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Biogeochemical Model Comparison in Terms of Microplankton-Detritus (MPD) Parameterisation

JAE-YOUNG LEE*[1], PAUL TETT[2] AND KYUNG-RYUL KIM[1]
[1]*OCEAN laboratory, Research Institute of Oceanography, School of Earth and Environmental Sciences, Seoul National University, Seoul 151-742, Korea*
[2]*School of Life Sciences, Napier University, Edinburgh EH10 5DT, U.K.*

Different model formulations in available models were compared with Microplankton-Detritus (MPD) model, and well documented FDM and ERSEM models were the candidate for these comparison. Different formulations in both candidate models were expressed in terms of MPD parameterization. Even though there are differences in the control of autotroph growth among models, it was found that some of the more important microplankton parameters expressed in comparable terms have broadly similar values in all the models. However, an important difference was proved to be the direct contribution of microheterotrophs to the Detritus compartment in FDM and ERSEM, whereas in MPD microplankton biomass passes to Detritus only by way of mesozooplankton grazing.

Key words: Biogeochemical Model, Microplankton, MPD, FDM, ERSEM

INTRODUCTION

In the light of our ever-increasing understanding of marine ecosystems, it is now possible to critically analyse the fundamental building blocks and pathways included within mathematical models that have different model structure and assumptions (Denman, 2003). After the discovery of the microbial loop (Azam *et al.*, 1983), these models have been improved for understanding the interactions within microbial food webs. However, the level of physiological detail incorporated within the models has varied markedly between different studies (Davidson, 1996; Haney and Jackson, 1996; Tett and Wilson, 2000).

Concerning different structure of the models, it is now possible to recognize the existing marine ecosystem models as three different models: microplankton-detritus (MPD) model (e.g. Tett, 1990); nutrient-phytoplankton-zooplankton (N-P-Z) model (e.g. Steel and Henderson, 1992; Edwards and Brindley, 1999) and/or nutrient-phytoplankton-zooplankton-detritus (N-P-Z-D) model (e.g. Baretta *et al.*, 1995); Fasham-Ducklow-McKelvive (FDM) Model (e.g. Fasham *et al.*, 1990). However, as mentioned by Tett and Wilson (2000), there is a surprising paucity of discussion regarding the implications of these different formulations, although numerous different model formulations exist. Therefore, in this paper we will compare relevant parts of well-documented and widely used model of FDM and the first version of ERSEM (European Regional Seas Ecosystem Model) (Baretta *et al.*, 1995) to the MPD model. In the comparison, parameters used in model of FDM and ERSEM were expressed in terms of MPD parameterization used by Lee *et al.* (2003). The objective of this comparison is to demonstrate how process descriptions differ and to bring out similarities in underlying biological parameters.

*Corresponding author: ocean_system@naver.com

COMPARISON OF MODEL EQUATIONS

Comparisons with autotroph equations in ERSEM and FDM

FDM (Fasham *et al.*, 1990) uses a nitrogen currency. There is a single phytoplankton compartment, which is parameterised for a surface mixed layer. The nonconservative part of the equation for phytoplankton nitrogen N_a is (in our symbols):

$$\beta_{Na} = (\mu_a - m_a - G)N_a \qquad \text{mmol N m}^{-3}\ \text{d}^{-1} \quad (1)$$

where the parentheticised right-hand terms are phy-

Table 1. General forms of symbols common in this paper

Symbol	General meaning	Units (in MP, if variable)
α	photosynthetic 'efficiency'	mmol C (mg chl)$^{-1}$ d^{-1} I^{-1}
B	biomass (as carbon)	mmol C m^{-3}
b	slope factor (e.g.) or inefficiency coefficient	-
β	(total) nonconservative flux for a substance	mmol m^{-3} d^{-1}
χ	chlorophyll:carbon ratio	mg chl (mmol C)$^{-1}$
e	relative (organic) excretion rate	d^{-1}
G	grazing pressure	d^{-1}
I	PAR	μE m^{-2} s^{-1}
i	relative ingestion rate	d^{-1}
K	(half)-saturation constant, as in or	S or I
μ	relative growth rate	d^{-1}
N	nitrogen associated with biomass	mmol N m^{-3}
Q	nutrient quota or content in biomass	Mmol nutrient (mmol C)$^{-1}$
r	biomass-related mineralisation/respiration rate	[mmol (mmol C)$^{-1}$] d^{-1}
Θ	Temperature	°C
u	biomass-related nutrient uptake rate	mmol (mmol C)$^{-1}$ d^{-1}
S	dissolved nutrient concentration	mmol m^{-3}
	NH: ammonium	
	NO: nitrate	
	SI: silicate	
	PO: phosphate	

Table 2. Standard values for phytoplankton parameter in FDM

Local symbol	Fasham *et al.* symbol	Description	Std value	Units
f_{ea}	g_1	phytoplankton DON excretion fraction (of production)	0.05	-
K_I		saturation irradiance (= $\mu_{max\,a}$ / α_a)	116	W m^{-2}
K_{in}	ψ	ammonium inhibition (of nitrate uptake) parameter	1.5	mmol NH_4^+ - N m^{-3}
K_{NHS}	K_1	half-saturation concentration for ammonium uptake	0.5	mmol N m^{-3}
K_{NOS}	K_1	half-saturation concentration for nitrate uptake	0.5	mmol N m^{-3}
m_a	μ_1	relative mortality rate	0.05	d^{-1}
q_a		phytoplankton N:C, inverse Redfield ratio	1/6.63	mmol N (mmol C)$^{-1}$
${}^{X}q^{N}$		phytoplankton chlorophyll yield from N (= χ_a /q_a)	1.59	mg chl (mmol N)$^{-1}$
α_a	α	P-I curve initial slope, maximum 'photosynthetic efficiency'	0.025	d^{-1} (W m^{-2})$^{-1}$
χ_a		chlorophyll: carbon ratio	12/50	mg chl (mmol C)$^{-1}$
	k_C	(coefficient of) PAR attenuation by phytoplankton	0.03	m^2 (mmol N)$^{-1}$
ε		==> chlorophyll-related version (k_C /${}^{X}q^{N}$)	0.02	m^2 (mg chl)$^{-1}$
k		coverts between units α of and Φ	4.15×0.0864	μE J^{-1} s d^{-1} nmol mmol^{-1}
Φ		photosynthetic quantum yield (=α_a /($k\varepsilon\chi_a$))	18	nmol C μE^{-1}
μ_{maxa}	V_p	maximum growth rate	2.9*	d^{-1}

for Bermuda station S; but in general based on Eppley (1972) according to Fasham *et al.* (1993), written here as: $\mu_{maxa}[\Theta°C]$= $\mu_{maxa}[0°C]\exp((0.063°C^{-1})\Theta°C)$, equivalent to Q_{10}=1.89; $\mu_{maxa}[0°C]$=0.6 d^{-1}.

toplankton relative growth rate (μ_a), relative mortality rate (m_a), and the grazing pressure to due zooplankton (G) (including microzooplankton). Mortality results in a direct conversion of phytoplankton to detritus. Standard parameter values in FDM are summarised in Table 2.

Growth rate is

$$\mu_a = (1-f_{ea})\mu_{maxa} f(I) f({}^{NH}S, {}^{NO}S) \quad \text{d}^{-1} \quad (2)$$

where ${}^{NH}S$ and ${}^{NO}S$ are nutrient concentration of ammo-

nium and nitrate. In contrast to the 'Cell-Quota, Threshold-Limitation' (CQTL) growth parameterisation in MP (Lee *et al.*, 2003), that of FDM (in Eqn. (2)) uses multiplicative growth kinetics with Monod-type dependency on external nutrient concentration. However, Cell Quota and Monod parameterisations can be equated when $dQ/dt = 0$, i.e. assuming steady state conditions (see Droop, 1983). Then, $\mu_a = u_a/Q_a$, with the Monod parameterisation assuming that 'yield' Q_a^{-1} is constant. When biomass is measured in units of the limiting nutrient, and there are no growth-related losses of nutrient after uptake (that is, growth efficiency is 100%, which is plausible for nitrogen), then the quota is 1, and growth and uptake may be equated, as in e.g. Dugdale (1967).

In Eqn. (2), f_{ea} is the fraction of phytoplankton production that is excreted as dissolved organic matter. The irradiance function is that of Smith (1936) and Talling (1957):

$$f(I) = \frac{I}{\sqrt{(K_I^2 + I^2)}}$$

in which the 'saturation irradiance' is in FDM written as a function of maximum growth rate (d^{-1}) and biomass-related photosynthetic efficiency α_a (d^{-1} I^{-1}):

$$K_I = \frac{\mu_{maxa}}{\alpha_a}$$

The nutrient function includes inhibition of nitrate uptake by ammonium:

$$f({}^{NH}S, {}^{NO}S) = \left(\frac{{}^{NH}S}{K_{NHS} + {}^{NH}S}\right) + \left(\frac{{}^{NO}S(e^{-Kin})^{NH}S}{K_{NOS} + {}^{NO}S}\right)$$

Nitrogen is linked to carbon and chlorophyll by fixed ratios, so that

$$X = {}^{X}q^{N}N_a \qquad \text{where: } {}^{X}q^{N} = \chi_a/q_a$$

and q_a^{-1} is the Redfield N:C ratio.

The most significant difference from MP is in the low value of α_a of 0.025 d^{-1} (W m^{-2})$^{-1}$ used as standard in FDM and implying a photosynthetic quantum yield of 18 nmol C per μE absorbed. The FDM value was based on measurements in the Sargasso Sea and may indicate nutrient-limited conditions here, although Fasham *et al.* (1993) concluded that the value "could be considered reasonably representative of a large part of the North Atlantic Ocean". In MP, such nutrient-limitation is expressed through a low chl:C ratio: so, for $Q_a = Q_{mina}$, $\chi_a = 0.1$ mg chl (mmol C)$^{-1}$, giving $\alpha\chi_a$(equivalent to FDM's α_a) of 0.029 d^{-1} (W m^{-2})$^{-1}$. Finally, the absence of a respiration term in Eqn. (2) is what would be expected of a model using a nitrogen currency, as micro-algae do not normally mineralise organic nitrogen.

ERSEM (Varela *et al.*, 1995) contains two autotroph compartments, representing the functional groups, diatoms (>20 μm cell size) and autotrophic flagellates (< 20 μm cell size). Biomass is quantified as carbon, although the model also deals with the cycling of nitrogen, phosphorus and silicon. In our notation and units, the main equation for nonconservative changes in carbon in a given autotroph compartment is:

$$\beta_{Ba} = (\mu_a - G)B_a \qquad \text{mmol C m}^{-3}\ \text{d}^{-1} \quad (3)$$

where B_a is biomass of autotroph compartment (mmol C m^{-3}). Grazing pressure G (d^{-1}) is that due to mesozooplankton in the case of diatoms, to mesozooplankton and microzooplankton (see heterotroph section) in the case of flagellates.

Growth rate is:

$$\mu_a = \mu_{maxa} f(I) f({}^{NH}S, {}^{NO}S, {}^{PO}S, {}^{SI}S) - r_a - e_a \quad \text{d}^{-1} \quad (4)$$

where r_a an e_a represent loss terms of respiration and excretion (see Eqn. (5) and (6)). Maximum growth rate varies with the difference between the actual temperature Θ and <Θ> the annual mean temperature for a given region:

$$\mu_{maxa} = \mu_{maxa}[\langle\Theta\rangle] f(\Theta) \qquad \text{d}^{-1}$$

where

$$f(\Theta) = Q_{10}^{((\Theta - \langle\Theta\rangle)/10^{\circ}\text{C})}$$

Q_{10} is 4.0, much higher than the value given by Eppley (1972), or used in MP or FDM. The irradiance function is that of Steele (1962):

$$f(I) = \left(\frac{I}{K_I}\right)\exp\left(-\left(\frac{1}{e}\right)\left(\frac{I}{K_I}\right)\right)$$

Varela *et al.* (1995) give this in a thick-layer version which also allows for the lack of photosynthesis at night. They make the saturation parameter K_I, which they call the 'optimum irradiance', a function of mixed-layer PAR, thus allowing for some measure of adap-

tation to changing light. However, the variation in K_I is relatively small, with a minimum value $K_{I\min}$ of 40 W (PAR) m^{-2}. The saturation parameter can be related to maximum photosynthetic rate and photosynthetic activity (Lederman and Tett, 1981):

$$K_I = \frac{P^B_{\max a}}{\alpha_a}$$

Equating the maximum photosynthetic rate $P^B_{\max a}$ with ERSEM's maximum growth rate, allows an estimate of maximum photosynthetic 'efficiency':

$$\alpha_a = \frac{\mu_{\max a}[\langle\Theta\rangle]}{\chi_a K_{I\min}} \text{ mmol C (mg chl)}^{-1}\ d^{-1}\ (\text{W m}^{-2})^{-1}$$

equivalent to 0.062 mmol C (mg chl)$^{-1}$ d^{-1} (μE m^{-2} s^{-1})$^{-1}$ in the case of diatoms. This value is close to that of MP autotrophs. These and other growth parameters are listed in Table 3.

Autotroph nutrient-limitation in this version of ERSEM I is both multiplicative and external:

$$f({}^{NH}S, {}^{NO}S, {}^{PO}S, {}^{SI}S) = \sqrt[3]{\left(\frac{S}{K_S+S}\right)\left(\frac{{}^{PO}S}{K_{PO_S}+{}^{PO}S}\right)\left(\frac{{}^{SI}S}{K_{SI_S}+{}^{SI}S}\right)} \quad \text{[diatom]}$$

$$f({}^{NH}S, {}^{NO}S, {}^{PO}S, {}^{SI}S) = \sqrt{\left(\frac{S}{K_S+S}\right)\left(\frac{{}^{PO}S}{K_{PO_S}+{}^{PO}S}\right)} \quad \text{[flagellates]}$$

where the suffix ^{PO} and ^{SI} repesent dissolved phosphate and silicate, and dissolved inorganic nitrogen concentration is represented by

$$S = {}^{NO}S + {}^{NH}S \qquad \text{mmol m}^{-3}$$

The value of the nitrogen half-saturation concentration is low compared with that of MP and FDM. It is, however, a value for growth, whereas that in MP is for uptake, and it can be shown (Tett and Droop, 1988) that half-saturation constants for growth are less than those for nutrient uptake.

Respiration includes rest, growth (called 'activity') and nutrient-stress components:

$$r_a = [r_{0a}] + b_a\,\mu_a + b_{Sa}(\mu_{\max a} f(I) - \mu_a) \qquad d^{-1} \qquad (5)$$

The terms are subject to temperature effects, either by way of maximum growth rate or directly. The rest term is zero during periods of illumination, having the values of Table 4 only during darkness. The dia-

Table 3. Standard values for phytoplankton growth parameter in ERSEM

Local symbol	Varela *et al.* name; *x* is replaced by 1: diatoms 2: flagellates	Description	Value for diatoms	Value for flagellates	Units
$\mu_{\max a}[\langle\Theta\rangle]$	*sumPxc$*	Maximum growth rate (at mean temperature)	2.5	2.0	d^{-1}
k_Θ		$=\ln(Q_{10})/10°C$	0.347	0.347	$°C^{-1}$
Q_{10}	*q10Px$*	increase in rate for 10°C increase in temperature	4.0	4.0	-
K_S	*chPxn$*	half-saturation conc. for diss. nitrogen control of growth	0.10	0.05	mmol N m^{-3}
K_{POS}	*chPxp$*	half-saturation conc.for phosphate control of growth	0.10	0.05	mmol P m^{-3}
K_{SIS}	*chPxs$*	half-saturation conc. for silicate control of growth	0.30	-	mmol Si m^{-3}
$K_{I\min}$	*clPIi$*	minimum optimal PAR, equivalent to 'saturation irradiance'	40	40	W m^{-2}
α_a		P-I curve initial slope, maximum 'photosynthetic efficiency' $= \mu_{\max a}[<\Theta>]K_{I\min}$	0.063	0.050	d^{-1} (W m^{-2})$^{-1}$
α		$= \mu_{\max}[\langle\Theta\rangle]/(\chi_a K_{I\min})$	0.26	0.104	mmol C (mg chl)$^{-1}$ d^{-1} (W m^{-2})$^{-1}$
		(converted at 4.15 μE J^{-1})	0.062	0.025	mmol C (mg chl)$^{-1}$ d^{-1} (μE m^{-2} s^{-1})$^{-1}$
${}^{X}q_a^N$	-	phytoplankton (min.) chlorophyll yield from N ($= \chi_a / q_a$)	1.4	2.6	mg chl (mmol N)$^{-1}$
χ_a	*uhPxc$*	Chlorophyll: carbon ratio	12/50	12/25	mg chl (mmol C)$^{-1}$
ε		(coefficient of) PAR attenuation by phytoplankton*	?	?	m^2 (mg chl)$^{-1}$
Φ		photosynthetic quantum yield ($= \alpha_a / (k\varepsilon\chi_a)$)	?	?	nmol C μE^{-1}

*not given; there is a reference to Baretta *et al.* (1988).

Table 4. Standard values for phytoplankton loss parameter in ERSEM

Local symbol	Varela *et al.* name	Description	Value for x=1 diatoms	for x=2 flagellates	Units
f_D	*pe_R1Cxc$*	fraction of phytoplankton lysis which becomes detritus (rest becomes labile DOM) [unclear]	0.20	0.50	-
b_{ea}	*pu_eaPx$*	coefficient of growth-dependent excretion	0.05	0.05	-
b_{la}	*pum_eoPx$*	coefficient of nutrient-stress- dependent lysis	0.30	0.30	-
K_{la}	*chB1eP2c$*	bacterial concentration for half-maximum effect of bacterial proteases on diatoms (only)	50	-	mmol C m^{-3}
r_{0a}	*srsPx$*	rate of rest respiration (in darkness)	0.25	0.15	d^{-1}
b_a	*pu_raPx$*	rate at which (activity) respiration increases with growth	0.10	0.25	
b_{Sa}	*pum_roPx$*	rate at which respiration increases with nutrient stress	0.05	0.05	

tom rest rate, 0.13 d^{-1} at mean temperature and for 12 hours of daylight in each 24 hours, implies a 24-hr mean rate of 0.065 d^{-1}, only a little more than the MP autotroph value. The effect of the 'slope' terms $b_{Sa}\,\mu_{\max a}\,f(I) + (b_a - b_{Sa})\mu_a$ will normally be less than $b_a\,\mu_a$ in MP, because of the higher value of b_a in MP. Nutrient stress is quantified in ERSEM as the difference between actual growth rate and potential rate $\mu_{\max a}\,f(I)$ under light-limitation alone.

Excretion includes 'lysis', a part of which (f_D) goes to detritus, the remainder to DOC, and growth-related 'activity excretion', all of which goes to DOC. The total rate is:

$$e_a = b_{ea}\,\mu_a + b_{la}(\mu_{\max a}\,f(I) - \mu_a)[(1 + f(B_b))] \qquad \text{d}^{-1} \qquad (6)$$

where b_{ea} is the coefficient of activity excretion and b_{la} is the coefficient of lysis. Lysis is held to be proportional to the extent of nutrient stress. In the case of diatoms only, the activity of bacterial protease is supposed to increase the lysis rate, according to a saturation function of bacterial biomass B_b:

$$f(B_b) = \frac{B_b}{K_{lb} + B_b}$$

Changes in phytoplankton nutrient in ERSEM are the result of uptake less excretion. Parameters for nitrogen, phosphorus and silicon kinetics are given in Table 5. We will start this account with phosphorus, which has no special features. For a given autotroph type,

$$\beta_{Pa} = ({}^{PO}u_a - e_a\,{}^{P}Q_a)B_a \qquad \text{mmol P m}^{-3}\ \text{d}^{-1} \qquad (7)$$

where biomass-related uptake rate

$${}^{PO}u_a = {}^{P}q_a(\mu_a - r_a) - m'\ \max\{0, ({}^{P}Q_a - {}^{P}q_a)\}$$

mmol P (mmol C)$^{-1}$ d^{-1}

The equation implies that uptake is driven mainly by the demand resulting from the carbon assimilation of net production. There may, however, also be excretion, which occurs when the actual phytoplankton phosphorus quota (${}^{P}Q_a = P_a / B_a$) exceeds the constant P:C ratio assigned to each type of phytoplankton. In writing Eqn. (7), we have slightly simplified the ERSEM equations, and have supplied the rate constant m' (d^{-1}) in the correction term, in order to emend an apparent dimensional error in Eq. (22) of Varela *et al.* (1995). The value of m' would need to be of the same order as μ_a. It is, however, not clear why the correction term is needed (except perhaps immediately after initialisation), since the actual quota should remain always the same as ${}^{P}q_a$. Finally, phosphorus lost in excretion

Table 5. Standard values for phytoplankton nutrient parameter in ERSEM

Local symbol	Varela *et al.* name	Description	Value for x=1 diatoms	for x=2 flagellates	Units
${}^{NH}p_a$	*xpref-N4n$*	relative preference for ammonium (over nitrate) uptake	3	3	
K_{NOS}	*chPxn$*	half-saturation concentration for nitrate uptake	0.10	0.05	mmol N m^{-3}
K_{NHS}	*chPxn$*	half-saturation concentration for ammonium uptake	0.10	0.05	mmol N m^{-3}
q_a	*qnPxc$*	phytoplankton 'maximum' (nominally constant) nitrogen content	0.172	0.188	mmol N (mmol C)$^{-1}$
${}^{P}q_a$	*qpPxc$*	phytoplankton 'maximum' phosphorus content	0.0132	0.0073	mmol P (mmol C)$^{-1}$
${}^{SI}q_a$	*qsPxc$*	phytoplankton maximum silicon content	0.21	-	mmol Si (mmol C)$^{-1}$

is distributed between detritus and DOM in a way that assumes different P:C ratios in particulate and soluble cell fractions.

The silicon equation is similar to that for phosphorus, but applies only to diatoms. That for nitrogen is also similar, but the total uptake of dissolved inorganic nitrogen is partitioned between nitrate and ammonium according to an ammonium preference factor ${}^{NH}p_a$ and the following equation:

$$ {}^{NO}f = \frac{f({}^{NO}S)}{{}^{NH}p_a f({}^{NH}S) + f({}^{NO}S)} \qquad (8) $$

where the saturation function is, for either nutrient

$$ f(S) = \frac{S}{K_S + S} $$

The fraction ${}^{NO}f$ of the required total nitrogen uptake flux is taken from nitrate, and the remainder from ammonium. The half-saturation constant has the same value for ammonium as for nitrate, and the same value as that used in the nutrient-limited growth equation.

Varela *et al.* (1995) remark that this ERSEM module was developed at NIOZ (Baretta *et al.*, 1988) before they joined the project. They suggest that an internal-nutrient model would describe phytoplankton growth better than does the external-limitation of Eqn. (3). This improvement is implemented in ERSEM II (Baretta-Bekker *et al.*, 1997), although the later version continues to assume that light and nutrients effects multiply. Apart from these differences in the growth function, the ERSEM autotroph model differs from the autotroph component of MP by including excretory and lytic losses. Such losses are assumed to take place largely independently of grazing or other interactions with heterotrophs. The losses of soluble organic material provide food for bacteria and hence support the microbial loop (see heterotroph section). MP implicitly includes these losses, and the corresponding heterotroph gains, completely within the microplankton compartment. The transfer of lysed autotroph particulate material to detritus in ERSEM, which corresponds to autotroph mortality in FDM, has no analogue in MP.

Comparisons with heterotroph equations in ERSEM and FDM

The ERSEM Microbial Food Web sub-model includes three explicit compartments for microheterotrophs (Baretta-Bekker *et al.*, 1997): bacteria, nanoflagellates, and microzooplankton. Dissolved organic matter is not explicitly represented, as it is assumed that such material, excreted by phytoplankton and protozoans, is immediately taken up by bacteria. The bacterial compartment also assimilates carbon from explicitly modelled particulate detritus, and so includes some of the bacterial activity that in the microplankton-detritus model is ascribed to the detrital compartment. In ERSEM, the bacteria provide the main food source for heterotrophic nanoflagellates (2-20 μm). Microzooplankton are "heterotrophic planktonic organisms from 20 to 200 μm SED, excluding .... naupliar/larval stages ... [and comprising] ciliates and other heterotrophic protists ... feeding on phytoplankton and heterotrophic nanoflagellates ... [and] itself ... [and] grazed by omnivorous zooplankton."

ERSEM's generalised non-conservative equation for a 'standard organism' of type $_i$ is (in our symbols):

$$ \beta_{Bi} = (\mu_i - m_i - G_i)B_i \qquad \text{mmol C m}^{-3}\ \text{d}^{-1} \qquad (9) $$

where m_i is (constant) mortality rate and grazing pressure G_i ("specific grazing rate") is the total for all predators. ERSEM uses neither of the terms 'specific growth rate' or 'ingestion rate' employed in MP (net growth in ERSEM refers to β_{Bi}). According to our definitions, however, (specific) growth rate would be the result in ERSEM of food uptake ui ${}^{C}u_i$ (mmol C (mmol C)$^{-1}$ d^{-1}) less (organic) excretion e_i and (mineralising) respiration r_i.

$$ \mu_i = i_i - r_i = {}^{C}u_i - e_i - r_i \qquad \text{d}^{-1} \qquad (10) $$

Ingestion is:

$$ i_i = u_i - e_i = k_1 {}^{C}u_i \qquad \text{d}^{-1} \qquad (11) $$

where:

$$ k_1 = (1 - f_{ei}(1 - f_{ai})) $$

Here, f_e is the fraction of unassimilated food that is excreted (lost into the detrital and implicit DOM pools), and f_a is assimilation efficiency. ERSEM (Fig. 2) defines assimilation as taking place after losses of captured carbon by activity respiration as well as by the 'messy feeding' implied by uptake-related excretion:

$$ \text{assimilation} = (1 - f_{ai}){}^{C}u_i = e_i + (r_i - r_{0i}) \qquad \text{d}^{-1} $$

$$ \text{assimilation efficiency, } f_{ai} = 1 - \frac{e_i + (r_i - r_{0i})}{{}^{C}u_i} $$

Respiration is a basal rate plus 'activity' respiration, the fraction of food uptake which is neither excreted or converted to biomass:

$$r_i = r_{0i} + {}^{C}u_i(1 - f_{ei})(1 - f_{ai}) \qquad \text{d}^{-1} \quad (12)$$

and so,

$$\mu_i = f_{ai}\,{}^{C}u_i - r_{0i} \qquad (13)$$

Combining Eqns. (11) and (13) gives:

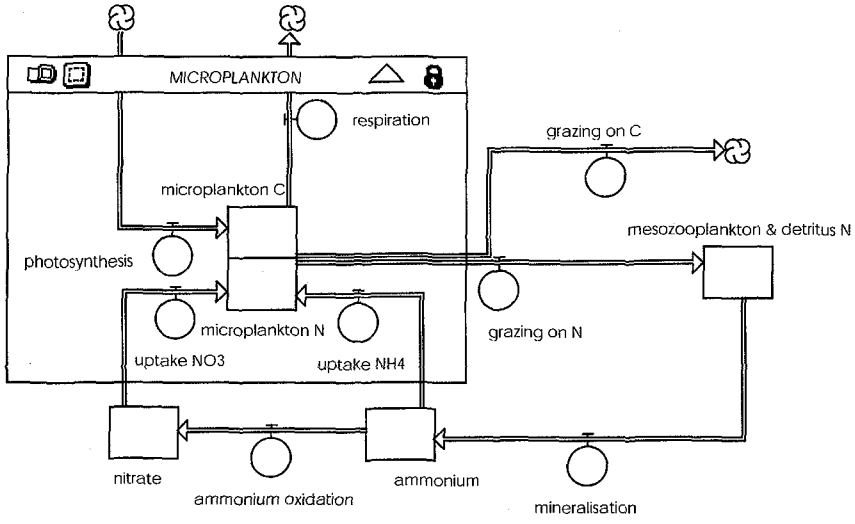
$$\mu_i = \left(\frac{f_{ai}}{k_{1i}}\right) i_i - r_{0i} \qquad \text{d}^{-1}$$

which may be compared with the MP equation for C-controlled growth for an example protozoan:

$$\mu_C = \frac{i_p - r_{0p}}{1 + b_p}$$

The two versions can be equated if ERSEM $f_{ai}/k_{1i} \equiv 1/(1+b_b)$ in MP, and ERSEM $r_{0i} \equiv r_{0p}/(1+b_p)$ in MP. Thus MP $b_p = (k_{1i}/f_{ai}) - 1$ in ERSEM.

(a) MP



(b) ERSEM

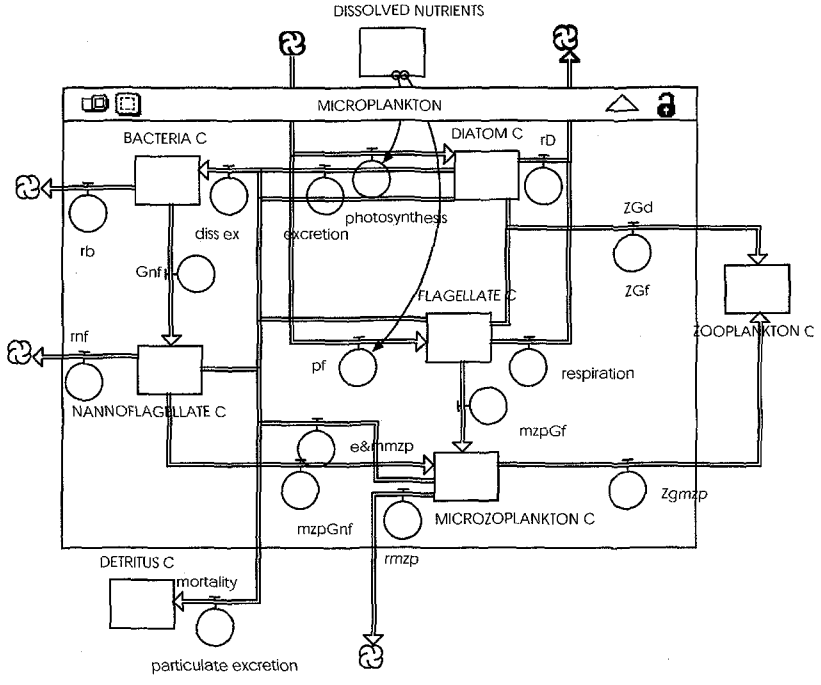


Fig. 1. Model comparisons. Relevant compartments and flow in (a) MP, (b) ERSEM and (c) FDM, shown according to the conventions of the modelling software STELLA.

(c) FDM

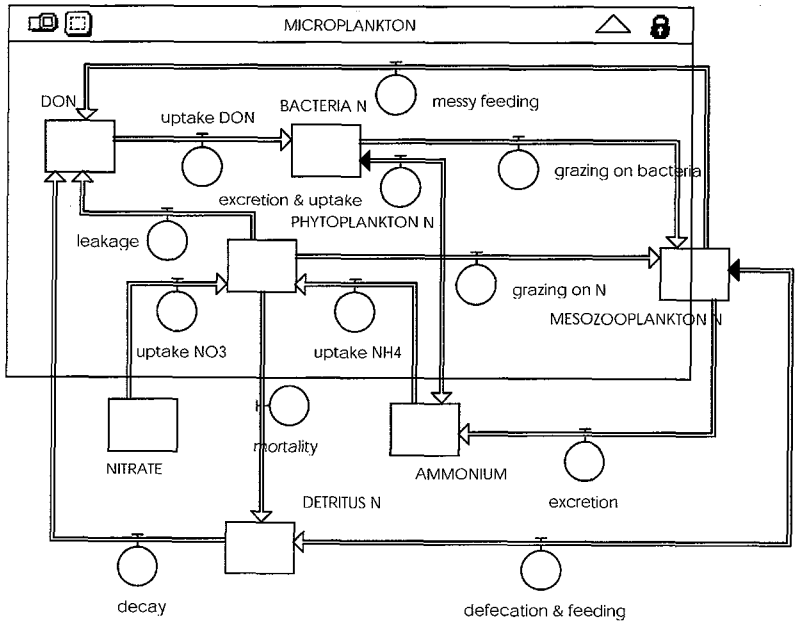


Fig. 1. Continued

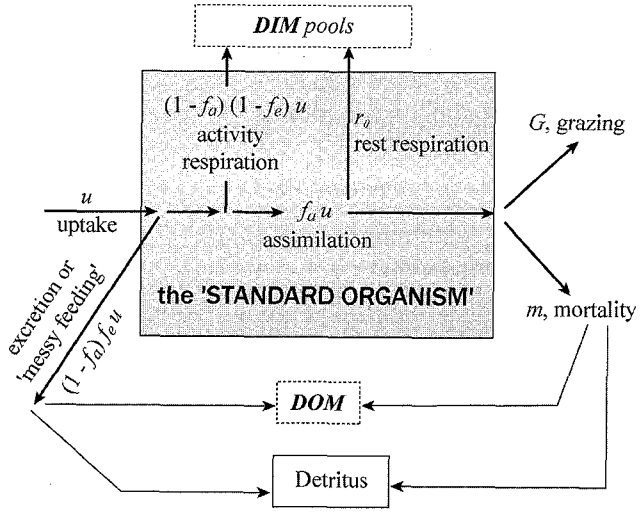


Fig. 2. The ERSEM 'standard organism' in the case of microheterotrophs.

Table 6 gives values of the relevant ERSEM parameters for each microheterotroph compartment. The pattern of carbon flow in ERSEM (see Fig. 1) tends to make bacteria the most abundant microheterotroph, followed by nanoflagellates. Therefore, the respiration slope b_h of MP heterotrophs constructed with ERSEM organisms is likely to be between 1.3 and 2.0, with r_{0h} less than 0.03 d^{-1}. However, the nanoflagellates and microzooplankton of ERSEM are partly cannibalistic, imposing, in effect, an extra respiratory tax. Thus the ERSEM-analagous b_h is likely often to exceed the MP value of 1.5.

ERSEM describes food uptake by saturation (Michaelis-Menten or Langmuir isotherm) kinetics:

$$ {}^{c}u_i = \frac{{}^{c}u_{\max i}\, B_f}{K_{Bfi} + B_f} \quad [\text{mmol C (mmol C)}^{-1}] \quad \text{d}^{-1} \quad (14) $$

where food concentration B_f is the result of totalling over all possible foods the product of concentration and 'availability' or preference $p_{i,j}$. A solution of Eqn. (14) for $B_f \gg KB_{fi}$ gives

$$ c_i = i_{\max i}/K_i = k_1\, {}^{c}u_{\max i}/K_{Bfi} \quad \text{m}^3 \text{ (mmol C)}^{-1} \text{ d}^{-1} $$

This allows (maximum) clearance rates to be calculated from the ERSEM parameters for maximum uptake ${}^{c}u_{max}$ and uptake half-saturation K_{Bfi} (Table 6). These rates are for 10°C. Combining them with some preference for the nanoflagellate clearance rate, and correcting to 20°C (because of the temperature-dependence of ERSEM ${}^{c}u_{\max}$), suggests a value for the ERSEM analogue of c_h of about 0.4 at 20°C. However, the 'availability' of foods is always less than one in ERSEM, and there is some cannibalism. Thus the ERSEM-analogue may be closer to the MP standard value of 0.2 m^3 (mmol C)$^{-1}$ d^{-1}.

ERSEM uses carbon as its main currency, but allows for variation in the nutrient:carbon ratio, or fraction, of the phytoplankton or detrital food of the microheterotrophs. In the model, bacteria, nanoflagellates or microzooplankton assimilate food without

Table 6. ERSEM (and derived MP or AH) parameters for heterotrophs (at 10°C)

Local symbol	ERSEM name*	Description	B1 bacteria	Z6 nano-flagellates	Z5 microzoo-plankton	Units (here)
f_a	$pu_{ST}\$$	assimilation efficiency	0.3	0.2	0.5	-
f_e	$pu\_ea_{ST}\$$	fraction excreted of unassimilated food; $1-f_e$ is 'activity' respired	(0)	0.5	0.5	-
f_D	$pe\_R1_{ST}\$$	particulate fraction of excretion	(0)	0.5	0.5	-
k_1		$= 1-f_e(1-f_a)$	0.7	0.6	0.75	
r_0	$srs_{ST}\$$	basal respiration rate	0.01	0.05	0.02	d^{-1}
${}^{C}u_{max}$	$sum_{ST}\$$	maximum food uptake rate	8.38	10.0	1.2	d^{-1}
K_{Bf}	$chu_{ST}c\$$	Food conc. half-saturating uptake	-	29	6.7	mmol C m^{-3}
Q_{10}	$q10_{ST}\$$	temperature coefficient.	2.95	2.0	2.0	$(10°C)^{-1}$
c		clearance rate $(=k_1{}^{C}u_{max} / K_{Bf})$	-	0.21	0.13	m^3 (mmol C)$^{-1}$ d^{-1}
b		slope of respiration on growth $(=(k_1 f_a)-1)$	1.3	2.0	0.5	-
p	$suP1\_{ST}\$$	availability (diatoms) for	-	0	0.5	-
	$suP2\_{ST}\$$	availability (phytoflagellates)	-	0.3	0.5	-
	$suB1\_{ST}\$$	availability (bacteria)	-	1.0	0	-
	$suZ6\_{ST}\$$	availability (nanoflagellates)	-	0.2	0.6	-
	$suZ5\_{ST}\$$	availability (microzooplankton)	-	0	0.2	-

*The *ST* component of the ERSEM name is replaced by *B1*, *Z5* or *Z6*.

changing its nutrient ratio. If this ratio exceeds q_{maxh}, the maximum nutrient:carbon ratio for the compartment, the excess nutrient is immediately returned to the inorganic nutrient pool. However, when "the difference between the actual and the maximum nutrient fraction becomes negative, nutrients are retained, until the maximum value is re-attained." Such a nutrient deficit does not otherwise affect microheterotroph rates. The maximum nitrogen fraction is 0.20 mol N (mol C)$^{-1}$ for protozoans and 0.25 mol N (mol C)$^{-1}$ for bacteria.

Finally, an important difference from MP is that in ERSEM the products of excretion and mortality "are partitioned over dissolved and particulate organic matter". Thus, ERSEM microheterotrophs contribute directly to the Detritus compartment, whereas MP microplankton biomass passes to Detritus only by way of mesozooplankton grazing.

FDM (Fasham *et al.*, 1990) includes compartments for DON (made by phytoplankton excretion), bacterial nitrogen, and zooplankton nitrogen, and most rates are relative to nitrogen. The "zooplankton compartment describes an animal which is a combined herbivore, bacterivore and detritivore...[with] parameters that are more typical of the herbivorous copepod part of this 'portmanteau' animal than the bacterivorous flagellate part." Nevertheless, the describing equation gives the bulk dynamics of a homogenous population and does not allow for delays between generations of animals. In our terms, it is:

$$\beta_Z = (\mu_Z - m_Z)Z \qquad \text{mmol N m}^{-3}\ \text{d}^{-1} \quad (15)$$

where

$$\mu_Z = \sum({}^{n}f_Z\ {}^{n}i_Z) - r_Z \qquad \text{d}^{-1}$$

The terms ${}^{n}f_Z$ and ${}^{n}i_Z$ are, respectively, assimilation efficiency and relative ingestion rate (d^{-1}) for food type n. Assimilation efficiency, relative excretion rate r_Z (mmol N (mmol N)$^{-1}$ d^{-1}) and relative mortality rate m_Z (d^{-1}) are assumed constant. The latter "parameterises both natural and predator mortality." The variable term is that for ingestion rate, exemplified for phytoplankton (nitrogen concentration N_a) as food:

$${}^{a}i = \frac{i_{maxZ}({}^{a}p)\ N_a}{K_{F_Z} + F} \qquad \text{d}^{-1} \quad (16)$$

F is the total concentration of food, summed over phytoplanktonic, bacterial and detrital nitrogen. The maximum relative ingestion rate i_{maxZ} (d^{-1}) and the half-saturation food concentration K_{F_Z} (mmol N m^{-3}) can be used to compute a maximum clearance rate equivalent to 0.15 m^3 (mmol zooplankton C)$^{-1}$ d^{-1}, given q_Z of 0.16 mmol N (mmol C^{-1}), the Redfield ratio (see Table 7). As well as being close to the MP value for c_h, this is similar to copepod clearance rates obtained

Table 7. Standard values for zooplankton parameters in FDM

Local symbol	FDM symbol	Description	Std value	Units
${}^{n}a_Z$, $n = a, b, D$	$\beta_1, \beta_2, \beta_3$	Assimilation efficiencies for diets of phytoplankton, bacteria or detritus	0.75	-
$i_{\max Z}$	g	maximum ingestion rate (relative to zooplankton biomass)	1.0	d^{-1}
c_Z		maximum clearance rate (=)	0.15	m^3 (mmol C)$^{-1}$ d^{-1}
K_{FZ}	K_3	(total) food concentration which half-saturates ingestion	1.0	mmol N m^{-3}
${}^{n}p_0$, $n = a, b, D$	p	preference for a food type when all foods equally abundant	??	
${}^{N}r\,{}^{N}Z$	μ_2	(N-)relative rate of N excretion	0.1	d^{-1}
${}^{N}r_Z$		(C-)relative rate of N excretion	0.015	mmol N (mmol C)$^{-1}$ d^{-1}
	ε	ammonium fraction of N excretion	0.75	
m_Z	μ_5	specific mortality rate	0.05	d^{-1}
	Ω	fraction of dead animals that become detritus ?? (the remainder minineralising to ammonium ??)*	0.33	q_Z
q_Z	-	N:C, inverse Redfield, ratio	1/6.63	mmol N (mmol C)$^{-1}$

Values are for Bermuda station S, but it does not appear from Fasham *et al.* (1993) that any are temperature-dependent.
*The value and definition of W are not quite clear.

(per animal) by Paffenhöfer (1971) and Paffenhöfer and Harris (1976), and thus a little controversial. Paffenhöfer's rates, obtained from animals cultivated in the laboratory, are an order of magnitude greater than measured by workers using 'wild' animals, and when related to biomass are of the same order as those for protozoans. Nevertheless, the Paffenhöfer rates seem correct, in that they, unlike the lower rates, will allow copepods to feed themselves at concentrations of phytoplankton encountered under typical conditions in the sea. So far as FDM is concerned, the similarity of biomass-related clearance rates for copepods and protozoans would seem to help justify their inclusion in the same model compartment.

Total food concentration is:

$$F = {}^{a}p_0\, N_a + {}^{b}p_0\, N_b + {}^{D}p_0\, N_D \quad \text{mmol N m}^{-3} \quad (17)$$

The terms in p_0 are the standardised preferences of the zooplankton for phytoplankton, bacteria and detritus, when these potential foods are presented in equal amounts. The actual preference for phytoplankton, for example, given a set of food abundances, is:

$${}^{a}p = \frac{{}^{a}p_0\, N_a}{F} \quad (18)$$

and this has the consequence that the simulated zooplankton exert the greatest grazing pressure (iZ) on the most abundant type of food, "equivalent to assuming that the zooplankton actively select the most abundant food organisms, or, as we are dealing with an aggregated entity, that particular sub-groups of zooplankton will develop to crop the most abundant organisms." Conversely, this description of grazing relieves grazed populations of grazing pressure when their abundance is low, and hence avoids driving phytoplankton or bacteria to extinction during simulations. Following Fasham *et al.*, we will call this a 'switching model' (although the change-over from one diet to another is continuous rather than abrupt), and it may have the advantage of stabilising the trophic network of FDM. Eqn. (16) seems equivalent to a Holling (1959) type III grazing function for any given prey type. Fasham *et al.* report that the use of Eqn. (18), ascribed to Hutson (1984), "increased the likelihood of a zooplankton population surviving the winter, thereby producing a more robust model."

The bacterial equation in FDM is

$$\beta_{Nb} = \mu_b\, N_b - {}^{b}i_Z\, Z \quad \text{mmol N m}^{-3}\ \text{d}^{-1} \quad (19)$$

where:

$$\mu_b = {}^{NH}u\ N_b + {}^{ON}u\ N_b - {}^{N}r\,{}^{N}b \quad \text{d}^{-1}$$

(The suffix N is added to the symbol u to emphasise that these uptake rates are relative to nitrogen biomass, in contrast to the carbon-related rates of MP and ERSEM. The FDM rates thus have dimensions of time^{-1}.) Parameter values are listed in Table 8. The bacteria are supposed to have a composition (q_b) of 5 mole carbon per mole of nitrogen. The uptake equations postulate a requirement for ammonium to supply the relative nitrogen deficiency of dissolved organic matter, assumed to have a C:N ratio (q_{ON})

Table 8. Standard values for bacterial parameters in FDM

Local symbol	FDM symbol	Description	Std value	Units
u^N_{maxb}	V_b	maximum N-relative ammonium or DON uptake rate	2.0	d^{-1}
u_{maxb}		maximum C-relative uptake rate ($=u^N_{maxb}\, q_h$)	0.4	mmol N (mmol C)$^{-1}$ d^{-1}
K_S	K_4	half-saturation concentration for nutrient uptake	0.5	mmol N m^{-3}
c_b		trophic transfer coefficient ($=u^N_{maxb}/K_S$)	0.8	m^{-3} (mmol C)$^{-1}$ d^{-1}
${}^{N}r\,{}^{N}b$	μ_3	(N-)relative rate of nitrogen excretion	0.05	d^{-1}
${}^{NH}q^{ON}$	η	ammonium:DON uptake ratio (assumes DOC:DON=8)	0.6	
q_b	-	nitrogen:carbon ratio	0.20	mmol N (mmol C)$^{-1}$

of 8. Thus,

$$ {}^{NH}uN_b = \frac{u^N_{maxb} S'}{K_S + S' + {}^{ON}S} \qquad d^{-1} $$

$$ {}^{ON}uN_b = \frac{u^N_{maxb}\, {}^{ON}S}{K_S + S' + {}^{ON}S} \qquad d^{-1} \qquad (20) $$

where

$$ S' = \min\{{}^{NH}S, {}^{ON}q^b\, {}^{ON}S\} \qquad \text{mmol N } m^{-3} $$

${}^{ON}q^b (=q_{ON}/q_b)$ is 0.6, the ratio of contents of nitrogen (relative to carbon) in DOM and bacteria. In the absence of ammonium, uptake (and hence growth) depends on DON concentration only; when ammonium is present the additional uptake of nitrogen allows faster growth. In the absence of DON, uptake is zero and hence growth is negative.

Finally, it may be noted in Table 8 that the transfer coefficient for bacteria has the deduced value of 0.8 m^3 (mmol C)$^{-1}$ d^{-1}. There are no equivalent values in MP or ERSEM for comparison but this high rate does not seem unreasonable given the large surface:volume ratio and potentially fast metabolic rate of bacteria.

DISCUSSION

The most crucial assumption of MP is that of a constant ratio of heterotrophs to autotrophs. A system comprising several species at each trophic level may form a more stable trophic web than implied by the quasi-Lotka-Volterra dynamics of autotrophs and heterotrophs so long as the protozoan consumers are catholic in their diet and able to switch between favoured foods. Fasham *et al.* (1990) were able to increase the robustness of FDM by assuming that the zooplankton compartment grazed more, at a given time, on the more abundant of phytoplankton, bacteria or detritus. "This assumption leads to a positive switching... which has a stabilizing effect on the predator-prey interaction ..." (Fasham *et al.* 1993). Taylor and Joint (1990) fitted a steady state microbial loop model to data from the Celtic Sea in summer, finding change in steady-state parameters during the course of the summer but support for the use of the steady state for any given time.

The comparisons with FDM and ERSEM show that, although these models differ substantially on structure from each other and from MP, some of the more important microplankton parameters have broadly similar values in all the models, when expressed in comparable terms. The models' differences in the control of autotroph growth are obvious. The other striking difference proves to be the direct production of detritus by microplankton in FDM and ERSEM.

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REFERENCES

Azam, F., T. Fenchel, J.G. Field, J.S. Gray, L.A. Meyer-Reil and F. Thingstad, 1983. The ecological role of water-column microbes in the sea. *Mar. Ecol. Prog. Ser.*, **10**: 257–263.

Baretta, J.W., W. Admiraal, F. Colijn, J.F.P. Malschaert and P. Ruardij, 1988. The construction of the pelagic submodel. In *Tidal flat estuaries. Simulation and analysis of the Ems estuary* (ed. Baretta, J. W. & Ruardij, P.), Ecological Studies, **71**: 77–104. Springer-Verlag, Heidelberg.

Baretta J.W., W. Ebenhöh and P. Ruardij, 1995. The European Regional Seas Ecosystem Model, a complex marine ecosystem model. *Neth. J. Sea Res.*, **33**: 233–246.

Baretta-Bekker, J.G., J.W. Baretta and W. Ebenhöh, 1997. Microbial dynamics in the marine ecosystem model ERSEM II with decoupled carbon assimilation and nutrient uptake. *J. Sea Res.*, **38**: 195–211.

Davidson, K., 1996. Modelling microbial food webs. *Mar. Ecol. Prog. Ser.*, **145**: 279–296.

Denman, K.L., 2003. Modelling planktonic ecosystems: parameterizing complexity. Prog. Oceanogr., **57**: 429–452.

Droop, M.R., 1983. 25 years of algal growth kinetics - a personal view. *Bot. Mar.*, **26**: 99–112.

Dugdale, R.C., 1967. Nutrient limitation in the sea: dynamics, identification, and significance. *Limnol. Oceanogr.*, **12**: 685–695.

Edwards, A.M. and J. Brindley, 1999. Zooplankton mortality and the dynamical behaviour of plankton population models. *Bull. Math. Biol.*, **61**: 303–339.

Eppley, R.W., 1972. Temperature and phytoplankton growth in the sea. *U. S. Fish. Wild. Ser. Bull.*, **70**: 1063–1085.

Fasham, M.J.R., H.W. Ducklow and S.M. McKelvie, 1990. A nitrogen-based model of plankton dynamics in the oceanic mixed layer. *J. Mar. Res.*, **48**: 591–639.

Fasham, M.J.R., J. L. Sarmineto, R.D. Slater, H.W. Ducklow and R. Williams, 1993. Ecosystem behaviour at Bermuda Station "S" and Ocean Weather Station "India": a general circulation model and observational analysis. *Global Biogeochemical Cycles*, **7**: 379–415.

Haney, J.D. and G.A. Jackson, 1996. Modelling phytoplankton growth rates. *J. Plankton Res.*, **18**: 63–85.

Holling, C.S., 1959. Some characteristics of simple types of predation and parasitism. *Can. Entomol.*, **91**: 385–398.

Hutson, V., 1984. Predator mediated coexistence with a switching predator. *Math. Biosci.*, **68**: 233–246.

Lederman, T.C. and P. Tett, 1981. Problems in modelling the photosynthesis-light relationship for phytoplankton. *Bot. Mar.*, **24**: 125–134.

Lee, J.-Y., P. Tett and K.-R. Kim, 2003. Parameterising a microplankton Model. *J. Korean Soc. Oceanogr.*, **38**: 185–210.

Paffenhöfer, G.-A., 1971. Grazing and ingestion rates of nauplii, copepods and adults of the marine planktonic copepod *Calanus helgolandicus*. *Mar. Biol.*, **11**: 286–298.

Paffenhöfer, G.-A. and R.P. Harris, 1976. Feeding, growth and reproduction of the marine planktonic copepod *Pseudocalanys elongatus* Boeck. *J. Mar. Biol. Ass. U.K.*, **56**: 327–344.

Smith, E.L., 1936. Photosynthesis in relation to light and carbon dioxide. *Proc. Nat. Acad. Sci. Amer.*, **22**: 504–.

Steele, J.H., 1962. Environmental control of photosynthesis in the sea. *Limnol. Oceanogr.*, **7**: 137–150.

Steele, J.H. and E.W. Henderson, 1992. The role of predation in plankton models. *J. Plankton. Res.*, **14**: 157–172.

Talling, J.F., 1957. The phytoplankton population as a compound photosynthetic system. *New Phytol.*, **56**: 133–149.

Taylor, A.H. and I. Joint, 1990. A steady-state analysis of the microbial loop in stratified systems. *Mar. Ecol. Prog. Ser.*, **59**: 1–17.

Tett, P., 1990. A three layer vertical and microbiological processes model for shelf seas. Proudman Oceanographic Laboratory, pp. 85.

Tett, P. and M.R. Droop, 1988. Cell quota models and planktonic primary production. In *Handbook of Laboratory Model Systems for Microbial Ecosystems* (ed. Wimpenny, J. W. T.), **2**: 177–233. CRC Press, Florida.

Tett, P. and H. Wilson, 2000. From biogeochemical to ecological models of marine microplankton. *J. Mar. Sys.*, **25**: 431–446.

Varela, R.A., A. Cruzado, and J.E. Gabaldón, J.E., 1995. Modelling primary production in the North Sea using the European Regional Seas Ecosystem Model. *Neth. J. Sea Res.*, **33**: 337–361.

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