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Diversity, distribution and abundance of nitrogen fixing microbes in the Oxygen Minimum Zones

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Nitrogen (N) is an essential nutrient that limits productivity in large parts of the world ocean. While denitrification and anammox are the major processes responsible for the removal of this nutrient from the oceans, input occurs mainly through nitrogen fixation. Estimates of marine N budgets suggest that losses exceed inputs, while models imply that nitrogen fixation should be enhanced in the vicinity of oxygen minimum zones, where the loss processes occur. Based on analysis of *nifH*, a key gene in nitrogen fixing microbes, we found that several clades of N-fixers are present and active in the OMZ and surface euphotic waters in the Eastern Tropical South Pacific (ETSP), Eastern Tropical North Pacific (ETNP) and Arabian Sea. These OMZ regions contain substantial *nifH* diversity, in both surface and anoxic waters. Surface waters contained greater diversity, but that was not due to presence of the well-known diazotroph, *Trichodesmium*, or other cyanobacteria. Sequences related to *Trichodesmium* were rare in the combined clone libraries from these three regions and were detected only in surface waters (Cluster I *nifH*), along with proteobacterial *nifH* phylotypes.

Most of the new sequences in three of the four Clusters of the conventional *nifH* phylogeny were not closely related to any sequences from cultivated Bacteria or Archaea. Cluster II was not represented in the OMZ samples. The most abundant Cluster I OTUs could be assigned to the Alphaproteobacteria, followed by the Gammaproteobacteria. *nifH* DNA and cDNA sequences with high identities to those of anaerobic microbes (Clusters III and IV *nifH*) were found in the anoxic waters. Although similar groups of *nifH* sequences were present in the three OMZs, strictly anaerobic sequences (Cluster III and IV) were better represented in the ETP ODZs. Most of the OTUs were not shared among regions, depths or DNA vs cDNA and sometimes were restricted to individual samples.

While measurements of N₂ fixation rates are not reported here, the abundance of cDNA sequences, estimated from quantitative PCR, implies that the genes are expressed and the cells harboring them are active. We previously reported low, but analytically significant, rates in anoxic depths in the ETNP, indicating that non-cyanobacterial N fixation might make a small contribution to the N budget of the ocean. Future work should focus on determining to what extent the diversity we detected actually represents biogeochemically significant reactions and what factors might control the activity of diazotrophs in the dark ocean.

Position

Senior Scientist

Affiliation

Princeton University

Email Address

ajayakum@princeton.edu

Are you a SFB 754 / Future Ocean member?

No

Primary author(s): JAYAKUMAR, Amal (Princeton University)

Co-author(s): Prof. WARD, Bess B (Princeton University)

Presenter(s): JAYAKUMAR, Amal (Princeton University)

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