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THE MICROBIAL FOOD WEB IN THE EUROPEAN REGIONAL SEAS ECOSYSTEM MODEL

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ABSTRACT

In the framework of the complex dynamical European Regional Seas Ecosystem Model (ERSEM) a module describing the microbial part of the pelagic ecosystem has been developed. The module contains the carbon and nutrient dynamics of pelagic bacteria, heterotrophic flagellates and microzooplankton and interacts with the other parts of the model via phytoplankton, particulate and dissolved organic matter and mesozooplankton. A short description of the module is given and the results are discussed. It is demonstrated that in an application of ERSEM to the North Sea there is a gradual shift in dominance from the continental coast boxes to the offshore deeper areas between the different food webs, from what in the literature is termed the classical food web to the microbial food web, concomitant with a gradual decrease in the efficiency of the microbial loop.

1. INTRODUCTION

ERSEM, the European Regional Seas Ecosystem Model, is a complex dynamical simulation model of the North Sea, developed by a group of nine European marine research institutes (Baretta *et al.*, 1995). ERSEM consists of three submodels: a transport submodel (Lenhart *et al.*, 1995; Radach & Lenhart, 1995), a submodel describing the pelagic system and one describing the benthic system (Ebenhöh *et al.*, 1995), including benthic nutrient regeneration (Ruardij & Van Raaphorst, 1995). Each submodel consists of several modules linked together (Blackford & Radford, 1995). Integration of the model and the exchange of information between the submodels is performed by a simulation software package (Ruardij *et al.*, 1995). The main modules of the pelagic submodel are modules for phytoplankton, zooplankton, microzooplankton and fish. The microzooplankton module describes the carbon and nutrient (N, P, Si) cycling by the state variables bacteria, heterotrophic nanoflagellates and microzooplankton. The state variables are functional groups, *i.e.* all species in a particular size class are aggregated into one biomass-based variable on the basis of their similar ecological function in terms of their trophic relationship with other functional groups. The explicit description of the nutrient flow through the microbial food web in addition to the carbon flow allows us to study the relative importance of nutrient recycling by the microbial food web *versus* its role as a link to higher trophic levels.

The microzooplankton module has been developed using the concepts established over the last two decades with regard to the role of single-celled organisms in pelagic environments. Many aspects of this role are treated in Bjørnsen & Riemann (1992).

For temperate, summer-stratified systems such as the North Sea the conceptual model of the seasonality in the microbial loop is as follows. In the central part of the North Sea there is a seasonal succession from a situation with a fully-mixed water column during winter and spring to a thermal stratification during summer. In spring the inorganic nutrients regenerated and advected during winter are converted by phytoplankton into organic form. Some of the biomass formed in spring bloom(s) sediments to the benthic system, and some is grazed by larger zooplankton. Only a small fraction of the gross primary production is released by the algae as dissolved organic matter. This concept of the food web has been established for a long time and forms the basis of Steele's (1974) model for the North Sea in which all primary production was assumed to be grazed by herbivorous zooplankton. It is known as the classical foodchain (Lenz, 1992).

However, in early spring there is very often a mismatch between primary production and grazing (Fransz & Gieskes, 1984), with a bloom being terminated by nutrient depletion and a very large proportion of the phytoplankton biomass rapidly sedimenting to the bottom. Near the end of a bloom under such conditions, high excretion and lysis give rise to a microbial system with strong similarities to the strati-

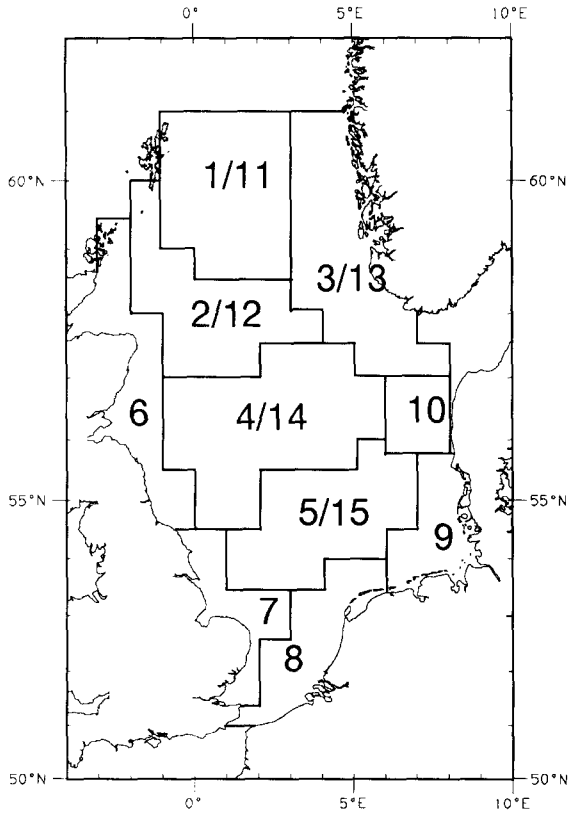


Fig. 1. ERSEM box structure. The deep boxes are divided into two layers, the top 30 m labelled as boxes 1 to 5 whilst the deep boxes are labelled 11 to 15.

fied summer situation.

During the period with summer stratification the concentration of dissolved nutrients above the thermocline is generally low and the phytoplankton is dominated by (small) flagellate phytoplankton. A potential explanation for this phenomenon is given by Aksnes & Egge (1991), who point out that small cells with a high surface to volume ratio have a higher affinity for nutrients than large cells. This implies that only small cells can proliferate in these nutrient-low waters. A relatively high percentage of the gross primary production ends up as dissolved organic matter, which is scavenged by bacteria; these are grazed mainly by heterotrophic nanoflagellates, which in turn may serve as food for ciliates and other microzooplankton, while the whole microzooplankton group forms a major food source for mesozooplankton. This pattern follows the ideas proposed by Pomeroy (1974) and is known as the microbial loop (Azam *et al.*, 1983).

The smaller autotrophic flagellates themselves are consumed by heterotrophic nanoflagellates and ciliates, extending the microbial loop to a microbial food web (Fenchel, 1988; Smetacek & Pollehne, 1986).

Cushing (1989), in discussing the transfer of energy by the different food chains, concludes that the traditional food web transfers most energy during the spring and autumn outbursts in temperate waters (under weakly stratified conditions, which imply meso- to eutrophic nutrient concentrations), but that the microbial food web dominates the strongly stratified and hence oligotrophic waters of the temperate summer. The permanently well-mixed coastal zones in such temperate seas then presumably could show either of the different food webs dominating, depending on the trophic status of the area.

There is no general consensus on which factor(s) determines the exudation of dissolved organic matter by phytoplankton. However, the ambient concentration of dissolved inorganic nitrogen has been shown to be negatively correlated with the release of dissolved organic matter relative to the total primary production (Joiris *et al.*, 1982), suggesting that nutrient stress stimulates the release of dissolved organic matter. Cell size may also be involved, smaller autotrophs (flagellates) with a relatively higher surface/volume ratio being more likely to lose dissolved organic matter through passive diffusion (Bjørnsen, 1988). However, Baines & Pace (1991) and Lignell (1990) show passive diffusion of exudates to be unlikely as a major mechanism. Lysis of *e.g.* (nutrient-)stressed algae is another source of dis-

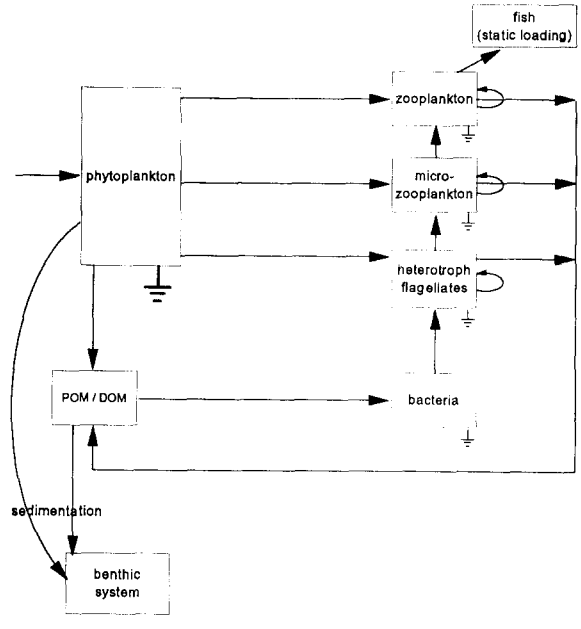


Fig. 2. The interactions of the state variables within the microzooplankton module and with other parts of the model.

solved organic carbon for the bacteria.

Input of dissolved nutrients by enhanced vertical mixing during wind events, local upwelling or nutrient input from land may distort the general picture of seasonal variation in the food web structure outlined here.

Transects through the shallow waters in the Southern Bight of the North Sea (Van Duyl *et al.*, 1990) and even across the much deeper Skagerrak (Kiørboe *et al.*, 1990) reveal hydrography-dependent variations in food web structure.

Where there are changes in time and/or space between these two food webs, there may also be a shift in the fluxes of carbon and nutrients.

The aim of this paper is to describe and discuss the microzooplankton module in ERSEM and the concept behind this module, to discuss some results and to compare the dominance of the two food webs mentioned above in different areas with what can be deduced from field observations.

2. MATERIAL AND METHODS

2.1. DESCRIPTION OF THE MODEL

The dynamical simulation model ERSEM describes the seasonal cycling of organic carbon, oxygen, and the macronutrients N, P, and Si in the North Sea. It represents the biological and nutrient dynamics in the water column, in the benthos underneath and the interaction between both systems. The water column may be seasonally stratified, in which case the column is divided into an upper layer of 30 m depth and a lower layer of the rest of the total depth.

For modelling purposes the North Sea has been divided into boxes similar to the ICES boxes (Fig. 1). In total there are 15 boxes; five upper and five lower boxes and five well-mixed ones (Lenhart *et al.*, 1995).

A transport submodel drives the transport processes across the boundaries of the system and between the spatial boxes, both horizontally and vertically between the upper and lower boxes.

The pelagic submodel consists of a set of interlinked modules. The phytoplankton module describes the phytoplankton dynamics, both of the diatoms and of the non-diatoms (Varela *et al.*, 1995), while the zooplankton module describes the dynamics of the herbivorous and the omnivorous mesozooplankton (Broekhuizen *et al.*, 1995) and the fish module concerns itself with the distribution of fish and their impact on the total system (Bryant *et al.*, 1995). The microbial food web module contains the state variables microzooplankton, heterotrophic nanoflagellates, and pelagic bacteria. In Fig. 2 the interactions of the state variables within the microzooplankton module and with the other parts of the model are given.

As mentioned earlier the biological state variables are modelled as functional groups. Each functional group is formulated using the concept of a 'standard organism' (Fig. 3). In this concept the universal biological processes of growth, food uptake, respiration, mortality, excretion and grazing are defined.

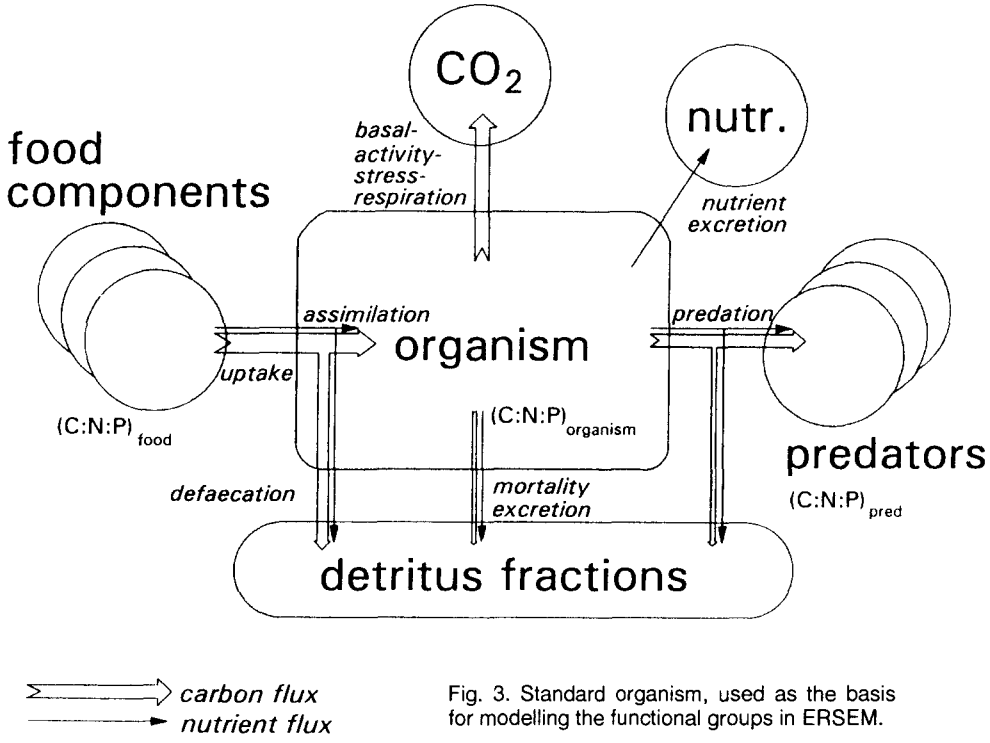


Fig. 3. Standard organism, used as the basis for modelling the functional groups in ERSEM.

2.1.1. CARBON DYNAMICS

The fundamental equation for net growth of the standard organism is

$$STc/dt = (sug_{ST} - (srt_{ST} + sd_{ST} + set_{ST} + sg_{ST})) \cdot STc$$

where

STc = the carbon biomass of the standard organism
sug_{ST} = specific uptake rate
srt_{ST} = specific total respiration rate
sd_{ST} = specific mortality rate
set_{ST} = specific total excretion rate
sg_{ST} = specific grazing rate

The processes determining the daily standing stock variations are both temperature dependent and dependent on the oxygen saturation. The temperature effect is quantified in the following equation:

$$et_{ST} = q10_{ST}\$^{(ETW - 10) \cdot 0.1}$$

where ETW is the water temperature and $q10_{ST}\$$ is the characteristic temperature coefficient, a state-variable-dependent parameter.

Uptake The specific uptake rate of the standard organism is dependent on temperature, on the parameter $sum_{ST}\$$, being the maximum uptake specific uptake rate, on rum_{ST}, which is the amount of food available and on the half saturation value $chu_{ST}c\$$ according to

$$sug_{ST} = sum_{ST}\$ \cdot rum_{ST}/(rum_{ST} + chu_{ST}c\$) \cdot et_{ST}$$

in which

$$rum_{ST} = \sum_{i=1}^{i=n} suFO_{iST}\$ \cdot FO_i$$

and FO_i = the different food or prey classes.

Respiration consists of two parts, standing stock respiration and activity respiration. The standing stock respiration is dependent on temperature while the activity respiration is dependent on the uptake rate, on the assimilation efficiency and on the activity excretion.

$$srt_{ST} = srs_{ST}\$ \cdot et_{ST} + sug_{ST} \cdot (1\text{-}pu_{ST}\$) \cdot (1\text{-}pu\_ea_{ST}\$)$$

in which the first part is the standing stock respiration and the second part is the activity respiration.

$srs_{ST}\$$ = rest respiration rate at 10°C
$pu_{ST}\$$ = assimilation efficiency
$pu\_ea_{ST}\$$ = excreted fraction of the non-assimilated uptake

Excretion The excretion rate is dependent on the uptake rate, on the assimilation efficiency and the activity excretion.

$$set_{ST} = sug_{ST} \cdot (1\text{-}pu_{ST}\$) \cdot pu\_ea_{ST}\$,$$

Thus in total the specific activity respiration and the specific excretion is a fraction $(1\text{-}pu_{ST}\$)$ of the specific uptake (sug_{ST}). The partitioning over respiration and excretion is determined by the parameter $pu\_ea_{ST}\$$.

Mortality The mortality rate has a temperature-independent part and a part dependent on the relative oxygen saturation, so

$$sd_{ST} = (1\text{-}eO2_{ST}) \cdot sd_{ST}o\$ + sd_{ST}\$$$

with $sd_{ST}o\$$ = oxygen-dependent mortality rate
and $sd_{ST}\$$ = temperature-independent mortality rate

The total of mortality and excretion products are partitioned over dissolved and particulate organic matter according to the value of the parameter $pe\_R1_{ST}\$$.

Grazing The specific grazing rate is dependent on the amounts of food (STc) available to the different predators (PR_i).

$$sg_{ST} = \Sigma\, su_{ST}PR_i\$ \cdot STc,$$

where $su_{ST}PR_i\$$ is the availability of the standard organism ST for predator PR_i.

2.1.2. NUTRIENTS

With the exception of nutrient excretion the nutrient dynamics are tightly coupled to the carbon dynamics. The uptake of nutrients by the primary producers is coupled to the gross carbon assimilation, which is dependent on the external nutrient limitation. Bacteria in the model do not take up inorganic nutrients directly, but take up dissolved organic nitrogen and phosphorus. Because of their high carbon respiration rates, the uptake of disolved organic nitrogen and dissolved organic phosphate is sufficient to acquire and maintain their C:N:P ratios which are lower than those of the phytoplankton; thus there is no direct competion with the phytoplankton for inorganic nutrients.
The nutrient excretion by the standard organism is

$$f_{ST}Nlp = (qp_{ST}c\text{-}qp_{ST}c\$) \cdot STc,$$ for phosphorus and

$$f_{ST}Nln = (qn_{ST}c\text{-}qn_{ST}c\$) \cdot STc,$$ for nitrate and ammonia,

with the parameters $qp_{ST}c\$$ and $qn_{ST}c\$$ defining the maximum nutrient (P or N) fraction in the carbon pool in the standard organism and with $qp_{ST}c$ and $qn_{ST}c$ being the actual nutrient (P or N) fractions in the carbon pool. When the difference between the actual and the maximum nutrient fraction becomes negative, nutrients are retained, until the maximum value is reattained.

2.2. THE FUNCTIONAL GROUPS IN THE MICROBIAL FOOD WEB

The differences between the functional groups mainly lie in the values of the parameters and particularly in the rate constants (Table 1). The values of the parameters are derived from allometric considerations (Moloney & Field, 1991; Moloney *et al.*, 1991), based on literature data or estimates in the food components on the uptake side and in the predators on the predation side.

2.2.1. HETEROTROPHIC NANOFLAGELLATES AND MICROZOOPLANKTON

Heterotrophic nanoflagellates in the model are defined as heterotrophic motile cells of 2 to 20 μm SED (Spherical Equivalent Diameter), which feed on bacteria, autotrophic flagellates and themselves. Microzooplankton is defined as heterotrophic planktonic organisms from 20 to 200 μm SED, excluding heterotrophic nanoflagellates and naupliar/larval stages of larger zooplankton and of benthic organ-

TABLE 1

Parameters of the microbial loop part of the ERSEM model. Naming convention: *Z5* = microzooplankton; *Z6* = heterotrophic nanoflagellates; *B1* = bacteria; *s* = specific, *u* = uptake, *r* = respiration, *d* = mortality, *e* = excretion, *g* = grazing (when it is the second character) or gross (when it is the third character), *t* = total, *m* = maximal, $ denotes a parameter.

state variables	*ST*	*Z5*	*Z6*	*B1*
environmental effects				
characteristic Q10	$q10_{ST}$\$	2.0	2.0	2.95
half oxygen saturation	$chr_{ST}o$\$	7.8125	7.8125	0.3125
uptake				
half saturation value	$chu_{ST}c$\$	80.0	350.0	-
maximum specific uptake rate at 10°C	sum_{ST}\$	1.2	10.	8.38
availability of *P2* for *ST*	$suP2\__{ST}$\$	0.5	0.3	-
availability of *P1* for *ST*	$suP1\__{ST}$\$	0.5	-	-
availability of *Z5* for *ST*	$suZ5\__{ST}$\$	0.2	-	-
availability of *Z6* for *ST*	$suZ6\__{ST}$\$	0.6	0.2	-
availability of *B1* for *ST*	$suB1\__{ST}$\$	0.0	1.0	-
availability of *R6* for *ST*	$suR6\__{ST}$\$	-	-	0.05
loss rates				
assimilation efficiency	pu_{ST}\$	0.5	0.2	0.3
assimilation efficiency at low ox	$pu_{ST}o$\$	-	-	0.2
excreted fraction of uptake	pu_ea_{ST}\$	0.5	0.5	-
respiration				
rest respiration rate at 10°C	srs_{ST}\$	0.02	0.05	0.01
mortality				
oxygen-dependent mortality rate	$sd_{ST}o$\$	0.25	0.25	-
temperature-independent mortality	sd_{ST}\$	0.05	0.05	0.0
excretion				
fraction of excretion prod to *R1*	pe_R1_{ST}\$	0.5	0.5	
nutrient dynamics				
max N fraction in carbon pool *ST* (Mol/g C)	$qn_{ST}c$\$	0.0167	0.0167	0.02084
max P fraction in carbon pool *ST* (Mol/g C)	$qp_{ST}c$\$	0.00185	0.00185	0.002083
other parameters				
feeding threshold	minfoodZ6\$	35		
silicate dissolution coefficient	pR6N5\$	0.02		
C/N ratio in fresh detritus (Redfield ratio)	pR6cR6n\$	6.625		
temperature dependency	q10N4N3\$	2.367		
relative nitrification rates	s4n3\$	0.01		

isms. The microzooplankton comprises ciliates and other heterotrophic protists, which are filter-feeders, feeding on phytoplankton and heterotrophic nanoflagellates. Because the microzooplankton is itself a large and diverse group it also feeds on itself. It is grazed by omnivorous zooplankton.

Most of the parameter values for these two groups have been taken from the Ems model (Baretta & Ruardij, 1988). In that model heterotrophic nanoflagellates and microzooplankton were implicitly aggregated into one functional group by allowing this functional group to feed on bacteria.

As it is doubtful that the larger microzooplankton feeds on bacteria (which have an SED of 0.2 to 2 μm), whereas heterotrophic nanoflagellates have been shown to do so extensively (Fenchel, 1986; Christoffersen, 1993), the heterotrophic nanoflagellates in this model have been defined as a separate state variable and the microzooplankton has been reparameterized to reflect its changed composition.

Extra parameters which do not appear in the Ems model, connected to the explicit modelling of the internal nutrient pools, are the maximal cell quota of nitrogen and phosphorus. For nitrogen the Redfield value would be 0.0126 mol N·g C^{-1}, equal to 5.67 g C·(g N)$^{-1}$. The chosen value, 0.0167 mol N·g C^{-1} is equal to 4.27 g C·(g N)$^{-1}$. This is lower than the values found in the literature which range from 4.5 (Moloney & Field, 1991) to 4.8 (*cf.* Jørgensen *et al.*, 1991). In the model it is assumed that the phytoplankton cells can accumulate nitrogen over the Redfield ratio. For the same reason for the phosphorus fraction in the carbon pool of 0.00185 mol P·(g C)$^{-1}$, equal to 13.86 g C·(g P)$^{-1}$, a value has been chosen larger than the value according to the Redfield ratio, being 0.00078 mol P·(g C)$^{-1}$, equal to 32.62 g C·(g P)$^{-1}$.

Except for the availability factors of the several food sources for microzooplankton and heterotrophic nanoflagellates that were estimated in a calibration procedure, there are a few parameters whose values differ for microzooplankton and heterotrophic flagellates, or are different from those used in the Ems model.

The first of them is the half saturation value of the food concentration. In the Ems model it was set to 200 mg C·m^{-3}, while ERSEM uses 80 mg C·m^{-3} for microzooplankton and 350 mg C·m^{-3} for the heterotrophic nanoflagellates. This value was determined from uptake experiments using fluorescently labelled bacteria (Havskum, pers. comm.).

Another difference in parameter values lies in the maximum specific uptake rate. In the Ems model it is set on 2, with literature values for bacteria and algae being in a range between 0.5 and 8 (Sorokin, 1981). In ERSEM, values of 1.2 and 10 are chosen for microzooplankton and heterotrophic nanoflagellates, respectively.

The assimilation efficiency for microzooplankton has been set higher than for the heterotrophic nanoflagellates, an intermediate value was used in the Ems model. Kopylov (1977 in Sorokin, 1981) stated that the assimilation efficiency for bacteria and algae is in the range between 30 and 60%.

In ERSEM lower values for the rest respiration have been chosen than were used in the EMS model, because of the lower reference temperature in ERSEM (10°C) than in the EMS model (12°C).

2.2.2. PELAGIC BACTERIA

The pelagic bacteria are assumed to be free-living heterotrophic bacteria in the water column with detritus as their food source. They form the main food source for the heterotrophic nanoflagellates.

Two forms of detritus are distinguished in the model, *viz.* particulate and dissolved. Both forms are products of excretion/lysis and mortality originating from primary and secondary producers, and are available as substrate for bacteria. The dissolved fraction in the model is treated as labile organic carbon: having a very short turnover time, it becomes fully available within hours of being produced as substrate for the bacteria. Because of its short turnover time it does not accumulate into appreciable concentrations, and for simplicity we do not represent it as an explicit state variable. Rather, we assume that the bacteria consume all labile organic carbon as it is produced.

In the model only a small fraction of the particulate detritus is available for mineralization by bacterioplankton at any time, reflecting the much longer turnover time of the particulate fraction.

The bacteria are modelled slightly differently from the standard organism in that the activity respiration is a fixed fraction of the uptake, while the standing stock (or rest) respiration is modelled as for the standard organism.

All dissolved bacterial excretion products are transformed into dissolved organic matter, which again becomes available as substrate for bacteria in the same time step. The bacterial uptake is the minimum of the potential uptake and the total amount of substrate available. The potential uptake is dependent on temperature, oxygen saturation, the maximum specific uptake rate at 10°C (the parameter sumB1$) and on the bacterial biomass itself, while the total amount of substrate available is the sum of all dissolved excretion and lysis products produced in the same time step and a fraction of the amount of particulate organic matter. The actual value of this fraction depends on the (varying) N:C ratio in detritus.

The temperature dependency, q10B1$, has been set at 2.95. This is at the lower end of what normally is observed in natural populations of bacteria incubated at different temperatures. Meyer Reil (1977) and Goche (1977) give values for Q10 between 2.2 and 4. A rather low value has been chosen because of the seasonal succession of mesophilic and psy-

chrophilic populations (Sieburth, 1976), and also because temperature acclimatization of bacterial populations to prevailing temperatures will result in a lower Q10 value.

The maximal specific uptake rate at 10°C has been taken from Moloney & Field (1991) based on allometric scaling. They calculated a maximal specific uptake rate of 8.38 for bacteria.

It has been assumed that from the pool of particulate detritus 5% is available for mineralisation by bacteria (Laane, 1982). This value is valid when the N:C ratio in detritus corresponds to the Redfield ratio, while in the model it in/decreases with in/decreasing N:C ratio.

The bacterial growth efficiency has been set at 30% for oxic situations and 20% for low oxygen situations. Both values are the same as for the Ems model. Middelboe *et al.* (1992) gave values between 21 and 45%.

The rest respiration rate is small, only 0.01%, as bacteria can persist in an inactive state for prolonged periods (cf. Heinänen & Kuparinen, 1992).

It has been assumed that bacteria suffer no non-grazing mortality and excrete no material. The reason for this is that the excretion and lysis products are available on the same day as substrate for bacteria again. The maximum ratio of nitrogen to carbon is taken to be 0.02084 (mmol $N \cdot mgC^{-1}$). Converted to carbon/nitrogen ratio expressed in g $C \cdot (g\ N)^{-1}$ this value is equal to 3.42. (For comparison the Redfield ratio by weight expressed in this unit is 5.67). This value is at the lower end of the range found in the literature (Moloney & Field, 1991: 4; Goldman *et al.*, 1987: 4.5; Jørgensen *et al.*, 1991: 3.8-6.1 extracted from several sources).

The corresponding value for phosphorus is 0.002083, which is equal to 12.3 g $C \cdot (g\ P)^{-1}$ (according to Redfield 32.6). This value has been chosen because bacteria may be expected to have a high P:C ratio due to their high content of nucleic acids (Thingstad, 1992).

3. RESULTS

The ERSEM model generates far more results than we can ever hope to verify with *in situ* data, because of the scarcity of relevant observational and experimental data on almost all aspects of the microbial food web in the North Sea.

To alleviate this problem, existing data on species composition and abundance have been analysed, aggregated into the functional groups used in the model and converted to mg $C \cdot m^{-3}$. Also, published results of *in situ* experiments on microbial food web dynamics have been used to test the model results.

3.1. VALIDATION DATA

The largest set of relevant data originates from the Natural Environmental Research Council (NERC) North Sea Community project (1988 to 1992). During the NERC North Sea survey water samples were collected monthly at 122 stations throughout the southern North Sea at three depths (surface, pycnocline/mid-depth and near-bottom) between August 1988 and October 1989. Data from this survey were assembled into an Oracle data base by the British Oceanographic Data Centre (BODC) and distributed on CD-ROM. For later analysis of microzooplankton samples were taken in duplicate, one sample being conserved with Lugol, the other with formaldehyde.

Phytoplankton and microzooplankton species were identified and counted in 221 of these samples by the Marine Analytical Service (UK) on behalf of the North Sea Directorate of the Department of Public Works (Rijkswaterstaat, NL). The most common phytoplankton species were grouped by size, to estimate biovolumes. The data are not included in the BODC data base, but have been aggregated into a data base at EMC. Carbon biomass has been calculated by applying conversion factors ($pgC \cdot cell^{-1}$) from different sources to the species counts. A. Pomeroy, B. Williams and M.R. Heath have kindly provided unpublished conversion factors for North Sea species. Conversion factors for the southern part of the North Sea were found in the data base by J. Berg, and finally missing conversion factors were calculated from biovolume data from the Kattegat (H.A. Thomsen, pers. comm.). Conversion factors could be derived for 90% of the species.

A comparison was made between *in situ* chlorophyll and the calculated chlorophyll values, using C:Chl ratios of 50, 25 and 100 for diatoms, autotrophic flagellates and *Phaeocystis*. This comparison revealed an overestimation of calculated chlorophyll during some blooms of *Gymnodinium simplex, Ceratium furca, Rhizosolenia styliformis* and *Rhizosolenia* sp. Lower conversion factors were applied on these occasions. However, in general, the C:Chl ratios used for calculating chlorophyll from carbon gave a good correspondence between calculated and observed values, indicating the chosen values to be reasonable.

The method used to estimate the carbon biomass of heterotrophic protists in the NERC samples, with Lugol preservation and counting by light microscope, may in general underestimate the biomasses of fragile and small heterotrophic protists. This applies especially to the heterotrophic nanoflagellates, only blooms of relatively large species can be expected to be recorded.

To be used for model verification purposes, the carbon biomass data were aggregated into the functional groups, diatoms, autotrophic flagellates, heterotrophic nanoflagellates and microzooplankton for each ICES box.

In addition to the NERC/BODC data set some of the results of the WINDOW and the EUZOUT expedi-

TABLE 2

Observed and simulated mean values over the period between July 14 and August 5 for the standing stock of bacteria, heterotrophic and autotrophic flagellates in mg $C \cdot m^{-3}$, bacterial and primary production in mg $C \cdot m^{-3} \cdot d^{-1}$, and the bacterial production expressed as percentage of the primary production, for the boxes 4/14, 5/15 and 8. The observations are from Van Duyl *et al.* (1990) and Riegman *et al.* (1990).

	box 4/14			*box 5/15*			*box 8*		
	observations		*ERSEM*	*observations*		*ERSEM*	*observations*		*ERSEM*
	mean	*SD*		*mean*	*SD*		*mean*	*SD*	
bacteria	7.37	3.26	36.82	17.97	7.57	42.76	34.9	24.11	53.5
heterotr. flag.	37.79	21.9	12.47	19.3	9.94	6.49	121.67	135.33	3.6
autrotr. flag.	51.6	40.74	67.07	28.7	20.6	71.53	60.06	50.31	58.9
bac. prod.(BP)	2.16	0.79	4.22	5.12	6.89	4.60	21.5	5.0	6.18
prim. prod.(PP)	-	-	9.93	-	-	15.53	-	-	30.86
(BP/PP).100	9-22	-	42.49	3-31	-	29.70	28	-	20

tions (Van Duyl *et al.*, 1990; Riegman *et al.*, 1990) have been used. Van Duyl *et al.* (*op. cit.*) give carbon biomass data for bacteria, heterotrophic and autotrophic flagellates, and data for bacterial production, while Riegman *et al.* (*op. cit.*) give phytoplankton biomass and production values for the period between July 14 and August 5. The stations along the transects, which went through the boxes 4, 5 and 8 have been mapped to the ERSEM boxes and the data converted from m^{-2} to m^{-3}. The mean values and their standard deviations are calculated for the appropriate ERSEM boxes and given in Table 2.

In February/March and in May/June 1988 Nielsen & Richardson (1989) studied carbon flows in the

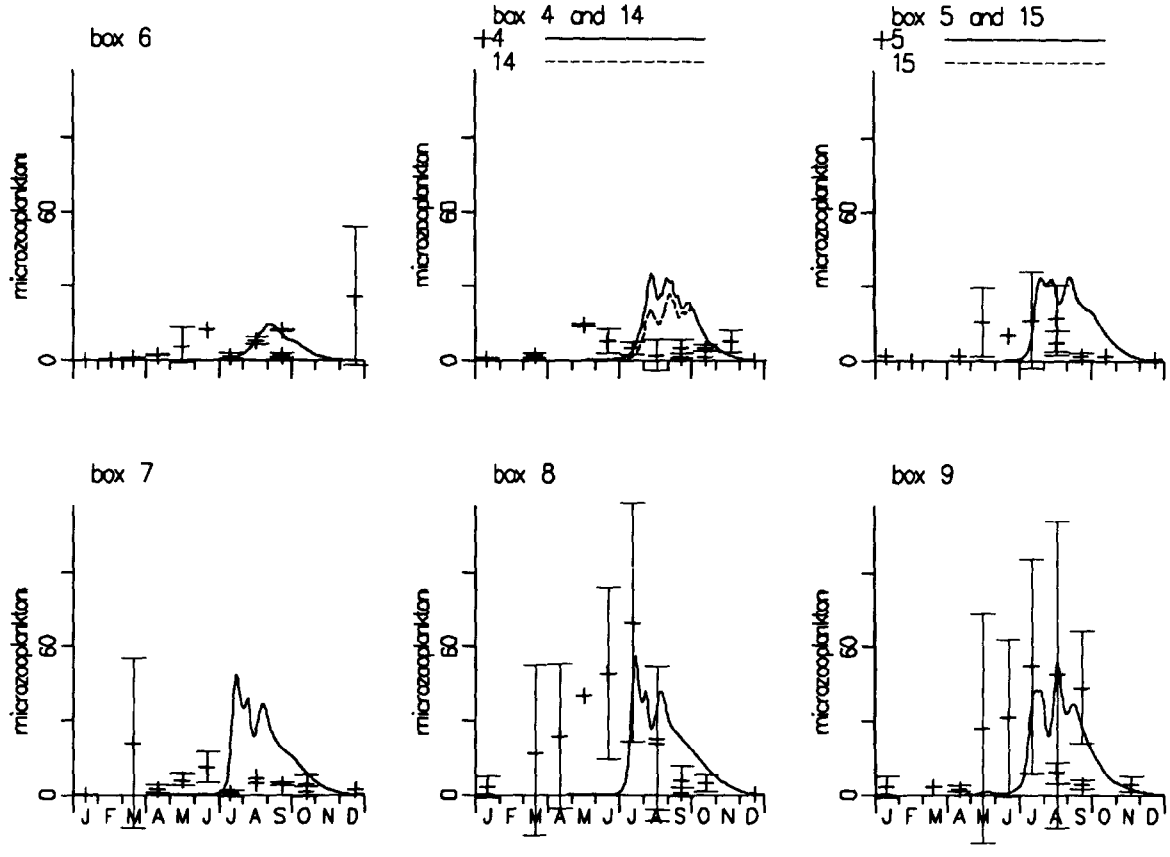
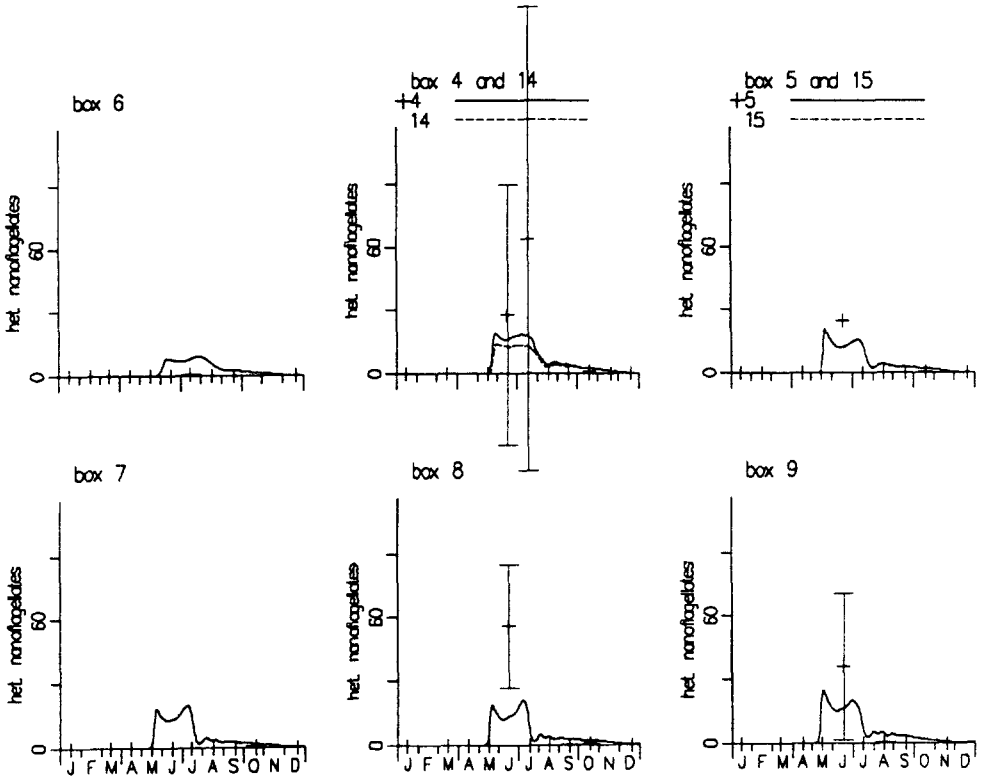
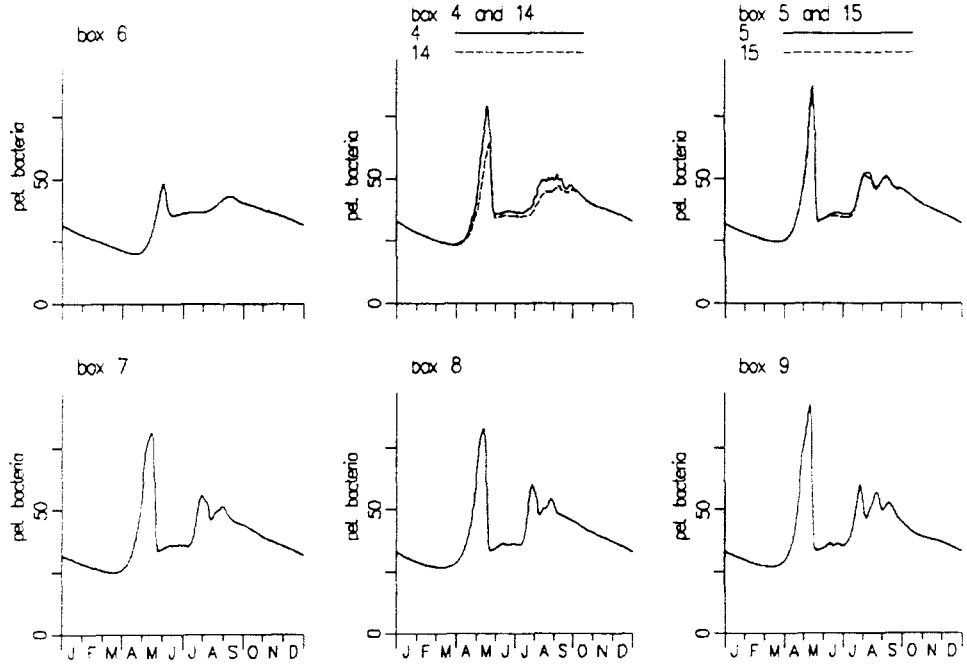


Fig. 4. Model results in mg $C \cdot m^{-3}$ with available field data (see text) of microzooplankton (above); heterotrophic nanoflagellates; (right, top) and bacterioplankton (right, bottom).


box 6
box 4 and 14
+4
14
box 5 and 15
+5
15
box 7
box 8
box 9
het. nanoflagellates
0
60
J F M A M J J A S O N D


box 6
box 4 and 14
4
14
box 5 and 15
5
15
box 7
box 8
box 9
pel. bacteria
0
50
J F M A M J J A S O N D

plankton community in various regions in the North Sea. From all the variables they measured, the standing stocks of the heterotrophic nanoflagellates and bacteria, as well as bacterial production are relevant as validation values for ERSEM. Values for the same variables can be extracted from a study by Nielsen *et al.* (1993), who investigated plankton dynamics and hydrodynamics in the Dogger Bank area (ERSEM boxes 4 and 5) two years later during May/June.

3.2. MICROZOOPLANKTON

The model results for microzooplankton biomass (Fig. 4a) in the coastal boxes 6, 8 and 9 in the second half of the year are similar to the NERC values, but in the first half year especially in box 8 the model severely underpredicts the microzooplankton biomass. The model predicts box 7 to be dynamically similar to the boxes 8 and 9, but the NERC data indicate microzooplankton biomasses to be lower in box 7 than in the continental coastal boxes. The simulated microzooplankton seasonal dynamics for the offshore boxes 4 and 5 have neither the right shape, nor the right maxima. Nielsen & Richardson (1989) only found few microzooplankton species in their samples and lumped them with the mesozooplankton species. Nielsen *et al.* (1993) calculated values between 1 and 5 mg $C \cdot m^{-3}$ south of the Dogger Bank in May/June and values higher than 10 mg $C \cdot m^{-3}$ on the Bank.

3.3. HETEROTROPHIC NANOFLAGELLATES

The NERC data for heterotrophic nanoflagellates (Fig. 4b) give values close to zero except for a peak in June, and for box 4 also during July. The model predicts values close to zero for the coastal boxes 6, 7, 8 and 9 for the whole year, with seasonal maxima in the period between May and July reaching values around 25 mg $C \cdot m^{-3}$, which is considerably lower than the maxima in the NERC/BODC data. The heterotrophic nanoflagellate biomasses for the boxes 4 and 5 measured by Van Duyl *et al.* (1990) are in the same range as the simulated values, but for box 8 much higher than both the model and the NERC/BODC values (Table 2). Heterotrophic nanoflagellates standing stock data observed for ERSEM box 5 by Nielsen & Richardson (1989) and by Nielsen *et al.* (1993) vary from lower than to within the range of the simulated values.

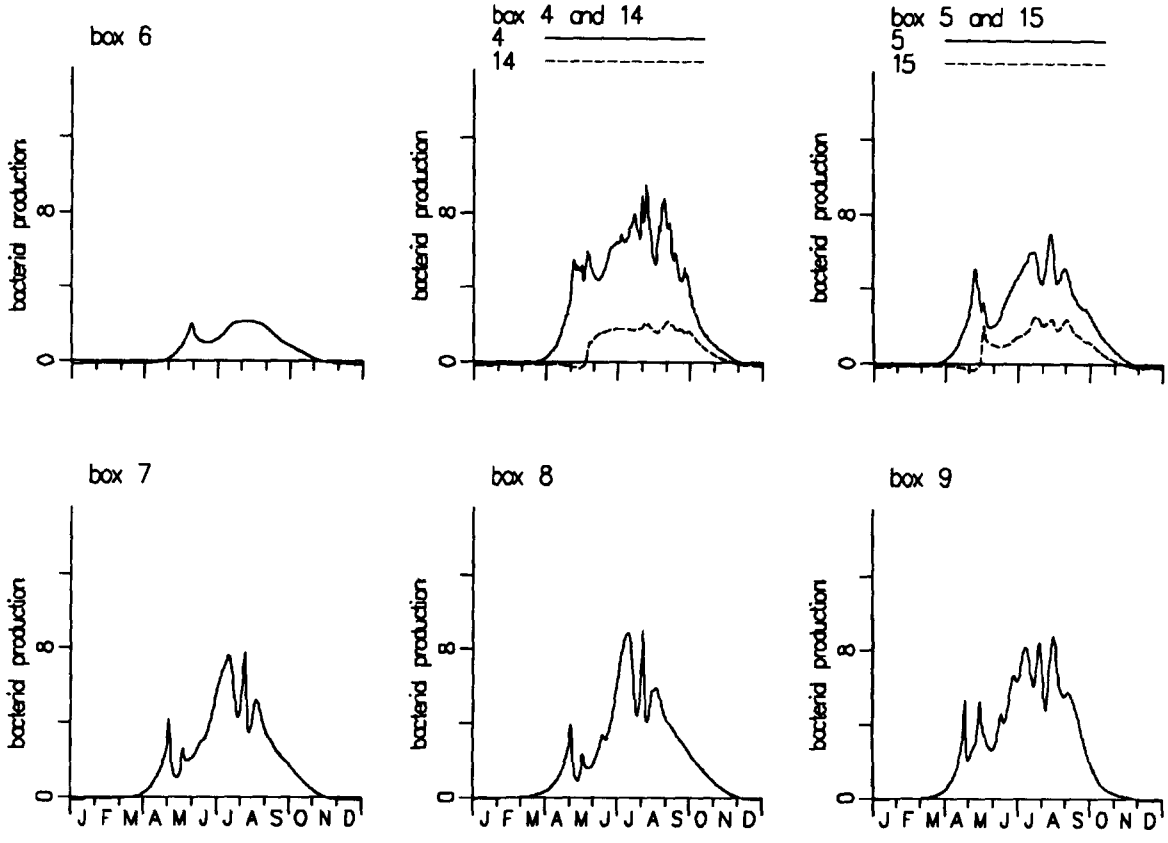


Fig. 5. Model results (mg $C \cdot m^{-3} \cdot d^{-1}$) of the bacterial production in the water column.

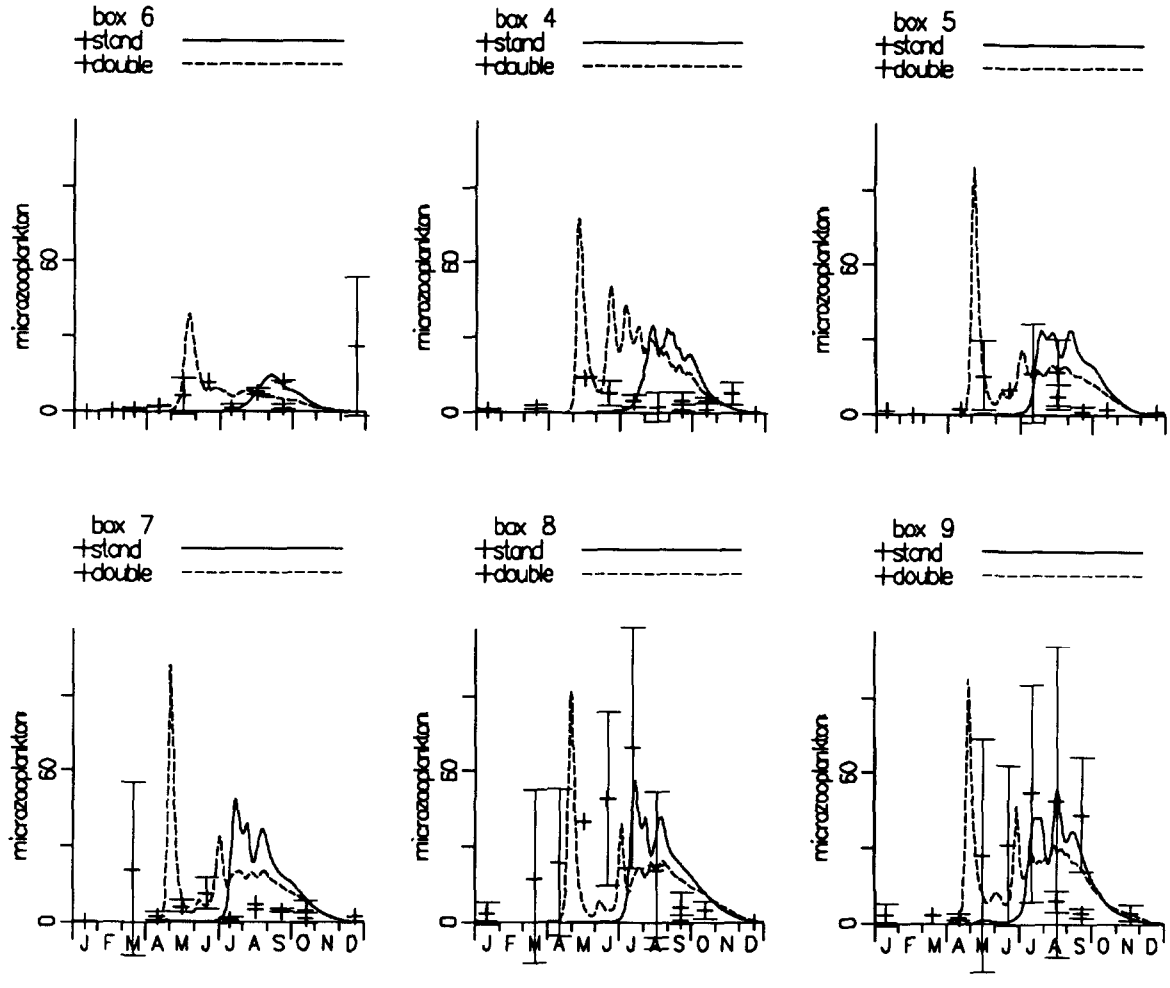


Fig. 6a. Comparison of the standard model results with field data of microzooplankton in box 8 (mg C·m^{-3}) with a sensitivity test with a doubled maximal rate of uptake (2.4).

3.4. BACTERIA

In comparison with the field data given by Van Duyl *et al.* (1990) the simulated bacteria biomasses (Fig. 4c and Table 2) for box 8 are in the right range, but too high for the other two boxes, especially for box 4. In comparison with data from Nielsen & Richardson (1989) the simulated winter values of the bacterial biomass are too high, while the May/June values are in the same range, as also is the case in comparison with Nielsen *et al.* (1993). The simulated bacteria production is shown in Fig. 5. The weighted mean of the simulated values for 5 and 15 is very close to the bacterial production measured by Van Duyl *et al.* (1990) (Table 2) and by Nielsen & Richardson (1989) and Nielsen *et al.* (1993). For box 4 and box 14 the bacterial production in the model is too high and for box 8 too low. Van Duyl *et al.* (*op. cit.*) also give the bacterial production as percentage of the primary production, calculated by Riegman *et al.* (*op. cit.*). Those values, averaged over ERSEM boxes are also given in Table 2 together with the model results. The values Nielsen *et al.* (1993) give for this ratio are higher: 13 to 26% for box 4, depending on the method used, and 55 to 78% for box 5, with ERSEM values averaged over the same period in May/June for boxes 4 and 5 of 15.74 and 15.86%, respectively. For the cruise period in February/March Nielsen & Richardson (1989) found in box 5 very low percentages (3 to 7%), while the ratios in the model were less than zero, because of negative bacterial production during that period.

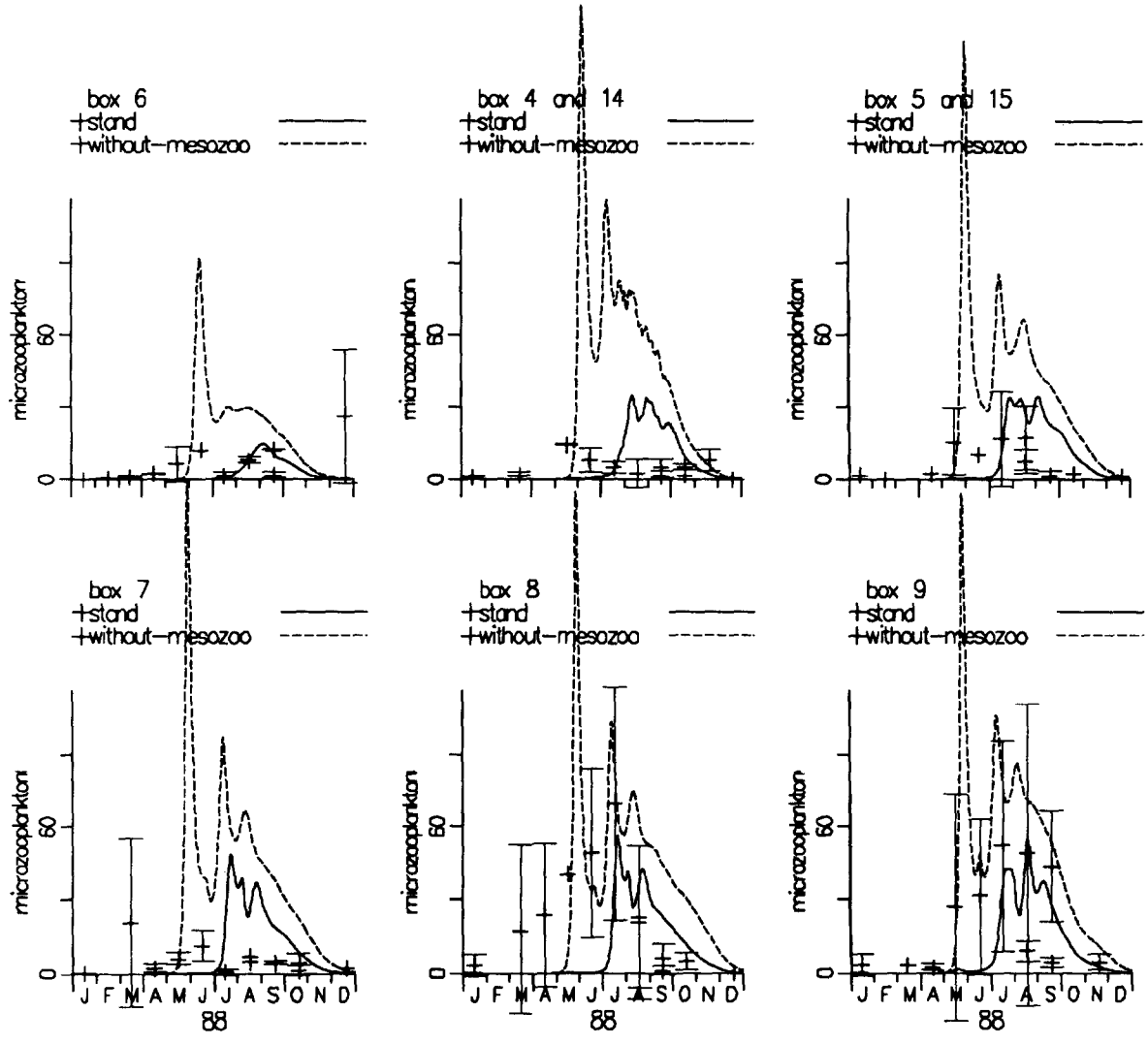


Fig. 6b. Comparison of the standard model results with field data of microzooplankton in box 8 (mg C·m^{-3}) with a sensitivity test excluding the mesozooplankton.

4. DISCUSSION

The reason(s) for the incorrect seasonality in microzooplankton abundance in the model are not entirely clear, but possibly the parameter value for the maximal rate of uptake is too low, so delaying net population growth until increased growth at higher water temperature (Q10 effect), by offsetting the internal and external losses.

A sensitivity test, running the model with a doubled maximal rate of uptake to the value of 2.4, indeed shows an improved seasonality for microzooplankton (Fig. 6a), but at the expense of generating a very pronounced spring maximum, which is not found in the data. During summer, especially in box 4, the microzooplankton in this model run exerts top-down control over the phytoplankton.

Another explanation may be that the grazing pressure by mesozooplankton in the model is too high in late spring, depressing microzooplankton biomass. As has been shown by Broekhuizen *et al.* (1995) the simulated biomass of the omnivorous mesozooplankton in late spring is higher than the observations. A coarse test of this hypothesis by excluding the mesozooplankton totally shows that the increase of the microzooplankton biomass indeed starts two months earlier. With the exception of box 8, this is in better accord with the data (Fig. 6b).

Both sensitivity analyses indicate that it is possible to improve the model's performance for at least some of the boxes. More tests could indicate more precisely which (interacting) processes, now included as con-

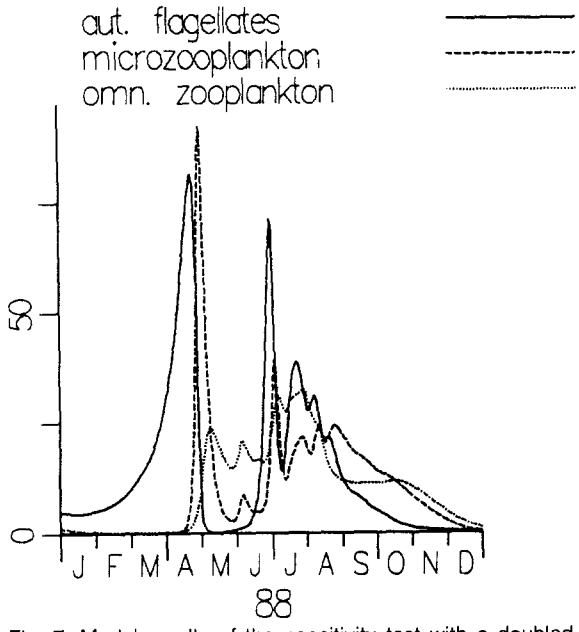


Fig. 7. Model results of the sensitivity test with a doubled maximal rate of uptake for the microzooplankton in box 8 (mg $C \cdot m^{-3}$), to show the tight coupling between autotrophic flagellates, microzooplankton and onmivorous mesozooplankton.

stant parameter values should be resolved to bring the model behaviour closer to reality.

In general, it seems phytoplankton-microzooplankton-mesozooplankton trophic interactions may be too rigidly defined in the model. This results in a rather rigid coupling of the dynamics of these groups, which in reality, because of small-scale variability (both in time and space) may be much looser. The degree of coupling can be shown in the output of the sensitivity test with the doubled microzooplankton uptake rate for box 8 (Fig. 7).

Another way of testing the realism of this model is with data from marine enclosure experiments (Baretta-Bekker *et al.*, 1994) by hindcasting the time-evolution of these experiments.

The conclusion of these hindcasts, which only involved the pelagic submodel of ERSEM, was that the simulated dynamics in the enclosures broadly reproduced the observed system dynamics for an oligotrophic control, but that the results for a nutrient-enriched enclosure were less convincing, especially concerning the nutrient dynamics. When the model system was given a nutrient pulse, mimicking the experiment, it correctly hindcast the resulting phytoplankton blooms and enhanced microbial food web

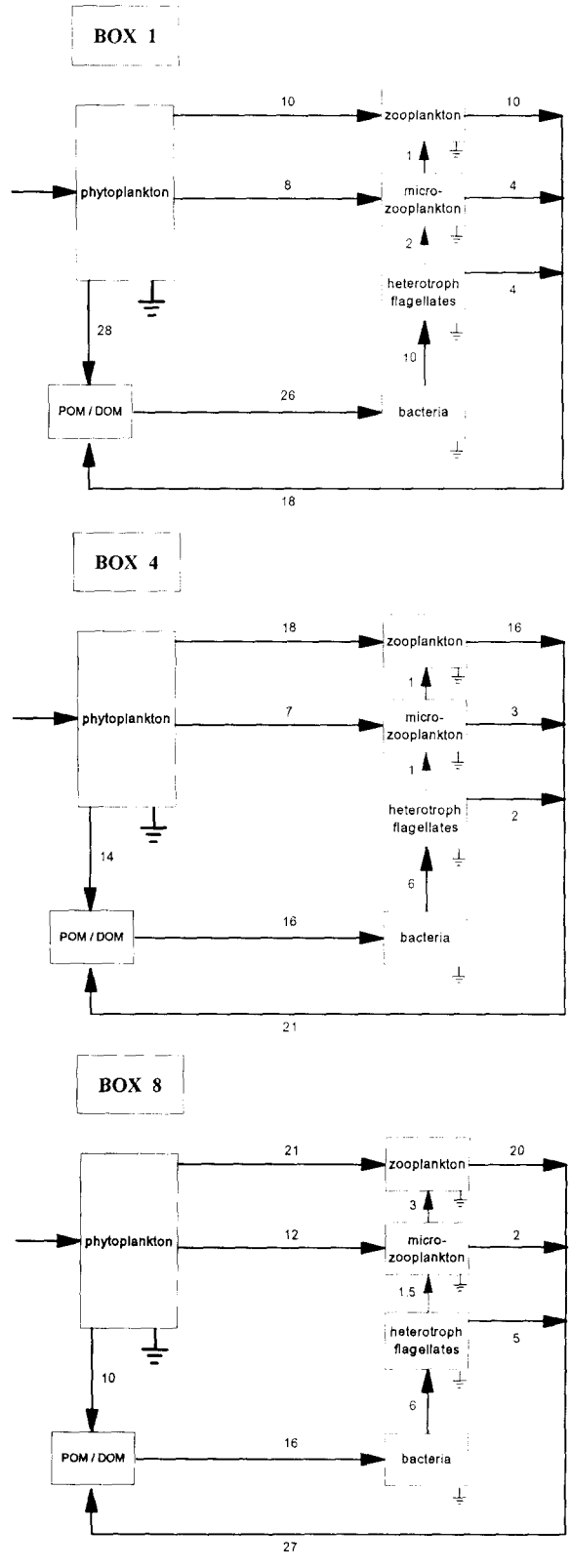


Fig. 8. Normalized carbon flows within the microbial food web for the boxes 1, 4 and 8. The calculated carbon flows have been normalized to the daily gross C assimilation of phytoplankton. All other fluxes are given as a percentage of this.

TABLE 3
Percentage of the total gross primary production flux going from phytoplankton to mesozooplankton (flux 1) and to dissolved and particulate organic matter (flux 2), with the microbial food web efficiency (MWE) in the ERSEM surface boxes.

box	*flux 1*	*flux 2*	*MWE*
1	10	28	0.11
2	19	16	0.11
3	18	19	0.13
4	18	14	0.12
5	19	12	0.15
6	32	9	0.12
7	23	11	0.16
8	21	10	0.16
9	19	12	0.17
10	21	12	0.17

activity, but it incorrectly hindcast the depletion of the nutrients, predicting higher than observed concentrations of phosphate, indicating that the nutrient dynamics as implemented in ERSEM are too simplistic and that mechanisms for luxury uptake as well as internal nutrient pools need to be incorporated.

The scarcity of *in situ* data on the various aspects of the microbial food web, especially the lack of rate measurements, have forced us to look for other verification methods. An indirect test of the realism (or lack of it) of the model is to look at the differences in energy-cycling between the different North Sea areas as predicted by the model, as such differences are emergent properties of the model.

In Fig. 8 the energy cycling for three of the ERSEM boxes along a gradient from near-shore to offshore is given. All the fluxes are expressed as percentage of the total primary production. There is a clear difference between the cycling in the non-stratified near-shore box 8 and the stratified deep offshore box 1, with the weakly stratified box 4 in the central North Sea occupying an intermediate position.

Near the coast, in box 8, the flux from phytoplankton to mesozooplankton is twice as large as the flux from phytoplankton to detritus. In box 1 the situation is the inverse, with the excretion flux even three times as large as the phytoplankton-mesoplankton flux. In Table 3 these fluxes have been given for all ten surface boxes.

The microbial food web efficiency (MWE), defined in Taylor & Joint (1990) as the ratio of the microbial grazer production consumed by (macro)zooplankton to the primary + bacterial production consumed by microbial grazers gives some indication of the relative role of the microbial food web in the various areas in the North Sea in transferring organic carbon to higher trophic levels.

The MWE values calculated from the model results are given in Table 3. They indicate that in the well-mixed coastal boxes the microbial food web functions at a higher efficiency than in the northerly, seasonally stratified boxes, with the central boxes occupying an intermediate position both in terms of vertical mixing and in MWE.

This result is in contrast with the expectation of Taylor & Joint (1990) that increased vertical mixing should result in declining MWE.

Also the degree of eutrophication in the different boxes, here taken to be represented by the annual-average NO_3-N and NH_4-N concentrations, plays a role in the MWE (Table 3), with higher average nutrient concentrations corresponding with higher MWE values. This agrees with the results obtained in mesocosm studies where nutrient enrichment resulted in higher MWE values (Baretta-Bekker *et al.*, 1994) than in the oligotrophic control. The model results for MWE generally confirm the counterintuitive conclusion of Riemann & Christoffersen (1993) that the efficiency of the microbial food web increases along a productivity gradient.

Thus, where the energy transfers from phytoplankton to all heterotrophs increase in absolute and relative terms, the relative efficiency of the microbial food web also increases by enhancing the transfer to mesozooplankton. According to the model, this occurs because there is a shift between the fluxes into the detritus pool. The flux from phytoplankton dominates in the seasonally stratified/oligotrophic areas, whereas the flux from mesozooplankton dominates in the well-mixed/eutrophic areas. The explanation why the model is able to reproduce this shift can be found in the phytoplankton module (Varela *et al.*, 1995). In nutrient-stressed situations phytoplankton will release more dissolved organic matter than in nutrient-rich situations. According to the literature there is a relation between ambient nutrient concentration and cell size (Riegman *et al.*, 1993), and between cell size and production of dissolved organic matter (Aksnes & Egge, 1991). In the model there is an enhanced release of dissolved organic matter in nutrient-stressed situations, so there is a negative relation between ambient nutrient concentration and

TABLE 4
Respiration by the microbial variables, expressed as percentage of the total gross primary production; nitrogen and phosphorus remineralisation by the microbial variables, expressed as percentage of the nitrogen and phosphorus fluxes into phytoplankton, respectively; and the total gross annual primary production (g $C \cdot m^{-2} \cdot a^{-1}$) in the ERSEM boxes 1 and 8 for two different model runs, the standard (= with bacteria) and without bacteria. The microbial variables are bacteria, heterotrophic nanoflagellates and microzooplankton.

	box 1		*box 8*	
	standard	*without bacteria*	*standard*	*without bacteria*
respiration	22	8	16	2
nitrogen recycling	40	1.2	1.2	30
phosph. recycling	26	0	23	0
prim. production	224	150	313	263

the production of dissolved organic matter, without taking into account the cell size. As the substrate/food supply to the microbial food web increases, the classical food web takes over, enhancing carbon transfer to mesozooplankton and thereby reducing respiratory losses of carbon in the lower trophic levels.

The response of the microbial variables to different hydrodynamical conditions and consequently different rates of nutrient supply are illustrated by comparison of boxes 1 (summer stratified, main nutrient supply variable by entrainment and mixing across the thermocline) and 8 (well-mixed, nutrient supply from rivers as well as directly from the sediment) (Table 4).

Clearly, with the relatively lower respiratory losses in the microbial variables in the eutrophic coastal box 8 the regeneration of nutrients is reduced. The higher carbon transfers to mesozooplankton reduce the microbial respiratory losses and explain the higher MWE in the coastal area. They also explain why Taylor & Joint (1990), using a steady-state model, expect MWE to decline with increased vertical mixing, as in their model respiratory losses do not vary.

The importance of the microbial loop in the system has been crudely tested by turning off the bacteria in the model. The respiratory fluxes in the microbial loop are much lower (Table 4) and fall to a few percent of phytoplankton carbon uptake, with the recycling fluxes of nitrogen and phosphorus being correspondingly lower. Annual gross primary production in this model run is 33% lower in box 1 and 17% lower in box 8, indicating recycling of nutrients to be more important in box 1. As the bacterioplankton is the only functional group able to scavenge dissolved organic matter, which comprises both dissolved organic nitrogen and dissolved organic phosphate, this large drop in recycling is to be expected. Again this result is in contrast to the conclusions of Taylor & Joint (1990) that bacteria are not important. Our conclusion would be that we need to find a better measure than MWE as it is not just the efficiency of the transfer that counts (because an inefficient carbon transfer regenerates relatively more nutrients for incorporation in primary production), but the proportion of carbon derived by the higher trophic levels from heterotrophic microbial components *versus* the amount derived directly from primary producers, taking into account the nutrients regenerated in the microbial food web.

5. CONCLUSION

This module cannot be considered to be complete, let alone completely correct as it neglects to take into account a number of, potentially significant, entities in the microbial loop, such as virus and picoalgae. Nor does it resolve mixotrophy, which may be important in nutrient-limited circumstances (*cf.* Thingstad *et al.*, 1993). On the other hand, incorporating as it does a fairly well-tested description of the major known processes of the microbial food web interacting with other system entities, the model results may be expected to provide a better estimate of the time- and space-dependent carbon- and nutrient fluxes in the North Sea than is presently possible with other approaches.

The fact that the present model does adapt to regional differences in the abiotic environment by adjusting the carbon and nutrient fluxes between the various functional groups so that under some circumstances a microbial food web occurs (box 1), while in other circumstances the traditional food chain dominates (box 8), encourages further development of this modelling approach to better understand the emergent properties of the ecosystem we model.

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