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Review

Potential roles for recently discovered chytrid parasites in the dynamics of harmful algal blooms

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ABSTRACT

Zoosporic true fungi belonging to the phylum Chytridiomycota, commonly referred to as chytrids, are ubiquitous in aquatic environments, however their role in phytoplankton population and eco-physiological dynamics is not fully understood. With the rising occurrence of harmful algal blooms (HABs) of phytoplankton worldwide, there is a growing need to investigate the factors affecting toxicity in algae, with a view to determining the significance of these factors in light of the current trends in global climate change. In this review we present current knowledge regarding the parasitism of phytoplankton by chytrids, including incidence of chytrid epidemics, methodologies used in their isolation and classification, their life cycles and infection strategies, and their potential role in toxin production in algae. We outline key areas in phytoplankton host–parasite dynamics that are poorly understood, discuss the potential roles of chytrids in these areas, and highlight future research directions for the furthering of our knowledge regarding algal ecophysiology. The synthesis of current knowledge in these fields will help researchers develop

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new hypotheses to further our understanding of primary production in aquatic ecology, and thus enhance our understanding of aquatic ecology, for more effective management of aquatic ecosystems.

1. Introduction

Many parasitic, mutualistic and saprotrophic species of zoosporic true fungi (supergroup Opisthokonta) have been frequently observed and described in a wide range of terrestrial and freshwater ecosystems, but only a few have been found in marine ecosystems (Sparrow, 1960; Karling, 1977; Powell, 1993; Barr, 2001; Shearer *et al*., 2007; Gleason *et al*., 2011, 2012b). Zoosporic true fungi include many species in the phyla Chytridiomycota, Blastocladiomyota, Neocallimastigomycota, and Monoblepharomycota and the *Olpidium* clade (James *et al*., 2006; Sekimoto *et al*., 2011; Voigt *et al*., 2013). These phyla are characterized by the production of motile zoospores as propagules with a single posteriorly directed whiplash flagellum, although species with several posteriorly directed flagella have been observed (Sparrow, 1960: Barr, 2001: James *et al*., 2006). Many of the species in Chytridiomycota (chytrids) have been observed to infect a large number of phytoplankton host species in freshwater ecosystems, particularly species of green algae (Chlorophyta), diatoms (Bacillariophyta) and blue-green algae (Cyanobacteria) (Sparrow, 1960; Canter, 1972; Kagami *et al*., 2007; Voigt *et al*., 2013; Lane and Carney, 2014). These parasites may play critical roles in regulating sizes of populations of phytoplankton hosts and may be responsible for the regulation of algal blooms in freshwater ecosystems (Canter and Lund, 1951; Ibelings *et al*., 2004; Sime-Ngando, 2012). The sudden appearance of large populations of zoosporic true fungi during an algal bloom has been called a chytrid epidemic (Sparrow, 1960; Ibelings *et al*., 2004).

The zoosporic true fungi that are parasites of phytoplankton are currently placed into two phyla, the Chytridiomycota and Blastocladiomycota, and into the *Olpidium* clade which has not yet been assigned to a phylum (James *et al*., 2006; Gutman *et al*., 2009; Sekimoto *et al*., 2011). However, with the exception of *Paraphysoderma*, species in the Blastocladiomycota and *Olpidium* clade have been poorly studied and inadequately characterized and therefore will not be considered in this review. In addition to true fungi, many species of fungus-like microorganisms (such as species of aphelids, cryptomycota, oomycetes, perkinsozoans, labyrinthulids, plasmodiophorids and possibly other phyla) are known to be zoosporic parasites of phytoplankton in aquatic ecosystems (Sparrow, 1960; Jones *et al*., 2011; Karpov *et al*., 2014), but only species of Chytridiomycota that potentially impact on the dynamics of harmful algal blooms (HABs) are considered in this review.

During asexual reproduction, most species of zoosporic true fungi produce large numbers of zoospores. A few species of *Paraphysoderma* and *Catenaria* produce amoebae (Gutman *et al*., 2009; Gleason and Lilje, 2009). Rapid growth and sporulation is characteristic of ruderal fungi. This strategy had been called the ruderal survival strategy, "r" selection or ecological strategy, by Dix and Webster (1995). This strategy makes chytid epidemics possible (Sparrow, 1960). Some zoosporic fungi have stress tolerant strategies, "s" selection or ecological strategies as well, particularly if they have sexual life cycles and produce zoospore cysts, resistant sporangia or resting spores. Some of the adaptations of chytrids for growth under extreme and stressful conditions have been discussed by Sparrow (1960) and Gleason *et al*. (2012a).

Laboratory research has shown that many zoospores are chemotactic, and presumably the zoospores of parasitic species can quickly find uninfected host cells in the field (Sparrow, 1960; Kagami *et al*., 2007; Gleason and Lilje, 2009; van den Wyngaert *et al*., 2014). In contrast, spores with thick cell walls are not chemotactic, and rely on high host population density to find new hosts. The zoospores of the parasites that do not find hosts are often grazed by predators or consumed by filter feeders before they settle to the bottom in aquatic ecosystems (Gleason and Lilje 2009; Kagami *et al*., 2014). This process facilitates the transfer of organic matter from producers to secondary consumers, and it is especially important for transfer from relatively inedible hosts at the producer level, such as diatoms and filamentous cyanobacteria, to higher trophic levels in the food web (Kagami *et al*., 2007, 2014; Sime-Ngando, 2012). Some parasitic species may play important roles in regulating the sizes and compositions of populations of host phytoplankton species (Ibelings *et al*., 2004).

Anderson *et al*. (2012b) provide an excellent general review of the ecology of the nature, composition, toxicology and ecology of harmful algal blooms, which are characterized by their inhibitory and/or deleterious effects on organisms who suffer exposure to them. HABs contain a mixed population of phytoplankton species (producers at the first trophic level in food webs). Some but not all of these species produce powerful toxins that are harmful to zooplankton and other invertebrate metazoans, vertebrates and/or even humans. Each toxin producing species produces a unique profile of toxins and some toxins are thought to accumulate in food webs (Christoffersen, 1996).

In the present review we focus on chytrid species (Chytridiomycota) known to be parasites of toxigenic unicellular or filamentous phytoplankton host species (Table 1). These parasites are all at the primary consumer trophic level and their host species are all at the producer trophic level in aquatic food webs. The present review considers in particular some of the important characteristics of the recently discovered parasitic chytrids in both marine and freshwater ecosystems. Species of cyanobacteria which are hosts for chytrids and which produce toxins have been observed predominantly in