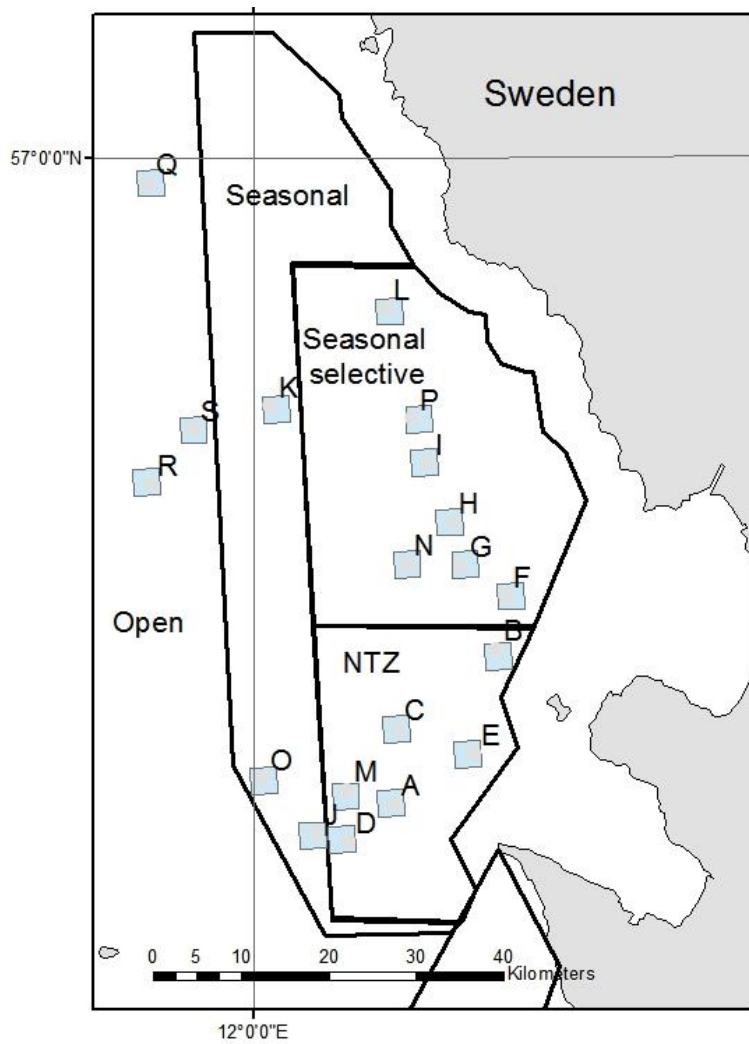


640

641 Figure 1. Hypothetical prey to consumer biomass ratios for different shaped  
 642 relationships between prey (top row) and consumer biomass (left column) and  
 643 trawling frequency. These relationships reflect the local, rather the population level,  
 644 effects. Because the prey is not mobile, their local response to trawling is assumed to  
 645 be neutral or negative. Consumers are mobile and therefore a wide variety of  
 646 responses is explored, even though the population level response to fishing will be  
 647 negative.

648

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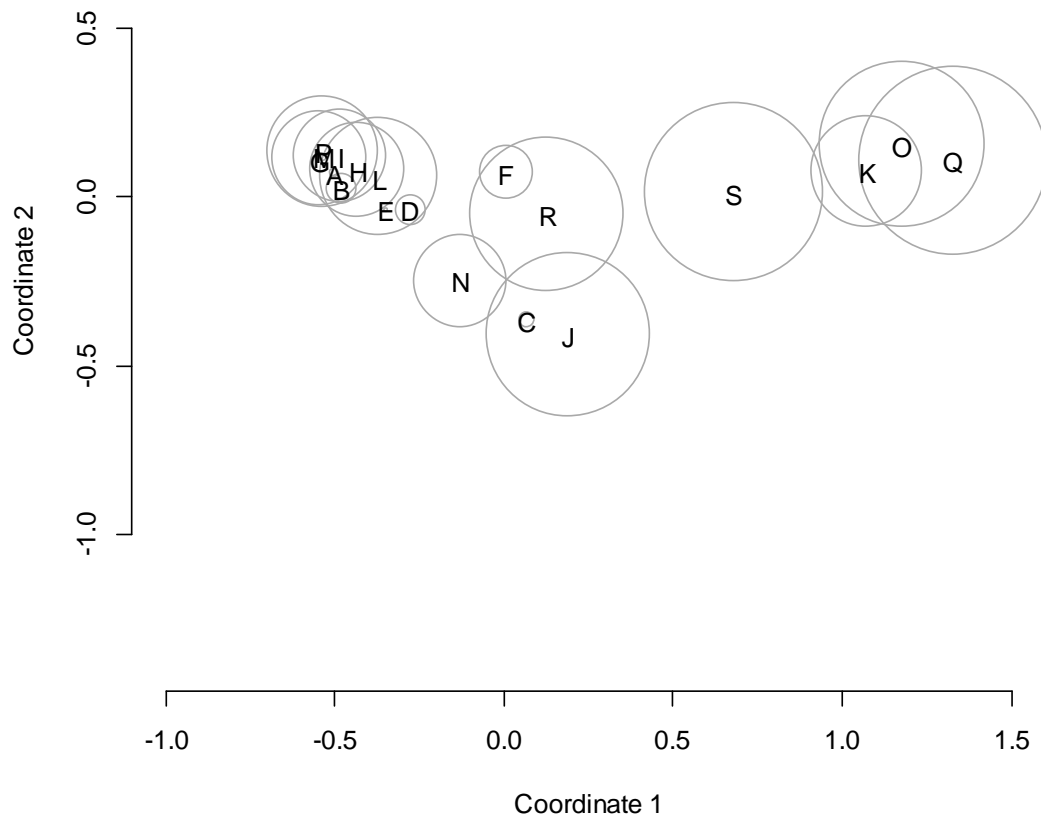


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652 Figure 2. The study area with the sampling stations and management area boundaries.

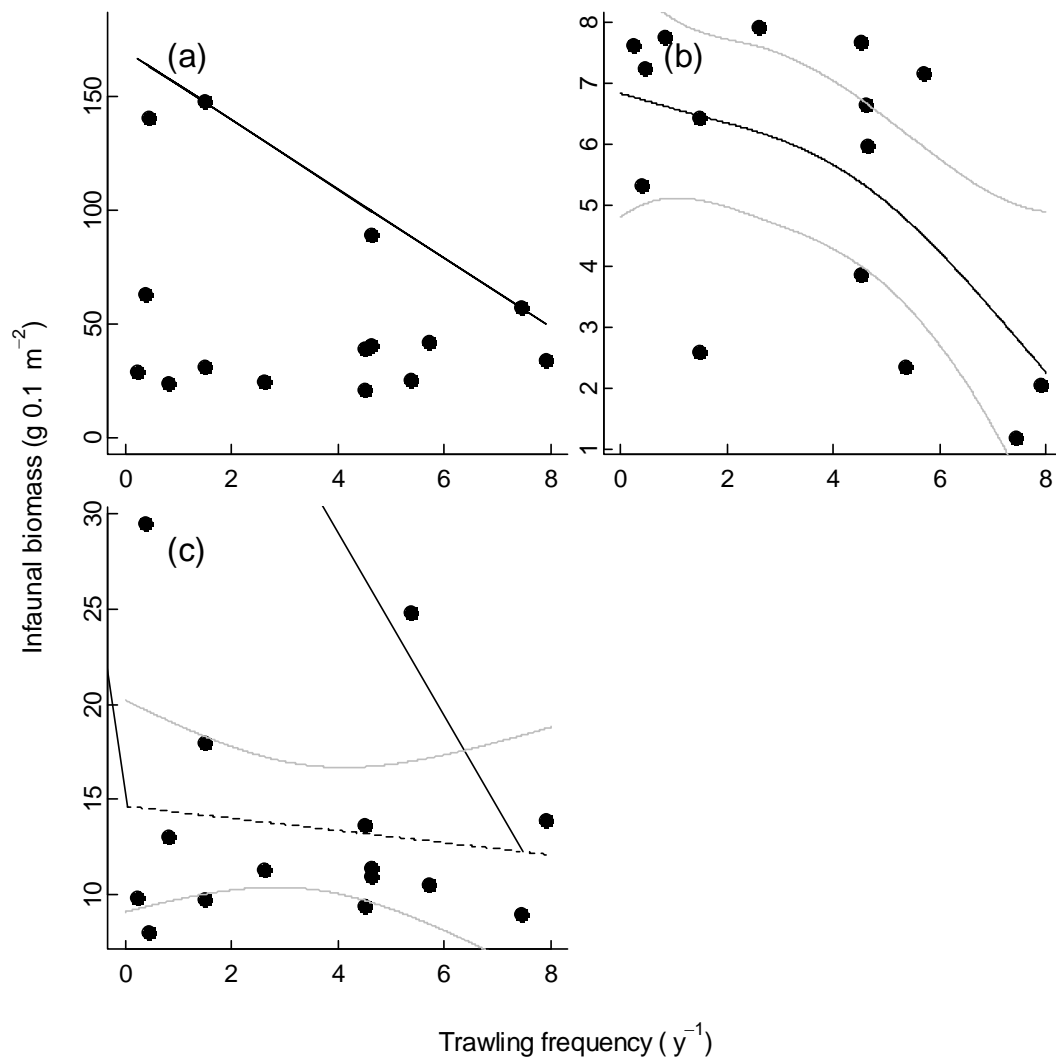
653 NTZ = No-take zone.



654

655 Figure 3. MDS plot of the site characteristics of the sampling stations. Bubble size is  
 656 proportional to the trawling intensity.

657



658

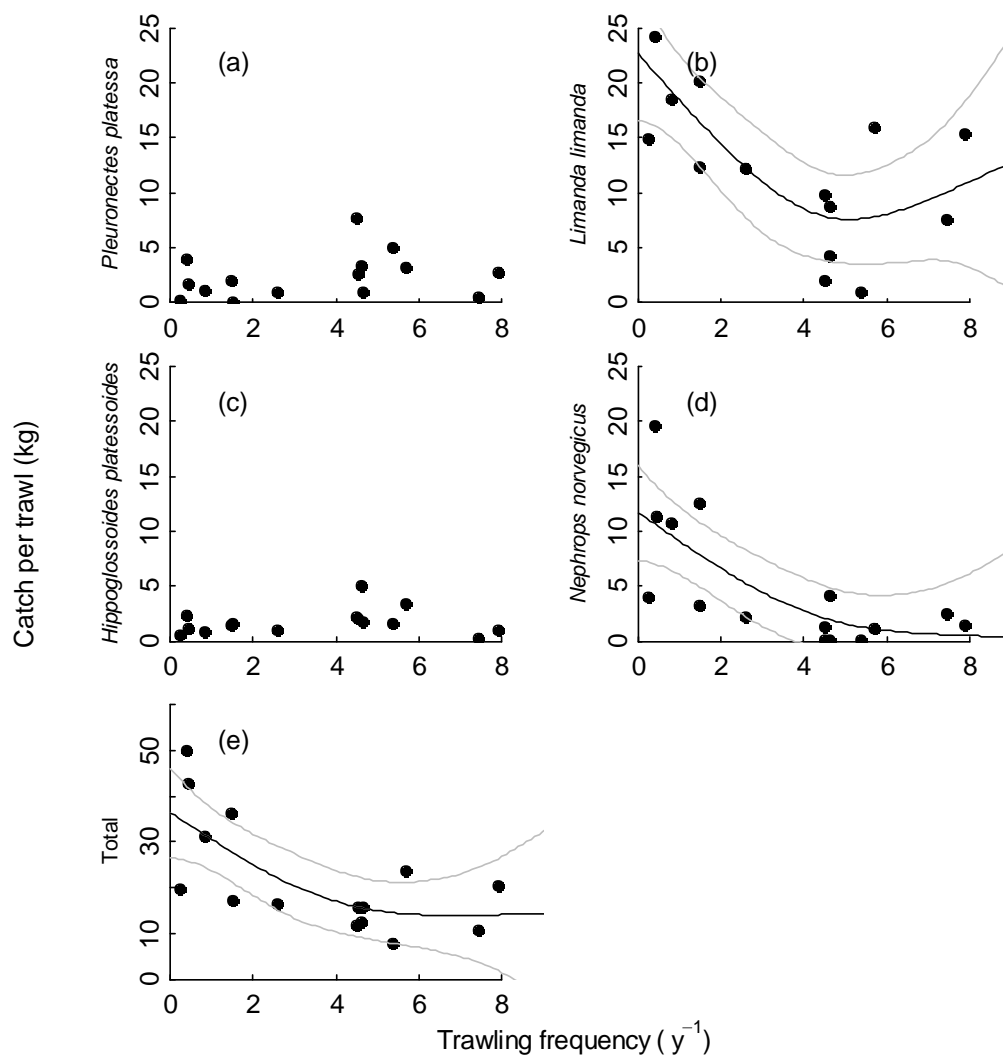
659 Figure 4. The effect of bottom trawling on the biomass of infaunal benthic invertebrates.

660 a) All infauna, solid line is 90% quantile regression, b) Plaice prey <0.2g, solid line is  
 661 fitted GAM, Grey lines indicate the 95% confidence interval,

662 c) Dab prey <0.63 g WW. The dashed line is the non-significant GAM for dab.

663





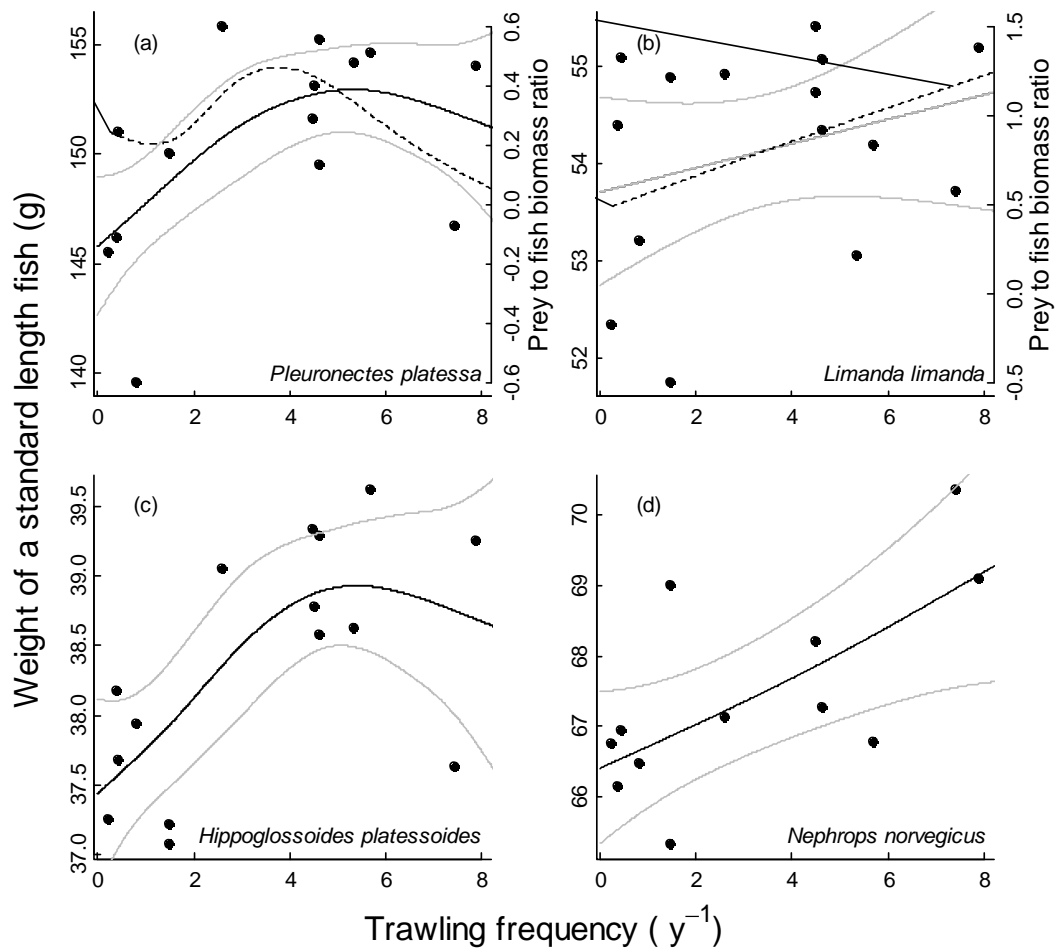
665

666

667 Figure 5. Mean fish biomass per trawl. a) Plaice, b) Dab, c) Long-rough, d) Norway

668 lobster, e) total of all four species. Grey lines indicate the 95% confidence interval.

669

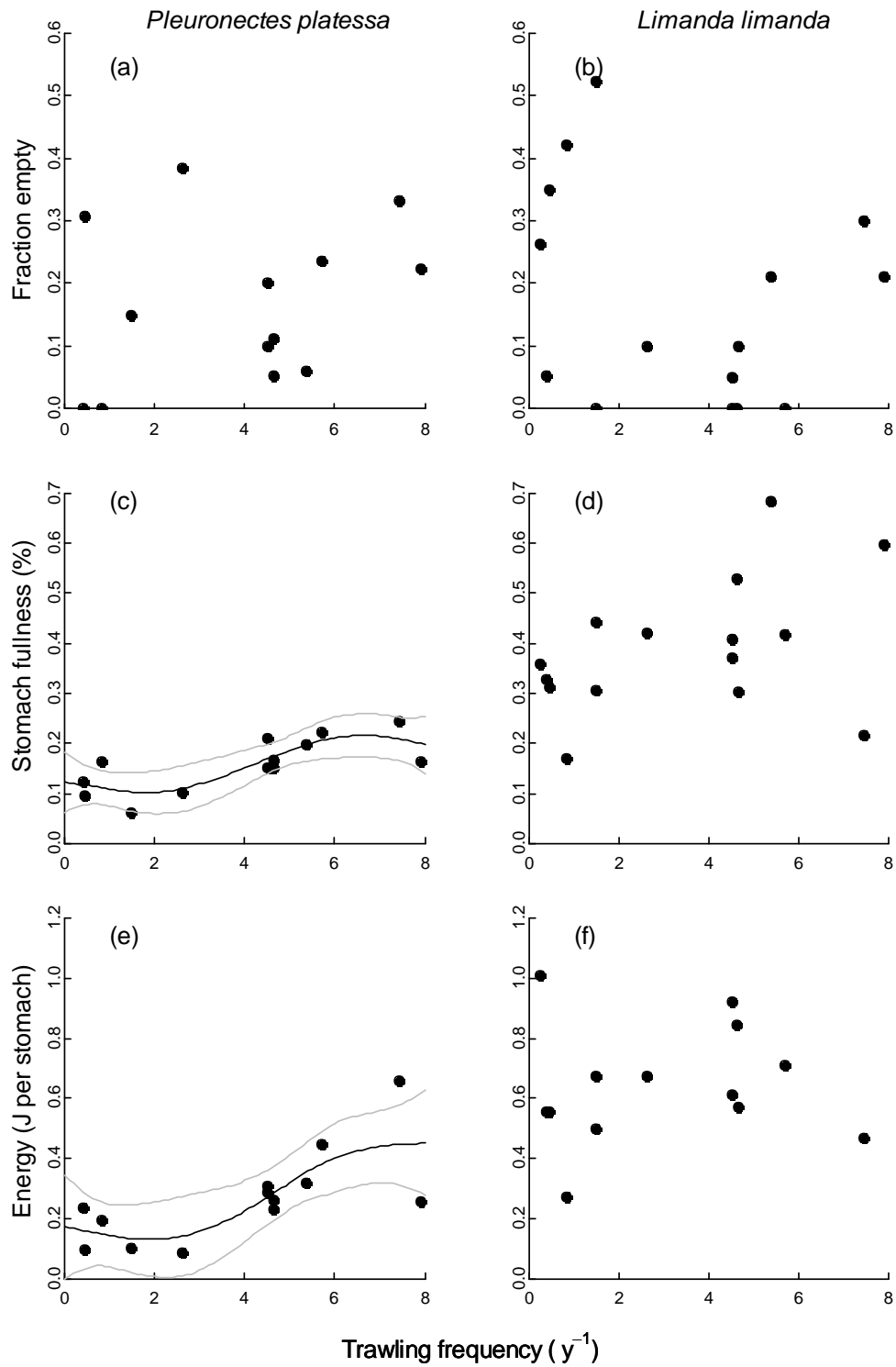


670

671 Figure 6. Weight of a standard length fish (as predicted from the GAMM plus the  
 672 residuals, solid black line) for a) plaice, b) dab, c) Long-rough dab and c) Norway  
 673 lobster. The dashed line (right y-axis) is the 'prey to consumer ratio' (g infaunal prey  
 674  $0.1 \text{ m}^{-2} \text{ kg fish}^{-1} \text{ trawl}^{-1}$ ) and is given for comparison with the weight-at-length. The  
 675 GAMM for dab is not significant.

676

677



679

680 Figure 7. Stomach contents of plaice and dab. a-b: fraction empty, c-d: stomach fullness

681 as a percentage of body weight. e-f: stomach energy content. a, c, e: plaice. b, d, f: dab.

682