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Assessing and predicting the relative ecological impacts of disturbance on habitats with different sensitivities

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Summary

1. Methods for assessing habitat sensitivity to human impacts are needed to gauge the sustainability of existing impacts, develop spatial management plans and support meaningful environmental impact assessments. These methods should be quantitative, validated, repeatable and applicable at the scales of impact and management.
2. Existing methods for assessing the sensitivity of marine habitats to human impacts have tended to rely on expert judgement and/or scoring systems. They are neither validated, quantitative nor repeatable.
3. We have developed a method that meets the criteria for assessing the sensitivity of seabed habitats to physical disturbance, and delineating and mapping habitat sensitivity at large spatial scales ($>10^5$ km^2). The method assumes that sensitivity is related to the recovery time of production or biomass, as predicted using a size-based model that takes account of the effects of natural disturbance.
4. As trawling disturbance is a major and widespread direct human impact on shelf seas, this was used as an example of anthropogenic physical disturbance. We mapped habitat sensitivity to trawling in 9-km^2 boxes across an area of 125 000 km^2 in the North Sea.
5. Habitat sensitivities varied widely, and a trawling frequency of 5 year^{-1} in the least-sensitive habitat had the same ecological effect as a trawling frequency of 0·3 year^{-1} in the most-sensitive habitat (based on production). When trawling effort was held constant but redirected to the least-sensitive habitats, the existing impacts on production and biomass were reduced by 36% and 25%, respectively.
6. *Synthesis and applications.* The method described in this paper enables managers to predict the implications of changing patterns of human impact on seabed habitats when establishing spatial management plans. In the context of fisheries management, this will support the identification and selection of fishing grounds that minimize the adverse ecological effects of fishing; the selection of closed areas (both representative and highly sensitive); the comparison of management options that might reduce the overall environmental impacts of fishing; and any future steps towards the application of environmental impact assessment in advance of fishery development.

Key-words: benthic invertebrate community, ecosystem approach to fisheries, ecosystem-based fishery management habitat sensitivity, marine protected areas, spatial management, trawling, vulnerability

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Introduction

Repeatable quantitative methods for identifying and delineating sensitive habitats are an essential prerequisite for the effective management of human activities (Bax & Williams 2001). Knowledge of sensitivity can be used to assess the sustainability of existing impacts, develop spatial management plans and support environmental impact assessment. Despite the need to identify and delineate sensitive habitats, available methods usually rely on expert judgement and/or scoring systems and are neither repeatable nor verifiable (Johnson

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& Gillingham 2004; Zacharias & Gregr 2005). This may not be an issue when comparing fundamentally different types of habitat, such as coral reefs and mobile sand in the marine environment (Hall-Spencer, Allain & Fossa 2002) or forest and grassland, but it is an issue when dealing with the full continuum of habitat types across subtle environmental gradients and their associated sensitivities to different impacts.

A suitable definition of sensitivity in the present context is that of Zacharias & Gregr (2005): the degree to which features of the environment (in the current context habitats) respond to stresses, where stresses are deviations of environmental conditions beyond the expected range. If sensitivity is to be measured and reported in a comparable way, and as habitat types and sources of stress are numerous in most environments, a widely applicable scale for measuring and reporting sensitivity is needed. One option is to treat sensitivity as the inverse of recovery time following a stress of defined magnitude and duration. This builds on the conceptual approach developed by Bax & Williams (2001), where sensitivity is highest when resistance and resilience are low. Resistance is defined as the initial resistance of a habitat to disturbance, and resilience is defined to be inversely proportional to recovery time.

In this study, we developed a quantitative, repeatable and validated method for estimating the sensitivity of marine habitats to stress. The method can be used to produce maps of habitat sensitivity for the marine environment. Consistent with Zacharias & Gregr (2005), our approach takes account of the effects of the range of natural stresses to which habitats are exposed. The method we present classifies the sensitivity of seabed habitats in relation to bottom-trawling disturbance. Direct changes in the relative abundances of species killed by fishing gears comprise the most widespread direct human impact on marine ecosystems. Disturbance caused by bottom-trawling is among the most widespread human impact on marine ecosystems, with >50% of many shelf seabeds impacted annually (Watling & Norse 1998; Hall 2002).

The method we present could readily be modified to classify sensitivity to other types of physical disturbance (e.g. aggregate dredging and cable laying) for which the response and recovery of biological attributes (e.g. biomass, diversity and production) have been ascertained. In qualitative terms, the sensitivities of seabed habitat to trawling disturbance are well known. Sensitive habitats are typically found in environments where there are low levels of natural disturbance resulting from wave erosion, currents at the seabed and temperature fluctuation (among others). Such habitats are characterized by the occurrence of large and old individuals (biota) that tend to be relatively abundant (Hall 1999). The response of a sensitive habitat to a given frequency and magnitude of disturbance is characterized by larger reductions in biomass, production and species richness of the associated fauna than those seen in a less sensitive habitat (Hiddink *et al*. 2006b).

Various conceptual models of the relationships between habitat sensitivity to trawling and habitat type have been proposed (Auster 1998; Jennings & Kaiser 1998) but these have limited application in management decision making because they do not provide quantitative predictions and are therefore not suitable for monitoring performance in relation to objectives or assessing the effects of mitigation measures.

With the advent of an ecosystem approach to fisheries (EAF) (Sinclair & Valdimarsson 2003), it is necessary to develop quantitative methods for predicting sensitivity to external forcing. This is because the EAF requires that managers take account of the ecosystem effects of fishing in management plans that are also intended to achieve sustainable exploitation of target species (Kaiser *et al*. 2002). Knowledge of habitat sensitivity would therefore support assessment and management. For example, methods for assessing and predicting the relative ecological impacts (where impact is defined as the reduction of some ecological function, such as production) of trawling disturbance in habitats with different sensitivities might provide a rational basis for assigning fishing access rights and identifying undesirable interactions between fishing and the environment. Moreover, the permissible spatial distribution and intensity of trawling on different habitats could be predicated on knowledge of sensitivity, and/or charges for access to fishing rights in different areas could be linked to measures of habitat sensitivity. Such processes might support the development of habitat quotas that are set to maintain a target habitat 'stock' (Holland & Schnier 2006). Estimates of sensitivity would also allow the production of habitat sensitivity maps. These could contribute to environmental impact assessment, if this process was required for new fisheries, by helping to identify areas where trawling would be expected to have the greatest environmental impact. Knowledge of the distribution of fish populations and the sensitivity of their habitats could also be used to redirect trawling to more resilient areas.

We developed a method for assessing the sensitivity of seabed habitats to bottom-trawling disturbance. The method assumes that sensitivity is related to the recovery time of biomass or production, as predicted using a validated size-based model that takes account of the effects of natural disturbance on habitat characteristics. The method was applied to seabed habitats in the North Sea and used to delineate and map habitat sensitivity at large spatial scales (> 10^5 km^2). Although we used the North Sea to illustrate the utility of the model, it could be developed and applied to other continental shelf areas for which the necessary physical and biological data exist. The distribution of habitat sensitivities was compared with the distribution of international bottom-trawling activity. We used the predictions of sensitivity to compare the relative environmental costs of trawling in habitats with different sensitivities and show how modifications to the existing distribution and intensity of trawling disturbance would affect the aggregate impacts of trawling. Our methods provide clear quantitative guidance for assessing the outcome, in terms of environmental costs and benefits (changes in the total biomass and production of benthic invertebrate communities), of different management options designed to support implementation of an EAF.

Methods

RECOVERY TIME AND SENSITIVITY

In this study, sensitivity is defined as the degree to which production and biomass in habitats respond to trawling disturbance. Sensitivity (S) is calculated from model estimates of the recovery time of production (T_P, i.e. the time that it takes the productivity of the benthic community to recover from a defined trawling impact) and biomass (T_B, the time that it takes the biomass to recover) following a specified trawling event, by assuming that sensitivity can be linked to recovery time using a relationship of the general form:

$$S = 1 - e^{-aT} \qquad \text{eqn 1}$$

where a is a scaling parameter that defines how quickly S approaches the asymptote. Qualitative results of our analyses are independent of the value of a. We used an exponential form for this relationship, rather than a linear relationship, because we considered it more important to be able to distinguish habitats that are insensitive from habitats that are sensitive to disturbance, rather than to distinguish habitats that are very sensitive from those that are extremely sensitive. This reflects the fact that environmental managers need to know in which areas disturbance is acceptable vs. areas where disturbance in not acceptable, and this exponential shape effectively focuses S on distinguishing between insensitive habitats on the on hand and the range from sensitive to highly sensitive on the other.

To describe sensitivity using a simple 0–1 scale, this function was modified to:

$$S_P = 1 - e^{-0{\cdot}25T_P} \qquad \text{eqn 2}$$

and

$$S_B = 1 - e^{-0{\cdot}1T_B} \qquad \text{eqn 3}$$

for production and biomass, respectively. The exponents were chosen so that S increased over the whole range of observed recovery times and was spread out over the range 0–1. As observed recovery times were longer for biomass, a smaller a was used for biomass.

We used a size-based model of the response of soft-sediment benthic communities to trawling disturbance to predict T_P and T_B. Details of the development and use of the model are given in Duplisea *et al*. (2002) and Hiddink *et al*. (2006b). In summary, the model contained 32 state variables, in two faunal groups (soft- and hard-bodied macrofauna). Growth of the population biomass in each body mass–organism type compartment was modelled by modifying Lotka–Volterra competition equations to give the population biomass flux for a compartment. The interaction between habitat type and trawling effects was 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, at the same body size, soft-bodied animals have a faster life history than hard-bodied animals, and therefore the latter dominate stable habitats and the former prevail in the more dynamic and disturbed habitats.

The model was validated by correlating observed benthic biomass with the biomass predicted by the model at 33 stations subject to a range of trawling intensities in four shallow, soft-sediment areas in the North Sea. Modelled increases in production (P) and biomass (B) can only take place through growth of the local population, as the model assumes that there is no migration between adjacent areas. Migration of benthic invertebrates is likely to be limited at the scale of the cells we used in this study (9 km^2). However, hard-bodied invertebrates are probably more mobile than soft-bodied, and this may lead to overestimation of recovery times for hard-bodied invertebrates (and therefore the whole community) in areas where trawling effort is spatially patchy. The sources of environmental data used to parameterize the model and the sensitivities of the model to changes in the values for its parameters are described by Hiddink *et al*. (2006b).

T_B and T_P are defined to be the time that it takes the biomass and productivity, respectively, of the benthic community to recover from a defined trawling impact, to 90% of the values predicted in the absence of trawling ($P_{0{\cdot}9}$ or $B_{0{\cdot}9}$; Hiddink, Jennings & Kaiser 2006c). Production and biomass in the absence of trawling were determined by running the model for 1500 time steps of 30 days without trawling. Then, after trawling once, the times for the community to recover to $P_{0{\cdot}9}$ and $B_{0{\cdot}9}$ were calculated. The resultant values of T_P and T_B were used to calculate S_P and S_B using equations 2 and 3, respectively.

TRAWLING IMPACTS

Trawling frequency was calculated from European Community Satellite Vessel Monitoring System (VMS) data (for more details see Dinmore *et al*. 2003; Hiddink *et al*. 2006b). For the Dutch beam-trawling fleet, VMS records were not available for all vessels. Therefore, effort–distribution as recorded by the VMS system was corrected to represent total trawling effort as recorded in logbooks by fishers (G. J. Piet, RIVO, unpublished data). To express trawling frequency, the North Sea was gridded at a scale of 9 km^2 and trawling intensity was expressed as the number of times each 9-km^2 grid cell was swept each year. In this calculation, it was assumed that trawlers fished at a speed of 5 knots, with a total fishing gear width of 24 m (two beam trawls each of 12 m wide or one otter trawl of 24 m wide). Therefore, at a VMS record frequency of once 2 h^{-1}, one satellite monitoring record in one grid cell represents a trawled area of 0·449 km^2, and one record in one grid cell in a 1-year period represents a trawling intensity of 0·050 year^{-1}.

The size-based model of trawling impacts was used to assess biomass and production of the whole benthic community for all cells in the southern North Sea, based on assumed trawling intensities of 0, 0·01, 0·05, 0·1, 0·25, 0·5, 0·75, 1, 2, 3 and 5 year^{-1}. The impact of these trawling intensities was calculated as the change in biomass and production for each cell. The relative effects of different trawling frequencies were compared as a function of S_P and S_B to identify frequencies of trawling that had comparable effects on biomass and production at different levels of S_P and S_B.

MANAGEMENT SCENARIOS

We used the modelled reduction in biomass and production to manage the ecological impact of bottom-trawling in five hypothetical scenarios. Two approaches were used: (i) to set the desired level of ecological impact and then distribute trawling effort accordingly; (ii) to set the desired level of trawling effort and distribute it so that the ecological impact is minimized or maximized.

The ecological impact caused by trawling depends on the trawling intensity, where intensity is defined as the number of times an area of the seabed is trawled completely each year. In applying the two approaches, we assumed that all areas that were trawled were trawled homogeneously at an intensity of 1 year^{-1}. We did this to provide a benchmark reference for scaling and interpreting results and it was not intended to be a reflection of reality. There is no need to assume a homogeneous distribution of trawling effort at 1 year^{-1} but this helps to simplify the comparison of the management scenarios. The ecological impact of trawling was estimated from the reduction in P and B at 1 trawl year^{-1} compared with a situation with no trawling. The five management scenarios are described in Table 1. In scenarios 1–3, trawling effort was distributed so that the maximum amount of trawling possible was carried out in the least-sensitive habitats up to the target ecological impact (25%, 50% and 100% of the current impact). In scenario 4, trawling effort was distributed so that the maximum amount of trawling possible was carried out in the least-sensitive habitats, and trawling only occurred in the more sensitive habitats when 100% of the area of the less sensitive habitats was already trawled 1 year^{-1}. Conversely, in scenario 5, trawling effort was distributed so that the maximum amount of trawling possible was carried out in the most-sensitive habitats, and trawling only occurred in the less sensitive habitats when 100% of the area of the most-sensitive habitats was already trawled 1 year^{-1}.

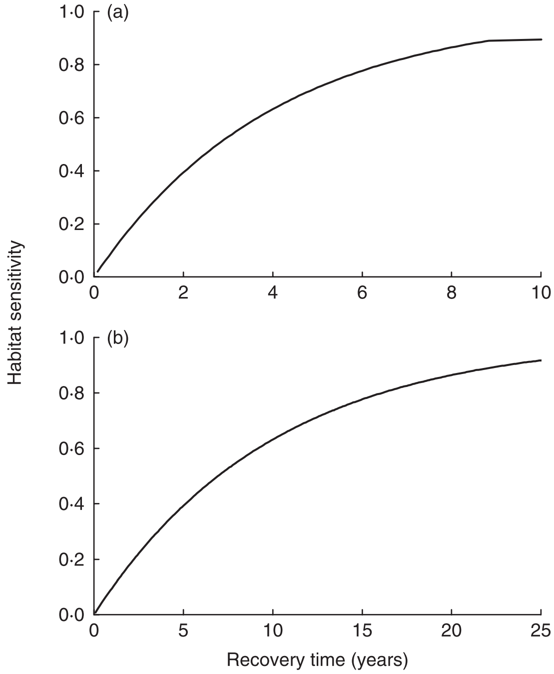

Fig. 1. Relationships between recovery time and sensitivity. (a) T_P and S_P; (b) T_B and S_B.

Table 1. Management scenarios

1	Reduce the ecological impact of bottom-trawling to 25% of current levels by changing trawling effort level and distribution
2	Reduce the ecological impact of bottom-trawling to 50% of current levels by changing trawling effort level and distribution
3	Keep the ecological impact of bottom-trawling at current levels by changing trawling effort level and distribution
4	Keep the trawling effort at current levels and minimize the ecological impact (most trawling in least-sensitive habitats)
5	Keep the trawling effort at current levels and maximize the ecological impact (most trawling in most-sensitive habitats)

Results

The values of sensitivity for biomass (S_B) and production (S_P) increased with recovery time for production (T_P) and biomass (T_B) (Fig. 1). The spatial distributions of S_B and S_P in the North Sea (Fig. 2) showed that they tend to be highest in the north-west North Sea and Oyster Ground area, and many areas with relatively high or low S_B and S_P are broadly the same in their spatial distribution. One deviation from this general pattern occurred in areas where $S_B > 0·8$ and there was slow recovery but low absolute biomass. This

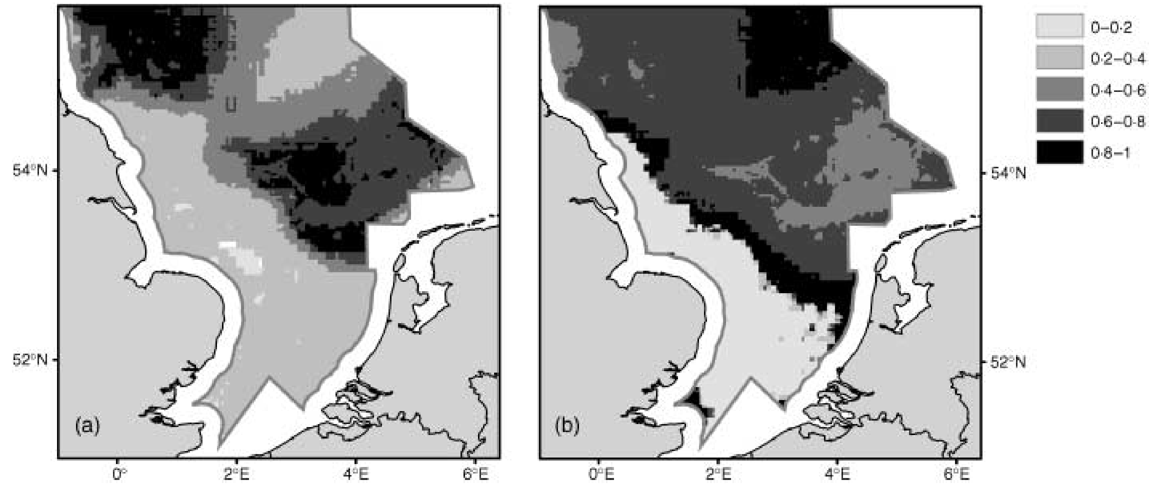

Fig. 2. Map of habitat sensitivity for production (a) and biomass (b) in the southern North Sea.

Table 2. Fraction of the area of North Sea seabed habitats assigned to sensitivity ranges (S). The total area of habitat was 125 000 km^2

	Fraction of area (%)	
S	Production	Biomass
0–0·2	1·2	20·7
0·2–0·4	42·6	0·9
0·4–0·6	20·2	13·7
0·6–0·8	20·9	51·9
0·8–1	15·0	12·8

occurred in a narrow band from north-east England (Flamborough head) to the central coast of the Netherlands (IJmuiden).

The largest proportions (> 40%) of the study area had sensitivities in the ranges S_P = 0·2–0·4 and S_B = 0·6–0·8 (Table 2). The environmental characteristics associated with different values of S are given in Appendix S1 (see the supplementary material). Trawling disturbance was generally higher in areas of lower sensitivity. Frequently trawled areas (> 1 year^{-1}) were uncommon and tended to occur primarily in areas of lower sensitivity (Fig. 3). However, some highly trawled areas corresponded with higher sensitivity (> 0·6). Thus trawling impacts would be expected to be much reduced if effort was reallocated to less sensitive habitats.

The magnitude of predicted trawling impacts on production and biomass were correlated with the S_P and S_B index (Fig. 4). These relationships were used to compare the relative effects of trawling on P and B in habitats with different sensitivities. For example, trawling 2 year^{-1} in a habitat with S_P = 0·2 is equivalent to trawling once every three years in a habitat with S_P = 0·4. Trawling 5 year^{-1} in habitat with S_P = 0·2 is equivalent to trawling four times every 10 years in habitat with S_P = 0·8. A trawling frequency of 5 year^{-1} in the least-sensitive habitat had the same ecological effect as trawling 0·3 year^{-1} in the most-sensitive habitat, based on production. At a trawling intensity of 1 year^{-1}, trawling 1 km^2 of habitat with S_P = 0·5 has an impact on production equivalent to trawling 3 km^2 of habitat with S_P = 0·2. The ecological impact increased with S_P, while the relationship between S_B and ecological impact was dome-shaped.

The ecological impact of trawling in the North Sea could be reduced substantially by allocating bottom-trawling to the least-sensitive habitats, even without reducing the overall trawling effort (Table 3). If trawling effort was increased, ecological damage could be kept at or below current levels (scenarios 2–3) by distributing trawling effort to the least-sensitive habitats. If trawling effort was kept at current levels, ecological damage could be reduced to 36% (production) or 25% (biomass) of current levels by redistributing trawling to the least-sensitive habitats (scenario 4). When trawling effort was concentrated in the most-sensitive habitats, the ecological impact changed to 135% (production) or 105% (biomass) of current levels (scenario 5).

Discussion

We have described a quantitative, field-data validated and repeatable method for assessing the sensitivity of seabed habitats to physical disturbance and delineating and mapping habitat sensitivity at large spatial scales. Although this approach was applied to North Sea seabed communities, and to assess sensitivity in relation to the additional physical disturbance associated with bottom-trawling, the model used to predict the recovery of production or biomass could readily be parameterized with different mortality functions to look at the effects of other types of disturbance, such as aggregate extraction, or modified to examine the effects of other types of fishing gear (Kaiser *et al*. 2006). The capacity to make quantitative predictions of sensitivity enables

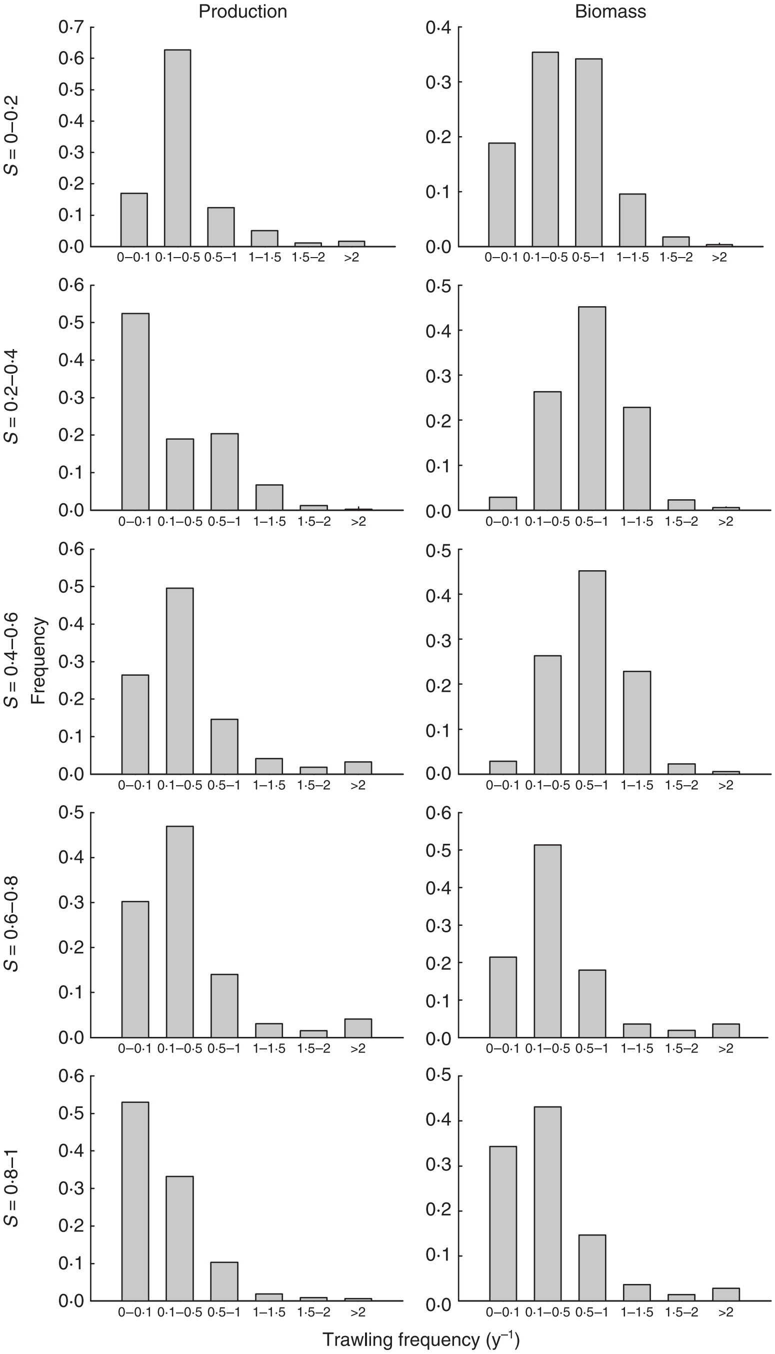

Fig. 3. Trawling frequencies in habitats with different sensitivities S (0, low sensitivity to 1, high sensitivity).

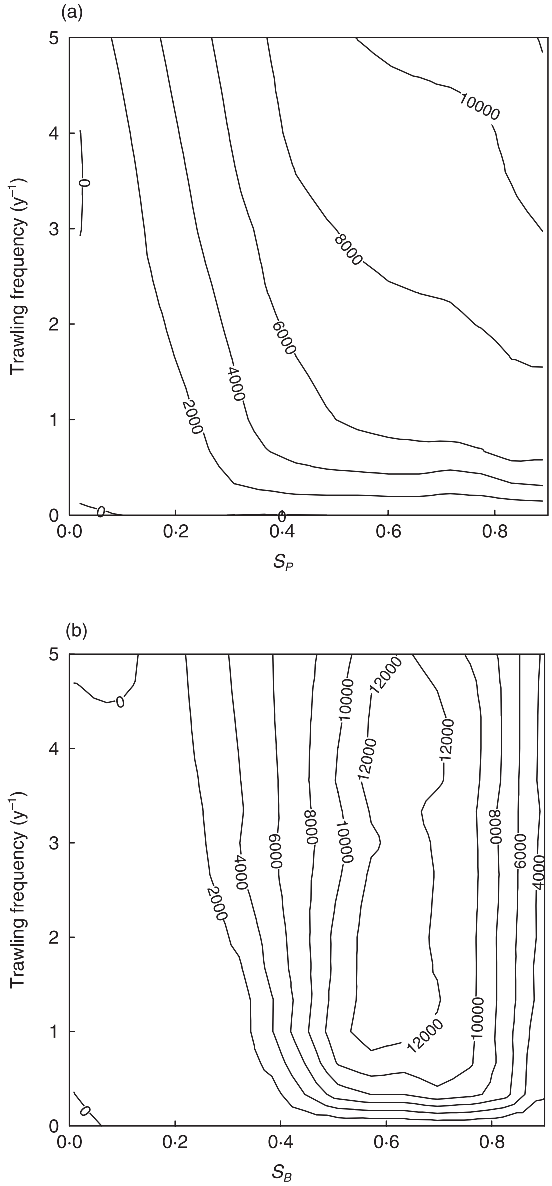

Fig. 4. Isoclines of equivalent reduction in benthic production (a) and biomass (b) as a result of trawling disturbance in relation to habitat sensitivity. The lines connect points of equal impact (mg m^{-2}) on production or biomass. Data have been smoothed using a Loess smoother.

managers to take account of habitat sensitivity explicitly when establishing spatial management plans. In the context of fisheries management, this will support the identification and selection of fishing grounds and closed areas (both representative and highly sensitive), the comparison of management options that might reduce the overall environmental impacts of fishing, and future steps towards environmental impact assessment in advance of fishery development. Currently, there exists a large range of policy commitments to maintain and promote the sustainability of the exploitation of marine living resources, for example to 'promote sustainable fisheries consistent with a diverse and resilient marine environment' (DARDNI *et al.* 2005) and to 'maintain the productivity of important and vulnerable marine and coastal areas' (WSSD 2002).

The proposed method for classifying habitat sensitivity provides a logical and ecologically meaningful basis for assessing and improving the effectiveness of management. Thus, by directing trawling to the least-sensitive habitats, ecological damage can be reduced without reducing total trawling effort. Coupled with knowledge of the distribution of target fish species, our approach may help identify fishing grounds where an appropriate balance between catch rates and environmental impacts might be achieved (Jennings 2000).

Table 3. The effect of different management scenarios on trawling effort and the ecological impact of trawling in the North Sea. Values shown in italics were set as constants, other values were derived from these. As cells are trawled at a frequency of 1 year^{-1}, the trawling frequency is equal to the fraction of the area trawled. *P*, production; *B*, biomass

	Trawling frequency (mean, year^{-1})		Ecological impact (relative to current levels) (%)	
Scenario	*P*	*B*	*P*	*B*
Current situation	*0·43*	*0·43*	*100*	*100*
1 Ecological impact reduced to 25% by changing trawling effort level and distribution	0·37	0·43	*25*	*25*
2 Ecological impact reduced to 50% by changing trawling effort level and distribution	0·50	0·57	*50*	*50*
3 Ecological impact kept equal by changing trawling effort level and distribution	0·68	0·79	*100*	*100*
4 Effort 100%, minimize ecological impact	*0·43*	*0·43*	36	25
5 Effort 100%, maximize ecological impact	*0·43*	*0·43*	135	105

Estimates of habitat sensitivity may be used to assign fishing access rights based on the ecological impact of trawling (Holland & Schnier 2006) and for identifying 'ecologically expensive' interactions between trawling and the environment, in which short-term financial gains result in long-term environmental degradation. In future studies, ecological impacts in terms of lost production or biomass might be expressed in terms of monetary value (Costanza *et al*. 1997; Chee 2004). Trawlers could then be charged differentially for access rights to fishing grounds (habitats), depending on their sensitivity (Holland & Schnier 2006). This is a form of ecosystem rent that assigns a monetary value to each habitat according to its sensitivity.

The choice of fishing location by trawlers would thus be expected to depend on the spatial distribution of ecosystem rent in relation to fishing profits. To predict these choices of fishing location, it would be necessary to model how the behaviour of fishermen is affected by the balance between the charges and expected fishing profits. Such models are relatively straightforward extensions of existing models that predict the spatial distribution of effort from the predicted behaviour of fishers (Hutton *et al*. 2004; Hiddink *et al*. 2006a).

Holland & Schnier (2006) recently proposed an individual habitat quota (IHQ) system that uses economic incentives to encourage habitat conservation. Individual quotas of habitat impact units (HIU) would be distributed to fishers, with a cumulative quota set for an area to maintain a target habitat 'stock'. The use of HIU by fishers thus reflects the amount of habitat damage that they cause by trawling. Holland & Schnier (2006) assumed that there was no spatial variation in habitat sensitivity to trawling, and that the absolute amount of trawling damage caused by trawling decreased exponentially with the number of previous trawling events (trawling history). Their approach could be developed further using our measures of the sensitivity of benthic communities, as the charges for trawling (use of HIU) would depend both on trawling history and on the sensitivity of the targeted area. The obvious advantage of this approach is that it becomes economically less attractive to fish in the most-sensitive areas and fisheries targeting relatively mobile fish would probably focus on areas where costs were lower (Holland & Schnier 2006). This approach could be developed further into a management system where gear types that fished on a habitat of given sensitivity would be charged differentially according to their relative impact and frequency of use. The impacts of different gears on different habitats could be assessed based on a meta-analysis of studies of the impacts of different gear types on different habitats (Kaiser *et al*. 2006).

Some problems have to be acknowledged with regard to ecosystem impact quotas. If such quotas are non-transferable, all the existing problems that result from non-transferability of fishing quotas (Arnason 2005) are likely to affect habitat impact quotas. Several fleets using different gears operate in the North Sea, with varying impact on the environment. Fleets fishing high-priced species would have an inherent advantage if ecosystem impact quotas were used, all other things being equal, as their profits in an area where they have to pay for a moderate impact may still be larger than the profits of other fisheries in areas where they have a low impact. Thus, if HIU are too cheap or too expensive relative to the profits of a fleet, HIU are unlikely to help ecosystem conservation. The risk also exists that quotas are monopolized for purposes other than the managers may have intended (e.g. by environmental organizations). Therefore, implementing HIU will not be simple.

Our analyses demonstrate that the allocation of bottom-trawling effort to less-sensitive habitats could lead to substantial reductions in the ecological impact of trawling, even without reductions in overall trawling effort. In this analysis, we assumed that all areas were suitable for trawling. However, benthic invertebrate production is typically low in areas that are least sensitive to trawling impacts, and it is possible that fish abundance, catch rates and total catch would also be low in these areas (Hoines & Bergstad 1999). If catch rates or total catch and habitat sensitivity were directly and positively related, then the redistribution of trawling would not provide any environmental benefits over and above a simple reduction of the total trawling effort. However, relationships between sensitivity and catch rates are unlikely to be direct and positive for at least three reasons. First, most North Sea species migrate, and while the areas occupied in some seasons may be sensitive and/or productive there will be times when, and places where, the fish can be caught over habitat of lower sensitivity. Secondly, aggregations of fish that are targeted by fishers can be very concentrated (particularly given the low abundance of many North Sea stocks) and the concentrations may reflect other drivers of habitat suitability, such as temperature, as well as the physical structure and productivity of the benthic habitat (Shepherd & Litvak 2004). Thirdly, trawlers often tend to trawl along tows that are recorded in their navigation systems and this results in patterns of effort that persist over many years (Auster & Langton 1999; Holland & Sutinen 2000). Additionally, at trawling intensities > 1 year^{-1}, the absolute differences between production and biomass at different levels of S_P and S_B are relatively small. Thus it seems unlikely that catch rates and habitat sensitivity will usually be directly and positively related, and thus it would be possible to redirect fleets to areas where the reductions in catch rates would be small in relation to the ecological benefits realized. Future studies should look in detail at the trade-offs between catch rate and ecological impact, and how they might vary seasonally, based on catch rate data and knowledge of fish migration.

The principal limitations of our method are that habitat sensitivity is measured in terms of production and biomass recovery rather than in terms of other attributes, such as diversity, that may be regarded as more important in a policy context. Moreover, the connectivity among habitats, habitat diversity and patch size were not accounted for in our model. Based on comprehensive validation, and the open nature of the North Sea marine environment, we consider these to be acceptable simplifications (Hiddink *et al.* 2006b). For other areas, the effects of disregarding connectivity and other processes would have to be assessed. The implementation of the management scenarios was also simplified by assuming that all areas are either not trawled or trawled once a year. Given that the reduction in production and biomass at low trawling intensities is large, while further increasing the trawling intensity in areas where trawling intensity is already high only has a small impact, a concentrated rather than a homogeneous distribution of a given level of effort will have a lower ecological impact. For all sensitivities, the relationship between trawling intensity and ecological impact flattens off at trawling intensities > 1 year^{-1}. This explains the seemingly counterintuitive result of scenario 5, where concentrating fishing effort in the most-sensitive habitats still only led to a very small increase in the ecological impact of trawling on biomass (104%). To avoid managers forming an unduly optimistic impression of the result of their actions, an assessment of the impacts when effort was not constrained to 1 year^{-1} would be necessary.

Concentrating trawling effort, regardless of the sensitivity of the habitat in which effort is concentrated, will reduce the aggregate ecological impact of trawling on that habitat. Trawlers could be encouraged to tow in defined narrow lanes (e.g. < 1 km wide) if it was essential to trawl in some areas of a sensitive habitat to maintain catch rates of some species. This would leave most of the habitat unimpacted, while the narrow lanes would facilitate immigration of commercial fish into the trawl path. The feasibility of such an approach depends on fish production rates in the untrawled areas, the movement of fish in relation to the trawl lanes, and the capacity of managers to monitor and regulate trawling activities reliably at this scale. With the advent of VMS, the spatial management of trawling at scales of a few kilometres is increasingly realistic.

Notwithstanding the limitations of our approach, we have shown that models of recovery time can be used to estimate habitat sensitivity and that the results can be used to map sensitive habitats, compare the sensitivity of habitats on a common scale and select spatial management strategies that minimize human impacts. Our methods do not rely on expert judgement and/or scoring systems that have commonly been adopted elsewhere (Zacharias & Gregr 2005) and, at least in the study area, are validated, repeatable and applicable at the scale of management.

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Supplementary material

The following supplementary material is available as part of the online article (full text) from http://www.blackwell-synergy.com.

Appendix S1. Characterization of the environment for the five sensitivity ranges.