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Robust biotic regulation of the deep ocean N:P ratio (Outstanding Young Scientist Lecture)

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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$16 required by the phytoplankton. Redfield and subsequent workers have suggested that it is due to N-fixing organisms being selected when N:P$<$16 but being out-competed when N:P$>$16. Models have shown this mechanism can work, but recent observations bring it into question. 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. To examine the impact of these discoveries, we adapt recent models to include non-Redfield stoichiometry of phytoplankton and limitation of N-fixers by resources other than P. This reveals 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, if competitive dynamics set the N:P threshold for N-fixation then 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. Decreases in phytoplankton C:P and N:P ratios over the past $\sim$1Gyr would have tended to decrease deep ocean N:P by increasing PO_4. 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. Even if Fe or light limitation makes 75% of the ocean unavailable to N-fixers, deep ocean N:P only drops to $\sim$13, because N-fixers reach higher densities when restricted to smaller fractions of the ocean's surface. Thus Redfield's mechanism for regulation of oceanic N:P is robust and it provides a remarkable example of global environmental variables

being set by biological requirements.