Aquatic Sciences (2026) 88:57
https://doi.org/10.1007/s00027-026-01287-2

Aquatic Sciences

REVIEW

# Drivers of aquatic zoosporic parasites in natural and artificial environments

Maya Stoyneva-Gärtner[1] · Hans-Peter Grossart[2,25] · Thijs Frenken[3] · Dirk S. Schmeller[4] · Laura Garzoli[5] · Serena Rasconi[6] · Elżbieta Wilk-Woźniak[7] · Albert Reñé[8] · Slawek Cerbin[9] · Cécile Lepère[10] · Caio César Pires de Paula[11,26] · Adeline Loyau[4] · Aleksandra Kudeń[9] · Ana Gavrilović[12] · Christian Lønborg[13] · Edward Walusiak[7] · Ifigenia Kagalou[14] · Ivana Trbojevic[15] · Jurica Jug-Dujaković[16] · Kristian Ivanov[1] · Lisa Morales[17] · Mahmut Sinan Erez[18] · Maija Balode[19] · Maja Berden Zrimec[20] · Martyna Budziak[7] · Miloš Stupar[15] · Miroslav Androv[1] · Petr Znachor[21] · Pietro Marchese[5] · Selene Chinaglia[5] · Slobodan Zlatković[22] · Télesphore Sime-Ngando[23] · Qëndrim Ramshaj[24] · Wojciech Krztoń[7] · Blagoy Uzunov[1]

Received: 12 November 2025 / Accepted: 1 March 2026

**Abstract**
This review, based on more than 500 scientific studies published between 1880 and 2025, summarises current knowledge on the complex relationships between aquatic zoosporic parasites (AZP) and their hosts, the physical and chemical properties of the environment and the many surrounding organisms, to outline the key drivers of AZP diversity, abundance and infection success. It emphasises the urgent need to focus research on the influence of global climate and undesirable anthropogenically driven changes, such as eutrophication, pollution and biological invasions. Knowledge gaps are identified, along with research needs to decipher the diverse responses of AZP to ongoing changes in abiotic and biotic drivers. We believe that the summarised data and highlighted open research questions will benefit future research and help to better conserve natural biodiversity and manage artificial aquatic systems.

**Keywords** Abiotic drivers · Aquacultures · Biotic drivers · Climate change · Global warming · Host-parasite systems

## Introduction

Parasitism and parasites are widely recognised as important drivers in the ecology and evolution of species, communities and ecosystems (Poulin 2007). They play an important role in maintaining the health of ecosystems through various ecological processes, including host population dynamics, energy flow and biodiversity (Hudson et al. 2006; Lafferty 2006; Miki et al. 2011). For centuries, the focus has traditionally been on terrestrial parasites that infest humans, animals or crops (e.g. Elsheikha and Khan 2011; Parwan et al. 2023), while far fewer studies have addressed their aquatic counterparts. In recent decades, however, parasites from different aquatic environments that have host-attached vegetative stages, but can reproduce asexually and infect the hosts through free-living flagellate spores (zoospores), and are therefore summarised under the term aquatic zoosporic parasites (AZP), have gained increasing attention in the scientific community. AZP have been described from various marine and inland waters and numerous aquaculture systems (e.g. Kühn et al. 1996; Reñé et al. 2021b; Masigol et al. 2023; Seto et al. 2023; Van den Wyngaert et al. 2025). They play an important ecological role in nature by regulating host density, genetic diversity and evolution, but they can also have a negative impact on aquaculture, leading to severe production losses and increased operating costs (e.g. Lafferty et al. 2008; Rasconi et al. 2012, 2014, 2022; Gsell et al. 2013b; Carney and Lane 2014; Kagami et al. 2014; Grossart and Rojas-Jimenez 2016; Schmeller et al. 2018; Asatryan et al. 2019; Tao et al. 2020; Gavrilović et al. 2022). Some AZP significantly affect total global biodiversity as invasive species, some of which are considered among the most destructive and highly infectious pathogens, putting at risk global populations of a wide range of hosts. Such highly impactful AZP include the amphibian pathogen *Batrachochytrium dendrobatidis* and the crayfish plague *Aphanomyces astaci* (e.g. Sewell et al. 2021; Basso et al. 2026). Although their taxonomy is currently undergoing a

---

Extended author information available on the last page of the article comprehensive revision, recent studies suggest that AZP species belong to phylogenetic lineages of seven phylum-level clades of early diverging fungi, i.e. Blastocladiomycota, Chytridiomycota, Aphelidiomycota, Rozellomycota and three unknown phylum-level clades, but also Oomycota, Labyrinthulomycota and Phytomyxea, as well as protists from Alveolata (Perkinsea). (Scholz et al. 2016; Van den Wyngaert et al. 2025). The hosts of AZP also come from different phylogenetic groups – from autotrophic algae and plants to heterotrophic organisms such as invertebrates, fish and amphibians. In addition, the hosts belong to different ecological groups and occupy different ecological niches, from plankton to benthos, and their spatial and temporal occurrence varies greatly, making the study of AZP even more complex.

Although the life cycles of host–parasite systems are closely linked, each participant can respond differently to changes in environmental variables (Gehman et al. 2018). The occurrence, maintenance and effectiveness of AZP infections are determined by a variety of ecological factors operating in aquatic ecosystems. Today, the health of these ecosystems is increasingly threatened by anthropogenic stressors, with climate change playing an increasingly important role: nowadays the Earth's average surface temperature has increased by 1.3–1.4 °C above the pre-industrial level (1850–1900) (Rodhe 2025), with changes in precipitation and a measured average sea level rise of 21–24 cm since 1880 (Lindsey 2022). Moreover, it has been shown that since 1970, global warming has been increasing at a roughly linear pace (Rohde 2025) and it is predicted that, depending on the level of greenhouse gas emissions (lowest possible or very high), at a warming of 1.5 °C, the global mean sea level would rise at least 0.3 m, or as much as 2 m above 2000 levels by 2100 (Lindsey 2022). In addition to this incremental warming with a gradual increase in temperature, climate change also manifests itself through episodic climate events such as heatwaves, which are increasing in frequency and severity (Claar and Wood 2020). It is widely believed that the rapid change in mean surface temperatures, with a projected increase of 1.4–5.8 °C over the next 75 years and increasing heat waves (Nelson 2005), is not only changing weather patterns but also disrupting the usual balance in nature. All gradual and pulse-like changes are altering aquatic habitats at an unprecedented rate and inevitably affecting their inhabitants in diverse and complex ways. There is growing concern about the role of climate change in influencing the life cycles and transmission patterns of AZP and their interactions with hosts. However, the specific relationship between climate change and AZP remains poorly understood. This knowledge gap emphasises the need for targeted research into how environmental changes affect their reproduction and spread, and what this means for the future health of aquatic ecosystems. In this review, we summarise the current state of expertise, the gaps in knowledge and highlight further research topics on the key drivers of AZP biodiversity, abundance and distribution. Taking into account the specific physical and chemical characteristics of their most important habitat, we first summarise the most important abiotic factors and then turn to the diverse, nonlinear biological interactions that influence AZP (Fig. 1). This does not mean that we give less importance to biological driving forces. In addition to discussing AZP drivers with a focus on the effects of current and future environmental change, we pay particular attention to other undesirable but strongly anthropogenically enhanced events such as eutrophication and biological invasions (e.g. Wells and Flynn 2022). By understanding all these drivers, we can better predict the future risks of aquatic diseases and implement strategies to manage their impact on biodiversity and ecosystem health under changing climate and increased anthropogenic pressure.

## Materials and methods

All information was compiled and reviewed using scientific databases such as Web of Science, Scopus, PubMed, Google Scholar, Research Gate and Academia. A large number of keywords were used, comprising the Latin and common names of the AZP and their hosts, combined with all terms relevant to the factors including specific organismal interactions. To keep the scope of the review manageable, we refer whenever possible to other reviews and summarising articles that provide more details and references. In this way, the review covers more than 500 scientific publications published in the period 1880–2025.

AZP terminology and classification has been harmonised with our recent publication on AZP biodiversity (Van den Wyngaert et al. 2025). Taxonomic affiliations and synonyms, both for the host and for the AZP, are only given when they appear for the first time in the text. All Latin names of AZP have been checked in the Index Fungorum and in the relevant modern taxonomic literature. For the term 'driver', we accept the Millennium Ecosystem Assessment (MA) definitions summarised by Nelson (2005, p. 74): 'A driver is any natural or human-induced factor that directly or indirectly causes a change in an ecosystem. A direct driver clearly influences ecosystem processes. An indirect driver has a more diffuse effect by modifying one or more direct drivers'. The definitions and order of drivers in the aquatic environment generally follow the classical hydrobiological sources (e.g. Hutchinson 1957; Wetzel 2001; Reynolds 2006). For each driver, the available information is organised in terms of hosts from autotrophs to heterotrophs and from freshwater to marine habitats.

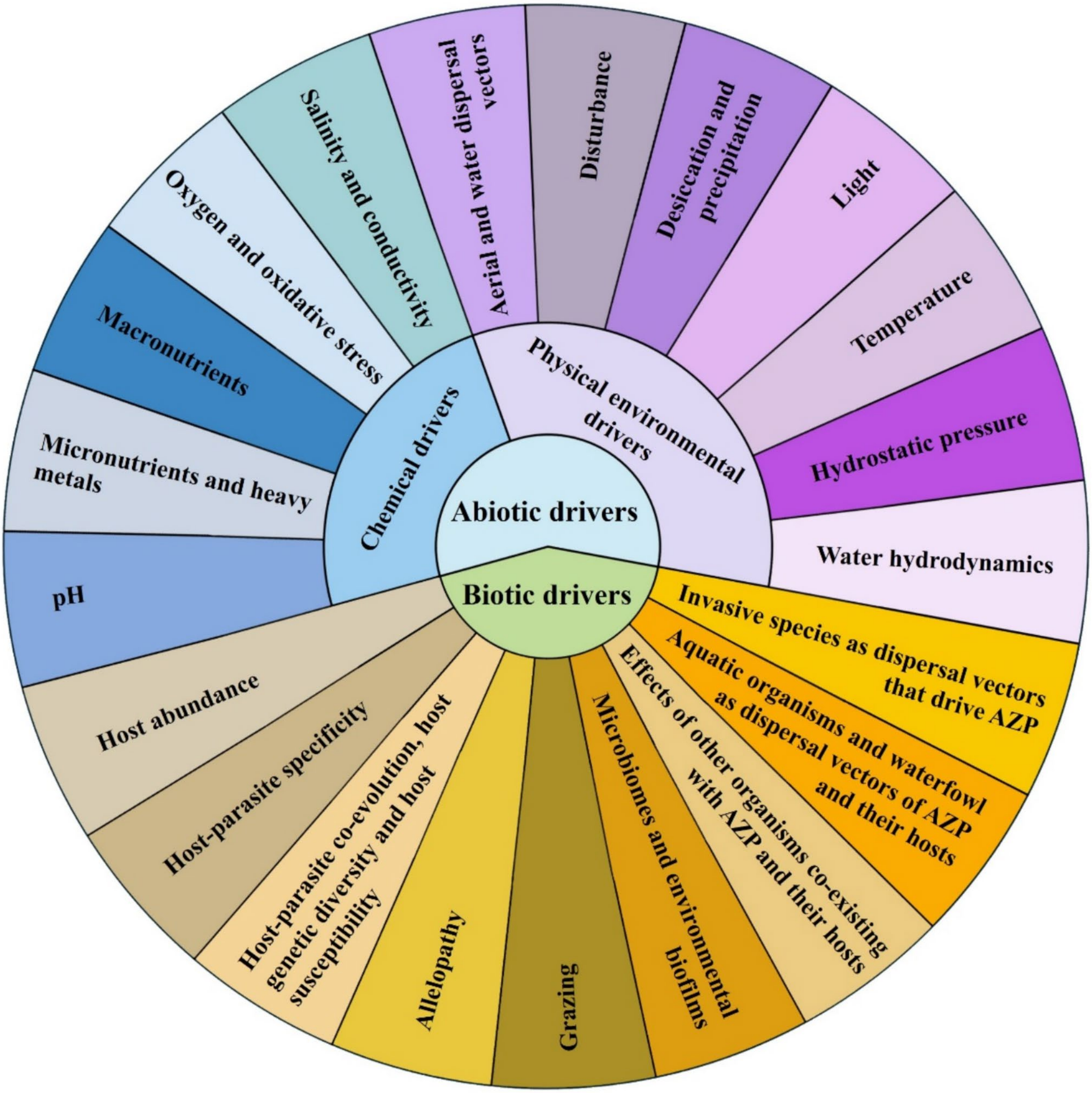


**Fig. 1** Abiotic and biotic drivers of AZP

## Results

### Abiotic drivers

Aquatic habitats cover about 72% of our planet, with the oceans accounting for 97.4% of all water on Earth, while lakes, rivers and atmospheric water account for only 0.02% (Reynolds 2006). The aquatic environment can be characterised by different physical states and is subject to different physical forces which also influence the chemical composition of the water layers. The most important abiotic factors that regulate the sinking, swimming, movement and dispersal of AZP and their hosts are summarised below.

#### Physical environmental drivers

The growth, reproduction and distribution of hosts and parasites and their interactions are strongly influenced by physical variables (Wolinska and King 2009; Kordas et al. 2011) – Fig. 2. Some environmental conditions can promote the

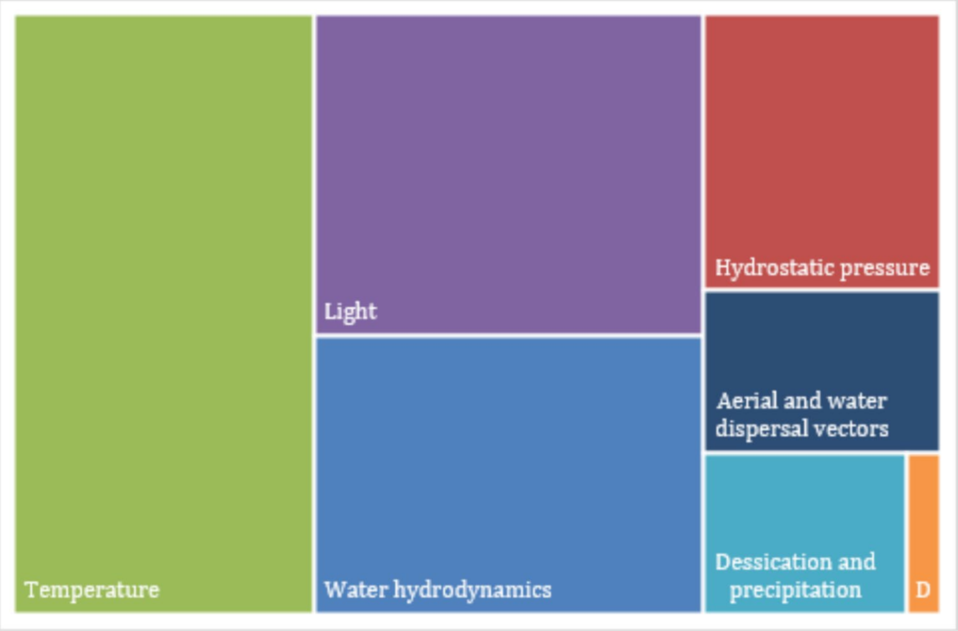


**Fig. 2** Physical drivers of AZP organised according to the degree of knowledge based on the number of publications on the topic. *D* disturbances

spread of parasites and diseases (Altizer et al. 2013) while others can provide hosts with conditions that offer a refuge from disease (Gsell et al. 2023).

**Water hydrodynamics** In all aquatic habitats, water masses are in constant motion, which is represented by turbulent and laminar flows (Reynolds 2006). Turbulence is characterised by chaotic changes in pressure and flow velocity, whereas in laminar flow, water flows in parallel layers without interruption between them (Batchelor 2000); it can be attenuated or amplified by basin morphometry, counter-currents, internal waves, wind and possibly tides, as well as by deflection due to the Earth's rotation (Coriolis forces), and thus determines the vertical and horizontal displacement of organisms (Reynolds 1997, 2006). Solar heating, which accounts for 99% of the heat in water bodies, changes the temperature and density gradients in the water layers and also plays a role. With strong warming and little wind, there is a difference in large and deep waters between the mixed surface layer (epilimnion) and the underlying water (hypolimnion), which is limited by the so-called thermocline (Reynolds 2006). In this way, the epilimnion is completely dynamic, and the vertical distribution of hosts and their parasites should match the highly variable vertical differentiation of the water column. In contrast, the water in shallow pools is completely mixed by the wind (Reynolds 2006).

Water turbulence and laminar flow (current) are also important for the horizontal distribution of certain groups of aquatic host organisms and their parasites. Overall, much less evidence has been collected for the spatial occurrence and biodiversity of AZP on planktonic algae in running waters, such as streams and rivers, than for standing inland waters (lakes, ponds, bogs, etc.) and oceans. The current and high turbulence may lead to lower species diversity and abundance of AZP in running waters, but the low number of AZP records from these habitats could also be explained by fewer field surveys. In any case, to the best of our knowledge, the available data refer to larger rivers with slower current velocities (Fabbro and Duivenvoorden 1996; Stoyneva 1998; Maier et al. 2013, 2016; Maier and Peterson 2014) and to some estuarine waters (Kazama 1972; Van Wichelen et al. 2006). Laboratory experiments have shown that high turbulence stimulates the growth rates of the large colonial pennate diatom *Asterionella formosa* in spring, allowing the alga to outcompete AZP and thus prevent the development of chytrid epidemics in rivers (Maier et al. 2013). In contrast, the reduction in flow velocity by barriers such as hydroelectric dams provides new niches with longer retention times, allowing diatoms to bloom and ensuring extended interaction time for chytrids to infect hosts (Maier et al. 2013; Maier and Peterson 2014). The lack of turbulence also enhances the attachment of AZP to host cells in marine habitats (Llaveria et al. 2010). Unlike algal AZP, parasites of insects, fishes and amphibians from different taxonomic groups have more often been recorded from rivers, streams and springs (e.g. Martin 1984; Czeczuga and Godlewska 2001; Combe et al. 2022; Jacinto-Maldonado et al. 2024).

In standing waters, there have been a few studies on the influence of water turbulence on host–parasite interactions and infection success, showing that it can have different effects depending on the strength of the turbulence and the species considered. Intermediate levels of turbulence in a poorly mixed waterbody can increase encounter rates between hosts and parasites, raising the chance that a parasite will find a suitable host (Zhang et al. 2024). AZP transmissions and infections are reduced under conditions of low turbulence and water stratification because stratification periods are often characterised by low nutrient concentrations and significantly lower phytoplankton abundance (Wetzel 2001), which reduces host density and thus the parasite infection rate. This was exemplified by consecutive epidemics of the chytrid *Zygorhizidium planktonicum* on the pennate diatom *Ulnaria acus* (Syn. *Synedra acus*), which occurred during the winter overturn, but were not observed in surface waters during spring stratification when host populations declined until the subsequent winter bloom (Doggett and Porter 1996). According to these authors, mixing of water layers can resuspend resting spores of chytrids, which are important for triggering AZP infections. Similarly, summer stratification strongly decreased AZP infections of zooplankton, such as *Daphnia pulicaria* by the chytrid *Polycaryum laeve*, while high turbulence in winter enhanced them (Johnson et al. 2009). In contrast, high water turbulence can significantly reduce chytrid infections in phytoplanktonic hosts that prefer stratified water, such as the prokaryotic blue-green algae (cyanoprokaryotes), more commonly known as cyanobacteria, as demonstrated by *Rhizophidium* sp. infections of filamentous *Planktothrix agardhii* (Wagner et al. 2023). Furthermore, in the case of AZP infections of *Planktothrix agardhii* in shallow water bodies, wind-driven high turbulence may hinder parasite transmission owing to impaired chemical communication or resuspension of sediments that physically prevent or reduce chytrid infections (McKindles et al. 2021b). The reduced infections in highly turbulent conditions could be due to the host-seeking behaviour of zoospores, as it was presumed in the case of the centric diatom *Coscinodiscus granii* and its parasitoid *Pirsonia diadema* (Kühn and Hofmann 1999). Strong turbulence, which leads to mixing of the water layers, can also result in the displacement of phytoplankton beyond the epilimnion in deep water bodies, where light limitation can reduce the transmission success of chytrids (Bruning 1991c, d) and other AZP.

**Hydrostatic pressure** Hydrostatic pressure results from gravity acting on all particles within a water column at a given depth and is determined by the weight of the overlying water per unit area (Lalli and Parsons 1997). As hydrostatic pressure is a downward force that increases with water depth, it is a significant abiotic factor influencing the host–parasite system in various waterbodies (Lalli and Parsons 1997). Therefore, actual depth is considered important for the distribution of aquatic organisms (Reynolds 1997, 2006; Xiao et al. 2021), and AZP are not exempt.

Few data support the presence of AZP in less explored benthic habitats strongly influenced by hydrostatic pressure. For example, AZP from different chytrid genera have been detected in marine micro- and macrophytobenthos hosts (Karling 1943; Gleason et al. 2011a; Gachon et al. 2017; Scholz et al. 2014; Ilicic et al. 2022, 2024; Murúa et al. 2020, 2023). Chytridiomycota and other AZP groups, such as Perkinsea, were consistently detected in the sediment, and their community structure remained stable over time (Chambouvet et al. 2011; Orsi et al. 2013; Xu et al. 2016, 2018; Picard 2017; Reñé et al. 2021b), suggesting that sediments contain a reservoir of diverse AZP that persist in a latent phase until favourable conditions allow their activation (Picard 2017; Reñé et al. 2021b; Fernández-Valero et al. 2022).

**Temperature** Temperature is one of the key drivers of environmental changes (e.g. seasonal events) and physiological traits in all organisms, including hosts and their parasites (Lafferty 2009; Wolinska and King 2009; Frenken et al. 2017b; Rajarajan et al. 2025). The response to changes in this physical factor depends on the optimum temperature of both host and parasite, as well as the prevailing temperature in their shared environment (Gsell et al. 2023). Therefore, temperature changes can strongly influence the success of AZP infections. For example, according to the thermal mismatch hypothesis (Cohen et al. 2017), AZP infections can be more successful when temperature conditions differ from the host's thermal optimum. Shifts in the timing of seasonal events caused by global warming can lead to a phenological mismatch (Stenseth and Mysterud 2002). Such phenological asynchrony occurs when the seasonal peak of consumer demand for a resource does not correspond with the peak of its availability (Gronchi et al. 2023). Desynchronisation of species-specific responses was among the earliest observations of trophic relationships in aquatic systems (Gronchi et al. 2023), but it also affects host–parasite relationships. If the thermal tolerance range of the host is greater than that of its parasite, temperature extremes at low or high levels may provide a disease-free refuge for the host, either because the parasite is inactive (e.g. in a dormant stage) or because it dies, being unable to withstand the temperature (Gsell et al. 2023). Experiments with *Asterionella formosa* and its chytrid parasite *Zygorhizidium planctonicum* confirmed that the narrower thermal tolerance range of the AZP provides the host with 'cold' and 'hot' thermal refugia, resulting in very little or no infection (Van Donk and Ringelberg 1983; Ibelings et al. 2011; Gsell et al. 2013a). Differences in temperature response and the resulting cold refugia for the host from chytrid infection have also been described for another freshwater phytoplankter, the filamentous cyanobacterium *Planktothrix rubescens* (Rohrlack et al. 2015; Rohrlack 2018; Wierenga et al. 2022). The hot refugium for the host has been hypothesised for *Planktothrix agardhii*: its infections by the chytrid *Rhizophydium* sp. mainly occurred between 19 °C and 23 °C (Wagner et al. 2023), while high temperatures (> 27 °C) inhibited the parasites (McKindles et al. 2021b).

The shape and amplitude of the thermal responses of algal hosts and AZP can be significantly altered by other interacting environmental factors, such as light or nutrient availability (Bruning 1991a, c, d; Wierenga et al. 2022). For example, warming accelerates the end of the spring bloom of the diatom *Synedra* sp., but the development of its chytrid parasites may have been restricted owing to increasing phosphorus limitation during the bloom (Frenken et al. 2017a). In cultures of the green freshwater flagellate alga *Haematococcus lacustris* (Syn. *Haematococcus pluvialis*), which is used for astaxanthin production, infections by *Paraphysoderma sedebokerense* (Blastocladiomycota) increased exponentially with temperature until an optimal temperature (30 °C) was reached, but could not establish at the low (< 15 °C) and high (40 °C) ends of the thermal tolerance range (Hoffman et al. 2008).

Temperature changes in the water column may not only create conditions that exceed the thermal tolerance limits of parasites and hosts but also influence the hydrodynamic environments in which they interact, as well as related light and nutrient regimes. Global warming, particularly the increasing frequency and intensity of heatwaves, is leading to greater summer stratification in both marine and deep freshwater ecosystems, affecting all food web components (e.g. Smale et al. 2019). These conditions reduce the vertical exchange of nutrients and passive phytoplankton, potentially resulting in greater nutrient depletion in the upper water layer (Boyce et al. 2010) and lower productivity, which in turn could lead to fewer and less nutritious hosts for parasites. While targeted studies on the effects of heatwaves on AZP are generally lacking, studies on other parasites have shown very different responses depending on factors such as the study area, host and parasite physiology and differences in their life cycles (Li et al. 2024).

With ongoing climatic changes, rising temperatures, changes in ice occurrence and shifts in the timing of snowmelt are also expected (Sharma et al. 2019). Decreasing snow and ice cover can directly lead to habitat loss for ice and snow algae and their associated parasites (Nakanishi et al. 2025). Loss of winter ice cover may also indirectly affect host–parasite interactions, as demonstrated by the loss of the cold-temperature refugium from chytrid infections of *Asterionella formosa* at low temperatures owing to warmer winters (Ibelings et al. 2011).

Temperature also controls dormancy and subsequent activation of resting spores, playing an important role in AZP periodicity. Both field and laboratory studies of the *Ulnaria acus*–*Zygorhizidium planctonicum* system revealed that resting spores of the parasite remained dormant at reduced hypolimnion temperatures (< 10 °C) but were activated and reached 70–80% germinability when temperatures increased to 10–16 °C (Doggett and Porter 1996).

The effect of temperature on amphibian chytrids and their infection dynamics is particularly well documented (e.g. Boyle et al. 2003; Turner et al. 2021; Haver et al. 2022). Optimal growth of the chytrid *Batrachochytrium dendrobatidis* occurs between 17 °C and 25 °C, and water temperatures below 17 °C slow fungal growth rates (Piotrowski et al. 2004), while high temperatures (> 27 °C), as with algal chytrids, kill the parasite within a few hours to days (Johnson et al. 2003; Piotrowski et al. 2004). This enables amphibian tadpoles to overcome chytrid infections (Geiger et al. 2011). Temperature also determines the interactions of *Batrachochytrium dendrobatidis* with other organisms, such as zooplankton feeders and the protective microbiome of amphibian skin (Haver et al. 2022, see below), and may explain the importance of seasonality in its infection dynamics (Clare et al. 2016).

Whether parasites have a higher or lower thermal adaptive capacity to global warming than their hosts requires further research. Some studies show no parasite adaptation to elevated temperatures in phytoplankton–fungus systems (Schampera et al. 2022), while other research predicts that AZP can adapt faster than their large-bodied hosts owing to their smaller size and shorter generation times (e.g. Cohen et al. 2017; Gsell et al. 2023). In contrast to the faster adaptation rates of smaller parasites, larger hosts may have a broader temperature tolerance range, and their acclimatisation capacity is positively correlated with body size (Rohr et al. 2018). This greater acclimatisation capacity could allow large-bodied hosts to use a wider temperature tolerance range than their parasites (Rohr et al. 2018; Gsell et al. 2023), potentially giving them an advantage under global warming.

**Light** In ecological studies, the term 'light' usually refers to the visible solar electromagnetic radiation spectrum with wavelengths from 400 to 700–750 nm, also known as photosynthetically active radiation (PAR), and ultraviolet radiation (UVR) with wavelengths of 280–400 nm (Zhang et al. 2020). Light intensity, i.e. the number of photons arriving at a defined surface per unit time, is highly variable at each location, with daily and annual fluctuations (Reynolds 1997). After underwater light attenuation, the spectrum and intensity of light perceived by aquatic host–parasite systems depend on their vertical position in the water column (Reynolds 2006) and on water transparency, which is influenced by the presence of organic and inorganic particles or the associated water turbidity (Wetzel 2001). Thus, underwater PAR and UVR penetration and water transparency depend on all physical, chemical, biological and even watershed processes, but they also regulate many biological, physical and chemical processes in aquatic systems (Zhang et al. 2020).

Host–parasite interactions and coexistence show considerable variability owing to differing light requirements of the host algae, which vary not only between species from different evolutionary lineages and taxonomic groups but also between algae from the same taxonomic group and even from the same genus (Round 1981). For example, the chytrid *Rhizophydium megarrhizum* infects two closely related phytoplanktonic species, *Planktothrix agardhii* and *Planktothrix rubescens*, which have contrasting light requirements and inhabit different depths: (1) *Planktothrix rubescens* is rich in the specific red pigment phycoerythrin, efficiently utilises green light (495–570 nm) and occurs in the metalimnion of stratified lakes; (2) in *Planktothrix agardhii*, the blue pigment phycocyanin predominates over phycoerythrin, allowing maximum growth rates in red light (620–750 nm), and the alga inhabits the epilimnion of stratified lakes or shallow waterbodies without stratification. However, experiments have shown that for both species, low light can provide a refugium from chytrid epidemics, while increased light availability can lead to the potential development of chytrids (Tao et al. 2020). Cells of the freshwater green alga *Tetradesmus obliquus* (Syn. *Scenedesmus obliquus*) infected with *Chytridium* sp. lysed only when exposed to blue light (Abeliovich and Dikbuck 1977). In addition to spectral composition, light intensity may affect algal hosts and thus their AZP. Experiments with *Planktothrix rubescens* showed that, although it grows optimally at higher light intensity under laboratory conditions, it can also grow at lower light intensity to avoid chytrid epidemics. This may explain its frequent occurrence in deeper lake layers (Rohrlack 2018; Wierenga et al. 2022). However, increased light availability can induce stress in other algal hosts, such as marine and ice diatoms, leading to a higher incidence of disease (Hassett and Gradinger 2016; Scholz et al. 2017).

Light can influence AZP directly or through indirect host-mediated effects and, together with temperature, can potentially explain seasonality in some AZP (Van den Wyngaert et al. 2022). In addition to the light requirements of the host, the occurrence and success of AZP infections in aquatic habitats also depend on the light requirements and behaviour of their zoospores, which play key roles in the dispersal, biogeographical range, ecological function and infection dynamics of AZP (Galindo et al. 2024). Light largely impacts the activity of photosynthetic microalgal and macroalgal hosts in both freshwater and marine habitats and likely influences the production of photosynthetic cues that chytrids may rely on to find suitable hosts through chemotaxis (Bruning 1991c; Muehlstein et al. 1988; Van den Wyngaert et al. 2014; Tao et al. 2020). Therefore, high light conditions and increased photosynthetic production can raise the probability of AZP finding hosts, and vice versa, as first demonstrated in Bruning's (1991a) experiments with the host–parasite system *Asterionella formosa–Rhizophydium planctonicum*. Other studies have also shown that low light levels or complete darkness hinder the attachment of zoospores to their hosts (Bruning 1991b, d; Scholz et al. 2017). Experiments with zoospores of *Rhizophydium planktonicum* showed that they are more active in bright light than in dim light (Canter and Jaworski 1980) and rarely adhere to the cells of *Asterionella formosa* under very low light conditions or in complete darkness, but once attached in the light, they remain alive and continue their development in the dark (Canter and Jaworski 1981). However, increased light penetration stresses ice algae and raises chytrid disease incidence under reduced snow cover in the Arctic (Hassett and Gradinger 2016). Not only the intensity, but also the duration of light exposure and spectral composition influence the development of AZP zoospores and the success of their infection, with species-specific responses. For example, day length has been shown to correlate positively with infection success (Scholz et al. 2017), and the spectral composition of light can influence parasite transmission, as shown for the zoospores of *Ulkenia* sp. (Labyrinthulomycota) which exhibited positive phototaxis to blue light (440–480 nm) produced by the marine bacterium *Vibrio fischeri*, but only under low light intensity conditions (Amon and French 2004).

Regarding UVR, there are limited and contradictory results on the sensitivity of AZP. According to Hite et al. (2016), high UVR negatively affects amphibian chytrids and increases their mortality, but may also harm their zooplankton grazers, potentially increasing the infection success of AZP. In the field, UVR led to a decrease of *Batrachochytrium dendrobatidis* infections in tadpoles (Ortiz-Santaliestra et al. 2011), while it had no effect in cultures (Johnson et al. 2003). Experimental exposure of amphibian larvae to high UVR resulted in higher infection rates by this chytrid, and the larvae carried a greater infection burden than those not exposed to elevated UVR (Cramp et al. 2022). Given the complexity of co-factors (e.g. presence of pathogens, low temperatures, species sensitivity to radiation) that may influence the response of both hosts and parasites to UVR, these factors need to be investigated in more detail (Haver et al. 2022).

With the growing human population, the role of anthropogenic light at night, which disrupts the normal photoperiod and is known as light pollution, is increasing (Poulin 2023). Although it affects aquatic systems, its impact on aquatic organisms, especially on AZP, is almost completely ignored (Poulin 2023).

**Desiccation and precipitation** Desiccation and drought can affect host–parasite systems both on land and in aquatic habitats. This is particularly true for amphibians and their chytrid parasites (especially *Batrachochytrium dendroba-*

*tidis*), which are highly susceptible to desiccation (Johnson et al. 2003; Piotrowski et al. 2004). Wetter regions and rainy seasons have been associated with more severe cases of chytridiomycosis in amphibians (Puschendorf et al. 2011; Valencia-Aquilar et al. 2016), and amphibians in constant contact with water are more susceptible to chytrid infections, whereas chytridiomycosis and related mortality remain low in dry environments (Haver et al. 2022). It remains unclear whether this is solely due to the drought sensitivity of the amphibian host, the protective skin microbiome, or pathogen characteristics. The occurrence of dry periods in some seasonal water bodies potentially provides a pathogen-free refugium for amphibians if the parasites cannot withstand drought (Scheele et al. 2015). This may also be hypothesised for other host–parasite systems and may explain a greater prevalence of AZP infections in larger water bodies.

**Disturbances** Disturbance in aquatic systems includes all processes that disrupt established conditions and is recognised as an important factor increasing heterogeneity at all levels (Naselli-Flores et al. 2003). This particularly affects biodiversity, as described by Connell's (1978) Intermediate Disturbance Hypothesis (IDH), a key ecological theory explaining patterns of species diversity in relation to the frequency and intensity of disturbances in ecosystems, and proposing that biodiversity is maximised at intermediate levels of disturbance. Natural and anthropogenic disturbances often co-occur, and their effects are frequently synergistically compounded (Archer and Stokes 2000). However, disturbances are more commonly associated with various anthropogenic activities (mining, livestock, fishing, wastewater discharges, agriculture, industrialisation and urbanisation) that lead to rapid transformation and pollution of aquatic ecosystems, severely affecting their biodiversity. Although data on the effects of pollutants and other human activities have previously been collected regarding different AZP and their hosts (e.g. Schmeller et al. 2018), the adverse effects of disturbances and disruption of steady states on host–parasite interactions have rarely been discussed (e.g. Jacinto-Maldonado et al. 2024). This contrasts with the broad acceptance of disturbances, such as extreme weather and floods, in altering seasonal events and causing shifts in phytoplankton assemblages (e.g. Gaedeke and Sommer 1986; Reynolds et al. 1993; Stoyneva 2003; Znachor et al. 2008; Shabarova et al. 2021).

**Dispersal via air and water** Many algae that host AZP have a large geographical range, although there are generally no obvious links between localities. It is assumed that they achieve their wide distribution passively through physical factors such as wind, water currents, rain, animal vectors or human activities (Kristiansen 1996b, 2008). The same transport vectors have been demonstrated for AZP, although little research has been conducted on the subject. For example, rainfall enhanced by wind can directly and indirectly influence AZP transmission and thus infection success. The detection of *Batrachochytrium dendrobatidis* zoospores in rainwater (Kolby et al. 2015) and fog samples (Prado et al. 2023) suggests that aerial transport may be possible and that its vectors may affect AZP from other hosts. In vitro experiments, in which *Batrachochytrium dendrobatidis* survived for up to 3 months in moist but sterile river sand, suggest that this AZP can be translocated by the movement of river sand (Johnson and Speare 2005).

Culture experiments with *Paraphysoderma sedebokerense* and its green algal hosts *Haematoccus lacustris* (Hoffman et al. 2008) and *Tetradesmus dimorphus* (Syn. *Scenedesmus dimorphus* – Letcher et al. 2016) have shown that the parasite's resting sporangia can retain infectivity after 3 to 4 weeks on agar (Hoffman et al. 2008). This enables widespread dispersion by water or wind after separation from the host until it finds a new suitable host (Letcher et al. 2016).

For aquatic organisms, water transport is the most common and long-distance dispersal mechanism (Kristiansen 1996a, b; Haver et al. 2022). The role of stream and river networks as natural transport corridors for various organisms, including pathogens and their hosts, has been summarised (Kristiansen 1996a, b; Meentemeyer et al. 2012; Rinaldo et al. 2018), although all mechanisms of abiotic dispersal of AZP, especially in complex landscapes, remain largely unknown (Haver et al. 2022). However, a review of current studies on the translocation of *Batrachocytrium dendrobatidis* by water movement in lakes or by downstream transport suggests that water connectivity is important in pathogen dispersal, particularly when facilitated by short distances between freshwater habitats (Haver et al. 2022).

Currently, a new form of facilitated water connectivity between non-adjoining waterbodies across various spatial scales, through the use of raw water transfers (RWTs), is rapidly increasing globally (Waine et al. 2024). These complex networks of purpose-built infrastructure – pipelines, tunnels and water supply canals – translocate large volumes of untreated freshwater and effectively create artificial corridors for aquatic organisms (Waine et al. 2024). Although RWTs pose a significant risk for the spread of invasive species and pathogens, there is limited awareness of RWTs among the scientific and nature conservation communities (Foster et al. 2025; Waine et al. 2025). At present, there are no studies on the spread of AZP by RWTs; however, considering their potential significant influence on biodiversity, we highlight these poorly understood, artificial, novel potential dispersal pathways of AZP.

## Chemical drivers

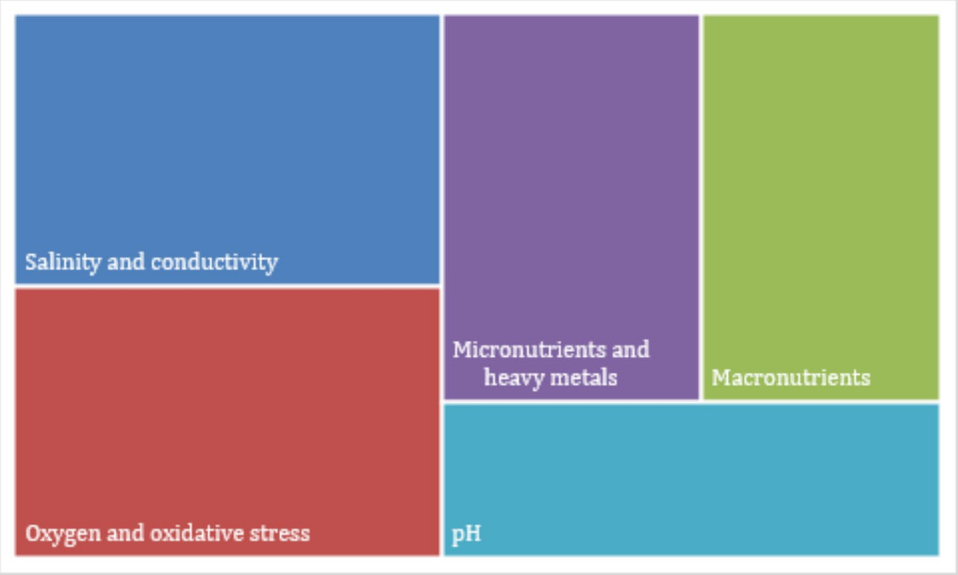
In addition to physical properties, the chemical composition of water is also important for aquatic life (Reynolds 1997). The solute content of water originates from several sources: the precipitation load, the geological basis of the catchment area, its geomorphological relief, and anthropogenic contributions to acidity, particulate matter and dissolved content. There is greater variation in the composition of major ions in inland waters than in marine systems (Reynolds 1997). The variability in the effects of different chemicals highlights the complexity of understanding the influence of water chemistry on host–AZP relationships (Chew et al. 2024) and its role as a driver of AZP diversity and abundance through its different components (Fig. 3).

**Salinity and conductivity** Salinity, defined as the total ion content in the water column, is closely related to water conductivity, which measures the ability of a solution to conduct electricity (Wetzel 2001). Salinity is among the key environmental variables controlling aquatic mycota (Harrison and Jones 1971; Walker and White 2017; Rojas-Jimenez et al. 2019; Guo et al. 2023; Peng et al. 2024) because changes in water ion concentration can affect the physiology of resident organisms by causing osmotic stress or inducing variations in ambient electric fields. In general, fungi can survive the adverse effects of osmotic stress by altering their morphogenetic programme or making structural and metabolic changes (Duran et al. 2010). Most AZP, and chytrids in particular, are known to prefer habitats with low osmotic potential, and very few live in marine or brackish waters (Sime-Ngando 2012; Rojas-Jimenez et al. 2019).

The distribution of fungi along salinity gradients depends on the physiological adaptations of different species. Recently, the application of molecular-genetic methods revealed that the overall diversity of marine microbenthic chytrids is primarily influenced by salinity (Ilicic et al. 2024). The decreased salinity increased the diversity of chytrids on benthic diatoms (Ilicic et al. 2022), but on several occasions led to outbreaks of marine seagrass (*Zostera marina*) infections by *Labyrinthula zosterae* (Muehlstein 1998; Muehlstein et al. 1991). In general, marine species can tolerate a wider range of salinities compared with freshwater species (Jones 2022). For example, plasticity in adaptation to salinity is less pronounced in chytrids of freshwater phytoplankton hosts such as *Planktothrix rubescens* (McKindles et al. 2021b) and in amphibian chytrids such as *Batrachochytrium dendrobatidis* (Heard et al. 2015, 2018; Bolom-Huet et al. 2023; Chew et al. 2024). High salinity disrupts osmotic balance, decreases parasite infections and likely creates a salt niche for amphibian hosts to escape chytrid infections (Stockwell et al. 2012, 2015a, b). The mechanism of this beneficial effect of increased salinity for amphibians has been explained by the inhibition of zoospores and reduced disease transmission (Clulow et al. 2018). However, data from a few other studies show no influence of salinity on the infection dynamics of amphibian parasites (for details see Chew et al. 2024).

**Oxygen and oxidative stress** Oxygen is a widely recognised essential element for life and is important for the distribution of organisms in aquatic environments (Verberk et al. 2011; Deutsch et al. 2020; Lobo et al. 2024). Zoosporic parasites from freshwater, brackish and marine environments are con-

**Fig. 3** Chemical drivers of AZP, organised according to the degree of knowledge based on the number of publications on the topic



sidered obligate aerobes whose growth is inhibited by low concentrations of dissolved oxygen (Gleason 1976; Barr 2001; Czeczuga and Godlewska 2001; Gleason et al. 2007, 2008; Sime-Ngando 2012). In a single study, two chytrids, *Rhizophydium sphaerotheca* and *Spizellomyces punctatus* (Syn. *Phlyctochytrium punctatum*), were shown to be facultative anaerobes, yet their growth was higher in oxygenated flasks (Goldstein 1960).

Low oxygen saturation levels and anaerobic conditions prevented the increase of *Chytridium* sp. infection and cell lysis of *Tetradesmus obliquus*, while varying the oxygen concentration between 3.5 and 13 mg $L^{-1}$ had no effect on chytrid infections (Abeliovich and Dikbuck 1977). Laundon and Cunliffe (2021) expand on the role of oxygen for chytrids by highlighting several questions related to reactive oxygen species (ROS) in host and parasite biology, particularly in parasite development and virulence. The term 'ROS' refers to a large family of oxidants derived from molecular oxygen, often as byproducts of cellular metabolism (Sies et al. 2022). Their accumulation and release into cells increase in response to various unfavourable environmental factors (such as increased salinity, heat or cold stress and pathogen attack), but they can also act as toxic molecules with strong antioxidant activity (Camejo et al. 2016). Therefore, ROS were thought to accumulate in hosts from different taxonomic groups as a defence against fungal parasitism (Canter and Jaworski 1979; Santhosh and Neuhauser 2024). However, AZP can also utilise them, and the review by Camejo et al. (2016) summarises data on the major enzymatic systems involved in ROS generation and the role of ROS as cell signalling components and parasite developmental cues during plant–pathogen interactions.

By studying the interaction between *Haematococcus lacustris* and *Paraphysoderma sedebokerense*, Yan et al. (2022) identified oxidative degradation as a strategy for fungal infestation. Two metabolites, 3-hydroxyanthranilic acid and hordenine, were identified and shown to stimulate infection by inducing oxidative stress, causing gene expression disorder and pigment degradation in algal cells. These metabolites generated hydroxyl radicals that destroyed subcellular components of algal cells, such as the cell wall, membranes and pyrenoid, thus increasing the susceptibility of algal cells to infection (Yan et al. 2022). Although in many pathogenic fungi the strong antioxidant glutathione is a virulence factor that helps to neutralise oxidative stressors generated by host immune cells (Wangsanut and Pongpom 2022), its role in the oxidative stress tolerance of AZP has not been investigated.

**Macronutrients** The resource requirements of AZP, which obtain their nutrients directly from hosts, include essential components of cell protoplasts needed in large quantities for organism development and growth (Reynolds 2006). These macronutrients include various forms of phosphorus (P) and nitrogen (N), which are constituents of nucleic acids and amino acids, respectively. Therefore, their availability in the aquatic environment is of great importance for the occurrence and maintenance of host–parasite systems. This availability, along with other environmental factors, plays an important role in the chytrid infection rate and thus in growth on algal hosts (Sime-Ngando 2012; Rasconi et al. 2012). For example, P limitation of *Asterionella formosa* led to reduced algal growth and thus facilitated the development of a *Rhizophydium* epidemic despite reduced zoospore production and parasite growth rate (Bruning 1991a).

AZP are sensitive to changes in N supply (Frenken et al. 2021) and a relatively high availability of N compared with P may also stimulate chytrid infection rates on cyanobacteria (Frenken et al. 2017a). Experiments with cultures of *Haematococcus lacustris–Paraphysoderma sedebokerense* likely revealed an important role of N in the development of parasite infection (Asatryan et al. 2019). In this study, the vegetative flagellate cells of the alga remained uninfected, but infection of its two resting stages (green, palmelloid stage and red, astaxanthin-rich cyst stage) was observed, with epidemics developing faster in the red cells when N was present. Although *Paraphysoderma sedebokerense* has long been known as the '*Haematococcus* parasite', it also has another green algal host, namely *Tetradesmus dimorphus* (Letcher et al. 2016). This 'new' host was easily infected when grown in a medium with low N levels (Letcher et al. 2016).

Although the effect of nutrients on AZP has been less specifically studied, given the ecological requirements of the hosts, it can be hypothesised that nutrient enrichment increases algal host availability and thus AZP infectivity (Rasconi et al. 2012). Although parasitic fungi are found across the full range from poor in nutrients (oligotrophic) to nutrient-rich (eutrophic) waterbodies (Kagami et al. 2007a; Rasconi et al. 2012), in oligotrophic conditions, AZP associations (e.g. various species of chytrid parasites on green algae and diatoms) have been detected in small quantities and with a generally low prevalence of infection (Rasconi et al. 2012). Total N and P, together with dissolved carbon (C), were positively correlated with *Batrachochytrium dendrobatidis* concentrations on frog swabs (Battaglin et al. 2016). However, according to other authors, these nutrients do not impact pathogen growth and infection outcomes regarding amphibian AZP (Chew et al. 2024).

For decades, nutrient enrichment, particularly by N and P, has occurred in various aquatic environments in a process known as eutrophication, which affects species composition, productivity and elemental cycles of aquatic organisms, including AZP (Smith et al. 2006). The role of AZP in material transfer within aquatic food webs increases with nutrient availability, and their key role in eutrophic systems has been demonstrated through both modelling and empirical results (Miki et al. 2011; Thongthaisong et al. 2022).

**Micronutrients and heavy metals** Many elements play a role in cell structures and their functions at relatively low concentrations (Reynolds 2006). Some of these micronutrients, such as sodium (Na), potassium (K), calcium (Ca), magnesium (Mg) and chlorine (Cl) are relatively abundant in water, while many others generally occur naturally in low concentrations (Reynolds 2006). The influence of these elements on AZP is poorly understood, although much knowledge has been accumulated about the hosts themselves. In sewage oxidation ponds, massive infections of *Tetradesmus obliquus* by *Chytridium* sp. were triggered by low concentrations ($<10^{-2}$ M) of $K^+$ and $Mg^{2+}$, while $Ca^{2+}$ and $Na^+$ had no effect (Abeliovich and Dikbuck 1977). The authors therefore hypothesised that it might be possible to prevent infection of mass cultures by replacing most $Na^+$ and $Ca^{2+}$ cations with $K^+$ and $Mg^{2+}$.

In the aquatic environment, some metals such as manganese (Mn,) iron (Fe), zinc (Zn), copper (Cu) and cobalt (Co), occur in quantities ranging from deficient to toxic concentrations (Reynolds 2006). Some of these metals are important for the homeostasis of fungi as they are required for various biochemical processes, usually as enzymatic cofactors. For example, Zn plays a crucial role as a large proportion of zinc-binding proteins are associated with critical functions including DNA binding, regulation of transcription, activity of transcription factors and response to chemical stimuli (Wilson et al. 2012; Staats et al. 2013), while Cu is necessary for the activation of metalloproteins (Festa and Thiele 2011). However, there is inconsistency in the reported impacts of both these metals on amphibian chytrids (e.g. Threlfall et al. 2008; Boisvert and Davidson 2011; Chew et al. 2024). At the same time, copper sulphate ($CuSO_4$) can act as fungicide against algal and amphibian chytrids (Fott 1967; Boisvert and Davidson 2011; Carney and Lane 2014). Fe is bound to many proteins and in this form is essential for metabolic pathways and physiological functions of living cells (Kontoghiorghes and Kontoghiorghe 2020).

Cadmium (Cd) is generally considered a toxic metal with no biological significance, although its catalytic role for carbonic anhydrase enzymes in marine diatoms has recently been discovered (Alterio et al. 2015). Cd tolerance in *Batrachochytrium dendrobatidis* appears to be controlled by the availability of glutathione, as since its depletion significantly affects the parasite's tolerance to Cd and silver (Ag) and moderately affects tolerance to Cu, Zn and lead (Pb) (Webb et al. 2024a, b).

Zoospores, which have a cell membrane rather than a cell wall, may be more sensitive than other AZP stages, such as the thick-walled sporangium (e.g. Berger et al. 2005). The metals mentioned above are transported in aquatic habitats mainly by surface run-off, which also exposes waterbodies to various agrochemical pollutants such as pesticides, fertilisers and veterinary pharmaceuticals. This diffuse pollution from agriculture is considered one of the main pressures on European waters (EEA 2024). Many organic micropollutants, including pesticides, are harmful to various organisms, including amphibians and their parasites (e.g. Johnson et al. 2003; Haver et al. 2022). However, it must be considered that while a particular compound may affect the parasite, it may have even more detrimental effects on the host, increasing its susceptibility to infection (Chew et al. 2024).

In addition to all the inorganic elements mentioned above, micronutrients also include certain vitamins, such as thiamine, biotin and cyanocobalamin (Reynolds 2006). Growth of the chytrid *Rhizophydium sphaerotheca* has been shown to depend on thiamine (Goldstein 1960). Some AZP may require vitamins, as demonstrated in a study on the oomycetes *Lagenidium callinectes* and *Haliphthoros milfordensis* in marine crustaceans (Bahnweg and Blang 1980).

**pH** The concentration of hydrogen ions ($H^+$) in a solution, traditionally measured as pH (Jensen 2004), is used to determine the acidity ($pH<7$) or basicity ($pH>7$) of aqueous solutions (Covington et al. 1985; Lim 2006). pH and closely related dissolved variables, such as dissolved organic matter, influence the biomass of aquatic microfungi (e.g. Jørgensen and Stepanauskas 2008). Recently, a substantial proportion of the carbon dioxide ($CO_2$) emitted by humans into the atmosphere has been absorbed by the oceans, progressively reducing their pH in a process known as 'ocean acidification' (Caldeira and Wickett 2003; Sabine et al. 2004; Ma et al. 2023). The decrease in pH is 0.1 units (from 8.2 to 8.1) compared with pre-industrial levels (Gruber et al. 2019), with some studies suggesting a further decrease to 7.8 by 2100 (Gattuso et al. 2015). Such changes are thought to favour the growth of marine fungi, some of which parasitise less resilient hosts, highlighting the need to assess the risk of increasing fungal infections in an ocean acidification scenario (Krause et al. 2013). In general, zoosporic fungi, and chytrids in particular, have been shown to tolerate low pH but not extremely high alkaline conditions (Gleason et al. 2008, 2010, 2011b). In cultures, growth of zoosporic strains was confirmed across the pH range 2.9–11.2; most isolates grow at pH between 4.7 and 8.9 but survived for 7 days at both pH 2.9 and pH 11.2 (Gleason et al. 2010). According to this study, many zoosporic fungi appear well adapted to a wider range of pH values than those found in the environments from which they were isolated, and, after brief exposure to pH extremes, they recover quickly.

An acidic cultivation strategy was developed to prevent contamination of *Haematococcus lacustris* cultures by *Paraphysoderma sedebokerensis* (Hwang et al. 2019). Instead of the commonly used neutral pH, an acidic condition ($pH=4$)

was applied during cultivation, resulting in significant inhibition of fungal contamination. The authors claim that this may be due to acid-induced denaturation of a surface protein of the parasite, which plays an important role in the parasite's recognition of the host.

According to some studies, amphibian chytrids have a very low tolerance to pH values outside the range of 6–8 (Piotrowski et al. 2004; Johnson and Speare 2005). However, inconsistency exists regarding the impacts of pH on their infection dynamics: one study showed increased infection in more alkaline conditions (pH > 6.5) (Kärvemo et al. 2018), while others reported high infection prevalence and intensity at low pH values (Battaglin et al. 2016; Valencia-Aguilar et al. 2016) or found no impact of pH (Chew et al. 2024).

## Biotic drivers

Although parasitism is one of the most common consumer strategies among organisms (Lafferty et al. 2008) and a common ecological interaction in most aquatic environments (e.g. Sime-Ngando 2012), AZP can be influenced by many biological factors and interactions. The main biological drivers (Fig. 4) are reviewed below.

### Host abundance

The presence and development of AZP infections depend primarily on the distribution of their hosts (e.g. Sime-Ngando 2012; Ilicic and Grossart 2022). Many AZP infect algal species from different taxonomic groups (Table 1), and evidence of them has been collected since the late nineteenth century (e.g. Wildeman 1890). Most data collected concern phytoplankton (e.g. Karpov et al. 2014; Frenken et al. 2017b; Van den Wyngaert et al. 2022), where hosts in freshwater are mainly representatives of green algae, diatoms and cyanobacteria, but also include desmids, zygnemaleans, dinoflagellates, yellow-green algae and glaucocystophytes (Table 1). In marine environments, phytoplankton hosts are predominantly dinoflagellates and diatoms, while benthic communities include a wide range of macroalgal hosts such as green algae from the class Ulvophyceae and brown algae, commonly known as kelp (and their associated microalgae – Fernández-Valero et al. 2023), as well as microbenthic diatoms (Table 1). AZP also infect green algae that develop on snow and ice, such as *Ancylonema nordenskioeldii*, *Ancylonema alaskana*, *Sanguina nivaloides* and *Chloromonas* sp., as well as microbenthic diatoms (Table 1). AZP not only infect algae in natural waters but are also widespread in mass algal cultures, where they frequently infect chlorophytes such as *Chlamydomonas*, *Haematococcus* and *Scenedesmus* s.l. (Table 1). It must be emphasised that AZP infect not only the vegetative algal cells but also some of their reproductive structures (e.g. sporangia and receptacles of brown algae; Karling 1943; Müller et al. 1999; Gachon et al. 2017) or resting stages, which are formed in large quantities to survive unfavourable conditions. Among these, infections have been reported on the cysts of the dinoflagellate *Ceratium hirundinella* (Canter 1961; Canter and Heaney 1984) and on the akinetes of cyanobacteria *Sphaerospermopsis aphanizomenoides* (Skuja 1948; Stoyneva-Gärtner et al. 2023) and *Dolichospermum macrosporum* (Syn. *Anabaena macrospora* – Sime-Ngando 2012, Gerphagnon et al. 2013, 2017). Other cells, such as *Dolichospermum* sp. heterocysts (cyanobacterial specialised nitrogen fixing cells) may also be infected by AZP (chytrids of the order Lobulomycetales) causing disturbances in the nitrogen fixation process (Xu et al. 2025). Despite their different taxonomic affiliations, the presence of susceptible

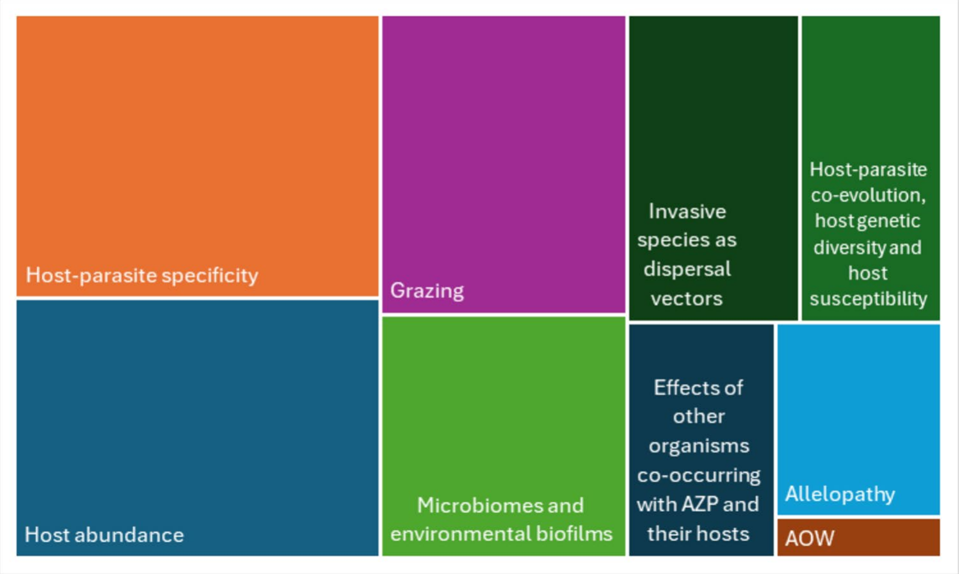


**Fig. 4** Biotic drivers of AZP organised according to the degree of knowledge based on the number of publications on the topic. *AOW* aquatic organisms and waterfowl as dispersal vectors of AZP

**Table 1** Algal hosts of AZP from different aquatic communities

| Aquatic community | Taxonomic group(s) | Refs. |
|---|---|---|
| Freshwater phytoplankton | Green algae, diatoms and cyanobacteria | Sparrow 1960; Canter 1951, 1967, 1972; Canter and Lund 1951, 1953; Batko 1975; Canter and Jaworski 1979, 1980, 1981, 1982, 1986; Sen 1988a, b; Canter and Beakes 1992; Canter-Lund and Lund 1995; Kagami et al. 2007a; Hanic et al. 2009; Sime-Ngando 2012; Gerphagnon et al. 2013, 2015; Gsell et al. 2013c; Voigt et al. 2013; Gleason et al. 2015; Takano et al. 2008; Van Wichelen et al. 2010, 2016; Sønstebø and Rohrlack 2011; Danz and Quandt 2023; Seto et al. 2020, 2023; Stoyneva-Gärtner et al. 2023; Wagner et al. 2023; Stoyneva-Gärtner and Uzunov 2024; Xu et al. 2025 |
| | Desmids | Canter 1961; Cook 1963; Canter and Lund 1969; Canter-Lund and Lund 1995; Kagami and Urabe 2002; Rasconi et al. 2011; Van den Wyngaert et al. 2017, 2023; Seto et al. 2023; Stoyneva-Gärtner and Uzunov 2024 |
| | Zygnemaleans | Canter-Lund and Lund 1995; Seto et al. 2023; Stoyneva-Gärtner and Uzunov 2024 |
| | Dinoflagellates | Alster and Zohary 2007 |
| | Yellow–green algae | Gromov et al. 1999; Karpov et al. 2014 |
| | Glaucocystophytes | Seto et al. 2023 |
| Freshwater phytobenthos | Green and yellow-green algae | Torruella et al. 2018; Stoyneva-Gärtner and Uzunov 2024 |
| Marine phytoplankton | Dinoflagellates and diatoms | Johnson 1967; Hanic et al. 2009; Chambouvet et al. 2011; Lepelletier et al. 2014; Gleason et al. 2015, Scholz et al. 2017; Reñé et al. 2021a, b; Fernández-Valero et al. 2022 |
| Marine macrobenthos | Green algae | Muehlstein et al. 1988; Ilicic et al. 2024 |
| | Brown algae (kelp) | Karling 1943; Gleason et al. 2011a; Gachon et al. 2017; Murúa et al. 2020, 2023 |
| Marine microbenthos | Diatoms | Muehlstein et al. 1988; Ilicic et al. 2024 |
| Snow and ice algae | Green algae and diatoms | Hassett and Gradinger 2016; Fiołka et al. 2021; Kobayashi et al. 2023; Nakanishi et al. 2025 |
| Mass freshwater algal cultures | Green algae | Fott 1967; Ilkov 1975; Shin et al. 2001; Hoffman et al. 2008; Han et al. 2013; Letcher et al. 2013, 2016; Carney and Lane 2014 |
| Marine aquacultures | Red algae | Badis et al. 2019, 2020 |

hosts in the environment allows the parasites to develop, transmit and increase their abundance.

Hosts of AZP also include aquatic vascular plants, such as seagrasses (*Zostera marina*—Muehlstein 1998; Muehlstein et al. 1991) and their pollen (e.g. Sparrow 1960; Stoyneva et al. 2013; Seto et al. 2023; Stoyneva-Gärtner and Uzunov 2024), while heterotrophic hosts include marine and freshwater amoebae and invertebrates (including rotifers, nematodes, mites, crustaceans and insects), amphibians and fish (Table 2). AZP of these groups infect not only adults, but

**Table 2** Heterotrophic hosts of AZP from different taxonomic groups

| Taxonomic group | Refs. |
|---|---|
| Protozoa (Amoebae) | Sparrow 1960; Corsaro et al. 2014a, b |
| Invertebrates (rotifers, nematodes, mites, crustaceans and insects) | Prowse 1954; Sparrow 1960; Green 1974; Batko 1975; Whisler et al. 1975; Bahnweg and Blang 1980; Burns 1980, 1985; Seymour et al. 1984; Martin 1987; Lord and Fukuda 1990; Glockling 1998; Gleason et al. 2008; Do Amaral et al. 2013; Valois and Burns 2016; Garcia et al. 2020; Masigol et al. 2023; Seto et al. 2023; Stoyneva-Gärtner and Uzunov 2024 |
| Amphibians | Berger et al. 1998, 2005; Czeczuga et al. 1998a; Longcore et al. 1999; Fisher and Garner 2007, 2020; Hyatt et al. 2007; Fisher et al. 2012 |
| Fish | Stirling 1880; Shanor and Saslow 1944; Florinskaya 1971; Ferguson and Ride 1980; Chien 1981; Lartseva 1986; Frick and Reinhold 1987; Dudka et al. 1989; Czeczuga and Muszynska 1998, 1999a, b; Lartseva and Dudka 1990; Hatai and Hoshiai 1992; Czeczuga and Godlewska 2001; Chukanhom and Hatai 2004; Fisher et al. 2012; Masigol et al. 2023 |

also eggs and various developmental stages such as larvae and tadpoles (e.g. Chukanhom and Hatai 2004; Seto et al. 2023).

It is widely recognised that parasite fitness depends on successful transfer from one host to another (Shaw et al. 2020) which requires host densities exceeding a critical threshold necessary for effective transmission and parasite development (Holt et al. 2003). Peaks in the abundance of susceptible algal hosts are indeed associated with peaks in the abundance of related parasitic species (e.g. Holfeld 2000; Ibelings et al. 2011; Gutiérrez et al. 2016; Taylor and Cunliffe 2016). Such patterns have been observed in various environments, from lakes (Rasconi et al. 2012) to marine settings (Hanic et al. 2009; Fernández-Valero et al. 2022, 2023), and are typical not only for classical AZP such as chytrids, but also for Perkinsea parasitoids (i.e. parasitic protists; Reñé et al. 2021b). The same applies to artificial freshwater systems for mass algal cultivation, where the chytrid *Rhizophydium scenedesmi* (Syn. *Phlyctidium scenedesmi*), *Amoeboaphelidium protococcarum* (Cryptomycota) and the blastoclad *Paraphysoderma sedebokerensis* cause severe production losses in green microalgae *Scenedesmus* s.l. (e.g. Fott 1967; Ilkov 1975), *Tetradesmus dimorphus* (Letcher et al. 2013) and *Haematococcus lacustris* (Han et al. 2013), respectively.

The high prevalence of AZP infections during algal blooms directly affects algal growth and leads to the termination or suppression of the bloom (e.g. Canter and Lund 1951; Van Wichelen et al. 2010; Gsell et al. 2013a; Sime-Ngando 2012), which, in turn, usually reduces the abundance and infection success of the causative AZP (e.g. Holfeld 2000; Sime-Ngando 2012). The presence of AZP and successful infections can influence the composition, succession, dominance and size structure of phytoplankton communities not only directly, but also by affecting interspecific competition between hosts and other algal species (e.g. Canter and Lund 1951; Van Donk and Ringelberg 1983; Van Donk 1989; Ibelings et al. 2004; Grami et al. 2011; Rasconi et al. 2012, 2014; Sime-Ngando 2012; Kagami et al. 2014). This occurs because, by parasitising one species and causing its population to decline, AZP alter competition among phytoplankton species, leading to an increase in the population of one or more competing algae. Several examples of such size- and composition-altering replacements confirm the general temporal shift from infection-inhibited large pennate diatoms (e.g. 50–70 µm in length: *Asterionella*, *Fragilaria*) to small non-infected centrics (e.g. 10 µm in diameter: *Stephanodiscus*) in deep lakes (e.g. Van Donk and Ringelberg 1983; Sommer 1987; Rasconi et al. 2011; Sime-Ngando 2012). Spatial shift in phytoplankton dominance was observed in the Danube River, from the heavily chytrid-infected small centric diatom *Stephanodiscus hantzschii* to the larger, uninfected pennate diatoms *Nitzschia acicularis* and *Diatoma elongata* (Stoyneva 1998). In marine waters, temporal replacement of large centric diatoms *Thalassiosira* and *Skeletonema* infected by chytrids by non-infected centric *Chaetoceros* was recorded (Gutiérrez et al. 2016). The results of physiological experiments with a widespread marine thraustochytrid and *Chaetoceros* suggest that parasitic systems target weaker phytoplankton individuals (Leshem et al. 2016) and thus improve population health (Laundon et al. 2021). Increased infections of stressed ice algae have also been recorded during field studies in Arctic marine systems (Hassett and Gradinger 2016). In contrast, other researchers claim that parasites grow better on healthy, non-stressed individuals, as has been shown for desmids and chytrids (Van den Wyngaert et al. 2014; Schampera et al. 2021).

It is worth noting that, in addition to free-swimming and chemotactic zoospores, some AZP can also reproduce by non-motile spores with thick cell walls (i.e. resting stages), which are not chemotactic and, after germination, usually need a high host density to infect new hosts (Gleason et al. 2015; Weldon et al. 2025).

A dependence of parasites on host density has been documented, though rarely, in zooplankton. For example, Valkanov (1931a, b) highlighted the more intensive development of *Hydatinophagus apsteinii* (Syn. *Aphanomyces hydatinae*) in the freshwater rotifer *Hydatina senta* during its mass growth following the snowmelt in February–March. The strong dependence of the zoospore–zooplankton interaction on high parasite efficiency has been indicated (Miki et al. 2011; Thongthaisong et al. 2022, 2025). Several studies show the selective pressure exerted by AZP from Blastocladiomycota (*Aphanomyces*, *Leptolegnia*, *Saprolegnia* and *Scoliolegnia*) on zooplankton populations of the genera *Boeckella*, *Daphnia* and *Parabroteas*, as well as on mosquito larvae (Whisler et al. 1974, 1975; Johnson et al. 2006; Gleason et al. 2008; Wolinska et al. 2008, 2009).

In other hosts, such as amphibians, density-dependent dynamics of infections has also been demonstrated. For example, experimental assessments of AZP disease transmission in *Rana mucosa* tadpoles have shown that the proportion of newly infected tadpoles increased with the number of previously infected individuals (Rachowicz and Briggs 2007). Similarly, a field experiment with tadpoles of *Alytes obstetricans* showed a rapid spread of infection once a single tadpole in a group was infected (Courtois et al. 2017). As these two species also produce overwintering larvae, they could act as super-spreaders, as their infected tadpoles usually do not die from the infection. This gives the pathogen time to multiply throughout the year and increase zoospore loads during winter in the ice-free, deeper parts of a lake, with potentially higher host densities during winter and early spring (Clare et al. 2016; Fernández-Beaskoetxea et al. 2016).

Fish mass mortality, particularly in salmonids, caused by excessive development of AZP has been known since the late nineteenth century (Stirling 1880). The AZP species most frequently responsible for losses in aquaculture and the wild are coregonids and acipenserids, mainly *Saprolegnia ferax*, *Saprolegnia monoica* and *Saproelgnia parasitica*, but also *Achlya americana*, *Achlya dubia*, *Achlya jlagellata*, *Achlya polyandra*, *Achlya proliferoides*, *Aphanomyces laevis*, *Dictyuchus sterilis*, *Leptolegnia caudata*, *Pythium proliferum*, and *Aphanomyces astaci* (see references in Table 2).

## Host–parasite specificity

The extent to which parasites can exploit different host species, known as host specificity, is considered an important trait of parasites (Poulin et al. 2011; Frenken et al. 2017b). Some AZP are host-specific and infect only a single host or a few related host taxa, while others are generalists and infect multiple species (Glockling et al. 2014). Field studies have often identified single chytrid species infecting one host species or its specific parts (e.g. Canter 1949, 1953; Holfeld 1998; Ibelings et al. 2004; Rasconi et al. 2009), which is most likely due to limited knowledge on this topic and the infrequent observation of host–parasite pairs in nature. However, in some cases, such as for the hosts *Asterionella formosa* and *Planktothrix* sp., chytrid infection was specific to genotypes or chemotypes of the same species (De Bruin et al. 2004; Kyle et al. 2015). For the chytrid *Rhizophydium algavorum*, a wide range of hosts from different taxonomic groups of algae (20 species from five green freshwater genera and one yellow–green alga) has been experimentally proved (Gromov et al. 1999), but some generalists infect hosts only within the same taxonomic group. For example, in marine environments, the parasitoid *Maranthos nigrum* (Perkinsea, Parviluciferaceae) and the chytrid *Dinomyces arenysensis* can infect different genera of dinoflagellates (Lepelletier et al. 2014; Reñé et al. 2021a; Fernández-Valero et al. 2022, 2023). A broad host spectrum encompassing several orders of brown algae has also been demonstrated for the chytrid *Chytridium polysiphoniae*, oomycete *Eurychasma dicksonii* and plasmodiophorid *Maullinia ectocarpii* (Müller et al. 1999; Maier et al. 2000). Similarly, in freshwaters, *Chytridium versatile* can infect ten different diatom species (Sparrow 1960). Another known generalist is the chytrid *Batrachochytrium dendrobatidis*, which can infect hundreds of amphibian species (Scheele et al. 2019) and is considered a pan-zootic chytrid (Torres-Sánchez et al. 2022). The fish parasite *Sphaerothecum destruens* has been found in a wide range of fishes (Charrier et al. 2016; Gunn et al. 2024), and many fish AZP can also infect planktonic crustaceans (Czeczuga et al. 2000), benthic crustaceans (Czeczuga et al. 1999) and shellfish (Czeczuga 2000). *Aphanomyces astaci* also infects a broad spectrum of crustaceans and fish (Czeczuga and Godlewska 2001; Masigol et al. 2023). In addition to field observations, cross-infection experiments (Gutman et al. 2009; Van den Wyngaert et al. 2018) and molecular studies (Kagami et al. 2021) confirm the coexistence of both specialist and generalist parasitic chytrids.

Regarding the hosts, a similar occurrence of specialists and generalists can be observed. Some hosts are infested by a single species, although specificity and virulence may vary widely, as demonstrated by experiments in which strains of *Rhizophydium* sp. infect only *Planktothrix* (McKindles et al. 2021a). In contrast, other hosts can harbour several parasitic species (e.g. Canter and Jaworski 1982; Letcher et al. 2013; Kagami et al. 2021). For example, *Asterionella formosa* has been found to be infected by more than two morphologically distinct chytrids (*Zygorhizidium* sp. and *Rhizophydium* sp.) (Canter 1969; Van Donk and Ringelberg 1983), and several species of AZP of the toxic marine diatom *Pseudonitzschia pungens* have been identified (Hanic et al. 2009). Recently, three different parasitic chytrids, *Algomyces stechlinensis*, *Endocoenobium eudorinae* and *Dangeardia mamillata*, were isolated from a common volvocacean species, *Yamagishiella unicocca* (Van den Wyngaert et al. 2018).

Many studies have emphasised the importance of host species composition and size for parasite infectivity. In freshwater chytrids, many infected phytoplankton hosts are large, such as species of *Asterionella*, *Fragilaria*, *Staurastrum*, *Staurodesmus*, *Dolichospermum*, *Planktothrix* and *Sphaerospermopsis* (e.g. Canter 1969; Sen 1988a, b; Kagami et al. 2007a, b; Rasconi et al. 2009, 2012; Ibelings et al. 2011; Weisbrod et al. 2020; Stoyneva-Gärtner et al. 2023). Large hosts are easier to target because the contact rate between host and parasite is inherently higher (Canter and Jaworski 1981; Sime-Ngando 2012). Larger cells contain more resources (e.g. greater amounts of organic carbon) for parasite nutrition (Lund 1957; Holfeld 1998; Kagami et al. 2007a). In addition, large hosts are less susceptible to grazing (e.g. Stoyneva et al. 2007; Charalampous et al. 2021), making them more attractive for successful parasite development. Thus, it is not surprising that large algae can be heavily infected even at low population densities (e.g. Lund 1957; Holfeld 1998; Sime-Ngando 2012; Rasconi et al. 2012). In contrast, for smaller hosts, such as the centric diatom species of *Melosira* or *Cyclotella*, infection was generally below 3% (Canter and Lund 1969; Sen 1988a, b; Holfeld 1998; Rasconi et al. 2012). Smaller hosts represent the so-called r-type strategy organisms which have high turnover and growth rates and produce many offspring, which could be problematic for parasites with slower growth rates (Rasconi et al. 2012).

### Host–parasite co-evolution, host genetic diversity and host susceptibility

Host–parasite interactions offer great potential for studying co-evolution mechanisms, as these interactions are generally very close and associated with high fitness costs (Thompson 2002). Co-evolution in –ost-parasite systems can occur in two ways, leading to different outcomes: (1) selective sweeps (i.e. successive fixation of beneficial mutations), which result in rapid gene evolution but low levels of standing genotypic variation, or (2) 'Red Queen dynamics', in which species must constantly evolve to avoid extinction and these sustained genotype frequency oscillations lead to long-term maintenance of genotypic diversity (Woolhouse et al. 2002; Frenken et al. 2017b). At the same time, many terrestrial studies indicate that high genetic diversity in host populations results in decreased parasite burdens (e.g. Gibson and Nguyen 2021). In aquatic environments, similar effects in preventing or at least slowing parasitic adaptation due to host genetic diversity have already been observed in the host–parasite system of *Asterionella formosa* and *Zygorhizidium planktonicum* (De Bruin et al. 2008).

The experimental study of *Rhizophydium megarrhizum* and various cyanobacterial strains, such as *Planktothrix agardhii* and *Planktothrix rubescens*, demonstrated that host genetic diversity increases resistance to disease, but can also be considered an important driver leading to rapid, sometimes novel and diverse, adaptations of the parasite to efficiently overcome host defences (Agha et al. 2018). Genetic diversification of natural host populations, promoted by high prevalence of parasitism, was demonstrated by studying genotypes of *Asterionella formosa* populations in three spring blooms under high and low parasite pressure, respectively (Gsell et al. 2013b).

Host–parasite co-evolution was demonstrated in experiments with two chytrid strains, Chy-Lys2009 and Chy-Kol2008, and their *Planktothrix* hosts (Sønstebø and Rohrlack 2011). Results from this study showed the strong selection pressure of parasites on host population, leading to its subdivision into coexisting chemotypes with periodic shifts in their composition, which in turn acts as a driving force resulting in AZP polymorphism. Further experiments with mono- and polycultures of different *Planktothrix agardhii* strains exposed to infection by several chytrid isolates demonstrated the importance of host specificity (genotypic or phenotypic determination of susceptibility) for parasite infection success (McKindles et al. 2023). In addition, the same study highlighted specific interactions between AZP and their hosts when involving diverse organismic communities allowing for co-occurrence, co-infection and competition between parasites.

Specificity and differential susceptibility of algal hosts to AZP were also demonstrated by in situ experiments with four marine diatoms, which showed a positive correlation between the abundance of chytrids (*Chytridium* sp. and *Rhizophydium* sp.) and that of their hosts (*Chaetoceros* sp., *Navicula* sp. and *Rhizosolenia* sp.), while there was no significant correlation with the abundance of *Nitzschia* sp. (Scholz et al. 2017). Experiments with infections of two bloom-forming colonial freshwater cyanobacteria (*Microcystis aeruginosa* and *Microcystis viridis*) showed a generally higher susceptibility of *Microcystis viridis* (85% infection prevalence) to *Chytridium microcystoides* (Van Wichelen et al. 2010). Recent studies by Van den Wyngaert et al. (2023) have also shown differences in susceptibility to infection between the original desmid host *Staurastrum* sp. and the experimentally infected desmid *Staurodesmus* sp. by the chytrid *Staurastromyces oculus*. This may reflect the co-evolutionary history and adaptation of this chytrid and its sympatric host *Staurastrum* sp. as an important driving force.

The susceptibility of the algal host population to parasite infection may vary depending on environmental factors (e.g. temperature—Gsell et al. 2022), as well as various other factors, ranging from compatibility between specific strains to the production of physical barriers and defences or the transition to resistant life cycle stages or morphologies. The specific infection relationships of host species depend on parasite genotype and important morphological characteristics of both hosts and parasites, which influence the infection process and shape host–parasite specificity (Sun et al. 2023). Laboratory experiments with the dinoflagellate *Alexandrium minutum* and its parasite *Parvilucifera sinerae* (Perkinsea) suggested that genes involved in infectivity and subsequent regulation of infection intensities could potentially be involved in co-evolution (Räberg et al. 2014).

Genetic studies on *Batrachochytrium dendrobatidis* from 14 amphibian hosts identified groups of differentially expressed genes among host environments with similar infection outcomes, demonstrating that this parasite exhibits plastic infection strategies when challenged by hosts with varying disease susceptibility (Torres-Sánchez et al. 2022). This study shows that host environments can exert different selection pressures, and that the success of multihost pathogens is promoted by an evolutionary factor such as plasticity of gene expression. According to available evidence for the co-evolution of *Batrachochytrium dendrobatidis* and its hosts, host susceptibility depends on the parasite's geographical distribution, with some hosts able to recover from parasite outbreaks. Parasite genotypes also vary in their geographical distribution and virulence, leading to geographical patterns of host genotype distribution (O'Hanlon et al. 2018; Carvalho et al. 2024).

The functional role of mucilage as a physical barrier against AZP has been demonstrated as one of the defence features of phytoplankton. For example, with its mucilage envelope, *Staurodesmus* is protected from infection by *Staurastromyces oculus*, but without it, it becomes susceptible (Van den Wyngaert et al. 2023). In contrast, other studies have shown the ability of some chytrid AZP, such as *Dangeardia mamillata*, *Algomyces stechlinensis*, *Endocoenobium eudorinae*, *Phlyctochytrium planicorne* and *Rhizophydium ubiquetum*, to penetrate the mucilage layer of coenobial flagellate chlorophyte algae (Canter 1950; Van den Wyngaert et al. 2018) or desmids (Canter 1961) with their rhizoids, probably using carbohydrate-active enzymes that can degrade complex mucilage polymers (Lange et al. 2019; Van den Wyngaert et al. 2023).

The role of autophagy as a defence pathway during infection, considered a key player in host–pathogen interactions (Evans et al. 2018), has been demonstrated in studies on marine brown algae (Murúa et al. 2020), as well as on freshwater diatoms (Canter and Jaworski 1979) and chlorophytes (Seto et al. 2020).

## Allelopathy

In aquatic ecosystems, chemical interactions such as allelopathy play key roles in regulating various physiological processes and biological interactions that strongly influence population structure, community organisation and ecosystem function (Hay 2009, 2014). Allelopathy is a biological phenomenon in which one organism produces one or more chemical compounds, called allelochemicals, that can influence the germination, growth, reproduction and even survival of other organisms (Stamp 2003; Sentenac et al. 2022). The term was originally created for direct biochemical interactions between neighbouring plants, but was later broadened to include all possible chemical interactions between organisms (Whittaker and Feeny 1971; Rice 1984; Stamp 2003). In this broader sense, organisms can not only be harmed but also benefit from allelochemicals (Whittaker and Feeny 1971; Stamp 2003). Thus, allelopathy can have both positive and negative effects, either promoting symbiotic relationships or eliminating competitors, thereby influencing species interactions and ecological balance. Although allelochemicals are primarily studied in terrestrial plants, they are also a recurrent focus of interest in aquatic ecosystems, particularly in interactions with planktonic parasites (Vallet et al. 2023; Vallet 2024). Aquatic parasites can alter host chemical cues, affecting community dynamics and impacting organisms at all trophic levels (e.g. Friesen and Detwiler 2021).

Research has shown that certain metabolic products of the host act as specific chemical signals—chemoattractants—that attract parasites. The zoospores of AZP (e.g. chytrids, blastoclads) are chemotactic and can quickly locate uninfected host cells (Sparrow 1960; Canter and Lund 1951; Gleason and Lilje 2009; Voyles et al. 2011; Van den Wyngaert et al. 2014; Wang et al. 2021). Zoospores of chytrid parasites can be attracted to cell extracts of stressed hosts and to certain dissolved carbohydrates (Scholz et al. 2017), or to small amino acids and carbohydrates that are by-products of photosynthesis (Muehlstein et al. 1988). In addition, the volatile compounds released by infected and uninfected hosts display different metabolic profiles, such as a reduction in antifungal compounds in chytrid-infected cells (Yoneya et al. 2021).

The excretion of primary or secondary metabolites as a host defence mechanism has been widely discussed in relation to algae and their production of toxins (phycotoxins), with all accumulated contradictory data arguing against the primacy and predominance of this protective function (Gärtner et al. 2021). A targeted study on *Planktothrix rubescens* has shown that its toxins (microcystins, microviridins and/or anabaenopeptins) can reduce susceptibility to chytrid infections and thus increase the host's chances of survival (Rohrlack et al. 2013). In contrast, observations on the microcystin-producing *Microcystis aeruginosa* and *Microcystis viridis* indicate that the toxins are not involved in host resistance to *Chytridium microcystoides* (Van Wichelen et al. 2010). Similar conclusions can be drawn from experiments on the variation of microcystin production in *Planktothrix agardhii* and *Planktothrix rubescens* which show that chytrid infection leads to limited or no release of this toxin (Agha et al. 2022). Weisbrod et al. (2020) reported selective parasitism of the chytrid *Rhizosiphon crassum* on a straight morphotype of the filamentous, bloom-forming cyanobacterium *Dolichospermum* sp. with increased toxin production (microcystins and anabaenopeptins), while the coiled morphotype of this alga was not infected despite the constant presence of chytrids in the environment. The authors interpreted this as a defence reaction to parasitism at the expense of lower competitiveness of the straight form compared with the co-occurring coiled morphotype. Abscisic acid is a chemical produced by *Tetradesmus obliquus* to protect the host from infection by the chytrid *Rhizophydium scenedesmi* (Puneva and Christov 2004; Puneva 2006).

## Grazing

In both freshwater and marine environments, phytoplankters are exposed to protozoans and metazoans that exert temporally and spatially variable feeding pressure (Reynolds 2006; Lürling 2021). Thus, phytoplankton must withstand grazing (Reynolds 2012), which is considered one of the largest loss processes and strongest selective forces on phytoplankton (Smetacek 2001; Lürling 2021). The altered structures of phytoplankton communities due to grazing are well documented. Such changes in the occurrence and availability of hosts inevitably lead to shifts in their AZP and infection success. For example, *Asterionella formosa* is less affected by

*Rhizophydium planctonicum* in summer, when zooplankton grazers are more active, than in winter (Rasconi et al. 2011). The presence of the generalist zooplankton grazer *Daphnia* can significantly reduce the intensity of chytrid infection on phytoplankton (Kagami et al. 2004; Lürling 2021).

In addition to these indirect effects of grazing on parasites through changes in host availability, evidence shows that grazing can also have direct effects on AZP by consuming their free-living zoospores (Thongthaisong et al. 2022), which are highly susceptible owing to their lack of cell walls (Gleason and Lilje 2009). Although AZP, and chytrids in particular, are generally thought to produce too many spores to be fully controlled by zooplankton grazing alone (Frenken et al. 2019), several studies have shown that crustaceans, ciliates and rotifers actively ingest zoospores in freshwaters (Kagami et al. 2007a, b, 2014; Gleason and Lilje 2009; Buck et al. 2011; Hamilton et al. 2012; Searle et al. 2013; Schmeller et al. 2014; Agha et al. 2016; Frenken et al. 2018; Thongthaisong et al. 2025). In marine systems, grazing on zoospores can also lead to fluctuations in the relative abundance of chytrids (Johansson and Coats 2002). Parasitic zoospores are a valuable food source with suitable dimensions for both types of zooplankton: selective or specialised grazers (e.g. rotifers) and non-selective or generalist grazers (e.g. filter-feeding cladocerans) (Gleason et al. 2009; Sime-Ngando 2012; Frenken et al. 2016; Lürling 2021; Abonyi et al. 2024). It is estimated that chytrid zoospores can supplement the zooplankton diet in freshwaters by up to 60% (Rasconi et al. 2014). Results also suggest that small zooplankton benefit nutritionally from chytrid zoospores during blooms of large diatoms, as they prevent losses from downstream transport and retain organic matter within the system (Maier et al. 2016). In the marine environment, next generation sequencing has shown that chytrids from diatoms account for a large proportion of sequence reads in the gut of the Arctic copepod *Calanus glacialis* (Cleary et al. 2017). Zoospores are not only an important food source in terms of quantity, but also contribute to food quality, as they transfer all the nutrients they have absorbed from large inedible algae directly to zooplankton (Gerphagnon et al. 2015). In addition, zoospores enhance trophic value by converting short-chain polyunsaturated fatty acids (PUFAs) from inedible hosts into long-chain PUFAs (Gerphagnon et al. 2019; Taube et al. 2019; Rasconi et al. 2020) or by enriching the biochemical composition of their hosts through de novo synthesis of sterols (Gerphagnon et al. 2019). Therefore, zoospores are considered a valuable food source for zooplankton and form an alternative trophic link between large inedible phytoplankton and zooplankton, known as the mycoloop (Kagami et al. 2007a, 2014; Miki et al. 2011; Frenken et al. 2020; Chen et al. 2024; Thongthaisong et al. 2022, 2025). Other notable trophic links involve bacteria and carbon transfer through the so-called fungal shunt (Klawonn et al. 2021), including pollen, from which organic carbon, normally unavailable to zooplankton, is efficiently transferred via chytrid fungi to higher trophic levels (Gerphagnon et al. 2019). In this way, AZP can also control the population dynamics of many invertebrate grazers such as crustaceans, rotifers, nematodes, arachnids (e.g. mites) and insects (Gleason et al. 2008), particularly in benthos (benthic shortcut) (Attermeyer et al. 2013). Thus, AZP themselves may serve as a driving force that alters the abundance, distribution and availability of their hosts, with profound consequences for their own evolution.

Herbivory can indirectly affect phytoplankton infections, for example through fragmentation of hosts caused by zooplankton, which provides more new infection sites for chytrid parasites to colonise (Frenken et al. 2020). Grazers may also reduce epidemics of virulent parasites by selectively grazing on and consuming infected cells or organisms, thereby maintaining population health (Packer et al. 2003). However, this effect has not yet been demonstrated for AZP.

### Microbiomes and environmental biofilms

The interactions between globally distributed communities enclosed in a gelatinous matrix, commonly referred to as biofilms (Sentenac et al. 2022), and AZP–host systems, as well as interactions between microbial communities coexisting with different AZP–host systems, may influence the occurrence and success of parasitic infections.

Interactions between algae and microbial communities have been studied mainly in the context of algal production systems, where algae coexist with various associated microorganisms (Dittami et al. 2014) that promote their growth (Hom et al. 2015) or support faster and more efficient removal of organic and inorganic wastes and hazardous substances (e.g. Su et al. 2012; Luo et al. 2014; Cavaliere et al. 2017). However, whether these associated or symbiotic microorganisms also help algae to ward off chytrid infections remains unclear. Significant changes in the native bacterial microbiome during AZP infection of algae were recorded in experiments with the freshwater green alga *Coelastrella vacuolata* (Syn. *Scenedesmus vacuolatus*) and its endoparasite *Amoeboaphelidium protococcarum* (Hoeger et al. 2022). The observed shifts in the functional and metabolic profiles of the bacteria during infection were driven by the release of nutrients and metabolites from decaying algal cells, resulting in increased bacterial metabolism of amino acids, lipids, nucleotides and carbohydrates, suggesting that the microbiome can adapt its metabolism to algal host die-off.

Research on the interactions between *Batrachochytrium dendrobatidis* and microorganisms is particularly advanced, with growing evidence highlighting the important role of amphibian skin-associated microbial communities and those from biofilms in infection dynamics and the likelihood of AZP occurrence (e.g. Woodhams et al. 2011; Bletz et al. 2013; Garner et al. 2016; Torres-Sánchez and Longo 2022; Loyau et al. 2024). Although in some cases the bacterial composition on the skin reflects the host and environment rather than any chytrid impact (Kruger 2020), it is broadly accepted that the severity of infection depends on the composition and/or richness of the skin microbiome (e.g. Brucker et al. 2008; Bates et al. 2018; Schmeller et al. 2022; Loyau et al. 2024). In addition, infection success is influenced by the abundance of chytrid-inhibitory taxa on amphibian skin (Bernardo-Cravo et al. 2020; Loyau et al. 2024) and by antifungal metabolites secreted by bacteria to inhibit parasite growth (e.g. Harris et al. 2006, 2009; Bell et al. 2013; Loudon et al. 2014; Woodhams et al. 2015; Niederle et al. 2019; Torres-Sánchez and Longo 2022; Ujszegi et al. 2023).

The effects of the microbiota on *Batrachochytrium dendrobatidis*, which prevent pathogen-induced morbidity and mortality, led to the formulation of the 'Adaptive Microbiome Hypothesis'. This hypothesis proposes that exposure to a pathogen can trigger the rapid proliferation of anti-pathogenic microbes, thereby reducing microbial diversity but increasing anti-pathogen function (Woodhams et al. 2023). This understanding of the individual host response may also apply to other AZP. However, our knowledge remains limited, and the recruitment process of protective microbes is largely unknown, though it may be related to host physiology and/or environmental factors (Davis et al. 2017; Flechas et al. 2019). Thus, the concept of the Disease Pyramid, which includes the host, pathogen, environmental factors and the microbiome, provides a comprehensive framework for future research into AZP (Bernardo-Cravo et al. 2020).

For *Batrachochytrium dendrobatidis*, it was further shown that the different compositions of biofilms in mountain lakes affect infection dynamics, and experiments confirmed that parasite zoospores are inactivated even by simple biofilms within a few hours (Sentenac et al. 2024). Besides biofilms associated with *Batrachochytrium dendrobatidis*, many other biofilms on amphibians may entrap zoospores, which are then consumed or displaced by the biofilm inhabitants or inactivated by biofilm metabolites (Chabaud et al. 2006; Rendueles and Ghigo 2012). Biofilm inhabitants may also include sessile or semi-sessile rotifers and ciliates, which have been shown to feed on AZP and chytrids in particular (Weitere et al. 2018; Mialet et al. 2013). Depending on their composition, biofilms can therefore be considered natural biological barriers that prevent AZP infections (Sentenac et al. 2024) and, in this respect, are considered biological drivers affecting AZP.

## Effects of other organisms co-occurring with AZP and their hosts, co-infections and hyper-parasitism

In aquatic environments, as in other parts of the world, host–parasite systems are surrounded by numerous other organisms that influence them through various physical, chemical and biotic interactions, extending beyond grazing, symbiotic microbiomes or environmental biofilms. For example, high densities of planktonic green algae negatively affected the abundance of zoospores of *Batrachochytrium dendrobatidis*, suggesting physical interference or allelopathy (Searle et al. 2013).

Besides the interactions between host and AZP, other parasites can also develop on, or in, the host and thus influence the host's susceptibility to infection and potential mortality. This is the case with pathogens such as *Hannemania* mites, which also persist and develop within the spongy epidermis and cause various detrimental effects on amphibians, such as deformities, reduced foraging ability, loss of chemosensory function and reduced reproduction and survival (Jacinto-Maldonado et al. 2024). In addition, mites can transport toxic cerium oxide nanoparticles into the bodies of amphibians during the larval period, increasing mortality, causing behavioural changes and inhibiting amphibian growth (Jacinto-Maldonado et al. 2022). Currently, a significant correlation has been observed between the intensity of chytrid infection and the abundance of mites and amphibian species (especially in *Lithobates yavapaiensis*), particularly in anthropogenically disturbed waters (Jacinto-Maldonado et al. 2024). Similar modulations may occur with co-infections of *Batrachochytrium dendrobatidis* and Ranavirus, particularly Frog Virus 3 (FV3), which, although not common (Bosch et al. 2020), has been documented in various amphibian populations worldwide (Olori et al. 2018; Thumsová et al. 2024; Yoldas et al. 2024). Some studies suggest that the chytrid and the virus may interact synergistically, potentially increasing infection intensity and disease progression in co-infected hosts (De Jesús Andino et al. 2024; Thumsová et al. 2024).

Despite their small size, individual AZP cells are complex environments and can be hyper-parasitised by other parasites (Seto et al. 2023). Thus, hyper-parasitism may be another biological driver of AZP, as suggested after the discovery of chytrid or rozellid hyper-parasites that infect other parasitic chytrids or oomycetes on phytoplankton. Examples include *Rhizophydium carpophilum* on endoparasitic *Olpidiopsis* infecting *Achlya*, *Chytridium parasiticum* or *Septosperma anomalum* on *Chytriomyces tabellariae* (Canter 1949) and on *Zygophlyctis asterionellae*, *Rozella parva* on *Zygorhizidium affluens* and *Rozella* spp. on chytrids or oomycetes (Sparrow 1932; Canter 1969; Canter and Jaworski 1986; Gleason et al. 2014; Frenken et al. 2017b; Letcher and Powell 2018), as well as additional chytrid and rozellid strains on algal AZP currently identified and sequenced by Seto et al. (2023). The ecological importance of hyper-parasitism has been demonstrated in phytoplankton studies, where hyper-parasitism of the primary parasite may reduce its impact by decreasing or suppressing the release of spores (Canter-Lund and Lund 1995; Frenken et al. 2017b).

### Aquatic organisms and waterfowl as dispersal vectors of AZP and their hosts

Dispersal is one of the most important drivers of biodiversity at both local and global levels and concerns both AZP and their hosts. In addition to physical dispersal vectors, aquatic organisms and waterfowl are important for the spatial distribution of AZP hosts such as algae (Kristiansen 1996a, b; Padisák et al. 2016). Following the classic studies by Proctor (1966) and Atkinson (1970, 1971, 1972, 1980), there has been little research demonstrating the importance of algal transport by birds over long distances along their migratory routes (Coesel et al. 1988; Cellamare 2010, 2013; Stoyneva 2016). Birds can also act as sentinels for potential disease outbreaks (Green and Elmberg 2014). In vitro studies of *Batrachochytrium dendrobatidis* have shown that it can survive 1–3 h of drying between transfers from sterile feathers to new culture media, supporting the idea of its possible translocation by birds (Johnson and Speare 2005). A few research papers have experimentally demonstrated the role of birds in the transport of aquatic invertebrates (for details see Charalambidou and Santamaría 2002; Figuerola et al. 2004; Green et al. 2023). Here, we would like to highlight the important findings of Brown (1933), which demonstrate that invertebrate reproduction can still occur after 26 h in the gut of birds and up to 14 days in the gut of amphibians and reptiles. This supports the concept of long-distance transport of aquatic invertebrates as AZP hosts. Aquatic insects (32 species of Odonata, Hemiptera, Diptera and Trichoptera in both larval and adult stages) were identified as dispersal vectors of 28 fish and crayfish AZP in six waterbodies with different trophic statuses (Czeczuga et al. 1998b, 1999b, 2000; Czeczuga and Godlewska 2001). The highest number of fish parasites developed on the water scorpion *Nepa cinerea* (16), while the lowest numbers (four species on each) were found on the larvae of the hawker dragonfly dragonfly *Anax imperator*, the phantom midge *Chaoborus cristallinus*, the fly *Paramormia decipiens* (Syn. *Pericoma decipiens*) and adult ground beetle *Hydroporus palustris*.

### Invasive species as dispersal vectors that drive AZP

Non-native (also known as alien, non-indigenous or allochthonous) species are defined as those capable of surviving and reproducing when introduced outside their former or current range (Kokociński et al. 2017; Soto et al. 2024). An invasive species is a widespread alien species that has an adverse effect on the invaded habitat, local ecosystems and species, thereby threatening local biodiversity (Colautti and MacIsaac 2004; Wilk-Woźniak and Najberek 2013; Kokociński et al. 2017). In the context of increasing globalisation and the associated exchange of goods (e.g. Stoyneva-Gärtner and Uzunov 2015), it is often difficult to distinguish between human-mediated movements, whether intentional or unintentional, and natural migration processes. Nevertheless, it appears likely that most current invasions are facilitated by global climate change (Walther et al. 2009).

The emergence of non-indigenous pathogenic AZP is an increasing threat to global health, biodiversity, food safety and the global economy (Fisher et al. 2012; Combe et al. 2022). When discussing AZP drivers, we consider invasive host species for their role as vectors in spreading their specific parasites. For example, *Aphanomyces astaci*, which causes crayfish plague in noble crayfish and many fish species, arrived in Europe from America via non-native crayfish imported for aquaculture and farming (Holdich et al. 2009; Svoboda et al. 2017; Martín-Torrijos et al. 2021). Owing to the high host mortality, *Aphanomyces* itself, as well as its non-native crayfish vectors, are listed by the IUCN as among the 100 worst invasive alien species in the world (Lowe et al. 2000).

Another prominent example of an AZP whose global presence has been driven by an invasive species is *Batrachochytrium dendrobatidis* (Voyles et al. 2009). It is currently distributed on all continents except Antarctica, where its amphibian hosts do not occur (Fisher et al. 2009). Vectors of this AZP and the related disease include the invasive African clawed frog *Xenopus laevis* and the American bullfrog *Lithobates catesbeianus* (Fisher et al. 2009; Scheele et al. 2019; Nie and Feng 2022; Carvalho et al. 2024). Parasite transport routes involve both indirect transmission via free-swimming zoospores and direct transmission of zoospores through host-to-host contact (Carvalho et al. 2024). Its sister species, *Batrachochytrium salamandrivorans*, is also considered an emerging fungal pathogen of salamanders and newts (Urodela) (Martel et al. 2014; EFSA 2018). Its origin is thought to be in East Asia, where it infects native salamanders without causing significant disease (Martel et al. 2014). Recently, it has been introduced into European amphibian populations, where it has caused severe declines, and in at least one case its spread has been linked to the presence of an invasive species (Lötters et al. 2020; Martel et al. 2020).

Within the non-fungal AZP, an emerging pathogen is *Sphaerothecum destruens*, an agent of a disease with high mortality among populations of cyprinids and salmonids, posing a threat to native European fishes and causing significant economic damage to their aquaculture (Charrier et al. 2016; Combe et al. 2022; Gozlan and Combe 2023). The most common biological driver of the pathogen worldwide is the highly invasive Asian gudgeon, the small cyprinid *Pseudorasbora parva* (Charrier et al. 2016; Combe et al. 2022), which appeared in Europe from China (e.g. Sana et al. 2017) through multiple invasions (Brazier et al. 2021).

## Discussion

During the past two decades, AZP have received increasing attention in the scientific community; however, our understanding of their physiology and ecology remains limited (Grossart and Rojas-Jimenez 2016; Grossart et al. 2019; Rasconi et al. 2022). This is hindered by the fact that we are far from knowing the true AZP biodiversity in all communities across various types of aquatic habitats and different geographical regions. Currently, research is dominated by studies in large lakes from temperate regions, while marine environments, deep-sea habitats and polar regions are gaining increasing attention. There is still little data from small water bodies, rivers and streams. Most AZP studies focus on chytrids and their phytoplankton or amphibian hosts, while much more observation and experimentation are needed for other host–parasite systems.

Analysis of the available literature reveals diversity of factors influencing the AZP success and that no single factor has been equally well studied for AZP across all taxonomic groups in different habitats and communities. Therefore, assessing the role of individual influencing factors and determining general patterns of AZP responses to environmental changes remains a challenge. The variability of the results obtained indicates that the effects of individual factors are often species-specific and may influence infection dynamics differently in various host–pathogen systems. For example, data collected to date on the effects of pH, salinity and heavy metals on different AZP are inconsistent and vary in a case-specific manner. All factors can either directly influence the diversity, distribution, growth and virulence of AZP or act in complex and often complicated ways in environments where host–parasite systems coexist with a variety of organisms. An additional complication in identifying major AZP drivers arises from the fact that, during their life cycles, AZP produce zoospores and non-motile resting stages that may have environmental requirements different from those of the adult stages. For example, AZP zoospores are naked and therefore more sensitive to factors such as drought, light, heavy metals and grazing (e.g. Gleason and Lilje 2009; Thongthaisong et al. 2022, 2025; Galindo et al. 2024). Regarding individual factors, most studies report on temperature effects on AZP. Although higher temperatures generally favour more infections (Gehman et al. 2018), many chytrids and some other AZP cannot grow at water temperatures above 23–27 °C (Boyle et al. 2003; Johnson et al. 2003; Piotrowski et al. 2004; McKindles et al. 2021b). Therefore, future global warming, with an increasing frequency of heat extremes, is expected to have a significant impact on the population sizes and diversity of AZP in aquatic environments. However, most empirical data on parasite fitness and disease progression have been measured immediately after sudden temperature increases, ruling out the possibility of parasite adaptation to continuously increasing temperatures. This suggests that disease progression under global warming is largely determined by the thermal tolerance range of both host and parasite (Schampera et al. 2020). Their development is strongly affected by shifts in the timing of seasonal events caused by global warming, leading to the so-called phenological mismatch, with differences in the resource requirements of hosts and parasites (e.g. Stenseth and Mysterud 2002; Gsell et al. 2023; Gronchi et al. 2023).

Trends in the future development of different AZP and relevant epidemics are likely to differ if only water temperature is considered. However, temperature never acts alone, and the AZP response can be strongly influenced by other natural environmental factors or anthropogenic impacts. In projected future scenarios resulting from global change, environmental conditions of various aquatic habitats and their biodiversity, including hosts and AZP, are expected to change. Among these changes is the anticipated warming of large parts of the world, especially during the winter season and at high latitudes (IPCC 2014; Sharma et al. 2019). Reduced glacier areas and shifts in the timing and intensity of snow and ice melt will decrease habitats for cryophilic AZP–host systems, leading to reduced diversity. Conversely, such events can also affect these host–parasite systems by altering the light regime and reducing salinity (e.g. Hassett and Gradinger 2016; Scholz et al. 2017; Ilicic et al. 2022). Thus, the influencing factors are manifold, especially in the context of global climate change, and the same factor can affect different AZP not only directly and indirectly, but often in opposing ways. The difficulty in predicting specific responses of various AZP also arises from the fact that gradual and pulse warming effects differ in magnitude and seasonality depending on the study area (e.g. lakes versus open ocean), region (e.g. polar versus tropical) and water depth (e.g. surface versus deep water layers).

There is virtual consensus that rising temperatures due to global climate change are leading to the spread of algal blooms (Paerl and Huisman 2009; Griffith and Gobler 2020) and floating plant cover (Kleinschroth et al. 2021), resulting in higher host density and a corresponding increase in AZP infection success (e.g. Holfeld 2000; Reñé et al. 2021b; Fernández-Valero et al. 2022, 2023). Conversely, mass development of algae and plants reduces light availability in the water column, which can hinder zoospore attachment to hosts, leading to reduced infection success (Canter and Jaworski 1980; Bruning 1991b, c, d; Scholz et al. 2017). Temperature fluctuations can also lead to changes in water stratification and the relevant spectral composition of available light: if the mixed surface layers become shallower during warming, AZP and their hosts will be exposed not only to more light, but also to more red or green light instead of blue light, which may favour parasite transmission and infection outcomes (e.g. Tao et al. 2020).

Climate change is expected to alter precipitation patterns both spatially and temporally, and increase the likelihood of extreme weather events, including heavy rainfall and droughts (IPCC 2014). Excessive water run-off from land to water can dilute ion concentrations, while seawater intrusion or a reduction in volume due to droughts can increase dissolved ion concentrations in freshwater (Kaushal et al. 2025). In both cases, such events may severely affect the physiology of both freshwater and marine AZP. If lower salinity promotes the development of AZP with lower salinity tolerance, there may also be a concomitant loss of halophilic AZP (e.g. Muehlstein 1998; Muehlstein et al. 1991). When discussing the impact of global warming and the expected drier conditions on AZP, it is important to emphasise their high susceptibility to desiccation, especially in amphibian parasites (e.g. Johnson et al. 2003; Haver et al. 2022). There is no doubt that increasing drought periods will affect waterbodies, especially smaller and temporary ones, resulting in a highly probable decline in host diversity and, subsequently, of AZP.

Another major problem for aquatic environments is eutrophication. Extensive literature already exists on its occurrence and consequences in freshwaters and coastal seas, and various approaches have been proposed to mitigate this generally undesirable but mainly human-induced phenomenon. Both the extent and impact of eutrophication, as well as the effectiveness of measures to prevent it, can vary greatly both spatially and temporally, but in all cases they affect aquatic life, including the distribution and abundance of AZP and their hosts. It should be noted that eutrophication increases pH to extreme levels owing to the depletion of dissolved inorganic carbon, exposing aquatic diversity, including AZP diversity, to the risk of species shifts or declines (Lobo et al. 2024). Elevated pH can impair the chemosensory abilities of organisms that rely on the perception of dissolved chemical cues for survival, as has been shown for predatory snails (Turner and Chislock 2010). Such ‘blinding’ may also be expected to affect the chemotactic, host-seeking zoospores of AZP (e.g. Sparrow 1960; Canter and Lund 1951; Muehlstein et al. 1988; Gleason and Lilje 2009; Wang et al. 2021). In addition, microbial decomposition of the organic matter from dense algal blooms caused by eutrophication leads to a strong reduction in dissolved oxygen, creating hypoxic or anoxic ‘dead zones’. The lack of oxygen negatively affects almost all aquatic organisms, including AZP, most of which are typical aerobes (e.g. Gleason 1976; Sime-Ngando 2012). Eutrophication is also accompanied by significant changes in the structure of aquatic communities. As AZP use their hosts as the main source of nutrients, the effects of nutrient enrichment or depletion are usually more pronounced in the hosts and typically affect the AZP indirectly. Thus, increased P and N concentrations generally stimulate algal growth and promote their parasites (Sime-Ngando 2012; Rasconi et al. 2012). However, greater epidemic success can also occur following a reduction in host growth in cases of nutrient limitation (Bruning 1991a).

From all collected data, we conclude that the diversity, dominance, infection rates and success of AZP depend largely on the presence and abundance of their hosts and, therefore, on the drivers of host abundance and distribution. In some cases, factors affect both AZP and their hosts in similar ways but with different intensities. This has been shown in experiments where fungicides harmful to the parasites may also affect the host and increase infection outcomes (Chew et al. 2024). Evidence has also been collected, albeit less frequently, that a particular ecological factor can affect the parasites and their hosts in opposing ways and, when it has a negative effect on the host, it can increase AZP infection success. This has been exemplified by the different effects of UVR on amphibians and their chytrids (Cramp et al. 2022; Haver et al. 2022). Similarly, the overall effect of global warming is predicted to be rather negative for amphibians, but may benefit their pathogens (e.g. Cohen et al. 2017; Haver et al. 2022).

Conversely, certain environmental conditions may limit the performance of parasites more than that of their hosts, thereby providing the hosts with environmental refugia from disease, as shown for chytrids in amphibians during drought (Scheele et al. 2015) and for many phytoplankters and their parasites with different thermal tolerance ranges (e.g. Van Donk and Ringelberg 1983; Ibelings et al. 2011; Wierenga et al. 2022; Wagner et al. 2023). However, whether parasites have higher or lower thermal adaptability to global warming than their hosts remains unclear for most host–parasite pairs. Most authors currently assume that AZP can adapt faster than their large-bodied hosts owing to their smaller size and shorter generation times (e.g. Cohen et al. 2017; Gsell et al. 2023), although it is also recognised that larger hosts have the advantage of a wider temperature tolerance range and greater acclimatisation capacity (Rohr et al. 2018; Gsell et al. 2023). Larger hosts appear to be favoured by AZP, especially in phytoplankton (e.g. Rasconi et al. 2012), indicating the importance of host size for algal AZP occurrence and success. Whether size is important in other host–AZP systems remains to be determined.

While abiotic factors, which strongly influence AZP and their hosts, are better understood, knowledge of biotic factors, which also play an important role in AZP diversity and abundance, remains limited. Very little research has addressed the potential for co-evolution, and little is known about the specific interactions between AZP and their hosts involving multiple organisms, including co-occurrence, co-infection and competition (e.g. De Bruin et al. 2008; Sønstebø and Rohrlack 2011; Gsell et al. 2013b; Lepelletier et al. 2014; Räberg et al. 2014; Agha et al. 2018; O'Hanlon et al. 2018; Torres-Sánchez et al. 2022; McKindles et al. 2023; Sun et al. 2023; Carvalho et al. 2024). Regarding biotic factors, we always consider that AZP are not only affected by biological relationships, but can also influence the composition, succession, dominance and size structure of host communities, which in turn can alter their own diversity, abundance and infection success. Such influence by AZP can occur not only directly through detrimental effects, but also indirectly by affecting interspecific competition between hosts and other species, as has been demonstrated in phytoplankton (e.g. Canter and Lund 1951; Van Donk and Ringelberg 1983; Rasconi et al. 2012, 2014; Kagami et al. 2014).

Our synthesis identifies grazing as one of the most important biotic factors for AZP. Grazing directly reduces host availability (Kagami et al. 2004; Rasconi et al. 2011; Lürling 2021) or acts by consuming zoospores via a specific trophic link, the mycoloop (e.g. Kagami et al. 2007a). As zooplankton may benefit nutritionally from zoospores, which are abundant, valuable food of suitable size (e.g. Rasconi et al. 2014, 2020; Gerphagnon et al. 2015, 2019; Lürling 2021; Abonyi et al. 2024), this can increase populations of certain grazers, affecting the abundance, distribution and availability of algal hosts, which in turn influences the development of AZP. However, grazing can also have the opposite effect and increase infection through host fragmentation, leaving more sites available for parasite colonisation (Frenken et al. 2020).

The interactions between AZP and microbiomes from different biofilms appear to be another important factor in AZP infection dynamics. This is particularly true for amphibian chytrids and the microorganisms associated with amphibian skin (e.g. Woodhams et al. 2011; Schmeller et al. 2022; Loyau et al. 2024). As the antifungal metabolites excreted by these organisms can inhibit parasite growth (e.g. Harris et al. 2006, 2009; Ujszegi et al. 2023), both the Adaptive Microbiome Hypothesis (Woodhams et al. 2023) and the Disease Pyramid Concept (Bernardo-Cravo et al. 2020) provide a comprehensive framework for future research into AZP and their biological drivers. In addition to excreting antipathogenic metabolites, microbiomes from amphibian skin and other biofilms can influence infection dynamics by trapping zoospores and inactivating or consuming them through biofilm inhabitants (e.g. Sentenac et al. 2024). These findings open new avenues for future research on this topic. As with the interactions between amphibian biofilms and AZP host systems, current findings on the relationships between other aquatic communities co-existing with AZP host systems highlight the complexity of these interactions and the need for further investigation of these biological drivers. We still know little about the effects of co-infection and hyper-parasitism, as well as the interactions between parasites, although it is well established that they can strongly modulate relationships with their hosts (e.g. Sparrow 1932; Canter 1949, 1969; De Jesús Andino et al. 2024; Thumsová et al. 2024; Yoldas et al. 2024). Consequently, targeted co-infection studies are needed in the future.

All biological factors are important, but given the increase in harmful algal blooms due to climate change (Wilk-Woźniak et al. 2024), understanding the allelopathic events and dependence of toxin production in hosts on their parasites will be useful for future management and conservation efforts related to aquatic habitats and their diversity. This protective mechanism experienced by hosts during parasite infection, as well as the release of volatile compounds or other organic metabolites, may increase their chances of fighting off AZP infections (Puneva and Christov 2004; Puneva 2006; Rohrlack et al. 2013; Yoneya et al. 2021; Agha et al. 2022), despite some conflicting results on this topic (Van Wichelen et al. 2010; Weisbrod et al. 2020).

Many questions remain unanswered, and further research is needed on all possible transport vectors of AZP, particularly concerning the increasing biological invasions. In this context, invasive host species, acting as transporters for the spread of their specific parasites, represent important AZP drivers. This is illustrated by the spread of emerging pathogens such as the noble crayfish plague (*Aphanomyces astaci*), the two causative agents of amphibian chytridiomycosis, *Batrachochytrium dendrobatidis* and *Batrachochytrium salamandrivorans*, as well as the fish-infecting *Sphaerothecum destruens* (Lowe et al. 2000; Martel et al. 2020; Gozlan and Combe 2023; Carvalho et al. 2024, etc.).

Our results emphasise the importance of complex physical, chemical and biological processes in the control of AZP and highlight the need for further research on this topic, as data on most factors remain limited and additional studies with broader scope are required. The following areas are poorly documented and lack sufficient evidence in the literature: (1) effects of oxygen and oxidative stress on AZP ecology, including the role of antioxidants such as glutathione; (2) macro- and micronutrient requirements of AZP; (3) physiological responses to osmotic stress and salinity tolerances of AZP; (4) effects of UVR on AZP; (5) role of disturbances in the diversity and abundance of AZP; (6) defensive role of autophagy during infection; (7) genomic data on AZP strains and their hosts, which are necessary for a better understanding of co-evolution and other biological drivers.

This review, based on an analysis of more than 500 papers, identifies significant research gaps and further open questions in various aspects of AZP biology and their role in the functioning of aquatic ecosystems: (1) the effect of transient climatic events (such as heatwaves) on host–parasite interactions; (2) the effects of light pollution on AZP; (3) potential of RWTs as novel transporting vectors of AZP; (4) the ability of AZP to acclimatise or adapt, and the speed of this process; (5) the selective shedding of infected cells or organisms via grazing, which maintains population health; (6) the role of associated or symbiotic microorganisms in the algal mucus and other mucilage layers that help hosts resist AZP infections; (7) viral infection of AZP and its consequences for disease outbreaks. How expected changes in environmental factors, particularly those caused by climate warming, eutrophication and biological invasions, will affect AZP biodiversity and functionality, as well as AZP strategies—especially whether generalists will be more successful than specialists—remain important open questions.

## Conclusions

There is already a substantial body of literature on the role of AZP and their functional diversity in natural and artificial aquatic habitats. Nevertheless, there is a significant need for a deeper understanding of the key factors promoting or constraining AZP diversity, distribution and infection success. The accumulated knowledge indicates that these are shaped by a complex interaction of environmental factors. Although the review raises further questions, it demonstrates the importance of identifying the abiotic and biotic drivers of AZP, especially in the context of climate change, eutrophication, water and light pollution, as well as biological invasions, to better predict environmental controls of disease dynamics. Despite the growing recognition of climate change as a dominant driver across various ecosystems, the specific impacts on AZP remain underexplored, and further research is needed to unravel the nuanced relationships between climate factors, parasite life cycles, host–parasite interactions and transmission patterns. This gap in understanding presents a significant challenge to managing and predicting disease outbreaks in aquatic environments, particularly in the context of global biodiversity conservation and aquaculture sustainability. Given the potential consequences for both aquatic biodiversity and human industries, it is essential to prioritise interdisciplinary research that integrates climate modelling, parasitology and ecological forecasting. Such research will enable more accurate predictions of disease risks and guide the development of adaptive management strategies. Ultimately, understanding the drivers of AZP dynamics in a changing climate will be crucial for mitigating future disease outbreaks, preserving aquatic ecosystems and ensuring the sustainability of aquatic resources. We hope that this review, which synthesises results on potential factors affecting AZP and outlines current knowledge gaps, will provide useful information for the design of further interdisciplinary research on AZP ecology.

**Acknowledgements** This article used the network of COST Action CA20125—Applications for zoosporic parasites in aquatic systems (ParAqua), https://www.cost.eu/actions/CA20125/, supported by COST (European Cooperation in Science and Technology) www.cost.eu. The study and article processing charges were funded by the European Union-NextGenerationEU, through the National Recovery and Resilience Plan of the Republic of Bulgaria, project no. BG-RRP-2.004-0008.

**Author contributions** BU and MSG: conceptualisation, vizualization and funding. MSG drafted the manuscript. All authors participated in editing of the text and providing references.

**Funding** The study was funded by the European Union-NextGenerationEU, through the National Recovery and Resilience Plan of the Republic of Bulgaria, project no. BG-RRP-2.004-0008.

**Data availability** No datasets were generated or analysed during the current study.

## Declarations

**Conflict of interest** The authors declare no competing interests.

**Ethical approval** Not applicable.

**Informed consent** Not applicable.

## References

Abeliovich A, Dikbuck S (1977) Factors affecting infection of *Scenedesmus obliquus* by a *Chytridium* sp. in sewage oxidation ponds. Appl Environ Microbiol 34(6):832–836. https://doi.org/10.1128/aem.34.6.832-836.1977

Abonyi A, Fornberg J, Rasconi S, Ptacnik R, Kainz MJ, Lafferty KD (2024) The chytrid insurance hypothesis: integrating parasitic chytrids into a biodiversity–ecosystem functioning framework for phytoplankton–zooplankton population dynamics. Oecologia 204:279–288

Agha R, Saebelfeld M, Manthey C, Rohrlack T, Wolinska J (2016) Chytrid parasitism facilitates trophic transfer between bloom-forming cyanobacteria and zooplankton (*Daphnia*). Sci Rep 6:35039

Agha R, Gross A, Rohrlack T, Wolinska J (2018) Adaptation of a chytrid parasite to its cyanobacterial host is hampered by host intraspecific diversity. Front Microbiol 9:921. https://doi.org/10.3389/fmic.2018.00921

Agha R, Gerphagnon M, Schampera C, Rohrlack T, Fastner J, Wolinska J (2022) Fate of hepatotoxin microcystin during infection of cyanobacteria by fungal chytrid parasites. Harmful Algae 118:102288. https://doi.org/10.1016/j.hal.2022.102288

Alster A, Zohary T (2007) Interactions between the bloom-forming dinoflagellates *Peridinium gatunense* and the chytrid fungus *Phlyctochytrium* sp. Hydrobiologia 578:131–139. https://doi.org/10.1007/s10750-006-0439-y

Alterio V, Langella E, De Simone G, Monti SM (2015) Cadmium-containing carbonic anhydrase CDCA1 in marine diatom *Thalassiosira weissflogii*. Mar Drugs 13(4):1688–1697. https://doi.org/10.3390/md13041688

Altizer S, Ostfeld RS, Johnson PTJ, Kutz S, Harvell CD (2013) Climate change and infectious diseases: from evidence to a predictive framework. Science 341(6145):514–519. https://doi.org/10.1126/science.1239401

Amon JP, French KH (2004) Photoresponses of the marine protist *Ulkenia* sp. zoospores to ambient, artificial and bioluminescent light. Mycologia 96(3):463–469. https://doi.org/10.2307/3762166

Archer S, Stokes C (2000) Stress, disturbance and change in rangeland ecosystems. In: Arnalds O, Archer S (eds) Rangeland desertification. Advances in vegetation science, vol 19. Springer, Dordrecht, pp 17–38

Asatryan A, Boussiba S, Zarka A (2019) Stimulation and isolation of *Paraphysoderma sedebokerense* (Blastocladiomycota) propagules and their infection capacity toward their host under different physiological and environmental conditions. Front Cell Infect Microbiol. https://doi.org/10.3389/fcimb.2019.00072

Atkinson K (1970) Dispersal of phytoplankton by ducks. Wildfowl 212:110–111

Atkinson K (1971) Further experiments in dispersal of phytoplankton by birds. Wildfowl 22:98–99

Atkinson K (1972) Birds as transporters of algae. Br Phycol J 7:319–321

Atkinson K (1980) Experiments in dispersal of phytoplankton by ducks. Br Phycol J 15:49–58

Attermeyer K, Premke K, Hornick T, Hilt S, Grossart HP (2013) Ecosystemlevel studies of terrestrial carbon turnover reveal contrasting roles for bacterial metabolism in different aquatic habitats. Ecology 94:2754–2766. https://doi.org/10.1890/130420.1

Badis Y, Klochkova TA, Strittmatter M, Garvetto A, Murúa P, Sanderson JC, Kim GH, Gachon CM (2019) Novel species of the oomycete *Olpidiopsis* potentially threaten European red algal cultivation. J Appl Phycol 31:1239–1250. https://doi.org/10.1007/s10811-018-1641-9

Badis Y, Klochkova TA, Brakel J, Arce P, Ostrowski M, Tringe SG, Kim GH, Gachon CM (2020) Hidden diversity in the oomycete genus *Olpidiopsis* is a potential hazard to red algal cultivation and conservation worldwide. Eur J Phycol 55(2):162–171. https://doi.org/10.1080/09670262.2019.1664769

Bahnweg G, Bland ChE (1980) Comparative physiology and nutrition of *Lagenidium callinectes* and *Haliphthoros milfordensis*, fungal parasites of marine crustaceans. Bot Mar 23(11):689–698. https://doi.org/10.1515/botm-1980-1105

Barr DJS (2001) Chytridiomycota. In: McLaughlin DJ, McLaughlin EG, Lemke PA (eds) The Mycota, vol VII. Part A. Springer-Verlag, New York, pp 93–112

Basso A, Paolini V, Martín-Torrijos L, Vladimir Sandoval-Sierra JV, Manfrin A, Diéguez-Uribeondo J, Pretto T (2026) Chronic *Aphanomyces astaci* infection in wild white-clawed crayfish: Risks and implications for breeding programs. J Invertebr Pathol 214:108434. https://doi.org/10.1016/j.jip.2025.108434

Batchelor G (2000) Introduction to fluid mechanics. Cambridge University Press, Cambridge

Bates KA, Clare FC, O'Hanlon S, Bosch J, Brookes L, Hopkins K, McLaughlin EJ, Daniel O, Garner TWJ, Fisher MC, Harrison XA (2018) Amphibian chytridiomycosis outbreak dynamics are linked with host skin bacterial community structure. Nat Commun 9:693. https://doi.org/10.1038/s41467-018-02967-w

Batko A (1975) *Zarys hydromikologii* [Hydromycology-an overview]. PWN, Warszawa (**in Polish**)

Battaglin WA, Smalling KL, Anderson C, Calhoun D, Chestnut T, Muths E (2016) Potential interactions among disease, pesticides, water quality and adjacent land cover in amphibian habitats in the United States. Sci Total Environ 566–567:320–332. https://doi.org/10.1016/j.scitotenv.2016.05.062

Bell SC, Alford RA, Garland S, Padilla G, Thomas AD (2013) Screening bacterial metabolites for inhibitory effects against *Batrachochytrium dendrobatidis* using a spectrophotometric assay. Dis Aquat Org 103:77–85

Berger L, Speare R, Daszak P, Green DE, Cunningham AA, Goggin CL, Slocombe R, Ragan MA, Hyatt AD, McDonald KR, Hines HB, Lips KR, Marantelli G, Parkes H (1998) Chytridiomycosis causes amphibian mortality associated with population declines in rain forests of Australia and Central America. Proc Natl Acad Sci U S A 95:9031–90336. https://doi.org/10.1073/pnas.95.15.9031

Berger L, Hyatt AD, Speare R, Longcore JE (2005) Life cycle stages of the amphibian chytrid *Batrachochytrium dendrobatidis*. Dis Aquat Org 68:51–63. https://doi.org/10.3354/dao068051

Bernardo-Cravo AP, Schmeller DS, Chatzinotas A, Vredenburg VT, Loyau A (2020) Environmental factors and host microbiomes shape host-pathogen dynamics. Trends Parasitol 36(7):616–633. https://doi.org/10.1016/j.pt.2020.04.010

Bletz MC, Loudon AH, Becker MH, Bell SC, Woodhams DC, Minbiole KPC, Harris RN (2013) Mitigating amphibian chytridiomycosis with bioaugmentation: characteristics of effective probiotics and strategies for their selection and use. Ecol Lett 16(6):807–820. https://doi.org/10.1111/ele.12099

Boisvert SP, Davidson EW (2011) Growth of the amphibian pathogen, *Batrachochytrium dendrobatidis*, in response to chemical properties of the aquatic environment. J Wildl Dis 47:694–698. https://doi.org/10.7589/0090-3558-47.3.694

Bolom-Huet R, Pineda E, Andrade-Torres A, Díaz-Fleischer F, Muñoz AL, Galindo-González J (2023) Chytrid prevalence and infection intensity in treefrogs from three environments with different degrees of conservation in Mexico. Biotropica 55(2):318–328. https://doi.org/10.1111/btp.13186

Bosch J, Monsalve-Carcaño C, Price SJ, Bielby J (2020) Single infection with *Batrachochytrium dendrobatidis* or *Ranavirus* does not increase probability of co-infection in a montane community of amphibians. Sci Rep 10:21115. https://doi.org/10.1038/s41598-020-78196-3

Boyce D, Lewis M, Worm B (2010) Global phytoplankton decline over the past century. Nature 466:591–596. https://doi.org/10.1038/nature09268

Boyle DG, Hyatt AD, Daszak P, Berger L, Longcore JE, Porter D, Hengstberger SG, Olsen V (2003) Cryo-archiving of *Batrachochytrium dendrobatidis* and other Chytridiomycetes. Dis Aquat Organ 56:59–64. https://doi.org/10.3354/dao056059

Brazier T, Cherif E, Martin JF, Gilles A, Blanchet S, Zhao Y, Gozlan R (2021) A tale of an invader: reconstructing the genomic history of invasive topmouth gudgeon (*Pseudorasbora parva*) populations. Authorea. https://doi.org/10.22541/au.161417292.23392023/v1

Brown CDJ (1933) A limnological study of certain freshwater polyzoa with special reference to their statoblasts. Trans Am Microsc Soc 52:271–316

Brucker RM, Harris RN, Schwantes CR, Gallaher TN, Flaherty DC, Lam BA et al (2008) Amphibian chemical defense: antifungal metabolites of the microsymbiont *Janthinobacterium lividum* on the salamander *Plethodon cinereus*. J Chem Ecol 34(11):1422–1429

Bruning K (1991a) Effects of phosphorus limitation on the epidemiology of a chytrid phytoplankton parasite. Freshw Biol 25:409–417

Bruning K (1991b) Effects of temperature and light on the population dynamics of the *Asterionella-Rhizophydium* association. J Plankton Res 13:707–719

Bruning K (1991c) Infection of the diatom *Asterionella* by a chytrid. I. Effects of light on reproduction and infectivity of the parasite. J Plankton Res 13(1):103–117

Bruning K (1991d) Infection of the diatom *Asterionella* by a chytrid. 2. Effects of light on survival and epidemic development of the parasite. J Plankton Res 13:119–129

Buck JC, Truong L, Blaustein AR (2011) Predation by zooplankton on *Batrachochytrium dendrobatidis*: biological control of the deadly amphibian chytrid fungus? Biodivers Conserv 20:3549–3553

Burns CW (1980) Occurrence of *Aphanomyces ovidestruens*, a fungus parasitic on copepods, in two eutrophic lakes. N Z J Mar Freshwater Res 14:23–29

Burns CW (1985) Fungal parasitism in a freshwater copepod: components of the interaction between *Aphanomyces* and *Boeckella*. J Invertebr Pathol 46:5–10

Caldeira K, Wickett ME (2003) Anthropogenic carbon and ocean pH. Nature 425:365

Camejo D, Guzmán-Cedeño Á, Moreno A (2016) Reactive oxygen species, essential molecules, during plant–pathogen interactions. Plant Physiol Biochem 103:10–23. https://doi.org/10.1016/j.plaphy.2016.02.035

Canter HM (1949) Studies on British chytrids: IV. *Chytriomyces tabellariae* (Schröter) n.comb. parasitized by *Septosperma anomalum* (Couch) Whiffen. Trans Br Mycol 32:16–21

Canter HM (1950) Fungal parasites of the phytoplankton. I: Studies on British chytrids, X. Ann Bot 14(2):263–289. https://doi.org/10.1093/oxfordjournals.aob.a083246

Canter HM (1951) Fungal parasites of the phytoplankton. II: Studies on British chytrids, XII. Ann Bot 15(2):129–156. https://doi.org/10.1093/oxfordjournals.aob.a083272

Canter HM (1953) Annotated list of British aquatic chytrids. Trans Br Mycol Soc 36:278–303. https://doi.org/10.1016/S0007-1536(53)80023-9

Canter HM (1961) Studies on British chytrids: XVII. Species occurring on planktonic desmids. Trans Br Mycol Soc 44(2):163–176. https://doi.org/10.1016/S0007-1536(61)80067-3

Canter HM (1967) Studies on British chytrids: XXVI.A critical examination of *Zygorhizidium melosirae* Canter and *Z. planktonicum* Canter. Linnean Soc London Proc Bot J 60(381):85–97. https://doi.org/10.1111/j.1095-8339.1967.tb00081.x

Canter HM (1969) Studies on British chytrids. XXIX. A taxonomic revision of certain fungi found on the diatom *Asterionella*. Bot J Linn Soc 62:267–278. https://doi.org/10.1111/j.1095-8339.1969.tb01970.x

Canter HM (1972) A guide to the fungi occurring on planktonic blue-green algae. In: Desikachary TV (ed) Taxonomy and biology of blue-green algae. University of Madras, Madras, India, pp 145–159

Canter HM, Beakes GW (1992) Formae speciales differentiation in the chytrid *Zygorhizidium planktonicum* Canter, a parasite of the diatoms *Asterionella* and *Synedra*. Nova Hedwigia 55:437–455

Canter HM, Heaney SI (1984) Observations of zoosporic fungi of *Ceratium* spp. in lakes of the English Lake District; importance for phytoplankton population dynamics. New Phytol 97(4):601–612. https://doi.org/10.1111/j.1469-8137.1984.tb03624.x

Canter HM, Jaworski GHM (1979) The occurrence of a hypersensitive reaction in the planktonic diatom *Asterionella formosa* Hassall parasitized by the chytrid *Rhizophydium planktonicum* Canter emend., in culture. New Phytol 82:187–206. https://doi.org/10.1111/j.1469-8137.1979.tb07574.x

Canter HM, Jaworski GHM (1980) Some general observations on zoospores of the chytrid *Rhizophydium planktonicum* Canter emend. New Phytol 84(3):515–531. https://doi.org/10.1111/j.1469-8137.1980.tb04559.x

Canter HM, Jaworski GHM (1981) The effect of light and darkness upon infection of *Asterionella formosa* Hassall by the chytrid *Rhizophydium planktonicum* Canter emend. Ann Bot 47:13–30. https://doi.org/10.1093/oxfordjournals.aob.a085987

Canter HM, Jaworski GHM (1982) Some observations on the alga *Fragilaria crotonensis* Kitton and its parasitism by two chytridiaceous fungi. Ann Bot 49:429–446

Canter HM, Jaworski GHM (1986) A study on the chytrid *Zygorhizidium planktonicum* Canter, a parasite of the diatoms *Asterionella* and *Synedra*. Nova Hedwigia 43:269–298

Canter HM, Lund JWG (1951) Studies on plankton parasites. III. Examples of the interaction between parasitism and other factors determining the growth of diatoms. Ann Bot 15:359–371

Canter HM, Lund JWG (1953) Studies on plankton parasites. II. The parasitism of diatoms with special reference to lakes in the English Lake District. Trans Br Mycol Soc 36:13–37

Canter HM, Lund JWG (1969) The parasitism of planktonic desmids by fungi. Oesterr Bot Z 116:351–377. https://doi.org/10.1007/BF01379634

Canter-Lund H, Lund JWG (1995) Freshwater algae: their microscopic world explored. Biopress Limited, Bristol

Carney LT, Lane TW (2014) Parasites in algae mass culture. Front Microbiol 5:278. https://doi.org/10.3389/fmicb.2014.00278

Carvalho T, Belasen AM, Toledo LF, James TY (2024) Coevolution of a generalist pathogen with many hosts: the case of the amphibian chytrid *Batrachochytrium dendrobatidis*. Curr Opin Microbiol 78:102435. https://doi.org/10.1016/j.mib.2024.102435

Cavaliere M, Feng S, Soyer OS, Jiménez JI (2017) Cooperation in microbial communities and their biotechnological applications. Environ Microbiol 19:2949–2963. https://doi.org/10.1111/1462-2920.13767

Cellamare M, Leitao M, Coste M, Dutartre A, Haury J (2010) Tropical phytoplankton taxa in Aquitaine lakes (France). Hydrobiologia 639:129–145. https://doi.org/10.1007/s10750-009-0029-x

Cellamare M, Pinto PT, Leitao M, Coste M, Boutry S, Haury J (2013) Using functional approaches to study phytoplankton communities in a temperate region exposed to tropical species dispersal. Hydrobiologia 702:267–282. https://doi.org/10.1007/s10750-012-1330-7

Chabaud S, Andres Y, Lakel A, Le Cloirec P (2006) Bacteria removal in septic effluent: influence of biofilm and protozoa. Water Res 40(16):3109–3114. https://doi.org/10.1016/j.watres.2006.06.008

Chambouvet A, Alves-de-Souza C, Cueff V, Marie D, Karpov S, Guillou L (2011) Interplay between the parasite *Amoebophrya* sp. (Alveolata) and the cyst formation of the red tide dinoflagellate *Scrippsiella trochoidea*. Protist 162(4):637–649. https://doi.org/10.1016/j.protis.2010.12.001

Charalambidou I, Santamaría L (2002) Waterbirds as endozoochorous dispersers of aquatic organisms: a review of experimental evidence. Acta Oecol 23(3):165–176. https://doi.org/10.1016/S1146-609X(02)01148-7

Charalampous E, Matthiessen B, Sommer U (2021) Grazing induced shifts in phytoplankton cell size explain the community response to nutrient supply. Microorganisms 9:2440. https://doi.org/10.3390/microorganisms9122440

Charrier A, Peudpiece M, Lesne M, Daniel P (2016) First report of the intracellular fish parasite *Sphaerothecum destruens* associated with the invasive topmouth gudgeon (*Pseudorasbora parva*) in France. Knowl Manag Aquat Ecosyst 417:44

Chen M, Gao H, Zhang J (2024) Mycoloop: modeling phytoplankton–chytrid–zooplankton interactions in aquatic food webs. Math Biosci 368:109134. https://doi.org/10.1016/j.mbs.2023.109134

Chew A, West M, Berger L, Brannelly LA (2024) The impacts of water quality on the amphibian chytrid fungal pathogen: a systematic review. Environ Microbiol Rep 16(3):e13274. https://doi.org/10.1111/1758-2229.13274

Chien CY (1981) Observations on the growth and morphology of saprolegniaceous fungi isolated from rainbow trout (*Salmo gairdneri*). Fish Pathol 15:241–247. https://doi.org/10.3147/jsfp.15.241

Chukanhom K, Hatai K (2004) Freshwater fungi isolated from eggs of the common carp (*Cyprinus carpio*) in Thailand. Mycoscience 45:42–48. https://doi.org/10.1007/S10267-003-0153-9

Claar DC, Wood CL (2020) Pulse heat stress and parasitism in a warming world. Trends Ecol Evol 35(8):704–715. https://doi.org/10.1016/j.tree.2020.04.002

Clare FC, Halder JB, Daniel O, Bielby J, Semenov MA, Jombart T, Loyau A, Schmeller DS, Cunningham AA, Rowcliffe M, Garner TWJ, Bosch J, Fisher MC (2016) Climate forcing of an emerging pathogenic fungus across a montane multi-host community. Philos Trans R Soc Lond B Biol Sci 371:20150454. https://doi.org/10.1098/rstb.2015.0454

Cleary AC, Søreide JE, Freese D, Niehoff B, Gabrielsen TM (2017) Feeding by *Calanus glacialis* in a high Arctic fjord: potential seasonal importance of alternative prey. ICES J Mar Sci 74(7):1937–1946. https://doi.org/10.1093/icesjms/fsx106

Clulow S, Gould J, James H, Stockwell M, Clulow J, Mahony M (2018) Elevated salinity blocks pathogen transmission and improves host survival from the global amphibian chytrid pandemic: implications for translocations. J Appl Ecol 55:830–840. https://doi.org/10.1111/1365-2664.13030

Coesel PFM, Duque SH, Arango G (1988) Distributional patterns in some Neotropical desmid species (algae, Chlorophyta) in relation to migratory bird routes. Rev Hydrobiol Trop 21(3):197–205

Cohen JM, Venesky MD, Sauer EL, Civitello DJ, McMahon TA, Roznik EA, Rohr JR (2017) The thermal mismatch hypothesis explains host susceptibility to an emerging infectious disease. Ecol Lett 20:184–193. https://doi.org/10.1111/ele.12720

Colautii RI, MacIsaac HJ (2004) A neutral terminology to define 'invasive' species. Divers Distrib 10(2):135–141. https://doi.org/10.1111/j.1366-9516.2004.00061.x

Combe M, Cherif E, Charrier A, Barbey B, Chague M, Carrel G, Chasserieau C, Foissy J-M, Gerard B, Gozlan Z, Guillouët J, Hérodet B, Laine M, Masseboeuf F, Mirkovic I, Nicolas D, Poulet N, Martin J-F, Gilles A, Gozlan RE (2022) Towards unravelling the Rosette agent enigma: spread and emergence of the co-invasive host-pathogen complex, *Pseudorasbora parva–Sphaerothecum destruens*. Sci Total Environ 806(2):150427. https://doi.org/10.1016/j.scitotenv.2021.150427

Connell J (1978) Diversity in tropical rain forests and coral reefs. Science 199:1302–1310

Cook PW (1963) Host range studies of certain *Phycomycetes* parasitic on desmids. Am J Bot 50:580–588. https://doi.org/10.1002/j.1537-2197.1963.tb07231.x

Corsaro D, Walochnik J, Venditti D, Müller KD, Hauröder B, Michel R (2014a) Rediscovery of *Nucleophaga amoebae*, a novel member of the Rozellomycota. Parasitol Res 113(12):4491–4498. https://doi.org/10.1007/s00436-014-4138-8

Corsaro D, Walochnik J, Venditti D, Steinmann J, Müller KD, Michel R (2014b) Microsporidia-like parasites of amoebae belong to the early fungal lineage Rozellomycota. Parasitol Res 113(5):1909–1918. https://doi.org/10.1007/s00436-014-3838-4

Courtois EA, Loyau A, Bourgoin M, Schmeller DS (2017) Initiation of *Batrachochytrium dendrobatidis* infection in the absence of physical contact with infected hosts – a field study in a high altitude lake. Oikos 126:843–851. https://doi.org/10.1111/oik.03462

Covington AK, Bates RG, Durst RA (1985) Definitions of pH scales, standard reference values, measurement of pH, and related terminology (Recommendations 1984). Pure Appl Chem 57(3):531–542. https://doi.org/10.1351/pac198557030531

Cramp RL, Ohmer MEB, Franklin CE (2022) UV exposure causes energy trade-offs leading to increased chytrid fungus susceptibility in green tree frog larvae. Conserv Physiol 10:coac038. https://doi.org/10.1093/conphys/coac038

Czeczuga B (2000) Zoosporic fungi growing on freshwater molluscs. Pol J Environ Stud 9(3):151–156

Czeczuga B, Godlewska A (2001) Aquatic insects as vectors of aquatic zoosporic fungi parasitic on fishes. Acta Ichthyol Piscat 31(2):87–104

Czeczuga B, Muszynska E (1998) Aquatic fungi growing on coregonid fish eggs. Acta Hydrobiol 40:239–264

Czeczuga B, Muszynska E (1999a) Aquatic fungi growing on the eggs of fishes representing 33 cyprinid taxa (Cyprinidae) in laboratory conditions. Acta Ichthyol Piscat 29(2):53–72

Czeczuga B, Muszynska E (1999b) Aquatic fungi growing on the eggs of various fish families. Acta Hydrobiol 41:235–246

Czeczuga B, Godlewska A, Krzeminska A (1998a) Aquatic fungi growing on the spawn of certain amphibians. Amphib-Reptil 19:239–251

Czeczuga B, Muszynska E, Godlewska A (1998b) Aquatic fungi on certain species of crayfish in water from different water bodies. Pol J Environ Stud 7:75–82

Czeczuga B, Kozlowska M, Godlewska A (1999) Zoosporic fungus species growing on dead benthos crustacean. Pol J Environ Stud 8:377–382

Czeczuga B, Godiewska A, Kozlowska M (2000) Zoosporic fungi growing on the carapace of dead zooplankton organisms. Limnologica 30:37–43

Danz A, Quandt CA (2023) A review of the taxonomic diversity, host-parasite interactions, and experimental research on chytrids that parasitize diatoms. Front Microbiol 14:1281648. https://doi.org/10.3389/fmicb.2023.1281648

Davis LR, Bigler L, Woodhams DC (2017) Developmental trajectories of amphibian microbiota: response to bacterial therapy depends on initial community structure. Environ Microbiol 19:1502–1517. https://doi.org/10.1111/1462-2920.13707

De Bruin A, Ibelings BW, Rijkeboer M, Brehm M, Van Donk E (2004) Genetic variation in *Asterionella formosa* (Bacillariophyceae): is it linked to frequent epidemics of host-specific parasitic fungi? J Phycol 40:823–830. https://doi.org/10.1111/j.1529-8817.2004.04006.x

De Bruin A, Ibelings BW, Kagami M, Mooij WM, Van Donk E (2008) Adaptation of the fungal parasite *Zygorhizidium planktonicum* during 200 generations of growth on homogeneous and heterogeneous populations of its host, the diatom *Asterionella formosa*. J Eukaryot Microbiol 55:69–74. https://doi.org/10.1111/j.1550-7408.2008.00306.x

De Jesús Andino F, Davydenko A, Webb RJ, Robert J (2024) The binding, infection, and promoted growth of *Batrachochytrium dendrobatidis* by the *Ranavirus* FV3. Viruses 16:154. https://doi.org/10.3390/v16010154

de Wildeman E (1890) Note sur quelques Saprolegniees parasites des algues. Bull Soc Belge Microbiol 16:134–139

Deutsch C, Penn JL, Seibel B (2020) Metabolic trait diversity shapes marine biogeography. Nature 585(7826):557–562. https://doi.org/10.1038/s41586-020-2721-y

Dittami SM, Eveillard D, Tonon T (2014) A metabolic approach to study algal–bacterial interactions in changing bloom environments. Wiley Online Library 23(7):1656–1660. https://doi.org/10.1111/mec.12670

Do Amaral Meirinho P, Nishimura PY, Pires-Zottarelli CLA, MochiniCarlos V, Pompêo MLM (2013) Olpidium gregarium, a chytrid fungus affecting rotifers populations in Rio Grande Reservoir, São Paulo State, Brazil. Biota Neotrop 13:356–359. https://doi.org/10.1590/S1676-06032013000100036

Doggett MS, Porter D (1996) Fungal parasitism of *Synedra acus* (*Bacillariophyceae*) and the significance of parasite life history. Eur J Protistol 32:490–497

Dudka IA, Isayewa NM, Davydov ON (1989) Saprolegniaceae inducing fish mycosis. Mycol Phytopathol 23:488–498

Duran R, Cary JW, Calvo AM (2010) Role of the osmotic stress regulatory pathway in morphogenesis and secondary metabolism in filamentous fungi. Toxins 2:367–381. https://doi.org/10.3390/toxins2040367

EFSA (2018) The 2018 European Union report on pesticide residues in food. https://www.efsa.europa.eu/en/efsajournal/pub/6057

Elsheikha HM, Khan NA (2011) Essentials of veterinary parasitology. Caister Academic Press, Poole

European Environment Agency (EEA) (2024) Europe's state of water 2024: the need for improved water resilience. EEA

Evans RJ, Sundaramurthy V, Frickel E-M (2018) The interplay of host autophagy and eukaryotic pathogens. Front Cell Dev Biol 6:118. https://doi.org/10.3389/fcell.2018.00118

Ferguson HW, Ride DW (1980) Post-spawning mortalities in brown trout *Salmo trutta* L. J Fish Diseas 3:153–160

Fernández-Beaskoetxea S, Bosch J, Bielby J (2016) Infection and transmission heterogeneity of a multi-host pathogen (*Batrachochytrium dendrobatidis*) within an amphibian community. Dis Aquat Org 118:11–20. https://doi.org/10.3354/dao02963

Fernández-Valero AD, Reñé A, Timoneda N, Sampedro N, Garcés E (2022) Dinoflagellate hosts determine the community structure of marine Chytridiomycota: demonstration of their prominent interactions. Environ Microbiol 24:5951–5965. https://doi.org/10.1111/1462-2920.16182

Fernández-Valero AD, Reñé A, Timoneda N, Pou-Solà N, Gordi J, Sampedro N, Garcés E (2023) The succession of epiphytic microalgae conditions fungal community composition: how chytrids respond to blooms of dinoflagellates. ISME Communications 3(1):103. https://doi.org/10.1038/s43705-023-00304-x

Festa RA, Thiele DJ (2011) Copper: an essential metal in biology. Curr Biol 21(21):877–883

Figuerola J, Green AJ, Black K, Okamura B (2004) Influence of gut morphology on passive transport of freshwater bryozoans by waterfowl in Doñana (southwestern Spain). Can J Zool 82(6):835–840. https://doi.org/10.1139/z04-055

Fiołka MJ, Takeuchi N, Sofińska-Chmiel W, Wójcik-Mieszawska S, Irvine-Fynn T, Edwards A (2021) Morphological and spectroscopic analysis of snow and glacier algae and their parasitic fungi on different glaciers of Svalbard. Sci Rep 11:21785. https://doi.org/10.1038/s41598-021-01211-8

Fisher MC, Garner WJ (2007) The relationship between the emergence of *Batrachochytrium dendrobatidis*, the international trade of amphibians and introduced amphibian species. Fungal Biol Rev 21:2–9

Fisher MC, Garner TWJ (2020) Chytrid fungi and global amphibian declines. Nat Rev Microbiol 18:332–343. https://doi.org/10.1038/s41579-020-0335-x

Fisher MC, Garner TW, Walker SF (2009) Global emergence of *Batrachochytrium dendrobatidis* and amphibian chytridiomycosis in space, time, and host. Annu Rev Microbiol 63:291–310. https://doi.org/10.1146/annurev.micro.091208.073435

Fisher MC, Henk DA, Briggs CJ, Brownstein JS, Madoff LC, McCraw SL, Gurr SJ (2012) Emerging fungal threats to animal, plant and ecosystem health. Nature 484:186–194. https://doi.org/10.1038/nature10947

Flechas SV, Acosta-González A, Escobar LA, Kueneman JG, Sánchez-Quitian ZA, Parra-Giraldo CM, Rollins-Smith LA, Reinert LK, Vredenburg VT, Amézquita A, Woodhams DC (2019) Microbiota and skin defense peptides may facilitate coexistence of two sympatric Andean frog species with a lethal pathogen. ISME J 13:361–373. https://doi.org/10.1038/s41396-018-0284-9

Florinskaya AA (1971) On finding *Saprolegnia* on eggs and fishes during artificial cultivation in the region of Leningrad. Trudy VNIIPRCh 18:222–226

Foster R, Bass D, Clark PF, Morritt D, Stebbing P (2025) Qualitative risk analysis of invasive pathogens spreading via raw water transfers in the UK. Sci Total Environ 986:179746. https://doi.org/10.1016/j.scitotenv.2025.179746

Fott B (1967) *Phlyctidium scenedesmi* spec. nova, a new chytrid destroying mass cultures of algae. Z Allg Mikrobiol 7:97–102. https://doi.org/10.1002/jobm.19670070203

Frenken T, Velthuis M, de Senerpont Domis LN, Stephan S, Aben R, Kosten S, van Donk E, Van de Waal DB (2016) Warming accelerates termination of a phytoplankton spring bloom by fungal parasites. Glob Change Biol 22:299–309. https://doi.org/10.1111/gcb.13095

Frenken T, Wierenga J, Gsell AS, van Donk E, Rohrlack T, Van de Waal DB (2017a) Changes in N:P supply ratios affect the ecological stoichiometry of a toxic cyanobacterium and its fungal parasite. Front Microbiol 8:1015. https://doi.org/10.3389/fmicb.2017.01015

Frenken T, Alacid E, Berger SA, Bourne EC, Gerphagnon M, Grossart H-P, Gsell AS, Ibelings BW, Kagami M, Küpper FC, Letcher PM, Loyau A, Miki T, Nejstgaard JC, Rasconi S, Reñé A, Rohrlack T, Rojas-Jimenez K, Schmeller DS, Scholz B, Seto K, Sime-Ngando T, Sukenik A, Van de Waal DB, Van den Wyngaert S, Van Donk E, Wolinska J, Wurzbacher C, Agha R (2017b) Integrating chytrid fungal parasites into plankton ecology: research gaps and needs: research needs in plankton chytridiomycosis. Environ Microbiol 19:3802–3822. https://doi.org/10.1111/1462-2920.13827

Frenken T, Wierenga J, van Donk E, Declerck SA, de Senerpont Domis LN, Rohrlack T, Van de Waal DB (2018) Fungal parasites of a toxic inedible cyanobacterium provide food to zooplankton. Limnol Oceanogr 63(6):2384–2393. https://doi.org/10.1002/lno.10945

Frenken T, Agha R, Schmeller DS, van West P, Wolinska J (2019) Biological concepts for the control of aquatic zoosporic diseases. Trends Parasitol 35(7):571–582. https://doi.org/10.1016/j.pt.2019.04.003

Frenken T, Wolinska J, Tao Y, Rohrlack T, Agha R (2020) Infection of filamentous phytoplankton by fungal parasites enhances herbivory in pelagic food webs. Limnol Oceanogr 65:2618–2626. https://doi.org/10.1002/lno.11474

Frenken T, Paseka R, González AL, Asik L, Seabloom EW, White LA, Borer ET, Strauss AT, Peace A, Van de Waal DB (2021) Changing elemental cycles, stoichiometric mismatches, and consequences for pathogens of primary producers. Oikos 130:1046–1055. https://doi.org/10.1111/oik.08253

Frick W, Reinhold H (1987) Nachweis und Epizootiologie fischpathogener *Saprolegnia*. Arten in Forellenzuchtanlagen. Monatsh Veterinaermed 42:712–716

Friesen OC, Detwiler DT (2021) Parasite-modified chemical communication: implications for aquatic community dynamics. Front Ecol Evol. https://doi.org/10.3389/fevo.2021.634754

Gachon CMM, Strittmatter M, Badis Y, Fletcher KI, West PV, Müller DG (2017) Pathogens of brown algae: culture studies of

Anisolpidium ectocarpii and *A. rosenvingei* reveal that the Anisolpidiales are uniflagellated oomycetes. Eur J Phycol 52(2):133–148. https://doi.org/10.1080/09670262.2016.1252857

Gaedeke A, Sommer U (1986) The influence of the frequency of periodic disturbances on the maintenance of phytoplankton diversity. Oecologia 71:25–28. https://doi.org/10.1007/BF00377315

Galindo LJ, Richards TA, Nirody JA (2024) Evolutionarily diverse fungal zoospores show contrasting swimming patterns specific to ultrastructure. Curr Biol 34(19):4567–4576. https://doi.org/10.1016/j.cub.2024.08.016

Garcia RD, Jara FG, Steciow MM (2020) Record of parasitic oomycetes on neotropical copepods in aquatic environments of Northwestern Patagonia (Argentina). Acta Limnol Bras 32:16. https://doi.org/10.1590/S2179-975X0719

Garner TWJ, Schmidt BR, Martel A, Pasmans F, Muths E, Cunningham AA, Weldon C, Fisher MC, Bosch J (2016) Mitigating amphibian chytridiomycoses in nature. Philos Trans R Soc Lond B Biol Sci 371:20160207. https://doi.org/10.1098/rstb.2016.0207

Gattuso JP, Magnan A, Billé R, Cheung WW, Howes EL, Joos F, Allemand D, Bopp L, Cooley SR, Eakin CM, Hoegh-Guldberg O, Kelly RP, Pörtner HO, Rogers AD, Baxter JM, Laffoley D, Osborn D, Rankovic A, Rochette J, Sumaila UR, Treyer S, Turley C (2015) Contrasting futures for ocean and society from different anthropogenic $CO_2$ emissions scenarios. Science 349(6243):4722

Gavrilović A, Klonis P, Rasconi S (2022) Report on the meeting of COST action "Applications for zoosporic parastes in aquatic systems" (CA20125 PARAQUA), Larnaca, Cyprus. Ann Sof Univ Fac Biol B2 Bot 106:45–56. https://doi.org/10.6066/GSU.BIOFAC.Bot.106.45-56

Gehman AM, Hall RJ, Byers JE (2018) Host and parasite thermal ecology jointly determine the effect of climate warming on epidemic dynamics. Proc Natl Acad Sci U S A 115(4):744–749. https://doi.org/10.1073/pnas.1705067115

Geiger CC, Küpfer E, Schär S, Wolf S, Schmidt BR (2011) Elevated temperature clears chytrid fungus infections from tadpoles of the midwife toad, *Alytes obstetricans*. Amphibia-Reptilia 32:276–280

Gerphagnon M, Latour D, Colombet J, Sime-Ngando T (2013) Fungal parasitism: life cycle, dynamics and impact on cyanobacterial blooms. PLoS ONE 8(4):e60894. https://doi.org/10.1371/journal.pone.0060894

Gerphagnon M, Macarthur DJ, Latour D, Gachon CMM, Van Ogtrop F, Gleason FH, Sime-Ngando T (2015) Microbial players involved in the decline of filamentous and colonial cyanobacterial blooms with a focus on fungal parasitism: microorganisms involved in cyanobacterial bloom decline. Environ Microbiol 17:2573–2587. https://doi.org/10.1111/1462-2920.12860

Gerphagnon M, Colombet J, Latour D, Sime-Ngando T (2017) Spatial and temporal changes of parasitic chytrids of cyanobacteria. Sci Rep 7:6056. https://doi.org/10.1038/s41598-017-06273-1

Gerphagnon M, Agha R, Martin-Creuzburg D, Bec A, Perriere F, Rad-Menéndez C, Gachon CMM, Wolinska J (2019) Comparison of sterol and fatty acid profiles of chytrids and their hosts reveals trophic upgrading of nutritionally inadequate phytoplankton by fungal parasites. Environ Microbiol 21:949–958. https://doi.org/10.1111/1462-2920.14489

Gibson AK, Nguyen AE (2021) Does genetic diversity protect host populations from parasites? A meta-analysis across natural and agricultural systems. Evol Lett 5(1):16–32. https://doi.org/10.1002/evl3.206

Gleason FH (1976) The physiology of the lower freshwater fungi Chapter 21. In: Gareth Jones EB (ed) Recent advances in aquatic mycology. Paul Elek Books Ltd., London, pp 543–572

Gleason FH, Lilje O (2009) Structure and function of fungal zoospores: ecological implications. Fungal Ecol 2:53–59

Gleason FH, Letcher PM, McGee PA (2007) Some aerobic Blastocladiomycota and Chytridiomycota can survive but cannot grow under anaerobic conditions. Australas Mycol 26:57–64

Gleason FH, Kagami M, Lefevre E, Sime-Ngando T (2008) The ecology of chytrids in aquatic ecosystems: roles in food web dynamics. Fungal Biol Rev 22:17–25. https://doi.org/10.1016/j.fbr.2008.02.001

Gleason FH, Kagami M, Marano AV, Sime-Ngando T (2009) Fungal zoospores are valuable food resources in aquatic ecosystems. Inoculum Newsl Mycol Soc Am 60:1–3

Gleason FH, Daynes CN, McGee PA (2010) Some zoosporic fungi can grow and survive within a wide pH range. Fungal Ecol 3:31–37. https://doi.org/10.1016/j.funeco.2009.05.004

Gleason FH, Küpper FC, Amon JP, Picard K, Gachon C, Marano AV, Sime-Ngando T, Lilje O (2011a) Zoosporic true fungi in marine ecosystems: a review. Mar Freshw Res 62:383–393

Gleason FH, MaranoAV DAL, Al-Shugairan N, Lilje O, Steciow MM, Barrera MD, Inaba S, Nakagiri A (2011b) Patterns of utilization of different carbon sources by Chytridiomycota. Hydrobiologia 659:55–64. https://doi.org/10.1007/s10750-010-0461-y

Gleason FH, Lilje O, Marano AV, Sime-Ngando T, Sullivan BK, Kirchmair M, Neuhauser S (2014) Ecological functions of zoosporic hyperparasites. Front Microbiol 5:244

Gleason FH, Jephcott TG, Küpper FC, Gerphagnon M, Sime-Ngando T, Karpov SA, Guillou L, van Ogtrop FF (2015) Potential roles for recently discovered chytrid parasites in the dynamics of harmful algal blooms. Fungal Biol Rev 29(1):20–33. https://doi.org/10.1016/j.fbr.2015.03.002

Glockling SL (1998) Isolation of a new species of rotifer attacking *Olpidium*. Mycol Res 102:206–208

Glockling SL, Marano AV, Lilje O, Gleason FH (2014) Zoosporic parasites of freshwater invertebrates. In: Gareth Jones EB, Hyde KD, Pang K-L (eds) Freshwater fungi: and fungal-like organisms. Walter de Gruyter, Berlin, Boston, pp 305–332

Goldstein S (1960) Physiology of aquatic fungi I. Nutrition of two monocentric chytrids. J Bacteriol 80:701–707

Gozlan RE, Combe M (2023) Emergence of the fungal rosette agent in the world: current risk to fish biodiversity and aquaculture. J Fungi (Basel) 9(4):426. https://doi.org/10.3390/jof9040426

Grami B, Rasconi S, Niquil N, Jobard M, Saint-Béat B, Sime-Ngando T (2011) Functional effects of parasites on food web properties during the spring diatom bloom in Lake Pavin: a linear inverse modeling analysis. PLoS ONE 6(8):e23273. https://doi.org/10.1371/journal.pone.0023273

Green J (1974) Parasites and epibionts of Cladocera. Philos Trans R Soc Lond 32:417–515

Green AJ, Elmberg J (2014) Ecosystem services provided by waterbirds. Biol Rev 89(1):105–122

Green AJ, Lovas-Kiss Á, Reynold C, Sebastián-González E, Silva GG, van Leeuwen CHA, Wilkinson DM (2023) Dispersal of aquatic and terrestrial organisms by waterbirds: a review of current knowledge and future priorities. Freshw Biol 68(2):173–190. https://doi.org/10.1111/fwb.14038

Griffith AW, Gobler CJ (2020) Harmful algal blooms: a climate change co-stressor in marine and freshwater ecosystems. Harmful Algae 91:101590. https://doi.org/10.1016/j.hal.2019.03.008

Gromov BV, Plujusch AV, Mamkaeva KA (1999) Morphology and possible host range of Rhizophydium algavorum sp. Nov. (Chytridiales)—an obligate parasite of algae. Protistology 1(2):62–65

Gronchi E, Straile D, Diehl S, Jöhnk KD, Peeters F (2023) Impact of climate warming on phenological asynchrony of plankton dynamics across Europe. Ecol Lett 26:717–728. https://doi.org/10.1111/ele.14190

Grossart H-P, Rojas-Jimenez K (2016) Aquatic fungi: targeting the forgotten in microbial ecology. Curr Opin Microbiol 31:140–145. https://doi.org/10.1016/j.mib.2016.03.016

Grossart H-P, Van den Wyngaert S, Kagami M, Wurzbacher C, Cunliffe M, Rojas-Jimenez K (2019) Fungi in aquatic ecosystems. Nat Rev Microbiol 17(6):339–354. https://doi.org/10.1038/s41579-019-0175-8

Gruber N, Clement D, Carter BR, Feely RA, van Heuven S, Hoppema M, Ishii M, Key RM, Kozyr A, Mauvest SK, Lo Monaco C, Mathis JT, Murata A, Olsen A, Perez FF, Sabine CL, Tanhua T, Wanninkhof R (2019) The oceanic sink for anthropogenic $CO_2$ from 1994 to 2007. Science 363(6432):1193–1199

Gsell AS, de Senerpont Domis LN, Van Donk E, Ibelings BW (2013a) Temperature alters host genotype-specific susceptibility to chytrid infection. PLoS ONE 8:e71737. https://doi.org/10.1371/journal.pone.0071737

Gsell AS, de Senerpont Domis LN, Verhoeven KJ, VanDonk E, Ibelings BW (2013b) Chytrid epidemics may increase genetic diversity of a diatom spring-bloom. ISME J 7:2057–2059. https://doi.org/10.1038/ismej.2013.73

Gsell AS, de Senerpont Domis LN, Naus-Wiezer SMH, Helmsing NR, Donk EV, Ibelings BW (2013c) Spatiotemporal variation in the distribution of chytrid parasites in diatom host populations. Freshw Biol 58:523–537. https://doi.org/10.1111/j.1365-2427.2012.02786.x

Gsell A, de Senerpont DL, van Donk E, Ibelings B (2022) Replication data for: temperature alters host genotype-specific susceptibility to chytrid infection. DataverseNL

Gsell AS, Biere A, de Boer W, de Bruijn I, Eichhorn G, Frenken T, Geisen SA, van der Jeugd H, Mason-Jones K, Meisner A, Thakur MP, van Donk E, Zwart MP, van de Waal DB (2023) Environmental refuges from disease in host-parasite interactions under global change. Ecology. https://doi.org/10.1002/ecy.4001

Gunn BK, Leary JH, Lee VM, Kirby AJ, Scott G, Camus AC (2024) First report of the emerging rosette agent (*Sphaerothecum destruens*) in a captive held native North American cyprinid, the warpaint shiner (*Luxilus coccogenis*, Cope). J Fish Dis 47(9):e13980. https://doi.org/10.1111/jfd.13980

Guo S-Y, Gareth Jones EB, Chiang MWL, Pang K-L (2023) Salinity and temperature affect growth rate of *Alphamyces chaetifer* and *Gorgonomyces haynaldii* (Chytridiomycota) isolated from coastal habitats of Taiwan. Bot Mar 66(4):345–352. https://doi.org/10.1515/bot-2023-0011

Gutiérrez MH, Jara AM, Pantoja S (2016) Fungal parasites infect marine diatoms in the upwelling ecosystem of the Humboldt Current System off Central Chile. Environ Microbiol 18(5):1646–1653. https://doi.org/10.1111/1462-2920.13257

Gutman J, Zarka A, Boussiba S (2009) The host-range of *Paraphysoderma sedebokerensis*, a chytrid that infects *Haematococcus pluvialis*. Eur J Phycol 44(4):509–514. https://doi.org/10.1080/09670260903161024

Gärtner G, Stoyneva-Gärtner M, Uzunov B (2021) Algal toxic compounds and their aeroterrestrial, airborne and other extremophilic producers with attention to soil and plant contamination: a review. Toxins 13:322. https://doi.org/10.3390/toxins13050322

Hamilton PT, Richardson JML, Anholt BR (2012) *Daphnia* in tadpole mesocosms: trophic links and interactions with *Batrachochytrium dendrobatidis*. Freshw Biol 57:676–683. https://doi.org/10.1111/j.1365-2427.2011.02731.x

Han D, Li Y, Hu Q (2013) Biology and commercial aspects of *Haematococcus pluvialis*. In: Richmond A, Hu Q (eds) Handbook of microalgal culture: applied phycology and biotechnology, 2nd edn. John Wiley and Sons, Oxford, pp 388–405

Hanic LA, Sekimoto S, Bates SS (2009) Oomycete and chytrid infections of the marine diatom *Pseudo-nitzschia pungens* (Bacillariophyceae) from Prince Edward Island, Canada. Botany 87(11):1096–1105. https://doi.org/10.1139/B09-070

Harris RN, Lauer A, Simon MA, Banning JL, Alford RA (2006) Addition of antifungal skin bacteria to salamanders ameliorates the effects of chytridiomycosis. Dis Aquat Org 83:11–16

Harris RN, Brucker RM, Walke JB, Becker MH, Schwantes CR, Flaherty DC, Lam BA, Woodhams DC, Briggs CJ, Vredenburg VT, Minbiole KPC (2009) Skin microbes on frogs prevent morbidity and mortality caused by a lethal skin fungus. ISME J 3:818–824. https://doi.org/10.1038/ismej.2009.27

Harrison J, Jones EG (1971) Salinity tolerance of *Saprolegnia parasitica* Coker. Mycopathol Mycol Appl 43:297–307

Hassett BT, Gradinger R (2016) Chytrids dominate arctic marine fungal communities. Environ Microbiol 18(6):2001–2009. https://doi.org/10.1111/1462-2920.13216

Hatai K, Hoshiai G (1992) Mass mortality in cultured coho salmon (*Oncorhynchus kisutch*) due to *Saprolegnia parasitica* Coker. J Wild Diseeas 28:532–535

Haver M, Le Roux G, Friesen J, Loyau A, Vredenburg VT, Schmeller DS (2022) The role of abiotic variables in an emerging global amphibian fungal disease in mountains. Sci Total Environ 815:152735. https://doi.org/10.1016/j.scitotenv.2021.152735

Hay ME (2009) Marine chemical ecology: chemical signals and cues structure marine populations, communities, and ecosystems. Ann Rev Mar Sci 1:193–212. https://doi.org/10.1146/annurev.marine.010908.163708

Hay ME (2014) Challenges and opportunities in marine chemical ecology. J Chem Ecol 40:216–217. https://doi.org/10.1007/s10886-014-0393-5

Heard GW, Thomas CD, Hodgson JA, Scroggie MP, Ramsey DSL, Clemann N (2015) Refugia and connectivity sustain amphibian metapopulations afflicted by disease. Ecol Lett 18:853–863. https://doi.org/10.1111/ele.12463

Heard GW, Scroggie MP, Ramsey DSL, Clemann N, Hodgson JA, Thomas CD (2018) Can habitat management mitigate disease impacts on threatened amphibians? Conserv Lett 11:1–10. https://doi.org/10.1111/conl.12375

Hite JL, Bosch J, Fernández-Beaskoetxea S, Medina D, Hall SR (2016) Joint effects of habitat, zooplankton, host stage structure and diversity on amphibian chytrid. Proc Biol Sci 283:20160832. https://doi.org/10.1098/rspb.2016.0832

Hoeger AL, Jehmlich N, Kipping L, Griehl C, Noll M (2022) Associated bacterial microbiome responds opportunistic once algal host *Scenedesmus vacuolatus* is attacked by endoparasite *Amoeboaphelidium protococcarum*. Sci Rep 12:13187. https://doi.org/10.1038/s41598-022-17114-1

Hoffman Y, Aflalo C, Zarka A, Gutman J, James TY, Boussiba S (2008) Isolation and characterization of a novel chytrid species (phylum Blastocladiomycota), parasitic on the green alga *Haematococcus*. Mycol Res 112(1):70–81. https://doi.org/10.1016/j.mycres.2007.09.002

Holdich DM, Reynolds JD, Souty-Grosset C, Sibley PJ (2009) A review of the everincreasing threat to European crayfish from non-indigenous crayfish species. Knowl Managt Aquatic Ecosyst 11:394–395. https://doi.org/10.1051/kmae/2009025

Holfeld H (1998) Fungal infections of the phytoplankton: seasonality, minimal host density, and specificity in a mesotrophic lake. New Phytol 138:507–517. https://doi.org/10.1046/j.1469-8137.1998.00126.x

Holfeld H (2000) Relative abundance, rate of increase, and fungal infections of freshwater phytoplankton. J Plankton Res 22(5):987–995. https://doi.org/10.1093/plankt/22.5.987

Holt RD, Dobson AP, Begon M, Bowers R, Schauber EM (2003) Parasite establishment in host communities. Ecol Lett 6:837–842. https://doi.org/10.1046/j.1461-0248.2003.00501.x

Hom EFY, Aiyar P, Schaeme D, Mittag M, Sasso S (2015) A chemical perspective on microalgal-microbial interactions. Trends Plant Sci 20(11):689–693

Hudson PJ, Dobson AP, Lafferty KD (2006) Is a healthy ecosystem can that is rich in parasites? Trends Ecol Evol 21:381–385

Hutchinson GE (1957) A treatise on limnology, vol. 1, geography, physics, and chemistry. John Wiley, London

Hwang S-W, Choi HI, Sim SJ (2019) Acidic cultivation of *Haematococcus pluvialis* for improved astaxanthin production in the presence of a lethal fungus. Bioresour Technol 278:138–144. https://doi.org/10.1016/j.biortech.2019.01.080

Hyatt AD, Olsen V, Boyle DB, Berger L, Obendorf D, Dalton A, Kriger K, Hero M, Hines H, Phillott R, Campbell R, Marantelli G, Gleason F, Colling A (2007) Diagnostic assays and sampling protocols for the detection of *Batrachochytrium dendrobatidis*. Dis Aquat Org 73:175–192. https://doi.org/10.3354/dao073175

Ibelings BW, De Bruin A, Kagami M, Rijkeboer M, Brehm M, Donk EV (2004) Host parasite interactions between freshwater phytoplankton and chytrid fungi (Chytridiomycota). J Phycol 40:437–453. https://doi.org/10.1111/j.1529-8817.2004.03117.x

Ibelings BW, Gsell AS, Mooij WM, Van Donk E, Van den Wyngaert S, de Senerpont Domis LN (2011) Chytrid infections and diatom spring blooms: paradoxical effects of climate warming on fungal epidemics in lakes. Freshw Biol 56:754–766. https://doi.org/10.1111/j.1365-2427.2010.02565.x

Ilicic D, Grossart H-P (2022) Basal parasitic fungi in marine food webs -a mystery yet to unravel. J Fungi 8:114. https://doi.org/10.3390/jof8020114

Ilicic D, Woodhouse J, Karsten U, Zimmermann J, Wichard T, Quartino ML, Campana GL, Livenets A, Van den Wyngaert S, Grossart H-P (2022) Antarctic glacial meltwater impacts the diversity of fungal parasites associated with benthic diatoms in shallow coastal zones. Front Microbiol 13:805694. https://doi.org/10.3389/fmicb.2022.805694

Ilicic D, Woodhouse J, Karsten U, Schimani K, Zimmermann J, Grossart H-P (2024) Chytrid fungi infecting Arctic microphytobenthic communities under varying salinity conditions. Sci Rep 14(1):25821. https://doi.org/10.1038/s41598-024-77202-2

Ilkov G (1975) Population dynamic relationships during *Phlyctidium scenedesmi* development in *Scenedesmus acutus* cultures. Appl Microbiol 6:104–110

Index Fungorum. IOP Publishing PhysicsWeb. https://www.indexfungorum.org/Index.htm. Accessed 26 September 2025

IPCC (2014): Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, Pachauri RK, Meyer LA (eds.)]. IPCC, Geneva

Jacinto-Maldonado M, Meza-Figueroa D, Pedroza-Montero M, Lesbarrères D, Robles-Morúa A, Navarro-Espinoza S, González-Grijalva B, Pérez-Segura E, Silva-Campa E, Angulo-Molina A, Paredes-León R (2022) Mites as a potential path for Ce-Ti exposure of amphibians. Front Environ Sci. https://doi.org/10.3389/fenvs.2022.870645

Jacinto-Maldonado M, Lesbarrères D, Rebollar EA, Basanta MD, González-Grijalva B, Robles-Morúa A, Álvarez-Bajo O, Vizuete-Jaramillo E, Paredes-León R, Meza-Figueroa D (2024) *Batrachochytrium dendrobatidis* and Hannemania mite's relationships with Mexican amphibians in disturbed environments. Front Amphib Reptile Sci. https://doi.org/10.3389/famrs.2024.1372993

Jensen WB (2004) The symbol for pH. J Chem Educ 81(1):21. https://doi.org/10.1021/ed081p21

Johansson M, Coats DW (2002) Ciliate grazing on the parasite *Amoebophrya* sp. decreases infection of the red-tide dinoflagellate *Akashiwo sanguinea*. Aquat Microb Ecol 28:69–78

Johnson TW (1967) Monocentric fungi on species of *Rhizosolenia* from saline habitats. Mycopathologia 32:281–290

Johnson ML, Speare R (2005) Possible modes of dissemination of the amphibian chytrid *Batrachochytrium dendrobatidis* in the environment. Dis Aquat Organ 65:181–186. https://doi.org/10.3354/dao065181

Johnson ML, Berger L, Philips L, Speare R (2003) Fungicidal effects of chemical disinfectants, UV light, desiccation and heat on the amphibian chytrid *Batrachochytrium dendrobatidis*. Dis Aquat Organ 57:255–260. https://doi.org/10.3354/dao057255

Johnson PTJ, Longcore JE, Stanton DE, Carnegie RB, Shields JD, Preu ER (2006) Chytrid infections of *Daphnia pulicaria*: development, ecology, pathology and phylogeny of *Polycaryum leave*. Freshw Biol 51:634–648

Johnson PTJ, Ives AR, Lathrop RC, Carpenter SR (2009) Long-term disease dynamics in lakes: causes and consequences of chytrid infections in *Daphnia* populations. Ecology 90:132–144. https://doi.org/10.1890/07-2071.1

Jones EBG, Ramakrishna S, Vikineswary S, Das D, Bahkali AH, Guo S-Y, Pang K-L (2022) How do fungi survive in the sea and respond to climate change? J Fungi 8(3):291. https://doi.org/10.3390/jof8030291

Jørgensen NOG, Stepanauskas R (2008) Biomass of pelagic fungi in Baltic rivers. Hydrobiologia 623:105–112

Kagami M, Urabe J (2002) Mortality of the planktonic desmid, *Staurastrum dorsidentiferum*, due to interplay of fungal parasitism and low light conditions. SIL Proc 28(2):1001–1005. https://doi.org/10.1080/03680770.2001.11901868

Kagami M, Van Donk E, Rijkeboer M, Ibelings BW (2004) *Daphnia* can protect diatoms from fungal parasitism. Limnol Oceanogr 49:680–685. https://doi.org/10.4319/lo.2004.49.3.0680

Kagami M, de Bruin A, Ibelings BW, Van Donk E (2007a) Parasitic chytrids: their effects on phytoplankton communities and food-web dynamics. Hydrobiologia 578:113–129. https://doi.org/10.1007/s10750-006-0438-z

Kagami M, von Elert E, Ibelings BW, de Bruin A, Van Donk E (2007b) The parasitic chytrid, *Zygorhizidium*, facilitates the growth of the cladoceran zooplankter, *Daphnia*, in cultures of the inedible alga, *Asterionella*. Proceedings of the Royal Society B: Biological Sciences 274(1617):1561–1566. https://doi.org/10.1098/rspb.2007.0425

Kagami M, Miki T, Takimoto G (2014) Mycoloop: chytrids in aquatic food webs. Front Microbiol 5:166. https://doi.org/10.3389/fmicb.2014.00166

Kagami M, Seto K, Nozaki D, Nakamura T, Wakana H, Wurzbacher C (2021) Single dominant diatom can host diverse parasitic fungi with different degree of host specificity. Limnol Oceanogr 66(3):667–677. https://doi.org/10.1002/lno.11631

Karling JS (1943) The life history of *Anisolpidium ectocarpii* gen. nov. et sp. nov., and a synopsis and classification of other fungi with anteriorly uniflagellate zoospores. Am J Bot 30(8):637–648

Karpov SA, Mamkaeva MA, Aleoshin VV, Nassonova E, Lilje O, Gleason FH (2014) Morphology, phylogeny, and ecology of the aphelids (Aphelidea, Opisthokonta) and proposal for the new superphylum Opisthosporidia. Front Microbiol 5:112. https://doi.org/10.3389/fmicb.2014.00112

Kärvemo S, Meurling S, Berger D, Höglund J, Laurila A (2018) Effects of host species and environmental factors on the prevalence of *Batrachochytrium dendrobatidis* in northern Europe. PLoS ONE 13:e0199852. https://doi.org/10.1371/journal.pone.0199852

Kaushal SS, Shelton SA, Mayer PM, Kellmayer B, Utz RM, Reimer JE, Baljunas J, Bhide SV, Mon A, Rodriguez-Cardona BM, Grant SB, Newcomer-Johnson TA, Malin JT, Shatkay RR, Collison DC, Papageorgiou K, Escobar J, Rippy MA, Likens GE, Najjar RG, Mejia AI, Lassiter A, Li M, Chant RJ (2025) Freshwater faces a warmer and saltier future from headwaters to coasts: climate risks, saltwater intrusion, and biogeochemical chain reactions. Biogeochem 168:31. https://doi.org/10.1007/s10533-025-01219-6

Kazama FY (1972) Ultrastructure and phototaxis of the zoospores of *Phlyctochytrium* sp., an estuarine chytrid. J Gen Microbiol 71:555–566. https://doi.org/10.1099/00221287-71-3-555

Klawonn I, Van den Wyngaert S, Parada AE, Arandia-Gorostidi N, Whitehouse MJ, Grossart HP, Dekas AE (2021) Characterizing the "fungal shunt": parasitic fungi on diatoms affect carbon flow and bacterial communities in aquatic microbial food webs. Proc Natl Acad Sci USA 118(23):e2102225118. https://doi.org/10.1073/pnas.2102225118

Kleinschroth F, Winton RS, Calamita E, Niggemann F, Botter M, Wehrli B, Ghazoul J (2021) Living with floating vegetation invasions. Ambio 50:125–137. https://doi.org/10.1007/s13280-020-01360-6

Kobayashi K, Takeuchi N, Kagami M (2023) High prevalence of parasitic chytrids infection of glacier algae in cryoconite holes in Alaska. Sci Rep 13:3973. https://doi.org/10.1038/s41598-023-30721-w

Kokociński M, Akçaalan R, Salmaso N, Stoyneva-Gärtner MP, Sukenik A (2017) Expansion of alien and invasive cyanobacteria. In: Meriluoto J, Spoof L, Codd JA (eds) Handbook of cyanobacterial monitoring and cyanotoxin analysis. Wiley, Chichester, pp 28–40. https://doi.org/10.1002/9781119068761.ch4

Kolby JE, Ramirez SD, Berger L, Griffin DW, Jocque M, Skerratt LF (2015) Presence of amphibian chytrid fungus (*Batrachochytrium dendrobatidis*) in rainwater suggests aerial dispersal is possible. Aerobiologia 31:411–419. https://doi.org/10.1007/s10453-015-9374-6

Kontoghiorghes GJ, Kontoghiorghe CN (2020) Iron and chelation in biochemistry and medicine: new approaches to controlling iron metabolism and treating related diseases. Cells 9(6):1456. https://doi.org/10.3390/cells9061456

Kordas RL, Harley CDG, O'Connor MI (2011) Community ecology in a warming world: the influence of temperature on interspecific interactions in marine systems. J Exp Mar Biol Ecol 400(1–2):218–226. https://doi.org/10.1016/j.jembe.2011.02.029

Krause E, Wichels A, Giménez L, Gerdts G (2013) Marine fungi may benefit from ocean acidification. Aquat Microb Ecol 69:59–67. https://doi.org/10.3354/ame01622

Kristiansen J (1996a) Biogeography of freshwater algae – conclusions and perspectives. In: Kristiansen J (ed) Biogeography of freshwater algae. Developments in hydrobiology, vol 118. Springer, Dordrecht, pp 159–161

Kristiansen J (1996b) Dispersal of freshwater algae - a review. In: Kristiansen J (ed) Biogeography of freshwater. Algae developments in hydrobiology, vol 118. Springer, Dordrecht, pp 151–157

Kristiansen J (2008) Dispersal and biogeography of silicascaled chrysophytes. Biodivers Conserv 17:419–426. https://doi.org/10.1007/s10531-007-9259-2

Kruger A (2020) Frog skin microbiota vary with host species and environment but not chytrid infection. Front Microbiol 11:1330. https://doi.org/10.3389/fmicb.2020.01330

Kühn SF, Hofmann M (1999) Infection of *Coscinodiscus granii* by the parasitoid nanoflagellate *Pirsonia diadema*: III. effects of turbulence on the incidence of infection. J Plankton Res 21:2323–2340. https://doi.org/10.1093/plankt/21.12.2323

Kühn SF, Drebes G, Schnepf E (1996) Five new species of the nanoflagellate *Pirsonia* in the German Bight, North Sea, feeding on planktic diatoms. Helgol Meeresunters 50(2):205–222. https://doi.org/10.1007/BF02367152

Kyle M, Haande S, Ostermaier V, Rohrlack T (2015) The red queen race between parasitic chytrids and their host, *Planktothrix*: a test using a time series reconstructed from sediment DNA. PLoS ONE 10(3):e0118738. https://doi.org/10.1371/journal.pone.0118738

Lafferty KD (2009) The ecology of climate change and infectious diseases. Ecology 90(4):888–900. https://doi.org/10.1890/08-0079.1

Lafferty KD, Dobson AP, Kuris AM (2006) Parasites dominate food web links. Proc Natl Acad Sci U S A 103(30):11211–11216. https://doi.org/10.1073/pnas.0604755103

Lafferty KD, Allesina S, Arim M, Briggs CJ, De Leo G, Dobson AP, Dunne JA, Johnson PTJ, Kuris AM, Marcogliese DJ, Martinez ND, Memmott J, Marquet PA, McLaughlin JP, Mordecai EA, Pascual M, Poulin R, Thieltges DW (2008) Parasites in food webs: the ultimate missing links. Ecol Lett 11:533–546. https://doi.org/10.1111/j.1461-0248.2008.01174.x

Lalli CM, Parsons TR (1997) Chapter 2 - the abiotic environment. In: Lalli CM, Parsons TR (eds) Biological oceanography: an introduction (Second edition). Butterworth-Heinemann, pp 16–38

Lange L, Barrett K, Pilgaard B, Gleason F, Tsang A (2019) Enzymes of early-diverging, zoosporic fungi. Appl Microbiol Biotechnol 103:6885–6902. https://doi.org/10.1007/s00253-01909983-w

Lartseva LV (1986) *Saprolegnia* on the spawn of sturgeons and salmons. Hydrobiol J 22:103–107

Lartseva LV, Dudka IA (1990) Dependence of Saprolegniaceae development on the sturgeon and salmon eggs fish productive quality. Mikol Fitopatol 24:112–116

Laundon D, Cunliffe M (2021) A call for a better understanding of aquatic chytrid biology. Front Fungal Biol 2:708813. https://doi.org/10.3389/ffunb.2021.708813

Laundon D, Mock T, Wheeler G, Cunliffe M (2021) Healthy herds in the phytoplankton: the benefit of selective parasitism. ISME J 15(7):2163–2166. https://doi.org/10.1038/s41396-021-00936-8

Lepelletier F, Karpov SA, Alacid E, Le Panse S, Bigeard E, Garcés E, Jeanthon C, Guillou L (2014) *Dinomyces arenysensis* gen. et sp. nov. (Rhizophydiales, Dinomycetaceae fam. nov.), a chytrid infecting marine dinoflagellates. Protist 165:230–244. https://doi.org/10.1016/j.protis.2014.02.004

Leshem T, Letcher PM, Powell MJ, Sukenik A (2016) Characterization of a new chytrid species parasitic on the dinoflagellate, *Peridinium gatunense*. Mycologia 108:731–743. https://doi.org/10.3852/15-197

Letcher PM, Powell MJ (2018) A taxonomic summary and revision of *Rozella* (Cryptomycota). IMA Fungus 9:383–399. https://doi.org/10.5598/imafungus.2018.09.02.09

Letcher PM, Lopez S, Schmieder R, Lee PA, Behnke C, Powell MJ (2013) Characterization of *Amoeboaphelidium protococcarum*, an algal parasite new to the Cryptomycota isolated from an outdoor algal pond used for the production of biofuel. PLoS ONE 8(2):e56232. https://doi.org/10.1371/journal.pone.0056232

Letcher PM, Lee PA, Lopez S, Burnett M, McBride RC, Powell MJ (2016) An ultrastructural study of *Paraphysoderma sedebokerense* (Blastocladiomycota), an epibiotic parasite of microalgae. Fungal Biol 120:324–337. https://doi.org/10.1016/j.funbio.2015.11.003

Li J, Guttmann N, Drew GC, Hector TE, Wolinska J, King KC (2024) Excess mortality of infected ectotherms induced by warming depends on pathogen kingdom and evolutionary history. PLoS Biol 22(11):e3002900. https://doi.org/10.1371/journal.pbio.3002900

Lim KF (2006) Negative pH does exist. J Chem Educ 83(10):1465. https://doi.org/10.1021/ed083p1465

Lindsey R (2023) Climate change: Global Sea Level. NOAA Climate. Gov. Retrieved from https://www.climate.gov/news-features/understanding-climate/climate-change-global-sea-level on 17th February 2026.

Llaveria G, Garcés E, Ross ON, Figueroa R, Sampedro N, Berdalet E (2010) Small-scale turbulence can reduce parasite infectivity to dinoflagellates. Mar Ecol Prog Ser 412:45–56

Lobo LQ, Izabel-Shen D, Albertsson J, Raymond C, Gunnarsson JS, Broman E, Nascimento FJA (2024) Salinity and resource availability as drivers of Baltic benthic fungal diversity. Environ DNA 6:e526. https://doi.org/10.1002/edn3.526

Longcore JE, Pessier AP, Nichols DK (1999) *Batrachochytrium dendrobatidis* gen. et sp. nov., a chytrid pathogenic to amphibians. Mycologia 91(2):219–227. https://doi.org/10.1080/00275514.1999.12061

Lord JC, Fukuda T (1990) A *Leptolegnia* (Saprolegniales) pathogenic for mosquito larvae. J Invertebr Pathol 55(1):130–132. https://doi.org/10.1016/0022-2011(90)90043-6

Lötters S, Wagner N, Albaladejo G, Böning P, Dalbeck L, Düssel H, Feldmeier S, Guschal M, Kirst K, Ohlhoff D, Preissler K, Reinhardt T, Schlüpmann M, Schulte U, Schulz V, Steinfartz S, Twietmeyer S, Veith M, Vences M, Wegge J (2020) The amphibian pathogen *Batrachochytrium salamandrivorans* in the hotspot of its European invasive range: past – present – future. Salamandra 56(3):173–188

Loudon AH, Holland JA, Umile TP, Burzynski EA, Minbiole KP, Harris RN (2014) Interactions between amphibians' symbiotic bacteria cause the production of emergent anti-fungal metabolites. Front Microbiol 5:441. https://doi.org/10.3389/fmicb.2014.00441

Lowe S, Browne M, Boudjelas S, De Poorter M (2000) 100 of the world's worst invasive alien species: a selection from the global invasive species database. The Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN).

Loyau A, Bouchali R, Sentenac H, Schmeller DS (2024) The commensal skin microbiome of amphibian mountain populations and its association with the pathogen *Batrachochytrium dendrobatidis*. Environ Microbiol 26(10):e16699. https://doi.org/10.1111/1462-2920.16699

Lund JWG (1957) Fungal diseases of plankton algae. In: Horton-Smith C (ed) Biological aspects of the transmission of diseases. Oliver and Boyd, Edinburgh, pp 19–23

Luo Y, Guo W, Ngo HH, Nghiem LD, Hai FI, Zhang J, Liang S, Wang XC (2014) A review on the occurrence of micropollutants in the aquatic environment and their fate and removal during wastewater treatment. Sci Total Environ 473–474:619–641. https://doi.org/10.1016/j.scitotenv.2013.12.065

Lürling M (2021) Grazing resistance in phytoplankton. Hydrobiologia 848:237–249. https://doi.org/10.1007/s10750-020-04370-3

Ma D, Gregor L, Gruber N (2023) Four decades of trends and drivers of global surface ocean acidification. Glob Biogeochem Cycles 37:e2023GB007765. https://doi.org/10.1029/2023GB007765

Maier MA, Peterson TD (2014) Observations of a diatom chytrid parasite in the lower Columbia River. Northwest Sci 88(3):234–245. https://doi.org/10.3955/046.088.0306

Maier MA, Peterson TD (2016) Enumeration of parasitic chytrid zoospores in the Columbia River via quantitative PCR. Appl Environ Microbiol 82(13):3857–3867. https://doi.org/10.1128/AEM.00084-16

Maier I, Parodi E, Westermeier R, Müller DG (2000) *Maullinia ectocarpii* gen. et sp. nov. (Plasmodiophorea), an intracellular parasite in *Ectocarpus siliculosus* (Ectocarpales, Phaeophyceae) and other filamentous brown algae. Protist 151:225–238. https://doi.org/10.1078/1434-4610-00021

Maier MA, Peterson TD, Needoba JA (2013) Dynamics of chytrid infections on diatoms in a turbulent river system. Ecological Society of America, 98th Annual meeting—Sustainable pathways: learning from the past and shaping the future, August 4–9, 2013, Minneapolis, USA

Martel A, Blooi M, Adriaensen C, Van Rooij P, Beukema W, Fisher MC, Farrer RA, Schmidt BR, Tobler U, Goka K, Lips KR, Muletz C, Zamudio KR, Bosch J, Lötters S, Wombwell E, Garner TW, Cunningham AA, Spitzen-van der Sluijs A, Salvidio S, Ducatelle R, Nishikawa K, Nguyen TT, Kolby JE, Van Bocxlaer I, Bossuyt F, Pasmans F (2014) Recent introduction of a chytrid fungus endangers Western Palearctic salamanders. Science 346(6209):630–631. https://doi.org/10.1126/science.1258268

Martel A, Vila-Escalé M, Fernández-Giberteau D, Martinez-Silvestre A, Canessa S, van Praet S, Pannon P, Chiers K, Ferran A, Kelly M, Picart M, Piulats D, Li Z, Pagone V, Pérez-Sorribes L, Molina C, Tarragó-Guarro A, Velarde-Nieto R, Carbonell F, Obon E, Martínez-Martínez D, Guinart D, Casanovas R, Carranza S, Pasmans F (2020) Integral chain management of wildlife diseases. Conserv Lett 13(2):e12707. https://doi.org/10.1111/conl.12707

Martin WW (1984) The dynamics of aquatic fungi parasitic in a stream population of the midge, *Chironomus attenuatus*. J Invertebr Pathol 44:36–45. https://doi.org/10.1016/0022-2011(84)90043-0

Martin WW (1987) Zoosporic parasites of aquatic insects: collection, identification, and culture. In: Fuller MS, Jaworski A (eds) Zoosporic fungi in teaching and research. Southeastern Publishing Corporation, Athens, pp 137–142

Martín-Torrijos L, Martínez-Ríos M, Casabella-Herrero G, Adams SB, Jackson CR, Diéguez-Uribeondo J (2021) Tracing the origin of the crayfish plague pathogen, *Aphanomyces astaci*, to the Southeastern United States. Sci Rep 11:9332. https://doi.org/10.1038/s41598-021-88704-8

Masigol H, van West P, Taheri SR, Fregeneda-Grandes J-M, Pârvulescu L, McLaggan D, Bliss TT, Mostowfizadeh-Ghalamfarsa R, Pourmoghaddam MJ, Grossart H-P (2023) Advancements, deficiencies, and future necessities of studying Saprolegniales: a semi-quantitative review of 1073 published papers. Fungal Biol Rev 46:100319. https://doi.org/10.1016/j.fbr.2023.100319

McKindles KM, Jorge AN, McKay RM, Davis TW, Bullerjahn GS (2021a) Isolation and characterization of Rhizophydiales (Chytridiomycota), obligate parasites of *Planktothrix agardhii* in a Laurentian Great Lakes Embayment. Appl Environ Microbiol 87:e02308-20. https://doi.org/10.1128/AEM.02308-20

McKindles KM, Manes MA, McKay RM, Davis TW, Bullerjahn GS (2021b) Environmental factors affecting chytrid (Chytridiomycota) infection rates on *Planktothrix agardhii*. J Plankton Res 43(5):658–672. https://doi.org/10.1093/plankt/fbab058

McKindles KM, McKay RML, Bullerjahn GS, Frenken T (2023) Interactions between chytrids cause variable infection strategies on harmful algal bloom forming species. Harmful Algae 122:102381. https://doi.org/10.1016/j.hal.2023.102381

Meentemeyer RK, Haas SE, Václavík T (2012) Landscape epidemiology of emerging infectious diseases in natural and human-altered ecosystems. Annu Rev Phytopathol 50:379–402. https://doi.org/10.1146/annurev-phyto-081211-172938

Mialet B, Majdi N, Tackx M, Azémar F, Buffan-Dubau E (2013) Selective feeding of bdelloid rotifers in river biofilms. PLoS ONE 8(9):e75352. https://doi.org/10.1371/journal.pone.0075352

Miki T, Takimoto G, Kagami M (2011) Roles of parasitic fungi in aquatic food webs: a theoretical approach. Freshw Biol 56(6):1173–1183. https://doi.org/10.1111/j.1365-2427.2010.02562.x

Muehlstein L (1998) Perspectives on the wasting disease of eelgrass *Zostera marina*. Dis Aquat Org 7:211–221. https://doi.org/10.3354/dao007211

Muehlstein LK, Amon JP, Leffler DL (1988) Chemotaxis in the marine fungus *Rhizophydium littoreum*. Appl Environ Microbiol 54:1668–1672. https://doi.org/10.1128/aem.54.7.1668-1672.1988

Muehlstein LK, Porter D, Short FT (1991) *Labyrinthula zosterae* sp. nov., the causative agent of wasting disease of eelgrass, *Zostera marina*. Mycologia 83(2):180–191. https://doi.org/10.1080/00275514.1991.12025994

Müller DG, Küpper FC, Küpper H (1999) Infection experiments reveal broad host ranges of *Eurychasma dicksonii* (Oomycota) and

*Chytridium polysiphoniae* (Chytridiomycota), two eukaryotic parasites of marine brown algae (Phaeophyceae). Phycol Res 47:217–223. https://doi.org/10.1046/j.1440-1835.1999.00165.x

Murúa P, Müller DG, Etemadi M, van West P, Gachon CMM (2020) Host and pathogen autophagy are central to the inducible local defences and systemic response of the giant kelp *Macrocystis pyrifera* against the oomycete pathogen *Anisolpidium ectocarpii*. New Phytol 226:1445–1460. https://doi.org/10.1111/nph.16438.c

Murúa P, Garvetto A, Egan S, Gachon CMM (2023) The reemergence of phycopathology: when algal biology meets ecology and biosecurity. Annu Rev Phytopathol 61:231–255. https://doi.org/10.1146/annurev-phyto-020620-120425

Nakanishi M, Michibata T (2025) How does cloud emissivity feedback affect present and future Arctic warming? Ocean-Land-Atmos Res 4:0089. https://doi.org/10.34133/olar.0089

Nakanishi H, Seto K, Takeuchi N, Kagami M (2023) Novel parasitic chytrids infecting snow algae in an alpine snow ecosystem in Japan. Front Microbiol 14:1201230. https://doi.org/10.3389/fmicb.2023.1201230

Naselli-Flores L, Padisák J, Dokulil M, Chorus I (2003) Equilibrium/steady-state concept in phytoplankton ecology. Hydrobiologia 502:395–403. https://doi.org/10.1023/B:HYDR.0000004297.52645.59

Nelson GC (2005) Drivers of ecosystem change: summary chapter. In: Hassan R, Scholes R, Ash N (eds) Ecosystems and human well-being: current state and trends, vol 1. Island Press, Washington, pp 73–76

Nie P, Feng J (2022) Global niche and range shifts of *Batrachochytrium dendrobatidis*, a highly virulent amphibian-killing fungus. Fungal Biol 126(11–12):809–816. https://doi.org/10.1016/j.funbio.2022.10.004

Niederle MV, Bosch J, Ale CE, Nader-Macías ME, Aristimuño Ficoseco C, Toledo LF, Valenzuela-Sánchez A, Soto-Azat C, Pasteris SE (2019) Skin-associated lactic acid bacteria from North American bullfrogs as potential control agents of *Batrachochytrium dendrobatidis*. PLoS ONE 14(9):e0223020. https://doi.org/10.1371/journal.pone.0223020

O'Hanlon SJ, Rieux A, Farrer RA, Rosa GM, Waldman B, Bataille A, Kosch TA, Murray KA, Brankovics B, Fumagalli M, Martin MD, Wales N, Alvarado-Rybak M, Bates KA, Berger L, Böll S, Brookes L, Clare F, Courtois EA, Cunningham AA, Doherty-Bone TM, Ghosh P, Gower DJ, Hintz WE, Höglund J, Jenkinson TS, Lin C-F, Laurila A, Loyau A, Martel A, Meurling S, Miaud C, Minting P, Pasmans F, Schmeller DS, Schmidt BR, Shelton JMG, Skerratt LF, Smith F, Soto-Azat C, Spagnoletti M, Tessa G, Toledo LF, Valenzuela-Sánchez A, Verster R, Vörös J, Webb RJ, Wierzbicki C, Wombwell E, Zamudio KR, Aanensen DM, James TY, Gilbert MTP, Weldon C, Bosch J, Balloux F, Garner TWJ, Fisher MC (2018) Recent Asian origin of chytrid fungi causing global amphibian declines. Science 360:621–627. https://doi.org/10.1126/science.aar1965

Olori JC, Netzband R, McKean N, Lowery J, Parsons K, Windstam ST (2018) Multi-year dynamics of ranavirus, chytridiomycosis, and co-infections in a temperate host assemblage of amphibians. Dis Aquat Organ 130(3):187–197. https://doi.org/10.3354/dao03260

Orsi W, Biddle JF, Edgcomb V (2013) Deep sequencing of subseafloor eukaryotic rRNA reveals active fungi across marine subsurface provinces. PLoS ONE 8(2):e56335. https://doi.org/10.1371/journal.pone.0056335

Ortiz-Santaliestra ME, Fisher MC, Fernández-Beaskoetxea S, Fernández-Benéitez MJ, Bosch J (2011) Ambient ultraviolet B radiation and prevalence of infection by *Batrachochytrium dendrobatidis* in two amphibian species. Conserv Biol 25:975–982. https://doi.org/10.1111/j.1523-1739.2011.01700.x

Packer C, Holt RD, Hudson PJ, Lafferty KD, Dobson AP (2003) Keeping the herds healthy and alert: implications of predator control for infectious disease. Ecol Lett 6:797–802

Padisák J, Gábor V, Gábor B (2016) Psychogeography of freshwater phytoplankton: traditional knowledge and new molecular tools. Hydrobiologia 764:3–27

Paerl HW, Huisman J (2009) Climate change: a catalyst for global expansion of harmful cyanobacterial blooms. Environ Microbiol Rep 1:27–37. https://doi.org/10.1111/j.1758-2229.2008.00004.x

Parwan S, Hallan S, Suchita S, Sood V (2023) Plant Pathology-Introduction, History and Importance. In: Advances in plant pathology. Sharma Publications, Jalandhar. https://www.researchgate.net/publication/374234547

Peng X, Amend AS, Baltar F, Blanco-Bercial L, Breyer E, Burgaud G, Cunliffe M, Edgcomb VP, Grossart H-P, Mara P, Masigol H, Pang K-L, Retter A, Roberts C, van Bleijswijk J, Walker AK, Whitner S (2024) Planktonic marine fungi: a review. J Geophys Res Biogeosci 129:e2023JG007887. https://doi.org/10.1029/2023JG007887

Picard KT (2017) Coastal marine habitats harbor novel early-diverging fungal diversity. Fungal Ecol 25:1–13. https://doi.org/10.1016/j.funeco.2016.10.006

Piotrowski JS, Annis SL, Longcore JE (2004) Physiology of *Batrachochytrium dendrobatidis*, a chytrid pathogen of amphibians. Mycologia 96(1):9–15. https://doi.org/10.2307/3761981

Poulin R (2023) Light pollution may alter host–parasite interactions in aquatic ecosystems. Trends Parasitol 39(12):1050–1059. https://doi.org/10.1016/j.pt.2023.08.013

Poulin R, Krasnov BR, Mouillot D (2011) Host specificity in phylogenetic and geographic space. Trends Parasitol 27:355–361. https://doi.org/10.1016/j.pt.2011.05.003

Poulln R (2007) Evolutionary ecology of parasites, 2nd edn. Princeton University Press, Princeton

Prado JS, Ernetti JR, Pontes MR, Toledo LF (2023) Chytrid in the clouds: an alternative passive transport of a lethal pathogen for amphibians. Hydrobiologia 850(9):2061–2073. https://doi.org/10.1007/s10750-023-05218-2

Proctor VW (1966) Dispersal of desmids by waterbirds. Phycologia 5:227–232

Prowse GS (1954) *Aphanomyces daphniae* sp. nov., parasitic on *Daphnia hyaline*. Trans Br Mycol Soc 37:22–28

Puneva ID (2006) Effect of abscisic acid and ontogenic phases of the host alga on the infection process in the pathosystem *Scenedesmus acutus - Phlyctidium scenenedesmi*. APP 28(5):395–400

Puneva I, Christov C (2004) Influence of abscisic acid and abscisic acid biosyntesis inhibitor fluridone on infection process in the pathosystem *Scenedesmus incrassatulus –Phlyctidium scenedesmi*. Compt Rend Acad Bulg Sci 57(8):33–38

Puschendorf R, Hoskin CJ, Cashins SD, McDonald K, Skerratt LF, Vanderwal J, Alford RA (2011) Environmental refuge from disease-driven amphibian extinction: environmental refuge from extinction. Conserv Biol 25:956–964. https://doi.org/10.1111/j.1523-1739.2011.01728.x

Räberg L, Alacid E, Garces E, Figueroa R (2014) The potential for arms race and Red Queen coevolution in a protist host–parasite system. Ecol Evol 4(24):4775–4785

Rachowicz LJ, Briggs CJ (2007) Quantifying the disease transmission function: effects of density on *Batrachochytrium dendrobatidis* transmission in the mountain yellow-legged frog *Rana muscosa*. J Anim Ecol 76:711–721. https://doi.org/10.1111/j.1365-2656.2007.01256.x

Rajarajan A, Cerbin S, Beng KC, Monaghan MT, Wolinska J (2025) Warming increases richness and shapes assemblages of eukaryotic parasitic plankton. Environmental Microbiome 20:76. https://doi.org/10.1186/s40793-025-00724-3

Rasconi S, Jobard M, Jouve L, Sime-Ngando T (2009) Use of Calcofluor White for detection, identification, and quantification of phytoplanktonic fungal parasites. Appl Environ Microbiol 75:2545–2553. https://doi.org/10.1128/AEM.02211-08

Rasconi S, Jobard M, Sime-Ngando T (2011) Parasitic fungi of phytoplankton: ecological roles and implications for microbial food webs. Aquat Microb Ecol 62(2):123–137. https://doi.org/10.3354/ame01448

Rasconi S, Niquil N, Sime-Ngando T (2012) Phytoplankton chytridiomycosis: community structure and infectivity of fungal parasites in aquatic ecosystems. Environ Microbiol 14:2151–2170. https://doi.org/10.1111/j.1462-2920.2011.02690.x

Rasconi S, Grami B, Niquil N, Jobard M, Sime-Ngando T (2014) Parasitic chytrids sustain zooplankton growth during inedible algal bloom. Front Microbiol 5:229. https://doi.org/10.3389/fmicb.2014.00229

Rasconi S, Ptacnik R, Danner S, Van den Wyngaert S, Rohrlack T, Pilecky M, Kainz MJ (2020) Parasitic chytrids upgrade and convey primary produced carbon during inedible algae proliferation. Protist 171(5):125768. https://doi.org/10.1016/j.protis.2020.125768

Rasconi S, Grossart H-P, Gsell A, Ibelings BW, van de Waal D, Agha R, Bacu A, Balode M, Beklioğlu M, Berden Zrimec M, Botez F, Butler T, Cerbin S, Cortina A, Cunliffe M, Frenken T, Garcés E, Gjyli L, Golan Y, Guerra T, Iacovides A, Idà A, Kagami M, Kisand V, Leshoski J, Marco P, Mazalica N, Miki T, Moza MI, Neuhauser S, Özkundakci D, Panksep K, Patcheva S, Pestoric B, Stoyneva MP, Pinto D, Polle J, Postolache C, Pozo Dengra J, Reñé A, Rychtecky P, Schmeller DSS, Scholz B, Selmeczy G, Sime-Ngando T, Tapolczai K, Tasevska O, Trbojevic I, Uzunov B, Van den Wyngaert S, van Donk E, Vanthoor M, Sarafiloska EV, Wood S, Znachor P (2022) Applications for zoosporic parasites in aquatic systems (ParAqua). ARPHA Preprints. https://doi.org/10.3897/arphapreprints.e94590

Rendueles O, Ghigo JM (2012) Multi-species biofilms: how to avoid unfriendly neighbors. FEMS Microbiol Rev 36(5):972–989. https://doi.org/10.1111/j.1574-6976.2012.00328.x

Reñé A, Alacid E, Gallisai R, Chambouvet A, Fernández-Valero AD, Garcés E (2021a) New Perkinsea parasitoids of Dinoflagellates distantly related to Parviluciferaceae members. Front Microbiol 12:701196. https://doi.org/10.3389/fmicb.2021.701196

Reñé A, Timoneda N, Sampedro N, Alacid E, Gallisai R, Gordi J, Fernández-Valero AD, Pernice MC, Flo E, Garcés E (2021b) Host preferences of coexisting *Perkinsea parasitoids* during coastal Dinoflagellate blooms. Mol Ecol 30(10):2417–2433. https://doi.org/10.1111/mec.15895

Reynolds CS (1997) Vegetation processes in the pelagic: a model for ecosystem theory. Ecology Institute, Oldendorf/Luhe

Reynolds CS (2006) Ecology of phytoplankton. Cambridge University Press, Cambridge, Ecology, Biodiversity and Conservation

Reynolds CS (2012) Environmental requirements and habitat preferences of phytoplankton: chance and certainty in species selection. Bot Mar 55:1–17. https://doi.org/10.1515/bot.2011.121

Reynolds CS, Padisák J, Sommer U (1993) Intermediate disturbance in the ecology of phytoplankton and the maintenance of species diversity: a synthesis. Hydrobiologia 249:183–188. https://doi.org/10.1007/BF00008853

Rice EL (1984) Allelopathy, 2nd edn. Academic Press, New York

Rinaldo A, Gatto M, Rodriguez-Iturbe I (2018) River networks as ecological corridors: a coherent ecohydrological perspective. Adv Water Resour 112:27–58. https://doi.org/10.1016/j.advwatres.2017.10.005

Rohde R (2025) Berkeley Global Temperature Report for 2024. Retrieved from https://berkeleyearth.org/global-temperature-report-for-2024/ on 17th February 2026.

Rohr JR, Civitello DJ, Cohen JM, Roznik EA, Sinervo B, Dell AI (2018) The complex drivers of thermalacclimation and breadth in ectotherms. Ecol Lett 21:1425–1439. https://doi.org/10.1111/ele.13107

Rohrlack T (2018) Low temperatures can promote cyanobacterial bloom formation by providing refuge from microbial antagonists. AIMS Microbiol 4:304–318

Rohrlack T, Christiansen G, Kurmayer R (2013) Putative antiparasite defensive system involving ribosomal and nonribosomal oligopeptides in cyanobacteria of the genus *Planktothrix*. Appl Environ Microbiol 79:2642–2647. https://doi.org/10.1128/AEM.03499-12

Rohrlack T, Haande S, Molversmyr Å, Kyle M (2015) Environmental conditions determine the course and outcome of phytoplankton chytridiomycosis. PLoS ONE 10(12):e0145559. https://doi.org/10.1371/journal.pone.0145559

Rojas-Jimenez K, Rieck A, Wurzbacher C, Jürgens K, Labrenz M, Grossart H-P (2019) A salinity threshold separating fungal communities in the Baltic Sea. Front Microbiol 10:680. https://doi.org/10.3389/FMICB.2019.00680

Round EF (1981) The ecology of algae. Cambridge University Press, Cambridge

Sabine CL, Feely RA, Gruber N, Key RM, Lee K, Bullister JL, Wanninkhof R, Wong CS, Wallace DWR, Tilbrook B, Millero FJ, Peng T-H, Kozyr A, Ono T, Rios AF (2004) The oceanic sink for anthropogenic $CO_2$. Science 305(5682):367–371

Sana S, Hardouin EA, Gozlan RE, Ercan D, Tarkan AS, Zhang T, Andreou D (2017) Origin and invasion of the emerging infectious pathogen *Sphaerothecum destruens*. Emerg Microbes Infect 6(8):e76. https://doi.org/10.1038/emi.2017.64

Santhosh A, Neuhauser S (2024) Host-parasite interaction between brown algae and eukaryote biotrophic pathogens. Curr Res Microb Sci 7:100306. https://doi.org/10.1016/j.crmicr.2024.100306

Schampera C, Wolinska J, Bachelier JB, de Souza Machado AA, Rosal R, González-Pleiter M, Agha R (2021) Exposure to nanoplastics affects the outcome of infectious disease in phytoplankton. Environ Pollut 277:116781. https://doi.org/10.1016/j.envpol.2021.116781

Schampera C, Agha R, Manzi F, Wolinska J (2022) Parasites do not adapt to elevated temperature, as evidenced from experimental evolution of a phytoplankton-fungus system. Biol Lett 18(2):20210560. https://doi.org/10.1098/rsbl.2021.0560

Scheele BC, Driscoll DA, Fischer J, Fletcher AW, Hanspach J, Vörös J, Hartel T (2015) Landscape context influences chytrid fungus distribution in an endangered European amphibian: chytrid fungus in ephemeral pond-breeding amphibians. Anim Conserv 18:480–488. https://doi.org/10.1111/acv.12199

Scheele BC, Pasmans F, Skerratt LF, Berger L, Martel A, Beukema W, Acevedo AA, Burrowes PA, Carvalho T, Catenazzi A, De la Riva I, Fisher MC, Flechas SV, Foster CN, Frías-Álvarez P, Garner TWJ, Gratwicke B, Guayasamin JM, Hirschfeld M, Kolby JE, Kosch TA, La Marca E, Lindenmayer DB, Lips KR, Longo AV, Maneyro R, McDonald CA, Mendelson J III, Palacios-Rodriguez P, Parra-Olea G, Richards-Zawacki CL, Rödel M-O, Rovito SM, Soto-Azat C, Toledo LF, Voyles J, Weldon C, Whitfield SM, Wilkinson M, Zamudio KR, Canessa S (2019) Amphibian fungal panzootic causes catastrophic and ongoing loss of biodiversity. Science 363:1459–1463. https://doi.org/10.1126/science.aav0379

Schmeller DS, Blooi M, Martel A, Garner TWJ, Fisher MC, Azemar F, Clare FC, Leclerc C, Jäger L, Guevara-Nieto M, Loyau A, Pasmans F (2014) Microscopic aquatic predators strongly affect infection dynamics of a globally emerged pathogen. Curr Biol 24(2):176–180. https://doi.org/10.1016/j.cub.2013.11.032

Schmeller DS, Loyau A, Bao K, Brack W, Chatzinotas A, De Vleeschouwer F, Friesen J, Gandois L, Hansson SV, Haver M, Le

Roux G, Shen J, Teisserenc R, Vredenburg VT (2018) People, pollution and pathogens – global change impacts in mountain freshwater ecosystems. Sci Total Environ 622–623:756–763. https://doi.org/10.1016/j.scitotenv.2017.12.006

Schmeller DS, Urbach D, Bates K, Catalan J, Cogălniceanu D, Fisher MC, Friesen J, Füreder L, Gaube V, Haver M, Jacobsen D, Le Roux G, Lin Y-P, Loyau A, Machate O, Mayer A, Palomo I, Plutzar C, Sentenac H, Sommaruga R, Tiberti R, Ripple WJ (2022) Scientists' warning of threats to mountains. Sci Total Environ 853:158611. https://doi.org/10.1016/j.scitotenv.2022.158611

Scholz B, Küpper FC, Vyverman W, Karsten U (2014) Eukaryotic pathogens (Chytridiomycota and Oomycota) infecting marine microphytobenthic diatoms – a methodological comparison. J Phycol 50:1009–1019. https://doi.org/10.1111/jpy.12230

Scholz B, Guillou L, Marano AV, Neuhauser S, Sullivan BK, Karsten U, Küpper FC, Gleason FH (2016) Zoosporic parasites infecting marine diatoms - a black box that needs to be opened. Fungal Ecol 19:59–76. https://doi.org/10.1016/j.funeco.2015.09.002

Scholz B, Vyverman W, Küpper FC, Ólafsson HG, Karsten U (2017) Effects of environmental parameters on chytrid infection prevalence of four marine diatoms: a laboratory case study. Bot Mar 60:419–431

Searle CL, Mendelson JR, Green LE, Duffy MA (2013) *Daphnia* predation on the amphibian chytrid fungus and its impacts on disease risk in tadpoles. Ecol Evol 3:4129–4138. https://doi.org/10.1002/ece3.777

Sen B (1988a) Fungal parasitism of planktonic algae in Shearwater. III. fungal parasites of centric diatoms. Arch Hydrobiol Suppl 79:167–175

Sen B (1988b) Fungal parasitism of planktonic algae in Shearwater. IV. parasitic occurrence of a new chytrid species on the blue-green alga *Microcystis aeruginosa* Kuetz emend. Elenkin. Arch Hydrobiol Suppl 79:177–184

Sentenac H, Loyau A, Leflaive J, Schmeller DS (2022) The significance of biofilms to human, animal, plant and ecosystem health. Funct Ecol 36(2):294–313. https://doi.org/10.1111/1365-2435.13947

Sentenac H, Schmeller DS, Caubet S, Carsin A, Guillet R, Ferriol J, Leflaive J, Loyau A (2024) Biofilms inactivate the free-living stage of *Batrachochytrium dendrobatidis*, the most destructive pathogen for vertebrate diversity. ISME J 18(1):wrae189. https://doi.org/10.1093/ismejo/wrae189

Seto K, Matsuzawa T, Kuno H, Kagami M (2020) Morphology, ultrastructure, and molecular phylogeny of *Aphelidium collabens* sp. nov. (Aphelida), a parasitoid of a green alga *Coccomyxa* sp. Protist 171:125728. https://doi.org/10.1016/j.protis.2020125728

Seto K, Simmons DR, Quandt CA, Frenken T, Dirks AC, Clemons RA, McKindles KM, McKay RML, James TY (2023) A combined microscopy and single-cell sequencing approach reveals the ecology, morphology, and phylogeny of uncultured lineages of zoosporic fungi. Mbio 14:e01313-23. https://doi.org/10.1128/mbio.01313-23

Sewell TR, Longcore J, Fisher MC (2021) Batrachochytrium dendrobatidis. Trends Parasitol 37:933–934. https://doi.org/10.1016/j.pt.2021.04.014

Seymour R, Cowgill UM, Klečka GM, Gersich FM, Mayes MA (1984) Occurrence of *Aphanomyces daphniae* infection in laboratory cultures of *Daphnia magna*. J Invertebr Pathol 43:109–113

Shabarova T, Salcher MM, Porcal P, Znachor P, Nedoma J, Grossart H-P, Seďa J, Hejzlar J, Šimek K (2021) Recovery of freshwater microbial communities after extreme rain events is mediated by cyclic succession. Nat Microbiol 6:479–488. https://doi.org/10.1038/s41564-020-00852-1

Shanor L, Saslow HB (1944) *Aphanomyces* as a fish parasite. Mycologia 36(4):413–415

Sharma S, Blagrave K, Magnuson JJ, O'Reilly CM, Oliver S, Batt RD, Magee MR, Straile D, Weyhenmeyer GA, Winslow L (2019) Widespread loss of lake ice around the Northern Hemisphere in a warming world. Nat Clim Chang 9:227–231. https://doi.org/10.1038/s41558-018-0393-5

Shaw CL, Hall SR, Overholt EP, Cáceres CE, Williamson CE, Duffy MA (2020) Shedding light on environmentally transmitted parasites: lighter conditions within lakes restrict epidemic size. Ecology 101(1):e03168. https://doi.org/10.1002/ecy.3168

Shin W, Boo SM, Longcore JE (2001) *Entophlyctis apiculata*, a chytrid parasite of *Chlamydomonas* sp. (Chlorophyceae). Can J Bot 79(9):1083–1089. https://doi.org/10.1139/b01-086

Sies H, Belousov VV, Chandel NS, Davies MJ, Jones DP, Mann GE, Murphy MP, Yamamoto M, Winterbourn C (2022) Defining roles of specific reactive oxygen species (ROS) in cell biology and physiology. Nat Rev Mol Cell Biol 23:499–515. https://doi.org/10.1038/s41580-022-00456-z

Sime-Ngando T (2012) Phytoplankton chytridiomycosis: fungal parasites of phytoplankton and their imprints on the food web dynamic. Front Microbiol 3:361. https://doi.org/10.3389/fmicb.2012.00361

Skuja H (1948) Taxonomie des Phytoplanktons einiger Seen in Uppland, Sweden. Symb Bot Upsal 9(3):1–399

Smale DA, Wernberg T, Oliver ECJ, Thomsen M, Harvey BP, Straub SC, Burrows MT, Alexander L, Benthuysen JA, Donat MG, Feng M, Hobday AJ, Holbrook NJ, Perkins-Kirkpatrick SE, Scannell HA, Gupta AS, Payne BL, Moore PJ (2019) Marine heatwaves threaten global biodiversity and the provision of ecosystem services. Nat Clim Chang 9:306–312. https://doi.org/10.1038/s41558-019-0412-1

Smetacek V (2001) A watery arms race. Nature 411:745

Smith VH, Joye SB, Howarth RW (2006) Eutrophication of freshwater and marine ecosystems. Limnol Oceanogr 51:351–355. https://doi.org/10.4319/lo.2006.51.1_part_2.0351

Sommer U (1987) Factors controlling the seasonal variation in phytoplankton species composition. A case study for a deep, nutrient rich lake. Prog Phycol Res 5:123–178

Sønstebø JH, Rohrlack T (2011) Possible implications of chytrid parasitism for population subdivision in freshwater cyanobacteria of the genus *Planktothrix*. Appl Environ Microbiol 77:1344–1351. https://doi.org/10.1128/AEM.02153-10

Soto I, Balzani P, Carneiro L, Cuthbert RN, Macêdo R, Tarkan AS, Ahmed DA, Bang A, Bacela-Spychalska K, Bailey SA, Baudry T, Ballesteros-Mejia L, Bortolus A, Briski E, Britton JR, Buřič M, Camacho-Cervantes M, Cano-Barbacil C, Copilaș-Ciocianu D, Coughlan NE, Courtois P, Csabai Z, Dalu T, De Santis V, Dickey JWE, Dimarco RD, Falk-Andersson J, Fernandez RD, Florencio M, Franco ACS, García-Berthou E, Giannetto D, Glavendekic MM, Grabowski M, Heringer G, Herrera I, Huang W, Kamelamela KL, Kirichenko NI, Kouba A, Kourantidou M, Kurtul I, Laufer G, Lipták B, Liu C, López-López E, Lozano V, Mammola S, Marchini A, Meshkova V, Milardi M, Musolin DL, Nuñez MA, Oficialdegui FJ, Patoka J, Pattison Z, Pincheira-Donoso D, Piria M, Probert AF, Rasmussen JJ, Renault D, Ribeiro F, Rilov G, Robinson TB, Sanchez AE, Schwindt E, South J, Stoett P, Verreycken H, Vilizzi L, Wang Y-J, Watari Y, Wehi PM, Weiperth A, Wiberg-Larsen P, Yapıcı S, Yoğurtçuoğlu B, Zenni RD, Galil BS, Dick JTA, Russell JC, Ricciardi A, Simberloff D, Bradshaw CJA, Haubrock PJ (2024) Taming the terminological tempest in invasion science. Biol Rev 99(4):1357–1390. https://doi.org/10.1111/brv.13071

Sparrow FK (1932) Observations on the aquatic fungi of Cold Spring Harbor. Mycologia 24:268–303

Sparrow FK (1960) Aquatic phycomycetes, 2nd edn. Michigan Press, Ann Arbor

Staats C, Kmetzch L, Schrank A, Vainstein M (2013) Fungal zinc metabolism and itsconnections to virulence. Front Cell Infect Microbiol 3:65. https://doi.org/10.3389/fcimb.2013.00065

Stamp N (2003) Out of the quagmire of plant defense hypotheses. Q Rev Biol 78(1):23–55

Stenseth NC, Mysterud A (2002) Climate, changing phenology, and other life history traits: nonlinearity and match- mismatch to the environment. Proc Natl Acad Sci U S A 99(21):13379–13381. https://doi.org/10.1073/pnas.212519399

Stirling AB (1880) Additional observations on fungus disease of salmon and other fish. Proc R Soc Edinb B Biol Sci 10:232–250. https://doi.org/10.1017/S0370164600043698

Stockwell MP, Clulow J, Mahony MJ (2012) Sodium chloride inhibits the growth and infective capacity of the amphibian chytrid fungus and increases host survival rates. PLoS ONE 7(5):e36942. https://doi.org/10.1371/journal.pone.0036942

Stockwell MP, Clulow J, Mahony MJ (2015a) Evidence of a salt refuge: chytrid infection loads are suppressed in hosts exposed to salt. Oecologia 177:901–910. https://doi.org/10.1007/s00442-014-3157-6

Stockwell MP, Storrie LJ, Pollard CJ, Clulow J, Mahony MJ (2015b) Effects of pond salinization on survival rate of amphibian hosts infected with the chytrid fungus. Conserv Biol 29:391–399

Stoyneva MP (1998) Spring-phytoplankton of the river Danube in the year 1990. River Syst 11(2):167–194 (**Arch Hydrobiol Suppl 115/2**)

Stoyneva MP (2003) Steady-state phytoplankton assemblages in shallow Bulgarian wetlands. Hydrobiologia 502:169–176. https://doi.org/10.1007/978-94-017-2666-5_15

Stoyneva MP (2016) Allochthonous planktonic algae recorded during the last 25 years in Bulgaria and their possible dispersal agents. Hydrobiologia 764:53–64. https://doi.org/10.1007/s10750-015-2334-x

Stoyneva MP, Descy J-P, Vyverman W (2007) Green algae in Lake Tanganyika: is morphological variation a response to seasonal changes? Hydrobiologia 578:7–16. https://doi.org/10.1007/s10750-006-0428-1

Stoyneva M, Uzunov B, Gärtner G (2013) First record of the parasitic aquatic oomycete *Ducellieria chodatii* from Pirin Mts (Bulgaria) with notes on its taxonomy, life cycle and ecology. Sydowia 65:1–12

Stoyneva-Gaertner MP, Uzunov BA (2024) Overview of studies on zoosporic parasites and their hosts in Bulgaria. Ann Sof Univ, Fac Biol Book 2- Bot 108:60–82. https://doi.org/10.60066/GSU.BIOFAC.Bot.108.60-82

Stoyneva-Gärtner MP, Uzunov BA (2015) An ethnobiological glance on globalization impact on the traditional use of algae and fungi as food in Bulgaria. J Nutr Food Sci 5:413. https://doi.org/10.4172/2155-9600.1000413

Stoyneva-Gärtner MP, Uzunov BA, Gärtner G, Androv MI, Ivanov KR (2023) Species composition of Cyanoprokaryota in the summer phytoplankton of 55 lakes and reservoirs, sampled in Bulgaria in the years 2018, 2019, 2021 and 2023. Ann Sof Univ, Fac Biol Book 2-Bot 107:57–113. https://doi.org/10.60066/GSU.BIOFAC.Bot.107.57-113

Su Y, Mennerich A, Urban B (2012) Synergistic cooperation between wastewater-born algae and activated sludge for wastewater treatment: influence of algae and sludge inoculation ratios. Bioresource Technol 105:67–73

Sun S-J, Calhoun SK, Duffy MA (2023) Host and parasite functional morphology jointly explain parasite specificity. Funct Ecol 37:1620–1627. https://doi.org/10.1111/1365-2435.14323

Svoboda J, Mrugała A, Kozubíková-Balcarová E, Petrusek A (2017) Hosts and transmission of the crayfish plague pathogen *Aphanomyces astaci*: a review. J Fish Dis 40:127–140. https://doi.org/10.1111/jfd.12472

Takano K, Ishikawa Y, Mikami H, Igarashi S, Hino S, Yoshioka T (2008) Fungal infection for cyanobacterium *Anabaena smithii* by two chytrids in eutrophic region of large reservoir Lake Shumarinai, Hokkaido, Japan. Limnology 9:213–218

Tao Y, Wolinska J, Hölker F, Agha R (2020) Light intensity and spectral distribution affect chytrid infection of cyanobacteria via modulation of host fitness. Parasitology 147:1206–1215. https://doi.org/10.1017/S0031182020000931

Taube R, Fabian J, Van den Wyngaert S, Agha R, Baschien C, Gerphagnon M, Premke K (2019) Potentials and limitations of quantification of fungi in freshwater environments based on PLFA profiles. Fungal Ecol 41:256–268. https://doi.org/10.1016/j.funeco.2019.05.002

Taylor J, Cunliffe M (2016) Multi-year assessment of coastal planktonic fungi reveals environmental drivers of diversity and abundance. ISME J 10:2118–2128. https://doi.org/10.1038/ismej.2016.24

Thompson JN (2002) Coevolution. In: Pagel M (ed) Encyclopedia of evolution. Oxford University Press, New York, pp 178–183

Thongthaisong P, Kasada M, Grossart H-P, Wollrab S (2022) Critical role of parasite-mediated energy pathway on community response to nutrient enrichment. Ecol Evol 12(12):e9622. https://doi.org/10.1002/ece3.9622

Thongthaisong P, Kasada M, Grossart H-P, Wollrab S (2025) Longer durability of host–parasite interaction increases host density. Oikos 6:e11029. https://doi.org/10.1111/oik.11029

Threlfall CG, Jolley DF, Evershed N, Goldingay RL, Buttemer WA (2008) Do green and golden bell frogs *Litoria aurea* occupy habitats with fungicidal properties? Aust Zool 34(3):350–360. https://doi.org/10.7882/AZ.2008.012

Thumsová B, Alarcos G, Ayres C, Rosa GM, Bosch J (2024) Relationship between two pathogens in an amphibian community that experienced mass mortalities. Conserv Biol 38:e14196. https://doi.org/10.1111/cobi.14196

Torres-Sánchez M, Longo AV (2022) Linking pathogen-microbiome-host interactions to explain amphibian population dynamics. Mol Ecol 31(22):5784–5794. https://doi.org/10.1111/mec.16701

Torres-Sánchez M, Villate J, McGrath-Blaser S, Longo AV (2022) Panzootic chytrid fungus exploits diverse amphibian host environments through plastic infection strategies. Mol Ecol 31(17):4558–4570. https://doi.org/10.1111/mec.16601

Torruella G, Grau-Bové X, Moreira D, Karpov SA, Burns JA, Sebé-Pedrós A, Völcker E, López-García P (2018) Global transcriptome analysis of the aphelid *Paraphelidium tribonemae* supports the phagotrophic origin of fungi. Commun Biol 1:231. https://doi.org/10.1038/s42003-018-0235-z

Turner AM, Chislock MF (2010) Blinded by the stink: nutrient enrichment impairs the perception of predation risk by freshwater snails. Ecol Appl 20:2089–2095. https://doi.org/10.1890/10-0208.1

Turner A, Wassens S, Heard G, Peters A (2021) Temperature as a driver of the pathogenicity and virulence of amphibian chytrid fungus *Batrachochytrium dendrobatidis*: a systematic review. J Wildl Dis 57(3):477–494. https://doi.org/10.7589/JWD-D-20-00105

Ujszegi J, Boros Z, Fodor A, Vajna B, Hettyey A (2023) Metabolites of *Xenorhabdus* bacteria are potent candidates for mitigating amphibian chytridiomycosis. AMB Express 13(1):88. https://doi.org/10.1186/s13568-023-01585-0

Valencia-Aguilar A, Toledo LF, Vital MVC, Mott T (2016) Seasonality, environmental factors, and host behavior linked to disease risk in stream-dwelling tadpoles. Herpetologia 72:98–106. https://doi.org/10.1655/HERPETOLOGICA-D-15-00013

Valkanov A (1931a) Über die Morphologie und Systematuik der Rotatorienbefallenden Oomyceten. Ann Sof Univ Phys-Math Fac 27(3):215–235

Valkanov A (1931b) Über die Morphologie und Systematuik der Rotatorienbefallenden Pilze. Arch Protistenkd 74:5–17

Vallet M (2024) Chemical ecology of plankton parasitism in algae. Bot Mar 67(3):11–229. https://doi.org/10.1515/bot-2023-0062

Vallet M, Kaftan F, Buaya A, Thines M, Guillou L, Svatoš A, Pohnert G (2023) Single-cell metabolome profiling for phenotyping parasitic diseases in phytoplankton. Front Anal Sci. https://doi.org/10.3389/frans.2022.1051955

Valois AE, Burns CW (2016) Parasites as prey: *Daphnia* reduce transmission success of an oomycete brood parasite in the calanoid copepod *Boeckella*. J Plankton Res 38:1281–1288. https://doi.org/10.1093/plankt/fbw055

Van den Wyngaert S, Vanholsbeeck O, Spaak P, Ibelings BW (2014) Parasite fitness traits under environmental variation: disentangling the roles of a chytrid's immediate host and external environment. Microb Ecol 68:645–656. https://doi.org/10.1007/s00248-014-0434-1

Van den Wyngaert S, Seto K, Rojas-Jimenez K, Kagami M, Grossart H-P (2017) A new parasitic chytrid, *Staurastromyces oculus* (Rhizophydiales, Staurastromycetaceae fam. Nov.), infecting the freshwater desmid *Staurastrum* sp. Protist 168:392–407. https://doi.org/10.1016/j.protis.2017.05.001

Van den Wyngaert S, Rojas-Jimenez K, Seto K, Kagami M, Grossart H-P (2018) Diversity and hidden host specificity of chytrids infecting colonial volvocacean algae. J Eukaryot Microbiol 65(6):870–881. https://doi.org/10.1111/jeu.12632

Van den Wyngaert S, Ganzert L, Seto K, Rojas-Jimenez K, Agha R, Berger SA, Woodhouse J, Padisák J, Wurzbacher C, Kagami M, Grossart H-P (2022) Seasonality of parasitic and saprotrophic zoosporic fungi: linking sequence data to ecological traits. ISME J 16(9):2242–2254. https://doi.org/10.1038/s41396-022-01267-y

Van den Wyngaert S, Kainz MJ, Ptacnik R (2023) Mucilage protects the planktonic desmid *Staurodesmus* sp. against parasite attack by a chytrid fungus. J Plankton Res 45:3–14. https://doi.org/10.1093/plankt/fbac071

Van den Wyngaert S, Cerbin S, Garzoli L, Grossart H-P, Gsell AS, Kraberg A, Lepère C, Neuhauser S, Stupar M, Tarallo A, Cunliffe M, Gachon C, Gavrilović A, Masigol H, Rasconi S, Selmeczy GB, Schmeller DS, Scholz B, Timoneda N, Trbojević I, Wilk-Woźniak E, Reñé A (2025) ParAquaSeq, a database of ecologically annotated rRNA sequences covering zoosporic parasites infecting aquatic primary producers in natural and industrial systems. Mol Ecol Resour 25:e14099. https://doi.org/10.1111/1755-0998.14099

Van Donk E (1989) The role of fungal parasites in phytoplankton succession. In: Sommer U (ed) Plankton Ecology. Springer-Verlag, Berlin, pp 171–194

Van Donk E, Ringelberg J (1983) The effect of fungal parasitism on the succession of diatoms in Lake Maarsseveen I (The Netherlands). Freshw Biol 13:241–251. https://doi.org/10.1111/j.1365-2427.1983.tb00674.x

Van Wichelen J, Muylaert K, van der Gucht K, Vyverman W (2006) Observations of little studiedprotists (chytrids and an amoeba) affecting phytoplankton populations in the upper reaches of the Schelde Estuary (Belgium). Belg J Bot 139:153–166

Van Wichelen J, van Gremberghe I, Vanormelingen P, Debeer A-E, Leporcq B, Menzel D, Codd GA, Descy J-P, Vyverman W (2010) Strong effects of amoebae grazing on the biomass and genetic structure of a *Microcystis* bloom (cyanobacteria). Environ Microbiol 12:2797–2813. https://doi.org/10.1111/j.1462-2920.2010.02249.x

Van Wichelen J, Vanormelingen P, Codd GA, Vyverman W (2016) The common bloom-forming cyanobacterium *Microcystis* is prone to a wide array of microbial antagonists. Harmful Algae 55:97–111. https://doi.org/10.1016/j.hal.2016.02.009

Verberk WCEP, Bilton DT, Calosi P, Spicer JI (2011) Oxygen supply in aquatic ectotherms: partial pressure and solubility together explain biodiversity and size patterns. Ecology 92(8):1565–1572. https://doi.org/10.1890/10-2369.1

Voigt K, Marano AV, Gleason FH (2013) 9 Ecological and economical importance of parasitic zoosporic true fungi. In: Kempken F (ed) Agricultural applications: the mycota, vol 11. Springer. Berlin, Heidelberg, pp 243–270

Voyles J, Young S, Berger L, Campbell C, Voyles WF, Dinudom A, Cook D, Webb R, Alford RA, Skerratt LF, Speare R (2009) Pathogenesis of chytridiomycosis, a cause of catastrophic amphibian declines. Science 326:582–585. https://doi.org/10.1016/j.micinf.2010.09.015

Voyles J, Rosenblum EB, Berger L (2011) Interactions between *Batrachochytrium dendrobatidis* and its amphibian hosts: a review of pathogenesis and immunity. Microbes Infect 13(1):25–32. https://doi.org/10.1016/j.micinf.2010.09.015

Wagner RS, McKindles KM, Bullerjan GS (2023) Effects of water movement and temperature on *Rhizophydium* infection of *Planktothrix* in a shallow hypereutrophic lake. Front Microbiol 14. https://doi.org/10.3389/fmicb.2023.1197394

Waine A, Robertson P, Pattison Z (2024) Understanding and classifying the raw water transfer invasion pathway. Biol Invasions 26:4035–4049. https://doi.org/10.1007/s10530-024-03432-0

Waine A, Robertson P, Pattison Z (2025) Integrated management of the raw water transfer invasion pathway. Manag Biol Invasions 16(1):227–246. https://doi.org/10.3391/mbi.2025.16.1.14

Walker GM, White NA (2017) Introduction to fungal physiology. In: Kavanagh K (ed) Fungi: biology and applications, 3rd edn. John Wiley & Sons, Hoboken, pp 1–35

Walther G-R, Roques A, Hulme PE, Sykes MT, Pyšek P, Kühn I, Zobel M, Bacher S, Botta-Dukát Z, Bugmann H, Czúcz B, Dauber J, Hickler T, Jarošík V, Kenis M, Klotz S, Minchin D, Moora M, Nentwig W, Ott J, Panov VE, Reineking B, Robinet C, Semenchenko V, Solarz W, Thuiller W, Vilà M, Vohland K, Settele J (2009) Alien species in a warmer world: risks and opportunities. Trends Ecol Evol 24(12):686–693. https://doi.org/10.1016/j.tree.2009.06.008

Wang Y, Verbrugghe E, Meuris L, Chiers K, Kelly M, Strubbe CN, Pasmans F, Martel A (2021) Epidermal galactose spurs chytrid virulence and predicts amphibian colonization. Nat Commun 12:578. https://doi.org/10.1038/s41467-021-26127-9

Wangsanut T, Pongpom M (2022) The role of the glutathione system in stress adaptation, morphogenesis and virulence of pathogenic fungi. Int J Mol Sci 23(18):10645. https://doi.org/10.3390/ijms231810645

Webb R, Rush C, Berger L, Skerrat t L, Roberts A (2024a) Glutathione is required for growth and cadmium tolerance in the amphibian chytrid fungus, *Batrachochytrium dendrobatidis*. Biochimie 220:22–30. https://doi.org/10.1016/j.biochi.2023.12.002

Webb RJ, Cuff C, Berger L (2024b) Glutathione-mediated metal tolerance in an amphibian chytrid fungus (*Batrachochytrium dendrobatidis*). Environ Toxicol Chem 43(7):1583–1591. https://doi.org/10.1002/etc.5885

Weisbrod B, Riehle E, Helmer M, Martin-Creuzburg D, Dietrich DR (2020) Can toxin warfare against fungal parasitism influence short-term *Dolichospermum* bloom dynamics? A field observation. Harmful Algae 99:101915. https://doi.org/10.1016/j.hal.2020.101915

Weitere M, Erken M, Majdi N, Arndt H, Norf H, Reinshagen M, Traunspurger W, Walterscheid A, Wey JK (2018) The food web perspective on aquatic biofilms. Ecol Monogr 88(4):543–559. https://doi.org/10.1002/ecm.1315

Wells K, Flynn R (2022) Managing host-parasite interactions in humans and wildlife in times of global change. Parasitol Res 121:3063–3071. https://doi.org/10.1007/s00436-022-07649-7

Wetzel RG (2001) Limnology. Lake and river ecosystems, 3rd Edition. Academic Press, San Diego

Whisler H, Zebold S, Shemanchuk J (1974) Alternate host for mosquito parasite *Coelomomyces*. Nature 251:715–716. https://doi.org/10.1038/251715a0

Whisler HC, Zebold SL, Shemanchuk JA (1975) Life history of *Coelomomyces psorophorae*. Proc Natl Acad Sci U S A 72:693–696. https://doi.org/10.1073/pnas.72.2.693

Whittaker RH, Feeny PP (1971) Allelochemics: chemical interactions between species: chemical agents are of major significance in the adaptation of species and organization of communities. Science 171(3973):757–770

Wierenga J, Thomas MK, Ranjan R (2022) Complex effects of chytrid parasites on the growth of the cyanobacterium *Planktothrix rubescens* across interacting temperature and light gradients. ISME Commun 2:93. https://doi.org/10.1038/s43705-022-00178-5

Wilk-Woźniak E, Najberek K (2013) Towards clarifying the presence of alien algae in inland waters – can we predict places of their occurrence? Biologia 68(5):838–844

Wilk-Woźniak E, Krztoń W, Budziak M, Walusiak E, Žutinič P, Udovič MG, Koreivienė J, Karosienė J, Kasperovičienė J, Kobos J, Toporowska M, Bańkowska-Sobczak A, Budzyńska A, Domek P, Dunalska J, Frąk M, Gołdyn R, Grabowska M, Jakubowska-Krepska N, Jasser I, Karpowicz M, Kokociński M, Kozak A, Mazur-Marzec H, Mądrecka-Witkowska B, Messyasz B, Napiórkowska-Krzebietke A, Niedźwiecki M, Pawlik-Skowrońska B, Pasztaleniec A, Pełechata A, Pełechaty M, Pęczuła W, Rosińska J, Szeląg-Wasielewska E, Mankiewicz-Boczek J, Wasilewicz M, Stević F, Maronić DŠ, Pfeiffer TŽ (2024) Harmful blooms across a longitudinal gradient in central Europe during heatwave: cyanobacteria biomass, cyanotoxins, and nutrients. Ecol Indic 160:111929. https://doi.org/10.1016/j.ecolind.2024.111929

Wilson D, Citiulo F, Hube B (2012) Zinc exploitation by pathogenic fungi. PLoS Pathog 8(12):e1003034. https://doi.org/10.1371/journal.ppat.1003034

Wolinska J, King KC (2009) Environment can alter selection in host–parasite interactions. Trends Parasitol 25:236–244. https://doi.org/10.1016/j.pt.2009.02.004

Wolinska J, King KC, Vigneux F, Lively CM (2008) Virulence, cultivating conditions, and phylogenetic analyses of oomycete parasites in *Daphnia*. Parasitology 135:1667–1678. https://doi.org/10.1017/S0031182008005052

Wolinska J, Giessler S, Koerner H (2009) Molecular identification and hidden diversity of novel *Daphnia* parasites from European lakes. Appl Environ Microbiol 75(22):7051–7059. https://doi.org/10.1128/AEM.01306-09

Woodhams DC, Bosch J, Briggs CJ, Cashins S, Davis LR, Lauer A, Muths E, Puschendorf R, Schmidt BR, Sheafor B, Voyles J (2011) Mitigating amphibian disease: strategies to maintain wild populations and control chytridiomycosis. Front Zool 8:8. https://doi.org/10.1186/1742-9994-8-8

Woodhams DC, Alford RA, Antwis RE, Archer H, Becker MH, Belden LK, Bell SC, Bletz M, Daskin JH, Davis LR, Flechas SV, Lauer A, Gonzalez A, Harris RN, Holden WM, Hughey MC, Ibáñez R, Knight R, Kueneman J, Rabemananjara F, Reinert LK, Rollins-Smith LA, Roman-Rodriguez F, Shaw SD, Walke JB, McKenzie V (2015) Antifungal isolates database of amphibian skin-associated bacteria and function against emerging fungal pathogens. Ecology 96:595–595. https://doi.org/10.1890/14-1837.1

Woodhams DC, McCartney J, Walke JB, Whetstone R (2023) The adaptive microbiome hypothesis and immune interactions in amphibian mucus. Dev Comp Immunol 145:104690. https://doi.org/10.1016/j.dci.2023.104690

Woolhouse MEJ, Webster JP, Domingo E, Charlesworth B, Levin BR (2002) Biological and biomedical implications of the co-evolution of pathogens and their hosts. Nat Genet 32:569–577. https://doi.org/10.1038/ng1202-569

Xiao X, Zhang Y, Wang F (2021) Hydrostatic pressure is the universal key driver of microbial evolution in the deep ocean and beyond. Environ Microbiol Rep 13:68–72. https://doi.org/10.1111/1758-2229.12915

Xu W, Luo Z-H, Guo S, Pang K-L (2016) Fungal community analysis in the deep-sea sediments of the Pacific Ocean assessed by comparison of ITS, 18S and 28S ribosomal DNA regions. Deep Sea Res I Oceanogr Res Pap 109:51–60. https://doi.org/10.1016/j.dsr.2016.01.001

Xu W, Gong L-F, Pang K-L, Luo Z-H (2018) Fungal diversity in deep-sea sediments of a hydrothermal vent system in the Southwest Indian Ridge. Deep Sea Res I Oceanogr Res Pap 131:16–26. https://doi.org/10.1016/j.dsr.2017.11.001

Xu X, Kasada M, Grossart H-P, Ibelings BW, Van den Wyngaert S (2025) A newly isolated chytrid fungus specialized in parasitizing heterocysts of the filamentous cyanobacterium *Dolichospermum* sp. Hydrobiologia. https://doi.org/10.1007/s10750-025-05911-4

Yan H, Ma H, Li Y, Zhao L, Lin J, Jia Q, Hu Q, Han D (2022) Oxidative stress facilitates infection of the unicellular alga *Haematococcus pluvialis* by the fungus *Paraphysoderma sedebokerense*. Biotechnol Biofuels Bioprod 15:56. https://doi.org/10.1186/s13068-022-02140-y

Yoldas T, Agyar Yoldas P, Cengiz Erismis U (2024) Investigation of the prevalence of co-infection by *Batrachochytrium dendrobatidis* and ranavirus in Turkey. In: Bacterial, viral, fungal and parasitic coinfections. IntechOpen. https://doi.org/10.5772/intechopen.115136.

Yoneya K, Miki T, Van den Wyngaert S, Grossart H, Kagami M (2021) Non-random patterns of chytrid infections on phytoplankton host cells: mathematical and chemical ecology approaches. Aquat Microb Ecol 87:1–15. https://doi.org/10.3354/ame01966

Zhang Y, Shi K, Zhou Q, Zhou Y, Zhang Y, Qin B, Deng J (2020) Decreasing underwater ultraviolet radiation exposure strongly driven by increasing ultraviolet attenuation in lakes in Eastern and Southwest China. Sci Total Environ 720:137694. https://doi.org/10.1016/j.scitotenv.2020.137694

Zhang J, Han X, Wang H (2024) Phytoplankton-chytrid-zooplankton dynamics via a reaction–diffusion–advection mycoloop model. J Math Biol 89(2):15. https://doi.org/10.1007/s00285-024-02113-9

Znachor P, Zapomělová E, Řeháková K, Nedoma J, Šimek K (2008) The effect of extreme rainfall on summer succession and vertical distribution of phytoplankton in a lacustrine part of a eutrophic reservoir. Aquat Sci 70:77–86. https://doi.org/10.1007/s00027-007-7033-x

## Authors and Affiliations

**Maya Stoyneva-Gärtner**[1] · **Hans-Peter Grossart**[2,25] · **Thijs Frenken**[3] · **Dirk S. Schmeller**[4] · **Laura Garzoli**[5] · **Serena Rasconi**[6] · **Elżbieta Wilk-Woźniak**[7] · **Albert Reñé**[8] · **Slawek Cerbin**[9] · **Cécile Lepère**[10] · **Caio César Pires de Paula**[11,26] · **Adeline Loyau**[4] · **Aleksandra Kudeń**[9] · **Ana Gavrilović**[12] · **Christian Lønborg**[13] · **Edward Walusiak**[7] · **Ifigenia Kagalou**[14] · **Ivana Trbojevic**[15] · **Jurica Jug-Dujaković**[16] · **Kristian Ivanov**[1] · **Lisa Morales**[17] · **Mahmut Sinan Erez**[18] · **Maija Balode**[19] · **Maja Berden Zrimec**[20] · **Martyna Budziak**[7] · **Miloš Stupar**[15] · **Miroslav Androv**[1] · **Petr Znachor**[21] · **Pietro Marchese**[5] · **Selene Chinaglia**[5] · **Slobodan Zlatković**[22] · **Télesphore Sime-Ngando**[23] · **Qëndrim Ramshaj**[24] · **Wojciech Krztoń**[7] · **Blagoy Uzunov**[1]

✉ Blagoy Uzunov
buzunov@uni-sofia.bg

[1] Department of Botany, Faculty of Biology, Sofia University "St. Kliment Ohridski", 8 Blvd. Dragan Tsankov, 1164 Sofia, Bulgaria

[2] Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Zur Alten Fischerhuette 2, 16775 Stechlin, Germany

[3] HAS green academy, Cluster Nature & Society, Onderwijsboulevard 221, 5223 DE 's-Hertogenbosch, The Netherlands

[4] Centre de Recherche sur la Biodiversité et l'Environnement (CRBE, UMR 5300), Université de Toulouse, CNRS, Toulouse INP, Université Toulouse, Toulouse, France

[5] Water Research Institute, National Research Council (CNR-IRSA), Largo Tonolli 50, 28922 Verbania, VB, Italy

[6] Université Savoie Mont Blanc, INRAE, CARRTEL, Thonon les Bains, France

[7] Institute of Nature Conservation, Polish Academy of Sciences, al. Adama Mickiewicza 33, 31-120, Kraków, Poland

[8] Department Marine Biology and Oceanography, Institut de Ciències del Mar (ICM-CSIC), Pg. Marítim de la Barceloneta, 37-49, 08003 Barcelona, Catalonia, Spain

[9] Department of General Zoology, Faculty of Biology, Adam Mickiewicz University, ul. Uniwersytetu Poznańskiego 6, 61-614 Poznań, Poland

[10] CNRS, Laboratoire Microorganismes: Génome et Environnement, Université Clermont Auvergne, ClermontFerrand, France

[11] Biology Centre CAS, Institute of Hydrobiology, Na Sádkách 7, 37005 České Budějovice, Czechia

[12] Faculty of Agriculture, University of Zagreb, Zagreb, Croatia

[13] Section for Marine Diversity and Experimental Ecology, Department of Ecoscience, Aarhus University, 4000 Roskilde, Denmark

[14] Laboratory of Sanitary Engineering- Quality of Water & Wastewater, Democritus University of Thrace, 67100 Xanthi, Greece

[15] Faculty of Biology, Institute of Botany and Botanical Garden "Jevremovac", University of Belgrade, Takovska 43, 11 000 Belgrade, Serbia

[16] M.J.D. Consulting, Stari Grad, Croatia

[17] Department F.-A. Forel for Environmental and Aquatic Sciences, University of Geneva, Geneva, Switzerland

[18] Department of Parasitology, Faculty of Veterinary Medicine, Afyon Kocatepe University, 03200 Afyonkarahisar, Türkiye

[19] Department of Experimental Hydrobiology, Latvian Institute of Aquatic Ecology, Daugavgrivas 6, Riga 1048, Latvia

[20] Algen, Algal Technology Centre, Llc, Ljubljana, Slovenia

[21] Department of Aquatic Microbial Ecology, Institute of Hydrobiology, Biology Centre CAS, Na Sádkách 7, 37005 České Budějovice, Czech Republic

[22] Agency for Ecological Consulting "Akvatorija", Belgrade, Serbia

[23] UMR CNRS 6023, Laboratoire Microorganismes: Génome et Environnement, Université Clermont Auvergne, Clermont-Ferrand, France

[24] Department of Biology, Faculty of Mathematics and Natural Sciences, University of Prishtina, St. "Mother Teresa", 10 000 Prishtina, Kosovo

[25] Institute of Biochemistry and Biology, Potsdam University, Maulbeerallee 2, 14469 Potsdam, Germany

[26] Faculty of Science, University of South Bohemia, Branišovská, České Budějovice 37005, Czechia