Phytoplankton community dynamics in a changing world

Ecological drivers of Microcystis and Naiadinium polonicum dominance

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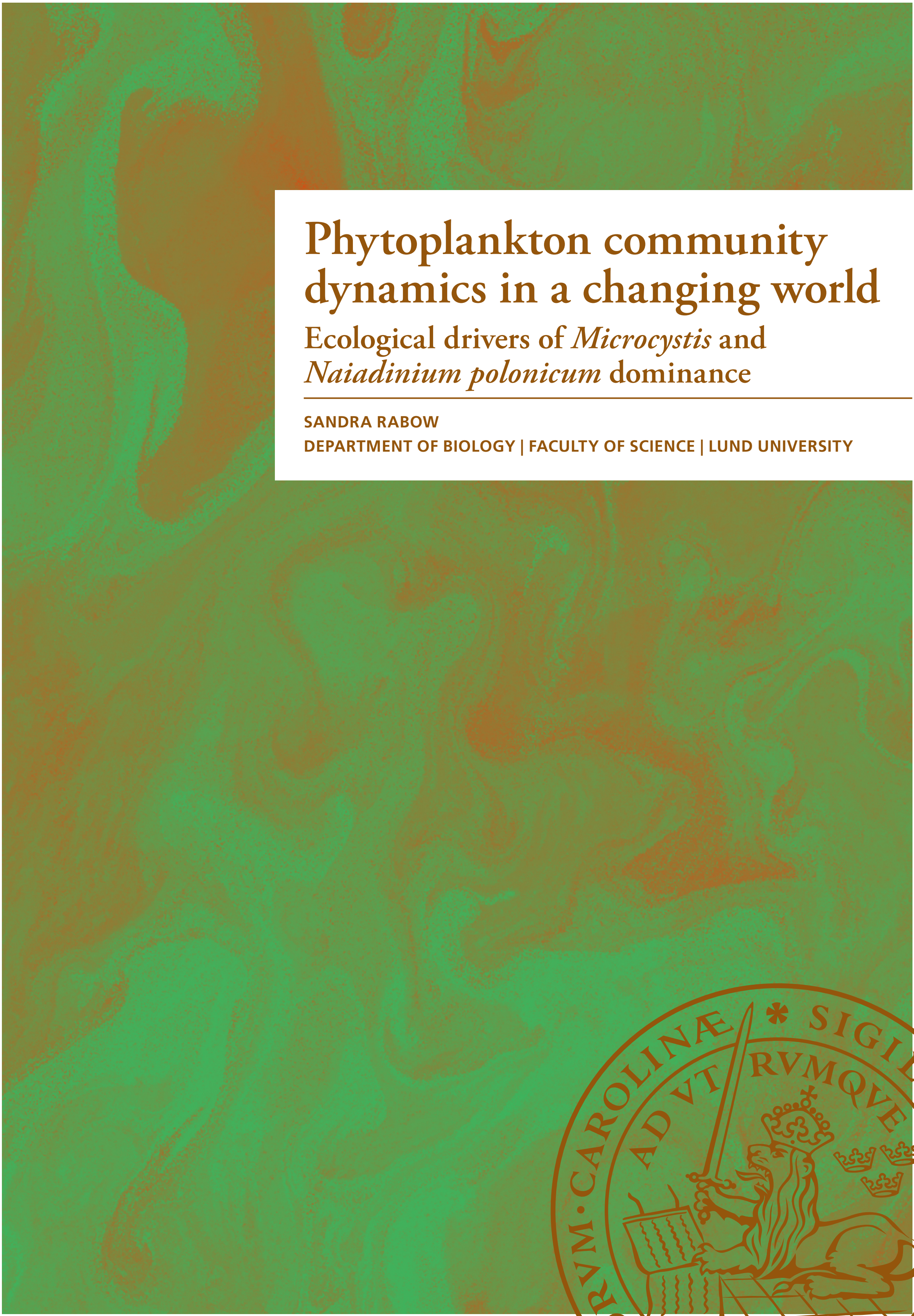

Phytoplankton community dynamics in a changing world

Ecological drivers of *Microcystis* and *Naiadinium polonicum* dominance

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Phytoplankton community dynamics in a changing world: Ecological drivers of *Microcystis* and *Naiadinium polonicum* dominance

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Sandra Rabow

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Key words: Harmful algal blooms, cyanobacteria, *Microcystis*, dinoflagellates, *Naiadinium polonicum*, functional traits, lakes, microcystins

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To phytoplankton enthusiasts,

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II. Rabow, S., Cai, S., Carlsson, P., & Rengefors, K. Earlier spring may explain dominance of the slow-growing dinoflagellate *Naiadinium polonicum* over the cyanobacterium *Microcystis* during a heatwave. *Manuscript.*

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Author contributions

I. KR and SR conceptualized the study. KR and EJ planned the sampling. SR and EJ performed field and laboratory work. SR analyzed the data and wrote the original manuscript. All co-authors read and edited the manuscript.

II. SR, SC, and KR conceptualized the study with help from PC. SR and SC performed laboratory work. SR analyzed the data and wrote the original manuscript. All co-authors read and edited the manuscript.

III. SR conceptualized the study. SR and JH designed the study with help from KR. JH performed laboratory work. SR analyzed the data and wrote the original manuscript. SR and KR read and edited the manuscript.

IV. EJ, KR and CL conceptualized the study. KR, EJ and TS planned the sampling. EJ performed field work. EJ and SR performed laboratory work. SR and EJ analyzed the data. EJ, SR and KR wrote the original manuscript. SR and KR read and edited the manuscript.

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Abstract

Lakes provide critical ecosystem services and are therefore particularly sensitive to disruptions such as harmful algal blooms (HABs). Cyanobacteria are the most common HAB-forming species in lakes, and their prevalence is expected to increase with climate change. However, during a 2018 heatwave in southern Sweden, Lake Vombsjön experienced an unexpected shift from its usual cyanobacterial dominance to a bloom of the dinoflagellate *Naiadinium polonicum*. This event provided a rare opportunity to examine how ecological drivers shape the population dynamics of cyanobacteria and dinoflagellates, two groups predicted to do well under future climate change scenarios due to shared functional traits, though freshwater dinoflagellates remain comparatively understudied. In particular, this thesis focuses on *Microcystis*, a toxin-producing cyanobacterium of global importance, and *N. polonicum*, a bloom-forming dinoflagellate whose autoecology is largely unresolved.

Across the first three papers, I examined field biomass dynamics, recruitment and growth responses to temperature, and allelopathic interactions between *Microcystis* and *N. polonicum*. In Lake Vombsjön, *N. polonicum* biomass was associated with higher temperatures, elevated soluble reactive phosphorus concentrations, water column stratification, and anoxic conditions near the sediment surface. While higher temperatures in 2018 did not directly enhance *N. polonicum* growth, temperature-dependent recruitment from sediments likely allowed it to establish earlier than *Microcystis*, whose recruitment was temperature independent. These findings point to seasonal timing as a key determinant of species dominance. Co-culture experiments revealed no evidence that *N. polonicum* inhibited *Microcystis*, whereas *Microcystis* was able to suppress *N. polonicum* growth at ecologically relevant densities.

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that they may become more prominent under future climate conditions, potentially impacting cyanobacteria bloom dynamics. Second, benthic life stages, particularly recruitment from sediments, must be incorporated into future research on cyanobacterial HABs. As climate change drives phenological shifts and alters pelagic conditions, understanding benthic-pelagic links will be essential for predicting and managing HAB events.

Popular Summary

Freshwater lakes provide drinking water, support ecosystems, and are central to recreation and tourism. However, these benefits are increasingly threatened by harmful algal blooms. Some of the algae that dominate these blooms even produce toxins that can make water unsafe for people, pets, and livestock. Climate change is expected to worsen this problem as warmer temperatures, stronger water column stratification, and changes in rainfall and nutrient inputs create conditions that favor bloom-forming algae.

Most research on harmful algal blooms in lakes has focused on cyanobacteria, a group of microorganisms that commonly form dense and sometimes toxic blooms. However, during a heatwave in 2018, something unexpected occurred in Lake Vombsjön, a drinking water lake in southern Sweden. Instead of a cyanobacterial bloom, the lake was dominated throughout the summer by a dinoflagellate species that had not previously been observed to form blooms there. This unusual event raised important questions about how different types of algae respond to extreme weather and climate change, and whether organisms other than cyanobacteria may become more common in the future.

In this thesis, I investigated why this shift occurred and what it can tell us about the conditions that favor different bloom-forming species. I focused on two types of algae: *Microcystis*, a cyanobacterium that frequently forms toxic blooms worldwide and poses major challenges for drinking water management, and *Naiadinium polonicum*, the dinoflagellate that dominated Lake Vombsjön in 2018. Although these organisms share traits that allow them to thrive in warm, stratified lakes, relatively little is known about how freshwater dinoflagellates respond to environmental change.

My results show that the success of *Naiadinium polonicum* in 2018 was likely due to timing. Algae often spend the winter months in lake sediments and must re-enter the water column in spring, a process referred to as recruitment. I found that *Naiadinium polonicum* recruitment depended on temperature, whereas *Microcystis* recruitment did not. Warmer conditions therefore likely allowed *Naiadinium polonicum* to emerge from sediments earlier in the season, giving it a head start before *Microcystis* could establish. These findings highlight that when environmental changes occur can be just as important as how large those changes are.

I also examined what determines the presence of toxic *Microcystis*, as opposed to non-toxic *Microcystis* in Lake Vombsjön, as well as another drinking water supply, Lake Ringsjön. Toxic *Microcystis* were more common when nitrogen levels were high, while the amount of toxins in the water was most strongly linked to phosphorus availability and overall cyanobacterial biomass. This supports the need to reduce both nitrogen and phosphorus inputs to lakes in order to effectively manage toxic blooms.

Overall, this thesis shows that harmful algal blooms in lakes are shaped by a combination of climate conditions, nutrient availability, and biological timing. It highlights the need to broaden research beyond cyanobacteria to include freshwater dinoflagellates, and to better incorporate recruitment processes into our understanding of bloom formation. As climate change increases the frequency of heatwaves and alters conditions in lakes, this knowledge will be essential for predicting and managing future bloom events and protecting freshwater sources.

Introduction

Lakes make up a relatively small proportion of Earth's continental land surface (~3%) (Downing et al., 2006), yet they provide some of our most important ecosystem services such as drinking water, irrigation, fishing, recreation, and tourism. One of the biggest threats to lakes is harmful algal blooms (HABs) (Brooks et al., 2016), defined here as any phytoplankton bloom that has a negative impact on human health and/or one or more ecosystem services. The most prolific HABs in lakes are those dominated by cyanobacteria: oxygen-producing bacteria that originated around 3 billion years ago and are responsible for triggering the oxygenation of Earth's atmosphere (Schirrmeister et al., 2015). Today, cyanobacteria are best known for their dense blooms, which can cause major problems for water quality. Issues associated with cyanobacterial HABs include low edibility and nutritional values for zooplankton (Porter, 1977), increased turbidity (Scheffer et al., 1993), high biomass and subsequent oxygen depletion (Rabalais et al., 2010), as well as the production of secondary metabolites, some of which are toxic for aquatic organisms, pets, livestock, and humans (Merel et al., 2013).

A growing concern is that climate change and extreme weather events will exacerbate what is already considered to be an increasing occurrence of cyanobacterial HABs (Carey et al., 2012; Gobler et al., 2024; Huisman et al., 2018; O'Neil et al., 2012; Paerl & Huisman, 2008). Climate change projections indicate that in temperate regions lakes will experience increased temperatures (Peeters et al., 2002), more intense and longer thermal stratification (DeStasio et al., 1996), and increased precipitation (IPCC, 2023; Meehl et al., 2005), which can lead to increased nutrient loading. Cyanobacteria are well known to thrive in nutrient-rich lakes (Paerl et al., 2016; Schindler, 1974), and warmer temperatures have been associated with a higher proportion of cyanobacterial biomass (Kosten et al., 2012). This has largely been attributed to the fact that temperature optima for cyanobacteria tend to be higher than those of eukaryotic algae (Reynolds, 2006). Rising temperatures also enable cyanobacterial species to expand their geographic range. For instance, the spread of *Raphidiopsis raciborskii* (basionym *Cylindrospermopsis raciborskii*) from tropical to temperate regions has been linked to an earlier spring (Wiedner et al., 2007). Indirect temperature effects, such as changes in thermal stratification and vertical mixing, are also expected to favor cyanobacteria, which can regulate their buoyancy and migrate vertically through the water column, accessing light near the surface and nutrients from deeper layers (Visser et al., 1997).

In Sweden, the summer of 2018 was marked by a heatwave resulting in a hydrological drought (Teutschbein et al., 2022). During this period, a sampling program was initiated in Lake Vombsjön to investigate *Microcystis* strain variation and toxin production. Lake Vombsjön is a eutrophic lake that supplies drinking water to approximately 400,000 inhabitants in southern Scania and is known to frequently experience cyanobacterial blooms (Alström et al., 2017; Johansson et al., 2019). However, contrary to expectations, no *Microcystis* or other cyanobacteria bloom occurred in 2018. Instead, the phytoplankton community was dominated throughout the summer by a dinoflagellate, *Naiadinium polonicum* (synonyms: *Peridiniopsis polonicum*, *Peridinium polonicum,* and *Glenodium gymnodinium*; Craveiro et al. 2015). No blooms of *N. polonicum* had previously been reported in Lake Vombsjön. Early seasonal succession and functional trait models have pointed out that cyanobacteria and dinoflagellates share important functional traits, such as large size and vertical motility, allowing them to do well under similar conditions (Reynolds et al., 2002; Sommer et al., 1986). Despite this, relatively few studies have examined how climate-driven changes may influence the population dynamics of freshwater dinoflagellates and, in turn, affect the development of cyanobacterial blooms in lakes.

The overarching aim of this thesis was to better understand which conditions favor cyanobacteria versus dinoflagellates by examining the factors that may have caused the shift in the phytoplankton community from being cyanobacteria to dinoflagellate dominated in Lake Vombsjön in 2018. Before defining the specific research questions, I provide a brief overview of phytoplankton community assembly, seasonal succession, and functional traits. I also describe the study system and focal organisms, *Microcystis* and *Naiadinium polonicum*, and discuss how the functional traits of these species may influence their responses to changes in the pelagic environment driven by climate change. Finally, I present examples from freshwater systems across multiple continents where alternating dominance between *Microcystis* and dinoflagellates has been observed, thereby placing my research into a broader context and highlighting the need to further investigate the ecological drivers determining *Microcystis* and *N. polonicum* success.

The theoretical framework

Phytoplankton community assembly

To identify the drivers behind cyanobacteria and dinoflagellate bloom formation, it is important to understand how communities are assembled. Community assembly is a combination of stochastic (random) and deterministic (selective) processes, by which species colonize, interact with other species, and establish a community (Young et al., 2001). Two ruling factors for community assembly include the 'species pool', which is the group of species that have the potential to colonize a habitat, and the 'filter', which are the abiotic and biotic factors that select for establishment (Figure 1) (Cornell & Harrison, 2014). These factors can be further subdivided into the physical environment (e.g., turbulence/vertical mixing and temperature), resources (e.g., light, carbon dioxide, nutrients), and natural enemies (e.g., predation, parasites, allelopathy) (Litchman & Klausmeier, 2008; Shea & Chesson, 2002). Competition can occur either through exploitative or interference mechanisms. Exploitative competition is a form of indirect competition that occurs when individuals deplete shared resources (Tilman et al., 1982), whereas interference competition is a direct form of competition via behaviors that prevents others from accessing resources (e.g., allelopathy, physical obstruction) (Case & Gilpin, 1974).

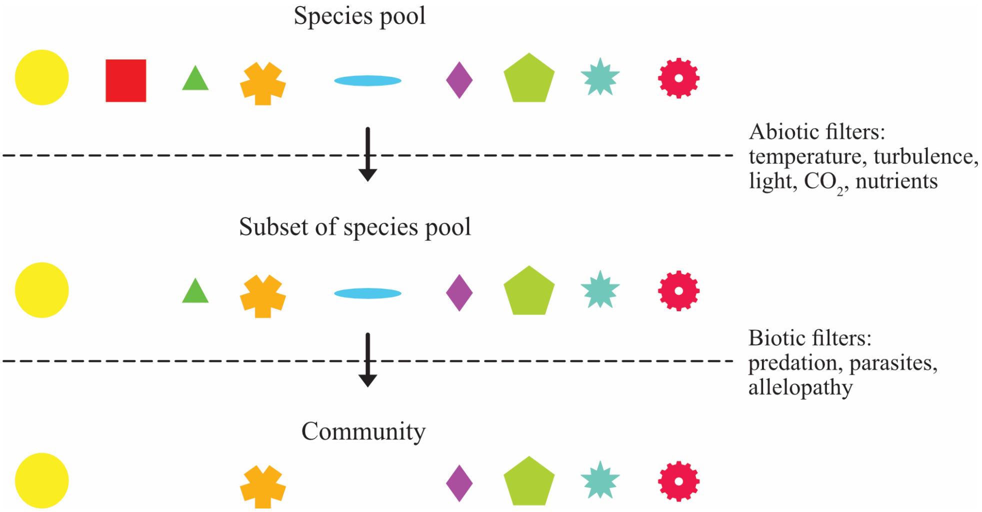

Figure 1. Schematic of species assembly processes. The group of species that have the potential to colonize a habitat (species pool) are sorted through abiotic and biotic filters before a community can be established.

Phytoplankton seasonal succession and functional traits

Given that the abiotic and biotic factors vary not only in space but also over time, phytoplankton communities change frequently throughout the year. As populations of species die, encyst, or settle to the sediments as resting stages, they are replaced by other species recruited from the species pool. Consequently, a predictable pattern of phytoplankton succession emerges, which can largely be determined by functional traits and the ecological niches that species occupy (Litchman & Klausmeier, 2008; Reynolds et al., 2002; Sommer et al., 2012; Sommer et al., 1986).

Functional traits are traits that strongly influence organismal performance (McGill et al., 2006; Violle et al., 2007). The most important traits for predicting phytoplankton seasonal succession and community composition are considered to be those that govern phytoplankton response to the abiotic and biotic factors driving community assembly (Litchman, 2023; Litchman & Klausmeier, 2008). Traits considered most relevant in this thesis are listed in Table 1 and grouped into four categories: morphological (cell or colony size), physiological (temperature response, nutrient and light utilization, nitrogen fixation, mixotrophy, and allelopathy), behavioral (motility) and life-history (sexual or asexual reproduction and resting stages).

Margalef (1978) pioneered the use of functional traits to predict the response of phytoplankton with r (small, high surface-to-volume ratios) versus K (large, motile, resistant to grazing) life history strategies to changes in nutrients and turbulence in marine environments. Reynolds (1988) extended this model using the same environmental gradients (nutrients and turbulence/mixing) but incorporated Grime’s (1979) adaptive strategies for coping with stress and disturbance. This resulted in the definition of three strategies for phytoplankton: competitive, stress-tolerant, or ruderal (CSR strategies) (Reynolds, 1988, 2006). Since then, subsequent studies have advanced the idea of using shared adaptive traits, rather than, for example, phylogenetic relatedness, to explain the distribution of species along environmental gradients (see e.g., Reynolds et al., (2002); Smayda & Reynolds, (2001)).

Although conceptually similar, modern trait-based frameworks have adopted a more quantitative approach (Litchman, 2023). For example, Edwards et al. (2013) showed that light utilization traits and maximum growth rates could predict how freshwater species abundances varied along light and nutrient gradients across lakes in the United States. Similarly, Ehrlich et al. (2020) showed that defense/edibility and maximum growth rates could largely explain phytoplankton seasonal succession in Lake Constance. Consequently, understanding and quantifying the functional traits of HAB-forming species, as well as their competitors, is crucial for improving our ability to predict and manage HABs in the future (Litchman, 2023).

Table 1. Key funtional traits for predicting phytoplankton seasonal succession and community composition with examples of how they can be quantified. Functional trait classification and definitions are adapted from Litchman and Klausmeier (2008) and Litchman (2023). The traits included in this table are not exhaustive, but are those considered to be most relevant in this thesis.

Trait type	Functional trait	Examples of how traits can be measured/quantified
Morphological	Cell size, shape	Diameter, length, width, surface area:volume ratio
	Coloniality	Colony size, filament length
Physiological	Temperature-dependent growth	T_{opt} (optimum temperature for growth), T_{min} and T_{max} (min and max temperture for growth), thermal niche width
	Nutrient-dependent growth (N, P, Si, Fe, etc)	μ_{max} (maximum growth rate), K_s (half-saturation constant for growth)
	Light-dependent growth	α (light affinity), I_{opt} (optimum irradiance), I_{out}^* (light intensity at bottom of a water column when culture is in steady state, see Huisman et al. (1999))
	Nitrogen-fixation	Presence/absence, maximum rate, density of heterocysts, dependence on environmental factors
	Mixotrophy	Presence/absence, max ingestion rate, prey size range
	Allelopathy	Presence/absence, dependence on environmental factors
Behavioral	Motililty	Presence/absence of flagella, gas vesicles, swimming speed, dependence on environmental factors
Life history	Sexual/asexual reproduction	Presence/absence, dependence on environmental factors
	Dormancy/resting stages	Presence/absence of cysts, akinetes, dependence on environmental factors

The study system

Disturbances such as heatwaves are known to drive changes in phytoplankton community assembly (Young et al., 2001). Given that cyanobacteria are widely expected to benefit from warmer conditions, the dominance of *Naiadinium polonicum* in Lake Vombsjön during the hot and dry summer of 2018 was highly unexpected. At the same time, despite their evolutionary divergence, early functional trait models grouped cyanobacteria, such as *Microcystis,* and dinoflagellates, such as *Ceratium hirundinella* and *Peridinium gatunense,* in the same functional group (Reynolds, 2006; Reynolds et al., 2002). This was due to shared traits including a preference for eutrophic lakes, large size conferring resistance to grazing, and the capacity for vertical migration, allowing access to both surface light and deeper nutrient pools (Reynolds, 2006; Reynolds et al., 2002). Despite these similarities, relatively few studies have investigated how freshwater dinoflagellates respond to climate change or which ecological factors favor dinoflagellates versus cyanobacteria.

In this thesis, I chose to examine how abiotic and biotic factors influence the success of the cyanobacterium *Microcystis* and the dinoflagellate *Naiadinium polonicum* in relation to their functional traits. *N. polonicum* was selected due to its unexpected bloom in 2018, whereas *Microcystis* was chosen as it is a common bloom-forming species in Lake Vombsjön (Alström et al., 2017; Johansson et al., 2019). Moreover, *Microcystis* is one of the most globally widespread and problematic bloom-forming cyanobacteria, posing significant risks to drinking water supplies in major freshwater systems such as Lake Taihu and Lake Erie (Qin et al., 2010; Watson et al., 2016). Understanding the conditions that promote *Microcystis* dominance is therefore of broad ecological and societal importance. Below, I provide a brief overview of Lake Vombsjön, *Microcystis*, and *Naiadinium polonicum*, and then discuss the functional traits relevant to their ecological success.

Lake Vombsjön

In southern Sweden, Lake Vombsjön (Figure 2) supplies drinking water to over 400,000 inhabitants in Burlöv, Malmö, Staffanstorp, Svedala, Vellinge, and parts of Lund and Eslöv (Alström et al., 2017). The lake is relatively small, with a surface area of 11.8 km^2 and a mean and maximum depth of 6.6 m and 16 m, respectively. Its catchment area covers approximately 450 km^2 and is predominantly agricultural. Lake Vombsjön is eutrophic and often experiences cyanobacterial blooms (Alström et al., 2017; Cronberg, 1996), defined here as cyanobacteria making up more than 50% of the total phytoplankton biomass.

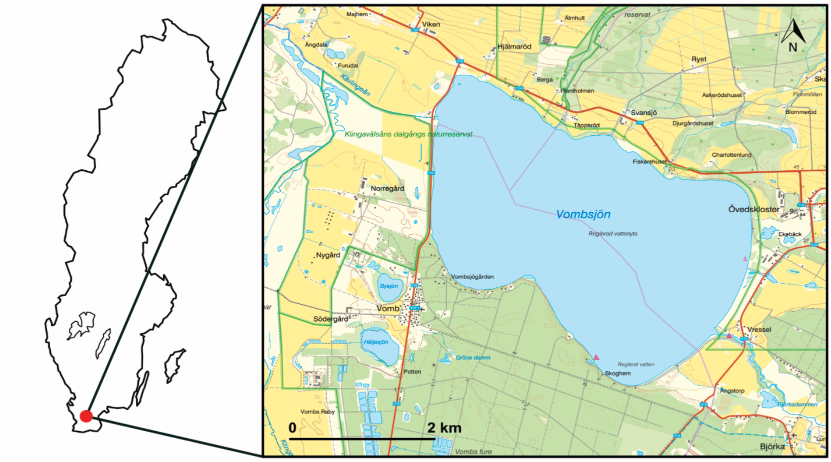

Figure 2. Map of Lake Vombsjön located in Scania, southern Sweden. The map is modified from © Lantmäteriet.

Microcystis

Microcystis Lemmermann belongs to the order Chroococcales and is one of the most widespread bloom-forming cyanobacteria in freshwater systems (Harke et al., 2016; O'Neil et al., 2012). Cells are spherical and typically 3-7 µm in diameter (Cronberg & Annadotter, 2006). In natural environments, *Microcystis* usually occur as colonies (Figure 3b), with colony morphology being used to divide *Microcystis* into different 'morphospecies'. The differentiation of species based on morphology is, however, not currently supported by genomic analysis of *Microcystis* based on average nucleotide identity values, 16S identity scores, and DNA-DNA hybridization values (Harke et al., 2016; Kondo et al., 2000). Blooms of *Microcystis* generally occur when water temperatures are above 15°C (Reynolds et al., 1981). *Microcystis* is known to produce compounds that have varying toxic effects, including microcystins (hepatoxin), anatoxin-a (neurotoxin), cyanopeptolines (cytotoxic) and BMAA (neurotoxin) (Meriluoto et al., 2017). Despite being the topic of intense scientific research, the functions, as well as the factors regulating the production of toxins, are not well understood (Harke et al., 2016).

Naiadinium polonicum

Naiadinium polonicum (Woloszynska) Carty (synonyms: *Peridiniopsis polonicum*, *Peridinium polonicum,* and *Glenodium gymnodinium*; Craveiro et al., 2015) is a thecate dinoflagellate with an oval shape (Figure 3b). Its dimensions are approximately 32-42 µm long, 27-36 µm wide, and 18-24 µm thick (Craveiro et al., 2015). *N. polonicum* (or one of its synonyms) has been identified in Europe (Moestrup & Calado, 2018; Roset et al., 2002), Israel (Pollingher & Hickel, 1991), Japan (Hashimoto et al., 1968), the Bahamas (Bjorneras et al., 2020), Chile (Ascencio et al., 2015), and Brazil (Sant'Anna et al., 1988). It is the only freshwater species known to produce ichthyotoxins (Oshima et al., 1989; Yotsu-Yamashita et al., 1998), which cause fish kills (Hashimoto et al., 1968; Oshima et al., 1989; Roset et al., 2002). Reported cases of fish kills are, however, rare and no fish kills were reported in Lake Vombsjön in 2018. There exists few studies pertaining to *N. polonicum*, thus its autecology is not well known and the conditions under which toxins are produced have not been investigated (Moestrup & Calado, 2018).

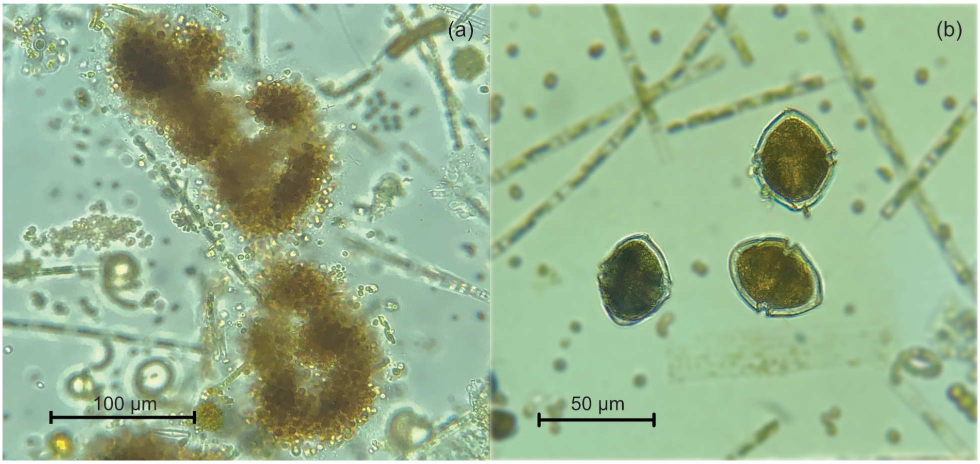

Figure 3. Images of (a) *Microcystis* and (b) *Naiadinium polonicum* from Lake Vombsjön, fixed with Lugol's solution. Images are taken from qualitative phytoplankton samples hence the high density of phytoplankton in the background.

Functional traits of *Microcystis* and *Naiadinium polonicum*

Below are details regarding relevant functional traits for *Microcystis* and *N. polonicum* (see Table 1). When specific information for *N. polonicum* is missing, I provide details for dinoflagellates in general. Mixotrophy and nitrogen fixation, as alternative nutrient acquisition strategies for dinoflagellates and cyanobacteria, respectively, were not included in this section since mixotrophy was not investigated during this thesis and *Microcystis* does not have the ability to fix nitrogen. Furthermore, the information presented below does not include findings from the papers in this thesis, which will be presented in the section "Main Findings".

Morphological

Phytoplankton morphology is often described as a 'master trait', since nearly all studies of phytoplankton traits include some aspect of cell size (Kruk et al., 2010; Litchman et al., 2010). Cell size is also closely linked to grazing pressure, with larger phytoplankton generally exhibiting greater resistance to grazers than smaller cells (Lurling & VanDonk, 1996; Pancic & Kiorboe, 2018). Although individual *Microcystis* cells are small (approximately 3-7 µm in diameter), *Microcystis* typically occurs as large colonies, often reaching maximum linear dimensions of

600-900 µm (Cronberg & Annadotter, 2006). In contrast, *Naiadinium polonicum* occurs as solitary, motile cells with the dimensions of approximately 32-42 µm long, 27-36 µm wide, and 18-24 µm thick (Craveiro et al., 2015). Thus, *N. polonicum* is smaller than other common dinoflagellates, such as *Ceratium* spp., whose maximum linear dimension can exceed 200 µm (Bustamante-Gil et al., 2021). It also lacks spines or horns, which provide other dinoflagellates with additional protection against grazing (Lurling, 2020).

Physiological

Temperature-dependent growth

The optimum temperature for *Microcystis* growth is reported to range between 28°C and 32.5°C (Lurling et al., 2013; Reynolds, 2006; Robarts & Zohary, 1987; Yang et al., 2020), with a minimum growth temperature between 10°C and 13°C (Robarts & Zohary, 1987; Yang et al., 2020) and a maximum growth temperature exceeding 36°C (Rossi et al., 2023; Yang et al., 2020). However, *Microcystis* blooms are often observed at temperatures well below their reported optima (Harke et al., 2016).

Dinoflagellates generally exhibit maximum growth rates at lower temperatures than those reported for *Microcystis*. For example, *Ceratium furcoides* has been reported to reach its maximum growth rate at 20°C, with no major differences observed between 17°C and 25°C (Butterwick et al., 2005). Although *N. polonicum* has not been studied under laboratory conditions, blooms have been documented in Japan and Spain at temperatures ranging from 20°C to 23°C (Hashimoto et al., 1968; Roset et al., 2002). Additionally, *N. polonicum* has been observed in the Bahamas, where surface water temperatures ranged from 23°C to 26°C (Bjorneras et al., 2020), suggesting that *N. polonicum* may have a higher optimum temperature for growth than other dinoflagellates.

Nutrient-dependent growth

The half-saturation constant (K_s), which is the concentration of external nutrients needed to sustain half the maximum nutrient uptake rate, has been widely used as an index of a species competitive ability to acquire nutrients at low concentrations (Reynolds, 2006; Smayda, 1997). Species with low K_s values are predicted to perform better when nutrient supply rates are low, whereas species with high K_s values tend to be more competitive when nutrient supply rates are high (Reynolds, 2006; Smayda, 1997). For nitrate and phosphate, *Microcystis* generally exhibits lower K_s values than dinoflagellates (Collos et al., 2005; Reynolds, 2006). Therefore, *Microcystis* is likely a better competitor for nutrients at low concentrations than are dinoflagellates.

Both *Microcystis* and dinoflagellates have been shown to possess alternative mechanisms for phosphorus acquisition that are likely important for their success in phosphorus-limited environments. These mechanisms include the luxury uptake (i.e., storage) of phosphorus (Baek et al., 2008; Jacobson & Halmann, 1982) and the production of alkaline phosphatases, enzymes that enable cells to utilize dissolved organic phosphorus (Harke & Gobler, 2013; Rengefors et al., 2003). In a paper by Rengefors et al. (2003), alkaline phosphatase activity was found to be much more common among dinoflagellate species than among cyanobacterial species in a natural population; however, neither *N. polonicum* nor *Microcystis* were included in that population.

Light-dependent growth

Microcystis, which forms surface scums, is best known for being high-light tolerant (Raps et al., 1983; Reynolds, 2006; Robarts & Zohary, 1992), with a high resistance to photoinhibition due to protective pigmentation (Paerl et al., 1983). At the same time, *Microcystis* has largely been considered a poor competitor under low light due to its colonial form (Kirk, 2010). However, Marinho et al. (2013) and Torres et al. (2016) showed *Microcystis* to be a better competitor at low light compared to low light specialists such as *Planktothrix agardhii* and *Raphidiopsis raciborskii*. Limited information regarding freshwater dinoflagellates makes it difficult to compare *Microcystis* and dinoflagellates directly.

For dinoflagellates, the majority of available data comes from marine environments, where dinoflagellates appear to do well in both high and low-light environments (Edwards et al., 2015; Smayda, 1997). This is also evident from the schematic summary of marine pelagic habitats by Smayda and Reynolds (2001), which predicts the success of different dinoflagellate functional groups along nutrient and light gradients. In general, dinoflagellates have been shown to aggregate in areas with elevated nutrient levels and low irradiance (Smayda, 1997). Photoadaptive strategies that enhance photosynthesis, such as increasing the size or number of photosynthetic units, enable dinoflagellates to perform well under low light conditions (Harding et al., 1983).

Allelopathy

Allelopathy is a well-documented form of interference competition among phytoplankton (Legrand et al., 2003; Prince et al., 2008). Allelochemicals are secondary metabolites that can disrupt essential functions in other prokaryotic and eukaryotic cells, sometimes resulting in cell death (Legrand et al., 2003). Their modes of action include damaging cell membranes, inhibiting protein activity, and altering or activating physiological processes (Legrand et al., 2003). Both *Microcystis* and dinoflagellates have been shown to produce allelochemicals that suppress the growth of competing species, including each other (Chia et al., 2018; Prince et al., 2008; Rengefors & Legrand, 2007; Vardi et al., 2002). For example, allelopathic interactions between *Peridinium gatunense* and *Microcystis* have been linked to a presence-absence pattern of these species in Lake Kinneret, Israel (Sukenik et al., 2002; Vardi et al., 2002). *Microcystis* has also been shown to exert allelopathic effects on green algae and other cyanobacteria (Dunker et al., 2017; Ma et al., 2015). Prior to my thesis work, nothing was known about the allelopathic potential of *N. polonicum*. However, allelopathy is common among bloom-forming marine dinoflagellates, such as the ichthyotoxic *Margalefidinium polykrikoides*.

Behavioral

Motility

Both *Microcystis* and dinoflagellates are known for their ability to move vertically through the water column. *Microcystis* produces gas vesicles under low-light conditions, which are hollow protein structures that provide buoyancy to cells (Walsby, 1994). During photosynthesis, cells accumulate carbohydrates, thereby counteracting the buoyancy provided by gas vesicles and causing cells to sink (Ibelings et al., 1991; Walsby, 1994). Floating and sinking velocities are affected by size; larger colonies move faster through the water column than do smaller colonies or single cells (Reynolds et al., 1987; Walsby, 1994).

Dinoflagellate motility depends on two flagella: one circles the cell in the girdle, providing both propulsive and spinning force, while the other is directed posteriorly along a longitudinal groove, the sulcus, and is thought to act like a rudder for steering (Hackett et al., 2004; Lee, 2018). Dinoflagellates are capable of directed swimming in response to a variety of parameters, including chemotaxis (chemical stimuli), phototaxis (light stimuli), and geotaxis (gravity stimuli) (Hackett et al., 2004; Lee, 2018).

Life history

Reproduction and resting stages

Dinoflagellates reproduce both asexually and sexually. Asexual reproduction occurs through vegetative cell division and is common under favorable environmental conditions. When conditions become limiting for growth, many dinoflagellates switch to sexual reproduction, producing temporary or dormant cysts (Kremp & Parrow, 2006; Pfiester, 1989). The success of dinoflagellates is largely determined by the transition between resting cysts and vegetative cells (Anderson & Rengefors, 2006). This includes cyst germination (excystment) and recruitment into the water column in the spring, which provides the initial inoculum, and cyst formation (encystment) in the fall, which ends the planktonic phase (Rengefors, 1998, 2020).

The main factors affecting excystment include an endogenous clock combined with a suitable germination temperature window (Rengefors & Anderson, 1998).

In contrast, *Microcystis* reproduces only asexually through vegetative cell division. There are no morphological distinctions between pelagic and benthic stages. Furthermore, *Microcystis* overwinters as both benthic and pelagic populations, with both populations representing important inoculum for summer blooms (Brunberg & Blomqvist, 2003; Verspagen et al., 2005). Recruitment of benthic colonies into the water column is thought to occur primarily through physical resuspension driven by mixing (Misson & Latour, 2012; Verspagen et al., 2004), while temperature plays a key role in regulating the reactivation of dormant cells already present in the pelagic zone (Yang et al., 2020).

Is *Microcystis* or *Naiadinium polonicum* more likely to benefit under future climate change scenarios?

Abiotic and biotic factors are key filters regulating the establishment and assembly of phytoplankton communities in lakes. Consequently, any change in physical conditions, resource availability, or, for example, zooplankton communities can lead to shifts in phytoplankton community composition. The ability of species to respond to changing conditions depends on their functional traits (Kruk et al., 2010; Litchman & Klausmeier, 2008; Reynolds et al., 2002). A number of review articles have addressed how cyanobacteria are likely to respond to climate change based on their functional traits (Carey et al., 2012; Harke et al., 2016; Huisman et al., 2018; O'Neil et al., 2012; Paerl & Huisman, 2008). Below, I expand on these studies and discuss how similarities and differences in functional traits between *Microcystis* and *Naiadinium polonicum* (or dinoflagellates in general) might influence their success in the context of a warming world.

Climate change is predicted to increase lake temperatures (IPCC, 2023; Peeters et al., 2002). Warmer temperatures have been positively correlated with a higher proportion of cyanobacterial biomass in lakes (Kosten et al., 2012), leading to predictions that cyanobacteria will become more dominant in a warmer world. This is partly because cyanobacteria generally grow better than many eukaryotic phytoplankton at temperatures above 25°C (Johnk et al., 2008; Paerl & Huisman, 2008; Robarts & Zohary, 1987). However, surface water temperatures in temperate regions, such as Sweden, may not consistently exceed 25°C. For instance, the highest recorded temperature in Lake Vombsjön during the 2018 heatwave was 24.3°C, while the two subsequent years peaked at 22.2°C and 23°C, respectively (**Paper I**). At the onset of this thesis work, there was limited information regarding the temperature optima of freshwater dinoflagellates, and no information for *N. polonicum*. Nevertheless, *N. polonicum* has been observed in warmer regions, such as the Bahamas, suggesting potential adaptation to higher temperatures. Given that surface water may not exceed 25°C, it is interesting to investigate whether *N. polonicum* or *Microcystis* benefit more from temperature increases in the 20°C-25°C range.

Indirect effects of warming, such as changes in thermal stratification and vertical mixing, are at least as important as direct effects because they govern the availability of light and nutrients to phytoplankton (Diehl et al., 2002; Salmaso, 2005; Schindler et al., 1996). One key functional trait that benefits both *Microcystis* and dinoflagellates under stratified conditions is vertical motility (Huisman et al., 2018; Smayda, 1997). However, *Microcystis* and dinoflagellates move vertically through the water column using different mechanisms. *Microcystis* adjusts its buoyancy through the production of gas vesicles and accumulation of carbohydrates, whereas dinoflagellates use flagella. Diel vertical migration patterns have been established for *Microcystis* (Ibelings et al., 1991; Kromkamp & Mur, 1984; Visser et al., 1997) and dinoflagellates (Cullen, 1985; Smayda, 1997), although nothing is currently known about the vertical migration behavior of *N. polonicum*. While it has been shown that *Microcystis* is particularly adept at moving towards the surface following mixing events to access light (Huisman et al., 2004), the extent to which it exploits sinking for nutrient acquisition is less understood. In contrast, dinoflagellates are known for actively positioning themselves at depths associated with favorable nutrient conditions (Heaney & Eppley, 1981; Smayda, 1997). Consequently, more research is needed to assess the competitive abilities of *N. polonicum* and *Microcystis* to access nutrients from deeper waters under stratified conditions.

Another critical functional trait related to both direct and indirect temperature effects is the recruitment of cells or colonies from sediments. In contrast to marine harmful algal blooms, recruitment has been largely overlooked in freshwater bloom dynamics. Cottingham et al. (2021) highlighted that most of the current knowledge regarding *Microcystis* focuses on its pelagic life stage. However, stratification, which is largely considered beneficial for *Microcystis*, can have contrasting effects on pelagic and benthic stages (Cottingham et al., 2021). A study by Misson and Latour (2012) demonstrated that mixing was the primary driver of benthic recruitment of *Microcystis* colonies, independent of light or temperature. Passive resuspension, such as wind-induced mixing or bioturbation, was also found to be important in field studies, more so than, for example, active changes in buoyancy of the cells (Verspagen et al., 2004). In contrast, *N. polonicum* forms resting cysts like other dinoflagellates, and the main factors regulating excystment in dinoflagellates have been shown to include an internal maturation period and a suitable temperature window (Rengefors & Anderson, 1998). This suggests that direct temperature effects are more likely to have an influence on *N. polonicum* recruitment, whereas indirect effects of temperature (changes in vertical mixing patterns) are more likely to have an influence on *Microcystis* recruitment.

In addition to temperature, climate change is expected to increase precipitation in temperate regions, particularly during winter, which may enhance nutrient inputs to lakes (Meehl et al., 2005). Stronger thermal stratification can also reduce oxygen near the sediment surface, leading to the release of phosphorus and other nutrients from sediments into the lake (Mortimer, 1942). Thus, nutrient regimes are likely to be altered by climate change. Considering half-saturation constants for *Microcystis* and dinoflagellates, *Microcystis* is likely the better competitor at low phosphorus concentrations. Therefore, higher phosphorus concentrations could increase the competitive ability of *N. polonicum*. At the same time, high phosphorus concentrations are synonymous with cyanobacterial blooms, including blooms of *Microcystis* (Schindler, 1974), so further research is needed on how different phosphorus concentrations affect *N. polonicum* versus *Microcystis* growth. If phosphorus is released from the sediments without vertical mixing, whichever species is more adept at vertical migration is likely to benefit under such conditions.

Finally, climate change and heatwaves have the potential to alter zooplankton communities, thereby influencing phytoplankton community assembly (Ratnarajah et al., 2023). For example, warming has been associated with a reduction in zooplankton body size (Albini et al., 2025; Campbell et al., 2021), which may reduce grazing pressure on larger or colonial phytoplankton such as *Microcystis*. Beyond changes in body size, warming has also been shown to drive phenological shifts in the timing of zooplankton peak biomass (Bailey & Hood, 2024; Mackas et al., 2012; Richardson, 2008), which will further impact grazing pressure on phytoplankton in ways currently not understood. Taken together, zooplankton community dynamics under future climate change scenarios are also likely to be critical for understanding shifts in phytoplankton community assembly.

Examples of alternating dominance between *Microcystis* and dinoflagellates in freshwater systems

The overarching aim of this thesis is to better understand the conditions that favor cyanobacteria versus dinoflagellates by examining the ecological factors that may have led *N. polonicum* to outcompete *Microcystis* during the 2018 heatwave in Lake Vombsjön. In this section, I present examples of other systems (Rostherne Mere, England; Lake Kinneret, Israel; and Garças Reservoir, Brazil) where shifts in the phytoplankton community have occurred, resulting in alternating dominance between *Microcystis* and different dinoflagellate species (*Ceratium* spp., *Peridinium gatunense*). I also summarize the ecological factors that have been proposed to drive dinoflagellate success in these systems. The final example, Garças Reservoir, is of particular interest because it represents a recent invasion of the dinoflagellate *Ceratium furcoides* in South America, leading to widespread changes in phytoplankton communities (Kruk et al., 2021; Silva et al., 2019).

Rostherne Mere, England

Rostherne Mere is a highly fertile and stratifying lake system located in Cheshire, England. In the late 1950s, there was a shift in the seasonal succession of phytoplankton from a diatom-*Ceratium*-*Aphanizomenon* sequence to a diatom-*Microcystis* or *Ceratium* sequence (Reynolds & Bellinger, 1992). What caused the transition in seasonal succession is not known, though one hypothesis is that it was related to an increase in nutrient supply to the lake. Based on phytoplankton community composition data collected over 18 years (between 1967 and 1989), Reynolds and Bellinger (1992) described the resulting interannual oscillations between *Microcystis* and *Ceratium* as "striking". Preferences of *Microcystis* and *Ceratium* were reported as largely indistinguishable with respect to the physical parameters considered (Secchi depth, water column stability, temperature). There was, however, evidence that conditions governing the recruitment and establishment of *Microcystis* and *Ceratium* were important factors in determining which species became dominant (Reynolds & Bellinger, 1992). In years when *Ceratium* established first, *Microcystis* was able to overtake *Ceratium* if the biovolume of *Ceratium* was below 7 $mm^3\ L^{-1}$ (1967 and 1972), but not if *Ceratium* biovolume was already above 10 $mm^3\ L^{-1}$ (1971, 1979, 1980, 1981, 1984). An exception occurred in 1989, when *Microcystis* overtook a dominant *Ceratium* population of over 20 $mm^3\ L^{-1}$ (Reynolds & Bellinger, 1992). In years when *Microcystis* established first, *Ceratium* either produced populations that remained small or failed to do so at all.

Lake Kinneret, Israel

Peridinium gatunense is a large thecate dinoflagellate (diameter: 44-60 μm) that dominated the Lake Kinneret phytoplankton community from the mid-1960s until 1996. In that year, no bloom formed for the first time, and since then *Peridinium* blooms have become irregular events (Zohary et al., 2012). At the same time, cyanobacteria increased from a minor component of the phytoplankton community to a more prominent one, with winter-spring blooms of the toxic *Microcystis* becoming commonplace in "non-*Peridinium* years" (Ninio et al., 2020; Vardi et al., 2002). The reason for this shift in phytoplankton community composition remains unclear, though a possible explanation is hydrological changes in the Hula Valley that significantly reduced the amount of water from this valley reaching Lake Kinneret via the Jordan River (Zohary et al., 2014). It has been hypothesized that water originating from the Hula Valley contains a specific growth factor for *P. gatunense* (Zohary et al., 2012). Consistent with this hypothesis, between 1996 and 2012 *Peridinium* tended to bloom in wet years characterized by high riverine inflow, when water from the Hula Valley was more likely to reach the Jordan River (Zohary et al., 2012). Hula Valley water was also found to stimulate the growth of *P. gatunense* cultures in the laboratory (Zohary et al., 2012). Additional laboratory studies have suggested that allelopathic interactions between *P. gatunense* and *Microcystis* may influence the population dynamics of these species (Sukenik et al., 2002; Vardi et al., 2002).

Garças Reservoir, Brazil

Ceratium furcoides is a large, invasive freshwater dinoflagellate that has recently extended its distribution in South America (Crossetti et al., 2019; da Silva et al., 2025; Kruk et al., 2021; Pacheco et al., 2021). Since the early 2000s, the Garças Reservoir in Brazil has experienced frequent and intense cyanobacterial blooms, primarily dominated by *Raphidiopsis raciborskii* and, to a lesser extent, *Microcystis* (Crossetti et al., 2019). During a drought event in 2014, *Ceratium furcoides* was recorded in the reservoir for the first time, coinciding with the partial removal of a macrophyte stand and substantial sediment disturbance (Crossetti et al., 2019). These disturbances led to marked increases in water transparency as well as soluble reactive phosphorus and ammonium concentrations. Furthermore, sediment disturbance seemed to promote the recruitment of *C. furcoides* (Crossetti et al., 2019). In the three years following its initial detection (2015-2017), *C. furcoides* was observed annually and accounted for more than 80% of total phytoplankton biomass at peak abundance. Over the same period, cyanobacterial biomass declined from a pre-2014 maximum of 104 $mm^3 L^{-1}$ (2008-2013) to a maximum of 69.5 $mm^3 L^{-1}$. New alternative states were observed in the reservoir, characterized by *Ceratium-Trachelomonas* dominance during mixing periods with high dissolved inorganic nitrogen (DIN) concentrations and *Microcystis-Cryptomonas* dominance during stratified periods with low DIN concentrations (Crossetti et al., 2019).

The examples above place the shift observed in Lake Vombsjön within a broader ecological context and demonstrate that alternating dominance between *Microcystis* and different dinoflagellate species has been observed in freshwater systems across multiple continents and a range of environmental conditions. In these systems, the success of dinoflagellates has been linked to several ecological factors, including recruitment timing, mixing regimes, nutrient availability, and allelopathic interactions. Nevertheless, the mechanisms determining whether *Microcystis* or dinoflagellates dominate remain poorly understood, highlighting the need for further studies that improve our ability to predict phytoplankton community outcomes under changing environmental conditions.

Aims and Research Questions

Climate change is expected to alter the pelagic environments of temperate lakes, leading to shifts in phytoplankton community composition. Cyanobacterial harmful algal blooms are predicted to increase under future climate change scenarios due to the functional traits of cyanobacteria. In contrast, the response of freshwater dinoflagellates, an evolutionarily divergent group of phytoplankton that shares key functional traits with cyanobacteria, such as vertical motility, remains poorly understood. Furthermore, little is known about competitive interactions between cyanobacteria and dinoflagellates in freshwater systems, despite their likely importance for community dynamics. Identifying the ecological conditions driving dominance, and linking these outcomes to functional traits, is essential for predicting and managing future cyanobacterial blooms.

In this thesis, I investigate the ecological conditions that favor cyanobacteria versus dinoflagellates by examining the population dynamics of the cyanobacterium *Microcystis* and the dinoflagellate *Naiadinium polonicum* in a temperate drinking water lake in relation to key abiotic and biotic factors. I also seek to verify and, where possible, quantify functional traits, including recruitment, growth rates, and allelopathic interactions, that may confer competitive advantages to either species. In my final paper, I narrow my focus to *Microcystis*, identifying the abiotic and biotic factors that best explain variation in the relative abundance of toxigenic and non-toxigenic strains in natural populations.

Specifically, the papers in this thesis address the following questions:

I. *Which ecological factors best explain differences in the success of Microcystis and Naiadinium polonicum in Lake Vombsjön?*

    In **Paper I**, I present a three-year field study examining the phytoplankton community alongside abiotic and biotic factors linked to key functional traits. Data were collected during the extreme drought year of 2018 and compared with subsequent years, 2019 and 2020. The aim was to identify recurring patterns and formulate hypotheses related to the question above that could subsequently be tested in the laboratory.

II. *How does temperature influence the recruitment and growth rates of Microcystis and Naiadinium polonicum isolated from Lake Vombsjön?*

In **Paper II**, I investigate the effects of temperature on recruitment from sediments and growth rates of *Microcystis* and *Naiadinium polonicum*. Multiple strains of each species, isolated from Lake Vombsjön, were included to account for intraspecific variation.

III. *Do secondary metabolites produced by Naiadinium polonicum inhibit the growth of Microcystis and vice versa?*

In **Paper III**, I examine whether secondary metabolites produced by *Naiadinium polonicum* inhibit the growth of *Microcystis*, and whether secondary metabolites produced by *Microcystis* inhibit the growth of *N. polonicum*. Strains from each species, isolated from Lake Vombsjön, were exposed to cell-free supernatants from the other species and were also grown in co-culture, allowing evaluation of allelopathic effects both in the presence and absence of direct cell-to-cell interactions.

IV. *Which abiotic and biotic factors best explain variation in the proportion of toxigenic Microcystis and microcystin concentrations in two eutrophic lakes in Scania?*

In **Paper IV**, I present a two-year field study in which qPCR was used to estimate the proportion of toxigenic and non-toxigenic *Microcystis* strains in natural populations. Microcystin concentrations in lake water samples were also measured. I then identify the abiotic and biotic factors that best explain variation in both the proportion of toxigenic strains and microcystin concentrations.

Research approaches and methodology

To answer the questions posed in the previous section, a combination of field studies and laboratory experiments were used in this thesis. The most important aspects of the approaches and methodology used in each of the papers are presented below.

Lake sampling

Paper I and **Paper IV** were based on field studies. For **Paper I**, Lake Vombsjön (Figure 2) was sampled over three seasons (2018-2020). Samples collected in 2018 (July-September) were combined with a more intensive sampling regime conducted during 2019 and 2020 (May-October). From the lake, samples were taken for determining phytoplankton and zooplankton communities, along with data on nutrients, light availability, and temperature. This was complemented with temperature and dissolved oxygen profiles from the deepest part of the lake, provided by the municipality-owned drinking water treatment company Sydvatten AB, as well as climatic data from the catchment area, including precipitation, river discharge, and global radiation, downloaded from online databases.

For **Paper IV**, Lake Vombsjön was sampled over two seasons (2018-2019) from July to September. In addition to Lake Vombsjön, another eutrophic lake located approximately 20 km north of Lake Vombsjön, Lake Ringsjön, was also sampled. The sampling regime was similar to that of **Paper I** and focused on testing relevant hypotheses regarding which variables were responsible for variation in toxigenic strains of *Microcystis* in natural populations. Samples were taken for determining phytoplankton and zooplankton communities, along with data on nutrients, temperature, dissolved oxygen, and pH. In addition, samples were taken for quantifying microcystin concentrations in lake water and to determine the proportion of toxigenic *Microcystis* using qPCR. Note that data were shared between **Paper I** and **Paper IV** for Vombsjön 2018.

In addition to field sampling, sediments were collected from Lake Vombsjön for **Paper II** and cultures were isolated from Lake Vombsjön for **Paper II** and **Paper III**. Sediment sampling took place in February, prior to the onset of favorable conditions for recruitment. Sediment cores were collected from the deepest part of the lake, and the top 2 cm were sliced on the boat. The sliced sediments were then thoroughly mixed and stored in sealed plastic containers filled to the brim, which were kept in the dark at 4°C until the start of the experiment in May of the same year. The deepest part of the lake was chosen because previous studies have shown that resting cells and cysts accumulate and are most abundant there (Rengefors, 1998).

Cultures of *Naiadinium polonicum* and *Microcystis* were isolated from Lake Vombsjön during 2020 and 2021, respectively. Following isolation, single cells (*N. polonicum*) or single colonies (*Microcystis*) were grown in individual wells of 48- or 96-well plates in a medium consisting of 50% filtered lake water and 50% MWC+Se medium (see below). Isolated strains of *Microcystis* were all identified as the morphospecies *M. botrys* Teiling, but since this is not a phylogenetically valid species, I refer to them simply as *Microcystis* (Johansson et al., 2025). As the strains grew, they were sequentially transferred to larger vessels while gradually increasing the proportion of MWC+Se medium. The established strains were non-axenic. They were maintained in culture flasks with ventilated caps in 100% MWC+Se medium at 20°C and 20-50 µmol m^{-2} s^{-1}. Prior to use in experiments, cultures were visually inspected to ensure that there was no unwanted contamination.

MWC+Se medium

MWC+Se medium was used to establish and maintain cultures, as well as in experiments, including the growth rate experiment in **Paper II** and allelopathy experiment in **Paper III**. The chemical composition of the MWC+Se medium was adapted from Guillard and Lorenzen (1972). Selenium was added to the original recipe because it has been shown to support dinoflagellate growth (Lindstrom, 1985). The full composition of the MWC+Se medium is provided in the supplementary material for **Paper III**.

Phytoplankton biomass estimation using microscopy

Microscopy was used throughout this thesis, mostly using a Nikon Eclipse TS100 (nicknamed Nicke), without whom this work would not have been possible. In **Paper I** and **Paper IV**, quantitative phytoplankton samples were counted using sedimentation chambers, and the phytoplankton community was determined to the finest taxonomical unit possible. In **Paper IV,** the whole phytoplankton community was counted, whereas in **Paper I** only cyanobacteria and dinoflagellates were counted. The number of cells per colony of *Microcystis*, which primarily occurred in colonial form, was estimated using a grid reticle and a previously determined number of cells per grid (Ekvall et al., 2013). Phytoplankton biovolumes were mainly calculated according to Hillebrand et al. (1999), deviations are referenced in text. Assuming cytoplasm density to be equal to that of water (1.0 g mL^{-1}), biomass (wet weight) was then estimated as 1 mm^3 L^{-1} = 1 mg L^{-1}. In **Paper II**, the same method was used to count *Microcystis* and *Naiadinium polonicum* present in the recruitment samples.

In addition to the above, microscopy was used to both set up and enumerate the results from the allelopathy experiments in **Paper III**. In this case, *Microcystis* was counted using a Palmer-Maloney chamber with a volume of 100 µL, while *Naiadinium polonicum* was counted using a Sedgewick-Rafter chamber with a volume of 1 mL. When possible, up to 400 cells were counted. Cultures of *Microcystis* were primarily composed of single cells, and therefore cell numbers could be determined directly without estimating the number of cells per colony.

Phytoplankton biomass estimation using fluorescence

Fluorescence is a common tool used in phytoplankton ecology. It involves exciting samples with a light source, causing pigments such as chlorophyll a to absorb light energy and elevate their electrons to a higher energy state. As the electrons return to their normal state, part of the absorbed energy is released as fluorescent light. By measuring the emitted light, which varies depending on pigment, it is possible to assess, among other things, phytoplankton abundance and composition in samples. In **Paper I**, a preliminary overview of the phytoplankton community was established on the day of sampling using an AlgaeLabAnalyser (ALA), which applies fluorescence measurements to categorize the phytoplankton community into one of the following groups based on pigment compositions: green algae, cyanobacteria, diatoms plus dinoflagellates, or cryptophytes. In **Paper II**, growth rates of monocultures were calculated from raw fluorescence units (RFUs) using a TD-700 Laboratory Fluorometer. To confirm that increases in RFUs corresponded to increases in cell number, a subset of samples was also counted using microscopy.

Quantitave Polymerase Chain Reaction (qPCR)

In **paper IV**, quantitative polymerase chain reaction (qPCR) was used to determine the proportion of toxigenic versus non-toxigenic *Microcystis* spp. in natural populations. During each qPCR cycle, the target DNA is denatured, sequence-specific primers anneal to their complementary sequences, and DNA polymerase extends the new strands. As amplification progresses, a fluorescence signal increases proportionally to the amount of amplified DNA. The point at which fluorescence exceeds a defined threshold is called the threshold cycle (Ct). This value is inversely proportional to the initial amount of target DNA and is quantified using a standard curve generated from known DNA concentrations included in each qPCR run.

For **paper IV**, population-specific primers were designed using the primer design tool Primer-BLAST. Primer sites were identified by aligning sequences of the *mcyF* and the *mcyJ* genes from 14 *M. botrys* strains isolated from Lake Vombsjön, the *M. aeruginosa* reference strain PCC7806L, and consensus sequence based on 190 (*mcyF*) or 176 (*mcyJ*) strains. To ensure genus-specificity, a custom database was created by performing local alignment searches of the sequences listed above using the online tool Standard Nucleotide BLAST and compiling accession numbers of all sequences not belonging to *Microcystis* spp. These accession numbers were then imported into Primer-BLAST to ensure that designed primer pairs did not match genera other than *Microcystis*. Genus specificity of the selected primers was further tested using microcystin-producing strains of *Planktothrix aghardii* and *Dolichospermum flos-aquae*. These species were chosen given their presence in Lake Vombsjön and Lake Ringsjön samples.

Enzyme-Linked Immunosorbent Assay (ELISA)

Microcystin concentrations in lake water samples were determined for **Paper IV** using a competitive ELISA kit, following the manufacturer's instructions. The assay is based on competition between free microcystins (sample antigens) and enzyme-labelled microcystins (reference antigens) for antibody binding sites. Depending on the concentration of sample antigens, more or less of the reference antigens can bind to the antibodies. The resulting color intensity, measured spectrophotometrically at 450 nm, is inversely proportional to toxin concentration and quantified against a standard curve.

Statistical analyses

To address the research questions for **Paper I** and **Paper IV**, multivariate statistical approaches were used. In **Paper I**, variables explaining variation in *Microcystis* and *Naiadinium polonicum* biomass were identified using a multiple linear regression combined with model averaging. This approach identifies predictors that are consistently important across a set of models with comparable predictive performance, allowing key explanatory variables to be isolated and used to formulate hypotheses. In **Paper IV**, significant predictors of variation in the toxigenic proportions of *Microcystis* and microcystin concentrations were identified using partial least squares (PLS) regression with variable importance in projection (VIP) values. This method is suited to handling datasets with many explanatory variables, as well as high multicollinearity among variables (Wold et al., 2001). Variables with VIP values greater than 1.0 were considered significant predictors (Wold et al., 2001).

In **Paper II**, generalized linear mixed models (GLMMs) with a negative binomial distribution were used to assess the effect of temperature and time on the recruitment of *Microcystis* and *Naiadinium polonicum*. The effects of temperature on cumulative recruitment and growth rates were evaluated using one-way ANOVAs with Tukey post hoc tests.

In **Paper III**, repeated-measures ANOVAs were used to test for treatment effects (exposure to the opposite species or its cell-free supernatant). Tukey post hoc tests were applied when significant interactions between time and treatment were detected.

Main findings

Temperature and soluble reactive phosphorus are important variables for *Naiadinium polonicum* dominance (Paper I)

The aim of this study was to understand how the heatwave of 2018 affected pelagic conditions in Lake Vombsjön and whether these changes led to a change in the phytoplankton community. Furthermore, I wanted to understand whether Microcystis and N. polonicum tended to be co-dominant or whether one outcompeted the other. Finally, I wanted to identify which ecological factors best explained the success of Microcystis and Naiadinium polonicum in the lake.

The hot and dry summer of 2018 appeared to have a strong impact on pelagic conditions in Lake Vombsjön. Surface water temperatures were higher than in subsequent years but never exceeded 25°C (Figure 4a), a threshold temperature often cited as being particularly favorable for cyanobacteria. In addition to warmer surface water temperatures, there was a stronger and more prolonged relative water column stability (used here as a proxy for thermal stratification) (Figure 4b), along with an extended period of hypoxia (dissolved oxygen < 2 mg L^{-1}) near the sediment surface (Figure 4c). In terms of nutrients, it was expected that reduced rainfall would lead to lower nitrogen and phosphorus concentrations in the lake. Interestingly, while total phosphorus and nitrogen concentrations were indeed lower in 2018, concentrations of soluble reactive phosphorus (SRP) were higher than in subsequent years (Figure 4d). This was likely due to the internal loading of SRP from sediments, a well-known phenomenon caused by hypoxic conditions near the sediment surface (Mortimer, 1942).

Historical phytoplankton data showed that cyanobacteria dominated the phytoplankton community in 11 out of 15 years on record. During the three-year field study, cyanobacteria dominated the summer phytoplankton community in 2019, with *Microcystis* being the most dominant genus among cyanobacteria at this time (Figure 5b). *Naiadinium polonicum* dominated during the summer of 2018 (Figure 5a), while green algae were most successful in the summer of 2020 (**Paper I**). In addition to 2018, *N. polonicum* biomass increased rapidly in the fall of 2020, following a rise in temperature and a spike in SRP concentrations in the lake (Figure 5c). The zooplankton community was also sampled to determine whether grazing on *Microcystis* or other cyanobacteria could have contributed to the dominance of *N. polonicum* in 2018. Our data showed that copepods dominated the zooplankton community in 2018 and that total biomass was higher than in subsequent years (**Paper I**). However, copepods are selective feeders that prefer eukaryotic phytoplankton over cyanobacteria as a food source (Ger et al., 2019). We therefore reasoned that *N. polonicum*, which is a suitable size for consumption by many copepod species (Hansen et al., 1994), served as a good food source for copepods in Lake Vombsjön, thereby contributing to their higher biomass.

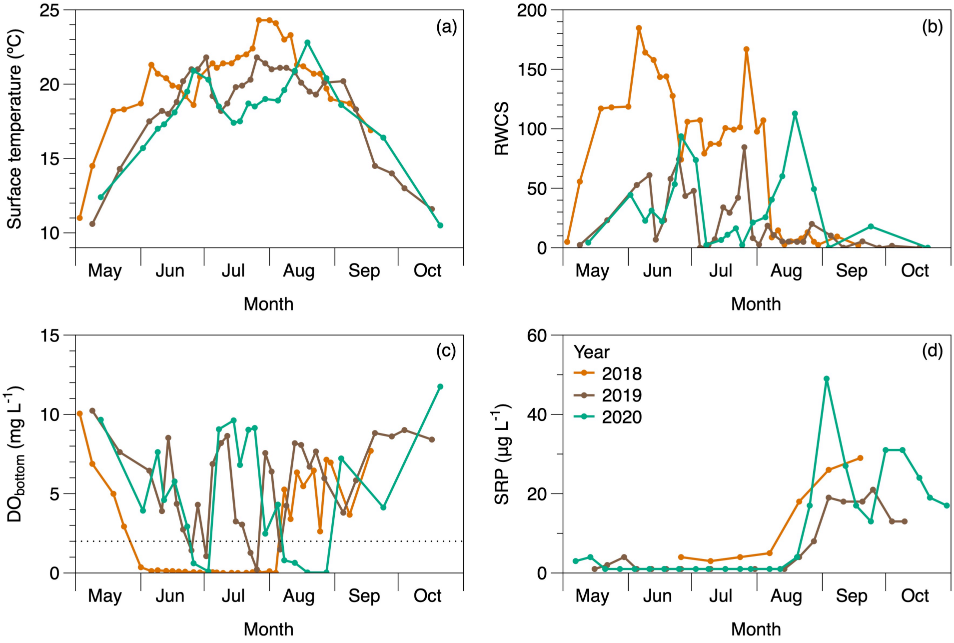

Figure 4. Data collected from Lake Vombsjön regarding (a) surface water temperature, (b) relative water column stability (RWCS), (c) dissolved oxygen near the sediment surface (DO$_{bottom}$), and (d) soluble reactive phosphorus (SRP). Dotted line in (c) corresponds to a dissolved oxygen concentration of 2 mg L^{-1}, below which conditions are considered hypoxic. This figure is adapted from **Paper I.**

A distinct presence-absence pattern was observed for *Microcystis* and *Naiadinium polonicum* in the lake, particularly during 2018 and 2019 (**Paper I**). Based on a multiple linear regression with model averaging, nitrate plus nitrite was identified as the only significant predictor for *Microcystis* biomass. The negative relationship between *Microcystis* and nitrate was likely due to nitrate uptake by *Microcystis* during growth (Chaffin et al., 2011). The strongest predictors for *N. polonicum* biomass were high surface water temperatures, elevated SRP concentrations, and low 30-day average outflow. *N. polonicum* biomass was also associated with high relative water column stability and hypoxia near the sediment surface, which were two factors that could not be included in the MLR analysis.

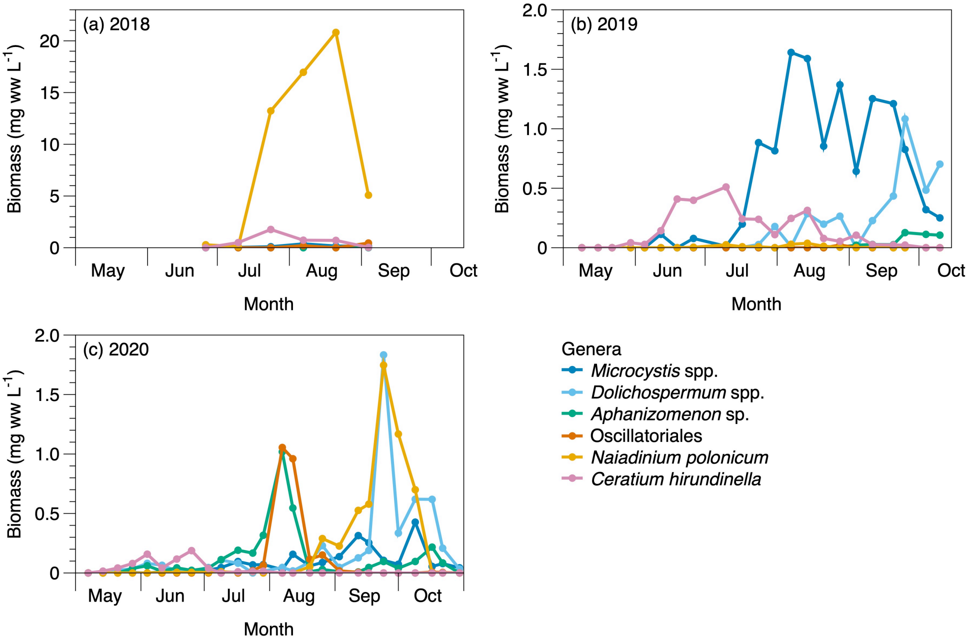

Figure 5. Cyanobacteria and dinoflagellate biomass from the phytoplankton community for (a) 2018 (June-September), (b) 2019 (May-October) and (c) 2020 (May-October). Only dominant phytoplankton genera/species were plotted, ww = wet weight. Note y-axis scale for 2018 is different from 2019 and 2020. This figure is adapted from **Paper I**.

These results indicate that both direct and indirect effects of temperature, as well as SRP concentrations, are important factors influencing the success and dominance of *Naiadinium polonicum*. Furthermore, the observed presence-absence pattern between *Microcystis* and *N. polonicum* led me to hypothesize that allelopathic interactions may contribute to the relative success of these species. In this thesis, I address hypotheses related to the direct effects of temperature on recruitment and growth rates of *N. polonicum* and *Microcystis* (**Paper II**) as well as allelopathic interactions between the two species (**Paper III**). Additional hypotheses arising from the results presented above, but beyond the scope of this thesis, include:

1. *Higher soluble reactive phosphorus concentrations increase the competitive ability of Naiadinium polonicum.*
2. *Naiadinium polonicum is more adept at vertical migration than Microcystis, benefiting N. polonicum during periods of strong relative water column stability.*

Earlier spring during heatwave may explain dominance of slow-growing *Naiadinium polonicum* over *Microcystis* (Paper II)

I hypothesized that increasing temperatures would have a positive effect on the recruitment of Naiadinium polonicum, but no effect on the recruitment of Microcystis. I further hypothesized that the relative increase in growth rates with rising temperatures, from 20℃ to 24℃, would be greater for Naiadinium polonicum than for Microcystis.

Recruitment of *Microcystis* and *N. polonicum* was monitored across five temperatures, from 8°C to 24°C in 4°C increments. *Microcystis* recruitment was significantly affected by time, with most cells recruiting on day 2 (Figure 6a), but showed no response to temperature (Figure 6a and 6b). In contrast, *N. polonicum* recruitment was significantly affected by both time and temperature, including a significant interaction between the two factors (Figure 6c). Recruitment generally occurred more rapidly at higher temperatures: at 8°C it was delayed, with most recruitment occurring between days 8-16, whereas at 12°C and 16°C it occurred primarily between days 4-10 (Figure 6c). Patterns at 20°C and 24°C were less distinct due to low overall recruitment. Cumulative recruitment of *N. polonicum* declined sharply above 12°C, with no significant difference between the 8°C and 12°C treatments (Figure 6d).

Growth rates of *Microcystis* and *Naiadinium polonicum* were also monitored over five temperatures, from 12°C to 28°C in 4°C increments. *Microcystis* growth rates increased significantly with rising temperatures (Figure 7a), while *N. polonicum* growth rates peaked at 20°C, with little difference observed between 16°C and 24°C (Figure 7b). This pattern was, however, strain-dependent given large intraspecific strain variability at 24°C (Figure 7b). Most importantly, Q_{10} values calculated for the temperature range 20°C to 24°C indicated a strong positive thermal dependence for *Microcystis* but a negative thermal dependence for *N. polonicum*.

Taken together, our results suggest that *N. polonicum* recruitment would not have increased in response to the relatively warm May temperatures in 2018, which averaged 16°C but reached 18°C. Furthermore, the increase in surface water temperatures during July would have favored *Microcystis* growth rather than *N. polonicum*. However, the earlier onset of spring warming in 2018 likely triggered earlier recruitment of *N. polonicum* from the sediment, as its recruitment is temperature dependent, whereas *Microcystis* recruitment is not, at least not for the temperature span included in this study. Using the average growth rate of *N. polonicum* at 20°C, we further determined that a prolonged period of favorable conditions would have been required for *N. polonicum* to attain the bloom biomass observed in 2018. Overall, these findings indicate that both the magnitude and timing of warming events can strongly shape phytoplankton community composition and bloom dynamics.

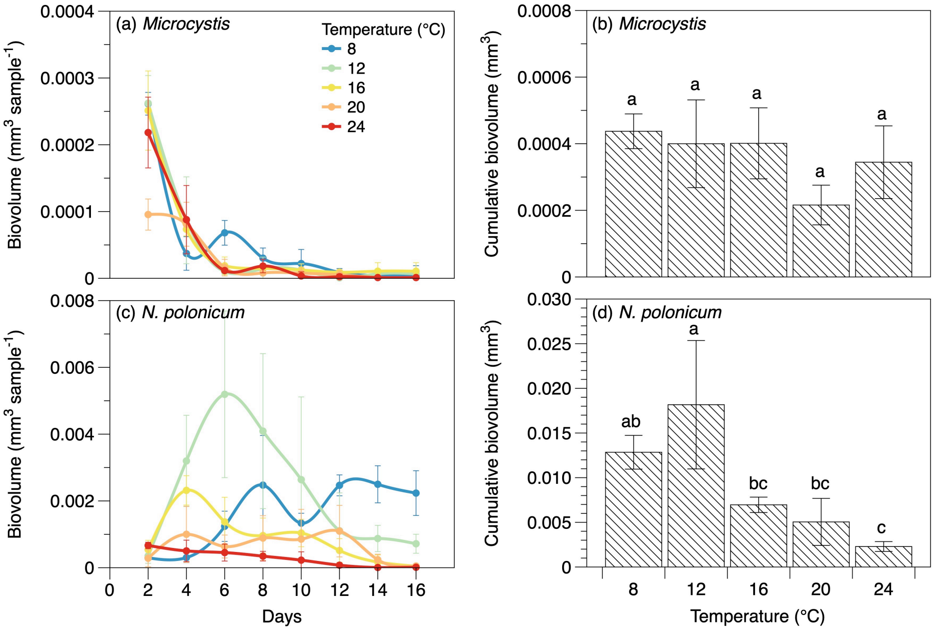

Figure 6. Recruitment of *Microcystis* (a) and (b) and *Naiadinium polonicum* (c) and (d) at five temperatures: 8°C, 12°C, 16°C, 20°C, and 24°C. Panels (a) and (c) show recruitment from samples taken every second day of the experiment. For statistical details see **Paper II**. Panels (b) and (d) show cumulative recruitment over the entire experiment. Letters indicate whether there is a significant difference in biovolume between temperatures based on a one-way ANOVA with a Tukey post hoc test. Note difference y-axes for each of the panels.

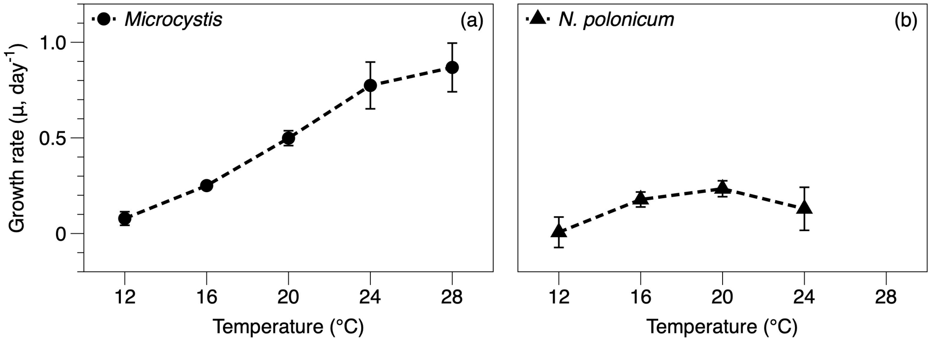

Figure 7. Mean growth rates (μ) calculated from four different strains of (a) *Microcystis* and (b) *Naiadinium polonicum* at five temperatures: 12°C, 16°C, 20°C, 24°C, and 28°C. *N. polonicum* cultures did not survive acclimation at 28°C. For statistical details see **Paper II**.

Rapid decline of *Naiadinium polonicum* grown in co-culture with *Microcystis* (Paper III)

I hypothesized that secondary metabolites produced by Naiadinium polonicum negatively affect Microcystis growth and that secondary metabolites produced by Microcystis negatively affect Naiadinium polonicum growth.

Contrary to our initial hypothesis, *N. polonicum* exhibited no inhibitory effect on *Microcystis* growth. Instead, both *N. polonicum* strains were strongly negatively affected when co-cultured with *Microcystis*. This inhibitory effect on *N. polonicum* was significant across all *Microcystis*:*N. polonicum* biovolume ratios tested (0.1:1, 0.5:1, 1:1, and 2:1) (Figure 8).

Interestingly, allelopathic effects were observed in co-culture but not when *N. polonicum* was exposed to the cell-free supernatant of *Microcystis*. However, there are several reported cases in which direct or indirect cell-to-cell interactions are required for inhibition to occur (Dunker et al., 2017; Mello et al., 2012). For example, Mello et al. (2012) investigated the allelopathic effects of *Raphidiopsis raciborskii* (basionym *Cylindrospermopsis raciborskii*) on *Microcystis* and found that growth inhibition occurred only when strains were exposed to filtrate from a mixed culture, not from a monoculture. Similarly, Song et al. (2017) found that signaling compounds released from the green algae *Chlorella vulgaris* increased secondary metabolite production in *Microcystis*, thereby enhancing its allelopathic effect on *C. vulgaris*.

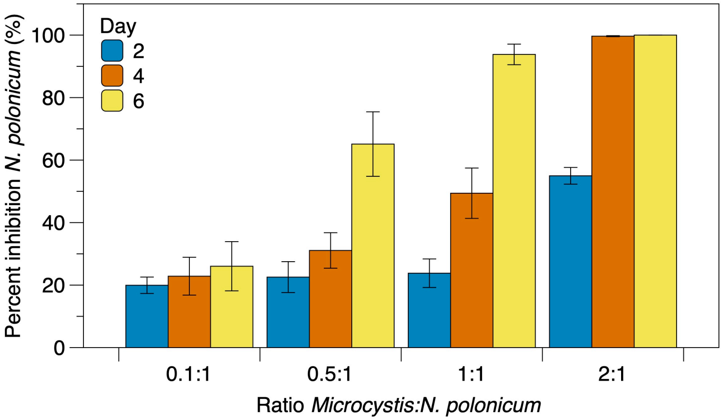

Figure 8. Percent inhibition of *N. polonicum* strain NPVO18-1 in co-cultures with *Microcystis* strain S1-119 at four different starting *Microcystis:N. polonicum* biovolume ratios: 0.1:1, 0.5:1, 1:1, and 2:1. The experiment was run for a total of 6 days with sampling on day 2, 4, and 6. For statistical details see **Paper III**.

Our results indicate that allelopathy cannot explain the dominance of *Naiadinium polonicum* in Lake Vombsjön. However, once *Microcystis* biomass begins to increase during the early bloom phase, it may have the potential to suppress *N. polonicum* and other competitors through the production of allelopathic secondary metabolites. This mechanism may be particularly important for outcompeting species that occupy similar ecological niches.

Nitrogen availability favors toxigenic *Microcystis* in lakes (Paper IV)

The aim of this study was to test whether toxigenic Microcystis strains were favored under nitrogen-rich conditions, high grazing pressure, and environmental conditions indicative of CO_2 limitation in the field.

Our results showed only moderate variation in the proportions of toxigenic versus non-toxigenic strains of *Microcystis* in Lake Vombsjön and Lake Ringsjön (Figure 9). In general, the proportion of toxigenic strains rarely exceeded 50%, with a mean of 30.7% ± 13%. Variation in the proportion of toxigenic strains could be partially explained by total nitrogen (TN) and dissolved inorganic nitrogen (DIN) concentrations (Figure 10a), with which toxigenic strains were positively correlated. Because microcystin is a nitrogen-rich metabolite and its production has been shown to increase under nitrogen-replete conditions (Brandenburg et al., 2020; Harke & Gobler, 2013; Wagner et al., 2021), it has been hypothesized that microcystin-producing strains have higher nitrogen requirements than non-producing strains. This could account for the positive correlation observed in this study.

Contrary to our expectations, the proportion of toxigenic strains was significantly negatively correlated with pH (Figure 10a). High pH is typically a consequence of high photosynthetic activity, which decreases dissolved CO_2 and increases bicarbonate and carbonate concentrations. Since microcystins have been suggested to facilitate carbon assimilation (Wei et al., 2024), I expected a higher proportion of toxigenic strains at higher pH. However, different *Microcystis* strains possess different genes involved in carbon assimilation (Sandrini et al., 2014). It is therefore possible that toxigenic strains in Lake Vombsjön and Lake Ringsjön lack genes for efficient bicarbonate uptake and are instead favored at lower pH, when CO_2 availability is higher.

We also observed a significant negative relationship between the proportion of toxigenic strains and copepod biomass (Figure 10a). This relationship, however, was driven primarily by conditions in Lake Vombsjön in 2018, when the phytoplankton community was dominated by the dinoflagellate *Naiadinium polonicum* (**Paper I**). *N. polonicum* likely represented a high-quality food source for copepods, resulting in increased copepod biomass (**Paper I**). When the 2018 data from Lake Vombsjön were excluded, no correlation between the proportion of toxigenic strains and copepod biomass was found. Thus, our findings do not support the hypothesis that microcystins function as a grazer deterrent.

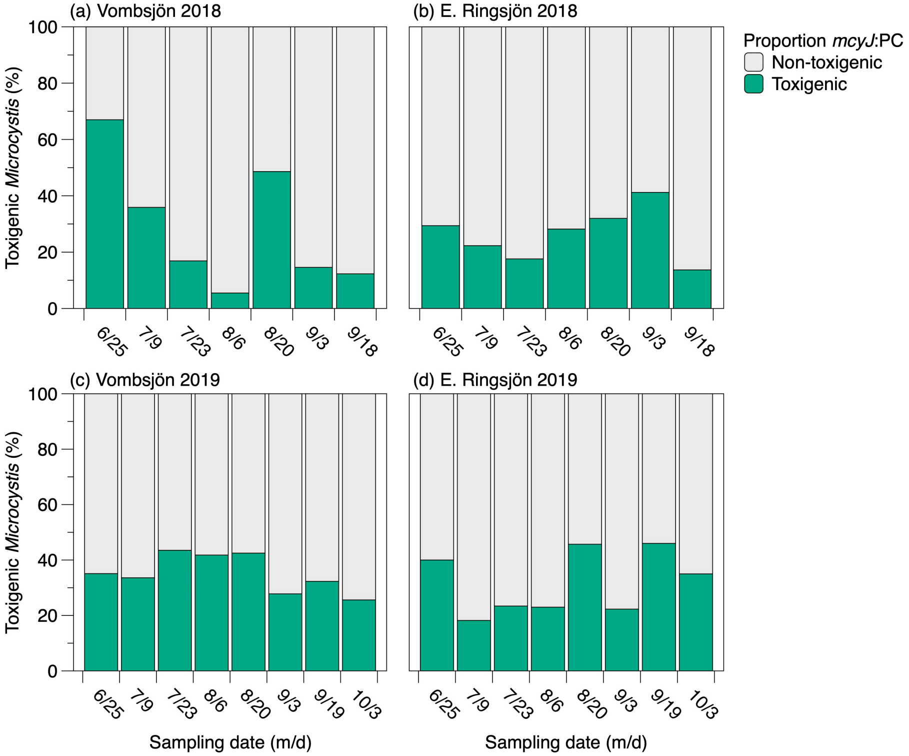

Figure 9. Barplots showing the proportion of *mcyJ* to PC gene copies also referred to as proportion toxigenic *Microcystis* for (a) Lake Vombsjön 2018, (b) Lake E. Ringsjön 2018, (c) Lake Vombsjön 2019, and (d) Lake E. Ringsjön 2019. Note different x-axes in the top and bottom row.

In addition to assessing the proportion of toxigenic *Microcystis*, we examined the relationship between microcystin concentrations and abiotic and biotic factors in the lakes. Microcystin concentrations were significantly positively correlated with phosphorus and significantly negatively correlated with nitrogen (Figure 10b), both of which are closely linked to *Microcystis* biomass accumulation. For example, **Paper I** identified a negative relationship between DIN and *Microcystis* biomass, likely reflecting nitrate uptake during periods of biomass accumulation. Furthermore, a strong relationship between soluble reactive phosphorus (SRP) and cyanobacteria biomass is well established (Schindler, 1974). Lake Vombsjön and Lake Ringsjön seem to undergo a seasonal transition from phosphorus to nitrogen limitation. During this shift, increasing phytoplankton biomass likely leads to nitrate depletion and a concomitant accumulation of SRP, which could explain the positive relationship between *Microcystis* biomass and SRP and the negative relationship with DIN.

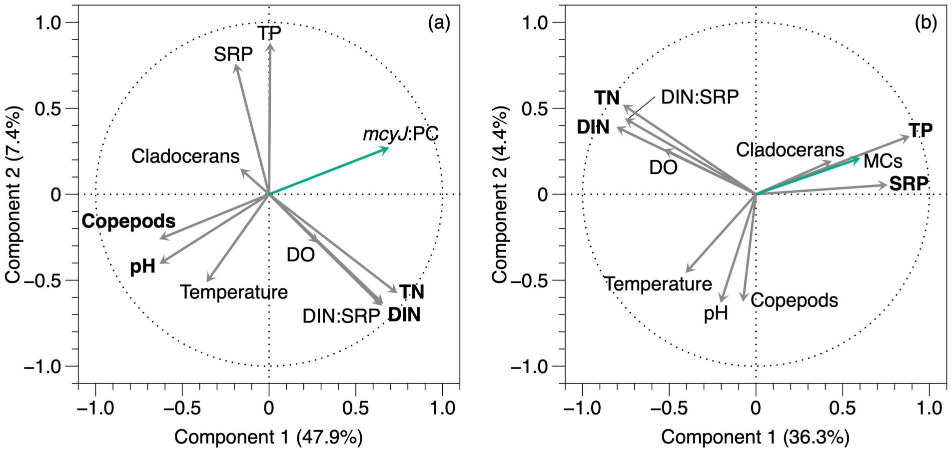

Figure 10. Correlation circle plots from partial least square (PLS) regression for response variables (a) proportion toxigenic *Microcystis* (*mcyJ*:PC); and (b) microcystin concentrations (MCs). The plots represent correlation of the variables along the first two components of the PLS regression. Variables in **bold** indicate significant effect of the environmental variable. Explanatory variables are soluble reactive phosphorus (SRP), total phosphorus (TP), dissolved inorganic nitrogen (DIN), total nitrogen (TN), ratio dissolved inorganic nitrogen to soluble reactive phosphorus (DIN:SRP), pH, temperature, dissolved oxygen (DO), copepod biomass (Copepods) and cladoceran biomass (Cladocerans).

Taken together, our results indicate that nitrogen availability favors toxigenic strains of *Microcystis*, whereas microcystin concentrations are more closely linked to SRP and overall *Microcystis* biomass. While management of harmful cyanobacterial blooms has traditionally focused on phosphorus reduction, our findings highlight the importance of controlling both phosphorus and nitrogen inputs to limit the proliferation of toxic cyanobacteria and mitigate harmful blooms in lakes.

Conclusions and Outlooks

Seasonal succession and functional trait models predict that *Microcystis* and dinoflagellates such as *Naiadinium polonicum* perform well under similar conditions due to similarities in their functional traits. At the beginning of my PhD research, it was unclear whether the success of *N. polonicum* in 2018 was driven primarily by stochastic processes or by identifiable ecological drivers. My thesis research indicates that temperature, one of the major environmental drivers expected to benefit cyanobacteria under future climate change scenarios, also plays an important role in dinoflagellate success. While increased temperatures in 2018 did not directly benefit *Naiadinium polonicum* recruitment or growth rates, we were able to establish that *N. polonicum* recruitment, which was temperature dependent, likely occurred earlier than *Microcystis* recruitment, which was independent of temperature within the tested temperature span. Given that *Microcystis* recruitment from sediments has been shown to be strongly dependent on mixing and resuspension (Misson & Latour, 2012; Verspagen et al., 2004), its recruitment in 2018 may have been further suppressed by the unusually strong relative water column stability observed that year. This interpretation is consistent with a recent review by Cottingham et al. (2021), which highlighted that while stratification tends to benefit pelagic stages of cyanobacteria, mixing is more favorable for their benthic life stages. These findings highlight that, in addition to magnitude, the timing of environmental change is a critical determinant of phytoplankton community composition.

Given the relatively slow growth rates of *N. polonicum*, earlier recruitment appears to have been essential for the species to reach the bloom biomass observed in 2018. This is consistent with the findings of Reynolds and Bellinger (1992), who showed that in a lake with alternating dinoflagellate (*Ceratium*) and *Microcystis* dominance, dinoflagellates were most successful in years when they were able to establish first and attain a critical biomass. In **Paper III**, I found no evidence to suggest that allelopathy contributed to the success of *N. polonicum*, for example through the suppression of *Microcystis* growth, at least not at ecologically relevant densities. By contrast, *Microcystis* was found to suppress the growth of *N. polonicum* at ecologically relevant densities, a trait that may be important for its own ability to establish and maintain high bloom biomass.

In addition to temperature, **Paper I** showed that *N. polonicum* was associated with elevated soluble reactive phosphorus (SRP), increased water column stability (a proxy for thermal stratification), and anoxic conditions near the sediment surface. Future work could investigate the relative vertical migration capacities of *N. polonicum* and *Microcystis* under stratified conditions. While vertical migration is commonly associated with cyanobacterial success in freshwater, the PEG model of seasonal succession, based on 19 temperate lakes, found that cyanobacteria were successful in eutrophic lakes irrespective of stratification, whereas higher proportions of dinoflagellates were observed only in stratifying lakes (Sommer et al., 1986). Furthermore, vertical motility has been identified as an important trait for marine dinoflagellates, which are otherwise inferior competitors for nutrients and light (Litchman, 2023; Smayda, 1997). Taken together, these findings suggest that stratification may be more important for the competitive ability of dinoflagellates, for example, to access nutrients only available in deeper layers, than for that of cyanobacteria.

Anoxic conditions near the sediment surface may also have indirectly influenced the success of *N. polonicum*. It is well established that anoxia promotes the internal loading of phosphorus and other micronutrients, such as iron and manganese, from sediments (Mortimer, 1942). Elevated SRP concentrations were also observed during an invasion and bloom of *Ceratium furcoides* in the Garças Reservoir, Brazil. I reason that while higher SRP concentrations in the water column likely enhanced *N. polonicum* growth in 2018, they are unlikely to fully explain its success, given that *Microcystis* exhibits faster growth rates under nutrient-replete conditions (**Paper II**). However, a potentially interesting avenue for future research is to investigate how dissolved organic carbon influences *N. polonicum* growth and whether this species exhibits mixotrophic capabilities, as dissolved organic carbon is also released under anoxic conditions and can be utilized by mixotrophic species only (Granéli et al., 1999; Peter et al., 2017).

In **Paper IV** of this thesis, I addressed a significant knowledge gap regarding factors that favor toxigenic strains of *Microcystis* in natural populations. We found no support for hypotheses relating to the suggested functions of microcystins, such as predator avoidance or enhanced carbon acquisition under low CO_2 concentrations. This could reflect the extensive ecotypic diversity of *Microcystis* strains (Johansson et al., 2025). Instead, toxigenic strains were positively associated with elevated nitrogen concentrations, likely due to the high nitrogen requirements of microcystins (Harke & Gobler, 2013). Microcystin concentrations themselves, however, were most strongly linked to phosphorus availability and overall *Microcystis* biomass, lending further support to the need for reductions in both nitrogen and phosphorus inputs to lakes as an effective strategy to mitigate toxic cyanobacterial blooms (Paerl et al., 2016).

To summarize, this thesis highlights two major takeaways. First, there is a critical need to expand research on freshwater dinoflagellates, which are currently underrepresented in phytoplankton ecology due to a strong focus on cyanobacterial species. A more comprehensive understanding of dinoflagellate functional traits, which can differ substantially from those of marine species (e.g., toxin production), is essential for improving predictions of phytoplankton dominance and bloom dynamics. Second, benthic life stages must be more explicitly incorporated into our understanding of cyanobacterial blooms. While climate change research has largely focused on pelagic processes, the results from this thesis highlight that sediment recruitment and benthic-pelagic coupling can play a crucial and currently underappreciated role in bloom development. As climate change and extreme weather events lead to phenological shifts and altered stratification regimes in lakes, understanding these benthic processes will be essential for predicting and managing future bloom events.

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II. Rabow, S., Cai, S., Carlsson, P., & Rengefors, K. Earlier spring may explain dominance of the slow-growing dinoflagellate *Naiadinium polonicum* over the cyanobacterium *Microcystis* during a heatwave. *Manuscript*.

III. Rabow, S., Hüller, J., & Rengefors, K. Allelopathy causes rapid decline of *Naiadinium polonicum* in co-culture with *Microcystis*. *Manuscript*.

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