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Review

The ecology of chytrids in aquatic ecosystems: roles in food web dynamics

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ABSTRACT

Chytrids are very important components of freshwater ecosystems, but the ecological significance of this group of fungi is not well understood. This review considers some of the significant environmental factors affecting growth and population composition of chytrids in aquatic habitats. The physical factors include primarily salinity, dissolved oxygen concentration and temperature. The biological factors include the role of chytrids as saprobes and parasites and methods of dispersal of propagules throughout the ecosystem. Dispersal depends upon both zoospores for short range and whole thalli for long range dispersal. Five roles for chytrids in food-web dynamics are proposed: (1) chytrid zoospores are a good food source for zooplankton, (2) chytrids decompose particulate organic matter, (3) chytrids are parasites of aquatic plants, (4) chytrids are parasites of aquatic animals and (5) chytrids convert inorganic compounds into organic compounds. New molecular methods for analysis of chytrid diversity in aquatic environments have the potential to provide accurate quantitative data necessary for better understanding of ecological processes in aquatic ecosystems.

1. Introduction

This review considers common habitats, physical factors affecting growth and population size, parasitism, mechanisms for dispersal and some significant roles in food web dynamics for chytrids in aquatic ecosystems. Information garnered from recent environmental DNA analysis is included. Much of the knowledge about the ecology of chytrids is sparse and fragmented in the literature. Sparrow (1960) provides an excellent discussion of some aspects of the ecology of chytrids which were known at that time, but this information needs to be brought up to date. By bringing together information from many sources published during the past fifty years into one comprehensive review it is hoped we might better understand the ecology of this poorly studied group of microorganisms.

In this review chytrids are defined to include all fungi in the Phylum Chytridiomycota as defined by Barr (2001). However, in the higher-level phylogenetic classification of the Fungi, most genera of chytrids are currently placed into three basal phyla, the Blastocladiomycota, Chytridiomycota and

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Neocallimastigomycota and into six orders, the Blastocladiales, Chytridiales, Monoblepharidales, Neocallimastigales, Rhizophydiales and Spizellomycetales (James et al. 2000; James et al. 2006; Letcher et al. 2006; Hibbett et al. 2007). The appropriate placement of several other genera, such as *Olpidium* and *Rozella*, may be outside these phyla, and many species have yet to be added to the molecular and TEM-based classification.

Most members of the three basal phyla reproduce asexually by releasing zoospores with a single posteriorly-directed whiplash flagellum (Sparrow 1960; Barr 2001). In a few species of the Neocallimastigales zoospores are multiflagellate (Trinci et al. 1994) or in at least one species of the Blastocladiales (Hoffman et al. 2008) and one species in the Monoblepharidales (Ustinova et al. 2000) the spores lack flagella. The thallus can be either monocentric, polycentric or filamentous (hyphal) (Sparrow 1960) and are able to grow either on top or within substrates.

Throughout the twentieth century mycologists have observed and described the morphology of many chytrids (Sparrow 1960; Karling 1977; Barr 2001). However, much of the taxonomy, which depended on thallus morphology, has proven not to be phylogenetically informative. Recently, impressive amounts of molecular data on DNA sequences in ribosomal and other genes from fungi maintained in culture have been published (James et al. 2000; James et al. 2006; Letcher et al. 2006; Hibbett et al. 2007). This information together with information from studies on the ultrastructure of zoospores has led to a new understanding of phylogenetic relationships.

In contrast, only a few studies have considered the ecology of chytrids, and so very little information is available on the ecology of these diverse groups of fungi. Some of this information has been reviewed by Sparrow (1960); Bremer (1976); Dick (1976); Gleason (1976); Masters (1976); Powell (1993); Barr (2001); Ibelings et al. (2004) and Kagami et al. (2007a), but these reviews focus primarily on other topics.

In addition, many aspects of the ecology of chytrids still remain poorly understood, particularly substrate specificity of saprobes, the nature of the interactions between parasites and their hosts and the effect of physical and biological factors on population size and composition. Furthermore, their roles in ecological processes such as carbon turnover and food-web dynamics remain unclear. Powell (1993); Lefèvre (2007) and Lefèvre et al. (2007) have suggested that chytrids sometimes have been either totally ignored or wrongly classified in many ecological studies especially on biodiversity of fresh water environments. Thus the ecological significance of this group of microorganisms remains to be fully appreciated.

2. Aquatic habitats

According to Barr (1987) members of the orders Blastocladiales and Spizellomycetales are more commonly found growing on solid substrates in soil where moisture content temperature and salinity vary considerably, whereas the Chytridiales and Rhizophydiales are more commonly found growing in bodies of water where these parameters are more constant (Barr 1987). However, members of many genera of chytrids have been observed in both soil and aquatic ecosystems (Sparrow 1960).

Different species of chytrids prefer different environments. Booth (1971b) and Amon and Arthur (1981) suggest the existence of ecotypes. Many physical and chemical factors such as temperature, salinity, dissolved oxygen concentration, mineral composition of the water, pH and light affect the species composition in chytrid communities in both aquatic and soil ecosystems (Paterson 1960; Sparrow 1960; Willoughby 1961a; Barr & Hickman 1967b; Booth 1971a; Bruning 1991a, b; Dubey et al. 1994; Gleason et al. 2007a, b). We expect that because each species has unique physiological capacities, each species operates in its own ecological niche. Here, we focus on three physical factors: salinity, temperature and dissolved oxygen concentration.

Salinity. Most species of chytrids have been observed from fresh water environments (Sparrow 1960; Barr 2001). In general chytrids prefer environments with low osmotic potentials. Some species can grow in slightly saline estuaries where sea water mixes with freshwater, but the growth of most freshwater and soil chytrids is not possible in undiluted sea water (Booth 1971b; Amon & Arthur 1981; Nielsen 1982; Gleason et al. 2006). Laboratory studies have shown that many freshwater and soil chytrids can grow on media supplemented with 1 % NaCl but not with 2 % NaCl (Chukanhom & Hatai 2004; Gleason et al. 2006). As expected, estuarine chytrids can tolerate a much broader range of NaCl concentrations than freshwater chytrids (Amon & Arthur 1981). Few chytrids have been reported from marine environments (Johnson & Sparrow 1961; Bremer 1976). However, recently several chytrid parasites of marine algae have been described (Amon 1984; Müller et al. 1999; Nyvall et al. 1999).

Temperature. Studies with pure cultures in the laboratory have shown that high temperatures can limit the growth of chytrids and that the maximum temperature for growth varies with each isolate. In one study the maximum temperature for growth of twenty three chytrids varied from 30 to 40 °C (Gleason et al. 2005). Only a few chytrids can grow at 40 °C, and no chytrids are known which can grow at temperatures above 45 °C (Booth 1971b; Nielsen 1982; Theodorou et al. 1994; Chukanhom & Hatai 2004; Gleason et al. 2005). The highest optima for growth have been reported for the Neocallimastigales which are adapted to the rumen and hindguts of herbivorous mammals where ambient temperatures approach 40 °C (Theodorou et al. 1994). Many chytrids cannot grow at temperatures over 30 °C (Gleason et al. 2005) and some aquatic chytrids cannot grow at temperatures over 25 °C (Boyle et al. 2003; Johnson et al. 2003; Piotrowski et al. 2004) or 23 °C (Longcore 1993). Therefore, a large increase in temperature of aquatic environments caused by thermal pollution or global warming could have significant effects on chytrid population size and diversity.

Dissolved oxygen concentration. Chytrids in the orders Blastocladiales, Chytridiales, Monoblepharidales, Rhizophydiales and Spizellomycetales are thought to be mostly obligate aerobes, and their growth rates are greatly inhibited by low dissolved oxygen concentrations (Gleason 1976; Barr 2001; Gleason et al. 2007a). Obligately aerobic chytrids have been isolated from freshwater, soil, brackish and marine environments. A few facultative anaerobes have been isolated from stagnant waters and tolerated low dissolved oxygen concentrations (Emerson & Natvig 1981; Whisler 1987). The chytrids in the Order Neocallimastigales have been isolated from the digestive systems of herbivorous mammals. All species in this order lack mitochondria are considered to be obligate anaerobes (Orpin 1994; Trinci *et al.* 1994; Rezaeian *et al.* 2004). Recently DNA assigned to the Neocallimastigales has been found in landfill sites (Lockhart *et al.* 2006).

3. Saprobes and parasites

Many species of chytrids in both the Blastocladiomycota and the Chytridiomycota are saprobes. These fungi are commonly found growing on a large variety of substrates in freshwater and soil environments (Sparrow 1960, pp. 1073-1104) and are important in the breakdown of insoluble macromolecules such as protein, chitin, starch and cellulose in dead fungal, plant and animal material (detritus) (Sparrow 1960; Goldstein 1960; Paterson 1967; Karling 1977; Whisler 1987; Barr 1987; Powell 1993; Barr 2001).

Many other species of Blastocladiomycota and the Chytridiomycota are parasites, infecting phytoplankton, zooplankton, fungi, plants and invertebrate animals (Sparrow 1960; Whisler *et al.* 1975; Masters 1976; Karling 1977; Powell 1993; Barr 2001; Ibelings *et al.* 2004; Johnson *et al.* 2006; Kagami *et al.* 2007a). Canter and her colleagues have documented chytrid parasites on a large number of phytoplankton species in the English Lake District (Ibelings *et al.* 2004; Kagami *et al.* 2007a). Chytrids have also been reported to be parasites of vertebrates: *Batrachochytrium dendrobatidis* infects the skin of various amphibian species (Berger *et al.* 1998; Fisher & Garner 2007; Hyatt *et al.* 2007) and *Allomyces arbuscula* is possibly a parasite of fish eggs (Chukanhom & Hatai 2004). The role of *Allomyces arbuscula* as a parasite of fish eggs needs further clarification. Some chytrids are even parasites on other chytrids (hyperparasitism) (Karling 1942; Couch 1945; Sparrow 1960; Seymour 1971; Karling 1977; Held 1980). Chytrid parasites of phytoplankton may be promiscuous (Paterson 1956, 1958; Gromov *et al.* 1999) or species specific (Kagami *et al.* 2007a; Holfeld 1998, 2000; Ibelings *et al.* 2004). Some species may infect a range of species within a genus (Barr & Hickman 1967a). Other species are possibly facultative parasites since they can be grown in pure culture without the host (Barr & Hickman 1967b; Alster & Zohary 2007). Some chytrids may be symbiotic, such as the rumen chytrids (Neocallimastigomycota) (Trinci *et al.* 1994).

4. Dispersal of propagules

The fungi in the Blastocladiomycota and Chytridiomycota always release zoospores into aquatic environments (Sparrow 1960). Large numbers of zoospores are often present during log phase growth in liquid culture media when chytrids complete their life cycle. When thalli in stationary phase are removed from the surface of solid culture media and placed in deionized water zoospores may be released quickly. However conditions for stimulation of zoospore release under natural conditions are not understood and may vary with species. Zoospores remain motile until they either attach to a substrate or deplete energy reserves (Suberkropp & Cantino 1973). Zoospores cannot swim far so that as a vehicle for dispersal they are useful only for short distances. Some chytrids produce amoeboid zoospores or motile cells without flagella which crawl over surfaces (Couch 1945; Sparrow 1960; Whisler *et al.* 1975; Dorward & Powell 1983; Chukanhom & Hatai 2004; Hoffman *et al.* 2008). Since zoospores lack a cell wall (Suberkropp & Cantino 1973; Dorward & Powell 1983; Powell 1994) they are sensitive to environmental factors such as changes in osmotic potential and moisture.

However hyphae, thalli, sporangia and zoospore cysts, often still attached to substrates or their hosts, are carried with the currents horizontally or vertically in the water column. Chytrids attached to substrates can be carried for long distances horizontally in streams, sink vertically into the benthic region and rise vertically again to the surface during lake turnover. Although chytrids have been isolated from benthic samples (Paterson 1967) the rates of growth and metabolism in benthic regions are unknown. Some chytrids cannot grow but can survive at least for short periods of time under anaerobic conditions (Gleason *et al.* 2007a). How long chytrids can survive in a dormant state in aquatic environments is not known. Johnson and Speare (2005) showed that *Batrachochytrium dendrobatidis* can survive and remain infectious in sterile moist river sand for up to 12 weeks.

Intact thalli, sporangia and possibly zoospore cysts of some species (particularly species in the Blastocladiales and Spizellomycetales) can be resistant to drying (Couch 1945; Willoughby 2001; Gleason *et al.* 2004; Gleason *et al.* 2007b; Hoffman *et al.* 2008). When dried on the surface of the soil or mud in vernal pools these dormant structures may become airborne and could travel long distances before they encounter conditions suitable for resumption of growth. Since keratin is a good substrate for the growth of many chytrids (Sparrow 1960), it may be possible for zoospores to attach to the feathers of aquatic birds. If the sporangia of these chytrids are resistant to drying, they could be transported over long distances as well. Johnson and Speare (2005) suggest that the sporangia of *Batrachochytrium dendrobatidis* (Chytridiales) which are sensitive to drying might be transported on feathers as long as the sporangia are not dried for over three hours. Thus the dispersal of some of these species is not dependent on zoospores swimming in water alone.

5. Roles in food-web dynamics

The roles of some groups of fungi in food web dynamics of terrestrial ecosystems (parasitic, saprophytic and symbiotic) have been intensively studied. For example, in a food web link referred to as the ‘fungal based energy channel’ terrestrial fungi are known to render unutilized resources (plant litter, woods, etc.) accessible to animals (Vega & Blackwell 2005; Wardle 2002). Fungal endophytes and mycorrhizal fungi can make plants more edible for herbivores, thus increasing herbivore growth, by altering plant morphology or nutritional quality (Wardle 2002). In marine environments zoosporic fungal-like protists in the Labyrinthulomycota play important roles in food web dynamics (Raghukumar 2002). Although chytrids have been isolated from both terrestrial and marine ecosystems (Sparrow 1960; Barr 2001), their roles in food web dynamics in these ecosystems are unknown. In freshwater ecosystems, very little attention has been paid to the role of all groups of fungi including chytrids in food web dynamics, although Dick (1976, p. 534) presented a flow diagram illustrating hypothesized roles of aquatic fungi in some of ecological processes in a lake ecosystem.

Recently, however, Kagami *et al.* (2007a) suggested several important roles for chytrids in aquatic food webs. Chytrids can significantly modify plant-animal interactions and change the flows of energy and nutrients in the food web (Kagami *et al.* 2007a). In addition, molecular techniques revealed that a significant part of the small hetrotrophic flagellate populations were very likely to be zoospores of parasitic or saprophytic species of chytrids that heretofore were misidentified as bacterivorous flagellates (Lefèvre 2007; Lefèvre *et al.* 2007). Although quantitative measurements have not yet been attempted, the amount and the quality of matter and energy transferred by chytrids to zooplankton may be significant in food-webs in aquatic environments. In this review we attempt to extend the concepts from the previous studies to the whole ecosystem by including both saprophytic and parasitic chytrids.

In particular we have expanded the conceptual view of aquatic ecosystems presented by Kagami *et al.* (2007a) to include saprobes. In addition we propose several potentially important roles for chytrids in phytoplankton food webs (Fig 1) and present ecological implications for the structure and functioning of aquatic ecosystems. In our synthesis we include the connections between the catchment area and the pelagic ecosystem, because matter input from the surrounding environment supports growth of many pelagic microorganisms and is important in the functioning of pelagic food webs.

(1) Chytrid zoospores as a food source for zooplankton

In general, the cytoplasm of chytrids contains storage carbohydrates such as glycogen (Camargo *et al.* 1969; Suberkropp & Cantino 1973), storage proteins (Suberkropp & Cantino 1973), a wide range of fatty acids, phospholipids, sterols and other lipids (Suberkropp & Cantino 1973; Powell 1978; Weete *et al.* 1989) and nucleic acids (Suberkropp & Cantino 1973). When chytrids reproduce, most of the cytroplasm is converted into zoospores which swim away to colonize new substrates or infect new hosts (Sparrow 1960). Zoospores are well within the range of a good particule size for zooplankton feeding behavior

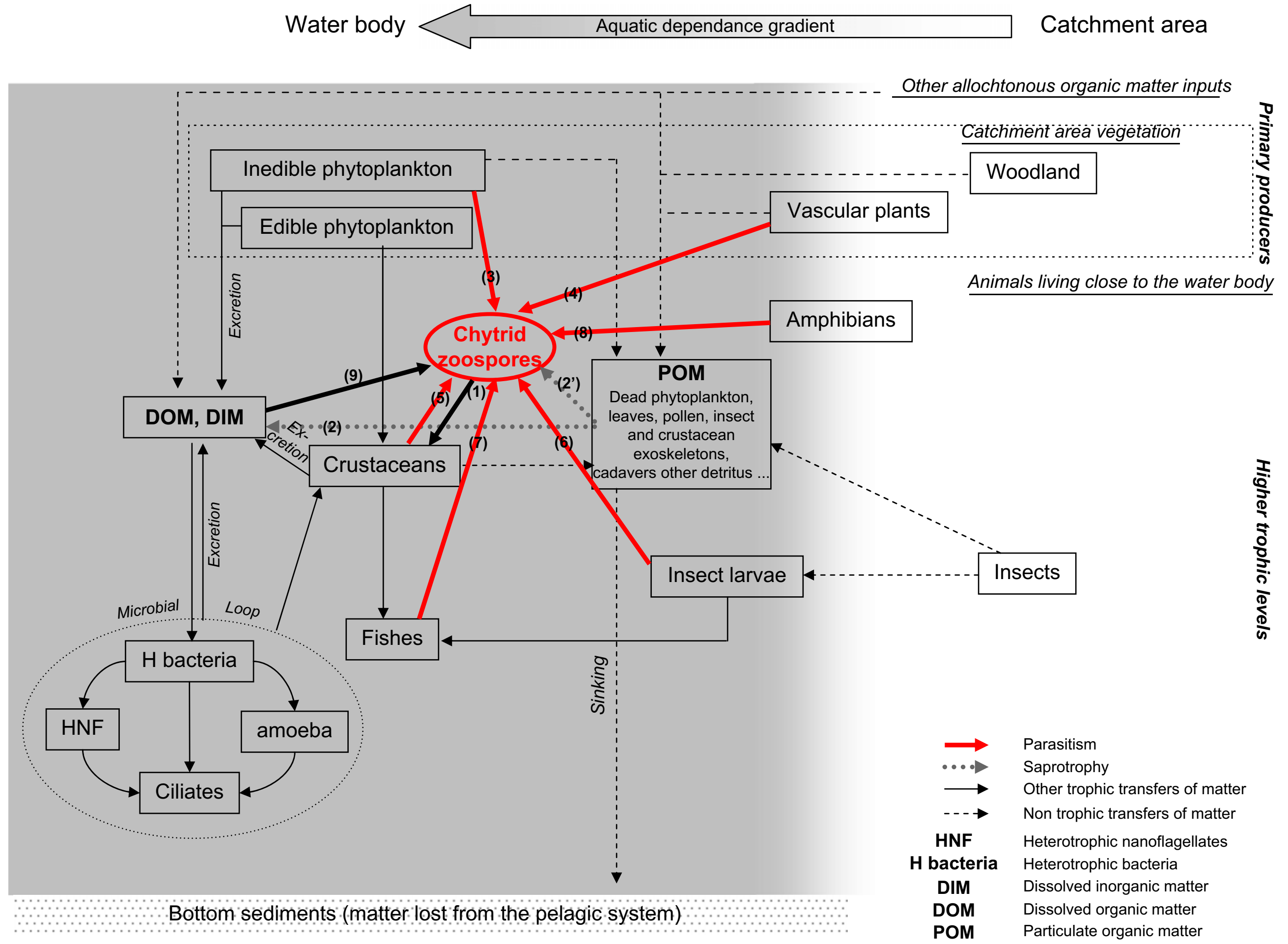

Fig. 1 – A diagram of a freshwater catchment including a generalized planktonic food web with producer and detritus based food chains. Zoospores from both parasitic and saprophytic chytrids are included in the chytrid zoospore pool.

(2–3 μm in diameter) and consequently, when fed upon, transfer matter to higher trophic levels in the food chain (Kagami *et al.* 2004, 2007b). For example, zoospores are efficiently grazed by crustcean zooplankton **(arrow 1** in Fig 1**)** such as *Daphnia* spp., before they grow into a mature thallus (Kagami *et al.* 2004, 2007b). Because our food web hypothesis is restricted to the pelagic zone of lentic ecosystems, we only consider the zoospore stage of the chytrid life cycle in our diagram (Fig 1).

Thus zoospores may provide organic compounds containing nitrogen, phosphorus and sulfur, mineral ions and vitamins to grazing zooplankton.

Zoospores are a particularly good food source because of their nutritional qualities. They are rich in polyunsaturated fatty acids (PUFAs) and contain high cholesterol concentrations (Kagami *et al.* 2007b). These PUFAs and cholesterol are known to promote growth and reproduction in crustacea (Muller-Navarra *et al.* 2000). This phenomenon, known as the 'trophic upgrading concept', is of significant importance in the aquatic food webs because it highlights not only the quantity but also the quality of the matter being transferred.

(2) Decomposition of POM by chytrids

In the pelagic system, the particulate organic matter (POM) pool contains a broad range of complex molecules, including both autochthonous (dead planktonic organisms, crustacean exoskeleton etc.) and allochthonous materials (plant leaves, pollen, others debris). This pool of particulate organic particles is susceptible to sinking through the water column and thus is thought to be lost by the pelagic system (Kagami *et al.* 2006). Chytrids can efficiently digest complex molecules such as chitin (found in crustacean and insect exoskeletons), cellulose (found in plant debris and some algae), proteins (found in snake skin and hair) and other detrital organic materials (Haskins 1939; Whiffen 1941; Sparrow 1960; Murray & Lovett 1966; Paterson 1960, 1967; Willoughby 1961a, b, 2001). So part of the POM might be solublized by saprophytic chytrids and become dissolved organic matter (DOM) and dissolved inorganic matter (DIM) (**arrow 2**). In addition, zoospores produced by saprophytic chytrids growing on POM might be transferred into higher trophic levels of the food chain **(arrow 2')** by being grazed by zooplankton.

(3) Infection of aquatic plants by chytrids

Phytoplankton. Many phytoplankton species are susceptible to parasitism by chytrids (Ibelings *et al.* 2004; Kagami *et al.* 2007a). Chytrid parasitism is one of the important factors controlling the seasonal succession of phytoplankton species (Van Donk & Ringelberg 1983; Holfeld 1998, 2000; Ibelings *et al.* 2004; Kagami *et al.* 2007a). By controling phytoplankton dynamics and blooms, chytrids can significantly affect primary production of aquatic systems.

In addition, because chytrids seem to preferentially infect large and less edible phytoplankton species (Kagami *et al.* 2007a), they may return energy and matter from large sinking cells back to the pelagic and to the higher trophic levels **(arrow 3)** (Kagami *et al.* 2006). This pathway, the "Mycoloop" (Kagami *et al.* 2007a), may reduce sinking fluxes and increase energy transfer from primary producers to consumers in the systems.

Vascular plants. Some chytrids are also known to infect vascular plants in terrestrial ecosystems (Barr 2001). For example chytrid species belonging to the genus *Olpidium* have been intensively studied as specific parasites in roots of several crop plants such as tabacco, lettuce, and cucumber (Powell 1993). It is possible for zoospores discharged from sporangia in the roots or zoospore cysts from plants living in or near water to enter aquatic ecosystems where zooplankton are present **(arrow 4)**. In some instances this could happen with species of *Physoderma* and with saprobic species that grow on scenescent and dead vascular plants.

(4) Infection of aquatic animals by chytrids

Chytrids are important parasites of many groups of aquatic invertebrates such as rotifers, nematodes, mites, crustaceans **(arrow 5)** and insects **(arrow 6)** (Sparrow 1960; Karling 1977; Martin 1987). Chytrid parasites may play significant roles in the control of population size of invertebrates in aquatic environments (Whisler *et al.* 1974, 1975; Martin 1984; Johnson *et al.* 2006). The use of *Coelomoyces* for the biological control of mosquito larvae has been investigated (Whisler *et al.* 1974, 1975). The chytrid *Polycaryum laeve* is highly pathogenic and can cause sharp decline in *Daphnia* populations in 14 lakes from North America (Johnson *et al.* 2006). Given the keystone importance of species of *Daphnia* as efficient grazers of phytoplanktonic organisms and other components of the microbial loop (bacteria, heterotrophic flagellates, ciliates), and as a food resource for planktivorous fishes, chytrids that negatively affect the dynamics of *Daphnia* populations have the potential to significantly influence the entire food web community.

Chytrids also infect several aquatic species of vertebrates. As previously stated the role of *Allomyces arbuscula* as a parasite or saprobe on fish eggs requires more investigation (Chukanhom & Hatai 2004). However zoospores from this chytrid are released into the water **(arrow 7)**. *Batrachochytrium dendrobatidis* is considered the main infectious agent responsible for the decline and extinction of numerous amphibian species worldwide (Berger *et al.* 1998; Fisher & Garner 2007; Hyatt *et al.* 2007) **(arrow 8)**.

(5) Converting inorganic compounds into organic compounds (DIM → DOM)

Chytrids may supply organic nitrogen, phosphorus and sulfur compounds in the food-web. Some chytrids can convert inorganic nitrogen (ammonium and nitrate ions), inorganic sulfur (sulfate ion) and inorganic phosporous (phosphate ion) into organic compounds **(arrow 9)**, since they can grow on synthetic media with only inorganic sources (Haskins & Weston 1950; Craseman 1954; Willoughby 1962; Murray & Lovett 1966; Nolan 1970; Hassan & Catapane 2000; Gleason *et al.* 2006; Midgley *et al.* 2006; Cantino 1955; Gleason 1976). Furthermore some chytrids may use insoluble sources of phosphorous which need to be solubilized before they can be absorbed (Midgley *et al.* 2006). Some chytrids can also use DNA as a source of phosphorous (Midgley *et al.* 2006). Organic compounds then become available to heterotrophic organisms in the ecosystem.

6. Future perspectives

Due to the small size and lack of distinctive morphological features, the identification of chytrids remains a difficult task in natural samples. Our inability to identify and quantify these small species has limited our understanding of their ecological significance. Therefore, new sensitive techniques are required.

Recently, environmental 18S ribosomal DNA surveys have analyzed planktonic assemblages of small eukaryotes in freshwater lakes and, surprisingly, have revealed a relatively high diversity within the phyla Blastocladiomycota and Chytridiomycota in these communities (Slapeta *et al.* 2005; Lefèvre 2007; Lefèvre *et al.* 2007). Many of the sequences tentatively assigned to chytrids have never been detected before. This suggests that the diversity of chytrids in aquatic ecosystems is much greater than previously thought and that conventional microscopic techniques have not provided a complete description of these microbial communities.

Molecular approaches such as Fluorescent *in situ* Hybridization and qantitative PCR seem to offer a promising alternative to reach *in situ* specific abundances of previously undetected taxa (Head *et al.* 1998; Caron *et al.* 2004). These techniques require the design of specific oligonucleotidic probes and primers targeting ribosmal genes. A quantitative PCR assay targeting a molecular-based clade of parasitic chytrids has already been successfully applied to one natural aquatic ecosystem (Lefèvre 2007; Lefèvre *et al.* 2007). The large fungal ribosomal gene database presently available provides numerous possibilities to design oligonucleotidic probes and primers specific to different taxonomic levels within the phylum of Chytridiomycota. There have been promising developments in the ability to directly monitor the dynamics of chytrid zoospores *in situ* using species-specific molecular probes and quantitative PCR (Walker *et al.* 2007). Application of these new molecular techniques should lead to a greater understanding of the ecological significance of chytrids in aquatic ecosystems.

7. Conclusion

Although the morphology of chytrids has been frequently studied throughout the last century, their ecology remains poorly understood. In this review five significant roles for chytrids in food web dynamics in aquatic ecosystems are proposed. These highlight the importance of chytrids in food web dynamics which has frequently been overlooked. A large number of phytoplankton and invertebrate species are impacted in some way by chytrid pathogens.

Saprophytic chytrids recycle detritus and provide food for many other organisms in food webs. Quantitative studies are needed to provide data for mathematical analysis of the processes in food webs in which chytrids are involved. Also we need better methods for classifying chytrids and measuring population size before we can more fully document community structure and the impact of environmental factors. Hopefully molecular methods will be adapted to provide accurate quantitative information for determining population composition in the field. This should lead to a better understanding of some of the processes involved in the functioning of aquatic ecosystems. We hope that this review will provide useful information for the design of further research on the ecology of chytrids in the future.

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