

Could our fisheries be more productive? Indirect negative effects of bottom trawl fisheries on fish condition

Jan G. Hiddink*, Andrew F. Johnson, Rachel Kingham and Hilmar Hinz

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

Summary

1. The nets used in bottom trawl fisheries cause mortality of benthic invertebrates and this can decrease the long-term availability of prey to exploited fish species by reducing the abundance of benthic invertebrates. This may have consequences for the sustainability of fisheries.

2. We assessed the impact of bottom trawling on the food availability of fish by comparing the condition of fish (as weight-at-length) in an area that had a steep commercial bottom-trawling gradient in the Irish Sea but otherwise homogeneous environmental conditions.

3. We found that the condition of the important commercial flatfish plaice *Pleuronectes platessa* was negatively related to trawling frequency, and this could be explained by a reduced production of the infaunal invertebrates they feed on. Density-dependent changes in competition over food could not explain this difference. No effect of trawling on the condition of the flatfish dab *Limanda limanda* was detected. Whiting *Merlangius merlangus* feeds primarily on fish, and therefore, no effect of bottom trawling on its condition was expected or detected.

4. This study therefore indicates that bottom trawl fisheries may have a negative effect on the condition of some of their target species, but not others, by reducing the abundance of their benthic prey.

5. *Synthesis and application.* Bottom trawls may indirectly affect the population size and growth rate of the target fish species and result in lower fishing yields. Such reductions in the yield and sustainability of fisheries are highly undesirable. The effects of bottom trawls may be mitigated by the modification of fishing gears or by minimizing the area of the seabed fished by bottom trawls.

Key-words: beam trawl, ecosystem approach to fisheries management, ecosystem-based management, fisheries yield, otter trawl, predator–prey interactions

Introduction

It is vital to understand how the wider ecosystem effects of fisheries affect the long-term sustainability of the populations being fished. The stocks of many commercial fish species, and in particular of demersal (groundfish) species, have collapsed under increasing exploitation pressure. Some have failed to recover or have shown much slower recoveries than expected after management measures, such as fishery closures, have been implemented (e.g. Hutchings 2000; Choi *et al.* 2004). A more detailed understanding of the indirect effects of demersal fishing practices on exploited species is vital for the implementation of stock recovery plans and the move towards an ecosystem approach to fisheries management (Link 2002).

Many fisheries for demersal fish and crustaceans use otter and beam trawls and many of these use heavy ground ropes

and chains to drive the fish from the seabed and into the nets. Bottom trawling causes widespread physical disturbance of benthic habitats and leads to reductions in biomass, production and species richness of benthic macro-invertebrates, (e.g. Jennings & Kaiser 1998; Hiddink *et al.* 2006; Hinz, Prieto & Kaiser 2009). Many important commercial fishes, such as flatfish and gadoids, feed on these benthic invertebrates for part or all of their life history. Bottom trawling thus not only reduces the population size of fish through direct removal, but also reduces the abundance of their prey (Auster & Langton 1999). This may affect the growth, population size and distribution of fish species. Alternatively, it has been hypothesized that low levels of bottom trawling may benefit the small benthic invertebrates that form the food source for some species of flatfish such as plaice by removing the large fauna that small benthos compete with for food and space. A modelling study by Hiddink, Rijnsdorp & Piet (2008) demonstrated an increased production in polychaete biomass at low levels of trawling.

*Corresponding author. E-mail: J.Hiddink@bangor.ac.uk

Biomass then strongly decreased again at higher trawling frequencies.

Using a simple model of the relationship between fishing effort, carrying capacity and yield, Fogarty (2005) showed that bottom trawl fisheries that reduce the carrying capacity of the ecosystem, by reducing prey availability for fish, have a lower maximum sustainable yield (MSY) which is reached at a lower fishing effort. Despite these potentially important indirect effects of bottom trawling on target populations, traditional fisheries management has not addressed these wider ecological consequences of fishing. Models that are used for fisheries management, for example to estimate the MSY, do not usually consider the implications of a decrease in food availability that can be associated with certain harvesting techniques (although some fisheries management models do include, and account for, variations in food supply because of harvesting of the forage fish [e.g. Walters *et al.* 2005]). Models generally assume that the growth of fish is density dependent, with reduced levels of exploitation showing increased fish population growth rates. Consequently, these models implicitly assume that the total food supply for the fish does not change, and therefore, the food intake per fish increases when fish are exploited. However, when fishing has negative effects on prey abundance, food availability decreases with decreasing fish stocks which means that no density-dependent increase in growth can be assumed. In other words, the carrying capacity of the system may be simultaneously reduced. This means that the MSY is lower than assumed from model outputs. This also means that the likelihood of overexploitation of the resource is higher.

Many studies have examined how bottom-trawling affects benthic invertebrates (meta-analysis in Kaiser *et al.* 2006). Fewer studies have examined the negative effect of bottom trawling on fish habitats and fish prey (e.g. Auster & Langton 1999), and only very modelling studies have considered what effect this may have on fish populations (Fogarty 2005; Hiddink, Rijnsdorp & Piet 2008). There has been little progress in quantifying the importance of this process for fish, and there is a paucity of empirical studies. A recent study by Shephard, Brophy & Reid (2010) examined length-at-age of plaice in the Celtic Sea in relation to large-scale trawling effort. They found that plaice on gravel showed significant declines in length-at-age with increasing trawling effort while plaice on sand showed significant increases in length-at-age. They propose that contrasting trawling effects reflect dietary differences between substrates as plaice on sand substrates predominantly consume polychaetes, which may proliferate at moderate trawling intensity on these substrates (Hiddink, Rijnsdorp & Piet 2008). Conversely, plaice on gravel substrates consume more fragile organisms such as echinoderms and bivalves that show marked declines with bottom trawling (Amezcuca, Nash & Veale 2003). The biochemical condition of benthivorous fishes was also higher in less frequently fished areas in the Mediterranean (Lloret & Planes 2003; Lloret, Demestre & Sánchez-Pardo 2007). Effects could, however, not be unequivocally related to fishing impacts in any of these studies as many confounding factors were readily identified because of the large study scales.

The objective of this study was to assess whether bottom trawling affects the fitness of fish species that feed on benthic invertebrates by changing their food availability. Separating the effect of trawl capture from the effect of prey availability on fish population size is difficult. Bottom trawl impacts on benthos occur in the trawl path, and most species of benthic invertebrates do not move over more than a metre a year. Many temperate commercial fish species can however move over hundreds of kilometres each year (e.g. plaice, Hunter, Metcalfe & Reynolds 2003; cod, Robichaud & Rose 2004). It is therefore difficult to assess whether changes in the local food availability translate into population scale effects for fish. The approach that we used here was to compare the weight-at-length of fish as a proxy for their condition in a small area that had a steep bottom-trawling gradient. Weight-at-length may be used as a proxy of fitness and depends on the balance of energy intake and expenditure. Weight-at-length is widely used as an index of the health of an individual because the routine use of biochemical measures of fat content is rarely practicable. This is based on the assumption that heavier fish of a certain length are in better condition, although the weight-at-length measures the shape of a fish rather than being a direct measure of the extent of fat reserves and has been extensively criticized for this (e.g. Davidson & Marshall 2010). Weight-at-length varies throughout the year because of the acquisition of resources during the summer, reduced food intake in the winter and then the release of spawning products during the spawning season. Estimates of weight-at-length may also be biased by variations in muscle water content. A positive relationship between weight-at-length and biochemical measurements of fat content has however been found for many species (see McPherson *et al.* 2011 for overview). When morphometric condition indices are used, they should ideally be validated before use to assess to what extent the index correlates to energy stores or protein content.

Changes in energy reserves and associated condition can have important consequences for the health of fish and therefore can influence survival and abundance. Reduced energy reserves can lead to reduced fecundity or quality of eggs and larvae although the strength of these relationships varies greatly between species (Marshall & Frank 1999; Blanchard, Frank & Simon 2003; Kennedy *et al.* 2008). Starvation because of exhaustion of energy reserves weakens fish and makes them more susceptible to predation and other stressors such as parasites. Changes in fish condition are likely to correlate with the food uptake of the fish for the weeks previous to sampling (Kennedy *et al.* 2008). Changes in condition can have a wide variety of effects and fish can compensate for decreases in condition in many ways such as reduced activity, and reduced investment in reproduction including skipping spawning (Rideout & Rose 2006).

We hypothesize that trawling negatively affects benthic invertebrate biomass (H1) and that the condition of fish that feed on these benthic invertebrates (benthivorous fish) is higher at high benthos biomass (H2a). The condition of fish that do not feed on benthic invertebrates is hypothesized to be unrelated to the biomass of benthic invertebrates (H2b). As benthic

biomass is lower at high trawling frequencies, it is hypothesized that the condition of benthivorous fish is lower at high trawling frequencies (H3a), while no such relationship is expected for non-benthivorous fish (H3b). The trawling frequency in the study area is higher than the level at which increases in the production of small infauna may be possible, and therefore, no positive effects of bottom trawls on prey availability and condition are expected. The results of this study indicate that bottom trawl fisheries may have a negative effect on the condition of some of their target species by reducing the abundance of their benthic prey.

This paper provides a major advance on previous work. The large spatial scale of past studies means that, although the results are more generally applicable, a larger scope exists for confounding the effects of bottom-trawling effort with other environmental variables that may affect fish growth such as primary production (Shephard, Brophy & Reid 2010). Furthermore, because of the large within ICES (International Council for the Exploration of the Sea) rectangle patchiness in the distribution of trawling effort, the fish that were examined by Shephard, Brophy & Reid (2010) were unlikely to have been feeding at locations that experienced the average trawling effort for that rectangle. The current study avoids such confounding effects as much as possible by examining the effect of bottom trawls on fish condition at a much smaller spatial scale.

Materials and methods

We examined the flatfishes plaice *Pleuronectes platessa* and dab *Limanda limanda* and the gadoid whiting *Merlangius merlangius*. These three species comprised 97% of the catch numbers made in the study area. Plaice is a benthivore that feeds primarily on small polychaetes and to a lesser extent on bivalves (Rijnsdorp & Vingerhoed 2001; Hiddink, Rijnsdorp & Piet 2008). Dab is a benthivore that feeds primarily on mobile crustaceans, polychaetes, fish and mollusc siphons (Braber & de Groot 1973). Whiting goes through an ontogenetic diet shift, feeding primarily on benthic amphipods and other

benthic invertebrates up to a size of about 14 cm, and switching to a diet of small fish such as the sandeel *Ammodytes tobianus* above this size (Pedersen 1999). No whiting < 14 cm were caught in our trawls. We assumed that plaice feed on prey sizes < 0.5 g (Hiddink, Rijnsdorp & Piet 2008), dab on prey < 2 and < 4 g for whiting (Appendix S1, Supporting Information). Weight-at-length has been shown to be a proxy for fitness in plaice (Kennedy *et al.* 2008), and although such information is not available for dab and whiting, it does not seem unreasonable that such correlations exist for these species.

The effects of chronic trawling on the weight-at-length of fish were investigated over a fishing ground in the north-eastern Irish Sea off the Cumbrian coast (Fig. 1). The main bottom-trawling activity that occurs on this fishing ground is otter trawling for Norway lobster *Nephrops norvegicus* and gadoid fish. The fishery operates throughout the year with a peak in activity from spring to early summer. Owing to the proximity to the coast, fishing vessels tend to operate on day trips, and the majority of vessels are under 20 m in length. The area is characterized by low-energy hydrodynamic conditions, and consequently, the substratum comprises mostly fine sand and muddy sediment. This study area was selected because Hinz, Prieto & Kaiser (2009) showed that chronic otter trawling had a significant negative effect on the biomass of infaunal benthic invertebrates. The area also displayed statistically homogeneous habitat characteristics (depth, sediment type, bottom temperatures and tidal currents) while at the same time showing a strong spatial gradient in trawling intensity (see Hinz, Prieto & Kaiser 2009 for details). We expected trawling effort to be spatially heterogeneous in areas of relatively homogeneous habitat because trawlers tend to fish along tows that are recorded in their navigation systems and are known to be free of obstructions that could damage the trawl gear (Auster & Langton 1999; Holland & Sutinen 2000). This pattern of effort within habitats persists over many years, and Dinmore *et al.* (2003) showed that unfished areas are not necessarily unsuitable for trawling. Therefore, at the scale of the study, trawling effort distributions were unlikely to be related to patterns in ecosystem productivity. If fishers concentrate in areas with a high ecosystem production, this would decrease the power to detect a negative effect of trawling on fish condition, and therefore, our conclusions would be conservative. Fifteen stations were selected for sampling, each station comprised of a 1 × 2 km box.

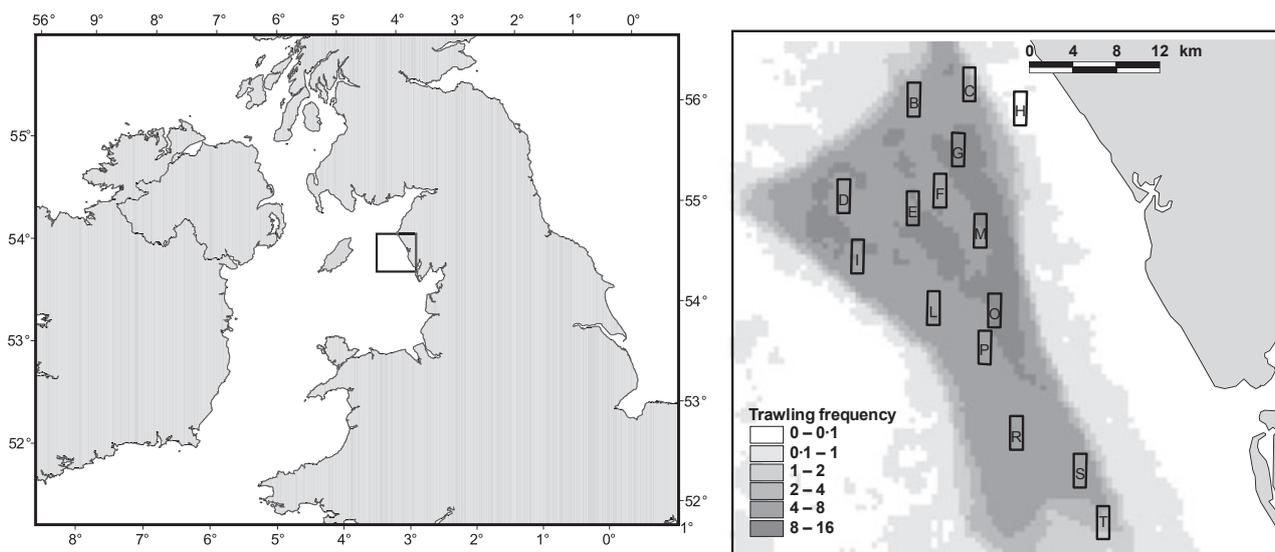


Fig. 1. Sampling stations and the distribution of bottom trawling frequency (year^{-1}) from 2004 to 2008 in the study area.

Tracking studies by Hunter, Metcalfe & Reynolds (2003) showed that plaice hardly moved in June, the month of our study. This means that plaice are unlikely to be moving much during the feeding season in summer and therefore that any relationship between trawling frequency and plaice condition is likely to be causally related to trawling. Very little is known about the small-scale and short-term movements of dab on their feeding grounds. A tag-recapture study of whiting recorded long-term displacement distances from 53 to 123 km over a period of year, which suggests they move over relatively small distances (Tobin *et al.* 2010). This lack of detailed knowledge on the movements of dab and whiting on their feeding grounds makes it more difficult to draw firm conclusions about these species. However, there is no reason to assume that dab is more mobile than plaice, but it seems likely that the benthic-pelagic whiting is more mobile than plaice.

EFFORT ESTIMATION

Recovery from bottom-trawling impacts can take well over 10 years (Hiddink, Jennings & Kaiser 2006), and therefore, trawling frequency was estimated over the 10 years previous to sampling. Spatially detailed estimates of trawling effort can be obtained from satellite or aircraft observations of vessels that are fishing, if the number of fishing hours that each observation represents, and the speed and size of fishing gear, is known. It was assumed that otter trawlers fished at a mean trawl speed of 2.5 knots (4.62 km h⁻¹) and used gear with a width of 60 m (Hinz, Prieto & Kaiser 2009). Trawling frequency at the sampling stations was calculated from fishery protection overflight observations from 1999 to 2004 as in Hinz, Prieto & Kaiser (2009) and European Community Satellite Vessel Monitoring System (VMS) data from 2004 to 2008 as in Hiddink *et al.* (2006). These two data sets complement each other in time, as high-quality overflight data, that cover all sizes of vessels, are not available after 2004 and VMS data are only available for small vessels (>15 m) after 2004. One-third of the fishing vessels that have their homeport in the two nearest ports of Whitehaven and Fleetwood are under 15 m and therefore not included in the recent VMS records (<http://marinemanagement.org.uk/fisheries/statistics/documents/vessels/under/090601.xls>). As more recent bottom trawling will have impacted infaunal invertebrates most strongly, the VMS data from 2004 to 2008 contributed two-third of our trawling frequency estimate, while the overflight data from 1999 to 2004 contributed one-third. Trawling frequency at the sampling stations varied between 0.5 and 11.9 trawl passes year⁻¹.

SAMPLING OF FISH AND INVERTEBRATE POPULATIONS

Fish and invertebrates were sampled at each station in June 2009. Two tows of 30-min duration were made at each station at a speed of three knots with a rock hopper otter trawl (distance across mouth of the net 16 m, head line height 3 m, 82-mm diamond mesh cod-end). The length (to the nearest mm) and weight (to the nearest g) of all common fish species in the catch was recorded on board. If the catch of a species in a haul was large (> 50 individuals), only the first three fish per cm-size class were weighed. The benthic invertebrates were sampled by taking five 0.1-m² day grabs at haphazard locations in the station box. Samples were sorted over a 1-mm sieve and preserved in 4% formalin for identification. Results from the five individual grabs were pooled before statistical analyses as replication within stations was aimed at increasing the accuracy and precision of our estimates of benthic production and not at obtaining estimates of within station

variability. The wet weight of each individual organism was estimated after blotting. The weight range of infaunal invertebrates consumed by analysed fish species was obtained from existing sources (See Appendix S1 and Fig. S1, Supporting Information) and the biomass of organism in this weight range was used to calculate infaunal production in the analyses. The food availability for fish was determined by the production rather than the biomass of invertebrates. We therefore calculated the production of benthic invertebrates per station for the relevant size ranges using the equation $\log_{10} P:B = -0.431 - (0.236 \times \log_{10} B)$, where P is production and B is the ash-free dry weight in g of the individual benthic organisms (Jennings *et al.* 2002) using conversion factors from wet weight to ash-free dry weight from Brey (2008). A very strong correlation exists between the observed biomass and calculated production at stations (d.f. = 13, $r = 0.987$, $P < 0.0001$).

FISH CONDITION

The condition of individual fish was estimated as the weight-at-length of the fish. In the rest of this paper, we will use 'condition' as a synonym of 'weight-at-length'. We used total fish weight for this proxy condition rather than eviscerated weight as higher numbers of fish could be processed that way. Using total weight implies that differences in gonad and stomach content weight between stations may have increased the variation in the condition. The 5% shortest and longest fish per species were excluded from all analyses to avoid biases that could be caused by particularly large or small fish. For the three fish species, only stations where more than 10 fish were caught were used to avoid biased condition estimates because of low numbers of fish. A total of 14 stations were considered for plaice, 15 stations for dab and 12 stations for whiting.

To account for the non-independence of fish condition measurements within a station, the effect of trawling or benthic production on the \log_{10} (weight) at \log_{10} (length) of fish was estimated using linear mixed effect models (Pinheiro & Bates 2000), using \log_{10} (length) and trawling or benthic production as fixed factors and using 'Station' as a grouping variable. The Akaike Information Criterion (AIC) was lower for this mixed model than for a generalized least squares regression without a random effect of station, and this showed that the random effect did improve the models. We selected a Gaussian correlation structure from a selection of alternative structures using the AIC to address the correlation that may exist because stations close to each other may exhibit more similar values than those further apart (Pinheiro & Bates 2000). As the interaction between \log_{10} (length) and trawling or benthic production was never significant, this term was excluded from analyses. The significance of the effect of trawling or infaunal production on condition is reported as the significance of the factor from the ANOVA. The significance of the relationship between fish abundance and trawling or infaunal production is tested using an ordinary least squares linear regression. Homogeneity of residuals was established through visual examination of plotted standardized residuals vs. fitted values.

Results

Areas that were more frequently trawled had a significantly lower production of infaunal invertebrates (Fig. 2, $R^2 = 0.58$, $F_{1,15} = 18.02$, $P < 0.001$). This effect remained significant when only the size classes of infauna that are potential food for plaice (<0.5 g, $R^2 = 0.55$, $F_{1,15} = 15.61$, $P = 0.002$), dab (<2 g, $R^2 = 0.55$, $F_{1,15} = 15.75$, $P = 0.002$) and whiting

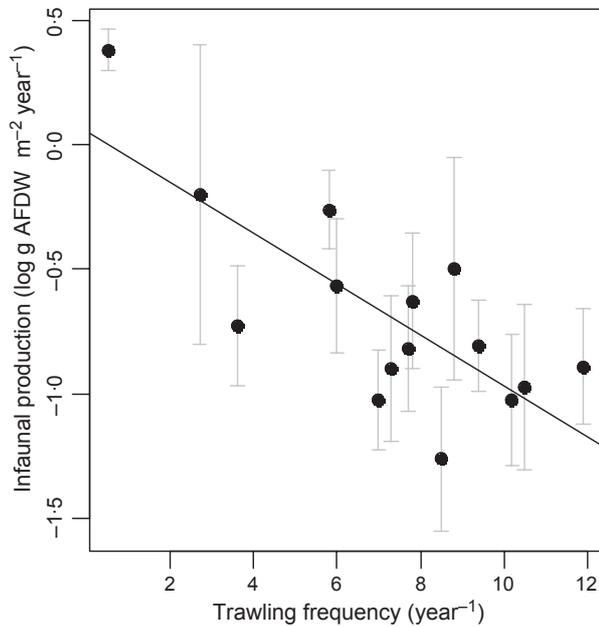


Fig. 2. Chronic bottom trawling has a strong negative impact on the biomass of infaunal invertebrates. Means \pm standard deviation of 5 replicate grabs.

(< 4 g, $R^2 = 0.54$, $F_{1,15} = 15.35$, $P = 0.002$) were considered.

We estimated the condition of plaice using 831 fish in the size range from 176 to 310 mm (mean 234, standard deviation 32), of dab using 1074 fish in the size range from 150 to 239 mm (mean 189, standard deviation 20) and of whiting for 228 fish

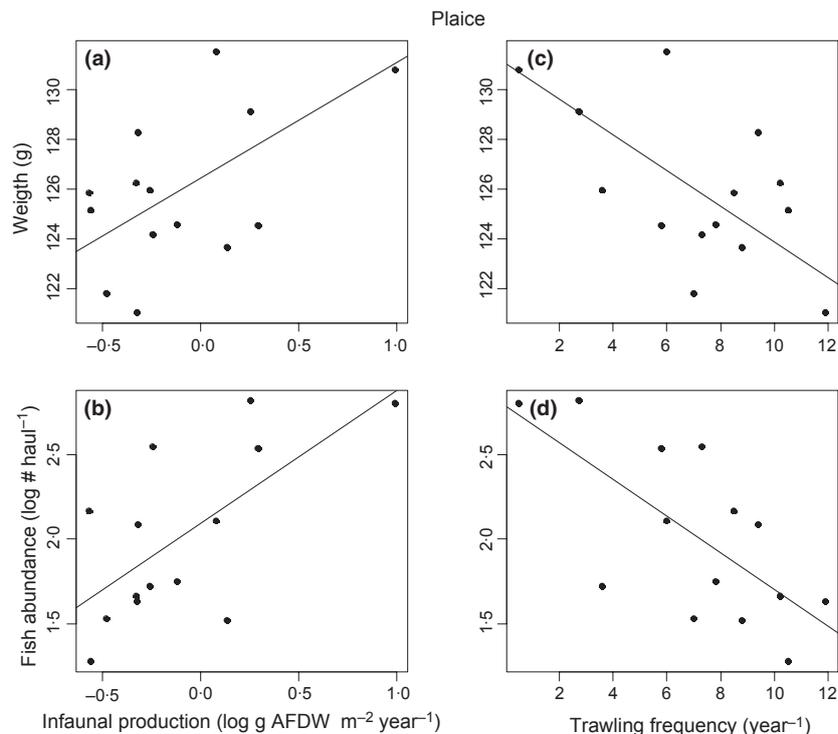
in the size range from 159 to 264 mm (mean 214, standard deviation 27). These whiting are therefore all within the size range that feed predominantly on non-benthic prey species.

Both the weight-at-length and the abundance of plaice were positively related to the production of infaunal invertebrates (condition: $F_{1,12} = 6.36$, $P = 0.027$, Fig. 3a, abundance: $R^2 = 0.43$, $F_{1,14} = 9.2$, $P = 0.011$, Fig. 3b). The condition of plaice was significantly negatively related to the bottom-trawling frequency ($F_{1,12} = 11.71$, $P = 0.005$, Fig. 3c). The weight of an average length plaice varied between 122 and 130 g, thus indicating a maximum 6% difference in condition between the low- and high-trawling-frequency stations. The abundance of plaice was lower at higher trawling frequencies ($R^2 = 0.47$, $F_{1,14} = 10.82$, $P = 0.006$, Fig. 3d).

The weight-at-length of dab was not significantly related to the production of infaunal invertebrates (condition: $F_{1,13} = 2.9$, $P = 0.112$, Fig. 4a) or to the trawling frequency (condition: $F_{1,13} = 2.33$, $P = 0.151$, Fig. 4c), but these non-significant effects have the same direction as was observed for plaice. Dab abundance was higher at stations with a higher infaunal production ($R^2 = 0.65$, $F_{1,14} = 24.63$, $P < 0.001$, Fig. 4b) and lower at stations with a high bottom-trawling frequency ($R^2 = 0.62$, $F_{1,14} = 20.8$, $P = 0.001$, Fig. 4d).

The weight-at-length and abundance of whiting were not related to the production of infaunal invertebrates (condition: $F_{1,8} = 0.2$, $P = 0.668$, Fig. 5a, abundance: $R^2 = 0.01$, $F_{1,11} = 0.03$, $P = 0.878$, Fig. 5b) or to the trawling frequency (condition: $F_{1,8} = 0.06$, $P = 0.819$, Fig. 5c), although there is the suggestion of a negative effect of bottom trawling on the abundance of whiting (abundance: $R^2 = 0.25$, $F_{1,11} = 2.01$, $P = 0.194$, Fig. 5d).

Fig. 3. Plaice, *Pleuronectes platessa*. Fish weight (plotted for an average size fish, $L = 235$ mm) (a) and fish abundance (b) relate positively to the production on infaunal invertebrates (< 0.5 g). In (a) and (b), the line is the fitted model for a fish of median length. The plotted weights are for a fish of median length predicted from a model that relates weight to length and station and uses station as a grouping factor. The deviations of the points from the line therefore represent the variation that is caused by station effects. These points are for illustration only and were not used in fitting relationships. The negative relationship between fish condition and trawling (c) arises from both the negative effect of the trawling on invertebrates (Fig. 2), and the fish feeding on the invertebrates. Bottom trawling reduced the abundance of fish (d).



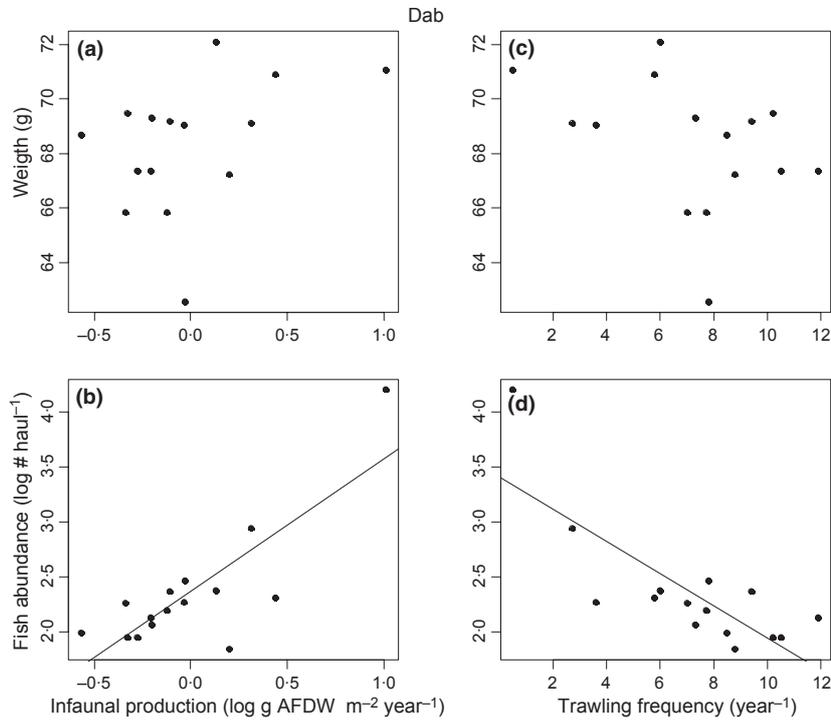


Fig. 4. Dab *Limanda limanda*. Fish weight (plotted for a median size fish, $L = 189$ mm) did not relate to infaunal production (a) or trawling frequency (c). Fish abundance relates positively to the production of infaunal invertebrates (< 0.2 g) (b) and negatively to bottom trawling (d). See Fig. 3 for an explanation of how plotted weights for (a) and (b) were derived.

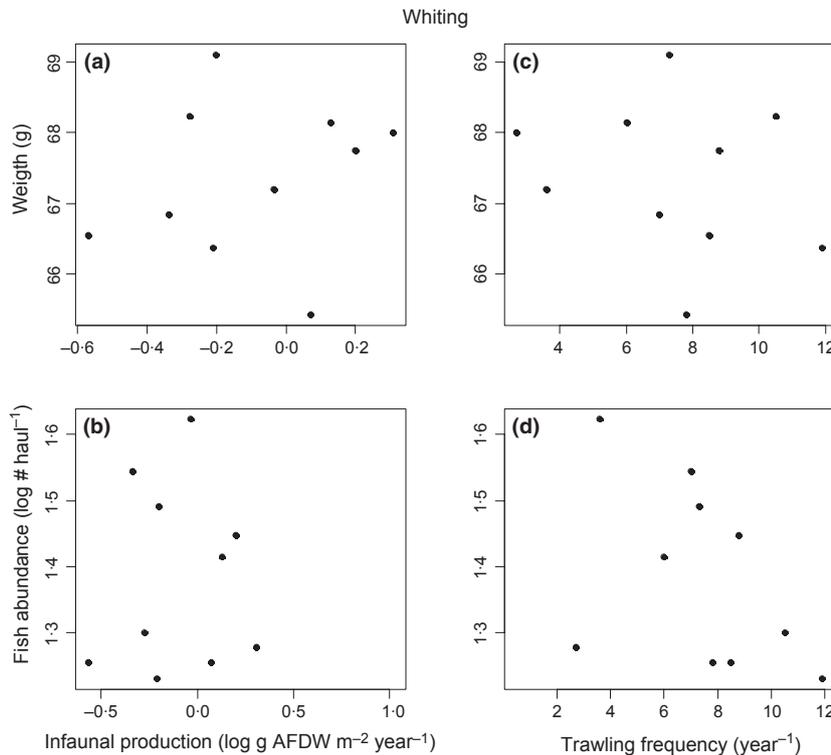


Fig. 5. Whiting, *Merlangius merlangus*. Fish weight (plotted for a median size fish, $L = 213.6$ mm) (a) and fish abundance (b) do not relate to the production of infaunal invertebrates (of < 4 g). As whiting do not predominantly feed on these invertebrates, there is no relationship seen between bottom trawling frequency and their condition. (c) Bottom trawling did not affect the abundance of whiting (d). See Fig. 3 for an explanation of how plotted weights for (a) and (b) were derived.

Discussion

Our results provide partial support for the hypothesis that bottom trawling negatively affects the fitness of benthivorous fish by reducing the availability of food. The condition of benthivorous plaice was negatively related to trawling frequency, and

this could be explained by a reduction in the production of infauna. Density-dependent effects such as competition could not have played a role in generating this relationship as plaice had the worst condition at the stations where they were least abundant and therefore where competition for food resources was expected to be the lowest. The hypothesized positive effect

of low trawling frequencies ($< 2 \text{ year}^{-1}$) on the abundance of the food for plaice or the condition of plaice (Hiddink, Rijnsdorp & Piet 2008) could not be detected in this study because only one of the stations covered this range of trawling intensities. This hypothesis therefore remains untested. The condition of benthivorous dab however was not related to trawling frequency or infaunal production and does therefore not support our hypotheses. The relationship between trawling and condition for the piscivorous whiting provides a 'control treatment' that takes account of any other effects bottom trawling may have on fish condition that are not related to food availability. As hypothesized, no effect of bottom trawling on the condition of whiting was detected.

The lack of an effect of trawling on dab may be explained by its diet composition, as dab has a highly opportunistic feeding strategy making it more adaptable to habitat and ecosystem change compared with other species (Hinz, Kröncke & Ehrich 2005). Dab might be able to feed and maintain its condition regardless of changes in benthic community structure, while more selective benthic feeders such as plaice might not be able to compensate for the loss of particular prey types. In addition, dab is known to scavenge more extensively than plaice and whiting on dead and dying invertebrates in trawled areas (Groenewold & Fonds 2000). This means that the food availability for dab is likely to be less strongly affected by bottom trawls than for plaice.

Bottom trawling reduced the abundance of the fish at the same time as reducing food production. The ramifications for the fish depend on the relationship between the amount of prey available and the demand on the reduced food supply by the remaining fish. Energetically, it is likely to be more costly to forage in low-production compared with high-production patches. In areas of low benthos, fish will have to spend more time searching for prey (e.g. Charnov 1976), and therefore, lowering their intake rates while increasing energy expenditure. This means that if bottom trawling leads to a decrease in the carrying capacity for benthos of the ecosystem, fish production is likely to drop, even if the amount of food per fish stays equal. Furthermore, fish numbers decrease linearly with fishing effort, but benthic invertebrate production has been shown in previous studies to drop very sharply even at low levels of bottom trawling (Hiddink *et al.* 2006). Fish numbers may not always decrease linearly with fishing effort because catchability can depend on fish density, but this effect tends to lead to a faster depletion of prey than of the fish. This means that both the amount of food production per fish and the food intake per fish is likely to decrease as a result of bottom trawling.

Any study using an observational approach has to consider the potential for confounding factors affecting conclusions. This study assumed that the condition of fish represented the local prey availability. The mobility of the fish in the study area is poorly known, and therefore, we cannot be sure that individuals captured at different stations had been feeding at that station for several weeks before sampling. However, it seems reasonable to assume that benthic flatfish are less mobile than the benthic-pelagic whiting. It is therefore conceivable that any effect of trawling on whiting condition could have been

masked by the movement of whiting between areas of different trawling frequency. This, however, does not affect the conclusions that trawling had a significant negative effect on the condition of plaice, as mobility would break up any spatial pattern in condition; therefore, these analyses are likely to underestimate any effect of trawling on condition. We could gain more certainty about the validity of our conclusions by sampling several benthivorous and several piscivorous species, both of differing mobilities, but the low fish diversity in the study area limited our analysis to three species. A problem of using weight-at-length as an indicator of food intake is that as food intake increases, the growth of 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. 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.

Fishing activities may stress fishes even when they are not caught. Fish present in frequently trawled areas may have escaped from fishing gears several times and this may negatively affect their condition (Chopin & Arimoto 1995), also generating a negative relationship between fish condition and trawling frequency. If such a scenario played an important role in our study area, such a negative effect of trawling on condition would be expected to exist for all three species and this was not observed in the current study. However, the higher mobility of whiting could have weakened any such pattern. Such shortcomings may be unavoidable when trying to study the large-scale effects of trawling, if such research is to progress at the speed required to support management decision-making.

The difference in condition for low and high trawling frequency stations was *c.* 6% for the size ranges of plaice that were sampled using our trawl. Thus, the biomass of fish present would have been 6% lower at more intensely trawled stations even if fish abundance was not affected by fishing. This difference in condition is likely to represent the effect of a reduced food intake in the weeks previous to sampling (Kennedy *et al.* 2008) and is likely to increase over the feeding season. On longer timescales, such reduced food intake is likely to lead to a reduced weight and length growth. Our 6% decrease is therefore likely to be an underestimate of the long-term impacts of bottom trawling on plaice biomass growth as we sampled at the start of the feeding season. A reduced condition is also likely to affect plaice reproduction. In studies on spawning, a 4–8% reduction in the condition of plaice resulted in a lower growth rate in vitellogenic oocytes and lower fecundity (Kennedy *et al.* 2008). Such a reduction in fish condition and the resulting reductions in growth and fecundity are likely to have population scale effects. These effects are likely to lead to lower population growth rates and a lower standing stock biomass. Any change in the carrying capacity of the ecosystem to support fish populations will lead to a lower MSY. As the weight of smaller, thinner fish is less valuable than the same weight of large fish, the effects of

a decrease in biomass yield will be aggravated by a reduction in the value of the fish per kilogram.

The negative effect of bottom trawling on plaice condition indicates that bottom trawling may indirectly affect the population size and growth rate of the target fish species and result in lower fishing yields. This study provides the basis for further studies that should be aimed at testing the hypotheses that the population size and yield of commercial fishes are lower than they could be without the secondary effects of bottom trawling. As indicated in the introduction, these are not effects that can be directly measured. It is difficult to assess the magnitude of such effects using current knowledge and will need a combination of ecosystem models, large-scale field campaigns and experimental studies that relate growth and fecundity to food availability. In addition, experimental studies are required where the effect of varying food availability on the length and weight growth and fecundity of fish is used to assess how differences in condition translate into differences in population biomass and reproductive success. Many such studies have been undertaken as part of research into aquaculture (e.g. Bromley, Ravier & Witthames 2000). It will be necessary to develop ecosystem models that describe the interaction between fisheries, fish and their prey. Such models should be able to integrate (i) size-based effects of bottom trawling on benthic invertebrates, (ii) predator-prey interactions between fish and invertebrates, (iii) the effect of different levels of food intake on the growth and reproduction of fish and (iv) how this translates into fish population dynamics in combination with exploitation. Once developed, such an ecosystem model would require validation using observed patterns from field campaigns. The current study both provides the justification for carrying out such modelling exercises and highlights some of the data that would be required for validation. Developing such an ecosystem model is a major undertaking and is beyond the scope of the current paper.

In conclusion, this study indicates that bottom trawl fisheries may have a negative effect on the condition of some of its target species by reducing the abundance of their benthic prey. This may therefore indirectly affect the population size and growth rate of the target fish species, resulting in lower fishing yields. The effects of bottom trawls may be mitigated by switching to gears that do not affect prey availability, such as gill nets or long-lines. Bottom trawls were developed to increase the catches of demersal fish, and the question remains whether it is possible to efficiently exploit demersal fish population without such gears. If this is not possible, an alternative approach may be to minimize the area of the seabed fished by bottom trawls by creating 'trawl lanes' that are fished at a high frequency, while leaving the remaining seabed untrawled. As noted above, infaunal biomass responds in a non-linear way to trawling (Hiddink *et al.* 2006). The first trawl pass will cause a severe reduction in the infaunal biomass, but one additional trawl pass in areas that are already trawled frequently will cause only a small additional reduction in the infauna. Concentrating the same amount of bottom trawling on a smaller area of seabed will reduce the overall impact on benthic inverte-

brates, thereby minimizing the effects on fish species feeding on these prey.

Acknowledgements

Joan Moranta, Chris Coleby, Phil Hollyman, Lowri Evans, Fiona Read, Mandy Lo and the officers and crew of RV Prince Madog are thanked for their efforts during sampling. Melanie Bergmann and Michel Kaiser contributed to whiting stomach content analyses.

References

- Amezcuza, F., Nash, R.D.M. & Veale, L. (2003) Feeding habits of the order Pleuronectiformes and its relation to the sediment type in the North Irish Sea. *Journal of the Marine Biology Association of the United Kingdom*, **83**, 593–601.
- Auster, P.J. & Langton, R.W. (1999) The effects of fishing on fish habitat. *Fish Habitat: Essential Fish Habitat and Rehabilitation* (ed L.R. Benaka), pp. 150–187. American Fisheries Society, Hartford, Connecticut.
- Blanchard, J.L., Frank, K.T. & Simon, J.E. (2003) Effects of condition on fecundity and total egg production of eastern Scotian Shelf haddock (*Melanogrammus aeglefinus*). *Canadian Journal of Fisheries and Aquatic Sciences*, **60**, 321–332.
- Braber, L. & de Groot, S.J. (1973) The food of five flatfish species (Pleuronectiformes) in the southern North Sea. *Netherlands Journal of Sea Research*, **6**, 163–172.
- Brey, T. (2008) Population dynamics in benthic invertebrates. *A Virtual Handbook*. Version 01.2. <http://www.thomas-brey.de/science/virtualhandbook/navlog/index.html>. In: Alfred Wegener Institute for Polar and Marine Research, Germany.
- Bromley, P.J., Ravier, C. & Witthames, P.R. (2000) The influence of feeding regime on sexual maturation, fecundity and atresia in first time spawning turbot. *Journal of Fish Biology*, **56**, 264–278.
- Charnov, E.L. (1976) Optimal foraging, the marginal value theorem. *Theoretical population biology*, **9**, 129–136.
- Choi, J.S., Frank, K.T., Leggett, W.C. & Drinkwater, K. (2004) Transition to an alternate state in a continental shelf ecosystem. *Canadian Journal of Fisheries and Aquatic Sciences*, **61**, 505–510.
- Chopin, F. & Arimoto, T. (1995) The condition of fish escaping from fishing gears—a review. *Fisheries Research*, **21**, 315–327.
- Davidson, D. & Marshall, C.T. (2010) Are morphometric indices accurate indicators of stored energy in herring *Clupea harengus*? *Journal of Fish Biology*, **76**, 913–929.
- Dinmore, T.A., Duplisea, D.E., Rackham, B.D., Maxwell, D.L. & Jennings, S. (2003) Impact of a large-scale area closure on patterns of fishing disturbance and the consequences for benthic communities. *ICES Journal of Marine Science*, **60**, 371–380.
- Fogarty, M.J. (2005) Impacts of fishing activities on benthic habitat and carrying capacity: approaches to assessing and managing risk. *Benthic Habitats and the Effects of Fishing*, **41**, 769–784.
- Groenewold, S. & Fonds, M. (2000) Effects of benthic scavengers of discards and damaged benthos produced by the beam-trawl fishery in the southern North Sea. *ICES Journal of Marine Science*, **57**, 1395–1406.
- Hiddink, J.G., Jennings, S. & Kaiser, M.J. (2006) Indicators of the ecological impact of bottom-trawl disturbance on seabed communities. *Ecosystems*, **9**, 1190–1199.
- Hiddink, J.G., Rijnsdorp, A. & Piet, G. (2008) Can bottom trawling disturbance increase food production for a commercial fish species? *Canadian Journal of Fisheries and Aquatic Science*, **65**, 1393–1401.
- Hiddink, J.G., Jennings, S., Kaiser, M.J., Queirós, A.M., Duplisea, D.E. & Piet, G.J. (2006) Cumulative impacts of seabed trawl disturbance on benthic biomass, production and species richness in different habitats. *Canadian Journal of Fisheries and Aquatic Sciences*, **63**, 721–736.
- Hinz, H., Kröncke, I. & Ehrich, S. (2005) The feeding strategy of dab *Limanda limanda* in the southern North Sea: linking stomach contents to prey availability in the environment. *Journal of Fish Biology*, **67** (Suppl. B), 125–145.
- Hinz, H., Prieto, V. & Kaiser, M.J. (2009) Trawl disturbance on benthic communities: chronic effects and experimental predictions. *Ecological Applications*, **19**, 761–773.
- Holland, D.S. & Sutinen, J.G. (2000) Location choice in New England trawl fisheries: old habits die hard. *Land Economics*, **76**, 133–149.

- Hunter, E., Metcalfe, J. & Reynolds, J. (2003) Migration route and spawning area fidelity by North Sea plaice. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 2097.
- Hutchings, J.A. (2000) Collapse and recovery of marine fishes. *Nature*, **406**, 882–885.
- Jennings, S. & Kaiser, M.J. (1998) The effects of fishing on marine ecosystems. *Advances in Marine Biology*, **34**, 201–352.
- Jennings, S., Nicholson, M.D., Dinmore, T.A. & Lancaster, J. (2002) The effect of chronic trawling disturbance on the production of infaunal communities. *Marine Ecology Progress Series*, **243**, 251–260.
- Kaiser, M.J., Clarke, K.R., Hinz, H., Austen, M.C.V., Somerfield, P.J. & Karakassis, I. (2006) Global analysis and prediction of the response of benthic biota to fishing. *Marine Ecology Progress Series*, **311**, 1–14.
- Kennedy, J., Witthames, P.R., Nash, R.D.M. & Fox, C.J. (2008) Is fecundity in plaice (*Pleuronectes platessa* L.) down-regulated in response to reduced food intake during autumn? *Journal of Fish Biology*, **72**, 78–92.
- Link, J.S. (2002) What does ecosystem-based fisheries management mean? *Fisheries*, **27**, 18–21.
- Lloret, J., Demestre, M. & Sánchez-Pardo, J. (2007) Lipid reserves of red mullet (*Mullus barbatus*) during pre-spawning in the northwestern Mediterranean. *Scientia Marina*, **71**, 269–277.
- Lloret, J. & Planes, S. (2003) Condition, feeding and reproductive potential of white seabream *Diplodus sargus* as indicators of habitat quality and the effect of reserve protection in the northwestern Mediterranean. *Marine Ecology Progress Series*, **248**, 197–208.
- Marshall, C.T. & Frank, K.T. (1999) The effect of interannual variation in growth and condition on haddock recruitment. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 347–355.
- McPherson, L.R., Slotte, A., Kvamme, C., Meier, S. & Marshall, C.T. (2011) Inconsistencies in measurement of fish condition: a comparison of four indices of fat reserves for Atlantic herring (*Clupea harengus*). *ICES Journal of Marine Science*, **68**, 52–60.
- Pedersen, J. (1999) Diet comparison between pelagic and demersal whiting in the North Sea. *Journal of Fish Biology*, **55**, 1096–1113.
- Pinheiro, J.C. & Bates, D.M. (2000) *Mixed Effect Models in S and S-Plus*. Springer, New York.
- Rideout, R.M. & Rose, G.A. (2006) Suppression of reproduction in Atlantic cod *Gadus morhua*. *Marine Ecology Progress Series*, **320**, 267–277.
- Rijnsdorp, A.D. & Vingerhoed, B. (2001) Feeding of plaice *Pleuronectes platessa* L. and sole *Solea solea* (L.) in relation to the effects of bottom trawling. *Journal of Sea Research*, **45**, 219–229.
- Robichaud, D. & Rose, G.A. (2004) Migratory behaviour and range in Atlantic cod: inference from a century of tagging. *Fish and Fisheries*, **5**, 185–214.
- Shephard, S., Brophy, D. & Reid, D. (2010) Can bottom trawling indirectly diminish carrying capacity in a marine ecosystem? *Marine Biology*, **157**, 2375–2381.
- Tobin, D., Wright, P.J., Gibb, F.M. & Gibb, I.M. (2010) The importance of life stage to population connectivity in whiting (*Merlangius merlangus*) from the northern European shelf. *Marine Biology*, **157**, 1063–1073.
- Walters, C., Christensen, V., Martell, S. & Kitchell, J. (2005) Possible ecosystem impacts of applying MSY policies from single-species assessment. *ICES Journal of Marine Science*, **62**, 558.

Received 11 January 2011; accepted 3 June 2011

Handling Editor: Melanie Austen

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Prey size selection by whiting and dab.

Fig. S1. The size distribution of prey in the stomach contents of dab and whiting.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.