CHAPTER 16

The Ecology of Chytrid and Aphelid Parasites of Phytoplankton

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CONTENTS

16.1 INTRODUCTION

Over the past decade, there has been a surge of research devoted to the study of zoosporic parasites of phytoplankton (Karpov et al. 2014a; Gleason et al. 2015; Lepère et al. 2015; Valois and Poulin 2015). While this paradigm shift in aquatic ecology is relatively new, chytrids parasitizing algae have been the focus of studies dating back to at least the early twentieth century (Atkinson 1909; Karling 1928a; Karling 1928b; Canter 1947; Sparrow 1951). Work focusing on aphelid parasites of phytoplankton has taken longer to emerge (Fott 1957; Schnepf et al. 1970; Schnepf et al. 1971; Schnepf 1972; Gromov 2000) and has not gained the attention given to chytrid ecology. The focus on zoosporic parasites of phytoplankton can be aligned with shifts in perspective in many fields; the problems associated with mass infection of algae cultured for biofuel (Collins et al. 2014), our evolving understanding of the role of parasites in food web structure and functioning (Jephcott et al. 2016b), and the extremely rapid generational turnover exhibited by

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microbial host-parasite systems leading to coevolutionary dynamics (De Bruin et al. 2008; Kyle et al. 2015). However, it seems more likely that the recent mass declines and extinctions in amphibian populations worldwide due to infection by the chytrid *Batrachochytrium dendrobatidis* (Longcore et al. 1999; Lips et al. 2006; Skerratt et al. 2007) is the reason for this surge of interest. Not only phytoplankton, but other groups of organisms such as zooplankton (Penalva-Arana et al. 2011), salamanders (Martel et al. 2014), and snakes (Allender et al. 2015), are susceptible to fungal infection, and interest in these relationships has burgeoned as a result.

Chytrids and Aphelids are flagellated fungi and belong to the phyla Chytridiomycota and Aphelidia, and supergroup Opisthokonta. These two phyla represent basal branches of the fungal phylogenetic tree only recently described within the last decade (James et al. 2006; Ishida et al. 2015). These lineages are old, in the evolutionary sense, having split off from the main fungal line 710–1060 million years ago (Lücking et al. 2009). This means that features displayed in the chytrids and aphelids were possibly displayed in the earliest fungi. This is supported by studies on the *Rozella* genus (phylum Cryptomycota), considered the most basal clade of fungi (James et al. 2006), and which is made up of zoosporic unicellular parasites and hyperparasites of chytrids and oomycetes (Held 1981). The Chytrdiomycota and Aphelidia represent a huge amount of uncharacterized genetic diversity in aquatic systems, with metagenomics surveys finding that uncultured or unclassified lineages are more common than established and well-described ones (Monchy et al. 2011; Karpov et al. 2013; Lazarus and James 2015). This is in keeping with the concept of microbial dark matter (Rinke et al. 2013), which is used to describe the uncharted branches of the tree of life. When studying the ecology of chytrids and aphelids, we should keep in mind that we do not possess a complete picture of the diversity of these organisms. As such, our understanding of their prevalence in aquatic ecosystems is inevitably limited.

The ecology of chytrid and aphelid parasites of phytoplankton is arguably the most important among parasitized organisms, as phytoplankton are responsible for a large proportion of primary production in aquatic ecosystems, and their response to stimuli dictates entirely whether a particular system perseveres, or collapses. Indeed, it is natural to ask the question: Will zoosporic parasitoids bring about a repeat of the amphibian crisis in another group of organisms? Besides the "ecological disaster" line of inquiry, we know that chytrids and aphelids are ubiquitous, have a global distribution (Figure 16.1), can cause significant and influential changes in food webs, most of which we are probably not yet aware (Gachon et al. 2010). As the environment changes around us due to our reckless and explosive inclination towards growth and consumption, so too do the relationships and dynamics between organisms. Invasive species may move further and further afield into new ecosystems at unprecedented rates, and the delicate balance between parasite and host may be thrown into disarray (Winder et al. 2004). It is for these reasons that our understanding of host-parasite relationships is becoming a crucial driving force in how we recognize ecosystems under the stress of a rapidly changing environment. In this chapter, we report on the current state of knowledge regarding chytrid and aphelid infection of phytoplankton, with emphasis placed on the ecology of these organisms in the context of anthropogenic environmental change, and the significance of parasitism in ecosystem functioning and evolution.

16.2 APHELIDIA

Aphelids are a poorly known group of parasites of algae that have raised considerable interest due to their pivotal phylogenetic position. Together with the Cryptomycota and the Microsporidia, they have been recently reclassified as Opisthosporidia, a sister group to the true fungi (Karpov et al. 2014b). Despite their huge diversity, as revealed by molecular environmental studies, and their interesting phylogenetic position, only three genera have been described (*Aphelidium*, *Amoeboaphelidium*, and *Pseudaphelidium*). Furthermore, validated 18S rRNA gene sequences exist only for *Amoeboaphelidium* species (Karpov et al. 2014b). The complex life cycle of aphelids encompasses several stages such as cyst, trophont, plasmodium, sporangium, and zoospore stage (Figure 16.2). Of these stages, the plasmodium stage, with a large central vacuole containing a residual body, is the most commonly observed phase in cultures as it is the longest lasting one in the life cycle and in this stage the plasmodium occupies all the space inside the host cell wall (Karpov et al. 2014b, Figure 16.2). The level of knowledge of aphelids is far outstripped by that of chytrids; this could be due to the fact that aphelids are not a "cosmopolitan" parasite as chytrids are, however it could be argued that the endobiotic nature of aphelids means they are far less likely to be observed in culture studies, while the sporangia of the epibiotic chytrids are easily identified under a light microscope.

16.2.1 Chlorophytes

Chlorophytes (green algae) are easily the best documented of the aphelid hosts. Aphelids are common parasitoids in many aquatic ecosystems (Karpov et al. 2014b), with species in *Aphelidium* and *Amoeboaphelidium* infecting many species of unicellular eukaryotic algae in the Chlorophyta in freshwater (Fott 1957; Gromov 2000). *Aphelidium* has been documented parasitizing *Coleochaeta* and *Scenedesmus*, while *Amoeboaphelidium* parasitizes *Ankistrodesmus*, *Chlorella*, *Chlorococcum*, *Kirchneriella,* and *Scenedesmus* (Zopf 1885; Fott 1957; Fott 1967; Gromov and Mamkaeva 1969; Gromov 2000).

The host range of some *Amoeboaphelidium* species has been investigated. Gromov and Mamkaeva (1969) measured

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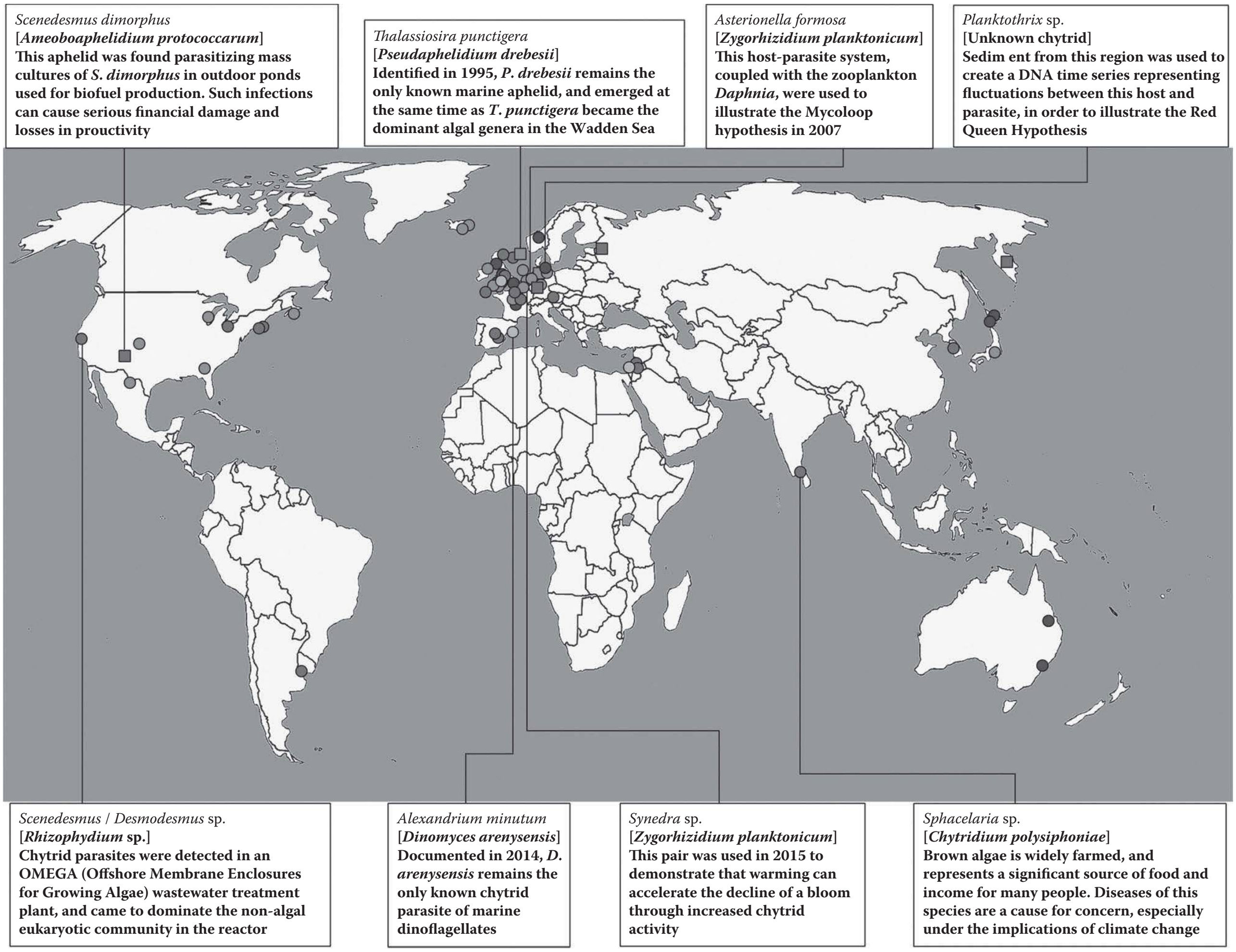

Scenedesmus dimorphus
[*Ameoboaphelidium protococcarum*]
This aphelid was found parasitizing mass cultures of *S. dimorphus* in outdoor ponds used for biofuel production. Such infections can cause serious financial damage and losses in prouctivity

Thalassiosira punctigera
[*Pseudaphelidium drebesii*]
Identified in 1995, *P. drebesii* remains the only known marine aphelid, and emerged at the same time as *T. punctigera* became the dominant algal genera in the Wadden Sea

Asterionella formosa
[*Zygorhizidium planktonicum*]
This host-parasite system, coupled with the zooplankton *Daphnia*, were used to illustrate the Mycoloop hypothesis in 2007

Planktothrix sp.
[Unknown chytrid]
Sedim ent from this region was used to create a DNA time series representing fluctuations between this host and parasite, in order to illustrate the Red Queen Hypothesis

Scenedesmus / Desmodesmus sp.
[*Rhizophydium* sp.]
Chytrid parasites were detected in an OMEGA (Offshore Membrane Enclosures for Growing Algae) wastewater treatment plant, and came to dominate the non-algal eukaryotic community in the reactor

Alexandrium minutum
[*Dinomyces arenysensis*]
Documented in 2014, *D. arenysensis* remains the only known chytrid parasite of marine dinoflagellates

Synedra sp.
[*Zygorhizidium planktonicum*]
This pair was used in 2015 to demonstrate that warming can accelerate the decline of a bloom through increased chytrid activity

Sphacelaria sp.
[*Chytridium polysiphoniae*]
Brown algae is widely farmed, and represents a significant source of food and income for many people. Diseases of this species are a cause for concern, especially under the implications of climate change

Figure 16.1 **(See color insert.)** World map showing the location of field studies that have documented parasitism on phytoplankton by chytrids and aphelids, with significant or novel incidences of infection described. Circles denote chytrid infections, squares denote aphelid infections. Reports were found by using a combination of "algae," "chytrid," and "aphelid" search terms in Web of Science.

the susceptibility of 226 different strains of green and yellow-green algae to infection by four isolates of *Amoeboaphelidium*. Four cultures of *Amoeboaphelidium protococcarum* were specific parasites of cells of the genus *Scenedesmus* and of some other genera of protococcous algae, while others were resistant. It was found that different *Scenedesmus* cultures were sensitive to some or all *Amoeboaphelidium* strains or were fully resistant. There was no apparent specialization of any of the parasite strains to particular *Scenedesmus* species (Gromov and Mamkaeva 1969).

16.2.2 Diatoms

Diatoms are a major group of algae, and are, depending on the region and seasonal parameters, among the most common species in phytoplanktonic and microphytobenthic realms. Diatoms are unicellular microalgae, although they can form colonies in the shape of filaments or ribbons (e.g., *Fragilaria*), fans (e.g., *Meridion*), zigzags (e.g., *Tabellaria*), or stars (e.g., *Asterionella*) (Van den Hoek et al. 1997). A unique feature of diatom cells is that they are enclosed within a cell wall made of silica (hydrated silicon dioxide)—the so-called frustule. These frustules show a wide diversity in for and are the main morphological characteristic for the identification of taxa in the literature (Hasle and Syvertsen 1996).

Only one species of aphelid, *Pseudoaphelidium drebesii* Schweikert and Schnepf, has been reported from marine ecosystems as a parasite of the centric diatom *Thalassiosira punctigera* (Castracane) Hasle (Schweikert and Schnepf 1997). The host-parasite pair were isolated from the Wadden Sea, Germany. Curiously, the discovery of *P. drebesii* only came about due to a shift in phytoplankton community structure that left its host, *T. punctigera*, as the dominant alga in the region (Schweikert and Schnepf 1996).

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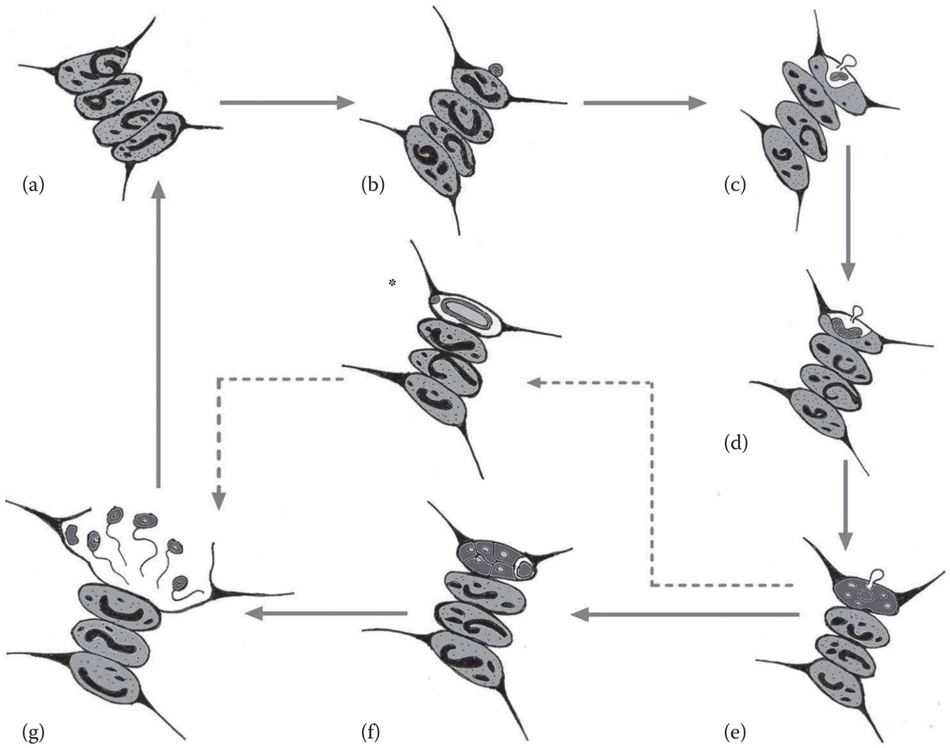

Figure 16.2 **(See color insert.)** The life cycle of Aphelidium, parasitizing the chlorophyte Scenedesmus. Zoospores chemotactically locate healthy host cells (a), and encyst themselves onto the cell surface (b). The parasite then migrates into the host cytoplasm (c) and begins to consume the host via phagotrophy (d). Once the host cytoplasm has been consumed, the parasite amoeba develops a plasmodium with several nuclei (orange) and a vacuole with a residual body (purple) (e). The plasmodium then divides into cells each with a single nucleus (f) and these are then released outside the dead host cell as infective zoospores (g). The asterisk and red dotted line represents the parasite forming a thick-walled resting cyst, which can then transition to the formation of uninuclear cells and release zoospores once environmental conditions are at an optimum.

16.2.3 Cyanobacteria

To date, no instances of cyanobacteria being parasitized by aphelids have been documented.

16.2.4 Dinoflagellates

To date, no instances of dinoflagellates being parasitiszd by aphelids have been documented.

16.2.5 Other

The aphelid *Aphelidium tribonemae* has been reported as a parasite of two species of yellow-green alga (Xanthophyta): *Tribonema gayanum* and *Botridiopsis intercedens* (Karpov et al. 2014b).

16.3 CHYTRIDIOMYCOTA

Chytrids are true fungi and are characterized by cell walls composed of chitin. There is considerable variation in the morphology of chytrids. The most prominent morphological feature of the thallus is the zoosporangium (James et al. 2006). The zoosporangium is a sac-like structure in which internal divisions of the protoplasm result in production of zoospores (Figure 16.3). Eucarpic chytrids are those that consist of a zoosporangium and filamentous rhizoids. In contrast, holocarpic chytrids produce thalli that are entirely converted into zoosporangia during reproduction. Chytrid thalli can be either monocentric, in which an individual produces only a single zoosporangium, or polycentric, in which an individual is composed of multiple zoosporangia produced on a network of rhizoids termed a rhizomycelium. Classically, chytrids were also described on the basis of whether they grow on the surface of (epibiotic) or within the cytoplasm of (endobiotic) their host cell (or substrate). Other characteristics historically used for taxonomy include the presence of a lid-like operculum, which opens upon sporangia maturation and allows the dispersal of zoospores (Sparrow 1960), and the apophysis, a protuberance that helps anchor the developing sporangia to the host (Figure 16.3). The ultrastructure of zoospores has become a key feature in the taxonomy of the Chytridiomycota (Barr 1981; Longcore 1995; Letcher and Powell 2014). Due to several morphological transitions during their life histories of the often intracellular, usually

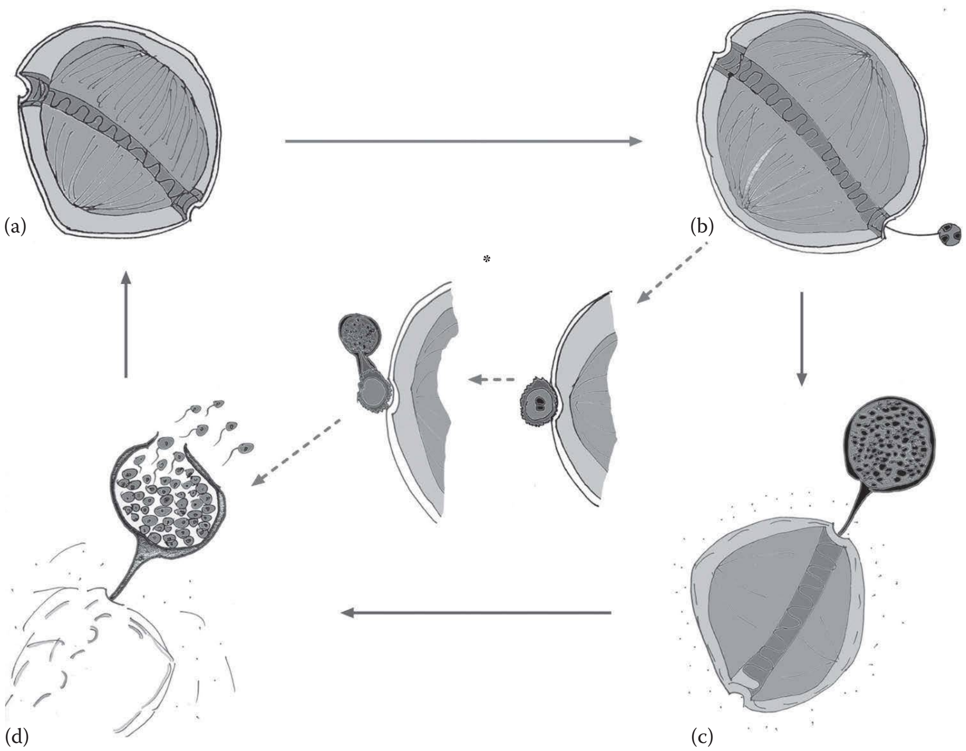

Figure 16.3 **(See color insert.)** Life cycle of *Dinomyces arenysensis* parasitizing the dinoflagellate Alexandrium. Zoospores chemotactically locate healthy host cells (a), encyst onto the host surface, reabsorb their flagellum, and establish a feeding tube which penetrates through the gap in the host thecal plates (b). The parasite feeds on the host, taking up lipids and starch granules, and develops into a sporangium with many dark nuclei. The parasite also develops rhizoids and an apophysis which help anchor the thallus within the host (c). Upon the death of the host cell, the sporangium opens, releasing many new infective zoospores (d). The red dotted arrows follow the sexual life cycle of the chytrid, where two developing sporangia will fuse into a thick-walled diploid resting spore. Once conditions become optimal, the resting spore will germinate a sporangium, which will release zoospores.

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holocarpic stages, microscopic identification of these parasitic species is not straightforward, especially in the mixed cultures often found in environmental samples.

16.3.1 Chlorophytes

The occurrence of chytrid parasites of chlorophytes is quite common, however the relationships between chytrids and chlorophytes have received only a cursory amount of attention. Ecological theories attached to parasitism, such as coevolution and population control, have been applied mostly to cyanobacteria and diatoms (Ibelings et al. 2011; Sonstebo and Rohrlack 2011). This is possibly because chlorophytes produce none of the debilitating toxins produced by other varieties of phytoplankton. Nonetheless, many chytrid parasites have been documented as parasites of chlorophytes. The genus *Rhizophydium* is a large group of species and contains many parasites of chlorophyta (Sparrow 1960). The host range of *Rhizophydium algavorum* is wide, a study examined 137 strains of chlorococcalean algae and found 33 were sensitive, representing 20 species of five genera (Gromov et al. 1999). Whereas the host range for *Paraphysoderma sedebokerensis* (nom. prov. Blastocladiomyota) is highly specific for *Haematococcus pluvialis*, but has a limited capacity to infect other green algae (Gutman et al. 2009). The infection of *Haemetococcus* is highly significant, as the alga is grown commercially for the production of the keto-carotenoid astaxanthin.

16.3.2 Diatoms

Taxonomy and occurrence of freshwater diatom parasites, especially true zoosporic fungi such as chytrids, have been studied since the 1940s (Ingold 1944; Canter 1947; Canter and Lund 1948). In most of these cases, occurrence and biomass of the infecting stages in the natural environment are still underreported and information about impacts on the community compositions and tropic levels are sparse.

Only a few host-chytrid systems are relatively well described, in particular the spring-bloom diatom *Asterionella formosa* Hassall and its two chytrid parasites: *Zygorhizidium planktonicum* Canter and *Rhizophydium planktonicum* Canter (Canter and Lund 1948; Van Donk and Ringelberg 1983). *Asterionella* often is a prominent contributor to the

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diatom spring bloom in lakes worldwide. Its blooms are frequently followed by chytrid epidemics with the prevalence of infection exceeding 90% in many cases (Ibelings et al. 2011).

Although true fungi are abundant in the marine environment, only relatively few species are known to infect plankton organisms (Gleason et al. 2011), and knowledge on the biological interactions and effects of fungal infections in marine plankton is still limited (Scholz et al. 2016a). From the literature, a few examples are known among the Chytridiomycetes, such as *Rhizophydium*, that are able to infect the marine diatoms *Pseudo-nitzschia* and *Chaetoceros* (Elbrächter and Schnepf 1998; Hancic et al. 2009; Wang and Johnson 2009). A recent monitoring survey conducted in the northern Icelandic Húnaflói near Skagaströnd (Scholz 2015; Scholz et al. 2016b), which is still ongoing, showed the presence of chytrids infecting representatives of different diatom taxa such as *Fragilaria*, *Chaetoceros,* and *Rhizosolenia* (Figure 16.3). Although several morphological features of the observed chytrids in this area point to the presence of *Rhizophydium* as described by Sparrow (1960) and Letcher and Powell (2012), the identity of this parasite is still not confirmed by molecular-taxonomical analysis and study of the zoospores by transmission electron microscopy.

In several cases, empty sporangia are found attached on dead phytoplankton cells (Rasconi et al. 2012), which is suggestive of the lethal issue of chytrid infection (Sime-Ngando, 2012). Pathogenic true zoosporic fungi such as chytrids are considered to be osmotrophic and digestion occurs outside the cell by excretion of extracellular enzymes (Gleason and Lilje 2009). These parasitic groups produce zoospores, which are often host specific, highly infective, and extremely virulent (Gleason et al. 2011). When conditions are favorable for growth, the asexual life cycle in many oomycetes and zoosporic fungi is completed relatively rapidly resulting in the release of a large number of zoospores into the water column (sporulation). According to Sparrow (1960), population densities can increase or decrease suddenly with changing environmental conditions. In several cases, pathogen periodicity was primarily related to host cell density (Anderson and May 1979; Ibelings et al. 2011), whereas no single physiochemical factor has been found that fully explains the dynamics of epidemics in the field (Van Donk and Bruning 1992), suggesting other biotic, probably cell-to-cell-specific processes. Holfeld (2000) suggested that the host cell size could be one of the driving forces in chytrid infection by enhancing the encounter rate between zoospores and host cells. This hypothesis is supported as large and/or colonial phytoplankton species are more susceptible to chytrid parasitism (Ibelings et al. 2004; Kagami et al. 2007a; Sime-Ngando 2012). In contrast, other studies showed that smaller or intermediate size classes were more frequently parasitized than larger ones (Koob 1966; Sen 1987).

There is evidence that parasitism inhibits the development of their hosts, and particular attention has been paid to the occurrence of fungi on diatoms, and to the effects of parasitism on their seasonal distributions (Canter and Lund 1948; Van Donk and Ringelberg 1983; Scholz et al. 2016b). For example, in the oligotrophic Lake Pavin (France), the spring development of the diatoms *Asterionella* and *Synedra* was found to be inhibited by the chytrid *Rhizophidium planktonicum*. In productive Lake Aydat (France), another diatom, *Fragilaria*, became abundant but the proliferation of their parasites, *Rhizophidium fragilariae*, interrupted their development (Rasconi et al. 2012).

Field observations showed that the development of *Asterionella* spring-blooms depends on water temperatures in early spring as *Asterionella* already reproduces at temperatures below 3°C, while the parasite is still inactive (Van Donk and Ringelberg 1983). This mismatch in thermal ranges provides the host with a low temperature window of disease-free population growth which bears consequences for the size the diatom spring bloom (Ibelings et al. 2011) and its genetic structure (Gsell et al. 2013a; Gsell et al. 2013b). Warmer winters in which water temperature stays above 3°C remove this window of opportunity since the parasite remains active, denying the host the ability to build up a bloom (Ibelings et al. 2011; Gsell et al. 2013c). These safe zones, driven by environmental conditions, are referred to as refuges in ecological studies.

The response of fungal zoospores to environmental factors might be species-specific (Gsell et al. 2013c; Kagami et al. 2007a). For instance, zoospores of *R. planktonicum* were not able to find and infect their host under very low light conditions (Bruning 1991a; Bruning 1991b), while zoospores of *R. sphaerocarpum* can infect their host even in the darkness (Barr and Hickman 1967). 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 (Kagami et al. 2007b). Recently, susceptibility to fungal infection was found to be highly strain-specific within *Asterionella formosa* host populations (De Bruin et al. 2004) and genetically different *A. formosa* strains differed in their susceptibility to parasite attack (Gsell et al. 2012).

Chytrid infections in marine diatoms were recently observed in *Pseudo-nitzschia pungens* (Grunow ex Cleve) Hasle from the ocean near Prince Edward Island, Canada (Hanic et al. 2009), and in several other species of diatoms during monitoring of intertidal surface sediments in the Wadden Sea area (Solthörn tidal flat, southern North Sea, Germany) and in north-west Icelandic coastal habitats, using ultrasound and gradient centrifugation for separation of diatom cells from the sediment matrix in combination with Calcofluor White staining of zoosporangia (Scholz et al. 2014; Scholz et al. 2016b). Although the identities of the species of these chytrids were not further determined, sporangium morphology indicated the presence of five different morphotypes, infecting mainly epipelic taxa of the orders Naviculales (e.g., *Navicula digitoradiata* [Gregory] Ralfs) and Achnanthales (e.g., *Achnanthes brevipes* Agardh) in the temperate Solthörn tidal flat (Scholz et al. 2014).

Similarly, the morphology of zoosporangia was also used to distinguish chytrids in sediment samples from the north-west Icelandic coast. Here, the diatom taxa infected by epibiotic parasites comprised representatives of the Bacillariales (*Cylindrotheca closterium* Ehrenberg, *Ceratoneis closterium* Ehrenberg), Fragilariales (*Fragilaria striatula* Lyngbye), and Naviculales (*Diploneis bombus* Ehrenberg) and other species. Figure 16.4 shows some examples of the infections found in north-west Iceland (Húna Bay and Isafjördur).

16.3.3 Dinoflagellates

Parasites of dinoflagellates may have a more important role than grazers in controlling dinoflagellate numbers (Montagnes et al. 2008). Much of the research has focused

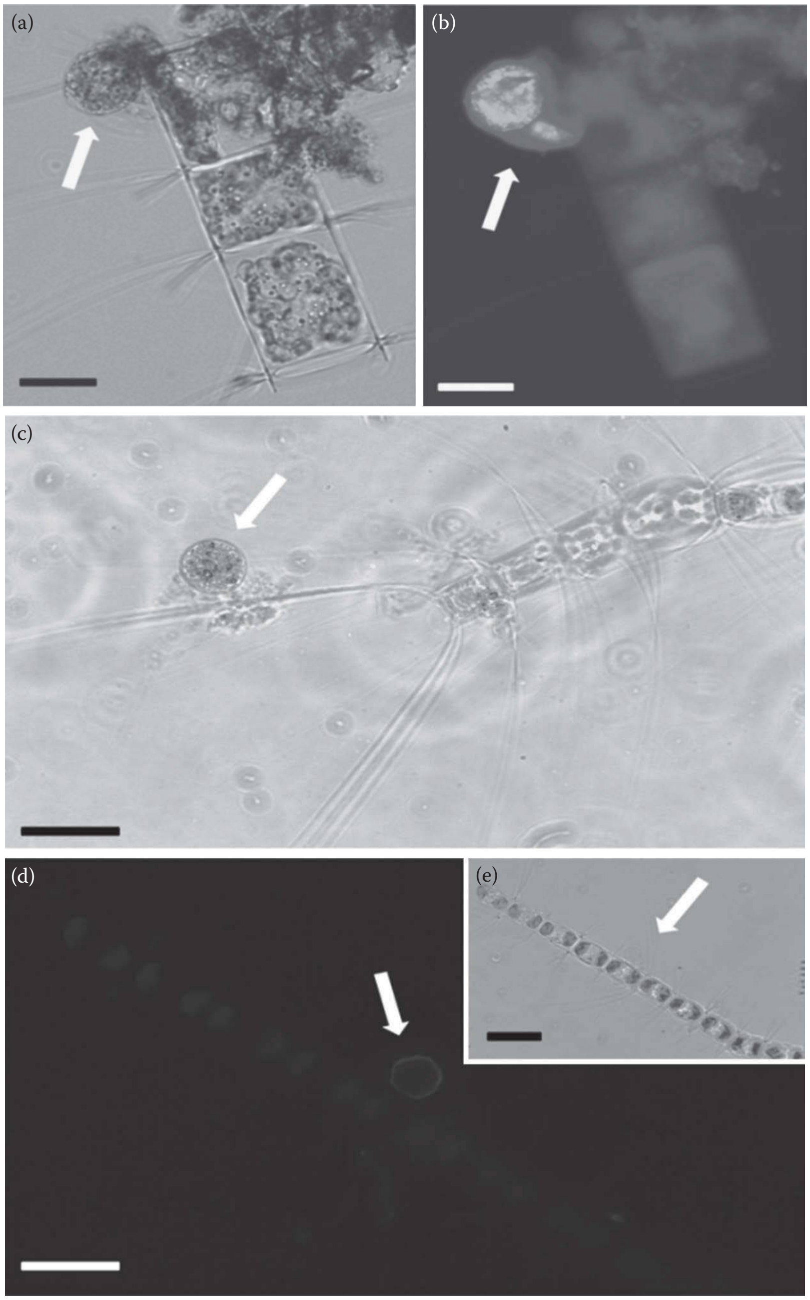

Figure 16.4 **(See color insert.)** Examples of chytrids infecting *Chaetoceros* sp. (a–e) observed in phytoplankton samples collected from the Húnaflói near Skagaströnd (northern Iceland) in 2015 and culture material. Pathogens were visualized using Calcofluor White stain in combination with transmission light and fluorescence excitation (UV-light, 330–380 nm) as described in Scholz et al. (2014). Bar: 100 µm.

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on the parasites from the heterotrophic dinoflagellate classes Perkinsea and Syndinea (Figueroa et al. 2008; Jephcott et al. 2016a). In contrast, *Dinomyces arenysensis* is the only parasitic chytrid species of marine dinoflagellates identified. It was found to be infecting *Alexandrium minutum* (Lepelletier et al. 2014; Jephcott et al. 2016a). Further experiments identified that while *D. arenysensis* infect most strains of *Alexandrium* sp. they showed a mix of sensitivities to infection. Except for *Scrippsiella trochoidea,* most of the other dinoflagellate species tested were either not infected or were resistant to the infection. This demonstrates that *D. arenysensis* has a broad host range unlike chytrid parasites found in freshwater environments (Lepelletier et al. 2014). While more chytrid parasites of dinoflagellates have been identified in freshwater environments, the data remains sparse.

Early work identified *Ceratium hirundinella* infected by *Amphicypelluselegans* (Ingold 1944). More recently, the bloom forming dinoflagellate *Peridinium gatunense* occurred annually in Lake Kinneret, Israel until the mid-1990s. Hereafter, the occurrence of blooms decreased. Zohary (2004) and Alster and Zohary (2007) reported that *P. gatunense* was infected by the chytrid identified as *Phlyctochytrium* sp. Detailed field work clearly showed the dynamics between host and parasite reported in other studies (Ibelings et al. 2004) where a phytoplankton bloom is closely followed by a significant increase in parasite infection. Interestingly, in this case, it is unlikely that the chytrid killed its host and it is possible that the parasite was behaving opportunistically and parasitizing weak or dead cells as a result of other stressors such as unfavorable growth conditions (Ibelings et al. 2004) or another infection (Alster and Zohary 2007). Importantly, the absence of *Peridinium gatunense* resulted in other phytoplankton species (cyanobacteria in particular) to bloom.

16.3.4 Cyanobacteria

Cyanobacteria are, unlike their eukaryotic phytoplankton counterparts, prokaryotes, and are usually considered the dominant phytoplankton variety in freshwater systems alongside the chlorophytes. This dominance is widely considered as increasing due to the warming and stratifying influence of climate change (Wagner and Adrian 2009; but see Anneville et al. 2015). They come in a wide array of shapes and sizes, being found in unicellular (*Microcystis*), filamentous (*Nodularia*), and colonial (*Nostoc*) forms. Chytrids as parasites of cyanobacteria are well documented (Gleason et al. 2015; Figure 16.5), however in contrast with diatoms, studies of chytrid parasitism of cyanobacteria have been conducted quite recently, most within a decade. Only one chytrid-cyanobacteria relationship has been especially well described, which is *Planktothrix* and *Zygorhizidium* (Rohrlack et al. 2013; Kyle et al. 2015). Further identified examples include *Anabaena macrospora* infected by *Rhizosiphon* sp. in France (Gerphagnon et al. 2013). Other studies, while able to identify the host, fail to identify the chytrid (Müller and Sengbusch 1983; Sigee et al. 2007; Takano et al. 2008).

Field studies of chytrids reveal highly pathogenic but specific parasites. Two chytrids, *Rhizosiphon crassum* and *R. akinetum*, infecting blooms of *A. macrospora* in Lake Pavin, France, reveal the presence of highly specific infection strategies across parasitic varieties. While the rhizoids of *R. crassum* crossed through both vegetative and akinete cells with no apparent preference, *R. akinetum*¸ true to its name, infected only akinete cells (Gerphagnon et al. 2013).

Studying the relationship between the chytrid *Rhizophidium megarrhizum* and the filamentous microcystin-producing *Planktothrix* has yielded significant ecological insight. Rohrlack et al. (2013) has used the host-parasite relationship to provide arguably the most concrete hypothesis of the purposes behind phycotoxin synthesis in phytoplankton, namely that phycotoxins could be part of a defense mechanism against parasitism. Strains of *Planktothrix* grown with knockout mutations for microcystin, anabaenopeptin, and microviridian production were significantly more susceptible to infection by four chytrid strains, when compared to their infectivity to the wild type with full oligopeptide synthesis capabilities. Furthermore, a historical relationship between chytrid parasites and *Planktothrix* was examined through the processing and analysis of sediment cores from Lake Kolbotnvannet in southeastern Norway. Chytrid and *Planktothrix* DNA from the cores was amplified and used to reveal changes in prevalence of known chemotypes of DNA typically found in Norway. Rather than showing a clear winner in the Red Queen arms race, as predicted by De Bruin et al. (2008), the results suggested that the relationship between the host and parasite was actually characterized by a stable coexistance.

16.3.5 Other

Raghukumar reported the infection of the marine brown alga *Sphacelaria* by the chytrid *Chytridium polysiphoniae.* Karpov et al. (2014a) established a new species of chytrid, *Gromochytrium mamkaeva*, that was found infecting the freshwater yellow-green alga *Tribonema gayanum.*

16.4 ECOLOGY

16.4.1 The Balance of Parasites

A characteristic of zoosporic parasitoids acting in natural aquatic environments is their tendency to “mimic” the rise and fall of biomass in phytoplankton as optimal bloom conditions occur and then subside. As more host material is available, chytrids and aphelids will reproduce and infect cells at a higher rate. The combined pressures of grazing,

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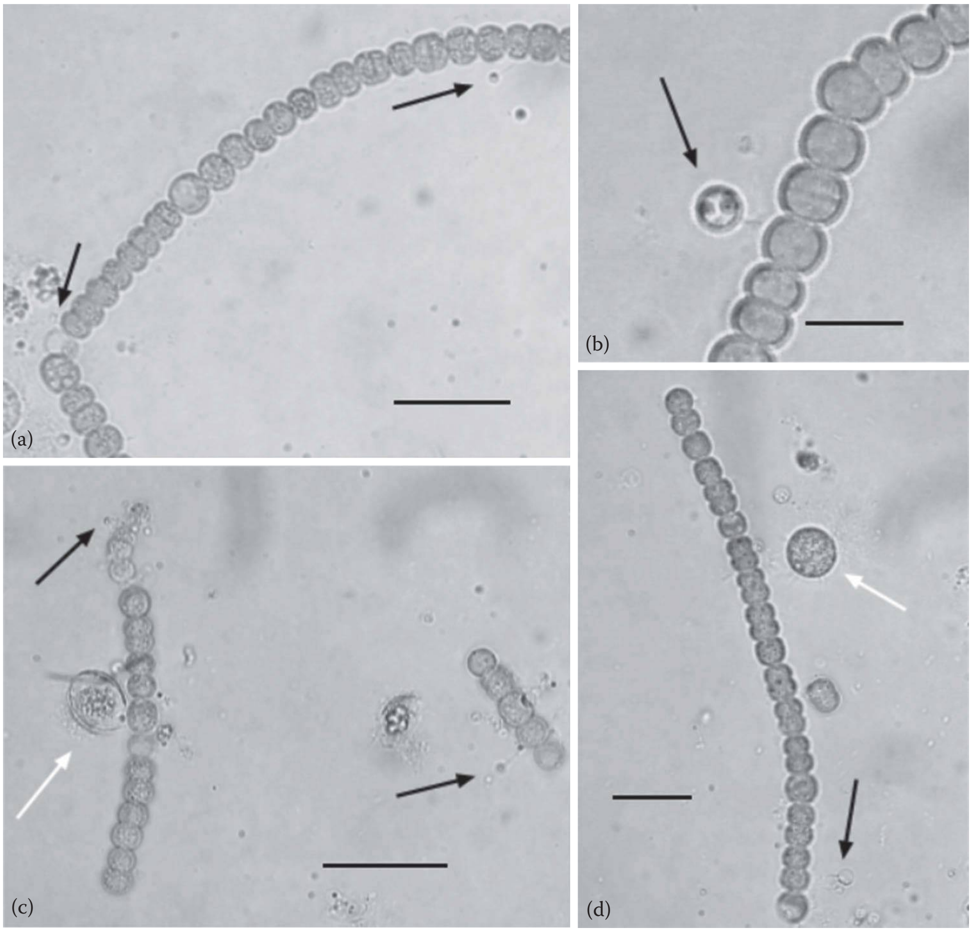

Figure 16.5 **(See color insert.)** Chytrids infecting *Anabaena* in Centennial Park, Sydney, Australia (a–d). White arrows identify sporangia, and black arrows identify zoospores. All scale bars: 50 µm. (Courtesy of DJ Macarthur.)

parasitism, and perhaps a change in optimal conditions, will result in the dissipation of phytoplankton blooms, and the resulting dearth of host material will result in a decline in chytrid and aphelid populations (Chambouvet et al. 2008). Both host and parasite, however, have the capability to form thick-walled resting cysts (Doggett and Porter 1996), which will typically reside in sediment until conditions return to optimal, and the blooming of phytoplankton is again followed by the zoosporic feeding frenzy. We term this dynamic the "balance of parasites," and assert that, as a result of evolutionary forces driving parasites who cannot maintain pace with their hosts to extinction, it is ubiquitous within ecosystems on earth. This hypothesis is supported by the assertion that roughly 50% of the biodiversity on earth is composed of parasites (Toft 1986; Hechinger 2015; Jephcott et al. 2016b), in that food webs can be seen as networks of interacting species, with each of these species balanced by parasitic elements. This concept can be applied further to coevolutionary dynamics, in that the selection of host genotypes that can resist parasitic infection are shadowed by the selection of parasite genotypes that can continue to infect.

16.4.2 The Red Queen and the Cheshire Cat

The Red Queen hypothesis is not a new one, being over forty years old (Van Valen 1973), however, today the ecological and biological significance attached to the theory is arguably at its peak, mostly due to the increasing awareness of the prevalence of parasitic activity in ecosystems. We now know that this activity can drive not only diversification in host populations (Singh et al. 2015), but also diversification in parasite populations (Schulte et al. 2013), and even mating behavior (Soper et al. 2014). The theory is not unanimously espoused: Gokhale et al. (2013) found that a mathematical representation of Red Queen dynamics which takes into account classic Lotka-Volterra dynamics tends to rapidly collapse rather than persist, which suggests that the dynamic is, rather than prolific in ecosystems, extremely rare. Similarly, Vermeij and Roopnarine (2013) found that

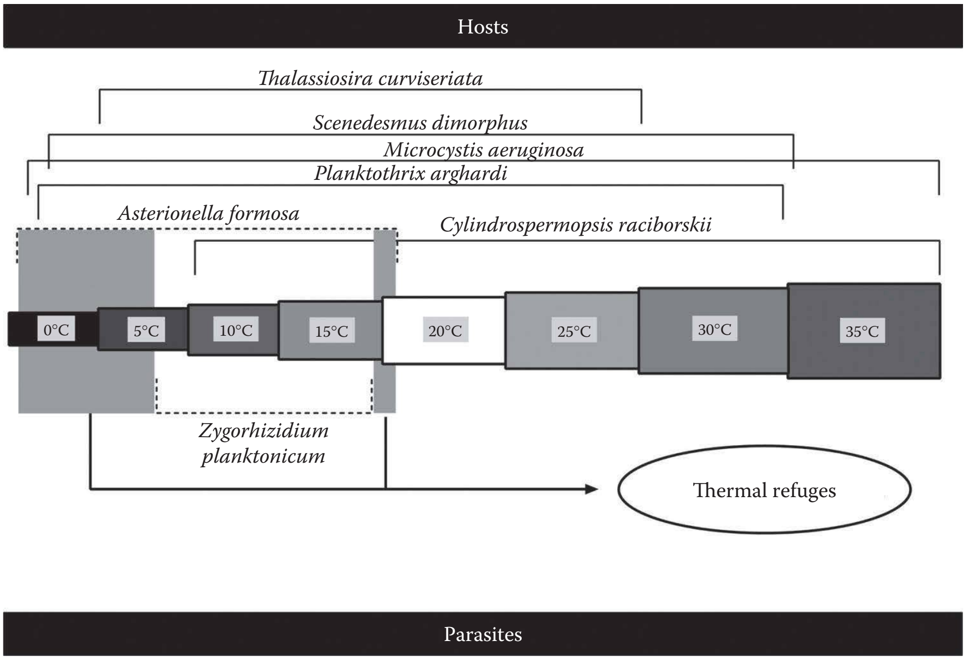

Figure 16.6 **(See color insert.)** Temperature ranges of some phytoplankton and one chytrid parasite. Typically, phytoplankton have a very wide temperature tolerance range. The narrower range of the chytrid *Zygorhizidium planktonicum* presents its host *Asterionella formosa* with thermal refuges, displayed as green areas. These indicate thermal zones where it may grow free of infection.

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several assumptions made by the Red Queen hypothesis, such as continuous evolutionary adaptation, were false, and that correcting these assumptions resulted in a dynamic that only took hold under rare and unusual ecological situations. Despite these criticisms, the Red Queen has many more allies than critics, and recent experimental evidence supports her place as a powerful and prevalent driving force in ecological networks.

The extent to which the Red Queen Hypothesis has been examined in phytoplankton parasite systems is extremely limited. De Bruin et al. (2008) exposed both uniclonal and multiclonal cultures of *Asterionella formosa* to its parasite *Zygorhizidium planktonicum* and measured changes in parasite fitness over 200 generations, and showed that fitness increased dramatically in new uniclonal cultures, but struggled to increase in new multiclonal cultures. This suggests that host populations of low genetic diversity are significantly more susceptible to parasitic activity than populations that are highly diverse. In contrast, Kyle et al. (2015) found that, in a lake system where only two chemotypes of *Planktothrix* were present and one significantly dominated over the other, the long-term host-parasite relationship between the dominant *Planktothrix* and its chytrid parasite showed a stable coexistence over many years, more than enough time for the chytrid to, theoretically, overwhelm its host and win the Red Queen arms race (Kyle et al. 2015). The fact that this has not occurred could be for several reasons, such as the presence of undetected hyperparasites that prevent the parasite fitness from increasing unchecked, or grazing activity of zooplankton that consume large amounts of zoospores and reduce the potential for infection, however we think it most likely that the seasonal dynamic of Lake Kolbotnvannet provides a thermal refuge for *Planktothrix*, which has a much wider temperature tolerance range than *Z. planktonicum*, its parasite (Figure 16.6). Further study is needed to properly address these theories.

The release of hosts from the Arms Race grip of Red Queen dynamics can possibly be induced through so-called Cheshire Cat dynamics. These processes involve a haplo-diploidy life cycle, where the diploid phase of the life cycle is vulnerable to infection, but the haploid phase is resistant. Transition from diploid to haploid phases induced by infection provides an escape mechanism for organisms under pressure from infective agents, and also ensures the selection of dominant genotypes without the risk of costly and slow sexual fusion (Frada et al. 2008). There is extremely limited data on these dynamics, and while they are a promising avenue of research, whether they play any role in relationships between zoosporic parasites and phytoplankton remains unknown.

16.4.3 Environmental Regulation

It is well known that the response of one organism to a change in environmental conditions can wildly differ from the response of another. A key factor in host-parasite

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relationships is that the host in almost all cases possesses more biomass than the parasite. This means that, in climate change scenarios where temperatures increase, the metabolic rates of parasites can be expected to increase by a greater margin than their hosts, as goes with a larger surface-to-volume ratio. As such numerous studies predict a greater incidence of disease will result from warming trends (Hoegh-Guldberg and Bruno 2010). This simple approximation, however, has not held true with regards to chytridiomycosis of amphibians, with studies illustrating a "climate-chytrid" paradox, where increases in temperature reduces infection rates and host mortality (Pounds et al. 2006; Heard et al. 2014). Similarly, when applied to zoosporic parasites of phytoplankton, there are conflicting accounts of the true effect of temperature on parasitism and community structure. Ibelings et al. (2011) examined data spread over a period of more than 30 years (1978–1982, 1984–1988, and 2007–2010), and found that, counter intuitively, warming did reduce the availability of a cold refuge for the host, but nonetheless impeded chytrid dominance due to the decreased availability of host material for infection. This was because, when denied the cold period to grow uninfected, the host suffered infections earlier in the year and failed to reach population levels that it would in colder years.

To counter the advantage of smaller organisms, which exhibit stronger responses to stimuli than larger organisms, larger hosts with a smaller surface-to-volume ratio will often have a wider tolerance to various stressors (Figure 16.6). This has been shown to be the case with *Zygorhizidium planktonicum*, which has a narrower range of thermal tolerance than its diatom host, *Asterionella formosa* (Gsell et al. 2013a; Figure 16.6). Despite this, it must be acknowledged that in this study, the temperatures tested covered a very wide range (1°C–21°C) and, while indicative of a possible "thermal refuge" for phytoplankton parasitized by zoosporic parasites, do not represent a realistic natural scenario. The effects of climate change will likely reduce the effectiveness of cold refuges, and hosts must, before reaching the safety of a warm refuge, persist through heightened parasitic activity. In lake-based mesocosm systems, increases of temperature resulted in both an increase in prevalence of infection and a faster decline rate of blooming *Synedra* diatoms (Frenken et al. 2016), suggesting that before the host reaches its thermal refuge, it must survive an increasingly active parasitic population. It must be kept in mind, however, that the mesocosms were also inhabited by zooplankton, and that the relative contributions of grazing and parasitism to bloom termination are unknown. Further research is needed here; on the one hand, Ibelings et al. (2011) shows support for the chytrid climate paradox, but relies on a data set that possesses large temporal gaps. On the other hand, Frenken et al. (2016) shows that rising temperature in chytrid-phytoplankton-zooplankton communities promotes bloom termination, but utilizes closed mesocosm systems. Rises in temperature may sway dominance towards pathogens, however many other factors act in cohesion that drive ecological succession. For example, a recent study has shown that salt loads can potentially provide amphibians with salt refuges, where chytrid infection potential is lowered when hosts are exposed to higher salinities (Stockwell et al. 2015). Invasion and introduction of foreign species has also been put forward as a significant factor (Rohr et al. 2008), as well as physical process that can provide additional refuges (De Wever et al. 2009; Llaveria et al. 2010). More work is needed to tease apart these complexities in order to determine the true driving effects of ecological shifts.

16.4.4 Food Webs

The Mycoloop is a relatively new concept (Kagami et al. 2007a), and is used to represent the consumption of chytrid zoospores by zooplankton during algal blooms that are infected with zoosporic parasites. This dynamic is highly significant, and is one of the two energy "shunts" in aquatic microbial systems (the other being the viral shunt) that can facilitate the transfer of energy up the food chain. This becomes especially important when primary producers are inedible to grazers, as grazers can instead consume zoospores and thus persist in food webs. Because the intracellular C:N ratio of phytoplankton is extremely variable, atmospheric carbon deposition is increasing, and phytoplankton nutrient use efficiency increases at higher temperatures, there is a significant risk of the food quality of phytoplankton to zooplankton decreasing over time given current climatic trends (De Senerpont Domis et al. 2014). One possible alleviation of this stress is for zooplankton to increasae their intake of chytrid zoospores, as zoospores are quite nutritious food, being rich in polyunsaturated fatty acids and cholesterol (Grami et al. 2011). Thus, although the presence of chytrids in aquatic food webs may be seen as a potential ecological threat, especially given the current amphibian crisis, the involvement of a wide variety of organisms makes this topic much more complex.

One step further from the Mycoloop described above is the incorporation of zoosporic parasites of phytoplankton into whole food web analyses, in order to quantify their impact on energy and elemental cycling in ecological networks. The incorporation of parasites into food webs has been a contentious issue over the years (Jephcott et al. 2016b), both because of the large numbers of parasites hypothesized to exist but remain unclassified, and also because of the incredible variation and complexity that make up a parasitic life style. Despite this, the importance of fungal parasites in aquatic food webs has been recognized, and is a driver of research attempting to elicit their ecological roles (Lepère et al. 2008; Jobard et al. 2010). Only one study to date has examined the quantitative effects of chytrid activity on food webs. Grami et al. (2011) undertook extensive sampling of Lake Pavin in France and quantified bacteria, heterotrophic nanoflagellates, nanoplankton and microphytoplankton, ciliates,

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metazooplankton, and chytrids. Field data were then used to construct a pelagic food web model, which was characterized by 53 carbon flows, and compartments representing each of the sampled groups. The study found that the inclusion of chytrids in the food web had a significant effect on the carbon flows of the network, with 21% of microphytoplankton production being utilized in sporangia development, and zoospores representing 38% of the diet of grazers. Furthermore, the flow of carbon through the system increased, carbon transfer to higher trophic levels was improved, and losses of phytoplankton through sedimentation were reduced, decreasing the production of detritus. The addition of chytrids also affected system properties, causing increases in trophic links and longer path lengths, which suggests an overall stabling influence (Grami et al. 2011). Further studies assessing the effects of chytrids in different systems will be valuable, both to our understanding of primary production and elemental transfer in systems, and to our knowledge of the effects of parasitic activity on trophic networks.

16.5 FUTURE PERSPECTIVES

16.5.1 Hyperparasites

Parasites of parasites, hyperparasites, have received scant attention in regards to the ecology of zoosporic parasites of phytoplankton. The genus *Rozella* is made up of fungal zoosporic parasites that exclusively parasitize parasitic chytrids and oomycetes. For example, *R. polyphagi* parasitizes the chytrid *Polyphagus euglenae*, which is itself a parasite of the photosynthetic protist *Euglena viridis* and *E. gracilis* (Powell 1984). Further studies on the *Rozella* genus beyond this point have focused exclusively on the prestigious status of the rozellid clade as the first discernable fungal lineage in molecular phylogenetic trees (Corsaro et al. 2014), until Gleason et al. (2014) hypothesized about several ecological principles regarding hyperparasite activity in phytoplankton-parasite systems. Currently, there is no further information regarding the role of these organisms in host and parasite dynamics; we believe this is one of many areas that need exploration in ecological parasitology.

16.5.2 Commercial Applications

Many commercial applications of algae are at risk of infection by chytrids and aphelids (Carney and Lane 2014). The mass culturing of algae is a rapidly expanding global industry with many applications, including aquacultural food production, wastewater treatment, production of nutritional supplements, and production of sustainable biofuels (Carney et al. 2015). A critical process of commercial algae production is strain selection, where strains are continually assessed and tested, and a single strain that exhibits the desired qualities is selected for growth to maximize productivity. However, this comes at a high price: the resulting mass cultures have an extremely low genetic diversity, and hence stand little chance against parasitic infection. Prevention is the first line of defense in these situations, however in outdoor ponds this is prohibitively difficult. Further possible strategies are the growth of multiclonal cultures to increase disease tolerance, or the utilization of compounds that exhibit desirable properties, such as fungicides. Recently, it has been shown that cyanobacteria produce a class of glycolipopeptides named hassallidins, which possess antifungal properties (Vestola et al. 2014). The isolation and mass production of these compounds, or even the growth of hassallidin producing species in cultures of commercial algae, could serve as a possible defense against potential chytrid and aphelid aggressors.

16.5.3 Communication Barriers

It is an unfortunate result of the merging of several areas of ecological research that the ecology of zoosporic parasites of phytoplankton is rather opaque to a general and indeed general scientific audience. Chytrids are parasites, and the action of parasites in food webs is a topic full of ambiguity (Jephcott et al. 2016b). Combine that with contrasting terminology from the fields of mycology, botany, disease ecology, and parasitology, and a relationship that should be regarded as the aquatic version of an aphid on a rose bush is instead barely recognized outside a specialist community. To compound this issue, there are a very wide variety of fungus-like parasites of phytoplankton, including Oomycetes, Perkinsozoa, and even parasitic Dinoflagellates (Scholz et al. 2016a; Jephcott et al. 2016a), and observed infections in phytoplankton may easily be mistakenly identified. For example, several papers in the literature report on infections of the commercially grown red alga *Porphyra* by the “chytrid” *Olpidiopsis* sp., however *Olpidiopsis* is not a chytrid, but an Oomycete, which are fungus-like protists more closely related to other alga (Arasaki et al. 1960; Ding and Ma 2005). The field is also rapidly evolving, with new species and groups being regularly described and their taxonomy sorted (Karpov et al. 2014a). However, as more work is being undertaken to further refine our knowledge of these organisms, the above issues will hopefully be resolved.

16.6 CONCLUDING REMARKS

Studying the ecology of chytrid and aphelid parasites of phytoplankton provides an opportunity to glimpse the underlying processes that shape primary production in aquatic ecosystems, and also provides ideal models of microbial evolution that lend evidential support to theoretical ecology (Table 16.1). In our world characterized by a severely declining biodiversity and increasingly rapid environmental

Table 16.1 A Selection of Chytrid and Aphelid-Associated Dynamics, Their Descriptions, and Whether They Have Been Observed or Not: Much Significance Attached to the Actions of Zoosporic Parasites of Phytoplankton Is Based on Very Little Data or Is Completely Hypothesized

Dynamic	Description	Observed or Hypothesized?
Energy shunting	Zoospores provide an alternate food source for zooplankton when phytoplankton are inedible	Observed
Community structuring	The pressure exerted on phytoplankton by chytrids and aphelids determines community structures in natural assemblages, and thus shapes the structure of food webs	Semiobserved[a]
Toxin defense mechanisms	In response to parasitic pressure, phytoplankton synthesize potent toxins that inhibit infection by chytrid and aphelids	Semiobserved[a]
Response to warming	Increasing temperatures will cause an unequal response from aquatic microbial communities, which will favour chytrids over phytoplankton	Semiobserved[a]
Coevolution	Parasitic activity acts as a selection force, suppressing strains of a host that are less able to resist infection, allowing strains that are resistant to proliferate	Semiobserved[a]
Bloom control	Chytrids and aphelids can control and suppress potentially harmful blooms of phytoplankton	Semiobserved[a]
Viral transfer	Through infection, chytrids and aphelids act as vehicles for viruses that can infect phytoplankton	Hypothesized
Biological dark matter	The early divergence of chytrids and aphelids provide supporting evidence for the large proportion of microbial dark matter that characterises the tree of life	Hypothesized
System collapse	Given the right variety of chytrids and aphelids, the entire population responsible for primary production in a system may be infected, resulting in the collapse of the system	Hypothesized
Horizontal gene transfer	Chytrids and aphelids may transfer genes to phytoplankton during infection	Hypothesized
Human infection	Over time chytrids have adapted to infect a broad range of organisms. This may, given time and the right circumstances, eventually include humans	Hypothesized

[a] Supported by very little evidence, or conflicting accounts.

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change, knowledge of these processes is becoming more and more valuable, as we strive to understand how our race is altering the ecological networks upon which our continued growth depends. To date, filling in the gaps in our knowledge of these networks is still a monumental task, however, as evidence mounts in support of a stronger ecological mindset, it is a task that is thankfully receiving more attention.

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