frontiers in Marine Science

EDITORIAL
published: 04 March 2021
doi: 10.3389/fmars.2021.664195

Editorial: Marine N_2 Fixation: Recent Discoveries and Future Challenges

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Keywords: N_2 fixation, marine N inventory, environmental controls, aphotic N_2 fixation, diversity, modeling

Editorial on the Research Topic

Marine N_2 Fixation: Recent Discoveries and Future Challenges

Marine N_2 fixation is one of the most critical processes in the ocean, controlling the bioavailability of nitrogen (N), an essential building block for the maintenance of biological activity (Falkowski, 1997). Technological advances in the field of genomics (Zehr et al., 1998) unveiled the existence of a wide variety of both N_2 fixers and N_2 fixation strategies, challenging our knowledge of the factors controlling this important process. Temperature, N deficiency, as well as iron (Fe) and phosphorus availability have been traditionally thought to be the main factors controlling diazotrophs's distribution. These factors now appear insufficient to describe the variety of physiologies associated with the diversity of N_2 fixers, and to explain the wider range of marine habitats occupied by these unique organisms (Zehr and Capone, 2020). At the same time, methodological limitations associated with the N_2 fixation rate measurement (Mohr et al., 2010) have cast some doubt on the robustness of historical data, further increasing the uncertainty of global N_2 fixation rates (Großkopf, 2012). These findings imply that we still have much to learn about the factors that control the magnitude and temporal and spatial variability of this important process, and its role in regulating ocean biogeochemistry. This Research Topic stems from two international workshops on the "Environmental Controls of Marine N_2 Fixation" aiming to connect the scientific community working on N_2 fixation. It gathers contributions from different expertise focusing on novel aspects of the physiology, ecology and biogeochemical role of diazotrophs, spanning from cellular to global scales with the aim of contributing to a more coherent understanding of the triggers and function of N_2 fixation in the marine environment.

Current independent estimates of global marine N_2 fixation from direct measurements, geochemical fingerprints on oceanic nutrient content and model simulations reviewed by Landolfi et al. in this Research Topic, range from about 100–200 $TgNy^{-1}$. Large uncertainties still remain from the lack of a comprehensive understanding of the environmental controls and ecological interactions of marine N_2 fixers. The application of molecular techniques allowed the detection of *nifH* genes in regions that extend far beyond the geographical domain of N_2 fixation originally associated to warm tropical oligotrophic waters. Using molecular fingerprinting Fernandez-Mendez et al. report on the detection of *nifH* genes in the Arctic Ocean, and the existence of a large genetic diversity that appears distinct from surrounding oceanic regions. This wider distribution is further supported by year-round measurable N_2 fixation rates in N-rich temperate waters of the upwelling system of the Iberian peninsula, that appear populated by genetically diverse diazotrophs as reported by the study of Moreira-Coello et al., challenging the traditional low-N paradigm. Oceanic environments are populated by diverse N_2 fixing organisms, including non-cyanobacterial diazotrophs. Albeit expressing low fixation rates non-cyanobacterial diazotrophs thrive both in photic and aphotic regions as reviewed by Moisander et al., potentially

OPEN ACCESS

Edited and reviewed by:
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Specialty section:
This article was submitted to Aquatic Microbiology, a section of the journal Frontiers in Marine Science

Received: 04 February 2021
Accepted: 11 February 2021
Published: 04 March 2021

Citation:
Landolfi A, Rabouille S and Mouriño-Carballido B (2021) Editorial: Marine N_2 Fixation: Recent Discoveries and Future Challenges. Front. Mar. Sci. 8:664195. doi: 10.3389/fmars.2021.664195

making a large contribution to global rates of N_2 fixation. In their perspectives Benavides, Bonnet et al. speculate that extrapolating the sparse low aphotic N_2 fixation rates for the whole mesopelagic NO_3-rich zone, would lead to a significant increase of the oceanic N inputs, largely compensating for the N loss via denitrification, and call for the consolidation of these extrapolations with future aphotic N_2 fixation rate measurement studies.

Several contributions address the control of diazotroph's biogeography by resource availability. While desert dust is considered a primary source of iron (Fe) to the ocean, its low solubility (<12%, Jickells et al., 2005) prompts phytoplankton adaptive strategies to access this micronutrient in bioavailable forms. In controlled laboratory experiments, Polyviou et al. report on the substrate specific physiological and transcriptomic responses of *Trichodesmium* for Fe acquisition from complex matrices. Direct vicinity between cell and dust particles may enhance Fe bioavailability to *Trichodesmium*, suggesting that modes of Fe-supply may be important for the niche determination of this important diazotroph. Benavides, Martias et al. discuss the role of dissolved organic matter as a possible complementary source of energy and nutrients for both cyanobacterial and non-cyanobacterial diazotrophs.

Gradoville et al. used high-throughput 16S rRNA and *nifH* gene sequencing and metagenomics to describe the microbiome associated with *Trichodesmium* colonies in the North Pacific subtropical gyre. They find that colony morphology appears to be tied to different epibiont communities, uncovering the links between physiological characteristics and ecological functions. The fate and mortality pathways of diazotrophs and their effect on biogeochemistry is just starting to be explored. In this collection, Kuznecova et al. provide new insight on the role of virus-host interaction. They investigate how viral infections affect the growth, N_2 fixation ability and gene expression of a bloom-forming heterocytous cyanobacterium *Aphanizomenon flos-aquae*.

Accurate rate measurements are key for assessing the global significance of N_2 fixation. In a combination of dedicated laboratory experiments and a literature meta-analysis Wannike et al. constrain the errors associated with the $^{15}N_2$ methods, that may lead to underestimate N_2 fixation rates measurements. They find that the errors associated with the lack of equilibration of $^{15}N_2$ are highly dependent on incubation time and experimental conditions. By comparing the retentive characteristics of filters for N_2 fixation rates measurements, in different settings from coastal waters to the Baltic Sea and Pacific Ocean, Bombar et al. warn on the potential underestimation of N_2 fixation by the use of borosilicate glass fiber filters (GF/F, Whatman) with a nominal pore size of $0.7\,\mu m$ that are inadequate to capture small cells. Caputo et al. conducted a comparative analysis of two symbiotic N_2-fixing cyanobacteria, the diazotrophs-diatoms associations (DDA) and diazotroph-prymnesiophyte known as UCYN-A, both providing fixed forms of N to the host. They warn on the pre-filtration step during qPCR *nifH* surveys that lead to systematic underestimation of large and chain-forming DDAs.

In summary, the contributions included in this Research Topic focused on novel aspects of the physiology and ecology of marine diazotrophs, addressing methodological limits and current gaps in our knowledge that make future predictions a challenge. These papers contribute toward a more comprehensive understanding of the controls of this key process, which is core for improving future predictions of marine N_2 fixers under a fast-evolving climate.

AUTHOR CONTRIBUTIONS

All authors listed have made a direct and intellectual contribution to the work, and approved it for publication.

ACKNOWLEDGMENTS

Papers featured in this Special Issue have been leveraged from two workshops on the Environmental Controls of Marine N_2 Fixation: Present Knowledge and Future Challenges that brought together a multidisciplinary group of marine N_2 fixation experts, from genomics to global biogeochemistry, to consolidate current knowledge and define key uncertainties in current understanding of marine N_2 fixation. We acknowledge the funding support from the Deutsche Forschungsgemeinschaft (DFG) project SFB754 and Euromarine 2015 Workshop grant.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.