ECOSYSTEM EFFECTS OF BOTTOM TRAWL FISHING

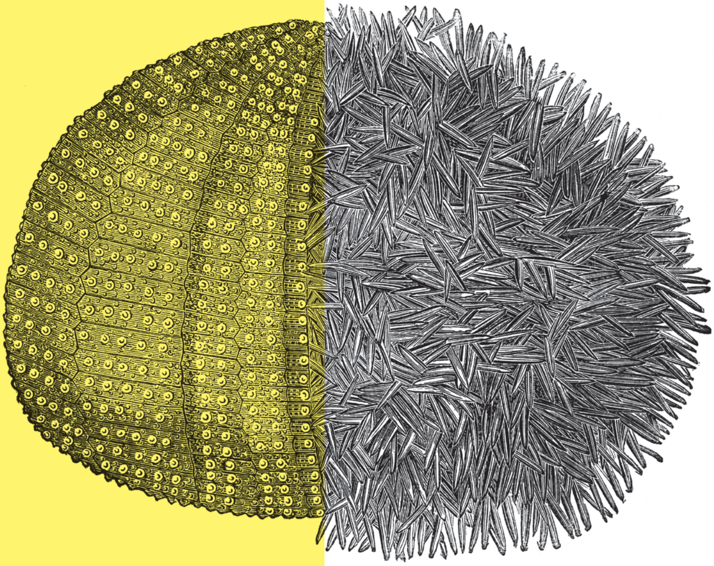

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TABLE OF CONTENT

Chapter 1

INTRODUCTION

OVERVIEW

Marine fisheries are an important contributor to global food security and nutrition and provide about 12% of the animal protein for direct human consumption (Bruinsma 2003). The global marine catch from wild fish stocks strongly increased from the middle of the 20th century until the 1990s and remained at approximately 80 million tonnes annually since (Garcia and Grainger 2005 and references therein).

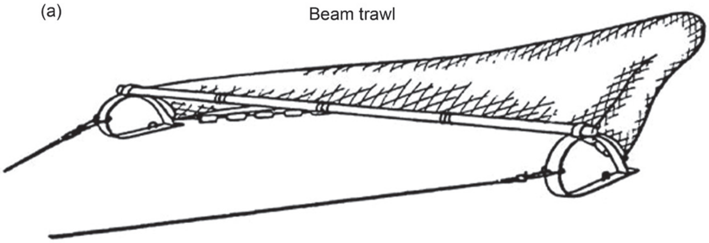
Without any doubt, fisheries have driven many target populations to low abundances (Hutchings 2000). Besides, they have affected non-target species, habitats and complete ecosystems (Dayton *et al*. 1995, Jennings and Kaiser 1998). These changes have been difficult to observe and fisheries management has for long focussed on maximizing the catch of a single target species. Recently, fisheries management started to move towards a management approach in which exploitation of target species is also linked to the environmental effects of the fishery (Hall and Mainprize 2004, Pikitch *et al*. 2004).

One of the most destructive fishing methods that are currently used is bottom trawling. Bottom trawls target demersal fish and benthic invertebrate organisms by dragging a net, or other collection device, over the seabed. Bottom trawl fishing is responsible for about one fourth of the global capture fisheries production (FAO 2009). The effects of trawling on the seabed and the benthic ecosystem have spurred numerous serious concerns starting in the 13th century (de Groot 1984), up to today (Kaiser *et al*. 2002, Puig *et al*. 2012). As a result, bottom trawling has a notoriously bad reputation and due to the side-effects it is thought, it will be hard to arrange into an ecosystem-based fisheries management framework. In this light, I have studied the ecosystem effects of bottom trawl fishing. This thesis largely focusses on bottom trawl fisheries at continental shelf areas that target benthivorous fish.

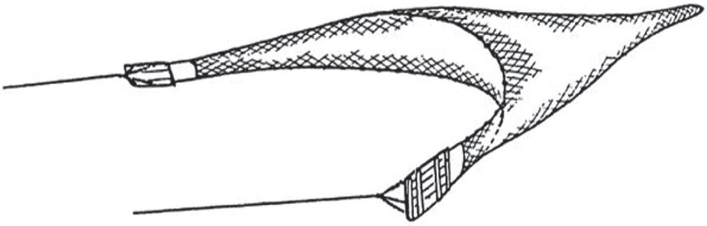
BOTTOM TRAWL FISHERIES

Bottom trawling is a type of fishing in which a net, or other collection device, is dragged over the seabed to catch demersal fish, crustaceans and shellfish. Bottom trawls account for 23% of the global fisheries yield (FAO 2009). Bottom trawl fisheries have a large spatial footprint of approximately 50 million square kilometre of habitat, of which almost half lies in continental shelf seas (Halpern *et al*. 2008). Some of these areas, such as the North Sea and the Georges Bank region, have been intensively trawled for many decades, are heavily trawled today, while trawling can be the most widespread source of human disturbance in the area (Fogarty and Murawski 1998, Eastwood *et al*. 2007, Rijnsdorp *et al*. 2008, Piet and Hintzen 2012).

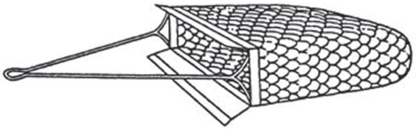
(a) Beam trawl



(b) Bottom otter trawl



(c) Dredges



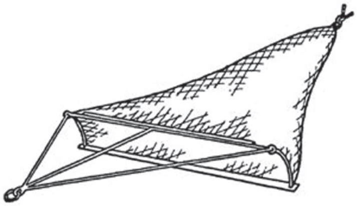


Figure 1.1 The most commonly used gears for bottom trawl fishing are beam trawls (a), otter trawls (b) and dredges (c) (copyright FAO 2001).

The most commonly used gears for bottom trawl fishing are beam trawls, otter trawls and dredges (figure 1.1). Beam trawl gears are generally used to catch flatfish species and shrimps. Their nets are kept open by a horizontal steel beam (FAO 2001). Beam trawling typically disturbs seabed sediment by scraping off sediment with tickler chains to scare the target species off the seabed, and, this may affect seabed sediment up to at least the first six centimetres (Bergman and Hup 1992, Watling and Norse 1998). Effects of otter trawl gears on the seabed are often restricted to the otter boards that stay in contact with the seabed to keep the net open, although impact will vary dependent on gear design (Watling and Norse 1998). Otter trawls are used to catch a wide variety of demersal and bottom species (FAO 2001). Finally, dredges consist of steel frames to which chain-mesh bags are attached that plough over and through the sediment (Watling and Norse 1998). Dredges are generally used to catch molluscs, such as oysters, clams, scallops and mussels.

All bottom trawl gears generate a substantial amount of bycatch of undersized fish and non-target species which are discarded at sea (Alverson *et al.* 1994). In some fisheries, the discarded bycatch even exceeds the marketable fraction of the catch (Kelleher 2005). In addition, bottom trawls cause resuspension of nutrients and organic material into the water column (Riemann and Hoffmann 1991, Grant *et al.* 1997, Pilskaln *et al.* 1998), modify seabed habitats (Dayton *et al.* 1995, Watling and Norse 1998, Kaiser *et al.* 2002, Puig *et al.* 2012), and impose mortality on benthic invertebrate organisms (hereafter also called benthos, figure 1.2) that are not retained by the net (Collie *et al.* 2000a, Kaiser *et al.* 2006). Bottom trawls cause a decline of large, sessile and low productive benthos, as these are most vulnerable to the direct passing of trawl gears and have slowest recovery rates. Short-lived, opportunistic benthos and scavengers/predators are less vulnerable or able to recover more rapidly, and such species usually dominate areas that are trawled frequently (Kaiser *et al.* 2006). The intensively trawled areas are generally less speciose (e.g. Collie *et al.* 1997, Thrush *et al.* 1998, Hiddink *et al.* 2006, Hinz *et al.* 2009) and are altered in their functional composition (Tillin *et al.* 2006, de Juan *et al.* 2007, Kenchington *et al.* 2007). The changes induced by bottom trawling on the benthic community may affect the food availability of benthivorous target fish (see below).

The effects of bottom trawling on a benthic community will also depend on the pre-fished community composition (Kaiser *et al.* 2002). This composition is largely affected by different habitat conditions, e.g. type of sediment and primary production, that change benthic communities in their richness, biomass and function (Probert 1984, Gray 2002, Bremner 2008). This may affect the vulnerability of the benthic community to the effects of bottom trawling. A lower vulnerability is often related to high amounts of natural disturbance (tidal-currents, waves or storms) in an area. High natural disturbance promotes species adapted to naturally occurring disturbance conditions and these species are expected to be relatively resistant to trawl disturbance (Kaiser 1998). In areas exposed to high natural disturbance, community responses to trawling also seem to be smaller or absent (e.g. Kaiser and Spencer 1996a, Collie *et al.* 2000b, Hiddink *et al.* 2006, Kaiser *et al.* 2006, Queirós *et al.* 2006, Tillin *et al.* 2006).

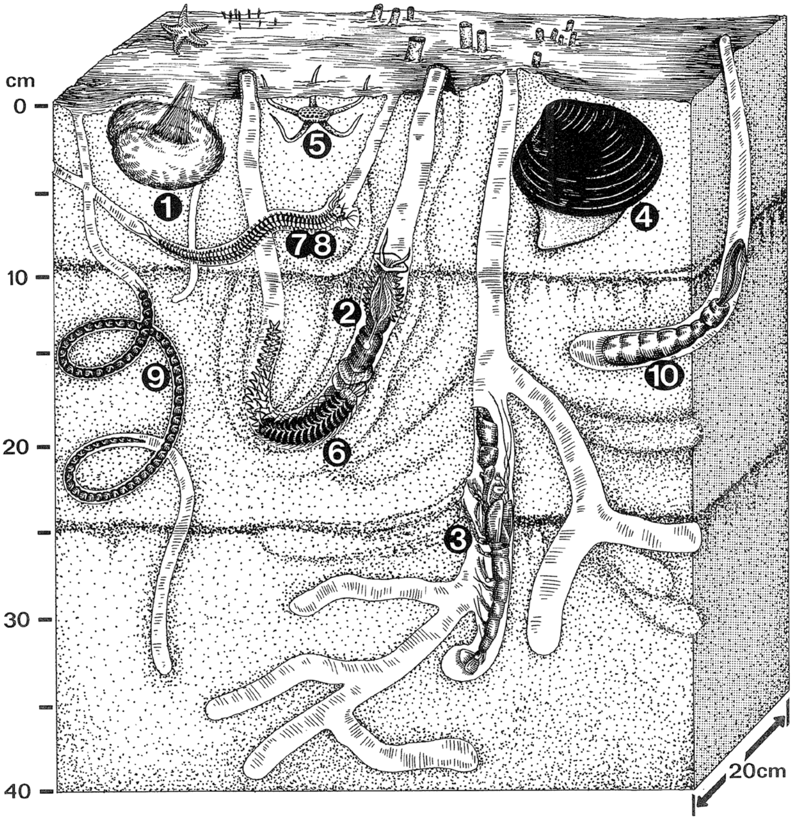


Figure 1.2 Block diagram showing spatial arrangements of dominant macrofauna organisms (benthos) in a muddy sediment in the Oysterground, North Sea. 1. *Echinocardium cordatum*, 2. *Chaetopterus variopedatus*, 3. *Callianassa subterranea*, 4. *Arctica islandica*, 5. *Amphiura filiformis*, 6. *Gatteana cirrosa*, 7. *Glycera rouxii*, 8. *Nereis sp*., 9. *Notomastus latericeus*, 10. *Echiurus echiurus*

(from de Wilde PAWJ *et al*. (1984) Netherlands Journal of Sea Research 18: 143-159, reprinted with permission of Elsevier)

TRAWL-INDUCED CHANGES IN FOOD FOR TARGET FISH

The impact of bottom trawls on the benthic community has led to the question how trawling influences the food availability of benthivorous target fish. Fishermen have for long suggested that trawling modifies the seabed habitat and makes it a more productive area for the target species. This “farming the sea” or “trawl-induced cultivation” has been topic of much debate. Usually, the benthic ecosystem is only described as food for target fish in this discussion, while trawling simultaneously interferes with other ecosystem processes of the benthos.

The first suggestion of trawl-induced changes in food for target fish is related to the direct damaging and killing effects of benthic organisms by trawl gears. This can provide prey that is otherwise protected from fish predation through e.g. their shell or position in the seabed. Such effects were first observed in trawled areas in Kiel Bay (Baltic Sea) where stomach contents of cod (*Gadus morhua*) and dab (*Limanda limanda*) contained high amounts of the large bivalve, ocean quahog (*Arctica islandica*), in frequently trawled areas, while this bivalve is generally protected from predation under natural conditions (Arntz and Weber 1970). Others found this scavenging behaviour of fish in trawled areas as well (de Groot 1984, Kaiser and Spencer 1994) and such behaviour also occurred in areas where discarded material reached the seabed (Wassenberg and Hill 1990, Kaiser and Spencer 1996b). The effect of these food subsidies on the population abundance of scavenging fish is not well understood, but is presumably weak (Groenewold and Fonds 2000). Yet, trawl-induced food subsidies may become an important part of the diet of individual fish over multiple months (Shephard *et al*. 2014).

There is limited evidence that these food subsidies have significantly contributed to the abundance of target fish and incorporation of this process for the management of the fish stock thus seems unimportant (although the food subsidies can be important for bird and marine mammal populations, see Heath *et al*. 2014). However, frequent trawling may also lead to trawl-induced shifts in the benthic community and influence the food availability for benthivorous fish. Changes in benthos in response to trawling have also been shown to alter the benthivorous fish diet compared with untrawled sites (Smith *et al*. 2013, Johnson *et al*. 2014) and historic times (Rijnsdorp and Vingerhoed 2001). This could have affected both growth rates and body condition of benthivorous fish compared with fish that feed in areas where benthic species have not been disturbed by trawling.

Changes in growth rates due to trawl impact were first suggested by Rijnsdorp & van Beek (1991) who observed growth rate increases in different age-classes of plaice (*Pleuronectes platessa*) and sole (*Solea solea*) in the North Sea from the 1960s. The changes in growth rates were only partly explained through density-dependent processes and coincided with increased bottom-trawl disturbance and eutrophication (Millner and Whiting 1996, Rijnsdorp and van Leeuwen 1996). A positive relationship between growth rates of plaice and trawling intensity was also observed in the Celtic Sea in sandy habitat (Shephard *et al*. 2010). This study also showed a negative effect of trawling on fish growth rates in gravelly habitat, potentially reflecting dietary differences between habitats and/or habitat-specific impacts of bottom trawls.

Changes in fish body condition in relation to trawl impact were first suggested by Choi *et al*. (2004), who observed a reduction in groundfish condition at the eastern Scotian Shelf off Novia Scotia from the 1970s onwards. This could potentially be the result of large depletions of groundfish prey through removals of fish and benthos biomass by fisheries. A negative relationship between fish body condition and trawling intensity was more systematically shown by Hiddink *et al*. (2011) in the Irish Sea. In this study, it was found that plaice body condition was reduced at increased trawling intensity, while effects of trawling on dab and whiting (*Merlangius merlangus*) condition were not detected. The decline in plaice condition was explained through a shift towards energy-poor prey and a potential decline in plaice foraging efficiency due to lower prey densities at the trawled sites (Johnson *et al*. 2014).

ECOSYSTEM-BASED FISHERIES MANAGEMENT OF BOTTOM TRAWL FISHING

During the last few decades, a large effort has been made to reduce overfishing. This has resulted in overall reductions of exploitation rates in some of the most heavily fished ecosystems (Worm *et al.* 2009). Trawl fishing has also been reduced for many fish stocks. This has, for example, resulted in relatively healthy groundfish stocks in the North Pacific Ocean off Alaska (Witherell *et al.* 2000) and in highest population abundances of North Sea plaice since the onset of the collection of fish stock data (ICES 2013).

There remains a task for fisheries managers to further reduce bottom fishing to protect trawled target stock, but a larger challenge in the near future will be to reduce the side-effects of trawl fishing on the benthic ecosystem. Concerns about these side-effects have already resulted in an ongoing shift from a single-species management perspective, towards a multispecies fisheries management in which ecosystem health is considered similarly important as the target species conservation (Pikitch *et al.* 2004). In European waters, this has resulted in the development of a marine management strategy in which the occurrence of certain benthic invertebrate species and habitats improves the quality status of the marine environment (European Commission 2010). Still, most management measures to protect either trawled target fish or conserve benthic ecosystems are implemented independent from each other. This is surprising as fish and benthos live in the same habitat, are affected by the same fisheries and are part of the same demersal food web.

A complete ecosystem-based management approach should integrate management decisions of the two different components. This means that there is a need to understand how direct and indirect effects of trawling on both benthos and fish translate into changes in the fish stock, the demersal food web and the structure and function of benthic communities. The **aim of this thesis** is to examine how the interactions between fisheries, fish and benthos affect exploitation of target fish and conservation of benthic ecosystems.

OUTLINE OF THE THESIS

Most of the fisheries management that deals with bottom trawls targeting benthivorous fish, either aims to protect the commercially interesting fish species or the benthic ecosystem. However, these two are tightly coupled, as trawling affects both the fish and benthic fish prey at the same time (Hiddink *et al.* 2011, Smith *et al.* 2013, Johnson *et al.* 2014). In **chapter 2** of this thesis, we examine how interactions between fisheries, fish and benthos affect the impact of trawling on the benthic ecosystem and the amount of target fish food, fish production and fisheries yield. This is studied by varying the relative importance of top-down and bottom-up processes in the benthic ecosystem and by fluctuating the energetic profitability of benthic fish prey species.

The food-web interactions between fish and benthos and trawl impact on benthos also have important implications for the effectivity of marine protected areas (MPAs) to conserve benthos, fish and fisheries yield. However, in current theory regarding the functioning of MPAs, also in relation to bottom trawl fisheries, trophic interactions in the benthic ecosystem are generally not taken into account. In **chapter 3** of this thesis, we discuss how food-web interactions that are potentially affected by bottom trawling may alter the effectiveness of MPAs to protect biodiversity and marine habitats (i), fish populations (ii), fisheries yield (iii) and trophic structure of the community (iv). The effectivity of MPAs for trawled fish stocks is further examined in **chapter 4** of this thesis, by exploring the trade-off between fisheries yield and the conservation of the benthic ecosystem.

Part of the trawl impact on benthos will depend on how much a benthic community is exposed to trawl fishing. Fisheries select areas because they are suitable for the trawl gears and because they have a high abundance of target fish (Fogarty and Murawski 1998, Rijnsdorp *et al.* 2006). These target fish often feed on benthic invertebrates and they are expected to accumulate in highly productive areas, attracted to a high availability of benthic fish food. In **chapter 5** of this thesis, we explore these interactions in an area covering the Dutch part of the North Sea by testing whether there is an interaction between trawl disturbance intensity and primary production and we examine how both factors together affect benthic species richness and biomass.

Within the spatial boundaries of bottom trawl fishing, there is large temporal variation in exposure to trawl impact. This originates from the seasonal patterns in the occurrence of target species. The temporal variation has largely been ignored in studies examining trawl effects on the benthic ecosystem (but see Piet and Quirijns 2009, Ellis *et al.* 2014, Lambert *et al.* 2014). In **chapter 6** of this thesis, we explore these temporal patterns in an area covering the Dutch part of the North Sea for the Dutch beam trawl fleet over a 10-year period. The observed temporal pattern is afterwards used to study how temporal variation in trawling intensity may affect impact of trawling on the benthic community and its potential for recovery.

The impact of bottom trawling on benthic communities is often suggested to be limited in areas exposed to high natural disturbance (Kaiser and Spencer 1996a, Collie *et al*. 2000b, Hiddink *et al*. 2006). This has led to the expectation that natural and trawl disturbance affect benthic communities in a similar way (Kaiser 1998). In **chapter 7** of this thesis, we test this hypothesis over gradients of commercial bottom trawling effort in eight areas in the North and Irish Seas, with data spanning many levels of natural disturbance. Community effects of trawling are examined using a biological trait-based approach.

In **chapter 8** of this thesis, an overview of the thesis findings is presented and I discuss what we can learn from trawl disturbance as an ecological experiment (i), whether there is evidence for trawl-induced cultivation or depletion of food for target fish (ii) and how we can manage bottom trawl fishing by understanding its impact (iii).

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Chapter 2

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

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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.

INTRODUCTION

There is global concern about the effects of bottom trawling on aquatic ecosystems (Kaiser *et al.* 2002, Puig *et al.* 2012). Bottom trawl fisheries target demersal fish, crustaceans and shellfish by towing a fishing gear over the seafloor, thereby not only manipulating the abundance of the target species, but also physically disturbing the seabed, damaging benthic organisms and potentially changing the functioning of the entire benthic ecosystem (Kaiser *et al.* 2002). The FAO estimates that bottom trawling accounts for 23% of the global fishery capture (FAO 2009). This type of fishery occurs predominantly in soft-bottom habitats on the continental shelf, where certain locations may be trawled as often as several times per year (Pilskaln *et al.* 1998, Rijnsdorp *et al.* 1998). The direct impact of the gear on the seabed is seen as a major impediment to sustainability in trawl fisheries (Kaiser *et al.* 2002). A wide variety of gear modifications and gear restrictions are in development to reduce the effect of bottom trawls on the seabed (Valdemarsen *et al.* 2007).

The occurrence and magnitude of mortality from bottom trawling on benthic invertebrates is highly species-dependent. Some, such as large bivalves and crustaceans, suffer high mortality with long recovery times while others, such as certain annelids are virtually unaffected (Kaiser *et al.* 2006). Generally, it is thought that hard-bodied and large benthic invertebrates are affected most, and that chronic trawling induces a shift in the benthic community towards smaller and soft-bodied species (Engel and Kvitek 1998, Kaiser *et al.* 2000, Duineveld *et al.* 2007). Smaller species are also often associated with shorter generation times, which could lead to higher resilience after disturbances (Jennings *et al.* 2001). The trawling-induced shift to smaller species has been shown in several modelling studies (Duplisea *et al.* 2002, Hiddink *et al.* 2008).

Some benthic invertebrates make up the food for flatfish which are targeted by specific bottom trawl fisheries. A debate is ongoing in the literature as to whether bottom trawling can actually increase the food availability for flatfish, by shifting the benthic community towards the ‘fish food’ species (Jennings *et al.* 2001, Jennings *et al.* 2002, Hiddink *et al.* 2008, Hiddink *et al.* 2011). Fuelling this debate, certain studies report increased growth rates of benthivorous flatfish, plaice (*Pleuronectus platessa*) and sole (*Solea solea*), coinciding with higher trawling intensity (Millner and Whiting 1996, Rijnsdorp and van Leeuwen 1996), which could be explained by a trawling-induced shift of productivity towards those benthic invertebrates that the flatfish feed on (Rijnsdorp and Vingerhoed 2001). Others have argued that bottom trawling has negative effects on the food availability (Hinz *et al.* 2009), or that these effects are substrate dependent (Shephard *et al.* 2010). However, none of these studies took into account the feedback effect of fish, feeding on benthic invertebrates, and the manipulation of fish abundance by fishing.

Here we study a model of these interactions among two different types of benthic invertebrates, a fish predator and bottom trawling as a source of mortality for both fish and benthic prey. We do this for a top-down controlled system, where abundances of benthic invertebrates are largely controlled by fish predation and for a bottom-up controlled system where resource limitation determines the abundances of benthic invertebrates, which in turn determines fish abundance. We study both configurations, because the mode of trophic control governs the occurrence and shape of trophic cascades in response to external manipulation of ecosystems, such as fisheries (Pace *et al.* 1999). Both forms of trophic control occur (Menge 2000) and many studies indicate the importance of both predation (for review see Seitz 1998), and competition (Peterson and Andre 1980, Peterson 1982, Nascimento *et al.* 2011) as structuring processes in soft-bottom habitats. It is unclear if there is a single predominant mode of trophic control in soft-bottom benthic ecosystems (Wilson 1991).

Our model describes the generic food web interactions between functional groups (not particular species) and the effects of varying trawling mortality on these groups. Our results apply to benthic ecosystems and bottom trawl fisheries in general. We show that the effects of trawling intensity on the abundances of benthic invertebrates, fish and fisheries yield, depend on the mode of trophic control of the community. Indirect positive effects of trawling on fish abundance and fisheries yield occur in a bottom-up controlled system, when resistant invertebrates are a more profitable prey for fish. The same positive effects may occur in top-down controlled systems when fish have a limited predation impact on benthos. The difference in trawling impact between top-down and bottom-up controlled benthic systems highlight that a mechanistic understanding of benthic community functioning is a prerequisite for successful management of trawled fish stocks and to conserve the benthic community.

METHOD

MODEL DESCRIPTION

We formulated and analysed two different models, dependent on the mode of trophic control, with fish and two benthic invertebrate prey species (hereafter: benthos). The prey differ in vulnerability to trawling and in their profitability to fish.

Benthos follows in both models semi-chemostat dynamics in absence of predation, with turnover rate r and maximum density B_{max}. Interspecific competition is modelled as a dependence of the maximum abundance of each benthos group on the density of the other, implicitly assuming competition for a shared, constant resource, such as space. Both competition for space and food have been observed in field studies in soft-bottom environments (Peterson and Andre 1980, Peterson 1982, Nascimento *et al.* 2011). Explicit modelling of resource competition between benthos using a dynamic resource would lead to competitive exclusion of one of the benthos groups (Hardin 1960).

TOP-DOWN CONTROLLED BENTHIC SYSTEM

The dynamics of both susceptible (B_S) and resistant (B_R) benthos and fish (S) in a top-down controlled system are described by the following ordinary differential equations:

$$\frac{dB_S}{dt} = r(B_{\max} - (B_S + B_R)) - (\alpha S + mf)B_S \tag{1}$$

$$\frac{dB_R}{dt} = r(B_{\max} - (B_R + B_S)) - (\alpha S + \frac{1}{\sigma}mf)B_R \tag{2}$$

$$\frac{dS}{dt} = \alpha S(g_{Bs}B_S + g_{Br}B_R) - (f + \mu)S \tag{3}$$

Predation mortality on the benthos follows a linear functional response, with fish attack rate α. The change in fish biomass depends on attack rate α, and on the abundance and conversion efficiencies g_{Bs} and g_{Br} of the prey species. Mortality rate of fish consists of the trawling intensity f (for fish trawling intensity equals mortality) and natural mortality μ. Benthos is subjected to the same trawling intensity f, but scaled by a factor m. The parameter σ represents the asymmetric trawling vulnerability between the benthos groups. As long as $\sigma > 1$, trawling mortality is always higher for the susceptible than for the resistant benthos, but note that mortality on each benthos group can be both higher or lower than on fish, dependent on m. The fish attack rate α is used to vary the strength of fish predation in a top-down controlled benthic system. At high α, there is a strong impact of fish predation on the abundance of benthos, whereas at low α, the numerical impact of fish feeding on benthos remain small.

BOTTOM-UP CONTROLLED BENTHIC SYSTEM

Benthos is entirely controlled by their resources in a bottom-up controlled system. The problem with such a system is that there is no non-trivial fish equilibrium. Because fish density is unregulated, it either goes extinct, or to infinity. One way to overcome this is by assuming that fish biomass is an instantaneous function of its environment, in terms of food and mortality. This approximation of equilibrium fish biomass is achieved by setting equation (3) equal to zero and solving for S (equation 6). The bottom-up regulated system is then described by:

$$\frac{dB_S}{dt} = r(B_{\max} - (B_S + B_R)) - mfB_S \tag{4}$$

$$\frac{dB_R}{dt} = r(B_{\max} - (B_R + B_S)) - \frac{1}{\sigma} mfB_R \tag{5}$$

$$\frac{dS}{dt} = \frac{\alpha(g_{Bs} B_S(t) + g_{Br} B_R(t))}{(f + \mu)} \tag{6}$$

Where equations (4) and (5) are equal to (1) and (2) minus the effect of fish feeding on benthos.

ASYMMETRY IN PREY PROFITABILITY

Since benthic species differ in energetic content, defence mechanisms against predation (shells, for example) and vertical position in the seabed, asymmetry in benthos edibility to fish may be expected. This asymmetry has been implemented in our model using the conversion efficiency g. This reflects our choice to keep the model as simple and generic as possible. Both higher conversion efficiencies of the resistant benthos group ($g_{Bs} < g_{Br}$) and higher efficiencies of the susceptible benthos group ($g_{Bs} > g_{Br}$) have been studied. Besides using the conversion efficiency, we have studied two alternative types of asymmetry (difference in productivity and in prey-specific edibility), and find no qualitative difference with our results (appendix 2.1).

PARAMETERIZATION

We used semi-chemostat dynamics to describe invertebrate growth, which means that no predator-prey cycles occur (de Roos *et al.* 2008). Parameters r and B_{max} can be chosen arbitrarily without affecting the qualitative behaviour of the model (de Roos *et al.* 2008). We assumed a 40-fold difference (σ=40) in trawling vulnerability between susceptible and resistant benthos groups. This is in line with direct beam trawl mortality estimates of 20-30% for susceptible and <0.5% for resistant species, particularly annelids (Bergman and van Santbrink 2000). However, trawling vulnerability between susceptible and resistant benthos groups may vary dependent on type of trawl and habitat (Kaiser *et al.* 2006). For that reason, the sensitivity of model outcome is tested in the result section for a range of σ values.

Piet *et al.* (2000) estimated the mean annual trawling mortalities for the most susceptible macrobenthic species in the Dutch sector of the North Sea at 31-44%. This is comparable with the mean annual fishing mortality for plaice and sole, 49% and 45% respectively, in the North Sea during the same period (ICES 2012). Hence, we set the trawling mortality of susceptible benthos equal to that of fish, while resistant benthos have mortalities 40 times as low ($1/\sigma$). We used fish natural mortality μ=0.1 y^{-1}, which is also used in stock assessments of plaice and sole (ICES 2012). Parameter values are summarized in table 2.1.

Table 2.1 Model parameters and their values.

Description	Symbol	Default value	Unit
Benthic growth rate	r	1	y^{-1}
Benthic carrying capacity	B_{max}	2.5	$m\,V^{-1}$
Fish attack rate	α	0 - 1	y^{-1}
Susceptible benthos conversion efficiency	g_{Bs}	0.3 or 0.6	$m\,m^{-1}$
Resistant benthos conversion efficiency	g_{Br}	0.3 or 0.6	$m\,m^{-1}$
Fish natural mortality	μ	0.1	y^{-1}
Trawling intensity	f	varied	y^{-1}
Benthos asymmetric vulnerability to trawling	σ	40	-
Scaled gear impact of trawling on benthos	m	0 - 4	-

Note: y = year, V = unit of volume, m = unit of mass

ANALYSIS

We showed the long-term effects of trawling on benthos and fish by numerical continuation of equilibrium biomass densities of the system with changing parameter values, using the software package Content (Kuznetsov *et al.* 1996). Trawling intensity f, attack rate α, conversion efficiencies g_{Bs} and g_{Br}, benthos asymmetric vulnerability to trawling σ and the scaled trawling impact on benthos m were all varied.

RESULTS

MODEL DYNAMICS OF BENTHOS AND FISH

In a bottom-up controlled system benthos biomass remains at carrying capacity (B_{max}), independent of fish attack rate, while the net biomass production remains at zero. Fish biomass increases linearly with increasing attack rate (figure 2.1, dashed lines).

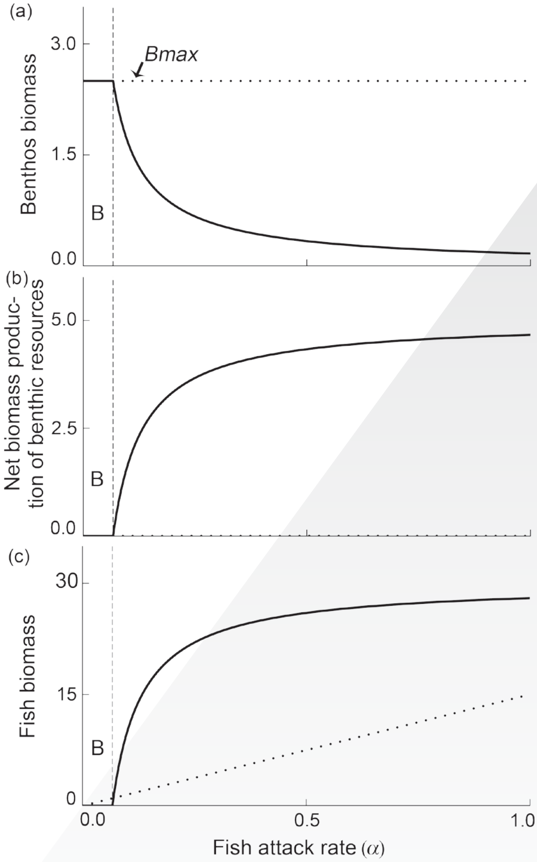

Figure 2.1 Benthos biomass (a), net biomass production of benthic resources $r(B_{max} - (B_S + B_R)) + r(B_{max} - (B_R + B_S))$ (b) and fish biomass (c) as function of the fish attack rate α (both (a) and (b) are the sum of B_S and B_R). The solid lines show model results when system is top-down controlled, while dotted lines show model outcome when system is bottom-up controlled (dotted line in (b) is at zero). At low values of α, fish cannot persist in a top-down controlled system (to the left of the vertical dashed lines). Higher values of α increase fish predation and this results in coexistence between both benthos and fish. B, persistence of benthos without fish. $f = 0$, $m = 0$, g_{Bs} and g_{Br} are both 0.6, all other parameters have default values.

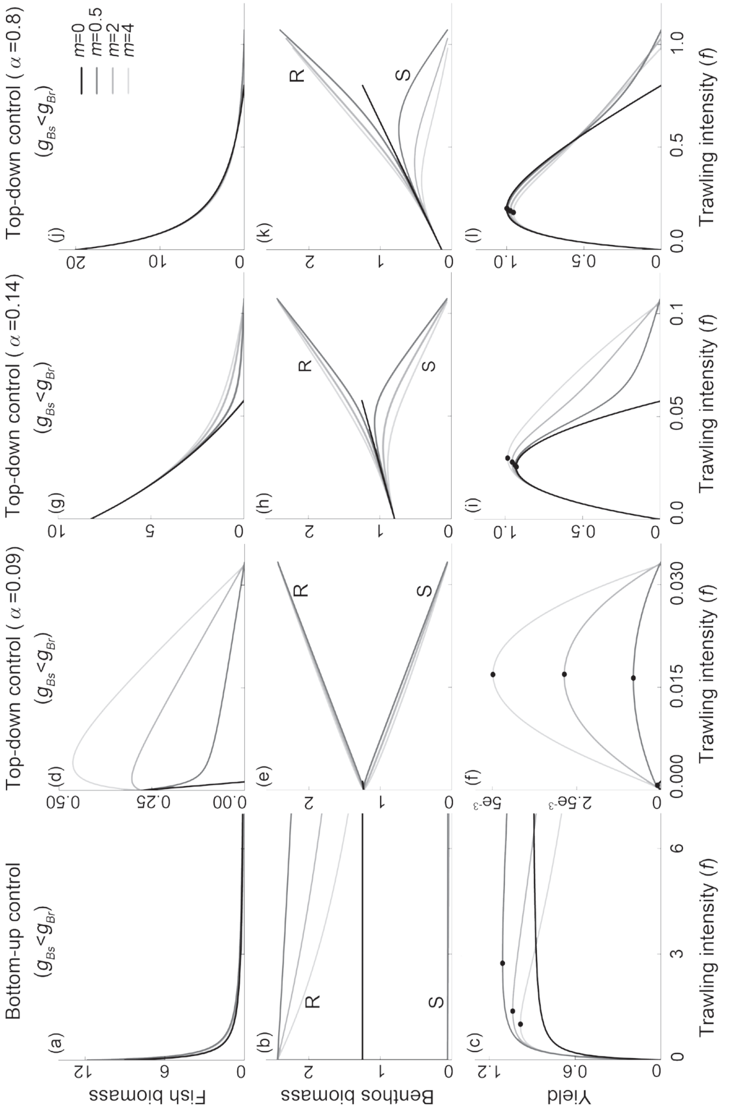

Figure 2.2 Impact of bottom trawling (by varying *f*) on fish biomass, benthos biomass and yield, the product of the trawling intensity (*f*) and fish density, in a bottom-up controlled system (a-c) and three systems with various strengths of top-down control (d-f, α = 0.8; g-i, α = 0.14; j-l, α = 0.09). Resistant benthos are more profitable food for fish ($g_{Bs} < g_{Br}$). The different grey coloured lines present different scaled trawling mortalities on benthos (*m*). Susceptible and resistant benthos (in b, e, h and k) have the same biomass levels at *m*=0. All lines above this black line (*m*=0) show biomass levels of resistant benthos (marked with R), while all lines below this black line show biomass levels of susceptible benthos (marked with S). The dots (in c, f, i and l) represent maximum sustainable yield levels. g_{Bs} = 0.3, g_{Br} = 0.6, all other parameters have default values.

Contrastingly, in a top-down controlled system there is a minimum fish attack rate (α) below which fish cannot persist even in absence of fishery and where benthos abundances equal carrying capacity (figure 2.1, solid lines). Close to this persistence threshold, fish equilibrium abundance is low and its effect on the benthos equilibrium densities limited. The presence of fish induces increased net biomass production of both benthos groups. This effect becomes more pronounced at higher attack rate as feeding by fish reduces competition among the benthos (figure 2.1b). The increased net production leads to strongly increased fish equilibrium abundance (figure 2.1c).

IMPACT OF BOTTOM TRAWL FISHERY ON BENTHOS AND FISH

Bottom trawling increases the mortality of fish and potentially of benthos, and changes the predation pressure on, and the competitive interactions between the two benthos prey groups. The ecosystem effects of trawling depend on whether the system is bottom-up or top-down controlled (figure 2.2).

In a bottom-up controlled system, fish predation has no effect on benthos. Therefore, when fishing only affects fish (m=0), trawling simply reduces fish density (figure 2.2a). When trawling does affect benthos (m>0), both benthos and fish respond to trawling. For any degree of asymmetry (σ>1) between the susceptible and resistant benthos, trawling causes susceptible benthos to lose competition with resistant benthos and this reduces susceptible benthos to very low abundance, while resistant benthos abundance strongly increases (these initial changes occur at low f and are not visible in figure 2.2b). Further increasing trawling intensity leads to a gradual reduction of the resistant benthos (figure 2.2b). When the resistant is also the more profitable benthos ($g_{Bs} < g_{Br}$), trawling increases the quality of the available prey for fish and can cause a positive relationship between fishing intensity and fish abundance. This positive relationship between trawling intensity and fish abundance occurs up to a certain maximum trawling intensity (f) (not visible in figure 2.2a as it occurs at very low levels of f), which decreases with the strength of the direct effect of trawling on benthos (m), but increases with σ, the degree of asymmetry of this effect on benthos (figure 2.3a, b).

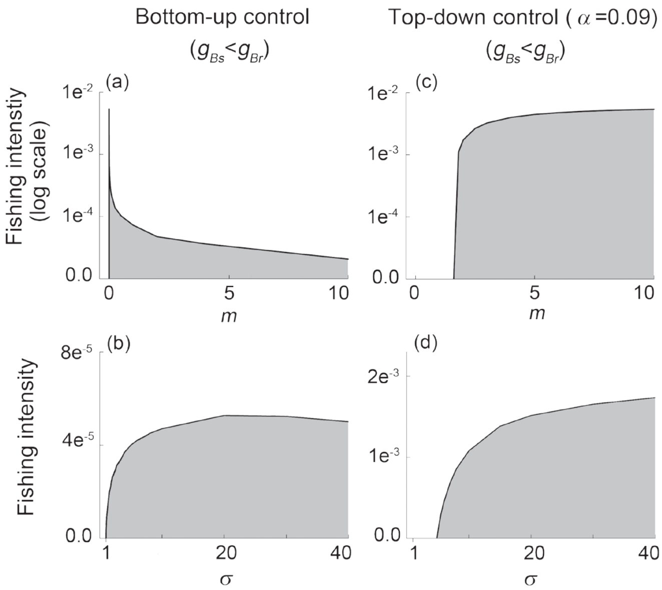

Figure 2.3 The increase in fish biomass (occurring inside the grey area) as a result of bottom trawling, in relation to the trawling intensity (*f*) and the scaled fishing mortality on benthos (*m*) (a, c) or the relative impact of bottom trawling on resistant compared to susceptible benthos (σ) (b, d) in a bottom-up controlled system (a-b) and a system with weak top-down control (α = 0.09, c-d). g_{Bs} = 0.3, g_{Br} = 0.6, m = 2 for (b, d), all other parameters have default values.

If, in a bottom-up controlled system, susceptible benthos is the more profitable prey ($g_{Bs} > g_{Br}$), the decline in fish abundance with trawling intensity is accelerated at higher m because the quality of the available prey is reduced (figure 2.4a). This results in less fish and lower fishery yields (figure 2.4b).

Under both strong and intermediate top-down control, (α=0.8 and 0.14), trawling reduces the abundance of fish (figure 2.2d, g). Initially, this leads to higher biomass of both benthos groups, as they suffer reduced predation mortality (figure 2.2e, h). When there is a direct effect of trawling on benthos (*m*>0), the positive effect on the susceptible benthos is reduced, while that on the resistant benthos is reinforced by reduced competition. This divergence is stronger, the larger the effect of trawling on benthos. At high trawling intensity, the upward trend is reversed in the susceptible species as direct trawling mortality outweighs reduced predation mortality.

With any degree of top-down control, trawling intensity drives fish to extinction at the point where fish intake can no longer compensate for mortality (figures 2.2d, g and j). Generally, this occurs at higher trawling intensity as fish

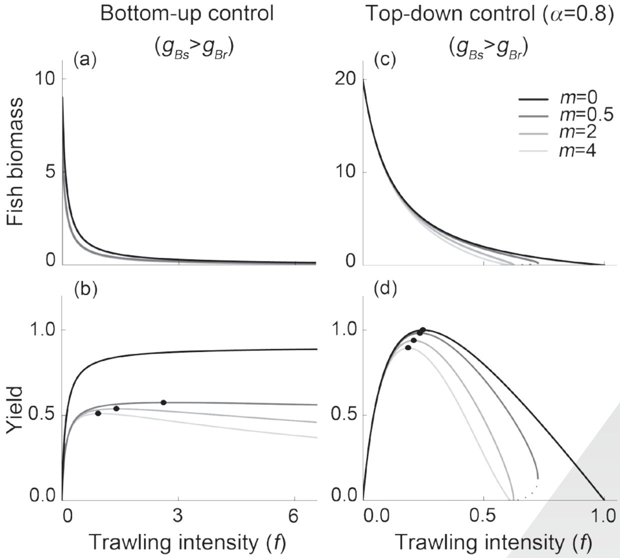

Figure 2.4 Impact of bottom trawling (by varying f) on fish biomass and yield, the product of the trawling intensity (f) and fish density, in both a system which is bottom-up controlled (a-b) and a strong top-down controlled system (c-d, α = 0.8). Susceptible benthos are more profitable food for fish ($g_{Bs} > g_{Br}$). Solid lines correspond to stable equilibria, dashed lines to unstable equilibria. g_{Bs} = 0.6, g_{Br} = 0.3, all else is similar to figure 2.2.

attack rate increases (compare figures 2.2f, i and l). When the resistant benthos group is also the more valuable fish food ($g_{Br}>g_{Bs}$), a direct effect of trawling on benthos (m>0) extends the range of trawling intensity under which fish can persist, because the food quality subsidy it incurs makes up for part of the added mortality on fish. Furthermore, under a range of trawling intensity, a direct effect of trawling on benthos increases both fish biomass (figure 2.2d, g and j) and fishery yield (figure 2.2f, i and l). The opposite occurs when susceptible benthos are more profitable prey (figure 2.4c, d): the stronger the direct effect of trawling on benthos (m), the lower the fish abundance and yield and the earlier fish go extinct.

A weakly top-down controlled system (α=0.09) behaves somewhat similar to a bottom-up controlled system, because fish have only a limited impact on benthos. It shows both increasing yield with higher m and a positive relationship between trawling and fish biomass (figure 2.2j, l). However, this positive relationship only occurs when both the trawling effect on benthos and the asymmetry in trawl susceptibility between benthos groups are large enough (figure 2.3c above m~1.6, 2.3d above σ~5).

IMPACT OF BOTTOM TRAWL FISHERY ON MAXIMUM SUSTAINABLE YIELD

In a bottom-up controlled system, maximum sustainable yield (MSY) is generally higher and occurs at higher trawling intensity, the smaller the effect of trawling on benthos. When there is no effect on benthos at all (m=0), maximum yield occurs at infinitely high trawling intensity and can hardly be classified as sustainable, because it occurs at infinitely low fish biomass (figure 2.2a, c).

As trawling intensity increases and fish abundance is reduced, any top-down regulated system behaves more ‘bottom-up’, as fish are decreasingly able to control benthos biomass. At weak and intermediate top-down control, this shift occurs relatively early and leads to an increased MSY with higher m (figure 2.2i, j). The same shift occurs in a strongly top-down controlled system but at fishing intensities higher than MSY, which, as a result, only lowers MSY with stronger trawling effect on benthos (figure 2.2f). The same decrease in MSY with increasing m occurs when the susceptible prey is the more profitable (figure 2.4b, d).

DISCUSSION

We have shown that direct mortality of trawl fishery on non-target benthic organisms can lead to persistence of fish up to higher trawling intensities, increased fish biomass and (maximum sustainable) fisheries yield, and a positive relationship between fish abundance and trawling intensity. The presence of these indirect effects depends on the mode and degree of trophic control (top down or bottom up) of the benthic organisms, and on the relative susceptibility of the most important benthic fish prey to trawling.

When the benthos which is the best quality fish food is also more resistant to trawling than the lower quality benthos, trawling mortality on benthos can lead to higher fish biomass, independent of the mode of trophic regulation. In top-down controlled systems, this also extends the maximum trawling intensity at which fish can persist. The increase in fish biomass leads to higher fishery yield under both top-down and bottom up control, and to higher MSY under all but the strongest top-down control. When susceptible benthos are the most profitable prey, trawling reduces fish abundance, yield and persistence of fish in all situations.

Under bottom-up and weak top-down control, a positive relationship between trawling intensity and fish biomass emerges as fishing increases the quality of the available prey to such an extent that it more than offsets the direct mortality it imposes on fish. This occurs over a wide range of non-target effects of trawling, but only at low trawling intensity (figure 2.3). It is hence expected primarily in newly-fished benthic ecosystems, where it could lead to an initial peak in fish abundance. Contrastingly, increased (maximum sustainable) yield and persistence of fish occur at higher trawling intensity, and so are more relevant to the management of highly exploited ecosystems.

Our analysis shows that in both top-down and bottom-up controlled systems, the abundance of the resistant benthos is positively related to trawling intensity, as a result of either reduced fish predation or interspecific competition. This corresponds with empirical observations of increased abundance of Annelids and polychaetes, generally considered resistant to trawling, in heavily trawled areas (Engel and Kvitek 1998, Kaiser *et al.* 2000, Duineveld *et al.* 2007). However, such observational data does not allow us to distinguish between the two possible mechanisms (reduced predation or competition).

Fishing generally leads to reduced abundance of susceptible benthos in our model. This is also found in a number of field studies which have shown a higher abundance of susceptible invertebrates, such as large bivalves and spatangoids, in areas with lower trawling intensities (Kaiser *et al.* 2000) or areas closed for bottom trawling (Murawski *et al.* 2000, Duineveld *et al.* 2007). Our model shows that the impact of bottom trawling on susceptible benthos can be mitigated by reducing the mortality imposed by trawling. This may be accomplished by either reducing fishing effort, or through technical adaptations reducing the direct impact of the trawl on the sea bed. Development of such less destructive trawls is an active field of research (Valdemarsen *et al.* 2007, Soetaert *et al.* 2015). Our results indicate that this may actually, dependent on the mode of trophic control and asymmetry in prey profitability, lead to reduced fish abundance and yield.

The trawling-induced effects on the food availability for fish affect MSY differently in top-down or bottom-up controlled systems (figure 2.2, yield). A positive effect of trawling on resistant benthos leads to an increased fish abundance and MSY in a bottom-up controlled system (figure 2.2a, c). This phenomenon occurs at trawling impacts on benthos which reflect those found in the North Sea. There are indications that in the North Sea, the more profitable prey (in particular polychaetes) are also more resistant to trawling (Rijnsdorp and Vingerhoed 2001), which is the configuration for which we find a positive effect of benthic trawling mortality on fish abundance and yield.

Several studies have found faster growth of benthivorous fish with higher trawling intensity (Millner and Whiting 1996, Rijnsdorp and van Leeuwen 1996, Shephard *et al.* 2010). Contrastingly, Hiddink *et al.* (2011) found, in the most comprehensive study on this interaction, a negative relation between the condition of plaice individuals and trawling frequency in a field study in the Irish Sea, while no effect of trawling was found on the condition of dab (*Limanda limanda*). They hypothesized that trawling could indirectly affect growth of target species, resulting in lower fisheries yield. This result is compatible with the model configuration with strong top-down control and/or the susceptible benthos being the most profitable prey, in which case there is no trawling-induced increase in fish resources and the highest MSY occurs when there is no impact of trawling on benthos at all (m=0 in figures 2.2f and 2.4b, d). In this case, the use of fishing gears that minimize benthic mortality would lead to higher abundance, catches and increased persistence of fish. To our knowledge there are no studies measuring the long-term consequences of indirect effects of trawling on fish abundance and MSY.

The response of our modelled community to trawling depends strongly on the asymmetry between the two benthos groups not only in their vulnerability to trawling, but also in their role in the food web. We have used the conversion efficiency parameter as a generic way to impose such asymmetry, but alternative mechanisms are easily conceivable. One alternative is a difference in edibility (or preference) of the benthos groups to fish. We have shown that the results of our analysis are qualitatively identical under this assumption (appendix 2.1). Another possibility is that one group has a higher intrinsic growth rate (is more r-selected, see MacArthur and Wilson 1967) and can more efficiently recolonize the ‘free space’ created by trawling. Assuming that such fast-growing species would generally be smaller, Jennings *et al.* (2002) hypothesized that increasing trawling intensity would coincide with smaller benthic invertebrates. Because fish are gape limited (Piet *et al.* 1998), a shift to smaller individuals in the benthic community means that a larger proportion is edible to fish. Jennings *et al.* (2002) did not find this effect in field data, but they have no information on fish presence or feeding in their study area, which may have confounded their results. Asymmetry in productivity between susceptible and resistant benthos (appendix 2.1) does not quantitatively change our results. The addition of size structure and size-dependent predation in the benthos community is beyond the scope of this study, but could profoundly affect community dynamics and response to trawling (van Kooten *et al.* 2005, de Roos *et al.* 2008).

Besides a shift towards more profitable prey, other mechanisms by which trawling may increase the food availability for benthivorous fish have also been suggested. The physical disturbance of the seabed and resulting resuspension of nutrients may have increased the primary productivity (Riemann and Hoffmann 1991, Pilskaln *et al.* 1998). This higher productivity could then lead to increased benthic productivity. Others have suggested that food subsidies due to discards and killed organisms in the trawl path can also positively affect the food availability for fish, by delivering easy prey for (scavenging) fish (Kaiser and Spencer 1994, Groenewold and Fonds 2000), but the effect of these food subsidies is considered relatively small on scavenger population levels in the southern North Sea (Groenewold and Fonds 2000).

The response of the benthic component in our model to trawling is consistent with other modelling studies (Duplisea *et al.* 2002, Hiddink *et al.* 2008), who did not incorporate fish predation. However, the interaction between fish and its benthic prey in our model has substantially increased the complexity of the response to trawling. To assess the importance of predation in marine benthic communities, caging experiments are still seen as the most valid method (Hall *et al.* 1990), but we know of no predator exclusion experiments conducted at the feeding grounds of commercially important benthivorous fish species.

In this study, we have examined a bottom-up controlled system and three systems with various strengths of top-down regulation. However, the mode of regulation is not a fixed property of natural systems, but depends on the state and history of the system. This is illustrated in our model, where top-down controlled benthic systems behave more bottom-up controlled as the fish population is depleted by fishery (figure 2.2d-i). Our results show that an assessment of the degree to which a system is bottom-up or top-down controlled should be central to any strategy of adaptive and ecosystem-based management of exploited fish stocks, because it is a key determinant of how the system responds to exploitation. For the North Sea, Heath (2005) suggested that macrobenthic species were predominantly top-down controlled. If this is correct, our results imply that a positive effect of trawling on the food availability of benthivorous fish is expected only at high trawling intensities. It also implies that gear adaptations minimizing damage to benthos may result in higher abundance of susceptible benthos.

Our work highlights that the relative importance of bottom-up and top-down processes is crucial for understanding the dynamics of benthic communities. We also show that incorrect assumptions regarding trophic control of the ecosystem can lead to dramatic failure of management of exploited benthivorous fish and the conservation of benthos. Unfortunately, little is known about the trophic regulation of marine benthic ecosystems worldwide, but our work highlights that further study is urgently needed in light of the recent worldwide push for ecosystem-based marine management (Pikitch *et al.* 2004).

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APPENDIX 2.1 ASYMMETRY IN PREY PROFITABILITY IN RESPONSE TO TRAWLING

The positive effects of trawling solely occur when resistant benthos have a higher prey profitability. Asymmetric prey profitability is established in the main manuscript by differences in conversion efficiencies between susceptible and resistant benthos. Besides these conversion efficiencies, we can propose two alternative mechanisms, differences in productivity and in prey edibility, that may lead to asymmetry as well:

We show for these two alternative types of asymmetry that positive effects of trawling may occur when resistant invertebrates are a more profitable prey for fish. This is illustrated in a model with weak top-down regulation, as we think that this system shows most complex behaviour. The results show that impact of trawling on benthos (*m*=4) may lead to a positive relationship between trawling intensity and fish biomass, higher fish biomass levels compared to m=0 at similar trawling intensities (hence higher yield) and increased persistence of fish at higher trawling intensities (figure A2.1). These positive effects are similar to the patterns described in the main manuscript. Both alternative types of asymmetry are described below.

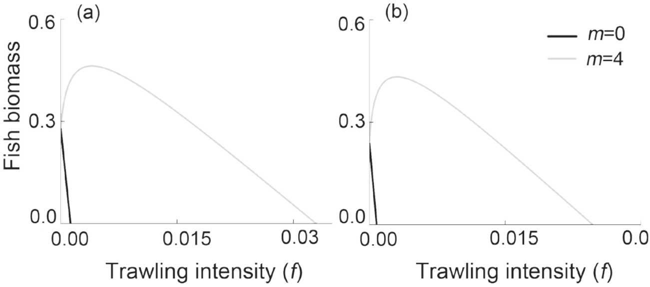

Figure A2.1 Impact of bottom trawling (by varying *f*) on fish biomass in two top-down controlled systems with low fish attack rates. The two systems differ in their mechanism to obtain asymmetry in prey profitability: (a) difference in productivity and (b) difference in prey edibility. The black and grey lines present different scaled trawling mortalities on benthos (*m*). Model description and parameterisation are described in the text of appendix A2.1.

DIFFERENCES IN PRODUCTIVITY BETWEEN SUSCEPTIBLE AND RESISTANT BENTHOS (FIGURE A2.1A)

Asymmetry in productivity can be established by assuming uneven carrying capacity levels between resistant benthos (R_{max}=2.5) and susceptible benthos (S_{max}=1.25). Additionally, a competition coefficient is needed which describes the negative impact of one benthos population on the other. The coefficient is based on body size. This means that susceptible benthos (assumed to be larger) have a stronger negative impact on the intrinsic growth rates of resistant benthos (cl=2) than resistant have on susceptible species (cs=0.5). In this situation, positive effects of trawling occur. Note that conversion efficiencies are equal (g=0.6), α=0.09, all other parameters have values similar to the main manuscript.

$$\frac{dB_S}{dt} = r(S_{\max} - (B_S + csB_R)) - (\alpha S + mf)B_S \tag{1}$$

$$\frac{dB_R}{dt} = r(R_{\max} - (B_R + clB_S)) - (\alpha S + \frac{1}{\sigma} mf)B_R \tag{2}$$

$$\frac{dS}{dt} = \alpha S(gB_S + gB_R) - (f + \mu)S \tag{3}$$

HETEROGENEITY IN PREY EDIBILITY (FIGURE A2.1B)

In the following ordinary differential equations heterogeneity in prey edibility (or preference) is included. The result is that fish feeds more on prey which is easier edible. The positive effects of trawling occur when resistant benthos is the most edible prey (ϱ_{Br}=0.6, ϱ_{Bs}=0.4). Note that conversion efficiencies are equal (g=0.6), α=0.14, all other parameters have values similar to the main manuscript.

$$\frac{dB_S}{dt} = r(B_{\max} - (B_S + B_R)) - (\alpha\rho_{Bs} S + mf)B_S \tag{4}$$

$$\frac{dB_R}{dt} = r(B_{\max} - (B_R + B_S)) - (\alpha\rho_{Br} S + \frac{1}{\sigma} mf)B_R \tag{5}$$

$$\frac{dS}{dt} = g\alpha S(\rho_{Bs} B_S + \rho_{Br} B_R) - (f + \mu)S \tag{6}$$

Chapter 3

USING MARINE RESERVES TO MANAGE BOTTOM TRAWL FISHERIES REQUIRES CONSIDERATION OF BENTHIC FOOD WEB INTERACTIONS.

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Keywords
benthos
bottom trawl fisheries
ecosystem-based fisheries management
fish-benthos interaction
marine reserves

Marine protected areas (MPAs) are widely used to protect exploited fish species as well as to conserve marine habitats and their biodiversity. They have become a popular management tool also for bottom trawl fisheries, a common fishing technique on continental shelves worldwide. Bottom trawls have an effect on their target species and may also affect other components of the benthic ecosystem and the seabed itself. This means that for bottom trawl fisheries, MPAs can potentially be used not only to conserve target species, but also to reduce the impact of these side-effects of trawling. However, protection may not always enhance all ecosystem components on which trawling has an impact, due to food-web interactions between target and non-target species. In current theory regarding the functioning of MPAs, also in relation to bottom trawl fisheries, such interactions among species are generally not taken into account. In this paper, we review how food web interactions that are potentially affected by bottom trawling may alter the effectiveness of MPAs to protect (i) biodiversity and marine habitats, (ii) fish populations, (iii) fisheries yield and (iv) trophic structure of the community. Our work shows that current theory related to MPAs is incomplete with regards to its ability to determine the effects of MPAs for bottom trawling. We provide a conceptual framework for future research to conserve exploited fish species and benthic marine habitats using area protection.

INTRODUCTION

Marine protected areas (MPAs, areas closed to fishing and other anthropogenic activities), are a popular management tool to protect exploited fish species and to conserve marine habitats and biodiversity (Gell and Roberts 2003, Lubchenco *et al.* 2003, Vandeperre *et al.* 2011). The basic idea is that closing an area to fishing activities creates a safe haven for the species and habitats affected by the fisheries and promotes the recovery of the natural marine ecosystem. The increased survival of the target species may enhance its density inside the MPA and also outside through spillover of eggs, larvae and/or adults (Rowley 1994).

A large number of empirical studies have shown the potential of MPAs through an increase in density, biomass and individual size of target species (Halpern 2003, Lester *et al.* 2009, Sciberras *et al.* 2013) and an increase in species diversity, ecosystem structure and functioning (Babcock *et al.* 1999, Halpern 2003). How and when such benefits of MPAs occur has also extensively been explored in modelling studies (for reviews see Guénette *et al.* 1998, Gerber *et al.* 2003, Baskett *et al.* 2007, Pelletier *et al.* 2008). The majority of these modelling studies focussed on the effects of MPAs on the direct relationship between the fishery and the fish stock and have ignored the possible side-effects of fishing.

Such side-effects are most prominent in bottom trawl fishing, which is a dominant fishing technique used in shelf areas worldwide. The impact of bottom trawls goes far beyond the direct effect on its target species, as trawls cause mortality through bycatch and gear-induced physical damage on non-targeted organisms (Alverson *et al.* 1994, Kaiser *et al.* 2006) and change benthic community structure and functional composition (Kaiser *et al.* 2000, Kaiser *et al.* 2002, Tillin *et al.* 2006). Bottom trawls may also disturb seabed habitat (Dayton *et al.* 1995, Puig *et al.* 2012) and perturb biochemical processes by resuspension of nutrients and organic material into the water column (Grant *et al.* 1997, Pilskaln *et al.* 1998).

Because of these strong side-effects, MPAs can potentially be used as a fisheries management tool that will also mitigate the side-effects of bottom trawling on the ecosystem. However, side-effects of bottom trawls may affect benthic prey species for the fish, targeted by the trawl fishery, as well as inedible invertebrates that compete for food with the edible ones. Hence, side-effects of trawling may indirectly affect the target fish through the effect on their food, further complicating the relationship between trawling intensity, yield and the target fish stock (van Denderen *et al.* 2013).

Such ecological interactions between target and non-target species obviously have important ramifications for the functioning of MPAs as tools to manage or mitigate the effects of bottom trawling. Yet, current theory on the functioning of MPAs is largely based on studies that ignore the complex interplay between bottom trawls, target fish and their benthic food. Acknowledging that such interactions may affect the effectiveness of MPAs as a fisheries management and conservation tool, is essential for their successful application as part of the ecosystem approach to fisheries.

In this paper, we take a first step towards an extension of MPA theory to include the side-effects of bottom trawling, by exploring how food web interactions that are potentially affected by (side-effects of) bottom trawling may alter the effectivity of MPAs, in particular in relation to four common goals of MPAs: to protect (i) biodiversity and marine habitats, (ii) fish populations, (iii) fisheries yield and (iv) trophic structure of the community. Our work provides a conceptual framework within which future research can be interpreted to conserve exploited fish species and benthic marine habitats from bottom trawling using MPAs.

SIDE-EFFECTS OF BOTTOM TRAWL FISHERIES

Bottom trawling, where a net or other collection device is dragged over the seabed, is the dominant technology used to catch demersal fish and benthic invertebrates (hereafter benthos). It is estimated that 23% of global fisheries or 20 million tons of seafood annually, comes from bottom trawling (FAO 2009). Bottom trawls generally catch substantial amounts of bycatch, of either undersized fish and non-target species, which are discarded (Alverson *et al.*, 1994). In some fisheries, the discarded bycatch approaches or exceeds the marketable fraction of the catch (Kelleher 2005). In addition, bottom trawls can damage seabed habitats (Watling and Norse 1998, Puig *et al.* 2012) and impose mortality on benthos (Collie *et al.* 2000, Kaiser *et al.* 2006).

Bottom trawls cause a decline to large, sessile and low productive benthos as these are most vulnerable to the direct passing of the trawl gears and have slowest recovery rates (Kaiser *et al.*, 2006). Short-lived, opportunistic benthos and scavengers/predators are generally less vulnerable or able to recover more rapidly, and such species usually dominate areas that are trawled frequently (Kaiser *et al.* 2006, Tillin *et al.* 2006). The intensively trawled areas are generally less speciose (e.g. Collie *et al.* 1997, Thrush *et al.* 1998, Hiddink *et al.* 2006, Hinz *et al.* 2009, van Denderen *et al.* 2014) and are altered in their functional composition by a reduced abundance of filter-feeding organisms (Tillin *et al.* 2006, de Juan *et al.* 2007, Kenchington *et al.* 2007).

Both the short-term effects of trawling, by discarding and mechanically damaging benthic organisms, and the asymmetric effect of trawling on benthos species and its effect on species composition lead to the question how trawling influences the food availability for the target fish. Discarded and mechanically damaged benthos form a potential food source for food scavenging invertebrates and fish (de Groot 1984, Wassenberg and Hill 1990, Kaiser and Spencer 1994, Groenewold and Fonds 2000) and it has been suggested that this is an important part of the diet of some fish (Shephard *et al.* 2014). Benthivorous fish also respond to trawl-induced shifts in benthic species composition with changes in their diet compared with untrawled sites (Smith *et al.* 2013, Johnson *et al.* 2014) and historic times (Rijnsdorp and Vingerhoed 2001). Such changes may affect fish growth rates and body condition. This has also been found in a number of studies, reporting positive and negative relationships between trawling intensity and the growth rates of target species (Millner and Whiting 1996, Rijnsdorp and van Leeuwen 1996, Shephard *et al.* 2010) and no or negative relationships between trawling intensity and fish condition (Hiddink *et al.* 2011). From theory, it is expected that trawling will increase food availability for target fish (and hence the productivity of the species), when benthos, which is the most profitable food source for fish, are relatively resistant to the effects of trawling, so that they can use more of the available resources when more sensitive competitors suffer from trawling mortality (van Denderen *et al.* 2013). So far, none of the empirical studies have found that the loss of susceptible benthos was (fully) compensated by an increase in resistant benthos, potentially increasing the food availability for target fish (Jennings *et al.* 2001, Hinz *et al.* 2009, Ingels *et al.* 2014), although Jennings *et al*. (2001) have found increased production per unit benthic biomass with increased trawling intensity.

Finally, bottom trawls disturb biogeochemical processes on the seafloor and cause resuspension of nutrients and organic material into the water column (Riemann and Hoffmann 1991, Grant *et al.* 1997, Pilskaln *et al.* 1998). Resuspension of nutrients has been suggested to change phytoplankton community composition and primary production (Riemann and Hoffmann 1991, Pilskaln *et al.* 1998), while resuspension of organic material may supply food to suspension feeders and increase their abundance (Grant *et al.* 1997). Both may indirectly affect food availability for benthivorous fish, due to a change in systems (primary and secondary) production.

COMMON GOALS OF MPAs

We review MPA functioning in relation to the protection of (i) biodiversity and marine habitats, (ii) fish populations, (iii) fisheries yield and (iv) trophic structure of the community (for overview see figure 3.1).

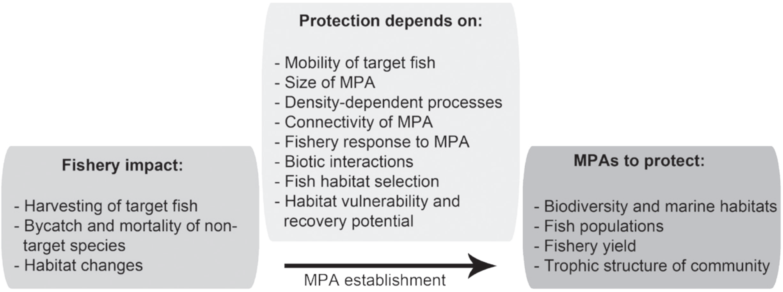

Figure 3.1 Overview of the role of MPAs to conserve different ecosystem indicators from the adverse effects of fishing. The box in the middle shows the processes that determine (often in interaction with each other) whether MPAs can induce benefits to (some of) the ecosystem indicators.

MPAs TO PROTECT BIODIVERSITY AND MARINE HABITATS

Two underlying rationales can be distinguished for establishing MPAs for biodiversity and habitat conservation: either to protect existing natural values or to allow for recovery of such values after they have been lost. The former are generally located in ecological hotspots that have a high diversity and contain (endemic) populations and/or habitat structures that are vulnerable to fisheries, but which have not been (heavily) affected by fisheries yet (Roberts *et al.* 2003). Such sites may also have high economic (e.g. tourism) and social (e.g. aesthetic appeal) values.

When an MPA is established in order to rebuild lost natural values, it is important to determine the potential for recovery. Recovery of some types of habitats, in particular those with complex structural properties (macrophytes, corals, sponge fields), may take decades or even centuries, while others may recover quick (Roberts and Hirshfield 2004, Kaiser *et al.* 2006). In some cases, it has also been suggested that fishing can shift the ecosystem to alternative stable states from which recovery to the pre-fished state is very difficult (Scheffer *et al.* 2001, Jensen *et al.* 2012).

In addition to the growth rates of the species involved, an important determinant of the potential (and speed) of recovery is whether the area can be recolonized by species that have disappeared. This is determined by its connectivity to other areas in which the species still occurs (Thrush *et al.* 2013, Lambert *et al.* 2014). Many marine benthic organisms produce pelagic larvae, which can disperse long distances before settlement (Kinlan and Gaines 2003). The ability for larval dispersal generally determines the connectivity between sites, especially for otherwise sessile benthos, and the dispersal distance of benthic larvae is considered crucial to calculate both the effective size of an MPA and the maximum distance between MPAs (Shanks *et al.* 2003).

MPAs TO PROTECT FISH POPULATIONS

Most cases of successful MPA implementation have been observed in fish with limited mobility. These species are often dependent on specific habitat-structures, such as reefs. For these species, it has been shown that MPAs generally increased their density, biomass and individual size (Halpern 2003, Lester *et al.* 2009, Sciberras *et al.* 2013). In some areas, this also led to higher abundance of fish (McClanahan and Mangi 2000) and marketable catch (Vandeperre *et al.* 2011) around the border of MPAs.

Fish protection by MPAs has been suggested to be less effective for species with high mobility (Horwood *et al.* 1998, Gerber *et al.* 2003, Kaiser 2005, Grüss *et al.* 2011). These species are often less dependent on specific habitats and move considerable distances within a year (Shipp 2003, Kaiser 2005). Protection of mobile species largely depends on the size of MPAs relative to the movement of the fish, and it has been suggested that protection of these populations will only lead to noticeable rebuilding of the population when 40% of the total area would be protected (Le Quesne and Codling 2009). Protection of certain life-stages is suggested as a more adequate option than implementing large MPAs for mobile species (Grüss *et al.* 2011, Beare *et al.* 2013). This may work when populations are regulated by processes in the protected life-stage (St. Mary *et al.* 2000, van de Wolfshaar *et al.* 2011).

The functioning of an MPA also depends on how density-dependence operates to regulate fish populations, in particular in absence of fishing. Some have found that density-dependent growth will reduce length at age within the MPA (and potentially the surrounding area) due to a build-up of biomass and increased competition (Gårdmark *et al.* 2006). Increased competition inside the MPA has also been suggested to reduce the reproductive output to levels lower than the fished area, making the MPA a larval sink (Claessen *et al.* 2009). Others have shown that the mechanism that regulates populations (density-dependent growth or movement) will affect whether there is an optimal reserve size that maximizes spillover (Kellner *et al.* 2008). All studies indicate that the functioning of MPAs is dependent on target species ecology (and hence model assumptions).

Effectiveness of an MPA to protect fish populations is also dependent on the response of the fishery to the closure. MPAs often lead to fisheries effort reallocation (e.g. Murawski *et al.* 2005) and this may counteract the positive effects on the target population inside the MPA and its spillover to surrounding areas

(Halpern *et al.* 2004). This has also been illustrated for North Sea cod (*Gadus morhua*) and Baltic cod, where temporal fisheries closures did not increase the cod population, partly due to fisheries effort reallocation outside the protected zone (Dinmore *et al.* 2003, Kraus *et al.* 2009).

MPAs TO PROTECT FISHERIES YIELD

Modelling studies have shown that MPAs can only increase fisheries yield in stocks that are overfished (fished with fishing mortality above F_{MSY}) before MPAs are implemented (for review see Gerber *et al*. 2003). Positive MPA effects on yield are limited to even higher fishing mortalities with the inclusion of density-dependent body growth (Gårdmark *et al*. 2006). MPAs reduce the yield of stocks that are exploited at a certain fishing effort below F_{MSY}, and this has been suggested as an important drawback to use MPAs for fisheries management compared with regular catch restrictions (Hilborn *et al*. 2006). This finding is also corroborated in field studies, where MPAs have often resulted in limited benefits to the yield (Hilborn *et al*. 2004). MPAs may decrease the variability in yield by reducing effects of environmental uncertainty (Mangel 2000).

MPAs TO PROTECT TROPHIC STRUCTURE OF THE COMMUNITY

MPAs may allow the trophic structure to recover. Fishing changes the size structure of the fish community by reducing the abundance of large fish, mainly high trophic level species, limiting the predation mortality on the smaller prey species (Daan *et al*. 2005, Andersen and Pedersen 2010). Top-down control may be re-enforced inside MPAs due to an increase of the predatory species that are now protected from the fisheries (for review see Pinnegar *et al*. 2000, Baskett *et al*. 2007).

INDIRECT FOOD WEB EFFECTS OF TRAWLING AND THEIR IMPLICATION FOR MPAs

The indirect food web effects of bottom trawl fisheries may affect the processes that determine MPA functioning (figure 3.2). We will discuss how these food web effects can change (i) the recovery potential inside an MPA, (ii) affect changes in trophic structure and (iii) influence protection of fish populations and fisheries yield.

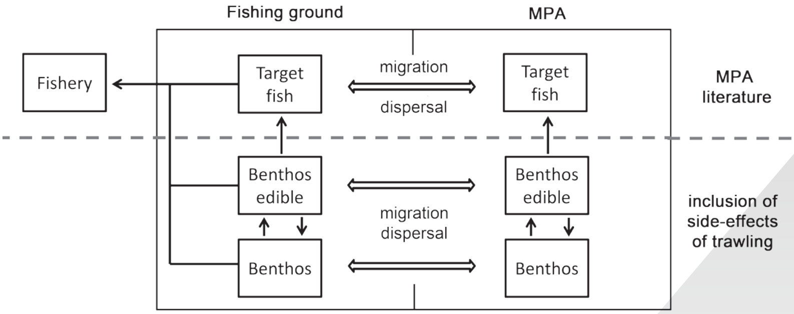

Figure 3.2 The interplay between bottom trawling and target fish and benthos in a fishing ground and an MPA. Fish and benthos migrate (as adults) or disperse (as eggs or larvae) between the different areas. All components above the dashed line have generally been studied to develop MPA theory.

BIOTIC INTERACTIONS CHANGE THE RECOVERY POTENTIAL OF DISTURBED HABITAT

Soft-bottom habitats that have been impacted by trawls are often dominated by opportunistic and fast-growing species (Kaiser *et al*. 2006). An MPA may potentially shift the system back towards a community with slow-growing species that are less resilient to the impact of trawling. Whether this occurs depends strongly on the successful colonization of sensitive species in the MPA. This success depends on whether larvae can reach, settle and survive in the MPA. Settlement and survival may be hampered by long-lasting changes to the habitat after bottom trawling (Piersma *et al*. 2001) and by the biotic interactions present as a result of bottom trawling.

Settlement can be prevented by the opportunistic benthic residents in the area that dominate through direct feeding on the larvae (by predators or deposit feeders), the smothering of the larvae (by bioturbators), filtering them from the water column as prey (by suspension feeders) or by denying them space to settle (tube-builders) (Woodin 1976, Hunt and Scheibling 1997). There is some evidence that such effects are strong enough to delay the recovery of sensitive species. This is best observed in defaunation experiments that show reduced colonization (Lu and Wu 2000, Montserrat *et al*. 2008) and coexistence (Lu and Wu 2000) in areas that are occupied by a resident community, compared with an area that is empty. Settlement success may also be reduced by resident species that can modify seabed sediment, making it less suitable for other organisms (van Nes *et al*. 2007). Such interactions indicate clearly that modification of the benthic ecosystem composition, as a result of the side-effects of bottom trawling, can reduce the recovery potential of an area after it has been designated an MPA and trawling has ceased. It is theoretically possible, if the resident community which formed under the effects of trawling is stable enough, that trawling induces an alternative stable state. We are not aware of empirical support for trawling-induced alternative stable states, but their existence would strongly reduce the value of MPAs as a recovery tool for the benthic ecosystem.

Larvae of sensitive species that manage to settle in the MPA have to survive and grow. This may be limited through competition for food with the resident community, reducing food intake of the settled larvae and eventually causing starvation. Survival and growth may also be limited as a result of increased predation of both fish and benthic invertebrate predators, that also benefit from the establishment of an MPA as it is also a safe haven for these species. Fish and benthic invertebrate predation has been shown to limit survival of newly arrived benthic larvae (Hunt and Scheibling 1997) and an increase in these predatory species may induce a stronger predation mortality on larval prey.

TRAWL EFFECTS ON BOTH FISH AND BENTHOS AFFECT TROPHIC STRUCTURE

It is often suggested that top-down control may be reinforced inside MPAs, due to an increase of the predatory species that are targeted by the fisheries (Pinnegar *et al*. 2000). In the case of benthivorous fish and their prey, this expectation is complicated by the fact that both are affected by the bottom trawl fishery. At low trawl intensity, fish density is relatively unaffected consequently so is the predation mortality on benthic prey, while at high trawl intensity, fish density and the importance of fish predation is reduced, but mortality induced by trawls on the prey is high. Hence, for benthos, direct mortality of trawling replaces predation mortality as fish abundance is reduced at high trawling intensity. The relative change in these two sources of mortality per unit trawling intensity determines whether the benthos will increase (reduced trawl mortality) or decrease (increased predation mortality) inside MPAs (van Denderen *et al*. 2013). This means that benthos vulnerable to trawl impact, which is not an important prey for fish, will likely benefit from MPAs, whereas benthos species that are less vulnerable to trawl impact or which are important prey for fish, may respond differently to MPA establishment.

There are a variety of studies that have shown top-down effects of benthivorous fish (and benthic invertebrate predators) on abundance of their benthic prey (Wilson 1991, Baum and Worm 2009). Top-down effects of fish on benthos are found predominantly in systems that are not intensively bottom trawled (but see

Heath 2005), as many of the areas fished by bottom trawls make it notoriously difficult to carry out (experimental) studies of the subtle relationships between target fish and benthic prey.

Even with limited predation mortality on benthos, reduced trawling mortality inside MPAs does not necessarily increase benthic biomass. This is because resistant benthos may compensate for the loss of biomass of the more sensitive species in a trawled habitat. Although establishment of an MPA may reverse this shift (if these sensitive species can settle and grow in the area, see *Biotic interactions change the recovery potential of disturbed habitat*), it will primarily change species composition towards more sensitive benthos. Benthic biomass inside MPAs may increase when trawling impact was too high and biomass compensation by resistant benthos limited. Benthic biomass may also increase when the sensitive species are more efficient in capturing food, enhancing the total carrying capacity of the area, or facilitate other benthos by providing resources or shelter, possibly reducing natural disturbance and predation (Thrush *et al*. 1992, Stachowicz 2001).

BIOTIC INTERACTIONS INFLUENCE PROTECTION OF TARGET FISH AND FISHERIES YIELD

Shifts in benthos species composition in response to changed trawling intensity affect fish food availability, fish production and fisheries yield (van Denderen *et al*. 2013). The net effect on fish abundance and yield depends on how the prey species of the target fish are affected by trawling.

When bottom trawling reduces benthic prey abundance, MPAs may increase food production for fish and hence support higher fish production than the surrounding trawled area. This mechanism further amplifies the expected build-up of fish biomass inside the MPA due to reduced mortality. The increased food production for fish results in higher fisheries yields if fish spillover into surrounding areas. If this mechanism (the increased fish food production in absence of trawling) is strong enough, fisheries yields with an MPA may even become higher than those under MSY with traditional quota-based management, when the increased fish production more than compensates for the loss of fishing grounds. Contrastingly, when less sensitive species are a particularly good food source for fish, trawling can actually enhance food production for fish and fisheries yield (van Denderen *et al*. 2013). This implies that an MPA may become less attractive for fish and may reduce the overall productivity of the target fish species and hence fisheries yield in the area.

The asymmetry in food availability between MPA and fished area will affect how fish forage and migrate between these different areas. Mobile fish search for food in a larger area than fish that have a high site fidelity and it may be expected that these mobile fish profit more easily from changes in benthic prey in response to trawling and establishment of MPAs. Besides changes in food availability, fish migration may also be affected by (side-)effects of trawling that induce behavioural differences in fish between the trawled area and the MPA. Such effects may be expected when areas differ in type of prey (and hence predator foraging behaviour), habitat structure or density of conspecifics. Ultimately, movement of fish will depend on how fish species select their habitat (e.g. based on specific structures or energetic profitability of prey) and how fish interact with their prey. Such findings show that MPAs may become suitable habitats for some fish species, while they reduce suitable habitat for others.

The overall productivity of the target fish species and hence the fisheries yield may also be affected by trawling-induced resuspension of nutrients and organic material. This has the potential to change both primary and secondary production (see also *Side-effects of bottom trawl fisheries*) and as such also the productivity of benthic prey. How establishment of an MPA will affect food production for fish will depend on how the resuspended material (indirectly) contributes to the productivity of benthic prey.

CONCLUSION

MPAs protect a habitat from human impact and this has made them a promising management tool also for bottom trawl fisheries, which affect many components of the benthic ecosystem in direct and indirect ways. Establishment of MPAs is often based solely on an understanding of the impact of the fisheries on the criterion to be protected. In this paper, we have argued that protection will not always enhance all ecosystem components on which trawling has an impact, due to the food web interactions between target and non-target species. The success of an MPA in achieving its management objectives is a balance between the direct benefit (less mortality on fish or benthos) versus indirect disadvantages (e.g. less fish prey or more predation mortality).

The importance of these indirect food web effects in relation to bottom trawling are currently not incorporated in studies that examine, both theoretically and empirically, the potential of MPAs for the management of bottom trawl fisheries and the conditions necessary for their successful application. In this work we have shown that the current theory regarding the functioning, design and implementation of MPAs is incomplete and must be extended to include food web interactions, in order to provide the scientific basis for the application of MPAs in the sustainable management of exploited fish stocks and to protect marine habitats and their biodiversity from bottom trawl fisheries.

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Chapter 4

EXPLORING THE TRADE-OFF BETWEEN FISHERIES YIELD AND CONSERVATION OF THE BENTHIC ECOSYSTEM IN TRAWLED FISH STOCKS.

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benthos
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marine protected areas
maximum sustainable yield

Marine protected areas (MPAs) are promoted as a valuable tool to protect marine habitat and biodiversity, while their potential for target fish populations and fisheries yield, compared to regular effort limitations, is ambiguous. However, many fishing techniques, such as bottom trawl fishing, have considerable impact beyond the extraction of target fish. In such a case, MPAs can potentially be used not only to protect target fish but also to reduce the adverse side-effects of the fisheries. In this study, we examined the effectivity of MPAs, compared to regular effort restrictions, to protect the benthic ecosystem from bottom trawl impact, while we incorporated the effects of both measures on the fisheries yield. This was done in a food-web model with multiple groups of benthos and a benthivorous fish, where benthos varied in mode of trophic regulation (i.e. top-down or bottom-up control). Our results show that protection of vulnerable benthos with MPAs generally results in higher or equal fisheries yields compared with a similar protection of benthos using effort restrictions. Only when benthic competitive interactions strongly reduce fish prey production in absence of fishing or when fish have limited mobility, there will be lower fisheries yields when benthos is protected with MPAs. This highlights the effectivity of MPAs for trawled target stocks when the management objective is beyond maximizing fisheries yield. The results demonstrate the importance of the benthic food web interactions in finding a balance between exploitation of trawled target stocks and conservation of marine habitats, which is the essence of the ecosystem approach to fisheries management currently being implemented.

INTRODUCTION

Marine protected areas (MPAs) are a well-established tool for the protection and restoration of threatened or degraded marine habitats (Halpern 2003, Lester *et al*. 2009, Edgar *et al*. 2014). They have also been used as a tool to protect harvested fish stocks and fisheries yield (Gell and Roberts 2003 and references therein), although their suitability in this respect is not quite as universally accepted compared to standard fisheries management by effort limitation (Hilborn *et al*. 2004, Gårdmark *et al*. 2006, Hilborn *et al*. 2006).

Bottom trawl fisheries are special in the sense that they have large effects on seabed habitat while catching target species (Jennings and Kaiser 1998). This causes declines in benthic diversity and changes in benthic community composition and ecosystem function (Kaiser *et al*. 2002, Thrush and Dayton 2002, Tillin *et al*. 2006). Bottom trawls account for 23% of global fisheries yield (FAO 2009) and have a large spatial footprint, approximately affecting 50 million square kilometre of habitat, of which almost half occurs at continental shelf seas (Halpern *et al*. 2008). In some of these areas, trawling is by far the most widespread source of human disturbance (Eastwood *et al*. 2007).

MPAs can potentially be used to protect trawled target fish and the benthic ecosystem from the adverse effects of bottom fishing (Murawski *et al*. 2000, Witherell *et al*. 2000). Such a protection will also affect the fisheries yield and, generally, it is suggested that an MPA will reduce yields whenever fishing intensities are below that which maximize yield (for review see Gerber *et al*. 2003). The effectivity of MPAs, compared to standard fisheries management by effort limitation, is less understood when the objective is not only to maximize fisheries yield but simultaneously to protect benthos vulnerable to bottom fishing. This is also complicated by the fact that protection of benthos and exploitation of target fish should not be viewed in isolation, as benthos affected by trawling include the prey species for benthivorous fish that are the target of the trawl fisheries (Jennings *et al*. 2001, Hiddink *et al*. 2008, van Denderen *et al*. 2013). How in such a food web context, protection of the benthic ecosystem from bottom fishing can be achieved with limited deviations from optimal fisheries yield has never been explored.

The purpose of this study is to examine how fisheries yield and the benthic component vulnerable to trawling are affected by MPAs and effort limitations. This is done in a model with multiple groups of benthos and fish in which benthos is bottom-up controlled, and determined in its abundance by its resource, or top-down controlled by the predation effects of fish. We study both types of trophic control as it is shown in a previous study that this largely determines the response of the benthic community to trawling (van Denderen *et al*. 2013). It is currently unknown whether there is a predominant mode of trophic control, while there are indications that both occur (Wilson 1991, Seitz 1998). Our results show that protection of vulnerable benthos with MPAs generally results in higher or equal fisheries yields compared with similar protection of benthos using effort restrictions. Only when benthic competitive interactions strongly reduce fish prey production in absence of fishing or when fish have limited mobility, there will be lower fisheries yields when benthos is protected with MPAs. The results highlight the effectivity of MPAs at fishing intensities below that which maximize yield whenever management deals with the ongoing process of balancing fisheries exploitation and conservation of marine benthic ecosystems.

METHOD

MODEL FORMULATION

We formulated two different models, dependent on mode of trophic control, with fish and four groups of benthos in two patches, a fishing ground and an MPA. In the bottom-up controlled model, benthos population dynamics are fully determined by competitive interactions and there is no feedback from fish feeding on the benthos. In the top-down controlled model, fish are dynamically modelled and control benthos abundance through predation mortality. In both models, benthos groups differ in sensitivity to trawling and suitability as food for fish (reflected in a different fraction of time spent foraging on each benthic group) (table 4.1).

Table 4.1 Differences in the four groups of benthos (with their names). Remaining parameter values are summarized in table 4.2.

Benthos index	Fraction of time spent foraging on benthic prey (α)	Sensitivity to trawling (σ)
1 (PR)	0.45 (P)	0.5 (R)
2 (NR)	0.05 (N)	0.5 (R)
3 (PS)	0.45 (P)	2.0 (S)
4 (NS)	0.05 (N)	2.0 (S)

Benthos groups follow semi-chemostat dynamics in absence of predation, with growth rate r and maximum population density $B^{MAX.}$ We use semi-chemostat dynamics because it describes an open population, where population growth rate is independent of abundance at low density. We consider this appropriate for benthic invertebrate species that typically have pelagic larval stages and larvae mixing over large distances (Caley *et al*. 1996). Interspecific competition among benthos groups is modelled as a dependence of the maximum abundance of each benthos group on the density of the others.

In the bottom-up controlled model, benthos density is entirely determined by their resource. Benthos (*B*) and fish (*P*) in both fishing ground (FG) and protected area (MPA) are described by:

$$\frac{dB_{FGi}}{dt} = r(\mathrm{B}^{MAX} - \sum_{j=1}^{j=4} B_{FG\,j}) - (f\sigma_i + \mu_B)B_{FGi} \tag{1}$$

$$\frac{dB_{MPAi}}{dt} = r(B^{MAX} - \sum_{j=1}^{j=4} B_{MPA\,j}) - \mu_B B_{MPAi} \tag{2}$$

$$P_{FG}(t) = \frac{g\varepsilon_{FG}(\mathrm{t})/(1+h\varepsilon_{FG}(\mathrm{t}))}{\mu_p + f} \tag{3}$$

$$P_{MPA}(t) = \frac{g\varepsilon_{MPA}(\mathrm{t})/(1+h\varepsilon_{MPA}(\mathrm{t}))}{\mu_p} \tag{4}$$

where i represents the four benthos groups (table 4.1). Mortality in benthos is based on natural mortality μ_B and, in the fishing ground, on trawling mortality, described by benthos sensitivity to trawling σj and the trawling intensity f. The change in fish density is described by a type II functional response and depends on the prey conversion efficiency g, fish handling time h and the prey encounter rate ε. The encounter rate depends on prey densities and the factors α that indicate the fraction of time that fish spends foraging on a particular benthic group:

$$\varepsilon_{FG} = \sum_{j=1}^{j=4} \alpha_j B_{FGj} \tag{5}$$

$$\varepsilon_{MPA} = \sum_{j=1}^{j=4} \alpha_j B_{MPAj} \tag{6}$$

Fish mortality is based on natural mortality μ_P and in the fishing ground, on trawling mortality f (assuming fish has a sensitivity to trawling of 1). Since fish is described by an instantaneous function of its environment (eq. 3-4), fish densities are proportional to the densities of their prey and instantaneously redistributed following a change in prey distribution. The model describes population densities (abundances per unit area) and the average benthos and fish density over both patches (i.e. total abundance) is the sum of the population densities in the MPA multiplied by the size of the MPA p and the population densities in the fishing ground multiplied by 1-p.

In the top-down controlled system, fish are dynamically coupled to benthic prey. The top-down controlled system is described by:

$$\frac{dB_{FGi}}{dt} = r(B^{MAX} - \sum_{j=1}^{j=4} B_{FGj}) - (f\sigma_i + \mu_B)B_{FGi} - \frac{\alpha_i B_{FGi}}{(1 + h\varepsilon_{FGi})} P_{FG} \tag{7}$$

$$\frac{dB_{MPAi}}{dt} = r(B^{MAX} - \sum_{j=1}^{j=4} B_{MPAj}) - \frac{\alpha_i B_{MPAi}}{(1 + h\varepsilon_{MPAi})} P_{MPA} \tag{8}$$

$$\frac{dP_{FG}}{dt} = \frac{\varepsilon_{FG}}{(1 + h\varepsilon_{FG})} gP_{FG} - (\mu_P + f)P_{FG} + e\frac{p^2}{1-p}(P_{MPA} - P_{FG}) \tag{9}$$

$$\frac{dP_{MPA}}{dt} = \frac{\varepsilon_{MPA}}{(1 + h\varepsilon_{MPA})} gP_{MPA} - \mu_P P_{MPA} + ep(\mathrm{P}_{FG} - P_{MPA}) \tag{10}$$

As before, fish feed on benthos according to a type II functional response, but contrary to the bottom-up controlled model, fish imposes predation mortality on benthos. The model again describes population densities of both benthos and fish. Fish exchange is based on diffusive mixing across the MPA border and depends on fish migration rate *e* and MPA size *p*. Mixing only occurs between MPA and fishing ground in an area with size *p*. When areas differ in size ($p \neq 0.5$), the migrating part of the population needs to be rescaled in its density towards the new area with a different size. If we assume *p* is equal to or smaller than 0.5 (i.e. up to half of the total area is an MPA), migration into and out of the MPA can be described by $ep(P_{FG}\text{-}P_{MPA})$ since exchange only occurs in an area with size *p*. However, the fishing ground is equal to or larger than size *p*, the area where mixing occurs, and this means that fish exchange into and out of the fishing ground should be rescaled in its density towards an area with size (1-*p*). This can be done by multiplying $ep(P_{MPA}\text{-}P_{FG})$ by the scaling factor *p*/(1-p).

MODEL PARAMETERIZATION AND ANALYSIS

The parameter values σ and α are used to create distinct differences between the 4 groups of benthos (table 4.1). The values chosen reflect our interest in the relative differences and responses to bottom trawling and fish predation. The parameter values B^{MAX}, *r* and *g* are taken from van Denderen *et al.* (2013). The value for parameter *h* will have no effect on the qualitative behaviour of the model (de Roos *et al.* 2008) and is set equal to 1. Natural mortality of benthos μ_B will, in absence of fish predation mortality, determine whether benthos abundances are close to their maximum density (B^{MAX}) and as such, whether there is a low or high net production of benthos. To examine the effects of both a low and high benthic production, μ_B is varied between 0.001 and 0.2. In the top-down controlled model, numerical dominance of fish on benthos is limited by setting fish natural mortality μ_P to a benthos-fish ratio of 2:1. The remaining parameter values, migration rate *e*, MPA size *p* and trawling intensity *f* are varied in the manuscript. All parameter values are summarized in table 4.2.

Table 4.2 Model parameters and their values.

Description	Symbol	Default value	Unit
Benthic growth rate	r	1	t^{-1}
Benthic carrying capacity	B^{max}	2.5	$m\ V^{-1}$
Benthic natural mortality	μ_B	0.001 or 0.2	t^{-1}
Fish assimilation fraction	g	0.6	$m\ m^{-1}$
Fish natural mortality	μ_P	0.109 or 0.17	t^{-1}
Trawling frequency	f	varied	t^{-1}
Fish handling time	h	1	t^{-1}
Fish migration rate	e	varied	t^{-1}
Size of MPA	p	varied	V

Note: t = unit of time, V = unit of volume, m = unit of abundance

We analyse how changes in catch restrictions (by varying *f*) and size of MPA (by varying *p*) affect abundance of vulnerable benthos (i.e. benthos groups that decline in response to trawling) and fishery yield in systems with top-down or bottom-up control of benthos. The findings are all compared with a situation where the fish population is fished at an intensity that maximizes fishery yield (F_{MSY}) without an MPA. Fishery yield is written as fish abundance in the fishing ground multiplied by the trawling intensity. The results show the equilibrium dynamics by numerical continuation of equilibrium densities of the system using the software package Content (Kuznetsov *et al*. 1996).

RESULTS

BOTTOM-UP CONTROL OF BENTHOS

The equilibrium abundances of all benthic groups in isolation (no competition for a shared resource) decline exponentially with trawling intensity (*f*), with the steepness of the decline determined by the value of its sensitivity (σ) (not shown). With benthic competition, benthos that is relatively sensitive to the impact of bottom trawling (NS and PS), declines in response to trawling (figure 4.1a). Their rate of decline is faster than in isolation, because it is accelerated through the effects of competition with benthos that is relatively more resistant to trawling (NR and PR). The resistant benthos benefits from the declining competitors and increase with trawling intensity up to a point where the added positive effects of reduced competition become smaller than the increasing negative effects of trawl mortality.

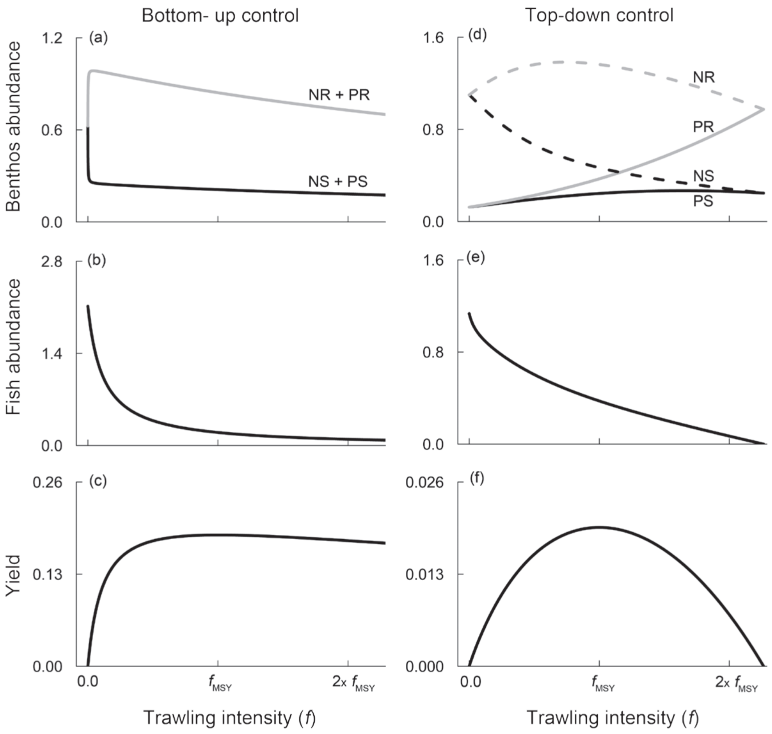

Figure 4.1 Impact of bottom trawling (by varying *f*) on benthos and fish abundance and fishery yield in a system with bottom-up (a-c) or top-down (d-f) control of benthos. The benthic names refer to table 4.1. p=0, e=0, μ_B=0.001, μ_P =0.109, all other parameters have default values.

The benthic groups that decline in response to trawling (NS and PS) may increase in abundance, compared with a trawl intensity at F_{MSY}, with a reduction in trawling intensity (effort limitation) (figure 4.1a), an MPA (figure 4.2a) or a combination of both management strategies (figure 4.3a). The lower the trawling intensities and/or the larger the MPA, the higher the benefits for vulnerable benthos (figure 4.3a). However, both management strategies will also decline the fishery yield (figure 4.1c and 4.2c) and protection of vulnerable benthos, at the least cost in terms of fishery yield, is achieved when an MPA is established (figure 4.3b). This occurs because a certain percentage increase in vulnerable benthos can be realised with a relatively small MPA, as the MPA causes a strong and non-linear increase in vulnerable benthos (see figure 4.1a at zero trawling intensity). As such, the fishery yield will decline less compared with a similar protection of vulnerable benthos using effort limitations.

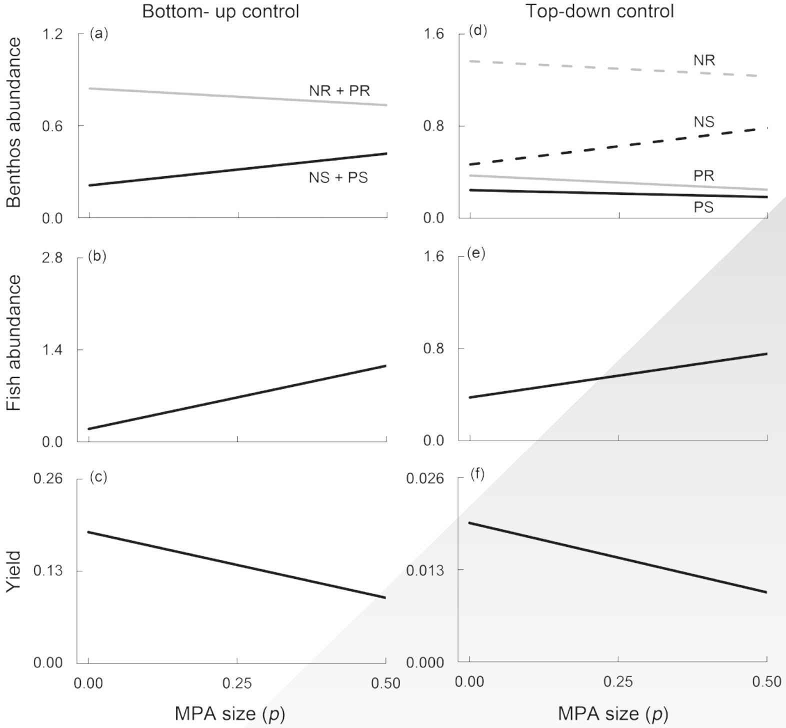

Figure 4.2 Effects of an MPA (by varying *p*) on benthos and fish abundance and fishery yield in a system with bottom-up (a-c) or top-down (d-f) control of benthos. The fishing intensity is similar to F_{MSY} at p=0 and there is no effort compensation for the loss of fishing area at increasing *p*. The benthic names refer to table 4.1. p=0, e=0, μ_B=0.001, μ_P=0.109, f=F_{MSY} at p=0 and that is 0.94 in (a-c) and 0.05 in (d-f), all other parameters have default values.

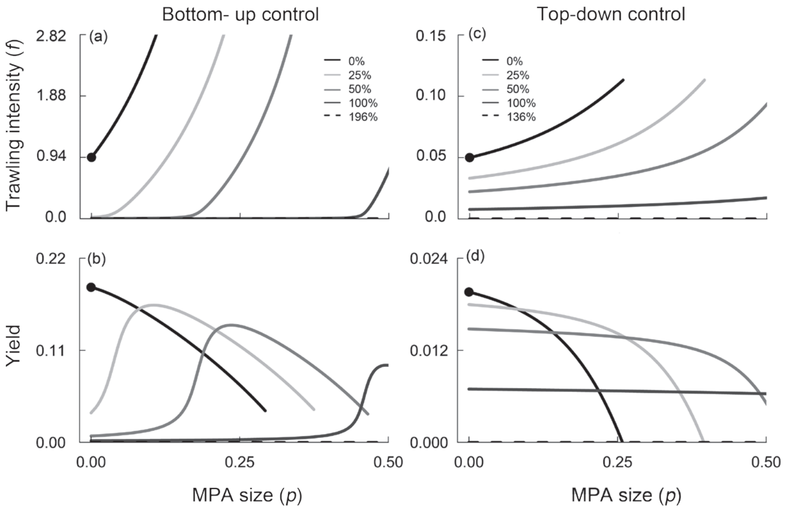

Figure 4.3 The percentage of increase in vulnerable benthos in relation to trawling intensity (*f*) and an MPA (*p*), compared with a situation without an MPA at F_{MSY} (represented by the dot), for a bottom-up (a) and top-down controlled (c) benthic community. Vulnerable benthos is defined as benthos that declines in response to trawling and this are the benthic groups PS and NS in (a), and, the benthic group NS in (c). The fishery yield, corresponding to the trawling intensity and MPA combination following the lines in panel (a) and (c), is shown in panel (b) and (d). The dashed lines present the percentage increase in vulnerable benthos without any trawling (f=0). e=0, μ_B=0.001, μ_P =0.109, all other parameters have default values.

TOP-DOWN CONTROL OF BENTHOS

Top-down control of fish on benthos limits benthos abundance. Benthos that is the most suitable prey (PS and PR) is most strongly reduced by fish. Trawling reduces fish abundance (figure 4.1e) and hence predation mortality of benthos. This directly translates into a higher equilibrium abundance of benthic prey (PS and PR) (figure 4.1d). Benthos that is relatively sensitive to bottom trawling and less suitable as fish prey (NS) declines in response to trawling. However, its decline is limited compared with a bottom-up controlled system, since increased trawl mortality reduces fish predation mortality on benthos as a result of fish harvesting. The decline is even further limited when fish predation on benthos becomes stronger (higher α), while less predation results in a benthos response that resembles bottom-up control. Similarly, the decline is accelerated with increased sensitivity of benthos to trawling impact (higher σ) and reduced with a lower σ.

The benthic group that is relatively sensitive to trawl impact and less suitable as fish prey (NS) is the only group that declines in response to trawling. This group can be protected with a reduction in trawling intensity (figure 4.1d), an MPA (figure 4.2d) or a combination of both management strategies (figure 4.3c).

Benefits of an MPA to protect the vulnerable benthic group (NS) are rather limited compared with bottom-up control of benthos as there is now no strong and non-linear decline of benthos in response to trawling (figure 4.1d). As a result, protection of the vulnerable benthic group (NS), at the least cost in terms of fishery yield, is in all situations achieved with a reduction in trawling intensity (figure 4.3d, highest yield values are at p=0).

FISH MIGRATION BETWEEN MPA AND FISHING GROUND

The results so far are shown without fish migration between fishing ground and MPA (e has been set to zero). With bottom-up control of benthos, effects of fish migration cannot be tested as fish densities are proportional to the densities of their prey and instantaneously redistributed following a change in prey distribution. In the model where benthos is top-down controlled, fish migration results in spillover from the MPA towards the surrounding fishing ground, as a result of different fish abundances between the two areas due to fish harvesting. Fish spillover has limited effect on the fishery yield (figure 4.4a), since the MPA is dominated by benthos less suitable as prey (NS, NP) (see figure 4.1d at zero trawling intensity). This limits benthic fish prey production inside the MPA through competition and subsequently fish production.

With increased natural mortality on benthos (μ_t = 0.2), benthos abundance is lower. This reduces benthic competition inside the MPA and increases benthic fish prey production and subsequently fish production. Fish spillover has now a positive effect on fishery yield and results in fishery yields that are close to a maximum yield without an MPA when fish mobility is sufficient (figure 4.4b). This happens when trawling intensities are increased in the fishing ground

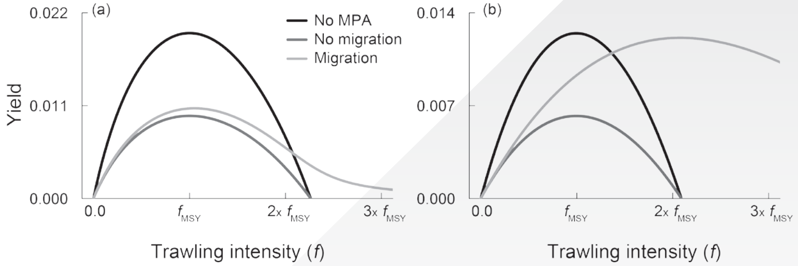

Figure 4.4 Impact of bottom trawling (by varying f) on fishery yield when there is a low (a) or high (b) benthic fish prey production in absence of fishing (by varying μ_B). The lines in both figures represent three scenarios: no MPA and no fish migration (p=0 , e=0; black lines), MPA without fish migration (p=0.5 , e=0; dark grey lines) and MPA with fish migration (p=0.5, e=0.3; light grey lines). The model does not take into account the effect of fishing effort displacement. μ_B=0.001 in (a) and 0.2 in (b), to keep the benthos-fish ratio 2:1 μ_P is varied as well and is 0.109 in (a) and 0.17 in (b), all other parameters have default values.

compensating for the loss of fishing area (the model does not take into account the effect of fishing effort displacement, see *Discussion* section). Due to these spillover effects, fishery yields are equal when effort limitations or an MPA are used to protect vulnerable benthos (NS) (figure 4.5). The percentage increase in vulnerable benthos abundance in response to protection (figure 4.5) is relatively small compared with the top-down controlled benthic community with a lower benthic natural mortality (figure 4.3c-d).

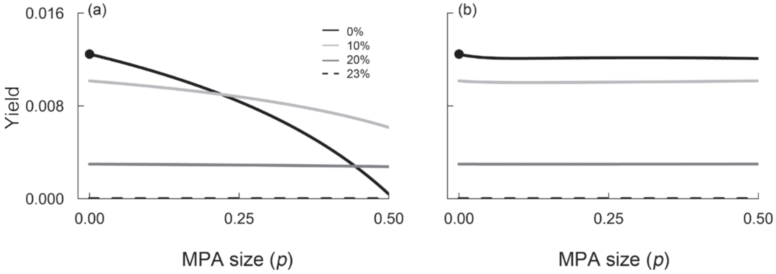

Figure 4.5 Changes in fishery yield, given a certain percentage increase in vulnerable benthos compared with a situation without an MPA at F_{MSY} (represented by the dot), in relation to MPA size (*p*) and trawling intensity (*f*) (not shown) without (a) and with (b) fish migration. Both figures show a top-down controlled benthic community with a relatively high benthic fish prey production in absence of fishing. e=0 in (a) and 0.3 in (b), μ_B=0.2, μ_P=0.17, all other parameters have default values.

DISCUSSION

The model simulations demonstrate how benthos vulnerable to bottom trawl impact can be protected by both effort restrictions and an MPA. The two management measures have different implications for the fisheries yield and our models show that the best management choice to protect benthos, while avoiding large deviations from optimal fisheries yield, will depend on benthos sensitivity to trawl impact, the mode of trophic regulation of the benthic community and fish mobility. Our results show that protection of vulnerable benthos with an MPA will be costly in terms of fisheries yield when benthic competitive interactions strongly reduce benthic fish prey production in absence of fishing or when fish have limited mobility. In all other cases, MPAs are favourable or equally acceptable compared to effort limitations to protect vulnerable benthos with the least deviation from optimal fisheries yield.

It is often suggested that the potential of MPAs to promote fisheries yield is limited to intensities beyond that which maximize yield F_{MSY} (for review see Gerber *et al*. 2003). These findings have been shown in models that only examined fisheries impact on fish, while bottom trawl fishing has considerable impact beyond the extraction of target fish. Our results show that relevance of MPAs to promote fisheries yield can be even further reduced with the inclusion of food-web interactions between fish and benthos. This occurs when benthos less suitable as fish prey dominates inside the MPA and limits benthic fish prey production, through competition, and subsequently fish production (figure 4.3c-d and 4.4a). However, our results also show that MPAs can become the best management measure at fishing intensities below F_{MSY} when the objective is not only to maximize fisheries yield but also to protect benthos vulnerable to bottom fishing.

Our results show the importance of the food-web interactions to understand the decline of benthos in response to bottom trawl impact (see also van Denderen *et al*. 2013). The rate of decline of benthos can be faster than in isolation when there is benthic competition and can be reduced when increased trawl mortality reduces fish predation mortality on benthos as a result of fish harvesting. The decline of benthos in response to trawling is usually predicted on the basis of benthos sensitivity to trawl impact, a parameter that varies among species, habitats and types of trawl gear (Collie *et al*. 2000, Kaiser *et al*. 2006). The trophic interactions hence present an additional mechanism to understand trawl impact on benthos.

This study shows how trawl (or natural) mortality on benthos increases benthic fish prey production, by reducing benthic competition, and enhances productivity of target fish. There are a variety of other indirect effects of bottom trawls on the benthic ecosystem that may also change productivity of target fish (for review see Collie *et al*. unpub.). This may be related to trawl-induced effects on specific habitat structures that are essential for target fish (Watling and Norse 1998), trawl-induced changes in primary and benthic productivity through resuspension of organic material (Grant *et al.* 1997, Pilskaln *et al.* 1998), fish preference for benthos that is relatively more or less resistant to trawl impact (van Denderen *et al.* 2013) or changes in fish foraging behaviour in response to trawling (Johnson *et al.* 2014). Such indirect effects can have important implications for the functioning of MPAs as a tool to manage and mitigate the effects of trawling on benthos and target fish (van Denderen *et al.* unpub.). How such effects may diverge from our findings will likely be context dependent, as uniform responses of these effects on target fish have not been found.

The MPA in our model acted as a fish source with a positive net spillover of fish to the fishing ground due to fish harvesting (see appendix 4.1, figure A4.1a). Due to these spillover effects, fisheries yields were equal when effort limitations or an MPA were used to protect vulnerable benthos (figure 4.5). However, these findings are all based on fish migration through diffusive mixing, while fish might also actively migrate to the most profitable area. Active migration of fish to the area with the highest prey encounter or fish intake rate will not affect our model dynamics (appendix 4.1). Fish will still spillover to the fishing ground as it is more profitable due to a higher abundance of benthos suitable as fish prey.

The effect of fisheries effort displacement in response to the establishment of an MPA is not included in our model. Inclusion of effort displacement will not affect our model results qualitatively as we assume fishery is homogenously spread. Effort displacement is of more importance in real areas affected by bottom trawling, since the fisheries is often patchily distributed (e.g. Rijnsdorp *et al.* 1998, Bellman *et al.* 2005, Murawski *et al.* 2005). This may reduce positive effects of MPAs on benthos due to a redistribution of fishing intensity to areas that were previously less affected by trawling and as such more sensitive to trawl impact (Dinmore *et al.* 2003, Hiddink *et al.* 2006). Based on these findings, Hiddink *et al.* (2006) suggested that without further management action, MPAs could best be established in areas that are lightly fished by bottom trawls as this will both protect areas from incidental trawling events and limit the redistribution of fishing effort.

The potential of MPAs to promote fisheries yield below fishing intensities that maximize yield, F_{MSY}, is often suggested to be limited. However, many fishing techniques, such as bottom trawl fishing, have considerable impact beyond the extraction of target fish (Jennings and Kaiser 1998). Our results show that MPAs can become the best management measure at fishing intensities below F_{MSY} when there is a combined evaluation of the effects of bottom trawling on target stock and the benthic ecosystem. The protective effects of MPAs, and the cost of this protection to the fisheries yield, depend on the mode of trophic regulation of the benthic community, the sensitivity of benthos to trawl impact and the mobility of target fish. The results highlight how an understanding of the direct and indirect effects of bottom fishing on demersal food webs will help management to reduce conflict between conservation and sustainable exploitation of marine ecosystems.

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APPENDIX 4.1 FISH MIGRATION

Fish exchange between MPA and fishing ground is modelled in the main manuscript through diffusive mixing. In this appendix, we show that active migration of fish to the area with the highest prey encounter or fish intake rate will not affect our model dynamics. Fish exchange between MPA and fishing ground is described in the main manuscript by:

$$e\frac{p^2}{1-p}(P_{MPA}-P_{FG}) \quad \text{and} \quad ep(\mathrm{P}_{FG}-P_{MPA})$$

We can describe active migration by including parameter *z*:

$$(1-z)e\frac{p^2}{1-p}(P_{MPA}-P_{FG}) \quad \text{and} \quad zep(\mathrm{P}_{FG}-P_{MPA})$$

When fish actively migrates towards the area with the highest prey encounter rate, parameter *z* is calculated by dividing the prey encounter rate inside the fishing ground by the sum of the prey encounter rates of both fishing ground and MPA:

$$z=\frac{\varepsilon_{FG}}{\varepsilon_{FG}+\varepsilon_{MPA}}$$

Active migration towards the area with the highest fish intake rate is calculated by dividing the fish intake rate inside the fishing ground by the sum of the intake rates of both fishing ground and MPA:

$$z=g\frac{\varepsilon_{FG}}{(1+h\varepsilon_{FG})}/(g\frac{\varepsilon_{FG}}{(1+h\varepsilon_{FG})}+g\frac{\varepsilon_{MPA}}{(1+h\varepsilon_{MPA})})$$

With active migration, there will still be nett spillover of fish from the MPA to the fishing ground (figure A4.1). This occurs because the fishing ground has highest prey encounter and fish intake rates due to a higher abundance of benthos suitable as fish prey (figure 4.1, main manuscript). Both types of active migration lead to similar amounts of fish spillover compared with diffusive mixing and this shows that our findings are robust against these different mechanisms of fish migration. Active migration can result in increased spillover of fish at high trawling intensities (figure A4.1b). However, this only occurs at intensities beyond that which maximize yield and, as such, it is irrelevant in relation to our findings.

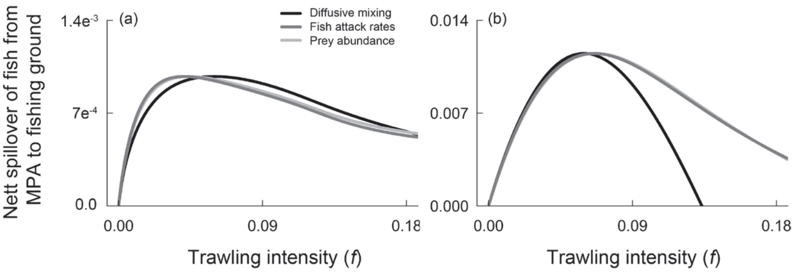

Figure A4.1 Impact of bottom trawling (by varying *f*) on the amount of nett spillover of fish from MPA to fishing ground when there is a low (a) or high (b) benthic fish prey production in absence of fishing (by varying μ_B). The three lines present the different mechanisms of fish migration. μ_B=0.001 in (a) and 0.2 in (b), to keep the benthos-fish ratio 2:1 μ_P is varied as well and is 0.109 in (a) and 0.17 in (b), e=0.3, p=0.5, all other parameters have default values.

Chapter 5

HABITAT-SPECIFIC EFFECTS OF FISHING DISTURBANCE ON BENTHIC SPECIES RICHNESS IN MARINE SOFT SEDIMENTS.

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primary productivity
species richness

Around the globe, marine soft sediments on continental shelves are affected by bottom trawl fisheries. In this study we explore the effect of this widespread anthropogenic disturbance on the species richness of a benthic ecosystem, along a gradient of bottom trawling intensities. We use data from 80 annually sampled benthic stations in the Dutch part of the North Sea, over a period of 6 years. Trawl disturbance intensity at each sampled location was reconstructed from satellite tracking of fishing vessels. Using a structural equation model, we studied how trawl disturbance intensity relates to benthic species richness, and how the relationship is mediated by total benthic biomass, primary productivity, water depth, and median sediment grain size. Our results show a negative relationship between trawling intensity and species richness. Richness is also negatively related to sediment grain size and primary productivity, and positively related to biomass. Further analysis of our data shows that the negative effects of trawling on richness are limited to relatively species-rich, deep areas with fine sediments. We find no effect of bottom trawling on species richness in shallow areas with coarse bottoms. These condition-dependent effects of trawling suggest that protection of benthic richness might best be achieved by reducing trawling intensity in a strategically chosen fraction of space.

INTRODUCTION

Identifying the factors that determine species richness has been central to community ecology. Much of the empirical and theoretical work has been dedicated to examine the relationships between species richness and both productivity (for review see Waide *et al.* 1999) and disturbance (for review see Sousa 1984). The text-book prediction is that richness is highest at an intermediate level of productivity or disturbance (Grime 1973, Connel 1978). However, negative and positive monotonic, U-shaped and non-significant relationships have also regularly been observed (Mackey and Currie 2001, Mittelbach *et al.* 2001, Hughes *et al.* 2007, Adler *et al.* 2011, Cusens *et al.* 2012). The shape of the pattern has been suggested to depend on the scale of the observations (Moore and Keddy 1989), environmental heterogeneity (Guo and Berry 1998) or the combined effects of disturbance and productivity on communities (Huston 1979, Kondoh 2001).

Despite the persistence of the hump-shaped relationship in the literature, there is both limited empirical support for it, and the mechanistic underpinning of the pattern has repeatedly been challenged (Abrams 1995, Fox 2013). This has led some authors to call for the development of new, mechanistic explanations for the observed relationships between productivity, disturbance and species richness (Adler *et al.* 2011, Fox 2013).

In this study we explore the effects of bottom trawl fishery disturbance and productivity on benthic richness in a soft-bottom habitat covering the Dutch part of the North Sea. This area is known to be intensively fished by beam trawlers, towing several tickler chains over the seafloor to chase their target species sole (*Solea solea*) and plaice (*Pleuronectus platessa*) (Rijnsdorp *et al.* 2008). This type of fishery incurs severe physical disturbance on the seabed up to at least the first 6 cm (Bergman and Hup 1992), which may have major impacts on benthic organisms, processes and functioning (Jennings and Kaiser 1998, Kaiser *et al.* 2002). Some intensively fished areas in the North Sea are trawled more than 10 times per year (Rijnsdorp *et al.* 1998, Piet and Hintzen 2012). The amount and timing of this trawl disturbance largely depends on the occurrence of commercial fish species, plaice and sole, in the area (Rijnsdorp *et al.* 2011). As these species feed on benthic invertebrate prey (Molinero and Flos 1992, Rijnsdorp and Vingerhoed 2001, Shucksmith *et al.* 2006), both fish species and subsequently fishery may be attracted to areas of high benthic productivity. This may result in an interaction between trawl disturbance intensity and benthic productivity on large spatial and temporal scales and may affect species richness.

Many studies have examined the relationship between productivity or (trawl) disturbance and benthic richness in marine soft sediments (*e.g.* Pearson and Rosenberg 1978, Collie *et al.* 2000, Hall *et al.* 2000, Huxham *et al.* 2000, Hiddink *et al.* 2006, Hinz *et al.* 2009). This is often done on small spatial and temporal scale, to reduce the confounding effect of habitat heterogeneity. How habitat heterogeneity interacts with both disturbance and productivity and how all together affect species richness is largely unknown. This is surprising, as marine soft-bottom habitats are the most common on earth and provide important ecosystem services, *e.g.* contributing to biogeochemical cycles and food production (Snelgrove 1999). One reason for our lack of knowledge is the inaccessibility of the marine habitat, which restricts the possibilities to conduct underwater experiments, especially on large spatial and temporal scales (Thrush *et al.* 1997). In some cases, large spatial and temporal scales are covered by benthic monitoring programs, usually constructed to acquire indications of ecosystems health. Although the data from such programs cannot replace the mechanistic knowledge obtained through manipulation experiments, it can be used to explore relationships between productivity and trawl disturbance and their combined effect on benthic communities.

Our analysis of data from a North Sea benthic monitoring program shows that the effects of trawl disturbance and productivity on benthic richness are both negative, but are positively related to each other. Both explain a relatively small amount of the variation in species richness. Within two subsets of sediment grain size gradients, there is either a negative effect of trawl disturbance on species richness or no effect. These habitat-specific effects emphasise the importance of the choice of spatial scale to assess the impact of trawl disturbance on benthic communities.

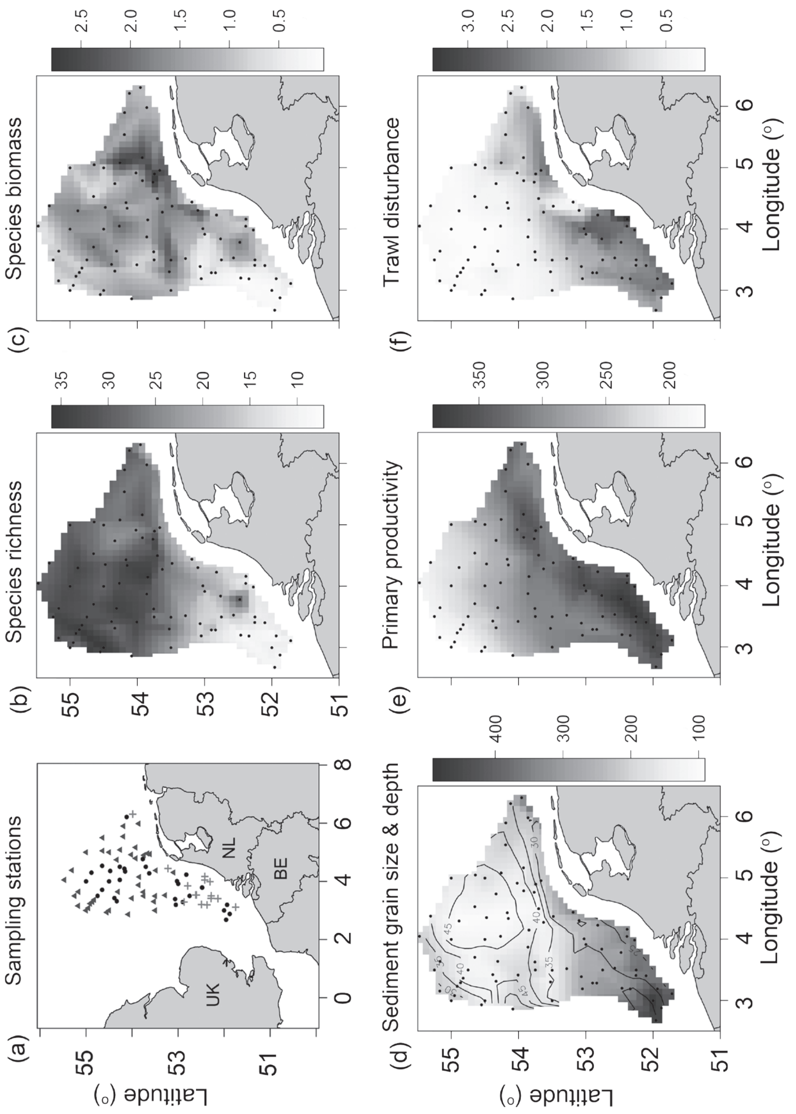

Figure 5.1 Maps of macrozoobenthos stations and the variables studied. (a) Macrozoobenthos stations sampled between 2002-2007 in the Dutch EEZ (all points). After exploration of the total data set, two subsets of the data with more homogenous sediment grain sizes were extracted, one with finer sediments, (125 - 235 µm, triangles) and one with coarser sediments (290 - 430 µm, plus signs). Subset selection is explained in the *Method* section. Panels (b-f) are created using point interpolation of the average of all years per station for species richness (b, colour scale; number), species biomass (c, colour scale; gram/sample), sediment grain size with depth contours (in meters) (d, colour scale; µm), primary productivity (e, colour scale; gr C/m^2/year) and trawl disturbance (f, colour scale; average fraction of surface area trawled per year).

METHODS

The effects of trawl disturbance and productivity on benthic species richness were examined using 6 years of data obtained from a benthic monitoring program in the Dutch part of the North Sea. Trawl disturbance intensity was estimated from Vessel Monitoring by Satellite (VMS) data (Hintzen *et al.* 2010, Piet and Hintzen 2012). We used primary productivity, calculated from the ecosystem model ERSEM (Baretta *et al.* 1995), as an approximation for benthic productivity and also included benthic biomass data, obtained from the monitoring program. Biomass has often been used to approximate productivity in terrestrial studies (Guo and Berry 1998, Mittelbach *et al.* 2001) but will be decoupled from productivity when there is strong predation. Biomass has also been used to indicate the strengths of competitive interactions (Gough *et al.* 1994). Finally, our analysis included both sediment grain size and water depth, which are seen as important factors to predict benthic richness in soft-bottom marine systems (Gray 2002) and hence help to prevent confounding effects.

MACROBENTHIC DATA COLLECTION

Data on macrobenthic richness and biomass were obtained from the Dutch monitoring program MWTL in the Dutch Exclusive Economic Zone (EEZ) (www.waterbase.nl). Benthos data were collected from 81 stations (2002-2005) and then from 79 (2006-2007) (figure 5.1). All selected stations were located outside the 12-mile zone, as these areas are less affected by coastal fisheries and natural disturbances. At all stations, samples were collected between March and June using a 0.078 m^2 Reineck box corer and sieved over a 1 mm mesh sieve (Daan and Mulder 2009). In the retained fraction of the sample, biota were manually separated from sediment and other material and identified to species level. When unknown (3 percent of the total biomass), biota were determined to higher taxonomic groupings (genus, family, order, class or phylum) and counted, when belonging to the same taxonomic grouping, as a single species in the calculation of species richness.

Total biomass per station per year was the sum of all individuals collected in grams ash free dry weight. Some individuals had biomass larger than the rest of the sample combined. These individuals, mostly large bivalves, are not effectively sampled with a Reineck box corer and were hence classified as outliers and removed. This occurred for 10 observations, sampled in 10 different stations and 5 different years. Finally, a sorting error in the data from 2006 made a portion of the observations unusable (pers. comm. Dutch Waterbase), this did not affect the outcome of the analysis for 2006 compared to the other years.

PRIMARY PRODUCTIVITY ESTIMATION

Primary productivity was obtained through predictions from GETM-ERSEM (General Estuarine Transport Model – European Regional Seas Ecosystem Model) (Baretta *et al.* 1995). GETM-ERSEM describes the temporal and spatial patterns of the biogeochemistry of the water column and sediment using two coupled hydrodynamic models. These models predicted total production of new phytoplankton biomass for each year (g C/ m^2/ y) per sampled macrobenthic station on a 10 x 10 km spatial scale. Total production was estimated for each area over a period of one year prior to the sampling date. These modelled productivities approximate measured primary productivity (Ebenhoh *et al.* 1997).

TRAWL DISTURBANCE

Trawl disturbance at the sampled locations was estimated from the VMS data. VMS data provided information for each fishing vessel on its position, speed and heading approximately every 2 hours. The VMS data was linked per fishing trip to vessel logbook data with information on vessel and gear characteristics (Hintzen *et al.* 2012). Only VMS data from vessels with beam trawl gear and large engine power (> 349 kW) were included in the analysis, as these dominated the study area (Rijnsdorp *et al.* 2008). We checked the activity of low-power vessels and confirmed that it was present at negligible intensity for all stations (results not shown). From this selected dataset, trawl disturbance was estimated on a fine spatial grid, 0.001° latitude by 0.001° longitude (approximating an area of 110 by 70 meter), to have the best approximation of disturbance at each sampling station using the method described in Hintzen *et al.* (2010) and Piet and Hintzen (2012). Trawl disturbance was expressed as the fraction of cumulative surface area trawled in each grid cell over a period of one year prior to the sampling date. This annual trawl disturbance estimation might not cover all benthic responses, as we know that recovery for benthic species following trawling disturbance may last more than one year (Kaiser *et al.* 2006). Some of these effects are indirectly picked up, since there is a clear correlation between disturbance at a station in one year and the year before (mean correlation coefficient = 0.89 using Pearson product-moment correlation).

HABITAT CHARACTERISTIC PARAMETERS

Median sediment grain size for each macrobenthic station per year was obtained from particle size analysis of sediments directly taken from the benthic monitoring program (www.waterbase.nl). Depth was extracted from bathymetric data on the North Sea for all sampled stations on a 1 x 1 km spatial scale (based on bathymetric data from www.helpdeskwater.nl and verified with bathymetric data from Deltares 2011).

STATISTICAL PROCEDURE

A structural equation model (SEM), a multivariate analysis of networks of causal relationships (Grace 2006), was used to examine the combined effects of productivity, disturbance, biomass, sediment grain size and depth on species richness. All the factors included in the model were expected to interact both directly and indirectly. In the SEM, depth was the exogenous variable, i.e. connected with all others (see for terminology of SEM: Grace *et al.* 2012). It was assumed that in addition to depth, both productivity and sediment grain size might explain variations in trawl disturbance, as we expect that these together might explain the spatial distribution of the target species in the area. The model connected the four variables (sediment grain size, depth, primary productivity and trawl disturbance) with biomass, and it was expected that these variables explained variation in species richness. The SEM had a double arrow between sediment grain size and productivity to represent a joint factor not included in the analysis (see *Discussion* section). The constructed SEM had as many pathways between the variables as there were degrees of freedom, which means that we started with a saturated model. The model was tested for each year separately to obtain indications of temporal variability for the different model pathways. When pathways were non-significant (p-value > 0.05) in 6 out of 6 years, they were removed, leading to a revised model for which we reviewed the distributional properties of the residuals at each node. After certain nodes were improved by transformation, i.e. a log-transformation for grain size and richness and a log(x+1) transformation for biomass, the final model was tested for overall model fit using a chi-square test. SEM analyses were performed using the package Lavaan in R (Rosseel 2012). SEM outcome per year is shown in table A5.1, A5.2 and A5.3 in appendix 5.1.

Because the results of the final SEM pointed towards examining the effects of the variables on richness and biomass according to different sediment grain sizes, rather than across a gradient, we divided the data according to grain size into two subsets. The subsets were derived by a stepwise reduction of the grain size range (in steps of 5 μm), aiming to preserve the largest number of sampled stations with a non-significant relation between grain size and species richness and biomass, while there was still a trawling disturbance gradient. Because we assumed interannual variation to explain part of the variation between years for all benthic stations, subset selection was done using a linear mixed model with year as random factor. The resulting two subsets of the data had grain sizes of 125 - 235 μm and 290 - 430 μm (figure 5.1 and 5.2). In each subset, linear-mixed models with year as random factor were constructed to re-examine the effects of disturbance, productivity and depth on richness and biomass, where biomass was log(x+1) transformed. Model fits were assessed using the Akaike Information Criterion (AIC) and the model with the lowest AIC was selected as best candidate. When other candidate models had a difference of 0 – 2 AIC units, we concluded that models were essentially equivalent and the model with fewest parameters was selected.

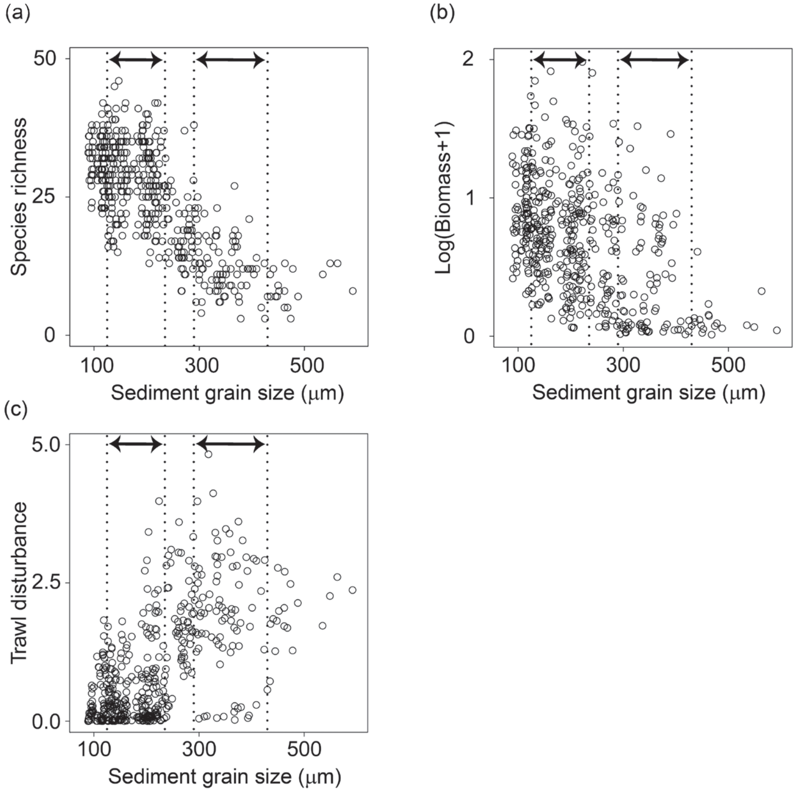

Figure 5.2 We selected two subsets of the data where sediment grain size had no significant effect on species richness (a) and biomass (b), while there was still a trawling disturbance gradient (c). The two subsets are marked by the arrows between the vertical dashed lines. The subset at relatively finer sediments varies between 125 - 235 μm and the other subset between 290 - 430 μm. Subset selection is explained in the *Method* section.

We examined linear relationships in all statistical procedures. Because unimodal patterns have been predicted for some of the variables studied here (between richness and disturbance and richness and productivity), we verified by testing model residuals that there were no clear unimodal relationships.

RESULTS

Bivariate correlations show that most variables strongly correlate with each other except between biomass and primary productivity, and biomass and trawl disturbance (table 5.1). Correlations between richness and trawl disturbance (figure 5.3a, r^2=0.36), primary productivity (figure 5.3b, r^2=0.25) and sediment grain size (figure 5.3d, r^2=0.55) are negative, while biomass (figure 5.3c, r^2=0.14) and depth (r^2=0.23) correlate positively with richness. Whether the changes observed in richness are direct effects of the gradient in the predictor variable or indirect effects governed by other predictor variables (affecting them together) is examined with a SEM, which allows us to study the relative strengths of the different factors in combination.

Table 5.1 Correlation coefficient matrix for all variables studied. We used untransformed data and all 6 years for the comparisons. The correlation coefficients and p-values were calculated using Pearson product-moment correlation.

	Biomass		Richness		Grain size		Depth		Primary productivity	
	Corr.	***P***	**Corr.**	***P***	**Corr.**	***P***	**Corr.**	***P***	**Corr.**	***P***
Richness	0.375	<0.001								
Grain size	-0.366	<0.001	-0.745	<0.001						
Depth	0.172	<0.001	0.485	<0.001	-0.646	<0.001				
Primary productivity	0.038	0.400	-0.506	<0.001	0.510	<0.001	-0.364	<0.001		
Trawl disturbance	-0.080	0.079	-0.603	<0.001	0.614	<0.001	-0.562	<0.001	0.613	<0.001

We started with a saturated SEM (see *Method* section) and tested whether pathways were non-significant in 6 out of 6 years. This was true for the pathways between trawl disturbance and biomass, which is unsurprising as there is no strong bivariate correlation (table 5.1); it was also true for the pathway between depth and species richness, which is unexpected as these are strongly correlated (table 5.1). Hence, depth only has an indirect effect on richness, passed on through the other endogenous variables (grain size, primary productivity, trawl disturbance and biomass).

All other pathways were at least two times significant in the six years tested and were retained in the final SEM (figure 5.4). The final model has a mean χ^2 of 3.58 (standard error χ^2 = 0.60), 2 degrees of freedom and p-values ranging between 0.06 and 0.36, which suggests that model structure supports the data. Based on the final model structure, we obtained the following results: (1) variation in benthic richness is reasonably well explained (mean r^2=0.69), but variation in biomass much less so (mean r^2=0.30); (2) sediment grain size, as the standardised coefficients show, has the strongest effect on both benthic richness and biomass; (3) trawl disturbance has a negative effect on richness and no

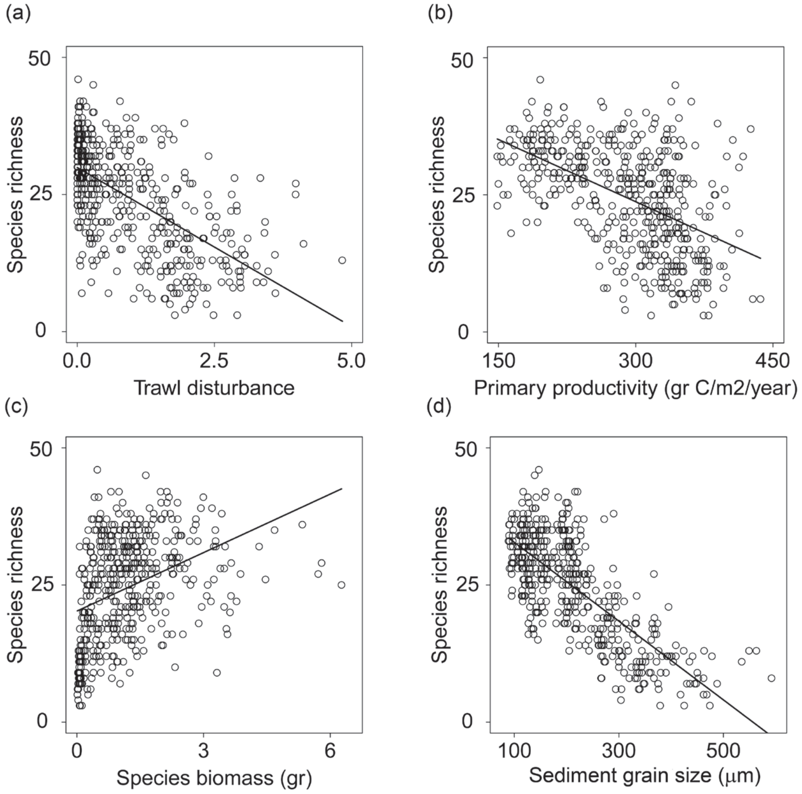

Figure 5.3 Bivariate correlations between species richness and trawl disturbance (a), primary productivity (b), species biomass (c) and sediment grain size (d). See Table 1 for correlation coefficient and significance values. The lines in the bivariate plots were constructed using linear regression.

effect on biomass; (4) biomass and primary productivity show a positive relationship, and have opposing relationships with richness (richness is positively correlated with biomass and negatively with primary productivity); (5) variation in trawl disturbance is largely explained by depth, primary productivity and sediment grain size (mean r^2=0.59).

The final structure of the SEM allowed us to examine the direction of the effect between richness and biomass in 5 of the 6 years (2003 did not meet the requirements to test the reciprocal interaction since depth had no effect on biomass and trawl disturbance had no effect on richness, see table A5.3 in appendix 5.1). In 3 of these 5 years, we observed a positive effect of biomass on richness (all p-values < 0.04), while we found no effect of richness on biomass.

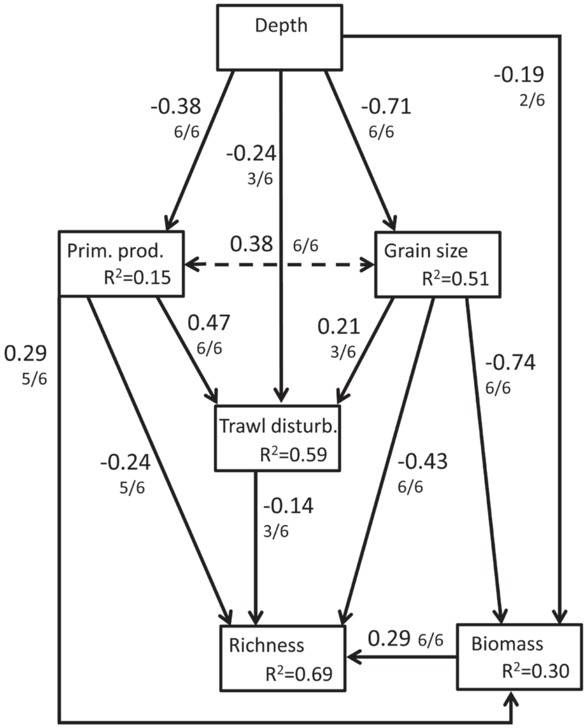

Figure 5.4 Final structural equation model (SEM) that fitted the data between 2002 – 2007 best (average $\chi^2 = 3.58$, standard error $\chi^2 = 0.604$, df = 2 and 6/6 times p-value > 0.06). Boxes represent our variables. The numbers next to the arrows are the mean standardised coefficients (based on these 6 years) and number of times that this pathway had a p-value lower than 0.05. The dashed line with arrows on both sides shows strong correlation but direction is unknown (see *Discussion* section). Model selection procedure and data transformations are explained in the main text.

Table 5.2 Model selection for richness and biomass in the data subsets. Model selection was based on AIC. The two or three models that fitted data best are shown (Δ AIC shows best candidate model by *). The names p1 and x1 refer to the first predictor variable in the same row, p2 and x2 to the second, etcetera. We used a linear mixed model with year as random factor. Biomass is log(x+1) transformed.

	Sediment grain size between 125 - 235 um (n=230 for 6 years)				
	Best model fits:	P-value	Estimated intercept	AIC	Δ AIC
Richness ~	Trawl disturbance + primary productivity	p1=0.004; p2=0.002	Y=36.3-2.0*x1-0.02*x2	1489.1	9.3
	Trawl disturbance + primary productivity + biomass	p1=0.001; p2<0.000; p3=0.001	Y=35.4-2.4*x1-0.03*x2+3.8*x3	1479.8	0.0*
Biomass ~	Trawl disturbance	p1<0.000	Y=0.65+0.187*x1	188.7	13.4
	Primary productivity	p1<0.000	Y=0.14+0.002*x1	179.1	3.8
	Trawl disturbance + primary productivity	p1=0.017; p2<0.000	Y=0.24+0.099*x1+0.002*x2	175.3	0.0*

	Sediment grain size between 290 - 430 um (n=84 for 6 years)				
	Best model fits:	P-value	Estimated intercept	AIC	Δ AIC
Richness ~	Biomass	p1<0.000	Y=10.3+5.9*x1	494.2	1.9*
	Trawl disturbance + biomass	p1=0.054; p2<0.000	Y=11.9-0.9*x1+6.1*x2	492.3	0.0
Biomass ~	Depth	p1<0.000	Y=1.41-0.03*x1	79.9	0.0*
	Depth + trawl disturbance	p1<0.000; p2=0.689	Y=1.47-0.04*x1-0.02*x2	81.7	1.8
	Depth + primary productivity	P1<0.000; p2=0.585	Y=1.72-0.04*x1-0.0007*x2	81.6	1.7

Given the strong effect of grain size on richness and biomass, we analysed whether the results of the SEM would still hold within subsets of the range of sediment grain size in our data. The subset with relatively small grain sizes (125 – 235 μm) covers almost the entire range of variability in all other variables, except for trawl disturbance which ranges between 0.0 – 4.0, as opposed to 4.8 (table A5.4 in appendix 5.2). Analysing this subset with a linear mixed model gives a similar outcome as the SEM for explaining variation in species richness (figure 5.4). Richness is best described by the combined effects of trawl disturbance (negatively correlated), primary productivity (negatively correlated) and species biomass (positively correlated) (table 5.2). Variation in biomass is best described by the combined effect of primary productivity and trawl disturbance (both positively correlated) (table 5.2). This differs from the SEM results, where trawl disturbance had no effect on biomass.

The subset with larger sediment grain size (290 – 430 μm) has smaller gradients in depth, primary productivity and biomass compared to the total data set, but covers the entire range of trawl disturbance intensity (table A5.4 in appendix 5.2). Analysing this subset gives a different outcome than the SEM for explaining variation in species richness. Richness is positively correlated with biomass but none of the other variables add any explanatory value. This is true even for the model that includes trawl disturbance (which only reduces the AIC with 1.9). Variation in biomass is best described by depth (table 5.2).

DISCUSSION

Our analysis demonstrates how a combination of direct and indirect effects in this soft-bottom marine habitat shape benthic species richness. Richness is mostly determined by the gradient in sediment grain size, and is negatively related to both primary productivity and trawl disturbance. The effects of disturbance on richness and biomass diverge within subsets of our data with a relatively homogenous grain size. These habitat-dependent effects have important implications for the conservation and restoration of marine benthic habitats.

We observed a negative relationship between productivity and richness in the SEM. This negative relationship could be the declining part of a hump-shaped pattern. Although the mechanisms behind this declining phase continue to be debated, two predicted mechanisms have received most attention in plant communities (Waide *et al.* 1999, Adler *et al.* 2011). The first mechanism implies that high productivity reduces the heterogeneity of limiting resources and that this results in a situation in which only the dominant competitors persist (Tilman and Pacala 1993). If so, competitive exclusion would show up in the data as a decline in species richness as biomass increases. However, in our data a positive relationship exists between richness and biomass. The second hypothesized mechanism requires the inclusion of disturbance (Huston 1979, Kondoh 2001). A negative relationship between productivity and richness may typically be observed at low disturbance (Kondoh 2001). It is unlikely that this is the underlying explanation in our area, as our results show a positive relationship between productivity and trawl disturbance.

In contrast to the negative relationship between productivity and richness, a positive relationship between biomass and richness was observed. The directionality of this effect was tested in our SEM (by including a reciprocal interaction between richness and biomass) (Grace 2006) and this showed that biomass affects richness, but not vice versa. One suggested explanation for the opposing responses of productivity and biomass on richness is the omnipresent impact of predation in soft-bottom habitats (for a review, see Wilson 1991 and Seitz 1998), since predation may decouple the strong correlation between productivity and biomass (Oksanen *et al.* 1981).

Within the subset of the data with larger grain sizes, no effect was found between productivity and benthic richness. This subset started at higher productivities compared to the other subset where a negative relationship with benthic richness was found. One possible explanation could be that the effect of productivity on richness is limited to low and intermediate productivity, while other factors determine richness at higher productivity.

In this study, we used primary productivity as the best approximation of benthic productivity. However, benthic production depends not only on the amount but also on the quality of organic matter that is available as food for benthos

(Dauwe *et al.* 1998). Variation in quality could thus decouple this relationship. This decoupling seems to have limited effects, as we still find a strong relationship in the SEM between trawl disturbance and primary productivity. This relationship was expected when areas with high productivity produce large quantities of fish food, to which the fish are attracted.

We observed a negative relationship between trawl disturbance and species richness in the SEM (figure 5.4). These negative effects have most commonly been described in areas with gradients of human disturbance (Mackey and Currie 2001). They are also observed in studies specifically examining the impact of bottom trawling on benthic richness (Collie *et al.* 2000, Hiddink *et al.* 2006, Hinz *et al.* 2009). However, the effects of disturbance on richness diverge within subsets of our data with a relatively coarse or fine grain size.

Within the subset of the data with coarser grain sizes, no effect was found between trawl disturbance and species richness, which was surprising as this subset had a large trawl disturbance gradient. This gradient ranged from two locations in a protected area (the Plaice Box), where beam trawl effort decreased by more than 90% after the establishment of the protected zone in 1989 (Beare *et al.* 2013), to different locations where trawl disturbance was estimated to be the highest in the entire data set. These findings lead to the question of whether fishing occurs predominantly in low diversity areas, where its effects matter least, or whether the benthic ecosystem in heavily fished areas adapts accordingly (and for the stations in the Plaice Box remains in this state). The former scenario suggests that there is limited need to protect benthic richness from trawl disturbance in this habitat. In contrast, the latter scenario suggests that the absence of trawl disturbance in the protected area has (so far) not induced benthos recovery. The opposing scenarios clearly show the limits to the use of species richness as indicator to examine effects of trawl disturbance on ecosystem health. Richness points only at one aspect of ecosystem health and a further exploration of trawl disturbance should look into possible changes in community structure or functioning, for example using a trait-based approach (Bremner 2008).

At finer sediment grain sizes, we observed a stronger negative relationship between disturbance and richness. This suggests that marine protected areas may work to protect benthic richness when placed in these habitats. Interestingly, we also saw a positive relationship between disturbance and biomass in these finer sediments. An increase in biomass in response to trawling was also observed with the model result by van Denderen *et al.* (2013). Based on the model, such an increase may be expected in a top-down controlled system where trawling reduces fish abundance and its predation impact on benthic prey, or in a bottom-up controlled system where trawling increases productivity of the area.

Patterns in benthic richness in our data are best explained by a complex structure of interacting variables. The high degree of interaction is clearly visible for the trawl disturbance gradient, which is largely related to (and explained by) habitat characteristics. To disentangle the relative strengths of the interacting variables on richness we used a SEM that included an unknown relationship between sediment grain size and primary productivity. The variables covaried, although there is no clear causal link between them. Both are high/large near the coast and low/small further away from the coast and this correlation is probably due to a third, confounding factor. This may also apply to other pathways in our SEM, although most were based on a better understanding of the causal mechanisms involved.

Assessing the strength of the different predictor variables in the SEM showed that sediment grain size had the strongest effect on benthic richness. Sediment grain size, it should be noted, is measured directly at the sampling locations together with the biological samples, and therefore may have higher accuracy than the estimates used for the other predictor variables. This may have influenced the statistical model outcome, for example some variables might have had more importance if the measurement errors had been lower. Besides the variables studied here, there are two others which likely interact with the other predictor variables to affect benthic richness: natural disturbance and fish abundance. Natural disturbance is expected to covary with depth and for that reason we also removed the number of points at very shallow sampling locations which are likely outliers in terms of natural disturbance (see *Method* section). As some have proposed, frequent natural disturbance may lower the relative impact of trawling on the benthic habitat (Hall 1994, Kaiser and Spencer 1996, Kaiser 1998, Diesing *et al.* 2013). Natural disturbance may thus interact with trawl disturbance and could be one of the reasons that we found no effect of trawl disturbance in the subset of the data with the largest grain size. The inclusion of fish (especially plaice and sole) and their predation impact on benthic prey could have an even more profound effect on benthic richness (and biomass). These effects on richness and biomass have been observed in many predator-prey studies (*e.g.* Paine 1966, Oksanen *et al.* 1981, Shurin *et al.* 2002).

In this study we explored how different factors interact and together affect species richness in a marine soft-bottom environment. Although the monitoring data do not allow us to determine the mechanisms behind these observed patterns, our results provide insight into the potential processes. While part of our results, in particular the negative relationship between disturbance and richness, corroborate earlier findings, other (combinations of) results were unexpected. This is especially the case for the negative relationship between richness and primary productivity and the positive relationship between richness and biomass. Another important result of our work is the habitat-specific response of trawl disturbance on benthic richness. This suggests a multivariate, non-linear relationship between these factors and hence indicates habitat-dependent effects of bottom trawl fisheries. Such a multivariate response has been suggested by others (*e.g.* Kaiser *et al.* 2006), but it has, to the best of our knowledge, never been shown to occur in one dataset, under the influence of a single type of fishing.

Our outcome emphasises the importance of the choice of spatial scale to assess the impact of trawl disturbance on the benthic community. It suggests that the right spatial scale depends on the heterogeneity of the habitat and the combined effects of trawl disturbance and productivity on the benthic community. A clearer understanding of the processes and patterns associated with benthic richness and biomass in these habitats is a requirement for the conservation of these systems and the management of their exploitation.

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APPENDIX 5.1 STRUCTURAL EQUATION MODEL OUTCOME PER YEAR

Table A5.1 Model fit of the final SEM for the 6 years of data (mean χ^2 of 3.58, standard error χ^2 = 0.60).

	2002	2003	2004	2005	2006	2007
χ^2	5.81	3.55	2.78	4.81	2.47	2.06
df	2	2	2	2	2	2
P-value	0.06	0.17	0.25	0.09	0.29	0.36

Table A5.2 Coefficient of determination (R^2) from the SEM for the 6 years of data and their mean and standard error. Sediment grain size and species richness are log-transformed and species biomass log(x+1).

	2002	2003	2004	2005	2006	2007	Mean	SE
Biomass	0.23	0.25	0.32	0.29	0.34	0.39	0.30	0.02
Richness	0.65	0.63	0.74	0.74	0.69	0.67	0.69	0.02
Grain size	0.51	0.49	0.50	0.50	0.51	0.53	0.51	0.01
Prim. productivity	0.06	0.11	0.14	0.19	0.09	0.32	0.15	0.04
Trawl disturbance	0.54	0.61	0.54	0.61	0.66	0.60	0.59	0.02

Table A5.3 Standardised coefficients and p-values per year for each pathway from the SEM and their mean, standard error and number of times that the p-values are lower than 0.05. Sediment grain size and species richness are log-transformed and species biomass log(x+1). Read tilde (~) as "is modelled as" and double tilde (~~) as "varies together with".

	2002		2003		2004		2005		2006		2007				
	Stand. coef.	P-value	Stand. coef.	P-value	Stand. coef.	P-value	Stand. coef.	P-value	Stand. coef.	P-value	Stand. coef.	P-value	Mean	SE	P-value < 0.05
Biomass ~ Grain size	-0.59	0.000	-0.53	0.000	-0.73	0.000	-0.71	0.000	-0.91	0.000	-0.95	0.000	-0.74	0.07	6
Biomass ~ Prim. prod.	0.28	0.010	0.30	0.005	0.27	0.013	0.30	0.008	0.20	0.064	0.39	0.001	0.29	0.03	5
Biomass ~ Depth	-0.11	0.441	0.04	0.791	-0.12	0.360	-0.12	0.379	-0.53	0.000	-0.29	0.026	-0.19	0.08	2
Richness ~ Grain size	-0.42	0.000	-0.44	0.000	-0.41	0.000	-0.41	0.000	-0.46	0.000	-0.43	0.000	-0.43	0.01	6
Richness ~ Trawl dist.	-0.20	0.028	0.06	0.608	-0.25	0.003	-0.26	0.004	0.02	0.818	-0.18	0.086	-0.14	0.06	3
Richness ~ Prim. prod.	-0.17	0.045	-0.36	0.000	-0.18	0.016	-0.13	0.120	-0.39	0.000	-0.21	0.045	-0.24	0.04	5
Richness ~ Biomass	0.32	0.000	0.34	0.000	0.25	0.000	0.41	0.000	0.25	0.000	0.18	0.023	0.29	0.03	6
Grain size ~ Depth	-0.71	0.000	-0.70	0.000	-0.70	0.000	-0.70	0.000	-0.72	0.000	-0.73	0.000	-0.71	0.01	6
Prim. prod. ~ Depth	-0.24	0.026	-0.34	0.001	-0.37	0.000	-0.43	0.000	-0.30	0.005	-0.57	0.000	-0.38	0.05	6
Trawl dist. ~ Prim. prod.	0.44	0.000	0.56	0.000	0.36	0.000	0.49	0.000	0.49	0.000	0.50	0.000	0.47	0.03	6
Trawl dist. ~ Depth	-0.42	0.000	-0.15	0.133	-0.20	0.056	-0.23	0.019	-0.36	0.000	-0.06	0.579	-0.24	0.05	3
Trawl dist. ~ Grain size	0.08	0.483	0.23	0.027	0.32	0.007	0.20	0.057	0.15	0.142	0.30	0.009	0.21	0.04	3
Grain size ~~ Prim. prod.	0.35	0.003	0.32	0.006	0.41	0.001	0.37	0.002	0.41	0.001	0.42	0.001	0.38	0.02	6

APPENDIX 5.2 VARIABLE RANGE IN THE TOTAL DATASET AND THE TWO SUBSETS

Table A5.4 The minimum, maximum and mean values for all variables in the total data set and in the two subsets for the 6 years of data.

		Total dataset (n=482)			Subset 125 - 235 µm (n=230)			Subset 290 - 430 µm (n=84)		
Variable	**unit**	**min**	**max**	**mean**	**min**	**max**	**mean**	**min**	**max**	**mean**
Richness	number	3	46	24.4	13	46	28.7	3	27	12.8
Biomass	g (dry weight)	0.01	6.27	1.18	0.06	6.27	1.31	0.01	3.57	0.68
Depth	m	22.2	55.9	36.3	26.2	55.9	37.5	22.2	36.2	28.7
Prim. productivity	g C/m^2/year	148.7	436.3	291.1	148.7	417.3	268.8	257.8	436.3	342.2
Grain size	µm	89	592	216.3	126	234	176.9	292	425	345.3
Trawl disturbance	fraction	0	4.83	0.95	0	3.98	0.57	0.02	4.83	1.97

Chapter 6

TEMPORAL AGGREGATION OF BOTTOM TRAWLING AND ITS IMPLICATION FOR THE IMPACT ON THE BENTHIC ECOSYSTEM.

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temporal effort distribution
Vessel Monitoring by Satellite (VMS)

Understanding trawling impacts on the benthic ecosystem depends to a large extent on the ability to estimate trawling activity at the appropriate scale. Several studies have assessed trawling at fine spatial scales on an annual basis, largely ignoring temporal patterns. In this study we analysed these temporal patterns in beam trawl effort intensity at 90 stations of the Dutch continental shelf of the North Sea for a period of 10 years, at a fine temporal (weekly) and spatial (110 by 70 meter) scale using Vessel Monitoring by Satellite (VMS) data. Our results show that trawling is aggregated in time and shows clear seasonality, related to the behaviour of the fleet and migration patterns of the target fish species. The temporal patterns affect the overall impact on and the recovery of the benthic community, as is illustrated with a benthic population model. Our results imply that trawling impact studies using high resolution data like VMS should take account of the possibility of temporal aggregation and seasonality in trawling in order to improve the assessment of the impact of trawling on the population dynamics of benthos.

INTRODUCTION

The impact of bottom trawl fishery on the seabed is a matter of concern already for some time (de Groot, 1984, Auster *et al.*, 1996, Jennings and Kaiser, 1998) and still remains one of the major challenges in ecosystem-based fishery management (Pikitch *et al.*, 2004). Bottom trawl gears disturb the seabed while catching bottom-dwelling target species and this affects non-target organisms and the functioning of the benthic ecosystem (Kaiser *et al.*, 2002). Assessing the possible effects of bottom trawling on the ecosystem depends to a large extent on our ability to estimate the distribution and intensity of trawling activities.

Many studies have shown that bottom trawl fishery is patchily distributed (Rijnsdorp *et al.*, 1998, Pitcher *et al.*, 2000, Ragnarsson and Steingrímsson, 2003, Bellman *et al.*, 2005, Murawski *et al.*, 2005). This highlighted the importance of an appropriate spatial scale to analyse the impact of trawling on benthic organisms and habitats. This appropriate scale is at a grid resolution where fishing effort becomes randomly distributed, i.e. when fishing effort averages accurately represent the area (Rijnsdorp *et al.*, 1998). The impact of trawling on benthic organisms and habitats at such spatial scales and the evaluation of the fisheries footprint have been described in several studies (*e.g.* Rijnsdorp *et al.*, 1998, Piet *et al.*, 2000, Dinmore *et al.*, 2003, Hiddink *et al.*, 2006a, Hiddink *et al.*, 2006b, Lee *et al.*, 2010, Jennings *et al.*, 2012, Lambert *et al.*, 2012, Piet and Hintzen, 2012).

Although all studies agreed on the use of a correct spatial scale, the question of an appropriate temporal scale has not received much attention (but see Piet and Quirijns 2009, Lambert *et al.* 2014 and Ellis *et al.* 2014). For most trawl impact studies, trawling intensity is expressed as an annual average. However, given the strong seasonality in many biological processes (including the benthic community), a yearly averaged trawling intensity is not necessarily the most appropriate scale. The seasonality in the life cycle of many benthic organisms means that their vulnerability to trawling potentially varies during the year. Trawl fishing itself is also seasonally organised (both in intensity and spatial distribution), and the temporal aggregation of trawling events (*e.g.* clustered in a short period or spread evenly through the year), will most likely cause a different impact and recovery of the benthic community.

This paper explores the temporal distribution of trawling intensity in a selection of stations on the Dutch continental shelf of the North Sea using Vessel Monitoring by Satellite (VMS) data of the Dutch beam trawl fleet over a 10-year period. Trawling patterns are analysed at a fine temporal (per week) and spatial scale. The observed temporal pattern in trawling is used in a benthic population model to examine trawl impact on benthos and compared to the impact in absence of such a temporal pattern. The results are discussed in relation to the fleet behaviour and the spatial dynamics of the target species of the Dutch trawling fishery.

MATERIAL AND METHODS

We selected 90 stations in the Dutch part of the North Sea to assess temporal patterns in beam trawl intensity between 2001-2010. These stations are sampling points of a macrobenthic monitoring program in the Dutch Exclusive Economic Zone (EEZ), representative for the benthic ecosystem of the area. The impact of trawling, based on yearly intensities, on benthic richness and biomass is presented in another study (van Denderen *et al.*, 2014).

VESSEL MONITORING BY SATELLITE (VMS) DATA

Trawling intensity at each station was estimated from VMS data that records information on its position, speed and heading approximately every 2 hours. The VMS data were analysed using the VMStools package (Hintzen *et al.*, 2012), which is available as add-on package for R software (R Core Team, 2013). VMS data were linked to logbook information to obtain vessel characteristics per fishing trip, such as gear type employed and engine power. VMS data from vessels with bottom trawl gear and an engine power > 349 kW were included in the analysis, as these are the dominant fishery in the study area (Rijnsdorp *et al.*, 2008). Data preparation of both VMS and logbook followed Hintzen *et al.* (2012).

The VMS data were restricted to Dutch fishing vessels, as information on foreign vessels was unavailable. This data deficiency is relatively small as trawl fishery in the Dutch EEZ is dominated by Dutch vessels (van Hal *et al.*, 2010). For some Dutch vessels, VMS data were available but logbook information on vessel characteristics was missing (varying per year between 0-5 % of the total VMS observations). For these instances, gear characteristics were derived from the European Fleet Register database (see http://ec.europa.eu/fisheries/fleet/index.cfm).

In the first years of the study period, directly after the introduction of VMS, coverage increased from about 60% of the fishing trips in 2001 (VMS data for the first 19 weeks were completely unavailable), to 70% in 2002 and 95% and higher from 2003 onwards. This data deficiency results in an underestimation of fishing activity in 2001 and 2002.

Since 2008, the Dutch beam trawl fleet started replacing the traditional tickler chain beam trawls with energy efficient alternatives such as the SumWing and the pulse trawl. As the SumWing still deploys tickler chains, they were included in our analyses. The vessels that switched to pulse trawling, three vessels in 2009 and one vessel in 2010, were excluded from the analysis as these gears have a substantially lower impact on benthos and presumably an altered spatial distribution of fishing effort (van Marlen *et al.*, 2014, Soetaert *et al.*, 2015).

DEFINING FISHING ACTIVITY

Beam trawling comprises three activities, floating, fishing and steaming, each characterised by a specific vessel speed range (Rijnsdorp *et al.*, 1998, Fock, 2008, Lee *et al.*, 2010). Fishing activity was identified for each vessel and year separately, largely following Poos *et al.* (2013). The analysis differed as we fitted a mixture of three normal distributions through the peaks, where the floating peak was half of a normal distribution (Benaglia *et al.*, 2009). An estimate of the area under the 'fishing' peak was used as an estimate of total fishing activity of that vessel in that year.

Selection of fishing activity purely based on speed profiles will underestimate the activity as there are periods of low speed during each fishing event where a vessel is hauling or shooting its gear. These periods will be classified as floating activity, while most of the time between the two hour pings will be fishing activity. Based on the findings by Rijnsdorp *et al.* (1998), hauling or shooting the gear occurs for about 5-10 % of the total fishing time. To correct these classifications, VMS points classified as floating, while positioned between two fishing points, were interpreted to represent fishing. This increased the number of VMS fishing positions by 7.0-7.9% per year.

SPATIO-TEMPORAL SCALE TO ASSESS TRAWLING INTENSITY

Trawling intensity at each station was assessed per week, corresponding to the weekly fishing trips characteristic of the Dutch trawling fishery (Rijnsdorp *et al.*, 2011).

We used the finest spatial grid possible that matches the inaccuracy of the VMS vessel position by GPS: 0.001° latitude by 0.001° longitude (approximating a grid cell of 110 by 70 meter). At this fine spatial grid, the VMS position of the vessel may be located in a different grid cell than the position of the gear. To correct for this difference, gear position for each VMS position was estimated using bathymetric data on the North Sea (http://portal.emodnet-hydrography.eu/), the heading of the vessel, and the assumption that the length of the gear cable is 4 times the water depth under the vessel (van Marlen *et al.*, 2014).

TRAWLING INTENSITY PER GRID CELL

To estimate trawling intensity at a spatial and temporal scale required for benthic impact studies, we obtained trawl distribution data at the scale of a gear track. For that reason, we reconstructed vessel trajectories between consecutive VMS fishing positions, using the cubic hermit spline method (Hintzen *et al.*, 2010). The trajectories were surrounded by a confidence interval, showing the probability that a vessel trawled an area (Hintzen *et al.*, 2010). The area trawled, projected onto a grid, was then calculated by multiplying the time interval between two VMS fishing points (hours) with the average speed between the points (meter/hour), the gear width of the vessel (meter) and the probability that the vessel trawled the grid (Piet and Hintzen, 2012). The area trawled in each grid was aggregated for all vessels per week and divided by the surface area of the grid. This resulted in a weekly trawling intensity, reflecting the proportion of surface area trawled per grid.

TRAWLING PATTERN ANALYSIS

Trawling pattern analysis was based on (1) the temporal pattern observed in trawling intensities, (2) a discrete benthic population model illustrating the implications of temporal patterns in trawling intensity on benthic impact, and (3) a calculation of the length of the recovery interval.

Temporal pattern in trawling intensity

We first explored the temporal distribution of trawling by examining temporal autocorrelation patterns with a time lag in weeks from 0 up to 104 weeks (two years). Then, we explored seasonal variation in trawling intensity. We classified stations with similar seasonal patterns using detrended correspondence analysis on the trawling intensities per week averaged over the years (Hill and Gauch, 1980). We used detrended correspondence analysis as regular correspondence analysis did not result in distinct groups of stations.

Benthic population model

We formulated a discrete benthic population model to study the implications of temporal patterns in trawling impact. The model followed semi-chemostat dynamics, with growth rate r and maximum density $Nmax$. Trawling mortality consisted of a mortality rate μ and a parameter f which defined a trawling event (f=1) or no fishing (f=0).

Population biomass is described by the following equation:

$$N(t+1) = N(t) + r(Nmax - N(t)) - \mu f(t)N(t)$$

Trawling events were constructed from the observed series of trawling intensities for each station. These intensities can be interpreted as the probability that a small station inside the grid cell is trawled in a given week. Whether a trawling event actually occurred was simulated by comparing the series of observed trawling intensities with randomly drawn numbers between 0 and 1. A trawling event (f=1) was recorded if the random number was smaller than or equal to the trawling intensity.

With this model, we tested the effect of temporal aggregation of events compared to a similar amount of events randomly picked through the time series. We also examined the effect of seasonality in trawling impact. Since seasonality may affect vulnerability of benthos to trawl impact in different ways (see *Discussion* section), we deliberately choose to account for seasonality in its most simplistic form by fluctuating the mortality rate μ according to weekly changes in seawater temperature from the Dutch North Sea (http://www.rijkswaterstaat.nl/water). Mortality rate was calculated as a constant multiplied by sea water temperature. This gives lowest mortality rates during winter and highest during summer. The average mortality rate was kept similar to the mortality rate without seasonality.

Recovery interval

The recovery time was calculated as the interval between two periods of frequent trawling (figure 6.1a). Such a period was defined as a period in which trawling events succeeded closer in time than a station-specific gap. The gap describes the maximum interval between two trawling events and is a measure of short-term autocorrelation for trawling intensity for each individual station. The gap was calculated by comparing the frequency distribution of weekly intervals between trawling events based on the observed pattern, with a frequency distribution of weekly intervals constructed from a random pattern (created by randomly selecting trawling intensities from the observed pattern) (figure 6.1b). For this comparison, trawl events were simulated for both patterns by comparing the series of observed trawling intensities with randomly drawn numbers between 0 and 1. This was repeated 10^5 times for the time period.

Afterwards, we estimated periods of frequent trawling and the recovery interval between these consecutive periods of frequent trawling (figure 6.1a). This was simulated using the trawling intensity data from 2002-2010 (2001 had missing values for the first 19 weeks and was not used). The simulation was run with 1000 repetitions, where repetitions followed in time to form a continuous time-series. After 1000 repetitions for each station, the mean of the recovery time was stable and could be compared to a recovery time calculated by dividing total time by total trawling intensity.

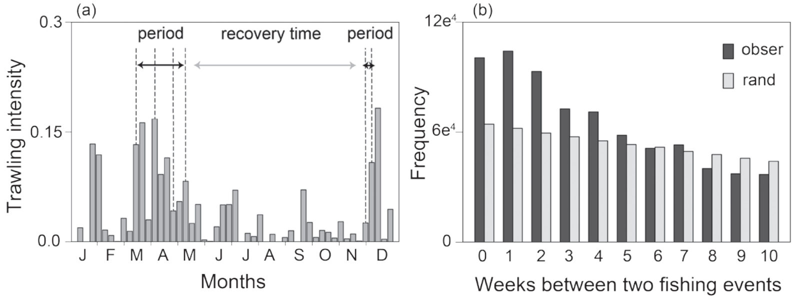

Figure 6.1 (a) Illustration of one simulation outcome for one station in one year. The grey bars represent observed trawling intensity per week and the vertical dashed lines show a trawling event based on one realisation of the simulation. A period of frequent trawling is defined as a period in which trawling events succeeded closer in time than expected when trawling events occur random in time. The recovery time is defined as the interval between two periods of frequent trawling. (b) Illustration of the calculation of a station-specific gap for the same station as in (a). The station-specific gap is 5 weeks, since the observed temporal pattern (obser) has a lower frequency of weekly intervals between two trawling events at 6 than the random pattern (rand).

RESULTS

TEMPORAL PATTERN IN TRAWLING INTENSITY

The selected stations differed substantially both in total trawling intensity and temporal pattern. Based on the weekly trawling intensity and the estimated temporal autocorrelation in trawling intensity, four typical trawling patterns were found (figure 6.2). Type 1 stations are fished at low intensity, with a mean intensity <0.2 per year, without any significant temporal autocorrelation (figure 6.3a, e). Most of these stations are located in the northern part of the Dutch EEZ, the Dogger Bank and Oyster Ground, while four are located in the Plaice Box near the Dutch coast, where large beam trawlers are not allowed to fish. Type 2, 3 and 4 stations have higher trawling intensities (mean intensity >0.2 per year), but differ in their temporal autocorrelation pattern. Type 2 stations lack significant temporal autocorrelation (figure 6.3b, f). Type 3 stations have a strong autocorrelation with a period of 1 and 2 years (figure 6.3c, g) and are located in the southern part of the area, closest to the coast. These are trawled with the highest intensities, up to a mean intensity of 2.6 times per year. Type 4 stations have a 1-year autocorrelation (figure 6.3d, h).

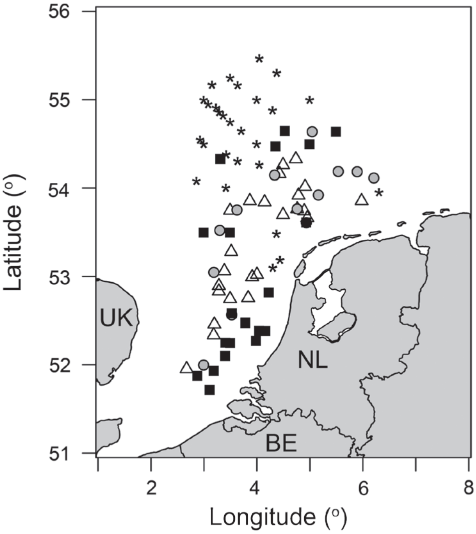

Figure 6.2 Selected stations for which we assessed temporal patterns in beam trawl intensity per week between 2001-2010 at a spatial scale of 110 by 70 meter. The stations are sampling points for a macrobenthic monitoring program in the Dutch Exclusive Economic Zone. In total, 28 stations had mean fishing intensity <0.2 per year (Type 1, marked with *), 26 stations had no autocorrelation (Type 2, open triangles), 21 stations showed strong temporal autocorrelation patterns for the two years tested (Type 3, black squares) and 15 stations showed autocorrelation only with one following year (Type 4, grey dots).

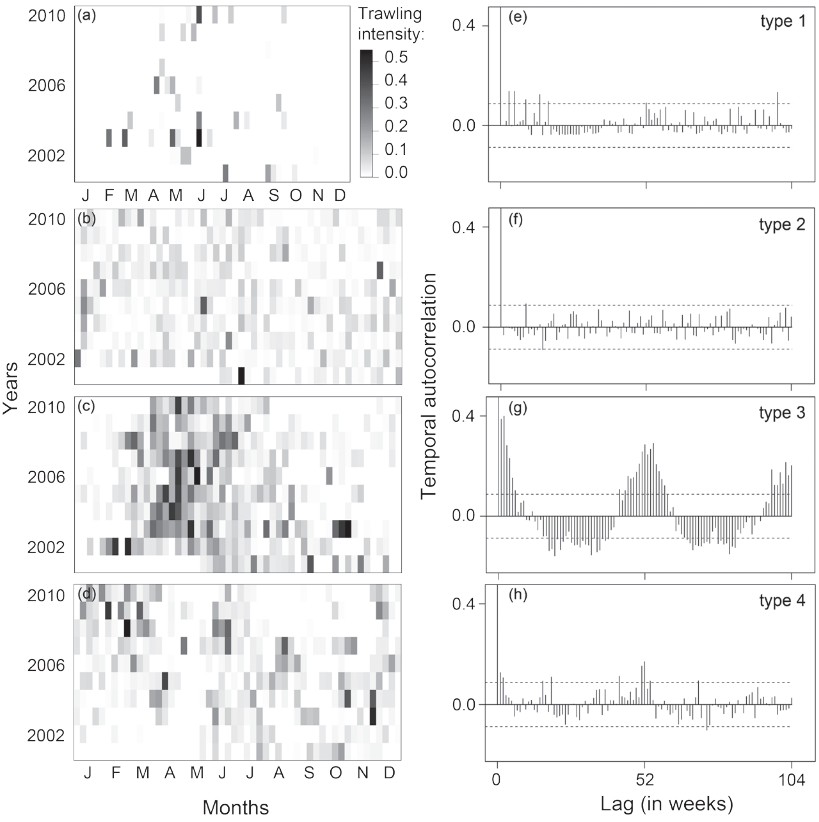

Figure 6.3 Trawling intensity patterns per week (a-d, each block is one week) and the temporal autocorrelation (ACF) with a time lag in weeks (e-h) for four stations with the observed trawling patterns (type 1 to 4). Data from the first 19 weeks in 2001 were unavailable. The dashed lines in (e-h) are the 95% confidence boundaries.

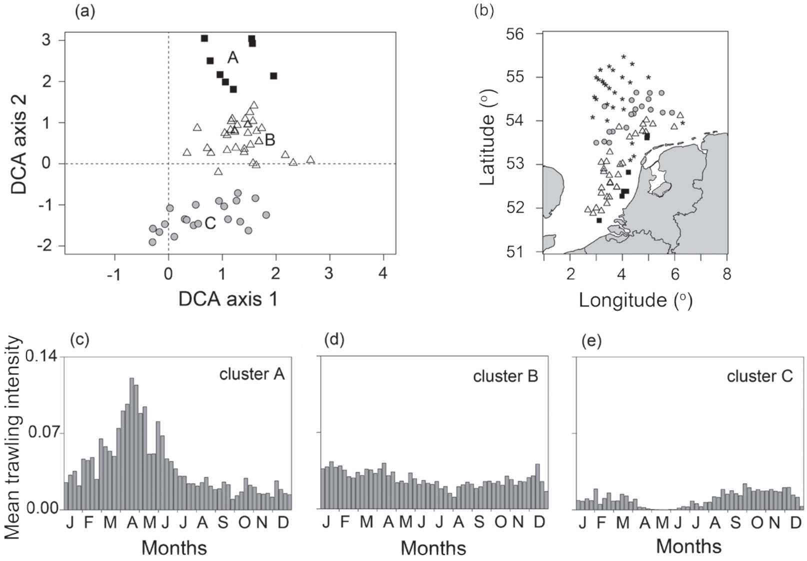

Figure 6.4 Seasonal variation in trawling intensity between three clusters, grouped on the basis of the detrended correspondence analysis (a) showing distinct locations (b) and different trawling intensity patterns (c-e). Cluster A: black squares, cluster B: open triangles, cluster C: grey dots. All points marked with * in (b) have mean trawling intensity <0.2 per year and were not included in the clustering. Each grey bar (c-e) represents a week.

Detrended correspondence analysis (only taking into account stations with mean annual trawling intensity >0.2) clustered the stations in three different groups (figure 6.4a). Stations in cluster A are the closest to the Dutch coast (figure 6.4b) and have a clear seasonality in trawling, with highest intensities between March and June (figure 6.4c). Stations in cluster B show no seasonality in trawling and are trawled throughout the year at equal intensity (figure 6.4d). Stations in cluster C are all located in the north and also show seasonality in trawling (figure 6.4e) with very low intensity between April and June.

BENTHIC POPULATION MODEL

Temporal aggregation of fishing events results in a lower amount of benthic biomass removed by trawling compared to random fishing events (figure 6.5a). This occurs as multiple events in a short period of time reduce population size and limit the amount of biomass removal from successive trawl events. Random trawl patterns give the population more time to recover between events and this results in a larger population size and more biomass removal. The magnitude of these effects depends on the mortality rate and the growth rate of the population (figure 6.5b). When the growth rate is low (speed of recovery limited), there will be less difference between temporal aggregation and random fishing events.

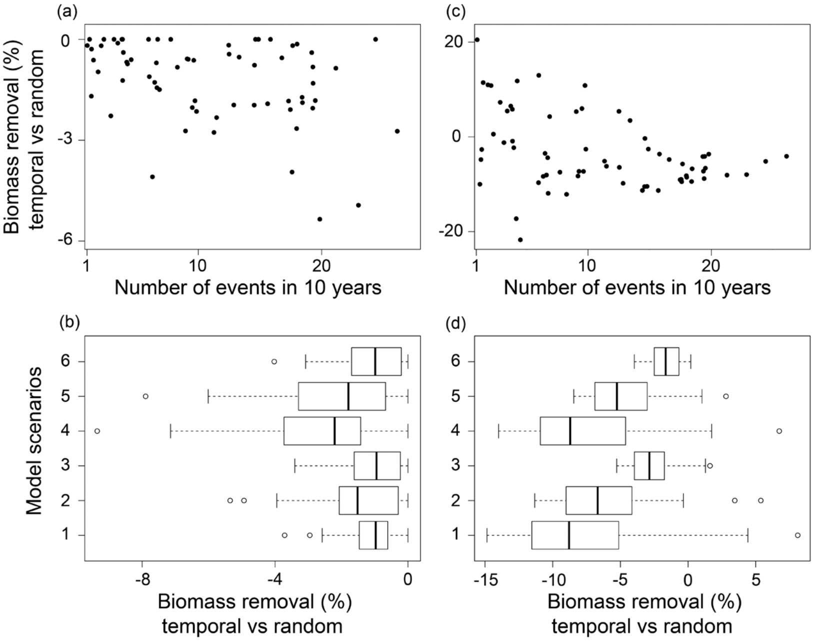

Figure 6.5 The outcome of the benthic population model shows the difference between the amount of benthic biomass removed using the observed temporal trawling pattern as compared to a random pattern for six scenarios of combinations of growth and mortality rates without (a and b) and with the inclusion of a seasonally varying vulnerability to trawling (c and d). This is presented for Scenario 2 for all stations that have at least 1 event in 10 years (a and c) and for all six scenarios in a box and whisker plot for stations with > 10 events in 10 years (b and d). When percentages are below zero, there is less biomass removed with the inclusion of temporal pattern. Model parameters: scenarios 1-3 in (b) $\mu=0.25$ in (d) average of $\mu=0.25$; scenarios 4-6 in (b) $\mu=0.75$ and in (d) average of $\mu=0.75$; scenarios 1 and 4 $r=0.12$; scenarios 2 and 5 $r=0.012$; scenarios 3 and 6 $r=0.0012$; $Nmax=5$ in all scenarios. Recovery (up to 95% of the original biomass) will take 0.5, 5 and 50 years after 1 event in (b) scenarios 1-3, respectively. Results show the outcome after 5000 simulations through the 10-year period.

When trawling vulnerability varies seasonally, temporally aggregated trawling removes more or less benthic biomass, compared to a random pattern, depending on the timing of the trawling event (figure 6.5c and d). This is the result of the seasonality in the temporal aggregation pattern, where stations are fished only during certain periods each year. In our case, mortality rate is lowest during winter and early spring and most of the stations with intensities >10 in 10 years have less benthic biomass removed (compared to a random pattern) with this seasonality in trawl vulnerability (figure 6.5d).

RECOVERY INTERVAL

The frequency distribution of station-specific gaps (for all stations with mean annual trawling intensity >0.2) show that most stations have a gap between trawling events of 4 weeks. Maximum gap was 11 weeks, while some stations had no short term autocorrelation of trawling intensity (i.e. more or less continuously fished) and hence no station-specific gap (figure 6.6a).

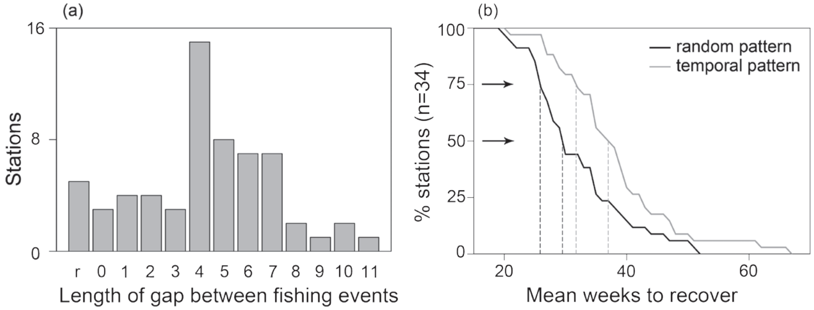

Figure 6.6 (a) Length of station-specific gaps between two trawling events for all stations with a mean trawling intensity <0.2 per year. r indicates that there is no temporal aggregation of trawling events and that events occur randomly through time. A gap of 0-11 indicates that there is temporal aggregation of trawling events and the strength of this aggregation is determined by the length of the gap (a gap of 0 indicates that only a trawl event directly after another trawl event occurred more frequently than random). (b) Difference between time to recover (i.e. no fishing) calculated from the random pattern (black line) and from the temporal pattern (grey line) for all stations that have mean yearly intensities >1 (n=34). The dashed lines show the minimum recovery time for the least impacted 75% and 50% of the stations.

The recovery times based on the observed temporal pattern using the station-specific gap are longest in the offshore stations, and shorter towards the coast (figure 6.7). These recovery times were compared with recovery times based on a random pattern (time/intensity) (figure 6.6b). Since the difference in recovery will be strongest for stations that have highest intensities, we selected those stations (n=34) with mean annual intensities >1. This shows that the minimum recovery time for all 34 stations is 19 weeks (no trawling period) when based on the random pattern and 21 weeks when calculated from the observed temporal pattern. Seventy five percent of the stations can recover for at least 25 weeks (random pattern) and 31 weeks (observed pattern), while fifty percent of the stations can recover at least 29 weeks (random pattern) or 37 weeks (observed pattern).

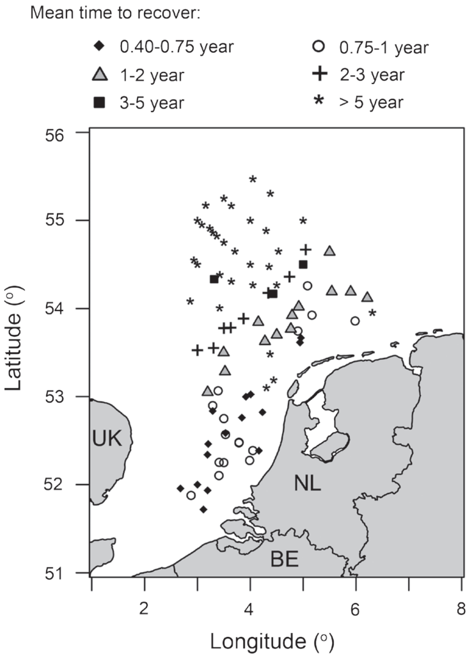

Figure 6.7 All 90 stations and their calculated mean recovery times based on the observed temporal pattern in fishing intensity.

DISCUSSION

In this study we analysed the temporal patterns of trawling intensity over a period of 10 years at a fine temporal (per week) and spatial (0.001° longitude by 0.001° latitude) scale and showed that trawling is temporally aggregated and varies seasonally in most stations that are strongly impacted by trawling.

ANNUAL PATTERNS IN TRAWLING INTENSITY

The autocorrelation patterns showed that for some stations, trawling intensity patterns are consistent between the different years studied. These annually repeated patterns suggest that part of the fishing behaviour is fixed to specific areas for certain weeks each year. Since fishermen concentrate their effort in areas (fishing grounds) where target species are abundant (Rijnsdorp *et al.*, 2011), the annual pattern also suggests that high concentrations of fish return to the same areas every year, which is even visible at the fine spatial scale we examined. This is also supported by the findings of Piet & Hintzen (2012) who showed strong overlap in area impacted by trawls from year to year. How much these fishing grounds contribute to the catches remains to be explored.

Other areas are less used as a fishing ground and this is clearly visible in the north-western part of the Dutch EEZ where many stations had almost no fishing impact over the last 10 years. This can be explained by the fact that there is less fish compared to other areas or the cost to get to this area may be too high. The first argument is in agreement to the relatively low catch rates of sole *Solea solea* in this area (Rijnsdorp *et al.*, 2006). Interestingly, the area is characterized by relatively fine sediments and a high benthic biomass and diversity (van Denderen *et al.*, 2014). Incidental trawling events in such areas can be avoided by totally excluding fishing through protection of the area. This will provide a great benefit to the benthic system, as these sites may be inhabited by vulnerable benthic organisms that normally need to recover over a long period of time after a trawling event (Jennings and Kaiser, 1998, Dinmore *et al.*, 2003).

TEMPORAL AGGREGATION OF TRAWLING INTENSITY

Most of the stations that were impacted by a trawl had short term autocorrelation in trawling intensity and this was estimated in our study using the station-specific gap. The short term autocorrelation is in agreement with Poos and Rijnsdorp (2007), who showed that high flatfish concentrations may persist up to three weeks, and with Rijnsdorp *et al.* (2000), who showed that vessels tend to return to a fishing ground in consecutive weeks.

The temporal aggregation of fishing intensity affects benthic impact as is shown in our benthic population model, although these effects were rather limited (maximum difference with random pattern is ~9%). It may be expected that these effects become larger when trawling intensity is higher (the highest mean intensity in our stations was 2.6 times a year). A small part of the Dutch EEZ is fished more than 10 times a year (Piet and Hintzen, 2012) and temporal aggregation of events may have more profound effects at these sites. Still, temporal aggregation coupled to seasonally fluctuating mortality rates showed already much larger effects in the benthic impact model (figure 6.5).

SEASONALITY IN TRAWLING INTENSITY

The observed seasonality in trawling intensity may be explained by the seasonal migration patterns of the target species, sole and plaice *Pleuronectes platessa*, of this fishery (Gillis *et al.*, 2008). This is most evident for sole, which migrates in spring to the coastal spawning grounds (ICES, 1965, de Veen, 1967, Rijnsdorp *et al.*, 1992). During this period, stations closest to the coast in cluster A have their highest intensities, while stations further offshore in cluster C have almost no fishery (figure 6.4c). These fishing patterns largely correspond to the findings by Rijnsdorp *et al.* (2006).

The seasonality in trawling intensity may influence the direct mortality of trawling on benthic species. In our model, this was constructed by varying the mortality rate according to weekly changes in seawater temperature. This was based on the observation that infaunal species show temporal changes in their burying depth, with largest depth in winter (Reading and McGrorty, 1978, Beukema, 1985, Hines and Comtois, 1985, Zwarts and Wanink, 1993). Hence for certain periods, benthos may occur below the penetration depth of the gear and trawling impact will be less. Seasonality may also affect direct mortality since many species vary in abundance, biomass and population structure during the year, largely driven by recruitment processes in spring and summer (Reiss and Kröncke, 2005). Since trawling mortality on benthos is size-dependent (Kaiser *et al.*, 2000), trawling will likely differ in its mortality on the benthos dependent on timing of a trawling event.

In addition, seasonality in trawling intensity may also change the population dynamics of benthos. Early demersal stages of benthic organisms may suffer from food-limited growth and survival in areas with relatively low production (Holland *et al.*, 1987, Reiss and Kröncke, 2005). Trawling mortality induced in the period prior to or during the phase when density-dependent regulation occurs may interfere with this density-dependent feedback, and speed up growth of the survivors.

RECOVERY TIME

In this study, we found that all selected stations had at least a mean recovery period of 21 weeks (19 weeks when ignoring the temporal aggregation). This time period may be long enough to allow recovery of benthic species with short-life spans (Kaiser *et al.*, 2006). Stations with the lowest trawling impact could recover over >5 years (figure 6.7), long enough to induce recovery of slow-growing large-biomass benthos when these settle again (Kaiser *et al.*, 2006).

How recovery of benthos is affected by the timing of a trawl event remains to be explored. It will likely depend on the mobility of the affected organism and its recruitment dynamics.

IMPLICATIONS FOR BENTHIC IMPACT ASSESSMENTS

Most trawling impact studies on benthic communities have estimated trawling intensity on an annual basis, ignoring temporal pattern within a year, while the benthic community is often sampled only once a year (Dinmore *et al.*, 2003, Hiddink *et al.*, 2006b, Piet *et al.*, 2007, Lambert *et al.*, 2012, van Denderen *et al.*, 2014). Annual average trawling intensities may not show a clear relationship with the degree of disturbance of the benthic community, because part of the impact of trawling is determined by the timing and temporal aggregation of trawling events. Whether an (multi-)annual estimate of trawling intensity or an estimate of the recovery period prior to the benthic sampling comprises the appropriate temporal scale to assess trawl impact will most likely be species-specific, dependent on the direct mortality rates induced by trawling and the speed of population recovery. To estimate a recovery period prior to the benthic sampling, the simulation approach applied in this paper could be used or a cumulative trawling intensity could be calculated (Lambert *et al.*, 2014).

CONCLUSIONS

In this study we have shown that there are strong temporal patterns in local trawling intensity in some of the stations studied. These patterns consist both of a short-term aggregation and seasonal variation in trawling intensity and are mostly observed in stations frequently impacted by the fishery. The temporal patterns are of relevance to our understanding of trawling impact on the seafloor community, because repeated trawling in a short period of time, alternated with longer undisturbed periods, have a different effect on invertebrate benthos than single trawling events which are randomly spaced in time. It is also important because benthos vulnerability to trawling may vary seasonally due to changes in population structure and behaviour. Our results imply that trawling impact studies using high resolution data like VMS should take account of the possibility of temporal aggregation and seasonality in trawling in order to improve the assessment of trawling impact on the benthic community.

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Chapter 7

SIMILAR EFFECTS OF BOTTOM TRAWLING AND NATURAL DISTURBANCE ON COMPOSITION AND FUNCTION OF BENTHIC COMMUNITIES ACROSS HABITATS.

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Bottom trawl fishing has widespread impact on benthic habitats and communities. The benthic response to trawl disturbance is influenced by the degree of natural disturbance in an area, as communities are also modified by the effects of currents and waves on the seabed (bed shear stress). In areas exposed to high natural disturbance, community responses to trawling also seem to be smaller or absent, leading to the possibility that natural and trawl disturbance affect benthic communities in a similar way. However, systematic tests of this hypothesis at large spatial scales and with data spanning many levels of natural disturbance have not been conducted. Here, we examine the effects of trawl and natural (tidal-bed shear stress) disturbance on benthic community composition over gradients of commercial bottom trawling effort in eight areas in the North and Irish Seas. Using a trait-based approach, that classified species by life-history strategies or by characteristics that provided a proxy for their role in community function, we found support for the hypothesis that trawl and natural disturbance affect benthic communities in similar ways. Both sources of disturbance caused declines in long-lived, hard-bodied, and suspension-feeding organisms. Because the effect of trawling and shear stress was similar, there was no detectable trawling effect on the composition or function of communities exposed to a high natural disturbance. Conversely, in three out of five areas with low bed shear stress, responses to trawling disturbance were detected. In these areas, increased trawling led to community compositions comparable with those in areas subject to high natural disturbance; being associated with either small-sized, deposit-feeding animals, or, mobile scavengers and predators. These observations together provide strong evidence for the similarity of the community states induced by trawling and natural disturbance. Knowledge of the interacting effects of trawling and natural disturbance will help to identify areas that are more or less resilient to trawling and support the development of management plans that account for the environmental effects of fishing.

INTRODUCTION

There is global concern about the negative effects of bottom trawl fisheries on the benthic ecosystem. Bottom trawl fisheries account for around 23% of global fisheries yield (FAO 2009) and are one of the most widespread sources of human disturbance affecting benthic communities in shallow shelf seas (Eastwood *et al.* 2007, Foden *et al.* 2011). The fishery physically disturbs the seabed by dragging a net, or other collection device, over the seabed to catch demersal fish and benthic invertebrate organisms. This modifies benthic habitats and induces mortality on target and non-target benthic invertebrates (Kaiser *et al.* 2002).

The effects of trawling vary markedly among benthic species (Collie *et al.* 2000b, Kaiser *et al.* 2006), as a result of their different vulnerability to a trawl pass (*e.g.* Bergman and van Santbrink 2000) and different recovery rates following impact, varying from months to many years (*e.g.* Lambert *et al.* 2014). Generally, studies have found that long-living, sessile and suspension-feeding organisms are particularly negatively affected by trawl disturbance (Tillin *et al.* 2006, de Juan *et al.* 2007, Kenchington *et al.* 2007), while opportunistic species, *e.g.* short-living polychaetes, are less affected (Kaiser *et al.* 2006).

The response of a benthic community to trawling will also depend on the prefished composition of the community (Kaiser *et al.* 2002). This composition is largely affected by the degree of natural disturbance, due to currents, waves or storms in an area (Thistle 1981, Probert 1984). Natural disturbance may erode seabed sediment, cause resuspension of organic matter (Morris and Howarth 1998) and may affect settlement of new recruits (Thistle 1981, Hunt and Scheibling 1997). Such effects promote species that are adapted to natural disturbance; species that usually have opportunistic life history strategies are also relatively resistant to trawl disturbance (Jennings and Kaiser 1998, Kaiser 1998). Indeed, changes in response to trawling seem to be smaller or absent in communities exposed to high natural disturbance (Kaiser and Spencer 1996, Collie *et al.* 2000a, Hiddink *et al.* 2006, Tillin *et al.* 2006), leading to the expectation that natural and trawl disturbance affect benthic communities in a similar way (Kaiser 1998). However, systematic tests of this hypothesis at large spatial scales and with data spanning many levels of natural disturbance have not been conducted.

Here, we combine existing and new data from studies of trawling impacts at sites throughout the North and Irish Seas to assess the effects of natural disturbance on the relationships between community composition and trawling intensity. Community composition was described using a trait-based approach that classified species by life-history strategies or by characteristics that provided proxies for their role in community function (Bremner 2008, Bolam *et al.* 2014). The changes in community composition and function were analysed to assess whether bottom trawling and tidal-bed shear stress, the force per unit area exerted on the seabed by the tidal currents, affected benthic communities in similar ways. Our results confirm the hypothesis that bottom trawling and shear stress have comparable effects on benthic community composition and function. We found no effects of trawl disturbance in areas subject to high shear stress, while in three out of five areas with more stable natural conditions, clear shifts were observed in trait composition in relation to trawling intensity. In these areas, trawling results in community compositions comparable with those in areas subject to high natural disturbance. Together, these observations provided strong evidence for the similarity of the community states induced by trawling and natural disturbance. These findings are relevant to management in that they may help to identify areas that are more or less resilient to trawl impact (sensu Diesing *et al.* 2013) and support the development of management plans that take into account the environmental effects of fishing.

METHODS

STUDY AREA

The effects of trawling were assessed in eight areas where soft-sediment benthic communities were sampled across a gradient in trawling disturbance. Seven areas are located in the North Sea, one in the Irish Sea (figure 7.1). Sampling sites were selected to cover the trawling intensity gradient in each area, while keeping the environmental conditions as homogenous as possible (table 7.1). The eight differed in terms of habitat type (expressed as depth, sediment type and primary productivity) and the degree of natural disturbance, predicted by calculating the force per unit area exerted on the seabed by the tidal currents (*i.e.* tidal-bed shear stress). Areas were categorised and named on the basis of their mean tidal-bed shear stress, assigning A to the area with the lowest shear stress and G to the highest. For six areas (A, B, D, E, F, G), homogeneity of other habitat characteristics was maximized by limiting the distance between sampling sites in the area and by selecting sites with similar habitat conditions (depth and sediment maps and/or habitat information from previous field studies; table 7.1, Ref. to area). For the two other areas (C, H), sampling sites were selected from monitoring sites in the Dutch Exclusive Economic Zone based on similarity of sediment grain size conditions (table 7.1, Ref. to area). Sample data from four areas (B, C, D, H), were published previously (table 7.1, Ref. to dataset), but have not been used to investigate benthic community composition and function.

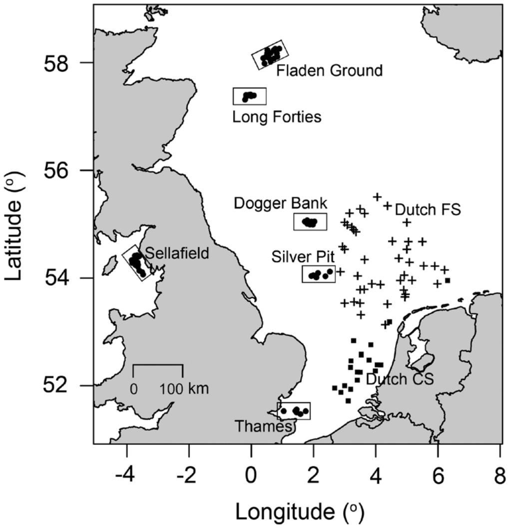


Figure 7.1 Map of the eight different study areas and associated sampling sites.

Table 7.1 Overview of the different study areas and their characteristics.
Areas are ranked on the basis of their mean tidal-bed shear stress (lowest in A, highest in H).
In four areas (B, C, D, H), collected samples have already been used in previous publications (see Ref. to dataset), but none of these have investigated benthic community composition and function.

Area code*	Number of stations (samples per station)	Sampling date (m ‘yy)	Sampling device (surf. area in m²)	Max. dist. between stations (km)	Depth (m)	Sediment type	Silt (%)	Prim. product. (gr C/m²/ year)	Trawling intensity (year⁻¹)	Shear stress (N/m²)	Ref.to dataset	Ref. to area
A	14 (5)	6 ’04	Day grab (0.1)	41	143-153	Mud	93-97	125-141	0.1-3.0	0.1-0.1		(5)
B	7 (5)	9 ’03	Hamon grab (0.1)	20	25-30	Sand	1-3	171-192	0.1-1.5	0.1-0.2	(1)	(1)
C	230 (1)	3-6 ‘02-07	Box corer (0.078)	264	26-56	Sand	0-21	149-417	0.0-4.0	0.0-0.4	(2)	(2)
D	15 (5)	6 ‘09	Day grab (0.1)	42	21-42	Muddy sand	42-89	-	0.5-11.9	0.2-0.3	(3,4)	(3,4,6)
E	6 (4)	7 ‘02	Box corer (0.078)	40	68-78	Muddy sand	9-27	173-184	1.8-99**	0.2-0.3		(7,8,9)
F	7 (2-5)	9 ‘03	Hamon grab (0.1)	19	74-83	Gravelly sand	2-6	183-198	0.1-1.6	0.3-0.4		(5)
G	6 (4)	7 ‘02	Box corer (0.078)	49	16-40	Sand	3-22	130-340	0-100**	0.5-1.1		
H	84 (1)	3-6 ‘02-07	Box corer (0.078)	329	22-36	Sand	0-1	258-436	0.0-4.8	0.4-1.4	(2)	(2)

** A: Fladen Ground, B: Dogger Bank, C: Dutch EEZ fine sediment, D: Sellafield, E: Silver Pit, F: Long Forties, G: Thames, H: Dutch EEZ coarse sediment*

*** note that areas E and G have a different trawl disturbance metrics compared with the other areas (see appendix 7.3)*

(1) Queirós et al. 2006, (2) van Denderen et al. 2014, (3) Hiddink et al. 2011, (4) Johnson et al. 2014, (5) Tillin et al. 2006, (6) Hinz et al. 2009, (7) Jennings et al. 2001a, (8) Jennings et al. 2001b, (9) Jennings et al. 2002.

BENTHIC SAMPLING AND TRAIT CLASSIFICATION

The number of benthic sampling sites ranged from 6 to 230 among areas, while number of samples taken at each site ranged from 1 to 5 (table 7.1). When there was more than one replicate per site, samples were pooled to provide an integrated estimate of the benthic community at each sampling site. The benthos was sampled using a 0.1 m^2 Day grab (area A and D), a 0.1 m^2 Hamon grab (area B and F) or a 0.078 m^2 Reineck box corer (area C, E, G and H). The different gears have a different penetration depth and sample a different surface area but they were selected because no single gear can operate effectively on all substrate types. However, all gears effectively sample the smaller epi- and infaunal component of the benthic ecosystem and provide a quantitative estimate of their abundance and biomass. Samples from all areas were sieved over a 1 mm mesh sieve and biota were identified to the lowest taxonomic level possible. Biomass per taxonomic group was estimated in grams ash free dry weight (area C and H) or wet weight (other areas). Biomass of some individuals was larger than the mean of all samples in the area combined (*e.g.* from a masked crab, *Corystes cassivelaunus*, a common otter shell, *Lutraria lutraria,* or a heart-urchin, *Echinocardium cordatum*). These large and low density individuals are not effectively sampled by the gears and were removed from the data. Large fauna were removed from data for 28 samples, representing 0.2% of all individuals and 17.7% of the total biomass.

We used a suite of ten biological traits to predict changes in the resilience and function of benthic communities in response to bottom trawling and shear stress. In total, trait information was obtained for 222 different genera and 59 unique higher taxonomic groupings (mostly 'family') for which abundance data were available (Bolam *et al.* 2014). Each trait considered was subdivided into multiple modalities (table 7.2). For each genera-trait combination, a single trait modality was assigned a score of one when the genus showed total affinity for that particular modality. When the genus could not be assigned unequivocally to a single trait modality, multiple modalities were assigned fractional scores that summed to one, depending on the affinity of that genus for that modality (Bolam *et al.* 2014). When genera could not be identified, traits were defined for higher taxonomic levels. From this genera-by-trait matrix (including the higher taxonomic levels), we calculated a table of sampling sites by biomass-weighted modalities. This was done for each sampling site by multiplying the total biomass per taxonomic grouping by the score for each trait modality. These were summed by modality to produce a biomass-weighted trait modality table for all sampling sites (Tillin *et al.* 2006, Bolam *et al.* 2014). Seven taxonomic groups, representing 0.5% of the biomass, were excluded from the analysis as no trait data were available.

It is important to note that 28-74% of the total sampling biomass in each area was dominated by one or two genera (heart urchins from the genera *Echinocardium* in four areas and *Brissopsis* in two areas, and, the razor clam, *Ensis*, and the brittle star, *Amphiura,* in one area). These dominant taxa overshadow the community responses that are the focus of this study (see appendix 7.1) and so we assessed the responses of these taxa to trawling separately.

Table 7.2 Benthic traits and their modalities. The abbreviations are corresponding to figure 7.2 and 7.5

Traits	Modalities	Abr.
Size (mm)	<20 20-100 101-200 >200	S<20 S20-100 S101-200 S>200
Morphology	Soft Exoskeleton	M_soft M_exo
Longevity (years)	<3 3-10 >10	L<3 L3-10 L>10
Larval development	Planktotrophic Lecithotrophic / direct	LD_plank LD_le/di
Egg development	Eggs shed in water Eggs on seabed Eggs brooded	ED_pela ED_bent ED_brood
Living habitat	Tube-dwelling Burrow-dwelling Free-living	LH_tube LH_burrow LH_free
Sediment position	Surface Shallow (0-5 cm) Mid-depth (5-10 cm) Deep (>10 cm)	SP_surf SP0-5 SP5-10 SP>10
Feeding type	Suspension feeder Deposit feeder Scavenger Predator	F_susp F_dep F_scav F_pred
Mobility	Sessile Swimmer/crawler Burrower	M_sessile M_swi/cr M_bur
Bioturbation activity	Diffusive mixing Surface deposition Others	BT_dif BT_dep BT_others

TRAWL DISTURBANCE, NATURAL DISTURBANCE AND HABITAT CONDITIONS

To assess the intensity of trawling and natural disturbance and to describe environmental factors that may affect community composition, we linked site-specific benthic data to estimates of trawl disturbance, tidal-bed shear stress and primary production for the same sites.

Estimates of the amount of trawl disturbance were based on both beam and/or otter trawls. Both types of trawling disturb seabed sediment and impact benthic communities (Kaiser *et al.* 2006). Trawl disturbance for areas A, B, C, D, F and H was estimated using satellite Vessel Monitoring System (VMS) data and expressed as the cumulative surface area trawled per year (the exact calculations are explained in previous articles, table 7.1, Ref. to area). This is the frequency with which, on average, the surface area of the site is trawled, expressed per annum. Trawl disturbance for area E and G was estimated from aerial survey data of fisheries inspection services (Jennings *et al.* 2001b).

Type of sediment, silt percentage and depth were site-specific data collected during the benthic sampling. The distinction in sediment type was based on the classification diagram of Folk (Folk 1954). Silt percentage was obtained from particle size analysis. Except for areas C and H, depth was directly measured at the benthic sampling location. Depths were extracted for areas C and H from bathymetric data of the North Sea (see van Denderen *et al.* 2014).

Tidal-bed shear stress was estimated using a two-dimensional hydrographical model. This model predicts shear stress (the force per unit area exerted on the seabed by the tidal currents: N/m^2) per sampled station on a 1/8° longitude by 1/12° latitude spatial scale. The shear stress calculations are explained in more detail in Hiddink *et al.* (2006).

Primary productivity was obtained through predictions from GETM-ERSEM (General Estuarine Transport Model—European Regional Seas Ecosystem Model) (Baretta *et al.* 1995). GETM-ERSEM describes the temporal and spatial patterns of the biogeochemistry of the water column and sediment using two coupled hydrodynamic models. These models predicted total production of new phytoplankton biomass for each year ($g\ C/m^2/y$) on a 10 x 10 km spatial scale. Total production was estimated for each sampling site, except for area D, over a period of one year prior to the sampling date. These modelled productivities approximate measured primary productivity (Ebenhoh *et al.* 1997).

STATISTICAL ANALYSIS

We first analysed the effect of trawling on trait composition for all areas together by aggregating the sampling sites for each area into a 'low' and 'high' trawl disturbance treatment. We then analysed the effects of trawling on trait composition for each area individually using the gradient in trawling disturbance rather than the two categories. Finally, we analysed the effects of trawling for a few dominant genera separately as their responses overshadow the community response to trawling (appendix 7.1).

For the first analysis, we examined the proportion of biomass per modality within trait categories, as this allowed us to compare areas that may vary greatly in their total biomass and that were sampled with different gears. We combined all sampling sites for each area by grouping them into a 'low' and 'high' trawl disturbance group. Since recovery from trawling probably takes at least 2.5 years (Blyth *et al.* 2004), we defined low disturbance at an intensity <= 0.2 per year as this means that there will be, on average, a trawl pass once every 5 years. All other sampling sites were grouped into the high trawl disturbance group. Since area D did not have any sampling sites with trawling intensities <= 0.2 per year, low trawl disturbance of area D was set at <= 0.5 per year. Finally, trawl disturbance of both area E and G was based on a different metrics. In both these areas, three sampling sites had a relatively low trawling disturbance index, while the other three sampling sites were gradually increasing. These were split accordingly. Differences in trait composition between areas and ‘low’ and ‘high’ trawl disturbance treatment were examined with a correspondence analysis that included bootstrapped p-values from a hierarchical cluster analysis (Suzuki and Shimodaira 2006).

We then analysed the effects of trawling on trait composition for each area separately using the trawling intensity gradient and biomass per modality (instead of proportion of biomass per modality). This was done with a redundancy analysis where we used the trawling intensity gradient as a predictor variable. With only one predictor variable present, the redundancy analysis is the multivariate analogue of linear regression (Legendre and Legendre 2012) and may be used to determine which trait modalities are positively or negatively correlated to trawl disturbance. Such an analysis may hence determine whether the observed shifts in response to trawling are relative, indicating that some organisms are less (negatively) affected by trawl disturbance than others, or absolute, indicating an increase in the biomass abundance of certain trait modalities at high trawl disturbance. The redundancy analysis assumes there is a linear relationship between the predictor variable and its response. For that reason trawl disturbance was log-transformed as we expected the trait modalities sensitive to trawl disturbance to decline exponentially (Tillin *et al.* 2006, Hiddink *et al.* 2011). Whether trawl disturbance had a significant effect on community composition for each area was tested using a permutation test. Since sampling sites in areas C and H covered a large spatial scale and were only selected on the basis of similar sediment grain size conditions, the effects of trawling in these two areas were examined using a partial redundancy analysis that controlled for the environmental conditions. All multivariate analyses were done using the package “Vegan” in program R (Oksanen *et al.* 2013).

Finally, we analysed the effects of trawling on a few dominant genera separately as their responses overshadow the community response to trawling (appendix 7.1). This was achieved by investigating the relationship between trawling intensity and log biomass.

RESULTS

EFFECTS OF TRAWLING ON TRAIT COMPOSITION FOR ALL AREAS COMBINED

We first analysed the effect of trawling on trait composition for all areas together by aggregating the sampling sites for each area into a ‘low’ and ‘high’ trawl disturbance treatment. This was done using a correspondence analysis based on trait composition. The correspondence analysis shows five different clusters, grouped at a p-value <0.05 (figure 7.2). Five of the areas (A, C, F, G and H) remain within the same cluster at low and high trawl disturbance and this suggests that their trait composition does not change with trawling (this is tested for each area individually below). The other three areas (B, D and E) have a similar trait composition at low trawling (figure 7.2a and 7.3), which is most associated with the modalities hard bodied (exoskeleton), a maximum longevity of >10 years and suspension feeding (figure 7.2b). Trawling causes significant

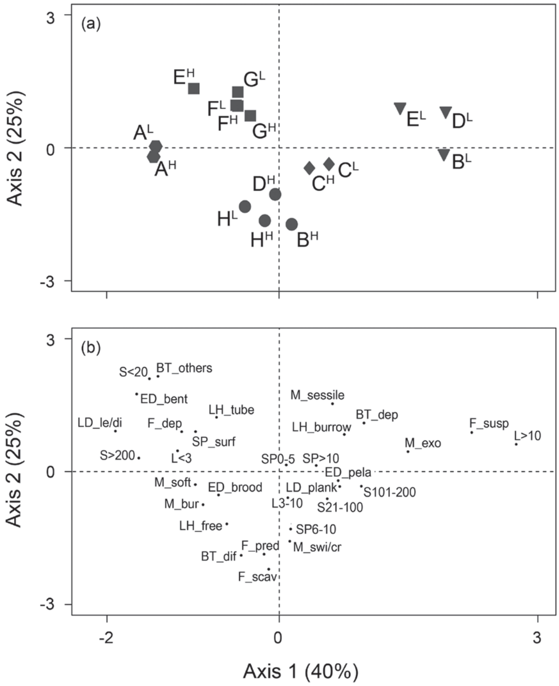
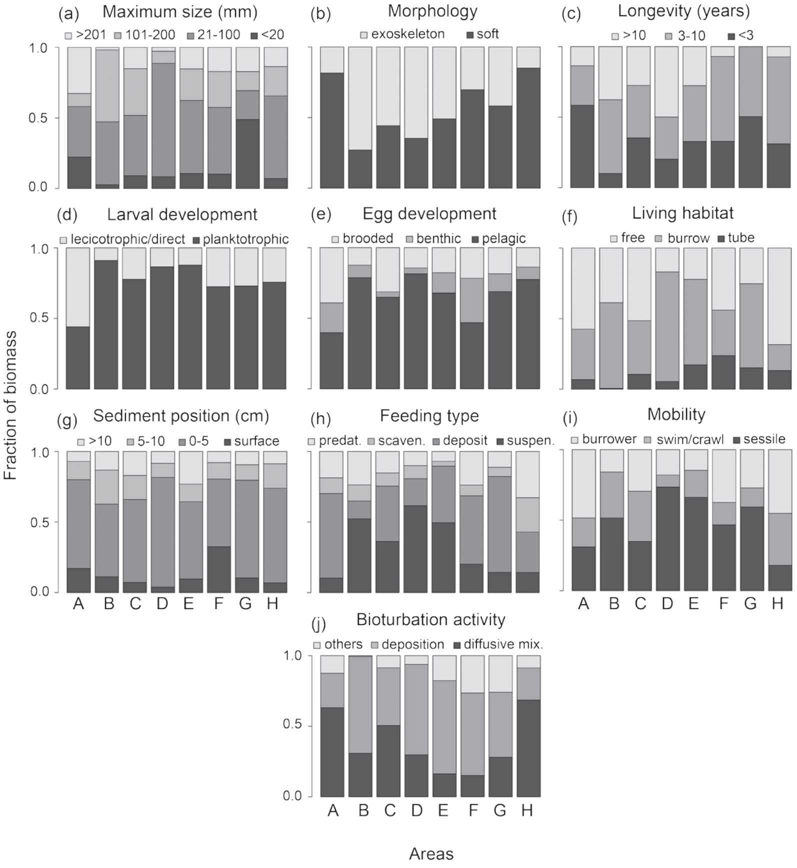


Figure 7.2 Outcome of the correspondence analysis based on trait composition for the different sampling areas (a), split into a ‘low’ (^{L}) and ‘high’ (^{H}) trawl disturbance treatment, and trait modalities (b). The correspondence analysis shows five different clusters in (a), grouped at a p-value <0.05 (represented by different symbols). The abbreviations in (b) correspond to the trait modalities in table 7.2.

changes in their trait composition and these changes lead to community compositions comparable with those in areas subject to high shear stress (figure 7.2 and 7.4): Area B and D cluster, at high trawl disturbance, with area H and this group is most associated with the modalities free living, swim/crawl, scavenger, predator and diffusive mixing activity; Area E clusters, at high trawl disturbance, with area F and G (figure 7.2a) and they are most strongly associated with the modalities small sized, short living, surface living, benthic egg development, tube dwelling, and deposit feeding.



A: Fladen Ground, B: Dogger Bank, C: Dutch EEZ fine sediment, D: Sellafield, E: Silver Pit, F: Long Forties, G: Thames, H: Dutch EEZ coarse sediment

Figure 7.3

Overview of the differences in trait composition for the eight areas at 'low' trawl disturbance. Figure panels show fractions of biomass per modality for all traits. Outcome is based on the mean of the sampling stations (replicates are pooled). Number of sampling stations (replicates) differ for each site: A: 2(5); B: 3(5); C: 92(1); D: 1(5); E: 3(4); F: 2(2 and 5); G: 3(4); H: 9(1).

No detectable effects of trawling are found in the area with the lowest shear stress (area A) and in area C. The trait composition of area A, at low and high trawl disturbance, is most associated with the modalities direct or lecicotrophic larval development, large sized, short living and soft bodied (figure 7.2 and 7.3). Area C is not strongly associated with any specific trait modalities.

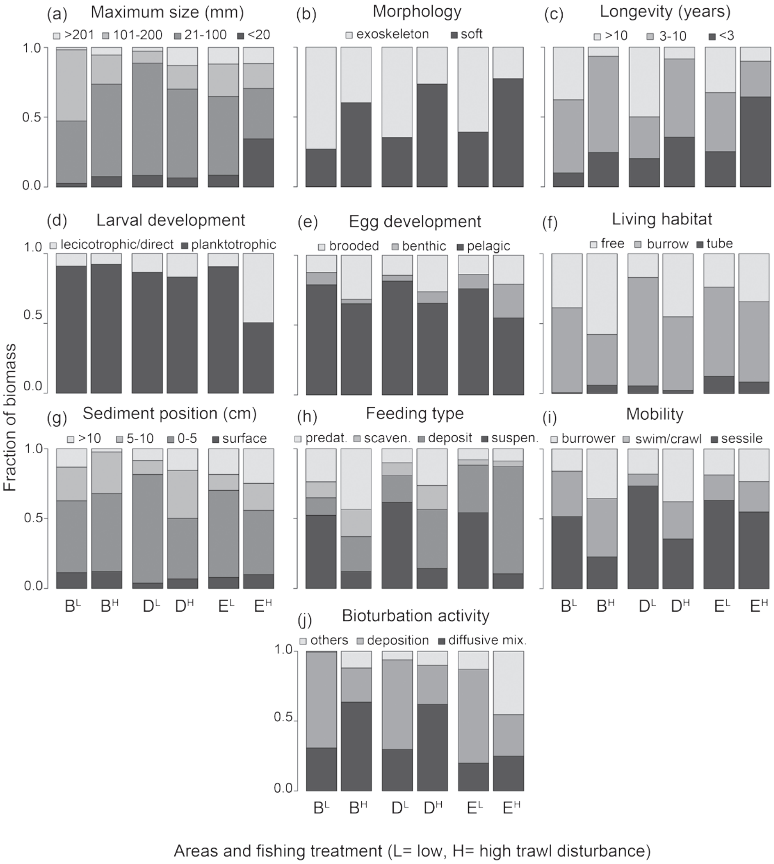


Figure 7.4 Overview of the differences in trait composition between sampling sites exposed to 'low' and 'high' trawl disturbance for the three different areas that show shifts in trait composition in response to trawling (figure 7.2). Figure panels show fractions of biomass per modality for the different traits. Outcome is based on the mean of the sampling sites (replicates are pooled). Number of sampling sites (replicates) differ for each area and 'low' and 'high' trawl disturbance treatment: B^L 3(5), B^H 4(5); D^L 1(5), D^H 14(5); E^L 3(4), E^H 3(4).

EFFECTS OF TRAWLING ON TRAIT COMPOSITION TESTED FOR EACH AREA SEPARATELY

The three areas that show shifts in trait composition (area B, D and E) are also significantly affected by trawling when they are individually analysed (figure 7.5). Trawling explains 52% of the variation in trait composition in B, 63% in D and 55% in E. A number of modalities are consistently and negatively correlated with trawl disturbance (figure 7.5) in all three areas. These are the modalities hard bodied (exoskeleton), sessile, suspension feeding, planktotrophic larval development, pelagic egg development, burrow dwelling, 0-5 cm positioned in the sediment, surface-deposition activity and with a maximum longevity of 3-10 or >10 years. A few abundant genera in these areas have all these modalities combined (such as *Dosinia*, *Spisula*, *Acanthocardia*, *Ensis*, *Phaxas* and *Abra*).

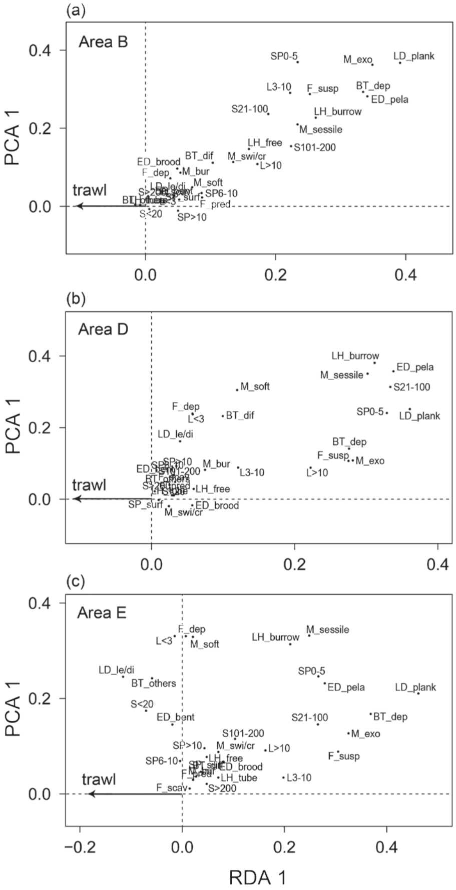


Figure 7.5 Outcome of the redundancy analysis for all areas (B, D and E) where trawl disturbance had a significant effect on community composition (all p-values <0.05). Abbreviations correspond to the trait modalities in table 7.2.

Trawling in area B and D is also negatively correlated to all other trait modalities and this means that the shift in trait composition is only based on relative increases. Contrastingly, trawl disturbance in area E is positively correlated with the modalities short-living, direct or lecicotrophic larval development and the bioturbation activity 'other'. This indicates absolute increases in biomass of these modalities in response to trawling, but these effects are not significant when tested using univariate statistics (appendix 7.2).

No significant effects of trawl disturbance on trait composition are observed in the other areas (all p-values in permutation tests > 0.24). Trawling explains only 9% of the variation in trait composition in A, 0.3% in C, 19.5% in F, 26% in G and 1.4% in H.

EFFECTS OF TRAWLING ON DOMINANT GENERA

Each study area is dominated in biomass by only one or two genera. The biomass of these genera are separately examined as their response to trawling confounded the community response (appendix 7.1). The relationships between trawling intensity and log biomass of each of these dominant genera is shown in table 7.3. The dominant genera in area D, *Amphiura* and *Echinocardium*, are negatively related in biomass to trawl disturbance, while no significant effects of trawling are observed in the other dominant genera.

Table 7.3 Trawl effects on four different genera that were not included in the trait-based analysis as their responses overshadow the community response (see appendix 7.1). Analysis is done using a linear regression model, genera biomass is log(x+1) transformed. The regression model for area C includes the effects of productivity and percentage silt, which are both significantly related to *Echinocardium* biomass (not shown).

Genera	Area	Intercept	Slope	R^2	P-value
Brissopsis	A	1.07	0.32	0.08	0.17
Echinocardium	B	1.48	-0.52	0.08	0.48
Echinocardium	C	-0.06	0.04	0.09	0.31
Echinocardium	D	2.45	-0.26	0.48	**0.003**
Amphiura	D	2.35	-0.26	0.57	**0.001**
Brissopsis	E	2.09	0.02	0.11	0.51
Echinocardium	H	0.27	-0.02	0.00	0.50
Ensis	H	0.14	0.00	0.01	0.92

DISCUSSION

We find no effects of trawling on functional benthic invertebrate community composition at locations with high natural disturbance (area F, G and H), while in three out of five areas with more stable natural conditions clear shifts are observed in trait composition in relation to trawling disturbance (area B, D and E). In these areas, trawling results in community compositions comparable with those in areas subject to high natural disturbance. Hence, our results provide strong support for the hypothesis that trawl and natural disturbance affect benthic communities in similar ways. Both sources of disturbance cause declines in long-lived, hard-bodied and suspension-feeding animals and these effects are likely to affect community function.

The comparable effects of trawl and natural disturbance may help to identify areas that are particularly susceptible or resistant to trawl disturbance. Such methods have already been proposed by Diesing *et al.* (2013), who estimated the probability that fishing disturbance exceeds natural disturbance on large spatial scales. They identified areas that are expected to be particularly vulnerable or resilient to bottom fishing without an understanding of the associated benthic communities. Our results confirm the applicability of their proposed method, but also its limitations as we found no detectable effects of trawling in the area with the lowest shear stress.

Trawl disturbance particularly reduced the occurrence of ten modalities of nine different traits in three areas subject to low shear stress. The same type of trait modalities have been observed to decline in previous studies (Kaiser *et al.* 2006, Tillin *et al.* 2006, Juan *et al.* 2007, Kenchington *et al.* 2007). These effects of trawling led, in our study, to community compositions comparable with those in areas subject to high natural disturbance; being dominated by either small-sized, deposit-feeding animals or by mobile scavengers and predators. The different community compositions between the areas in response to trawling seem not to be related to differences in the range of the trawl disturbance gradient (appendix 7.3). It is unclear why these areas have different community compositions. A composition with many scavenging organisms, as found in some of our areas subject to high natural or trawl disturbance, may be expected when disturbed sites have relatively high abundances of exposed or damaged and dead organisms (Collie *et al.* 1997, Groenewold and Fonds 2000, Ramsay *et al.* 2000)

In our results, the clearest indication of changes in community function in response to trawling is the strongly negative association of surface deposition (a modality of bioturbation) with trawl disturbance. This is mainly the result of a decline in suspension-feeding organisms. A decline in the abundance of this functional group means that less organic material is put onto the seabed, which potentially reduces benthic secondary production (Gili and Coma 1998, Snelgrove 1999, Pearson 2001, Lohrer *et al.* 2004, Thrush and Dayton 2010).

A decline in benthic production in response to trawling may reduce the amount of benthos available as prey for the benthivorous target species of the fishery. This would suggest that trawl fisheries could increase fish production and fisheries yield with gear modifications that limit trawl mortality on benthos (Hiddink *et al.* 2011, van Denderen *et al.* 2013).

We detected no effects of trawling in the area characterized by the lowest shear stress (area A). The community composition of this area, at both low and high trawl disturbance, is most similar to a naturally perturbed community, but differs as many organisms are large sized and have direct or lecicotrophic larval development. These types of development are often observed in deep areas with limited amounts of planktonic food (Vance 1973). Indeed, area A is located deepest and has the lowest primary productivity of our study areas. Food limitation has also been observed in the area for one long-living suspension feeder, *Arctica islandica*, which had very low growth rates (Witbaard *et al.* 1999).

In this study, we examined the smaller epi- and infaunal component of the benthic ecosystem. This resulted in a relatively low power to detect the effects of trawling on larger epifauna (species like shrimps, starfish and sea pens). In two of the areas where we detected no effects of trawling (A and F), trawl effects have been found on trait composition for larger epifauna sampled using a small beam trawl (Tillin *et al.* 2006). In these datasets, long-living and suspension-feeding trait modalities were particularly negatively affected by trawl disturbance. Furthermore, we found no effects of trawling in area C, while trawl effects have been reported on benthic species richness in this area (van Denderen *et al.* 2014). Conversely, we observed fishing effects in area B, whereas no effects of trawling were detected in this area on larger epifauna (Tillin *et al.* 2006). These comparisons show that trawling can have differential effects on different components of the benthos, with the result that impacts may be overlooked unless several sampling gears and community indicators (*e.g.* diversity, biomass and trait composition) are used.

The effects of trawling were in all areas examined over a gradient of commercial bottom trawling intensity. Such a comparative analysis can result in differences in community composition along the trawling gradient, that seem to be related to fishing impact, while in fact these patterns result from the fishery selecting areas with a particular community composition, where they catch the most fish (see also Tillin *et al.* 2006). Such effects may be especially relevant at large spatial scales (scales at which the fishery fleet operates) where a large part of the variation in fishing effort can be explained by gradients in environmental conditions (van Denderen *et al.* 2014). However, others have shown that unfished habitats are not necessarily unsuitable for fishing (Dinmore *et al.* 2003) and it has been suggested that part of the fishery behaviour is just fixed to areas that are known to be free from obstructions that could damage the gear (Holland and Sutinen 2000). In addition, it has been suggested that trawl effects on benthic communities can have a much larger impact than is expected from small changes in environmental conditions (see Tillin *et al.* 2006).

This is also true for our study areas, where even large differences in seabed sediment (mainly differences in silt content) between area B and E (table 7.1) resulted in similar trait compositions (figure 7.2 and 7.4).

In a previous study in area E, Jennings *et al.* (2001a) examined whether there was an absolute increase in biomass of benthic infauna in response to trawling. In their study, they investigated the benthic infauna as an aggregated group and they did not find such effect. They recommended that future trawl studies should focus on the smallest macrofauna (and meiofauna) as these have sufficiently fast life cycles to benefit from trawl disturbance. Precisely these types of species are also positively correlated to bottom trawl gears in our study in area E, although their increase is not statistically significant when trait modalities are individually analysed (appendix 7.2). The increase is mostly related to high abundance of organisms from the family Scalibregmatidae and to a lesser extent Sipunculidae at the trawled stations. The increase may be expected when the species that are not so sensitive to trawl disturbance benefit from an increase in the available food, due to a decline of their more sensitive competitors (Jennings *et al.* 2002, Hiddink *et al.* 2008, van Denderen *et al.* 2013).

Most of the study areas were dominated in biomass by only one or two genera. The biomass of these genera were separately analysed as their response to trawling confounded the community response (appendix 7.1). Except for area D where *Amphiura* and *Echinocardium* decreased significantly in biomass, none of the dominant genera showed a response, despite their sensitivity to trawl gears (Bergman and van Santbrink 2000, Callaway *et al.* 2007). The lack of response may be due to a low sampling efficiency of grabs and cores for these genera, which are large in body size. Some of these genera contain species that are important habitat facilitators (Lohrer *et al.* 2004, van Nes *et al.* 2007, Lohrer *et al.* 2013) and these may facilitate other benthos by providing resources and shelter (Thrush *et al.* 1992, Stachowicz 2001). Effects of trawling on these facilitators may hence indirectly affect the benthic component that is the focus of this study.

We conclude that high levels of natural disturbance that affect soft-sediment habitats will lead to community compositions and functions that are more resilient to a given level of trawling disturbance than those found in areas with less natural disturbance. Such asymmetric impacts of bottom fishing will help to identify areas that are particularly susceptible or resilient to trawling and thereby support the development of spatial management plans that deal with the ongoing process of balancing fishery exploitation and conservation of marine benthic ecosystems.

ACKNOWLEDGEMENT *We thank J. Aldridge, N.T. Hintzen and P. Ruardij for their help in assembling the data. This research was partially supported through the policy support research programme (BO) of the Dutch Ministry of Economic Affairs to P.D.vD. and T.vK., the FP7 project BENTHIS (312088) to A.D.R. and T.vK and J.G.H and a grant of the Schure Beijerinck Popping Fund of the Royal Netherlands Academy of Arts and Sciences to P.D.vD.*

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APPENDIX 7.1 DOMINANT GENERA

In most of the areas, there are a few dominant genera that represent 28-74% of the total sampling biomass; this are heart urchins from the genera, *Echinocardium* (four areas) and *Brissopsis* (two areas), and a razor clam, *Ensis*, (one area) and a brittle star, *Amphiura* (one area) (see table 7.3). Including these dominant taxa in our trait-based analysis reveals two different clusters, instead of 5, grouped at a p-value <0.05 (figure A7.1). The first cluster incorporates all area x trawl disturbance treatment combinations that contain at least one of these dominant genera, while the other cluster contains all area x trawl disturbance treatment combinations lacking such species. The results hence clearly show that these dominant genera overshadow the community response to trawl disturbance that is the focus of this study. As such, we decided to assess the responses of these taxa to trawling separately.

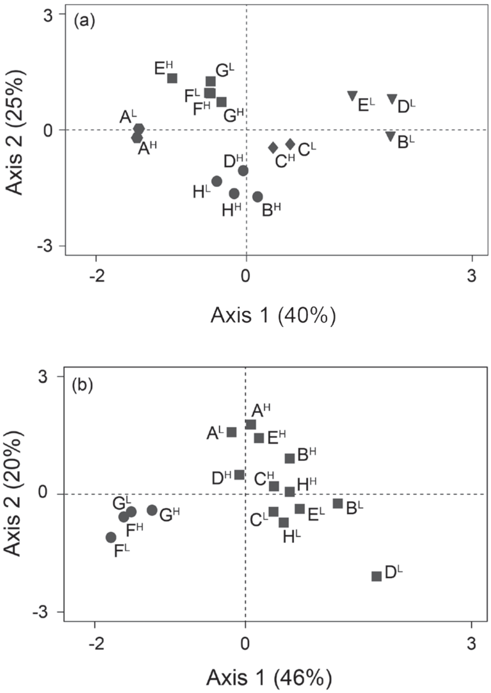

Figure A7.1 Outcome of the correspondence analysis based on trait composition for the different sampling areas without (a) and with (b) the inclusion of the dominant genera. The different sampling areas are split into a ‘low’ (^{L}) and ‘high’ (^{H}) trawl disturbance treatment. The correspondence analysis shows five different clusters in (a) and 2 in (b), grouped at a p-value <0.05 (represented by different symbols).

APPENDIX 7.2 TRAIT MODALITIES THAT CORRELATED POSITIVELY WITH TRAWL DISTURBANCE

Table A7.1 The three trait modalities that were positively correlated to trawl disturbance in area E using a redundancy analysis. The positive correlations are not significantly related to trawling when tested with a linear regression model.

Trait modality	Intercept	Slope	R^2	P-value
Size<20	1.64	0.93	0.03	0.41
Lecithotrophic / direct larval dev.	1.53	1.51	0.02	0.35
Bioturbation activity others	3.61	0.77	0.16	0.60

APPENDIX 7.3 DIFFERENCES IN TRAWL DISTURBANCE

We found a different community shift in response to trawling between area B, D and area E. This different shift could be related to differences in the length of the trawl disturbance gradient between the areas. Since trawl disturbance for area E is estimated from aerial survey data of fisheries inspection services (figure A7.2), it is hard to compare with area B and D. Trawl disturbance has also been estimated for area E by Hiddink *et al*. (2006), using satellite Vessel Monitoring System (VMS) data. They found a maximum trawling intensity of ~5.5 per year. This suggests that the range of the trawling intensity gradient in area E is located between area B (up to 1.5 per year) and D (up to 11.9 per year) and it indicates that the different community responses to trawling are not related to differences in amount of trawl disturbance between areas.

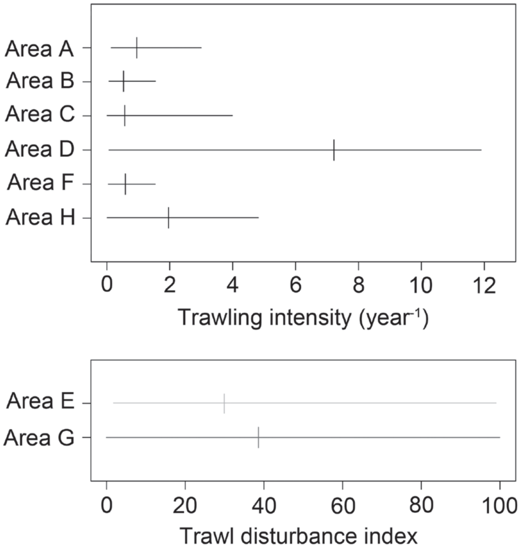

Figure A7.2 The minimum, maximum and mean (vertical lines) of trawl disturbance for each of the areas based on a yearly trawling intensity or a trawl disturbance index.

REFERENCES APPENDIX 7.3

Hiddink JG, Jennings S, Kaiser MJ, Queirós AM, Duplisea DE and Piet GJ. (2006) Cumulative impacts of seabed trawl disturbance on benthic biomass, production, and species richness in different habitats. Canadian Journal of Fisheries and Aquatic Sciences 63: 721-736.

Chapter 8

SYNTHESIS

THESIS SUMMARY

In this thesis, I examined the ecosystem effects of bottom trawl fishing. I focussed on the direct and indirect effects of trawling on both benthos and benthivorous fish and how these effects translate into changes in the fish stock, the demersal food web and the composition and function of benthic communities.

The first research chapter of this thesis (**chapter 2**) describes the interactions between fisheries, fish and benthos and how these affect the impact of trawling on the benthic ecosystem, the amount of target fish food, fish production and fisheries yield. When the direct negative effects of trawling (mortality) on benthos are considered in a food-web perspective, the ultimate effects of trawling on both fish and benthos are strongly mediated by the relative importance of top-down and bottom-up processes in the benthic ecosystem. When benthos competes for the same food, and when the seafloor is trawled, the species which are not so sensitive can use more of the available food, left by their more sensitive competitors. If these less sensitive benthos is a particularly good food source for fish, the benefits can even percolate through to fish, so that the production of fish is stimulated by the negative effect of trawling on benthos. Alternatively, when sensitive benthos is the most profitable food source, trawling leads to a lower production of fish compared with a fishery without impact on benthos.

The trophic interactions between fish and benthos also have important implications for the effectivity of marine protected areas (MPAs) to conserve the benthic ecosystem, fish populations, fisheries yield and the trophic structure of the community, as discussed in **chapter 3**. MPAs may potentially be used simultaneously to protect trawled target fish and the benthic ecosystem. However, their potential for the fisheries yield is not as well established as regular effort limitations. **Chapter 4** of this thesis shows that MPAs, compared to regular effort limitations, can become the best management measure for the fisheries yield when the objective is not only to maximize yield but also to protect benthos vulnerable to bottom fishing. Only when benthic competitive interactions strongly reduce fish prey production in absence of fishing or when fish have limited mobility, there will be lower fisheries yields when benthos is protected with MPAs.

Chapter 5 of this thesis describes the interaction between trawl disturbance intensity and primary production for the Dutch beam trawl fishery fleet that targets plaice (*Pleuronectes platessa*) and sole (*Solea solea*) in the Dutch part of the North Sea. It shows that a large part of the spatial variation in trawling intensity, up to 60%, is explained by a positive relationship with primary productivity and, to a lesser extent, sediment grain size and depth. The positive relationship between productivity and trawling intensity may be the result of an accumulation of plaice and sole in highly productive areas, attracted to a high availability of benthic fish food. The findings highlight how environmental conditions mediate bottom trawl fishing intensity and as such the exposure of benthos to trawling. The environmental conditions not only determine how much benthos is exposed to trawling, but they also directly affect benthic species richness and biomass. This leads to habitat-specific effects of bottom trawling on benthic diversity.

Within the spatial boundaries of the Dutch part of the North Sea, there is also large temporal variation in exposure to trawl impact. **Chapter 6** of this thesis presents these temporal patterns for the Dutch beam trawl fishery fleet for a period of 10 years. It shows that trawl fishing is aggregated in time and displays clear seasonality, related to the behaviour of the fleet and migration patterns of target species. The temporal patterns are of relevance to our understanding of trawling impact on the seabed community, because repeated trawling in a short period, alternated with longer undisturbed periods, have a different effect on invertebrate benthos than single trawling events which are randomly spaced in time. It is also important because benthos vulnerability to trawling may vary seasonally due to changes in population structure and behaviour.

Finally, **chapter 7** of this thesis supports the hypothesis that natural and trawl disturbance affect benthic communities in similar ways. Both sources of disturbance cause declines in long-lived, hard-bodied, and suspension-feeding organisms. No effects of trawling are found in areas with high natural disturbance, while in three out of five areas with low natural disturbance, responses to trawling disturbance are detected. In these areas, trawling results in community compositions comparable with those in areas subject to high natural disturbance. Together, these observations provide strong evidence for the similarity of the community states induced by trawling and natural disturbance.

Overall, this thesis shows how a mechanistic understanding of the factors that determine interactions between fisheries, benthivorous target fish and benthos is a prerequisite for successful management of trawled fish stocks and conservation of the benthic ecosystem. In the remaining part of chapter 8, I discuss what we can learn from trawl disturbance as an ecological experiment (i), whether there is evidence for trawl-induced cultivation or depletion of food for target fish (ii) and how we can manage bottom trawl fishing by understanding its impact (iii).

WHAT CAN WE LEARN FROM TRAWL DISTURBANCE AS AN ECOLOGICAL EXPERIMENT?

Disturbance is thought to shape community diversity, structure and functioning, for example through the intermediate disturbance hypothesis. This hypothesis predicts a hump-shaped pattern between the intensity or frequency of disturbance and the number of species present in an area (Grime 1973, Connell 1978). The pattern arises as at low disturbance, competitive exclusion may limit species richness, whereas at high disturbance, all but the most disturbance-tolerant species are excluded. At intermediate disturbance, species coexist and this causes the hump-shaped pattern. The pattern has been observed in many field studies, but has not been successful as a general ecological theory as even more examples have counteracted the pattern (Mackey and Currie 2001). In addition, the theoretical foundations have been challenged (Shea *et al.* 2004, dos Santos *et al.* 2011, Fox 2013). As a result, some have suggested to move away from testing richness-disturbance patterns and use a biological-trait approach to determine the mechanisms by which disturbance affects communities (Haddad *et al.* 2008, Mouillot *et al.* 2013). Such an analysis can also help to predict the vulnerability of ecological communities to disturbance and changes in ecological functioning of the communities in response to disturbance.

Given the strong disturbing effects of trawling and the many studies that have investigated trawl impact on benthic richness and community structure, we can ask the question whether studying trawling impact contributes to our understanding of disturbance effects on ecological communities. Below, I discuss the effects of trawl disturbance on benthic species richness and community composition (using trait-based approaches) and I explain how the observed changes in community composition may affect benthic ecosystem function.

EFFECT OF TRAWL DISTURBANCE ON SPECIES RICHNESS

Figure 8.1 shows an overview of all trawl disturbance-benthic species richness relationships that I could find from a literature review using the search terms provided in appendix 8.1. These studies (n=43) all showed long-term effects of trawl disturbance on benthic richness. Most studies reported a negative relationship (63%) between trawl disturbance and richness, while 30% of the studies showed no effect and 7% a positive monotonic relationship (figure 8.1). In contrast, the meta-analysis by Mackey and Currie (2001), who collected richness-disturbance relationships of 116 studies, showed that at least one third of the studies reported a positively monotonic or peaked relationship between richness and disturbance, while negative relationships were much less observed (figure 8.1). Yet, their meta-analysis did not consider trawl impact as a disturbing factor and very few of the studies included in the analysis examined marine benthic richness at continental shelf areas. This indicates, that richness-trawl disturbance patterns in marine benthic communities somehow deviate from the earlier found patterns in richness-disturbance relationships. Below, I discuss whether trawl impact is a type of disturbance to be different from the ones included in the meta-analysis, or whether marine benthos differs in its community dynamics from other types of communities and as such in its response to disturbance.

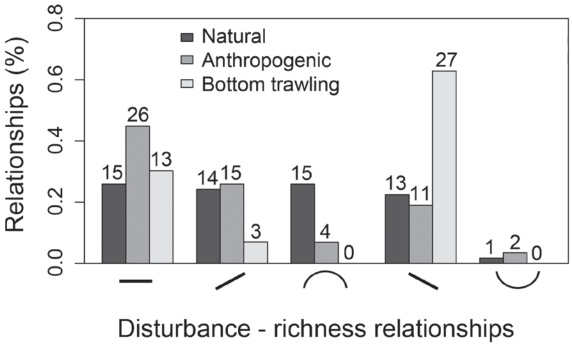

Figure 8.1 Overview of disturbance - species richness relationships for natural, anthropogenic (as extracted from a figure from Mackey and Currie 2001) and bottom trawling disturbance. The search criteria and selected bottom trawl impact studies are shown in Appendix 8.1.

Bottom trawl impact as a disturbing factor

In the meta-analysis, Mackey and Currie (2001) defined disturbance as a "temporally discrete event that abruptly kills or displaces individuals or that directly results in the loss of biomass". Based on this definition, bottom trawl disturbance is similar to the disturbances included in the meta-analysis. Finding many negative relationships between benthic richness and trawl disturbance can then be related to the way in which trawl disturbance affects the benthic community compared with the studies in the meta-analysis. It may differ when the initial effect of trawling already induces such a strong disturbance impact on the benthic community that it will only decline benthic richness. This may be true, since a first trawling event already imposes strong mortality on benthos (Jennings and Kaiser 1998). If correct, it may then be expected, that bottom trawls that have less impact on benthos can exhibit a positive effect on benthic richness at low trawl frequency, but this has not been found in any of the studies I assessed.

Marine soft-sediment environments

Another explanation of the many negative relationships between species richness and trawl disturbance could be that competitive exclusion is not so important in the areas that are most impacted by bottom trawls. These soft-bottom habitats are suggested to be substantially different from hard-substrate marine environments, due to their three-dimensional structure. It is suggested that this structure may reduce the strength of competitive interactions (Wilson 1991, Seitz 1998, Stanley 2008). Moreover, although the importance of competition for food and/or space in marine soft sediments has been suggested (Peterson and Andre 1980, Peterson 1982, Nascimento *et al.* 2011), no study ever showed competitive exclusion of species (Wilson 1991). This could be caused by the often demographically open population dynamics of marine benthos, where local offspring production plays no substantial role in the supply of recruiting larvae (Caley *et al.* 1996, Kinlan and Gaines 2003). These open dynamics may enhance the persistence of inferior competitors through the inflow of new recruits from distant sources (Hixon *et al.* 2002). This may limit competitive exclusion of species and a positive relationship of richness with disturbance. Still, experiments show increased colonization (Lu and Wu 2000, Montserrat *et al.* 2008) and possibly higher species coexistence (Lu and Wu 2000) in defaunated areas compared with areas occupied by a resident benthic community. This suggest that competition can be important in these systems and implies that trawl disturbance could reduce competitively dominant species and increase benthic biodiversity.

Indeed, three studies did observe a positive relationship between trawl disturbance and benthic richness. However, in at least one of these three, richness became higher due to an increase of mobile, scavenging species (Mangano *et al.* 2013). These are not the typical organisms that would normally be competitively excluded at low disturbance, as they feed on a different resource (although there could be competition for space). The increase in scavenging species in response to trawl disturbance, and, as such, total benthic richness, may hence be based on a different mechanism than described within the context of the intermediate disturbance hypothesis. It may have simply emerged because trawl-induced mortality on benthos and fish increased the amount of food for scavengers.

EFFECT OF TRAWL DISTURBANCE ON COMMUNITY COMPOSITION

Bottom-trawl disturbance leads to changes in benthic community composition (Dayton *et al.* 1995, Kaiser *et al.* 2000), arising as some benthos species are more vulnerable to the impact of a gear or can recover more rapidly than other benthos. The vulnerability of the benthic community to trawling and effect of trawling on functioning of the benthic ecosystem are most clear when benthos is split into different groups based on traits related to life history, morphology and ecological niche of the species.

Tillin *et al.* (2006) conducted the first comprehensive trait-based analysis in which trawl impact on the benthos was investigated. Their study shows clearly how trawling affects the functional composition of the benthic community by inducing shifts from large, sedentary and suspension-feeding species towards motile species and infaunal and scavenging organisms. The decline of large, sedentary and suspension-feeding benthos is also observed in other studies that used a trait-based approach (de Juan *et al.* 2007, Kenchington *et al.* 2007).

It is less clear in these studies whether trawl impact also resulted in a similarly perturbed community composition. A systematic test of the response of the community composition of benthos to trawling is described in chapter 7 of this thesis. The results indicate that in response to trawling communities with relatively similar compositions shift to communities dominated by either mobile scavengers and predators, or small-sized, deposit-feeding animals. The shifts are largely the result of relative changes in species biomass, although there is some indication of an absolute increase of small-sized benthos.

A consistent finding in the trait-based analyses is the trawl-induced decline of suspension-feeding organisms. It is likely that these have a certain morphology and/or life-history strategy that makes them particularly vulnerable to trawl impact. A decline in the abundance of this functional group may limit the amount of organic material that is put into the seabed and can reduce benthic production and affect biogeochemical cycles (Gili and Coma 1998, Snelgrove 1999, Pearson 2001, Lohrer *et al.* 2004, Thrush and Dayton 2010). The decline of suspension-feeding organisms also reduces food-web complexity of the benthic ecosystem, which at sites with high trawl disturbance mostly consists of deposit feeders, predators and scavengers (chapter 7). Understanding how these trawl-disturbed benthic communities, with impoverished complexities, are affected in their food-web dynamics, stability and functioning is still at an early stage. However, given the severe effects of bottom trawling on the benthic community in some areas, it could arguably become the most relevant contribution of trawl impact studies to general ecological theory.

TRAWL-INDUCED CULTIVATION OR DEPLETION OF FOOD FOR TARGET FISH

There are different mechanisms by which trawl impact on the benthic ecosystem may affect food availability and productivity of benthivorous fish. In this thesis, I have largely focussed on the mechanism that originates from a trawl-induced shift in the benthic species composition (chapter 2-4). Some of the other mechanisms, *e.g.* trawl-induced suspension of organic material or trawl-induced changes to the habitat, are discussed in chapter 3 and they are furthermore reviewed in Collie *et al.* (unpub.). As such, I will not reiterate them here and I will focus on trawl-induced shifts in benthos and how these may affect the food availability for fish, fish production and consequently the fisheries yield. I will discuss these effects first theoretically (i), and, afterwards I will review empirical evidence in benthos of this process (ii) and discuss future research directions to determine how trawl-induced shifts in benthos may affect food for benthivorous fish (iii).

THEORETICAL FRAMEWORK – BENTHOS, FISH AND FISHERIES

The first model investigating the effects of trawling on benthos in relation to a shift in species composition was described by Duplisea *et al.* (2002). Due to the nature of bottom trawl impact, the authors created a model with multiple groups of benthos that differed in size and morphology (hard or soft bodied). Benthos competed for a single resource and large hard-bodied benthos was competitively superior without trawl impact. The analysis shows that trawling may reduce the total biomass and biomass of large benthos, while it releases small benthos from resource competition, consequently resulting in an increase of their biomass. The model was afterwards extended by Hiddink *et al.* (2008), who coupled relationships between growth, mortality and the environment to incorporate interactive effects between the habitat type and trawl impact (following Hiddink *et al.* 2006b). This study also shows that benthos is expected to decline in response to trawling, while production and biomass of smaller benthos peaks at low trawl intensities due to a decline of the larger, competitively superior species. The increase of smaller benthos supports the idea that trawling potentially enhances food availability for fish that feed on small, soft-bodied prey.

Both studies did not incorporate the effect of fish predation on the benthos and the effect of fishing on fish abundance. How this affects trawl impact dynamics on the benthic ecosystem is shown in chapter 2 of this thesis. The model in chapter 2 describes a system in which benthos dynamics are controlled by resource competition (bottom-up control) or fish predation (top-down control). In a system in which benthos is bottom-up controlled, the benthos shows a response to trawl fishing like discussed by Duplisea *et al.* (2002) and Hiddink *et al.* (2008). In such a system, whether trawl impact on benthos increases the food availability for benthivorous fish largely depends on the energetic profitability for fish of the benthos that is relatively resistant to trawling. When this occurs, fish biomass will increase at low trawl intensities and fisheries yield will be higher compared with a system where there is no trawl impact on benthos. The model dynamics are different for a system in which benthos is top-down controlled. This configuration results in an initial increase of both susceptible and resistant benthos in response to trawling as both benefit from declining fish predation mortality due to fish harvesting. In a top-down controlled system, trawling may result in a higher fisheries yield at high trawling intensity and a higher persistence of fish compared with a system where there is no trawl impact on benthos. Contrastingly, when fish prey is relatively vulnerable to trawl impact, increasing trawl intensity reduces fish biomass, fisheries yield and fish persistence compared with a fishery that has no trawl impact on benthos.

The model described in chapter 2 was used to examine the consequences of an interaction between the vulnerability of benthos to trawling and the energetic profitability of benthos for fish. Benthos that is relatively resistant to the impact of trawl gears are often suggested to be the more profitable fish prey. It is argued that characteristics that make them less vulnerable to trawling also result in a higher energetic profitability for fish. This is most clearly related to the size and morphology of benthos. Small and soft-bodied benthos is often less affected by bottom trawl gears (Duplisea *et al.* 2002). It is also expected to be more profitable prey items for benthivorous fish, which are constrained in prey selection by their gape width (Piet *et al.* 1998). However, other benthic characteristics that make species relatively resistant to trawl impact are expected to correspond less to a higher prey profitability; *e.g.* species that live deep in the sediment are more resistant to trawling, while they are harder to catch by fish. Such species may benefit from a decline in more vulnerable competitors, which would not constitute increasing food availability for target fish. Hence, knowledge of the preference of fish for its benthic prey and the energetic profitability of this prey are needed to understand the effect of trawl-induced changes in fish food availability.

The advantage of the modelling work is that it clarifies which processes are important (*i.e.* asymmetric vulnerability to trawling and energetic profitability of fish prey) and shows the mechanisms through which these processes affect the fish population. The consequences of trawl impact are hard to tackle in the field, as the nature of the system makes it notoriously hard to understand the complete and clear picture. However, different aspects of the impact of bottom trawls on the benthic community in relation to food for benthivorous fish have been examined in the field.

EMPIRICAL EVIDENCE OF TRAWL-INDUCED CHANGES IN BENTHIC PREY FOR FISH

The effects of trawling on benthos in relation to food for benthivorous fish was studied first by Jennings *et al.* (2001). The study shows no absolute increase in biomass or production of infaunal benthos in the Silver Pit area in the North Sea in response to trawling, although the production per unit benthic biomass was found to increase with increased trawling intensity. Comparable negative effects of bottom trawl disturbance on benthic production and/or biomass have been found in many other studies (*e.g.* Hermsen *et al.* 2003, Hiddink *et al.* 2006b, Queirós *et al.* 2006). Jennings *et al.* (2001) recommended that future trawl studies should focus on the smallest macrofauna and meiofauna as these have sufficiently fast life cycles to benefit from trawl disturbance. Precisely these small macrofauna species were found to be positively correlated (not significant) with bottom trawl disturbance in data from the Silver Pit area in chapter 7 of this thesis. The findings suggest an absolute increase in short-living benthos with lecithotrophic or direct larval development. In contrast, no increase of biomass in response to a trawl-induced decline of larger benthos has been observed for meiofaunal benthos (nematodes) (Hinz *et al.* 2008), although such increases were suggested in a mesocosm experiment, where total nematode abundance (biomass was not tested) was higher in the absence of large macrofauna (Ingels *et al.* 2014). There is hence no firm evidence from the above trawl-impact studies that the biomass of part of the benthos increases in response to trawling when others decline. This suggests that most studies reporting trawl-induced shifts in species composition refer to relative shifts; some (groups of) species are less affected by the trawls and as such increase proportionally in response to trawling. A relative increase of certain benthic species will not enhance the food availability for benthivorous fish, as the abundances of benthos decline (or remain constant). This may decline body condition and productivity of benthivorous fish (Hiddink *et al.* 2011, Johnson *et al.* 2014). However, it should be noted that studies testing species-specific responses over a trawl disturbance gradient often find increases of some species, despite a reduction in total (trait/benthic group) biomass (*e.g.* Hinz *et al.* 2008, Hinz *et al.* 2009, Johnson *et al.* 2014). These findings highlight that species-specific testing of trawl responses could be needed to understand trawl-induced effects on the benthic food web.

FUTURE DIRECTIONS TO DETERMINE TRAWL-INDUCED FOOD WEB EFFECTS

Theory indicates there could be positive indirect effects of trawling on target fish food, fish production and fisheries yield. However, the only suggestions of positive effects in the field are based on positive relationships between trawling intensity and growth rates of plaice (Rijnsdorp and van Leeuwen 1996, Shephard *et al.* 2010) and sole (Millner and Whiting 1996) in large-scale correlative studies in which other processes, such as gradients in primary production, are hard to disentangle from the effects of fishing. Alternatively, there is limited empirical evidence of trawl-induced cultivation of food for fish based on the benthic response to trawling. Many studies have shown declines in benthic species biomass and/or production, and, suspension-feeding organisms are particularly negatively affected by trawling. At this stage, most evidence is hence found for trawl-induced depletion of food for target fish in chronically fished areas, as a result of direct trawl mortality on fish prey and/or an overall reduction in benthic productivity through a decline in suspension-feeding organisms (see chapter 8, what can we learn from trawl disturbance as an ecological experiment?). A trawl-induced depletion of food for target fish will have negative consequences for the fish production, fisheries yield and fish persistence.

Evidence of these effects is, admittedly, only coming from studies examining the response patterns of benthos and fish along trawling gradients and as such they only show local population dynamics. A clearer understanding of indirect effects of trawling on target fish food can be derived through a mechanistic understanding of the benthic ecosystem. This may be achieved by determining the relative importance of bottom-up and top-down processes in the benthic ecosystem and by examining foraging behaviour of benthivorous target fish. To assess this, there is a clear need for experimental set-ups in the field (*e.g.* caging experiments and recovery studies), mesocosms (*e.g.* controlled impact studies) and laboratory (*e.g.* fish behavioural studies).

HOW TO MANAGE BOTTOM TRAWL FISHERIES BY UNDERSTANDING ITS IMPACT

The aim of all trawl disturbance studies is, eventually, to understand how the benthic ecosystem, including the target species of fisheries, should be managed. Interestingly, most measures to protect benthos are decoupled from management of target fish. Decoupling of policy aimed to protect benthos and fish may lead to remarkable failures of management as not all ecosystem components on which trawling has an impact will increase once they are protected (chapter 2-4). Successful protection will depend on the balance between direct benefits (less trawl mortality on fish or benthos) versus indirect disadvantages (*e.g.* less fish prey or more predation mortality).

A management strategy that deals with trawled fish stocks needs to account for the effect of trawling on the benthos. In case trawling induces a negative effect on the most profitable food items for target fish, trawling will result in a lower fish production, fisheries yield and persistence of fish at high trawling mortalities compared with trawl gears with less impact on benthos (chapter 2). Management actions that reduce the impact of trawling on benthos could hence increase fish production, fisheries yield, and, reduce the trawl mortality of vulnerable benthos. This may be achieved through technological innovations, such as the pulse trawl, which reduces the impact of trawling on benthos strongly (van Marlen *et al.* 2014, Soetaert *et al.* 2015), and through the establishment of MPAs. It is even possible that, as hypothesized in chapter 3 of this thesis, negative effects of MPAs on the fisheries yield (occurring when the stock is fished below a fishing mortality at maximum sustainable yield (MSY), see Gerber *et al.* 2003) are outweighed by positive effects of a reduced impact of trawling on fish food.

Alternatively, if the most trawl-resistant benthos is the more profitable type of food for fish, trawling with high impact on benthos may lead to higher fish biomass, fisheries yield and fish persistence compared with fisheries with less impact on benthos (chapter 2). A reduction of the impact of trawling on benthos, through technological innovations or MPAs, will in this case reduce the productivity of the stock, although it will limit trawl mortality on benthos. Fisheries management that promotes fish stock exploitation at MSY, the current strategy in European waters, is then confronted with a wide range of possible MSYs depending on the amount of trawl mortality on benthos at a given fishing intensity. In such a situation, there is a need for fisheries management to define how much of the benthos may be impacted to maintain a certain productivity of the target stock. Although this sounds futuristic, such effects may already be on going in the North Sea through the recent introduction of pulse trawl gears that target plaice and sole with less impact on benthos compared with traditional beam trawls (Soetaert *et al.* 2015).

The paragraphs above illustrate how fisheries management can account for the indirect effects of fishing to exploit trawled fish stocks. The objective is still to maximize fisheries yield, and, as such, there is no full integration between the conservation of benthic habitat and exploitation of target fish. A management strategy that deals with both these components has to select a measure that gives most protection to the benthic ecosystem, at the least cost in terms of fisheries yield. In isolation, benthos may best be protected by MPAs as trawling is expected to have largest impact during a first event (Jennings and Kaiser 1998, Dinmore *et al.* 2003), while fisheries yield is highest when effort restrictions are set to a fishing mortality at MSY (Gerber *et al.* 2003, Hilborn *et al.* 2004). In chapter 4 of this thesis a combined evaluation of benthos and fisheries yield, while accounting for food-web interactions between fish and benthos, shows that protection of benthos with MPAs may result in a higher or equal fisheries yield compared with a similar level of protection of benthos with effort restrictions. Only if competitive interactions in the benthos strongly reduce benthos production in absence of fishing or when fish have limited mobility, fisheries yields decrease when benthos and fish are protected with MPAs.

These findings highlight the importance of food-web interactions to understand bottom-trawl effects on the benthic ecosystem and to impose suitable management measures to protect the system. For the sake of clarity these findings are all shown for constant environmental conditions and a fishery that is homogenously spread. In real areas impacted by bottom fishing, there are environmental gradients in *e.g.* productivity, sediment type and natural disturbance, that affect benthic community composition, richness, food-web interactions and bottom trawl intensity and impact. Fisheries managers could also use this information to reduce the environmental effects of bottom fishing, with limited costs to fisheries yield. Below, I will discuss how this may work out when it is acknowledged that some areas are of limited importance to fisheries, while fisheries affect other areas only mildly. Both aspects have a temporal component, since trawl fishing is seasonally organized (chapter 6).

AREAS OF LIMITED IMPORTANCE TO THE FISHERY

There is large spatial variation in bottom trawling intensity. Some areas are fished multiple times each year while others remain unaffected over periods of multiple years (Piet and Hintzen 2012). This information may be used to identify areas that can be closed to fishing in order to protect the benthic ecosystem from trawl impact. It may be expected that a closure of the frequently fished areas will largely affect fisheries behaviour (Halpern *et al.* 2004, Murawski *et al.* 2005). This may lead to negative effects on benthic communities, despite the establishment of an MPA, due to displaced fishing activity towards more sensitive or previously unfished areas (Dinmore *et al.* 2003, Hiddink *et al.* 2006a). Alternatively, closing areas less used by fisheries will result in limited fisheries effort displacement, while protection may still provide a great benefit to the benthic ecosystem; these incidentally trawled sites may be inhabited by vulnerable benthic organisms that normally need to recover over a long period of time after a trawling event (Jennings and Kaiser 1998, Dinmore *et al.* 2003). Based on these findings, Hiddink *et al.* (2006a) suggested that without additional management action, area closures in lightly fished areas are expected to be the most effective strategy to minimize the environmental effects of bottom fishing.

Additionally, habitat conditions probably differ between frequently and incidentally trawled sites. This is likely because fisheries select habitats that are suitable for their trawl gears and have high abundances of target fish (Fogarty and Murawski 1998, Rijnsdorp *et al.* 2006). Habitat conditions also affect the benthic ecosystem and this causes an interaction between habitat conditions, bottom trawling intensity and the vulnerability of benthos to trawling impact. These interactions were examined in chapter 5 of this thesis. The most striking result was that we found that areas exposed to high fishing intensities were relatively species-poor, probably the result of high primary productivities and coarse-grained sediments. Negative effects of trawling on benthic species richness in these areas were not detected. Alternatively, negative effects of trawling on benthic richness were found in species-rich areas that were less used by the fishery. Some of these species-rich areas were only incidentally affected by trawl fishing over the last 10 years (chapter 6). Together, these findings highlight how in this case, limiting incidental trawling events will lead to protection of areas that have highest benthic diversity, while they are vulnerable to bottom fishing. The generality of this finding may be worth exploring for other habitats and trawled target species.

Similarly, fisheries management could close areas that are only fished during certain periods of the year (see chapter 6 for examples), presumably because they are only temporally inhabited by target fish. These fish can still be caught in other areas during other seasons. This suggests that closure of such an area will have limited impact on fisheries yield, while vulnerable benthos is year-round protected. However, to reach such limited effects on fisheries yield, there is need for the fisheries to be flexible in their intensity throughout the year. A similar spatiotemporal distribution of fishing intensity could be enforced when fisheries have to compensate for fishing a vulnerable habitat, *i.e.* using a fishing-impact credit system (van Riel *et al.* 2013, Batsleer *et al.* unpub.)

AREAS THAT ARE LESS AFFECTED BY FISHERY

Variation in habitat conditions affects benthic ecosystems in their richness, biomass, community structure and function (Probert 1984, Gray 2002, Bremner 2008). This, on its turn, affects the vulnerability of the benthic community to bottom trawling at a given level of trawling intensity and causes habitat-specific effects of trawling. These effects have been shown in many studies and it is often indicated that community responses to trawling in areas exposed to high natural disturbance (currents, waves and storms) seem to be smaller or absent (*e.g.* Kaiser and Spencer 1996, Collie *et al.* 2000, Hiddink *et al.* 2006b, Kaiser *et al.* 2006, Queirós *et al.* 2006, Tillin *et al.* 2006). In chapter 7 of this thesis, we tested this hypothesis at large spatial scales and with data spanning many levels of natural disturbance. We found strong evidence for the similarity of the community states induced by trawling and natural disturbance. Based on the interactive effects on the benthic community, Diesing *et al.* (2013) calculated the probability that fishing disturbance exceeds the amount of natural disturbance for the English part of the North Sea. This can be an indication to identify areas, without an understanding of the benthic community, that are most vulnerable to fishing impact. The interactive effects between trawl and natural disturbance can hence support the development of management measures that include the environmental effects of bottom fishing.

Protection of benthos from bottom trawls is completely linked to spatial fisheries management. However, there is often also a strong temporal aspect to trawl fishing intensity and this has largely been neglected in management plans to protect the benthic ecosystem so far. The temporal patterns in bottom fishing may arise from migration patterns in target species that lead to temporal aggregation of fish. These temporal patterns are of relevance to our understanding of trawling impact on the seabed community because benthos vulnerability to trawling may vary seasonally due to changes in population structure and behaviour (chapter 6). This may affect the amount of benthic by-catch (Dunn *et al.* 2011) as well as trawl-induced benthic mortality (chapter 6). Fisheries management could account for these temporally fluctuating vulnerabilities of benthos through seasonal closures. Such closures may disproportionally reduce trawl impact on benthos. Interestingly, temporal closures have already been developed to protect target fish, especially of fish aggregations during their spawning period (van Overzee and Rijnsdorp 2015).

CONCLUSIONS

Review papers and meta-analysis clearly show that bottom trawling negatively affects benthic habitats and species (Collie *et al.* 2000, Kaiser *et al.* 2002, Thrush and Dayton 2002, Kaiser *et al.* 2006). Moreover, it should be acknowledged that the effects of bottom trawling on the benthic community depend on habitat and gear type, biotic interactions in the benthic ecosystem and timing and magnitude of (historic) trawl events. Understanding how such factors affect bottom trawl impact will help the development of successful management measures of trawled fish stocks that take into account the environmental effects of bottom fishing.

A complete ecosystem-based fisheries management approach also asks for full integration of the benthic ecosystem and its trawled fish stock. This will help to predict how direct and indirect effects of trawl mortality on both benthos and fish translate into changes of the fish stock, the fisheries yield, the demersal food web and the structure and function of benthic communities. This thesis shows how only a mechanistic understanding of the factors that determine interactions between fisheries, fish and benthos may lead to such integration. It is this type of information that is needed to shift the ecosystem approach to fisheries management from a policy objective towards an effective instrument for successful management of trawled fish stocks and the conservation of the benthic ecosystem.

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APPENDIX 8.1 OVERVIEW OF TRAWL DISTURBANCE – RICHNESS RELATIONSHIPS

Table A8.1 shows an overview of all trawl disturbance-benthic species richness relationships that I could find from a literature review. Studies were selected from Scopus using the search terms ((TITLE(trawl*) OR TITLE(fishing) OR TITLE(fisheries) AND TITLE-ABS-KEY(epifauna*) OR TITLE-ABS-KEY(infauna*) OR TITLE-ABS-KEY(meiofauna*) OR TITLE-ABS-KEY(megafauna*) OR TITLE-ABS-KEY(benthic) OR TITLE-ABS-KEY(benthos) AND TITLE-ABS-KEY(number of taxa) OR TITLE-ABS-KEY(*diversity) OR TITLE-ABS-KEY(richness) OR TITLE-ABS-KEY(number of species))). The search resulted in 258 studies of which title and abstract were scanned for long-term effects of bottom trawl impact on benthic species richness (based on comparisons between active fishing grounds and untrawled sites or experimentally trawled areas with sampling for at least 1 year after the first trawling event). Note that the list provided is not comprehensive and shows a summary of trawl impact for different types of gear, habitats and sampling protocols. Studies sampling benthos using multiple types of gear and/or multiple areas were counted individually when they were separately examined in the study.

Table A8.1 Overview of the 43 selected trawl disturbance – richness relationships.

Response	Reference
Negative	van Denderen *et al.* 2014
No	van Denderen *et al.* 2014
Negative	Mangano *et al.* 2014
Negative	Handley *et al.* 2014
Negative	Pusceddu *et al.* 2014
Negative	Sheehan *et al.* 2013
Negative	Cook *et al.* 2013
Positive	Mangano *et al.* 2013
No	Atkinson *et al.* 2011
Negative	Atkinson *et al.* 2011
No	Currie *et al.* 2011
Negative	Reiss *et al.* 2009
Negative	Althaus *et al.* 2009
Negative	Grizzle *et al.* 2009
No	Svane *et al.* 2009
Negative	Hinz *et al.* 2009
Negative	Hinz *et al.* 2009
Negative	Asch and Collie 2008
No	Schejter *et al.* 2008
Negative	Hinz *et al.* 2008

Negative	Hinz *et al*. 2008
Negative	de Biasi and de Ranieri 2006
Negative	Vergnon and Blanchard 2006
Negative	Hiddink *et al*. 2006
No	Hiddink *et al*. 2006
No	Hiddink *et al*. 2006
No	Hiddink *et al*. 2006
No	Henry *et al*. 2006
Negative	Blanchard *et al*. 2004
Negative	Blyth *et al*. 2004
Negative	Cryer *et al*. 2002
Negative	Schratzberger and Jennings 2002
No	Schratzberger *et al*. 2002
Negative	Chícharo *et al*. 2002
Positive	Chícharo *et al*. 2002
No	Kenchington *et al*. 2001
Negative	Koslow *et al*. 2001
Negative	McConnaughey *et al*. 2000
Positive	Tuck *et al*. 1998
Negative	Collie *et al*. 1997
No	Kaiser and Spencer 1996
Negative	Kaiser and Spencer 1996
No	van Dolah *et al*. 1991

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SAMENVATTING

Bodemberoerende trawlvisserij is een vismethode die via verstoring van de bodem verschillende soorten demersale vis, schelp- en schaaldieren vangt. De visserij is verantwoordelijk voor ongeveer 25% van de wereldwijde vangsten en heeft een geschatte 50 miljoen vierkante kilometer van de zeebodem bevist. De verstorende effecten van de vistuigen op de zeebodem hebben geleid tot grote maatschappelijke ongerustheid over het welzijn van bodemdieren en het functioneren van het bodemecosysteem.

Trawlvisserij, met name boomkor-, borden- en dredgevisserij, staat bekend om haar grote hoeveelheden bijvangst van ondermaatse doelsoorten en van soorten die geen commerciële waarde hebben. De hoeveelheid bijvangst is in sommige visserijen meer dan de helft van de totale vangst. Daarnaast leidt de bodemberoering tot verandering in de habitat en veroorzaken de tuigen, naast de sterfte via bijvangst, ook directe sterfte onder ongewervelde bodemdieren (benthos). Deze sterfte geldt met name voor grote, sessiele en improductieve benthossoorten, die over het algemeen gevoelig zijn voor de directe effecten van de visserij en langzaam herstellen van deze verstoring. Kortlevende, opportunistische benthossoorten, aaseters en predators zijn minder gevoelig voor de effecten van de visserij en/of kunnen sneller herstellen. Deze soorten domineren dan ook gebieden die vaak bevist worden. De beviste gebieden hebben over het algemeen een lagere benthische soortenrijkdom, met vooral verlies van soorten die voedsel uit het water filteren.

De negatieve bij-effecten van vistuigen op het benthische ecosysteem hebben geleid tot maatregelen ter bescherming van dit systeem, onder meer via het sluiten van gebieden voor de visserij en het stimuleren van vistuigen die sterfte onder het benthos verlagen. De meeste van deze maatregelen zijn onafhankelijk genomen van maatregelen ten behoud van de commerciële demersale vis, die vooral beheerd wordt via beperkingen in visserij-inspanning. Dit is opmerkelijk omdat benthos en vis sterk aan elkaar gekoppeld zijn: veel getrawlde demersale vis foerageert op benthos en de visserij zorgt onder zowel vis als benthos voor sterfte. **Dit proefschrift** beschrijft de ecosysteemeffecten van bodemberoerende trawlvisserij. Het onderzoekt hoe directe en indirecte effecten van de visserij op benthos en commerciële vis kunnen leiden tot veranderingen in de vispopulatie, het demersale voedselweb en de samenstelling en het functioneren van bodemgemeenschappen.

Het eerste onderzoekshoofdstuk (**hoofdstuk 2**) beschrijft de voedselweb-interacties tussen vis en benthos in een modelstudie. Er is onderzocht hoe deze voedselweb-interacties de productie van commerciële vis en de visserijopbrengst beïnvloeden. Het laat zien dat de effecten van vistuigen op het benthos zowel productieverhogend als -verlagend kunnen werken op vis en visserijopbrengst. Dit ontstaat door een verschuiving in de concurrentieverhouding binnen het benthos. Bodemberoering is productieverhogend wanneer relatief ongevoelige benthossoorten het belangrijkste voedsel voor vis vormen en profiteren van de visserij door een afname van gevoelige benthossoorten die minder aantrekkelijke prooien zijn. Het omgekeerde gebeurt wanneer de gevoelige benthossoorten het belangrijkste voedsel voor vis vormen. Afhankelijk van deze interacties zullen maatregelen aan vistuigen ter bescherming van benthos, tot meer of minder vis, visproductie en visserijopbrengst leiden.

De voedselweb-interacties kunnen ook een belangrijke rol spelen bij de effectiviteit van mariene reservaten voor het behoud van benthos, vis en visserijopbrengst en dit is bediscussieerd in **hoofdstuk 3**. Mariene reservaten zijn een aantrekkelijke maatregel voor het beheer van de negatieve effecten van trawlvisserij omdat ze zowel het benthische ecosysteem als de commerciële vis kunnen beschermen. Er is gesuggereerd dat reservaten echter niet leiden tot een hogere visserijopbrengst, die optimaal is via de juiste visserij-inspanningsmaatregelen. In **hoofdstuk 4** van dit proefschrift is in een modelstudie onderzocht hoe de visserijopbrengst het beste kan worden beheerd, gegeven een bepaalde mate van bescherming van benthos, gevoelig voor deze visserij. Het hoofdstuk laat zien dat mariene reservaten, vergeleken met visserij-inspanningsmaatregelen, vaak leiden tot een hogere of gelijke visserijopbrengst wanneer rekening wordt gehouden met de bescherming van benthos. Alleen wanneer concurrentie in het benthos de productie van benthische prooidieren voor vis verlaagt, of wanneer vis niet mobiel genoeg is, zullen er lagere visserijopbrengsten zijn bij bescherming van het gevoelige benthos door middel van mariene reservaten.

Een deel van het effect van de visserij op het benthische ecosysteem hangt af van de mate van bevissing van een gebied. De visserij selecteert gebieden die geschikt zijn voor hun vistuigen en waar ze veel vis kan vangen. Het is waarschijnlijk dat visserij op benthivore vis zich concentreert in productieve gebieden omdat daar veel benthivore vis zit, aangetrokken door een grote hoeveelheid en/of hogere productie van benthische prooidieren. In **hoofdstuk 5** is de interactie tussen visserij-inspanning en primaire productiviteit onderzocht in het Nederlandse deel van de Noordzee aan de hand van verspreidingsgegevens van de Nederlandse boomkorvloot, met name vissend op schol (*Pleuronectus platessa*) en tong (*Solea solea*). Een groot deel van de verspreiding van de visserij, tot 60%, kan worden verklaard aan de hand van een positieve relatie met productiviteit en in mindere mate sediment type en bodemdiepte. De positieve relatie onderbouwt de hypothese dat vis aangetrokken wordt tot productieve gebieden waar veel voedsel aanwezig is. Tegelijk laten de resultaten zien dat zowel productiviteit als de abiotische condities sterk bepalen waar de visserij plaatsvindt en als zodanig waar het benthische ecosysteem wordt blootgesteld aan de visserij. Deze factoren hebben daarnaast ook een direct effect op benthische diversiteit en biomassa. Dit zorgt voor gebiedsafhankelijke effecten van bodemvisserij. In laagproductieve gebieden met fijn sediment is er een negatieve relatie tussen soortenrijkdom en bodemvisserij, terwijl er in de productievere gebieden met grof sediment geen relatie te vinden is. Juist die laatste gebieden worden het sterkst bevist.

Naast de ruimtelijke verspreiding van trawlvisserij in het Nederlandse deel van de Noordzee, is er ook een sterke temporele variatie wanneer deze bevissing optreedt. **Hoofdstuk 6** van dit proefschrift beschrijft deze temporele patronen voor de Nederlandse boomkorvloot gedurende een periode van 10 jaar. Het hoofdstuk laat zien dat bevissing van een bepaald gebied vaak gebeurt binnen een korte periode in het jaar. De visserij heeft ook sterke seizoenspatronen, de migratiepatronen van de doelsoorten, schol en tong, volgend. Kennis van de temporele patronen wordt vrijwel niet gebruikt om zowel het effect van trawlvisserij op het benthos te schatten, als om beheermaatregelen te ontwikkelen ter bescherming van het benthische ecosysteem. Aan de hand van een benthospopulatiemodel wordt er in hoofdstuk 6 getoond dat de temporele patronen wel degelijk relevant zijn. Enerzijds geeft een gepiekte bevissing in een bepaald gebied een lagere sterfte aan benthos dan een zelfde hoeveelheid bevissing die willekeurig plaatsvindt over het jaar. Daarnaast zijn er aanwijzingen dat de gevoeligheid van benthos voor bodemberoering varieert over de seizoenen, vanwege enerzijds een veranderende populatieopbouw, als anderzijds seizoensgebonden gedrag.

De negatieve effecten van trawlvisserij op het benthische ecosysteem zijn vaak minder aanwezig in hoogdynamische gebieden waar de bodem verstoord wordt door stormen en getijdenstromen. Dit heeft geleid tot de hypothese dat zowel trawlvisserij als natuurlijk verstoring dezelfde effecten veroorzaken op bodemgemeenschappen. Deze hypothese is getest in **hoofdstuk 7** voor acht verschillende gebieden in de Noordzee en Ierse zee die allemaal een gradiënt hebben in visserij en tegelijk verschillen in mate van natuurlijke verstoring. De resultaten laten zien dat beide typen verstoring leiden tot een afname in langlevende, harde benthossoorten die voedsel uit het water filteren. Geen effecten van bodemvisserij zijn gevonden in hoogdynamische gebieden, terwijl er in drie van de vijf andere gebieden sterke verschuivingen in de samenstelling van de bodemgemeenschap zijn gevonden. In deze gebieden heeft bodemberoering geleid tot een bodemgemeenschap die lijkt op de bodemgemeenschap in een hoog dynamisch gebied, met veel mobiele aaseters en predatoren of kleine, detritusetende benthossoorten. Tezamen ondersteunen deze resultaten dan ook de hypothese dat zowel visserijverstoring als natuurlijke verstoring dezelfde effecten veroorzaken op bodemgemeenschappen.

Concluderend laat dit proefschrift zien dat begrip van de interacties tussen visserij, benthivore vis en benthos noodzakelijk is voor het beheren van commerciële benthivore vis en het beschermen van het benthische ecosysteem. Deze informatie is nodig om tot een succesvolle ecosysteembenadering van het visserijbeheer te komen.

CURRICULUM VITAE

Daniël van Denderen is born on Monday the 22th of December 1986, in Leeuwarden, the Netherlands. After obtaining his VWO diploma from the Kennemer Lyceum, Overveen in 2005, he starts the study Biology at Leiden University. In the third year of his bachelor program, he starts a research project supervised by dr. W. Tamis on the risk of invasive plant seeds imported through fodder. He discovers that, in practice, this means he is counting seeds for a few months. In 2008, Daniël starts the MS Animal Biology in Leiden. In his first master project, supervised by Prof. dr. M. Richardson and dr. S. Ali, he examines the toxicity response of zebrafish embryos to a pyrethroid insectide. In practice, this means he is now counting eggs for a few months. A summer school organized by the Tropical Biology Association in Tanzania helps him to become passionate about ecology. Afterwards, he starts a research project at IMARES Wageningen University under supervision of dr. R HilleRisLambers and dr. T van Kooten examining size-based interactions between herring and cod in the North Sea. In practice, this means he is examining size-based interactions between "herring" and "cod" in the "North Sea", and, as such it is a very successful match. After finishing his masters *cum laude*, he returns 8 months later to IMARES Wageningen University for his PhD research supervised by Prof. dr. A.D. Rijnsdorp and dr. T. van Kooten. Coming years, Daniël will work as a postdoctoral researcher at the Centre for Ocean Life, DTU-Aqua, Denmark.

LIST OF PUBLICATIONS

van Denderen PD, Hintzen NT, van Kooten T and Rijnsdorp AD. (2015) Temporal aggregation of bottom trawling and its implication for the impact on the benthic ecosystem. ICES Journal of Marine Science 72: 952-961.

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DANKWOORD

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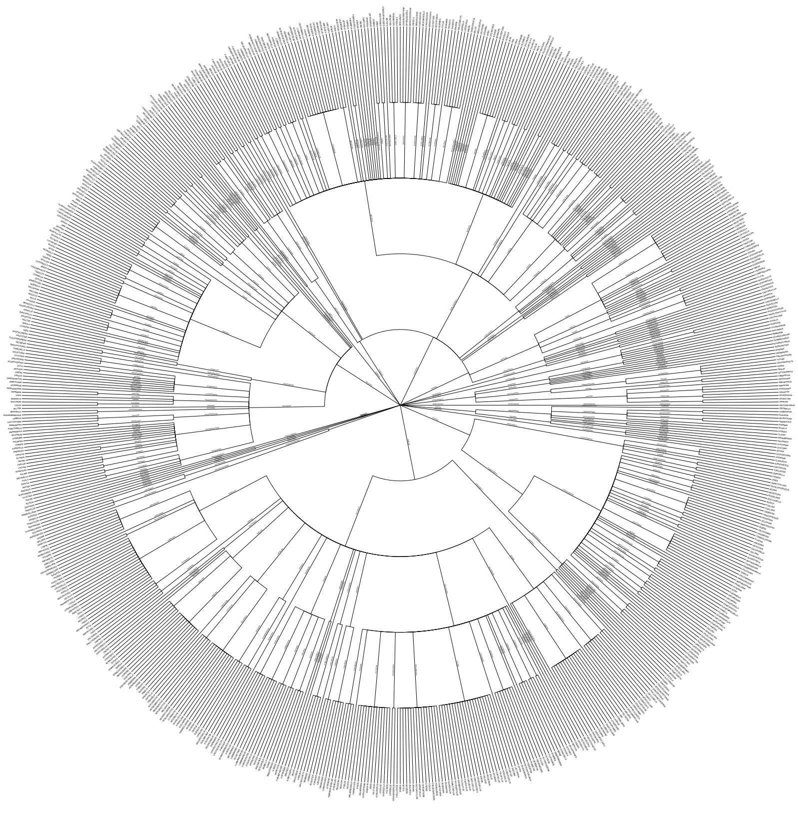

Phylogenetic tree based on the taxonomic classification of infaunal benthic invertebrate genera found across the European continental shelf (constructed by C. Doorenweerd). Benthos data from Bolam *et al.* (2014) Journal of Sea Research. 85: 162-177 and www.benthis.eu.

Training and supervision plan		Graduate School WIAS
Name PhD student	Daniël van Denderen	
Project title	Ecosystem Effects of Bottom Trawl Fishing	
Group	IMARES Fish & Aquaculture and Fisheries	
Daily supervisor	Dr. Tobias van Kooten	
Supervisor	Prof. dr. Adriaan D. Rijnsdorp	
Project term	from 01-05-2011 – until 01-05-2015	
Submitted	18-05-2015 – certificate	

Education and training	Year	Credits*
The basic package		
WIAS introduction course	2012	1.5
Ethics and philosophy in aquatic life sciences	2012	1.5
Scientific Exposure		
Mathematical models in ecology and evolution, Groningen	2011	1.0
International flatfish symposium, IJmuiden	2011	1.5
IMARES PhD day, Texel (oral, poster)	2011-2013	2.9
International symposium on the ecology of the Wadden Sea, Texel	2011	1.5
Netherlands annual ecology meeting, Lunteren (oral 3x)	2012-2015	5.4
WIAS science day, Wageningen (oral, poster)	2013, 2015	2.6
Workshop North Sea and Wadden Sea modelling, Texel	2013	0.3
INTECOL Ecology: into the next 100 years, London (oral)	2013	2.5
ICES Annual Science Conference, Reykjavik (oral)	2013	2.5
Effects of fishing on benthic fauna and habitats, Tromsø (oral)	2014	2.0
Workshop: trawling impact on benthic ecosystems	2014	0.6
Seminar at Danish Technical University AQUA, Copenhagen	2014	1.0
Current themes in ecology, Wageningen	2014	0.3
In-depth studies		
ELME: Enhancing linkage in mathematics and ecology Michigan State University	2012	4.5
Modelling and Analysis of Innovation and Competition Processes Politecnico di Milano	2014	1.5
Resource-Consumer Interactions: Hunger, Health and Horror Driebergen	2014	2.0
Professional skills support courses		
Writing for academic publication	2013	3.0
Research skills training		
Preparing own PhD research proposal	2011	6.0
External training period at CEFAS Lowestoft, UK	2013	2.0
Didactic skills training		
Supervising MSc theses	2011, 2013	3.5
Management skills training		
Organisation IMARES PhD day	2012, 2013	1.5
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