

Entry

Marine Fungi: Opportunities and Challenges

Micael F. M. Gonçalves , Ana C. Esteves  and Artur Alves 

CESAM, Department of Biology, University of Aveiro, 3810-193 Aveiro, Portugal; acesteves@ua.pt (A.C.E.); artur.alves@ua.pt (A.A.)

* Correspondence: mfm@ua.pt

Definition: Marine fungi play a crucial role in energy flow and nutrient recycling, mediating the cycling of dissolved organic matter in marine environments. However, despite being a prolific group of organisms, marine fungi have been largely neglected for a long time. Besides their importance in the marine food web, marine fungi represent an active source of natural products. Over the last years, researchers have focused on studying marine organisms to discover new metabolites with antibacterial, antiviral, and anticancer activities. Moreover, with the advances in high-throughput sequencing technologies and mass spectrometry techniques, genomic and metabolomic approaches have revealed to be of paramount importance in natural products discovery. The marine mycobiome includes many organisms still to be identified, and the ones already known are still underutilized in biotechnological applications. For this reason, it is undeniable that exploring the marine mycobiome including new habitats and substrates, even those of remote access, is fundamental for describing the true magnitude of the Earth's mycobiome.

Keywords: marine fungi; diversity; taxonomy; biological activities; metabolomics; genomics



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1. Introduction

Fungi are ubiquitous organisms widely distributed in ecosystems, including marine environments [1–3]. Marine environments represent the last frontier of biodiversity. Even though marine habitats account for 70% of the surface of the planet, they still remain biologically unexplored. Fungi are key players in terrestrial and marine environments representing a substantial proportion of the microbial diversity on Earth [1].

Over time, different definitions of marine fungi have been used. Marine fungi were originally defined based on their physiological characteristics, such as the requirement of more than 30% salinity to grow [4]. The first attempt to define ‘marine fungi’ and still the most quoted definition was given by Kohlmeyer and Kohlmeyer [5]. These authors restricted ‘marine fungi’ to two ecological groups: obligate and facultative marine fungi. Obligate marine fungi are those that grow and sporulate exclusively in a marine or estuarine habitat; facultative marine fungi are those from freshwater or terrestrial milieus, able to grow and sporulate in marine environments. However, this distinction is not always easy nor clear to establish, and it is somehow controversial. Later, Jones et al. [6] labelled ‘obligate’ marine fungi as those isolated from submerged substrates or sediments from marine environments. The term “marine-derived fungi” has been extensively used in the field of natural product chemistry [7]. Recently, Pang et al. [8] reviewed the use of the terms “marine fungi” and “marine-derived fungi” and proposed a wide-ranging definition. These authors replaced Kohlmeyers’ definition by a broader concept. From this point forward, marine fungi are defined as any fungus able to: (i) grow and/or sporulate (on substrata) in marine environments; (ii) form symbiotic relationships with other marine organisms; or (iii) adapt and evolve or be metabolically active in marine environments.

In the past, marine fungi were viewed as an exotic group, relatively species-poor, with low abundance. Over the last two decades the use of culture-independent approaches and, more recently, of next-generation sequencing methods have started to disclose a

considerable hidden fungal diversity from a wide range of environments [9]. In this respect, only recently, marine fungi have attracted attention and are yet to find a prominent place in biotechnology [3].

Marine fungi are a biochemically diverse group of organisms representing a promising source of novel bioactive natural compounds. The secondary metabolites produced by marine fungi include terpenes, steroids, polyketides, peptides, alkaloids, and polysaccharides. These metabolites are mainly associated with antimicrobial, anticancer, antiviral, antioxidant, and anti-inflammatory activities [3,10]. Considering this wide range of activities, these metabolites hold great promise since they can be used for drug discovery and medical, pharmaceutical, agriculture and cosmetic applications [3]. Besides being a source of bioactive compounds, marine fungi are also recognized for their metabolic capacities for bioremediation. This capacity aids, for instance, in the degradation of recalcitrant cell wall compounds (marine fungi express catalases, laccases, peroxidases) and environmental contaminants (e.g., toxic pollutants and microplastics) [11].

2. Origin and Diversity of Marine Fungi

The origin of fungi remains unclear. Fungi are presumed to have evolved in the late Proterozoic, about 900–570 million years ago (mya) (Figure 1) [12–15]. However, according to the Ongeluk fossils, the fungal clade is considerably two to three times older than current age estimates [16]. The basalt from the Palaeoproterozoic Ongeluk Formation in South Africa suggests that fungi have inhabited submarine volcanoes approximately 2400 mya. Most of the species described in marine ecosystems have relations to terrestrial species. In fact, fungi transitioned several times from marine to terrestrial environments, and vice versa [17]. During evolution in the Precambrian (from the formation of Earth about 4600 mya to the beginning of the Cambrian Period, about 541 mya), cooling events and marine salinity decrease, resulted in the increase of dissolved oxygen, allowing the transition of non-marine early fungi to marine niches [18]. The existence of a terrestrial runoff or different migration trajectories from terrestrial to marine environment [19] was accompanied by several adaptations in response to these environmental changes [20]. However, the origin of marine fungi is still discussed.

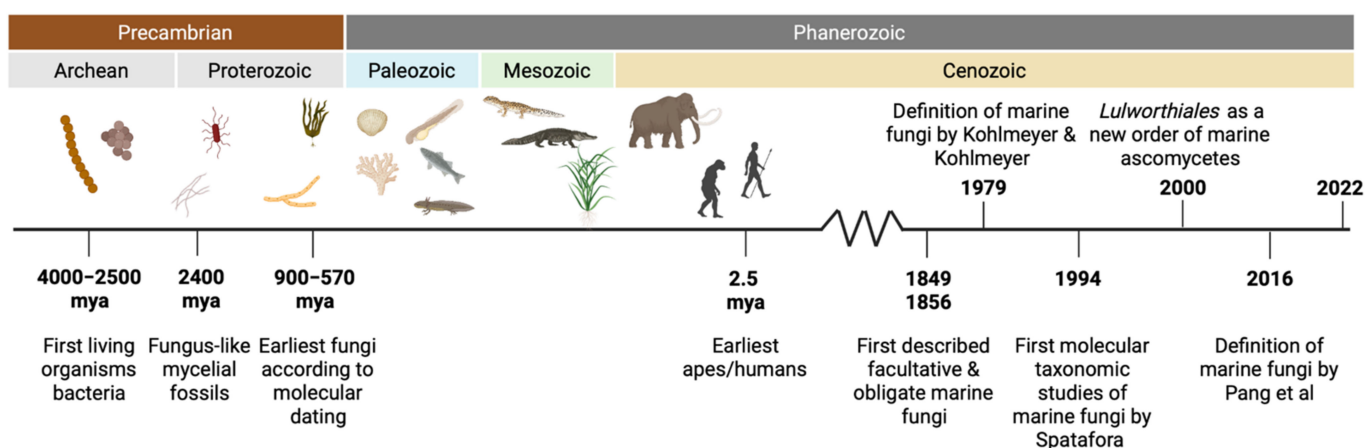


Figure 1. Timeline showing important events concerning marine fungi taxonomy. Mya: millions of years ago.

2.1. Challenges and Adaptions

Fungi in the sea face substantial challenges compared to the terrestrial compartment. Figure 2 shows some of these challenges, and the molecular and morphological adaptations of fungi to thrive in the marine environment. High levels of salinity lead to osmotic and ionic stress. However, fungi can control their turgor through a conserved pathway known as the high-osmolarity-glycerol (HOG) signaling pathway. This pathway is responsible for

the regulation of the salt efflux pumps and the production of osmolytes compatible with cellular functions [21]. Another evident molecular adaptation is the production of gels and slimes by lignicolous marine fungi (colonizers of driftwood or submerged wood) which may retain secreted enzymes at the substrate [21]. Additionally, a range of morphological adaptations in fungal structures and in the spore-dispersion strategies contributes for the success of marine fungi (Figure 2). One example of morphological-adapted fungi are chytrids (Chytridiomycota), also known as zoosporic true fungi, that depend on their zoospores for dispersal in water [22]. Although chytrids are one of the early diverging fungal lineages [22], and are the most common fungal group in marine habitats [23–26], there is no sufficient evidence to show that the ancestral chytrids were marine [27]. This gap is largely due to the lack of molecular data in Chytridiomycota [22].

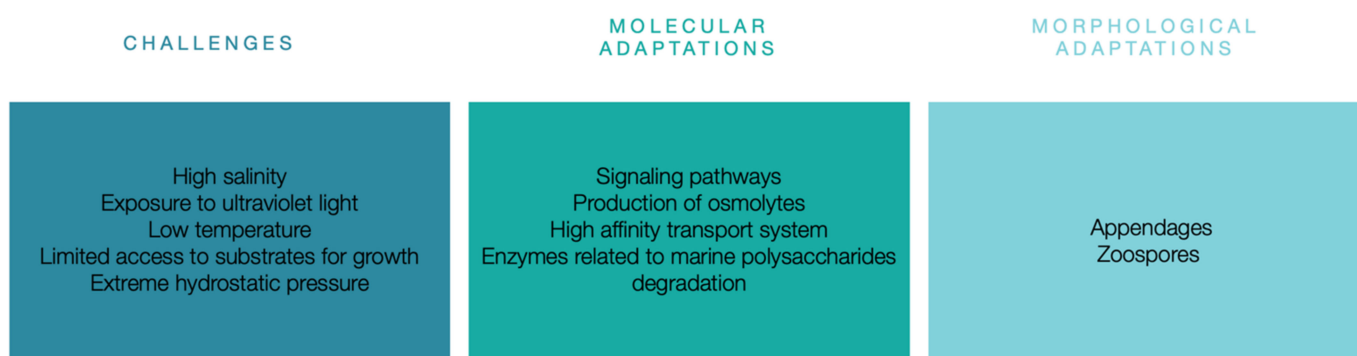


Figure 2. Challenges and adaptations of marine fungi to the marine environment.

2.2. Diversity

Recent advances in high throughput sequencing technologies stimulated a new wave of research in marine mycology, revealing an increase of fungal diversity in the marine realm. However, using culture dependent methods, the most common taxa which have been recovered are predominantly allied to the phyla *Ascomycota* and *Basidiomycota*, to which more than 90% of the total described marine species belong [22]. In marine environments, the phylum *Ascomycota* is represented by the subphyla *Pezizomycotina*, *Saccharomycotina* and *Taphrinomycotina*, while *Basidiomycota* is represented by *Agaricomycotina*, *Pucciniomycotina* and *Ustilaginomycotina* [1,28].

The subphylum *Pezizomycotina*, includes the classes *Dothideomycetes*, *Eurotiomycetes* and *Sordariomycetes*, which comprise the highest number of species described [7]. In this context, some of these classes include many marine hyphomycetes, a diverse ecological group that contains species able to alternate their life cycle between aquatic and terrestrial habitats. This ecological group is often associated with leaf litter, driftwood, water, algae, marine animals, and halophytes. Marine hyphomycetes have probably also evolved from terrestrial fungi with some morphological adaptations to colonize marine habitats. Yet, attempts to taxonomically resolve several taxa *incertae sedis* in these subphyla are currently ongoing. Additionally, yeast-like fungi within the phyla *Ascomycota* and *Basidiomycota* have been found in marine environments [1].

The total fungal diversity has been the subject of much discussion. It is estimated that the number of fungal species ranges from 1.5 to 5.1 million [29,30]. Marine fungi represent less than 1% of the known species [10,29,30], thus remaining a poorly characterized group. It has been estimated that the number of marine fungi range from 10,000 to 12,500 species [29], although more recently Garzoli et al. [31] suggested that up to 1 million species are yet to be discovered. The most up-to-date number of described marine fungal species until February 2021 is only 1901, distributed in 769 genera, 226 families, 88 orders, 22 classes and seven phyla into *Aphelidiomycota*, *Ascomycota*, *Basidiomycota*, *Blastocladiomycota*, *Chytridiomycota*, *Mortierellomycota* and *Mucoromycota* (Figure 3, www.marinefungi.org (accessed on 9 January

2022) [32]). This estimate includes yeasts and filamentous fungi and other basal fungal lineages.

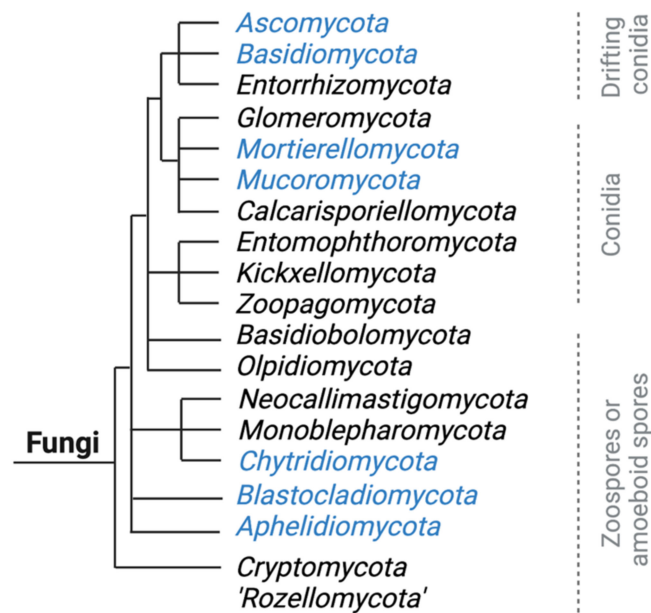


Figure 3. Fungal tree of life including the updated phylum-level classification of fungi, illustrating the morphological characteristics of the spores that are adapted for dispersal in marine habitats. Phyla which contain marine fungal lineages are depicted in blue.

Over the last two decades, attempts to understand the diversity and function of fungi in marine habitats has also been made through culture-independent approaches [23,26,33]. More recently, next-generation sequencing methods have been used to disclose a considerable number of fungal species from a wide range of marine environments [23,34]. However, from the known marine fungal species, some of them have a limited number of ITS (internal transcribed spacer region) sequences and are mostly identified based on the conserved 28S or 18S rRNA genes (large and small subunits of ribosomal RNA, respectively). The analysis of these conserved regions is not always reliable to delimitate fungal species. Therefore, multi-gene phylogenetic analyses allied with morphological characteristics are crucial for a correct species identification. Furthermore, genome sequencing approaches are critical to understand the evolution of fungi particularly those associated with early diverging lineages [22].

3. Diversity of Marine Fungi Habitats and Their Ecological Roles

Fungi are key players in terrestrial and marine environments representing a substantial proportion of the microbial diversity on Earth [22]. However, even though marine habitats account for 70% of the surface of the planet, they remain biologically unexplored. This is especially evident when considering microbial life in these environments, most specifically its fungal component. Despite many difficulties to isolate fungal species from marine environments, researchers continue to make progresses towards uncovering marine fungal species by exploring new habitats. Marine fungi have been recovered from organic and inorganic substrata (Figure 4): mangrove plants, macroalgae, seagrass, coral reef, drift- and submerged wood, sponges, sea ice, sea garbage, and coastal and open-ocean water columns [35–37]. As mentioned, using high-throughput sequencing technologies, researchers have also found marine fungal species on deep-sea and benthic sediments, hydrothermal vents, oxygen-deficient environments and in global surface waters [23,26,33]. Table 1 summarizes studies (from 2015) of marine fungi diversity covering different substrata.

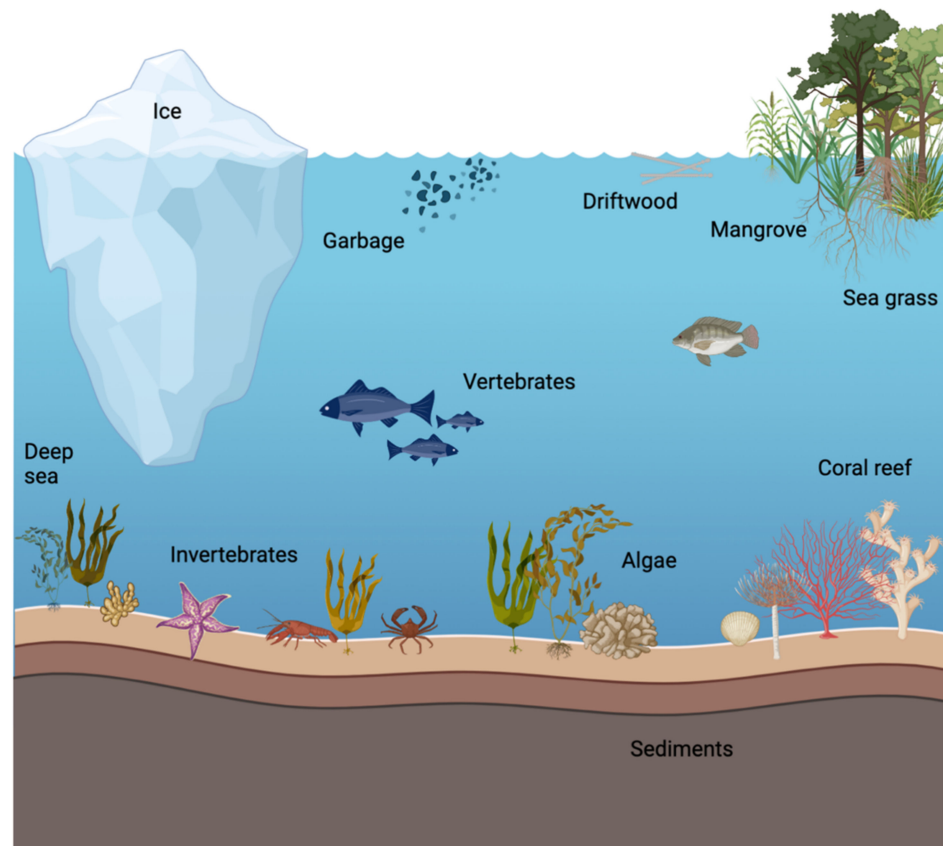


Figure 4. Diversity of marine fungal habitats. The figure was created with BioRender.com (accessed on 9 January 2022) [38].

Table 1. Substrata from which marine fungi have been identified. Only research published after 2015 were included.

Substrata	Studies
Algae	[31,35,39–56]
Corals	[37,57,58]
Invertebrates	[59–61]
Mangroves	[2,62–73]
Ocean crust	[74–77]
Plastic debris	[78–89]
Salt marsh plants	[81–83]
Sandy beaches	[84,85]
Seagrasses and seaweeds	[51–53,55,86–98]
Sea and ice water	[23–25,42,44,45,82,99–111]
Sediments or soil	[23,26,46,99–101,112–131]
Sponges	[40,44,58,100,132–138]
Wood (drift or submerged)	[42,44,46,64,114,139–148]

Although marine fungi are ubiquitous, some fungal species are found only in certain geographic regions, such as the tropics, subtropics, temperate or polar waters [149], or in specific substrates (Table 1).

To sustain the biodiversity and marine ecosystem functioning, the energy fixed by primary photosynthetic producers in the ocean is controlled to various trophic levels [22]. Microorganisms play a key role in nutrient recycling and in the regulation of energy flow in marine ecosystems [22]. From these microorganisms, marine fungi are one of the major components in marine food webs and occur as saprobes, mutualists, endobionts and parasites [22]. As saprobes, fungi can colonize and transform the organic matter originated from plants, algae, and animals into valuable nutrients. As mutualists, fungi can be associated to organisms such as sponges or protozoans, where both individuals benefit. As endobionts, fungi can provide energy to the host or even be commensals benefiting from host protection. As parasites of phytoplankton, macrophytes, algae, and animals' marine fungi can cause leaching of dissolved organic matter and destruction of their host populations [22]. *Cryptomycota* and *Chytridiomycota* are considered as early diverging fungal lineages, displaying physiological adaptations for inhabiting aquatic ecosystems, and contributing to marine food webs [150]. For example, Senga et al. [151] showed that parasitic fungi, such as chytrids (*Chytridiomycota*), utilize living diatoms efficiently. Additionally, chytrids can change the quality and quantity of algal dissolved organic matter, thus influencing higher trophic levels. Therefore, by virtue of chytrids' interactions with diverse living or dead organisms, marine fungi can transform and incorporate organic matter into the food web regulating the energy flow in marine ecosystems [1]. Similarly, members of *Cryptomycota* are parasitic zoosporic fungi exhibiting a similar life cycle to chytrids (e.g., free-swimming stage), and are typically found in freshwater, soil and in some marine habitats. In addition to chytrids, *Cryptomycota* fungi are dynamic players on microbial food webs and can parasitize many phytoplankton species such as diatoms, green algae, and dinoflagellates [152]. Despite the potential role of *Chytridiomycota* and *Cryptomycota* as mycopesticide formulations, such is still unexplored, mainly due to cultivation difficulties.

4. A Source of Potential Bioactive Compounds

The identification of novel natural products appears to be a robust approach to the approval of new drugs and therapies [34]. Therefore, there is the need to create new, safer, eco-friendly, and sustainable substances as alternatives to chemically synthesized products. Natural products are pharmacologically or biologically active chemical compounds or molecules (often below 1000 Da), found in nature and produced by a biological source [34]. Additionally, high molecular weight compounds such as proteins and polysaccharides also may show therapeutics potential. Referred to as secondary metabolites, these compounds are not directly involved in any primary function related to growth, development, and reproduction of an organism [153]. However, they are more commonly associated with organism's survival prospects, such as, defense, competition, and communication [154].

Penicillin, the first natural product antibiotic, produced by the fungus *Penicillium notatum* (syn. *P. rubens* and previously known as *P. chrysogenum*) was discovered by Sir Alexander Fleming in 1928 [155]. This event fueled the exploration of microorganisms as sources for antibiotics, initiating the golden era for the discovery of other natural products from fungi. Some studies were focused on an intensive exploration of new natural products with biologically active properties, from marine sources. Initially, the study of marine natural products was limited to organisms easy to collect such as corals and sponges. For example, the toxin tedanolide was isolated from the sponge *Tedania ignis*, while prostaglandins were isolated from the Caribbean Sea whip *Plexaura homomalla* [156]. Moreover, many natural products may also be synthesized by marine microorganisms [157]. In this respect and considering that only about 5% of the world's fungal taxa have been described, marine fungi have recently attracted attention for being a plentiful source for new chemical entities. However, marine fungi still represent an underexplored group, and researchers are yet to discover their full biotechnological potential [158–161].

In 1945, the first group of natural products from marine fungi was described as cephalosporins, a class of β -lactam antibiotics isolated from the *Acremonium chrysogenum* (previously known as *Cephalosporium chrysogenum*) [162]. Later, in 1977, Okutani identified

gliotoxin as a new type of the antibiotic diketopiperazine isolated from a marine fungus *Aspergillus* sp. obtained from deep-sea sediments [163]. Thenceforward, the number of antibiotic compounds isolated from marine fungi was rapidly increasing [162]. More than 3500 marine fungal secondary metabolites have already been reported [164], but a high number surely remains untapped. Such may be related to the unexploited marine ecological niches and their almost ubiquitous distribution, as well as to the high number of silent biosynthetic clusters in the genomes [34,159]. Figure 5 shows some classes of metabolites produced by marine fungi and their associated biological activities.



Figure 5. Diversity of metabolites' classes produced by marine fungi and their biological activities with potential applications.

Most of the research on secondary metabolites of marine fungi have been focused on a few genera: *Penicillium*, *Aspergillus*, *Fusarium*, and *Cladosporium* [60,159]. However, studies of natural products from marine fungi continue to increase and have been expanded to other genera [159]. These studies have demonstrated that marine fungi represent a tremendous source of secondary metabolites for drug discovery [157]. The number of studies published increases every year, with most of them coming from species associated with different substrata and new habitats. Most of these metabolites are derivatives of those found on terrestrial fungi but hold significant differences in their biological activities (sometimes more effective and more specific).

Currently, 14 marine natural products are approved as drugs and more than 30 natural products are in different phases of clinical trials [165]. Despite the large number of new natural products from marine fungi, Plinabulin (diketopiperazine class) is the only one isolated from a marine fungus (*Aspergillus* sp.) that is currently under clinical trials by BeyondSpring Pharmaceuticals [165]. This compound is currently in the late-stage of a world-wide phase III clinical trial for anticancer therapy of non-small cell lung cancer and for the reduction of chemotherapy-induced neutropenia [166]. Despite the research efforts towards marine fungi, most studies are focused only on the description of new natural compounds with in vitro biological activities. A simplified representation of the fungal marine natural product drug discovery pipeline is shown in Figure 6. Therefore, after the drug discovery process, efficient approaches to produce enough quantities of the interest compound for clinical trials need to be implemented. Silber et al. [162] already listed different biotechnological approaches in all stages of the discovery-to-development of antibiotics from marine fungi.

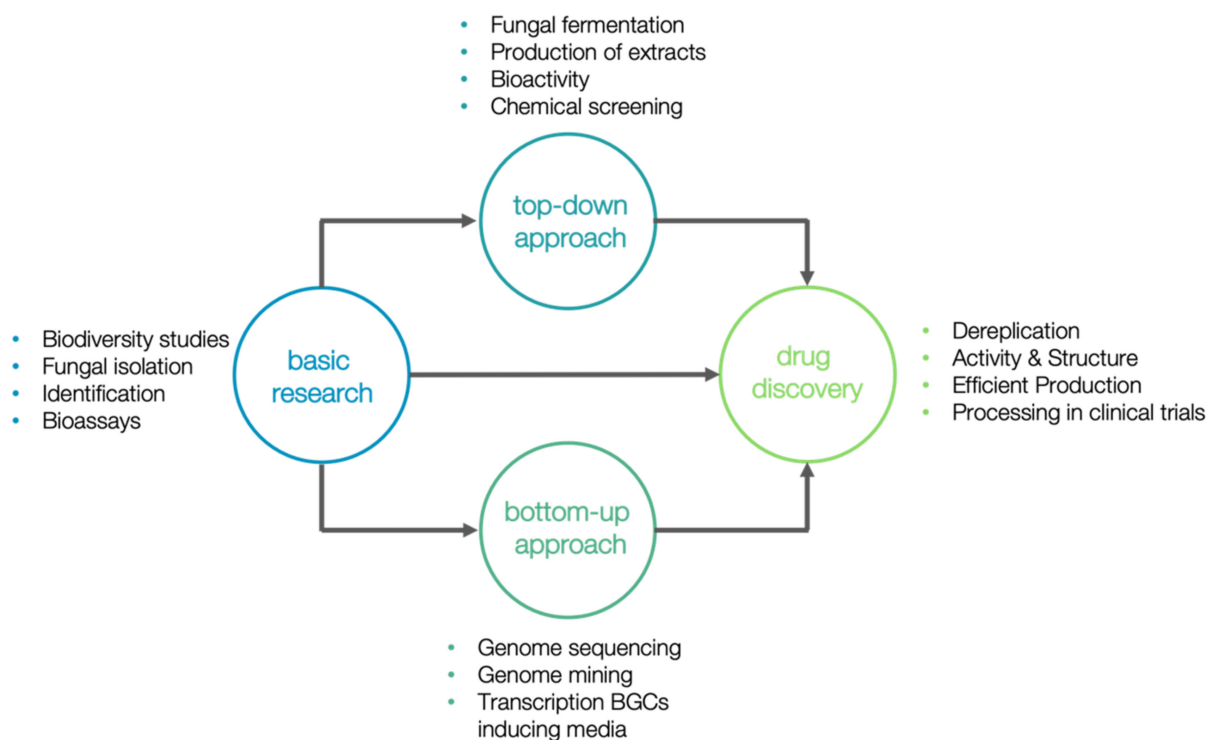


Figure 6. General representation of the pipeline for drug discovery in marine fungi.

4.1. Metabolomics Approaches

Omics (genomic, transcriptomic, proteomic, and metabolomic approaches) have become popular due to the advances in high-throughput sequencing technologies, bioinformatic tools and mass spectrometry techniques. Metabolomic approaches have embraced the discovery of natural products [34]. Mass spectrometry (MS) is a highly sensitive analytical tool used for the identification and quantification of metabolites [167]. Analytical techniques (e.g., nuclear magnetic resonance (NMR)) and several types of mass analyzers are used for metabolomic studies, such as capillary electrophoresis mass spectrometry (CE-MS), gas chromatography mass spectrometry (GC-MS), liquid chromatography mass spectrometry (LC-MS), and matrix-assisted laser desorption/ionization mass spectrometry (MALDI-MS).

Mass spectrometry has a significantly higher sensitivity and resolution than NMR [168], that requires a relatively simple sample preparation step and generates large amounts of data that remain challenging to handle. Despite MS-based approaches being able to quantify the metabolic profile in different sample matrices, the metabolites' capacity to ionize in a particular analyzer deeply influences data. MS-based approaches have become popular both in targeted and untargeted studies, due to their potential to identify an array of diverse metabolites by an organism [169,170]. On the other hand, NMR-based approaches have advantages compared to MS. NMR is quantitative, highly reproducible, and has the possibility of not using standards to elucidate the compounds [168]. NMR is also a non-destructive technique, which allows MS-based approaches to be used as complementary. The use of these two approaches is information-rich, becoming more popular for the discovery of new metabolites. Table 2 sums up the recent studies of marine fungi's metabolome using different techniques. The most used techniques are GC-MS and LC-MS [171]. GC-MS separates a mixture of compounds according to their compound's volatility/molecular weight, while LC-MS separates according to compound polarity or hydrophobicity for example. However, LC-MS represents the most versatile approach for profiling extracts [172].

Metabolomics has become an essential analytical tool for the drug discovery process. Nonetheless, as metabolomics of marine fungi is still in its infancy, the identification of marine natural products, remains challenging [160]. Untargeted metabolomics generate

massive data sets. However, analysis is time consuming, due to the lack of user-friendly bioinformatic annotation pipeline tools and open access data repositories. Furthermore, the prediction of biological activity of the secondary metabolites identified is a challenging task—if not impossible—because small structural differences in the molecules may lead to different bioactivities [34].

Recently, Rotter et al. [173] listed an overview of databases useful for the marine biotechnology pipelines. Briefly, the major MS/MS data organization tool and open access is the Global Natural Products Social (GNPS) Molecular Networking. However, most of the specific databases that already contain some marine natural products from fungi, such as Marine Lit and Dictionary of Natural Products, are not open access. Recently, Van Santen et al. [174] developed the Natural Products Atlas, an open access database for microbial natural products discovery. In any case, at our knowledge, there is no marine fungi-specific database combining mass spectra data.

Table 2. Different MS techniques used on marine fungi metabolomics.

Technique	Species	Host/Habitat	Studies
GC-MS	<i>Grammothele fuligo</i> , <i>Rigidoporus vinctus</i> , <i>Cystobasidium minutum</i> , <i>Candida railenensis</i> , <i>Pichia kudriavzevii</i> , <i>Aspergillus</i> sp., <i>Penicillium chrysogenum</i>	Algae	[175–177]
GC-MS	<i>Emericella</i> sp., <i>Aspergillus unguis</i>	Sponge	[178,179]
GC-MS	<i>Aspergillus versicolor</i>	Sediments	[180]
GC-MS	<i>Aspergillus flavus</i> , <i>Penicillium echinulatum</i> , <i>Microascus croci</i> , <i>Penicillium purpurogenum</i>	Seaweed	[181]
GC-MS/LC-MS	<i>Penicillium brevicompactum</i>	Anemone	[182]
GC-MS/LC-MS	<i>Botryosphaeria</i> sp., <i>Piriformospora indica</i>	Algae	[183,184]
GC-MS/NMR	<i>Aspergillus sydowii</i>	Sponge	[185]
LC-MS	<i>Trichoderma reesi</i> , <i>Trichoderma atroviride</i> , <i>Aspergillus welwitschiae</i>	Sponge	[186,187]
LC-MS	<i>Aspergillus allahabadii</i> , <i>Aspergillus ochraceopetaliformis</i> , <i>Aspergillus</i> sp., <i>Penicillium</i> sp.	Sediments	[188–190]
LC-MS	<i>A. sydowii</i> , <i>P. chrysogenum</i>	Corals	[191]
LC-MS	<i>Aspergillus affinis</i> , <i>A. sydowii</i>	Sea water	[169,192]
LC-MS	<i>Emericellopsis cladophorae</i>	Algae	[170]
LC-MS	<i>Cladosporium cladosporioides</i>	Seaweed	[193]
LC-MS/NMR	<i>Oidiodendron griseum</i> , <i>Aspergillus flavipes</i>	Sediments	[194,195]

4.2. Genomic Approaches

Marine fungal genomes' sequencing adds more in-depth information to search for natural products from these microorganisms. The increasing number of fungal genomes sequenced has revealed that fungi contain an enormous potential for secondary metabolite production. Biosynthetic gene clusters (BGCs) can be involved in different biosynthetic pathways, resulting in a variety of possible final products [117]. However, most of these BGCs have not been linked to their corresponding natural products [34]. So far, only approximately 4000 fungal species have completed or ongoing genome projects [196], with more than 8000 genomes available. The shortage of marine fungal genomes in public databases, such as Genome–NCBI (National Center for Biotechnology Information) (<https://www.ncbi.nlm.nih.gov/> (accessed on 9 January 2022) [197]) and JGI Genome Portal (Joint Genome Institute) (<https://genome.jgi.doe.gov/portal/> (accessed on 9 January 2022) [198]), impairs the fast identification of BGCs, thus hampering the discovery of natural products from these microorganisms. Table 3 shows an overview of the marine fungal genomes sequenced that are deposited at Genome–NCBI and at JGI databases. *Ascomycota* is

the phylum that contains more sequenced marine fungal genomes (21 isolates of 12 different families).

The ‘unculturable’ fungal species represent one of the major problems and challenges for marine mycology. Isolation into pure culture remains the gold standard for the identification, description, and genome sequencing of new marine fungal species. Another challenge for marine natural products identification is, as mentioned before, that BGCs may remain silent under laboratory culture conditions. To overcome this, different methods have been developed to ‘awaken’ or stimulate the expression of silent genes. Among these methods to induce the production of BGC coded compounds, we can highlight: (1) the use of epigenetic modifiers of natural or chemical elicitors (microbial cells components, microbial lysates, or non-biological origin compounds) and (2) the co-cultivation with other species [199]. These strategies are known as OSMAC (One Strain Many Compounds) approach [200]. OSMAC makes use of altering cultivation parameters or adding elicitors to activate silent and poorly expressed BGCs in microorganisms to induce the expression of more natural products [201].

Table 3. Overview of the marine fungal genomes sequenced.

Family or Class	Species	Strain	Host/Substrate	NCBI Accession Number	JGI Project ID
<i>Aspergillaceae</i>	<i>A. affinis</i>	CMG 70	Sea water	JAGXNN000000000	-
	<i>Aspergillus flocculosus</i>	CBS 112785	Saltern	-	1052366
<i>Bionectriaceae</i>	<i>Emericellopsis maritima</i>	TS7	Sponge	JAFMPH000000000	1092660
	<i>E. cladophorae</i>	MUM 19.33	<i>Cladophora</i> sp.	JAGIXG000000000	-
<i>Chaetomiaceae</i>	<i>Achaetomium macrosporum</i>	CBS 532.94	Mangrove mud	-	1151607
	<i>Trichocladium antarcticum</i>	CBS 123565	Antarctic lichen	-	1018949
<i>Dothideomycetes</i>	<i>Lineolata rhizophorae</i>	ATCC 16933	Marine environment	JAAEJC000000000	1051209
<i>Halojulellaceae</i>	<i>Halojulella avicenniae</i>	ATCC 66911	Roots of <i>Avicennia</i>	-	1042899
<i>Halosphaeriaceae</i>	<i>Corollospora maritima</i>	CBS 119819	Marine detritus	-	1024020
<i>Lulworthiaceae</i>	<i>Lindra thalassiae</i>	JK4322	<i>Thalassia</i> sp.	-	1070663
<i>Pleosporaceae</i>	<i>Decorospora gaudefroyi</i>	CBS 332.63	<i>Salicornia</i> sp.	JAADKE000000000	1032354
	<i>Paradendryphiella salina</i>	CBS 112865	<i>Fucus serratus</i>	CAAAGB000000000	-
<i>Sporormiaceae</i>	<i>Westerdykella ornata</i>	CBS 379.55	Mangrove mud	JAAEJA000000000	1019763
<i>Teratosphaeriaceae</i>	<i>Hortaea werneckii</i>	MC848	Sea water	PRJNA641248 PRJNA428320	-
		EXF-2788	Hypersaline water		
		MC873	Sea water		
		EXF-120	Hypersaline water		
<i>Torpedosporaceae</i>	<i>Torpedospora radiata</i>	EXF-10513	Deep sea water	-	1019473
		JK5252C	Woody debris		
<i>Trichocomaceae</i>	<i>Penicillium antarcticum</i>	<i>Eurotium rubrum</i>	Dead Sea brine	-	1078839
		IBT 31811	Seaweed	MDYN000000000	1188177
<i>Atheliaceae</i>	<i>Digitatispora marina</i>	008cD1.1	Driftwood	-	1081701
<i>Chytridiaceae</i>	<i>Chytridium lagenaria</i>	Arg66	Algae	-	1098839

5. Conclusions and Prospects

Marine fungi have been studied since the first record of a marine species. However, despite their widespread distribution and abundance, marine fungi have been largely neglected. Since isolation into pure culture remains the gold standard for discovery and description of novel taxa, the use of different methods for isolation, culture media, incubation temperatures, and damp/moist chamber incubation, may contribute for the increase

of fungal diversity. Environmental alterations, such as the seasonality could also yield different diversity. However, climate changes can also have a major impact on the food web dynamics in the marine fungal communities as well as alter their structure causing unpredictable consequences. It is widely accepted that the climate is changing at a global level, and it is also essential to understand these impacts on marine fungi dynamics.

It is recognized that marine fungi represent a potential source of secondary metabolites for drug discovery. Although genome-wide sequencing allows the detection of BGCs involved in different biosynthetic pathways in marine fungi, there is still limited of genomes available. Therefore, it is crucial to broaden this field of investigation into underexplored marine taxa, to infer about the lifestyles, ecological roles, evolutionary history, and regulatory mechanisms.

Despite the research motivation, a holistic and integrated approach is necessary to ensure the success of any conservation management strategy or economic use of marine fungi. Therefore, all fungal species recorded in each study should be isolated and preserved in reference culture collections to provide the authentic biological material. This material will not only increase the accuracy of the taxonomic assignments but will also be useful for further biotechnological purposes.

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