Journal of the Korean Society of Oceanography
Vol. 39, No. 4, pp. 222–233 December 2004

Comparison of a Microbiological Model Simulation with Microcosm Data

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Using nitrogen as the limiting nutrient, the default version of a microplankton-detritus model linked chlorophyll concentration to the autotroph nitrogen. However, phosphorus dynamics were added to simulate the results of a microcosm experiment. Using standard parameter values with a single value of microheterotroph fraction in the microplankton taken from the observed range, the best simulation successfully captured the main features of the time-courses of chlorophyll and particulate organic carbon, nitrogen and phosphorus, with root-mean-square error equivalent to 29% of particulate concentration. A standard version of microbiological model assumes complete internal cycling of nutrient elements; adding a term for ammonium and phosphate excretion by microheterotrophs did not significantly improve predictions. Relaxing the requirement for constant microheterotroph fraction resulted in an autotroph-heterotroph model AH, with dynamics resembling those of a Lotka-Volterra predator-prey system. AH fitted the microcosm data worse than did MP, justifying the suppression of Lotka-Volterra dynamics in MP. The paper concludes with a discussion of possible reasons for the success of the simple bulk dynamics of MP in simulating microplankton behaviour.

Key words: Microbiological Model, Microcosm Experiment, Microplankton

INTRODUCTION

Tett (1990) proposed a microbiological model with three pelagic compartments and 6 independent state variables:

- microplankton organic carbon and nitrogen (and non-independent chlorophyll);
- detrital organic carbon and nitrogen;
- dissolved ammonium and nitrate (and non-independent oxygen);

The microbiological (or microplankton-detritus) model (MP) was embedded in a 3-layer physical framework, and the combination named L3VMP. The microplankton compartment was defined as including planktonic microheterotrophs (protozoa and bacteria) as well as photoautotrophic phytoplankton. Mesozooplankton were represented as a grazing pressure rather than a dynamic compartment. This microplankton-detritus model has been used in a number of studies (Huthnance *et al.*, 1993; Hydes *et al.*, 1997; Smith and Tett, 2000; Tett and Grenz, 1994; Tett *et al.*, 1993; Tett and Smith 1997; Tett and Walne, 1995; Wilson and Tett 1997; Hydes *et al.*, 1997) with some variations in the process equations and parameter values.

Earlier versions of the microplankton equations were given as part of the model L3VMP (Tett, 1990; Tett and Grenz, 1994; Tett and Walne, 1995), and by Smith and Tett (2000) as part of the model SED-BIOL. However, because earlier accounts of MP (Tett *et al.*, 1993; Tett and Walne, 1995) tested the microplankton equations as part of the physical-microbiological model L3VMP, the aim of the present work is to test MP on its own, using data from a microcosm experiment (Jones *et al.*, 1978a; Jones *et al.*, 1978b). MP assumes a constant relation between autotroph and heterotroph processes in the microplankton compartment, and so the tests also involved simulations with a model AH in which this assumption was relaxed, allowing microautotrophs and microheterotrophs to vary independently.

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MICROCOSM EXPERIMENT

Jones *et al.*, (1978a; 1978b) and Jones (1979) report results from a microcosm experiment ('H' of a series) which allows a test of MP. The microcosm was filled with 19 dm^3 of 200 µm-screened water taken from the Scottish sea-loch Creran in July 1975, enriched with nitrate, silicate, vitamins and trace minerals, and incubated in a water bath at 10°C, corresponding to sea water temperature at the time. It was exposed, through a green filter, to light from a north-facing window, approximating in amount and colour balance the irradiance a depth of 4 m in the loch. The contents of the microcosm were gently stirred, and continuously diluted at 0.21 d^{-1} with 0.45 µm-filtered, nutrient-enriched, water taken from the loch at intervals during the experiment. The aim of the dilution was to reduce wall effects and remove detritus and populations of non-dividing cells.

Samples were taken regularly for measurement of pigments and organic carbon, nitrogen and phosphorus retained on glass fibre filters. 'Chlorophyll' and chlorophyll-equivalent pheopigments were extracted into 90% acetone and measured by fluorescence before and after acidification (Holm-Hansen *et al.*, 1965). What was called 'chlorophyll' includes chlorophyll a and chlorophyll-*a* equivalent amounts of some other pigments, especially chlorophyllide a (Gowen *et al.*, 1983). C and N were measured after combustion in an elemental analyser, and P by wet oxidation to phosphate (Tett *et al.*, 1985). Concentrations of dissolved nutrients were measured at the start of the experiment and in the vessel supplying the diluent. Water samples were preserved with Lugol's iodine and analysed with an inverted microscope for abundance and mean size of phytoplankton and protozoa (Tett, 1973). Phytoplankton abundances given in Jones (1979) have been converted to carbon concentrations using mean cell volumes observed during the experiment, and carbon contents of 0.12 pg C μm^{-3} for diatoms and 0.18 pg C μm^{-3} for other microplankters.

The experiment had three phases during 6 weeks (Fig. 1). During the first phase (up to day 8), initial, relatively high, concentrations of detritus were diluted, most microplankters decreased in abundance and some species disappeared. During phase 2, at least 5 species of diatoms increased in parallel as the growth-limiting element switched from nitrogen to phosphorus. At the end of this phase there remained 10 taxa from the 15 recorded at the start of the experiment, the most important loss being ciliates, replaced by zooflagellates. At the start of phase 3, on day 30, the microcosm reactor and reservoir were enriched with phosphate. The resulting increase in biomass confirmed control by phosphorus.

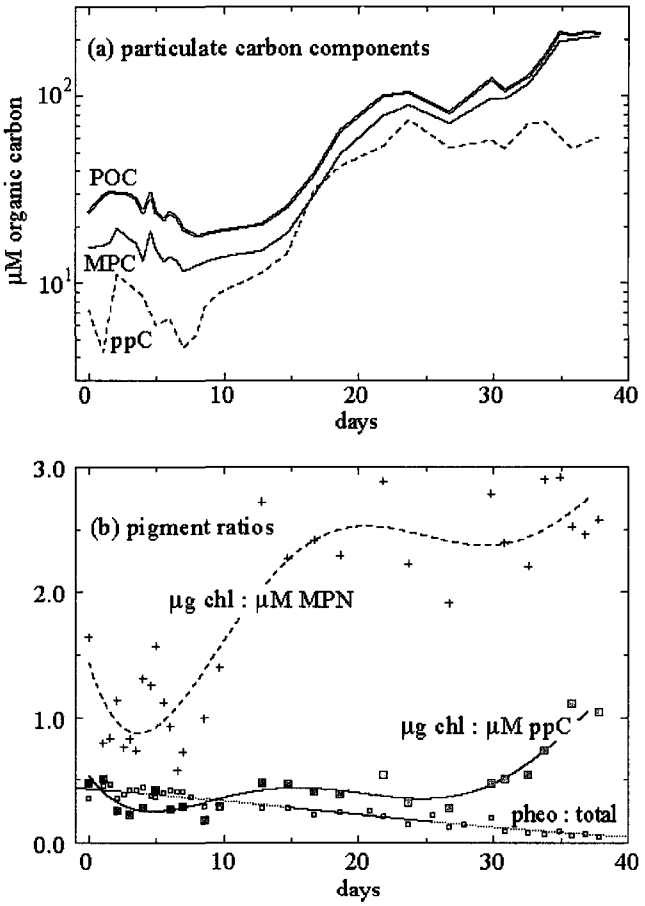

Fig. 1. Results from a microcosm experiment. Total particulate organic carbon and nitrogen (POC and PON) were determined after combustion. Photosynthetic pigments (pheo ='pheopigment' and chl='chlorophyll') measured by fluorescence. Phytoplankton organic carbon (ppC) was estimated by microscopy. Microplankton organic matter (MPC and MPN) estimated from corresponding POM×chl/(chl+pheo).

On the basis of other work in Creran, detritus probably made up at least half the initial particulate organic carbon (POC). Although about 80% of this detritus should have been removed by dilution during phase 1, the continued presence of pheopigments, and their increase during phase 2, suggests that new detritus was formed, either as a result of protozoan grazing or of cell death. Nevertheless, a continuing decrease in the ratio of pheopigment to total pigment (Fig. 2) indicated a diminishing ratio of detritus to microplankton. Estimates of microplankton particulates(carbon, MPC; nitrogen, MPN; and phosphorus, MPP) were made by multiplying POC, PON or POP by the ratio of 'chlorophyll' to total pigments ('chlorophyll' plus

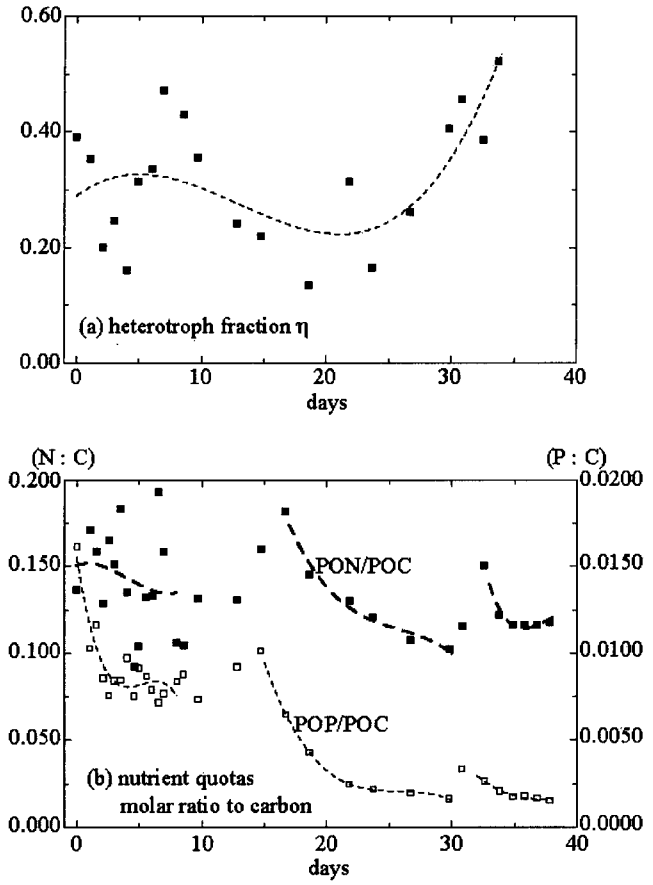

Fig. 2. The microcosm experiment, continued. (a) The heterotroph fraction η estimated from hetC/MPC for days 0-8 (where hetC is microscopically heterotroph carbon), then from (MPC-ppC)/MPC. (b) Microplankton nutrient quotas, estimated as Q=PON/POC and ${}^{P}Q$=POP/POC. Total particulate organic carbon and nitrogen (POC and PON) were determined after combustion. Total particulate organic phosphorus (POP) was determined by wet oxidation.

pheopigments) on the assumption that fresh detritus had the same C:N:P:pigment ratio as microplankton and contained pheopigment instead of 'chlorophyll'.

The methods used for microscopy revealed only some photosynthetic and heterotrophic picoplankton, and might have underestimated protozoans because of failure to preserve the most fragile naked dinoflagellates and ciliates. Other studies (Tett *et al.*, 1988) have, however, shown that picophytoplankton make only a small contribution to phytoplankton biomass in these waters, which are, generally, dominated by diatoms. Microscopic estimates of phytoplankton carbon (ppC) may thus be considered reliable. Microscopic estimates of microheterotroph carbon (mhC) were, however, mostly lower than estimates from the difference between MPC and ppC, and the heterotroph fraction η was estimated as (MPC-ppC)/MPC from day 8 onwards. Values of η decreased from about 0.4 to a minimum of 0.2, rising again towards 0.6 by day 35.

The ratio of 'chlorophyll' to microscopically estimated phytoplankton carbon remained constant (apart from measurement error) at about 0.5 mg chl (mmol C)$^{-1}$ during phases 1 and 2, increasing to more than 1 mg chl (mmol C)$^{-1}$ after day 35. It is possible that the biomass contributions of the dominant diatoms (*Cerataulina pelagica* and *Leptocylindrus danicus*) were underestimated at this time. If so, the values of η after day 35 would be unreliable. Data used for comparison with simulation are thus taken from days 8 to 35 (inclusive) only.

MODEL

The model needed to take account of P limitation. The full set of equations for state variables in version MP+*P* was:

$$\text{carbon: } \frac{dB}{dt} = (\mu - D)B \qquad \text{mmol C m}^{-3}\text{d}^{-1} \quad (1a)$$

$$\text{nitrogen: } \frac{dN}{dt} = ({}^{NO}u - D\,{}^{N}Q)B \qquad \text{mmol N m}^{-3}\text{d}^{-1} \quad (1b)$$

$$\text{phosphorus: } \frac{dP}{dt} = ({}^{PO}u - D\,{}^{P}Q)B \qquad \text{mmol P m}^{-3}\text{d}^{-1} \quad (1c)$$

$$\text{nitrate: } \frac{d^{NO}S}{dt} = -{}^{NO}u\,B - D({}^{NO}S - {}^{NO}S_r)$$

$$\text{mmol N m}^{-3}\text{d}^{-1} \quad (1d)$$

$$\text{ammonium: } \frac{d^{NH}S}{dt} = -{}^{NH}u\,B - D({}^{NH}S - {}^{NH}S_r)$$

$$\text{mmol N m}^{-3}\text{d}^{-1} \quad (1e)$$

$$\text{phosphate: } \frac{d^{PO}S}{dt} = -{}^{PO}u\,B - D({}^{PO}S - {}^{PO}S_r)$$

$$\text{mmol P m}^{-3}\text{d}^{-1} \quad (1f)$$

$$\text{quota: } {}^{N}Q = N/B \text{ and } {}^{P}Q = P/B$$

$$\text{mmol (mmolC)}^{-1} \quad (1g)$$

$$\text{chlorophyll: } X = {}^{X}q\,{}^{N}N \qquad \text{mg chl m}^{-3} \quad (1h)$$

where D is dilution rate and S_r is the concentration in the reservoir from which diluent is drawn. Because silicate was added in excess, its dynamics were ignored. There was no grazing term because mesozooplankton had been removed by the 200 μm screen. Because of the absence of simulated grazing, there was no formation of detritus during simulations. The mineralisation of the observed detritus was assumed to be slow, and

hence was ignored.

Extra, or modified, rate equations to default equation were

$$\mu = \min\{\mu(I), \mu({}^{N}Q), \mu({}^{P}Q)\} \quad \text{d}^{-1} \tag{2}$$

where

$$\mu({}^{P}Q) = \mu_{\max}\left(1-\left(\frac{{}^{P}Q_{\min}}{{}^{P}Q}\right)\right) \quad \text{d}^{-1}$$

$${}^{P}Q = P/B \qquad \text{mmol P (mmol C)}^{-1}$$

$${}^{PO}u = {}^{PO}u_{\max} f({}^{PO}S) f_{in1}({}^{P}Q) - [{}^{P}r_h]$$

$$\text{mmol P (mmol C)}^{-1}\,\text{d}^{-1} \tag{3}$$

where

$$f({}^{PO}S) = \begin{cases} \dfrac{{}^{PO}S}{K_{POS} + {}^{PO}S} & : {}^{P}Q \le {}^{P}Q_{\max} \\ 1 & : {}^{P}Q \le {}^{P}Q_{\max} \end{cases}$$

$$f_{in1}({}^{P}Q) = 1 - \left(\frac{{}^{P}Q - {}^{P}q_h\eta}{{}^{P}Q_{\max} - {}^{P}q_h\eta}\right)$$

The phosphate uptake equation allows excretion when ${}^{P}Q > {}^{P}Q_{max}$. In addition, an optional 'phosphorus respiration' term in Eqn. (3) was expanded in the same way as ammonium excretion (see Eqn. (32) of Lee *et al.* (2003)):

$${}^{P}r_h = \mu(((1+b_h)q^{+} - q_h) + r_{0h}q^{+})$$

$$\text{mmol P (mmol C)}^{-1}\text{d}^{-1} \tag{4}$$

where

$$q^{+} = \begin{cases} \dfrac{{}^{P}Q - {}^{P}q_h\eta}{1-\eta} & : {}^{P}Q \ge {}^{P}q_h \\ {}^{P}q_h & : {}^{P}Q < {}^{P}q_h \end{cases}$$

Finally, it was thought that the strong phosphorus-limitation designed into the experiment might influ-

Table 1. General forms of symbols and parameters common in this paper

Symbol	General meaning	Units (in MP, if variable)
B	biomass (as carbon)	mmol C m^{-3}
N	nitrogen associated with biomass	mmol N m^{-3}
P	Phosphorus associated with biomass	mmol P m^{-3}
Q	nutrient quota or content in biomass	mmol nutrient (mmol C)$^{-1}$
S	dissolved nutrient concentration	mmol m^{-3}
S_h	dissolved nutrient concentration in the reservior	mmol m^{-3}
u	biomass-related nutrient uptake rate	mmol (mmol C)$^{-1}$ d^{-1}
K	(half)-saturation constant, as in K_{NHS}	S
q	fixed quota	mmol nutrient (mmol C)$^{-1}$
b	slope factor (e.g. $\Delta r/\Delta\mu$) or inefficiency coefficient	-
η	heterotroph fraction (of biomass)	-
c	clearance rate or transfer coefficient	m^3 (mmol C)$^{-1}$ d^{-1}
r	biomass-related mineralisation/respiration rate e.g) r_{0h}: basal respiration of heterotroh	[mmol (mmol C)$^{-1}$] d^{-1}
I	PAR	μE m^{-2} s^{-1}
μ	relative growth rate	d^{-1}
Identifiers	(used in the form of subscript or superscript)	
	a: autotrophic	h: (micro) heterotropic
	N: (organic) nitrogen	P: (organic) phosphorus
	NH: (diss.) ammonium	
	NO: (diss.) nitrate	PO: (diss.) phosphate
Qualifiers	(used in the form of subscript)	
	min(minimum) value; max(imum) value	
	0: basal of threshold value (≈minimum)	

ence nitrate uptake, and hence an optional modification was added to the default equation of nitrate uptake with ammonium inhibition (see Eqn. (52) of Lee *et al.* (2003):

$$^{NO}u = {}^{NO}u_{\max} f({}^{NO}S) f_{in}({}^{NH}S) f_{in1}(Q)[f_{in3}({}^{P}Q)] \qquad (5)$$

where

$$f_{in3}({}^{P}Q) = \begin{cases} \dfrac{{}^{P}Q - {}^{P}Q_{\min}}{{}^{P}Q_{\max} - {}^{P}Q_{\min}} & :\mu({}^{P}Q) < \mu({}^{N}Q) < \mu(I) \\ 1 & :\mu({}^{P}Q) > \mu({}^{N}Q) \end{cases}$$

PHOSPHORUS SUBMODEL AND OTHER NON-STANDARD PARAMETER VALUES

Initial values of ${}^{P}Q_{\min}$ and ${}^{PO}u_{\max}$ were estimated from microplankton particulates, following the procedures used by Jones *et al.* (1978a) (for total particulates). ${}^{P}Q_{\max}$ was taken as the largest observed ratio of POP to POC. K_{POS} had the value given by Jones *et al.* (1978a).

The only parameter that caused difficulty was ${}^{P}q_h$, the microheterotroph ratio of P to C. The Redfield ratio is 9.4 mmol P (mol C)$^{-1}$, and the results of Caron *et al.* (1990) suggest optimum values of 13.3 mmol P (mol C)$^{-1}$ for protists. Substituting such values into

$${}^{P}Q_{\min a} = \frac{{}^{P}Q_{\min} - {}^{P}q_h\eta}{1-\eta}$$

together with the initial value of 1.3 used for ${}^{P}Q_{\min}$, gave ${}^{P}Q_{\min a}<0$ for most values of η. As the measurements of POP and POC used to estimate the phosphorus subsistence quota seem reliable, the implication is that some microheterotrophs must have had phosphorus content much below the Redfield value. There is evidence that bacteria can grow with ${}^{P}Q_b$ less than 1 mmol P (mol C)$^{-1}$ (Currie and Kalff 1984). Whatever the explanation, the difficulty for the simulations was that $({}^{P}Q - {}^{P}q_h\eta)$ in equations such as Eqn. (3) could not be allowed to go negative. The solution was to set ${}^{P}q_h\eta$ equal to ${}^{P}Q_{\min}$, implying q_h of 4.1 mmol P (mol C)$^{-1}$ for η of 0.25.

Some phosphorus parameters were adjusted to minimise the MP+*P* prediction error with η of 0.25. A plot of 'chlorophyll' against MPN for days 8-35 had a slope of 2.8, which provided the initial estimate of ${}^{X}q^{N}{}_{a}$ (approximated by ${}^{X}q^{N}/(1-\eta)$) of 3.7 mg chl (mmol N)$^{-1}$, adjusted to 3.0 by fitting. The adjusted values (Table 2) were used in all other simulations.

INITIALIZATION AND EXTERNAL FORCING

Simulations were initialized on day 8, at the beginning of phase 2, with values for the particulate state variables *B*, *N* and *P* set to MPC, MPN and MPP estimated from observed particulates. Values of external forcing variables are given in Table 3. The simulations used a retrospectively estimated approximate 24-hr mean value of 50 μE m^{-2} s^{-1} for *I*; no account was taken of natural variation in light, although self-shading, which brought about a maximum reduction in mean irradiance of 10%, was simulated. However, PAR was not limiting in any simulation reported here.

NUMERICAL METHODS

The equations of MP+*P* were numerically integrated using repeated Euler forward difference solutions. Standard time-step was 0.01 day; results were not meaningfully different with Δt of 0.005 and 0.02 day. Making allowance for dilution, the simulations conserved total nitrogen and phosphorus exactly.

Agreement between values of a simulated Y' and observed Y variable was assessed by calculating a sum of squares of the differences between corresponding logarithms:

Table 2. Phosphorus submodel, and other non-standard, parameters in MP+P

Parameter	Jones *et al.* (1978b) value, from total particulates	Recalculated from MP particulates	After fitting	Units
${}^{P}Q_{\max}$		10.5	15	mmol P (mol C)$^{-1}$
${}^{P}Q_{\min}$	1.02	1.3	1.5	mmol P (mol C)$^{-1}$
${}^{P}q_h$		${}^{P}Q_{\min}/\eta$		mmol P (mol C)$^{-1}$
${}^{P}u_{\max}$	2.4@10°C	5@20°C/10(with excr.)	6@20°C/11(with excr.)	mmol P (mol C)$^{-1}$ d^{-1}
K_{PO}	0.21	-	0.21	mmol P m^{-3}
${}^{X}q^{N}$	2.16-3.04 (Gowen *et al.*, 1992)	2.8		mg chl (mmol N)$^{-1}$
${}^{X}q^{N}{}_{a}$		3.7 (η=0.25)	3.0	mg chl (mmol N)$^{-1}$

Table 3. Forcing for the microcosm simulations

Symbol for quantity	Description of quantity	Value(s) or equation	Units
${}^{NO}S_r$	reservoir nitrate	100	μM
${}^{PO}S_r$	reservoir phosphate	0.28 (day 0-19), 0.20 (day 20-30.4), 0.70 (day 30.5-40)	μM
I	reactor PAR	I_0 (1-exp(-ζ))/ζ	μE m^{-2} s^{-1}
I_0	external PAR	50	μE m^{-2} s^{-1}
ζ	reactor mean optical pathlength	$z(\lambda_w+\varepsilon X)$	
z	reactor mean photon pathlength	0.1	m
λ_w	seawater attenuation coefficient	0.2	m^{-1}
D	reactor dilution rate	0.21	d^{-1}
Θ	temperature in reactor	10	°C

$$\mathrm{SOSD}(Y) = \sum_{n_Y}(\log_{10}(Y'[t_j]) - \log_{10}(Y'[t_j]))^2$$

where there were j=1 to n_Y observations in the time-series $Y(t)$. The logarithmic transformation was used to normalise and homogenise errors, and to allow the assessment of an overall goodness of fit to concentrations varying with time by an order of magnitude and between variables by several orders of magnitude. A root-mean-square prediction error was calculated for each variable from

$$s(Y) = \sqrt{SOSD(Y)/n_Y}$$

The observations were those of concentrations of MPC, MPN, MPP and 'chlorophyll', corresponding to model state variables B, N, P, X. An overall error was calculated from

$$s = \sqrt{\frac{(SOSD(B)+SOSD(N)+SOSD(P)+SOSD(X))}{(n_B+n_N+n_P+n_X)}}$$

RESULTS

Fig. 3 and 4 shows the results of running simulations for standard MP+P with η of 0.20, 0.25 and 0.30. Fig. 5 shows extent of agreement between observed and simulated microplankton growth rate. Fig. 6 gives the fitting errors as a function of η, showing best overall fit, with prediction error of 0.108, at η of 0.27. Results for B and N were especially satisfactory (with $s(B)$ falling to 0.079 at η=0.27 and $s(N)$ to 0.068 at η=0.29). Despite adjustment to ${}^{X}q^{N}_{a}$, chlorophyll prediction were less good, with $s(X)$ showing a minimum of 0.105 (η=0.25). This may reflect greater day-to-day variability in pigments.

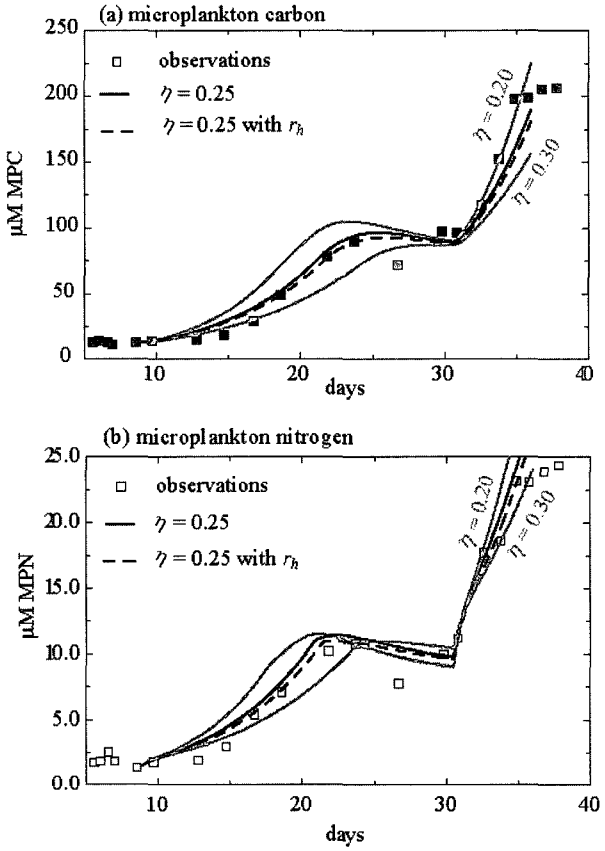

Fig. 3. MP+P simulations of particulates in the microcosm. The lines show concentrations of microplankton components predicted during days 8-35 by MP+P simulation with η=0.20, 0.25 and 0.30, and also by MP+P+r_h with η=0.25. The points show concentration duduced from observations.

Whereas the fits for carbon, nitrogen and chlorophyll show clear minima, that for phosphorus did not. This was a result of using η-independent parameters in the phosphorus sub-model. It is clear that this sub-model is less satisfactory than that for carbon and nitrogen, since $s(P)$ was 0.148 at η=0.25, despite preliminary adjustment of most P-model parameters.

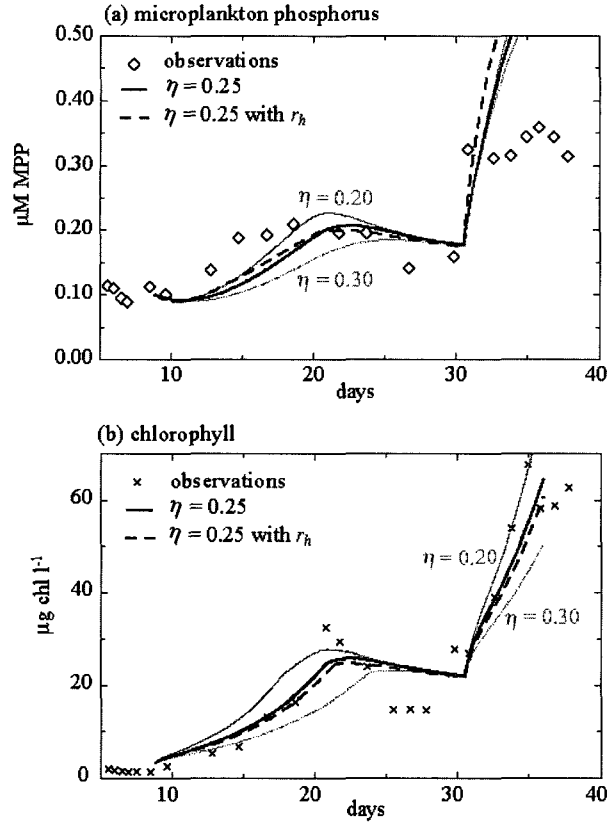

Fig. 4. Simulations of particulates, continued. (a) Simulated P and observed (MPP) microplankton organic phosphorus. (b) Simulated X and observed (chl) microplankton chlorophyll.

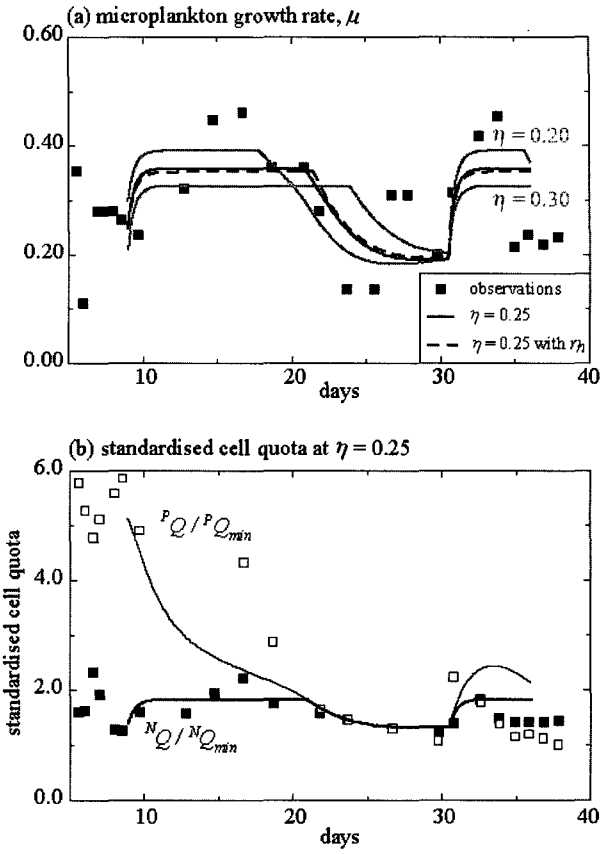

Fig. 5. MP+P simulations of μ and Q in the microcosm. MP+P and MP+P+r_h simulations compared with values deduced from microcosom observations: (a) Mcroplankton growth rate μ compared with values estimated from $\Delta(\ln(\mathrm{MPC}))/\Delta t + D$; (b) Standardized cell quotas ($Q/Q_{\min}$) compared with estimates from ratios of particulate elements: $Q_{\min}$=0.0825 N (mmol C)$^{-1}$ and $^{P}Q_{\min}$=1.5 mmol P (mmol C)$^{-1}$.

Fig. 3 through 6 also show the effect of adding terms (Eqn. 4) for heterotroph mineralisation of nitrogen and phosphorus. Simulation with MP+P+r_h, including excretion, required recalculation (Table 2) of the value for maximum uptake rate of phosphate, since the previous calculation did not take account of remineralisation losses. Best fit was now obtained with η of 0.25, giving a slightly improved overall error of 0.107. $s(N)$ reached a minimum of 0.066 at η= 0.27. Simulated free ammonium reached a maximum of 0.04 µM.

The standard runs of MP+P included suppression of nitrate uptake by limiting phosphorus (Eqn. 5). Removing this coupling gave a best fit at η of 0.27 and increased the overall error to 0.114.

AN UNCONSTRAINED AUTOTROPH-HETEROTROPH MODEL (AH)

The behaviour of MP is constrained by the constant ratio of autotrophs to heterotrophs. This constraint was relaxed in the model AH, which used the autotroph rate equations and heterotroph rate equa-

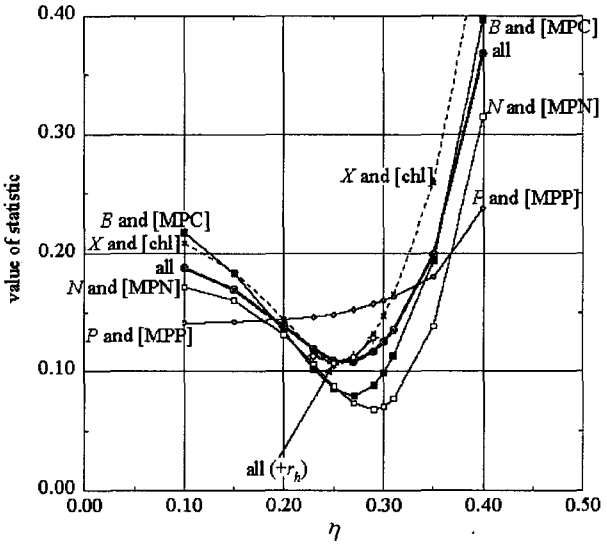

Fig. 6. Fit of MP+P with changes in η. Effect of the assumed value of the heterotroph fraction η on the fit of MP+P simulations to observations. Additional points show best fit for option MP+P+r_h with heterotroph excretion.

tion in Table 2 and 5 of Lee et al. (2003), respectively. The differential equations for AH were

autotroph carbon: $\frac{dB_a}{dt} = (\mu_a - c_h' B_h - D)B_a$ (6.1a)

heterotroph carbon: $\frac{dB_h}{dt} = (c_h' B_a - r_h - D)B_h$ (6.1h)

autotroph nitrogen: $\frac{dN_a}{dt} = \left(\frac{u_a}{Q_a} - c_h' B_h - D\right)N_a$ (6.2a)

heterotroph nitrogen: $\frac{dN_h}{dt} = (c_h' N_a - {}^N r_h)B_h - D\,N_h$ (6.2h)

autotroph phosphorus: $\frac{dP_a}{dt} = \left(\frac{{}^P u_a}{{}^P Q_a} - c_h' B_h - D\right)P_a$ (6.3a)

heterotroph phosphorus: $\frac{dP_h}{dt} = (c_h' P_a - {}^P r_h)B_h - DP_h$ (6.3h)

dissolved ammonium:

$$\frac{d^{NH}S}{dt} = -{}^{NH}u_a B_a + {}^N r_h B_h + D({}^{NH}S_r - {}^{NH}S) \quad (6.4)$$

dissolved nitrate: $\frac{d^{NO}S}{dt} = -{}^{NO}u_a B_a + D({}^{NO}S_r - {}^{NO}S)$ (6.5)

dissolved phosphate:

$$\frac{d^{PO}S}{dt} = -{}^{PO}u_a B_a + {}^P r_h B_h + D({}^{PO}S_r - {}^{PO}S) \quad (6.6)$$

chlorophyll: $X = {}^X q\, {}^N a N_a$ mg m^{-3} (6.7)

All the rates of change have units of mmol m^{-3} d^{-1}. AH simulations were initialised as for MP+*P*, assuming an initial heterotroph fraction of 0.25. This fraction was also used to calculate values of autotroph and heterotroph parameters for phosphorus dynamics (Table 2) in cases where microplankton parameter values had been obtained or fitted directly.

The only parameter value not already used by MP+*P* was the heterotroph transfer coefficient, or volume clearance rate, c_h'. The equation pair (6.1) resembles a set of Lotka-Volterra predator-prey equations. In order to increase the possibility of a stable equilibrium in such a system (Hastings, 1996), the transfer coefficient was given a Holling (Holling, 1959) type II functional response:

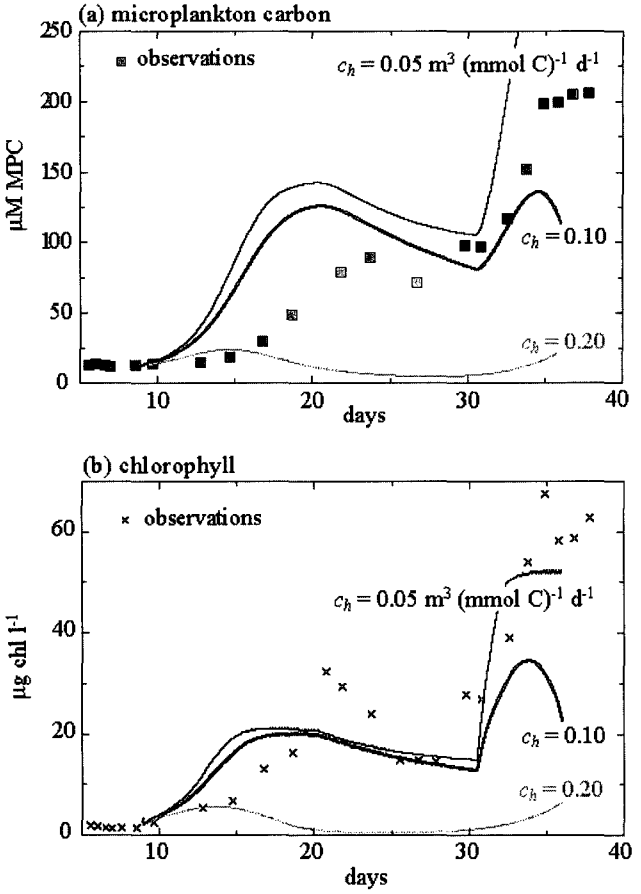

Fig. 7. AH simulations of particulates in the microcosm. Simulations with the unconstrained autotroph-heterotroph model AH, for c_h=0.05, 0.10 and 0.20 m^3 (mmol C)$^{-1}$ d^{-1} (at 20°C), compared with values deduced from observations. Time-series of: (a) simulated microplankton biomass (B=B_a +B_h) compared with MPC; (b) simulated chlorophyll (X=X_a) compared with [chl].

$$c_h' = \frac{c_h}{1 + \left(\frac{B_a}{K_{Ba}}\right)} \quad (7)$$

where c_h is the maximum clearance rate at the given temperature.

The food concentration K_{Ba} for half saturation of ingestion was taken as 50 mmol autotroph C m^{-3}. Fig. 7 compares the results of simulations using c_h of 0.20, 0.10 and 0.05 m^3 (mmol C)$^{-1}$ d^{-1} (at 20°C) with values deduced from the microcosm observations. The 'standard' value of 0.2 for maximum clearance rate (actually close to 0.1 m^3 (mmol C)$^{-1}$ d^{-1} at the temperature of the microcosm) resulted in a very poor fit.

Fig. 8(a) shows plots of heterotroph biomass against autotroph biomass for simulations with the same values of c_h. The diagonal line is the corresponding plot from MP+*P* with η=0.25, with overall fitting error

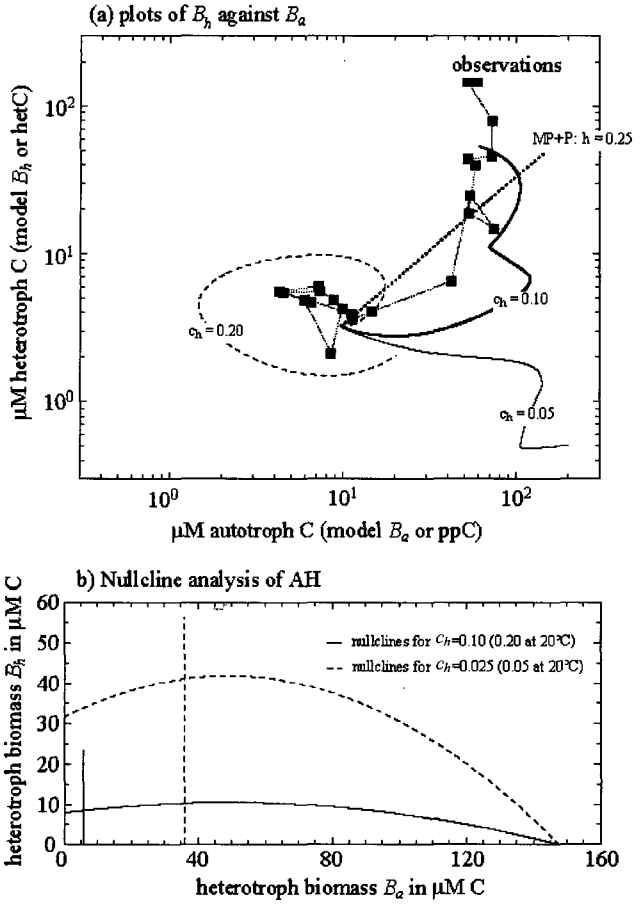

Fig. 8. Phase plots of AH and MP simulations and microcosm results. Observations shown by squares in (a): autotroph biomass from microscopic observations (ppC); heterotroph biomass from MPC-ppC. In (b), $B_{max\ a}$ was taken as 186 mmol C m^{-3}, from ${}^{PO}S_i/{}^{P}Q_{mina}$, and $\mu_{max\ a}$ was 1.0 d^{-1} 10°C.

(for MPC, MPN, MPP and chlorophyll) of 0.108. Even the best fit of AH, with c_h of 0.09 m^3 (mmol C)$^{-1}$ d^{-1} (at 20°C), gave an overall error of 0.241.

NULLCLINE ANALYSIS

Eqn. (6.1) can be made the subject of nullcline analysis (Hastings, 1996), given the replacement of $\mu_a(I, Q)$ by a simplified density dependence:

$$\frac{dB_a}{dt} = 0 = \left(\mu_{maxa}\left(1-\frac{B_a}{B_{maxa}}\right)-c_h'B_h-D\right)B_a \quad (8.1a)$$

$$\frac{dB_a}{dt} = 0 = (a\,c_h'B_a-D)B_h \quad (8.2h)$$

where a=1/(1+b_h), which neglects r_{0h}. Taking into account the saturation function of Eqn. (6.2) for c_h', these equations lead to the nullclines:

$$B_a = \frac{1}{\left(\frac{a\,c_h}{D}-\frac{1}{K_{Ba}}\right)} \quad \therefore \frac{dB_h}{dt} = 0$$

$$B_h = \left[\left(\mu_{max}\left(1-\frac{B_a}{B_{max}}\right)-D\right)\left(1+\left(\frac{B_a}{K_{Ba}}\right)\right)\right]/c_h$$

$$\therefore \frac{dB_h}{dt} = 0$$

which are plotted in Fig. 8(b) for several values of c_h.

The nullclines intersect on the rising part of that for B_h, which suggests (Hastings, 1996) that any equilibrium should be unstable. Although this does not take account of the other processes described by equations (6.2) to (6.5), it does help to explain the oscillatory behaviour shown in Fig. 8, especially that displayed by the simulation with c_h of 0.20 m^3 (mmol C)$^{-1}$ d^{-1} (at 20°C).

DISCUSSION

The most crucial assumption of MP is that of "*a constant ratio of heterotrophs to autotrophs*". The unconstrained autotroph-heterotroph model AH failed to simulate, adequately, the time-courses of state variables during the microcosm experiment. In contrast, the microplankton model MP was able to describe the observations quite well, despite - or, perhaps, because of - assuming a fixed ratio of autotrophs to heterotrophs.

AH may be too simple to represent, properly, the heterogeneous nature of the experimental microplankton. A system comprising several species at each trophic level may form an more stable trophic web than implied by the quasi-Lotka-Volterra dynamics of AH, 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 stablising 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.

AH and MP are fairly compared because both models drew on the same set of parameter values for autotrophs and heterotrophs. They combined them,

Table 4. Phosphorus submodel parameters for autotrophs and heterotrophs in AH

Parameter	Value	Units	How calculated (with η=0.25)
${}^{P}Q_{\max a}$	15	mmol P (mol C)$^{-1}$	same as ${}^{P}Q_{\max}$
${}^{P}Q_{\min a}$	1.5	mmol P (mol C)$^{-1}$	same as ${}^{P}Q_{\min}$
${}^{P}q_{h}$;	6	mmol P (mol C)$^{-1}$	${}^{P}Q_{\min}/\eta$
${}^{P}u_{\max a}$	14.7@20°C	mmol P (mol C)$^{-1}$ d^{-1}	${}^{P}u_{\max}/(1-\eta)$
K_{PO}	0.21	mmol P m^{-3}	

however, in different ways. In the case of MP, the ratio of autotroph to heterotroph biomass was fixed during any one simulation, resulting in particular values of the microplankton parameters that were derived from the autotroph and heterotroph parameters. The value of η was varied between model runs to improve the fit of simulations to observations. In the case of AH, the relative biomasses of autotrophs and heterotrophs were free to change. Thus, autotroph and heterotroph parameter values were, in effect, combined dynamically, as the implicit value of η was changed by the model during a simulation. In contrast with MP, which had to be supplied with a value of η but made no use of the trophic transfer coefficient c_h, AH simulations used η only to calculate initial values of autotroph and heterotroph biomasses but required a value for c_h. The clearance coefficient's value was varied in order to improve the fit of AH simulations to observations, but gave no fit as good as that obtained with MP.

The value of η=0.25 giving the best fit of MP+*P* was within the range (0.15-0.52) calculated from the microcosm observations between days 8 and 35. It may also be compared with estimates derived from the literature (Table 5).

There is, clearly, no universal value of η. Furthermore, the data in Table 5, and the existence of several sets of trophic pathways amongst plankton, Legendre and Rassoulzadegan (1995) suggest that the value of η should change seasonally in temperate waters, with low values during the early stages of diatom-dominated Spring bloom and higher values when a recycling, Microbial-Loop, community is established in Summer. There is analagous variability in space (Holligan *et al.*, 1984; Richardson *et al.*, 1998). MP as it presently stands cannot deal with such seasonal or spatial changes, but Tett and Smith (1997) have described a 'two-microplankton' model, which allows the value of η to change dynamically over a range set by the value in each of the two microplanktons.

Did the microcosm data provide a good test of MP? Jones *et al.* (1978b) argued that the behaviour of the experimental microplankton was natural in respect of maintaining "the occurrence of typical sea-loch species, their growth in parallel with the same species in the loch [from which they were innoculated] ..., the coherence of growth curves ... and ... moderate diversity". The model was successful in simulating a biomass increase of an order of magnitude during an experiment in which growth rates varied as a result of changes in available nutrient. Although the phosphorus submodel added to MP had some deficiencies, MP predictions for carbon and nitrogen remained accurate during the switch from N to P limitation. In these respects, MP has been severely tested. Against this claim, it might be argued that the range of biomasses observed in the microcosm lay at the upper end of the natural range, and that a scenario involving a shift

Table 5. Estimates of the heterotroph fraction .

Site	Season	Autotroph mmol C m^{-3}	Hetero-troph mmol C m^{-3}	Micro-plankton mmol C m^{-3}	η	Reference
Scottish coastal: Easdale Quarry	May - August	8.1	3.6	11.7	0.31	Tett *et al.* (1988)
Scottish coastal: Loch Creran	whole year	6.6	3.8	10.4	0.36	Tett *et al.* (1988)
English Channel: mixed	July	6.8	1.6	8.2	0.19	Holligan *et al.* (1984)
English Channel: stratified	July	1.4	2.0	3.4	0.58	Holligan *et al.* (1984)
Canadian coastal: CEPEX	July -August	10.4	1.3	11.7	0.11	(Williams, 1982)
Area-integrated gobal means		mmol C m^{-2}	mmol C m^{-2}	mmol C m^{-2}		
'Coastal' euphotic zone or similar	mean of all data (n≥82)	191	71	262	0.27	Gasol *et al.* (1997)
'Open Ocean' euphotic zone or similar	mean of all data (n≥119)	164	135	299	0.45	Gasol *et al.* (1997)

from *N* to *P* limitation would be unusual for natural marine plankton. The most important switch in limitation for microplankton in temperate waters is from light to nutrient control during the transition from Spring to Summer conditions. The model L3VMP, which combines MP, detritus and a physical submodel, has been successfully used to simulate the Spring Bloom in the central North Sea (Tett and Walne 1995). Even so, it will be desirable to test MP with experimental data which includes a shift from light to nitrogen control of growth.

ACKNOWLEDGEMENT

This work was supported by Korean Science & Engineering Foundation (KRF-R08-2004-000-10261-0). We would like to thank to Dr. Chang-Keun Kang in Pusan National University and Dr. Woo-Jeung Choi in National Fisheries Research & Development Institue (NFRDI) for their valuable comments and suggestion.

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Manuscript received November 22, 2004
Revision accepted December 22, 2004
Editorial handling: Chang-Keun Kang