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Who are the marine fungi?

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Fungi are widespread throughout marine habitats. Most marine fungi are microscopic, either microfungi, yeasts, or swimming zoospore-producing groups such as the Chytridiomycota ('the chytrids'). The macroscopic exceptions are the marine lichens along coastlines. Marine mushrooms are yet to be discovered. The functional roles of marine fungi include parasites (e.g., infecting phytoplankton; Hassett & Gradinger, 2016), saprotrophs recycling organic matter (e.g., degrading phytoplankton-produced polysaccharides; Cunliffe et al., 2017) and in symbiosis with other marine life (e.g., seaweeds; Bonthond et al., 2022). Here, I briefly summarize my perspective of marine fungi with an emphasis on identity. Looking into the crystal ball, I see a possible near future for marine mycology highlighting some conceptual and technical developments.

The first marine fungus was described in the middle of the 19th century and subsequently for several decades, early pioneers (e.g., Sparrow, 1936; Sutherland, 1915) extended a list of new species. The first proposal of a definition to identify marine fungi came in the mid-20th century and was simply based around the physiological ability to grow in seawater (Barghoorn & Linder, 1944). Earlier studies had already shown that some fungi collected from the marine environment are the same or at least similar to non-marine taxa (Sparrow, 1937), and an updated definition of marine fungi was made to separate the obligate marine fungi (i.e., fungi that only grow and sporulate in the marine environment) from facultative marine fungi (i.e., fungi that are from the non-marine ecosystems that are still able to grow and sporulate in the marine

environment) (Kohlmeyer & Kohlmeyer, 1979). The definition of a marine fungus was further developed to identify any fungus able to grow and/or sporulate in the marine environment or adapt and evolve or be metabolically active in the marine environment or form symbiotic relationships with other marine organisms (Pang et al., 2016). From the first described marine fungus, the legacy of collecting, characterizing, and cataloguing continues with an expanding compendium of marine fungal diversity (Jones et al., 2015, 2019). All this work is made possible through collecting samples, observing fungi living on substrates, stimulating spore production, growing fungi and/or cultivation on artificial media, with taxonomy from morphology and more recently in combination with DNA barcoding of phylogenetic marker genes. Jan Kohlmeyer with Brigitte Volkmann-Kohlmeyer need to be acknowledged here because they were some of the most prolific collectors and identifiers of marine fungi in the 20th and early 21st century with their herbarium of more than 25,000 specimens now held at the New York Botanical Garden. Cultivation-based approaches to identify would-be marine fungi are of course not perfect, and proof that the isolated fungus is active in the marine environment is important. Such information will help to distinguish the genuine marine fungi from cultured contaminants washed in from non-marine ecosystems that are present but not active (Kohlmeyer & Kohlmeyer, 1979).

As with many topics in environmental microbiology, the advent and subsequent application of DNA-based molecular ecology tools in the late 20th century offered a panacea to some limitations of culture-based

approaches and yet opened a Pandora's Box of issues likely to vex any typical 'Reviewer 2'. From early clone libraries and other now apparently obsolete techniques (e.g., my personal favourite was denaturing gradient gel electrophoresis), through to the current importunate production of high-throughput next-generation metabarcode libraries, we have an almost overwhelming bounty of apparent marine fungal diversity studies to peruse. These data-dense DNA surveys have allowed a new interpretation of marine fungal diversity that is different to the 'Kohlmeyer-type' view, including congruent spatial surveys that in some cases traverse entire ocean basins (e.g., Hassett et al., 2020) and temporal analysis from multiyear time-series (e.g., Taylor & Cunliffe, 2016). With adequate resources that are available to many researchers but not all, these DNA-based approaches are relatively quick and easy to conduct, and provide access to the field for those without the training or patience needed for identification covered in the previous paragraph.

Writing with the perspective of an eternal optimist, my gaze into the crystal ball is more of a wish list for the near future of marine mycological research, including a call for the wider inclusion of marine fungi in contemporary marine microbial and general marine science. As a general observation, there needs to be improved integration of fungi into wider understanding of the structure and function of marine ecosystems. Fungi still seem lacking from a consensus view of marine ecosystems at all levels. For example, I checked current editions of marine microbiology textbooks I use for undergraduate teaching and found marine fungi are included in some (Munn, 2020) but not others (Gasol & Kirchman, 2018). Who is responsible for this improved integration and how could this be achieved? Perhaps in part, this could be delivered with truly holistic whole system level approaches in marine science in which entire ecosystems are considered together, with fungi included alongside the usual suspects (bacteria, phytoplankton, etc.) in marine ecosystem functioning. Historic biases, including those associated with sampling approaches and assessment tools, can now be overcome to some extent with contemporary and inclusive methodologies à la *Tara Ocean*, for example.

We need a more realistic view of the identity of marine fungi that considers and combines both the culture dependent and independent approaches. Many of the marine fungi identified with culture-independent DNA-based tools are not on lists of 'obligate marine fungi' but are instead currently taxa more familiar to non-marine habitats and potentially fall into Kohlmeyer's category of 'facultative marine fungi'. The relatively short DNA sequences from metabarcoding and choice of phylogenetic marker genes [normally the internal transcribed spacer (ITS) DNA between small-subunit ribosomal RNA (rRNA) and large-subunit rRNA genes or part of the small-subunit rRNA gene] means

at best only genera are typically resolved with other studies having coarser taxonomic resolution that is difficult to fully interpret. Overcoming the limitations of interpreting the typical short sequences that constrain most metabarcoding surveys would be worthwhile. More sequence data could improve taxonomic resolution of marine fungi and therefore progress our understanding of the phylogeny of taxa that are similar but still different and currently not differentiated. Longer read metabarcoding is promising because it captures entire and multiple phylogenetic marker genes. How long read metabarcoding needs to be to distinguish the closely related marine and non-marine relatives should be assessed. Phylogenetic placement of the recently discovered marine fungus *Emericellopsis atlantica* in a clade of other marine relatives versus other species in the same genus and other non-marine clades required concatenated six-gene analysis (Hagestad et al., 2021). The level of resolution needed to distinguish marine fungi across all major groups needs exploring.

'Nothing in biology makes sense except in the light of evolution' Theodosius Dobzhansky. As well as improving DNA-based taxonomic resolution, developing a better understanding of the identity of marine fungi would also be supported by a clearer view of their evolution and therefore systematics. This includes improved insight into terrestrial and freshwater-to-marine transition events, which are critical in determining marine fungal evolutionary history and contemporary diversity. Compared to other microbial eukaryotes, terrestrial/freshwater to marine transition events have occurred many more times with fungi and often only 'recently' in an evolutionary sense (Jamy et al., 2022). Why and how did these transition events specifically occur in the fungi? The why could include the regular transport of terrestrial and freshwater fungi to marine ecosystems via estuaries into coastal waters or fungi living in dynamic marginal habitats and ecotones at the land-sea coastal fringe such as on intertidal seaweeds and mangroves. The how is likely, in part, related to the incredible adaptive capabilities of fungi underpinning their ability to conquer distinct niches and general resilience/plasticity. An impact of these rapid and recent transitions to marine is that there is not much change in the phylogenetic marker genes currently used (Jamy et al., 2022). This could account for why many marine fungi in short read metabarcode studies appear the same or similar to terrestrial/freshwater fungi.

Identity and functional biology are frequently overlapping concepts in environmental microbiology. The two-component research question '*who is doing what?*' is probably a key aspect of many of our endeavours. More knowledge of the functional biology of marine fungi is also required. Think about nitrogen fixation in the marine environment and you might also be thinking about the marine diazotrophic cyanobacterium genus *Trichodesmium*. Oil degradation and the hydrocarbonoclastic genera *Alcanivorax* or *Cycloclasticus*.

Marine primary production and the diatoms (*Chaetoceros*, *Skeletonema*, etc.). Comparable levels of established understanding of the links between functional biology and identify of marine fungi are yet to be widely considered, with some groups such as the marine chytrids especially poorly studied (Laundon & Cunliffe, 2021). Here is an example to illustrate potential. The widespread yeast *Malassezia* was initially a surprising member of the marine mycobiome with close non-marine relatives typically found living on skin (Amend, 2014); however, assimilation of ^{13}C -labelled diatom-produced organic matter in stable isotope probing (SIP) experiments have shown that marine *Malassezia* are active saprotrophs in coastal waters (Cunliffe et al., 2017) and the open ocean (Orsi et al., 2022).

Insightfully, Kohlmeyer and Kohlmeyer (1979) outlined what they called ‘unsolved major problems’ in marine mycology, which included the need for the quantification of biomass, abundance and activity. Some progress has been made since 1979 to address their concerns, but more work is needed. Only very few studies have quantified marine fungal biomass and abundance (e.g., Gutiérrez et al., 2011; Priest et al., 2021), certainly much less than other marine microbial groups. Marine fungal activity has been determined now in several different ways. Seeing is believing and some marine fungi are conspicuous in their activity, such as marine chytrids that are observed infecting diatoms in sea ice (Hassett & Gradinger, 2016) and the open ocean (Gutiérrez et al., 2016). With new ‘single spore’ DNA barcode techniques developed for freshwater chytrid parasites (Kagami et al., 2021), the identity of the marine chytrid parasites in action is possible. The lichens are perhaps the most obvious marine fungi in their activity, we see them living along coastlines with their symbionts (Christmas et al., 2021). Activity has been shown through ^{13}C assimilation in SIP-type experiments with examples already mentioned (Cunliffe et al., 2017; Orsi et al., 2022). RNA-based studies of marine fungi have also been conducted, such as metatranscriptome indications of functional biology in the open ocean (Christmas & Cunliffe, 2020). This work is still only a handful of studies from a small number of researchers, especially when compared to other marine microbial groups such as bacteria and protists. Greater exploration of marine fungal abundance, biomass (including production and turnover), and activity across all marine habitats and under changing conditions could be the ammunition needed to convince the wider marine microbiological and broader marine science community to include fungi in their view of the marine world.


AUTHOR CONTRIBUTIONS

Michael Cunliffe: Conceptualization (lead); writing – original draft (lead); writing – review and editing (lead).

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