Culturable and Molecular Diversity of Marine Fungi

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Fungi are considered terrestrial and oceans are a “fungal desert”. However, with the considerable progress made over past decades, fungi have emerged as morphologically, phylogenetically, and functionally diverse components of the marine water column. Although their communities are influenced by a plethora of environmental factors, the most influential include salinity, temperature, nutrients, and dissolved oxygen, suggesting that fungi respond to local environmental gradients.

coastal pelagic water column culturable fungi

1. Current Consensus of Culturable Diversity

Traditionally, marine fungi included higher (i.e., filamentous fungi in Basidiomycota and Ascomycota) and lower (i.e., zoosporic fungi in Chytridiomycota, Oomycetes, and Labyrinthulomycetes) fungi [1]. However, the latest update on their phylogeny has grouped them into evolved branches (Ascomycota, Basidiomycota, Blastocladiomycota, and Chytridiomycota) and basal lineages (Cryptomycota, Microsporidia, and Aphelida) [2]. The first inventory of cultured marine fungi described 209 species of higher filamentous fungi, 177 species of marine-occurring yeasts, and less than 100 species of the lower marine fungi [3]. This was followed by reports of 467 [4], 530 [5], 1112 [6], and 1257 [7] species of marine fungi. Currently, about 1900 marine fungal species, distributed across seven phyla (Aphelidiomycota, Ascomycota, Basidiomycota, Blastocladiomycota, Chytridiomycota, Mucoromycota, and Microsporidia), 22 classes, 88 orders, 226 families, and 769 genera, are documented (www.marinefungi.org, accessed on 1 May 2022). *Halosphaeriaceae* is the largest family of marine fungi, consisting of 141 species across 59 genera, and the most specious genera are *Candida* (64 species), *Aspergillus* (47 species), and *Penicillium* (39 species) [6]. The documented number (ca.1900 species) is much less than the estimated 10,000 species [4], which suggests that the oceans harbor a high fungal diversity, which is yet to be fully described.

2. Mycoplankton Diversity

2.1. Microscopic Forms and Culturable Diversity

Fungi in the water column, commonly referred to as mycoplankton or planktonic fungi, were microscopically detected as individual filaments or hyphal aggregates, yeast forms, as well as picoeukaryote-associated and phytoplankton-associated zoosporic and cryptomycota forms [8][9][10][11][12]. The size range of individual filamentous forms is generally 1–3 μm in diameter and 10–200 μm in length [8][10], but in aggregate, they could reach up to 20 μm in diameter and >50 µm in length in coastal regions. The zoosporic forms (chytrids) in the coastal waters show a typical spherical sporangium (1–10 µm diameter) and rhizoid structure over 2 µm in length [13][14]. Some of these fungal forms with different lifestyles have been found to co-exist in the coastal water column [8]. The most common form of planktonic fungi encountered is yeast forms (size < 5 µm diameter), which have been found in a wide range of oceanic regions [15][16][17][18]. On the other hand, filamentous forms have been discovered mostly in coastal and coastal-upwelling regions [8][10][18].

Using culture-based methods, researchers characterized the culturable diversity of marine fungi mostly in nutrient-rich sediments. Those studies provided evidence for the presence of fungi in sediments, including subsurface, deep-sea, and anoxic sediments of different oceanic regions (Table S1). Apart from the most common ascomycetous and basidiomycetous fungi, several novel culturable fungi were also reported from marine sediments (Figure S1). Nevertheless, a vast majority of the fungi sampled from sediments are close to, or within, clades of terrestrial fungi.

Most earlier studies revealed that a large proportion of culturable diversity in the water column comprised of yeasts, including *Rhodotorula*, *Rhodosporidium*, *Metchnikowia*, *Torulopsis*, *Kluyveromyces*, *Aureobasidium,* and *Cryptococcus* [15][16][17][18][19]. The common filamentous fungi and molds cultured from seawaters were *Aspergillus*, *Trichoderma*, *Arthrinium*, *Cladosporium, Penicillium*, *Cystobasidium*, *Exophiala*, *Graphium*, *Lecanicillium*, *Purpureocillium*, *Acremonium*, *Coniothyrium*, *Simplicillium, and Mucor* [18][20][21][22][23]. Yeasts and filamentous fungi were even reported from extreme habitats such as the hypersaline waters of Qatar, including the halo- and psychro-tolerant, red-pigmented yeast *Rhodotorula mucilaginosa*, and melanized filamentous fungi *Cladosporium* and *Alternaria* [24]. Filamentous fungi were also reported from the oil-spill-contaminated marine site where the predominant genera were found to be *Penicillium*, *Aspergillus*, and *Trichoderma* [25].

The Ascomycota and Basidiomycota are the major phyla in both water (**Figure 1**) and sediment samples. The total sequence diversity of water samples was lower than that of the sediment samples, which could be a result of the poor availability of growth substrates in the water column or a low sampling effort. Interestingly, both filamentous and yeast forms of fungi were found in the global pool of culturable fungi isolated from the water column.

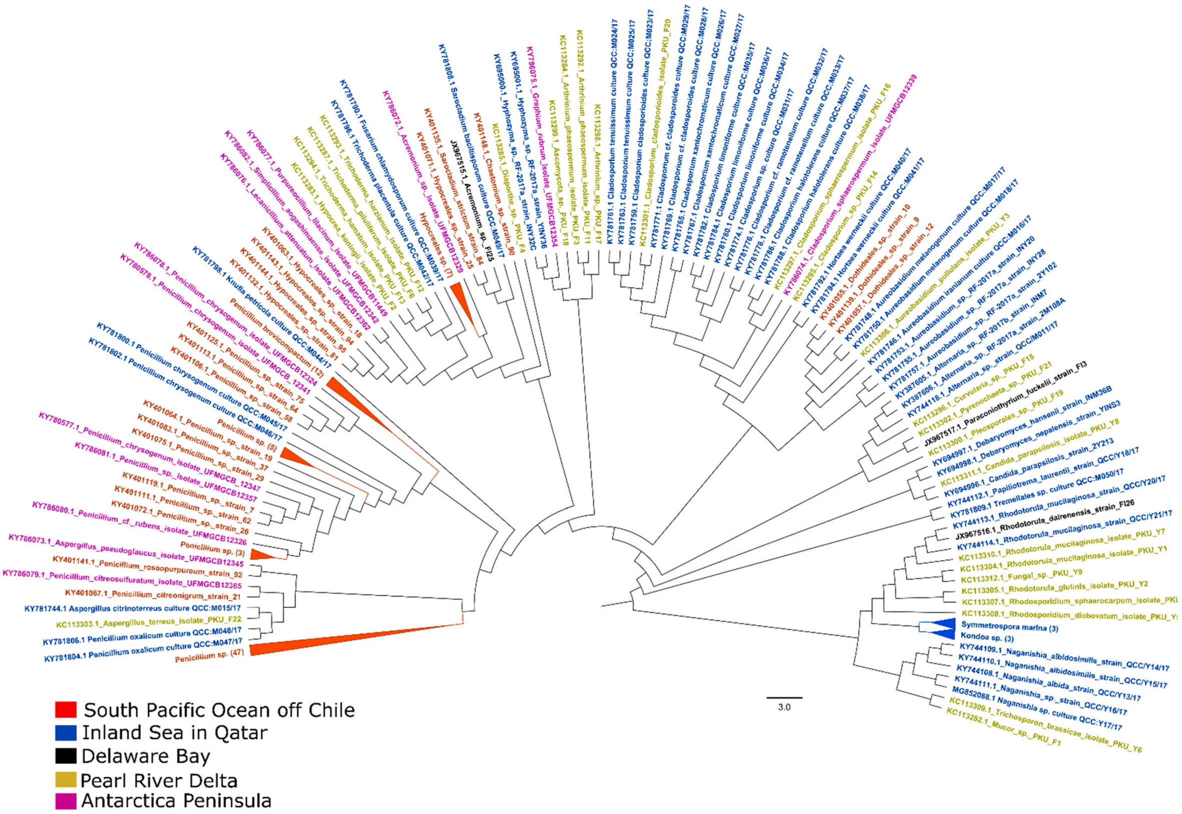

Figure 1. Maximum-likelihood (ML) tree of culturable fungi isolated from representative marine waters. A total of 192 ITS sequences of culturable fungi isolated from the water column (coastal and pelagic) across the globe were retrieved from the NCBI Nucleotide database. Sequences in the tree were aligned with MUSCLE using default settings. Phylogenetic analysis was performed using FastTree2.1 software (version 2.1, developed by Morgan N. Price, Berkeley, CA, USA) for the construction of the ML tree, which used the Shimodaira–Hasegawa test to estimate the reliability of each split in the tree. The sampling coordinates of the South Pacific Ocean off Chile [20], Inland Sea in Qatar [24], Delaware Bay [23], Pearl River Delta [21], and Antarctica Peninsula [22] are available in the corresponding publications.

Overall, culture-based studies indicate that mycoplankton diversity is limited to filamentous fungi and ascomycetous and basidiomycetous yeasts. The probable reasons for such a seemingly low diversity could be less sampling effort or nutrient-poor water column. Moreover, culture-based studies are known for their inherent biases, including the selective enrichment of a few phyla and difficulty in isolating host-associated fungi.

2.2. Molecular Diversity and Dynamics of Mycoplankton

Past culture-based studies have revealed the presence of yeasts and filamentous fungi. However, they failed to discover the zoosporic fungi in the marine water column. On the contrary, high-throughput sequencing (HTS) efforts revealed a lot more diversity, including the prevalence of zoosporic fungi, in several marine habitats [14][18][26][27][28][29]. Moreover, molecular surveys of marine eukaryotes detected fungi not only in the euphotic zone of the global ocean [30] but also in the entire water column [31]. Unfortunately, molecular surveys of eukaryotes could not provide any evidence for the extent of fungal diversity in the coastal and open-ocean waters.

Over the last decade, efforts were made to investigate the diversity of mycoplankton in both coastal and open-ocean waters (**Table 1**). The spatial analyses of planktonic fungi, based on DNA fingerprinting, could reveal the dynamics of positive fungal genotypes [10][32] and the presence of only Dikarya [33]. Especially in Hawaiian coastal waters, the exclusive presence of Dothideomycetes (four species) and dominance of Basidiomycota, including several novel phylotypes (42 species), were documented. The fungal communities displayed a noticeable spatial (lateral and vertical) diversity, with the vertical diversity profile being different for coastal and open-ocean waters [33]. Similarly, in the upwelling ecosystem off the coast of Central Chile, the fungal diversity was distinct, with a higher richness at the near-shore site than that of the off-shore site and a tendency to decrease with depth [32]. However, due to the inherent biases of fingerprinting techniques, this could only provide a limited view of fungal diversity. With the application of HTS, recent studies provide a deeper assessment of planktonic fungal communities and uncover many OTUs, classified into a wide range of phyla and several unclassified and possibly novel fungi from coastal waters (**Table 1**). Most of these studies documented the predominance of Dikarya and the prevalence of Chytridiomycota in coastal waters. However, a few studies also provided evidence for the occurrence of Cryptomycota (also known as Rozellomycota), Mucoromycota, Glomeromycota, and Neocallimastigomycota. Overall, the HTS approach provided evidence for the presence of zoosporic and basal phyla and altered the earlier notion that Dikarya fungi are exclusive inhabitants of the ocean.

Table 2. Application of high-throughput sequencing (HTS) methods in the assessment of fungal diversity of marine water columns.

Method	Target Region	Primers	Number of OTUs	Phyla	Sampling Region	Reference
454 Pyrosequencing	18S (V4)	TAReuk454FWD1 and TAReukREV3	71	Chytridiomycota and Dikarya*	European near-shore sites	[12]
454 Pyrosequencing	18S (V4)	TAReuk454FWD1 and TAReukREV3	23,263 seqs.	Chytridiomycota, Dikarya, and Cryptomycota	Arctic and temperate biomes	[34]
454 Pyrosequencing	ITS	ITS1F and ITS4	-	Coastal water: Chytrids (36%) Open ocean: Rhizophydiales (30%)	Tasman Sea, and East Australian Current	[35]
454 Pyrosequencing	ITS1	ITS1F and ITS2	3468	Dikarya, Chytridiomycota, Mucroromycotina, and Cryptomycota	Dongchong Bay, China	[36]
Illumina HiSeq	ITS1	ITS1F and ITS2	1483	Dikarya, Chytridiomycota,	Bohai Sea	[26]

Method	Target Region	Primers	Number of OTUs	Phyla	Sampling Region	Reference
				Mucoromycota, and Cryptomycota		
Illumina Hiseq	ITS	528F and 706R	91	Dikarya, Glomeromycota, Chytridiomycota, and Cryptomycota	Mariana Trench	[37]
Illumina Hiseq	ITS2	ITS3 and ITS4	8701	Dikarya, Chytridiomycota, Glomeromycota, and Rozellomycota	East China Sea water column and sediments	[29]
Illumina Hiseq	ITS2:	ITS3 and ITS4	4028	Dikarya, Chytridiomycota, and Mucoromycota	Western Pacific Ocean (Epi-Abyssopelagic zone)	[38]
Illumina MiSeq	ITS	ITS1F and ITS4	582	Dikarya and Chytridiomycota	Plymouth, UK	[27]
Illumina Miseq	ITS	ITS1F and ITS4	2796	Dikarya and Chytridiomycota, Glomeromycota, and Neocallimastigomycota	Piver's Island Coastal Observatory (PICO), USA	[28]
Ion-Torrent	LSU	LR0R and EDF360R	2305	Ascomycota, Basidiomycota, and Chytridiomycota	Piver's Island	[39]

* Dikarya: Ascomycota and Basidiomycota.

dynamics Plymouth found that Dikarya and Chytridiomycota were both dominant and dynamic, with several abundant and dominant orders [27]. Similarly, another multi-year study of fungal diversity at Piver's Island Coastal Observatory (PICO), USA, a coastal mesotrophic ocean site, showed not only the dominance of Ascomycota but also interannually indicated seasonal patterns of Basidiomycota, Chytridiomycota, and Mucoromycotina [28]. Particularly, Chytridiomycota (order Rhizophydiales) and Mucoromycotina were detected in winter and Glomeromycota in early winter and spring. In addition, the highest richness and diversity of fungi during winter and the lowest during summer were detected at PICO. Contrastingly, in the coastal waters of the Bohai Sea, Chytridiomycota (order Rhizophydiales) dominated Ascomycota and Basidiomycota in April, indicating a possible association with phytoplankton bloom [26]. Temporal changes in the community composition of fungi were also evident during different stages of algal bloom in the coastal waters of Shenzhen [36]. Several genera prevailed in the pre-bloom stage; however, only *Malassezia* dominated the onset and the peak bloom stages. *Saitoella* and *Lipomyces* gradually succeeded *Malassezia* and eventually, *Rozella* dominated the terminal stage. Notably, the bloom decline stage exhibited a higher diversity than the pre-and peak-bloom stages. Collectively, the above time series studies suggest that fungi respond to seasonality and phytoplankton dynamics, which supports the view that they are residents of the coastal water column and are most likely metabolically active biomass.

Similar to the coastal water column, several lines of evidence indicated a high molecular diversity of fungi, including several unidentified and potentially novel species, in the open-ocean water column. For example, a high diversity of fungi, with the predominance of Dikarya, was reported for the first time in waters of the open-ocean transect from the Hawaiian coast to Australia [40]. Within Ascomycota and Basidiomycota, the family Nectriaceae and genus *Malassezia,* respectively, were the most common open-ocean fungi. Unfortunately, only Dikarya were documented, probably due to the insufficient coverage of the clone libraries. However, later studies that adopted HTS additionally uncovered several basal phyla (**Table 1**). For example, a study of the epi- to abyssopelagic zone of the Western Pacific Ocean documented OTUs that were assigned to Ascomycota, Basidiomycota, Chytridiomycota, and Mucoromycota, with Ascomycota as the most dominant phylum [38]. Furthermore, the classes Sordariomycetes, Eurotiomycetes, Dothideomycetes, Saccharomycetes, and the order Malasseziales were found to dominate the fungal communities. Compared to other zones, a higher OTU richness and distinct fungal community were evident in the epipelagic zone. Yet, another study of the water column suggested an increasing number of OTUs of the ascomycetous genus *Aspergillus* from coastal to open-ocean waters [29]. Contrastingly, in the waters of the South Pacific Ocean, Chytridiomycota (order Rhizophydiales) was reported as one of the dominant fungi. The occurrence of chytrids in oceanic waters suggested that their ecological importance in open oceans was similar to that in coastal water columns [35].

In summary, most molecular surveys of planktonic fungi report the dominance of Dikarya and suggest that many fungal OTUs in both coastal and open-ocean waters are yet to be described. Furthermore, by reprocessing more than 600 HTS datasets and analyzing 4.9×10^9 sequences (4.8×10^9 shotgun metagenomic reads and 1.0×10^8 amplicon sequences), a recent study found that every fungal phylum is represented in the global marine planktonic mycobiome [41]. However, the global marine mycobiome is generally predominated by Ascomycota, Basidiomycota, and Chytridiomycota. Particularly, the coastal and open-ocean fungal communities show the dominance of ascomycetous classes, such as Sordariomycetes, Eurotiomycetes, Dothideomycetes, Saccharomycetes, and Pezizomycetes. These findings corroborate previous culture-based studies, which report the prevalence of members of classes Dothideomycetes and Sordariomycetes in mangroves and coastal waters [42][43]. These classes of fungi are suggested to have adaptations (dispersal and attachment) for sustenance in marine environments [7][44]. Contrary to ascomycetous fungi, basidiomycetous fungi appear scarce, with Ustilaginomycetes, Agaricomycetes, Exobasidiomycetes, Wallemiomycetes, and Tremellomycetes being generally detected [26][27][45]. Interestingly, molecular surveys uncover a richer diversity of basidiomycetous classes than culture-based methods, where only Exobasidiomycetes, Agaricomycetes, and Ustilaginomycetes are described [7]. Furthermore, only *Pleosporales, Dothideales, Capnodiales, Eurotiales, Malasseziales*, *Hypocreales,* and *Rhizophydiales* appear ubiquitous from molecular surveys, despite the 74 known orders of culturable marine fungi [7]. The diverse and dynamic patterns of fungi in oceanic waters similar to nutrient-rich coastal waters, which emerged from molecular surveys, raise questions about their modes of nutrition and roles in oligotrophic conditions. More importantly, the differences in the abundances evident across space and time support the proposition that planktonic fungi are viable and responsive to environmental changes.

3. Environmental Drivers of Mycoplankton Diversity

Environmental factors are known to play an important role in regulating microbial community structure and diversity [46][47]. In terrestrial realms, fungi have unique requirements, and species segregate along environmental gradients [48][49]. Likewise, several lines of evidence suggest the role of environmental factors in shaping the fungal diversity of the water column (**Table 2**). For example, phytoplankton and primary production, nutrients, salinity, organic matter, seasonality, DO, and temperature have been reported as the key factors that govern mycoplankton diversity. In parallel, it has been suggested that riverine inputs of fungi might be responsible for a higher fungal richness in coastal sites than that in off-shore sites [32]. The other less-reported environmental factors such as ocean currents, hydrographic conditions, depth, DO, COD, nitrate, flow, conductivity, insolation, pH, DIC, oxygen concentration, riverine inputs, tidal actions, dispersal, and biological interactions were also shown to influence fungal communities of seawater columns [8][28][29][35][36][45][50][51]. These environmental associations of mycoplankton can potentially have several ecological implications, including spatiotemporal variations, organic matter decomposition, niche differentiation, host–parasite interactions, and the regulation of phytoplankton bloom (**Table 2**), which are yet to be fully established. Undoubtedly, the associations of fungi with a multitude of environmental factors, evident from the above studies, suggest that fungi respond to environmental gradients, and their communities can be shaped by local conditions. Although significant differences among oceanographic regions were identified, latitudinal gradients of the richness and diversity of marine fungi were not observed [41]. This was unlike the pattern observed for planktonic marine bacteria [52]. Perhaps with the availability of more HTS datasets, it would be essential to expand the collection of reference loci and genomes to determine the typical environmental drivers of planktonic fungi [41].

Table 2. Factors affecting fungal assemblages in water columns of different marine habitats and their ecological implication.

Strongly Correlated Factors	Region	Ecological Implication	Reference
Chlorophyll *a*, temperature, phytoplankton biomass	Hawaiian coast	Spatial variations	[33]
Phytoplankton, nutrients (nitrate, phosphate, nitrite), and location	West Pacific Warm Pool	Organic matter decomposition	[40]
Chlorophyll *a*, organic matter, and warm conditions	Upwelling ecosystem off the coast of Central Chile	Organic matter decomposition	[10]
High nitrogen availability, reduced salinity, temperature, phytoplankton, organic matter	Coastal station off Plymouth	Temporal variations, niche differentiation, and host–parasite interactions	[27]
Salinity, temperature, oxygen, and nutrients	Tasman Sea, East Tasman Sea, and East Australian Current	Biogeochemical cycling and spatial variations	[35]
Depth, dissolved oxygen, and nitrate	Across the globe	Local environmental conditions govern assemblages	[50]
Temperature, salinity, nitrate, nitrite, ammonium, and phosphate	Coastal region Dongchong Bay	Fungi regulate phytoplankton bloom	[36]

Strongly Correlated Factors	Region	Ecological Implication	Reference
Temperature, depth, salinity, riverine input, location	Upwelling ecosystem off the coast of Central Chile	Organic matter decomposition	[32]
Dissolved nitrogen, particulate phosphorous silicate, pH, salinity, chlorophyll *a*	Coastal water column	Spatial variations	[26]
Dissolved oxygen and depth	East China Sea water and sediments	Ocean currents govern assemblages	[29]
Temperature, pH, insolation, dissolved inorganic carbon	Waters of Piver's Island Coastal Observatory (PICO)	Temporal variations	[28]
Depth, temperature, and dissolved oxygen	Epi- to abyssopelagic zones of the Western Pacific Ocean	Distinct zonation of assemblages in the water column	[38]
Salinity	Baltic Sea	Salinity threshold separates assemblages	[53]

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