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Long-term trends and seasonal variation in host density, temperature, and nutrients differentially affect chytrid fungi parasitising lake phytoplankton

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Abstract

1. Parasites are generally considered the most commonly occurring type of consumers, yet their biomass and population dynamics are rarely quantified at community level.
2. Here, we used 12 years of weekly or fortnightly monitoring data (518 time points) to determine the occurrence of chytrids, fungal parasites of phytoplankton, to assess their seasonality and long-term (seasonally-detrended) dynamics in the pelagic plankton community of a temperate, eutrophic, and polymictic lake.
3. Chytrid infections were observed in c. 75% of all samples with recurrent infections in multiple host taxa. Infection prevalence was highest in spring, but infections occurred throughout the entire year with an average of 2.3 host taxa infected per time point (ranging from 0 to 10 host taxa) and an average infection prevalence of 2.78% (ranging from 0% to 47.35%). Infected host biomass equalled that of the carnivorous zooplankton and decreased over time, while infection prevalence remained unchanged. Seasonal infection prevalence increased with phytoplankton biomass, but decreased with increasing temperature and phosphorus concentrations, reflecting that peak prevalence occurred in spring when temperature and phosphorus concentrations were relatively low. In contrast, seasonally-detrended prevalence increased with temperature, but decreased with increasing phosphorus concentrations.
4. Chytrids are a common component of the pelagic plankton community with sizeable biomass and removing an—at times—substantial proportion of the primary production, challenging the long-standing underrepresentation of parasites in ecological studies.

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5. Chytrids responded differentially to seasonal variation and long-term trends in host density, water temperature and nutrient availability, highlighting the need to disentangle seasonal signals from long-term changes.

KEYWORDS

host–parasite interactions, parasitism, phosphorus, seasonality, temperature

1 | INTRODUCTION

Parasites are the most commonly occurring type of consumers (Lafferty et al., 2006; Dobson et al., 2008), and as such have also been coined *missing links* in aquatic and terrestrial food-webs (Lafferty et al., 2008; Sommer et al., 2012). Even though parasites can represent substantial biomass in natural ecosystems and affect a wide range of ecosystem processes (Hatcher et al., 2012; Kuris et al., 2008; Sures et al., 2017), their dynamics and biomass are rarely quantified at community level. Moreover, environmental variation can modulate the outcome of host–parasite interactions (Wolinska & King, 2009) but we still lack insight in the contribution of specific environmental variables on host–parasite dynamics in natural communities. Assessing baseline data on occurrence and biomass as well as the environmental factors associated with parasite infections will improve our understanding of the role of parasites in natural ecosystems.

Chytrids parasitising phytoplankton represent an interesting study system to assess the role of parasites in natural ecosystems due to their widespread occurrence and dominance in aquatic fungal communities (Beng et al., 2021; Comeau et al., 2016; Ortiz-Álvarez et al., 2018). Epidemics of host-specific chytrids can control size and timing of phytoplankton blooms and thereby influence their seasonal succession (Van Donk & Ringelberg, 1983). Moreover, chytrids can increase the intraspecific diversity of their host populations by preferentially infecting common host geno- or chemotypes (Agha, Gross, Rohrlack, et al., 2018; Gsell, de Senerpont Domis, Verhoeven, et al., 2013; Sønstebo & Rohrlack, 2011). By producing zoospores, nutritious and edible infectious lifestages (Gleason et al., 2009), chytrids can upgrade the biochemical composition of their hosts (Gerphagnon et al., 2019), serve as trophic links from large-sized, inedible phytoplankton to zooplankton consumers (i.e., the mycoloop [Kagami et al., 2014]), and thereby support zooplankton growth during inedible phytoplankton blooms (Agha et al., 2016; Frenken et al., 2018). As parasites of phytoplankton, chytrids influence carbon quality and cycling in aquatic ecosystems (Grami et al., 2011; Rasconi et al., 2020; Senga et al., 2018). However, most studies on the ecology of parasitic chytrids have only covered snapshots in time or focused on individual host–parasite model systems. The lack of baseline data on chytrid occurrence, and their seasonal and long-term dynamics in complex communities, hinders our understanding of the role of chytrids in aquatic ecosystems (Frenken, Alacid, et al., 2017; Sime-Ngando, 2012).

Environmental conditions are known to influence parasite fitness (Wolinska & King, 2009) and the seasonal and long-term patterns of parasite occurrence (Canter & Lund, 1948; Van Donk & Ringelberg, 1983). For parasites both the host environment (e.g., host density) and the abiotic environment are relevant. In laboratory experiments and field observations chytrid transmission has been shown to increase with host density once a minimum host density threshold was surpassed (Holfeld, 1998; Ibelings et al., 2011). Environmental conditions such as temperature and nutrient concentrations fluctuate with the seasons, while global change adds directional change across years (IPCC, 2013). Physiological rates increase with temperature (Brown et al., 2004), leading to the expectation that warmer temperatures also result in faster parasite generation times and infection spread (Marcogliese, 2008). In diatom and cyanobacterium host–chytrid systems, chytrid prevalence of infection showed an optimum curve relationship with temperature, with very cold and very warm conditions inhibiting parasite infections (Agha, Gross, Gerphagnon, et al., 2018; Gsell, de Senerpont Domis, Van Donk, et al., 2013; Rohrlack et al., 2015). Nutrient enrichment and subsequent changes in the elemental composition of hosts can result in higher infection prevalence due to higher production and nutritional quality of hosts (Frenken et al., 2021; McKenzie & Townsend, 2007). However, changes in host community composition due to eutrophication can also result in decreases in parasitism as well-defended or toxin-producing species may become dominant (Budria, 2017). Chytrids have shown relatively low carbon to nutrient ratios, indicating their relatively high nutrient requirements (Frenken, Wierenga, et al., 2017; Kagami et al., 2007; Sánchez Barranco et al., 2020). Nutrient enrichment experiments and model simulations have also shown that the net effect of eutrophication depends on the relative changes in host and chytrid growth rates. Eutrophication can lead to a higher infection prevalence, but also to the paradox of enrichment when overshooting infection cycles drive the host population size below the minimum host density necessary for maintenance of infection (Gerla et al., 2013). Conversely, nutrient limitation may also lead to enhanced, albeit short-lived chytrid success as the parasite can outgrow the host population (Bruning, 1991; Frenken, Wierenga, et al., 2017).

Here, we analysed 12 years of weekly (partly fortnightly) data on multiple chytrid parasites and their pelagic phytoplankton hosts in a shallow, temperate, eutrophic lake to infer occurrence, biomass (i.e., infected host biomass), seasonal and long-term (seasonally-detrended) prevalence of infection dynamics in phytoplankton under natural conditions. As phytoplankton host density, nutrient

concentrations, and water temperature show the typical seasonal variations of temperate eutrophic lakes, we additionally assessed the response of chytrid infection prevalence to potential long-term trends in phytoplankton host density, nutrient concentrations, and water temperature. We expected that: (1) chytrid infection prevalence would scale with phytoplankton biomass and therefore also follow the seasonal dynamics and long-term trends of phytoplankton; and (2) chytrid infection prevalence would increase with water temperature—up to an optimum—and nutrient concentrations following the seasonal dynamics as well as long-term trends in associated environmental factors.

2 | MATERIALS AND METHODS

2.1 | Study site

Müggelsee (N 52.438489, E 13.645173; northern Germany) is a eutrophic, shallow (mean depth of about 4.9 m, maximum depth 8 m), and polymictic lake with a surface area of 7.3 km² and a theoretical retention time of 6–12 weeks (Shatwell & Köhler, 2019). From 2005–2017, the lake was monitored at weekly (or fortnightly when ice-covered) time intervals. Physical variables (e.g., temperature) were measured in situ. Additionally, integrated volumetrically weighted water samples were taken at 1-m intervals from the surface to the bottom at five different stations across the lake, accounting for possible spatial heterogeneity. These samples were analysed for the pelagic phytoplankton and zooplankton community compositions as well as concentrations of soluble reactive phosphorus (SRP) and dissolved nitrate (NO₃), see (Driescher et al., 1993; Gerten & Adrian, 2000) for more details on sampling and sample processing. Since 1979, mean summer surface water temperature increased, while external nutrient loads decreased, leading to an overall decrease in phytoplankton biomass (Shatwell & Köhler, 2019). The rapid invasion of quagga mussels (*Dreissena rostriformis bugensis*) in 2012 was responsible for a further decrease in total phosphorous concentrations and phytoplankton biomass in the water column (Wegner et al., 2019).

2.2 | Plankton counting and identification

Plankton samples were taken from the epi- and hypolimnion separately, or from an integrated water column sample when the lake was mixed. Phytoplankton samples were fixed with Lugol's iodine solution and counted according to the Utermöhl method (Utermöhl, 1958). Phytoplankton taxa were identified at species or higher taxonomic levels, in some cases with additional separation into 5 µm-wide size classes (e.g., in centric diatoms, *Cryptomonas* spp, *Aulacoseira* spp, *Peridinium* spp, *Gymnodinium* spp), resulting in 158 taxa over the entire study period (Table S1 Phytoplankton). Taxon biovolume was determined from standard measurements of 50 cells or filaments (Mischke & Behrendt, 2007; Padisák & Adrian, 1999) to

calculate the dry-weight biomass of phytoplankton taxa assuming a specific weight of 1 g/cm³.

Zooplankton samples were concentrated from a 20-L sample to 100 mL using a 30-µm plankton net and fixed with formaldehyde (4% final concentration). Zooplankton were identified and counted at species or higher taxonomic levels, resulting in 104 different taxa (Table S2 Zooplankton). Zooplankton abundances were converted into dry-weight biomass (mg/L) based on taxa-specific size estimates and dry mass conversion factors reported elsewhere (Gsell et al., 2016; Hébert et al., 2016).

Additionally, the plankton samples were concentrated over a 5-µm plankton mesh, fixed with formaldehyde (4% final concentration) and stored as long-term reference samples. Epilimnion (when the lake was stratified) or integrated water column samples (when the lake was mixed) were used to count chytrid infections of phytoplankton combining the thick blood smear method with fluorescence microscopy (Kawamoto, 1991; WHO, 2019) by staining 50 µl of the sample with 50 µl of 0.1% Calcofluor White (C₄₀H₄₄N₁₂O₁₀S₂, Fluorescent Brightener 28; Merck KGaA) that binds selectively to chitin and cellulose and fluoresces bright blue under UV excitation (Hageage & Harrington, 1984; Klawonn et al., 2021; Rasconi et al., 2009). The complete subsample was pre-screened for infected phytoplankton taxa (i.e., cells with attached chytrid sporangium) using an inverted fluorescence microscope (Leica DMI 4000B, Leica Microsystems B.V.) equipped with a filter for UV excitation (filtercube A, excitation band-pass filter 340–380 nm). If pre-screening detected infections, 200 cells (in single celled taxa) or all cells in 25 colonies / filaments of infected phytoplankton taxa were counted for proportion of infected cells. In some instances, the counts target was not reached due to low biomass in the sample. As the morphology of sporangia is not indicative of the chytrid species and DNA extraction from formaldehyde fixed samples was not feasible, overall chytrid-infected host biomass per host taxon was used as a measure of parasite biomass, calculated by multiplying the proportion of infected host cells with the host biomass recorded for those sampling days. As hosts cease to reproduce once they are infected by chytrids and each infection is fatal, the infected host biomass was considered the extended phenotype of the chytrid parasite (Dawkins, 2016). In the following, we treat infected host biomass as equal to chytrid parasite biomass and use this measure to calculate the parasite population dynamics.

2.3 | Data analyses

2.3.1 | General analysis strategy

The data analysis was organised in four consecutive steps: (1) summary statistics of phytoplankton and their chytrid parasites to assess occurrence and prevalence of infection as well as chytrid biomass (i.e., biomass of infected host) relative to those of the other trophic levels (producers, primary and secondary consumers); (2) illustration of seasonal dynamics and testing of temporal trends of phytoplankton

biomass, chytrid biomass and infection prevalence using Theil–Sen regressions; (3) testing relationships and temporal precedence between chytrid prevalence and seasonal phytoplankton biomass, surface water temperature (termed temperature hereafter), dissolved SRP, and dissolved NO_3 using Theil–Sen regressions and calculation of cross-correlation coefficients; and (4) identifying global change effects on chytrid prevalence against seasonally-adjusted time series (anomaly time series) of temperature, SRP, and NO_3 . All statistical analyses and graphing were performed in R version 3.5.1 (R Core Team, 2018) and package ggplot2 (Wickham, 2016) and Microsoft Excel.

2.3.2 | Summary statistics

For the study period (1 August 2005 to 17 December 2017), the proportion of time points with observed chytrid infections was calculated for the total phytoplankton community and per host taxon. Moreover, the average infection intensity (i.e., number of host taxa infected) and the average infection prevalence (i.e., the proportion of the bulk phytoplankton biomass infected) was assessed. The relationship between occurrences of host taxa and infections was tested by a Pearson correlation. To visually inspect differences in biomass between four predetermined trophic levels (i.e., producers, parasites, primary consumers, and secondary consumers), the biomass of each taxon was summed per trophic level and plotted as violin plots.

Temporal trends and seasonal dynamics

To visualise temporal trends and seasonal dynamics of chytrid infections on phytoplankton, we imputed values of missing samples (122 out of 640, longest gap = 3 weeks) by Kalman filtering. Most of the missing values occurred during winter when sampling frequency was fortnightly. Temporal trends of phytoplankton biomass, chytrid infected biomass, and infection prevalence were tested using the non-parametric Theil–Sen regression for trend slopes on weekly time series (Theil, 1992) using the *mblm* package (R Core Team, 2018). Theil–Sen regression has been employed in climatology but also gains traction in ecological studies as it calculates the median slope out of all possible pairwise combinations of datapoints in the dataset. Thereby it removes (at least partially) temporal autocorrelation, provides robustness to outliers, and does not require a priori assumptions on measurement errors (Fernandes & Leblanc, 2005; Frei et al., 2020; Zhang et al., 2019). Time series of phytoplankton and chytrid biomass were plotted to illustrate temporal dynamics, with additional boxplot of fortnightly phytoplankton biomass and infection prevalence to depict seasonal dynamics.

Relationships and temporal patterns

Relationships of chytrid prevalence with phytoplankton biomass, temperature, SRP and NO_3 were tested using Theil–Sen regressions on weekly observation data. Moreover, temporal precedence was assessed by calculating cross-correlation coefficients for chytrid infection prevalence against phytoplankton biomass, temperature, SRP, and NO_3 using the *ccf* function (R Core Team, 2018).

Cross-correlation coefficients help identify lags of the predictor that best predict the response value at a given timestep. Given the generation times of phytoplankton and their chytrid parasites (Frenken et al., 2018), we assessed lags of ± 2 weeks. To avoid introducing potential bias in the cross-correlation coefficients due to the starting date, we repeated the calculations starting with each week of the first year, resulting in a set of 52 cross-correlation coefficients per predictor and lag tested.

Long-term effects of changing temperature and nutrients

To assess whether environmental change (i.e., warming and changes in nutrient availability) affect the success of chytrid infections, the response of chytrid prevalence to long-term changes in temperature, SRP, and NO_3 was tested using Theil–Sen regressions on weekly time series that were seasonally detrended by correcting for the long-term average of each week (Mazzi & Ladiray, 2018). For context, we also estimated long-term trends in the seasonally-detrended data of temperature, SRP, and NO_3 using Theil–Sen regressions.

3 | RESULTS

3.1 | Chytrid infections on phytoplankton

Over the study period (1 August 2005 to 17 December 2017: 640 weeks), 387 out of 518 time points (74.7%) contained at least one infected phytoplankton taxon. On average, 2.3 host taxa were infected per time point ($SD = 1.3$, ranging from 0 to 10 host taxa). The average prevalence of infection on bulk phytoplankton biomass was 2.78% ($SD = 5.39$, ranging from 0% to 47.35%). Overall, 52 infected phytoplankton taxa or taxon groups were observed, of which 17 taxa showed recurrent infections (i.e., at least four time points with infections observed). Recurrently infected host taxa belonged to diatoms ($n = 8$), cyanobacteria ($n = 5$) and green algae ($n = 4$; Figure 1). Host taxa that occurred more often were not necessarily more often infected (Pearson's $r [15] 1.9447, p = 0.07$). The predetermined trophic levels (phytoplankton, herbivorous zooplankton, carnivorous zooplankton, and chytrids) showed differences in their biomass distributions, although visual inspection suggested that chytrid biomass roughly equalled that of carnivorous zooplankton (Figure 2).

3.2 | Seasonal dynamics and long-term trends

Seasonal time courses of phytoplankton and chytrid biomass illustrated that many phytoplankton blooms were tracked by an increase in chytrid biomass; however, a few blooms showed little or even no infection (e.g., summer blooms 2007 and 2012 in Figure 3). Generally, phytoplankton biomass followed the typical bloom dynamics for shallow lakes with blooms in spring and summer, while infection prevalence showed just a slight peak in spring. Notably, chytrid infections occurred throughout the entire year, including the winter season (Figure 3). While phytoplankton and chytrid biomass

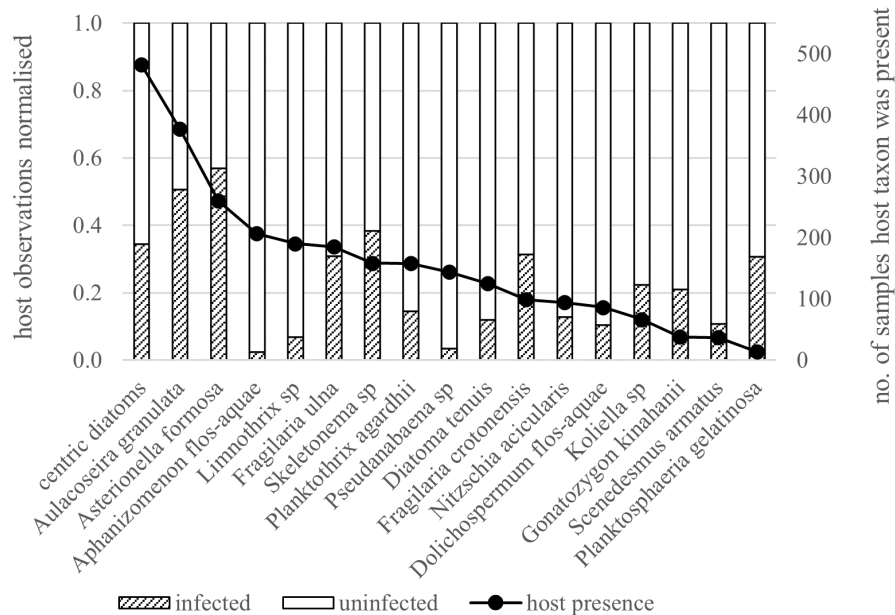


FIGURE 1 Rarely occurring host phytoplankton taxa are not necessarily less frequently infected by chytrids. Stacked bar plot of 17 recurrently infected phytoplankton taxa or taxa groups (e.g., single centric diatoms). Each host taxon bar is normalised to the number of samples in which it occurred. Hatched bars show the proportion of samples in which the host taxon was present and infected, white bars show the proportion of samples in which the host was present and not infected. Dots indicate the number of samples each host taxon occurs in the dataset (out of 518 weekly or fortnightly samples during the period 2005–2017)

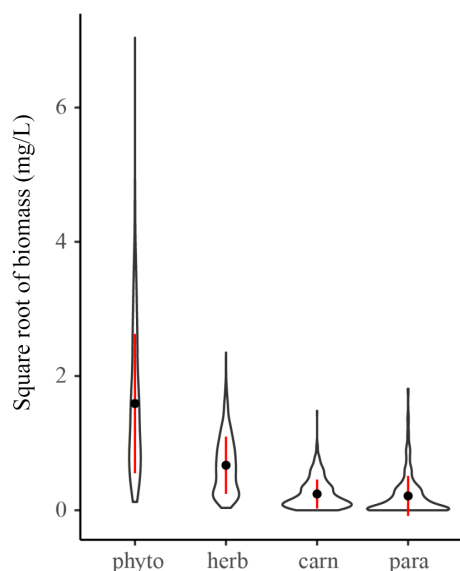


FIGURE 2 Average chytrid biomass is on par with that of the carnivorous zooplankton. Violin plot of biomasses (mg/L) for predetermined trophic levels phytoplankton (phyto), herbivorous zooplankton (herb), carnivorous zooplankton (carn), and chytrid parasites of phytoplankton (Para), with the dot and bars indicating mean and standard deviation. Data were square-root transformed for plotting

showed a slight but significant decline over time ($-0.28 \text{ mg L}^{-1} \text{ year}^{-1}$ and $-0.0015 \text{ mg L}^{-1} \text{ year}^{-1}$ respectively), infection prevalence showed no significant change (Table 1).

3.3 | Relationships and temporal patterns in seasonal data

Seasonal infection prevalence showed a positive relationship with host biomass and slight but significant negative relationships

with temperature and SRP, while NO_3 had no influence (Table 2). Assessment of cross-correlation coefficients indicated that host biomass showed the highest correlation with prevalence at lag -1 and lag 0 ($\rho = 0.13 \pm 0.008 \text{ SD}$), suggesting that increases in phytoplankton biomass lead increases in chytrid prevalence by up to 1 week (Table S3). Temperature and NO_3 showed the highest correlation with prevalence at lag -2 (temperature: $\rho = -0.1 \pm 0.005$; NO_3 : $\rho = 0.09 \pm 0.002$), suggesting that these predictors may lead prevalence by 2 weeks or more. SRP showed the strongest (although still weak) correlation with prevalence at lag 0 and lag $+1$ ($\rho = -0.18 \pm 0.003$), suggesting that changes in SRP do not directly lead to changes in infection prevalence (Table S3).

3.4 | Long-term effects of changing temperature and nutrients

Seasonally-detrended time series (i.e., anomaly time series) were assessed for effects of long-term environmental change in absence of seasonal variation. Anomaly infection prevalence increased with anomaly temperature but decreased with anomaly SRP and NO_3 (Table 3). Over the study period, anomaly SRP showed a slight but significant decrease while anomaly NO_3 significantly increased, and anomaly temperature showed no significant trend (Table 3).

4 | DISCUSSION

Our assessment of 12 years of chytrid–phytoplankton associations in a eutrophic lake revealed that multiple phytoplankton taxa carried chytrid infections at any given time of the year. Infection prevalence reached up to 47% indicating that chytrid parasites can, at times, remove a substantial part of the phytoplankton community as each infection is deadly for the host. Chytrid biomass was

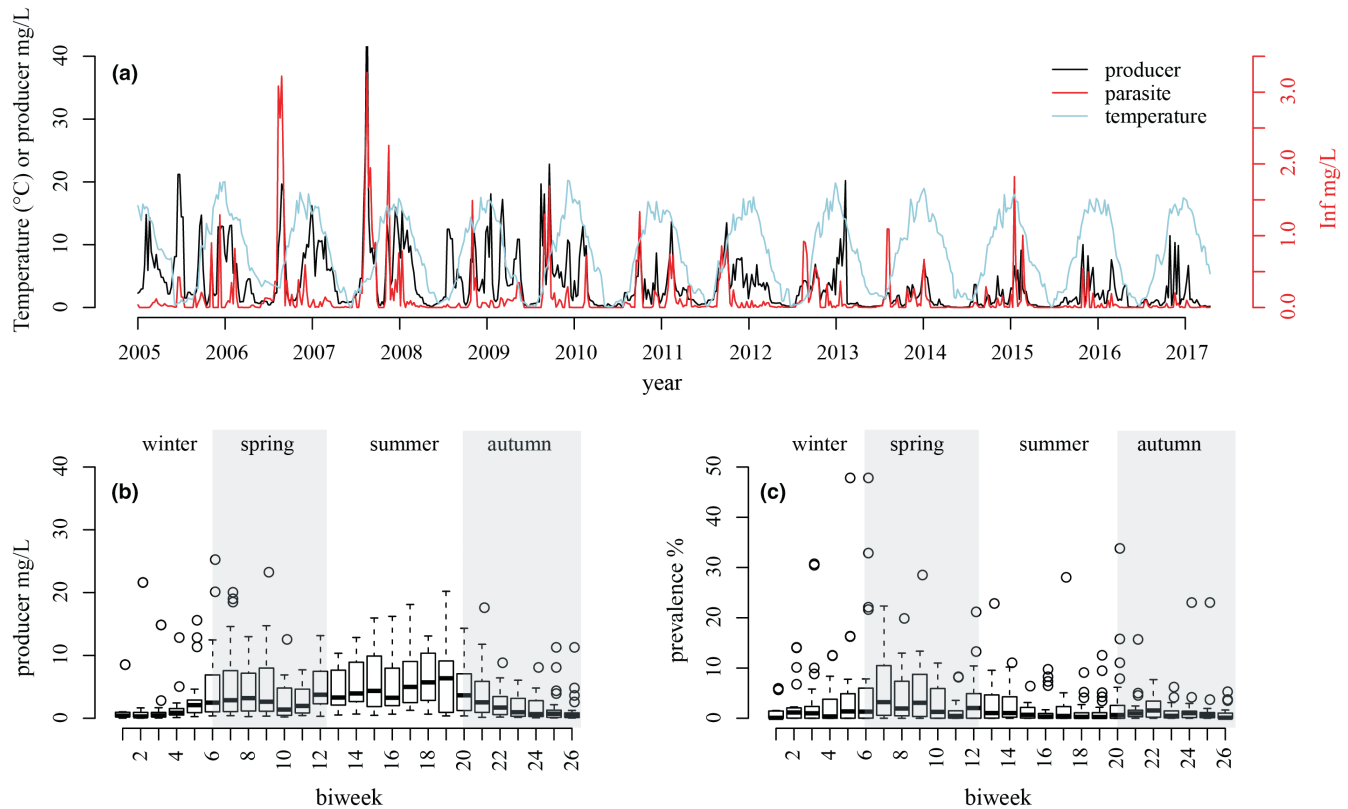


FIGURE 3 (a) Time series (top) of producer biomass (mg/L, black), chytrid biomass (mg/L, red), and water surface temperature ($^{\circ}\text{C}$, blue); note that producer biomass and temperature scale on a shared axis (left) and differ from the chytrid biomass axis (right). Boxplots (bottom) showing biweekly averages over the course of 26 biweeks (i.e., 1 year) of (b) producer biomass (mg/L), and (c) infection prevalence (% of phytoplankton biomass infected) over the study period. Note that these time series include Kalman imputed values for missing values

TABLE 1 Temporal trends of host biomass (mg/L), chytrid biomass (mg/L), and infection prevalence (%) calculated as Theil–Sen slope estimates on seasonal observation data

Predictor	Response	Slope estimate (per week)	Residual SD	df	Pr(> V)
Time	Host biomass	-0.0054	4.839	638	<0.001
Time	Chytrid biomass	-2.803×10^{-5}	0.386	638	<0.001
Time	Prevalence	8.97×10^{-5}	5.755	638	0.074

Note: Significant relationships ($p < 0.05$) are indicated in bold.

TABLE 2 Relationships of infection prevalence with host biomass (mg/L), temperature ($^{\circ}\text{C}$), SRP (mg/L), and NO_3 (mg/L) on seasonal observation data

Predictor	Response	Slope estimate (per week)	Residual SD	df	Pr(> V)
Phytoplankton biomass	Prevalence	0.1192	5.685	638	<0.001
Temperature	Prevalence	-0.0092	5.685	638	0.027
SRP	Prevalence	-0.0026	5.708	638	<0.001
NO_3	Prevalence	0	5.762	638	0.417

Note: Significant relationships ($p < 0.05$) are indicated in bold.

overall on par with that of the carnivorous zooplankton. Given the importance of carnivorous zooplankton in trophic interactions and nutrient and energy transfer in freshwater lakes (DeMott, 1989), other, overlooked trophic groups of equal biomasses, such as chytrid parasites, could be assumed to be of similar importance

for lake food webs. While infections occurred throughout the whole year with no apparent low-infection season, the greatest prevalence generally occurred in spring. Overall, phytoplankton and chytrid biomass decreased over time, while prevalence of infection showed no long-term trend, indicating that the rate of

Predictor	Response	Slope estimate (per week)	Residual SD	df	Pr(> V)
Temperature anomaly	Prevalence anomaly	0.03462	1.78	638	<0.001
SRP anomaly	Prevalence anomaly	-0.9422	54.93	638	<0.001
NO ₃ anomaly	Prevalence anomaly	-0.00627	0.27	638	<0.001
Time	Temperature anomaly	1.582×10 ⁻⁵	1.79	638	0.1807
Time	SRP anomaly	-0.04625	53.11	638	<0.001
Time	NO ₃ anomaly	6.262×10 ⁻⁵	0.27	638	<0.001

Note: Significant relationships ($p < 0.05$) are indicated in bold.

TABLE 3 Theil–Sen regressions of anomaly time series to assess relationships of infection prevalence (%) with temperature (°C), SRP (mg/L), and NO₃ (mg/L), as well as long-term trends of temperature, SRP, and NO₃ on seasonally-detrended data

infection did not change despite changes in phytoplankton biomass and other environmental factors. Analysis of the seasonal and anomaly data showed differential relationships between infection prevalence and potential drivers of infection (host biomass, water surface temperature, SRP, and NO₃), highlighting the importance of distinguishing between seasonal variation and long-term trends when assessing the effects of environmental variables associated with infection.

4.1 | Occurrence, seasonal dynamics, and long-term trends of chytrids

Almost 75% of all analysed samples showed chytrid infections on one or several phytoplankton taxa belonging to diatoms, cyanobacteria, and green algae. Several host taxa showed recurrent infections; however, the most commonly occurring phytoplankton taxa were not necessarily infected proportionally more often than less commonly occurring taxa. In contrast to observations in other lakes where cyanobacteria were highly infected by chytrids (Rasconi et al., 2012; Rohrlack et al., 2015), here, commonly occurring cyanobacteria (e.g., *Aphanizomenon flos-aquae*) only rarely carried infections, hinting to potential defence mechanisms against chytrid infections in cyanobacteria (Sønsteibø & Rohrlack, 2011). However, commonly occurring diatoms (e.g., *Aulacoseira granulata*) as well as more rarely occurring diatoms (e.g., *Fragilaria crotonensis*) were rather regularly infected by chytrids, suggesting either highly efficient host finding mechanisms or a generalist infection strategy in their associated chytrids (Gleason et al., 2008).

Chytrid infections of phytoplankton in Müggelsee occurred throughout the entire year. Many phytoplankton blooms in spring or summer were closely tracked by chytrid infections. However, a few blooms were hardly infected, as for example the 2007 summer bloom (dominated by centric diatoms, *A. granulata*, *A. flos-aquae*, and *Planktothrix aghardii*) and the 2012 summer bloom (dominated by *P. aghardii*, centric diatoms, and *A. granulata*), even though all these phytoplankton taxa can be infected by chytrids in Müggelsee. Similar interannual differences in susceptibility of phytoplankton

blooms to chytrid infections have been observed also in other meso- to eutrophic lakes and have been either attributed to absence of matching host or parasite genotypes (Holfeld, 1998; Kagami et al., 2021) or physico-chemical conditions that were not conducive for parasite spread (Canter & Lund, 1948; Gsell, De Senerpont Domis, Naus-Wiezer, et al., 2013; Van Donk & Ringelberg, 1983). Like in several other case studies of lakes with diatom spring blooms (Canter & Lund, 1948; Holfeld, 1998; Van Donk & Ringelberg, 1983), in Müggelsee, infection prevalence was highest in spring, indicating that spring periods provided chytrids with host communities and sufficient host biomass to promote infection spread despite the generally lower temperatures during these periods. We also observed chytrid infections during the winter period, often on typical spring bloom taxa such as centric diatoms. This contrasts with previous studies suggesting that colder winter periods provide phytoplankton with a cold-temperature refuge from disease as shown in model systems such as the diatom *Asterionella formosa* or the cyanobacterium *P. aghardii* (Ibelings et al., 2011; Rohrlack et al., 2015). However, our results tie in well with a DNA metabarcoding study exploring seasonal patterns in overall parasite diversity and occurrence performed on Lake Müggelsee samples (Beng et al., 2021). Beng et al. (2021) found that Chytridiomycota were the most abundant and diverse group of parasites in the lake with strong seasonal diversity patterns and near complete species turn over across seasons, while seasonal differences in relative abundance depended on the year. Their findings support our results that chytrid abundance is probably influenced by differences in intra- and interannual dynamics of their phytoplankton host populations as well as in abiotic conditions.

Both phytoplankton and chytrid biomass decreased over time while prevalence of infection remained unchanged in the seasonal data. The decrease in phytoplankton biomass was most likely to be associated with decreasing nutrient loading in Müggelsee (Shatwell & Köhler, 2019) and increased grazing pressure by invasive quagga mussels (*Dreissena rostriformis bugensis*) (Wegner et al., 2019). However, the net rate of infection was not affected by concurrent changes in phytoplankton densities and environmental factors. When relating prevalence to potential drivers,

infection prevalence increased with phytoplankton biomass, but contrary to our expectation, decreased with temperature and SRP. The positive response of infection prevalence to increases in phytoplankton biomass tie in well with results of studies focusing on interactions between specific phytoplankton-chytrid host-parasite systems documenting host biomass dependency (Bruning et al., 1992; Holfeld, 1998; Ibelings et al., 2011). Furthermore, increases in phytoplankton biomass lead increases in chytrid prevalence by up to 1 week, suggesting that chytrids can track phytoplankton hosts relatively fast. The negative relationship between temperature and infection prevalence in the seasonal data was unexpected as several chytrid species have shown a clear positive temperature dependence—up to an optimum - in field and experimental data (Agha, Gross, Gerphagnon, et al., 2018; Bruning et al., 1992; Gsell, de Senerpont Domis, Van Donk, et al., 2013; Ibelings et al., 2011; Rohrlack et al., 2015). The negative relationship between infection prevalence and SRP in the seasonal data contradicts laboratory studies that have shown higher per capita reproduction in chytrids on nutrient replete hosts with favourable elemental composition (Bruning, 1991; Frenken, Wierenga, et al., 2017). However, nutrient-depleted hosts show lower population growth rates and can therefore be outgrown by the parasite, leading to high chytrid prevalence under low phosphorus conditions (Bruning, 1991). Here, the negative relationships may also just reflect that chytrid prevalence is highest in spring when chytrids track phytoplankton spring blooms while temperature and SRP concentrations are relatively low. However, these relationships may be affected or even confounded by untested environmental variables, in particular grazing on zoospores by zooplankton (Frenken et al., 2020; Kagami et al., 2014), which warrants further exploration of the network position of chytrid infections in the planktonic food web.

The long-term relationship between temperature and infection prevalence in the anomaly data showed a positive correlation between prevalence and temperature and aligns well with the general expectation that disease incidence increases with higher temperatures (Lafferty & Mordecai, 2016). The negative relationship between anomaly prevalence and SRP is more difficult to explain as chytrids are nutrient demanding as expressed in their relatively low carbon to nutrient ratios compared to that of their host taxa (Frenken, Wierenga, et al., 2017; Kagami et al., 2007; Sánchez Barranco et al., 2020). However, changes in nutrient and mixing conditions in a lake typically also result in changes in the phytoplankton community composition (Reynolds, 1984), often promoting a dominance of cyanobacteria in phosphorus rich systems (Rigosi et al., 2014). Increased occurrence and duration of stratification events have led to a higher proportion of buoyant cyanobacteria capable of N-fixation (e.g., *Aphanizomenon*) in the Müggelsee phytoplankton community. As phytoplankton taxa vary in their susceptibility to chytrid infections and the Müggelsee cyanobacteria taxa seem to be less susceptible to infection in general, changes in community composition due to changes in nutrient conditions may well lead to lower parasite load in some nutrient rich waters (Budria, 2017).

4.2 | Chytrid biomass in plankton

Chytrid biomass represented on average 2.8% of the phytoplankton biomass. While these percentages may be an overestimation of infection when mistaking epibionts as chytrid infections, the calcofluor white staining allowed good differentiation of chitinous structures of chytrid sporangia from empty sheaths of, for example, epibiotic choanoflagellates (Rasconi et al., 2009). It is more likely that the reported chytrid biomasses are an underestimation as not all phytoplankton taxa remained preserved equally well with softer bodied Chlorophyceae, Chrysophyceae and Cryptophyceae crumbling to an extent that any potential chytrid infections were not discernible anymore. Nevertheless, chytrid biomass reached as much as 47.4% of the total phytoplankton biomass present in the lake. While field-based studies have shown that chytrid infections of dominant bloom-forming phytoplankton species can reach up to 90% prevalence (Canter & Lund, 1948; Holfeld, 1998; Ibelings et al., 2011), these findings have rarely been generalised to the biomass of the entire phytoplankton community (but see Rasconi et al., 2012). Considering that chytrid infections are deadly and preclude further reproduction of the host, the infected host biomass can be seen as the extended phenotype of the chytrid parasite. In this line of reasoning, chytrids can, at times, make up a substantial part of the plankton biomass by infecting an appreciable proportion of the phytoplankton community, in the present case approximately equal to the biomass represented by omni-carnivorous zooplankton. Given the high efficiency of chytrids in exploiting their phytoplankton hosts and their sizeable biomass, our findings lend credible support to the mycoloop (Kagami et al., 2014) in which chytrids transfer carbon and nutrients from inedible, primary producers to higher trophic levels (Grami et al., 2011; Rasconi et al., 2020; Sánchez Barranco et al., 2020). Moreover, our results highlight that parasites represent an underestimated amount of biomass in ecosystems (Kuris et al., 2008). Hence, their effects not only influence the fitness and population dynamics of hosts but also represent a potential sink or prey (Frenken et al., 2018; Gleason et al., 2008; Kagami et al., 2014; Sime-Ngando, 2012) with potential subsidiary ecosystem scale effects.

In our assessment of 12 years of phytoplankton-chytrid interactions in Müggelsee, we showed that chytrid infections exert considerable pressure on primary production throughout the whole year, including the winter period. At times, chytrids represented a substantial part of plankton biomass, substantiating our claim that parasites should be included in freshwater lake ecosystem and food-web studies both as a component and as a factor influencing nutrient fluxes and energy transfer. While chytrid biomass generally increased with phytoplankton biomass, commonly occurring phytoplankton taxa were not necessarily more often infected than rarely occurring ones, indicating either highly efficient host finding mechanisms or a generalist infection strategy of the chytrids involved. Chytrid biomass was highest in spring, hence, they did not show the positive relationship with temperature or nutrients expected from laboratory studies, highlighting that care needs to be taken when extrapolating expectations from laboratory studies to

more complex natural systems that often are characterised by high interannual variability in phytoplankton biomass and community composition (Dakos et al., 2009). Finally, our study also highlights the value of preserving sample collections for future analyses of the effects of organism groups that have been overlooked in the past (Bell et al., 2018).

AUTHOR CONTRIBUTIONS

Conceptualisation: A.S.G., J.W., S.H., R.A. Developing methods: A.S.G., J.W., S.T., D.Ö. Data analysis: A.S.G. Preparation of figures and tables: A.S.G., J.W., S.H., R.A. Conducting the research: A.S.G., K.P. Data interpretation, writing: A.S.G., J.W., K.P., S.T., D.Ö., S.H., E.v.D., B.W.I., R.A.

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DATA AVAILABILITY STATEMENT

The data analysed for this study is freely available through the IGB Freshwater Research and Environmental Database of the Leibniz Institute of Freshwater Ecology and Inland Fisheries (<https://fred.igb-berlin.de/>).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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