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Malassezia is widespread and has undescribed diversity in the marine environment

Ronja M. Steinbach [a], Fouad El Baidouri [a,b], Lorna M.Y. Mitchison-Field [c,d], Fang Yun Lim [e], Joanne Ekena [f], Ellysa J.D. Vogt [f,g], Amy Gladfelter [c,f], Ashleigh B. Theberge [e], Anthony S. Amend [h,*]

[a] School of Life Sciences, University of Hawai'i at Mānoa, 2538 McCarthy Mall, Edmondson 216, Honolulu, HI, 96822, USA
[b] Harvard T.H. Chan School of Public Health, Boston, MA, 02115, USA
[c] Marine Biological Laboratory, Woods Hole, MA, 02543, USA
[d] Department of Biology, Johns Hopkins University, Baltimore, MD, 21218, USA
[e] Department of Chemistry, University of Washington, Box 351700, Seattle, WA, 98195, United States
[f] Department of Cell Biology, Duke University, Durham, NC, 27710, USA
[g] Department of Biology, University of North Carolina at Chapel Hill, Chapel Hill, NC, 27599, USA
[h] Pacific Biosciences Research Center, University of Hawai'i at Mānoa, 1993 E West Rd, Honolulu, HI, 96822, USA

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ABSTRACT

There is substantial fungal diversity in marine environments where uncharacterized species may play important ecological roles. *Malassezia*, a genus of yeast generally associated with mammalian skins, is an example of a seemingly abundant marine fungus in ocean environments. Accumulating evidence indicates that *Malassezia* is widespread in the ocean. However, we know little about its diversity, role, and distribution. To address these gaps in our knowledge, we analyzed 127 marine samples collected from marine rocks, sediment, water, and various organisms, from the coasts of Hawai'i, Washington, and Massachusetts. We then used *Malassezia*-specific 28S primers in a nested PCR approach to amplify all present *Malassezia*, and performed Illumina sequencing from which we generated a possible phylogeny. Based on our phylogenetic results, we circumscribed 20 potentially novel clades that might represent new species. Our findings are consistent with *Malassezia* having substantial novel diversity and a high prevalence in the marine environment.

1. Introduction

Although fungi play important roles in terrestrial and aquatic environments, their diversity and distribution are poorly characterized. Common estimates for fungal diversity range from 1.5 million to over 5 million species (Blackwell 2011) with the lower estimated range steadily increasing (Hawksworth and Lücking 2017; Jones et al., 2019). Aided by the rise of molecular techniques, the rate of discovery has risen to around 1,800 species per year (Hawksworth and Lücking 2017). Presently, there are between 120,000 and 142,273 described species (Jones et al., 2019), which accounts for less than 10% of estimated extant fungi (Hawksworth and Lücking 2017). Of the described fungi, the large majority are terrestrial with only around 1,900 described fungi in the marine environment (https://www.marinefungi.org/) (Jones et al., 2019; El Baidouri et al., 2021; Ettinger et al., 2021). However, there are estimated to be at least 10,000 species of marine fungi (Jones 2011; Amend et al., 2019; Lee et al., 2019; Rabbani et al., 2021) and many are likely amphibious, living in both aquatic and terrestrial ecosystems (El Baidouri et al., 2021). In terrestrial ecosystems, fungi are highly diverse organisms that play important ecological roles. By all appearances they are important and widespread in the marine environment as well (Tisthammer et al., 2016; Amend et al., 2019; Gladfelter et al., 2019; Jones et al., 2019; Lee et al., 2019). One common fungus found in our oceans is the genus *Malassezia* (Amend et al., 2012; Amend 2014; Ettinger et al., 2021; Garmendia et al., 2021).

Malassezia has been most studied in the terrestrial environment. Members of this genus associate with mammalian skin (Amend et al., 2012; Findley et al., 2013; Amend 2014; Theelen et al., 2018; Guillot and Bond 2020; Ianiri and Heitman 2020; Ianiri et al., 2020) where they appear to exhibit some host specificity (Ianiri and Heitman 2020). One

* Corresponding author.
E-mail address: amend@hawaii.edu (A.S. Amend).

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reason that *Malassezia* is commonly found on mammal skins is likely due to their dependence on lipids; they are unable to synthesize long chain fatty acids and therefore require external sources, which also makes them difficult to cultivate (Amend 2014; Wu et al., 2015; Theelen et al., 2018; Amend et al., 2019; Guillot and Bond 2020). In fact, *Malassezia* are the most prevalent member of human skin's mycobiota (Findley et al., 2013; Wu et al., 2015). While not usually harmful, *Malassezia* is considered an opportunistic pathogen and is traditionally associated with several skin conditions including atopic dermatitis (eczema), dandruff, and other mild skin conditions (Findley et al., 2013; Amend 2014; Soares et al., 2015). Recently, *Malassezia* was linked to severe diseases such as pancreatic cancer and Crohn's disease (Limon et al., 2019; Ianari et al., 2022). While past studies focused on *Malassezia* in terrestrial habitats, new questions about their diversity and ecology in the ocean have risen with the discovery that *Malassezia* is found on, in, and independent of hosts in an expansive range of locations (Amend 2014; Garmendia et al., 2021).

The genus *Malassezia* is nested in the phylum Basidiomycota and subdivision Ustilaginomycotina (Wu et al., 2015; Ianiri and Heitman 2020). They are more closely related to plant pathogens than to other human pathogens (Wu et al., 2015; Ianiri and Heitman 2020). Currently, there are 18 accepted taxa— *M. furfur, M. pachydermatis, M. sympodialis, M. globosa, M. restricta, M. obtusa, M. slooffiae, M. dermatis, M. japonica, M. yamatoensis, M. nana, M. caprae, M. equina*, *M. cuniculi, M. arunalokei, M. brasiliensis, M. psittaci,* and *M. verpertillionis*—but further studies suggest that there are several other undescribed species (Soares et al., 2015; Wu et al., 2015; Theelen et al., 2018; Guillot and Bond 2020).

Past studies have found *Malassezia* to be widespread in the oceans under diverse environments and lifestyles, ranging from free-living individuals in extreme environments such as hydrothermal vents to those associated with hosts such as stony corals (Amend et al., 2012; Amend 2014; Garmendia et al., 2021; Zeng et al., 2021). One of the most challenging obstacles to identifying host-associated marine fungi is the co-amplification of the host's DNA when using fungal primers to amplify the Internal Transcribed Spacer (ITS) or the 18S rDNA regions (Kutty and Philip 2008; Amend et al., 2019; Rabbani et al., 2021). Other studies have attempted to use different DNA target regions, phylum-specific primers, and nested PCRs to avoid the preferential amplification of host DNA, with little success (Rabbani et al., 2021). To overcome these difficulties, and to minimize contamination from host DNA and other fungal species to a greater extent, we used *Malassezia*-clade specific primers, from the large ribosomal subunit (28S rDNA).

The purpose of this study is to shed light on the diversity of marine *Malassezia* by studying the occurrence of putative *Malassezia* in various locations, hosts, and substrates. Considering the limited number of research studies on marine fungal diversity, we expected to find significant undescribed diversity of marine *Malassezia,* constituting potentially novel clades.

2. Materials and methods

2.1. Study site, sampling, and sample preparation

Samples for this study were collected in nearshore habitats in three locations: 1) Friday Harbor, Washington, 2) Woods Hole, Massachusetts, and 3) in the Waimea Bay area of North Shore Oʻahu, Hawaiʻi.

Sampling from Hawaiʻi was conducted at seven sites within the Pupukea Marine Conservation Area. A broad range of algae (across all three phyla) and animals and environmental samples were collected from each site, for a total of 443 samples (Table S1). The samples collected on Oʻahu were a part of a larger study (Amend et al., 2022) conducted by a consortium of interdisciplinary researchers at the University of Hawaiʻi at Mānoa. A more detailed protocol based on the sample type is available at https://dx.doi.org/10.17504/protocols.io.btz2np8e (Amend 2021).

Samples from Washington were collected at two sites: Friday Harbor Labs docks and the Eagle Cove Beach intertidal area. The marine sponges and ascidians collected from the two sites were scraped off of dock fenders and kept in cold seawater until they were ready for processing. No permits were necessary for these samples, however permission was obtained from the Director of the Friday Harbor Labs, Dr. Megan Dethier. A total of 14 samples were used from Washington (Table S1). Samples from Woods Hole, Massachusetts were collected from two locations: Seawater tanks at the Marine Resources Center (MRC) at University of Chicago Marine Biological Laboratory and from Fay Beach near Woods Hole, Massachusetts. Samples were rinsed and kept in cold seawater until they could be frozen. Sample DNA was extracted using the DNeasy PowerSoil Pro Kit (Qiagen NV, Venlo, Netherlands). Samples were beaten in the provided tubes using a Powerlyzer 24 (Qiagen) and extracted following the manufacturers protocol. There were 7 samples from Woods Hole, Massachussetts (Table S1).

Marine sample tissues from Hawaiʻi were rinsed with sterile ultrapure water to remove any excess salt. Between 100 and 250 mg of the tissue samples were freeze dried, and then homogenized using sterile 5 mm glass beads and a benchtop vortexer. A 50 mg subsample of the freeze dried material (or a single swab or filter, depending on the sample type), was added to a 2 mL tube containing garnet beads, 60 μL of Qiagen SL solution, and 4 μL of RNase A. Samples were macerated in a Fast Prep 96 Homogenizer at 1,600 RPM for 3 min and extracted on a KingFisher™ Flex™ System (Thermo Fisher Scientific, Waltham, MA, USA) with a MagAttract PowerSoil KF Kit (Qiagen) following the manufacturer's protocol. The prepared DNA samples were then stored in a −20 °C freezer and re-organized into plates with the aid of the iPipet program (Zielinski et al., 2014).

Marine samples from Washington were washed with distilled water, aliquoted into 50 mL tubes, sorted into species, labeled, and then frozen at −20 °C. For the DNA extraction, the samples were beat using 0.5 mm Zirconia/Silica beads (Biospec) and then the DNeasy Powerlyzer Powersoil Kit (Qiagen) was used, following the manufacturer's protocol.

2.2. Molecular analysis

Preliminary research showed that direct amplification of *Malassezia* from environmental samples was inconsistent, probably due to a combination of low cell numbers, thick cell walls that are difficult to lyse, and/or secondary structure issues with the primers that were an unavoidable compromise due to the few sites discriminating between *Malassezia* and other Fungi. For this reason, we used a nested PCR approach. First, we amplified a ~920 bp section of the 28S ribosomal DNA (rDNA) large subunit (LSU), using universal fungal primers—LR0R/LR5 (Vilgalys and Hester 1990; Rehner and Samuels 1994) (Appendix). PCRs were prepared in a laminar flow hood and used Phusion Hot Start II DNA Polymerase (ThermoFisher) (Supplements Table S2) to amplify genomic DNA for 22 cycles (Supplements Table S3). At least four negative controls were present for each plate along with DNA extraction negative controls. One μl of product was used as template for a second PCR (Supplements Table S2) using custom *Malassezia* specific primers (Illum_Mala_28S_F2:

TCGTCGGCAGCGTCAGATGTGTATAAGAGACAGCGCGTTGTAATCTCGAGACG and Illum_Mala_28S_R2 GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAGCCACCCAAAAACTCGCACA, orientation 5′ to 3' with an overhang complimentary to an Illumina index adaptor oligo.) The primers were designed to amplify 536 base pairs of the 28S. This second PCR was run for 30 cycles (Table S3). To minimize the risk of contamination, the second PCR was conducted on a separate lab bench, using separate equipment, and consumables were disinfected with 10% bleach solution, sterile water, and 70% ethanol. Finally, 1 μl of this amplicon was used as template in which 8 bp indexed adapters were added onto the amplicons over ten cycles (Tables S4 and S5). Although the high number of cycles in a nested PCR increases likelihood of PCR errors and contamination, we were unable to consistently amplify DNA without

this added step. In all cases, negative controls either did not produce sequence data, or produced comparatively small number reads, none of which were identified as *Malassezia*.

Amplicons were imaged after the second PCR on 1.5% agarose gels. To check for the presence of dimers, a bioanalyzer High Sensitivity DNA Analysis assay was performed. Finally, the samples were sent to the Advanced Studies in Genomics, Proteomics and Bioinformatics (ASGPB) at the University of Hawai'i at Mānoa, for Illumina MiSeq sequencing using V2 paired-end 250 bp chemistry.

2.3. Sequence processing

Primer and adapter sequences were removed from de-multiplexed FastQ sequences using Cutadapt (Martin 2011), in R. These were then processed using the DADA2 (Callahan et al., 2016) pipeline in which reads were truncated (250 forward, 200 reverse), merged via concatenation (there was no overlap between reads), and filtered such that reads exceeding 0 "N" nucleotides, or an EE score of 1 are omitted, truncated at the first instance of a truncQ value of 2 or greater, error-corrected and binned into amplicon sequence variants (ASVs). Putative chimeras were identified and removed using the "Denovo" method in DADA2 (Callahan et al., 2016). Taxonomic assignments using the DADA2 algorithm were based on the RDP LSU fixed training set V2 with a minimum bootstrap confidence level of 70. Raw FastQ sequences are available in NCBI's BioProjects, SRA accession PRJNA734665. R scripts to reproduce analyses are available in the Supplements section.

2.4. Phylogenetic reconstruction

All sequences identified as members of the Exobasidiomycetes (353 ASVs) were included in an alignment containing 1,178 sequences from 18 known *Malassezia* species (Fig. 1) and two outgroups using MAFFT v7.427 (Price et al., 2009). The alignment was used to build a Maximum Likelihood tree using FastTree (Price et al., 2009, 2010) under the GTR model with a proportion of invariable sites and with gamma distribution. To assess branch support 100 fast-global bootstraps were used. Taxa that were not monophyletic with reference *Malassezia* were excluded from subsequent analysis. The tree was used for taxonomic assignment of the 353 putative *Malassezia* ASVs as shown in Fig. 1. While concatenated Forward and Reverse sequences potentially provide more informative sites for phylogenetic reconstructions, we were concerned that this method might increase the likelihood of chimeric sequences (or the false detection of non-chimeric sequences). Therefore, we additionally reconstructed a phylogenetic tree using only the forward sequences to explore *Malassezia* diversity. This process has a lower likelihood of producing chimeras, and a greater sequencing depth since fewer reads are discarded as a result of lower quality reverse reads. 469 putative forward *Malassezia* ASVs and 1183 sequences belonging to the known *Malassezia* species were used to build a phylogenetic tree under the GTR model with a proportion of invariable sites and with gamma distribution in FastTree (Fig. S1). Because the resulting topologies were essentially identical between the two datasets, we present the results from combined forward and reverse reads here (Fig. 1).

2.5. Biogeography

To investigate the distribution and biogeography of putative *Malassezia* clades, the ASV contingency table was combined with sample metadata and the phylogeny using the Phyloseq package (McMurdie and Holmes, 2013). We omitted samples with fewer than 10 *Malassezia* sequences. We categorized the samples based on the Earth Microbiome Project Ontology (EMPO) level 3 categories (Thompson et al., 2017), which organizes samples based on whether associated with hosts, and if so, the identity of those hosts (in our case: animal, algae, sediment, water, and rock swabs). In the EMPO, algae are nester under the level 3 category label of 'plant.' We plotted heatmaps using the Bray Curtis Dissimilarity matrix based on the EMPO level 3 category and the location (the state in which the samples were collected).

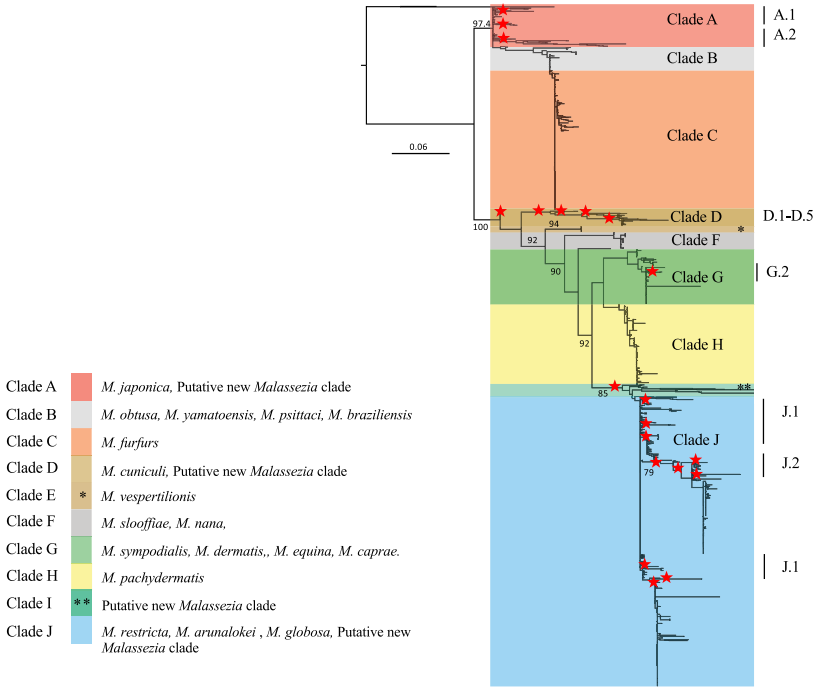

Fig. 1. Hypothesized phylogeny with putative new clades circumscribing accepted Malassezia taxa. Red stars indicate locations on the phylogeny where one or more novel species may be present. This phylogeny was reconstructed using both forward and reverse reads. Asterisks are used to indicate where a different clade is, when the clade was too small to be labeled directly on the phylogeny.

3. Results

3.1. Sequencing results

From an initial 5,406,615 paired sequences obtained, 3,139,907 sequences were retained following filter, trimming, and merge functions. When dereplicated, a total of 29,514 amplicon sequence variants (ASVs) were left. A large number of these were flagged as potential bimeras (24,190), which were subsequently culled. With the chimeras removed, we retained a final table of 524 samples that contained 5,324 putative *Malassezia* ASVs. Of those 524 samples, 211 had greater than 50% target amplification (*Malassezia*), while the remaining samples had more than 50% co-amplification of other taxa. After pruning out samples with fewer than 10 *Malassezia* reads, we retained 279 unique ASVs from 127 samples.

3.2. Marine Malassezia diversity

Phylogenetic analysis of our combined forward and reverse sequence data revealed putatively novel diversity, including 10 monophyletic clades with significant bootstrap support in agreement with the current taxonomy. However, some of the species that are considered genetically distinct (e.g. *M. globosa*, *M. restricta and M. arunalokei*, Fig. 1, Clade J), formed a single clade. Surprisingly, despite the phylogenetic conservation of this locus, we identified several novel clades separated from known species by substantial branch length with high bootstrap support. These results were supported by the phylogeny reconstructed using only the forward sequences. Despite the lower number of informative sites and comparatively weak support in this tree, the main putative new clades and potential *Malassezia* species were retained (See Fig. S1).

3.3. Host and geographic specificity

Heatmaps plotted for sample by host EMPO level 3 did not show clear evidence of geographic or host-type affinities (Fig. 2; Fig. 3; Fig. 4; Fig. S2; Tables S6–S9). Statistical analysis of whether sample type or location predict *Malassezia* composition are problematic due to the asymmetrical sample sizes, and their contributions to differences in beta-diversity dispersion, which increases the likelihood of Type I (false positive) errors. Nevertheless, one clade was only detected in the MA field site, and others were unique to algal samples ('plant' category). Nevertheless, the lack of apparent patterning in the distribution of *Malassezia* across the three sampling locations is notable and runs counter to expectations.

4. Discussion

Results from the phylogenetic reconstruction support the hypothesis of undescribed, novel diversity of marine *Malassezia*. We identified ten novel monophyletic clades with significant bootstrap support, and circumscribed 20 putative new species or clades (Fig. 1). Despite the high levels of novel diversity that we detected, this diversity is likely a conservative underestimate since the LSU is comparatively slowly evolving and unlikely to differentiate close relatives (Schoch et al., 2012). For instance, Clades A, D, G and Clade J (Fig. 1) contained numerous (323) sequences that grouped together with known *Malassezia* species in the same clades, but were genetically distinct, indicating that these sequences may represent new species of their own. Some sequences (26) that formed completely new clades (e.g. Clade I) and were clearly distinct from the known species, and may represent new clades or even multi-species complexes. In Clade J, for example, using our target region of the 28S, it was impossible to distinguish, *M. restricta*, *M. arunalokei*,

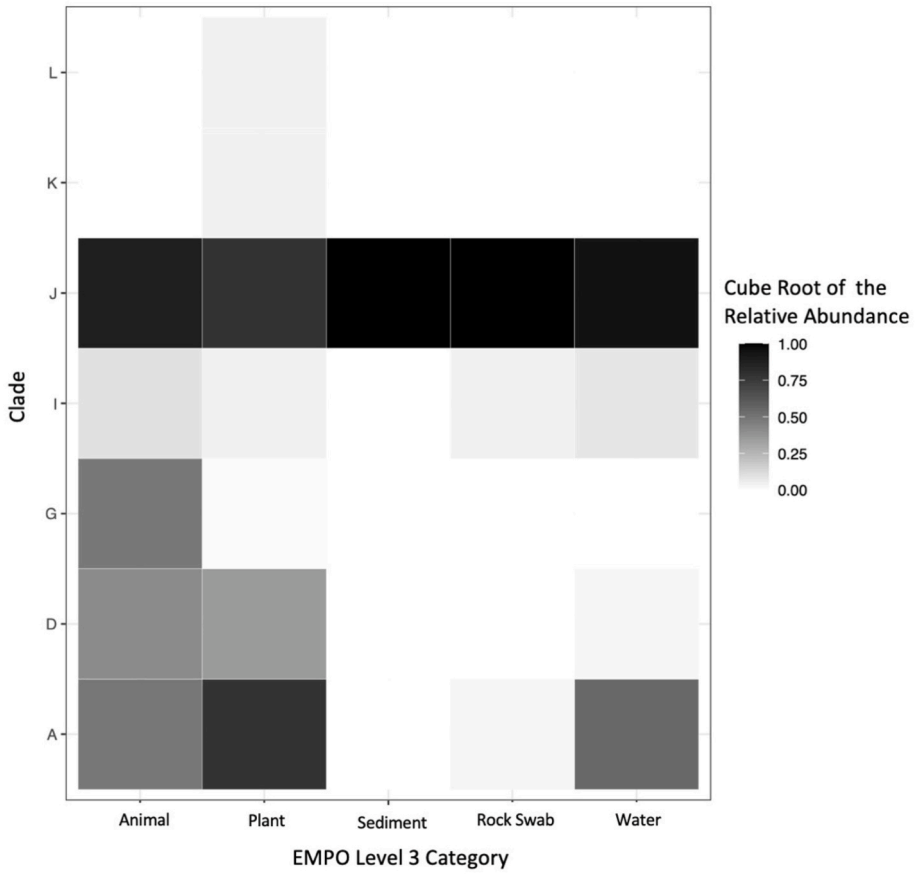

Fig. 2. Heatmap showing the relative abundance of Malassezia clades as hypothesized by the new phylogeny, in the EMPO Level 3 categories.

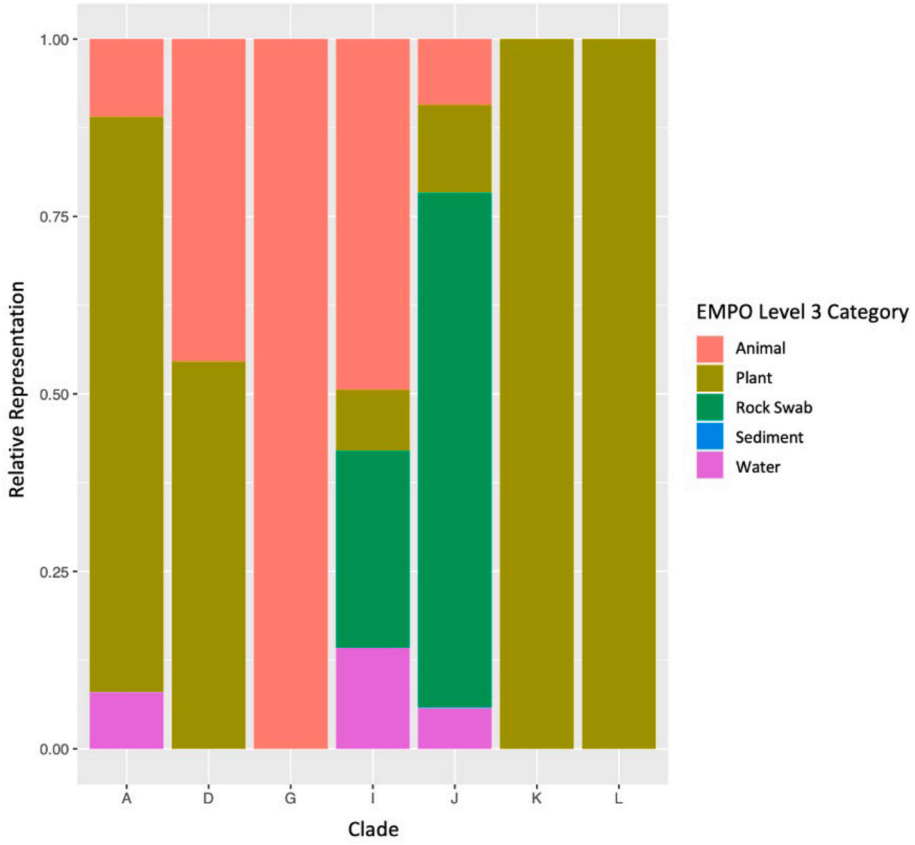

Fig. 3. Justified bar chart showing the relative representation of each EMPO Level 3 category, for each clade. The total number of reads per clade were: A: 239,591, D: 23,312, G: 24,568, I: 338, J: 1,662,639, K: 22, and L: 44.

and *M. globosa* (Fig. 1, Clade J), likely due to their genetic proximity and the lack of informative sites in our marker gene. As with many other studies, our selection of genetic marker was constrained by sequence base pair limits of the Illumina platform, the availability of primer regions conserved throughout the target clade, and database coverage enabling tree-building and primer design. Longer-read technologies, higher throughput technologies, or enrichment procedures such as host depletion or FACS might help overcome these limitations in future studies. However, this high sequence diversity in the conserved LSU region suggests that new *Malassezia* species and clades are yet to be described. *Malassezia* has been exceptionally difficult to culture in laboratory setting due to their lipid dependence, however, finding ways to isolate them may help with the characterization of these novel species. It will be interesting to see if there are different requirements for isolating terrestrial and marine *Malassezia*, given temperature differences and halotolerance, although some studies have shown little to no difference in growth rates in freshwater or seawater (Jones et al., 2022). From this study, the abundance and diversity of marine species, the validity, and the definition of the entire *Malassezia* genus may need to be revisited.

There are advantages and disadvantages to using forward and reverse reads versus using only forward reads. By using both forward and reverse, we obtained longer sequences but higher rates of chimeras, and therefore lower confidence in the sequences. Using only the forward reads, we obtained shorter sequences, but had higher confidence in them. Due to the tradeoff in using one method over the other (forward and reverse and forward only) we created phylogenies using both methods (Fig. 1; Fig. S1). Both cases provide evidence of novel diversity that were almost entirely congruent.

The question of how *Malassezia* overcomes its dependence on external lipids remains unanswered (Amend 2014; Wu et al., 2015; Theelen et al., 2018; Amend et al., 2019; Guillot and Bond 2020). We expect that those host associated strains obtain their lipids from their hosts in the same manner that terrestrial *Malassezia* does (Gioti et al., 2013; Theelen et al., 2018; Guillot and Bond 2020; Ianiri and Heitman 2020). The free-living *Malassezia* detected from rock swabs, water samples, and sediments are hypothesized to obtain their lipids from some other source, for example from plankton, although the true source has yet to be determined (Orsi et al., 2016). Alternatively, it is possible that the *Malassezia* being detected are not metabolically active; fungal propagules are prevalent in the ocean (Gladfelter et al., 2019) and one possibility is that the reads obtained in this study and others come from such transient propagules. However, DNA Stable Isotope Probing has found that at least some *Malassezia* is actively assuming the role of a saprotroph in coastal waters by assimilating particulate organic carbon from algae (Cunliffe et al., 2017). Further studies are needed to answer these open questions about *Malassezia* in the ocean to provide insights into the potential ecological roles that marine *Malassezia* may be playing, beyond their known role as pathogens on some marine animals (Pang et al., 2021) and saprotrophic tendencies (Cunliffe et al., 2017).

In addition to presenting strong evidence for undescribed diversity, the phylogeny offers further support for other hypotheses regarding their prevalence in the ocean. For example, it can bolster the hypothesis that *Malassezia* may have evolved into and out of the ocean, potentially on numerous occasions (Amend 2014). Many of the *Malassezia* species that we find in our oceans are also found in terrestrial ecosystems. Furthermore, *Malassezia* found both on land and in the ocean are intermingled both within and among the clades. If there had been a single evolutionary event in which terrestrial and marine *Malassezia* split lineages, we would expect to see distinct marine and terrestrial clades, which is not the case. A formal evolutionary transition analysis is needed to confirm this hypothesis, preferably based on more than a single locus. *Malassezia,* therefore, presents an unusual evolutionary

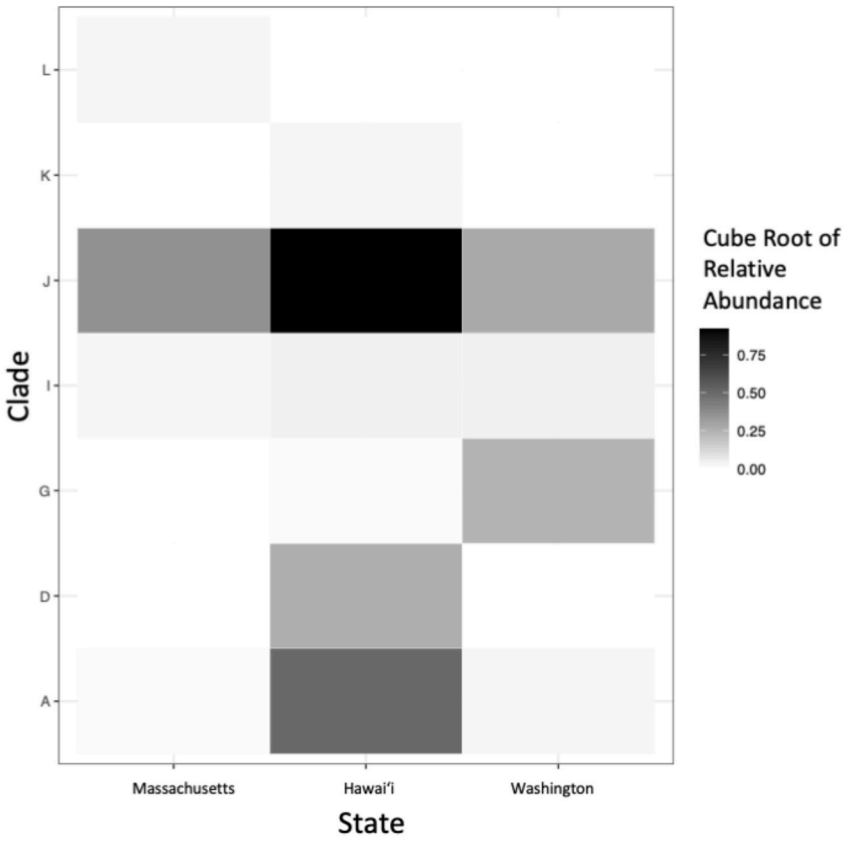

Fig. 4. Heatmap showing the relative abundance of Malassezia clades as hypothesized by the new phylogeny, by the state where samples were collected.

topology for which we have yet to find an explanation. Alternatively, the phylogeny can add support to the hypothesis that many of these species are amphibious (El Baidouri et al., 2021). While *Malassezia* has frequently been found in environmental DNA samples (Amend et al. 2014) and thus could reasonably be carried into the ocean by terrestrial hosts, wind, and/or runoff, it is highly unlikely that the source of all *Malassezia* found in marine systems comes from terrestrial sources, given how widespread it is and that we are finding it associated with a variety of marine hosts. Further studies are necessary to better understand the evolution and ecological role of *Malassezia*.

For the biogeographical distribution of *Malassezia*, we saw interesting trends that warrant further investigation. Our sampling design did not allow for an in-depth examination of host-affinity. However, our results show that *Malassezia* is widespread—found in three geographically distant and ecologically different locations that are spread between two different oceans—and appears to be generalist with regards to host/habitat associations. This apparent generalism is notable and runs counter to expectation, due to this yeast's putative lipid dependence, which had led us to hypothesize greater specificity. In the future, a sampling approach and project design targeted at answering these questions might determine whether these affinities are biological reality or sampling artifacts and can increase the depth of our understanding of this unexpected phenomenon.

Our findings offer new insights into the diversity and distribution of marine fungi. There is substantial uncharacterized diversity in this unique fungal genus. However, these results indicate several unexplained phenomena that should be high priorities for future research. How has this fungus successfully dispersed to nearly all parts of the ocean? How many times and when did *Malassezia* transition from land to sea? As interest into the diversity and distribution of marine fungi increases, the case study of *Malassezia* might serve as a model for other fungi inhabiting nearshore habitats.

Declaration of competing interest

All sources of funding have been acknowledged and the authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.funeco.2023.101273.

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