The importance of the form of the quota curve and control of non-limiting nutrient transport in phytoplankton models

KEVIN J. FLYNN*
INSTITUTE OF ENVIRONMENTAL SUSTAINABILITY, SWANSEA UNIVERSITY, WALLACE BUILDING, SINGLETON PARK, SWANSEA SA2 8PP, WALES, UK

*CORRESPONDING AUTHOR: k.j.flynn@swansea.ac.uk

Received November 16, 2007; accepted in principle January 10, 2008; accepted for publication January 13, 2008; published online January 27, 2008

INTRODUCTION

Originating almost 40 years ago (Droop, 1968), quota models are widely used to describe phytoplankton growth as a function of internal nutrient status. There are various quota-based models in the literature developed from the original empirically based works of Droop (Droop, 1968) and Caperon and Meyer (Caperon and Meyer, 1972). The form of the response curve relating the nutrient quota to organism growth rate (μ) varies between being linear and strongly hyperbolic, depending on the nutrient element and the organism, while the model representation depends also upon the quota equation type. The original Droop model defines the quota–μ curve as a fixed hyperbolic function of the current and minimum quotas. Others have used more complex hyperbolic descriptions (e.g. Davidson and Gurney, 1999; Flynn, 2001; Baklouti et al., 2006), while at the other extreme one could assign a simple linear response (Geider et al., 1998; Moore et al., 2002). In ecosystem models, usually an element:C quota form is used (e.g. Moore et al., 2002; Blackford et al., 2004). Operating quota models on a cell basis is also problematic because of changes in size during the cell cycle and with changes in nutrient status.
Of the nutrients affecting phytoplankton growth, the quota model is inappropriate for the description of 

1985) confound interpretation of cell-based nutrient quota $\mu$ relationships (Flynn, 2008).

Of the nutrients affecting phytoplankton growth, the quota model is inappropriate for the description of Si-limited growth (Si cannot in reality be redistributed within the cell to support growth in the absence of new Si obtained from outside of the cell), while the need for Fe is so variable (depending on light, respiration and N-source consumption which affect the demand for Fe from Fe-linked physiological process) that the minimum quota (Fe:C) and form of the quota–$\mu$ curve is expected to be similarly highly variable (Flynn, 2003).

N and P are the most important of the macro nutrients for quota-style modelling. The interface between N and P dynamics has been largely examined in connection with the critical (internal) N:P ratio at which N and P co-limit growth (Rhee and Gotham, 1980; Flynn, 2002; Leonardos and Geider, 2004).

Transport of the limiting nutrient element is a function of external nutrient availability, of the intracellular nutrient status, of temperature and light; models attempt to mimic these interactions (Laws and Chaloup, 1990; Geider et al., 1998; Armstrong, 2006). Some form of control is then required on the transport of the non-limiting nutrient (Droop, 1975; Davidson and Gurney, 1999; Flynn, 2001). In physiological terms, the control of nutrient transport is achieved by repression of the synthesis and/or operation of transporters. While in reality, this is related to the internal concentration of metabolites (typically early products of nutrient assimilation, as implemented for N nutrition by Flynn et al., 1997), a more empirical relationship can be made to the element:cell or element:C quotas (Morel, 1987; Flynn, 2003).

Although the biological control of transport operates on a continuum, and the maximum transport rate varies with nutrient status (typically being elevated as nutrient stress develops, e.g. Gotham and Rhee, 1981; Terry, 1982; Syrett et al., 1986) in a model the crudest control is to set a maximum rate (typically as a function of the maximum growth rate and maximum quota—Goldman and McCarthy, 1978) and to halt transport when the element:C quota attains a critical level. The critical level could exceed the maximum quota ($Q_{\text{max}}$; i.e. that required to sustain optimal growth); Flynn thus differentiated between $Q_{\text{max}}$ and $Q_{\text{abs}}$, the latter being the absolute maximum possible quota value, above which transport cannot proceed irrespective of any other factor (Flynn, 2003). When considering only a single nutrient, maximum transport rate in a simple model can be balanced with maximum growth rate, and there is no need to invoke such a transport cessation function. The value of the critical level at which transport is halted (in biological terms, fully repressed) could be considered as a variable with other factors (Droop, 1974, 1975; Davidson and Gurney, 1999), and indeed with the form of the nutrient being taken up; the control of ammonium transport differs from that of nitrate (Flynn et al., 1997, 1999). In contrast, one could tie the transport of non-limiting nutrients to that of the limiting nutrient, so maintaining, for example, a constant cellular N:P, while C:(N:P) varies. The balance of nutrient transports and assimilations has important ramifications for the growth rate of the organism (as a function of the shape of the quota–$\mu$ curve), the removal of both limiting and non-limiting nutrients (Flynn, 2005a), and subsequently for the operation of the ecosystem that consumes the algal biomass. The latter has a temporal if not spatial effect on nutrient recycling, while the stoichiometric value of the phytoplankton has a direct and important effect on consumer growth (Hessen and Andersen, 1992; Grover, 2003; Mitra and Flynn, 2005, 2006).

The aim of this work is to compare the performance of multi-nutrient quota models configured with different response curves for controlling growth and also for controlling the transport of the non-limiting nutrient. In order to do this, a model was configured to describe the data of Elrifi and Turpin (Elrifi and Turpin, 1985), who give data for nutrient quota relationships with growth rate. These data show not only the expected differences between the form of the N and P quota–$\mu$ curve shapes, but also a contrast between the controls of N and P transport when these are the non-limiting nutrients (results consistent with Healey and Hendzel, 1975; Terry, 1982). The model developed to describe these data was then used in a Turing-style test to compare the behaviour of alternate model structures. The results of the current study clearly show that the form of the quota–$\mu$ curve and also of the control of the non-limiting nutrient acquisition can be important determinants for the models ability to behave in an appropriate fashion.

### METHOD

There are few data sets available in the literature to enable a comparison between N and P quota models. The data used for this work were obtained by a digitalization of the graphs in Elrifi and Turpin (Elrifi and Turpin, 1985) (using Un-Scan-It v6, Silk Scientific Corp., USA) followed by transformations as required to obtain nutrient:C (N:C and P:C) quota–$\mu$ relationships both for limiting and non-limiting nutrients. The data
show not only how $\mu$ varies with the quota of the limiting nutrient, but also how the quota for the non-limiting nutrient varies with growth being limited by another nutrient (Fig. 1).

The aim here is to compare the impacts of the response curves relating quota to growth rate for the limiting nutrient, and relating quota to transport rate for the non-limiting nutrient, as shown in the data (Fig. 1). There are several variants of the quota model in the literature; the exact mathematical form used is not important in this context as long as it possesses the required flexibility to describe the data with sufficient fidelity. Below, a simple model structure is described to attain this aim.

### Quota–$\mu$ relationship for the limiting nutrient

The Droop (Droop, 1968) quota relationship [equation (1)] relates growth to the current quota ($Q$), minimum quota ($Q_{\text{min}}$) and a theoretical maximum growth rate at infinite $Q$ ($\mu_{\text{max}}$). For values of $Q$ over a realistic range ($Q_{\text{min}}$ to $Q_{\text{max}}$), equation (1) can be rewritten as equation (2); the curve form can now be seen as fixed as a function of $Q_{\text{min}}$: $Q_{\text{max}}$ such that the wider the range the more hyperbolic is the quota–$\mu$ relationship.

$$\mu = \mu_{\text{max}} \cdot \left(1 - \frac{Q_{\text{min}}}{Q}\right)$$

$$\mu = \frac{\mu_{\text{max}}}{\left(1 - \frac{Q_{\text{min}}}{Q_{\text{max}}}\right)}$$

The Caperon–Meyer (Caperon and Meyer, 1972) quota description [equation (3)] introduces a curve-defining parameter $K_q$ that carries the same units as $Q$. This rectangular-hyperbolic description is essentially a derivation of the Michaelis–Menten enzyme kinetics equation, where the substrate concentration is described by $Q - Q_{\text{min}}$. This function enables a fully variable curve description. However, constant $\mu_{\text{mcCM}}$ is required to scale the quota response to give an output between $\mu$ and $\mu_{\text{max}}$, so that a different value of $\mu_{\text{mcCM}}$ is required for each nutrient type described.

$$\mu = \mu_{\text{mcCM}} \cdot \left(\frac{Q - Q_{\text{min}}}{(Q - Q_{\text{min}}) + K_q}\right)$$

Flynn (Flynn, 2002) described a normalized rectangular hyperbolic (RH) description, the $^n$Quota equation [equation (4)].

$$\mu = \frac{\mu_{\text{max}}}{(1 + K_Q) \cdot (Q - Q_{\text{min}})} \cdot \left(\frac{Q - Q_{\text{min}}}{(Q - Q_{\text{min}}) + K_Q \cdot (Q_{\text{max}} - Q_{\text{min}})}\right)$$

$K_Q$ is a dimensionless parameter [unlike $K_q$ in equation (3)] that can be readily compared between nutrient types (that have very different numeric values and ranges for $Q$), and different quota bases (cell or C). From a survey of the literature, $K_Q$ for N ($^nK_Q$) tends to be high ($> 3$), while $^pK_Q$ tends to be low $< 0.3$ (Flynn, 2008). Equation (5) defines the value of $K_Q$ for the placement in equation (4) that will reproduce the Droop quota–$\mu$ relationship [as otherwise described by equation (2)]. The value of $K_Q$ required ($K_Q^{\text{equiv}}$) is a fixed function of $Q_{\text{min}}$ and $Q_{\text{max}}$; the greater $Q_{\text{max}}$: $Q_{\text{min}}$ the smaller is $K_Q^{\text{equiv}}$, and the tighter is the hyperbolic curve.

$$K_Q^{\text{equiv}} = \frac{Q_{\text{min}}}{Q_{\text{max}} - Q_{\text{min}}} = \left(\frac{Q_{\text{max}}}{Q_{\text{min}}} - 1\right)^{-1}$$

---

Fig. 1. Data digitalized and transformed from Elrifi and Turpin (Elrifi and Turpin, 1985) for Selenastrum minutum, from N-limited and P-limited cultures. Panel (a) shows the relationship between N:C and growth rate ($\mu$); panel (b) is for P:C versus $\mu$. The $^n$Quota fits are from equation (4) fitted to the N or P limited data series. Also shown is the steady-state output of the Control model (Table III).
Equation 6 gives a quota description that assumes a linear quota–μ relationship (e.g. Geider et al., 1998; Moore et al., 2002); this recognizes that phytoplankton have variable stoichiometry, but not that there may be a curvi-linear relationship in the quota–μ relationship. To obtain a description using equation (4) that equates to equation (6), the value of KQ simply needs to be made large (KQ > 5).

\[
\mu = \mu_{\text{max}} \cdot \frac{Q - Q_{\text{min}}}{Q_{\text{max}} - Q_{\text{min}}}
\] (6)

For the analysis given here, three alternative quota–μ descriptions were considered; Droop, linear and RH.

The normalized quota description given in equation (4) \(q^{\text{Quota}}\) was used for the base model, as the curve form can be readily altered to describe all three of the required quota–μ descriptions.

Fits of thenQuota function to the experimental data of Elrifi and Turpin (Elrifi and Turpin, 1985) are shown in Fig. 1; equation (4) was fitted to the data for the quota for limiting nutrients using an iterative procedure (Sigma Plot v.9) yielding the quota constants (NCo, NGm, PCo, PCm in Table I, and KQ values shown in Fig. 1. The value of \(N^{KQc}\) (KQ for the N:C–μ relationship when N is limiting) set at 10 gives a linear relationship, while \(P^{KQc}\) is much lower, at 0.44, describing a hyperbolic quota–μ relationship when P is limiting.

The forms of the alternative quota–μ response curves for N and P are shown in Fig. 2. The linear quota configuration is only different from the RH \(q^{\text{Quota}}\) form for the P:C description, as the optimal \(q^{\text{Quota}}\) form is linear for the N:C–μ relationship (Fig. 2a).

### Quota-transport relationship for the non-limiting nutrient

The other part of the model requires a regulation of the transport of the non-limiting nutrient, with reference to the degree of nutrient stress being imparted by the limiting nutrient. Again three alternative approaches were considered. The experimental data shows a strong contrast for \(m\) and N:C versus \(m\) and P:C when the nutrient is non-limiting (Fig. 1). The shape of the non-limiting nutrient:C quota–μ relationship is dictated by the physiological status which triggers cellular regulatory

<table>
<thead>
<tr>
<th>Table I: Definition of parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parameter</td>
</tr>
<tr>
<td>-----------</td>
</tr>
<tr>
<td>algNP</td>
</tr>
<tr>
<td>conQ</td>
</tr>
<tr>
<td>conT</td>
</tr>
<tr>
<td>KtN</td>
</tr>
<tr>
<td>KtP</td>
</tr>
<tr>
<td>NCabs</td>
</tr>
<tr>
<td>NCm</td>
</tr>
<tr>
<td>NCo</td>
</tr>
<tr>
<td>PCabs</td>
</tr>
<tr>
<td>PCm</td>
</tr>
<tr>
<td>PCo</td>
</tr>
<tr>
<td>Um</td>
</tr>
<tr>
<td>Cu</td>
</tr>
<tr>
<td>KQN</td>
</tr>
<tr>
<td>KQP</td>
</tr>
<tr>
<td>NCrep</td>
</tr>
<tr>
<td>NCu</td>
</tr>
<tr>
<td>Nup</td>
</tr>
<tr>
<td>PCrep</td>
</tr>
<tr>
<td>PCu</td>
</tr>
<tr>
<td>Pup</td>
</tr>
<tr>
<td>TN</td>
</tr>
<tr>
<td>TP</td>
</tr>
<tr>
<td>C</td>
</tr>
<tr>
<td>N</td>
</tr>
<tr>
<td>NC</td>
</tr>
<tr>
<td>P</td>
</tr>
<tr>
<td>PC</td>
</tr>
</tbody>
</table>

*aThese parameters are operationally auxiliaries, as defined in Table II.

These are grouped as constants (Con), auxiliaries (Aux, see also Table II and Appendix I), and state variables (StVar). Parameters with no indicated units are dimensionless. Values of conQ and conT define different model configurations—see Table III.
responses. One may thus mechanistically employ the relationship between the quotas for limiting and non-limiting nutrients to control non-limiting nutrient transport in a model. Hence, transport of nutrient X (Xt) occurs as a RH (Michaelis–Menten) function of external concentration, with reference to a half saturation constant $k_t$ and a maximum transport rate $X_{t\text{max}}$, as modulated by a function ($f$) of the quotas of both N:C and P:C [equation (7)].

$$X_t = X_{t\text{max}} \cdot f(N:C, P:C) \cdot \frac{X}{X + k_t} \tag{7}$$

From Fig. 1 it can be seen that the value of N:C at which N transport halts decreases as the value of P:C declines with P-limitation (closed symbols, Fig. 1). In contrast, the value of P:C at which P transport halts increases as the value of N:C declines with N-limitation (open symbols, Fig. 1). In Fig. 3 are shown the relationships describing the critical values of the non-limiting quota that completely represses (halts) transport of the non-limiting nutrient as functions of the limiting nutrient quota, for N transport in Fig. 3a, and P transport in Fig. 3b. The form of the equation controlling N transport (defined in the final model by auxiliary NCrep, Table I) includes the multiplier 0.55 because the optimal model configuration described the data best using an inflexion in the response curve at PC$_{\text{max}}$=0.55 (see Fig. 3a, noting the absence of the data around the point of inflexion which may have enabled a better empirical description of the relationship).

There are two additional configurations for controlling transport to that described above. In one, the quota of the non-limiting nutrient at which non-limiting nutrient transport is repressed is set as the maximum possible quota, QCabs (Flynn, 2003). Alternatively, the cellular N:P is fixed, while C:(N:P) varies (as in
Lancelot et al., 2000 implementation of the model of Shuter, 1979). In all instances, the complete repression of the transport of the non-limiting nutrients was achieved (rather coarsely) by not allowing transport if the quota value of that element exceeded a critical value. This generates a simple mechanism which, while it lacks the fidelity of more complex feedback regulations (Flynn, 2003), works well enough for the purpose at hand (see Discussion).

The kinetics of nutrient transport has been simplified to assume no increase in transport velocity with nutrient stress, as is expected in reality for both N and P (Gotham and Rhee, 1981; Terry, 1982; Flynn et al., 1999). In the absence of other information, the half saturation values for N and P transport were set at 1 and 0.1 μM respectively. Initially, the maximum transport rate [\(X_{\text{max}}\) in equation (7)] was set as \(\mu_{\text{max}} Q_{\text{max}}\) (Goldman and McCarthy, 1978), and was so implemented for N transport (auxiliary TN in Table II). However, it was noted that the model could not attain the correct P:C when N was limiting unless the maximum rate of P transport was doubled over this value (hence the multiplier 2 in the equation for TP, Table II). As typically the P transport maximum exceeds that required by more like an order of magnitude (Gotham and Rhee, 1981; Terry, 1982) the value of this multiplier is conservative.

Model

The model used in this study is described in Tables I–III; the equations are given in plain ASCII text form to aid their coding into a simulation platform. (Non-ASCII versions of the equations given in Table II are given in Appendix 1.) The model contains five state variables describing changes in C-biomass [\(C\); equation (8)], nitrogen and phosphorus carbon-quotas [\(N\) and \(P\); equation (9), respectively], and external nutrient nitrogen and phosphorus [\(N\) and \(P\); equation (10), respectively].

\[
\frac{dC}{dt} = C \cdot \text{Cu} \tag{8}
\]

\[
\frac{dNC}{dt} = N_{\text{up}} - N \cdot C \cdot \text{Cu} \quad \frac{dPC}{dt} = P_{\text{up}} - P \cdot C \cdot \text{Cu} \tag{9}
\]

\[
\frac{dN}{dt} = C \cdot N_{\text{up}} \quad \frac{dP}{dt} = C \cdot P_{\text{up}} \tag{10}
\]

The model makes use of Boolean switches to enable the testing of three alternative quota descriptions (\(Q_Q\)) and three alternative transport control mechanisms (\(Q_T\)). These configurations are summarized in Table III. Alternative \(Q_Q\) settings were as follows: \(Q_Q = 1\), values of \(Q_Q\) as derived from the experimental data (Fig. 1); \(Q_Q = 2\), values of \(Q_Q\) describe Droop kinetics as per equation (5); \(Q_Q = 3\), assuming a linear function achieved by setting \(Q_Q = 10\); see also Fig. 2. A threshold function selecting the quota of the most limiting element then controls growth (Flynn, 2003). The alternative \(Q_T\) settings were: \(Q_T = 1\), using a dynamic regulation in accordance with experimental data (Figs 1 and 3); \(Q_T = 2\), terminating transport if \(Q_T\) attained a critical, absolute maximum value of \(Q_T\) (i.e., \(Q_{\text{abs}}\)); \(Q_T = 3\), tying transport of the non-limiting nutrient to that of the limiting nutrient such that the internal ratio of \(N/P\) was held fixed (at the Redfield mole ratio value of 16; mass ratio 7.23).

The operation of the most flexible model (i.e. configured with \(Q_Q = 1\) and \(Q_T = 1\), run in steady-state over a range of nutrient concentrations in order to generate outputs comparing \(N:C\) and \(P:C\) quotas and growth rates, shows a good fit to the experimental data (Fig. 1). This demonstrates not only the correct relationship between the limiting nutrient:C quota and \(\mu\), but

### Table II: Equations defining auxiliaries, displayed in ASCII text format

<table>
<thead>
<tr>
<th>Auxiliary</th>
<th>Equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cu</td>
<td>Um*MIN(NCu,PCu)</td>
</tr>
<tr>
<td>KQN</td>
<td>(conQ=1)*10+(conQ=2)*1/(NCm(NCo-1)+(conQ=3)*10</td>
</tr>
<tr>
<td>KQP</td>
<td>(conQ=1)*0.44+(conQ=2)*1/(PCm(PCo-1)+(conQ=3)*10</td>
</tr>
<tr>
<td>NCrep</td>
<td>(T=1)*((PC&gt;PCm)<em>0.55</em>NCm+((PC&lt;PCm)<em>0.55</em>(1+PC+0.1021))+((T=2)*NCabs+(T=3)*algNL))+(algNP&gt;NC(PC))</td>
</tr>
<tr>
<td>NCu</td>
<td>(NC&lt;NCm)<em>1+(KQN</em>(NC-NCo)/(NC-NCo)+KQP*(NCm-NCo)+NC&gt;NCo)</td>
</tr>
<tr>
<td>Nup</td>
<td>T*N+K+N</td>
</tr>
<tr>
<td>PCrep</td>
<td>(T=1)<em>((NC&gt;NCm)<em>PCm+(NC&lt;NCm)</em>(-1.5703</em>NC^2+0.9462*NC+0.0578))+(T=2)*PCabs+(T=3)*algNL</td>
</tr>
<tr>
<td>PCu</td>
<td>(PC&lt;PCm)<em>1+(KQP</em>(PC-PCo)@((PC-PCol+KQP*(PCm-PCo)+PC&gt;PCm)</td>
</tr>
<tr>
<td>Pup</td>
<td>T<em>P</em>(F+K(P)</td>
</tr>
<tr>
<td>TN</td>
<td>Um<em>NCm</em>(NCrep&gt;NC)<em>1</em>(T&lt;T)+1.5*(T&gt;T)</td>
</tr>
<tr>
<td>TP</td>
<td>Um<em>PCm</em>2*(PCrep&gt;PC)<em>1</em>(T&lt;T)+1.5*(T&gt;T)</td>
</tr>
</tbody>
</table>

Boolean operators take the value 0 if false, or 1 if true. See also Fig. 3a and b concerning the definitions of NCrep and PCrep. See Appendix 1 for non-ASCII equations.
also the correct description of the quota when the counter nutrient became limiting. This model was deemed to give the best likely fit to the data and hence used as the Control model for the Turing-type tests conducted against the other, less flexible, configurations.

To ensure broad equality between the behaviour of different model configurations, the values of the maximum growth rate and half saturation constants for nutrient transport in the test models were tuned to the steady-state output of the Control model (Table III). This ensured similar growth kinetics at different limiting nutrient concentrations (Fig. 4). All models were run on Powersim Constructor (Isdalstø, Norway), and tuned to data using Powersim Solver v.2, utilizing an evolutionary algorithm to minimize the likelihood of locating local minima. Initial simulations under steady-state conditions over a range of external N and P concentrations showed that because configuration ConQ = 3 spent much time switching nutrient transport on and off (to maintain a constant algal N:P), it could not match the growth rate of the Control unless the maximum rate of transport was increased by a factor of ca. 1.5 (hence the multiplier 1.5 in the equations for the conQ=3 implementations of TN and TP in Table II). Again, as typically the N and P transport maximum exceeds that required (i.e. as set by $\mu_{\text{max}}Q_{\text{max}}$) by a considerable margin (Gotham and Rhee, 1981; Terry, 1982; Flynn et al., 1999) the use of such a low value multiplier is quite acceptable from a mechanistic point of view.

Figure 5 shows a comparison between the quota relationships and $\mu$ for all five configurations running at steady-state (constant nutrient concentrations); these plots are directly comparable with those in Fig. 4. For these runs, the model was run until internal rate processes were constant (i.e. the values of equations (9), describing changes in nutrient quotas, were zero). While the Control model fits the experimental data well (see Fig. 1), there is considerable variation between the behaviour of the Control and of the other configurations even though the behaviour with respect to the limiting nutrient and growth rate is similar (Fig. 4). The purpose of this paper is to consider what effects are caused by the operation of these different model variants (with their contrasting quota–$\mu$ and non-limiting nutrient transport regulation controls) in dynamic scenarios.

In nature, behaviour under steady-state is of lesser importance than responses to perturbations. Accordingly, it is important to consider the behaviour of models running under dynamic situations in which, for example, phytoplankton growth continues at the expense of previously accumulated nutrients. For the dynamic comparison between configurations, the models (configured according to Table III) were placed within scenarios in which either N or P became limiting (mole nutrient N:P of either 4 or 80; “N-limit”, “P-limit” respectively), or with the nutrient N:P set at the mole Redfield value (N:P of 16; “NP co-limit”). Either a slow or fast chemostat-style dilution rate (10 or 40% of the maximum growth rate; “low D”, “high D” respectively) was applied in order to compare the behaviour of the different configurations under either a wide nutrient-status range (low D) or a more narrow range; the latter is arguably more important in nature, where extremes of nutrient limitation are less likely. In addition, part way through the

### Table III: Definitions of model configurations

<table>
<thead>
<tr>
<th>Model</th>
<th>conQ</th>
<th>conT</th>
<th>Um (day$^{-1}$)</th>
<th>KtN (µgN L$^{-1}$)</th>
<th>KtP (µgP L$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>1</td>
<td>1</td>
<td>1.68</td>
<td>14.00</td>
<td>3.10</td>
</tr>
<tr>
<td>Droop</td>
<td>2</td>
<td>1</td>
<td>1.59</td>
<td>15.80</td>
<td>5.41</td>
</tr>
<tr>
<td>Linear</td>
<td>3</td>
<td>1</td>
<td>1.61</td>
<td>8.57</td>
<td>1.09</td>
</tr>
<tr>
<td>Qabs</td>
<td>1</td>
<td>2</td>
<td>1.61</td>
<td>8.66</td>
<td>1.92</td>
</tr>
<tr>
<td>Fixed NP</td>
<td>1</td>
<td>3</td>
<td>1.70</td>
<td>16.06</td>
<td>1.61</td>
</tr>
</tbody>
</table>

Values of the maximum growth rate (Um) and the half saturation constants for N and P transport (KtN, KtP) are shown for the alternate models employed. The Droop, Linear, Qabs and Fixed NP models were all tuned to the Control model output in steady-state (see Fig. 4). conQ and conT are switches used in the equations in Table II. See also Table I.
Fig. 5. Comparisons between quota–μ relationships of the Control and test models. The Control curves (bold continuous lines) are the same as those shown as “model output” in Fig. 1. Panels show performance of different model configuration: Droop (a), Linear (b), Qabs (c) and Fixed NP (d); see also Table III. The arrows indicate the direction of change in the non-limiting quota value as the other nutrient becomes increasingly limiting; thick arrows for Control, thin arrows for the alternative model form.
simulation, the algal population was culled to 5%, so that the next period of growth was in the presence of external and internal nutrient regimes in part a function of the activity of the previous growth period.

Deviations of test model output from the Control were calculated using equation (11), where \( x \) is the Control model value and \( y \) the test model value at the same time point, \( \text{MAX}_x \) is the maximum value of the Control value in the time series in question, and \( n \) is the number of time points (here, the model output was considered every 0.125 day, over 25 day, so \( n = 200 \), ignoring the start point).

\[
\text{dev} = \frac{\sum ((x-y)/\text{MAX}_x)^2}{n} \cdot 100 \quad (11)
\]

While this equation scales the deviations relative to the range of the parameter range so aiding comparison between parameter types, the relative importance of obtaining a good fit for one parameter at the possible expense of another is rather subjective, and depends on the application envisaged for the model. By inspection of the plots and the calculated deviations, the author is of the opinion that in this work a deviation calculated by equation (11) greater than 1 indicates a potentially important difference between the model outputs.

**RESULTS**

The results from the N-limiting scenario (Fig. 6) show a close agreement between the Control and Linear configurations (these share the same shape N:C quota–\( \mu \) shape—Fig 2a). The Droop configuration, however, reported a higher C biomass, and more extreme N:C and P:C excursions. This reflects the fact that the Droop quota–\( \mu \) curves are more hyperbolic for both nutrients than is described by the Control model as fitted to the data (Figs 1 and 2a and b). There are no consequential differences between using the simple limitation of P transport when P:C attained PCabs, as in the Qabs configuration, rather than the experimentally derived control of P transport (see Figs 1 and 5). However, linking the transport of N and P together, to maintain a fixed algal N:P gave gross errors in the reporting of the non-limiting nutrient (P) and of the internal quota (P:C); see Fixed NP configuration in Fig. 6. These differences are common between the low and high dilution scenarios; note the less extreme ranges of N:C and P:C in the Control outputs in the high dilution series.

In the P-limiting scenario (Fig. 7), not only is the Droop configuration in disagreement with the Control, but now the Linear model also produces a strongly contrasting behaviour. These differences are in all aspects of growth, nutrient consumption and quota (Table IV). The performance of the Qabs configuration is now also poor; this reflects the linkage between N:C and P:C in P-limiting cells (Figs 1 and 5), whose inappropriate reporting by this configuration leads to an over consumption of N and an excessive N:C (arrowed parts in Figs 5a and 7). The Fixed NP configuration is again poor. The differences are common in qualitative terms between dilution scenarios.

The NP co-limitation scenario (supply nutrient N:P = 16) shows the least disagreements between the model types (Fig. 8, Table IV). The Droop configuration still over estimates C biomass, while the Qabs version still overstates P:C. The behaviour of the Fixed NP configuration is much closer to that of the Control than it was under N or P limitations (Figs 6–8).

The deviations calculated using equation (11) are given in Table IV, showing that P-limited conditions were most problematic for all the test configurations, and also that the Droop and Fixed NP configurations performed at greatest odds versus the Control. Most points of disparity were in the algal C biomass and the reported N:C and P:C quotas.

**DISCUSSION**

While the multi-nutrient (C,N,P) model used as the Control configuration provides a computationally compact and effective simulation of the experimental data (Fig 1), the emphasis here is not placed upon the minutia of model code. Rather, this paper primarily considers the importance or otherwise of describing the quota–\( \mu \) relationship using Droop, linear or rectangular hyperbolic curves, and of using alternative contrasting mechanisms to control the transport of the non-limiting nutrient.

The behaviour of phytoplankton towards nutrient limitation is part of their phenotypic character, defining how one species or taxonomic group may fair in competition with others (Turpin and Harrison, 1979; Spijkerman and Coesel, 1998; Ahn et al., 2002). The emphasis in most studies (experimental and modelling) in this respect has been upon a single limiting nutrient, with or without light-limitation (e.g. Zevenboom et al., 1980; Watanabe et al., 1987; Geider et al., 1998). Rather fewer studies report changes in the physiological status of non-limiting nutrient acquisition (e.g. Terry, 1982; Elrifi and Turpin, 1985; John and Flynn, 2002). Even where only one nutrient type is considered, there may be various routes of element entry, each with different kinetic descriptors; ammonium versus nitrate is the
most studied and modelled interaction here (Flynn et al., 1997, 1999). The critical interactions in the context of modelling these processes lay at the levels of nutrient transport (initial acquisition) and then subsequent assimilation and promotion of growth. This work demonstrates the importance of getting these descriptions correct, both with respect to the limiting nutrient and also for the non-limiting nutrients. The importance of this issue lays not only in the implications for the growth of subsequent (simulated) generations of phytoplankton (Flynn, 2005a), but also for the growth of zooplankton whose behaviour is affected by the stoichiometric-linked quality of their feed (Hessen and Andersen, 1992; Grover, 2003). The importance of the latter, simply for a single nutrient, has been shown by Mitra et al. (Mitra et al., 2007). Where changes in nutrient status are associated with the development of grazing deterrents (Mitra and Flynn, 2005, 2006) the importance of the correct description of phytoplankton stoichiometry is all the greater.

In the quest to describe ecologically important planktonic events, modellers have described phytoplankton using various approaches. Typically approaches have been Monod (assuming invariant, Redfield fixed, 

Fig. 6. Comparisons of model outputs under conditions of N-limitation (initial nutrient mole N:P of 4, under a dilution rate equating to (a) 10% or (b) 40% of the maximum growth rate (low D, or high D respectively). Panels show algal biomass, external nutrient concentrations, and N:C and P:C quotas (mass ratios).
C:N:P), quota (classically Droop), or Shuter (Shuter, 1979), the latter assuming variable C:(N:P) but fixed N:P. The Droop model uses a fixed descriptor formulation linking quota to growth [see equations (1) and (2)], which is inappropriate for the N quota (e.g. Figs 1, 2a and 5). The N:C quota–μ relationship appears typically linear (NKQC > 5 for over a dozen contrasting algal species; Flynn, unpublished), and it may be tempting to assume that other quota relationships are also linear (Moore et al., 2002). However, the results of this work show the dangers of assuming a hyperbolic relationship where there is none (i.e. here for N), or linear where there is none (i.e. here for P); the Linear configuration was particularly unsatisfactory here when P was limiting (Figs 6–8; Table IV).

The interface between nutrient transport and quota control is a critical part of the description (Flynn, 2002, 2003; Klausmeier et al., 2004); as the immediate interface with the environment, it is as much if not more important than the internal (quota-driven) regulation of growth (Flynn, 2002). It is as much part of the defining phenotypic characterization as are the initial slope of

Fig. 7. Comparisons of model outputs under conditions of P-limitation (initial nutrient mole N:P of 80). Otherwise, as Fig. 6.
The photosynthesis-irradiance curve ($\alpha$) and Chl:C. We know that the maximum rate of nutrient transport ($T_{\text{max}}$) varies with nutrient status. $T_{\text{max}}$ typically increases with nutrient stress (Gotham and Rhee, 1981; Terry, 1982; Syrett et al., 1986) but there is great variability both with respect to the magnitude of the change in $T_{\text{max}}$ and the form of the relationship which significantly affects model behaviour (Flynn, 2002). Thus, $T_{\text{max}}$ for nitrate does not show the order of magnitude variation that it does for ammonium, and it may also decline when cells are severely N-stressed (Flynn et al., 1999). The relationship between limitation by some substrate (e.g. N as ammonium versus nitrate) as well as for the control of the transport of the non-limiting nutrient. The importance of the latter has long been appreciated (Droop, 1974, 1975), but has typically involved relatively complex equations. Previously Flynn (Flynn, 2001, 2003) employed sigmoidal functions to regulate transport with reference to the quota. This was done because, for ammonium versus nitrate, regulatory switching between growth limiting substrates using an all-or-nothing mechanism can result in unwanted oscillations in model behaviour. Here, however, where regulation was required of a non-limiting substrate, such a course switch does not affect growth dynamics; only the transport of the non-limiting nutrient exhibits violent changes (not shown) but overall dynamics are little altered. This enabled the use of a simple model construct (Tables I–III, “Control” variant) that described the original experimental data well (Fig. 1).

The relationship between transport and the nutrient quotas (defined by NCrep and PCrep in Table II) had a great effect on model performance. The simplest expectation is that there is a single quota value (namely $Q_{\text{abs}}$) at which transport stops. Indeed, by definition it must stop when $Q$ attains $Q_{\text{abs}}$. Flynn (Flynn, 2003) introduced $Q_{\text{abs}}$ to differentiate between quota values that affected growth (between $Q_{\text{min}}$ and $Q_{\text{max}}$) and higher quota values. This is particularly important for N when ammonium is being used (growth using ammonium need not be any faster than on nitrate, but supports a higher N:C; Flynn et al., 1999) and for P (an excess of which may be accumulated as polyphosphate in those organisms capable of such synthesis, Watanabe et al., 1987). Reference to a diminution of transport as $Q$ approaches $Q_{\text{abs}}$ also gives a ready mechanism for the description of light limited growth (where nutrient:C quotas may increase coupled with a decrease in $\mu$); this gives a mechanistic model construct in contrast to the approach suggested by Armstrong (Armstrong, 2006).

Assuming that $Q_{\text{abs}}$ can be used as a carte-blanche terminator of transport ($Q_{\text{abs}}$ model configuration as used here), when in fact it should be halted at a different quota value depending on which nutrient limits growth (see Figs 1, 3a and b and 5), can have important implications (cf. Control versus $Q_{\text{abs}}$ in Figs 6–8). However, the resultant erroneous behaviour is minor compared with that associated with using a fixed N:P as the target switch to regulate transport of the non-limiting nutrient (Fixed NP configuration in Figs 6–8; Table IV).

Ecosystem modellers generally, and with good cause, seek the simplest description that captures the gist of what they consider as typical biological behaviour. While it is unrealistic to attempt a description of all species of phytoplankton, the cold reality is that we do not know to what extent we can generalize phytoplankton behaviour even for the construction of C,N,P based models because we simply lack the data for the comparison. There are several factors that have conspired to worsen the situation, such as the lack of

### Table IV: Deviations, calculated using equation (11), between the Control and test model configurations

<table>
<thead>
<tr>
<th>Dilution</th>
<th>Scenario</th>
<th>Figure</th>
<th>Test Model</th>
<th>Parameter deviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low D</td>
<td>N-limit</td>
<td>6a</td>
<td>Droop</td>
<td>C 0 N 0 P 0 N:C 0 P:C 0</td>
</tr>
<tr>
<td>Low D</td>
<td>P-limit</td>
<td>7a</td>
<td>Fixed NP</td>
<td>C 0 N 0 P 0 N:C 0 P:C 0</td>
</tr>
<tr>
<td>High D</td>
<td>N-limit</td>
<td>6b</td>
<td>Droop</td>
<td>C 0 N 0 P 0 N:C 0 P:C 0</td>
</tr>
<tr>
<td>High D</td>
<td>P-limit</td>
<td>7b</td>
<td>Fixed NP</td>
<td>C 0 N 0 P 0 N:C 0 P:C 0</td>
</tr>
<tr>
<td>Low D</td>
<td>co-limit</td>
<td>8a</td>
<td>Droop</td>
<td>C 0 N 0 P 0 N:C 0 P:C 0</td>
</tr>
<tr>
<td>High D</td>
<td>co-limit</td>
<td>8b</td>
<td>Fixed NP</td>
<td>C 0 N 0 P 0 N:C 0 P:C 0</td>
</tr>
</tbody>
</table>

Those values in bold (i.e. >1) are considered significant [see text for Equation (11); Figs 6–8]. Deviations are dimensionless.
measurements of the fate of non-limiting nutrients, and the measurement of so many quotas on a cell rather than C-biomass basis. Data are needed at least of the sort used here (Elrifi and Turpin, 1985) for phytoplankton from different taxonomic groups, and using different substrate types (ammonium, nitrate, urea, inorganic and organic P etc.). Once in possession of such data, the normalized quota, $^{a}Q_{\text{quota}}$, construct of equation (4) enables a ready comparison of the quota curve shapes that one may suspect as being important as phenotypic descriptors. Knowing the typical values for $KQ$ and the ranges of $Q_{\text{min}}$, $Q_{\text{max}}$ and $Q_{\text{abs}}$ for different groups of organisms would help greatly. From what data are available it appears that $^{a}KQ$ is typically $>5$, while $^{b}KQ$ is less than 0.2 (as judged from Fig. 1, data presented in Morel, 1987; Grover, 1991; Ducobu et al., 1998).

In the absence of hard information with which to design and parameterize models of phytoplankton, one is left to make guesstimates, assumptions and to tune models to what few data are available. This is problematic because, for example, a similar relationship between growth rate and the concentration of the

---

**Fig. 8.** Comparisons of model outputs under conditions of NP-limitation (initial nutrient mole N:P of 16). Otherwise, as Fig. 6.
limiting nutrient can be attained using various combinations of quota description, maximum growth rate and half saturation constant for nutrient transport (Fig. 4; Flynn, 2005a). Attempting to tune the results of the dynamic runs generated by the different configurations to the Control output (as per Figs 6–8) showed that the Linear model (which is incapable of describing the correct hyperbolic P:C quota - $\mu$ description) most closely followed the performance of the Control model when using much higher $\mu_{\text{max}}$ ($U_m$ in Table I) and $K_t$ values (results not shown). This combination of $\mu_{\text{max}}$ and $K_t$ had the effect of enforcing a stronger hyperbolic relationship at the external interface (transport) compensating for the lack of one at the internal interface (quota) within the Linear quota configuration. However, blindly altering transport and quota descriptions in this fashion can lead to the use of constants that are beyond biological justification. In addition, while the alternative model configurations could be better tuned to the dynamic output of the Control by such manipulations, the resultant “optimal” values for $\mu_{\text{max}}$ and $K_t$ differed between each scenario (low N, low P, low D, high N). It is thus important that as many parts of the model behave individually in an realistic a fashion as possible (within reasonable bounds of complexity), so that a failing in one part does not require compensation elsewhere (Mitra et al., 2007).

Ultimately, whether using models that can demonstrate questionable behaviour is deleterious to the whole ecosystem simulation depends on the conditions under which the model is used. Thus, while the Fixed NP configuration generally performed poorly here (Figs 6–8; Table IV), the conditions under which such a construct was used by Lancelot et al. (Lancelot et al., 2000) was concerned primarily with non-N-P limitation. A more basic question then, is why not always use a model that best describes phytoplankton behaviour? If the typical values of $K_{QN}$ and $K_{QP}$ were known for placement in the “Quota formula [equation (4)], and we already have ball-park figures of ca. 5 and 0.2 respectively, then it would not be necessary to use a default Droop or linear quota configuration.

In conclusion, the relationships between the nutrient:C quota and growth rate and transport are suspected critical phenotypic determinants whose formulation has been shown here to have considerable influence over total simulation behaviour. Our modelling of these facets of behaviour should be accorded appropriate recognition. Much work is required to parameterize these interactions for different phytoplankton groups. This is an important prerequisite for the construction of phytoplankton functional type models (Flynn, 2005b).

ACKNOWLEDGEMENTS

I wish to thank Ian Davies (Swansea, UK), Michael Droop (Oban, UK) and Dougie Spiers (Strathclyde, UK) for their assistance and motivation.

APPENDIX 1

Non-ASCII format versions of the equations given in Table II

\[
\begin{align*}
Cu &= U_m \cdot (\text{MIN}(NCu, PCu)) \\
KQN &= (\text{con}Q = 1) \cdot 10 + (\text{con}Q = 2) \cdot \frac{1}{(NCm/NC0) - 1} + (\text{con}Q = 3) \cdot 10 \\
KQP &= (\text{con}Q = 1) \cdot 0.44 + (\text{con}Q = 2) \cdot \frac{1}{(PCm/PC0) - 1} + (\text{con}Q = 3) \cdot 10 \\
NCrep &= (\text{con}T = 1) \cdot ((PC > PCm \cdot 0.55) \cdot NCm + (PC \leq PCm \cdot 0.55) \cdot 5 \cdot (PC + 0.1021)) + (\text{con}T = 2) \cdot NCabs + (\text{con}T = 3) \cdot (\text{algNP} > \frac{NC}{PC}) \\
NCu &= (NC \leq NCm) \cdot \frac{(1 + KQN) \cdot (NC - NC0)}{(NC - NC0) + KQN \cdot (NCm - NC0)} + (NC > NCm) \\
Nup &= TN \cdot \frac{N}{N + KiN} \\
PCrep &= (\text{con}T = 1) \cdot ((NC > NCm) \cdot PCm + (NC \leq NCm) \cdot (-4.5703 \cdot NC^2 + 0.9462 \cdot NC + 0.0578)) + (\text{con}T = 2) \cdot PCabs + (\text{con}T = 3) \cdot (\text{algNP} < \frac{NC}{PC}) \\
PCu &= (PC \leq PCm) \cdot \frac{(1 + KQP) \cdot (PC - PC0)}{(PC - PC0) + KQP \cdot (PCm - PC0)} + (PC > PCm) \\
Pup &= TP \cdot \frac{P}{P + KiP} \\
TN &= U_m \cdot NCm \cdot (NCrep > NC) \cdot (1 \cdot (\text{con}T < 3) + 1.5 \cdot (\text{con}T = 3)) \\
TP &= U_m \cdot PCm \cdot (PCrep > PC) \cdot (1 \cdot (\text{con}T < 3) + 1.5 \cdot (\text{con}T = 3)).
\end{align*}
\]
REFERENCES


