

# Can bottom trawling disturbance increase food production for a commercial fish species?

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**Abstract:** Fishery closures and marine protected areas are increasingly being used as tools to achieve sustainable fisheries. The “plaice box”, a gear restriction area in the North Sea that was established to reduce the bycatch of undersized plaice (*Pleuronectes platessa*), is considered ineffective because there has been a shift in the distribution of juvenile plaice to the waters that remained open to bottom trawlers. Here we examine the hypothesis that bottom trawling benefits the small benthic invertebrates that form the food source for plaice and that the plaice box had a negative impact on food production for plaice. A size-based model of benthic communities indicates that the production of prey was low without trawling and maximal in areas that are trawled once to twice a year. Therefore, bottom disturbance may improve the feeding conditions for species that feed on small invertebrates. As plaice aggregate at the locations with the highest benthic biomass, this may explain the observed redistribution to areas outside the plaice box. We conclude that the plaice box may not have been the most appropriate measure to protect plaice from discarding and that the species’ ecology should be considered when choosing the most appropriate management measure to achieve an objective.

**Résumé :** Les fermetures de la pêche et les zones de protection marine servent de plus en plus d’outils pour obtenir des pêches durables. Le « cantonnement à plies », une zone de restriction des engins de pêche dans la mer du Nord établie pour réduire la capture accessoire de plies (*Pleuronectes platessa*) de taille inférieure à la limite, est considérée inefficace car il y a eu un déplacement dans la répartition des plies vers les eaux qui restent disponibles aux navires de chalutage de fond. Nous examinons ici l’hypothèse selon laquelle le chalutage de fond favorise les petits invertébrés benthiques qui constituent la source de nourriture des plies et que le cantonnement à plies a un impact négatif sur la production de nourriture des plies. Un modèle des communautés benthiques basé sur la taille indique que la production de proies est basse en l’absence de chalutage et qu’elle est maximale dans les zones où il y a du chalutage une ou deux fois par an. C’est pourquoi, la perturbation du fond peut améliorer les conditions alimentaires pour les espèces qui se nourrissent de petits invertébrés. Comme les plies se rassemblent dans les sites de biomasse benthique maximale, cela peut expliquer le redéploiement des plies vers les zones extérieures au cantonnement à plies. Nous concluons que le cantonnement à plies ne s’est peut-être pas avéré être la méthode la plus appropriée pour protéger les plies du rejet à la mer; il faut donc tenir compte de l’écologie de l’espèce lors du choix de la mesure de gestion la plus appropriée pour réaliser un objectif.

[Traduit par la Rédaction]

## Introduction

Marine protected areas (MPAs) are areas where the environment is protected in some way and include marine reserves, no-take zones, and fishery closures (Kelleher 1999). MPAs are increasingly being used as a tool for achieving sustainable fisheries. There exists an extensive literature on the contributions of MPAs to achieve conservation goals (meta-analysis in Halpern 2003). However, the fishery benefits of MPAs are ambiguous (Willis et al. 2003; Gårdmark et al. 2006), and the negative effects of displacement of fishing effort from the closed areas to areas that remain open may

be larger than the positive effects in the closed areas (Dinmore et al. 2003; Hiddink et al. 2006a).

The “plaice box” is a 38 000 km<sup>2</sup> gear restriction area (a type of MPA) in the southeastern North Sea that was established to reduce the bycatch of undersized plaice (*Pleuronectes platessa*) in heavily trawled coastal nursery grounds. Large mature plaice are distributed more widely and further offshore than juveniles (Rijnsdorp and van Leeuwen 1996). The plaice box was closed to trawlers with an engine power >300 hp (1 hp = 746 W) for part of the year in 1989 and for the whole year since 1995. There are no spatial restrictions on fishing by trawlers with an engine power <300 hp and fishing effort by these vessels in the plaice box has increased since 1989. Nevertheless, total trawling effort in the plaice box was reduced by more than 90%, and most of this effort was redistributed into adjacent areas (Pastoors et al. 2000). At the time of closure, it was expected that this closure would result in an increase in plaice stocks of 25%–35% (Grift et al. 2004), but instead plaice spawning stock biomass has declined strongly (Pastoors et al. 2000). There also seems to have been a shift in the spatial distribution of juvenile plaice to the deeper offshore waters that have remained open to all trawlers (Van Keeken et al. 2007). Therefore, the plaice box is currently

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less effective than anticipated in reducing the capture and discarding of juvenile plaice (Grift et al. 2004). Several explanations for the decrease in abundance of juvenile plaice in the plaice box have been put forward, such as decreasing eutrophication, climate change, and a decrease in intraspecific competition in offshore areas and an increase in predation risk in shallow waters (Van Keeken et al. 2007). Another explanation, which is endorsed by fishermen, is that bottom trawling “farms the sea” (Rijnsdorp and Van Beek 1991). The idea behind this is that ploughing the seabed with heavy beam trawls increases the production of the small benthos that flatfish feed on by removing the large fauna that small benthos compete with over food and space. Benthic production is the amount of biomass that is generated by benthic invertebrates in a year and therefore determines the amount of food that becomes available for higher trophic levels. According to this hypothesis, the reduction of fishing effort in the plaice box has led to a decrease in bottom disturbance, an increase in the abundance of large-bodied invertebrates, and a concordant reduction in the production of flatfish food. Aggregation of juvenile plaice in the habitats with the highest production of food will then result in a redistribution to the heavily trawled areas outside the plaice box (Rijnsdorp and Vingerhoed 2001; Grift et al. 2004; Van Keeken et al. 2007). Evidence for aggregation at the scales we examine in this paper has not been studied for plaice, but has been found for Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) in the North Sea (Blanchard et al. 2005; Hiddink et al. 2005).

Previous studies have shown that bottom trawling has a negative effect on the total production of benthic invertebrate communities (Jennings et al. 2001; Hermsen et al. 2003; Hiddink et al. 2006b). The abundance of large invertebrates is strongly reduced by chronic trawling disturbance because of their slow life history (Jennings et al. 2001), and models suggest that reduced competitive interactions between these large invertebrates and small invertebrates may lead to an increase in the abundance of the latter (Duplisea et al. 2002). Plaice diets consist primarily of these small infaunal invertebrates, in particular polychaetes and to a lesser extent bivalves (Wyche and Shackley 1986; Piet et al. 1998; Rijnsdorp and Vingerhoed 2001). Therefore, the production of plaice food may have decreased in the plaice box when trawling effort was reduced.

In the current study, we explore the hypothesis that a reduction in trawling disturbance in the plaice box had a negative impact on the production of food for plaice by using an established size-based model of invertebrate communities (Hiddink et al. 2006b). Here, we assess the size range of food items taken by plaice from stomach content analysis. The size-based model is then used to predict the production of the prey of plaice inside and outside the plaice box. Most studies to date that have considered MPAs as fisheries management tools have examined the effects of MPAs on fish populations through population dynamics and dispersal. The current study is one of the first to consider the effect of an MPA on the trophic ecology of a commercial fish species. Understanding the impact of bottom trawl fisheries on the production of their food for commercial fish is of vital importance when designing and evaluating the utility of MPAs.

## Materials and methods

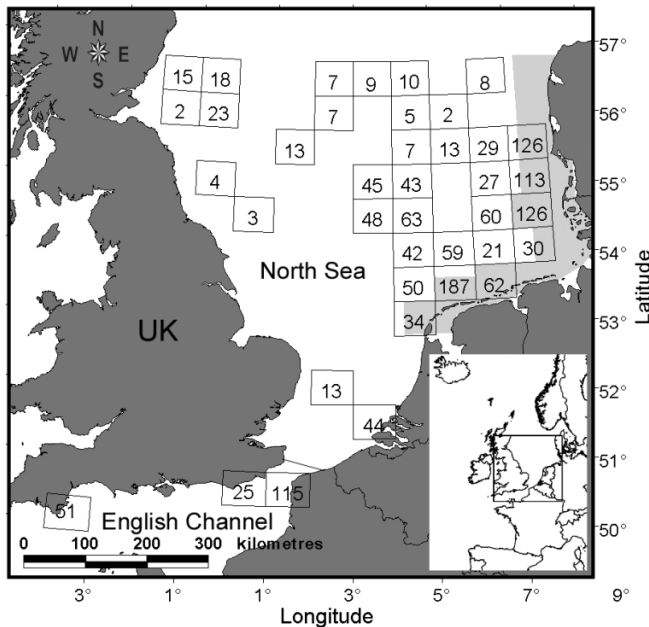
In this paper, we estimate food availability for plaice using a model, rather than by examining empirical data on plaice diet, for several reasons. Direct comparison of the diet of plaice is unlikely to be productive when trying to assess differences in food availability between locations when fish show density-dependent habitat selection and distribute themselves over food resources according to the ideal free distribution (Fretwell and Lucas 1969; Shepherd and Litvak 2004). The ideal free distribution dictates that the fish are distributed in a way that the same amount of food is available for each fish. In this case, no differences in the diet between fish inside and outside the MPA would be expected, and a previous study has shown that no such differences exist (Rijnsdorp and Vingerhoed 2001). Currently, no large-scale data on the abundance of benthic invertebrates for the plaice box and surrounding area exists, and the little data that exists does not allow separation of benthic communities into size classes and is therefore unsuitable for our analysis. Ideally, we would manipulate trawling effort in experimental areas in and outside the plaice box and record the response of benthic communities to these manipulations. However, such large-scale manipulations of fishing effort are currently not within our reach. For these reasons, we tackle our question by combining general diet data with a model that predicts the impact of trawling on benthic communities. This approach can test the hypothesis that changes in benthic production explain changes in the distribution of juvenile plaice, but does not test or reject alternative hypotheses. It should therefore be seen as a starting point for future modelling and empirical studies on the indirect effects of trawling and MPAs.

### Plaice stomach contents

Plaice were collected for stomach content analysis in the North Sea (NS) and the English Channel (EC) (Fig. 1). Plaice were assigned to 5 cm length classes. NS samples were collected in 1996 and used in a separate previous analysis (Rijnsdorp and Vingerhoed 2001). In short, stomachs of plaice were collected inside and outside the plaice box on several cruises from April to September 1996 using beam trawls. In total, 1337 stomachs containing food were sampled. More details of the sampling methods are given in Rijnsdorp and Vingerhoed (2001).

Plaice stomachs ( $n = 222$ ) were collected from 11 stations in the EC in August 2002. Stomachs were preserved in 8% buffered formalin. The sampling protocol is described in more detail by Hinz et al. (2006). The abundance and wet weight (WW) of all dry-blotted prey was recorded and assigned as soft or hard. “Soft” are soft-bodied animals like polychaetes, and “hard” are animals with a hard exoskeleton like bivalves, echinoderms, and crustaceans. Unidentified remains were ignored in the analysis (EC: 5.2% by weight; NS: <1% by weight). The digestive state and the level of intactness of prey items were not recorded, and this will have caused an underestimate of the weight of prey (Hyslop 1980). All individual food items in the stomach were assigned to  $\log_2$  weight (g WW) classes. The classes are reported as the lower end of the class interval.

**Fig. 1.** The number of plaice (*Pleuronectes platessa*) stomachs sampled per ICES (International Council for the Exploration of the Sea) rectangle in the North Sea (data from Rijnsdorp and Vingerhoed 2001) and the English Channel. The extent of the plaice box is indicated by grey shading.



### Plaice abundance – benthos abundance relationships

The abundance of plaice was related to the biomass of infaunal invertebrates using samples collected on nine stations in the EC in August 2002. At each station, three–five 0.1 m<sup>2</sup> Day grabs were taken and sieved over a 1 mm mesh. Animals were sorted to species and wet-weighted individually after blotting. The total biomass of invertebrates <0.5 g WW·m<sup>-2</sup> was calculated. Plaice abundance was estimated in daylight hours using a 4 m beam trawl fitted with a chain matrix and an 82 mm diamond mesh cod end with a 40 mm square mesh liner. Four tows of 20 min duration were made at each site at speed of 4 kn (1 kn = 1.853 km·h<sup>-1</sup>). Details of the sampling stations and methodology are given in Hinz et al. (2006) and Shucksmith et al. (2006).

### Benthos model

We used a size-based model of the response of soft-sediment benthic communities to trawling disturbance that has been validated with extensive field data to examine the large-scale impact of trawling disturbance on benthic production. Details of the model are given in Duplisea et al. (2002) and Hiddink et al. (2006b). In summary, the model contains 32 state variables in two faunal groups (soft and hard macrofauna): 16 for soft (1.9–500 mg) and 16 for hard (50 – 60 000 mg). At the same size, soft have life-history characteristics that allow them to grow faster than hard. Duplisea et al. (2002) give the life-history parameters for soft and hard in all size classes. Soft and hard were assumed to be in competition over food or space (Wilson 1990). Growth of the population biomass in each body mass – organism type compartment is modelled by modifying Lotka–Volterra competition equations to give

the population biomass flux for a compartment. The interaction between habitat type and trawling effects is modelled by including relationships between growth, mortality, and the environment in the model. Thus, sediment type affects trawling mortality, sediment erosion rates affect natural mortality, the effect of bed shear stress modifies population growth rate, and the chlorophyll *a* content of the sediment affects carrying capacity. The interaction of organisms with the environment is independent of body type and depends solely on their life-history parameters. As soft- and hard-bodied invertebrates have different life-history parameters in the model, the latter dominate stable habitats and the former prevail in the more dynamic and disturbed habitats. A critical assumption of the benthos model is that there is competition between different size classes of benthic invertebrates. This means that without disturbance large animals out-compete the smaller animals. The impact of plaice predation on benthic biomass was not considered. The model has been validated using benthic biomass and production estimates from 33 stations subject to a range of trawling frequencies in four areas in the NS. For a detailed description of the model, validation, and the environmental data sets that were used, see Hiddink et al. (2006b). The model was run to equilibrium in 1500 time steps of 30 days for each individual cell in the NS, assuming fishing effort was constant over this period.

Benthic production was modelled for 9 km<sup>2</sup> cells in the plaice box ( $n = 2461$ ) and a reference area within 50 km of its borders ( $n = 2925$ ). These areas are comparable, but not identical, in environmental conditions. Sediment composition was particularly divergent, with mud and muddy sand covering 34% of the area outside the plaice box and only 3% inside the plaice box. Average depth was 22 m inside the plaice box and 35 m in the adjacent area. Apart from trawling frequency, none of the environmental parameters showed a sudden change that coincided with the boundary of the plaice box. To the north (56°N) and east (8°E), the modelled area was limited by the availability of environmental data.

### Trawling effort

Trawling frequency was calculated from European Community Satellite Vessel Monitoring System data of Dutch beam trawl vessels and raised to the total fishing effort of the Dutch fleet (for more details see Dinmore et al. 2003; Hiddink et al. 2006b). To distinguish fishing from other activities (e.g., steaming), this approach uses the speed of the vessel and knowledge on the range of speeds per gear type at which fishing is conducted (Piet et al. 2007). As this approach is not perfect and the results of this study are sensitive to spurious fishing registrations, notably in the plaice box, we added another filter and removed all registrations of the larger vessels (>300 hp) that are not allowed to fish in the box. These registrations were generally found on routes to and from fishing ports and were therefore considered unlikely to represent illegal fishing. Trawling frequency was expressed as the number of times each 9 km<sup>2</sup> grid cell was swept each year. Although there is interannual variation in fishing effort, we used the mean trawling frequencies for the period 2000–2004 and assumed these are representative for the most recent period. To check the sensitivity of our

**Table 1.** The six most abundant (by weight) prey items in plaice *Pleuronectes platessa* stomachs from the English Channel and North Sea.

Species	Phylum	Fraction by weight
<b>English Channel</b>		
<i>Lanice conchilega</i>	Annelida	0.43
<i>Ensis arcuatus</i>	Bivalvia	0.07
<i>Nephtys</i> spp.	Annelida	0.05
<i>Amphiura</i> spp.	Echinodermata	0.04
<i>Echinocardium cordatum</i>	Echinodermata	0.03
<i>Notomastus latericeus</i>	Annelida	0.03
Total		0.64
<b>North Sea</b>		
<i>Pectinaria</i> spp.	Annelida	0.16
<i>Nereis</i> spp.	Annelida	0.14
<i>Ensis</i> spp.	Bivalvia	0.10
<i>Spisula</i> spp.	Bivalvia	0.08
<i>Liocarcinus holsatus</i>	Crustacea	0.06
<i>Upogebia</i> spp.	Crustacea	0.05
Total		0.59

conclusions to the trawling effort estimates, we corrected the Dutch trawling effort data to represent international (including The Netherlands) and historic trawling regimes (1990–1995) using International Council for the Exploration of the Sea (ICES) fishing effort data per ICES rectangle, assuming that the small-scale effort within the rectangles remained the same (Hiddink et al. 2006a). The Dutch fishing effort is therefore a subset of the international fishing effort. This resulted in four different effort estimates: Netherlands 2000–2004, International 2000–2004, Netherlands 1990–1995, and International 1990–1995. The years 1990–1995 are considered most representative of the period in which the distribution of juvenile plaice shifted to more offshore areas. The Dutch beam trawl fleet represented about 75% of the international trawling effort in the plaice box from 2000 to 2004 (Van Keeken et al. 2007).

### Environmental data

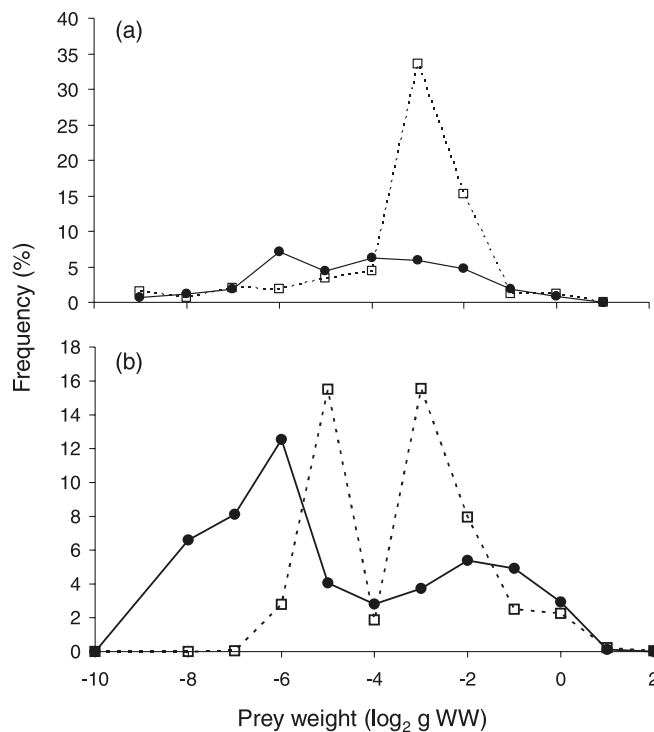
The sources of habitat data are described by Hiddink et al. (2006b). Additional seabed sediment composition data were obtained for the German Bight (Figge 1981) and for Danish waters (Bundesanstalt für Bodenforschung and Unesco 1970).

## Results

### Stomach contents

The most dominant prey of plaice in the EC and the NS were several species of infaunal polychaetes (Table 1). Very few prey over 2 g WW ( $\log_2$  class 0) and below 4 mg WW ( $\log_2$  class -8) were found in plaice stomachs (Fig. 2). In the EC, most prey were found in the soft -3  $\log_2$  weight class (125–250 mg WW). In the NS, the soft-bodied fauna showed a bimodal frequency distribution, with many prey items in the -5 (31–63 mg) and -3 (125–250 mg WW)  $\log_2$  weight classes. This bimodal distribution was caused by the

**Fig. 2.** Frequency distribution of prey in plaice (*Pleuronectes platessa*) stomach content per  $\log_2$  weight class (g wet weight, WW): (a) English Channel, (b) North Sea. Circles and solid lines represent hard-bodied infauna; squares and broken lines indicate soft-bodied infauna.



high abundance of the polychaete *Magelona* spp. in the -5 size class and by the high abundance of the polychaete *Pectinaria* spp. in the -3 size class. Most hard-bodied fauna in the stomachs weighed between 4 and 31 mg ( $\log_2$  weight classes -8 to -6).

Small plaice ingested smaller prey than large plaice; the modal size of prey in the stomach was significantly positively related to plaice length class, although only a small fraction of the observed variation in prey weight was explained by plaice length ( $R^2 = 0.20$ ; area:  $F_{[1,1179]} = 158$ ,  $p < 0.001$ ; size class:  $F_{[1,1179]} = 150$ ,  $p < 0.001$ ). At the same size, plaice ingested smaller prey in the EC than in the NS. Juvenile plaice (up to 25 cm, 1–2 years old) primarily ingested prey in the -4 to -3  $\log_2$  size class (62.5–250 mg). In both the NS and the EC, soft-bodied invertebrates dominated the stomach contents of 15–25 cm plaice by weight (EC = 64%, NS = 60%).

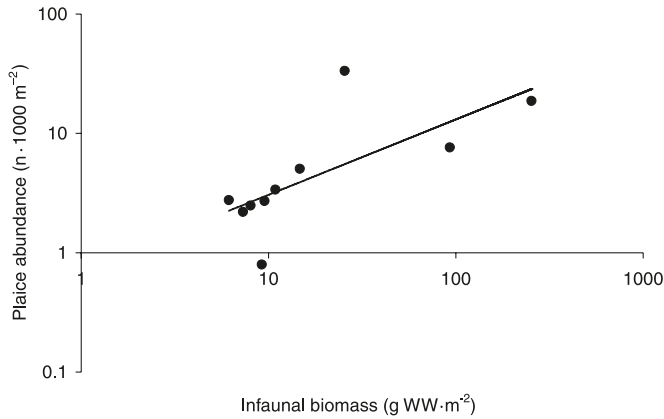
### Relation between plaice abundance and benthic biomass

In the EC, plaice were more abundant on stations with a high biomass of small benthic invertebrates (Fig. 3,  $R^2 = 0.50$ ,  $F_{[1,8]} = 8.11$ ,  $p = 0.021$ ).

### Model predictions

The modelled response of production to trawling was very similar inside and outside the plaice box (Fig. 4). Total production of the whole benthic community was highest without trawling, but production of animals <0.5 g peaked at trawling frequencies of 0.25 year<sup>-1</sup>. The production of small (<500 mg) soft- and hard-bodied invertebrates reacted dif-

**Fig. 3.** Relationship between plaice (*Pleuronectes platessa*) abundance and food availability in the English Channel.



ferently to trawling disturbance (Fig. 4). The production of hard-bodied invertebrates decreased strongly with trawling to virtually nothing at a trawling frequency of 0.5 year<sup>-1</sup>. Production of soft-bodied invertebrates was low at very low trawling frequencies, but increased to a maximum at trawling frequencies of 0.5–1 year<sup>-1</sup> and decreased slowly with further increasing trawling frequencies.

Trawling effort was much higher outside than inside the plaice box and was particularly intense in the southeastern NS outside the boundary (Fig. 4a and Fig. 5a). Typical international trawling frequencies in the plaice box (<0.5 year<sup>-1</sup>) resulted in a high production of hard-bodied invertebrates and a low production of soft-bodied invertebrates (Fig. 4). International trawling frequencies in the reference area around the plaice box (>2 year<sup>-1</sup>) resulted in a maximal production of soft-bodied invertebrates, but a low production of hard-bodied invertebrates.

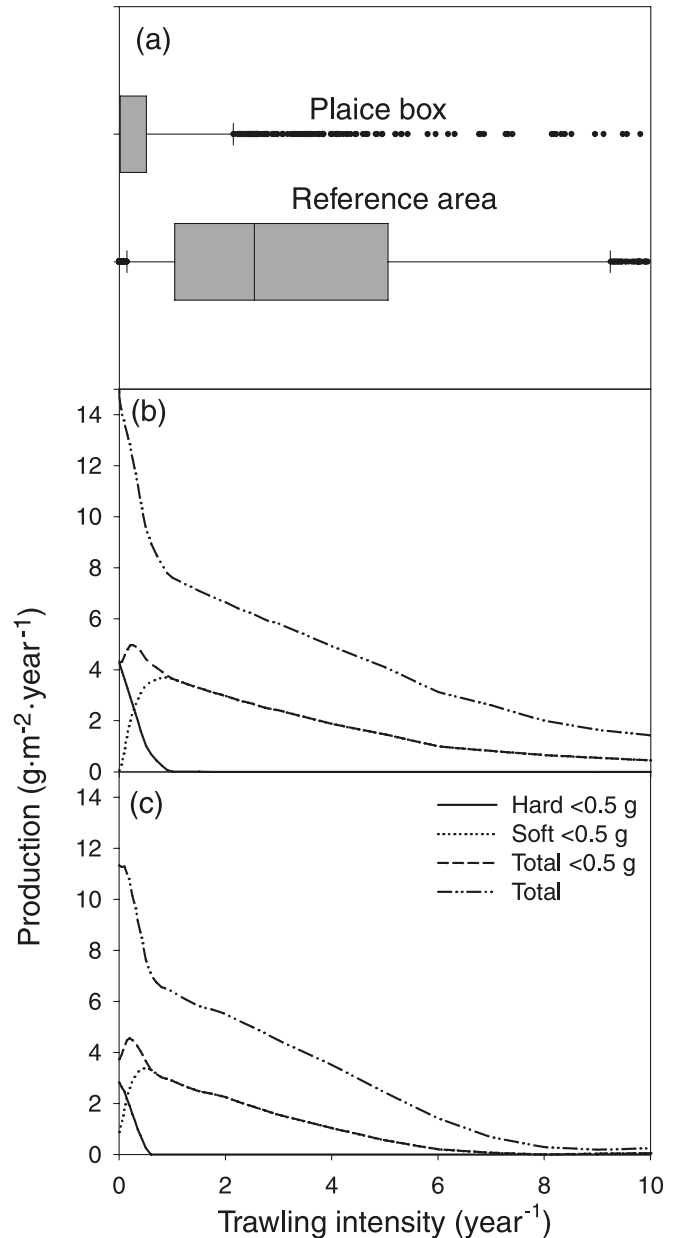
The modelled production of small, soft-bodied invertebrates (<500 mg) showed a gradient that coincided with the boundary of the plaice box and was 1.5 to 2 times lower (depending on the effort estimate used) in the plaice box than in the reference area (Fig. 5b, Table 2). Total benthic production (all size classes and both soft- and hard-bodied invertebrates) was much higher than the production of small, soft-bodied invertebrates and was 1.5 to 2 times higher in the plaice box than in the reference area (Fig. 5c).

The effect of different estimates of fishing effort on the relative benthic production inside and outside the plaice box was relatively small (Table 2). For all four effort estimates, total benthic production was higher in the plaice box, while production of small, soft-bodied benthic invertebrates was higher outside the plaice box.

**Discussion**

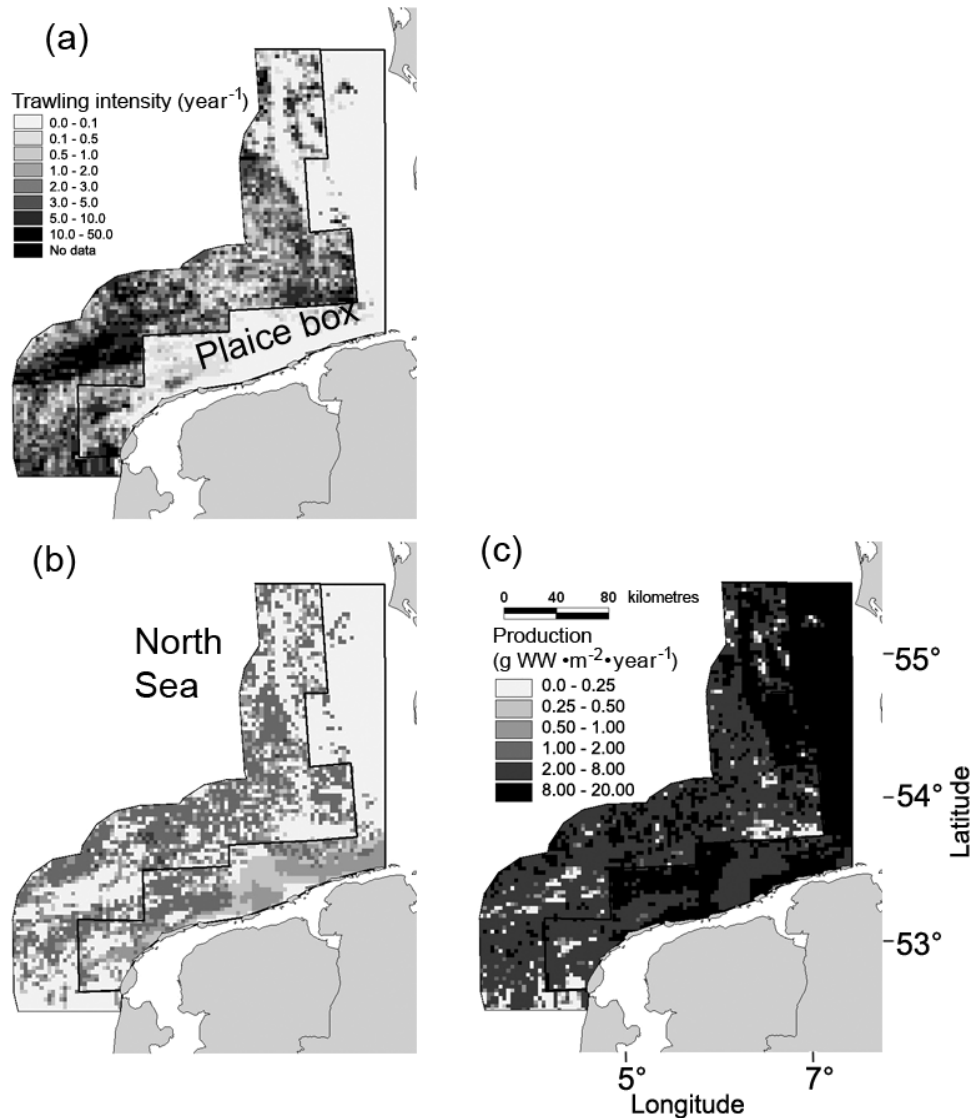
The plaice box has successfully reduced discarding of juvenile plaice within this MPA (Grift et al. 2004). Our analysis provides support for the hypothesis that the reduction of fishing effort in the plaice box has led to a decrease in bottom disturbance and may lead to a concordant reduction of the production of flatfish food in the plaice box. Decreasing trawling disturbance favours large, inedible (for plaice), benthic invertebrates over small, edible invertebrates. As a result of this indirect effect, production of small, soft-bodied

**Fig. 4.** (a) Box and whisker plot of trawling frequency (international effort 2000–2004) in the plaice box and the reference area. The boundaries of the boxes indicate the 25th and the 75th percentiles, the line within the box marks the median, and the whiskers indicate the 90th and 10th percentiles. Outlying points are plotted as individual points; outliers over 10 are not shown. The median for the plaice box is 0. (b) The average modelled relationship between trawling frequency and benthic production in the plaice box. (c) The average modelled relationship between trawling frequency and benthic production in the reference area in the southeastern North Sea.



invertebrates (and food availability for plaice) is predicted to be higher outside the plaice box. These model results thus provide support for the idea that disturbing the seabed with bottom trawls may increase food production for fish species that feed on small invertebrates. These predictions have not been corroborated by empirical results for the plaice box area (although the model has been validated in the southern

**Fig. 5.** Trawling frequency and modelled benthic invertebrate production in and around the plaice box: (a) international trawling frequency 2000–2004; (b) production of small, soft-bodied invertebrates (<500 mg); (c) production of the whole benthic community.



**Table 2.** Average modelled benthic production in and outside the plaice box for four trawling effort estimates.

	Average trawling frequency (year <sup>-1</sup> )		Total production (g·m <sup>-2</sup> )		Production of small, soft-bodied invertebrates (g·m <sup>-2</sup> )	
	Plaice box	Control	Plaice box	Control	Plaice box	Control
Netherlands 2000–2004	0.33	3.00	11.55	7.15	0.36	0.83
International 2000–2004	0.45	3.96	11.27	6.33	0.36	0.69
Netherlands 1990–1995	0.57	4.48	11.25	6.01	0.35	0.64
International 1990–1995	0.93	6.09	10.97	5.22	0.34	0.51

**Note:** Average trawling frequency describes the average trawling frequency in space and indicates the total fishing effort levels in and outside the plaice box in the different scenarios.

NS; Hiddink et al. 2006b), and this means the proposed mechanism may explain observed distribution patterns of juvenile plaice, but not that alternative hypotheses have been rejected (see below). Thus, the positive relationship between plaice abundance and benthic biomass may be the consequence of the redistribution of plaice to maximize their food intake and results in a gradual shift out of the protected area into the areas that remain open to bottom trawling. This

implies that the plaice box was probably not the most appropriate management measure to protect undersized plaice from discarding, as the undersized fish will redistribute so that they reach the highest densities in areas that are fished. The use of other management measures such as a larger mesh size and a decrease of the overall trawling effort could therefore have been more effective tools to achieve a sustainable exploitation of plaice.

The relationship between plaice size and prey size only explained a small fraction of the observed variation in prey sizes. However, over 80% of prey for all size classes of plaice were smaller than 0.5 g. This means that the conclusions of this paper are unlikely to be sensitive to the exact relationship between body weight of plaice and prey size. It also means that although adult plaice eat larger prey than juveniles, they still eat relatively small prey and are therefore unlikely to move inshore to benefit from the increased abundance of large invertebrates there.

Alternative hypotheses that may explain the decline in plaice stocks and the shift in the distribution of juvenile plaice, such as an increase in water temperature due to climate change, a reduction of eutrophication, a reduction in intraspecific competition, or an increase in predation risk in shallow waters (Van Keeken et al. 2007), have not been examined in this study and remain to be tested, either separately or in concert. Water temperature in the NS has increased considerably since the establishment of the plaice box (Perry et al. 2005) and in the plaice box area in particular (Van Keeken et al. 2007) and may play a role in explaining the changes in distribution patterns of plaice.

Even though bottom disturbance by trawling may improve feeding conditions for plaice, bottom trawling can have undesirable effects on the ecosystem and other commercial fisheries (e.g., on fish species that feed on large invertebrates, such as Atlantic cod). This paper illustrates that closed areas may not be a suitable management measure to protect juvenile plaice, but does not suggest that bottom trawling has a net positive effect on this species, the ecosystem, or the exploitation in general. The net effect of bottom trawling disturbance on plaice populations depends on the balance between the positive effect on food supply of juvenile plaice versus the negative effect of increased juvenile bycatch mortality. The decision to create MPAs should therefore be based on an assessment of the impact of the MPA on all components of the ecosystem, as the impact on different ecosystem components can be different.

Over time, there seems to have been a shift in the south-eastern NS from fish that eat large benthic invertebrates (such as Atlantic cod and rays) to ones that eat small worms (such as plaice, dab (*Limanda limanda*), and common sole (*Solea solea*)). It has been well established that the life-history characteristics of large species make them more vulnerable to the effects of exploitation (e.g., Jennings et al. 1999), and as all the large fish tend to eat large food, it is difficult to disentangle the effects of life history and food. Nevertheless, this mechanism could explain that the effect of bottom trawling on the food sources of these animals (negative for species such as Atlantic cod and rays, positive for the small flatfish) contributed to the observed shift in the composition of the fish fauna from large species to smaller, worm-eating species.

A critical assumption of the benthos model for the current study is that there is competition between different size classes of benthic invertebrates and that without disturbance large animals out-compete the smaller animals. There are good indications that competition among benthic invertebrates exists (for an overview see Wilson 1990). The correspondence between observed and modelled size spectra in the NS indicates that our model realistically reproduces

these interactions (Duplisea et al. 2002). To date there is no conclusive empirical evidence that production of small benthic invertebrates increases with trawling disturbance, but some studies suggest that such a release from competition due to trawling disturbance may occur (Jennings et al. 2001; Tanner 2003). However, the reason why trawling studies do not commonly find an increase in small benthos with increasing trawling may be that the range of trawling frequencies that is sampled often does not include many (or any) stations with low trawling frequencies ( $<0.3 \text{ year}^{-1}$ , even though this is often in the most common trawling frequency category (Hiddink et al. 2007)); therefore, the power to detect a hump-shaped relationship is low (e.g., see fig. 5c in Hiddink et al. 2006b). The current study therefore indicates that it is important that future studies include low disturbance frequencies and that the response of different size classes of animals to disturbance is analysed separately.

Some of the areas in which plaice were collected for stomach content analysis were heavily trawled, which implies that large, hard-bodied benthos may not have been available as prey. This means that the diet of plaice in our analysis may be biased towards small, soft-bodied prey. However, as Rijnsdorp and Vingerhoed (2001) found no differences between the diet of plaice in and outside the plaice box, the diet as recorded in this study probably reflects the true preference of plaice.

Understanding how habitat selection relates to food abundance is central to predicting the effect of closed areas on the distribution of plaice. Little is known about the habitat selection of plaice  $>1$  year old, but there are some indications that plaice aggregate in locations with good feeding conditions (Hinz et al. 2006). In the EC, adult plaice were most abundant at locations where tubeworms (which were abundant in the stomachs) were abundant (Shucksmith et al. 2006). In another gear restriction area in the EC, large plaice were less abundant and experienced slower growth rates than in an adjacent open access area (Blyth-Skyrme et al. 2006). Future studies could elucidate the role of food abundance in determining plaice distribution by examining plaice abundance (Hinz et al. 2003), abundance of relevant food sources, and plaice condition (e.g., as in Hiddink et al. 2005).

In this study, we implicitly assumed that the availability of benthic food sources affects the distribution of the plaice population, and the negative impact of plaice predation on benthic biomass was not considered. Some fish predators exert a top-down control in benthic food webs (Worm and Myers 2003), and it has been argued that changes in predation pressure by fish in the North Sea due to their exploitation have caused changes in the benthic invertebrate community (Frid et al. 1999; Heath 2005). In such a situation, the current benthic model would not provide accurate predictions of the level of benthic production because fish predation is likely to affect the biomass and size distribution of the benthos. Adding a predator to the benthos model may solve this problem.

Our results support the hypothesis that bottom disturbance may improve the feeding conditions for small-mouthed commercial fish species, such as plaice, that feed on small-sized benthic invertebrates. Bottom trawling may lead to an increase of small, soft-bodied organisms at the expense of

large fauna, and plaice mostly eat these smaller, soft-bodied species. If juvenile plaice aggregate at the locations with the best feeding conditions, they will follow the fishery, which leads to the conclusion that the plaice box may not have been the most appropriate management measure to protect undersized plaice from discarding.

The general implication of this study is that in fisheries management, MPAs are not necessarily the preferred tool to achieve a specific management objective and that when deciding which tool(s) to use, the ecology of the target species should be taken into account.

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