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Assessing an efficient “Instant Acclimation” approximation of dynamic phytoplankton stoichiometry

BEN A. WARD*

SCHOOL OF GEOGRAPHICAL SCIENCES, UNIVERSITY OF BRISTOL, UNIVERSITY ROAD, BRISTOL BS8 1SS, UK

*CORRESPONDING AUTHOR: b.a.ward@bristol.ac.uk

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The variable elemental ratios of carbon to essential nutrients in marine organic matter affect the productivity of marine food-webs and the sequestration of carbon in the deep ocean. It is important that models of these systems are able to correctly reproduce observed trends. “Dynamic Quota” models have achieved some success in this regard, but the computational expense of transporting each state variable in ocean models has prevented many large-scale models from moving beyond a simpler “Fixed Stoichiometry” formulation. This article compares the Dynamic Quota and Fixed Stoichiometry models to a recent “Instant Acclimation” model, which combines the stoichiometric flexibility of the Dynamic Quota model with the computational efficiency of the Fixed Stoichiometry model. The Instant Acclimation model is mathematically equivalent to the Dynamic Quota model at equilibrium, and provides an accurate approximation under a wide range of dynamic conditions. The accuracy and computational efficiency of the Instant Acclimation model recommend it as a candidate for incorporating flexible stoichiometry into marine ecosystem models, especially in situations where the number of model state-variables is restricted.

KEYWORDS: phytoplankton; quota; dynamic; equilibrium; balanced; approximation; efficient

INTRODUCTION

Marine phytoplankton represent an important nexus in the Earth system. The photosynthetic transformation of inorganic nutrients and carbon dioxide into living biomass sustains fluxes of energy and biomass through the food web, supporting almost all life in the ocean. This

includes the fisheries that provide essential nutrition to more than half the human population (Hollwed *et al.*, 2013). The supply of essential nutrients to the sunlit ocean surface also sustains a downward flux of organic carbon on the order of 10 billion tonnes each year (Hain *et al.*, 2014). This “biological carbon pump” is thought to lower atmospheric carbon concentrations by as much as

200 ppm (relative to a hypothetical abiotic ocean; Parekh *et al.*, 2006), with clear implications for global climate.

These important fluxes through the system are affected by the stoichiometric ratios in which carbon is coupled to limiting nutrients in organic biomass. While it has long been noted that that marine organic matter has a well-defined global average C:N:P stoichiometry of ~106:16:1 (Redfield, 1934), this single ratio masks considerable variability. Particulate N:C and P:C ratios decrease with nutrient drawdown during blooms (Davidson *et al.*, 1999), and show related spatial trends between the eutrophic subpolar gyres and the oligotrophic subtropical gyres (Körtzinger *et al.*, 2001; Martiny *et al.*, 2013). The variability of particulate stoichiometry in the ocean appears to be driven by related trends in the stoichiometry of plankton. For example, Figure 1 shows the stoichiometry of the chlorophyte *Selenastrum minutum*, in continuous cultures under either nitrate or phosphorus limitation (Elrifi and Turpin, 1985). The biomass ratio of the limiting nutrient to carbon tends to increase with the equilibrium growth rate, while the non-limiting nutrient to carbon ratio is a more complex function of the nutrient supply ratio and the growth rate. All other things being equal, higher nutrient-to-carbon ratios in organic matter will inhibit both ecosystem productivity and the sequestration of carbon within the ocean interior (Ayata *et al.*, 2014; Galbraith and Martiny, 2015). It is

therefore important to develop models that can account for this variability.

Although many contemporary models of marine ecosystems contain independent state variables for a number of potentially limiting nutrients, phytoplankton biomass is most typically represented in terms of just a single nutrient element, to which carbon and other essential elements are coupled in a constant ratio (Follows *et al.*, 2007; Kwiatkowski *et al.*, 2014). These “Fixed Stoichiometry” models cannot account for the observed non-Redfieldian coupling of carbon and nutrients in organic matter. This can be achieved with more complex “Dynamic Quota” models that account for flexible stoichiometry by including independent state variables for carbon and nutrient biomasses, with separate functions for the acquisition of each resource (Caperon, 1968; Droop, 1968). Phytoplankton take up nutrients as a function of environmental nutrient concentrations, while carbon synthesis is set as a function of light availability and cellular stoichiometry. Dynamic Quota models have proved useful in terms of accounting for observed trends in the stoichiometry of organic matter (Moore *et al.*, 2002; Ward and Follows, 2016), but their application at the global scale has been restricted by practical and scientific concerns associated with their increased complexity, relative to simpler fixed stoichiometry models. An additional phytoplankton state variable must be added for each nutrient element, and the

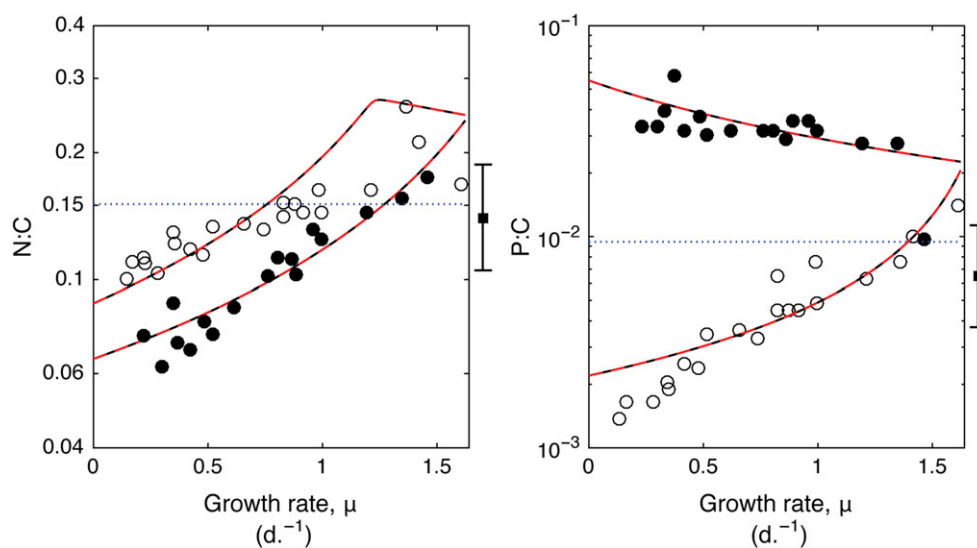


Fig. 1. Equilibrium N:C and P:C stoichiometry of *Selenastrum minutum* (Elrifi and Turpin, 1985), with model fits under N-limitation (filled circles) and P-limitation (open circles). The black and red lines indicate the (identical) output from the Dynamic Quota and Instant Acclimation models. The dotted blue lines indicate output from the Fixed Stoichiometry model (C:N:P = 106:16:1). All three models make use of the same empirical parameters (Table II), which were adjusted to give the best subjective fit to the observations. The N-limited model solutions were determined with incoming N and P concentrations each set to 10 mmol m^{-3} . The P-limited solutions were determined with the incoming N concentration increased to 400 mmol m^{-3} . The error bars to the right of each figure describe the observed distribution of C:N and P:N of particulate organic matter in the surface 50 m of the ocean (Martiny *et al.* 2014). The central mark is the geometric mean, while the whiskers span ± 1 geometric standard deviation.

model formulation also requires the specification of a greater number of empirically uncertain model parameters.

A potential solution to this problem was recently presented by Smith *et al.* (2016), who derived a dynamic “Instant Acclimation” model that combines the simplicity and mathematical efficiency of the Fixed Stoichiometry model with the stoichiometric flexibility of the Dynamic Quota model. Burmaster (1979) first demonstrated that an equilibrium version of the Instant Acclimation model is mathematically equivalent to the Dynamic Quota model, but this equivalence is not guaranteed to hold in a dynamic environment, when nutrient uptake and growth are often imbalanced. It is not yet clear what impact this might have on model performance within a dynamic ecosystem. This article addresses this issue by comparing a Fixed Stoichiometry and a Dynamic Quota model with the alternative Instant Acclimation model (Smith *et al.*, 2016). If the temporal decoupling of nutrient uptake and growth are relatively unimportant, then the Instant Acclimation model may provide an accurate and computationally inexpensive approximation of the full Dynamic Quota model. The aim of this article is therefore to assess the validity and

computational efficiency of the Instant Acclimation model within a simplified, but dynamic, model environment.

THE PHYTOPLANKTON GROWTH MODELS

The three models each represent the growth of a phytoplankton population within an idealized model chemostat. This can be thought of as a highly simplified analogy to the surface ocean, with a biologically productive surface layer supplied by the influx of nutrient-enriched waters from the thermocline. The equations for all three models are fully defined in Tables I and II. In each case, dissolved nitrogen and phosphorus are fed into the model chemostat at rate κ and with incoming nutrient concentrations R_N^{supply} and R_P^{supply} . Phytoplankton growth within the chemostat is limited by nutrient availability, with temperature and light limitation additionally accounted for with an imposed scalar, γ (Appendix A). Nutrients and phytoplankton are washed out of the chemostat at the same rate at which nutrient medium is

Table I: Summary of the model differential equations and auxiliary variables. Instantly acclimated quotas are indicated with tildes (\tilde{Q}_i)

	Model 1: 'Dynamic Quota'	Model 2: 'Instant Acclimation'	Model 3: 'Fixed Stoichiometry'
	Dynamic Quota	Balanced growth	
	Flexible Stoichiometry		Fixed Stoichiometry
State variables			
$dR_i/dt =$	$\kappa (R_i^{\text{supply}} - R_i) - \rho_i B_C$	$\kappa (R_i^{\text{supply}} - R_i) - \mu \hat{Q}_i B_C + \psi_i$	
$dB_i/dt =$	$\rho_i B_C - \kappa B_i$	-	
$dB_C/dt =$	$B_C (\mu - \kappa)$	$B_C (\mu - \kappa)$	
Composite parameters and variables			
$\mu =$	$\gamma \min \left[\mu_N^{\infty} \left(1 - \frac{Q_N^{\min}}{Q_N} \right), \mu_P^{\infty} \left(1 - \frac{Q_P^{\min}}{Q_P} \right) \right]$	$\min \left[\frac{\mu_{r,N}^{\max} \beta_N R_N}{\mu_{r,N}^{\max} + \beta_N R_N}, \frac{\mu_{r,P}^{\max} \beta_P R_P}{\mu_{r,P}^{\max} + \beta_P R_P} \right]$	
$\rho_i =$	$\frac{\rho_i^{\max} \alpha_i R_i}{\rho_i^{\max} + \alpha_i R_i} \cdot \frac{Q_i^{\max} - Q_i}{Q_i^{\Delta}}$	-	
$\mu_{r,i}^{\max} =$	-	$\frac{\gamma \mu_i^{\infty} \rho_i^{\max} Q_i^{\max}}{\gamma \mu_i^{\infty} Q_i^{\min} + \rho_i^{\max} Q_i^{\max} / Q_i^{\Delta}}$	
$\beta_i =$	-	α_i / Q_i^{\min}	
$Q_i^{\Delta} =$	$Q_i^{\max} - Q_i^{\min}$		
$Q_i =$	B_i / B_C	$\frac{\rho_i^{\max} \alpha_i R_i Q_i^{\max}}{\rho_i^{\max} \alpha_i R_i + \mu (\rho_i^{\max} + \alpha_i R_i) Q_i^{\Delta}}$	S_i
$B_i =$	-	$\hat{Q}_i B_C$	$S_i B_C$
Correction factor			
$\psi_i =$	-	see Equations C.1 and C.2	0

Table II: Model parameters after calibration to observations of *Selenastrum minutum* (Elrifi and Turpin, 1985)

Parameter	Symbol	Value	Units
Maximum population growth rate	μ^{\max}	1.64	d ⁻¹
Theoretical asymptotic growth rate as $Q_N \rightarrow \infty$	μ_N^{∞}	2.23	d ⁻¹
Theoretical asymptotic growth rate as $Q_P \rightarrow \infty$	μ_P^{∞}	1.82	d ⁻¹
Nitrate uptake affinity	α_N	1.80	m ³ (mmol C) ⁻¹ d ⁻¹
Phosphate uptake affinity	α_P	1.00	m ³ (mmol C) ⁻¹ d ⁻¹
Maximum nitrate uptake rate	ρ_N^{\max}	0.90	mol N (mol C) ⁻¹ d ⁻¹
Maximum phosphate uptake rate	ρ_P^{\max}	0.06	mol P (mol C) ⁻¹ d ⁻¹
Minimum cellular nitrogen quota	Q_N^{\min}	0.065	mol N (mol C) ⁻¹
Minimum cellular phosphorus quota	Q_P^{\min}	0.0022	mol P (mol C) ⁻¹
Maximum cellular nitrogen quota	Q_N^{\max}	0.39	mol N (mol C) ⁻¹
Maximum cellular phosphorus quota	Q_P^{\max}	0.055	mol P (mol C) ⁻¹
Chemostat dilution rate	κ	0.60	d ⁻¹
Nitrate concentration in supply medium	R_N^{supply}	16.0	mmol N m ⁻³
Phosphate concentration in supply medium	R_P^{supply}	2.0	mmol P m ⁻³
“Redfieldian” N:C stoichiometry	S_N	16/106	mol N (mol C) ⁻¹
“Redfieldian” P:C stoichiometry	S_P	1/106	mol P (mol C) ⁻¹

fed in. For the sake of simplicity any other loss terms are assumed to be negligible relative to this dilution effect.

Model 1: The “Dynamic Quota” model

The full dynamic model includes state variables for dissolved nitrogen and phosphorus (R_N and R_P), and the phytoplankton population is represented in terms of its carbon, nitrogen and phosphorus biomass (B_C , B_N and B_P). Although not considered here, estimates of population cell density would require knowledge of the cellular carbon content (C_{cell}). Elrifi & Turpin (1985) reported uniform values for $C_{\text{cell}} = 0.70$ pmol C (cell)⁻¹ for equilibrium growth rates up to 1.5 d⁻¹ (with C_{cell} increasing to 1.04 pmol C (cell)⁻¹ as the growth rate approaches its maximum value). Variability in the cellular carbon content is not considered here, although it should be noted that such changes may play a role in the regulation of cellular nutrient-to-carbon ratios (Garcia *et al.*, 2016). Dissolved carbon is also omitted from the model because its availability is assumed to be non-limiting to growth.

Phytoplankton growth rates are defined according to their cellular nutrient-to-carbon biomass ratios, or “quotas” (where, $i = N$ or P).

$$Q_i = \frac{B_i}{B_C} \quad (1)$$

The gross rate of carbon synthesis (μ) is a rectangular-hyperbolic function of the most-limiting

internal nutrient quota (Caperon, 1968; Droop, 1968), increasing from zero when either quota is equal to a minimum value of $Q_i = Q_i^{\min}$, towards an asymptotic value of μ_i^{∞} as $Q_i \rightarrow \infty$. As plankton can never actually obtain this infinite quota for either nutrient, the values of μ_i^{∞} are neither observable nor (in isolation) biologically meaningful. Precise estimates of μ_i^{∞} can however be inferred from steady-state observations of the maximum population growth rate, μ_{\max} (see equation B.17 in Appendix B, and Table II). (Note that this gives different values of μ_i^{∞} for the hypothetical growth rates at infinite N quota and at infinite P quota.)

The cellular nutrient quotas increase by nutrient uptake (ρ_i), defined as Michaelis–Menten functions of the environmental nutrient concentrations (R_i). These functions also include an uptake regulation term that restricts nutrient uptake as the quotas become full. This term is required to avoid the Instant Acclimation model becoming intractable when light-limited growth is close to or equal to zero. With the exception of this uptake limitation term, the dynamic model is equivalent to the multi-nutrient phytoplankton growth model first described by Legović and Cruzado (1997), and later examined by Klausmeier *et al.* (2004).

Model 2: The “Instant Acclimation” model

The dynamic quota model can be simplified by assuming that at any point in time the ratio of nutrient uptake (ρ_i) to carbon synthesis (μ) is in balance with the cellular quota (Q_i). In practice, this “balanced growth” assumption (Burmester, 1979; Smith *et al.*, 2016) is achieved by assuming that the quotas adjust instantly to the environmental conditions, such that the instantly acclimated quota (\tilde{Q}_i) is given by the following equation:

$$\tilde{Q}_i = \frac{\rho_i}{\mu} \quad (2)$$

This assumption allows us to define μ solely as function of physiological traits and (external) environmental conditions, including light, temperature and nutrients (Table I). We no longer require a prognostic equation for B_i , which is now given as the product of B_C and \tilde{Q}_i .

We can calculate the rates of change of dissolved nutrients (dR_i/dt) by replacing ρ_i with the product of the carbon-specific growth rate, μ , and the instantly acclimated quota, \tilde{Q}_i . It is, however, important to note that in order to conserve mass we must also account for the instantaneous adjustment of the cellular quotas. Smith *et al.* (2016) showed that this can be achieved by including a mass correction term (ψ_i) that precisely accounts for the nutrient uptake or release associated with the adjustment

of the cellular quota (see Appendix C and Smith *et al.*, 2016). When the entire system is in equilibrium, the mass balance terms decrease to zero, such that the Instant Acclimation model gives identical results to the Dynamic Quota model (Burmaster, 1979; Smith *et al.*, 2016).

Model 3: The “Fixed Stoichiometry” model

The Instant Acclimation model can be further simplified by assuming the nutrient quotas take predetermined fixed values.

$$\tilde{Q}_i = S_i \quad (3)$$

Under this assumption, plankton nutrient uptake and N and P biomasses are defined as for Model 2, with the exception that $\tilde{Q}_i = S_i$ and $\psi_i = 0$ (Table I). The “Fixed Stoichiometry” model forms the basis of many global marine ecosystem models (Fasham *et al.*, 1993; Le Quéré *et al.*, 2005; Follows *et al.*, 2007), being favoured for its computational efficiency and relative simplicity. The fixed ratio S_i is most typically set to the “Redfieldian” C:N:P ratio of 106:16:1 (Redfield, 1934).

MODEL ANALYSIS

Equilibrium solutions

The previous section defined three closely related models of phytoplankton growth in an idealized chemostat environment. The model equations can be solved analytically for a system-level equilibrium by assuming all rates of change are equal to zero. The associated equilibrium solutions (each denoted with an overbar) are defined for the three models as follows, with the subscripts “lim” and “non” denoting the limiting and non-limiting nutrient elements.

$$\bar{R}_{\text{lim}} = \frac{\mu^{\text{max}} \kappa}{\beta_{\text{lim}} (\mu^{\text{max}} - \kappa)} \quad (4)$$

$$\bar{B}_{\text{lim}} = \bar{R}_{\text{lim}}^{\text{supply}} - \bar{R}_{\text{lim}} \quad (5)$$

$$\bar{B}_C = \frac{\bar{B}_{\text{lim}}}{\bar{Q}_{\text{lim}}} \quad (6)$$

$$\bar{R}_{\text{non}} = \bar{R}_{\text{non}}^{\text{supply}} - \frac{\bar{Q}_{\text{non}}}{\bar{Q}_{\text{lim}}} (\bar{R}_{\text{lim}}^{\text{supply}} - \bar{R}_{\text{lim}}) \quad (7)$$

$$\bar{B}_{\text{non}} = \bar{B}_C \bar{Q}_{\text{non}} \quad (8)$$

For the sake of clarity, the solutions are presented in simplified form using the composite parameters μ^{max} and β_i (Table I). The full solutions are much more cumbersome, especially for the non-limiting nutrient and its associated phytoplankton biomass, and are not shown here. The equilibrium solutions are the same for all three models, with the exception that the cellular stoichiometries \tilde{Q}_i are either defined as emergent traits (Dynamic Quota and Instant Acclimation), or set to predetermined fixed values (Fixed Stoichiometry, $\tilde{Q}_i = S_i$).

With nothing to set them apart at equilibrium, the two flexible stoichiometry models (Dynamic Quota and Instant Acclimation) give identical results for all five variables. The Fixed Stoichiometry model also provides identical solutions in terms of the equilibrium limiting nutrient (\bar{R}_{lim}) and limiting nutrient biomass (\bar{B}_{lim}). These solutions are independent of the cellular quota, which is the only factor that separates the fixed and flexible stoichiometry models at equilibrium. On the other hand, the remaining three model variables are dependent on the emergent or fixed cellular stoichiometry, and hence the Fixed Stoichiometry model may produce different equilibrium solutions for the non-limiting nutrient (\bar{R}_{non}), the non-limiting nutrient biomass (\bar{B}_{non}) and the carbon biomass (\bar{B}_C).

Figure 1 shows equilibrium solutions to the three models as a function of an increasing equilibrium dilution rate ($\kappa = \mu$). The Dynamic Quota and Instant Acclimation models are identical, regardless of the dilution rate. Both of these flexible stoichiometry models are able to reproduce most of the observed variation of the cellular limiting-nutrient to carbon ratios ($r^2 = 0.61$ for N:C and 0.86 for P:C). The two models also reproduce most of the observed variability in the non-limiting nutrient quotas ($r^2 = 0.77$ for N:C and 0.73 for P:C). The Fixed Stoichiometry model is unable to capture any of this variability. For any single value of κ , the equilibrium solutions of the Fixed Stoichiometry model could be adjusted to exactly match those of the two flexible stoichiometry models (by changing the imposed value of S_i to match \tilde{Q}_i). However, given that the flexible equilibrium quotas change as a function of the environment, there is no single value for S_i that would be applicable under all conditions.

Nutrient drawdown

Equations 4–8 and Fig. 1 demonstrate that the ability to account for flexible cellular stoichiometry may have an important influence on our predictions of steady state carbon and nutrient dynamics. It is also clear that the ability of the Dynamic Quota model to account for the temporal decoupling of nutrient uptake and carbon synthesis has absolutely no effect on the equilibrium

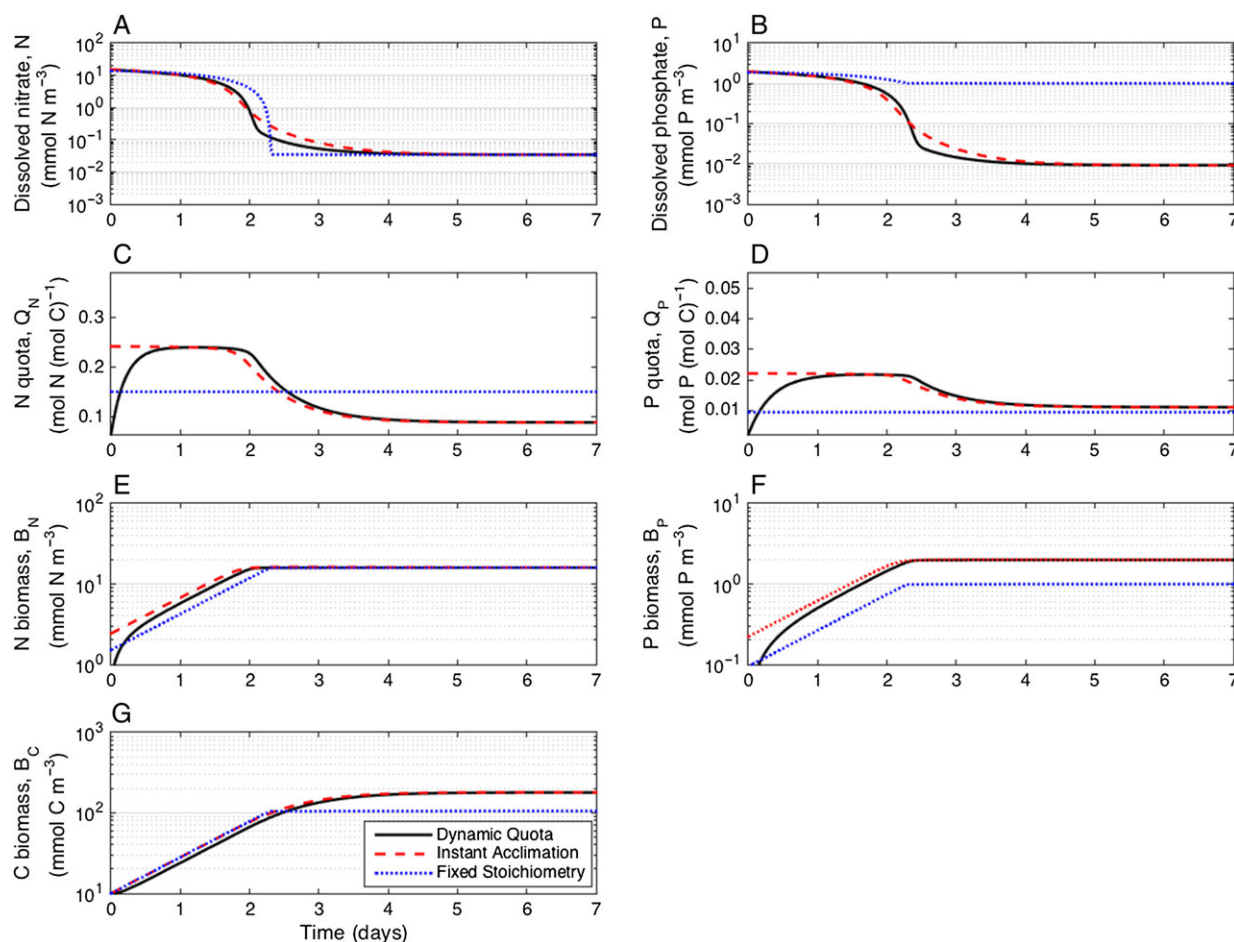


Fig. 2. Model behaviour when initialized with abundant nutrients and a small initial population of phytoplankton. These simulations have a constant dilution rate and incoming nutrient concentrations (parameter values are listed in Table 2). (A) Dissolved nitrate; (B) dissolved phosphate; (C) phytoplankton nitrogen quota; (D) phytoplankton phosphorus quota; (E) phytoplankton nitrogen biomass; (F) phytoplankton phosphorus biomass and (G) phytoplankton carbon biomass.

behaviour of the model, relative to the simpler Instant Acclimation model (simply because this decoupling does not occur at equilibrium). This section and the following explore whether perturbations from equilibrium will cause the two flexible stoichiometry models to yield conflicting behaviour, as nutrient uptake and carbon synthesis become decoupled in the Dynamic Quota model.

Figure 2 shows the response of the three models as the chemostat is inoculated with a small initial population of nutrient starved cells. This can be considered as analogous to a natural phytoplankton bloom, where a small initial population grows rapidly in the presence of initially abundant nutrients and in the absence of significant zooplankton grazing pressure. The nutrient concentrations within the chemostat start at their input concentrations, with an incoming excess of phosphorus ensuring nitrogen limitation. The models were solved numerically using the Matlab “ode45” solver. In all

cases, dissolved nitrogen is drawn down to a low equilibrium concentration as phytoplankton biomass accumulates. At the end of the seven day run, the system is effectively at equilibrium and, as expected, the equilibrium states of the Dynamic Quota and Instant Acclimation models are identical. The equilibrium concentrations of dissolved nitrogen and phytoplankton nitrogen biomass are also matched by the Fixed Stoichiometry model. The Fixed Stoichiometry model strongly overestimates the equilibrium dissolved phosphorus concentration and underestimates the equilibrium carbon and phosphorus phytoplankton biomass.

Despite their equivalence in terms of some or all state variables at equilibrium, Fig. 2 shows that all three models differ in terms of their transient behaviour during nutrient drawdown. In general, the flexible stoichiometry models exhausts the limiting nutrient more slowly than the Fixed Stoichiometry model. This occurs

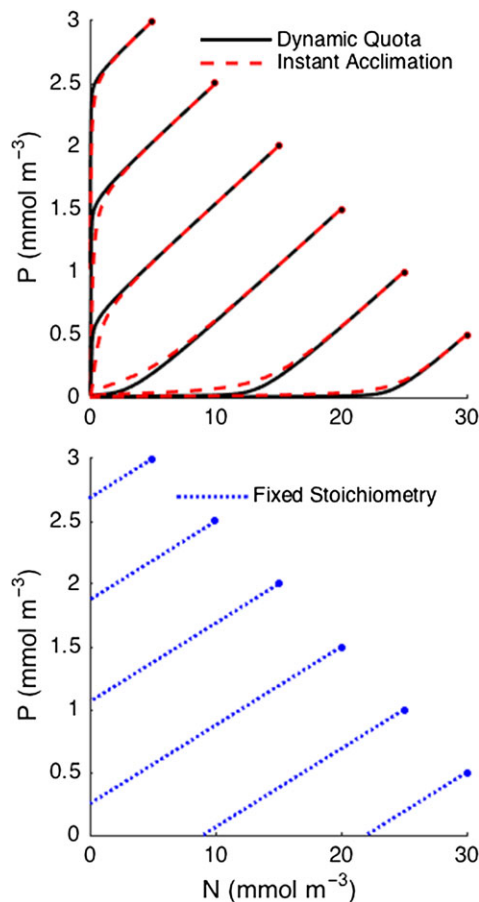


Fig. 3. Nutrient drawdown trajectories for a range of N:P supply ratios. The two flexible stoichiometry models are in the upper panel. The fixed stoichiometry model is in the lower panel. The top-right endpoints indicate the incoming nutrient concentrations, while the opposite ends of each line indicate the equilibrium nutrient concentrations.

because the flexible nutrient quotas decline as nutrients become depleted, decreasing the demand for scarce nutrients relative to carbon synthesis and slowing the pace of nutrient drawdown. This effect is most pronounced in the Instant Acclimation model, because (unlike in the Dynamic Quota model) the stoichiometric response is instantaneous (Smith *et al.*, 2016).

Figure 3 shows the relative drawdown of dissolved nitrogen and phosphorus in experiments across a range of input nutrient ratios. In each case the model chemostat was inoculated as before, with a small initial population of nutrient starved cells. Regardless of the incoming nutrient ratio, the two flexible stoichiometry models are able to draw down both limiting and non-limiting nutrients close to zero. This occurs because uptake of the non-limiting nutrient continues even as the limiting nutrient is exhausted. This behaviour is not seen in the Fixed Stoichiometry model, for which the complete drawdown

of the limiting nutrient prevents any further drawdown of the non-limiting nutrient. Figure 3 also shows that although the two flexible stoichiometry models both equilibrate in the same steady state, the Instant Acclimation model follows a slightly different trajectory to the Dynamic Quota model. This occurs because the Instant Acclimation and Dynamic Quota models adjust their stoichiometry to the changing environmental conditions on somewhat different timescales, as described above.

Response to ongoing perturbations

The response of the three models to rapid environmental perturbations can be assessed by imposing an irregular environmental forcing function (defined in Appendix A), varying (in opposite phase) the light-limitation term (γ) and the incoming nutrient concentrations (R_N^{supply} and R_P^{supply}). This section explores the response to a (somewhat arbitrary) forcing function with a period of 15 days, as shown in Fig. 4H. The aim of this function is to provide a highly dynamic environment, challenging the two balanced growth models to reproduce the behaviour of the Dynamic Quota model (rather than to provide an accurate representation of any particular ocean environment). The response to forcing of different periods is explored in the following section.

The behaviour of the three models in response to the variable forcing is shown in Fig. 4. In each case, the models were evaluated for 45 days, during which time a repeating cycle was achieved. In almost all respects, the Instant Acclimation model tracks the Dynamic Quota model very closely. There are, however, some discrepancies. In general, the nutrient quotas and nutrient biomasses respond slightly more quickly and show slightly greater variability in the Instant Acclimation model. This is attributable to the phytoplankton stoichiometry changing instantly in response to the environment. On the other hand, the dissolved nutrient concentrations respond more slowly, and show less variability in the Instant Acclimation model. This is attributable to the damped uptake response described above.

The Fixed Stoichiometry provides a markedly less accurate approximation of the Dynamic Quota model. The dissolved nitrogen concentration is closely matched throughout the forcing period, but the nitrogen biomass is only reproduced during periods when the nutrient input is low and the light-limited growth rate is high (i.e. when nitrogen is limiting to growth). During periods where nitrogen is not limiting, the nitrogen biomass is underestimated several-fold. The opposite pattern is seen for the phytoplankton carbon biomass, which is reproduced accurately when nutrient input is high and growth is limited by γ . During periods when γ is high

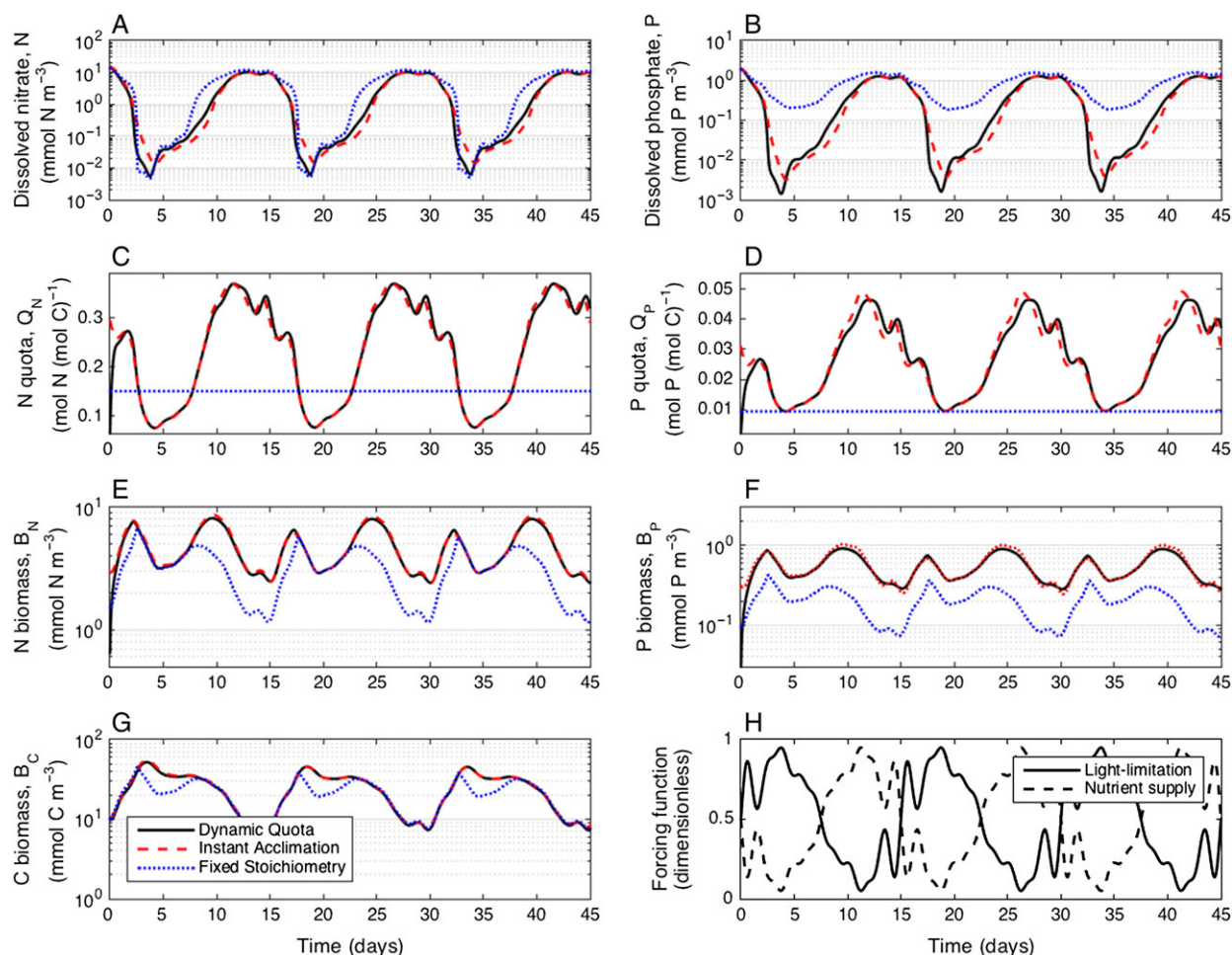


Fig. 4. Results of the three models in response to variable nutrient input and light limitation. **(A)** Dissolved nitrate; **(B)** dissolved phosphate; **(C)** phytoplankton nitrogen quota; **(D)** phytoplankton phosphorus quota; **(E)** phytoplankton nitrogen biomass; **(F)** phytoplankton phosphorus biomass; **(G)** phytoplankton carbon biomass and **(H)** environmental forcing functions.

and the nutrient input is low, the carbon biomass is strongly underestimated. The Fixed Stoichiometry model also provides a very poor approximation of the Dynamic Quota model in terms of the (non-limiting) dissolved phosphorus concentration and the phytoplankton phosphorus biomass.

Timescales of perturbation

The 15-day period examined in the previous section was chosen arbitrarily to simulate the dynamic nature of the marine ecosystem. Although the Instant Acclimation model reproduces the Dynamic Quota model very well, it is not clear whether its performance might breakdown on different timescales. Figure 5 shows the fidelity of the Instant Acclimation and Fixed Stoichiometry models to the Dynamic Quota model, under sinusoidal environmental forcing across a range of timescales. In each case, the

models were run until a repeating cycle was achieved, with the period of forcing varied in 10 logarithmically spaced increments between 0.1 and 100 days. The means of each state variable during the last period of forcing were compared between models, with the figure showing differences relative to the Dynamic Quota model. The Instant Acclimation model provides an accurate approximation of the Dynamic Quota model as long as the forcing period is longer than ~ 12 h. Below this, the Instant Acclimation underestimates phytoplankton C, N and P biomass. This appears to be related to the instantaneous response to the light-and-temperature-limitation factor (γ). The bias at high frequencies disappears when the Instant Acclimation model was re-evaluated with a 24 h running mean applied to γ ("Instant Acclimation 24"). With this filter applied, the Instant Acclimation model provides an accurate representation of the Dynamic Quota at all frequencies of environmental forcing. This is not the case for

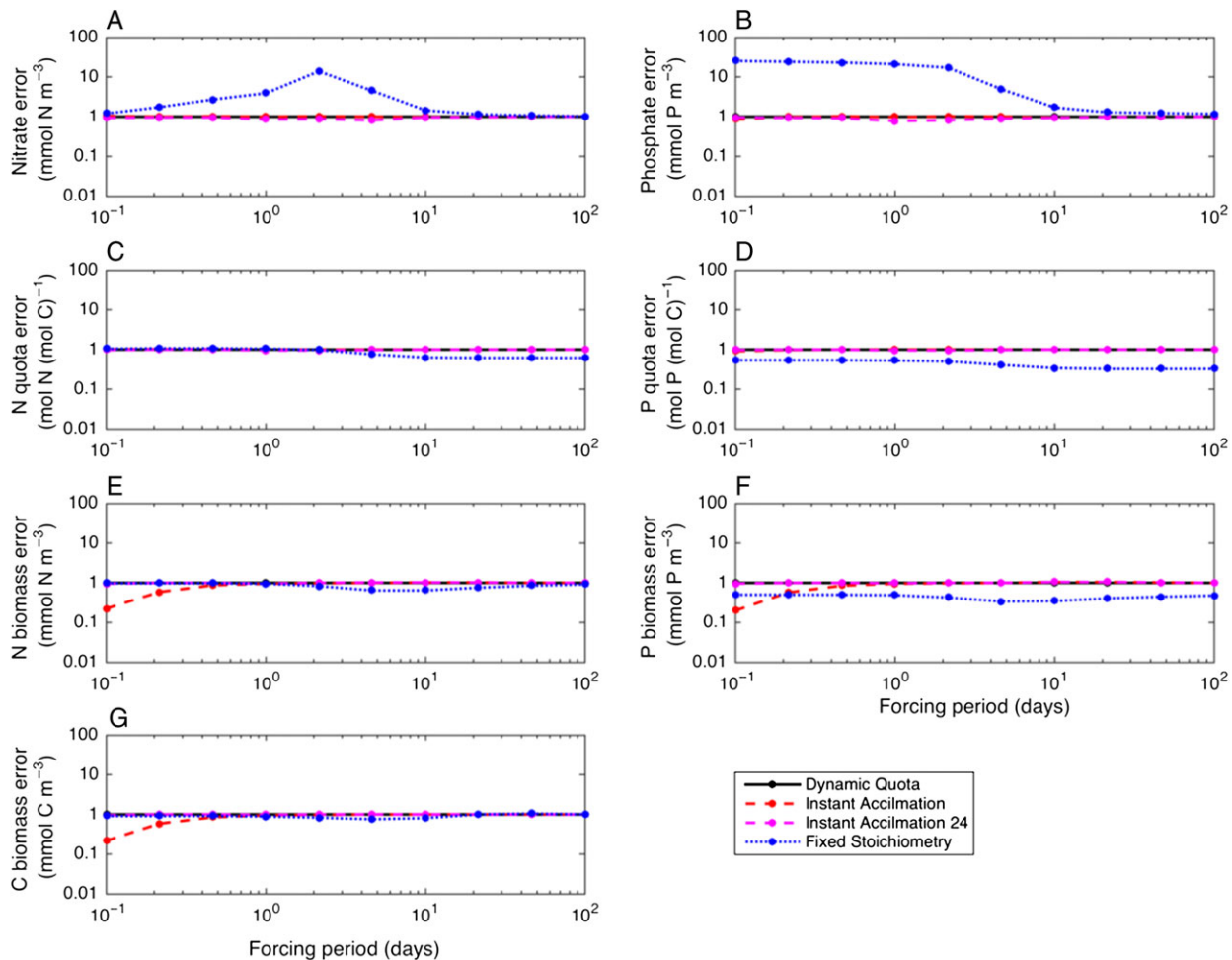


Fig. 5. Relative errors of the Instant Accilimation and Fixed Stoichiometry model in comparison to the Dynamic Quota model, as a function of the environmental forcing period. Each state variable was compared in terms of its mean value during the last cycle of environmental forcing. The Instant Accilimation model was evaluated twice, the second time with a 24-h running mean applied to the environmental forcing function, γ (“Instant Accilimation 24”). Panels show errors in (A) dissolved nitrate; (B) dissolved phosphate; (C) phytoplankton nitrogen quota; (D) phytoplankton phosphorus quota; (E) phytoplankton nitrogen biomass; (F) phytoplankton phosphorus biomass and (G) phytoplankton carbon biomass.

the Fixed Stoichiometry model, which shows notable biases in all the model variables, at some or all frequencies of environmental forcing. These biases were not meaningfully improved by the application of a 24 h running mean to γ (not shown).

DISCUSSION

Globally important fluxes of carbon and essential nutrients through the marine ecosystem are mediated by planktonic nutrient uptake and photosynthesis. These two processes are not rigidly coupled at the cellular level, and phytoplankton growth can be described as a two step process comprising resource-dependent nutrient uptake, followed by biomass synthesis that is

regulated by the size of the cellular quota (Caperon, 1968; Droop, 1968; Legović and Cruzado, 1997). For each phytoplankton population included in an ecosystem model, this approach requires explicit model state variables for the phytoplankton biomass of carbon and each potentially limiting nutrient element. The additional complexity relative to fixed stoichiometry models may be associated with increased uncertainty, and also incurs additional computational expense, particularly when each state-variable needs to be transported through a spatially resolved ocean model (Kwiatkowski *et al.*, 2014). These constraints have limited the use of dynamic quota models, particularly at the global scale. The use of fixed stoichiometry models is nonetheless at odds with observations that show considerable variability in the C:N:P stoichiometry of phytoplankton cells

and marine particulate organic matter (Fig. 1). This limits our ability to understand and accurately represent the coupled cycles of carbon and essential nutrients in ocean models (Ayata *et al.*, 2014).

Smith *et al.* (2016) derived a simplified approximation of the Dynamic Quota model that was extended here to account for multiple nutrients. This Instant Acclimation model combines the physiologically constrained flexible stoichiometry of the Dynamic Quota model with the lower complexity and computational expense of the Fixed Stoichiometry model. The Instant Acclimation model provides a better approximation of the Dynamic Quota model than the Fixed Stoichiometry model, and this appears to be the case regardless of the timescales on which the system is perturbed (as long as high frequency variation in the light-limitation term are suppressed; Fig. 5b). The relative simplicity of the Instant Acclimation model in relation to the Dynamic Quota model suggests that it may be appropriate for application at the global scale, but any potential gains in computational efficiency need to be weighed against the computational cost of solving the physiological equations themselves (which may, in some cases, require very short time-steps). The impact of dynamic environmental forcing on this aspect of computational efficiency was evaluated by running the three models with a sinusoidal environmental forcing function applied to either the incoming nutrient concentrations (R_N^{supply} and R_P^{supply}) or to the light and temperature limitation factor (γ). The period of the sinusoidal function was varied between 0.1 and 100 days, recording in each case the average number of time-steps per day required for stable integration (by the Matlab ode45 solver) during the last cycle of environmental forcing. In response to forcing of the incoming nutrient concentrations, Fig. 6A shows that

the Instant Acclimation model was the most efficient of the three models, regardless of the forcing period. On the other hand, Fig. 6B shows that the Instant Acclimation model was the most efficient only when the light limitation term was forced with a period of more than ~ 1 day. When the forcing period was decreased below this, integration of the Instant Acclimation model required disproportionately short time-steps. Figure 6C shows that the Instant Acclimation model did not suffer from this increased inefficiency when the daily light cycle was removed (by applying a 24 h running mean to γ).

It appears that a very short time-step is required to account for the instantaneous adjustment of the cellular quota in response to rapid variation of the light and temperature limited growth rate, γ (Table 1). This issue can be better understood by considering the hypothetical response of the Instant Acclimation model to a rapid onset of darkness. The equation for \bar{Q}_i in Table 1 shows that the quota is equal to Q_i^{max} when $\gamma = 0$. If we consider the stable, nitrogen-limited community in Fig. 2, a sudden onset of darkness would lead to an equally rapid jump in both the nitrogen quota, and the overall nitrogen biomass. This would require the almost instant acquisition of more than 50 mmol N m^{-3} through the “mass correction” term, ψ_N . This is 500 times more than the $\sim 0.1 \text{ mmol N m}^{-3}$ dissolved in the growth medium, and hence the model solver requires an extremely short time-step.

Although the Instant Acclimation model includes fewer state variables than the Dynamic Quota model, its tight coupling to the light cycle suggests that the requirement for a very short time-step could, in some circumstances, outweigh any gains in computational efficiency associated with the spatial transport of state variables. However, in applications where the diel cycle is not of primary interest, our results suggest that the Instant

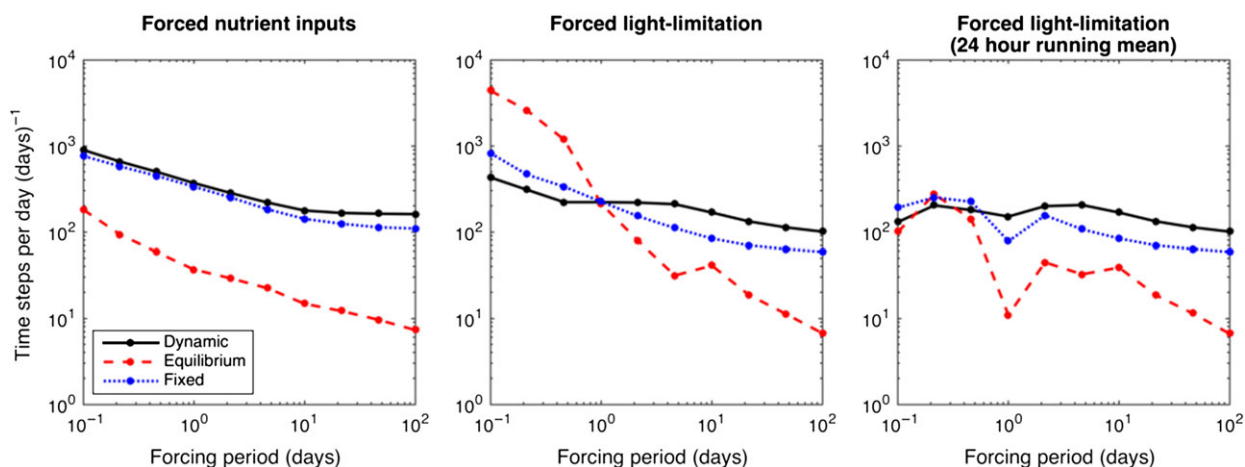


Fig. 6. Mean time-step frequency in Matlab ode45 as a function of the environmental forcing period.

Acclimation model should allow efficient representation of flexible phytoplankton stoichiometry in global ecosystem models that currently (and erroneously) assume fixed stoichiometry. Such a step would allow an increase in both model realism and computational efficiency. The use of the same mathematically consistent model hierarchy applied here would also allow a precise assessment of the impact of flexible stoichiometry and dynamic sub-cellular processes on marine ecosystems and biogeochemistry. Such analyses have been performed previously, but any findings must be weighed against inconsistencies in both the structure and parameterization of the different models (Ayata *et al.*, 2014).

Development of the Instant Acclimation model within three-dimensional ocean models will require further work to assess its suitability outside the idealized environments considered here. It remains to be seen how well the simpler model will handle sources and sinks attributable to advection and diffusion of living plankton cells. One particular issue is that without state variables for planktonic nitrogen and phosphorus, these will not be available for transport. Instead, only planktonic carbon can be transported, and it must be assumed that all associated nutrient biomass is obtained locally. The validity of this assumption will require further study, ideally in a suite of ocean circulation models across a range of spatial resolutions (with an associated range of time-scales). In addition, the utility of the Instant Acclimation model remains to be assessed within a more complex community model.

CONCLUSIONS

The Instant Acclimation model provides an accurate approximation of the Dynamic Quota model under a wide range of dynamic environmental conditions. This performance is achieved despite the removal of two of the five state variables originally included in the Dynamic Quota model. The Instant Acclimation model appears to represent a viable alternative to much less physiologically accurate Fixed Stoichiometry models that are currently in use within a number global ocean modelling environments. An upcoming challenge will be to redevelop the Instant Acclimation model within more complex ecological and environmental modelling frameworks.

SUPPLEMENTARY DATA

Supplementary data is available at *Journal of Plankton Research* online.

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