Trends in
Microbiology

Forum

Element cycling and microbial life in the hadal realm

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Hadal trenches represent the deepest oceanic realm and were once considered to be deprived of life. However, trenches act as important depocenters for organic matter with highly elevated microbial activity. In this forum, we discuss the biogeochemistry of the hadal realm and its microbial communities thriving at extreme hydrostatic pressure.

Introduction

The hadal zone accounts for 45% of the oceanic depth range (6–11 km) and covers ~1% of the global seabed. The area is dominated by 27 trench systems that stretch along tectonic subduction zones forming long, narrow, and bathymetrically isolated environments. The name, derived from the realm of death in Greek mythology, implies that trenches were believed to be too inhospitable for life and of little biogeochemical relevance. Furthermore, the extreme depth made it challenging to sample and to explore hadal ecosystems. Only recently have technological advances made it possible to directly observe, sample, and measure processes at such depths and provided completely novel insights and perspective on the importance of the hadal realm.

Hadal trench sediments have large inventories of organic material and pollutants

The V-shaped hadal trenches are located in seismic active areas with frequent earthquakes (Figure 1) [1]. This can induce mass wasting events where material from the sides of the trench is mobilized and focused along the trench axis [1]. The events not only translocate previously deposited material but also carry fresh carrion, and associated tsunamis have been shown to facilitate extensive material transport from land and coast to the trench interiors [2]. The events may result in burial of younger and fresher organic material in subsurface sediments (Figure 1). Besides these extreme events, continued downslope material focusing via nepheloid layers is probably also at play in trench systems (Figure 1) [3]. Hadal sediments are thus characterized by high sedimentation rates and are estimated to sequester 70 times more organic carbon than abyssal plain sediments (at 3–6 km of depth) per square meter [3]. Despite their relatively small areal extent, hadal trenches may therefore be important for carbon sequestration in the deep ocean. Recent findings further suggested that hadal trenches not only act as depositories for organic material but also accumulate high levels of pollutants and are thus affected by anthropogenic activity despite their remoteness and great depth [4,5].

Elevated microbial activity in hadal trench sediments

Benthic oxygen uptake is an excellent proxy for organic carbon mineralization in marine sediments. Using autonomous lander systems, it has been documented that hadal sediments have shallow O_2 penetration depths and have markedly higher O_2 consumption rates than adjacent abyssal sediments [6]. This confirms that hadal sediments not only accumulate redeposited, resilient material but also are enriched with more labile organic material that is accessible for microbial mineralization [7].

The benthic mineralization – also at hadal depth – correlates to the productivity of the surface ocean and varies extensively among different trench systems [6]. This implies that a fraction of organic material remains nutritious after the descent and that spatiotemporal variations in surface production affect microbial processing even at the greatest depths. The tight pelagic-benthic coupling appears to be related to pressure-induced inhibition of microbial degradation of sinking particulate organic material (POC) [8,9]. Phytoaggregates, zooplankton carcasses, and fecal pellets are produced and colonized by microbes in the surface ocean. Despite extensive community shift, there is little *de novo* colonization during the descent, and pressure appears to inhibit the activity of the microbial communities that originate from the surface [9]. Therefore, labile POC reach greater depth than would be anticipated from onboard degradation experiments performed without accounting for the pressure increase experienced by the descending community [8].

Despite well-oxygenated bottom waters, the elevated microbial activity in the organic carbon-enriched hadal sediment results in relatively shallow oxygen penetration depth. Oxygen extends decimeters or meters in abyssal settings but may reach only a few centimeters in hadal settings [6,10]. So, although organic carbon mineralization in abyssal settings is almost entirely driven by aerobic respiration, hadal sediments may hold highly active anaerobic microbial communities, and the distinct redox zonation known from coastal settings reemerges in hadal sediments [10]. However, in contrast to coastal sediments, hadal sediments are distinctly laminated and have little bioturbation (Figure 1) [3]. Thus, reoxidation of reduced constituents from anaerobic mineralization is limited, and iron sulfides from metal respiration and sulfate reduction may accumulate. The high benthic oxygen consumption in hadal settings may therefore even underestimate the total organic carbon mineralization. The high hadal mineralization rate also fosters an intense benthic nitrogen cycle where anammox bacteria and, to a lesser extent, denitrifies

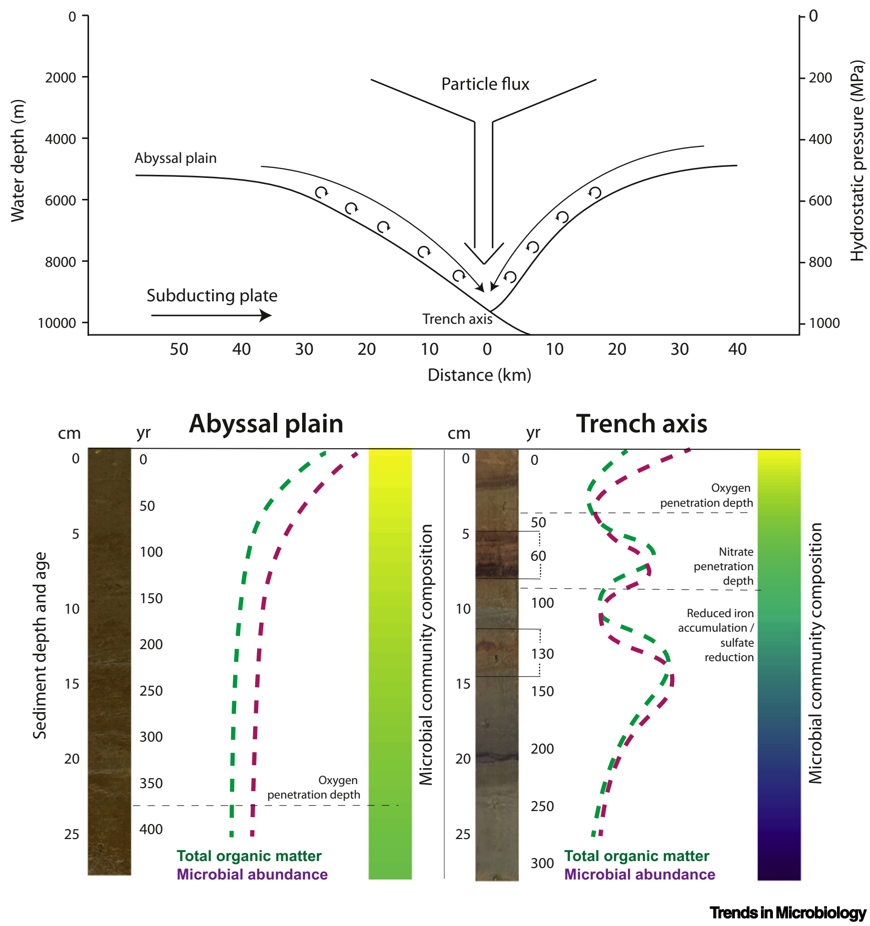

Figure 1. Conceptual diagram of the hadal trench systems. Top panel: trench systems function as important depocenters for organic material. Generally, the particle flux from the productive surface ocean decreases with depth. However, at ~4000 meters, this attenuation is partially halted as microbial mineralization of sinking particles is inhibited by increasing hydrostatic pressure. Additionally, hadal trenches receive near-bed lateral inputs via gravity-driven downslope material transport, a transport that is greatly intensified during seismically driven mass wasting events. Bottom panel left: abyssal plain sediments are exposed to a relatively stable sedimentation rate, and, once deposited, the organic material is gradually degraded by pressure-tolerant microbial communities. The most nutritious organic material is degraded at the surface; thus, the abundance of microbes and the concentration of organic matter will decline with sediment depth. Bottom panel right: by contrast, the intensified and dynamic deposition at the trench axis leads to a highly variable downcore content of organic matter with several subsurface maxima that also is reflected in the microbial abundance. The intensified mineralization activity results in shallow O_2 penetration depth and steep redox zonation, as known for sediments deposited at the ocean margin. Although the microbial abundances mirror the downcore distribution of organic matter patterns, microbial community composition does not. Instead, in both hadal and abyssal settings, microbial community composition changes gradually with sediment depth, with more pronounced community changes observed in hadal sediments due to steeper redox zonation. These gradual changes persist through redox zones and likely indicate the high resilience and slow turnover of microbial communities in deep sea sediments.

converts fixed and bioavailable nitrogen into inert dinitrogen [10].

The relative importance and the linkage of redox processes at hadal depth differ from those encountered in either coastal or abyssal settings, but the fundamental pathways remain the same. The processing, however, is mediated by microbial communities that flourish at extreme hydrostatic pressure, raising some fundamental questions regarding the adaptation, nature, and origin of hadal microbial communities.

Microbial processing at extreme hydrostatic pressure

The discovery of microorganisms thriving only at elevated hydrostatic pressure, known as ‘piezophiles,’ coupled with hadal sediments being the deepest marine realm, may intuitively suggest that hadal microbial communities are dominated by unique, highly specialized taxa. But the involvement of a wide range of metabolic processes in hadal mineralization also implied that numerous microbial lineages must have adapted to the challenges posed by high hydrostatic pressure.

Recent research suggests that ~85% of mesopelagic microbes are tolerant to high hydrostatic pressures, whereas only ~5% are truly piezophiles [8]. The remaining 10%, which are pressure-sensitive, primarily comprise members of Bacteroidetes and Alteromonas [8]. However, these pressure-sensitive microbes remain viable and become up to 100-fold more metabolically active when depressurized and incubated at atmospheric conditions [8]. Such increases in microbial activity have previously been observed in recovered deep sea sediment and have been attributed to enhanced activity of pressure-resilient microbes stimulated by dissolved organic carbon (DOC) leakage from disintegrating pressure-sensitive linages.

The activity of autotrophic anammox bacteria should be affected not by an ambient increase in DOC but rather by direct physiological effects following recovery. However, despite the highly complex cell structures of anammox bacteria, preliminary comparisons of *in situ* versus onboard incubations suggested that anammox bacteria were relatively resilient to pressure changes and piezotolerant rather than piezophilic, but this preliminary observation needs to be substantiated by more measurements [10]. Surprisingly, the anammox community was found to be highly diverse and non–monophyletically related within anammox bacteria. Similarly, preliminary investigations suggest that active sulfate respiring bacteria at hadal depth are represented by the multiple families of sulfate reducers and exhibited high genomic diversity. This implies a potentially tight genomic connection between bacterial populations in the water column, shallow sediments, and those found in hadal sediments. This further indicates that for microorganisms, hydrostatic pressure is not a selective force that is evolutionarily difficult to overcome as it is for higher life forms. It is, however, important to emphasize that trustworthy assessment of microbial process rates require more *in situ* measurements using specialized, innovative instrumentation.

A microbial seed that changes its habitat

The ubiquitous tolerance to high hydrostatic pressure among microbial lineages is also apparent, considering that approximately one-third of all described microbial phyla can be detected in hadal sediments [11]. But despite a constant influx of microbial cells via sinking POC and mass wasting events, hadal microbial communities still differ significantly from those found at adjacent abyssal settings [12,13]. The relative contribution of mass wasting events to microbial community composition as well as the causes for microbial dissimilarity between trenches remains unclear.

Within a trench, microbial communities exhibit remarkable similarity along the hundreds of kilometer-long axes, whereas most of the community variation occurs on a centimeter scale downcore [7]. A critical aspect of benthic microbial community assembly in hadal sediments is limited mixing and burial by novel deposition that outpace microbial dispersal [14]. Thus, microbial innovation in the form of evolutionary adaptations to hadal conditions is constantly buried and lost from the surface, meaning that the entire seed, including all anaerobic microbial lineages, for a microbial community needs to pass through the water column before settling [7]. The composition of this seeded community then successively changes with increasing sediment depth (Figure 1). Two apparent selective forces contribute to the observed community changes: (i) the composition and availability of organic matter and (ii) the successive depletion of electron acceptors [14].

Benthic microbes often specialize in degrading specific polymers and substrates, and they possess an arsenal of enzymes to do so. However, we currently lack an understanding of the relative contribution of each of these processes to the oxidation of deposited organics and the sustaining of the microbial community in the seabed. The successive depletion of electron acceptors is apparent from porewater gradients and distinct redox zonations, but because microbes typically use the more favorable electron acceptors almost until depletion, the selective force within a given zone is probably uniform. A drastic change then occurs between the redox zones, such as the nitrogenous and ferruginous zones, where the aerobic and nitrogen respiring community is replaced by a fermenting, iron, and sulfate-reducing community (Figure 1). On the basis of sedimentation age data, cell counts, and data on microbial community composition, the half-life period for the decay rate of microbial cells in hadal sediments is estimated to be 125 to 419 years [11]. These findings contrast with previous estimates on microbial mortality rates as induced by viral lysis, concluding that the microbial communities in deep sea sediments are overturned every 90 days [15]. The importance of viruses for benthic microbial communities is elusive, but rather than acting as top–down controls, viruses may act as important vectors for dispersing beneficial genetic traits among benthic microbes.

Concluding remarks and future perspectives

Hadal trenches have been proved to act as quantitatively important depositories of organic matter with high inventories of pollutants and with intensified mineralization mediated by surprisingly active and diverse microbial communities thriving at extreme hydrostatic pressure. But trenches are also very different, reflecting variations in surface production, distance to land, and tectonic and hydrographic forcings, shaping life and element cycling in the respective trenches. So far, we have only investigated a small subset of trench systems, and extensive efforts, including *in situ* instrumentation, are required to fully appreciate the role of the hadal realm for life, biodiversity, and biogeochemical function of the global ocean.

Acknowledgments

The study was supported by Danish National Research Foundation through the Danish Center for Hadal Research, HADAL (grant DNRF145).

Declaration of interests

The authors declare no competing interests.

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https://doi.org/10.1016/j.tim.2024.07.004

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