

Impact of a large-scale area closure on patterns of fishing disturbance and the consequences for benthic communities

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Seasonal area closures of fisheries are primarily used to reduce fishing mortality on target species. In the absence of effort controls, fishing vessels displaced from a closed area will impact fish populations and the environment elsewhere. Based on the observed response of the North Sea beam trawl fleet to the closure of the “cod box” and an existing size-based model of the impacts of beam trawling, we predict the effects of seasonal area closures on benthic communities in the central North Sea. We suggest that repeated seasonal area closures would lead to a slightly more homogeneous distribution of annual trawling activity, although the distribution would remain patchy rather than random. The increased homogeneity, coupled with the displacement of trawling activity to previously unfished areas, is predicted to have slightly greater cumulative impacts on total benthic invertebrate production and lead to localized reductions in benthic biomass for several years. To ensure the effective integration of fisheries and environmental management, the wider consequences of fishery management actions should be considered *a priori*. Thus, when seasonal closures increase the homogeneity of overall disturbance or lead to the redistribution of trawling activity to environmentally sensitive or previously unfished areas, then effort reductions or permanent area closures should be considered as a management option. The latter would lead to a single but permanent redistribution of fishing disturbance, with lower cumulative impacts on benthic communities in the long run.

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Introduction

Temporarily closed areas may be used to protect target stocks from mortality at a specific stage of the life history, such as when a species aggregates to spawn (Halliday, 1998; Horwood *et al.*, 1998). The value of temporarily closed areas as a management tool has to be assessed on a case-by-case basis, and depends on the biology of the target species and the dynamics of the fishery. It is well recognised that temporary area closures lead to effort displacement if they are not accompanied by catch or effort controls (Rijnsdorp *et al.*, 2001). From the perspective of stock management, effort displacement may be undesirable because it may increase mortality on other species or life history stages of the target species outside the closed area (Fogarty and Murawski, 1998; Horwood *et al.*, 1998).

With the advent of the ecosystem approach to fisheries management, it is necessary to account for environmental consequences of management actions. When fishing grounds are closed, vessels may disperse more widely (Fogarty and Murawski, 1998; Frank *et al.*, 2000), to search for profitable sites, and to escape the increased competition from vessels congregating along the boundaries of the closed area (Rijnsdorp *et al.*, 2000). Skippers may also postpone their fishing activities until later in the season, when their regular grounds reopen (Rijnsdorp *et al.*, 2001).

Trawling disturbance affects the structure and diversity of benthic communities (Jennings and Kaiser, 1998; Hall, 1999; Kaiser and de Groot, 2000). Large, slow-growing species are particularly vulnerable to trawling disturbance (Engel and Kvitek, 1998; Kaiser *et al.*, 2000; Bergman and van Santbrink, 2000a), while smaller individuals and species suffer lower mortality rates (Gilkinson *et al.*, 1998).

Differential vulnerability to trawling leads to lower biomass and production of communities in heavily trawled areas and a dominance by smaller, faster growing individuals and species (Jennings *et al.*, 2001).

Although there are relatively few restrictions on the areas that can be fished by beam trawlers, the distribution of fishing activity is patchy on many scales (Rijnsdorp *et al.*, 1998; Jennings *et al.*, 1999). For instance, more than half the North Sea is not fished by the beam trawl fleet and yet small areas in the south-eastern part are trawled more than 10 times per year (Rijnsdorp *et al.*, 1998). Only within small areas of 1×1 n miles is fishing activity randomly distributed. The patchiness of trawling disturbance has an important bearing on the persistence of benthic animals. Both empirical and theoretical studies have shown that the relative impacts on benthic production are greater when areas are trawled for the first time or trawled infrequently (Duplisea *et al.*, 2002). Thus, untrawled areas can support rich communities that cannot persist elsewhere. Duplisea *et al.* (2002) developed a size-based model to assess the impacts of trawling on benthic production. For invertebrates in the range of 1 μ g to 80 g (shell free wet weight), the model predicted that larger species could only survive in some fishing grounds because trawling disturbance was patchy.

Area closures will be most effective in areas where effort is concentrated, and therefore involve major effort displacement. When the closures end, effort will be redistributed again, resulting in necessarily greater homogeneity of effort over a longer period than if no closure had been enforced. Since many fleets from many nations may be affected by area closure, an assessment of the ecosystem consequences requires detailed information (preferably at scales of 1×1 n miles if effort at this scale is randomly distributed) on the spatial and temporal distribution of all fishing vessels over large sea areas. Such information was previously not available for international fleets operating in the central North Sea. However, with the advent of the European Community Satellite Vessel Monitoring System (VMS), introduced on 1 January 2000, it has been possible to track the position of the whole North Sea >24 m beam trawl fleet at 2 h intervals.

A recent example of a temporary area closure in the North Sea is the “cod box” of 2001. This closure was imposed because the cod (*Gadus morhua*) stock was considered to be outside safe biological limits and at serious risk of collapse (Cook *et al.*, 1997; ICES, 2001). Accordingly, the EU Council asked the Commission to establish a plan to protect the cod stock during the spawning season and to deter discarding and misreporting of cod in all fisheries. The resultant Cod Recovery Plan included (1) closed areas, (2) technical measures and (3) comprehensive proposals for longer-term measures. Stage 1 (Commission Regulation (EC) No 259/2001) came into force on 14 February 2001. An area of more than 40 000 square miles, almost a fifth of the North Sea, was closed to fisheries likely to catch cod for 75 days. The areas closed

included some of the main fishing grounds for the international beam trawl fleet (Jennings *et al.*, 1999), and led to the displacement of large beam trawlers to adjacent areas (Rijnsdorp *et al.*, 2001).

Our aim is to predict the effects of area closure on fishing effort distributions and the production of benthic communities. In addition, we compare the effects of observed effort distributions with the effects of uniformly or randomly distributed effort on the same fishing grounds and determine how the spatial scale of analysis affects the results. Our analyses focus on the response of the international beam trawl fleet to the cod box closure, as assessed by satellite monitoring.

Methods

Study area

The study area extends over 3° latitude and 5° longitude in the central North Sea (Figure 1), which is fished by beam trawlers and includes part of the 2001 cod box. Since effort distribution was examined at scales of 1×1 to 8×8 n miles, we trimmed the area to 176×176 n miles by excluding the northern and eastern boundaries. Within the area, depth ranges between 25 and 100 m. Sand, sandy gravel and muddy sand are the dominant sediment types, with

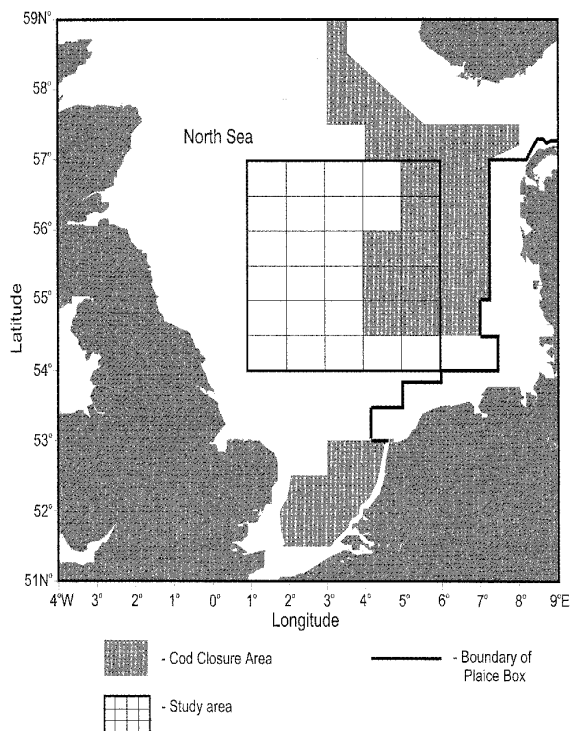


Figure 1. Location of the study area with ICES rectangles (0.5° latitude by 1° longitude) relative to the “cod box” and “plaice box” (east of the marked boundary).

intermittent patches of shell fragments and silt (British Geological Survey and Geological Survey of Denmark and Greenland, unpublished). The area excludes the “plaice box”, established in 1989 to reduce fishing mortality on young plaice and prohibited for large beam trawlers (Piet and Rijnsdorp, 1998).

Estimates of trawling disturbance

Trawling intensity was determined using records from the VMS. From 1 January 2000 onwards, all EC fishing vessels over 24 m were required to report their location, via satellite, to monitoring centres in their flag states, at 2-h intervals. The only exception is made for vessels that undertake trips of <24 h or fish exclusively within territorial waters (Dann *et al.*, 2002). Since not all member states were receiving full records during the first months of operation, we only used data from 1 July 2000 to 30 June 2002 in the analysis.

The VMS does not indicate whether a vessel is fishing when it sends positional data, but the speed of a vessel can be derived from two consecutive records. Accordingly, the raw data were gated to eliminate vessels travelling at speeds greater than 8 knots. These vessels were assumed to be steaming rather than fishing. Some vessels were also transmitting signals more frequently than once every 2 h from November 2001, and these additional signals were excluded.

Patterns of fishing effort were assessed at scales of 1×1 , 2×2 , 4×4 and 8×8 n miles. Satellite location records were assigned to each square for the periods from 1 July 2000 to 30 June 2001 (including cod box closure from 14 February 2001 to 1 May 2001) and 1 July 2001 to 30 June 2002 (reference period). The mean trawling frequency (F) in each square was calculated as:

$$F = \frac{2RD}{A},$$

where R is the number of location records received from the square in 1 year, D is the area disturbed per hour trawling (assuming all beam trawlers tow 2×12 m wide beams at 6 knots) and A is the area of the square. Thus we assigned the 2 h of trawling associated with one VMS record to a single square.

Effects on benthic production

The effects of the frequency of trawling disturbance on benthic biomass and production were assessed with a size-based model (Duplisea *et al.*, 2002). The model contained 37 state variables defined on the basis of body size and faunal group (five meiofauna, 16 soft-bodied macrofauna and 17 hard-bodied macrofauna). The growth of population biomass in each compartment was modelled independently using modified Lotka–Volterra competition equations, under the assumptions that (1) soft- and hard-bodied

macrofauna were in competition, and (2) meiofauna did not compete with either macrofauna group. The development and validation of the model is described in detail by Duplisea *et al.* (2002).

Model simulations were run to a steady state for 1000 time steps with a step size of 30 days. Because it is a steady-state model, we assume that patterns of effort distribution or redistribution observed in a single year would apply in subsequent years. The total annual production ($\text{g m}^{-2} \text{year}^{-1}$) of infaunal invertebrates >0.04 g wet weight was predicted for each year using 21 values of trawling frequency. Production was also calculated on the basis that (1) trawling disturbance was uniformly distributed among squares and (2) that trawling disturbance was random (modelled with a Poisson distribution).

Results

When VMS data for the closure period were excluded from the analysis, the gross distribution of trawling activity was similar in the year of the closure and the reference year (Figure 2a, c). When data for the closure period were included (Figure 2b, d), an area to the west of the cod box was more intensively trawled in the year of closure (Figure 2b; 56° – 57° N, 2° – 4° E) than in the reference year. Figure 3 shows patterns of trawling effort by 75-day periods in the 2 years relative to the closure in 2001. Effort was clearly displaced to the west of the cod box during closure and moved in again afterwards (Figure 3a), while such a response did not occur in 2002 (Figure 3b). Outside the period of closure, effort distribution was broadly similar in the 2 years.

While effort was more widely distributed in the year of the cod box closure, total trawling effort was lower (Table 1). However, in both years, approximately 60% of the area was not fished at the scale of 1 n miles grid (Figure 4), which is double the proportion expected if the effort distribution were random. As the scale of analysis increased the proportion of the area that would be considered “unfished” decreased, although even at a scale of 8×8 n miles, around 10% would still be unfished (Figure 4). Because of differences in the number of VMS records in the 2 years (Table 1), we estimated the proportion of the area that was unfished, over and above the random (Poisson) expectation, in each period. In the absence of the cod box closure, 36% was unfished, as opposed to 30% when the cod box was in place.

The analysis of trawling frequencies in 1×1 n miles squares showed that patterns of beam trawling were not random (Figure 5). Approximately 30% of squares were trawled 0.1 – 0.5 times year^{-1} , while almost 70% would be trawled at this frequency if effort were randomly distributed. A greater proportion of squares was trawled at low frequency during the year of cod box closure, reflecting

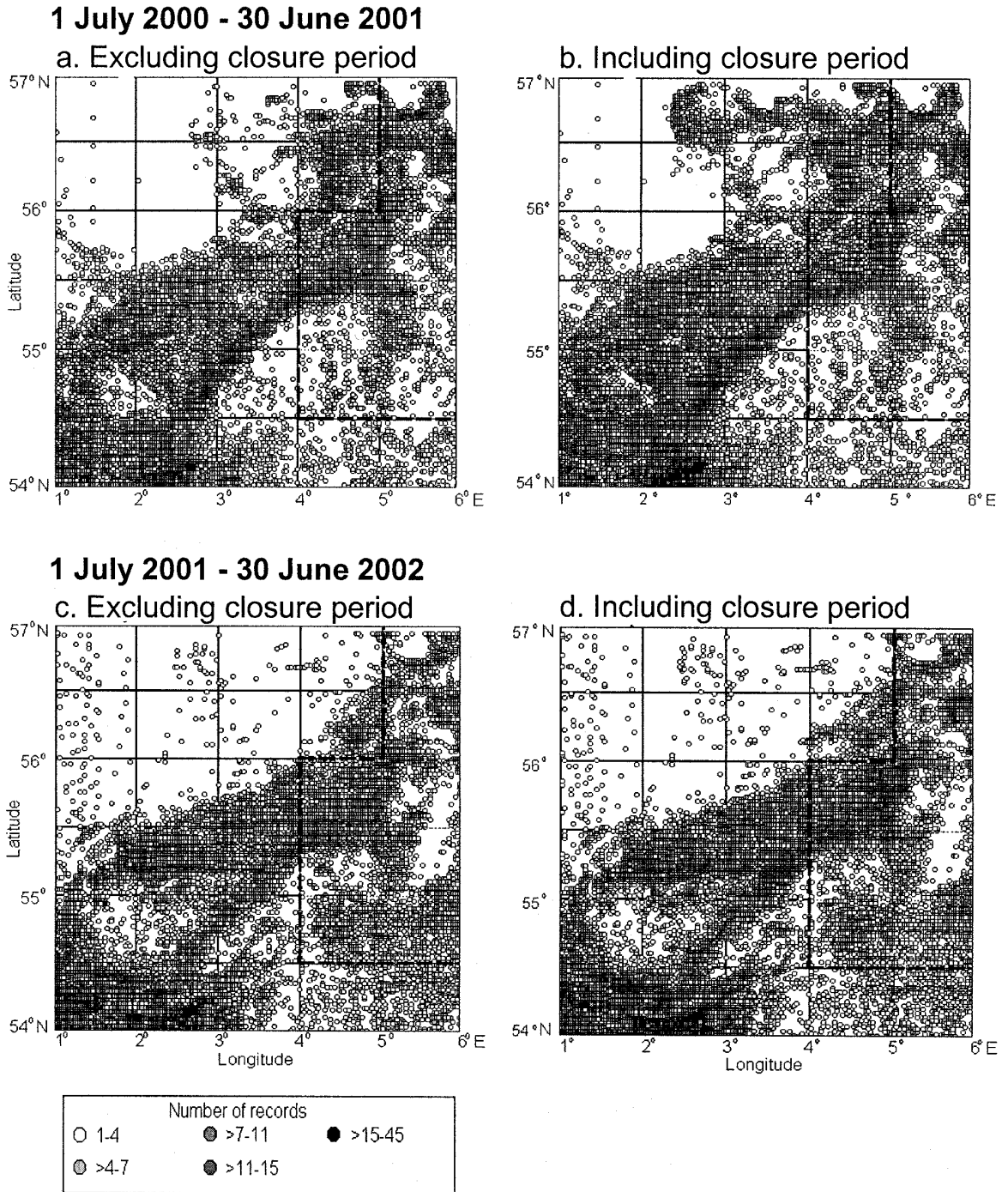


Figure 2. Frequency distribution of VMS records from beam trawlers in the study area: (a) excluding and (b) including VMS records from the closure period in the year from 1 July 2000 to 30 June 2001, and (c) excluding and (d) including VMS records from the closure period in the year from 1 July 2001 to 30 June 2002. The dashed line indicates the western boundary of the “cod box”.

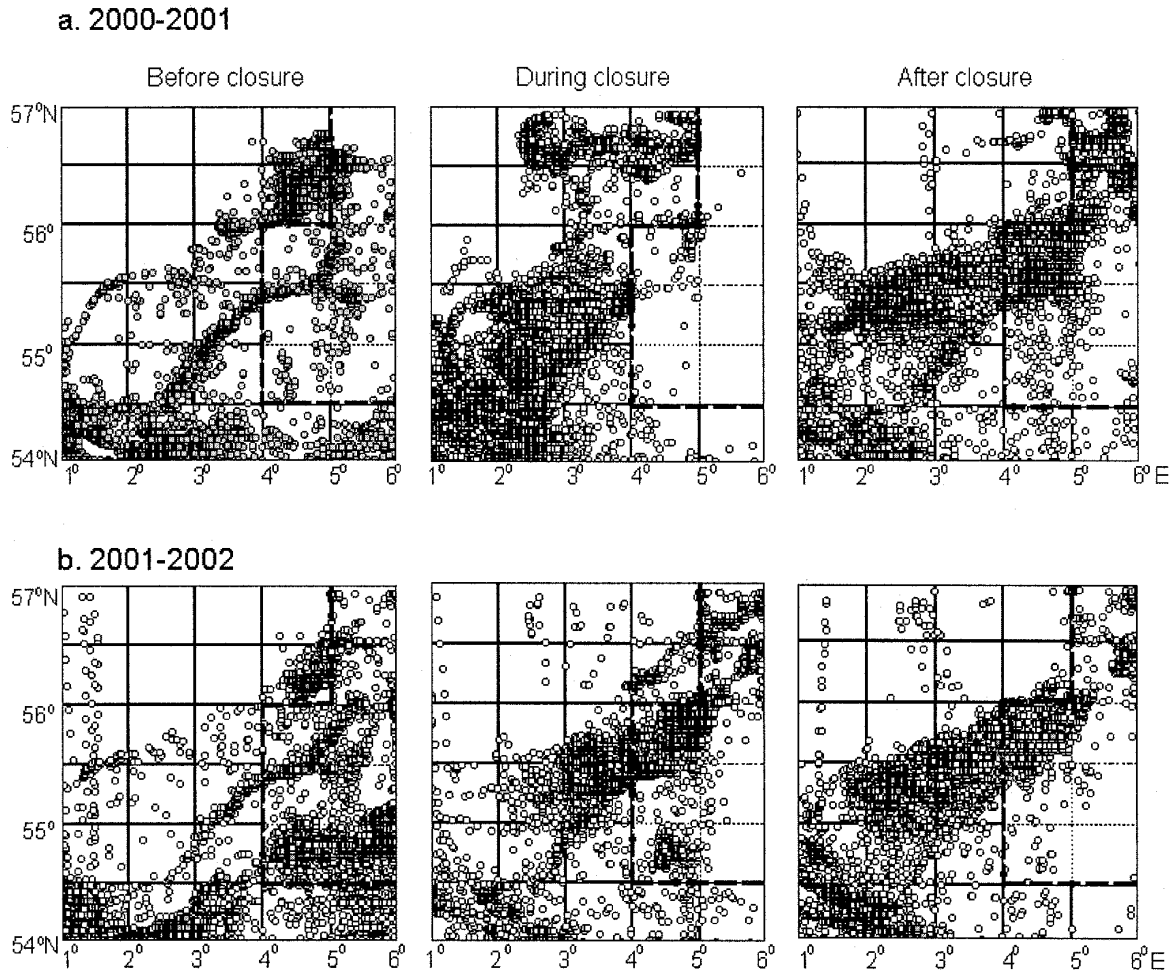


Figure 3. Frequency distribution of VMS records from beam trawlers by 75-day periods in (a) 2000–2001 before, during and after the cod box closure, and (b) 2001–2002 during the same periods.

Table 1. Number of satellite signals received from beam trawl vessels fishing in the study area between 2000 and 2002.

Month	2000	2001	2002
1		1413	2809
2		1143	2341
3		7286	3647
4		4449	3069
5		3230	3354
6		2896	3302
7	1941	3436	
8	3089	3727	
9	5306	4979	
10	3689	5231	
11	2234	4037	
12	1174	2251	
Sum (1/7–30/6)	37850		41883

the redistribution of effort to otherwise unfished areas (Figure 3a).

While the closure led to a small increase in the spatial homogeneity of annual trawling effort, the effort distribution was still far from random. A more pronounced effect was the displacement of effort to previously unfished areas. At the scale of 1 n miles, 25% of the squares were fished in both years (Table 2). However, in 2000–2001 an additional part of the area was newly trawled as a result of effort displacement.

According to the size-based model, production of the benthic infaunal community would decrease with increased trawling disturbance. Based on the observed frequencies of trawling disturbance at a scale of 1×1 n miles, total production was slightly lower when there was an area closure (Table 2). Similar results were obtained at larger scales. At the scale of 1×1 n miles, predicted production was lowest when effort distribution was uniform. However,

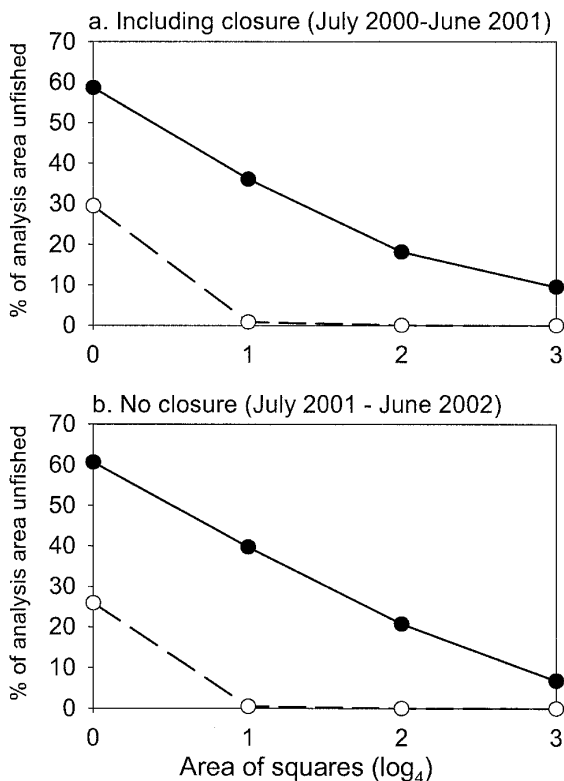


Figure 4. Proportion of the study area that would be considered “unfished” at different scales of analysis from (a) 1 July 2000 to 30 June 2001 and (b) 1 July 2001 to 30 June 2002. The “cod box” area closure took place in the earlier period (a). The continuous line indicates the observed percentage of unfished squares and the broken line indicates the proportion of squares that would be unfished if the same total effort was randomly (Poisson) distributed.

estimated production in both the closure and reference period was higher than production based on a random (Poisson) effort distribution (7 and 10%, respectively; Table 2).

To examine the consequences of effort redistribution, we modelled the recovery time of previously unimpacted communities that were trawled for the first time during the cod box closure. Recovery was measured as the time taken for different components of the benthic fauna to return to 95% of their unimpacted biomass. Simulations of trawling one to four times during the 12-week closure, after running the model to steady state without trawling, suggested that recovery could take up to 10 years for large, hard-bodied macrobenthic organisms (Table 3). This approach assumed that growth and natural mortality were negligible over the 12-week period, and that trawling ceased completely thereafter. The calculated recovery times do not account for immigration effects. Although predicted recovery takes longer at higher levels of disturbance, the first trawl pass caused the greatest reduction in benthic biomass while

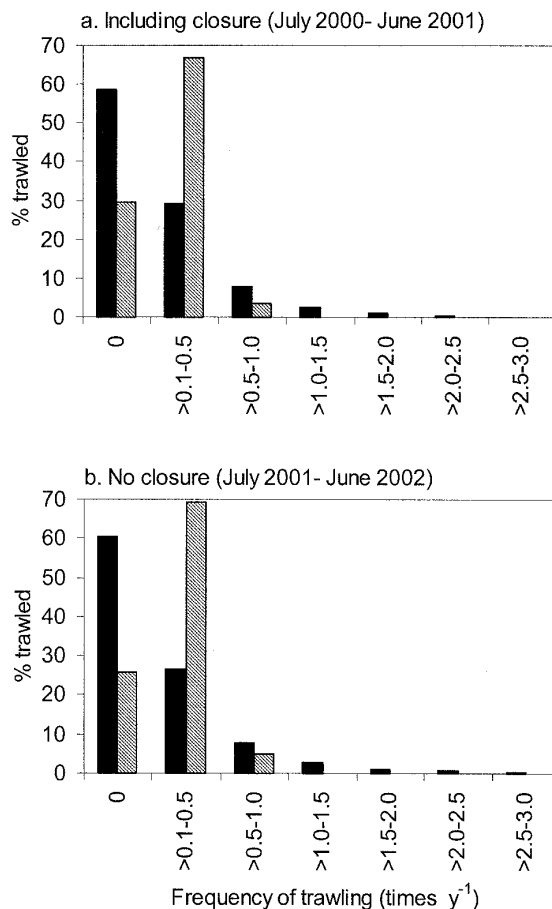


Figure 5. Comparison of observed trawling frequencies (solid bars) at a scale of 1×1 n miles² with the random (Poisson) expectation (shaded bars) from (a) 1 July 2000 to 30 June 2001 and (b) 1 July 2001 to 30 June 2002.

subsequent passes had proportionally less effect. Meiofauna had the fastest recovery of between 2 and 4 months.

Discussion

Imposition of a temporary closed area in the central North Sea led to redistribution of international beam trawling effort. The larger macrofauna would require several years to recover from the impacts of effort displaced to previously unfished areas. Repeated imposition of such a seasonal area closure would lead to small long-term reductions in the mean production of benthic communities. However, while the homogeneity of trawling effort increased in the year of closure, the distribution of effort was still relatively patchy and had less impact on benthic communities than would be expected if effort distribution were uniform or random.

Fishing patterns under normal management regimes are spatially similar from year to year, reflecting the patchiness of suitable fishing grounds and the availability of the target

Table 2. (A) Frequency distribution of squares fished in one or both years in relation to grid scale. (B) Predicted total production (10^6 t year⁻¹) and mean production (g m^{-2} year⁻¹) of benthic infauna >0.04 g wet weight in relation to grid scale given different assumptions about the effort distribution. Predicted changes in production are expressed as percentages relative to the random expectation (observed-random) for each year (small apparent discrepancies are due to rounding).

		Scale of analysis							
		1 × 1 n miles		2 × 2 n miles		4 × 4 n miles		8 × 8 n miles	
(A) Frequency distribution		N	%	N	%	N	%	N	%
Total no. of squares		30976		7744		1936		484	
Fished in both years		7768	25.1	3706	47.9	1385	71.5	422	87.2
Fished only in year 1		5053	16.3	1253	16.2	201	10.4	16	3.3
Fished only in year 2		4447	14.4	965	12.5	150	7.7	16	3.3
Not fished in either year		13708	44.3	1820	23.5	200	10.3	17	3.5
(B) Production		Total	Mean	Total	Mean	Total	Mean	Total	Mean
July 2000 to June 2001 (Area closure)	Uniform	5.43	51.0	5.43	51.1	5.43	51.1	5.43	51.1
	Random	5.58	52.4	5.43	51.1	5.43	51.0	5.40	50.8
	Observed	5.95	56.0	5.75	54.0	5.61	52.8	5.52	51.9
	Obs-Rand (g)		3.5		3.0		1.8		1.1
	Obs-Rand (%)		7.0		6.0		3.0		2.0
July 2001 to June 2002 (reference)	Uniform	5.28	49.6	5.28	49.6	5.28	49.6	5.28	49.6
	Random	5.41	50.9	5.28	49.7	5.28	49.6	5.26	49.5
	Observed	5.98	56.2	5.79	54.5	5.65	53.1	5.53	52.0
	Obs-Rand (g)		5.3		4.8		3.5		2.5
	Obs-Rand (%)		10.0		10.0		7.0		5.0

species, specifically plaice *Pleuronectes platessa* and sole *Solea solea*, for the North Sea beam trawl fleets (Rijnsdorp *et al.*, 1998). However, with the imposition of the cod box closure, beam trawlers were denied access to their favoured grounds and as a consequence, effort was redistributed temporarily to grounds to the west of the closed area. Previous studies of effort displacement resulting from changes to fisheries management regimes are scarce. Pastoors *et al.* (2000) reported on the response of beam trawlers to the closure of the plaice box (Figure 1) in 1989. Fishing effort, while decreasing initially, was largely redistributed to the borders of the box. A study of the immediate effects of the cod box closure by Rijnsdorp *et al.* (2001) showed that in the first week after closure the

number of trips made by beam trawlers to the open grounds immediately adjacent to the closure area had doubled. Much of the effort distribution to the “open north” area reported by Rijnsdorp *et al.* (2001) is equivalent to displacement to the west of our study area.

Because the initial effects of fishing on biomass, production, diversity and trophic structure are the most important ones (Jennings and Kaiser, 1998), displacement of fishing effort to previously unfished areas can have a disproportionate impact on the benthic community. In rarely fished sites, the benthic fauna is more likely to be dominated by organisms suited to a regime of low anthropogenic disturbance, such as fragile free-living large-bodied species or biogenic habitat forming species

Table 3. Predicted recovery times for different groups of benthic organisms to reach 95% of unimpacted biomass (i.e. statistically indistinguishable from unimpacted—see main text) after trawling a previously unfished area 1–4 times during the 12-week cod box closure.

Group	Size range	Pristine B (g m^{-2} wet weight)	F (%)	Recovery time (months)			
				1	2	3	4
Meiofauna	1–200 μg	0.02	0.2	2	3	4	4
Soft macrofauna	1.9–500 mg	2.75	0.2	18	34	40	45
Hard macrofauna	88 mg to 105 g	21.85	0.1	67	92	108	124

which are slow growing and vulnerable to heavy gear (Bergman and van Santbrink, 2000b). If new fishing grounds are explored, these fragile species would suffer high mortality rates from the first trawling event. In the short-term, mortality rates as high as 90% have been recorded for sea urchins and 30–40% for large bivalves (Bergman and van Santbrink, 2000b). The model results suggest that the recovery time for the biomass of large macrofauna, even after just one trawl pass, is about 5 years. This is rather slower than recovery times observed in some empirical studies, but those would include the effects of immigration (Collie *et al.*, 2000). The modelled recovery times of meiofauna are consistent with the observation that these assemblages recover quickly from acute trawling disturbance (Schratzberger *et al.*, 2002). The effects of effort displacement in other fisheries might have even greater consequences than those predicted here. For example, displacement of trawlers from shallow shelf seas to the shelf edge and the deep sea could impact highly diverse and previously undisturbed communities such as biogenic coral reefs (Hall-Spencer *et al.*, 2002).

The temporary closure of the cod box also led to a small increase in the homogeneity of effort distribution over the year. Patchiness is correctly assessed over a whole year because there are significant seasonal (intra-annual) changes in fleet distribution that reflect the migrations of fish populations and the effects of weather conditions. Thus, a snapshot from one season may give a false impression of the true spread of fishing effort. The model showed that the increased homogeneity of effort was likely to lead to a relatively small reduction in benthic production.

Following effort displacement caused by the area closure, the annual distribution of trawling effort was still more patchy than uniform or random. A patchy distribution would not guarantee the preservation of a wide range of undisturbed community types if effort distribution reflected the distribution of specific habitat types. For example, if beam trawlers fished solely on sandy-mud *Arctica islandica* communities, patchiness might make things worse for this particular community. However, while large-scale patterns in effort distribution do reflect the gross distribution of habitat types, there is still much patchiness within habitats. Thus, there are consistent spatial variations in annual trawling effort at scales of a few kilometres even when substrate type does not change (Rijnsdorp *et al.*, 1998; Jennings *et al.*, 2002). These patterns within habitats persist over many years, possibly because skippers store tows yielding large catches in navigational systems and repeat tows that have been proven free of obstructions. Rijnsdorp *et al.* (1998) showed that, within the most heavily trawled ICES areas in the southern North Sea, 15% of the area is trawled less than once a year, and 4% less than once every 5 years. The more sensitive organisms may only survive in these areas because fishing distribution does not change much on annual basis (Duplisea *et al.*, 2002).

Our approach assumes that the size-based model of fishing impacts on production adequately describes the response of the benthic community to trawling disturbance. This is unlikely to be the case when production will also be affected by spatial variations in depth, primary production, sediment characteristics and water movement. A more rigorous analysis would require a model that accounts for the effects of physical characteristics as well as trawling disturbance on production, and uses habitat-specific mortality functions that account for the variable penetration of gear in different sediments (Duplisea *et al.*, 2002). However, even if such a model were developed, it could not be applied over large areas of the North Sea because small-scale habitat maps are not available. Notwithstanding, our approach demonstrates a process for describing the effects of effort redistribution on benthic production and provides preliminary estimates of the magnitude of such an effect over a large area of the central North Sea characterized by soft sediments.

The spatial scale of analysis has a critical effect on any interpretation of fishing impacts. An impact assessment at large spatial scales gives a false impression of the unfished area and analysis at smaller scales shows that the truly unfished area is much larger (Rijnsdorp *et al.*, 1998). Our results suggest that analysis at the scale of, for instance, ICES rectangles, is not sufficient to predict effects of fishing on benthic communities. Rather, analysis should be conducted at the smallest possible scales. VMS data might be used more effectively if the frequency of signals was increased and the fishing tracks of individual vessels could be reconstructed. This would allow swept areas to be calculated at any scale from the total distance of trawl track crossing a specified area in a specified time period.

The VMS has not been designed for scientific purposes and its primary use is to monitor vessel positions for enforcement purposes. Consequently, there are some potential problems with the use of these data. Thus, the system does not hold full records of gear type and some beam trawlers may have been mis-classified. Because we needed to gate the data based on vessel speed to eliminate those vessels that were only steaming through an area, vessels that were not actively fishing may be included in the analysis. This may apply to signals received from within the cod box during the closure. Despite these concerns, the VMS data have enabled scientists to examine the behaviour of the entire international beam-trawl fleet in much greater detail than has previously been possible.

To ensure the effective integration of fisheries and environmental management, it is important to consider the wider consequences of fishery management actions (e.g. Ecosystem Principles Advisory Panel, 1999; Link, 2002). Because seasonal area closures may increase the spatial homogeneity of trawling disturbance and lead to displacement of effort to previously unfished areas, it is desirable to conduct *a priori* assessments of potential effects of

management measures on the marine ecosystem. When effects are expected to be negative, then the effects should be costed against potential management benefits for the target stocks and, if appropriate, alternate management options should be explored. These might include permanent area closures that lead to a single but permanent redistribution of fishing disturbance.

Area closures have been proposed to meet a number of management objectives, ranging from the reduction in fishing mortality to the conservation of benthic biodiversity (Shackell and Martin Willison, 1995). Our analysis shows how an analysis of fleet responses can be used to predict the effects of a closure on one aspect of ecosystem function. The next step is to develop predictive models that describe how the fishing fleet responds to management action and to couple these with models of the ecosystem effects of fishing disturbance.

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References

- Bergman, M. J. N., and van Santbrink, J. W. 2000. Fishing mortality of populations of megafauna in sandy sediments. *In* Effects of Fishing on Non-Target Species and Habitats: Biological, Conservation and Socio-Economic Issues, pp. 49–68. Ed. by M. J. Kaiser and S. J. de Groot. Blackwell Science, Oxford.
- Bergman, M. J. N., and van Santbrink, J. W. 2000. Mortality in megafaunal benthic populations caused by trawl fisheries on the Dutch continental shelf in the North Sea in 1994. *ICES Journal of Marine Science*, 57: 1321–1331.
- Collie, J. S., Hall, S. J., Kaiser, M. J., and Poiner, I. R. 2000. A quantitative analysis of fishing impacts on shelf sea benthos. *Journal of Animal Ecology*, 69: 785–798.
- Cook, R. M., Sinclair, A., and Stefansson, G. 1997. Potential collapse of North Sea cod stocks. *Nature*, 385: 521–522.
- Dann, J., Millner, R., and De Clerck, R. 2002. Alternative uses of data from satellite monitoring of fishing vessel activity in fisheries management: II. Extending cover to areas fished by UK beamers. Report of EC Project 99/002.
- Duplisea, D. E., Jennings, S., Warr, K. J., and Dinmore, T. 2002. A size-based model of the impacts of bottom trawling on benthic community structure. *Canadian Journal of Fisheries and Aquatic Science*, 59: 1785–1795.
- Ecosystem Principles Advisory Panel 1999. Ecosystem-Based Fishery Management. NOAA National Marine Fisheries Service, Silver Spring, MD.
- Engel, J., and Kvittek, R. 1998. Effects of otter trawling on a benthic community in Monterey Bay National Marine Sanctuary. *Conservation Biology*, 12: 1204–1214.
- Fogarty, M. J., and Murawski, S. A. 1998. Large-scale disturbance and the structure of marine ecosystems: fishery impacts on Georges Bank. *Ecological Applications*, 8: S6–S22.
- Frank, K. T., Shackell, N. L., and Simon, J. E. 2000. An evaluation of the Emerald/Western Bank juvenile haddock closed area. *ICES Journal of Marine Science*, 57: 1023–1034.
- Gilkinson, K., Paulin, M., Hurley, S., and Schwinghamer, P. 1998. Impacts of trawl door scouring on infaunal bivalves: results of a physical trawl door model/dense sand interaction. *Journal of Experimental Marine Biology and Ecology*, 224: 291–312.
- Hall, S. J. 1999. The Effects of Fishing on Marine Ecosystems and Communities. Blackwell, Oxford.
- Halliday, R. G. 1998. Use of seasonal spawning area closures in the management of haddock fisheries in the Northwest Atlantic. *Northwest Atlantic Fisheries Organization Scientific Council Studies*, 12: 27–36.
- Hall-Spencer, J., Allain, V., and Helge Fossa, J. 2002. Trawling damage to Northeast Atlantic ancient coral reefs. *Proceedings of the Royal Society of London*, 269: 507–511.
- Horwood, J. W., Nichols, J. H., and Milligan, S. 1998. Evaluation of closed areas for fish stock conservation. *Journal of Applied Ecology*, 35: 893–903.
- ICES 2001. Report of the ICES Advisory Committee on Fisheries Management. ICES Cooperative Research Report 246.
- Jennings, S., and Kaiser, M. J. 1998. The effects of fishing on marine ecosystems. *Advances in Marine Biology*, 34: 201–352.
- Jennings, S., Alvsvag, J., Cotter, A. J. R., Ehrich, S., Greenstreet, S. P. R., Jarre-Teichmann, A., Mergardt, N., Rijnsdorp, A. D., and Smedstad, O. 1999. Fishing effects in northwest Atlantic shelf seas: patterns in fishing effort, diversity and community structure III. International trawling effort in the North Sea: an analysis of spatial and temporal trends. *Fisheries Research*, 40: 125–134.
- Jennings, S., Dinmore, T. A., Duplisea, D. E., Warr, K. J., and Lancaster, J. E. 2001. Trawling disturbance can modify benthic production processes. *Journal of Animal Ecology*, 70: 459–475.
- Jennings, S., Nicholson, M. D., Dinmore, T. A., and Lancaster, J. E. 2002. The effects of chronic trawling disturbance on the production of infaunal communities. *Marine Ecology Progress Series*, 243: 251–260.
- Kaiser, M. J., and de Groot, S. J. (eds) 2000. The effects of fishing on non-target species and habitats: biological, conservation and socio-economic issues. Blackwell Science, Oxford.
- Kaiser, M. J., Ramsay, K., Richardson, C. A., Spence, F. E., and Brand, A. R. 2000. Chronic fishing disturbance has changed shelf sea benthic community structure. *Journal of Animal Ecology*, 69: 494–503.
- Link, J. S. 2002. What does ecosystem-based fisheries management mean? *Fisheries*, 27: 18–21.
- Pastors, M. A., Rijnsdorp, A. D., and Van Beek, F. A. 2000. Effects of a partially closed area in the North Sea (plaice box) on stock development of plaice. *ICES Journal of Marine Science*, 57: 1014–1022.
- Piet, G. J., and Rijnsdorp, A. D. 1998. Changes in the demersal fish assemblage in the south-eastern North Sea following the establishment of a protected area (plaice box). *ICES Journal of Marine Science*, 55: 420–429.
- Rijnsdorp, A. D., Buys, A. M., Storbeck, F. S., and Visser, E. G. 1998. Micro-scale distribution of beam trawl effort in the southern North Sea between 1993 and 1996 in relation to the trawling frequency of the sea bed and the impact on benthic organisms. *ICES Journal of Marine Science*, 55: 403–419.

- Rijnsdorp, A. D., Dol, W., Hoyer, M., and Pastoors, M. A. 2000. Effects of fishing power and competitive interactions among vessels on the effort allocation on the trip level of the Dutch beam trawl fleet. *ICES Journal of Marine Science*, 57: 927–937.
- Rijnsdorp, A. D., Piet, G. J., and Poos, J. J. 2001. Effort allocation of the Dutch beam trawl fleet in response to a temporarily closed area in the North Sea. *ICES CM 2001/N*: 01.
- Schratzberger, M., Dinmore, T. A., and Jennings, S. 2002. Impacts of trawling disturbance on the biomass and community structure of meiofauna. *Marine Biology*, 14: 83–93.
- Shackell, N. L., and Martin Willison, J. H. (eds) 1995. *In Marine Protected Areas and Sustainable Fisheries*. Science and Management of Protected Areas Association, Halifax, Nova Scotia.