



# Bacterial and Fungal Diversity in Sediment and Water Column From the Abyssal Regions of the Indian Ocean

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The deep sea is the largest environment on Earth, comprising important resources of commercial interest. It is composed of a wide variety of ecosystems, which is home to often unique organisms that are yet to be described. The deep-sea is one of the least studied environments, where research is strongly linked to technological access and advances. With the recent advances in the next-generation sequencing and bioinformatics tools, there is an enhanced understanding of microbial diversity and ecological functions in deep sea. Multidisciplinary programs are being undertaken to investigate into microbial communities in diverse marine environments. As compared to other Oceans, the deeper parts of Indian Ocean are still poorly sampled and studied for bacterial, and more so fungal diversity. The studies reporting usage of modern sequencing tools to describe uncultured microbial diversity have seen a rise in numbers in the last decade. In this review, we summarize the important findings of research works carried on bacterial and fungal diversity from the abyssal regions of the Indian Ocean and provide our views on possible future paths.

**Keywords:** benthic, bioinformatics, deep sea, metagenomic, next-generation sequencing

## INTRODUCTION

### The Deep-Sea – What Lies Beneath?

The abyssal plain (also referred to as the deep-sea) is normally located between 3000 and 6000 m deep in the global ocean. It includes biogenic sediments, ocean waters from the bathypelagic (ranging from 1000 to 4000 m) and abyssopelagic (ranging from 4000 to 6000 m) zones, and occasionally manganese nodules (da Silva et al., 2013; Corinaldesi, 2015). The deep-sea environment plays important roles in nutrient cycling, carbon sequestration and biomass production (Barbier et al., 2014; Danovaro et al., 2014, 2017). Light intensity decreases with depth within this region, and photosynthetic production is arrested due to the absence of sunlight. The

temperatures nearing freezing ( $-1^{\circ}\text{C}$  to  $4^{\circ}\text{C}$ ) and the paucity of organic matter at the seafloor bed are the key features of the deep sea that control benthic productivity and biomass (Jørgensen and Boetius, 2007). Characteristically, the biota of the deep-sea are “food limited,” since it is solely dependent on organic matter input from the photic zone (Danovaro et al., 2017).

Despite the “harsh” conditions, there is a large variety of deep-sea organisms. The diversity of deep-sea benthic communities has intrigued researchers. Over the last two decades, deep-sea explorations have led to the discovery of novel ecosystems and diverse microbes. Gartner et al. (2011) studied the effect of hydrostatic pressure on the microbial communities from the deep sea sediments of Eastern Mediterranean and revealed that Gamma-proteobacteria had selective advantage over others under mimicked nutrient supply in elevated pressure conditions. Marine microbial communities are important for the structure and dynamics of food webs, global biogeochemical cycles, and the remineralization of organic matter (Jørgensen and Boetius, 2007; Parvathi et al., 2020; Wei et al., 2020). The microbial processes occurring along the seafloor are essential in sustaining primary and secondary production in the water column. In deep-sea sediments, the most significant fraction of taxonomic richness and biomass is contributed by the Bacteria and Archaea, which represent around 90% of the total benthic biomass. Multidisciplinary efforts across the globe are undertaken to characterize the microbial communities in different marine environments. For example, the *Sorcerer II* Global Ocean Sampling expedition (2003–2004) carried out in the Atlantic and Pacific Oceans; the TARA Ocean expedition (2009–2013) carried out in the Atlantic, Pacific and Indian Ocean. Despite this, the deep-sea environment remains one of the most understudied ecosystems on earth.

The total microbial counts in the marine sediments is estimated to be  $2.9 \times 10^{29}$  –  $5.4 \times 10^{29}$  cells, contributing to 3.6% of the entire living biomass on Earth (Kallmeyer et al., 2012; Parkes et al., 2014), and bacterial endospores in the upper kilometer of marine sediment are estimated between  $2.5 \times 10^{28}$  and  $1.9 \times 10^{29}$  (Wörmer et al., 2019). Stratification of the microbial communities is dependent on the depth of the sediment; wherein cell counts are inversely proportional to depth (Inagaki et al., 2003; Parkes et al., 2005; Inagaki et al., 2006; Biddle et al., 2008; Fry et al., 2008; Teske, 2013; Ciobanu et al., 2014; Inagaki et al., 2015; Chen et al., 2017). Additionally, microbial abundance is inversely proportional to the age of marine sediments and is higher in organic-rich anoxic sediments than oligotrophic oxic sediments (Kallmeyer et al., 2012; D'Hondt et al., 2015). Studies carried out on pore-water suggested that the microbial activity in the sub-seafloor environment is extremely low, with means respiration rates ranging between  $2.8 \times 10^{-18}$  and  $1.1 \times 10^{-14}$  moles of electrons per cell per year (D'Hondt et al., 2004; Hoehler and Jørgensen, 2013; D'Hondt et al., 2015).

Although efforts are there to develop newer methods for studying deep sea organisms, the biodiversity in abyssal plains remains one among the least understood (da Silva et al., 2013). In addition, commercial mining of marine mineral resources has

regained attention in recent times due to rising global demands and the belief that marine resources would someday replace land-based resources (Molari et al., 2020). The Indian Ocean has attracted attention as a potential mining site for polymetallic nodules; enriched in minerals such as manganese, iron, copper, cobalt, nickel and rare-earth elements (Wegorzewski and Kuhn, 2014). This has increased the curiosity among the scientific community in gaining insights about ‘sedimentary life’ in the Indian Ocean. The Indian Ocean is the third largest ocean, yet it remains among the most underexplored oceans in terms of biodiversity, especially microbial diversity (Hood et al., 2009; Wang et al., 2018). Mining of the deep sea nodules might result in perturbations in the deep-sea environments (Miller et al., 2018); hence, it is important to explore and record the biota present in deep-sea sediments. Among the biota present, microbes are considered important as they are believed to play a key role in organic matter mineralization, thereby affecting the global biogeochemical cycles and carbon sequestration capacity of oceans. This review is aimed at highlighting the bacterial and fungal diversity derived from the abyssal deep-sea environments (including water, hydrothermal vents, polymetallic nodules and sediment) of the Indian Ocean.

## BACTERIAL DIVERSITY OF THE ABYSSAL REGIONS OF THE INDIAN OCEAN INFERRED USING CULTURING METHODS

The deep sea microbes are difficult to isolate due to poor understanding about their nutritional requirements and lack of novel methods and incubation conditions. Despite this, considerable efforts have been invested in culturing of deep-sea bacteria, mainly to under their taxonomic novelty, physiological adaptations and biotechnological potentials (Zengler et al., 2002).

The first study, by Johnson et al. (1968), investigated the bacterial composition in the sediments of the Indian Ocean. After this, extensive studies have been carried out to gain an understanding about the topography and benthic life in deep-sea sediments of the Central Indian Ocean Basin (CIOB) (Parulekar et al., 1982; Chandramohan et al., 1987; Nath and Mudholkar, 1989; Sharma and Rao, 1992; Sharma and Kodagali, 1993; Ingole et al., 1999; Ingole et al., 2001). The microbial standing stock in the CIOB was measured (Raghukumar et al., 2001) and the results showed a relatively homogenous distribution of bacteria, indicative of possible active microbial processes and a stable ecosystem. The bacterial counts in the sediments were found to be in the range  $10^{10}$ – $10^{11}$  cfu  $\text{g}^{-1}$ , higher than those found in sediments of the Pacific and Atlantic Oceans. Furthermore, perturbations in the CIOB stimulated the retrievable bacterial counts from sediments. This resulted in an increase in the culturable bacterial diversity, wherein *Acinetobacter* and *Moraxella* species that were dominant before the disturbance were replaced by *Acinetobacter*, *Coryneforms*, *Enterobacter*, *Marinococcus*, *Pseudomonas*, and *Staphylococcus* (LokaBharathi and Nair, 2005). Disturbances in the sediment

caused by anthropogenic influence could result in a re-emergence of the buried sedimentary organic material accessible for microbial degradation. This could result in the alteration of bacterial communities therein and thereby impact the ecological process within the ecosystem.

In recent times, researchers have focused on isolation, cultivation and screening of deep-sea microbes for biotechnological applications. Aiming to identify bacteria with potential biotechnological applications, Gawas et al. (2019) isolated 43 heterotrophic bacteria belonging to the phyla Proteobacteria, Actinobacteria, and Firmicutes, from nodule associated sediments of the first generation mining site and preservation reference zone of the CIOB. This is among the first reports of *Oceanobacillus* (Firmicutes) and *Brachybacterium* (Actinobacteria) in the CIOB, although these genera have been previously reported from deep-sea sediments of the Pacific and the Atlantic Oceans. Padmanaban et al. (2019) investigated the metabolic potential of bacteria isolated from deep-sea sediments of the Indian Ocean, mainly from the Bay of Bengal and the Andaman Sea. They isolated and screened 34 bacteria for their potential to produce extracellular hydrolases such as caseinase,  $\alpha$ -amylase, urease, gelatinase, lipase, DNase and the production of anti-bacterial metabolites against human clinical pathogens. These 34 bacterial isolates were affiliated to Firmicutes, Proteobacteria and Actinobacteria, with Firmicutes and Actinobacteria being the dominant phyla, which was also confirmed through metagenomic studies.

Fifty-one bacteria capable of degrading polyaromatic hydrocarbons, belonging to 29 genera, were isolated from the deep seawater column (3946 – 4746 m) above the South-West Indian Ridge. The majority of the isolated bacteria were grouped under Proteobacteria (88%), followed by Bacteroides (6%), Actinobacteria (4%), and Firmicutes (2%). Of these isolates, 34 isolates showed the ability to use phenanthrene as a sole carbon source, wherein 20 isolates belonged to Alpha-proteobacteria within the genera, *Alterierythroacter*, *Citricella*, *Erythroacter*, *Kaistia*, *Lutibacterium*, *Maricaulis*, *Martelevella*, *Mesorhizobium*, *Novosphingobium*, *Pseudomonas*, *Phenylobacterium*, *Roseovarius*, *Rhodobacter*, *Salipiger*, *Stappia*, *Sphingopyxis*, *Sphingomonas*, *Tistrella*, and *Thalassospira*. Within the Gamma-proteobacteria, isolates belonged to the genera *Alkaligenes*, *Alkanovorax*, *Halomonas*, *Idiomarina*, *Marinobacter*, *Pseudoidiomarina*, and *Pseudomonas*. *Muricauda* and *Salegentibacter* (Bacteroides), *Bacillus* (Firmicutes) and *Microbacterium* (Actinobacteria) also showed phenanthrene-degrading potential (Shao et al., 2015). Moreover, in addition to bioprospecting, isolation of bacterial cultures could yield novel findings with respect to new species within the environment or an undocumented functional role. Yuan et al. (2009) isolated a novel hydrocarbon-degrading bacterium from the deep sea waters of the Indian Ocean and named it *Novosphingobium indicum*, referring to the Ocean from which the type strain was isolated. Another study reported a unique lineage of *Aquificales* in the Edmon hydrothermal vent and the Kairei vent field of the Central Indian Ridge (Reysenbach et al., 2002). *Bhargavaea cecembensis*, a novel Gram-positive, sporulating bacterium, was isolated from sediments of the Chagos-Laccadive ridge system in the

Indian Ocean (Manorama et al., 2009). *Acuticoccus sedimeni* was reported from sediments collected from Indian Ocean from a depth of 2946 m (Lai et al., 2019). This strain was isolated from sediments enriched with poly aromatic hydrocarbons (PAHs) as sole source of carbon and energy. This also shows that the novel strains obtained from deep-sea sediments could have applications in field of bioremediation too like PAH degradation. Cao et al. (2017) reported a novel thermophilic sulfur-reducing bacterium, *Desulfurobacterium indicum* from sulfide sample collected from a depth at 2771 m from a high temperature hydrothermal vent in the Indian Ocean. Ren et al. (2014) reported a Mn-oxidizing bacterial strain, *Fulvimarina manganooxydans* from a Fe and Mn-rich hydrothermal plume in the south-west Indian Ocean. Wang J. et al. (2020) reported a novel planctomycete, *Gimesia benthica*, from the bottom water samples collected with a multi-corer from a depth of 4213 m in Northwest Indian Ocean. Most of the Planctomycetes strains are known for their role in global carbon and nitrogen cycles (Wagner and Horn, 2006). Shivaji et al. (2007) and Bhadra et al. (2008) have reported novel *Brevibacterium oceani* and *Microbacterium indicum* species, respectively, from Chagos Trench in Indian Ocean. Qiu et al. (2021) reported a halotolerant *Halomonas sedimenti* from the deep sea sediment (2699 m) of the Southwest Indian Ocean. Xie et al. (2021) have reported a novel hydrogen and sulfur-oxidizing chemolithoautotroph, *Sulfovorulum indicum*, from deep sea hydrothermal plumes in the Northwestern Indian Ocean. This reiterates the fact that there is a lot more to be explored from the abyssal depths of the Oceans, and it is a very good source of novel bacterial isolates for understanding the diversity and also useful for biotechnological applications.

All the research findings discussed above underline the importance of traditional isolation and cultivation of bacteria, as they allow the possibility of genome sequencing and bioprospecting for biomolecules and industrially relevant processes. Although isolation and culturing of bacteria help us provide holistic information regarding the microorganism, this may not always be feasible due to the stringent nutritional requirements and limited methods available for their isolation. For these reasons, researchers are now focusing on culture-independent methods to gain insights into diversity and ecological roles of deep sea life forms. Additionally, these tools allow for detection of the viable but non-cultivable fraction of the sedimentary microbial community (Polymenakou et al., 2009; Schauer et al., 2010).

## BACTERIAL DIVERSITY IN THE ABYSSAL REGIONS OF THE INDIAN OCEAN BASED ON CULTURE-INDEPENDENT METHODS

Despite technological advances, only 5% of the ocean floors have been scientifically explored. There is a lacuna in understanding the distribution patterns, diversity and ecological roles played by microbes within the infinite seafloor (Corinaldesi, 2015).

Describing marine microbial communities is vital to catalog the genetic diversity in a region and understand the functional roles of these organisms in the ecological processes of marine ecosystems. Deep-biosphere bacteria are extremely difficult to cultivate due to their incredibly slow growth rates, hence the number of pure cultures available for in-depth studies does not exceed a few hundred (Jørgensen and Boetius, 2007). Microbial communities interact with each other to exchange nutrients, biochemical products and chemical signals. The presence of this complex community cannot be detected based on traditional cultural methods. Recent developments in molecular fingerprinting techniques have been instrumental in providing new insights into bacterial diversity and their response to environmental heterogeneity (Varliero et al., 2019). The use of

molecular methods has made it possible to analyze microbial communities without the conventional isolation and culturing techniques. Molecular analysis using rRNA as a marker began in the early 1970s based on Sanger's sequencing. This was replaced by the next-generation sequencing (NGS) techniques such as Illumina, Ion Torrent and Roche/454, which are reliable and efficient tools for studying microbial communities. **Table 1** summarizes select studies carried out using NGS in the last decade from the abyssal regions of the Indian, Pacific and Atlantic Oceans. This shows that abyssal regions of the Indian Ocean are less explored as compared to the Pacific and Atlantic Oceans.

Marine bacteria, being metabolically diverse, significantly impact the nutrient composition and energy flow in both:

**TABLE 1** | Un-cultured bacterial and fungal diversity reported (last 10 years) from the abyssal regions of different Oceans using different next-generation sequencing platforms.

S. No.	Area	Sample	Depth (m)	NGS platform	Gene	References
1	Indian Ocean	Sediment	5000	454 pyrosequencing	16S rRNA (V6)	Zinger et al. (2011)
2	Indian Ocean	Sediment	2784	454 pyrosequencing	16S rRNA (V3–V4)	He et al. (2016)
3	Indian Ocean	Sediment	4800	Illumina HiSeq	16S rRNA (V3–V4)	Wang et al. (2018)
4	Indian Ocean	Sediment	3000	Illumina MiSeq	16S rRNA (V3–V4)	Parvathi et al. (2020)
5	Indian Ocean	Sediment	3776	Illumina MiSeq	16S rRNA (V3)	Sinha et al. (2019)
6	Indian Ocean	Water	3000–4000	Ion S5 TM XL	16S rRNA (V3–V4)	Gao et al. (2021)
7	Indian Ocean	Sediment	2086	Illumina MiSeq	ITS1	Zhang et al. (2016a)
8	Indian Ocean	Sediment	2813	Illumina HiSeq	ITS	Xu et al. (2018)
9	Pacific Ocean	Sediment	3953	454 pyrosequencing	16S rRNA (V6)	Zinger et al. (2011)
10	Pacific Ocean	Sediment	2982	454 pyrosequencing	16S rRNA (V3–V4)	He et al. (2016)
11	Pacific Ocean	Fe-Mn nodules	3573	Illumina MiSeq	16S rRNA (V4)	Zhang et al. (2015)
12	Pacific Ocean	Water	2665	Illumina HiSeq	16S rRNA	Anantharaman et al. (2016)
13	Pacific Ocean	Sediment	4970–5620	Illumina MiSeq	16S rRNA	Dong et al. (2016)
14	Pacific Ocean	Water	3000	Illumina MiSeq	16S rRNA	Lindh et al. (2017)
15	Pacific Ocean	Sediment	4200	Illumina MiSeq	16S rRNA	Lindh et al. (2017)
16	Pacific Ocean	Water	3000	Illumina HiSeq	16S rRNA	Li et al. (2018)
17	Pacific Ocean	Sediment	2980	Illumina HiSeq	16S rRNA	Wu et al. (2019)
18	Pacific Ocean	Water	5000	Illumina MiSeq	16S rRNA	Wei et al. (2020)
19	Pacific Ocean	Sediment	4129	Illumina MiSeq	16S rRNA (V3–V4)	Molari et al. (2020)
20	Pacific Ocean	Water	4000	Illumina HiSeq	16S rRNA (V3–V4)	Wang M. et al. (2020)
21	Pacific Ocean	Sediment	6000	Illumina HiSeq	16S rRNA (V3–V4)	Wang M. et al. (2020)
22	Pacific Ocean	Sediment	4700–10902	Illumina MiSeq	16S rRNA (V4–V5)	Hiraoka et al. (2020)
23	Pacific Ocean	Sediment	3156–7837	Illumina MiSeq	16S rRNA (V3–V4)	Zhang et al. (2021)
24	Pacific Ocean	Sediment	4500, 5315	Illumina HiSeq	ITS2	Xu et al. (2019)
25	Pacific Ocean	Sediment	3500–5500	Illumina HiSeq	ITS2	Luo et al. (2020)
26	Pacific Ocean	Sediment	5527	Illumina HiSeq	ITS1	Yang et al. (2020)
27	Pacific Ocean	Sediment	3200	Illumina MiSeq	18S rRNA (V7–V8)	Rojas-Jimenez et al. (2020)
28	Atlantic Ocean	Water	4600	454 pyrosequencing	16S rRNA (V6)	Zinger et al. (2011)
29	Atlantic Ocean	Sediment	3860	454 pyrosequencing	16S rRNA (V6)	Zinger et al. (2011)
30	Atlantic Ocean	Water	4000	454 pyrosequencing	16S rRNA (V6)	Ghiglione et al. (2012)
31	Atlantic Ocean	Water	2990	454 pyrosequencing	16S rRNA (V3–V4)	He et al. (2016)
32	Atlantic Ocean	Sediment	2949	454 pyrosequencing	16S rRNA (V3–V4)	He et al. (2016)
33	Atlantic Ocean	Sediment	3760–4869	Illumina MiSeq	16S rRNA (V3–V4)	Varliero et al. (2019)
34	Atlantic Ocean	Sediment	2728	Ion Torrent PGM	16S rRNA (V3–V4)	Queiroz et al. (2020)
35	Atlantic Ocean	Water	4000	Illumina MiSeq	16S rRNA	Coutinho et al. (2021)
36	Atlantic Ocean	Fe-Mn Crust	4000	Illumina MiSeq	16S rRNA (V3–V4)	Bergo et al. (2021)
37	Atlantic Ocean	Sediment	2720	Ion Torrent PGM	ITS	Nagano et al. (2017)
38	Atlantic Ocean	Sediment	3734	Illumina MiSeq	ITS1	Vargas-Gastélum et al. (2019)

the sediments as well as the overlaying water column; thus, governing the critical biogeochemical cycles (Arrigo, 2005; Fennel et al., 2005; Emerson et al., 2010). Distinct biological patterns have been revealed in marine environments due to the advances in sequencing techniques. For example, Proteobacteria is found to be dominant in the Atlantic Ocean sediments and the deeper depths of the Arctic and Pacific Oceans (Fuhrman et al., 1993; Schauer et al., 2010). Seasonal changes have been reported in the Pacific Ocean, with Bacteroidetes being more abundant than Proteobacteria in winter (Suh et al., 2014). Compared to other Oceans, studies with respect to the Indian Ocean are in their infancy (Wang et al., 2016).

The first culture-independent molecular study in the Indian Ocean was carried out in the Edmon hydrothermal vent (3300 m) on the Central Indian Ridge (Hoek et al., 2003). Sequencing of 150 clones of the amplified 16S rDNA revealed the incidence of 26 unique bacterial phylotypes. The majority of the clones were affiliated with the Epsilon-proteobacteria. Among the Epsilon-proteobacteria, more than 40% of the phylotypes were closely related to *Nautilia lithotrophica*, a thermophilic chemoautotrophic sulfur reducer isolated from deep-sea vents; while the majority of the remaining sequences clustered with uncultured clones. Epsilon-proteobacteria displays wide metabolic diversity, but most are hydrogen- and sulfur-oxidizing chemolithoautotrophs. They play significant roles in carbon and sulfur cycles and are also dominant in the active hydrothermal vents in the Pacific and Atlantic Oceans. One of the 150 clones analyzed was identified as *Hydrogenobacter thermolithotrophum*, which is the first report of the incidence of this genus in deep-sea hydrothermal environments.

Studies on sediments obtained from the Afanasiy- Nikitin seamount in the Equatorial East Indian Ocean revealed a unique bacterial diversity depending on the depth of the sediment (Khandeparker et al., 2014). Sixty-four clones obtained from the top surface sediments classified into Firmicutes (63%) and Gamma-proteobacteria (37%). Within the Firmicutes, *Bacillus* was dominant, followed by *Dolosigranulum*. *Pseudomonas*, and *Shigella* or in some cases *Escherichia* were prominent among the Gamma-proteobacteria. The 58 clones obtained from deeper sediments (200 m) were dominated by the Gamma-proteobacteria (66%) represented by *Pseudomonas* and *Enterobacteriaceae*, followed by Beta-proteobacteria (34%) represented by *Limnobacter* and *Burkholderiales*. Hence, it can be said that bacterial communities are stratified based on the depth of the sediment. Gamma-proteobacteria members are metabolically versatile and abundant in various environments, including the cold deep ocean, hydrothermal region, nodule province, polluted continental area, and water column. Gamma-proteobacteria is known to mediate sulfide reduction and oxidation, which is one of the most important microbial chemosynthetic pathways in deep-sea hydrothermal ecosystems.

Li et al. (2014) examined the microbial diversity inhabiting the exterior (black Fe-Mn oxides) as well as the interior (white carbonates) of carbonate sediments of the Southwest Indian Ridge (SWIR). Analyses of the 16S rRNA gene of the 145 clones indicated that diverse bacteria are associated

with the exterior and interior of the sediments. Ninety-three phylotypes were obtained from the clone analysis, among which a large majority belonged to the Proteobacteria (alpha, beta, gamma, and delta), followed by the Acidobacteria (22.07%), Actinobacteria and Bacteroidetes (6.9%); and a small fraction classified as Chloroflexi, Deferribacteres, Nitrospirales, Planctomycete, Verrucomicrobia, and uncultured taxonomic groups WS3. *Nitrospira*, which plays a role in nitrogen cycling in the conversion of nitrites to nitrates, is widespread in marine environments and has been reported from metal-rich sediments of Pacific Ocean. Deferribacteres and Nitrospirales are known metal reducers and could play a role in the formation of metal oxides. These bacterial groups detected are common in deep-sea sediments and participate in various biochemical processes such as recycling nutrients (carbon, nitrogen, sulfur) and trace metals (iron and manganese).

Another study conducted in the SWIR, analyzed the bacterial communities within inactive hydrothermal vents (Zhang et al., 2016b). Samples were collected at two different sites for comparison using the Illumina MiSeq2500 platform, and it was found that the Proteobacteria and Bacteroidetes were dominant at both locations. The major classes in the two samples were  $\alpha$ -proteobacteria, followed by Gamma-proteobacteria, Sphingobacteria, Beta-proteobacteria, and Flavobacteria. Alpha- and Gamma-proteobacteria are known to mediate sulfide reduction and oxidation. Sphingobacteria and Flavobacteria are known degraders of biopolymers in sedimentary organic matter. Thus, the bacterial community identified could be involved in nitrogen and sulfur cycling and metal metabolism, suggesting that they may play important ecological roles in inactive deep-sea hydrothermal vents (Zhang et al., 2016b). Furthermore, the diversity and abundance varied between the two samples isolated from the two adjacent sites (E 50.9277°, S 37.6251°, and E 50.9643°, S 37.6174°), suggesting that the ambient environmental parameters probably influence the formation of microbial communities, even within the same oceanic ridge. Environmental conditions are considered to have a strong influence on microbial biogeography (Li et al., 2009). Several studies in Pacific and Atlantic Oceans have also previously shown that spatial distances affect microbial diversity (Papke et al., 2003; Whitaker et al., 2003; Martiny et al., 2006; Ramette and Tiedje, 2007; Schauer et al., 2010; Zinger et al., 2011).

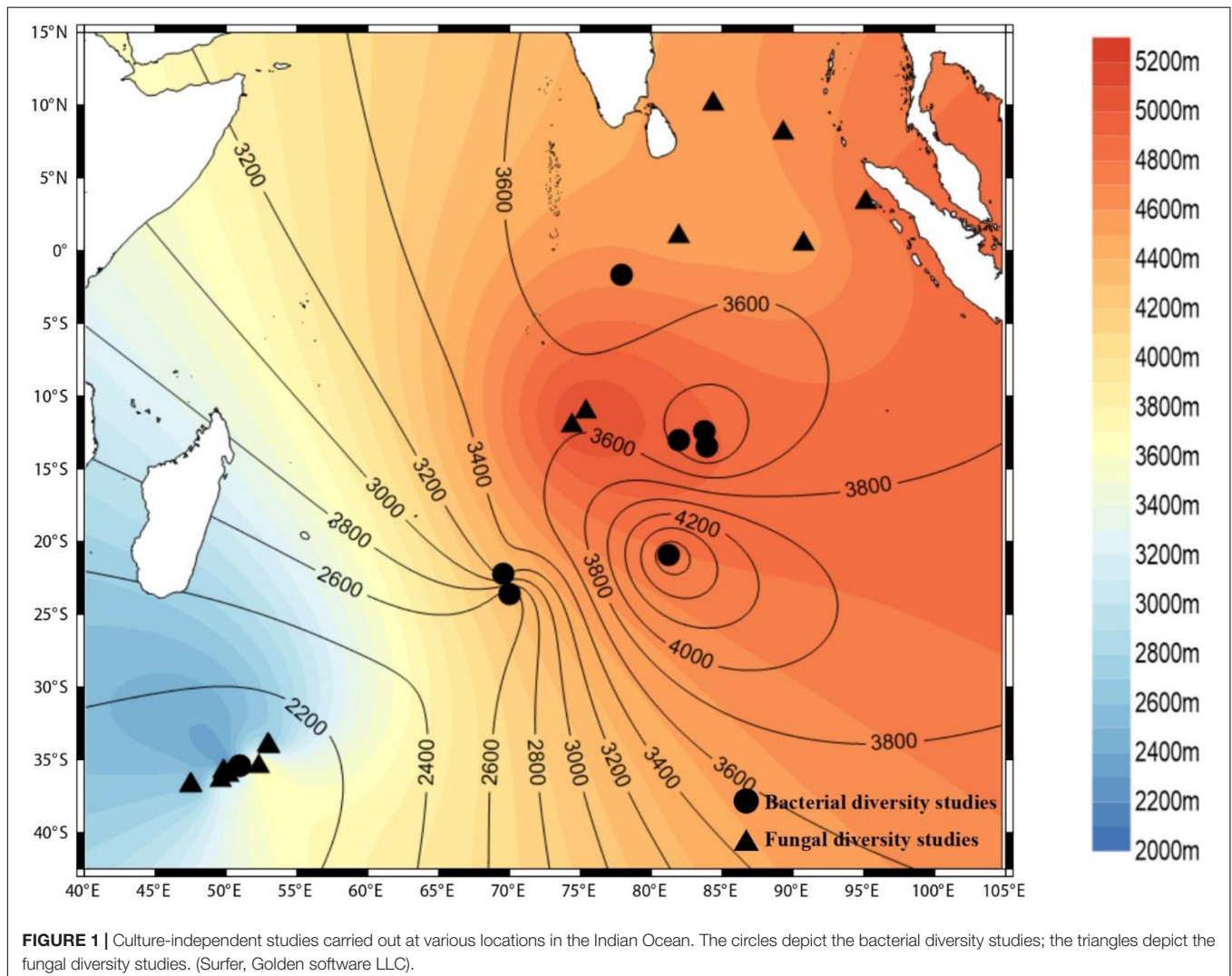
Bacterial diversity from rare earth elements-rich sediment (4800 m) in the Indian Ocean was characterized using the Illumina HiSeq platform (Wang et al., 2018). The results revealed the occurrence of 49 different phyla, among which the most abundant bacteria were Proteobacteria, with Gamma-proteobacteria being present in all sections of the core; followed by Firmicutes (27.95%), Actinobacteria (5.45%), Bacteroidetes (4.03%), Cyanobacteria (1.71%), and Chloroflexi (0.68%). The major genera included, *Lactobacillus*, *Profundibacterium*, *Shigella*, *Escherichia*, *Pseudoalteromonas*, *Vibrio*, *Propionibacterium*, *Alteromonas*, *Enterobacter*, *Sphingomonas*, and *Staphylococcus*. The results also revealed that the microbial diversity at this site was less sensitive to changes in the vertical depth within the sediment core; however, the abundance of bacteria changed with the vertical depth

profile. *Pseudomonas* and *Alteromonas*, which are predicted to play a role in building matrix outside cells to induce or control mineralization, suggest that these bacteria possibly play a role in the formation of polymetallic nodules in the Indian Ocean. Another study using the Illumina MiSeq platform was conducted on sediments from the Bay of Bengal region of the Indian Ocean also showed that bacterial diversity within the deep-sea sediments is quite similar (Parvathi et al., 2020). Proteobacteria dominated the sediments, followed by Firmicutes, Cyanobacteria, Bacteroidetes, Actinobacteria, Chloroflexi, and Planctomycetes. Alpha-proteobacteria was the most abundant class among Proteobacteria, followed by Gamma-proteobacteria and Delta-proteobacteria, and are known to mediate sulfide reduction and oxidation. Planctomycetes have a suggestive role in methane oxidation. *Wolbachia* belonging to  $\alpha$ -proteobacteria was found to be the dominant genus in the deep-sea. Functional analysis revealed that dehalogenation activities were higher in *Wolbachia* dominated sediments, hinting at the role of these bacteria in biogeochemical cycles of chlorine, iodine, bromine and halogenated carbon substrates.

All of these findings portray the importance of diversity studies within an environment. Bacteria are highly adaptive and sensitive to environmental perturbations. The bacterial community structure differs depending on the features of the environment, the nutrient profiles, the vertical zonation, and the interior and exterior of sediments obtained from the same ecological niche. Therefore, cataloging the diversity of bacteria is of paramount importance to fully understand the processes taking place in a particular environment. Unfortunately, the Indian Ocean is yet to be explored, and a large portion of the Indian Ocean remains under-explored and under-sampled (Figure 1).

## FUNGAL DIVERSITY IN THE ABYSSAL REGIONS OF THE INDIAN OCEAN

Compared to the exploration of bacterial diversity in the Indian Ocean, fungal diversity studies are still in their infancy. The first report on the isolation of deep-sea fungi from a



depth of 4450 m from the Atlantic Ocean was published by Roth et al. (1964). Although the role and diversity of deep-sea fungi remains largely ambiguous, their ecological significance is being recognized. Numerous studies have reported isolation of fungal isolates from deep-sea environments including hydrothermal vents and the Mariana Trench (Takami et al., 1997; Gadanho and Sampaio, 2005; Nagahama et al., 2006, 2008). Fungal diversity in the deep-sea realm has been investigated by both traditional culturing and modern culture-independent methods.

The ability of fungi to adapt/thrive under deep-sea conditions in the Indian Ocean was first discussed by Raghukumar and Raghukumar (1998). Wherein two isolates, *Aspergillus ustus* and *Graphium* sp. obtained from calcareous shells in the sediments from the Arabian Sea and the Bay of Bengal, demonstrated conidial germination and hyphal growth at conditions mimicking the deep-sea environment, i.e., high pressures and low temperature. Following this, another study, based on culturing, reported the presence of fungi at a depth of 5904 m in the Chagos trench of the Indian Ocean (Raghukumar et al., 2004). They comprised non-sporulating as well as sporulating forms, identified as *Aspergillus sydowii*, and present up to 370 m depth of the core subsection mbsf. A total of 181 fungal cultures were isolated from 5000 m depth in the CIOB, most of which were terrestrial sporulating species belonging to *Aspergillus*, *Penicillium*, and *Cladosporium* genera (Damare et al., 2006). The presence of *Aspergillus terreus* in the sediments was confirmed in these studies using immunofluorescence techniques. Singh et al. (2010) isolated 16 filamentous and 12 yeast cultures, belonging to the Ascomycota and Basidiomycota, from sediments of the CIOB at depths of 5000 m. This was the first report of isolation of filamentous fungi (*Capronia*, *Exophiala*, *Sagenomella*, and *Tilletiopsis*) from deep-sea sediments, showing that the Indian Ocean basin is a host to a unique diversity of fungi.

The first culture-independent report on fungal diversity from the Indian Ocean sediments was published by Singh et al. (2011). A total of 39 OTUs, belonging to 32 fungal taxa, majorly the Ascomycota and Basidiomycota, were retrieved from 5000 m depth. Within the Ascomycota, members of Sordariomycetes, Dothideomycetes, and Saccharomycetes were identified. Members belonging to Tremellomycetes, Microbotryomycetes, and Ustilaginomycetes were identified within the Basidiomycota. This study revealed heterogeneity with respect to the fungal diversity in deep-sea sediments. In a comparative study using culture-dependent and culture-independent techniques, it was found that the fungal diversity altered vertically with the increase in the depth of the sediment (Singh et al., 2012a,b). Furthermore, 19 fungi belonging to 12 genera were obtained via culture-based methods, wherein a higher diversity was obtained (42 unique OTUs) using sequencing techniques. This was also confirmed in another study in the Eastern Indian Ocean, wherein 45 OTUs were obtained using sequencing approaches compared to 20 culturable fungal phylotypes (Zhang et al., 2014). The culturable fraction was dominated by filamentous fungi, including *Aspergillus*,

*Penicillium*, *Simplicillium*, *Cladosporium*, and *Phoma*. Moreover, six of the twenty culturable fungal isolates and 20 of the 45 OTUs were first time reports from deep-sea sediments. A more significant fraction of fungal phylotypes was recovered using targeted environmental sequencing than the conventional culturable techniques from deep-sea sediments of hydrothermal vents in the Southwest Indian Ridge (Xu et al., 2018). In this study, 79 fungal taxa were identified from sediments, whereas isolates belonging to only 14 taxa could be cultivated. In a recent study, 42 OTUs and 10 different fungal phylotypes belonging majorly to *Aspergillus*, *Penicillium*, *Ophiocordyceps*, and *Phoma* could be recovered (Tang et al., 2020). All the findings discussed here suggest that sediments from the abyssal regions of the Indian Ocean are dominated by Ascomycota and Basidiomycota. Fungi detected in deep-sea sediments are similar to those present in the terrestrial environment, indicating the possibility of connectivity between these two environments, mediated by either aerial dispersal or terrestrial runoff.

## CONCLUSION

The deep-sea is a largely unexplored area and is attracting attention in recent times due to the presence of polymetallic nodules. The mining of polymetallic nodules found in the Indian Ocean has been viewed as an alternative to terrestrial mining; therefore, it is important to understand the marine life existing in these regions. However, the knowledge about the inhabitants of the deep-sea ecosystem is limited. Furthermore, information on possible effects of anthropogenic disturbances due to deep-sea mining on the ecosystem and its dwellers is yet to be generated. Although newer technology such as submersibles and drilling tools are made available, similar efforts have not yet been made to explore the microbial diversity thoroughly in the Indian Ocean deep-sea.

This review has summarized the important findings on distribution and diversity of bacterial and fungal communities in the abyssal regions of the Indian Ocean. The deep-sea environments of the Indian Ocean possess diverse assemblages of bacteria and fungi, including novel taxa and new records of species that could be endemic to the region (For example, *Novosphingobium indicum*). The bacterial distribution in the Indian Ocean differs with respect to the depth of the sediment as well as spatial distances between the sampling locations, probably due to the differing environmental conditions. A variety of bacteria, with unique metabolic abilities for biotechnological potentials such as industrial and medical applications (extracellular hydrolases and anti-bacterial metabolites), have been retrieved from the Indian Ocean. Moreover, bacteria (*Pseudomonas* and *Alteromonas*) that may play a key role in formation of polymetallic nodules have been detected in sediments from the Indian Ocean. The presence of metal-utilizing bacteria (*Acinetobacter*) in samples from the Indian Ocean suggest for an environmentally induced adaptation mechanism due to the richness of metals in sediments. Although the third largest Ocean in the world, only a

small fraction of the Indian Ocean deep-sea environments has been sampled, most of the high-throughput sequencing studies carried out mainly focus on the water column. Metagenomic and functional gene studies are lacking from the abyssal depths. Therefore, extensive sampling and functional gene characterization and quantification of microbes and their activities in the abyssal regions of the Indian Ocean need to be carried out to build the knowledge with respect to their diversity and the ecological processes they affect.

## AUTHOR CONTRIBUTIONS

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

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