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Effects of demersal trawling on ecosystem functioning in the North Sea: a modelling study

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ABSTRACT: Demersal trawling causes chronic and widespread disturbance to the seabed in shallow shelf seas potentially leading to changes in function and trophic structure of benthic communities and with important implications for the processing of primary production and the wider functioning of the marine ecosystem. We used a coupled physical-ecological model (the European Regional Seas Ecosystem Model (ERSEM) with the General Ocean Turbulence Model (GOTM)) to investigate the impact of demersal trawling on the benthic and pelagic ecosystems of generic stratified and unstratified water columns in the central North Sea. Perturbation experiments were used to simulate trawling events using estimates of mortality of benthic fauna caused by different fishing gears in different habitats, derived from a meta-analysis of over 100 trawling disturbance experiments reported in the literature. The results suggest that the biogeochemical impact of demersal trawling is most significant in regions where gear type, trawl frequency and bed type cause high levels of filter feeder mortality. This results in substantially increased oxygen content of the benthic system and significant changes in its biogeochemistry (increased phosphorus absorption, increased nitrification of ammonia, reduced silicate cycling). The impacts of these changes on the overlying pelagic ecosystem are, however, buffered by the physical environment and the ability of phytoplankton to vary their internal cell nutrient contents. Analysis of recovery of the benthic system on complete cessation of demersal trawling suggests that the system will return to its original state within 5 yr, except in extreme cases where the deposit or filter feeder function is effectively removed, when a permanent change in the function of the benthic ecosystem may result.

KEY WORDS: ERSEM · Ecosystem · Change · Benthic-pelagic coupling · Trawling impact · Ensemble models · Nutrient cycling · Disturbance experiments

INTRODUCTION

Towed bottom fishing gears are thought to be one of the largest global anthropogenic sources of disturbance to the seabed and its biota (Watling & Norse 1998, Auster & Langton 1999, Kaiser et al. 2006). The current drive towards an ecosystem approach in fisheries management requires consideration of the implications of habitat deterioration and potential for restoration consequent on this activity (e.g. Pikitch et al. 2004). In particular, demersal trawling causes chronic and widespread disturbance to the seabed of shallow shelf seas (Collie et al. 1997, 2000). Gear types range from beam and otter trawls, which are basically nets with rollers or chains in contact with the bottom, to drags which have large teeth or bars which dig into the bottom. The degree of disturbance is a function of both the sediment and the gear type used (Eleftheriou & Robertson 1992, Auster & Langton 1999). Such disturbances may lead to changes in function and trophic structure of benthic communities and consequently have important implications for the processing of primary production, and may alter biogeochemical cycles, perhaps even globally (Watling & Norse 1998).

Recent work (Jennings et al. 2001) has demonstrated that the frequency of trawling in the central North Sea ranged between 0.2 and 6.5 times yr^{-1}. Trawling is especially problematic where the return interval — the

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time from one dredging or trawling event to the next — is shorter than the time it takes for the ecosystem to recover (Watling & Norse 1998). Chronic trawling disturbance leads to dramatic reductions in the biomass of infauna and epifauna, but these reductions are not reflected by changes in the trophic level of the community (Jennings et al. 2001). Recovery after disturbance is often slow because recruitment is patchy and growth to maturity takes years, decades, or more for some structure-forming species (Watling & Norse 1998).

Kaiser et al. (2006) undertook a meta-analysis of 101 different fishing impact experiments in the environment, mostly reported in the published literature. The direct effects of different types of fishing gears were found to be strongly habitat-specific with the most severe impact occurring in biogenic habitats in response to scallop dredging. The biota of soft-sediment habitats such as muddy sand were surprisingly vulnerable, with predicted recovery times measured in years. Slow growing large-biomass biota such as sponges and soft corals took much longer to recover (up to 8 yr and beyond) than biota with shorter lifespans such as polychaetes (<1 yr). Their results give the first possible basis for predicting the outcome of using different fishing gears in a variety of habitats.

Previous modelling studies of trawling impacts in the southern North Sea (Duplisea et al. 2001) imply that the removal of macrobenthos by trawling could strongly impact benthic biogeochemical processes, which in turn could affect the carbon flow through the ecosystem. For example this has been observed in systems where large suspension feeders (such as the horse mussel *Atrina zelandica*) were removed, resulting in an observed increase in the oxygen content of the benthic system (Warwick et al. 1997).

According to Duplisea et al. (2001) the presence of macrobenthos helps to stabilise sediment chemical storage and fluxes to reach equilibrium. Recovery times for biota reported from a meta-analysis by Collie et al. (2000) vary between 100 and 500 d, the later coinciding with the most complete data sets. The projected recovery times for biota from the meta-analysis of Kaiser et al. (2006) indicate time scales of 2 to 5 yr, which are similar to that reported for a scallop fishery closure in the Irish Sea (Bradshaw et al. 2000).

The purpose of the present study was to address questions of the magnitude of impact of demersal trawling on gross structural properties of benthic systems and the effects these changes have on benthic nutrient recycling and pelagic production. We used a model to investigate the following hypotheses about the impact of fishing: (1) the removal of suspension feeders will lead to a more oxic benthic system; (2) benthic ecosystem function recovers to pre-trawling levels within 5 yr of the cessation of trawling (e.g. Collie et al. 2000, Kaiser et al. 2006).

To investigate these links we used a coupled physical-ecological water-column model. This model is a synthesis of the European Regional Seas Ecosystem Model (ERSEM, Baretta et al. 1995) as modified by Blackford et al. (2004) and the General Ocean Turbulence Model (GOTM, Umlauf et al. 2005). The simulations were of generic stratified and unstratified water columns in the central North Sea that are typical of the North West European shelf. We performed a number of perturbation experiments to simulate trawling events using estimates of the mortality of benthic fauna caused by different fishing gears in different habitats derived from the meta-analysis of Kaiser et al. (2006). We investigated medium- to long-term impacts of trawling events (timescales of up to 10 yr) with different mean return intervals, rather than the instantaneous impacts on the system.

METHODS

Ecosystem model. ERSEM is a generic ecosystem model that was originally developed and applied in the context of the North Sea (e.g. Baretta et al. 1995, Allen et al. 2001). It has also been successfully applied to the Mediterranean Sea (Allen et al. 2002, Siddorn & Allen 2003), the Adriatic Sea (Allen et al. 1998, Vichi et al. 1998) and the Arabian Sea (Blackford & Burkill 2002).

ERSEM represents the ecosystem as a network of physical, chemical and biological processes. A schematic of the pelagic trophic links is given in Fig. 1. A 'functional group' approach is used to describe the biota. The ecosystem is divided into 3 functional types: primary producers, consumers and decomposers, and subdivided on the basis of trophic links and/or size.

Physiological (ingestion, respiration, excretion and egestion) and population (growth and mortality) processes are included in the descriptions of functional group dynamics. These dynamics are described by fluxes of carbon and nutrients between functional groups. Each functional group is defined by a number of components, namely carbon, nitrogen, and phosphorus and, in the case of diatoms silicon, each of which is explicitly modelled.

The ERSEM pelagic foodweb is shown in Fig 1. Detailed descriptions of the pelagic submodels and parameters of the version of ERSEM used can be found in Blackford et al. (2004, and references therein).

The benthic model (Fig. 1) describes 3 layers, an oxic layer, a denitrifying layer and an anaerobic layer. The benthic foodweb consists of aerobic and anaerobic bacteria, meiobenthos (all heterotrophs between protozoa and 1 mm), suspension feeders (feeding directly on the pelagic system) and deposit feeders (feeding on benthic detritus and other benthic organisms). It

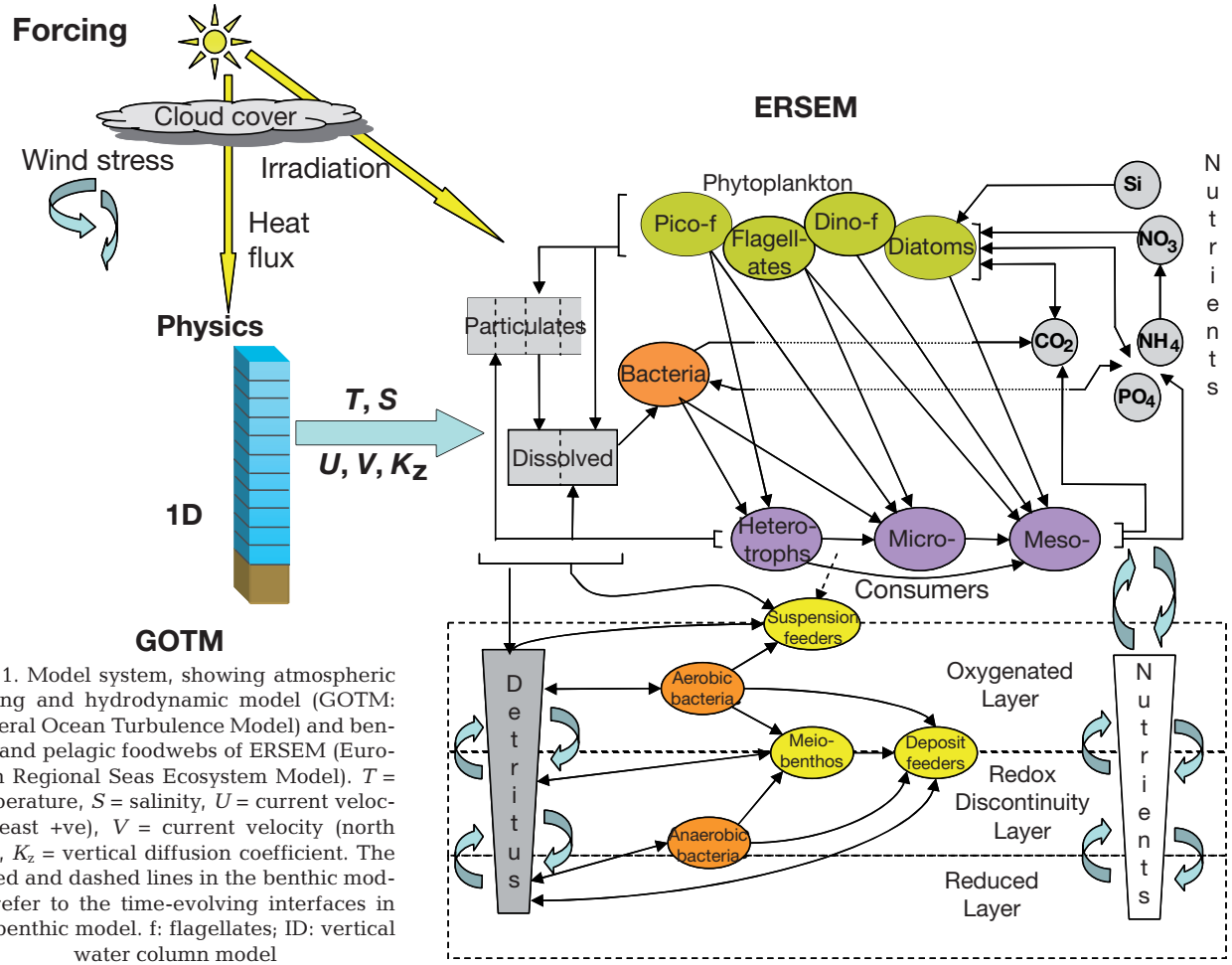

Fig. 1. Model system, showing atmospheric forcing and hydrodynamic model (GOTM: General Ocean Turbulence Model) and benthic and pelagic foodwebs of ERSEM (European Regional Seas Ecosystem Model). T = temperature, S = salinity, U = current velocity (east +ve), V = current velocity (north +ve), K_z = vertical diffusion coefficient. The dotted and dashed lines in the benthic models refer to the time-evolving interfaces in the benthic model. f: flagellates; ID: vertical water column model

should be noted that individual species may behave as both deposit and suspension feeders, thus straddling more than one functional group; consequently, functional groups comprise particular types of behaviour rather than species lists.

The benthic system is driven by the settling of overlying detritus and filter-feeding by suspension feeders. Detritus is remineralised by bacteria releasing phosphate and ammonia into the sediment porewaters. Other chemical processes include nitrification of ammonia, phosphate–sediment interactions and the dissolution of silicate. Nutrients are released from the porewaters into the overlying water column. These flux rates are enhanced by biomass-dependent parameterisations of bioirrigation; a monod function is used to describe the increase in bioirrigation rate as macrobenthic biomass increases. Detailed descriptions of both the equations and parameters can be found in Ebenhöh et al. (1995) and Blackford (1997).

Simulations. Simulations were carried out using water column model representations of 2 distinct stations in the North Sea. (1) Stn CS (55° 30′ N, 0° 50′ E): seasonally stratified, depth 85 m, with moderate benthic influence; (2) Stn AB (52° 40′ N, 2° 25′ E): permanently mixed, depth 50 m, with strong benthic influence.

Both were extensively sampled during the NERC North Sea programme of 1988 and 1989.

The simulations are of a repeating year and forced with reanalysis of meteorological information (ERA40) from the European Centre for Medium-range Weather Forecasting (ECMWF) and relaxed to observed temperature and salinity profiles for 1989. Further details of the simulations and setups, including comprehensive validation, can be found in Allen et al. (2004) and Blackford et al. (2004).

In order to simulate trawling events we made the following assumptions:

- The oxic layer had been removed (set close to zero)
- Deposit feeders, suspension feeders, aerobic bacteria and meiofauna all experience mortality (determined by meta-analysis; Table 1)
- All C, N and P generated is placed in the benthic detrital pool, reflecting the impact of mortality and maintaining the mass balance of the model.

Table 1. Mortality rates (%) under different scenarios

Trawl type/ bed type	Suspension feeders	Deposit feeders	Bacteria and meiofauna
Beam/sand	–73	–23	–67
Beam/gravel	–15	–67	–42
Otter/mud	–31	–18	–29
Otter/sand	–4	–23	–15

In Galveston Bay, USA, observations of the immediate impact of shrimp trawling on the oxic layer indicate that the upper 1 cm of the sediment was re-suspended (Warken et al. 2003). As heavier trawling gear (beam and otter trawls that penetrate to depths of around 6 cm; Duplisea et al. 2001) is used in the North Sea and the oxic depths are generally much less than 1 cm (e.g. Lohse et al. 1993), we assumed that the oxic layer had been removed.

Trawling mortality data, derived from meta-analysis of the scale of trawling impact (Kaiser et al. 2006), is specific to a particular combination of trawling gear and sediment type. Our analysis was performed on the only the 2 functional groups for which there was enough data to determine the effects, i.e. DF (deposit feeders) and SF (suspension feeders). Studies of the immediate impact of scallop drags indicate significant microbial mortality (ca. 50%) in the disturbed layer (Watling et al. 2001). As the meta-analysis of Kaiser et al. (2006) does not provide microbial mortality for each trawl/bed type, we assumed that microbial mortality is dependent on gear and bed type and is therefore the same as that for the whole community (average mortality of all organisms killed during trawling in the experiments considered). Similarly, the mortality rates for meiobenthos were assumed to be the same as those for the whole community.

For each scenario we made an ensemble simulation. Each experiment consisted of 20 simulations with an average of either 2 or 5 trawling events yr^{-1} occurring randomly for 5 yr, followed by 5 yr with no trawling. We chose a 5 yr 'no take' period (Kaiser et al. 2006) because this is the observed timescale for recovery of the benthic community on cessation of scallop fishing in the Irish Sea (Bradshaw et al. 2000).

We then analysed the mean behaviour of the ensemble. An ensemble approach incorporates realistically randomly spaced trawling events in time (a simple Poisson process) and the results are very sensitive to the frequency and number of disturbances (Fig. 2). Our methodology allowed us to investigate the cumulative impacts of trawling on the system when the disturbance frequency was less than the recovery time of the system.

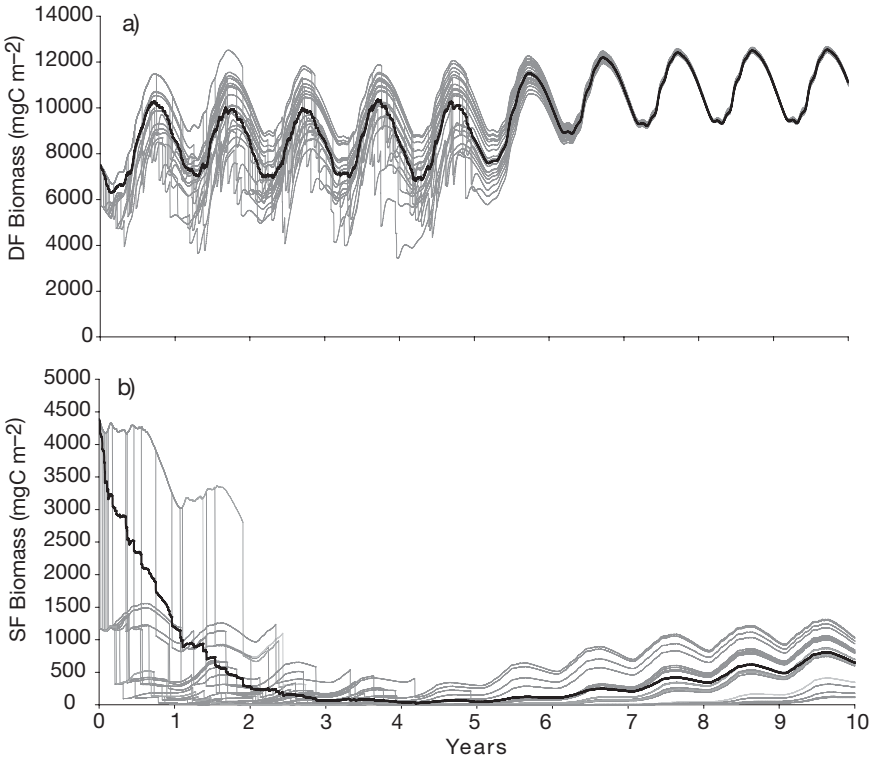

Fig. 2. Example of variability in trawling impact on (a) deposit feeder (DF) and (b) suspension feeder (SF) biomass induced by random timing of trawling events of the same average frequency (2 yr^{-1}) and gear type/bed type (i.e. beam trawling/sand) at the unstratified (AB) site. The 20 ensemble simulations are indicated by thin grey lines, the ensemble mean by the thick black line

Statistical methods. Model outputs were placed into a common format of mean percentage change from control levels, the latter simulated under conditions of no trawling impact. The main model variables subject to further statistical treatment were (1) biomass change in suspension and deposit feeders and in meiofauna, (2) benthic nutrient flux change in phosphate, nitrate and ammonia, (3) depth of oxic layer, and (4) net pelagic primary production.

Mean values of all variables over the replicate simulations were recorded at the end of each of the simulated 10 yr period (5 yr impact followed by 5 yr recovery). The variable set obtained at the end of Year 5 and again at the end of Year 10 were subjected to multivariate analysis, in order to generate an effective simultaneous display of the whole system at those

times. Principal components analysis (PCA, e.g. Chatfield & Collins 1980) was used for this, since the outputs are continuous variables for which standard Euclidian distance is an appropriate distance measure (e.g. Clarke et al. 2006).

The purpose of the PCA is to display, in 2-dimensional space, the appropriate relationship between different status scenarios, i.e. gear type–seabed, gear type–trawl, frequency–stratification, in terms of the similarity of changes they induce in the modelled biomass and flux variables. Provided that the first 2 principal axes (PC1 and PC2) account for much of the total variance in the full variable set, which can happen (as it does here) when there are strong intercorrelations between the modelled variables, then points that are close together on the PCA plot indicate impact or recovery conditions that are similar. Furthermore, the PC axes are simple linear combinations of the model variables, so that the sign of a linear coefficient and its magnitude indicate the direction and strength of the change in that variable across (PC1) or up (PC2) the plot. This can be further emphasised, visually, by superimposing selected variables (e.g. percentage change in suspension feeder biomass) as circles of increasing size (proportional to the value of the variable) onto the points in the PCA plot (see, e.g., Figs. 5 & 7). In a slight variation of the normal procedure, the PCA plots herein use filled circles to indicate negative changes and open circles to indicate positive changes.

Finally, the variables in this case were all on a common scale (% change from control), so it was not necessary to normalise the data before performing PCA. In this way, the variables with the greatest percentage change as a result of the trawling scenarios will make the greatest contribution to the principal axes, as is desirable. This is sometimes referred to as a covariance-based PCA (in contrast with a correlation-based PCA which first normalises all variables to obtain zero mean and unit standard deviation).

All multivariate analyses and displays used the PRIMER software (Plymouth Routines In Multivariate Ecological Research Version 6, Clarke & Gorley 2006).

RESULTS

Reference simulations

At the unstratified site, the annual mean simulated biomass of deposit feeders (DF) was 7754 mg C m^{-2} and that of the suspension feeder (SF) was 4940 mg C m^{-2}, compared with an observed mean DF biomass of 6925 mg C m^{-2} and a mean SF biomass of 4577 mg C m^{-2} for the surrounding region (ERSEM Box 8; Ebenhöh et al. 1995). At the stratified site the annual mean simulated DF biomass was 3901 mg C m^{-2} and SF biomass 2018 mg C m^{-2}, compared with observed mean DF biomass of 3241 mg C m^{-2} and mean SF biomass of 2142 mg C m^{-2} for the surrounding region (ERSEM Box 14; Ebenhöh et al. 1995). In both cases the simulated biomass values were of the same order of magnitude as the observations.

Recovery after a single trawling event

The simulated impact after a single trawling event on DF and SF and their recovery at the unstratified site are shown in Fig. 3; the stratified site (not shown) exhibits similar behaviour. Not surprisingly, the short-term scale of impact reflects the mortality rates in Table 1 and beam trawling has more impact than otter trawling, the impact of a single otter trawl being a disturbance of <20% of the initial condition. Noticeable recovery begins after 2 to 3 wk. Appendix 2 of Kaiser et al. (2006) gives the following descriptions of

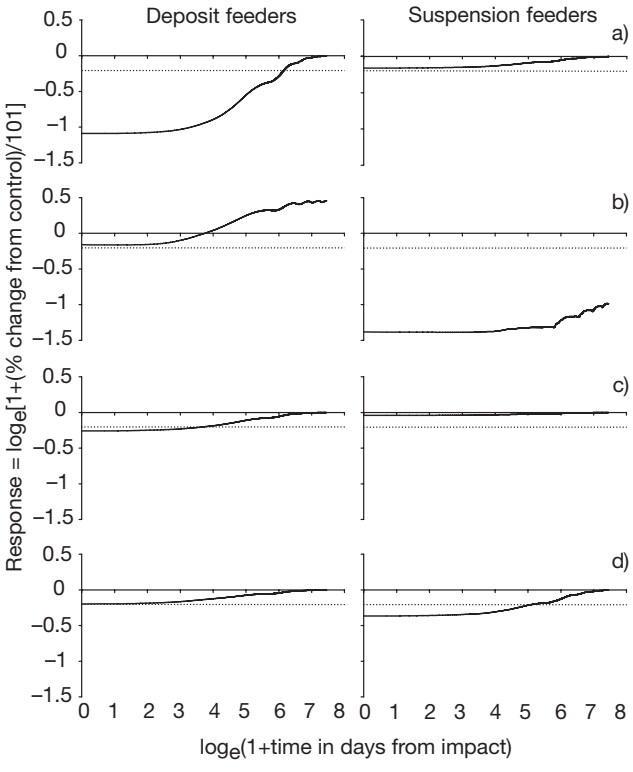

Fig. 3. Recovery times for deposit and suspension feeders after a single trawling event. (a) Beam trawling in gravel, (b) beam trawling in sand, (c) otter trawling in sand, (d) otter trawling in mud. Dotted line indicates recovery to 20% of initial level. Scale for *x*-axis: 2 = 1 wk, 3.5 = 1 mo, 5.9 = 1 yr, 7 = 3 yr; *y*-axis: −1.5 = −78%, −1 = −64%, −0.5 = −40%, −0.25 = −22%, 0 = no change, 0.25 = +29%, 0.5 = +65% (these scales are consistent with the data of Kaiser et al. 2006)

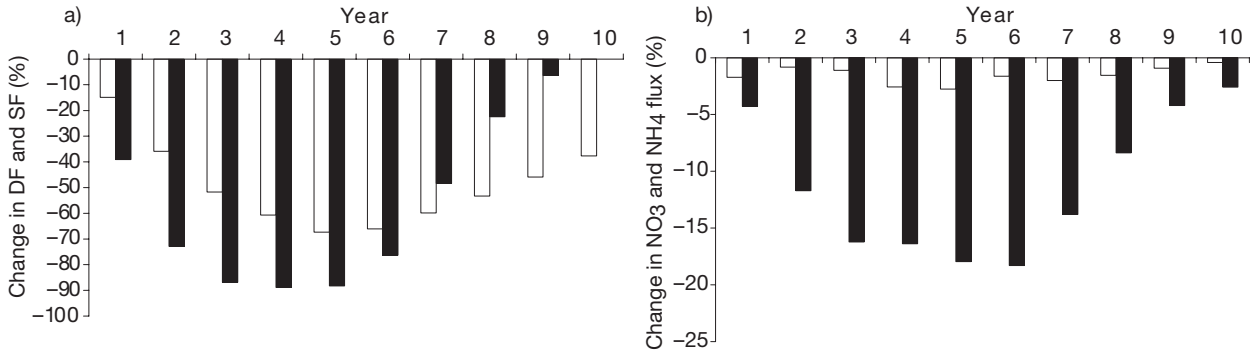

Fig. 4. Mean annual percentage change in ensemble simulations due to beam trawling in sand at a trawl frequency of twice a year for (a) deposit feeders (white bars), and suspension feeders (black bars), and (b) nitrate (white bars) and ammonia (black bars) for each year of simulation compared with the reference (unperturbed) simulation at the stratified site (Stn CS)

the potential impact of a single trawling event: for beam trawling gravel (BTG), there is no data on recovery but a significant initial drop; for beam trawling in sand (BTS), there is no data on recovery but a strong initial drop; for otter trawling in mud (OTM), it takes 1 to 4 d for recovery to 20% of the initial conditions; for otter trawling in sand (OTS), there is no evidence for a drop or subsequent change, and the model reflects this limited information. In the case of simulated BTS where the impact on SF is much larger than on DF, the DF quickly recover to a higher level than the initial level and consequently suppress the recovery of SF which has not recovered to the 20% level after 5 yr, indicating that differential mortality rates on functional groups may have a significant impact on recovery.

Ensemble simulation: basic response

An example of the mean impact for ensemble simulations of 5 yr of disturbance followed by 5 yr recovery upon SF and DF is shown in Fig. 4. This example considers beam trawling in sand (the condition giving the greatest mortality of the 4 scenarios, Table 1) at the stratified station, trawled on average twice each year. After 5 yr trawling, 88% of the SF and 67% of the DF biomass has been removed. After 5 more years with no further impact, the DF have recovered but the biomass of SF is still 40% less than control simulations with no trawling impact. The recovery periods are of similar magnitude to those reported from meta-analysis of experimental studies in Kaiser et al. (2006). For the benthic pelagic exchange of nitrogen, after 5 yr the flux of ammonia has decreased by 20%, while the drop in nitrate is <5%. After 5 yr recovery, the nutrient

Table 2. Effects of disturbance. Change in biomass of benthic fauna, benthic nutrient flux and net primary production after 5 yr trawling as a percentage of the untrawled state, at both the unstratified (AB) and stratified (CS) sites at trawl frequencies of 2 and 5 trawls yr^{-1}. –: no scenario performed

	Unstratified				Stratified			
	Beam trawl		Otter trawl		Beam trawl		Otter trawl	
	2	5	2	5	2	5	2	5
Suspension feeders								
Sand	−99.0	−99.9	−7.8	−9.1	−88.3	−99.9	−2.4	+5.47
Mud	–	–	−68.3	−90.8	–	–	−46.5	−73.8
Gravel	−24.3	−43.8	–	–	+12.0	−23.5	–	–
Deposit feeders								
Sand	+13.1	−18.3	−25.3	−72.4	−67.3	−96.8	−68.3	−97.4
Mud	–	–	−24.5	−64.2	–	–	−57.0	−92.9
Gravel	−88.6	−99.99	–	–	−99.6	−99.99	–	–
Meiofauna								
Sand	−56.7	−58.5	+8.0	+79.3	+14.7	+3.9	+41.6	+62.9
Mud	–	–	+2.8	+49.6	–	–	+24.6	+37.7
Gravel	+78.5	+118.8	–	–	+61.5	+45.1	–	–
Phosphate flux								
Sand	−23.7	−24.5	−0.9	−3.6	−10.9	−15.6	−1.4	−1.5
Mud	–	–	−14.5	−21.0	–	–	−5.8	−9.7
Gravel	−4.3	−12.3	–	–	−1.8	−5.3	–	–
Nitrate flux								
Sand	+30.4	+17.4	−12.7	−14.6	−2.8	−14.5	−7.2	−13.7
Mud	–	–	−1.7	−0.3	–	–	−5.5	−12.9
Gravel	−13.0	−0.04	–	–	−5.3	−11.8	–	–
Ammonium flux								
Sand	−38.7	−38.6	+1.4	−6.6	−18.0	−17.3	+2.1	+5.7
Mud	–	–	−19.7	−31.5	–	–	−6.8	−9.4
Gravel	−3.2	−20.9	–	–	−0.5	−2.3	–	–
Net primary production								
Sand	−2.2	−3.0	−0.1	−1.0	−2.6	+1.5	−0.8	−1.8
Mud	–	–	−1.2	−2.7	–	–	−1.2	−2.7
Gravel	−3.4	−2.6	–	–	−2.0	−5.2	–	–

fluxes have returned to normal. Differences in the response of the 2 sites are highlighted by comparison of Fig. 4 (sand) with Figs. 2 & 3 which show beam trawling in sand at the unstratified site. At the shallower station where benthic–pelagic coupling is stronger, the removal of suspension is almost 100% after 5 yr and the DF have replaced SF.

Effects of disturbance: Years 1 to 5

Table 2 summarises the impact of both beam and otter trawling at different frequencies on different bed types at both stratified (CS) and unstratified (AB) sites. One clear trend emerges from this table: trawling frequency is important. Not surprisingly, the impact is greater the more frequently the site is trawled. Beam trawling generally causes larger reductions in benthic biomass (Table 2), than otter trawling. However the biogeochemical consequences are not so clear-cut (Table 2). The biomass losses due to beam trawling are consistent with the 56% reduction in biomass estimated by Hiddink et al. (2006), based on a size-based model of the impact of the international beam trawling fleet in the North Sea. The standard deviations of the ensemble means demonstrate that ensemble variability ranks as SF ~ DF > nutrient fluxes > primary production (Table 3), reflecting the relative levels of impact of trawling disturbance in different parts of the ecosystem system. High levels of variability (Table 3, Fig 2) illustrate the importance of the return interval, with several trawling events in quick succession causing the biomass to collapse.

Principal component analysis of these results (Table 2) is presented in Fig. 5. The first component explains 74% of the variability and is the following linear combination of the modelled percentage changes from control (untrawled) conditions: PC1 = 0.45DF – 0.51SF – 0.685MF (meiofauna) – $0.1P_{flux}$ + $0.15NO_{3flux}$ – $0.17NH_{4flux}$ – 0.001PP (primary production) – $0.09O_{flux}$. It is dominated by biomass changes, essentially a contrast of deposit feeders with suspension feeders (+meiofauna), with suspension feeders decreasing across the plot (Fig. 5b) and deposit feeders increasing (Fig. 5c). The decrease in suspension feeders is associated with significant reductions in the benthic flux of phosphate, ammonia and an increase in the oxic layer (Fig. 6). The correlations between suspension feeders and these variables are very strong in all cases (PO_4 flux r = 0.91; NH_4, r = 0.86; oxic layer depth r = 0.89). The deposit feeder mortality is associated with a decrease in nitrate flux. The second PC explains about 18% of the variability. It is defined as PC2 = –0.48DF – 0.77SF + 0.33MF – $0.12P_{flux}$ – $0.02NO_{3flux}$ – $0.19NH_{4flux}$ – 0.007PP – $0.12O_{flux}$ and expresses an overall biomass loss (Fig. 5b,c) and the trawling frequency.

Table 3. Standard deviation for change in biomass of benthic fauna, benthic nutrient flux and net primary production after 5 yr trawling as a percentage of the untrawled state, at both the unstratified (AB) and stratified (CS) sites at trawl frequencies of 2 and 5 trawls yr^{-1}. –: no scenario performed

	Unstratified				Stratified			
	Beam trawl		Otter trawl		Beam trawl		Otter trawl	
	2	5	2	5	2	5	2	5
Suspension feeders								
Sand	10.8	1.1	8.6	13.3	13.2	0.2	5.7	11.6
Mud	–	–	47.5	13.3	–	–	16.2	14.2
Gravel	29.1	42.5	–	–	16.3	17.3	–	–
Deposit feeders								
Sand	26.1	24.8	22.8	30.0	13.7	4.4	15.6	3.7
Mud	–	–	19.3	26.4	–	–	14.7	6.7
Gravel	20.7	0.02	–	–	0.9	0.0003	–	–
Meiofauna								
Sand	1.2	15.8	8.7	24.2	5.8	18.3	12.12	3.3
Mud	–	–	4.0	15.4	–	–	8.7	3.6
Gravel	18.7	6.4	–	–	4.5	8.6	–	–
Phosphate flux					–			
Sand	10.1	4.6	5.8	8.1	2.6	2.2	0.0	1.8
Mud	–	–	20.4	10.4	–	–	2.9	2.5
Gravel	10.7	5.8	–	–	2.0	2.5	–	–
Nitrate flux								
Sand	8.3	7.8	10.3	12.4	3.1	6.3	3.7	4.2
Mud	–	–	10.1	13.0	–	–	3.6	2.7
Gravel	7.0	10.3	–	–	2.8	3.2	–	–
Ammonium flux								
Sand	9.0	5.2	7.3	10.3	1.2	3.8	2.6	2.8
Mud	–	–	35.8	14.1	–	–	3.5	3.3
Gravel	18.2	7.3	–	–	3.0	2.7	–	–
Net primary production								
Sand	0.3	0.5	0.08	0.3	0.8	1.1	0.3	0.3
Mud	–	–	0.8	0.4	–	–	0.4	0.7
Gravel	0.7	0.08	–	–	0.3	0.3	–	–

Recovery after cessation of trawling: Years 6 to 10

Table 4 summarises the recovery of the simulated systems 5 yr after the cessation of trawling, on different bed types at both stratified (CS) and unstratified (AB) sites. Once again the clear trend emerges that trawling frequency is important. Not surprisingly, the recovery is dependent on the frequency at which the site is trawled;

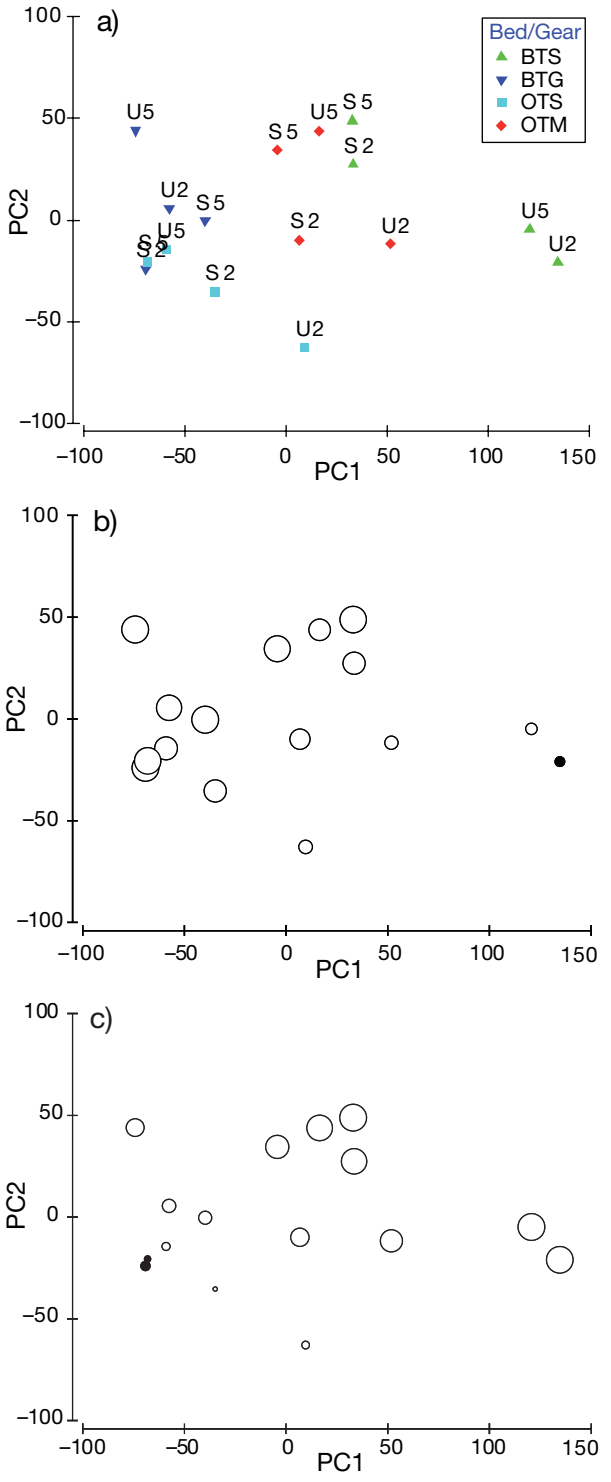

Fig. 5. Principal components analysis of trawling impact (5 yr point). (a) Impact as a function of gear type, substrate and station (BT = beam trawling, OT = otter trawling, S = sand, G = gravel, M = mud, U = unstratified, S = stratified, 2 and 5 = mean number of trawling impacts yr^{-1}); (b) impact on deposit feeders; (c) impact on suspension feeders. ○: negative values (circle size increases with increasing biomass loss, with largest circle corresponding to 99% biomass loss); ●: positive values (circle size increases with increasing biomass)

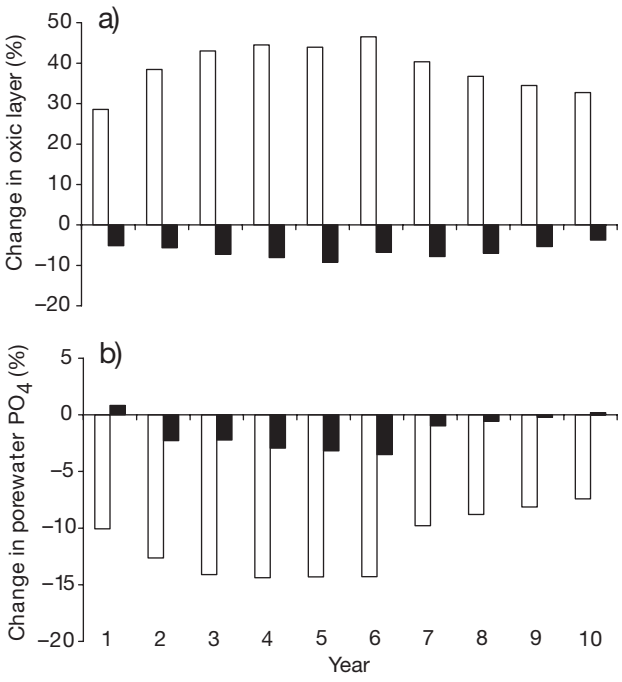

Fig. 6. Changes in (a) oxic layer depth and (b) porewater phosphate for beam trawling in sand (white bars) and gravel (black bars) at the unstratified (AB) site at a trawling frequency of twice a year

the greater the trawling impact the slower the recovery. Sites that have been beam trawled recover more slowly than those that have been otter trawled. Beam trawling generally causes larger reductions in benthic biomass (Table 4). The response of the biogoechemcial fluxes to recovery depends on the type of trawling; beam trawled simulations exhibit significant deviations from the initial conditions, while fluxes in otter trawled simulations generally lie within 5% of the reference solution (Table 4).

The standard deviations for the ensemble means demonstrate that ensemble variability is only large for SF, DF, phosphate and ammonia fluxes at those sites that have been beam trawled (Table 5), reflecting the relative levels of the impact of trawling disturbance in different parts of the ecosystem system.

Fig. 7a shows the PCA of the same variables (Table 4) after a 5 yr recovery period (no trawling). Again the first PC is primarily a measure of the impact on deposit and suspension feeders (Fig. 7b,c). The points on the PCA cluster in 3 regions: (1) those where the suspension feeders have not recovered, characterised by increased oxygen and reduced phosphate and ammonia; (2) those where the system has recovered (most variables are close to the unperturbed state); (3) those where the deposit feeders have been replaced by suspension feeders. The latter are charac-

Table 4. Effects of recovery. Change in biomass of benthic fauna, benthic nutrient flux and net primary production after 5 yr trawling followed by 5 yr no trawling as a percentage of the untrawled state, at both the unstratified (AB) and stratified (CS) sites at trawl frequencies of 2 and 5 trawls yr^{-1}. –: no scenario performed

	Unstratified				Stratified			
	Beam trawl		Otter trawl		Beam trawl		Otter trawl	
	2	5	2	5	2	5	2	5
Suspension feeders								
Sand	–86.0	–99.98	–0.1	–10.9	–37.7	–79.8	+7.8	+50.9
Mud	–	–	–5.8	–2.9	–	–	+2.5	+35.3
Gravel	+0.7	+22.7	–	–	+57.5	+57.8	–	–
Deposit feeders								
Sand	+45.0	+44,9	–0.1	+6.6	–0.1	–92.0	–36.0	–95.7
Mud	–	–	–0.7	–11.1	–	–	–24.3	–87.7
Gravel	–16.9	–99.0	–	–	–99.1	–100.0	–	–
Meiofauna								
Sand	–55.5	–56.2	+0.0	+21.2	+18.9	+41.1	+19.7	+67.9
Mud	–	–	+0.0	+21.3	–	–	+11.5	+59.6
Gravel	+8.8	+128.0	–	–	+71.2	+71.2	–	–
Phosphate flux								
Sand	–20.8	–15.9	+0.0	–3.9	–1.7	–12.8	+0.1	+1.9
Mud	–	–	–0.6	–3.8	–	–	–0.34	+0.5
Gravel	+0.0	–7.3	–	–	+2.81	+1.9	–	–
Nitrate flux								
Sand	+30.7	18.4	+0.1	+3.6	–0.4	–10.7	–0.6	–2.2
Mud	–	–	+0.9	+5.7	–	–	+0.0	–2.3
Gravel	+0.9	+6.4	–	–	–1.8	–1.7	–	–
Ammonium flux								
Sand	–34.5	–27.7	+0.0	–11.3	–2.6	–8.5	0.7	+4.6
Mud	–	–	–1.1	–11.1	–	–	–0.5	+2.3
Gravel	+0.5	–15.9	–	–	+4.7	+4.1	–	–
Net primary production								
Sand	+0.0	–4.9	+0.0	–3.4	–2.7	0.9	–0.9	–2.2
Mud	–	–	+0.0	–2.5	–	–	–1.0	–3.1
Gravel	–1.8	–2.7	–	–	–2.4	–6.9	–	–

terised by a reduction in net primary production because of increased grazing pressure from filter feeders.

Recovery trajectories

These disturbance and recovery patterns are further illustrated by a PCA of the temporal evolution of displacement and recovery for different gear and bed types at the unstratified site (AB), trawling frequency 5 yr^{-1} (Fig. 8). This site/trawl frequency combination is chosen because is illustrates all 3 of the aforementioned responses. The initial disturbances caused by beam trawling are much larger than those caused by otter trawling; the beam trawled simulations reaching a maximum perturbed state after 2 yr compared with 4 to 5 yr for the otter trawl. Almost total recovery for both types of otter trawling is clearly shown, whilst impact of beam trawling is far more significant with no perceptible recovery detected: beam trawling in both sand (SF loss) and gravel (DF loss) give distinct trajectories and end points. It appears that the system will recover to its original state as long as the compound average mortality of either suspension or deposit feeders is less than about 90%. If the mortality exceeds these thresholds, we see a shift in ecosystem function, at least over the timescales of the simulations.

DISCUSSION

Benthic species contribute to the flow of carbon and nutrients between the water column and bottom (benthic pelagic coupling), form habitats (Auster & Langton 1999) and provide important food sources for demersal fish (Greenstreet et al. 1997). Demersal trawling disturbs benthic habitats and species, and can reduce diversity, biomass and production (Hall 1999, Kaiser & De Groot 2000).

It is apparent from our PCA that there are biogeochemical differences between those gear and seabed types that heavily impact suspension feeders and those that impact deposit feeders. When suspension feeders are removed we see a substantial increase in the depth of the oxic layer (Fig. 6a) and a corresponding decrease in porewater phosphate (Fig. 6b). This is because phosphate absorption onto sediments is much greater in the oxic layer (Ruardij & van Raaphorst 1995) and consequently more phosphate is retained by the benthic system. It also allows higher rates of nitrification of ammonia, resulting in the release of more nitrate and less ammonia. There is also a reduction in the silicate flux of up to 10%. The removal of the suspension feeders appears to reduce the benthic oxygen demand significantly, resulting in a more oxic system and a change in both phosphorus and nitrogen chemistry, as observed by Warwick et al. (1997). Studies of the effect on sediment chemistry of the burrowing heart urchin *Brissopsis lyrifera* which oxygenates the sediment (Widdicombe & Austen 1997), demonstrate that increasing oxygenation results in increased phosphate binding due to oxidative precipitation and also in a possible increase in nitrate production. While we recognise that *B. lyrifera* is not a suspension feeder, the observed biogeochemical responses to biologically induced oxygenation are the same.

Table 5. Standard deviation for change in biomass of benthic fauna, benthic nutrient flux and net primary production after 10 yr trawling as a percentage of the untrawled state, at both the unstratified (AB) and stratified (CS) sites at trawl frequencies of 2 and 5 trawls yr^{-1}. –: no scenario performed

	Unstratified				Stratified			
	Beam trawl		Otter trawl		Beam trawl		Otter trawl	
	2	5	2	5	2	5	2	5
Suspension feeders								
Sand	7.4	49.0	0.1	0.2	1.9	32.8	6.8	9.2
Mud	–	–	5.7	5.6	–	–	2.9	32.8
Gravel	13.8	0.8	–	–	4.5	0.4	–	–
Deposit feeders								
Sand	1.6	0.1	0.1	2.1	18.5	8.2	22.2	5.7
Mud	–	–	0.6	1.2	–	–	15.9	8.2
Gravel	68.2	9.4	–	–	2.4	0.0	–	–
Meiofauna								
Sand	0.2	2.3	0.0	0.3	11.7	3.4	14.9	5.5
Mud	–	–	0.0	0.2	–	–	9.4	3.4
Gravel	39.0	0.3	–	–	2.3	0.0	–	–
Phosphate flux								
Sand	2.4	20.3	0.0	0.0	0.0	4.3	1.8	0.0
Mud	–	–	1.1	2.0	–	–	0.0	4.3
Gravel	3.6	0.0	–	–	0.0	0.0	–	–
Nitrate flux								
Sand	1.4	9.2	0.0	0.2	0.8	3.5	0.9	0.4
Mud	–	–	0.8	1.0	–	–	0.4	3.5
Gravel	1.9	0.2	–	–	0.3	0.0	–	–
Ammonium flux								
Sand	5.5	44.4	0.3	0.9	1.9	9.5	1.0	0.3
Mud	–	–	1.7	4.6	–	–	0.3	9.5
Gravel	10.4	1.4	–	–	0.0	0.1	–	–
Net primary production								
Sand	1.5	1.4	0.0	0.1	1.2	2.8	0.5	0.2
Mud	–	–	0.2	0.9	–	–	0.5	2.8
Gravel	1.4	0.3	–	–	0.2	0.2	–	–

Removal of deposit feeders leads to the system becoming slightly more anoxic and a slight decrease in porewater phosphate. The impact on the overlying pelagic production varies between a 1.5% increase (BTS, stratified) to a –5% decrease (BTG, stratified). It may initially seem surprising that large changes in the nutrient supply do not result in a significant change in the primary production of the system. There are several reasons for this: There are 2 opposing influences on production, a restriction in the nutrient supply and a reduction in the grazing pressure when suspension feeders are removed. The ability of phytoplankton to adjust their internal nutrient ratios (C:N, C:P) allows them to buffer production against changes in the nutrient supply (Allen et al. 2006). Also, model primary production is mainly a function of the physical structure of the overlying water column and the availability of light (Allen et al. 2004), drivers which do not change because we use a repeating year forcing on the model. Their contributions always appear to outweigh the impact of changes in benthic–pelagic coupling.

When considering these results we have to understand the limitations of the model processes and assumptions. The ERSEM benthic models (Ebenhöh et al. 1995, Ruardij & van Raaphorst 1995, Blackford 1997) were designed to simulate the inputs, transformations and export of carbon, nitrogen, phosphate and silicate through the benthic system. To do this, the ecosystem structure is considered in terms of function rather than species composition, dividing the foodweb into bacteria (aerobic and anaerobic), meiofauna, suspension feeders and deposit feeders. In doing so, we effectively make the assumption that ecosystem function is independent of species diversity over the range of disturbance investigated.

Auster & Langton (1999) discussed 2 responses of shifts in community structure after disturbance: (1) The successional model, whereby communities change sequentially and is based on 1 community of organisms producing a set of local conditions which make the environment unsuitable for continued survival but suitable for another set of organisms. This is essentially how a functional group ecosystem model such as ERSEM behaves, and this type of behaviour is observed in soft substrate benthic communities. (2) The disturbance-mediated and stochastic model. Shifts in community type are produced by competition and disturbance (e.g. trawling, predation, grazing) that can result in unpredictable community types because they are based on the pool of recruits available in the water column at the time the niche space becomes free. Empirical studies indicate that these shifts are generally found in hard substrate communities (e.g Horn 1976, Witman 1987). As we are considering soft substrates (sand, gravel, mud) in our study, ERSEM is an appropriate tool.

In this study we perturbed a functional-group ecosystem model to investigate the consequences of demersal trawling on both biogeochemistry and ecosystem function. The disturbance and recovery patterns are emergent properties of the perturbed model and are a function of its structure parameterisation and environmental forcing. As the environmental forcing is that of a repeating year, the unperturbed state generally acts as an attractor as the model recovers (Fig 7, Table 4). The exceptions are heavy beam trawling (SF or DF mortality exceeds 90%, average of 5 trawls yr^{-1})

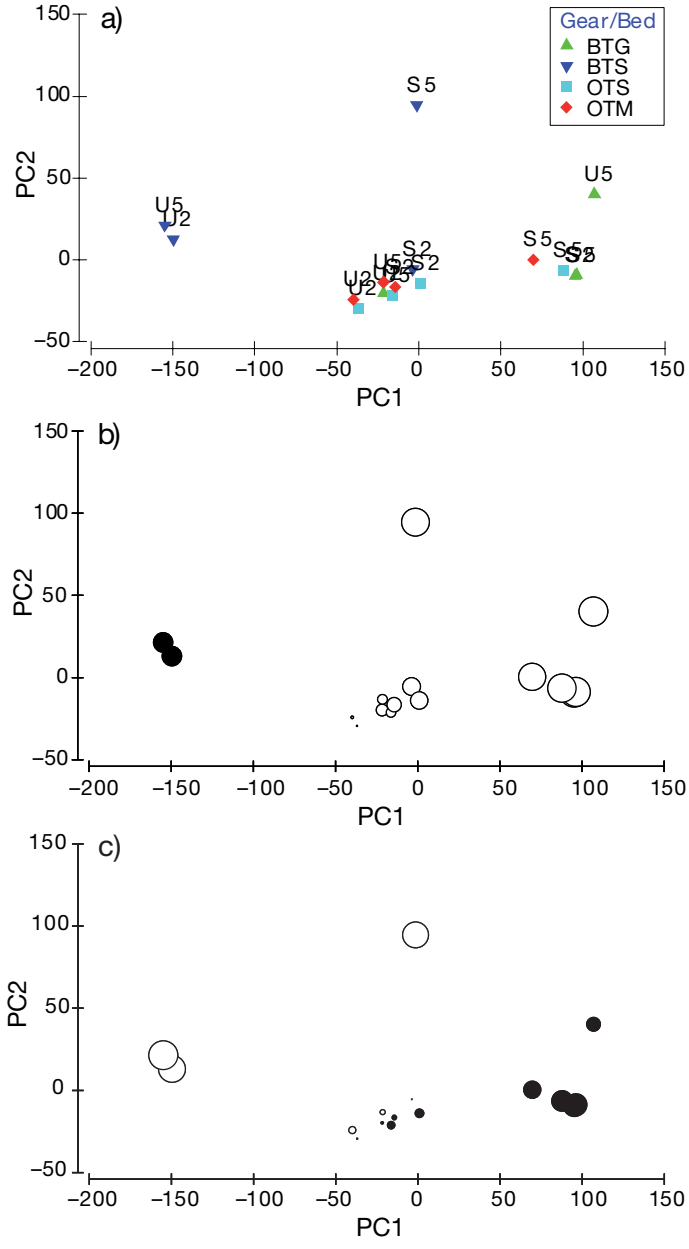

Fig. 7. Principal components analysis of recovery (10 yr point) from trawling impact. (a) Recovery as a function of gear type, substrate and station; (b) impact on deposit feeders; (c) impact on suspension feeders. ○: negative values (circle size increases with increasing biomass loss, with largest circle corresponding to 99% biomass loss); ●: positive values (circle size increases with increasing biomass). Numbers and abbreviations as in Fig. 5 legend

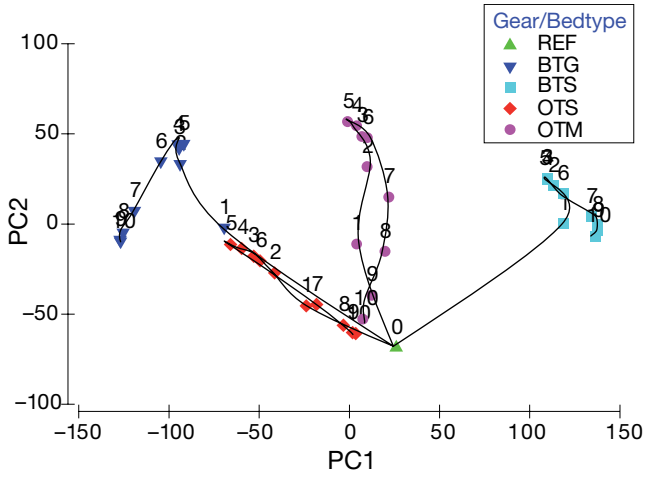

Fig. 8. Example trajectories in PCA space of disturbance (Years 1 to 5) and recovery (Years 6 to 10) using different gear/bed types at the unstratified (AB) site at an average trawling frequency of 5 yr^{-1}. REF: unperturbed reference simulation. Abbreviations as in Fig. 5 legend

for which we see a shift in ecosystem function, at least over the timescales of these simulations. In reality, the environment is constantly changing, which may prevent the disturbed system from returning to its original state. It should be noted that our models do not take account of the spatial movement of benthic animals. In practice, areas of high trawling impact may be recolonised by organisms from the surrounding regions or by the settlement of planktonic organisms, leading to faster rates of recovery than our simulations suggest. These impacts are however difficult to quantify at sites with strong tidal currents and mobile substratum. Trawling changes the community, but it recovers rapidly (e.g. Thrush et al. 1995, Kaiser et al. 1998), although the recovery times for previously untrawled muddy areas can be at least 18 mo (Tuck et al. 1998). We can speculate that these effects would have more impact at the unstratified site where the tidal currents are much stronger. Nor do our models take into account resuspension of sediments and effects of currents on sediment mixing and fluxes of carbon and nutrients. This again may be particularly significant at the unstratfied site where the tidal mixing is strong enough to resuspend sediments.

The absence of predation by demersal fish may also impact recovery times but can probably be discounted, as estimates of benthic faunal mortality due to predation by fish show the effect to be very small (mean mortality rate of 0.1% d^{-1}, Bryant et al. 1995). Another possible process impacting recovery is the addition of discards.

Trawling effort in the North Sea is very patchy (Rijnsdorp et al. 1998), with some regions being trawled > 4 times each year while others are not trawled at all. To assess the cumulative effects of trawling on biogeochemical processes in the North Sea we could apply this methodology of trawling disturbance to the existing 3D POLCOMS ERSEM models of the North Sea (Allen et al. 2001). This would allow us to

explore the impacts and recovery times of existing fishing effort and the potential impacts of different management and conservation strategies.

CONCLUSIONS

Our modelling study suggests that the biogeochemical impact of demersal trawling is most significant in regions where gear type, trawl frequency and seabed type cause high levels of filter-feeder mortality. This results in a substantial increase in the oxygen content of the benthic system and significant changes in its biogeochemistry (increased phosphorus absorption, increased nitrification of ammonia, reduced silicate cycling) which confirms our first hypothesis that removal of suspension feeders leads to a more oxic benthis system.

With regard to our second hypothesis, that the benthic ecosystem recovers within 5 yr of trawling cessation, analysis of the recovery of the benthic system on the complete cessation of demersal trawling suggests that the benthic system will generally return to its original state within 5 yr. Important exceptions are extreme situations where the deposit or filter feeder function is effectively removed, when a permanent change in the functioning of the benthic ecosystem could occur.

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