

Review

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Arctic marine fungi: from filaments and flagella to operational taxonomic units and beyond

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Abstract: Fungi have evolved mechanisms to function in the harsh conditions of the Arctic Ocean and its adjacent seas. Despite the ecological and industrial potential of these fungi and the unique species discovered in the cold seas, Arctic marine fungi remain poorly characterised, with only 33 publications available to date. In this review, we present a list of 100 morphologically identified species of marine fungi detected in the Arctic. Independent molecular studies, applying Sanger or high-throughput sequencing (HTS), have detected hundreds of fungal operational taxonomic units (OTUs) in single substrates, with no evidence for decreased richness of marine fungi towards northern latitudes. The dominant fungal phyla may be substrate-specific, as sea-ice and seawater seem to host more Chytridiomycota and Basidiomycota than Ascomycota-dominated driftwood and sediments. Molecular studies have revealed the presence of the Chytridiomycota and Leotiomyces in Arctic waters, with mounting evidence suggesting a significant role in nutrient and carbon cycling. The high detection frequency of Leotiomyces is partly due to OTUs from marine *Cadophora* (Helotiales) that are indistinct from terrestrial strains. Knowledge of Arctic marine fungi has rapidly increased in recent years. Nevertheless, some bottlenecks, such as limited OTU identification persist and more researchers are encouraged to join the study of Arctic marine fungi.

Keywords: Chytridiomycota; Helotiales; high-throughput sequencing; morphology; polar.

Marine fungi in the Arctic

Microorganisms, such as fungi, interface key eco-physiological processes between organisms and the abiotic environment that influence all life on earth. The impacts on human life can be both harmful and beneficial. Benefits derived from marine fungal activity include sustainable discoveries that help solve anthropogenic problems, such as use in bioremediation (Raghukumar 2000) or as a source for new drug candidates and cosmeceuticals (Ebel 2012, Balboa et al. 2015). The negative impacts on our society result from the activity of marine pathogenic fungal strains that cause diseases in aquaculture systems that can be difficult and costly to manage (Gachon et al. 2010, Hatai 2012). Marine fungi contribute to biofouling of anthropogenic substrates in the sea (Jones et al. 1972, Björndal 2012) that cause substantial economic costs, e.g. when wooden constructions such as piers need to be rebuilt, and cultural heritage objects are degraded (Salamone et al. 2016). Positive ecological effects of marine fungal activity include contributions to ecosystem services, such as nutrient and carbon cycling at lower trophic levels through parasitism of zooplankton, phytoplankton and seaweeds (Sparrow 1960, Gutiérrez et al. 2016, Jephcott et al. 2016), degradation of seagrasses and seaweeds (Hyde et al. 1998, Zuccaro et al. 2003, Baral and Rämä 2015), and the establishment of mutualistic relationships with marine autotrophs (Garbary and London 1995, Garbary and MacDonald 1995). At higher trophic levels, marine fungi act as parasites and pathogens of animals, yet little is known about the impact parasitic fungi have on populations of marine mammals, fishes and invertebrates (cf. Hatai 2012). Even less is known about the ecological roles of marine fungi in the cold waters of the Arctic that sustain shorter food webs than warmer regions.

The Arctic is the circumpolar area between the North Pole and the Arctic Circle at 66°33'N that encompasses the northern regions of North America, Greenland, Eurasia, and the shallow seas that separate these landmasses. The Arctic Ocean and its adjacent seas, including the Barents Sea, Beaufort Sea, Chukchi Sea, East Siberian Sea, Greenland Sea, Kara Sea, Laptev Sea, Baffin Bay and Hudson

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Bay, are typically cold, with average sea surface water temperatures of the warmest calendar month $<+10^{\circ}\text{C}$ (Maslowski et al. 2004, Locarnini et al. 2010, Marchenko 2012). Geographically, some of these areas extend south of the Arctic Circle but, due to the cold water, they are functionally considered Arctic seas. In these seas, microorganisms, including fungi, have evolved advanced eco-physiological and chemical mechanisms to survive in extremely low temperatures and darkness during winter months. These features make marine fungi a very interesting study object for both academia and industry (Raghukumar 2008).

Climate change is predicted to have the biggest environmental effects at high latitudes in the Northern Hemisphere (ACIA 2004); consequently, the Arctic is being studied at an increasing rate. Experiments investigating Arctic soil fungi have indicated that the structure of fungal communities is changing in response to climate warming (Timling and Taylor 2012), but similar experiments are not available for fungi in the marine environment, though seawater temperature and pH are predicted to change in the Arctic (Doney et al. 2012). It has been shown in a microcosm study that marine fungal communities respond to slight changes in seawater pH (Reich et al. unpublished). Seawater temperature drives the distribution of marine fungi at a global scale (Booth and Kenkel 1986) and it is likely that small changes in environmental parameters cause changes in species distributions that eventually may have cascading effects on the Arctic ecosystems over time.

Based on current knowledge, the number of filamentous marine fungi is highest in tropical and temperate regions and is suggested to decrease towards the poles (Shearer et al. 2007). In the terrestrial realm, no evidence has been found for decreased fungal richness of soil fungi within the Arctic area, whereas global sampling using a high-throughput sequencing (HTS) technique has revealed decreasing richness towards the poles (Timling and Taylor 2012, Tedersoo et al. 2014). Shearer et al. (2007) noted that the Arctic was one of the regions in special need for the exploration of Arctic marine fungi, with only 28 species of filamentous ascomycetes known, including one undescribed species; however, no species inventories were provided in this publication. Based on a single study, Pang et al. (2011) provided a preliminary account of Arctic marine fungi that included 12 species, including four new to science. Indeed, several published studies indicate that the Arctic hosts unique fungal species, which participate in ecological phenomena of major importance (Rämä et al. 2014a, Hassett and Gradinger 2016). Obviously, the changing climate and

the unexplored nature of Arctic marine mycobiota, with potentially major ecological functions, warrant further studies on high latitude marine fungi.

The study efforts made in marine mycology during this and the previous century have resulted in 33 publications dealing with marine fungi in the Arctic (Figure 1). The majority of these publications have dealt with fungi in Arctic waters, where the average sea surface temperature of the warmest calendar month is below $<+10^{\circ}\text{C}$ (Hughes 1974). These publications can be further grouped into morphological and molecular studies, based on the method used to identify fungi (Figure 1). In the current work, we present a review of the studies of true fungi in the Arctic marine environment and a brief history of Arctic marine mycology. Based on the studies conducted across the Arctic region, we compiled a list of morphologically identified fungi that have been detected and isolated from the marine environment. Furthermore, we evaluate the new knowledge these studies have produced for the scientific community with an emphasis on recent results obtained with DNA-based methods.

Morphological studies

Marine fungi have historically been documented in the Arctic; however, neither Shearer et al. (2007) nor Pang et al. (2011) mentioned older (pre-1990) morphological diversity contributions, largely detailed from the Atlantic Arctic region. In some parts of the Arctic, such as Russia, numerous studies have been published that describe the morphological diversity of fungi. For the most part, the Russian publications have appeared in Russian journals in the native language, and have consequently been less distributed among the international marine mycological community.

In general, there are scattered records of marine fungi in the Arctic, collected during the 1800s and 1900s. For example, *Pleospora triglochicola* J. Webster was collected in Northern Norway in 1895 (Rehm 1896, Webster 1969, Rämä et al. 2014a), and Petersen (1905) described *Rhizophydium olla* H.E. Petersen [= *Algochytrops polysiphoniae* (Cohn) Doweld] based on material from Greenland. As we have not conducted a thorough study on herbarium material dispersed around the globe, it is uncertain whether the Norwegian collection is the first observation of Arctic marine fungi. More published descriptions started to appear in the 1960s, pioneered by Aleem (1962) and Artemchuk (1972, 1974, 1975, 1981) in the former USSR's White Sea and

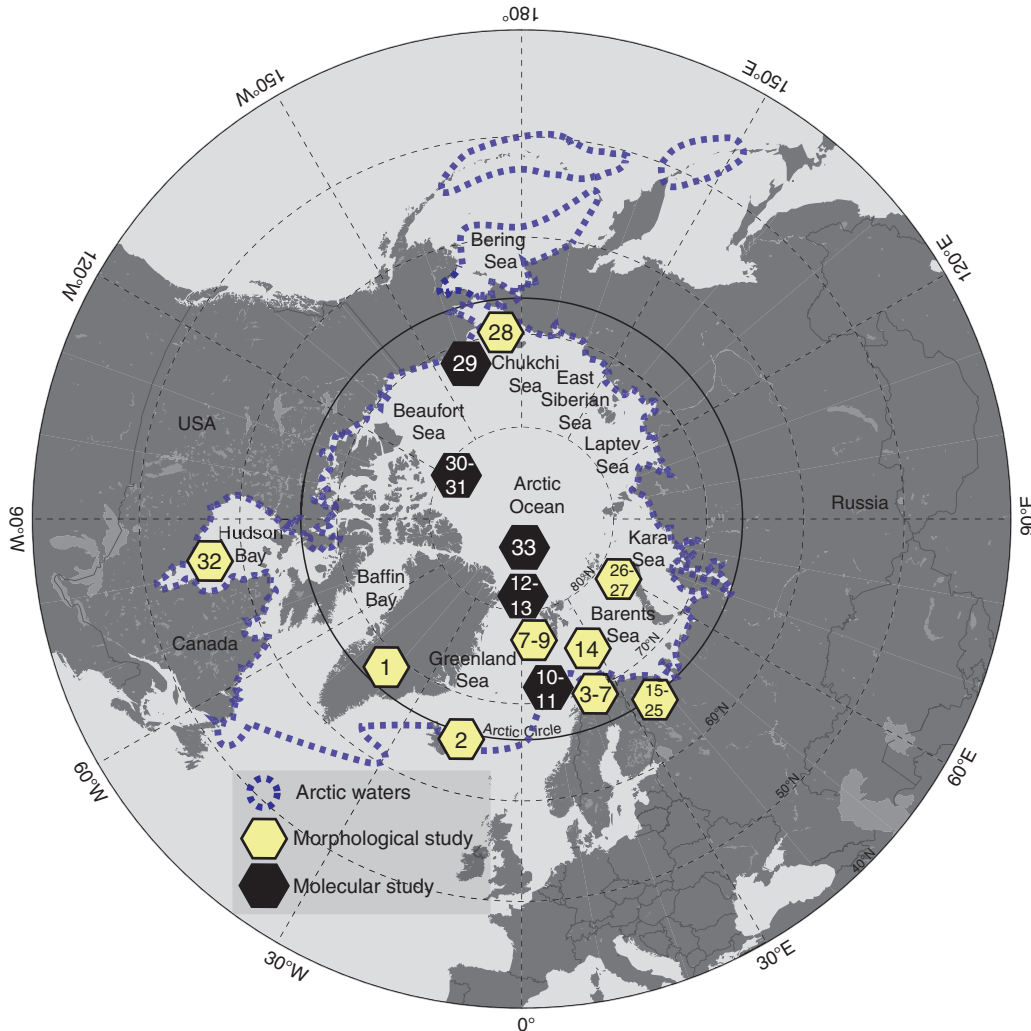


Figure 1: Research locations of marine fungi in the Arctic.

Arctic waters are delineated by the +10°C isotherm that is drawn following Hughes (1974) and Locarnini et al. (2010). Polygons indicate approximate study locations for studies on fungi (studies on fungal-like organisms are excluded): (1) Petersen (1905), (2) Cavaliere (1968), (3) Rehm (1896), (4) Eriksson (1973), (5) Baral and Rämä (2015), (6) Rämä et al. (2014a), (7) Pang et al. (2011), (8) Pang et al. (2008), (9) Pang et al. (2009), (10) Rämä et al. (2014b), (11) Rämä et al. (2016), (12) Zhang et al. (2015), (13) Zhang et al. (2016), (14) Schaumann (1975), (15) Meilik and Petrov (1966), (16) Artemchuk (1974), (17) Kuznetsov (1979), (18) Sogonov and Marfenina (1999), (19) Bubnova (2009), (20) Bubnova and Kireev (2009), (21) Bubnova (2010), (22) Konovalova and Bubnova (2011), (23) Konovalova et al. (2012), (24) Kireev et al. (2015), (25) Bubnova (2016), (26) Kirtsideli et al. (2012), (27) Bubnova and Nikitin (2017), (28) Bubnova and Konovalova unpublished, (29) Hassett and Gradinger (2016), (30) Hassett et al. (2016), (31) Comeau et al. (2016), (32) Booth (1981), (33) Blanchette et al. (2016).

Barents Sea area, as well as by Schaumann (1975) in the Nordic countries. During this time, there was no published work from the North American Arctic (cf. Johnson and Sparrow 1961). However, Terry W. Johnson Jr. was active in the Nordic countries and published several papers on marine fungi and fungal-like organisms from Iceland, building on the work he initiated in the 1960s (e.g. Johnson 1968, 1971, 1972, 1973), some coauthored by his colleagues and students (Cavaliere 1968, Johnson and Cavaliere 1968, Johnson and Howard

1968). Many of Johnson's works were conducted in temperate waters south of the Arctic Circle and often gave no exact location for the observations. For this reason, only a few Arctic water records made in Northern and Eastern parts of Iceland are included in this review. In the following decades, few mycological studies were published from the Arctic region (Booth 1981, Sogonov and Marfenina 1999), whereas research activity has increased in the 21st century (Tchesunov et al. 2008, Bubnova 2009, 2010, 2016, Bubnova and Kireev 2009,

Konovalova and Bubnova 2011, Konovalova et al. 2012, Rämä et al. 2014a, Kireev et al. 2015).

Cumulative research conducted since Rehm (1896) has resulted in 100 species of marine fungi reported from the area north of the Arctic Circle, of which *Cladosporium macrocarpum* is reported here for the first time from the Arctic (Table 1). This number includes filamentous species and one common yeast species, *Debaryomyces hansenii*. Fungal-like organisms (e.g. Oomycota, mesomycetozoa, thraustochytrids) that were studied by mycologists in the past, and many yeasts isolated from marine habitats (e.g. Gunde-Cimerman et al. 2005) are excluded from our inventory. Sixty-one species have been detected or isolated from truly Arctic waters, including seven species that were previously only known from temperate waters of the Arctic region (Table 1). Additionally, we have compiled a list of 88 fungal species that have been detected or isolated from marine habitats in the Arctic, but whose ecology remains unclear (Table 2). More data are needed to confirm whether these species are marine taxa (*sensu* Pang et al. 2016).

Gathering species occurrence data from the Arctic is a major step forward in understanding the distribution patterns of species, especially for the truly Arctic waters that remain insufficiently explored. Fungi classified as strictly marine taxa, such as Lulworthiales and Halosphaeriaceae, are underrepresented in our list and should be the subject of increased focus in the future. We chose to exclude tens of species from the White Sea area in Russia that were included in thesis works and subsequently determined to be unreliable (Kuznetsov 2003, Bubnova 2005, Konovalova 2012), as no voucher material was deposited in collections for confirmation. The excluded records are mostly included in Tchesunov et al. (2008) that is available in English at <http://en.wsbs-msu.ru/>.

We have just started to gain a more complete understanding of the marine fungal diversity in the Arctic. Based on our incomplete understanding of fungal taxa in northern latitudes, our synthesised list of fungal species suggests that the Arctic region is rich in marine fungal taxa. The 25 morphological studies published from the Arctic during the last 120 years are obviously not enough to establish a comprehensive list of all the species present in Arctic areas; consequently, much more sampling is needed to compare Arctic fungal diversity to warmer environments or the Antarctic. For example, seaweed-associated fungal species are barely studied in the Arctic (but see Konovalova and Bubnova 2011, Konovalova 2012), though kelp forests and algal beds cover vast areas of the Arctic shallow seafloor

and are expected to host novel fungal species (Zuccaro et al. 2003, Jones 2011). Morphological investigations are time consuming and require specialised taxonomic expertise. More efficient tools are needed to expedite the exploration of the marine mycobiota, as we do not know how Arctic species will adapt under forecasted environmental changes, such as receding sea ice-cover and increasing temperatures. Sanger sequencing and HTS are established tools that can be used to assess fungal diversity in the Arctic marine environment. Integrating morphological techniques with molecular tools have given promising results that will be addressed in the following section.

Molecular studies

Until the 1990s, mycological diversity studies were largely based on morphological examination of fruiting bodies and culture isolates. The wide application of first-generation sequencing techniques, based on Sanger sequencing and molecular fingerprinting methods (e.g. denaturing gradient gel electrophoresis and restriction fragment length polymorphism), introduced new possibilities for characterising fungal diversity. Buchan et al. (2002) and Zuccaro et al. (2003) used DNA fingerprinting methods for profiling marine fungal communities, whereas Spatafora et al. (1998) led the way for molecular identification and evolutionary studies on marine fungi based on Sanger sequencing. By pairing Sanger sequencing with cloning of DNA extracted directly from substrates, it became possible to survey non-fruiting members of the communities (Rondon et al. 2000). However, inherent biases associated with cloning methodologies exclude a sizable fraction of microbial diversity (see e.g. marine studies Stoeck et al. 2007, 2009).

The second molecular revolution in fungal ecology took place during the mid-2000s, when new HTS techniques were introduced. HTS can produce thousands of sequences (reads) per sample in a single run and may be used to create taxonomic profiles of fungal communities at a fraction of the costs associated with culturing and subsequent Sanger sequencing of axenic cultures (Liu et al. 2012). HTS techniques also detect species that are fastidious, impossible to culture, or are non-fruiting. The possible drawbacks of HTS include extensive bioinformatic processing of large datasets and the non-selective sequencing of artefactual DNA sourced from dead organisms. The first available HTS platform was 454 pyrosequencing (Margulies et al. 2005), which

Table 1: Morphologically identified marine fungi found in the Arctic region.

Species	Country; Substrate ¹	References	Arctic/ temperate
Fungi			
Basidiomycota			
Exobasidiomycetes			
Exobasidiales			
<i>Tilletiopsis albescens</i> Gokhale	Russia; A	22	-/+
Agaricomycetes			
Russulales			
<i>Digitatispora marina</i> Doguet ^{a,3}	Norway; D	6, 10	+/+
Ascomycota			
Dothideomycetes			
Capnodiales			
<i>Aureobasidium pullulans</i> (de Bary) Abnaud	Russia; A, L	18, 22	-/+
<i>Cladosporium cladosporioides</i> (Fresen.) G.A. de Vries	Russia; A, L, S, W	18, 19, 20, 21, 22, 27	+/+
<i>C. herbarum</i> (Pers.) Link	Russia; L, S, W	18, 19, 20, 26	+/+
<i>C. macrocarpum</i> Preuss ²	Russia; S	28	+/-
<i>C. sphaerospermum</i> Penz.	Russia; A, L, W	18, 20, 21, 22, 27	+/+
<i>Sphaerulina orae-marais</i> Linder	Norway; Sa	6	-/+
<i>Stigmidium ascophylli</i> (Cotton) Aptroot	Russia; A	23	-/+
Pleosporales			
<i>Alternaria alternata</i> (Fr.) Keissler ^{a,3}	Russia; A, L, S, W	18, 19, 20, 22, 27, 28	+/+
<i>A. botrytis</i> (Preuss) Woudenberg et Crous	Russia; A	20	-/+
<i>A. raphani</i> J.W. Groves et Skolko	Russia; L	18	-/+
<i>Asteromyces cruciatus</i> Moreau et F. Moreau ex Hennebert ^a	Norway; D	6, 10	+/-
<i>Coniothyrium cerealis</i> E. Müll.	Russia; A	22	-/+
<i>Dictyosporium pelagicum</i> (Linder) G.C. Hughes ex E.B.G. Jones	Canada; D	32	+/-
<i>Paradendryphiella arenariae</i> (Nicot) Woudenberg et Crous	Russia; A, S	19, 20	-/+
<i>P. salina</i> (G.K. Sutherl.) Woudenb. et Crous.	Russia; A, L, S	18, 19, 20, 22, 24	-/+
<i>Phaeosphaeria neomaritima</i> (R.V. Gessner et Kohlm.) Shoemaker et C.E. Babc.	Russia; H	25	-/+
<i>Phoma herbarum</i> Westend. ^a	Russia; A, S, W	19, 22, 26, 28	+/+
<i>Pleospora triglochinicola</i> J. Webster	Norway, Russia; H	3, 25	+/-
Mytilinidiales			
<i>Halokirschsteiniothelia maritima</i> (Linder) Boonmee et K.D. Hyde ^{a,3}	Iceland, Norway; D	2, 6, 10	+/+
Eurotiomycetes			
Chaetothyriales			
<i>Capronia ciliomaritis</i> (Kohlm.) E. Müll., Petrini, P.J. Fisher, Samuels et Rossman	Canada, Norway; D	6, 32	+/+
Eurotiales			
<i>Aspergillus candidus</i> Link	Russia; L	18	-/+
<i>A. carneus</i> Blochwitz	Russia; L	18	-/+
<i>A. ficuum</i> (Reichardt) Thom et Currie	Russia; A	20	-/+
<i>A. flavus</i> Link ³	Russia; L, S	18, 27, 28	+/+
<i>A. fumigatus</i> Fresen.	Russia; L	18	-/+
<i>A. glaucus</i> (L.) Link	Russia; A	20	-/+
<i>A. niger</i> Tiegh.	Russia; A, L, W	18, 20, 22, 26	+/+
<i>A. pulvirulentus</i> (McAlpine) Thom	Russia; A	20	-/+
<i>A. wentii</i> Wehmer	Russia; S	19	-/+
<i>A. versicolor</i> (Vuill.) Tirab.	Russia; A	22	-/+
<i>Beauveria bassiana</i> (Bals.-Criv.) Vuill.	Russia; A, S	19, 22	-/+
<i>Penicillium aurantiogriseum</i> Dierckx	Russia; A, L, S, W	18, 19, 20, 21, 22, 26, 28	+/+
<i>P. brevicompactum</i> Dierckx	Russia; A, L, W, S	18, 19, 20, 21, 22, 26	+/+
<i>P. canescens</i> Sopp	Russia; A, L, W, S	18, 20, 21	+/+
<i>P. chrysogenum</i> Thom	Russia; A, L, W, S	18, 19, 20, 21, 26	+/+
<i>P. citrinum</i> Thom	Russia; L, S, W	18, 19, 21, 26	+/+

Table 1 (continued)

Species	Country; Substrate ¹	References	Arctic/ temperate
<i>P. commune</i> Thom	Russia; S	21	+/-
<i>P. expansum</i> Link	Russia; L, S, W	18, 19, 26	+/+
<i>P. glabrum</i> (Wehmer) Westling ⁵	Russia; A, L, S, W	18, 19, 20, 22, 26, 28	+/+
<i>P. griseofulvum</i> Dierckx	Russia; L	18	-/+
<i>P. janczewskii</i> K.M. Zalesky	Russia; L, S	18, 19	-/+
<i>P. lanosum</i> Westling	Russia; S, W	19, 21, 26	+/+
<i>P. miczynskii</i> K.M. Zalesky	Russia; S	21	+/-
<i>P. montanense</i> M. Chr. et Backus	Russia; L	18	-/+
<i>P. paxilli</i> Bainier	Russia; S	19	-/+
<i>P. raistrickii</i> G. Sm.	Russia; A, S	19, 20, 22	-/+
<i>P. restrictum</i> J.C. Gilman et E.V. Abbott	Russia; S	19	-/+
<i>P. simplicissimum</i> (Oudem.) Thom	Russia; L, S, W	18, 19, 21, 26	+/+
<i>P. spinulosum</i> Thom	Russia; L, S, W	18, 19, 21, 26	+/+
<i>P. thomii</i> Maire C	Russia; A, L, S, W	18, 19, 22, 26, 28	+/+
<i>P. waksmanii</i> K.M. Zalesky	Russia; L	18	-/+
Leotiomycetes			
<i>Incertae sedis</i>			
<i>Pseudogymnoascus pannorum</i> (Link) Minnis et D.L. Lindner ⁴	Russia; A, L, S, W	18, 19, 21, 22, 26, 28	+/+
Helotiales			
<i>Amylocarpus encephaloides</i> Curr. ^a	Canada, Norway; D	7, 6, 10, 32	+/+
<i>Cadophora malorum</i> (Kidd et Beaumont) W. Gams ^a	Russia; W	26	+/+
<i>Calycina marina</i> Rämä et Baral ^{a,3}	Norway; A	4, 5, 6	+/+
Saccharomycetes			
Saccharomycetales			
<i>Debaryomyces hansenii</i> (Zopf) Lodder et Kreger ^a	Russia; A	22, 26	+/+
Sordariomycetes			
Diaporthales			
<i>Phialophorophoma litoralis</i> Linder ^{a,3}	Norway; D		+/-
Hypocreales			
<i>Acremonium fuci</i> Summerb., Zuccaro et W. Gams	Russia; A, S	19, 20, 22	-/+
<i>A. furcatum</i> (Moreau et V. Moreau) ex W. Gams	Russia; S	19	-/+
<i>A. pesicinum</i> (Nicot.) W. Gams	Russia; L	18	-/+
<i>A. potronii</i> Vuill.	Russia; A	22	-/+
<i>A. tubakii</i> W. Gams	Russia; S	19	-/+
<i>Chaetomium difforme</i> W. Gams	Russia; A	20	-/+
<i>C. globosum</i> Kunze ex Fries ^a	Russia; A	20, 22, 28	+/+
<i>Gelasinospora tetrasperma</i> Dowding	Russia; A	22	-/+
<i>Gliomastix murorum</i> (Corda) S. Hughes ³	Russia; S	19, 27	+/+
<i>Sarocladium strictum</i> (W. Gams) Summerb.	Russia; A, S, W	19, 20, 21, 22, 27	+/+
<i>Trichoderma atroviride</i> P. Karst.	Russia; S	19	-/+
<i>T. hamatum</i> (Bonord.) Bainier	Russia; S	19, 21	+/+
<i>T. harzianum</i> Rifai	Russia; S	19	-/+
<i>T. koningii</i> Oudemans	Russia; L, S	18, 19, 21	+/+
<i>T. viride</i> Pers.	Russia; A, L, S, W	18, 19, 20, 26, 28	+/+
Lulworthiales			
<i>Lulwoana uniseptata</i> (Nakagiri) Kohlm., Volkm.-Kohlm., J. Campb., Spatafora et Gräfenhan ^a	Norway; D	6	+/-
<i>Lulworthia halima</i> (Ellis et Everh.) Cribb et J.W. Cribb	Canada, Norway; D	6, 7, 10, 14, 32	+/+
<i>Lulworthia</i> spp. ^a	Norway; D	6, 7, 10, 14	+/+
Microascales			
<i>Appendichordella amicta</i> (Kohlm.) R.G. Johnson, E.B.G. Jones et S.T. Moss	Canada; D	32	+/-
<i>Ceriosporopsis halima</i> Linder	Canada, Iceland; D	2, 32	+/+
<i>Corollospora luteola</i> Nakagiri et Tubaki	Norway; D	6	+/-
<i>Halosphaeriopsis mediosetigera</i> (Cribb et J.W. Cribb) T.W. Johnson	Canada; D	32	+/-

Table 1 (continued)

Species	Country; Substrate ¹	References	Arctic/ temperate
<i>Havispora longyearbyensis</i> K.L. Pang et Vrijmoed	Norway; D	6, 7, 8	+/-
<i>Lautisporopsis circumvestita</i> (Kohlm.) E.B.G. Jones, Yusoff et S.T. Moss	Norway; D	7, 6	-/+
<i>Naïs inornata</i> Kohlm.	Canada, Norway; D	6, 32	+/+
<i>Nereiospora comata</i> (Kohlm.) E.B.G. Jones, R.G. Johnson et S.T. Moss	Canada, Norway; D	6, 32	+/-
<i>N. cristata</i> (Kohlm.) E.B.G. Jones, R.G. Johnson et S.T. Moss	Canada, Norway/Russia; D	14, 32	-/+
<i>Remispora maritima</i> Linder	Canada, Norway; D	6, 32	+/+
<i>R. pileata</i> Kohlm.	Norway; D	6	+/-
<i>R. quadri-remis</i> (Höhnk) Kohlm.	Canada, Norway; D	6, 32	+/+
<i>R. spitsbergensis</i> K.L. Pang et Vrijmoed	Norway; D	6, 9	+/-
<i>R. stellata</i> Kohlm. ^a	Canada, Norway; D	6, 32	+/+
<i>Sablecola chinensis</i> E.B.G. Jones, K.L. Pang et Vrijmoed	Norway; D	7	-/+
<i>Toriella tubulifera</i> (Kohlm.) Sakay., K.L. Pang et E.B.G. Jones	Canada, Norway; D	7, 14, 32	+/-
<i>Tubakiella galerita</i> (Tubaki) Sakay., K.L. Pang et E.B.G. Jones	Canada, Norway/Russia; D	14, 32	+/-
Chytridiomycota			
Chytridiales			
<i>Spizellomyces palustre</i> A. Gaertn. ex D.J.S. Barr	Canada; L	32	+/-
Rhizophydiales			
<i>Algochytrops polysiphoniae</i> (Cohn) Doweld	Greenland (Denmark); A	1	+/-
<i>Rhizophydium angulosum</i> Karling	Canada; L	32	+/-
<i>R. sphaerotheca</i> Zopf	Canada; L	32	+/-
<i>Uebelmesseromyces harderi</i> M.J. Powell et Letcher	Canada; L	32	+/-
Fungi			
<i>Incertae sedis</i>			
<i>Olpidium maritimum</i> Höhnk et Aleem	Russia; F, L, W	16, 17	-/+

The table contains species included in Jones et al. (2015).

References are listed in legend to Figure 1. The division between Arctic and temperate waters follows Hughes (1974), and taxonomy follows Jones et al. (2015) and Index Fungorum (www.indexfungorum.org).

^aSpecies supported by sequence data.

¹Substrate abbreviations: A, algae; D, dead wood; F, foam; H, halophyte; L, littoral ground and soil; S, sediment; Sa, saprotroph in different substrates; W, seawater.

²First marine record from Arctic region published here.

Cladosporium macrocarpum **Russia, Chukchi Sea**, bottom sediments, 40 m depth, 67°32'14"N.

³First record from Arctic waters published here.

Digitatispora marina **Norway, Finnmark**, Berlevåg, Tanafjorden, Store Molvik, on intertidal wood (*Pinus* sp.), 70°38'42"N, 22°14'4"E, 6.IX.2010, T. Rämä 3070.

Alternaria alternata **Russia, Barents Sea**, bottom sediments, 304 m depth, 08.X.2014, K. Bubnova 14-200-55.

Halokirschsteiniiothelia maritima **Norway, Svalbard**, Adventfjorden, Longyearbyen, on intertidal wood (*Pinus* sp.), 78°14'59.83"N, 15°30'30.79"E, 15.VII.2011, T. Rämä 3122; Kongsfjord, Hukbogen, station M11HEL0590, on wood in splash zone, 78°58'45"N, 11°17'4"E, 01.X.2011, T. Rämä 3124; Smeerenburgfjorden, station M11HEL0435, on drifting wood (*Pinus* sp.), 79°40'9.86"N, 11°11'7"E, 03.X.2011, T. Rämä 3127.

Aspergillus flavus **Russia, Chukchi Sea**, bottom sediments, 73 m depth, 71°42'43"N, 174°53'07"W, 08.IX.2012, K. Bubnova 12-02-28.

Calycina marina **Norway, Svalbard**, Hinlopenstretet, Gyldenøyene, station M16HEL1413, decaying *Fucus* sp. in splash zone, 12.VIII.2016, T. Rämä.

Phialophorophoma litoralis **Norway, Finnmark**, Hasvik, Sørøya, Nordsandfjorden, on driftwood (*Betula* sp.), 15.VIII.2010, T. Rämä 3051D.

Gliomastix murorum **Russia, Barents Sea**, bottom sediments, 242 m depth, 08.X.2014, K. Bubnova 14-200-51.

⁴*Geomyces pannorum* is considered as a synonym for *Pseudogymnoascus pannorum* (Index Fungorum). In Jones et al. (2015) both names were used, i.e. the same taxon was included twice.

⁵*Penicillium frequentans* is considered as a synonym for *P. glabrum* (Index Fungorum). In Jones et al. (2015) both names were used, i.e. the same taxon was included twice.

for several years produced the longest sequence reads, long enough to cover, for example, the fungal internal transcribed spacer 1 (ITS1) or ITS2 region (Liu et al. 2012), but whose efficacy was limited by inaccurate base

calling in homopolymer regions. Another popular platform that was used at the beginning of the second molecular revolution is Illumina sequencing (Bennett 2004, Bentley et al. 2008). The Illumina read length is shorter

(currently single strand maximum of 300 base pairs; at <http://www.illumina.com>) than the 454 pyrosequencing platform's (700 bp; Liu et al. 2012). The number of 454 pyrosequencing studies published will start to decrease in the coming years, as Roche has terminated the support for this platform, whereas Illumina sequencing is still being developed and the length of the sequencing reads is expected to grow. Other second generation platforms include Ion Torrent (e.g. used in Picard 2017), PacBio and MinION, but these technologies remain to be fully applied to marine fungi. Third generation techniques such as single-cell sequencing provide exciting future opportunities as genome sequences or transcriptomes can be obtained from single-cells rapidly and at low-cost.

The number of second-generation HTS studies targeting marine fungi has seen a rapid increase in the 2010s. The first studies started appearing less than a decade ago (Alexander et al. 2009, Stoeck et al. 2009) and, since then, the techniques have been applied to anoxic waters (Stoeck et al. 2010) and deep-sea habitats (Alexander et al. 2009, Le Calvez et al. 2009, Orsi et al. 2013). Results of HTS studies are difficult to compare due to the different types of environmental samples sequenced, DNA locus selected (e.g. ITS, 28S and 18S), data processing methods and sequencing techniques used. The richness of fungi is usually measured as numbers of Operational Taxonomic Units (OTUs), which can be defined using different sequence similarity cut-off values of sequencing reads. Usually these OTUs are defined to correspond to a species based on an averaged estimate of intraspecific variation of a given gene marker, such as the ITS (Nilsson et al. 2008). Comparing OTU counts from different substrates obtained using varying survey inputs can, at best, give us a rough estimate of the richness of fungal communities. Unfortunately, rarefaction curves seldomly reach saturation, meaning only a subset of the total community has been sampled (e.g. Rämä et al. 2016).

Richness of marine fungi in the Arctic

Recent molecular studies of Arctic marine fungi have focused on driftwood (Rämä et al. 2014b, 2016, Blanchette et al. 2016), sediments (Zhang et al. 2015, Hassett and Gradinger 2016), seawater and sea-ice (Comeau et al. 2016, Hassett et al. 2016, Hassett and Gradinger 2016), and water from brackish (and fresh) water habitats (Zhang

et al. 2016). These studies have shown that marine habitats in the Arctic host fungal assemblages consisting of potentially hundreds of species.

A HTS study revealed 113 fungal OTUs in eight sediment samples from a high Arctic fjord (Zhang et al. 2015). The OTUs were defined based on a 97% sequence similarity cut-off value of the ITS rDNA region. Blanchette et al. (2016) sequenced 103 fungal species out of 177 cultures that were isolated from 80-driftwood logs in Greenland, Iceland and the Lena River Delta (Russia). A much higher richness was detected in 50 recently stranded logs in Norway by coupling two study approaches. Rämä et al. (2014b, 2016) found altogether 904 OTUs (Rämä unpublished; same OTU definition as Zhang et al. 2015). By plating wooden cubes and targeting the ITS and 28S rDNA regions with Sanger sequencing of the cultured isolates, Rämä et al. (2014b) detected 143 OTUs, of which 46 were detected also using the 454 pyrosequencing approach (Rämä unpublished). The number of shared OTUs was surprisingly low, even though it is known that method-related biases cause different fungi to be detected using different study methods (Ovaskainen et al. 2010, Lindner et al. 2011).

Comparable richness of fungi was also found by Hassett et al. (2016), who detected 450 fungal OTUs (97% similarity of 18S rDNA sequences) in 12 sea-ice samples analysed. Zhang et al. (2016) detected 641 OTUs (same OTU definition as in Zhang et al. 2015) in their most recent study of aquatic fungi at 78°55'N, while the two estuarine samples contained 165 and 146 OTUs. The relatively low number of OTUs in this study is likely due to under-sampling, since only a total of two litres of estuarine water was sampled in two proximate locations. Comeau et al. (2016) were concerned about the problem of under-sampling and analysed approximately 15,000 post-filtered 18S rDNA pyrosequencing reads derived from 164 marine samples from Russian and the North American Arctic. Based on 98% 18S rDNA similarity as a cut-off value, Comeau et al. (2016) detected 2799 OTUs in Arctic seawater. Interestingly, only 149 of these OTUs were shared with Atlantic water samples and 35 with Arctic freshwater and sea-ice samples.

The current knowledge is too limited for drawing conclusions about the richness of Arctic marine fungi. However, the number of recovered OTUs in different studies is high, especially if OTU counts from individual substrates are compared to the number of marine fungi known (1112 species; Jones et al. 2015). Independent OTU counts from different substrates support the estimate of at least 12,000 marine fungal species (Jones and Pang 2012). In fact, it may be that 12,000 species is still an

underestimate, as the genetic diversity detected in single studies is so high. Given the assumption that a single OTU corresponds to a species, it is hard to believe that 5–10%, even 23% (Comeau et al. 2016), of all marine fungal species would be found in single studies made in the harsh Arctic environment. However, it is worth bearing in mind that the OTU numbers may contain several terrestrial species that are not repeatedly isolated from, nor adapted to live in, this environment and should not be called marine fungi (Pang et al. 2016).

Phylogenetic diversity of Arctic marine fungi

Molecular studies conducted in the Arctic have revealed that different fungal phyla dominate in different marine habitats. Driftwood and sediments seem to host mostly ascomycetes, with relative frequency among OTUs varying between 55% and 85% in different studies (Rämä et al. 2014b, 2016; Zhang et al. 2015; Blanchette et al. 2016). However, Chytridiomycota (chytrids) dominated fungal communities (50–99% relative abundance across different months) in sediments under land fast-ice near Barrow, Alaska (Hassett and Gradinger 2016). Sediments under land fast-ice may be distinct in the taxonomic composition of their fungi, because high phytoplankton biomass provides niches for marine parasitic fungi, such as Chytridiomycota (see below). Based on HTS studies, ascomycetes are abundant in seawater and sea-ice samples under high snowpack and tend to supplement chytrid-dominated fungal communities (Comeau et al. 2016; Hassett et al. 2016; Hassett and Gradinger 2016; Zhang et al. 2016).

Molecular methods may challenge the morphology-based view that Sordariomycetes, Dothideomycetes, Eurotiomycetes and Saccharomycetes are the dominant groups of marine fungi (Jones and Pang 2012; Jones et al. 2015), although in some molecular studies the above-mentioned groups were dominant (Zuccaro et al. 2003, 2008). At least in the Arctic, this dominance pattern cannot be proved based on the few published studies. The molecular studies conducted at high latitudes, and especially the ones applying HTS, have revealed that other taxonomic classes of fungi dominated in Arctic marine substrates. In two out of three HTS studies that presented the taxonomic profile of detected OTUs in detail, other fungal classes were more frequent. In North Atlantic driftwood, Leotiomyces was the most frequent fungal class with 21% relative frequency of OTU occurrence

(Rämä et al. 2016). Applying a culturing approach on the same study logs, Sordariomycetes were found to be the most frequently detected fungal class (40% frequency; Rämä et al. 2014b), which indicates that members of this fungal class are selected for in culturing (using standard methods for culturing marine filamentous fungi). In estuarine water samples from the high Arctic, Microbotryomycetes were found to be predominant with 28% frequency (Zhang et al. 2016), whereas Sordariomycetes were detected with only 0.25% frequency. The other frequent groups of marine fungi, such as Eurotiomycetes and Dothideomycetes, were detected with 5% and 1% frequency, respectively. In Zhang et al. (2016), basidiomycetes were most frequent (together with chytrids); for example, Tremellomycetes (including both yeast-like and filamentous forms) had a 5% frequency of occurrence.

Agaricomycetes (Basidiomycota) is a frequent class of fungi detected in Arctic marine HTS studies. It is in the top five most frequent taxonomic classes of fungi in three out of four molecular studies that listed the taxa of detected fungal OTUs (Rämä et al. 2014b, 2016; Zhang et al. 2016). The high frequency of Agaricomycetes was likely due to the OTUs belonging to the fungal orders Agaricales and Sebaciales (Zhang et al. 2015). Interestingly, the ascomycetous fungal order Helotiales contributed most to the dominance of Leotiomyces in Rämä et al. (2014b, 2016) and Zhang et al. (2015) with relative frequency of 17%, 21% and 12%, respectively.

Cadophora (Helotiales)

The high frequency of Leotiomyces and Helotiales OTUs in molecular studies is partly due to the large abundance of fungal species within the genus *Cadophora* Lagerb. et Melin. The genus was described as a blue stain fungus of conifers in Scandinavia (Lagerberg et al. 1927). Later, it was morphologically identified from conifers (Land et al. 1987) and wood pulp in pulp mills of North America (Martin 1938, Brewer 1958). In marine morphological studies, *Cadophora* has been infrequently detected (Bubnova 2009, Bubnova and Nikitin 2017), and it is likely that this asexual genus has been overlooked or confused with *Phialophora* Medlar that is morphologically similar, but molecularly distinct from *Cadophora* (Gams 2000, Harrington and McNew 2003). Indeed, it was not until first-generation molecular studies that it became apparent how frequent and predominant *Cadophora* species are in the Arctic (Rämä et al. 2014b, Blanchette et al. 2016), also confirmed

Table 2: Morphologically identified fungi detected in, or isolated from, marine habitats in the Arctic region.

Species	Country; Substrate ¹	References	Arctic/ temperate
Fungi			
Basidiomycota			
Tremellomycetes			
Tremellales			
<i>Cryptococcus albidus</i> (Saito) C.E. Skinner	Russia; A	22	-/+
Ascomycota			
Incertae sedis			
<i>Acrodontium hydnicola</i> (Peck) de Hoog	Russia; A	22	-/+
<i>A. salmoneum</i> de Hoog	Russia; A	22	-/+
<i>Pseudeurotium hygrophilum</i> (Sogonov, W. Gams, Summerb. et Schroers)	Russia; S	19, 21, 27	+/+
Minnis et D.L. Lindner			
Dothideomycetes			
Capnodiales			
<i>Septoria ascophylli</i> Melnic et Petrov	Russia; A	15	-/+
Pleosporales			
<i>Alternaria alternariae</i> (Cooke) Woudenb. et Crous	Russia; A	20, 22	-/+
<i>A. tenuissima</i> (Kunze) Wiltshire	Russia; W	26	+/+
<i>Boeremia exigua</i> (Desm.) Aveskamp, Gruyter et Verkley	Russia; S	19, 21	-/+
<i>Epicoccum nigrum</i> Link	Russia; A	22	-/+
<i>Phoma leveillei</i> Boerema et G.J. Bollen	Russia; A	22	-/+
<i>Ulocladium chartarum</i> (Preuss) E.G. Simmons ³	Russia; A, S	22, 27	+/+
<i>U. consortiale</i> (Thüm.) E.G. Simmons	Russia; A	20, 22	-/+
Eurotiomycetes			
Chaetothyriales			
<i>Exophiala dermatitidis</i> (Kano) de Hoog	Russia; A	22	-/+
<i>Phialophora cinerescens</i> (Wollenw.) J.F.H. Beyma	Russia; A, S	19, 22	-/+
Eurotiales			
<i>Aspergillus clavatus</i> Desm.	Russia; A, L, W	18, 20	-/+
<i>Eurotium herbariorum</i> (Weber ex F.H. Wigg.) Link ex Nees	Russia; A	20	-/+
<i>Penicillium asperosporum</i> Smith ²	Russia; S	27	+/-
<i>P. atramentosum</i> Thom	Russia; S, W	26, 28	+/+
<i>P. bilaiae</i> Chalab.	Russia; L	18	-/+
<i>P. chermesinum</i> Biourge	Russia; S, W	19, 26, 28	+/+
<i>P. corylophyllum</i> Dierckx	Russia; S	19	-/+
<i>P. crustosum</i> Thom	Russia; L	18	-/+
<i>P. dierckxii</i> Biourge ²	Russia; S	28	+/-
<i>P. echinulatum</i> Raper et Thom ex Fassatiava	Russia; L	18	-/+
<i>P. hirsutum</i> Dierckx	Russia; S, W	21, 26	+/-
<i>P. italicum</i> Wehmer	Russia; S	19	-/+
<i>P. jensenii</i> K. M. Zalessky	Russia; A, W	20, 22, 26	+/+
<i>P. madriti</i> G. Sm. ²	Russia; S	27	+/-
<i>P. melinii</i> Thom	Russia; L	18	-/+
<i>P. multicolor</i> Grig.-Man. et Porad.	Russia; A, S	20, 21	+/+
<i>P. nalgiovense</i> Laxa	Russia; S	19, 21, 28	+/-
<i>P. palitans</i> Westling	Russia; S	19	-/+
<i>P. purpurescens</i> (Sopp) Biourge	Russia; S	21	+/-
<i>P. purpureogenum</i> Stoll	Russia; A	22	-/+
<i>P. roseopurpureum</i> Dierckx	Russia; S	19, 21	+/+
<i>P. sclerotiorum</i> J.F.H. Beyma	Russia; A	20	-/+
<i>P. steckii</i> K. M. Zalessky	Russia; S	19	-/+
<i>P. velutinum</i> J.F.H. Beyma	Russia; S	21	+/-
<i>P. vinaceum</i> J.C. Gilman et E.V. Abbott	Russia; S	19	-/+
<i>P. vulpinum</i> (Cooke et Massee) Seifert et Samson	Russia; L	18	-/+
<i>Talaromyces variabilis</i> (Sopp) Samson	Russia; A, S	19, 22	-/+
Onygenales			
<i>Chrysosporium merdarium</i> (Ehrenb.) J. W. Carmich	Russia; A, W	20	-/+

Table 2 (continued)

Species	Country; Substrate ¹	References	Arctic/ temperate
Leotiomycetes			
<i>Incertae sedis</i>			
<i>Pseudogymnoascus roseus</i> Ralio	Russia; S	19, 21	+/+
Helotiales			
<i>Botrytis cinerea</i> Pers.	Russia; A, L, W	18, 22, 26	+/+
<i>Cadophora fastigiata</i> Lagerb. et Melin ³	Russia; S	19, 27	+/+
Thelebolales			
<i>Thelebolus microsporus</i> (Berk et Broome) Kimbr. ^a	Russia; W, S	26, 28	+/+
Orbiliomycetes			
Orbiliales			
<i>Dactilella aquatica</i> (Ingold) Ranzoni	Russia; L	18	-/+
Saccharomycetes			
Saccharomycetales			
<i>Dipodascus geotrichum</i> (E.E. Butler et L.J. Petersen) Arx	Russia; A	22	-/+
Sordariomycetes			
<i>Incertae sedis</i>			
<i>Plectosphaerella cucumerina</i> (Lindf.) W. Gams	Russia; A	22	-/+
<i>Verticillium dahliae</i> Kleb.	Russia; A, W	20	-/+
Amphisphaeriales			
<i>Broomella acuta</i> Shoemaker et E. Müll.	Russia; A	22	-/+
Hypocreales			
<i>Acremonium charticola</i> (Lindau) W. Gams ^a	Russia; L	18, 28	+/+
<i>A. chrysogenum</i> (Thirum. et Sukapure) W. Gams	Russia; A, S	19, 20, 22	-/+
<i>A. kiliense</i> Grütz	Russia; A, L, S, W	18, 19, 20, 22	-/+
<i>A. rutilum</i> W. Gams	Russia; A, S	19, 22	-/+
<i>Cylindrocarpon cylindroides</i> Wollenw.	Russia; A	22	-/+
<i>Emericellopsis minima</i> Stolk	Russia; S	19	-/+
<i>Fusicolla aquaeductuum</i> (Radlk. et Rabenh.) Gräfenhan, Seifert et Schroers ²	Russia; S	28	+/-
<i>Fusarium oxysporum</i> Schltdl.	Russia; A, S	19, 20, 22	-/+
<i>Gibberella fujikuroi</i> (Sawada) Wollenw.	Russia; L, S	18, 19	-/+
<i>Isaria farinosa</i> (Holmsk.) Fr.	Russia; A, L, S	18, 19, 22	-/+
<i>Lecanicillium lecanii</i> (Zimm.) Zare et W. Gams	Russia; A, S	21, 22, 28	+/+
<i>Metarhizium carneum</i> (Duché et R. Heim) Kepler, Rehner et Humber	Russia; L	18	-/+
<i>M. marquandii</i> (Masse) Kepler, S.A. Rehner et Humber	Russia; L	18	-/+
<i>Pochonia suchlasporia</i> (W. Gams et Dackman) Zare et W. Gams	Russia; S	19	-/+
<i>Tolypocladium cylindrosporum</i> W. Gams	Russia; S	19, 21, 28	+/+
<i>T. geodes</i> W. Gams	Russia; S	21	+/-
<i>T. inflatum</i> W. Gams	Russia; S	19, 21, 28	+/+
<i>T. microsporum</i> (Jaap) Bissett	Russia; S	21	+/-
<i>Trichoderma citrinum</i> (Pers.) Jaklitsch, W. Gams et Voglmayr	Russia; S	21	+/-
<i>T. deliquescens</i> (Sopp) Jaklitsch	Russia; A	20	-/+
<i>T. polysporum</i> (Link) Rifai	Russia; S	21	+/-
Melanosporales			
<i>Harzia acremonioides</i> (Harz) Costantin	Russia; A	20	-/+
Microascales			
<i>Acaulium acremonium</i> (Delacr.) Sandoval-Denis, Guarro et Gené	Russia; A	20	-/+
<i>Cephalotrichum stemonitis</i> (Pers.) Nees	Russia; L	18	-/+
<i>Microascus paisii</i> (Pollacci) Sandoval-Denis, Gené et Guarro ²	Russia; S	27	+/-
<i>Scopulariopsis hibernica</i> A. Mangan ^{a,3}	Russia; S	28	+/-
<i>Wardomyces anomalus</i> F.T. Brooks et Hansf.	Russia; S	19	-/+
Sordariales			
<i>Papulaspora halima</i> Anastasiou	Canada; D or S	32	+/-
Zygomycota			
Mucorales			
<i>Absidia glauca</i> Hagem	Russia; L	18	-/+
<i>Mucor hiemalis</i> Wehmer	Russia; A, L, S, W	18, 19, 22, 26	+/+

Table 2 (continued)

Species	Country; Substrate ¹	References	Arctic/ temperate
<i>M. racemosus</i> f. <i>sphaerosporus</i> (Hagem) Schipper	Russia; A, W	20	-/+
<i>Rhizopus stolonifer</i> (Ehrenb.) Vuill. var. <i>stolonifer</i>	Russia; A	20	-/+
<i>Umbelopsis isabellina</i> (Oudem.) W. Gams ²	Russia; S	27	+/-
<i>U. ramanniana</i> (Möller) W. Gams	Russia; L	18	-/+
Chytridiomycota			
Chytridiales			
<i>Chytridium lagenaria</i> Schenk	Russia; W	16	-/+
<i>Rhizophydium globosum</i> (A. Braun) Rabenh	Russia; A	16	-/+
<i>Tylochytrium pollinis-pini</i> (A. Braun) Doweld	Russia; W	16	-/+

The table contains species whose ecological role in the marine environment is unclear. References are listed in the legend to Figure 1. The division between Arctic and temperate waters follows Hughes (1974), and taxonomy follows Jones et al. (2015) and Index Fungorum (www.indexfungorum.org).

²Species supported by sequence data.

¹Substrate abbreviations: A, algae; D, dead wood; L, littoral ground and soil; S, sediment; W, seawater.

²First marine record from Arctic region published here.

Penicillium asperosporum **Russia, Kara Sea**, bottom sediments, 128 m depth, 77°53'0.01"N, 80°15.051'E, 26.VIII.2014, K. Bubnova 14-200-08.

Penicillium dierckxii **Russia, Chukchi Sea**, bottom sediments, 59 m depth, 71°21'N, 171°17'21"W, 11.IX.2012, K. Bubnova 12-02-51.

Penicillium madriti **Russia, Barents Sea**, bottom sediments, 277 m depth, 09.X.2014, K. Bubnova 14-200-30.

Fusicolla aquaeductuum **Russia, Chukchi Sea**, bottom sediments, 45 m depth, 67°27'11"N, 169°37'05"W, 30.VIII.2012, K. Bubnova 12-02-05.

Microascus paisii **Russia, Kara Sea**, bottom sediments, 128 m depth, 77°53'0.01"N, 80°15.051'E, 26.VIII.2014, K. Bubnova 14-200-11.

Umbelopsis isabellina **Russia, Kara Sea**, bottom sediments, 128 m depth, 77°53'0.01"N, 80°15.051'E, 26.VIII.2014, K. Bubnova 14-200-19.

³First record from Arctic waters published here.

Ulocladium chartarum **Russia, Kara Sea**, bottom sediments, 128 m depth, 77°53'0.01"N, 80°15.051'E, 26.VIII.2014, K. Bubnova 14-200-09.

Cadophora fastigiata **Russia, Barents Sea**, bottom sediments, 203 m depth, 09.X.2014, K. Bubnova 14-200-35.

Scopulariopsis hibernica **Russia, Chukchi Sea**, bottom sediments, 64 m depth, 11.IX.2012, K. Bubnova 12-01-037 and 12-01-43.

using a second-generation HTS technique (Rämä et al. 2016). The Arctic (and Antarctic) habitats of *Cadophora* include soil and old expedition huts made of driftwood (Blanchette et al. 2004, 2010, Arenz and Blanchette 2009, Arenz and Blanchette 2011), freshwater lakes (Gonçalves et al. 2012) and marine sediments and wood (Jurgens et al. 2009, Rämä et al. 2014b, 2016). Interestingly, some species occurring in the sea [*C. luteo-olivacea* (J.F.H. Beyma) T.C. Harr. et McNew and *C. melinii* Nannf.] were also detected in grape vines worldwide (Gramaje et al. 2011, 2014, Navarrete et al. 2011, Travadon et al. 2015). Besides the saprotrophic life history, the genus is detected as an endophyte in various green plants and mosses in both high latitudes and temperate-tropical areas (Tosi et al. 2002, Chen et al. 2010, Rosa et al. 2010, Gramaje et al. 2011, Zhang and Yao 2015). *Cadophora* seems to possess phenotypic plasticity that has helped it to tolerate varying environmental conditions; consequently, it is a dominant taxon with bipolar distribution in cold and saline environments, as concluded already by Blanchette et al. (2016). *Cadophora* is hypothesised to be a key organism capable of initiating nutrient cycles

and energy flows from dead organic materials in high latitudes.

The wood decay pattern caused by *Cadophora* species is soft rot that is typical for marine ascomycetes (Barghoorn and Linder 1944, Duncan 1960, Blanchette et al. 2004). Members of the genus *Cadophora* are able to cause soft rot both in marine and terrestrial habitats, which naturally raises the question whether the strains are distinct between these two environments. In order to answer this question, we constructed a phylogeny of the publicly available *Cadophora* sequences that were derived from terrestrial and marine strains (Figure 2). We detected no separation between marine and terrestrial strains based on the barcoding marker ITS2. *Cadophora* strains from terrestrial and marine environments cluster together. *Cadophora luteo-olivacea*, for example, has been independently isolated from Arctic driftwood, submerged wood and algae in the Mediterranean, deep subsurface sediments, willow wood in the Antarctic and water mint stems along inland riversides. Our analysis gives more evidence of the morphological plasticity of this genus, and underscores that distinct phenotypes are

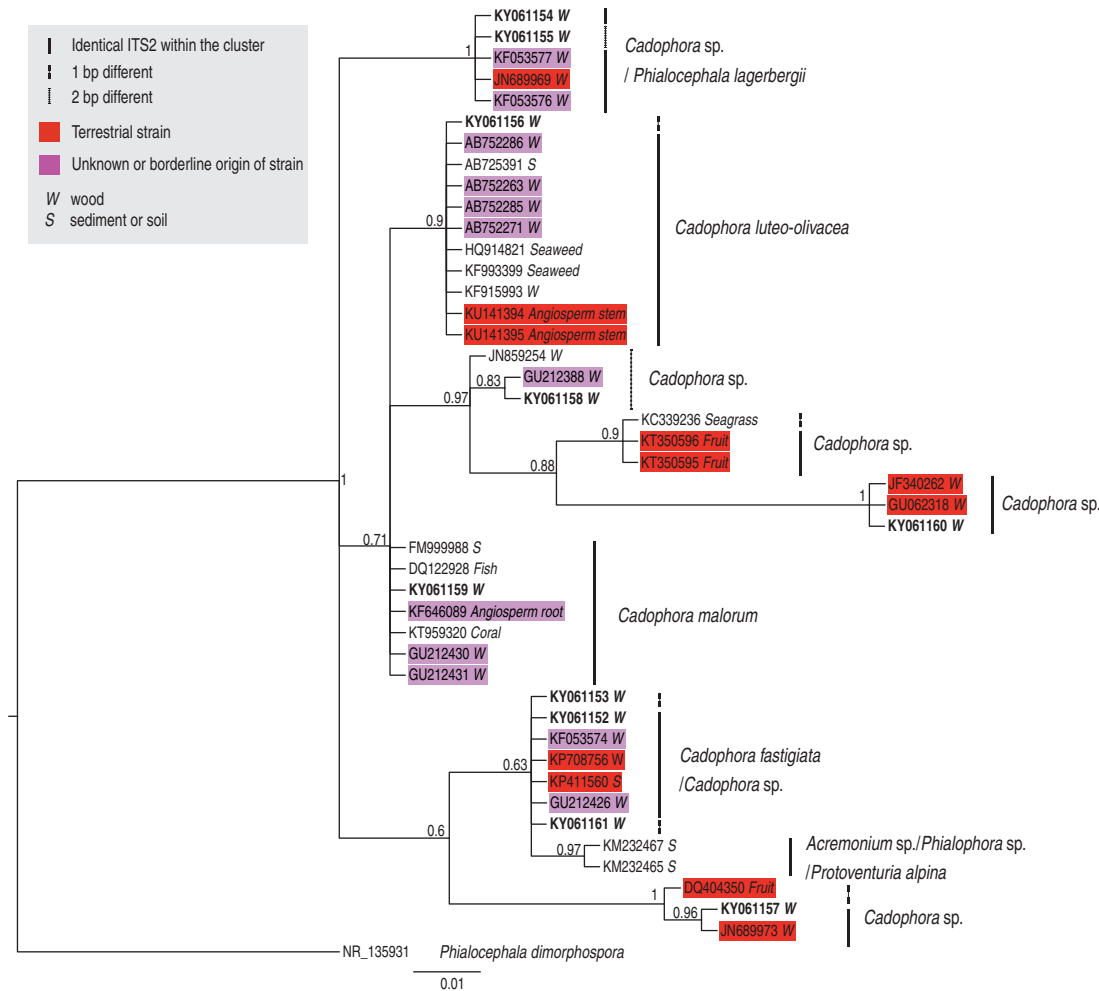


Figure 2: ITS2 phylogeny of *Cadophora* strains from the marine and terrestrial environment.

Strain labels include accession numbers in the National Center for Biotechnology Information's Nucleotide database, source environments and substrates of isolation. Sequences published as part of this study are in bold. Cluster identities are based on top megablast matches against the non-redundant (nr) database. Sequence from the type specimen of *Phialocephala dimorphospora* W.B. Kendr. was used as an outgroup for the analysis. Node support is given as posterior probabilities (PP) at the nodes and the scale bar shows estimated substitutions per site. The ITS2 alignment that was constructed contained 154 characters and 45 sequences. The analysis was run in Mr Bayes v. 3.2.4 (Ronquist et al. 2012) using a GTR model with γ -distributed rate variation across sites. The 20 million generations analysis using four chains in each of the three runs reached stationary and produced in total 60,003 trees, of which first 15,000 were discarded as burnin. The remaining trees were used to calculate the posterior probability (PP) support values for the nodes of a consensus tree produced using the 50% majority rule option.

able to persist both on land and in the sea. The genus *Cadophora* obviously includes marine species, but these are not restricted to marine habitats.

Chytridiomycota

First recognised as algal parasites in the mid-1800s (Braun 1851) and historically dismissed as ecologically inconsequential (Powell 1993), the Chytridiomycota are now understood to be voracious parasites of algae, fungi and

amphibians, capable of terminating algal blooms, delaying the onset of maximum algal densities, and altering microbial successions in aquatic ecosystems (e.g. Ibelings et al. 2004, Adl and Gupta 2006, Kagami et al. 2007, Lepère et al. 2008, Frenken et al. 2016). Chytrids possess various saprophytic modes of nutrition and use recalcitrant substances, such as plant pollen, cellulose, lignin, chitin and keratin (Sparrow 1960) as carbon and energy sources. Chytrids are globally distributed and can be found in deep sea sediments (Lopez-Garcia et al. 2001), manure (Simmons et al. 2012), arid sand dunes (Wakefield et al. 2010), soil, limnetic, and marine systems (Powell and Letcher 2012).

The presence and ecological role of chytrids in Arctic marine environments has historically remained uncertain; yet early morphological surveys of biological diversity in sea ice suggested the existence of parasitic Chytridiomycota on diatoms (e.g. Horner and Schrader 1982). Recent HTS studies across the Arctic have detected chytrids in polynyas (Terrado et al. 2011), sea ice (Hassett et al. 2016), sediment (Zhang et al. 2015, 2016), open-water (Comeau et al. 2016), and associated with wooden substrates (Rämä et al. 2016). The ecological niches occupied by chytrids in the Arctic marine environment still remain uncertain; however, chytrids have been observed parasitising large pennate diatoms across the western Arctic (Hassett et al. 2016) and detected in the gut content of Bering Sea zooplankton (Cleary et al. 2016). The presumed fastidious nature of algal symbionts has challenged the success of culturing-based studies of chytrids, resulting in the absence of any chytrid isolates from the Arctic marine environment; consequently, HTS studies have given a deeper understanding of the ecology associated with chytrids in the Arctic.

The diversity of the Chytridiomycota was historically understood in terms of morphological differences that guided a morphotypic species concept (e.g. operculation of the zoosporangium, rhizoid-branching patterns, and monocentric versus polycentric thallus development; Sparrow 1960). While these morphological characteristics established the framework for early taxonomy, they were phylogenetically erroneous due to the phenotypic plasticity of chytrids (Paterson 1963), resulting in molecular polyphyly (e.g. James et al. 2006). Global morphotypic species diversity circumscribed the Chytridiales to include 7 families, nearly 100 genera and almost 1000 species; however, many of these species were incompletely described and are likely to be synonyms (Karling 1977). The Chytridiales now contains two families and at least 14 described genera (Powell and Letcher 2012), based on the ultrastructure of the flagellated reproductive zoospore (e.g. Barr 1980) and molecular phylogeny (e.g. James et al. 2006). Today, 28S and ITS1-ITS2 rDNA loci are used reliably in molecular phylogenetic studies of chytrids, in conjunction with zoospore ultrastructure and thallus morphology to characterise chytrid species (e.g. Vélez et al. 2011, Powell et al. 2013, Davis et al. 2016), underscoring that general morphology alone cannot be reliably used to assess chytrid species diversity.

Classical taxonomic studies of morphology have described five high-latitude marine chytrid species (four from the Hudson Bay region and one from Greenland) belonging to the genera *Rhizophyidium* Schenk ex Rabenh., *Phlyctochytrium* J. Schröt., and *Uebelmesseromyces* M.J.

Powell et Letcher (as *Rhizophlyctis* A. Fisch. in the literature) (Table 1). Since these early observations, substantial taxonomic revisions have occurred, resulting in the elevation of the genus *Rhizophyidium* to the taxonomic order Rhizophydiales (Letcher et al. 2008), the reclassification of *Phlyctochytrium palustre* A. Gaertn. to *Spizellomyces palustris* (Barr 1984), the reclassification of *Rhizophlyctis harderi* Uebelm. to *Uebelmesseromyces harderi* (Powell et al. 2015), and the merging of the synonymous species *Rhizophyidium olla* H.E. Petersen and *Chytridium polysiphoniae* Cohn to *Algochytrrops polysiphoniae* (Letcher and Powell 2012, Doweld 2014). Reclassification of several of these species was conducted with non-Arctic type material (Barr 1984, Powell et al. 2015); consequently, the species diversity of the Chytridiomycota in Arctic marine environments remains uncertain.

Molecular HTS studies have detected a diverse population of chytrids across the Arctic, classified as the Chytridiales (Terrado et al. 2011, Majaneva et al. 2012, Hassett and Gradinger 2016), Rhizophydiales (Zhang et al. 2015), Mesochytriales, Gromochytriales, Lobulomycetales (Hassett and Gradinger 2016) and other unknown lineages (Zhang et al. 2015). The accuracy of HTS-generated read classification is challenged considerably by the genetic locus targeted (typically 18S rDNA; Panzer et al. 2015), the number of base pairs generated and the database used for taxonomic classification. Short 18S rRNA gene loci likely do not contain enough genetic information to resolve sequence reads to the taxonomic order level, as fungal taxonomy and phylogenetics typically use the more informative 28S rDNA locus (Letcher et al. 2008). Additionally, some taxonomic libraries (e.g. SILVA release 119) classify the Cryptomycota as “Chytridiomycota: *incertae sedis*”.

To circumvent the challenges associated with HTS-generated read classification, clone-based studies offer an alternative for assessing fungal diversity. Historically, fungal sequences have comprised <1% of total eukaryotic 18S rDNA clone libraries from marine environments (Massana and Pedrós-Alió 2008, Richards et al. 2012), suggesting a low incidence of fungi in marine environments; however, one 28S rDNA clone-based study from the Arctic identified a low-diversity (pair-wise) population of chytrids from 54 fungal clones that branch sister to the Lobulomycetales (Hassett et al., 2016). Overall mean pair-wise 28S rDNA genetic distance between species within the Lobulomycetales is estimated at 0.09 (unpublished data) and 0.056 between clones generated from across the Arctic (Hassett et al. 2016). Consequently, low pair-wise differences suggest minimal chytrid species diversity in the Arctic, based on sparse clone data.

Conclusions and future perspectives

The morphological and molecular work on marine fungi has greatly improved our understanding of marine fungal biology and ecology. However, the ecological roles and diversities of dikaryotic fungi and the Chytridiomycota in high latitude marine environments remain to be fully elucidated. More DNA barcoding of these fungi, i.e. more collecting and culturing coupled with morphological identification and sequencing of marker genes, is a requisite for improving fungal sequence databases. These will in turn facilitate increased OTU identification and more in-depth knowledge of Arctic marine fungal communities, obtained through molecular studies.

Arctic seas are rich in life and include numerous habitats and substrates that are known, or assumed, to host marine fungi. These substrates are not well studied, and some are barely explored within a mycological context, such as the extensive algal beds of the shallow seafloor. Cold-water coral reefs formed by *Lophelia pertusa* L. are another example of an overlooked habitat that most likely hosts plenty of novel fungal diversity. Recent advancements in molecular diversity studies and morphological observations have detected a pan-Arctic distribution of the Chytridiomycota that suggests uncharacterised contributions to the Arctic carbon budget and a role in regulating algal bloom dynamics. Consequently, we believe that increased focus should be given to understanding chytrid-algal relationships and the biotic and abiotic factors that regulate these interactions.

The Arctic is a remote and challenging place to work in. It is vast, cold and exposed. However, there are several research stations, and even universities, located at high latitudes that function as excellent bases for studies of Arctic marine fungi. We would like to encourage marine mycologists to conduct research in the vast circumpolar Arctic region, as the marine fungi there remain understudied with enormous potential for new discoveries.

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Graphical abstract

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Arctic marine fungi: from filaments and flagella to operational taxonomic units and beyond

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Review: We summarise the study efforts made in marine mycology in the Arctic region during the last 120 years and discuss the new knowledge that has been obtained using molecular methods.

Keywords: Chytridiomycota; Helotiales; high-throughput sequencing; morphology; polar.

