

Cumulative impacts of seabed trawl disturbance on benthic biomass, production, and species richness in different habitats

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Abstract: Bottom trawling causes widespread disturbance of sediments in shelf seas and can have a negative impact on benthic fauna. We conducted a large-scale assessment of bottom trawl fishing of benthic fauna in different habitats, using a theoretical, size-based model that included habitat features. Species richness was estimated based on a generalized body mass versus species richness relationship. The model was validated by sampling 33 stations subject to a range of trawling intensities in four shallow, soft sediment areas in the North Sea. Both the model and the field data demonstrated that trawling reduced biomass, production, and species richness. The impacts of trawling were greatest in areas with low levels of natural disturbance, while the impact of trawling was small in areas with high rates of natural disturbance. For the North Sea, the model showed that the bottom trawl fleet reduced benthic biomass and production by 56% and 21%, respectively, compared with an untrawled situation. Because of the many simplifications and assumptions required to synthesize these data, additional work is required to refine the model and evaluate applicability in other geographic areas. Our model enables managers to understand the consequences of altering the distribution of fishing activities on benthic production and hence on food web processes.

Résumé : Le chalutage de fond cause une perturbation générale des sédiments sur les plates-formes marines et peut avoir un impact négatif sur la faune benthique. Nous avons évalué sur une grande échelle les effets de la pêche au chalut de fond sur la faune benthique dans des habitats différents à l'aide d'un modèle théorique basé sur la taille qui inclut des caractéristiques du milieu. Nous avons estimé la richesse spécifique en nous basant sur une relation entre la masse corporelle généralisée et la richesse spécifique. Le modèle a pu être validé par l'échantillonnage de 33 stations soumises à des intensités diverses de chalutage dans quatre régions à sédiments mous de la mer du Nord. Tant le modèle que les données de terrain montrent que le chalutage réduit la biomasse, la production et la richesse en espèces. L'impact du chalutage est maximal dans les zones à perturbations naturelles peu importantes et faible dans les zones de fortes perturbations naturelles. Dans la mer du Nord, le modèle prédit que la flotte de chalutage de fond réduit la biomasse et la production benthiques respectivement de 56 % et de 21 %, par comparaison aux zones non soumises à la pêche. Puisqu'il a fallu faire de nombreuses simplifications et présuppositions afin de synthétiser ces données, il faudra beaucoup de travail additionnel pour raffiner le modèle et pour vérifier s'il s'applique à d'autres régions géographiques. Notre modèle permet aux gestionnaires de comprendre les conséquences du changement des répartitions des activités de pêche sur la production du benthos et, par conséquent, sur les processus du réseau alimentaire.

[Traduit par la Rédaction]

Introduction

Fisheries research traditionally has been driven by the requirement to manage stocks of the harvested species. However, research in the last two decades has increasingly focused on the environmental effects of fishing on non-target fauna and marine habitats (Hall 1999; Sinclair and Valdimarsson 2003) and on ecosystem-based approaches to man-

agement that take account of these impacts (Murawski 2000; Brodziak and Link 2002; Link 2002). The impacts of bottom trawls on the seabed are a particular environmental concern because trawls can modify seabed habitat, disrupt food web processes, and extirpate vulnerable species (e.g., Hall 1999). Most existing knowledge of the direct effects of bottom fishing is based on site-specific and relatively small-scale experimental studies (Collie et al. 2000) and comparisons among

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areas subject to known levels of fishing effort (e.g., Hermesen et al. 2003). However, it is not possible to meaningfully extrapolate these results to the scale of the fishery because (i) the results of individual studies usually apply to specific habitat types, while many habitat types are impacted by whole fisheries, (ii) the spatial distribution of habitat type and other environmental factors affecting the benthic community is unknown or not mapped throughout the area fished, and (iii) information on the spatial and temporal distribution of the fishing impact is inadequate (Jennings et al. 2005). The absence of methods for assessing trawling impacts at the scale of the fishery has impeded the development of ecosystem-based management, and attempts to ameliorate the effects of bottom trawling have thus far focused on small-scale area closures to protect vulnerable habitat (e.g., cold-water coral reefs, Hall-Spencer et al. 2002) rather than on management of the overall impact on benthic biomass, production, or diversity.

In coastal seas, the major sources of seabed disturbance are nearbed currents, wind-induced waves (Hall 1994), and bottom trawling and dredging (Jennings and Kaiser 1998). Fishing vessels that target flatfish, gadoids, scallops, and other benthic animals use beam trawls, otter trawls, and scallop dredges that disturb the seafloor to varying depths (from 2 to 20 cm) and kill a substantial fraction of the benthic fauna in the path of the fishing gear. In a global analysis of the effects of bottom fishing, Collie et al. (2000) found that one trawling pass reduced the mean abundance of animals by up to 55%. As benthic invertebrates form the major food source for many commercially exploited fish species, the effects of trawling on the production of benthic communities are of direct relevance for the management of commercial fish stocks and other ecosystem functions the benthos provide (e.g., Link 2002; Widdicombe et al. 2004).

Communities found in locations with high rates of natural disturbance should have characteristics that provide resilience to additional disturbance, since any vulnerable species are unable to become established in conditions of frequent disturbance. Accordingly, the impact of trawling is expected to be proportionately higher at locations that experience low levels of natural disturbance (e.g., deeper water sites) and lower at locations with high levels of natural disturbance (e.g., areas frequently subject to wave action) (e.g., Jennings and Kaiser 1998; Watling and Norse 1998). Despite the potential significance of natural disturbance in determining benthic community responses to trawling impacts, this relationship remains unquantified.

Analyses based on body size consistently explain the fundamental aspects of community structure at many scales and in many ecosystems (Brown and West 2000; Kerr and Dickie 2001). Body size also determines responses to mortality. Since species with smaller body sizes have higher intrinsic rates of increase and can withstand higher rates of mortality, trawled benthic communities tend to be dominated by smaller individuals and species (Kaiser et al. 2000; Duplisea et al. 2002). Ultimately, reductions in the abundance of larger individuals due to trawling may lead to reductions in local species richness. Thus, if all size classes that contain the adults of a given species are lost, then the species becomes extinct, unless it is supported by recruitment or immigration from elsewhere. The cumulative effect of local species loss

will be manifest as regional reductions in species richness. If there are consistent relationships between species number and body size in communities, models of trawling impacts on community size composition could readily be developed to predict the direct effects of fishing on species richness.

Here, we assess for the first time the large-scale impacts of an entire bottom trawl fishery on benthic production, biomass, and species richness in the North Sea. The assessment draws on an existing size-based approach for assessing trawling impacts on benthic communities (Duplisea et al. 2002), with new model development to allow for the effects of habitat parameters on the dynamics of benthic communities and to predict the effects of trawling on species richness. The model estimates benthic biomass, production, and species richness in 9 km² cells throughout the main fishing grounds prosecuted by the North Sea beam trawl fleet, based on the frequency of trawling effort recorded from the satellite vessel monitoring system (VMS) and environmental parameters of habitat type (sediment type, depth, shear stress, and chlorophyll *a* content of the sediment). Model outputs are extensively validated with field data. Although the model is parameterized and validated using data from the North Sea, the generality of the size-based model ensures that the approach is likely to be applicable in other shallow shelf seas.

Materials and methods

Model development

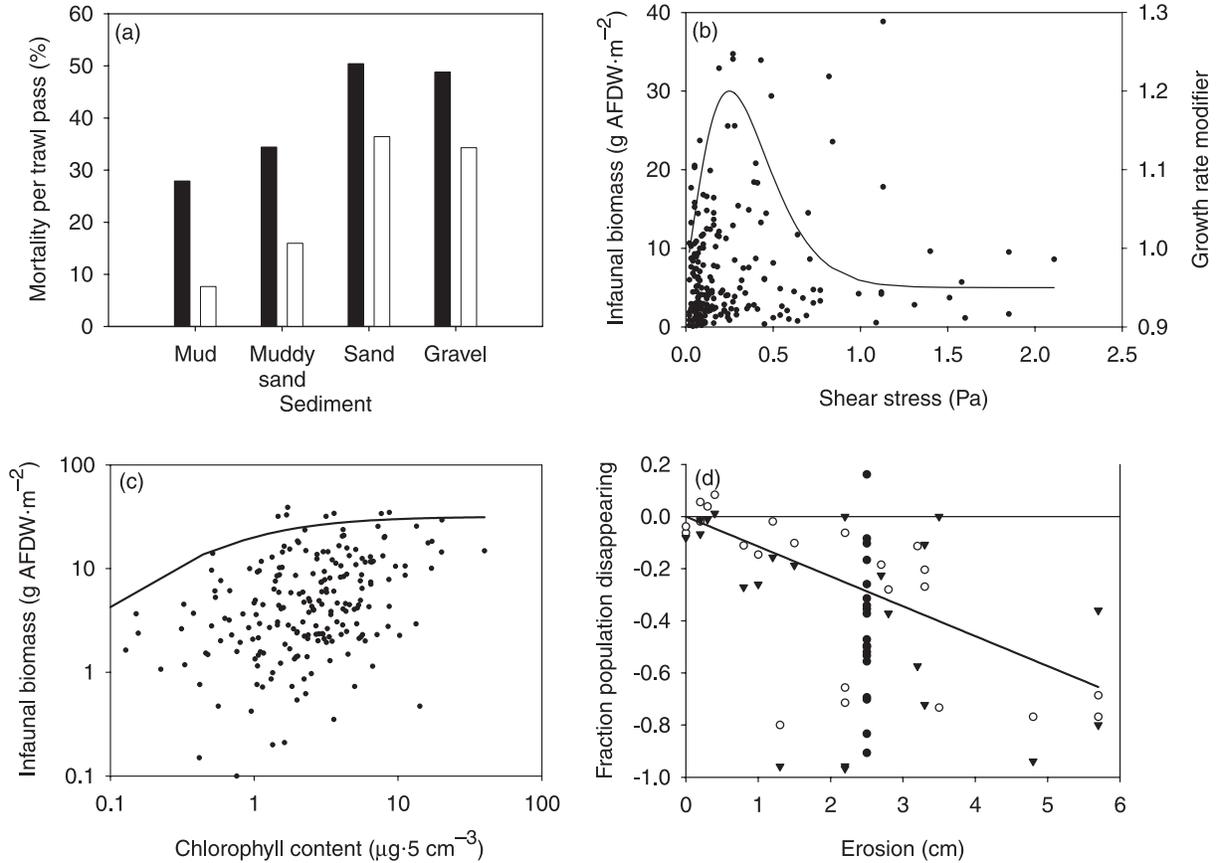
State variables in the model were defined on the basis of body size and two faunal groups: soft-bodied macrofauna (SOFT), such as polychaetes, and hard-bodied macrofauna (HARD), such as bivalves and crustaceans. The model contained 32 state variables: 16 SOFT (1.9–500 mg) and 16 HARD (50–60 000 mg). Since the 32 state variables represented only two groups differing in body size, there were only two sets of parameters, and the model was relatively simple in both structure and parameter demands. Growth of the population biomass in each body size and organism type compartment was modelled by modifying the basic Lotka–Volterra competition equations to give the population biomass flux for a compartment:

$$(1) \quad \frac{dB_i}{dt} = B_i r_i \left(\frac{C_i - B_i - \alpha_{ij} B_j}{C_i} \right) - B_i \text{Mort}_i$$

where *i* and *j* are competing groups of organisms, *B_i* is the biomass of animals in compartment *i*, *r* is the specific growth rate, *C_i* is the carrying capacity for compartment *i*, *B_j* is the biomass of competitor *j*, *α_{ij}* is the competitive influence of a unit of the competitor *j* biomass on the carrying capacity of population *i*, and *Mort_i* is the mortality rate of compartment *i*. SOFT and HARD were assumed to be in competition (Wilson 1990). Table 2 in Duplisea et al. (2002) summarizes all parameter values for all size classes of the three faunal groups.

The interaction between habitat type and trawling effects was modelled by including relationships between growth and the environment and between mortality and the environment. We included the effect of (i) sediment type on trawling mortality, (ii) bed shear stress on population growth rate,

Fig. 1. Parameterization of the model. (a) % mortality for a single trawl pass (beam and otter trawl) for hard- (solid) and soft-bodied (open) invertebrates on four sediment categories. (b) The relationship between infaunal biomass in the North Sea and bed shear stresses due to the M_2 tide. The plotted line relates shear stress to the growth rate modifier in the model (right axis). (c) Infaunal biomass and chlorophyll *a* content of the sediment in the North Sea. See the text for a description of the fitted regression line. (d) The fraction of the population of infaunal animals disappearing and sediment erosion. Solid circles, Zühlke and Reise (1994); open circles, hurricane (Yeo and Risk 1979); solid triangles, storm (Yeo and Risk 1979). The regression line was fitted through all data points. AFDW, ash-free dry weight.



(iii) chlorophyll *a* content of the sediment on carrying capacity, and (iv) sediment erosion on mortality.

Trawling mortality in different sediments

Mortality caused by a single trawl pass on different sediments was estimated from a meta-analysis of experimental studies, including studies carried out in North Sea, by Collie et al. (2000). This is currently the most extensive quantitative database describing the direct effects of trawling on the abundance of benthic species. Only those studies that examined the effects of otter trawling and beam trawling on gravel, mud, muddy sand, and sand habitats in the subtidal zone were included. Because we wanted to estimate the mortality caused by a single trawl pass, we included only those studies that examined the effect of a single trawling event and that sampled the substratum within 10 days of that event. As one trawling event could consist of one or more trawl passes, the effect size was corrected by assuming that the passage of every trawl led to the same proportional reduction. Each species in the database was assigned to the classes SOFT or HARD. The impact of trawling on a species (percent increase or reduction after trawling compared with the condition before trawling or a control area) was $\ln(x + 101) - \ln(101)$ transformed to normalize the data (Collie et al. 2000). The impact of one trawl pass was calculated from the coefficients

of a two-way analysis of variance (ANOVA), with sediment type and faunal group as factors. After the analysis, figures were back-transformed to give percent mortality caused by one trawl pass. In total, 381 records from 24 experimental manipulations from 10 studies were used. There was no evidence for body-size-dependent mortality in these data and so no size dependence was assumed. Mortality rates were higher for HARD than for SOFT and were higher for coarser sediments (gravel, sand) than for finer sediments (mud, muddy sand) (Fig. 1a). There was a significant effect of sediment ($F_{[3,376]} = 4.9$, $p = 0.0025$) and faunal group ($F_{[1,376]} = 5.4$, $p = 0.0205$) on trawling mortality. Trawling mortality was implemented as a discrete, annual event. This is probably realistic given that most trawling in the North Sea appears to be clustered in time on a small scale. We assumed no direct effect of sediment on benthic growth or on mortality rates (Snelgrove and Butman 1994). Instead we assumed that any correlations between sediment type and benthic community biomass could be explained through the correlation of sediment type with shear stress, chlorophyll *a* content, and erosion rates.

Shear stress

Currents and the associated seabed shear stress can influence food availability for benthic communities (Jenness and

Duineveld 1985) and benthic secondary production (Warwick and Uncles 1980; Wildish and Peer 1983). High shear stress results in scouring and high current velocities inhibit feeding activity, but some water movement at the seabed is necessary to supply food to the benthos. Below a certain current velocity threshold, food particles transported from other areas may begin to sink to the seabed, where they become available as food to the benthos (Creutzberg 1984). Therefore, we assumed that bottom shear stress affected the biomass of benthic communities primarily through growth rate. A quantile regression showed that infaunal biomass at 209 stations (VLIZ 1986) is limited by M_2 bottom shear stress (generated by the M_2 , or semidiurnal, component of the tidal current) according to a second-order polynomial optimum relationship (90th quantile, $p = 0.034$, $R_1 = 0.053$) (for more information on quantile regression, see Cade et al. 1999) (Fig. 1b). Visual examination of the relationship among benthic biomass, shear stress, and chlorophyll *a* content of the sediment indicated that there was no interaction between the effect of shear stress and chlorophyll *a* content of the sediment. The relationship between growth rate and shear stress was modelled by multiplying the density-dependent growth rate, as calculated by the Lotka–Volterra equation, with a factor that describes the effect of shear stress on the growth rate. The relationship was modelled as a Gaussian curve according to

$$(2) \quad G = G_{\min} + (G_{\max} - G_{\min}) e^{-\frac{(S - S_m)^2}{V}}$$

where G is the shear-dependent growth rate modifier, G_{\min} is the minimal growth rate (0.95), G_{\max} is the maximal growth rate (1.2), S is shear stress^{0.5}, S_m is the shear stress^{0.5} at which the maximum growth rate is reached (0.5), and V is the variance of the Gaussian curve (0.075).

Carrying capacity

Carrying capacity in the model is simply a scaling factor. Thus, absolute values do not affect the model outcomes, but the relative differences between size classes and stations do. The biomass of benthic communities in a habitat can be limited by the input of food (Beukema and Cadee 1997). The base of the benthic food chain in generally fuelled by microalgae. We used a type II functional response to describe how benthic biomass (g ash-free dry weight·m⁻²) in the North Sea was limited by the chlorophyll *a* content of the sediment using data from the North Sea Benthos Survey in April–May 1986 (VLIZ 1986) using upper boundary analysis (Blackburn et al. 1992): infaunal biomass = 54.6 chlorophyll *a* / (1 + 1.72 chlorophyll *a*), $R^2 = 0.66$, $F_{[1,12]} = 23.3$, $p = 0.0004$ (Fig. 1c).

Sediment erosion due to disturbance by waves and tides

Additional to the normal mortality rates, which relate to body size, sediment movement due to wave action caused by wind and tides can be a major cause of mortality among benthic animals and has been shown to affect secondary production (Emerson 1989). The relationship between sediment erosion and benthos mortality was parameterized using mortality and erosion data from Zühlke and Reise (1994) and Yeo and Risk (1979) and can be described by the following equation: benthos population reduction (%) = 0.14 erosion depth (cm), $R^2 = 0.34$, $n = 67$, $p < 0.0001$ (Fig. 1d). SOFT

and HARD were assumed to be affected in the same way, as there was no data to justify discriminating between these groups. Yearly mortality rate due to sediment erosion was modelled as erosion mortality = 1 – (1 – mortality per storm)^{number of storms}. A storm was defined as an event where the significant wave height was over 4 m.

Modelled relationships between body mass and species richness

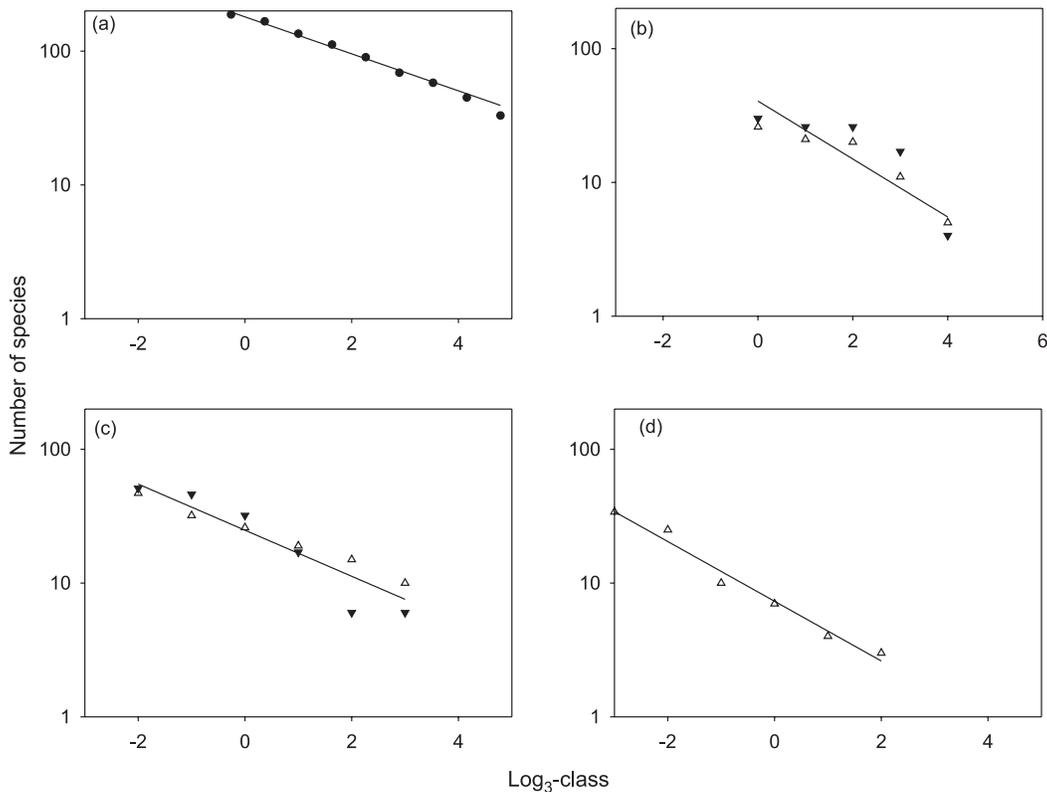
To relate the reduction in biomass of a body mass class to species loss, it was necessary to (i) describe the relationship between the number of species in each body mass class and body mass and (ii) identify a threshold biomass reduction at which species loss was assumed to occur.

In most taxonomic groups and ecosystems, the relationship between species richness and body size is strongly right-skewed log-normal. Above the modal size class, the relationship between species numbers and body size is generally log-linear (Gaston and Blackburn 2000). The relationship between species richness and body mass was determined from the slope of a regression of the number of species in log₃ body mass classes versus log body mass. All species of free-living infauna and epifauna recorded in the central North Sea by Jennings et al. (2002b) were used to determine this relationship, and the heaviest body mass class to which species were assigned was based on their maximum recorded body mass (since maximum observed body mass in trawled areas will fall in response to elevated mortality; for more details see Jennings et al. 2002b). Thus, smaller body mass classes had more species than large body mass classes, as they contain both juveniles of large species and adults of small species. The relationship between the log number of species and log body mass for the body mass range considered was linear (Fig. 2a, $R^2 = 0.993$, $F_{[1,8]} = 952$, $p < 0.001$). If it is assumed that a species is found in its adult body mass class and in all smaller body mass classes as juveniles, the number of adult species in a body mass class can be described by the slope (derivative) of the relationship describing species number versus body mass (number of adult species per log₃ body mass = 65 exp(–0.35 log₃ body mass)). The relationship between size and species richness that is determined here is valid for soft-sediment communities in the North Sea, and the exact shape of the relationship may differ for other areas and habitats.

The average ratio of size at maturity to maximum body size is two-thirds of body length for species in which growth is described by a Von Bertalanffy growth equation (Charnov and Berrigan 1990). Assuming that body mass increases linearly with the cube of length, the predicted body mass at maturity is 30% of maximum body mass, and almost all mature individuals of a species will be found in the top log₃ body mass class of its size distribution. Adult individuals of each species were assumed to be present only in the heaviest log₃ body mass class. To test the validity of this assumption, we estimated the empirical ratio of the body mass at maturity (W_{mat}) to the maximum body mass (W_{max}) as reported in published literature. If length rather than body mass was reported, we assumed that body mass scaled to length cubed (Charnov 1993).

Species were assumed to be extirpated if the adult biomass fell by 95% from unimpacted levels. This assumption

Fig. 2. The number of species per \log_3 body mass class in the North Sea. (a) Central North Sea, data from Jennings et al. (2002b). (b) Epifauna sampled with a 2 m beam trawl. (c) Large infauna sampled with a toothed dredge. (d) Small infauna sampled with a Hamon grab. Lines are least squares regression lines through all data points. Open triangles, Dogger Bank (DB); solid triangles, North-west Rough (NW).



follows from the World Conservation Union (IUCN) criterion (A1) that a species is critically endangered when adult abundance declines by 90% over 10 years or three generations (Hilton-Taylor 2000). The average, unimpacted biomass per \log_3 body mass class was obtained by running the model with trawling intensity set to zero for the Dutch and British sectors of the North Sea in the area south of 56°N , as this was the area for which all environmental data were available. The areas inside the coastal 12 nautical mile (1 n.mi. = 1.853 km) zone and the “plaice box” (a gear restriction area to protect juvenile European plaice, *Pleuronectes platessa*) were excluded from the analysis, because no reliable fishing effort data were available for these areas.

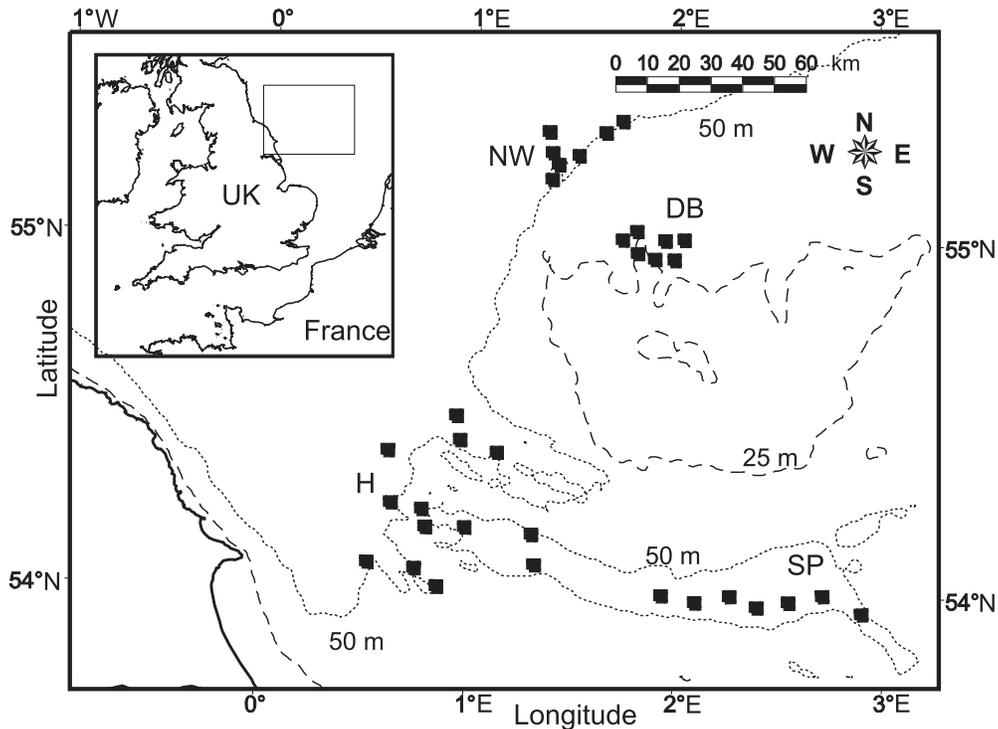
In the model, the loss of the adult size classes did not affect the abundance of the smaller size classes. Despite the local extirpation of a species, we assumed that the biomass of the juveniles of those species that were lost could be replaced by juveniles and adults of smaller body size species. This is consistent with the Lotka–Volterra competition equation model formulations.

Habitat data for the North Sea

Data on sediment, depth, shear stress, and chlorophyll *a* content of the sediment were necessary to validate the model and to make large-scale predictions of the effects of trawling on biomass and production in the North Sea. Sediment data were obtained from digital British Geological Survey (BGS) sediment maps for the North Sea (BGS 2002). Because the relationship between sediment and trawling mortality was

parameterized for four sediment classes only (gravel, mud, muddy sand, sand), the BGS classification (Wentworth Folk classification in 15 classes) was simplified into these four classes. All sediments with gravel content of more than 5% were classified as gravel. For sediments with less than 5% gravel, a sand:mud ratio of more than 9:1 was classified as sand. Sediments with a sand:mud ratio between 1:1 and 9:1 were classified as muddy sand, and sediments with a sand:mud ratio smaller than 1:1 were classified as mud. Depth was interpolated using inverse distance weighing from a 1 n.mi. resolution data set. A two-dimensional hydrodynamic model of the northwest European shelf, originally developed at the Proudman Oceanographic Laboratory, UK, was used to predict the mean depth M_2 tidal current at a spatial resolution of $1/8^\circ$ longitude by $1/12^\circ$ latitude (approximately 8 km). Bed shear stresses due to the M_2 tide were then calculated using a quadratic expression, with bed stress dependent on the predicted maximum ellipse current and an appropriate bed friction coefficient, which we assumed to have a value of 0.0025 (Howarth and Proctor 1992). Sediment erosion rates due to the combined effects of currents and wind-induced waves were modelled as the maximum erosion for a single event (i.e., the maximum erosion depth that occurred over the whole year). They do not take account of bedload transport or modifications to current associated with bedforms (J.N. Aldridge, CEFAS, Lowestoft, NR33 0HT, UK, unpublished data). On average, there are 4.75 major storms of similar magnitude in a year (Centre for Environment Fisheries and Aquaculture Science 2004). The chloro-

Fig. 3. Overview of the study areas and sampling stations in the North Sea. Stations subject to different levels of trawling disturbance within the four areas: DB, Dogger Bank; H, Hills; NW, Northwest Rough; SP, Silver Pit. The 25 and 50 m depth contours are shown.



phyll *a* content of the sediment was interpolated using inverse distance weighing from the data for 209 stations in the North Sea, which were spaced by 0.5° longitude and latitude (VLIZ 1986).

Trawling effort

Trawling effort was calculated from European Community Satellite Vessel Monitoring System (VMS) data. From 1 January 2000 onwards, all European Community fishing vessels over 24 m were required to report their location, via satellite, to monitoring centres in their flag states, at 2 h intervals. The only exception is made for vessels that undertake trips of <24 h or that fish exclusively within 12 n.mi. of the shoreline (Dann et al. 2002). The proportion of fishing vessels <24 m is probably very low in the offshore areas we examined. The VMS data does not indicate whether a vessel is fishing when it sends position data, but the speed of a vessel can be derived from two consecutive records. Accordingly, vessels travelling at speeds greater than 8 knots and stationary vessels were eliminated as these vessels were assumed not to be fishing (for more details see Dinmore et al. 2003). As the composition of the benthic community is determined by the trawling history, the number of trawl passes per nine square kilometre cell per year was calculated from the number of records in a cell in the period from 1 July 2000 to 31 December 2002. For the calculation of trawling intensity (year⁻¹), it was assumed that trawlers fished at a speed of 5 knots, with a total fishing gear width of 24 m (i.e., two beam trawls each of 12 m wide or one 24 m wide otter trawl) (Davidse and De Wilde 2001). Therefore, one record represents a trawled area of 0.449 km², and one record in a 9 km² cell over the 2.5 year period therefore represents a trawling intensity of 0.0198 year⁻¹. The lower limit to the

scale at which trawling effort could be evaluated was defined by the resolution of the VMS records. The 9 km² scale as used is close to the 1 × 1 n.mi. scale at which fishing effort becomes random (Rijnsdorp et al. 1998). 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. Additional trawling intensity figures were obtained from records of vessel sightings by fishery protection aircraft as described by Jennings et al. (2001). Within each area, the number of fishing beam or otter trawlers were counted and corrected for the number of visits as a measure of trawling intensity.

Effect of trawling on production, biomass, and species richness in different habitats

Empirical assessments of the effects of trawling were based on measurements of biomass, production, and species richness at sites subject to different levels of fishing intensity in up to four areas with different habitat types. These assessments were used to test model predictions. Data for two of these areas (Silver Pit (SP) and Hills (H)) were taken from Jennings et al. (2001, 2002a) and reanalyzed and summarized in this paper.

Experimental design

Each area was characterized by strong gradients in trawling intensity across a homogenous habitat (Fig. 3, Table 1). We expected trawling effort to be spatially heterogeneous in areas of relatively homogeneous habitat because trawlers tend to fish along tows that are recorded in their navigation systems and are known to be free of obstructions that could damage the trawl gear (Auster and Langton 1999; Holland

Table 1. Environmental and sampling characteristics of the sampled areas in the North Sea.

(a) Environmental characteristics.								
	Dogger Bank		Hills		Northwest Rough		Silver Pit	
Sediment	Sand		Sand		Sand		Muddy sand	
Depth (m)	25–30 (27.3±2.0)		39–62 (51.4±5.3)		49–63 (53.1±5.2)		54–73 (65.3±7.0)	
Bed shear stress (Pa)	0.11–0.17 (0.14±0.02)		0.37–0.76 (0.54±0.12)		0.10–0.15 (0.13±0.02)		0.18–0.30 (0.23±0.04)	
Erosion (cm)	0.04–0.07 (0.05±0.01)		0.12–0.21 (0.16±0.03)		0.07–0.09 (0.08±0.01)		0.04–0.09 (0.06±0.02)	
Chl <i>a</i> in sediment ($\mu\text{g}\cdot 5\text{ cm}^{-3}$)	4.9–5.6 (5.4±0.3)		2.5–5.0 (3.6±0.8)		3.7–4.3 (4.0±0.3)		2.9–6.4 (4.2±1.2)	
Trawling intensity (year^{-1})	0.20–4.88 (1.45±1.97)		0.06–2.35 (0.67±0.72)		0.05–8.17 (2.46±2.90)		0.53–5.38 (1.94±1.80)	

(b) Sampling characteristics per sampling gear.								
	Dogger Bank		Hills		Northwest Rough		Silver Pit	
	Stations × samples	Sampling date	Stations × samples	Sampling date	Stations × samples	Sampling date	Stations × samples	Sampling date
2 m beam trawl	7 × 3	Sept. 2003	13 × 6	Nov. 1999 and May 2000	7 × 3	Mar. 2003	6 × 6	Nov. 1999 and May 2000
Anchor dredge	—	—	13 × 6	Nov. 1999 and May 2000	—	—	6 × 6	Nov. 1999 and May 2000
Toothed dredge	7 × 3	Sept. 2003	—	—	7 × 3	Mar. 2003	—	—
Hamon grab	7 × 5	Sept. 2003	—	—	—	—	—	—
Box corer	—	—	—	—	—	—	24 × 10	Nov. 2000 and Apr. 2001

Note: Data for environmental characteristics represent range, with mean ± standard deviation in parentheses. Chl *a*, chlorophyll *a*.

and Sutinen 2000). This pattern of effort within habitats persists over many years, and Dinmore et al. (2003) showed that unfished areas are not necessarily unsuitable for trawling. Therefore, at the scale of the study, trawling effort distributions were unlikely to be related to patterns in ecosystem productivity. If fishers nevertheless concentrate in areas with a high ecosystem production, this would decrease the power to detect a negative effect of trawling on benthic production, and therefore our conclusions would be conservative.

Within each area, 7–24 stations were sampled. Areas had the same sediment type (BGS sediment maps) and local environmental conditions, but the stations within areas were subject to different trawling intensities (Table 1). Stations were defined as 6.25 km² boxes. The maximum distance between stations within an area varied between 19 and 62 km. Trawling intensities, as calculated from the VMS data, were additionally verified by counting trawl marks on sidescan sonar images of the seabed obtained at the time of sampling (Friedlander et al. 1999).

In the analysis of macrofauna from the SP, station 7 from Jennings et al. (2001, 2002a) was excluded because it was situated on the Dutch continental shelf. As a result, effort figures were probably not consistent with data from UK waters. It was also classified as having a different sediment type. VMS fishing effort figures that became available after Jennings et al. (2001, 2002a) were included in our analysis, allowing all 24 stations in the UK sector to be used as replicates (conversion of eight stations × three replicates design to 24 stations × one replicate design).

Estimation of trawling disturbance

We used the VMS data to calculate trawling intensity as described earlier. The H and SP were sampled in 1999 prior

to the introduction of VMS recording, but it was assumed that patterns in fishing effort were stable over time, thus making it possible to compare the effect of trawling in the different areas on a common trawling intensity scale. There was a significant positive relationship between VMS trawling intensity and the relative trawling intensity calculated from overflight observations for the stations in the SP and H areas at a scale of 3 km × 3 km ($R^2 = 0.72$, $F_{[1,17]} = 45.0$, $p < 0.0001$). This suggests that the trawling effort distribution was reasonably stable through time and that current VMS data could reasonably be used as a surrogate for fishing effort when the SP and H areas were sampled.

Sampling of the invertebrate community

Epifauna were defined as those species that live on the seabed or burrow in it temporarily, while infauna were defined as those for which parts of the body remains more or less permanently in the substratum. Most epifaunal invertebrates are part of the HARD component in the model, while both HARD and SOFT are represented in the infauna. The different components of the benthic community were used as indicators of total benthic community biomass in validation of the model.

We sampled the different components of the benthic community with several sampling devices, partly because of the sediment characteristics in the different areas. Communities of small infaunal invertebrates were sampled with a 0.1 m² NIOZ box corer in the SP area and with a 0.1 m² Hamon grab in the Dogger Bank (DB) area. Samples were passed through a 1 mm sieve; all animals were picked off the sieve and preserved in 4% buffered formalin. Because the Hamon grab penetrates less deeply into the sediment (<10 cm, often less than 5 cm) than the NIOZ box corer (>20 cm), biomass estimates among gears were not directly comparable. Larger

infaunal animals were sampled with an anchor dredge (Kaiser et al. 1998) in the SP and H areas and with a toothed dredge in the Northwest Rough (NW) and DB areas. The anchor dredge was towed across the seabed for 1 min. A subsample of 0.2 m³ of sediment was taken from each anchor dredge sample and sieved through a 1 mm square mesh. All free-living infaunal species retained by the mesh were removed for processing. The toothed dredge had twelve 15 cm long teeth across the 120 cm wide mouth opening and a 5 mm × 5 mm mesh liner and was towed at a speed of 1.5 knots for 3 min. Epifaunal invertebrates were sampled with a 2 m beam trawl fitted with a chain mat and a 2 mm mesh liner (Jennings et al. 1999). The beam trawl was towed at a speed of 1.5 knots for 5 min. All organisms taken in the beam trawl and toothed dredge sample were removed for processing. Start and end positions for the beam trawl and toothed dredge hauls were recorded at DB and NW using the ships' differential global positioning system (DGPS) and the towed distance (m) calculated from these positions. The towing period was timed from the moment that the net contacted the seabed until the moment of hauling. For H and SP, the trawled distance with the beam trawl was not recorded and was assumed to be the average of the distances trawled on DB and NW, which was 300 m. As the same sampling protocol was used in all areas, this assumption may increase the variation in the estimates of biomass per square metre, but not does affect the bias in the estimates. The number of replicate samples, which were taken at haphazard locations within each box, is given in Table 1.

Biomass estimates

All preserved animals from the replicate grabs were sorted and identified to the lowest practicable level in the laboratory, and wet mass was determined after blotting. Animals were identified only in the NW and DB areas. All animals from the replicate beam trawl and dredge samples were identified and individually weighed on heave-compensated balances. Hermit crabs (Paguridae) were weighed after removal from their shells, but animals that secreted their own shells were weighed with the shells intact. Most individuals estimated to weigh less than 0.5 g were preserved and weighed on return to the laboratory. We did not apply shrinkage factors to account for weight changes following preservation, as these were not available for the very wide range of species included in our samples, and blotted weight was recorded in each case (Jennings et al. 2001). Subsequent conversions between wet weight (WW) and ash-free dry weight (AFDW) were made using conversion factors provided by Brey (2001). In the grab and core samples, only infauna with a WW < 1 g were considered in biomass analyses, and only infauna >0.78 mg and <62.5 mg AFDW were considered in production analyses. Animals outside these limits were considered not to have been sampled quantitatively and might have greatly increased the variance in our production estimate. This caused an underestimate of total infaunal production. We only considered epifaunal animals from the beam trawl samples and infaunal animals from the dredge samples

Production estimates

Production was calculated from individual body weights using allometric relationships. For all epifauna and for the

infauna sampled with the dredges, we used the production–biomass ($P:B$) relationship $\log_{10} P:B = -0.233 \log_{10} B - 0.197$ (Jennings et al. 2001). For small infauna sampled with corers–grabs, we used the relationship $\log_{10} P:B = -0.236 \times \log_{10} B - 0.431$ (Jennings et al. 2002a). Calculated estimates of biomass and production are not identical to those reported by Jennings et al. (2001, 2002a) because conversion factors were updated and different selection criteria were used (as described earlier) to make sure that data from all areas were analyzed in the same manner.

Species richness analysis

Loss of diversity was reported as a proportional loss of species from body mass classes >0.2 g. This approach was adopted because the number of local species will be smaller than the number of regional species, and we wanted to apply the model consistently at different scales. In adopting this approach, we assumed that the slope of the regression of the number of species in \log_3 body mass classes vs. \log body mass was a constant in all communities. We tested this by comparing the slope for the entire central North Sea species pool against the slopes for the sampled (local) communities. We also reported losses of diversity in proportional terms, as none of the sampling methods used to validate model outputs sampled the whole community (as modelled).

The hypothesis that large species decreased at a faster rate than small species with trawling disturbance was tested by comparing the slopes of the regression of species number against trawling intensity (number of species lost per unit trawling effort) for four body mass classes for the three sampling gears used. All species were categorized in one of four \log_3 body mass classes (<0.33, 0.33–1, 1–3, and >3 g WW) based on the mass of the largest individual of the species from any station from any of the four sample areas. We only examined species richness in the body mass classes that were considered to be sampled efficiently by the benthic sampling gear and sieves utilized (\log_3 body mass classes: grabs, –3 to 2; toothed dredge, –2 to 3; 2 m beam trawl, 0 to 4). No comparisons of species richness across gear types were made because the different areas sampled by the gears did not allow this.

Sediment parameters

A sediment sample was taken for particle-size analysis at each station in the DB and SP areas to check whether significant relationships existed between sediment characteristics and trawling intensity. Sediment samples were wet-sieved through a 500 μm sieve, and the fraction greater than 500 μm was oven-dried at 90 °C for 24 h. This fraction was then dry-sieved at 0.5 phi intervals, down to 1 phi (500 μm) and weighed. The fraction smaller than 500 μm was freeze-dried and analyzed on a Coulter LS 130 laser sizer. The laser sizer results were combined with the dry-sieve results to give the full particle size distribution. As no grabbing or coring could be carried out in the H and NW areas, no sediment data beside BGS sediment maps (BGS 2002) were available for these areas.

Large-scale effects of trawling

The model was used to examine the effect of bottom trawling on benthic productivity in the Dutch and British

sectors of the North Sea in the area south of 56°N. The areas inside the coastal 12 n.mi. zone and the plaice box were excluded from the analysis, as vessels fishing in these areas are generally not required to record their position through VMS, possibly causing a strong underestimation of trawling intensity in these areas. The whole area was evaluated by calculating biomass and production for each 9 km² cell by running the model for 1500 time steps, using the habitat and trawling intensity data described earlier. Biomass and production were compared with a situation without fishing by running the model for the same cells, setting trawling intensity to zero. Total production and biomass was summed over all cells in this area and compared between the normal and no-trawling situation.

Results

Tests of assumptions

We found the $W_{\text{mat}}/W_{\text{max}}$ ratio for 11 species from 43 populations of bivalves, gastropods, and polychaetes. There was a significant correlation between body mass at maturity and maximum body mass ($n = 43$, $r = 0.87$, $p < 0.001$), with a slope of 0.28. Analysed at the species level, on average the body mass at maturity was 35% of the maximum body mass. (For a table of the $W_{\text{mat}}/W_{\text{max}}$ ratios, see Supplemental Appendix S1.²) The slope of the relationship between species richness and body mass was similar for the central North Sea and the different faunal groups in the two areas that were sampled in this study (Figs. 2a–2d; ANOVA: group (as in Figs. 2a–2d), $F_{[1,33]} = 66$, $p < 0.001$; body mass, $F_{[1,33]} = 37$, $p < 0.001$; group \times body mass interaction, $F_{[1,33]} = 0.03$, $p = 0.85$).

Model predictions

The model predicted that trawling reduced biomass, production, and species richness of benthic invertebrate communities. The effects of trawling were generally stronger on biomass than on production (Fig. 4). The model predictions showed that the impact of the first passage of a trawl has the greatest effect, while an increase of trawling effort on communities that were already heavily trawled had little additional effect on production or biomass for all habitats. As expected, when shear stresses and erosion rates occur at the optimum value for the growth and survival of the benthos (0.25 Pa and 0 cm, respectively), the modelled production, biomass, and species richness was higher than when values were further away from the optimum (0.75 Pa and 1 cm) (Fig. 4). The model demonstrated that there was an interaction between natural disturbance and fishing disturbance; in situations of high natural disturbance (erosion), biomass, production, and species richness were low irrespective of fishing disturbance. Consequently, additional fishing disturbance had a much smaller effect on the benthos in situations with a high than with a low natural disturbance. At the same level of natural disturbance and trawling intensity, benthic communities on mud and muddy sand were less affected by trawling than those on sand and gravel. Carrying capacity at

a particular location changed the amount of biomass supported, but did not change the shape of the response curves.

Biomass, production, and species richness in the North Sea

For the DB and SP areas, there were no significant correlations between the sediment composition parameters and trawling intensity, indicating that local variations in trawling intensity were not influenced by fishers' knowledge of sediment type (Pearson correlations of trawling intensity and mud and sand content by weight, DB: $n = 7$; sand $r = -0.11$, $p = 0.814$; mud $r = -0.02$, $p = 0.974$; SP: $n = 24$; sand $r = -0.30$, $p = 0.16$; mud $r = 0.30$, $p = 0.16$).

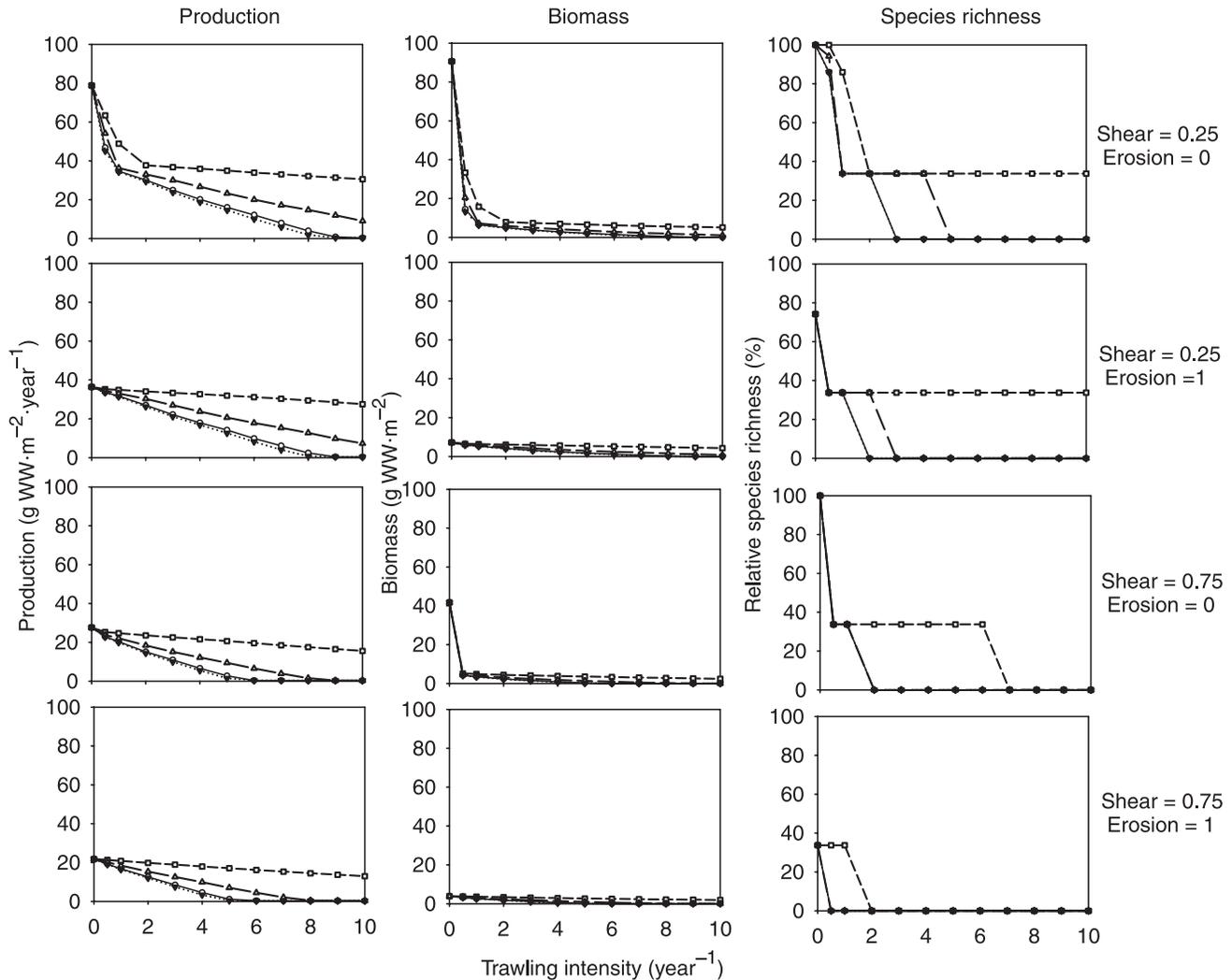
Relationships between trawling and benthic community parameters were examined after log₁₀-transformations of biomass, production, and trawling intensity (Figs. 5a–5g). For epifauna (2 m beam trawl samples), there was a significant negative effect of trawling on biomass and production; for small infauna (box corer and Hamon grab samples), there was a significant negative effect of trawling on biomass (Table 2). We found no effect of trawling on the biomass and production of infauna sampled using the dredges, and we found no significant interactions between the area and trawling intensity for any of the three sampling methods (Table 2). Trawling had a negative impact on species richness for epifauna and grab-sampled infauna, but not for dredge-sampled infauna (Figs. 5h–5i; Table 2). The initial impact of trawling on biomass, production, and species richness was higher than the additional impact of subsequent trawling events in areas that were already heavily trawled, as indicated by the log-linear relationship among biomass, production, species richness, and trawling intensity.

Validation of model using the field studies

The model was tested by comparing the model predictions of biomass with observed biomass and species richness at the stations that were sampled during the field studies. We used modelled biomasses for the whole community (all faunal groups and all size classes) in all tests. Within areas and sampling gear types, all correlations between the observed biomass in the North Sea and that predicted by the model except one were positive, and 8 out of 12 of these correlations were significant (Table 3). When the observed and predicted values from different areas were combined in one correlation per gear type, all correlations were significantly positive (Table 3). The most extensive data set was for the epifauna sampled with the 2 m beam trawl, with comparable data for all four areas. Accordingly, the relationship between the observed and predicted biomass was highly significant (Table 3; Fig. 6), although the low R^2 indicates that there is a high level of unexplained variation. The original model did not include habitat features (Duplisea et al. 2002) and could not explain the observed variation in biomass of epifauna at this scale (Pearson's correlation coefficient = 0.054, $n = 33$, $p = 0.77$). (A sensitivity analysis of the effect of the parameterization of carrying capacity, trawling mortality, shear-stress-related growth, and erosion-related mortality on the

²Supplementary data for this article are available on our Web site (<http://cjfas.nrc.ca>) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 4090. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

Fig. 4. The relation among trawling intensity, production, biomass, and species richness of benthic communities on four sediment types as calculated by the model. Production, biomass, and relative species richness are given for two levels of shear stress (Pa), two levels of erosion (cm), and four sediment types. Open circle, gravel; solid triangle, sand; open triangle, muddy sand; open square, mud. WW, wet weight.



correlation between observed and modelled biomass is provided in Supplemental Appendix S2.²)

For species richness within areas, the correlation between observed and modelled species richness was positive for all combinations of areas and sampling gear, although the correlation was never significant (Table 3). Combining the data for the four areas, this correlation was significant for the epifauna sampled with the 2 m beam trawl, but not for the infauna sampled with the grab or the dredge. Species with large body mass disappeared at a faster rate than small species when subjected to trawling (Fig. 7; general linear model with gear type as a categorical factor and body mass class as a continuous variable: gear type, $F_{[2,14]} = 0.79$, $p = 0.47$; body mass class, $F_{[1,14]} = 5.54$, $p = 0.033$; interaction $F_{[2,14]} = 1.13$, $p = 0.35$).

Effect of current trawling levels on biomass and production of benthic communities

According to the model, benthic biomass in the Dutch and UK sector of the North Sea is currently 56% lower than

would be expected in the absence of bottom trawling. Benthic production in the Dutch and UK sectors of the North Sea was 21% lower, consistent with a shift in the benthic community towards smaller individuals and species with higher $P:B$ ratios.

Discussion

This is the first large-scale study of the effect of the interaction between habitat and trawling on benthic biomass, production, and species richness and the first model of the benthic impacts of fishing at the scale of a fishery. Both the model and the field data showed that on shallow, soft sediment habitats, trawling had a large negative effect on biomass and the production of benthic communities in all habitats and that the strength of the impact was linked to the characteristics of the habitat. The initial impact of the first trawl pass was large, while further increasing the trawling intensity in areas where trawling intensity was already high had a smaller additional effect on biomass and production. The model pre-

Fig. 5. Biomass, production, and species richness of benthic communities in different habitats in the North Sea and trawling intensity with least squares regression lines. (a) Biomass for epifauna with 2 m beam trawl, (b) biomass for infauna with dredge, (c) biomass for infauna with cores-grabs, (d) production for epifauna with 2 m beam trawl, (e) production for infauna with dredge, (f) production for infauna with cores-grabs, (g) species richness for epifauna with 2 m beam trawl, (h) species richness for infauna with toothed dredge, (i) species richness for small infauna with Hamon grab. Cross and long dash, Dogger Bank; solid triangle and dotted line, Silver Pit; open square and grey line, Northwest Rough; open circle and solid line, Hills. WW, wet weight; AFDW, ash-free dry weight.

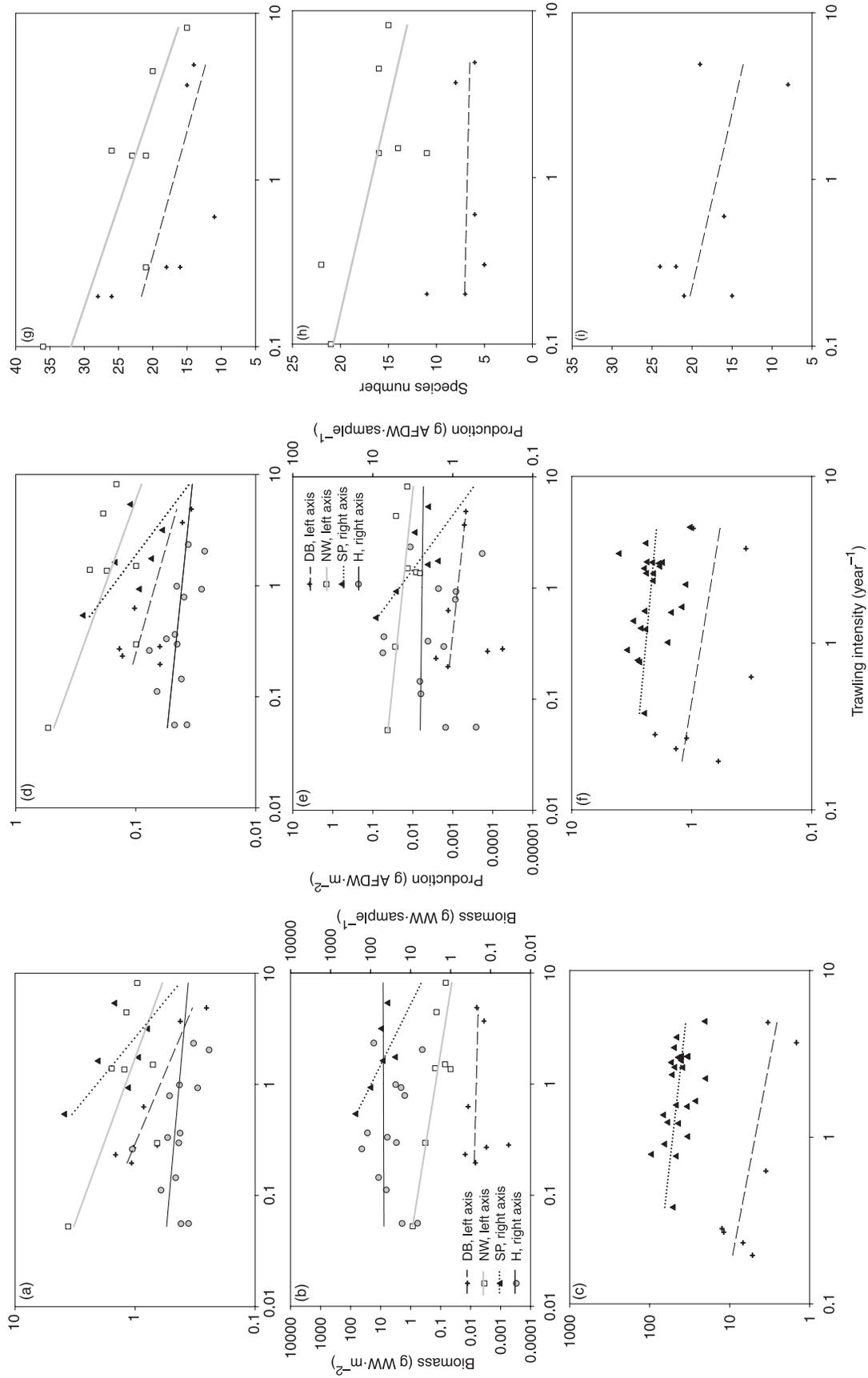


Table 2. Statistical parameters of the regression relationships among biomass, production, and trawling intensity (all log₁₀-transformed) for four locations and three types of sampling gear for biomass, production, and species richness.

	<i>R</i> ²	Area			Trawling intensity			Area × trawling intensity			Residual df
		df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>	
Biomass											
2 m beam trawl	0.72	3	15.5	<0.001	1	14.29	0.0008	3	1.40	0.26	25
Dredges	0.95	3	162.1	<0.001	1	2.32	0.14	3	1.34	0.28	25
Corer-grab	0.87	1	176.0	<0.001	1	18.15	0.002	1	1.28	0.26	27
Production											
2 m beam trawl	0.75	3	20.7	<0.001	1	12.33	0.0017	3	0.80	0.50	25
Dredges	0.94	3	138.9	<0.001	1	0.89	0.35	3	0.44	0.072	25
Corer-grab	0.55	1	29.2	<0.001	1	3.74	0.064	1	0.06	0.80	27
Species richness											
2 m beam trawl	0.60	1	3.53	0.089	1	11.33	0.0071	1	0.10	0.75	10
Dredges	0.83	1	42.8	<0.001	1	2.81	0.12	1	2.76	0.13	10
Corer-grab	0.27	—	—	—	1	1.87	0.23	—	—	—	5

Table 3. Correlation coefficients between observed and modelled biomass and species richness in four areas in the North Sea for three gear categories (Pearson correlation).

Area	2 m beam trawl	Dredges ^a	Box corer – Hamon grab ^b
Biomass			
DB	0.81 (7, 0.027)*	0.14 (7, 0.58)	0.68 (7, 0.095)
NW	0.83 (7, 0.022)*	0.98 (7, <0.001)*	—
SP	0.89 (6, 0.015)*	0.96 (6, 0.002)*	0.30 (24, 0.155)
H	0.36 (13, 0.20)	0.00 (13, 0.99)	—
Combined	0.63 (33, <0.001)*	AD: 0.46 (19, 0.048)* TD: 0.75 (14, 0.002)*	—
Species richness			
DB	0.737 (7, 0.059)	0.138 (7, 0.767)	0.578 (0.17)
NW	0.692 (7, 0.085)	0.749 (7, 0.053)	—
Combined	0.575 (14, 0.032)*	0.079 (14, 0.78)	—

Note: The *n* and *p* values are given in parentheses, respectively. An asterisk (*) indicates significance after step-up false discovery rate correction, an alternative to Bonferroni corrections (Garcia 2004), with a family-wise *p* = 0.10. DB, Dogger Bank; NW, Northwest Rough; SP, Silver Pit; H, Hills; AD, anchor dredge; TD, toothed dredge.

^aBiomass data included both toothed and anchor dredges; species richness data included only the toothed dredge.

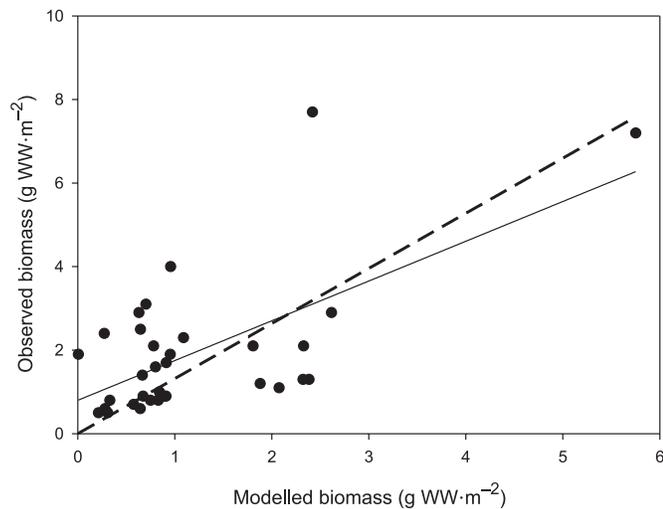
^bBiomass data included both box corer and Hamon grab; species richness data included only the Hamon grab.

dicted that the biomass of benthic communities in habitats subject to high levels of natural disturbance was less affected by additional trawling disturbance than the community in naturally stable habitats. The effect of trawling was predicted to be smaller on muddy than on sand and gravel sediments, but this effect is relatively unimportant compared with the effect of natural disturbance. In real ecosystems, sediment type and natural disturbance rates are likely to be correlated, with muddy sediments in locations with low natural disturbance and coarser sediments in areas with higher natural disturbance. The field data showed that the least affected area (H) was known to be dynamic in terms of sediment transport and has high levels of erosion and shear stress. The deeper areas NW and SP, which had the lowest erosion rates, were more severely affected by trawling. Large species disappeared at a faster rate in response to trawling than small species, as would be expected given the

less resilient life histories of larger animals. This study demonstrates that reductions in species richness in response to chronic trawling disturbance occur primarily because of this loss of large body mass species.

The biomass of infauna and epifauna at 33 stations from four areas in the North Sea were significantly and positively related to the biomass predicted by the model for most of the sampled communities. For epifauna, which were sampled in a comparable way at the largest scale, there was a highly significant correlation between the observed and modelled biomass and the scale of the four areas. The original model (Duplisea et al. 2002), which did not include habitat features, could not explain large-scale patterns in benthic biomass. This shows that habitat interacts with trawling in determining the effects of trawling on benthic communities and that the mechanisms in the model increased our ability to predict the effect of trawling. For infaunal invertebrates, positive

Fig. 6. Modelled community biomass and observed epifaunal biomass. Solid line: least squares regression with both slope and intercept fitted; $R^2 = 0.39$, $F_{[1,31]} = 20.2$, $p < 0.001$. Broken line: intercept removed; $R^2 = 0.29$, $F_{[1,32]} = 75.04$, $p < 0.001$. WW, wet weight.

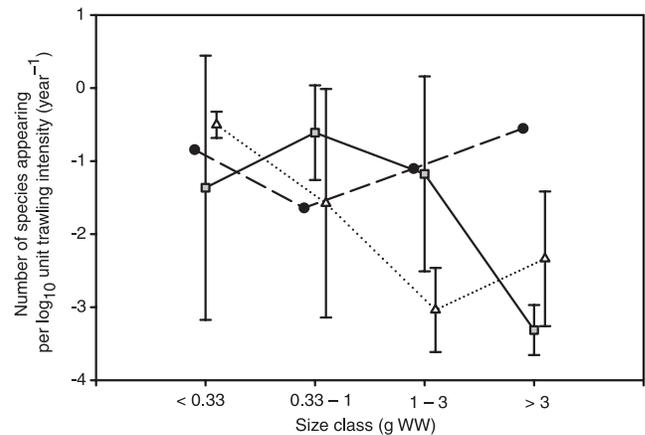


correlations between observed and modelled species richness were not significant, probably because the predicted biomasses were less precise than for epifauna.

These results show that size-based models can be used to predict large-scale patterns in biomass, production, and species richness of benthic invertebrate communities. The model predicted that benthic community biomass was reduced by 56% and production by 21% owing to trawling in the southern North Sea, but this does not imply that 44% of the benthic community is not affected by trawling. This is because the model does not account for shifts in the species composition of communities that are not reflected in simple biomass or production estimates. For example, the intensive exploitation of fish communities often results in species that are more resilient to fishing, thereby replacing those that are not, even though the total abundance may not change (e.g., Dulvy et al. 2000). Large-scale reductions in the production of benthic communities will affect energy flow through the ecosystem. Part of the food otherwise used by the benthic community, predominantly phytoplankton and detritus, might remain unused. This may lead to a greater accumulation of detritus on the sea floor with impacts on microbial communities or the storage of organic matter in sediments or may result in more phytoplankton grazing in the pelagic food chain (Duplisea et al. 2001).

The absolute effects of trawling are smaller in areas with poor growth conditions and high natural disturbance rates because there is less initial biomass. This conclusion is primarily based on the model, which assumes that different benthic groups (soft- and hard-bodied macrofauna) and size classes can only differ in growth and mortality rates. This does not take into account the specific adaptations of species to disturbance. For example, fragile, emergent epifaunal species, like the sea pen (*Virgularia mirabilis*), are likely to be particularly vulnerable to trawling, while species that are tough, flexible, and can easily repair damage, like the starfish (e.g., *Asterias rubens*), may be resilient (Ramsay et al.

Fig. 7. Number of species change (\pm standard error) per unit trawling intensity for four body mass classes. Solid circle, small infauna; shaded square, large infauna; open triangle: epifauna. WW, wet weight.



2001). If there are species of similar size that differ greatly in vulnerability to trawling, and if resilient species can quickly fill the niche of vulnerable species after trawling, the actual impact of trawling on biomass and production may be smaller than the model predicts. If the species that go extinct occupy unique niches in the ecosystem, which may be common in marine systems (Micheli and Halpern 2005), resources can remain unused after species extinction, thereby reducing community production (Loreau et al. 2002). Extinction of key species may affect other important ecosystem services, such as nutrient cycling and primary production (Lohrer et al. 2004; Solan et al. 2004; Widdicombe et al. 2004). We did not account for such possibilities in our simple model, but further developments could usefully do so if and when adequate data become available to support model development and validation.

Limitations

Because of the many simplifications and assumptions required to synthesize these data, additional work is required to refine the model and evaluate applicability in other geographic areas. The present model does not include predictions for biogenic habitats, like *Modiolus* and *Sabellaria* reefs, where the main habitat features are formed by the animals themselves, with a high diversity of associated species. We would expect substantial trawling effects on production processes and trophic structure in such habitats (Collie et al. 2000), as many of the most vulnerable animals are among those responsible for forming habitat. Indeed, other recent studies have shown that the impact of chronic trawling on production and biomass of benthic communities was severe in biogenic habitats (Bordehore et al. 2003).

The model explained 39% of the observed variation in biomass of epifauna, which indicates that a major part of the variation in biomass in the North Sea remains unexplained. As the fitted intercept of the relationship does not equal zero, the impact of trawling is probably overestimated by the model. However, if the relationship is forced through the origin, the model still explains 29% of observed variation and does not deviate much from the relationship, including an

intercept. Thus, the model does not capture the real world perfectly, and the modelled values are based on numerous assumptions and relationships that all have a degree of uncertainty. Therefore, we do not know how accurate and precise our estimates of the North Sea-wide impact of trawling on the biomass and production of benthic communities are. The model is also deterministic rather than stochastic and reveals nothing about expected variation in the ecosystem. The sensitivity analysis demonstrated that the correlation of modelled and observed biomass is not particularly sensitive to changes in the parameterization of the model.

North Sea trawl fisheries have a long history, but we only used 2.5 years of recent data for model validation. Given the disproportionate effect of the "first" trawl disturbance, this may explain some of the unexplained variation in the relationship between observed and modelled biomasses. However, the relatively strong correlation between trawling effort as calculated from recent VMS and older, over-flight data showed that effort distribution patterns were relatively stable.

Analyses and modelling of the biomass, production, and species diversity of benthic communities at a large scale is inevitably ambitious, and we had to make many simplifications and generalizations, particularly to parameterize the model to examine large-scale ecological processes. We have to accept these shortcomings if research on large-scale distribution patterns of communities, and in particular on large-scale effects of trawling, in marine ecosystems is to progress at the speed required to support management decision-making. Our model greatly simplifies the structure of the benthic community and ignores recruitment processes that could be limiting at the highest levels of trawling disturbance. However, large infaunal organisms may also play facilitating roles (e.g. Norkko et al. 2002), and in this case, the model will have underestimated the impact of trawling. Instead of compensation for the effect of trawling within the community by small animals, the eradication of large animals will accelerate the loss of smaller animals.

The model assumes that competition is a key mechanism in structuring benthic invertebrate communities. Currently, there is no consensus over the relative importance of competition, predation, and facilitation in marine soft-bottom communities, but competition can play an important role (Branch 1984; Wilson 1990). However, large infaunal organisms may also play important facilitating roles (e.g., Norkko et al. 2002), and in this case, the model will have underestimated the impact of trawling instead of compensating for the effect of trawling within the community, since eradication of large animals will accelerate the loss of smaller animals. However, given the reasonably good fit between observed and predicted biomasses, competition cannot be rejected as a structuring mechanism based on our results.

We deliberately ignored the processes that link the reproductive output of mature individuals to the recruitment of juveniles, which is very poorly known at present. Moreover, migration was ignored. Together, ignoring recruitment and migrations means that recovery from trawling can only occur through local growth of biomass. As a result of this, recovery from trawling is slow, and the model may overestimate the impact of trawling. Therefore, it is important to include these dispersion processes in future developments of the model. The model does not capture seasonal cycles in

the recruitment and growth of benthic animals, since growth was treated as continuous. In reality, recruitment of juveniles occurs on a seasonal basis for most species, and growth rates of new biomass are highly dependent upon season in accordance with temperature and primary production. In the real world, one might expect different effects if trawling occurs immediately before adults spawn, compared with later (for example), just after new juveniles have settled. However, as there is no seasonal trend in trawling intensity over the year on a large scale, we expect that this process causes no systematic bias in the effect of trawling as estimated by the model.

Extinction thresholds were set as a proportion of the mean biomass by body mass class in the absence of trawling disturbance. A consequence of this formulation is that species richness can only increase in the areas where the biomass of small animals was depressed below the mean by the dominance of more competitive, large animals. Such instances occurred in areas where natural disturbance was lower than the mean value. Since the empirical data did not show any dome-shaped relationships between trawling and species richness, our assumption does not seem unreasonable. As such, given the constraints of our data, we did not find any evidence to support predictions of the Intermediate Disturbance Hypothesis (Connell 1978), which predicts the highest species richness at intermediate levels of disturbance. Another potential source of bias in this study was that all individuals could not be identified to species. This means that the number of species, particularly in smaller body mass classes, was probably underestimated. This would have resulted in an underestimate of the effect of trawling on species richness.

A further potential critique of our model is that the interaction of habitat and trawling is explained by the inclusions of 10 more habitat parameters, while relatively few data points (33 in four areas) are available for validation. However, most of the model parameters do have an empirical and theoretical basis and were based on empirical observations, thus avoiding one part of the overfitting problem (Ginzburg and Jensen 2004). Almost all relationships between habitat and growth or mortality used in the model were based on empirical data and were significant, even though some had a low R^2 value. Given that four different habitat features plus trawling act simultaneously, it is not surprising that individual habitat features each explain less than 20% of the observed variation. If one factor explained a major part of the variation, hardly any variation would be left that could be explained by other factors.

In conclusion, these results suggest that the use of a size-based model may help to understand the spatial patterns and changes in biomass, production, and species richness in relation to trawling. Overall, our results have shown that trawling affects biomass, production, and species richness of benthic invertebrate communities at a large scale and that the effect of trawling depends on habitat type. Thus, trawling not only reduces fish stocks, but also reduces the abundance of benthic food for commercial fish in a wide range of habitats and hence the carrying capacity of benthivorous species. Therefore, it seems important that fisheries managers consider both the direct and indirect effects of trawling on fish stocks. Given the interaction between habitat and the effect of trawl-

ing, it may be possible to reduce the impact of trawling on benthic production by redirecting trawling effort from vulnerable to resilient habitats. Moreover, because we observed a nonlinear relationship between trawling and benthic biomass or production, increasing the heterogeneity of fishing effort would also reduce the large-scale impact of trawling. Our new approach for predicting the effects of mortality and environmental factors on species richness is based on the general principles of allometry and a generalized body mass versus species richness relationship, and thus it may be used more widely for predicting spatial patterns of species richness. This model could have practical use for predicting the effects of trawling and natural disturbance on communities. However, as the models are underpinned by the size dependence of vulnerability (i.e., mortality is size dependent), such models could not be applied when vulnerability was determined by size-independent impacts (e.g., pollution).

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