A size-based model of the impacts of bottom trawling on benthic community structure

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Abstract: Bottom trawling causes widespread disturbance to the sediments in shallow-shelf seas. The resultant mortality of benthic fauna is strongly size dependent. We empirically demonstrate that beam trawling frequency in the central North Sea had a greater effect on fauna size distribution in a soft sediment benthic community than variables such as sediment particle size and water depth. Accordingly, we simulated the impacts of trawling disturbance on benthos using a model consisting of 37 organism size classes between 1 µg and 140 g wet weight. The model produced a production–biomass versus size relationship consistent with published studies and allowed us to predict the impacts of trawling frequency on benthos size distributions. Outputs were consistent with empirical data; however, at high yet realistic trawling frequencies, the model predicted an extirpation of most macrofauna. Empirical data show that macrofauna persist in many heavily trawled regions; therefore, we suggest that trawling by real fisheries is sufficiently heterogeneous to provide spatial refuges less impacted by trawling. If correct, our analyses suggest that fishery management measures that do not reduce total effort but do lead to effort displacement and spatial homogenization (e.g., temporarily closed areas) may have adverse effects on the systemic persistence of intermediate- and large-sized macrofauna.

Résumé : Le chalutage de fond cause une perturbation importante des sédiments dans les mers peu profondes du plateau continental. Nous démontrons de façon empirique que la fréquence de chalutage à perche dans la région centrale de la mer du Nord a un effet plus prononcé sur la distribution de fréquence des tailles de la faune dans une communauté benthique sur sédiments mous que des variables telles que la taille des particules des sédiments et la profondeur de l'eau. C'est pourquoi, nous avons simulé les impacts de la perturbation due au chalutage sur le benthos à l'aide d'un modèle qui comprend 37 classes de taille d'organismes, allant de 1 µg à 140 g de masse humide. Le modèle génère une relation entre la production/biomasse et la taille qui est compatible avec les données publiées et il nous permet de prédire les impacts de la fréquence de chalutage sur la distribution de fréquence des tailles du benthos. Les résultats du modèle sont compatibles avec les données empiriques; cependant, à des fréquences élevées, mais réalistes, de chalutage, le modèle prédit l'élimination de presque toute la macrofaune. Les données empiriques indiquent que la macrofaune persiste dans plusieurs des régions de chalutage intense; ainsi, nous croyons que le chalutage dans des conditions réelles de pêche est suffisamment hétérogène pour laisser des refuges spatiaux qui sont moins affectés. Si elles sont exactes, nos analyses laissent croire que les mesures de gestion des pêches qui ne réduisent pas l'effort total de pêche, mais qui mènent au déplacement de cet effort et à une homogénéisation spatiale (e.g. des régions fermées temporairement) peuvent avoir des effets négatifs sur la persistance systémique de la macrofaune de taille intermédiaire et grande.

[Traduit par la Rédaction]

Introduction

Trawling disturbance has wide-ranging impacts on the diversity, structure, and productivity of benthic communities (Dayton et al. 1995; Jennings and Kaiser 1998; Hall 1999). Knowledge of these impacts is based primarily on empirical studies that describe biological differences among communities subject to different levels of trawling disturbance (Thrush et al. 1998; Collie et al. 2000; Kaiser et al. 2000). Such studies are essential for understanding trawling impacts; however, future demands on science will be for quantitative methods

predicting changes in communities resulting from trawling. An improved understanding of mechanisms would help to this end by describing how changing patterns and intensities of trawling disturbance affect benthic communities.

At least two factors must be considered when examining effects of trawling on benthic populations: the immediate mortality inflicted by trawling gear and the longer-term ability of populations to cope with this mortality. As both of these processes are functions of body size, size-based models are likely to provide a useful framework to examine questions concerning impacts of trawling activities on the

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entire benthic community rather than smaller studies on one or a few species.

Trawling leads to the mortality of benthic invertebrates because they are crushed directly by the trawl, exposed to predators by the passage of the trawl, or are caught in the net and die after capture and return to the sea (Ramsay et al. 1997; Bergman and van Santbrink 2000a, 2000b). Within and among species, the mortality rates suffered by the smallest individuals may be lower because they may be pushed aside by the pressure wave in front of the trawl (Gilkinson et al. 1998). Larger individuals usually suffer higher mortality if they are in the path of the trawl, although actual mortality rates are dependent on their distribution in the sediment. Thus, deeper-burrowing individuals may not come into contact with fishing gear because trawls rarely penetrate more than 6 cm into sand–mud sediments (Lindeboom and de Groot 1998; Bergman and van Santbrink 2000a, 2000b). Burrowing depth may increase with body size for some bivalves (Zaklan and Ydenberg 1997), and so larger individuals may be less vulnerable to mortality. Despite the trawling mortality refuge for some large individuals and observations of decreased mortality relative to intermediate-sized species (Bergman and van Santbrink 2000a, 2000b), large species usually show the greatest decreases in abundance following chronic (long-term) trawling disturbance. This is because large body size is correlated with slower growth, lower annual reproductive output, and lower intrinsic rates of natural increase (Charnov 1993; Brey 1999). Thus populations of large species, despite suffering lower mortality, may be less able to withstand these mortality rates than populations of smaller species.

In recent years, fishery managers have been asked to account for the ecosystem effects of fishing when formulating management plans (e.g., Ecosystem Principles Advisory Panel 1999). Trawling effects on benthic communities are a key concern because they may affect food availability for commercial fishes, modify food webs, and reduce diversity (Rijnsdorp and Millner 1996; Rijnsdorp and van Leeuwen 1996; Jennings and Kaiser 1998). Although we know many impacts of trawling from several studies, managers lack quantitative tools that allow them to predict the responses of benthic communities to changes in the intensity and distribution of trawling disturbance. Changes in the intensity and distribution of disturbance could result from catch or effort controls or technical measures such as the imposition of a closed area; hence, a quantitative predictive capacity is needed to assess the implications and efficacy of such management actions.

In this study, we use empirical data to show the effects of beam trawling disturbance and sediment characteristics and depth on the structure of the infaunal size spectrum in central North Sea fishing grounds. Having demonstrated that trawling disturbance rather than sediment type or depth has the overriding effect on the size structure of the community, we develop a size-based model to examine how spatial and temporal patterns of trawling disturbance affect the production, biomass, and size composition of the infaunal community. The model is parameterized from literature data and by using allometric methods (Yodzis and Innes 1992). We compare model outputs with previously published field data that describe the effects of beam trawling on the production and size composition of benthic communities.

Methods

Effects of trawling disturbance on size structure of the benthic community

We assessed the effects of trawling disturbance and environmental factors on the size structure of the benthic community at seven sites of 1 nautical mile × 1 nautical mile (1 nautical mile = 1.852 km) in the Silver Pit, an important beam trawling ground in the central North Sea. Silver Pit sites generally have fine sediments with high water content and range in depth from 59 to 72 m (Table 1). Silver Pit is more famous as the site of a well-preserved, unique, small crater created by the impact of an extraterrestrial object about 60 million years ago (Stewart and Allen 2002), but the effects of this crater underlying >300 m of tertiary sediment were not considered in our analysis. Further details of the study sites are reported in a companion study (Jennings et al. 2001).

The infaunal invertebrate community at each site was sampled with an anchor dredge during winter and summer. The anchor dredge samples on an appropriate scale for the study of fishing effects (over areas of m^2) and integrates small-scale patchiness of the larger macrofauna (individual body mass >0.0625 g wet weight). Three randomly located replicate tows were completed at each site in each season from the R/V *Corystes*. Winter samples were collected from 22 November to 8 December 1999, and summer samples were collected from 1 to 3 May 2000. A subsample of 0.2 m^3 of sediment was taken from each anchor dredge sample and sieved through 1 mm square mesh. All free-living infaunal species retained by the mesh were removed for processing. All individuals were weighed, either fresh using heave-compensated balances or after preservation in 4% seawater–formalin buffered with 3 g·L^{-1} sodium acetate, and were assigned to log$_2$ body size categories. Biomass by size class was reported as the mean for the six replicates at each site. Biomass size spectra were normalized by dividing the biomass in a given body mass class interval by the width of that class interval. Trawling disturbance at each site was estimated from records of vessel sightings by fishery-protection aircraft as described by Jennings et al. (2001) and reported as sightings of beam trawlers per unit of searching effort (SPUE) (Table 1). The mean depth at each site was calculated from six measurements taken at random locations during the deployment of the anchor dredge. Five randomly located sediment cores were taken at each site, and one subsample from each core was taken with a 5.5 cm diameter perspex tube inserted to a depth of 10 cm; these samples and overlying water were frozen to –20°C pending analysis. In the laboratory, thawed 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 on a top pan balance (precision = 0.01 g). The fraction smaller than 500 µm was freeze-dried and analyzed on a Coulter LS 130 laser sizer (Beckman Coulter, Inc., Fullerton, Calif.). The laser sizer results were combined with

Table 1. Environmental and fishing effort at the Silver Pit study sites.

Site	Water depth (m)	Trawling effort (SPUE × 10^3)	Sediment diameter (mm)	Mean % mud–clay
S1	72±1.2	3.2	0.08±0.015	25
S2	69±1.6	7.9	0.09±0.017	21
S3	67±0.7	14	0.05±0.009	36
S4	65±0.7	12.4	0.06±0.014	25
S5	60±2.9	19.4	0.08±0.025	27
S6	59±0.2	13.7	0.03±0.004	45
S7	60±0.8	0.7	0.02±0.002	34

Note: Depth is the mean depth based on six random measurements during sampling. Beam trawl disturbance is expressed as mean sightings per unit searching effort (SPUE) of beam trawlers by fishery-protection flights. Site codes follow Jennings et al. (2001).

the dry-sieve results to give the full particle size distribution. The mean particle size diameter and sorting coefficient were calculated from these results (Dyer 1986).

Multidimensional scaling (MDS) was used to investigate the biotic relationships between sites. In this analysis, we treated each of the infaunal $\log_2$ body mass classes from –4 to 7 as if it were a species in a conventional community analysis (Schwinghamer 1988) and produced a similarity matrix for the seven sites using a Bray–Curtis similarity measure. The biomass in each of the 12 size classes was $\log_{10}$-normalized biomass (the mean values in the size spectra shown in Jennings et al. 2001).

To examine the relationships between the size structure of the infaunal community, depth, trawling disturbance, and sediment characteristics, we used the BIOENV procedure of Clarke and Ainsworth (1993). This selects the environmental variables best explaining community pattern by maximizing a rank correlation between environmental and community similarity matrices. The environmental similarity matrix was calculated using square root transformed mean depth, trawling disturbance (SPUE), and mean sediment diameter, using a Euclidean distance measure. This community similarity matrix underlies the MDS plot. Mean sediment diameter was used as a surrogate for percent sand and mud–clay when calculating the environmental similarity matrix because there were highly significant correlations between mean sediment diameter and the percentages of sand and mud–clay. All empirical data analyses were conducted using SAS and PRIMER.

Model development

Our model of a soft-sediment benthic community was developed as a difference model in S, version 4, the language used by the program S-Plus 6 (Insightful Corp., Seattle, Wash.). State variables in the model were defined on the basis of body size and three faunal groups: meiofauna (MEIO), soft-bodied macrofauna (SOFT), and hard-bodied macrofauna (HARD). The model contained 37 state variables, five of which were meiofauna, 16 SOFT, and 17 HARD (Table 2). Though there were 37 state variables, they represented only three groups differing in body size. Hence, there were only three sets of parameters and the model is relatively simple in both structure and parameter demands.

Growth of population biomass in each body size – organism type compartment was modeled by modifying the basic Lotka–Volterra competition equations:

$$(1) \quad \frac{dG_i}{dt} = B_i r_i \left(\frac{C_i - B_i - \alpha_{ij} \dfrac{\displaystyle\sum_j^J B_j}{J}}{C_i} \right)$$

where i and j are competing groups of organisms, G_i is the gross population growth of compartment i, N_i is the number of individuals in the population i, r_i is the specific rate of weight increase of an individual in population i, C_i is the biomass carrying capacity for population i, B is the biomass of a population i or j, α_{ij} is the competitive influence of a unit of the competitor j biomass on the carrying capacity of population i, and J is the number of compartments of competitor j. SOFT and HARD were assumed to be in competition, but MEIO were not assumed to compete with either of the other groups.

The carrying capacity of a compartment was set at a fixed level in all compartments for each of the three faunal groups of organisms. The competitive reduction of carrying capacity of one compartment by biomass in another was done on a group-wide basis. That is, the biomass of HARD negatively affects the carrying capacity of SOFT in the same manner. As a result, the effects of competition are spread over several size classes.

The α_{ij} values for Lotka–Volterra competition are difficult to determine from experimental data as they are products of the model formulation. Accordingly, we derived a value using a prey overlap index for soft- and hard-body benthos from an Ecopath model (Pauly et al. 2000) of the Celtic Sea (J.K. Pinnegar, Centre for Environment, Fisheries and Aquaculture Science, Lowestoft Laboratory, Pakefield Rd., Lowestoft, Suffolk NR33 0HT, United Kingdom, personal communication) in conjunction with specific growth rates as

$$(2) \quad \alpha_{ij} = O_{ij}\left(1 - \frac{(\overline{r_j})^\delta}{(\overline{r_i})^\delta + (\overline{r_j})^\delta}\right)$$

where α_{ij} is the conversion of a unit of competitor j's biomass from the carrying capacity of competitor i, and O_{ij} is the proportional overlap of shared prey in the diets of competitors i and j, by weight. Food overlap, O_{ij}, is an output of Ecopath models (Pauly et al. 2000) and varies between 0 and 1. $\overline{r_j}$ and $\overline{r_i}$ are the average specific growth rates (eq. 5) of competitors j and i averaged over size classes. In this case i and j are faunal categories (e.g., HARD or SOFT) rather than individual size classes. Competitive difference, δ, either reduces or increases the difference between the values α_{ij} and α_{ji}. Competitive difference, δ, values of <1 decrease the difference ($\alpha_{ij} - \alpha_{ji}$) in the competitive ability of a competitive pair, whereas δ values >1 increase the difference. The same δ value was used for each pair of α determinations.

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Table 2. Model state variables and parameters.

State variable	Shell-free wet weight (mg)	Total wet weight (mg)	Weight class	Carrying capacity (mg sfwwt·m⁻²)	k (year⁻¹)	W_∞ (mg sfwwt)	Specific growth rate (year⁻¹)	M_{nat}	M_{trl}	O	δ	α
MEIO 1	0.001	0.001	−20	10	4	0.25	26.8	25.03	0.2	—	—	—
MEIO 2	0.005	0.005	−18	10	4	0.25	24.9	23.28	0.2	—	—	—
MEIO 3	0.02	0.02	−16	10	4	0.25	19.0	17.71	0.2	—	—	—
MEIO 4	0.06	0.06	−15	10	4	0.25	9.1	8.57	0.2	—	—	—
MEIO 5	0.2	0.2	−13	10	4	0.25	0.71	0.74	0.2	—	—	—
SOFT 1	1.9	1.9	−10	1200	0.85	700	8.97	8.42	0.2	0.64	0.5	0.23
SOFT 2	5	5	−8	1200	0.85	700	8.76	8.23	0.2	0.64	0.5	0.23
SOFT 3	10	10	−7	1200	0.85	700	8.45	7.94	0.2	0.64	0.5	0.23
SOFT 4	20	20	−6	1200	0.85	700	7.85	7.38	0.2	0.64	0.5	0.23
SOFT 5	40	40	−5	1200	0.85	700	6.77	6.38	0.2	0.64	0.5	0.23
SOFT 6	80	80	−4	1200	0.85	700	5.04	4.77	0.2	0.64	0.5	0.23
SOFT 7	100	100	−4	1200	0.85	700	4.35	4.13	0.2	0.64	0.5	0.23
SOFT 8	125	125	−3	1200	0.85	700	3.62	3.45	0.2	0.64	0.5	0.23
SOFT 9	200	200	−3	1200	0.85	700	2.08	2.02	0.2	0.64	0.5	0.23
SOFT 10	225	225	−3	1200	0.85	700	1.73	1.69	0.2	0.64	0.5	0.23
SOFT 11	300	300	−2	1200	0.85	700	0.99	1	0.2	0.64	0.5	0.23
SOFT 12	350	350	−2	1200	0.85	700	0.69	0.72	0.2	0.64	0.5	0.23
SOFT 13	400	400	−2	1200	0.85	700	0.48	0.53	0.2	0.64	0.5	0.23
SOFT 14	450	450	−2	1200	0.85	700	0.33	0.39	0.2	0.64	0.5	0.23
SOFT 15	475	475	−2	1200	0.85	700	0.27	0.33	0.2	0.64	0.5	0.23
SOFT 16	500	500	−1	1200	0.85	700	0.23	0.3	0.2	0.64	0.5	0.23
HARD 1	50	87.5	−4	6000	0.2	140 000	1.66	1.63	0.26	0.64	0.5	0.41
HARD 2	100	175	−3	6000	0.2	140 000	1.66	1.63	0.26	0.64	0.5	0.41
HARD 3	200	350	−2	6000	0.2	140 000	1.65	1.62	0.26	0.64	0.5	0.41
HARD 4	300	525	−1	6000	0.2	140 000	1.65	1.62	0.27	0.64	0.5	0.41
HARD 5	400	700	−1	6000	0.2	140 000	1.64	1.61	0.27	0.64	0.5	0.41
HARD 6	500	875	−1	6000	0.2	140 000	1.63	1.6	0.27	0.64	0.5	0.41
HARD 7	1000	1750	0	6000	0.2	140 000	1.61	1.58	0.29	0.64	0.5	0.41
HARD 8	3200	5600	2	6000	0.2	140 000	1.49	1.47	0.35	0.64	0.5	0.41
HARD 9	10 000	17 500	4	6000	0.2	140 000	1.18	1.18	0.44	0.64	0.5	0.41
HARD 10	18 500	32 375	5	6000	0.2	140 000	0.88	0.9	0.27	0.64	0.5	0.41
HARD 11	23 000	40 250	5	6000	0.2	140 000	0.76	0.79	0.15	0.64	0.5	0.41
HARD 12	28 000	49 000	5	6000	0.2	140 000	0.64	0.68	0.06	0.64	0.5	0.41
HARD 13	35 000	61 250	5	6000	0.2	140 000	0.50	0.46	0.02	0.64	0.5	0.41
HARD 14	42 000	73 500	6	6000	0.2	140 000	0.40	0.27	0.01	0.64	0.5	0.41
HARD 15	50 000	87 500	6	6000	0.2	140 000	0.30	0.17	0.01	0.64	0.5	0.41
HARD 16	60 000	105 000	6	6000	0.2	140 000	0.21	0.11	0.01	0.64	0.5	0.41

Note: Weight class is $\log_2$ total wet weight (g). Carrying capacity is in shell-free wet weight (sfwwt). Specific growth is calculated from the von Bertalanffy growth curve where the von Bertalanffy growth rate is k (year⁻¹) and the asymptotic weight is W_∞. Natural mortality (M_{nat}) is calculated from specific growth using the relationship from Brey (1999). M_{trl} is the direct mortality rate of fauna resulting from the single passage of a beam trawl. O is the proportional overlap in common diet between the competitive groups SOFT and HARD. The Lotka–Volterra competition coefficient, α, describes the reduction in the carrying capacity of a group by a unit of biomass of the competitor; e.g., a unit of HARD biomass reduces the carry capacity of SOFT by 0.41 units. The exponent in the Lotka–Volterra competition term derivation, which determines the difference in competitive abilities of a competitive pair, is δ.

If there is no overlap in prey ($O_{ij} = 0$), then i and j do not share any food resources and α_{ij} is 0. This means that i and j do not compete. The limits of α_{ij} as r_j approaches 0 or infinity are O_{ij} or 0, respectively. Therefore a slower-growing prey has a competitive advantage because it reduces the carrying capacity of its competitor. Relatively fast-growing competitors have reduced competitive ability. We consider this a reasonable assumption because slow-growing species often allocate resources to the development of protective structures, whereas fast-growing species often allocate a greater proportion of resources to reproductive output (e.g., Charnov 1993).

The carrying capacity level in the model is simply a scaling factor, i.e., the absolute levels do not affect the model outcomes but the relative difference between size classes and the mechanism itself are important. It must be noted though that the carrying capacity will affect the model dynamics, so greater care needs to be exercised in choosing carrying capacity for a dynamic model. Carrying capacity, C, was chosen as follows:

(3) $C_{ALL} = 1$

$C_{HARD} = C_{ALL}$

$C_{SOFT} = C_{HARD}/5$

$C_{MEIO} = C_{HARD}/600$

C_{ALL} can then be scaled to reflect the level of biomass in the benthos. The factors for SOFT and MEIO were chosen because they roughly correspond to the relative biomasses of these faunal groups in soft sediment biomass size spectra described in the literature (Schwinghamer 1981; Duplisea 2000) and for the Silver Pit area of the central North Sea (Jennings et al. 2001). All model parameter values are documented here (Table 2) and can be found in the model code (available from first author and for download at http://www.qc.dfo-mpo.gc.ca/iml/en/scientists/DupliseaDE/default.htm).

Growth was modeled using the von Bertalanffy growth equation for weight (Quinn and Deriso 1999):

(4) $W(t) = W_\infty(1 - e^{-kt})^3$

where body weight of an individual, W, is a function of time, t. The Brody growth coefficient is k and W_∞ is the theoretical asymptotic weight of the individual. Then, by taking the first derivative of eq. 4 and dividing it by the body size at the corresponding time, an expression is obtained for specific growth, r, as a function of time and body weight:

(5) $r \equiv \dfrac{dW/dt}{W(t)} = \dfrac{3k_i e^{-kt}}{1 - e^{-kt}}$

Each of eqs. 4 and 5 was calculated over an appropriate period of time such that the maximum weight was achieved and there was a good range of points at all body sizes to determine a relationship. A log-linear model was then was fitted to these two series, so that we could derive an allometric growth curve for each set of von Bertalanffy growth parameters as

(6) $\log(r) = aW + b$

Fig. 1. Specific growth rate of SOFT as a function of soft body size as determined by the von Bertalanffy growth formulation for the SOFT set of parameters. The fitted straight line shown was used to estimate specific growth rate for every body size of SOFT. A similar curve was constructed for each set of growth parameters. Organism shell-free wet weight is abbreviated as sfwwt.
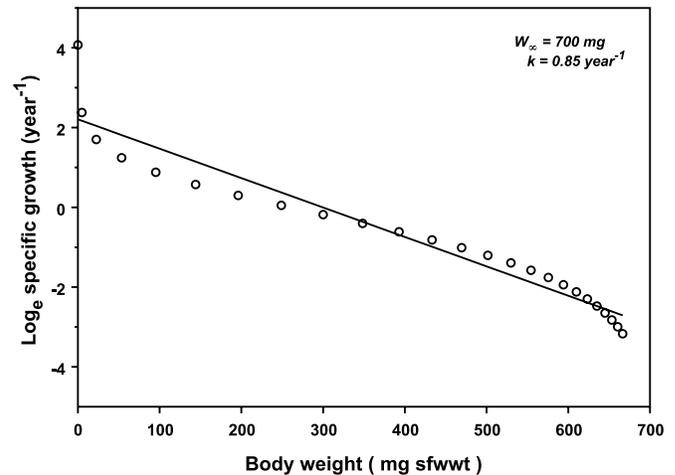
where r is the specific growth rate of an individual, W is the body weight of the individual, and a and b are the fitted coefficients. This fits a linear curve to data that appears as a rotated sigmoidal (Fig. 1). The sigmoidal curve is a function of the von Bertalanffy form of asymptotic growth.

Von Bertalanffy growth rate values (Table 2) were taken from Brey (1999), where SOFT k values are characteristic of organisms such as polychaetes and amphipods and HARD k values are characteristic of those for bivalves and echinoderms. The W_∞ values were based on the largest organisms recorded in the literature or recorded on surveys conducted in the North Sea by the Centre for Environment, Fisheries and Aquaculture Science (CEFAS) research vessels. Von Bertalanffy growth parameters for meiofauna were not available in the literature and thus von Bertalanffy growth may not be accurate for MEIO; however, in the absence of other information, we continued to use it for the sake of internal consistency.

Instantaneous mortality rates were modeled from specific growth rate using an empirically determined relationship (Brey 1999):

(7) $M_{nat} = 0.082 + 0.93r$

where M_{nat} is the instantaneous natural mortality rate and r is the specific growth rate per year of organisms type size i. Because this relationship primarily applies to small soft-bodied invertebrates, it was modified for the hard organisms by reducing M_{nat} values by factors 1.2, 1.7, 2.1, and 2.6, respectively, for the four largest size classes of hard organisms (Table 2). These values were chosen by "tuning" them so that the modeled production–biomass (P/B) versus body size slope matched empirical curves while keeping a progression of increasing division factors with size.

Mortality resulting from trawling activity was modeled with a continuous formulation:

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(8) $\text{Mort} = 1 - e^{-(M_{trl}F + M_{nat})}$

where Mort is the proportion of the population dying per unit time, M_{trl} is the instantaneous mortality rate resulting from trawling activity, and M_{nat} is the instantaneous natural mortality rate. Trawling effort, F, is the number of times per year that an area of the bottom is swept by a trawl.

The mortality rates that result from a single pass of a beam trawl were compiled from Lindeboom and de Groot (1998) and Bergman and van Santbrink (2000*a*, 2000*b*) (Fig. 2; Table 2). We fitted a size-dependent mortality curve to these data to estimate the direct mortality rate on each faunal group and size class. The relationship between HARD mortality was modeled as a Gaussian curve where trawling caused at least 1% mortality and the maximum mortality was 44% (Fig. 2*a*; Table 2):

(9) $M_{trl(HARD)} = M_{hmin} + (M_{hmin} - M_{hmax})e^{\frac{(W_h - \overline{W}_h)^2}{V_h}}$

where $M_{trl(HARD)}$ is the mortality rate which varies between the minimum mortality rate (M_{hmin}) and maximum mortality rate (M_{hmax}), W_h is the body weight of compartments of h, $\overline{W}_h$ is the mean body weight of HARD, and V_h is the variance of the Gaussian curve describing mortality as a function of size.

The relationship between SOFT and MEIO mortality versus body size was modeled with a simple linear relationship of slope = 0 and intercept halfway between the maximum and minimum observed mortality. The data do not justify the use of a more complex functional form (Fig. 2*b*).

Direct mortality rates (Fig. 2; Table 2), which vary between 0 and 1, were considered to be equivalent to continuous mortality rates for modeling mortality (eq. 8). Continuous mortality usually overestimates survivorship by 2–10% for a trawling mortality rate of 0.2 and up to five trawl passes per year.

Equations 1–9 were combined to give the population biomass flux for a compartment:

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

The model results reported here are for simulations run to steady state with a 30-day time step. Other time steps were used, but because this model is implemented as a difference equation, instabilities arise at large time steps. As time step length decreases, the model makes a better approximation to the continuous formulation used for trawling mortality.

We used the model to simulate the impacts of trawling frequencies ranging from 0 to 10 times per year. This covers the range of trawling frequencies commonly observed on beam trawl fishing grounds in the North Sea (Rijnsdorp et al. 1998; Jennings et al. 1999), although some small patches of ground may be trawled more frequently (Rijnsdorp et al. 1998). Model results are generally presented in the convention of normalized size spectra (Platt and Denman 1977) where biomass in a size category is divided by the width of that category and the result is plotted as $\log_2$ body size versus $\log_2$-normalized biomass.

Fig. 2. Direct mortality of (*a*) hard-bodied and (*b*) soft-bodied organisms of different body sizes following a single pass of a 12-m beam trawl. The curves were used to parameterize trawling mortalities for (*a*) HARD and (*b*) SOFT and MEIO. (A secondary *x* axis scaling in body weight class is shown that is consistent with other figures.) Data compiled from Lindeboom and de Groot (1988) and Bergman and van Santbrink (2000*a*, 2000*b*). Organism wet weight is abbreviated as wwt and organism shell-free wet weight as sfwwt.
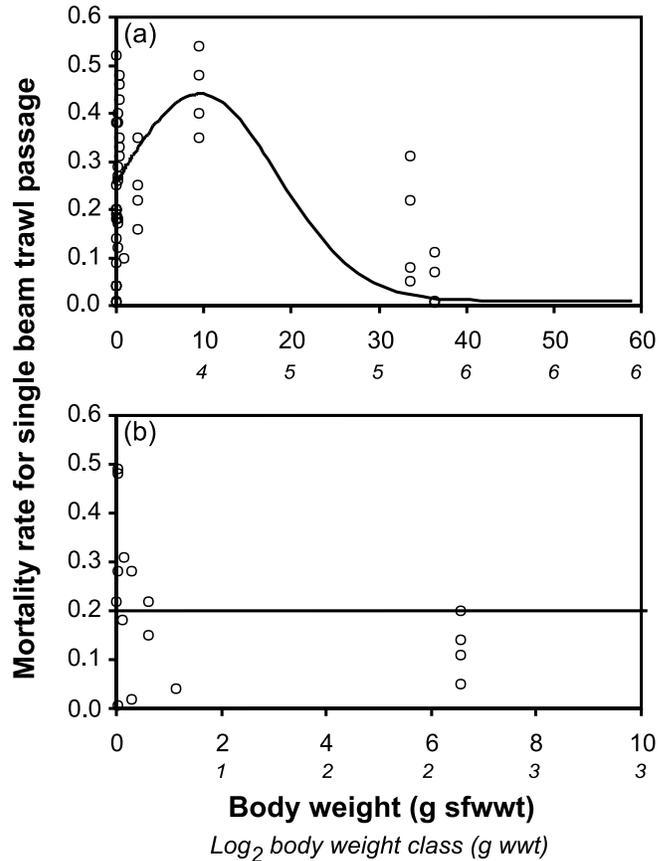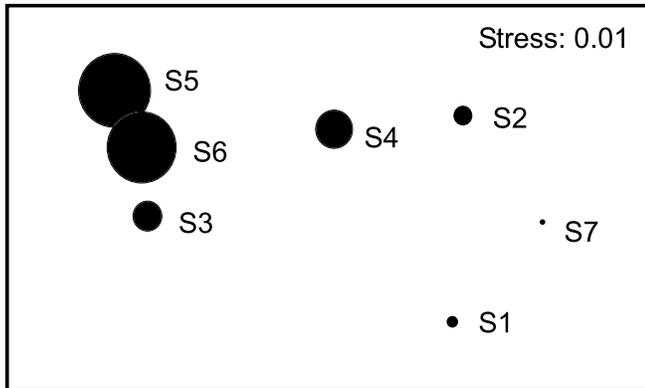

Results

Effects of trawling disturbance on size structure of the benthic community

Trawling disturbance varied by a factor of 27 among the Silver Pit study sites (Table 1). An MDS plot with trawling disturbance superimposed (Fig. 3) suggested that the size structure of the infaunal communities was largely influenced by trawling disturbance, with sites subject to higher levels of disturbance (S4 and S5) clearly separated from those sites where trawling disturbance was low (S1 and S7). When the BIOENV procedure was used to select the environmental variables best explaining the size structure, the single environmental variable that best grouped the sites in a manner consistent with the size-based community patterns was trawling disturbance (PW = 0.63). No other environmental variable or combination of environmental variables grouped the sites as effectively, the best alternative being the combination of trawling disturbance and mean sediment diameter (PW = 0.62).

Fig. 3. Multidimensional scaling (MDS) plot as produced by the BIOENV procedure showing the relationship between seven sites in the Silver Pit based on the size structure of the benthic communities. Areas of symbols are proportional to the level of trawling disturbance (see Sightings per unit effort (SPUE), Table 1).

Fig. 4. Production–biomass ratio (P/B) versus body size as produced by the present model. For comparison, the empirically determined line for benthic fauna described by Schwinghamer et al. (1986) is depicted as a broken line. The fitted line produced by the model has a slope of –0.20 and intercept of –0.22 year^{-1}. Organism wet weight is abbreviated as wwt.

Model predictions

Over all modeled organism size classes, the model generated a P/B versus body mass relationship of –0.20 and a within-macrofauna slope of –0.32 (Fig. 4). The modeled normalized biomass size spectrum for a community unaffected by trawling disturbance fell within the range of biomass size spectra determined empirically for sites in the Silver Pit (Fig. 5). The modeled normalized biomass size spectra exhibited a trough in biomass in the size transition between meiofauna and macrofauna and humps in biomass associated with meiofaunal and macrofauna size classes. These spectra corresponded to an increasing interval size spectrum (not normalized spectrum) with maximum biomass occurring at the largest body size (Fig. 5).

The model predicted a reduction in total biomass and in the biomass of larger size classes with trawling (Figs. 6a, 6b, 7). Size classes >1 g wet weight composed most of the total biomass and were most affected by trawling, whereas the smaller size classes were not so heavily affected by trawling and only accounted for a small proportion of total biomass (Fig. 7). There was a small mortality refuge for the largest size class. This resulted from the modeled low mortality rate for larger animals, which may burrow to greater depths than intermediate-sized individuals. At weight classes near –5 (about 0.03 g wet weight), the biomass of organisms was low in the absence of trawling mortality. As trawling intensity increased, however, their biomass also increased because of a competitive release afforded by the reduction in biomass of their larger competitors (Fig. 6b). At the highest trawling intensities, this competitive release was countered by direct mortality, and the biomass maximum moved to an even smaller body size.

For the meiofauna, our model predicted that the largest size classes, with low specific growth rates, would be impacted by relatively low levels of trawling activity. However, the smaller meiofauna, which are very productive and have fast generation times, appear to be relatively unaffected by trawling disturbance (Fig. 6a).

Total biomass and biomass of organisms >1 g wet weight decreased by a factor of 3–4 with an increase in trawling fre-
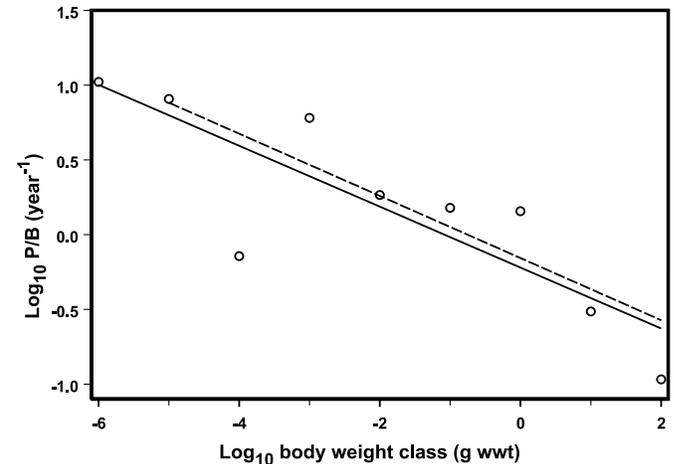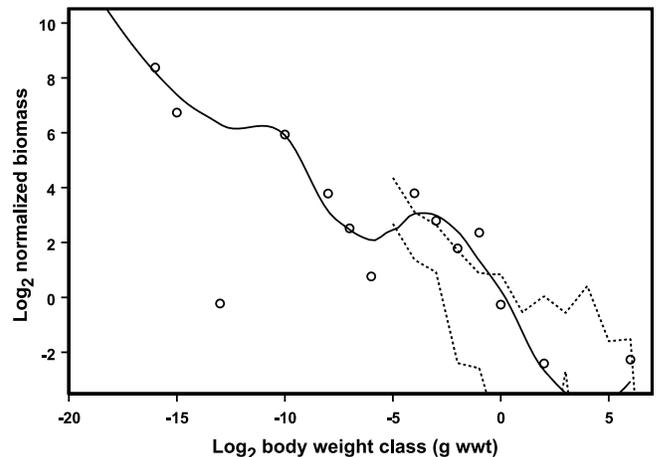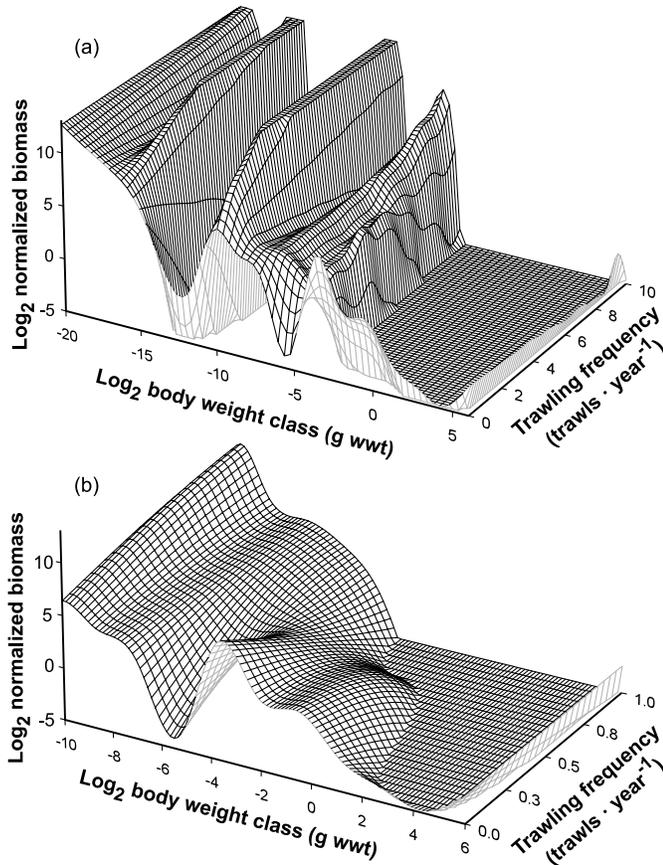
Fig. 5. Modeled biomass size spectrum of benthic organisms in an undisturbed community. The range of empirical data from all sampling stations in the Silver Pit region of the central North Sea is shown as the two broken lines. A spline smoother fitted to the modeled points is shown as the solid line. Organism wet weight is abbreviated as wwt.

quency from 0 to 10 times per year (Fig. 7). Total production was more sensitive to trawling, showing a decline of more than tenfold over the same trawling frequency range. Largest declines in biomass and production occurred at the initial stages of trawling activity (i.e., at low levels of levels of trawling).

A sensitivity analysis of selected model parameters indicated that von Bertalanffy growth rates were usually most important in determining modeled steady state biomass in SOFT and HARD. Furthermore, their importance increased with trawling frequency. As might be expected, the direct trawling mortality estimates were very important in determining community response to trawling activity. A detailed

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Fig. 6. Normalized biomass size spectra of a simulated steady state community at different levels of simulated trawling intensity. (*a*) The entire spectrum over a trawling intensity range of 0–15 times per year. (*b*) The same spectrum as in (*a*) in greater detail for larger size classes in the trawling range of 0–1 times per year. Organism wet weight is abbreviated as wwt.
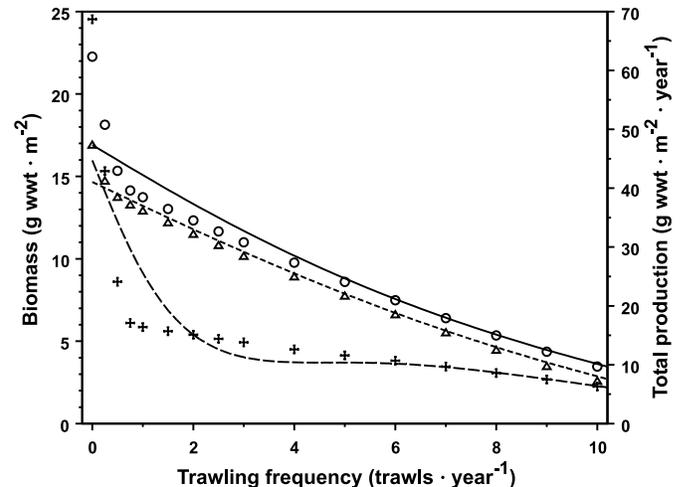
Fig. 7. Total biomass and biomass in size classes >1 g wet weight (wwt) of the modeled benthic community versus trawling intensity: solid line and circles, total biomass; short-dashed line and triangles, biomass in organism sizes >1 g wet weight (wwt); and long-dashed line and crosses, production. Lines represent spline smoothers through the modeled data points.

sensitivity analysis is available from the author and at http://www.qc.dfo-mpo.gc.ca/iml/en/scientists/DupliseaDE/default.htm.

Discussion

Trawling disturbance, as opposed to measured environmental factors, had an overriding effect on the size structure of the benthic infaunal community in the Silver Pit. This size-based response provided a compelling reason to develop a size-based model of the effects of trawling disturbance on benthic community structure. The resultant model was internally consistent and generated *P/B* versus body mass relationships consistent with those reported in empirical studies (Schwinghamer et al. 1986; Dickie et al. 1987), and the modeled size spectra, total biomass, and total production have empirical support from the companion study to the present work (Jennings et al. 2001).

The model showed a clear decline in total community biomass, biomass of larger macrofauna, and a total production with increases in trawling frequency and sustained trawling activity. That is, there is initially a large decline in the community *P/B* followed by a gradual increase. This is consistent with small, fast-growing fauna with low biomass con-

tributing relatively more to community production with trawling frequency. This is corroborated by the decline of large fauna in the biomass spectrum with increased trawling frequency. Change of specific production or respiration is a phenomenon known to occur in disturbed communities where the community is dependent on more resilient smaller fauna (Duplisea and Hargrave 1996). These fauna are often not the macrofauna used by fish as food; hence, it is unlikely that their production would be transferred to the fisheries-related food web.

Our model is applicable to the trawling impacted infaunal communities of mobile sand–mud sediments in the central North Sea. Any application of the model to other locations would require new empirical estimates of mortality functions because mortality rates are strongly dependent on the size-related distribution of animals in the sediment and the penetration depth of the fishing gear (Lindeboom and de Groot 1998). The model outputs implied that the biomass of the larger fauna is reduced by trawling disturbance, consistent with the results of empirical studies in the central North Sea (Jennings et al. 2001). However, the model suggested that this reduction in biomass was not a direct function of body size at all trawling intensities because some of the largest animals suffered lower trawling mortality than intermediate-sized animals (Bergman and van Santbrink 2000*a*, 2000*b*). At moderate trawling intensity, for example, the model suggested that the biomass of intermediate-sized fauna was reduced in relation to that of the largest animals because the largest animals suffered lower mortality than moderate-sized animals that lived closer to the surface of the sediment (Bergman and van Santbrink 2000*a*, 2000*b*). However, at higher trawling intensities, the relatively low population growth rates of the largest animals were not high enough to sustain any elevated mortality resulting from trawling, and their biomass de-

creased in relation to that of intermediate-sized animals with higher population growth rates. Because the size – trawling mortality relationship is a key component of this model, further empirical work should aim at its amelioration.

We made a number of simplifying assumptions when formulating the model, and although the model is implemented in a dynamic form, it is presently valid only at steady state. We modeled the population growth of three types of organisms in several size classes, but there is no growth between size classes to link the growth of individuals through the size spectrum. Therefore, the abundance of large HARD, for example, is not directly related to the abundance of small HARD. Moreover, we ignored the processes that link the reproductive output of mature individuals to the recruitment of juveniles, which is very poorly known at present. Both these factors could be incorporated in subsequent developments of the model and would be needed for its application in system-wide management of trawl fishery impacts.

The asymptotic growth formulation that we used means that an organism approaching its maximum size will have a growth rate tending to zero. Therefore, in some parts of the size spectrum, there is low biomass because there is only a very low population growth rate of organisms there. This is both real because biomass troughs are observed in benthic and pelagic size spectra (Schwinghamer 1981; Sprules and Goyke 1994) and an artefact arising from only three different growth trajectories being used rather than the continuum that would be present in a multispecies community. In the present model, the location of near-zero biomass values corresponded with those observed in real spectra (e.g., Schwinghamer 1981), but it is important not to overinterpret bumps in the size spectrum of individual organism types.

We assumed that mortality could be estimated from specific growth using a published empirical relationship (eq. 6). This relationship was interpolated between the sizes of MEIO 5, SOFT 11–15, and HARD 10–12, but we had to extrapolate it to other size categories. As a result, predicted mortality rates may be too high or low for some categories; however, when trawling mortality contributes a large proportion of total mortality, errors in modeling natural mortality are less important. Further improvements to the model should account for mortality in a more mechanistic manner that models mortality rates for all size categories.

At the lowest trawling intensities, the model predicted that there was a "dip" in the biomass of small macrofauna, but this dip was lost at higher trawling intensities. This is a result of competition, where the high biomass of large fauna at low trawling intensities reduces the biomass of smaller fauna. As trawling intensity increases, the biomass of larger macrofauna is reduced and the smaller macrofauna can compete more effectively. These outputs suggest that the processes structuring trawled and untrawled benthic communities will be very different, with untrawled communities in areas of low natural disturbance dominated by larger macrofauna that limit the growth of smaller individuals. For meiofauna, our model predicted that the largest size classes, with low specific growth rates, would be impacted by relatively low levels of trawling activity. However, the smaller meiofauna that are very productive and have fast generation times appear to be relatively unaffected by trawling disturbance.

Unfortunately, at present, there are few empirical data to determine whether the predicted changes in MEIO resulting from trawling are consistent with those that actually occur in meiobenthic communities (Schratzberger et al. 2002).

Clearly, the current model would need further modification and testing before the outputs are used for quantitative prediction and to support management advice. The size-based approach to modeling trawling impacts, however, should be recognized for its many useful properties such as simple structure, low parameter demands, and general applicability to entire communities rather than specific taxa. Moreover, because so many characteristics of organism metabolism, community structure, and trawl-induced organism mortality are size-based, the present model structure provides a useful and biologically grounded description of the community and its response to trawling.

Both the model and existing empirical studies suggest that North Sea populations of intermediate- and large-sized macrofauna cannot tolerate moderate (~2 passes·year^{-1}) levels of trawling disturbance (Piet et al. 2000; Rumohr and Kujawski 2000; Jennings et al. 2001). However, there is little evidence for the extirpation of intermediate- and large- sized macrofauna over the whole of the central North Sea, even though their abundance is much reduced. We suggest that their persistence is a consequence of the patchiness of trawling disturbance at many scales, with some areas of the seabed trawled five or more times per year while others are virtually untrawled. If the same trawling effort were distributed homogeneously, it is unlikely that populations of these animals would persist. In the North Sea, the significance of patchiness in trawling disturbance is likely to be considerable. At the scale of the ICES (International Council for the Exploration of the Sea) rectangle (211 rectangles of 0.5° latitude by 1° longitude: area of rectangle 3720 km^2 at 53°N), 50% of rectangles are beam-trawled for less than 2000 h·year^{-1} (Jennings et al. 1999). Because a typical beam trawler tows two 12 m wide beams at 6 knots (11 km·h^{-1}), it will impact 534.5 km^2 of the seabed in 2000 h. Thus, in rectangles subject to 2000 h beam trawling·year^{-1} and with a truly homogeneous effort distribution in the rectangle, it would take at least 7 years to trawl the entire rectangle once. Both our model and empirical studies suggest that this frequency of trawling (0.14 times·year^{-1}) would have a relatively minor effect on the benthic infaunal community in sandy sediments.

At the North Sea scale, of course, the distribution of trawling effort among rectangles reflects the presence of sand and sand–mud habitats that can be beam-trawled, so not all lightly trawled rectangles may support comparable populations of intermediate- and large-sized macroinfauna. When distributions of trawling disturbance are examined at even finer scales on comparable habitats, the patchiness in disturbance is still apparent. Rijnsdorp et al. (1998), for example, looked at the patchiness of beam trawling effort on the fishing grounds used by the Dutch fleet in the southern and central North Sea. The degree of patchiness decreased as the resolution of their analyses was increased from 30 × 30, to 10 × 10, to 3 × 3, to 1 × 1 nautical miles. In 1 × 1 nautical mile boxes, the distribution of effort was considered random in 90% of cases. In eight of the most heavily trawled ICES

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rectangles in the southern North Sea (total area 7200 nautical mile^2), 5% of the area was trawled less than once in 5 years and 70% was trawled more than once per year. Because trawling frequencies of greater than once per year would exterminate some of the intermediate-sized macrofauna, we can only assume that their persistence in parts of the North Sea is due to their presence in occasionally trawled areas and habitats unsuitable for trawling, both of which can also act as sources of recruitment.

It is also important for the persistence of intermediate-sized macrofauna that similar patterns of spatial heterogeneity in trawling effort are maintained from year to year. Over the 4 years of the Rijnsdorp et al. (1998) study, this appeared to be the case. In the absence of changes to management strategies that result in the relocation of effort, some consistency in spatial effort distribution is expected from year to year because trawlers will tend to return to tows that are stored on their navigation systems and known to be clear of obstructions. We suggest that management measures that reduce patchiness in trawling disturbance or affect the persistence of spatial patterns in effort over time are likely to have greater effects on benthic communities than those that encourage small areas to be fished repeatedly.

Acknowledgements

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