Lake ecosystem responses to climate warming

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What we do know we don't know

is less important than

what we don't know we don't know

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Zusammenfassung

Die drastische Erhöhung der globalen Oberflächentemperatur besonders während der letzten Jahrzehnte ist zu einem bedeutenden Teil anthropogenen Ursprungs, und es besteht wissenschaftlicher Konsens, dass die Klimaerwärmung weiter fortschreiten wird. Da physikalische, chemische und biologische Prozesse in Seen besonders schnell auf Veränderungen in Umweltbedingungen reagieren, ist die Bewertung der Effekte der Klimaerwärmung auf Seeökosysteme ein integraler Bestandteil der limnologischen Forschung, speziell hinsichtlich zu erwartender Erwärmungstrends in den kommenden Jahren und Jahrzehnten. Der Fokus der vorliegenden Arbeit lag auf der Identifizierung von saisonalen strukturellen und funktionellen Veränderungen auf abiotischen sowie biotischen Systemebenen im Müggelsee, einem polymiktischen Flachsee in Berlin, wobei der Schwerpunkt der Untersuchung auf der Sommersaison lag. Besondere Berücksichtigung lag dabei auf der Unterscheidung von klimabedingten Veränderungen und Veränderungen, die durch andere Umweltfaktoren, wie Nährstoffverfügbarkeit, gesteuert wurden.

In einer ersten Studie habe ich den Zeitpunkt und die Art struktureller Langzeitänderungen auf abiotischen und biotischen Systemebenen hinsichtlich der Frage untersucht, ob und welche Änderungsmuster auf den verschiedenen Stufen innerhalb der trophischen Kaskade auftreten und inwiefern diese Muster einer Hierarchie innerhalb des Systems folgen. Dabei lag als Hypothese zugrunde, dass Veränderungen auf unteren Systemebenen eher abrupt auftreten, während das Antwortverhalten höherer Systemebenen gradueller erfolgt. Eine weitere Fragestellung in diesem Kontext war, ob aggregierte Systemebenen (Physik, Nährstofflimitation, Phytoplankton und Zooplankton) erkennbare Veränderungsmuster zeigten und ob diese Veränderungen chronologisch von Physik nach Plankton eintraten sowie ob es hier jahreszeitliche Charakteristika gab. Es konnte keine Hierarchie von Veränderungen auf verschiedenen Systemebenen nachgewiesen werden, die Mehrzahl der Veränderungen war abrupter permanenter Natur, was darauf hindeutet, dass diese Veränderungen von großskaligen klimatischen Oszillationen oder überschrittenen Grenzwerten getrieben wurden. Das Gros der Systemvariablen zeigte keine systematischen Veränderungen, wahrscheinlich als Folge von Kompensationsprozessen auf höheren trophischen

bzw. stärker aggregierten Systemebenen, als Ergebnis simultan wirkender Effekte von Erwärmung und klimaunabhängigen Veränderungen im Trophiegrad. Dennoch haben sich die komplexen Veränderungen auf den verschiedenen Systemebenen in deutlichen und chronologischen Änderungen auf Ebene der Systemkomponenten manifestiert, von Änderungen auf physikalischer Ebene über Phyto- zu Zooplankton. Der Zeitpunkt und die Höhe dieser Veränderungen differierte klar zwischen Frühling und Sommer, sehr deutlich zeigte sich z.B., dass sich die Erwärmungstrends im Frühjahr etwa vier Jahre früher als im Sommer in der physikalischen Systemkomponente niederschlugen. Weiterhin manifestierte sich die Veränderung in der Nährstoffkomponente im Sommer im Jahre 1990, zwei Jahre früher als die Veränderung in der physikalischen Komponente, was im Gegensatz zum Frühjahr zu einem Versatz der Chronologie von Physik zu Nährstoffen geführt hat.

Um die Auswirkungen der Sommererwärmung, speziell über verstärkte thermische Schichtung, auf verschiedene Eigenschaften der Planktongemeinschaft zu untersuchen, habe ich die Entwicklung von Diversität, Biomasse und Artenzusammensetzung der Hauptgruppen des Phyto- und Zooplanktons im Verlauf langlebiger Schichtung (mehrere Wochen) gegenüber lang andauernder Durchmischung untersucht. Es konnte gezeigt werden, dass thermophile Arten der cyclopoiden Copepoden direkt durch höhere Wassertemperaturen befördert wurden, während Cyanobakterien indirekt von einer stabilen Schichtung profitierten. Demgegenüber sind Diatomeen direkt durch hohe Wassertemperaturen und indirekt durch Sedimentationsverluste aufgrund fehlender Durchmischung während längerer Schichtungsperioden benachteiligt. Die Diversität des Planktons zeigt allerdings kaum klimagetriebene Veränderungen, jedoch die Zusammensetzung der Planktongemeinschaft, was darauf schließen lässt, dass die Diversität noch nicht sehr stark durch Klimaveränderungen beeinträchtigt ist, die strukturelle Position eines bestimmten Artensatzes jedoch durch andere Arten, die besser an hohe Temperaturen und stabile Bedingungen angepasst sind, eingenommen werden kann. Die funktionelle Rolle einer veränderten Artenzusammensetzung kann jedoch substantiell differieren, wie z.B. die Verschiebung zu erhöhter N-Fixierung innerhalb des Systems mit zunehmender Schichtungslänge, hervorgerufen durch die Ersetzung von nicht N-fixierendem Phytoplankton durch N-fixierende Blaualgen.

Das vermehrte Auftreten von Blaualgenblüten während der letzten Jahre wird verstärkt der Klimaerwärmung zugeschrieben. Um die hypothetische Verbindung zwischen Klimaerwärmung und Blaualgenblüten im Sommer zu verifizieren, habe ich die für die Blaualgenentwicklung während thermischer Schichtung bestimmenden Faktoren ermittelt und hierbei den Klima- vom Nährstoffeffekt separiert. Die absolute Phosphorkonzentration war der Haupttreiber für die Dominanz von Blaualgen, jedoch konnte gezeigt werden, dass der indirekte Klimaeffekt über stabile Schichtung, und nicht der direkte Temperatureffekt, die Dominanz von Blaualgen förderten. Eine Schichtungslänge von > drei Wochen bzw. eine Stabilität der Wassersäule > 44 g cm cm^{-2} führten zu einer deutlichen Zunahme des Anteils der Blaualgen an der Gesamtbiomasse innerhalb eines kritischen Bereichs der TP-Konzentration (70 bis 215 μg L^{-1}). Diese Studie ist die erste quantitative Bewertung von Nährstoff- und klimarelevanten Schwellwerten für das Auftreten von Blaulalgenblüten.

Die Klimaerwärmung hat zu einer Reihe von Veränderungen auf verschiedenen Ebenen des betrachteten Systems geführt. Am deutlichsten zeigte sich der Klimaeffekt in der erhöhten Ausbildung langlebiger Schichtungsereignisse im Sommer, ein Trend, der sich in den nächsten Jahren aufgrund der fortschreitenden Klimaerwärmung sehr wahrscheinlich noch verstärken und die physikalischen Eigenschaften im See prägen wird. Es konnte klar gezeigt werden, dass diese Änderungen auf der physikalischen Systemebene substantielle Veränderungen auf höheren trophischen Ebenen bewirkt haben. Trotz dieser zum Teil sehr deutlichen Änderungen scheint die Diversität des Planktons (noch) nicht sehr stark beeinträchtigt zu sein. Dieser Umstand wird getragen durch substantielle Veränderungen in der Artenzusammensetzung hin zu Arten, die an warme und stabile Bedingungen angepasst sind. Hierzu zählen N-fixierende und zum Teil toxische Blaualgen, die in ihrer Bedeutung sehr wahrscheinlich zunehmen und dadurch die Funktionalität innerhalb des Systems zu erhöhter N-Fixierung und Toxinproduktion verschieben werden.

Neben klimatischen Änderungen werden Seen zusätzlich stark beeinflusst durch die Bedingungen und Ereignisse, die innerhalb des Einzugsgebietes auftreten. Urbanisierung oder verstärkte Landnutzung können zum Eintrag von chemischen Kontaminanten und so zu Veränderungen im Trophiegrad führen. Die mannigfaltigen Einflüsse auf Seen können sich abschwächen oder gegenseitig potenzieren, aber

auch unabhängig voneinander wirken. Die gemeinsame Wirkung verschiedener Effekte kann dabei zeitlich variieren und hängt wesentlich vom Arteninventar ab. Die gefundenen Wirkungen korrekt den möglichen Ursachen zuzuordnen, ist in diesem Zusammenhang von fundamentaler Bedeutung. Zusätzlich sollte der Bestimmung von Schwellwerten, deren Überschreiten substantielle und möglicherweise unumkehrbare Verschiebungen im System zur Folge haben kann, verstärkt Forschungspotenzial gewidmet werden, denn dies ist möglich und hinsichtlich potenzieller Managementoptionen nötig, um unerwünschte Veränderungen im System im Voraus zu erkennen und zu vermeiden.

Summary

Data collected over the last few decades indicate that average global surface temperatures have been steadily rising, a trend that has been associated, to a large degree, with the emission of greenhouse gases into the atmosphere. Physical, chemical and biological processes of lakes have been shown to be particularly vulnerable to changing environmental conditions. Evaluating the effects of climate change on lake ecosystems, therefore, is an integral component of limnological research, especially with respect to concerns about significant warming that may occur in the future. Specifically, this study focused on identifying climate-induced structural and functional changes within the abiotic and biotic system levels of Müggelsee, a shallow polymictic lake in Berlin. The goal of this study was to differentiate between climate-driven changes and those that are triggered through other factors, such as nutrient availability, with emphasis on the summer situation.

In an initial study, I determined the timing and type of abiotic and biotic changes that occurred in the spring and summer, assuming that lower system levels are going to respond sooner and more abruptly than higher system levels and that there is a hierarchy of those changes across the food chain. Moreover, I assessed the change patterns of aggregated system components (physics, nutrient limitation, phytoplankton and zooplankton), expecting that measurable biotic changes would follow, chronologically, changes at the abiotic level. No hierarchical response pattern with increasing system level was detected, however, abrupt permanent changes were the most prominent response pattern observed, suggesting they may be driven by large scale climatic oscillations and by surpassed thresholds. Moreover, the majority of time series did not display any long-term trend, pointing to compensation processes among higher trophic levels and higher levels of aggregation resulting from, e.g., simultaneously acting forces of warming trends and climate-independent changes in trophic state. Nevertheless, the complexity of response patterns at the single system level manifested clear chronological regime shifts for aggregated system components, from abiotic to biotic in spring and summer. The timing and magnitude of those changes differed, however, substantially between seasons. Lake warming trends during the spring, for example, were detected four years earlier than similar patterns in the summer. Moreover, contrary to spring, the nutrient effect in summer, evident in 1990, preceded the warming effect by two years, offsetting the chronology from physics to nutrients.

To analyze the effects of summer warming and, in particular, enhanced thermal stratification, on plankton community properties such as diversity and biomass, I examined the temporal evolution of phytoplankton and zooplankton community properties as well as community composition over an extended period of time (several weeks), during which the lake demonstrated continuous thermal stratification or water column mixing, respectively. Data indicate that thermophilic cyclopoid copepods benefited directly from higher water temperatures, whereas cyanobacteria were indirectly favored by stable, stratified conditions. Conversely, diatoms were less well adapted to conditions during stratification, and were discouraged both directly by higher water temperatures and indirectly by sinking losses when the water was not as well mixed. While there was no strong pattern of plankton diversity response to warming, large shifts in plankton biomass and community composition were identified. These results suggest that diversity is not (yet) strongly affected by recent warming patterns, providing compelling evidence that the structural role of any particular set of affected species can be assumed by a different species assemblage that is well adapted to higher temperatures and stratified conditions. However, the functional role of an altered species assemblage may differ substantially, like e. g., the observed shift towards nitrogen(N)-fixation within the system with increasing length of thermal stratification, mediated through the replacement of non N-fixing phytoplankton by N-fixing cyanobacteria species.

Finally, I quantitatively investigated the hypothetical link between climate and cyanobacteria bloom formation during the summer. The focus of this study was to identify major determinants of cyanobacteria performance during periods of thermal stratification, and to distinguish climate- from nutrient-driven forces. Although total phosphorus (TP) concentration was the principal force driving cyanobacteria contribution to total algal mass, climate induced changes in the thermal regime, rather than direct temperature effects, positively influenced cyanobacteria dominance. Stratification periods exceeding three weeks and exhibiting a Schmidt stability > 44 g cm cm^{-2} favored cyanobacteria proliferation within a critical TP concentration range (70 to 215 μg L^{-1}). This study provides the first quantitative

assessment of nutrient- and climate-related thresholds for the occurrence of cyanobacteria blooms.

Climate warming has caused substantial structural shifts in the lake ecosystem. The most striking effect was on the lake's physical environment, with an increase in the length of time the lake is thermally stratified during the summer. Continued warming of the climate will further enhance periods of summer stratification and profoundly alter the abiotic characteristics of the lake. The data showed that these changes at the abiotic level were manifested across multiple trophic levels. Despite these significant and measurable changes, overall diversity of the lake plankton community does not seem to be strongly affected. The lack of substantive shifts in the diversity measurements are probably due to the effective replacement of historically dominant species by those adapted to warmer and more stable conditions. However, anticipated changes in community composition towards increasing importance of N-fixing and/ or toxin-producing cyanobacteria during the summer may shift functional lake properties towards accelerated N-fixation and higher toxin-production. By their very nature, lakes are highly influenced by conditions and events within their watershed, or catchment. Urbanization or the expansion of agriculture can lead to the influx of chemical contaminants and a higher nutrient load, which can influence the lake's trophic status. The various influences on a lake system may be additive, antagonistic or simply independent of each other. Which action will occur can shift with time and may be affected by the particular species that are present. It is clear that abiotic and biotic lake functions are complex and the impact of anthropogenic factors on those functions is not easily defined, particularly under current climatic conditions. However, we have reached a quantitative level in climate impact research by actually being able to define critical thresholds of climate-driven forces for cyanobacteria dominance in summer. Further limnological research should thus focus on the distinction between various effects, and the determination of effects thresholds, beyond which significant and potentially irrevocable changes are likely to occur. By developing a more thorough, quantitative understanding of these factors, it may be possible to make accurate predictions of future trends under given climatic scenarios, and implement warning systems along with reasonable and effective mitigation steps to counter undesirable systemic alterations.

1. General Introduction

Climate change

The preconditions for Earth's climate are determined by the planet's position relative to the sun, that is, inclination of the axis (obliquity), shape of the orbit (eccentricity) and direction of the axis tilt (precession). All of these cycles slowly change on different temporal scales, ranging from (approximately) 23,000 years (precession), to 41,000 years (obliquity), to 100,000 years (eccentricity). The position of our planet within this so-called Milankovitch cycle is the key factor that determines the amount of solar energy impinging upon earth's upper atmosphere at any given time (Milankovitch 1948). Currently, the Earth is in the cooling phase of a Milankovitch cycle, which should naturally result in a decline in global temperatures (Firth and Fisher 1992). A growing body of evidence indicates that this is not the case. The disparity between predicted and actual temperature trends is due to changes in albedo (primarily controlled through the proportion of cloud cover) and alterations in longwave radiation back into space (affected by the concentration of greenhouse gases). The average global temperature has shown a documented increase by about 0.7°C between 1906 and 2005, with all years since 1997 being the warmest on record (Trenberth et al. 2007); an additional increase of about 1.8°C to 4°C is predicted by the end of this century (Meehl et al. 2007).

Changes on a global scale, including biological and climatic, typically occur at a relatively slow pace over many years or decades, making it difficult to document significant shifts, but even harder to convince decision-making governmental bodies, and the general populace, that the changes are real. Recently, however, climatic regime shifts, that is, abrupt and sustained changes of the climatic system (Scheffer and Carpenter 2003), have occurred in the mid 1970s and the late 1980s. These shifts corresponded to an abrupt increase in measured air temperatures in the northern hemisphere and occurred simultaneously over a large spatial scale (Hare and Mantua 2000; Hurrell et al. 2001).

Climate-induced changes to a lake's physical characteristics

Ice cover in winter and thermal stratification in summer are the primary lake properties that determine the intrinsic physical conditions for abiotic and biotic lake processes (Hutchinson 1957; Wetzel 2001). The timing and intensity of these lake conditions were affected, on a large scale, by climate. Higher atmospheric temperatures reduced the ice cover on temperate lakes in the northern hemisphere (Weyhenmeyer et al. 2004; Magnuson et al. 2006; Blenckner et al. 2007). This sequence of events was synchronized by large-scale climatic fluctuations, like the North Atlantic Oscillation (NAO) (Gerten and Adrian 2002a; Blenckner et al. 2007). Increases in summer water temperatures have been documented (Adrian et al. 2006; Austin and Colman 2007) along with prolongation (Livingstone 2003; Winder and Schindler 2004) and intensification of summer thermal stratification (King et al. 1997). The timing and magnitude of warming trends differed between seasons, winter/ spring warming preceded summer warming in large parts of Europe (Gerten and Adrian 2000; Adrian et al. 2006; Blenckner et al. 2007).

Recent studies indicate that climate change may cause lakes to alter their mixing status, transforming dimictic lakes to monomictic if ice cover is reduced, or polymictic lakes to monomictic, if the period of summer stratification is extended and insufficient energy is available to induce turnover (Kirillin 2003; Boehrer and Schultze 2008; Livingstone 2008).

Changes in trophic status

In addition to climate change, lakes can experience other environmental perturbations that are often triggered, or exacerbated, by human activity; this includes eutrophication (Wetzel 2001; Smith and Schindler 2009). During the 1960s and 1970s vastly expanded use of chemical fertilizers to enhance agricultural production, combined with few controls on point and nonpoint source runoff, led to significantly altered trophic conditions in many lakes, resulting in eutrophic, and hypertrophic, conditions (Schindler 1977; Edmondson 1993). Recognition of the detrimental impacts of uncontrolled nutrient inputs has resulted in beneficial restoration efforts in recent decades that have improved the trophic conditions of many waterbodies (Sas 1989; Jeppesen et al. 2007b; Søndergaard et al. 2007). Reduction in nutrient load has led to lower nutrient lake concentrations (Anneville et al. 2005; Jeppesen et al. 2005; Jeppesen et al. 2007b) which, in turn, reduced phytoplankton biomass (Willen 1992; Jeppesen et al. 2005; Köhler et al. 2005), with subsequent impacts on zooplankton through changes in food availability (Brett et al. 2000; Dickman et al. 2008; Van Donk et al. 2008).

Effects of warming on plankton communities

The effects of winter and spring warming on plankton phenology and biomass in the spring have been studied in some detail (reviewed by Gerten and Adrian 2002a; Blenckner et al. 2007). Earlier occurrence and expansion of phytoplankton populations has been reported (Adrian et al. 1999; Weyhenmeyer et al. 1999; Peeters et al. 2007), as has the associated advanced spring dynamics of daphnid communities (Straile and Adrian 2000; Winder and Schindler 2004; Blenckner et al. 2007). These changes from historical conditions have been attributed to large scale climatic fluctuations (Gerten and Adrian 2002a; Blenckner et al. 2007). By contrast, plankton communities did not show comparable patterns of synchronous and coherent response to warming trends during the summer season (Adrian et al. 2006; Blenckner et al. 2007). However, some general tendencies of shifts in plankton communities during the summer have been observed within the last years and decades. Recently, cyanobacteria blooms in summer have received attention as numerous reports have documented their more frequent occurrence (Mooij et al. 2005; Guo 2007; Jacoby and Kann 2007), giving rise to the assumption that the taxonomic group may benefit from higher temperatures (Jöhnk et al. 2008; Paerl and Huisman 2008). Furthermore, there is already evidence that the strength of thermal stratification can alter the community composition of phytoplankton towards small-sized phytoplankton species and species able to perform buoyancy (Strecker et al. 2004; Rühland et al. 2008; Winder and Hunter 2008). Global warming may affect phytoplankton directly by increased temperatures or indirectly via prolongation of thermal stratification, depending on the physiological demands of individual taxa (Paerl 1988a; Reynolds et al. 2002). Summer crustacean communities are generally dominated by slow-growing species with complex and longer life-cycles that exhibit species-specific responses to environmental stimuli (Adrian et al. 2006; Blenckner et al. 2007). Studies have shown that, during the summer, some species of copepods responded directly to higher temperatures by earlier occurrence in the pelagic phase, later onset of diapause, an increase in abundance or a combination of one or more of these phenomena (Gerten and Adrian 2002b; Adrian et al. 2006; Seebens et al. 2007). Such responses are not necessarily restricted to a single lake, but are widespread within a geographic region (Blenckner et al. 2007). Climate warming may also influence lake functioning by altering diversity, e.g., by invasion (Holzapfel and Vinebrooke 2005; Rahel and Olden 2008) or extinction (McIntyre et al. 2007). Despite those data that indicate these climate-induced modifications of lentic biological communities are occurring, little is known about the quantitative relationships between the effects of changing climate and biological diversity in lake ecosystems (MA 2005). A recent study by Burgmer et al. (2007) did not find evidence for climate induced changes in diversity of macrozoobenthos communities in several Swedish lakes and McKee et al. (2002) reported little to no effects of warming on diversity and abundance of cladocerans and copepods in well-mixed microcosms.

Thesis outline

In this thesis, I investigated how, and to what extent, warming of the climate altered structural and functional lake properties during the spring and particularly during the summer. All studies were based on decadal long-term records (1980 – 2007) of Müggelsee, a shallow polymictic productive lake in Berlin (Germany). Müggelsee has experienced warming trends of ~0.7°C per decade since 1980 and nutrient load reduction beginning in the early 1990s, a common situation for many north temperate lakes (George et al. 1990; Anneville et al. 2005; Jeppesen et al. 2005). The *in situ* measurements of physical, chemical and biological variables were taken weekly in the summer within the framework of the Müggelsee long-term monitoring program at the Leibniz-Institute of Freshwater Ecology and Inland Fisheries, established in 1979. My approach was to initially generate a systematic and comprehensive overview of the timing and type of long-term changes (1980 – 2004) on all system levels and system components for both the spring and the summer (Chapter 2), to further analyze climate-induced intraannual changes in structure and functioning of the dominating phytoplankton and zooplankton groups (cyanobacteria, diatoms, rotifers, cladocerans, and cyclopoid copepods) during the summer as related to thermal regime (Chapter 3), and, finally, as a specific case study, to assess the particular abiotic and biotic conditions that determine cyanobacteria performance in periods of thermal stratification during the summer (Chapter 4).

The main hypotheses and questions investigated in this thesis were the following:

(1) The timing and type of response of potential long-term change among different system levels occurred in a hierarchy-dependent manner, from rather abrupt changes at the abiotic and the lower trophic levels to more gradual changes at the higher levels. Those changes manifested in chronological shifts of abiotic (physics and nutrients) and biotic (phytoplankton and zooplankton) system components. To test this hypothesis, I determined the timing and type of overall long-term system changes that were occurring for the physical, chemical and planktonic variables, separating the spring and the summer season, in 1980 – 2004 (Chapter 2). According to system theory, changes in physical properties and on plankton species level were expected to respond rather abruptly, while higher trophic levels and higher levels of integration were expected to change rather gradually. Therefore, I assumed an increasing proportion of gradual changes compared to abrupt changes along the trophic cascade, leading from simple to complex organization, and from short to long life cycles. Moreover, shifts in system components were assumed to occur chronologically, from abiotic to biotic system components.

(2) Summer warming significantly changed abiotic lake properties, in particular during extended periods of thermal stratification. Those changes altered phytoplankton and zooplankton diversity and community structure and favored species well adapted to higher water temperatures and more stable, stratified conditions. To address this hypothesis, I tested for climate-induced changes in thermal properties such as higher surface water temperature and prolonged and intensified periods of thermal stratification and subsequent effects on plankton community properties (diversity, biomass and abundance) and community composition, of the major phytoplankton and zooplankton groups, assuming that effects are manifold and operate either directly via accelerated water temperature or indirectly via stable stratified conditions or both (Chapter 3). In particular, I tested the

temporal evolution of all community properties, i. e., diversity, biomass, and abundance, (1) in the long-term (1982 – 2007), and (2) during prolonged periods when the lake was thermally stratified and mixed, respectively, in relation to the length of respective periods. Moreover, I determined abiotic factors that correlated to community properties during stratified and mixed periods.

(3) Increased summer water temperatures and periods of thermal stratification enhanced cyanobacteria bloom formation and off-set the recent reduction in algal mass. I tested this hypothesis by identifying critical abiotic and biotic thresholds relating to performance of the cyanobacteria during the summer, hypothesizing that increased summer temperatures and periods of thermal stratification will enhance cyanobacteria bloom formation and off-set the recent reduction in algal mass (Chapter 4).

2. Exploring lake ecosystems: hierarchy responses to long-term change?

Carola Wagner and Rita Adrian

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Abstract

Shifts in climate regime have provoked substantial trophic- and species-dependent changes within ecosystems. With growing concerns of present global warming, we examined potential lake ecosystem responses, natural hierarchy responses (i.e. immediate responses at lower system levels as opposed to delayed responses at higher system levels), and possible shifts among abiotic (physics, nutrients) and biotic (phytoplankton, zooplankton) system components. Specifically, we analyzed decadal data collected from Müggelsee, a lake in Berlin, Germany, for climate induced abiotic and biotic changes, their timing and type, and classified them as abrupt permanent, gradual permanent, abrupt temporary, or monotonic. We further categorized variable changes as a function of system hierarchy, including lake physics (ice, temperature, stratification), nutrients (phosphorus, nitrogen, silicate), plankton, and levels of integration (i.e. species, taxonomic groups, and total plankton). Contrary to current theory, data suggests abrupt responses did not occur in a hierarchy-dependent manner, nor was a clear pattern observed among functional system based categories. Abrupt permanent changes were the most prominent response pattern observed, suggesting they may be driven by large scale climatic oscillations and by surpassed thresholds, as noted in previous case studies. Gradual changes coincided with affected abiotic parameters spanning an expansive time range; for example, climatic effects in spring preceded changes in nutrient limitation. Variables displaying no long-term changes pointed to compensation processes caused by e.g. simultaneously acting forces of warming trends and climate independent changes in trophic state. Nevertheless, the complexity of response

patterns at the single system level manifested clear chronological regime shifts in abiotic and biotic parameters in spring and, to a lesser extent, in summer. With regard to projected global warming, the majority of currently unaffected system levels may face impending thermal thresholds, achievement of which would result in an accelerated shift in ecosystem state.

2.1. Introduction

Recent climatic regime shifts, in the mid 1970's and late 1980's, were accompanied by changes in the El Niño-Southern Oscillation and North Atlantic Oscillation (Philander 1990; Hurrell et al. 2001), and have induced substantial changes in both aquatic and terrestrial ecosystems (Post and Stenseth 1998; Reid et al. 1998; Ottersen et al. 2001; Gerten and Adrian 2002a; Straile et al. 2003; Edwards and Richardson 2004). The magnitude of response to seasonal warming trends differs among trophic levels and species with different life history strategies, and is dependent on the timing, magnitude, and direction of climate change (Adrian et al. 2006; Blenckner et al. 2007). Change within a single trophic level can cascade throughout the food web via direct interactions, indirect relationships, temporal disparity, and feedback regulation (Cushing 1990; Stenseth and Mysterud 2002; Winder and Schindler 2004; Straile et al. 2007). Furthermore, a latency period of more than a year may exist between climate change and ecosystem response (e.g. Straile et al. 2007).

Given the complexity of relationships within an ecosystem, response to climate change is likely to be multifaceted, trophic level specific, and possibly delayed. Moreover, simultaneous external forces such as changing climate and climate independent improvements in trophic state (Jeppesen et al. 2003), can amplify or circumvent effects (Jeppesen et al. 2005; Matzinger et al. 2007; Wilhelm and Adrian 2007), thus modifying overall ecosystem response (Elliott et al. 2006; Huber et al. 2008).

Despite strong evidence of climate induced response among lake ecosystems, the form of temporal response (gradual vs. abrupt) remains heavily debated. The hierarchy theory, first applied in ecology by Overton (1972, 1974) and Allen and Starr

(1982), postulates that lower levels (i.e. planktonic species in lake ecosystems) respond immediately and adapt quickly to environmental disturbances, such as surpassed temperature and food availability thresholds. Conversely, higher levels, which are constrained and dependent on lower levels, are believed to respond to disturbances slowly and less frequently (Allen et al. 1984). Further, asymmetric interaction between adjacent levels may elicit no to minute changes among higher levels due to compensation processes within the system. Therefore, the responsiveness of higher levels cannot be extrapolated or predicted based on lower level responses (O'Neill 1988; Gaedke et al. 1996; Vasseur and Gaedke 2007).

O'Neill 1988 stated that the configuration of a system may remain stable even if immense changes occur among varying levels. But once the system is disrupted, it is the rapid dynamics of the lower levels that could force the system into a new configuration. This impending transition between stable system states may occur abruptly (Scheffer et al. 2001) or gradually (Walker and Meyers 2004). Numerous studies have been conducted to reveal regime shifts in terrestrial (e.g. Foley et al. 2003; Schmitz et al. 2006), marine (e.g. deYoung et al. 2004; Alheit et al. 2005), and lake ecosystems (Jeppesen et al. 1998; Ibelings et al. 2007). Of note, the term *regime shift* is often used generically, implying a phenomenon rather than a specific mechanism (Scheffer and Carpenter 2003).

To obtain a more comprehensive understanding of long-term system response patterns at singular abiotic and biotic levels, as well as aggregated levels, we investigated hierarchy responses in Müggelsee, a polymictic lake in Berlin, Germany, including lake physics, nutrients, plankton species, taxonomic groups, and total plankton; and we analyzed data collected from 115 temporal series from 1980 to 2004, including surface water temperature, ice formation, thermal stratification events, nutrient limitation, phytoplankton, and zooplankton. Specifically, we questioned the temporal responsiveness of potential long-term change, and hypothesized that physical variable responses would occur rapidly, with more gradual responses among higher trophic levels. Further, we addressed whether regime shifts manifest chronologically in a trophic level dependent manner, and determined the yearly state of different system components (physics, nutrient limitation, phytoplankton, zooplankton) in reference to the long-term mean via the calculated system component state index.

2.2. Material and methods

Study site

Müggelsee, a shallow polymictic and eutrophic lake southeast of Berlin, Germany (52°26´N, 13°39´E) has an average retention time of 40 days. The lake has an approximate area of 7.3 km^2, with maximal and mean depths of 7.9 m and 4.9 m, respectively. Its physical and limnological characteristics have been previously described (Driescher et al. 1993). Over the past three decades the lake has been subject to seasonal warming trends (2.4 K and 2.3 K in spring and summer; Adrian et al. 2006) and decreased nutrient loading beginning in the early 1990s (Köhler et al. 2005).

Physical variables

Surface water temperature was recorded daily between 08:00 and 09:00 h at two different sites during the duration of the study period: (1) at the lake's north shore using an AD590 temperature transducer from January 1980 to June 2002; and (2) at an anchored lake station 300 m from shore using an AD592 temperature transducer from June 2002 to December 2004. Due to different sampling sites, water temperature data collected after June 2002 were transformed based on linear regression ($R^2 = 96\%$) of temperatures measured between July and August 2002. On average, lake station temperatures were 0.1°C below north shore temperatures. Forward movements of annually recurring events have been demonstrated (Adrian et al. 2006), thus data were represented as seasonal mean water temperatures in spring and summer (for definition of seasons see *Phenology*). Additionally, we tested for monthly mean water temperatures in March, April and May (integrated in the physical variables of the spring season) and in June, July, August and September (integrated in the physical variables of the summer season). For pragmatic reason the number of days when the lake was covered with ice (usually between December and April) was integrated in the physical variables of the spring season.

The threshold for lake thermal stratification was set at a difference of 1°C between surface and 5 m depth temperatures. Data were represented as the number of biweeks of summer stratification per year.

Biotic sampling

Sampling of lake biota occurred biweekly between 1980 and 2004. Detailed descriptions of sampling methodologies and processing have been previously reported (Gerten and Adrian 2000). Determination to species level was made for zooplankton over the entire study period; however, such high taxonomic resolution for the phytoplankton was only available after 1994, except for rather conspicuous diatom and cyanobacteria species. Analyses included comparison of mean algal biomass and zooplankton abundance during spring and summer.

Limiting nutrient concentrations

Nutrient concentrations (soluble reactive phosphorus, SRP; total soluble nitrogen including nitrate and nitrite, nitrogen; soluble reactive silicate, SRSi) were measured biweekly from 1980 to 2004. Data exceeding limiting threshold concentrations of 10 µg L^{-1} SRP and 72 µg L^{-1} nitrogen delineated by Köhler et al. (2005), and 500 µg L^{-1} SRSi delineated by Sas (1989) were categorized by sample date and expressed as the number and the percentage of biweeks per season which exhibited nutrient limitation.

Classification of plankton into hierarchical levels

Sampled plankton was classified based on species and taxonomic groups, and analyzed as a function of season (spring and summer; for definition see - *Phenology*). Available data on ciliates are limited to conspicuous species, which were easily identified in the zooplankton samples. Analysis of taxonomic levels, phytoplankton (cyanobacteria, diatoms, cryptophytes, chlorophytes) and zooplankton (daphnids, bosminids, calanoid copepods, cyclopoid copepods), were conducted using biomass and abundance, respectively. Seasonal total algal biomass and abundance of herbivorous cladocerans, copepods, and rotifers represented the inclusive plankton level.

Phenology

Phenological events, cyclical events in nature, were reported as the biweek of occurrence during the year for the following : ice–off date, maximal algal biomass in spring, initiation of the clear-water phase (maximal Secchi depth after the spring algal bloom), maximal daphnid abundance, first appearance of *Dreissena polymorpha* larvae, first appearance of the five summer cyclopoid copepod species (*Acanthocyclops robustus, Diacyclops bicuspidatus, Mesocyclops leuckarti, Thermocyclops crassus, Thermocyclops oithonoides*), maximal abundance of the five summer cyclopoid copepod species. We only chose phenology events that were clearly identifiable.

Since we observed marked changes in the dates of phenological events during spring and summer, as previously reported (Adrian et al. 2006), season onset was standardized according to ice-off (spring) and the clear-water phase (summer, the time of maximal Secchi depth). For years with no ice development (1988 – 1990), the ice-off date was set to biweek 2, the earliest ice-off date in the past 25 years. For years with no clear-water phase (1980, 1988, 1989), the date of lowest diatom biomass before summer was substituted as diatoms substantially declined after the spring peak during all examined years. The end of the summer season was defined as biweek 20 (the end of September) due to lack of a discrete and reliable biotic or abiotic marker.

System variables

To obtain comparable values for seasonal-specific records, the mean of respective variables were calculated based on the standardized season for each year. To determine the type of long-term change we conducted the following steps. (i) The nonparametric Pettitt test (Pettitt 1979) was applied to all time series to detect the most probable year when changes occurred as a preselection measure (significance level was set to 10%). (ii) Type of change was analyzed by applying curve estimations to time series containing significant changes (as defined by the Pettitt test), and estimating the parameters of theoretical models (for full description see Web Appendix 1). We then described two main aspects of the variables' behaviour: persistence (permanent or temporary change) and speed of change (abrupt or gradual; detailed in Web Appendix 1). (iii) The remaining time series, which exhibited no significant year of change, were tested for monotonic trends over the entire study period using the non-parametric rank-based Kendall τ_B correlation coefficient (Helsel and Hirsch 2002). The significance, direction, and strength of the trend were calculated.

System component state indices

Data concerning timing and type of change were aggregated by determining the transient behaviour of abiotic and biotic variables during spring and summer, separately. Abiotic indices comprised water temperature and nutrient limitation time series for both seasons, ice duration and ice–off dates, and number of summer biweeks exhibiting thermal stratification. We performed separate analyses for physical and nutrient time series to track climate vs. nutrient driven components in the system state. Biotic variables included all plankton time series including phenology, as described above. Aggregated phytoplankton and zooplankton variables were analyzed separately. Indices included time series for which no significant long-term trends had been recorded. In total, four system component state indices (physics, nutrient limitation, phytoplankton, zooplankton) were calculated for each season (spring and summer).

The main principle of the system component state index is to standardize all relevant system variables and to determine whether the yearly state of the system component is above or below the long-term mean. As an alternative to the ecosystem state index calculation proposed by Hare and Mantua (2000), we used the standard deviation for the entire period, and determined the long-term trend (Kendall's τ_B) to reverse time series with negative trends. This was necessary, as a specific year for system state shifts was not assumed but subsequently determined using the Pettitt-test as described above (see *System variables*).

2.3. Results

System variables

Of the system variables tested, 37% (42 of 115) showed either a systematic pattern change (28 variables; see Fig. 2.1 for an example of each model fit) or a monotonic long-term trend (14 variables; Fig. 2.2). For a detailed overview of the curve fit and trend analysis output see Table 2-1 and Table 2-2. Table 2-1 and 2 also outline the type and year of change, direction and speed of change, as well as document the complexity of the observed change patterns. Abrupt change was observed in 22 cases (20 permanent, two temporary), whereas gradual fit was adequate for six variables. Trends in physical and nutrient limitation variables were limited to abrupt and monotonic, whereas all types of change were observed for plankton variables (Fig. 2.2). Sixty three percent of the system variables tested displayed no significant changes (lower panel in Fig. 2.2).

Changes in the abiota

All abiotic time series demonstrating significant change followed the abrupt permanent model or a monotonic trend for both spring and summer (Fig. 2.2). Abrupt changes in temperature occurred in spring of 1989, while a trend in summer warming began in 1992, as well as an increase in the number of biweeks the lake was thermally stratified (Table 2-1). All physical time series demonstrating significant changes displayed increasing trends. Silicate limitation vanished abruptly in spring of 1996, whereas Müggelsee was affected by monotonic decreases in phosphorus and increases in nitrogen limitation in summer (Fig. 2.2).

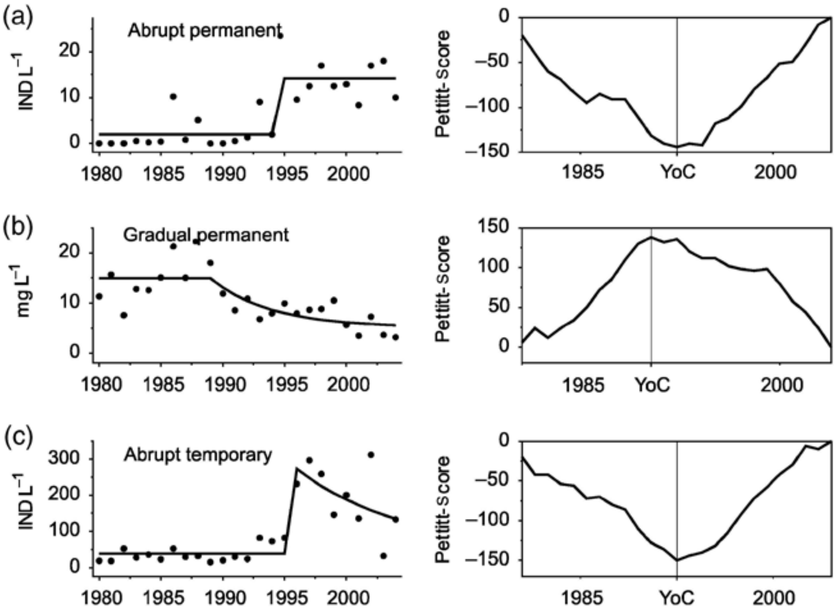

Fig. 2.1: Representative curve estimations: (a) abrupt permanent change (summer peak abundance of *Thermocyclops oithonoides*); (b) gradual permanent change (mean summer total algal biomass); (c) abrupt temporary change (mean summer abundance of *Dreissena polymorpha* larvae). Dots depict observations; lines delineate model predictions. Corresponding plots of the Pettitt statistics over time along with the year of change (YoC) are depicted to the right.

Changes in the biota

Responses of biological variables included all types of change (abrupt permanent, gradual permanent, abrupt temporary, monotonic), and no general pattern or hierarchy was observed. Monotonic changes alone were observed among the phytoplankton species level, whereas abrupt and gradual change patterns were observed among higher hierarchical levels, such as taxonomic groups and total algal biomass (Fig. 2.2). All types of change were observed among zooplankton species, while zooplankton taxonomic groups only displayed abrupt change patterns (Table 2-1, Fig. 2.2) and monotonic trends (Table 2-2, Fig. 2.2). The highest level of zooplankton aggregation only exhibited abrupt changes (Table 2-1, Fig. 2.2), specifically the mean abundance of copepods during summer. The direction of change within the biota was consistent; to illustrate, phytoplankton biomass decreased and abundances of cyclopoid copepods and ciliates increased as a function of time, while, daphnid abundance decreased regardless of season (Table 2-1 and 2).

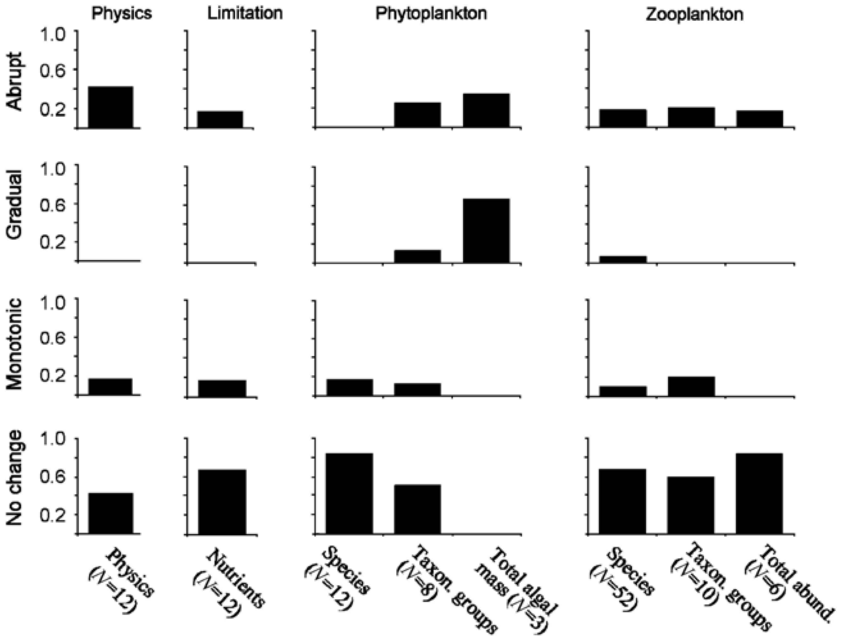

Fig. 2.2: Percentage of system variables that exhibited change among tested variables from the following categories: physics, nutrient limitation, phytoplankton, and zooplankton (number of tested variables in brackets). Physical variables consist of timing of ice-out, ice duration, mean water temperatures in spring, the months March, April, and May for the spring season, and number of biweeks exhibiting thermal stratification, mean water temperatures in summer, the months June, July, August, and September for the summer season. Variables of nutrient limitation consist of number and percentage of biweeks with nutrient limitation for SRP, nitrogen, and SRSi in spring and summer. Plankton variables were subdivided into hierarchy levels. The phytoplankton taxonomic groups (Taxon. groups) consist of cyanobacteria, diatoms, cryptophytes, and chlorophytes in spring and summer. The phytoplankton total biomass level (Total algal mass) consists of mean and peak total biomass in spring and mean total biomass in summer. The zooplankton taxonomic groups (Taxon. groups) consist of daphnids, bosmininds, calanoid copepods, and cyclopoid copepods in spring and summer, timing of daphnids spring peak and daphnids spring peak. Zooplankton total abundance (Total abund.) consists of rotifers, herbivorous cladocerans, and copepods in spring and summer. Based on model fits, the proportion of abrupt change patterns is shown in the upper panel, gradual change patterns in the second panel and monotonic changes in the third panel. Additionally, the lower panel gives the proportion of time series in each category, which exhibited no change. Vertical bars sum up to 1 (100%).

System component state indices

System component states changed abruptly, with the exceptions of phytoplankton in spring and zooplankton in summer that displayed a gradual transition to a new state (Fig. 2.3). All changes in system component state indices were permanent, with the exception of nutrient limitation in spring. In spring of 1988, 1991, and 1995, distinct system component states were separated for physical, phytoplankton, and zooplankton system components, respectively, indicative of the chronological change from abiotic to biotic system components. In summer of 1992, 1990, 1990, and 1990 changes in system component states manifested for physical, nutrient limitation, phytoplankton, and zooplankton system components, respectively (Table 2-1, Fig. 2.3). In this case, the chronology of abiotic components was offset because the timing of external nutrient reduction (in 1990) preceded the climate signal by two years (1992; Table 2-1).

2.4. Discussion

Response latency and response rate of individual components elicited by environmental changes, such as global warming, are critical to proper ecosystem function due to potential loss of inter-level synchrony, for example, predator prey interactions (Cushing 1990; Winder and Schindler 2004). Here we report complex changes at the single system level, as well as the impact of those changes on abiotic and biotic aggregated levels in a lake model, which is subject to global warming and a reduction in external nutrient loading (see *Study site*). Prominent results include that the majority of observed changes were systematic, response diversity at the single system level manifested, however, clear shifts in system component states for abiotic and biotic system components, and chronology was season-dependent. Importantly, 63% of single system variables did not display significant long-term changes.

Hierarchy of change

The majority of changes occurred abruptly; however, changes within the hierarchy were not dependent on level, and showed no clear pattern regardless of method of hierarchy classification, e.g. abiotic/biotic, species, or taxonomic group. Similarly, abrupt permanent responses were prominent among single system levels, as well as aggregated abiotic vs. biotic system component states, suggesting changes were driven by surpassed thresholds or following the well known sudden responses related to large scale climatic oscillations such as the North Atlantic Oscillation (NAO). Using previously reported case studies for Müggelsee (Adrian et al. 2006; Wilhelm and Adrian 2007; Huber et al. 2008) or rivers and marine

Table 2-1: Model fit for time series (1980-2004) with a significant year of change (YoC) (see Appendix 1 for more detail).

			Model type	Direction of change	b_0	b_1	δ	b_1*	R^2
Spring									
System variables									
Mean water temperature in March	1989	0.050	ap	increase	2.7	1.8	-	4.5	36%
Mean water temperature in spring	1989	0.016	ap	increase	8.5	1.6	-	10.1	40%
Number of biweeks with silicate limitation	1996	0.007	ap	decline	1.7	-1.7	-	0	39%
Percentage of biweeks with silicate limitation	1996	0.007	ap	decline	0.29	-0.29	-	0	47%
Mean biomass of cyanobacteria	1991	0.001	gp	decline	2.9	-1.3	0.5	0.2	47%
Mean biomass of cryptophytes	1993	0.015	ap	decline	1.5	-0.7	-	0.8	42%
Mean total algal biomass	1993	0.001	gp	decline	14.4	-4.0	0.6	4.4	64%
Maximal total algal biomass	1993	0.002	ap	decline	28.7	-17.6	-	11.1	50%
Mean abundances of *Codonella cratera*	1991	0.001	ap	increase	339	2700	-	3039	80%
Mean abundances of *Tintinnopsis fluviatile*	1991	0.067	ap	increase	138	201	-	340	30%
Timing of spring peak of *Daphnia galeata*	1992	0.020	at	earlier	11.8	-2.0	0.9	-	44%
Maximal abundances of *Daphnia galeata*	1991	0.001	gp	decline	87.0	-16.2	0.8	1.7	47%
Mean abundances of *Cyclops kolensis*	1994	0.000	gp	increase	0.1	5.2	0.5	9.7	90%
Mean abundances of cyclopoid copepods	1994	0.000	ap	increase	4.2	6.8	-	11.0	64%
System component state indices									
Physics (N=6)	1988	0.003	ap	-	-0.72	1.06	-	0.34	37%
Phytoplankton (N=13)	1991	0.002	gp	-	-0.41	0.25	0.7	0.52	69%
Zooplankton (N=28)	1995	0.001	ap	-	-0.32	0.80	-	0.48	74%
Summer									
System variables									
Mean water temperature in June	1992	0.067	ap	increase	18.0	1.4	-	19.4	29%
Mean water temperature in August	1994	0.032	ap	increase	20.0	2.0	-	22.0	39%
Number of biweeks with thermal stratification	1992	0.037	ap	increase	4.8	2.1	-	6.9	32%
Mean biomass of cyanobacteria	1990	0.006	ap	decline	8.7	-5.5	-	3.2	45%
Mean total algal biomass	1990	0.002	gp	decline	14.9	-1.8	0.8	5.0	60%
Mean abundances of *Codonella cratera*	1992	0.002	ap	increase	60.8	248.5	-	309.3	53%
Mean abundances of *Daphnia galeata*	1994	0.001	gp	decline	27.1	-8.0	0.7	2.0	56%
Mean abundances of *Leptodora kindtii*	1988	0.001	ap	decline	1.4	-1.1	-	0.3	56%
Mean abundances of *Dreissena polymorpha* larvae	1995	0.000	at	increase	37.9	262.4	0.9	-	74%
Timing of first appearance of *Diacyclops bicuspidatus*	1994	0.025	ap	later	10.4	4.0	-	14.4	36%
Mean abundances of *Thermocyclops oithonoides*	1994	0.001	ap	increase	0.6	3.6	-	4.2	72%
Maximal abundances of *Thermocyclops oithonoides*	1994	0.001	ap	increase	2.0	15.2	-	17.2	71%
Mean abundances of daphnids	1992	0.012	ap	decline	66.1	-29.8	-	36.3	32%
Mean abundances of copepods	1988	0.003	ap	increase	139	158	-	297	57%
System component state indices									
Physics (N=6)	1992	0.001	ap	-	-0.45	0.86	-	0.41	31%
Nutrient limitation (N=6)	1990	0.077	ap	-	-0.47	0.79	-	0.32	31%
Phytoplankton (N=10)	1990	0.007	ap	-	-0.44	1.24	-	0.80	73%
Zooplankton (N=40)	1990	0.001	gp	-	-0.35	0.23	0.7	0.35	80%

Variables are categorized in terms of hierarchy (physics → nutrients → phytoplankton → zooplankton). Fitted models are: ap=abrupt permanent change; gp=gradual permanent change; at=abrupt temporary change. Significance (p) refers to the Pettitt-test. Model parameters are: b_0=the mean level in sub-period 1; b_1=the level shift at t_0 due to the model fit; b_1*= the (asymptotic) mean level in sub-period 2; δ = speed of adaptation for gradual and temporary model fit; R^2= explained variance.

ecosystems (e.g. Hari et al. 2006; Pörtner and Knust 2007), we identified a number of thresholds, including those for temperature, initiating zooplankton growth (Gerten and Adrian 2000; Winder and Schindler 2004; Adrian et al. 2006; Wilhelm and Adrian 2007), air temperature and wind speed, initiating spring algal growth (Peeters et al. 2007), oxygen (Pörtner and Knust 2007; Wilhelm and Adrian 2008), timing of nutrient limitation versus predation pressure (Elliott et al. 2006; Huber et al. 2008), initiation of thermal stratification (Schindler et al. 1990; Peeters et al. 2007) and its associated length and frequency which initiate nutrient pulses (Wilhelm and Adrian 2008).

Table 2-2: Trend statistics for time series (1980-2004) that displayed continuous monotonic trends according to Kendall's τ_B.

Spring	τ_B	p<
Mean water temperature in May	0.391	0.006
Mean biomass of *Limnothrix redekii*	-0.684	0.000
Maximal abundances of *Daphnia cucullata*	-0.310	0.035
Mean abundances of *Leptodora kindtii*	-0.352	0.027
Mean abundances of *Eudiaptomus graciloides*	0.441	0.003
Mean abundances of calanoid copepods	0.307	0.032
Mean abundances of copepods	0.293	0.040
Summer		
Mean water temperature in summer	0.305	0.033
Percentage of biweeks with SRP limitation	-0.358	0.016
Number of biweeks with nitrogen limitation	0.328	0.032
Mean biomass of *Limnothrix redekii*	-0.603	0.000
Mean biomass of diatoms	-0.441	0.002
Mean abundances of *Tintinnopsis fluviatile*	0.420	0.003
Mean abundances of *Eudiaptomus graciloides*	0.370	0.010

Significance was calculated as a two-sided p-value. Time series are sorted by season and system level in ascending order.

Besides these threshold driven changes ecosystem responses over large parts of Europe have been related to regime shifts in the climate associated with changes in the NAO (Hurrell et al. 2001). Prominent abrupt changes in e.g. ice phenology or the spring plankton phenology basically followed the abrupt changes in the NAO in the late 1980s (Weyhenmeyer et al. 1999; Gerten and Adrian 2000; Livingstone 2000; Temnerud and Weyhenmeyer 2008; see also the 1988 abrupt shift in the spring physical system component in Fig. 2.3). As such, they were found to be coherent across a wide range of European lakes (Straile and Adrian 2000; Blenckner et al. 2007). Those NAO driven abrupt shifts are also well known for marine (e.g. Edwards and Richardson 2004; Alheit et al. 2005) and terrestrial ecosystems (e.g. Menzel et al. 2005).

Species and taxonomic groups

Limnothrix redekii was the only phytoplankton species analyzed (comprised at maximum 36% of spring and 4.4% of summer total algal mass on long-term average), which displayed a significant monotonic change. The observed decrease in *L. redekii* biomass coincided with a switch from a phosphorus to a nitrogen limiting system during summer. *L. redekii,* a non-nitrogen fixing species, was replaced by N_2-fixing species (Köhler et al. 2005). Abrupt, gradual, and monotonic responses were observed at the algal taxonomic group level. Decline in the mean seasonal total algal mass exhibited a gradual response pattern during spring and summer, congruent with the broad temporal range of changing abiotic forces and internal counteracting effects. To illustrate, in spring temperature increase (1989) preceded silicate limitation by seven years (1996); in summer, reduction in external nutrient loading (1990) preceded the climate signal by 2-4 years; moreover, the decline in external phosphorus load was counteracted by internal phosphorus releases from anaerobic sediments due to an increase in the thermal stratification period two years prior (Wilhelm and Adrian 2008; see also below). Interestingly, decline in mean summer total algal biomass preceded the spring decline by three years, suggesting seasonal specific responses to changes in the catchment, warming trends, and internal feedback; or seasonal specific plankton communities differ in their response to environmental forces (Adrian et al. 2006; Blenckner et al. 2007).

Crustacean zooplankton species were more threshold-driven than rotifers, as significant changes were only observed on the species level for the crustacean community and *Dreissena polymorpha*. Based on previous reports, observed changes within the zooplankton species level were related to temperature driven phenology shifts (*Daphnia galeata, Diacyclops bicuspidatus*), increase in thermophilic species (*Thermocyclops oithonoides*), or surpassed temperature and oxygen thresholds (e.g. *Dreissena polymorpha* larvae) (Gerten and Adrian 2000; Gerten and Adrian 2002a; Adrian et al. 2006; Wilhelm and Adrian 2007). The general increase in copepods and the decline in daphnids are in line with the prominence of copepods in less productive lakes, as Müggelsee has shifted from a hypereutrophic to a eutrophic state, although mechanisms remain undetermined.

Time series displaying no change

In climate impact research, we usually focus on observed changes but do not mention system variables, which show no response to the known changes in the climate. Also, climate induced changes often overlap with other environmental changes such as eutrophication (Jeppesen et al. 2003) or acidification (Schindler et al. 1996), influencing overall ecological responses (Huber et al. 2008). In our case study lake (Müggelsee), which was both imposed to strong changes in the climate as well as to an improvement in trophic state (Köhler et al. 2005; Huber et al. 2008) 63 % of the studied variables, spanning all system levels, showed no significant change (Fig. 2.2). Variables, which show no responses in a system, which otherwise exhibits huge changes, give indications for compensation processes in the ecosystem. Those can derive from counteracting effects of positively and negatively temperature driven effects itself or compensation due to multiple environmental forces. An example of compensating temperature effects has been observed for *Dreissena polymorpha*. Positive effects of an earlier reach of critical temperature thresholds for the first spawning event of *Dreissena polymorpha* - resulting in a longer spawning season – can be counteracted by an enhancement of temperature driven anoxia during summer, negatively affecting survivorship of the adult mussels (Wilhelm and Adrian 2007). Climate change has been argued to counteract effects of re-oligotrophication (Wilhelm and Adrian 2008). To illustrate - the trophic state induced decrease in the magnitude of algal mass in the early 1990s in Müggelsee (Köhler et al. 2005) was counteracted by climate induced increases in internal nutrient pulses, causing short term algal blooms of mostly cyanobacteria (Wilhelm and Adrian 2008). The reduction in total phosphorus and total nitrogen loading in the early 1990s resulted in an immediate decline in the total nitrogen concentrations in the lake, whereas the lake sediments acted as a net phosphorus source under warming induced anoxic conditions – causing the switch from phosphorus toward nitrogen limitation (Table 2-2; Köhler et al. 2005) - leaving the system with a sustained limitation situation. Those nitrogen depleted conditions during summer have been shown to be on the increase in shallow northern European lakes due to changes in external nitrogen loading, including nitrogen deposition, and by changes in the climate (Weyhenmeyer et al. 2007). Within the plankton community, the loss of summer daphnids may to some extent be compensated for by the rise in calanoid as well as cyclopoid copepods (Table 2-2). Finally, extreme events such as heat waves may induce a collapse of one species (e.g. *Dreissena polymorpha*; Wilhelm and Adrian 2007) but favour other species (e.g. cyanobacteria; Jöhnk et al. 2008) in particular years. The long lasting effects of those climate driven extreme events for population development or compensation processes in subsequent years are hardly understood. In that respect, extreme events provide an opportunity to test the sensitivity of lake ecosystems under future climate scenarios and to define critical thresholds beyond which abrupt changes are to be expected (Jankowski et al. 2006; Mouthon and Daufresne 2006; Wilhelm and Adrian 2007).

Chronology of shifts in system component states

While there is no evidence of a hierarchy of change among single system levels, system component state indices provided strong evidence of chronological changes, abiota → biota → trophic level (phytoplankton/ zooplankton), in spring and to a lesser extent in summer. The physical system component shifted abruptly in spring 1988, coinciding with the climatic regime shift synchronized by the NAO (Hurrell et al. 2001), as has been observed in numerous aquatic (Blenckner et al. 2007) and terrestrial ecosystems (for review see Visser and Both 2005), e.g. water temperature and ice formation in freshwater systems across Europe exhibited coherent abrupt changes in the late 1980s (Weyhenmeyer et al. 1999; Gerten and Adrian 2000; Livingstone 2000; Weyhenmeyer et al. 2004; Hari et al. 2006). The reduction in external nutrient supply (1990) occurred two years after the climatic signal (Köhler et al. 2005) and the immediate manifestation of an increase in the number of nutrient

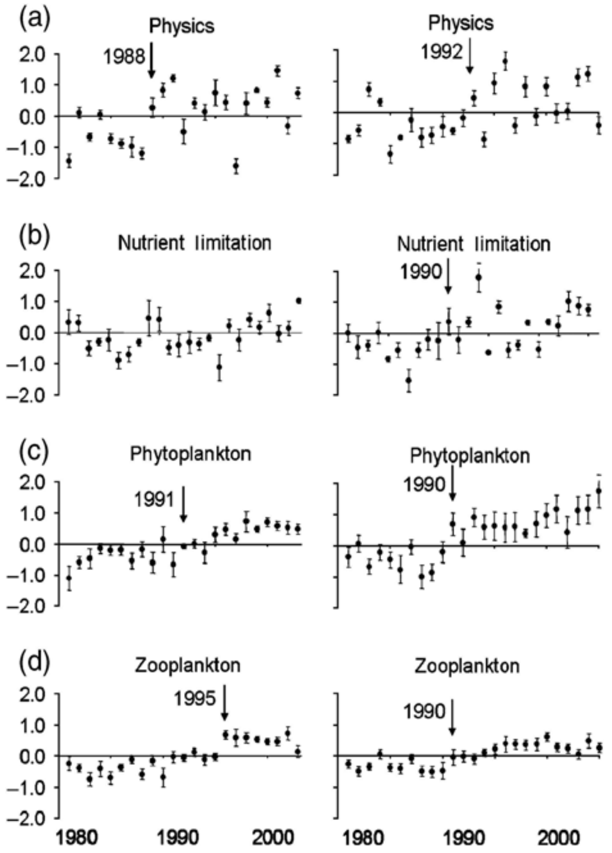

Fig. 2.3: System component state indices for lake physics (temperature, ice, stratification), nutrient limitation (SRP, nitrogen, SRSi), phytoplankton (species, taxonomic groups, total algal mass), and zooplankton (species, taxonomic groups, higher aggregated levels such as rotifers, copepods and herbivorous cladocerans) in spring (left column) and summer (right column). The system component state index refers to yearly means and standard errors. Arrows indicate the year when shifts in the system component state were initiated. SRP, soluble reactive phosphorus; SRSi, soluble reactive silicate.

limiting weeks in summer but not spring. A chronological alteration in functional hierarchy was observed when the spring nutrient effect (1990) preceded the summer warming effect (1992), offsetting the chronology from physics to nutrients. The system component state index for nutrient limitation exhibited high interannual variability in its long-term change pattern during both seasons, as nutrient limitation in Müggelsee switched from predominately phosphorus to nitrogen limitation (Table 2-2), silicate limitation was irrelevant after 1996 (Huber et al. 2008), and internal nutrient loading increased with stratified periods beginning in summer 1992. The abrupt decline in summer algal mass was potentially initiated by changes in trophic state (1990), since predominate herbivores (daphnids) declined abruptly in the summer of 1992, and copepod abundance remained static until 1994 (Table 2-1). In spring, strong climate induced shifts in phytoplankton phenology (1979-1987 vs. 1988-1998) (Adrian et al. 1999; Gerten and Adrian 2000) were later influenced by changes in trophic state (1994-2005) (Huber et al. 2008), buttressing the gradual change displayed by spring phytoplankton. Summer zooplankton displayed a gradual change synchronous with the phytoplanktonic change, with a transition period of four years wherein summer warming was established. Moreover, the influence of spring warming on copepod species is well documented (Gerten and Adrian 2000; Adrian et al. 2006), and probably contributed to the gradual change.

Interestingly, shifts in biota were more apparent and persistent compared to abiota, potentially due to response latency periods associated with warming trends (with the exception of the established immediate climate induced changes in plankton phenology; Weyhenmeyer et al. 1999; Gerten and Adrian 2000; Straile 2000). Causes of latency response among biota are numerous and include, pools of resting stages; species specific life history traits such as generation time, age, timing of spawning (Straile et al. 2007); and redundant functionality among species. Conversely, physical system components are less stable, driven by interannual variability associated with the temporal progression of warming trends or extreme events. To illustrate, the abiotic spring system component index was lowest in 1996, a year with a long ice cover period, and the summer index was highest in 1995 and 2003, years with heat waves. In contrast, biotic indices generally stayed above the long-term mean once they had shifted to a new regime. However, it is important to note that a portion of the aforementioned differences may be attributable to the different number of variables constituting aggregated abiotic and biotic indices.

Coherent vs. site-specific responses

The question whether the observed changes in Müggelsee are part of a more general pattern or site-specific turned out to be highly dependent on system level and season. Surface water temperature rises and changes in ice and spring plankton phenology are by far the most coherent responses of lake ecosystems toward climate warming world wide (Weyhenmeyer et al. 1999; Gerten and Adrian 2000; Livingstone 2000; Livingstone 2003; Magnuson et al. 2000; Straile et al. 2003; Arhonditsis et al. 2004; Winder and Schindler 2004; Coats et al. 2006; Austin and Colman 2007).

Nevertheless, Weyhenmeyer et al. (2004) report non-linear responses of lake ice break-up dates along a longitudinal gradient in Swedish lakes and Livingstone et al. (2005) point to altitude dependent differences in lake surface water temperature responses in lakes in the Swiss Alps. The observed increase in thermally stratified conditions during summer in Müggelsee (Table 2-1) is, however, very likely a generally found pattern of change for polymictic shallow lakes of the northern hemisphere. Although the observed changes in nutrient dynamics were highly affected by changes in the catchment, and are thus rather lake specific, nitrogen limitation seems to become a more general phenomenon in shallow lakes in the context of global warming (see also discussion above; Weyhenmeyer et al. 2007).

Contrary to lake physics, climate induced changes in the biota have been shown to be less coherent; the strength in coherence generally declines from physical variables up the food web (Blenckner and Hillebrand 2002). Moreover, individual trophic levels and species with differing life history traits are known to react differently (Adrian et al. 2006; Blenckner et al. 2007). Nevertheless, the observed rise in cyclopoid copepods in Müggelsee is in line with findings in other European lakes; overlapping forces of changes in the climate and improvements in trophic state were most likely underlying mechanisms for those coherent responses (Straile and Geller 1998; Blenckner et al. 2007).

Coherence in climate induced changes can be hampered by the fact that there are other anthropogenically induced environmental changes influencing ecological response variables such as re-oligotrophication. Well known examples are the decrease of e.g. phytoplankton biomass as a result of reduced nutrient loads in Lake Washington (Edmondson 1991) or Lake Constance (Sommer et al. 1993). As the temporal overlap between climate change and restoration efforts are site specific, the overlapping effects of these multiple forces are rather system specific (Straile 2000; Winder and Schindler 2004; Elliott et al. 2006; Huber et al. 2008). A more recent observation, however, is the increase in the frequency of cyanobacteria blooms in the context of global warming, which is predicted to become more intense under future climate scenarios (e.g. Jöhnk et al. 2008) and may thus become a coherent response in many productive lake ecosystems. Indeed, a recent study of our case study lake confirms these findings. Climate induced increases in the frequency and duration of thermally stratified events during summer in Müggelsee (Table 2-1) positively influenced the dominance of cyanobacteria (Wagner and Adrian 2009b). Cyanobacteria bloom formation may thus be considered a good indicator of climate induced changes as they critically rely on water column stability (Paerl 1988b), which, in a warmer world, will change in favor of cyanobacteria in dimictic (McCormick and Fahnenstiel 1999) as well as in polymictic productive lake ecosystems (Table 2-1; Wilhelm and Adrian 2008).

The Müggelsee case study reported here illustrates long-term changes are systematic in nature, and not decreed by food web hierarchy. Sudden shifts in system state are, therefore, difficult to foresee and may be seasonally dependent. In the context of projected climate warming, most of the unaffected system levels are likely to approach thermal thresholds, thereby accelerating the continuous shifting in system component states. Thus, the significant ecological challenges of identification of critical thresholds and comprehension of external force and internal feedback equilibrium must be overcome in order to offset climate interannual variability and its associated effects.

Acknowledgements

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2.5. Appendix 1

Detection of changes in distribution

We implemented the non-parametric, rank-based Pettitt- test (Pettitt 1979). The null hypothesis of this test is that there is no change in the common distribution function of the examined variable over time. It is based on the Mann-Whitney statistics:

$$U_{t,N} = \sum_{i=1}^{t} \sum_{j=t+1}^{N} D_{ij} \tag{1}$$

where $D_{ij} = \mathrm{sgn}(X_i - X_j)$ measures the numerical order of two observations with the signum function $\mathrm{sgn}(X) = \begin{cases} 1, \text{if } X > 0 \\ 0, \text{if } X = 0 \\ -1, \text{if } X < 0 \end{cases}$. The value k of the test statistics $K_N = \max_{1 \le t < N} \left| U_{t,N} \right|$ with the asymptotic two-sided significance level

$$p_a \approx 2 \exp[-6 \times k^2 \times (N^3 + N^2)^{-1}] \tag{2}$$

is then used for testing whether a change in the distribution is probable. The first sub-period ranges from the beginning of the series to the year prior to the year when a change is most probable (determined by K_N); the second sub-period lasts until the end of the time series. To circumvent the problem that the Pettitt test also detects significant changes in a time series, which shows a continuous monotonic trend over time without a systematic change in behaviour (Coops 1992; Sneyers 1997), we visually inspected the time series prior to analysis. Time series with continuous changes were analysed by Kendall’s correlation coefficient.

Curve estimation

The type of change in a particular time series was analysed by curve fitting for those time series for which a significant change had been determined. Modified from intervention analysis, three models were applied that test whether the mean level of the series changes permanently or only temporarily and whether the change occurs suddenly or gradually (Box and Tiao 1975; McDowall et al. 1980). We assumed that the time series are in an equilibrium state until the change happens, so they are sufficiently described by their mean level until the year when change is initiated. Additionally, we do not expect autocorrelation. These assumptions have to be tested (see chapter: Model selection). The three applied models have the following parameters in common: the value of the dependent variable y_t, the indicator variable I_t following $I_t = \begin{cases} 0, \text{ if } \mathrm{t} < \mathrm{t}_0 \\ 1, \text{ if } \mathrm{t} \geq \mathrm{t}_0 \end{cases}$, the year when change is obvious (t_0), the average level of the time series until the year of change (b_0) and the level shift (b_1) at time t_0. Units for y_t, b_0 and b_1 are equivalent to the unit for the considered data set (e.g. IND x L^{-1} for zooplankton abundances).

Model description

Abrupt permanent change – This model is characterized by an abrupt shift in the mean level of the series (see Fig. 2.1a). This type of change is also referred to as a step change or jump (Yamamoto et al. 1986). It can be described by the following equations:

$$y_t = \begin{cases} b_0 + \varepsilon_{1t}, & \text{if } \mathrm{t} < \mathrm{t}_0 \\ b_0 + b_1 + \varepsilon_{2t}, & \text{if } \mathrm{t} \geq \mathrm{t}_0 \end{cases}, \tag{3}$$

Utilising the indicator variable I_t, equation (3) is equivalent to $Ey_t = b_0 + b_1 \times I_t$ with Ey_t the expectation of y_t.

The estimated average level of the second sub-period is calculated as:

$$b_1^* = b_0 + b_1. \tag{4}$$

The residuals ε_{jt} of subperiod j ($j \in \{1,2\}$) are random errors (white noise), i.e. they are assumed to be normally distributed with an expectation of zero along with a constant variance and to be free of autocorrelation. Diagnostic checks for testing these assumptions are explained in the model selection part. The assumptions about the residuals are the same for the gradual permanent change and the abrupt temporary change.

Gradual permanent change – A gradual permanent change is also characterized by a shift in the mean level at t_0, the level shift is, however, reached gradually. That means that the final permanent new level b_1^* of the series is not established before a certain period of time has passed. The speed of convergence for the level shift is expressed by the dimensionless parameter δ with $\delta > 0$. For the system to be stable, δ has to fulfil the convergence criterion $\delta < 1$, otherwise the level would increase or decrease exponentially over time. If δ is close to zero, the series reaches its final state very quickly, whereas a δ close to one indicates a longer period of adaptation. The following equations (abbreviations see equation 3) describe this type of change:

$$y_t = \begin{cases} b_0 + \varepsilon_{1t}, & \text{if } \mathrm{t} < \mathrm{t}_0 \\ y_{t-1} + b_1 \times \delta^{t-t_0} + \varepsilon_{2t}, & \text{if } \mathrm{t} \geq \mathrm{t}_0 \end{cases} \tag{5}$$

or equivalently, $Ey_t = b_0 + b_1 \times \dfrac{\delta^{t-t_0+1} - 1}{\delta - 1} \times I_t$.

To calculate the asymptotic average level of the second sub-period, we determined

$$b_1^* = b_0 + \frac{b_1}{1-\delta}. \tag{6}$$

Abrupt temporary change – The abrupt temporary change implies a sudden abrupt change, which then, however, slowly decays until the earlier mean level of the time series is reached again (Fig. 2.1c). Similarly to the gradual permanent fit, the parameter δ refers to the speed of convergence; it determines the time needed to reach the original average level of the time series. This model is expressed by the equation system (abbreviations see equation 3):

$$y_t = \begin{cases} b_0 + \varepsilon_{1t}, & \text{if } \mathrm{t} < \mathrm{t}_0 \\ b_0 + b_1 \times \delta^{t-t_0} + \varepsilon_{2t}, & \text{if } \mathrm{t} \geq \mathrm{t}_0 \end{cases} \tag{7}$$

which is equivalent to $Ey_t = b_0 + b_1 \times \delta^{t-t_0} \times I_t$.

The abrupt temporary change is equivalent to the abrupt permanent model if $\delta = 1$. Please note that $b_1^* = b_0$.

Model selection

To select the best model, we tried to fit each of the three models of change to all considered time series by minimizing the mean squared error (squared difference between observation and prediction adjusted by the number of observations). For the model fits, we selected the timing t_0 from a range of possible years (year of change according to the Pettitt test ± 3 years).

To evaluate the model fit, in a first step, the residuals, i.e. the differences between observations and predictions, were tested for normality, constant variance and freedom of autocorrelation. Normality was tested by applying the Shapiro-Wilks test – which is optimal for small sample sizes – for each of the two sub-periods and each model. The null hypothesis of this test is an underlying normal distribution (rejection is not what we desire); we set the significance level to 0.1 in order to balance the type one and type two errors. For some series, we faced the problem of non-normally distributed observations in the first sub-period. We decided to include models with observations mainly close to zero because the rejection of normal distributed values is due to the skewness of the distribution of the data, but not to a change in location. The problem of residual distribution must be handled case-specifically. Furthermore, the residuals were tested for autocorrelation by determining the Durbin-Watson-statistics d (Durbin and Watson 1951), calculated as

$$d = \frac{\sum_{i=2}^{n} (\varepsilon_i - \varepsilon_{i-1})^2}{\sum_{i=1}^{n} \varepsilon_i^{\,2}}. \qquad (8)$$

Critical values for d are tabled in time-series texts, they depend on the number of observations, the number of parameters and the significance level. Commonly, statistical tools provide a test for autocorrelation based on the Durbin-Watson-statistics. Thirdly, the residuals should be analyzed by graphical means by plotting them against time and against the response variable to explore whether they still show any non-random structure.

In a second step, the change parameter b_1 was tested for significance. Models with non-significant parameters were excluded, because a change is not probable then. In a third step, the additional parameter δ was tested for significance. If δ is estimated to be different from zero, the three-parameter model with the higher explained variance is superior to the other three-parameter model. To choose between the two- and three-parameter models, we checked whether the estimation of one additional parameter is reasonable based on the higher proportion of explained variance. A measure to appraise this balance is the adjusted R^2 (R_a^2) based on the mean squared error (Helsel and Hirsch 2002), which can be calculated easily from the explained variance R^2 as

$$R^2{}_a = R^2 - \frac{m \times (1 - R^2)}{n - m - 1} \tag{9}$$

with m the number of estimated parameters and n the number of observations. We chose the model with the higher R_a^2

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3. Consequences of changing thermal regime on plankton diversity and community composition in a polymictic lake

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(intended for Freshwater Biology)

Abstract

Changes in diversity and community structure as a result of global warming are a growing concern in ecological studies, as those properties substantially contribute to ecosystem functioning. Shallow polymictic lakes, a lake type we focus on here, are exceptionally prone to changing climate, as they quickly respond to atmospheric warming with enhanced water temperature and changes in thermal regime. In this study, we analyzed the effect of climate warming, mediated through enhanced thermal stratification, on the plankton diversity and structure of Müggelsee, a shallow polymictic lake. We tested for changes in plankton community properties, such as richness, evenness, Shannon Wiener index, biomass, abundance and community composition of cyanobacteria, diatoms, rotifers, cladocerans, and cyclopoid copepods during periods of thermal stratification and mixing during the summer in 1982 - 2007. Abiotic lake properties differed substantially between periods of stratification and mixing of equal length, with consistenly higher surface water temperatures and lower epilimnetic nutrient concentrations when the lake was stratified. We identified climate-related long-term changes in plankton community properties. Cyanobacteria and cladoceran community properties and diatom biomass showed decreasing long-term trends, rotifer community properties showed increasing long-term trends, whereas no clear pattern of long-term change was observed for the cyclopoid copepods. However, an increase in the length of thermal stratification coincided with higher richness, Shannon Wiener index and abundance of cyclopoid copepods and higher abundance of rotifers, likely as a direct response to increased water temperatures, lower diatom richness, Shannon Wiener index and biomass, both directly adversely affected by higher water temperatures and indirectly adversely affected by sinking losses due to reduced mixing, and higher biomass of

cyanobacteria, favored indirectly by stable stratified conditions. During periods of continuous lake mixing, community properties stayed remarkably unaffected by the length of mixing, and only few changes, such as an increase in diatom biomass, were observed. Community composition changed remarkably, especially towards plankton groups and species well adapted to higher temperatures, like cyclopoid copepods, or to stratified conditions, like cyanobacteria genera, both of which we expect to further profit from ongoing climate warming. Opposite, diatoms may face increasingly worse environmental conditions in the future, and thus further decrease in relevance within the plankton community. Anticipating further climate warming, this shift in community composition may substantially alter lake functional properties, e. g., towards higher relevance of nitrogen-fixation when cyanobacteria gain importance during enhanced thermal stratification in the summer, whereas plankton diversity may not even change remarkably.

3.1. Introduction

The issue of how climate warming alters structural and functional properties of ecosystems is of major interest in climate impact research both in the terrestrial and the aquatic realm. There is growing concern that future climate change in concert with changes in other environmental conditions (e. g. trophic status, biotic exchange) may have severe impacts on ecosystem processes and properties, resulting in profound changes related to phenology, biomass, diversity and community composition, as has already been shown for the past decades (reviewed by MA 2005; Rosenzweig et al. 2007). Most importantly, species loss is considered the main impact of changing environmental conditions, in particular for terrestrial communities (MA 2005; Wilson et al. 2007; Deutsch et al. 2008), and extinction rates are predicted to accelerate drastically until 2050 (MA 2005).

However, ecosystem responses to changing climate may differ quite substantially between aquatic and terrestrial ecosystems (Giller et al. 2004; Hillebrand et al. 2007). Specifically, shallow lakes, the lake type we focus on here, are notably prone to climate warming, as they showed immediate responses to increased air temperatures (Gerten and Adrian 2002a; Wilhelm and Adrian 2008). Most strikingly, physical lake properties shifted towards reduced ice-cover in winter/ spring (Livingstone 2000; Winder and Schindler 2004; Weyhenmeyer et al. 2004), higher water temperatures in spring and summer (Adrian et al. 2006; Hari et al. 2006; Austin and Colman 2007) and enhanced and intensified thermal stratification during summer (King et al. 1997; Livingstone 2003; Winder and Schindler 2004), subsequently provoking oxygen depletion in the hypolimnion and stimulation of nutrient pulses from the sediment (Søndergaard et al. 2003; Wilhelm and Adrian 2008).

Climate warming may directly and indirectly favor plankton species with high optimal growth temperatures and/ or species well adapted to stratified conditions, as has been shown for thermophilic species, like cyclopoid copepods (Gerten and Adrian 2002b; Adrian et al. 2006; Blenckner et al. 2007) or buoyant and N-fixing cyanobacteria species (Jöhnk et al. 2008; Paerl and Huisman 2008; Wagner and Adrian 2009b). Effects include increases in biomass and abundance, and moreover, changes in phenology, e. g., the earlier occurrence and/ or prolonged presence of thermophilic species in the pelagic zone, as has been shown for copepods (Adrian et al. 2006; Seebens et al. 2007). Conversely, species adapted to lower water temperatures and well-mixed conditions, like e. g. diatoms (Reynolds et al. 2002), may experience a reduction in favorable conditions for growth and thus, likely become less important, resulting in alterations of the relative community composition as has been shown for several plankton communities (Adrian et al. 2006; Rühland et al. 2008; Winder and Hunter 2008). With regard to the projected warming of 1.8°C to 4°C by the end of this century (Meehl et al. 2007), summer conditions in lakes will evolve towards higher water temperature and pronounced thermal stratification, thus certainly shifting the plankton community to higher relevance of species well adapted to those conditions (Jöhnk et al. 2008; Winder et al. 2009; Wagner and Adrian 2009b).

In addition to particular species-specific responses, effects of climate change may be regulated by complex interactions, indirect relationships and feedback regulations and may cascade throughout the entire food web (Cushing 1990; Stenseth and Mysterud 2002; Straile et al. 2007). Moreover, time-lagged responses between climate change and biotic response may occur (Gerten and Adrian 2002b; Straile et al. 2007). Furthermore, superimposed effects, like climate-independent changes in trophic status (Jeppesen et al. 2003; Søndergaard et al. 2007), can have additive or antagonistic effects (Jeppesen et al. 2005; Matzinger et al. 2007; Wilhelm and Adrian 2007).

However, there is no evidence so far that climate warming alters diversity in lake ecosystems. A recent study by Burgmer et al. (2007) did not provide evidence, that macroinvertebrate diversity in several Swedish lakes responded to climate warming, and McKee et al. (2002) did not observe significant effects of climate warming on zooplankton diversity. Biotic exchange processes, like dispersal (Hillebrand and Blenckner 2002; Matthiessen and Hillebrand 2006) and invasion of exotic species (Rahel and Olden 2008) may occur more frequently with ongoing climate warming prospectively altering existing communities. North European lakes, e. g., have been invaded by the tropic toxin-producing cyanobacterium *Cylindrospermopsis raciborskii* within the last decades (Wiedner et al. 2007), and the species has already been observed in our study site Müggelsee in recent years.

In the present study, we examined the effect of climate warming, mediated through changes in the thermal regime, assuming that effects are manifold and operate either directly via accelerated water temperature or indirectly via stable stratified conditions or both. We analyzed potential warming effects on diversity, biomass, abundance and community composition of the phytoplankton and zooplankton community of Müggelsee, a shallow polymictic lake in Berlin. The lake experienced pronounced summer warming trends of ~0.7°C per decade since 1980 (Adrian et al. 2006) and a significant increase of periods when the lake is thermally stratified in summer (Wagner and Adrian 2009a, b). To this end, we analyzed the following community properties: richness, evenness, Shannon Wiener index, biomass, abundance, and additionally community composition, of cyanobacteria, diatoms, rotifers, cladocerans and cyclopoid copepods, as they constitute the main groups of the plankton community, in the course of the past three decades and in relation to the length of periods of thermal stratification vs. mixing during summer for the period 1982 – 2007. In particular, we tested for the temporal evolution of all community properties by determining (i) long term trends during stratified versus mixed periods within the past three decades; (ii) the temporal evolution in the course of thermally stratified and mixed periods; and (iii) abiotic factors determining community properties, separated for periods of extended thermal stratification and mixing, respectively.

3.2. Materials and Methods

Study site

Müggelsee is a shallow polymictic lake in the southeast of Berlin, Germany (52°26´N, 13°39´E). Its mean depth is 4.9 m with a maximal depth of 7.9 m and a covered area of approximately 7.3 km^2. The lake is eutrophic, the anthropogenic nutrient load has been continuously decreasing since the early 1990s (Köhler et al. 2005). Besides reductions in nutrient load, Müggelsee has been subject to seasonal warming trends, the surface water temperature in summer has increased by 2.3 K over the last three decades (Adrian et al. 2006). A comprehensive limnological characterization is given in Driescher et al. (1993).

Sampling and sample processing

Between 1982 and 2007, samples of physical, chemical and planktological variables were taken weekly during summer. Water temperature profiles were taken at 0.5m steps during summer. Summer was defined as the period between clear-water phase and end of September (Wagner and Adrian 2009a). The lake was defined to be thermally stratified when the water temperature difference between surface (0.5m) and 5m exceeded 1°C (Wetzel 1990), and each sampling date was classified as “mixed” or “stratified” accordingly. Long stratification events were defined if stratification was recorded on ≥2 consecutive weeks (Wagner and Adrian 2009b). Accordingly, long mixing events were defined if the lake was defined as mixed on ≥2 consecutive weeks. Stability of the water column was determined via the Schmidt stability index ($g\ cm\ cm^{-2}$; Soranno 1997).

Nutrients (soluble reactive phosphorus (SRP), total phosphorus (TP), nitrate (NO_3^-), ammonium (NH_4^+), total nitrogen (TN), soluble reactive silicate (SRSi)) were collected separately from the upper (0.5m – 3.5m, henceforth referred to as epilimnion) and the lower (4.5m – 7.0m; henceforth referred to as hypolimnion) water column when the lake was stratified. During mixing, composite samples throughout the entire water column were taken. We determined concentration of dissolved nitrogen (sum of NO_3^- and NH_4^+).

Phytoplankton samples were taken from the epilimnion, whereas the zooplankton were collected as composite sample over the entire water column. In case of the cyanobacteria, the diatoms and the rotifers, high taxonomic resolution to species level was carried out since 1995, while the remaining zooplankton were determined to species level over the entire study period.

Community properties

For the period 1995 – 2007, we determined richness on species level as well as on genus level for cyanobacteria, diatoms and rotifers, and a comparison between those estimates revealed a high overlap (linear regression, R^2 = 73%, 84%, and 87%, respectively). Thus, determining diversity on genus level seems to be suitable for considering diversity over the entire study period.

To generate an overall picture of change patterns in diversity, we not only calculated species/ genus richness, but also incorporated additional aspects of diversity, in particular evenness and the Shannon Wiener index, as those indices include not only the number of present taxa, but also their relative distribution, measures more appropriate to describe certain facets of community structure with respect to the link between diversity and ecosystem functioning (MA 2005; Hillebrand et al. 2007; Gamfeldt and Hillebrand 2008). Diversity indices were estimated for cyanobacteria (9 genera) and diatoms (10 genera) as well as for rotifers (10 genera), cladocerans (9 species) and cyclopoid copepods (5 species). Zooplankton abundance were $\log_{10}$ – transformed due to the skewness in the particular distributions.

We investigated community composition of the existing genera and species by estimating average absolute and relative biomass/ abundance distributions for the phytoplankton and the zooplankton groups (including taxa, which contributed at least 5% contribution in any given week). Those averages were calculated in the course of events, from one to eight weeks separately, both for periods of thermal stratification and mixing. In the following, the term “community properties” refers to richness, evenness, Shannon Wiener index, phytoplankton biomass, and zooplankton abundance.

Statistical analyses

We tested for long-term trends in community properties by means of correlation analysis. We determined Kendall's τ_B correlation coefficient for yearly averages (Helsel and Hirsch 2002) and calculated significance, direction and strength of the trend. Accordingly, we tested for trends in community properties with increasing event length of stratification and mixing events. We tested for differences in community properties between stratification and mixing by means of the Wilcoxon test (Helsel and Hirsch 2002). We used the paired test in order to adjust for year-specific characteristics and thus, to adjust for long-term changes in temperature regime and trophic status. We tested for differences in lake characteristics and community properties between stratification and mixing for different event lengths (from one to eight weeks) by means of the Mann-Whitney test (Helsel and Hirsch 2002), the significance level for each pairwise test was Bonferroni - adjusted by the number of simultaneous tests (8 tests, $\alpha = 0.0063$).

Additionally, analyses were performed separately for the periods 1982 – 1993 vs. 1994 – 2007 to account for confounding effects of summer warming (Wagner and Adrian 2009a) and the reduction in nutrient load (Köhler et al. 2005). We found that the unidirectional changes within events were equivalent regardless of the period, however, biomass of cyanobacteria and diatoms were consistently lower in the later period. As we focus on 'relative' changes rather than on 'absolute' values, we show the results for the whole study period.

To assess the relationship between abiotic factors and community properties, we conducted correlation analyses between water temperature, Schmidt stability, nutrient concentrations and community properties by determining Kendall's τ_B correlation coefficient (Helsel and Hirsch 2002). This analysis was performed separately for stratification and mixing events to account for potentially different mechanisms driving plankton responses between the regimes.

3.3. Results

Abiotic conditions

In summer, Müggelsee is mixed with irregularly interruptions of periods of thermal stratification (Fig. 3.1). During the study period (1982 – 2007), we determined 26 long stratification events and 66 long mixing events. Those events varied in length between two and eight weeks for stratification events and between two and 17 weeks for mixing events, respectively (Table 3-1). The frequency of stratification events increased significantly during the study period (τ_B=0.466, *p*<0.05). The seasonal distribution of mixing and stratification events did not display any long-term trend, neither in the onset of the first event (usually June for stratification events and May/ June for mixing events) nor in the terminus of the last event (usually August for stratification events and September for mixing events; Fig. 3.1).

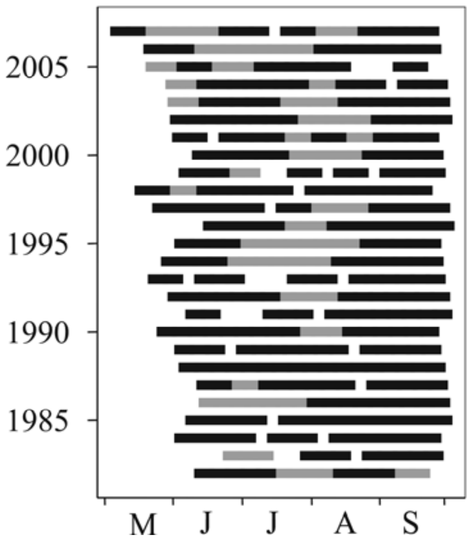


Fig. 3.1: Thermal regime of Müggelsee during summer between 1982 and 2007. Black bars indicate continuous records of mixing, grey bars represent continuous records of thermal stratification.

Surface water temperature differed substantially between stratification and mixing events (Fig. 3.2). In the course of thermal stratification events, epilimnetic water temperature steadily increased, while it decreased in the course of mixing events, resulting in significant differences in epilimnetic water temperatures between stratification and mixing for equal event lengths from two to eight weeks (Mann Whitney test, $p<0.0063$; Fig. 3.2 a).

Table 3-1: Number of events of different lengths for thermal stratification and mixing in Müggelsee between 1982 and 2007.

Event length (weeks)	Thermal stratification	Mixing
2	10	13
3	5	10
4	4	7
5	3	13
6	0	6
7	2	7
≥8	2	10

Water column stability steeply increased in the second week of continuous stratification and remained at a constant level until stratification breakdown. The stability index did not differ from zero in case of continuous lake mixing (data not shown).

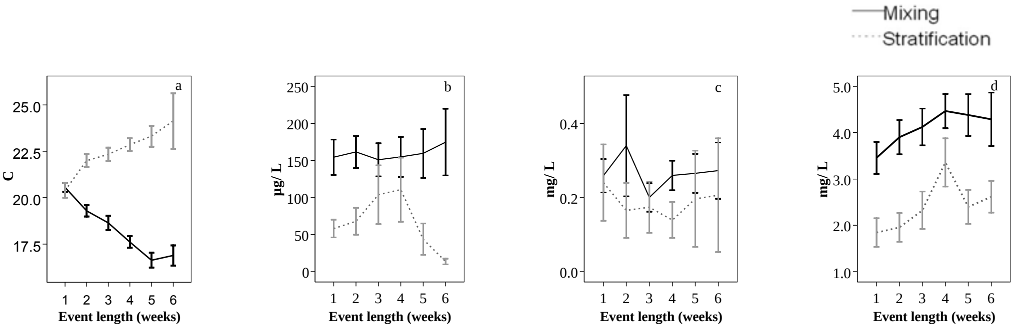


Fig. 3.2: Development of surface water temperature (a), epilimnetic concentrations of SRP (b), nitrogen (c) and SRSi (d) in the course of thermal stratification (gray lines) vs. mixing (black lines). We depict means with standard errors for event lengths between one and six weeks.

Epilimnetic nutrient concentrations were consistently lower in case of stratification compared to mixing (Fig. 3.2 b-d), but did not differ significantly between stratification and mixing for equal event length. Stratification events of >4 weeks led to decreases of SRP concentrations in the epilimnion (Fig. 3.2 c), whereas no clear patterns were observed for dissolved nitrogen (Fig. 3.2 b) and SRSi (Fig. 3.2 d).

Long-term trends of community properties (1982 – 2007)

Yearly mean diversity and biomass of cyanobacteria decreased significantly during the study period (Table 3-2), comparable in case of stratification and mixing. Diatom biomass showed a significant decrease, while no such trends were detected for diatom diversity. Neither cyanobacteria nor diatom diversity and biomass differed significantly between periods of mixing and stratification in the long-term (Table 3-2).

Rotifers consistently exhibited increasing diversity and abundance, both in case of stratification and mixing (Table 3-2). Furthermore, we detected significant higher values for genus richness and abundance of rotifers in case of thermal stratification compared to mixing. Conversely, cladocerans showed decreasing trends for diversity and abundance in case of mixing and stratification. We found no differences between mixing and stratification for cladoceran diversity and abundance (Table 3-2). Significant long-term trends for cyclopoid copepods covered a decrease of richness in case of mixing and an increase of evenness in case of stratification. Species richness, Shannon Wiener index and abundance of cyclopoid copepods were significantly higher when the lake was stratified (Table 3-2).

Table 3-2: Long-term trends (1982 – 2007) of yearly averages of community properties (richness, evenness, Shannon Wiener index, biomass and abundance) of cyanobacteria, diatoms, rotifers, cladocerans and cyclopoid copepods. Given are the long-term means and the long-term trends (as a result of the correlation analysis), separated for periods of mixing (Mix) and thermal stratification (Strat). Significant differences resulting from the Wilcoxon test between yearly means in mixed vs. stratified periods are marked by 'x' in the column 'Diff'.

	Richness (Number of genera/ species)					Evenness					Shannon Wiener Index					Biomass (mg L^{-1})/Abundance (Ind L^{-1})				
	Mean		Diff	Long-term trend		Mean		Diff	Long-term trend		Mean		Diff	Long-term trend		Mean		Diff	Long-term trend	
	Strat	Mix		Strat	Mix	Strat	Mix		Strat	Mix	Strat	0.5		Strat	Mix	Strat	Mix		Strat	Mix
Cyanobacteria	2.8	2.7		-.349(*)	-.327(*)	0.5	0.5		-0.107	-0.225	0.5	0.5		-.320(*)	-.317(*)	5.7	5.2		-.500(**)	-.409(**)
Diatoms	2.8	2.8		-0.037	0.080	0.6	0.5		-0.120	0.175	0.5			-0.060	0.169	3.0	3.7		-.440(**)	-.409(**)
												0.7								
Rotifers	5.3	5.0	x	.317(*)	0.133	0.5	0.5		.313(*)	0.237	0.8	1.1		.353(*)	.274(*)	2.8	2.7	x	.407(**)	.280(*)
Cladocerans	5.4	5.7		-.606(**)	-.526(**)	0.6	0.6		-.320(*)	-.458(**)	1.0	0.6		-.480(**)	-.526(**)	1.8	1.8		-.353(*)	-.403(**)
Cyclopoid copepods	2.8	2.4	x	-0.220	-.308(*)	0.8	0.7		.367(*)	0.231	0.7	0.7	x	-0.120	-0.169	1.0	0.8	x	-0.127	0.009

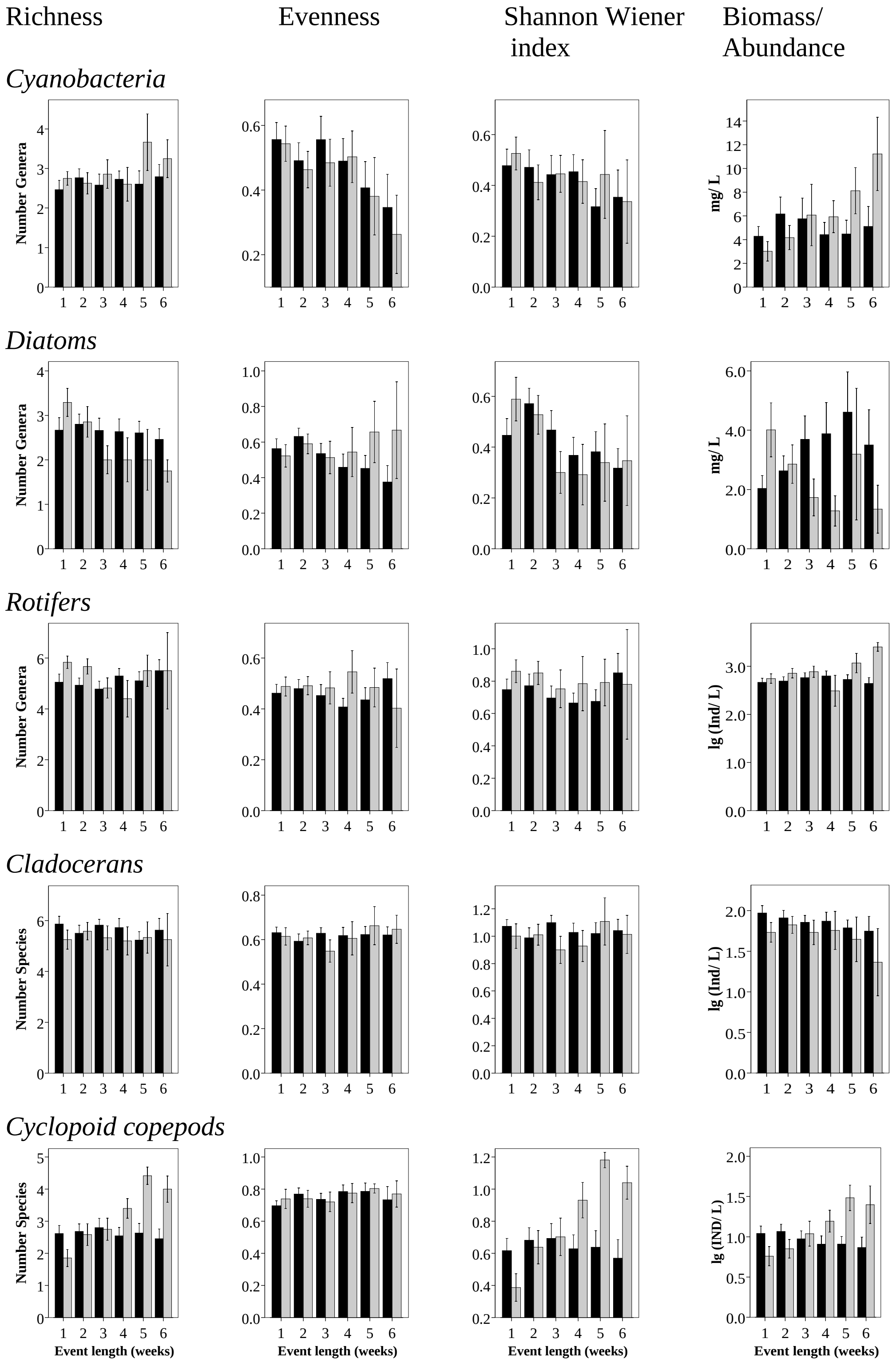
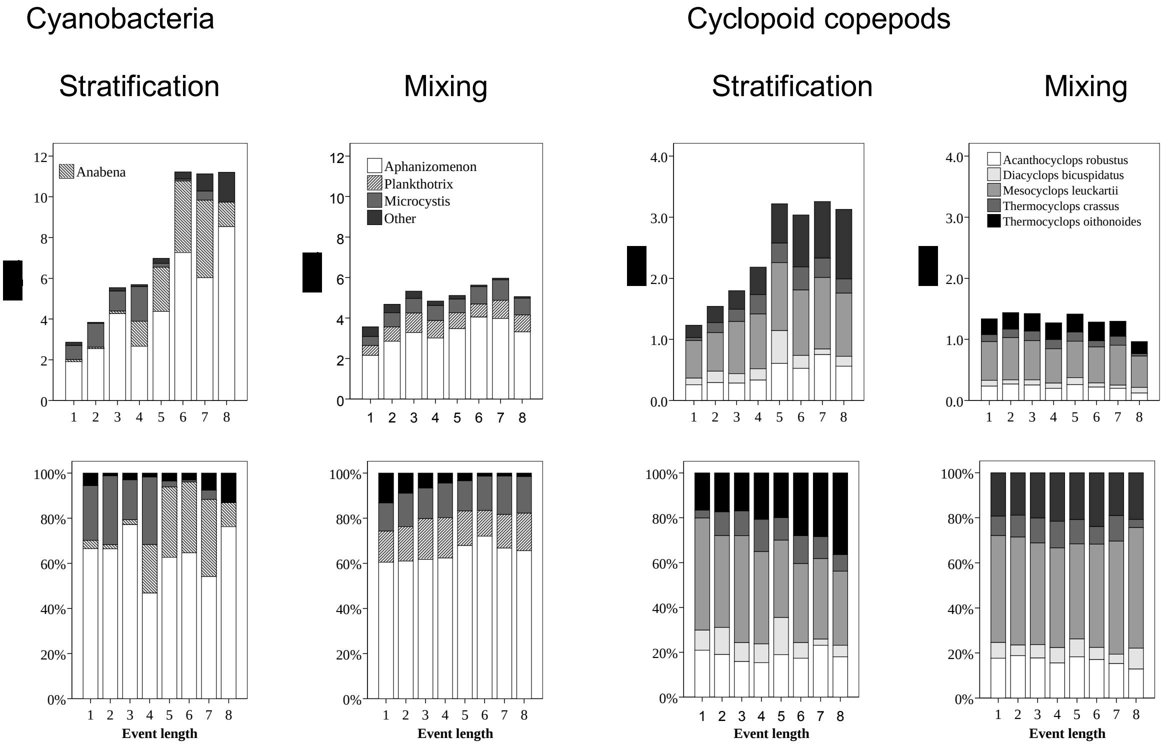


Fig. 3.3: Diversity, phytoplankton biomass (cyanobacteria and diatoms; panels 1 and 2) and zooplankton abundance (rotifers, cladocerans, and cyclopoid copepods; panels 3 – 5) in the course of thermal stratification (grey bars) vs. mixing (black bars). We present means with standard error in the course of event duration between one and six weeks for diversity indices (Richness, Evenness, Shannon Wiener index; columns 1-3) and biomass/ abundance (column 4) (lg=log10).

Temporal evolution of community properties and composition with event length

Cyanobacteria biomass increased significantly with the length of thermal stratification (Table 3-3, Fig. 3.3), while it remained constant during mixing events. Cyanobacteria community properties during mixing showed no unidirectional change in the course of events, regardless of thermal regime (Fig. 3.3; Table 3-3). No significant differences in community properties between stratification and mixing events of equal length were observed (Mann-Whitney tests, p>0.0063) for the cyanobacteria. This holds for all comparisons of community properties of the remaining phytoplankton and zooplankton between stratification and mixing events of equal length. We identified changes in cyanobacteria community composition, which was in general dominated by three species, two of which where *Aphanizomenon* and *Microcystis*, however, *Plankthotrix,* a genus well adapted to mixed conditions (Reynolds et al. 2002), was replaced by buoyant N-fixing *Anabaena* (Paerl 1988a; Reynolds et al. 2002) in case of thermal stratification (Fig. 3.4). Diatom genus richness, Shannon Wiener index and biomass significantly decreased in the course of thermal stratification, whereas diatom biomass increased with increasing length of mixing (Table 3-3, Fig. 3.3). Diatom community was dominated by *Aulacoseira*, single centric diatoms and *Fragilaria* both under stratified and mixed conditions.

Rotifer abundance increased in the course of stratification and mixing events, whereas rotifer diversity stayed unaffected by event length (Table 3-3, Fig. 3.3). Community composition of rotifers was rather uniform in the course of events. *Keratella*, *Trichocera* and *Synchaeta* dominated rotifer community, regardless of event type and event length. *Conochilus* occurred in case of stratification, while, *Kellicotta* and *Brachionus* were found if the lake was mixed. Cladocerans did not exhibit unidirectional changes, neither in diversity nor in abundance, regardless of thermal regime (Table 3-3, Fig. 3.3). Approximately, 50% of the cladoceran community consisted of daphnids, whose importance decreased slightly with increasing length of stratification mainly caused by a decrease of abundance of *Daphnia galeata*. Cyclopoid copepods showed strong increases in diversity (except for evenness) and abundance in the course of stratification, but no changes in the course of mixing (Table 3-3, Fig. 3.3). In general, *Mesocyclops leuckartii* showed highest abundances (up to 50% of cyclopoid copepod community abundance), but with increasing length of thermal stratification the two thermophilic species *Thermocyclops crassus* and *Thermocyclops oithonoides* gained relevance both in relative and absolute abundance (Fig. 3.4). During mixing, no change in community composition was observed (Fig. 3.4).


Cyanobacteria

Cyclopoid copepods

Stratification

Mixing

Stratification

Mixing

Fig. 3.4: Community composition for cyanobacteria (two left panels) and cyclopoid copepods (two right panels) in the course of thermal stratification (column 1 and 3) and mixing (column 2 and 4) in summer for event lengths between one and eight weeks. The upper panel shows absolute values for cyanobacteria biomass and copepod abundance, the lower panel shows the respective relative biomass and abundance. Values for the cyanobacteria genera *Anabaena* and *Planktothrix* are striped to point out their particular thermal preference and replacement. Genera and species, which contribute less than 5% to the respective biomass and abundance at any given week, are summarized into ‘other’.

Table 3-3: Results of correlation analysis between Richness (Number of genera/ species), Evenness, Shannon Wiener index, biomass, abundance and abiotic factors, separated for periods of stratification and mixing for different plankton groups in the period 1982 – 2007. Given are significant correlations (Kendall's τ_B, $p<0.05$). Duration = Event length, WT = surface water temperature, SRP = soluble reactive phosphorus, SRSi = soluble reactive silicate.

	Stratification							***Mixing***				
	Duration (weeks)	**WT (°C)**	**Stability (g cm cm^{-2})**	**SRP (µgL^{-1})**	**Nitrogen (mg L^{-1})**	**SRSi (mg L^{-1})**		**Duration (weeks)**	**WT (°C)**	**SRP (µgL^{-1})**	**Nitrogen (mg L^{-1})**	**SRSi (mg L^{-1})**
Richness (Number of Genera/ Species)												
Cyanobacteria				-0.166								
Diatoms	-0.235			-0.254		-0.303				-0.242		-0.257
Rotifers												
Cladocerans			-0.162									
Cyclopoid copepods	0.372	0.436										
Evenness												
Cyanobacteria		-0.160		0.188								
Diatoms								-0.108				
Rotifers												
Cladocerans												
Cyclopoid copepods								0.111				
Shannon Wiener index												
Cyanobacteria												
Diatoms	-0.200			-0.182		-0.199				-0.122		-0.161
Rotifers												
Cladocerans												
Cyclopoid copepods	0.367	0.353	0.172									
Biomass (mgL^{-1})/ Abundance (Ind L^{-1})												
Cyanobacteria	0.223					0.259				0.231		0.253
Diatoms	-0.211	-0.214	-0.180	-0.191		-0.230		0.184		-0.184	-0.142	-0.207
Rotifers	0.178	0.205	0.232						0.163			
Cladocerans												
Cyclopoid copepods	0.245	0.302										

Drivers of community properties

Diversity of cyanobacteria did not show significant correlations with abiotic factors, except for weak correlations between richness and SRP and between evenness and water temperature and SRP in case of stratification (Table 3-3). Cyanobacteria biomass, however, showed positive correlations with SRSi and SRP, the latter only in case of mixing. Richness and Shannon Wiener index of diatoms were negatively correlated with nutrient concentrations, in particular SRP and SRSi. Additionally, diatom biomass was negatively correlated with water temperature and Schmidt stability when the lake was stratified (Table 3-3).

Significant correlations between zooplankton community properties and physical factors were rare and, except for the cyclopoid copepods, rather weak (Table 3-3). We found no relationship between rotifer diversity and physical factors; however, rotifer abundance was positively correlated with water temperature and stability. Species richness of cladocerans was negatively correlated with Schmidt stability during stratification. Richness, Shannon Wiener index and abundance of cyclopoid copepods showed strong positive correlations with water temperature when the lake was stratified, but not in case of mixing (Table 3-3).

3.4. Discussion

Climate induced modifications in thermal regime

The most apparent impact of summer warming on physical lake properties of Müggelsee were those in water temperature and the mixing regime. The number of events and the time, when the lake was stratified in summer, increased significantly over the study period (Fig. 3.1; Wagner and Adrian 2009a). While in the early period only half of the years were affected by a long stratification event, we found at least one long event per year since 1994 (Fig. 3.1). Thus, climate warming induced a higher proportion of stratification and especially long stratification events (Wilhelm and Adrian 2008, Wagner and Adrian 2009b). In contrast to continuous mixing, a long period of thermal stratification considerably changes lake properties, e. g. by an increase in lake surface water temperature and stability, nutrient depletion in the epilimnion (Fig. 3.2) and nutrient pulses from the sediment when the lake bottom becomes anoxic (Søndergaard et al. 2003; Wilhelm and Adrian 2008). Hence, we can regard periods of thermal stratification as climate-induced disturbances of the system, and they remarkably alter abiotic lake characteristics and consequently biotic properties.

Phytoplankton

The long-term decreasing trend in biomass for both the cyanobacteria and the diatoms is clearly an effect of reduced nutrient load, as has already been shown for Müggelsee (Köhler et al. 2005), as well as for many productive lakes that experienced nutrient load reductions due to tremendous restoration efforts in recent decades (Sommer et al. 1993; Jeppesen et al. 2005; Schindler 2006). We found no significant effects of event length on the diversity of cyanobacteria, neither in case of stratification nor in case of mixing. As cyanobacteria generally profit from stable conditions (Paerl 1988b; Reynolds et al. 2002; Wagner and Adrian 2009b), biomass of cyanobacteria increased with increasing length of stratification, leading to the development of cyanobacteria blooms (Jöhnk et al. 2008; Wagner and Adrian 2009b). The replacement of *Plankthotrix*, a genus well adapted to mixing conditions, by buoyant N-fixing *Anabaena*, which is favored by stratified conditions (Reynolds et al. 2002; Wagner and Adrian 2009b), when comparing periods of mixing and stratification, respectively, reflected that community composition may vary according to species-specific demands, however, great changes in functionality may not result in strong changes in diversity (Hillebrand et al. 2007). Anticipating future climate warming, polymictic lakes may undergo a transition to dimictic thermal conditions (Boehrer and Schultze 2008; Livingstone 2008), subsequently shifting the system to a higher importance of cyanobacteria during the summer and thus, in combination with a shift of the system to enhanced N-limitation during the summer (Wagner and Adrian 2009a), altering system functionality towards accelerated N-fixation. Moreover, several cyanobacteria species are toxin-producers, e. g. *Anabaena* (Sotero-Santos et al. 2008) or the tropical invader *Cylindrospermopsis* (Wiedner et al. 2007), which has already been observed in Müggelsee (unpubl. data). Hence, lake functionality is expected to additionally shift to higher importance of toxin production (Paerl and Huisman 2008).

Opposite to cyanobacteria, diatoms showed not only decreasing trends in biomass, but also in diversity (Table 3-3) when the lake was stratified. This decrease in diversity is likely a result of sinking losses due to the absence of required turbulence in the epilimnion. Apparently, diatoms are unable to cope with conditions when stratification exceeds two weeks in length (Fig. 3.3) – diversity as well as biomass consistently showed a steep decline between second and third week of continuous thermal stratification, and additionally, biomass decreased with increasing stability (Table 3-3). A further prominent change in lake properties in the course of stratification is the increase in epilimnetic water temperature. Since the second week of stratification, epilimnetic water temperature exceeded 22°C, a temperature range, which is rather inauspicious for diatoms (Snoeijs 1990; Davison 1991; Coles and Jones 2000), resulting in a substantial negative relationship between biomass and temperature (Table 3-3). We observed no relationship between biomass and water temperature, when the lake was mixed (Table 3-3), indicating that temperature during mixing was in a more favoring range for diatom growth (<20°C, if the lake is mixed for ≥ 2 weeks; Fig. 3.2a), while higher temperatures during stratification (>22°C, if the lake is stratified for ≥ 2 weeks; Fig. 3.2a) already had adverse effects, pointing to a direct adverse temperature effect during stratification. Nutrient limitation is likely of minor importance, as we observed negative correlations between community properties and nutrient concentrations in case the lake was stratified with lower nutrient concentrations in the epilimnion as compared to higher nutrient concentrations during lake mixing (Fig. 3.2 b-d), in agreement with actual lake nutrient concentrations, which are not in a limiting range in particular for SRSi and SRP during the summer (Wagner and Adrian 2009a).

Thermal stratification has converse effects on cyanobacteria and diatoms; while cyanobacteria seem to be favored, diatoms are poorly adapted to prolonged periods of thermal stratification. However, the mechanisms seem to differ for those groups and we found evidence that climate warming had direct effects or indirect effects or both. Stratified conditions clearly favored buoyant and N-fixing cyanobacteria species, such as *Anabaena* and *Aphanizomenon* (Paerl 1988b; Reynolds et al. 2002; Wagner and Adrian 2009b), replacing non N-fixing non-buoyant species such as

Plankthotrix (Fig. 3.4). Those taxa could gain higher importance during long stratification events that led to nitrogen limitation in the epilimnion (Nõges et al. 2008; Wagner and Adrian 2009b). The striking abrupt decline in diversity and biomass of diatoms and the fairly constant levels in the first two weeks and the later weeks, respectively, gives evidence that the main effect occurred indirectly via reduced mixing, however, direct adverse effects of higher temperatures during stratification were observed, too. During the first two weeks, when stratification is not yet fully pronounced, diatoms can persist in the epilimnion, but once the system is stratified for three consecutive weeks, diatoms sink to the lake bottom and won't be transported back into the epilimnion due to reduced mixing. This conclusion is further supported by the uniformity of genus richness and Shannon index and the increase in biomass if the lake is continuously mixed (Fig. 3.3, Table 3-3), pointing to a persistence of diatoms in the epilimnion and growing biomass as a result of permanent access to resources (light and nutrients).

Zooplankton

The thermophilic species (*Thermocyclops crassus* and *Thermocyclops oithonoides*) became more important in terms of absolute and relative abundances with increasing stratification length (doubling on average in absolute and relative abundance when stratification exceeds four weeks, Fig. 3.4), but remained stable in the course of mixing. This gives evidence for a strong direct temperature effect that promoted a rapid growth, which is further supported by the strong positive correlations with water temperatures during stratification. Thus, cyclopoid copepods are likely directly favored by climate warming, however, the effect of higher water temperatures is only relevant in case of stratification but not during periods of mixing. This is in line with the coherent response of cyclopoid copepods to climate forcing during summer reported for several European lakes (Blenckner et al. 2007). The increase in diversity and abundance of cyclopoid copepods during thermal stratification indicates that food limitation could be neglected. Moreover, cyclopoid copepods might profit from their ability to feed omnivorous (Adrian and Frost 1993; Work and Havens 2003), e. g., they are able to ingest cyanobacteria and rotifers, which, opposite to diatoms, increase in biomass and thus, in relative importance as food resource for zooplankton when lake stratification is long-lived (Fig. 3.3).

Fast-growing rotifers probably profited directly from higher temperatures, diversity and abundance increased during the study period with consistently higher values during stratification in general (Table 3-2). Rotifer abundance increased with increasing water temperature during stratification, however, no such effect was observed for diversity or in case of mixing. Thus, rotifers likely profited directly from higher water temperatures, which match their optimal growth range (Wetzel 2001; Pavon-Meza et al. 2005).

Diversity and abundance of cladocerans showed strong declines in the long-term, but did not show any clear response towards event length or abiotic factors, neither for stratification nor for mixing events (Table 3-3). The summer decline of daphnid biomass may be partly explained by fish predation (Boersma et al. 1996; Mehner 2000; Benndorf et al. 2001), however, the long-term decline might also be a result of reoligotrophication in terms of declining food quality, as the biomass of diatoms, an important food resource for most importantly daphnids (Brett et al. 2000; Wetzel 2001), decreased substantially (Table 3-2). However, we did not find any evidence for direct or indirect adverse warming effects on cladoceran diversity or abundance (Table 3-3).

Conclusions

We found little evidence that climate warming has influenced overall plankton diversity, during the study period (1982 – 2007) only subtle climate-related changes in diversity indices have been observed (Table 3-2). However, we identified strong effects of warming reflected in changes of biomass and community composition when comparing periods of thermal stratification and mixing and in the course of thermal stratification (Fig. 3.3, Fig. 3.4). This study provided evidence that climate warming affects relative species composition and functionality more severely than diversity. With increasing length of thermal stratification, the phytoplankton community shifted towards higher importance of buoyant species capable of N-fixation (*Aphanizomenon*, *Anabaena*; Reynolds 1984; Paerl 1988b), and within the zooplankton community species with higher thermal tolerances; most importantly thermophilic cyclopoid copepod species (*Thermocyclops oithonoides, Thermocyclops crassus*) gained relevance. By contrast, diatoms are less well adapted to higher water temperatures and stratified conditions, according to their ecological demands (Reynolds et al. 2002) and showed decreasing trends in biomass and diversity with increasing length of thermal stratification. With regard to further climate warming (Meehl et al. 2007), we expect the alteration in community composition observed in the course of thermal stratification to accelerate, as thermal stratification will gain further significance in the future. Thus, the system is likely to shift towards higher importance of cyanobacteria and cyclopoid copepods and reduced importance of diatoms during the summer. To what extent those shifts in community composition will affect diversity remains speculative. Except for richness and Shannon Wiener index of cyclopoid copepods, there is not much evidence for climate impacts on diversity (Table 3-3; McKee et al. 2002). Specifically, we did not identify factors that may determine evenness of plankton groups. The importance of diversity for aquatic ecosystem functioning has been documented (MA 2005; Hillebrand et al. 2007; Gamfeldt and Hillebrand 2008), however, shifts in community composition may have as severe impacts on ecosystem functioning as diversity (Hillebrand et al. 2007), like e. g., an increasing importance of N-fixing and/ or toxin-producing cyanobacteria during the summer may shift functional lake properties towards accelerated N-fixation and higher toxin-production (Nõges et al. 2008; Wiedner et al. 2007; Wagner and Adrian 2009b), a likely effect when anticipating further global warming (Meehl et al. 2007).

Acknowledgements

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4. Cyanobacteria dominance – quantifying the effects of climate change

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(Limnology and Oceanography **54**: 2460-2468)

Abstract

An increase in cyanobacteria bloom formation within lakes has been forecasted due to global warming. We investigated the particular physical and chemical thresholds for cyanobacteria performance in a lake model system: the polymictic eutrophic Müggelsee, which has been affected by significant warming trends and substantial reductions in external nutrient load. To identify key physical and nutrient thresholds favoring cyanobacterial performance, we applied classification tree analysis to water temperature, Schmidt stability, oxygen, pH, nutrients (including phosphorus, nitrogen, and their relative ratios), and zooplankton abundance during periods of summer thermal stratification. Although total phosphorus concentration (TP) was the principal force driving cyanobacteria contribution to total algal mass, climate induced changes in the thermal regime, rather than direct temperature effects, positively influenced cyanobacteria dominance. Stratification periods exceeding four weeks and exhibiting a Schmidt stability > 44 g cm cm^{-2} favored cyanobacteria proliferation within a critical TP concentration range (70 to 215 μg L^{-1}). The dominating genera *Aphanizomenon*, *Anabaena,* and *Microcystis* achieved highest biomass in case when total nitrogen concentrations exceeded 1.29 mg L^{-1}, stratified conditions exceeded a duration of three weeks, and TP concentrations exceeded 215 μg L^{-1}, respectively. Given the observed broad range of TP thresholds within which climate warming enhances the probability of cyanobacteria dominance, the incidence of cyanobacteria blooms will certainly increase in many lakes under future climate scenarios.

4.1. Introduction

Cyanobacteria dominance and bloom formation has been a persistent concern of freshwater ecologists, historically due to the formation of nuisance blooms during lake eutrophication (Edmondson 1993; Paerl and Huisman 2008). More recently, cyanobacteria bloom formation is hypothesized to increase in the context of global warming (Mooij et al. 2005; Jeppesen et al. 2007a), which would counteract the tremendous lake restoration measures taken in the recent decades (Jeppesen et al. 2007a).

It is well established that the success of cyanobacteria is a result of complex and synergistic environmental factors rather than a single dominant variable (Huyenstrand et al. 1998; Dokulil and Teubner 2000). However, many of these factors are altered directly and indirectly by temperature, resulting in positive selection pressure for cyanobacteria due to their optimal growth at higher temperatures compared with other algal groups (Reynolds 1984). The indirect positive effects of temperature are manifold. First, buoyant species profit from the stable thermal conditions that coincide with high temperatures (for review *see* Paerl 1988a; Dokulil and Teubner 2000), conditions which are likely to become prolonged (Gerten and Adrian 2001; Winder and Schindler 2004; Wilhelm and Adrian 2008) and more intense under future climate scenarios, such as observed within dimictic lakes (Winder and Schindler 2004). Subsequent oxygen depletion in the hypolimnion stimulates nutrient release at the sediment-water interface (Søndergaard et al. 2003; Wilhelm and Adrian 2008) and high hypolimnetic temperatures also stimulate the mineralization of organic matter, which contributes to the accumulation of dissolved nutrients in the hypolimnion (Søndergaard et al. 2003). Access to these increased nutrient pools will be limited to migrating species such as buoyant cyanobacteria (Reynolds 1984; Paerl 1988a). These indirect climate driven enhancements in nutrient availability, particularly phosphorus, alter the eutrophic conditions of the lake ecosystem in favor of cyanobacteria.

Whether phosphorus and nitrogen concentrations, or nutrient ratios such as total nitrogen: total phosphorus (TN:TP), are crucial for cyanobacterial prominence is still under debate (Smith 1983; Downing et al. 2001). As many bloom forming species are capable of fixing atmospheric nitrogen, there is a general consensus among scientists that cyanobacteria dominate at low TN:TP ratios (Smith 1983). However, a recent study by Downing et al. (2001) who reported that total nitrogen and phosphorus concentrations, rather than nutrient ratios, were superior predictors of cyanobacteria relative biomass in 99 lakes around the world refutes this theory.

Given the predicted further warming of at least 1.8°C until the end of this century (Meehl et al. 2007), and because climate warming induced changes can be linked to cyanobacterial physiology and morphology, there is good reason to expect that global warming will indeed lead to a proliferation of cyanobacteria blooms. However, the statement ‘blooms like it hot’ recently published by Paerl and Huisman (2008), implies a fact, what is rather a hypothesis. This statement neglects the fact that cyanobacteria are a diverse group from which different species are likely to respond differently to climate driven changes in lakes, which themselves are different; e.g., shallow polymictic lakes may differ greatly in their response from deep, dimictic lakes. In polymictic lakes e.g., the frequency and duration of stratified conditions will increase (Wilhelm and Adrian 2008), while the overall duration of summer stratification or the depth of the thermocline will be affected in dimictic lakes (McCormick and Fahnenstiel 1999; Gerten and Adrian 2001). How the forecasted increase in storm events (Christensen et al. 2007) may counteract the probability of bloom formation mediated by increasingly stable conditions remains speculative (Howard and Easthope 2002).

At present, there are insufficient data to confirm the belief that cyanobacteria are already benefiting from warmer temperatures and will benefit even more in the future. The present study quantitatively investigates the hypothetical link between climate and cyanobacteria bloom formation for a highly productive polymictic lake that underwent substantial reductions in external nutrient load during the last few decades that resulted in an improvement in trophic status from hypertrophic to eutrophic, i.e., a decline in total algal mass but with cyanobacteria still being the dominant group (comprising 40% of the total algal mass; Köhler et al. 2005; Wagner and Adrian 2009a).

In a previous study, we were able to illustrate that climate induced changes in spring phytoplankton bloom phenology in this lake were modified by trophic state alterations (Huber et al. 2008). In the present study, we explore whether the trophic state of the lake imposes boundaries on climate driven cyanobacteria blooms during summer. Given the increasing threat of global warming we hypothesize that increased summer temperatures and periods of thermal stratification will enhance cyanobacteria bloom formation and off-set the recent reduction in algal mass, a situation widely applicable across the northern temperate zone due to tremendous restoration efforts (Edmondson 1993; Jeppesen et al. 2007a). To this end, we analyzed three decades of data on physical and chemical variables as well as zooplankton abundance, to identify major determinants of cyanobacteria performance during periods of thermal stratification, and to distinguish climate- from nutrient-driven forces.

4.2. Methods

Study site

Müggelsee is a highly eutrophic, polymictic lake located at 52°26'N, 13°39'E in Berlin, Germany, with a surface area of 7.3 km^2, a mean depth of 4.9 m and a maximum depth of 7.9 m. The surrounding topography is flat and the lake basin is oriented east-west and exposed to prevailing south westerly winds. For further details on lake morphometry and the catchment area see Driescher et al. (1993). Over the last three decades of observation, the lake has been subjected to seasonal warming trends (~2.3°C during summer, Adrian et al. 2006) and decreased nutrient loading beginning in the early 1990s (Köhler et al. 2005). Intermittent thermal stratification during summer is common (Fig. 4.1a) with consequent effects on temperature, oxygen, internal nutrient load, and phytoplankton development (Wilhelm and Adrian 2008).

Data collection

Physical, chemical, and planktological variables were recorded weekly during the summers between 1982 and 2007. Summer was defined as the period between the clear water phase (maximal Secchi depth after the spring algal bloom) and the end of September. Water temperature and oxygen profiles were recorded from 0 m to 7 m water depth at 0.5 m intervals (Gerten and Adrian 2002a). The lake was considered to be thermally stratified when the water temperature on the surface (0.5 m depth) and at a depth of 5.0 m differed by more than 1°C (Wilhelm and Adrian 2008). The strength of thermal stratification was described by the Schmidt stability index (Soranno 1997). Recently, Wilhelm and Adrian (2008) reported the thermal stratification pattern of Müggelsee in 2003-2006 using water temperature profile measurements collected hourly from the automated lake station (http://www.igb-berlin.de/abt2/ms/ms_dat.shtml). Stratification events less than one week in duration were frequent; as well, there were longer stable stratification events of one to eight weeks, which mirrored local meteorological forcing (Wilhelm et al. 2006). As data prior to 2003 were only collected weekly, in the present study our investigation is limited to stratification events longer than one week in duration, i. e., water column stratification lasting for at least two consecutive weekly profile measurements from 1982-2007. To test the reliability of this methodology we compared our stratification events with stratification events determined by Wilhelm and Adrian 2008) based on daily profile measurements. Six of the defined events between 2003 and 2006 based on weekly records were congruent in timing and duration with those defined by Wilhelm and Adrian (2008), and only one event was wrongly classified as a long stratification event in our study. Thus, the method used here seems suitable for defining stratification events.

During stratification, two mixed samples from the upper (0.5 m -3.5 m, henceforth referred to as epilimnion) and lower (4.5 m – 7.0 m, henceforth referred to as hypolimnion) water layers were collected separately for nutrient (soluble reactive phosphorus (SRP), total phosphorus (TP), nitrate (NO_3), ammonium (NH_4), total nitrogen (TN), soluble reactive silicate (SRSi)) and phytoplankton analyses. Between 1982 and 1998, phytoplankton analyses were restricted to the epilimnion. From 1999 onwards, phytoplankton was additionally analyzed in the hypolimnion. Zooplankton were collected as composite sample throughout the entire water column during the entire investigation period (1982-2007). Detailed descriptions of sampling and processing have been previously reported in Driescher et al. (1993).

Statistical analysis

Differences in temporal trends (the number of stratification events per year), thermal characteristics (event duration, epilimnetic and hypolimnetic water temperatures, event stability) and seasonal patterns (first and last event onset, end of last event) of stratification events were determined via Kendall's τ_B correlation coefficient (Helsel and Hirsch 2002). Long-term trends and trends in stratification dependent cyanobacterial biomass and contribution were analyzed accordingly.

Classification and regression tree analysis

The cyanobacteria fraction of total algal biomass was determined and the resulting percentages were classified into tiers of 10% increments ranging from 10% to 80% cyanobacterial contribution. Organizing the data this way facilitated the identification of main predictor variables of cyanobacteria performance. For each classification, a dichotomous variable was assigned that indicated if the tiered percentage level was exceeded (value 1) or not (value 0). Unless stated otherwise, ‘contribution’ refers to cyanobacteria contribution to total algal mass.

Classification tree analysis (De'ath and Fabricius 2000; utilizing SPSS version 15.0 for Windows) was applied to all contribution classes of cyanobacteria. Regression tree analysis was applied individually to the biomass of the most prominent genera during stratification, which accounted for 95% of cyanobacteria biomass, namely *Aphanizomenon*, *Anabaena,* and *Microcystis.* Classification and regression tree analysis is a recursive technique used for extracting key variables and thresholds within a multivariate data set in order to determine the most likely inducer of variability among category and numeric response variables, respectively. Beginning with the initial response variable distribution, the data set is divided into exclusive subsets based on predictor variables; variables that produce the most homogenous partitions according to Chi Square multiple comparisons (*see Stopping rules and validation* below). For each generated partition the procedure is repeated for the remaining predictor variables until a stopping rule (*see* below) is achieved; in the present study, we used the CHAID algorithm (Chi-squared Automatic Interaction Detection; Biggs et al. 1991) for the segmentation process, which allows for multiple splits. The output of the classification and regression tree analysis is a graphical representation (a schematic tree where partitions are represented by nodes) that indicates significant predictor variables, their sequence, thresholds, and interactions, as well as statistical significance and distribution within each generated partition.

Stopping rules and validation: Multiple comparisons of partitions were conducted based on Chi-Square statistics according to Pearson with Bonferroni adjustment. The significance level was set to 5%. Since the algorithm continues if further partitions are significant, we limited tree depth to three to avoid overspecification. The minimum number of cases among 'parent nodes' (i.e., a split with further segmentation) was set to 20, and 'child nodes' (i.e., a split without further segmentation) was set to 10. Model selection was validated by a ten-fold cross-validation.

Predictor variables: Data measured at depths of 0.5 m and 5 m for water temperature (°C), oxygen (mg L^{-1}), pH, as well as duration of thermal stratification (weeks) and Schmidt stability (g cm cm^{-2}) were included in classification and regression tree analysis. Also included were epilimnetic and hypolimnetic concentrations of total phosphorus (TP) (μg L^{-1}), soluble reactive phosphorus (SRP), total nitrogen (TN) (mg L^{-1}), nitrate (NO_3), ammonium (NH_4), soluble inorganic nitrogen (NO_3+NH_4), soluble reactive silicate (SRSi), mass ratios of TN:TP and NO_3:TP, and zooplankton genera (abundance per liter of rotifers, cladocerans, daphnids, bosminids, calanoid and cyclopoid copepods, copepodites and nauplii). Secchi depth was analyzed as an indicator of light availability and a possible predictor variable; however, results indicated it was dependent upon cyanobacteria biomass, and it was therefore excluded from the predictor variable dataset (results not shown).

4.3. Results

Thermal Regime

A total of 26 stratification events ranging in duration between two and eight weeks were observed in Müggelsee (Fig. 4.1a, b). While stratification event frequency increased significantly during the study period (τ_B=0.466, *p*<0.05), thermal characteristics did not display significant long-term trends. The earliest thermal stratification onset was May, and the latest occurred in September (Fig. 4.1a). Event seasonal distribution was homogenous, and no significant long-term trends were observed in the onset of the first and last stratification event, or the end of the last event (*see* Fig. 4.1a).

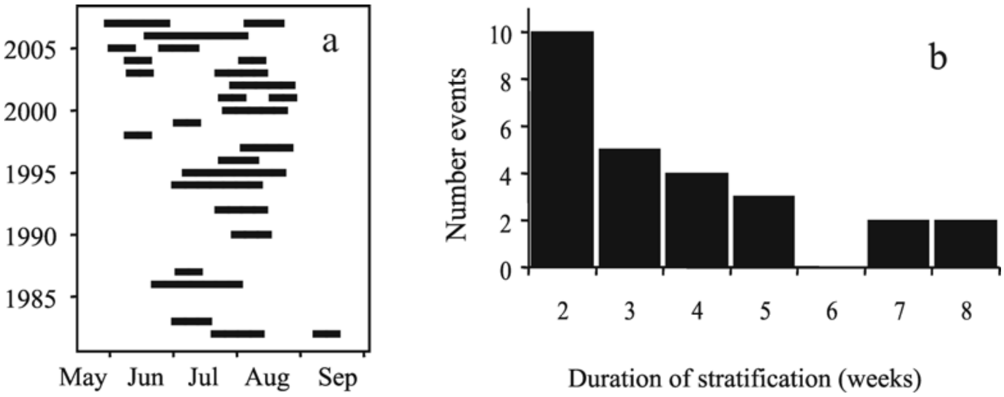

Fig. 4.1: (a) Thermal stratification events in Müggelsee between 1982 and 2007. Each bar represents a single event with a thermal stratification period of two consecutive weeks or longer. The length of the bars corresponds to the duration of the stratification event (two to eight weeks). (b) Frequency distribution for stratification events of different durations.

Development of cyanobacteria

During the study period, summer mean cyanobacteria biomass and contribution to total algal mass decreased (τ_B= -0.509, *p*<0.01; τ_B= -0.453, *p*<0.01, respectively; Fig. 4.2a) but increased with the length of stratification (τ_B= 0.857,

p<0.01; τ_B= 0.929, p<0.01, respectively; Fig. 4.2b). Biomass of the genera *Aphanizomenon* (τ_B= 0.857, p<0.01) and *Anabaena* (τ_B= 0.643, p<0.05) increased with the length of stratification, while *Microcystis* (τ_B= -0.500, p<0.10) biomass decreased slightly (Fig. 4.2b). Cyanobacteria mean contribution increased from 25% during the first week of stratification to ≥ 50% after stratification of four weeks or longer (Fig. 4.2b). High contributions of cyanobacteria were concurrent with high cyanobacteria biomass, which translated to an elevated probability of bloom formation (Fig. 4.2c). Hypolimnetic cyanobacteria biomass estimates for a shorter time period (1999-2007) comprised 1% - 58% (on average 15%) of the cyanobacteria biomass (Fig. 4.2d). The relative contribution of the dominant genera *Aphanizomenon, Anabaena*, and *Microcystis* changed with duration of thermal stratification.

Table 4-1: Regression tree analysis results for the most prominent cyanobacteria genera in Müggelsee. The most important predictor variables, thresholds, and intervals are listed along with respective category biomass. Information on the ecological demands of the three genera is summarized according to Paerl (1988a) and Reynolds et al. (2002).

Genus	Most important predictor	Thresholds and intervals			Ecological demands
Aphanizomenon	TN (mg L^{-1})	≤1.01	(1.01; 1.29)	>1.29	N_2-fixing, buoyancy regulation
	Biomass (mg L^{-1})	0.6	2.7	6.9	
Anabaena	Duration of thermal stratification (weeks)	≤ 3 weeks	> 3 weeks		N_2-fixing, prefers stratified conditions, buoyancy regulation
	Biomass (mg L^{-1})	0.1	2.2		
Microcystis	TP (μg L^{-1})	≤70	(70; 215)	>215	Prefers N- and P-enriched waters, favored by P-pulses, buoyancy regulation
	Biomass (mg L^{-1})	0.1	0.6	3.2	

Contribution of cyanobacteria predictors

The classification trees for ≥ 30%, ≥ 50%, and ≥ 70% cyanobacteria contribution to total algal biomass (Fig. 4.3) were chosen since they separate the major driving forces underlying cyanobacteria development. The ≥ 30% tree represents the ≥ 10% to ≥ 30% contribution, and the ≥ 50% tree represents the ≥ 40% to ≥ 70% contribution. The ≥ 50% tree shows when cyanobacteria reached dominance and the ≥ 70% tree when the duration of stratification was replaced by Schmidt stability as a separating driving force (*see* also Fig. 4.4).

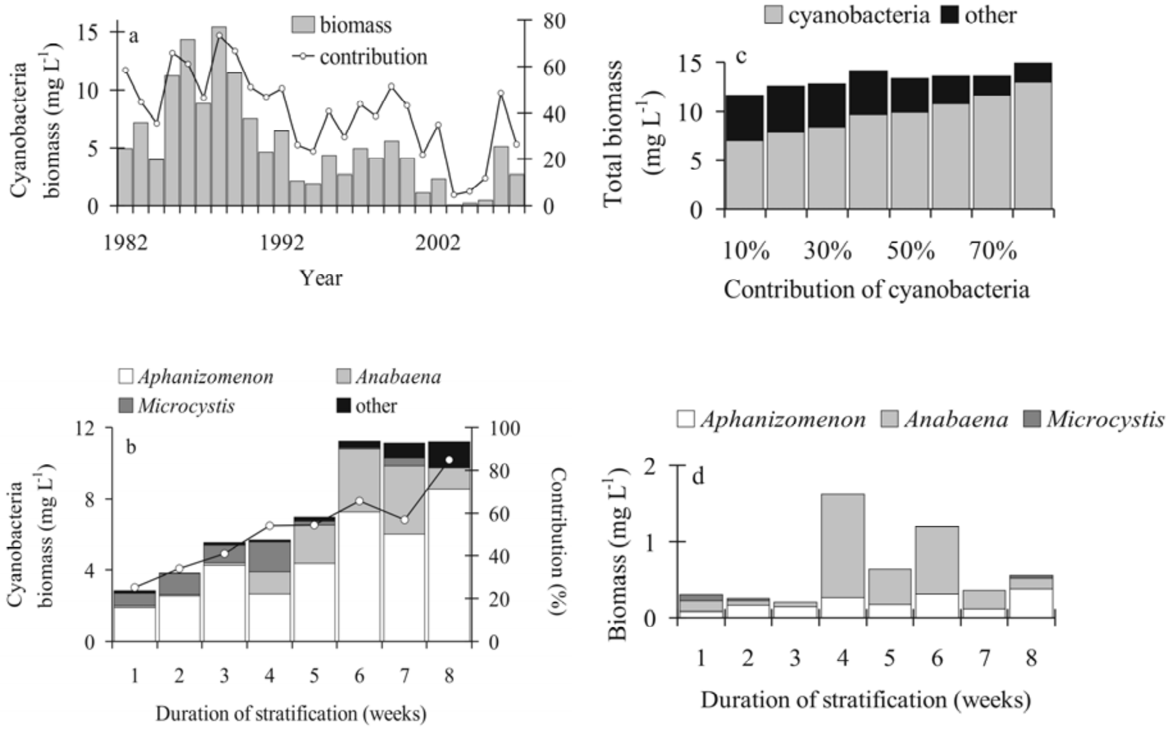

Fig. 4.2: (a) Mean epilimnetic cyanobacteria biomass and contribution to total algal mass during the study period (1982–2007). (b) Mean epilimnetic cyanobacteria biomass and contribution to total algal mass during thermal stratification events of different durations. Biomass was segregated into the dominant genera *Aphanizomenon*, *Anabaena*, *Microcystis*, and other cyanobacteria (other). (c) Mean epilimnetic biomass of cyanobacteria and other algae for surpassed cyanobacterial contributions to total algal biomass, i. e., the 10% bar shows the biomass of cyanobacteria and other algae, if the proportion of cyanobacteria exceeds 10% (10% - 100%), the 20% bar shows the biomass of cyanobacteria and other algae, if the proportion of cyanobacteria exceeds 20% (20% - 100%), etc. It documents that an increasing contribution of cyanobacteria to total algal biomass coincided with an increase in their absolute biomass; indicating the risk of bloom formations once they become dominant. (d) Mean hypolimnetic biomass of the dominating genera *Aphanizomenon*, *Anabaena*, and *Microcystis* during thermal stratification events of different duration.

Subdominant contributions of cyanobacteria: Total nitrogen was the dominant factor for cyanobacteria contributions of up to 30% (Fig. 4.3a; nodes 1, 2). When TN concentration exceeded 1.01 mg L^{-1}, a contribution of ≥ 30% occurred with a probability of 82% (Fig. 4.3a, node 2). In contrast, TN concentrations below 1.01 mg L^{-1} reduced the probability of a ≥ 30% contribution to 28% (Fig. 4.3a, node 1). Within this partition, additional separating factors were TP concentration (Fig. 4.3a;

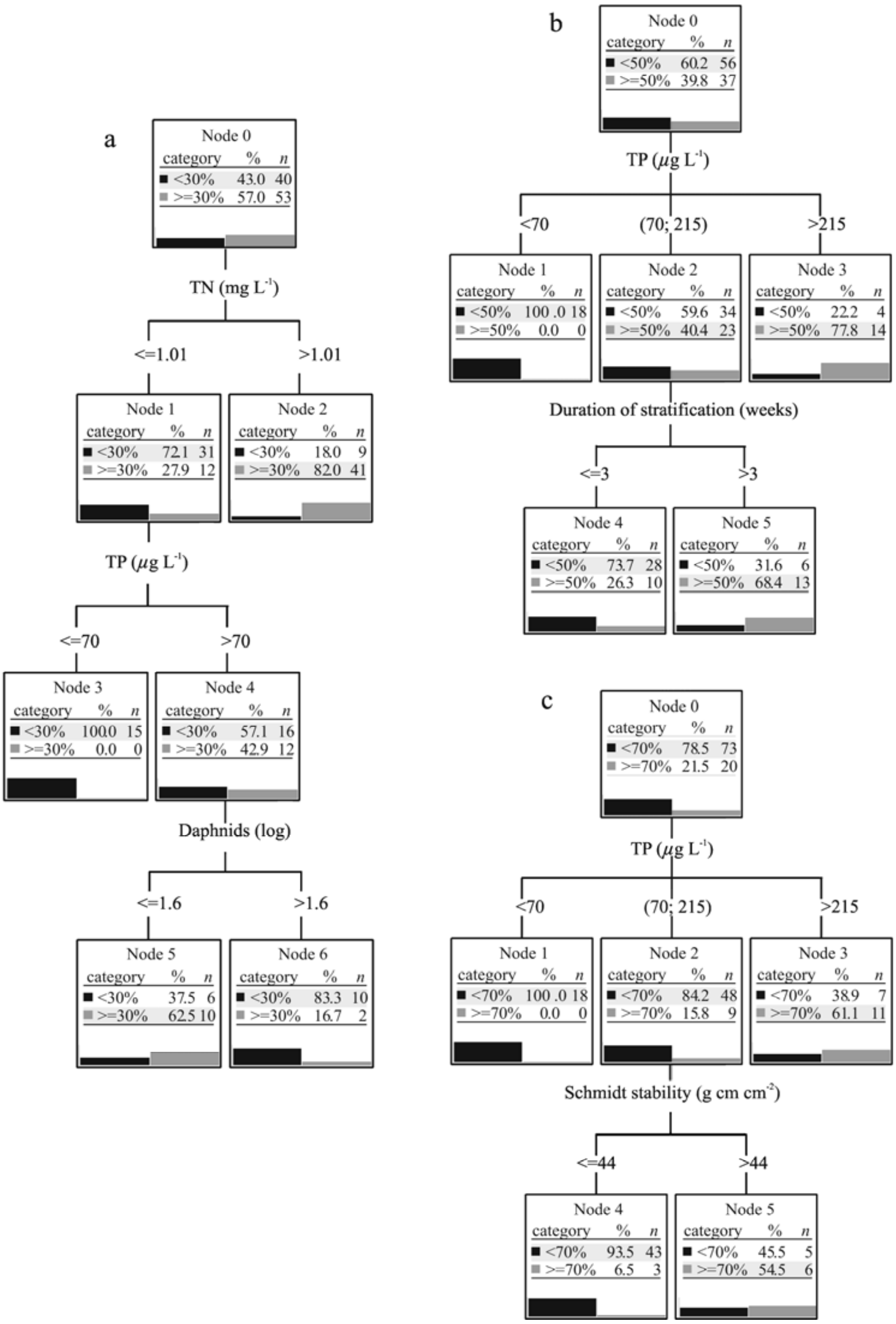

Fig. 4.3: Classification trees for (a) ≥ 30%, (b) ≥ 50%, and (c) ≥ 70% contribution of cyanobacteria to total algal mass. Node 0 represents the initial distribution for two categories: (1) cyanobacteria contribution below the specified threshold (black bar), and (2) cyanobacteria contribution above the specified threshold (grey bar). Each node similarly contains information pertaining to the distribution. Given are the percentage (%) and number (*n*) of cases for respective contribution categories. The extracted predictor variables represent the link, TN = total nitrogen, TP = total phosphorus, Daphnids (log) = log abundance of daphnids, Duration = Duration of stratification, and stability = Schmidt-stability.

nodes 3, 4) and daphnid abundance (Fig. 4.3a; nodes 5, 6). Low concentrations of TP (≤ 70 μg L^{-1}) reduced the probability of ≥ 30% contribution (as well as ≥ 20% contribution, data not shown) to zero (Fig. 4.3a; node 3). Thus, if TN and TP were below 1.01 mg L^{-1} and 70 μg L^{-1}, respectively, the contribution of cyanobacteria was limited to 20%. Generally, zooplankton was of minor importance (Fig. 4.3a; nodes 5, 6).

Dominance of cyanobacteria: Total phosphorus was a crucial factor for cyanobacteria dominance (a contribution of 50% to 70%; Fig. 4.3b, c; nodes 1 - 3). At a TP concentration of ≤ 70 µg L^{-1} the probability of cyanobacteria reaching a ≥ 50% contribution was zero (Fig. 4.3b; node 1), while concentrations > 215 µg L^{-1} increased the probability of reaching a ≥ 50% or ≥ 70% contribution to 78% (Fig. 4.3b; node 3) and 61% (Fig. 4.3c; node 3), respectively. At a TP level in the intermediate range of 70 to 215 µg L^{-1} the duration of thermal stratification determined whether cyanobacteria achieved dominance: a ≥ four week stratification period increased the probability of cyanobacteria reaching ≥ 50% of total algal mass from 26% (Fig. 4.3b; node 4) to 68% (Fig. 4.3b; node 5), and when Schmidt stability exceeded 44 g cm cm^{-2} the probability of a ≥ 70% contribution was 55% (Fig. 4.3c; node 5). Further, Schmidt stability was the most important predictor variable for a ≥ 80% contribution. The probability of a ≥ 80% contribution was 55% if Schmidt stability exceeded 44 g cm cm^{-2} compared to a probability of 14% if Schmidt stability was ≤ 44 g cm cm^{-2} (tree not shown). All predictor variables and their relative importance over the complete range of cyanobacteria contribution (≥ 10% to ≥ 80%) are summarized in Fig. 4.4.

Main factors controlling biomass of dominant cyanobacteria genera: Additionally, we tested major predictors of biomass for the dominating cyanobacteria genera (Table 4-1). *Aphanizomenon* biomass was influenced by TN concentration, *Anabaena* biomass by the duration of stratification, and *Microcystis* biomass by TP concentration, in concordance with well documented ecological demands. The dominating genera primarily consisted of the following species: *Aphanizomenon flos-aquae*, *Anabaena flos-aquae*, *Anabaena crassa*, and *Microcystis aeruginosa*.

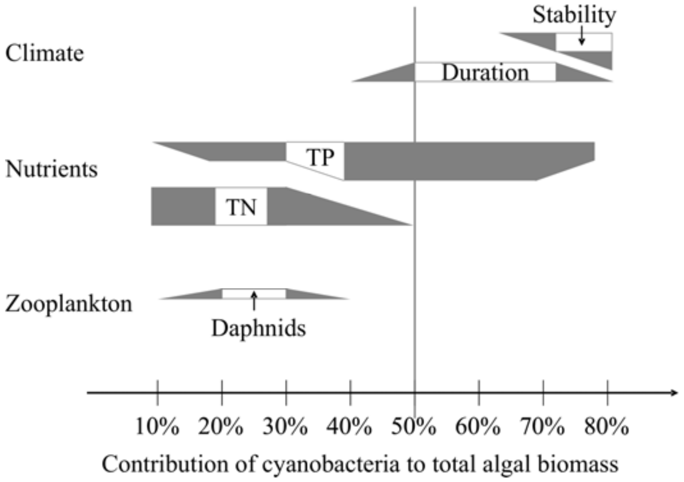

Fig. 4.4: Classification tree analysis results for increased cyanobacteria contribution to total algal biomass (≥ 10% to ≥ 80%). Factors are categorized by climate, nutrients, and zooplankton. Bar height corresponds to the importance of the respective factor. The highest bars represent the most important factors, bars with an intermediate height depict factors that were chosen for the second partition, and short bars represent factors chosen in the third partitioning step. Vertical line highlights 50% cyanobacteria contribution, indicating cyanobacteria dominance.

4.4. Discussion

The effects of global warming include a predicted increase in cyanobacteria bloom formation due to the direct effects of higher water temperature, the longer period of thermal stratification, and increased internal nutrient loads, all of which are beneficial to cyanobacteria (Jöhnk et al. 2008; Paerl and Huisman 2008; Wilhelm and Adrian 2008). Our results confirm these predictions and provide threshold values for cyanobacteria dominance. Climate induced probability for the achievement of cyanobacteria dominance was restricted to TP concentrations of 70 - 215 μg L^{-1} (Fig. 4.3b, c). Below and above the critical TP range, the probability of cyanobacteria dominance was zero and 80%, respectively (Fig. 4.3b, nodes 1 and 3), indicating that bloom formation was independent of climate; however, within the critical TP range, climate warming strongly enhanced the probability of cyanobacteria dominance via an extension of a stable stratification period, with a critical length of ≥ 4 weeks (Fig. 4.3b). Further, climate was the primal force for a cyanobacteria contribution of ≥ 80% (Fig. 4.2c), if Schmidt stability surpassed the critical threshold of 44 g cm cm^{-2}, which yielded the development of strong blooms. This threshold was usually surpassed in climate induced prolonged stratified periods (Wilhelm and Adrian 2008). Zooplankton abundance was of minor importance, and observed effects were limited to daphnids and subdominant cyanobacteria contributions (Fig. 4.3a, Fig. 4.4), confirming that cyanobacteria are resistant towards grazing, particularly at high densities (Lampert 1987).

Absolute TP and TN concentrations, rather than nutrient ratios, were the most important drivers of cyanobacteria biomass during stratification events in Müggelsee (Fig. 4.4), buttressing previous findings by Lathrop et al. (1998), and Downing et al. (2001). During stratification, TN:TP ratios were consistently less than 20:1, and hence within the spectrum favoring N-fixing cyanobacteria (cyanobacteria favorable TN:TP ratio below 20; Smith 1983; Steinberg and Hartmann 1988). The critical TP threshold for the prevention of cyanobacteria bloom formation in Müggelsee over the last three decades, as reported here, was in agreement with thresholds identified in lakes around the world (Dokulil and Teubner 2000; 50 μg L^{-1}; Downing et al. 2001; 70 μg L^{-1}). Given the broad range of TP concentration (70-215 μg L^{-1}) critical to the stimulation of cyanobacteria bloom formation, it is reasonable to infer that climate warming will enhance the probability of cyanobacteria bloom formation in shallow lakes, which tend to be productive – hence within the observed critical TP range.

We found no evidence that cyanobacteria profited directly from increased water temperatures (Adrian et al. 2006). The average epilimnetic summer temperature during thermal stratification (1982 – 2007 mean = 21.6°C) already fell within a temperature range favorable to cyanobacteria (McQueen and Lean 1987), but inauspicious for diatoms (approximately 36% of total algal mass in Müggelsee during summer), which were negatively influenced by water temperatures above 20.5°C (C. Wagner unpubl. data). Climate driven effects were indirect, critically the prolonging and enhancing the stability of thermal stratification periods (Fig. 4.3, Fig. 4.4).

The indirect effects of temperature on stratification conditions are two-fold: species either prefer a stable water column (e.g., especially *Anabaena*; Paerl 1988a) or they profit from an internal phosphorus load within the hypolimnion (e.g., buoyant *Microcystis* and *Anabaena;* Bormans et al. 1999), or both (Table 4-1). Stratification in eutrophic lakes generally results in enhanced nutrient supply, specifically phosphorus, which is mediated by low oxygen and elevated hypolimnetic temperature, thus stimulating overall hypolimnetic phosphorus accumulation (Søndergaard et al. 2003). In Müggelsee, thermal stratification results in an immediate oxygen depletion and subsequent high phosphorus accumulation in the hypolimnion (Wilhelm and Adrian 2008). Other than in deep lakes, migration amplitudes for *Microcystis* and *Anabaena* of several meters (Ibelings et al. 1991; Bormans et al. 1999) are sufficient to actually reach the rich hypolimnetic nutrient pool in shallow lakes such as Müggelsee (maximum depth 8 m), where an average of 15% of the cyanobacteria biomass was found in the hypolimnion (Fig. 4.2d). This gives direct evidence that buoyant species of the genera *Microcystis* and *Anabaena* may indeed profit from the climate induced elevated internal phosphorus load (Steinberg and Hartmann 1988; Jöhnk et al. 2008). This is in line with the robust increase in the proportion of phosphorus demanding *Microcystis* after the onset of stratification (Fig. 4.2b; Table 4-1). However, *Microcystis* was replaced by *Anabaena*, a nitrogen-fixing genus that thrives in stable water columns (Table 4-1, Paerl 1988a), when the duration of stratified conditions exceeded four weeks (Fig. 4.2b, Table 4-1). Congruent with the N decrease associated with external nutrient reduction during the past few decades (Köhler et al. 2005; Wagner and Adrian 2009a), the N-fixing genera *Aphanizomenon* and *Anabaena* (Paerl 1988a; Reynolds et al. 2002) gained significance within the ecosystem resulting in an increased contribution to total algal mass (Fig. 4.2b). All prominent cyanobacteria genera within Müggelsee (Fig. 4.2b) prefer phosphorus enriched waters to varying degrees (Paerl 1988a; Steinberg and Hartmann 1988), including migrating species (e.g., *Microcystis*) that profit from climate induced internal hypolimnetic phosphorus pulses (Olsen et al. 1989) and species capable of N-fixation in the N depleted epilimnion (e.g., *Anabaena*). Species that have adapted to stable water columns and are N-fixation capable should profit the most under predicted climate warming scenarios, i.e., the occurrence of prolonged and increasingly stable thermal stratification events. Underlying mechanisms for the replacement of *Microcystis* by *Anabaena*, which both profit from stable conditions, are not fully extractable from observational data. There is, however, strong evidence that nitrogen limitation may have been crucial for *Anabaena* to outcompete *Microcystis*. Indeed, data on cyanobacteria composition in the hypolimnion for a shorter time period (1999 – 2007; Fig. 4.2d) revealed enhanced biomass of *Anabaena* during long lasting stratified periods, whereas *Microcystis* was only found during short stratified periods of 1-2 weeks duration. A decrease in buoyancy in several cyanobacteria genera, including *Microcystis*, under N and P limitation has been consistently reported from numerous studies (Konopka et al. 1987; Klemer et al. 1996). Thus, under nitrogen limiting conditions as observed in Müggelsee (Wagner and Adrian 2009a), nitrogen- fixing species such as *Anabaena* gain an advantage over non N- fixing species of *Microcystis*. This advantage may be further enhanced if epilimnetic SRP concentrations become additionally limiting during stratification events, as recently documented for Müggelsee (Wilhelm and Adrian 2008).

In our polymictic lake, we predict *Anabaena* will profit most under future climate scenarios, as it has already increased during the longer stratification events observed in the present study (Fig. 4.2b). Our results capture the well known ecological demands of the cyanobacteria community, a community typically found in eutrophic shallow lakes including dimictic one's (Steinberg and Hartmann 1988; Reynolds et al. 2002), extremely well. Hence, the observed role of climate warming in enhancing the risk of cyanobacteria bloom formation provides valuable quantitative thresholds of the major driving forces with respect to phosphorus and thermal stratification. Those thresholds can be used to make projections of cyanobacteria dominance under future climate scenarios. It is worth keeping in mind, however, that physical conditions in polymictic lakes differ substantially from shallow dimictic lakes; in particular, hypolimnetic water temperature is higher compared to dimictic shallow lakes due to the frequent alteration between mixed and stratified conditions and lower stability, leading to higher phosphorus release rates from the sediment – not only after the breakdown, but also during stratification (Søndergaard et al. 2003; Wilhelm and Adrian 2008).

Climate change will counteract the tremendous efforts to reduce lake external phosphorus loads to eutrophic lakes by fostering internal nutrient release from sediments in dimictic and polymictic lakes (Wilhelm and Adrian 2008). Lakes at the edge of the lower TP threshold, not yet dominated by cyanobacteria, may thus experience cyanobacteria dominance under future climate scenarios. The changes in cyanobacteria bloom formation observed in the present study occurred during a mean rise in summer air temperature of ~0.7°C per decade (Adrian et al. 2006).

Based on projections under various emission scenarios (Meehl et al. 2007), global surface temperatures will increase by 1.8 – 4.0°C by the end of this century, further enhancing the duration and frequency of thermal stratification periods in shallow lakes and thereby increasing the probability of cyanobacteria blooms. With respect to lake management, our results clearly show that lake TP concentrations below the critical threshold of 70 μg L^{-1} are necessary to mitigate predicted temperature increases.

Based upon the predicted climate scenarios, cyanobacteria blooms will increase and thus pose a threat to recreational water use and the consumable water supply. However, the trophic state, itself influenced by climate warming, determines the thresholds associated with enhanced probability. The field of climate effect research has achieved the capability to quantify critical system thresholds for climate driven responses. Given that all cyanobacteria genera prominent in Müggelsee and those dispersed in other eutrophic shallow lakes are potential toxin producers (Paerl 1988a; Steinberg and Hartmann 1988), cyanobacteria blooms are likely to again become problematic in western countries, such as they were in the 1960s and 1970s, a period of heavy lake eutrophication.

Acknowledgements

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5. General Discussion

Climate-induced changes on abiotic and biotic system levels

Climate warming was manifested in lakes at all system levels. In the northern hemisphere, reductions in the duration of ice cover (Weyhenmeyer et al. 1999; Livingstone 2000; Magnuson et al. 2000), increases in epilimnetic water temperatures (Gerten and Adrian 2002b; Austin and Colman 2007) and extension of summer stratification (Livingstone 2003; Winder and Schindler 2004) have been documented, thus changing the physical boundaries for the plankton community. The most coherent and synchronous response to warmer temperatures appeared to be earlier succession of plankton communities in the spring (Gerten and Adrian 2000; Straile 2002; Rusak et al. 2008). However, warming effects were highly season-specific (Adrian et al. 2006; Blenckner et al. 2007; Chapter 2), and temperature-related impacts to various trophic levels that occurred during the summer are less well studied (Adrian et al. 2006; Blenckner et al. 2007; Straile and Stenseth 2007). In this thesis, I studied several aspects of the impact of climate on lakes, with emphasis on summer conditions, under special consideration of superimposed changes in trophic status.

The occurrence of thermal stratification during the summer in polymictic lakes has increased substantially during the last few decades due to atmospheric warming. In particular, the frequency of long-lived thermal stratification events has risen (Livingstone 2008; Wilhelm and Adrian 2008; this thesis), and this trend is likely to continue and intensify (Livingstone 2008). It has been predicted that the number of days when Müggelsee is stratified in the summer will increase by 10 between 2000 and 2050 (Kirillin 2003), and that this increase will be accompanied by a predicted 1°C change in water temperature (Fig. 5.1). This prediction is based on climate scenarios from the Potsdam Institute of Climate Impact Research (PIK). Gaining a comprehensive understanding of the effects of thermal stratification may provide insights into the future condition of lakes, particularly if extended stratification becomes more common and triggers altered lake characteristics, higher water temperatures and a more stabilized water column (King et al. 1997; Livingstone 2003; Jankowski et al. 2006).

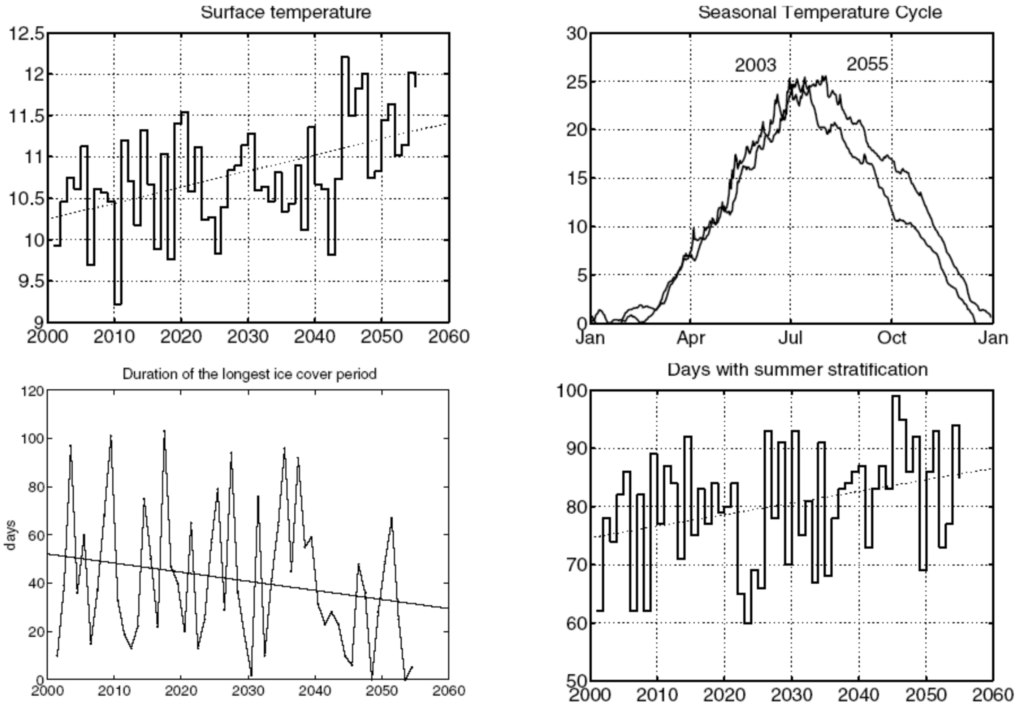

Fig. 5.1: Predictions of surface water temperature (°C), seasonal temperature cycle (°C) (upper panel), duration of ice cover and summer stratification (lower panel) for Müggelsee, 2001 – 2055. The predictions are derived from the TeMiX – model, developed by Dr. Georgyi Kirillin (IGB Berlin); the model was run with climate scenarios developed at the Potsdam Institute of Climate Impact Research (PIK). Charts were taken from Kirillin (2003).

Under such limnetic conditions, oxygen depletion at the lake bottom is likely to occur and be accompanied by subsequent nutrient pulses into the hypolimnion (Søndergaard et al. 2003; Jankowski et al. 2006; Wilhelm and Adrian 2008), thus counteracting the improvements in trophic status (Blenckner et al. 2002; Jeppesen et al. 2005; Wilhelm and Adrian 2008; Chapter 4). Thermal stratification of long duration, therefore, can be regarded as a significant disturbance of the aquatic system, which is likely to alter plankton composition but not necessarily diversity (Chapter 3).

The nature of responses for physical system variables and system components was mostly abrupt permanent (Chapter 2), which is in line with the rising concerns that immediate and drastic changes in systems may occur if the system is forced across critical thresholds (Alley et al. 2003; Scheffer and Carpenter 2003), as has already been shown for climate change and subsequent regime shifts in entire ecosystems (Scheffer et al. 2001; Walker and Meyers 2004; Alheit et al. 2005). Specifically, the amount of thermal stratification in Müggelsee increased abruptly in

1992 (Chapter 2; Table 2-1), and moreover, the number of long-lived thermal stratification events doubled since 1994 compared to the early period (1982 – 1993; Chapter 3; Fig. 3.1), and we observed at least one long-lived stratification event in the late period. Thus, the abrupt permanent increase in the abundance of thermophilic cyclopoid copepods in 1994 (Chapter 2; Table 2-1) was not surprising, as they directly profited from increased water temperatures, but only during periods of thermal stratification (Chapter 3; Table 3-3). For the cyclopoid copepods, the abrupt increase in thermal stratification may thus have been related to a surpassed threshold initiating a substantial and sustained increase in thermal stratification in 1994 (Chapter 4, Fig. 4.1). Therefore, the surprisingly coherent responses of summer abundances of cyclopoid copepods over large spatial scales to climate fluctuations (Blenckner et al. 2007) may indeed be driven by warming, however, this was probably not a temperature effect *per se*, but particularly temperature during stratification, as only water temperature in stratified periods, which was significantly higher than during lake mixing (Chapter 3, Fig. 3.2), showed a strong positive correlation to the abundance of cyclopoid copepods (Chapter 3, Table 3-3). We could not estimate, however, to what extent potential top-down effects by fish may have changed, as there are no appropriate data available for Müggelsee.

For the phytoplankton, superimposed effects of climate warming and nutrient load reduction may have acted antagonistically or additively, due to physiological demands of algae species (Reynolds et al. 2002). Lake nutrient status in summer changed abruptly in 1990 (Chapter 2, Table 2-1), as did the summer biomass of phytoplankton and, specifically, cyanobacteria (Chapter 2, Table 2-1). However, climate warming may have counteracted the effects of reduced nutrient load (Jeppesen et al. 2005; Paerl and Huisman 2008), in particular, cyanobacteria growth was favored during extended periods of thermal stratification (Chapter 4, Fig. 4.2b). However, regarding cyanobacteria as a taxonomic group neglects the fact that species specific responses may vary according to their ability to perform buoyancy and N-fixation (Paerl 1988a; Reynolds et al. 2002). Indeed, community composition of cyanobacteria shifted towards higher importance of N-fixing buoyant cyanobacteria, like *Anabaena*, with increasing length of thermal stratification (Chapter 3, Fig. 3.4; Chapter 4, Table 4-1). Conversely, warming and nutrient load reduction have acted in the same adverse direction in case of the diatoms, the change in trophic status led to a gradual overall decrease in diatom biomass in the summer (Chapter 2, Table 2-2), and in addition, the increase in periods of long-lived thermal stratification during the summer discouraged diatom growth both directly by enhanced water temperatures and indirectly by higher sinking losses due to reduced mixing (Chapter 3, Table 3-3, and Fig. 3.3), which is in line with changes reported in recent studies (Strecker et al. 2004; Rühland et al. 2008; Winder et al. 2009). Given the prospected further increase in periods of thermal stratification in the future (see above), I conclude that the system is likely to shift towards a phytoplankton community consisting of species well adapted to stable and stratified conditions, like buoyant cyanobacteria able to perform N-fixation (e. g., *Anabaena*; Paerl 1988a; Reynolds et al. 2002). In addition, some of those taxa are toxin-producers (as is, e. g., *Anabaena*; Sotero-Santos et al. 2008; Wiedner et al. 2008). Thus, lake functional properties may shift towards accelerated N-fixation and toxin-production when anticipating further global warming (Paerl and Huisman 2008). However, strong climate-related changes in community composition did not reflect in substantial changes in plankton diversity yet (Chapter 3), in line with findings so far, that there is little evidence that climate warming already showed signs of adverse effects on the diversity of aquatic communities (McKee et al. 2002; Burgmer et al. 2007). However, there is consensus that future climate change, in combination with concomitant changes in abiotic and biotic lake processes, such as changes in trophic status, higher rate of invasion of exotic species or dispersal processes, may have severe impacts on the diversity of plankton communities and thus on ecosystem functioning, as has already been shown for terrestrial ecosystems (MA 2005; Rosenzweig et al. 2007).

Confounding effects

The given examples demonstrate that responses to altered environmental conditions may be related to one factor only (temperature during stratification for the cyclopoid copepods) or to the combined effects of several factors (enhanced thermal stratification within critical nutrient thresholds for cyanobacteria dominance). Lakes in general are subject to multiple stressors, and the impacts of those stressors vary with the type, number and intensity, as well as the size and inherent buffering capacity of the particular lentic system (Gerten and Adrian 2001). Müggelsee is a typical representative of a polymictic temperate lake of the northern hemisphere. It has been exposed to a variety of natural and anthropogenic environmental changes in recent decades; in particular climate warming, and changes in the catchment characteristics (e.g., reduction in nutrient load), operating simultaneously in many temperate lakes (George et al. 1990; Anneville et al. 2005; Jeppesen et al. 2005; Chapter 2), yet their spatial scales are unquestionably different. While climate change is a global phenomenon (Hurrell et al. 2001; Trenberth et al. 2007), regional land use and local catchment characteristics are more important in affecting a lake's trophic status (Søndergaard et al. 2003; Köhler et al. 2005; Carpenter et al. 2007). Thus, the response of each lake to climate warming is strongly determined by individual characteristics related to nutrient availability (Jeppesen et al. 2005; Weyhenmeyer et al. 2007; Huber et al. 2008). Discriminating between the distinctive effects of climate change and nutrient load reduction on the one hand, and the combined climate–nutrient effect on the other hand, is a major challenge for understanding lake ecosystem functioning (Carvalho and Kirika 2003; Jeppesen et al. 2005; Elliott et al. 2006) and an important prerequisite for predicting lake response based on climate scenarios (Carvalho and Kirika 2003; Mooij et al. 2005). To address this issue, different approaches can be used. A commonly used method is detrending, or removing the long-term trend from the relevant time series and studying the effect of an additional factor on the detrended time series (George et al. 2004; Jankowski et al. 2006). However, the removal of any long-term trend does not allow for the separation of individual and joint effects of multiple stressors. To make that differentiation, additional methods were applied, including correlation/regression techniques (Hakanson et al. 2007; Weyhenmeyer et al. 2007; Wilhelm and Adrian 2007), modelling approaches (Elliott and May 2008; Huber et al. 2008), the latter technique also allowed the development of simulations under different scenarios, and meta–analysis, which is a way to determine the effect size for different stressors over a large number of ecosystems (Blenckner et al. 2002; Blenckner et al. 2007). In this thesis, I analyzed temporal shifts in the physical components and nutrient status of the lake, and found that significant effects occurred both simultaneously and chronologically, but there were differences between seasons in how these effects were manifested (Chapter 2). In addition, I was able to determine nutrient and climatic thresholds associated with the occurrence of cyanobacteria dominance in the summer (Chapter 4) by using classification tree analysis, a powerful but easily-applied method for distinguishing between effects (De'ath and Fabricius 2000). This technique provides a very intuitive graphical representation of individual, and joint, effects on the system being studied.

Temporal scales

A fundamental challenge in limnological research is choosing the appropriate time scale for the particular study question (Levin 1992; Mac Nally and Quinn 1998; Whittaker 2000). System perturbations as well as internal processes may act on very different temporal scales (Greathouse et al. 2006; Peters et al. 2007; Takimoto et al. 2009). Fluctuations on a fine temporal scale cannot be detected using data of a rather coarse temporal resolution. Conversely, general patterns on a decadal scale may not be detected using high temporal resolution data (Anderson 1995; Cumming et al. 2006; Kitron et al. 2006). Whereas global warming, in general, acts on a coarse temporal scale of years to decades, localized weather conditions can shift quickly and result in very rapid warming (or cooling) events that may precipitate significant disturbances in the system on a weekly (e.g., heat waves) or even an hourly (e.g., storms and heavy rain events) scale. Reduction of the anthropogenic nutrient load can operate on a rather coarse temporal scale of years and decades (Köhler et al. 2005; Jeppesen et al. 2007b), but climate-induced internal nutrient pulses occur on a finer temporal scale of a few days or even hours (Wilhelm and Adrian 2008). Similarly, ecosystem responses and processes can occur over decades, as has been shown for distinct system component states (Chapter 2), as well as on an intraannual scale, (e.g., plankton diversity and cyanobacteria performance (Chapters 3, 4)). Even finer temporal scales may be applicable to some events. Wilhelm and Adrian (2008), for example, were able to show that summer thermal stratification events of less than one day were very common. Furthermore, the speed of a species` growth and response is highly dependent on its growth rate that is, in turn, often related to its position in the trophic cascade. Based on an analysis of long-term, weekly *in situ* measurements, we were able to capture changes and trends ranging from decadal (Chapter 2, 3) to weekly (Chapters 3, 4).

Advances in limnology: New technologies

Recently, new technologies, such as buoys and floating stations, have allowed for not only the monitoring of physical lake properties, like vertical temperature or oxygen profiles, but also biological markers, such as chlorophyll and phycocyanin concentrations, at high temporal resolution. Current technology allows data to be recorded every second, or even more frequently, and provided to the technician or scientist *in real time*. This ability to accurately log information at an astonishing rate has resulted in a rapid and monumental shift in the dimension of data quantity, thus yielding results that may not be comparable to existing long-term data. Continuous weekly measurements of *in situ* data over 30 years, for example, would have resulted in a total of 1,500 observations, which is approximately the number of single-day observations when data are collected every minute. Thus, data management strategies must be improved and optimized according to the new requirements; new analytical tools will certainly be necessary. Meeting these challenges will only be possible if expertise from different fields is brought together in an interdisciplinary scientific environment. A first attempt is GLEON, the **G**lobal **L**ake **E**cological **O**bservatory **N**etwork (http://www.gleon.org), a grassroots network of researchers from the fields of limnology, ecology, information technology, statistics and engineering. GLEON is attempting to gain new ecosystem understanding by providing the technical and analytical tools to perform meta-analysis based on high-frequency abiotic and biotic data from lakes all over the world. Using this information, it will be possible to study the impact of perturbations on lake properties and their propagation up the food web by applying mechanistic approaches to reveal and model fundamental processes that are driving changes. By obtaining data on a very fine temporal scale, certain thermal or chemical tolerance thresholds that previously were unidentifiable can a quantified, based upon which the implementation of “early warning systems” may be possible to alert impending thresholds in time to avert them (Carpenter et al. 2008; Biggs et al. 2009). Finally, by applying the same approaches to multiple lakes at different geographic locations, similarities and differences can be identified and patterns, if present, may be clarified.

Conclusions

The purpose of this study was to explore the connection between increasing global temperature and particularly summertime effects on a polymictic lake under consideration of simultaneously acting forces such as changes in trophic status. This study visualized expedient methods to (a) analyze changes within the entire ecosystem through a system-integrating approach, and (b) separate the effects that are associated with climate from those that are directly related to nutrients, and determine the critical thresholds of these key factors.

Accelerated warming of lake water, beginning in early spring and continuing during the summer, altered the physical properties of the lake by raising water temperature and enhancing thermal stratification leading to sustained shifts in the physical system component and to subsequent shifts on biological system levels in the long-term as well as on an intraannual scale of several weeks. Although a variety of structural and functional changes have been observed on all levels, overall diversity of the lake was maintained, primarily through substantial shifts in community composition. Thermophilic taxa that are highly tolerant of elevated environmental temperatures, and those that prefer stable water column conditions, are more likely to out-compete plankton, which is better adapted to lower temperatures and mixed conditions, to become dominant in thermally-altered ecosystems. To prevent undesired shifts in lake communities, such as blooms of cyanobacteria, it will be necessary to determine critical thermal and nutrient thresholds and initiate effective, reasonable management measures. By now, climate impact research has reached the stage to be able to separate distinct and joint effects of simultaneously acting forces from existing time series.

Referring back to the original statement at the very beginning of this thesis, I would conclude that, while our knowledge about the effects of climate change on lake ecosystems has grown substantially in recent years due to available decadal records on lake properties, there is still an insufficient amount of information to fully understand the complexity and magnitude of possible impacts. Increasing availability of highly sophisticated and accurate detection equipment and access to high-resolution temporal data will allow for development of very detailed insights into lake processes. I am convinced that, with these new information acquisition systems, limnology is on the verge of a new era of lake ecosystem understanding.

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