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Indirect Effects of Bottom Fishing on the Productivity of Marine Fish

Jeremy Collie¹, Jan Geert Hiddink², Tobias van Kooten³, Adriaan D. Rijnsdorp³, Michel J. Kaiser², Simon Jennings^{4,5}, Ray Hilborn⁶

¹Graduate School of Oceanography, University of Rhode Island, Narragansett, RI 02882, USA

²School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey, LL59 5AB, UK

³Wageningen Institute for Marine Resources and Ecosystem Studies, 1970 AB IJmuiden, The Netherlands

⁴Centre for the Environment, Fisheries and Aquaculture Science, Lowestoft Laboratory, Pakefield Road, Lowestoft, Suffolk, NR33 0HT, UK

⁵School of Environmental Sciences, University of East Anglia, Norwich Research Park, Norwich, NR4 7TJ, UK

⁶School of Aquatic and Fisheries Science, University of Washington, Seattle, WA 98195

Corresponding author:

Jeremy Collie

Graduate School of Oceanography

University of Rhode Island

Narragansett, RI 02882, USA

telephone: 401-874-6859

fax: 401-874-6240

e-mail: jcollie@uri.edu

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Abstract

One quarter of marine fish production is caught with bottom trawls and dredges on continental shelves around the world. Bottom-towed fishing gears typically kill 20 to 50 percent of the benthic invertebrates in their path, depending on gear type, substrate, and vulnerability of particular taxa. Particularly vulnerable are epifaunal species, which stabilize the sediment and provide habitat for benthic invertebrates. To identify the habitats, fisheries, or target species most likely to be affected, we review evidence of the indirect effects of bottom fishing on fish production. Recent studies have found differences in the diets of certain species in relation to bottom-fishing intensity, thereby linking demersal fish to their benthic habitats at spatial scales of ~10km. Bottom fishing affects diet composition and prey quality rather than the amount of prey consumed; scavenging of discarded bycatch makes only a small contribution to yearly food intake. Flatfish may benefit from light trawling levels on sandy seabeds, while higher intensity trawling on more vulnerable habitats has a negative effect. Models suggest that reduction of the carrying capacity of habitats by bottom fishing could lead to lower equilibrium yield and a lower level of fishing mortality to obtain maximum yield. Trawling effort is patchily distributed—small fractions of fishing grounds are heavily fished, while large fractions are lightly fished or unfished. This patchiness, coupled with the foraging behavior of demersal fish may mitigate the indirect effects of bottom fishing on fish productivity. Current research attempts to scale-up these localized effects to the population level.

Keywords: beam trawl, benthic disturbance, dredge, fish yield, otter trawl

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Introduction

Demersal fisheries using otter trawls, beam trawls and scallop dredges are widespread on continental shelves and account for about one quarter of the world capture fisheries production (FAO 2009). These gears 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 among different gears and habitats.

While these changes in benthic ecosystems are conservation issues in themselves, 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 (Auster and Langton 1999; Shucksmith *et al.* 2006). 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 that provide refuges, such as sponges and corals, could also increase exposure of juvenile fish to predators. These indirect effects of trawling through changes in habitat and food availability occur in parallel with the direct removal of target fish biomass that would occur with any fishing gear. For these indirect effects to be detected, their negative effects on fish productivity would need to be large relative to the release from intra-specific competition, which results from the reduction of any stock when it is fished. Here, we would like to assess the magnitude of indirect effects of trawling on fish populations, and whether they are important relative to the direct mortality of fish caused by exploitation.

We review the indirect effects of bottom fishing on target species (mostly fish, but also crustaceans such as prawns and mollusks such as scallops). This review is structured around the main indirect mechanisms (Fig. 1) by which trawling could affect fish productivity: 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 target species by dead and dying animals in the trawl path or discards and 5) through changes induced in primary productivity. We will examine the available modeled and empirical evidence in the literature, and use a simple food-web

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 (Collie *et al.* 2000; 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. Throughout the remainder of the paper, we use the term bottom trawling generically for all mobile bottom-fishing gear, including beam trawls, otter trawls and dredges.

Effects of bottom trawling on biogenic habitat and fish refugia

Bottom trawls can affect habitat structure through the removal of sessile epifauna, including soft corals, hydroids and sponges, and can cause changes in the sediment composition and relief. Such changes can reduce the amount of shelter available for fish, or the extent of suitable habitats (Auster and Langton 1999; Lindholm *et al.* 2014). Sessile 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 below).

Commercially important fish and shellfish species use benthic habitats in different ways and at different stages in the life cycle (Kritzer *et al.* 2016). Many studies 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, shell or filamentous hydroid substrate for the settlement, attachment, and survival of their juveniles. Silver hake *Merluccius bilinearis* juveniles orient to sand waves to maintain a hydrodynamic advantage in areas with strong seabed currents (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 and Brown 1993; Tupper and Boutilier 1995). As the cod age, habitat associations persist but become more facultative as their vulnerability to predation decreases with size (Gregory and 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 that directly relate bottom-trawling impacts to habitat use by fish are scarce and outlined below. A large-scale experiment was conducted on the northwest shelf of Australia to test the relative importance of inter and 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 snapper species. 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 of the seabed 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.

Effects of bottom trawling 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 (Brown and Trebilco 2014). Coinciding with an increase in fishing effort, the abundance of small fish steadily and significantly increased in absolute numbers over large parts of the North Sea while the abundance of large (predatory) species declined (Daan *et al.* 2005). 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 simply result from prey release as a result of predator exploitation. The section above 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. Below, 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 few 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 and Cole 1999). Seastars prey on scallops and are also killed by trawls and dredges (Jenkins et

al 2001). If their mortality per unit effort 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 can have a large bycatch of their predator cod (Valentinsson and Ulmestrand, 2008). In the Firth of Clyde, overfishing of groundfish released *Nephrops* from predation pressure (Thurstan and Roberts 2010). Brander and Bennet (1986) modeled the interaction of cod and *Nephrops* in the Irish Sea. They predicted that the total value of cod plus *Nephrops* catch could be increased by reducing the fishing mortality rate on *Nephrops* and increasing fishing pressure on cod, thereby reducing predation mortality.

In summary, there is evidence that target invertebrate species benefit from reduced mortality when their predators are also captured by bottom trawls. In five of the 12 examples cited by Brown and Trebilco (2014), fisheries for vertebrate predators caused increases in the abundance of invertebrate prey species. 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.

Effects of bottom trawling 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 measured 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 of

km. At this scale, chronic and frequent fishing can lead to wide-spread depletion of benthic invertebrate prey species (Hiddink et al. 2006; Hinz et al. 2009). 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 could 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.* (2007) examined the relationship between the lipid content of the muscle tissue of red mullet *Mullus barbatus* and 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 muscle lipid reserves and hence lower body condition. Similarly, Hiddink *et al.* (2011) found that the condition of 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.* (2011) 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 the same heavily trawled areas of the seabed. Smith *et al.* (2013) related differences in the abundance of benthic species to trawling intensity on gravel habitats of Georges Bank. The diets of haddock *Melanogrammus aeglefinus* and winter flounder *Pseudopleuronectes americanus*, both benthic feeders, reflected these differences in species composition. The most insightful study to date is that of Johnson *et al.* (2015) who 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, popular among fishermen, is that bottom trawling “farms the sea”. Bottom trawling may benefit the small benthic invertebrates that form the food source for exploited flatfish by removing the large fauna that compete with small benthos for food and space (Rijnsdorp and Vingerhoed 2001). Bottom trawling would therefore have a positive effect on food production for species that eat small worms and other small invertebrates. 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 intensities, and that incidence of this important prey item in the diet of some flatfish species increased at high trawling (Engel and 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 was unlikely to have a positive or negative effect on their contribution to fish diets. Meta-analyses indicate that, while small benthic species increase in *relative* abundance in response to bottom trawling, on average all taxa decrease in *absolute* abundance (Collie *et al.* 2000, Kaiser *et al.* 2006).

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. Fish feeding in disturbed areas appear able to maintain stomach fullness even as the composition and possibly the energy content of the prey varies.

Energy subsidies generated by bottom trawling

The assemblage of potential prey available to predatory fish can be altered in the short term through the injured or dying fauna, carrion or displaced biota that occur as a result of the direct physical disturbance created immediately in the track and 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 the potential food source (Kaiser and Spencer 1994; Link and Almeida 2002).

Although there have been considerable improvements in the selectivity of some bottom trawls, many non-target fish and invertebrates are still captured by many gears and fisheries. The non-target fish species and benthic invertebrates that are retained in the net are discarded with variable survival, which depends on the configuration of the fishing gear and the prevalent environmental conditions (Kaiser and 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 groundfish (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 (typically between 20 and 50% (Collie *et al.* 2000, Kaiser *et al.* 2006)) and in addition may expose infaunal invertebrates that are normally unavailable to fish predators. For example, Rumohr and Krost (1991) reported the flesh of the clam *Arctica islandica* in the stomachs of cod collected in the vicinity of trawling activity, while Link and Almeida (2002) found that longhorn sculpins *Myoxocephalus octodecemspinosus* fed on the tissues of scallops in areas subjected to scallop dredging. These large bivalves would normally not be available as a food source for these fishes. Such exposed material may be an important food source for scavenging fish and invertebrates if normal

sources of food are limiting and may encourage fish to remain within areas where food resources are scarce.

The food subsidies generated by towed bottom fishing gears flow to scavenging seabirds (Garthe *et al.* 1996), marine mammals and pelagic fish (Hill and Wassenberg 2000), demersal fish and benthic invertebrates (Groenewold and Fonds 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 and Spencer 1994, 1996; Kaiser and Ramsay 1997; Groenewold and Fonds 2000; Hill and Wassenberg 2000). 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 and Fonds 2000). These short-term effects 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). This section attempts to estimate the importance of this food subsidy for demersal fish species.

We assume that the physiological importance of scavenging on carrion that results from trawling depends on what fraction of the energy requirements of fish are met 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 distribution and frequency of trawling disturbance 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 of 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 and Spencer 1994; Kaiser and Ramsay 1997).

Here, we assume that the 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 fish in the trawled area increases by a factor of three after trawling, then (if catchability remains constant) it can be assumed that fish were attracted from an area 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 and Spencer 1994, 1996; Kaiser and Ramsay 1997; Demestre *et al.* 2000; Groenewold and Fonds 2000), and three that examined the stomach contents of fish before and after trawling (Kaiser and Spencer 1994; Kaiser and Ramsay 1997; Groenewold and 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 (Fig. 2a). 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 (Fig. 2b). 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 and Hargrave 1987; Groenewold and Fonds 2000; Bozzano and Sardà 2002), but much smaller than for seabirds, which range from 3 km to 8.5 km (Skov and 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 is necessarily simplistic given the data available and only provides an approximation 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 ($>1 \text{ nm}^2$), the vast majority of fish will not cross from one cell to the next in response to trawling, and the local trawling effort in a cell will therefore be the relevant effort for a fish. If we assume that an area is trawled once a year, trawling effort is distributed homogeneously 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 fish can eat 2.16 times more than they would otherwise be eating 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 take the actual distribution of bottom trawling effort in the North Sea in 2003 as an example (Hiddink *et al.* 2006), this would translate into an

extra 6.0 days of food for the average fish (interquartile range 0.13 – 6.2 days). This suggests that the contribution of carrion to the diet of fish is limited, even in heavily trawled areas like the North Sea.

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 and 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) available, 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.

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 and 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.* 2001), exposure of anoxic layers, release of contaminants, increasing biological oxygen demand (Reimann and Hoffman 1991), and the smothering of feeding and respiratory organs. Suspension feeders may 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. By contrast, elevated levels of suspended particulate matter decreased the growth rates of juvenile king scallops *Pecten maximus* (Szostek *et al.* 2013). Deposit feeding benthos may be negatively affected by trawling due to a loss of surficial sediments and a reduction of the food quality (Watling *et al.* 2001; Mayer *et al.* 1991). 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.

The release of nutrients from the sediment may stimulate primary production; conversely, increased turbidity resulting from suspended sediment may decrease light penetration and hence primary production. Current evidence from models suggests that these processes may have a fairly limited effect on overall primary production (Allen and Clarke 2007). Overall, the available evidence suggests that bottom trawling will only lead to small indirect increases or decreases in the amount of phytoplankton primary production and thus to correspondingly small changes in the food that is available to animals higher in the food chain and fish populations. For other locally important primary producers, such as seagrasses, trawling may lead to reductions in their distribution and abundance, through sedimentation and effects on light availability as well as direct impacts (González Correa *et al.* 2005), and this is also expected to reduce their contribution to local primary production.

In summary, knowledge on the effect of bottom trawling on the resuspension of sediments is limited. The available evidence suggests that it is most prominent in fine sediments. Chronic trawling may reduce the food conditions of benthic detritivores and have a small effect on primary production.

The effect of bottom trawls on fish productivity

In the previous sections we examined the mechanisms; this section examines whether evidence supports the hypothesis that bottom trawling can change the productivity of fish populations. Here, we look at the effects of bottom trawling on the growth of fish and the growth and size of fish populations. Changes in fish condition and growth may become apparent if the feeding opportunities for fish are indirectly affected by trawling, but changes in fish population growth, productivity and size may be hard to detect because of the high natural variation in recruitment and dynamics of commercial fish populations.

The body of empirical evidence for effects of trawling on fish growth is rather limited. Most studies have examined the indirect effects of trawling 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 Celtic Sea, the length-at-age of plaice was lower in more heavily trawled areas on gravel and mud but was higher on sand habitats (Shephard et al. 2010). Plaice in the gravel habitats typically feed on more fragile fauna, such as echinoderms and bivalves, that are more susceptible to trawling. In the North Sea, with a sand dominated seabed, beam-trawl effort has been positively correlated to length-at-age and growth of sole *Solea solea* (Millner and Whiting 1996; De Veen 1976) and plaice (Rijnsdorp and van Leeuwen 1996) but the effect for plaice seems to have disappeared in recent years (Beare *et al.* 2013). On the gravel substrates of northern Georges Bank, length distributions of haddock, yellowtail flounder and cod were shifted to smaller sizes in trawled areas (Smith *et al.* 2013).

The response of fish condition and growth to bottom trawling depends on the interplay between reduced benthic prey abundance and reduced competition for benthic food as fish density declines. In the Irish Sea, plaice abundance and benthic prey declined with increased trawling intensity, but plaice abundance declined more slowly (Hiddink *et al.* 2011). Therefore, the ratio of prey-to-predator biomass and condition of plaice declined monotonically with trawling effort. A recent study in an area of the Kattegat with a steep gradient in bottom trawling intensity allowed the effects on fish and benthic prey abundance to be disentangled (Hiddink *et al.* 2016). This study assessed the impact of bottom trawling on food availability, condition, and stomach contents of three flatfishes, and *Nephrops norvegicus*. Because the abundance of competitors, such as other plaice, dab and *Nephrops*, initially decreased faster than the abundance of prey, an increase in the condition and stomach contents of plaice was recorded up to trawling frequencies of 5 to 6 times per year. Beyond this level, prey abundance dropped faster than competitor abundance and in response, condition fell. These results support the idea that when the abundance of the prey declines in response to exploitation, the ratio of the prey-to-consumer biomass will determine whether exploitation will result in an increase or a decrease in the food intake and condition of the predator.

On longer time-scales, comparison of the growth patterns between modern (AD 1984–1999) and historical otoliths (AD 1200–1925) revealed a considerable 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, such that the effects of trawling and eutrophication are hard to disentangle. Alternatively, a depletion of these stocks may have resulted in more benthic food per fish, and fisheries-induced evolution may have influenced growth rates (Jørgensen *et al.* 2007).

Modelling approaches have been used to explain these empirical patterns (Hiddink *et al.* 2008; van Denderen *et al.* 2013). The models show that the interactions among 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. Hiddink *et al.* (2008) developed a model of benthic invertebrate communities in sedimentary habitats, which was parameterized for the North Sea, and used to evaluate the effect of trawling on the diet of plaice. Model results showed that low levels of trawling (once or twice per year) may increase in the productivity of small polychaetes, thereby improving the feeding conditions for plaice. Higher trawling frequencies resulted in lower benthic production of all size classes and functional groups. 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 in which susceptible benthos have higher energy quality.

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.

Model exploration of the indirect effects of bottom fishing

Existing evidence for indirect effects of trawling on fish productivity is rather limited to a few studies of few species in a small number of ecosystems where there are many potentially confounding variables,

such that the results differ in sign and magnitude. Scaling-up these changes to effects on the population is a further challenge, addressed in very few modeling studies (Hiddink *et al.* 2008; Van Denderen *et al.* 2013). To consider systematically and generically the population-level consequences of the indirect effects of trawling over the life cycle of a fish, we can build on the habitat-dependent production model of Sainsbury (1991), in which the carrying capacity of the fish species depended on the proportion of habitat occupied by large and small benthos, primarily sponges. A similar model was used to demonstrate that the combination of fishing disturbance on the habitat and direct fishing mortality on the target stock reduced the equilibrium yield, causing the maximum yield to be obtained at a lower level of fishing effort (Fogarty 2005).

We extend this approach with a dynamically coupled model of habitat (H), benthic invertebrate prey (B), and target fish species (F), to examine the potential magnitude and implications of indirect trawling effects. The equations describing this coupled system are:

$$\begin{aligned}\frac{dH}{dt} &= r_H(1 - H) - q_H EH \\ \frac{dB}{dt} &= r_B(B_{max} - B) - a_F BF - q_B EB \\ \frac{dF}{dt} &= \gamma a_F BF - PF(a_{PH}H + a_P(1 - H)) - \mu_F F - q_F EF\end{aligned}$$

where fish predators are P and trawling intensity is E . The parameters q_H and q_B are the respective effects of trawling on habitat and benthic prey, relative to the catchability of fish q_F (relative in the sense that when $q_H=1$, the effect 'per unit E ' on habitat equals that on fish). Parameters were chosen that are biologically realistic for these taxa (Table 1), with ranges to illustrate the processes in Fig. 1.

The growth rate of habitat is described as a "semi-chemostat" such that the rate of increase is maximal when $H=0$. This formulation avoids cyclic dynamics of the coupled system. The habitat carrying

capacity is scaled such that H varies between 0 and 1. Benthos is also modeled as a semi-chemostat with B_{max} scaled relative to habitat. Benthos is preyed on by fish with attack rate coefficient a_F . Fish feed on benthos, and turn it into fish biomass with conversion efficiency γ .

It is assumed that biogenic habitat modifies the strength of the fish-predator interaction (dashed arrow in Fig. 1) such that predators have a 10-fold higher attack rate outside 'habitat' than inside. Thus, if habitat extent is reduced by trawling, predation mortality increases. We assume predator abundance P to be constant (in essence, predators become a fixed 'natural mortality' for the fish). We did not include a dynamic equation for predators because the consequences of harvesting predator-prey systems have been well studied (e.g. by Brander and Bennett 1986 and others).

Equilibrium abundance of the model system was calculated numerically using the software MATCONT (Dhooge *et al.* 2003) for a range of fishing efforts, E . We also numerically integrated the equations to investigate how the recovery rate of the fish population depends on the rate of habitat recovery. Six scenarios were run; their letters correspond to the linkages in Fig. 1. Each scenario investigated the consequences of varying the strength of each of the links in turn, while holding the other links constant (Fig. 3).

(a) **Fishing down habitat.** Fishing affects habitat but not the benthic invertebrate prey ($q_B=0$). Increasing q_H substantially decreases the equilibrium yield and the maximum sustainable level of fishing mortality (Fig. 3a). With $q_H=0.2$, yield is already reduced by more than half. Interestingly, the effort level for maximum yield decreases for intermediate levels of q_H and then increases for high levels of q_H , at which point the habitat is depleted at the same rate as the fish. At high levels of q_H , there is no further reduction in fish yield because $H=0$ and the fish can survive in a disturbed habitat.

(b) **Effect of predator abundance.** In this scenario predator abundance was not modeled explicitly; instead equilibrium predator abundance was decreased sequentially, as would occur with predator fishing. Habitat vulnerability $q_H=1$, so with $P=1$, the purple curve in Fig. 3b is the same as the yellow one

in Fig. 3a. As predator abundance declines, equilibrium yield of the target fish species increases.

Without predators, the habitat refuge is no longer important.

(c) **Fishing down prey.** In this scenario fishing affects the benthic prey but not the habitat ($q_H = 0$). With increased vulnerability of the benthos to fishing, the maximum yield declines slightly, but the yield curves become much more dome shaped, such that yield is reduced to zero at a much lower effort level (Fig. 3c). The high sensitivity to benthic disturbance occurs because fish production depends entirely on benthic prey.

(d) **Scavenging.** To simulate the effect of scavenging, a proportion f_C of the benthos killed by trawling is assumed to be turned into carrion (C). Carrion is reduced by fish predation and other decomposition. We add a differential equation for carrion to the system given by

$$\frac{dC}{dt} = f_C q_B E B - a_{FC} F C - \mu_C C$$

where a_{FC} is the fish attack rate on carrion and μ_C is the consumption rate of carrion by species other than the modelled scavenger. The term $\gamma a_{FC} F C$, the carrion intake multiplied by the conversion efficiency, is added to the fish equation as an additional resource. We have assumed that carrion consumption is relatively rapid ($\mu_C = 1$) and that fish are more effective feeding on carrion than on benthos ($a_{FC} = 1.5$). We vary the fraction of fishing-induced dead benthos biomass that ends up as edible carrion (f_C). In this scenario, $q_B = 1$, such that the blue curve in Fig. 3d is the same as the yellow curve in Fig. 3c. Adding edible carrion to the system somewhat increases the maximum yield, which also occurs at higher trawling intensity. It also allows fish to sustain higher trawling intensity before going extinct.

(e) **Prey needs habitat.** In this scenario the preferred benthic prey are assumed to be habitat dependent by setting the carrying capacity of benthos to $B_{max} \times H$. The predator attack rate was set at 0.1

both inside and outside the habitat to isolate the effect of fishing the habitat on the benthos. In this scenario both the maximum yield and the maximum sustainable fishing effort declines sharply with increasing effort for levels of q_H lower than those in Scenario 1 (Fig. 3e).

(f) **Stock recovery in depleted habitat.** The parameters for this recovery scenario are the same as Scenario 1. Note that $q_H=0.2$ depletes the habitat to 0.25. The fish population starts at 1 (<10% of its equilibrium abundance) and then recovers with $E=0$. With increasing initial habitat depletion, the fish stock takes longer to recover because the habitat takes longer to recover (Fig. 3f).

These scenarios show that bottom trawling has mostly negative, but some positive effects on fish yields. The conversion of benthos to prey for scavengers and the reduction of the abundance of predators both increased yields, while yield declined when fishing affected the habitat of fish and benthos, and the benthos directly. These outputs therefore indicate that it is important to understand the strength of the interactions between prey, habitat, fish and their predators and how these are affected by trawling. The model results suggest that the relative importance of these interactions will determine whether their net effect on fish yield is positive or negative. Thus it is unsurprising that the few empirical studies of these processes have mixed results.

Discussion

There are several mechanisms through which bottom trawling can affect the productivity of exploited fish populations; these mechanisms push in different directions with different magnitudes. Although the empirical evidence to quantify the magnitude of each mechanism is quite limited, some generalizations are possible. Biogenic habitats are most vulnerable to bottom trawling disturbance, which can reduce the carrying capacity of fish species by increasing the predation risk to habitat-dependent juvenile stages or reducing the abundance of habitat-dependent prey. Several crustacean species have indirectly benefited from reductions of their fish predators. Flatfish species that feed on

vulnerable benthic prey are most likely to be affected by trawl-induced mortality of benthic macrofauna. In this case, the indirect effect of fishing is to reduce the sustainable exploitation rate of the target species. The effect of trawling on benthic prey can be mitigated to some extent if some of the benthos is available as carrion. While important on short time scales, carrion makes only a small contribution to the annual diet of scavengers. Sediment resuspension by trawling is most important in fine-sediment habitats, where it may have a small effect on primary production and the feeding of benthic detritivores. The general pattern seems to be that the effects of bottom trawling on fish productivity are negative but small relative to the direct effects of reductions in abundance by exploitation.

Bottom fisheries that are currently harvested at sustainable rates must be exploiting species that are able to withstand both the direct and indirect effects of exploitation. For species with a strong dependence on biogenic habitat, the indirect effect of bottom fishing would be to shift the equilibrium yield downward with minor changes in the fishing effort at which MSY would be attained (Fig. 3a). There are some historical suggestions that shelf ecosystems supported higher yields prior to the introduction of mechanized bottom fishing (Bolster 2008), but it is difficult to tell whether high historical catches represented higher productivity or simply fishing down large standing stocks. In the case of Europe, where several population collapses have been recorded, bottom trawl fisheries expanded rapidly in the early 20th century (Kerby *et al.* 2012); such effects would have occurred before the start of standardized fisheries time series. Some species that are exploited with trawls have experienced population collapses, for example cod, ling *Molva molva* and spurdog *Squalus acanthias* (Cook *et al.* 1997; Choi *et al.* 2004). These species eat benthic invertebrates as juveniles and could be negatively affected when young, but all are piscivorous as adults. Nevertheless, the juveniles of these species may depend on habitat complexity for refuges from predation. Based on the estimated rates of fishing mortality, it is much more likely that the direct effects of exploitation caused the declines. However, strong habitat dependence could delay the recovery of a depleted stock, as shown in Figure 3f.

If the predators of the target species are also fished, habitat becomes less important as a refuge from predation. As shown with the food-web model, depleting the predators can result in a yield curve equivalent to the case in which there is effect of bottom fishing on habitat ($q_H=0$ in Fig. 3a). This could be the current situation for heavily depleted fish communities. If so, recovery of predator populations would also require recovery of biogenic habitat to reduce predation on the target fish stock.

Effects of bottom trawling on benthic prey resources

Exploitation of a target fish populations always results in a decrease in the population size. According to fisheries theory, the subsequent reduction in competition for resources leads to an increased growth rate of the remaining fish population, resulting 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.

The interplay between these two processes is illustrated with the food-web model. As the target fish stock is reduced by fishing, predation mortality on the benthos (a_{BF}) diminishes, thereby increasing the per capita production of benthos and fish. This increase in per capita production is countered by the direct effect of fishing on the benthos (q_{BE}). As the vulnerability of benthos to fishing increases, the yield curve for fish becomes increasingly narrow. The maximum yield declines only slightly because the benthic productivity is maintained but the fishing effort for MSY and the maximum sustainable fishing effort decline markedly. This mechanism would imply that a bottom trawl fishery for the target fish species could sustain a lower level of fishing mortality than a fishing gear that didn't impact the benthos, but that the equilibrium yield would be similar for both fisheries. Such an effect on fishing mortality reference points would be difficult to distinguish, given that it would have occurred early in the development of the trawl fishery.

Certain species that have sustained exploitation with bottom trawls for decades, such as plaice, may have benefited from trawling through increases in their food supply, while having little reliance on complex refuges as they bury in the sediment for protection (Gibson 1994; Brown and Trebilco 2014). The occurrence of density-dependent growth in some benthivorous fish, such as haddock on Georges Bank (Brodziak *et al.* 2008), suggests that the per capita availability of prey resources increases when the fish stock declines. In this case, the reduction of predation on benthos outweighs the direct mortality of the fishing gear on benthos. However, cases of density-dependent growth appear to be rare for bottom-trawled species. Lorenzen and Enberg (2002) found evidence for density-dependent growth in only two out of seven bottom-trawled fish stocks, while they found evidence for density-dependent growth in seven of nine other fish stocks.

Using data from the North Sea, Heath (2005) showed that the depletion of demersal fish species may have released the benthos from predation pressure, leading to an increase in benthic production. A complete 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 used production-to-biomass ratios to convert measured body sizes into production estimates (e.g. 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 would need to be measured using repeated sampling for each benthic species present in the community separately.

The effect of bottom fishing on benthic prey is mitigated to some extent if fish scavenge on the prey killed by bottom trawls. The empirical studies we have reviewed indicate that scavenging on carrion generated by bottom trawling makes a small but positive contribution to the diets of some demersal fish. Inclusion of scavenging in the food-web model increased equilibrium fish yield only slightly but

extended the range of sustainable fishing effort (Fig. 3d). Some benthic prey species are associated with biogenic habitat. Examples include species of shrimp, decorator crabs, and tubicolous polychaetes that live in mussel beds (Collie *et al.* 2005). In this case, it is the benthic prey not the target fish species that depend on habitat cover. Both the equilibrium yield (as in Scenaria 1) and the fishing effort for MSY (as in Scenario 3) decline with increased habitat vulnerability to fishing.

Bottom fishing affects fish populations and benthic fauna at different spatial scales because fish are more mobile than their benthic prey. Fishing reduces fish abundance at the scale of the population, while effects on the benthos are local, at the scale of a trawl. Demersal fish feed over areas of 10s of km, integrating over prey patches. Since bottom fishing is patchy over these spatial scales, fish can also integrate over disturbed and undisturbed areas. This may be one reason that stomach fullness does not vary for fish caught in disturbed and undisturbed areas (Dell *et al.* 2013; Johnson *et al.* 2015). Modelling studies of the effects of bottom trawling on fish feeding (Hiddink *et al.* 2008; van Denderen *et al.* 2013, this study) have not accounted for spatial patchiness. Existing spatial models of benthic disturbance do not yet include feedback from the disturbance to fish productivity (Dichmont *et al.* 2008). As a result, the mechanisms illustrated by the models of fish feeding are likely to be attenuated by spatial variability. Studies of fish movement suggest that some demersal fish species move relatively short distances while foraging, compared with their longer seasonal migrations (Dunn and Pawson 2002; Hunter *et al.* 2009). Recent studies that have sampled fish diets and benthic prey resources on spatial scales that are relevant to fish feeding (Smith *et al.* 2013, Johnson *et al.* 2015) do find differences in diet and growth across disturbance gradients. Evidence is accumulating that bottom trawling can affect fish feeding, but the magnitude of this effect is attenuated by spatial patchiness in trawling and prey resources.

Future research to support management decisions

From a research perspective, there is a need to study the mechanistic links between fish and the physical attributes of their habitat to go beyond simple habitat associations. *In situ* tracking of fish in areas of different trawling activity is needed to measure the foraging ranges of demersal fish and whether they may spend more time in high-quality habitats. Fish that feed in areas disturbed by bottom fishing may spend more time foraging, which potentially exposes them to a higher predation risk. Even when maintaining stomach fullness, fish may consume prey with lower energy content, thereby reducing their net rate of energy intake (Kaiser *et al.* 1992). Laboratory experiments are needed to test the effects of prey densities and energy quality on foraging effort and behavior.

A major unresolved question is whether food availability per fish will increase or decrease with bottom trawling? The answer to this question will be species specific, depending on habitat use and diet at different life-history stages, dietary plasticity and the nature of predator-prey interactions. Secondly, 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. A third challenge is 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 the 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.

The impacts and consequences of bottom trawling depend on the spatial 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. Numerous trawl-impact studies, conducted at the scale of individual tows,

have adequately demonstrated the mechanism of seabed disturbance. Trawl-impact studies now need to be conducted at the scale of the fishery, in order to identify thresholds for acceptable intensities and distributions of disturbance given different management and conservation goals.

Conclusions

In conclusion, bottom trawling causes a high level of local mortality to benthic fauna, especially emergent epifauna. Over all cases, the negative effects of bottom trawling on target fish species outweigh the positive effects, but indirect and direct effects are difficult to distinguish. Historically, trawling may have modified habitat and reduced the carrying capacity of fish stocks. For fish species that depend on benthic 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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Table 1: Parameter values of the habitat-benthos-fish model and their interpretation.

Parameter	Value	Meaning
r_H	0.1	Habitat growth rate
r_B	1	Benthic invertebrate prey growth rate
B_{max}	5	Maximum benthic prey abundance
a_F	1	Attack rate of fish on benthic prey
γ	0.5	Conversion efficiency
P	0.1, 0.2, 0.5, 1	Predator abundance
a_{PH}	0.1	Predator attack rate on fish inside habitat
a_P	1	Predator attack rate on fish outside habitat
E	varied	Trawling effort
q_H	0, 0.2, 1, 2	Trawling relative effect on habitat
q_B	0, 0.2, 1, 2	Trawling relative effect on benthic prey
q_F	1	Trawling relative effect on fish
μ_F	0.1	Fish background mortality rate
f_c	0,0.2,0.5,1	Fraction of dead benthos consumed as carrion

Figure Captions

Figure 1. Schematic representation of the effects of trawling on different components of the ecosystem reviewed in this study. Solid lines are the links included in the habitat-benthos-fish model; broken lines are discussed in the paper but not included in the model. Arrows depict positive effects; lines with circles depict negative effects. Letters correspond to the model scenarios.

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.

Figure 3: Equilibrium fish yield as a function of Fishing effort for the scenarios of the effects of bottom trawling: (a) Fishing down habitat; (b) Effect of predator abundance; (c) Fishing down prey; (d) Scavenging; (e) Prey needs habitat; (f) Stock recovery in depleted habitat. H_0 indicates the initial level of habitat depletion.

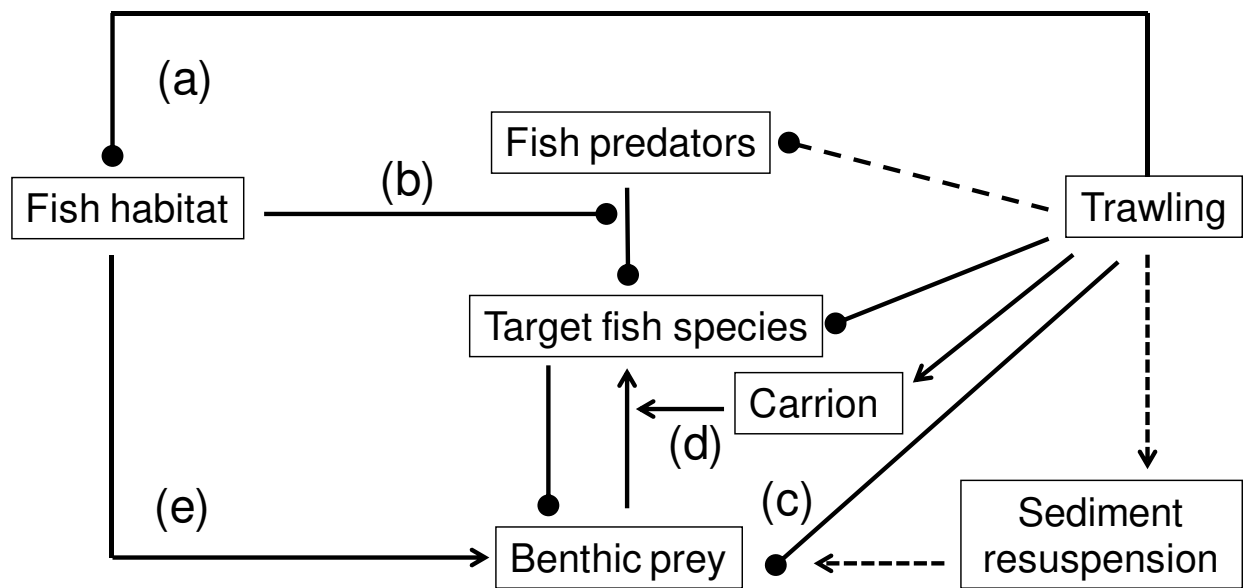


Figure 1.

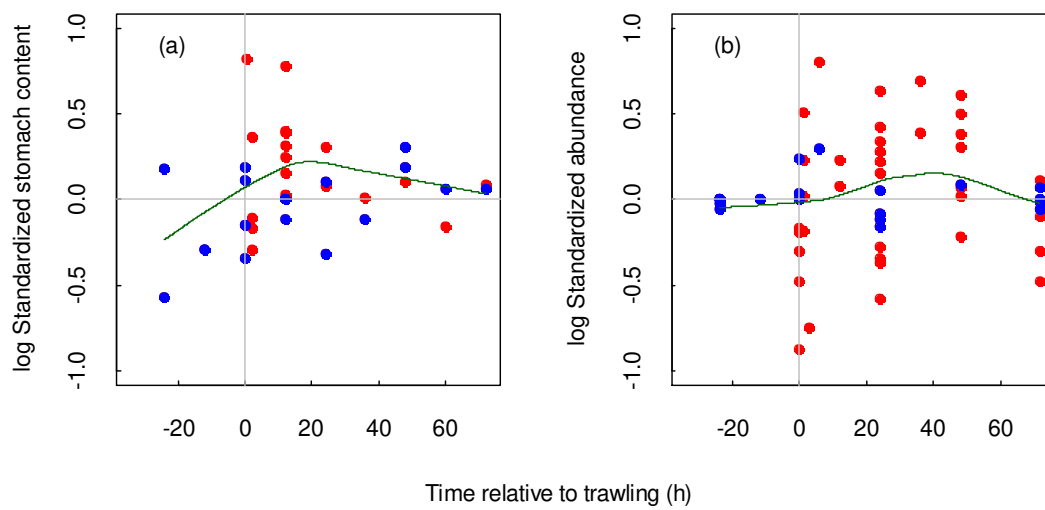


Figure 2.

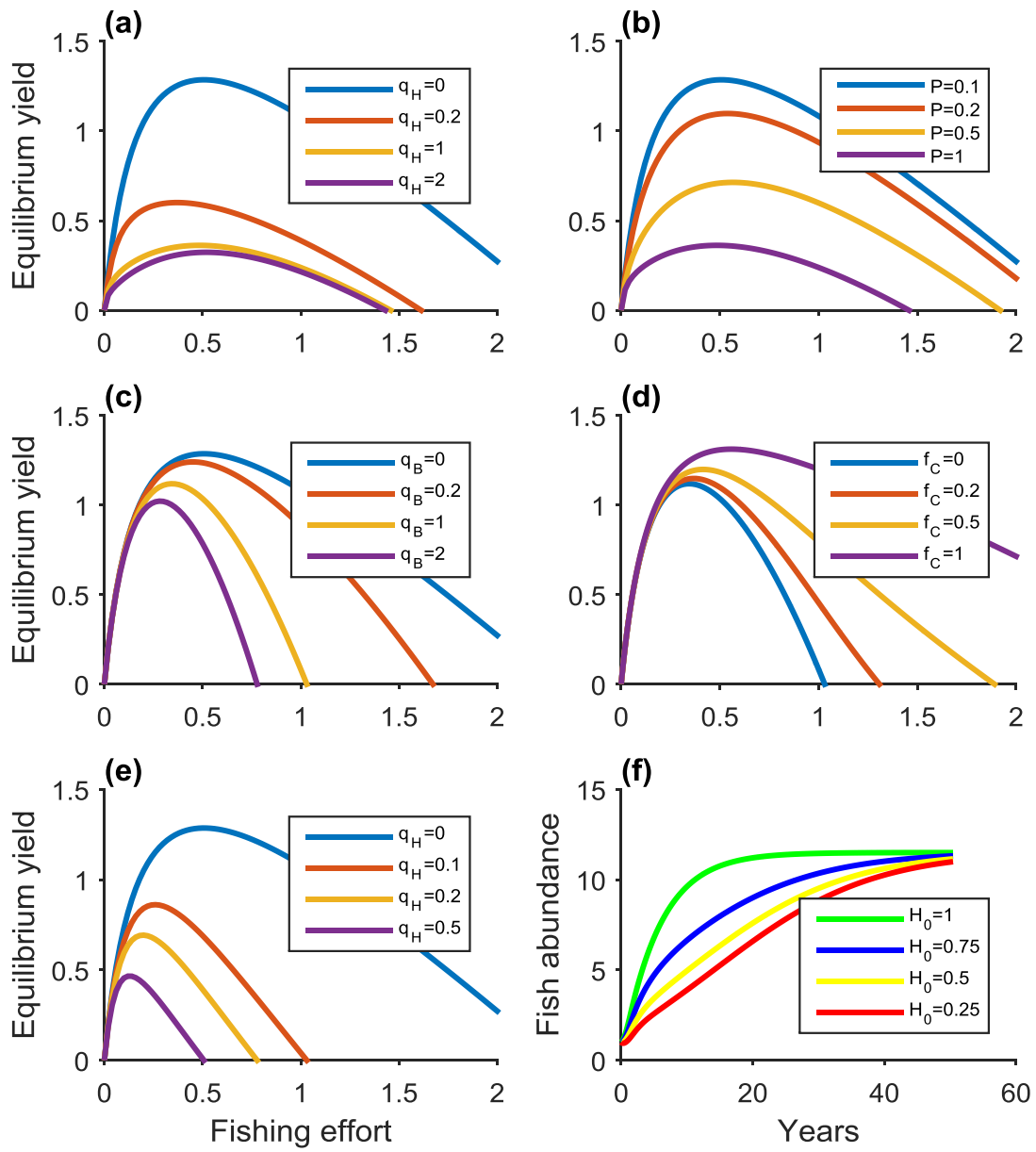


Figure 3