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**Co-evolution of
phytoplankton and
ocean N:P ratios**

T. M. Lenton and
C. A. Klausmeier

Co-evolution of phytoplankton C:N:P stoichiometry and the deep ocean N:P ratio*

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Abstract

There is a long-established, remarkable correspondence between the nitrogen-to-phosphorus ratio $N:P \sim 15$ of deep ocean water and the “Redfield ratio” of $N:P \sim 16$ required by phytoplankton. Redfield and subsequent workers have suggested that it is due to N-fixing organisms being selected when $N:P < 16$ but being out-competed when $N:P > 16$. Models have shown this mechanism can work, but recent observations reveal that the real system is more complex. First, the C:N:P stoichiometry of phytoplankton varies with growth rate, nutrient and light limitation, species and phylum. Second, although N-fixation is sometimes P-limited and suppressed by N-addition, there is also evidence for Fe-limitation, light-limitation and P and Fe co-limitation of N-fixers. Here we adapt recent models to include non-Redfieldian stoichiometry of phytoplankton and limitation of N-fixers by resources other than P. We show that the deep ocean N:P is set by the N:P threshold that triggers N-fixation, and is not directly related to the N:P ratio of sinking material. However, assuming competitive dynamics set the N:P threshold for N-fixation, it will be close to the N:P requirement of non-fixers (rather than that of N-fixers) and consequently so will the deep ocean N:P ratio. Theoretical limits on the N:P requirements of phytoplankton suggest that since the deep ocean became well oxygenated, its N:P has remained within the range 7.7–32.3. Decreases in phytoplankton C:P and N:P ratios over the past ~ 1 Gyr are predicted to have driven a decrease in deep ocean N:P, probably via increasing PO_4 . Even if Fe or light limitation restrict N-fixers to a fraction of the surface ocean, they reach higher densities there, minimising variations in deep ocean N:P. Thus Redfield’s mechanism is robust and we expand it to suggest that phytoplankton C:N:P and deep ocean N:P have co-evolved.

1 Introduction

There is a well-known correspondence between the average proportions of N and P in marine organic matter – the “Redfield ratio” of $N:P \sim 16$ – and the composition of the

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5 deep ocean with N:P~15. Redfield (1934) suggested that an explanation "... may be sought in the activities of those bacteria which form nitrogenous compounds or liberate nitrogen in the course of the decomposition of organic matter" intuiting that "... in a world populated by organisms of these two types the relative proportion of phosphate and nitrate must tend to approach that characteristic of protoplasm in general..." In his later work, Redfield (1958) proposed that: "When living in an environment containing a deficiency of nitrate relative to phosphate, the growth and assimilation of the nitrogen-fixing organisms might tend continually to bring the proportions of nitrogen and phosphorus nearer to that characteristic of their own substance." Subsequent workers
10 (Broecker and Peng, 1982; Tyrrell, 1999; Lenton and Watson, 2000) have expressed the mechanism in terms of competition between N-fixing organisms that are selected when N:P<16 and non-fixers that out-compete them when N:P>16. This mechanism assumes that under P-limiting conditions N-fixers have a lower growth rate than non-fixers, because of the high energy cost of N-fixation, whilst under sufficiently N-limiting
15 conditions N-fixers have a higher growth rate than non-fixers.

The canonical value of ~16 for the N:P Redfield ratio represents an average for today's phytoplankton. It has long been known that the Redfield ratios of phytoplankton vary with growth rate (Goldman et al., 1979) and light regime (Goldman, 1986). Nutrient replete phytoplankton cultures (with consequently high growth rates) have a mean
20 N:P of 10.1 across 34 studies, in contrast to marine particulate matter with a mean N:P of 16.4 across 27 studies (Geider and La Roche, 2002). It was thought that N:P~16 might represent some kind of optimum for phytoplankton, but no theoretical basis has been found for this (Klausmeier et al., 2004). Instead, the optimum composition of phytoplankton predicted under exponential growth is 8.2, whilst under light limitation it
25 is 35.8, nitrogen limitation 37.4, and phosphorus limitation 45.0. Furthermore, different phyla or super-families of differing antiquity have different N:P, with older "greens" having higher N:P than younger "reds" (Quigg et al., 2003). This raises the question (Falkowski and Davis, 2004; Arrigo, 2005): Would a systematic shift in the Redfield ratios alter deep ocean composition? We address this question by generalising two ex-

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isting models (Tyrrell, 1999; Lenton and Watson, 2000) to allow variation of the Redfield ratios.

The question provokes a deeper one: What sets the deep ocean N:P ratio? Some authors still make statements, which can be traced back to Redfield (1934), to the effect that the ratio of major nutrients N:P~15 in the deep ocean directly reflects the average Redfield ratio (N:P~16) of sinking organic matter being remineralised in the water column. Whilst the gradient (~15) of a plot of ocean NO₃ versus PO₄ measurements reflects the ratio in which N and P are remineralised, where the line of points intercepts an axis – typically at the origin or close to it, at a low value of PO₄ – demands a different explanation. This is because the cycle of uptake in the surface ocean and remineralisation at depth redistributes NO₃ and PO₄, but cannot alter their absolute or relative amounts in the ocean as a whole, which depend on net input to or removal from the ocean. The ocean mixing time (<10³ yr) is shorter than the residence time of NO₃ (~3×10³ yr) (Codispoti, 1995; Lenton and Watson, 2000), which is in turn shorter than that of PO₄ (~1.8×10⁴ yr) (Ruttenberg, 1993; Lenton and Watson, 2000). Hence mixing tends to homogenize the processes setting the concentrations of both nutrients. Furthermore, we can consider a timescale over which PO₄ is relatively constant but NO₃ can vary due to imbalances of input (primarily N-fixation) and output (primarily denitrification) processes. The essence of Redfield's mechanism is that one of these processes – N-fixation – responds to any deficit of NO₃ relative to the N:P requirement of average phytoplankton (non-fixers), whilst the other process – denitrification – tends to continually remove NO₃ and thus maintain a small N:P deficit and corresponding population of N-fixers.

Recent discoveries have the potential to further complicate Redfield's mechanism: Although N-fixation is sometimes P-limited and suppressed by N-addition, there is also evidence for Fe-limitation (Berman-Frank et al., 2001; Mills et al., 2004), light-limitation (Hood et al., 2004) and P and Fe co-limitation (Mills et al., 2004) of N-fixers. This raises the question: Given that N-fixers may be limited to restricted areas of the world ocean, can they still regulate deep ocean N:P? We address this question by adapting one of

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the existing models (Tyrrell, 1999) to restrict N-fixers to a fraction of the surface ocean.

2 Methods

Here we briefly describe the two models adapted for this study. For full explanations of their formulation see Lenton and Watson (2000) and Tyrrell (1999).

5 2.1 LW model

Lenton and Watson (2000) (henceforth LW) model deep ocean reservoirs of nitrate (actually available nitrogen) and phosphate, and a reservoir of atmospheric oxygen expressed as the concentration in water ventilating the deep ocean. The limiting nutrient in water up-welled to the surface ocean is assumed to be completely used up, generating a corresponding concentration of new production (C here instead of N , to avoid confusion with Tyrrell's N):

$$C = \min(r_{C:N}NO_3, r_{C:P}PO_4) \quad (1)$$

Here we generalize the original model (M1) of LW to allow independent variation of the C:N and C:P Redfield ratios of new production (sinking organic matter from the surface layer), denoted $r_{C:N}$ and $r_{C:P}$, and the N:P threshold below which N-fixation occurs, denoted $r_{N:P,Fix}$. The generalized equation for N-fixation (F_{N-Fix}) is:

$$F_{N-Fix} = \frac{k_3}{k_p} \left(PO_4 - \frac{NO_3}{r_{N:P,Fix}} \right) \quad (2)$$

All constants are retained including the initial N-fixation flux $k_3=8.7 \times 10^{12}$ mol N yr⁻¹ and the initial normalizing values: the average deep ocean nutrient concentrations of $PO_{4(0)}=2.2 \mu\text{mol kg}^{-1}$ and $NO_{3(0)}=30.9 \mu\text{mol kg}^{-1}$ from World Ocean Atlas data, a representative oxygen concentration of $O_{2(0)}=331.5 \mu\text{mol kg}^{-1}$ for water ventilating the deep ocean, and an average carbon concentration of new production in surface waters

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of $C_0=226.0 \mu\text{mol kg}^{-1}$. The derived constant $k_P=\text{PO}_{4(0)}-\text{NO}_{3(0)}/16=0.26875 \mu\text{mol kg}^{-1}$ represents the surplus PO_4 remaining in surface waters after NO_3 has been removed by new production. Denitrification in the water column depends on the anoxic fraction of the ocean, A , which is given by:

$$A = 1 - k_1 \frac{\text{O}_2}{\text{O}_{2(0)}} \frac{C_0}{C} \quad (3)$$

where the initial oxidic fraction, $k_1=0.86$, hence the initial anoxic fraction $A_0=0.14$.

For the nitrate reservoir, N-fixation in the surface ocean is balanced by water column denitrification (initially $k_4=4.3 \times 10^{12} \text{ mol N yr}^{-1}$), a fixed flux of sedimentary denitrification (k_4), and organic nitrogen burial in sediments (initially $0.1 \times 10^{12} \text{ mol N yr}^{-1}$):

$$\frac{d\text{NO}_3}{dt} = k_8 \left(\frac{k_3}{k_P} \left(\text{PO}_4 - \frac{\text{NO}_3}{r_{\text{N:P,Fix}}} \right) - k_4 \frac{A}{A_0} - k_4 - \frac{k_2}{b_{\text{C:N}}} \left(\frac{C}{C_0} \right)^2 \right) \quad (4)$$

where $k_8=7.1 \times 10^{-22} \text{ kg}^{-1}$ converts from reservoir size in mol to average concentration, the initial organic carbon burial flux $k_2=3.75 \times 10^{12} \text{ mol C yr}^{-1}$ and the C:N burial ratio $b_{\text{C:N}}=37.5$.

Input to the phosphate reservoir comes from weathering (initially $k_5=3.6 \times 10^{10} \text{ mol P yr}^{-1}$) and removal occurs due to iron-sorbed phosphorus (Fe-P) burial (initially $k_6=0.6 \times 10^{10} \text{ mol P yr}^{-1}$), organic phosphorus (Org-P) burial (initially $1.5 \times 10^{10} \text{ mol P yr}^{-1}$) and calcium-bound phosphorus (Ca-P) burial (initially $k_7=1.5 \times 10^{10} \text{ mol P yr}^{-1}$):

$$\frac{d\text{PO}_4}{dt} = k_8 \left(k_5 W - \frac{k_6}{k_1} (1 - A) - \frac{k_2}{b_{\text{C:P}}} \left(\frac{C}{C_0} \right)^2 - k_7 \left(\frac{C}{C_0} \right)^2 \right) \quad (5)$$

where W is a normalised weathering forcing parameter (i.e. $W=1$ at present day), and $b_{\text{C:P}}=250$ is the C:P burial ratio.

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Net addition of oxygen occurs due to organic carbon (Org-C) burial and net removal due to oxidative weathering:

$$\frac{dO_2}{dt} = k_9 \left(k_2 \left(\frac{C}{C_0} \right)^2 - k_2 W \right) \quad (6)$$

where $k_9 = 8.96 \times 10^{-24} \text{ kg}^{-1}$ converts from atmospheric oxygen reservoir size in mol to concentration dissolved in surface waters ventilating the deep ocean.

The system was solved analytically for steady state following the method in the Appendix of LW but for an unknown limiting nutrient, yielding:

$$\frac{C}{C_0} = W^{\frac{1}{2}} \quad (7)$$

$$\frac{O_2}{O_{2(0)}} = W^{\frac{3}{2}} \quad (8)$$

$$PO_4 = \frac{NO_3}{r_{N:P-Fix}} + k_P (4.025 - 3.025W) \quad (9)$$

$$A = 1 - k_1 W \quad (10)$$

Steady state for O_2 is lost when $A \rightarrow 0$, which from Eq. (10) gives an upper limit on $W = 1.163$ (above this, O_2 increases monotonically).

2.2 TT model

Tyrrell (1999) (henceforth TT) models nitrate and phosphate in two boxes, the surface and deep ocean, and includes explicit competition between N-fixing and non-fixing organisms in the surface ocean. However, the TT model does not include any cycling of carbon or oxygen, hence the effects of changes in C:P and C:N Redfield ratios cannot be addressed.

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We extended the TT model in two ways. First, nitrogen-fixers and other phytoplankton are given different N:P stoichiometry (R_{NF} and R_O respectively). Second, the surface layer of the ocean is split into a fraction where nitrogen-fixers can grow (f_A) and a fraction where they cannot ($f_B=1-f_A$), due to light, iron, or temperature-limitation. These two parts are not directly coupled, but both exchange nutrients and dead biomass with the deep layer. The subscripts A , B and D refer to the two surface boxes and the deep box, respectively. NF is the standing stock of N-fixers and O that of other phytoplankton. P and N are the concentrations of PO_4 and NO_3 , respectively. All other symbols and parameter values are as in Tyrrell (1999).

The population dynamics are described by:

$$\frac{dNF_A}{dt} = \mu'_{NF} \cdot \frac{P_A}{P_A + P_H} \cdot NF_A - M \cdot NF_A \quad (11)$$

$$\frac{dO_A}{dt} = \mu'_O \cdot \min\left(\frac{P_A}{P_A + P_H}, \frac{N_A}{N_A + N_H}\right) \cdot O_A - M \cdot O_A \quad (12)$$

$$\frac{dO_B}{dt} = \mu'_O \cdot \min\left(\frac{P_B}{P_B + P_H}, \frac{N_B}{N_B + N_H}\right) \cdot O_B - M \cdot O_B \quad (13)$$

where $P_H=3 \times 10^{-5}$ mol P m^{-3} and $N_H=5 \times 10^{-4}$ mol N m^{-3} are half-saturation constants for growth on PO_4 and NO_3 respectively, $\mu'_{NF}=87.6 \text{ yr}^{-1}$ and $\mu'_O=91.25 \text{ yr}^{-1}$ are maximum growth rates for N-fixers and other phytoplankton respectively, and $M=73 \text{ yr}^{-1}$ is mortality.

Nutrient concentrations in the surface ocean boxes are described by:

$$\begin{aligned} \frac{dP_A}{dt} = & -\mu'_{NF} \cdot \frac{P_A}{P_A + P_H} \cdot \frac{NF_A}{R_{NF}} - \mu'_O \cdot \min\left(\frac{P_A}{P_A + P_H}, \frac{N_A}{N_A + N_H}\right) \cdot \frac{O_A}{R_O} + M \cdot SR \cdot \frac{NF_A}{R_{NF}} \\ & + M \cdot SR \cdot \frac{O_A}{R_O} + \frac{K \cdot (P_D - P_A)}{SD} + \frac{RP}{SD} \end{aligned} \quad (14)$$

$$\begin{aligned} \frac{dN_A}{dt} = & -\mu'_O \cdot \min\left(\frac{P_A}{P_A + P_H}, \frac{N_A}{N_A + N_H}\right) \cdot O_A + M \cdot (SR - 0.75 \cdot DN) \cdot NF_A \\ & + M \cdot (SR - 0.75 \cdot DN) \cdot O_A + \frac{K \cdot (N_D - N_A)}{SD} + \frac{(RN + AN)}{SD} \end{aligned} \quad (15)$$

$$\frac{dP_B}{dt} = -\mu'_O \cdot \min\left(\frac{P_B}{P_B + P_H}, \frac{N_B}{N_B + N_H}\right) \cdot \frac{O_B}{R_O} + M \cdot SR \cdot \frac{O_B}{R_O} + \frac{K \cdot (P_D - P_B)}{SD} + \frac{RP}{SD} \quad (16)$$

$$\begin{aligned} \frac{dN_B}{dt} = & -\mu'_O \cdot \min\left(\frac{P_B}{P_B + P_H}, \frac{N_B}{N_B + N_H}\right) \cdot O_B + M \cdot (SR - 0.75 \cdot DN) \cdot O_B \\ & + \frac{K \cdot (N_D - N_B)}{SD} + \frac{(RN + AN)}{SD} \end{aligned} \quad (17)$$

where $SD=500$ m is the depth of the surface layer, $SR=95\%$ is the fraction of total primary productivity regenerated in the surface layer, and $K=3.0$ m yr⁻¹ is the mixing coefficient between the surface and the deep. $RP=2.0 \times 10^{-4}$ mol P m⁻² yr⁻¹ is the river input of P. $RN=6.0 \times 10^{-3}$ mol N m⁻² yr⁻¹ is the river input of N, $AN=7.5 \times 10^{-3}$ mol N m⁻² yr⁻¹ is the atmospheric input of N, $DN=1.5\%$ is the fraction of total N uptake that is converted to N₂ via denitrification.

Deep ocean nutrient concentrations are given by:

$$\begin{aligned} \frac{dP_D}{dt} = & M \cdot DR \cdot \frac{NF_A}{R_{NF}} \cdot \frac{f_A \cdot SD}{DD} + M \cdot DR \cdot \frac{O_A}{R_O} \cdot \frac{f_A \cdot SD}{DD} + M \cdot DR \cdot \frac{O_B}{R_O} \cdot \frac{f_B \cdot SD}{DD} \\ & - \frac{K \cdot (P_D - f_A P_A - f_B P_B)}{DD} \end{aligned} \quad (18)$$

$$\begin{aligned} \frac{dN_D}{dt} = & M \cdot (DR - 0.25 \cdot DN) \cdot NF_A \cdot \frac{f_A \cdot SD}{DD} + M \cdot (DR - 0.25 DN) \cdot O_A \cdot \frac{f_A \cdot SD}{DD} \\ & + M \cdot (DR - 0.25 DN) \cdot O_B \cdot \frac{f_B \cdot SD}{DD} - \frac{K \cdot (N_D - f_A N_A - f_B N_B)}{DD} \end{aligned} \quad (19)$$

where $DD=3230$ m is the depth of the deep layer, and $DR=4.8\%$ is the fraction of total primary productivity regenerated in the deep layer (leaving 0.2% to be permanently incorporated into sediments).

Setting $f_A=1$ and $R_{NF}=R_O=16$ ($=R_{ORG}$) recovers the original TT model. These equations were solved numerically with a Fortran program and using Mathematica software.

3 Results

3.1 What controls deep ocean N:P?

From the analytical solution of the LW model for steady state (Sect. 2.1), rearranging Eq. (9), we find the following relationship between available nitrogen (NO_3) and phosphorus (PO_4) in the deep ocean (valid for normalised weathering forcing $0 \leq W \leq 1.163$):

$$\frac{\text{NO}_3}{\text{PO}_4} = r_{\text{N:P,Fix}} \left(1 - \frac{k_P (4.025 - 3.025W)}{\text{PO}_4} \right) \quad (20)$$

For close to present day weathering $W \sim 1$, deep ocean N:P is set slightly below the N:P threshold that triggers N-fixation ($r_{\text{N:P,Fix}}$), because $k_P = 0.26875 \mu\text{mol kg}^{-1}$ is small. Denitrification in the water column and sediments, plus a small amount of organic nitrogen burial, continually remove N from the ocean, thus lowering N:P and supporting a counter-balancing flux of N-fixation. Decreasing weathering increases the deficit of deep ocean N:P below the threshold triggering N-fixation, whereas increasing weathering (within the limit $W \leq 1.163$) reduces the deficit. The actual concentrations of NO_3 and PO_4 , and which limits new production, are determined by $r_{\text{C:N}}$, $r_{\text{C:P}}$, $r_{\text{N:P,Fix}}$, the constraint (20), and the steady state solution for new production (C) in surface waters:

$$\min(r_{\text{C:N}}\text{NO}_3, r_{\text{C:P}}\text{PO}_4) = C_0 W^{\frac{1}{2}} \quad (21)$$

If we fix the weathering forcing parameter at $W = 1$ (thus making PO_4 input to the ocean and O_2 removal from the atmosphere constant), then $\text{O}_2 = \text{O}_{2(0)}$, $C = C_0$ (from Eqs. 7 and 8), the ocean has a constant anoxic fraction, $A = A_0 = 0.14$, and:

$$\frac{\text{NO}_3}{\text{PO}_4} = r_{\text{N:P,Fix}} \left(1 - \frac{k_P}{\text{PO}_4} \right) \quad (22)$$

$$\min(r_{\text{C:N}}\text{NO}_3, r_{\text{C:P}}\text{PO}_4) = C_0 \quad (23)$$

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where $C_0=226.0 \mu\text{mol kg}^{-1}$. Only one of $\text{NO}_3=226/r_{\text{C:N}}$ and $\text{PO}_4=226/r_{\text{C:P}}$ as limiting is consistent with the value of the other nutrient calculated from Eq. (22). If $r_{\text{C:N}} \times r_{\text{N:P,Fix}} \leq r_{\text{C:P}}$ then NO_3 must be limiting, if $r_{\text{C:N}} \times r_{\text{N:P,Fix}} > r_{\text{C:P}}$ then PO_4 can be limiting. LW took $r_{\text{C:N}}=117/16=7.3125$ and $r_{\text{C:P}}=117$ from nutrient data analysis (Anderson and Sarmiento, 1994) and assumed $r_{\text{N:P,Fix}}=r_{\text{C:P}}/r_{\text{C:N}}=16$, corresponding to a steady state $\text{PO}_4=2.2 \mu\text{mol kg}^{-1}$ and $\text{NO}_3=30.9 \mu\text{mol kg}^{-1}$, i.e. deep ocean N:P=14.0 (a little below observations).

The N:P ratio of the deep ocean tracks changes in the N:P threshold for N-fixation (Eqs. 20 and 22). To illustrate this, let us conduct a thought experiment and assume that a systematic shift occurs in phytoplankton stoichiometry to $r_{\text{C:N}}=7.5$ and $r_{\text{C:P}}=75$ (i.e. N:P=10 in new production, based on average values from culture studies; Geider and La Roche, 2002), but there is no change in $r_{\text{N:P,Fix}}=16$. In the new steady state, $\text{PO}_4=3.0 \mu\text{mol kg}^{-1}$, $\text{NO}_3=43.7 \mu\text{mol kg}^{-1}$ i.e. deep ocean N:P=14.6 has changed very little and P now limits new production. Conversely, if we arbitrarily assume $r_{\text{N:P,Fix}}=10$ but keep the original $r_{\text{C:N}}=7.3125$ and $r_{\text{C:P}}=117$ (i.e. N:P=16 in new production) the new steady state has $\text{PO}_4=3.36 \mu\text{mol kg}^{-1}$, $\text{NO}_3=30.9 \mu\text{mol kg}^{-1}$, i.e. deep ocean N:P=9.2 has dropped significantly and N is extremely limiting to new production. Finally, if we assume $r_{\text{C:N}}=7.5$, $r_{\text{C:P}}=75$ and $r_{\text{N:P,Fix}}=r_{\text{C:P}}/r_{\text{C:N}}=10$ then, $\text{PO}_4=3.28 \mu\text{mol kg}^{-1}$, $\text{NO}_3=30.1 \mu\text{mol kg}^{-1}$ i.e. deep ocean N:P=9.2 and N limits new production. Thus, a systematic change in phytoplankton C:N:P can alter the concentrations of NO_3 and PO_4 in the deep ocean but cannot significantly alter their ratio, unless it also alters the N:P threshold for N-fixation.

3.2 What sets the N:P threshold for N-fixation?

In Redfield's (1958) mechanism the N:P level triggering N-fixation cannot be decoupled from the N:P ratio of the phytoplankton because the latter sets the threshold below which N-fixers are selected and N-fixation occurs. This can be explained in terms of competitive dynamics (Schade et al., 2005): If the N:P supply ratio in the water is

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below the N:P requirement of non-fixers, then they will use up all the N and leave some P remaining. N-fixers can utilise this P and in so doing add fixed N to the system. This will continue until the N:P supply ratio approaches the N:P requirement of the non-fixers, at which point the N-fixers tend to be out-competed because N-fixation is an energy demanding process.

If we impose the condition that $r_{N:P,Fix} = r_{C:P} / r_{C:N} = r_{N:P}$ in the LW model, then $NO_3 = 226 / r_{C:N}$ and is always limiting, $PO_4 = 226 / r_{C:P} + k_P$, hence the deep ocean N:P ratio is:

$$\frac{NO_3}{PO_4} = r_{N:P} \left(\frac{1}{1 + r_{C:P} k_P / 226} \right) \quad (24)$$

In the original TT model, competition between N-fixers and non-fixers is explicit and they have identical N:P ratios ($r_{N:P} = R_O = R_{NF}$, which was R_{ORG} in TT's notation). N-fixers are given a lower maximum growth rate on P because of the energy demands of N-fixation. For the default parameter settings including a fixed weathering flux of P to the ocean, deep ocean $PO_4 = 1.75 \mu\text{mol kg}^{-1}$ and the deep ocean N:P ratio is given by:

$$\frac{NO_3}{PO_4} = \frac{(r_{N:P} \times 1.475) + 2}{1.75} \quad (25)$$

Hence in both models, deep ocean N:P tracks change in the phytoplankton N:P ratio ($r_{N:P}$), dropping further below it the more the Redfield ratio is increased. In the TT model, deep ocean PO_4 is fixed, which is equivalent to fixing the C:P Redfield ratio in the LW model. In both cases, deep ocean N:P linearly tracks the phytoplankton N:P ratio entirely through changes in NO_3 . The only difference between the models is in the default gradient (0.84 in TT, 0.88 in LW) and offset (1.14 in TT, 0 in LW) of the relationship.

Contrary to Redfield (1958) (as quoted in Sect. 1), it is the N:P ratio of non-fixers (rather than N-fixers) that sets the N:P threshold for N-fixation. Hence although N-fixers often have a higher N:P ratio than non-fixers (Klausmeier et al., 2004) with reported

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N:P values for N-fixing *Trichodesmium* colonies ranging from 18.3 (Sañudo-Wilhelmy et al., 2001) to 125 (Karl et al., 1992), this should have little effect on the N:P of deep water, because their density is regulated by the N:P requirements of the non-fixers. Our extension of the TT model to include different N:P ratios for the different functional groups confirms this: steady-state deep water N:P ratio is 14.6 when N-fixers have an N:P ratio of 16 and 14.7 when N-fixers have an N:P ratio of 125.

3.3 What if the Redfield ratios vary?

Theoretical limits on the N:P requirements of phytoplankton of 8.2–45.0 have been established (Klausmeier et al., 2004). Exponential growth favours greater allocation to P-rich assembly machinery and hence a lower N:P ratio. Competitive equilibrium favours greater allocation to P-poor resource-acquisition machinery and hence a higher N:P ratio. Whether light, N, or P is limiting has a second-order effect, with P-limitation favouring the least allocation to assembly and the highest N:P ratio.

Corresponding limits on deep ocean N:P can be derived for the TT model and for the LW model with either fixed $r_{C:P}$ or fixed $r_{C:N}$ (Table 1). All three model variants give similar results. Fixed $r_{C:N}$ in the LW model is the most defensible, because existing data indicate that phytoplankton C:N is less variable than N:P and C:P (Geider and La Roche, 2002; Quigg et al., 2003). This model variant suggests that deep ocean N:P has a maximum range of 7.7–32.3 (i.e. about a factor of 2 in either direction).

We can also use the LW model to consider the effect on ocean composition of systematic changes in the phytoplankton C:N:P over evolutionary time (Quigg et al., 2003). Table 2 shows the predicted ocean composition if it were dominated by each of a series of phyla/super-families of decreasing antiquity. This indicates that a general decrease in N:P ratios of marine phytoplankton over the past ~1 Gyr would have tended to decrease deep ocean N:P. This is predicted to have occurred via increasing ocean PO_4 , due to the general decrease in phytoplankton C:P, whereas the relative constancy of the phytoplankton C:N ratio would not have forced NO_3 .

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3.4 What if phosphorus weathering also varies?

The above inferences assume weathering forcing (W) is fixed, which has not been the case (Bergman et al., 2004; Lenton and Watson, 2004). The biological colonisation of the land surface has tended to accelerate weathering, in particular of phosphorus. Retaining the dependence on weathering forcing in the LW model but assuming $r_{N:P,Fix} = r_{N:P}$ gives:

$$\frac{\text{NO}_3}{\text{PO}_4} = r_{N:P} \left(1 - \frac{4.025 - 3.025W}{1 + 226/r_{C:P}k_P} \right) \quad (26)$$

Thus a general increase in weathering forcing (W) toward the present, due to biotic colonisation of the land surface would have tended to increase deep ocean N:P, bringing it closer to the N:P of the phytoplankton. This may have counteracted a decline in deep ocean N:P driven by a declining N:P Redfield ratio. An order of magnitude increase in W from 0.1 to 1 over the past ~1000 Myr is probably an upper limit, and for $r_{C:P} = 117$ as at present, this raises deep ocean N:P from ~55% to ~88% of the Redfield ratio. A factor of two increase in W is more reasonable and $W = 0.5$ gives deep ocean N:P ~69% of the Redfield ratio.

In contrast, 1000 Myr ago the N:P Redfield ratio could have been ~29 (averaging the values for Prasinophyceae and Chlorophyceae in Table 2; Quigg et al., 2003). This suggests a decline in the N:P Redfield ratio could have dominated over an increase in weathering and generated an overall decline in deep ocean N:P. Lowering weathering forcing (W) reduces both NO_3 and PO_4 , the former more than the latter. Thus the inferred overall increase in deep ocean N:P over the past ~1000 Myr could have involved an increase in NO_3 (driven indirectly by increasing weathering) as well as a proportionally larger increase in PO_4 (driven primarily by declining N:P of phytoplankton).

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3.5 What if N-fixation is restricted to a fraction of the surface ocean?

Having explored how variation in the Redfield ratios and phosphorus weathering could have altered deep ocean N:P, we finish by considering the potential impact of limitations on N-fixation. We find that deep ocean N:P is remarkably well regulated as N-fixation is restricted to a progressively smaller fraction (f_A) of the surface ocean (Fig. 1). As f_A is reduced from 1 to 0.33, steady state deep ocean N:P declines from 14.6 to 11.5, for example, when only 50% of the ocean is available to N-fixers, deep N:P is 12.9. As f_A is reduced below 0.33, the system undergoes a Hopf bifurcation to an oscillating solution, and deep N:P actually increases, oscillating in the range 13.5–13.7 for $f_A=0.329$. As f_A is reduced further, deep N:P declines in a non-linear fashion, for example, when only 25% of the ocean is available to N-fixers, the deep N:P oscillates in the range 12.8–13.0, whereas when N-fixers are restricted to 15% of the surface ocean, deep N:P is still 11.5–11.7. As f_A tends to zero, deep ocean N:P also tends to zero, and in the absence of N-fixers, the oscillations disappear.

Such homeostatic biotic control over whole ocean stoichiometry is maintained because N-fixers reach higher densities when restricted to smaller fractions of the ocean's surface, compensating for their reduced distribution. Although the predicted values of deep N:P fall below those observed, this is sensitive to the choice of model parameters. If we assume that the N:P Redfield ratio of non-fixers (R_O) is somewhat greater than 16, this can compensate for restricting N-fixers to a fraction of the ocean's surface, for example, with $f_A=0.5$, $R_O=18$ recovers a deep ocean N:P=14.3.

4 Discussion

Existing explanations of the correspondence between phytoplankton N:P and deep ocean N:P have often included the tenets that: (1) C:N:P = 106:16:1 represents a biochemical optimum for the phytoplankton, (2) N:P of sinking material sets deep ocean N:P, (3) N-fixation occurs when up-welled N:P < 16. These points have all been chal-

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lenged here and elsewhere and are revised as follows: (1) As Redfield recognised, phytoplankton C:N:P=106:16:1 simply represents an average of the present phytoplankton community, there is as yet no evidence that it is optimal, and C:N:P is now known to vary with growth conditions, among species, and (probably) over evolutionary time. (2) The N:P ratio that triggers N-fixation sets the N:P ratio of the deep ocean (referring here to the average concentrations of N and P, not the proportions in which they are remineralised), which is not directly related to the N:P ratio of sinking material (or any other process that merely redistributes N and P within the ocean). (3) The N:P uptake ratio of other plankton determines the N:P threshold for N-fixation, and hence indirectly sets deep ocean N:P. Furthermore, N-fixation can be limited by Fe, light or other factors, such that N-fixers are restricted to a modest fraction of the surface ocean, but they can still maintain deep ocean N:P relatively close to the N:P of other phytoplankton.

The other side of Redfield's mechanism is that denitrification somewhat lowers deep ocean N:P, thus maintaining a population of N-fixers. This needs elaborating given the recent discoveries that anaerobic ammonium oxidation ("anammox"; $\text{NH}_4^+ + \text{NO}_2^- \rightarrow \text{N}_2 + 2\text{H}_2\text{O}$) in the ocean water column and sediments, is responsible for significant removal (up to 30–50%) of fixed nitrogen (Dalsgaard et al., 2003; Kuypers et al., 2003). Anammox may thus contribute to lowering deep ocean N:P. However, the nitrite (NO_2^-) used in the anammox reaction at depth appears to be supplied by denitrification (of NO_3^-), and both processes occur under anaerobic conditions. Hence there is no qualitative change to the overall negative feedback between the amount of available N in the ocean and its removal. For example, an increase in fixed N will lead to an increase in new production in N limited regions, which will promote anoxia at depth, tending to increase denitrification and anammox, both of which remove fixed N.

An additional mechanism not modelled herein is that phosphorite formation and consequent P removal from the ocean can be associated with fixed N removal (Piper and Codispoti, 1975; Schulz and Schulz, 2005). Qualitatively this acts in the right direction

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to stabilise the deep ocean N:P ratio, although its effect will clearly depend on the (as yet unknown) proportions in which N and P are removed.

Our model based analysis suggests that long-term changes in the average phytoplankton N:P Redfield ratio can drive changes in deep ocean N:P, on timescales longer than the $\sim 10^4$ year residence time of PO_4 . The greater variability in C:P than C:N Redfield ratios implies that such stoichiometrically driven changes in deep ocean N:P occur primarily through changes in PO_4 . Hence a suggested decline in N:P and C:P Redfield ratios over evolutionary time (Quigg et al., 2003) implies a corresponding decline in the deep ocean N:P ratio, occurring via an increase in PO_4 .

The lower PO_4 we predict in the mid-Proterozoic 1200–1000 Ma (Table 2) is consistent with much lower PO_4 in the early Proterozoic 1900 Ma, followed by a rise in PO_4 due to less removal on iron oxides (Bjerrum and Canfield, 2002). A further rise in PO_4 over the last ~ 1000 Myr is consistent with an increase in phosphorus weathering flux from the continents due to the biological colonisation of the land surface. Land colonisation may have been stepwise, with one burst in the Neoproterozoic, perhaps involving the first lichens (Lenton and Watson, 2004; Yuan et al., 2005), and a second in the early Phanerozoic with the rise of vascular land plants (Lenton, 2001). Corresponding increases in atmospheric oxygen (Lenton, 2001; Lenton and Watson, 2004) would have suppressed anoxia and denitrification (plus anammox) thus increasing NO_3 and bringing deep ocean N:P closer toward whatever was the average phytoplankton N:P at the time.

In this scenario, the higher N:P ratios of older phyla/super-families do not reflect adaptation to external drivers of ocean composition, because although phosphorus input was probably lower when they arose, so was atmospheric oxygen, making denitrification (and anammox) more extensive and leading to a lower predicted deep ocean N:P. We suggest that the evolution of the composition of the organisms drove ocean composition rather than vice versa. This extends Redfield's (1958) argument for the present ocean by adding an evolutionary time dimension. We describe our scenario as "co-evolution" of phytoplankton C:N:P stoichiometry and deep ocean N:P because the

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composition of the environment is predicted to track evolutionary changes in the composition of the organisms. The question then becomes; what is driving the evolution of phytoplankton composition?

To make further progress we suggest that a model of competing populations with differing stoichiometry could be nested within a model of ocean composition subject to external drivers. The populations themselves could exhibit phenotypic plasticity in their stoichiometry as their resource allocation varies in response to prevailing conditions (Klausmeier et al., 2004). However, acknowledging that phytoplankton composition may adapt (within limits) to the composition of the ocean, as well as alter it, will make disentangling cause and effect even more difficult. Circular reasoning is a common problem in any feedback system with closed loops of cause and effect, and we have struggled to avoid it here. We suspect that the real system is even more complex than we have envisaged.

5 Extensions to the carbon cycle

Our argument that changes in phytoplankton composition drive changes in ocean composition has interesting potential extensions to the carbon cycle. On short timescales, an increase in C:N and C:P Redfield ratios will give rise to increased carbon export from the surface ocean (new production). However, our modelling suggests that on timescales longer than their residence times, the ocean NO_3 and PO_4 reservoirs adjust such that new production tends to be fairly constant. This is consistent with the stability of the $\delta^{13}\text{C}$ record (Schidlowski, 1988).

In one of many hypotheses to explain the lower CO_2 at the Last Glacial Maximum, Broecker and Henderson (1998) suggest that a 50% increase in plankton N:P and deep ocean N (with the same plankton C:N) could drive the requisite increase in the organic carbon pump. Such an increase in plankton N:P demands a shift from “reds” to “greens” (Quigg et al., 2003) and/or a more nutrient or light limited regime in the surface ocean (Klausmeier et al., 2004). More importantly, the models we have examined

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suggest deep ocean N, and new production are self-regulated. A 50% increase in phytoplankton N:P does not in itself drive an increase in deep ocean N (e.g. Table 2). Indeed a 50% increase in deep ocean N and carbon export can only occur with a similar increase in weathering input of P to the ocean.

5 The potential effects of CO₂ on phytoplankton composition are of interest for both the glacial world of lower CO₂ and the present and future world of increasing CO₂. Increases in C:N and C:P with increasing CO₂ have been seen in a naked strain of *Emiliania huxleyi* (Leonardos and Geider, 2005). Increases in C:N and inorganic carbon drawdown also occur under elevated CO₂ in mesocosm experiments (Riebesell, et al., 2006). This suggests a potential negative feedback in which increasing CO₂ generates an enhanced organic carbon pump and vice versa. This only adds to the difficulty of explaining lower glacial CO₂ levels.

6 Conclusion

15 Despite potential variability in phytoplankton stoichiometry, weathering supply of phosphorus to the ocean, and widespread Fe and/or light limitation of N-fixation, we find that Redfield's mechanism can still regulate deep ocean N:P somewhat below the proportions that trigger N-fixation in those areas of the ocean where it is limited by P and suppressed by N addition. Furthermore, deep ocean N:P is unlikely to have varied by more than a factor of two in either direction since the deep oceans became well oxygenated. We extend Redfield's mechanism to suggest that within these bounds, the evolution of phytoplankton composition drove long-term changes in ocean composition. Decreases in phytoplankton C:P and N:P ratios over the past ~1 Gyr are predicted to have driven a decrease in deep ocean N:P, via increasing PO₄.

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Table 1. Limits on ocean composition predicted from theoretical limits on the N:P stoichiometry of phytoplankton (Klausmeier et al., 2004) using the TT and LW models.

Limit	Phytoplankton N:P	Predicted N:P of deep ocean		
		TT	LW with $r_{C:P}=117$	LW with $r_{C:N}=7.3$
Control	16	14.6	14.0	14.0
Exponential growth	8.2	8.1	7.2	7.7
Light limitation	35.8	31.3	31.4	27.3
N-limitation	37.4	32.7	32.8	28.2
P-limitation	45.0	39.1	39.5	32.3

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Table 2. Expected ocean composition if dominated by various phyla of phytoplankton. Predicted from the Redfield ratios found by (Quigg et al., 2003) and the adapted LW model, assuming the N:P Redfield ratio is the threshold below which N-fixation occurs.

Phylum/superfamily (and age)	C:N:P ratio	NO ₃ (μmol kg ⁻¹)	PO ₄ (μmol kg ⁻¹)	NO ₃ :PO ₄
Prasinophyceae (1200 Myr)	200:25:1	28	1.4	20
Chlorophyceae (1000 Myr)	200:33:1	38	1.4	27
Dinophyceae (440 Myr)	140:13:1	21	1.9	11
Prymnesiophyceae (210 Myr)	60:9:1	32	4.0	8.0
Diatoms (<200 Myr)	70:10:1	32	3.5	9.2

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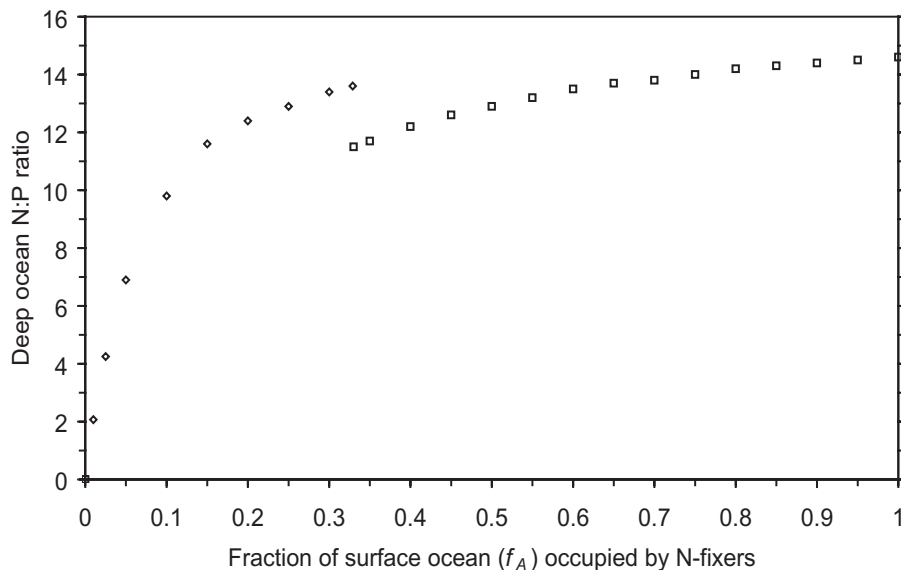


Fig. 1. Dependence of the steady state deep ocean N:P ratio on the fraction of the surface ocean occupied by N-fixers (f_A). Predicted by the extended TT model assuming an N:P Red-field ratio of 16 for both N-fixers and other phytoplankton. Squares symbols indicate a stable solution, diamond symbols a limit cycle (oscillating solution). The oscillations are small, with a maximum amplitude of $\sim 0.75\%$ (e.g. 13.3–13.5 for $f_A=0.3$), and the diamonds are plotted at the mid point of the oscillations. The transition from a stable steady state to a limit cycle occurs in the range $f_A=0.329$ – 0.330 .

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