Anoxia in the snow

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*Substantial amounts of denitrification and other anaerobic metabolisms can occur in anoxic microenvironments within marine snow particles, according to model simulations. This microbial activity may have a global impact on nitrogen cycling.*

The vast majority of the global ocean contains plenty of oxygen, allowing aerobic respiration of organic carbon. Some organisms are also capable of respiring other compounds such as nitrate or sulfate, but generally these metabolisms are confined to oxygen minimum zones that make up less than 1% of the global ocean volume\(^1\). These oxygen depleted regions play a key role in controlling the oceanic nutrient inventory, as they host 30 to 50% of oceanic nitrogen loss\(^2\). However, molecular and experimental data suggests that anoxic microenvironments might exist outside of oxygen minimum zones in sinking organic-rich aggregates in oxygenated waters\(^3\)-\(^5\). Writing in *Nature Geoscience*, Bianchi and co-authors\(^6\) report that estimates of nitrogen loss in the water column could double when anaerobic metabolisms occurring in anoxic microenvironments are considered. Microbial processes in these microenvironments also explain observations of sulfate reduction and cadmium enrichment.

Aggregates, commonly known as marine snow, form in the sunlit surface oceans and can include phytoplankton, detritus and fecal pellets\(^7\). Throughout a particle’s journey towards the seafloor, organic matter is consumed as oxygen is respired. When respiration rates exceed diffusion of oxygen into the particle from the surrounding water, then the centre can become anoxic\(^8\) (Fig. 1). The formation and extent of anoxia within a particle is dependent on the aggregate size, carbon reactivity, and the oxygen concentration in the ambient water; anoxic microenvironments can occur even in fully oxygenated waters if aggregates are large enough, generally greater than one millimetre in diameter\(^9\).

Once oxygen has been depleted, organic matter is respired using other abundant oxidants in the order of free energy yield. The most favorable oxidant after oxygen is nitrate, which is sequentially reduced, via nitrite and nitrous oxide, to dinitrogen gas, whereupon it is lost from an ecosystem. Once nitrate is exhausted, sulfate reduction becomes the most dominant process. The links between these anaerobic metabolisms and carbon rich particles have been investigated in the context of oxygen minimum zones and in laboratory formed aggregates\(^9\)-\(^12\), but whether anoxic microenvironments influence nutrient cycling in oxygenated ocean waters is less well known.

Bianchi *et al.*\(^6\) address this knowledge gap by using a size-resolved model to predict the onset and rates of anaerobic metabolisms within sinking particles throughout the oceans. Rates of denitrification and sulfate reduction within particles are controlled by a complex interplay of processes that are challenging to reproduce in experimental setups; numerical simulations allow the authors to account for factors such as aggregate properties and size spectra, as well as seawater chemistry. The model reproduces particle features observed in the eastern tropical South Pacific.
Ocean and the Mauritanian upwelling zone, including trace metal enrichment in particles due to sulfide precipitation. The resulting global estimation of particle-associated denitrification shows substantial activity throughout large regions of the tropics and the subtropical and subarctic North Pacific, where water column oxygen is low. If correct, the additional nitrogen loss in particles would result in a doubling of the estimated rate of water column denitrification.

Due to the lack of experimental data, the new size resolved model makes some assumptions about the kinetics and diversity of anaerobic metabolisms. One assumption is that anaerobes are present and ready when favourable conditions arise; another is that respiration rates scale to the free energy yield of each pathway, for example that denitrification has a free energy yield that is 99% of oxygen respiration. In sensitivity tests, changing respiration rates of denitrification to 50% of oxygen respiration rates, instead of 99%, only results in a 20% reduction in nitrogen loss. However, this step down is poorly constrained, with no experimental evidence to suggest whether denitrification rates are 5, 50 or 90% that of oxygen respiration. Hopefully this work will inspire the research needed to constrain these assumptions. Further refinements will also come as more metabolisms are added to the model. So far, nitrate reduction to dinitrogen gas is considered as a single process in the model, but nitrate respiration to nitrite or ammonium in particles may also be important processes\(^9\,^{12}\). These metabolisms, along with nitrification, do not result in dinitrogen production, so may reduce the simulated loss of bioavailable nitrogen.

Nevertheless, the upward revision of water column nitrogen loss rates presented in the paper alters the balance of the marine nitrogen budget, with sinks apparently exceeding sources. Bianchi et al. suggest that it is unlikely that the oceans will run out of bioavailable nitrogen in the coming centuries. Instead, they argue that either an increase in the source term, nitrogen fixation, is required, which has been upwardly revised several times in the past decade\(^{13}\), or, alternatively, the distribution of nitrogen sinks in the ocean needs to be reassessed. A ratio of approximately 2:1 between benthic and pelagic fixed nitrogen removal has been inferred based on isotopic constraints\(^{14}\). However, localized depletion of nitrate in anoxic microenvironments should result in a weaker isotopic fractionation. Hence, some of the nitrogen loss currently assigned to sediments may be occurring within anoxic microenvironments instead.

Bianchi et al.\(^6\) have shown that anoxic microenvironments in aggregates are an overlooked niche in the oceans, potentially doubling the rate of pelagic denitrification compared to estimates from oxygen minimum zones alone. Their simulations provide a new appreciation of heterogeneity in elemental cycling in the global ocean and may require a revision of our understanding of the marine nitrogen budget and its sensitivity to climate change.

References
Figure 1. Suggested caption: Particle microenvironments. In well-oxygenated waters, particles are degraded by microbes using aerobic metabolisms. However, if the availability of oxygen decreases, these particles can form anoxic microenvironments where nitrate and sulfate respiration occur. Bianchi et al.\textsuperscript{6} use numerical simulations to show that denitrification in these microenvironments results in substantial loss of bioavailable nitrogen from the water column. Images provided courtesy of Morten H. Iversen (Alfred Wegener Institute for Polar and Marine Research and MARUM, University of Bremen)