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Review

'Marine fungi' and 'marine-derived fungi' in natural product chemistry research: Toward a new consensual definition

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ABSTRACT

The discovery of new natural products from fungi isolated from substrata in marine environment has increased dramatically over the last few decades, cumulating in over 1000 new metabolites. The term 'marine-derived fungi' is used extensively in these reports, and it refers to the environment from which the fungi are isolated, in contrast to the classical ecological definition of 'marine fungi' as obligate and facultative inhabitants of the marine environment. In a significant number of reports, the origins of substrata or habitat relationships of strains referred to as 'marine-derived fungi' are unknown or whether a seawater medium was used for their isolation. In August 2014, a workshop held at the University of Prince Edward Island, Canada was convened to discuss a series of topics related

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to marine fungal natural product research. A central discussion topic was "What constitutes a marine fungus?" There was a general agreement that a review of the definition of a marine fungus would be beneficial to the marine fungal natural product community, together with an evaluation of the suitability and relevance of the use of the term 'marine-derived fungi'. We here propose a revised, broad definition of a marine fungus as 'any fungus that is recovered repeatedly from marine habitats because: 1) it is able to grow and/or sporulate (on substrata) in marine environments; 2) it forms symbiotic relationships with other marine organisms; or 3) it is shown to adapt and evolve at the genetic level or be metabolically active in marine environments'.
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1. Introduction – history of marine mycology and associated natural products discovery

The field of marine mycology has evolved tremendously since its inception. The first marine fungi were described in the 1850s, and early studies of marine fungi focused mainly on seaweeds (Sutherland, 1915, 1916). The subdiscipline of marine mycology was conceived based on Barghoorn and Linder's exhaustive investigation of wood-inhabiting marine fungi (Barghoorn and Linder, 1944). Pioneering efforts in the field were dedicated to deciphering the diversity of marine fungi from different marine substrata, *i.e.* submerged wood, seaweeds and salt marsh grasses in temperate areas, mainly in Europe and North America (Sutherland, 1915, 1916; Barghoorn and Linder, 1944; Kohlmeyer and Kohlmeyer, 1979). As the field advanced into the late 1970's, morphological studies of marine fungi, especially those affiliated with the Halosphaeriaceae, using light and electron microscopy, were subsequently used to classify taxa (Jones and Moss, 1978; Jones, 1995). All of these marine fungi were collected on substrata in intertidal zones, and classified based on characteristics of sporulating (sexual or asexual) structures. Since the 1990s, molecular-based studies of marine fungi, using rDNA phylogenetic analyses, have dominated the field (Spatafora *et al.*, 1998; Jones *et al.*, 2009; Suetrong *et al.*, 2009; Sakayaroj *et al.*, 2011; Hyde *et al.*, 2013). In 1996, diversity estimates of marine fungi were placed at around 1500 species and by 2011, diversity estimates were projected to include over 10,000 species (Jones, 2011). To date, a total of 1112 marine fungi have been documented (including yeasts) from marine sources (Jones *et al.*, 2015). According to Jones *et al.* (2009), classification of many marine fungi remains a confused and unresolved issue; particularly because of a narrow, prior definition of what constitutes a marine fungus.

Concurrent to the development of the field of marine mycology, there has been a voluminous output in natural product research from fungi isolated from substrata in different marine habitats, including marine animals, seaweeds and sediments, with many new bioactive compounds being described each year (Rateb and Ebel, 2012; Blunt *et al.*, 2013; Ebada and Proksch, 2015). An exponential increase in the rate of discovery of new natural products from "marine-derived" fungi has occurred over a period spanning 1970–2010, cumulating in over 1000 new metabolites described by the middle of 2010 (Overy *et al.*, 2014). These so-called 'marine-derived' fungi had an impact early on in the history of drug discovery from fungi. The cephalosporin β-lactam antibiotics (Fig. 1A–C) were discovered about 15 y after the penicillins from *Acremonium chrysogenum* (previously known as "*Cephalosporium acremonium*"). Giussepe Brotzu, a professor of Hygiene at the University of Cagliari, Sardinia, Italy formulated a hypothesis about why young people that were swimming at "Su Siccu" Bay, at the site where the city sewer system drained into the sea never contracted typhoid fever (Hamilton-Miller, 2000). Although the disease was endemic to the area, there were no cases of typhoid fever related to bathing in these sewage-contaminated waters. He decided to take a water sample from the bay and tested its effect on *Salmonella enterica* subsp. *enterica* (serovar Typhi), *Yersinia pestis*, *Brucella melitensis*, *Vibrio cholerae*, and *Staphylococcus aureus*, leading to observations of potent antibacterial activities which he followed with improvised experiments with humans using concentrated culture broths. Investigations on Brotzu's fungus in England eventually led to the isolation of cephalosporins P, N and C (Burton and Abraham, 1951; Newton and Abraham, 1954; Abraham and Newton, 1961).

In recent decades, renewed interest in fungi obtained from marine substrata has significantly expanded the catalog of fungal natural products, including many novel chemical scaffolds. One metabolite, halimide (Fig. 1D), a potently cytotoxic diketopiperazine phenylahistine from a marine-derived *Aspergillus ustus* isolate, led to the synthesis of plinabulin (NPI-2358) – a molecule that reached phase II trials as an angiogenesis inhibitor for preventing tumors and scar tissue development (Mita *et al.*, 2010). A current issue in the field of marine fungal natural product research is that an increasing majority of fungal isolates obtained from marine habitats and examined for new and novel natural products belong to well-known terrestrial genera, such as *Aspergillus* (Fig. 2C) and *Penicillium*. This raises questions as to whether these genera are capable of growth in saline habitats, do they constitute stable and active populations in the marine environment and what is their associated ecological role(s) (Höller *et al.*, 2000; Jensen and Fenical, 2002; Kohlmeyer and Volkmann-Kohlmeyer, 2003; Overy *et al.*, 2014). Inversely correlated with the increased attention given to chemistry of marine-derived fungi has been an apparent rejection of the exploration of terrestrial soil fungi because they are perceived as exhausted sources of new natural products, even though genomics clearly indicates this is not the case (Bérdy, 2012). A

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