



Mini-review

The igneous oceanic crust – Earth's largest fungal habitat?

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ABSTRACT

In recent years the igneous oceanic crust has been recognized as a substantial microbial habitat and a scientific frontier within Geology, Biology, and Oceanography. A few successful metagenomic investigations have indicated the presence of Archaea and Bacteria, but also fungi in the seafloor igneous crust. A comprehensive fossil record supports the presence of fungi in these deep environments and provides means of investigating the fungal presence that complements metagenomic methods. Considering the vast volume of the oceanic crust and that it is the largest aquifer on Earth, we put forward that it is the largest fungal habitat on the planet. This review aims to introduce a yet unexplored fungal habitat in an environment considered extreme from a biological perspective. We present the current knowledge of fungal abundance and diversity and discuss the ecological role of fungi in the igneous oceanic crust.

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1. Introduction

Coordinated scientific drilling and exploration have during the last three decades recognized a deep biosphere in the deep-sea sediments and a seafloor biota that was previously unknown (Schrenk et al., 2009). So far, the emphasis has been on prokaryotes but, although neglected at the beginning, the presence of eukaryotes including fungi in these environments is now being investigated (Orsi et al., 2013a,b). It is evident that fungi occur in abundance and high diversity in such varied environments as the deep-sea sediments (Nagano et al., 2010; Orsi et al., 2013a,b), at hydrothermal vents (Gadanhó and Sampajo, 2005; López-García et al., 2007; Connell et al., 2009), and at methane cold-seeps (Nagano et al., 2010; Nagahama et al., 2011).

The underlying igneous oceanic crust, on the other hand, is still more or less unexplored in terms of biology. Considering that deep sea sediments are estimated to contain the largest proportion of Earth's microorganisms (Whitman et al., 1998; Schrenk et al., 2009), it would be reasonable to assume that a significant biosphere is hosted in deep crustal environments as well. However, owing to sampling issues, next to nothing is known about microbial life in the igneous crust. Apart from a few successful molecular

studies that have shown the presence of Archaea and Bacteria in seafloor basalts (Mason et al., 2010; Orcutt et al., 2010; Lever et al., 2013) the concept of a deep biosphere in seafloor crust is based on a fossil record (Staudigel et al., 2008; Ivarsson et al., 2012, 2013a; Bengtson et al., 2014). Ichnofossils in volcanic glass represent the most studied fossil type (Staudigel et al., 2008) but fossilized microorganisms in open pore spaces have, during the last 10 yr, become more acknowledged and investigated (Ivarsson et al., 2008a,b; Peckmann et al., 2008). Unexpectedly, a majority of the fossilized microorganisms are the remains of fungal communities. The fungi seem to play an important ecological role in the igneous oceanic crust as they exist in symbiosis with chemoautotrophic prokaryotes, decompose organic matter from overlying sediments, dissolve and form minerals, and are involved in cycling of elements (Ivarsson et al., 2012, 2013a, 2015a,b,c; Bengtson et al., 2014). It is obvious that the igneous oceanic crust is a previously unrecognized and unexplored fungal niche that might be of great importance considering the distribution of fungi both spatially and in time. This review aims at presenting the occurrence, diversity, and ecological role of fungi in one of Earth's most extreme environments – the igneous oceanic crust.

2. The igneous oceanic crust as a microbial habitat

The igneous oceanic crust consists of three main parts: an upper 500–1000 m section of permeable basalts, a middle layer down to

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~1.5 km of sheeted dikes, and a deeper layer to about 4 km depth of gabbroic rock (Fig. 1). The total rock volume is $2.3 \times 10^{18} \text{ m}^3$, which is 6–10 times the total volume of the marine sediments. The upper layer is characterized by extensive fracturing, about 10% porosity, and with permeabilities of about 10^{-12} to 10^{-15} m^2 (Bach and Edwards, 2004; Orcutt et al., 2011). Fractures created by tension release or quick cooling occur with varying size and frequency, as do vesicles as a result of pressure release during magma extrusion. Thus, subseafloor basalts contain coherent systems of microfractures and vesicles interconnected with each other in which seawater and hydrothermal fluids circulate. Roughly 60% of the oceanic crust is hydrologically active and the total fluid volume that is held within the oceanic crust corresponds to 2% of the total ocean (Orcutt et al., 2011). The entire water volume of the ocean circulates through the oceanic igneous crust every 10^5 – 10^7 years, which means that the oceanic igneous crust is the largest aquifer system on Earth (Fisher and Becker, 2000; Orcutt et al., 2011). Indirectly this means that the oceanic igneous crust is the largest potential microbial habitat on Earth. Microorganisms are passively transported or actively migrate through this system wherever pore space and fluid flow permit. The host rock and secondary mineralizations of the fracture walls are used for colonization and anchoring of microbial communities (Figs. 1 and 2A,B), and the minerals of the host rock can be used as energy sources for the microorganisms. Little is known of metabolic reactions in the subseafloor crust because of restricted accessibility of live microbial communities, and discussions on possible metabolic pathways tend to be rather

speculative. However, in the absence of sunlight, a majority of the deep subseafloor biosphere is thought to consist of chemototrophs; organisms that obtain energy from inorganic sources and synthesize all necessary organic compounds from inorganic carbon sources, in contrast to photoautotrophs that utilize solar energy.

Basalts exposed at the seafloor, and thus more accessible compared to deeper basalts, are commonly coated with biofilms mainly dominated by Bacteria according to quantitative molecular studies like PCR or FISH (Edwards et al., 2003; Sudek et al., 2010; Templeton et al., 2009). Taxonomically, the microbial communities are dominated by Actinobacteria, Bacteroidetes, Chloroflexi, Firmicutes, Planctomycetes, and Proteobacteria phyla (Mason et al., 2007, 2008; Einen et al., 2008; Santelli et al., 2008; Santelli et al., 2009). The Archaea are much less known but tend to be dominated by members of Crenarchaeota and Thaumarchaeota (Thorseth et al., 2001; Fisk et al., 2003; Lysnes et al., 2004; Mason et al., 2007). Eukaryotes, including fungi, have been reported from dredged basalts (Connell et al., 2009) and hydrothermal vent sites (López-García et al., 2007).

Subseafloor basalts are more difficult to access and sample than seafloor-exposed basalts, and molecular studies from such environments are therefore sparse. Alpha-, Beta-, and Gammaproteobacteria lineages in gabbroic layers (Mason et al., 2010) have been reported as well as anaerobic Archaea such as *Archaeoglobus* and *Methanosarcina* (Cowen et al., 2003; Orcutt et al., 2010). Lever et al. (2013) reported *Methanosarcinales*, anaerobic methane-oxidizing

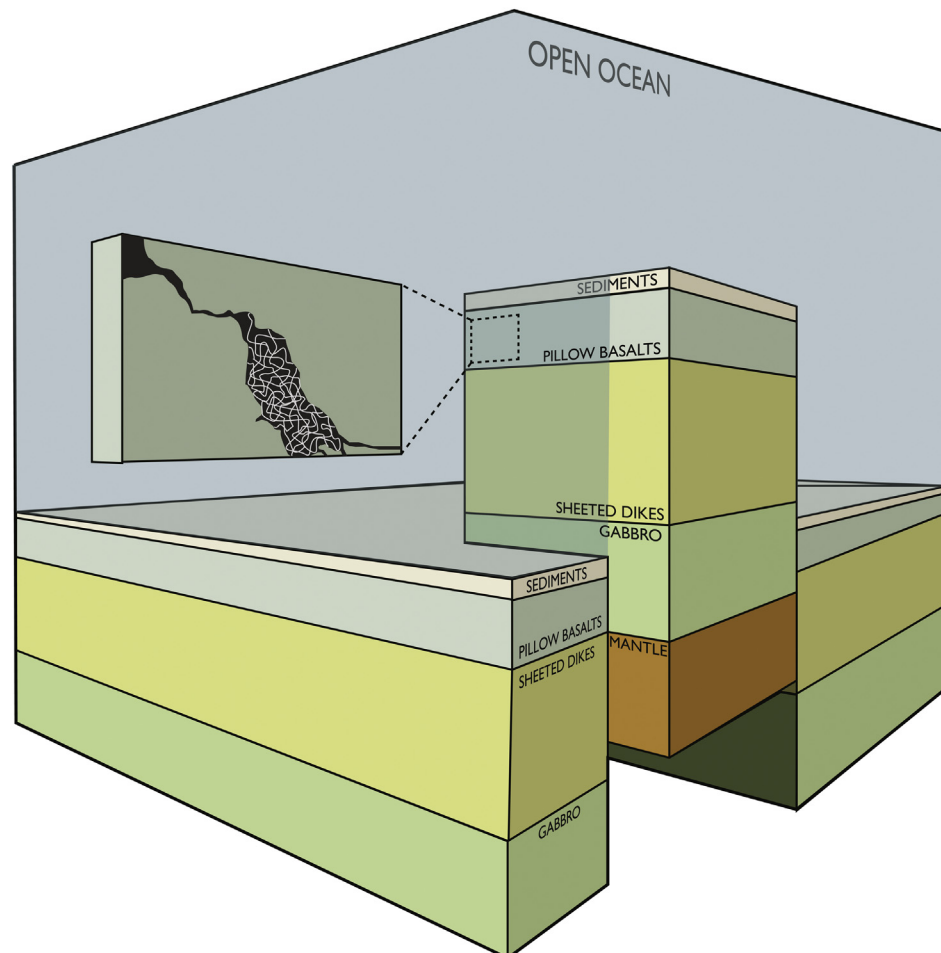


Fig. 1. Diagram showing the oceanic crust and endolithic habitats.

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