Marine Fungal Ecology in the Molecular Era

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Abstract

The marine environment is an intriguing one and provides a range of wonderful ecological niches to explore the ecology and biodiversity of marine microorganisms. Fungi are possibly by far the most abundant "lifeforms" in the marine environments but largely unexplored. Most studies on marine fungi were from coastal habitats, and they are mainly surveys employing traditional techniques such as microscopy and/or culture-dependent methods which suggest poor diversity of marine fungi (less than 1%) predominated by *Dikarya*. In fact, open oceans were largely considered as "fungal desert" given their inaccessibility and lack of appropriate methods to recover these organisms from these harsh environments. With recent technological advances and developments in molecular techniques involving advanced DNA sequencing technologies, marine mycologists have started to unravel unseen microbial species and better understand the structural and functional diversity of environmental fungal communities. These molecular genomic tools provided insights into genetic diversity especially pertaining to recovery of uncultured fungal organisms, discovery of novel fungal lineages, as well as the metabolic diversity of these complex fungal communities. Particularly, the culture-independent techniques involving environmental cloning, next-generation sequencing are revealing a higher fungal diversity from environmental DNA samples collected from surface waters in open seas, sediments in coastal, benthic and deep sea environments, hydrothermal vents and oxygen-deficient environments. In addition to the diversity, whole genome sequencing, RNA-Seq and microarray

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technologies in transcriptome profiling have provided a better understanding of potentially active fungal communities. With the use of these culture-independent methods, several undescribed fungal taxa termed as "dark matter fungi" belonging mainly to zoosporic fungi such as *Blastocladiomycota*, *Chytridiomycota*, *Cryptomycota*, and *Neocallimastigomycota* and *Zygomycota* including *Entomophthoromycota*, *Kickxellomycotina*, *Mortierellomycotina*, *Mucoromycotina*, and *Zoopagomycotina* lineages have been retrieved from marine habitats. Many of these nameless and faceless taxa of the early diverging clusters are microscopic in nature with special nutritional requirements and are difficult to isolate in vitro. *Cryptomycota*, the recently described phylum, established using phylotypes based exclusively on environmental sampling, has been shown to be highly diverse, abundant and ubiquitous in distribution. The marine fungal ecology has changed paradigms in the molecular era. The diversity and ecology of marine fungi recovered from the use of molecular tools are discussed in this book chapter.

Keywords
Next-generation sequencing · Phylotypes · Environmental DNA · Deep-sea environment · Sediments · Nucleic acid primers · Environmental cloning

6.1 Introduction

Marine mycology has evolved as a specialized branch of science only in the recent past. Although marine fungi are an ecologically and physiologically defined group, they are taxonomically diverse. Kohlmeyer and Kohlmeyer (1979) have proposed a definition of marine fungi wherein those fungi that grow and sporulate exclusively in a marine or estuarine habitat were considered as obligate marine fungi and those from a freshwater or terrestrial milieu, able to grow and possibly also sporulate in the marine environment, were considered as facultative marine fungi. Marine fungi have long been studied following two techniques including (1) direct examination method where the fungi occurring on natural samples alone (e.g., driftwood, mangrove wood) were studied by observing under dissection/stereo-zoom microscopes to locate fungal propagules/fruiting structures and identify them and (2) culture techniques where soil samples beneath the mangroves or beaches are isolated into appropriate agar media (Hyde et al. 2000; Newell 1976). The former technique retrieves obligate marine fungi if the samples were inundated in marine waters or facultative marine fungi if the samples were collected from aerial parts of mangrove plants or shoreline plants, most of the fungi isolated by the latter technique, i.e., culture plates on agar media result in isolation of common terrestrial fungi, viz., species of *Aspergillus* and *Penicillium* commonly known as "marine-derived fungi." In a modified definition of marine fungi proposed by Pang et al. (2016), both the groups of fungi have been recognized as marine fungi, and their definition states that "a marine fungus is one that could be recovered repeatedly from marine

habitats because (1) it is able to grow and/or sporulate (on substrata) in marine environments; (2) it forms symbiotic relationships with other marine organisms; or (3) it is shown to adapt and evolve at the genetic level or be metabolically active in marine environments."

Fungi play important roles as decomposers involved in regeneration of nutrients in detritus environments in addition to being parasites and symbionts (Webster and Weber 2007). The same is true in the case of marine fungi also where they produce organic detritus supporting large animal community (Kohlmeyer and Kohlmeyer 1979) and decompose the detrital organic matter in marine ecosystems and indulge in nutrient regeneration cycles (Fell and Master 1980; Hyde et al. 1998; Newell 1996 and Raghukumar et al. 1994, 1995) in addition to acting as breeding and nursery grounds in commercial fisheries (Jones and Alias 1997). Though fungi are thought to be major contributors of degradation of decaying plant substrata and animal remains along coastal and surface marine habitats (Kohlmeyer and Kohlmeyer 1979 and Newell 1996), only 1% (1112 species) of the known fungi are from marine environments (Jones et al. 2015), and hence questions have been raised about the importance of fungal communities in marine habitats (Richards et al. 2012) as it is suggested that fungi are nondiverse as well as low in abundance in marine habitats (Burgaud et al. 2009; Kis-Papo 2005 and Le Calvez et al. 2009). Presence of low fungal abundance in upper seawater column samples was reported by Richards et al. (2015) excepting those that occur on phytoplankton. Pang and Jones (2017), however, cautioned about interpretations of results of molecular studies as seawater is a highly dispersive and diluted medium and is not a growth substrate when compared to sediments which represent a niche for settlement of fungal propagules. They reasoned out mentioning that fungi in these substrata might not represent the actively involved marine populations since many fungal propagules could be originated from freshwater or terrestrial environments. However, relatively a higher diversity is reported from the deep-sea environments when compared to surface waters in both culture-dependent and culture-independent studies in addition to indicating their active ecological roles in deep-sea habitats (Edgcomb et al. 2011; Manohar and Raghukumar 2013; Raghukumar et al. 2004 and Singh et al. 2010, 2011, 2012). In many of these studies, it was also found that there are significant differences in the deep-sea fungal diversity between targeted environmental sequencing and conventional cultivation methods (Le Calvez et al. 2009; Singh et al. 2012 and Zhang et al. 2014). Hence a combined approach of both these methods has been suggested to get exact assessment of fungal diversity in deep-sea habitats (Xu et al. 2017).

More than 1112 marine fungal species in 472 genera are known (Jones et al. 2015). The number now stands at 1206 (Pang and Jones 2017). Jones (2011) projected that there could be more than 10,000 marine fungal species. Until the 1970s, most of the research on marine fungi concentrated on their taxonomy (Hyde et al. 2000; Jones et al. 2009). Subsequently, considerable amount of information has become available on several ecological aspects including geographical distribution, frequency of occurrence, vertical zonation, and succession (Alias et al. 1995; Booth and Kenkel 1986; Fryar 2002; Hughes 1974; Hyde and Jones 1988, 1989; Hyde

1988a, b, 1989a, b, 1990a, b; Hyde and Lee 1995; Kohlmeyer and Kohlmeyer 1979; Sarma and Vittal 2000, 2001; Sarma and Hyde 2001). However, all these studies were based on the microscopic observations and enumeration of fungal occurrences when they are in the reproductive phase. In the context of fungal succession, Fryar (2002) presented the problems in studying ecological succession studies of fungi as more often such studies remain to be "sequence of fungal sporulation" instead of "mycelial succession." The reason is at morphology and light microscopy level, where the fungi could be identified based on the fruiting structures only and not based on the mycelia or hyphae on natural samples. Furthermore, the mycelia indicate the active roles of fungi more credibly when compared to the reproductive structures/propagules. In addition to this, a single fungus may sporulate over the entire surface of the substratum and hence only presence or absence could be noted down but number of individuals cannot be quantified as such since sporulation could be from a single mycelium (Jones and Hyde 2002). One cannot deny the importance of microscopy and cultural studies in fungal diversity studies. Direct microscopic analysis and cultural studies are useful approaches for quick diversity estimates (albeit semi-quantitative) and cost-effective. These approaches, however, may not be reliable and underestimate diversity (e.g., Jeewon et al. 2018). Under cultural conditions, species that share similar physiological conditions and exhibit similar cultural characteristics may be different species (Jeewon et al. 2002, 2003a; Liu et al. 2010; Promputtha et al. 2005, 2007; Swe et al. 2009). There are also other major drawbacks such as inefficiency of growth medium used, long-time consumption, laborious and tedious laboratory procedures, lack of experts to enable proper identification, and high risk of contamination by fast-growing fungi (Jeewon and Hyde 2007, 2016). These problems could be circumvented by molecular tools which have revolutionized ecological studies of fungi in the past two decades. However, questions may come whether molecular techniques can discriminate between dormant spores, actively growing mycelium and senescing mycelium.

6.2 Molecular Methods and Marine Fungal Ecology

Molecular methods especially those based on PCR (polymerase chain reaction) to amplify taxonomically informative primer regions in environmental DNA samples clubbed with clonal library construction, DNA sequencing, and phylogenetic analyses that target fungi have usually sampled regions within the ribosomal RNA regions, particularly the small subunit rDNA (18S) and ITS regions (Richards et al. 2012). These approaches have been very useful for resolving species relationships across different taxonomic levels (Jeewon et al. 2003a; Wang et al. 2007; Hongsanan et al. 2017; Jeewon et al. 2017) and to establish novel sexual fungal species (Cai et al. 2006; Duong et al. 2004; Zhang et al. 2008), asexual fungal species (Kodsueb et al. 2007; Pinnoi et al. 2007; Tsui et al. 2006; Vijaykrishna et al. 2004), link sexual and asexual fungal species (Jeewon et al. 2003b; Karunarathna et al. 2017), or discover novel fungal species or new host records from marine environments (Devadatha et al. 2018a, b; Li et al. 2018; Swe et al. 2008a, b; Vinit et al. 2018a, b).

Though ITS regions are handy to determine species diversity and could be employed for ecosystem comparisons, when well-defined taxonomic groups are targeted, it has limited usage during interpretation of higher-level phylogenetic relationships and identifying novel groups since it provides a weak resolution among deeper branching relationships in the fungi (Richards et al. 2012; Horton and Bruns 2001). Due to this reason, some workers have concentrated on selection of SSU rRNA gene marker to study fungal diversity on higher taxonomic groups because this marker does not discriminate between closely related fungal species (Bass et al. 2007; Jebaraj et al. 2009; Richards et al. 2012). To circumvent this problem, multigene phylogenetic analyses including SSU, 5.8S, and large subunit (LSU 28S) sequences that could provide strong phylogenetic support for lower as well as higher phylogenetic levels are currently being used (Jeewon et al. 2009, 2013; Jones et al. 2011; Senanayake et al. 2018a; Wanasinghe et al. 2018; Zhao et al. 2007). In addition, to overcome bias associated with single gene phylogenies, DNA sequence-based analyses on protein-coding genes have been very common to investigate phylogenetic relationships among fungi (Luo et al. 2017; Senanayake et al. 2017, 2018b).

Studies based on morphology and culture-based studies of marine fungi have so far reported 1112 species (Jones et al. 2015). These are mainly fungi isolated from sediments and lignocellulosic substrates occurring in the coastal habitats. However, culture-dependent and culture-independent approaches from both surface waters and deep-sea environments by various workers have revealed some interesting results. For example, DNA-based sequence analyses of 49 SSU rDNA environmental clone libraries recovered totally 1077 sequences from soil, freshwater, and marine samples and also suggest that fungi, with only 124 sequences (11.5%), are comparatively nondiverse and low in abundance in upper as well as surface marine ecosystems (Richards and Bass 2005). A similar trend was observed by Massana and Pedrós-Alió (2008) when they examined 23 coastal water libraries comprising 1349 clones and 12 open ocean libraries comprising 826 clones but could recover only 16 fungal clones (0.8%) of the total marine SSU rDNA sequences processed. Usage of a different technique involving 454 sequencing of eukaryotic SSU rDNA from marine coastal waters also suggests fungal diversity to be nondiverse with less than 5% of the total OPUs (operational taxonomic units) recovered, although this technique indicated an increased diversity than clone library methods (Stoeck et al. 2010). The usage of multi-gene analyses may improve this impasse.

6.3 Marine Fungal Diversity and Abundance in Upper and Surface Open Sea Waters

Fungi have absorptive mode of nutrition (osmotrophy) that involves secretion of enzymes, breaking down of complex biopolymers, and absorption of the nutrients from the breakdown products. Such a lifestyle makes them to feed on organically rich plant and animal substrata or organic remains in soils, sediments, and detritus environments and requires attachment to respective substrata. Probably, due to these ecological characteristics, fungal diversity and abundance have been found to be

low in several upper as well as surface marine water column samples studied (Kis-Papo 2005; Richards and Bass 2005). Hence, these environments are not likely to support organisms that thrive basically by attaching to larger physical substrata and adopting osmotrophy, presumably because both the enzymes secreted and their target nutrients would have been lost due to rapid diffusion into the liquid environment. Based on environmental DNA sequence analyses of marine water from upper column, Richards et al. (2015) also supported that marine fungi occur in low diversity and low abundance within this region. However, it was also clear from this study that although amplicons are detected in low numbers, unclassified OTUs can be diverse and dominated by *Chytridiomycota*, followed by *Ascomycota* and *Basidiomycota*. The other reason is the existence of the variations between photosynthesis and biomass accumulation on land as well as at sea. In terrestrial environments, the carbon is fixed into larger and composite plant tissues that are rich in energy as well as nutrients and are tough to digest. Such an aspect would have driven the evolution of osmotrophic lifestyle among the fungi with specialized plant and fungal associations leading to higher fungal diversity. However, in the open seas, the primary producers are small and unicellular lacking complex energy and nutrient-rich compounds. Accordingly, the type of fungal diversity found on land is largely missing in the open seas. Instead, as the open seas have only unicellular photosynthetic organisms and phagotrophic grazers in the surface waters, the diversity and abundance of detrital microbiota develop according to this trophic relationship which is very low (Richards et al. 2012). However, as depth increases, crossing the photozone, the particulate matter reaches the sediments thus increasing its availability for saprotrophs, including fungi, paving the way for detritus processing. In fact, the fungi have been reported to be predominantly active eukaryotic microbes in these environments (Edgcomb et al. 2011; Takishita et al. 2006).

6.4 Marine Fungal Diversity and Abundance in Deep Sea Environments

The deep-sea environmental sampling of sediments and hydrothermal vents for mycocommunities using SSU DNA clone library methods, though has shown a low diversity of fungi in the overall analysis, have indicated a predominance of ascomycete and basidiomycete forms. Further, most of these forms belong to yeast morphotypes suggesting that these taxa were easily recoverable or that they were dominant in these environments. Also, seven clusters of distinctive sequences were recovered of which six potentially represents new fungal lineages in marine environments (Bass et al. 2007). When environmental DNA (eDNA) methods using a different primer set from that in the above study was undertaken to analyze samples from deep-sea hydrothermal vents, many novel fungal lineages were recovered including three unknown phylotypes within the *Basidiomycota* and novel phylotypes close to *Chytridiomycota* (Le Calvez et al. 2009).

Culture sampling from deep-sea sediments revealed the yeast form *Cryptococcus surugensis* (Nagahama et al. 2003). On the other hand, molecular analysis of

eukaryotic diversity in marine sediments by Takishita et al. (2006) revealed a different species of *Cryptococcus* (*C.curvatus*). This evidently points out that species diversity at the genus level might be higher than expected and if one relies only on cultural or only molecular data, fungal diversity estimates could be erroneous. When both DNA- and RNA-based diversity profiles were targeted to identify the eukaryotic microbial communities in deep-sea sediment cores, a high incidence of basidiomycetous yeast sequences close to existing *Cryptococcus* as well as *Malassezia* species were recovered (Edgcomb et al. 2011), with a large percentage (42%) of sequences retrieved from RNA-derived libraries cladding with *Cryptococcus* sequences. One of the advantages of conducting studies with RNA-derived libraries is that they also indicate about the metabolically active taxa in sedimentary ecosystems (Edgcomb et al. 2011).

The diversity of mycocommunities from 10 different deep-sea sediment samples was investigated by Nagano et al. (2010) using polymerase chain reaction-mediated ITS regions of rRNA gene clone analysis. The results, in addition to showing common terrestrial fungal species, indicated the presence of a group of major deep-sea phylotypes belonging to the phylum *Ascomycota* in addition to a novel phylotype cladded in deep branches within the phylum *Chytridiomycota* with *Rozella* spp. that are considered to be the closely related organisms (Table 6.1).

The fact that most of the fungi retrieved from deep-sea environmental samples clade closely to known terrestrial fungi suggesting that fungi of terrestrial or marine surface environments are adept at making transition to deep-sea habitats as evidenced in laboratory experiments which reported fungi capable of tolerating high hydrostatic pressure by altering their membrane composition (Simonato et al. 2006).

Basically, deep-sea regions are characterized by low temperatures, higher hydrostatic pressures, absence of light, and finally a very low biological diversity, and hence diversity and abundance of fungi are low when compared to coastal sediments. Further, most of the culturable fungi retrieved are common terrestrial forms (Damare et al. 2008; Singh et al. 2010). However, the number of novel phylotypes obtained from the deep-sea environments is higher when compared to other marine habitats (Manohar and Raghukumar 2013). Fungi play an active ecological role in the deep-sea environments as proven by metabolically active sequences found in RNA-based libraries (Edgcomb et al. 2011).

The ecological roles of fungi in the deep realm of Canterbury basin sediment cores, New Zealand, were studied by Rédou et al. (2014) by using 454-pyrosequencing pointed at small subunit (18S) ribosomal RNA and DNA in addition to fungal ITS1 regions. Though a total of 17,672 sequences were retrieved for five samples from 346 to 1711 mbsf (meters below seafloor) depths, only 18 operational taxonomic units (OTUs) were detected in this study but still enlightens the potentially important ecological roles of fungi in the deep-see environment. Taxa belonging to the fungal classes *Dothideomycetes*, *Exobasidiomycetes*, *Eurotiomycetes*, *Microbotryomycetes*, *Saccharomycetes*, *Sordariomycetes*, *Tremellomycetes*, and *Wallemiomycetes* were observed. The 18SrDNA analyses revealed three clusters: (I) *Cryptococcus surugaensis*, *Filobasidium globisporum*, and *Wallemia muriae* were retrieved from the deeper sediment horizon depth; (II) *Exophiala dermatitidis*,

Table 6.1 List of fungal species retrieved through culture-independent analyses from marine environments

S.No.	Name of the species	Taxonomic group	Primer	Sample nature	References
1	*Absidia glauca*	*Mucoromycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
2	*Acaulospora laevis*	*Glomeromycetes*	ITS	Sagami Bay, Japan coast	Nagano et al. (2010)
3	*Apusomonas proboscidea*	*Apusozoa*	18S rDNA	Deep-sea sediment cores, Peru Margin/ Trench	Edgcomb et al. (2011)
4	*Aspergillus flavus*	*Eurotiomycetes*	18S rDNA	Deep-sea sediment cores, Peru Margin/ Trench	Edgcomb et al. (2011)
5	*Aspergillus penicillioides*	*Eurotiomycetes*	ITS	Izu-Ogasawara Trench, Japan coast	Nagano et al. (2010)
6	*Aureobasidium pullulans*	*Dothideomycetes*	18S rDNA	deep-sea sediment cores, Peru Margin/ Trench	Edgcomb et al. (2011)
7	*Babjeviella inositovora*	*Saccharomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
8	*Basidiobolus haptosporus*	*Basidiobolomycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
9	*Basidiobolus meristosporus*	*Basidiobolomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
10	*Basidiobolus microsporus*	*Basidiobolomycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
11	*Basipetospora chlamydospora*	*Eurotiomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)

(continued)

Table 6.1 (continued)

S.No.	Name of the species	Taxonomic group	Primer	Sample nature	References
12	*Batcheloromyces leucadendri*	*Dothideomycetes*	ITS 1	Deep-sea Canterbury basin sediment cores, New Zealand	Rédou et al. (2014)
13	*Bensingtonia subrosea*	*Agaricostilbomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
14	*Blastocladiella emersonii*	*Blastocladiomycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
15	*Blyttiomyces helicus*	*Chytridiomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
16	*Bullera arundinarieae*	Tremellomycetes	18SrDNA	European near shore samples	Richards et al. (2015)
17	*Candida ethanolica*	*Saccharomycetes*	18SrDNA	European near shore samples	Richards et al. (2015)
18	*Candida parapsilosis*	*Saccharomycetes*	ITS	Sagami Bay, Japan coast	Nagano et al. (2010)
19	*Candida sagamina*	*Saccharomycetes*	18S rDNA	Deep-sea sediment cores, Peru Margin/ Trench	Edgcomb et al. (2011)
20	*Candida sylvanorum*	*Saccharomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
21	*Chytridium olla*	*Chytridiomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
22	*Chytridium polysiphoniae*	*Chytridiomycetes*	18S rDNA	Deep-sea sediment cores, Peru Margin/ Trench; European near shore samples	Edgcomb et al. (2011); Richards et al. (2015)

(continued)

Table 6.1 (continued)

S.No.	Name of the species	Taxonomic group	Primer	Sample nature	References
23	*Chytriomyces angularis*	*Chytridiomycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
24	*Chytriomyces confervae*	*Chytridiomycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
25	*Clydaea vesicular*	*Lobulomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
26	*Cokeromyces recurvatus*	*Mucoromycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
27	*Colacogloea peniophorae*	*Microbotryomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
28	*Cordyceps gunnii*	*Sordariomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
29	*Cryptococcus aureus*	*Tremellomycetes*	18S rDNA	Deep-sea sediment cores, Peru Margin/ Trench	Edgcomb et al. (2011)
30	*Cryptococcus carnescens*	*Tremellomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
31	*Cryptococcus cellulolyticus*	*Tremellomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
32	*Cryptococcus curvatus*	*Tremellomycetes*	18S rDNA	Deep-sea Canterbury basin sediment cores, New Zealand	Rédou et al. (2014)
33	*Cryptococcus dimennae*	*Tremellomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
34	*Cryptococcus marinus*	*Tremellomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)

(continued)

Table 6.1 (continued)

S.No.	Name of the species	Taxonomic group	Primer	Sample nature	References
35	*Cryptococcus pseudolongus*	*Tremellomycetes*	ITS 1, 18S rDNA	Deep-sea Canterbury basin sediment cores, New Zealand, deep-sea sediment cores, Peru Margin/ Trench	Rédou et al. (2014), Edgcomb et al. (2011)
36	*Cryptococcus psychrotolerans*	*Tremellomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
37	*Cryptococcus saitoi*	*Tremellomycetes*	ITS 1	Deep-sea Canterbury basin sediment cores, New Zealand	Rédou et al. (2014)
38	*Cryptococcus skinneri*	*Tremellomycetes*	ITS	Sagami Bay, Japan Coast	Nagano et al. (2010)
39	*Cryptococcus surugaensis*	*Tremellomycetes*	18SrDNA	Deep-sea Canterbury basin sediment cores, New Zealand	Rédou et al. (2014)
40	*Cyberlindnera jadinii*	*Saccharomycetes*	ITS 1	Deep-sea Canterbury basin sediment cores, New Zealand	Rédou et al. (2014)
41	*Cyberlindnera macularae*	*Saccharomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
42	*Debaryomyces hansenii*	*Saccharomycetes*	18S rDNA	European near shore samples; Arabian coast, India	Richards et al. (2015)
43	*Delfinachytridium mesopotamicum*		18S rDNA	European near shore samples	Richards et al. (2015)

(continued)

Table 6.1 (continued)

S.No.	Name of the species	Taxonomic group	Primer	Sample nature	References
44	*Diversispora spurca*	*Glomeromycetes*	18SrDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
45	*Endogone lactiflua*	*Endogonomycetes*	18SrDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
46	*Endogone pisiformis*	*Endogonomycetes*	18SrDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
47	*Elmerina caryae*	*Tremellomycetes*	ITS 1	Deep-sea Canterbury basin sediment cores, New Zealand	Rédou et al. (2014)
48	*Entophlyctis helioformis*	*Chytridiomycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
49	*Entrophospora semiglobiferus*	*Glomeromycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
50	*Exophiala dermatitidis*	*Eurotiomycetes*	18S rDNA	Deep-sea Canterbury basin sediment cores, New Zealand	Rédou et al. (2014)
51	*Exophiala spinifera*	*Eurotiomycetes*	ITS 1	Deep-sea Canterbury basin sediment cores, New Zealand	Rédou et al. (2014)

(continued)

Table 6.1 (continued)

S.No.	Name of the species	Taxonomic group	Primer	Sample nature	References
52	*Filobasidium globisporum*	*Tremellomycetes*	18S rDNA	Deep-sea Canterbury basin sediment cores, New Zealand, deep-sea sediment cores, Peru Margin/ Trench	Rédou et al. (2014), Edgcomb et al. (2011)
53	*Fimicolochytrium jonesii*	*Spizellomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
54	*Fomes fomentarius*	*Agaricomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
55	*Fusarium solani*	*Sordariomycetes*	18S rDNA	Deep-sea Canterbury basin sediment cores, New Zealand	Rédou et al. (2014)
56	*Gaertneriomyces semiglobifera*	*Spizellomycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
57	*Gaertneriomyces tenuis*	*Spizellomycetes*	18SrDNA	European near shore samples	Richards et al. (2015)
58	*Galactomyces candidum*	*Saccharomycetes*	ITS 1	Deep-sea Canterbury basin sediment cores, New Zealand	Rédou et al. (2014)
59	*Gamsiella multidivaricata*	*Mucoromycetes*	18SrDNA	European near shore samples	Richards et al. (2015)
60	*Geosiphon pyriformis*	*Zygomycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)

(continued)

Table 6.1 (continued)

S.No.	Name of the species	Taxonomic group	Primer	Sample nature	References
61	*Geotrichum candidum*	*Saccharomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
62	*Geotrichum klebahnii*	*Saccharomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
63	*Glomeralla lagenaria*	*Sordariomycetes*	ITS	Izu-Ogasawara Trench, Japan coast	Nagano et al. (2010)
64	*Harpella meridianalis*	*Harpellomycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
65	*Hyaloraphidium curvatum*	*Chytridiomycetes*	18 SrDNA	European near shore samples	Richards et al. (2015)
66	*Isaria farinosa*	*Sordariomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
67	*Kondoa malvinella*	*Agaricostilbomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
68	*Kuzuhaea moniliformis*	*Zoopagomycetes*	18 SrDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
69	*Lacustromyces heimalis*	*Cladochytriomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
70	*Leptosphaerulina chartarum*	*Dothideomycetes*	ITS 1	Deep-sea Canterbury basin sediment cores, New Zealand	Rédou et al. (2014)
71	*Leucosporidiella muscorum*	*Microbotryomycetes*	ITS 1	Deep-sea Canterbury basin sediment cores, New Zealand	Rédou et al. (2014)
72	*Limacella glischra*	*Agaricomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)

(continued)

Table 6.1 (continued)

S.No.	Name of the species	Taxonomic group	Primer	Sample nature	References
73	*Linderina pennispora*	*Kickxellomycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
74	*Lobulomyces angularis*	*Lobulomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
75	*Lobulomyces poculatus*	*Lobulomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
76	*Malassezia furfur*	*Exobasidiomycetes*	18S rDNA	deep-sea sediment cores, Peru Margin/ Trench	Edgcomb et al. (2011)
77	*Malassezia pachydermatis*	*Exobasidiomycetes*	18SrDNA	Deep sea Canterbury basin sediment cores, New Zealand	Rédou et al. (2014)
78	*Martensiomyces pterosporus*	*Kickxellomycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
79	*Maunachytrium keaense*	*Lobulomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
80	*Metschnikowia colocasiae*	*Saccharomycetes*	ITS	Izu-Ogasawara Trench, Japan coast	Nagano et al. (2010)
81	*Metschnikowia continentalis*	*Saccharomycetes*	ITS	Izu-Ogasawara Trench, Japan coast	Nagano et al. (2010)
82	*Metschnikowia kamakouana*	*Saccharomycetes*	ITS	Izu-Ogasawara Trench, Japan coast	Nagano et al. (2010)

(continued)

Table 6.1 (continued)

S.No.	Name of the species	Taxonomic group	Primer	Sample nature	References
83	*Meyerozyma guilliermondii*	*Saccharomycetes*	18S rDNA	Deep-sea Canterbury basin sediment cores, New Zealand; European near shore samples	Rédou et al. (2014) and Richards et al. (2015)
84	*Mortierella cystojenkini*	*Mortierellomycetes*	18 SrDNA	European near shore samples	Richards et al. (2015)
85	*Mortierella wolfii*	*Mortierellomycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
86	*Mrakia frigida*	*Tremellomycetes*	18S rDNA	Deep-sea sediment cores, Peru Margin/ Trench	Edgcomb et al. (2011)
87	*Mycogloea macrospora*	*Spiculogloeomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
88	*Neokarlingia chitinophila*	*Polychytriomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
89	*Neurospora crassa*	*Sordariomycetes*	18S rDNA	Deep-sea sediment cores, Peru Margin/ Trench	Edgcomb et al. (2011)
90	*Obelidium mucronatum*	*Chytridiomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
91	*Olpidium brassicae*	*Olpidiomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
92	*Orbilia auricolor*	*Orbiliomycetes*	18S rDNA	Arabian coast, India	Jebraj et al. (2009)
93	*Orbilia fimicola*	*Orbiliomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)

(continued)

Table 6.1 (continued)

S.No.	Name of the species	Taxonomic group	Primer	Sample nature	References
94	*Orphella haysii*	*Trichomycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
95	*Paraglomus brasilianum*	*Paraglomeromycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
96	*Penicillium chrysogenum*	*Eurotiomycetes*	ITS	Izu-Ogasawara Trench, Japan coast	Nagano et al. (2010)
97	*Penicillium minioluteum*	*Eurotiomycetes*	ITS 1	Deep-sea Canterbury basin sediment cores, New Zealand	Rédou et al. (2014)
98	*Phlyctochytrium arcticum*	*Chytridiomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
99	*Physoderma macularae*	*Physodermatomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
100	*Pichia guilliermondii*	*Saccharomycetes*	18S rDNA	Deep-sea sediment cores, Peru Margin/ Trench	Edgcomb et al. (2011)
101	*Pichia heedii*	*Saccharomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
102	*Pichia membranifaciens*	*Saccharomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
103	*Piptocephalis corymbiferae*	*Zoopagomycetes*	18SrDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)

(continued)

Table 6.1 (continued)

S.No.	Name of the species	Taxonomic group	Primer	Sample nature	References
104	*Pleurostomophora richardsiae*	*Sordariomycetes*	ITS 1	Deep-sea Canterbury basin sediment cores, New Zealand	Rédou et al. (2014)
105	*Podochytrium dentatum*	*Chytridiomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
106	*Polychytrium aggregatum*	*Cladochytriomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
107	*Protomyces lactucaedebilis*	Taphrinomycetes	18S rDNA	Arabian coast, India	Jebraj et al. (2009)
108	*Puccinia poarum*	*Pucciniomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
109	*Pucciniastrum epilobii*	*Pucciniomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
110	*Radiomyces spectabilis*	*Mucoromycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
111	*Rhinocladiella similis*	*Eurotiomycetes*	ITS 1	Deep-sea Canterbury basin sediment cores, New Zealand	Rédou et al. (2014)
112	*Rhizidium endosporangiatum*	*Chytridiomycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
113	*Rhizophlyctis harderi*	*Rhizophlyctidomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
114	*Rhizophlyctis rosea*	*Rhizophlyctidomycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
115	*Rhodosporidium dacryoidum*	*Microbotryomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)

(continued)

Table 6.1 (continued)

S.No.	Name of the species	Taxonomic group	Primer	Sample nature	References
116	*Rhodosporidium diobovatum*	*Microbotryomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
117	*Rhodosporidium kratochvilovae*	*Microbotryomycetes*	ITS 1	Deep-sea Canterbury basin sediment cores, New Zealand	Rédou et al. (2014)
118	*Rhodotorula bacarum*	*Microbotryomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
119	*Rhodotorula lamellibrachiae*	*Microbotryomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
120	*Rhodotorula laryngis*	*Microbotryomycetes*	ITS	Izu-Ogasawara Trench, Japan coast	Nagano et al. (2010)
121	*Rhodotorula marina*	*Microbotryomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
122	*Rhodotorula minuta*	*Microbotryomycetes*	ITS 1	Deep-sea Canterbury basin sediment cores, New Zealand; European near shore samples	Rédou et al. (2014) and Richards et al. (2015)
123	*Rhodotorula mucilaginosa*	*Microbotryomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
124	*Rhodotorula rosea*	*Microbotryomycetes*	ITS	Izu-Ogasawara Trench, Japan coast	Nagano et al. (2010)
125	*Rhodotorula yarrowii*	*Microbotryomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
126	*Rhopalomyces elegans*	*Zoopagomycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)

(continued)

Table 6.1 (continued)

S.No.	Name of the species	Taxonomic group	Primer	Sample nature	References
127	*Roccella fuciformis*	*Arthoniomycetes*	18S rDNA	Arabian coast, India	Jebraj et al. (2009)
128	*Saccharomyces cerevisiae*	*Saccharomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
129	*Scutellospora calospora*	*Glomeromycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
130	*Sirobasidium brefeldianum*	*Tremellomycetes*	18SrDNA	European near shore samples	Richards et al. (2015)
131	*Spiromyces aspiralis*	*Kickxellomycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
132	*Spiromyces minutus*	*Kickxellomycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
133	*Spizellomyces acuminatus*	*Spizellomycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
134	*Spizellomyces dolichospermus*	*Spizellomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
135	*Spizellomyces plurigibbosus*	*Spizellomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
136	*Sporobolomyces hasegawianum*	*Microbotryomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
137	*Sporobolomyces inositophilus*	*Microbotryomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
138	*Syncephalis depressa*	*Zoopagomycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)

(continued)

Table 6.1 (continued)

S.No.	Name of the species	Taxonomic group	Primer	Sample nature	References
139	*Torpedospora radiata*	*Sordariomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
140	*Tremella moriformis*	*Tremellomycetes*	ITS 1	Deep-sea Canterbury basin sediment cores, New Zealand,	Rédou et al. (2014),
141	*Trichosporon aquatile*	*Tremellomycetes*	18S rDNA	Deep-sea sediment cores, Peru Margin/ Trench	Edgcomb et al. (2011)
142	*Trichosporon mucoides*	*Tremellomycetes*	18S rDNA, ITS	Deep-sea Canterbury basin sediment cores, New Zealand, Izu-Ogasawara Trench, Japan coast	Rédou et al. (2014), Nagano et al. (2010)
143	*Trimorphomyces papilionaceus*	*Tremellomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
144	*Triparticalcar arcticum*	*Spizellomycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
145	*Uromyces aritriphylli*	*Pucciniomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)
146	*Ustilago shiraina*	*Ustilaginomycetes*	18S rDNA	Deep-sea sediment cores, Peru Margin/ Trench	Edgcomb et al. (2011)
147	*Xerocomus chrysenteron*	*Agaricomycetes*	18S rDNA	Deep-sea sediment cores, Peru Margin/ Trench	Edgcomb et al. (2011)

(continued)

Table 6.1 (continued)

S.No.	Name of the species	Taxonomic group	Primer	Sample nature	References
148	*Wallemia muriae*	*Wallemiomycetes*	18S rDNA	Deep-sea Canterbury basin sediment cores, New Zealand	Rédou et al. (2014)
149	*Zoophagus insidians*	*Zoopagomycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
150	*Zygopolaris ephemeridarum*	*Harpellomycetes*	18S rDNA	Near wreck of Bismarck, Brest, France in Atlantic Ocean	Bass et al. (2007)
151	*Zygorhizidium planktonicum*	*Chytridiomycetes*	18S rDNA	European near shore samples	Richards et al. (2015)

Malassezia pachydermatis, *Meyerozyma guilliermondii*, *Pleurostomophora richardsiae*, and *Trichosporon mucoides* were found in sediment samples that have a low organic carbon concentration; (III) *Cryptococcus curvatus*, *Cyberlindnera jadinii*, *Fusarium solani*, *Leptosphaerulina chartarum*, and *Trichoderma* sp. were found in shallowest depths and correlated with methane concentration. Similarly, ITS1 sequence analyses also resulted in three clusters (I) *Cryptococcus saitoi*, *Leucosporidiella muscorum*, *Rhodosporidium kratochvilovae*, *Rhodotorula* sp., and *Tremella moriformis*; (II) *Batcheloromyces leucadendri*, *Chaetothyriales sp*., *Elmerina caryae*, *Exophiala spinifera*, *P. richardsiae*, *Penicillium* sp., and *Rhinocladiella* sp.; and (III) *Cryptococcus jadinii*, *C. pseudolongus*, *Galactomyces candidum*, *L. chartarum*, and *Trichosporon* sp., and most of the OTUs were only found at a given depth (Rédou et al. 2014). The above study clearly demonstrates that the use of different primer sets yields different results. This difference in taxon recovery from the same habitats highlights that the selection of appropriate genes is crucial in determining fungal diversity and it would be far more judicious to use several gene markers as compared to only one.

Studies on culturable mycocommunities from deep-sea sediment core samples from Canterbury basin, New Zealand, resulted in isolation of more than 200 filamentous fungi (68%) and yeasts (32%) (Rédou et al. 2015). This study provides proof of deep-subsurface mycocommunities having ability to survive, adapt, grow, and interact with other microbial communities in addition to highlighting that the

deep-sediment environment is one more ecological niche for fungi. Further, all the fungal taxa isolated were well-known in terrestrial habitats indicating the ability of terrestrial fungi to adapt to deep-subsurface conditions (Rédou et al. 2015). Based on 18S rDNA sequence data, it has been reported that yeasts tend to dominate fungal diversity in deep ocean floor and that huge hydrostatic pressure is not a barrier to life (Bass et al. 2007).

Employing amplicon pyrosequencing, eukaryotic 18SrRNA sequences were investigated by Orsi et al. (2013) and found a distinct set of fungi across different marine subsurface regions such as continental margins, ridge flanks, and abyssal plains near Peru Margin, Eastern Equatorial Pacific, and Mid-Atlantic Ridge. The subseafloor mycocommunities and their populations had a statistically significant correlation with various environmental parameters including nitrate, sulfide, total organic carbon (TOC), and dissolved inorganic carbon (DIC). Such correlation was also supported by terminal restriction length polymorphism (TRFLP) analyses of fungal rRNA (Orsi et al. 2013). In the North Pond (1.6 mbsf) the sequences associated with *Antrodia*, *Apioplagiostoma*, *Cordyceps*, *Cryptococcus*, *Cyberlindnera*, *Doassansia*, *Erythrobasidium*, *Filobasidium*, *Hannaella*, *Hyphodontia*, *Mycena*, *Powellomyces*, *Peyronellaea*, and *Sterium* were retrieved that represent sediment age of 0.1–2 MYA. From Hydrate Ridge (1.8 mbsf) *Cordyceps*, *Crinipellis*, *Cryptococcus*, *Entoloma, Leucosporidium*, and *Mycena* were retrieved, which represent sediment age of 0.1 MYA. In the Benguela Upwelling System (4.61 mbsf) *Acidomyces*, *Neurospora*, *Sordaria*, *Candida*, *Hydropus*, *Mycena*, *Steccherinium*, *Stereum*, *Filobasidium*, *Rhodotorula*, *Rhodosporidium*, *Diversispora*, and *Glomus* were retrieved and these represent sediment age of 0.03 MYA. From the Eastern Equatorial Pacific (45.3 mbsf), *Alternaria*, *Antrodia*, *Apioplagiostoma*, *Camarops*, *Candida*, *Cryptosporella*, *Cyberlindnera*, *Cryptococcus*, *Dioszegia*, *Discula*, *Filobasidium*, *Helicogloea*, *Mycena*, *Neurospora*, *Peyronellaea*, *Phruensis*, *Rhizoctonia*, *Rhodotorula*, *Sporobolomyces*, and *Sterigmatomyces* were retrieved that represent sediment age of 2.77 MYA. From Peru Margin (48.1 mbsf), *Cryptococcus*, *Glyphium*, *Geopyxis*, *Knufia*, *Lentinula*, *Mycena*, *Rhotorula*, and *Trichosporum* were retrieved, and these taxa represent sediment age of 2.6 MYA (Orsi et al. 2013).

The deep sea environment, in particular, the sediments, must be inhabited by many undiscovered species, but our knowledge is still limited and fragmentary because our methods available do not allow us to fully recover all species from those habitats. High-throughput approaches have shed a new perception of deep-sea fungal community ecology. One of the latest studies dealing with deep-sea sediment samples is that of Nagano et al. (2018) in Brazil. The authors reported similar fungal diversity as other previous work with *Aspergillus*, *Penicillium*, psychrotrophic fungi, and red-pigmented basidiomycetous yeasts as dominant fungi. Interestingly, ubiquitous taxa such as *Aspergillus*, *Pestalotiopsis*, and *Trichoderma* have also been recovered, and these have been reported to be able to degrade petroleum hydrocarbons. This points out that many of these fungi could be significant bioremediators that can potentially be exploited to combat pollution problems.

6.5 Deep-Sea Hydrothermal Vents

The fungal diversity of deep-sea hydrothermal samples from East Pacific Rise at the Elsa site, Pacific Ocean, and Mid-Atlantic Ridge at Menez Gwen site, employing small-subunit rRNA (18SrDNA) gene sequences amplified by culture-independent PCR using DNA extracts, was investigated by Le Calvez et al. (2009). The results showed that *Chytridium polysiphoniae*, *Rhizophlyctis rosea*, *Spizellomycete* sp., *Powellomyces s*p., *Rhizophydium* sp., *Kappamyces laurelensis* belonging to *Chytridiomycota*; *Cryptococcus* sp., *Filobasidium* sp., *Bullera nakhonratchasimensis*, *Kockovaella kimperatae*, *Feliomyces ogasawarensis*, *Exida uvapsassa*, *Auricularia polytricha*, and *Fibulorhizoctonia* sp. belonging to *Basidiomycota* were present. In addition to this culture-dependent studies employing molecular techniques revealed the presence of *Penicillium tardum*, *Wangiella dermatidis*, *Phaeococcomyces exophialae*, *Capronia acutiseta*, *Graphium* sp., *Exophiala jeanselmei*, *Phialophora* sp., *Rhinocladiella atrovirens*, *Exophiala* sp., *Helicoon fuscosporium, Spliocaea oleagina*, *Tricodelitschia munkii*, *Phaeotrichum benjamini, Hortaea werneckii*, *Aureobasidium pullulans*, *Diaporthe eres*, *Acremonium* sp., *Tritirachium* sp., *Engyodontium album*, *Nadsionella nigra*, *Pochonia chlamydosporia*, and *Tolypocladium cylindrosporum* (Le Calvez et al. 2009). Further, many of the species recorded in this study through culture-independent methods were not known even at higher taxonomic levels in the *Chytridiomycota*, *Ascomycota*, and *Basidiomycota*. A combined culture-dependent and culture-independent sequence-based study on fungal distribution and diversity at a deep-sea hydrothermal vent site at the Mid-Atlantic Ridge of the South Atlantic Ocean undertaken by Xu et al. (2017) revealed that the mycocommunity was dominated by members belonging to *Ascomycota* and *Basidiomycota*. In addition, several novel phylotypes, i.e., 28 of 65 total fungal OTUs from clone library construction and 2 out of 19 cultural fungal phylotypes, were recovered indicating the presence of unrevealed diversity of fungi in this habitat. Also, they found that the mycocommunities in the chimney samples were different from those found in three sulfide samples. Further, their qPCR studies have shown that fungal LSU rRNA gene copy numbers ranged from 5.88×10^5 to 6.77×10^6 copies/gram rock of wet weight. Also, their results showed that *Ascomycota* was 2–3 times more abundant than the *Basidiomycota* (Xu et al., 2017). Within the *Ascomycota* they found *Sordariomycetes* to be the most dominant group followed by *Dothideomycetes*, *Saccharomycetes*, *Eurotiomycetes*, and *Leotiomycetes*.

6.6 Anoxic Marine Environments

Fungi are often found as saprotrophs in terrestrial environments that are low in oxygen and have cellular and genomic adaptations for survival in anoxic environments (Embley et al. 2006; Gojkovic et al. 2004). Vast areas of marine

environments are anoxic. Fungal sequences closely related to *Fusarium* species in deep-sea anoxic environments, using SSU DNA clone libraries, have been reported by Jebraj et al. (2009). Further, Jebaraj and Raghukumar (2009) have demonstrated that *Fusarium* strains isolated from anoxic deep-sea samples could utilize nitrate for respiration and accumulate nitrite thus indicating a role in anaerobic denitrification in marine environments. When multiple fungal-specific SSU rDNA primer sets and a universal eukaryotic-specific marker were used to amplify SSU sequences from samples of oxygen-depleted regions of the Arabian sea, a greater diversity of fungi was found in the fungal-specific marker genes than the clone libraries constructed using universal eukaryotic primers (Jebaraj et al. 2009). Further, this study also indicated the necessity of using different primers to regulate PCR biases, and chances of missing fungal diversity when universal primer sets alone were used. In the same study, 56% of the total 48 phylotypes branched within the ascomycete radiation and 41% within basidiomycetes with only 2% belonged to lower fungi (Jebraj et al. 2009). While culture-dependent studies suggest the presence of a higher percentage of filamentous forms in deep-sea environments, the molecular analyses of sediment and water samples from marine environments using SSU rDNA marker genes by Richards et al. (2012) indicate that *Dikarya* (Ascomycetes and Basidiomycetes) are the most likely recoverable marine fungal lineages with a high percentage of sequences recovered within *Dikarya* belonging to well-known yeast groups. Earlier Alexander et al. (2009) also reported predominance of fungi from sediment samples from the hypersaline anoxic deep-sea basin of L'Atalante using SSU rDNA sequence analyses. The detection of fungal hyphae in anoxic sediments in mangrove habitat using Calcoflour staining and epifluorescene microscopy and using 454 pyrosequencing of nuclear ribosomal ITS regions with the latter technique revealing dominance of *Agaricomycetes* in the *Basidiomycota* has been reported (Arfi et al. 2012). Clades close to the basidiomycetous yeast *Malassezia*; *Rozella* and allied clusters belonging to *Cryptomycota*; well-known fungal taxa belonging to *Penicillium*, *Eupenicillium,* and *Aspergillus*; and basal clones close to *Chytridiomycota*, in addition to several novel sequences have been reported from different anoxic environments including coastal anoxic sediments of Bolinas tidal flat (Dawson and Pace 2002), L'Atlantic basin at a depth of 3500 m (Alexander et al. 2009), Arabian sea from depths of 25–200 m (Jebaraj et al. 2010; Manohar and Raghukumar 2013), Methane cold seeps, South China Sea at depths ranging from 350 to 3000 m (Lai et al. 2007), Methane cold seep, Sagami Bay at a depth of 1080 m (Nagahama et al. 2011; Takishita et al. 2007), Kagoshima bay at a depth of 204 m (Takishita et al. 2005), Cariaco basin at a depth of 340 m (Stoeck et al. 2006), and Gotland deep, Baltic Sea at depths of 200–240 m (Stock et al. 2009). In addition to the diversity of fungi, an active role for fungi also has been reported in marine anoxic habitats including denitrification (Manohar and Raghukumar 2013; Stief et al. 2014), tolerating hypersalinity in the deep hypersaline anoxic basins (DHABs) [Alexander et al. 2009].

6.7 Fungal Pathogens in Marine Environment

Fungal pathogens closely related to terrestrial fungi are specifically present in marine mammals. These include *Aspergillus* (aspergillosis), *Blastomyces* (blastomycosis), *Candida* (candidiasis), *Coccidioides* (coccidioidomycosis), *Cryptococcus* (cryptococcosis), *Fusarium* (fusariomycosis), *Malassezia* (dermatitis), and several disease-causing zygomycetes (Higgins 2000). *Aspergillus sydowii*, which is common in terrestrial environments, is found in coral reeves as a pathogen of sea fan corals (Alker et al. 2001). An unidentified fungal pathogen occurring in shallow reef habitat that spreads dense black fungal bands was found causing the death of coralline algae (Raghukumar and Ravindran 2012). Fungi parasitize virtually all groups of marine animals in the marine environment and attack both wild and cultivated marine animals (Hatai 2012; Marano et al. 2012; Porter 1986; Ramaiah 2006; Shields and Overstreet 2007). Among the several groups, Oomycetan taxa cause diseases on a wide range of hosts but prominently attack invertebrates during seed production of marine crustaceans including shrimps and crabs (Hatai 2012; Marano et al. 2012; Beakes et al. 2014). The prominent members are *Halipthoros*, *Halioticida*, and *Halocrusticida* belonging to Haliphthorales, which are exclusively marine (Beakes et al. 2014). Other genera of the Oomycetes that cause diseases among marine animals are *Atkinsiella*, *Lagenidium*, and *Sirolpidium* (Beakes et al. 2014). A *Fusarium* sp. has been identified as a disease-causing agent of American lobsters (Cawthorn 2011). Interestingly this genus has been represented in various environmental DNA analyses (Richards et al. 2012). Several ascomycete fungi are known to be pathogens of marine algae (Kohlmeyer and Kohlmeyer 1979). Pathogenic fungal signatures belonging to *Exophiala dermatitidis* and *Trichosporon dermatis* (Gadanho and Sampaio 2005) from hydrothermal vents in Mid-Atlantic Rifts southwest of the Azores archipelago employing metagenomics were reported. Clones related to the yeast *Malassezia furfur* have been reported from hydrothermal vents of the Lost city (Lopez-Garcia et al. López-Garcia et al. 2007), Rainbow (Bass et al. 2007) in the Mid-Atlantic Ridge.

6.8 Marine Fungal Diversity in Coastal Regions

Coastal regions have a large availability of organic matter to consumers as detritus due to terrestrial run-off and high primary production often leading to eutrophication (Danovaro and Pusceddu 2007). Mangroves, coral reefs, salt marshes, shore line plants, and different halophytic plants are different habitats having different niches in the coastal habitats that offer substrata for colonization of marine fungi. Driftwood was considered to support a higher number of fungi in the past (Kohlmeyer and Kohlmeyer 1979). However, this was overtaken by mangroves which support relatively a higher number of marine fungi (Hyde et al. 2000). Fungal diversity in mangroves has been explored by several workers (see Jones and Alias 1997; Hyde and Lee 1995; Sarma and Hyde 2001). Around 656 fungi were reported from mangroves of the world up to 2003 (Schmidt and Shearer 2003). In mangroves, the taxa

belonging to the group *Dothideomycetes* are rich and diverse when compared to *Sordariomycetes* (Suetrong et al. 2009). Earlier only microscopic observations were used for identification of marine fungi from mangrove substrata. In recent times, the culturable fungi are also supplemented with DNA sequence data, and several new genera and new species are published with support from phylogeny (Abdel-Wahab et al. 2010; Devadatha et al. 2017, 2018a, b, c). Molecular diversity analysis using pyrosequencing method revealed a high fungal diversity with *Agaricomycetes* predominating in coastal mangrove regions (Arfi et al. 2012). Spatiotemporal variations play a role in determining the fungal community compositions in the ocean. Water temperature and salinity drive community compositions of wood-inhabiting marine fungi (Booth and Kenkel 1986) in addition to log attachment (fixed vs. free-floating) and location (Rama et al. 2014).

Various ecological aspects of marine fungi in mangroves have been investigated. These include (1) frequency of occurrence (Alias et al. 1995; Borse 1988; Hyde 1988a, 1989a, b, 1992; Hyde and Jones 1989; Hyde et al. 1990; Jones and Alias 1997; Sarma and Hyde 2001; Sarma et al. 2001; Sridhar and Maria 2006; Volkmann-Kohlmeyer and Kohlmeyer 1993), (2) host and substrate specificity (Alias and Jones 2000; Hyde 1990a; Hyde and Alias 2000; Hyde and Jones 1988; Hyde and Lee 1995; Poonyth et al. 1999; Sarma and Vittal 2000, 2001), (3) succession (Hyde 1991; Leong et al. 1991, and Kohlmeyer et al. 1995), (4) spatiotemporal variations (Aleem 1980; Hyde 1989a; Alias et al. 1995; Sarma and Vittal 1998–1999), (5) vertical distribution (Hyde 1988b, 1989b,c 1990b; Hyde and Jones 1988; Jones and Tan 1987; Kohlmeyer et al. 1995; Sarma and Vittal 2002), (6) salinity and horizontal distribution (Aleem 1980; Hyde 1992; Hyde and Sarma 2006; Kohlmeyer and Kohlmeyer 1979), and (7) geographical distribution (Hyde and Lee 1995; Jones and Alias 1997; Kohlmeyer 1983, 1987; Schmidt and Shearer 2004). However, all these studies are based on morphology and microscopy. It is well known that fungi could be identified at a microscopic level based on their fruiting structures/reproductive propagules. Many mycologists consider that fruiting structures by and large do not indicate the active roles of fungi unlike the mycelia. To this extent, the location and identity of mycelia on natural samples are difficult. Several novel techniques are explored to study the mycelial fungi including particle filtration technique (Bills and Polishook 1994; Polishook et al. 1996). A large number of fungi isolated through the particle filtration technique remain nonsporulating and hence require molecular analyses to identify them. Several of these fungi seem to be novel but due to lack of sporulation they remain uncharacterized. Nevertheless, these morphological investigations provide qualitative assessments of diversity and ecological data, though the quantitative data is often questioned due to the reason that "only mycelial state is considered as functionally involved in various metabolic activities and not the sporulation stage." Future studies should include attempts of direct isolation of fungal DNA from lignocellulosic substrata and check whether "yet to be cultured fungi" also could be found. The same would also expand the scope of diversity and ecological investigations of fungi colonizing lignocellulosic substrata from mangroves and other such habitats. It is surprising that recent research review papers omitted a discussion on the ecological data of morphological investigations (e.g.,

Richards et al. 2012). There is a need to integrate the diversity and ecological information from both morphological and molecular analyses.

Few studies employing molecular tools to understand the ecology of marine fungi in sediments and water samples have been carried out near mangroves and other coastal habitats. Molecular studies on planktonic diversity of fungi from some coastal locations of Brazil (Cury et al. 2011), coral reefs of Hawaii (Gao et al. 2008; Gao et al. 2010), and mangrove regions (Arfi et al. 2012) have resulted in the identification of fungal organisms belonging to *Ascomycota*, *Basidiomycota*, and *Chytridiomycota* in addition to few cladding into novel environmental clusters (Manohar and Raghukumar 2013). Though fungi were largely considered to be pathogens in the coral reef ecosystems (Kim et al. 2006; Vega Thurber et al. 2009; Yarden et al. 2007), the metagenomics and functional diversity analyses of microbiota in this ecosystem have revealed that fungi are dominant community and are involved even in the nitrogen cycling (Wegley et al. 2007). Many fungi isolated from sponges and other organisms in corals have shown varied secondary metabolites that have wide applications (Zhuo et al. 2011).

Most of the fungal OTU clusters identified from European near shore water column samples predominantly belonged to chytrid-like and yeast *Dikarya* phylotypes (Richards et al. 2015). Filamentous fungal forms such as Pezizomycotina seem to be less suited for marine water column environments than soils and sediments which have solid substrates rich in organic matter (Richards et al. 2012, 2015). The investigations involving ion semiconductor sequencing (Ion Torrent) of the ribosomal large subunit (LSU/28S) to explore fungal diversity from water as well as sediment samples taken from four habitats in North Carolina revealed dominance of taxa belonging to *Ascomycota* and *Chytridiomycota* (Picard 2017). Further, this study also revealed that sand flats and wetland sediments have the highest diversity, although benthic sediments could harbor a higher proportion of novel sequences. Another interesting study focusing on metatranscriptomics analysis of mangrove habitats around Mauritius have also led to an interesting study where the potential roles of different microorganisms could be elucidated (Rampadaruth et al. 2018).

6.9 Coral-Associated Marine Fungi

The facultative marine fungi seem to play ecologically important roles in coral environments of Lakshadweep Islands, India, and Great Barrier Reef, Australia (Ravindran et al. 2001; Morrison-Gardiner 2002; Yarden 2014; Yarden et al. 2007). Species belonging to *Alternaria*, *Aspergillus*, *Aureobasidium*, *Cladosporium*, *Fusarium*, *Penicillium*, *Hormonema*, *Phialophora*, and *Phoma* have been reported from different healthy scleractinian corals (Ravindran et al. 2001). The obligate marine fungi reported from corals include *Koralionastes* and *Corallicola* of Koralionastaceae family (Kohlmeyer and Volkmann-Kohlmeyer 1992). A study on coral-associated fungal ribosomal DNA amplicons of *Acropora hyacinthus* coral colonies from neighboring natural pools with varying water temperatures suggested a high diversity of *Basidiomycetes* and *Ascomycetes* such as novel lineages. Colonies

from a warmer pool comprised phylogenetically more diverse mycocommunities than from colder pool (Amend et al. 2012). Four taxa were retrieved in all coral colonies sampled in this study and they seemed to represent obligate associates. Further, the DNA and RNA (mRNA sequences) analyses indicated a metabolically active and diverse marine fungal communities in the corals (Amend et al. 2012). Ecological roles of endolithic fungi such as denitrification have been reported from corals (Wegley et al. 2007).

The mycocommunities, along with *Symbiodinium* and bacteria, related to the Caribbean coral *Siderastrea siderea*, taken from two depths viz., 17 and 27 m on Conch Reef in the Florida Keys, were studied by Bonthond et al. (2018) employing the high-throughput amplicon sequencing targeting ITS rRNA gene. In this study, even though they used fungal-specific primers (Nikolcheva and Bärlocher 2004), only 22.2% of the 790,398 quality-filtered ITS2 reads were fungal while the remaining belonged to other eukaryotes. Although 184 fungal OTUs were assumed to belong to fungal kingdom using the UNITE reference database in the Mothur pipeline, their additional comparison of the complete fungal OUT sequence set along the GenBank database revealed 145 OTUs have high similarity to nonfungal sequences. Hence they could relate only 39 fungal OTUs having similarity hits to fungi or Mesomycetozoa. Among these, a large number (34) of OTUs belonged to *Ascomycota*, while only 2 OTUs belonged to *Basidiomycota*, 2 to Mesomycetozoa, and 1 OUT to Entomorphthoromycota. It was also found by these workers that ITS2 similarity with sequences from GenBank was notably low, i.e., 91%, which is indicative of the presence of a higher novel diversity connected with *S. siderea*. The most abundant fungus was found most similar (76%) to sequences belonging to Lulworthiales in the class *Sordariomycetes* (Bonthond et al. 2018). While endolithic fungi (fungi thriving within the skeleton) may invade coral tissues at times of stress (Yarden 2014), the fungi also have been shown to parasitize on endolithic algae (Le Campion-Alsumard et al. 1995). Samples of *S. siderea* collected from the same reef but with differences in the depth did not show any difference in mycocommunities (Bonthond et al. 2018). These authors recommended that more conserved markers such as the SSU or LSU rRNA should be employed to characterize fungal diversity colonizing corals.

6.10 Conclusions and Future Perspectives

A list of marine fungi retrieved through culture-independent studies from different marine habitats is shown in Table 1. It could be seen from the table that (1) many fungi are known terrestrial fungi, (2) several new phylotypes are encountered from the marine habitats and they await formal recognition, and (3) *Dikarya* dominate the list of fungi of which *Ascomycota* are rich in diversity. Though the table is still not exhaustive, it could be deduced that the number and diversity of marine fungi retrieved through culture-independent studies is also low. The molecular tools are helping us to identify the ecosystem functioning and the role of fungi in marine environments in addition to the diversity.

Employing novel molecular tools to discover fungi and their ecological significance is exciting but the laborious nature, time, and cost of sophisticated machinery deter further research. Next-generation sequencing has revolutionized microbial ecology, but we are still recovering some common fungal organisms similar to terrestrial organisms. Are those studies still reflecting only a fraction of those cryptic taxa? Are these "DNA-based taxa" especially those novel phylotypes which are genetically different from known ones more ecologically and functionally important than common ubiquitous fungi? There is a dire need to assess their physiological roles in vitro, but the problem is that most of the taxa cannot be cultured. Hence novel methods must be brought forward so that these organisms can be grown under laboratory conditions to permit further experimentations and use approaches discussed by Reich and Labies (Reich and Labes 2017). The overwhelming majority of marine fungal taxa, especially from deep sea and harsh environments still remain to be described. How to translate the loner sequences (OTUs) into official taxonomic names and make them nomenclaturally valid to facilitate taxonomy is an aspect which is still in a transitional stage. The other problem is how to properly identify these novel phylotypes. At some point, one would be very tempted to label them as new species but based on what DNA sequence similarities or differences? These aspects need to be worked out. Whenever any taxonomic novelties and potential phylogenetic relationships are proposed based on environmental DNA, one should do so with extreme precautions as it could lead to a number of future problems (Hongsanan et al. 2018). So far, most DNA-based studies have used only one gene region which represents only a short fragment of the whole genome. It is common practice nowadays to use multigene phylogeny, especially those from protein-coding genes as they are more informative. How far can we go in designing primers for these regions and target a wider diversity of marine fungi? From a phylogenetic perspective, most studies have revealed that these marine organisms possibly have complex evolutionary scenarios and these need to be dealt with. In addition, given that those fungi adapt to extreme environments, the possibility that they can be exploited for medicinal, pharmaceutical, bioprospecting, and bioremediation potential should not be neglected.

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