Parameterising a Microplankton Model

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.*

This paper describes and assesses the parameterisation of MP, the microplankton compartment of the carbon-nitrogen microplankton-detritus model. The compartment is 'the microbial loop in a box' and includes pelagic bacteria and protozoa as well as phytoplankton. The paper presents equations and parameter values for the autotroph and microheterotroph components of the microplankton. Equations and parameter values for the microplankton as a whole are derived on the assumption of a constant 'heterotroph fraction'. The autotroph equations of MP allow variation in the ratios of nutrient elements to carbon, and are largely those of the 'cell-quota, threshold-limitation' algal growth model, which can deal with potential control of growth by several nutrients and light. The heterotroph equations, in contrast, assume a constant elemental composition. Nitrogen is used as the limiting nutrient in most of the model description, and is special in that MP links chlorophyll concentration to the autotroph nitrogen quota.

Key words: Microplankton, Phytoplankton, Microbial Loop, Cell-Quota

INTRODUCTION

Descriptions of biological-physical interactions in the sea must take account of physical transports (which conserve the total quantity of transported variables) and of non-conservative biological or chemical processes (which convert one variable into another). An equation which summarises both causes of variation, and which forms the basis of (Eulerian) vertical-process models, is:

$$\frac{\partial Y}{\partial t} = \underbrace{-\frac{\partial \varphi_Y}{\partial z}}_{\text{flux divergence}} + \underbrace{\beta_Y}_{\text{nonconservative processes}} \qquad (1)$$

where the vertical flux is:

$$\varphi_Y = \langle (w + w' + w_Y)(Y + Y') \rangle$$

$$\approx \underbrace{-Kz\frac{\partial Y}{\partial z}}_{\text{eddy mixing}} + \underbrace{(w + w_Y)\, Y}_{\text{water advection \& particle sinking}}$$

The equation describes the rate of change at a given point in the sea of a generalised biological variable Y which is a function of time t and height z above the sea bed. The equation must be repeated, and numerically solved, for every state variable in a

*Corresponding author: ocean_system@naver.com

model. It is desirable to minimise the list of such variables, not only in order to minimise computer storage and calculation (especially in 2D or 3D models, or during the repeated simulations necessary for parameter optimisation), but also because of Occam's Razor ('do not unnecessarily multiply explanations') and on account of practical and theoretical difficulties in estimating parameters (which, in general, increase with variable number).

Taking into account this need for parsimony in state variables, Tett (1990b) proposed a microbiological model (Fig. 1(a)) 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 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. The microplankton-detritus model has
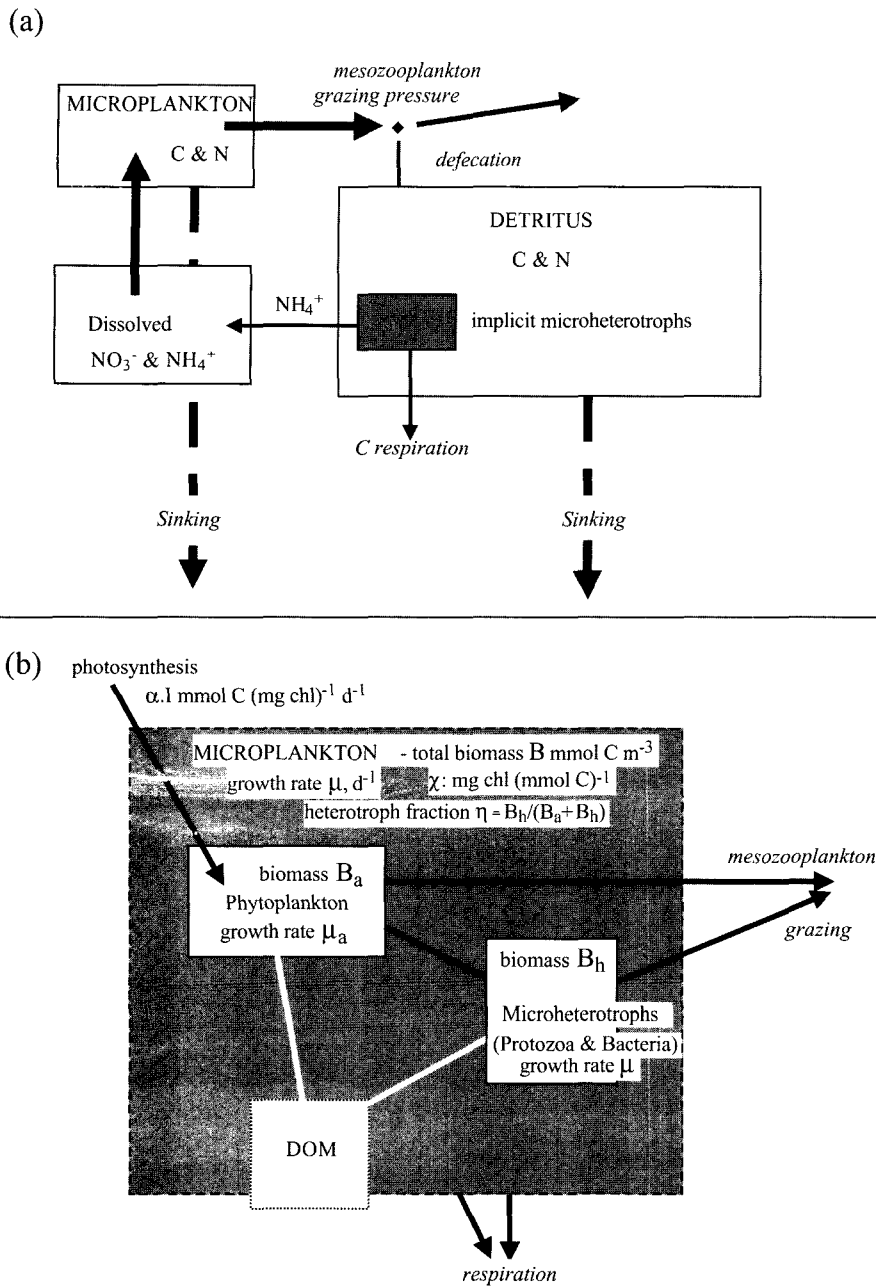
Fig. 1. The microplankton-detritus model. (a) The complete microbiological model of Tett (1990b), with slowly-mineralising detritus compartment; (b) The microplankton compartment (MP), showing the implicit microbial loop in a box.

been used in a number of studies (Huthnance et al., 1993; Hydes ei 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., 1996) with some variations in the process equations and parameter values.

This paper concerns the microplankton compartment (Fig. 1(b)), which was proposed by Tett (1987) as a relatively simple way of parameterising the most important (for water quality models) of the processes in the 'microbial loop' (Azam et al., 1983; Williams, 1981). The aim of the paper is to describe this param-

eterisation in more detail than given by Tett (1990b) or than was possible in subsequent papers, and to discuss more fully the basis and consequences of the assumptions employed to obtain a simple description. Earlier versions of the microplankton equations were given as part of the model L3VMP (Tett 1990b; Tett and Grenz, 1994; Tett and Walne, 1995), and by Smith and Tett (2000) as part of the model SED-BIOL. 'MP' will denote the equation set here proposed. Table 1 lists common symbols used throughout this report for all the models.

THE MICROPLANKTON COMPARTMENT

The microplankton compartment of MP is deemed to contain all pelagic micro-organisms less than 200 µm, including heterotrophic bacteria and protozoa (zooflagellates, ciliates, heterotrophic dinoflagellates, etc) as well as photo-autotrophic cyanobacteria and micro-algae (diatoms, dinoflagellates, flagellates, etc). This definition (Tett, 1987) employs an earlier use

(Dussart, 1965) of the term 'microplankton' than that suggested by Sieburth (1979), who contrasted microplankton to picoplankton and nanoplankton. Flows of energy and materials through and between the organisms of the microplankton link them in the 'microbial loop' (Azam *et al.*, 1983; Williams, 1981). Microplankters reproduce mainly by binary division, in contrast to mesozooplankton, such as copepods, which typically have relatively long periods of individual
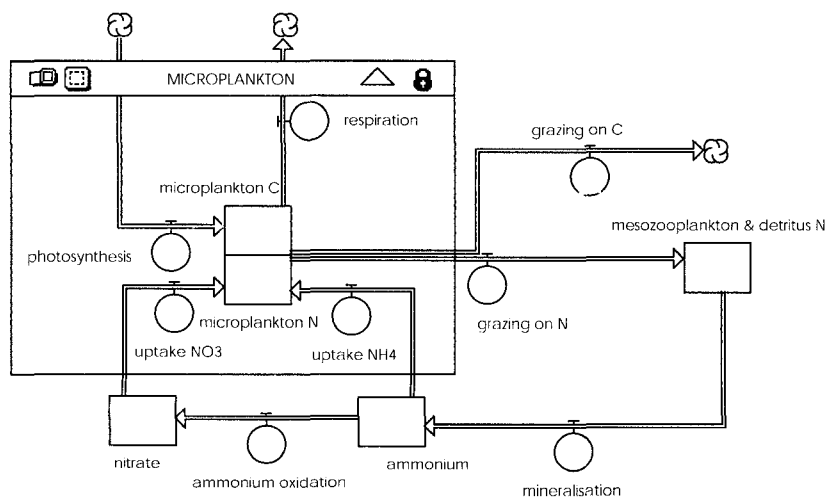
(a) ML
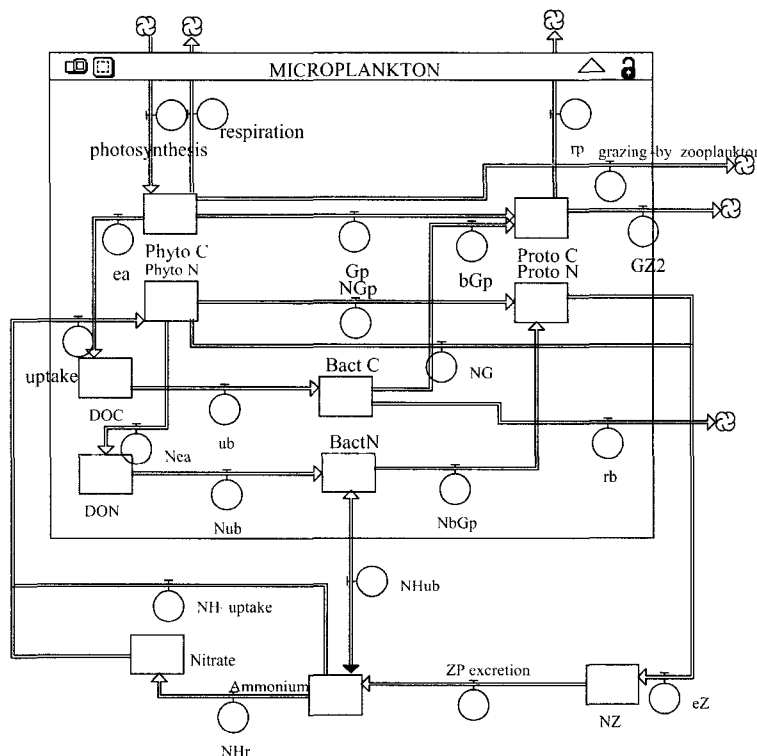
(b) MP

Fig. 2. Model comparisons. Relevant compartments and flows in (a) ML of Tett and Wilson (2000), and (b) MP, shown according to the conventions of the modelling software STELLA. The large rectangle shows the limits of the MP microplankton compartment or its analogue.

growth after the laying of many eggs by those few females that survive to maturity. Many of the microbial populations in the loop have turnover rates of order 10^{-1} d^{-1} during the productive season, and can be parameterised as a unit without unduly distorting the response of the model on time-scales of a few days or longer.

Models of the microbial loop can be recognised by their explicit inclusion of compartments for heterotrophic bacteria and their consumers. The loop as thus defined has been modelled by several authors, including Baretta-Bekker et al. (1995) as part of ERSEM, Fasham et al. (1990) in FDM, and Taylor and co-workers (Taylor et al., 1993; Taylor and Joint, 1990). Wilson and Tett (1997) compare Microbial Loop (ML) and Microplankton (MP) models (Fig. 2(a)). Their version of MP has 2 independent state variables and 12 parameters in the description of the microplankton compartment itself; the analogous compartments of ML (phytoplankton, bacteria, protozoa and dissolved organic matter) have 6 independent state variables and 27 parameters. These numbers demonstrate the relative simplicity of MP, which is 'the microbial loop in a box'.

The microplankton compartment of MP contains several trophic levels, and thus would seem to confuse the distinction between autotrophs and heterotrophs. However, the distinction is not clear-cut in microplanktonic organisms. Not only do phytoplankton respire, but some protozoans retain ingested chloroplasts and some micro-algae can grow heterotrophically or mixotrophically. The microplankton may thus be seen from a functional viewpoint as a suspension of chloroplasts (and cyanobacteria) and mitochondria (and heterotrophic bacteria) with associated organic carbon and nitrogen. Tett (1987) proposed a model in which bulk "photoautotrophic processes are made simple functions of chlorophyll concentration, representing algal biomass...; heterotrophic processes are made simple functions of ATP concentration, representing total microplankton biomass ... and including the algal component." The model was used to estimate carbon fluxes in an enclosed coastal microplankton (Tett et al., 1988), and the concept of the microplankton in MP developed from that work. The microplankton model distinguishes autotrophic from heterotrophic processes rather than autotrophic from heterotrophic organisms.

Originally (Tett, 1990b), the single microplankton compartment of MP was seen as predominantly algal in character, with a heterotroph 'contamination' merely

exaggerating the effect of the heterotrophic processes of the algae themselves - for example, implicitly increasing the microplankton's respiration rate. In the treatment that follows, however, the effects of an autotroph-heterotroph mixture are taken explicitly into account. This involves the parameter η, the ratio of microheterotroph to microplankton biomass:

$$\eta = \frac{B_h}{(B_a + B_h)} \tag{2}$$

where subscripts a and h indicate autotrophs (phytoplankton) and (pelagic micro-) heterotrophs (protozoa and heterotrophic bacteria). In the equations hereunder, terms without subscripts refer to the microplankton as a whole. It is a crucial assumption of this version of MP that the value of the heterotroph fraction does not change during a simulation. Variation in η has been addressed by models (Tett and Smith, 1997) using two MP compartments that vary in their relative contribution to total biomass and which differ in η. Tett and Wilson (2000) and Wilson and Tett (1997) examine the effect of treating η as a forcing variable.

It is further assumed that organic matter excreted by phytoplankton or leaked during 'messy feeding' by protozoans is re-assimilated by microplankton bacteria so rapidly that the turnover times of pools of labile dissolved organic matter are less than a day. Thus the existence of such pools can be ignored. It is, similarly, assumed that inorganic nutrients (ammonium, phosphate) excreted by microheterotrophs are rapidly re-assimilated by the autotrophs and thus retained within the microplankton. This assumption is further examined in the sections of 'microplankton rate equations'.

MICROPLANKTON EQUATIONS OF STATE

The microplankton compartment has two independent state variables, organic carbon B:

$$\frac{\partial B}{\partial t} = -\frac{\partial \varphi_B}{\partial z} + \beta_B \qquad \text{mmol C m}^{-3}\text{d}^{-1} \tag{3}$$

and organic nitrogen N:

$$\frac{\partial N}{\partial t} = -\frac{\partial \varphi_N}{\partial z} + \beta_N \qquad \text{mmol N m}^{-3}\text{d}^{-1} \tag{4}$$

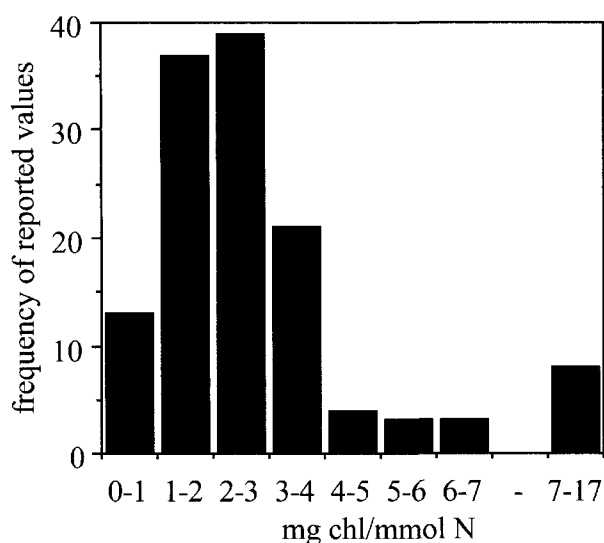Two other variables are linked to the above; the nitrogen quota:

Fig. 3. Chlorophyll:nitrogen yield. Histogram of the frequency of values of the ratio of chlorophyll (g) to nitrogen (moles) in cultured marine algae growing at irradiances less than 300 μE m^{-2} s^{-1}. Literature data for *Chaetoceros gracilis*, *Dunaliella tertiolecta*, *Gymnodinium sanguineum*, *Pavlova lutheri*, *Skeletonema ostatum*, and *Thalassiosira pseudonana*.

$$Q = N/B \qquad \text{mmol N(mmol C)}^{-1} \qquad (5)$$

and the chlorophyll concentration:

$$X = \chi B \qquad \text{mg chl m}^{-3} \qquad (6)$$

where χ is the variable ratio of chlorophyll to microplankton carbon, with a value that depends on Q.

Microplankton carbon is the sum of autotroph and heterotroph contributions:

$$B = B_a + B_h = B(1 - \eta) + B\eta \qquad \text{mmol C m}^{-3} \quad (7)$$

In the case of microplankton nitrogen,

$$N = N_a + N_h = Q_a B_a + q_h B_h = (Q_a(1 - \eta) + q_h \eta)B$$
$$\text{mmol N m}^{-3} \quad (8)$$

where Q_a is the variable autotroph nutrient quota and q_h is a constant heterotroph nutrient quota (mmol N (mmol C)$^{-1}$).

The flux divergences in Eqn. (3) and (4) are not of concern here. The nonconservative term for microplankton carbon rate of change in Eqn. (3) can be expanded:

$$\beta_B = \beta_{Ba} + \beta_{Bh} = (\mu_a - c_h B_h - G)B_a$$
$$+ (c_h B_a - r_h - G)B_h \qquad \text{mmol C m}^{-3} \text{ d}^{-1} \quad (9)$$

where μ_a is the relative growth rate (d^{-1}) of the autotrophs; G is mesozooplankton grazing pressure

b$_1$, b$_2$ and b$_3$ are bacteria
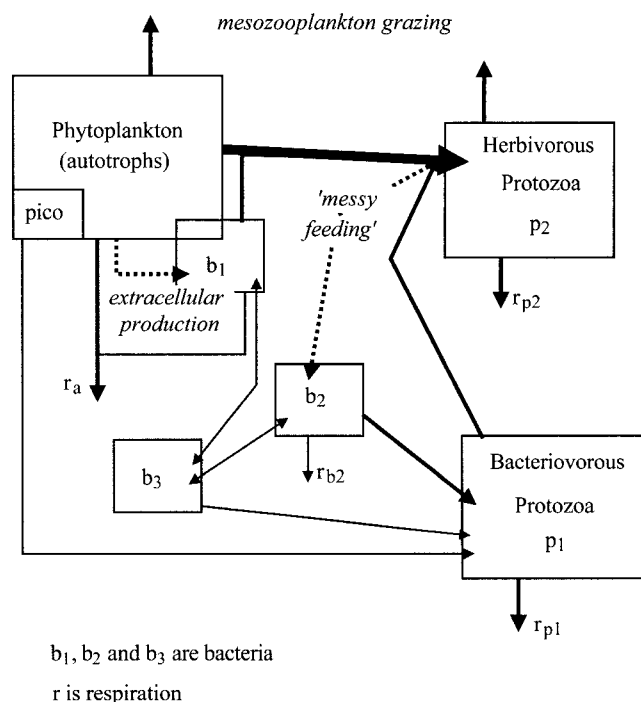
r is respiration

Fig. 4. Conceptual model of interactions between bacteria and other microplankton.

(the instantaneous probability per unit time that a microplankter will be consumed by a copepod or similar animal); it is assumed that *this pressure applies equally to heterotrophs and autotrophs*; $c_h B_h$ is the 'transfer pressure' (d^{-1}) on autotrophs due to microplankton heterotrophs; it is analogous to the mesozooplankton grazing pressure; r_h is the relative respiration rate (d^{-1}) of microplankton heterotrophs.

If the heterotrophic component were solely herbivorous protozoa, then c_h might be seen as a clearance rate (volume of water made free of autotrophs by the grazers, per unit grazer biomass and time). However, there are other ways in which organic matter is transferred from producers to consumers, including photosynthetic and grazing-induced leakage of Dissolved Organic Matter (DOM) which is assimilated by bacteria, in turn grazed by protozoa (Fig. 4). $c_h B_h B_a$ (mmol C m^{-3} d^{-1}) is thus best understood as the total organic carbon flux from autotrophs to microplankton heterotrophs. Details of the routes are of no importance so long as the transfer term appears identically (except for opposite sign) in β_{Ba} and β_{Bh}, and so cancels. It is thus assumed that all DOM produced by leakage is labile and rapidly assimilated by other microplankters. It is also assumed by MP that protozoans do not defecate, and hence the only intrinsic loss of carbon experienced by the micro-

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. Δr / $\Delta\mu$) or inefficiency coefficient	-
β	(total) nonconservative flux for a substance	mmol m^{-3} d^{-1}
c	Clearance rate or transfer coefficient	m^3 (mmol C)$^{-1}$ d^{-1}
χ	Chlorophyll: carbon ratio	mg chl (mmol C)$^{-1}$
e	Relative (organic) excretion rate	d^{-1}
ε	Photosynthetic pigment attenuation cross- section	m^2 (mg chl)$^{-1}$
Φ	Photosynthetic quantum yield	nmol C μE^{-1}
G	Grazing Pressure	d^{-1}
η	Heterotroph fraction (of biomass)	-
I	PAR	μE m^{-2} s^{-1}
i	Relative ingestion rate	d^{-1}
K	(half)-saturation constant, as in K_S or K_I	S or I
k	Miscellaneous constants	various
μ	Relative growth rate	d^{-1}
N	Nitrogen associated with biomass	mmol N m^{-3}
p	Preference (e.g. for one diet compared with other)	-
Q	Nutrient quota or content in biomass	mmol nutrient (mmol C)$^{-1}$
q	Fixed quota	mmol nutrient (mmol C)$^{-1}$
r	Biomass-related mineralisation/respiration rate	mmol (mmol C)$^{-1}$ d^{-1}
S	Dissolved nutrient concentration	mmol m^{-3}
Θ	Temperature	°C
u	Biomass-related nutrient uptake rate	mmol (mmol C)$^{-1}$ d^{-1}

heterotrophs is through their respiration:

$$\mu_h = c_h\, B_a - r_h \quad \text{d}^{-1} \tag{10}$$

It may be noted that microheterotroph growth rate μ_h must be the same as microplankton growth rate μ if the heterotrophs are to remain a constant fraction of the microplankton. However, μ_h need not appear explicitly in the microplankton equation of state, because the transfer term $c_h\, B_h\, B_a$ cancels in Eqn. (9), which can then be simplified:

$$\beta_B = (\mu - G)B \quad \text{mmol C m}^{-3}\text{d}^{-1} \tag{11}$$

where microplankton growth rate is:

$$\mu = \mu_a(1 - \eta) - r_h\eta \quad \text{d}^{-1} \tag{11a}$$

As with carbon, so with microplankton nitrogen. The non-conservative term for rate of change in Eqn. (4) can be expanded:

$$\beta_N = \beta_{Na} + \beta_{Nh} \quad \text{mmol N m}^{-3}\text{d}^{-1}$$

$$= (u_a - (c_h\, B_h + G)Q_a)B_a + (c_h\, Q_a\, B_a - {}^N r_h - G\, q_h)B_h \tag{12}$$

where u_a is autotroph biomass-related nutrient uptake rate, in the case of nitrogen the sum of ammonium and nitrate uptakes (mmol N (mmol C)$^{-1}$ d^{-1}); $^N r_h$ is the heterotroph ammonium excretion rate (mmol N (mmol C)$^{-1}$ d^{-1});

As in the case of carbon, the transfer of nitrogen from autotrophs to heterotrophs is not a loss when included within the microplankton compartment, and Eqn. (12) simplifies to:

$$\beta_N = uB - GN = (u - GQ)B \quad \text{mmol N m}^{-3}\text{d}^{-1} \tag{13}$$

where

$$Q = Q_a(1 - \eta) + q_h\eta \quad \text{mmol N (mmol C)}^{-1} \tag{13a}$$

$$u = u_a(1 - \eta) - {}^N r_h\eta \quad \text{mmol N (mmol C)}^{-1}\text{d}^{-1} \tag{13b}$$

The following sections expand the autotroph and heterotroph rate terms in these equations.

Table 2. Autotroph rate equations used in MP

Growth	$\mu_a = \min\{\mu_a(I), \mu_a(Q)\}$ where	d^{-1}
	$\mu_a(Q) = \mu_{\max a}\left(1 - \dfrac{Q_{\min a}}{Q_a}\right) : Q_a \geq Q_{\min a}$	
	$\mu_a(I) = \alpha \, \chi_a \, I - r_a$	
	where $\alpha = k \, \varepsilon \, \Phi$	mmol C (mg chl)$^{-1}$ d^{-1} (μE m^{-2} s^{-1})$^{-1}$
	$\chi_a = {}^X q_a^N \, Q_a$	mg chl (mmol C)$^{-1}$
Respiration	$r_a = \begin{bmatrix} r_{0a} + b_a \, \mu_a & : & \mu_a > 0 \\ r_{0a} & : & \mu_a \leq 0 \end{bmatrix}$	d^{-1}
Nutrient uptake	$u_a = u_{\max a} \, f(S) f_{in}(Q_a) \, [\, f_{in}({}^{NH}S)\,]$ where	mmol N (mmol C)$^{-1}$ d^{-1}
	$f(S) = (S/(K_S + S)) : S \geq 0$	
	$f_{in}({}^{NH}S) = 1/(1 + ({}^{NH}S/K_{in})) : {}^{NH}S \geq 0$	[inhibits NO_3^- uptake]
	$f_{in}(Q_a) = 1 - (Q_a/Q_{\max a}) : Q_a \leq Q_{\max a}$	
Temperature	$\mu_{\max a} = \mu_{\max a}[20°C] \, f(\Theta)$	d^{-1}
	$u_{\max a} = u_{\max a}[20°C] \, f(\Theta)$	d^{-1}
	where $f(\Theta) = \exp(k_\Theta(\Theta - 20°C))$	
	$\Theta = $ temperature	°C

AUTOTROPH (PHYTOPLANKTON) EQUATIONS

The autotroph equations used by MP are summarised in Table 2. They are largely derived from the 'Cell-Quota, Threshold-Limitation' (CQTL) model of Droop (Droop, 1968), and others (Caperon, 1968; Fuhs, 1969; Paasche, 1973; Rhee, 1973), reviewed by Droop (1983) and Rhee (1980). Tett and Droop (1988) review estimates of CQTL parameter values. At the heart of the model is the concept of a variable cell nutrient quota (Eppley and Strickland, 1968), changing as a result of nutrient uptake and of the dilution of nutrient by biomass during growth:

$$\frac{dQ_a}{dt} = u_a - \mu_a \, Q_a \quad \text{mmolnutrient (mmol C)}^{-1}\text{d}^{-1} \quad (14)$$

Such variability allows 'luxury uptake' of nutrient in excess of immediate need for growth (Kuenzler and Ketchum, 1962; Mackereth, 1953), the stored nutrient being available for later use. Despite the name 'cell quota', the variable is normally measured as the ratio of population nutrient to biomass (Droop,

1979), although the biomass has sometimes been expressed in terms of numbers of cells. Droop (1968) showed that vitamin B_{12}-limited growth of the prymnesiophyte *Pavlova* (=*Monochrysis*) *lutheri* was a function of the cell quota of the vitamin, and Caperon (1968) showed a similar dependency of N-limited growth on the N:C ratio of the prymnesiophyte *Isochrysis galbana*. The simplest form (Droop, 1968) of the Cell-Quota function for growth is

$$\mu_a = \mu_{\max a}\left(1 - \frac{Q_{\min a}}{Q_a}\right) : Q_a \geq Q_{\min a} \quad (15)$$

where $Q_{\min a}$ is the minimum cell quota that supports life (but not growth), and $\mu_{\max a}$ gives the notional growth rate at infinite (and therefore, unrealisable) cell quota. Caperon's version has an extra parameter:

$$\mu_a = \mu_{\max a}\left(\frac{Q_a - Q_{\min a}}{k_{Qa} + Q_a - Q_{\min a}}\right) : Q_a \geq Q_{\min a}$$

but, as argued by Droop (1983), this is the same as Eqn. (15) when $k_{Qa} = Q_{\min a}$, and so there is little case for introducing the third parameter when observations

cannot well distinguish the value of the internal half-saturation constant k_{Qa} from that of the threshold quota Q_{mina}. For consistency in notation within MP, we use for Droop's symbol k_Q. For simplicity, Droop's symbol μ'_m for maximum growth rate (at infinite Q) is written as μ_{max}, but this should not be confused with the use of μ_{max} in the Monod (or similar) growth equation, where the maximum rate is that at infinite external nutrient concentration.

Droop (1974; 1975) and Rhee (1974) showed that there was a threshold, rather than multiplicative, relationship between two potentially limiting nutrients, and Droop et al. (1982) extended threshold-limitation theory to include irradiance I:

$$\mu_a = \min \{\mu_a(I), \ \mu_a(^1Q_a), \ \mu_a(^2Q_a), \ ...\} \quad d^{-1} \quad (16)$$

This states that, at a given instant, phytoplankton growth rate depends solely on the factor that predicts the least growth rate. Standard MP uses only the first two terms: $\mu_a(I)$ and $\mu_a(Q_a)$ for nitrogen.

The irradiance function includes photosynthesis and respiration:

$$\mu_a = p(I) - r_a \quad d^{-1}$$

The function $p(I)$ could be any of the photosynthesis-irradiance equations reviewed by Jassby and Platt (1976) and Lederman and Tett (1981), but the use of a linear equation simplifies integration over an optically thick layer (Tett, 1990a) and is a good approximation under most light-limiting conditions (Droop et al., 1982). Thus MP's light-controlled growth equation is:

$$\mu_a(I) = \alpha \ \chi_a \ I - r_a = k \ \varepsilon \ \Phi \ \chi_a \ I - r_a \quad d^{-1} \quad (17)$$

where photosynthetic 'efficiency' α (a parameter which does not need subscripting when defined in relation

to chlorophyll) is made up from a phytoplankton attenuation cross-section ε (m^2 (mg chl)$^{-1}$) and a photosynthetic quantum yield Φ (nmol C μE^{-1}): the constant k serves to convert units. Droop et al. (1982) showed that photosynthetic efficiency was high in light-limited Pavlova, and lower when the algae were nutrient-controlled. MP treats the efficiency parameters ε and Φ as constants (in a given simulation), on the grounds that they are not used to calculate nutrient-controlled growth rate. However, the algal-biomass-related photosynthetic efficiency α_a ($d^{-1} I^{-1}$) decreases with increasing nutrient limitation because of the relationship, discussed below, between chlorophyll content and the cell quota.

As discussed by Tett and Droop (1988) and Tett (1990a) there is evidence that micro-algal respiration depends more on growth rate than on temperature (some temperature effect being expected because $\mu(Q)$ depends in part on $\mu_{max} f(\Theta)$). In MP, respiration is made up of a basal and a growth-rate-related component:

$$r_a = \begin{bmatrix} r_{0a} + b_a \ \mu_a & : & \mu_a > 0 \\ r_{0a} & : & \mu_a \leq 0 \end{bmatrix} \quad d^{-1} \quad (18)$$

Values of the parameters r_{0a} and b_a were based on measurements made using algal cultures. However, in the case of r_{0a} in particular, the literature gives a wide range of estimates (Table 3). The standard value of 0.05 d^{-1} for basal respiration r_{0a} was chosen because higher values would make it difficult for simulated algae to survive under winter conditions. A respiration slope b_a of 0.5 is supposed to take account of the effects of epiphytic bacteria, as discussed in the section of 'heterotroph equations'.

MP defines nutrient uptake in relation to carbon biomass. Most studies concerning nutrient-limited growth have found that the uptake of a limiting nutrient at extracellular concentration S (mmol m^{-3}) can

Table 3. Estimates of respiration parameters

Species	b_a	r_{0a}, d^{-1}	Source
Dunaliella tertiolecta	0.74	0.028	(Laws and Wong 1978)
Dunaliella tertiolecta		0.24	(Richardson et al., 1983)
Gonyaulax polyedra		0.41	(Richardson et al., 1983)
Leptocylindrus danicus		0.03	(Richardson et al., 1983)
Pavlova lutheri	0.18	0.082	(Laws and Caperon, 1976)
Pavlova lutheri		0.15	(Droop et al., 1982)
Pavlova lutheri	0.48	0.028	(Laws and Wong, 1978)
Skeletonema costatum		0.04	(Richardson et al., 1983)
Thalassiosira alleni	0.20	0.037	(Laws and Wong, 1978)

be described by the Michaelis-Menten equation:

$$u_a = u_{\max a}\left(\frac{S}{K_S + S}\right) \quad \text{mmol nutrient (mmol C)}^{-1}\text{d}^{-1}$$

(19)

The parameter $u_{\max a}$ specifies the uptake rate at infinite concentration of the external nutrient; the half-saturation parameter K_S gives the nutrient concentration at which uptake is half the maximum rate. Some authors (e.g. Droop, 1974; Paasche, 1973) added a parameter S_0, the threshold for uptake:

$$u_a = u_{\max a}\left(\frac{S - S_0}{K_S + (S - S_0)}\right) \quad : \quad S \geq S_0$$

Droop (1974; 1975) distinguished between the uptake of the nutrient currently controlling growth and the uptake of another nutrient, and Droop et al. (1982) proposed an equation for the uptake of a nutrient when another nutrient, or light, was controlling growth:

$$u_{na} = u_{\max a}\left(\frac{S}{K_S + S}\right)\rho$$

where the 'coefficient of luxury':

$$\rho = R_m/(\Lambda(R_m - 1) + 1)$$

and, for light in control of growth:

$$\Lambda = (S/K_S)(K_I/I) \quad : \quad (I/K_I) \leq (S/K_S)$$

whereas, for another nutrient (2) in control of growth (Droop 1974):

$$\Lambda = (^1S/^1Q_{\min})(^2Q_{\min}/^2S) \quad : \quad (^2S/^2Q_{\min}) \leq (^1S/^1Q_{\min})$$

K_I is a saturation constant for (absorbed) irradiance and R_m is the maximum value of ρ.

The autotroph nutrient uptake equation used in MP is simpler than this. It does not distinguish controlling from non-controlling nutrient. Instead, it regulates uptake so as to prevent the cell quota from exceeding a realistic upper limit, $Q_{\max a}$:

$$u_a = u_{\max a} \; f(S) \; f(Q_a)$$

$$\text{mmol nutrient (mmol C)}^{-1} \; \text{d}^{-1} \quad (20)$$

where:

$$f(S) = S/(K_S + S) \quad : \quad S \geq 0$$

$$f(Q_a) = 1 - (Q_a / Q_{\max a}) \quad : \quad Q_a \leq Q_{\max a}$$

This equation preserves the essential features (luxury

uptake, partial suppression of the uptake of a currently non-controlling nutrient) of CQTL theory without using the maximum luxury coefficient R_m, which is difficult to measure. $Q_{\max a}$ is the greatest amount of nutrient that a phytoplankton cell can store, and may be higher than the value (as given in Tett and Droop, 1988) for a limiting nutrient required by the theory of Droop et al. (1982) or the maximum observed in a chemostat. The standard value used in MP is a typical maximum N:C ratio observed in axenic algal batch cultures.

CQTL theory has been shown to apply to many types of micro-algae, and cyanobacteria, limited by the nutrient elements nitrogen, phosphorus, silicon and iron and the vitamin, B_{12} (Droop, 1983). It is thus general purpose. Nevertheless, each nutrient has special features that may need to be taken into account. In the case of nitrogen, considered here as the most likely limiting nutrient element in the sea, the special feature is the distinction between oxidised and reduced forms. This distinction between nitrate (plus nitrite) and ammonium is important in relation to water quality and the estimation of new, as opposed to recycled, production. Uptake of nitrate must be followed by its reduction, and so uses more energy and reducing power than does assimilation of ammonium. MP uses a relatively simple inhibition term (Harrison et al., 1987) to describe suppression of nitrate uptake by ammonium:

$$f_{in}(^{NH}S) = \frac{1}{1 + (^{NH}S / K_{in})} \quad : \quad {}^{NH}S \geq 0 \quad (21)$$

This term is applied to Eqn. (19), and may be contrasted with the treatment of the process in more detailed models (e.g. Flynn et al., 1997; Flynn and Fasham, 1997).

The next part of the parameterisation involves the ratio of chlorophyll to autotroph organic carbon, χ_a. The ratio is known to vary (from 0.04 to 1 mg chl (mmol C)$^{-1}$) as a function of temperature, irradiance and nutrient status (Baumert, 1996; Cloern et al., 1995; Geider et al., 1997; Laws and Bannister, 1980; Sakshaug et al., 1989). However, such variability was not dealt with explicitly by Droop's CQTL theory, perhaps because the chlorophyll content of cells of Pavlova lutheri appears to be rather invariant. Droop et al. (1982) showed that photosynthetic energy yield decreased as P. lutheri became increasingly nutrient-limited. Although Baumert (1996) suggested that microalgae have several strategies for adapting pho-

tosynthesis to changes in relative supplies of photons and nutrients, this version of MP deals implicitly with the light-nutrient interaction by means of a simple equation for the phytoplankton ratio of chlorophyll to carbon:

$$\chi_a = {}^{X}q_a^{N} Q_a \quad \text{mg chl (mmol C)}^{-1} \tag{22}$$

In earlier versions of MP (Smith and Tett, 2000; Tett and Walne, 1995) we allowed the microplankton chlorophyll: nitrogen ratio ${}^{X}q^{N}$, and by implication ${}^{X}q_a^{N}$, to vary between 2 and 1 mg chl (mmol N)$^{-1}$ as the microplankton nutrient quota varied from maximum to minimum. A similar approach was taken by Doney et al. (1996), who had 1 mg chl (mmol N)$^{-1}$ at saturating irradiance increasing to 2.5 mg chl (mmol N)$^{-1}$ at zero light. In this version of MP, however, we treat ${}^{X}q^{N}$ as a constant. Its value was estimated from data for algal cultures (Fig. 3). The pigment data (Caperon and Meyer, 1972; Levasseur et al., 1993; Sakshaug et al., 1989; Sosik and Mitchell, 1991; Sosik and Mitchell, 1994; Tett et al., 1985; Zehr et al., 1988) were obtained by 'standard' spectrophotometric or fluorometric methods, and thus overestimate chlorophyll a determined by precise chromatographic methods (Gowen et al., 1983; Mantoura et al., 1997). Nevertheless, they are appropriate for a model intended for comparison with observations made by the same 'standard' field methods. The culture data show a wide range of values of the ratio of chlorophyll to nitrogen without any clear overall pattern in relation to cell size, growth rate or irradiance (below 300 μE m^{-2} s^{-1}). Ignoring a few values of more than 7 mg chl (mmol N)$^{-1}$, the median was 2.2 mg (mmol N)$^{-1}$, and this was taken as an initial value for ${}^{X}q_a^{N}$. It may be compared with maximum values of 3.6 to 4.8 in a model which allowed the ratio of chlorophyll to nitrogen to vary dynamically (Geider et al., 1998).

CQTL theory does not include the effects of temperature (see Tett and Droop, 1988), and it is therefore assumed (as is almost universal, but not self-evident) that the temperature effect is multiplicative. Thus the maximum rate parameters $\mu_{\text{max}a}$ and $u_{\text{max}a}$ were given a Q_{10} of 2, a little higher than the value of 1.88 given by Eppley (1972). The temperature function in MP is:

$$f(\Theta) = \exp(k_{\Theta}(\Theta - 20°C)) \tag{23}$$

which can also be written as $Q_{10}((\Theta - 20°C)/10°C)$, so that k_{Θ} is $\ln(Q_{10})/10°C$. Eqn. (23) is thus essentially the same as Eppley's function. When the difference

between the actual and reference temperature is a small fraction of the Kelvin temperature, then Eqn. (23) is also a good approximation to the equation of Arrhenius:

$$f_A(\Theta) = \exp(k_A(\Theta_{ref}^{-1} - \Theta^{-1}))$$
$$\approx \exp(k_A(\Theta - \Theta_{ref}) / \Theta_{ref}^{2})$$

where the temperature is given in degrees Kelvin and Θ_{ref} is the reference temperature. k_{Θ} in Eqn (23) is equivalent to k_A / Θ_{ref}^{2} in the Arrhenius equation (and $\Theta_{ref}^{2} \approx \Theta\Theta_{ref}$). Table 4 lists autotroph parameter values used in MP.

HETEROTROPH EQUATIONS

The microheterotrophs in MP include several functional types of marine pelagic bacteria and protozoa, and the most general difficulty concerns how to make a simple parameterisation of the key processes in which these organisms are involved. A second difficulty is that their growth physiologies are less well known than those of algae. Although there have been many studies of feeding and growth efficiencies, there have been few that have examined carbon-nitrogen dynamics under well-controlled conditions, because of the difficulty of maintaining well-defined populations of delicate protozoa, or bacteria with largely unknown nutritional needs, under such conditions in the laboratory. The solution to these problems adopted by MP is to treat the heterotrophic component as (a) a single compartment, with properties (b) constrained (mathematically) by the need to conserve totals of elements and (physiologically) by the assumed tendency of the microheterotrophs to maintain an optimal elemental composition (Caron et al., 1990; Goldman et al., 1983).

Simplifying the description of heterotrophic processes

In the conceptual model for the implicit contents of MP (Fig. 4), bacteria are allocated to one of three categories:

- b_1, bacteria assimilating DOM leaked by phytoplankton during photosynthesis or cell lysis, and returning this DOM, less a respiratory tax, to the microplankton pool;
- b_2, bacteria assimilating DOM leaked from microplankters during messy feeding by protozoa, and returning this DOM, less a respiratory tax, to the

Table 4. Autotroph parameters used in MP and AH with nitrogen as potentially limiting nutrient.

		Ref	Value	Range	Units
$u_{max\,a}$	maximum relative rate of: nitrate uptake ammonium uptake	1	at 20°C 0.5 1.5	0.2-0.8 ?	mmol N $(mmol\ C)^{-1}\ d^{-1}$
K_S	half-saturation concentration for uptake of: nitrate ammonium	1	0.32 0.24	0.2-5 0.1-0.5'	mmol N m^{-3}
K_{in}	ammonium concentration giving half-inhibition of nitrate uptake	2	0.5	0.5-7	mmol N m^{-3}
$Q_{max\,a}$	maximum cell nitrogen content	1, 3	0.20	0.15-0.25	mmol N $(mmol\ C)^{-1}$
$Q_{min\,a}$	minimum cell nitrogen content	1	0.05	0.02-0.07	mmol N $(mmol\ C)^{-1}$
$\mu_{max\,a}$	maximum (nutrient-controlled) growth rate	1	2.0 at 20°C	1.2-2.9	d^{-1}
ε	PAR adsorption cross-section	4	0.02	0.01-0.04	m^2 (mg chl)$^{-1}$
Φ	photosynthetic quantum yield	5	40	40-60	nmol C μE^{-1}
k	converts $\varepsilon\,\Phi$ to typical units of α		0.0864		s d^{-1} nmol mmol^{-1}
α	photosynthetic efficiency, (derived from $k\,\varepsilon\,\Phi$)		0.069		mmol C (mg chl)$^{-1}$ d^{-1} $(\mu E\ m^{-2}\ S^{-1})^{-1}$
r_{0a}	basal respiration rate	6	0.05	0.03-0.41	d^{-1}
b_a	rate of increase of respiration with growth rate $(\Delta r_a/\Delta\mu_a)$	6	0.5	0.2-0.7	-
$x_{q_a}^{\,N}$	ratio of chlorophyll to nitrogen	7	2.2	0.5-7	mg chl (mmol N)$^{-1}$
k_Θ	temperature coefficient		0.069		°C^{-1}

Sources:
(1) Tett and Droop (1988) with standard values largely after Caperon and Meyer (Caperon and Meyer 1972a,b) for diatoms and prymnesiophytes.
(2) Standard value from Harrison et al. (1987); higher values from Maestrini et al (1986)
(3) Maximum value is that observed in a batch cultures of Nannochloropsis atomus by Setiapermana (1990) .
(4) Standard value for moderately clear coastal water; range related to water type (lowest in turbid coastal) (Tett 1990a).
(5) Tett (1990a) and Tett et al. (1993).
(6) See text and Table 2.   (7) See text and Fig. 3.

microplankton pool;
• b_3, dormant bacteria, making no contribution to any microplankton process, but adding carbon and nitrogen to the microplankton pool.

The argument that a given size of predator can ingest only a restricted range of prey sizes suggests considering (at least) two categories of protozoa:

• p_1, bacterivorous protozoa (zooflagellates and smaller ciliates) feeding on picoplanktonic autotrophs and heterotrophs;

• p_2, herbivorous and carnivorous protozoa (dinoflagellates and larger ciliates) feeding on autotrophs larger than picoplanktonic size and on the bac-

terivorous protozoa.

Microbial loop models represent several of these components by explicit compartments. The aim here is, however, to consider how this diversity of organisms might be approximated by a single microheterotroph compartment which can itself be subsumed into the microplankton compartment of MP.

The b_1 bacteria are, mainly, those attached to cell walls or found in the viscous, perhaps glycosaminoglycan (=mucopolysaccharide) enriched, layer surrounding each algal cell. In either case they will be consumed by grazers at the same time as their hosts. 'Extracellular production', or DOM excreted by micro-

algae, characteristically at high irradiances, is thought to be largely glycollate (Fogg, 1991) and so is a source of carbon with little nitrogen. If bacterial metabolism tends to preserve a balanced N:C ratio of 0.22 (Goldman and Denett, 1991), then bacterial respiration is likely to take a high proportion of this DOM, unless the bacteria have access to another source of organic matter rich in nitrogen, or unless they compete with algae for ammonium. The excreted DOM is assumed by MP to be immediately assimilated by b_1 bacteria, and is thus ignored because *these bacteria are treated as part of the autotroph component*, giving it a somewhat higher relative respiration rate than is measured in axenic cultures of micro-algae.

Another source of DOM is cell lysis after viral attack or during 'messy feeding' by protozoans. This DOM, with the C:N ratio of its source, is assumed in MP *to pass efficiently to the microheterotroph component*, although at the cost of a respiratory tax. The route, by way of b_2 bacteria and p_1 protozoans, *re-assimilates labile DOM before any can diffuse away from the region of production*. The assumption of efficient transfer requires that bacterial uptake rates are relatively high and do not saturate at the concentrations of labile DOM that might be generated by realistic rates of protozoan feeding. It is also assumed that the relative physical fluxes, given by terms such as φ_{Bb2}/B_{b2}, are the same for each microheterotroph component. This might be the case if all the components of Fig. 4 are conceived of as occurring together within packets of water defined by the Kolmogorov scale (Lazier and Mann, 1989) and dominated by viscous rather than inertial (including eddy-diffusive) forces.

The significance of the transfers shown in Fig. 4 can be examined by listing the processes which result in net gain or loss to the microheterotrophs as a whole. These processes are 'net ingestion', 'net mesozooplankton grazing loss', and 'total respiration'. Conversions which take place (or are assumed to take place) wholly within the heterotroph compartment can be ignored in constructing a unitary parameterisation of this compartment. Such conversions include: interchanges between b_2 and b_3, as some active bacteria become dormant, and *vice versa*; and the leakage of DOM during messy feeding and its subsequent rapid re-assimilation by b_2 bacteria.

'Net ingestion' is obtained by summing the protozoan consumption of autotrophs:

$$c_{p2}B_{p2}B_{a2} + c_{p1}B_{p1}B_{a1} \approx c_h B_h B_a \quad \text{mmol C m}^{-3}\text{d}^{-1} \quad (24)$$

where the suffixes $a2$ and $a1$ stand, respectively, for large (i.e. >2 µm) autotrophs (including associated heterotrophic b_1 bacteria) and small (picoplanktonic) autotrophs. The coefficients c_p refer to protozoan volume clearance rates, in m^3 (mmol protozoan C)$^{-1}$ d^{-1}. The simplification in Eqn. (24) results from the definitions that $B_a=B_{a2}+B_{a1}$ and $B_h=B_{p1}+B_{p2}+B_{b2}+B_{b3}$, and so requires that

$$c_h = c_{p1}(B_{p1}/B_h)(B_{a2}/B_a) + c_{p2}(B_{p2}/B_h)(B_{a1}/B_a) \quad (25)$$

The bulk heterotroph transfer coefficient c_h can be treated as a parameter if the proportions of the two kinds of protozoa, and the two kinds of autotroph, remain constant. Because of the effect of the value of B_{a1}/B_a on c_h, it seems likely that the value of c_{p2} normally has the strongest effect on c_h, giving way to c_{p1} only when picophytoplankton are the dominant autotrophs. Thus, the value of c_h must lie between $c_{p2}((B_{p1} + B_{p2})/B_h)$ and $c_{p1}((B_{p1} + B_{p2})/B_h)$.

'Net mesozooplankton grazing losses' from the microheterotrophs were assumed in Eqn. (9) and (12) to be $G\,B_h$ for carbon and $G\,q_h\,B_h$ for nitrogen, where G is the grazing pressure due to copepods and other mesozooplankton. This formulation assumes grazing without selection, a contestable assumption. It was discussed by Huntley (1981), who reported studies on *Calanus* spp. He concluded that for "phytoplankton > 20 µm in diameter there appeared to be no selective ingestion according to the size, shape or species." It is, however, likely that bacteria and small zooflagellates will be grazed less effectively than larger microplankton by mesozooplankton, and thus that the grazed flux from the heterotrophs will be less than $G\,B_h$ in the ratio $B_{p'}/B_h$, where $B_{p'}$ includes B_{p2} and some or none of B_{p1}. This 'undergrazing' of microheterotrophs may need further consideration.

'Total heterotroph respiration' is the sum of contributions from b_2 bacteria and the protozoans; b_3 bacterial respiration is assumed insignificant, and b_1 respiration is included in that of the autotrophs. Thus,

$$r_h B_h = r_{p1}B_{p1} + r_{p2}B_{p2} + r_{b2}B_{b2} \quad \text{mmol C m}^{-3}\text{d}^{-1} \quad (26)$$

If it is assumed that the respiration of each component is linearly related to growth rate, then

$$r_h = r_{0h} + b_h\mu \quad \text{d}^{-1} \quad (27)$$

where μ is microheterotroph and microplankton relative growth rate and

$$r_{0h} = r_{0b2}(B_{b2}/B_h) + r_{0p1}(B_{p1}/B_h) + r_{0p2}(B_{p2}/B_h)$$

$$b_h = b_{b2}(B_{b2}/B_h)(\mu_{b2}/\mu) + b_{p1}(B_{p1}/B_h)(\mu_{p1}/\mu)$$
$$+ b_{p2}(B_{p2}/B_h)$$

Some evidence for linearity comes from Fenchel and Findlay (1983), who reviewed published estimates of protozoan respiratory rates and concluded that during "balanced growth, energy metabolism is nearly linearly proportional to the growth rate constant". The expansion for b_h in Eqn. (27) contains the multiplying terms (μ_{b1}/μ) and (μ_{p1}/μ) which imply that it is necessary for the intrinsic growth rate of the bacterial population to exceed that of the bacterivore population, and their rate that of the protistivores, in order that all the microheterotroph components may in MP change at the same relative rate as the microplankton as a whole. Given the assumption of fixed ratios of components, r_{0h} and b_h can be treated as parameters, with the value of r_{0h} within the range defined by r_{0b2}, r_{0p1} and r_{0p2} unless B_{b3} is large. The value of b_h, however, will be larger than the component values b_{b2}, b_{b1} and b_{p2}, because of the effects of component growth rates. This additional 'respiratory tax' paid by the microheterotroph compartment is the main device for parameterising the extra losses resulting from several trophic transfers.

Growth of the microheterotroph compartment under C or N control

It is assumed that heterotroph (biomass-related) growth is either carbon or nitrogen limited,

$$\mu_h = \min\{\mu_C, \mu_N\} \quad d^{-1} \tag{28}$$

Under carbon limitation,

$$\mu_C = i_h - r_h \quad d^{-1} \tag{29}$$

where i_h ($=c_h B_a$) is food intake rate per unit heterotroph carbon biomass, the result of ingestion of particles or uptake of dissolved organic matter (DOM). Respiration rate r_h has already been assumed to be related to growth rate (Eqn. 27), leading to:

$$\mu_C = (i_h - r_{0h})/(1 + b_h) \quad d^{-1} \tag{30}$$

Under nitrogen limitation,

$$\mu_N = (i_h Q_a - {}^N r_h)/q_h \quad d^{-1} \tag{31}$$

where Q_a is food N:C ratio, q_h is heterotroph N:C

ratio and $^N r_h$ is heterotroph biomass-related rate of ammonium excretion. It is assumed that, unlike the autotrophs, the microheterotrophs have a constant N:C ratio, and that, under nitrogen-limited conditions, ammonium excretion rate is related to growth rate by the same parameters that control respiration rate under C-limited conditions:

$$^N r_h = q_h\, r_h = q_h(r_{0h} + b_h\, \mu_N)$$

$$\text{mmol N (mmol C)}^{-1} d^{-1} \tag{32}$$

Substituting this in Eqn. (31) gives:

$$\mu_N = (i_h(Q_a/q_h) - r_{0h})/(1 + b_h) \tag{33}$$

Which of μ_N and μ_C is lowest depends on the N:C ratio of the food in relation to the optimal N:C ratio of heterotrophs. Carbon limitation must obtain when $Q_a > q_h$, and N limitation when $Q_a < q_h$, since in the latter case the food is poorer in N than the microheterotrophs that ingest it. A form of the growth equation covering both limiting conditions is:

$$\mu_h = (i_h\, q^* - r_{0h}) / (1 + b_h) \quad d^{-1} \tag{34}$$

where

$$q^* = \begin{bmatrix} 1 & : & Q_a \ge q_h & [C - limiting] \\ Q_a/q_h & : & Q_a < q_h & [N - limiting] \end{bmatrix}$$

Carbon respiration and ammonium excretion must be set by the difference between food intake and the growth need:

$$r_h = i_h - \mu_h \quad d^{-1} \tag{35}$$

$$^N r_h = i_h\, Q_a - \mu_h\, q_h \quad \text{mmol N (mmol C)}^{-1} d^{-1} \tag{36}$$

Substituting i_h by $(\mu_h (1 + b_h) + r_{0h}) / q^*$ from Eqn. (34), gives:

$$r_h = \mu_h(((1 + b_h) / q^*) - 1) + (r_{0h} / q^*) \quad d^{-1}$$

$$= \begin{bmatrix} \mu_h(((1 + b_h)q_h/Q_a) - 1) + (r_{0h}q_h/Q_a) & [N - limiting] \\ \mu_h b_h + r_{0h} & [C - limiting] \end{bmatrix} \tag{37}$$

$$^N r_h = \mu_h(((1 + b_h) Q_a / q^*) - q_h) + (r_{0h} Q_a / q^*)$$

$$= \begin{bmatrix} \mu_h((1 + b_h)Q_a - q_h) + (r_{0h}Q_a) & [C - limiting] \\ (\mu_h b_h + r_{0h})q_h & [N - limiting] \end{bmatrix}$$

$$\text{mmol N (mmol C)}^{-1} d^{-1} \tag{38}$$

Table 5. Heterotroph rate equations used in MP

Growth	$\mu_h = (i_h q^* - r_{0h})/(1 + b_h)$ where $$q^* = \begin{bmatrix} 1 & : & Q_a \geq q_h \\ Q_a/q_h & : & Q_a < q_h \end{bmatrix}$$	d^{-1}
C ingestion	$i_h = c_h B_a$ [MP-cancels out]	d^{-1}
net N uptake	$u_h = \mu_h q_h = i_h Q_a - {}^N r_h$	mmol N (mmol C)$^{-1}$ d^{-1}
NH$_4^+$ excretion	${}^N r_h = i_h Q_a - \mu_h q_h$ $$= \begin{bmatrix} \mu_h((Q_a - q_h) + b_h Q_a) + r_{0h} Q_a & [C-limiting] \\ \mu_h b_h q_a + r_{0h} q_h & [N-limiting] \end{bmatrix}$$	mmol N (mmol C)$^{-1}$ d^{-1}
Respiration	$r_h = i_h - \mu_h$ $$= \begin{bmatrix} \mu_h b_h + r_{0h} & [C-limiting] \\ \mu_h(((1 + b_h)q^*) - 1) + r_{0h}/q^* & [N-limiting] \end{bmatrix}$$	d^{-1}
Temperature	$f(\Theta) = \exp(k_\Theta(\Theta - 20^\circ C))$	

Eqn. (37) shows that more carbon is respired under N-limiting conditions, and Eqn. (38) shows that more nitrogen is mineralised under C-limiting conditions. In effect, the N:C ratios of food and heterotroph are harmonised by 'burning off' the unwanted portion of the excess element. Finally, the equation for nitrogen assimilation, or net uptake, is:

$$u_h - \mu_h q_h = i_h Q_a - {}^N r_h \quad \text{mmol N (mmol C)}^{-1} \text{ d}^{-1}$$
<div align="right">(39)</div>

The heterotroph N:C ratio q_h is an important parameter. Protozoan optima of $0.15 - 0.16$ (Caron et al., 1990; Davidson et al., 1995) and bacterial optima of 0.22 mol N (mol C)$^{-1}$ (Goldman and Dennett, 1991), suggest a standard value for q_h of 0.18 mol N (mol C)$^{-1}$.

Table 5 summarises the microheterotroph equations. Unlike the autotroph equations, these have not been empirically validated, but follow from assuming that (i) the protozoan-bacterial mixture has a constant composition, and (ii) exhibits threshold-limited growth with mineralisation as the only loss of C and N. They predict that growth efficiency, defined (for $i_h >> r_{0h}$) as $\mu_h / i_h = q^*/(1 + b_h)$, must be less under nutrient-controlled conditions (when $q^* = Q_a/q_h < 1$) than under C-controlled conditions. Evidence cited below suggests that this is the case for some single-species populations and for mixtures of micro-organisms. The

rest of this section considers the remaining heterotroph parameters (r_{0h}, b_h and c_h).

Respiration

Eqn. (30) embodies the assumption of linearly growth-dependent respiration for carbon-limited microheterotrophs. Here is the growth equation with protozoan or bacterial subscripts:

$$\mu_{Cp} = (i_p - r_{0p})/(1 + b_p) \quad d^{-1} \tag{40a}$$

$$\mu_{Cb} = (i_b - r_{0b})/(1 + b_b) \quad d^{-1} \tag{40b}$$

where i_p is the relative ingestion rate (d^{-1}) at which protozoa ingest biomass. The analogous i_b is the relative rate at which bacteria assimilate DOM.

Fuller (1990) studied ingestion and growth in 12 combinations of marine protozoans and algae in batch cultures (Table ι Gross Growth Efficiency (GGE) was estimated by dividing predator specific growth rate by specific food ingestion rate, using maximum rates when accurately estimated. In 6 cases he obtained significant regressions of growth rate on ingestion, of general form $\mu = a + b_i$ i. These may be compared with Eqn. (40a) for the carbon-limiting case, when $b_i = 1/(1 + b_p)$. When nitrogen limits growth, b_i should be smaller. Thus, it is Fuller's higher values of b_i that point to the most appropriate values of b_p for MP: between 1 and 3. The data cannot be used

Table 6. Dependence of growth rate on ingestion rate (Fuller, 1990)

Grazer/food	GGE	(s.e.)	regression, $\mu = a+b_i i$				b_p
			a, d^{-1}	(s.e.)	b_i	(s.e)	
Euplotes sp. & Dunaliella primolecta	0.02	(0.01)					*
Euplotes & Oxyrrhis marina	0.04	(0.01)	0.01	0.01	0.023	0.004	*
Euplotes & Oxyrrhis & Dunaliella	0.29	(0.03)					2.5
Oxyrrhis & Dunaliella tertiolecta	0.55	(0.06)	0.05	(0.13)	0.49	(0.10)	1.0
Oxyrrhis & Brachiomonas submarina	0.47	(0.04)	0.21	0.07	0.25	0.05	1.1, 3.0
Oxyrrhis & Chlamydamonas spreta	0.08	(0.01)	0.05	0.07	0.07	0.03	*
Oxyrrhis & Nannochloropsis oculata	0.42	(0.05)	0.06	0.18	0.33	0.11	1.4, 2.0
Pleurotricha sp. & Brachiomonas	0.07	(0.01)					*
Strombidium sp. & Pavlova lutheri	0.24	(0.05)					3.2
Uronychia sp. & Dunaliella	0.02	(0.01)					*
Uronychia & Oxyrrhis	0.10	(0.03)					*
Uronychia & Oxyrrhis & Dunaliella	0.32	(0.03)					2.1

GGE is 'Gross Growth Efficiency'; the slope coefficient b_p = GGE^{-1} - 1. Additionally, where regression coefficients a and b_i were given by Fuller, a second value of the slope was estimated from $b_p = b_i^{-1}$-1. Low values of b_p were assumed to represent N-limited conditions, in which $b_i \approx (Q_a/q_p)/(1+b_p)$; hence these b_p values are not given as Fuller did not report food nitrogen.

to estimate r_{0p}, because the regression intercepts are positive (they should be negative), although in most cases not significantly so.

Hansen (1992) estimated a growth/ingestion yield of 0.36 for the heterotrophic dinoflagellate *Gyrodinium spirale* feeding on the autotrophic dinoflagellate *Heterocapsa triquetra*. This value corresponds to b_p=1.8, within the range of 1 to 3 taken from Fuller's results. However, the corrsponding basal rates were large: even *Gyrodinium* populations previously kept on a maintenance ration, and then starved, decayed at 0.19 d^{-1}.

Fenchel and Findlay (1983) reviewed published estimates of protozoan respiratory rates. They concluded that "the data show a surprisingly large variance when similarly sized cells or individual species are compared. This is attributed to the range of physiological states in the cells concerned. The concept of basal metabolism has little meaning in protozoa. During balanced growth, energy metabolism is nearly linearly proportional to the growth rate constant; at the initiation of starvation, metabolic rate rapidly declines." Later in the paper they state that in "small [starved] protozoa the respiratory rate per cell may eventually decrease to 2–4% of that in growing cells." This contrasts with Hansen's decay rate for starved *Gyrodinium*. MP follows Fenchel and Findlay in assuming a low basal respiration rate. As Fuller's pelagic protozoa (*Strombidium, Pleurotricha* and *Oxyrrhis*) had maximum growth rates of 0.4 to 1.3 d^{-1}, the value of the basal respiratory rate r_{0p} was taken as 0.02

d^{-1}. Fenchel and Findlay estimated food conversion efficiency ($\approx b_i$ when r_{0p} small) in the range 0.4 to 0.6 for protozoa growing under good conditions; these values support the use of a value of about 1.0 for b_p.

Caron *et al.* (1990) tabulated ranges of GGE from published studies of 25 single species and mixed assemblages. The minima (for nutrient-limited conditions?) range from 1 to 64% with a median of 12%, the maxima (for C-limited conditions?) from 11 to 82% with a median of 49%. The latter value corresponds to b_p of 1.04.

As in the case of protozoan b_p, bacterial b_b can be estimated from growth efficiencies if basal respiration is assumed low. Goldman and Dennett (1991) obtained GGE of 47% to 60% for natural populations of marine bacteria grown with added sources of nitrogen and carbon. Calculating b_b from (GGE^{-1} - 1) gives values between 0.7 and 1.2. Danieri *et al.* (1994) obtained a wide range of efficiencies for bacterial growth in mesocosms and the Bay of Aarhus, but most of their values were between 15% and 45%. Growth with added glycine had mean GGE of 32%, whereas growth on added inorganic nutrients had mean GGE of 16%. Taking 32–45% for C-limited bacteria, b_b = 1.2 to 2.1.

The assumption that starved bacteria become dormant is equivalent to supposing that r_{0b} is zero. Hence the standard value of r_{0b} will be taken as the protozoan value of 0.02 d^{-1}. The 'best' estimates of b_p and b_b are likely to be the lowest observed values,

of about 1.0; however, b_h is required to be larger than this, and so the standard value is set at 1.5.

Ingestion and clearance

Although terms in c_h cancel in the equations of MP, values will be useful in examining heterotroph-autotroph interactions. On theoretical grounds, protozoan specific ingestion rate i_p should be a saturation function of food concentration B_f:

$$i_p = c_p B_f \left(1/(1 + (B_f/K_{Bf}))\right) \quad \mathrm{d}^{-1} \tag{41}$$

The explanation is that clearance slows as animals spend more time digesting food. Thus c_p is a maximum clearance rate. Writing $i_p = c_p B_f$ is a linearisation which is appropriate for the low food concentrations $(B_f < K_{Bf})$ that are typical of most natural waters. When c_p is not given explicitly, it can be calculated from the solution of Eqn. (41) for $(B_f \gg K_{Bf})$.

$$c_p = i_{\max p}/K_{Bf} \quad \mathrm{m}^3 \text{ (mmol protozoan C)}^{-1}\mathrm{d}^{-1}$$

When examined over a wide range of cell sizes, biomass-related rates of clearance and ingestion decrease with increasing cell size (Fuller, 1990). However, there is considerable variability amongst organisms of similar size. I have relied on the data (Table 7) of Fuller (1990), who measured ingestion rates of several laboratory-grown marine ciliates, and a dinoflagellate, feeding on various algae. In some cases Fuller found that food concentration had to exceed a threshold before grazing took place. Adding this threshold B_{0f} to the half-saturation concentration K_{Bf}

gives estimates of the food concentration above which ingestion begins to saturate; the median value is 30 mmol C m^{-3}. According to Table 7, the median protistivorous protozoan ingests a maximum of 3.15 times its own biomass daily, and has a maximum clearance rate of 0.21 m^3 (mmol protozoan C)$^{-1}$d^{-1}. However, Fuller's values ranged from 0.026 to 0.69 m^3 (mmol C)$^{-1}$ d^{-1} d^{-1}, which may be understood as demonstrating the difficulty of making the measurements as well as showing the effects of dependence of clearance or ingestion rates on predator prey size, prey size, and prey nutritional status.

For comparison, the results of a study (Davidson et al., 1995) of the dinoflagellate *Oxyrrhis marina* feeding on the prymnesiophyte alga *Isochrysis galbana*, gives a (maximum) clearance rate of 0.009 m^3 (mmol C)$^{-1}$ d^{-1}, when the data are appropriately converted. Grazing data (Hansen, 1992) for the dinoflagellate *Gyrodinium spirale* feeding on the (autotrophic) dinoflagellate *Heterocapsa triquetra* gives 0.038 m^3 (mmol C)$^{-1}$ d^{-1}. Observations of tintinnid ciliates feeding on small autotrophic flagellates give clearance rates just above 1.0 m^3 (mmol C)$^{-1}$ d^{-1} (Heinbokel, 1978). Caron et al. (1985) reported a study of the zooflagellate *Paraphysomonas imperforata*. After conversion to my units, clearance rates on a diet of bacteria ranged from 0.021 to 0.040 m^3 (mmol C)$^{-1}$ d^{-1}, those on a diet of the anomalous diatom *Phaeodactylum tricornutum* ranged from 0.024 to 0.061 m^3 (mmol C)$^{-1}$ d^{-1}. Literature reviewed by Caron et al. gave a very wide range of bacterivore clearance rates, from 0.05 to 4.5 m^3 (mmol C)$^{-1}$ d^{-1}.

Given these ranges, and the uncertainties involved in deriving c_h from c_p, the standard value of c_h has

Table 7. Ingestion and related parameters (Fuller, 1990)

Grazer/food	$i_{\max p}$, d^{-1}	K_{Bf}, mmol m^{-3}	B_{0f}, mmol m^{-3}	$K_{Bf}+B_{0f}$, mmol m^{-3}	c_p, dm^3 mmol^{-1} d^{-1}
Euplotes sp. & Dunaliella primolecta	3.32	9.5	6.4	16	348
Euplotes & Oxyrrhis marina	4.81	172	0	172	26
Euplotes & Oxyrrhis & dunaliella	2.24	3.2	33	36	694
Oxyrrhis & Dunaliella tertiolecta	2.02	9.7	1.6	11	208
Oxyrrhis & Brachiomonas submarina	2.10	9.9	3.7	14	211
Oxyrrhis & Chlamydamonas spreta	4.80	22	5.1	27	215
Oxyrrhis & Nannochloropsis oculata	2.26	8.5	0.8	9	268
Pleurotricha sp. & Brachiomonas	8.32	2.5	65	68	?
Strombidium sp. & Pavlova lutheri	2.98	-	-	-	-
Uronychia sp. & Dunaliella	4.74	66	-1.6	64	72
Uronychia & Oxyrrhis	3.56	58	6.8	65	61
Uronychia & Oxyrrhis & dunaliella	2.42	16	14	30	149
Median	3.15	10	5	30	210

Table 8. Heterotroph parameters used in MP

		Std value	Range	Units
c_h	(maximum) transfer rate, expressed as clearance, relative to heterotroph biomass [temperature: $c_h = c_h[20°C]f(\Theta)$]	0.2 at 20°C	0.01-4.5	m^3 (mmol C)$^{-1}$ d^{-1}
q_h	Nitrogen: carbon ratio	0.18	0.15-0.22	mmol N (mmol C)$^{-1}$
r_{0h}	Basal (biomass-related) respiration rate	0.02	0.00-0.05	d^{-1}
b_h	Slope of graph of r_h on μ_h	1.5	1-3	
k_Θ	Temperature coefficient	0.069		°C^{-1}

been taken as 0.2 m^3 (mmol C)$^{-1}$ d^{-1}, close to the median of Fuller's value. Table 8 lists the full set of microheterotroph parameter values.

MICROPLANKTON RATE EQUATIONS

The microplankton equations derived in the section of microplankton equations of state are summarised in Table 9. Our purpose now is to derive versions of the equations for growth and nutrient uptake which do not include explicit autotroph or heterotroph variables such as μ_a or $^N r_h$, but only microplankton variables and parameters (which can be recognised by the absence of a or h subscripts). In this version of MP, with explicit η, most microplankton parameters will be derived from autotroph and heterotroph parameters, using the assumption of constant η.

The starting point is the equation for the intrinsic growth rate of the microplankton. This rate must be the same as that of the microheterotrophs if autotroph and heterotroph biomasses are to remain in constant proportion:

$$\mu = \mu_h = \mu_a(1 - \eta) - r_h\eta \qquad d^{-1} \qquad (42)$$

Under light-limiting conditions, μ_a is given by Eqn. (17) and so Eqn. (42) is

$$\mu = (\alpha \chi_a I - r_a)(1 - \eta) - r_h\eta \qquad d^{-1} \qquad (43)$$

where α is photosynthetic efficiency (mmol C fixed (mg chl)$^{-1}$ d^{-1} (unit of irradiance)$^{-1}$) and χ_a is the ratio of chlorophyll to autotroph carbon. (Photosynthetic efficiency is not subscripted when related to chlorophyll: the same value applies to both autotrophs and the microplankton because heterotrophs do not add chlorophyll to the microplankton total). For light-limited autotrophs, respiration rate is a function of growth rate (Eqn. 18):

$$r_a = \begin{bmatrix} r_{0a} + b_a\mu_a: & \mu_a > 0 & d^{-1} \\ r_{0a} & : & \mu_a \le 0 \end{bmatrix} \qquad (44)$$

It is convenient to assume that autotrophs and heterotrophs are always in analogous physiological states - i.e. both are either simultaneously nitrogen-limited or simultaneously carbon-limited at a given time. This excludes some possible combinations of limitation states (Fig. 5). It is not a fundamental requirement, but serves to simplify MP equations, avoid discontinuities, and reduce the number of logical tests to be made during numerical simulations. Thus, assuming that heterotroph carbon-limitation always corresponds to autotroph light-limitation, the simplest form

$$r_h = r_{0h} + b_h \mu \qquad d^{-1} \qquad (45)$$

of Eqn. (37) can be used for respiration in Eqn. (43):

Table 9. MP equations derived from equations of state

Carbon biomass	$\beta_B = (\mu - G)B$	mmol C m^{-3}d^{-1}
where: growth rate	$\mu = \mu_h = \mu_a(1 - \eta) - r_h\eta$	d^{-1}
Nitrogen in biomass	$\beta_N = uB - GN = (u - GQ)B$	mmol N m^{-3}d^{-1}
where: nutrient quota	$Q = Q_a(1 - \eta) + q_h\eta$	mmol N (mmol C)$^{-1}$
uptake rate	$u = u_a(1 - \eta) - ^N r_h\eta$	mmol N (mmol C)$^{-1}$d^{-1}

$Q_{\max a} = 0.20$

heterotrophs C-limited

$Q_a \geq q_h$

autotrophs light-limited

$\mu_a = f(I)$

$q_h = 0.18$

autotrophs N-limited

$\mu_a = f(Q_a)$

heterotrophs N-limited

$Q_a < q_h$

$Q_{\min a} = 0.05$

axis of Q_a, mmol N (mmol C)$^{-1}$, as food for heterotrophs

$\mu_h > 0$

$\mu_a > 0$

$\mu = 0$

$\mu_h < 0$

$\mu_a < 0$

$\mu = -r_0$

axis of microplankton growth rate μ (d^{-1})

in this region,
autotroph growth in excess of maintenance
supplies maintenance needs of heterotrophs
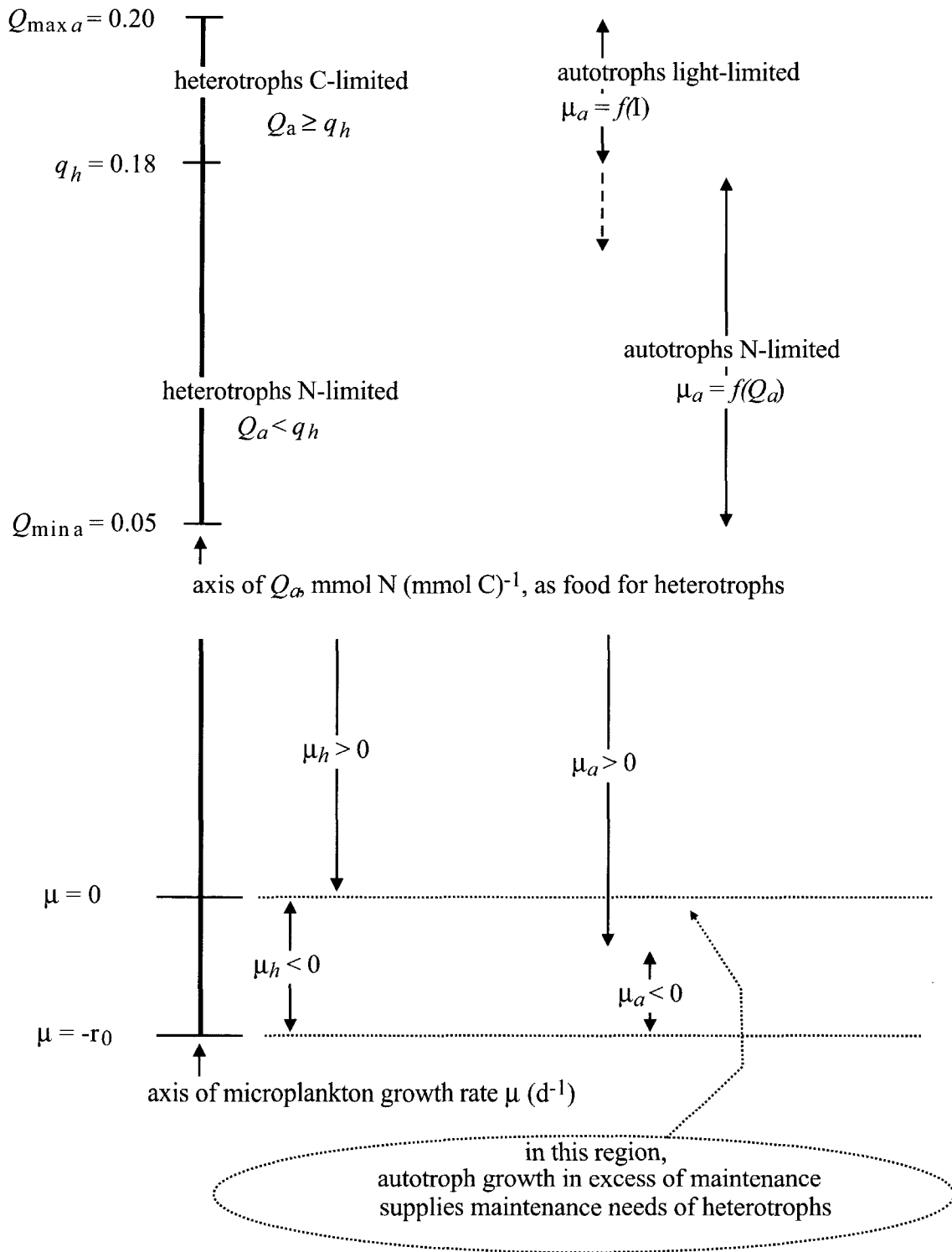
Fig. 5. Limitations states of MP. The diagram concerns the assumption that heterotrophs and autotrophs are always in the same state of limitation. The shaded regions show combinations of limitation states that are excluded in the interests of simplicity.

$$\mu = (\alpha \chi_a I - (r_{0a} + b_a \mu_a))(1 - \eta) - (r_{0h} + b_h \mu) \eta$$

growth rate:

$$\text{d}^{-1} \qquad (46)$$

$$\mu_a = (\mu + r_h \eta)/(1 - \eta) \quad \text{d}^{-1}$$

Eqn. (42) can be re-arranged to give autotroph

Combining this with Eqn. (45) results in:

$$\mu_a = (\mu(1 + b_h\eta) + r_{0h}\eta)/(1 - \eta) \quad d^{-1}$$

which can be substituted in Eqn. (46) to give:

$$\mu = (\alpha\chi_a I - (r_{0a} + b_a((\mu(1 + b_h\eta)$$
$$+ r_{0h}\eta)/(1 - \eta)))) (1 - \eta) - (r_{0h} + b_h\mu)\eta$$

This is not as complicated as it seems. The autotroph and heterotroph terms can be re-written as microplankton parameters, leading to:

$$\mu = (\alpha I \chi - r_0)/(1 + b) \quad d^{-1} \quad (47)$$

where the terms are:
the ratio of chlorophyll to microplankton carbon,

$$\chi = \chi_a(1 - \eta) \quad \text{mg chl(mmolC)}^{-1}$$

$$= \begin{bmatrix} {}^X q_a^N(Q_{min} - q_h\eta) & : Q \le Q_{min} \\ {}^X q_a^N(Q - q_h\eta) & : Q_{min} < Q < Q_{max} \\ {}^X q_a^N(Q_{max} - q_h\eta) & : Q \ge Q_{max} \end{bmatrix}$$

The basal respiration rate,

$$r_0 = r_{0a}(1 - \eta) + r_{0h}\eta(1 + b_a) \quad d^{-1}$$

and the respiration slope,

$$b = \begin{bmatrix} b_a(1 + b_h\eta) + b_h\eta & : \mu > 0 \\ 0 & : \mu \le 0 \end{bmatrix}$$

In this equation, the chlorophyll: carbon ratio has been expanded using the two equivalencies:

$$\chi_a = {}^X q_a^N Q_a \quad \text{and} \quad Q = Q_a(1 - \eta) + q_h\eta$$

See below for Q_{max} and Q_{min}. Finally, the condition when $\mu \le 0$ is a simplification of two conditions ($\mu \le 0$ and $\mu_a \le 0$) (see Fig. 5). As a result of the simplifications, Eqn. (47) has essentially the same form as the autotroph Eqn. (17), but its parameters take account of the heterotroph contributions to respiration and biomass.

Under nitrogen-limiting conditions, Eqn. (42) becomes:

$$\mu = \mu_{maxa}(1 - (Q_{min\,a}/Q_a))(1 - \eta) - r_h\eta \quad d^{-1} \quad (48)$$

by inclusion of Eqn. (15). Q_a is the (variable) autotroph cell quota. Rearrangement of the Eqn. (13a) for Q gives:

$$Q_a = (Q - q_h\eta)/(1 - \eta) \quad \text{mmol N (mmolC)}^{-1}$$

Substituting this into Eqn. (48), and writing the result in terms of microplankton parameters, results in:

$$\mu = \mu_{max} f_1(Q) - r_h\eta \quad d^{-1}$$

where

$$f_1(Q) = (Q - Q_{min})/(Q - q_h\eta) \quad : Q \ge Q_{min}$$

$$\mu_{max} = \mu_{max\,a}(1 - \eta) \quad d^{-1}$$

$$Q_{min} = Q_{min\,a}(1 - \eta) + q_h\eta \quad \text{mmolN(mmolC)}^{-1}$$

Q_{min} is the minimum microplankton nutrient quota. μ_{max} is the limit for microplankton relative growth rate as Q becomes infinite. The final steps are the expansion of the limits and r_h. The simplifying assumption that heterotrophs as well as autotrophs are nitrogen-limited, allows use of a cut-down version of Eqn. (37):

$$r_h = \mu_h(((1 + b_h)/q^*) - 1) + (r_{0h}/q^*) \quad d^{-1}$$

where $q^* = Q_a/q_h$
Attempting a treatment in terms of microplankton variables:

$$\mu = \mu_{max} f_1(Q)/(1 + ((1 + b_h) f_2(Q) - \eta) - r_{0h} f_2(Q)$$
$$d^{-1} \quad (49)$$

where

$$f_1(Q) = \begin{bmatrix} (Q - Q_{min})/(Q - q_h\eta) & : Q \ge Q_{min} \\ 0 & : Q < Q_{min} \end{bmatrix}$$

$$f_2(Q) = \begin{bmatrix} q_h\eta(1 - \eta)/(Q - q_h\eta) & : Q \ge Q_{min} \\ q_h\eta(1 - \eta)/(Q_{min} - q_h\eta) & : Q < Q_{min} \end{bmatrix}$$

Eqn. (49) is complicated, and can be approximated (Fig. 6) as:

$$\mu = \mu_{max} f_3(Q) \quad (50)$$

where

$$\mu_{max} = \mu_{max\,a}(1 - \eta)/(1.2 - \eta) \quad d^{-1}$$

$$f_3(Q) = (Q - Q_{min})/Q$$

$$= \begin{bmatrix} 1 - (Q_{min}/Q) & : Q \ge Q_{min} \\ 0 & : Q < Q_{min} \end{bmatrix}$$

$$Q_{min} = Q_{min\,a}(1 - \eta) + q_h\eta \quad \text{mmol N (mmolC)}^{-1}$$
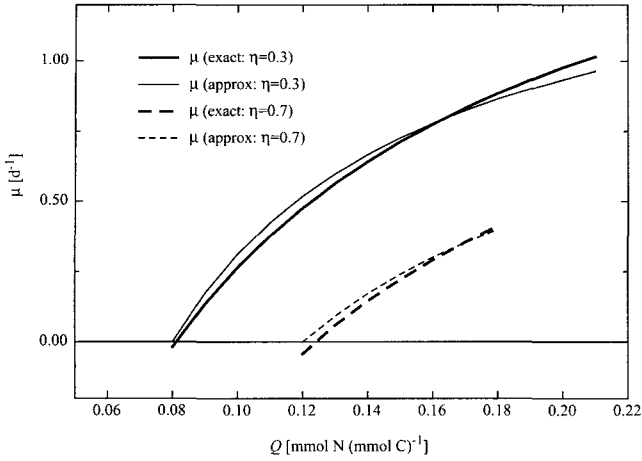
Fig. 6. Growth rate. Comparisons of microplankton nutrient-limited growth according to the more exact equation (49) and the approximation (50).

This is the form used in earlier versions of MP (Smith and Tett, 2000; Tett 1990b; Tett and Grenz, 1994; Tett and Walne, 1995), although the definitions of μ_{max} and Q_{min} were, in most cases, implicit (i.e. parameter values for algae were adjusted for the presence of microheterotrophs without taking explicit account of η). $f_3(Q)$ is the cell-quota function of Droop (1968). The term $(1.2 - \eta)$ in the definition of μ_{max} was obtained empirically, and the term $r_{0h} f_2(Q)$ for the effect of microheterotroph basal respiration on growth was omitted as insignificant. No upper limit is applied in $f_3(Q)$ because the function's value asymptotically approaches 1.

The final step is to deal with uptake of nutrients. In MP, autotrophs can take up both nitrate and ammonium:

$$u = u_a(1 - \eta) - {}^N r_h \eta$$
$$= ({}^{NO}u_a + {}^{NH}u_a)(1 - \eta) - {}^N r_h \eta$$
$$\text{mmol N (mmol C)}^{-1} \text{d}^{-1} \qquad (51)$$

It is assumed that nitrate uptake can be inhibited by the presence of ammonium as well as by a high cell quota, but never involves excretion. Substituting microplankton for autotroph parameters in Eqn. (20) results in:

$$^{NO}u = {}^{NO}u_a(1 - \eta) = {}^{NO}u_{max} \, f({}^{NO}S) f_{in}({}^{NH}S) f_{in1}(Q)$$
$$(52)$$

where

$$^{NO}u_{max} = {}^{NO}u_{max\,a}(1 - \eta) \quad \text{mmolN(mmolC)}^{-1}\text{d}^{-1}$$

$$f({}^{NO}S) = {}^{NO}S / (K_{NOS} + {}^{NO}S)$$

$$f_{in}({}^{NH}S) = 1 / (1 + ({}^{NH}S + K_{in}))$$

$$f_{in1}(Q) = \begin{bmatrix} 1 - ((Q - q_h\eta)/(Q_{max} - q_h\eta)) \end{bmatrix} : Q \le Q_{max}$$
$$\begin{bmatrix} 0 \end{bmatrix} : Q > Q_{max}$$

$$Q_{max} = Q_{max\,a}(1 - \eta) - q_h\eta \quad \text{mmolN(mmolC)}^{-1}$$

Q_{max} is the maximum nitrogen:carbon ratio which should occur in the microplankton. The nitrate and ammonium functions are meaningful only for $S \ge 0$, and $f_{in1}(Q)$ only for $Q \ge q_h$.

Ammonium uptake is not inhibited by nitrate, but should include the heterotroph excretion term. It could also be negative if the microplankton nitrogen quota exceeds a maximum. Rewriting Eqn. (20) for ammonium, and with microplankton parameters:

$$^{NH}u = {}^{NH}u_{max} \, f({}^{NH}S) \, f_{in2}(Q) - {}^N r_h \eta \qquad (53)$$

where

$$^{NH}u_{max} = {}^{NH}u_{max}(1 - \eta) \quad \text{mmolN(mmolC)}^{-1}\text{d}^{-1}$$

$$f({}^{NH}S) = \begin{bmatrix} {}^{NH}S/(K_{NHS} + {}^{NH}S) \end{bmatrix} : Q \le Q_{max}$$
$$\begin{bmatrix} 1 \end{bmatrix} : Q > Q_{max}$$

$$f_{in2}(Q) = 1 - ((Q - q_h\eta)/(Q_{max} - q_h\eta)) : Q \ge Q_{min}$$

$$Q_{max} = Q_{max\,a}(1 - \eta) + q_h\eta \quad \text{mmolN(mmolC)}^{-1}$$

The term for ammonium excretion by microheterotrophs can be taken from Eqn. (38) by replacing q^* defined with autotroph parameters by q^+ defined with microplankton parameters:

$$^N r_h = \mu(((1 + b_h)q^+ - q_h) + r_{0h}q^+)$$
$$\text{mmolN(mmolC)}^{-1}\text{d}^{-1} \qquad (54)$$

where

$$q^+ = \begin{bmatrix} (Q - q_h\eta)/(1 - \eta) : Q \ge q_h \end{bmatrix}$$
$$\begin{bmatrix} q_h \end{bmatrix} : Q < q_h$$

This is complicated because ${}^N r_h$ is a function of two variables, Q and $\mu(I, Q)$. Test cases (Fig. 7) show that uptake predicted by Eqn. (53), with ${}^N r_h$ defined by Eqn. (54), does not become negative. This is because excreted ammonium leads to an increase in the ambient concentration and so gives rise to additional uptake. Thus, in accord with the view that excreted material (but not respired carbon) is recy-
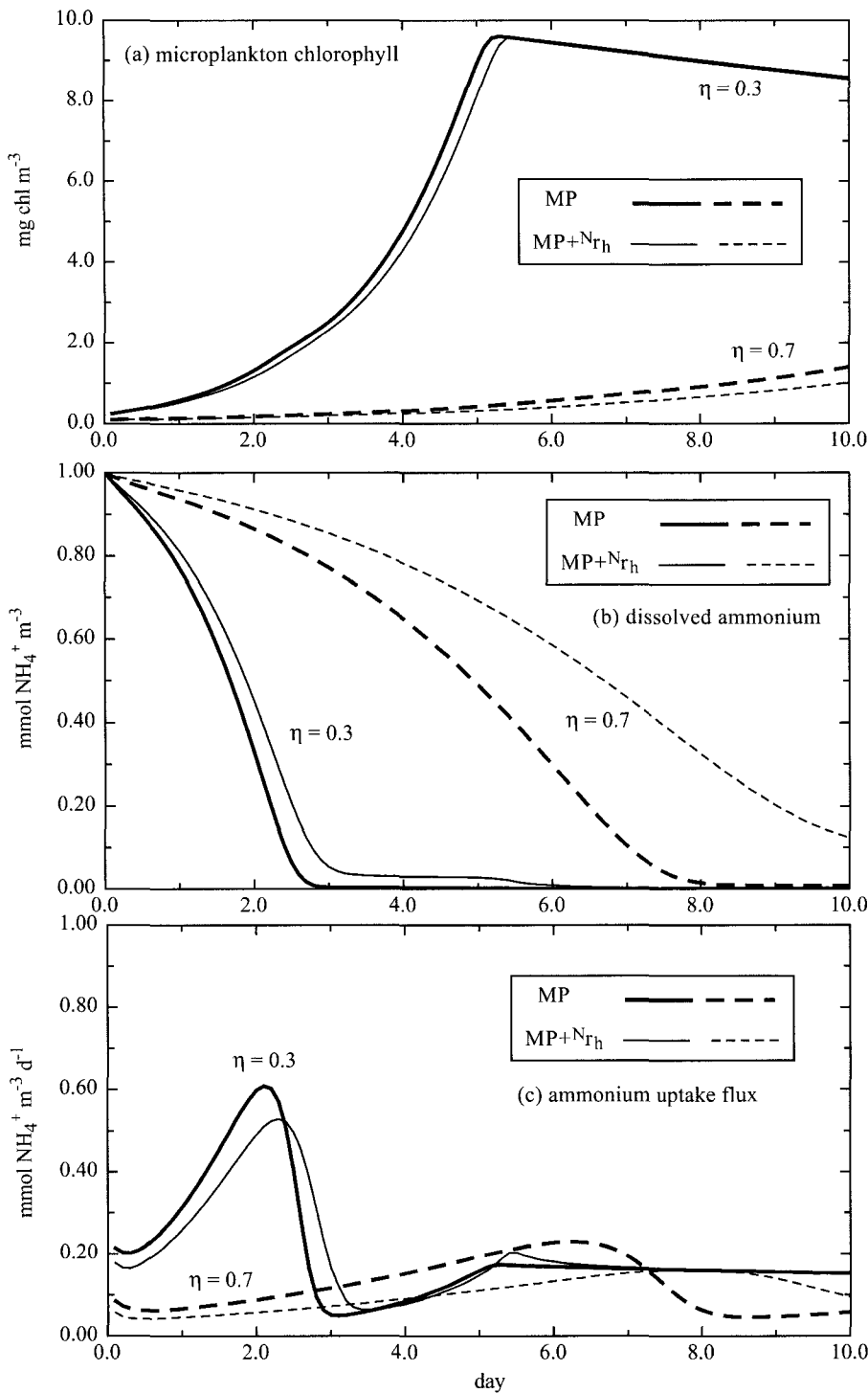
Fig. 7. Test case for ammonium uptake. Eqn. (53) to (55) examined in a syatem with state variables ^{NH}S (initial concentration 1 mmol m^{-3}), ^{NO}S (6 mmol m^{-3}), B (1 mmol m^{-3}) and N (0.15 mmol m^{-3}). Growth according to Table 10 with $I = 50$ μE m^{-2} s^{-1} and all parameters given standard values. There was a constant mesozooplankton grazing pressure of 0.05 d^{-1}, with 50% ammonium recycling. Microplankton parameters calculated from standard autotrophy and heterotroph parameters with $\eta = 0.3$ and 0.7. The equation at issue is $^{NH}u = {}^{NH}u_{max} f\ (^{NH}S) f_{in2}(Q)$ $[-{}^{N}r_h]$. The ammonium respiration term being included in MP $+ {}^{N}r_h$ and excluded from MP. Ammonium uptake flux is shown in the third panel, and was always positive. The standard simplication, omitting $^{N}r_h$, was better for lower values of η.

cled within the microplankton, the default option in MP assumes that there is no ammonium excretion by the microplankton (except in special circumstances, see below), and so the definitive equation for ammonium uptake is:

$$^{NH}u = {}^{NH}u_{max}\, f(^{NH}S)\, f_{in2}(Q) \qquad (55)$$

where the parameters and included functions are as in Eqn. (53). This equation does allow for ammonium to be excreted, but only when $Q > Q_{max}$ (when $f_{in2}(Q) < 0$). Such a condition is possible, for example when irradiance is very low and as a result light-controlled growth is negative because of the effects of respiration. Without allowing (in the model) for

Table 10. MP rate equations

Growth rate	
$\mu = \min\{\mu(I),\ \mu(Q)\}$	d^{-1}
$\mu(I) = (\alpha I\ ^X q_a^N\ (Q - q_h \eta) - r_0)/(1 + b)$	d^{-1}
$\mu(Q) = \mu_{\max}(1 - (Q_{\min}/Q))$	d^{-1}

uptake rate	

$$u = {}^{NO}u + {}^{NH}u \qquad\qquad \text{mmolN(mmolC)}^{-1}\text{d}^{-1}$$

$(NO_3^-) \qquad {}^{NO}u = {}^{NO}u_{\max}\ f({}^{NO}S)\ f_{in}({}^{NO}S)f_{in1}(Q)$

$(NH_4^+) \qquad {}^{NH}u = {}^{NH}u_{\max}\ f({}^{NH}S)\ f_{in2}(Q)\quad [-{}^N r_h]$

where

$$f({}^{NO}S) = {}^{NO}S/(K_{NOS} + {}^{NO}S)$$

$$f({}^{NH}S) = \begin{bmatrix} {}^{NH}S/(K_{NHS} + {}^{NH}S) & : & Q \leq Q_{\max} \\ 1 & : & Q > Q_{\max} \end{bmatrix}$$

$$f_{in}({}^{NH}S) = 1/(1 + ({}^{NH}S/K_{in}))$$

$$f_{in1}(Q) = \begin{bmatrix} (1 - ((Q - q_h \eta)/(Q_{\max} - q_h \eta))) & : & Q \leq Q_{\max} \\ 0 & : & Q > Q_{\max} \end{bmatrix}$$

$$f_{in2}(Q) = 1 - ((Q - q_h \eta)/(Q_{\max} - q_h \eta))$$

$$\begin{bmatrix} & optional & \\ {}^N r_h = \mu((1 + b_h)q^+ - q_h) + r_{0h}\ q & & \text{mmolN(mmolC)}^{-1}\text{d}^{-1} \\ \text{where} & & \\ & q^+ = (Q - q_h \eta)/(1 - \eta) : Q \geq q_h & \\ & q_h \qquad\qquad : Q < q_h & \end{bmatrix}$$

variables	
I : PAR experienced by microplankton,	$\mu E\ m^{-2}\ s^{-1}$
Q : microplankton nitrogen:carbon ratio,	mmol N (mmol C)$^{-1}$
${}^{NH}S$: sea-water ammonium concentration,	mmol m^{-3}
${}^{NO}S$: sea-water nitrate concentration,	mmol m^{-3}
Θ : temperature experienced by microplankton,	$^\circ$C

parameters		
heterotroph fraction,	$\eta = B_h/(B_a + B_h)$	
photosynthetic efficiency,	$\alpha = k\ \varepsilon\ \Phi$	mmol C (mg chl)$^{-1}$ d^{-1} ($\mu E\ m^{-2}\ s^{-1}$)$^{-1}$
yield of chlorophyll from N,	${}^X q^N = {}^X q_a^N (1 - \eta)$	mg chl (mmol N)$^{-1}$
basal respiration rate,	$r_0 = r_{0a}(1 - \eta) + r_{0h}\eta(1 + b_a)$	d^{-1}
respiration slope,	$b = \begin{bmatrix} b_a(1 + b_h \eta) + b_h \eta & : & \mu > 0 \\ 0 & : & \mu \leq 0 \end{bmatrix}$	
max. N-limited growth rate,	$\mu_{\max} = \mu_{\max}(1 - \eta)/(1.2 - \eta)$	d^{-1}
minimum N quota,	$Q_{\min} = Q_{\min a}(1 - \eta) + q_h \eta$	mmol N (mmol C)$^{-1}$
maximum N quota,	$Q_{\max} = Q_{\max a}(1 - \eta) + q_h \eta$	mmol N (mmol C)$^{-1}$
max. NO$_3$ uptake,	${}^{NO}u_{\max} = {}^{NO}u_{\max a}(1 - \eta)$	mmol N (mmol C)$^{-1}$ d^{-1}

Table 10. continued

max. NH₄ uptake,	$^{NH}u_{max} = {^{NH}u_{max\,a}}(1 - \eta)$	mmol N (mmol C)$^{-1}$ d^{-1}
half-sat. conc., NH₄ uptake,	K_{NHS} = autotroph value	mmol N m^{-3}
half-sat. conc., NO₃ uptake,	K_{NOS} = autotroph value	mmol N m^{-3}
half-sat. conc., NH₄ inhibition,	K_{in} = autotroph value	mmol N m^{-3}
temperature effects		
max. growth rate,	$\mu_{max\,a} = \mu_{max\,a}[20°C]\,f(\Theta)$	d^{-1}
max. uptake rate,	$u_{max\,a} = u_{max\,a}[20°C]\,f(\Theta)$	d^{-1}
temperature effect:	$f(\Theta) = \exp(k_\Theta(\Theta - 20°C))$	

nitrogen excretion, the autotroph (and hence microplankton) cell quota would, in these circumstances, continue to increase far above the maximum quota. Finally, $f(^{NH}S)$ is meaningful only for $^{NH}S \geq 0$, and $f_{in2}(Q)$ only for $Q \geq q_h\eta$. These points, however, are matters to be considered during numerical simulation rather than as part of the model.

This concludes the derivation of the microplankton equations that commenced in the section of 'microplankton equations of state'. These growth and uptake equations are summarised in Table 10, together with the definitions of microplankton parameters in terms of autotroph and heterotroph parameters. These definitions allow parameter values to be calculated from Tables 3 and 8, given a value of η. Under the assumption of constant η, a microplankton parameter has a constant value so long as there is constancy in the algal and heterotroph values from which it is derived. Numerical simulations of micorplankton growth thus require micorplankton parameter values to be calculated once only, before the start of numerical integration.

DISCUSSION

The most crucial assumption of MP is that of *a constant ratio of heterotrophs to autotrophs*. There is, clearly, no universal value of η. Furthermore, the data in Table 11, 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 analogous 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.

The second most important assumption of MP is that of *complete internal recycling*. Under this assumption it is implicit that DOM is excreted by phytoplankton, or leaked by protozoa, and that protozoa excrete ammo-

Table 11. Estimates of the heterotroph fraction

Site	Season	Autotroph mmol C m^{-3}	Heterotroph mmol C m^{-3}	Microplankton 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)

nium. However, these processes are not described explicitly because the excreted material is supposed to be rapidly and completely re-assimilated by microplankton components. This assumption was explored for the microcosm case by including the '+ $^{N}r_h$' option (for ammonium, and phosphate, excretion and re-uptake) in some simulations. In these cases there was insufficient improvement in the fit of the simulations to the observations to justify the inclusion of the excretion option. The more general results in Fig. 7 suggest, however, that the option might be worth including in simulations with a higher value of η than used in the microcosm case.

Physical models of the sea are based on well-known equations of motion, even in cases when the products of chaotic fluctuations in velocity and concentration are approximated by Fickian diffusion. Although the equations describing simple biological systems also show chaotic tendencies, it is as yet uncertain how much of the variability in natural marine ecosystems derives from sum of the 'simple chaos' of many subsystems, and how much from fluctuating physical forcing. As Hastings (1996) remarks, many biological systems have been observed to be more stable than would be expected if they behaved according to Lotka-Volterra dynamics. One explanation for such stability would be a system with many alternative pathways, for which the Internet would be a more suitable metaphor than the billiard table of classical physics. If this be the case, then the relatively simple mathematics which have proven successful in describing physical systems, cannot be used with biological systems. Nevertheless, there may be a bulk level of analysis at which some important properties of marine pelagic ecosystems can be captured by small sets of relatively simple differential equations. The ability of MP to simulate events during the microcosm experiment of Jones et al. (1978), or during the seasonal cycle in the central North Sea (Tett et al., 1993; Tett and Walne, 1995), encourages this view.

Demonstrating such points about marine ecosystems made up of pelagic micro-organisms was not the original aim of the work reported here, and we do not wish to make strong claims on the basis of the ability of MP to fit some sets of observations. Nevertheless, it is a convenience to be able to use a simple model to simulate important bulk properties of these ecosystems.

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