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Mini-review

Fungal diversity in deep-sea extreme environments

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ABSTRACT

The deep-sea is one of the most mysterious and unexplored extreme environments, holding great potential and interest for science. Despite extensive studies on deep-sea prokaryotes, the diversity of fungi, one of the most ecologically important groups of eukaryotic micro-organisms, remains largely unknown. However, the presence of fungi in these ecosystems is starting to be recognised. Many fungi have been isolated by culture-dependent methods from various deep-sea environments, with the majority showing similarity to terrestrial species. However, culture-independent methods have revealed many novel fungal phylotypes, including novel fungal lineages recently described as Cryptomycota, which are suspected to lack typical fungal chitin-rich cell walls. Although true fungal diversity and its role in deep-sea environments is still unclear, the intention of this review is to assess current knowledge of the diversity of fungi in these ecosystems and to suggest future direction for deep-sea fungal research.

Introduction

The deep-sea is recognised as an extreme environment. It is characterised by the absence of sunlight, predominantly low temperatures (<4 °C but occasionally >400 °C close to hydrothermal vents) and high hydrostatic pressure (up to 110 MPa). The deep-sea normally refers to oceans greater than 200 m depth. With nearly three quarters of the Earth's surface area being covered by ocean, the average depth of which is 3 800 m, the vast majority of our planet thus comprises deep-sea environments. Although once thought to be an uninhabitable milieu owing to its extreme conditions, the deep-sea environment is now recognised as highly dynamic, hosting a wealth of unique organisms. In particular, the discovery of hydrothermal vents, methane cold-seeps and surrounding ecosystems has resulted in completely new concepts for considering energy sources available for sustaining life in deep oceans (Lonsdale 1977; Cavanaugh 1985; Grassle 1985).

As in other environments, micro-organisms play an important role in deep-sea ecosystems. Since the first foray into deep-sea research, with the development of advanced instrumentation for sampling and researching life at great depths, the presence and ecological importance of deep-sea bacteria and Archaea has been extensively researched (Horikoshi 1998; Jørgensen & Boetius 2007; Dubilier *et al.* 2008; Lauro & Bartlett 2008; Dekas *et al.* 2009; Takai & Nakamura

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2011). In contrast, fungi, one of the most extremotolerant and ecologically important groups of micro-organisms, have been relatively underexplored in deep-sea environments. Although their true abundance and importance within these ecosystems is not yet understood, this review presents recent knowledge of fungal diversity in the deep-sea.

Fungal diversity in deep-sea environments

Although the presence of fungi in deep-sea environments was not well recognised until very recently, the isolation of deep-sea fungi was first reported approximately 50 yr ago from the Atlantic Ocean at a depth of 4450 m (Roth *et al.* 1964). Since this first report, others have been published on the isolation of fungi, including novel species (mostly yeasts) from several deep-sea environments, e.g. hydrothermal vents and the deepest of the seas, the Mariana Trench (Takami *et al.* 1997; Gadanho & Sampaio 2005; Nagahama *et al.* 2006, 2008). Although the true role and diversity of deep-sea fungi remains largely unclear, the significance of fungi in deep-sea environments is starting to be recognised, with more intensive investigations in recent years.

Fungal diversity in deep-sea environments has been investigated by both conventional culture-dependent methods (Nagahama *et al.* 2001; Raghukumar *et al.* 2004; Gadanho & Sampaio 2005; Damare *et al.* 2006; Le Calvez *et al.* 2009; Burgaud *et al.* 2009; Connell *et al.* 2009; Jebaraj *et al.* 2010; Singh *et al.* 2010) and culture-independent methods (Bass *et al.* 2007; Lopez-Garcia *et al.* 2007; Lai *et al.* 2007; Le Calvez *et al.* 2009; Jebaraj *et al.* 2010; Nagano *et al.* 2010; Sauvadet *et al.* 2010; Singh *et al.* 2011; Eloe *et al.* 2010; Quaiser *et al.* 2011; Nagahama *et al.* 2011). The taxonomic distribution of fungal diversity in deep-sea environments from recent studies is shown in Table 1, and the sample details and methods in Table 2. Fungi reported from deep-sea environments mostly belong to the Phylum Ascomycota, with a few yeast species belonging to the Basidiomycota. At present, there are no reports of zygomycetes and Chytridiomycota having been isolated from deep-sea environments. Since zygomycetes have not been detected by culture-independent methods either, it appears likely that these fungi are very rare or non-existent in deep-sea environments. However, this cannot be concluded with any certainty, as the primers that have been used may not amplify zygomycetes from deep-sea environments, and culturing methods may not be appropriate. For instance, we have isolated a novel psychrophilic fungus whose optimum growth temperature is $<4\,^{\circ}C$. Observations indicate that this fungus is most closely related to the zygomycete *Mucor hiemalis* (unpublished data). Chytridiomycota have been detected as one of the major fungal components in several deep-sea environments, such as hydrothermal vents and methane cold-seeps, but only by culture-independent methods (Table 1).

Ascomycota

Eurotiomycetes are the most frequently detected fungal taxa from deep-sea environments within the phylum Ascomycota, followed by the classes Saccharomycetes, Dothideomycetes and Sordariomycetes. The majority of species belonging to the Eurotiomycetes are members of the *Aspergillus/Penicillium*

Table 1 – Fungi recorded from deep-sea extreme environments by culture-independent and culture-dependent methods

Methods	Culture-independent												Culture-dependent								
Reference*	1	2	3	4	5	6	7	8	9	10	11	12	13	3	14	15	7	16	17	18	19
Ascomycota																					
Dothideomycetes	●	●			●	●	●		●	●		●	●	●	●		●	●			●
Eurotiomycetes	●	●			●	●	●	●	●	●	●		●	●	●	●	●	●		●	
Leotiomycetes									●		●				●	●					
Saccharomycetes	●			●	●		●		●	●	●	●	[a]			●			●	●	
Sordariomycetes				●	●		●		●	●	●	●	●	●	●	●	●	●			
DSF-Group1[b]	●								●	●	●										
Basidiomycota																					
Agaricomycetes	●		●	●					●							●					
Cystobasidiomycetes												●	[a]				●	●	●	●	
Entorrhizomycetes							●		●												
Exobasidiomycetes	●	●	●	●	●	●	●		●	●		●			●		●	●			
Microbotryomycetes	●				●	●			●			●	[a]			●		●	●	●	●
Tremellomycetes	●		●	●	●	●				●	●	●				●		●		●	●
Ustilaginomycetes						●	●					●					●				
Wallemiomycetes				●	●																
Chytridiomycota																					
Chytridiomycetes	●		●	●																	
Other basal lineage																					
Cryptomycota[b]	●								●		●										
Basal clone group I[b]	●							●	●												

a Taxa expected from morphology.
b Unknown groups containing highly novel phylotypes.
* Numbered references indicated in Table 2.