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An analysis of benthic biological dynamics in a North Sea ecosystem model

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Abstract

This paper presents an overview and analysis of the benthic biological submodel of the European Regional Seas Ecosystem Model II (ERSEM II). This submodel consists of a detailed model description of the benthic system which is integrated with a marine ecosystem model which attempts to address the full range of pelagic and benthic biogeochemical and physical processes. The submodel simulates the seasonal dynamics of a number of functional groups, ranging from decomposers to predators and their interaction with detrital matter in the sediments. The improvements and extensions to the benthic biology submodel compared with the previous published version of the European Regional Seas Ecosystem Model are described. The improvements comprise: the reformulation of turbation and irrigation as functions of faunal activity, the inclusion of oxygen stress limitations and mortalities, a refinement of the description of detritus, additions to the diet of the filter feeders in line with the extensions to the primary production module and an extensive re-parameterisation. Using the $1^\circ \times 1^\circ$ North Sea application, the submodel predictions are compared with data and the performance of the submodel assessed. Using the results of the submodel, the relation between benthic biological dynamics and its principal determinants, depth and overlying production is examined. The model is found to give qualitatively correct results. The transition in community type from anaerobe/deposit feeder in the south to a more mixed community in the north, involving aerobes and meiobenthos is also correctly predicted by the model. The biology is demonstrated to have a strong influence on nutrient efflux. The lack of resuspension/deposition processes is identified as the most significant omission from the current model. © 1997 Elsevier Science B.V. All rights reserved.

Keywords: ecosystem model; benthos; North Sea; ERSEM

1. Introduction

The North Sea benthic communities have been described by several authors, most notably Eleftheriou and Basford (1989), Kunitzer et al. (1992) and Heip et al. (1992) using results from the North Sea Benthic Survey (NSBS). They describe a system in which the principal determinant of the macrobenthos is depth,

with the 70 m contour nominally separating northern and southern community types, although the transition occurs between 50 and 100 m depth. Although influenced by the different water masses involved, this trend is judged to be a product of the variation in food supply reaching the sea floor — both in terms of quality and quantity — (Buchanan, 1963). To the north of the region the consumption of phytoplankton by copepod populations and the greater decomposition of the faecal pellets that is possible during their longer journey to the sea floor is thought to

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limit benthic food supply (Krause, 1981; Fransz and Gieskes, 1984). The influence of temperature is also thought to be significant in maintaining the north–south trend (Jones, 1950; Glemarec, 1973), with only cold-water species found below the 100 m contour and exclusively warm-water species above the 30 m line. The North Sea as a whole is largely influenced by the influx of Gulf Stream waters from the north-west and anthropogenically affected coastal inputs. It comprises an area of approximately 750 000 km², including a diverse range of circulation patterns and a coastline contributing a run off of 300 km³/year derived from a heavily populated and industrialised catchment area of 850 000 km².

The generic European Regional Seas Ecosystem Model (ERSEM, summarised in Baretta et al., 1995) has been applied to a set of physical forcing data describing the North Sea at a resolution of 1° × 1°, under the second phase of the ERSEM programme. The physical forcing data recreate the regional temperature, light and circulation patterns which largely control the productive environment from which the benthos ultimately derives its food and also include riverine inputs. The model includes dynamically coupled representations of pelagic production, the microbial processes, mesozooplankton, benthic sediment chemistry and benthic biology, simulating fluxes of carbon, nitrogen, phosphate and silicate. It is a description and examination of this latter submodel that provides the subject of this paper. As with most benthic systems, the North Sea benthos comprises a complex patchwork of communities, sediments and topography. A model of the scale and complexity of ERSEM does not aim to describe such a level of detail, rather the goal is to reproduce the general trends of the region, in such a way that the cycling of energy and nutrients within the benthos and between the benthos and the overlying water column is accurately portrayed.

2. The submodel

2.1. *The conceptual structure of the benthic submodule*

The benthic biological submodel detailed here is conceptually similar to that described by Ebenhöh et al. (1995), the submodel version produced during

the first phase of the ERSEM project. The current version is fully documented in Radford (1996). The salient features of the submodel and modifications from the ERSEM-I version are described below.

Within ERSEM the benthic system is considered a three-layered physical and chemical structure, comprising oxygenated, oxidised and reduced sediment layers through which organic detritus is distributed. A number of biological functional groups are considered to interact within these layers and with the overlying pelagic system. The nutrient fluxes between the layers and between the benthic and the pelagic system are described by the benthic nutrient submodel (Ruardij and Van Raaphorst, 1995). Detritus is resolved into a number of categories, namely dissolved, particulate and refractory. The vertical distribution of the detrital material is mediated by the biological activity of the components included in the submodel.

The structure of the food web has been developed according to a commonly accepted view of benthic functionality as discussed by Fedra et al. (1976), Chardy and Dauvin (1992) and others. It may be conceived of as two loosely coupled food webs. The first web represents the 'surface' route of recycling via the filter feeders and epibenthic predators. The second represents the 'subsurface' route involving bacteria, meiobenthos, deposit feeders and infaunal predators. A complication that hampers this functional group modelling approach is the tendency for individual macrobenthic species to straddle more than one functional group. For example many species utilise both deposit and filter modes of feeding. It is important therefore to consider the functional groups as not representing a set list of species, but as representing particular modes of energy cycling. The trophic structure of the benthic submodel is shown in Fig. 1, where each link shows a predation or uptake pathway for carbon and the nutrients, nitrogen and phosphorus. In addition respiration, faeces production and nutrient excretion and uptake are explicitly modelled. Pseudo-cannibalistic uptakes are a feature of both the meiobenthos and the two predator groups.

The state variables defined by the benthic modules are given in Table 1. These may be divided into mass state variables which must obey mass conservation laws and the morphological states which describe

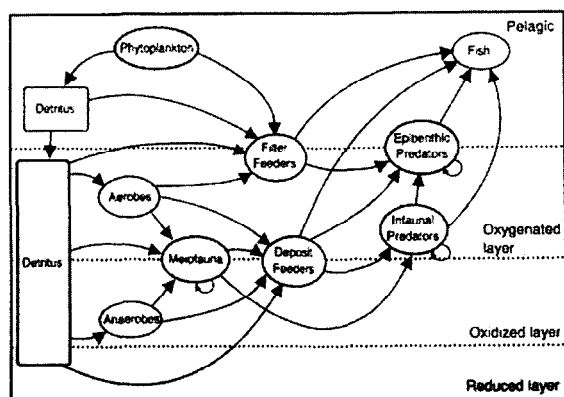


Fig. 1. The benthic food web and the sediment layers.

the structure of the sediment. The mass states may be further subdivided into the functional groups (biology), the detrital state variables and the inorganic chemical states. In principle all ERSEM functional and detrital groups are considered to comprise carbon, nitrogen, phosphorus and sometimes silicon in varying proportions and so have to be described by up to four separate variables. However, the zoobenthic functional groups are considered to have fixed C:N:P ratios and hence can be described by one dynamic mass state variable (carbon) accompanied by a set of nutrient ratio parameters. Detrital matter is described by decoupled, dynamically varying carbon and nutrient state variables.

Parameterisation and measurement of many benthic processes is inherently complicated. There are many reasons for this, some important ones being, the relative inaccessibility of the benthos which limits sampling programmes, the difficulty of establishing benthic communities in mesocosms which limits process studies and the high degree of heterogeneity, even at small scales (De Wolf, 1989), which makes blind sampling prone to high variability. In addition, the difficulty in extrapolating species specific measurements to the functional group or community level adds further uncertainties. Hence most parameterisations are not derived directly from values quoted in the literature but are a synthesis of process measurements, fitting and educated guesswork. The preference factors defining the feeding matrix are given in Table 2. The parameter set for the heterotrophs is given in Table 3 and for the decomposers in Table 4.

Table 1

State variables directly relevant to the benthic biology submodel

State	Unit	Description
Functional groups		
Y1c	mg C m ⁻²	Epibenthic predators or megabenthos
Y2c	mg C m ⁻²	Deposit feeders, macrobenthos
Y3c	mg C m ⁻²	Suspension/filter feeders, macrobenthos
Y4c	mg C m ⁻²	Meiobenthos
Y5c	mg C m ⁻²	Infaunal predators, macrobenthos
H1c	mg C m ⁻²	Aerobic bacteria/decomposers
H2c	mg C m ⁻²	Anaerobic bacteria/decomposers
Detrital state variables		
Q1c	mg C m ⁻²	Dissolved detrital carbon
Q1n	mmol N m ⁻²	Dissolved detrital nitrogen
Q1p	mmol P m ⁻²	Dissolved detrital phosphate
Q1s	mmol Si m ⁻²	Dissolved detrital silicate
Q6c	mg C m ⁻²	Particulate carbon
Q6n	mmol N m ⁻²	Particulate nitrogen
Q6p	mmol P m ⁻²	Particulate phosphate
Q7c	mg C m ⁻²	Refractory carbon
Q7n	mmol N m ⁻²	Refractory nitrogen
Q7p	mmol P m ⁻²	Refractory phosphate
Inorganic state variables		
K1p	mmol P m ⁻²	Aerobic layer phosphate
K11p	mmol P m ⁻²	Oxidized layer phosphate
K21p	mmol P m ⁻²	Reduced layer phosphate
K3n	mmol N m ⁻²	Aerobic layer nitrate
K13n	mmol N m ⁻²	Oxidized layer nitrate
K23n	mmol N m ⁻²	Reduced layer nitrate
K4n	mmol N m ⁻²	Aerobic layer ammonium
K14n	mmol N m ⁻²	Oxidised layer ammonium
K24n	mmol N m ⁻²	Reduced layer ammonium
K5s	mmol Si m ⁻²	Aerobic layer silicate
K15s	mmol Si m ⁻²	Oxidised layer silicate
K25s	mmol Si m ⁻²	Reduced layer silicate
K6e		Aerobic layer reduction equivalent
K26e		Reduced layer reduction equivalent
G2o	mmol O ₂ m ⁻²	Benthic oxygen
G3c	mmol C m ⁻²	Benthic carbon dioxide
G4n	mmol N m ⁻²	Benthic
Structural state variables		
D1m	m	Depth of aerobic layer
D2m	m	Depth of reduced surface
xD2m	m	Constrained depth of reduced surface
D3m	m	Penetration depth of Q7c
D4m	m	Penetration depth of Q7n
D5m	m	Penetration depth of Q7p
D6m	m	Penetration depth of Q6c
D7m	m	Penetration depth of Q6n
D8m	m	Penetration depth of Q6p
D9m	m	Penetration depth of Q6s
Pelagic state variables		
P1c	mg C m ⁻³	Diatoms
P2c	mg C m ⁻³	Flagellates
P3c	mg C m ⁻³	Picoalgae

Table 2

Prey preference factors for the benthic biology

Grazer	Food source													
	Q1	Q7	Q6	H1	H2	Y4	Y2	Y5	Y3	Y1	R6	P1	P2	P3
H1	1.0	1.0	1.0											
H2	1.0	1.0	1.0											
Y4			0.3	1.0	1.0	1.0								
Y2			0.1	1.0	1.0	1.0								
Y5						0.5	1.0	3.0						
Y3			0.1	1.0							1.0	1.0	1.0	1.0
Y1							0.7	0.5	1.0	5.0				

Q1: dissolved organics; Q6: particulate detritus; Q7: refractory particulates; H1: aerobic bacteria; H2: anaerobic bacteria; Y1: epibenthic predators; Y2: deposit feeders; Y3: suspension feeders; Y4: meiobenthos; Y5: infaunal predators; R6: pelagic detritus; P1: pelagic diatoms; P2: pelagic flagellates; P3: pelagic picophytoplankton.

2.2. The heterotrophic physiological modules

Each of the heterotrophic groups: meiobenthos, deposit feeders, suspension feeders, infaunal predators and epibenthic predators, share the same set of physiological processes but they differ in the parameterisation of these processes and the set of food sources. The processes affecting the consumers are represented in Fig. 2. They are uptake, assimilation and faeces production, respiration, mortality and nu-

trient release. Each diet is modified by applying a preference weighting to each food source (Table 2). The mathematical basis of the modules is the same as described in Ebenhöh et al. (1995), reporting on the first phase of ERSEM, but several extensions have been applied since and are now described.

During the second phase of the ERSEM programme several aspects of the submodel were enhanced. Of key importance to the benthic modules was the extension of pelagic primary production

Table 3

Heterotrophic parameters

Process	Unit	Functional group				
		Y1	Y2	Y3	Y4	Y5
Q ₁₀ value (10°C)	–	2.0	2.0	2.0	2.0	2.0
Max specific uptake rate	d ⁻¹	0.03	0.11	0.09	0.40	0.08
Michaelis uptake constant	mg C m ⁻²	5000.0	4000.0	300.0	1000.0	5000.0
Feeding threshold	mg C m ⁻²	50.0	125.0	50.0	50.0	100.0
Excreted fraction of prey	–	0.30	0.35	0.35	0.25	0.30
Excreted fraction detritus	–		0.80	0.85	0.40	
Respired fraction of prey	–	0.25	0.35	0.4	0.45	0.30
Nutrient dilution factor	–	0.8	0.8	0.8	0.8	0.8
Respiration	d ⁻¹	0.0027	0.0027	0.0027	0.01	0.0027
Mortality	d ⁻¹	0.002	0.001	0.001	0.01	0.003
Max. O ₂ stress mortality	d ⁻¹	1.0	1.0	1.0	1.0	1.0
Exploitable water column	m				1.0	
Detrital layer available	m		0.3	0.0025		
Crowding low threshold	mg C m ⁻²			2500.0		
Crowding half saturation	mg C m ⁻²			7000.0		
Crowding coefficient	–			1.3		
Contribution to bioturbation	–	0.5	1.0			0.5
Contribution to bioirrigation	–		1.0		0.2	1.0

Y1: epibenthic predators; Y2: deposit feeders; Y3: suspension feeders; Y4: meiobenthos; Y5: infaunal predators.

Table 4
Decomposer parameters

Process	Unit	Functional group	
		H1	H2
Q_{10} value (10°C)	–	2.0	2.0
Fast decomposition rate for particulate detritus	d^{-1}	$2.0E-4$	$2.0E-4$
Slow decomposition rate for particulate detritus	d^{-1}	$2.0E-5$	$2.0E-5$
Decomposition rate for refractory detritus	d^{-1}	$2.0E-6$	$2.0E-6$
Decomposition rate for dissolved organics	d^{-1}	0.0005	
Excreted fraction	–	0.1	
Excreted fraction detritus	–	0.1	
Respired fraction	–	0.3	0.3
Respiration	d^{-1}	0.02	0.02
Mortality	d^{-1}	0.05	0.05
Fraction of mortality to dissolved detrital material	–	0.1	
Layer depth causing half max. mortality	m	0.001	0.01
Preference of nutrient content	–	2.0	2.0

H1: aerobic bacteria; H2: anaerobic bacteria.

from two functional groups (diatoms and flagellates) to four (now including picoplankton and inedible phytoplankton). This improved the seasonal description so that some production occurs throughout the annual cycle. In turn this enhanced the over-wintering behaviour of the pelagic functional groups and hence provided a more balanced supply of detritus to the sea floor. The food sources of the suspension feeders now include one of the new phytoplankton groups, picoplankton and additionally the benthic aerobic bacteria. The rationale for this being that

bacteria are considered to adhere to detritus particles which (resuspended) already constituted one of the suspension feeders food sources. Excretion of deposit feeders has been redistributed over both the aerobic and anaerobic layers, in direct relation to the proportion of uptake derived from each layer. Whilst this is certainly a simplification of deposit feeder behaviour and physiology, as an assumption taken over the entirety of the deposit-feeding functional group it is probably not unreasonable.

Two new uptake limitation factors have been introduced to the heterotrophic process descriptions: an oxygen stress limitation for all the heterotrophic functional groups and a spatial or crowding limitation applied to the suspension feeders only. In addition a mortality effect due to severe oxygen stress has been included for the heterotrophs.

The rationale for a spatial limitation arose from the tendency in earlier model versions for suspension feeders to achieve unrealistic biomass values due to unconstrained utilisation of their pelagic food sources, a problem exacerbated by the introduction of picoalgae and dinoflagellates into the model. However, a crowded sea floor has been observed to adversely affect uptake by suspension feeders via intraspecific spatial interference (Olscher and Fedra, 1977). This process has been modelled where e_C represents the proportion of maximal uptake rate achievable, Y represents the density of suspension feeders, the constant, s , gives a soft threshold to the onset of the process and h provides the defining half rate constant. x is a measure of effective biomass contributing to the crowding formulation:

$$x = \frac{Y^2}{Y + s}$$

and the limitation on uptake (e_C) is defined by:

$$e_C = 1.0 - \frac{x}{x + h}$$

This is parameterised according to Olscher and Fedra (1977) so that a 40% reduction in uptake is found in populations with high densities (about 7000 mg C m^{-2}). Interference is only considered to be operational above densities of 2500 mg C m^{-2} . However, on reflection, a more intuitive modified Michaelis-Menten function can provide a near identical response and is recommended for future

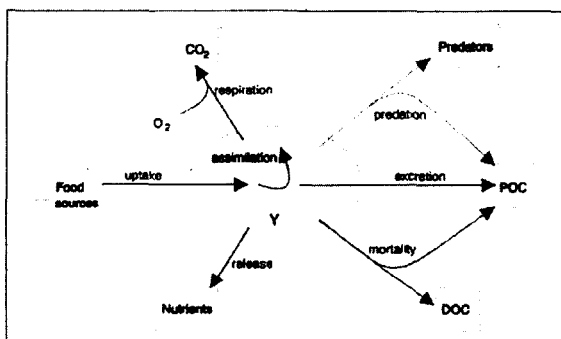


Fig. 2. The heterotrophic physiological model.

versions:

$$e_c = 1 - \frac{Y^c}{Y^c + k_m^c}$$

where Y represents the biomass contributing to the crowding response, k_m the half rate constant and the exponent c modifying the slope or severeness of the response.

Episodic mass mortalities of the benthic system have been observed, for example, in the northern Adriatic for a number of years but also in the German Bight during the early 1980s. This is due to acute near-bed oxygen depletion, in turn caused by high surface water nutrient inputs, eutrophication and strong vertical stability (Stachowitsch, 1984; Justic et al., 1987; Lozan et al., 1990). A formulation of oxygen stress has thus been introduced to the five consumer groups represented in the model. This takes two forms. Firstly there is a reduction of the food uptake rate at low oxygen concentrations, again using a modified Michaelis-Menten function:

$$e_o = \frac{[O_2]^3}{[O_2]^3 + K_m^{O_2}},$$

where e_o represents the proportion of maximum uptake rate achieved at the prevailing oxygen concentration and $[O_2]$ represents the concentration of oxygen in the water column. The physiological complexities of modelling the limitation on respiration caused by low oxygen levels and the subsequent feedback to assimilation and food uptake have been avoided by allowing O_2 stress to directly affect uptake.

Secondly a mortality induced by very low oxygen saturations has been introduced:

$$s = (1.0 - e_o) \cdot s_{\max}$$

where s , the daily mortality, is a function of the maximum daily mortality.

A cubic Michaelis-Menten function has been used to allow survival at very low oxygen saturations, as found in populations well adapted to oxygen stress, whilst allowing steep catastrophic mortality response when O_2 falls below the survival threshold.

Activity respiration of the benthic heterotrophs has been reparameterised from data given by Warwick and Price (1975).

2.3. The decomposer physiological modules

The sediment in the model has a three-layered structure comprising oxygenated, oxidised and reduced layers. Ideally a minimum of three functional types of bacteria should be modelled to complement this structure, namely aerobic, nitrate reducing and sulphate reducing. However, as there is no explicit inclusion of methane and sulphate in the current model, only two types of bacteria are modelled, aerobic and anaerobic, the latter combining the functionality of both the nitrate and sulphate reducers.

Fig. 3a illustrates the underlying principles of bacterial degradation. Bacteria produce extra-cellular enzymes, which decompose the particulate detrital material (POC) into a dissolved form, labile DOC, which rapidly loses part of its nutrient content. The utilisable DOC is therefore assumed to be nutrient poor and necessitates the uptake of extra nutrients from the pore water.

However, as DOC is relatively labile the module has used a simplification so that the decomposers degrade POC directly and the nutrient loss on conversion to DOC is modelled as part of the as-

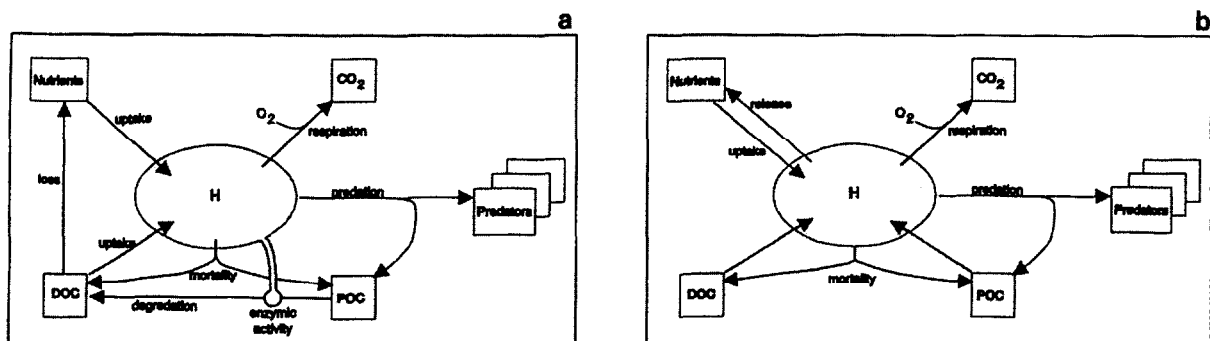


Fig. 3. (a) A standard decomposer physiological model; (b) the simplified decomposer physiological model used in ERSEM.

similation/excretion process. Hence nutrient uptake generally reverses to a nutrient release. The bacterial processes as modelled within ERSEM are shown in Fig. 3b. The process descriptions remain unchanged from the ERSEM-I version.

2.4. Detritus

A new state variable, refractory organic detritus, comprising carbon, nitrogen and phosphorus components has been introduced. This provides a food source for aerobic and anaerobic bacteria only. The degradation rate for the refractory organic detritus is a factor ten smaller than that for particulate organic matter. The distribution with depth of refractory detritus is modelled in a similar way to the other detrital groups. About 10% of pelagic particulate detritus is assumed to become refractory benthic detritus after sedimentation.

2.5. Bioturbation and bioirrigation

Although not described by state variables as such, the sediment pore waters are important as they allow for the mobility of nutrient ions across the sediment interface and in the sediment itself. ERSEM derives the pore-water nutrient variables (phosphate, nitrate, ammonium and silicate) directly from the sediment nutrient state variables. Molecular diffusion (σ^{mol}) of the pore-water nutrients is enhanced by the movement of the pore water, mainly due to the activity of biota that inhabit burrows and spaces in the sediment. For simplicity this extra movement is treated as enhanced diffusion. The diffusion itself is modelled as part of the nutrient submodules (Ruudij and Van Raaphorst, 1995). The purpose of the bioirrigation formulation is to calculate these enhancement factors.

Bioirrigation is modelled as a function of the sediment dwelling functional groups (meiobenthos, deposit feeders and infaunal predators) that are considered to enhance the porosity of the sediment via their activities. Bioirrigation is now modelled as a function of activity rather than as a function of the biomass, as previously. The contribution of each functional group is weighted (p^{irr}) and the net uptake of food (flux^{net}) is taken as a representation of activity, so that:

$$Y^{\text{irr}} = \sum p^{\text{irr}} \cdot \text{flux}^{\text{net}}$$

when summed for each of the three functional groups gives irrigational activity Y^{irr} .

A Michaelis-Menten function determines the apparent diffusion (σ) as a proportion of the maximum enhancement due to irrigation ($\sigma_{\text{irr}}^{\text{max}}$) plus the basal molecular diffusion rate (σ^{mol}):

$$\sigma = \sigma^{\text{mol}} + \sigma_{\text{irr}}^{\text{max}} \cdot \frac{Y^{\text{irr}}}{Y^{\text{irr}} + h}$$

The macrobenthos also strongly affects the transport of particulate matter through the sediment profile via bioturbation (Gerino, 1990). ERSEM treats this in an analogous way to diffusion/irrigation by assuming a basal bioturbation factor (τ^{phys}) as an approximation of physically induced turbation with an enhancement due to biological activity. This factor changes the vertical distribution of detritus in the sediment so that:

$$Y_{\text{tur}} = \sum p^{\text{tur}} \cdot \text{flux}^{\text{net}}$$

when summed for each of the functional groups considered to contribute towards the process, gives bioturbational activity Y_{tur} . The deposit feeders and both the predator groups are considered to be active in this respect. The omission of suspension feeders as bioturbators, on the basis that most of their activity represents the assimilation of suspended matter into the sediment, rather than the reworking of the sediment itself, is contentious and deserves consideration for future model developments.

A Michaelis-Menten function determines the bioturbation factor (τ) as a proportion of the maximum enhancement due to biota ($\tau_{\text{tur}}^{\text{max}}$):

$$\tau = \tau^{\text{phys}} + \tau_{\text{tur}}^{\text{max}} \cdot \frac{Y_{\text{tur}}}{Y_{\text{tur}} + h_{\text{tur}}}$$

Bioturbation changes the vertical distribution of detritus, slowly burying it and thereby increasing its average depth. This process is offset by the continuous addition of detritus at the surface. Consumption and defecation/excretion can act in both directions. The model assumes an exponential distribution of detritus with depth, a simplification that allows a reasonable representation of the process, given the overall detail included in the module. A further advantage is that this can be represented by one parameter, D .

The change in detrital penetration depth is modelled by:

$$\Delta D = \frac{\tau^{\text{bas}} \cdot \tau \cdot (1.0 - e^{\eta/D})}{D}$$

Where the basal bioturbation rate is τ^{bas} , the enhancement due to biota τ , the present penetration depth D and bioturbation depth parameter η (m).

2.6. The physical model

The full North Sea simulations are driven from forcing derived from the model of Backhaus (1983, 1985), modified by Pohlmann (1996a,b,c). Its usage in the context of the ERSEM model is described by Lenhart et al. (1995). For ERSEM II the resultant circulation patterns have been applied to a one by one degree grid ranging from the straits of Dover (51°N) to a northern boundary at 61°N, protruding

into the Skagerrak to 10°E and otherwise bounded by the UK and continental coasts (Fig. 4a). This configuration with a total of 130 boxes and known as the ND130 setup, was chosen largely for the ease of generating validation and forcing data, whilst providing a significant improvement in resolution and hydrodynamic accuracy over the ND15 setup with 15 boxes as used in ERSEM I. Of the 85 cells thus defined, 45, principally in the north of the region, are considered as two layered due to the existence of thermal stratification in the summer. These cells comprise a top box of 30 m with a bottom box extending from 30 m to the sediments, making 130 boxes in all, of which 85 have a benthic interface. In addition to the horizontal and vertical advection generated by the Pohlmann model, the ecology is also forced by time series for radiation, temperature, suspended matter and riverine inputs.

One disadvantage of this increased resolution is

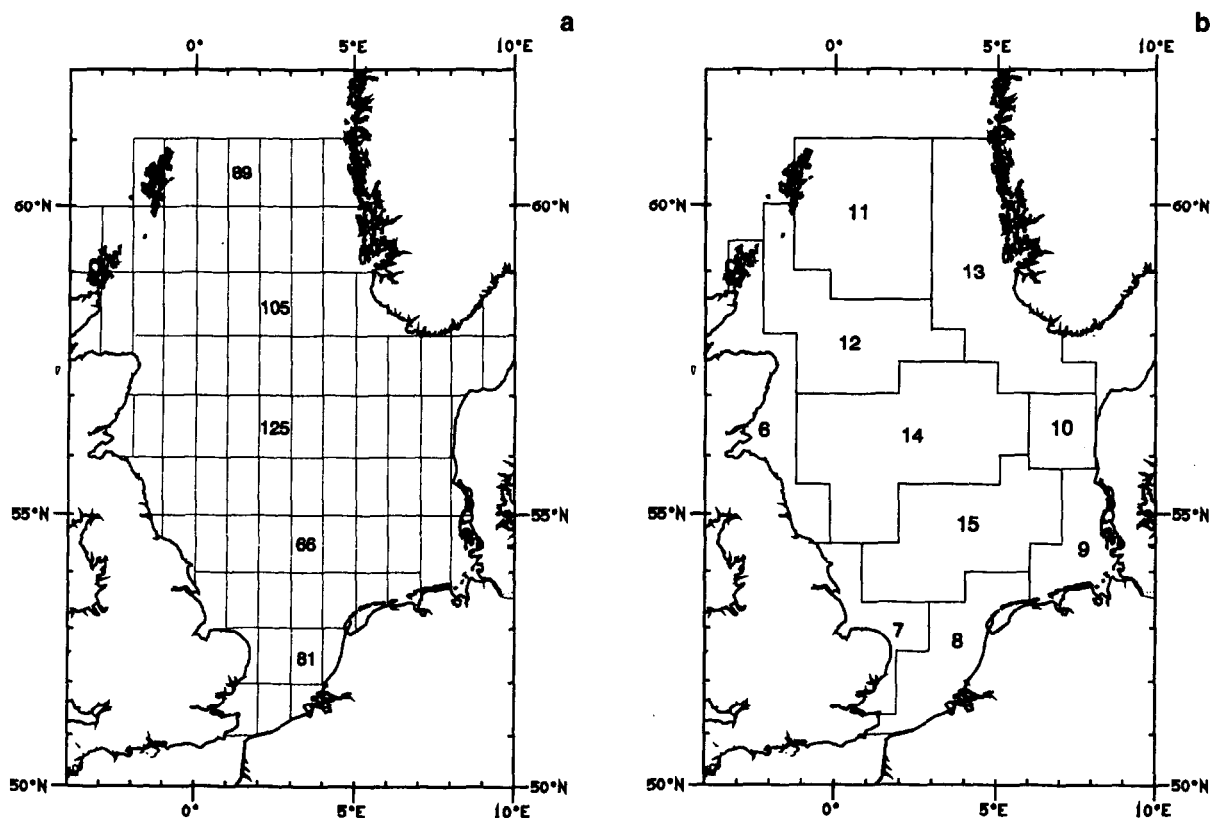


Fig. 4. (a) The degree squares of the North Sea ND130 model. Box numbers for the results illustrated in Table 7 are shown; (b) the large ERSEM boxes used for the ND15 model.

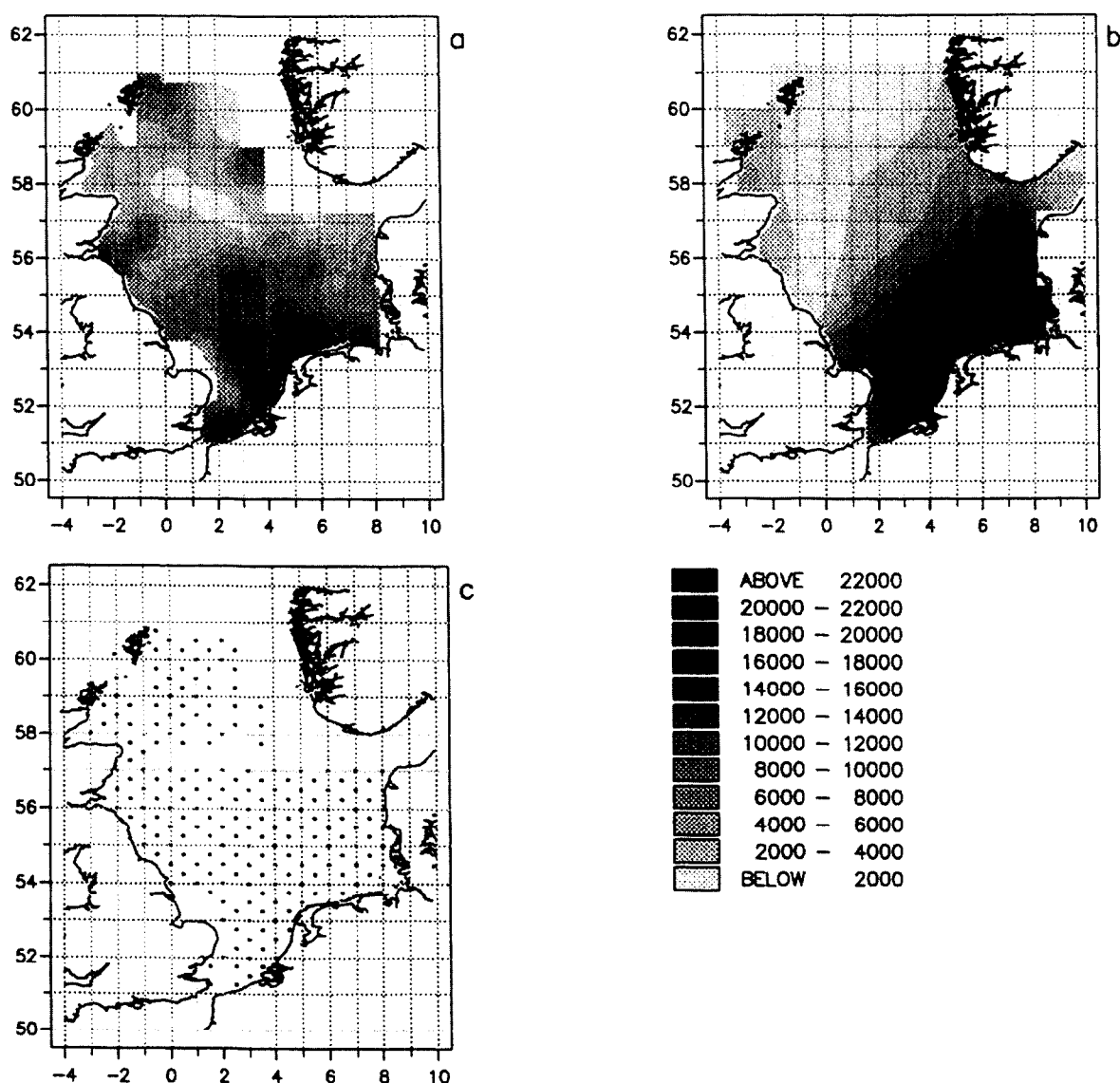


Fig. 6. (a) Contoured macrofaunal NSBS data as annual mean biomass in g C m^{-2} ; (b) contoured macrofaunal model results (annual mean biomass in g C m^{-2}); (c) sampling grid for the North Sea Benthic Survey.

tion of the model would preclude this. Perhaps more seriously, for example, the submodel seemingly overpredicts the faunal biomass of the German Bight. A number of factors might account for this. This area is very variable in terms of its faunal content (Stripp, 1969), the fauna of this area being highly correlated with sediment type (Salzwedel et al., 1985), an interaction which the present submodel neglects, not including resuspension/deposition processes. Further,

the predominantly sandy sediments of this shallow region are prone to the disturbance both from tidal effects and severe weather events. Neither of these processes, which would tend to limit the biomass of the benthos, are included in the ERSEM submodel. The area is also prone to episodic mass mortalities in the benthos due to oxygen depletion. This phenomenon does not occur in the ERSEM simulations described here due to the coarse spatial resolution. A

in the treatment of results. Presenting the results for each of 85 boxes would generate much text but little understanding. Additionally, validation data at this scale tends to be sparse. Thus many of the results presented here have been generated by transforming the output from the ND130 model onto the ND15 configuration used in ERSEM I, based on the large ICES boxes (Fig. 4b) (ICES, 1983). This transformation has been generated by simply calculating the mean for each state variable from every $1^\circ \times 1^\circ$ cell that falls into each of the large ERSEM-I boxes at each time step. Cells that overlap are treated by an appropriate weighting according to area.

3. Submodel validation and analysis

Fig. 5a,b shows the correlation of modelled annual mean macrofaunal biomass with data from the North Sea Benthic Survey (NSBS) (Kunitzer et al., 1992). Macrofauna are taken to be represented by the sum of deposit feeders, suspension feeders and infaunal predators. Fig. 5a aggregates the NSBS data on the North Sea model grid of $1^\circ \times 1^\circ$ (Fig. 4a). At this scale, between 0 and 5 sampling stations fall into each model grid square. Whilst a general correlation is apparent, at this scale the degree of variability in the data is very high compared to the mean. It is necessary to note the limitations of the NSBS data. Whilst the spatial coverage is excellent, seasonality is not recorded as each station was sampled only once, either in April/May (central and southern regions) or January (northern regions). The estimates of annual means have been generated using the fol-

lowing two assumptions; that biomass minima occur in April, prior to the fallout from the spring bloom re-energising the benthos, and that the seasonal maxima is twice the minima. Coupled with the variation inherent in a patchy benthic system, the data must be viewed as qualitative rather than quantitative. A consistent anomaly with the comparison of model and data at the $1^\circ \times 1^\circ$ scale is the underprediction by the model of areas with a biomass over about 13 g C m^{-2} . Biomasses of this magnitude are observed on the continental coast in shallow areas in the vicinity of major river plumes. This may point to either a lack of suspension deposition processes in the model which may sustain the benthic biota, or to an effect of resolution, with the model being still too coarse to generate the conditions in the vicinity of the coast. Indeed, if both data and model results are transformed to the large ERSEM boxes (Fig. 4b), increasing by an order of magnitude the number of samples within each model box, then the correlation between the two is greatly improved as shown by Fig. 5b.

When the mapped macrofaunal results are compared with the survey results (Fig. 6a–c) a limitation of the submodel results becomes apparent. The submodel does make a good prediction of the depth-generated north–south trend in biomass found in the benthos of the region, which is quantitatively correct. However, the submodel can be seen to be performing less well in a number of specific regions. As already mentioned, the submodel does not reproduce the smaller features found by the NSBS in the vicinity of the continental coast, but the relatively coarse resolu-

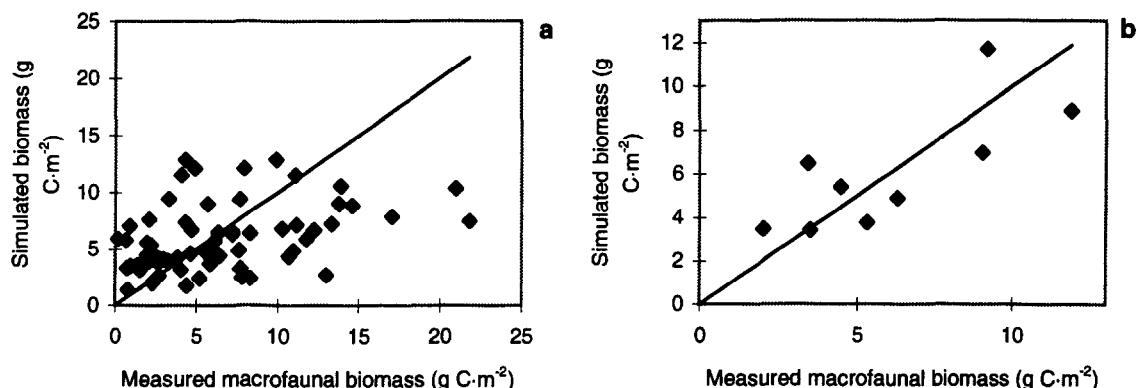


Fig. 5. (a) Correspondence of model results with data (one degree grid). The line illustrates 1:1 correspondence; (b) correspondence of model results with data (aggregated into the large ERSEM boxes). The line illustrates 1:1 correspondence.

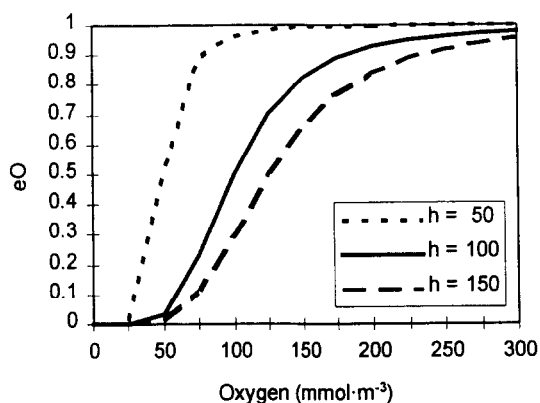


Fig. 7. Response to oxygen stress parameterisation for half limitation values of $h = 150$ (long dashes), $h = 100$ (solid line) and $h = 50$ (short dashes) $\text{mmol O}_2 \cdot \text{m}^{-3}$.

sensitivity analysis on the oxygen stress parameters in ERSEM shows the result of increasing the half limitation value from 0 (i.e. effectively turned off, as used for the standard runs reported on here) to $150 \text{ mmol O}_2 \cdot \text{m}^{-3}$ (Fig. 7, Table 5). This has the effect of reducing the excessive predator biomasses produced by the model, whilst potentially improving the accuracy of the macrofaunal results. However, the correct parameterisation of this process must ultimately be decided by the experimentalists, which is why it remains turned off in the ERSEM standard runs.

The apparent anomaly in the vicinity of the Fladen ground ($58^\circ 40' \text{N } 1^\circ \text{E}$) is a product of an extremely high measurement at only one of the NSBS stations and is certainly a feature that the ERSEM model is too coarse to expect to mimic. The sub-model does begin to show an increase in biomass along the eastern edge of the Norwegian Trench as seen in the data, but does not reproduce the higher biomass found by the NSBS extending in a north-westerly direction from the continental coast into the central North Sea. This feature (as well as the Fladen Ground) may be due to the proliferation of richer muddy sediments in these areas (Eisma, 1981), again signalling the lack of resuspension/deposition processes as an important omission from the current submodel.

The individual components of the macrobenthos (Fig. 8) generally mirror the north–south trend exhibited by the macrofaunal data. Suspension feeders

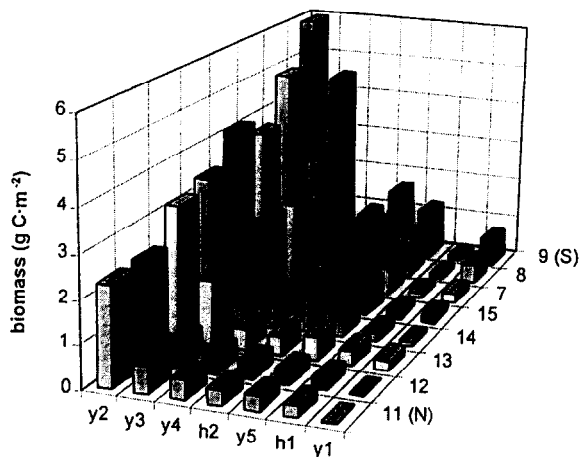


Fig. 8. The annual mean biomass ($\text{g C} \cdot \text{m}^{-2}$) of the benthic functional groups aggregated into the large ERSEM boxes (Fig. 4b) arranged approximately by descending latitude.

are relatively more influenced by the depth of the water column as the availability of the more nutritious living phytoplankton is severely curtailed below the photic zone. The more uniform trend in deposit feeders reflects the distribution of their principal food source, detritus.

Considering the other components of the biological model, the distribution of meiobenthos (Fig. 8), although perhaps under-estimated in the south due to excessive predation, does just indicate an increase in biomass north of 57° , a feature noted by the NSBS (Heip and Craeymeersch, 1995). A sensitivity analysis shows that the controlling factor for meiobenthic biomass in the model is predation, both intra-specific and from deposit feeders (Table 6). However the effects of altering these parameters are uniform across the modelled region. Anaerobic bacteria dominate in the southern North Sea (Fig. 8), with aerobic bacteria gaining importance towards the better oxygenated north (Fig. 8). These trends are generally in agreement with data and hypotheses that are available. Bacteria are generally found to be predicted by the organic content of the sediment which the model also shows (Fig. 9). Van Duyl and Kop (1994) found a weak relation between organic carbon content of the sediment and bacterial biomass but a stronger one with the sediment pigment content. However, this distinction between qualities of detritus is lacking in the model, so the observed result is unsurprising.

Table 5

The results of oxygen stress parameter sensitivity analysis

Box	6	7	8	9	10	11	12	13	14	15	Average
Half saturation = 0.0 mmol O ₂ m ⁻³											
Y1	2.1	4.9	10.3	14.9	3.5	0.3	0.3	2.3	1.0	1.9	
Y2	0.7	1.9	0.7	1.1	2.0	0.8	1.5	0.8	0.9	0.9	
Y3	0.5	1.4	0.7	1.3	2.2	1.2	2.1	3.4	0.3	0.5	
Y5	2.9	9.3	4.0	6.6	12.3	1.9	3.3	2.4	4.4	3.8	
YMC	0.7	1.8	0.7	1.3	2.3	0.9	1.6	1.2	0.8	0.8	
YMC											1.21
All											2.94
Half saturation = 50.0 mmol O ₂ m ⁻³											
Y1	2.0	4.8	10.1	14.7	3.5	0.3	0.3	2.3	1.0	1.9	
Y2	0.7	1.9	0.7	1.1	2.0	0.8	1.4	0.8	0.9	0.9	
Y3	0.5	1.4	0.6	1.2	2.2	1.2	2.1	3.4	0.3	0.5	
Y5	2.9	9.2	4.0	6.5	12.2	1.9	3.3	2.4	4.4	3.8	
YMC	0.7	1.8	0.7	1.3	2.3	0.9	1.6	1.2	0.8	0.8	
YMC											1.20
All											2.90
Half saturation = 100.0 mmol O ₂ m ⁻³											
Y1	1.2	2.4	5.4	9.1	2.2	0.2	0.2	1.3	0.5	0.9	
Y2	0.6	1.8	0.7	1.1	2.0	0.8	1.3	0.8	0.8	0.9	
Y3	0.4	1.0	0.5	1.0	1.7	0.9	1.5	2.5	0.2	0.3	
Y5	2.2	7.3	3.3	5.7	10.6	1.4	2.4	1.9	3.3	3.0	
YMC	0.6	1.6	0.6	1.1	2.0	0.8	1.4	1.0	0.6	0.7	
YMC											1.04
All											2.12
Half saturation = 150.0 mmol O ₂ m ⁻³											
Y1	0.4	0.4	1.0	2.6	0.7	0.1	0.0	0.4	0.1	0.2	
Y2	0.4	1.5	0.6	1.0	1.8	0.5	0.9	0.6	0.6	0.8	
Y3	0.2	0.5	0.2	0.5	0.9	0.4	0.7	1.3	0.1	0.2	
Y5	1.0	3.3	1.8	3.7	7.0	0.6	0.9	0.9	1.3	1.4	
YMC	0.4	1.1	0.5	0.9	1.5	0.5	0.9	0.7	0.4	0.5	
YMC											0.73
All											1.03

Results are given as a proportion of figures obtained from the North Sea Benthic Survey.

Y1: epibenthic predators; Y2: deposit feeders; Y3: suspension feeders; Y5: infaunal predators; YMC: total macrobenthos (Y2 + Y3 + Y5).

Bacterial biomass in the top 5 mm, roughly representing the aerobic layer, as reported by Van Duyl et al. (1993) is in accordance with modelled aerobic decomposer biomass. Measured bacterial biomass over the top 63 mm of the sediment (1–10 g C m⁻²) (Van Duyl and Kop, 1994) is, however, significantly higher than that produced by the submodel (1.5 g C m⁻²). There is good agreement between measured and modelled aerobic layer depth.

Little quantitative data concerning the seasonality of the benthos of the North Sea exists. The general understanding is that the seasonality of the benthos is

determined by the timing of the onset of spring production and the consequent rise in detrital sedimentation (e.g. Buchanan et al., 1978). Hence the lower trophic levels are thought to show annual maxima in the early summer, whilst that of the higher trophic levels occurs in autumn. Fig. 10 shows results for three of the large ERSEM boxes (Fig. 4b), representing a well-mixed and coastal-influenced zone off the Belgium/Dutch coast (box 8), a stratified mid North Sea area (box 14) and a northern box (11) strongly influenced by Atlantic inflow. The submodel shows the seasonality clearly (Fig. 10a–e), with bacterial

Table 6

The results of meiobenthic (Y4) predation sensitivity analysis and the effect on macrobenthos (YMC)

Box	6	7	8	9	10	11	12	13	14	15
Standard parameterisation, Y2 uptake = 0.11 d^{-1} , Y4 cannibalism = 1.0										
Y4	432	552	702	907	837	455	467	491	532	634
YMC	3559	6331	8815	11616	10578	3307	3345	5226	4749	6817
Y2 uptake = 0.10 d^{-1}										
Y4	1.11	1.14	1.12	1.11	1.12	1.13	1.12	1.15	1.13	1.14
YMC	0.90	0.92	0.94	0.95	0.94	0.88	0.88	0.92	0.90	0.92
Y2 uptake = 0.09 d^{-1}										
Y4	1.23	1.28	1.25	1.23	1.25	1.27	1.25	1.31	1.28	1.29
YMC	0.80	0.84	0.86	0.89	0.88	0.75	0.75	0.81	0.78	0.83
Y4 cannibalism = 0.5										
Y4	1.44	1.43	1.44	1.43	1.47	1.47	1.46	1.45	1.45	1.43
YMC	0.85	0.89	0.91	0.92	0.92	0.84	0.83	0.85	0.87	0.87

The sensitivity results are given as the proportion of the standard run annual mean biomass.

activity increasing in response to the spring bloom and remaining at high levels throughout the summer whilst detrital input remains high. Aerobic bacteria are much more strongly associated with the spring–summer growing season than the anaerobes. This accords reasonably with Van Duyl et al. (1993) and Van Duyl and Kop (1994), who found bacterial activity peaking in late summer. Meiobenthos closely follows its bacterial substrate in seasonality with the slower growing macrobenthos showing maxima during September to November depending on latitude, again according to received wisdom. The later maxima for the larger biota in the north may in part be influenced by the warmer winter temperatures experienced there.

The range of the seasonal signal agrees with the generally accepted understanding of benthic ecology (Buchanan et al., 1978).

Fig. 11a,b illustrates the relation between depth and modelled net primary production, detrital input, suspended food and macrobenthic biomass. The relationship between food supply and biomass is reasonably linear (Fig. 11c). In the absence of physical processes affecting the benthic modules this is perhaps not surprising. However, it does hypothesise a relationship, deviations from which could be indicators of communities strongly affected by sediment or disturbance. The relationship between available food and net primary production in the overlying water column (Fig. 11a) is also clear. Where available food falls below that expected from the production, depth is found to be the explanation, in accordance with Buchanan (1963), Krause (1981) and Fransz and Gieskes (1984).

Table 7 shows mean daily fluxes for a series of modelled boxes running approximately north to south as shown in Fig. 4a. Box 81 is situated just off the Dutch coast whilst box 89 is on the northern boundary of the modelled region, midway between Shetland and Norway. There is a northward trend of increasing depth with the exception of boxes 66 and 125, which although of similar depth, differ in that the former is mixed and the latter is stratified. This is seen to have a strong effect on the uptake of pelagic food by the suspension feeders.

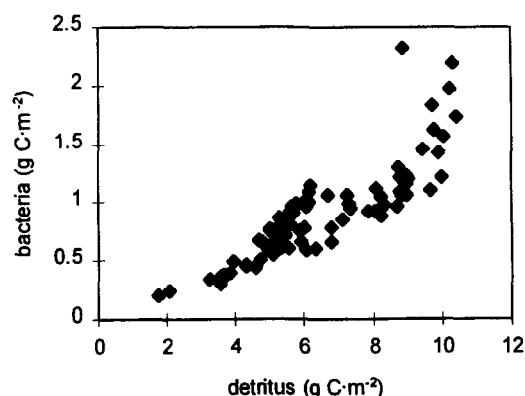


Fig. 9. The relationship between modelled total bacterial biomass and benthic detritus (both in g C m^{-2}).

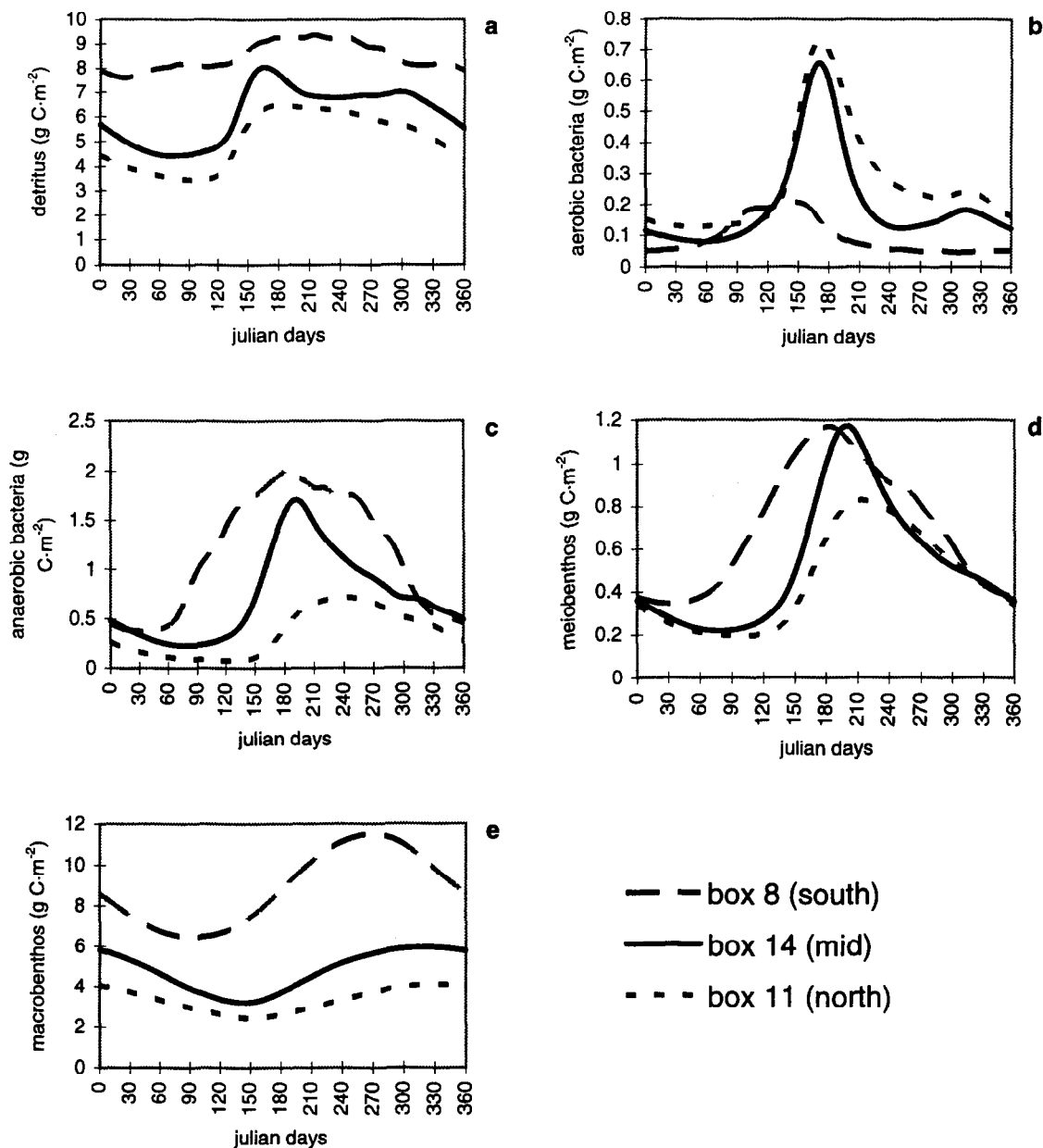


Fig. 10. The modelled seasonal cycle for (a) detritus; (b) aerobic bacteria; (c) anaerobic bacteria; (d) meiobenthos; (e) macrobenthos (all in g C m^{-2}) for three zones of the North Sea corresponding to the large ERSEM boxes as numbered 8 (long dashes), 14 (solid) and 11 (short dashes) in Fig. 4b.

The fluxes indicate that the macrobenthos derive a significant part of their diet directly from the detritus as do the meiobenthos. The meiobenthos are seen to be strong competitors with bacteria for detritus, a trend that increases towards the north. Fluxes

through the anaerobes and deposit feeders dominate those of the aerobic layer and suspension feeders in the south with this dominance decreasing with latitude. Direct uptake of phytoplankton by suspension feeders is only significant in the shallow south.

The aerobes are, however, the only group to show a strong increase with depth due to eutrophic conditions in shallower waters. Meiofauna do not show a significant trend with depth, principally because of the decrease in predation pressure in deeper columns. Bacterial carbon assimilation agrees well with mea-

surements reported by Van Duyl et al. (1993). Three to four times the amount of energy is cycled through the benthos in the south compared with the north.

The regeneration of nutrients into the water column is shown in Fig. 12a,b. Phosphate, ammonium and silicate regeneration are found to be highly correlated with macrofaunal biomass and hence at least partly with bioturbational activity. There is no apparent correlation with nitrate efflux. The exceptionally high nitrogen loading of the Rhine is responsible for the one negative flux (into the sediment) observed (but not shown). The benthic biology is shown to have a very significant effect on the nutrient fluxes of the system. Summer effluxes predicted by the sub-model (Fig. 12 shows annual mean efflux) are in very good agreement with those reported by Van Duyl et al. (1993) both being about an order of magnitude less than the annual mean.

4. Discussion

The spatial resolution of the ERSEM North Sea application implies that the aim for the benthic sub-model can be no more than to reproduce the macro trends found in this region. A representation of benthic patchiness and small scale coastal features is far beyond the scope of the current implementation.

As the benthic system derives its food from the pelagic, the accuracy of the pelagic simulations is of crucial importance when attempting to model the benthos. The pelagic modules of ERSEM generally function well (Ebenhöh et al., 1997; Baretta-Bekker et al., 1998), but have a tendency to underpredict the northern copepod blooms and, perhaps as a consequence, overpredict chlorophyll in the north of the region. There may then be a tendency for the benthos in the northern boxes to be oversupplied with food. The coarse vertical resolution of the model may well be responsible for limiting the accuracy with which the quality of the food supply to the benthos can be predicted.

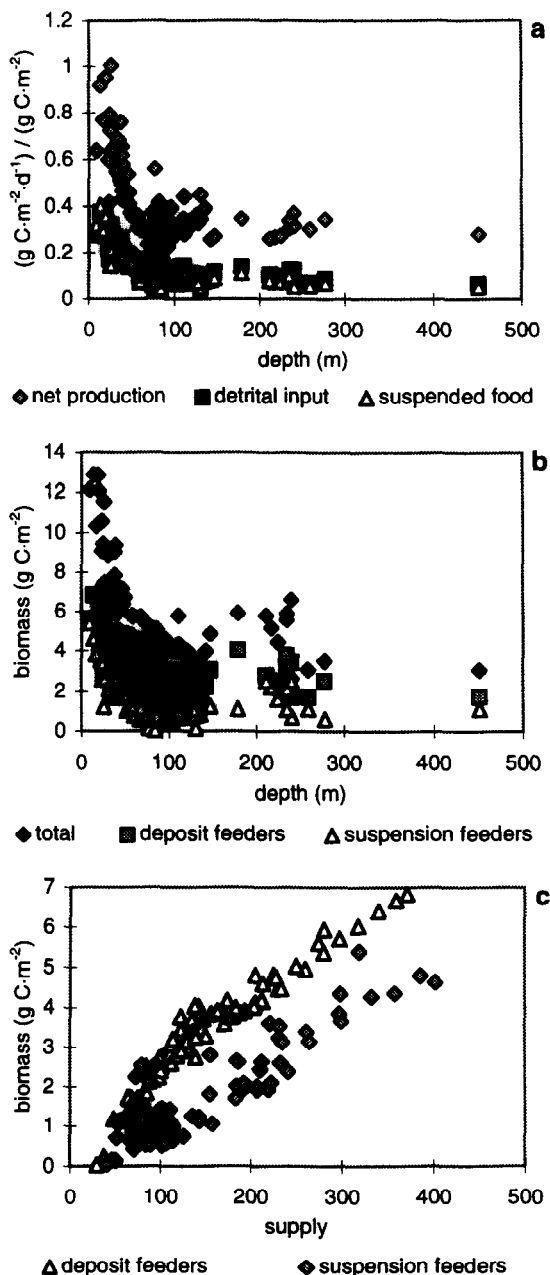


Fig. 11. (a) The relation between depth and net primary production, detrital input (both $g\ C\ m^{-2}\ d^{-1}$) and suspended food ($g\ C\ m^{-2}$); (b) the relation between benthic biomass and depth; (c) the relation between suspension feeders and suspended food (both $g\ C\ m^{-2}$) and between deposit feeders and detrital input (respectively $g\ C\ m^{-2}$ and $g\ C\ m^{-2}\ d^{-1}$).

Table 7

Mean daily fluxes between the benthic components ($\text{mg C m}^{-2} \text{d}^{-1}$)

Flux from	Q6					H1			H2		Y4	R6	PI
to	H1	H2	Y2	Y3	Y4	Y2	Y3	Y4	Y2	Y4	Y2	Y3	Y3
Box 89 (north)	35.3	62.8	16.9	5.4	63.6	6.0	3.9	9.4	17.5	24.0	17.2	5.6	0.1
Box 105	30.5	81.4	18.0	4.0	63.3	5.3	2.8	8.2	22.6	30.0	18.3	4.4	0.1
Box 125	30.0	121.5	21.6	5.3	66.2	5.3	3.2	7.4	34.4	43.2	21.8	6.4	0.3
Box 66	43.6	198.6	44.2	28.8	128.2	5.7	11.5	8.1	56.0	57.9	39.5	39.3	6.5
Box 81 (south)	20.6	358.3	52.1	59.0	155.5	1.7	7.5	2.7	103.2	102.1	53.9	94.0	17.0

Y2: deposit feeders; Y3: suspension feeders; Y4: meiobenthos; H1: aerobic bacteria; H2: anaerobic bacteria; R6: pelagic detritus; Q6: benthic detritus; PI: pelagic phytoplankton. For locations of boxes see Fig. 4a.

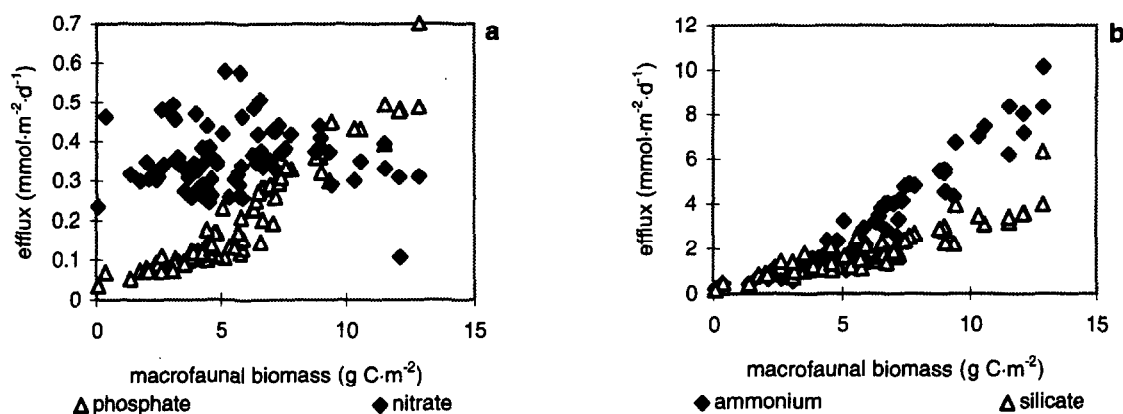


Fig. 12. The relation between macrofaunal biomass and nutrient effluxes (a) phosphate and nitrate; (b) ammonium and silicate.

Other limitations within the current implementations of ERSEM include the lack of an explicitly modelled near-bed layer, which certainly has different properties compared with the general pelagic system; and of processes such as tidally driven resuspension which would tend to increase suspended matter in the bottom layer of the water column. This results in a different sediment structure (sandy gravel) in the shallower regions compared with the muddier sediments found elsewhere. The different physical niches and food types result in different community types. Although sediments, after depth, are thought to be the next major determinant of benthic assemblages, ERSEM does not explicitly include a description of sediment type with respect to its effect on the biota. In turn biota can have significant effects on the stability of the sediment (Jumars and Nowell, 1984). These omissions have been to some extent dealt with by allowing the suspension feeders access to the top layer of sediment (which

one might expect to be generally resuspended) and some other assumptions, but remain as areas demanding further work. For example reduced oxygen saturations are often found close to the sediment during the summer months, where the lower stratified layer is thin and energy input is low (e.g. the Kattegat). The coarse vertical resolution of ERSEM is unable to reproduce this phenomenon so an important limitation on the benthic system is absent. Nor does ERSEM mimic the storm driven resuspension events which can have catastrophic effects on benthic communities.

Much more remains to be explored, perhaps verified and undoubtedly improved within the version of the benthic biological module reported on here. However, in spite of the limitations mentioned, the correspondence with data for the benthic variables indicates that many of the most significant interactions between the benthic and pelagic system have been captured in the model. There are certainly lim-

its to a biomass-based model of this type, and very similar results (in terms of biomass and regeneration) may be obtained from simpler models. A key task remains the coupling of physical sediment processes with the biology, and perhaps a re-examination of the way that detritus is considered in models of this kind. However, models of this complexity do indicate with some success the complex interactions and feedbacks between ecosystem elements, and thus provide a tool with which to focus questions for future benthic studies.

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