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Report on empirical and modelled small and large scale interactions between benthos, fish and trawl fisheries, focusing on the effect of trawling on fish condition

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SUMMARY

This report collates the work that has been carried out under Task 4.6. It brings together the results of several different studies that have examined the effect of bottom trawling on the food intake, condition and population productivity of trawled demersal fish populations. It combines the results of empirical and modelling studies, and synthesizes the available knowledge from the literature in order to give the most comprehensive overview of the topic so far.

Some effects of bottom trawling, both positive and negative, on the food intake and condition of commercial fished species was evident at local scales and in models, but such effects were not detected over larger spatial scales. The detected empirical effects at local scales were quite subtle. An effect that can be hard to detect at the local scale will be even weaker when viewed at the shelf sea scale. The effect on those populations that range widely will also be rather small and diffuse. As mentioned before, the effects can be both positive and negative, but there exists only little empirical evidence for positive effects. The models predict that the effects of trawling can be substantial and both positive and negative, but only under a limited set of conditions, at low trawling for species with specific diet. It seems that the flexibility of the diet of fish helps them in overcoming effects of trawling, especially when they can shift to less sensitive prey, which lead to increases in food availability.

In conclusion, the large amount of work done under this WP shows that there is no strong evidence to suggest that bottom trawling has substantial positive or negative effects on commercial fish populations by affecting their food supply.

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1 INTRODUCTION

Demersal fisheries using otter and beam trawls and scallop dredges are widespread, and typically use heavy ground ropes and chains to drive fish from the seabed into nets. Physical disturbance from such fisheries can cause significant changes in the seabed ecosystem. The ecological effects of bottom fishing with trawls and dredges on non-target benthic invertebrates have been summarized in review papers (Jennings and Kaiser 1998) and meta-analyses that quantify the mortality of benthic invertebrates in relation to fishing gear, depth, and sediment type (Collie et al. 2000, Kaiser et al. 2006). These studies found that the effects of bottom trawling on benthic invertebrates include reductions of biomass, diversity and body size, changes in the functional trait composition of the community, and that the effects are different between different gears and habitats.

These changes in the benthic ecosystems are conservation issues in themselves, but there is also ongoing concern that bottom fishing may impact the productivity of demersal fish species that depend on these habitats for food and shelter, such as cod, haddock and many species of flatfish (Auster and Langton 1999). Productivity is defined here as the rate of increase in the biomass of a fish population, and therefore directly relates to the potential yield of a fishery. For example, trawling may negatively affect prey availability, potentially leading to reduced food intake, body condition and therefore yield of fishes in chronically trawled areas. Removal of sessile epifauna, like sponges and corals, that provide refuges could also increase exposure of juvenile fish to predators. These indirect effects of trawling through changes in habitat and food availability occur next to the direct removal of target fish biomass that would occur with any fishing gear. For these indirect effects to be important, their negative effects on fish productivity would need to be larger than the effect of the release from competition caused by the reduction in fish stocks that any fishery causes. Here, we would like to assess how large the indirect effects of trawling on fish populations are, and whether they are important relative to the direct mortality of fish caused by exploitation.

This report brings together the results of several different studies that have examined the effect of bottom trawling on the food intake, condition and population productivity of trawled demersal fish populations. It combines the results of empirical and modelling studies, and synthesizes the available knowledge from the literature in order to give the most comprehensive overview of the topic so far.

SYNTHESIS OF THE LITERATURE

2 INDIRECT EFFECTS OF BOTTOM FISHING ON THE PRODUCTIVITY OF MARINE FISH

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2.1 Introduction

Demersal fisheries using otter and beam trawls and scallop dredges are widespread, and typically use heavy ground ropes and chains to drive fish from the seabed into nets. Physical disturbance from such fisheries can cause significant changes in the seabed ecosystem. The ecological effects of bottom fishing with trawls and dredges on non-target benthic invertebrates have been summarized in review papers (Jennings & Kaiser, 1998) and meta-analyses that quantify the mortality of benthic invertebrates in relation to fishing gear, depth, and sediment type (Collie *et al.*, 2000; Kaiser *et al.*, 2006). These studies found that the effects of bottom trawling on benthic invertebrates include reductions of biomass, diversity and body size, changes in the functional trait composition of the community, and that the effects are different between different gears and habitats.

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We present a review of both empirical and modeling studies of the indirect effects of bottom fishing on target species (mostly fish, but also crustaceans such as prawns and molluscs such as scallops). This review is structured around the main indirect mechanisms (Fig. 1) by which trawling could affect fish productivity. These are: by affecting 1) the habitat of the fish target species, 2) the abundance of fish predators of the target species, 3) the abundance of the prey of the target species, 4) through energy subsidies provided to the target species through discards and 5) through changes induced in primary productivity. We will examine the available modeled and empirical evidence in the literature, and use a heuristic model to compare the direction and magnitude of the indirect effects on habitat relative to the direct mortality. The effect of bottom trawling on the seabed depends on the habitat and the fishing gear that is used (Kaiser *et al.*, 2006), while the effect on the productivity of a fish is likely to depend on its habitat requirement, diet and predators. The ultimate objective of this work is therefore to be able to predict which habitats, fisheries, or target species are likely to experience important indirect effects of bottom fishing.

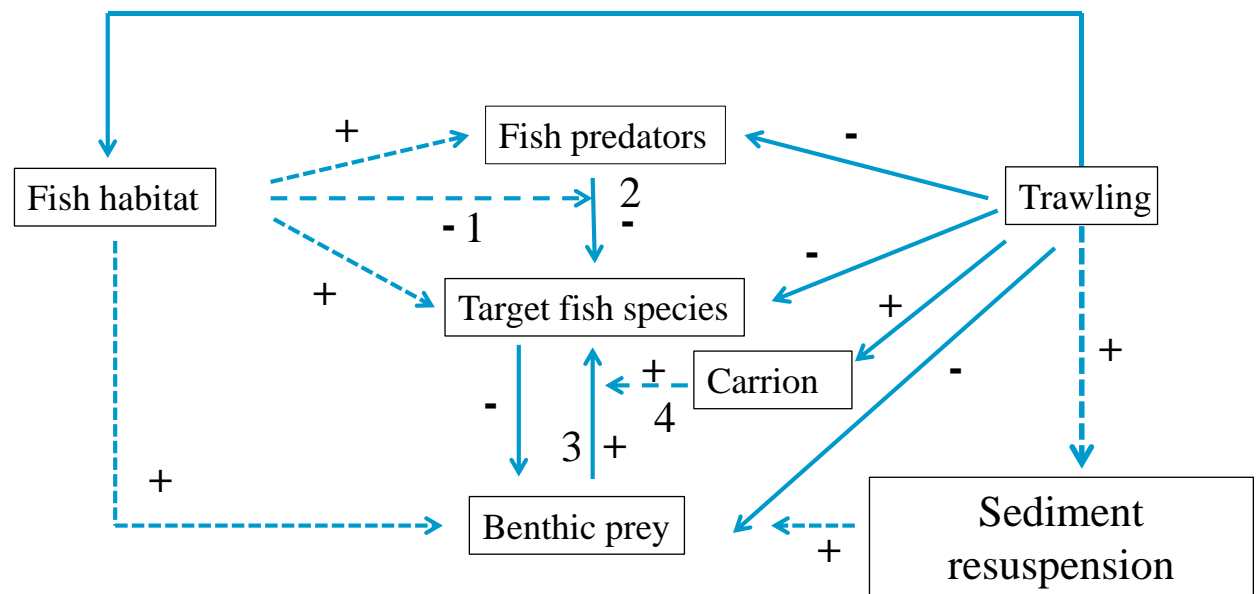


Figure 1. Schematic representation of the effects of trawling on different components of the ecosystem used for illustration in this study. Solid arrows are the known links between trawling and components of the ecosystem that could affect fish production. The dotted arrows indicate those effects of trawling for which there is some qualitative support in the published literature. Numbers indicate the section in which the link is discussed. + and – indicate the direction of the effect, some effects can have both positive and negative effects.

2.2 Effects of bottom fishing on fish refugia and habitat extent

Bottom trawls can affect habitat structure through the removal of sessile epifaunal like soft corals, hydroids and sponges, and can cause changes in the sediment composition and relief. Such changes can be hypothesized to reduce the amount of shelter available for fish, or the extent of suitable habitats (Auster & Langton, 1999; Lindholm *et al.*, 2014). Benthic epifauna stabilize the sediment and provide three-dimensional structure to an otherwise two-dimensional seafloor. These epifaunal species also harbor benthic invertebrates, which are the prey of demersal fish species (see section 3). To varying degrees, these habitat features are sensitive to bottom trawling and dredging (Auster and Langton 1999). Commercially important fish and shellfish species use benthic habitats in different ways and at different stages in the life cycle. There are many studies that show that fished species depend on these benthic habitat features that may be affected by bottom trawling, of which we give some examples here. Some pelagic species, such as herring *Clupea harengus*, have demersal eggs that require substrates with sufficient aeration to ensure development. Scallops and oysters require a gravel or shell or filamentous hydroids substrate for the settlement, attachment, and survival of their juveniles. Silver hake *Merluccius bilinearis* juveniles orient to sand waves to maintain a hydrodynamic advantage (Auster *et al.*, 1997) The preference of many demersal fish and invertebrate species for complex habitats is thought to confer a survival advantage, especially for the vulnerable juvenile stages. Juvenile Atlantic cod, *Gadus morhua*, are most abundant on cobble substrates, where their mottled coloration makes them less visible to predators (Lough *et al.*, 1989; Gotceitas & Brown, 1993; Tupper & Boutilier, 1995). As the cod age, habitat associations persist but become more facultative as their vulnerability to predation decreases with size (Gregory & Anderson, 1997). Plaice *Pleuronectes platessa* densities correlated with the abundance of emergent tube-dwelling polychaetes, which are a valuable food source for plaice and sensitive to bottom trawling (Shucksmith *et al.*, 2006).

Studies directly relating fish habitat availability with bottom trawling impacts are scarce and outlined below. A large-scale experiment was conducted on the northwest shelf of Australia to test the relative importance of inter-specific interactions, intra-specific interactions, and trawl-induced modification of

benthic habitats in regulating the species composition of the fish community (Sainsbury, 1991). The experiment consisted of sequentially closing two areas to bottom trawling, while leaving a third area open. The experimental results most strongly supported the benthic-habitat hypothesis, that trawl-induced modification of benthic habitats regulates the species composition of the fish community (Sainsbury *et al.*, 1997). After five years of closure, the percent cover of benthic epifauna increased, along with the catch rate of two snappers. The cover of large sponges increased slowly, suggesting recovery times of decades. Laboratory experiments conducted by (Lindholm *et al.*, 1999) indicated higher survival of Atlantic cod in habitats with epifaunal cover. A follow-up modeling study linked trawling disturbance to habitat to population-level effects on cod survival (Lindholm *et al.*, 2001). They found the effect of habitat disturbance to be more pronounced when the cod stock was at low abundance, such that the available nursery habitat was not saturated. In this scenario, habitat disturbance would create an additional source of mortality on a depleted cod stock, which could delay its recovery.

In summary, there are many studies that show that fish rely on habitats that may be affected by trawling, but the number of studies that have explicitly studied the effect of bottom trawling on habitat availability for target fish species is very limited.

2.3 Effects of bottom fishing on the predators of target species

In mixed-species fisheries, bottom trawls can reduce the abundance of predator species, thereby enhancing the productivity of prey species. Because bottom trawls are size selective, larger predator species have a higher catchability than smaller prey species. This size selectivity, combined with the fact that small species have higher intrinsic rates of increase than larger ones, means that prey species can indirectly benefit from fishing their predators. There are many examples of prey increases due to declining abundances of predatory fish stocks; for example in open ocean ecosystem of the Central Pacific the abundance of small pelagic stingrays increased as the abundance of their large shark predators decreased (Ward & Myers). Here we consider only the special case in which both predator and prey are caught by the same bottom fishing gear and the prey is a target species, while the predator is caught as a non-target or bycatch species. We will not consider effects that are simply the result of prey release as a result of predator exploitation. Section 1 showed that one of the main roles of seabed habitat is as a refuge from predation. If predators are fished down however, the presence of a habitat refuge may no longer be important. In section 5, we explore this phenomenon with simple models; first we examine the empirical evidence.

There are examples of trawl fisheries that catch the prey and predator simultaneously, but none of these studies have quantified the magnitude of such effects on the target, prey, species. For example, in the Gulf of Mexico, shrimp fisheries have a large bycatch of red snapper, which prey on juvenile shrimp (Gallaway & Cole, 1999). Sea stars prey on scallops and are also killed by trawls and dredges (Jenkins *et al* 2001). If their mortality per unit effect exceeds that of the scallops, the scallops would receive an indirect benefit. Another example of such a system is the otter trawl fishery for the Norway lobster *Nephrops norvegicus*, which has a large bycatch of their predator cod *Gadus morhua* (Valentinsson & Ulmestrand, 2008).

In summary, there is evidence that target species of fish and invertebrates benefit from reduced mortality when their predators are also captured by bottom trawls. The magnitude of this benefit depends on the relative catchability and rate of increase of prey and predator species. Prey and predator species are typically targeted by different fishing fleets with specific gears, such that the degree of overlap in mixed-species trawl fisheries amounts to bycatch of one species or the other.

2.4 Effects of bottom fishing on fish prey resources

The effects of bottom trawling on the availability and quality of prey resources for fish predators have been inferred from a number of studies that have studied the diet composition of fish sampled from

trawled areas and areas subjected to lower levels of trawl impact or across a gradient of trawl disturbance. The potential prey available to predatory fish can be altered in the short term through the carrion or displaced biota that occur as a result of the direct physical disturbance created immediately within the wake of towed bottom fishing gear. These short term effects are covered in the next section and are distinct from the larger-scale consequences of fishing patches of seabed at the scale of 10s km. At this scale, chronic and frequent fishing can lead to wide-spread depletion of benthic invertebrate prey species (Hiddink *et al.*; Hinz *et al.*). This leads to the possibility that fish that occur within these prey depleted patches persist in a food impoverished environment for prolonged periods of time, particularly if their movement is limited. Furthermore, sporadic fishing within these areas may serve to retain the fish within these areas if they are attracted to the short term pulses of carrion generated. The degradation of the prey resource could occur via three pathways: 1) a simple reduction in abundance and biomass of prey, 2) a reduction in prey energy density (J g^{-1} prey) or 3) an increase in energetic costs associated with foraging to maintain a constant level of stomach fullness and energy content.

A number of studies provide evidence to support different aspects of these pathways. (Lloret *et al.*) examined lipid content of the muscle tissue of red mullet *Mullus barbatus* and the prey availability in trawled and untrawled areas. They found that polychaete prey biomass and abundance was lowest in trawled areas and that the red mullet from these areas had lower lipid reserves and hence body condition. Similarly, (Hiddink *et al.*) found that the condition of a flatfish (plaice *Pleuronectes platessa*) was negatively related to trawling frequency. The observed reduction in condition was explained by a reduced production of the infaunal invertebrates upon which the plaice feed. Importantly, (Hiddink *et al.*) were able to disentangle this observation from potential density-dependent changes in competition over food. While plaice were affected by the reduction in prey biomass, other more generalist species such as dab *Limanda limanda* or piscivorous species such as whiting *Merlangius merlangus* were not affected by the reduced benthic biomass in heavily trawled areas of the seabed. Shephard *et al.* (2010) observed similar responses for plaice in the Celtic Sea, observing declines in the length-at-age in gravel, but not sand, habitats. Plaice in the gravel habitats typically feed on more fragile fauna that (such as echinoderms and bivalves) that are more susceptible to trawling. The most insightful study to date is that of (Johnson *et al.*) that showed that flatfish were able to maintain their stomach fullness despite the reduction of local prey biomass and abundance. However these fish had reduced body condition, which is most likely explained by the additional energetic costs of searching in a reduced prey field. Dell *et al.* (2013) also found differences in the composition of the diet of eight fish species between low and high fishing intensity areas in a tropical prawn fishery, and also found that stomach fullness did not differ between low and high trawling areas.

An alternative hypothesis, which is endorsed by fishermen, is that bottom trawling “farms the sea”. Bottom trawling may benefit the small benthic invertebrates as form the food source for exploited flatfish by removing the large fauna that small benthos compete with over food and space and that bottom trawling therefore has a positive effect on food production for species that eat small worms. A comparison of fish diets between a high- and low-trawling area in Monterey Bay found that the abundance of an opportunistic worm species was higher at high trawling, and that incidence of this important prey item in the diet of some flatfish species increased at high trawling (Engel & Kvitek, 1998). However, Jennings *et al.* (2002) found no change in the biomass of small infaunal polychaetes with chronic trawling and concluded that beam trawling disturbance does not have a positive or negative effect on their food supply for flatfish. Beyond these observations, no empirical datasets are available to test this hypothesis, but a modelling study by Hiddink *et al.* (2008a) indicates that the production of small invertebrate prey was low without trawling and maximal in areas that are trawled once to twice a year. Therefore, modelling suggests that bottom disturbance may improve the feeding conditions for species that feed on small invertebrates.

In summary, there is empirical evidence that shows that bottom trawling reduces the availability of food for commercial fish species, while there is little support for increases in food production at low trawling intensities.

2.5 Energy subsidies generated by bottom fishing

The assemblage of potential prey available to predatory fish can be altered in the short term through the carrion or displaced biota that occur as a result of the direct physical disturbance created immediately within the wake of towed bottom fishing gear. The chemical cues released from the damaged tissue of biota in the trawl path and cues generated as the gear passes across the seabed (sediment clouds, noise from ground gear) attract fish from the surrounding area to feed on the carrion.

Although there have considerable improvements in the selectivity of some bottom trawls, the retention of by-catch of both fish and invertebrates remains a considerable challenge. The non-target fish species and benthic invertebrates that are retained in the net are discarded with variable survival thereafter, which is affected by the context of the fishing gear and the prevalent environmental conditions (Kaiser & Spencer, 1995). Offal that results from gutting the fish at sea is also discarded. In most places scavenging seabirds eat approximately 99% of the offal and 90% of the discarded roundfish (Garthe *et al.*, 1996). Most of the other material that is discarded becomes available as a potential food subsidy to demersal fish and other scavengers (Garthe *et al.*, 1996). In addition to the material generated from discarding of by-catches, bottom towed fishing gears also kill variable fractions of the benthic invertebrates that live on the seabed (generally around 20-50% (Kaiser *et al.*, 2006) and in addition may expose infaunal invertebrates that are normally unavailable to fish predators. For example, Rumohr & Krost (1991) reported the flesh of the clam *Arctica islandica* in the stomachs of cod collected in the vicinity of trawling activity, while (Link & Almeida, 2002) found that longhorn sculpins *Myoxocephalus octodecemspinosus* fed on the tissues of scallops in areas subjected to scallop dredging. This material may be an important food source for scavenging fish and invertebrates if normal sources of food are limiting.

The food subsidies generated by towed bottom fishing gears flow to scavenging seabirds (Garthe *et al.*, 1996), marine mammals and pelagic fish (Hill & Wassenberg, 2000), demersal fish and benthic invertebrates (Groenewold & Fonds, 2000). Past studies have shown that this material contributes significantly to the food intake of seabirds in some areas, and has resulted in an increase in seabirds populations and foraging behaviour (Garthe *et al.*, 1996). A single disturbance event from a beam trawl pass can generate enough food to meet the energetic requirements of local benthic scavenger populations for 5-21 days (Groenewold & Fonds, 2000). These short-term effects area can lead to higher concentrations of fish within the trawl path for a period of 24-72 h after the initial impact (Kaiser and Spencer 1994; Fonds and Groenewold 2000; Demestre et al. 2000). Studies have identified and/or quantified scavenging behaviour and increases in food consumption in relation to trawl disturbance in flatfish, gadoids, sharks, snappers, gurnards, sea scorpions, dragonets, nemipterids (Kaiser & Spencer, 1994, 1996; Kaiser & Ramsay, 1997; Groenewold & Fonds, 2000; Hill & Wassenberg, 2000). This section attempts to estimate the importance of this food subsidy for demersal fish species.

We assume that the physiological importance of scavenging on trawl catches depends on what fraction of the energy requirements of fish is made up by this scavenging activity. This importance is likely to depend on the following factors:

- The frequency of trawling in an area;
- The attraction area over which a fish can detect an area of trawl disturbance;
- The capability of the fish to respond to and locate the trawl disturbed area;
- The amount of additional food a fish eats after a trawling event once in the trawled area;
- The suitability and energy density of the carrion or prey made available;
- The physiological processing time required to digest and assimilate the energy.

The frequency of trawling is routinely calculated from VMS records (Lambert *et al.*, 2012), but the attraction area and the amount of discards eaten have only been quantified in a few studies. Studies that examined the importance of scavenging on trawl discards usually examine the

abundance fish and/or their stomach contents at different time intervals before and after experimentally trawling an area of one to tens of thousands of m², and sometimes also in control areas (Kaiser & Spencer, 1994; Kaiser & Ramsay, 1997).

Here, we assume that attraction area can be estimated from the increase in the abundance of fish in the trawled area after fishing. For example, if the abundance of a fish in the trawled area increases by a factor three after trawling, then (if catchability remained constant), it can be assumed that fish immigrated from an area that was three times larger than the experimentally trawled area, and the distance over which fish are attracted therefore can be estimated. This assumes that *all* the fish from the adjacent area move into the trawled area.

We found five studies that examined changes in the abundance of five fish species (Kaiser & Spencer, 1994, 1996; Kaiser & Ramsay, 1997; Demestre *et al.*, 2000; Groenewold & Fonds, 2000), and three that examined the stomach contents of fish before and after trawling (Kaiser & Spencer, 1994; Kaiser & Ramsay, 1997; Groenewold & Fonds, 2000) for ten fish species. From each of these studies, we extracted the time at which the fish were sampled relative to the experimental trawling, and their abundance or a measure of stomach fullness. Because we extracted values for different species of fish in different areas, all measures were standardized to the mean of all untrawled stomachs/abundances, either before trawling or in control areas, and log-transformed to centre no-responses around zero.

Fish stomach contents in the trawled areas increased to a peak that was 1.65 times greater than ambient stomach contents 20h after the trawl disturbance occurred and returned to their ambient stomach contents three days post trawl disturbance (Figure 3a). The total area under the curve represents the total amount of extra food eaten over the studied period and equals a subsidy of 1.16 relative to 'normal' stomach contents.

Fish that immigrated into the trawled area reached a peak in abundance that was 1.42 times the ambient abundance after 30h, and returned to ambient abundance within 3 days (Figure 3b). If we assume that fish do not leave the trawl disturbed area after they have reached satiation, the total area under the curve represents the total quantity of additional fish present over the studied period and equals an additional presence of 0.60 'normal' fish densities. The reported experimentally trawled areas had a width of 30-35m, this indicates that the attraction area is very small at around 0.6 times this width, c. 50m. These estimates of attraction area are in the same order of magnitude as values from the literature for baited cameras and traps (Sainte-Marie & Hargrave, 1987; Groenewold & Fonds, 2000) (Bozzano & SardÀ 2002), but much smaller than for seabirds, which range from 3 km to 8.5 km (Skov & Durinck, 2001). Taken together, these values indicate that a trawled area supported 1.6 times the normal number of fish and that all fish present consumed 2.16 times the amount of normally ingested food. Our approach here is very simplistic and is only aimed at giving an order of magnitude estimate of the importance of scavenging in the diet of these fish species.

The next step is to estimate how often a trawl passes within 50m of a fish over the course of a year. As the estimated attraction area is much smaller than the cell size that is generally used for estimating bottom trawling effort using VMS (>1 nm²), the vast majority of fish will not cross from one cell to the next in attraction to trawl paths, and the local trawling effort in a cell will therefore be the relevant effort for a fish. A typical trawling frequency for a cell will be once a year, while about 30% of the seabed will remain unfished, while some areas will be fished >10 times a year (Hiddink *et al.*, 2006). If we assume that an area is trawled once a year, trawling effort is distributed homogenously in a cell, and tracks lie parallel, and are 50m wide, there would be at most two trawl tracks within the attraction area of a fish over the course of a year. As a fish can eat 2.16 times more than normally after trawling, trawling activity would be equivalent to a very modest 4.3 extra days of food, or 1.2% of their normal annual energy budget. If we use the actual distribution of bottom trawling effort in the North Sea in 2003 (Hiddink *et al.*, 2006), this would translate into an extra 6.0 days of food for the average fish (interquantile range 0.13 – 6.2 days). This suggests that the contribution of carrion to the diet of fish is limited, even in the most heavily trawled areas.

It is not clear to what extent these short-term increases in food intake are offset by long-term decreases in the abundance of prey due to the trawl impact on invertebrates. Using a different approach, (Kaiser & Hiddink, 2007) estimated that the production of carrion only compensates for 22% of the reduction in production at the seabed. However, if bottom trawling makes prey that are normally outside the limits of a predator's capabilities (such as large clams), bottom trawling may increase the production of food for demersal fish. Two studies that used stable isotope analyses to examine if a scavenging signature could

be detected in demersal fish, found some evidence of the importance of scavenging in the diets of whiting *Merlangius merlangus* and megrim *Lepidorhombus whiffiagonis*, but no effect for a range of other species (Badalamenti *et al.*, 2008; Shephard *et al.*, 2013). In conclusion, scavenging on carrion generated by trawling makes a positive but small contribution to the diets of demersal fish.

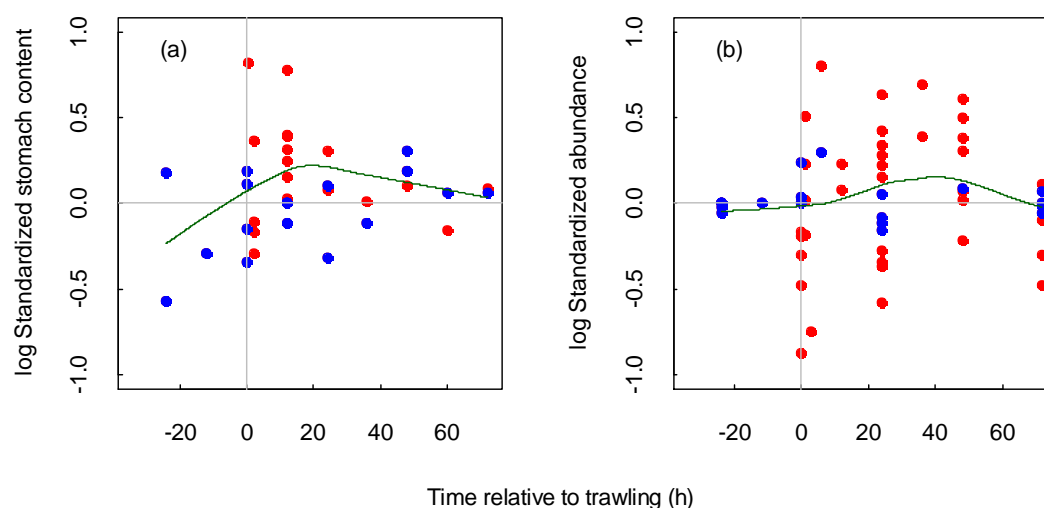


Figure 2. The relative changes in abundance (a) and stomach content (b) of fish before and after bottom trawling. Blue points indicate samples before trawling and in control areas, while red points indicate samples after trawling in the trawled area. The black line is the fitted loess smoother through the before-trawling points and red after-trawling points.

2.6 Sediment resuspension and primary production

Sediment resuspension due to bottom trawling is most significant in deeper areas with softer sediments where levels of natural disturbance due to wave and tidal action are low (Duplisea *et al.*, 2001). Bottom trawling has been shown to enhance sediment resuspension with measured concentrations up to 500 mg l^{-1} being much larger than the concentrations resuspended by natural events (de Madron *et al.*, 2005; Tjensvoll *et al.*, 2013). Because finer particles will be brought into suspension more quickly and will sink more slowly, trawling modifies the physical properties of the sediment (de Madron *et al.*, 2005); (O'Neill & Summerbell, 2011). Chronically trawled sediments along the continental slope of the north-western Mediterranean Sea are characterized by significant decreases in organic matter content (Pusceddu *et al.*, 2014). For example, a strong decrease in the mud fraction and an increase in the fine sand fraction was observed over a period of 35 years in the sediments of the Bay of Biscay (Hily *et al.*, 2008). Sediment resuspended as a result of bottom fishing will have a variety of effects including: the release of nutrients held in the sediment (Duplisea *et al.*, 2002), exposure of anoxic layers, release of contaminants, increasing biological oxygen demand (Reimann and Hoffman 1991), smothering of feeding and respiratory organs. Suspension feeders may however also benefit from enhanced levels of POM as shown for scallops (*Placopecten magellanicus*) on Georges Bank (Grant *et al.*, 1997). Resuspension events occurred with sufficient frequency, and the residence time of the resuspended sediment was long enough to provide a consistent nutritional benefit. Deposit feeding benthos may be negatively affected by trawling due to a loss of surficial sediments and a reduction of the food quality (Mayer *et al.*, 1991; Watling *et al.*,

2001). Sediment resuspension by trawling, in particular its effect on particulate organic matter (POM), may have important trophodynamic consequences as it may affect the availability and quality of food for suspension feeding and deposit feeding benthos. This can therefore indirectly increase or decrease the amount of food that is available to fish populations.

The release of nutrients from the sediment may stimulate primary production, while increased turbidity because of suspended sediment may decrease primary production. Current evidence from models suggests that this may have a fairly limited effect on overall primary production (Allen & Clarke, 2007).

2.7 The effect of bottom trawls on fish productivity

In the previous sections we examined the mechanisms, in this section examines if there is direct evidence to support the hypothesis that bottom trawling can change the productivity of fish populations. Changes in fish condition, growth and population size may become apparent if the productivity of fish populations is affected by trawling, but changes in fish productivity are hard to detect because of the high natural variation in recruitment of commercial fish populations. A second problem is that fish will be selective feeders and not all benthic species will be vulnerable to trawling. Hence, the response will depend on this selectivity in combination with the specific response of the preferred food to the effect of trawling.

The body of empirical evidence for these effects is rather limited. Most studies have examined the effect on the condition, growth or length-at-age of flatfish. Even within this taxonomic group, evidence is pointing in opposite directions for different species and populations. In the Irish Sea, the relative weight and length-at-age of plaice was lower in more heavily trawled areas on gravel and mud but was higher on sand (Shephard *et al.*, 2010; Hiddink *et al.*, 2011b). In the North Sea, a sand dominated sea, an apparent positive effect of beam trawling on the growth rates of plaice (Rijnsdorp & van Leeuwen, 1996) seems to have disappeared in recent years (Beare *et al.*, 2013). Beam-trawl effort in the North Sea was positively correlated to length-at-age and growth of sole *Solea solea* (Millner & Whiting, 1996) (De Veen, 1976). This work suggest that flatfish on sand may benefit from light trawling levels, but that higher intensity trawling on more vulnerable habitats will have a negative effect. Two studies in other areas and on other species, found negative correlations between the intensity of bottom trawling and the muscle lipid levels of red mullet *Mullus barbatus* (Lloret *et al.*, 2007) and the lengths of haddock *Melanogrammus aeglefinus*, Atlantic cod *Gadus morhua* and winter flounder *Pseudopleuronectes americanus* (Smith *et al.*, 2013).

On longer time-scales, comparison of the growth patterns between modern (AD 1984–1999) and historical otoliths (AD 1200–1925) revealed a major increase in growth rate of haddock, whereas growth changes were not observed in saithe *Polachius virens* and only in the smaller size classes of plaice and cod (Bolle *et al.*, 2004). These observed growth rate changes in plaice and cod occurred within the 20th century and coincided with increase in trawling impact on the benthos, which may have enhanced the productivity of opportunistic benthic species. However, a simultaneous increase in eutrophication of the North Sea occurred and the effect of trawling and eutrophication are hard to disentangle. Alternatively a depletion of these stocks have resulted in more benthic food per fish.

Modelling approaches have been used to explain these empirical patterns (Hiddink *et al.*, 2008b; van Denderen *et al.*, 2013). The models show that the interactions between different species of

benthic invertebrates (differences in their sensitivity to and recovery from trawling disturbance) and the food selection of fish species (do they eat sensitive or resilient benthos?) are key for understanding the effect of bottom trawling on fish food intake. Van Denderen *et al.* (van Denderen *et al.*, 2013) showed that the ecosystem response to trawling depends on whether the abundance of benthos is top-down or bottom-up controlled. Fishing may result in higher fish abundance when the benthos that is the best-quality fish food is also much more resistant to trawling than non-preferred food. These positive effects occur in bottom-up controlled systems and systems with limited impact of fish feeding on benthos, resembling bottom-up control. Fishing leads to lower yields and fish persistence in all configurations where susceptible benthos are more profitable prey. A model by Hiddink *et al.* (Hiddink *et al.*, 2008b) showed that only low levels of trawling may result in an increase in the productivity of small polychaetes, but that higher trawling frequencies result in a lower benthic production in all size classes and functional groups.

In conclusion, the effect of trawling of fish productivity is likely to depend on the species' feeding habits and the environmental conditions. There is a body of evidence that suggests that flatfish living in naturally disturbed sandy habitats may benefit from low levels of bottom disturbance, but that in other species, in other habitats, and at higher levels of trawling fish productivity is negatively affected.

2.8 Discussion

The evidence presented in the preceding sections shows that are several mechanisms through which bottom trawling can affect the productivity of exploited fish populations. The direction and magnitude of these different effects are different. The empirical evidence supporting the hypothesis that bottom trawling reduces the productivity of fish populations is very limited, and as many studies recording positive as negative effects were found. It is possible that the different mechanisms are cancelling each other out. The ultimate objective of this work was to be able to predict which habitats, fisheries, or target species are likely to experience important indirect effects of bottom fishing. It seems that we have only achieved this objective to a limited degree. The general pattern seems to be that the effects on bottom trawling on fish productivity are negative but small, but that the effects of low levels of trawling could be positive for flatfish on sandy bottoms.

Fisheries that are currently persisting a high yield must be exploiting species that are able to withstand both the direct and indirect effects of exploitation. If they were not, the fishery would have collapsed. As such, indirect trawling effects on productivity of currently exploited populations are unlikely to be severe as in such situations the population would have collapsed long ago. In fact, species that have been coping well with exploitation using bottom trawls, such as plaice *Pleuronectes platessa*, may have benefited from trawling though increases in their food supply, while having little reliance on complex refuges as they bury in the sediment for taking cover (Brown & Trebilco, 2014). In contrast, some species are exploited using trawls and have experienced population collapses, for example cod *Gadus morhua*, ling *Molva molva* and spurdog *Squalus acanthias* (Greenstreet & Hall, 1996; Choi *et al.*, 2004). These species eat benthic invertebrates as juveniles and could be negatively affected when young, but all of these species are piscivores as adults (<http://www.fishbase.org>). Nevertheless, the juveniles of these species may depend on habitat complexity for refuges from predation. It is therefore far from evident that the indirect effects of bottom trawling have played any role in the collapse of these species as it is much more likely that the direct effects of exploitation caused the declines.

2.8.1 Simultaneous reductions in carrying capacity and fish population size

Exploitation of a target fish populations is always going to result in a decrease in the population size. Fisheries ecology assumes that the subsequent reduction in competition over resources leads to an increased growth of the remaining fish and results in a surplus production of fish that can be sustainably harvested. Any reductions in the availability of benthic food and refuge for commercial fish as a result of bottom trawling are therefore occurring simultaneous to a decline in the requirement for these resources. As the energy requirement per gram of body weight of small fish is higher than for larger fish (), the energy requirements will decline less than the biomass of the fish stock, but there will be a decline in energy requirements nevertheless. If the effect of bottom trawling on the target species is larger than the effect on the resources they need (which is possible when the 'catchability' of the fish is higher than that of the benthic invertebrates, or when recovery of the benthic invertebrates is faster), an increase in the amount of prey available per fish is possible, and increasing growth of fish with increasing bottom trawling can be expected. In such situations bottom trawling may still reduce the productivity of commercial fish stocks relative to a situation where the fish are exploited using other techniques, but this effect will be impossible to detect using current techniques. Similar reasoning can also be applied to the provision of refuge by benthic fauna, but with the added effect that the abundance of predators may be reduced and therefore the requirement for refuges may be reduced too.

A proper assessment of how benthic food production changes with exploitation requires a quantification of benthic production dynamics including any top-down effects of fish predation on benthos. Most studies that have examined the effect of bottom trawling on benthic production have estimated production using production to biomass ratios to convert measured body sizes into production estimates (Hiddink *et al.*, 2006), but such an approach is not suitable for detecting these subtle effects because it cannot capture the effect of density-dependent growth on production. Instead, benthic production will need to be measured using repeated sampling for each benthic species present in the community separately.

Density-dependent increases in growth occur in trawled fish populations would suggest that these indirect trawling effects are relatively unimportant. Intriguingly, (Lorenzen & Enberg, 2002) found evidence for density-dependent growth in only 2 out of 7 bottom-trawled fish stocks, while they found evidence for density-dependent growth in 7 out of 9 other fish stocks.

2.8.2 The spatial scale of trawling, the spatial scale of the fisheries, and top-down effects

Most studies that have sampled benthic invertebrates over gradients of commercial bottom trawling intensities within areas with homogeneous habitat (<100 km) have found a decline in the biomass of benthic invertebrates with increasing trawling (Engel & Kvitek, 1998; Hiddink *et al.*, 2006). These observations apparently conflict with the model outputs in section 7 that predict an increase in benthic invertebrates with more bottom trawling. This apparent contradiction can occur in systems where benthos can increase in abundance when it is released from predation by fish, when the fish is reduced in abundance by trawling. A second requirement is that the fish populations are more mobile than their benthic prey. In such a situation, the fishery affects the fish populations at the scale of the population, while the benthos is affected locally, at the scale of a trawl (Figure 3). Heath (2005) showed using data from the North Sea that the depletion of demersal fish species may have released the benthos from predation pressure, and leading to an increase in benthic production. There is currently no consensus on whether a reduction in fish predation can result in an increase of benthic invertebrates. This

is obviously an important question to answer because if it is it is very unlikely that bottom trawling will indirectly reduce the productivity of fish.

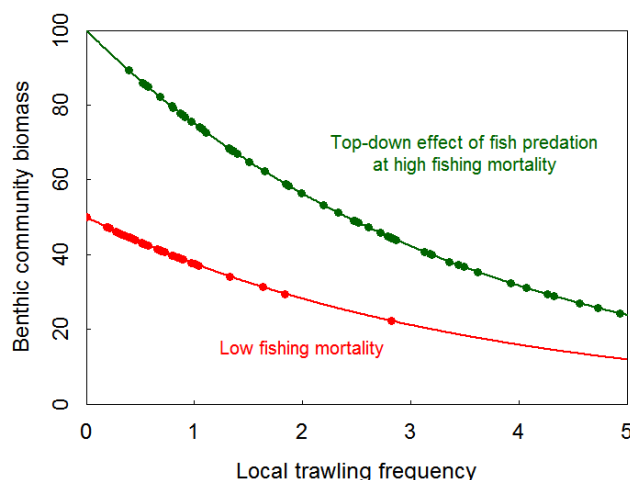


Figure 3. The hypothesized relationship between trawling frequency and benthic invertebrate biomass in top-down and bottom-up controlled ecosystems. Bottom trawling reduces the abundance of benthic invertebrates in the trawl path. The abundance of the target fish species is also reduced by trawling activity, but because fish are mobile, fish abundance is reduced at larger spatial scales than benthos abundance. In a top-down controlled ecosystem, where high levels of fish predation suppress the abundance of benthic invertebrates, a high fishing mortality on fish will release benthic invertebrates from top-down control and the overall abundance of benthos will therefore increase. As a result of this, a negative relationship will still exist between trawling frequency and benthic biomass at local scales, but the relationship will be at a higher level than in a situation with a low fishing mortality. If fish predation does not reduce the abundance of benthos (bottom-up control), the relationship between benthic biomass and trawling frequency will not change with increasing fishing mortality. The data points on the lines illustrate what the distribution of benthic biomasses could be at high and low fishing mortality (assuming spatial variation in the actual trawling frequencies but a higher mean trawling frequency in the high fishing mortality situation). This illustrates that benthic biomass could increase, under specific conditions, on a regional scale even when bottom trawling kills benthic invertebrates.

2.8.3 The way forward

Both costs and benefits of bottom fishing to fish populations have been highlighted, but impacts and consequences depend on the scale and intensity of fishing, the habitats affected and the objectives of conservation and fisheries management. We show that current debate would be better informed and contribute more to management if studies of predominantly local impacts could be scaled-up to assess their collective effects on populations, fisheries and ecosystems. This would contribute to identifying thresholds for acceptable intensities and distributions of disturbance given different management and conservation goals.

Given that we have not come up with a clear answer, there are several remaining challenges. A first challenge is to get a better handle on strength of top-down effects of fish predation on benthos. Without this it is impossible to assess whether food availability per fish will increase or decrease with bottom trawling. In addition to this, a second challenge is that we need empirical evidence to test if there is ever an increase in food abundance for fish at low levels of trawling at local scales. Thirdly, it is necessary to study how the density-dependence of growth varies with different levels of trawling intensity for

benthivorous fish. This would elucidate how the interaction of the depletion of food sources of fish by trawling and reduction in the predation pressure on benthos by depletion of the fish affect fish growth. Such an analysis will show whether or not exploitation with trawls leads to increase in growth that is anticipated in fisheries models, if it does not this is a sign that trawling erodes the ability of the ecosystem to support the fishery.

2.9 Conclusions

In conclusion, bottom trawling causes a high level of mortality to benthic fauna, especially emergent epifauna. In most cases, the indirect effects of bottom fishing on target fish species seem small compared with the direct effects. Historically, trawling may have modified habitat and reduced the carrying capacity. For fish species that depend on benthic fauna this epifauna for food and shelter, productivity and hence sustainable harvest may decline with increasing levels of bottom fishing disturbance. In some cases, these disturbance effects can be traced to changes in the feeding and growth of demersal flatfish. In most cases these indirect effects are small compared with the direct mortality cause by fishing. A likely possible explanation for this is that the distribution of fishing effort is very patchy—small fractions of fishing grounds are heavily fished, while large fractions are lightly fished or unfished. The indirect effects of bottom fishing are therefore also likely to be localized, for example to flatfish species living on vulnerable habitats. This would suggest that management measures that minimize the footprint of fishing will lead to higher yields than measures that spread fishing activity more widely and evenly across the seabed.

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MODELLING STUDIES

3 WHEN DOES FISHING LEAD TO MORE FISH? COMMUNITY CONSEQUENCES OF BOTTOM TRAWL FISHERIES IN DEMERSAL FOOD WEBS

P. Daniel van Denderen, Tobias van Kooten and Adriaan D. Rijnsdorp

Abstract

Bottom trawls are a globally used fishing gear that physically disturb the seabed and kill non-target organisms, including those that are food for the targeted fish species. There are indications that ensuing changes to the benthic invertebrate community may increase the availability of food and promote growth and even fisheries yield of target fish species. If and how this occurs is the subject of ongoing debate, with evidence both in favour and against. We model the effects of trawling on a simple ecosystem of benthivorous fish and two food populations (benthos), susceptible and resistant to trawling. We show that the ecosystem response to trawling depends on whether the abundance of benthos is top-down or bottom-up controlled. Fishing may result in higher fish abundance, higher (maximum sustainable) yield and increased persistence of fish when the benthos which is the best-quality fish food is also more resistant to trawling. These positive effects occur in bottom-up controlled systems and systems with limited impact of fish feeding on benthos, resembling bottom-up control. Fishing leads to lower yields and fish persistence in all configurations where susceptible benthos are more profitable prey. Our results highlight the importance of mechanistic ecosystem knowledge as a requirement for successful management.

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

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A copy of the paper is available on the BENTHIS website.

EMPIRICAL STUDIES

4 EFFECTS OF BOTTOM TRAWLING ON FISH FORAGING AND FEEDING

Johnson, A.F., Gorelli, G., Jenkins, S.R., Hiddink, J.G., and Hinz, H.

Abstract

The effects of bottom trawling on benthic invertebrates include reductions of biomass, diversity and body size. These changes may negatively affect prey availability for demersal fishes, potentially leading to reduced food intake, condition and yield of fishes in chronically trawled areas. Here, the effect of trawling on the prey availability and diet of the commercially important flatfish species, plaice (*Pleuronectes platessa*) and dab (*Limanda limanda*), was investigated over a chronic trawling intensity gradient in the Irish Sea. Previous work in this area has shown that trawling negatively affects the condition of plaice but not of dab. The present study showed that reductions in local prey availability did not result in reduced feeding of fish. Even at frequently trawled sites with low prey biomass, both plaice and dab managed to maintain constant levels of stomach fullness and gut energy contents. Dietary shifts in plaice towards energy-poor prey items were, however, evident when prey species were analysed individually and a potential decrease in foraging efficiency was seen as the most plausible cause for the reduced body condition observed. Understanding the relationship between trawling, benthic impacts, fish foraging and resultant body condition is an important step in designing successful mitigation measures for future management strategies in bottom trawl fisheries.

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<http://classic.rspb.royalsocietypublishing.org/content/282/1799/20142336.full>

A copy of the paper is available on the BENTHIS website.

5 THE EFFECT OF TRAWLING INTENSITY ON THE WEIGHT-LENGTH RELATIONSHIP OF FLATFISH¹

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5.1 Introduction

Bottom trawling affects the biomass and species composition of the benthic ecosystem and consequently affect the growth of benthivorous fish species. Previous studies have reported both positive and negative effects of bottom trawling on the growth. In this study, we analysed the condition factor of individual fish recorded during routine research vessel surveys in the south-eastern North Sea in late summer. Condition factor was standardised for each year for males and females separately in order to reflect the relative condition of the sampled individuals relative to the population mean. Condition factor was analysed in relation a suite of environmental variables including the primary and secondary production estimated with a regional ecosystem model (ERSEM), depth, geographic location and trawling intensity.

5.2 Methods

Fish samples. Fish were sampled during the annual Beam Trawl Survey carried out in August-September by IMARES in the southern-eastern North Sea. Weight, length, gender and age were determined and the location of the sample was recorded. In total 13088 plaice and 6144 sole were collected in the period between 2002 and 2012. Condition factor was estimated as the residual of the glm-model of the log-transformed body weight and log-transformed length, including gender and the interaction between gender and the log-transformed length. The condition factor was estimated for each year separately.

Environmental variables. Density of plaice and sole were estimated for each sampling station. Trawling intensities were estimated for the 10x10 km square around each sampling station based on VMS data of the Dutch beam trawl fleet. Temperature data and biological productivity were obtained from the ERSEM model (van Denderen et al., 2014).

5.3 Results

Condition factors of plaice and sole varied in space and was highest in the coastal zone (Figure 1). The effect of environmental variables on body condition and their possible interactions was explored using a structural equation analysis. The analysis showed that temperature and productivity are negatively correlated with depth, while productivity is positively correlated with temperature. Trawling intensity is positively correlated with depth, temperature and productivity. The condition of plaice is significantly correlated with depth and benthic productivity. Depth has a negative effect, while productivity has a positive effect. The effect of trawling, temperature and density were not significant (Figure 2 upper panel). For sole, the condition was negatively related to trawling intensity. Sole density was positively correlated with productivity.

¹ This paper was presented at the 9th Flatfish Ecology Symposium, 9-14 November 2014, Cle Elum, Washington, USA

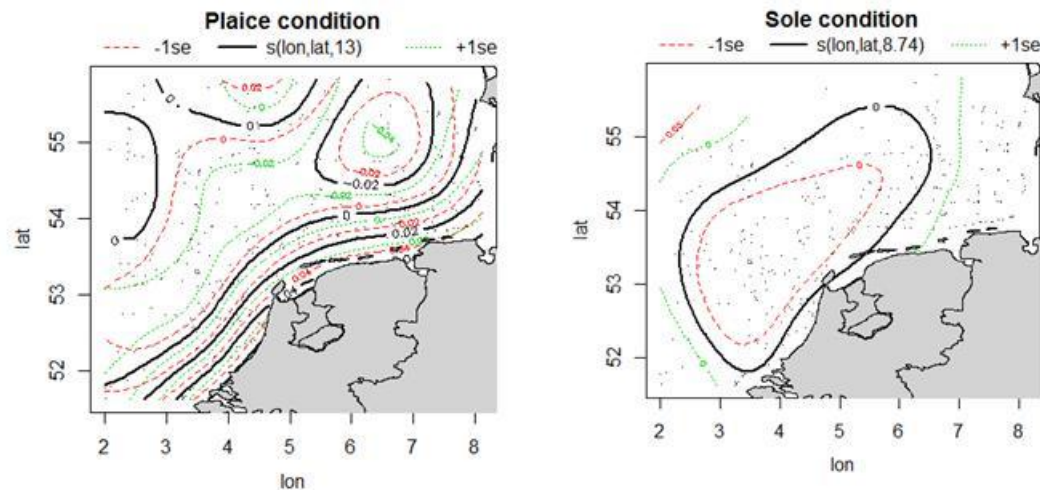


Figure 1. Spatial pattern in the relative condition factor of plaice (left) and sole (right).

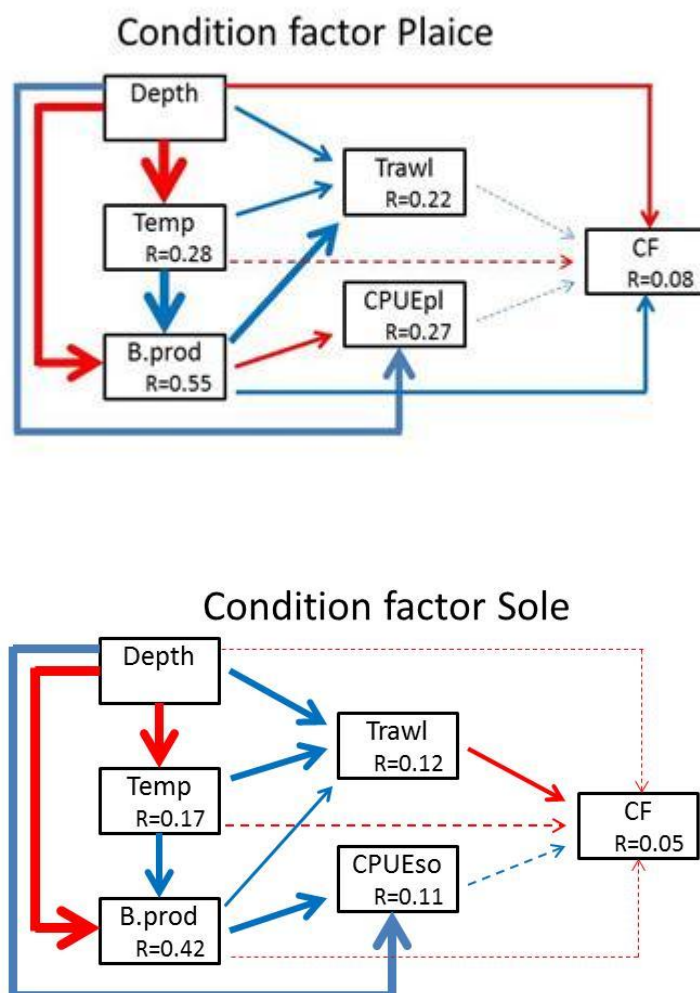


Figure 2. Structural equation analysis of the relative body condition in plaice (upper panel) and sole (lower panel). Full lines show significant effects. Dotted lines show insignificant effects. Red arrows indicate negative effects. Blue arrows indicate positive effects. The R-values in the boxes show the correlation coefficient of the significant environmental variables.

To further investigate these relationships, allowing for non-linearity, a GAM approach was applied. The GAM-model including only the variables that are biologically meaningful (temperature, secondary production, plaice density and trawling intensity) explained 20% of the deviance in condition.

The analysis indicates that condition may decrease with increasing trawling intensity. The relationship estimated for temperature and secondary production are (partly) as expected. However, the relative high condition at low secondary production in plaice is unexpected. Also the increase in condition at high plaice densities is surprising, but may indicate that plaice aggregate in areas where there is plenty of food.

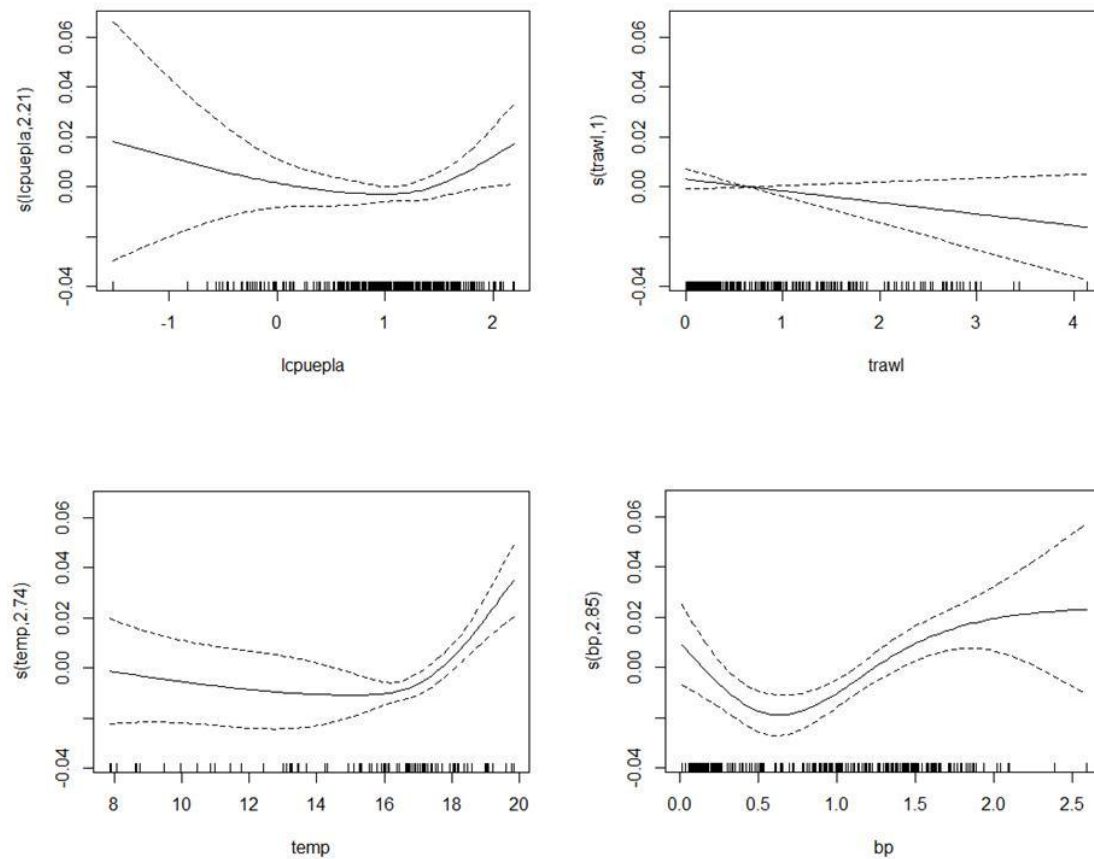


Figure 3. Plaice. Result of the GAM analysis of the condition factor in relation to density (lcpuepla), trawling intensity (trawl), temperature (temp) and secondary production (bp).

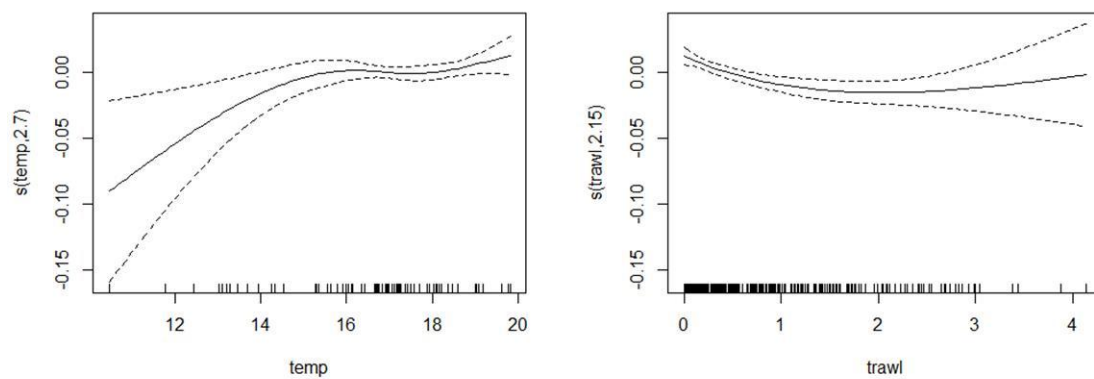


Figure 4. Sole. Result of the GAM analysis of the condition factor in relation to temperature (temp) and trawling intensity (trawl).

5.4 Conclusions

- Trawling influences benthic ecosystem
- The trawling impact differs across habitats
- No impact detected in areas of high natural disturbance
- Top-down or bottom-up control
- Habitat dependent effects may explain the contradictions in the literature on effect on food benthivorous flatfish
- Condition analysis suggests a slight negative effect of trawling
- Dedicated sampling along trawling gradients required for further investigation

5.5 References

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6 THE EFFECT OF BOTTOM TRAWLING ON THE CONDITION OF FISH DEPENDS ON THE CHANGE IN THE RATIO OF BENTHIC PREY TO FISH CONSUMERS

Jan Geert Hiddink¹, Joan Moranta², Stephen Balestrini¹, Marija Sciberras¹, Marine Cendrier¹, Rosie Bowyer¹, Michel J Kaiser¹, Mattias Skold³, Patrik Jonsson³, Francois Bastardie⁴, Hilmar Hinz⁵

6.1 Abstract

1. Bottom trawl fisheries are wide-spread and cause mortality of benthic invertebrates and this can decrease the availability of prey to target fish species. Exploitation also reduces the abundance of the fish species themselves. Modelling studies have shown that bottom trawling could lead to both increases and decreases in fish production, but so far empirical evidence to test these ideas has been very limited. We hypothesize that the effect of bottom trawling on the food intake and condition of fish depends on how the ratio of prey to consumers changes with increasing fishing pressure.
2. We simultaneously assessed the impact of bottom trawling on the food availability, condition and stomach contents of three flatfish and Norway lobster in an area in the Kattegat that had a steep commercial bottom-trawling gradient but otherwise homogeneous environmental conditions.
3. For the plaice, prey biomass initially decreased more slowly than the biomass of fish, and as a result the amount of food available per plaice increased before decreasing at higher trawling frequencies $>5 \text{ y}^{-1}$. This pattern was mirrored in both the condition and stomach contents of plaice, which both peaked at intermediate levels of trawling, and for long rough dab.
4. No effect of trawling on dab prey and condition was found. Norway lobster condition increased as abundance decreased with trawling.
5. Together these results support the idea that when the abundance of both the prey and the target predator are affected by exploitation, which of these declines more quickly will determine whether exploitation will result in an increase or a decrease of the food intake, condition and growth rates of the target species.
6. *Synthesis and application.* Bottom trawls may result in lower fishing yields compared to fishing gears that do not affect prey availability. Understanding the relationship between trawling, benthic impacts, fish foraging and resultant body condition is an important step in designing successful mitigation measures for future management strategies in bottom trawl fisheries. 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.

Keywords: *Pleuronectes platessa*, *Limanda limanda*, *Hippoglossoides platessoides*, *Nephrops norvegicus*, Otter trawl, Beam trawl, Scallop dredge, ecosystem effects of fishing, Kattegat, Marine protected area, *Amphiura*

6.2 Introduction

Demersal fisheries using otter and beam trawls and scallop dredges are widespread, and typically use heavy ground ropes and chains to drive fish and shellfish from the seabed into nets. Physical disturbance from such fisheries can cause significant changes in the seabed ecosystem. Previous studies have found that the effects of bottom trawling on benthic invertebrates include reductions of biomass, diversity and body size, changes in the functional trait composition of the community, and that the effects are different between different gears and habitats (Hiddink *et al.*, 2006; Kaiser *et al.*, 2006; Tillin *et al.*, 2006). These changes in the benthic ecosystems are conservation issues in themselves, but there is also ongoing concern that bottom fishing may impact the demersal fish species that depend on these habitats for food, such as cod *Gadus morhua*, haddock *Melanogrammus aeglefinus* and many species of flatfish (Auster & Langton, 1999). Trawling potentially leads to changes in food intake, body condition and therefore yield of fishes in chronically trawled areas (Fogarty, 2005).

Trawling may affect prey availability both negatively and positively, depending on the diet of fish and the intensity of trawling. The total biomass of benthic invertebrates and of large benthic invertebrates in particular decreases strongly with increasing trawling in most habitats (Hiddink *et al.*, 2006), and this is therefore likely to result in a reduction of the amount of food available to many benthivorous fish species. However, modelling studies suggest that low levels of bottom trawling may benefit the small benthic invertebrates that form the food source for some fish species, by removing the large benthic fauna that small benthic prey compete with for food and space (Hiddink *et al.*, 2008; van Denderen *et al.*, 2013). Very high intensities of trawling are likely to ultimately also remove those small prey. A model by Van Denderen *et al.* (2013) showed that the fish population response to trawling depends on whether the abundance of their benthic prey is top-down or bottom-up controlled. They assumed that within the benthos, fish prey are competing over resources with other benthos that is not eaten by fish, and that fish prey were less vulnerable to trawling than the non-prey. They found that in bottom-up controlled systems trawling may result in higher fish abundance and higher yield of fish, but not in top-down controlled ecosystems.

Empirical support for such increases in food availability with trawling is however largely lacking so far. Jennings *et al.* (2002) found no change in the biomass of small infaunal polychaetes with chronic trawling and concluded that beam trawling disturbance does not have a positive or negative effect on their food supply for flatfish. The only empirical study to record changes in food supply for fish is a comparison of fish diets between a high- and low-trawling area in Monterey Bay that found that the abundance of an opportunistic worm species was higher at high trawling, and that incidence of this important prey item in the diet of some flatfish species increased at high trawling (Engel & Kvitek, 1998).

These indirect effects of trawling through changes in food availability occur at the same time as the direct removal of target fish biomass that would occur with any fishing gear. Changes in prey abundance are only likely to have a negative effect on the food intake of fish if any negative effects on prey availability are larger than the decline in fish stocks that any fishery causes, and the prey to fish ratio declines. I.e. any reduction in the abundance of the benthic prey due to fishing would need to be faster than the reduction in the target fish stock.

Empirical studies that have examined the effect of trawling on both benthic prey and the fish simultaneously are very scarce. Lloret *et al.* (2007) found that polychaete prey biomass and abundance was lowest in trawled areas and that the red mullet *Mullus barbatus* from these areas had lower lipid reserves and hence body condition. Similarly, the condition of the flatfish plaice *Pleuronectes platessa* was negatively related to trawling frequency in the Irish Sea. The plaice in this area were able to maintain their stomach fullness despite the reduction of local prey biomass and abundance, and the reduced body condition was best explained by the additional energetic costs of searching in a reduced prey field (Hiddink *et al.*, 2011; Johnson *et al.*, 2015). Shephard *et al.* (2010) observed declines in the length-at-age in gravel with increasing trawling, but not sand, for plaice in the Celtic Sea.

Here we assessed the impact of bottom trawling on the food availability of fish by simultaneously measuring the abundance of prey, the food intake by fish, the resulting condition of fish and the abundance of fish in an area that had a steep commercial bottom trawling gradient in the Kattegat but otherwise homogeneous environmental conditions. This is the first study that has measured all these parameters simultaneously, and is therefore able to explore how both changes in prey availability and fish abundance with trawling interact to cause changes in the stomach contents and the condition. Similar previous work has often not been in a position to detect the potential increases in prey abundance at low levels of trawling because too few areas with low trawling were available for sampling. In this study we avoid this problem by sampling in and outside areas where trawling has been restricted.

The main objective of this study is to disentangle the effects of changes in prey availability with trawling on fish food intake from the effects of changes in competition over food sources that are caused by reduction in fish stocks due exploitation. We hypothesize that food intake and the resulting condition of benthivorous fish relates positively to the biomass of their prey and negatively to the biomass of competitors of benthivorous species. As both prey and fish biomass are expected to go down with increasing bottom trawling, the effect of the food availability per fish will depend on which one of those will decline faster, and fish condition could increase as well as decrease. Figure 1 illustrates how different shapes of the relationship between prey and fish biomass and trawling frequency can result in very different prey to fish biomass ratios (i.e. the amount of food available per fish). Subtle differences in the shape of the curve can result in the effect of trawling on the food/fish ratio changing from a declining relationship (Figure 1b, c and f) to an optimum curve (Figure 1d, g and h), and effectively any shape of relationship seems possible.

6.3 Methods

We studied three species of benthivorous flatfish (plaice *Pleuronectes platessa*, dab *Limanda limanda*, long rough dab *Hippoglossoides platessoides*) and Norway lobster *Nephrops norvegicus*. These four species comprised 89% of our catch biomass in the study area. Plaice feeds on small polychaetes and to a lesser extent on bivalves (Rijnsdorp & Vingerhoed, 2001). Dab feeds on mobile crustaceans, polychaetes, fish and mollusc siphons (Braber & de Groot, 1973). Long rough dab feeds on shrimps and shrimp-like crustaceans, ophiurid brittle stars and polychaetes (Lande, 1976; Klemetsen, 1993; Ntiba & Harding, 1993; Amezcua *et al.*, 2003). Norway lobster feeds on a great diversity of prey, including crustaceans, molluscs, polychaetes, echinoderms and fish (Cristo & Cartes, 1998; Parslow-Williams *et al.*, 2002) and may even do some suspension feeding (Loo *et al.*, 1993). 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 the other species, it does not seem unreasonable to assume that such correlations exist for these other species.

6.3.1 Outline

The effects of chronic trawling on the weight-at-length of fish was investigated over a muddy fishing ground and associated closed areas in the southern Kattegat (Figure 2) in August 2013. The main bottom-trawling activity that occurs on this fishing ground is otter trawling for Norway lobster (*Nephrops norvegicus*) and gadoid fish. Three different types of closed areas with different restrictions were created in this area in 2008 to protect cod stocks, and this created a gradient in trawling effort (Vinther & Eero, 2013). The area was divided in a permanently closed area, a seasonally closed area, a seasonally closed area where gears that do not target cod are allowed, and a permanently open area. This management regime had been in place for 5 years when we sampled the area in August 2013. At each of the stations we sampled the infaunal benthic invertebrates using a grab and the fish and Norway lobster using a trawl. Permission to sample inside the closed areas was obtained from Havs och Vatten myndigheten in Sweden.

6.3.2 Station selection

We selected 19 sampling stations on mud between 25 and 40m depth (HELCOM, 2007) that covered a large range of fishing pressure, with stations in all different types of closed areas. Each station was defined as a box of 3x3 km. We reviewed station characteristics after the survey with the most up to date fishing pressure estimates and actual sediment composition information in order to exclude stations that were outliers in terms of sediment composition, depth and fishing pressure using Multi-Dimensional Scaling (see Results).

6.3.3 Fishing pressure estimates

Fishing pressure was estimated using European Community Satellite Vessel Monitoring System (VMS) data. The yearly seabed area (km²) swept by a fishing gear was estimated for each station for a three year and half period from 2010 to Aug 2013. These fishing pressures were estimated on the 19 stations by computing the accumulated swept areas within a year from all the bottom-contact fishing gears (otter and bottom pair trawls) by Danish and Swedish vessels larger than 15 m. We used Danish and Swedish official catch and effort statistics for combining VMS data with logbook data, together with estimates regarding the dimensions of the different gears. The relationships between gear dimensions and vessel size (e.g. trawl door spread and vessel engine power (kW)) for different gear groups were used to assign quantitative information of bottom contact (e.g. width of gear) to each logbook trip, and the extended logbook data were combined with interpolated vessel tracks based on VMS data (Hintzen *et al.*, 2012). The required vessel size information, in terms of engine power (kW) and vessel length overall in metres, was collected, together with the gear specifications in a pan-European industry-based questionnaire survey (Eigaard *et al.*, 2015). This study enabled statistical modelling of the vessel size or vessel engine power ~ gear size relationships for different métiers (combinations of gear types and target species) to be conducted and deduce the width of the sweep of each of the (VMS interpolated) fishing event taking place across the stations. Trawling intensity is expressed here as the swept area ratio (γ^{-1} , the mean number of km² fished / the area of each station, 9km²).

6.3.4 Sampling of fish and invertebrate populations

Fish and invertebrates were sampled at each station in August 2013. Two tows of 30 min duration were done at each station with otter trawl (distance across mouth of the net 25 m, 80 mm mesh cod-end) at a speed of 3 knots between 7.45 and 17.00h. The total catch number and weight per species was measured. The length (to the nearest mm) and weight (to the nearest g) of the individual fish in the catch was recorded on board. If the catch of a species in a haul was large (>50 individuals), a subsample of ≥ 50 fish was measured and weighed. For Norway lobster, the carapace length and the total weight was measured for intact male lobsters. Females and males with missing limbs were excluded. The benthic invertebrates were sampled by taking five 0.1 m² Smith-McIntyre grab at haphazard locations in the station box. A 50ml sediment sample was retained for grain size analysis and the rest of the sample were sorted over a 1 mm sieve and preserved in 4% formalin for identification. Results from the 5 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. All invertebrates were identified to the highest practicable taxonomic resolution (mostly Genus or Family) and the wet weight of each individual organism was estimated after blotting. For some analysis wet weight was converted to energy (J) using conversion factors from Brey (2015).

Average particle sizes and particle size distributions were determined using a Malvern laser diffraction particle sizer (Blott & Pye, 2001).

6.3.5 Fish condition

Throughout the rest of this paper, ‘fish’ will be used to indicate both the 3 flatfish species and Norway lobster. 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 condition proxy 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. Only stations where more than 10 fish were caught were used for condition estimates to avoid biased condition estimates due to low numbers of fish.

6.3.6 Stomach contents

Plaice and dab of total body length 182–299 mm and 168–274 mm, respectively, were selected for stomach content analysis. These size ranges minimized the likelihood of incorporating ontogenetic changes in diet and allow comparison with Johnson *et al.* (2015) who used the same size ranges. Stomachs of up to 20 individuals of each species per station were extracted and stored in 8% buffered formalin for processing. The mass of the entire stomach (whether full or empty) and total mass of prey contents were recorded after blotting. Prey items were then separated, identified to the highest taxonomic resolution possible, counted, weighed and measured. In total, 200 plaice and 295 dab stomachs were analysed. The fraction of empty stomachs was reported separately; remaining analyses only examined stomachs that had some contents to avoid including fish that had regurgitated their stomach contents. To investigate differences in energy content of the prey species consumed, the mean energy content per stomach was calculated using biomass conversion factors (Brey, 2015). The level of stomach fullness to which plaice and dab fed at each site was calculated as the mean stomach content weight as a percentage of body biomass. Stomach contents of long rough day and Norway lobster were not examined.

6.3.7 Analyses

Because we were aiming to detect whether bottom trawling can result in decreases, increases or humped responses in prey availabilities, stomach contents and fish condition, we used Generalized Additive Models (GAM) and Generalized Additive Mixed Models (GAMM) as those allow any shape of relationship to be fitted. Most analyses were performed using GAM using mean values per station as the response variable and trawling frequency (y^{-1}) as the driver. To account for the non-independence of fish condition measurements within a station, the effect of trawling or benthic production on the $\log_{10}(\text{weight})$ at $\log_{10}(\text{length})$ of fish was estimated using GAMM from the package *mgcv* in R (Zuur *et al.*, 2009; Wood, 2015), using $\log_{10}(\text{length})$ and trawling as fixed factors and using ‘Station’ as a grouping variable and a Gaussian error distribution. As the interaction between $\log_{10}(\text{length})$ and trawling was not significant, this term was excluded from analyses. Homogeneity of residuals was established through visual examination of plotted standardized residuals versus fitted values.

6.4 Results

6.4.1 Environmental conditions

Particle size analysis and subsequent MDS indicated that four stations (K, O, Q and S) were less muddy than the other stations in combination with a high trawling intensity (Table S1, Figure 3). To avoid confounding of sediment composition with trawling intensity these stations were excluded from further analyses. The trawling intensity on the remaining station ranged from 0.2 to 7.9 y^{-1} . Some bottom trawling was recorded even in the areas that were closed to all trawling.

6.4.2 Infauna

The community of infaunal invertebrates was dominated by the brittlestars *Amphiura* spp. by numbers and by the ocean quahog *Arctica islandica* and sea urchin *Spatangus purpureus* by biomass. Together these three species comprised 92% of all invertebrate biomass. Mean total community biomass was not significantly related to trawling intensity (Figure 4a, Table 1a), but bottom trawling limited the total biomass that could be found at a station (90% quantile regression, $p = 0.029$). This pattern can be explained if we assumed that the long-lived, fragile, low-density but high-biomass *Arctica* and *Spatangus* are particularly vulnerable to trawling activities. Whether or not these are collected in 5 x 0.1m² of samples is unpredictable even if they are present, and therefore a lower total biomass may be obtained even at low trawling stations, but high biomass is never found at high trawling stations.

A comparison of the weight distribution of the infauna and the stomach contents of plaice and dab indicated that the fish select only the smaller infauna as prey (Figure S1); 97.5% of plaice prey was <0.20g while 97.5% of dab prey was <0.630g. *Amphiura* was very dominant and made up 22% of the total biomass of invertebrates, but 76% of biomass <0.20 g and 84% of biomass below 0.63g. Other species in the prey size classes are mostly polychaetes and bivalves. Plaice prey biomass declined slowly at lower trawling frequencies and more quickly above trawling frequencies of 5 y^{-1} , while no significant relationship between dab prey abundance of trawling was found (Figure 4b-c, Table 1a).

6.4.3 Fish biomass

Most fish that were caught were around 20 cm in length, while *Nephrops* had a carapace length of around 5 cm (Table S2). Dab and *Nephrops* biomass was about five times higher than those of plaice and long rough dab. The biomass per trawl of dab and *Nephrops* (and as a consequence also the total fish biomass) declined quickly with increasing trawling intensity and levelled off at a trawling intensity of 5 y^{-1} (Figure 5, Table 1b). The abundance of plaice and long rough dab did not react to trawling. Other abundant species in the catch were *Gadus morhua*, *Microstomus kitt*, *Merluccius merluccius*, *Scophthalmus rhombus* and *Eutrigla gurnardus*.

6.4.4 Fish condition

The weigh-at-length peaked around 5 times y^{-1} for both plaice and long rough dab (Figure 6, Table 1c). Dab weight-at-length did not respond to trawling, while *Nephrops* weight-at-length increased with increasing fishing pressure (Figure 6, Table 1c). The difference between the highest and lowest condition recorded was around 4% for plaice, long rough dab and *Nephrops*.

Figure 6a and b also gives the 'prey to consumer biomass ratio' for plaice and dab for comparison with the fish condition. This ratio was calculated by dividing the fitted GAM for prey by the fitted GAM for fish biomass. We used total fish biomass as the measure of the abundance of consumers because in particular plaice abundance was low in comparison with the abundance of competitors, and therefore the abundance of competing species was considered a better proxy for the abundance of competitors than the abundance of plaice alone. The 'prey to consumer biomass ratio' for plaice also peaked around 5 y^{-1} and showed a similar pattern to plaice weight-at-length. The 'prey to consumer biomass ratio' for dab increased and also showed a similar pattern to (the non-significant) dab weight-at-length. This

comparable pattern therefore suggests that both competitor abundance and prey availability affect the food intake by these fish.

6.4.5 Stomach contents

Overall, dab stomachs were much fuller than plaice stomachs. The most common prey item in the stomach of both species was the brittlestar *Amphiura*, but the rest of the diet is more focused on polychaetes and bivalves for plaice and more on crustaceans for dab (Figure S2). Even though *Amphiura* has a low energy density (Table S3), it still contributes most energy to the diet of both species at most stations. The percentage of empty stomachs did not respond to trawling in either of the two species (Figure 7a-b, Table 1d). Stomach fullness and the stomach energy content approximately doubled over the trawling gradient for plaice, but did not change with trawling for dab (Figure 7c-f, Table 1d).

6.5 Discussion

The results from this study support our hypothesis that food intake and the resulting condition of benthivorous fish relates positively to the biomass of their prey and negatively to the biomass of competitors of competing fish. For plaice, prey biomass initially decreased more slowly than the biomass of consumers, and as a result the amount of food available per plaice increased before decreasing at higher trawling frequencies. This pattern was mirrored in both the condition and stomach contents of plaice, which both peaked at intermediate levels of trawling. No significant effect of trawling on dab prey abundance was detected, and as fish biomass decline the prey/consumer ratio increased moderately for dab. Although not significant, again this pattern was mirrored in both the condition and stomach contents of dab, which both showed increases. No diet information was available for long rough dab, but the condition reacted to bottom trawling in a similar way to plaice, which suggest they may be relying on a similar diet. *Nephrops* condition increased linearly with increasing trawling, suggesting that their food sources did not react strongly to trawling, and that a release from competition was the overriding factor driving the increase in condition for this species. Together these results support the idea that when the abundance of both the prey and the target predator are affected by exploitation, it is important to know which of these declines more quickly as this will determine whether exploitation will result in an increase or a decrease of the food intake, condition and growth rates of the target species. Our results show that the assumption of Van Denderen *et al.* (2013) that prey abundance will increase with trawling was not supported, but our results do emphasize that it is important to take top-down effect of fish predation on benthic prey into account when trying to assess the effect of bottom trawling on fish productivity.

Energetically, it is likely to be more costly to forage in low-prey compared with high-prey patches. In areas of low benthos, fish will have to spend more time searching for prey, and therefore increasing energy expenditure. The prey to consumer ratio that we calculated does not take this into account. If this effect is important it would be expected that the effect of trawling on fish condition is stronger than the effect on stomach contents, but this was not evident from our results. As the functional responses of demersal fish foraging on benthic prey are unknown, we cannot do a quantitative assessment of this effect.

The effects of trawling on fish condition were modest (around a 4% increase over the trawling gradient for plaice, long rough dab and Norway lobster relative to an untrawled situation). Our analysis shows that the effect of trawling on fish condition results from two different effects: the effect of trawling on prey availability and the effect of the reduction in fish stocks by exploitation. The effect on prey availability is a local effect, while the effect of exploitation is fish populations that range widely is going to occur over a larger scale. When evaluated at the scale of the fish population, the effect of prey availability will be weaker as only about ¼ of the seabed is trawled at frequencies over 1 y⁻¹ (Jennings & Lee, 2012). The effect of reductions in competition over food will be stronger over larger scales however as fish are more mobile than their prey, and can forage away from areas that have depleted prey populations. This means that the effect of trawling on the condition and prey availability per fish is likely to be more positive when evaluated over larger scales.

An important assumption in our analyses was that the different species at least partly share the same food sources. Given the dominance of *Amphiura* in the environment, and in the stomachs of plaice and dab, this does not seem an unreasonable assumption. *Nephrops* was one of the most abundantly caught species at all stations, but because we fished in the day when they are mostly hiding in their burrows, it is likely that *Nephrops* was many times more abundant than the flatfish species together, and therefore even a partial prey overlap will have resulted in *Nephrops* being an important competitor for the flatfish.

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. Previous work suggests that flatfish forage within quite limited areas (de Castro *et al.*, 2015). 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 in the time that they built up their condition (weeks) before sampling. This, however, does not affect the conclusions that trawling had an effect on the condition of three of the species, as mobility would break up any spatial pattern in condition; therefore, these analyses are likely to underestimate any effect of trawling on condition. This is confirmed by comparing the magnitude of the effect of trawling on condition with the effect on stomachs contents; the effect on condition was much smaller than the effect on the stomachs. As the stomach contents reflect the food intake in the previous 24h and the condition the previous weeks, this confirms that fish mobility weakens the observed effects.

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 *et al.*, 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.

Implications

A general assumption in fisheries management is that fish productivity increases with exploitation because of a reduction in competition over food and other resources. Our results show that this assumption seems reasonable for *Nephrops* and dab, but not for plaice and long rough dab. Although condition and food intake for these two species increase up to 5 times trawling y^{-1} , these results do not show that bottom trawling has a positive effect on the prey availability as sometimes has been suggested. Instead, it shows that bottom trawling above a frequency of 5 y^{-1} reduces the carrying capacity of the ecosystem to support production of plaice and long rough dab, compared to a fishing gear that would not have an effect on the food of the fish. 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, but it seems unlikely that such gears can efficiently exploit demersal fish population. Our results suggest that production of plaice be maximized by fishing areas at an intensity of less than 5 y^{-1} . This may not be compatible with management for biodiversity conservation though as biodiversity benefits from concentrating fishing activities as much as possible (Jennings *et al.*, 2012).

6.6 Acknowledgements

This research was supported the by FP7 project BENTHIS (grant agreement no. 312088), the FP7 project ASSEMBLE (grant agreement no. 227799) and the Sven Loven Centre for Marine Sciences.

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6.8 Tables

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.

a. Infauna per 0.1 m² GAM

Parameter	n	res.df	F	p
Total infauna	15	13	1.176	0.298
Infauna <0.20 g WW	15	12.4	4.175	0.041
Infauna <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

6.9 Figures

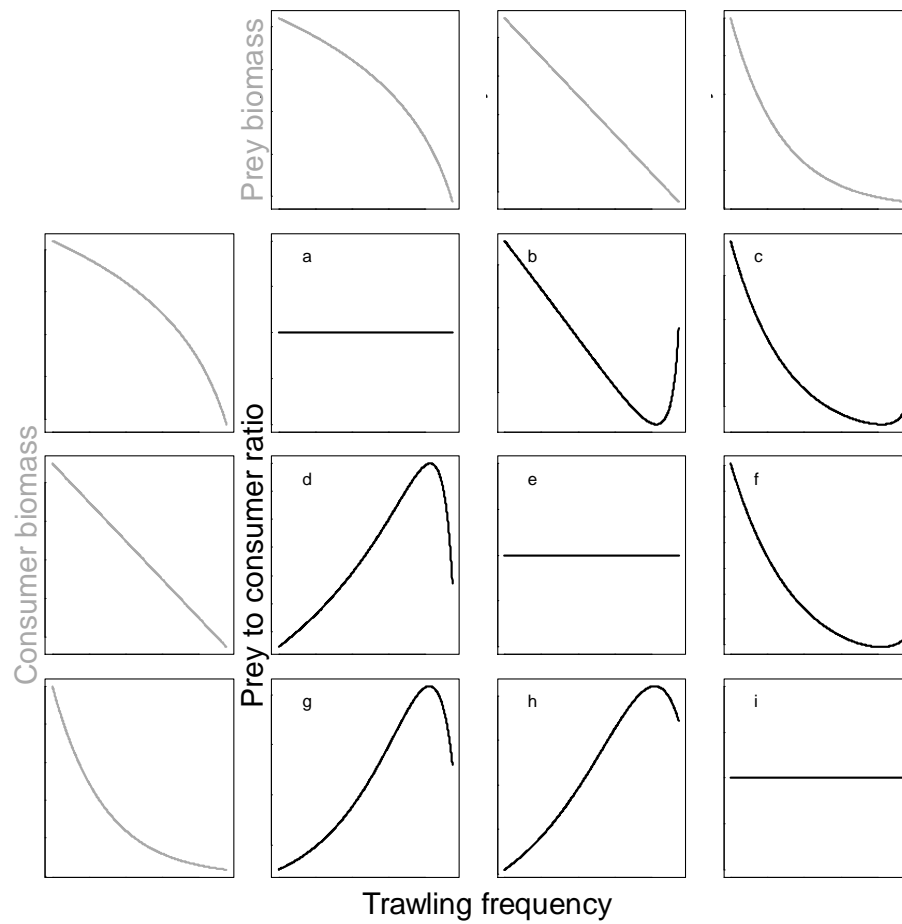


Figure 1. Hypothetical prey to consumer biomass ratios for different shaped relationships between prey (top row) and consumer biomass (left column) and trawling frequency.

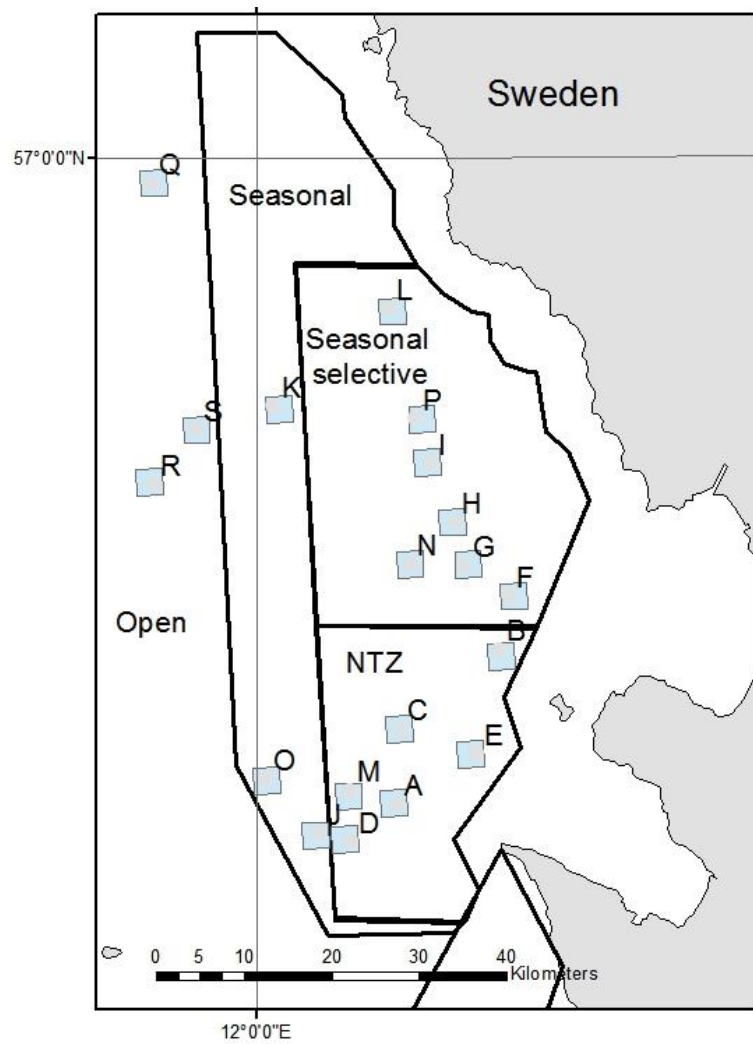


Figure 2. Map of the study area with the sampling stations and MPA boundaries indicated. NTZ = No take zone.

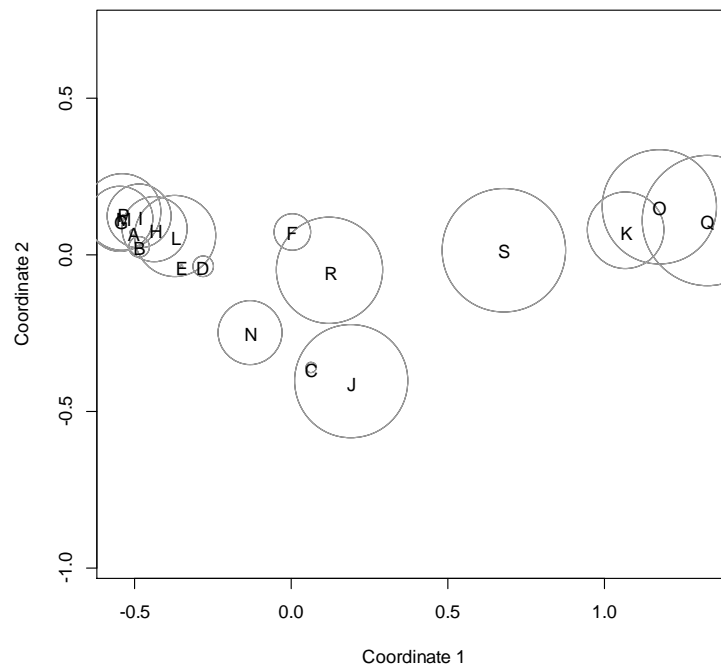


Figure 3. MDS plot of the site characteristics of the sampling stations (depth and sediment parameters). The size of the bubble is proportional to the trawling intensity.

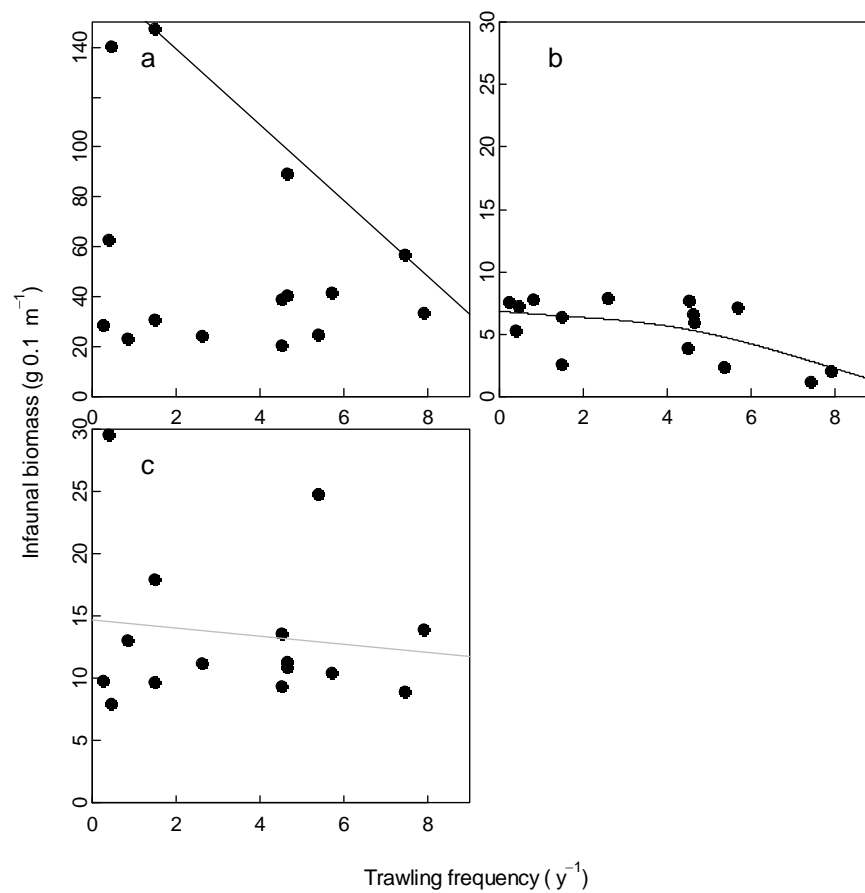


Figure 4. The effect of bottom trawling on the biomass of infaunal benthic invertebrates in the Kattegat. a) All infauna, solid line is 90% quantile regression, B) Plaice prey <0.2g, solid line is fitted GAM. c) Dab prey <0.63 g WW. The grey line is the non-significant GAM for dab.

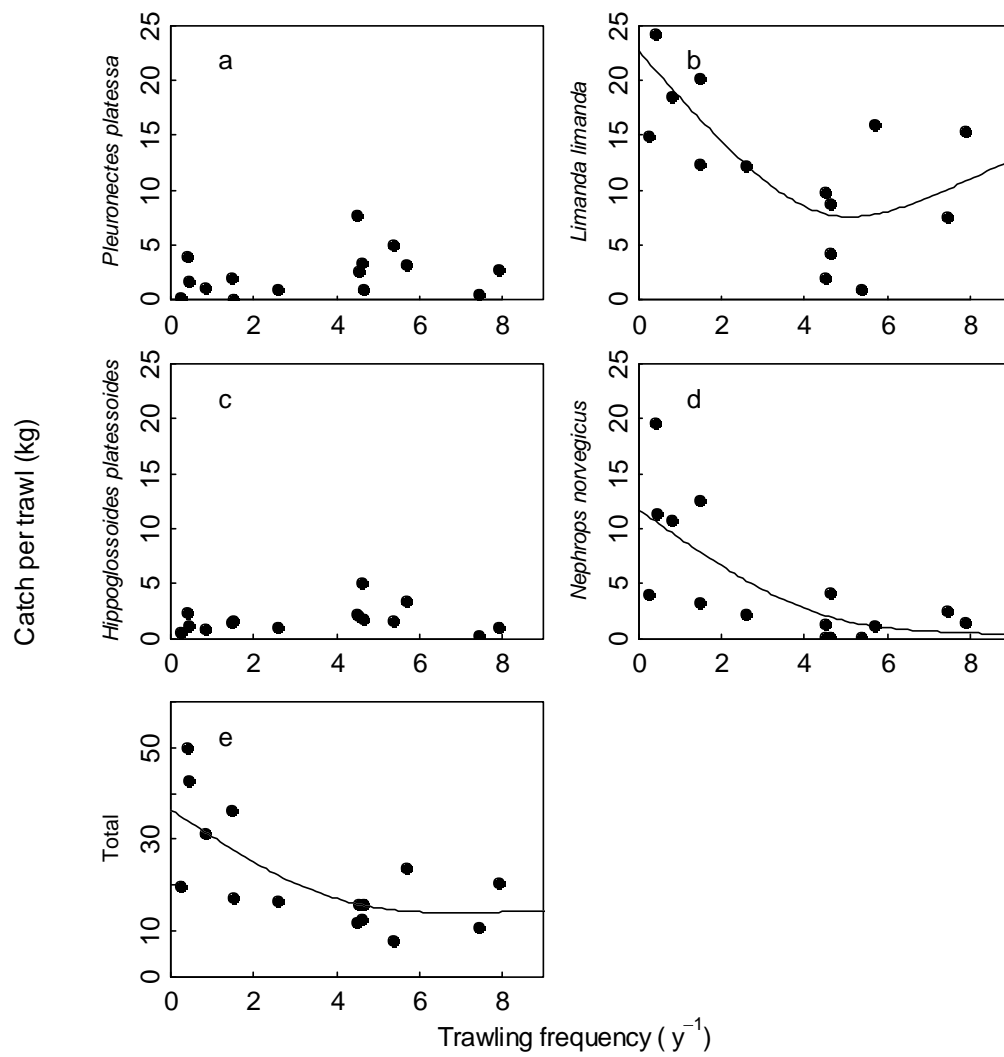


Figure 5. Fish biomass per trawl. a) Plaice, b) Dab, c) Long rough dab, d) Norway lobster, e) total of all four species.

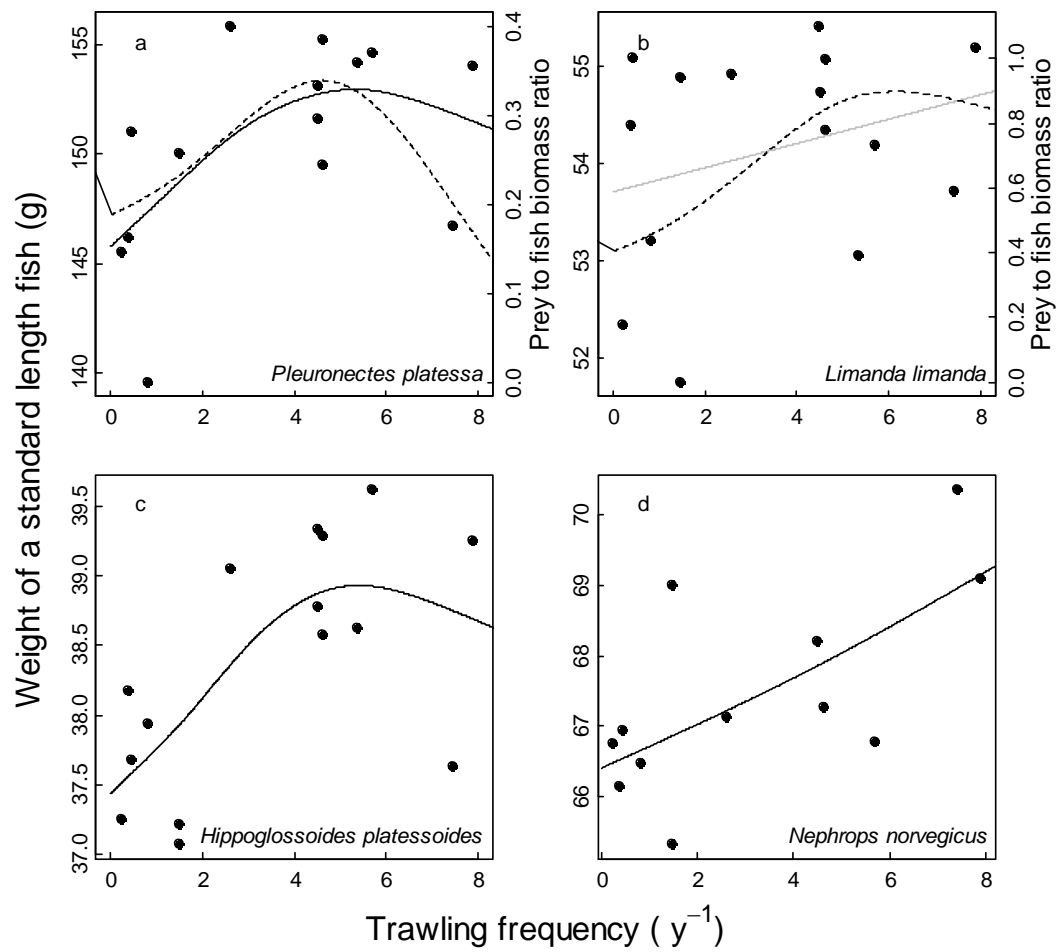


Figure 6. Weight of a standard length fish (as predicted from the GAMM plus the residuals) for a) plaice, b) dab, c) long rough dab and c) Norway lobster. The dashed line (right y-axis) is prey to consumer ratio (g infaunal prey $0.1 \text{ m}^{-2} \text{ kg fish}^{-1} \text{ trawl}^{-1}$). The grey line is the non-significant GAM for dab.

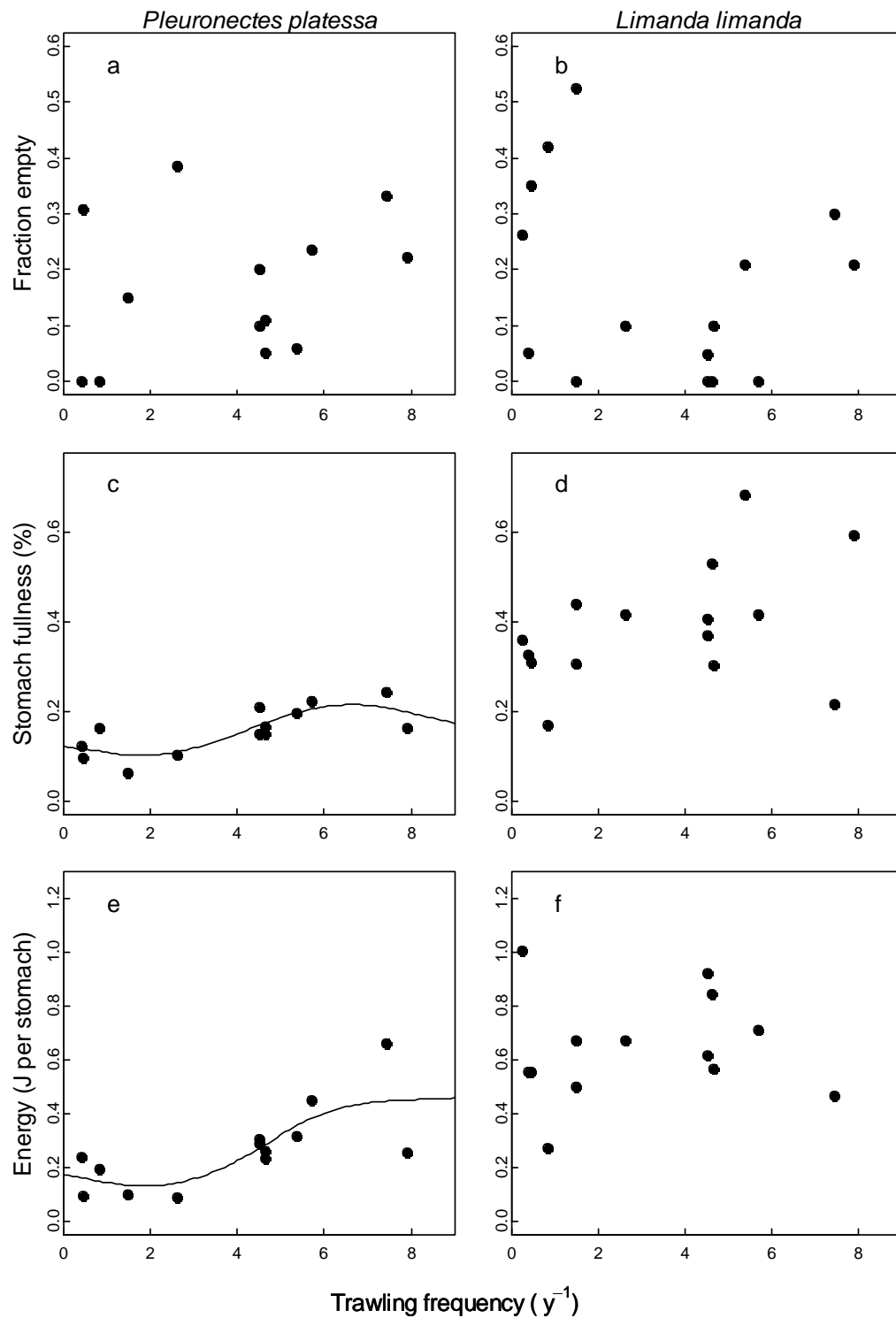


Figure 7. Stomach contents of plaice and dab. a-b: fraction empty, c-d: stomach fullness as a percentage of body weight. e-f: stomach energy content. a, c, e: plaice. b, d, f: dab.

Online supplementary material.**Tables**

Table S1. Site characteristics of the sampling stations. Stations in italics were excluded from further analysis because they combined higher fishing effort with coarser sediment and could therefore have confounded the outcomes.

Station	Latitude (°)	Longitude (°)	Depth (m)	Mud and silt (%)	Sediment			Closure		Swept area ratio (y ⁻¹)
					10% quantile (µm)	Median grain size (µm)	90% quantile (µm)			
A	56.339	12.260	31	100	2	8	35	No take zone		0.4
B	56.498	12.449	27	100	3	9	36	No take zone		1.5
C	56.416	12.266	32	85	3	12	172	No take zone		0.8
D	56.302	12.174	31	99	3	10	60	No take zone		1.5
E	56.391	12.406	27	100	2	10	51	No take zone		0.2
F	56.552	12.468	28	99	3	20	76	Selective seasonal closure		2.6
G	56.584	12.386	31	100	2	9	29	Selective seasonal closure		4.6
H	56.628	12.369	34	100	3	10	38	Selective seasonal closure		4.6
I	56.689	12.324	34	100	3	9	32	Selective seasonal closure		4.5
J	56.310	12.115	31	78	3	13	223	Seasonal closure		7.9
<i>K</i>	<i>56.748</i>	<i>12.032</i>	<i>34</i>	<i>52</i>	<i>4</i>	<i>117</i>	<i>355</i>	<i>Seasonal closure</i>		<i>5.4</i>
L	56.848	12.247	34	100	3	10	44	Selective seasonal closure		5.7
M	56.353	12.172	33	100	2	8	30	No take zone		0.4
N	56.585	12.286	39	93	3	10	104	Selective seasonal closure		4.5
<i>O</i>	<i>56.366</i>	<i>12.018</i>	<i>32</i>	<i>43</i>	<i>4</i>	<i>156</i>	<i>344</i>	<i>Seasonal closure</i>		<i>8.0</i>
P	56.735	12.296	35	100	2	9	29	Selective seasonal closure		5.4
Q	56.976	11.802	37	40	5	186	473	Open to all fishing		9.1
R	56.668	11.809	38	94	3	21	107	Open to all fishing		7.4
<i>S</i>	<i>56.723</i>	<i>11.888</i>	<i>40</i>	<i>76</i>	<i>4</i>	<i>59</i>	<i>223</i>	<i>Open to all fishing</i>		<i>8.6</i>

Table S2. Size of the fish in the catch. Total length for the fish, carapace length for *Nephrops norvegicus* (mm)

Species	5% quantile	Median	95% quantile
<i>Pleuronectes platessa</i>	163	259	329
<i>Limanda limanda</i>	151	180	219
<i>Hippoglossoides platessoides</i>	139	181	219
<i>Nephrops norvegicus</i>	40	51	67

Table S3. Mean energy density of different prey group items. Energy density is reported as the mean per group and was calculated from the biomass-weighted conversion factors of the lower taxa that are making up these groups.

Group	Energy density (J g ⁻¹ WW)
<i>Amphiura</i>	1.878
Annelida	3.384
Bivalve	3.031
Crustacea	4.389
<i>Glycera</i>	3.523
Other	3.253

Table S3. Number of stomachs analysed per station

Station	Dab	Plaice
A	20	13
B	21	0
C	20	8
D	19	20
E	20	0
F	20	13
G	20	9
H	20	19
I	18	20
J	19	18
L	19	17
M	19	20
N	20	20
P	20	17
R	20	6

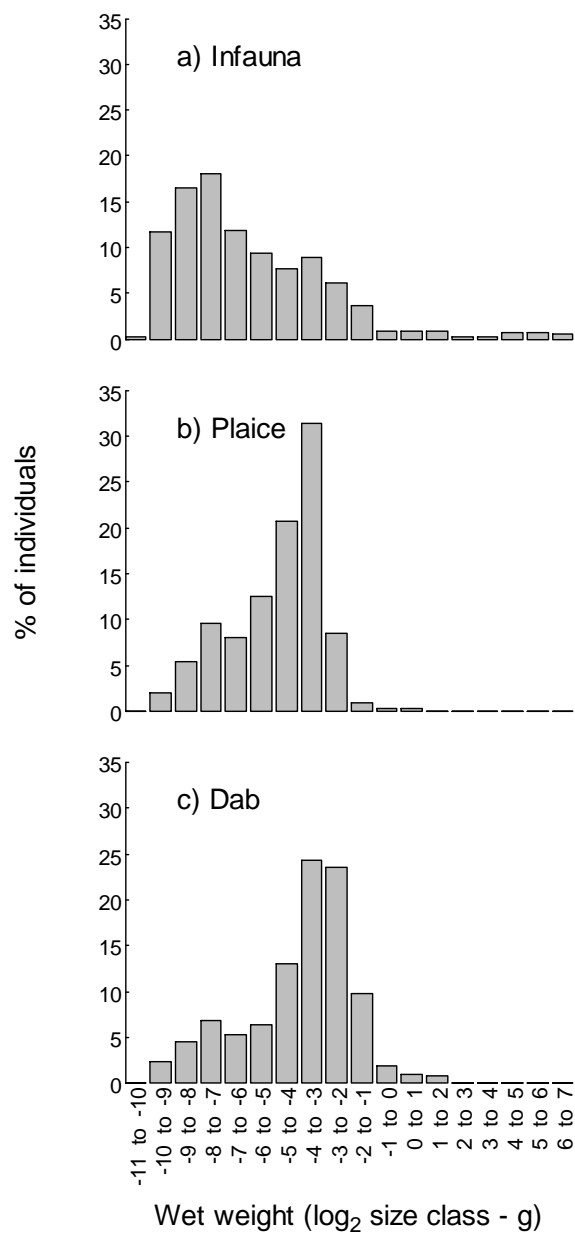


Figure S1. Weight distribution of a) infauna, b) plaice stomach contents and c) dab stomach contents in \log_2 weight classes.

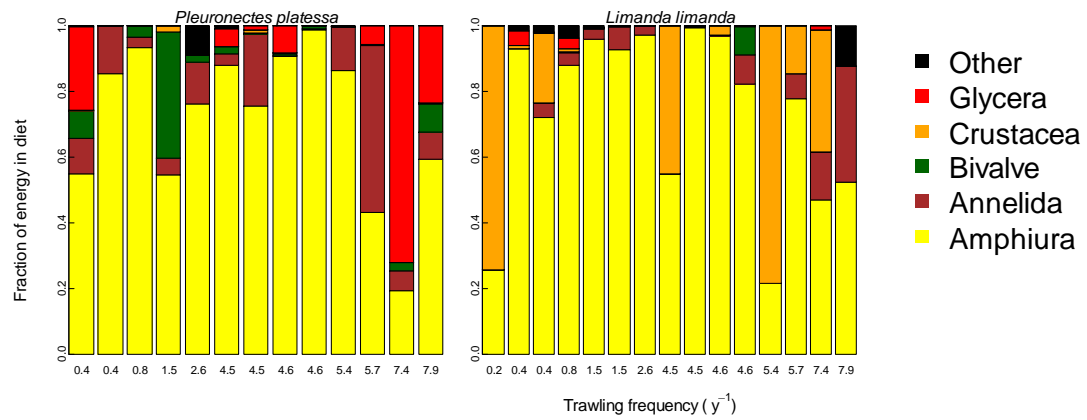


Figure S2. Stomach content composition by energy contribution (J) for plaice and dab. The stations are ranked by trawling intensity.

7 STOCK-SCALE EFFECTS OF BOTTOM TRAWLING ON THE GROWTH OF COMMERCIAL FISH SPECIES

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7.1 Introduction

If the effects of bottom trawling on benthic invertebrates cause a major change in the amount of food that is available for fish to eat, it could be expected that large-scale changes in the growth of fish occur. It is likely that a lower food availability will result in a lower maximum size of fish (Lorenzen and Enberg 2002). On the other hand, exploitation of fish stocks will also reduce their abundance and biomass, and therefore reduce the food requirements for the fish stock. If we ignore the effect of bottom trawling on fish food for now, it can be expected that fish growth goes up with increasing levels of exploitation, because competition of their food resources will decline with declining fish stocks. For example, Lorenzen and Enberg (Lorenzen and Enberg 2002) showed that the maximum size of many fish stocks, L_{∞} , increases when the biomass of the fish stock decreases. In fact, classic fisheries models assume that fish production increases with declining fish abundance exactly because of this decrease in competition (Jennings, Kaiser *et al.*).

Density-dependent increases in growth in trawled fish populations would suggest that these indirect trawling effects of fish food availability are relatively unimportant, while an absence of density-dependent increases in growth, or even decreases in growth with decreasing stocks, would suggest that bottom trawling is reducing the ability of the ecosystem to support fish production. Intriguingly, Lorenzen and Enberg (Lorenzen and Enberg 2002) found evidence for density-dependent growth in only 2 out of 7 bottom-trawled fish stocks, while they found evidence for density-dependent growth in 7 out of 9 other fish stocks.

It is necessary to study how the density-dependence of growth varies with different levels of trawling intensity for benthivorous fish. This would elucidate how the interaction of the depletion of food sources of fish by trawling and reduction in the predation pressure on benthos by depletion of the fish affect fish growth. Such an analysis shows whether or not exploitation with trawls leads to increase in growth that is anticipated in fisheries models. If it does not this is a sign that trawling erodes the ability of the ecosystem to support the fishery.

Here we aim to test whether bottom trawling reduces the ability of the ecosystem to support the fishery. We will test the hypothesis that density-dependent increases in growth are stronger for fish that rely less on benthic food sources, and lower or even negative in fish that feed exclusively on benthic invertebrates.

7.2 Methods

7.2.1 Outline

We will use the method of Lorenzen and Enberg (Lorenzen and Enberg 2002) to estimate the strength of density-dependence of growth on fish stock biomass. We use long-term time-series of fish length-at-age and stock abundance to estimate how the maximum length of fish populations changes as a function of the abundance of competitors. They estimated this as the parameter g , which is the change in L_{∞} in cm for an increase in the biomass of the fish species by 1 kg ha^{-1} . Normally it is expected that g is positive, when

L_{∞} decreases with an increase in the abundance of competitors. Here we expect that g is larger for piscivorous and zooplanktivorous species than for bottom-trawled benthivorous species.

An important assumption of this approach is that variations in stock size are caused by varying levels of fishing pressure, which is probably valid over the time periods of many decades that we study here.

7.2.2 Time series of weight-at-age of North Atlantic commercial fish stocks

We extracted time series of the weight-at-age, stock biomass, fishing mortality, and temperature of 32 stocks of 8 North Atlantic commercial fish species (cod *Gadus morhua*, saithe *Pollachius virens* L., haddock *Melanogrammus aeglefinus*, whiting *Merlangius merlangus*, hake *Merluccius merluccius*, herring *Clupea harengus*, plaice *Pleuronectes platessa* L. and sole *Solea solea* L.) from stock assessment reports and other sources (e.g. <http://www.ices.dk>). These species differ in their dependence on benthic food sources. Some species are benthivorous throughout their life (plaice, sole), some show ontogenetic shifts towards increasing piscivory in later life (haddock, cod, whiting, saithe and hake), and herring never eats any benthos. The degree of benthivory of these species is ranked in this order for further analysis, and our hypothesis therefore expects g to be smaller or negative for the flatfish species and larger for the species later in the list.

Data were obtained from virtual population analysis (stocks sizes and fishing mortality) and regular biological monitoring of fishery-dependent samples (weight-at-age). We analysed body size of fish stocks from both sides of the North Atlantic (ICES and NAFO areas) because these stocks are well documented and long time-series are available. Plaice and sole are restricted to the North-East Atlantic, while the other four species range across the North Atlantic Ocean. The number of stocks analysed per species varied from 1 to 9 (Table 1). The stocks analysed represent management units rather than fully distinct populations. For each stock we created tables of mean length-by-age and abundance-by-age. Where only weight data were available, these were converted to length using length–weight relationships for the study populations from Fishbase.org. We excluded from our analysis *i*) those years for which time series of cohort weight data were identical (indicating a lack of data at the start of the VPA), *ii*) the oldest year class of each cohort (because this year class sometimes represents the mean weight for several ages combined), *iii*) stocks that contained <10 cohorts (to ensure that statistical power was sufficient).

In studies where total stock biomass was reconstructed, this was expressed as biomass density, by dividing biomass by the relevant statistical area. As the distribution of most populations is spatially heterogeneous, the biomass-density estimates are in effect averages over relatively large areas.

7.2.3 Estimation of growth parameters

A von Bertalanffy growth model was used to predict mean length $L_{pred,a,t}$ of age group a at time t from the observed mean length of the cohort in the previous year ($L_{obs,a-1,t-1}$):

$$L_{pred,a,t} = L_{\infty B} - (L_{\infty B} - L_{obs,a-1,t-1}) \exp(-K)$$

where L_B is the asymptotic length at the average observed (or reconstructed) biomass density B during the year (t_1 to t_1^{-1}):

$$L_{\infty B} = L_{\infty L} - g \left(\frac{B_{t-1} + B_t}{2} \right)$$

The values of $L_{\infty L}$, K and g were estimated using the nls-function in R. Stocks were excluded from further analysis if the estimated value of K was not significantly different from zero.

7.3 Results

After removing 5 species where estimated value of K was not significantly different from zero, all estimated values of $L_{\infty L}$ seemed within the expected range (Figure 1 and Table 1). Significant density-dependence of growth was found for 12 out of 32 species. g was significantly positive for 8 species and significantly negative for 4 species (Table 2).

Table 1. Estimates and significance of g for each of the fish stocks considered. The p -value indicates whether g is significantly different from 0. ΔAIC indicates the difference in AIC between model with and without density dependence, a ΔAIC of <2 indicates that there is little evidence for density-dependence of growth, and a negative ΔAIC means that inclusion of density-dependence of growth in the model made it worse.

Species	Stock	g (cm ha ⁻¹ kg ⁻¹)	L_{∞} (cm)	K (y ⁻¹)	Biomass (kg.ha ⁻¹)	p -value	ΔAIC
<i>Clupea harengus</i>	25_29_32	-0.34	17	0.26	13.2	0.000	80.0
<i>Clupea harengus</i>	31	-0.17	17	0.32	9.4	0.000	27.6
<i>Clupea harengus</i>	28	3.67	26	0.22	2.1	0.000	45.9
<i>Gadus morhua</i>	Baltic_22_24	1.53	149	0.13	13.3	0.044	2.4
<i>Gadus morhua</i>	I_II	2.81	216	0.06	6.3	0.002	8.2
<i>Gadus morhua</i>	I_II Coastal	-22.93	155	0.08	0.6	0.367	-1.1
<i>Gadus morhua</i>	IV_VIIa_IIIa	-0.35	129	0.17	7.9	0.286	-0.9
<i>Gadus morhua</i>	IIIa	4.83	166	0.12	2.8	0.008	5.9
<i>Gadus morhua</i>	Va	0.22	142	0.13	28.6	0.188	-0.2
<i>Gadus morhua</i>	Vb1	1.66	126	0.13	5.4	0.099	1.1
<i>Gadus morhua</i>	VIIa	-1.54	123	0.2	3.2	0.157	0.1
<i>Gadus morhua</i>	VIIek	-0.44	132	0.23	3.4	0.816	-1.9
<i>Melanogrammus aeglefinus</i>	I_II	6.23	99	0.13	1.0	0.000	31.1
<i>Melanogrammus aeglefinus</i>	Vb1	0.21	74	0.18	5.7	0.616	-1.7
<i>Melanogrammus aeglefinus</i>	VIIbk	0.03	65	0.31	22.1	0.593	-1.7
<i>Merlangius merlangus</i>	IV_VIIId_IIIa	-1.32	34	0.34	5.9	0.000	13.3
<i>Merluccius merluccius</i>	IIIa_IV_VI_VII_VIIIabd	0.18	164	0.05	1.3	0.972	-2.0
<i>Pleuronectes platessa</i>	IIIa	1.46	48	0.22	3.9	0.452	-1.4
<i>Pleuronectes platessa</i>	IV	-0.04	45	0.24	7.2	0.814	-1.9
<i>Pleuronectes platessa</i>	VIIa	0.59	42	0.31	1.8	0.420	-1.3
<i>Pleuronectes platessa</i>	VIIId	-0.19	45	0.23	5.0	0.725	-1.9
<i>Pleuronectes platessa</i>	VIIe	4.29	54	0.17	0.8	0.065	1.5
<i>Pleuronectes platessa</i>	VIIIfg	2.08	46	0.22	0.6	0.477	-1.5
<i>Polachius virens</i>	I_II	3.52	127	0.1	2.1	0.077	1.2
<i>Polachius virens</i>	Va	0.92	157	0.07	8.5	0.138	0.3
<i>Polachius virens</i>	Vb1	4.47	180	0.08	11.0	0.000	30.6
<i>Solea solea</i>	IIIa	-3.13	32	0.41	0.7	0.086	1.0
<i>Solea solea</i>	IV	2.28	39	0.42	1.2	0.000	11.5
<i>Solea solea</i>	VIIa	4.92	41	0.24	1.0	0.000	15.6
<i>Solea solea</i>	VIIId	-0.49	34	0.38	4.3	0.531	-1.6
<i>Solea solea</i>	VIIe	-3.52	37	0.27	0.9	0.001	8.4
<i>Solea solea</i>	VIIIfg	7.60	51	0.21	0.7	0.032	2.7

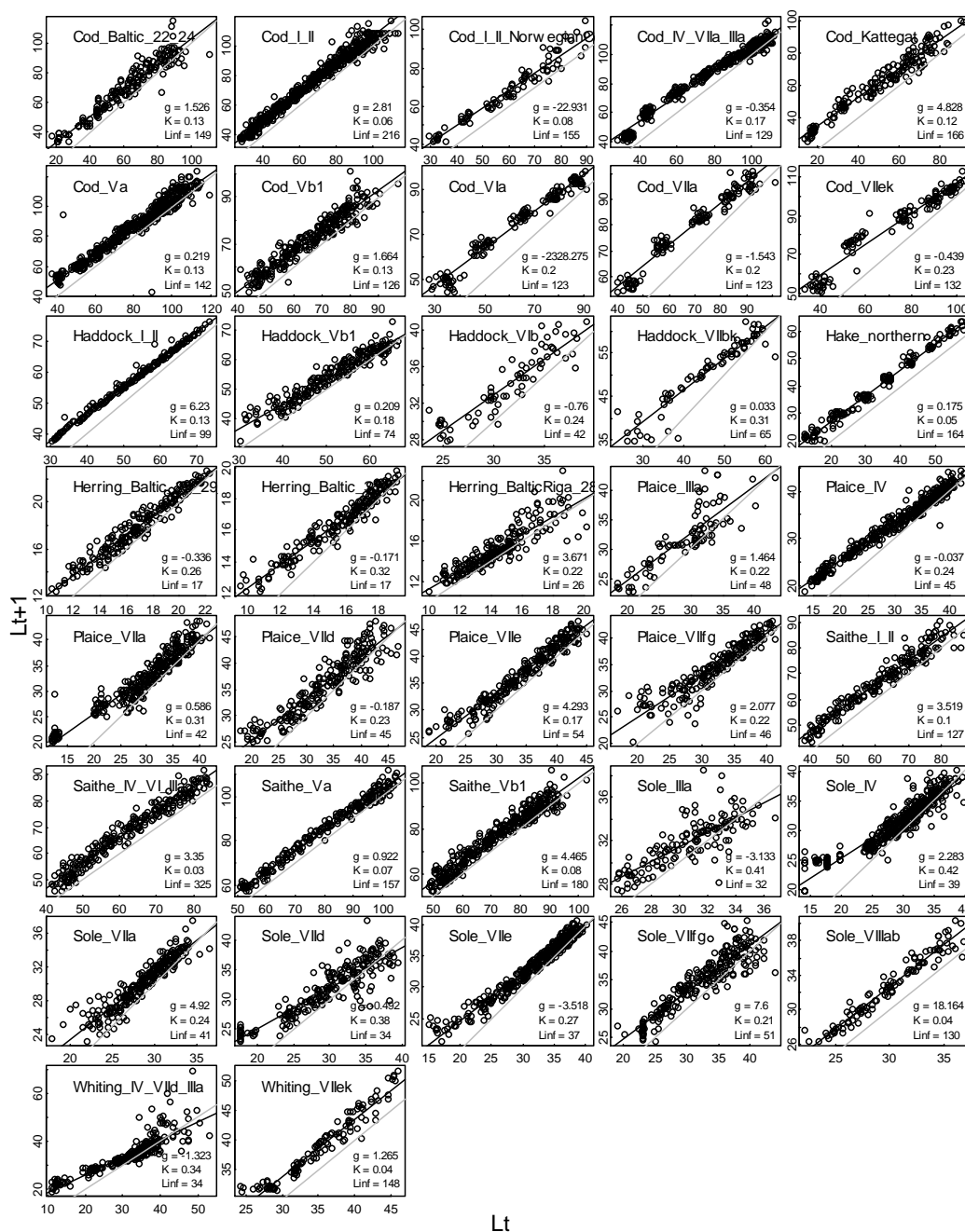


Figure 1. The relationship between L_t and L_{t+1} for each of the fish stocks. L_{∞} is the point where the fitted black line crosses the grey (1:1) line. The variation around the fitted relationships is partly explained by variations in stock biomass for stocks where $g \neq 0$. Species that are present in this figure but not in Table 1 were excluded because the estimated K values was not significantly different from zero. Examples of such species are Saithe_IV_VI_IIIa and Sole_VIIlab.

Table 2. Number of significant effects of g in the fitted models.

	Number of stocks
Significant negative g	4
Significant positive g	8
No significant effect of g	20

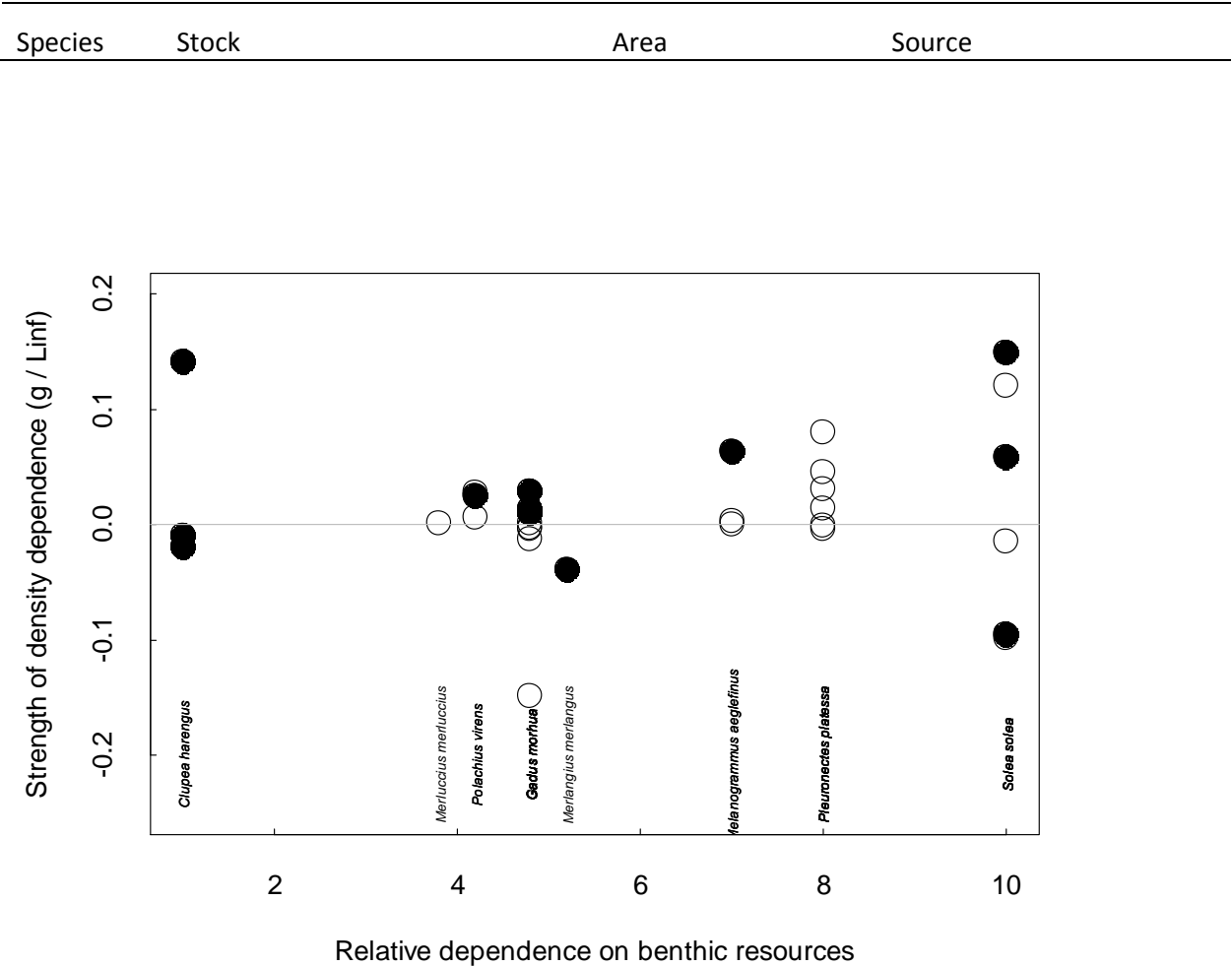


Figure 2. The relationship between the affinity of species to benthic food and habitat and the strength of density-dependence for growth. The facilitate comparison between different species, the strength of density dependence is expressed as $g L_{\infty}^{-1}$ (units $kg^{-1} ha^{-1}$). This therefore indicates the proportional decrease in L_{∞} per $kg ha^{-1}$ increase in biomass. Solid points represent stocks where g was significantly different from zero, open points where g was not significantly different from zero.

We did not find any relationship between the magnitude of g and the dependence of species on benthic resources (Figure 2). The hypothesis that g would be smaller for species that depend more on benthic resources is therefore not supported. The only hint of such a pattern occurring is the observation that the most negative g was found for sole, which is the most strictly benthivorous species, but sole was also the species with the highest observed g .

7.4 Conclusion

The hypothesis that g would be smaller for species that depend more on benthic resources is not supported by these results. This implies that there is no evidence to support the idea that the carrying capacity of the ecosystem to support benthivorous fish is reduced by the bottom trawling fisheries that are targeting these fish species. If such an effect exists, it is therefore likely to be quite small, and this an indication that the effect of bottom trawling on fish productivity is unlikely to be large and to be occurring over large scales.

Cod	Celtic Sea	VIIe-k	(ICES 2006d; ICES 2008d)
Cod	Faroe plateau (Vb1)	Vb1	(ICES 2006a; ICES 2008a)
Cod	Georges Bank	5Z	(Mayo and Terceiro 2005)
Cod	Gulf of Maine	5Y	(Mayo and Terceiro 2005)
Cod	Icelandic	Va	(ICES 2006a; ICES 2008a)
Cod	Kattegat	IIIa	(ICES 2007b)
Cod	Northeast Arctic, Barents Sea (I, II)	I, II	(Hyllen ; ICES 2007a)
Cod	North Sea	IV, IIIa, VIId	(ICES 2007e; ICES 2009d)
Cod	West Scotland	Via	(ICES 2006c; ICES 2008c)
Cod		3NO	(Power, Healey <i>et al.</i> 2005)
Cod		3P	(Bratley, Cadigan <i>et al.</i> 1999)
Haddock	Faroe (Vb)	Vb	(ICES 2007e; ICES 2009c)
Haddock	Icelandic	Va	(ICES 2006a; ICES 2008a)
Haddock	Northeast Arctic, Barents Sea	I, II	(ICES 2007a; Navarrete, Menge <i>et al.</i> 2000)
Haddock	North Sea	IV, IIIa	(ICES 2007e; ICES 2009d)
Haddock	West Scotland	Vla	(ICES 2007f; ICES 2008c)
Haddock		4TVW	(Frank, R.K. Mohn <i>et al.</i> 2001)
Herring	Autumn Spawn	4TV	(LeBlanc, Poirier <i>et al.</i> 2006)
Herring	Baltic	25-27, 28.2, 29, 32	(ICES 2007b; ICES 2009a)
Herring	Baltic	30	(ICES 2007b; ICES 2009a)
Herring	Baltic	31	(ICES 2007b)
Herring	North Sea	IV, VIId, IIIa	(ICES 2007c; ICES 2009b)
Herring	Norwegian Spring Spawning	I, II	(ICES 2007d; Toresen and Østvedt 2000)
Herring	Spring Spawn	4TV	(LeBlanc, Poirier <i>et al.</i> 2006)
Herring		4VWX	(Power, Clark <i>et al.</i> 2006)
Herring		5YZ	(Overholtz, Jacobson <i>et al.</i> 2003)
Plaice	Eastern Channel	VIId	(ICES 2008b; ICES 2009d)
Plaice	Irish Sea	VIIa	(ICES 2007f; ICES 2008c)
Plaice	North Sea	IV	(ICES 2008b; ICES 2009d)
Saithe	Faroe	Vb	(ICES 2007e; ICES)
Saithe	Icelandic (Va)	Va	(ICES 2006a; ICES 2008a)
Saithe	Northeast Arctic, Barents Sea	I, II	(ICES 2007a; ICES 2013)
Saithe	North Sea	IV, VI, IIIa	(ICES 2007e; ICES 2009d)
Saithe		4VWX5YZ	(Stone, P. Perley <i>et al.</i> 2006)
Sole	Bay of Biscay	VIIIa,b	(ICES 2006b)
Sole	Celtic Sea	VIIIfg	(ICES 2006d; ICES 2008d)
Sole	Irish Sea	VIIa	(ICES 2007f; ICES 2008c)
Sole	North Sea	IV	(ICES 2007e; ICES 2009d)
Sole	Western Channel	VIIe	(ICES 2006d; ICES 2008d)

Table S1. Sources of the data used for each of the stocks used in the analyses.

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8 GENERAL DISCUSSION

This report collates the work that has been carried out under Task 4.6. It brings together the results of several different studies that have examined the effect of bottom trawling on the food intake, condition and population productivity of trawled demersal fish populations. It combines the results of empirical and modelling studies, and synthesizes the available knowledge from the literature in order to give the most comprehensive overview of the topic so far.

Some effects of bottom trawling, both positive and negative, on the food intake and condition of commercial fished species was evident at local scales and in models, but such effects were not detected over larger spatial scales. The detected empirical effects at local scales were quite subtle. An effect that can be hard to detect at the local scale will be even weaker when viewed at the shelf sea scale. The effect on those populations that range widely will also be rather small and diffuse. As mentioned before, the effects can be both positive and negative, but there exists only little empirical evidence for positive effects. The models predict that the effects of trawling can be substantial and both positive and negative, but only under a limited set of conditions, at low trawling for species with specific diet. It seems that the flexibility of the diet of fish helps them in overcoming effects of trawling, especially when they can shift to less sensitive prey, which lead to increases in food availability.

In conclusion, the large amount of work done under this WP shows that there is no strong evidence to suggest that bottom trawling has substantial positive or negative effects on commercial fish populations by affecting their food supply.