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Review

Impacts of mesomycetozoean parasites on amphibian and freshwater fish populations

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ABSTRACT

Fungal and fungal-like parasites and the diseases which they cause have been increasingly associated with amphibians and fish population declines at a global scale. This review summarises our current knowledge of the Mesomycetozoea, a poorly-studied group of fungal-like parasites that includes emerging virulent parasites capable of causing high mortality rates in fish and amphibian populations. This review considers the potential impact of emerging parasites in this class on global aquatic biodiversity. Several aspects of the biology of mesomycetozoean parasites are associated with the potential to drive hosts to extinction, including their high virulence under certain conditions, low host specificity, and a free-living infectious stage. In addition, mesomycetozoeans are currently being introduced into novel environments and hosts via the global freshwater wildlife trade. These parasites have been linked to dramatic population declines in at least one native fish throughout Europe, and there are indications that they are already impacting amphibian populations in America and Europe. The impact of mesomycetozoeans on freshwater biodiversity is likely to increase in response to stressors such as global climate change and habitat modification. Surveillance for mesomycetozoean parasites in the field and in specimens transported in the aquatic wildlife trade needs to be increased, and a tighter control of the aquatic wildlife trade is urgently needed.

1. Introduction

In recent decades there has been an increasing awareness of the roles of fungal and fungal-like parasites in wildlife population declines and species extinctions, particularly species in the Chytridiomycota, Oomycota and Mesomycetozoa (Berger *et al.*, 1998; Anderson *et al.*, 2004; Frick *et al.*, 2010, Gozlan et al., 2010b, Glockling *et al.* 2013), to the point of

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threatening ecosystem services (Gozlan *et al.*, 2005, 2006; Pennisi, 2010). As a striking example, in the last several decades the infectious disease chytridiomycosis has contributed to a rapid and widespread decline in amphibian populations on a global scale. The disease, caused by *Batrachochytrium dendrobatidis* (phylum Chytridiomycota, order Chytridiales) is currently implicated in the decline of at least 200 amphibian species (Skerratt *et al.*, 2007) and is the most commonly reported amphibian parasite (Johnson and Paull, 2011). In addition, many species of Oomycota, particularly in the genus *Saprolegnia*, are known to be common parasites of fish and of amphibian eggs (Ruthig and Provost-Javier 2012; van den Berg *et al.* 2013).

While there is no doubt about the significance of chytridiomycosis, a central question remains about a range of dramatic population declines attributable to other groups of fungal-like parasites that are likely to go unnoticed (Kent, 2000; Gozlan *et al.*, 2005, 2006; Pereira *et al.*, 2005; Pessier, 2008; Gozlan, 2012). One of these relatively poorly-studied classes of fungal-like organisms, the Mesomycetozoea (Ragan *et al.*, 1996), includes emerging parasites associated with high mortality in fish (Olson *et al.*, 1991; Rahimian and Thulin, 1996; Arkush *et al.*, 1998, 2003; Marty *et al.*, 1998; Hershberger *et al.*, 2002; Gozlan *et al.*, 2005, 2009; Andreou *et al.*, 2012) and frog populations (Pascolini *et al.*, 2003; Pereira *et al.*, 2005; Di Rosa *et al.*, 2007).

Mesomycetozoeans have a number of key biological features typical of parasites capable of causing host extinction including high virulence under certain conditions, the presence of long-lived environmental stages, a broad host range, and the potential for spread via international trade (Fisher *et al.*, 2012). However, the role of mesomycetozoean parasites in fish and amphibian population declines has received remarkably little attention, despite their association with population mass mortalities since the early 1990's.

In this review, we discuss recent research on mesomycetozoean parasites of amphibians and freshwater fishes. We predict that by reviewing the current state of knowledge on mesomycetozoean parasites, particularly those belonging to the order Dermocystida, a more general pattern of infection will emerge across both fish and amphibians, contributing to the epidemiological understanding of these pathogens.

2. Phylogeny and general characteristics of mesomycetozoean parasites

The class Mesomycetozoea is a monophyletic group of protists, which is placed near the point of animal-fungal divergence in the Opisthokont supergroup in the tree of life (Baldauf, 2003; Marshall *et al.*, 2008; Marshall and Berbee 2011; Mendoza *et al.*, 2002; Paps *et al.*, 2013; Vilela and Mendoza, 2012). In this supergroup, most species have mitochondria with flat plate-like cristae, and when zoospores are present, they usually have one posteriorly directed whiplash flagellum. The presence of chitin in the cell wall is not a universal characteristic of the class as there is evidence of its presence in some species (Spangaard *et al.*, 1996; Herr *et al.*, 1999) and absence in others (Trotter and Whisler, 1965). The class is divided into two, phylogenetically well-supported orders, Dermocystida and Ichthyophonida (Mendoza *et al.*, 2002). The species in these orders have different morphologies and life cycles. While all Mesomycetozoea produce endospores (i.e. with cell walls), some Dermocystida also produce zoospores and some Ichthyophonida also produce amoebae, both of which lack cell walls (Mendoza *et al.*, 2002; Glockling *et al.*, 2013).

Overall, the Mesomycetozoa have osmotrophic nutrition with currently known species either parasitic (e.g. invertebrates, fish, amphibians, birds and mammals), or commensal to their animal hosts (e.g. the nutrient rich digestive tract of invertebrates) (Mendoza *et al.*, 2002; Glockling *et al.*, 2013). No species is known to be a saprotroph. Most species are found in aquatic environments, both freshwater and marine, although a few are terrestrial (Glockling *et al.*, 2013). Despite the fact that many mesomycetozoean parasites cause diseases in human and animal populations, they remain poorly understood, largely as a result of the inability of these organisms to be maintained in pure culture and the delayed recognition of existence of the class itself (Mendoza *et al.*, 2002). The discovery of new species within this class has rapidly increased during the last decade (e.g. Feldman *et al.*, 2005; Jøstensen *et al.*, 2002; Marshall and Berbee, 2011; Lord *et al.*, 2012) but basic biological information including, geographical distribution, life-cycle and relationship with the natural environment are still absent for most mesomycetozoeans (Mendoza *et al.*, 2002). Most known mesomycetozoean parasites of amphibians and fish belong to the order Dermocystida while a few belong to the order Ichthyophonida (Mendoza *et al.*, 2002) (see Tables 1 and 2).

3. Symptoms and pathogenicity

3.1. *Amphibian host*

Mesomycetozoean infections are often macroscopically visible. Infection of amphibians by *Amphibiocystidium* can be inferred by the presence of small (~1 cm), multifocal nodules or pustules or a variable shape, appearing white under translucent skin and typically concentrated in the ventral dermis (Densmore and Green, 2007; Raffel *et al.*, 2008, Fig 1) *Amphibiocystidium* may also infect the liver (Raffel *et al.*, 2008). *Ichthyophonus* sp. infection in amphibians is often associated with severe swelling of the axial musculature, and frequently associated with ulcerations (Raffel, 2006, Fig 2). These ulcerations often have secondary infections with bacteria and fungi (Herman, 1984; Raffel, 2006). However, the pathogenesis and impact of mesomycetozoean parasites in amphibian hosts remains poorly studied (Mikaelian *et al.*, 2000; González-Hernández *et al.*, 2010). Pathology and mortality has been reported in infected individuals (Moral, 1913), and newts visibly infected with *Amphibiocystidium* have a significantly lower survival rate in captivity than uninfected newts (Raffel *et al.*, 2008). Although only correlative, these studies show that mesomycetozoean infection in amphibians can be lethal under certain circumstances. This is not surprising in light of the severe impacts observed in fish populations infected with mesomycetozoea (Arkush *et al.*, 1998; Gozlan *et al.*, 2006; Peeler *et al.*, 2011; Andreou *et al.*, 2011). Most mesomycetozoean