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Climate induced impacts on lake functioning in summer

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LIST OF ABBREVIATIONS

A_L	Absorption coefficient for long-wave radiation
A_S	Absorption coefficient for short-wave radiation
C	Cloud cover
DIN	Dissolved inorganic nitrogen
$DL_{5,8,12}$	Day lengths at the timing of spring water temperatures of 5 °C, 8 °C, 12 °C
DO	Dissolved oxygen
DO_h	Dissolved oxygen (hourly measured)
DO_w	Dissolved oxygen (weekly measured)
E	Heat content
e_a	Water vapour pressure
E_L	Emission coefficient of the atmosphere
e_s	Saturation vapour pressure
f	Wind function
G	Global radiation
G_0	Clear-sky global radiation
H_B	Emission of long-wave radiation
H_C	Convection and conduction
H_{calc}	Net heat flux into the lake (calculated)
H_E	Evaporation and condensation
H_F	Inflow and outflow (heat flux)
H_L	Absorption of long-wave atmospheric radiation
H_{meas}	Net heat flux into the lake (measured)
H_P	Precipitation (heat flux)
H_S	Absorption of short-wave solar radiation
NAO	North Atlantic Oscillation
NH_4	Ammonium
NO_3	Nitrate
Q	Discharge
r_h	Relative humidity
SRP	Soluble reactive phosphorus
SRSi	Soluble reactive silicon
T_0	Epilimnetic temperature

$T_{0,dtr}$	Daily epilimnetic temperature range
$T_{0,max}$	Daily maximum epilimnetic temperature
$T_{0,min}$	Daily minimum epilimnetic temperature
T_{air}	Air temperature
$T_{air,dtr}$	Daily air temperature range
$T_{air,max}$	Daily maximum air temperature
$T_{air,min}$	Daily minimum air temperature
T_{eq}	Equilibrium temperature
$T_{eq,dtr}$	Daily equilibrium temperature range
$T_{eq,max}$	Daily maximum equilibrium temperature
$T_{eq,min}$	Daily minimum equilibrium temperature
T_{inflow}	Mean inflow temperature
u_{10}	Wind speed 10 m above the lake surface
WT	Water temperature
$WT_{5,8,12}$	Timing of spring water temperature of 5 °C, 8 °C, 12 °C

ZUSAMMENFASSUNG

Es gibt bereits viele Hinweise dafür, dass Seen sehr sensibel auf die anthropogen verursachte Klimaerwärmung reagiert haben. Bis jetzt haben sich die Studien der Klimafolgenforschung hauptsächlichst auf die Auswirkungen der Erwärmung im Winter und Frühling konzentriert. Über den Einfluss der Klimaerwärmung auf Seen in den gemäßigten Breiten im Sommer ist weniger bekannt. In der vorliegenden Doktorarbeit habe ich einige Faktoren, welche die Reaktion von Seen auf die Erwärmung im Sommer vermutlich stark mitbestimmt haben, untersucht. Der Schwerpunkt lag dabei auf klimatisch induzierten Auswirkungen auf die thermische Charakteristik und die Phänologie und Abundanz des Planktons eines flachen und polymiktischen Sees (Müggelsee, Berlin).

Zuerst wurde der Einfluss der Klimaerwärmung auf die Phänologie und Abundanz des Planktons in verschiedenen Jahreszeiten untersucht. Das schnellwachsende Phyto- und Zooplankton (*Daphnia*) im Frühjahr hat sich vorwiegend synchron vorverschoben, wohingegen Veränderungen des Sommerzooplanktons deutlich artspezifisch und nicht synchron waren. Die Phänologie oder Abundanz einiger Sommercopepoden hat sich entsprechend der individuellen thermischen Anforderungen innerhalb bestimmter Entwicklungsstufen, wie zum Beispiel der Emergenz von der Diapause im Frühling, verändert. Die Studie unterstreicht, dass nicht nur der Grad der Erwärmung, sondern auch dessen Zeitpunkt innerhalb des Jahres von großer ökologischer Bedeutung ist. Die asynchronen Veränderungen im Sommerplankton haben möglicherweise zu einem Versatz von eng gekoppelten Räuber-Beute-Beziehungen geführt. Somit könnte die Klimaerwärmung sich über die trophische Kaskade fortpflanzende Effekte auch im Müggelsee ausgelöst haben.

Um die Auswirkungen des Klimawandels auf die thermischen Eigenschaften des Sees zu erforschen, habe ich die Langzeitentwicklung der täglichen epilimnischen Temperaturextrema während des Sommers untersucht. Durch diese Studie wurde zum ersten Mal für Seen gezeigt, dass die täglichen epilimnischen Minima (Nacht) stärker angestiegen sind als die Maxima (Tag), wodurch sich der tägliche epilimnische Temperaturbereich deutlich verringert hat. Diese Tag-Nacht-Asymmetrie in der epilimnischen Temperatur wurde durch eine erhöhte Emission von Langwellenstrahlung aus der Atmosphäre während der Nacht verursacht. Dies unterstreicht, dass nicht nur Erhöhungen der Lufttemperatur, sondern auch Änderungen anderer meteorologischer Variablen wie der Windgeschwindigkeit, der Luftfeuchte und der Bewölkung eine wichtige Rolle bei der Bestimmung der Seetemperatur im Hinblick auf weitere Klimaveränderungen spielen werden.

Zudem wurde eine Kurzzeitanalyse zum Schichtungsverhalten des polymiktischen Sees durchgeführt, um die Häufigkeit und Dauer von Schichtungsereignissen und deren Einfluss auf den gelösten Sauerstoff, die gelösten Nährstoffe und das Phytoplankton zu untersuchen. Selbst während der längsten Schichtungsereignisse (Hitzewellen 2003 und 2006) unterschieden sich die Auswirkungen auf den See von denen, welche in flachen dimiktischen Seen während der kontinuierlichen Sommerschichtung auftreten. Die hypolimnische Temperatur war höher, was die Sauerstoffzehrung und die Akkumulation von gelösten Nährstoffen begünstigt hat. Zudem führte jedes lange Schichtungsereignis am Ende zu einem Nährstoffeintrag in die euphotischen Zone, was die Bildung mehrerer Phytoplanktonblüten während des Sommers ausgelöst hat. Die thermische Schichtung wird in Zukunft sehr wahrscheinlich zunehmen. Dies lässt darauf schließen, dass die Planktonentwicklung in polymiktischen Seen viel anfälliger für Änderungen im Hinblick auf projizierte Klimaveränderungen sein wird gegenüber flachen dimiktischen Seen.

Abschließend wurde eine Studie über Lang- und Kurzzeitveränderungen in der Entwicklung der planktischen Larven der Muschel *Dreissena polymorpha* durchgeführt, um den Einfluss der Veränderungen im thermischen und trophischen Regime des Sees zu analysieren. Die Klimaerwärmung und die Verringerung in der externen Nährstofffracht haben die Abundanz der Larven stark beeinflusst indem sie jeweils auf bestimmte Entwicklungsphasen dieser Art während der warmen Jahreszeiten gewirkt haben. Der Anstieg in der Abundanz und der Länge der Larven stand im Zusammenhang mit dem Rückgang der Nährstofffracht und der Veränderung der Phytoplanktonzusammensetzung. Die Hitzewellen in den Jahren 2003 und 2006 haben diesen positiven Effekt auf die Larvenabundanz jedoch durch ungünstige Sauerstoffkonzentrationen während der sehr langen Schichtung aufgehoben. Die Klimaerwärmung kann demzufolge entgegenwirkende Effekte in produktiven flachen Seen, in welchen die externe Nährstofffracht reduziert wurde, auslösen.

Aus diesen Ergebnissen schließe ich, dass nicht nur die Art des Klimawandels und damit der Zeitpunkt der Erwärmung und das Auftreten von Extremen wie Hitzewellen, sondern auch standortspezifische Bedingungen wie Schichtungsverhalten und Trophiegrad entscheidende Faktoren sind, welche die Auswirkungen der Klimaerwärmung auf interne Seeprozesse im Sommer bestimmen. Somit sollte sich die weiterführende Klimafolgenforschung für Seen darauf konzentrieren, wie verschiedene Seetypen auf die komplexen Umweltveränderungen im Sommer reagieren, damit ein umfassenderes Verständnis über den Einfluss von anthropogen verursachten Veränderungen auf Seen der gemäßigten Breiten erreicht wird.

SUMMARY

There is already strong evidence that temperate lakes have been highly vulnerable to human induced climate warming during the last century. Hitherto climate impact studies have mainly focussed on the impacts of the recent long-term warming in winter and spring and little is known on the influence of climate warming on temperate lakes in summer. In the present thesis, I studied some aspects, which may have been strongly involved in determining the response of a lake to climate warming in summer. Thereby I have focussed on climate induced impacts on the thermal characteristics and the phenology and abundance of summer plankton in a shallow polymictic lake (Müggelsee, Germany).

First, the influence of climate warming on the phenology and abundance of the lake plankton was investigated across seasons. Fast-growing spring phytoplankton and zooplankton (*Daphnia*) advanced largely synchronously, whereas long-term changes in the phenology of slow-growing summer zooplankton were clearly species-specific and not synchronised. The phenology and/or abundance of several summer copepod species changed according to their individual thermal requirements at decisive developmental stages such as emergence from diapause in spring. The study emphasises that not only the degree of warming, but also its timing within the annual cycle is of great ecological importance. The asynchronous changes in summer plankton may have resulted in mismatches of tightly coupled predator-prey relationships that have been disrupted by climate warming, implying propagating effects of climate warming across the trophic cascade.

To analyse the impact of climate change on the thermal characteristics of the lake, I examined the long-term development of the daily epilimnetic temperature extrema during summer. The study demonstrated for the first time for lakes that the daily epilimnetic minima (during nighttime) have increased more rapidly than the daily epilimnetic maxima (during daytime), resulting in a distinct decrease in the daily epilimnetic temperature range. This day-night asymmetry in epilimnetic temperature was likely caused by an increased nighttime emission of long-wave radiation from the atmosphere. This underlines that not only increases in air temperature, but also changes in other meteorological variables such as wind speed, relative humidity and cloud cover may play an important role in determining the lake temperature with respect to further climate change.

Furthermore, a short-term analysis on the mixing regime of the polymictic lake was conducted to examine the frequency and duration of stratification events and their impacts on dissolved oxygen, dissolved nutrients and summer phytoplankton. Even during the longest stratification events (heatwaves in 2003 and 2006) the thermal characteristics of the lake differed from those typically found in shallow dimictic lakes, which exhibit a continuous stratification during summer. Particularly, hypolimnetic temperatures were higher, favouring the depletion of oxygen and the accumulation of dissolved nutrient in the hypolimnion. Moreover, each longer stratification event was followed by a nutrient pulse into the euphotic zone, inducing several phytoplankton blooms during summer. Thermal stratification will be very likely amplified in the future, thus, I conclude that, for example, the plankton development in polymictic lakes is more vulnerable to alterations in the thermal regime than in shallow dimictic lakes with respect to projections of further climate change during summer.

Finally, a long-term case study on the long and short-term changes in the development of the planktonic larvae of the freshwater mussel *Dreissena polymorpha* was performed to analyse the impacts of simultaneous changes in the thermal and in the trophic regime of the lake. Both the climate warming and the decrease in external nutrient load were important in determining the abundance of the pelagic larvae by affecting different features of the life-history of this species throughout the warm season. The long-term increase in the abundance and length of larvae was related to the decrease in external nutrient loading and the change in phytoplankton composition. However, the recent heatwaves in 2003 and 2006 have offset this positive effect on larval abundance, due to unfavourable low oxygen concentrations that had resulted from extremely long stratification events, mimicking the effects of nutrient enrichment. Climate warming may thus induce counteracting effects in productive shallow lakes that underwent lake restoration through a decrease in external nutrient loading.

I conclude that not only the nature of climate change and thus the timing of climate warming throughout the seasons and the occurrence of climatic extremes as heatwaves, but also site-specific lake conditions as the thermal mixing regime and the trophic state are crucial factors governing the impacts of climate warming on internal lake processes during summer. Consequently, further climate impact research on lake functioning should focus on how the different lake types respond to the complex environmental forcing in summer, to allow for a comprehensive understanding of human induced environmental changes in lakes.

CHAPTER I
GENERAL INTRODUCTION

Recent environmental changes and impacts on ecosystems

Environmental changes apparent during the last century until today are mainly of anthropogenic origin, due to the steadily increasing population and its high resource consumption (Prentice et al. 2001). There is no doubt about human induced **climate warming** within the last century (Meehl et al. 2004); the global mean air temperature has increased by 0.6 ± 0.2 K since the late 19th century (Folland et al. 2001). Interestingly, over large areas of the earth's surface this long-term warming is known to be proceeding faster during nighttime than during daytime and this day-night asymmetry in warming has resulted in a reduction of the daily air temperature range (Karl et al. 1993, Folland et al. 2001). During the last 50 years a mean reduction in the daily air temperature range of about 0.4 K was found over the land surface (Braganza et al. 2004). The overall increase in global surface temperature has led to spatially and temporally varying changes in the hydrological cycle of the Earth, which increased the risk of extreme precipitation and drought (Folland et al. 2001). In addition, **human land use** by intensified production is steadily becoming a force of global importance (Foley et al. 2005), particularly because of the deposition of nutrients and pollutants.

There are a variety of studies concerning the recent impact of global and regional environmental changes on physical and biological properties of terrestrial and aquatic environments, which provide strong evidence for the vulnerability of ecosystems to intense human induced impacts (e.g. Gitay et al. 2001, Smith et al. 2006). The most obvious ecological trends reported for aquatic and terrestrial ecosystems are advancements of phenological events and shifts in geographical species ranges (e.g. Walther et al. 2002, Parmesan and Yohe 2003, Menzel et al. 2006), and changes in species abundance and community structure (e.g. Hays et al. 2005, Smith et al. 2006). Even subtle changes such as the reduced daily air temperature range have led to significant impacts on terrestrial species (Alward et al. 1999, Turnbull et al. 2004, Whitney-Johnson et al. 2005, Xu and Zhou 2005).

Impacts on freshwater ecosystems

Impacts of climate warming on **thermal conditions** of freshwater ecosystems are widely documented, especially for northern hemispheric temperate lakes (reviewed by Gerten and

Adrian 2002a, Mooij et al. 2005). Rising air temperatures resulted in shortened ice-cover periods (e.g. Weyhenmeyer et al. 1999), increasing epilimnetic (e.g. Schindler et al. 1990, Livingstone and Dokulil 2001) and, especially in deep lakes, hypolimnetic temperatures (e.g. Ambrosetti and Barbanti 1999, Dokulil et al. 2006), an advanced onset of thermal stratification (Gerten and Adrian 2001), an increased lake stability (e.g. King et al. 1997, Coats et al. 2006) and changes in thermocline depth (e.g. Coats et al. 2006). These climate-driven changes in the thermal structure of lakes are known to have been synchronised by the North Atlantic Oscillation (NAO) among lakes in Europe, as this large-scale climatic fluctuation has led to coherent long-term changes in winter and spring (Straile et al. 2003). The magnitude of the observed responses of the thermal characteristics to climate warming have varied substantially within a lake throughout the course of the year (Gerten and Adrian 2002b) and among lakes with different sizes, thermal structures and mixing regimes, indicating different climatic "memories" of the diverse lake types (e.g. Straile and Adrian 2000, Gerten and Adrian 2001). So far, very little work has been done on analyzing the impact that the day-night asymmetry in rising air temperatures might have on the long-term warming of the epilimnion of lakes (Livingstone 2003, Wilhelm et al. 2006; Chapter III). Climatic changes that affected the water cycle resulted in changes of the hydrological regime of lakes (Gitay et al. 2001). Decreases in the water discharge of lakes due to decreased precipitation resulted in a prolongation of the water residence time, which had profound effects on nutrient conditions of lakes (e.g. Schindler 1996) increasing the importance of internal processes in lakes.

Shallow lakes are known to quickly respond to actual weather conditions and are thus particularly prone to changes in climate (c.f. Mooij et al. 2005). Temperate shallow lakes are often polymictic, i.e. they become fully mixed repeatedly during summer due to wind and convection, in comparison to dimictic lakes that are continuously stratified throughout the warm season. Thermal stratification and, hence, the **mixing regime** of a lake strongly determines the lake properties during summer, such as the hypolimnetic dissolved oxygen and nutrient concentrations (Marsden 1989, Søndergaard et al. 2003) and the epilimnetic phytoplankton biomass and composition (Reynolds 1997, Ptacnik et al. 2003, Huisman et al. 2004). For polymictic lakes changes in climate do not only affect thermal conditions but also the frequency and duration of intermittent thermal stratification events, affecting chemical and biological lake processes (Chapter IV). Therefore, shallow polymictic lakes may be more strongly affected by changes in climatic forcing factors during summer than shallow dimictic lakes.

Changes in thermal conditions induced by climate warming are known to affect **biological processes** in freshwater ecosystems. Numerous studies documented changes in composition and abundance of phyto- and zooplankton (reviewed by Gerten and Adrian 2002a), macroinvertebrates (Burgmer et al. 2007) and fish species (Hari et al. 2006) in lakes and streams of Northern Europe. Changes in the spring phenology – the timing of seasonal succession events – of lake plankton were often most pronounced in comparison to changes in species composition and showed coherent patterns among lakes in Europe, synchronised by the winter NAO index (Straile et al. 2003, Blenckner et al. in press). Particularly, earlier occurrences of the phytoplankton spring bloom in warmer years due to shortened ice-cover periods were reported (Adrian et al. 1999, Weyhenmeyer et al. 1999), as well as earlier timings of the clear-water phase induced by *Daphnia*, due to increased winter or spring temperatures (Müller-Navarra et al. 1997, Straile 2000, Scheffer et al. 2001).

Little is known whether the species responses to climate warming are synchronous throughout the course of the year. Because of differences in the ecology of lake plankton, responses to variations in environmental conditions (especially in water temperature and light availability) are species-specific, as for instance shown for climate warming induced changes in zooplankton species (Chen and Folt 2002, Gerten and Adrian 2002b). In spring, the plankton communities are characterised by fast-growing species, which are adapted to the prevailing steep temporal gradients in temperature and light conditions (Reynolds 1984, Sommer et al. 1986). During summer, by contrast, temporal fluctuations of temperature and light are small and slow-growing zooplankton species predominate (e.g. copepods), whose complex life cycles span several months. Climate induced phenology shifts of slow-growing summer plankton species may be less synchronised than phenology shifts of fast-growing spring species, as the longer life cycles of summer species may prevent synchronous changes (Adrian et al. 2006; Chapter II). Thus, environmental changes as climate warming could provoke a decoupling in the phenology of predator-prey relationships in lakes (Stenseth and Mysterud 2002, Winder and Schindler 2004, Mooij et al. 2005), especially during summer.

Besides the influence of climatic conditions on biological properties of freshwater ecosystems, **nutrient availability** is of major importance. Over the past centuries increasing "cultural eutrophication" (term introduced by Hasler 1947) has affected many aquatic systems by anthropogenic nutrient loading, which caused an intensification of all biological activity and typically led to dramatic changes in the composition and structure of food webs (reviewed by Smith et al. 2006). However, within recent decades, ongoing re-oligotrophication processes in lakes are increasingly reported, which mainly resulted from improved wastewater treatments (Anderson et al. 2005). Responses of lakes to a decreased external nutrient load include changes in plankton and fish composition (e.g. Gaedke and Wickham 2004, Jeppesen et al. 2005) and decreases in phytoplankton biomass resulting in a higher water clarity (e.g. Jeppesen et al. 2005, Köhler et al. 2005). However, responses of phytoplankton biomass and composition to a reduced nutrient load were also shown to be more complex. Dokulil and Teubner (2005) reported a delay in the reduction of the total phytoplankton biovolume of Mondsee, Austria, which was caused by species-specific timings in the response of the phytoplankton to the nutrient reduction. And in Lake Constance the re-appearance of phytoplankton summer blooms was observed in several years after the decrease in nutrient load, likely due to simultaneous variations in local weather conditions and related hydrodynamical processes (Gaedke 1998).

Simultaneous changes in forcing factors in lakes and the value of long-term data

Within longer periods of time almost always several driving factors that influence fresh-water ecosystems are changing simultaneously as for instance the above described anthropogenic induced **changes in climate and nutrient loading** within the past decades. Limnologists are becoming increasingly aware that the interpretation of cause-and-effect relationships may be complicated by concomitantly occurring environmental changes as suggested by Jeppesen et al. (2005), who anticipate confounding effects of global warming to reductions in nutrient loading of lakes. Often it remains difficult to separate between the effects of several changing factors; however, there is increasing evidence that various changes in lake ecosystems can be attributed to either changes in climate or in nutrient load through the analysis of long-term data series (George et al. 1990, Scheffer et al. 2001, Edmondson et al. 2003, Anneville et al. 2005). Less is known about how climate change and re-oligotrophication interact, especially how warming could potentially interfere with any recovery from the eutrophication process (Wilhelm and Adrian 2007; Chapter V). For example, the water column stability during summer is known to increase in response to climate warming (King et al. 1997), strongly favouring buoyant phytoplankton species as cyanobacteria and motile flagellates (Reynolds 1997). This might enhance the formation of severe algal blooms (e.g. Huisman et al. 2004, Mooij et al. 2005), which would offset the effect of a reduced nutrient load on the phytoplankton biomass.

To ascertain the particular importance of environmental changes in both climate and nutrient loading on lakes, **long-term data series** spanning several decades are very valuable. On the one hand, the impact of past or historical environmental changes on lake physics, chemistry and biology can be assessed by means of statistical analysis (as for most of the above cited studies, Chapters II and III). On the other hand, modelling approaches using adequate long-term data sets provide useful tools for simulating potential effects of distinct environmental changes on different components of ecosystems (De Stasio et al. 1996, Peeters et al. 2002, Gooseff et al. 2005). Global projections of future climate conditions using different scenarios of future forcing agents (Cubasch et al. 2001) are also available at regional and local scales (The Max Planck Institute for Meteorology in Germany, 2006) and even for distinct lake catchments in Europe (P. Samuelsson, SMHI Sweden, unpublished data). These projections reveal a general increase in air temperature and reductions in wind speed and precipitation during summer and increasing trends for the duration of summer heat waves in central Europe within this century. Besides model analysis, the occurrence of **extreme environmental events** is very useful in determining the impact of intense changes in one of the major driving factor of lake ecosystems (Chapters IV and V). The European heat wave in summer 2003 (Schär et al. 2004), for example, provided an excellent opportunity to study how freshwater ecosystems are likely to function in respect to future climate warming (e.g. Jankowski et al. 2006, Mouthon and Daufresne 2006).

OUTLINE OF THE THESIS

Rationale

Hitherto climate impact studies particularly on temperate lakes have mainly focussed on the influence of the recent long-term warming in winter and spring, for which the winter NAO index proved very important in highlighting the coherence in responses among different lakes across Europe. Climate warming has led to coherent increases in epilimnetic temperatures among lakes and to largely synchronous advances in phenological events in winter and spring within and among lakes (reviewed by Straile et al. 2003), including Müggelsee (Gerten and Adrian 2000). However, relatively little is known on the impacts of the overall summer warming on temperate lakes (e.g. Benndorf et al. 2001). During this season specific characteristics of shallow lakes as the thermal and trophic regime and species specific life-histories and requirements seem to be more important in determining the response of a lake to climate change than large scale climate fluctuations as the NAO (Gerten and Adrian 2002a).

Specifically, there is a lack of knowledge on whether the response of summer plankton to climate warming in a lake is synchronised among species as known for spring. In summer, indirect effects of increases in the water temperature throughout the course of the year may be more important for summer species than the direct water temperature effects observed in spring. Furthermore, little is known on the impact of recent climatic extremes concerning the air temperature on temperate lakes in summer (Jankowski et al. 2006). Besides the asymmetric long-term warming in the daily air temperature extrema, the occurrence of heat waves may affect the epilimnetic temperature and the mixing regime of lakes. Polymictic lakes may be particularly vulnerable with respect to projected increases in the frequency and severity of heat waves in the future (Cubasch et al. 2001). In addition to changes in climate European lakes are very often affected by simultaneous changes in external nutrient loading (e.g. George et al. 1990, Scheffer et al. 2001, Anneville et al. 2005), which complicates the interpretation of changes in the development of summer plankton.

In this thesis, I investigated the impact of climate warming on thermal and biological properties of a shallow temperate lake in summer. Müggelsee (Berlin, Germany) was chosen as study lake, since there is already strong evidence for climate induced changes in its ice duration, water temperature and plankton phenology (Adrian et al. 1999, Gerten and Adrian 2000 and 2002b). As many temperate shallow lakes (c.f. Anderson et al. 2005)

Müggelsee is eutrophic and experienced considerable changes in both climate and external nutrient loading within the last decades (Köhler et al. 2005). Hence, this lake is very suitable for studying the impact of climate variations and of overlapping changes in several environmental driving factors on shallow and productive temperate lakes in general.

Approach of this thesis

First, the influence of climate warming on the phenology and abundance of lake plankton was investigated across seasons (Chapter II). It was hypothesised that climate induced phenology shifts of slow-growing summer plankton species are less synchronised than phenology shifts of fast-growing spring species, as the difference in the length of the life cycles of summer species may prevent from synchronous changes in response to climate warming.

Thereafter, I studied the impact of climate warming on the thermal characteristics of the lake in summer. Since the warming in air temperature is known to be proceeding faster at night than during the day, a long-term study on the development of the daily extrema of the epilimnetic summer temperature was performed (Wilhelm et al. 2006, Chapter III). Air temperature is a major driving factor of the surface water temperature and, hence, the day-night asymmetry in warming may also be present in the epilimnion of lakes. Furthermore, a short-term analysis on the mixing regime of the polymictic lake was made to analyse the frequency and duration of stratification events in summer and their effects on dissolved oxygen, dissolved nutrients and phytoplankton composition and functionality (Chapter IV). The occurrence of heat waves within the study period provided an excellent opportunity to assess the functioning of polymictic lakes with respect to the projected future climate warming.

Finally, a case study on the long-term development of the planktonic larvae of the freshwater mussel *Dreissena polymorpha*, which represent the most sensible stage in the life-history of this species, was performed (Wilhelm and Adrian 2007, Chapter V). The pelagic larvae are affected by the thermal and trophic conditions of the lake throughout the warm season from spring to fall and I aimed at separating the effects of the simultaneous changes in water temperature and nutrient availability on the long and short term changes in larval abundance and length.

CHAPTER II

Life-history traits of lake plankton species may govern their phenological response to climate warming

Rita Adrian, Susann Wilhelm & Dieter Gerten (2006)

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Abstract

A prominent response of temperate aquatic ecosystems to climate warming is changes in phenology – advancements or delays in annually reoccurring events in an organism's life cycle. The exact seasonal timing of warming, in conjunction with species-specific life-history events such as emergence from resting stages, timing of spawning, generation times, or stage-specific prey requirements, may determine the nature of a species' response. We demonstrate that recent climate induced shifts in the phenology of lake phytoplankton and zooplankton species in a temperate eutrophic lake (Müggelsee, Germany) differed according to differences in their characteristic life cycles. Fast-growing plankton in spring (diatoms, *Daphnia*) showed significant and synchronous forward movements by about one month, induced by concurrent earlier ice break-up dates (diatoms) and higher spring water temperature (*Daphnia*). No such synchrony was observed for slow-growing summer zooplankton species with longer and more complex life cycles (copepods, larvae of the mussel *Dreissena polymorpha*). Although coexisting, the summer plankton responded species-specifically to seasonal warming trends, depending on whether the timing of warming matched their individual thermal requirements at decisive developmental stages such as emergence from diapause (copepods), or spawning (*Dreissena*). Others did not change their phenology significantly, but nevertheless, increased in abundances. We show that the detailed seasonal pattern of warming influences the response of phyto- and zooplankton species to climate change, and point to the diverse nature of responses for species exhibiting complex life-history traits.

Introduction

A prominent response of temperate aquatic (Weyhenmeyer et al. 1999, Gerten and Adrian 2000, Edwards and Richardson 2004) and terrestrial ecosystems (Walther et al. 2002) to climate warming is changes in phenology (i.e. annually reoccurring events such as the timing of first occurrence, or the timing when population maxima are reached; for a review see Gerten and Adrian 2002a, Straile et al. 2003). Some coexisting species may respond to climate change at similar rates and thus maintain synchrony, whereas for other coexisting species, loss of synchrony may lead to a decoupling of tightly coupled interactions (Cushing 1990, Stenseth and Mysterud 2002, Winder and Schindler 2004). Besides winter warming, spring and summer are now also subject to warming in Central Europe (Houghton et al. 2001).

The detailed seasonal timing of warming can determine the nature of a species' response, depending on whether species-specific life-history events such as emergence from resting stages spawning or generation times, are matched by the time window during which the warming occurs. Plankton communities in temperate lakes are characterised in spring by a dominance of fast-growing species, which are adapted to the prevailing steep temporal gradients in temperature and light conditions (Reynolds 1984, Sommer et al. 1986), resulting in immediate and likely synchronous phenology shifts to climate warming (Weyhenmeyer et al. 1999, Gerten and Adrian 2000, Straile and Adrian 2000 – but see Winder and Schindler 2004). During summer, by contrast, temporal gradients of temperature and light are small. Slow-growing zooplankton species predominate (e.g. copepods), whose complex life cycles span several months. Such plankton are thus prone to warming events across seasons (Gerten and Adrian 2002b) that do not necessarily coincide. For example, changes in daylength-specific temperatures during spring along with a concurrent warming during winter and spring may significantly influence the emergence of resting stages, and cause mismatches between species later in the year.

Our hypothesis is that climate induced phenology shifts of slow-growing summer plankton species are less synchronised than phenology shifts of fast-growing spring species, as the longer life cycles of summer species may prevent from synchronous changes in response to climate warming. To test this hypothesis, we investigated the interactive effects of warming on the performance of fast (algae, *Daphnia*) vs. slow growing (cyclopoid copepods, larvae of the mussel *Dreissena polymorpha*) lake plankton species, using multi-decadal time series (24 years) from a shallow eutrophic lake in Germany (Müggelsee). The rationale behind our choice of taxa was to compare species, which differ substantially in their life- history traits and their life span – processes that are all subject to season-specific changes in water temperature. In addition, all taxa are common in Europe (Maier 1994, Næss et al. 1993).

Parthenogenetically reproducing *Daphnia* are able to respond rapidly to environmental changes, exhibiting exponential growth over a period of several weeks in spring. Temperature and photoperiod are important cues for the emergence of *Daphnia* resting eggs (Cáceres 1998). Cyclopoid copepods, on the other hand, undergo a complex life cycle that encompasses many preadult stages (six nauplii stages and five copepodid stages before they moult into the adult stage), spanning a period of several weeks to months (Maier 1994). Each larval stage has distinct prey requirements: nauplii are strictly herbivorous (Hansen and Santer 1995), while late copepodids and adults are omnivorous (Brandl and Fernando 1978, Adrian and Frost 1993). Most of the copepod species studied here undergo diapause in the sediment in a late copepodid stage during winter (Maier 1994), which is most likely also the case in Müggelsee, as adults are absent from the pelagic zone during winter and early spring. Photoperiod is the main cue stimulating diapause and emergence of copepodids, although this effect may be modified, in particular, by water temperature (Næss et al. 1993, Hairston 1998). Moreover, egg development, clutch size and growth rate at each life-history stage are positively related to ambient temperature (Vijverberg 1980, Maier 1989). *D. polymorpha* is the only freshwater mussel to reproduce via pelagic larvae (Borcherding 1991), whereas this strategy is commonly found in marine systems. A free-swimming planktonic larva hatches from the egg and remains suspended in the water column for about 8-10 days before settling to the substratum. *D. polymorpha* mussels have a life span of 5-6 years (McMahon 1991). An individual mussel participates in 3-4 annual spawning events, with the first spawning event is known to be determined by water temperature (Borcherding 1991).

We show that the detailed seasonal pattern of warming is crucial for the individual response of various phyto- and zooplankton species to climate change, and relate this evidence to the fact that the species exhibit different life-history traits. For species with complex and long life-history traits, it seems important whether the seasonal timing of warming matches their individual thermal requirements at decisive developmental stages.

Materials and Methods

Phenology events (see below) were determined from long-term high-resolution records (1979-2003) of ice break-up dates (daily), water temperature (WT) in 0.5 m depth (daily), and phyto- and zooplankton abundances (mostly weekly) in Müggelsee, a small (7.3 km^2), shallow (maximum depth 8 m), eutrophic, polymictic lake in Berlin, Germany (52°26'N, 13°39'E). A detailed description of the sampling methodologies is given in Gerten and Adrian (2000). Air temperature records (1967-2002) were provided by the German

Weather Service for the nearby station of Berlin-Schönefeld.

Given the weekly sampling intervals of the plankton, phenology events are expressed as week of the year for the following events in the seasonal plankton succession: the timing of first appearance (*Daphnia*; adult cyclopoid copepods *Thermocyclops oithonoides, Diacyclops bicuspidatus, Mesocyclops leuckarti, Acanthocyclops robustus*; larvae of *D. polymorpha*) and last appearance in the pelagic zone (copepods), the timing of peak abundance in spring (phytoplankton, *Daphnia*) and summer (copepods), and the magnitude of the peak abundance of the copepod species. As the overall abundances of *Dreissena* larvae result from multiple spawning events during summer (McMahon 1991), we calculated the sum of the abundances derived from each sampling date as an estimate of the total number of larvae being released in the course of one summer. The timing of appearance and disappearance of species was determined as follows. The first appearance represents the date when a species was observed for the first time followed by a lasting presence of that species in the pelagic zone, while the disappearance represents the last observation of a species after a continuous presence. To determine the potentially combined effects of changes in WT and light conditions (relevant for the emergence of zooplankton resting stages), we extracted the dates when WT in spring first reached 5 °C, 8 °C and 12 °C, respectively ($WT_{5,8,12}$), which are biologically relevant temperature thresholds (Reynolds 1984, Peters and De Bernardi 1987, Borcherding 1995), along with the corresponding day lengths (in hours (h); $DL_{5,8,12}$).

The nonparametric Mann-Kendall trend was used to detect significant monotonous trends over time (Helsel and Hirsch 1992). As this test was applied for each monthly time series separately (i.e. one value per year, n = 19-25), autocorrelation was negligible. Only for time series with trends, we plotted their cumulative *z*-scores, i.e. the deviations from the long-term mean of the series divided by its standard deviation (Lozán and Kausch 1998). The cumulative *z*-score plots indicate the transient behaviour, and specifically help to distinguish periods with predominantly positive anomalies from periods with predominantly negative anomalies (years that distinguish these periods are herein referred to as "years of change"). As the *z*-scores are standardised values, the plots enable direct comparison of the years of change for different variables, irrespective of their absolute values. Differences between the sub-periods as identified by the cumulative *z*-score plots were tested for significance using the nonparametric Mann-Whitney test.

To analyse whether the phenology changes actually were related to concurrent warming, we calculated their Spearman ρ correlation coefficients with mean WT of the respective preceding months, $WT_{5,8,12}$, $DL_{5,8,12}$, the ice break-up date and the above mentioned cardinal phenology events. Abundances were log-transformed (ln ind. L^{-1}) prior to correlation analysis.

Food conditions for the summer species – i.e. total algal mass, phytoflagellate mass (the main food source for nauplii, which are the bottleneck in copepod development), and total rotifer abundances (prey for late copepodid stages and adult copepods) – were examined for the growing season of these species (April through September). All computations were performed using SAS 8.02 and SPSS 9.0.

Results and Discussion

Warming trends

During the investigation period (1979-2003), the study lake (Müggelsee) experienced significant warming of surface WT in different seasons (trends: winter, +1.02 K; spring, +2.40 K, summer, +2.31 K). These warming trends were not identical, but commenced

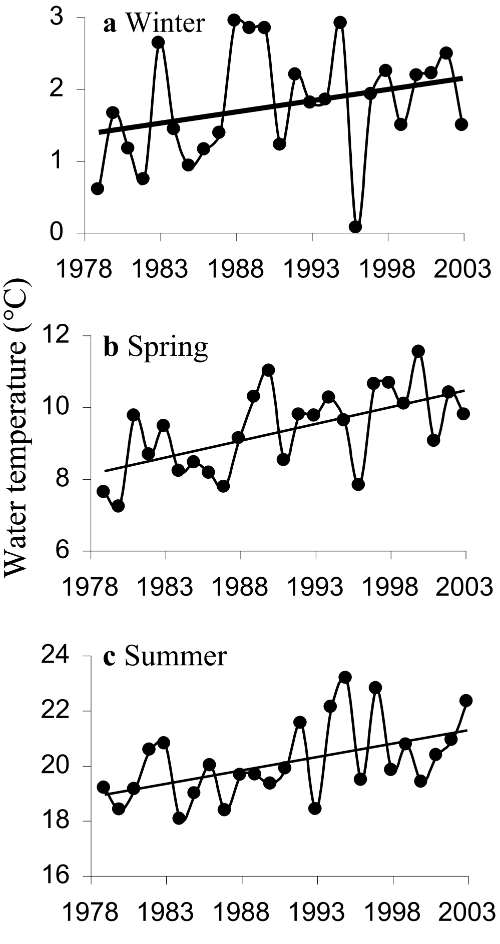

Fig. II-1 Mean near-surface water temperature (°C) of Müggelsee derived from daily measurements in (a) winter (December-February); (b) spring (March-May); and (c) summer (June-August), 1979-2003. The straight lines indicate the linear trends over time based on the Kendall-Theil robust line.

successively (Figs II-1 and II-2 a, c and e; Table II-1); the years of change lay in 1988 (winter), 1989 (spring), and 1994 (summer), respectively. Biologically relevant threshold WTs of 5 °C, 8 °C and 12 °C ($WT_{5,8,12}$) were reached up to 2 weeks earlier in spring in the latter years, which corresponds to lower light availability on these days (i.e. their day lengths $DL_{5,8,12}$ were shortened by up to 1.6 h; Table II-1). The upward trends in WT followed the trends in concurrent air temperature (except for winter temperatures), which were also evident in a longer time period (air temperature 1967-2002: winter +2.39 K, spring +1.97 K, summer +0.84 K). The winter/ spring warming was accompanied by shorter periods with ice cover (43 days) and earlier ice break-up dates (3.5 weeks) (Table II-1, Fig. II-3).

Changes in phenology during spring

Phytoplankton and zooplankton phenology advanced significantly in spring, largely synchronously with the sequential winter (phytoplankton) and spring warming (zooplankton). The phytoplankton bloom, of which diatoms comprised >80%, occurred around 4.5 weeks earlier from the year 1988 as compared to the preceding decade (Table II-1). Evidently, this advancement was related to the shorter period with ice cover (Fig. II-3) and associated improvements in turbulence and light conditions (Weyhenmeyer et al. 1999, Gerten and Adrian 2000). The relationship between ice conditions and the timing of the bloom is signalled by the synchronicity of the year of change of both events, 1988 (Figs II-2 and II-3; Table II-1), and their strong correlation ($p<0.001$).

Peak abundances of the *Daphnia* populations, which typically predominate after the breakdown of the phytoplankton bloom, also advanced by about 2 weeks (Fig. II-3; Table II-1). The same pattern of change was also found for single *Daphnia* and *Bosmina* species (data not shown), i.e. these plankton species responded synchronously to the spring warming. In contrast to the phytoplankton, the earlier timing of the peak abundances of *Daphnia* was largely decoupled from the winter situation and a direct response to elevated WT in spring and particularly in May ($p<0.001$), which is also indicated by the synchronicity of the year of change in the *Daphnia* and the spring WT time series (1989/1990; Fig. II-2 c and d). The first appearance of adult *Daphnia* in spring was closely related to WT_5 and DL_5 ($p<0.01$); the day length that corresponds to WT_5 was reduced by 1.6 h during the study period (DL_5 in Table II-1). Although photoperiod is an important cue for the emergence of *Daphnia* resting eggs (Cáceres 1998), this reduction in DL obviously was not critical for their emergence: if DL (i.e. light availability) would have

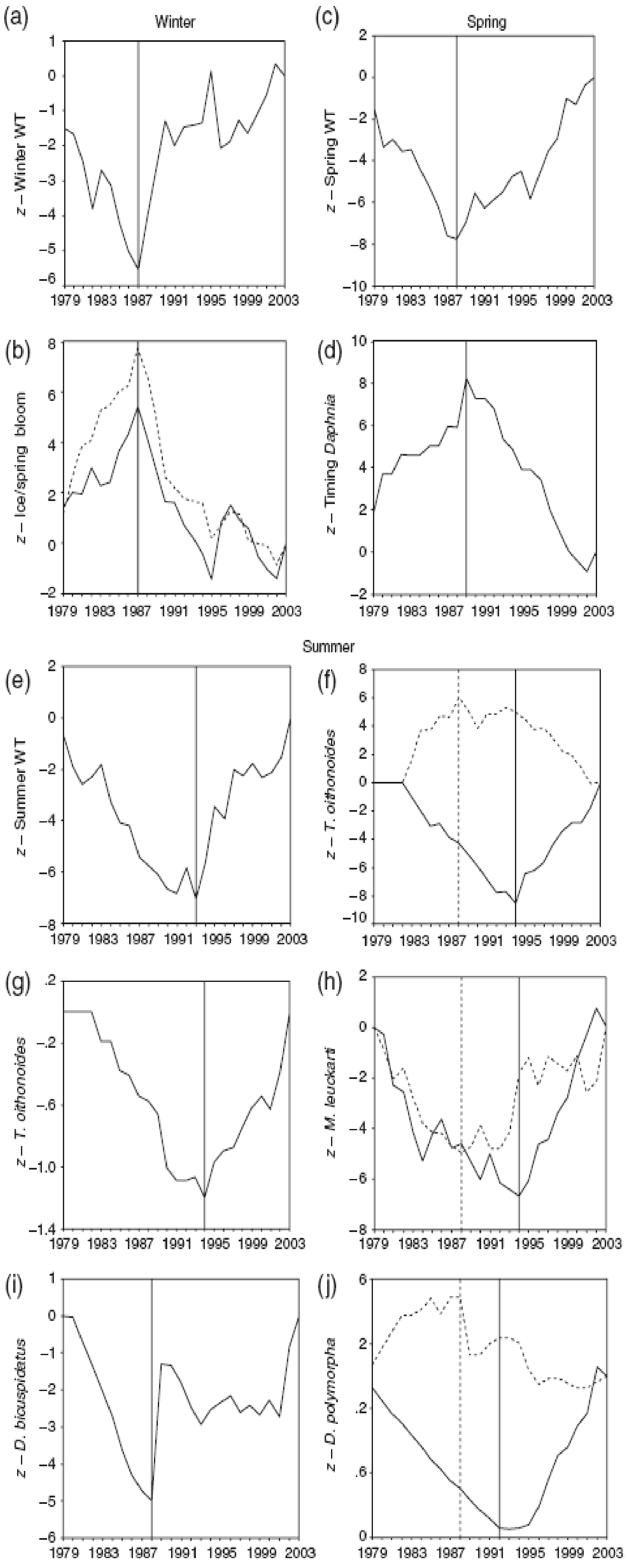

Fig. II-2 Cumulative *z*-score plots of (a) mean winter (December-February) surface WT of Müggelsee; (b) ice duration (solid line) and timing of the spring phytoplankton bloom (dashed line); (c) mean spring (March-May) surface WT; (d) timing of *Daphnia* spring maximum; (e) mean summer surface WT (June-August); (f) start of the pelagic phase of *Thermocyclops oithonoides* (dashed line) and magnitude of the *T. oithonoides* summer abundance maximum (solid line); (g) end of the pelagic phase of *T. oithonoides*; (h) magnitude of the *Mesocyclops leuckarti* summer abundance maximum (dashed line) and timing of the *M. leuckarti* summer abundance maximum; (i) magnitude of the *Diacyclops bicuspidatus* summer abundance maximum, (j) start of the pelagic phase of *Dreissena polymorpha* larvae (dashed line) and cumulative sum of the summer abundances of *D. polymorpha* larvae (solid line). Note the synchronicity in the timing of change between WT in winter (1987) and spring (1988) and phenology events in the spring plankton in opposition to the asynchronous responses of the summer species.

prevented the emergence in a sufficient number of years, the correlation between the timing of the first appearance and DL_5 would be lower than the correlation with WT_5, which is not the case. An interesting question is, however, whether the reduction in DL influences such features as *Daphnia* clone selection of emerging resting eggs.

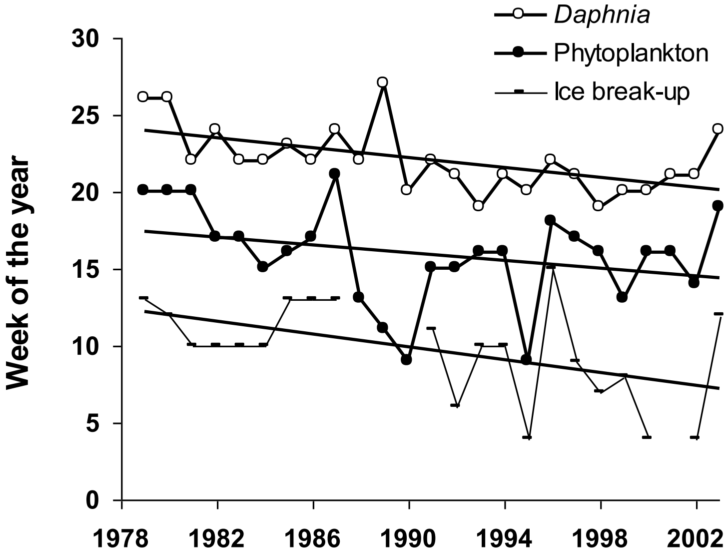

Fig. II-3 Annual timing of key phenology events in spring in Müggelsee, 1979-2003: ice break-up, spring phytoplankton bloom and peak abundance of *Daphnia* in spring. Significant phenology shifts of these events lay in the order of 1 month (Table II-1). The straight lines indicate the linear trends over time based on the Kendall-Theil robust line. Gaps in the ice break-up dates indicate years without ice (1988, 1989, 1990) or with rare ice formation.

This study documents an observed synchronous forward movement, of 2-4 weeks, for spring phenology events of fast-growing lake plankton species in response to a significant warming in winter and spring (Fig. II-2 a-d). This synchrony indicates that they all responded rapidly to warmer conditions, although these changes were not causally linked. The observed earlier occurrence of fast-growing phyto- and zooplankton in spring is not restricted to the lake under examination here, as it has also been reported for other, distant lakes (Weyhenmeyer et al. 1999, Straile 2000, Winder and Schindler 2004). The timing of ice break-up is a major driver of spring phytoplankton phenology in ice covered lakes of the temperate zone (Adrian et al. 1999, Weyhenmeyer et al. 1999). Underlying mechanisms driving the spring phytoplankton developments are, however, different in large lakes or marine systems, which lack the development of ice (Straile 2000, Edwards and Richardson 2004). In these ecosystems, phytoplankton phenology remained relatively fixed in time, despite analogous warming in winter and early spring.

Table II-1. Significance levels (p) according to Mann-Kendall trend test for phenology events and peak abundances in spring and summer in Müggelsee, 1979-2003 (copepods, 1980-2003).

	p <	Sub-periods	Medians of s.-periods
Air temperature			
Winter (Dec-Feb)	ns		
Spring (Mar-May)	0.05	79-88/89-02	8.3 °C / 9.5 °C
Summer (Jun-Aug)	0.05	79-90/91-02	17.3 °C / 18.5 °C
Water temperature			
Winter (Dec-Feb)	0.1	79-87/88-03	1.2 °C / 2.2 °C
Spring (Mar-May)	0.01	79-88/89-03	8.3 °C / 10.1 °C
Summer (Jun-Aug)	0.01	79-93/94-03	19.3 °C / 20.8 °C
WT5 (Mid Mar: 12 ± 2.5w)	0.05	79-88/89-03	14.0 w/ 10.0 w
WT8 (Begin Apr: 14 ± 1.4 w)	ns		
WT12 (Begin May: 18 ± 1.2 w)	0.01	79-91/92-03	18.0 w / 17.0 w
Day length at specific WT			
DL5	0.05	79-88/89-03	12.8 h / 11.2 h
DL8	ns		
DL12	0.001	79-91/92-03	15.1 h / 14.3 h
Ice break-up date	0.02	79-87/88-03	12.0 w / 8.5 w
Spring species			
Timing phytoplankton spring bloom (Mid Apr: 15 ± 3.2 w)	0.01	79-87/88-03	20.0 w / 15.5 w
Timing *Daphnia* peak (Mid May: 22 ± 2.1 w)	0.01	79-89/90-03	23.0 w / 21 w
Summer species			
Copepods (from 1980 only)			
Start pelagic phase			
Thermocyclops oithonoides (Mid May: 21 ± 5.3 w)	0.01	80-87/88-03	27.5 w / 18.0
Mesocyclops leuckarti (Begin Apr: 14 ± 3.6 w)	ns		
Diacyclops bicuspidatus (Mid Apr: 16 ± 7.9 w)	ns		
Acanthocyclops robustus (End May: 22 ± 6.3 w)	ns		
End pelagic phase			
T. oithonoides (Begin Oct: 41 ± 3.3)	0.001	80-93/94-03	39.0 w / 42.5 w
M. leuckarti (Begin Oct: 41 ± 3.0 w)	ns		
D. bicuspidatus (Mid Sep: 38 ± 5.7 w)	ns		
A. robustus (End Sep: 40 ± 3.5 w)	0.05	80-85/86-03	36 w / 41 w
Timing summer peak			
T. oithonoides (Begin Aug: 32 ± 3.3 w)	ns		
M. leuckarti (Begin Aug: 33 ± 2.3 w)	0.01	80-94/95-03	32 w / 35 w
D. bicuspidatus (End Jul: 29 ± 4.5 w)	ns		
A. robustus (Begin Aug: 32 ± 4.0 w)	ns		
Magnitude summer peak			
T. oithonoides	0.001	80-94/95-03	1.6 / 16.0 IndL^{-1}
M. leuckarti	0.05	80-88/89-03	17.1 / 30.0 IndL^{-1}
D. bicuspidatus	0.001	80-93/94-03	1.5 / 5.0 IndL^{-1}
A. robustus	ns		
Dreissena polymorpha larvae			
Start pelagic phase (Begin May: 19 ± 3.0 w)	0.05	79-88/89-03	21.0 w / 19.0 w
Magnitude summer peak	0.001	79-92/93-03	344 / 2769 IndL^{-1}

The respective two periods were determined from cumulative *z*-score plots (see Methods) and tested with the Mann-Whitney test; they all differed significantly from each other. WT$_5$, WT$_8$, and WT$_{12}$ refer to the week when water temperature first reached 5 °C, 8 °C and 12 °C, respectively; DL$_5$, DL$_8$, and DL$_{12}$ refer to the corresponding day lengths. The average week ± standard deviation of the phenology events is given in brackets.

Changes in phenology during summer

In summer the phenological shifts in the predominating zooplankton were clearly species-specific (Table II-1) and not synchronised (Fig. II-2 e-j) as were the changes in winter/spring. *T. oithonoides* – the most thermophilic of the four copepod species studied – appeared much earlier in spring (9.5 weeks) and also ended its pelagic phase notably later in autumn (3.5 weeks) in more recent years (Table II-1; Fig. II-4). The earlier start of the

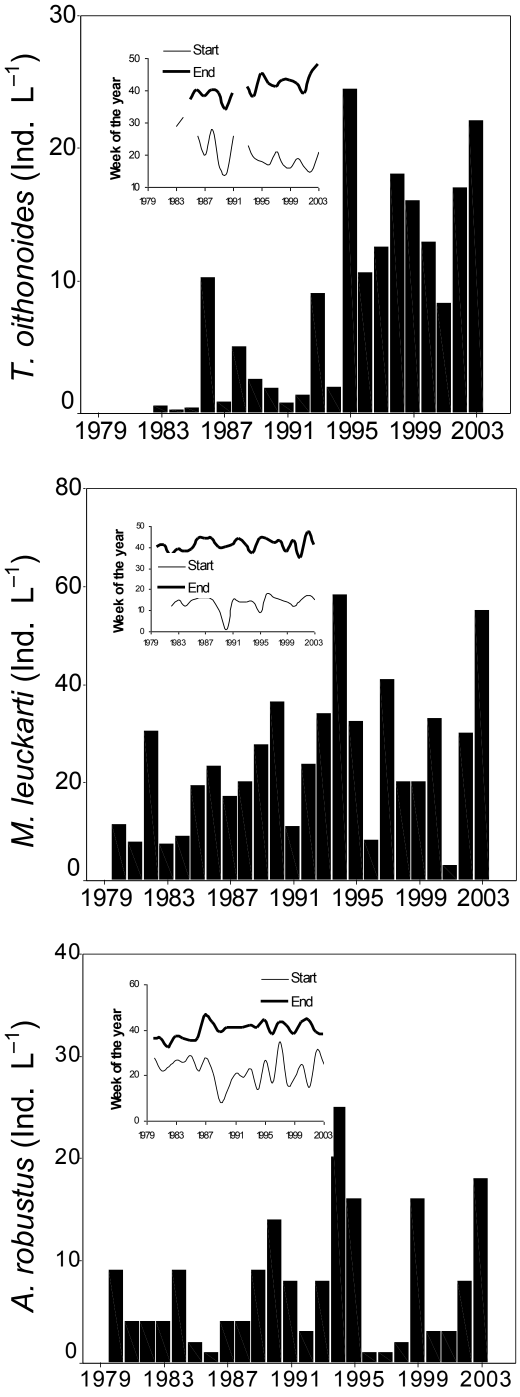

Fig. II-4 Magnitude of annual peak abundances of adult *T. oithonoides*, *M. leuckarti* and *A. robustus* in summer in Müggelsee, 1980-2003. The inner plots shows the week of the year when adults were first detected in the pelagic zone (start) and their disappearance in fall (end).

pelagic phase was synchronised with the timing of winter/spring warming (Table II-1; Fig. II-2). Furthermore, annual peak abundances of *T. oithonoides* significantly increased during the study period ($p<0.001$, Table II-1; Fig. II-4), which, however, coincided with summer warming (Table II-1; Fig. II-2). Phenologies of *D. bicuspidatus* and *M. leuckarti* exhibited no systematic change, but both populations demonstrated increased peak abundances (Table II-1; Fig. II-4). *A. robustus*, a species adapted to a broad temperature range (Maier 1989), extended its pelagic phase into autumn but the magnitude of its peak abundance remained unchanged (Table II-1; Fig. II-4). *M. leuckarti* reached its abundance peaks 3 weeks later in more recent years (Table II-1).

Importantly, the start of the pelagic phase of adult *T. oithonoides* was correlated with WT_5 ($p<0.05$), WT_8 ($p<0.05$) and DL_8 ($p<0.01$). This suggests that WT of around 5-8 °C and DL of around 13.3 h (average DL between 1979 and 2003), which are usually surpassed in March/April, are key requirements for the emergence of this species from diapause. Other factors were probably also important for the emergence of these species (especially since WT_8 and DL_8 did not change significantly over the study period, see Table II-1). Light availability is known to be important for the emergence of cyclopoid copepods in both limnetic (Watson and Smallman 1971) and marine ecosystems (Teasdale et al. 2004). The earlier emergence could also have been a consequence of the extension of the pelagic phase in autumn, since the later in the season diapause is initiated in some cyclopoid copepods, the shorter it lasts (Teasdale et al. 2004). Furthermore, the first appearance of adult copepods is only a proxy for the emergence of larval stages, which unfortunately have not been classified to species level in Müggelsee.

The magnitudes of the peak abundance of three out of the four copepod species were correlated with WT in May and/or June only ($p<0.05$). This suggests that the early appearance in the pelagic zone by more than 1 month allows the development of an extra generation, which may have contributed to the enhanced peak abundances during summer (Table II-1; Gerten and Adrian 2002b). For *T. oithonoides* it has been shown that warmer water temperatures do indeed allow the completion of a further generation (Næss et al. 1993), if food is not limiting. Although Müggelsee has undergone a reduction in total algal mass in the past years as a consequence of reduced inflow and nutrient load (Köhler et al. 2005), concentrations of e.g. phytoflagellates – a key resource for nauplii, the bottleneck in copepod development – remained at or above known limitation levels for cyclopoids, 0.2-0.3 mgC L^{-1} for *M. leuckarti* and *Cyclops vicinus* nauplii (Hansen and Santer 1995). From June till August, the critical period of nauplii development for summer cyclopoid species, phytoflagellate mass did not differ between the two sub-periods 1979-1988 and 1989-2003 (Fig. II-5). These subperiods were chosen in analogy to the change in the start of the pelagic phase in spring of the most responsive summer copepod species, *T. oithonoides*; the same pattern was found e.g. for the sub-periods 1979-1992 vs. 1993-2003, which are more representative for the observed changes in other summer species. Average total algal mass was generally lower in the latter years and more often below known threshold concentrations (6.6 mgCL^{-1} for adult *Tropocyclops*; Adrian and Frost 1992). However, during June-August – the main growing season of the studied copepods – differences in total algal mass were not significant (Fig. II-5; see overlap in 95% confidence intervals). The total number of rotifers – an important prey for late copepodid stages and adult cyclopoid copepods – did not change significantly in the course of the investigation period (Fig. II-5). The same was true for nauplii, which also belong to the prey spectrum of adults (data not shown). The decreases in total algal prey are therefore not a major driver of the observed changes in phenology, especially since most summer species increased in their abundances, which is not to be expected when food resources become limiting.

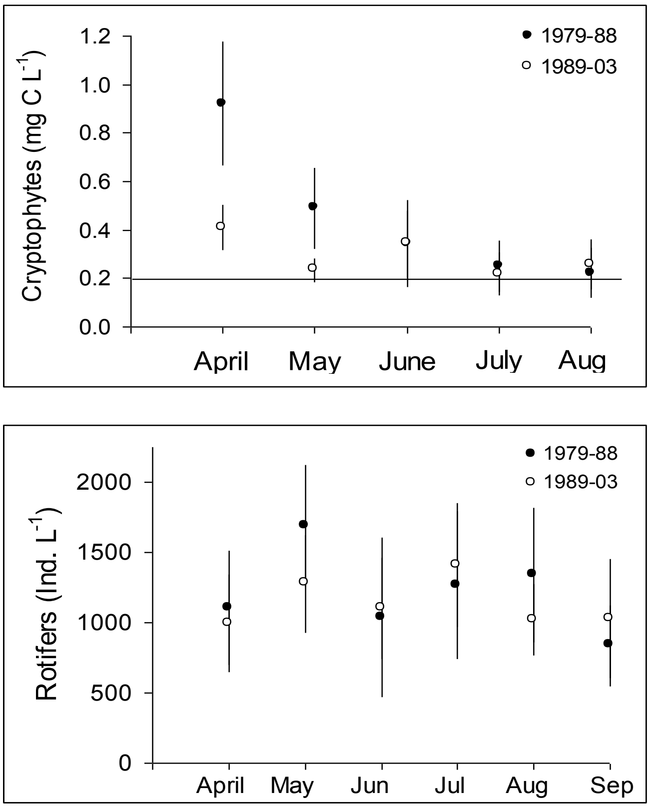

Fig. II-5 Monthly means of phytoflagellates mass (cryptophytes), total algal mass and rotifer abundances in Müggelsee from April to August/September for the periods 1979-1988 and 1988-2003. Each data point represents monthly means ± 95% confidence level. The horizontal line in the upper graph indicates the food threshold concentration of copepod nauplii for phytoflagellates (0.2 mgCL^{-1}, see text).

Changes in the population development of *D. polymorpha* larvae were probably a consequence of the warming events in both winter/spring and in summer. Their pelagic phase started on average 2 weeks early (year of change 1989, concurrent with spring warming, Figs II-2j and II-6; Table II-1), and they reached significantly higher peak abundances from 1993 onwards, concurrent with summer warming (Fig. II-2j). The start of their pelagic phase was correlated with WT in May ($p<0.05$) and specifically with WT_{12} ($p<0.01$), which was usually surpassed in May. It is well known that adult *Dreissena* start to spawn when ambient water temperatures reach 12 °C (Borcherding 1995). The findings of the present study clearly indicate that a spring warming in this temperature range induces early spawning of *Dreissena* mussels in lakes where algal prey is not limiting. As fecundity in terms of gonad size or number of oocytes per female is determined by winter/spring temperature and prey conditions (Borcherding 1991, 1995), the increase in the summer abundance appears to be already initiated by winter/spring conditions (Wilhelm and Adrian, unpublished data).

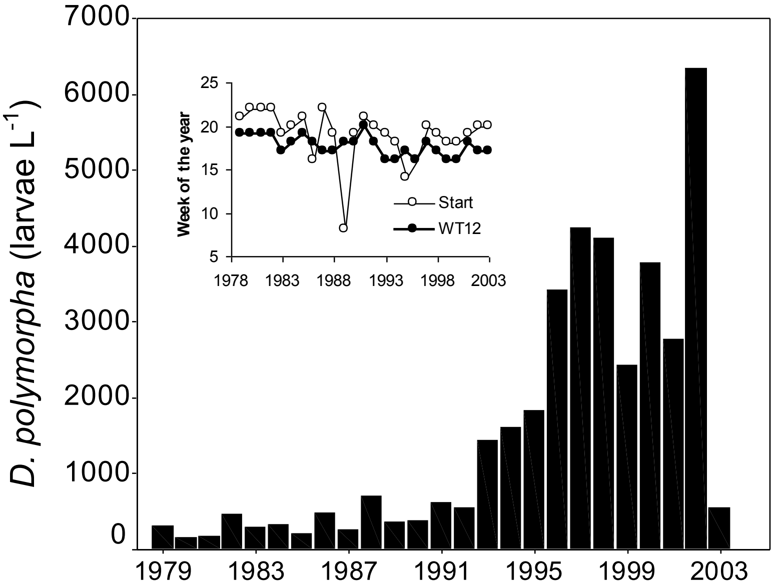

Fig. II-6 Sum of the abundances of pelagic *Dreissena polymorpha* larvae (individuals L^{-1}) in summer in Müggelsee, 1979-2003. The inner plot shows the week of the year when larvae were first detected in the pelagic zone (Start) and the timing of WT12, the temperature threshold when *Dreissena* mussels start to spawn.

Consequences of summer warming have rarely been examined so far in lakes (but see Gerten and Adrian 2002b) – thus, underlying mechanisms of change are not fully understood. During summer, responses seem to be more complex and more species-specific, as this study demonstrates. Furthermore, responses in summer will likely be of a more indirect nature. For example, warming should affect the intensity and duration of thermal stratification of lakes (Schindler et al. 1990), with repercussions on turbulence and nutrient conditions, finally affecting phytoplankton development. The early spawning of *Dreissena*, however, can be directly attributed to the early attainment of the 12 °C threshold temperature. Stage-specific food requirements of summer species may add to the complexity in their response to environmental changes such as global warming and/or reduction in eutrophication. Moreover, as we have shown, summer species can be already influenced by previous winter/spring warming, such that warming events earlier in the season may propagate in time and, thus, confound processes in summer. To what extent the increase in abundances on the one hand and the extension of the pelagic phase on the other hand of some summer species affect food web interactions will be discussed elsewhere (Adrian, in preparation).

Conclusions

The detailed seasonal pattern of warming influences the response of floral and faunal species to climate change. We show that fast- vs. slow-growing lake plankton species differed with respect to the synchrony of change in response to higher WT. Populations of fast-growing species, adapted to spring-specific steep gradients in temperature and light conditions, are able to directly respond to warming trends (Figs II-2b and d and II-3). This is likely also a reason why the rate of change in spring plankton phenology is somewhat higher than mean advancements in the spring phenology phases for plant and animal species of terrestrial ecosystems (5.1 days per decade; for review see Badeck et al. 2004).

By contrast, slow-growing species with longer and more complex life cycles are potentially affected by multiple warming events in the course of a year, which do not necessarily lead to changes in their phenologies. Warming may be required over the entire growing period or at least during decisive development stages. Larvae, for example, often represent the bottleneck in a species' life cycle with respect to population development or dispersal, such that warming during sensitive developmental stages – such as emergence from diapause or spawning – is of particular importance for aquatic and terrestrial ecosystems. Moreover, individual effects of multiple warming events within a year may propagate throughout the growing season and perhaps into the next year. The asynchronous timing of the seasonal warming trends (spring warming started around 1989, summer warming started around 1994), may have contributed to the diverse nature of observed changes in the copepod and *Dreissena* phenologies on the one hand and changes in peak abundances on the other hand, which were not per se interrelated (Fig. II-2 f-j).

Our findings imply that intra- and inter-annual differences in the timing of warming, along with differences in species' life-history strategies, potentially cause disruptions of established species interactions in freshwater ecosystems. But, as our results also suggest, these mismatches are more likely to occur during summer, when species with long and complex life cycles dominate.

One challenge is to estimate thresholds of further changes in the phenology of species under future climate change scenarios, that predict further warming (Räisänen et al. 2004). Apparently, the extent to which plankton phenology can advance in spring is limited. The presence or absence of ice, and the WT at specific day lengths, appear to be important variables setting these thresholds as they are important drivers of phytoplankton development (Reynolds 1984), but they are also important cues for the emergence of zooplankton resting stages (Cáceres 1998, Vandekerkhove et al. 2005). During summer, changes in the strength of thermal stratification, or in the case of polymictic lakes, changes in the frequency of stratified periods, may set some of the boundaries of the responses of the summer species.

Acknowledgements

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CHAPTER III

Long-term response of daily epilimnetic temperature extrema to climate forcing

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Abstract

Twenty years (1983-2002) of hourly summer temperature data from the epilimnion of Müggelsee, a shallow lake in northern Germany, showed a long-term increase, with the rate of increase of the daily minima (nighttime temperatures) exceeding that of the daily maxima (daytime temperatures). This does not simply reflect the long-term behaviour of air temperature, which did not exhibit a significant degree of day-night asymmetry. A sensitivity analysis based on a heat balance model revealed that the daily extrema of the lake surface equilibrium temperature responded differently not only to shifts in air temperature, but also to shifts in wind speed, relative humidity and cloud cover, suggesting that long-term changes in all four variables contribute to day-night asymmetry in the epilimnetic temperature. A comparison of nighttime and daytime estimates of the heat flux components into the lake indicates that the emission of long-wave radiation from the atmosphere is likely to be the main process responsible for day-night asymmetry in the epilimnetic temperature. While this process is partially dependent on air temperature, it is also dependent on relative humidity and cloud cover. The influence of long-term changes in these additional driving variables on epilimnetic temperatures cannot therefore be neglected.

Introduction

Over large areas of the earth's surface, long-term warming is known to be proceeding faster at night than during the day (e.g. Karl et al. 1993, Kukla and Karl 1993), probably as a result of an increase in low-level cloud cover associated with an increase in air pollution (Dai et al. 1999, Satheesh et al. 1999). There is some evidence that terrestrial biota may already be responding to such asymmetric air temperature increases involving anomalously high rates of nocturnal warming. The primary production of the dominant native C_4 grass *Bouteloua gracilis* in Colorado, for instance, is decreasing as a result of nocturnal warming, whereas the abundance and production of exotic and native C_3 forbs is increasing

(Alward et al. 1999). Nocturnal warming has also been shown to result in an increase in the dark respiration of the tree *Populus deltoides* (Turnbull et al. 2004), and a rise in the rate of development of the cabbageworm *Pieris rapae* (Whitney-Johnson et al. 2005).

Empirical studies show that water temperatures close to the surface of lakes closely follow ambient air temperatures (e.g. McCombie 1959, Shuter et al. 1983, Livingstone and Lotter 1998). The results of model studies predicting that rising air temperatures will result in increasing epilimnetic temperatures (e.g. Hondzo and Stefan 1993, Stefan et al. 1998, Peeters et al. 2002) are supported by the existence of long-term historical data series demonstrating that, over the past few decades, such increases have indeed occurred (e.g. Schindler et al. 1990, Gerten and Adrian 2002a, Livingstone 2003). However, despite the likelihood that the rise in epilimnetic temperature may be more closely related to nighttime processes, such as the inhibition of nighttime cooling, than to daytime processes (Livingstone 2003), very little work has been done on analysing the impact that day-night asymmetry in rising air temperatures might have on the long-term warming of lake epilimnia. Specifically, there is a lack of knowledge on whether day-night asymmetry involving a long-term decrease in the daily temperature range might also be present in lake epilimnia, although lake biota would be likely to respond to such a phenomenon. The present study attempts to rectify this omission.

One of the areas with a marked degree of day-night asymmetry in long-term regional warming is central Europe (e.g. Heino et al. 1999). Here, we examine a unique 20-yr set of hourly air and water temperature data recorded between 1983 and 2002 for Müggelsee, a shallow, polymictic lake in northern Germany, with a view to investigating the long-term behaviour of the daily water temperature extrema and their relationship to that of the daily air temperature extrema. We focus on the months of June, July and August, when the diel cycle in epilimnetic temperature is most pronounced and when the daily maximum approaches the tolerance threshold for some aquatic species. To ascertain the meteorological driving factors most likely to be responsible for long-term changes in the daily epilimnetic temperature extrema, and hence in the daily epilimnetic temperature range, a sensitivity analysis based on the heat budget and equilibrium temperature approach of Edinger et al. (1968) is performed.

Materials and methods

Study site

Müggelsee is a shallow, eutrophic lake situated 34 m above sea level (a.s.l.) in Berlin, Germany (52°26'N, 13°39'E). It has a mean depth of 4.9 m, a maximum depth of 8 m, and it covers an area of about 7.3 km^2. It is one of the intercalated lakes of the River Spree, with an average residence time of 6-8 weeks. Within the last 25 years Müggelsee has experienced considerable changes in lake catchment and climate. In response to a decrease in external nutrient loading, phytoplankton biomass has declined and its composition has changed (Köhler et al. 2005). Concurrently, higher water temperatures in spring and summer have caused the earlier appearance of various copepods and a prolongation of their period of activity (Gerten and Adrian 2002b).

Data

The epilimnetic temperature of Müggelsee was recorded hourly at a depth of 0.5 m in June, July and August from 1983 to 2002, using an AD590 temperature transducer mounted on a jetty. Daily minimum and maximum water temperatures ($T_{0,min}$ and $T_{0,max}$, respectively) were extracted from the hourly data. There were a total of 20 gaps in the water temperature data, with a mean duration of 3.5 d and a maximum duration of 6 d. These gaps were filled by linear interpolation. The daily water temperature range ($T_{0,dtr}$) was computed as $T_{0,max} - T_{0,min}$. For each year from 1983 to 2002, annual summer means of $T_{0,min}$, $T_{0,max}$ and $T_{0,dtr}$ were computed based on the 92 daily values from 1 June to 31 August. All analyses described below were conducted both on the interpolated data and on the original non-interpolated data. There was no significant difference between the two sets of results; the results presented here are those derived from the interpolated water temperature time series.

Daily meteorological data, covering the same period as the Müggelsee water temperature data, were available from Berlin-Schönefeld airport (52°23'N, 13°31'E; 46 m a.s.l.), located 10 km southwest of Müggelsee. Data available from this station included daily minimum and daily maximum air temperatures ($T_{air,min}$ and $T_{air,max}$, respectively). Hourly mean data on wind speed and relative humidity were also available, from which nighttime (defined as 20:00 h to 08:00 h) and daytime (08:00 h to 20:00 h) means were calculated. Cloud cover data were obtained from Berlin-Tempelhof airport (52°29'N, 13°24'E; 48 m a.s.l.), located 20 km west of Müggelsee. Cloud cover was recorded three times a day (in octals) at 7:30, 14:30 and 21:30 CET, and daily mean cloud cover was defined as the arithmetic mean of the three recorded values, converted to a fraction between 0 and 1. The daily air temperature range ($T_{air,dtr}$) was computed as $T_{air,max} – T_{air,min}$. Analogously to water temperature, annual summer means of $T_{air,min}$, $T_{air,max}$ and $T_{air,dtr}$ were computed for each year from 1983 to 2002. No record of any change in observation methods during the study period was found.

In the year 2002, from 1 June to 31 August, water temperature profiles and meteorological data were measured at 5-min intervals at a lake station anchored 300 m from the lakeshore in 5.5 m water depth. The water temperature profiles were recorded from 0.5 m to 5.0 m depth using a chain of AD592 temperature transducers spaced at intervals of 0.5 m. The meteorological data measured included air temperature, global radiation, wind speed, relative humidity and air pressure; precipitation was measured simultaneously on the roof of a building located near the lakeshore. The water temperature and meteorological data were aggregated to yield hourly means that were used in the calculation of the heat budget of the lake during summer 2002.

The simultaneous availability of meteorological data measured directly at the lake and at Berlin-Schönefeld airport from 1 June to 31 August 2002 also allowed the applicability of the airport data to the lake to be assessed. The lake and airport time-series were extremely highly correlated, with the proportion of shared variance (R^2) between them being 96% for daily mean air temperature, 92% for daily mean relative humidity and 83% for daily mean wind speed (with $p<0.001$ in all cases). The mean difference between the lake and airport time-series was 0.2 K for daily mean air temperature, -9.6% for daily mean relative humidity and –0.6 ms^{-1} for daily mean wind speed. Thus air temperature at the lake was slightly underestimated by the airport data, while relative humidity and wind speed were overestimated. However, this did not affect long-term trends in the data.

The water temperature of the River Spree, by far the most important inflow to Müggelsee, was measured weekly each Monday morning at 1 m depth at the inlet to the lake. The weekly data were interpolated linearly at daily intervals. The rate of inflow to the lake was measured daily at the Freienbrink monitoring station, located on the River Spree 13 km upriver from the inlet.

Heat budget model and equilibrium water temperature

The method chosen to analyse the effects of meteorological forcing on the epilimnetic temperature utilised the equilibrium temperature approach of Edinger et al. (1968). This approach is based on a heat budget model in which the net heat flux into a lake, H_{calc} (Wm^{-2}), is computed as the sum of the major heat exchange terms:

$$(1) \qquad H_{calc} = H_S + H_L + H_B + H_E + H_C + H_F + H_P$$

The processes underlying these terms are the absorption of short-wave solar radiation (H_S) and long-wave (infra-red) atmospheric radiation (H_L) incident at the lake surface; the emission of long-wave (infra-red) radiation from the lake surface (H_B); the exchange of latent heat by evaporation and condensation (H_E); the exchange of sensible heat by convection and conduction (H_C); heat exchange due to mass exchange via the inflow and outflow (H_F); and heat exchange by precipitation directly on to the lake surface (H_P). Heat exchange through the lake bottom is normally considered to be negligible compared to heat exchange across the air-water interface (Ragotzkie 1978).

The short-wave solar radiation absorbed (H_S) is given by:

$$(2) \qquad H_S = A_S\,G$$

where G is the incident global radiation (Wm^{-2}), which is highly dependent on cloud cover (e.g. Kasten and Czeplak 1980), and A_S is an absorption coefficient for short-wave radiation that was set to 0.906 following Kuhn (1978).

The long-wave atmospheric radiation absorbed by the lake (H_L) is given by:

$$(3) \qquad H_L = A_L\,E_L\,\sigma(T_{air} + 273.15)^4$$

where the absorption coefficient A_L of the water for long-wave radiation was set to 0.97 (Anderson 1954), σ is the Stefan-Boltzmann constant (56.7×10^{-9} $Wm^{-2}K^{-4}$), T_{air} is the air temperature (°C), and E_L is the emission coefficient of the atmosphere. Using the formula of Brutsaert (1982), this latter is given by:

$$(4) \qquad E_L = 1.24\,[e_a / (T_{air} + 273.15)]^{1/7}\,(1 + 0.17\,C^2)$$

where e_a is the water vapour pressure (hPa), given by the product of the saturation vapour pressure e_s (hPa) and the relative humidity r_h (%):

(5) $e_a = e_s r_h / 100$

e_s was obtained from the Magnus formula (Murray 1967):

(6) $e_s = 6.1078 \exp[(17.2694\, T_{air}) / (237.36 + T_{air})]$

and C is the degree of cloud cover (ranging from 0 to 1). C was estimated empirically from the ratio of incident global radiation (G) to clear-skies global radiation (G_0) using the equation of Kasten and Czeplak (1980):

(7) $G/G_0 = 1 - aC^b$

with a = 0.72 and b = 3.2, values that are considered to be representative for Germany (Kasten et al. 1984). The degree of cloud cover during nighttime was estimated by linear interpolation of daytime values.

The emission of long-wave radiation from the lake surface (H_B) proceeds according to the Stefan-Boltzmann law with an emission coefficient of 0.97:

(8) $H_B = -0.97\, \sigma(T_0 + 273.15)^4$

where T_0 is the surface water temperature (°C).

The loss of latent heat by evaporation from the lake surface (H_E) is influenced by wind speed:

(9) $H_E = -f\,(e_s - e_a)$

where f is the wind function ($Wm^{-1}hPa^{-1}$), here given by modifying the wind function of McMillan (1971) by including an air stability term (Dingman 1972) to yield the following equation as used by Kuhn (1978) and by Livingstone and Imboden (1989):

(10) $f = 4.4 + 1.82u_{10} + 0.26\,(T_0 - T_{air})$

where u_{10} is the wind speed 10 m above the lake surface (ms^{-1}). Assuming a logarithmic wind speed profile, the wind speed at the standard meteorological height of 10 m was estimated to be 8% greater than the actual measured wind speed 4 m above the lake surface.

The convective exchange of sensible heat (H_C) is also dependent on wind speed:

$$(11) \quad H_C = -Rf\,(T_0 - T_{air})$$

where R is the Bowen coefficient (Bowen 1926), dependent on air pressure, which relates H_C to H_E.

The heat exchange due to the inflow and outflow (H_F) is given by:

$$(12) \quad H_F = Qc_p\rho(T_{inflow} - T_0)/A_0$$

where Q is the lake discharge (m^3s^{-1}), c_p is the specific heat of water at constant pressure (4200 $Jkg^{-1}K^{-1}$), ρ is the density of water (1000 kgm^{-3}), T_{inflow} is the mean inflow temperature (°C), and A_0 is the lake surface area (7.3×10^6 m^2 for Müggelsee).

The effect of direct precipitation on the lake surface (H_P) on the heat flux of the lake is given by:

$$(13) \quad H_P = Pc_p\rho(T_{air} - T_0)$$

where P is the precipitation rate (ms^{-1}).

The model was verified by comparing the net heat flux calculated from the meteorological data (H_{calc}) with the net heat flux calculated directly from the measured lake temperature data (H_{meas}), given by:

$$(14) \quad H_{meas} = dE/dt$$

where E is the heat content of the lake per unit area. Assuming constant values for c_p and ρ, E was obtained as follows by integration of the hourly volume-weighted temperature profiles:

$$(15) \quad E = \frac{c_p\rho}{A_0}\int_0^{z_m} T_z\,A_z\,dz$$

where T_z and A_z are the temperature and isobath area, respectively, at depth z, and z_m is the maximum lake depth.

The equilibrium temperature T_{eq} of Edinger et al. (1968), defined as the surface temperature that would result in zero net heat flux, is the temperature that theoretically would ultimately be reached by the water surface under stationary environmental conditions. T_{eq} is computed by setting $H_{calc} = 0$ and solving equation 1 for $T_{eq} = T_0$. T_{eq} continually changes in response to variations in meteorological forcing; simultaneously, T_0 is continually being driven exponentially toward T_{eq} by the difference between the two. Under ordinary circumstances, T_0 will cross T_{eq} twice a day, as warming and cooling trends alternate in response to the diurnal cycle (Edinger et al. 1968). A further characteristic of the response of water temperature to meteorological forcing is the time lag that exists between the occurrence of the daily maximum equilibrium temperature and the occurrence of the daily maximum water temperature, which may approach a maximum of 6 h for the diel cycle (Edinger et al. 1968). T_{eq} exhibits a much larger diel amplitude than does the lake water surface temperature T_0, owing mainly to the strong diel variation in H_S and H_E (Edinger et al. 1968, Marti and Imboden 1986).

Exponential smoothing

Based on the example of lakes in Greenland, Kettle et al. (2004) introduced a method of modelling lake surface water temperature empirically based on the exponential filtering of ambient air temperature. As shown by Kettle et al. (2004), this approach is interpretable physically in terms of a sensible heat exchange model (e.g. Rodhe 1952, Billelo 1964), where the rate of change of T_0 with time is driven by the difference between T_{air} and T_0 and is proportional to this difference. The governing differential equation is that of Newton's Law of Cooling:

$$(16) \quad dT_0/dt = k(T_{air} - T_0)$$

The solution to equation 16 can be written as follows:

$$(17) \quad \begin{aligned} T_0(t) &= T_{air}(t) + [T_0(0) - T_{air}(t)]\, e^{-kt} \\ &= e^{-kt}\, T_0(0) + [1 - e^{-kt}]\, T_{air}(t) \end{aligned}$$

showing that T_0 follows T_{air} exponentially. Over a time-step δt from $t–\delta t$ to t, it follows that:

$$(18) \quad T_0(t) = e^{-k\delta t}\, T_0(t–\delta t) + [1 – e^{-k\delta t}]\, T_{air}(t)$$

Setting $\alpha = 1 – e^{-k\delta t}$ yields the difference equation for an exponential filter, where α is the exponential smoothing coefficient:

$$(19) \quad T_0(t) = (1 – \alpha)\, T_0(t–\delta t) + \alpha\, T_{air}(t)$$

Thus the sensible heat exchange model described by differential equation 16 is mathematically equivalent to applying exponential smoothing to the ambient air temperature. The smoothing coefficient α, which is dependent on the sampling interval δt, is confined to the interval [0, 1], with smoothing being absent at $\alpha = 1$ and increasing to a maximum as $\alpha \to 0$. Exponential filtering reduces the variance of a time-series and introduces a time delay. The approach of Kettle et al. (2004) – i.e. equation 19 – has been used successfully to model the surface temperature of mountain lakes in the Swiss Alps (Livingstone et al. 2005) and the Tatras (Šporka et al. 2006) based on air temperature alone, although Kettle et al. (2004) also included clear-sky solar radiation in their original model.

To take account of meteorological driving variables other than just air temperature, the same approach can be applied to the equilibrium temperature, as the rate at which T_0 is driven towards T_{eq} is proportional to $T_{eq} – T_0$, which results in T_0 tending towards T_{eq} exponentially (e.g. Edinger et al. 1968, Sweers 1976, Livingstone and Imboden 1989):

$$(20) \quad dT_0/dt = k(T_{eq} – T_0)$$

Replacing T_{air} by T_{eq} in equations 17-19, it follows that differential equation 20 is equivalent to applying exponential smoothing to the equilibrium temperature:

$$(21) \quad T_0(t) = (1 – \alpha)\, T_0(t–\delta t) + \alpha\, T_{eq}(t)$$

Viewed purely empirically, double exponential smoothing (i.e. smoothing the exponentially smoothed data a second time) would be more suited to time-series in which a trend is present, Holt-Winters smoothing would cope better with periodic data, and a combination of both techniques would cope best with time-series that contain both a trend and a periodic component. However, the advantages of the physical interpretability of equations 19 and 21 outweigh any empirical advantage, which might be conferred by full double exponential Holt-Winters smoothing (which also requires two additional smoothing parameters). In the following, we use equations 19 and 21 with $\delta t = 1$ h to model lake surface temperature not only in terms of the air temperature T_{air} alone, but also in terms of the equilibrium temperature T_{eq}.

Results

Long-term changes in daily air and water temperature extrema and ranges

For the 20-yr period 1983-2002, we illustrate a comparison of the time-series of the summer means of $T_{0,min}$ and $T_{0,max}$ (Fig. III-1a) with the summer means of $T_{air,min}$ and $T_{air,max}$ (Fig. III-1b). Although the four time-series exhibit similarities in their temporal structure, there are also substantial differences in behaviour, especially in the long-term.

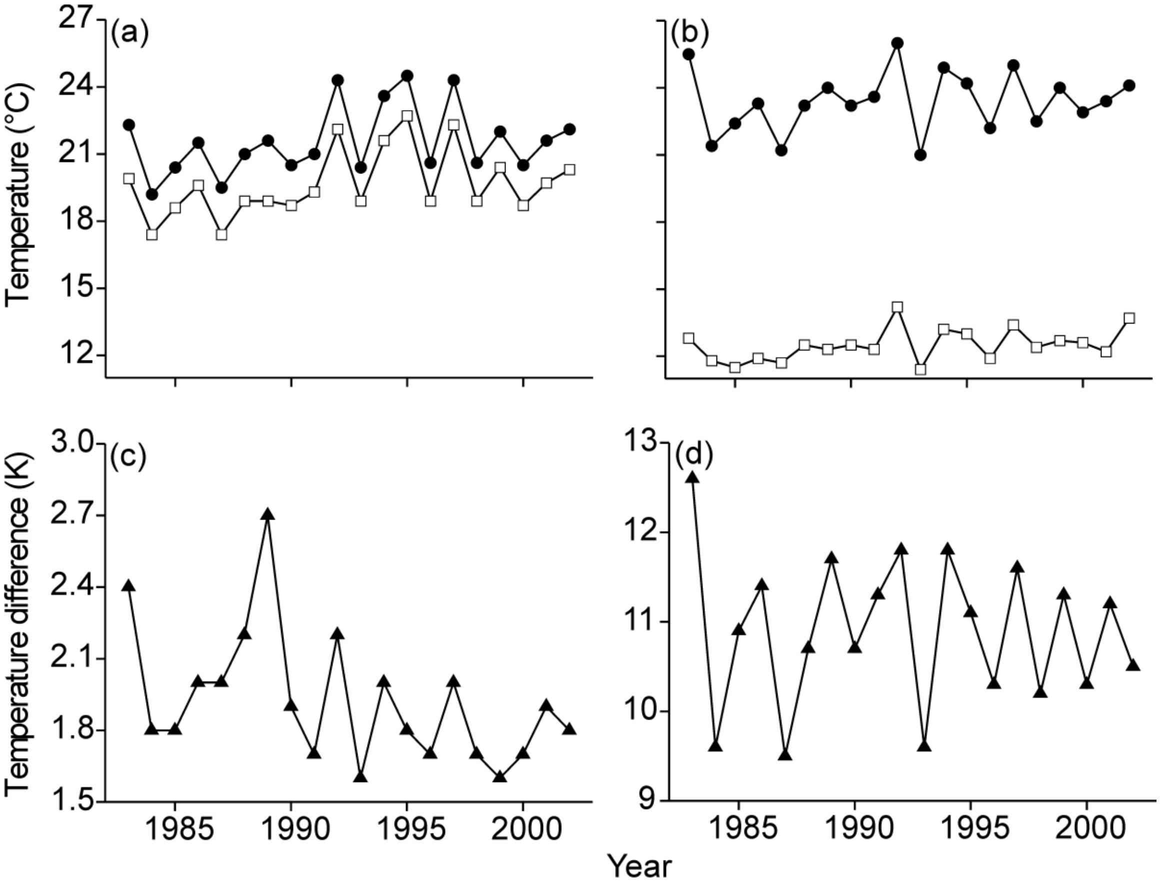

Fig. III-1 Summer (June-August) means of (a) daily minimum epilimnetic temperature ($T_{0,min}$, □) and daily maximum epilimnetic temperature ($T_{0,max}$, ●), (b) daily minimum air temperature ($T_{air,min}$) (□) and daily maximum air temperature ($T_{air,max}$, ●), (c) daily epilimnetic temperature range ($T_{0,dtr} = T_{0,max} - T_{0,min}$) and (d) daily air temperature range ($T_{air,dtr} = T_{air,max} - T_{air,min}$) for Müggelsee from 1983 to 2002.

To test for the presence of linear trends in these non-normally distributed time-series, the Theil-Sen trend, defined as the median of all possible slopes between the data points, taken pairwise (Theil 1950, Sen 1968), was computed and tested for statistical significance at the $p<0.1$ level using the non-parametric Kendall tau statistic (Helsel and Hirsch 1992). A significant increasing trend was confirmed in both $T_{0,min}$ and $T_{air,min}$, but not in either $T_{0,max}$ or $T_{air,max}$ (Table III-1). The long-term changes in daily water and air temperature extrema described above are reflected in the corresponding daily temperature ranges (Fig. III-1c and d). Although the daily air temperature range ($T_{air,dtr}$) exhibited no detectable long-term trend, the daily water temperature range ($T_{0,dtr}$) showed a distinct decreasing trend ($p=0.05$) (Table III-1). In all cases, the Theil-Sen trends in the water temperature time-series were stronger than those in the corresponding air temperature time-series (Table III-1).

Table III-1. Statistics of the epilimnetic temperature of Müggelsee and of the air temperature at Berlin-Schönefeld airport, 10 km from Müggelsee.

	Overall median temperature (°C)	Median absolute deviation (K)	Theil-Sen trend (Kyr^{-1})	p
$T_{0,min}$	19.1	0.5	0.083	0.06
$T_{0,max}$	21.3	0.8	0.069	ns
$T_{0,dtr}$	1.9	0.2	–0.016	0.05
$T_{air,min}$	12.4	0.5	0.054	0.08
$T_{air,max}$	23.4	0.8	0.054	ns
$T_{air,dtr}$	11.0	0.6	–0.015	ns

$T_{0,min}$, mean summer daily minimum epilimnetic temperature; $T_{0,max}$, mean summer daily maximum epilimnetic temperature; $T_{0,dtr}$, mean summer daily epilimnetic temperature range ($= T_{0,max} - T_{0,min}$). $T_{air,min}$, $T_{air,max}$, $T_{air,dtr}$, analogous values for air temperature. Summer was defined as 1 June - 31 August and the period covered was 1983 to 2002. Significance levels (p) of the Theil-Sen trend were calculated from the Kendall tau statistic (ns, not significant at the $p<0.1$ level).

Heat budget model and equilibrium water temperature

The calculated overall mean net heat flux into the lake (H_{calc}) during summer 2002 was 6.9 Wm^{-2}. An analysis of the individual heat flux terms contributing to H_{calc} (Fig. III-2a) confirmed that in Müggelsee, as in other lakes, the emission and absorption of long-wave radiation at the lake surface are the most important processes involved, with H_B (–413.7 Wm^{-2}) having the highest magnitude and H_L (354.2 Wm^{-2}) the second highest. H_S (180.9 Wm^{-2}) and H_E (–96.4 Wm^{-2}) were also important terms, with H_S being the most important forcing term during the daylight hours. The contribution of H_C (–15.9 Wm^{-2}) was relatively minor, and that of H_F (–1.7 Wm^{-2}) was negligible. The heat flux H_P due to precipitation was the least important on average (-0.7 Wm^{-2}), but decreased to as low as -102 Wm^{-2} during individual precipitation events. Thus H_P can be relevant to the lake heat budget in the short term.

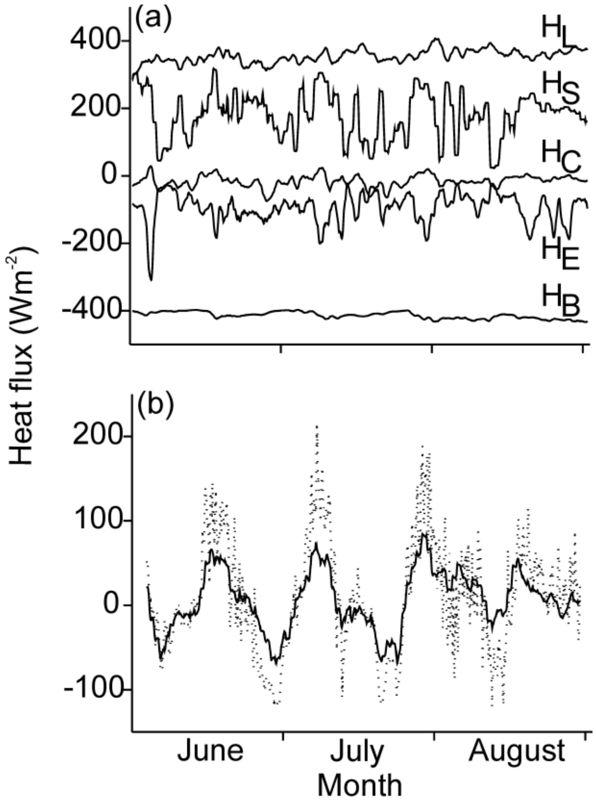

Fig. III-2 Time series of the heat flux into Müggelsee during summer 2002. (a) 24-hour moving averages of the individual heat flux terms of eq. 1 (note that the very small terms H_F and H_P are not shown as they would be indistinguishable from zero on this plot); (b) comparison of 5-day moving averages of the net heat flux calculated from eq. 1 (H_{calc}, solid line) with 5-day moving averages of the net heat flux obtained from temperature profile measurements (H_{meas}, dotted line).

A comparison of calculated and measured heat fluxes revealed that, although the amplitude of the diel variation in H_{meas} was not well accounted for by H_{calc}, averaging over several days drastically reduced the discrepancy between the two time-series, so that H_{calc} provided a good estimate of longer-period temporal variations in H_{meas} (Fig. III-2b). Discrepancies between H_{meas} and H_{calc} at higher frequencies are likely to be irrelevant, since the high-frequency variability of H_{meas} is almost certain to be predominantly an artefact due to seiching. When stratified, Müggelsee exhibits basin-wide circulation in response to wind pulses that set up internal seiches, thus causing local variations in the depth of the thermocline (Lorke 1998). This process can produce huge, rapid changes in H_{meas}, which depends on temperature profiles measured at only one location in the lake that do not in fact reflect the situation pertaining in the water body as a whole. This interpretation is supported by the results of a comparison of H_{meas} during periods of stratification (when seiching can occur) with H_{meas} during periods of homothermy (when seiching cannot occur), which revealed that the variability of H_{meas} was much higher during the former than during the latter.

Hourly values of the equilibrium temperature (T_{eq}) calculated from the heat budget model are compared with corresponding values of the measured temperature at 0.5 m, which is here taken to represent the lake surface temperature (T_0) (Fig. III-3a). The mean value of T_{eq} (20.6 °C) agreed very well with that of T_0 (21.3 °C). The amplitudes of the diel cycles of T_0 and T_{eq}, however, were vastly different, with that of T_{eq} (mean value of 12.9 K) exceeding that of T_0 (0.7 K) by a factor of about 18 (Fig. III-3a). This agrees with the theoretical conclusions of Edinger et al. (1968), who showed that the diel amplitude of T_0, which is driven by T_{eq}, can be only a small proportion of the diel amplitude of T_{eq} itself.

The exponential smoothing approach of Kettle et al. (2004) was used to model T_0 empirically based on air temperature (T_{air}) alone using equation 19 with $\delta t = 1$ h. An optimum value of the smoothing coefficient α was determined by minimising the root mean square error (RMSE) between the measured and modelled time-series of T_0. The optimum fit was found for $\alpha = 0.010$, yielding an overall RMSE of 2.7 K. The model successfully reproduced the main features of the temporal structure of T_0, although the modelled values were consistently somewhat low (on average, 2.2 K) and the high-frequency variability was suppressed (Fig. III-3b). The exchange coefficient $k = -[\ln(1-\alpha)]/\delta t$ corresponding to $\alpha = 0.010$ and $\delta t = 1$ h is 0.24 d^{-1}, which agrees well with the value of k corresponding to the mean value of α found by Kettle et al. (2004) for lakes in southwest Greenland ($\alpha = 0.23$, $\delta t = 1$ d, $k = 0.26$ d^{-1}).

An analogous approach was then employed to model T_0 based on T_{eq} instead of T_{air}, using equation 21 with $\delta t = 1$ h. Since T_{eq} incorporates the forcing effects not only of air temperature, but also of the other relevant meteorological variables (mainly wind speed, relative humidity and cloud cover), equation 21 should yield a better simulation of T_0 than equation 19. This was indeed found to be the case; the optimum value found for the smoothing coefficient ($\alpha = 0.015$; i.e. $k = 0.36$ d^{-1}) yielded an RMSE of 0.9 K, substantially better than the value obtained in the case of T_{air}. The model successfully reproduced not only the main features of the temporal structure of T_0, but much of its high-frequency structure as well (Fig. III-3b). The superiority of an approach based on smoothing T_{eq} rather than T_{air} is most obvious in the later part of the summer (Fig. III-3b),

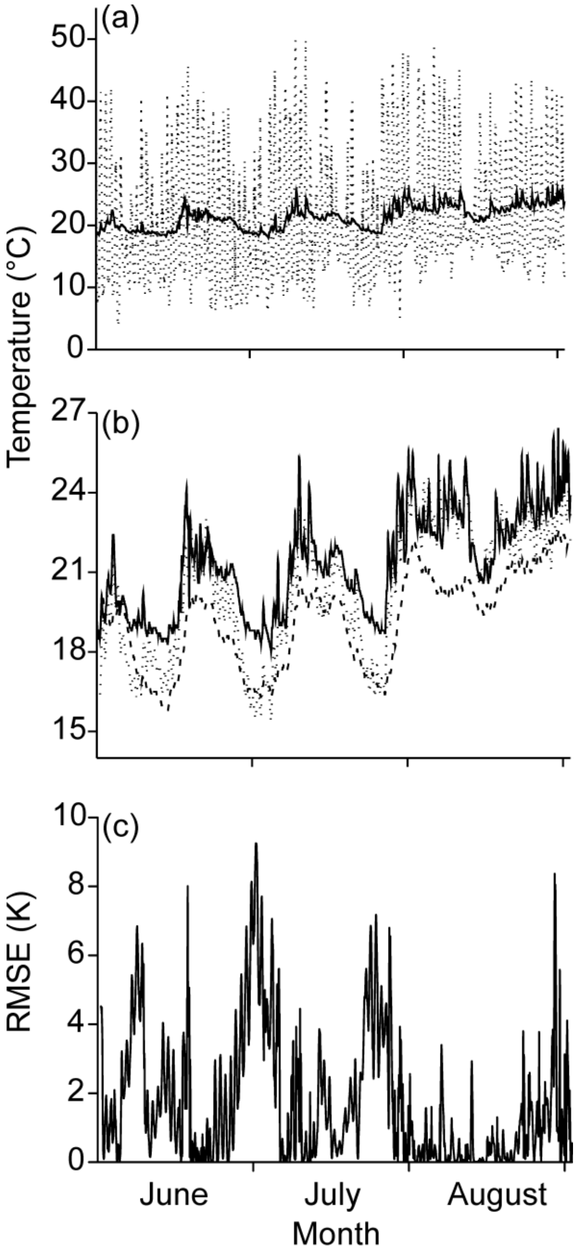

Fig. III-3 Comparison of the measured epilimnetic temperature of Müggelsee (T_0) with the air temperature measured at Berlin-Schönefeld airport (T_{air}) and with the calculated equilibrium temperature of the lake surface (T_{eq}) during summer 2002: (a) comparison of unsmoothed hourly values of T_0 (solid line) and T_{eq} (dotted line); (b) comparison of hourly values of T_0 (solid line) with hourly values of T_{air} (dashed line) and T_{eq} (dotted line) smoothed using eqs. 19 and 21; (c) the root mean square error (RMSE) between T_0 and T_{eq} (smoothed).

when the RMSE was generally very low (Fig. III-3c). Comparing the ability of equations 19 and 21 to reproduce the measured values of $T_{0,min}$, $T_{0,max}$ and $T_{0,dtr}$ (Table III-2), it again emerges that the approach based on T_{eq} (equation 21) is superior to that based on T_{air} (equation 19), with consistently lower RMSE values in all cases. The simulation of $T_{0,dtr}$, with an RMSE of only 0.3 K, was exceptionally good. A linear regression of $T_{0,min}$ on $T_{air,min}$ after smoothing, and of $T_{0,max}$ on $T_{air,max}$ after smoothing, yielded R^2 values of 0.82 and 0.76, respectively. The corresponding R^2 values for linear regressions based on $T_{eq,min}$

and $T_{eq,max}$ after smoothing – 0.88 in both cases – were distinctly higher. A linear regression of the daily temperature range $T_{0,dtr}$ on $T_{eq,dtr}$ after smoothing ($R^2 = 0.52$) also yielded better results than a linear regression of $T_{0,dtr}$ on $T_{air,dtr}$ after smoothing ($R^2 = 0.26$). This clearly demonstrates the improvement in fit achieved by basing the model on T_{eq} rather than T_{air}.

Table III-2. Root mean square errors (RMSE) between observed values of $T_{0,min}$ and between smoothed values of $T_{air,min}$ and $T_{eq,min}$; between observed values of $T_{0,max}$ and smoothed values of $T_{air,max}$ and $T_{eq,max}$; and between observed values of $T_{0,dtr}$ and smoothed values of $T_{air,dtr}$ and $T_{eq,dtr}$ for summer 2002.

	RMSE (K)	
	T_{air}	T_{eq}
$T_{0,min}$	1.8	1.1
$T_{0,max}$	4.0	0.8
$T_{0,dtr}$	0.8	0.3

Smoothing was accomplished by using eq. 19 with $\alpha = 0.010$ for T_{air} and eq. 21 with $\alpha = 0.015$ for T_{eq}. See Table III-1 for definitions of symbols.

Modelling the effect of the meteorological driving variables on the daily water temperature extrema

The heat exchange processes described by equations 1-13 are dependent on very few driving variables. In addition to clear-sky solar radiation, which is essentially a predetermined astronomical variable, the most important of these are air temperature, wind speed, relative humidity and cloud cover (e.g. Edinger et al. 1968, Sweers 1976, Livingstone and Imboden 1989). Because T_0 is determined predominantly by T_{eq}, a sensitivity analysis based on the heat budget model can be used to determine the relative influence of these driving variables on the daily extrema of T_{eq}, and hence on $T_{0,min}$ and $T_{0,max}$. This was done by calculating T_{eq} not only based on the hourly measured meteorological data, but also based on the values that result when these data are decreased and increased by amounts corresponding to the lower and upper quartiles of each input data set, respectively. For each of the hourly time-series of air temperature, wind speed, relative humidity and cloud cover from 1 June to 31 August 2002, the median and the upper and lower quartiles were calculated. For each of the four time-series, two new time-series were created by decreasing each hourly value in the original time-series by the difference between the median and the lower quartile, and by increasing each hourly value in the original time-series by the difference between the upper quartile and the median.

This allowed the effect on T_{eq} of lowering or raising each of the four variables by one quartile to be determined. This non-parametric approach made it unnecessary to make any assumptions about the form of the probability distributions of the driving variables.

An increase (decrease) in either air temperature or relative humidity resulted in an increase (decrease) in both $T_{eq,min}$ (Fig. III-4a) and $T_{eq,max}$ (Fig. III-4b). Although an increase (decrease) in either wind speed or cloud cover resulted in a decrease (increase) in $T_{eq,max}$ (Fig. III-4b), variations in these two driving variables had essentially no effect on $T_{eq,min}$ (Fig. III-4a). $T_{eq,min}$ reacted most sensitively to variations in relative humidity and air temperature, whereas $T_{eq,max}$ reacted most sensitively to changes in cloud cover and relative humidity.

The effect of variations in the four meteorological driving variables differed between nighttime ($T_{eq,min}$) and daytime ($T_{eq,max}$) (Fig. III-4a and b). This day-night asymmetry in the effects of each meteorological driving variable resulted in corresponding increases or decreases in $T_{eq,dtr}$ (Fig. III-4c). Increases (decreases) in either wind speed or cloud cover resulted in corresponding decreases (increases) in $T_{eq,dtr}$ that, in the case of cloud cover, were substantial. The effect of variations in air temperature and relative humidity on $T_{eq,dtr}$ were comparatively slight.

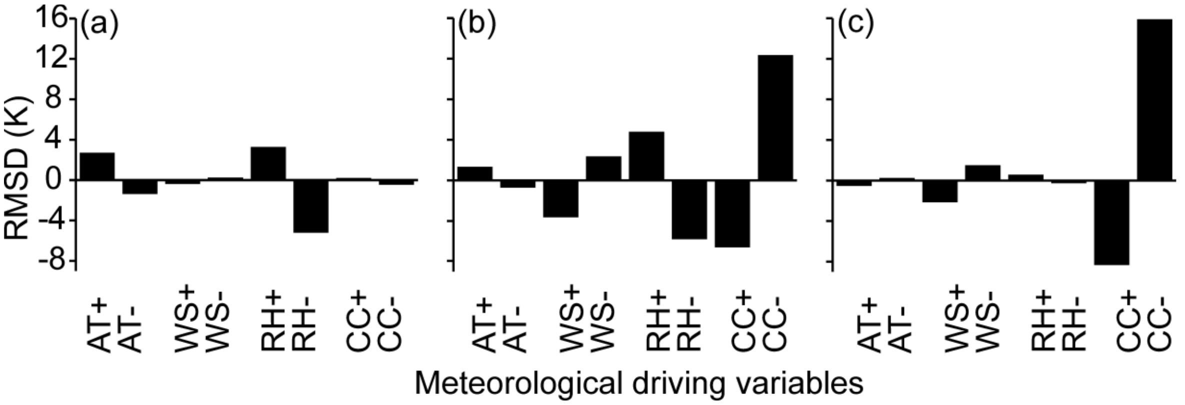

Fig. III-4 The root mean square deviation (RMSD) between the equilibrium temperature of the surface of Müggelsee during summer 2002 calculated (i) from measured meteorological data and (ii) by increasing (+) and decreasing (–) the meteorological driving variables air temperature (AT), wind speed (WS), relative humidity (RH) and cloud cover (CC) by amounts corresponding to the upper and lower quartiles of the data measured during the period 1983-2002. (a) RMSD for the daily minimum equilibrium temperature ($T_{eq,min}$), (b) RMSD for the daily maximum equilibrium temperature ($T_{eq,max}$), (c) RMSD for the daily equilibrium temperature range ($T_{eq,dtr} = T_{eq,max} - T_{eq,min}$).

During the period 1983-2002, the summer means of air temperature, wind speed, relative humidity and cloud cover varied within the ranges 16.2-20.4 °C, 3.0-3.9 ms^{-1}, 62.1-76.6% and 46.9-64.0%, respectively. While there was no obvious long-term change in either air temperature or relative humidity, both wind speed and cloud cover appeared to undergo a slight long-term increase. However, given the high degree of interannual variability, these apparent long-term increases were not statistically significant, and therefore in themselves do not offer a convincing explanation for the long-term changes in $T_{0,min}$, and hence in $T_{0,dtr}$.

To investigate the causes and consequences of the long-term increase in $T_{0,min}$ in more detail, nighttime and daytime estimates of the most important meteorologically dependent heat flux terms were computed from equations 2-11 for each day of each summer from 1983 to 2002. During both night and day, H_F and H_P were assumed to be negligible. During the night, H_S was assumed to be zero. Nighttime estimates of H_L, H_B, H_E and H_C were computed from $T_{air,min}$, $T_{0,min}$, C (daily mean), u_{10} (nighttime mean) and r_h (nighttime mean); daytime estimates of H_L, H_B, H_S, H_E and H_C were computed from $T_{air,max}$, $T_{0,max}$, C (daily mean), u_{10} (daytime mean) and r_h (daytime mean). The lack of data on cloud cover during the night necessitated the use of the daily mean cloud cover (actually a daytime mean) to compute both nighttime and daytime estimates. For both nighttime and daytime, the estimates were then averaged to provide separate estimates of the nighttime and daytime heat flux terms for each summer from 1983-2002. The respective Theil-Sen trends were then computed and tested for significance using the Kendall tau test as before (Table III-3).

Of the five major components of the heat flux, two – H_S and H_E – exhibited no significant long-term trend in either their nighttime or daytime estimates. Terms H_B and H_C exhibited no significant long-term trend in their daytime estimates, but did exhibit significant decreasing trends in their nighttime estimates. Finally, both the daytime and nighttime estimates of H_L exhibited a significant increasing trend, with the nighttime trend exceeding the daytime trend by 37%.

The long-term behaviour of the heat flux terms can be explained in terms of the relevant driving variables. The only driving variables to exhibit a statistically significant long-term trend are $T_{0,min}$ and $T_{air,min}$. During the night, a long-term increase in lake surface water temperature automatically results in the increased emission of long-wave radiation from the lake surface (equation 8), causing a long-term decrease in H_B. The long-term increase in $T_{0,min}$ exceeds that in $T_{air,min}$ by 54% (Table III-1); this difference in trend suffices to induce a long-term increase in nighttime convective heat loss (equation 11); i.e. a long-term decrease in H_C. The emission of long-wave radiation from the atmosphere (H_L) is a comparatively complex process that is driven by air temperature, relative humidity and

Table III-3. Statistics of meteorological driving variables and corresponding estimates of the nighttime and daytime heat flux terms into Müggelsee during summer.

	Overall median value	Median absolute deviation	Theil-Sen trend	p
Nighttime				
u_{10}	3.0 $\mathrm{ms^{-1}}$	0.2 $\mathrm{ms^{-1}}$	0.018 $\mathrm{ms^{-1}yr^{-1}}$	ns
r_h	77.6%	3.4%	0.204% $\mathrm{yr^{-1}}$	ns
H_L	305.8 $\mathrm{Wm^{-2}}$	3.0 $\mathrm{Wm^{-2}}$	0.512 $\mathrm{Wm^{-2}yr^{-1}}$	0.004
E_L	0.83	0.01	0.001 $\mathrm{yr^{-1}}$	0.06
SB_L	377.1 $\mathrm{Wm^{-2}}$	2.8 $\mathrm{Wm^{-2}}$	0.288 $\mathrm{Wm^{-2}yr^{-1}}$	0.08
H_B	–401.5 $\mathrm{Wm^{-2}}$	3.0 $\mathrm{Wm^{-2}}$	–0.458 $\mathrm{Wm^{-2}yr^{-1}}$	0.04
H_E	–37.3 $\mathrm{Wm^{-2}}$	6.7 $\mathrm{Wm^{-2}}$	0.032 $\mathrm{Wm^{-2}yr^{-1}}$	ns
H_C	–52.3 $\mathrm{Wm^{-2}}$	5.4 $\mathrm{Wm^{-2}}$	–0.563 $\mathrm{Wm^{-2}yr^{-1}}$	0.05
Daytime				
u_{10}	4.0 $\mathrm{ms^{-1}}$	0.2 $\mathrm{ms^{-1}}$	0.012	ns
r_h	63.6%	3.1%	–0.105% $\mathrm{yr^{-1}}$	ns
C	58.9%	4.1%	0.172% $\mathrm{yr^{-1}}$	ns
H_S	182.5 $\mathrm{Wm^{-2}}$	6.5 $\mathrm{Wm^{-2}}$	0.064 $\mathrm{Wm^{-2}yr^{-1}}$	ns
H_L	376.7 $\mathrm{Wm^{-2}}$	2.8 $\mathrm{Wm^{-2}}$	0.373 $\mathrm{Wm^{-2}yr^{-1}}$	0.04
E_L	0.89	0.01	0.000 $\mathrm{yr^{-1}}$	ns
SB_L	438.2 $\mathrm{Wm^{-2}}$	4.9 $\mathrm{Wm^{-2}}$	0.317 $\mathrm{Wm^{-2}yr^{-1}}$	ns
H_B	–413.5 $\mathrm{Wm^{-2}}$	4.6 $\mathrm{Wm^{-2}}$	–0.406 $\mathrm{Wm^{-2}yr^{-1}}$	ns
H_E	–114.6 $\mathrm{Wm^{-2}}$	18.1 $\mathrm{Wm^{-2}}$	–0.431 $\mathrm{Wm^{-2}yr^{-1}}$	ns
H_C	12.1 $\mathrm{Wm^{-2}}$	3.2 $\mathrm{Wm^{-2}}$	–0.226 $\mathrm{Wm^{-2}yr^{-1}}$	ns

The equivalent statistics of the epilimnetic temperature of Müggelsee (T_0) and of the air temperature at Berlin-Schönefeld (T_{air}) are listed in Table III-1. u_{10}, wind speed at Berlin-Schönefeld airport; r_h, relative humidity at Berlin-Schönefeld airport; C, cloud cover at Berlin-Tempelhof airport; H_S, heat flux due to absorption of short-wave (solar) radiation; H_L, heat flux due to absorption of long-wave (atmospheric) radiation; E_L, emission coefficient of the atmosphere; $SB_L = \sigma(T_{air} + 273.15)^4$, heat flux emitted from a black body by Stefan-Boltzmann radiation (eq. 3); H_B, heat flux due to the emission of long-wave radiation from the lake surface; H_E, heat flux due to latent heat exchange; H_C, heat flux due to convective heat exchange. Summer was defined as 1 June - 31 August and the period covered was 1983 to 2002. Significance levels (p) of the Theil-Sen trend were calculated from the Kendall tau statistic (ns, not significant at the $p<0.1$ level). The units of the Theil-Sen trend are the respective units of the variable concerned per year.

cloud cover. Taken individually, none of these driving variables exhibits a significant long-term daytime trend; taken together, however, the long-term changes in all three variables do yield a statistically significant long-term increase in daytime H_L (Table III-3). Given the significant increasing trend in $T_{air,min}$, the long-term increase in nighttime H_L is not only much more highly significant than that in daytime H_L, it is also 37% greater in magnitude (Table III-3). The main process responsible for the significant long-term increase in $T_{0,min}$ is therefore the emission of long-wave radiation from the atmosphere. Looking at this process in more detail, during the night a significant long-term increase is detected not only in $T_{air,min}$ (and in the factor $\sigma(T_{air,min} + 273.15)^4 = SB_L$), but also in the factor E_L, the emission coefficient of the atmosphere (Table III-3). From equations 4-6, an increase in E_L can result because of the increase in e_s, and hence in e_a, that would result from an increase in $T_{air,min}$. However, it can also result from an increase in e_a associated with an increase in relative humidity, or from an increase in cloud cover. However, the lack of a statistically significant trend in either of the latter two meteorological variables suggests that the long-term increase in the nighttime values of E_L are also predominantly the result of the long-term increase in $T_{air,min}$.

Discussion

An asymmetric increase in the daily air temperature extrema, leading to a decrease in the daily air temperature range, has characterised recent climate warming throughout the Northern Hemisphere (e.g. Karl et al. 1993). Our study demonstrates for the first time that an analogous phenomenon can be detected in lake epilimnetic temperatures. During summer, from 1983 to 2002, $T_{0,min}$ in Müggelsee increased more rapidly than $T_{0,max}$, resulting in a distinct decrease in $T_{0,dtr}$. However, the decrease in $T_{0,dtr}$ cannot be explained simply in terms of a response to $T_{air,dtr}$, which in fact remained essentially constant during the study period.

Various studies have shown that daily minimum air temperatures have generally been rising faster than daily maximum air temperatures not only globally (e.g. Easterling et al. 1997), but also in central Europe (e.g. Wibig and Glowicki 2002), including Germany (Heino et al. 1999). This is not always the case, however: according to Brázdil et al. (1996), the daily air temperature range in central Europe changed very little between 1951 and 1990. In agreement with this, we find that both $T_{air,min}$ and $T_{air,max}$ in Berlin rose by ~0.05 Kyr^{-1} during our 1983-2002 study period, resulting in essentially no long-term change in $T_{air,dtr}$. Air temperature is arguably the most important of the meteorological variables driving T_{eq}, and hence T_0, since it is involved in most daily heat exchange processes (e.g. Edinger et al. 1968). However, substantial discrepancies with respect to both fluctuations and long-term trends exist between $T_{0,min}$ and $T_{air,min}$, and between $T_{0,max}$ and $T_{air,max}$. These discrepancies lead to even more pronounced discrepancies between $T_{0,dtr}$

and $T_{air,dtr}$. Thus the asymmetric increase in $T_{0,min}$ and $T_{0,max}$ is unlikely to be interpretable in terms of air temperature alone; the influence of other meteorological driving variables must also be taken into account.

In addition to air temperature, the most important meteorological driving variables involved in determining the lake heat budget, and thus T_{eq} and T_0, are wind speed, relative humidity and cloud cover (e.g. Edinger et al. 1968). The good fit between measured values of T_0 and exponentially smoothed values of T_{eq} indicates that an analysis of the sensitivity of $T_{eq,min}$ and $T_{eq,max}$ to variations in these driving variables can be interpreted to show their relative influence on $T_{0,min}$ and $T_{0,max}$. The results of the sensitivity analysis demonstrate that each of the four meteorological driving variables has a perceptible effect on one or both of $T_{eq,min}$ and $T_{eq,max}$. The pronounced effects of relative humidity and cloud cover on the magnitude of T_{eq} agree with the results of Marti and Imboden (1986) and Livingstone and Imboden (1989), who showed the strong dependence of the net heat flux on these variables.

The effects of the meteorological driving variables on $T_{eq,min}$ and $T_{eq,max}$ are not only substantial, they are also asymmetric. The greatest degree of day-night asymmetry in the effects of these variables was exhibited by cloud cover, and to a lesser extent by wind speed, suggesting that these two variables may have contributed substantially to the diel asymmetry in T_{eq}, and hence to the discrepancy between $T_{0,dtr}$ and $T_{air,dtr}$. Because of the nonlinearities inherent in the equations describing the heat flux terms, fluctuations in the daily means of the driving variables can therefore induce a degree of day-night asymmetry in T_{eq} – and hence in T_0 – without day-night asymmetry necessarily having to be present in the driving variables themselves.

The presence of day-night asymmetry in the driving variables themselves makes the situation more complex. Computation of nighttime and daytime estimates of the individual heat flux components based on a coarse day-night separation of the driving variables revealed significant long-term increases in nighttime heat loss from the lake due to the emission of infra-red radiation from the lake surface and to convective processes in the atmospheric boundary layer above the lake surface, which in both cases can be confidently traced back to the observed long-term increase in epilimnetic temperature. These processes are essentially negative feedback processes that automatically regulate lake temperatures, preventing them from increasing steeply when subjected to increasing heat input (e.g. Peeters et al. 2002). This increasing heat input can only result from increases in incident radiation, either short-wave (H_S) or long-wave (H_L), both of which generally account for a very high proportion of the incoming heat flux. An increase in incident short-wave (solar) radiation can be ruled out not only because it exhibits no significant long-term trend during the study period, but also because any increase in incident solar radiation would clearly affect daily maximum (daytime) water temperatures much more strongly than daily minimum (nighttime) temperatures. This leaves the long-term increase in incident long-term atmospheric radiation as the only likely root cause of the overall long-term gross increase in heat input. Not only is H_L the only component of the heat balance to exhibit a statistically significant increasing long-term trend, but this trend is also substantially steeper during nighttime than during daytime. Although H_L is the most difficult of all the major heat flux terms to parameterise (Edinger et al. 1968), it is clear that air temperature, relative humidity and cloud cover are the major meteorological variables that determine it. The only relevant meteorological driving variable with a statistically significant increasing nighttime trend is air temperature, which has both a direct effect on H_L via Stefan-Boltzmann emission, and an indirect effect because it influences the emission coefficient of the atmosphere. Thus, despite the fact that the epilimnetic temperature can be modelled more accurately based on the equilibrium temperature than on air temperature alone, and although it can be shown that driving variables other than air temperature – especially cloud cover – have a substantial influence on the equilibrium temperature, the only variable that we can confidently assert to be at least partly responsible for the long-term increase in the daily minimum epilimnetic temperature, and hence for the daily temperature range in the epilimnion, is the daily minimum air temperature. Nevertheless, there are strong indications that relative humidity and cloud cover should not be neglected in future modelling studies, as any long-term increase in either of these variables will act to support the effect of a long-term increase in daily minimum air temperature on the nighttime emission coefficient of the atmosphere, and hence on the nighttime emission of long-wave atmospheric radiation. This is the process that is predominantly responsible for the phenomenon of day-night asymmetry in the epilimnetic temperature.

The results of this study are not only of physical, but also of biological significance. The importance of water temperature as an ecological factor in lakes is undoubted, since it is a dominant regulator of nearly all physico-chemical cycles, and consequently of lake metabolism and productivity (Wetzel 2001). The potential biological relevance of the long-term decrease in the daily epilimnetic temperature range resulting from the increase in the daily minimum is less clear, since this is the first time to our knowledge that this phenomenon has been observed. Demonstrating experimentally the ecological implications of such a decrease is, however, likely to be a challenging task.

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CHAPTER IV

The impact of long summer stratification events on dissolved oxygen, dissolved nutrients and phytoplankton in a polymictic lake

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Under revision for *Freshwater Biology*

Abstract

In comparison to dimictic lakes, temperate polymictic lakes exhibit frequent and irregular interruptions of thermal stratification by mixing. From hourly measured water temperature profiles the mixing regime of a polymictic lake (Müggelsee, Germany) was determined from 2003 to 2006. Stratification events lasting less than one day were by far the most frequent but during summer prolonged thermal stratification events occurred one to three times a year, lasting from about 1 week to 2 months. During stratification events the hypolimnetic temperature continuously increased, stimulating the depletion of dissolved oxygen and the accumulation of dissolved nutrients (especially of phosphorus). Limiting dissolved oxygen concentrations affected up to 66% (< 5 mg L^{-1}) and 40% (< 2 mg L^{-1}) of the total lake volume. The breakdown of each long stratification event was followed by a pulse of dissolved nutrients into the euphotic layer. These multiple nutrient pulses resulted in the development of phytoplankton blooms, the magnitude of which depended on the previously accumulated dissolved phosphorus and silicon. During stratification the functional phytoplankton composition shifted from species that are sensitive to stratification to species that are tolerant to or favoured by stratification. Contrary to predictions, cyanobacteria did not generally profit from rising water temperatures or prolonged stratification events. Even during extremely long stratification events the thermal characteristics and the nutrient accumulation were not generally comparable to those observed in shallow dimictic lakes during summer stratification. In the future, summer stratification events will be very likely amplified with respect to projected climate changes. Consequently, the dissolved oxygen depletion and dissolved nutrient accumulation in the hypolimnion may increase, stimulating the formation of phytoplankton blooms.

Introduction

Shallow lakes are widespread across the northern hemisphere and because of their morphometry are often polymictic, experiencing alternating periods of mixing and thermal stratification during summer driven by prevailing weather conditions (Wetzel 2001). These lakes quickly respond to actual weather conditions and are thus particularly prone to changes in climate. Impacts of climate warming on thermal conditions of temperate lakes are widely documented for dimictic lakes (reviewed by Gerten and Adrian 2002a), including shortened ice-cover periods (e.g. Weyhenmeyer et al. 1999), increasing water temperatures (e.g. Schindler et al. 1990), an advanced onset of thermal stratification (Gerten and Adrian 2001) and an increased lake stability (e.g. King et al. 1997). Modelling studies based on future climate scenarios suggest further amplifications in these changes in the thermal characteristics of dimictic lakes (De Stasio 1996, Peeters et al. 2002). Effects of climate warming on polymictic lakes are less well understood (Gerten and Adrian 2001). Here changes in climate may not only affect single thermal characteristics as water temperature but also the mixing regime in general and thus the frequency and duration of intermittent thermal stratification events.

Prolonged thermal stratification in the context of climate warming has already been shown to particularly influence hypolimnetic oxygen conditions (Jankowski et al. 2006), enhancing stress to aquatic organisms (Weider and Lampert 1985, Seager et al. 2000, Wilhelm and Adrian 2007). Moreover, nutrient release processes at the sediment-water interface are supported by oxygen depletion and by high hypolimnetic temperatures (Marsden 1989, Søndergaard et al. 2003). Higher hypolimnetic temperatures also stimulate the mineralisation of organic matter, which contributes to the accumulation of dissolved nutrients in the hypolimnion (Søndergaard et al. 2003). The internal nutrient loading, especially of phosphorus, is important for the nutrient budget of productive polymictic lakes (Riley and Prepas 1984, Scheffer 1998), because alternating stratification and mixing events cause – other than in dimictic lakes – multiple nutrient pulses into the euphotic layer during summer.

For phytoplankton the strength and frequency of turbulence governed by the mixing regime of a lake is a primary factor influencing growth and competition (Ptacnik et al. 2003, Huisman et al. 2004). Particularly buoyant species like cyanobacteria are advantageous over non-motile species (e.g. diatoms) in a stratified water column (Reynolds 1997). The breakdown of thermal stratification is followed by nutrient pulses into the euphotic zone inducing phytoplankton blooms (c.f. French and Petticrew 2007), which is a well known phenomenon in dimictic lakes after the overturn in fall (Sommer et al. 1985).

Previous studies on the mixing regime of temperate polymictic lakes and the impacts on dissolved oxygen, nutrients and the plankton community (Weithoff et al. 2000, Watts et al. 2001, Wiedner et al. 2002), including those on Müggelsee (e.g. Behrendt et al. 1993, Kleeberg and Dudel 1997), were often limited to short periods of time or to a low sampling frequency. However, high frequency measurements are especially important for the study of polymictic lakes, because their thermal characteristics vary on short time scales (Wetzel 2001).

To account for this high temporal variability we measured water temperature profiles at hourly intervals between 2003 and 2006. We determined the frequency, duration and intensity of stratification events and aimed at ascertaining the impact of long stratification events on hypolimnetic dissolved oxygen, dissolved nutrient concentrations (phosphorus, nitrate, silicon) and on phytoplankton biomass and functional composition. The investigation period includes the European heatwave in 2003 (Schär et al. 2004) and the recent extremely warm summer in 2006 and thus provides an excellent opportunity to assess the functioning of polymictic lakes with respect to the projected future climate warming (Cubasch et al. 2001).

Materials and methods

Study site

The Müggelsee is a shallow, eutrophic and polymictic lake in eastern Berlin, Germany. It has a mean depth of 4.9 m, a maximum depth of 8 m and covers an area of 7.3 km^2. The lake is flushed by the River Spree and had a mean theoretical water retention time of 25-28 weeks during the summer months (June, July and August) from 2003 to 2005 (S. Wilhelm, unpublished data). The surrounding topography is flat and the lake basin is oriented from East to West, hence, the lake is highly exposed to the prevailing winds from Southwest.

Data

The water temperature profile of the lake from 2003 to 2006 was recorded at 5-min intervals at a lake station anchored 300 m offshore using a chain of AD592 temperature transducers (Analog Devices, Norwood, USA) that were deployed from 0.5 to 5.0 m water depth at 0.5-m intervals. Water temperature measurements were used from April to October (except for 2003 when recordings started at the end of May) and were aggregated to yield hourly means. The lake was defined as thermally stratified if the water temperature difference exceeded 1 K between the surface (0.5 m depth) and 5.0 m depth (at the lake station). This water temperature difference ranged from 1.0 to 11.1 K and was also used to characterise the intensity of stratification, because the water column stability – estimated by the square of the Brunt-Väisälä frequency (c.f. Behrendt et al. 1993) – could not be calculated due to the lack of hourly conductivity profiles in 2003. From 2004 to 2006 hourly stratification intensity and the Brunt-Väisälä frequency-based stability were signifycantly correlated ($r = 0.99$, $p<0.001$), indicating the applicability of the stratification intensity based on water temperature alone.

During stratification the thermocline depth that separates the upper from the lower water layer (referred to epilimnion and hypolimnion in the following) was defined as the depth where the maximum temperature difference between two consecutive measurement depths occurred. This depth ranged from 0.75 to 4.75 m at intervals of 0.5 m. Water temperature profiles exhibiting double thermoclines were characterised using the deepest thermocline. Thermocline depths located beneath 5.0 m due to internal seiches that occur in the lake (Lorke 1998) were set to 4.75 m (in 139 incidents with a mean duration of 4.5 hours). Mean epilimnetic and hypolimnetic water temperatures were computed based on the profile measurements above and below the thermocline depth.

At the lake station hourly profiles of dissolved oxygen concentrations (DO) were measured from 2004 to 2006 from 0.5 to 5.0 m depth at 0.5-m intervals using a YSI 6600 probe (YSI Inc., Yellow Springs, USA) that was mounted on a winch. Since hourly DO profiles at the lake station were not available for 2003, weekly DO profiles were used from 2003 to 2006, measured at the deepest part of the lake from 0.5 to 7.0 m at 0.5 m intervals with a Hydrolab probe (Hach Corporation, Loveland, USA). The hourly and weekly DO concentrations averaged over the lake profile showed no significant difference for the years 2004 to 2006 (Wilcoxon paired-sample test, $p>0.05$). Thus, hourly DO (DO_h) and weekly DO (DO_w) measurements could equally be applied in the analysis. Both DO_h and DO_w were used to determine the relative frequency, quantity and duration of lake volumes containing less than 5 and 2 mg DO L^{-1}. These concentrations are known to limit the growth and survival of aquatic organisms, especially of fish species (e.g. Alabaster and Lloyd 1982). We identified the water depth below which DO was lower than 5 mg L^{-1} (2 mg L^{-1}) and calculated the affected lake volume (in %) by means of the hypsographic curve of the lake. The volume beneath the depth of 7 m corresponds to a total lake volume of 1.1% and beneath 5 m depth (about average lake depth) to 18.7%. For DO_h the affected lake volume was computed from 18.7% onwards, due to the maximum water depth of 5 m at the lake station. The hypolimnetic means of DO_w and DO_h were computed based on the profile measurements below the thermocline depth.

Dissolved nutrients, i.e. soluble reactive phosphorus (SRP), nitrate (NO_3), ammonium (NH_4) and soluble reactive silicon (SRSi), and phytoplankton biomass (fresh weight) from 2003 to 2006 were determined at weekly intervals (Driescher et al. 1993). During the absence of thermal stratification a mixed sample over the lake profile was taken (mean lake conditions), whereas during stratification two mixed samples were taken separately, representing the upper (0.5-3.5 m depth) and lower (4.5-7.0 m depth) water layers (Driescher et al. 1993). The separation of the upper and lower water layer may not always correspond to the epi- and hypolimnion as determined by the thermocline depth. Nevertheless, the two mixed samples representing the upper and lower water layers compare well with the mean thermocline depth as calculated in the present study (3.5 ± 1.3 m; see Results). Epilimnetic phytoplankton species were assigned to functional groups according to Reynolds et al. (2002), with each group being more likely to occur under particular environmental conditions such as mixing or stratification (Table IV-1). To analyse the overall phytoplankton composition during and after a stratification event, the dominant functional group was selected from each weekly sample. A phytoplankton bloom during and after long stratification events was defined as at least a doubling of biomass compared to the last sampling before stratification or before complete mixing.

Table IV-1. Dominant phytoplankton functional groups of Müggelsee according to Reynolds et al. (2002) during summer from 2003 to 2006.

Codon	Description	Representatives	Sensitivity
C	larger diatoms	*Stephanodiscus*	stratification
P	summer diatoms	*Aulacoseira, Fragilaria*	stratification
S1	filamentous cyanobacteria	*Planktothrix*	neither
X2	eutrophic nanoplankter	*Chrysochromulina*	mixing
Y	nanoplanktonic flagellates	*Cryptomonas, Rhodomonas*	neither
H1	nitrogen-fixing cyanobacteria	*Aphanizomenon*	mixing
L_M	motile colonies	*Ceratium*	mixing

Data analysis

To examine the mixing regime of Müggelsee we compiled a frequency distribution of the duration of stratification events between 2003 and 2006 and analysed their seasonal distribution. All further analyses were conducted with the data associated with stratification events with a duration of more than one week, as data on nutrients and phytoplankton were derived from weekly sampling intervals only. Mean values of hourly stratification intensity, thermocline depth, epilimnetic and hypolimnetic water temperature and weekly hypolimnetic DO_w, dissolved nutrients and phytoplankton biomass were calculated for each event and the Kruskall-Wallis H test was applied to test for significant differences between events. The Wilcoxon paired-sample test was used to test for differences in dissolved nutrient concentrations between the epi- and the hypolimnion. Spearman correlation was performed to test for relationships between physical, chemical and biological variables (i.e. stratification duration and intensity, hypolimnetic temperature DO_w and DO_h, dissolved nutrients and phytoplankton biomass). To evaluate the relationship between the thermal characteristics of the lake and each of the depending chemical or biological variable partial correlation analysis (e.g. Lozán and Kausch 1998) was performed. The proportion of shared variance (r) was calculated between each of the influencing variables (i.e. stratification duration, intensity, thermocline depth and hypolimnetic temperature) and the depending variable (hypolimnetic DO, SRP or epilimnetic phytoplankton functional groups), to describe the strength of the relationship between two variables whilst taking away the effects of the other influencing variables.

Results

Mixing regime

From 2003 to 2006, 150 stratification events of different duration were recorded between April and October. Very short events with a duration of less than 1 day were by far the most frequent, representing 79.3% of all events (Fig. IV-1a). Long events that lasted for more than 1 week occurred with an incidence of 5.3% or 8 events in total and lasted from 1.3 to 8.6 weeks (Fig. IV-1a and b). First stratification events occurred in March or April and the last in October or November. The onset of long stratification events was found from the end of May to the end of August (Fig. IV-1b). During fall the lake was usually completely mixed, while during summer the amount of stratification exceeded that of mixing (Fig. IV-1c). The longest stratification events developed during the European summer heat waves in 2003 and 2006 (events 1 and 2 in Table IV-2; Fig. IV-1b).

Physical characterisation of long stratification events

The eight prolonged stratification events were characterised by a wide range in their duration (Table IV-2), an overall mean thermocline depth of 3.5 ± 1.3 m and a mean stratification intensity of 3.5 ± 2.3 K (maximum of 11.1 K in 2006). The stratification events showed a high variability in thermocline depth and stratification intensity within and between events (Fig. IV-2a and b; Table IV-2). On the one hand, thermocline depth and

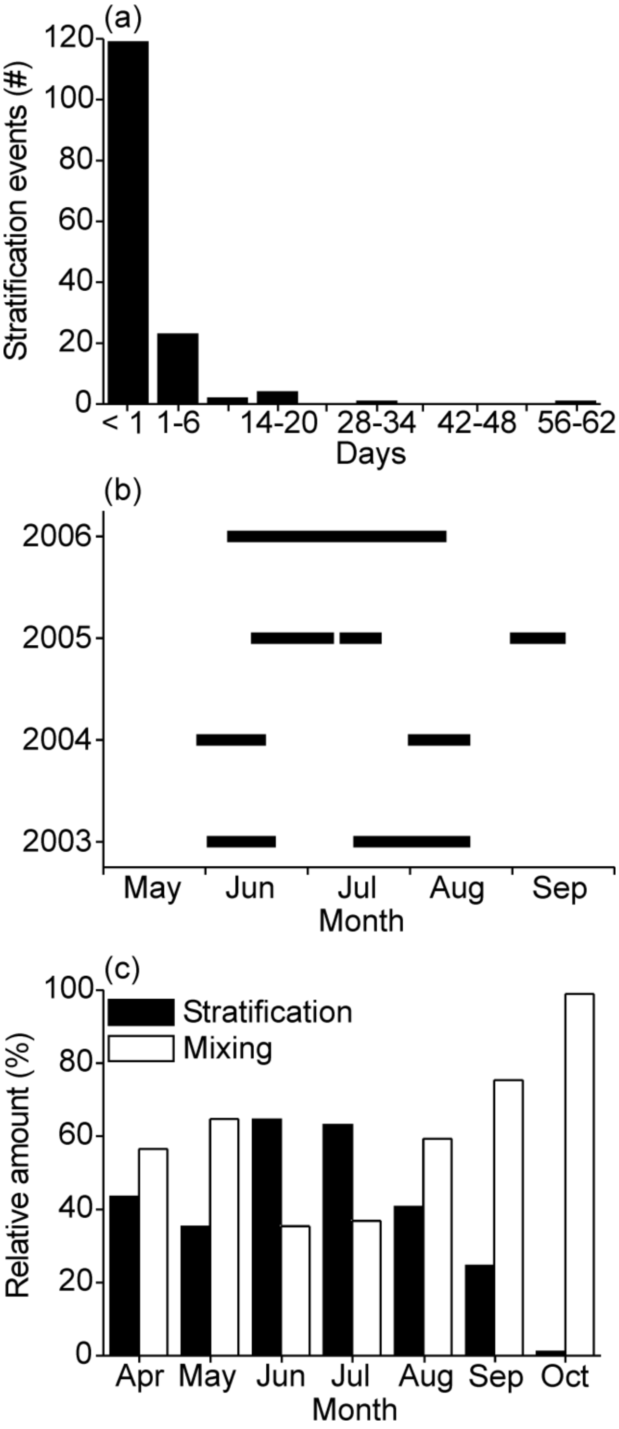

Fig. IV-1 The mixing regime of Müggelsee from 2003 to 2006: (a) duration of stratification events, (b) distribution of the eight prolonged summer stratification events and c) seasonal distribution of mixing and stratification.

stratification intensity exhibited stable periods as well as rapidly occurring steep changes during each event – even obvious after averaging over 48 h (Fig. IV-2) – but revealed no substantial correlation with each other. On the other hand, significant differences for thermocline depth and intensity between the events (both $p<0.001$) were found. The thermocline decreased significantly with increasing duration of stratification ($r = 0.40$,

$p<0.05$; Fig. IV-2a). Mean epilimnetic temperature per event ranged between 21.3 and 24.4 °C and was positively correlated with mean stratification intensity ($r = 0.81$, $p<0.05$). Mean hypolimnetic temperature per event ranged from 15.7 to 21.5 °C (Table IV-2) and was significantly correlated with the duration of stratification ($r = 0.60$, $p<0.01$), indicating an increase in hypolimnetic temperature with increasing stratification duration.

Table IV-2. Characterisation of long stratification events from 2003 to 2006 (mean values and standard deviation).

							Phytoplankt. (mgL^{-1})	
Event (#)	Duration (h)	Thermocline (m)	Intensity (K)	Hypolimn. temp. (°C)	DO_w (mgL^{-1})	SRP (μgL^{-1})	Strati-fication	Peak (after)
1	1456	3.8 ± 1.0	5.0 ± 2.5	19.6 ± 2.6	2.3 ± 2.5	328 ± 331	8.2 ± 5.3	13.1
2	751	3.4 ± 1.3	3.8 ± 1.6	21.5 ± 1.4	2.6 ± 0.8	359 ± 145	1.8 ± 0.6	14.9
3	496	3.3 ± 1.4	3.1 ± 1.8	18.8 ± 1.5	3.6 ± 2.7	70 ± 53	1.9 ± 1.9	-
4	432	3.9 ± 1.1	2.9 ± 2.0	20.1 ± 1.4	1.8 ± 0.6	124 ± 33	3.0 ± 2.4	6.1
5	410	3.5 ± 1.4	2.0 ± 1.0	15.7 ± 1.4	7.1 ± 2.0	33 ± 8	2.7 ± 0.9	7.0
6	356	3.2 ± 1.3	2.5 ± 1.2	20.8 ± 0.8	2.4 ± 0.7	183 ± 67	1.0 ± 0.2	12.6
7	325	2.8 ± 1.5	1.7 ± 0.9	20.0 ± 0.4	6.1 ± 0.7	207 ± 3	10.3 ± 6.3	10.4
8	223	2.9 ± 1.2	2.3 ± 1.3	21.0 ± 0.9	4.0 ± 4.8	64	2.5 ± 1.2	14.3

DO_w, weekly hypolimnetic dissolved oxygen; SRP, hypolimnetic soluble reactive. Events are sorted by their duration and there was only one sample for SRP during event 8. The epilimnetic peak biomass after breakdown of stratification cannot be given for event 3, because at the first sampling after breakdown of stratification the next event had started.

Dissolved Oxygen

Hypolimnetic DO_w concentrations were highly variable (Table IV-2) but no statistically significant difference was found between the events. Oxygen depletion (DO_w) affected up to 40% (< 5 mg L^{-1}) and 25% (< 2 mg L^{-1}) of the total lake volume (Fig. IV-3a). On an hourly basis oxygen depletion (DO_h) affected up to 66% (< 5 mg L^{-1}) and 40% (< 2 mgL^{-1}) of the total lake volume (Fig. IV-3a). These low oxygen conditions were usually rather short-lived lasting for 1 to 12 hours (Fig. IV-3b), but persisted up to a maximum of 9 days (DO_h < 5 mg L^{-1}) during the extreme summer in 2006. To determine the influence of the thermal characteristics of the lake on hypolimnetic DO_h and the lake volumes containing less than 5 and 2 mg DO_h L^{-1}, partial correlation analysis was performed. All tested thermal lake characteristics were important in determining overall DO concentrations (Table IV-3). This was not the case when considering the lake volumes affected by the two threshold concentrations as both were, e.g., unaffected by thermocline depth.

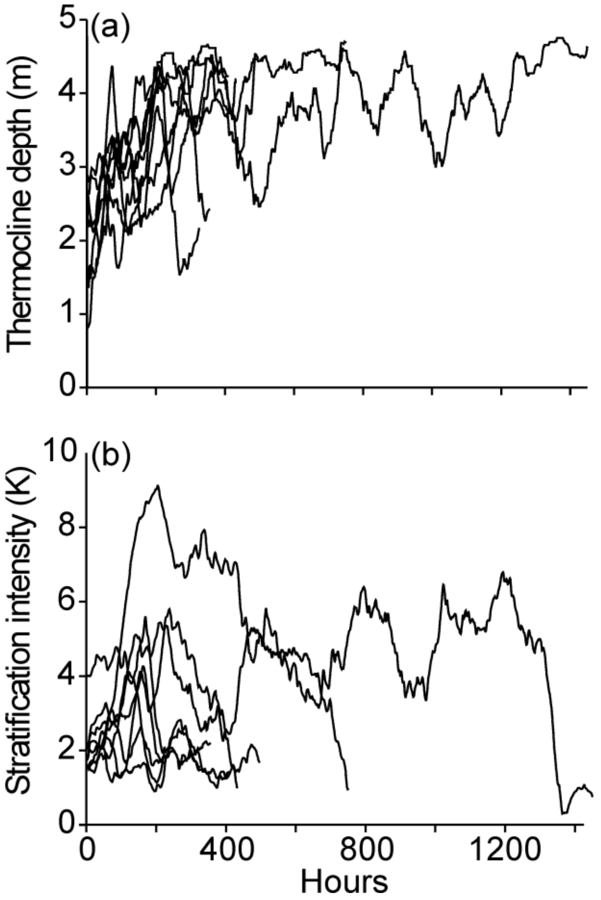

Fig. IV-2 Time series of the eight prolonged stratification events of Müggelsee from 2003 to 2006: 48-h moving averages of (a) thermocline depth and (b) stratification intensity.

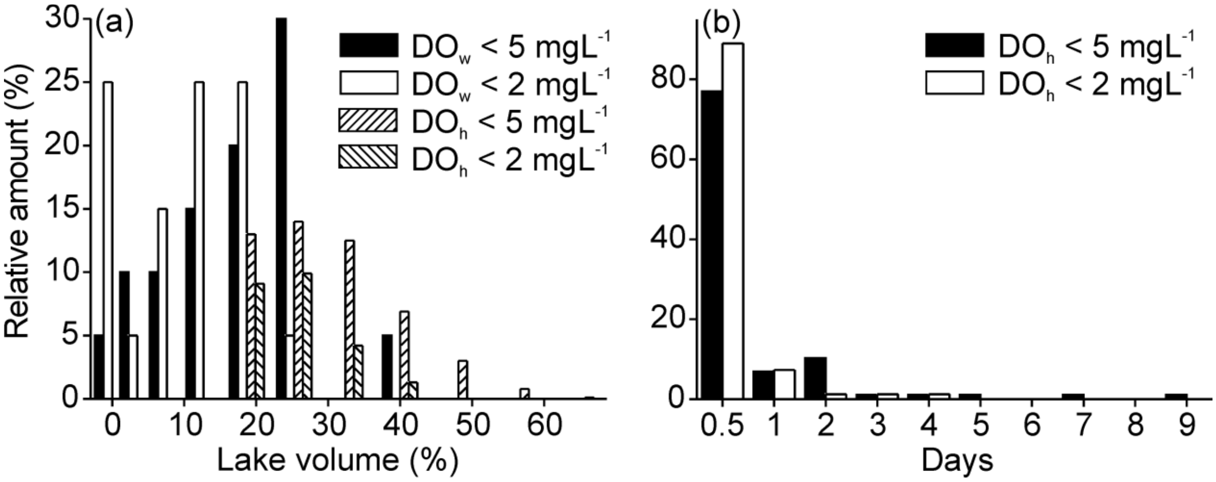

Fig. IV-3 Hypolimnetic dissolved oxygen conditions during stratification: (a) frequency of affected lake volumes containing less than 5 and 2 mg L^{-1} of weekly (DO_w) and hourly (DO_h) measured dissolved oxygen and (b) duration of hourly measured dissolved oxygen concentrations (DO_h) of less than 5 and 2 mg L^{-1}.

Table IV-3. Partial correlation coefficients (r) between the thermal characteristics of the lake and dissolved oxygen, SRP and epilimnetic phytoplankton.

		Lake volume			Functional group	
	DO_h (mgL^{-1})	DO_h < 5 mgL^{-1}	DO_h < 2 mgL^{-1}	SRP (µgL^{-1})	C (mgL^{-1})	X2 (mgL^{-1})
Stratification duration	–0.28**	0.17**	0.44**	0.71**	ns	ns
Stratification intensity	–0.37**	0.41**	0.28**	ns	ns	0.41*
Thermocline depth	–0.54**	ns	ns	–0.49*	–0.49*	ns
Hypolimnetic temperature	–0.23**	0.25**	ns	0.44*	ns	ns

DO_h, hourly hypolimnetic dissolved oxygen; SRP, hypolimnetic soluble reactive phosphorus; ns, not significant at $p<0.5$; *, significant at $p<0.05$; **, significant at $p<0.01$.

Nutrients

Epi- and hypolimnetic concentrations of dissolved nutrients exhibited a wide range between and within stratification events, particularly SRP (Tables IV-2 and IV-4), and were significantly higher in the hypolimnion than in the epilimnion (for all nutrients $p<0.01$). In contrast to hypolimnetic DIN and SRSi that generally remained at lower concentrations, hypolimnetic SRP concentrations strongly increased during most stratification events (Table IV-4) as obvious from the high mean values and their large standard deviations (Table IV-2). The magnitude of the hypolimnetic SRP accumulation mainly depended on the duration of stratification but also on thermocline depth and hypolimnetic temperature (Table IV-3). After the breakdown of stratification mean SRP concentrations increased by a factor of 3.3, DIN by 2.8 and SRSi by a factor of 1.2 as compared to previous epilimnetic concentrations (Table IV-4). The increase in SRP concentrations after mixing depended on hypolimnetic SRP concentrations reached by the end of each stratification event ($r = 0.93$, $p<0.01$). For DIN ($r = 0.52$, $p>0.05$) and SRSi ($r = 0.70$, $p>0.05$) concentrations no such significant relationship was found.

Table IV-4. Ranges of dissolved nutrients during and directly after breakdown of stratification events (c.f. Table IV-2) in the epi- and hypolimnion.

	During stratification		After mixing
	Epilimnion	Hypolimnion	Epilimnion
SRP (µgL^{-1})	4 - 138	26 - 933	34 - 267
DIN (mgL^{-1})	0.03 - 0.18	0.05 - 1.5	0.05 - 0.33
SRSi (mgL^{-1})	0.1 - 5.9	0.9 - 6.9	0.8 - 5.6

SRP, soluble reactive phosphorus; DIN, dissolved inorganic nitrogen; SRSi, soluble reactive silicon.

Phytoplankton

Mean epilimnetic phytoplankton biomass during the eight stratification events was highly variable (Table IV-2), and so was the phytoplankton composition. Nevertheless, some general pattern was found. Before the onset of stratification the functional groups C, Y and L_M (c.f. Table IV-1) dominated the summer phytoplankton (Fig. IV-4a). With the beginning of stratification functional groups P and X2 became dominant, while group C lost dominance after 1 week of stratification. The functional group H1 representing cyanobacteria appeared during the longest stratification event in 2006 only. During most events (5 of 8 events) maximum phytoplankton biomass was recorded 1 to 6 weeks after the onset of stratification, otherwise phytoplankton biomass remained rather stable or decreased steadily in the course of stratification. Functional groups C, P or H1 dominated the phytoplankton during the peak of a bloom. We tested the influence of the thermal conditions on the dominant functional groups and found that groups C and X2 were significantly correlated with thermocline depth or with the stratification intensity (Table IV-3). There were no significant correlations between the concentrations of dissolved nutrients and the biomass of distinct functional groups in the epilimnion.

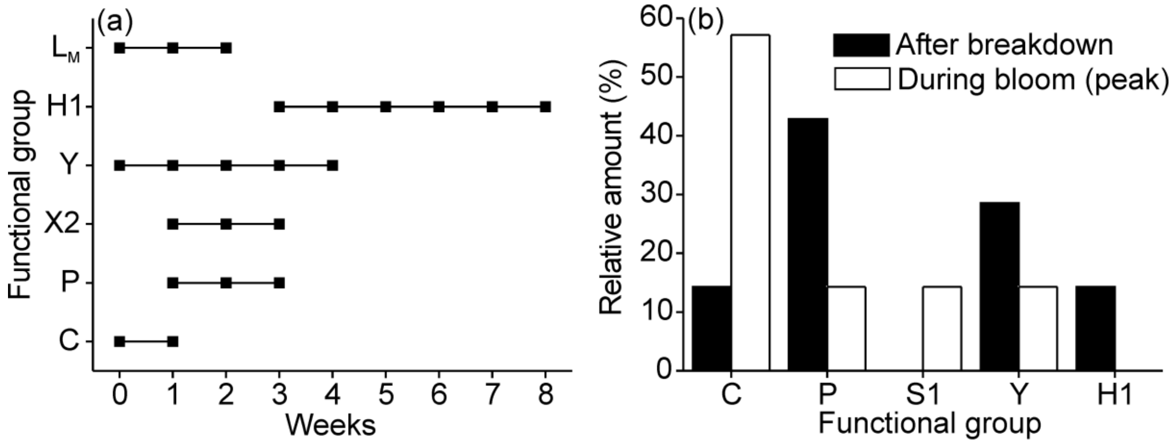

Fig. IV-4 Dominant phytoplankton functional groups of Müggelsee during summer from 2003 to 2006: (a) during stratification (note that the week before the onset of stratification was referred to as week 0) and (b) directly after breakdown of stratification and during the biomass peak of the phytoplankton blooms.

After the breakdown of the stratification events the phytoplankton composition was mostly dominated by functional groups P and Y (Fig. IV-4b). Each stratification event was followed by a phytoplankton bloom occurring about 3 weeks after complete mixing. The peak biomass of these phytoplankton blooms (Table IV-2) was on average 5.5 times higher than the biomass of the last epilimnetic sample before breakdown of stratification and was mostly dominated by functional group C (Fig. IV-4b). Only the extremely long event in 2006 was followed by a bloom of cyanobacteria (group S1). Except for DIN, we found significant relationships between hypolimnetic SRSi ($r = 0.86$) and SRP ($r = 0.71$, both $p<0.05$) concentrations reached by the end of stratification and the magnitude of the subsequent phytoplankton bloom.

Discussion

Mixing regime

In Müggelsee thermal stratification turned out to be more frequent than mixing during summer from 2003 to 2006. Between June and August 1 to 3 prolonged stratification events occurred per year, which highly varied in their length from about 1 week to 2 months and which reached maximum durations during the extremely warm summers in 2003 and 2006. The stratification event in 2006 was the longest on record between 1979 and 2006 (S. Wilhelm, unpublished data).

Even during the extremely long stratification events the thermal characteristics of the lake differed from those typically found in shallow dimictic lakes, which exhibit a continuous stratification during summer. The water temperature difference between lake surface and bottom (stratification intensity) was rather small (mean of 3.5 K), because long stratification events built up during summer when mean lake temperatures were already quite high. Therefore, hypolimnetic temperatures were much higher than in shallow but dimictic lakes that start to stratify earlier in the year (e.g., about 7-15 °C for Upper Rock lake, Agbeti et al. 1997; about 5-13 °C for Heiligensee, Gerten and Adrian 2001). In addition, hypolimnetic temperatures increased with increasing duration of a stratification event, most likely caused by heat conduction from the epilimnion to the hypolimnion during periods of low stratification intensity (Imberger and Patterson 1990). This process results in an extension of the epilimnion leading to a deepening of the thermocline throughout the period of thermal stratification (Fig. IV-2). The strong short-term variations in stratification intensity and thermocline depth in Müggelsee were mainly caused by variations in meteorological forcing at the lake surface (c.f. Wilhelm et al. 2006) and by internal seiches generated by wind (c.f. Lorke 1998), which is generally known for lakes exhibiting thermal stratification (Imberger and Patterson 1990, Imboden and Wüest 1995).

Effects of long stratification on dissolved oxygen, nutrients and phytoplankton

As expected, hypolimnetic DO_h depletion was strongly linked to the actual thermal conditions (Table IV-4). Interesting is the discrepancy between the duration of stratification (weeks to months) and the rather short-lived DO_h depletion in the hypolimnion (hours to days). This may be attributed to the frequent occurrence of internal seiches in Müggelsee (c.f. Lorke 1998), causing the thermocline to tilt (Imboden and Wüest 1995). This tilting of the thermocline leads to a "dis- and reappearance" of the hypolimnetic layer (at the near-shore measuring station), resulting in alternating high and low oxygen concentrations in deeper waters at rather short time intervals (Imboden and Wüest 1995). Deeper parts in the middle of the lake (5-8 m) are likely much longer affected by limiting DO_h concentrations, since these regions are not as strongly influenced by the tilting of the thermocline as near-shore regions. Oxygen depletion in Müggelsee was less severe than in shallow dimictic lakes, where the hypolimnion remains at low DO concentration throughout the course of summer stratification (Adrian et al. 1995, Scheffer 1998). This confirms an earlier study by Behrendt et al. (1993), who considered Müggelsee to be well supplied with DO_w. However, their study was based on the period 1979-1990, when the epilimnetic temperature lay about 1.5 K below the average summer water temperature reached from the mid 1990s onwards (Adrian et al. 2006, Wilhelm et al. 2006). Therefore it is likely that long stratification events have been less frequent or shorter during the colder period 1979-1990, resulting in less oxygen depletion. From 2003 to 2006, in contrast, hypolimnetic DO_h often dropped below biologically relevant threshold concentrations, affecting up to two thirds of the total lake volume.

We previously pointed out that the freshwater mussel *Dreissena polymorpha* may have been inhibited from reproduction due to unfavourable low DO conditions during the European summer heat wave in 2003 (Wilhelm and Adrian 2007). This extreme event also caused decreasing densities and species richness in the mollusc communities in a French river (Mouthon and Daufresne 2006). As in 2003, the abundance of *D. polymorpha* larvae in 2006 distinctly decreased with the onset of the extremely long stratification event without recovering (data not shown), which provides further evidence for a negative impact of longer lasting low oxygen concentrations on the reproduction of this species. Impacts of prolonged stratification on other organisms of the lake are not yet known or analysed. However, benthic organisms, zooplankton and fish species may also be influenced by low hypolimnetic DO concentrations in that they abandon not inhabitable lake sites (Watts et al. 2001, Järvalt et al. 2005) and/or experience changes in survival, growth and reproduction (Weider and Lampert 1985, Hamburger et al. 2000, Seager et al. 2000). Particularly, species interaction, e.g. in predator-prey relationships, may be influenced by stressful low DO conditions, because prey may be hindered to react to predators or their ability to use habitat refugia may be reduced (Moore and Townsend 1998, Dawidowicz et al. 2002, Saloom and Duncan 2005).

The alteration of mixing and long stratification events may enhance the hypolimnetic SRP accumulation, making polymictic lakes even more vulnerable to the internal eutrophication than shallow dimictic lakes (c.f. Riley and Prepas 1984). There are two mechanisms that are relevant in polymictic other than in dimictic lakes. First, the frequent alternation of stratification and mixing may stimulate phosphorus release processes by decreasing high SRP gradients at the sediment-water interface that hamper further phosphorus release (Marsden 1989). Second, the higher hypolimnetic temperatures during stratification enhance both the mineralisation of hypolimnetic organic matter and the SRP release from the sediment and, hence, stimulate the hypolimnetic phosphorus accumulation (Scheffer 1998, Søndergaard et al. 1999 and 2003). Direct temperature effects on the phosphorus release from anaerobic sediment are particularly prone in iron reach sediments (Scheffer 1998), the sediment type found in Müggelsee (Kleeberg and Dudel 1997). Therefore, overall SRP release rates during summer stratification may be higher in productive shallow polymictic than in productive shallow dimictic lakes (c.f. Riley and Prepas 1984, Scheffer 1998).

In comparison to shallow dimictic lakes that usually experience one nutrient pulse from deep waters not before complete overturn in late summer or fall (Scheffer 1998), the polymictic Müggelsee exhibited multiple nutrient pulses during summer. The magnitude of the epilimnetic nutrient enrichment of DIN and SRSi, in contrast to SRP, did not signifycantly depend on their hypolimnetic concentrations before complete mixing of the lake. This may be attributed to the sampling procedure, since epilimnetic dissolved nutrients were determined from a mixed sample between 0.5 and 3.5 m (c.f. Materials and methods). As the thermocline deepened with increasing duration of stratification epilimnetic waters diluted the hypolimnetic sample, resulting in an underestimation of hypolimnetic nutrient concentrations. In case of DIN and SRSi that exhibited small differences in their concentration between the epi- and hypolimnion this effect likely obscured a significant relationship as found for SRP.

The upwelling of hypolimnetic nutrient rich water positively affected the phytoplankton biomass resulting in phytoplankton blooms (mainly of diatoms), which has been frequently reported for eutrophic lakes (Riley and Prepas 1984, MacIntyre 1998, French and Petticrew 2007). The different magnitudes in peak biomass and therefore in the intensity of a bloom depended on the amount of SRP and SRSi distributed over the entire water column, indicating that the phytoplankton after breakdown of stratification was mainly limited by SRP or SRSi but not by DIN. This contradicts the interpretation by Köhler et al. (2005), who proposed a change towards nitrogen limitation concurrent with the decrease in external nutrient load in Müggelsee. However, they used total phosphorus and total nitrogen concentrations for their analysis.

The alteration between stratification and mixing clearly altered the functional phytoplankton composition. During stratification the dominance shifted from diatoms exhibiting a negative correlation with thermocline depth (group C) to small species exhibiting a positive correlation with stratification intensity (group X2) and to motile colonies that are tolerant to or favoured by stratification (groups L_M and H1), which is a well known process in stratifying lakes (Reynolds 1997, Ptacnik et al. 2003, Huisman et al. 2004). The dominance of summer diatoms (group P) until 3 weeks of stratification is surprising, since they are sensitive to stratification (Reynolds et al. 2002). Ptacnik et al. (2003) observed no decreasing cell densities for the summer diatom *Fragilaria* in enclosure experiments in a deep lake up to 9 m mixing (or thermocline) depth. Therefore, the shallow Müggelsee in comparison to deeper lakes may promote the persistence of small summer diatoms for a longer period of time during stratification through the relatively low thermocline depth and, hence, the small epilimnion exhibiting sufficient turbulence for sinking species (c.f. Reynolds 1997). The effect of thermal stratification on the functional phytoplankton composition increased with increasing duration of stratification events. Thus, short and less intense stratification events (duration of 1-3 weeks) in polymictic lakes may not negatively affect summer diatoms (group P) or promote small and motile species like flagellates and cyanobacteria (groups X2, L_M, H1).

The lack of cyanobacteria during and after stratification events from 2003 to 2005 is surprising, because they usually dominated over diatoms during summer in the years prior to our investigation period (Köhler et al. 2005). During three stratification events from 2003 to 2005 a steadily decreasing or stable phytoplankton biomass was observed, probably indicating a constant epilimnetic nutrient depletion or strong zooplankton predation (Reynolds 1997). Since motile and nitrogen-fixing cyanobacteria (group H1) that are favoured by stratification and low nitrogen concentrations (Reynolds et al. 2002) and that are less suitable for zooplankton (e.g. De Bernardi and Giussani 1990) did not establish during these events, it is possible that other nutrients, particularly SRP, limited the epilimnetic phytoplankton growth as discussed above for the magnitude of phytoplankton blooms after mixing.

Implications for future climate changes

Simulation analysis using two different regional climate models (RCM's) and future scenarios for the Müggelsee catchment reveal a general increase air temperature (by about 3.0-5.0 K) and reductions in wind speed (by about 0.5-1.5 ms^{-1}) and precipitation (by about 5-20 mm) within the next decades during summer (P. Samuelsson, SMHI Sweden, unpublished data). The Max Planck Institute for Meteorology in Germany recently published climate projections for the 21. century, reporting an increased probability for the occurrence of summer heat waves in central Europe; temperatures prevailing during the heat wave in 2003 will probably be very common by the end of this century (http://www.mpimet.mpg.de/fileadmin/grafik/presse/Klimaprojektionen2006.pdf).

According to these future projections stratification events in Müggelsee may occur more often and/or feature higher water temperatures, longer durations and stratification intensities within the next decades. The extremely long and intense stratification events in 2003 and 2006 may have already shown "the shape of things to come". In contrast to the hypolimnetic temperature of shallow dimictic lakes, which will likely decrease along with further global warming (Gerten & Adrian 2001), hypolimnetic temperatures of polymictic shallow lakes will likely increase. An amplification in stratification duration and hypolimnetic temperature would result in an increase in the severity of dissolved oxygen depletion as predicted for dimictic and polymictic lakes of the temperature zone with respect to future climate warming (Fang and Stefan 1997). Following from this, the hypolimnetic nutrient accumulation, the frequency and magnitude of nutrient pulses and the magnitude of subsequent phytoplankton blooms are likely to increase. This implies that this enhanced internal phosphorus loading during summer would strongly counteract the reduction in external load (Kleeberg and Dudel 1997, Søndergaard et al. 2003, Köhler et al. 2005). For the phytoplankton we cannot confirm that an increase in water temperature will favour the dominance of cyanobacteria as anticipated by Huisman et al. (2004) and Mooij et al. (2005). The period from 2003 to 2006 was distinctly warmer than the 1980s (Adrian et al. 2006, Wilhelm et al. 2006) and, except for 2006, did not promote cyanobacteria but rather diatoms.

Conclusions

Our analysis on the mixing regime of Müggelsee revealed that the thermal characteristics of the lake even during extremely long stratification events were not generally comparable to those of shallow dimictic lakes during summer stratification. Particularly hypolimnetic temperatures were much higher in the polymictic lake, favouring the hypolimnetic oxygen depletion and the accumulation of dissolved nutrients (especially of SRP). Thermal stratification directly affected the phytoplankton functional composition and indirectly stimulated the phytoplankton growth through the upwelling of nutrient rich hypolimnetic waters. These frequently occurring nutrient pulses are specific for polymictic lakes in contrast to shallow dimictic lakes that experience one nutrient pulse not before the complete overturn in fall. We assume that chemical and biological processes that are determined by thermal stratification will be amplified in the future with respect to projected climate changes. Hence, climate change may induce an internal nutrient accumulation and subsequent phytoplankton biomass growth that may generally be stronger for polymictic lakes than for shallow dimictic lakes.

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CHAPTER V

Long-term response of *Dreissena polymorpha* larvae to physical and biological forcing in a shallow lake

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Abstract

Müggelsee, a shallow eutrophic lake (Berlin, Germany), has been subject to global warming and concurrent reductions of anthropogenic nutrient loading during the past decades. Here, we focus on the recent increase in abundance of *Dreissena polymorpha* larvae. We aimed at ascertaining whether the change in abundance of larvae was driven by changes in climate, especially by climate warming, and/or by the concurrent changes in trophic state of the lake. Both the numbers of small, newly developed larvae and their lengths have increased in recent years, suggesting that conditions for overall reproductive success have improved. The timing of the increase in abundance of larvae was matched by changes in nutrient loading and phytoplankton biomass, induced by a reduced inflow of nutrients into the lake. Besides a correlation between the first appearance of larvae in each year and the timing of the requisite temperature for first spawning (12 °C), no relationship between changes in water temperature and abundance, length and survival rates of larvae was found. However, a sudden drop in abundance of larvae in 2003 may be primarily attributed to low dissolved oxygen conditions during an unusually long period of stratification, induced by anomalous meteorological conditions. The increase in length and survival rates of larvae was most likely due to changes in food composition, which followed the decrease in nutrient availability, and to changes in the occurrence of planktivorous fish. The results suggest that the first appearance of larvae per year and the decline in abundance of larvae in 2003 were driven by climatic influences, while the overall increase in abundance and length of *D. polymorpha* larvae in Müggelsee was more likely caused by changes in the trophic state of the lake rather than by climate warming.

Introduction

Impacts of recent changes in physical and biological conditions have been widely documented for freshwater (Gerten and Adrian 2002a, Anderson et al. 2005) and marine

(Marcus 2004, Hays et al. 2005) ecosystems and have mainly been related to climate warming and changes in nutrient loading, which affect the trophic state of habitats. In the past decades lakes were often subject to the concomitant influence of climate warming and re-oligotrophication (Anneville et al. 2002, Edmondson et al. 2003, Anneville et al. 2005, Jeppesen et al. 2005) and so was Müggelsee (Köhler et al. 2005), our study lake in Berlin, Germany. Warming from winter until summer has caused substantial changes in the phenology of ice cover, phytoplankton and zooplankton communities in spring (Gerten and Adrian 2000 and 2002b). Furthermore, phytoplankton biomass has declined and its composition has changed, due to reduced external nutrient loading (Köhler et al. 2005). However, often it remains difficult to link alterations in species or communities to concurrently changing forcing factors, such as changes in climate and nutrient availability, because of the array of environmental factors that regulate the survival, growth and reproduction of species (Wetzel 2001), especially during summer.

Concurrently with the reported changes in lake plankton of Müggelsee, the maximum abundance of larvae of *Dreissena polymorpha* (Pallas) reached during summer has increased (Chapter II). *D. polymorpha*, also known as zebra mussel, is a neozoon that expanded its range dramatically over the past 200 years (Stańczykowska 1977, Kinzelbach 1995). It was first recorded in 1827 in lakes around Berlin (Oderbrecht 1957). *D. polymorpha* is unusual among freshwater molluscs in having free-swimming larvae and a flexible reproductive cycle, which together facilitate a rapid spread of this non-native species (Stoeckmann and Garton 2001). The influences of environmental factors on this "pest" species were extensively studied – reinforced by the rapid spread of *D. polymorpha* into the Great Lakes of North America (Hebert et al. 1989) – providing a good base for studying the impact of concurrent changes in forcing factors on *D. polymorpha* larvae. Water temperature, pH, calcium content and trophic state are known to be highly relevant for the survival, growth and reproduction of *D. polymorpha*, affecting the life cycle continuously throughout the year (Stańczykowska and Lewandowski 1993, Nichols 1996). Water temperature is important for the start of oogenesis and spawning of adult *D. polymorpha* (Borcherding 1991) and for survival and development of larvae (Sprung 1993). Nutrient availability influences the colonisation success of *D. polymorpha* (Stańczykowska and Lewandowski 1993). Trophic-related food composition and oxygen conditions are known to affect not only adult *D. polymorpha*, but also their larvae (Stańczykowska 1977, Stoeckmann and Garton 2001, Wacker and Elert 2002).

Following up a recent study on the phenology of *Dreissena polymorpha* larvae (Chapter II), the purpose of this study is to examine whether the dramatic increase in abundance of *D. polymorpha* larvae in Müggelsee was related to climate warming or to the concurrent decline in nutrient availability or both. The strong increase in larvae and, hence, the possible increase in adult *Dreissena polymorpha*, may provoke important changes in the composition of planktonic and benthic communities of Müggelsee, as reported for other lakes (Nalepa and Schloesser 1992). For our analysis we used a unique long-term data set on the appearance, abundance and length of *D. polymorpha* larvae and on environmental variables that reflect thermal and trophic conditions, such as water temperature, nutrient loading, phytoplankton biomass and dissolved oxygen, before and during the reproductive season between 1988 and 2004. We focused on potential underlying mechanisms that drive annual and monthly abundances of larvae, the timing of first and last occurrences of larvae, and larval length. Further analysis on larval length were conducted to determine whether survival rates and survivorship curves that were estimated from size-frequency distributions of larvae changed within the period under study. All environmental variables were analysed for relationships with the appearance, abundance, length and survival rates of *D. polymorpha* larvae.

Materials and methods

Study site

Müggelsee, a shallow (mean depth 4.9 m) and eutrophic lake in Berlin, Germany (52°26' N, 13°39' E), covers an area of about 7.3 km^2 and is flushed by the River Spree. The mean discharge declined by about 34% between the periods 1980-1990 and 1997-2003 (Köhler et al. 2005), but mean monthly water retention time of the lake was rather long with about 11-19 weeks for May to August between 1988 and 2004 (S. Wilhelm, unpublished data).

Data

The abundance of epilimnetic *Dreissena polymorpha* veliger larvae (henceforth larvae) was estimated from a mixed sample taken at five different stations across the lake at weekly sampling intervals between 1988 and 2004. Sampling details are fully described in Köhler et al. (2005). The study period was chosen because of the high sampling frequency that reduces the uncertainty at determining the timing of larval appearance and spawning events (biweekly sampling between 1979 and 1987). However, the same point in time was found for the incipient increase in the abundance of larvae, when the longer time series from 1980 to 2004 was considered (C. Wagner and R. Adrian, submitted). The beginning and ending of the pelagic occurrence refer to the first and last week within a year when larvae were found in the samples. Unusual counts of < 1 ind. L^{-1} during winter were not considered, since these larvae probably survived during winter in the pelagic zone (cf. Nichols 1996). For 1989 the beginning of the pelagic occurrence could not be defined because of an unusual first appearance of 1 ind. L^{-1} in February (three months early), with a subsequent linear increase of about 1 ind. L^{-1} per week until the middle of June. That year was excluded from the calculations of annual mean abundance of larvae, which was computed as the mean number of larvae found during their pelagic occurrence (henceforth reproductive season). Monthly mean abundance of larvae was calculated for May to September, which corresponded to the period of pelagic occurrence of the larvae. The frequency and timing of spawning events was estimated from peak abundances of larvae throughout the annual reproductive season; peaks were defined as local maximum abundances with preceding and succeeding abundances of lower levels. An analysis on the size distribution of larvae during peak abundances in July revealed that all peaks were strongly dominated by small larvae. Local maxima of < 5 larvae L^{-1} at the beginning and the end of the reproductive season were not considered as peaks.

Epilimnetic phytoplankton biomass, zooplankton abundances and nutrient concentrations (total phosphorus and nitrogen) were determined from weekly samples, as well as depth profiles of water temperature and dissolved oxygen concentrations, as described in Köhler et al. (2005). Phytoplankton is, besides bacteria, a primary food source for both the adults and larvae of *D. polymorpha* (Sprung 1995). We did not distinguish between edible and non-edible phytoplankton prey, because most of the ingestible phytoplankton species (1-5 µm size for larvae) were not identified to species level before 1995. For analysis total phytoplankton biomass and total biomasses of cyanobacteria, bacillariophyceae, chrysophyceae, cryptophyceae, dinophyceae and chlorophyceae were used. In general, there exists a competitive rather than predatory interaction between larvae and other zooplankton species, because only few copepods are known to feed on larvae (Liebig and Vanderploeg 1995). For studying competition between larvae and zooplankton, abundances of ciliates, rotifers, cladocerans and copepods. Temperature and chemical conditions, such as total phosphorus and dissolved oxygen, are known to be important factors affecting growth, reproduction and survival of *D. polymorpha* (Stańczykowska and Lewandowski 1993, Nichols 1996). Depth profile measurements of water temperature and dissolved oxygen were averaged over the profile, so that average conditions for the survival of adult mussels from the benthic zone and of larvae from the pelagic zone could be examined. All environmental variables were aggregated to monthly means. Unfortunately, there are no long-term records of adult *D. polymorpha* mussels for Müggelsee.

The lengths of larvae (± 10 µm) were measured for each year from weekly preserved samples from July (the month with maximum abundances of larvae), so that we could examine the long-term development of the size-frequency distributions of larvae during the study period. The sampling size for the length measurements was determined from the estimated abundance of larvae per sample; about 15% of all larvae per sample were randomly selected under a microscope, and their lengths (widest dimension) were measured at ×10 magnification. This procedure ensured a good comparability, since the probability of measuring rare lengths (e.g. large larvae) was similar among samples. For samples with low abundance levels of larvae a higher proportion of larvae was measured to assure a sufficient sampling size for statistical analysis, i.e. at an abundance of about 40 larvae L^{-1} at least 20 larvae were measured. Samples containing < 20 larvae L^{-1} were excluded from the analysis. Results from weekly samples were aggregated for the whole month July. The yearly maximum length of larvae for July was defined as the mean of the largest 10% of the measured larvae.

Larval stage was identified in addition to the length of larvae; however, a distinction between veliconcha and pediveliger larvae (cf. Ackerman et al. 1994) was unfortunately not possible, because larvae with a developed foot were never found in the samples. This can be attributed to withdrawal of soft parts into the shell due to preservation of samples, as larvae with a velum were very rarely observed. Since we could not distinguish between all planktonic larval stages, we classified measured larvae into three different groups according to their length, with a maximum overlap of two larval stages. The first group (small larvae) included exclusively D-veliger larvae from 70-110 µm; the second group (medium larvae) included D-veliger and veliconcha larvae from 120-160 µm; the third group (large larvae) was made of by veliconcha and pediveliger larvae from 170-290 µm. For each group the relative annual abundance in July was computed and was used to split up the monthly mean abundance of larvae from July into the three different size groups. Survival rates from small to medium, medium to large and small to large larvae in July were computed as the percentage remainder from the younger to the older size group for each year (cf. Fig. V-3).

Data analysis

All analyses described below were conducted both with and without the data of 2003, because of the exceptional low abundance of larvae during that year. There was no significant difference between the two sets of results; the results presented here are those derived from the data set not including 2003.

To examine whether the annual and monthly mean abundances of larvae, the timing of first and last occurrences of larvae, the frequency of spawning events per year and monthly water temperature changed during the study period, we calculated the non-parametric Mann-Kendall test statistic Z to test for monotonic trends in the time series (Sneyers 1975). The Mann-Kendall trend test was chosen because distribution of data did not satisfy normality, but homogeneity of data was confirmed and no serial correlation was detected.

The annual mean abundances of larvae were transformed into *z*-scores, which are the deviations from the long-term mean of the series divided by its standard deviation, and the plot of the cumulative sums (CUSUMS) of the *z*-scores was used to search for a change point in the temporal development of this time series (Page 1955). The CUSUM plot indicates the transient behaviour and helps specifically to distinguish periods with predominantly positive anomalies from periods with predominantly negative anomalies. Based on the maximum deviation at 1995, the time series of the annual mean abundances was separated into a cluster with lower abundance levels (1988-1995, henceforth cluster A) and a cluster with higher abundance levels (1996-2002 and 2004, henceforth cluster B). Based on significantly different maximum lengths in July (Mann-Whitney $U = 0.0$, $p<0.01$, $N = 16$), the time-series of the annual mean abundances of larvae were separated into two other clusters (Fig. V-1) with either a small mean maximum length of 153.4 ± 3.9 µm (1988-1990 and 1993, henceforth cluster C) and a large mean maximum length of 203.1 ± 15.3 µm (1991, 1992, 1994-2002 and 2004, henceforth cluster D). For each cluster mean values for the abundance and survival rates of larvae were formed from corresponding years and the nonparametric Mann-Whitney U-Test was applied to test for significant differences between clusters A and B and C and D. We compiled larval size-frequency distributions for the clusters A to D from all particular length measurements of the corresponding years to estimate survivorship curves (cf. Wetzel 2001) of the larvae during their planktonic phase that describe the survival from small to large, i.e. from young to old, larvae including all intermediate lengths. The size frequency distributions of clusters are advantageous compared to distributions of single years, as spawning events within July of one year cannot reproduce a characteristic survivorship curve for *D. polymorpha* larvae, since spawning may occur first in mid or late July so that large larvae may not be included in the analysis. Combining several years compensates this effect. To test for distribution differences between corresponding clusters the χ^2-test was used.

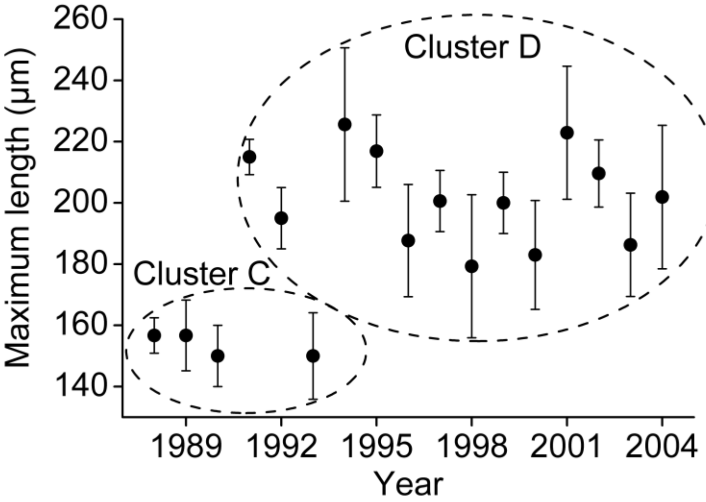

Fig. V-1 Annual maximum length and standard deviation of *D. polymorpha* larvae in July from 1988 to 2004. Enclosed by circles are years belonging to either cluster C (1988-1990 and 1993) or cluster D (1991-1992, 1994-2002 and 2004). Data of 2003 are not associated with either cluster (see "Materials and methods" for further description).

Spearman correlation was performed to evaluate the influence of monthly water temperature, nutrient and dissolved oxygen concentrations, phytoplankton biomass and zooplankton abundances on the abundance of larvae from June to July (the months with significant increases in larval abundances), on their maximum length and on the survival rates of the three size groups, estimated for July. When significant correlations were found for subsequent months, data from weekly measurements were averaged over the respective period and correlation analysis was rerun to summarise the results.

Results

Appearance and abundance of larvae

On average, the first appearance of *D. polymorpha* larvae in the pelagic zone was in May (week 19 ± 1) and the last appearance was in September/October (week 41 ± 4) throughout the study period. Both the first and the last appearance showed no long-term trends and thus, the duration of pelagic occurrence of larvae (spawning season) did not change during the study period. The first peak abundance or spawning event was on average in week 20 ± 2 and showed no temporal long-term trend during the study period. However, the annual mean abundance of larvae increased considerably (Fig. V-2). This increase was statistically significant (Z = 2.87, $p<0.01$) as well as the increase in mean abundance in June (Z = 3.29, $p<0.01$) and July (Z = 3.74, $p<0.001$), but not in other months. The mean annual abundance of larvae for cluster A (43.3 ± 19.0 ind. L^{-1}) was significantly lower than for cluster B (159.6 ± 66.6 ind. L^{-1}) (U = 0.0, p = 0.001).

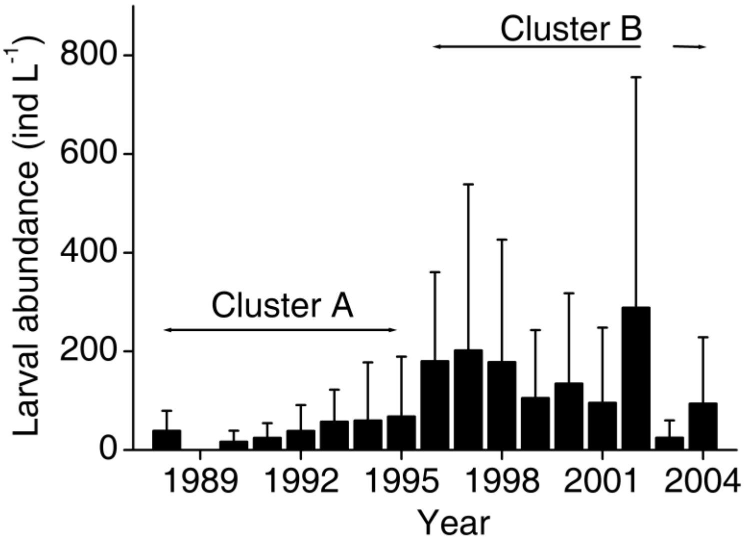

Fig. V-2 Annual mean abundance and standard deviation of *D. polymorpha* larvae from 1988 to 2004. Arrows indicate cluster A (1988-1995) and cluster B (1996-2002 and 2004). Data from 2003 are not associated with either cluster (see "Materials and methods" for further description).

Frequency of spawning events

No change in the frequency of spawning events was detected within the study period. The annual mean was estimated with 5 ± 1 spawning events. Note that the number of spawning events is not necessarily related to individual mussels; spawning can be highly synchronised, but mussel aggregations may be spatially far apart, which can lead to multiple spawning events from different sub-populations within the lake. The high variability in abundance of larvae within one year, which is due to several spawning events (followed by a strong decline in larval abundance until the next spawning), is reflected in the large standard deviations of the annual mean (Fig. V-2).

Length of larvae

Trends to increasing abundances were observed for small and large larvae ($p<0.01$) and, especially, for medium larvae ($p<0.001$) (Fig. V-3). For small and medium larvae ($p<0.01$ for both) and for large larvae ($p<0.05$) the abundances were significantly lower for cluster A than for cluster B. For cluster C, abundances of small larvae ($p<0.05$) and, especially of medium and large larvae ($p<0.01$ for both), were lower than for cluster D. The abundance of large larvae equalled zero for cluster C, whereas high abundance levels were estimated for cluster D (Fig. V-3). Maximum length in July (Fig. V-1) was not significantly correlated to mean abundance of larvae from June to July ($R^2 = 0.11$, $p = 0.2$, $N = 16$).

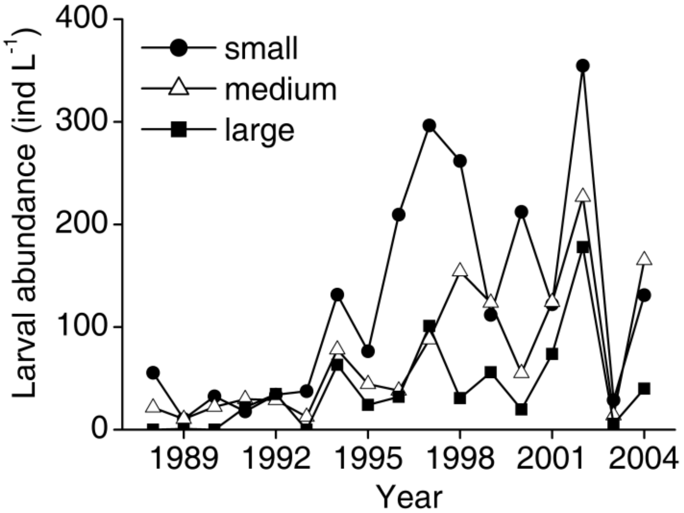

Fig. V-3 Monthly mean abundance of size groups of *D. polymorpha* larvae for July from 1988 to 2004.

Survivorship curves and survival rates of larvae

The size-frequency distributions from clusters A to D showed a good fit to an exponential decay model (Fig. V-4), indicating a constant death rate from small to large larvae for Müggelsee as is often assumed for larvae (cf. Wetzel 2001). This contradicts results from Schneider et al. (2003) and Stoeckel et al. (2004), who found development-specific mortality rates. As our sampling procedure (see method section) not allows to trace distinct cohorts of larvae within the lake, a direct comparison to these studies was not possible. The size-frequency distribution for cluster A was significantly different from those of cluster B (Fig. V-4a, b) ($\chi^2 = 40.5$, $p<0.01$, $N = 1737$), although no differences in survival rates for the three size groups were found (Table V-1). In cluster C none of the larvae had grown larger than 170 µm (Fig. V-4c). Clusters C and D (Fig. V-4c, d) showed different size-frequency distributions ($\chi^2 = 51.3$, $p<0.001$, $N = 1737$), even if we only used the length range from 70 to 170 µm for analysis ($\chi^2 = 32.8$, $p<0.001$, $N = 1532$). The annual survival rates from small and medium larvae to large larvae were significantly lower for cluster C than for cluster D ($U = 0.0$ and $p<0.01$ for both), but no significant differences were found for the survival rates from small to medium larvae (Table V-1).

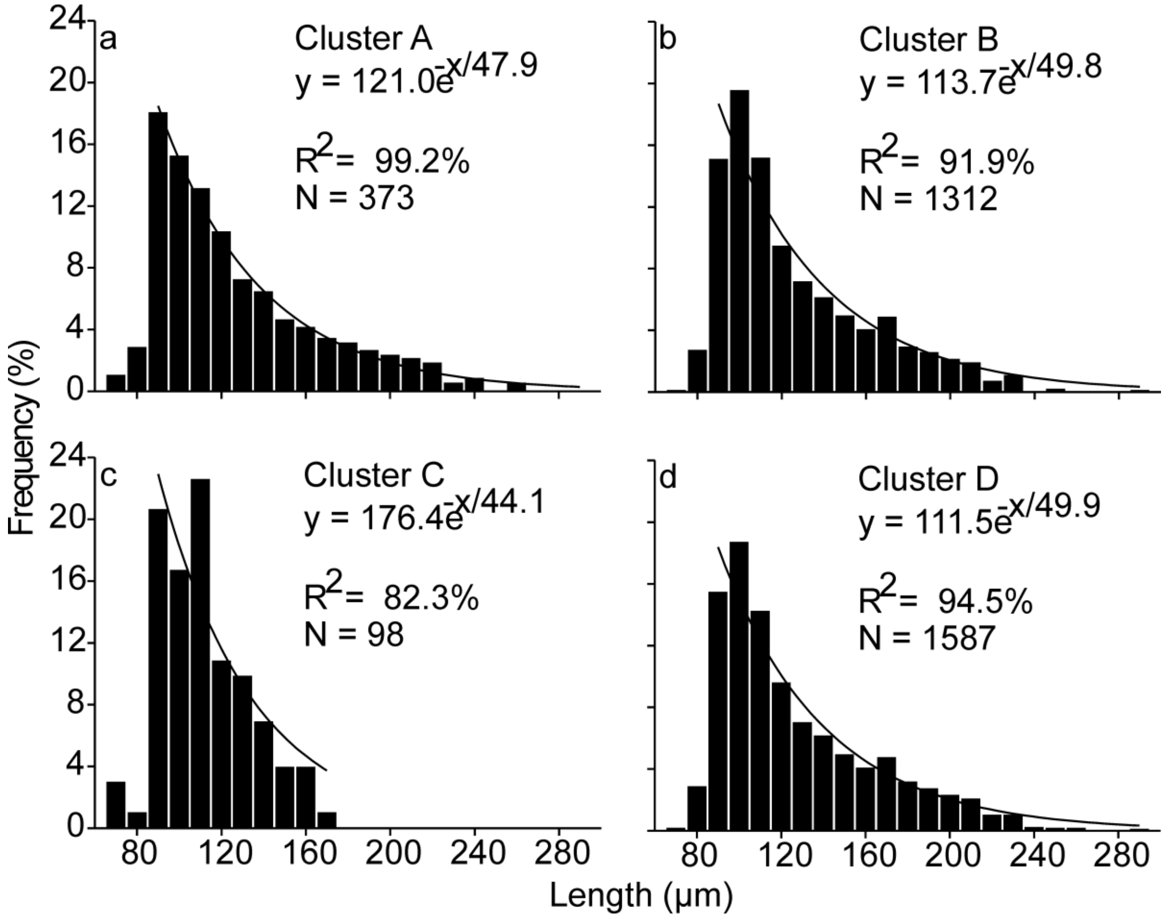

Fig. V-4 Size-frequency distribution for *D. polymorpha* larvae in July: (a) cluster A, (b) cluster B, (c) cluster C and (d) cluster D. Lines represent fitted exponential decay models starting at 90 µm length.

Table V-1. Mean survival rate and standard deviation (percentage) of *D. polymorpha* larval size groups for clusters A to D.

Size groups	Cluster A (1988-1995)	Cluster B (1996-2002, 2004)	Cluster C (1988-1990, 1993)	Cluster D (1991, 1992, 1994-2002, 2004)
Small-to-medium larvae	76.4 ± 43.3	71.7 ± 44.2	58.9 ± 32.4	79.2 ± 45.2
Medium-to-large larvae	41.9 ± 47.8	53.3 ± 24.0	1.9 ± 3.9	62.8 ± 29.2
Small-to-large larvae	39.6 ± 49.8	34.5 ± 21.1	1.9 ± 3.9	48.7 ± 35.6

Environmental conditions

Mean water temperature during the reproductive season ranged from 16.6 to 20.4 °C between 1988 and 2004 and increased significantly in May and June ($p<0.1$) and especially in August ($p<0.05$). A significant correlation was found between the timing when 12 °C water temperature was reached and the timing of first appearance of larvae in the pelagic zone (Fig. V-5). However, no significant relationship between water temperature and abundance of larvae or their maximum length was found. Chemical and biological conditions of the lake were significantly related to abundance (Fig. V-6) and maximum length of larvae. We found negative correlations between mean total phosphorus contents for the period March to July and the mean abundance of larvae from June to July (Fig. V-6a). Mean total phytoplankton biomass was correlated with abundance of larvae for the period March to May (Fig. V-6b), but not for the summer months. The long-term development of some phytoplankton groups was related to the increase in abundance of larvae; we found negative correlations for cyanobacteria (R^2 = 0.73, $p<0.001$) and bacillariophyceae (R^2 = 0.64, $p<0.001$) and a positive correlation for chlorophyceae (R^2 = 0.25, $p<0.05$). Larval abundance was related to the dissolved oxygen concentration in June (Fig. V-6c), but no relationship for oxygen conditions in previous months was detected. It is interesting to note that the lowest concentration of dissolved oxygen was 6.9 ± 1.8 mg L^{-1} in June 2003, the year with the exceptional low abundance levels of larvae during summer. A positive correlation was found between mean ciliate abundances and larvae abundances (Fig. V-6d), whereas a negative correlation was found with mean cladoceran abundances (Fig. V-6e) for the period June to July. No relationship was found between abundances of larvae and abundances of rotifers and copepods.

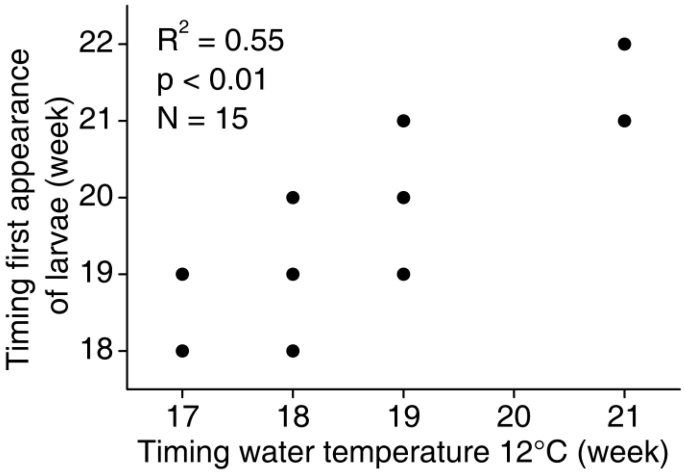

Fig. V-5 Spearman correlation between the timing of the first appearance of *D. polymorpha* larvae and the timing of 12 °C water temperature per year.

The maximum length of larvae correlated negatively with mean total phosphorus concentration (R^2 = 0.35, $p<0.05$) and phytoplankton biomass (R^2 = 0.36, $p<0.05$) for the period March to July, but neither dissolved oxygen conditions prior the reproductive season nor during this period were related to maximum length of larvae. Yearly survival rates of larvae from the three different size groups were not correlated with any physical, chemical, or biological variables.

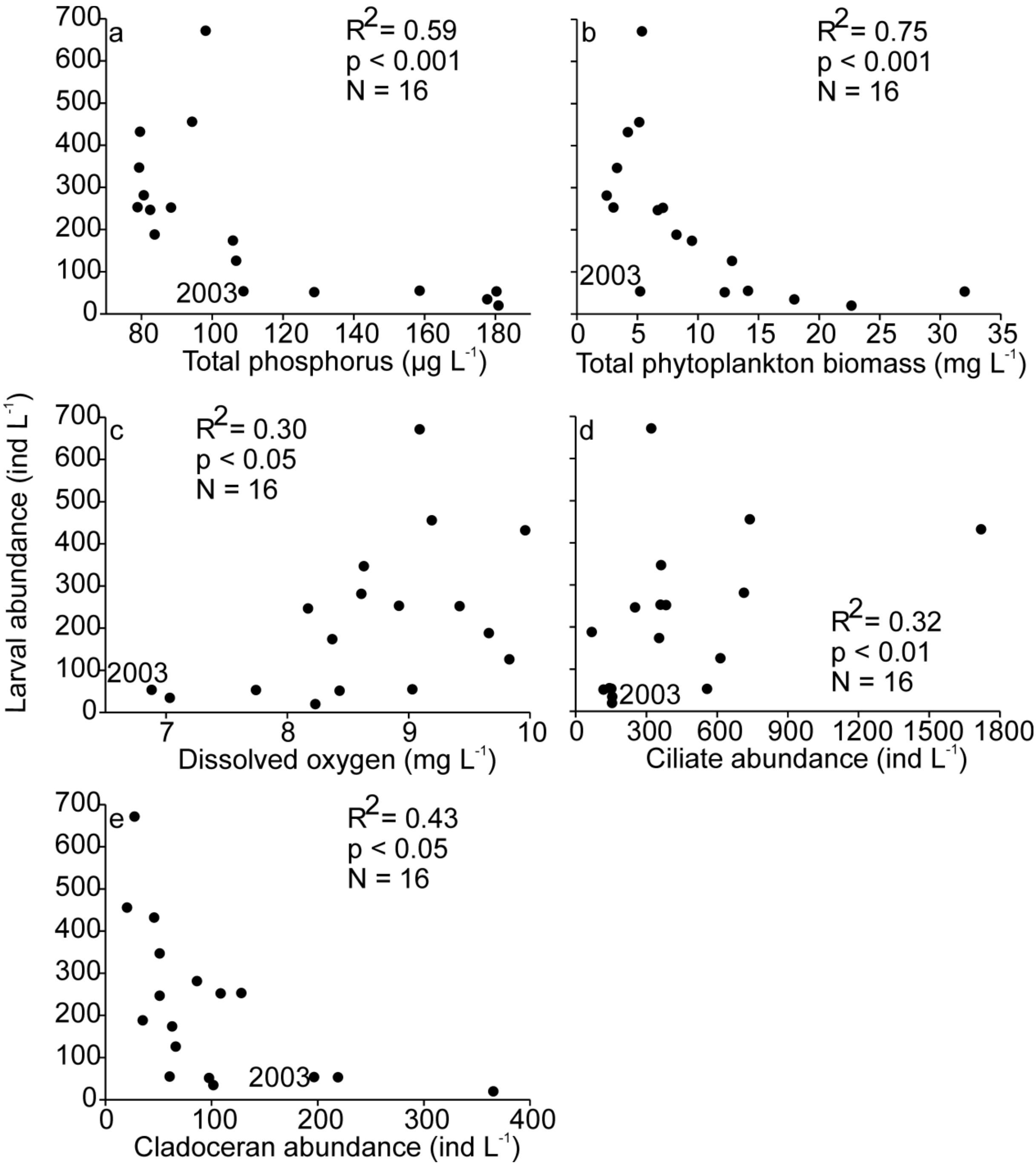

Fig. V-6 Spearman correlation between the abundance of *D. polymorpha* larvae from June to July and (a) total phosphorus from March to July, (b) total phytoplankton biomass from March to May, (c) dissolved oxygen in June, (d) ciliate abundance from June to July and (e) cladoceran abundance from June to July. Marked data from 2003 were not included in the analysis (see "Materials and methods" for further description).

Discussion

The present results show that the annual mean abundance of *D. polymorpha* larvae in Müggelsee has increased since 1995, although the abundance of larvae in 2003 drastically dropped to very low levels. Not only the abundance of small larvae but also the abundances of medium and large larvae have increased; large larvae were hardly present in the epilimnetic samples in the early years (cluster C).

The increase in abundance of larvae cannot be explained by a change in the duration of the spawning season or by the overall spawning frequency, since no shift in spawning season and frequency occurred within the study period. The rise in abundance of larvae was restricted to an increase in abundance in June and July, which resulted not only from increased abundances of all larval size groups, but also from a general increase in length of larvae. This implies that both the production of larvae from mussels and the survival of larvae in the pelagic zone were increased, suggesting that conditions for the reproduction of *D. polymorpha* have been improved during the study period. Unfortunately, there are no long-term data on the abundance or reproductive effort of adult mussels in Müggelsee, thus we cannot identify any changes in the population. Nevertheless, the timing of the appearance, the abundance and also the maximum length of larvae were related to environmental conditions prior and during the reproductive season. This suggests that not only larvae, but also the adult *D. polymorpha* population before first spawning were influenced by changes in environmental conditions.

Water temperature is an important factor affecting growth, reproduction and survival of *D. polymorpha*. Many studies agreed that a temperature threshold of 12 °C provides a requisite condition for gamete maturation and thus, for the onset of first spawning (reviewed by Nichols 1996). For Müggelsee this temperature threshold could be confirmed for the first appearance of larvae in the pelagic zone (Fig. V-5, see also Chapter II). Therefore, it is unlikely that the onset of gamete production of mussels was limited by factors such as food availability prior to the reproductive season during the study period, as the first appearance of larvae was not delayed (Borcherding 1991, Neumann et al. 1993). In a recent study, which was based on a longer time period (1979-2003), we showed that the pelagic phase of *D. polymorpha* started on average two weeks earlier concurrent with spring warming (Chapter II). Abundance, length and survival of larvae were not correlated to monthly mean water temperature before and during the reproductive season. This indicates that water temperature was not a limiting factor for production and development of larvae during the study period, as also reported by Burla and Ribi (1998) for Lake

Zürich, where mean annual counts of juvenile and mussels were not correlated with mean water temperature.

The increase in abundance of larvae was negatively correlated with total phosphorus, which was reduced by more than 50% from the hypertrophic (1979-1990) to the eutrophic period (1997-2003) in Müggelsee, due to a reduced inflow into the lake (Köhler et al. 2005). Our findings are in accordance with many studies, which have found that increased nutrient loadings may be the cause of a decrease in population density (reviewed by Stańczykowska and Lewandowski 1993). According to Stańczykowska and Lewandowski (1993) *D. polymorpha* was absent or did not occur in substantial numbers in polymictic lakes of the Mazurian Lakeland at phosphorus concentrations higher than 100 µg L^{-1}. Except for 2003, mean total phosphorus from March to July was below a threshold of 100 µg L^{-1} between 1996 and 2004 (cluster B), but exceeded this value between 1988 and 1995 (cluster A). Therefore, it is likely that living conditions for *D. polymorpha* based on nutrient conditions had been improved during the latter years.

Following the reduction in nutrient loading in Müggelsee, total phytoplankton biomass declined gradually, mainly caused by a decrease in cyanobacteria biomass (Köhler et al. 2005). Food quantity prior to the reproductive season affects the gamete production of mussels; Borcherding (1995) found that gamete production decreased at a low food availability. However, the abundance of larvae in June to July increased while total phytoplankton biomass decreased from March to May, which indicates that the production of gametes by adult mussels was probably not limited by food quantity during the study period (Fig. V-6b). However, food quality seems to have changed probably due to alterations in the composition of the phytoplankton community; cyanobacteria and bacillariophyceae were negatively correlated to the abundance of larvae, whereas chlorophyceae were positively correlated with the abundance of larvae. Several studies suggest that rather food quality than food quantity is an important factor for growth and reproduction of *D. polymorpha*; when fed a poor diet that lacked essential fatty acids adult mussels experienced a high mortality (Schneider et al. 1998, Stoeckmann and Garton 2001). A poor food quality did not support the development of larvae as well (Vanderploeg et al. 1996, Wright 1996, Wacker and Elert 2002). Therefore changes in food composition after 1995 probably improved the conditions for growth and reproduction of *D. polymorpha* in Müggelsee, since cyanobacteria, which are considered a low quality food (Dionisio Pires et al. 2004) have shown decreasing biomasses, while chlorophyceae, which are generally considered a high quality food (Dionisio Pires et al. 2004), increased in biomasses. The increase in high quality algal biomass despite an overall reduction in food quantity may have positively affected larval development.

Low oxygen conditions are not suitable for successful growth and reproduction of *D. polymorpha* (Stańczykowska 1977). Indeed, we found higher abundances of larvae at higher dissolved oxygen concentrations (Fig. V-6c) after 1995, suggesting that reproduction of *D. polymorpha* was favoured from 1995 onwards. In 2003 an unusual decline in the abundance of larvae occurred from June onwards, which was associated with a very low mean oxygen concentration at this time. This drop in dissolved oxygen concentrations was due to an unusual prolonged phase of thermal stratification of the lake driven by a high air temperature at low wind speeds; usually, polymictic Müggelsee stratifies for a longer time-period only in August, associated with a decrease in dissolved oxygen concentration in the hypolimnion (S. Wilhelm, unpublished data). It is well documented that native and introduced freshwater mussels are able to survive a short-term exposure (less than 5 days) to anoxic or hypoxic conditions in their habitat (Johnson and McMahon 1998). In June 2003 the oxygen saturation in Müggelsee at 7 m depth was below 6.5% and from 3 to 4 m depth the oxygen saturation was partly below 50% at mean water temperatures from 20 to 23 °C for three successive weekly samplings. Johnson and McMahon (1998) reported 50% mortality for adult mussels at an oxygen saturation of 7.5% after 10 days and 100% mortality after 15 days (at 25 °C). Walz (1973) found that *D. polymorpha* could survive for 9 days without oxygen at a water temperature of 19 °C. Although *D. polymorpha* can survive for some time at very low oxygen concentrations, these conditions may not be conducive to growth or successful reproduction (Woynarovich 1961). Therefore, it is likely that *D. polymorpha* in Müggelsee may have experienced unfavourable oxygen conditions produced by a heat wave in central Europe in summer 2003 (Schär et al. 2004), which prevented a successful reproduction during the reproductive season. In 2004 reproduction was comparable to the years prior to 2003, suggesting that the mussel population in Müggelsee may have been rather inhibited from reproduction than experiencing a high mortality in 2003.

Ciliates and cladocerans are not known to prey on *D. polymorpha* larvae, therefore the main interaction between larvae and both zooplankton groups is competition for shared algal resources. The opposed changes for ciliates and cladocerans in accord with the increase in abundance of larvae (Fig. V-6d, e) suggest that changes in zooplankton may have not affected the development of larvae.

The duration of the planktonic life span of larvae was lengthened in 1991, 1992 and 1994 to 2004 (cluster D), since the survival rates from small and medium larvae to large larvae have increased (Table V-1). The mortality of large larvae has decreased, as their abundance and length have both increased. Mortality of larvae in field populations has been attributed to a variety of causes, such as problems in finding settlement substratum, specific environmental conditions and predation (Nichols 1996). There are no data on substrate availability in Müggelsee. However, substrate seemed to play – at least for the earlier years – a minor role for survival of larvae, since for some years despite a low abundance of larvae (1991, 1992 and 2003; Fig. V-2) and thus, less competition for substrate, a high maximum length of larvae was reached (Fig. V-1). In other words, competition for substrate due to high larval abundance can affect larval length in that larvae that have already reached settling size, but cannot find a suitable substrate for settlement, will continue growth beyond settlement size until they find a substrate or die. Additionally, the largest mean maximum length of 156.7 ± 11.5 µm reached in 1988 to 1990 and 1993 (cluster C) was still below 200 µm, the length above which larvae are in general considered to be competent to settle (Stoeckel et al. 2004). This suggests that the majority of larvae in the earlier years lacked favourable conditions for a successful development until settling size. The increase in maximum length of larvae in July was correlated with the decrease in total phosphorus and total phytoplankton biomass from March to July, which implies that conditions prior and during the appearance of larvae have been improved. Larvae were unlikely limited by food availability, since they reached larger lengths despite a reduced and altered phytoplankton biomass. As noted above for abundances of larvae, it is likely that an altered food composition improved larval development in the latter years.

Predation is another reported cause of larval mortality. Fish including their larvae, some copepods and even adult *D. polymorpha* are known to feed on larvae (Nichols 1996). Large larvae are mainly preyed upon by planktivorous fish and their larvae (Wellborn 1994, Molloy et al. 1997). Our results show that overall survival of large larvae did increase. However, the survival rates of small to medium larvae, which are especially preyed by copepods (Liebig and Vanderploeg 1995) and adult mussels (MacIsaac et al. 1991), did not increase. Unfortunately, there are no long-term data on fish counts for Müggelsee; however, data on annual catches of fish species during the study period could be obtained from the Fischereiamt, Berlin (Fischereistatistik, unpublished data). Annual catches of the main species bream (*Abramis brama*), roach (*Rutilus rutilus*) and zander (*Sander lucioperca*), which are known to feed on larvae (Molloy et al. 1997), decreased between 1988 and 1991, but were relatively stable thereafter. Note that the decrease in fish catch was related to a drop in commercial fishery following the reunification of Germany in 1989/1990; however, stocking of fish was also reduced at the same time, pointing to a probable stable fish abundance on a lower level with the beginning of the 1990s. Mills et al. (1995) showed that in years when planktivorous fish were abundant and larvae sparse, planktivorous fish could substantially reduce larval numbers in a fairly short period. Therefore, it is likely that improved food composition and/or a probable decrease in fish abundance have enhanced conditions for survival of large larvae within the years of cluster D.

Besides changes in climate and nutrient loading, predation is an important factor determining adult mussel densities and thus their reproductive effort. *D. polymorpha* provide a potential food source for diving waterfowl such as coot (*Fulica atra*) (Stańczykowska 1977) and fish such as bream and roach (Molloy et al. 1997), which are very common in Müggelsee (Driescher et al. 1993, T. Becker and S. Hilt, unpublished data). There are no long-term data on waterfowl and fish abundance for Müggelsee and, therefore, a direct comparison with abundances of larvae was not possible. However, bream and roach abundances are presumed to have decreased in recent years as noted above, which may have had a positive influence on adult *D. polymorpha* densities.

In conclusion, the timing of the increase in abundance of *Dreissena polymorpha* larvae of Müggelsee was matched by changes in nutrient loading and phytoplankton biomass and composition, induced by a reduced inflow of nutrients into the lake. However, we cannot conclude whether the increase in abundance of larvae resulted from either higher adult population density or higher reproduction of adult mussels in response to improved environmental conditions. The sudden drop in abundance of larvae in 2003 can possibly be attributed to longer lasting low dissolved oxygen concentrations in June followed from an unusual long period of stratification, accompanied by a high total phosphorus concentration, which may have inhibited mussel reproduction. The increase in length and survival of larvae was most likely due to changes in food composition and fish predation pressure. Our results suggest that the increasing abundance of *D. polymorpha* larvae in Müggelsee was more likely caused by changes in trophic state rather than by climate warming; however the influence of weather and climate cannot be neglected referring to the sudden drop in abundance of larvae in 2003.

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CHAPTER VI
GENERAL DISCUSSION AND CONCLUSIONS

Climate induced impacts on lake functioning in summer

Besides shorter ice durations and earlier ice break-ups in winter and spring, increased summer temperatures and particularly the occurrence of heat waves within recent decades have increased the concerns among limnologists studying temperate lakes. So far, much is known about climate induced impacts on lake properties during winter and spring and there is striking evidence that the interannual variability in limnological variables is partly synchronised among lakes exposed to the same climatic regime (Gerten and Adrian 2002a, Straile et al. 2003, Anneville et al. 2005). In summer, the direct and indirect effects of climate warming on lakes are less comprehensively studied and during this season the influence of large-scale climate fluctuations as the NAO are anticipated to be of minor importance in comparison to site-specific conditions (Straile et al. 2003). Thus, it is difficult to extrapolate from local studies and to predict how lakes might respond to climate change in summer. Here I discuss some aspects, which may be strongly involved in determining the response of a lake to climate warming in summer and which may define the degree of spatial coherence among lakes, in the view of my results.

My study showed that climate warming has induced changes in the phenology of the lake plankton throughout the examined seasons. However, the changes among the summer zooplankton were not synchronous as found for the plankton in spring (Adrian et al. 2006; Chapter II). The fast-growing spring phytoplankton and *Daphnia* were directly affected by the warming in winter and spring and thus advanced at more or less similar rates maintaining the synchrony in their species interaction, which has also been observed in Swedish lakes (Weyhenmeyer et al. 1999). By contrast, long-term changes in the phenology of slow-growing summer zooplankton were clearly species-specific and not synchronised as found for the plankton in spring. The different slow-growing summer copepod species showed unique alterations in their phenology and abundance. *Thermocyclops oithonoides* and *Acanthocyclops robustus* showed a different lengthening of their pelagic phase, according to their individual thermal requirements at decisive developmental stages such as emergence from diapause in spring. Other copepods as *Mesocyclops leuckarti* and *Diacyclops bicuspidatus* did not change in phenology but increased in abundances according to higher spring water temperatures (c.f. Gerten and Adrian 2002b). Since the influence of increased summer water temperatures proved not important in determining the development of these copepods, a direct effect of increased summer temperatures can be mainly excluded. Past and recent average summer temperatures were well within the optimum range of the different species. A further increase in summer temperature may probably lead to limitations in the growth of certain species that are exposed to temperatures at or exceeding their upper thermal tolerances, as e.g. *D. bicuspidatus* (Maier 1989). This study strongly highlights and confirms that not only the degree of warming, but also its timing within the annual cycle is ecologically important (Adrian et al. 1999, Benndorf et al. 2001, Gerten and Adrian 2002b). If the long-term warming would have been less pronounced in spring, probably only minor and insignificant changes in the phenology of summer copepod species would have been observed.

The observed asynchronous changes in summer zooplankton may have led to disruptions in predator-prey relationships involving the examined copepod species. This is an important fact concerning further climate impact studies across the trophic cascade of the lake, since a mismatch in the timing of reproduction or peak biomass to optimal food availability will have profound effects on the development of the predator population (Cushing 1990). Along with the recent global warming the mistiming in species interactions across the trophic cascade has already been observed in terrestrial (reviewed by Harrington et al. 1999) and aquatic ecosystems (Edwards and Richardson 2004, Winder and Schindler 2004). The results suggest that climate induced trophic mismatches in Müggelsee may have been more probable in summer than in spring. However, this may change with respect to further climate warming (Cubasch et al. 2001). So far, climate induced synchronous changes in spring plankton were found in ice covered temperate lakes (Weyhenmeyer et al. 1999, Gerten and Adrian 2000, this study), but not in non-freezing temperate lakes (Lake Constance, Straile and Adrian 2000 and Lake Washington, Winder and Schindler 2004). In non-freezing lakes variances in the timing of the spring phytoplankton were not determined by light availability but rather by other driving factors such as the wind driven onset of thermal stratification in Lake Constance (Gaedke et al. 1998). A further climate warming probably may arise asynchronous changes in the phenology of spring plankton in freezing lakes (including Müggelsee) following from extremely warm winters featuring very short or no ice covers at all. Whereas in summer, further increases in water temperature across the seasons may not only promote strong shifts in the phenology and abundance of the prevailing species and thus mismatches in species interactions, but also changes in overall plankton composition. Thermophilic species such as the copepod *T.*

oithonoides may be strongly favoured, as well as species that are less sensitive to or benefit from amplifications in the stratification pattern.

The recent climate warming during summer has not only been associated with a general increase in air temperature across the Northern Hemisphere (Folland et al. 2001), but also with a reduction in the diurnal air temperature range over the second half of the 20th century (Easterling et al. 1997). My study demonstrated for the first time that this reduction in daily temperature range was also present in the epilimnion of a lake (Wilhelm et al. 2006; Chapter III). During summer the daily epilimnetic minima (during nighttime) have increased more rapidly than daily epilimnetic maxima (during daytime). This day-night asymmetry in epilimnetic temperature does not reflect the long-term changes in air temperature that did not exhibit a significant decrease in daily air temperature range in Berlin, Germany, which contradicts the findings of most studies on this phenomenon on global and regional scales (e.g. Easterling et al. 1997, Heino et al. 1999, Wibing and Glowicki 2002). The nighttime emission of long-wave radiation from the atmosphere is likely to be the main process responsible for the day-night asymmetry in the epilimnetic temperature. This process is determined by the meteorological variables air temperature, relative humidity and cloud cover (Edinger et al. 1968). Thus, my results underline that the epilimnetic temperature is not solely determined by air temperature, although lake surface temperatures have been successfully modelled based on the exponential filtering of air temperature alone (e.g. Kettle et al. 2004, Livingstone et al. 2005, Šporka et al. 2006). Variations in air temperature and other driving meteorological variables such as relative humidity and cloud cover may play an important role in determining the epilimnetic temperature with respect to further climate change.

Projections on future climate within the 21st century reveal an increase in global mean surface temperature by 1.4 to 5.8 K (1990-2100), which is a much more rapid rate of warming than during the 20th century (Cubasch et al. 2001). On a regional scale, summer air temperatures in northern Europe were projected to increase even more strongly in comparison to the global mean (Ruosteenoja et al. 2003), with increases of 0.7 to 2.2 K in the near future (2010-2039) and of 1.6 to 6.5 K in the far future (2070-2099). This increase in summer air temperature will be accompanied by reductions in wind speed and cloud cover (about 0.5 to 1.5 ms^{-1} and 5% to 20% for the Müggelsee catchment from 2070 to 2100, P. Samuelsson, SMHI Sweden, unpublished data). Furthermore, future climate projections reveal an increase in the frequency and magnitude of climate extremes around the globe (Cubasch et el. 2001). In temperate regions and especially in Europe the occurrence of heat waves and droughts will be particularly amplified during summer (Max Planck Institute for Meteorology 2006).

The projected climatic changes and especially the amplification of heat waves will have profound consequences on lakes during summer and, hence, any assessment of the impact of climate change on lakes should include an estimation of the potential effects of such extreme events. The extremely long and intense stratification events that occurred in Müggelsee during the recent heat waves in 2003 (Schär et al. 2004) and 2006 may have already shown “the shape of things to come” within the next decades (Chapter IV). These heat waves had led to a hypolimnetic dissolved oxygen depletion (see also Wilhelm and Adrian 2007; Chapter V) and nutrient accumulation (especially of dissolved phosphorus) of enormous magnitudes in the eutrophic lake. Jankowski et al. (2006) also observed an extraordinarily strong hypolimnetic oxygen depletion during the heat wave in 2003 in two Swiss lakes. In northern Europe the warmest summer on record occurred one year earlier in 2002, causing similarly strong impacts on hypolimnetic oxygen and nutrient accumulation in a Swedish lake (Weyhenmeyer et al. 2004). Both extreme stratification events in Müggelsee were followed by particularly heavy phytoplankton blooms, which were stimulated through the upwelling of the highly nutrient enriched hypolimnetic waters, as observed for other productive lakes (Riley and Prepas 1984, French and Petticrew 2007).

The effects of the extremely long stratification events on the chemical and biological processes in the polymictic lake were not generally comparable to those observed during the summer stratification of shallow dimictic and productive lakes. Particularly, hypolimnetic temperatures were much higher in the polymictic lake (c.f. Agbeti et al. 1997, Gerten and Adrian 2001), strongly stimulating the hypolimnetic oxygen depletion and dissolved nutrient mineralisation and accumulation (Scheffer 1998, Søndergaard et al. 2003). Therefore, dissolved nutrient – especially internal phosphorus – accumulation rates during summer are very likely higher in shallow polymictic than in shallow dimictic lakes as observed in two shallow Canadian lakes of different mixing regime (Riley and Prepas 1984). Furthermore, polymictic lakes experience multiple alternations between stratification and mixing during summer and, hence, phytoplankton growth is more frequently stimulated by the upwelling of nutrient enriched water in contrast to shallow dimictic lakes that experience a nutrient pulse not before the complete overturn in fall (Scheffer 1998). Thus, the distinct nature of the mixing regime strongly determines the functioning of productive shallow lakes during summer, particularly the magnitude of the internal nutrient loading and the associated phytoplankton development.

From my results I conclude that polymictic lakes are more vulnerable to alterations in the thermal regime than shallow dimictic lakes with respect to further climate change during summer. This assertion may not be generalizable among all polymictic lakes, since there is a huge range in the characteristic of polymixis in temperate shallow lakes (Gorham and Boyce 1989, Padisák and Reynolds 2003). The polymictic mixing regime during summer can be strongly dominated by wind induced mixing (e.g. Dutch lakes, Mooij et al. 2005) or by intermittent thermal stratification (e.g. Müggelsee, Germany, this study) or can exhibit any state in between. Padisák and Reynolds (2003) suggested the use of the Wedderburn formulation (including the impact of wind fetch) to determine and distinguish the stratification behaviour of shallow lakes. Consequently, lakes exhibiting lake depths and lengths similar to Müggelsee would very likely show analogous responses in their mixing regime to climate warming, if not sheltered from wind action. Polymictic lakes that stratify for only very short periods, e.g. on a daily basis, may not be as strongly affected by climate change as polymictic lakes that exhibit stratification for several days or weeks.

So far, the role of polymixis with respect to climate change is only sparsely examined (Zhang and Prepas 1996, French and Petticrew 2007, this study) although there are many shallow and potentially polymictic lakes particularly in the Northern Hemisphere, mainly formed through the Pleistocene glaciation (Wetzel 2001). These lakes quickly respond to actual weather conditions and are thus particularly prone to changes in the polymictic mixing regime according to changes in climate. I strongly suggest that further climate impact studies on shallow lakes should involve a thorough determination of the nature of the mixing regime, especially since mean or maximum lake depth are not sufficient in describing the behaviour of a shallow lake along with climate change (c.f. Padisák and Reynolds 2003).

In conclusion there is to say that the extend of spatial coherence in climate induced responses among lakes in summer may stronger vary between the different limnological variables as in spring, depending on the degree of direct effects of climate change. Particularly, changes in the daily development of epilimnetic temperatures may be highly coherent among lakes exposed to similar climatic regimes, since the upper water layer is directly affected by ambient climate and weather conditions (Edinger et al. 1968). However, the extend and magnitude of the spatial coherence may be less pronounced as for climate induced changes in the daily air temperature range around the globe (Fig. VI-1), since not only air temperature but also other meteorological driving factors such as cloud cover were found to be highly important in determining the daily epilimnetic temperature range. There is already strong evidence for a high degree of coherence in mean lake surface temperatures among Northern Hemispheric lakes in all seasons (Benson et al. 2000, Livingstone and Dokulil 2001, Livingstone and Padisák, in press). Livingstone and Dokulil (2001) found that the spatial coherence in central Europe during summer was related to large-scale variations in high altitude cloud cover and thus appeared to be of a more regional nature than found for the spatial coherence in winter and spring.

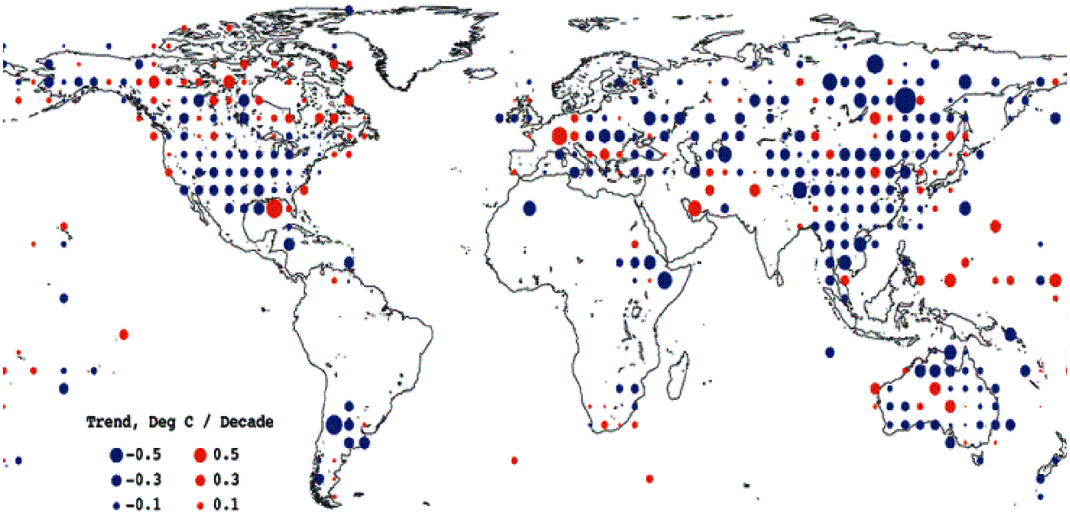

Fig. VI-1 Trends in annual daily air temperature range (°C/decade), from 1950 to 1993, for non-urban stations only, updated from Easterling et al. (1997). Decreases are in blue and increases in red. Redrawn from Folland et al. (2001).

In contrast, more indirectly climate driven lake processes such as the hypolimnetic dissolved oxygen depletion and internal nutrient loading that strongly depend on site-specific conditions as the mixing regime may only show minor regional coherence. Here, not only the geographical position but also the morphology and the trophic state of a lake are highly relevant factors confounding spatial coherence, which are also known to partly limit spatial and temporal coherence especially in biotic properties among lakes in spring (Straile et al. 2003). I expect the smallest degree of spatial coherence among climate induced changes in the phenology and abundance of aquatic organisms in summer, since my results emphasised the clearly indirect nature of climate induced impacts in this season and their strong dependency on site-specific conditions as the mixing and the trophic regime. Hence, there is a need for comparative studies on climate driven responses across geographical and climatic gradients as well as across the different thermal and trophic conditions of lakes to enhance our knowledge on climate induced effects on lakes and the level of spatial coherence in limnological variables among lakes during summer.

Simultaneous changes in climate and nutrient availability in lakes

Moss et al. (2003) concisely expressed one of the major issues in freshwater science: “Climate is changing. Existing impacts of nutrients in freshwater systems remain”. Studies on temperate lakes increasingly take into account more or less simultaneous impacts of changes in both the climate and the nutrient availability, particularly of the reduction in nutrient loading (George et al. 1990, Carvalho and Kirika 2003, Anneville et al. 2005, Jeppesen et al. 2005), including Müggelsee (Köhler et al. 2005). All of these long-term studies have underlined the difficulty of separating the effects of the concomitantly occurring changes. Climate warming and decreases in nutrient loading have resulted in complex responses of lake plankton, both directly or indirectly (through changes in zooplankton abundance) provoking declines in phytoplankton biomass (Carvalho and Kirika 2003) and changes in phyto- and zooplankton abundance and composition (Anneville et al. 2005, Adrian et al. 2006, Wilhelm and Adrian 2007; Chapters II and V).

Some limnologists anticipate that the effects of climate change likely offset the positive impact of the reduced nutrient loading on shallow temperate lakes, mimicking the effects of nutrient enrichment (Jeppesen et al. 2005, Mooij et al. 2005). The results of my study provide strong evidence for counteracting effects of climate warming – especially of the recent heatwaves in 2003 and 2006 – to the reduced external nutrient load in Müggelsee. On the one hand, these heatwaves caused severe oxygen depletions and, hence, drastic declines in *Dreissena polymorpha* larvae, albeit the positive effect of the improved environmental conditions on the larvae due to the decreased external nutrient load (Wilhelm and Adrian 2007; Chapter V). On the other hand, the heatwaves provoked particularly heavy phytoplankton blooms following from an intense internal nutrient loading, although the phytoplankton biomass had strongly declined through the reduction in external nutrient loading (Chapter IV). The magnitude of these phytoplankton blooms was comparable to blooms that occurred during the hypertrophic period in the 1980s (Köhler et al. 2005). However, less productive and/or deeper lakes might not show such counteracting effects along with future climate change. Therefore, it is very important to understand and to be able to predict the response of different lakes to changes in several important driving environmental factors, especially when concerning the lake management with respect to future climate conditions.

Consequently, further climate impact studies on lakes using long-term data analyses could be distinctly enhanced by conducting micro- or macrocosm experiments or by performing analyses supported by process based models. The microcosm experiments by

Moss et al. (2003) proved very useful in studying the influence of changes in three influencing environmental factors – warming, nutrient addition and fish – on the functioning of shallow lake ecosystems. Thereby, the warming treatments produced considerably smaller effects on the phytoplankton community than nutrients or fish additions. Furthermore, Elliot et al. (2006) successfully used the well validated model PROTECH (Phytoplankton RespOnses To Environmental Change) to experiment with the effects of increased water temperature and increased nutrient load on phytoplankton succession and productivity for a large lake in the English Lake District. The best approach in this regard may, however, be the conceptual model introduced by Blenckner (2005), which includes the landscape and internal interactions to help explain different responses of individual lakes to climatic variations. By using a "landscape filter" including the geographical position, catchment characteristics and the morphology of a lake as well as an "internal filter" including the lake history and biotic/abiotic interactions, this concept helps to explain WHY lakes respond individually to changes in climate.

Conclusions

The results of this thesis shed light on some key aspects that are important in determining the response of lakes to climate warming in summer. Not only the nature of climate change and thus the timing and the magnitude of climate warming throughout the seasons and climatic extremes such as heatwaves, but also lake-specific conditions as the mixing regime and the trophic state are crucial in controlling climate induced impacts on internal lake processes. There is, however, already some evidence that human induced changes in the environment produce synergistic effects in lakes, which superimpose and/or counteract each other. Hence, it is highly important to ascertain how individual lakes respond to complex environmental changes, especially with respect to the projected future climate change. The systematic long-term monitoring of lakes should therefore be continued or further promoted and, on a wider international scale, national databases should be combined (c.f. Blenckner 2005). Furthermore, process based models comprising an extensive input of lake and catchment specifics will be of major importance to allow for a comprehensive understanding of human induced environmental changes in lakes. This knowledge together with clear communication between scientists and decision makers will greatly facilitate the lake management and the assessing of adaptation strategies, which compensates for human induced influences on freshwater ecosystems.

REFERENCES

Ackerman JD, Sim B, Nichols SJ, Claudi R (1994) Review of the early life history of zebra mussels (Dreissena polymorpha): comparisons with marine bivalves. Can J Zool 72:1169-1179

Adrian R, Deneke R, Mischke U, Stellmacher R, Lederer P (1995) Long-term study of the Heiligensee (1975-1992) – evidence for effects of climatic change on the dynamics of eutrophied lake ecosystems. Arch Hydrobiol 133:315-337

Adrian R, Frost TM (1992) Comparative feeding ecology of *Tropocyclops prasinus mexicanus* (Copepoda, Cyclopoida). J Plankton Res 14:1369-1382

Adrian R, Frost TM (1993) Omnivory in cyclopoids: comparison of algae and invertebrates as food for three, differently sized species. J Plankton Res 15:643-658

Adrian R, Walz N, Hintze T, Hoeg S, Rusche R (1999) Effects of ice duration on the plankton succession during spring in a shallow polymictic lake. Freshw Biol 41:621-632

Adrian R, Wilhelm S, Gerten D (2006) Life-history traits of lake plankton species may govern their phenological response to climate warming. Glob Change Biol 12: 652-661

Agbeti MD, Kingston JC, Smol JP, Watters C (1997) Comparison of phytoplankton succession in two lakes of different mixing regime. Archiv für Hydrobiologie 140:37-69

Alabaster JS, Lloyd R (1982) Water quality criteria for freshwater fish. Butterworths, London

Alward RD, Detling JK, Milchunas DG (1999) Grassland vegetation changes and nocturnal global warming. Science 283:229-231

Ambrosetti W, Barbanti L (1999) Deep water warming in lakes: an indicator of climatic change. J Limnol 58:1-9

Anderson ER (1954) Energy budget studies. In: Water loss investigations: Lake Hefner studies. U.S. Geological Survey Professional Paper 269. pp. 71-118

Anderson NJ, Jeppesen E, Sondergaard M (2005) Ecological effects of reduced nutrient loading (oligotrophication) on lakes: an introduction. Freshw Biol 50:1589-1593

Anneville O, Ginot V, Druart JC, Angeli N (2002) Long-term study (1974-1998) of seasonal changes in the phytoplankton in Lake Geneva: a multi-table approach. J Plankton Res 24:993-1007

Anneville O, Gammeter S, Straile D (2005) Phosphorus decrease and climate variability: mediators of synchrony in phytoplankton changes among European peri-alpine lakes. Freshw Biol 50:1731-1746

Badeck FW, Bondeau A, Böttcher K, Doktor D, Lucht W, Schaber J, Sitch S (2004) Responses of spring phenology to climate change. New Phycol162:295-309

Behrendt H, Nixdorf B, Pagenkopf WG (1993) Phenomenological description of polymixis and influence on oxygen budget and phosphorous release in Lake Müggelsee. Int Rev Ges Hydrobiol 78:411-421

Benndorf J, Kranich K, Mehner T, Wagner A (2001) Temperature impact on the midsummer decline of *Daphnia galeata*: an analysis of long-term data from the biomanipulated Bautzen Reservoir (Germany). Freshw Biol 46:199-211

Benson BJ, Lenters JD, Magnuson JJ, Stubbs M, Kratz TK, Dillon PJ, Hecky RE, Lathrop RC (2000) Regional coherence of climatic and lake thermal variables of four lake districts in the Upper Great Lakes Region of North America. Freshw Biol 43:517-27

Bilello MA (1964) Method for predicting river and lake ice formation. J Appl Meteorol 3:38-44

Blenckner T (2005) A conceptual model of climate related effects on lake ecosystems. Hydrobiologia 553:1-14

Blenckner T, Adrian R, Livingstone DM, Jennings E, Weyhenmeyer GA, Aonghusa CN, George DG, Jankowski T, Järvinen M, Nõges T, Straile D, Teubner K (in press) Large-scale climatic signatures in lakes across Europe: A meta - analysis. Glob Change Biol

Borcherding J (1991) The annual reproductive cycle of the freshwater mussel *Dreissena polymorpha* Pallas in lakes. Oecologia 87:208-218

Borcherding J (1995) Laboratory experiments on the influence of food availability, temperature and photoperiod on gonad development in the freshwater mussel *Dreissena polymorpha*. Malacologia 36:15-27

Bowen IS (1926) The ratio of heat losses by conduction and by evaporation from any water surface. Physic Review 27:779-787

Braganza K, Karoly DJ, Arblaster JM (2004) Diurnal temperature range as an index of global climate change during the twentieth century. Geophys Res Lett 31: L13217, doi:10.1029/2004GL019998

Brázdil R, Budikova M, Auer I, Bohm R, Cegnar T, Fasko P, Lapin M, GajicCapka M, Zaninovic K, Koleva E, Niedzwiedz T, Ustrnul Z, Szalai S, Weber RO (1996) Trends of maximum and minimum daily temperatures in central and southeastern Europe. Int J Climatol16:765-782

Brutsaert WH (1982) Evaporation into the Atmosphere. Reidel, Dordrecht, The Netherlands

Burgmer T, Hillebrand H, Pfenninger M (2007) Effects of climate-driven temperature changes on the diversity of freshwater macroinvertebrates. Oecologia 151:93-103

Burla H, Ribi G (1998) Density variation of the zebra mussel *Dreissena polymorpha* in Lake Zürich, from 1976 to 1988. Aquat Sci 60:145-156

Cáceres CE (1998) Interspecific variation in the abundance, production, and emergence of *Daphnia* diapausing eggs. Ecology 79:1699-1710

Carvalho L, Kirika A (2003) Changes in shallow lake functioning: response to climate change and nutrient reduction. Hydrobiologia 506:789-796

Chen CY, Folt CL (2002) Ecophysiological responses to warming events by two sympatric zooplankton species. J Plankton Res 24:579-589

Coats R, Perez-Losada J, Schladow G, Richards R, Goldman C (2006) The warming of Lake Tahoe. Clim Change 76:121-148

Cubasch U, Meehl GA, Boer GJ, Stouffer RJ, Dix M, Noda A, Senior CA, Raper S, Yap KS (2001) Projections of future climate change. In: Houghton JT et al. (eds) Climate Change 2001: The scientific basis. Cambridge University Press, Cambridge, pp 525-582

Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv Mar Biol 26:249-293

Dai A, Trenberth KE, Karl TR (1999) Effects of clouds, soil moisture, precipitation, and water vapor on diurnal temperature range. J Clim 12:2451-2473

Dawidowicz P, Prejs A, Engelmayer A, Martyniak A, Kozłowski J, Kufel L, Paradowska M (2002) Hypolimnetic anoxia hampers top-down food-web manipulation in a eutrophic lake. Freshw Biol 47:2401-2409

De Bernardi R, Giussani G (1990) Are blue-green algae a suitable food for zooplankton? An overview. Hydrobiologia 200:29-41

De Stasio BT, Hill DK, Kleinhans JM, Nibbelink NP, Magnuson JJ (1996) Potential effects of global climate change on small north- temperate lakes: Physics, fish, and plankton. Limnol Oceanogr 41:1136-1149

Dingman SL (1972) Equilibrium temperatures of water surfaces as related to air temperature and solar radiation. Water Resour Res 8:42-49

Dionisio Pires LM, Jonker RR, Van Donk E, Laanbroek HJ (2004) Selective grazing by adults and larvae of the zebra mussel (*Dreissena polymorpha*): application of flow cytometry to natural seston. Freshw Biol 49:116-126

Dokulil MT, Jagsch A, George GD, Anneville O, Jankowski T, Wahl B, Lenhart B, Blenckner T, Teubner K (2006) Twenty years of spatially coherent deepwater warming in lakes across Europe related to the North Atlantic Oscillation. Limnol Oceanogr 51:2787-2793

Dokulil MT, Teubner K (2005) Do phytoplankton communities correctly track trophic changes? An assessment using directly measured and palaeolimnological data. Freshw Biol 50:1594-1604

Driescher E, Behrendt H, Schellenberger G, Stellmacher R (1993) Lake Müggelsee and its environment - natural conditions and anthropogenic impacts. Int Rev Ges Hydrobiol 78:327-343

Easterling DR, Horton B, Jones PD, Peterson TC, Karl TR, Parker DE, Salinger MJ, Razuvayev V, Plummer N, Jamason P, Folland CK (1997) Maximum and minimum temperature trends for the globe. Science 277:364-367

Edinger JE, Duttweiler DW, Geyer JC (1968) The response of water temperatures to meteorological conditions. Water Resour Res 4:1137-1143

Edmondson WT, Abella SEB, Lehman JT (2003) Phytoplankton in Lake Washington: long-term changes 1950-1999. Arch Hydrobiol Suppl 139:275-326

Edwards M, Richardson AJ (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430:881-884

Elliott JA, Jones ID, Thackeray SJ (2006) Testing the sensitivity of phytoplankton communities to changes in water temperature and nutrient load, in a temperate lake. Hydrobiologia 559:401-411

Fang X, Stefan HG (1997) Simulated climate change effects on dissolved oxygen characteristics in ice-covered lakes. Ecol Mod 103:209-229

Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, Gibbs HK, Helkowski JH, Holloway T, Howard EA, Kucharik CJ, Monfreda C, Patz JA, Prentice IC, Ramankutty N, Snyder PK (2005) Global consequences of land use. Science 309:570-574

Folland CK, Karl TR, Christy JR, Clarke RA, Gruza GV, Jouzel J, Mann ME, Oerlemans J, Salinger MJ, Wang S (2001) Observed Climate Variability and Change. In: Houghton JT et al. (eds), Climate Change 2001: The Scientific Basis. Cambridge University Press, Cambridge, pp. 99-181

French TD, Petticrew EL (2007) Chlorophyll-*a* seasonality in four shallow eutrophic lakes (northern British Columbia, Canada) and the critical roles of internal phosphorus loading and temperature. Hydrobiologia 575:285-299

Gaedke U (1998) Functional and taxonomical properties of the phytoplankton community of large and deep Lake Constance: Interannual variability and response to re-oligotrophication (1979-1993). Arch Hydrobiol Spec Issues Advances in Limnology 53:119-141

Gaedke U, Ollinger D, Bäuerle E, Straile D (1998) The impact of the interannual variability in hydrodynamic conditions on the plankton development in Lake Constance in spring and summer. Arch Hydrobiol Spec Issues Advances in Limnology 53:565-585

Gaedke U, Wickham SA (2004) Ciliate dynamics in response to changing biotic and abiotic conditions in a large, deep lake (Lake Constance). Aquat Microb Ecol 34:247-261

George DG, Hewitt DP, Lund JWG, Smyly WJP (1990) The relative effects of enrichment and climate change on the long-term dynamics of *Daphnia* in Esthwaite Water, Cumbria. Freshw Biol 23:55-70

Gerten D, Adrian R (2000) Climate-driven changes in spring plankton dynamics and the sensitivity of shallow polymictic lakes to the North Atlantic Oscillation. Limnol Oceanogr 45:1058-1066

Gerten D, Adrian R (2001) Differences in the persistency of the North Atlantic Oscillation signal among lakes. Limnol Oceanogr 46:448-455

Gerten D, Adrian R (2002a) Effects of climate warming, North Atlantic Oscillation, and El Niño-Southern Oscillation on thermal conditions and plankton dynamics in Northern Hemispheric lakes. The Scientific World Journal 2:586-606

Gerten D, Adrian R (2002b) Species-specific changes in the phenology and peak abundance of freshwater copepods in response to warm summers. Freshw Biol 47:2163-2173

Gitay H, Brown S, Easterling W, Jallow B (2001) Ecosystems and their goods and services. In: McCarthy JJ et al. (eds) Climate Change 2001: Impacts, adaptations, and mitigation of climate change. Cambridge University Press, Cambridge, pp 234-342

Gooseff MN, Strzepek K, Chapra SC (2005) Modelling the potential effects of climate change on water temperature downstream of a shallow reservoir, lower Madison River, MT. Clim Change 68:331-353

Gorham E, Boyce FM (1989) Influence of lake surface area and depth upon thermal stratification and the depth of the summer thermocline. J Great Lakes Res 15:233-245

Hairston NG Jr (1998) Time travelers: what's timely in diapause research? Arch Hydrobiol Spec Issues Advances in Limnology 52:1-15

Hamburger K, Dall PC, Lindegaard K, Nilson IB (2000) Survival and energy metabolism in an oxygen deficient environment. Field and laboratory studies on the bottom fauna from the profundal zone of Lake Esrom, Denmark. Hydrobiologia 432:173-188

Hansen AM, Santer B (1995) The influence of food resources on the development, survival and reproduction of the two cyclopoid copepods: *Cyclops vicinus* and *Mesocyclops leuckarti*. J Plankton Res 17:631-646

Hari RE, Livingstone DM, Siber R, Burkhardt-Holm P, Güttinger H (2006) Consequences of climatic change for water temperature and brown trout populations in Alpine rivers and streams. Glob Change Biol 12:10-26

Harrington R, Woiwod I, Sparks TH (1999) Climate change and trophic interactions. Trends Ecol Evol 14:146-150

Hasler AD (1947) Eutrophication of lakes by domestic sewage. Ecology 28:383-395

Hays GC, Richardson AJ, Robinson C (2005) Climate change and marine plankton. Trends Ecol Evol 20:337-344

Hebert PDN, Muncaster BW, Mackie GL (1989) Ecological and genetic studies on *Dreissena polymorpha* (Pallas): a new mollusc in the Great Lakes. Can J Fish Aquat Sci 46:1587-1591

Heino R, Brázdil R, Forland E, Tuomenvirta H, Alexandersson H, Beniston M, Pfister C, Rebetez M, Rosenhagen G, Rosner S, Wibig J (1999) Progress in the study of climatic extremes in northern and central Europe. Clim Change 42:151-181

Helsel DR, Hirsch RM (1992) Statistical methods in water resources. Elsevier, Amsterdam, The Netherlands

Hondzo M, Stefan HG (1993) Regional water temperature characteristics of lakes subjected to climate change. Clim Change 24:187-211

Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Dai X, Maskell K, Johnson CA (2001) Climate change 2001: The scientific basis. Contribution of working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge

Huisman J, Sharples J, Stroom JM, Visser PM, Kardinaal WEA, Verspagen JMH, Sommeijer B (2004) Changes in turbulent mixing shift competition for light between phytoplankton species. Ecology 85:2960-2970

Imberger J, Patterson JC (1990) Physical limnology. Adv Appl Mech 27:303-475

Imboden DM, Wüest A (1995) Mixing mechanisms in lakes. In: Lerman A, Imboden DM, Gat JR (eds) Physics and chemistry of lakes, Springer, pp 83-138

Jankowski T, Livingstone DM, Bührer H, Forster R, Niederhauser P (2006) Consequences of the 2003 European heat wave for lake temperature profiles, thermal stability, and hypolimnetic oxygen depletion: Implications for a warmer world. Limnol Oceanogr 51:815-819

Järvalt A, Krause T, Palm A (2005) Diel migration and spatial distribution of fish in a small stratified lake. Hydrobiologia 547:197-203

Jeppesen E, Sondergaard M, Jensen JP, Havens KE, Anneville O, Carvalho L, Coveney MF, Deneke R, Dokulil MT, Foy B, Gerdeaux D, Hampton SE, Hilt S, Kangur K, Köhler J, Lammens EHHR, Lauridsen TL, Manca M, Miracle MR, MOSS B, Noges P, Persson G, Phillips G, Portielje R, Schelske CL, Straile D, Tatrai I, Willen E, Winder M (2005) Lake responses to reduced nutrient loading - an analysis of contemporary long-term data from 35 case studies. Freshw Biol 50:1747-1771

Johnson PD, McMahon RF (1998) Effects of temperature and chronic hypoxia on survivorship of the zebra mussel (*Dreissena polymorpha*) and Asian clam (*Corbicula fluminea*). Can J Fish Aquat Sci 55:1564-1572

Karl TR, Jones PD, Knight RW, Kukla G, Plummer N, Razuvayev V, Gallo KP, Lindseay J, Charlson RJ, Peterson TC (1993) A new perspective on recent global warming - asymmetric trends of daily maximum and minimum temperature. Bull Am Meteorol Soc 74:1007-1023

Kasten F, Czeplak G (1980) Solar and terrestrial radiation dependent on the amount and type of cloud. Sol Energy 24:177-89

Kasten F, Dehne K, Behr HD, Bergholter U (1984) Die räumliche und zeitliche Verteilung der diffusen und direkten Sonneneinstrahlung in der Bundesrepublik Deutschland. BMFT-FB-T 84-125:1-128

Kettle H, Thompson R, Anderson NJ, Livingstone DM (2004) Empirical modeling of summer lake surface temperatures in southwest Greenland. Limnol Oceanogr 49:271-282

King JR, Shuter BJ, Zimmerman AP (1997) The response of the thermal stratification of South Bay (Lake Huron) to climate variability. Can J Fish Aquat Sci 54:1873-1882

Kinzelbach R (1995) Neozoans in European Waters - Exemplifying the worldwide process of invasion and species mixing. Experientia 51:526-538

Kleeberg A, Dudel GE (1997) Changes in extent of phosphorus release in a shallow lake (Lake Großer Müggelsee; Germany, Berlin) due to climatic factors and load. Mar Geol 139:61-75

Köhler J, Hilt S, Adrian R, Nicklisch A, Kozerski HP, Walz N (2005) Long-term response of a shallow, moderately flushed lake to reduced external phosphorus and nitrogen loading. Freshw Biol 50:1639-1650

Kuhn W (1978) Aus Wärmehaushalt und Klimadaten berechnete Verdunstung des Zürichsees. Vierteljahrschrift der naturforschenden Gesellschaft in Zürich 123:261-283

Kukla G, Karl TR (1993) Nighttime warming and the greenhouse-effect. Environ Sci Technol 27:1468-1474

Liebig JR, Vanderploeg HA (1995) Vulnerability of *Dreissena polymorpha* larvae to predation by Great-Lakes calanoid copepods - the importance of the bivalve shell. J Great Lakes Res 21:353-358

Livingstone DM (2003) Impact of secular climate change on the thermal structure of a large temperate central European lake. Clim Change 57:205-225

Livingstone DM, Dokulil MT (2001) Eighty years of spatially coherent Austrian lake surface temperatures and their relationship to regional air temperature and the North Atlantic Oscillation. Limnol Oceanogr 46:1220-1227

Livingstone DM, Imboden DM (1989) Annual heat balance and equilibrium temperature of Lake Aegeri, Switzerland. Aquat Sci 51:351-369

Livingstone DM, Lotter AF (1998) The relationship between air and water temperatures in lakes of the Swiss Plateau: a case study with palaeolimnological implications. J Paleolimnol 19:181-198

Livingstone DM, Lotter AF, Kettle H (2005) Altitude-dependent differences in the primary physical response of mountain lakes to climatic forcing. Limnol Oceanogr50:1313-1325

Livingstone DM, Padisák J (in press) Large-scale coherence in the response of lake surface-water temperatures to synoptic-scale climate forcing during summer. Limnol Oceanogr

Lorke A (1998) Investigation of turbulent mixing in shallow lakes using temperature microstructure measurements. Aquat Sci 60:210-219

Lozán JL, Kausch H (1998) Angewandte Statistik für Naturwissenschaftler. Parey, Berlin

MacIntyre S (1998) Turbulent mixing and resource supply to phytoplankton. In: Imberger J (ed) Physical processes in lakes and oceans, Coastal and estuarine studies, AGU, pp 539-567

MacIsaac HJ, Sprules WG, Leach JH (1991) Ingestion of small-bodied zooplankton by zebra mussels (*Dreissena polymorpha*) - can cannibalism on larvae influence population dynamics. Can J Fish Aquat Sci 48:2051-2060

Maier G (1989) The effect of temperature on the development times of eggs, naupliar and copepodite stages of five species of cyclopoid copepods. Hydrobiologia 184:79-88

Maier G (1994) Pattern of life history among cyclopoid copepods of central Europe. Freshw Biol 31:77-86

Marcus N (2004) An overview of the impacts of eutrophication and chemical pollutants on copepods of the coastal zone. Zool Stud 43:211-217

Marsden HW (1989) Lake restoration by reducing external phosphorus loading: the influence of sediment phosphorus release. Freshw Biol 21:139-162

Marti DE, Imboden DM (1986) Thermische Energieflüsse an der Wasseroberfläche: Beispiel Sempachersee. Schweiz Z Hydrol 48:196-229

McCombie AM (1959) Some relations between air temperatures and the surface water temperatures of lakes. Limnol Oceanogr 4:252-258.

McMahon RF (1991) Mollusca: Bivalvia. In: Thorp JH, Covich AP (eds) Ecology and classification of North American freshwater invertebrates. Academic Press, pp 315-399

McMillan W (1971) Heat dispersal - Lake Trawsfynydd cooling studies. In: Symposium on freshwater biology and electrical power generation, part I, session 1. pp 41-80

Meehl GA, Washington WM, Ammann CM, Arblaster JM, Wigley TML, Tebaldi C (2004) Combinations of natural and anthropogenic forcings in twentieth-century climate. J Clim 17:3721-3727

Menzel A, Sparks TH, Estrella N, Koch E, Aasa A, Ahas R, Alm-Kübler K, Bissolli P, Braslavská O, Briede A, Chmielewski FM, Crepinsek Z, Curnel Y, Dahl Å, Defila C, Donnelly A, Filella Y, Jatczak K, Måge F, Mestre A, Nordli Ø, Peñuelas J, Pirinen P, Remišová V, Scheifinger H, Striz M, Susnik A, van Vliet AJH, Wielgolaski F, Zach S, Zust A (2006) European phenological response to climate change matches the warming pattern. Glob Change Biol 12:1969-1976

Mills EL, Ogorman R, Roseman EF, Adams C, Owens RW (1995) Planktivory by alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) on microcrustacean zooplankton and dreissenid (Bivalvia, Dreissenidae) veligers in southern Lake Ontario. Can J Fish Aquat Sci 52:925-935

Molloy DP, Karatayev AY, Burlakowa LE, Kurandina DP, Laruelle F (1997) Natural enemies of zebra mussels: predators, parasites, and ecological competitors. Rev Fish Sci 5:27-97

Mooij WM, Hülsmann S, De Senerpont Domis LN, Nolet BA, Bodelier PLE, Boert PCM, Dionisio Pires LM, Gons HJ, Ibelings BW, Noordhuis R, Portielje R, Wolfstein K, Lammens EHRR (2005) The impact of climate change on lakes in the Netherlands: a review. Aquat Ecol 39:381-400

Moore MK, Townsend VR Jr (1998) The interaction of temperature, dissolved oxygen and predation pressure in an aquatic predator-prey system. Oikos 81:329-336

Moss B, MCKee DM, Atkinson D, Collings SE, Eaton JW, Gill AB, Harvey I, Hatton K, Heyes T, Wilson D (2003) How important is climate? Effects of warming, nutrient addition and fish on phytoplankton in a shallow lake microcosm. J App Ecol 40:782-792

Mouthon J, Daufresne M (2006) Effects of the 2003 heatwave and climatic warming on mollusc communities of the Saône: a large lowland river and of its two main tributaries (France). Glob Change Biol 12:441-449

Müller-Navarra DC, Guss S, Von Storch H (1997) Interannual variability of seasonal succession events in a temperate lake and its relation to temperature variability. Glob Change Biol 3:429-438

Murray FW (1967) On the computation of saturation vapor pressure. J Appl Meteorol 6:203-204

Nalepa TF, Schloesser DW (1992) Zebra mussels: Biology, Impacts, and Control. Lewis Press, Boca Raton, Florida

Neumann D, Borcherding J, Jantz B (1993) Growth and seasonal reproduction of *Dreissena polymorpha* in the River Rhine and adjacent waters. In: Nalepa TF, Schloesser DW (eds) Zebra mussels: Biology, Impacts, and Control Lewis Press, Boca Raton, Florida, pp 95-109

Nichols SJ (1996) Variations in the reproductive cycle of *Dreissena polymorpha* in Europe, Russia, and North America. Am Zool 36:311-325

Næss T, Nilssen JP, Demmo R (1993) Individual lake characteristics modify life cycle and diapause habitat of two neighbouring populations of the cyclopoid copepod *Thermocyclops oithonoides*. Can J Zool 71:1663-1672

Oderbrecht W (1957) Ausbreitung der Wander- oder Zebramuschel in Europa. Urania Monatschrift über Natur und Gesellschaft 20:24-27

Padisák J, Reynolds CS (2003) Shallow lakes: the absolute, the relative, the functional and the pragmatic. Hydrobiologia 506:1-11

Page ES (1955) A test for a change in a parameter occurring at an unknown point. Biometrika 42:523-527

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37-42

Peeters F, Livingstone DM, Goudsmit GH, Kipfer R, Forster R (2002) Modeling 50 years of historical temperature profiles in a large central European lake. Limnol Oceanogr 47:186-197

Peters RH, De Bernardi R (1987) *Daphnia*. Memorie dell′ Istituto Italiano die Idrobiologia 45:1-502

Prentice IC, Farquhar GD, Fasham MJR, Goulden ML, Heimann M, Jaramillo VJ, Kheshgi HS, Le Quéré C, Scholes RJ, Wallace DWR (2001) The carbon cycle and atmospheric carbon dioxide. In: Houghton JT et al. (eds) Climate Change 2001: The Scientific Basis. Cambridge University Press, Cambridge, pp 183-237

Ptacnik R, Diehl S, Berger S (2003) Performance of sinking and nonsinking phytoplankton taxa in a gradient of mixing depths. Limnol Oceanogr 48:1903-1912

Ragotzkie RA (1978) Heat budgets of lakes. In: Lerman A (ed) Lakes: Chemistry, Geology and Physics. Springer Verlag, pp 1-19

Reynolds CS (1984) The ecology of freshwater phytoplankton. Cambridge studies in Ecology. Cambridge University Press, Cambridge

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

Reynolds CS, Huszar V, Kruk C, Naselli-Flores L, Melo S (2002) Towards a functional classification of the freshwater phytoplankton. J Plankton Res 24:417-428

Riley ET, Prepas EE (1984) Role of internal phosphorus loading in two shallow, productive lakes in Alberta, Canada. Can J Fish Aquat Sci 41:845-855

Rodhe B (1952) On the relation between air temperature and ice formation in the Baltic. Geogr Ann 34**:**175-202

Ruosteenoja K, Carter TR, Jylhä K, Tuomenvirta H (2003) Future climate in world regions: an intercomparison of model-based projections for the new IPCC emissions scenarios. The Finnish Environment 644, Finnish Environment Institute

Saloom ME, Duncan RS (2005) Low dissolved oxygen levels reduce anti-predation behaviours of the freshwater clam *Corbicula fluminea*. Freshw Biol 50:1233-1238

Satheesh SK, Ramanathan V, Xu LJ, Lobert JM, Podgorny IA, Prospero JM, Holben BN, Loeb NG (1999) A model for the natural and anthropogenic aerosols over the tropical Indian Ocean derived from Indian Ocean Experiment data. J Geophys Res 104:27421-27440

Schär C, Vidale PL, Luthi D, Frei C, Haberli C, Liniger MA, Appenzeller C (2004) The role of increasing temperature variability in European summer heatwaves. Nature 427:332-336

Scheffer M (1998) Ecology of shallow lakes. Chapman and Hall, London

Scheffer M, Straile D, van Nes EH, Hosper H (2001) Climatic warming causes regime shifts in lake food webs. Limnol Oceanogr 46:1780-1783

Schindler DW, Beaty KG, Fee EJ, Cruikshank DR, Debruyn ER, Findlay DL, Linsey GA, Shearer JA, Stainton MP, Turner MA (1990) Effects of climatic warming on lakes of the central boreal forest. Science 258:967-970

Schindler DW (1996) Widespread effects of climate warming on freshwater ecosystems of North America. Hydrol Proc 11:1044-1069

Schneider DW, Madon SP, Stoeckel JA, Sparks RE (1998) Seston quality controls zebra mussel (*Dreissena polymorpha*) energetics in turbid rivers. Oecologia 117:331-341

Schneider DW, Stoeckel JA, Rehmann CR, Blodgett KD, Sparks RE, Padilla DK (2003) A developmental bottleneck in dispersing larvae: implications for spatial population dynamics. Ecol Lett 6:352-360

Seager J, Milne I, Mallett M, Sims I (2000) Effects of short-term oxygen depletion on fish. Env Toxicol Chem 19:2937-2942

Sen PK (1968) Estimates of the regression coefficient based on Kendall's tau. Journal of the American Statistical Association 63:1379-1389

Shuter BJ, Schlesinger DA, Zimmerman AP (1983) Empirical predictors of annual surface water temperature cycles in North American lakes. Can J Fish Aquat Sci 40:1838-1845

Smith VH, Joye SB, Howarth RW (2006) Eutrophication of freshwater and marine ecosystems. Limnol Oceanogr 51:351-355

Sneyers R (1975) Sur l'analyse statistique des séries d'observations. Note technique 143, WMO, Geneva, Switzerland

Sommer U (1985) Seasonal succession of phytoplankton in Lake Constance. BioScience 5:351-357

Sommer U, Gliwicz ZM, Lampert W, Duncan A (1986) The PEG-model of seasonal succession of planktonic events in fresh waters. Arch Hydrobiol 106:433-471

Søndergaard M, Jensen JP, Jeppesen E (1999) Internal phosphorus loading in shallow Danish lakes. Hydrobiologia 408:145-152

Søndergaard M, Jensen JP, Jeppesen E (2003) Role of sediment and internal loading of phosphorus in shallow lakes. Hydrobiologia 506:135-145

Šporka F, Livingstone DM, Stuchlík E, Turek J, Galas J (2006) Water temperatures and ice cover in the lakes of the Tatra Mountains. Biologia 61:77-90

Sprung M (1993) The other life: An account of present knowledge of the larval phase of *Dreissena polymorpha*. In: Nalepa TF, Schloesser DW (eds) Zebra mussels: Biology, Impacts, and Control Lewis Press, Boca Raton, Florida, pp 39-53

Sprung M (1995) Physiological energetics of the zebra mussel *Dreissena polymorpha* in Lakes. 2: Food uptake and gross growth efficiency. Hydrobiologia 304:133-146

Stańczykowska A (1977) Ecology of *Dreissena polymorpha* (Pall.) (Bivalvia) in lakes. Polskie Archiwum Hysrobiologii 24:461-530

Stańczykowska A, Lewandowski K (1993) Thirty years of studies of *Dreissena polymorpha* ecology in Mazurian lakes of northeastern Poland. In: Nalepa TF, Schloesser DW (eds) Zebra mussels: Biology, Impacts, and Control Lewis Press, Boca Raton, Florida, pp 3-37

Stefan HG, Fang X, Hondzo M (1998) Simulated climate change effects on year-round water temperatures in temperate zone lakes. Clim Change 40:547-576

Stenseth NC, Mysterud A (2002) Climate, changing phenology, and other life history traits: nonlinearity and match-mismatch to the environment. Proc Natl Acad Sci USA 99:133379-13381

Stoeckel JA, Padilla DK, Schneider DW, Rehmann CR (2004) Laboratory culture of *Dreissena polymorpha* larvae: spawning success, adult fecundity, and larval mortality patterns. Can J Zool 82:1436-1443

Stoeckmann AM, Garton DW (2001) Flexible energy allocation in zebra mussels (*Dreissena polymorpha*) in response to different environmental conditions. J North Am Benthol Soc 20:486-500

Straile D (2000) Meteorological forcing of plankton dynamics in a large and deep continental European lake. Oecologia 122:44-50

Straile D, Adrian R (2000) The North Atlantic Oscillation and plankton dynamics in two European lakes – two variations on a general theme. Glob Change Biol 6:663-670

Straile D, Livingstone DM, Weyhenmeyer GA, George DG (2003) The response of freshwater ecosystems to climate variability associated with the North Atlantic Oscillation. In: Hurrel JW, Kushnir Y, Ottersen G, Visbeck M (eds) The North Atlantic Oscillation: Climatic Significance and Environmental Impact. Geophys Monogr 134, pp 263-279

Sweers HE (1976) A nomogram to estimate the heat-exchange coefficient at the air-water interface as a function of wind speed and temperature; a critical survey of some literature. J Hydrol 30:375-401

Teasdale M, Vopel K, Thistle D (2004) The timing of benthic copepod emergence. Limnol Oceanogr 49:884–889

Theil H (1950) A rank-invariant method of linear and polynomial regression analysis I-III. Proceedings of Koninklijke Nederlandse Akademie van Wetenschappen 53:386-1412

Turnbull MH, Tissue DT, Murthy R, Wang XZ, Sparrow AD, Griffin KL (2004) Nocturnal warming increases photosynthesis at elevated CO2 partial pressure in *Populus deltoides*. New Phytol 161:819-826

Vanderploeg HA, Liebig JR, Gluck AA (1996) Evaluation of different phytoplankton for supporting development of zebra mussel larvae (*Dreissena polymorpha*): The importance of size and polyunsaturated fatty acid content. J Great Lakes Res 22:36-45

Vijverberg J (1980) Effects of temperature in laboratory studies on development and growth of Clodocera and Copepods from Tjeukemeer, The Netherlands. Freshw Biol 10:317-340

Wacker A, von Elert E (2002) Strong influences of larval diet history on subsequent post-settlement growth in the freshwater mollusc *Dreissena polymorpha*. Proc R Soc Lond B Biol Sci 269:2113-2119

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416:389-395

Walz N (1973) Studies on the biology of *Dreissena polymorpha* Pallas in the Lake of Constance. Arch Hydrobiol Suppl 42:452-482

Watson NHF, Smallman BN (1971) The role of photoperiod and temperature in the induction and termination of an arrested development in two species of freshwater cyclopid copepods. Can J Zool 49:855-862

Watts JM, Swan BK, Tiffany M, Hurlbert SH (2001) Thermal, mixing, and oxygen regimes of the Salton Sea, California, 1997-1999. Hydrobiologia 466:159-176

Weider LJ, Lampert W (1985) Differential response of *Daphnia* genotypes to oxygen stress: respiration rates, haemoglobin content and low-oxygen tolerance. Oecologia 65:487-491

Weithoff G, Lorke A, Walz N (2000) Effects of water-column mixing on bacteria, phytoplankton, and rotifers under different levels of herbivory in a shallow eutrophic lake. Oecologia 125:91-100

Wellborn GA (1994) Size-biased predation and prey life-histories - A comparative study of freshwater amphipod populations. Ecology 75:2104-2117

Wetzel RG (2001) Limnology. Academic Press, San Diego, CA

Weyhenmeyer GA, Blenckner T, Pettersson K (1999) Changes of the plankton spring outburst related to the North Atlantic Oscillation. Limnol Oceanogr 44:1788-1792

Weyhenmeyer GA, Persson G, Willén E (2004) Miljöövervakning i Mälaren 2003. SLU-Report, Dept. of Environmental Assessment, Uppsala, Schweden

Whitney-Johnson A, Thompson M, Hon E (2005) Responses to predicted global warming in *Pieris rapae* L. (Lepidoptera): Consequences of nocturnal versus diurnal temperature change on fitness components. Environ Entomol 34:535-540

Wibig J, Glowicki B (2002) Trends of minimum and maximum temperature in Poland. Clim Res 20:123-133

Wiedner C, Nixdorf B, Heinze R, Wirsing B, Neumann U, Weckesser J (2002) Regulation of cyanobacteria and microcystin dynamics in polymictic shallow lakes. Arch Hydrobiol 155:383-400

Wilhelm S, Hintze T, Livingstone DM, Adrian R (2006) Long-term response of daily epilimnetic temperature extrema to climate forcing. Can J Fish Aquat Sci 63:2467-2477

Wilhelm S, Adrian R (2007) Long-term response of *Dreissena polymorpha* larvae to physical and biological forcing in a shallow lake. Oecologia 151:104-114

Winder M, Schindler DE (2004) Climate change uncouples trophic interactions in an aquatic ecosystem. Ecology 85:2100-2106

Woynarovich E (1961) The oxygen consumption of *Dreissena polymorpha* (Lamellibranchiata) at different temperatures. Annales Instituti Biologici Tihany 28:211-216

Wright DA, Setzler Hamilton EM, Magee JA, Kennedy VS, McIninch SP (1996) Effect of salinity and temperature on survival and development of young zebra (*Dreissena polymorpha*) and quagga (*Dreissena bugensis*) mussels. Estuaries 19:619-628

Xu Z, Zhou G (2005) Effects of water stress and nocturnal temperature on carbon allocation in the perennial grass, *Leymus chinensis*. Physiol Planet 123:272-280

Zhang Y, Prepas EE (1996) Regulation of the dominance of planktonic diatoms and cyanobacteria in four eutrophic hardwater lakes by nutrients, water column stability and temperature. Can J Fish Aquat Sci 53:621-633

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