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Mini-review

Multiple zoosporic parasites pose a significant threat to amphibian populations

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ABSTRACT

There is substantial evidence for the dominant role of *Batrachochytrium dendrobatidis* in amphibian population dynamics. However, a wide range of other pathogens could also be important in precipitating amphibian population declines, particularly in the face of climate change or other stressors. Here we discuss some examples of zoosporic parasites in the Chytridiomycota, Mesomycetozoa, Perkinsozoa and Oomycota, all of which infect amphibians in freshwater habitats. The pathosystem model provides an excellent basis for understanding host–parasite interactions. Chemotactic zoopores and several families of proteases facilitate infection. Introduction of non-native host may accelerate the dispersal of these parasites. Unlike *B. dendrobatidis* some of the other zoosporic parasites grow well at or slightly above 25 °C, and their growth rates are likely to increase with global warming. The interactions of parasites with each other and the combined effect of simultaneous infection with multiple species in amphibian populations remain to be carefully studied.

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Introduction

Chytridiomycosis is a disease which infects many species in all major lineages of amphibians, including Anura (frogs and toads), Caudata (salamanders) and Gymnophiona (caecilians) (Gower et al., 2013). This disease is caused by the zoosporic true fungus *Batrachochytrium dendrobatidis* (Chytridiomycota).

Although *B. dendrobatidis* has been considered to be responsible for many of the recently reported mass-mortality events and population declines in amphibians due to infectious disease globally, it is becoming increasingly obvious that the spectrum of pathogens infecting amphibians is much wider than previously recognized (Pessier, 2008). In addition to *B. dendrobatidis*, a range of other zoosporic parasites are likely to

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be important in precipitating amphibian declines, particularly in the face of climate change or other stressors (Alford et al., 2007; Di Rosa et al., 2007; Pounds et al., 2007). Furthermore, in addition to zoosporic parasites, other groups of parasites are associated with population declines in amphibians. These include viruses, bacteria, fungi, platyhelminthes, mesozoa, nematoda, and annelida (Green et al., 2002; Raffel et al., 2008; Berger et al., 2009; Duffus and Cunningham, 2010; Hartigan et al., 2013). Although secondary infection by a variety of microorganisms may follow primary infections, this review focuses on primary infections by zoosporic parasites.

Many species of parasites in the Chytridiomycota, Blastocladiomycota, Olpidium (clade), Mesomycetozoea, Aphelidea, Cryptomycota, Perkinsozoa, Oomycota, Hyphochytriomycota, Labyrinthulomycota and Phytomyxea are known to infect vascular plants, large algae, phytoplankton, protists, fungi, invertebrates, and vertebrates, and all are dispersed by mobile propagules (Sparrow, 1960). Zoosporic parasites in these taxonomic groups along with their saprotrophic relatives are commonly observed in soil, freshwater and marine ecosystems and were formerly placed by Sparrow (1960) into the aquatic phycomyces based on morphological characteristics. However, these groups of phylogenetically unrelated fungi and fungal-like organisms are currently scattered into different supergroups in the tree of life based on rDNA and other gene sequences (Baldauf, 2003; Adl et al., 2005). The infective propagules of the parasites in these groups are usually zoospores, but can also be amoebae or walled spores or cysts. rDNA sequences from putative species belonging to these groups have been found frequently in samples from environmental surveys collected from freshwater and marine ecosystems (Jones et al., 2011; Lepère et al., 2008; Sime-Ngando, 2012). New techniques and research designs have greatly increased our understanding of the composition and dynamics of microbial communities in these ecosystems (Mangot et al., 2009, 2013).

In this paper we discuss some examples of well-known zoosporic parasites in four phyla, the Chytridiomycota, Mesomycetozoea, Perkinsozoa and Oomycota, which infect amphibians in freshwater habitats. First, we briefly compare the phylogeny and general characteristics of the four phyla and highlight key differences in their morphologies and life cycles. Next we discuss some recent examples of significant declines in host population sizes presumably caused by these parasites. Then we describe two models for analysis of host–parasite interactions. We also review some of the strategies which zoosporic parasites use to attack their hosts. We consider the evidence that infection prevalence in hosts can be accelerated by the introduction of non-native species carrying virulent parasites and by the impacts of global warming. Finally, we introduce the potential roles of zoosporic parasites in extinction of species. We propose that many declines in the sizes of the populations of amphibians are caused either by simultaneous infection by multiple parasites in different genera or by different genotypes of the same parasite together, and influenced by environmental factors. We also suggest that different diseases may impact different stages of the life cycle of the host. This hypothesis applies to populations and not to individuals. Interactions between pathogens in the same individual are not considered here, in

part because this topic has received little attention. Although the topic of fungal diseases of amphibians was extensively reviewed by Berger et al. (2009), a significant amount of new literature has been published since that review, and indeed analyses from different points of view are needed.

Phylogeny and general characteristics of zoosporic parasites of amphibians

The zoosporic parasites of amphibians considered in this review are placed into four phyla: Chytridiomycota, Mesomycetozoea, Oomycota and Perkinsozoa. The Chytridiomycota are true fungi which propagate primarily by uniflagellated zoospores and have thalli with cell walls containing chitin. They are considered to be primitive fungi in phylogenetic studies based on rDNA sequence data (James et al., 2006). The Mesomycetozoea are basal to the true fungi (including the Chytridiomycota) and have evolved near the point of fungi–animal divergence (Mendoza et al., 2002). The Mesomycetozoan parasites propagate by zoospores, amoebae or walled endospores (Mendoza et al., 2002; Marshall and Berbee, 2011, 2013), although many species lack either zoospores or amoebae. Some species may have chitin in their walls (Spanggaard et al., 1996). The zoospores of Chytridiomycota and Mesomycetozoea are uniflagellate with one posteriorly directed whiplash flagellum, and their mitochondria have flat, plate-like cristae. Both of these two groups of fungi and fungus-like organisms are currently placed in the Opisthokont supergroup in the tree of life (Baldauf, 2003; Adl et al., 2005).

The phylogenetic position of Perkinsozoa has long been controversial. They have been alternatively affiliated to Apicomplexa and then as an early branch of Dinoflagellata (Coss et al., 2001; Brugerolle, 2002). Recently, using multi-protein analysis, Perkinsozoa were finally described as an independent lineage positioned at the divergence between the phyla of Apicomplexa and Dinoflagellata (Zhang et al., 2011). In contrast, the Oomycota are heterotrophic stramenopiles. The phylogeny of the Oomycota has been recently reviewed by Beakes et al. (2012). Both the Perkinsozoa and the Oomycota have biflagellate zoospores. The posterior flagellum is a whiplash type and the anterior one is a tinsel type with mastigonemes. Their mitochondria have tubular cristae. Both the Perkinsozoa and the Oomycota are placed in the Chromalveolata supergroup (Baldauf, 2003; Adl et al., 2005).

The Oomycota have cellulose in their cell walls. Little is known about Perkinsozoa cell wall structure, but early studies based on cytochemical analyses suggested that the cell wall might be composed of cellulose and hemicellulose (Stein and Mackin, 1957). More recently, Montes et al. (2002) have identified in *Perkinsus atlanticus* one major protein involved in the cell wall structure, PWP-1 (~230 kDa), that is linked by disulfide bonds to the other cell wall constituent. The presence of disulfide protein complexes in the wall cell structure of *Perkinsus* sp. may explain the resistance to chemical and mechanical disruption (Montes et al., 2002).

All stages of the life cycles of zoosporic parasites in these four phyla have been described in detail by Longcore et al. (1999) for Chytridiomycota, Mendoza et al. (2002) for Mesomycetozoea, Van West (2006) for Oomycota and Villalba et al.

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