A new source of 'new' nitrogen in the sea

Open-ocean ecosystems on Earth are characterized by low concentrations of fixed, bioavailable nitrogen (N), which would appear to make them a suitable niche for the proliferation of N_2-fixing prokaryotes. However, N_2-fixing prokaryotes also prefer environmental conditions defined by high phosphorus (P), high iron (Fe) and low oxygen (O_2); near-surface open-ocean habitats are chronically depleted in P and Fe and, typically, are well oxygenated (e.g. O_2 = 200–250 μM).

Historical investigations conducted in candidate tropical and subtropical habitats of the world's oceans have generally failed to support the ecological prediction of N_2-fixing microorganism dominance. Existing conceptual and mathematical models of biogeochemical cycling in the ocean therefore generally ignore N_2 fixation as a key metabolic process.

In their now-classic treatise on nutrient dynamics in the sea, Dugdale and Goering[1] introduced the unifying concept of 'new' (i.e. nutrients imported to the local environment from surrounding regions) vs 'regenerated' (i.e. nutrients that are locally remineralized) forms of nitrogen. They were careful to emphasize that there were several potential sources of new N for the euphotic zone, each of equal value but with potentially different ecological consequences. As there were few data on N_2-fixation rates when their paper was published, importation of nitrate from below the euphotic zone was considered to provide the majority of new N in the sea.

Now, thirty years after the new production concept was introduced, there is increasing evidence that rates of oceanic N_2 fixation could have been systematically underestimated or, perhaps, have increased in relative importance over time. This new evidence comes from several independent lines of investigation. One of the most interesting and provocative modern data sets is that derived from the application of novel molecular methods to detect the presence and abundance of N_2-fixing microorganisms either by hybridization or amplification of nitrogenase genes (*nif*; the enzyme system used to reduce N_2 to ammonia), as described by Zehr *et al.* in the February 2000 issue of this journal[2]. Application of these methods to open-ocean biomes in the North Atlantic and North Pacific Oceans has revealed a spectrum of previously uncharacterized *nif* gene phylotypes. Furthermore, significant *nif* phylotype diversity was apparent both within and between open-ocean ecosystems. These novel data sets, when considered in concert with other recent reports of high rates of oceanic N_2 fixation, support the hypothesis that N_2 fixation is a major source of new N over vast regions of the world's oceans. It now appears that up to 50% of ecosystem new N could be derived from N_2 fixation[3–6] (D.M. Karl *et al.*, unpublished). Dugdale and Goering[1] were careful to warn initially that if N_2 fixation was (later) found to be a quantitatively important pathway for nutrient supply, then a revision of the new vs recycled N conceptual framework would be necessary.

I submit that the time has come for a reconsideration of the new production paradigm. There is much at stake in this re-assessment. First, the net rate of carbon dioxide sequestration into the interior portion of the ocean is directly controlled by the source(s) of new N. If the nitrate flux dominates, there will be no net carbon sequestration because the bidirectional mass fluxes of C and N would be nearly in balance, as predicted by the new production–export production model[7]. Alternatively, if N_2 fixation sustains a significant amount of new and export production in open-ocean ecosystems, then net carbon dioxide will be sequestered. Furthermore, N_2 fixation in the world's oceans could be controlled by the atmospheric deposition of Fe, which itself is a variable, climate-sensitive parameter. Total atmospheric dust transport is also affected by humankind, including population demographics, global economies and land-use patterns. These complex natural and anthropogenic interactions, with multiple potential feedback loops, provide a mechanism for biogeochemical variability in otherwise 'stable and homogeneous' biomes. In this regard, the seascape might be a slave to the landscape, and there is no question that the latter has changed significantly over the past 250 years.

If the conceptual framework of new and regenerated production is discarded, it could take many years for it to be replaced with a new, ecumenical theory of nutrient dynamics in the sea. There is no doubt in my mind that additional, important discoveries of novel unexpected marine microorganisms will be made as we continue to explore our planet and these future discoveries might also challenge existing dogmas. One immediate and major task before us is to isolate and identify these recently discovered 'virtual' N_2-fixing microorganisms in order to move forward towards the much larger challenge of *in situ* processes. As Tom Brock correctly stated nearly 40 years ago, 'Ecology is physiology under the worst possible conditions'. The report by Zehr *et al.*[2] brings us a step closer to a more complete ecological understanding of Earth's largest biome.

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