

Figure 2. Temporally precise counter-singing in pairs of *S. teguina*.

(A) An example *S. teguina* counter-singing interaction. Sound waveforms are presented for each vocal partner. (B) All vocal interactions in a day ($n = 101$) wherein Mouse #2 (in red) often responds to the vocalizations of Mouse #1 (in black). (C) Probability of Mouse #2's vocal onsets during counter-singing with Mouse #1. Figure modified from Okobi *et al.* (2019).

pharmacological inactivation of the orofacial aspect of motor cortex, we found that, while the ability to sing remains intact, vocal coordination is severely compromised. These results suggest a hierarchical arrangement, in which song production is mediated by subcortical structures, while the processes capable of coordinating rapid vocal exchanges are controlled cortically. Taken together, multiple lines of evidence point towards a crucial role of motor cortex in *S. teguina* vocal exchanges, enabling us to understand its role in a natural, ethologically relevant social behavior.

What makes singing mice interesting for neuroscience?

Understanding the neural mechanisms that allow the brain to perceive sensory input and generate appropriate motor responses is a central theme in neuroscience and is traditionally studied in the lab by training animals to associate simple sensory cues with motor outputs. Although counter-singing behavior in

S. teguina is a complex sensorimotor behavior, it does not require any training, enabling the study of neural dynamics underlying natural social interactions.

Are singing mice amenable to laboratory study? Yes. They breed throughout the year, and a colony can be maintained in the laboratory relatively easily. Importantly, they exhibit robust vocal behaviors even in a laboratory setting, and many of the natural interactions can be artificially tested using speaker playback assays. Because they are Muroid rodents, reagents developed for lab mice can readily be adopted to the singing mice, including neural circuit-mapping and optogenetic control of specific neuronal subtypes. Studying vocal communication in *S. teguina* and related species provides a great opportunity to understand how the interplay between ecology, evolution and neuroscience shapes social cognition.

Where can I find out more?

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Primer Marine fungi

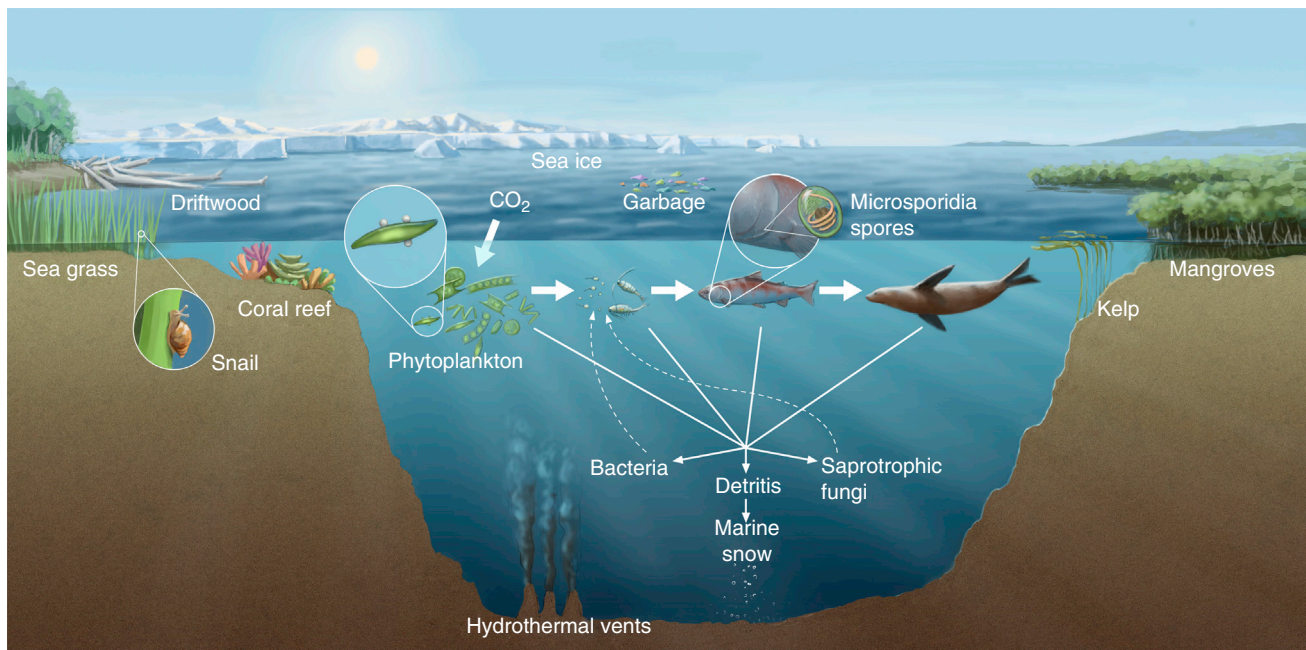
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Fungi play a dominant role in terrestrial environments where they thrive in symbiotic associations with plants and animals and are integral to nutrient cycling in diverse ecosystems. Everywhere that moisture and a carbon source coexist in the terrestrial biosphere, fungi are expected to occur. We know that fungi can be devastating to agricultural crops, both in the field and during their storage, and cause mortality in immunocompromised patients in numbers that rival the deaths from malaria. Yet fungi can also be harnessed as sources of food, chemicals and biofuels when humans exploit fungal metabolism. Despite their central role in the health and disease of the terrestrial biosphere, much less is known about the function and potential of marine fungi. Are fungi ubiquitous in marine environments as they are on land? Do they play the same or similar roles in these ecosystems? Here we describe the state of knowledge about the abundance and functions of fungi in the marine environment with a goal to stimulate new inquiry in this very open area.

Fungi in the ocean

Although you will not find them on restaurant menus or on the album covers of psychedelic rock bands, marine fungi do exist. In fact, they exist in every marine habitat where researchers have bothered to look: from hydrothermal vents, subsurface deep-sea sediments, and arctic ice, to surface waters, salt marshes and sandy beaches at low tide (Figure 1). Marine fungi are especially adept at living on or inside other living things like algae, corals, sponges and even other fungi. Even primary producers like dinoflagellates and diatoms are commonly infected by marine fungi, a dynamic that might play an important role in global carbon cycles. Although few researchers have tried to quantify their actual biomass, it seems that this can even exceed that of bacteria, particularly in habitats rich in organic carbon.





Current Biology

Figure 1. Diversity of marine fungal habitats and the ecological roles of marine fungi.

Fungi function as parasites at many trophic levels. The importance of chytrid fungi in parasitism of marine phytoplankton is increasingly recognized, and fungal parasites are also known from invertebrates, fish, and even top predators such as seals and dolphins, which are susceptible to cryptococcosis. Little is known about fungal parasites of fish, but the best-known examples are the intracellular parasites known as microsporidia. Fungi also function as major saprotrophs in oceans, converting detritus and algae into fungal biomass that, along with bacterial heterotrophs, become consumed by zooplankton and form a microbial loop connecting recalcitrant polymers derived from primary productivity to the rest of the food chain. Fungi are known to be excellent at degrading wood, for example, the marine mushrooms *Nia* and *Halocyphina* found on driftwood, and these adaptations also facilitate their ability to degrade plastics. Future exploration of fungi inhabiting the Great Pacific garbage patch is warranted. Fungi and their propagules are particularly diverse in marine sediments, even at the great depths of the ocean. Fungi function also as endosymbionts, such as the endophytes of sea grasses and mangrove trees. It is believed that a farming-like mutualism evolved between *Littoraria* snails and intertidal fungi inhabiting the seagrass *Spartina*; snails graze on live grass primarily to prepare the leaf as a substrate for fungal growth, which they then consume. Fungi can be isolated from living and dead seaweeds, but knowledge on fungal function and diversity in kelp beds is minimal. The fungal relationship with corals is complex, and the diversity of fungi on coral reefs numbers in the hundreds of species, most of whose roles in this habitat are uncertain. Fungi also are being detected in Arctic sea ice, and fungi are even associated with invertebrates and sediments near deep-sea vents thousands of meters below sea level. These habitats are rich in the fungal groups Chytridiomycota and Cryptomycota, early diverging lineages that may have never evolved a terrestrial ancestor, unlike the majority of marine fungi. Illustration by John Megahan.

Given their widespread distribution and abundance, it may be surprising that marine fungi receive considerably less attention than either their terrestrial counterparts or other marine microbes. However, marine fungi are easily overlooked. Only a handful, so far as we are aware, form anything remotely resembling the conspicuous fruiting bodies, like mushrooms, in their natural habitat. Throughout the twentieth century, a handful of pioneering researchers used time-consuming culturing techniques to characterize marine fungal diversity, although inherent biases in this process greatly limited the assessment of their true diversity. In particular, obligate biotrophs and unculturable so-called ‘early diverging lineages’ were just not detected.

Challenges to assessing fungal diversity in the marine environment

Paradoxically, most major fungal groups diversified long before their plant and animal counterparts invaded land, yet there are only about 1,000 or so described species that are largely derived from terrestrial ancestors. Although it is thought that potentially as few as 1% of marine fungi have been identified, what we do know thus far is, in large part, because of the pioneering work by Jan, Erika and Brigitte Kohlmeyer, who identified over 150 new species and 50 genera of marine fungi through the arduous work of collecting in diverse habitats around the world. They painstakingly developed methods and preserved 25,000 specimens along with field notes in the New York Botanical Garden herbarium,

which remains today a vast resource for understanding marine fungal biodiversity. In today’s world, there is vanishing support for such classic collection endeavors, which have been replaced by more high-tech and high-throughput identification methods.

It wasn’t until the advent of DNA-sequencing technology that the extensive diversity of marine fungi began to be appreciated. But large-scale DNA-sequencing projects are not the panacea that marine mycologists once hoped for. Although a handful of high-profile ocean expeditions (for example, the Global Ocean Sampling Expedition, the International Census of Marine Microbes, and the Tara Ocean Expeditions) have provided an impressively broad molecular sampling of marine microbes, their

methods tend to exclude or minimize fungal identification. Because the typical bacterium is roughly an order of magnitude smaller than the typical fungal spore (and smaller still than the typical hypha), size fractionation achieved by 'pre-filters' excludes fungi before nucleic acids are even extracted. Primer bias is also problematic: so called 'general' eukaryotic primers miss much of fungal phylogenetic diversity, and even the most 'fungal-specific' primers tend to co-amplify zooplankton and other invertebrates that collect on filters and swamp out fungal data. Shotgun-sequencing approaches, which mitigate priming biases, nevertheless tend to overlook fungi, which are underrepresented in reference databases. In addition to the comparatively limited collection effort, the relative low abundance of fungal DNA (as compared to bacteria) and the tendency for fungi to be patchy in space and time have frustrated large-scale assessments of diversity and distribution of marine fungi.

Discovering new marine fungi

Despite these difficulties, researchers continue to make progress towards uncovering marine fungal diversity by exploring new habitats and leveraging modern techniques. Although global biodiversity hotspots such as the coral triangle or 'unexplored' regions of our deep ocean trenches and subsurface surely harbor exciting and unanticipated surprises, DNA metabarcoding shows that numerous undescribed marine fungi exist even in the most accessible habitats, such as the near coastal surface waters and sediments. The pioneering work of the Kohlmeyers preceded similar cultivation efforts around the world, and innumerable cultures abound in freezers and slants at universities and research institutes, including popular repositories like the Westerdyk Institute, the American Type Culture Collection, or the marine culture collection at Geomar. Many of these efforts have been buoyed by funding to search for novel natural products. To date there has been little effort to coordinate these living collections, much less interrogate them systematically for novel species. Lamentably, very few isolates from

the Kohlmeyers' collections, nor other large marine fungal collections, are linked to publically available DNA-sequence data.

Although isolation into pure culture remains the gold standard for discovery and description of new marine fungi, novel methods in imaging and genome sequencing might be an expedient way to infer something about the lifestyles, ecological roles, and evolutionary history of newly discovered fungal taxa. For example, the use of fluorescent stains and clade-specific DNA probes have been used to visualize and describe the size, flagellation, host association, and cell-wall composition of members of Cryptomycota, a phylum that is common in aquatic habitats but which lacked cultivated isolates. Such imaging techniques, coupled with advances in microfluidics and flow cytometry, make it possible to isolate single targeted cells from a natural environment, subject them to various physiochemical conditions, and sequence their expressed genes or even entire genomes. Such strategies may be essential for understanding the functions of 99% of undocumented marine diversity, much of which is composed of as-yet unculturable species.

Fungal contributions to the marine environment

In the transition zones of salt marshes and mangrove swamps, the functions of marine fungi are likely quite similar to those of their counterparts in terrestrial ecosystems: establishing symbioses with flowering plants, playing key roles in nutrient cycling and degradation of cellulose materials. The functions of fungi in the deep sea, the water column, in coral reefs and within plankton communities is less well established; however, there is evidence of fungal activity throughout these diverse regions of the marine environment.

Pathological associations are easiest to identify, and fungal infection has been associated with disease in macroalgae, coral, crustaceans and even marine mammals. Around the world, fungi have been blamed for coral death in reefs that are likely already stressed. In the case of coral, knowledge of mycobiome composition and function is limited, although it is

clear that fungi associate with healthy reefs, reside in the calcium skeleton, and likely decompose senescent rubble. Fungal pathogenesis of phytoplankton is well established in freshwater where infection is thought to be critical for nutrient cycling. The extent of marine fungal pathology of phytoplankton is less established in salt water; however, evidence is mounting from direct microscopic observations (Figure 2) and intriguing spatial and temporal correlations that population cycles may be synchronized in several ocean contexts. These dynamics could ultimately be central to reallocating atmospheric carbon to sediments and might implicate marine fungi as a critical player in ocean carbon sequestration. There is also evidence of fungal activity in the sediments of the deep sea, where they may play a similar role in nutrient cycling as in terrestrial environments. As assays for activity become more sensitive and it becomes clear how to identify fungal-rich habitats, functional roles of fungi in marine environments as well as global geochemistry cycles should become more evident.

Adaptations required to survive in the marine ecosystem

Aquatic and marine fungi face substantial challenges compared to their terrestrial counterparts. Namely, they must tolerate high salinity, exposure to ultraviolet light, limited access to substrates for growth, and in some cases substantial hydrostatic pressure. Furthermore, being in water brings distinct dispersal challenges.

The most obvious stressor in the oceans is the high salinity leading to osmotic and ionic stress. At ~0.6 M NaCl, seawater might conceivably halt the growth of most fungi, which have rigid cell walls and grow and divide under substantial turgor pressure. However, marine fungi are not typically halophilic; although some can tolerate very high salinity, they do not show a preference for it, and similarly, most non-marine fungi can grow to some degree in near-seawater concentrations of salt. How do fungi control turgor in a hypertonic environment? The answer seems in part tied to a conserved pathway known as the high-osmolarity-glycerol signaling pathway that upregulates

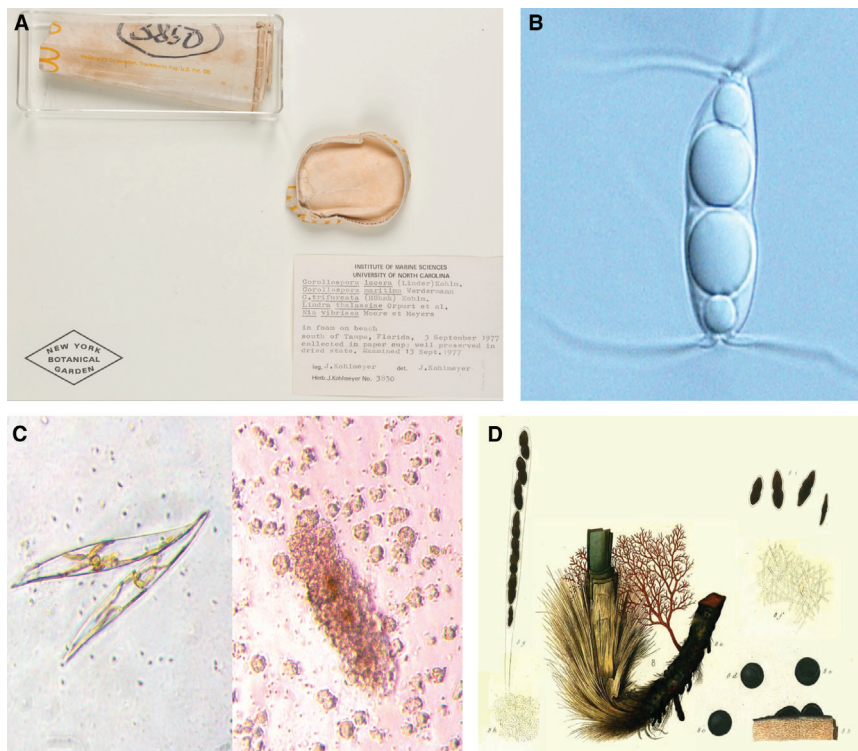


Figure 2. Images of marine fungal diversity.

(A) A collection of five marine fungal species collected by Jan Kohlmeyer from Florida sea foam in a McDonald's cup, a part of the marine mycology collection at the New York Botanical Garden. (B) Ascospore of common *Arenariomyces trifurcatus*. Note the conspicuous winged appendages presumed to aid in buoyancy and dispersal (photo credit: Ka Lai Pang). (C) A diatom, *Pleurosigma*, during initial infection by marine fungal zoospores and one week later (photo credit: Brandon Hassett and Marti Amargant). (D) A plate depicting *Sphaeria posidoniae* (= *Halothia posidoniea*), the first described marine fungus, observed on the rhizomes of *Spartina* in coastal Algeria and published in 1850, by Desmazière in *Plantes Cryptogames, Durieu de Mais*.

salt efflux pumps and creates osmolytes compatible with cellular functions. Another factor may be that fungi evolved for growth at high environmental osmolyte concentrations because they grow within their food and compete for uptake of sugars and other osmolytes generated by enzyme activity.

Life in the sea requires additional adaptations, in addition to a tolerance for salinity. High ultraviolet exposure may explain the prevalence of so-called black yeasts in marine environments that produce high levels of melanin in saline conditions. Gels and slimes are produced by wood-decaying marine fungi that may be involved in retaining secreted enzymes at the substratum. Another obvious adaptation for dispersing in an aquatic environment is the presence of a flagellum; indeed, that may account for the abundance of flagellated

fungi (chytrids and cryptomycetes) in some aquatic ecosystems. However, the efficiency of the flagellum may be debated in coastal ecosystems where tidal forces should provide a much greater movement. In these habitats, marine Ascomycota and Basidiomycota are known to have spore adaptations, such as extensive appendages that keep them in the water column longer (Figure 2B). Finally, extreme hydrostatic pressures found in the deep ocean require adaptations at the transcriptional or protein-coding level, as proteins are less stable and membranes less fluid. Interestingly, relatives of the human pathogen *Candida albicans* (which changes morphology in response to a host) change shape in response to hydrostatic pressure, indicating that not only are fungi tolerating extreme pressure, they are reacting and using this cue for cell-fate decision making.

Are marine fungi amphibious?

These intense environmental parameters raise an important, and at this point unresolved, conundrum about the origin of marine fungi and the possibility that some fungi are truly amphibious. One of the most unusual characteristics of marine fungi is that many of the same families, even some of the same species, are found both above and below the high tide line. This is particularly true of members of the Dikarya (Ascomycetes and Basidiomycetes), which are well characterized from habitats like soils and plants. Transitioning from land to a habitat such as a deep sea sediment requires tremendous physiological dexterity given the above-mentioned factors. Remarkably, fungi appear to have made such transitions repeatedly, and phylogenetic analysis shows that many marine fungi, even the most abundant or common, are nested within lineages known from terrestrial habitats.

An easy explanation for the high overlap in species between land and sea is the physiology of fungal spores, which can be produced in high numbers and are easily dispersed. If a spore originated on land and was somehow blown or washed into the ocean, its DNA would be detectable, regardless of whether or not it was still viable or metabolically active. By analogy, we should not consider *Veillea* jellyfish (by-the-wind-sailors) amphibious, even though they regularly wash up on the beach. So, it is only fair to consider fungi as 'marine' if they are able to perform some of life's basic necessities (for example, forage for food, grow, manufacture proteins, reproduce) whilst underwater. By way of example, let's consider one of the most common apparently amphibious species, *Malassezia restricta*, which is found in habitats as wide ranging as hydrothermal vents, corals, Antarctic soils and human skin. Is it really alive underwater?

Presumably, *Malassezia*, and other fungi with comparable distributions, must be innately tolerant of a range of environmental conditions that few other organisms can match in order to survive on both land and in sea. In the case of *Malassezia*, multiple lines of evidence indicate that this is the case: a high abundance and prevalence of DNA (including from locations thousands of

kilometers from a shoreline) indicates likely reproduction, putatively novel diversity indicates evolution, and detection of RNA transcripts involved in basic ‘housekeeping’ functions suggest that *Malassezia* in the ocean are alive and active. Although other species have received less scrutiny, available evidence suggests that marine fungi, on the whole, are actual contributing members of their aquatic ecosystems. Several studies have shown that marine fungi are partitioned by habitat, by environmental variables like temperature, salinity, and oxygen, and by nutrient levels such as dissolved inorganic carbon and sulfide, indicating that fungi are responsive to their environment. In a global study of marine fungi, proximity to land did not predict which fungi would be present, suggesting that terrestrial input is not a major component of marine fungal diversity.

Applications of marine fungi

The potential applications of marine fungi are vast, and their utility may pave a way forward for increased interest and funding in the field. The greatest effort in applied marine fungal research relates to the discovery and isolation of novel natural products, including secondary metabolites with antibacterial and anticancer properties. Although published research has focused primarily on a handful of readily cultivated ascomycetes such as *Aspergillus*, *Penicillium* and *Fusarium*, novel phylogenetic targets from a greater diversity of hosts and habitats are increasing steadily as is the discovery of new compounds. Future collaborations between marine fungal ecologists, evolutionary biologists and natural-product chemists may be a fruitful endeavor for all involved.

Considerably less studied are the potential roles that fungi might play in buffering the impacts of the anthropocene. Fungi are highly abundant in keystone marine species such as reef-building corals and sponges. Aside from their comparatively well-documented role in pathology, the functional roles of most of these symbionts are unknown. Nevertheless, coral microbiome compositions, including fungi, are impacted by, and likely impact, bleaching as a response to warming

ocean temperatures. Studies involving experimental evolution and probiotic microbial transplants are seen as one of the last hopes for thermo-susceptible coral species. Might fungi be the help these animals need?

If fungi have a superpower, it is their ability to degrade and metabolize recalcitrant polymers. Fungi, as a matter of fact, were the first organisms to degrade lignin: leading to a period of rapid diversification and reallocation of global carbon. Might marine fungi have another trick up their sleeves? Fungi are effective at metabolizing hydrocarbons, and can be used in bioremediation of contaminated sites following oil or petroleum spills. Even without active management, fungi quickly dominated sediments in the Gulf of Mexico following the Deepwater Horizon oil spill. Evidence suggests that some fungi even degrade plastics such as polyurethane. In fact, the ‘plastisphere’ is a large and growing habitat in the ocean, whose associated microbial diversity — and its potential role in plastic removal — is vast and little explored. A marine fungal solution to marine plastics has not yet been discovered, but plastic-eating species almost certainly exist in our oceans. It is therefore possible that the powers of this microbial community could potentially be engineered to degrade the Great Pacific garbage patch. We can only hope that if humans are unable to solve this environmental crisis on our own, fungi might eventually evolve to do it for us.

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