

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						
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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.
- We assessed the impact of bottom trawling on the food availability, condition
 and stomach contents of three flatfishes and Norway lobster in an area in the
 Kattegat that is characterized by a steep commercial bottom-trawling gradient
 due to the establishment of an area closed to all fisheries, but otherwise
 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 Long45 rough dab.
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 4. No effect of trawling on dab prey and condition was found. Conversely, the
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- 5. Together these results support the idea that when the abundance of the prey
 declines in response to exploitation, the ratio of the prey to consumer biomass
 will determine whether exploitation will result in an increase or a decrease of
 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 biomass, diversity and the body-size of benthic invertebrates (Hiddink et al. 2006; 66 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.

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 prev 100 item in the diet of some flatfish species) increased at high levels of trawling (Engel & 101 Kvitek, 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 observed declines in the length-at-age of plaice with increasing trawling over gravelbut 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 commercially targeted in the area and usually discarded when caught. Plaice feed 167 168 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 (Amezcua, 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 (km²) 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 $(y^{-1}, the mean number of km^2 fished / the area of the area of the swept area ratio (y^{-1}, the mean number of km^2 fished / the area of the area of the swept area ratio (y^{-1}, the mean number of km^2 fished / the area of the swept area ratio (y^{-1}, the mean number of km^2 fished / the area of the swept area ratio (y^{-1}, the mean number of km^2 fished / the area of the swept area ratio (y^{-1}, the mean number of km^2 fished / the area of the swept area ratio (y^{-1}, the mean number of km^2 fished / the area of the swept area ratio (y^{-1}, the mean number of km^2 fished / the area of the swept area ratio (y^{-1}, the mean number of km^2 fished / the area of the swept area ratio (y^{-1}, the mean number of km^2 fished / the area of the swept area ratio (y^{-1}, the mean number of km^2 fished / the area of the swept area ratio (y^{-1}, the mean number of km^2 fished / the area of the swept area ratio (y^{-1}, the mean number of km^2 fished / the area of the swept area ratio (y^{-1}, the mean number of km^2 fished / the area of the swept area ratio (y^{-1}, the mean number of km^2 fished / the area of the swept area ratio (y^{-1}, the mean number of km^2 fished / the area of the swept area ratio (y^{-1}, the mean number of km^2 fished / the area of the swept area ratio (y^{-1}, the mean number of km^2 fished / the area of the swept area ratio (y^{-1}, the mean number of km^2 fished / the area of the swept area ratio (y^{-1}, the mean number of km^2 fished / the area of the swept area ratio (y^{-1}, the swept area ratio ($ 228 each station, 9km²).

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 estimates. Benthic invertebrates were sampled by taking five 0.1 m² Smith-McIntyre 240 241 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

Plaice and dab of body length 182-299 mm and 168-274 mm, respectively, were 262 263 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 identified to the highest taxonomic resolution possible, counted, weighed and 266 267 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 log₁₀(weight) at log₁₀(length) of fish was estimated using GAMM from the package 284 mgcv in R (Wood 2015; Zuur et al. 2009), using log₁₀(length) and trawling as fixed 285 factors and using 'Station' as a grouping variable and a Gaussian error distribution. As 286 the interaction between $log_{10}(length)$ 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.

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290 Results
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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
- 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 they may not be present in 5 x $0.1m^2$ grabs even when they were present at station. As a result, both high 313 314 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

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

336

337 Fish and Nephrops biomass

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

345

346 Fish condition

Weigh-at-length peaked at a trawling intensity of c. 5 times y⁻¹ for both plaice and Longrough dab (Figure 6, Table 1c). Weight-at-length for dab did not respond to trawling,
while *Nephrops* weight-at-length increased with increasing fishing intensity (Figure 6,
Table 1c). The difference between the highest and lowest condition recorded was
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 comparison with the abundance of competitors, and therefore the abundance of all 358 359 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

Foraging in areas where prey abundance is low is more energetically costly than foraging in areas where prey is more abundant due to the increased search time (Croy & Hughes 1991). If this increase in energy expenditure at low prey abundance is substantial, it could be expected that the effect of trawling on fish condition is stronger than the effect on stomach contents; fish may still fill their stomach at low prey abundance but need to expend more energy to do so. However, such a stronger effect 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

An important assumption was that consumers compete for food and that growth wasdensity-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 effects. 463

A problem of using weight-at-length as an indicator of food intake is that as food intake increases, both length and weight may increase which means that a higher food intake will not be reflected in a straightforward increase in length-at-weight (Lloret, Shulman & Love 2014). The length ranges of fish in our samples included both juveniles and adults, and juvenile fish are likely to invest more energy into length growth than adults. This effect will therefore have decreased our ability to detect differences in food intake 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 species increased with trawling intensity up to a frequency of 3 to 5 v^{-1} , there was no 480 481 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.

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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-
- 516 hub/fish-stomach-records/
- 517

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- 632 Tables
- 633

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

a. Biomass of infauna, g WW per 0.1 m². GAM

Parameter		res.df	F	Р				
Total infauna WW		13	1.176	0.298				
Plaice infauna prey <0.20g WW		12.4	4.175	0.041*				
Dab infauna prey <0.63 g WW		13	0.244	0.630				
b. Fish biomass per trawl. GAM								
Species		res.df	F	Р				
Pleuronectes platessa		12.5	0.717	0.494				
Limanda limanda		12.0	7.049	0.007*				
Hippoglossoides platessoides		11.9	2.202	0.144				
Nephrops norvegicus		12.3	7.301	0.007				
Total		12.2	6.043	0.013				
c. Fish condition. GAMM								
Species	n	res.df	F	Р				
Pleuronectes platessa		367.9	6.399	0.002*				
Limanda limanda		912.0	1.201	0.273				
Hippoglossoides platessoides		878.9	7.143	0.001*				
Nephrops norvegicus		467.9	5.853	0.014				
d. Fish stomach contents. GAM								
Species		res.df	F	Р				
Pleuronectes platessa % empty	13	11.0	0.803	0.389				
Limanda limanda % empty		12.2	1.555	0.247				
Pleuronectes platessa fullness		8.9	4.849	0.024				
Limanda limanda fullness		13.0	2.750	0.121				
Pleuronectes platessa energy		9.3	4.340	0.034				
Limanda limanda energy		13.0	2.550	0.134				

639 **Figures**



640

Trawling frequency

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.



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

653 NTZ = No-take zone.



Figure 3. MDS plot of the site characteristics of the sampling stations. Bubble size isproportional to the trawling intensity.





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,
- c) Dab prey <0.63 g WW. The dashed line is the non-significant GAM for dab.
- 663



Figure 5. Mean fish biomass per trawl. a) Plaice, b) Dab, c) Long-rough, d) Norway
lobster, e) total of all four species. Grey lines indicate the 95% confidence interval.



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

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Figure 7. Stomach contents of plaice and dab. a-b: fraction empty, c-d: stomach fullness
as a percentage of body weight. e-f: stomach energy content. a, c, e: plaice. b, d, f: dab.