# Using MPAs to address regional-scale ecological objectives in the North Sea: modelling the effects of fishing effort displacement

Simon P. R. Greenstreet, Helen M. Fraser, and Gerjan J. Piet

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The use of Marine Protected Areas (MPAs) to address regional-scale objectives as part of an ecosystem approach to management in the North Sea is examined. Ensuring that displacement of fishing activity does not negate the ecological benefits gained from MPAs is a major concern. Two scenarios are considered: using MPAs to safeguard important areas for groundfish species diversity and using them to reduce fishing impacts on benthic invertebrates. Appropriate MPAs were identified using benthic invertebrate and fish abundance data. Fishing effort redistribution was modelled using international landings and fishing effort data. Closing 7.7% of the North Sea to protect groundfish species diversity increased the fishing impact on benthic invertebrates. Closing 7.3% of the North Sea specifically to protect benthic invertebrates reduced fishing mortality by just 1.7–3.8%, but when combined with appropriate reductions in total allowable catch (TAC), 16.2–17.4% reductions in fishing mortality were achieved. MPAs on their own are unlikely to achieve significant regional-scale ecosystem benefits, because local gains are largely negated by fishing effort displacement into the remainder of the North Sea. However, in combination with appropriate TAC reductions, the effectiveness of MPAs may be enhanced.

**Keywords:** benthic mortality, ecosystem approach to fishery management, fishing effort displacement, groundfish species diversity, MPAs.

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*S. P. R. Greenstreet and H. M. Fraser: FRS Marine Laboratory, PO Box 101, 375 Victoria Road, Aberdeen AB11 9DB, UK. G. J. Piet: Wageningen IMARES, IJmuiden, Haringkade 1, 1976 CP IJmuiden, The Netherlands. Correspondence to S. P. R. Greenstreet: tel: +44 1224 295417; fax: +44 1224 295511; e-mail: greenstreet@marlab.ac.uk.*

## Introduction

In recent decades, the potential impact of fishing on the broader marine ecosystem has raised serious concerns (Jennings and Kaiser, 1998; Hall, 1999; Ormerod, 2003) and has prompted a revolution in marine resource management, from traditional, single-species management to an ecosystem approach to management (EAM; Gislason *et al.*, 2000; Sainsbury and Sumaila, 2001; Hall and Mainprize, 2004; Cury and Christensen, 2005; Garcia and Cochrane, 2005). The perceived poor performance of conventional fishery management (Hilborn, 2004; Jennings, 2004; Frid *et al.*, 2005) has led to increased interest among marine resource managers in Marine Protected Areas (MPAs; Gaylord *et al.*, 2005; Friedlander *et al.*, 2007), implying that MPAs could provide an alternative to traditional fishery management that would be more successful in achieving both fishery and conservation objectives (Roberts *et al.*, 2001; Gell and Roberts, 2003). However, basic differences exist between the two approaches (Baelde, 2005). MPAs have been primarily advocated to address specific, local-scale issues (e.g. Willis *et al.*, 2003; Abesamis and Russ, 2005; Parnell *et al.*, 2006; Barrett *et al.*, 2007), whereas traditional fishery management has generally addressed regional-scale population issues. Indeed, the place-based paradigm of MPAs may actually compromise the ability of the population-based paradigm of traditional fishery management to monitor and assess fishery resources consistent with current methods and legislation (Field *et al.*, 2006). The emerging EAM represents the evolution of traditional fishery management to incorporate environmental and conservation aspirations, but it was never intended that the scale of perspective should change (Cury, 2004). The EAM was intended to take a holistic view: to safeguard the whole marine ecosystem at a regional scale (Pikitch *et al.*, 2004). The increasing belief that MPAs can provide an essential element of the EAM (e.g. Lubchenco *et al.*, 2003; Browman and Stergiou, 2004) takes for granted that they can bridge the "scale gap".

Many commercially valuable species are currently over-exploited (Cook *et al.*, 1997; Myers and Worm, 2003), and non-targeted fish species are also caught (Greenstreet and Rogers, 2000). In the northern North Sea, this fishing mortality has reduced demersal fish species diversity (Greenstreet and Rogers, 2006). Otter and beam trawls, the most common fishing gears in the North Sea (Jennings *et al.*, 1999, 2000), contact the seabed, damaging or killing benthic invertebrates (Bergman and van Santbrink, 2000; Collie *et al.*, 2000; Kaiser *et al.*, 2006). Conserving and restoring biodiversity are key concerns in many of the policy drivers underpinning the development of the EAM (Greenstreet, 2008). The use of MPAs to address marine ecosystem issues has been advocated in international policy documents, such as the Convention for the Protection of the Marine Environment of the Northeast Atlantic (OSPAR) and the EC Habitats and Marine Strategy Directives. However, it is not clear precisely what MPAs can and cannot deliver. MPAs have been used globally to protect commercial fish stocks and particular marine species, communities, and habitats that are at risk from fishing activity (Carr and Reed, 1993; Allison *et al.*, 1998; Houde, 2001;

Roberts *et al.*, 2001; Botsford *et al.*, 2003; Gerber *et al.*, 2003). They may well be beneficial at the local scale, i.e. within the closed area (Halpern, 2003), but whether or not they can deliver regional-scale (e.g. North Sea-wide) management objectives is less clear. Because many MPAs will be subject to fishing restrictions, a major concern focuses on the effects of fishing activity displaced from areas closed to fishing to alternative locations (Rijnsdorp *et al.*, 2001; Dinmore *et al.*, 2003). Such displaced fishing activity may have serious unintended consequences, perhaps even resulting in net losses for the marine ecosystem rather than gains. This raises the possibility that MPAs may prove inadequate to meet regional-scale management objectives within an EAM.

In this paper, we consider two closed area scenarios:

(i) using MPAs to protect regions of the North Sea where the species diversity of the demersal fish community is greatest;

(ii) using MPAs as a means of reducing fishing mortality on the benthic invertebrate community.

Issues with the first scenario have been explored elsewhere in this volume (Fraser *et al.*, 2009). Here, we consider the consequences associated with effort displacement of introducing MPAs to safeguard groundfish biodiversity on a second component of the marine ecosystem, the benthic invertebrate community. With regard to the second scenario, we are concerned that effort displacement may actually prevent MPAs that are intended to reduce fishing mortality in non-target components of marine ecosystems from achieving their goals. Finally, we consider how introducing measures to limit effort displacement might help MPAs to address regional-scale ecological objectives.

## MPA scenarios

In the terrestrial environment, land specifically designated for conservation objectives amounts to 8–10% of the total area (British Ecological Society, 1996). We therefore consider scenarios in which 7–8% of the area of the North Sea is designated as MPAs, amounting to 14 or 15 ICES statistical rectangles. We have not necessarily selected ICES rectangles with the greatest fish diversity or benthic mortality index values. Instead, we have selected groups of contiguous rectangles with relatively high conservation value, giving a smaller number of MPAs, each of two rectangles or more in size. This is generally a better design strategy for the conservation of species diversity (Halpern, 2003; Neigel, 2003) and can be more easily enforced.

### *MPAs to safeguard groundfish biodiversity*

Recent analyses of North Sea groundfish survey data have provided maps of spatial variation in demersal fish species diversity that take account of species- and size-related variation in catchability in the survey trawl and the sampling effort requirements necessary to provide robust measures of species diversity (Fraser *et al.*, 2007, 2008; Greenstreet and Piet, 2008). These maps provide the best indication of the most appropriate ICES rectangles to close to fishing to conserve groundfish species diversity (Fraser *et al.*, 2009). Cluster analysis of the species relative-abundance data revealed three distinct community types. High-diversity rectangles and representing each major community type were designated as potential MPAs (Figure 1). In total, 14 rectangles were selected, amounting to 46 595 km$^2$, 7.7% of the total North Sea area.

### *MPAs to reduce benthic fishing mortality*

Benthic invertebrate communities also vary in species composition and structure between the northern and southern North Sea (Figure 2a). A benthic invertebrate fishing mortality model was recently developed (Greenstreet *et al.*, 2007; Piet *et al.*, 2007). The model utilizes international fishing effort data (Greenstreet *et al.*, 2007), information related to the deployment of different types of fishing gear (Piet *et al.*, 2000, 2007; Greenstreet *et al.*, 2007), and

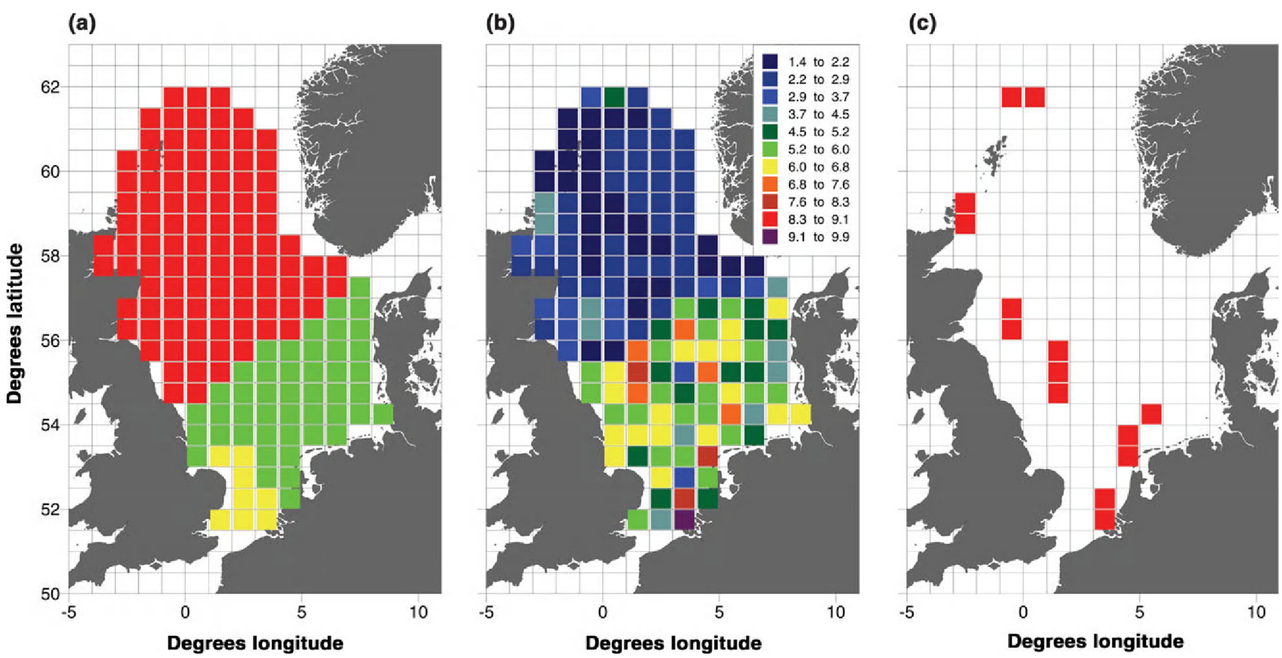


**Figure 1.** Spatial variation across the North Sea in (a) groundfish species assemblage type and (b) Hill's (1973) $N_1$, based on the groundfish survey data raised to account for catchability; (c) selection of ~7.7% of the North Sea area as MPAs designed to conserve the most species-diverse regions within each of the three main assemblage types.

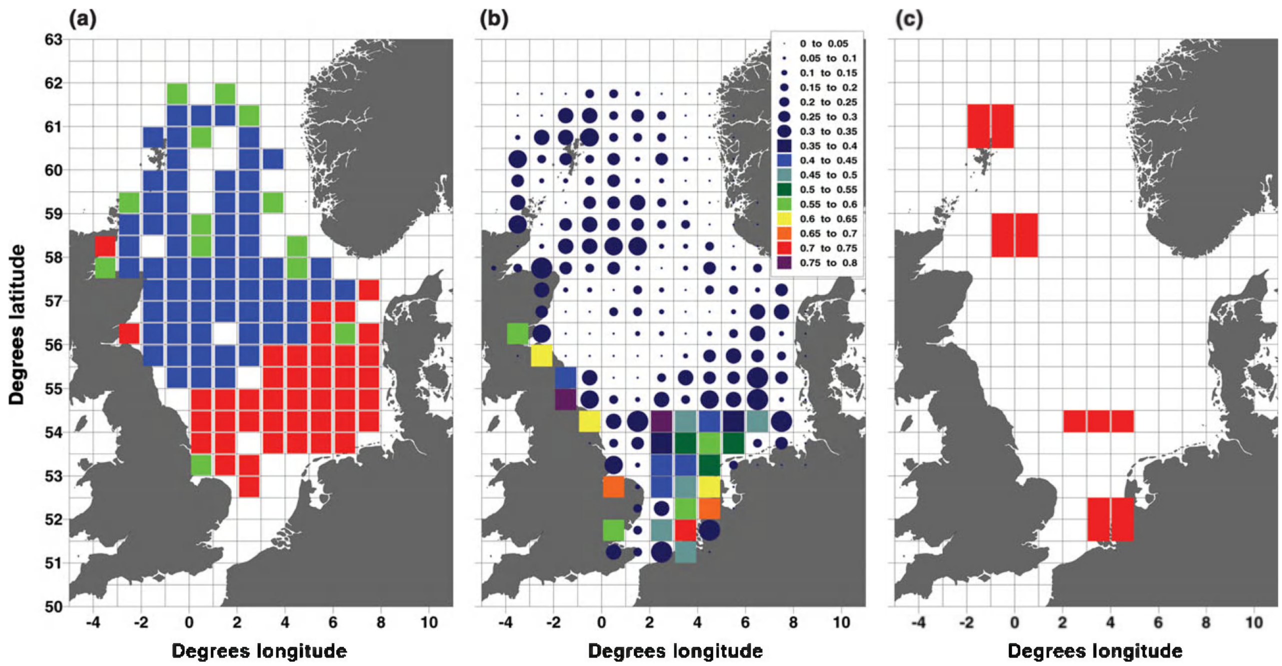


**Figure 2.** Spatial variation across the North Sea in (a) epibenthic invertebrate species assemblage type and (b) modelled annual benthic invertebrate fishing mortality rate; (c) selection of ~7.3% of the North Sea area as MPAs designed to reduce benthic invertebrate fishing mortality, with the objective of protecting rectangles in each of the main community types.

estimates of the "per event" mortality suffered by different types of benthic organism affected by different types of fishing gear (Kaiser *et al.*, 2006). The model was run to provide maps of spatial variation in benthic invertebrate fishing mortality (Figure 2b). Rectangles were selected for designation as MPAs from both main community types. Rectangles with the greatest mortality were selected on the basis that this strategy might achieve the greatest reduction in benthic fishing mortality for the least restriction to the fishing industry. In total, 15 rectangles were selected, amounting to 44 255 km$^2$, 7.3% of the total North Sea area.

The rectangles selected for MPA status under these two scenarios provided protection for areas with the greatest groundfish species diversity [based on Hill's (1973) $N_1$ diversity metric] and prevented fishing in the areas where benthic fishing mortality before MPA designation was greatest (Figure 3).

## Effort displacement model

The model utilizes international fishing effort and landings for the period 1997–2004 in 215 North Sea ICES rectangles (Greenstreet *et al.*, 2007). Figure 4 indicates the available landing and effort data and provides an example of the analyses carried out to generate catch per unit effort (cpue) data.

Following the designation of selected ICES rectangles as no-fishing MPAs, the amount of landings normally taken from

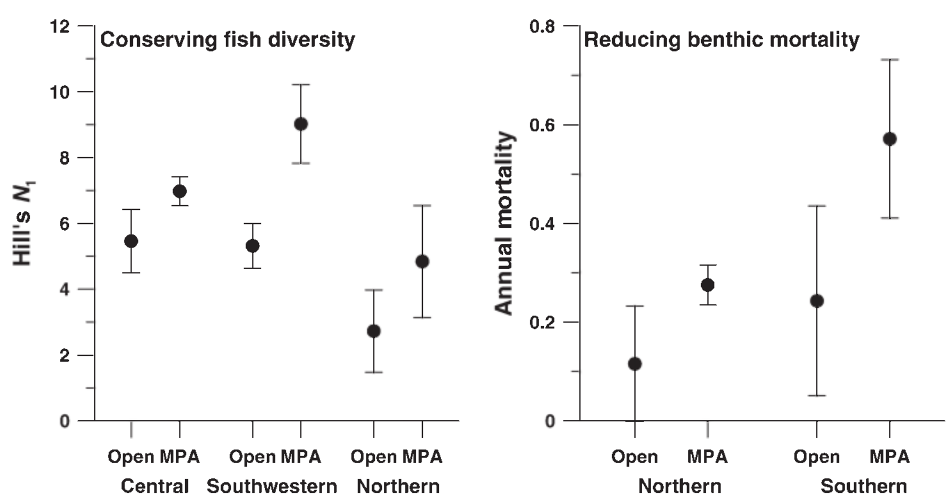


**Figure 3.** Mean (±1 s.d.) Hill's (1973) $N_1$ species diversity index and benthic invertebrate annual mortality estimate in rectangles designated as MPAs and rectangles remaining open to fishing in the three fish and two benthic community types under two MPA scenarios aimed at conserving fish species diversity or reducing benthic invertebrate fishing mortality.

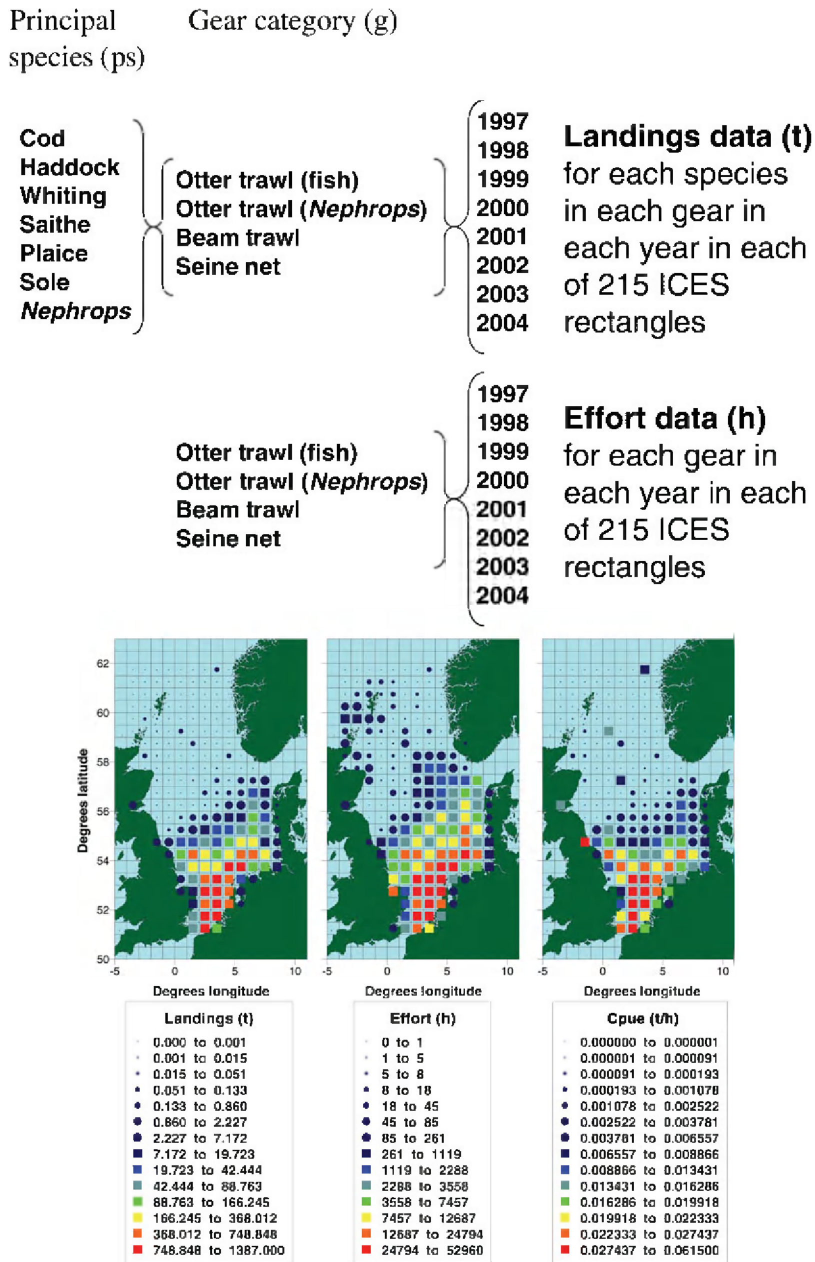


**Figure 4.** Schematic indicating available international landings and effort data (Greenstreet *et al.*, 2007); an example for sole caught by beam trawl indicating data averaged over the period 2001–2004 illustrates the generation of cpue data.

these rectangles is first determined directly from the international landings data (Greenstreet *et al.*, 2007). Figure 5 shows this information expressed as proportions of total landings averaged over the whole 8-year period. In the absence of simultaneous reductions in total allowable catch (TAC) by these amounts, these landings will be made up by increasing fishing effort in rectangles outside the MPAs; fishing effort will be displaced.

The displacement effect was estimated by calculating the additional landings of the principal species (ps) targeted by each main gear category (g) from each rectangle (r) remaining open to fishing that are required to balance landings normally taken from the closed MPA rectangles. The model assumes that, following the establishment of MPAs, landings are taken from rectangles remaining open to fishing in the same ratios as before MPA introduction, so that

$$L_{\mathrm{add,ps,g,r}} = \frac{L_{\mathrm{prior,ps,g,r}}}{\sum_{r=x}^{\mathrm{OPEN}} L_{\mathrm{prior,ps,g,r}}} \cdot \sum_{r=y}^{\mathrm{MPA}} L_{\mathrm{prior,ps,g,r}}. \qquad (1)$$

$L_{\mathrm{add,ps,g,r}}$ and $L_{\mathrm{prior,ps,g,r}}$ are, respectively, the additional landings in any given ICES rectangle remaining open to fishing following cessation of fishing in the MPA rectangles and the landings in that rectangle before the establishment of the MPAs. $\sum_{r=x}^{\mathrm{OPEN}} L_{\mathrm{prior,ps,g,r}}$ and $\sum_{r=y}^{\mathrm{MPA}} L_{\mathrm{prior,ps,g,r}}$ are the total landings before the establishment of the MPAs from all rectangles

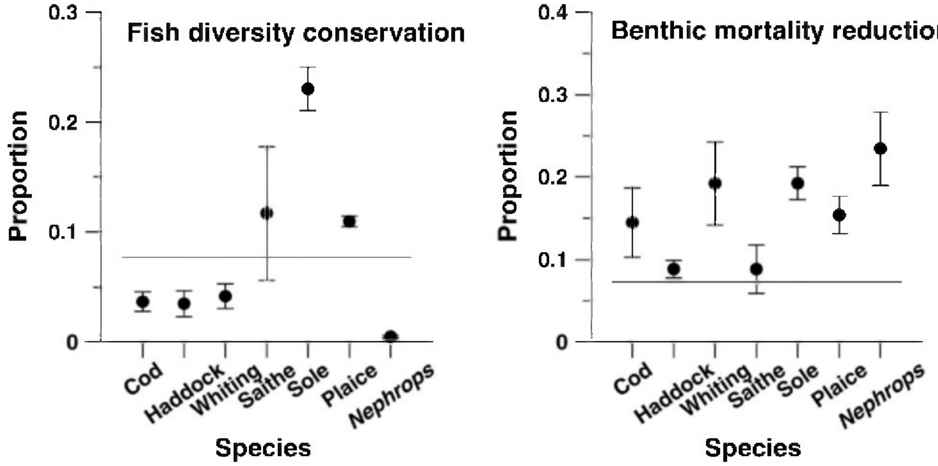


**Figure 5.** Mean ($\pm$1 s.d.) proportion of total landings of each species over the period 1997–2004 ($n = 8$) taken from ICES rectangles designated as MPAs under two scenarios: conserving groundfish species diversity and reducing benthic invertebrate fishing mortality. The solid line indicates the minimum expected proportion given the proportion of the North Sea included in the designated MPAs.



remaining open to fishing and all rectangles designated as part of an MPA, respectively. The additional effort by each gear in each rectangle remaining open to fishing ($E_{\mathrm{add,ps,g,r}}$) required to take the additional landings of the principal species targeted by the gear can be calculated knowing the cpue of the species and gears in question in each rectangle ($\mathrm{cpue}_{\mathrm{ps,g,r}}$),

$$E_{\mathrm{add,ps,g,r}} = \frac{L_{\mathrm{add,ps,g,r}}}{\mathrm{cpue}_{\mathrm{ps,g,r}}}. \tag{2}$$

Finally, as a result of this additional fishing effort in the rectangles remaining open to fishing, other commercially important species will also be caught. The additional landings of these species from each rectangle open to fishing can be determined knowing the cpue of each species in each main gear in each rectangle,

$$L_{\mathrm{add,s,g,r}} = E_{\mathrm{add,ps,g,r}} \cdot \mathrm{cpue}_{\mathrm{s,g,r}}. \tag{3}$$

Note the change in the subscript, from ps to s, in the landings and cpue terms to denote that we are no longer considering the species that are the principal target species of each gear.

## Model analyses

For each MPA scenario, the effort displacement model was run using annual average data for two periods, 1997–2000 and 2001–2004. In each case, the benthic invertebrate fishing mortality model was applied to the effort distributions before the introduction of MPAs and again following the designation of MPAs, using the effort distribution outputs from the effort displacement model. In this way, the consequences to benthic communities of using MPAs to protect fish communities, and the effectiveness of MPAs as a means of reducing the impact of fishing on benthic communities, could be explored.

## Model results

### *MPAs to safeguard groundfish biodiversity*

Sole, plaice, and saithe were the species most affected by the closure of rectangles aimed at protecting groundfish species diversity (Figure 5). The effort displacement model was run, assuming sole to be the principal target of beam trawlers and saithe the principal target of otter trawlers (directed at fish). On this basis, sufficient amounts of all other species were caught as bycatch to make up the shortfalls in landings normally taken in the MPA rectangles. In fact, bycatches generally exceeded shortfalls, suggesting that discarding would be necessary to maintain total landings within permitted TACs. Without detailed knowledge of current discard practices, it is not possible to judge the practical significance of this. For both species and main gear categories, the increase in fishing effort outside the MPAs exceeded the amount of effort that occurred previously within the MPAs. One of the consequences of closing these 14 rectangles was therefore an overall increase in fishing effort by beam and otter trawlers across the whole North Sea (Table 1). Application of the benthic fishing mortality model to the redistributed fishing effort data suggested that, in the absence of measures to restrict the displacement of fishing effort, closing these rectangles to safeguard fish biodiversity resulted in an overall increase in the impact of fishing on benthic invertebrate communities at the North Sea regional scale (Table 1).

### *MPAs to reduce benthic fishing mortality*

Landings of *Nephrops*, sole, and whiting were most affected by the closure of rectangles aimed at reducing benthic invertebrate fishing mortality (Figure 5). The effort displacement model was therefore run, assuming sole to be the principal target of beam trawlers, whiting to be the principal target of otter trawlers (directed at fish), and *Nephrops* to be the principal target of *Nephrops* otter trawlers. On this basis, sufficient amounts of all other species, except whiting, were taken as bycatch to make up the shortfalls in landings normally taken in the MPA rectangles. Failure to make up the whiting landings was caused by a marked reduction in gadoid bycatch taken by *Nephrops* trawlers after effort was relocated. Running the model using other otter trawl (directed at fish) strategies failed to find a solution for this; for example, further increasing effort by otter trawlers targeting whiting resulted in bycatches of other gadoid species that would have required unrealistically high levels of discarding to avoid exceeding TACs. In nearly all cases, displacement of fishing effort resulted in more

**Table 1.** Effort displacement model results for two MPA scenarios: protecting areas of great groundfish species diversity and reducing benthic invertebrate fishing mortality at the North Sea scale.

| MPA scenario | Period | | | | | |
|---|---|---|---|---|---|---|
| | 1997–2000 | | | 2001–2004 | | |
| Protecting areas of great groundfish species diversity | | | | | | |
| Gear category | Beam | Otter trawl (F) | Otter trawl (N) | Beam | Otter trawl (F) | Otter trawl (N) |
| Target species | Sole | Saithe | * | Sole | Saithe | * |
| MPA landings (t) | 4 628 | 6 584 | * | 4 331 | 14 620 | * |
| MPA effort (h) | 199 416 | 42 467 | * | 189 067 | 40 312 | * |
| Open effort "prior" (h) | 801 901 | 1 160 913 | * | 647 316 | 850 006 | * |
| Open effort "after" (h) | 1 033 115 | 1 258 318 | * | 858 521 | 1 005 133 | * |
| Δ Effort open (h) | 231 213 | 97 405 | * | 211 205 | 155 127 | * |
| Δ Effort open (%) | 28.8 | 8.4 | * | 32.6 | 18.3 | * |
| Δ Effort NS (h) | 31 797 | 54 939 | * | 22 138 | 114 815 | * |
| Δ Effort NS (%) | 3.2 | 4.6 | * | 2.6 | 12.9 | * |
| Δ Benthic *F* (%) | 1.2 | | | 3.5 | | |
| Reducing benthic invertebrate fishing mortality at the North Sea scale | | | | | | |
| Gear category | Beam | Otter trawl (F) | Otter trawl (N) | Beam | Otter trawl (F) | Otter trawl (N) |
| Target species | Sole | Whiting | *Nephrops* | Sole | Whiting | *Nephrops* |
| MPA landings (t) | 3 816 | 2 729 | 1 782 | 3 484 | 1 594 | 3 273 |
| MPA effort (h) | 199 404 | 200 195 | 106 249 | 166 467 | 143 997 | 159 227 |
| Open effort "prior" (h) | 801 913 | 1 003 185 | 245 072 | 669 916 | 746 321 | 278 664 |
| Open effort "after" (h) | 984 086 | 1 169 205 | 296 447 | 835 924 | 909 489 | 379 321 |
| Δ Effort open (h) | 182 173 | 166 020 | 51 375 | 166 008 | 163 168 | 100 657 |
| Δ Effort open (%) | 22.7 | 16.5 | 21 | 24.8 | 21.9 | 36.1 |
| Δ Effort NS (h) | −17 231 | −34 175 | −54 874 | −459 | 19 171 | −58 570 |
| Δ Effort NS (%) | −1.7 | −2.8 | −15.6 | −0.1 | 2.2 | −13.4 |
| Δ Benthic *F* (%) | −3.8 | | | −1.7 | | |

For each scenario, the displacement model strategies applied are indicated. Target species landings and main gear category effort in the MPA rectangles are indicated [Otter trawl (F) and Otter trawl (N) refer to otter trawl directed at fish and *Nephrops*, respectively], as is the amount of effort by the gear in the rectangles remaining open to fishing both before and after the introduction of MPAs; change (Δ) in effort by the gear in the open rectangles and across the North Sea (NS), both as hours and as a percentage, are indicated; consequences for benthic invertebrate fishing mortality (*F*), on the scale of the North Sea, predicted by the benthic mortality model, are given.

efficient fishing operations; fishing was displaced to rectangles where, on average, cpue for each target-species–main-gear combination was greater. As a result, fishing effort increases in rectangles outside the MPAs were generally smaller than the amount of effort normally expended within the MPA rectangles for the same amount of each target species landed (Table 1). Consequently, the MPA strategy provided some benefit to benthic invertebrate communities at the North Sea scale (Table 1). However, in both periods, the actual proportional reduction in North Sea benthic invertebrate fishing mortality was smaller than the proportional reduction in fishable area.

The MPA strategy for reducing the regional-scale benthic invertebrate fishing mortality that we examined, closing rectangles where benthic fishing mortality was greatest, resulted in the MPAs incorporating some of the most heavily fished rectangles in the North Sea. Cpue may have been lower in the MPA rectangles because of the depletion of stocks by these high levels of fishing activity. Nevertheless, the capacity for these rectangles to maintain relatively high catch levels over time must clearly underpin the attraction of these areas to fishers. It is questionable whether or not rectangles outside the MPAs would be able to maintain their initially high cpue after fishing activity in these areas increased following the introduction of the MPAs. Under such circumstances, we speculate that the effort displacement model probably underestimates the amount of effort in rectangles outside the MPAs that would actually be required to make up for landings normally taken within the MPAs. If so, benefits to the benthic invertebrate community of reduced fishing mortality at the whole North Sea scale may well also be overestimated.

For this MPA scenario, the benthic invertebrate model was run a second time, but this time preventing any displacement of fishing effort into areas outside the MPAs. Essentially, this simulated the introduction of MPAs combined with a simultaneous reduction in TACs, equivalent to the amount of fish normally taken from the MPAs. This strategy resulted in reductions in benthic invertebrate fishing mortality North Sea wide of 16.2 and 17.4% over the periods 1997–2000 and 2001–2004, respectively, representing a marked improvement in the ecological benefit gained from the introduction of MPAs alone.

## Discussion

To determine the efficacy of MPAs as a tool for use within an EAM, a regional or seascape perspective is necessary (Friedlander *et al.*, 2007). We have considered potential regional-scale conservation objectives for a North Sea EAM that protects fish biodiversity hotspots and reduces benthic invertebrate fishing mortality, and analysed simulations covering the entire North Sea to assess the regional-scale benefits from closing ∼8% of the area to fishing. MPAs can benefit fish species diversity (Russ and Alcala, 1989; Halpern, 2003; Lubchenco *et al.*, 2003; Friedlander *et al.*, 2007; McClanahan *et al.*, 2007), with the response often most apparent among larger bodied fish (Guidetti, 2006; Barrett *et al.*, 2007). Although less frequently examined, similar results have also been noted for benthic invertebrates (Duineveld *et al.*, 2007). These particular objectives are therefore suited to MPA management, but are MPAs the most appropriate tool to address these issues? Within a holistic EAM, different objectives should not be considered separately. Finding that MPAs intended to conserve fish biodiversity raised benthic fishing mortality at the North Sea scale was therefore not desirable. Local reductions in benthic fishing mortality within the MPAs were outweighed by the increased fishing mortality elsewhere in the North Sea, resulting from fishing effort displacement. This raises the question, can MPAs actually achieve any regional-scale reduction in benthic invertebrate fishing mortality? Our second simulation suggested a qualified yes. However, in both periods for which our models were run, the proportional reduction in North Sea scale benthic invertebrate fishing mortality was <4%, yet nearly 8% of the area was closed to fishing. MPAs alone appear inefficient at reducing fishing impact on the North Sea benthic invertebrate community.

In assessing the validity of these conclusions, various aspects of our analyses should be examined. First, our simulations consider an MPA designation amounting to 8% of the North Sea, yet to achieve conservation goals effectively, up to 30% or more of any marine region may need to be closed to fishing (Horwood, 2000; Pauly *et al.*, 2002; Gell and Roberts, 2003; Gladstone, 2007). For decades, scientists have argued that substantial reductions in fishing effort were necessary to address declines in North Sea fish stocks. Yet, despite reductions in these valuable natural resources, short-term social and economic costs were too high for the issue of long-term sustainability to be addressed adequately (Jennings, 2004). There is little to suggest that this situation has changed, at least to the extent that managers might consider designating as much as 30% of the North Sea as MPAs. In the UK and other European countries with North Sea interests, ∼8% of the land is set aside for conservation purposes (British Ecological Society, 1996). We have simply assumed that a similar fraction of the marine area might be designated as MPAs to address conservation issues.

Second, we did not simply select the highest fish diversity or benthic fishing mortality rectangles for MPA status. Instead, groups of adjacent rectangles with relatively high conservation value were identified, creating fewer, larger MPAs. In some circumstances generally associated with larval dispersal processes, MPA networks consisting of more, smaller reserves might be advantageous (e.g. Gaines *et al.*, 2003). However, the importance of reserve size is more often emphasized, particularly in northern latitudes, where mobile fish species are involved (Halpern, 2003; Baskett *et al.*, 2005; Martell *et al.*, 2005; Gurd, 2006; Laurel and Bradbury, 2006; Parnell *et al.*, 2006; Barrett *et al.*, 2007). Few large MPAs have been designated around the world, but the Scotian Shelf and Georges Bank in the northwestern Atlantic provide two examples. These are similar in latitude to the North Sea, hold similar groundfish communities, and are similar in size to the MPAs simulated here (Fisher and Frank, 2002; Murawski *et al.*, 2005). In practice, it would be easier to enforce compliance with fewer, larger MPAs.

Third, we have assumed a very simple rationale underpinning the redistribution of fishing effort following the implementation of our two MPA schemes. We assume that fishers have knowledge of catch rates throughout the North Sea and redistribute their effort throughout the area remaining open to fishing according to these catch rates (e.g. Hutton *et al.*, 2004; Hiddink *et al.*, 2006). Other alternative redistribution models could apply; for example, effort could be redistributed in line with previous effort distributions or influenced by cpue following some form of ideal free distribution (e.g. Gillis and Peterman, 1998). Behavioural processes, such as following previous habits or vessel aggregation, would also tend to redistribute effort into the more heavily fished regions of the North Sea (Allen and McGlade, 1986; Dorn, 1997; Pradhan and Leung, 2004). Economic factors, such as catch value, cost of fuel, and distance to alternative fishing grounds, could also influence the redistribution of effort (Hutton *et al.*, 2004; Mardle and Hutton, 2004). Natural predators appear to reach their hunting decisions by balancing costs and benefits in this way (Stephens and Krebs, 1986), and several studies have likened the decision-making process in fishing operations to those used by natural predators (Gillis and Peterman, 1998; Dorn, 2001; Bertrand *et al.*, 2007). These alternative redistribution models are therefore conceptually easy to construct within the analytical framework presented here, and this is the subject of continuing research. However, although different redistribution models might ultimately result in different fishing effort distributions, we have no reason to believe that this would significantly affect our overall conclusions.

More complex effort redistribution patterns may also emerge. Fish abundance within MPAs generally increases (Polacheck, 1990; Pipitone *et al.*, 2000; Côté *et al.*, 2001; Fisher and Frank, 2002; Halpern, 2003; Willis *et al.*, 2003; McClanahan and Graham, 2005; Friedlander *et al.*, 2007; McClanahan *et al.*, 2007), particularly among larger fish (Willis *et al.*, 2003; Barrett *et al.*, 2007), resulting in density-dependent emigration of fish out of the MPA into adjacent areas (Alcala and Russ, 1990; McClanahan and Kaunda-Arara, 1996; Russ and Alcala, 1996; McClanahan and Mangi, 2000; Fisher and Frank, 2002; Russ *et al.*, 2004; Abesamis and Russ, 2005). Consequently, fishers may be drawn to "fish the line" in areas bordering MPAs (Roberts *et al.*, 2001; Murawski *et al.*, 2005; Kellner *et al.*, 2007). Modelling such effort redistributions requires consideration not only of the effort that occurred previously within each MPA, but also the attraction of effort to MPA boundaries that would normally have been deployed outside the MPAs. MPA-induced recoveries of fish abundance generally occur over relatively long time-scales (e.g. Russ and Alcala, 2003; Micheli *et al.*, 2004; McClanahan and Graham, 2005), suggesting that such effort distributions might develop over time. The simple model examined here may therefore be more appropriate for the period (up to 5–10 years) following MPA implementation.

Both positive and negative effects of MPAs on benthic invertebrates have been demonstrated and shown to be a trade-off between recovery in closed areas and declines in areas to which trawling activity was displaced. Beneficial effects were greatest when relatively lightly fished areas were closed (Hiddink *et al.*, 2006), almost certainly because of curvilinear, asymptotic, relationships between ICES rectangle-scale fishing effort levels and the resultant benthic invertebrate fishing mortality (Greenstreet *et al.*, 2007). Displacing fishing effort to an already heavily fished area, where fishing mortality lies in the asymptotic region of the curve, causes relatively little additional mortality.

Conversely, adding the same amount of effort to lightly fished areas, where fishing mortality is on the linear ascending portion of the curve, causes substantial additional mortality. Clearly the former situation is more desirable and is more likely when relatively lightly fished areas are selected for MPA designation. The more heavily fished areas remain available to fishers and are, by definition, clearly attractive to them. This suggests that the criteria for selecting ICES rectangles for our MPA simulations could be improved and will need to be considered when defining MPA strategies as part of an EAM. Dinmore *et al.* (2003) noted that introduction of the "cod box", intended to reduce the mortality of juvenile cod, resulted in displacement of fishing activity into previously unfished areas, causing considerable damage to benthic communities. Determining the most effective MPA strategies to reduce the impact of fishing on the North Sea benthic invertebrate community, using the benthic mortality and effort displacement modelling approaches employed here, is the focus of ongoing research.

Because MPAs tend to enhance fishery yields, it has been argued that fishers should not suffer from their implementation (Gerber *et al.*, 2003; Russ *et al.*, 2004; Gaylord *et al.*, 2005; but see Gardmark *et al.*, 2006). This can only be the case, however, if fishers reap the benefits of the spillover effect by increasing fishing activity levels outside MPAs. Inevitably, therefore, MPAs will affect areas outside their boundaries through the displacement of fishing effort (Halpern *et al.*, 2004; Murawski *et al.*, 2005). Only when catches associated with spillover exceed catches normally taken from within the MPAs, so increasing cpue outside the reserves, will effort displacement be negligible (Sanchirico *et al.*, 2006). This is difficult enough to achieve with MPAs designed specifically to enhance fishery yield and is unlikely to happen with MPAs with broader conservation objectives.

Hiddink *et al.* (2006) noted that the beneficial effects of MPAs for benthic communities were enhanced when combined with measures to restrict effort displacement; an observation strongly corroborated by the results we report here. Simultaneously reducing TACs by the amount of landings normally taken from the MPAs resulted in no increase in fishing effort outside the MPAs. Under these circumstances, the effectiveness of MPAs designed to reduce the impact of fishing on benthic invertebrate communities was substantially increased, and MPAs that are intended to protect fish biodiversity hotspots should also actually benefit benthic invertebrate communities rather than harming them. However, imposing TAC reductions to limit effort displacement, simultaneously with the introduction of MPAs, invariably leads to reduced catch rates (Hilborn *et al.*, 2006). Within an EAM, spatial control of fishing effort through the introduction of MPAs aimed at conservation objectives may be most effective when combined with actions, such as TAC reductions, designed to reduce overall levels of fishing effort (Zeller and Russ, 2004). On the other hand, it has been argued that regional-scale conservation goals might be better achieved simply through a general reduction in fishing effort, rather than by closing specific areas to fishing (Kaiser, 2005; Holland and Schnier, 2006).

## Conclusions

With adequate data, MPAs to protect areas with greatest groundfish species diversity can be designated. Without TAC reductions equivalent to the landings normally taken from these areas, however, fishing effort will be displaced to areas remaining open to fishing. In fact, to compensate for landings normally taken in the MPAs, fishing effort increased regionally across the North Sea, resulting in increased benthic invertebrate fishing mortality at the North Sea regional scale. In the absence of measures to limit effort displacement, MPAs to protect groundfish communities have unfortunate consequences for benthic invertebrate communities. In the absence of measures to restrict effort displacement, closing 7.3% of the North Sea to fishing, where benthic fishing mortality rates are greatest, resulted in only minimal reduction in North Sea regional-scale benthic fishing mortality. The models discussed here can, however, be used to explore more effective MPA strategies. When TACs are reduced by amounts equivalent to the landings normally taken from the MPAs, then substantial reduction in North Sea regional-scale benthic mortality was achieved. MPAs combined with appropriate catch limitation measures may be much more effective in achieving ecological objectives within an EAM.

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