Review

Brandon T. Hassett[a,*], Tobias R. Vonnahme[a], Xuefeng Peng, E.B. Gareth Jones and Céline Heuzé

Global diversity and geography of planktonic marine fungi

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Abstract: Growing interest in understanding the relevance of marine fungi to food webs, biogeochemical cycling, and biological patterns necessitates establishing a context for interpreting future findings. To help establish this context, we summarize the diversity of cultured and observed marine planktonic fungi from across the world. While exploring this diversity, we discovered that only half of the known marine fungal species have a publicly available DNA locus, which we hypothesize will likely hinder accurate high-throughput sequencing classification in the future, as it does currently. Still, we reprocessed >600 high-throughput datasets and analyzed 4.9×10^9 sequences (4.8×10^9 shotgun metagenomic reads and 1.0×10^8 amplicon sequences) and found that every fungal phylum is represented in the global marine planktonic mycobiome; however, this mycobiome is generally predominated by three phyla: the Ascomycota, Basidiomycota, and Chytridiomycota. We hypothesize that these three clades are the most abundant due to a combination of evolutionary histories, as well as physical processes that aid in their dispersal. We found that environments with atypical salinity regimes (>5 standard deviations from the global mean: Red Sea, Baltic Sea, sea ice) hosted higher proportions of the Chytridiomycota, relative to open oceans that are dominated by Dikarya. The Baltic Sea and Mediterranean Sea had the highest fungal richness of all areas explored. An analysis of similarity identified significant differences between oceanographic regions. There were no latitudinal gradients of marine fungal richness and diversity observed. As more high-throughput sequencing data become available, expanding the collection of reference loci and genomes will be essential to understanding the ecology of marine fungi.

Keywords: Baltic Sea; Blastocladiomycota; Chytridiomycota; Dikarya; Red Sea; rRNA.

[a]**Brandon T. Hassett and Tobias R. Vonnahme:** These authors contributed equally to this review.
***Corresponding author: Brandon T. Hassett,** Department of Arctic and Marine Biology, University of Tromsø – The Arctic University of Norway, 9037 Tromsø, Norway, e-mail: brandon.hassett@uit.no
Tobias R. Vonnahme: Department of Arctic and Marine Biology, University of Tromsø – The Arctic University of Norway, 9037 Tromsø, Norway
Xuefeng Peng: Marine Science Institute, University of California Santa Barbara, Santa Barbara, CA, USA
E.B. Gareth Jones: Department of Botany and Microbiology, College of Science, King Saud University, P.O. Box 2455, Riyadh 11451, Kingdom of Saudi Arabia
Céline Heuzé: Department of Earth Sciences, University of Gothenburg, Box 460, 405 30 Gothenburg, Sweden

Introduction

The Fungi are globally distributed members of marine ecosystems (Tisthammer et al. 2016, Morales et al. 2019), whose abundances are tied to phytoplankton (Taylor and Cunliffe 2016), organic matter (Ortega-Arbulú et al. 2018), and elevated photon fluxes (Hassett and Gradinger 2016). Marine fungi have been detected in the sub-seafloor (Orsi et al. 2013), in coastal marine sediments (Picard 2017), throughout the Arctic (Rämä et al. 2017), and cultured extensively in temperate and tropic regions (Jones and Pang 2012a). Marine fungi were known to exist since the 1800s and their diversity has been explored through many vigorous culturing and morphological-based diagnostic studies (Johnson and Sparrow 1961, Kohlmeyer and Kohlmeyer 1979). There are currently between 120,000 and 143,273 accepted fungal species (Hawksworth and Lucking 2017, www.indexfungorum.org); of these, 1255 species have been recovered from the marine realm (Jones et al. 2015, 2019). Even though fungi comprise substantial quantities of biomass in the marine realm (Gutiérrez et al. 2011, Bochdansky et al. 2017, Hassett et al. 2019), their activity is not represented in marine ecosystem models (Worden et al. 2015).

Marine fungi behave as saprobes and symbionts that can recycle nutrients (Gutiérrez et al. 2011). Marine fungi have been reported from a wide range of substrates, such as wood, culms of angiosperms (*Posidonia* K.D. Koenig,

Spartina Schreb.), manmade materials (polyurethane), and as parasites of marine animals (copepods, fish), algae (diatoms, brown seaweeds), corals, and sponges (Chakrarvarity 1974, Pivkin 2000, Lin et al. 2002, Nagai 2002, Proksch et al. 2008, Zheng et al. 2009, 2013, Pang et al. 2011, Jones and Pang 2012b, Debbab et al. 2013, Yao et al. 2014, Gutiérrez et al. 2016, Gnavi et al. 2017, Raghukumar 2017), especially in pursuits of natural product discovery (Bugni and Ireland 2004, Pan et al. 2008, Schulz et al. 2008). Marine fungi have historically been defined as those capable of reaching reproductive maturity while completely or partially inundated with seawater salinity of at least 30 during some point in their life cycle (Johnson and Sparrow 1961), though broader definitions have since been applied (Pang et al. 2016). Many common terrestrial/freshwater fungal species within *Cladosporium* Link, *Saccharomyces* Meyen *ex* Hansen, *Fusarium* Link, *Aspergillus* P. Micheli *ex* Haller, *Penicillium* Link can grow in environments with salinity >30 (e.g. Morrison-Gardiner 2002, Schulz et al. 2008). As a result, the definition of a marine fungus is not founded in a unifying evolutionary history, if one exists. Moreover, the genetically encoded underpinnings that interface and give rise to either osmoregulation or osmoconformation within any broadly distributed marine-terrestrial fungal species remain to be fully elucidated.

The known long-distance travel of fungal spores through the atmosphere (Hovmøller et al. 2008) and inferred sourcing of fungal spores from local terrestrial environments like pollen (Heusser 1988), indicate that a fraction of fungi detected in the marine realm are almost certainly of terrestrial origin (Frölich-Nowoisky et al. 2012). Some research postulates that aquatic environments may be an ideal place for long distance fungal dispersal to occur (Golan and Pringle 2017). Furthermore, some fungal species that are known to exist both on land and in the marine realm can survive in seawater for at least 8 months (Hassett et al. 2019). Paired with 0.13 m s^{-1} current velocity (Johnson and McPhaden 2001), some fungi can theoretically travel the distance between New Zealand and Antarctica. Consequently, the abundance and corresponding genetically detected biogeography of marine fungi should certainly be influenced by the reproductive success and subsequent dispersal of terrestrial fungi, especially among many members of the Dikarya, which are evolved for aerial dispersal (James et al. 2006). Despite substantial overlapping range distributions, freshwater and marine fungal communities are significantly different (Panzer et al. 2015).

Efforts to assess the composition of marine fungal communities have been guided by contemporary taxonomy (i.e. defining what was considered to be within the Fungi), and constrained by sampling effort and the application of the most-advanced methodologies to inform ecology (e.g. culturing versus cloning versus high-throughput sequencing). For example, given their ease of cultivation, marine yeasts within the Ascomycota and Basidiomycota were historically believed to be the most abundant fungi in the pelagic ocean (Fell 2012), despite their variable density (1–200 cells l^{-1}) in seawater (Nagahama 2006, Fell 2012). Sequencing efforts have identified marine fungal taxa with known yeast forms as some of the most abundant fungi (Bass et al. 2007, Panzer et al. 2015). However, with increasing capacity to sample an environmental community with high-throughput sequencing (HTS), novel insights (e.g. hyperabundances of zoosporic taxa) are being generated. From these combined efforts, every fungal phylum has now been detected in the ocean.

The use of HTS has resulted in an increased focus on the zoosporic fungi and their relevance in aquatic microbial food webs (Grossart et al. 2016). Intuitively, flagellated fungi seem most suited for life in the open ocean, as they possess phototactic (Kazama 1972) and chemotactic (Muehlstein et al. 1988) motility, which can be used to overcome sinking and low substrate concentrations in pelagic marine environments; however, other fungi are able to modulate their own sinking rates by possessing spherical lipid complexes that can confer buoyancy (Grolig et al. 2006). In the euphotic zone, the zoosporic Chytridiomycota fungi occupy a niche by seasonally parasitizing diatoms, particularly during blooms (Hassett and Gradinger 2016, Taylor and Cunliffe 2016). Diatoms' silica frustules serve as an effective barrier to many types of grazers (Hamm et al. 2003). Yet, Chytridiomycota can break through this barrier and, upon maturation, produce numerous zoospores that can be consumed by zooplankton. This trophic dynamic, termed the "mycoloop" (Kagami et al. 2014), likely contributes to organic matter recycling and biological turnover within the euphotic zone, which confers a potential reduction of particulate organic matter export. The relevance of the Chytridiomycota to higher trophic levels appears to be seasonal, generally peaking during the spring phytoplankton bloom in high-latitude marine environments (Cleary et al. 2017). Other zoosporic fungi include the Aphelida, Cryptomycota, Neocallimastigomycota, Olpidiomycota, and select members formerly within the Zygomycota, whose relative abundance in marine environments appears to be generally low, according to the limited number of DNA studies (e.g. Cheung et al. 2010, Jebaraj et al. 2010, Livermore and Mattes 2013, Hassett and Gradinger 2016), though with emerging exceptions (Rojas-Jimenez et al. 2019). While we can infer the ecological roles of these understudied fungi in the pelagic ocean from their better-characterized freshwater counterparts, there is currently little evidence outside of sporadic observations that they exist in marine environments.

The objective of this review is to summarize the known diversity, richness, and associated spatial patterns of the marine fungi. Specifically, we focus this review on planktonic fungi, including those fungi from the coastal (defined here as marine systems disproportionally influenced by the terrestrial realm, including the Mediterranean Sea and Baltic Sea) and pelagic realms. We first summarize the morphology based diversity and then supplement this compilation by analyzing publicly available nucleotide sequencing databases. The efforts of various HTS studies from across the world provide a unique opportunity to explore global patterns of planktonic fungal diversity. To capitalize on the availability of these datasets, we reprocessed and analyzed 659 (286 18S rRNA amplicon and 373 shotgun sequencing) datasets from across the world (Figure 1).

Morphologic-based diversity of planktonic marine fungi

Historically, studies of marine fungal diversity relied on microscopy and subsequent morphological identification (e.g. Sparrow 1973) to assess community composition. Many historical descriptions of marine fungi detailed diversity to a higher taxonomic level (e.g. Horner and Schrader 1982), or not at all. For example, Höhnk (1961) isolated fungi from seawater during a voyage of the Anton Dohrn for the International Geophysical Year project on the Greenland Shelf; however, even the taxonomic phylum from many of these fungi was never determined. Partially in response to the seemingly low concentration of planktonic marine fungi, substrates were used to increase the success of recovery to expand descriptions of diversity. Specifically, sterile manmade panels (Jones and Le Campion-Alsumard 1970) and wood were deployed into the sea (Meyers and Reynolds 1958, Byrne and Jones 1974) at depths up to 3975 m (Kohlmeyer and Kohlmeyer 1979). From these early efforts, approximately 60 pelagic fungi were recovered from test timber blocks (Table 1). Nearly all recovered species were identified as common, globally distributed yeasts and Ascomycota, such as *Antennospora quadricornuta* (Cribb *et* J.W. Cribb) T.W. Johnson, *Cirrenalia macrocephala* (Kohlm.) Meyers *et* Moore, and *Trichocladium alopallonella* (Meyers *et* Moore) Kohlm. *et* E. Kohlm. A few fungi were recovered from only one location, hinting at discrete geographic localization. As some of these recovered fungi are very common in sea foam (Tokura et al. 1982, Nakagiri 1989), the perceived discrete patterns detected in these early studies are now known to be driven by sampling effort (Finlay 2002).

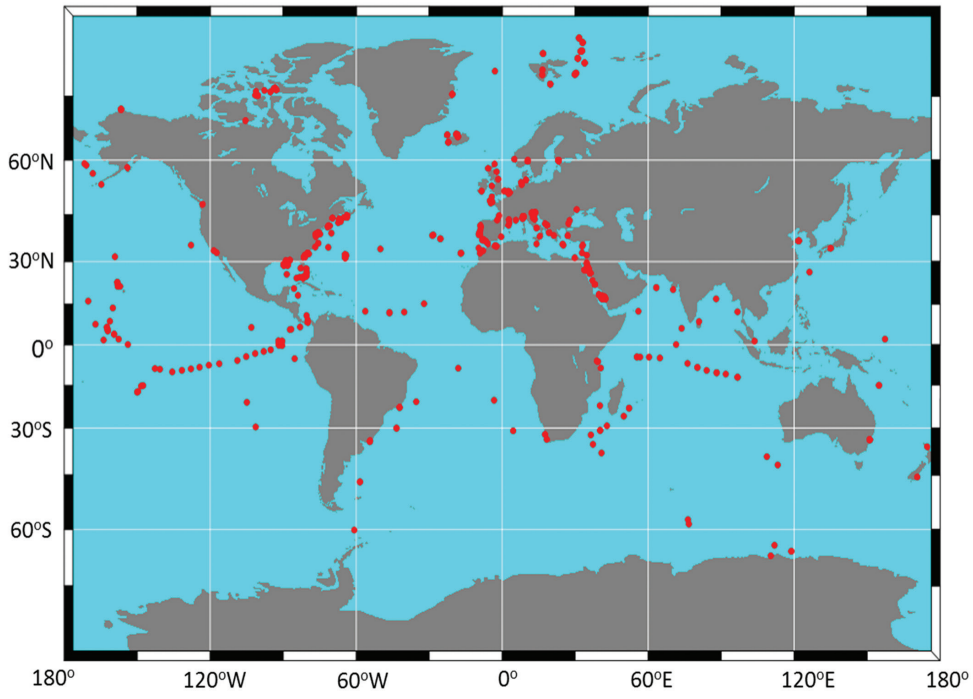

Figure 1: Global map displaying high-throughput sequencing data sampling sites in red that were used in this review for analysis. Some points represent multiple datasets.

Table 1: Selected common marine fungi recovered by submerging wood test panels.

Fungus	Country
Alternaria maritima G.K. Sutherl.	UK, Sweden, South Africa (Atlantic Coast)
Antennospora quadricornuta (Cribb *et* J.W. Cribb) T.W. Johnson	Antigua, Bahama, Haiti, British Honduras, Kuwait, Puerto Tahiti, Trinidad
Ceriosporopsis halima Linder	Antarctic (Atlantic coast), Argentina, Denmark, Japan, Sweden, South Africa
Cirrenalia macrocephala (Kohlm.) Meyers *et* R.T. Moore	France, Denmark, Ghana, Hong Kong, India, Italy, Japan, Sweden, UK, USA
Corollospora maritima Werderm.	Alaska, Antarctic, Argentina, Canada, Italy, Japan, South Africa
Dictyosporium pelagica (Linder) G.C. Hughes *ex* E.B.G. Jones	France, Denmark, Ghana, Hong Kong, Kuwait, UK
Halenospora varia (Anastasious) E.B.G. Jones	Hong Kong, Italy, Sweden, USA (Salton Sea)
Halosphaeria appendiculata Linder	Canada, Denmark, Italy, Kuwait, South Africa (Atlantic coast) Sweden, UK
Halosphaeriopsis mediosetigera (Cribb *et* J.W. Cribb) T.W. Johnson	Alaska, Antarctic, Argentina, Canada, Italy, Japan, South Africa
Lulwoana uniseptata (Nakagiri) Kohlm., Volkm.-Kohlm., J. Campb., Spatafora *et* Gräffenhan (Often as asexual morph *Zalerion maritimum*)	Antarctica, Africa (Atlantic Coast), Italy, Kuwait
Lulworthia floridana Meyers	Aden, Denmark, India, Italy, Singapore, Africa (Atlantic Coast), UK
Nereiospora comata (Kohlm.) E.B.G. Jones, R.G. Johnson *et* S.T. Moss	Antarctica, Denmark, Ghana, Italy, Sweden, UK
Nereiospora cristata (Kohlm.) E.B.G. Jones, R.G. Johnson *et* S.T. Moss (Often as asexual morph *Monodictys pelagica*)	Denmark, France, Hong Kong, Italy, Sweden
Okeanomyces cucullatus (Kohlm.) K.L. Pang *et* E.B.G. Jones (Often as asexual morph *Periconia prolifica*)	Indonesia, Ghana, Hong Kong, Kuwait
Remispora quadri-remis (Höhnk) Kohlm.	France, Ghana, Hong Kong, Italy, Sweden
Trichcladium alopallonella (Meyers *et* R.T. Moore) Kohlm. *et* Volkm.-.Kohlm.	Aden, Alaska, Antarctic, Argentina, Canada, Ghana, Hong Kong, India, Sweden, UK

Yeasts were some of the earliest observed and remain one of the most well-documented groups within the marine fungi (Kriss et al. 1952, Meyers et al. 1967a) that are now known to have a global distribution (Kriss 1963, Fell 1976, Kohlmeyer and Kohlmeyer 1979). Some yeasts appear to have a limited dispersal, such as select *Metschnikowia* Kamienski species in tropical waters in the Indian Ocean, *Blastomyces parvus* (Emmons *et* Ashburn) Jiang, Sigler *et* de Hoog in warmer Antarctic waters (Fell and Statzell-Tallman 1971), and *Candida natalensis* (van der Walt *et* Tscheuschner) south of the Indo-Pacific polar front. Yeasts are regularly found in unexpected environments, such as the sulfidic depth of the Black Sea (Kriss 1963) and up to ~4000 m depth (e.g. Nagahama 2006), underscoring their wide distribution.

Yeasts are a polyphyletic group of organisms belonging to the Ascomycota and Basidiomycota that are usually characterized by unicellular growth (Kutty and Philip 2008, Fell 2012). The study of marine pelagic yeasts was stimulated by the US Program in Biology, International Indian Ocean Expedition through which 25 species of yeasts were eventually isolated (Fell 1967). Currently, 214 marine yeast species in 65 genera (27 families) are known to exist in marine environments (Jones et al. 2019). Common genera of marine yeasts include *Cryptococcus* Vuill., *Debaryomyces* Lodder *et* Kreger-van Rij *ex* Kreger-van Rij, *Metschnikowia*, *Candida* Berkhout, *Torulopsis* Cif., *Rhodotorula* F.C. Harrison, *Kluyveromyces* Van der Walt, and *Rhodosporidium* Banno (Kutty and Philip 2008). However, most marine yeasts belong to the genera *Candida* (64 species), *Rhodotorula* (10 species), *Pichia* E.C. Hansen, and *Kazachstania* Zubkova (Table 2). Species within *Candida* and *Rhodotorula* appear to be the predominant genera encountered in culturing-based studies (Fell 2012, Jones et al. 2015). Ecologically, marine yeasts are known to degrade a wide range of biomass and hydrocarbons, and parasitize marine macrofauna (Kutty and Philip 2008). While observations indicate that yeast abundance is correlated with substrate availability (Nagahama 2006), there is still a lack of understanding of the environmental controls that regulate their distribution and activity.

As culturing poses a serious bottleneck at recovering diversity, and global sampling efforts are too few to determine large patterns of diversity, we chose to explore diversity and richness through nucleotide-based studies by mining publicly available sequencing databases and conducting analyses on phylogenetically classified nucleotide data.

Table 2: Pelagic marine yeasts isolated from seawater.

Species	Geographical location	Authority
Azymocandida mycoderma (Reess) E.K. Novák *et* Zsolt (=*Candida mycoderma* (Reess) Lodder *et* Kreger-van Rij)	Indian Ocean	Fell (1967)
Blastobotrys parvus (Fell *et* Statzell) Kurtzman *et* Robnett	Southern Ocean	Fell (1976, 2012)
Candida acidothermophilum Masuda, Kato, Takayama, Kida *et* Nakan.	North Sea	Meyers et al. (1967b)
C. albicans (C.P. Robin) Berkhout	Indian Ocean	Fell (1967)
C. atlantica (Siepmann) S.A. Mey. *et* Simione	Atlantic Ocean; Indian Ocean	Fell (1967), Meyers (1967b)
C. atmosphaerica Santa María	Indian Ocean	Fell (1967)
C. diddensii (Phaff, Mrak *et* O.B. Williams) Fell *et* S.A. Mey.	North Sea, Black Sea	Meyers et al. (1967a,b)
C. glabrata (H.W. Anderson) S.A. Mey. *et* Yarrow	Taiwan	Chen et al. (2009)
C. guilliermondii (Castell.) Langeron *et* Guerra	Black Sea, Indian Ocean	Meyers (1967a), Fell (1967)
C. lusitaniae Uden *et* Carmo Souza	North Sea	Meyers et al. (1967a)
C. natalensis Van der Walt *et* Tscheuschner	Pacific Ocean	Fell (1976)
C. neustonensis C.F. Chang *et* S.M. Liu	Taiwan	Chang et al. (2010)
C. parapsilosis (Ashford) Langeron *et* Talice	Biscayne Bay, Black Sea, Indian Ocean	Roth et al. (1962), Fell (1967), Meyers et al. (1967a)
C. polymorpha Y. Ohara *et* Nonom. *ex* M.T. Sm. *et* Batenburg-van der Vegte	Black Sea, Indian Ocean	Fell (1967), Meyers (1967a)
C. rugosa (H.W. Anderson) Diddens *et* Lodder	Indian Ocean	Fell (1967)
C. suecica Rodr. Mir. *et* Norkrans	Swedish west coast	De Mianda and Norkrans (1968)
C. tenuis Diddens *et* Lodder	Indian Ocean	Fell (1967)
C. torresii (Uden *et* Zobell) S.A. Mey. *et* Yarrow	Torres Strait, Australia	Van Uden and Zobell (1962)
C. tropicalis (Castell.) Berkhout	North Sea, Black Sea, Bombay, Taiwan, Indian Ocean	Fell (1967), Meyers et al. (1967a,b), Chen et al. (2009)
C. zeylanoides (Castell.) Langeron *et* Guerra	North Sea	Meyers et al. (1967b)
Cyberlindnera jadinii (Sartory, R. Sartory, Weill *et* J. Mey.) Minter	Black Sea	Meyers et al. (1967a)
Cryptococcus infirmominiatus (Okun.) Phaff *et* Fell	Black Sea	Meyers et al. (1967a)
Cystobasidium pallidum (Lodder) A.M. Yurkov, Kachalkin, H.M. Daniel, M. Groenew., Libkind, V. de Garcia, Zalar, Gouliamova, Boekhout *et* Begerow (= old name *Rhodotorula palida* Lodder)	Indian Ocean	Fell (1967)
Cy. minutum (Saito) A.M. Yurkov, Kachalkin, H.M. Daniel, M. Groenew., Libkind, V. de Garcia, Zalar, Gouliamova, Boekhout *et* Begerow	North Sea, in a bloom of *Noctiluca milliare*, Black Sea	Fell (1967), Meyers et al. (1967a,b)
Debaryomyces hansenii (Zopf) Lodder *et* Kreger	Atlantic Ocean, North Sea, Bombay, Indian Ocean	Bhat and Kachwalla (1955), Meyers et al. (1967b)
Glaciozyma antarctica (Fell, Statzell, I.L. Hunter *et* Phaff) Turchetti, Connell, Thomas-Hall *et* Boekhout	Atlantic Ocean	Fell et al. (1969)
Hanseniaspora uvarum (Niehaus) Shehata, Mrak *et* Phaff *ex* M.T. Sm.	North Sea, Taiwan, Indian Ocean	Fell (1967), Meyers et al. (1967b), Chen et al. (2009)
Kazachstania jiainica C.F. Lee *et* Chun H. Liu	Taiwan	Chen et al. (2009)
K. yakushimaensis (Mikata *et* Ueda-Nishim.) Kurtzman	East Taiwan	Chen et al. (2009)
Kluyveromyces aestuarii (Fell) Van der Walt	Torres Strait, Australia	Van Uden and Zobell (1962)
Kodamaea ohmeri (Etchells *et* T.A. Bell) Y. Yamada, Tom. Suzuki, M. Matsuda *et* Mikata	East Taiwan	Chen et al. (2009)
Leucosporidium scottii Fell, Statzell, I.L. Hunter *et* Phaff	Atlantic Ocean, Atlantic Peninsula, Weddell Sea	Fell et al. (1969)
Metschnikowiella bicuspidata (Metschn.) T. Kamienski	Pacific Ocean	Fell (1976)

Table 2 (continued)

Species	Geographical location	Authority
M. krissii (Uden *et* Cast.-Branco) Uden	Pacific Ocean	Fell (1976)
M. zobellii (Uden *et* Cast.-Branco) Uden	Atlantic Ocean	Meyers et al. (1967b)
Meyerozyma guilliermondii (Wick.) Kurtzman *et* M. Suzuki	Bombay	Fell (1967)
Moesziomyces bullatus (J. Schröt.) Vánky	Atlantic	Meyers et al. (1967b)
Naganishia albida (Saito) Xin Zhan Liu, F.Y. Bai, M. Groenew. *et* Boekhout [old name = *Cryptococcus albidus* (Saito) C.E. Skinner]	Black Sea, Indian Ocean	Fell (1976), Meyers et al. (1967a)
Papiliotrema laurentii (Kuff.) Xin Zhan Liu, F.Y. Bai, M. Groenew. *et* Boekhout	Black Sea	Meyers et al. (1967a)
Pichia fermentans Lodder	Indian Ocean	Fell (1967)
P. kudriavzevii, Boidin, Pignal *et* Besson	East Taiwan	Chen et al. (2009)
Prosporobolomyces hispanicus (= *Sp. hispanicus*) Peláez *et* C. Ramírez) E.K. Novák *et* Zsolt	Indian Ocean	Fell (1967)
Rhodotorula babjevae (Golubev) Q.M. Wang, F.Y. Bai, M. Groenew. *et* Boekhout	Atlantic	Meyers et al. (1967b)
R. diobovata (S.Y. Newell *et* I.L. Hunter) Q.M. Wang, F.Y. Bai, M. Groenew. *et* Boekhout	Atlantic Ocean	Meyers et al. (1967b)
R. dairenensis (T. Haseg. *et* Banno) Fell, Samp. *et* Gadanh	Biscayne Bay	Roth et al. (1962)
R. glutinis (Fresen.) F.C. Harrison	Black Sea, Indian Ocean	Meyers et al. (1967a), Fell (1976)
R. graminis Di Menna	Black Sea, Indian Ocean	Fell (1967), Meyers et al. (1967a)
R. mucilaginosa (A. Jörg.) F.C. Harrison (= *Rhodotorula rubra* (Demme) Lodder)	Biscayne Bay, North Sea, Black Sea, Indian Ocean	Roth et al. (1962), Fell (1967), Meyers et al. (1967a,b)
Rhodosporidiobolus odoratus (= *Sp. odorus*) (J.P. Samp., Fonseca *et* E. Valério) Q.M. Wang, F.Y. Bai, M. Groenew. *et* Boekhout	Indian Ocean	Fell (1967)
Saccharomyces cerevisiae Meyen *ex* E.C. Hansen	Indian Ocean	Fell (1976)
Sa. chevalieri Guillierm.	Bombay	Bhat and Kachwalla (1955)
Sa. italicus T. Castelli	Bombay	Bhat and Kachwalla (1955)
Spencerozyma crocea (= *R. crocea*) (Shifrine *et* Phaff) Q.M. Wang, F.Y. Bai, M. Groenew. *et* Boekhout	Indian Ocean	Fell (1967)
Sporobolomyces pararoseus H.C. Olson *et* B.W. Hammer	Black Sea, North Sea	Meyers et al. (1967a,b)
Sp. roseus Kluyver *et* C.B. Niel	Black Sea	Meyers et al. (1967a)
Sterigmatomyces halophilous (= *Sp. halophilous*) Fell	Indian Ocean	Fell (1967)
Torulaspora delbrueckii (Lindner) Lindner	Bombay, East Taiwan	Bhat and Kachwalla (1955), Chen et al. (2009)
Wickerhamomyces anomalus (E.C. Hansen) Kurtzman	Taiwan	Chen et al. (2009)

Marine fungi and high-throughput sequencing

The use of molecular phylogenetics to understand fungal evolution and inform taxonomy has generated extensive databases of nucleotide data derived from cultured and uncultured fungi. These databases are, in turn, used to inform HTS studies of richness and diversity. An extensive search of the National Center for Biotechnology Information (NCBI) nucleotide database (Supplementary methods) revealed that only half of the fungi known to exist in the marine realm are represented by a DNA locus (Supplementary Figure S1) of either terrestrial or marine origin. Of the marine fungi that are represented by a DNA sequence, the majority are represented by the large ribosomal subunit (28S rRNA), followed by the internal transcribed spacer (ITS) region, and finally the small ribosomal subunit (18S rRNA). The ITS region has been proposed as the formal molecular locus/barcode of fungi (Schoch et al. 2012); however, it is too variable to address the phylogeny of higher taxonomic ranks (Lindahl et al. 2013) without an 18S rRNA complement (Panzer et al. 2015) and disproportionally skews HTS-amplicon-based studies of fungal abundances, relative to loci within the 18S or 28S ribosomal subunit-encoded region (De Filippis et al. 2017). The 28S rRNA subunit is more variable than the 18S rRNA subunit and is consequently more informative for taxonomic resolution of the fungi. However, NCBI's Sequence Read Archive (SRA) is disproportionally represented by 18S rRNA marine datasets (Panzer et al. 2015), thereby currently necessitating the use of 18S amplicon datasets to surmise any large-scale spatial phenomena.

An alternative approach to single locus amplicon-based studies is shotgun metagenomics. Shotgun sequencing provides a less-biased sequencing approach that is not reliant on primer matches in PCR-based marker gene analyses (Tedersoo et al. 2015). Furthermore, shotgun sequencing can link taxonomy to function through analysis of encoded functional genes (e.g. Morales et al. 2019). However, the successful annotation of extra-rDNA operon data is dependent on curated databases that contain genome-wide information. There are currently (21 November 2018) 3905 fungal genomes archived in NCBI: 3032 from the Ascomycota, 691 from the Basidiomycota, and 182 from other fungal lineages. Combined with annotated transcripts and proteins, these data contribute to NCBI's RefSeq database that contains molecular data for 85,308 organisms, including 604 fungal genera. Of all 604 represented fungal genera, only 73 marine fungal genera are in the RefSeq database. As only half of the known marine fungal species have been assigned a molecular barcode and only 12% of marine fungal genera are represented in the RefSeq database, the phylogenetic classification and subsequent interpretation of HTS studies seem as limited by molecular information derived from described organisms, as sequences derived from organisms not yet known to science (e.g. Richards et al. 2012). Even though half of the marine fungi do not have any associated molecular data, HTS still offers immense possibilities to understanding global patterns of marine fungal diversity (Nilsson et al. 2018), especially at various taxonomic resolutions (such as phylum level), where databases are likely not as limiting. Even still, hierarchal database taxonomies used for classification can lag substantially behind novel evolutionary insights (Bass et al. 2018) and taxonomic revisions (Tedersoo et al. 2018).

Shotgun sequencing of marine fungal communities

We conducted a global analysis of shotgun sequencing datasets deposited in Metagenomic Rapid Annotations using Subsystems Technology (MG-RAST) (Glass et al. 2010), derived primarily from Global Ocean Sampling Expedition (e.g. Rusch et al. 2007), Tara Oceans (Pesant et al. 2015), Ocean Sampling Day (Kopf et al. 2015), and the Deepwater Horizon oil spill (Yergeau et al. 2015). We selected all marine samples and subsequently filtered out databases that were missing associated metadata, such as GPS location and depth of sampling (Supplementary Methods). After eliminating datasets with missing metadata, we analyzed 373 databases that contained 4.7×10^9 total sequences (two orders of magnitude more than other studies), of which 1.8×10^9 were annotated (minimum 65% identity and e-value cutoff $= 10^{-8}$). Analysis of these reads revealed that 4,130,526 (0.22%) of all reads (including non-annotatable reads, prokaryotes, and metazoans) were assigned to fungi. From all datasets, fungi comprised 7.8% of all eukaryotic sequences. Of these reads, the Ascomycota comprised 76.2% of all annotated fungal reads, followed by the Basidiomycota with 18.1%, the Microsporidia at 2.1%, the Chytridiomycota at 1.6%, unclassified fungal reads at 1.3%, the Blastocladiomycota at 0.2%, and finally the Glomeromycota at 0.2%. These proportions are consistent with other shotgun sequencing studies (Morales et al. 2019). When databases were normalized for comparison, these fungal phyla comprised comparable fractions of relative abundances throughout the world's oceans, irrespective of location, date of sampling, or environmental conditions (Supplementary Figure S2).

Site-specific spatial analysis using non-metric multidimensional scaling (NMDS) revealed a single mixed cluster of samples whose spatial distance was influenced by a predominance of Ascomycota, Basidiomycota, and the Microsporidia (Supplementary Figure S2). The mechanism for the grouping of the Microsporidia with the Dikarya is uncertain; however, the closely related Cryptomycota are known parasites of other fungi (Letcher et al. 2017). Spatially segregating, non-grouping sites were dominated by the Blastocladiomycota, Chytridiomycota, unclassified fungi, and the Glomeromycota. As many reads were not classified, it is difficult to conclusively discern biological patterns in light of known database limitations that result in a high proportion of sequences without annotations. Still, the tight clustering of many sample sites predominated by the Dikarya and Microsporidia suggest that a core group of these fungi could predominate in planktonic marine fungal communities and that site-specific characteristics could disproportionally favor the growth of Chytridiomycota, Blastocladiomycota, and Glomeromycota. The co-occurrence of an oil spill in the Gulf of Mexico and the hyperabundance of several fungal phyla after this spill support this hypothesis, especially as some phylogenetically basal fungi are known degraders of recalcitrant substances (Powell 1993). Alternatively, environmental filtering can eliminate taxa with less tolerance to perturbations or stressful environmental conditions, suggesting that basal fungi might be more tolerant to environmental irregularities. Regardless, the generally homogenous proportions of phyla detected across all sites was surprising.

The homogeneous patterns observed by analyzing sequences at the taxonomic phylum level led us to suspect

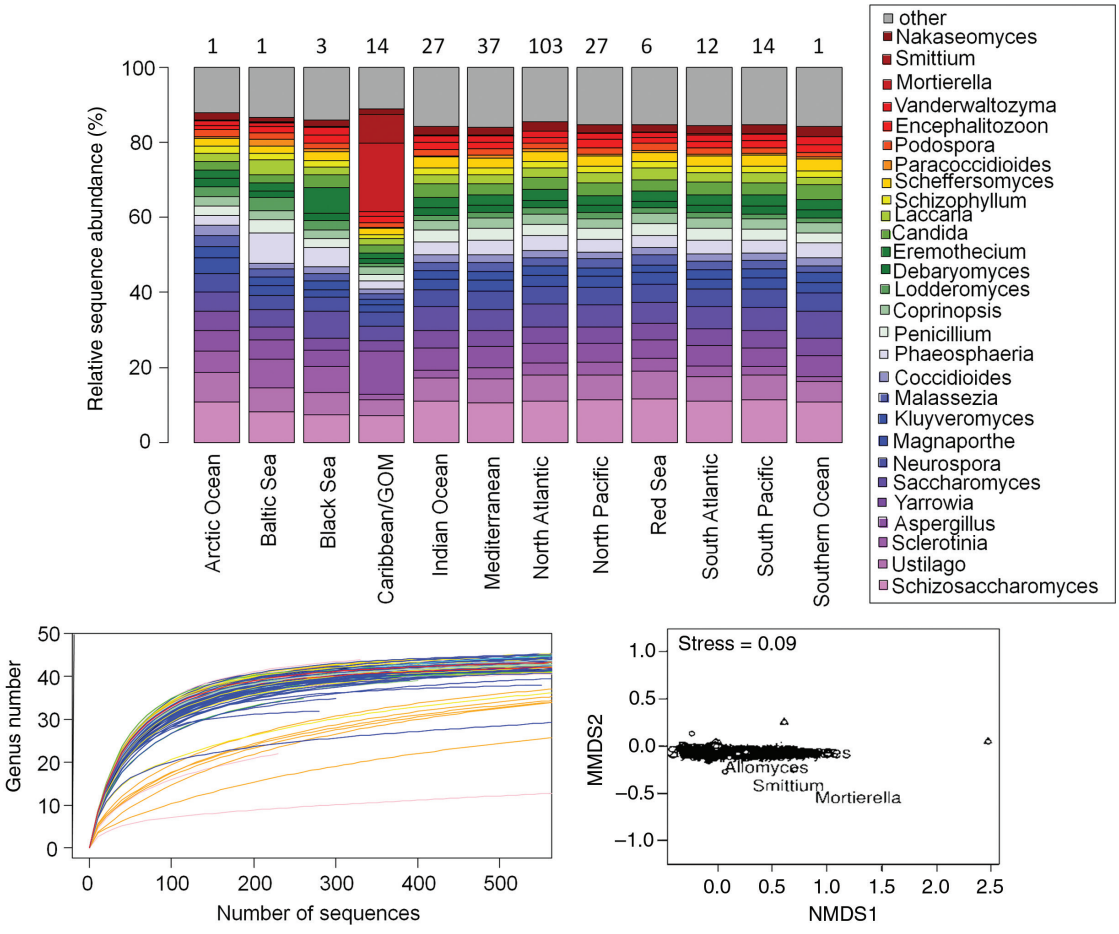

Figure 2: Shotgun sequencing data sourced from MG-RAST and manually binned into various oceanographic regions of the world. (Top) Relative abundances (using annotation e-value of 10^{-8}) of fungal genera. Numbers across the top of histogram bars denote the number of datasets used in the analysis. Numbers at top of histogram do not match the total number of databases analyzed, as many samples had no fungal sequences remaining after subsampling. GOM is Gulf of Mexico. (Bottom left) Rarefaction curves showing the number of fungal genera detected as a function of the number of fungal sequences analyzed before database normalization. (Bottom right) Genera-based non-metric multidimensional scaling (NMDS) spatial analysis with indicator taxa displayed, illustrating overlapping, similar fungal communities.

that we were masking discernible abundance differences. However, even at the genus level, we identified a similar homogeneous pattern of fungal taxa throughout the world's oceans (Figure 2). The stable community composition of classified fungal genera across different marine ecosystems remains surprising, especially as the less biased approach of shotgun sequencing (i.e. no amplification) lends greater confidence to their real proportions in the environment. Future research can leverage metatranscriptomic analyses of RNA to help discern the active versus the latent fungal fraction in the environment.

Site-specific spatial analysis of genera-classified reads revealed, again, one large cluster of spatially grouping samples (Figure 2). This main cluster was supplemented by spatially outlying sites predominated by sequences classified as *Allomyces* E.J. Butler (Blastocladiomycota), *Smittium* R.A. Poisson (Kickxellomycota), and *Mortierella* Coem. (Mucoromycota). Statistical analysis (two-way ANOVA) using Inverted Simpson diversity estimates identified that the Gulf of Mexico was statistically different ($p < 0.00002$) from all sites. Supplemental analysis using Chao1 identified that the Gulf of Mexico was statistically different from the North Pacific (two-way ANOVA, $p = 0.00005$), South Pacific ($p = 0.0014$), and Indian Ocean ($p = 0.009$). These differences were likely driven by the oil spill, as well as the metatranscriptomics data that comprised the majority of these data within this sampling site. Excluding the Gulf of Mexico, there were no differences in fungal diversity between any of our samples, irrespective of oceanographic regions, water depth, or proximity to land (Supplementary Figure S3). Rarefaction analysis of fungal genera suggests that most pelagic marine sites have approximately 40 fungal genera (Figure 2). However, few rarefaction curves actually reached a true asymptote, suggesting that a large fraction of fungal diversity either exists in lower quantities and can only be recovered with significant shotgun sequencing of the environment or that recovered diversity is not detectable due to current database limitations.

Marine fungal community analysis using 18S rRNA genes

The potential cost constraints associated with achieving adequate sequencing depth to adequately sample a community, as well as current database limitations associated with shotgun sequencing, pose major constraints to describing marine fungal diversity. Amplicon-based HTS analyses, in principle, offer a targeted approach to inventorying taxonomically informative loci, especially for those taxa that might exist in lower abundances. Analysis of 286 NCBI 18S rRNA databases (Table S1, Supplementary methods) that represent HTS studies conducted in various seas and oceans (e.g. Celussi et al. 2018; Enberg et al. 2018; Edgcomb et al. 2011; Flaviani et al. 2018; Hassett et al. 2017; Pearman et al. 2017; Stern et al. 2015) identified that the fungi comprised 1.3% of all eukaryotic sequences from marine environmental datasets. Many fungal sequences from this study were only classifiable to higher taxonomic levels (Figure 3), consistent with other published findings (Comeau et al. 2016, Hassett et al. 2017, Nagano et al. 2017, Picard 2017), suggesting either novel lineages and/or under-populated reference databases. Of the SILVA-classified fungi, the Ascomycota comprised on average 43% of all fungi globally, followed by the Chytridiomycota with 36%, the Basidiomycota with 27%, and then other fungal clades that contributed less than 1% of relative abundance. The under-representation of the Microsporidia and elevated Chytridiomycota in amplicon-based studies, relative to our shotgun sequencing data, is apparent and could indicate primer bias associated with the amplification of these groups.

Site-specific NMDS of individual samples revealed spatially partitioned fungal communities within different oceans. Indicator taxa within the Dikarya comprised a central-grouping core, while sites with flagellated fungal indicator species spatially segregated to the margins (Supplementary Figure S4). The homogeneous pattern of fungal taxa observed through shotgun sequencing was not observed with amplicon sequencing, consistent with other studies that found varying environmental conditions structuring fungal communities (Jeffries et al. 2016).

Globally, over the entire ocean depth, the mean salinity over the last 10 years is 34.6 with a standard deviation of 1 (Supplementary methods). The Baltic Sea and the Red Sea are both connected to the global ocean through one very narrow and shallow opening; hence, their salinity is mostly controlled by precipitation/evaporation and river runoff. As many large snow-melt fed rivers flow into the Baltic (Bergström and Carlsson 1994), the top 100 m of that sea are extremely fresh (average salinity of 7, or 27 standard deviations away from the global average). The Red Sea in contrast is characterized by year-round evaporation (Sofianos et al. 2002), making that sea hypersaline (average salinity of 40, or 5 standard deviations away from the global average). Marine environments with atypical salinity regimes, such as sea ice and the Red Sea, as well as the estuarine Baltic Sea, had elevated proportions of Chytridiomycota (Supplementary Figure S4), irrespective of substantially different temperatures, which

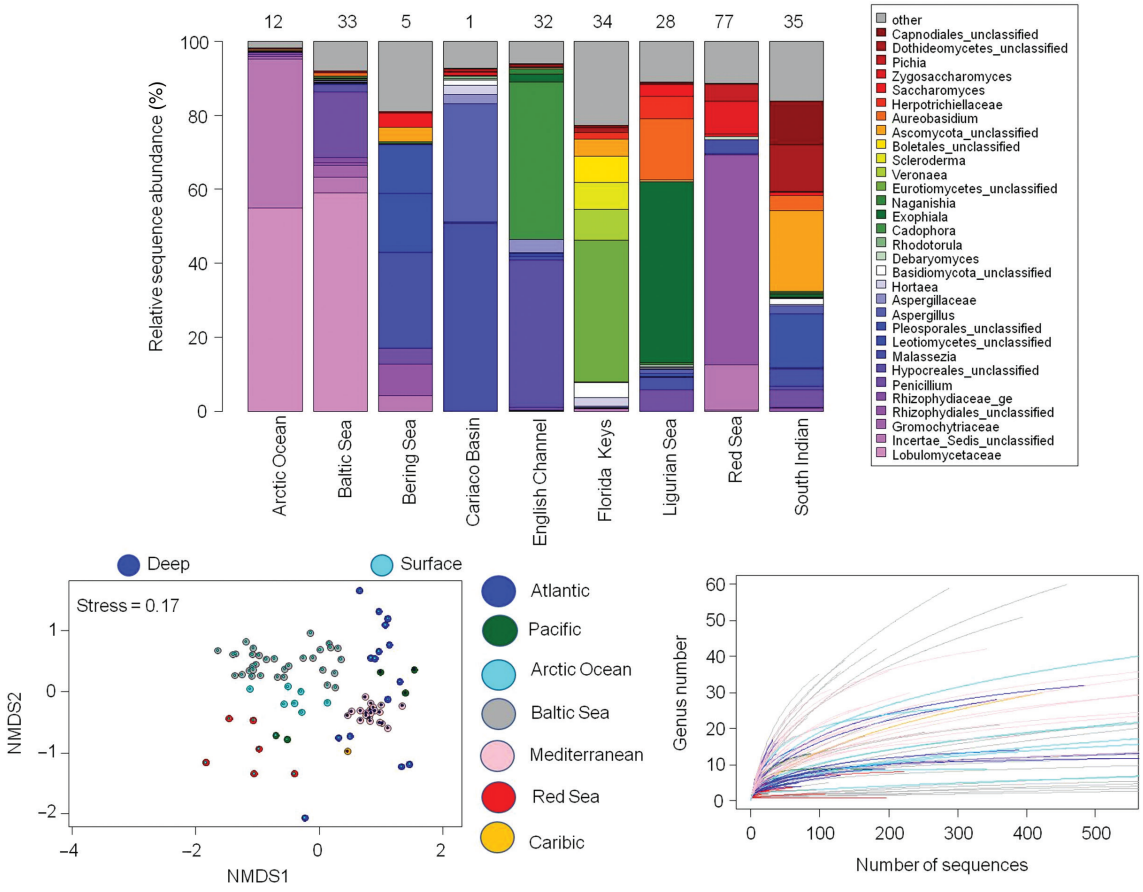

Figure 3: 18S rRNA amplicon sequencing of global high-throughput sequencing datasets.
Number at top of histogram indicates the number of samples used in this analysis. Numbers at top of histogram do not match the total number of databases analyzed, as many samples had no fungal sequences remaining after subsampling. (Top) Histogram of lowest-level classification of marine fungal taxa using SILVA-classified datasets from various regions of the world. (Bottom left) Non-metric multidimensional scaling (NMDS) spatial analysis of normalized sequencing datasets displaying color-coded sites with embedded colors representing sites from deeper (>35 m) and shallower depths. (Bottom right) Rarefaction curves showing the number of fungal genera detected as a function of the number of fungal sequences analyzed before database normalization.

structure marine microbial (Sunagawa et al. 2015) and terrestrial fungal communities (Kivlin et al. 2011). These results support the known effects of salinity on structuring marine fungal communities (Mohamed and Martiny 2011), especially in the Baltic Sea (Rojas-Jimenez et al. 2019). The Red Sea, Baltic Sea, and Arctic sea ice sites were all sequenced with the Illumina platform. This consistency helps ameliorate any concerns associated with conclusions derived from comparisons across sequencing platforms. The abundances and relevance of the Chytridiomycota at global scales remain largely unknown, as their recoverability and associated diversity in culturing surveys appears low (Jones et al. 2015), relative to the recoverability of their DNA and associated clone-based diversity from the marine environment (Hassett et al. 2017).

Spatial partitioning of fungal groups was also evident at the genus level, where about 40 groups constituted the majority of fungal observation (Figure 3). The highest richness was detected in samples from >100 m depth in the Mediterranean Sea and shallow samples within the Baltic Sea. The lowest diversity was detected in the Red Sea (Supplementary Figure S5). In the Arctic Ocean and Baltic Sea, Chytridiomycota members with closest affinity to the Lobulomycetales contributed large fractions of total fungal observations, as described previously (Hassett et al. 2017). In the Bering Sea and Red Sea, Chytridiomycota communities were comprised of sequences with closest affinity to the Gromochytriales and Rhizophydiales. The Rhizophydiales is the largest and most diverse of all Chytridiomycota orders that contains described marine isolates (Lepelletier et al. 2014). Furthermore, the Gromochytriales and Lobulomycetales are under-populated Chytridiomycota taxonomic orders that contain seven (Seto and Degawa 2015, Van den Wyngaert et al. 2018) and two species, respectively (Karpov et al.

2018); consequently, it is not surprising to detect Chytridiomycota sequences with closest affinity to these under-populated orders. Unclassifiable members within the fastidious and enigmatic *Malassezia* Baill. (Amend 2014), as well as common fungi within the Leotiomycetes, Trichocomaceae, Hypocreales, *Cadophora* Lagerb. *et* Melin, and numerous yeast-forming species were frequently detected. Marine yeasts primarily within the genera *Rhodotorula*, *Naganishia* Goto, *Saccharomyces*, and *Zygosaccharomyces* Nishiw. were found frequently in hypersaline environments, and were supplemented by contributions from *Pichia, Wickerhamomyces* Kurtzman, Robnett *et* Basehoar-Powers, and *Hortaea* Nishim. *et* Miyaji. Pigmented yeasts within *Rhodotorula* were detected in Arctic Ocean sea ice near Svalbard, along with *Naganishia*, which contains species isolated from hypersaline environments (Fotedar et al. 2018). *Zygosaccharomyces* was detected almost exclusively from the Red Sea.

Site-specific spatial analysis of these samples revealed that spatially segregated sites were driven by a predominance of fungi classified within the Chytridiomycota taxonomic order Rhizophydiales, as well as taxa allied to *Pichia*, *Scleroderma* Pers., *Wickerhamomyces*, *Hyphodontia* J. Erikss., and *Fusarium*. Rarefaction analysis of fungal genera suggests that most pelagic marine sites have approximately 20–30 classifiable fungal genera, plus a substantial fraction of unclassified sequences binned at the phylum level that would likely inflate the number of detected genera considerably. We used a combination of rarefaction curves, diversity indices, and Analysis of Similarities (ANOSIM; Table 3) to determine whether fungal communities in different oceanographic regions were distinct. Some sites were significantly different, such as the Arctic Ocean and Red Sea, while other sites were quite similar, such as the ice-covered Arctic Ocean and Baltic Sea. The most similar regions were the Bering Sea and the Cariaco Basin. Several sites were equally dissimilar (e.g. Arctic Ocean-Ligurian Sea, Baltic Sea-Red Sea, South Indian Ocean-Ligurian Sea). These large regional differences in fungal community structure are consistent with smaller regional studies that found community composition changing with distance from shore (Burgaud et al. 2013) and different nutrient regimes (Jeffries et al. 2016). As environmental conditions selectively favor the growth of specific taxa at smaller scales, it is not surprising to find statistically different fungal communities associated with larger distinct oceanographic regions. Though these phylogenetically classified sequences are informative, more distance-based analysis, such as those being generated through *UniEuk* (Berney et al. 2017) will help to more accurately elucidate biogeography.

Latitudinal gradients of marine fungi and biological hotspots

In terrestrial environments, the decline of species richness with increasing latitude has remained a central dogma in global biogeography (Hillebrand 2004). Discerning causalities for this covariation remain debatable, but has historically modulated around the nexus of various phenomena to explain endemism, such as: center of origin (Vavilov 1951), geological separation (McCoy and Heck 1976), solar radiation's effects on evolutionary speed (Rohde 1992), and dispersal (Thorson's Rule, Mileikovsky 1971), which is further scaled according to latitudinal distribution gradients (Rapopart's Rule, Stevens 1989). Local diversity is partially structured by large-scale biogeographical patterns of a specific taxon (Wiens and Donoghue 2004) that can be further shaped by disturbances (Townsend et al. 2003), biological interactions (Menge and Sutherland 1976), and seasonality (Marquardt et al. 2016). However, this trend does not necessarily apply to

Table 3: Two-way ANOSIM analysis displaying false discovery rate-adjusted p-values.

	Arctic Ocean	Baltic Sea	Bering Sea	Cariaco Basin	English Channel	Florida Keys	Liguarian Sea	Red Sea
Arctic Ocean								
Baltic Sea	0.1067							
Bering Sea	0.0208	0.0055						
Cariaco Basin	0.1604	0.0555	0.5					
English Channel	0.0055	0.004	0.018	0.1243				
Florida Keys	0.0446	0.0055	0.012	0.3429	0.0454			
Liguarian Sea	0.004	0.004	0.004	0.0858	0.004	0.0208		
Red Sea	0.004	0.004	0.0454	0.1586	0.0103	0.059	0.004	
South Indian Ocean	0.018	0.004	0.12	0.2647	0.0252	0.12	0.0055	0.0208

If $p > 0.05$, communities were considered statistically similar.

marine environments, especially for microbial life (Sunagawa et al. 2015).

Though larger (>1 mm) organisms display distinct biogeography (De Bie et al. 2012), many eukaryotic microbial taxa do not exhibit discernible spatial partitioning (Finlay 2002). Local:global species ratios for some eukaryotic microbial taxa are quite high (80%, Finlay and Clarke 1999), suggesting that high dispersal rates and the formation of resting spores can produce globally distributed homogeneous resting spores, such as seed banks (Lennon and Jones 2011). Consequently, it was hypothesized that among the eukaryotic microbes, many perceived biogeographical differences are the result of sampling effort (Finlay 2002), as opposed to dispersal limitations. The oceans are a contiguous ecosystem, whose circulation patterns connect all water bodies over decadal to centennial time scales. In marine environments, plankton dispersal is determined by local abundance, which is scaled with body size (Soininem et al. 2013, Villarino et al. 2018). Consequently, communities of smaller organisms are more likely to have a worldwide distribution (Djurhuus et al. 2017, Flaviani et al. 2018, Villarino et al. 2018).

If the success of dispersal is dependent on size and local abundance then the differential and usually complex growth patterns of fungal hyphae (Gutiérrez et al. 2011) should result in uneven dispersal patterns in the marine environment. Our analysis based on shotgun metagenomic reads found no discernible differences between richness or diversity and latitude (Figure 4). Our amplicon-based studies identified the highest richness values at 60° north (Supplementary Figure S6). Overall, we find no evidence for a decrease in diversity or richness with increasing latitude in the marine environment, consistent with other marine studies of fungal diversity (Tisthammer et al. 2016), but different from other shotgun sequencing analyses (Morales et al. 2019).

At global scales, we hypothesize that there are multiple phenomena responsible for the absence of any discernible biogeographical patterns in the datasets we re-analyzed. These reasons can be categorized as limitations driven by the absence of a marine fungal biomarker, the existence of various dispersal phenomena beyond ocean currents, and methodology limitations. First, a combination of differential osmotolerance and uncertain evolutionary histories confounds the conclusive identification of a marine fungus. For example, Zuluaga-Montero et al. (2010) undertook a phylogenetic study of *Aspergillus flavus* Link strains from terrestrial and marine sites and concluded there is no clade particular to the marine environment. Sivaramanan (2014) grew four common terrestrial fungi (*Aspergillus*, *Cladosporium*, *Helminthosporium* Link and *Trichoderma* Pers. species) to determine their growth on seawater media and demonstrated their halophilic nature; although of terrestrial origin, they have an individual preference, as well as tolerance, to the marine environment (Saritha et al. 2012). Consequently, if terrestrial input exceeds local marine diversity then a marine biogeography signal would be challenging to discern with amplicon data alone, especially if marine fungal communities are predominated by common terrestrial fungi.

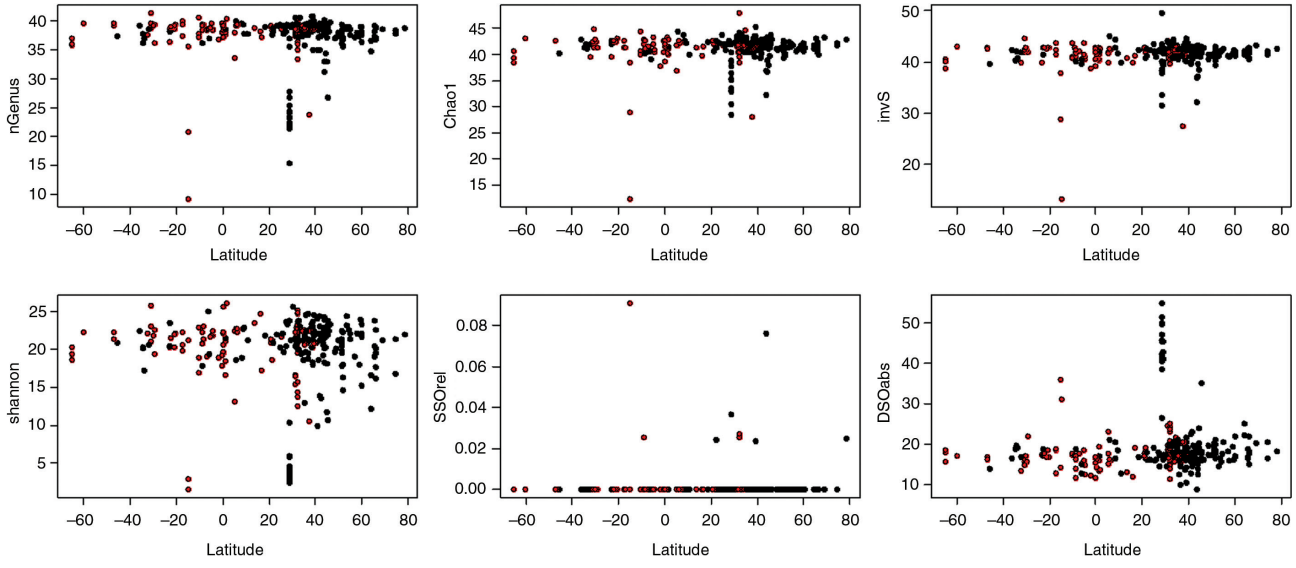

Figure 4: Shotgun sequencing data analyzed from metagenomic rapid annotations using subsystems technology (MG-RAST) of deposited datasets plotting richness and diversity as a function of latitude.
Red colors depict open ocean samples. Black colors depict coastal samples.

Zuccaro et al. (2004) in a phylogenetic study, showed that a new marine *Acremonium* species isolated from *Fucus* spp. grouped in a monophyletic marine clade comprising *Emericellopsis*, *Stanjemonium*, and *Acremonium* Link species. Consequently, the discernment of some marine taxa can be achieved with molecular phylogeny. The inconclusive evolutionary history of the marine fungi confounds the application of a working ecological definition. If the ocean really is a massive sink for terrestrial-sourced fungi, of which a large fraction can reproduce in the marine realm, biogeographical patterns of oceanic fungal diversity and richness should be nearly impossible to discern from a marine-exclusive perspective. Regardless, our amplicon-based study found the highest marine fungal genera-based richness in the Baltic Sea and Mediterranean Sea. If the fungi are indeed evolutionarily transitioning from terrestrial environments to the marine ecosystems (Spatafora et al. 1998, Hibbett and Binder 2001), coastal areas and enclosed seas with substantial terrestrial influence should be biological hotspots for marine fungal diversity in various stages of this evolutionary transition. The highest fungal richness that we identified in the Baltic Sea and Mediterranean Sea marginally supports this hypothesis. Furthermore, if multiple independent transitions of fungi from terrestrial to marine environments occurred then there should be several geographic areas with elevated diversity, as a result of more time for speciation.

Second, the small size (~2–10 µm diameter) of conidia is not limiting for dispersal and consequently should be distributed widely (Finlay 2002). In addition, both physical, such as advection (Hovmøller et al. 2008) and biological phenomena, such as the movement of fungal propagules by animals (Singh et al. 2016) aid in the wide-distribution of both marine and terrestrial fungi throughout the marine realm. Moreover, the evolved fungal appendages that aid in flotation and adhesion to substrate (Hyde et al. 1993, Jones 1994), coupled with the known association of fungi with marine driftwood (Rämä et al. 2016), suggests another mechanism for long-distance dispersal in the marine realm that could help eliminate detectable biogeography. Endemic marine fungal taxa should augment the discernment of biogeography and aid in assessments of latitudinal gradients. Marine fungal endemism seems likely, especially with regard to obligate parasites and other biotrophic taxa. Fungi have been found in association with macroalgal communities (Loque et al. 2010) and are known to exist as biotrophs in the terrestrial realm (Tedersoo et al. 2010). Consequently, it seems likely that obligate biotrophs would be associated, and ultimately regionally limited, with endemic marine macroalgae (Phillips 2001). Even still, our data find no evidence of latitudinal gradients, irrespective of likely endemic taxa.

Lastly, taxonomic classification of microbial communities depends on the size, quality, and breadth of reference database, which we tried to circumvent by classifying at various taxonomic levels. Regardless of classification scheme or sequencing approach implemented, we found that databases limited our ability to spatially analyze taxonomically classified sequences, especially those sequences derived from zoosporic fungi. These limitations likely resulted in multiple genera binned at higher taxonomic levels, which may or may not have masked discernible differences between latitude and diversity. Recent surveys using molecular techniques suggest that most planktonic fungal communities are comprised of novel species and assemblages (Wang et al. 2014, Jones et al. 2015, Jeffries et al. 2016). To eventually discern if these observations are driven by truly novel species or, alternatively, described species not yet represented in databases, we have generated a list of marine fungal species that are missing molecular information (Table S2).

Conclusions

By reviewing the biogeography of marine planktonic fungi, we discovered significant gaps in scientific knowledge that challenge our understanding of marine fungal ecology. First, there are few culturing observations from the open ocean, which is primarily a result of undersampling. Second, we found that ~50% of described marine fungi are missing an assigned rDNA locus in public databases. Third, the substantial range-overlap between terrestrial and marine fungal species underscores the missing evolution-based understanding needed to characterize and define a marine fungus. Though we found no evidence for any relationship between fungal richness/diversity and latitude, as previously described (Morales et al. 2019), it seems possible that if terrestrial fungi are sourced into the sea (Frölich-Nowoisky et al. 2012), and if terrestrial fungal richness decreases with latitude (Tedersoo et al. 2014) then detectable fungal richness in the marine environment should decrease with latitude, especially if the terrestrial input exceeds local marine diversity.

Analysis of fungal community structure identified that the only atypical shotgun sequencing dataset was from the Gulf of Mexico, which was predominated by the Chytridiomycota. These data were supported by amplicon-based sequencing, which found that Chytridiomycota

dominated fungal communities in areas with atypical salinity regimes, including the Arctic Ocean, Red Sea, and Baltic Sea. These data suggest that this under-studied clade of marine fungi might have greater ecological relevance than is currently believed. Moreover, the uncharacterized relevance and diversity of other zoosporic taxa, as well as missing molecular information for half of known marine fungi, provides ample opportunities to contribute to marine mycology.

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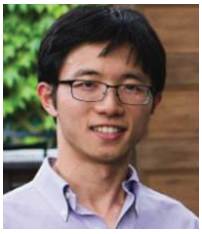
Bionotes

Brandon T. Hassett
Department of Arctic and Marine Biology, University of Tromsø – The Arctic University of Norway, 9037 Tromsø, Norway
brandon.hassett@uit.no

Brandon T. Hassett is a post-doctoral research fellow at UiT – The Arctic University of Norway in Tromsø. Dr. Hassett received his PhD in marine biology from University of Alaska Fairbanks in 2016, his MSc in plant pathology from Texas A&M University in 2012, and his BSc from La Roche University in 2007. Dr. Hassett is a microbial ecologist, specializing in plant-microbe interactions, sea ice ecology, and mycology. Dr. Hassett draws on his understanding of contemporary taxonomy and applies an array of molecular tools to study the diversity and functionality of microbial eukaryotes.

Tobias R. Vonnahme
Department of Arctic and Marine Biology, University of Tromsø – The Arctic University of Norway, 9037 Tromsø, Norway

Tobias Reiner Vonnahme is a PhD Candidate at UiT – The Arctic University of Norway, Tromsø. His research background lies in marine microbial ecology, bioinformatics, and biogeochemistry. His current focus lies on microbial carbon cycling in the seasonal ice zone including mixotrophy, and nitrification using isotope probing, modelling and metagenomics approaches. He received his Master at the Max-Planck Institute for Marine Microbiology in Bremen about impacts of deep-sea mining on microbial communities and biogeochemical cycling.



Xuefeng Peng
Marine Science Institute, University of California Santa Barbara,
Santa Barbara, CA, USA

Xuefeng (Nick) Peng is a postdoctoral scholar at the Marine Science Institute, University of California, Santa Barbara. His primary research interests lies in marine biogeochemistry and microbial ecology. As a Simons Postdoctoral Fellow in Microbial Ecology, his work focuses on the impact of marine fungi on marine nitrogen and carbon cycles. He received his PhD from the Department of Geosciences, Princeton University, where he studied marine nitrogen cycling in oceanic oxygen minimum zones and salt marsh sediments.

E.B. Gareth Jones
Department of Botany and Microbiology, College of Science, King Saud University, P.O. Box 2455, Riyadh 11451, Kingdom of Saudi Arabia

Professor Jones has devoted 60 years to the study of marine fungi, obtained PhD from the University of Leeds, UK and was awarded the DSc from the University of Wales. Gareth has worked extensively in Asia and supervised circa 100 PhD/MSc students by research and published circa 600 research articles. Besides marine mycology, he has studied marine biofouling, biodeterioration of materials, and wood decay by fungi. Gareth recently initiated the website HYPERLINK "http://www.marinefungi.org" www.marinefungi.org which documents our current knowledge of marine fungi.

Céline Heuzé
Department of Earth Sciences, University of Gothenburg, Box 460, 405 30 Gothenburg, Sweden

Céline Heuzé is a physical oceanographer and Associate Senior Lecturer (bitr. Universitetslektor) in climatology at the University of Gothenburg, Sweden. Her research focuses on the transport of oceanic heat by global deep waters and their interaction with the rest of the climate system at high latitudes, using global climate modelling, in-situ hydrographic data, and satellite remote sensing. She obtained her PhD in physical oceanography in 2015 from the University of East Anglia, UK, in collaboration with the UK Met Office.

Graphical abstract

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