



OPEN ACCESS

EDITED AND REVIEWED BY
Andreas Teske,
University of North Carolina at Chapel Hill,
United States

*CORRESPONDENCE
Tori M. Hoehler
✉ tori.m.hoehler@nasa.gov

RECEIVED 07 December 2023
ACCEPTED 11 December 2023
PUBLISHED 04 January 2024

CITATION
Hoehler TM, Amend JP, Jørgensen BB,
Orphan VJ and Lever MA (2024) Editorial:
Studies on life at the energetic edge – from
laboratory experiments to field-based
investigations, volume II.
Front. Microbiol. 14:1351761.
doi: 10.3389/fmicb.2023.1351761

COPYRIGHT
© 2024 Hoehler, Amend, Jørgensen, Orphan
and Lever. This is an open-access article
distributed under the terms of the [Creative
Commons Attribution License \(CC BY\)](#). The use,
distribution or reproduction in other forums is
permitted, provided the original author(s) and
the copyright owner(s) are credited and that
the original publication in this journal is cited, in
accordance with accepted academic practice.
No use, distribution or reproduction is
permitted which does not comply with these
terms.

Editorial: Studies on life at the energetic edge – from laboratory experiments to field-based investigations, volume II

Tori M. Hoehler^{1*}, Jan P. Amend², Bo Barker Jørgensen³,
Victoria J. Orphan⁴ and Mark A. Lever⁵

¹Exobiology Branch, NASA Ames Research Center, Moffett Field, CA, United States, ²Department of Earth Sciences and Department of Biological Sciences, University of Southern California, Los Angeles, CA, United States, ³Department of Biology, Aarhus University, Aarhus, Denmark, ⁴Department of Geological and Planetary Sciences, California Institute of Technology, Pasadena, CA, United States, ⁵Marine Science Institute, The University of Texas at Austin, Austin, TX, United States

KEYWORDS

energy limitation, deep biosphere, aquatic sediments, cryopeg, serpentinizing systems, hydrothermal systems

Editorial on the Research Topic

[Studies on life at the energetic edge – from laboratory experiments to field-based investigations, volume II](#)

Among the diverse inhabitants of Earth's biosphere, microorganisms reign supreme in their capabilities to occupy an expansive range of ecological niches. We often conceive of the fringes of our biosphere in terms of physicochemical "extremes", but perhaps the most pervasive environmental challenge to microbial life is that of extreme energy limitation (Hoehler and Jørgensen, 2013; Lever et al., 2015; Bradley et al., 2020). Globally, for example, the marine deep biosphere occupies a volume and hosts a biomass comparable to that of the overlying oceans, yet that deep biosphere is sustained by an energy flux about 1,000 times lower (Hoehler et al., 2023). Both in the sub-seafloor and in the continental subsurface, these energy-starved organisms exist at the interface between the inhabited and uninhabited realms of our planet. To understand their physiology in the face of extreme energy limitation would, therefore, be to understand the capabilities and limitations of the ultimate arbiters of chemical exchange between the biosphere and the geosphere.

Our awareness and understanding of life at the energetic edge has grown considerably over the last few decades, yet much remains to be learned. What factors determine the minimal energy requirements of microorganisms, and how do those requirements vary with the physicochemical environment? What physiological traits promote survival under extreme energy limitation? Do those traits evolve as a specific adaptation to energy limitation, or are they a fortuitous result of adaptation to other conditions (exaptation)? Do any physiological differences relating to energy limitation translate to differing capabilities and limitations with respect to biogeochemical processing? Natural ecosystems provide a unique window into populations exposed to energy limitation over long timescales that are intractable in laboratory settings. This special Research Topic focuses on such systems: on advances being made at the frontiers of environmental microbiology.

Jaussi et al. quantified cell-specific catabolic energy yields in several marine sediments, for both the total cell population and for sulfate-reducing bacteria (SRB), specifically. They observed that cell-specific energy yields for the total population diminished over orders of

magnitude with increasing sediment depth (age), but yields for SRB specifically appeared to reach a stable minimum much higher than that of the overall population. Taxonomic or metabolic differences thus appear to factor significantly into minimum energy requirements. This study leveraged sensitive radiotracer techniques to measure metabolic process rates. For those interested in pursuing similar techniques, Schubert and Kallmeyer have offered a deep dive into the methodology and optimization of liquid scintillation counting (LSC)—a “how-to” guide for pushing the sensitivity of radiotracer methods to the levels required for characterizing life at the energetic edge. Kanaan et al. modeled the energy requirements of microbes entrapped in a “cryopeg”—a volume of brine isolated within permafrost for 40,000 years. While subzero temperatures could potentially depress microbial energy requirements, the findings instead suggest that the need to produce extracellular enzymes and cryo- and osmoprotectant compounds results in an average per-cell requirement comparable to that observed by Jaussi et al. for SRB and well above that observed for non-SRB in cold marine sediments.

Two studies focused on microbial adaptations in serpentinizing systems, where water–rock reactions drive the fluid chemistry toward high pH and highly reducing and extremely CO₂-poor conditions. Thieringer et al. used metagenome analyses to investigate differences in ecophysiology among three distinct populations of CO₂-reducing methanogens. While all were found to share the potential for DNA scavenging, possibly as a strategy to mitigate phosphorus and nitrogen limitation, genomic differences suggest that organisms inhabiting the most alkaline fluids adopt distinctly different strategies for coping with this energetically challenging environment—a niche differentiation that supports their coexistence. Working in the same system, Rempfert et al. performed a comprehensive analysis of membrane-forming intact polar lipids (IPLs). The lipidome, dominated by diether glycolipids, reflects a unique combination of membrane adaptations—including pervasive modifications likely associated with phosphate limitation—to enable microorganisms’ survival in these conditions.

Three studies considered underexplored metabolic potential in the environment. Holden and Sistu reviewed the drivers of formate cycling by CO₂-reducing *Methanococci* and organotrophic *Thermococci*. Both have the genetic potential to produce H₂ from formate and subsequently catabolize H₂, but it is not known whether such production is prevalent relative to the direct utilization of environmental H₂. By considering H₂ and formate concentrations in hydrothermal fluids and environmental distributions, genomes, and biochemical data on *Methanococci* and *Thermococci*, Holden and Sistu argue that both preferentially utilize H₂, while formate becomes important primarily under low-H₂ conditions. Sonke and Trembath-Reichert analyzed published metagenomic and -transcriptomic datasets from a wide range of habitats to investigate the potential importance of oxalate as a microbial energy source. While oxalate is widespread in many environments, both in association with minerals and released by photosynthetic organisms, its typically very low dissolved concentrations suggest rapid turnover. Sonke and Trembath-Reichert demonstrate widespread potential for microbial oxalotrophy, especially in marine environments, where

oxalotrophy is thermodynamically favorable and may represent a widely overlooked microbial energy source. Vigderovich et al. used a series of incubation experiments to explore the relationship between iron reduction and aerobic methanotrophy in lake sediments. Rates of methanotrophy and, perhaps surprisingly, accumulation of ferrous iron were both enhanced by the addition of oxygen to hematite-amended incubations. The results suggest a complex interplay between these aerobic and anaerobic microbially mediated processes and a potential role for iron recycling in the survival of aerobic methanotrophs under hypoxic conditions.

Finally, Weeks et al. considered “the edge” for photosynthetic microorganisms. Working in 12 Yellowstone hot springs, they characterized microbial community composition and a suite of physicochemical variables across the “photosynthetic fringe”—the region in which an outflow channel visibly transitions from chemotrophic to highly pigmented photosynthetic microbial communities. While changes in temperature, pH, and sulfide content have been previously proposed to control the location of the transition, such factors only explain about 35% of the variation in community composition, indicating that the microbial community of photosynthetic fringe environments is a more complex interplay of these and other factors.

With this special Research Topic, we invite you to explore these recent advances in understanding life at the energetic edge!

Author contributions

TH: Writing—original draft. JA: Writing—review & editing. BJ: Writing—review & editing. VO: Writing—review & editing. ML: Writing—original draft, Writing—review & editing.

Funding

The author(s) declare financial support was received for the research, authorship, and/or publication of this article. TH was supported by the NASA Planetary Science Division’s ISFM program.

Acknowledgments

This special collection of articles accompanies the 4th International Workshop on Microbial Life under Extreme Energy Limitation (MicroEnergy 2022), which took place in Sandbjerg, Denmark, in September 2022. We gratefully acknowledge Kasper Urup Kjeldsen and Hans Røy for their many contributions to the organization of the workshop and the Aarhus University Research Foundation, the Carlsberg Foundation, the Center for Dark Energy Biosphere Investigations (C-DEBI), Frontiers in Microbiology, and the Gordon and Betty Moore Foundation for their financial support of the workshop.

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.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

References

- Bradley, J. A., Arndt, S., Amend, J. P., Burwicz, E., Dale, A. W., Egger, M., and LaRowe, D. E. (2020). Widespread energy limitation to life in global subseafloor sediments. *Sci. Adv.* 6, eaba0697. doi: 10.1126/sciadv.aba0697
- Hoehler, T. M., and Jørgensen, B. B. (2013). Microbial life under extreme energy limitation, *Nature Rev. Microbiol.* 11, 83–94. doi: 10.1038/nrmicro2939
- Hoehler, T. M., Mankel, D. J., Girguis, P. R., McCollom, T. M., Kiang, N. Y., and Jørgensen, B. B. (2023). The metabolic rate of the biosphere and its components, *Proc. Natl. Acad. Sci. U. S. A.* 120, e2303764120. doi: 10.1073/pnas.2303764120
- Lever, M. A., Rogers, K. L., Lloyd, K. G., Overmann, J., Schink, B., Thauer, R. K., Hoehler, T. M., and Jørgensen, B. B. (2015). Life under Extreme Energy Limitation: A Synthesis of Laboratory- and Field-Based Investigations, *FEMS Microbiol. Rev.* 39, 688–728. doi: 10.1093/femsre/fuv020