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PHYTOPLANKTON WORKSHOP

Parasitic chytrids: their effects on phytoplankton communities and food-web dynamics

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Abstract Many phytoplankton species are susceptible to fungal parasitism. Parasitic fungi of phytoplankton mainly belong to the *Chytridiomycetes* (chytrids). Here, we discuss the progression made in the study of chytrids that parasitize phytoplankton species. Specific fluorescent stains aid in the identification of chytrids in the field. The established culturing methods and the advances in molecular science offer good potential to gain a better insight into the mechanisms of epidemic development of chytrids and coevolution between chytrids and their algal hosts. Chytrids are often considered to be highly host-specific parasites, but the extent of host specificity has not been fully investigated. Chytrids may prefer larger host cells, since they would gain more resources, but whether hosts are really selected on the basis of size is not clear. The dynamics of chytrids epidemics in a number of studies were partly explained by environmental factors such as light, temperature, nutrients, pH, turbulence and zooplankton grazing. No generalization was made about the epidemic conditions; some state unfavorable conditions for the host growth support epidemic development, while others report epidemics even under optimal growth conditions for the host. Phytoplankton is not defenseless, and several mechanisms have been suggested, such as a hypersensitivity response, chemical defense, maintaining a high genetic diversity and multitrophic indirect defenses. Chytrids may also play an important role in food webs, because zoospores of chytrids have been found to be a good food source for zooplankton.

Keywords Host–parasite interactions · Epidemics · Host specificity · Cell size · Defense · Food webs

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Introduction

Fungal parasitism on phytoplankton is still a neglected subject, although progress has been made during the last decades. We are not the first to make this observation (see e.g. Cook, 1963; Masters, 1976; Reynolds, 1984; Van Donk & Bruning, 1992). This neglect is partly a consequence of the nature of

parasitic infections: they often escape the notice of non-specialists, and their epidemic development is often unpredictable, which has made it difficult to study chytrids in relation to other factors affecting phytoplankton populations (Reynolds, 1984; Van Donk, 1989). On the other hand, Bruning (1991c) emphasized that fungal parasitism, unlike grazing or sedimentation, is a loss factor which is directly perceptible. This should facilitate field investigations, especially when specific fluorescent stains—which avoid confusion with other attached non-parasitic organisms—are used (Müller & Sengbusch, 1983). In addition, established culture systems make experimental work possible, which should help to unravel the mechanisms underlying epidemic development.

The work devoted to taxonomy and occurrence of algal parasites by a relatively small number of researchers in the 1940s, 1950s and 1960s (Ingold, 1940, 1941, 1944; Canter, 1946, 1947a, b, c; Canter & Lund, 1948; Canter, 1949a, b, c, 1950a, b, c, 1951; Canter & Lund, 1951; Canter, 1953; Canter & Lund, 1953; Canter, 1954, 1960, 1961, 1966, 1967, 1968, 1969; Canter & Lund, 1969) may give the impression that ''fungal parasites have been studied for a considerable period of time, and indeed much has been learned about the occurrence of chytrids from these works.

Molecular science has progressed a great deal since the 1960s. Molecular studies now firmly place the *Chytridiomycetes* within the fungal kingdom (Bowman et al., 1992; Tehler et al., 2000). The progress of molecular techniques and the well established cultural system offer us new possibilities to study chytrid dynamics with a higher resolution than before, and to challenge some research questions that have not yet been solved. Intriguing questions include coevolution between phytoplankton and chytrids, or the role of chytrids in the food-web dynamics. In this paper, we give a general description of chytrids with relatively detailed attention to methods used in the study of chytrids, and a special emphasis on more recent developments in this research. This paper complements and builds on information summarized in an earlier review (Ibelings et al., 2004). We refer the taxonomy and life cycle of chytrids to Ibelings et al. (2004), and to Chytrid Fungi Online: (http://www.bama.ua.edu/~nsfpeet) where recent updates of chytrids taxonomy can be found.

Visualization of chytrids

Chytrids may remain undetected by non-specialists or are often confused with other organisms, for instance flagellates such as *Bicosoeca* (Canter Lund & Lund, 1995). These flagellate protozoans feed on bacteria, and do not harm the algae to which they are attached. Special dyes and key morphological differences are helpful to identify and distinguish chytrids from other organisms with a chytrid-like appearance. Zoospores of chytrids have a single straight flagellum (Canter, 1967), and a spherical body (2–3 μm in diameter) containing a conspicuous oil globule and a single nucleus. This oil globule is already quite visible (at a magnification of 400×), but can also be stained with Nile Red (Kudoh, 1990). The nucleus can be stained with 4′,6-diamidino-2-phenilindole (DAPI) or Syber green (Noble & Fuhrman, 1998). Before staining, the samples should be fixed with glutaraldehyde (1% final concentration). Therefore, 1-mL samples are put into Utermohl counting chambers, to which 100 μg L^{-1} of Nile Red and 50 μg L^{-1} of 4′,6-diamidino-2-phenilindole (DAPI) were added (both in final concentrations). The samples are then incubated for 30 min in the dark at room temperature. Nile Red stains the oil globule of the zoospores, emitting a characteristic orange fluorescence under green excitation (525 nm). DAPI stains the nucleus emitting blue fluorescence under ultraviolet (UV) excitation (365 nm).

Chytrids in the different stages of their life cycle (attached zoospores, sporangia and empty sporangia) can be stained with CalcoFluor White (Müller & Sengbusch, 1983). Three drops of 10% KOH solution and three drops of 0.1% CalcoFluor White solution were added to 1-mL samples in Utermohl counting chambers, after which the samples were incubated for 10 min. CalcoFluor White binds to chitin, a cell wall component of chytrids. The sample should be fresh or fixed with gultaraldehyde, but not with Lugol's solution. A more detailed protocol can be obtained at Mycology online (http://www.mycology.adelaide.edu.au/).

Culturing chytrids

With some effort parasitic chytrids can be isolated from lakes using elongated micropipettes and an inverted microscope and maintained in the laboratory. The isolated infected host cells are transferred into fresh uninfected host cultures, which then are kept under favorable environmental conditions for growth of the chytrids (relatively high light and temperature, see Bruning, 1991b). This way, parasite cultures are obtained as a non-axenic batch culture (Canter & Jaworski, 1978; Bruning, 1991d). Freshly isolated infected host cells can also be used for the short-term experiments without maintaining in the laboratory (Van Donk & Ringelberg, 1983; Kagami & Urabe, 2002).

The chytrid, *Zygorhizidium planktonicum* can be maintained on its host algae, *Asterionella formosa*, in non-axenic batch cultures, using the following procedure: 150-mL 1-week-old uninfected *A. formosa* host culture can be infected with 5 to 10-mL of a 1-week-old *Z. planktonicum* culture. The *A. formosa* host cultures can be maintained on a modified Chu-10 medium (Stein, 1973) at 40 μmol quanta m^{-2} s^{-1} with a 14:10 h light :dark cycle and a temperature of 18°C. Culture conditions should be modified according to the particular growth rates of chytrids and host algae (Bruning, 1991b).

Highly infected host cultures are characterized by multiple infected cells and free-swimming zoospores in the medium. Filtering of infected host cultures, using filters with a specific pore size (e.g. 5 μm mesh) makes it possible to separate the fungal zoospores from its algal host cells. This procedure is particularly appropriate if the host alga is larger than the fungal zoospores (2–3 μm). This method is useful not only to obtain fungal zoospores for experiments, but also to prevent the possible development of a resistant host strain (only zoospore suspensions are transferred to new host cultures, instead of using an infected host culture for inoculation of new host cultures, where the risk of transferring resistant hosts is increased). Culturing chytrids without host algae is also possible in artificial media (Barr & Hickman, 1967b) or on agar plates (Barr, 1987). Both methods with or without host algae, however, need special attention that bacteria should not outgrow the chytrids.

Parameters for fungal infection

The most common parameter quantifying the impact of chytrids on their host populations is the so-called prevalence of infection (proportion of infected cells, the percentages of infected cells) (Bruning et al., 1992; Holfeld, 2000a). This parameter is calculated by dividing the number of infected cells by the total number of host cells, and is often expressed as the percentages of infected cells. However, the prevalence of infection is not always the best parameter to quantify the severity of fungal attacks.

Another parameter to investigate the severity of fungal epidemics is the mean intensity of infection, which is a quantification of the mean number of fungi (attached zoospores and sporangia) per host cell in a population. This parameter is calculated by dividing the total number of fungi attached to algal cells by the total number of host cells (Holfeld, 2000a). This parameter normalizes the host cell density, and expresses how many fungi succeed in attachment to their host. Multiple infections (more than one parasite per host cell) can be expressed only by the mean intensity of infection. Multiple infections can have a large impact on host death rate, and to take this into account mean intensity of infection is more informative than the prevalence of infection.

A third important parameter is the abundance of free-swimming zoospores in lake water. This parameter has hardly been used, and only a few studies were carried out in natural lakes (Kudoh, 1990). This parameter may give an idea whether the prevalence of infection is dependent on the abundance of zoospores or on the successful attachment of the zoospores to the host cell.

Experimental studies (Bruning, 1991a, d, e) estimated four growth parameters to formulate a population dynamics model to calculate the specific growth rate of the chytrid at a given host density. The following parameters were included in the model: (1) the number of zoospores produced per sporangium; (2) the development time of the sporangia; (3) the infective lifetime of

the zoospores; and (4) the infectivity constant, a measure for the effectivity of the mechanism by which zoospores find the host and infect it. From those four parameters, three new parameters can be calculated: (1) the maximum growth rate of the parasite, (2) the threshold host density for the development of an epidemic, and (3) the threshold host density for survival of the parasite (Bruning, 1991a, b).

Phytoplankton–chytrids interactions

Host specificity

Chytrids are often considered to be highly host-specific parasites. However, the extent to which chytrids are truly host-specific has not been fully investigated. Some fungi are known to have narrow host ranges, while some had very broad host range (Gromov et al., 1999b).

The specific attachments of zoospores onto a particular host or group of algal species seem to indicate that specific signals are involved in the attraction of zoospores. Glycoproteins at the zoospore surface has been suggested to be the potential site involved in encystment or recognition of environmental cues (Powell, 1994). Marine (non-parasitic) chytrids species (*Rhizophydium*) were found to be positively attracted to both amino acids and carbohydrates (Muehlstein et al., 1988), indicating that chemical cues (chemotaxis) might be involved in recognizing potential host algae. Holfeld (2000b) suggested that zoospore losses on the wrong host are prevented because the attraction to cells is reversible. Recently, chemotaxis was suggested to be even strain specific by the experiments tracking the zoospores movement toward host cells. The swimming behavior of zoospores of the parasitic chytrid *Z. planktonicum* toward potential host algae (*A. formosa*) was observed to differ between susceptible host strains and resistant ones (De Bruin et al. unpublished). However, further tests are needed to investigate the behavior of zoospores more thoroughly. In contrast, Canter & Jaworski (1981) and Canter & Jaworski (1982) found that the attraction of chytrid zoospores to algal hosts was not specific at all. Specifically, attraction of zoospores was recorded for a wide range of hosts, including diatoms, green algae and cyanobacteria. Host specificity would occur during encystment of the zoospores rather than at the earlier stage of chemotaxis (Doggett & Porter, 1995). Zoospores of *Z. planktonicum*, a parasite of three *Synedra* species, sometimes loosely adhered to *A. formosa*, but germ tube intrusion was never observed (Doggett & Porter, 1995). Since *Z. planktonicum* is a well-known parasite of *A. formosa* (see Ibelings et al., 2004), the findings of Doggett & Porter (1995) also indicated that host selection in *Z. planktonicum* was confined to either *Synedra* or *Asterionella*, as reported by Canter & Jaworski (1986) and Canter et al. (1992).

Host cell size versus fungal infection

A possible factor in the selection of potential hosts by the fungal zoospores may be host cell size, although this factor has not yet been well studied. Algal cell size has been found to be an important feature influencing phytoplankton loss factors in general, and has a major effect on vulnerability to zooplankton grazing and sinking rate (Smayda, 1970; Lampert, 1974; Sterner, 1989).

It might be possible that chytrids prefer larger host cells to small ones for several reasons. First, the larger host cells might cause an increase in parasite fecundity, because larger cells contain more resources, which might increase growth of the parasite. In fact, the final sporangium size and host cell size were found to be positively correlated (Holfeld, 2000a). Second, host species with a larger cell volume can be infected at a lower population density (Holfeld, 1998). As a result of being attracted to larger host algae, chytrids may escape from being grazed upon by zooplankton, if the infected host cells remain too large for zooplankton to be ingested (Kagami et al., 2005).

Infecting larger host cells might have some disadvantages for chytrids as well. Some chytrids (*Rhizophydium planktonicum*) are less infective at lower temperature and/or under low light / darkness (Bruning, 1991b). Therefore, if larger host cells sink faster to the deeper layers (cold and dark) of the lake (Smayda, 1970), fungal parasites may not be able to infect or complete their life cycle.

It seems that parasitic chytrids prefer larger host species (Sommer, 1987). Large algae, which are fairly resistant to grazing by zooplankton, are often found being attacked by fungal parasites. In addition, fungal parasitism seems less likely on host cells of smaller size, especially picoplankton (Canter Lund & Lund, 1995; Raven, 1998). The small size of these species may constitute too small contribution of resources for the completion of the parasite life cycle. In fact, chytrids infecting picoplankton have not been reported yet, although viruses attacking picoplankton species were reported (Suttle & Chan, 1994; Wilson & Mann, 1997; Bailey et al., 2004). In addition to cell size, colony formation (and especially colony forms) might have an impact on host selection, because chytrids can infect more than one cell of an algal filament by growing through the filament, or reach spatially distant host cells by means of branched rhizoids (Canter Lund & Lund, 1995). Furthermore, zoospores may find neighboring host cells more easily if the host cells are arranged in a colony of some form. In some cases, parasitic chytrids were found to infect more *A. formosa* cells associated in colonies than the unicellular forms, and more parasitize *A. formosa* non-stellate colonies than stellate ones among colonies (Bertrand et al., 2004). However, more data are definitely needed to test this hypothesis.

Within host populations, size selectivity is still not clear. Some studies showed that infected cells tend to be larger than uninfected cells (Holfeld, 2000a), while other studies showed that smaller or intermediate size classes were more parasitized than larger ones (Koob, 1966; Sen, 1987a). Recently, susceptibility to fungal infection was found to be highly strain-specific within *A. formosa* host populations (De Bruin et al., 2004). Genetically different *A. formosa* strains differed in their susceptibility to parasite attack. Thus, not only host cell size but also its genetic make-up should be considered when size selectivity of chytrids within host populations is studied.

Fungal epidemics in the field

In lakes, phytoplankton blooms crashed relatively rapidly (over the course of a few weeks), at times when a high prevalence of infection (more than 90%) with parasitic chytrids was observed (Van Donk & Ringelberg, 1983; Kagami & Urabe, 2002). Fungal infection on single algal species (or a small range of related species) may favor the development of other algal species. Thus fungal parasitism can be an important factor controlling phytoplankton seasonal succession. Fungal parasitism, however, has received less attention in controlling algal population dynamics compared to physic-chemical factors and grazing by zooplankton (Sommer et al., 1986). The marked effects of chytrids on natural phytoplankton populations and communities in lakes are: (1) delaying the timing of maximum algal numbers or decrease the size of peak population densities (Canter & Lund, 1951), (2) the replacement of a dominant species by another species (Canter & Lund, 1951; Reynolds, 1973; Van Donk & Ringelberg, 1983), and (3) steering the outcome of interspecific competition among subdominant species (Canter & Lund, 1969).

Conditions for fungal epidemics

The development of fungal epidemics is unpredictable and fluctuates with time and space. These fluctuations have been partly explained by abiotic factors, such as temperature (Barr & Hickman, 1967a; Masters, 1971a; Blinn & Button, 1973; Van Donk & Ringelberg, 1983; Sen, 1987a; Kudoh & Takahashi, 1990), light (Barr & Hickman, 1967a; Blinn & Button, 1973; Abeliovich & Dikbuck, 1977; Kumar, 1978b; Canter & Jaworski, 1979, 1981; Bruning, 1991b, d; Kagami & Urabe, 2002), nutrients (Bruning, 1991a), pH (Sen, 1987a), turbulence (Doggett & Porter, 1996; Kuhn & Hofmann, 1999), and biotic factors, such as *Daphnia* grazing on fungal zoospores (Kagami et al., 2004). There are two contrasting statements concerning the necessary environmental conditions for the development of a fungal epidemic. One is that fungal epidemics within phytoplankton populations may arise more easily when growth conditions for the host are unfavorable (Canter & Lund, 1948; Canter & Lund, 1969; Masters, 1971a; Reynolds, 1984; Kagami & Urabe, 2002). In contrast, Van Donk & Ringelberg (1983) and Sen (1987a) observed that fungal epidemics occurred during optimal external conditions for the host.

The development of a fungal epidemic depends on the specific growth rate of host and parasite populations. Fungal parasites can only become epidemic when the parasite population increases faster than the host population. Thus in theory, a fungal parasite may become epidemic under conditions when algal growth is depressed (for instance at low nutrient levels), or when fungal growth is enhanced (i.e., when host densities are high). If environmental factors depress fungal growth more than algal growth, this factor will obviously hamper epidemic development.

The response of fungal zoospores to environmental factors might be species-specific. For instance, zoospores of *R. planktonicum* were not able to find and infect their host under very low light conditions (Canter & Jaworski, 1981; Bruning, 1991d), while zoospores of *R. sphaerocarpum* can infect their host even in the darkness (Barr & Hickman, 1967a). These species-specific growth characteristics also make it difficult to generalize whether fungal epidemics may arise more easily when the growth conditions for the host are unfavorable or optimal.

Although experimental work by Bruning (1991a, b, d, e) showed that the direct effects of environmental factors on chytrids life history can be separated from indirect effects that affect the parasite via environmental effects on host density, it is still hard to specify exactly which factors determine fungal epidemics in the field. This may be explained by the fact that several environmental parameters commonly change simultaneously in aquatic systems. In addition, host density effects may override the effects of other factors (Kudoh & Takahashi, 1990). Besides, several factors affect host-parasite dynamics in complex ways (Sen, 1988a; Bruning, 1991b; Doggett & Porter, 1996). For instance, epidemics of a parasitic chytrid on its diatom host were favored by high light intensities when the water temperature was high, but low light intensities were required when the water temperature was low. However, epidemics were not possible below a certain threshold value of the host density, irrespective of temperature and light conditions (Bruning, 1991b).

It should also be noted that host cell mortality was not proportional to the fungal infection rate, and that mortality effects of the parasite varied according to environmental factors such as temperature (Kudoh & Takahashi, 1990). Most previous studies have focused primarily on fungal dynamics (infection rates), and did not measure the mortality rate of the host algae (population decline rates). Host cells can be heavily infected by parasites and may still survive under high light conditions, whereas they would be more vulnerable (higher mortality) under reduced light (Kagami & Urabe, 2002).

Host defense

One of the intriguing questions is: 'how can the host survive (and even bloom regularly), despite recurring epidemics with a high prevalence of infection (>90%) by a highly virulent parasite? It is believed that a part of the host population escapes from infection, and serves as an inoculum for the next bloom. When a fungal epidemic reduces the host density to a very low number, it makes it hard for the parasite zoospores to find the last few remaining host cells. It has been shown for some diatom species that they form ''seed banks'' on the lake sediments, from where resuspended cells could provide the inoculum for the next bloom (Jewson, 1992; Itakura et al., 1997; McQuiod et al., 2002). These seedbanks are preserved under cold and dark conditions on the sediment, and this may enable the host to (temporarily) escape from parasite attack (Ibelings et al., 2004). These deeper lake areas might hence work as refuges for the host. Note that this is not always the case, that cysts of *Ceratium* were found infected only on the lake sediment and not while they were suspended in the water column (Canter Lund & Lund, 1995).

Another form of defense of the host against parasite attack is a so-called hypersensitivity response. This type of defense is well described in (terrestrial) plant studies. The hypersensitivity response is a form of programmed cell death: a burst of superoxide production, and the expression of specific defense genes (White et al., 2000). A hypersensitive response in diatom *A. formosa* is characterized by a quick death of the algal host cell, shortly after infection (Canter Lund & Lund, 1995). This way, the attached zoospores fail to

develop into sporangia (Canter & Jaworski, 1979), curbing epidemic development of the fungus.

Another type of defense, a form of induced chemical defense, was suggested by Pohnert (2000). The release of unsaturated aldehydes from mechanically wounded diatom cells (e.g. *Asterionella* and *Thalassiossira*) was shown to act as highly active fungicides against fungi like *Schizophyllum* and *Aspergillus nidulans*. The enzymatically produced unsaturated aldehydes, are also know to suppress copepod reproduction (Ianora et al., 2004). Rigorous tests are needed to examine whether these metabolites are effective against chytrids under natural conditions.

It is well known that some algae can defend themselves against grazers by changing their morphology (e.g., forming large colonies or aggregates or by producing spines) (Van Donk et al., 1999). Siliciumoxide (SiO_2), Calcium carbonate ($CaCO_3$), and certain polysaccharides in algal tissues were suggested to restrict the access of parasites, like viruses, amoebae, dinoflagellates and fungi to the host protoplast (Smetacek, 1999; Hamm et al., 2003; Raven & Waite, 2004). However, silicification seems not to prevent the chytrids infection on diatom, because chytrids on diatoms are ecologically significant (Table 1). Chytrids penetrate the diatom protoplast using a rhyizoidal system (Van Donk & Bruning, 1992), probably inserting a feeding tube between silicified wall segments (Fig. 1) after enzymic digestion of the organic components of the wall (Smetacek, 1999). Unlike the diatom cell, a porose silica wall with an overlapping system of girdle bands, there is only one entry point on siliceous *Mallomonas* cell or any other chrysophyte spore for the germ tube of the parasite (Canter Lund & Lund, 1995). This entry is via the single hole in the cell wall which is plugged by non-siliceous matter. Even with this one entry point, fungal zoospores managed to settle themselves on the plug itself (Canter Lund & Lund, 1995). Mucilage around cells doesn't seem to restrict the access of parasites to the protoplast either, because chytrids are also common on *Sphaerocystis*, *Microcystis* and *Eudorina*, in which fungi reaches algal cells by penetrating and elongating their threads through the mucilage into the protoplasts (Canter Lund & Lund, 1995).

There may also be other evolutionary defense mechanisms by which algal host cells may protect themselves from parasite attack. The Red Queen hypothesis (Bell, 1982) states that the evolutionary struggle with parasites has selected for sexual reproduction among hosts, resulting in genetically variable offspring. High levels of genetic variation within *A. formosa* host populations from Lake Maarsseveen were found by the use of molecular markers (De Bruin et al., 2004). Every host strain was found to have a unique AFLP (amplified fragment length polymorphism) banding pattern, and these high levels of genetic variation may be explained by recombination (sexual reproduction). In addition it was demonstrated that genetically different host strains differed in their susceptibility to different isolates of the parasitic chytrid *Z. planktonicum* (Fig. 2) (De Bruin et al., 2004). Thus, as stated by the Red Queen hypothesis, algal hosts may maintain a high level of genetic diversity to fend off parasites and buffer their population against widespread epidemics. Furthermore, laboratory serial passage experiments using the *Asterionella–Zygorhizidium* system showed that parasite fitness during 200 generations of growth improved rapidly on a genetically uniform host population in comparison to a population constructed from multiple strains (De Bruin et al., submitted for publication). This indicates that a high level of genetic variation within host population may hold back parasite evolution. Although recombination through sexual reproduction is an important mechanism through which genetic diversity is created and maintained, sexual reproduction has never been observed in *Asterionella* populations (Maberly et al., 1994; Canter Lund & Lund, 1995).

Multitrophic indirect defenses (Van Donk, 2005) have been described in many terrestrial and marine ecosystems (Dicke, 1999; Strom et al., 2003). These studies show that plants produce substances which attract natural enemies of the plant's attacker, resulting in an increase of predation on the herbivores, which in turn, reduces the grazing pressure of these herbivores on plants. In freshwater ecosystem, cyanobacteria were found to excrete organic substances that attract flagellates eating parasitic viruses of the

Table 1 Chytrids and their host phytoplankton genera

Host	Cell volume (μm^3)	Chytrids	Reference
Anabaena	94–320	*Chytridium*, *Rhiozosiphon*, *Phlyctidium*, *Blastocladiella*, *Scherffeliomyces*	1, 12, 13, 14, 16, 22, Paterson (1960), Canter & Willoughby (1964)
Ankistrodesmus	11–590	*Zygorhizidium*	14
Ankyra	3–67	Unidentified chytrids	Holfeld (1998)
Aphanizomenon	7–50	*Chytridium*, *Phlyctidium*, *Rhizophidium*	12, 22, 24
Apiocystis		*Rhizophidium*	10
Astericiccys		*Rhizophidium*	16
Asterionella	350–650	*Chytridium*, *Chytriomyces*, *Rhizophidium*, *Septosperma*, *Zygorhizidium*, unidentified chytrids	1, 14, 18, 23, 25, Beakes et al. (1988, 1992, 1993), Canter & Jaworski (1978, 1979, 1980), Kudoh & Takahashi (1992), Sommer (1987), Bertrand et al. (2004)
Asterococcus		*Phlyctochytirium*	16
Betrachosperium		Unidentified chytrids	1
Botryococcus	89	Chytridium, unidentified chytrids	1, Masters (1971b)
Bulbochaete		*Chytridium*	Sparrow (1936)
Ceratium	29080–62670	*Zygorhizidium*, *Rhizophydium*	1, Canter & Heaney (1984), Sommer (1987), Heaney et al. (1988)
Characium		*Chytridium*, *Rhizophydium*	1
Chaetoceros		*Rhizophydium*	26, Webster (1970)
Chara		*Diplophlyctis*, *Entophlyctis*	13, Richard (1951)
Chlamydocapsa		*Zygorhizidium*	1
Chlamydomonas	650	*Dangeardia*, *Entophlyctis*, *Polyphagus*, *Phlyctochytirium*, *Rhizophidium*, *Scherffeliomyces*	13, 21, Johns (1964), Shin et al. (2001), Ingold (1941)
Chlorococcalean algae		*Rhizophydium*	Gromov et al. (1999a)
Chlorococcum		*Mesochytrium*	Gromov et al. (2000)
Chlorogronium		*Phlyctidium*	13
Chlorogonium		Unidentified chytrids	1
Chrysamoeba	340	Unidentified chytrids	Holfeld (1998)
Chrysocapsa		*Dangeardia*	21
Chrysochaete		*Dangeardia*	20
Chrysomonad		*Rhizophidium*	14
Chrysophxis		*Rhizophidium*	14
Cladophora		*Olpidium*, *Phlyctochytirium*, *Rhizophidium*	13, Sparrow (1936, 1952)
Closterium	820–9200	*Ancylistes*, *Entophlyctis*, *Micromycopsis*, *Myzocytium*, *Micromyces*, *Olpidium*, *Phlyctochytirium*	1, 3, 7, 8, 13, 20, Cook (1963)
Cocconeis	4600	*Chytridium*	4
Coelastrum	610–780	*Zygorhizidium*	Sen (1988c)
Cosmarium	22000	*Myzocytium*, *Phlyctochytirium*, *Rhizophidium*	3, 16, 22, 27, Webster (1970)
Cryptomonas	1700–5337	*Rhizophydium*	19
Cyclotella	200–3100	*Zygorhizidium*	Sen (1988b)
Cylindrocystis		*Endodesmidium*	7
Cylindrospermopsis		Unidentified chytrids	Fabbro & Duivenvoorden (1996)
Dacrymyces		Unidentified chytrids	Canter & Ingold (1984)
Desmidium		*Myzocytium*	4
Dictyosphaerium	10–80	*Rhizophydium*, *Zygorhizidium*	1, Sen (1988c)
Dinobryon	2000–4200	*Rhizophydium*, *Zygorhizidium*	9, 14
Elakatothrix	260	*Zygorhizidium*	14
Eremosphaera		*Olpidium*, *Rhizophydium*	13

Table 1 continued

Host	Cell volume (μm^3)	Chytrids	Reference
Eudorina	320–586	*Dangeardia*, *Endocoenobium*, *Polyphagus*, *Rhizophydium*, *Zygorhizidium*	1, 2, 13, Ingold (1940), Johns (1964)
Euglena	9700–11000	*Entophlyctis*, *Olpidium*, *Polyphagus*, *Psuedosphaerita*, *Scherffeliomyces*	13, Sparrow (1936), Anderson et al. (1995), Johns (1964)
Fragilaria	300–755	*Chytridium*, *Podochytrium*, *Rhizophydium*, *Zygorhizidium*	4, 9, 25, Canter & Jaworski (1982), Sommer (1987), Sparrow (1936), Sen (1987b)
Gemellicystis		*Rhizidium*, *Rhizophydium*	9, 12, 14
Gonatozygon		*Myzocytium*	3, 19
Heliozoa?		*Chytriomyces*	17
Hyalobryon		*Rhizophidium*	12, 24
Hyalotheca		*Olpidium*	6
Kirchneriella	7–110	*Zygorhizidium*	1
Lyngbya		*Rhizophidium*	24
Mallomonas	940–9000	*Chytridium*, *Pseudopileum*, *Septosperma*	1, 21, 25
Melosira	190–2000	*Chytridium*, *Podochytrium*, *Rhyzidiopsis*, *Rhizophydium*, *Zygorhizidium*	10, 13, 18, Sparrow (1936), Sommer (1987), Sen (1988b)
Microcystis	10–110	*Chytridium*, *Rhizidium*	1, 22, Sen (1988a)
Mougeotia	1086–27000	*Chytridium*, *Micromyces*, *Olpidium*, *Phlycidium*, *Zygorhizidium*	4, 5, 7, 13, Sparrow (1936)
Netrium		*Endodesmidium*	7
Nitella		*Chytridium*, *Diplophlyctis*, *Entophlyctis*	13, Sparrow (1936)
Nitzschia	310–320	*Chytridium*	4
Ochromonas	2800	*Chytridiium*	1
Oedogonium		*Chytridium*, *Rhizophydium*	4, 11, 13
Oocystis	100–970	*Chytridium*, *Diplochytridium*, *Lagenidium*, *Zygorhizidium*	Masters (1971a), Cook (1963), Sen (1988c), Lopezllorca & Hernandez (1996)
Oscillatoria	130–46600	*Rhizophidium*	12, 22
Pandorina	450	*Dangenardia*, *Polyphagus*, *Zygorhizidium*	13, Sen (1988a), Johns (1964), Blinn & Button (1973), Blinn (1973)
Pediastrum	910–2200	*Phlyctidium*, *Zygorhizidium*	Masters (1971c), Doggett & Porter (1994)
Penium		*Myzocytium*	3, 21
Peridinium	4700	*Amphicypellus*, *Phlyctochytirium*	1, 14, 16, Ingold (1944), Alster & Zohary (2006)
Pinnularia		*Podochytrium*	1
Pseudosphaerocystis		*Rhizophydium*	1
Pythium		*Rozella*	13
Rhizosolenia	2000	*Zygorhizidium*	14, 18, 25
Scenedesums	92–440	*Chytridium (Schenepf)*, *Phlyctidium*	Lukavsky (1970), Abelovich & Dikbuck (1977), Masters (1971c), Puneva et al. (2000)
Sphaerocystis	74	*Rhizophidium*, *Zygorhizidium*	1, 10, 12
Spharozyga		*Chytridium*	22
Spirogyra	31000	*Chytridium*, *Entophlyctis*, *Lagenidium*, *Micromyces*, *Phlyctochytirium*, *Rhizidium*, *Rhizophydium*	1, 2, 13, 27, Sparrow (1936), Webster (1970), Masters (1971a), Paterson (1960), Barr & Hickman (1967a, b)
Spirotaenia		*Rhizophydium*	5
Spondylosium	10000	*Phlyctochytirium*, *Rhizophydium*	16, 22, Paterson (1960)
Staurastrum	4920–82000	*Chytridium*, *Myzocytium*, *Phlyctochytirium*, *Phlyctidium*, *Rhizophydium*, *Zygorhizidium*	3, 14, 15, 16, 20, 21, 22, 27, Sen (1988a), Webster (1970), Kagami & Urabe (2002)
Staurodesmus		*Chytridium*, *Phlyctochytirium*, *Rhizophydium*	1, 16, 27, Webster (1970)

Table 1 continued

Host	Cell volume (μm^3)	Chytrids	Reference
Stephanodiscus	220–15980	Zygorhizidium, unidentified chytrids	Sommer (1987), Sen (1988b), Holfeld (2000a, b)
Stylosphaeridium		*Rhizophidium*	9
Synedra	160–3800	*Septolpidium*, *Zygorhizidium*	13, 14, 18, 25
Tabellaria	820	*Chytridium*, *Chytriomyces*	25
Tetmemorum		*Micromycopsis*	7
Tribonema		*Chytridium*, *Rhizophidium*	13, Sparrow (1936)
Ulothrix		*Rhizophidium*	13
Uroglena	98–150	*Zygorhizidium*	9, 14
Vaucheria		*Entophlyctis*	13, Sparrow (1936)
Volvox	60	*Polyphagus*	13, Johns (1964)
Volvulina		*Polyphagus*	Johns (1964)
Xanthidium	62000	*Myzocytium*	3, 19
Zygnema		*Micromycopsis*, *Olpidium*, *Rhizophydium*	7, 13

References frequently used were shown by numbers: 1. Canter-Lund & Lund (1995); 2. Canter (1946); 3. Canter (1947a); 4. Canter (1947b); 5. Canter (1947c); 6. Canter (1949a); 7. Canter (1949b); 8. Canter (1949c); 9. Canter (1950a); 10. Canter (1950b); 11. Canter (1950c); 12. Canter (1951); 13.Canter (1953); 14. Canter (1954); 15. Canter (1960); 16. Canter (1961); 17. Canter (1966); 18. Canter (1967); 19. Canter (1968); 20. Canter (1969); 21. Canter (1971); 22. Canter (1972); 23. Canter & Lund (1948); 24. Canter & Lund (1951); 25. Canter & Lund (1953); 26. Canter & Lund (1968); 27. Canter & Lund (1969). The range of host cell volumes are listed if the data is available (Reynolds, 1984; Ichise et al., 1995; Kagami & Urabe, 2001)

cyanobacteria (Murray, 1995). It is possible that algae might also excrete some kind of infochemical, which may attract enemies (predators or parasites) of chytrids. Predation on the zoospores of chytrids has been found for certain zooplankton species, like *Daphnia*, the ciliate *Cyclidium*, and the Chrysophyte *Ochromonas* (Canter Lund & Lund, 1995; Kagami et al., 2004). Hyperparasitism, parasites infecting parasites, was found for the chytrid *Zygorhizidium affluens*. This parasite was frequently parasitized by another chytrid *Rozella* sp. (Canter, 1969). Although the impact

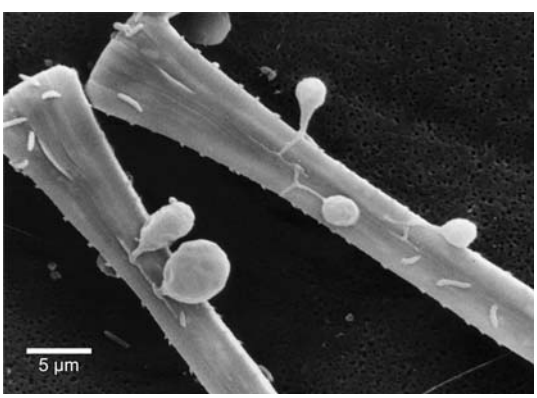

Fig. 1 Scanning electron microscopy image of *A. formosa* cells (rod-shapes) infected by *Z. planktonicum* (spheres). Photo by Van Donk

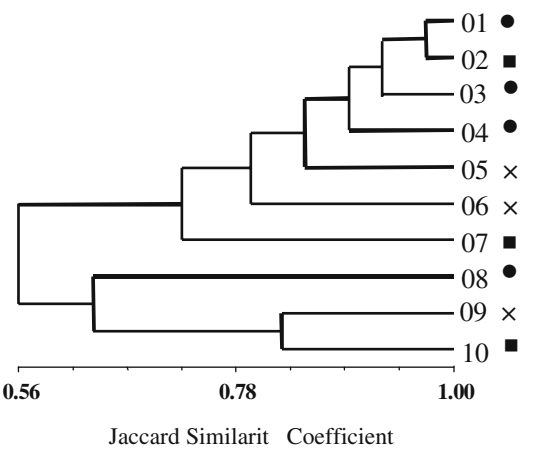

Fig. 2 Genotypic similarity among *Asterionella formosa* strains isolated from Lake Maarsseveen, obtained by AFLP fingerprinting (modified after De Bruin et al., 2004). Susceptibilities to parasite attack by *Zygorhizidium planktonicum* from Lake Maarsseveen differ among host strains, indicated as: (•) highly susceptible, (■) moderately susceptible, and (×) resistant

of these hyperparasites was not high enough to save the parasitized algae from their death (Canter Lund & Lund, 1995), hyperparasitism can reduce the impact of a fungal infection by reducing the production of spores by the primary parasite.

Impact of chytrids on food web dynamics

Parasites are generally neglected in food web studies, although their importance in food web dynamics has been emphasized by Marcogliese and Cone (1997). Recently, a new possible role of chytrids in aquatic food webs has been put forward. It has been suggested that the zoospores of chytrids are a good food source for zooplankton like *Daphnia* (Kagami et al., 2004). Zoospores of the chytrid *Z. planktonicum*, the fungal parasite of *A. formosa*, were found to be grazed efficiently by *Daphnia* (Kagami et al., 2004), since their size (2–3 μm) was well within the preferred range of food particle size for zooplankton (Geller & Müller, 1981). The density of zoospores during an epidemic may be in the same order of magnitude (or even more) than the density of edible phytoplankton cells (i.e., several thousands per milliliter). This implies that fungal zoospores may be a food source of some importance for *Daphnia* during fungal epidemics.

Phytoplankton species that are susceptible to fungal infection seem to be mainly large species, which are less grazed by large zooplankton (Sommer, 1987). Our experiments revealed that under the dominance of inedible algae (*Asterionella*), *Daphnia* could grow and survive well (only) if zoospores of the parasitic fungus were present (Kagami et al. unpublished). Since the infected *Asterionella* colonies remained inedible for *Daphnia* (Kagami et al., 2005), the higher growth rates in the treatments with fungi should be ascribed to grazing on fungal zoospores. The results indicate that fungi may enhance the reproduction and growth of *Daphnia*, especially when large inedible phytoplankton species dominate the phytoplankton community.

Large phytoplankton species are believed to be lost by sinking from the euphotic zone instead of being grazed (Malone, 1980; Legendre & Le Fevre, 1991; Kiørboe, 1993). When these large inedible phytoplankton species are infected by fungi, however, nutrients within these cells are consumed by parasitic fungi, some of which in turn are grazed by *Daphnia*. This new pathway has been dubbed the 'Mycoloop' since nutrients from large inedible algae are transferred to zooplankton via the zoospores of parasitic fungi that have 'consumed' nutrients from their algal hosts. The mycoloop may occasionally play an important role in shaping aquatic systems, by altering the material flow from settled algae to cells that are available to the pelagic food webs (Fig. 3).

One of the remarkable characteristics of fungal zoospores is the possession of an oil globule (Canter, 1967). Lipid analyses of fungal zoospores revealed that fungal zoospores are rich in polyunsaturated fatty acids (PUFAs), and contain high cholesterol concentrations (Kagami et al., unpublished). The analyses support the idea that fungal zoospores are food of good quality for *Daphnia*, since PUFAs and cholesterols are known to be essential for *Daphnia* growth and reproduction (Müller-Navarra et al., 2000). Thus, fungi might facilitate the growth of zooplankton not only via transferring energy (nutrients) from inedible algae to zooplankton, but also due to high nutritional quality of the chytrids themselves.

Future perspectives

It is essential to collect more data to obtain a better insight in the general patterns of the fungal distribution in aquatic ecosystems and to test/confirm the ideas described above. In lakes, for instance, estimating zoospore abundance is especially needed in addition to the data on the prevalence of infection. Furthermore, the presence and the roles of chytrids have not yet been investigated in marine and river ecosystems. Only a few chytrids have been found in estuary (Kazama, 1972) and on marine diatoms, such as *Licmophora hyaline* (Kumar, 1978a; Kumar, 1980) and *Coscinodiscus oculus iridis* (Taylor, 1976). Chytrids are also known on marine algae

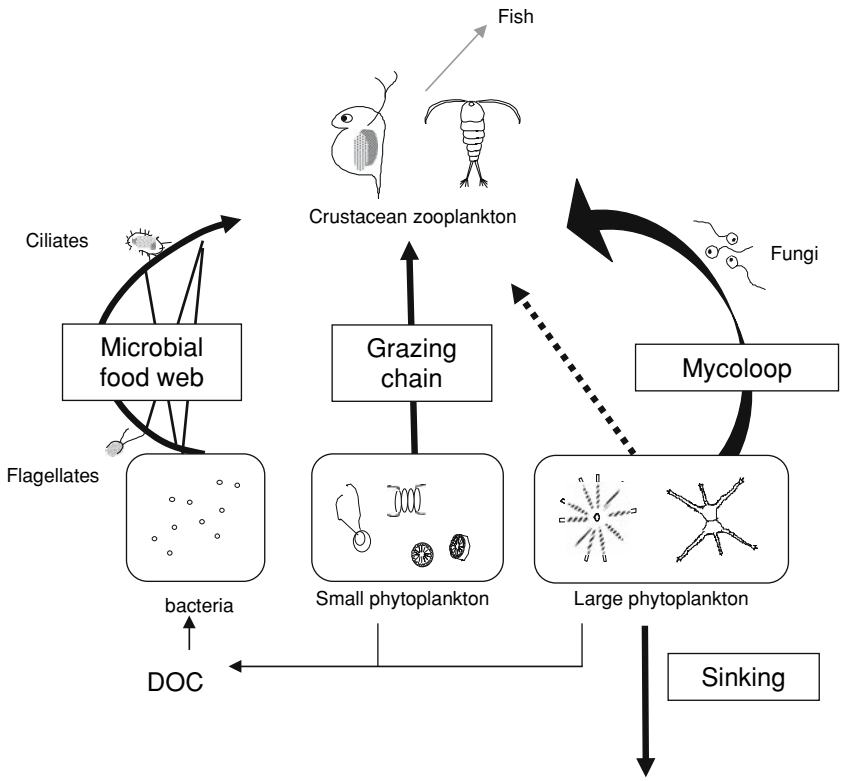

Fig. 3 Diagram of planktonic food webs. Large inedible algae can be incorporated into food webs instead of sinking to the lake bottom, if they are infected by chytrids, some of which in turn are grazed by *Daphnia*. This new pathway is named as ''Mycoloop''

Cladophora (Raghukumar, 1986). In addition, in a river, a single chytrid has been reported (Fabbro & Duivenvoorden, 1996).

The key drivers of aquatic ecosystem change (eutrophication, increasing temperature and UV radiation, habitat alteration, invasive species and pollution) may alter the impact of parasites on their host populations. Since fungal parasites perform better during diatom blooms that occur during warmer springs (Van Donk & Ringelberg, 1983), climate change may enhance fungal growth, which might increase the importance of fungal parasites in ecosystems. Some phytoplankton species may become more susceptible to chytrids due to the increase of UV radiation, as reported for instance in a chytrid–amphibians relationship (Blaustein et al., 1994; Blaustein & Kiesecker, 2002).

Some stressors may also increase host density, which increases the encounter rate between host and parasites. Eutrophication due to habitat alteration has been suggested as a driver of elevated parasitic infection in amphibian populations (Johnson & Chase, 2004). Specifically, eutrophication might cause a shift in snails species composition towards the potential host species (*Planorbella* spp.) of the chytrid *Ribeiroia ondatrae*, which increased amphibian malformation caused by *Ribeiroia* infection (Johnson & Chase, 2004). If eutrophication increases the abundance of large inedible algae as predicted by models (Leibold, 1989; Grover, 1995; Leibold, 1996), thus it may increase the impact of chytrids, since large inedible algae seem to be common as hosts to parasitic chytrids (Sommer, 1987). Furthermore, under environmental stress the host range of parasites may change, bringing completely new phytoplankton taxa under parasite attack. Long-term data, paleolimnological analysis and experiments may provide the evidence for the impact of environmental fluctuations on phytoplankton–chytrids interactions.

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