Nitrogen, phosphorus, iron and oceanic primary production

Tyrrell developed a simple two-box model of oceanic nitrogen and phosphorus cycles to describe the regulation of both nitrate and phosphate concentrations in the global ocean. Competition between nitrogen-fixing and other phytoplankton controls levels of nitrate, continually pushing molar concentrations to slightly less than 16 times those of phosphate. A ratio below 16 in surface waters is interpreted as indicating nitrate deficit, hence proximate control of primary productivity by nitrate. Results of the model show that phosphate is the ultimate limiting nutrient, because extra phosphate in the system supports the proliferation of N₂-fixers which can add new nitrogen to the ocean.

It was recently proposed that a widespread deficit of nitrate in the ocean, for example as presently observed, is caused by iron-limitation of marine N₂-fixation. That is, when iron is sufficiently abundant to satiate N₂-fixers, the ratio of nitrate to phosphate in the ocean will increase to 16. Tyrrell's model accounts for a nitrate deficit with no recourse to effects of iron, leading him to discount the biogeochemical significance of iron limitation as it relates to N₂-fixation and oceanic levels of N and P. Even when subjected to extensive sensitivity analysis, the model consistently predicts a deficit of nitrate in the surface layer.

Additional calculations (Fig. 1) indicate that the model's prediction of a nitrate deficit in surface waters of the ocean is uncertain. The molar ratio of nitrate to phosphate in the surface layer, $R_s$, is very sensitive to chosen values for the Michaelis-Menten half saturation constants for growth of phytoplankton on nitrate ($K_s(\text{NO}_3)$) vs. phosphate ($K_s(\text{PO}_4)$). A 20% increase of $K_s(\text{NO}_3)$ to 0.6 mmol m⁻³ from the assumed 0.5 mmol m⁻³ obliterates the predicted nitrate deficit in surface waters, bringing $R_s$ to 16. The uncertainty in $K_s(\text{NO}_3)$ is 0.1 to 4.2 mmol m⁻³ (ref. 4 cited in ref. 1), corresponding to $R_s = 2.7$ to 112 mol mol⁻¹.

Small changes in the maximum growth rate for other phytoplankton, $\mu'_O$ (d⁻¹), compared to 0.24 d⁻¹ for N₂-fixers, also strongly influence $R_s$ (Fig. 1). There is little experimental basis for excluding assumed growth rates that lead to $R_s = 16$.

This simple analysis, based directly on Tyrrell's model, suggests that regulation of oceanic N₂-fixation by iron cannot be excluded as a potentially important influence on cycles of nutrients and primary productivity in the ocean.

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