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ECOSYSTEMS

Can Organisms Regulate Global Biogeochemical Cycles?

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ABSTRACT

Global biogeochemical cycles are being profoundly affected by human activities; therefore, it is critical to understand the role played by organisms in their regulation. Autotrophic organisms can regulate nutrient abundance at local scales through resource consumption, but most resources are inaccessible to them at global scales, either because of physical barriers or because of the presence of non-assimilable chemical forms of nutrients. Here we present a generic model of resource access limitation and apply it to the oceanic cycles of iron, phosphorus, and silicon to examine whether phytoplankton can regulate the concentrations of these key nutrients. Our model predicts that autotrophs cannot at the same time strongly impact accessible nutrients and exert perfect regulation on inaccessible nutrients. We show that the ability of organisms to regulate inaccessible nutrient pools strongly depends on passive physical and chemical flows, and on the fraction of the system that is accessible to organisms. Components of global climate change such as increasing water column stratification might result in a further decrease of the biotic regulation of inaccessible nutrients in freshwater and marine systems.

Key words: biogeochemical cycles; nutrient cycling; regulation; Earth system; resource access limitation; anthropogenic impacts.

INTRODUCTION

Anthropogenic alteration of biogeochemical cycles is a major component of current global environmental changes (Schlesinger 1997). Human activities are profoundly modifying the global biogeochemical cycles of key elements, such as carbon, nitrogen, phosphorus, and oxygen (Benitez-Nelson 2000; Falkowski and others 2000; Gruber and Galloway 2008; Gruber 2011), mostly through changes in nutrient supply. For example, human activities release carbon dioxide to the atmosphere, which in turn increases its dissolution in oceans (Gruber 2011), whereas fertilizer application increases the supply of nitrogen and phosphorus in terrestrial ecosystems and oceans (Benitez-Nelson 2000; Gruber and Galloway 2008). Given these massive alterations, it is critical to understand to what extent and how global biogeochemical cycles are naturally regulated. Part of this regulation is due to physical and chemical processes. For example, in the carbon cycle, an increase in the partial pressure of CO_2 in the atmosphere induces increased dissolution of CO_2 in the ocean, leading to some regulation of the partial pressure of atmospheric CO_2 (Falkowski and others 2000). Organisms also play a significant part in the regulation of the Earth system (for example, Canfield 2014; Lenton and Watson 2011), but the extent of their regulating ability at global scales is much less clear.

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Author contributions ML conceived the idea, ASA and ML built and analyzed the model, ASA wrote the first draft of the manuscript, and both authors contributed substantially to revisions.
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The issue of the extent to which organisms are able to regulate their environment at large spatial and temporal scales has been debated for several decades (Loreau 2010). The near constancy of the composition, pH and temperature of the terrestrial atmosphere over long time scales led Lovelock and Margulis (1974) to propose the Gaia hypothesis, which assumes that organisms restrict variations in environmental conditions to a habitable range through feedback mechanisms. This hypothesis has been controversial, in particular, because evolution by natural selection does not necessarily promote large-scale environmental regulation (see Lenton 1998; Free and Barton 2007; Tyrrell 2013 for reviews). The hypothesis that water chemistry is regulated by phytoplankton in oceans provides another example of regulation by organisms of their environment at global scales. The mean N:P ratio of phytoplankton seems to be relatively constant at large scales (Redfield 1934, 1958; Karl and others 1993), although phytoplankton stoichiometry can vary depending on local conditions (Klausmeier and others 2004; Franz and others 2012) and phytoplankton growth strategies (Arrigo 2005). Redfield (1934) highlighted the similarity between this mean N:P ratio of 16:1 and that of ocean deep waters. He hypothesized that the intracellular content of phytoplankton could be central in this pattern and that the phytoplankton could maintain it through nitrogen fixation, denitrification, and recycling. Modeling studies support the hypothesis that Redfield ratios are controlled by the compensatory dynamics between nitrogen-fixing and non-fixing phytoplankton (Tyrrell 1999; Lenton and Watson 2000a; Weber and Deutsch 2012) and the diversity of metabolic N:P requirements of phytoplankton (Weber and Deutsch 2012).

One key issue with all the hypotheses that assume regulation of global environmental conditions or resources is that organisms typically act on their environment locally, at small space and time scales. At such small scales, organisms are known to modify their environment through a wide range of processes such as resource consumption, metabolism, and habitat modification, thereby creating strong feedbacks with, and possibly regulation of, their environment (Kylafis and Loreau 2008, 2011). One example is nitrogen fixers, whose metabolic activities release fixed nitrogen in the environment, thereby increasing nitrogen availability for other organisms. Feedbacks that link organisms and their environment and potentially generate environmental regulation at global scales are increasingly understood regarding the cycles of key nutrients such as oxygen, carbon, and nitrogen (Lenton and Watson 2000a, b, 2011; Weber and Deutsch 2012; Canfield 2014), but a general theoretical framework is still missing. Changes in the stocks or concentrations of inorganic nutrients can have massive effects on the physical characteristics of the global environment and on biodiversity (Smith and others 1999; Diaz and Rosenberg 2008; Smith and Schindler 2009). Therefore, it is important to clarify the main feedback mechanisms that can contribute to the regulation of inorganic nutrient pools by organisms at global scales.

Resource consumption is the most common biotic process leading to local regulation of inorganic nutrient pools. As the resource is consumed, its abundance tends to decrease to a level where its consumption balances consumers' basal metabolism and mortality, leading to top-down control of the resource by the consumers (Loreau 2010). Top-down resource control, however, occurs only inasmuch as the resource is accessible to consumers. Resource access limitation is common, often because of spatial barriers. For instance, plants have access to soil nutrients only in the vicinity of their rooting system in terrestrial ecosystems (Huston and DeAngelis 1994; Loreau 1996). Another cause of resource access limitation is the chemical form of nutrients, which can be unusable by some organisms. For instance, only nitrogen fixers are able to assimilate N_2, with the result that non-fixers have access only to part of the nitrogen available in their environment. The fact that organisms access only a small part of the resources available in their environment leads to an important question: Are organisms—in particular autotrophic organisms—able to indirectly regulate nutrient pools to which they do not have direct access? Inaccessible nutrient pools are often much larger than accessible ones, and thus one may expect biotic regulation of these pools to be strongly limited.

Our goal in this work is to elucidate the ability of organisms to regulate the pools of inorganic nutrients in both accessible and inaccessible form, and thereby the biogeochemical cycles of these nutrients at large spatial scales. We first build and analyze a simple generic model of resource regulation with resource access limitation. The model describes the dynamics of a limiting inorganic nutrient in two pools, one accessible and the other inaccessible to autotrophic consumers. We then provide applications of our model to the biogeochemical cycle of three key nutrients in the ocean. The first case study is the oceanic iron cycle, in which we consider that phytoplankton can use only part of the iron in seawater (Baker and Croot 2010; Boyd and Ellwood 2010). Assimilable iron is scarce in several oceanic regions, where it drives phytoplankton growth (Fung and others 2000; Moore and others 2001; Krishnamurthy and others 2010). Thus, it is interesting to assess the extent to which autotrophs can regulate the oceanic cycle of iron in response to increasing atmospheric deposition (Jickells and others 2005; Boyd and others 2010). The second case study is the oceanic phosphorus cycle. Phosphorus presents an example of physical resource access limitation as phytoplankton can only access nutrients in the surface ocean, either because of the thermocline or because of the limited depth of the euphotic layer. The interest of studying phosphorus is that it plays a major role in limiting phytoplankton growth in the ocean (Sañudo-Wilhelmy and others 2001; Elser and others 2007) and its biogeochemical cycle is strongly affected by agricultural activities (Benitez-Nelson 2000; Bouwman and others 2009). The last example is the oceanic silicon cycle. Just as dissolved phosphorus, only part of silicic acid is accessible to phytoplankton in the ocean due to physical barriers. Silicic acid is a key nutrient in the ocean as it is used by diatoms and influences their distribution (Martin-Jézéquel and others 2000; Yool and Tyrrell 2003; Sarthou and others 2005). This case study is of special interest since it provides an example of the regulation of nutrient pools in response to a decrease in nutrient supply by anthropogenic activities (Laruelle and others 2009; Tréguer and De La Rocha 2013), in contrast to phosphorus and iron, the supply of which increases.

Model and Methods

Our generic model explores the constraints on biotic regulation which arise from the presence of inaccessible nutrient pools (Huston and DeAngelis 1994; Loreau 1996, 2010) in global biogeochemical cycles (Figure 1; Table 1), either because of spatial barriers or because of non-assimilable chemical forms. In this model, we assume that a single inorganic nutrient limits the growth of autotrophic organisms that consume it. The inorganic nutrient occurs in two distinct pools, one that is accessible to organisms, and the other that is inaccessible to them. α represents the fraction of the total volume of the system (that is, the sum of the volumes of both accessible and inaccessible pools, noted $V_a + V_i$) that is accessible to organisms. In the case of chemical limitation, we consider that the environment is homogeneous, such that the accessible and inaccessible forms of the limiting nutrient occur in the same volume (that is, $V_a = V_i$), and thus $\alpha = V_a/(V_a + V_i) = 0.5$. N_a and N_i are nutrient concentrations in the accessible and inaccessible pools, respectively. The two nutrient pools are connected by passive flows governed by the physics or chemistry of the system. We distinguish between the transfer rate from the accessible to the inaccessible pool, k_a, and that from the inaccessible to the accessible pool, k_i. Both pools have nutrient inflows and outflows from and to the external world. S_a and S_i refer to the nutrient supply to the accessible and inaccessible pools, respectively, and q_a and q_i refer to the nutrient turnover rates in the accessible and inaccessible pools, respectively.

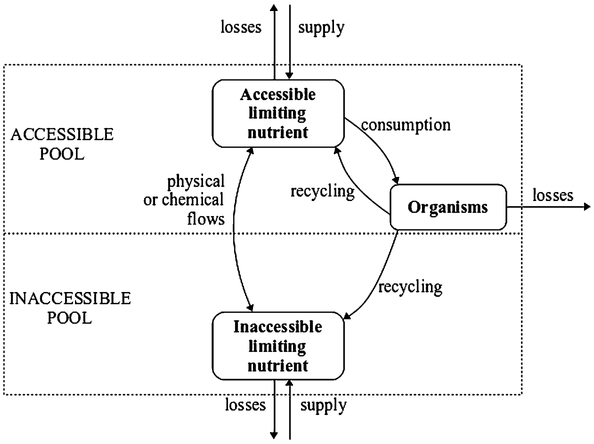

Figure 1. Generic model of nutrient dynamics with resource access limitation. *Boxes* and *arrows* represent stocks and flows, respectively.

Organisms, with concentration B, have a traditional resource-dependent functional response to the concentration of the accessible inorganic nutrient, $g(N_a)$, leading to top-down control at equilibrium. They recycle part of the inorganic nutrient in both accessible and inaccessible forms. m is the turnover rate of nutrient in organisms, λ is the fraction of dead organic matter that is lost from the system, and rec_a refers to the fraction of recycling that occurs in the accessible pool. We first use mass balance to obtain a model that tracks nutrient masses. By dividing nutrient mass by the volume of the pool concerned, we then obtain the following model that tracks nutrient concentrations (Figure 1):

Table 1. Model Parameters

Symbol	Description	Units
α	Fraction of the system that is accessible to organisms	
m	Mortality rate of autotrophic organisms (including grazing)	y^{-1}
μ	Maximum growth rate of autotrophic organisms	y^{-1}
N_H	Half saturation constant of the growth of autotrophic organisms for the accessible nutrient	$\mu mol\ m^{-3}$
λ	Fraction of organic matter that is not recycled	
rec_a	Fraction of recycling that occurs in the accessible pool	
k_a	Transfer rate from the accessible to the inaccessible pool	y^{-1}
k_i	Transfer rate from the inaccessible to the accessible pool	y^{-1}
S_a	Nutrient supply to the accessible pool	$\mu mol\ m^{-3}\ y^{-1}$
S_i	Nutrient supply to the inaccessible pool	$\mu mol\ m^{-3}\ y^{-1}$
q_a	Nutrient turnover rate in the accessible pool	y^{-1}
q_i	Nutrient turnover rate in the inaccessible pool	y^{-1}

$$\begin{aligned}\frac{dN_a}{dt} &= S_a-(k_a+q_a)N_a+\frac{1-\alpha}{\alpha}k_iN_i\\ &\quad+[m\,rec_a(1-\lambda)-g(N_a)]B\\ \frac{dN_i}{dt} &= S_i+\frac{\alpha}{1-\alpha}k_aN_a-(k_i+q_i)N_i\\ &\quad+\frac{\alpha}{1-\alpha}m(1-rec_a)(1-\lambda)B\\ \frac{dB}{dt} &= [g(N_a)-m]B.\end{aligned} \tag{1}$$

A simple measure of the efficiency with which organisms regulate nutrient concentrations against variations in nutrient supply is one minus the elasticity of the equilibrium nutrient concentration in pool x with respect to nutrient supply to pool y:

$$\rho_{x,y} = 1-\frac{S_y}{N_x}\times\frac{\partial N_x}{\partial S_y}, \tag{2}$$

$\rho_{x,y}$ is defined as the regulation coefficient of the nutrient concentration in pool x with respect to changes in the nutrient supply to pool y. When $\rho_{x,y} = 0$, there is no regulation (that is, the proportional variation in nutrient concentration x is equal to that in nutrient supply y). At the other extreme, when $\rho_{x,y} = 1$, there is perfect regulation (that is, there is no variation in nutrient concentration x as a result of that in nutrient supply y). Note we calculate the regulation coefficient for the nutrient concentration at equilibrium; thus perfect regulation does not exclude variations in the nutrient concentration during transient dynamics. When $0 < \rho_{x,y} < 1$, regulation is partial. Note that biota can sometimes over-regulate the nutrient concentration in pool x, in which case $\rho_{x,y} > 1$. Some cases where $\rho_{x,y} < 0$ can also occur; regulation is then negative, that is, organisms amplify variations in nutrient supply.

The impact of each parameter on each regulation coefficient was determined by the partial derivative of the regulation coefficient with respect to that parameter. When the sign of the partial derivative was not obvious but constant over the whole interval of parameter values, we determined the values of the regulation coefficients when the parameter is set to first its maximum and then its minimum to emphasize if possible the general impact of the parameter studied on the regulation coefficients (Table 2).

To illustrate the general predictions of our model, we apply it to the biogeochemical cycles of iron, phosphorus, and silicon in the global ocean. Soluble iron is thus accessible to organisms, whereas particulate iron is inaccessible. In the case of chemical limitation, $\alpha = V_a/(V_a + V_i) = 0.5$. Recycling produces soluble iron, thus in this application $rec_a = 1$. The examples of the phosphorus and silicon cycles correspond to physical limitations. Note that in the phosphorus cycle, there is no supply of dissolved phosphorus to the deep ocean (that is, $S_i = 0$, Benitez-Nelson 2000). Thus, in this special case, only the regulation of nutrient pools with respect to changes in the supply to the surface ocean is studied.

In numerical simulations, the functional response of phytoplankton to an accessible nutrient is modeled with a Michaelis–Menten function:

$$g(N_a) = \frac{\mu N_a}{N_a + N_H}, \tag{3}$$

where μ is the maximal growth rate of phytoplankton and N_H is the half-saturation constant for a nutrient in accessible form.

Table 2. Impact of Parameters on Biotic Regulation of the Inaccessible Nutrient Pool

Parameter	Impact on $\rho_{\mathrm{i,a}}$	Impact on $\rho_{\mathrm{i,i}}$
Transfer rate from the accessible to the inaccessible pool (k_{a})	+	+
Fraction of the system and that is accessible to organisms (α)	+	+
Nutrient turnover rate in the accessible pool (q_{a})	−	+
Nutrient turnover rate in the inaccessible pool (q_{i})	+	−
Accessible nutrient concentration at equilibrium (N_{a}^{+})	+	+
Fraction of recycling that occurs in the accessible pool ($\mathrm{rec_a}$)	+	+ when $S_{\mathrm{a}}(k_{\mathrm{a}}+q_{\mathrm{a}})N_{\mathrm{a}}^{+} < 0$ − when $S_{\mathrm{a}}(k_{\mathrm{a}}+q_{\mathrm{a}})N_{\mathrm{a}}^{+} > 0$
Fraction of organic matter that is not recycled (λ)	+	+ when $S_{\mathrm{a}}(k_{\mathrm{a}}+q_{\mathrm{a}})N_{\mathrm{a}}^{+} < 0$ − when $S_{\mathrm{a}}(k_{\mathrm{a}}+q_{\mathrm{a}})N_{\mathrm{a}}^{+} > 0$

$\rho_{i,a}$ is the regulation coefficient of the inaccessible nutrient pool with respect to changes in the accessible nutrient supply. $\rho_{i,i}$ is the regulation coefficient of the inaccessible nutrient pool with respect to changes in the inaccessible nutrient supply. The + and − symbols denote a positive and a negative impact of the paramenter on the regulation coefficient, respectively.

To perform numerical simulations, we chose parameter values within the range of values found in the literature (see Tables TS1, TS2, and TS3 in Supporting Information) to be as realistic as possible. We either increased or decreased nutrient supply by 50% after one-third of the simulation time to assess the strength of the regulation of nutrient pools in the present ocean. We increased iron and phosphorus supplies, whereas we decreased the supply of silicic acid, in agreement with current trends due to anthropogenic activities (Bouwman and others 2009; Boyd and others 2010) (Laruelle and others 2009; Tréguer and De La Rocha 2013).

RESULTS

Model (1) has two equilibria, one in the absence and the other in the presence of organisms. An analysis of the flows between nutrient pools helps to better understand the results (Figure 2). The equilibrium concentrations in the absence of organisms (denoted by a− superscript) are as follows:

$$\begin{aligned} N_{\mathrm{a}}^{-} &= \frac{S_{\mathrm{a}}\alpha(k_{\mathrm{i}}+q_{\mathrm{i}})+k_{\mathrm{i}}S_{\mathrm{i}}(1-\alpha)}{\alpha[q_{\mathrm{a}}(k_{\mathrm{i}}+q_{\mathrm{i}})+k_{\mathrm{a}}q_{\mathrm{i}}]} \\ N_{\mathrm{i}}^{-} &= \frac{S_{\mathrm{i}}(1-\alpha)+k_{\mathrm{a}}\alpha N_{\mathrm{a}}^{-}}{(1-\alpha)(k_{\mathrm{i}}+q_{\mathrm{i}})} \\ B^{-} &= 0. \end{aligned} \tag{4}$$

The equilibrium concentrations in the presence of organisms (denoted by a+ superscript) are as follows:

$$\begin{aligned} N_{\mathrm{a}}^{+} &= g^{-1}(m) \\ N_{\mathrm{i}}^{+} &= \frac{-[\alpha k_{\mathrm{a}}N_{\mathrm{a}}^{+}+S_{\mathrm{i}}(1-\alpha)][1-\mathrm{rec_a}(1-\lambda)]+\alpha(1-\mathrm{rec_a})(1-\lambda)[-S_{\mathrm{a}}+N_{\mathrm{a}}^{+}(k_{\mathrm{a}}+q_{\mathrm{a}})]}{(1-\alpha)\{k_{\mathrm{i}}(1-\mathrm{rec_a})(1-\lambda)-(k_{\mathrm{i}}+q_{\mathrm{i}})[1-\mathrm{rec_a}(1-\lambda)]\}} \\ B^{+} &= \frac{-S_{\mathrm{a}}\alpha(k_{\mathrm{i}}+q_{\mathrm{i}})-k_{\mathrm{i}}S_{\mathrm{i}}(1-\alpha)+\alpha N_{\mathrm{a}}^{+}[q_{\mathrm{a}}(k_{\mathrm{i}}+q_{\mathrm{i}})+k_{\mathrm{a}}q_{\mathrm{i}}]}{\alpha m\{k_{\mathrm{i}}(1-\mathrm{rec_a})(1-\lambda)-(k_{\mathrm{i}}+q_{\mathrm{i}})[1-\mathrm{rec_a}(1-\lambda)]\}} \\ &= \frac{(N_{\mathrm{a}}^{+}-N_{\mathrm{a}}^{-})[q_{\mathrm{a}}(k_{\mathrm{i}}+q_{\mathrm{i}})+k_{\mathrm{a}}q_{i}]}{m\{k_{\mathrm{i}}(1-\mathrm{rec_a})(1-\lambda)-(k_{\mathrm{i}}+q_{\mathrm{i}})[1-\mathrm{rec_a}(1-\lambda)]\}}, \end{aligned} \tag{5}$$

where g^{-1} refers to the inverse function of g.

Note that the total amount of nutrient in the system is

$$N_{\mathrm{tot}} = \alpha N_{\mathrm{a}} + (1-\alpha)N_{\mathrm{i}} + \alpha B. \tag{6}$$

In the presence of organisms, any variation in the supply of nutrient in accessible form is entirely absorbed by organisms because of their top-down control on the accessible nutrient pool, and thus $\rho_{\mathrm{a,a}} = 1$ (Figures 3A, 4A, 5A). Perfect regulation is explained by a strong negative feedback loop between phytoplankton and the accessible pool (path 2–3 in Figure 2A). Variations in the supply of

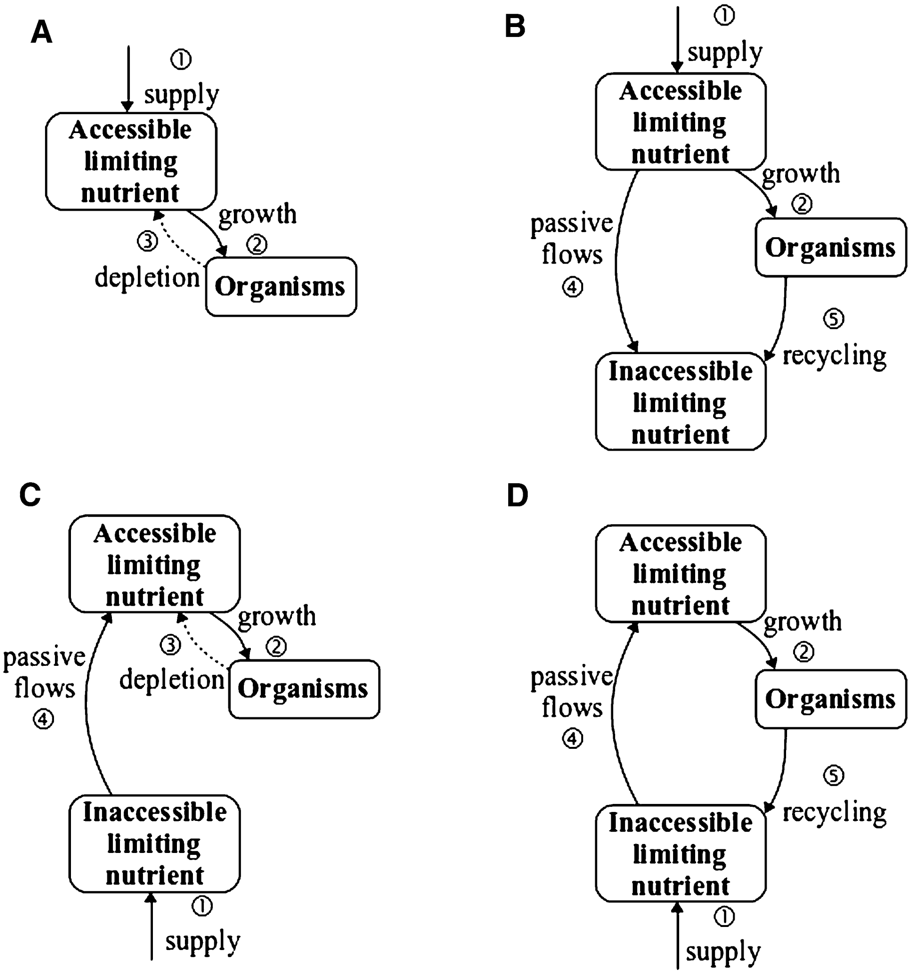

Figure 2. Regulation processes in the generic model. **A** Impact of the supply of a limiting nutrient in accessible form on its concentration in the accessible pool. **B** Impact of the supply of a limiting nutrient in accessible form on its concentration in the inaccessible pool. **C** Impact of the supply of a limiting nutrient in inaccessible form on its concentration in the accessible pool. **D** Impact of the supply of a limiting nutrient in inaccessible form on its concentration in the inaccessible pool. *Bold arrows* indicate a direct relationship (for example, an increase in the concentration of the accessible limiting nutrient results in an increase in biomass). *Dashed arrows* indicate an inverse relationship (for example, an increase in biomass results in a decrease in nutrient concentration in the accessible pool).

the accessible nutrient impact organisms' growth, which may alter the intensity of the recycling flow to the inaccessible nutrient pool. Therefore, the inaccessible nutrient concentration is only partially or negatively regulated because it varies in the same direction as the supply of nutrient in accessible form (paths 1–4 and 1–2–5 in Figure 2B):

$$\rho_{\mathrm{i,a}} = \frac{-[\alpha k_{\mathrm{a}} N_{\mathrm{a}}^{+} + S_i(1-\alpha)][1-\mathrm{rec_a}(1-\lambda)] + \alpha N_{\mathrm{a}}^{+}(k_{\mathrm{a}} + q_{\mathrm{a}})(1-\mathrm{rec_a})(1-\lambda)}{-[\alpha k_{\mathrm{a}} N_{\mathrm{a}}^{+} + S_i(1-\alpha)][1-\mathrm{rec_a}(1-\lambda)] + \alpha(1-\mathrm{rec_a})(1-\lambda)[-S_{\mathrm{a}} + N_{\mathrm{a}}^{+}(k_{\mathrm{a}} + q_{\mathrm{a}})]}. \tag{7}$$

Note that regulation of the inaccessible nutrient concentration with respect to changes in the accessible supply is perfect when there is no recycling to the inaccessible pool (that is, $\mathrm{rec_a} = 1$), as is the case with the iron cycle in the ocean (Figure 3A). In the numerical simulations of the oceanic cycles of silicon and phosphorus, part of the dead organic matter

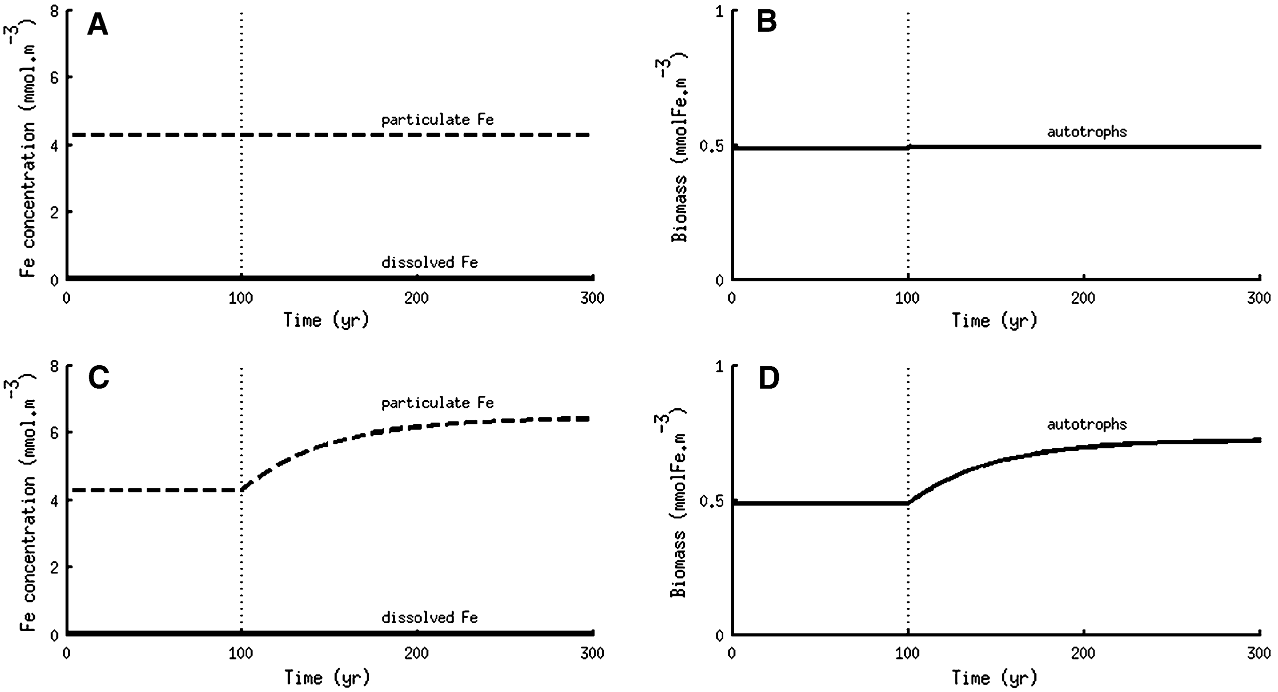

Figure 3. Regulation of iron concentrations in the ocean. Nutrient supply is increased by 50% after a third of the simulation time (*dotted vertical line*). Simulations are performed from the application of the generic model to the oceanic cycle of iron with realistic parameter values. *Bold lines* and *dotted lines* are for the dissolved and particulate iron pools, respectively. **A** Regulation of iron concentrations in case of an increase in the supply of dissolved iron ($\rho = 1$ for both pools). **B** Impact of an increase in the supply of dissolved iron on the biomass of autotrophic organisms. **C** Regulation of iron concentrations in case of an increase in the supply of particulate iron ($\rho = 1$ and $\rho = 2.3 \times 10^{-3}$ for the dissolved and particulate pools, respectively). **D** Impact of an increase in the supply of particulate iron on the biomass of autotrophic organisms.

is recycled in the deep ocean (that is, $\text{rec}_a < 1$). Changes in the supply of phosphorus and silicic acid to the surface ocean affect the growth and concentration of autotrophic organisms (Figures 4B, 5B) and then impact the strength of the recycling flow of organic matter to the deep ocean. Thus, regulation of the deep-ocean nutrient concentration with respect to a change in the supply to the surface ocean is partial ($\rho_{i,a} = 0.44$ and 0.18 in Figures 4A, 5A, respectively). Recycling to the inaccessible pool has a negative impact on regulation of changes in the accessible nutrient supply (Table 2), because any change in this supply alters the growth of organisms and thus the intensity of the recycling flow to the inaccessible pool. The efficiency of this regulation is also higher when the relative volume of the accessible pool, α, and the transfer rate from the accessible pool to the inaccessible one, k_a, are larger (Table 2). As changes in nutrient supply are totally absorbed in the accessible pool, variations of these two parameters in the direction indicated contribute to the dilution of changes in biotic flows to the inaccessible pool. Regulation of the inaccessible nutrient concentration with respect to changes in accessible nutrient supply is also more efficient when the turnover rates q_a and q_i are smaller and larger, respectively (Table 2).

There is also perfect regulation of the accessible nutrient concentration with respect to changes in the supply of the nutrient in inaccessible form because of top-down control (negative feedback loop, path 2–3 in Figure 2C), and thus $\rho_{a,i} = 1$ (Figures 3C, 4C). The concentration of the nutrient in inaccessible form is either partially or negatively regulated with respect to changes in its supply ($\rho_{i,i} = 2.3 \times 10^{-3}$ and 0.78 in Figures 3C, 4C, respectively) because there is a positive relationship between the supply and the concentration of the nutrient in inaccessible form (path 1–4–2–5 in Figure 2D):

$$\rho_{\mathrm{i,i}} = \frac{-\alpha k_{\mathrm{a}} N_{\mathrm{a}}^{+}[1-\mathrm{rec}_{\mathrm{a}}(1-\lambda)] + \alpha(1-\mathrm{rec}_{\mathrm{a}})(1-\lambda)[-S_{\mathrm{a}} + N_{\mathrm{a}}^{+}(k_{\mathrm{a}}+q_{\mathrm{a}})]}{-[\alpha k_{\mathrm{a}} N_{\mathrm{a}}^{+} + S_i(1-\alpha)][1-\mathrm{rec}_{\mathrm{a}}(1-\lambda)] + \alpha(1-\mathrm{rec}_{\mathrm{a}})(1-\lambda)[-S_{\mathrm{a}} + N_{\mathrm{a}}^{+}(k_{\mathrm{a}}+q_{\mathrm{a}})]}. \qquad (8)$$

The efficiency of this regulation is higher when the relative volume of the accessible pool, α, is larger, when the transfer rate from the accessible pool to the inaccessible one, k_{a}, is larger, and when the turnover rates q_{a} and q_{i} are larger and smaller, respectively (Table 2). The effect of these four parameters is intuitive as variations of these parameters in the direction indicated contribute to increase the impact of the biotic control of the accessible nutrient relative to that of the independent physical and chemical processes that affect inaccessible nutrient dynamics. We might intuitively expect recycling to the inaccessible pool to have a positive impact on the regulation of changes in the inaccessible nutrient supply, because it increases the control of organisms on the inaccessible pool. However, this occurs only under particular conditions (Table 2).

For both regulation coefficients, note that the regulation efficiency of the inaccessible nutrient concentration is higher when the equilibrium nutrient concentration in the accessible pool, N_{a}^{+}, is larger (Table 2). This effect is somewhat counter-intuitive as we might expect intuitively that the stronger the top-down biotic control on the accessible nutrient through resource depletion, the

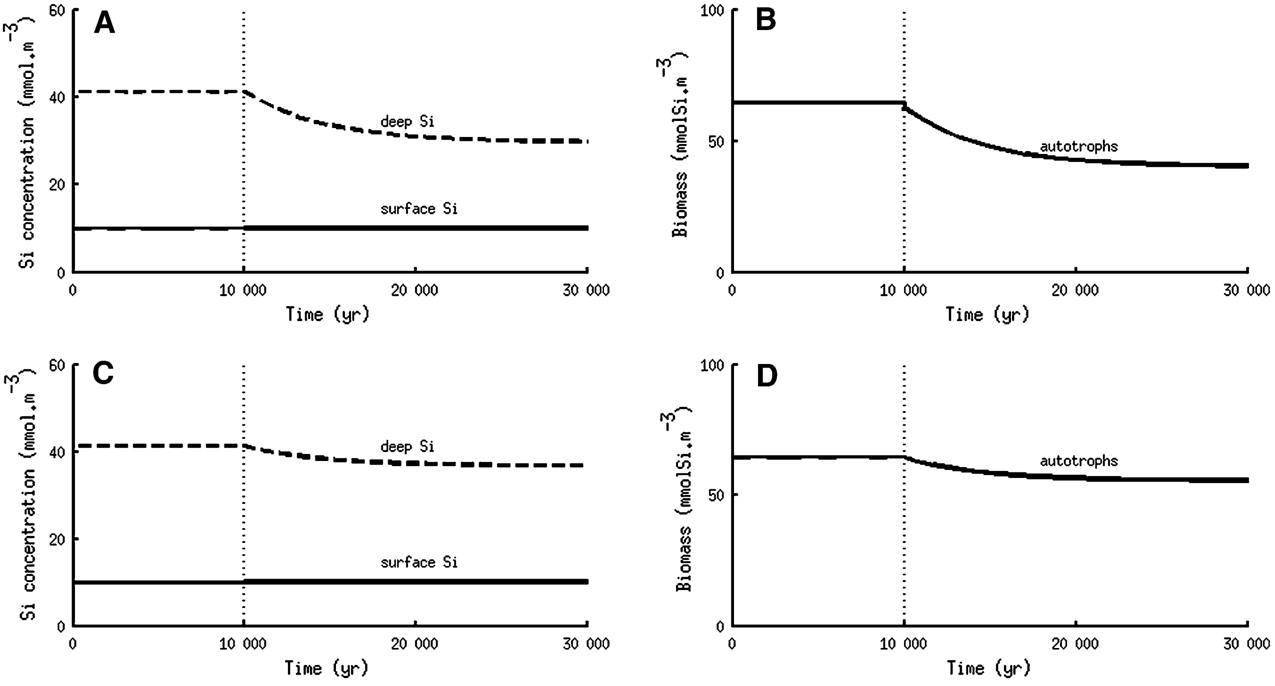

Figure 4. Regulation of silicic acid concentrations in the ocean. Nutrient supply is decreased by 50% after a third of the simulation time (*dotted vertical line*). Simulations are performed from the application of the generic model to the oceanic cycle of silicic acid with realistic parameter values. *Bold lines* and *dotted lines* are for the surface and deep silicic acid pools, respectively. **A** Regulation of silicic acid concentrations in case of a decrease in the supply of surface silicic acid ($\rho = 1$ and $\rho = 0.44$ for the accessible and inaccessible pools, respectively). **B** Impact of a decrease in the supply of surface silicic acid on the biomass of autotrophic organisms. **C** Regulation of silicic acid concentrations in case of a decrease in the supply of surface silicic acid ($\rho = 1$ and $\rho = 0.78$ for the accessible and inaccessible pools, respectively). **D** Impact of a decrease in the supply of deep silicic acid on the biomass of autotrophic organisms.

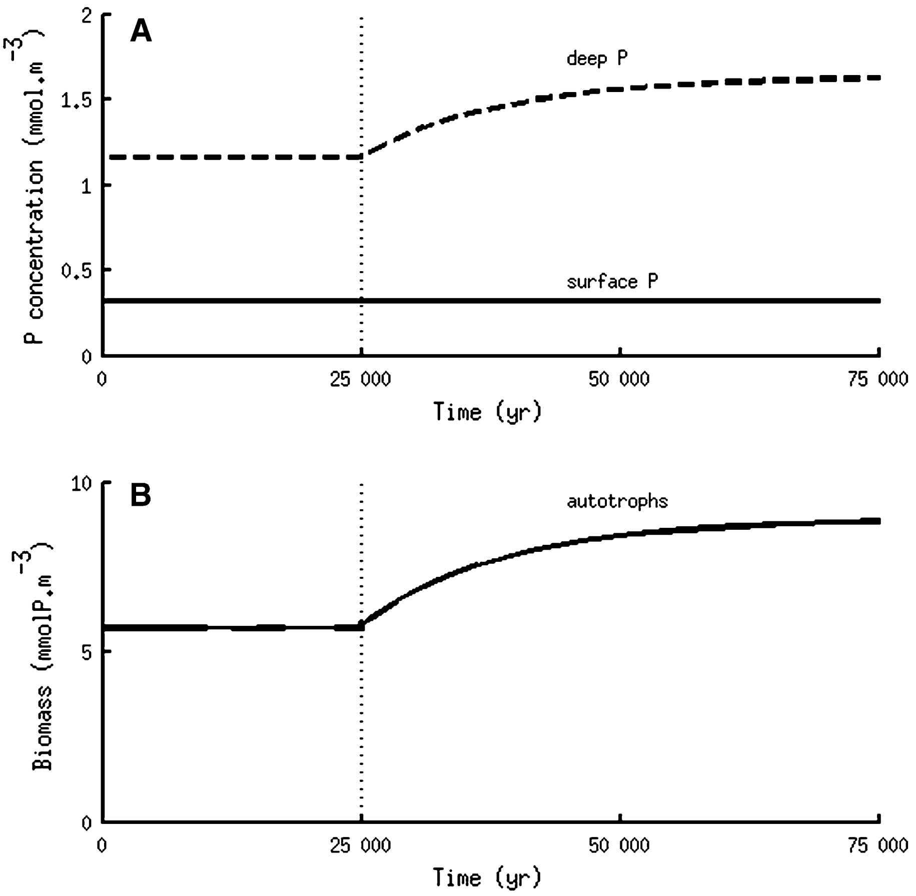

Figure 5. Regulation of phosphorus concentrations in the ocean. Nutrient supply is increased by 50% after a third of the simulation time (*dotted vertical line*). Simulations are performed from the application of the generic model to the oceanic cycle of phosphorus with realistic parameter values. *Bold lines* and *dotted lines* are for the surface and deep phosphorus pools, respectively. **A** Regulation of phosphorus concentrations in case of an increase in the supply of surface phosphorus ($\rho = 1$ and $\rho = 0.18$ for the accessible and inaccessible pools, respectively). **B** Impact of an increase in the supply of surface phosphorus on the biomass of autotrophic organisms.

stronger the indirect biotic regulation of the inaccessible nutrient. Thus, our generic model of a single nutrient cycle predicts that organisms have only a limited ability to regulate nutrient pools that are not directly accessible to them. Because inaccessible pools are often larger than accessible ones and external forcing often occurs through changes in nutrient supply, regulation of the system as a whole by the biota is expected to be limited.

In the cases of the current oceanic cycles of iron, silicon, and phosphorus, numerical simulations performed with realistic parameter values show that accessible nutrient pools are perfectly regulated. In contrast, regulation of inaccessible nutrient pools is in most cases partial, and once even non-existent ($\rho_{\mathrm{i,i}} = 2.3 \times 10^{-3}$, Figure 3C), although we can observe a response in the growth of autotrophic organisms (Figures 3D, 4D, 5D). These three examples suggest that for both chemical and physical nutrient limitations, nutrient cycles are not efficiently regulated by autotrophic organisms at global scales, although the strength of the biotic regulation of the different pools can quantitatively vary depending on the characteristics of each biogeochemical cycle (Figures 3, 4, 5).

DISCUSSION

The Importance of Physical and Chemical Processes in the Regulation of Biogeochemical Cycles

Our model highlights the importance of passive physical and chemical processes that govern transfers between accessible and inaccessible nutrient pools, in the regulation of biogeochemical cycles. It is well known that nutrient dynamics in ecosystems are strongly impacted by physical processes (for example, Karl 2002; Boyd and Ellwood 2010; Franz and others 2012 for marine ecosystems) and chemical reactions (for example, Falkowski and others 2000; Karl 2002). This phenomenon is revealed in our model by the importance of parameter k_a in the regulation coefficients. Thus, physical and chemical processes that govern transfer rates between pools can have a strong influence on the regulation of inaccessible limiting nutrients.

The intensity of chemical and physical flows between the accessible and inaccessible nutrient pools is highly affected by the characteristics of the environment. An example is water column stratification in freshwater and marine systems, which reduces the intensity of physical flows between water layers (that is, downwellings and upwellings, governed by parameters k_a and k_i, respectively), as well as the relative volume of the upper accessible layer (α) (Riebesell and others 2009). Global climate change is expected to increase stratification through increased sea surface temperature and decreased sea surface salinity (Gruber 2011; Rees 2012). By decreasing parameters k_a and α, increased water column stratification could strongly reduce the potential for biotic regulation of inaccessible nutrients in lakes and oceans. At the same time, the decrease in the depth of the upper layer (related to the parameter α) is likely to intensify the recycling flow to the inaccessible nutrient pool because sinking particles will take less time to reach the deep inaccessible layer. As recycling of organic matter by microorganisms consumes oxygen, an increase in oxygen depletion in deep waters is likely to occur (Diaz and Rosenberg 2008). The increasing eutrophication of deep waters and the spreading of oxygen minimum zones may then have dramatic consequences on freshwater and marine food webs (Diaz and Rosenberg 2008; Stramma and others 2008; Doney 2010).

Biotic Regulation on Global Scales

The potential for biotic regulation of the Earth system has been hotly debated, whether it relates to the Gaia hypothesis (Lovelock and Margulis 1974; Lenton 1998; Free and Barton 2007; Tyrrell 2013) or to Redfield ratios in the ocean (Redfield 1934, 1958). Our simple generic model of resource access limitation sheds new light on this longstanding debate. Strong biotic regulation of global biogeochemical cycles implicitly assumes that nutrients are accessible to organisms. But, in reality, resource access limitation is pervasive; massive amounts of nutrients globally are inaccessible to organisms because of physical or chemical barriers. Our model and its applications to the oceanic cycles of iron, silicon, and phosphorus predict, as expected intuitively, that autotrophic organisms should be able to strongly regulate the concentrations of limiting nutrients in accessible nutrient pools because of their top-down control on these pools. But our model also predicts that any variation in nutrient supply should be only partially or negatively regulated in inaccessible nutrient pools because organisms have only indirect access to these pools. In the application to the iron cycle, however, the absence of recycling in the inaccessible pool lead variations in the supply of accessible, dissolved iron to be entirely absorbed by organisms, and thus regulation of the concentration of inaccessible iron with respect to a change in the supply of accessible iron is perfect (Figure 3A).

Our model further shows that either autotrophic organisms have a strong impact on accessible pools and exert weak regulation on the rest of the system, or they have a weak impact on accessible pools and exerts moderate regulation on the rest of the system. Thus, strong biotic regulation of global biogeochemical cycles or of the Earth system as a whole seems unlikely because of the inaccessibility to organisms of large amounts of their resources at the global scale. Our predictions focus on the regulation of biogeochemical cycles by autotrophic organisms. Other biotic and abiotic processes could reinforce regulation of biogeochemical cycles by creating negative feedbacks, such as fires in the oxygen cycle (for example, Lenton and Watson 2000b; Lenton 2001) and microbial populations that control the denitrification and the anammox processes in the nitrogen cycle (Seitzinger and others 2006; Brandes and others 2007), and are likely to play an important role in the regulation of global biogeochemical cycles (Karl 2002). However, some other processes create positive feedbacks that can destabilize the system, for example, the positive climate-CO_2 feedback that occurs through thermal stratification and decreased solubility of CO_2 in seawater (for example, Denman and others 2007).

We assumed top-down control of inorganic nutrients by a single trophic level in our model. The addition of a second trophic level would lead the ecosystem to be controlled by herbivores instead of autotrophs. Consequently, we may expect decreased regulation of both accessible and inaccessible nutrient pools. Numerical simulations, however, suggest that regulation is little affected by the addition of herbivores in our generic model, except for the regulation of the accessible nutrient concentration with respect to changes in the nutrient supply to the inaccessible pool (results not shown). Although the addition of a second trophic level does have a quantitative impact on nutrient regulation, numerical simulations suggest that it does not qualitatively alter our predictions regarding the regulation of the inaccessible nutrient concentration.

Possible Applications of Our Model

We presented applications of our model to the cycles of iron, silicon and phosphorus in the global ocean. Numerical simulations performed with realistic parameter values illustrate the fact that global biogeochemical cycles are not efficiently regulated by autotrophic organisms (Figures 3, 4, 5). However, the oceanic cycles of the three key nutrients do not seem to be regulated in the same range. Phytoplankton appears to be completely unable to regulate the concentration of particulate iron with respect to an increase in its supply ($\rho_{\mathrm{i,i}} = 2.3 \times 10^{-3}$, Figure 3C), whereas the silicon cycle appears to be quite efficiently regulated with respect to changes in its supply to the deep ocean ($\rho_{\mathrm{i,i}} = 0.78$, Figure 4C). This difference could be due to the absence of recycling of organic matter to the inaccessible pool in the iron cycle, which strongly decreases the ability of phytoplankton to impact and possibly regulate the inaccessible nutrient pool.

In the application to the Si cycle, our estimate of the Si standing stock of autotrophs is 60 μmol m^{-3}, in agreement with experimental data of 17–217 μmol m^{-3} in the upper 120 m of the ocean (Adjou and others 2011; Tréguer and De La Rocha 2013). Likewise, the simulated stock of P in the organisms represents 1.74% of the total stock of P in the surface ocean, which is comparable with values of 0.03–6.45% found in the literature (Loh and Bauer 2000). In the application to the Fe cycle, organisms contain more than 9 times more Fe than dissolved Fe in the water column in our numerical simulations. A possible explanation for this high proportion is that dissolved Fe is scarce in the ocean (for example, Baker and Croot 2010; Boyd and Ellwood 2010). The simulated concentrations of silicic acid and phosphorus in the surface and deep ocean are in the same range as field measurements, although simulated deep-water concentrations are a little lower than experimental data, for both Si and P (Loh and Bauer 2000; Tréguer and De La Rocha 2013). The concentrations of dissolved phosphorus are also consistent with field measurements (Loh and Bauer 2000). Numerical simulations also predict a dissolved Fe concentration of 51.4 nmol m^{-3}, a high concentration compared to the measured concentration of 1–2 nmol m^{-3} in surface waters (for example, Boyd and Ellwood 2010). However, these measures are not contradictory, as our estimated concentration of dissolved Fe includes dissolved Fe in the whole water column, and the dissolved Fe concentration is higher in deep waters than in surface waters. Thus, the applications of our simple model predict relatively realistic concentrations in both biotic and abiotic pools.

We applied our theory to the example of the biogeochemical cycles of iron, phosphorus, and silicon in the ocean, but this theory could also help to study the ability of organisms to regulate nutrient pools at large spatial scales in other systems where access to resources is limited. For instance, oceanic and freshwater systems are often separated in two layers, either by a thermocline or because of the limited depth of the euphotic layer. These systems are heavily impacted by anthropogenic activities, in particular through water eutrophication (Smith and others 1999; Carpenter 2005; Smith and Schindler 2009). Our generic model could be applied to either oceanic or freshwater systems to assess the ability of organisms to regulate the concentration of nutrients such as N, P, and Fe that often limit primary production and are increasingly supplied to freshwater (and then marine) ecosystems by human activities. Another possible application is nutrient dynamics in soils inside and outside plant rooting systems and the ability of plants to mitigate the increased supply of nutrients used in fertilizers, such as N and P (Bouwman and others 2009; Vitousek and others 2009). However, the application of our model to the N cycle would require inclusion of a second type of autotrophic organisms, that is, nitrogen fixers (for example, Vitousek and Field 1999; Tyrrell 1999). Our model could also be extended to biogeochemical cycles of two nutrients consumed by two groups of autotrophic organisms to assess how competition between two functional groups of autotrophs impacts regulation of nutrient concentrations as well as nutrient ratios. Such a stoichiometric extension could be used to address the issue of the regulation of Redfield ratios in the ocean and determine how organisms can exert a strong control on nutrient ratios in their environment when they are unable to efficiently regulate nutrient concentrations. Thus, the theory and model of resource access limitation we have started to develop here offer promising tools to resolve long-standing issues and debates over the potential for biotic regulation of various components of the Earth system.

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