



# Marine Fungi

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**Abstract**

Marine fungi are found in almost every marine habitat explored. From surface waters to kilometers below the seafloor fungi appear ubiquitous and contribute to global biogeochemical processes as saprotrophic degraders or parasites at numerous trophic levels. The purpose of this chapter is to review the increasing amount of knowledge on the diversity and adaptive capabilities of marine fungal communities along with their metabolic functions which can be hijacked and used for biotechnological applications. Specifically, the aim is to provide an overview of a number of innovative approaches to optimize the search for novel enzymes and bioactive compounds.

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**Keywords**

Adaptation · Bioremediation · Biotechnology · Diversity · Marine fungi · Secondary metabolites

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## 5.1 Introduction

The vast expanse of the ocean biome still holds many mysteries even though major advances have been achieved in understanding microbial diversity, biogeography, and ecology. There are still important knowledge gaps to fill regarding some microbial groups and especially marine fungi. While fungi are critically important on land for ecosystem functioning and carbon cycling their ecological roles in marine food webs and carbon cycling are still largely overlooked. And yet fungal communities have been found in almost every marine habitat explored from the surface of the ocean to kilometers below ocean sediments where they function mostly as saprotrophic degraders or parasites at numerous trophic levels. The aim of this chapter is to provide a state-of-the-art summary of existing knowledge on the diversity and adaptive capabilities of marine fungal communities along with their functions which can be hijacked and used for biotechnological applications.

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## 5.2 From Culture-Based to Next-Generation Sequencing Methods to Access Marine Fungal Life

The fungi are a fascinating group that circumscribes morphologically diverse microorganisms with non-trivial roles in virtually any ecosystem. A clear answer to the question “what is a fungus” is not easily given because the quest to identify synapomorphy/synapomorphies to unify the fungi has failed (Naranjo-Ortiz and Gabaldón 2019) and led to Bruns’ Law: “there is no fungal synapomorphy, get used to it” (Richards et al. 2017). Moreover, as molecular phylogenetics guides taxonomy the limits of the fungal kingdom are expanding as new phyla are being introduced (Galindo et al. 2020). Knowing this, it appears that a clear answer to the question “what is a marine fungus” is not straightforward. The definition of marine fungi has been subject of discussion for a long time (see Rédou et al. 2016a). However, a consensual definition has now been proposed and seems to be adopted by the scientific community (Pang et al. 2016). In this study, a consortium of marine mycologists proposed a broad definition of a marine fungus “as any fungus that is 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 organisms, or (3) it adapts and evolves at the genetic level or is metabolically active in a marine environment.” This definition appears consistent with the one proposed by Rédou et al. (2016a) indicating that “Marine fungi display long-term presence and metabolic activities in a marine habitat as revealed by their adaptations (ecophysiological profile), active metabolism (rRNA), gene expression (mRNA), catalytic functions (proteome), or specific metabolites (metabolome) resulting from their biotic and abiotic interactions.” In this chapter these definitions of marine fungi are adopted.

There are many ways of targeting fungi in a marine sample from using microscopy to omic-based approaches. Direct observations of fungal structures have been largely used in early studies (e.g., Barghoorn and Linder 1944; Johnson and Sparrow 1961; Kohlmeyer and Kohlmeyer 1979) and are still used in numerous studies to qualitatively and quantitatively highlight the fungal diversity through cell visualization and quantification (e.g., Bochdansky et al. 2017; Burgaud et al. 2010; Gutiérrez et al. 2010; Hassett et al. 2019; Priest et al. 2020) but also cell morphology (e.g., Mitchison-Field et al. 2019). However, culture-dependent and molecular methods have clearly stolen the show.

Culturing has the advantage that it allows to generate genetic libraries of marine fungal isolates. These libraries can then be analyzed by using a variety of genetic markers or even be fully sequenced for further genomic or comparative genomic approaches coupled with (comparative) transcriptomics. This is often necessary in order to make a definitive species assignment. Oftentimes, short high-throughput sequencing reads that target conserved genetic loci (e.g., the 18S small ribosomal subunit) do not have sufficient taxonomic resolution to reliably identify species or genera, especially if clade segregation was based on full-length concatenated sequences. To this end, culturing approaches can be more advantageous. For example, Kumar et al. (2018) analyzed two marine fungi from the North Sea, namely

*Calcarisporium* sp. and *Pestalotiopsis* sp. and unraveled numerous biosynthetic gene clusters of which some are involved in the production of secondary metabolites with antimicrobial activities. These data are unobtainable by targeted loci metabarcoding sequencing analyses. A transcriptomic-based study has also demonstrated that fungi can adapt to changes in temperature, salinity, and acidity by up- or down-regulation of stress-related genes. This was shown for the marine fungus *Aspergillus terreus* strain NTOU4989 which was isolated from a hydrothermal vent system under a combined set of growth conditions of different temperature, pH, and salinity (Pang et al. 2020). Culturing has the important advantage of providing an opportunity to thoroughly characterize isolates through ecophysiological screening including tolerance to temperature, salinity, pH, and hydrostatic pressure (e.g., Burgaud et al. 2009; Burgaud et al. 2010; Rédou et al. 2015). Moreover, cultures allow to study their metabolic potential as well as their ability to grow on different carbon sources (e.g., Quémener et al. 2020). Numerous culturing techniques can be used to understand the culturable diversity of fungi of a specific marine habitat such as direct plating (e.g., Li et al. 2014; Vrijmoed 2000; Zuccaro et al. 2004), particle filtration, and dilution to extinction plating coupled with mid/high-throughput culturing (e.g., Quémener et al. 2020), or in situ culturing (see Overy et al. 2019). Some other culturing-based approaches appear promising such as those using microcapillaries (see L'Haridon et al. 2016), isolation chip (Nichols et al. 2010), and fluorescent activated cell sorter combined with microfluidics (Lambert et al. 2017). Although promising, such techniques have not been applied to understand the diversity and richness of marine fungi. However, culturing is facing some issues. The most important of these issues is the culturability of presumed fastidious organisms, which explains why it is thought that potentially as few as 1% of marine fungi have been identified so far (Gladfelter et al. 2019).

These fastidious organisms, the anticipated presence of obligate symbionts, and the laborious and resource-intensive efforts associated with culturing fungi from samples collected from often remote locations pose a major constraint on its broad implementation. To this end, molecular methods have provided a less-biased and sometimes more efficient way of assessing the full fungal community. Earlier applications of molecular methods utilized to study marine fungi have been based on molecular fingerprinting and cloned sequences (e.g., Fell and Newell 1998). Now the wider implementation of Next-Generation Sequencing (NGS) platforms has become the gold standard although cloning-based approaches are still useful and utilized (Hassett et al. 2017). This era of omics has ushered in the ability to generate independent, yet comparative broad assessments of marine fungal richness and diversity by targeting nucleotide sequences primarily through rRNA gene metabarcoding of taxonomically informative loci (18S, 28S, ITS). As the field continues to advance more nuanced approaches aimed at inventorying the metabolically active fraction through mRNA analyses (e.g., Orsi et al. 2013a) and ecologically targeted approaches with DNA stable isotope probing methods are being utilized (Cunliffe et al. 2017). As the focus begins to shift from understanding diversity toward functionality microarray analyses (e.g., Hassett et al. 2019) and shotgun sequencing (Christmas and Cunliffe 2020) are being utilized in order to

thoroughly assess the functional gene repertoire and gene expression patterns of fungi in the marine environment. The efficacy of these high-throughput approaches to resolve longstanding questions in marine mycology is rapidly increasing but still depends on reference databases. As of 2019, only ~50% of all marine fungi were represented by a nucleotide sequence and less than 20% of marine fungal genera were represented in the NCBI RefSeq database (Hassett et al. 2019). Balancing the limitations of culturing and molecular approaches often requires a dual approach to thoroughly understand marine fungal communities in terms of their diversity, activity, structuration, and ecological functions.

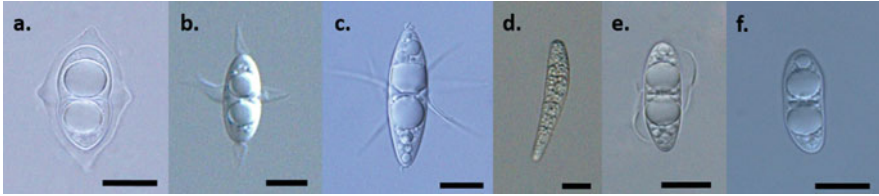
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### 5.3 Habitat Specific Community Composition or over-Dispersion?

The picture of marine fungal diversity remains largely pixelated even though in the past decade new studies have highlighted the importance of this group of microorganisms. Answering the question whether marine fungi are over-dispersed or endemic would help to better understand the broad-scale habitat and geographic differences among marine fungal communities.

#### 5.3.1 Plant-Based Habitats

Saprophytic fungi occurring on plant substrates are the most well-studied group of marine fungi. Since the monumental study of wood-inhabiting fungi by Barghoorn and Linder (1944) many new species of marine fungi have been described from wood in diverse habitats including wood buried in sandy beaches, decaying wood in mangroves, and drift or trapped wood on rocky shores. Wood-inhabiting marine fungi form fruiting bodies on wood and cause soft-rot decay mainly by producing cellulases and laccases (Bucher et al. 2004). Marine Dothideomycetes and Sordariomycetes belonging to the Ascomycota are dominant together with a few Basidiomycota. These identifications were based on the observation of fruiting bodies and also on culture-independent techniques using 454 pyrosequencing of the ribosomal ITS and of the 18S rRNA gene (Arfi et al. 2012a; Jones et al. 2015). Marine lignicolous basidiomycetes are mainly intertidal species and belong to the Agaricomycetes with reduced and enclosed fruiting bodies, loss of ballistospory, and evolution of spore appendages (Hibbett and Binder 2001). Marine lignicolous ascomycetes are phylogenetically diverse but mainly belonging to the Pleosporales in the Dothideomycetes and Microascales (Halosphaeriaceae) in the Sordariomycetes class forming exposed or immersed perithecia (Jones et al. 2015). As revealed by Rämä et al. (2014) Hypocreales and Helotiales also represent important taxonomic groups in which fungal communities from Arctic intertidal and seafloor logs were obtained using culture-based techniques. Apothecium-type of ascomata is uncommon with only 10 described species (Baral and Rämä 2015) possibly due to the inability to withstand wave action (Suetrong and Jones 2006).



**Fig. 5.1** Plant-inhabiting marine fungi from diverse habitats. (a) Ascospore of *Ebullia octonae* with a sheath. (b) Ascospore of *Halosphaeriopsis appendiculata* with polar and equatorial spoon-shaped appendages. (c) Ascospore of *Halosphaeriopsis mediosetigera*. (d) Clavate-shaped ascospore of *Buergenerula spartinae*. (e) Ascospore of *Natantisporea retorquens* with bipolar unfurling appendages. (f) Ascospore of *Lignicola laevis* (Scale bar 10  $\mu\text{m}$ )

These ascomycetes have evolved diverse morphologies to adapt to a marine lifestyle, i.e. deliquescing asci and ascospore appendages of different morphology and ontogeny (Fig. 5.1a–c) (Pang 2002). Two of the largest lineages of marine lignicolous ascomycetes, the Halosphaeriaceae and the Lulworthiales, were derived from terrestrial ancestors (Spatafora et al. 1998). Phylogenetic studies of the ribosomal RNA genes revealed further independent lineages into the marine environment in the Ascomycota: Dyfrolomycetales (Hyde et al. 2013), Tirisporellales, Torpedosporales (Jones et al. 2015), and Savoryellales (Boonyuen et al. 2011). This confirmed the high diversity of Ascomycota on wood substrates.

Marine fungi also grow on the decaying intertidal part of saltmarsh plants such as *Spartina* spp., *Juncus roemerianus*, and *Phragmites australis*, and the palm *Nypa fruticans*. Many species of marine fungi are host-/substrate-specific (Calado and Barata 2012; Pilantanapak et al. 2005). In particular, fungi associated with *Spartina* spp. have been well studied in US and Portuguese salt marshes where they are involved in nutrient cycling (Newell and Wasowski 1995). Diverse laccase genes were detected from the fungal community associated with *Spartina alterniflora*, which may suggest their involvement in lignin mineralization (Lyons et al. 2003). A total of 132 species of marine fungi have been documented to live saprophytically on *Spartina* spp. with the dominant groups belonging to the classes Dothideomycetes and Sordariomycetes (Calado and Barata 2012). *Phaeosphaeria halima*, *Phaeosphaeria spartinicola*, *Mycosphaerella* sp., *Byssothecium obiones*, and *Buergenerula spartinae* (Fig. 5.1d) are common taxa living on *Spartina* spp. in US saltmarshes (Buchan et al. 2002; Newell et al. 1996; Walker and Campbell 2010). Many of these species have fully functional asci for forcible expulsion of spores (Newell 2001). These species are also common in Portuguese saltmarshes along with *Natantisporea retorquens* (Fig. 5.1e) (Barata 2002; Calado et al. 2015). Based on an automated ribosomal intergenic spacer analysis (ARISA) the fungal community composition of *J. roemerianus* appears to be different from the one of *Spartina alterniflora* in the US saltmarsh. This suggests a host/substrate specificity of these plants (Torzilli et al. 2006). A total of 136 taxa have been recorded on *J. roemerianus* (Calado and Barata 2012). Many of those are not marine but grow on the terrestrial exposed parts of the plant. Common taxa on *J. roemerianus* include

*Loratospora aestuarii*, *Papulosa amerospora*, *Aropsiclus junci*, *Anthostomella poecila*, *Physalospora citogerminans*, *Scirrhia annulata*, *Massarina ricifera*, and *Tremateia halophile* (Newell and Porter 2000). Over 300 fungal species most of which asexual have been documented on the intertidal plant *P. australis* (Calado and Barata 2012). Common fungal species include *Cladosporium* spp., *Colletotrichum* sp., *Didymella glacialis*, *Halosarpheia phragmiticola*, *Lignincola laevis* (Fig. 5.1f), *Phaeosphaeria* sp., *Phoma* sp., *Phomatospora berkeleyi*, *Phomopsis* sp., *Septoriella* spp., and *Trichoderma* sp. (Luo and Pang 2014).

Mangrove plants support diverse fungal communities. Currently, about 500 fungi are known from mangrove habitats associated with 69 mangrove plants, sediments, and seawater with data from 80 countries (Jones et al. 2019; Schmit and Shearer 2004). Eighteen species identified as Ascomycota (e.g., *Antennospora quadricornuta*, *Halorosellinia oceanica*, *Sammeyersia grandispora*), asexual morphs (i.e., *Bactrodesmium linderi*, *Hydraena pygmaea*, *Periconia prolifica*), and Basidiomycota (i.e., *Calathella mangrovei*, *Halocyphina villosa*) have been listed as the core mangrove fungi (Jones 2011; Jones et al. 2019; Pang et al. 2011). From the palm tree *Nypa fruticans* in Brunei Hyde (1992) discovered 43 species whereas another study reported 135 species with 90 Ascomycota, 3 Basidiomycota, and 42 asexual fungi (Loilong et al. 2012). A higher fungal diversity occurred on the leaf base compared to the other tissues of this intertidal plant including inflorescence, leaf, leaf midrib, rachis, and aerial parts (Hyde and Alias 2000). Host specificity is pronounced with an estimated 40 endemic species (Hyde and Alias 2000). For example, *Aniptodera intermedia* and *Linocarpon appendiculatum* were found only on *N. fruticans* although this palm tree grows alongside mangrove tree species (Besitulo et al. 2010; Loilong et al. 2012). Using 454 pyrosequencing of the ITS of rRNA gene regions, Arfi et al. (2012a) found that the Agaricomycetes was the dominant fungal class in mangrove soil and that fungi may play a role in the decomposition of organic matter in the anoxic organic-rich sediments. However, the pathogenic genera such as *Diaporthe*, *Mycosphaerella*, *Phaeoramularia*, and *Ramulispora* were well represented in the leaves and branches of the two mangrove trees *Avicennia marina* and *Rhizophora stylosa* (Arfi et al. 2012b). The shift in community composition between sediments and healthy leaves highlights a switch in the ecological function of fungi from the submerged parts to aerial parts of mangrove trees.

Sea grasses have also been examined for endophytic fungi albeit colonization frequency and diversity were relatively low compared to terrestrial plants (Alva et al. 2002; Devarajan et al. 2002). Ascomycetes mostly belonging to the orders *Eurotiales*, *Hypocreales*, and *Capnodiales* appear dominant on seagrasses (Sakayaroj et al. 2012; Venkatachalam et al. 2015). Common genera include *Aspergillus*, *Cladosporium*, *Paecilomyces*, and *Penicillium*, which are typical asexual fungi of seawater and sediment (Sakayaroj et al. 2012; Venkatachalam et al. 2015). The few basidiomycetes found on *Enhalus acoroides* may represent mycorrhizal relationships (Sakayaroj et al. 2010) suggesting that fungal communities occurring on plant-based habitats are diverse and play different ecological roles. This trend was confirmed in a study focusing on the seagrass *Posidonia oceanica*

sampled in the coastal waters of the Elba Island in Italy (Poli et al. 2020). Ascomycetes represented 97% of the culturable diversity and, except for the genera *Penicillium* and *Aspergillus* for which representatives were isolated from all sites and plant parts, the diversity was homogeneously distributed in the classes Dothideomycetes (mainly *Pleosporales* and *Capnodiales*), Eurotiomycetes (mainly *Eurotiales*), and Sordariomycetes (mainly *Hypocreales* and *Microascales*). This was consistent with the results of an ITS-based metabarcoding study where the fungal alpha-diversity on different tissues (leaves, root, and rhizome) was significantly lower than that of the surrounding sediments (Ettinger and Eisen 2019; Wainwright et al. 2019a). Fungal communities on plants were dominated by the classes Dothideomycetes, Eurotiomycetes, Agaricomycetes, and Saccharomycetes for the seagrass *Enhalus acoroides* collected from Singapore and Peninsular Malaysia while the mycobiome of the seagrass *Zostera marina* appeared more complex in terms of diversity with the occurrence of the classes Sordariomycetes, Dothideomycetes, Saccharomycetes along with the basidiomycetous classes Agaricomycetes, Cystobasidiomycetes, and Malasseziomycetes as well as the *Chytridiomycota* and *Aphelidomycota*.

### 5.3.2 Coastal Waters

Compared to plant-based habitats the marine water column has much lower quantities of organic carbon substrate available for heterotrophic communities such as fungi. While the open ocean on one end of the spectrum is characterized by the lowest number and amounts of substrates and consequently fungal abundance and diversity, coastal waters on the other end of the spectrum harbor diverse fungal communities. Both culturing and metabarcoding methods revealed that fungi from the *Dikarya* phyla *Ascomycota* and *Basidiomycota* dominate most marine environments (Duan et al. 2018; Gao et al. 2010; Li et al. 2016a, 2016b, 2018; Taylor and Cunliffe 2016; Wang et al. 2018, 2019). For example, in Chinese coastal regions *Ascomycota* and *Basidiomycota* are dominant in seawater and sediment (Li et al. 2016a, 2016b, 2018; Wang et al. 2018, 2019) with large abundances of Dothideomycetes, Leotiomycetes, Eurotiomycetes, Agaricomycetes, Malasseziomycetes, and Tremellomycetes.

Most studies mentioned above were based on metabarcoding methods targeting the internal transcribed spacer (ITS) region. In studies where the small and large subunits of the ribosomal RNA genes were targeted early-diverging fungi from the phylum *Chytridiomycota* were recognized as representing a large part of the overall community (Picard 2017; Richards et al. 2015; Wang et al. 2017). Chytrid fungi in the marine environment are best known as diatom parasites (Gutiérrez et al. 2016; Hassett and Gradinger 2016) and probably play an important role in the transfer of organic matter and nutrients in marine food webs. The low representation of *Chytridiomycota* in studies targeting the ITS region is likely a result of the paucity of the reference sequences belonging to marine basal fungal clades, i.e., *Chytridiomycota* and *Cryptomycota* in the UNITE database (Kõljalg et al. 2013)



as many marine chytrid observations are based on morphological characteristics (e.g., Sparrow 1973).

In coastal ecosystems the main factors controlling fungal diversity include salinity, dissolved oxygen, and nutrient conditions. Salinity is recognized as one of the most important elements determining fungal diversity and community (Hassett et al. 2019; Jones 2000, 2011; Rojas-Jimenez et al. 2019; Taylor and Cunliffe 2016). Transitions in fungal communities along a salinity gradient were observed in Rhode Island (Mohamed and Martiny 2011) and the Delaware Bay (Burgaud et al. 2013), respectively. In the coastal waters off Plymouth, UK, mycoplankton alpha-diversity was negatively correlated with salinity with the highest values during periods of decreased salinity (Taylor and Cunliffe 2016). In the East China, Sea fungal communities in different water masses were mainly influenced by dissolved oxygen and water depth (Li et al. 2018). Nutrient conditions including ammonia, phosphate, and silicate were significantly correlated with fungal OTU richness or sequence read abundance in the coastal ecosystems of Plymouth (Taylor and Cunliffe, 2016) and North Carolina (Duan et al. 2018), respectively. Also, in the coastal waters of Hawaiian and North Carolina, positive correlations between fungal diversity and phytoplankton biomass were found (Gao et al. 2010; Duan et al. 2018). A similar pattern was observed in the upwelling ecosystem off the coast of Chile (Gutiérrez et al. 2011). A study based on 18S rRNA metabarcoding coupled to CARD-FISH highlighted the fungal diversity and biomass during a phytoplanktonic bloom in the North Sea and underscored the occurrence of *Cryptomycota* reaching cell concentrations similar to those in freshwater habitats (Priest et al. 2020).

The coastal mycobiome is strongly influenced by riverine input and ocean currents. Some terrestrial fungi that are well known from habitats such as soil and plants were often abundant in coastal areas suggesting the dispersal of terrestrial fungi to the marine environment (Amend et al. 2019; Richards et al. 2012). This dispersal occurs mainly via the riverine inputs, which enhance mycoplankton richness and shape community composition in coastal waters (Taylor and Cunliffe 2016; Wang et al. 2019). In the East China Sea, the coastal water mass harbored a high abundance of the typical terrestrial and freshwater fungal genus *Byssochlamys* suggesting the riverine inputs of fungi by the Yangtze River (Li et al. 2018). Other studies also detected the riverine inputs of fungi to coastal ecosystems (Wang et al. 2018, 2019). Planktonic fungi can travel long distances by hitchhiking on ocean currents. For example, the Kuroshio current contributes to the passive dispersal of fungi especially species affiliated to the genus *Aspergillus* along the shelf of the East China Sea (Li et al. 2018), which would lead to a great influence on biogeographic distribution pattern of marine fungi on a regional or even a global scale.

### 5.3.3 Algae

Macroalgae are colonized by various microorganisms collectively referred to as the microbiota. These microorganisms are interacting with their host throughout its life cycle impacting the physiological state of the host (Egan et al. 2013; Singh and

Reddy 2015; Wahl et al. 2012). The key role of these associated microorganisms in the algal development led to the concept of the holobiont in which the algae and its microbiota are defined as an entity (Egan et al. 2013). While the bacteria have been extensively studied macroalgae harbor also a large diversity of fungi which needs to be included in the study of algal microbiota. The first report of an obligate mycophycobiosis between the Fucales *Ascophyllum nodosum*, *Pelvetia canaliculata*, and the fungal endosymbiont *Stigmatidium ascophylli* (formerly *Mycosphaerella ascophylli*) dates back more than a century (Cotton 1907; Stanley 1991) and it has been suggested that the symbiont may protect the algae host from desiccation while obtaining nutrients in exchange (Decker and Garbary 2005; Garbary and London 1995; Garbary and Macdonald 1995). Similarly, the fungal symbiont *Turgidosculum ulvae* colonizes the inner tissue of the green alga *Blidingia minima* and induces dark spots that are never consumed by host predatory gastropods (Kohlmeyer and Volkmann-Kohlmeyer 2003).

Many filamentous fungi colonize the algal inner tissues without causing any apparent damage or disease (Debbab et al. 2012; Porrás-Alfaro and Bayman 2011) and such asymptomatic colonization by marine fungi remains mostly uninvestigated (Fries 1979; Harvey and Goff 2010; Loque et al. 2010; Jones and Pang 2012; Zuccaro et al. 2003). Thanks to DNA sequencing the fungal diversity in marine substrata has been unraveled and now it constitutes the second biggest known marine reservoir of fungi after sponges (Rateb and Ebel 2011). This diversity encompasses mutualistic symbionts, opportunistic pathogens, parasites, and saprophytes (Jones and Pang 2012; Rédou et al. 2016a; Richards et al. 2012; Zuccaro and Mitchell 2005). Studies based on a culturing approach showed that *Ascomycota* is the dominant endophyte of algae (Flewelling et al. 2013a, b; Godinho et al. 2013; Zuccaro et al. 2003, 2008). The study of the culturable fungal endophytic community associated with the inner tissues of the brown algae *L. digitata*, *S. latissima*, *A. nodosum*, and *P. canaliculata* confirmed the dominance of the *Ascomycota* and pointed out that the species belonged especially to the Sordariomycetes and the Dothideomycetes (Vallet et al. 2018). The proportion of taxa recovered within the main orders and classes were more or less similar to those described for marine fungi associated with plants or algae when compared to the public SSU rRNA reference databases (Panzer et al. 2015). The taxonomic diversity and abundance of isolates differed between the algal organs suggesting a potential tissue and host preference. This pattern of fungal colonization may be explained by the differences in chemical composition and defense in algal species and organs (Cosse et al. 2009; Megan et al. 2001; Thomas et al. 2014). However, aside from the cosmopolitan *Paradendryphiella arenaria*, which occurred in all four plant species investigated, few marine fungi sensu stricto or unknown species have been previously isolated. Instead, most of the recovered strains were closely related to terrestrial phytopathogens (37%), endophytes (21%), or a miscellaneous group of lignivore, soil-borne, and air-borne saprophytes (28%). Several genera, i.e., *Acremonium*, *Coniothyrium*, *Botryotinia*, *Phaeosphaeria*, and *Cordyceps* were not previously isolated from marine algal hosts (Flewelling et al. 2013b; Godinho et al. 2013). In particular, sequences matching the phytopathogens *Phoma exigua* and

*Botryotinia fuckeliana* were retrieved leading to the hypothesis that these strains might be opportunistic pathogens plausibly able to colonize an otherwise compromised alga.

Microbiota associated to the brown alga *Saccharina latissima* studied by high-throughput Illumina-based DNA sequencing highlighted that the fungal community was dominated by *Ascomycota* (54.6%) and *Basidiomycota* (45.3%) in particular *Mycosphaerellaceae*, *Psathyrellaceae*, and *Bulleribasidiaceae* (Tourmeroché et al. 2020). This result is consistent with previous metabarcoding studies on fungal communities associated with macroalgae which reported a predominance of *Ascomycota*, followed by *Basidiomycota* (Agusman and Dan-qing 2017; Wainwright et al. 2019b). However, important differences between the seaweed associated microbiota and the surrounding seawater microbiota were recorded suggesting that the seaweed has the capacity to recruit its microbiota. This phenomenon described as a “microbial gardening” hypothesis has been demonstrated in the green alga *Ulva* which enriches its environment by attracting and stimulating the growth of microorganisms necessary for its morphogenesis (Wichard et al. 2015). The fungal communities associated with *S. latissima* algal tissues were highly diverse and it turned out that the fungal diversity was spatially organized within the sampled algal tissues. Hitherto, no core fungal microbiota has been identified from numerous algal samples through snapshots of microbial diversity, suggesting that a functional core microbiota should be given more consideration to better understand the ecology of the host.

### 5.3.4 Deep-Sea and Deep Subsurface

Fungi are thought to play various roles in the deep sea including the decomposition of organic matter (Ivarsson et al. 2015a), in mineral weathering (Bengtson et al. 2014), and in manganese (Ivarsson et al. 2015b) and arsenic (Dekov et al. 2013) cycling. Deep-sea fungi also play a role as putative symbionts with chemoautotrophic bacteria and archaea in oceanic crust habitats (Bengtson et al. 2014). In terms of diversity and more precisely morphology a study of fungal marker genes in 11 deep-sea samples from around the world (1500–4000 m depth) suggested that certain yeast forms dominated the low-diversity fungal communities (Bass et al. 2007). However, this trend does not appear to be generalizable mostly because of the wide array of habitats in the deep sea.

#### 5.3.4.1 Deep-Sea Habitats

Fungi can be transported into the deep sea along with sinking organic material (algae, plant material, wood, and particulate organic carbon) as active cells, spores, or mycelial filaments (Lorenz and Molitoris 1997). Initial investigations of microbial eukaryotes in the deep sea utilized “universal” eukaryotic PCR primers that likely underestimated the diversity and abundance of fungi obscuring their relevance. Interest in the possible importance of fungi for deep-sea ecosystems was galvanized when living fungi were found in deep-sea sediments of the deepest ocean realm the

Mariana Trench (Takami et al. 1997, 1999). Since then, only a low number of studies of bathypelagic and abyssopelagic zones and unique deep-sea habitats such as hydrothermal systems have been conducted that specifically investigated fungal diversity.

Our knowledge of fungal diversity is in fact based on studies of marker genes (predominantly the internal transcribed spacer (ITS) of rRNA genes from environmental samples) and documentation of the fruiting bodies and culture characteristics of isolates from deep-sea sediment samples (Bass et al. 2007; Nagano et al. 2010; Raghukumar et al. 2004; Singh et al. 2010, 2012; Xu et al. 2014, 2016; Zhang et al. 2016). Marker gene sequencing has the advantage of detecting rare species and taxa that are currently unculturable or present only as vegetative mycelia as well as to recover the signatures of many putatively novel taxa (Lai et al. 2007; Nagano et al. 2017; Wang et al. 2018; Xu et al. 2016, 2017, 2019; Zhang et al. 2016).

Several studies provided insights into the extent of undescribed fungal diversity in deep-sea hydrothermal vent habitats. These include a culture-based study of yeast diversity in Mid-Atlantic Ridge sediments that revealed that 33% of the isolates were new phylotypes (Gadanhó and Sampaio 2005). Burgaud et al. (2009) examined the culturable diversity of filamentous fungi associated with shrimps, mussels, alvinellids, tubeworms, sediments, hydrothermal chimney rocks, and other types of samples from hydrothermal sites at the mid-Atlantic Ridge, South-west Pacific-Lau Basin, and the East Pacific Rise. The authors suggested that isolates from animals may be opportunistic pathogens or facultative parasites. Physiological studies on the strains in the collection of Burgaud et al. (2009) (including previously unknown phylotypes) included the assessment of their ability to grow under marine conditions. This demonstrated that not all fungal isolates should be considered as terrestrial “stowaways.” Analyses of sediments collected from the East Pacific Rise and the Mid-Atlantic Ridge and Lucky Strike hydrothermal sites using marker genes and culturing efforts revealed previously unidentified species of *Ascomycota* and *Basidiomycota* as well as a novel ancient evolutionary lineage of *Chytridiomycota* (Le Calvez et al. 2009). Hydrothermal sediments along the Mid-Oceanic Ridge in the East Pacific and the South Indian Oceans were investigated using culture-based and culture-independent approaches and revealed that *Ascomycota* dominated over *Basidiomycota* (Tang et al. 2020). In addition to some putatively novel taxa (less than 97% similarity to sequences in GenBank) culture-based approaches recovered 97 isolates belonging to 7 genera and 10 species including *Penicillium*, *Rhodotorula*, *Meyerozyma*, *Ophiocordyceps*, *Vishniacozyma*, *Aspergillus*, and *Phoma*. Most (5/7) genera were also detected using marker gene approaches (5.8S ITS along with 18S rRNA genes) confirming the importance of the classes Eurotiomycetes, Dothideomycetes, and Sordariomycetes in the marine environment from coastal waters to the deep biosphere. Fungi have also been found living in association with deep-sea animals at hydrothermal sites along the Mid-Atlantic Ridge, South Pacific Basins, and East Pacific Rise (Burgaud et al. 2010) and their growth potential under elevated hydrostatic pressure has been evaluated (Burgaud et al. 2015). Whether these are commensal, pathogenic, or mutualistic associations and whether the nature of the association can change under different conditions remain to be

determined. ITS marker gene sequences reveal many of the same dominant genera in samples from the northwest Pacific Magellan Seamount area (Luo et al. 2020). However, illustrating the unique fungal community composition that can be found at different locations at the Magellan Seamounts, *Basidiomycota* comprised the majority of OTUs (44%) with representation also from the phyla *Ascomycota* (25%) and minor representation from the phyla *Mortierellomycota*, *Chytridiomycota*, *Mucoromycota*, *Glomeromycota*, and *Monoblepharidomycota* (Luo et al. 2020). Five genera were common in most of the samples including *Aspergillus*, *Cladosporium*, *Fusarium*, *Chaetomium*, and *Penicillium* (representing once again the classes Eurotiomycetes, Sordariomycetes, and Dothideomycetes) all of which have been reported worldwide in marine settings. Studies of deep-sea hydrothermal sediments suggest there is much we still have to learn about fungal diversity in these habitats.

Examination of whale falls in the South Atlantic Ocean revealed a considerable diversity of previously unidentified fungi indicating that still much is unknown about this kingdom in the marine environment (Nagano et al. 2020). Molecular studies show that deep-branching basal (or “lower”) fungi and more precisely *Cryptomycota* are common in deep-sea methane cold-seep sediments (Nagahama et al. 2011). The deep sea appears to be a hot spot for discovery of additional early-diverging lineages that will help to elucidate the evolution of fungi. *Ascomycota* dominated ribosomal RNA ITS marker gene libraries from sediments of subtropical southern and northern Yellow Sea and the Bohai Sea where 816 operational taxonomic units that included 130 known genera, 36 orders, 14 classes, and 5 phyla were identified (Li et al. 2016a, b). Yeasts affiliated to the *Basidiomycota* and *Ascomycota* (particularly the genera *Rhodotorula*, *Rhodospiridium*, *Candida*, *Debaryomyces*, and *Cryptococcus*) appeared to be typical of deep-sea environments.

Fungal diversity in deep-sea sediments appears to be highly variable and possibly correlated with environmental factors that include sediment sources, organic carbon and nitrogen levels, geographical distance from land, latitude, temperature, salinity, and depth (Li et al. 2016a, b), although some researchers did not find such a strong correlation between these factors and fungal community composition (Luo et al. 2020). An increasing number of studies of the deep-sea suggest that fungal populations and saprophytic fungi contribute to the turnover of organic carbon and likely are important players in many nutrient cycles. For example, deep-sea fungi identified as *Dikarya* may play an important role in the degradation of lignin in deep marine realms because this group of fungi is present and is known to possess the ability to degrade lignin (Nagahama et al. 2011). Culture-based studies of deep-sea isolates from marine hypoxic sediments have shown that some fungi participate in denitrification under anaerobic conditions (Jebaraj and Raghukumar 2010).

#### 5.3.4.2 Deep Subsurface Sediments and Oceanic Crust

Knowledge of deep-sea fungi has now been extended into the deep subsurface biosphere, which includes sedimented and lithified realms, and which represents one of the largest reservoirs of microbial communities. The “deep biosphere” is defined here as ocean floor sediments that can only be accessed with drilling and are

too deep to be accessed with typical over-the-side gravity coring or submersible-assisted push coring. Microbial communities in deep biosphere habitats must cope with increasing temperature and hydrostatic/lithostatic pressures, low water activity (low water availability for biochemical reactions), and often nutrient-poor conditions (Gaboyer et al. 2019). Sufficient sediment pore spaces and veins or fractures in rocks are also required for subsurface microbial life to provide connectivity to fluids that can supply nutrients and electron donors and acceptors. Fungi and/or their biosignatures have been detected in deep (up to thousands of meters below the seafloor, mbsf) subsurface sediments of the Peru Margin, North Pond, Hydrate Ridge, Central Indian Basin, Benguela Upwelling System, South Pacific Gyre, Eastern Equatorial Pacific, Canterbury Basin, and off the Shimokita Peninsula in Japan (Ciobanu et al. 2014; Damare et al. 2006; Edgcomb et al. 2010; Inagaki et al. 2015; Liu et al. 2017; Orsi et al. 2013a, b; Rédou et al. 2014, 2015), the basaltic upper ocean crust (Ivarsson et al. 2012, 2016), and even in the gabbroic lower ocean crust (Quémener et al. 2020). Fungal diversity and culturability generally decrease with depth below seafloor (Rédou et al. 2014, 2015). Although many of these studies provide evidence that fungi are metabolically active in the deep subsurface their role in and impact on biogeochemical cycles and their interactions with other microbiota are uncertain.

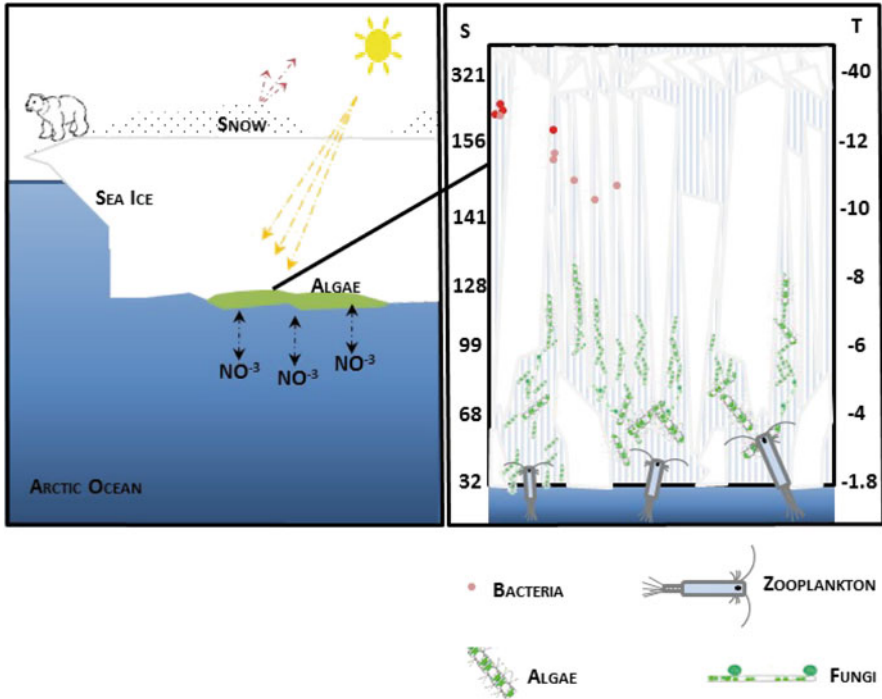
Fungal activities reported (on the basis of mRNA) in deep subsurface sediments and crust include organic matter recycling (Orsi et al. 2013a; Orsi 2018; Pachiadaki et al. 2016; Quémener et al. 2020) and biosynthesis of antimicrobial compounds, presumably used in competition with other microorganisms for available carbon and energy (Navarri et al. 2016). Fungal communities are thought to have a symbiotic interdependence with chemoautotrophic bacteria in basalts (Bengtson et al. 2014) and to participate in degradation of refractory organic matter and in manganese and arsenic cycling (Dekov et al. 2013; Ivarsson et al. 2015b). Additionally, anaerobic fungal lineages may support the energy needs of subsurface methanogens and hydrogen-consuming bacteria through the production of hydrogen as an end product of their fermentative energy metabolism (Drake and Ivarsson 2017; Drake et al. 2017; Hackstein et al. 2019; Ivarsson et al. 2016). Many fungal taxa detected in the deep biosphere appear to be ubiquitous taxa to deep sea and deep subsurface biosphere habitats including the genera *Penicillium*, *Aspergillus*, *Cladosporium*, and *Debaryomyces* (Hirayama et al. 2015; Li et al. 2019; Manohar et al. 2014; Nagano et al. 2010, 2017; Pang et al. 2019; Polinski et al. 2019; Zhang et al. 2016). As an example, members of *Aspergillus* have a wide distribution in marine biomes from coastal waters (Li et al. 2019) to the deep-sea (Burgaud et al. 2009) and deep subsurface sediments (Damare et al. 2006; Xu et al. 2017). *Aspergillus* species are known that they adapt to high hydrostatic pressures (Damare et al. 2006) and deep-sea yeasts affiliated to *Candida/Debaryomyces* as well as other fungal genera can grow at pressures ~25-40 MPa (Burgaud et al. 2015; Raghukumar et al. 2010). Laboratory tests of growth of fungal isolates from the lower ocean crust using diverse substrates suggest their ability to utilize a wide array of carbon compounds (Quémener et al. 2020). In addition to utilizing necromass and fluid-derived carbon such metabolic flexibility may be an important adaptation to survive in the lower

ocean crust where sources of carbon and energy delivered via fluid flows are likely ephemeral and variable. Expression of genes unique to fatty acid metabolism and peroxisomal biogenesis suggests that fungi maintain membrane integrity and may use fatty acids as an energy source (Quémener et al. 2020). This is consistent with laboratory studies that demonstrated fungal growth on fatty acids as a sole carbon source under aerobic conditions (Hynes et al. 2006). Recycling of proteins into central metabolism may be an additional adaptation to cope with limited carbon availability. Carbon-related stress responses can induce expression of hydrolases, cell wall degrading enzymes, and secondary metabolites (e.g., polyketides) as a means for fungal survival. Detection of expressed fungal genes for these processes as well as genes associated with cell division and senescence in deep crustal samples suggests a heretofore unknown ratio of senescent vs. active cells (Quémener et al. 2020). Future studies of the deep subsurface biosphere will hopefully include microscopy approaches that can tell us more about the physical associations of fungi with organic matter and about the abundance of active/vegetative cells in different habitats.

### 5.3.5 Polar Waters

The strong seasonal fluxes of temperature and light in high-latitude regions provide unparalleled opportunities to study the effects of environmental parameters on biological systems, which can aid in the elucidation of phenomena in regions with less pronounced natural gradients or fluxes. Within polar environments semi-porous sea ice is among the more unique physical features, which can harbor high densities of biota in close proximity (generally  $\mu\text{m}$ – $\text{mm}$  scale) within brine channels. As ice crystals thermodynamically form in marine environments the water molecules assemble into a lattice structure that physically excludes ions, which consequently accumulate into reticulate networks that are conceptualized as brine channels. The salinity and volume of these brine channels are partially governed by temperature: as the ice gets colder the salinity of brine increases as channel volumes decrease (Cox and Weeks 1983) (Fig. 5.2). The hypersalinity of sea ice brine and the constrained space within brine channels can exert strong selection on organisms (Caron and Gast 2010) including those seeking refuge from predators (Bluhm et al. 2017) and those not adapted to exist in the presence of elevated ion concentrations (Firth et al. 2016).

The rapid return of light in the spring fuels the development of massive under-ice algal blooms with associated primary productivity rates upwards to  $23.0 \text{ mg C m}^{-3} \text{ h}^{-1}$  (Gradinger 2009). In turn, this strong seasonal pulse of fresh primary production supports the life histories of diverse secondary producers including osmotrophic eukaryotes. With the return of summer comes seasonally elevated temperatures that melt snow, ice, and thaws surface terrestrial soils leading to location-variable seasonal freshening of polar seas (e.g., Bendtsen et al. 2014; Porter et al. 2019) and terrestrial export of organic material (Kaiser et al. 2017; Wadham et al. 2019). Although polar environments experience strong seasonality of light, temperature, and sea ice coverage the Arctic and Antarctic ecosystems are



**Fig. 5.2** Simplified and basic sea ice schematic and conceptually illustrating organisms inhabiting brine channels. Temperature (T) and its corresponding salinity (S) according to the equations of Cox and Weeks (1983) are displayed on the vertical axes. The brine volume fraction increases with temperature which is not represented here

markedly different: (1) The Arctic Ocean is surrounded by land, whereas the Antarctic is surrounded by water, (2) The Arctic Ocean's close proximity to land leads to it receiving  $\sim 11\%$  of the global river discharge (McClelland et al. 2012) and is consequently disproportionately affected by terrestrial processes. In contrast, the Southern Ocean is considered a more or less closed system (Fraser et al. 2018), and (3) The Arctic has in recent history contained larger quantities of multi-year ice, whereas the Antarctic is primarily a first-year ice-covered region. These differences probably result in diverging patterns of microbial richness and diversity (e.g., Bowman et al. 2012) and certainly confound the effective likening of associated biology within these different systems.

The biogeographical patterns of polar marine fungi as with nearly all marine fungal species are currently nebulous because under-sampling due to the limited number of studies prevents to discern true endemism. Although nebulous, there are emerging patterns of the relationship between specific environmental variables and marine fungal communities but these relationships appear to be scale-dependent. Specifically, at global scales pelagic marine fungi do not exhibit latitudinal gradients of species richness or diversity (Hassett et al. 2020; Tisthammer et al. 2016)



indicating that polar seas should not be unique in fungal species richness, even though new species have been described (e.g., Fell et al. 1969; Pang et al. 2008) and unique clades of fungi molecularly detected (Comeau et al. 2016; Hassett et al. 2017). Species checklists from culturing efforts have been discussed elsewhere for the Arctic (Rämä et al. 2017) and Antarctic (Godinho et al. 2019; Ogaki et al. 2019). At regional scales throughout the world marine fungal community composition regularly co-occurs with salinity (Hassett et al. 2020; Jeffries et al. 2016; Rojas-Jimenez et al. 2019; Taylor and Cunliffe 2016). However, Arctic marine fungal communities are frequently heterogenous (Perini et al. 2019) with weak to no relationships detected between salinity and geography (Comeau et al. 2016; Hassett et al. 2017). In polar regions, ascribing an effect of salinity on the composition of marine fungal communities is challenging and should be done cautiously especially in the Arctic, which contains many distinct hydro-morphological domains (Bluhm et al. 2015). Specifically: (1) the co-occurrence of a unique microbial community with low salinity during the sea ice melt season is most likely a detection of distinct brine channel communities being released into the water column (e.g., Rapp et al. 2018) as opposed to the result of stable environmental filtering/selection processes, (2) the disproportionately large quantities of freshwater that are discharged into polar waters are also source of terrestrial organisms (e.g., Collins et al. 2010) thereby creating unique communities which co-occur at lower salinity, and (3) sea ice brine salinity is calculated as a function of temperature. Hence, without carefully controlled experiments it is difficult to separate the covarying effects of temperature from salinity.

Lower latitude regional drivers of fungal communities do not appear to be robust uniform predictors of polar marine fungal community composition. However, local environmental differences such as specific substrate availability (e.g., Lacerda et al. 2020) and photon flux can explain the distribution of polar marine fungal communities. Specifically, the effect of higher light transmission into the water column at polynyas and under low localized snowpack on sea ice can result in a Chytridiomycota-predominated system (Hassett and Gradinger 2016; Hassett et al. 2017; Terrado et al. 2011). Many of these Arctic marine chytrids are parasites of diatoms (Hassett and Gradinger 2016; Hassett et al. 2020; Horner and Schrader 1982). The effect of light on *Chytridiomycota* and their parasitic activity on algae has been documented in experimental studies (Muehlstein et al. 1987; Scholz et al. 2017; Tao et al. 2020). Emerging evidence demonstrates that *Chytridiomycota* possess gene clusters associated with virulence (van de Vossenberg et al. 2019). If marine *Chytridiomycota* also possess virulence-associated genes like many diatoms possess defense response pathways such as those involving oxylipins (Johnson et al. 2020), marine *Chytridiomycota* may be disproportionately governed by the genetics of host and parasite according to various disease paradigms (e.g., Scholthof 2007), as opposed to exclusively environmental factors such as salinity. Reversible encystment of chytrid zoospores to host surfaces (Doggett and Porter 1994) lends additional evidence to the importance of biological interactions in governing local abundances. In addition to the factors that affect biological interactions spatially constrained brine channels harbor elevated proportions of *Chytridiomycota* relative

to open water (Comeau et al. 2016; Hassett et al. 2019). These brine channels also harbor elevated diatom densities (Gradinger 2009). Consequently, if *Chytridiomycota* abundances are governed by the molecular underpinnings of host–parasite interactions, then these elevated concentrations of both host diatoms and parasitic *Chytridiomycota* are likely amplified by principles of epidemiology such as lower dispersal time of infectious propagules in spatially constrained spaces. The atypical salinity patterns within sea ice could indeed serve as an amplification of *Chytridiomycota* abundances thereby creating an ideal niche for parasitic flagellated fungi. Saprotrophic chytrids have been previously reported in the Arctic Ocean (Sparrow 1973) and in association with fecal pellets (Hassett et al. 2019) although their diversity and ecological contributions remain to be elucidated.

In summary, the Arctic and Antarctic contain many cosmopolitan fungi, which support hypotheses of over-dispersal in marine realms. However, fungi in polar marine environments shift into habitat-specific communities seemingly driven by a preponderance of *Chytridiomycota*. The unique feature of constrained space within sea ice brine channels, hypersalinity of this brine, and high concentration of hosts has allowed this habitat-specific phenomenon to be putatively identified. This underscores the potential of the large gradients and fluxes in polar environments for answering outstanding questions in marine science.

In conclusion, fungi have been reported from every marine realm. From the Arctic to the Antarctic from surface waters to kilometers below the seafloor marine fungi are seemingly ubiquitous and certainly contributing to global biogeochemical processes. As the phylogenetic limits of the fungal kingdom both expand to include additional clades while existing clades are segregated into additional phyla it is expected that the reported marine fungal diversity increases with increasing sampling efforts especially among early-diverging taxa. This will lead to answers to outstanding questions of biogeographical patterns of species diversity, which will allow conclusions regarding over-dispersal.

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## 5.4 Adaptation of Marine Fungi

Many surveys have highlighted a high diversity of ubiquitous marine fungal species with a dominance of the filamentous genera *Penicillium*, *Cladosporium*, *Aspergillus*, *Fusarium*, and *Trichoderma* and the yeast genera *Candida*, *Rhodotorula*, *Cryptococcus*, and *Hortaea*. Detection of such fungi related to known freshwater or terrestrial groups in the ocean is surprising and suggests effective adaptive capabilities of these fungi for biotic and abiotic stresses related to the marine environment. The term “adaptation” is defined as any adjustment of an organism that makes it better suited to live in a given environment (Rédou et al. 2016a) either in terms of adaptive evolution (at the genetic level) or adaptive response (at the expression level). Evidence of real activity in the marine environment has been obtained using microscopic features, e.g., the germination of *Acremonium fuci* conidia only in the presence of *Fucus serratus* algal tissues (Zuccaro et al. 2004), or ecophysiological features, e.g., a shift from terrestrially-adapted to marine-

adapted fungal lifestyles along a sediment core (Rédou et al. 2015), or an ability to grow under elevated hydrostatic pressure (Burgaud et al. 2015; Damare et al. 2006). Modern high-throughput omics approaches based on rRNA and mRNA sequencing have also allowed to reveal the activity and functions of numerous ubiquitous fungal species in different marine habitats (Edgcomb et al. 2010; Orsi et al. 2013a; Orsi 2018; Pachiadaki et al. 2016; Quémener et al. 2020).

Comparative genomics/transcriptomics of marine vs. terrestrial isolates of the same species appears as powerful approaches to gain insights into the physiological capabilities, evolution, and adaptation of marine fungi. Assuming that habitats control genome evolution or genome adaptations it should be possible to observe the up- or down-regulation of specific genes or pathways when comparing marine to terrestrial representatives of the same species. Based on available data on halophilic fungi, namely *Eurotium rubrum*, *Hortaea werneckii*, and *Wallemia ichthyophaga* comparative genomics highlighted a high number of genes coding for proteins with a higher proportion of acidic amino acid residues, of genes related to stress response (A-/B-barrel proteins, catalases), of genes coding for hydrophobins and polyol synthesis, and of genes related to DNA processing and damage (Kis-Papo et al. 2014; Lenassi et al. 2013; Zajc et al. 2013). Complementary comparative transcriptomics revealed that most of these genes were highly expressed under high salinity conditions.

Evidence of adaptation to the marine environment can also be figured out based on marine fungal secondary metabolism. Genomic and transcriptomic analyses of *Scopulariopsis brevicaulis*, a well-known terrestrial fungus, isolated from a sponge revealed the gene/gene clusters responsible for the synthesis of anti-cancerous scopularides only found in marine conspecific *S. brevicaulis* (Kumar et al. 2015). Available genomes of marine fungi such as *Corollospora maritima* and *Lindra thalassiae* are available at the Joint Genome Institute. An overview of their secondary metabolite gene clusters revealed many non-ribosomal peptide synthetase (NRPS) genes, polyketide synthase (PKS) genes, and terpene-encoding genes in their genomes that may be involved in the production of unique secondary metabolites and could be explained as an adaptation to life in the marine environment. Metabolomics thus appears as another interesting approach to provide concrete evidence regarding the real in situ activity and interactions of ubiquitous marine fungi through their ability to produce a wide spectrum of secondary metabolites, which differ from those of their terrestrial counterparts (Bhakuni and Rawat 2005).

Despite their ecological importance marine fungi have been largely overlooked by marine microbiologists because they were considered by them to be inactive in the marine environment. Studies highlighting their presence, activity, and function in numerous marine habitats and their putative importance paved the road for an integrated analysis and to delve deeper into their adaptation to the marine environment and their capacities to cope with changes such as hydrostatic pressure, salinity, and temperature (see Rédou et al. 2016a).

The many ways of marine fungi to cope with biotic and abiotic stresses thanks to their adaptive capabilities make them an interesting subject for biotechnology.

Numerous capabilities can be hijacked from their first ecological functions and used for biotechnological applications with the idea to contribute with solutions to pressing societal/environmental challenges. The most important applications recognized to date are enzymes. For example, enzymes able to degrade complex polymers (e.g., hydrocarbons and plastics) can be applied in bioremediation. In addition, secondary metabolites of marine fungi are known for their antimicrobial activities.

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## 5.5 Accessing the Bioremediation Potential of Marine Fungi

Marine fungi are interesting as producers of enzymes with an industrial value such as cellulases, amylases, xylanases, lipases, proteases, and laccases (Rao et al. 2017). The adaptive potential of marine fungi providing them with a high ability to withstand many types of stressful conditions allows for the synthesis of a wide array of enzymes with different temperature and pH optima (Bonugli-Santos et al. 2015). To date, marine fungal enzymes have been mostly obtained from marine fungi isolated from seawater, sediments, or mangroves and, to a lesser extent, from deep-sea habitats.

### 5.5.1 Degradation of Hydrocarbons

Fungi have a high tolerance to hydrocarbons (Al-Nasrawi 2012) and more than 100 genera (Prince 2005) play important roles in the biodegradation of hydrocarbons in soils and sediments. Filamentous fungi such as *Cladosporium* and *Aspergillus* are among those known to participate in aliphatic hydrocarbon degradation. The genera *Cunninghamella*, *Penicillium*, *Fusarium*, *Mucor*, and *Aspergillus* are among those known to take part in the degradation of aromatic hydrocarbons (Al-Nasrawi 2012; Passarini et al. 2011; Steliga et al. 2012). While most filamentous fungi investigated to date are unable to fully mineralize aromatic hydrocarbons, they facilitate the degradation of the more recalcitrant hydrocarbons in the environment by secreting extracellular enzymes that transform these compounds into intermediates of lower environmental toxicity and increased susceptibility to bacterial decomposition (Steliga et al. 2012). The poor bioavailability of many hydrocarbon components is considered to be a major rate limiting factor in the hydrocarbon remediation process (Das et al. 2014). Biosurfactants act as surface-active amphiphilic compounds with a hydrophobic and hydrophilic moiety that interact with phase boundaries in a heterogeneous system to solubilize organic compounds (Sen et al. 2017). The entire phenomenon enhances the bioavailability of contaminants for microbial degradation through better solubilization of hydrocarbons in water or water in hydrocarbons (Banat et al. 2014). Chemical surfactants exist such as carboxylates, sulfonates, and sulfates but biosurfactants have several advantages over these such as lower toxicity and higher biodegradability (Shekhar et al. 2015). While a majority of biosurfactants described is of bacterial origin with producers affiliated to *Pseudomonas*,

*Acinetobacter*, and *Bacillus* the importance of the production of biosurfactants by yeasts and filamentous fungi is increasingly recognized. Fungal producers are affiliated to the yeasts *Candida*, *Pseudozyma*, and *Rhodotorula* (Sajna et al. 2015; Sen et al. 2017) and to the filamentous fungi *Cunninghamella*, *Fusarium*, *Phoma*, *Cladophialophora*, *Exophiala*, *Aspergillus*, and *Penicillium* (Lima et al. 2016; Silva et al. 2014) all of them with numerous representatives in the marine environment.

### 5.5.2 Degradation of Plastics

Plastics have become the most common form of waste in the environment and represent a major and growing environmental threat at the global scale. An estimation indicated that of the 8300 million metric tons (Mt) of virgin plastics produced so far ~80% accumulated in landfills or in the environment (Geyer et al. 2017). Annual plastic waste input from land into the ocean varies from 4.8 to 12.7 Mt. representing 1.75 to 4.65% of the 275 Mt. of plastic waste generated annually (Jambeck et al. 2015). In terms of global composition of marine litter plastics account for ~62%. Plastics also contribute to 49% of the litter composition in the seafloor and 81% at the sea surface (Sánchez 2020).

Essential characteristics that are responsible for the resistance of plastics to biodegradation include a long chain polymer structure made of carbon, silicon, hydrogen, nitrogen, oxygen, and chloride, high molecular weight (MW), absence of a favorable functional group, hydrophobicity, and crystallinity (Urbanek et al. 2018). Nevertheless, plastics are rapidly covered by organic matter collectively referred to as the “ecocorona,” which decreases the hydrophobicity of the surfaces and facilitates microbial colonization (Wright et al. 2020). Microplastics thus constitute a new ecological niche for microbial communities defined as the “plastisphere” (Amaral-Zettler et al. 2020; Zettler et al. 2013).

Not only bacteria but also fungi form biofilms on plastic surfaces mainly dominated by *Chytridiomycota*, *Cryptomycota*, and *Ascomycota* (Jacquin et al. 2019). In the framework of an exposure experiment (PET drinking bottles deployed at several stations in the North Sea) and using a metabarcoding approach, Oberbeckmann et al. (2016) revealed different microeukaryotic communities including fungi and more precisely the *Ascomycota*, *Basidiomycota*, and *Chytridiomycota*. These observations were supported by another metabarcoding approach that revealed similar phyla on PolyEthylene (PE) samples during an exposure experiment in the Belgian part of the North Sea (De Tender et al. 2017) leading to the identification of the species *Cladosporium cladosporioides*, *Fusarium redolens*, and *Mortierella alpina* as putative PE degraders. The abundant presence of *Chytridiomycota* could result in different kinds of parasitic or saprotrophic relationships with the primary producers that are also present in the plastic biofilms, mediating the carbon, nutrient, and energy transfer into the food webs (Kettner et al. 2017). Moreover, marine plastics are often covered with polysaccharide-rich diatom

biofilms, which could explain the attachment and association of fungi with biofilms on plastics (Lacerda et al. 2020).

While some fungi may be hitchhikers on plastics benefiting from a substrate covered with organic matter, some fungi appear to have the ability to biodegrade plastics as, for example, *Zalerion maritimum*. This marine fungus is able to biodegrade PE, which is one of the most widely used polymers and thus one of the main polymers found in the environment (Paço et al. 2017).

The biodegradation of plastics takes place in 4 steps: (1) Microbial biofilm formation decreasing the buoyancy and hydrophobicity of the plastic (Rai et al. 2020). Fungi have the ability to produce hydrophobins, which represent an important tool for bioremediation purposes since they act as natural biosurfactants increasing attachment to plastic hydrophobic substrate and thus its bioavailability (Sánchez 2020). (2) The generation of biofilms is followed by biodeterioration that weakens the polymer integrity and produces cracks and pores. (3) After biodeterioration, the carbon skeleton of plastics is destabilized through enzymatic depolymerization with amidases, oxidases, laccases, and peroxidases (e.g., the conversion of polymers into monomers that are assimilated into microbial biomass). (4) Mineralization as a final but rate-determining step where the polymers are completely degraded resulting in the release of final products such as, for example, CO<sub>2</sub> and H<sub>2</sub>O (Rai et al. 2020).

Thus, fungi including marine species have (1) abilities to produce hydrophobin for surface coating to attach hyphae/cells/spores to hydrophobic substrates, (2) a machinery of unspecific enzymes able to catalyze diverse reaction mechanisms, and (3) cellular ability to penetrate three-dimensional substrates making them highly convenient for plastic degradation (Sánchez 2020).

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## 5.6 Hints to Ecological Roles Inferred from Secondary Metabolites

### 5.6.1 Secondary Metabolites (or Specialized Metabolites): A Definition

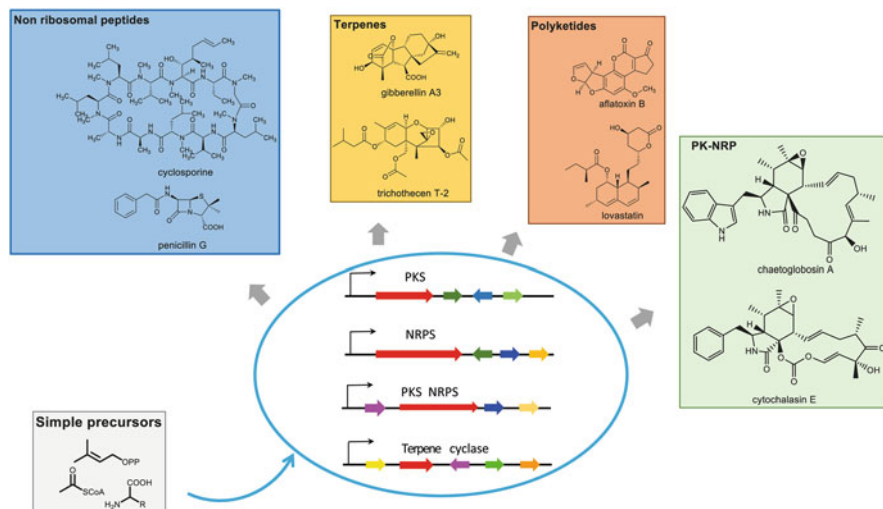
Organisms grow and develop using abiotic and/or biotic resources they find in their environment. The so-called primary metabolism is dedicated to the production of what is inherent to their development such as cell membranes, proteins for basic cellular functions, or nucleic acids for DNA. These primary constitutive metabolites are necessary for growth as they are involved in energy storage, cell machinery, and structure of organisms. These metabolites are universal and common in organisms. In contrast, the so-called secondary metabolites are produced in response to a plethora of different stimuli and are not considered to be essential for the organism. However, secondary metabolites often respond to diverse needs such as defense against predators, communication with other organisms, or adaptation to environmental changes. Actually, secondary metabolites are produced by organisms for specific functions which can be sometimes essential for their survival at a specific moment (e.g., mate recognition or settlement cues). Even if the production of these

metabolites is not universal and often limited to certain species under specific conditions, they are not less important. Secondary metabolites are produced to fulfill specific functions or to interact with specific biological targets. For all these reasons, the term “secondary”, which has been used for a long time, tends to be replaced by “specialized,” to avoid any misinterpretation on “secondary” as being less important than “primary” and to better reflect the distribution of these metabolites to restricted taxa.

Thanks to their intrinsic privileged interactions with living material, many secondary metabolites are used as valuable compounds for therapeutic targets thus providing interesting leads for the pharmaceutical industry. Among the drugs that have been approved since 1980, more than one third actually corresponds to compounds derived from natural products (mainly being secondary metabolites) and the drug discovery pipeline still continues to add new drugs of natural origin (Newman and Cragg 2020).

Microorganisms such as bacteria and fungi are invaluable for the discovery of drugs and/or lead compounds. Indeed, these microorganisms produce a huge variety of antimicrobial agents and the screening for secondary metabolites produced by microorganisms became highly generalized after the discovery of penicillin. Metabolites from fungi also lead to the discovery of potent compounds for other applications than antibiotics. This is, for instance, the case for lovastatin the lead compound for a series of drugs that lower cholesterol levels and cyclosporine currently used to suppress the immune response after transplantation operations (Numata et al. 1993). Secondary metabolites are central to the ecology of many fungi and allow their diverse interactions with other organisms. For instance, gliotoxin is a virulence factor and penicillin is an antibiotic whose ecological role lies in fungal defense against bacteria while  $\alpha$ -amatoxin is considered to serve as a constitutive chemical defense.

Secondary metabolites are produced from elementary bricks provided by the primary metabolism such as amino acids, sugars, and fatty acids. Various biosynthetic pathways have been described leading to different classes of compounds such as polyketides, alkaloids, or peptides. Surprisingly, the number of building blocks is small compared to the huge number of compounds that can be built. These pathways are governed by chemical reactions, many of which are catalyzed by specific enzymes encoded in the genome of the organisms. Indeed, most fungal secondary metabolites are encoded by biosynthetic gene clusters (BGCs). Each cluster typically contains the majority of the genes participating in the production of a given secondary metabolite. These genes are located adjacent to each other in the genome and are therefore called “clustered.” BGCs contain genes encoding proteins governing the biosynthesis of the backbone of the metabolite (e.g., polyketide synthases (PKSs), non-ribosomal peptide synthetases (NRPSs), prenyltransferases, and terpene cyclases) as well as genes encoding for tailoring enzymes that modify this backbone (epimerases, methyl-transferases, and hydroxylases), proteins involved in metabolite transport, transcription factors involved in regulation of the BGCs expression, and proteins that confer resistance to the activity of the secondary metabolite (Rédou et al. 2016a).



**Fig. 5.3** Schematic fungal BGCs and their secondary metabolites

The availability of a growing number of sequenced fungal genomes and their analyses by bioinformatics revealed that the number of genes encoding the highly conserved PKS and NRPS is much larger than anticipated, even in strains that have been extensively studied for the formation of natural products. Thus, fungi possess more potential secondary metabolic biosynthetic clusters than reported metabolites of which the identity, structure, and function often remain unknown. In fungi, the main biosynthetic pathways described include polyketides, terpenes, non-ribosomal peptides, alkaloids, and shikimate pathways (Fig. 5.3). With this machinery in hands, fungi are known to be prolific producers of secondary metabolites. The diversity of structures produced by fungi from elemental bricks arising from the primary metabolism appears huge, if not infinite.

## 5.6.2 Marine Fungal Chemodiversity

In the marine environment (micro)organisms have developed adaptations to cope with numerous stimuli through expression of specific biosynthetic pathways for defense or communication. It is well-known that there is an extremely harsh competition between (micro)organisms in the marine environment. On some tropical coral reefs, for example, there can be as many as 1000 species per  $m^2$  meaning that the organisms need to find ways to co-exist. This is where chemical cues and chemical communication take place.

While in 1992, only 15 fungal metabolites had been described from the marine environment (Fenical and Jensen 1993); this number increased tremendously over the last decades (Blunt et al. 2016; Bugni and Ireland 2004; Daletos et al. 2018; Rateb and Ebel 2011). So far, more than 3500 secondary metabolites have been



isolated from fungi collected in the marine environment. According to the open-source Natural Product Atlas (NPA, accessed in October 2020) (van Santen et al. 2019), marine fungal secondary metabolites now represent approximately 22% of all metabolites isolated from fungi.

Marine fungi have yielded many clinically-relevant natural products, including antibiotics (Blunt et al. 2018; Demain 2014; Rateb and Ebel 2011; Svahn et al. 2012). The antibiotics include gliotoxin from a deep-sea strain of *Aspergillus* sp. (Fan et al. 2016) and indanonaftol A from a marine *Aureobasidium* sp. (Biabani and Laatsch 1998). The biosynthesis of various secondary metabolites by fungi usually coincides with their life cycle (Calvo et al. 2002) and with fungal strategies to inhabit and survive in diverse ecological niches. Identification of fungal secondary metabolites can be challenging since it can require appropriate culture conditions that mimic the conditions of different extreme habitats such as those found in the deep sea and deep biosphere. As an example, few secondary fungal metabolites have been successfully isolated under high-pressure conditions (>90 atm) to date because of the technological constraints of recovering and culturing piezophile or piezotolerant fungal strains at elevated pressures (Kumar et al. 2015). The bioactive molecules that have been isolated from deep sea fungi include various secondary metabolites with biotechnological potential (Nicoletti and Trincone 2016). The majority of secondary metabolites isolated so far are derived primarily but not exclusively from strains belonging to two genera: *Penicillium* and *Aspergillus* (Petersen et al. 2020; Arifeen et al. 2020). These include biomolecules with anti-inflammatory, cytotoxic, antimicrobial, antifungal, and antiviral activities (Wang et al. 2015).

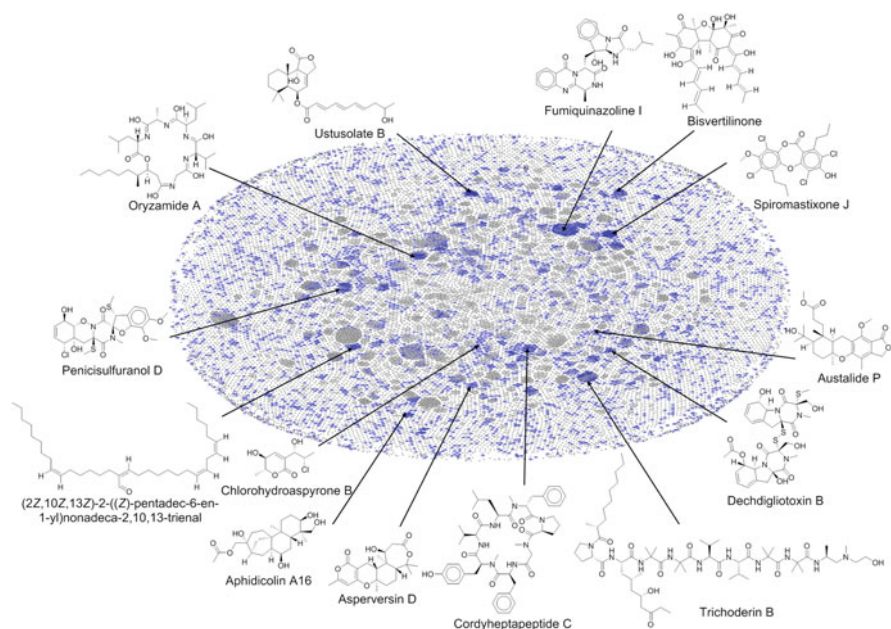
New polyketides (aspilactonol, aspiketolactonols, aspyronol, epiaspinonediol), alkaloids (meleagrins D and E, sorbicillamines, brevicompanines D–H, circumdatin F and G, and cyclopiamides), steroid and terpenoid derivatives (sterolic acid, breviones) were isolated from *Aspergillus* and/or *Penicillium* strains collected from deep sea hydrothermal vents (2255 m), and from deep sea sediments in the Pacific Ocean (~5000 m depth) and South China Sea (4593 m depth) (Chen et al. 2014; Fredimoses et al. 2015; Li et al. 2012; Xu et al. 2015; Zhang et al. 2018). Alkaloids from *Penicillium* sp. exhibit anti-inflammatory activity and weak or moderate cytotoxicity against cancer cell lines (Du et al. 2009). The terpenoids and steroid metabolites showed antiviral effects against HIV-1 and cytotoxicity against lung and breast cancer cells (Li et al. 2012). The cytotoxicity of two new C9 polyketides (spyronol and epiaspinonediol) and wentilactones (terpenoids) identified in *Aspergillus* sp. was tested against human leukemia cells and they turned out to be potential antitumor agents (Xu et al. 2015). Phenolic compounds from *Aspergillus* sp. (from 2326 and 3002 m depth; South China Sea) showed antifouling activities and possibly activate transcription factors related to detoxification mechanisms (Wu et al. 2016). Phenolic compounds from deep sea *Aspergillus* sp. were identified as potential antiviral agents against Herpes Simplex Virus 1 (HSV-1) (Wu et al. 2016). *Alternaria* sp. isolated from sediments at 3927 m depth (South China Sea) produced new perylenequinones that inhibit transcriptional

and epigenetic regulators (e.g., BRD4) that participate in cancer development (Ding et al. 2017).

Fungal polyketides (engyodontiumones, clindanones A–B), thiazole analogs (acaromyester A), and polypeptides (simplicilliumtides A–I) from *Engyodontium* sp., *Cladosporium* sp., *Simplicillium* sp., and *Acaromyces* sp. isolated from deep-sea sediments (3415 and 3739 m depth) in the South China Sea and the Indian Ocean (3471 and 4571 m depth) likely exhibit moderate to pronounced antitumor effects against lymphomas and cancer cells (Gao et al. 2016; Yao et al. 2014; Zhang et al. 2016). Other secondary fungal metabolites include terpenes (spirograterpene A, conidiogenone C and I, aspewentin A and D–H, asperethers A–E, asperolides D and E, and guignarderemophilane F) and cyclic lactones (butanolide A). These were all isolated from *Penicillium* sp. from deep waters (2284 m depths) and deep sediments (1393 m depth) at Prydz Bay of Antarctica. These compounds present antiallergic effects similar to common antihistamines (e.g., loratadine) and are thought to inhibit the protein tyrosine phosphatase 1B (PTP1B) which production is implicated in type-2 diabetes (Zhou et al. 2017). Fungal strains that belong to the family Lindgomycetaceae, isolated from deep sediments in the Greenland Sea, produce lindgomycin that shows antibiotic activity similar to chloramphenicol (Wu et al. 2015). Canescenin A and B (polypeptides) and nitrogen-bearing heterocyclic compounds (e.g., piperazine derivatives) isolated from deep-sea *Penicillium* sp., *Aspergillus* sp., and *Dichotomomyces* sp. have also been scanned for antibacterial activity (Dasanayaka et al. 2020; Fan et al. 2016; Wang et al. 2016). Dichotocejpins isolated from *Dichotomomyces* sp. seems to exhibit antifungal activity because of their inhibitory activity against  $\alpha$ -glucosidase (Fan et al. 2016). Terpenes and polyketides from the piezotolerant deep-sea fungi *Ascotricha* sp. and *Phialocephala* sp. have cytotoxic and antifungal activities (Ganesh Kumar et al. 2019; Zhang et al. 2018). In silico studies demonstrated that ascotrichin isolated from *Ascotricha* sp. can fit into serotonin receptors presenting a potential target for the development of drugs related to central nervous system disorders (Ganesh Kumar et al. 2019).

### 5.6.3 Marine Fungal SMs and Specificity to the Marine Environment

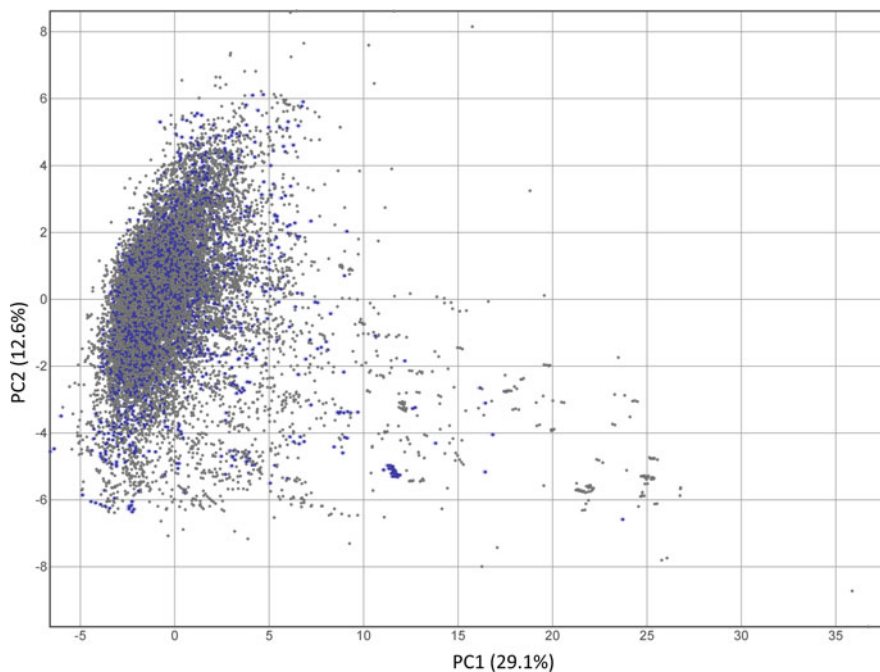
While some of the secondary metabolites have also been found in terrestrial fungi, others may be specific to the marine environment. By clustering all fungal metabolites described so far in the literature based on structure similarity it became clear that compounds isolated from the marine environment (highlighted in blue on Fig. 5.4) represent diverse skeletons. Some clusters of compounds were already described as produced by strains from the terrestrial environment while others such as spirostaxinones were only found in marine organisms such as the deep-sea-derived fungus *Spiromastix* sp. (Niu et al. 2014). These molecules were able to decrease oxidized low-density lipoprotein-induced lipid over-accumulation and



**Fig. 5.4** Similarity chart of the 17,441 fungal metabolites described in the Natural Product Atlas with metabolites first isolated from strains collected in the marine environment highlighted in blue. Each structure is represented by a dot and structures are clustered based on their similarity using the “Frag Fp” descriptor (on “data warrior” software, Sander et al. 2015). Some representative examples of natural skeletons isolated from the marine environment (blue clusters) are given

decrease intracellular cholesterol concentration, which is of potential interest in the treatment of atherosclerosis (Wu et al. 2015).

Specificity to the marine environment still remains difficult to assess on a chemical basis. Many examples have shown that after being isolated from a marine fungus the same molecule was later identified from a terrestrial species (e.g., communesins, Hayashi et al. 2004; Numata et al. 1993). Detecting an original compound produced by a fungus collected in the marine environment does not preclude it might be also found from a terrestrial strain. However, investigation of the chemodiversity produced by marine fungi in comparison to all fungal metabolites described so far in the NPA database shows some interesting points. First, while the overall chemical space occupied by fungal metabolites whether marine or not appears quite similar (Fig. 5.5), some specific physicochemical properties from fungal metabolites isolated in the marine environment could be highlighted. For example, drug likeness and halogen count in the molecules isolated from this environment appeared to be much higher (Fig. 5.6), which is consistent with the marine environment being rich in halogens, which leads to marine organisms to include these atoms in their metabolism. In fact, some studies already revealed the potential of marine fungal strains to produce halogenated metabolites (Roullier et al. 2016). While cheminformatic analyses of fungal metabolites have

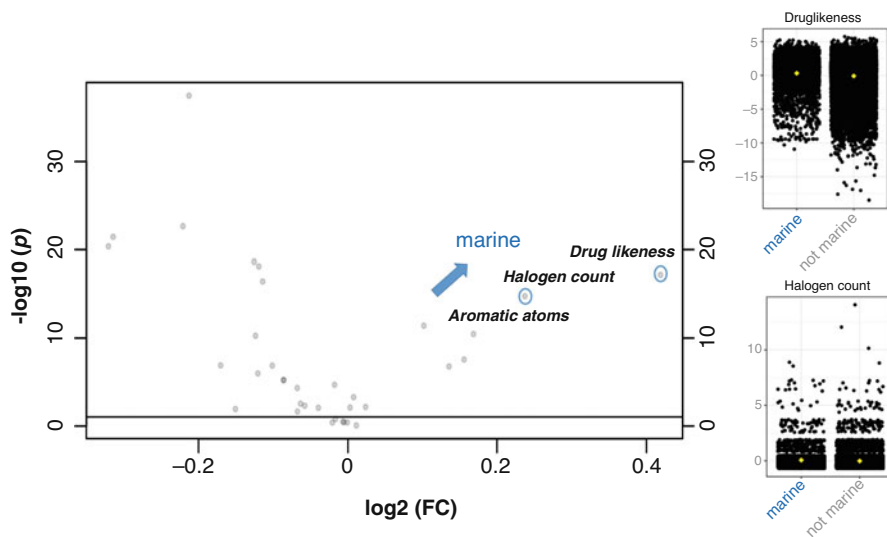


**Fig. 5.5** Representation of chemical space overlapping of fungal metabolites with metabolites first isolated from strains collected in the marine environment highlighted in blue. This graph was generated using “data warrior” software (Sander et al. 2015) after calculating different chemical properties and performing a principal component analysis

already shown that they are as structurally diverse as other natural products and cover relevant chemical space with drug-like physicochemical properties (González-Medina et al. 2016), the representation here shows that the marine environment may be even more interesting in this perspective. Marine fungal products then represent promising candidates for therapeutics. So far, plinabulin is the only marine fungal synthetic analog that has entered clinical trials now reaching phase III for the treatment of non-small cell lung cancer (Gomes et al. 2015).

#### 5.6.4 New Methods to Access the Marine Fungal Metabolome

Numerous approaches are available to investigate the fungal metabolome either based on culture-independent methods (e.g., genome mining, genetic engineering, heterologous expression) or culture-based ones (e.g., OSMAC, cocultivation, time-scale studies) (See Rédou et al. 2016a). Some new methods have been developed and seem ready to be used to access the marine fungal metabolome such as, for example, microscale platforms (Barkal et al. 2016), the development of CRISPR-Cas9 systems for filamentous fungi (Nødvig et al. 2015; Zhang et al. 2017), or molecular



**Fig. 5.6** Volcano plot presenting the most significant differentiating marine fungal metabolites (based on the same physicochemical properties calculated for the PCA)

networking (Oppong-Danquah et al. 2018). It is not the aim to describe all these approaches here but rather to list the putative next strategies to use in order to foster new research and generate novel knowledge on marine fungal metabolomics (see also Hautbergue et al. 2018; Hoang et al. 2018; Overy et al. 2019).

### 5.6.5 Marine Fungal Chemical Ecology: Ecological Role of Marine Fungal Metabolites

Efforts over the past decade to expand culture collections of terrestrial, freshwater, marine, and deep biosphere microbial fungi coupled with expanding databases with fungal genomic data are providing insights into the extent of fungal (including novel) diversity as well as the diverse metabolic capabilities of fungi.

Numerous studies have been done on the ecological role of chemical mediation by marine fungi. For instance, it has been shown that endophytic fungi associated with brown algae are able to protect the algal model *Ectocarpus siliculosus* against pathogenic infection through the production of fungal metabolites belonging to the pyrenocine series. A protection effect of the pyrenocines has been observed against oomycetes (i.e., *Olpidiopsis pyropiae* and *P. porphyrae*) infecting the economically important red seaweed *Pyropia* (Vallet et al. 2018). These findings suggest that brown algae-derived endophytes may determine the infection outcome of algal pathogens by chemically protecting their host through the production of chemicals. Brown algae-derived endophytic fungi interact with their host but are also likely to interact with bacteria within the algal holobiont to maintain the host–microbiota

equilibrium and thus contributing to maintain health of their hosts (Deveau et al. 2018; Hassani et al. 2018). The mechanisms underlying bacterial–fungal homeostasis remain unclear although they appear crucial for the macroalgal physiology. Evidence of a specific cell–cell signaling named “quorum sensing” among bacterial and fungal endophytes interactions of brown algae was provided by Tourneroche et al. (2019). Quorum sensing (QS), which allows bacteria to coordinate gene expression based on the density of specific signaling molecules, is of particular interest because it is essential for virulence, colonization, biofilm formation, and toxin production (Atkinson and Williams 2009). While the inhibitory activity against quorum sensing had been previously detected in marine fungi (Martín-Rodríguez et al. 2014), Atkinson and Williams (2009) demonstrate the importance of chemical communication, especially quorum sensing and quorum quenching (inhibition of QS), among bacteria and fungi sharing the same marine holobiont (*S. latissima*). The key role of QS in marine fungi functioning has been emphasized by a study carried out on the marine fungus *Paradendryphiella salina* isolated from several healthy brown macrophyte species (Vallet et al. 2020). Indeed, *P. salina* produces novel  $\alpha$ -hydroxy  $\gamma$ -butenolides that interfere with the bacterial quorum sensing system inhibiting QS phenotypes of the pathogenic bacterial *Pseudomonas aeruginosa*. Ultra-performance liquid chromatography–high-resolution mass spectrometry (UHPLC-HRMS)-based comparative metabolomics revealed the presence of the main  $\alpha$ -hydroxy  $\gamma$ -butenolides among all the *P. salina* strains isolated from different hosts as well as a high metabolic variability related to the alga-host species suggesting that the harboring algal species might have a substantial influence on fungal metabolism. Collectively, these findings strengthen the hypothesis of a key role of microbial chemical signaling which may occur within the algal holobiont.

In challenging habitats where there may be limited carbon availability the stress responses of fungi likely include processes that are known to induce expression of hydrolases, cell wall degrading enzymes, and secondary metabolites as means of survival (García-Lepe et al. 1997; Kim et al. 2011). This idea that interactions are mainly driven by chemical mediation is supported by metatranscriptome data from deep biosphere samples that show expression of genes associated with hydrolytic and polyketide biosynthetic genes (Quémener et al. 2020). Polyketides can have antimicrobial and antifungal properties and are frequently associated with fungal survival under nutrient limitation where competition for scarce resources is intense (Sheridan et al. 2015). This was recently using culture-based approaches highlighting deep subsurface fungi as able to produce antimicrobial compounds, presumably used in competition with other microorganisms for available carbon and energy (Navarri et al. 2016).

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## 5.7 From (Meta)Genomes to Bioactive Molecules

Rapid progresses in DNA-sequencing methods in the last decade from Sanger sequencing to various types of short read sequencing as well as advances in modern biology and biotechnology approaches have reached a point, where exploring

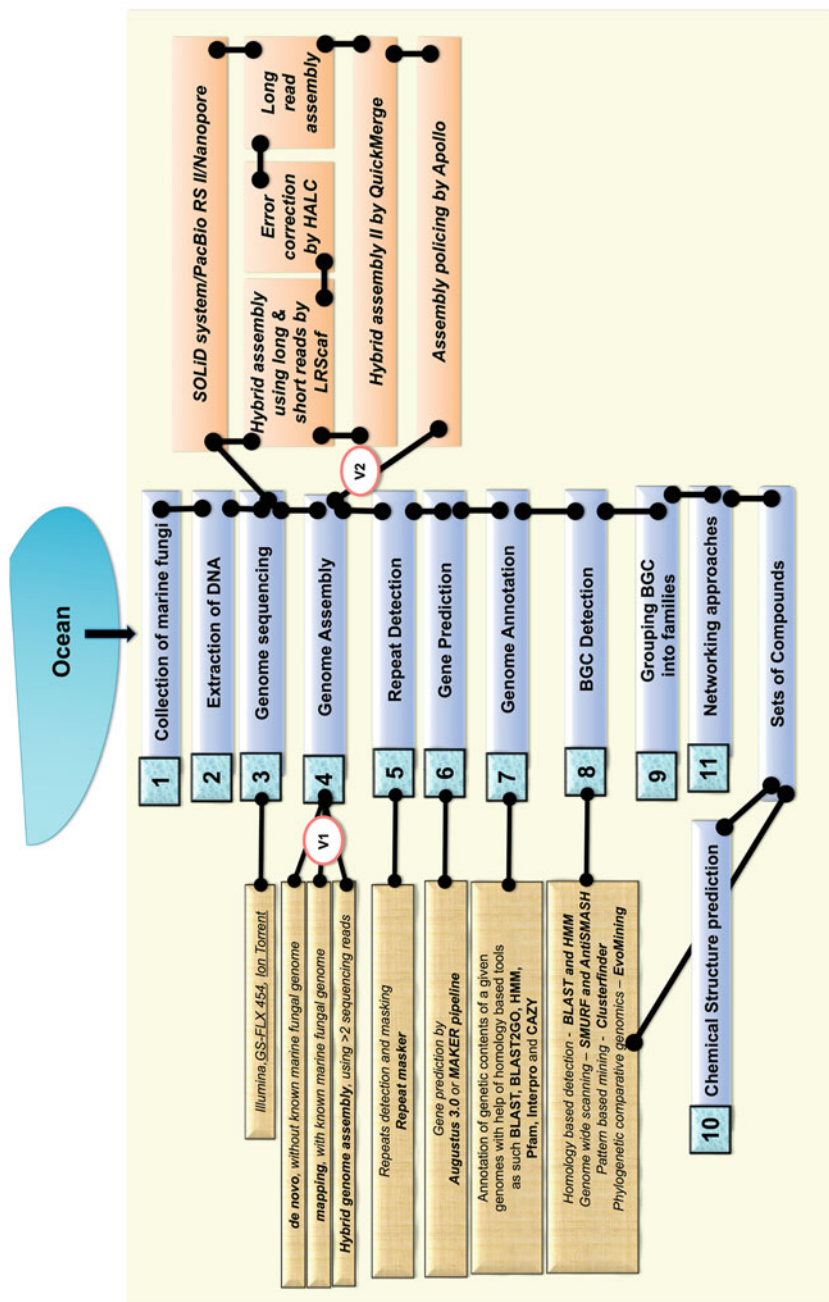
genetic information for any species of interest has become a quest requiring only a few months of time. This era of genome sequencing is often referred to as the era of “Desktop genomics.” Short read sequencing methods are collectively called Next-Generation Sequencing (NGS) methods and the primary NGS platforms include: the Roche GS-FLX 454 pyrosequencer, MiSeq, HiSeq, and Genome Analyzer II platforms (Illumina), SOLiD system (Life Technologies/Applied Biosystems), Ion Torrent and Ion Proton (Life Technologies), and the PacBio RS II system (Pacific Biosciences) (Culligan et al. 2013; Metzker 2010).

Fungal genome sequencing and analyses began with yeast models (Goffeau 2000; Goffeau et al. 1996) and were followed by the filamentous fungus *Neurospora crassa* (Galagan et al. 2003). Within 14–15 years ~50 fungal genomes were obtained using Sanger sequencing. In 2010 the *Sordaria macrospora* genome was sequenced using more than one NGS method (Nowrousian et al. 2010). This accelerated other fungal genome sequencing projects using NGS methods. To date, over 1000 fungal genomes have been sequenced thanks to the 1000 fungal genomes project aiming to cover all groups of fungi (Grigoriev et al. 2014). However, there are only a few marine fungal genomes sequenced to date, which are primarily derived from EU-funded projects, like “Marine Fungi” (FP7, 2011–2014) and “MaCuMBA: Marine Microorganisms: Cultivation Methods for Improving their Biotechnological Applications” (FP7, 2012–2016).

Fungi generally produce four different types of secondary metabolites (SMs), namely polyketides (PKS), non-ribosomal peptides (NRPS), terpene or hybrid molecules such as PKS-NRPS or PKS-terpenes (Keller et al. 2005). The majority of fungal secondary metabolites derives from either non-ribosomal peptide synthetases (NRPSs) or polyketide synthases (PKSs) while only a few are hybrid NRPS-PKS (Brakhage 2013). Generally, SM-encoding genes are organized in discrete clusters (Brakhage 2013; Keller et al. 2005) called biosynthetic gene clusters (BGCs). The genomes of filamentous fungi possess up to 70 BGCs encompassing from 30–80 kb regions on fungal chromosomes or scaffolds (Bok et al. 2015). Production of SMs is regulated by cluster-specific transcription factors and global regulators within BGCs (Brakhage 2013; Keller et al. 2005). SMs are highly relevant for drug discovery particularly for new antibiotics and pharmaceuticals (Newman and Cragg 2020). There is huge potential in fungal bioactive compounds which are expected to serve many roles for future drugs (Montaser and Luesch 2011).

Here, we propose a general pipeline for genome sequencing and annotation of marine fungi using short and long read sequencing (Fig. 5.7).

1. The first step is collecting samples from the targeted marine environment.
2. The second step is bringing samples to the laboratory to establish enrichment cultures under laboratory conditions, to isolate individual fungal strains, and to extract genomic DNA. If the aim is to process a metagenomic analysis, then DNA extraction directly from marine samples can be performed with described methods and some modifications (see Kumar et al. 2015).
3. The third step is genome sequencing using next-generation methods like the Illumina platforms, which are also cost-effective choices. However, a hybrid



**Fig. 5.7** Overview of genomic and metagenomic assemblies and annotation analyses based on short and long read DNA-sequencing data derived from marine fungi originating from the marine environment



assembly of data from two or more methods is recommended. For instance, the genome of *Scopulariopsis brevicaulis* LF580 has been sequenced using a combination of three methods (Kumar et al. 2015).

4. The fourth step is genome assembly, which assembles reads into genomic fragments called contigs or larger scaffolds. Genome assembly can be achieved in two ways. De novo genome assembly is used when a closely related fungal genome is not known and reads are assembled by genome assemblers without prior knowledge of chromosomes. Alternatively, in case the genome of a closely related fungus is available smaller reads can be mapped to the chromosomes of that close relative's fungal genome and this method is called genome mapping. When more than one type of genome sequencing reads is obtained using different sequencing platforms a hybrid genome assembly can be performed and this can increase the quality and coverage of the overall assembly by allowing longer reads to bridge gaps or scaffold shorter reads. There are several genome assemblers available for genome assembly and can be chosen depending on the requirements and types of genomic reads. A good example is documented in the genome assembly of *Scopulariopsis brevicaulis* LF580 (Kumar et al. 2015) with (a) an initial genome assembly performed using Roche 454 reads and the Newbler assembler (Margulies et al. 2005) coupled with (b) an assembly based on a de Bruijn graph through a de novo assembler in the CLC Genomics workbench (Knudsen and Knudsen 2013) which used different types of reads from Illumina and Ion Torrent and (c) a hybrid genome assembly that was achieved using three different types of reads. The genome assembly normally produces genomes assembled into contigs with contigs joined to form scaffolds, which leads this method to be called "genome scaffolding."

The Roche 454 sequencing platform has been fading out of use while third generation sequencing platforms that produce longer reads like PacBio/Nanopore became more important. These sequencing methods have slowly become the standard for generating hybrid assemblies. Long read-sequencers minimize the issue of read length from the second-generation sequencing technologies (e.g., Illumina) however they often contain up to 15% sequencing errors. To decrease sequencing errors tools like HALC (Bao and Lan 2017) can be used, however Canu (Koren et al. 2017) has its own built-in tool to correct sequencing errors. The output of error correction tools can be used for long read sequence assemblers such as Canu which assembles sequencing data into long-range scaffolds. Similarly, HALC output can be submitted for hybrid assembly using tools such as LRScf (Qin et al. 2019) which combines draft genome assembly of short reads with long reads sequencing data. This hybrid assembly approach produces a more accurate assembly than short read assemblers alone. Furthermore, to refine genome assembly a LRScf hybrid assembly can be combined with a Canu assembly using QuickMerge (Chakraborty et al. 2016) tools to obtain more continuity in final genome assembly output.

5. Step five is the detection of repeat elements and masking of repetitive elements, which is an essential step as these elements hamper gene predictions in the next step. This detection and masking are performed using RepeatMasker and

RepeatProteinMasker software programs (<http://www.repeatmasker.org>) using the fungal transposon species library as an input. This library contains all known fungal transposon elements.

6. Step six is gene prediction which can be performed using either the Augustus suite (Stanke and Morgenstern 2005) or within the MAKER 2.0 pipeline (Cantarel et al. 2008).
7. Step seven is gene annotation which can be performed with the help of homology detection tools such as BLAST homology searches (Altschul et al. 1997), the OMICSBOX tool (Gotz et al. 2008), and the Kyoto Encyclopedia of Genes and Genomes (KEGG) database (Kanehisa et al. 2010). Predicted proteins of a given genome can be scanned for protein domains using Pfam (Finn et al. 2014) and InterPro (Hunter et al. 2012) protein domain collections using HMMER 3.0 (Finn et al. 2011). Additionally, gene annotations can be performed when the objective of the analyses is known. In case it is necessary to annotate carbohydrate active enzymes of a marine fungal genome scanning the entire proteome against either the CAZy database (Levasseur et al. 2013; Lombard et al. 2014) or the dbCAN database (Yin et al. 2012) can be used. This type of analysis is often known as analysis of genes of interests (Kumar et al. 2014). For example, when plant pathogen fungal genomes are sequenced the sets of pathogen specific genes are looked upon for annotation.
8. Step eight is the detection of BGCs and is performed following four different steps. Initially, putative biosynthetic genes are identified using either BLAST (Altschul et al. 1997) or HMMER 3.0 (Finn et al. 2011). This scanning is performed using a collection of known biosynthetic genes. Secondly, two state-of-the-art tools, namely Secondary Metabolite Unique Regions Finder (SMURF) (Khaldi et al. 2010) and antibiotics & Secondary Metabolite Analysis SHell (antiSMASH) (Blin et al. 2013) are recommended for whole genome scanning of putative BGCs. Furthermore, the functional domains of PKSs and NRPSs can be identified as previously described (Hansen et al. 2014), using a combination of tools, namely antiSMASH (Blin et al. 2013), NCBI Conserved Domain Database (Marchler-Bauer et al. 2011), InterPro (Hunter et al. 2012), and the PKS/NRPS Analysis Web-site (Bachmann and Ravel 2009). Pattern-based approaches can be employed by using *clusterfinder* modules within antiSMASH (Blin et al. 2013). Phylogenetic and comparative genome methods can also be used for BGC detection and analysis with help of genome browsers and specialized tools like EvoMining (Cruz-Morales et al. 2015).
9. Steps nine, ten, and eleven aim at to first group similar BGCs into families based on sequence and domain similarities. Then, mass-spectroscopy-based networking approaches can help in the detection of molecules predicted by genomes. Predictions of small molecule structure using knowledge of BGCs are laborious tasks although antiSMASH (Blin et al. 2013) makes an attempt to predict structures. This is challenging because our knowledge of fungal BGCs is limited and rigorous classification and indexing systems for BGCs do not yet exist. The scientific community has determined a standard for carefully cataloging BGCs, potentially important enzymes, and structural records present in the literature and

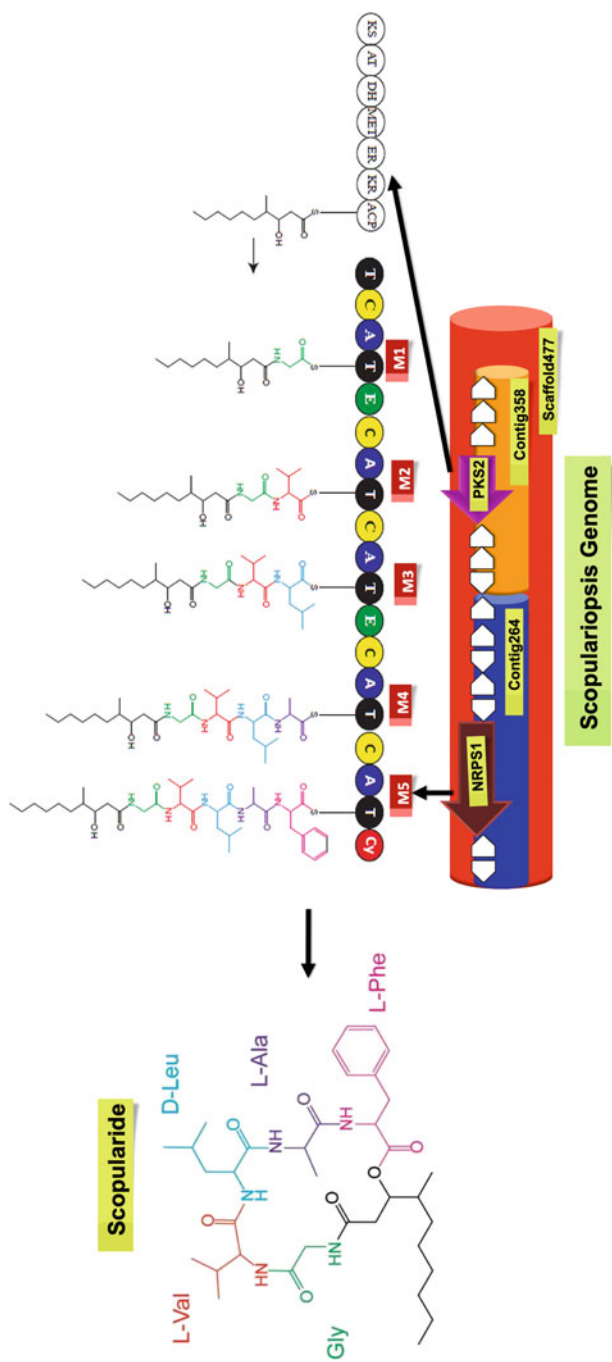
this will be incorporated into genome standards such as the Minimum Information about a Biosynthetic Gene cluster (MIBiG) (Medema et al. 2015). This will help in the near future for accurately predicting molecules from genomes. Further details for genome mining of BGCs can be found in the recent reviews (Boddy 2014; Medema and Fischbach 2015; Weber 2014).

Initial studies of marine fungal BGCs have been performed within the framework of EU-funded projects, namely “Marine Fungi” (FP7, 2011–2014) and “MaCuMBA: Marine Microorganisms: Cultivation Methods for Improving their Biotechnological Applications” (FP7, 2012–2016) during which five marine fungal genomes were sequenced and their BGCs were mined for further genetic engineering and production of selected bioactive compounds (Kumar et al. 2015; Kumar et al. 2018; Rédou et al. 2016b, c). These five marine fungi (namely *Scopulariopsis brevicaulis*, *Pestalotiopsis* sp., *Calcarisporium* sp., *Cadophora* sp., and *Cryptococcus* sp.) were sequenced using different sequencing techniques and expression profiles of SM-genes were analyzed (Kumar et al. 2015, 2018; Rédou et al. 2016b, c). These studies revealed that marine-derived fungi have high contents of SM-encoded genes and not all SM clusters are active under one particular condition as became evident from RNA-Seq based expression profiling of SM clusters (Kumar et al. 2015, 2018; Rédou et al. 2016b, c). These genomic analyses yielded evidence for several promising bioactive compounds with potential roles as antibiotics and anti-cancer metabolites.

Marine-derived fungi are considered as an excellent source of bioactive compounds and their genomes harbor many biosynthetic gene clusters (BGCs) from which these natural compounds are produced (Kumar et al. 2015, 2018; Rédou et al. 2016b, c). The genome sequence of the marine fungal strain of *Scopulariopsis brevicaulis* LF580 revealed 18 BGC clusters including one hybrid NRPS-PKS cluster (Fig. 5.8) which codes for anti-cancerous scopularides (Kumar et al. 2015). This cluster and remaining clusters were characterized using UV-mediated mutagenesis for the production of SM compounds through RNA-sequencing, proteomics, and comparative genomic approaches (Kramer et al. 2015; Lukassen et al. 2015). The other marine fungi *Pestalotiopsis* sp., *Calcarisporium* sp., *Cadophora* sp., and *Cryptococcus* sp. contain a total of 67, 60, 15, and 4 BGCs, respectively, emphasizing the high variability of such SM-encoding genes in marine fungal genomes.

Computational genome mining approaches alone cannot solve all problems associated with identifying fungal BGCs. Several BGC are silent under standard laboratory conditions leaving a plethora of bioactive compounds uncharacterized (Brakhage 2013). Hence, screening each fungus under a wide range of conditions appears essential to activate silent clusters.

Taken together, genome mining and detection of BGC involved in the production of bioactive compounds hold great potential. This is because initial genome mining reveals several different types of BGCs in marine fungal genomes. Heterologous expression systems have already been developed for the entire set of intact fungal BGCs using fungal artificial chromosomes (Bok et al. 2015). It is a matter of time



**Fig. 5.8** An example of genome mining strategies for the marine fungal strain *Scopulariopsis brevicaulis* LF580 illustrates production of anti-cancerous scopularides by the hybrid BGC of NRPS1 (five modular M1-M5) and PKS2. Modified from Kumar et al. (2015)

before BGCs will be characterized in heterologous systems. This holds great promise for the future of drug discovery for which genome mining of BGCs plays a fast and cost-effective role.

**Acknowledgements** AK is a recipient of Ramalingaswami Re-Retry Faculty Fellowship (Grant; BT/RLF/Re-entry/38/2017) from Department of Biotechnology (DBT), Government of India (GOI). BTH is supported by the Seasonal Ice Zone Ecology Project (SIZE). VE acknowledges funding from the National Science Foundation grants OCE-1658031 and OCE-1829903. GB and AP acknowledge funding from the French National Research Agency grant ANR-19-CE04-0001-01 (Mycoplast).

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