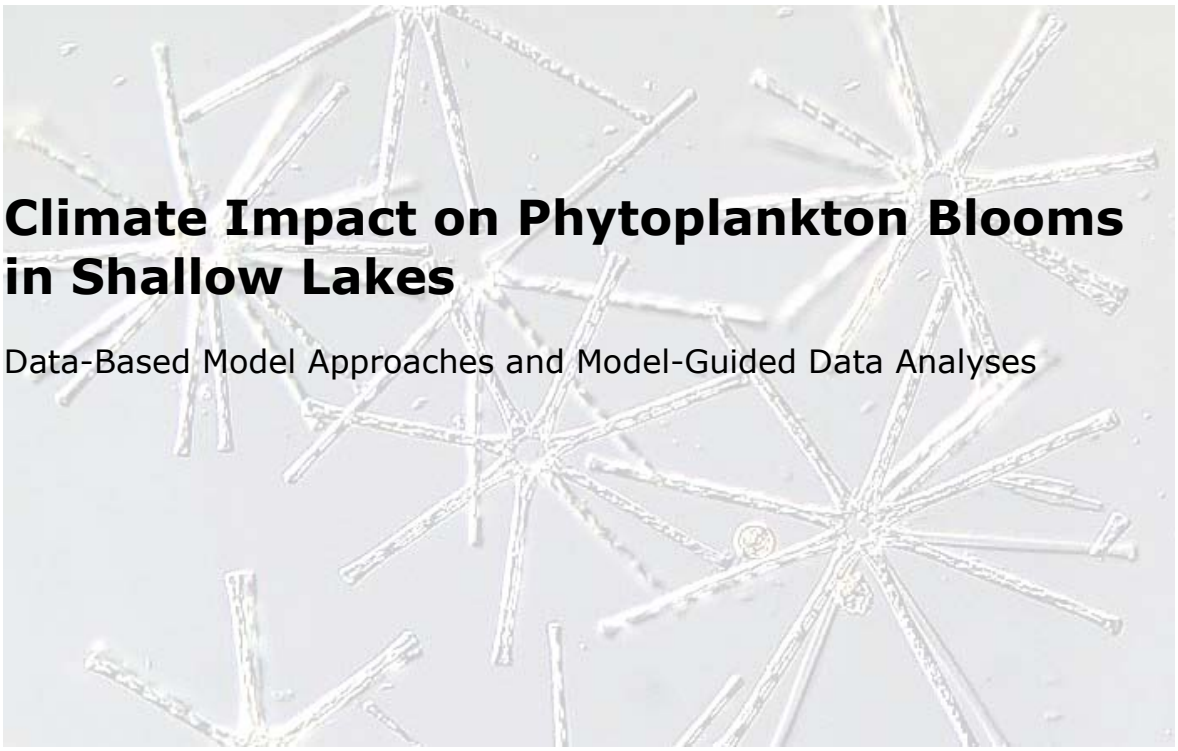

Climate Impact on Phytoplankton Blooms in Shallow Lakes

Data-Based Model Approaches and Model-Guided Data Analyses

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PhD Thesis

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2009

Institut für Biochemie und Biologie
Arbeitsgruppe für Ökologie und Ökosystemmodellierung

Climate impact on phytoplankton blooms in shallow lakes

Data-based model approaches and model-guided data analyses

Kumulative Dissertation

zur Erlangung des akademischen Grades
„doctor rerum naturalium"
(Dr. rer. nat.)
in der Wissenschaftsdisziplin „Ökologie"

eingereicht an der
Mathematisch-Naturwissenschaftlichen Fakultät
der Universität Potsdam

von
Veronika Emilie Charlotte Huber
Potsdam, den 20. November 2009

Published online at the
Institutional Repository of the University of Potsdam:
URL http://opus.kobv.de/ubp/volltexte/2010/4234/
URN urn:nbn:de:kobv:517-opus-42346
http://nbn-resolving.org/urn:nbn:de:kobv:517-opus-42346

Dem Baron auf den Bäumen

Contents

Summary

Lake ecosystems across the globe have responded to climate warming of recent decades and are expected to further change in the future. Anticipating impacts that are detrimental to water quality is critically important given that lakes constitute a major part of the earth's freshwater resources. A central concern is the climate impact on phytoplankton, including algae and cyanobacteria, since it forms the basis of the food chain and decisively influences water quality.

Climate impacts on freshwater phytoplankton are far from clear yet. Correctly attributing observed changes to altered climatic conditions is complicated by multiple anthropogenic influences. Due to successfully implemented measures to contain eutrophication, many lakes have simultaneously experienced increases in water temperature and reductions in nutrient load in the recent past.

With this thesis, I contribute to a better understanding of the climate impacts on phytoplankton in shallow lakes. The results shed light on

i) mechanisms underlying warming induced changes in the seasonal timing of the phytoplankton spring bloom (phenology shifts), in particular under varying nutrient availability (trophic state);
ii) the risk that climate change disrupts the temporal coupling of predator and prey (zooplankton and phytoplankton) in spring;
iii) the question whether summer heat wave events favour nuisance blooms of cyanobacteria; and
iv) the influence of seasonal warming patterns on cyanobacteria via effects on thermal stratification and food web interactions.

I also examine two different approaches to model phytoplankton spring phenology and focus on disentangling effects of climate change and nutrient enrichment.

My analyses were, for the most part, based on a long-term data set of physical, chemical and biological variables of Müggelsee, a shallow, polymictic lake in north-eastern Germany, which was subject to a simultaneous change in climate

and trophic state during the past three decades. To analyse the data, I constructed a dynamic simulation model, implemented a genetic algorithm to parameterize models, and applied statistical techniques of classification tree and time-series analysis.

Results achieved with the dynamic simulation model indicated that the mechanisms driving phytoplankton spring phenology in shallow lakes depend on the trophic state. They also suggested that nutrient enrichment amplifies the temporal advancement of the phytoplankton spring bloom, triggered by high winter and spring temperatures. Also, warming decoupled the phytoplankton from the zooplankton spring peak only under high nutrient supply. However, in contrast to observations of other studies, this temporal predator-prey mismatch did not cause the subsequent decline of the predator.

A novel approach to model phenology, which allows generating analytical prediction, was parameterized based on experimental data. It proved useful to assess the timings of population peaks of an artificially forced zooplankton-phytoplankton system. Mimicking climate warming by lengthening the growing period advanced algal blooms and consequently also peaks in zooplankton abundance.

Investigating the reasons for the contrasting development of cyanobacteria during two recent summer heat wave events, I found that anomalously hot weather did not always promote cyanobacteria in the nutrient-rich lake studied. The seasonal timing and duration of heat waves determined whether critical thresholds of thermal stratification, decisive for cyanobacterial bloom formation, were crossed.

In addition, the temporal patterns of heat wave events influenced the summer abundance of some zooplankton species, which as predators may serve as a buffer by suppressing phytoplankton bloom formation. Inter-annual differences in water temperature during specific temporal windows explained most of the contrasting responses of two zooplankton subgroups (cyclopoid copepods and bosminids) to recent heat wave events.

In conclusion, this thesis adds to the growing body of evidence that lake ecosystems have strongly responded to climatic changes of recent decades. It

reaches beyond many previous studies of climate impacts on lakes by focussing on underlying mechanisms and explicitly considering multiple environmental changes. Key findings show that while nutrients remain the primary agents that determine the magnitude of phytoplankton blooms future climate change may counteract successfully implemented measures to fight lake eutrophication, e.g., by favouring cyanobacteria. They also indicate that climate impacts are more severe in nutrient-rich than in nutrient-poor lakes. Hence, to develop lake management plans for the future, limnologists need to seek a comprehensive, mechanistic understanding of overlapping effects of the multi-faceted human footprint on aquatic ecosystems.

General introduction

0.1 Concepts and motivation

Climate change impact on lake ecosystems—Aquatic and terrestrial ecosystems across the globe have strongly responded to climate change of the recent past (Parmesan and Yohe 2003; IPCC 2007). Lakes are considered especially suitable indicators of ongoing climate change due to integration of changes occurring in the entire catchment area and the prevalence of temperature driven processes (Williamson *et al*. 2009). Climate induced changes have been recorded regarding lake physics, chemistry and biology all over the world (Adrian *et al*. 2009; Blenckner *et al*. 2007). A better mechanistic understanding of the observed changes is crucial to anticipate the effects of expected further warming on lakes. Detecting change that is detrimental to water quality is critically important given that lakes constitute a major part of earth's freshwater resources (Gleick 1996).

Phytoplankton blooms and multiple anthropogenic influences on lake ecosystems—Phytoplankton is the principal primary producer in most lakes forming the basis of the food chain (Wetzel 2001). Given suitable conditions these microscopic organisms grow extremely rapidly building up considerable biomass in a comparatively short time ('blooms') (e.g., Sommer and Lengfellner 2008). Certain phytoplankton species (cyanobacteria) float up to the water surface developing green scums that can be observed as macroscopic phenomena (Ibelings *et al*. 2003; Huisman *et al*. 2005). In addition, some of these species produce toxins that may pose a threat to human health (Chorus 1999).

Due to their important role for water quality, phytoplankton blooms and the underlying mechanisms have long been subjects of scientific interest (e.g., Lund 1950). Supply of large amounts of phosphorus (and to a lesser extent nitrogen) to the water has been established as a major driving force of phytoplankton blooms (Schindler 1974; Vollenweider and Kerekes 1982). This knowledge allowed for effective lake management successfully containing eutrophication of

lakes through reduction of nutrient inputs to freshwater bodies (Schindler 2006).

Climate impacts recorded in recent years have brought renewed interest in the mechanisms underlying phytoplankton blooms. Meteorological variability has been shown to affect the timing and magnitude of phytoplankton blooms in lakes (see following paragraphs). Some of these studies concluded that ongoing and future climate warming might counteract successfully achieved lake restoration efforts of the past (Schindler 2006). However, the effects of climate change on phytoplankton blooms are far from clear yet, with impacts varying depending on ecosystem type, species involved and prevailing food web interactions (Straile and Adrian 2000; Wiltshire *et al*. 2008; Adrian *et al*. 2009).

Numerous lakes have experienced climate change as well as a reduction in nutrient loading (re-oligotrophication) at the same time (Jeppesen *et al*. 2005; Köhler *et al*. 2005). Yet, up to now only few attempts have been made to disentangle the effects of these simultaneous environmental changes (but see Elliott *et al*. 2006; Feuchtmayr *et al*. 2009; Law *et al*. 2009). The results of this thesis contribute to closing this important research gap. Accurately attributing observed changes to climatic influences is crucial for the development of effective lake management plans in the future.

Plankton spring phenology—The seasonal plankton growth pattern in temperate lakes with moderately to high nutrient supply (eutrophic lakes) is marked by a bloom of phytoplankton in spring (Sommer *et al*. 1986). Typically it is followed by a population increase of zooplankton, which ultimately graze down the phytoplankton producing a period of high water transparency in late spring/early summer (the so-called 'clear-water phase'). A synchronous advancement in the phenology (timing) of these events concurrent with increasing winter and spring water temperatures has been demonstrated for a large number of lakes in the northern hemisphere (Gerten and Adrian 2000; Straile 2002; Adrian *et al*. 2009). There have been, however, also studies suggesting that the spring dynamics of phytoplankton and zooplankton species are not necessarily accelerated in parallel (Winder and Schindler 2004a; de Senerpont Domis *et al*. 2007a). This poses the risk of a mismatch in timing of

prey availability and zooplankton reproduction, with potential detrimental effects cascading up the food chain.

To anticipate phenology shifts under future climate warming and to assess the threat of predator-prey mismatch, a mechanistic understanding of the spring dynamics of plankton is required. Early studies investigating climate impacts on plankton phenology have been purely observational. Important mechanistic insights are beginning to emerge based on controlled experiments in laboratory microcosms (e.g., Nicklisch *et al*. 2008) as well as mesocosms, which have the advantage of better simulating natural conditions (e.g., Berger *et al.* 2007; Sommer *et al*. 2007). Modelling the effect of climate warming on phytoplankton spring blooms in lakes and reservoirs is another important approach to gain a better mechanistic understanding of the processes involved (e.g., Tirok and Gaedke 2007, Peeters *et al*. 2007a). However, few of these modelling studies have dealt with shallow lakes so far, where mechanisms underlying the phytoplankton spring dynamics are known to differ substantially from deep lakes (see however Scheffer *et al*. 2001; Elliott *et al*. 2006). The modelling approaches used in this thesis shed some light on these mechanisms and offer promising avenues for phenology projections under future climate warming yet to be undertaken.

Summer heat wave impact on phytoplankton—What we consider extreme summer heat today could become average conditions by the end of this century in many regions of the globe (Schär *et al*. 2004; Battisti and Naylor 2009). The impact of past heat wave events on lakes therefore provide us with the opportunity to study how these aquatic ecosystems could evolve under future climate change. Central Europe has experienced extreme summer heat in recent years, most prominently in 2003, which has strongly affected freshwater ecosystems (Jankowski *et al*. 2006; Daufresne *et al*. 2007; Wilhelm and Adrian 2007, 2008).

The seasonal succession of plankton in lakes has been shown to be influenced not only by the magnitude of temperature changes but also by their timing within the season (Adrian and Straile 2000; Gerten and Adrian 2002, Wagner and Benndorf 2007). This is to be expected for species with complex life-cycles,

whose stages are known to be differentially sensitive to temperature (Moore *et al*. 1996; Chen and Folt 2002). It might also stem from interactions between temperature and other environmental factors (Giebelhausen and Lampert 2001), in particular food availability and predation, which are of varying importance in the course of the year (Sommer *et al*. 1986). The strong temperature anomalies occurring during heat waves make these extreme events particularly suitable opportunities to study the effects of different temporal patterns of warming on lakes.

Due to their preference for high water temperatures and stable thermal stratification, as generally prevailing under heat wave conditions, cyanobacteria are often considered to be favoured by summer hot spells (Paerl and Huisman 2008). Heat waves have been recorded to increase the risk of cyanobacteria bloom formation in some lakes (Jöhnk *et al*. 2008). However, whether this is a general trend to be expected remains controversial; e.g., Wagner and Adrian (2009) have recently demonstrated that the response of cyanobacteria to prolonged and intensified stratification in a shallow lake is strongly species-specific and depends on whether critical thresholds of nutrient (phosphorus and nitrogen) concentrations have been passed. Despite the generally assumed resistance of cyanobacteria to grazing, a few studies have also suggested that food web interactions, susceptible to be strongly affected by heat waves as well, can become decisive for bloom triggering (Vanni *et al*. 1990; Sarnelle 2007). Taking the detailed seasonal pattern of meteorological forcing and potential food web interactions into account, this thesis allows to narrowing down specific circumstances under which future global warming is likely to favour cyanobacteria blooms in shallow lakes.

0.2 Data basis, objectives and outline of thesis

Data basis—This thesis focuses on two types of phytoplankton blooms that are typically observed in nutrient-rich, temperate lakes during the course of the season (Sommer *et al*. 1986): diatom spring blooms and cyanobacteria summer blooms (Fig. 0.1). While I concentrated on issues of bloom timing (phenology) in spring (chapter 1 and 2), I was mainly interested in the magnitudes of blooms in summer (chapter 3). The climate impact on summer zooplankton populations

were also investigated (chapter 4), because food web interactions were revealed as potential drivers of phytoplankton bloom formation.

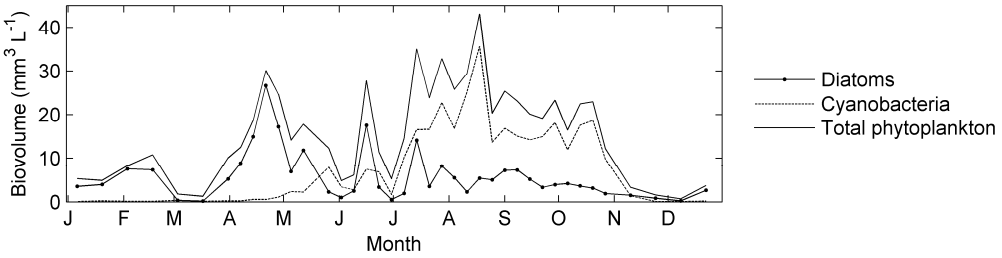

Fig. 0.1. Typical seasonal succession of phytoplankton in eutrophic lakes of the temperate zone. The spring bloom of phytoplankton is dominated by diatoms; cyanobacteria contribute most to summer blooms. Source: Müggelsee (Fig. 0.2); data of 1986 (this year was chosen because succession patterns were especially representative of eutrophic lakes).

Except for chapter 2, all analyses were based on a long-term data set of physical, chemical and biological variables, which has been established at a shallow, polymictic lake in north-eastern Germany (Müggelsee, Fig. 0.2) since 1979. During the last three decades the lake has experienced a trend of rising air and water temperatures (Fig. 0.3 a,b) while also undergoing a change from extremely high nutrient loading (hypertrophic phase) to reduced, yet still elevated nutrient supply (eutrophic phase) (Fig. 0.3 c).

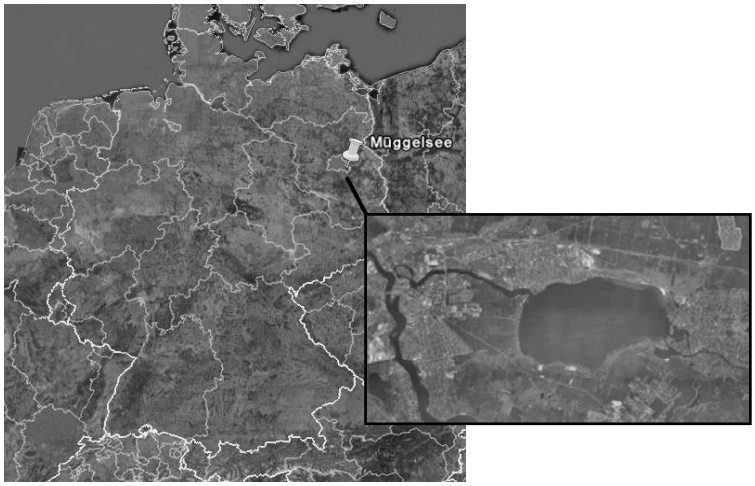

Fig. 0.2. Geographical location of study site Müggelsee (52°26'N, 13°39'E) in north-eastern Germany. Source: Google Earth 2009.

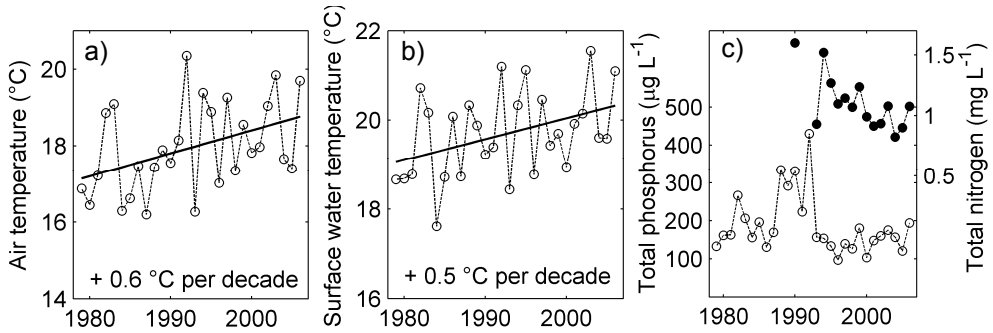

Fig. 0.3. Simultaneous change in climatic conditions and trophic state at Müggelsee. Inter-annual variability and long-term trends of mean summer (June-August) a) air temperature b) surface water temperature and c) total concentrations of phosphorus and nitrogen. Source: Panels a and b-c are based on daily measurements from nearby meteorological station Schönefeld and weekly water temperature measurements from Müggelsee, respectively.

Objectives—The dataset of Müggelsee, exceptional for its long temporal coverage, comprehensiveness and documentation of multiple environmental changes, provided me with the opportunity to study the following *overarching* research questions (for an overview on how these relate to the general concepts introduced in section 0.1 see Fig. 0.4)

Concerning the spring situation:

(1) How does a change in nutrient loading to lakes (change in trophic state) modify climate induced phenology shifts of phytoplankton in spring?

(2) Which mechanisms underlie the advancement of the phytoplankton spring bloom observed as a response to winter and spring warming; and which processes need to be incorporated into phenology models?

(3) Is there a risk that climate change triggers a de-synchronization of phytoplankton-zooplankton interactions (mismatch) in spring?

Concerning the summer situation:

(4) Are cyanobacteria blooms generally favoured by summer heat wave conditions in nutrient-rich, shallow lakes?

(5) Does the seasonal pattern of meteorological forcing determine the effect of heat waves on cyanobacteria, possibly via effects on thermal stratification and/or food web interactions?

(6) Is climate change likely to counteract successfully implemented measures to contain eutrophication and to suppress cyanobacteria blooms?

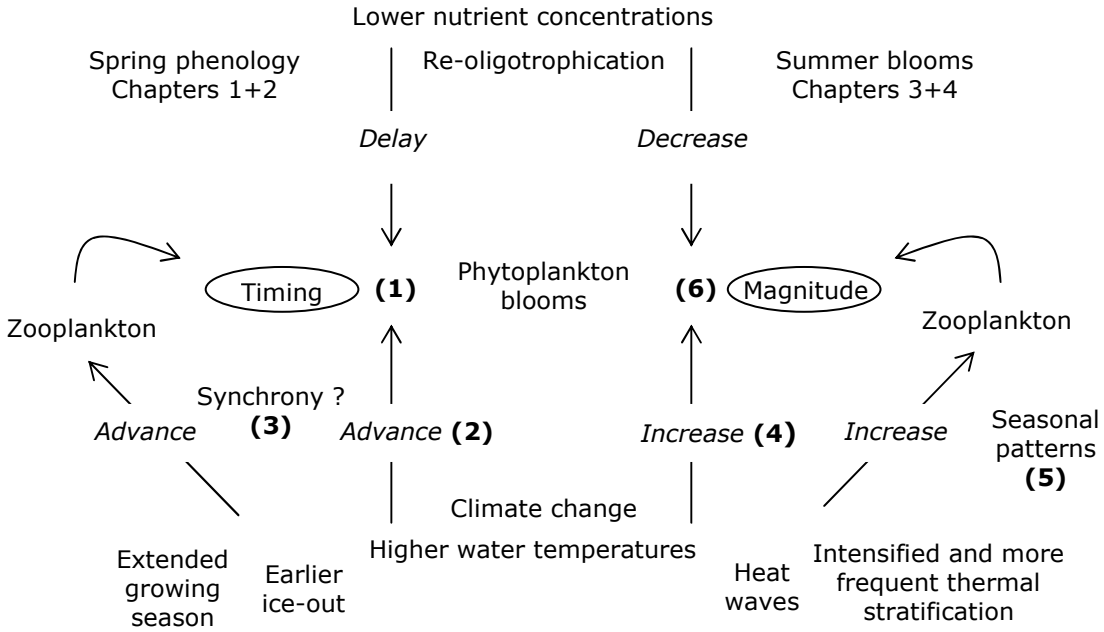

Fig. 0.4. Overview of main processes and overarching research questions (bold numbers; see text) investigated in this thesis. Presumable effects of climate change and re-oligotrophication on timing and magnitude of phytoplankton blooms are marked italic. For corresponding conclusions drawn from the results of this thesis see section 5.5 (p. 128)

Outline—The specific research questions addressed and methods applied are outlined as follows:

In **chapter 1**[1], I investigated the reasons for the relative delay of the timing of the diatom spring bloom after ice-free warm winters in recent years at Müggelsee, compared to previous years of similar meteorological conditions. Following the hypothesis that climatic conditions and trophic state were both influential I disentangled the effects of these simultaneous environmental changes on the diatom spring phenology. The analysis used a newly constructed

[1]Published as Huber V., R. Adrian & D. Gerten (2008). Phytoplankton response to climate warming modified by trophic state. *Limnology and Oceanography,* **53**, 1-13.

process-based model, which was forced by observed meteorological variables. It allowed simulating the diatom spring population together with dynamics of most important nutrients (phosphorus and silicate) and the major zooplankton grazers (*Daphnia*).

A novel approach to model seasonally forced predator-prey dynamics was employed in **chapter 2**[2]. In contrast to the process-based model applied in chapter 1 this model framework can be tackled analytically and allows general predictions on predator-prey phenology as a function of growing-season length. Controlled laboratory experiments with a zooplankton-phytoplankton system were undertaken to parameterize the model and quantitatively test predictions.

The starting point of my investigations in **chapter 3**[3] was that, contrary to expectations, cyanobacteria biovolume remained at an all record-low during the heat wave summer of 2003 at Müggelsee. This observation was contrasted with the heavy proliferation of cyanobacteria during the summer of 2006, which was also marked by anomalously hot weather. I used results of classification tree analysis to identify crucial factors explaining the observed contrast in cyanobacteria development. Findings pointed to the importance of seasonal patterns of meteorological forcing and resulting differences in the thermal stratification regime. It also became apparent that some zooplankton species had reached exceptionally high abundances during the heat wave summer of 2003, potentially contributing to the suppression of cyanobacteria.

These latter results motivated the analyses documented in **chapter 4**[4]. The objective was to identify seasonal periods during which temperature changes were crucial for the summer development of cyclopoid copepods and bosminids. Based on this knowledge, I aimed at better understanding the differing impact of recent heat wave events (2003, 2006 and 2007) on these two zooplankton groups. Linear regressions of moving averages allowed screening the seasonal

[2]Published as Steiner C.F., A.S. Schwaderer, V. Huber, C.A. Klausmeier & E. Litchman (2009). Periodically forced food chain dynamics: model predictions and experimental validation. *Ecology*, **90**, 3099-3107

[3]In revision for *Global Change Biology* as Huber V., C. Wagner, D. Gerten & R. Adrian. To bloom or not to bloom: Contrasting development of cyanobacteria during the European heat waves of 2003 and 2006 in a shallow lake.

[4]In revision for *Freshwater Biology* as Huber V., D. Gerten & R. Adrian. A matter of timing: heat wave impact on crustacean zooplankton.

dynamics of zooplankton, water temperature and other environmental factors for periods of highest correlations.

In the general discussion and concluding section, I discuss how the main results of this thesis contribute to answering the overarching research questions raised here, and how some of the analyses could be carried on to further improve the proposed answers to these questions.

Chapter 1

Phytoplankton response to climate warming modified by trophic state

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Published as Huber V., R. Adrian and D. Gerten (2008) Phytoplankton response to climate warming modified by trophic state. *Limnology and Oceanography*, **53**(1): 1-13.

1.1 Abstract

We investigated the combined effect of reduced phosphorus supply and warmer winter and spring conditions on the diatom spring bloom of a shallow lake. Simulations with a simple dynamic model indicated that reduced ice cover and increasing water temperatures resulted in a more intense and earlier bloom independently of phosphorus concentrations. However, whereas the collapse of the bloom was caused by silicate limitation under high phosphorus supply, it was caused by Daphnia grazing under reduced phosphorus supply. This switch from a bottom-up to a top-down driven collapse of the diatom spring bloom explains why, despite similarly mild winters, the bloom was observed earlier under high than under reduced phosphorus supply in the lake studied. Thus, an assessment of possible changes in nutrient loading is crucial when anticipating how phytoplankton could evolve under future climate warming.

1.2 Introduction

Increasing anthropogenic pressure requires a better understanding of how ecosystems react to multiple environmental stressors. During the last decades many freshwater systems were subject to both a changing climate and changes in trophic state due to reduced nutrient supply (Jeppesen *et al*. 2005). Yet, most analyses of long-term data of these systems focused either on the effect of climate change or on the effect of changes in trophic state. Few studies have tried to disentangle the combined effect of rising temperatures and changing nutrient supply on freshwater ecosystems (e.g., Horn 2003; Elliott *et al*. 2006).

Abiotic factors, influenced by climatic conditions and trophic state, are the primary drivers of phytoplankton succession in spring (Sommer *et al*. 1986). In lakes of the temperate zone, the phytoplankton spring bloom is predominantly initiated by increasing light availability (Sommer 1994), which is directly determined by solar radiation and day length and also indirectly depends on specific lake features such as water transparency and depth. In deep lakes, phytoplankton starts growing once strong mixing ceases and phytoplankton is no longer constantly transported out of the euphotic zone (Peeters *et al*. 2007a). In many shallow lakes, the phytoplankton spring bloom is initiated once the ice-cover melts, inducing a change in the underwater regime of light and turbulence (Adrian *et al*. 1999; Weyhenmeyer *et al*. 1999).

With the exception of very nutrient-rich lakes where grazer-resistant algae dominate early in the year, the phytoplankton spring bloom then collapses leading to a biomass minimum in late spring/early summer called the clear water phase (Sommer *et al*. 1986). The collapse of the phytoplankton spring bloom is attributed to different environmental factors. First, many studies have shown that zooplankton grazing rates (mainly by Daphnia) often exceed algal production rates in early summer, thus producing the clear water phase (Lampert *et al*. 1986). Second, nutrient limitation (potentially combined with increasing sinking losses) can induce a collapse of the phytoplankton bloom before grazing becomes important (Lund 1950; Smayda 1971). And third, a sharp increase in sinking losses due to the onset of stratification can also cause

the collapse of the algal bloom if stable summer stratification develops in moderately deep lakes (Winder and Schindler 2004b).

In lakes across the northern hemisphere, climate warming has induced forward shifts in the timing of the phytoplankton spring maximum and the clear water phase (Gerten and Adrian 2000; Straile 2002). On the one hand, these phenology shifts have been attributed to a direct effect of increased water temperatures on zooplankton grazers (Straile and Adrian 2000) and to a lesser extent to a direct effect of increased water temperatures on phytoplankton growth (Adrian *et al*. 1999). On the other hand, warming more indirectly affects the phytoplankton spring bloom through its effect on ice cover and the lake mixing regime (Adrian *et al*. 1999; Winder and Schindler 2004b; Peeters *et al*. 2007a). Furthermore, it is a classical result from eutrophication studies that in many lakes annual (or seasonal) phytoplankton biomass is correlated to annual (seasonal) phosphorus loading (Vollenweider and Kerekes 1982; Jeppesen *et al*. 2005). In addition to the effect of nutrient availability on phytoplankton productivity, trophic state is also known to affect the phytoplankton succession patterns, including the timing of the phytoplankton spring bloom (Sommer 1994).

Disentangling the effect of climate and nutrients on phytoplankton growth has proved challenging in the past. In a study of the effect of re-oligotrophication on the phytoplankton growth in a drinking water reservoir, Horn (2003) found that phytoplankton biomass did not decrease despite falling nutrient concentrations and hypothesized that this was because of a change in spring overturn duration dependent on weather conditions. In a modelling study, Elliott *et al*. (2006) showed that the phytoplankton spring peak always occurred earlier under higher temperatures, but it was species-specific as to whether increasing nutrient concentrations delayed the peak or advanced it further. When Scheffer *et al*. (2001) stated that the probability of a clear water phase increases with the temperature of a lake, a controversy arose as to whether they had sufficiently accounted for changes in the trophic state (and management regimes) of the lakes studied (Jeppesen *et al*. 2003; Scheffer *et al*. 2003;Van Donk *et al*. 2003).

The shallow lake studied here, Müggelsee, provides an opportunity to gain a better understanding of the combined effect of climate warming and changes in

trophic state on the phytoplankton spring development. The lake experienced a reduction of more than 50% in both total phosphorus and total nitrogen loading from a hypertrophic period, 1979–1990, to a eutrophic period, 1997–2003 (Köhler *et al*. 2005). In spring, phytoplankton is dominated by diatoms in this lake, and phosphorus and silicate are the potentially limiting factors, whereas nitrogen limitation most likely only plays a role in the summer (Köhler *et al*. 2000; Köhler *et al*. 2005). Climate-induced changes of physical lake features and resulting phenology shifts in the plankton community are well documented for this lake (Adrian *et al*. 1999; Straile and Adrian 2000). In particular, a forward shift of the phytoplankton spring bloom of about 1 month was found concurrently with earlier ice break-up dates from 1979–1987 to 1988–2003 (Gerten and Adrian 2000; Adrian *et al*. 2006). However, although ice break-up dates were generally a good predictor of the timing of the phytoplankton spring bloom, the bloom occurred relatively late in recent mild years with early ice-out.

In this study, we asked whether the climate signal detected in the phytoplankton time series was altered by decreasing phosphorus loading to the lake. Specifically, we investigated whether the relative delay of the phytoplankton spring bloom in recent years could be attributed to the observed change in trophic state. Based on long-term data (1979–2005) of physical, chemical, and biological variables, we constructed a deterministic model that simulates the dynamics of diatom biovolume, the potentially limiting nutrients (silicate and phosphorus), and Daphnia grazing in winter and spring. Using this model, we performed simulation experiments to explore how increased water temperatures and reduced ice cover affected the timing and intensity of the diatom spring bloom under conditions of high and reduced phosphorus loading (hypertrophic and eutrophic phase). These model simulations suggested a switch in bloom collapse mechanisms, rendering the phytoplankton response to climate warming strongly dependent on trophic state.

1.3 Methods

Study site—Müggelsee is a shallow, polymictic lake situated in the southeast of Berlin (52°26'N, 13°39'E). It spans an area of 7.3 km^2 with a mean depth of 4.9 m and a maximum depth of 7.9 m. The lake is moderately flushed by the river

Spree with a retention time of approximately 6–8 weeks (Köhler *et al*. 2005). The climate at this lake is governed by maritime and continental influences. Winter climate shows a high degree of inter-annual variability, with the monthly mean air temperature in January, the coldest month, varying within the approximate range of -7°C to +5°C (Adrian and Hintze 2000). Ice-cover duration varied between 0 days and 125 days in 1979–2005 with an average ice cover of 43 ± 33 SD days. Additional information on physical and limnological characteristics of Müggelsee is documented in Driescher
et al. (1993).

Data basis—From 1979 to 2005, water samples for nutrient and plankton analysis were taken weekly during the growing season and biweekly during winter. A detailed description of the sampling methodologies and sample processing is given in Gerten and Adrian (2000). Time-series of aggregated biovolume of total phytoplankton and aggregated biovolume of diatoms (Bacillariophyceae) were used in this study. For model development, we focussed on diatoms because these constituted about 81 % of total phytoplankton biovolume in Müggelsee during the spring peak (Fig. 1.1A). As grazers, only daphnids (mainly *Daphnia galeata*, *Daphnia hyalina*, *Daphnia cucullata*, and their hybrids) were considered in the model, however, other zooplankton groups (ciliates, cyclopoid, and calanoid copepods) were accounted for in a supplementary screening of factors that potentially influence the phenology of diatoms. Long-term records of physical factors (water temperature, ice cover, global radiation, light extinction) and weekly measurements of nutrients (total phosphorus concentration [TP] and dissolved silicate concentration [DSi]) were used as forcing variables in the model or for the purpose of parameter estimation (cf. Table 1.1). Water temperatures were hourly means (8 - 9 h) recorded daily near the lake surface at 0.3 m depth (from September 2002 onwards at 1–2 m depth during winter and at 0.5 m during spring and summer). Ice cover was assessed daily categorizing whether the lake was fully (>80 % of the lake surface) or partially covered with ice. Long-term records of mean daily global radiation were provided by Deutscher Wetterdienst for the station in Potsdam (52°04'N, 13°06'E) for 1979–2002; from 2003–2005 records from a

measurement station at the shore of Müggelsee were used. Incident photosynthetically available radiation (PAR) was considered to be 43% of global radiation. This was based on the assumption that on average 7% of global radiation are reflected at the water surface (estimated from measurements at Müggelsee in spring 2002, 2004, 2005, n=262) and that 46% of global radiation are photosynthetically available (Köhler *et al*. 2000). Light extinction coefficients were estimated based on light measurement in the water column (0-5 m) during 1993 – 2003 and transmittance through ice was assessed using measurements in the winter of 1995/1996.

Definition of phenology events—Ice-out date was defined as the week (or day of the year for model analysis) when the lake was free of all ice in spring. The *timing of the diatom spring bloom* was defined as the week (day of the year) when maximal biovolume of diatoms was observed after ice-out in spring. In years when several local maxima were observed (occurring in 6 out of 27 years) the timing of the highest peak was considered. The maximal biovolume was considered as the *magnitude* of the bloom. Also, we defined the *end* of the bloom as the week (day of the year) when minimal diatom biovolume was observed after the spring peak. This coincided with the clear water phase (defined as time of highest Secchi depth in late spring) during most years. We defined the *intensity* of the bloom as the mean biovolume from the beginning of the year until the end of the bloom. The timing of the *Daphnia* spring peak was defined as the first, clearly distinguishable maximum in spring (with densities >= 68 ind L^{-1}).

Model core—The spring diatom phenology model used here builds upon a phytoplankton growth model for a closed system proposed by Diehl *et al*. (2005) and modified according to an approach used by Klausmeier *et al*. (2004). It is a point-like model based on the assumption that the whole water column is well-mixed and phytoplankton is homogenously distributed in the water column, which is realistic for shallow, polymictic Müggelsee in spring. Our model is constructed in order to simulate diatom dynamics in winter and spring only (Jan – mid-Jun). The core of the model consists of four differential equations (Eqs. 1-4) describing changes in diatom biovolume and the dynamics of the potentially

limiting nutrients phosphorus and silicate (definitions and units of state variables, parameters, and forcing variables are summarized in Table 1.1).

$$\frac{dA}{dt} = \left(\mu(T,I,Q,Si) - \left(\frac{v}{z} + F_D(T) c_D D \right) \right) A \quad (1)$$

$$\frac{dQ}{dt} = \rho_{\max} F_A(T) \frac{P}{H_P + P} - \mu(T,I,Q,Si) Q \quad (2)$$

$$\frac{dP}{dt} = r_P \left(P_{tot} - P - QA \right) - \rho_{\max} F_A(T) \frac{P}{H_P + P} A \quad (3)$$

$$\frac{dSi}{dt} = r_{Si} \left(S_{tot} - Si - Q_{Si} A \right) - A Q_{Si} \mu(T,I,Q,Si) \quad (4)$$

Biovolume concentration of diatoms A (mm^3 L^{-1}) increases through temperature, light, and nutrient dependent growth (integrating all internal processes such as primary production, respiration, exudation, and lysis) and decreases through sedimentation and temperature dependent *Daphnia* grazing. Sedimentation loss rate was calculated as the ratio of sinking velocity v (m day^{-1}) to mixing depth z (m). For simplicity, we assumed that filtration rates are independent of prey density (type I functional response) so that *Daphnia* grazing loss rate is the product of clearance rate c_D (L ind^{-1} day^{-1}) and *Daphnia* density D (ind L^{-1}).

The temperature dependence of grazing and other *Daphnia* related process rates (see below) were described by the Q_{10}-rule:

$$F_D(T) = 2^{\left(\frac{T - T_{ref}}{10°C} \right)} \quad (5)$$

where T (°C) is the seasonally changing water temperature and T_{ref} (°C) is the reference temperature. This is an experimentally backed approach (Norberg and DeAngelis 1997), commonly used in minimal models of phytoplankton-zooplankton interaction (Scheffer *et al*. 2001; Peeters *et al*. 2007a). The algal growth rate, which is dependent on water temperature, light intensity I (W m^{-2}), silicate concentration Si (mg L^{-1}), and phosphorus cell quota Q (µg P mm^{-3}), was calculated as

$$\mu(T,I,Q,Si) = \mu_{\max} F_A(T) L_1(T,I) \min\left(L_2(Si), L_3(Q) \right) \quad (6)$$

where $\mu_{\max}$ (day^{-1}) is the maximum specific growth rate, L_1, L_2, and L_3 are

Table 1.1 State variables, parameters, and forcing variables for the diatom phenology model. *: forcing variables; **: parameters varied in the robustness test (cf. methods); values in brackets: parameter intervals used during calibration (if available from the literature as indicated); conversion factor for carbon content of algal biovolume used: 0.12 mg C mm^{-3} (Rocha and Duncan 1985).

Symbol	Definition	Unit	Default value	Source
A	Diatom biovolume	$mm^3\ L^{-1}$	—	—
μ_{max}	Maximum per capita growth rate	day^{-1}	0.94** (0.7-2.4)	calibrated (Andersen 1997)
z	Mixing depth = mean lake depth	m	4.9	Driescher *et al*. 1993
Ice*	Ice cover	dimensionless	—	—
P	Concentration of dissolved phosphorus available to diatoms	$\mu g\ L^{-1}$	—	—
H_P	Half-saturation constant of phosphorus uptake	$\mu g\ L^{-1}$	60** (5-60)	calibrated (Bowie *et al*. 1985)
Q	Phosphorus cell quota (P : biovolume)	$\mu g\ P\ mm^{-3}$	—	—
Q_{max}	Maximum phosphorus cell quota	$\mu g\ P\ mm^{-3}$	6.7** (1-7.5)	calibrated (Sommer 1994; Diehl *et al*. 2005; Andersen 1997)
Q_{min}	Minimum phosphorus cell quota	$\mu g\ P\ mm^{-3}$	0.5	Köhler *et al*. 2000; Diehl *et al*. 2005
ρ_{max}	Maximum phosphorus uptake rate	$\mu g\ P\ mm^{-3}\ day^{-1}$	4.9** (0.2-12)	calibrated (Arhonditsis and Brett 2005; Bowie *et al*. 1985)
r_P	Recycling rate of detrital phosphorus	day^{-1}	0.38** (0.05-0.5)	calibrated
P_{tot}	Maximal concentration of phosphorus	$\mu g\ L^{-1}$	—	independent estimation (cf. methods)
Si	Concentration of dissolved silicate	$mg\ L^{-1}$	—	—
H_{Si}	Half-saturation constant of silicate limited algal growth	$mg\ L^{-1}$	0.035** (0.03-0.5)	calibrated (Sommer 1994)
Q_{Si}	Silicate cell quota (Si:biovolume)	$mg\ Si\ mm^{-3}$	0.047** (0.03-0.1)	calibrated (Arhonditsis and Brett 2005; Sommer 1991)
r_{Si}	Recycling rate of sedimented silicate	day^{-1}	0.01	Lampert and Sommer 1999
Si_{tot}	Maximal concentration of silicate	$mg\ L^{-1}$	—	independent estimation (cf. methods)
I_0*	Incident light intensity: 43 % of daily global radiation	$W\ m^{-2}$	—	—
k_{ice}	Transmittance through ice	dimensionless	0.2	independent estimation (data of 1996)
H_I	Half-saturation constant of light limited algal growth	$W\ m^{-2}$	3.2** (0.2-8)	calibrated (Bowie *et al*. 1985)
K_{bg}	Background light extinction coefficient in the water column	m^{-1}	0.89	independent estimation (cf. methods)
k_A	Biomass specific light extinction coefficient	$L\ mm^{-3}\ m^{-1}$	0.07	independent estimation (cf. methods)
v	Sinking velocity of diatoms	$m\ day^{-1}$	0.65	Schellenberger *et al*. 1983
T*	Water surface temperature	°C		—
T_{ref}	Reference temperature	°C	20	—
T_{opt}	Optimal temperature for diatom growth kinetics	°C	20	Arhonditsis and Brett 2005
kT_A	Temperature constant for diatom growth kinetics	$°C^{-2}$	0.004	Arhonditsis and Brett 2005
D	Density of *Daphnia*	$ind\ L^{-1}$	—	—
M	Density-dependent mortality of *Daphnia*	day^{-1}	—	—
c_D	Clearance rate of *Daphnia*	$L\ ind^{-1}\ day^{-1}$	0.005	Wetzel 2001 and references cited therein
f	Fecundity parameter of *Daphnia* (surviving eggs/fertile individuals)	dimensionless	4.6 (0.1-9)	calibrated
τ	Relaxation time of density-dependent mortality of *Daphnia*	day	1 (1-45)	calibrated
m_D	Mortality parameter of *Daphnia*	$(ind\ L^{-1})^{-dd}\ day^{-1}$	0.52 (0.1-1)	calibrated
dd	Exponent for density-dependent mortality of *Daphnia*	dimensionless	0.23 (0.1-1)	calibrated

limitation functions described below and $F_A(T)$ is the temperature function used for diatom growth constants and process rates. For the latter we adopted the optimum curve suggested by Arhonditsis and Brett (2005)

$$F_A(T) = \exp\left(-kT_A\left(T - T_{opt}\right)^2\right) \quad (7)$$

where kT_A (°C $^{-2}$) describes the strength of the temperature effect and T_{opt} (°C) is the optimal temperature for diatom growth processes. Co-limitation of several resources was accounted for by using Liebig's minimum function for phosphorus and silicate that are considered strictly essential resources (Tilman 1982). Light was assumed to be an interactive essential resource (Rhee and Gotham 1981; Post *et al*. 1985), and, therefore, a multiplicative approach was adopted. Extinction was calculated according to the Lambert-Beer law including self-shading of algae. Based on this, mean underwater light intensity I (W m^{-2}) was determined by integrating over mixing depth:

$$I = \frac{1}{z}\int_0^z I_0 \exp\left(-(K_{bg} + k_A A)s\right) ds = \frac{I_o\left(1 - \exp\left(-(K_{bg} + k_A A)z\right)\right)}{(K_{bg} + k_A A)z} \quad (8)$$

where K_{bg} (m^{-1}) is the background extinction coefficient, and k_A (L mm^{-3} m^{-1}) the diatom biovolume specific extinction coefficient. The incident light I_0 (W m^{-2}) was reduced to $k_{ice}I_0$ when the lake was at least partially ice-covered. Light limitation of diatom growth was modelled using a Monod-approach:

$$L_1(T, I) = \frac{I}{F_A(T)H_I + I} \quad (9)$$

where H_I (W m^{-2}) is the half-saturation constant for light-limited growth, which is assumed to change with temperature. This temperature dependency of H_I assures that strongly light-limited growth is temperature independent (the initial slope of the hyperbolic curve is constant), as suggested by empirical studies of the interaction of light and temperature on algal growth (Post *et al*. 1985). We checked that this affected the growth in colder and warmer years similarly and, thus, was not an important control for the differences between colder and warmer years. Since silicate is not stored by phytoplankton, we assumed a constant silicate cell quota Q_{Si} (mg Si mm^{-3}) and also modelled the diatom growth dependency on silicate availability with a Monod-equation (Sommer 1994):

$$L_2(Si) = \frac{Si}{H_{Si} + Si} \tag{10}$$

where H_{Si} (mg L^{-1}) is the half-saturation constant for silicate-limited growth. In contrast, growth dependency on a variable phosphorus cell quota (Q) was accounted for by using a Droop-model approach (Droop 1983), modified as suggested by Wernicke and Nicklisch (1986):

$$L_3(Q) = \left(1 - \exp\left(-(\ln 2)\left(\frac{Q}{Q_{\min}} - 1\right)\right)\right) \tag{11}$$

Here, growth is increasingly limited by phosphorus shortage ($L_3(Q)$ approaches 0) when the cell quota Q approaches the minimum cell quota Q_{min}, while phosphorus limitation decreases as Q increases ($L_3(Q)$ approaches 1). The phosphorus cell quota increases through phosphorus uptake and decreases through algal growth (Eq. 2). To model the relationship between dissolved phosphorus available to diatoms P (μg L^{-1}) and uptake rate, we applied Michaelis-Menten kinetics, where ρ_{max} (μg P mm^{-3} day^{-1}) is the maximal phosphorus uptake rate and H_P (μg L^{-1}) the half-saturation constant for phosphorus uptake (Eqs. 2 and 3).

Phenomenological approach to nutrient dynamics—The concentration of dissolved phosphorus available to diatoms increases through recycling of detrital phosphorus with a recycling rate of r_P (day^{-1}) and decreases through phosphorus uptake (Eq. 3). Instead of explicitly considering the processes that lead to the recycling of nutrients such as the remineralization of phosphorus trapped in sedimented algae and the cycling of phosphorus through grazing, we chose a phenomenological approach and considered a closed system with a maximal phosphorus concentration of P_{tot} (μg L^{-1}). We neglected all phosphorus potentially stored in grazers, so that the pool of recyclable phosphorus could be calculated as the phosphorus, which was neither dissolved in the water column nor included in algae (P_{tot} - P - QA). To estimate the maximal phosphorus concentration potentially available to diatoms (P_{tot}), we used an empirical relationship based on diatom and phosphorus data measured during winter and spring 1979-2005. In fact, the annual mean diatom biovolume between the beginning of the year and the end of the bloom (A_{bloom}) and the annual mean total

phosphorus concentration during the same period (TP_{bloom}) showed a significant linear relationship:

$$A_{bloom} = 0.14\ TP_{bloom} - 7.37 \qquad (n=27,\ R^2=0.64,\ p<0.001) \qquad (12)$$

We then assumed that a fixed amount of phosphorus (given by the interception of the regression line with x-axis TP^*=52 μg L^{-1}) was locked in other compartments (such as bacteria, other phytoplankton species, zooplankton, and phosphorus bound to iron or calcite) and not available to diatoms. Thus, we calculated the maximal phosphorus concentration (P_{tot}) available to diatoms each year as the difference between TP_{bloom} and TP^*.

In a similar approach, dissolved silicate was assumed to increase through the recycling of sedimented silicate with a recycling rate of r_{Si} (day^{-1}) and to decrease through growth of diatoms with a fixed silicate cell quota Q_{Si} (Eq. 4). The pool of recyclable silicate was calculated analogous to the pool of recyclable phosphate ($Si_{tot} - Si - Q_{Si}A$), with the difference that the maximal silicate concentration (Si_{tot}) in the model was estimated as the maximal concentration of DSi observed in Müggelsee for each year.

The Daphnia sub-model—Several studies have found that the development of *Daphnia* biomass in spring is driven primarily by temperature and relatively independent of food availability (Straile and Adrian 2000; Gerten and Adrian 2000; Benndorf *et al*. 2001). When food becomes limiting in late spring and early summer other algal groups besides diatoms (mainly Cryptophyceae and Chlorophyceae) contribute to *Daphnia* food in Müggelsee. We, therefore, did not couple *Daphnia* to simulated diatom biovolume and included possible food limitation of *Daphnia* later in the season only implicitly through density-dependent mortality. (In fact, the phenomenological approach presented here resulted in a better model performance than a classical predator-prey approach, with *Daphnia* coupled to diatoms.) Density-dependent mortality M (day^{-1}) was simulated using a general formulation adopted from Tirok and Gaedke (2007):

$$\frac{dM}{dt} = \frac{1}{\tau}\left(m_D D^{dd} - M\right) \qquad (13)$$

where m_D ((ind $L^{-1})^{-dd}$ day^{-1}) and dd (dimensionless) modulate the strength of the density-dependent mortality and τ(day) corresponds to a relaxation time.

Reproduction was calculated as a function of temperature dependent egg development time $dev(T)$ (day) based on the empirical relationship given by Bottrell *et al*. (1976):

$$dev(T) = \exp\left(3.3956 + 0.2193\ln(T) - 0.3414\left(\ln(T)\right)^2\right) \quad (14)$$

Using a fecundity parameter f (dimensionless), which roughly combines the proportion of reproductively active individuals in the population with the number of eggs per individual, the rate of change in *Daphnia* population density D (ind L^{-1}) was then calculated following Eq. 15:

$$\frac{dD}{dt} = \left(\frac{f}{dev(T)} - F_D(T)M\right)D \quad (15)$$

where $F_D(T)$ corresponds to the Q_{10} rule (Eq. 5).

Model initialization—Since our model did not allow simulating the whole annual cycle, it had to be initiated each year. Initial values for diatom biovolume concentration A_0 were the mean of the last observation in the previous year and the first observation in the current year. The phosphorus cell quota Q was initially set to the maximal cell quota Q_{max}. The initial concentration of dissolved phosphorus available to diatoms P_0 (dissolved silicate Si_0) was calculated as the difference between the maximal phosphorus (silicate) concentration P_{tot} (S_{tot}) and phosphorus (silicate) initially stored in diatoms A_0Q_{max} (A_0Q_{Si}). Initial values for *Daphnia* densities D_0 corresponded to first observations of each year, and density-dependent mortality M was set to the steady state condition $m_D D_0^{dd}$.

Parameter calibration, model validation, and robustness against changes in parameters—Part of the parameter values were independently estimated from the data or directly taken from the literature (as indicated in Table 1.1). The other parameters (four parameters of the *Daphnia* sub-model and eight parameters of the core model describing the algal-nutrient dynamics) were calibrated, if possible based on biologically plausible intervals as documented in the literature (cf. Table 1.1). For this purpose, we split the data set into two sub-periods: 1979-1992 for calibration and 1993-2005 for validation. We used a genetic algorithm (adopted from Tietjen and Huth 2006) to efficiently search the parameter space and to find the parameter set that optimizes the fit between

the model and the data (for details on the calibration procedure see Appendix).

For model validation we assessed model performance as measured by Willmott's (1982) index of agreement (*IoA*). It describes the modelling quality with respect to the variance and the mean $(\overline{O})$ of the observations. *IoA* = 0 indicates complete disagreement between predicted (P_i) and observed values (O_i), while *IoA* = 1 indicates complete agreement:

$$IoA = 1 - \frac{\sum_{i=1}^{n}(P_i - O_i)^2}{\sum_{i=1}^{n}\left(\left|P_i - \overline{O}\right| + \left|O_i - \overline{O}\right|\right)^2} \qquad (16)$$

The index was calculated for the calibration (1979-1992) and the validation period (1993-2005) separately. The data used were (a) the observed and predicted diatom biovolume and *Daphnia* abundance (IoA_b) and b) the observed and predicted timing of the diatom and *Daphnia* spring peak (IoA_t). In the former case, we used all weekly measurements until the end of the simulation period (mid-Jun) summing over all years considered ($\overline{O}$ is not the seasonal but the long-term mean). We thereby assessed the ability of the model to reproduce the observed seasonal dynamics during winter and spring. In the latter case, calculations were based on yearly estimations of the timing of the peak.

The robustness of the model was tested by varying the calibrated parameters of the diatom model (Table 1.1) by +/- 20% as suggested by Omlin *et al*. (2001) for moderately inaccurate parameters. Timing and intensity of the simulated diatom blooms were then calculated for all of these parameter combinations (n= 1944; three parameter values were excluded that lay outside the biologically plausible interval) and the resulting distributions depicted with boxplots (Fig. 1.2 A, B).

Control run and simulation experiments—In order to assess how climate warming affected diatom spring phenology under different trophic states, we ran a number of simulation experiments. The validated model, which was forced by current environmental factors (ice cover, water temperature, global radiation, maximal phosphorus, and silicate availability) served as a control (abbreviated 'C'). Scenarios consisted of setting one or several of these environmental forcing

factors to data of extreme years while using current data for the remaining factors.

The effect of missing ice cover and increased water temperatures (warming scenario abbreviated 'W') was assessed by running the model for every year on climate data from 1990, but keeping current data of global radiation and nutrient availability. The winter and spring (Jan-May) of 1990 was exceptionally warm with average water temperatures being 1.6 °C higher than the long-term mean of 1979-2005.

Hypertrophic conditions (abbreviated 'HYP') were simulated by calculating the upper limit of phosphorus concentrations available (P_{tot}) based on the maximum of the observed mean total phosphorus concentrations in spring (TP_{bloom} = 135 μg L^{-1} in 1988, see Fig. 1.1A). Likewise, eutrophic conditions (abbreviated 'EU') were simulated based on the minimum of observed mean total phosphorus concentrations in spring (TP_{bloom} = 62 μg L^{-1} in 2001, see Fig. 1.1A). Maximum and minimum of mean total phosphorus concentrations observed in the time-series were assumed to represent two different trophic states according to Köhler *et al*. (2005). These authors classified a hypertrophic (1979-1990), transient (1991-1996) and eutrophic phase (1997-2003) at Müggelsee based on data of external and internal nutrient loading.

We also investigated the effect of silicate and the effect of *Daphnia* grazing on diatom spring phenology. Silicate limitation was turned off (abbreviated 'NSi') by fixing the silicate limitation factor at 1. *Daphnia* grazing was turned off (abbreviated 'ND') by setting the *Daphnia* grazing constant to 0. Results of simulation experiments were depicted with boxplots showing the inter-annual variability (1979-2005) of the intensity (Fig. 1.3) and timing (Fig. 1.4) of the diatom spring bloom under different scenarios. All model simulations and statistical tests were performed using Matlab 6.5 and 7.0 (MathWorks, Inc.).

1.4 Results

Diatom spring phenology—The magnitude and the timing of the diatom spring peak in Müggelsee showed a strong inter-annual variability during 1979-2005 (Fig. 1.1). While high diatom biovolumes were reached in the spring of the late

80s and early 90s, biovolumes have decreased strongly in the last decade. These changes in diatom biovolume were correlated with changes in mean total phosphorus concentrations (TP) measured in spring (Spearman's δ = 0.79, p<0.001, Fig. 1.1A).

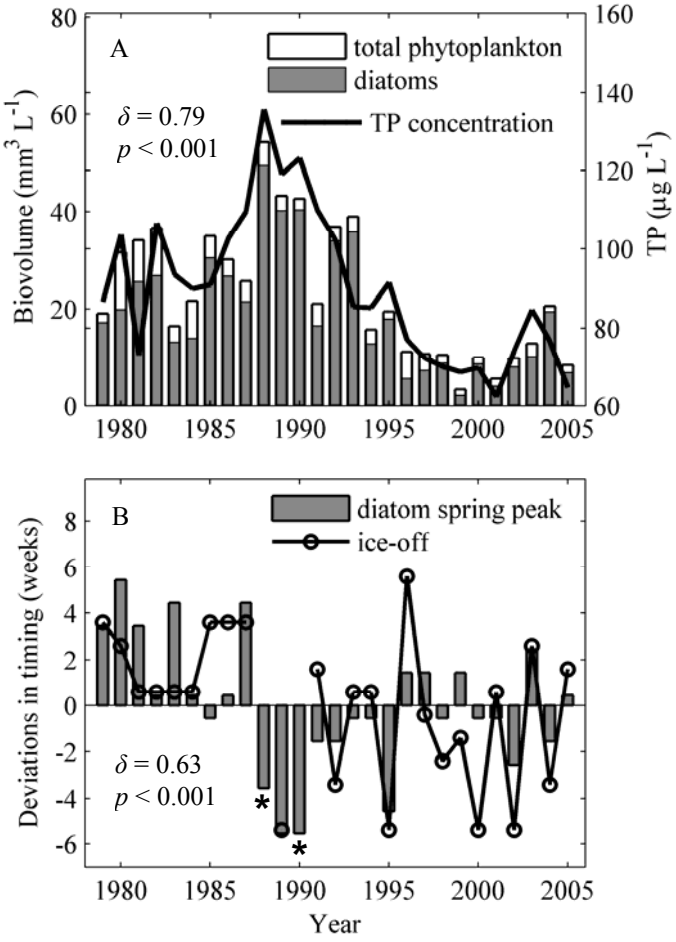

Fig. 1.1. Inter-annual variability of the (A) magnitude and (B) timing of the diatom spring peak in Müggelsee. (A) Biovolumes (mm^3 L^{-1}) of diatoms (grey bars) and total phytoplankton (open bars) in the week of the spring peak and mean total phosphorus concentrations (µg L^{-1}) until the end of the bloom (solid line). (B) Timing (week) of the diatom spring peak (grey bars) and ice-out dates (open circles) shown as departures from the long-term mean (1979-2005). Asterisks mark years with missing ice cover. Spearman's δ are given for the correlations between the magnitude of the diatom spring peak and mean total phosphorus concentrations (panel A) and the timing of the diatom spring peak and the timing of ice-out (panel B).

Moreover, the timing of the diatom spring peak showed a positive correlation with the timing of ice-out during the whole study period (δ = 0.63, p<0.001, Fig. 1.1B). Yet, while years with early ice-out or missing ice cover led to early diatom spring peaks in the late 80s and 90s (years 1988, 1989, 1990, 1995), diatom

spring peaks occurred relatively late despite early ice-out in recent years (2000 and 2002). Correlation analysis did not reveal any significant relationship between the timing of ice-out and the magnitude of the diatom spring peak (δ = 0.05, p>0.1) nor between the mean total phosphorus concentrations in spring and the timing of the diatom spring peak (δ = -0.22, p>0.1). We applied the diatom phenology model to investigate these relationships further.

Model performance and robustness against changes in parameters—The model very well predicts the intensity and timing of the diatom spring bloom in Müggelsee for the time span considered (with, respectively, 54 % and 68% of the observed inter-annual variability explained, Fig. 1.2A, B). The index of agreement indicated that the model succeeded in reproducing the timing of the diatom spring peak both during years used for calibration (1979-1992, IoA_t = 0.92) and during years used for validation (1993-2005, IoA_t = 0.85). The same was true for the model's ability to predict the overall dynamics of diatom biovolume in spring (IoA_b = 0.81 for calibration years, IoA_b = 0.66 for validation years). With the exception of a few years the model performance was relatively robust against changes in calibrated parameter values with highest uncertainty (boxplots in Fig. 1.2A, B). The large variability in the predicted timing of the diatom spring peak during some years (Fig. 1.2B) occurred when multiple peaks developed, thus, they result from the phenology definition applied. Also, the submodel well predicted *Daphnia* spring dynamics: Model performance in years that were used for validation (1993-2005, IoA_t = 0.69, IoA_b = 0.74) was about the same as model performance in years that were used for calibration (1979-1992, IoA_t = 0.73 , IoA_b = 0.79). The timing of the *Daphnia* spring peak and therefore also the onset of the grazing impact on diatoms was sufficiently well reproduced by the model (with 44 % of the observed inter-annual variability explained, Fig. 1.2C).

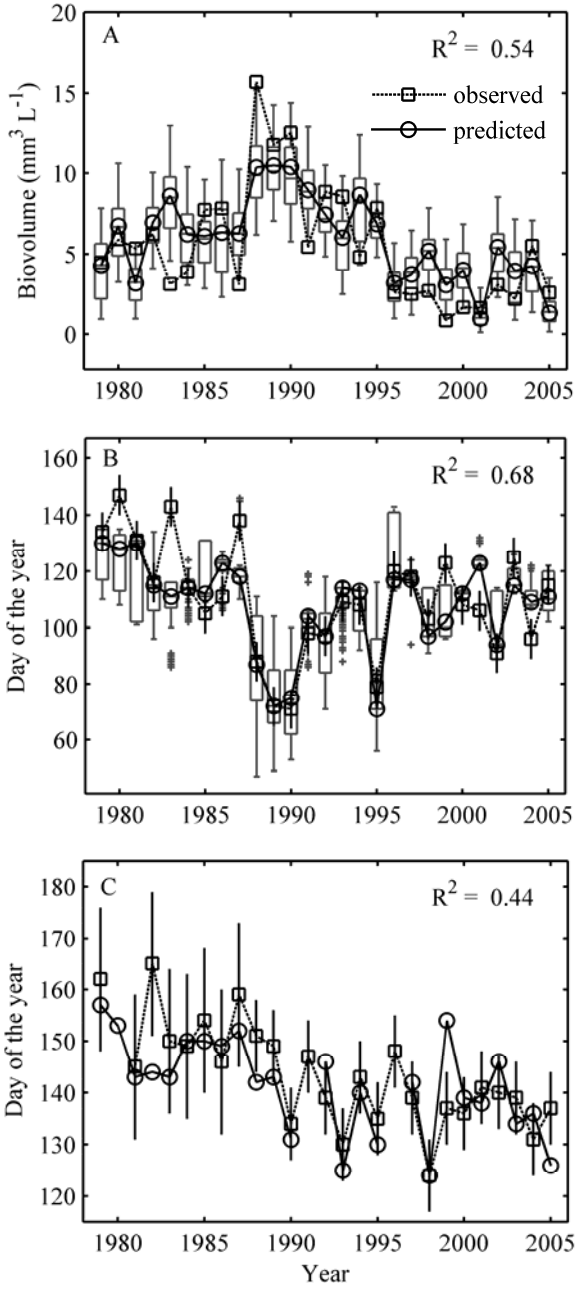

Fig. 1.2. Model performance and robustness against changes in parameters. Observed (squares) and predicted (circles) (A) intensity of the diatom spring bloom, (B) timing of the diatom spring peak and (C) timing of the *Daphnia* spring peak. Intensity of the diatom spring bloom is calculated as the mean annual biovolume until the end of the bloom. Vertical black lines (in panels B and C) show ± 7 days (± 14 days), i.e., the uncertainty due to sampling frequencies of one week (two weeks for *Daphnia* until 1987). Missing data points (in panel C) correspond to years when no *Daphnia* peak was observed/predicted until the end of the simulation period. Boxplots (in panels A and B) depict the effect of varying the eight calibrated parameters by ± 20 % (n=1944, cf. methods), the horizontal lines show the median, lower and upper quartile, the whisker extend at most to 1.5 times the interquartile range and the crosses point to outliers.

Simulation experiments and the intensity of the diatom spring bloom—Simulation experiments indicated that the strength of the warming effect on the intensity of the diatom spring bloom was dependent on trophic state (Fig. 1.3). Simulating warm conditions, with missing ice cover and higher water temperatures in all years ('W' in Fig. 1.3), significantly increased the mean biovolume of the diatom spring bloom compared to the control ('C') run (Wilcoxon rank test, $p<0.001$). We separated hypertrophic from eutrophic conditions by simulating very high ('HYP') and reduced ('EU') phosphorus supply respectively in all years. Additionally simulating warm conditions provoked a significant increase ($p<0.001$) of the bloom intensity under both trophic states (compare 'HYP' with 'HYPxW' and 'EU' with 'EUxW' in Fig. 1.3). Yet, the increase of the mean biovolume due to warming was smaller under eutrophic than under hypertrophic conditions. Thus, in our simulations a reduction in nutrient supply attenuated the effect of climate warming on the intensity of the phytoplankton spring bloom.

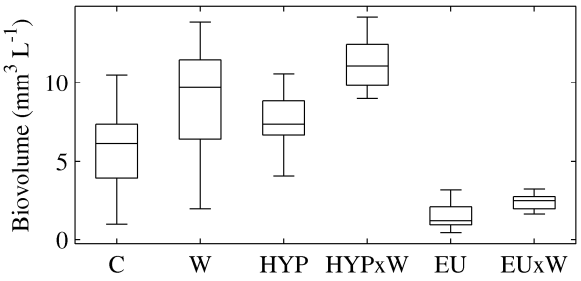

Fig. 1.3. The effect of warming on the intensity of the diatom spring bloom under different trophic states. Boxplots depict inter-annual variability of the intensity of the diatom spring bloom (1979-2005, $n=27$) under different scenarios (cf. methods): A control ('C') run using environmental forcing factors as observed (corresponding to predicted values in Fig. 1.2), simulated warm conditions with increased water temperatures and no ice cover ('W'), simulated hypertrophic conditions ('HYP'), hypertrophic conditions combined with warming ('HYPxW'), eutrophic conditions ('EU'), and eutrophic conditions combined with warming ('EUxW'). Boxplot details as in Fig. 1.2.

Simulation experiments and the timing of the diatom spring peak—Trophic state also influenced the effect of climate warming on the timing of the diatom spring peak (Fig. 1.4). Simulating warm conditions ('W' in Fig. 1.4A) resulted in an earlier peak when compared to the control ('C') run (Wilcoxon rank test, $p<0.001$). These changes were reinforced when additionally simulating increased availability of phosphorus, i.e., hypertrophic conditions ('HYPxW' in Fig. 1.4A).

In contrast, decreased availability of phosphorus, i.e., eutrophic conditions, counteracted the effect of climate warming on the timing of the diatom spring peak ('EUxW' in Fig. 1.4A). Comparing our simulations with the observed timing of the peak during years with mild winter conditions and early ice-out (circles in Fig. 1.4A) suggests that the relative delay of the diatom spring peak in recent mild years (Fig. 1.1B) can be attributed to the observed shift in trophic state. We explored this further by analysing the mechanisms that induce the collapse of the spring bloom and thereby determine the timing of the peak.

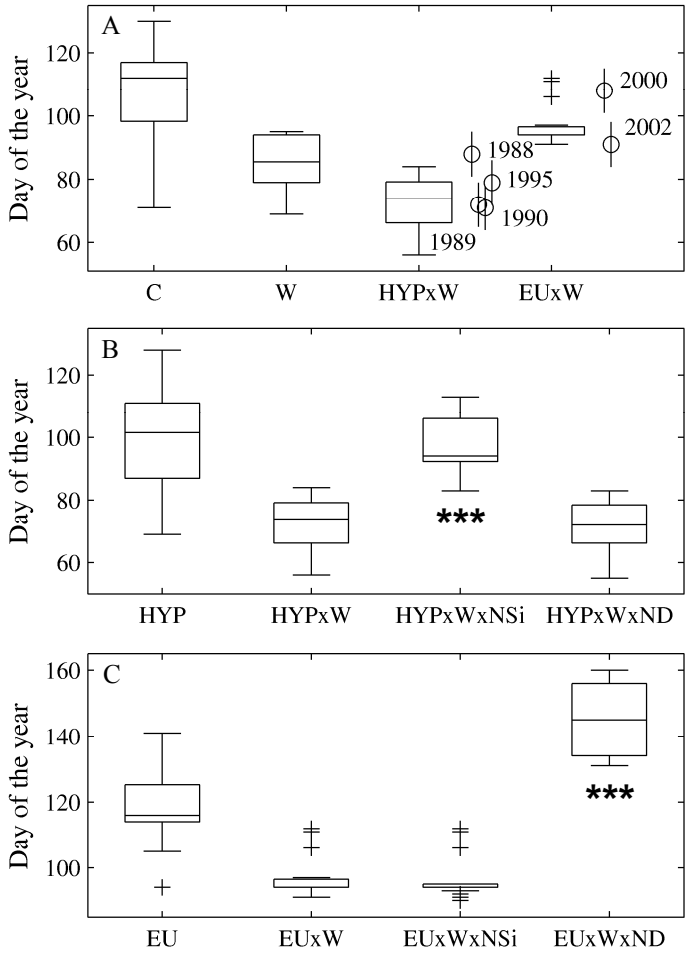

Fig. 1.4. (A-C) The effect of warming on the timing of the diatom spring peak under different trophic states. Boxplots depict inter-annual variability of the timing of the diatom spring peak (1979-2005, n=27) under different scenarios: Abbreviations are 'NSi' for simulations without silicate limitation and 'ND' for simulations without *Daphnia* grazing. Other abbreviations as in Fig. 1.3. Circles (in panel A) mark the observed timing of the diatom spring peak during years of early ice-out (cf. Fig. 1.1B) with vertical lines depicting ± 7 days, i.e., the uncertainty due to the sampling frequency of one week. Asterisks (in panels B, C) mark results of simulations that differ significantly from warming scenarios ('HYPxW' and 'EUxW'), as determined by Wilcoxon rank tests (p<0.001). Boxplot details as in Fig. 1.2.

Bloom collapse mechanisms under different trophic states—Analysing the role of silicate limitation and *Daphnia* grazing showed that the mechanisms, which underlie diatom spring phenology, differ under hypertrophic and eutrophic conditions (Fig. 1.4B, C). While under hypertrophic conditions (Fig. 1.4B) neglecting silicate limitation strongly decelerated the warming-induced forward shift of the peak ('HYPxW' vs. 'HYPxWxNSi', $p<0.001$), the effect of warming persisted when silicate limitation was neglected under eutrophic conditions (Fig. 1.4C, 'EUxW' vs. 'EUxWxNSi', $p>0.1$). By contrast, neglecting *Daphnia* grazing had hardly any effect on the timing of the peak under simulated hypertrophic conditions (Fig. 1.4B, 'HYPxW' vs. 'HYPxWxND', $p>0.1$), whereas the effect of warming was annulled and the peak delayed significantly under eutrophic conditions (Fig. 1.4C, 'EUxW' vs. 'EUxWxND', $p<0.001$). Hence, while the collapse of the bloom was caused by silicate limitation under very high phosphorus supply (hypertrophic conditions), it was caused by *Daphnia* grazing under reduced phosphorus supply (eutrophic conditions).

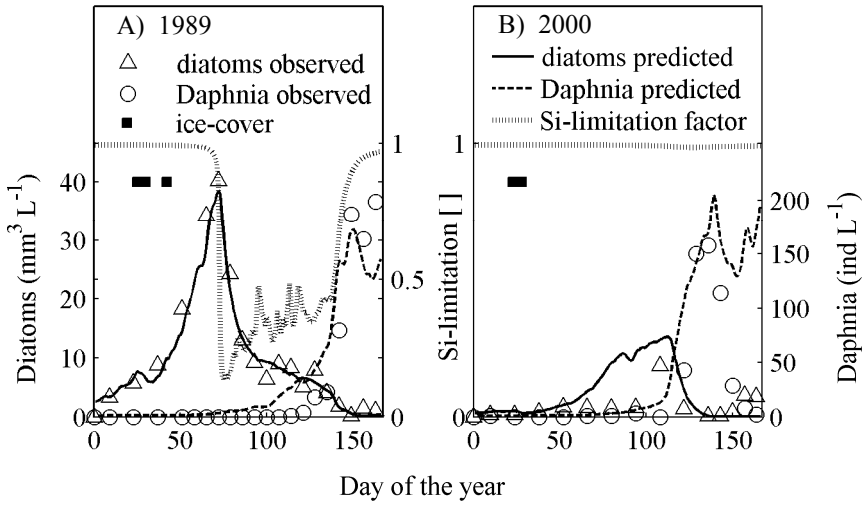

Fig. 1.5. Observed and predicted spring dynamics of diatom biovolume and *Daphnia* density during two years of early ice-out: (A) 1989 (hypertrophic phase) and (B) 2000 (eutrophic phase). The thick shaded line shows silicate limitation as indicated by the model, with a value of 1 corresponding to no limitation.

Two example years, which both experienced relatively warm conditions in winter, illustrate that the collapse of the diatom spring bloom can, as found above, be induced by different environmental factors depending on the trophic

state (Fig. 1.5). The model indicates that the diatom spring bloom was terminated through silicate limitation in 1989 (i.e., in the hypertrophic phase) as suggested by our simulation experiments (Fig. 1.4B). In contrast, the diatom spring bloom in 2000 (i.e., in the eutrophic phase) did not collapse until *Daphnia* densities became important, again in accordance with our simulation results (Fig. 1.4C). Correspondingly, minimal dissolved silicate concentrations measured in Müggelsee until the end of the diatom spring bloom differed between the phases of very high (1979-1996) and reduced phosphorus supply (1997-2005) (Fig. 1.6). While during the hypertrophic (and transient) phase they often reached the detection limit of 0.1 mg L^{-1}, below which diatom growth is likely to be silicate limited, during the eutrophic phase they always remained on a level where silicate limitation is unlikely.

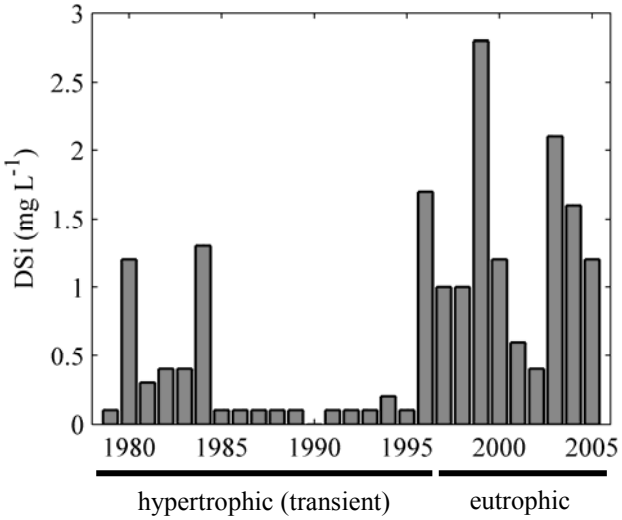

Fig. 1.6. Minimal concentrations of dissolved silicate (mg L^{-1}) during the diatom spring bloom in Müggelsee, measured during phases of high (hypertrophic and transient 1979-1996) and reduced phosphorus supply (eutrophic 1997-2005).

1.5 Discussion

Our model well reproduced observed spring dynamics of diatoms (and *Daphnia*) in Müggelsee during 1979-2005. Simulation experiments indicated that the effect of climate warming on both the timing and intensity of the diatom spring bloom was reinforced through high phosphorus availability (hypertrophic conditions), while decreasing phosphorus availability (eutrophic conditions), as prevailing in the last decade, counteracted the warming effect. Further analysis

suggested that the collapse of the bloom was caused by silicate limitation during hypertrophic conditions. In contrast, silicate concentrations did not reach the limitation threshold during eutrophic conditions such that the bloom was terminated by *Daphnia* grazing. This switch in bloom collapse mechanisms explains why the phytoplankton response to mild winter and spring conditions differed between the periods of very high and reduced phosphorus loading in the lake studied here.

Plausibility of bloom collapse mechanisms—Diatom biovolume in Müggelsee is dominated by small centric species in spring (<30 μm), which belong to the preferred food size range of *Daphnia.* In fact, the mean yearly contribution of centric diatom species to total diatom biovolume until the clear water phase was 65 ± 18 SD % (n=27) in our study period. In addition, larger diatoms such as *Asterionella formosa* and *Fragilaria crotonensis*, also present in Müggelsee, have been found to be suppressed by *Daphnia* in other freshwater lakes (Vanni and Temte 1990). The role of silicate limitation during the diatom spring bloom is well documented in marine systems (Allen *et al*. 1998), but has also been shown to be important in freshwater systems (Lund 1950). Thus, both of our explanations for the collapse of the diatom bloom are plausible.

The bloom collapse mechanisms proposed here might also contribute to a better understanding of the effects of climate warming on phytoplankton phenology described in other studies. Interestingly, in a simulation study by Elliott *et al*. (2006), increasing the nutrient (phosphorus and nitrogen) load enhanced the warming-induced forward shift of the spring peak of the diatom species *Asterionella* sp., whereas the timing of the spring peak of the two non-diatom species *Chlorella* sp. and *Plagioselmis* sp. was delayed under increased nutrient load. This finding is in accordance with our results assuming that in Eliott *et al*.'s (2006) simulations increasing phosphorus and nitrogen availability resulted in higher growth rates of *Asterionella* sp. and subsequently in an earlier collapse of the peak caused by silicate limitation. In contrast, *Chlorella* sp. and *Plagioselmis* sp., which were not limited by an additional nutrient, peaked later in that study because they could fully exploit the larger resource base.

1.5 Discussion

Potential food web consequences of a switch in bloom collapse mechanisms—A bloom collapse induced by silicate limitation, as suggested for mild years during the hypertrophic phase of Müggelsee (Fig. 1.4B), decouples diatoms from *Daphnia* (Fig. 1.5). We wondered whether this decoupling of predator and prey had any consequences for the growth success of *Daphnia*. In fact, Winder and Schindler (2004*a*) have shown that a climate-induced decoupling of the phytoplankton bloom from the onset of *Daphnia* growth in spring can produce a mismatch situation causing a decline in *Daphnia* abundance. However, in a supplementary analysis, we did not find any relationship between the number of weeks elapsed between the phytoplankton peak and the *Daphnia* maximum in spring (as an indicator of the potential mismatch) and *Daphnia* densities in late spring and summer (not shown). Moreover, when *Daphnia* started growing in spring, the diatom biovolume always stayed above 0.2 mg C L^{-1} (approximately 1.7 mm^3 L^{-1}), which is regarded as the food limitation threshold for *Daphnia* (Lampert 1978). Considering that besides diatoms other phytoplankton species contribute to *Daphnia* food, it is not surprising that although the phytoplankton spring peak is decoupled from *Daphnia* growth in some years, we do not find any evidence for a mismatch situation between phytoplankton and *Daphnia* in this nutrient-rich lake.

Phenomenological approach to phosphorus limitation—A strong correlation between phytoplankton biomass and total phosphorus concentrations as found in spring for Müggelsee (Eq. 12) does not necessarily indicate that algal growth rates are indeed limited by phosphorus (Sommer 1994). Yet, we chose the phenomenological approach presented here, based on the assumption that decreasing concentrations of total phosphorus reflect decreasing concentrations of phosphorus available for algal growth. In fact, previous studies have pointed to increasingly phosphorus limited phytoplankton spring growth in Müggelsee (Köhler *et al*. 2000; Köhler *et al*. 2005). Such a limitation is plausible, as concentrations of soluble reactive phosphorus fell below the limitation threshold of 10 μg L^{-1} during the phytoplankton spring bloom in all years (Köhler *et al*. 2005).

When estimating the maximal phosphorus available for diatom growth, we assumed that a constant amount (TP^*=52 μg L^{-1}) is locked in other compartments (such as bacteria, other phytoplankton species, zooplankton, and phosphorus bound to iron or calcite) each year (cf. methods). This is a strong assumption because, intuitively, the amount of phosphorus locked in other compartments should decrease as total phosphorus concentrations decrease in the lake. We, therefore, performed two additional regressions (cf. Eq. 12) of mean spring diatom biovolume (A_{bloom}) on mean spring total phosphorus concentrations (TP_{bloom}) for the periods 1979-1993 (high TP concentrations) and 1994-2005 (reduced TP concentrations). The estimation of the phosphorus locked in other compartments was clearly not lower under reduced total phosphorus concentrations (TP^*=56 μg L^{-1}, p<0.001, R^2=0.54) than under high total phosphorus concentrations (TP^*=47 μg L^{-1}, p<0.01, R^2=0.41). This supports our assumption that, during the study period, a relatively equal amount of phosphorus was not available to diatoms independently of trophic state. Interestingly, a large amount of particulate phosphorus in Müggelsee and its inflow is bound to iron and not available to phytoplankton growth (Kirchner 1997). Better understanding the phosphorus limitation of phytoplankton in Müggelsee definitively requires further research, however, the main conclusions of this study are independent of the exact mechanisms which determine the intensity of algal biovolume under different trophic states.

Other model simplifications—Model development poses the challenge to find a balance between including the key processes while keeping the model as simple as possible. This process necessarily leads to the exclusion of mechanisms that are known to be important in other systems. For instance, we are aware of the fact that grazing by copepods and ciliates can be an important loss factor for phytoplankton early in the year (Huber and Gaedke 2006; Tirok and Gaedke 2006; Peeters *et al*. 2007a). Yet, a model that included the effect of winter grazers (based on observed densities and clearance rates from the literature) as additional forcing factors negligibly improved the fit of the model (not shown). We also ignored that the maximal uptake rate of phosphorus ρ_{max} can be dependent on cell quota (Morel 1987). The reason for this was that the

regulation of nutrient uptake rates is poorly understood yet (Klausmeier *et al*. 2004) and modelling the negative feedback of internal nutrient stores on uptake rates has hardly affected the system behaviour in similar models (Klausmeier *et al*. 2004, Diehl *unpubl.*). Also, studies of phytoplankton physiology have clearly demonstrated that it is not only the average light availability but day length that influences phytoplankton growth rates (Nicklisch and Kohl 1989). Accounting for the latter mechanism would certainly be one of the many steps to render the model more realistic.

The importance of considering changes in trophic state besides climate warming—Previous studies on the phytoplankton response to climate warming in Müggelsee did not find any effect of nutrients (Adrian *et al*. 1999; Gerten and Adrian 2000). This might be explained by the shorter time-series used in these studies ending in the late 90s, when the nutrient effect might not have been apparent yet. Another explanation could be that, as found here, simple correlation analysis is not the right tool to detect more subtle relationships as those between the trophic state and the timing of the phytoplankton spring bloom. Our results are clearly in accordance with other observational and modelling studies, showing that the effect of climate warming on the phytoplankton spring bloom can be counteracted by decreasing nutrient concentrations (Eliott *et al*. 2006; Jeppesen *et al*. 2005). These authors explain their findings by the well-known positive effect of increasing temperatures and the negative effect of decreasing nutrient concentrations on phytoplankton growth (Wernicke and Nicklisch 1986). Here, we show that decreasing phosphorus concentrations do not only imply a gradual shift of increasingly phosphorus-limited algal growth, but a qualitative switch from a bottom-up driven (by silicate limitation) to a top-down controlled (by *Daphnia* grazing) collapse of the phytoplankton spring bloom.

The interaction between climate warming and a change in nutrient loading can be expected to occur in other aquatic ecosystems of different trophic state (such as meso- or oligotrophic lakes) and of different types (such as deep lakes or marine systems). The mechanisms underlying this interaction might differ between the ecosystems. However, there are some indications that the switch in

bloom collapse mechanisms that we propose here for the shallow, heavily loaded lake might also be relevant for other systems. Schelske and Stoermer (1971) first postulated a relationship between eutrophication and the increasing occurrence of silicate limitation of diatom growth for the deep, oligotrophic Lake Michigan. This relationship has also been described for marine systems, such as the heavily loaded, mesohaline part of Chesapeake Bay and for coastal waters of the North Sea (Conley *et al*. 1993). Thus, it is conceivable that a switch from an algal bloom collapse induced or at least accelerated by silicate limitation to a collapse induced by some other factor (such as grazing or sedimentation) takes place in the course of a load reduction in these systems as well. Simultaneous climate warming should then amplify the changes brought about by a shift in trophic state just as it has been found in this study.

1.6 Conclusions

In conclusion, other studies have pointed to the risk of falsely attributing observed changes in aquatic ecosystems to climate warming (Jeppesen *et al*. 2003; Van Donk *et al*. 2003; Jeppesen *et al*. 2005). Here, we emphasize the necessity of gaining a better understanding of the mechanisms that underlie phenology shifts and other climate-induced changes in aquatic ecosystems. For instance, it has become increasingly clear that the mechanisms determining the phytoplankton response to climate warming differ strongly between shallow and deep lakes (Adrian *et al*. 1999; Peeters *et al*. 2007a). Our results show that it is equally important to consider the trophic state of a lake when investigating the mechanisms underlying the effect of global warming on phytoplankton bloom formation. In view of future climate warming, further studies are needed to determine how climatic conditions influence the external and internal nutrient loading of lakes (e.g., Malmaeus *et al*. 2006). Moreover, other anthropogenic interventions (such as land use and management changes), which influence the nutrient supply to lakes and rivers, have to be taken into account in order to establish more realistic scenarios of freshwater ecosystems under anticipated climate change.

1.7 Acknowledgements

We thank Sebastian Diehl for his helpful comments during the model construction process and on the method section of the manuscript, Ursula Gaedke for advising us on many model related questions, Andreas Nicklisch and Jan Köhler for their advice on phytoplankton dynamics in Müggelsee and all scientists and technicians involved in the collection and compilation of the long-term data set. We are also grateful to Don Scavia and one anonymous referee for giving valuable comments on the first version of the manuscript. The German Research Foundation (DFG) supported Veronika Huber within the program AQUASHIFT (SPP 1162).

1.8 Appendix

Genetic algorithm—A genetic algorithm is a computational search technique inspired by evolutionary biology that allows approximating solutions to optimization problems. Here, the aim is to find a parameter set that optimizes the fit between the (sub-) model and the data. The genetic algorithm comprises four major building blocks: the initialization of parameter sets (the creation of the initial 'population'), the selection of the best parameter sets based on model performance (selection based on 'fitness'), the recombination of the selected parameter sets ('crossover'), and randomly altering parameter values ('mutation'). In this study, the sequence of selection, crossover, and mutation was repeated for 1000 generations. After the last generation, one final selection procedure was run and the parameter set with the best performance (the highest fitness) provided the default parameter values (cf. Table 1.1) for the subsequent model analysis.

We separately calibrated, first, the *Daphnia* sub-model and, second, the diatom core model. In the following, we describe the design of the genetic algorithm for the diatom core model and then mention a few changes specific to the *Daphnia* sub-model.

Creation of an initial population—The genetic algorithm was initialized by creating a suit of 36 parameter sets, which proved to be sufficient for our calibration problem. Each parameter set consisted of 8 calibration parameters that were drawn randomly from the biologically plausible intervals given in Table 1.1.

Selection based on fitness—The differential equations (Eqs. 1-4) were solved for each of the 36 parameter sets created during the initialization process (using the solution for *Daphnia* density from Eqs. 13-15 as a forcing variable). For each solution, the fit between the model and the data was assessed by calculating the weighted mean absolute deviation between predicted (pB_i) and observed (oB_i) diatom biovolumes (modified from Willmott 1982)

$$MAD_b = \frac{\sum_{k=1}^{n_y} \frac{\sum_{i=1}^{n_k} |pB_i - oB_i| oB_i}{n_k}}{n_y} \quad \text{(A1)}$$

where n_y is the number of years in the calibration period, and n_k are the different numbers of observations during each year. The algorithm also calculated the mean absolute deviation between predicted (pT_i) and observed (oT_i) timing of the diatom spring peak.

$$MAD_t = \frac{\sum_{k=1}^{n_y} |pT_k - oT_k|}{n_y} \quad \text{(A2)}$$

The performance of a parameter set (the fitness F of an individual) was defined as

$$F = \frac{w_T}{MAD_t} + \frac{w_B}{MAD_b} \quad \text{(A3)}$$

where w_T and w_B are weighting factors that we chose to set to 1 and 5 respectively. The choice of the weighting factor required several trial runs of the calibration algorithm, examining the distributions of MAD_t and MAD_b, and adjusting the weighting factors until a satisfactory, qualitative fit of the model to the data was reached. Once the performance of each parameter set was evaluated, a total of 6 parameter sets were selected: the two sets that produced the highest fitness, and four other parameter sets randomly with a probability proportional to their fitness F.

Crossover—A new suit of parameter sets was constructed by keeping the 6 parameter sets chosen in the selection procedure and by recombining all possible pairs of these parameter sets (producing 30 new additional parameter sets). The recombination imitates the chromosomal crossover with each parameter set representing a string of genes. It consisted of cutting the parameter string of two sets at a random position and creating two new sets by combining the corresponding parts of the parameter strings.

Mutation—Random changes were imposed on all new parameter sets except for the parameter set that produced the best model performance. Each parameter

'mutated' with a probability of 0.4 by adding (deducting) a value drawn randomly from the mutation range, which is half of the corresponding biological plausible parameter interval. If the new parameter value lay outside the given parameter interval, the parameter was set to the maximal (minimal) allowed value.

Calibrating the Daphnia sub-model—Since the *Daphnia* sub-model required the calibration of fewer parameters, it was sufficient to run the genetic algorithm with a suit of 16 parameter sets, choosing 4 during each selection procedure. The fitness function consisted of the sum of the indices of agreement IoA_t and IoA_b (as described in the method section of the manuscript) and of the reciprocals of MAD_t and MAD_b.

Chapter 2

Periodically forced food chain dynamics: model predictions and experimental validation

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Published as Steiner C.F., A.S. Schwaderer, V. Huber, C.A. Klausmeier and E. Litchman (2009) Periodically forced food chain dynamics: model predictions and experimental validation. *Ecology*, **90**, 3099-3107.

2.1 Abstract

Despite the recognition of the importance of seasonal forcing in nature, remarkably few studies have theoretically explored periodically forced community dynamics. Here we employ a novel approach called "successional state dynamics" (SSD) to model a seasonally forced predator-prey system. We first generated analytical predictions of the effects of altered seasonality on species persistence and the timing of community state transitions. We then parameterized the model using a zooplankton-phytoplankton system and tested quantitative predictions using controlled experiments. In the majority of cases, timing of zooplankton and algal population peaks matched model predictions. Decreases in growing period length delayed algal blooms, consequently delaying peaks in zooplankton abundance. Predictions of increased probability of predator extinction at low growing period lengths were also upheld experimentally. Our results highlight the utility of the SSD modeling approach as a framework for predicting the effects of altered seasonality on the structure and dynamics of multitrophic communities.

2.2 Introduction

Approaches to modeling consumer-resource interactions have frequently relied on the assumption that systems are at equilibrium and that parameters governing species vital rates are fixed through time. While such approaches have proven powerful in identifying key ecological mechanisms and processes, most ecologists recognize that many natural systems experience temporally varying environmental conditions that can buffet populations, enhance background mortality rates, and drive population trajectories far from steady-state conditions. Hence, perceived patterns of community structure may actually be in flux as populations are frequently within transitory phases due to external forcing (Hastings 2001, 2004; Jäger *et al*. 2008). The overriding influence of temporal heterogeneity on community dynamics is most readily apparent in temperate and high latitude systems in which seasonal variation imposes periods of active somatic and population growth followed by periods of depressed metabolic activity, dormancy and increased mortality. Predicting the long-term consequences of such periodic forcing on the dynamics and structure of communities is a challenge to ecologists and may prove especially vital in the near future as large-scale climate change threatens to alter the strength and timing of seasonality in many natural systems (Walther *et al*. 2002; Parmesan and Yohe 2003).

Despite the recognition of the importance of temporal variability and seasonal forcing in nature, remarkably few studies have theoretically explored how periodic mortality events alter community dynamics within spatially homogeneous, closed systems (though see Scheffer *et al*. 1997; Ives *et al*. 2000). One obstacle towards theoretical advancement is the lack of analytical techniques for exploring the effects of large perturbations with long period lengths. Recently, Klausmeier (unpublished manuscript) outlined a general methodology for theoretically examining the effects of seasonal mortality events on community dynamics, based on earlier work (Litchman and Klausmeier 2001). Called "successional state dynamics" (SSD), the model framework treats compositional succession of a community as a path taken through different community equilibria during an active growing period which is periodically reset

to a near empty state during a period of intensified mortality (e.g., the winter season).

Here we employ the SSD approach to model the dynamics of a periodically forced food chain composed of a single top predator and a single prey. We generate quantitative predictions of the effects of growing season length on the timing of key state transitions of the system using a simple planktonic system as a model basis. We then test these predictions using controlled laboratory experiments. Planktonic communities are excellent model systems for examining the impacts of seasonal forcing on community dynamics as they are known to exhibit repeatable patterns of seasonal succession in nature (Sommer *et al*. 1986; Sommer 1989). Moreover, alterations in seasonality and growing season length are believed to have strong effects on zooplankton-algal dynamics and the timing of key events such as spring algal blooms, peaks in zooplankton abundance, and the clear water phase (Straile and Adrian 2000; Straile 2002; Mooij *et al*. 2005; Berger *et al*. 2007; Huber *et al*. 2008). Hence, model development and experimental validation using simplified modules of these systems are important first steps towards understanding natural variation in seasonal patterns.

Model predictions—In-depth analysis of the effects of periodic forcing on community dynamics using the SSD approach will be presented in a future paper (Klausmeier unpublished manuscript). Here we outline the salient features and predictions of the SSD food chain model. The SSD approach models seasonal succession as a path through possible community equilibria (or "states") of the non-forced system. In a system composed of a single zooplankton predator (Z) and its phytoplankton prey (P), there are three possible community states: prey present and predator absent, predator and prey both present, and the empty state (both predator and prey absent). Given these possible states, there are only two nontrivial successional trajectories the system may take following winter mortality: 1) the empty state to prey present and 2) the empty state to prey present to a state with both predator and prey present. The SSD model assumes that changes in log transformed predator and prey densities approach a linear form over time (Fig. 2.1A).

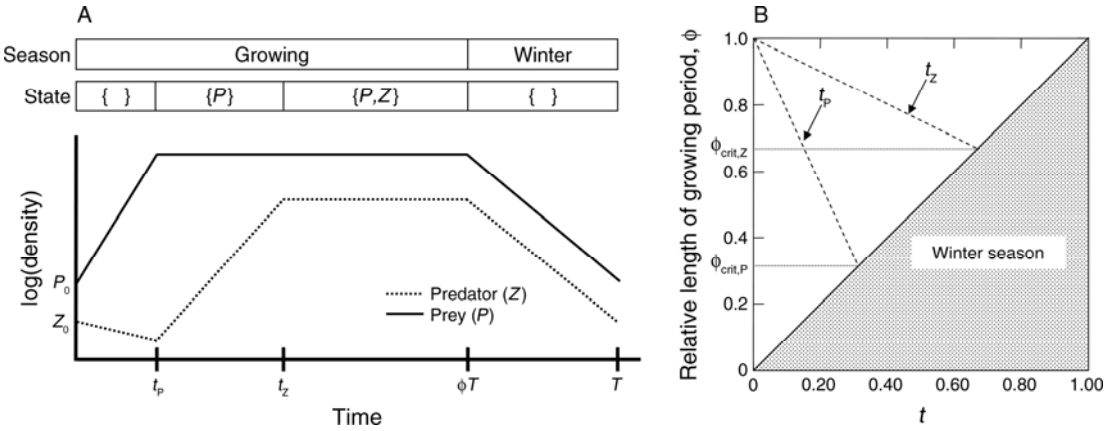


Fig. 2.1. General predictions of the SSD food chain model in which length of the year (T) has been standardized to equal 1 (shown are predictions for a hypothetical predator and prey). A) Example dynamics of predator and prey over a single growing season in which relative growing period length (ϕ) is long enough to permit both predator and prey persistence. At the start of the growing season the community transitions from the empty state {}, to the prey only state {P} at time t_p, to the predator and prey state {P, Z} at time t_Z, and back to the empty state at time ϕT. B) Predicted transition times (dashed diagonal lines) to the prey only state (t_P) and the prey and predator present state (t_Z) for a range of ϕ values. As the length of the growing season increases towards a limit of ϕ=1 (no winter season), the predicted timings converge towards t=0 and a state in which both predator and prey persist at equilibrium densities for the duration of the year. Decreasing the proportion of the year devoted to growth relative to the winter (decreasing ϕ) causes prey to invade later in the growing period and delays the state transition from prey alone to predator plus prey. Shown also are critical ϕ values that permit invasion and persistence by the prey ($\phi_{crit,P}$) and the predator ($\phi_{crit,Z}$).

Note that in figure 2.1 and henceforth the length of the year (T) has been standardized to equal 1. In a system that can support zooplankton and phytoplankton, phytoplankton invade the empty state {} at initial density (P_0) following winter and increase exponentially at their maximal growth rate until reaching a threshold density (K_p) at time t_p (Fig. 2.1A). Zooplankton enter the empty state {} at initial density (Z_0) and decline at their background mortality rate during this phase. In the prey only state {P}, phytoplankton are at a threshold level and zooplankton increase at their maximal growth rate until peaking at their threshold density (K_z) at time t_z. In this state {P, Z}, both zooplankton and phytoplankton populations are unchanging until the final empty state {}, when both populations experience winter mortality. As population dynamics in these different phases are simple functions of exponential growth and mortality rates, they can be easily represented

mathematically. The long term population growth rate of phytoplankton (Λ_P) averaged over a period is:

$$\Lambda_P = \lambda_{\mathrm{P},\{\ \},\mathrm{growing}}\, t_P + \lambda_{\mathrm{P},\{\ \},\mathrm{winter}}(1-\phi) \tag{1}$$

where $\lambda_{P,\{\},\mathrm{growing}}$ is its growth rate when invading the empty state early in the growing season, t_p is the proportion of the year required for phytoplankton to reach equilibrium when invading (after which net growth rate equals zero), and $\lambda_{P,\{\},\mathrm{winter}}$ is its mortality rate during the winter season weighted by the proportion of the year that is winter (1-ϕ). For the invading predator (Z), long term growth averaged over a period is:

$$\Lambda_Z = \lambda_{\mathrm{Z},\{\ \},\mathrm{growing}}\, t_P + \lambda_{\mathrm{Z},\{\mathrm{P}\},\mathrm{growing}}\,(t_Z - t_P) + \lambda_{\mathrm{Z},\{\ \},\mathrm{winter}}(1-\phi) \tag{2}$$

where $\lambda_{Z,\{\},\mathrm{winter}}$ is the predator's winter mortality rate, $\lambda_{Z,\{\},\mathrm{growing}}$ is its growth rate when invading the empty state (which is assumed to be negative and equal to its background mortality) and $\lambda_{Z,\{\mathrm{P}\},\mathrm{growing}}$ is its exponential growth rate following successful prey invasion (at time t_p) which proceeds until the predator reaches an equilibrium density at time t_z.

Model predictions of the effects of relative length of the growing period (ϕ) on the timing of state transitions can be easily ascertained by assuming that the system has settled to a stable seasonal trajectory, setting equations 1 and 2 to zero and solving for t_p and t_z (Klausmeier unpublished manuscript). Doing so produces the following relationships:

$$t_P = \frac{-\lambda_{\mathrm{P},\{\ \},\mathrm{winter}}(1-\phi)}{\lambda_{\mathrm{P},\{\ \},\mathrm{growing}}} \tag{3}$$

$$t_Z = \frac{-\lambda_{\mathrm{Z},\{\ \},\mathrm{growing}}\, t_P + \lambda_{\mathrm{Z},\{\mathrm{P}\},\mathrm{growing}}\, t_P - \lambda_{\mathrm{Z},\{\ \},\mathrm{winter}}(1-\phi)}{\lambda_{\mathrm{Z},\{\mathrm{P}\},\mathrm{growing}}} \tag{4}$$

Furthermore, critical ϕ values that permit successful invasion of predator and prey can also be determined. The minimum ϕ permitting invasion and persistence by the prey ($\phi_{\mathrm{crit,P}}$) is found by setting $\phi_{\mathrm{crit,P}}=\phi=t_p$ and solving equation 3. Similarly, the minimum ϕ permitting predator invasion ($\phi_{\mathrm{crit,Z}}$) is found by

setting $\phi_{crit,Z}=\phi=t_z$ in equation 4 and solving for $\phi_{crit,Z}$. Doing so produces the following:

$$\phi_{crit,P}=\frac{\lambda_{P,\{\ \},winter}}{\lambda_{P,\{\ \},winter}-\lambda_{P,\{\ \},growing}} \quad (5)$$

$$\phi_{crit,Z}=\frac{\lambda_{Z,\{\ \},winter}\lambda_{P,\{\ \},growing}+\lambda_{Z,\{P\},growing}\lambda_{P,\{\ \},winter}-\lambda_{Z,\{\ \},growing}\lambda_{P,\{\ \},winter}}{\lambda_{Z,\{\ \},winter}\lambda_{P,\{\ \},growing}-\lambda_{Z,\{\ \},growing}\lambda_{P,\{\ \},winter}-\lambda_{Z,\{P\},growing}\lambda_{P,\{\ \},growing}+\lambda_{Z,\{P\},growing}\lambda_{P,\{\ \},winter}} \quad (6)$$

General predictions from equations 3-6 are fairly intuitive and shown in figure 2.1B. Dashed lines represent predicted timings of state transitions (t) in relation to relative growing period length (ϕ). Shown are predictions for transitions to the prey only state {*P*} and the prey and predator present state {*P,Z*}. As the length of the growing season increases towards a limit of ϕ=1 (no winter season), the predicted timings converge towards t=0 and a state in which both predator and prey persist at equilibrium densities for the duration of the year. Decreasing the proportion of the year devoted to growth relative to the winter (decreasing ϕ) increases the severity of winter mortality. Consequently, prey invade the system later in the growing period and the state transition from prey alone to predator plus prey is delayed (Fig. 2.1B). If the growing season is too short (below $\phi_{crit,Z}$ in Fig. 2.1B), predators are unable to invade and persist and the system only transitions to a state with the prey present; growing seasons less than $\phi_{crit,P}$ exclude both predators and prey.

We tested the SSD model predictions using an experimental food chain composed of a single species of zooplankton as a predator and a single species of phytoplankton as its prey. We empirically derived estimates of exponential growth and background mortality rates for our species and then generated quantitative predictions of critical ϕ values ($\phi_{crit,P}$ and $\phi_{crit,Z}$) and the timing of state transitions (t_p and t_z) under different growing period lengths. These predictions were then compared to observed experimental transition times and patterns of zooplankton/phytoplankton persistence.

2.3 Methods

Experimental system—Experiments were conducted using a laboratory-based system consisting of the rotifer *Brachionus calyciflorus* as a predator and the flagellated green alga *Chlamydomonas reinhardtii* as its prey (all species are hereafter referred to by genus). We obtained *Brachionus* cultures from Florida Aqua Farms (Dade City, FL, USA), while *Chlamydomonas* was a wild type strain (#CC-2935) obtained from the *Chlamydomonas* Genetics Center (Duke University, Durham, NC, USA). *Brachionus* cultures were fed the same *Chlamydomonas* strain used in the experiment and all stock cultures were maintained using the same medium and environmental conditions as in the experiment. Experimental vessels consisted of 1000mL flasks loosely capped with aluminum foil and filled with 800mL of COMBO medium; medium was prepared as in Kilham *et al*. (1998) except that phosphorus was added at a lowered concentration of 490 μg/L to minimize formation of non-motile algal cells (Harris 1989). All flasks were housed and randomly ordered in a single environmental chamber at 25°C under 24 hour light; flasks were rotated on the chamber shelves daily. During the experiment, flasks were manually mixed and had 10% of their volume removed and replaced with fresh medium once daily (removed medium served as a zooplankton and phytoplankton sample). Both *Brachionus* and *Chlamydomonas* are motile and found in the water column; manual mixing helped ensure that nutrients and organisms remained relatively homogenous in their distributions. *Brachionus* were enumerated using a dissecting scope while *Chlamydomonas* were counted using a CASY particle counter. As *Brachionus* males do not actively feed and were rare, population densities of *Brachionus* were based only on counts of females. All experimental materials were autoclave-sterilized prior to use.

We tested the capacity of our model to predict the timing of state transitions for different relative growing period lengths. Experimentally, the proportion of the year devoted to the growing period (ϕ) versus winter can be easily manipulated by periodically imposing different levels of winter mortality via a single, large-scale mortality event. For example, an imposed mortality event of 90% of the community would correspond to a longer winter period compared to a mortality event with 50% removal. We employed five relative growing period treatments:

ϕ = 0.65, 0.70, 0.75, 0.80, and 0.85, with each treatment replicated four times. Our previous pilot experiments and model simulations showed that *Brachionus* and *Chlamydomonas* could persist at these ϕ levels and that the ϕ=0.65 treatment was close to the critical ϕ ($\phi_{crit,Z}$) for *Brachionus,* allowing us to test the effects of decreased ϕ on the probability of predator extinction. To experimentally impose winter mortality, a percentage of the community was removed by volume from each flask, added to a new flask and then brought to 800mL total with fresh, sterile medium. Percentage of volume *D* removed for each treatment was calculated using $D = \exp(\lambda_{\{\},winter}(1-\phi)T') \cdot 100$, where $\lambda_{\{\},winter}$ is the winter mortality rate for both predator and prey arbitrarily set to -1 day^{-1}, and *T*' is the absolute length of the full period (growing season plus winter). *T*' can be easily calculated from $\phi T' = t_{max}$ where t_{max} is the time the organisms where allowed to grow between mortality events (set to 14 days for all treatments). A fourteen day growing length was chosen based on preliminary experiments which showed that *Brachionus* densities peaked and equilibrated by day 14.

At the start of the experiment, 20 cells/mL of *Chlamydomonas* were added to all experimental flasks. Algae were allowed to reproduce for seven days at which time *Brachionus* individuals were haphazardly isolated from stock cultures and added at a density of 0.125 individuals/mL. Zooplankton were allowed to reproduce for 14 days, reaching a peak in density; we refer to this initial growth period as "year 0". On day 14, the first winter mortality event was imposed and communities were allowed to numerically respond for 14 days; we refer to this growth period as "year 1". A second winter mortality was then imposed and communities were again allowed to respond for another 14 days ("year 2") at which time the experiment was terminated.

Quantitative predictions and data analysis—To generate quantitative predictions of the timing of state transitions for our treatments, we parameterized our model using data from year 1 of the experiment. Estimates of species growth rates, background mortality rates (λ's), initial densities (P_0 and Z_0) and threshold densities (K_p and K_z) were obtained by fitting the log-linear

SSD model structure (as in Fig. 2.1A) simultaneously to ln transformed *Brachionus* and *Chlamydomonas* densities using a genetic algorithm (Haupt and Haupt 1998). Unlike conventional parametric model fitting, we employed a rule-based approach to obtain the SSD model fits. Fitting the SSD model structure translates to parameterizing rules that are used to numerically project the community forward in time as in Fig. 2.1A (Klausmeier unpublished manuscript). These rules dictate λ's based on the state of the system and determine how state transitions occur in the system. Specifically, populations grow or shrink exponentially at rates determined by the current state of the system (i.e., which species are at their threshold abundances). Transitions take place when a population is projected to reach its threshold abundance or when winter occurs. The procedure consisted of repeating the following steps: 1) time increments to all potential state transitions are calculated; 2) the temporally closest transition is chosen to occur; and 3) population densities and the state of the system are updated accordingly (Klausmeier unpublished manuscript). While conventional gradient search methods are not appropriate for this type of rule-based model parameterization, other optimization techniques such as genetic algorithms can easily handle these problems. For details on the genetic algorithm procedure used see Appendix B. Models were fit to data from each treatment replicate separately. After obtaining λ estimates for each replicate from the model fits, critical ϕ values ($\phi_{crit,P}$ and $\phi_{crit,Z}$) were calculated by solving equations 5 and 6 for all possible combinations of λ's (n = 20 for $\phi_{crit,P}$, and n = 20^3 for $\phi_{crit,Z}$). Similarly, we calculated transition times (t_p and t_z) based on all combinations of λ's (equations 3 and 4) for all treatment level ϕ values (ϕ = 0.65, 0.7, 0.75, 0.8, and 0.85). Predictions for mean critical ϕ values and transition times were determined by calculating the mean (and standard deviations) of the resultant distributions.

Model predictions generated from our year 1 model fits were compared to observed transition times from year 2 of the experiment. To estimate transition times in year 2, we again fit the SSD log-linear model to ln transformed year 2 data for each replicate separately using the genetic algorithm (as for year 1). This yielded estimates for initial densities (P_0 and Z_0), threshold densities (K_p and K_z) and vital rates (λ's) for each replicate. Instead of calculating transition

times using equations 3 and 4 (as for year 1), these parameters were used to numerically determine transition times. We employed the same method described above to numerically project the community forward in time; transitions were determined to take place when a population was projected to reach its threshold abundance or when winter occurred (Klausmeier unpublished manuscript). All transition times are presented as proportions of the full period (winter plus growing seasons). Observed and mean predicted transition times were compared using one sample t-tests. We also calculated type II error rates (β values) for each t-test and its observed p-value. In a few rare instances, *Brachionus* and *Chlamydomonas* densities fell below the limits of sampling detection following winter mortality. Rather than exclude these data points, we added a constant to these values equivalent to the detection limit density. Model fitting was performed using Matlab; statistical tests were performed using Systat.

2.4 Results

Time series and model fits for all treatments and replicates can be found in supplementary figures A2.1 and A2.2 (Appendix A). Model fits converged quickly for both year 1 and 2 with parameter estimates exhibiting negligible change over time and high congruence among repeated reinitializations of the genetic algorithm after 300000 generations (Appendix A: Fig. A2.3). In general, the log-linear SSD model captured observed *Brachionus* dynamics well, with the majority of R^2 values greater than 0.90 (Fig. 2.2; Appendix A: Fig. A2.1 and A2). Model fits were weaker for *Chlamydomonas*, accounting for a smaller proportion of variation compared to *Brachionus* in all replicates (Fig. 2.2; Appendix A: Fig. A2.1 and A2.2). Lower R^2 values for *Chlamydomonas* were largely due to declines in algal abundance following invasion by *Brachionus*.

Transition times observed in year 2 of our experiment and model predictions for each treatment level are listed in Table 2.1. Figure 2.3 displays means from the model prediction distributions and mean observed transition times. As can be seen, observed transition times in year 2 showed good qualitative agreement with model predictions (Fig. 2.3; Table 2.1). As the relative length of the growing period was reduced, both t_p and t_z were predicted to occur later in the growing

season. This trend was observed for both *Brachionus* and *Chlamydomonas* but was only strongly expressed at lower ϕ values, i.e. at higher levels of seasonal forcing (Fig. 2.3). Delays in *Chlamydomonas* transition times were evident at the four lowest ϕ treatments while *Brachionus* exhibited delays at the three lowest ϕ treatments (Fig. 2.3).

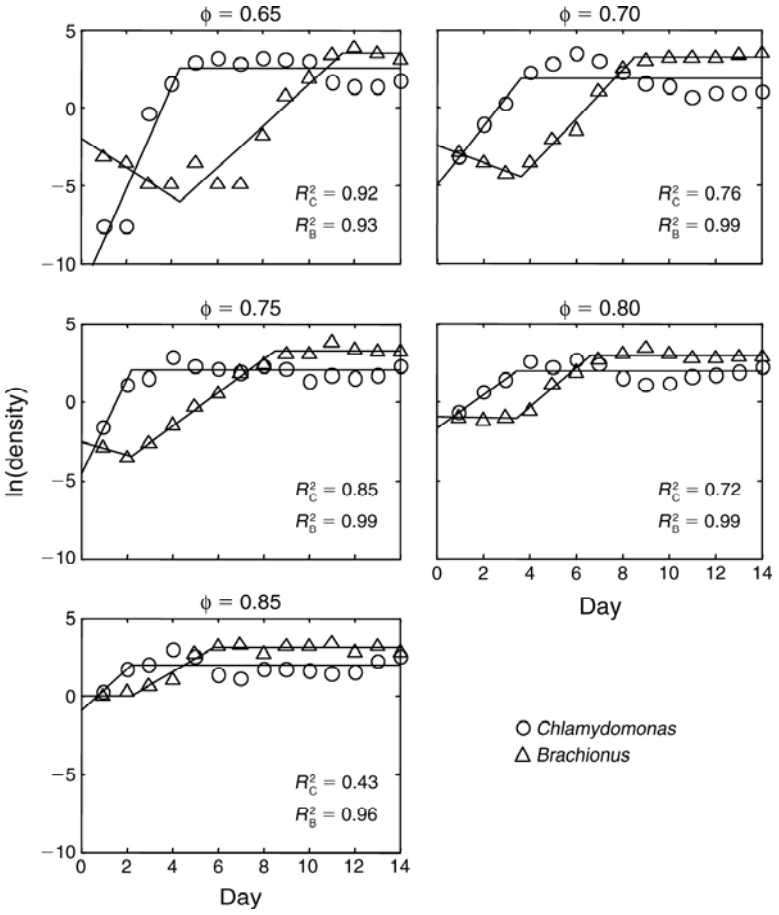


Fig. 2.2. Examples of food chain dynamics in year 2 of the experiment and model fits generated by the genetic algorithm. R^2 subscripts refer to genus names. *Brachionus* densities are given in units of #/mL; *Chlamydomonas* densities have been rescaled to units of #/10^{-5} mL. Results are for replicate #2 (year 1 and year 2 data and fits for all replicates can be found in Appendix A).

Quantitative agreement with model predictions was strongest for *Chlamydomonas* at ϕ levels 0.7-0.8 (Table 2.1). Differences between observed and predicted transition times for these treatments were weak, exhibiting *p*-values all greater than 0.40 (Table 2.1), while differences were evident in the ϕ=0.65 and ϕ=0.85 treatments (Table 2.1). Type II error rates for ϕ levels 0.7-0.8

also were moderate to high, ranging between 0.26 and 0.43 (Table 2.1). Thus, there was a reasonably high probability of failing to detect differences between our observed and predicted transition times when differences may have actually been present in these treatments. Quantitative agreement between observed and predicted transition times for *Brachionus* were strongest in the three lowest ϕ treatments (Table 2.1); significant differences were only detected at the two highest ϕ levels (Table 2.1). As with *Chlamydomonas*, type II error rates were also fairly high for several of the treatments in which no significant differences were detected (Table 2.1).

Table 2.1. Mean predicted and mean observed transition times for phytoplankton (t_p) and zooplankton (t_z) for each relative growing period treatment (ϕ).

ϕ	Mean Predicted t_p	Mean Predicted t_z	Mean Observed t_p	Mean Observed t_z	Obs vs Pred t_p P	Obs vs Pred t_p β	Obs vs Pred t_z P	Obs vs Pred t_z β
0.65	0.216	0.491	0.202	0.500	0.034	0.000	0.817	0.176
0.7	0.185	0.456	0.180	0.442	0.478	0.406	0.453	0.415
0.75	0.154	0.416	0.162	0.384	0.718	0.262	0.320	0.446
0.8	0.123	0.368	0.144	0.393	0.415	0.427	0.058	0.425
0.85	0.093	0.283	0.162	0.382	0.052	0.423	0.037	0.418

Note: *P*-values and type II error rates (β) are for one-sample t-tests comparing observed and predicted transition times

Year 1 fits produced mean critical ϕ values of $\phi_{crit,P}$=0.37 (SD=0.11) for *Chlamydomonas* and $\phi_{crit,Z}$=0.63 (SD=0.09) for *Brachionus* (Fig. 2.3). The latter value was close to our lowest ϕ treatment (ϕ=0.65; Fig. 2.3), and *Brachionus* indeed went extinct in two replicates of this treatment following winter mortality in year 2 (extinction was verified by exhaustively sampling flasks at the termination of the experiment). These replicates were excluded from analyses.

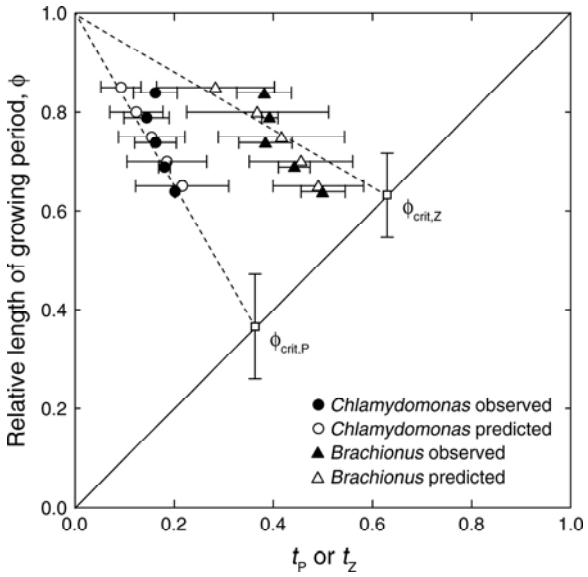


Fig. 2.3. Mean predicted transitions times (+/-SD) and mean observed transition times (+/-SD) for *Chlamydomonas* (t_P) and *Brachionus* (t_Z) (circles and triangles, respectively). Observed values have been offset vertically to better display error bars. Shown also are mean predicted critical ϕ values (+/-SD) for *Chlamydomonas* ($\phi_{crit,P}$) and *Brachionus* ($\phi_{crit,Z}$) (open squares). The dashed lines are extrapolated predictions from the critical ϕ values (as in Fig. 2.1B).

2.5 Discussion

While most ecologists recognize the potential of periodic forcing to strongly impact community dynamics, theoretical examinations have remained surprisingly uncommon. This is particularly true of freshwater planktonic systems in which seasonal succession is a well-recognized facet of temperate systems, receiving profuse empirical investigation, but where theoretical treatments and quantitative modeling of seasonal dynamics have been rare (though see Scheffer *et al*. 1997; de Senerpont Domis *et al*. 2007a). The SSD approach offers a tractable technique for examining generalizable food web structures within a dynamic seasonal framework, permitting analytical and quantitative predictions of the effects of altered seasonality on patterns of species coexistence and the timing of community state transitions.

For simple food chains, the SSD model predicts that increasing the length of the growing season relative to winter increases the probability of predator-prey persistence. This prediction was supported by our experimental system. *Brachionus* populations persisted in the four highest ϕ treatments for the duration of the experiment but went extinct at the start of year 2 in two

replicates of the ϕ=0.65 treatment – the treatment with the shortest relative growing period and most severe winter mortality. This treatment level was very close to the critical ϕ for *Brachionus* predicted by our model ($\phi_{crit,Z}$=0.63) below which extinction is expected.

In addition to facilitating predator/prey persistence, increasing growing period length relative to winter was predicted to hasten invasion by both predator and prey during the active growing season. Thus, transition times (t_p and t_z) were expected to occur earlier in the year with increasing levels of ϕ. This prediction is consistent with long-term patterns of zooplankton-algal dynamics in natural systems in which warming trends have advanced seasonal community development (e.g., Straile 2002). Our experiment provided further evidence of shifts in successional dynamics with altered seasonality; both *Chlamydomonas* and *Brachionus* exhibited accelerated transitions times with increasing ϕ, although effects of extended growing seasons on zooplankton-algal peaks were more strongly expressed in the lower ϕ treatments. For both *Chlamydomonas* and *Brachionus*, observed transition times tended to occur later than predicted at the two highest period lengths (ϕ=0.80 and 0.85).

Deviations between observed and predicted timings could be due to several factors. First, a key assumption when generating our model predictions was that the system had settled onto a stable seasonal trajectory. This assumes that species' initial densities at the start of the growing season are unchanging from year to year. However, it was possible that two rounds of winter mortality were insufficient to attain stability in our experimental system. When comparing *Chlamydomonas* initial densities obtained from our model fits for each replicate, we found no differences between years (Appendix A: Fig. A2.4). However, *Brachionus* showed evidence of lower initial densities in year 2 compared to year 1 with differences being strongest in the three highest ϕ treatments (Appendix A: Fig. A2.4). Low densities early in the growing period should translate into delayed peaks in abundance later in the growing period potentially explaining t_z values higher than predicted.

Another assumption of our model was that species' vital rates (λ) were constant across ϕ treatments and across years. This assumption was not upheld in our

experimental system. First, the large standard deviations exhibited by our prediction distributions (Fig. 2.3) expose the large amount of variation in λ estimates among replicates in year 1. This variation was not only generated by process and measurement error but by variation among treatments as well; significant differences in *Brachionus* growth rates were detected among ϕ levels in year 1 (Appendix A: Fig. A2.5). Furthermore, variation among treatments was also evident in year 2; *Brachionus* growth rates were higher than the year 1 average for the three lowest ϕ treatments and lower than the year 1 average for the two highest ϕ treatments (Fig. 2.4). A similar trend was observed for *Chlamydomonas* growth rates; however differences among treatments were statistically weaker (Appendix A: Fig. A2.6). Systematic variation in *Brachionus* invasion rates with growing period length may account for deviations between observed and predicted t_z values. Lower than average rates in the ϕ=0.80 and 0.85 treatments should lead to transition times that occur later than mean predicted timings.

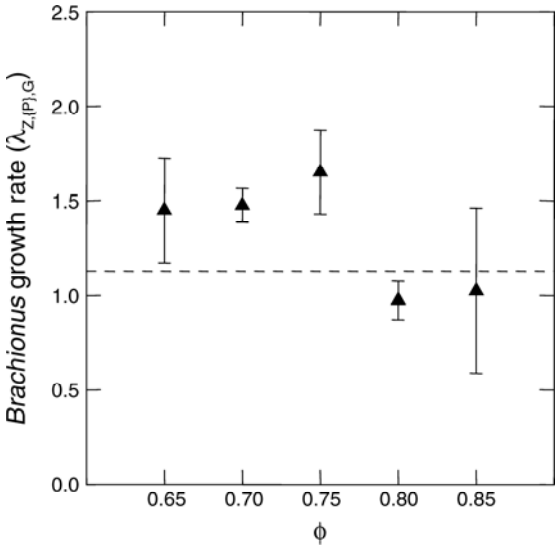


Fig. 2.4. Variation in *Brachionus* growth rates ($\lambda_{Z,\{P\},growing}$) across ϕ treatments in year 2. Shown are means and standard errors. The dashed line represents the mean growth rate generated from year 1 (averaged across ϕ treatments). There was a weak effect of ϕ on $\lambda_{Z,\{P\},growing}$ using one-way ANOVA (P=0.09).

We can only speculate on the cause of variation in zooplankton growth rates among our treatments. One possibility is that algal nutritional quality varied among ϕ treatments early in the growing period. In treatments with shorter

growing periods, *Chlamydomonas* populations started at much lower densities at the initiation of the growing season and thus experienced exponential growth for longer periods of time. For example, algal densities, on average, increased up to four orders of magnitude in the ϕ=0.65 treatment and less than two orders of magnitude in the ϕ=0.85 treatment in year 2 (Fig. 2.2). Algal populations that experience nutrient saturated conditions and exponential growth for longer periods of time should exhibit higher cellular nutrient content (i.e., lower carbon:phosphorus and carbon:nitrogen content) and thus could be of greater nutritional quality for zooplankton. Moreover, *Chlamydomonas* cells grown under nutrient saturated conditions are known to be more easily digested by zooplankton compared to nutrient-limited cells (van Donk *et al*. 1997), further increasing the probability that algal populations in low ϕ treatments were of better quality for *Brachionus*. Whether covariation between zooplankton maximal growth rates and growing season length is a peculiarity of our model system or a generalizable feature of natural planktonic systems is an open question. While our highly simplified system may have amplified such effects, it is not inconceivable that this phenomenon could occur in natural systems, delaying expected zooplankton population peaks. If of sufficient magnitude, our model could be easily altered to allow for changes in zooplankton growth rates with changing ϕ in order to increase quantitative predictive power.

Finally, it is important to note the inherent mismatch between the time scales employed in our model and experiment. The dominant forcing period in natural aquatic ecosystems is one year. In contrast, the SSD approach assumes the limit of infinite period forcing in which species dynamics approach log-linear (as in Fig. 2.1A) and which maintains analytical tractability (Klausmeier unpublished manuscript). Numerical results show that this approximation is reasonable for systems forced at the annual scale (Klausmeier unpublished manuscript). Our laboratory system was forced with an effective period of 16.5–21.5 days; longer periods would have required larger winter dilutions, which would have resulted in less than one rotifer per flask in our 800 mL experimental volumes. Thus, the time scales of our mathematical and laboratory models varied in opposite directions from the natural systems they were intended to mimic, potentially generating discrepancies between our predictions

and empirical results. As ϕ decreased in our experiments, the assumptions of the SSD model were better met, which may account for the stronger match between observed and predicted transition times and the better fits seen in supplemental figures A2.1 and A2.2 (Appendix A).

2.6 Conclusions

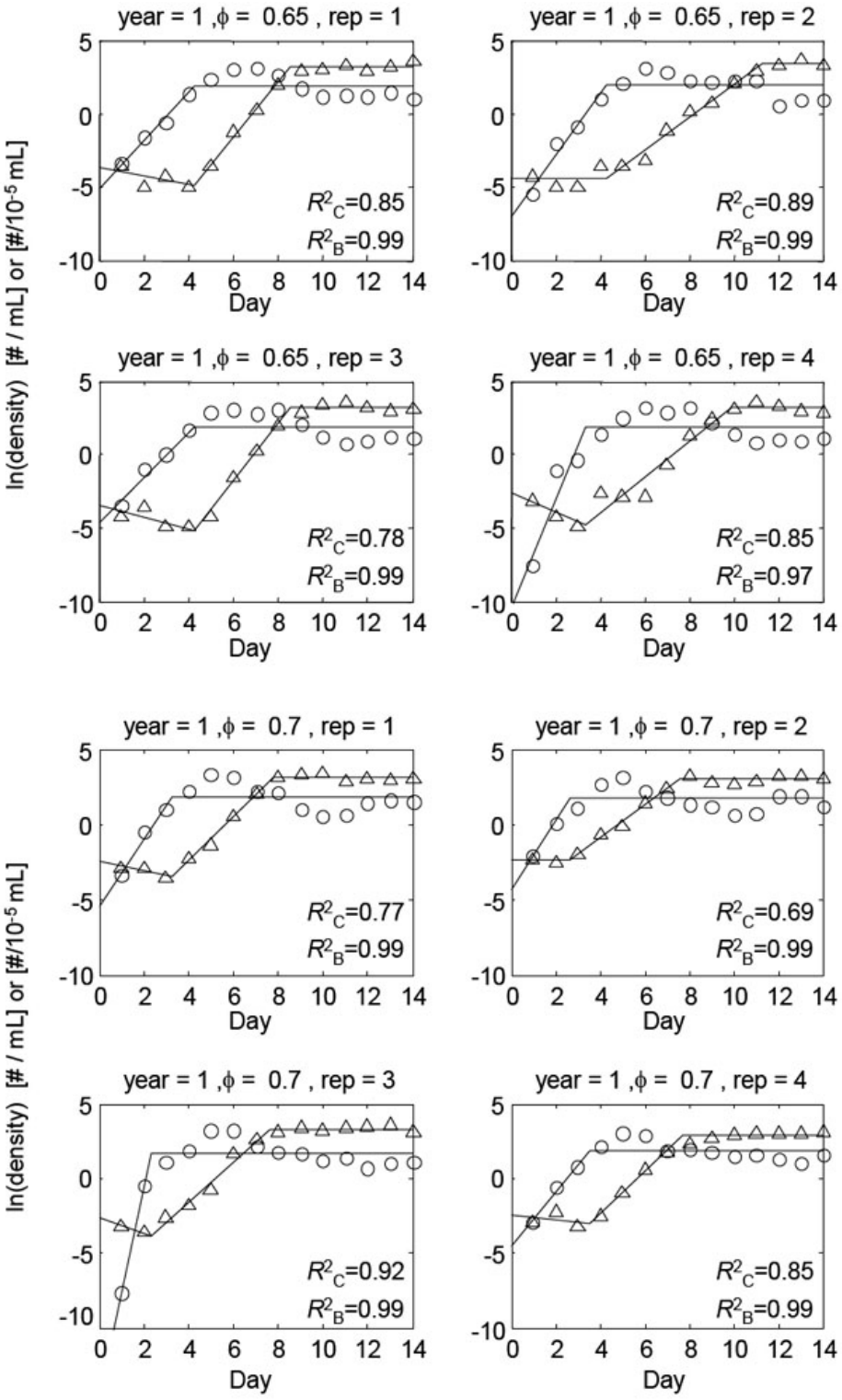
The growing reality of climate change has necessitated more in-depth examination of the role of seasonal forcing and altered seasonality on the structure and dynamics of natural communities (Walther *et al*. 2002; Parmesan and Yohe 2003; Menzel *et al*. 2006; Berger *et al*. 2007; Cleland *et al*. 2007; Huber *et al*. 2008). As increases in average mean temperatures may increase the number of ice-free days temperate lakes experience, the effective length of the growing season is also predicted to increase. How such alterations impact the timing of spring algal blooms and zooplankton population peaks is a vital question facing aquatic ecologists. Our model provides a simple but tractable framework for exploring the dynamic consequences of variation in large-scale seasonal events. We show both theoretically and empirically that the probability of zooplankton population persistence increases with increasing growing period. Furthermore, the timing of zooplankton and algal population blooms depends greatly on the relative length of the growing season with the timing of algal/zooplankton population peaks occurring progressively earlier in the year with increasing growing period. Such advances in the seasonal timing of plankton population peaks have been detected in many long-term data sets (e.g., Winder and Schindler 2004a, 2004b; Huber *et al*. 2008). Our model framework could help to better understand the mechanisms underlying such phenological changes. Given the low number of parameters required by the approach, the successional state dynamics framework can be easily altered to address alternative food web structures while retaining analytical tractability. Moreover, the model's minimal parameter requirement has the advantage of being relatively easy to parameterize empirically and generate quantitative predictions. Thus, compared to more complex, process-based numerical models, the SSD framework could be a more promising approach for generating projections of plankton phenology under future climate warming.

2.7 Acknowledgements

Author contributions: CFS, VH and CAK wrote the paper; CFS and VH analyzed the data ; AS, CAK, CFS and EL designed the experiment; AS and CFS performed the experiment; CAK and EL developed the SSD model; VH wrote the genetic algorithm. We thank D. Shumway, P. Woodruff and A. Morgan for laboratory assistance; M. Evans, J. Mellard, and K. Yoshiyama for valuable comments on the manuscript; and G. Fussmann and S. Ellner for helpful advice on model fitting. This research was supported by National Science Foundation grant DEB-0610532 and a grant from the James S. McDonnell Foundation to CAK and EL. VH was supported by the German Research Foundation (DFG SPP 1162) and the German Academic Exchange Service (DAAD). This is contribution number 1495 of the Kellogg Biological Station.

2.8 Appendix A – supplementary figures

Fig. A2.1. Year 1 data and model fits. Circles are *Chlamydomonas*; triangles are *Brachionus*. R^2 subscripts refer to genus names. *Brachionus* densities are given in units of #/mL while *Chlamydomonas* densities have been rescaled to units of #/10^{-5} mL.



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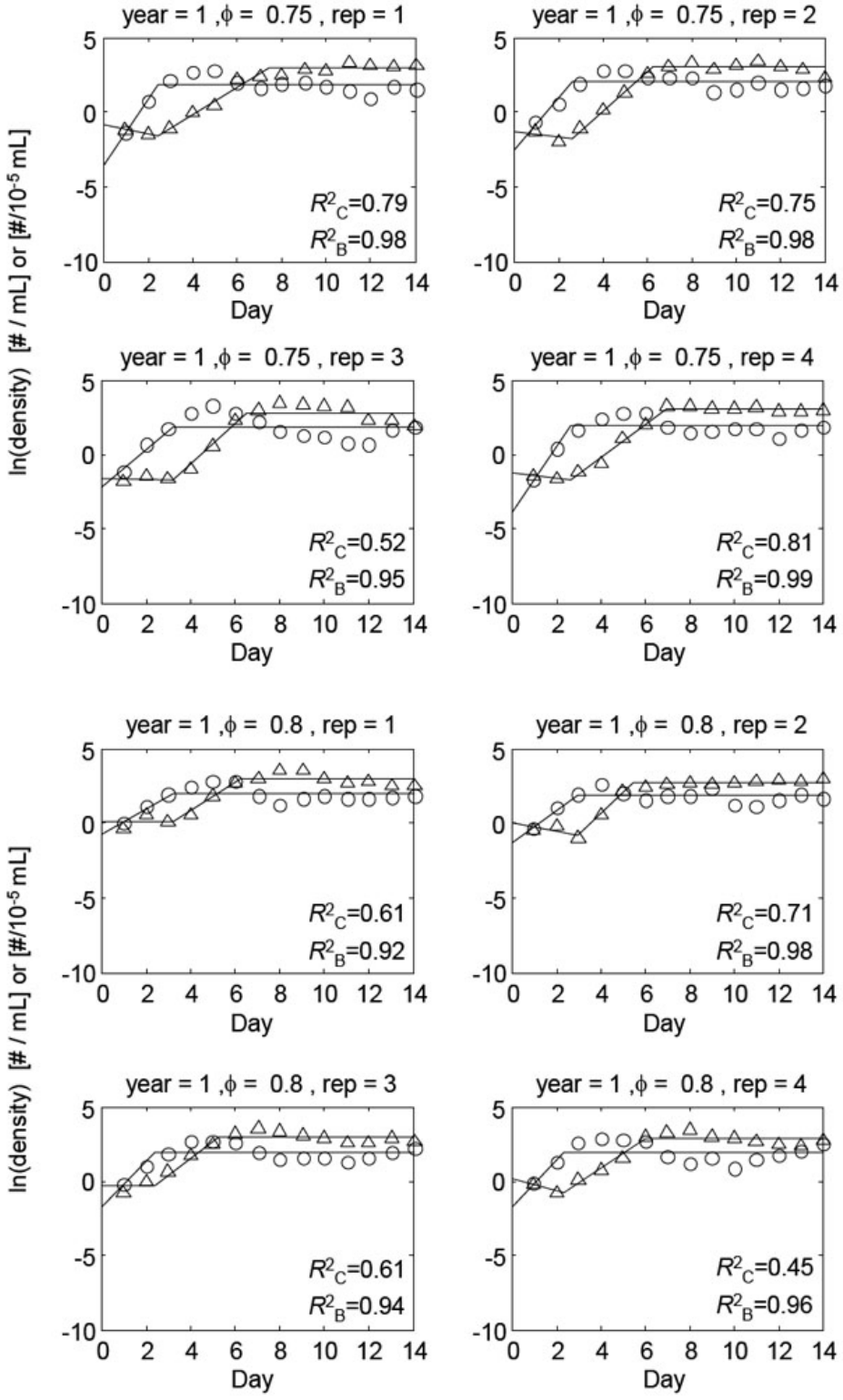

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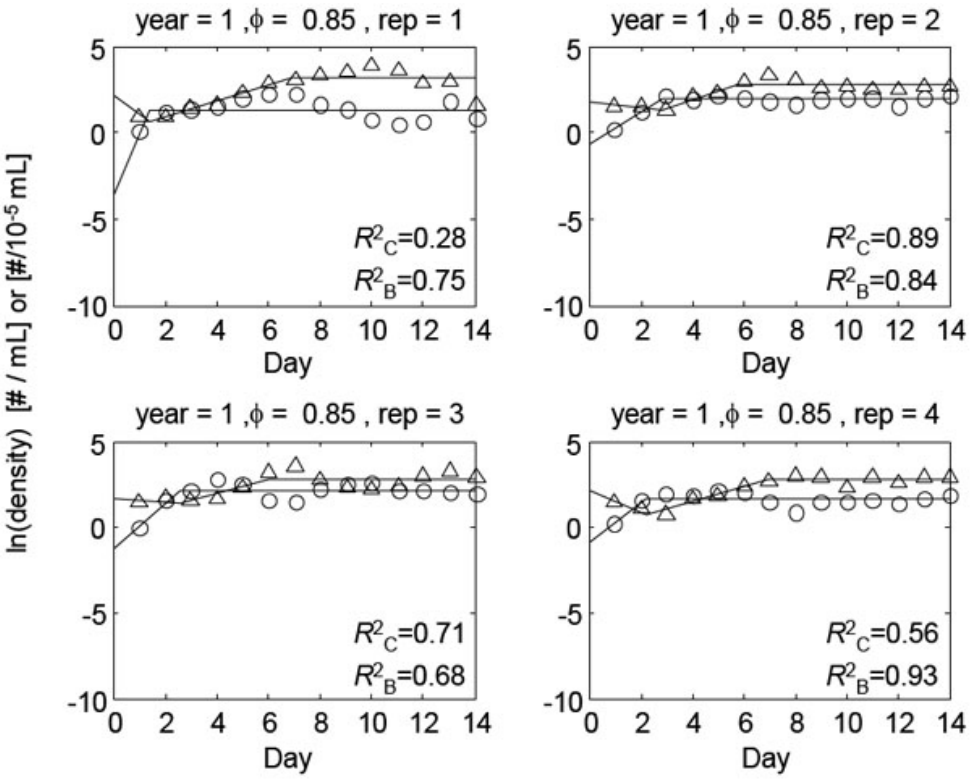
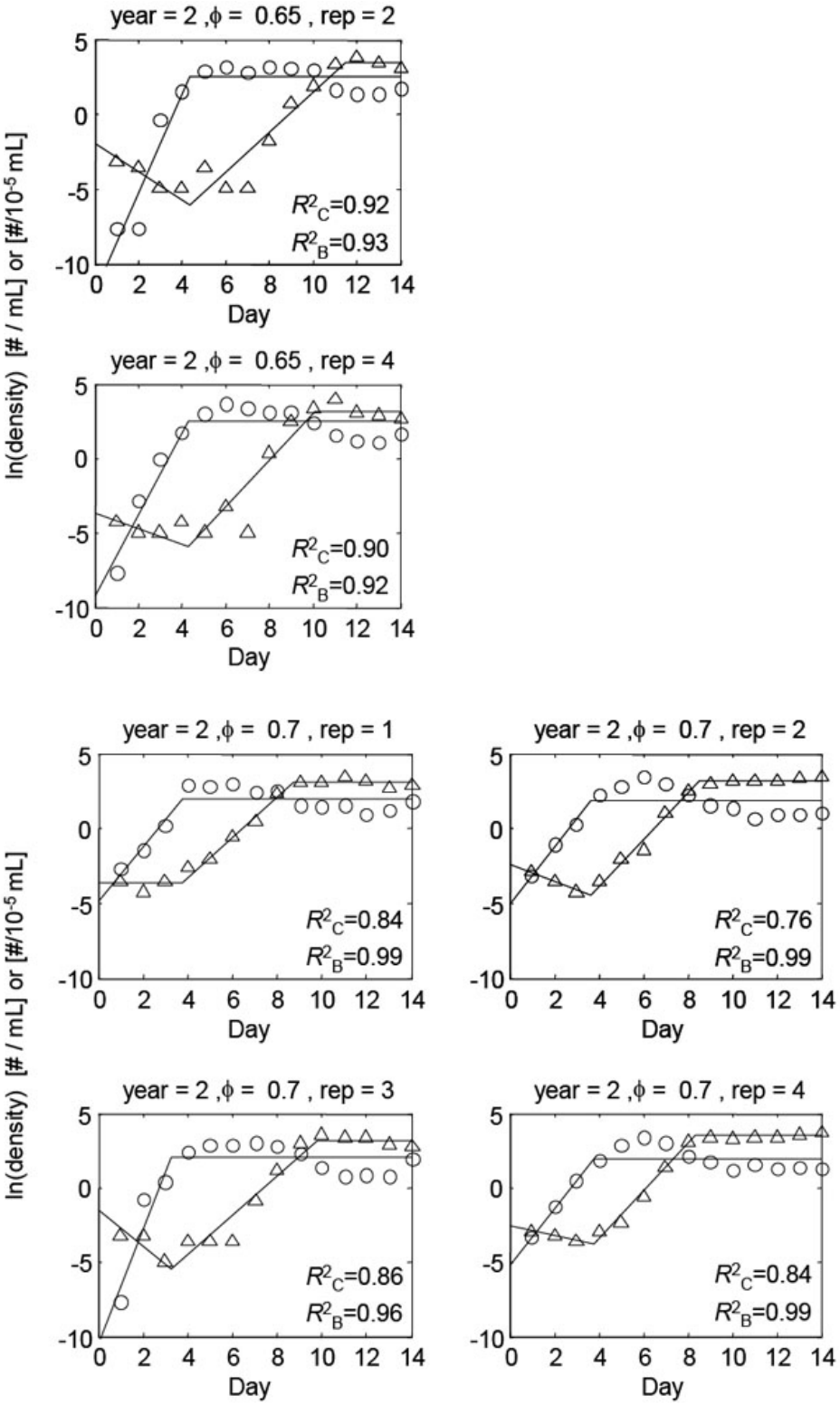


Fig. A2.2. Year 2 data and model fits. Circles are *Chlamydomonas*; triangles are *Brachionus*. R^2 subscripts refer to genus names. *Brachionus* densities are given in units of #/mL while *Chlamydomonas* densities have been rescaled to units of #/10^{-5} mL. Replicates 1 and 3 of the ϕ=0.65 treatment were not used in analyses and are not displayed due to extinction of *Brachionus* at the start of year 2.



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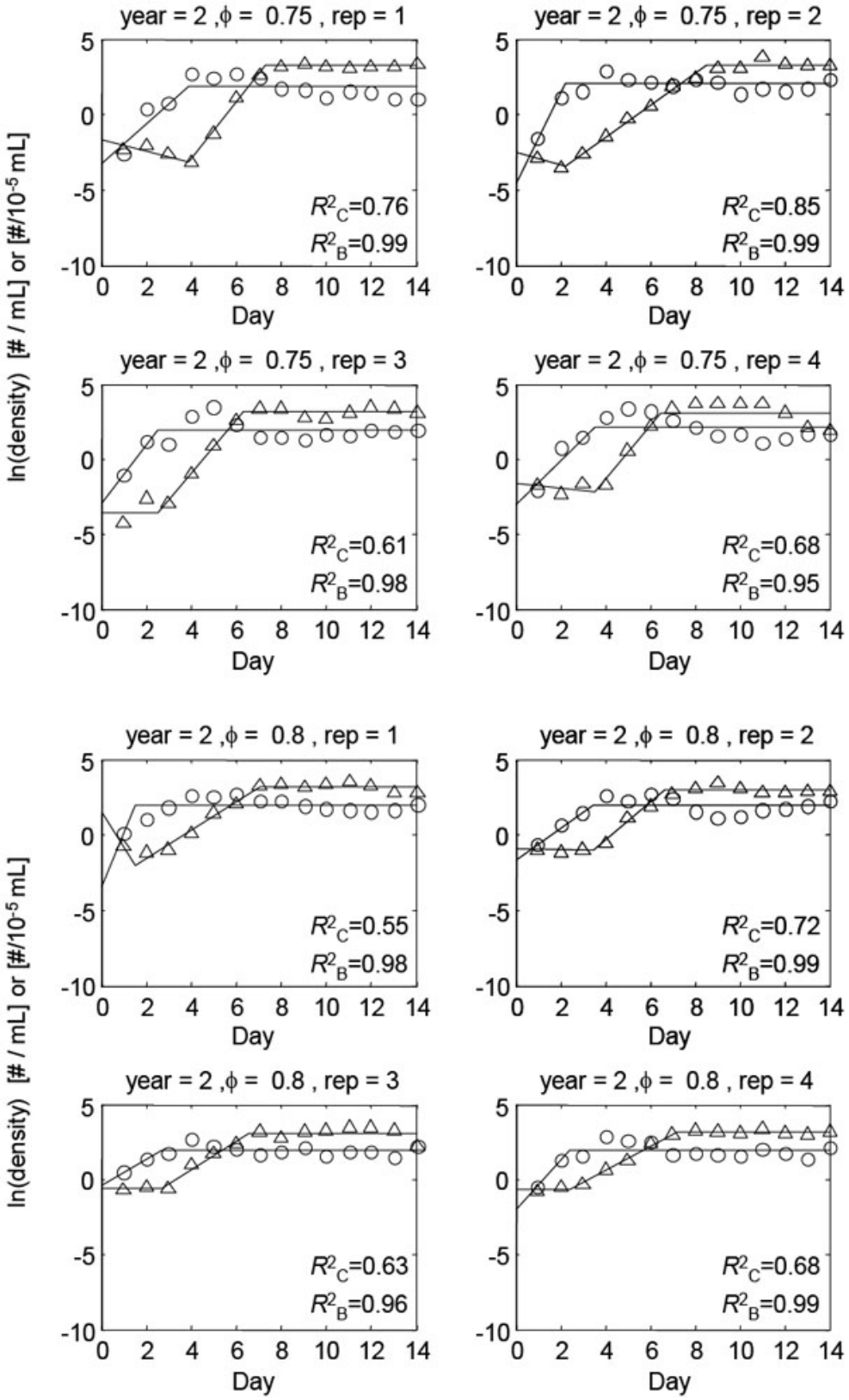

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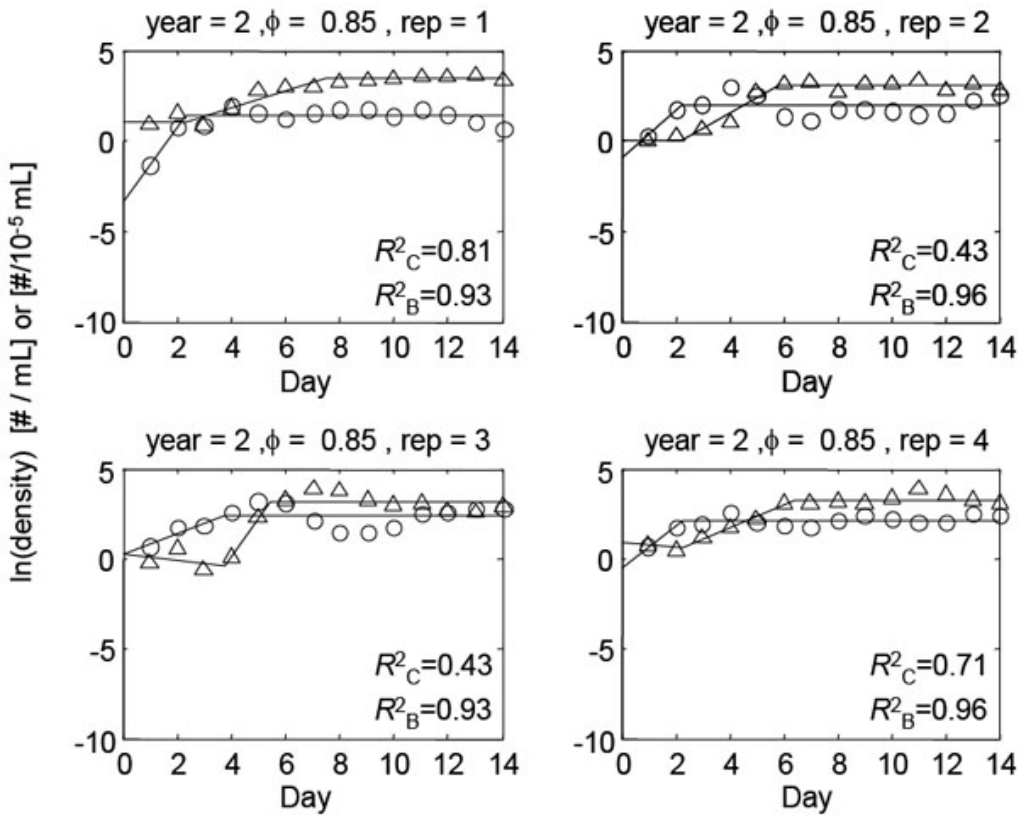
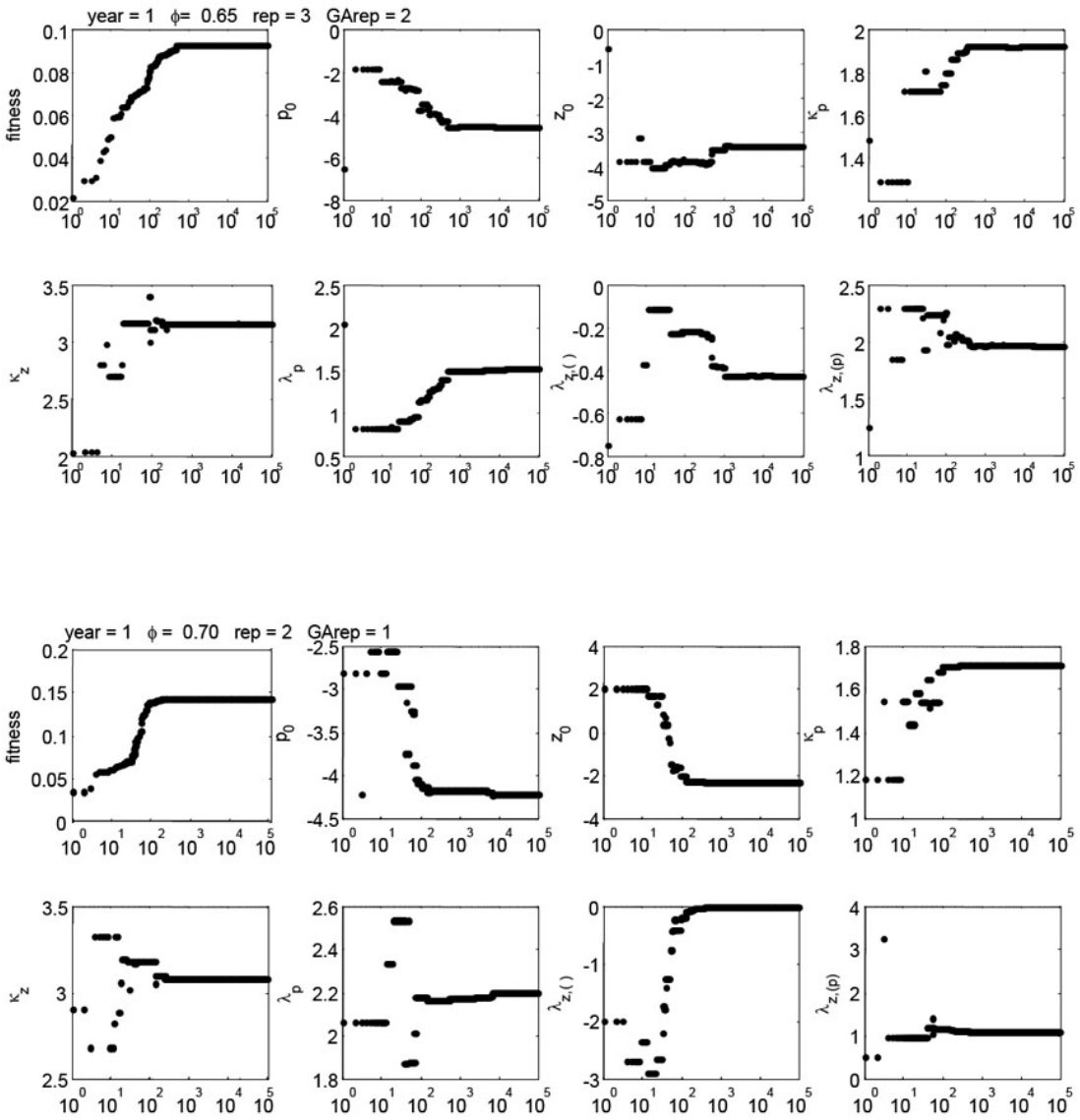


Fig. A2.3. Parameter and fitness convergences generated by the genetic algorithm over time. Representative examples are given for selected initiations of the algorithm (GArep) and for selected replicates of each ϕ treatment in year 1 or year 2. Time on the x-axis has been log transformed to better display changes early in the time series.



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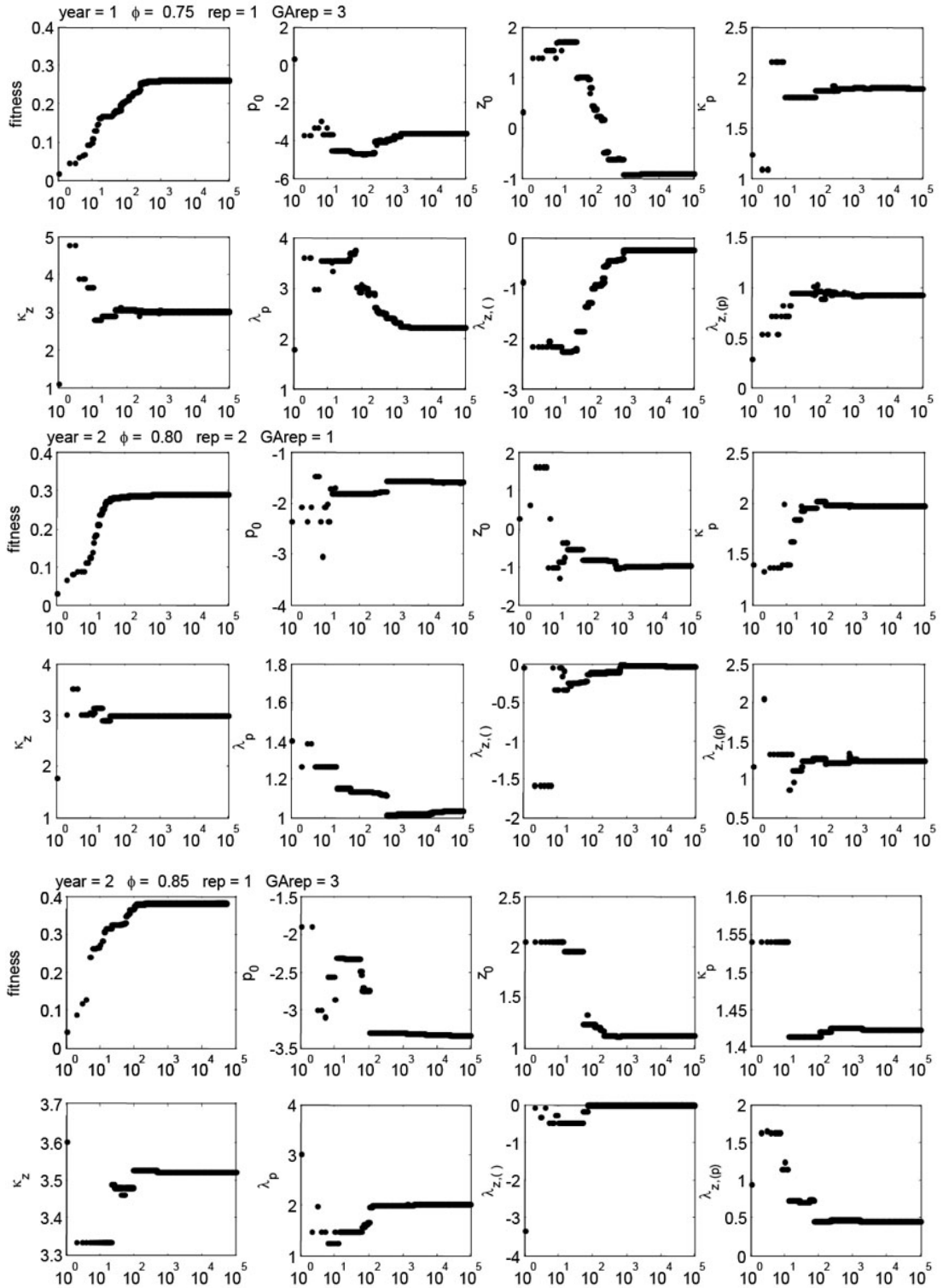


Fig. A2.4. Variation in initial *Brachionus* and *Chlamydomonas* densities across ϕ treatments and between year 1 and year 2. Estimates of initial densities were obtained from the SSD model fits for each replicate. Shown are means and standard errors. Year and ϕ effects were tested using ANOVA. A significant effect of ϕ was detected for *Chlamydomonas* (P<0.0001), but no effect of year or an interaction were present (all P>0.40). Significant effects of ϕ (P<0.0001) and year (P<0.034) were present for *Brachionus*; no interaction was detected (P=0.11).

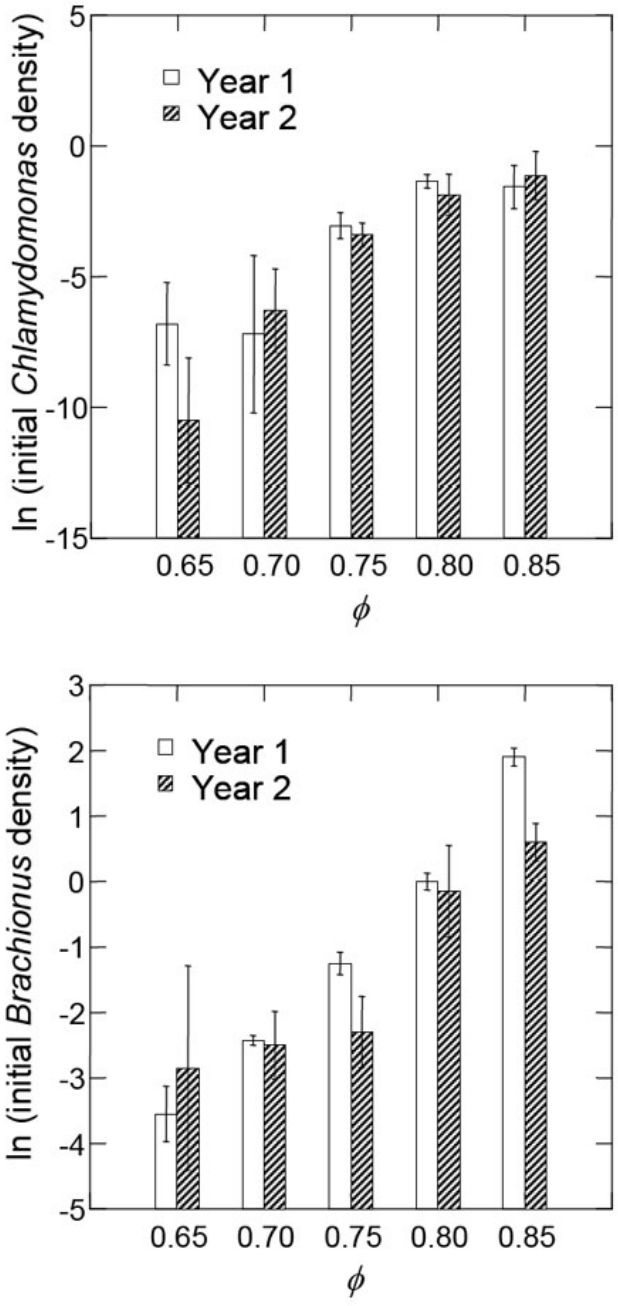


Fig. A2.5. Variation in *Brachionus* growth rates across ϕ treatments in year 1. Shown are means and standard errors. Growth rates varied among ϕ treatments (P<0.001, one-way ANOVA).

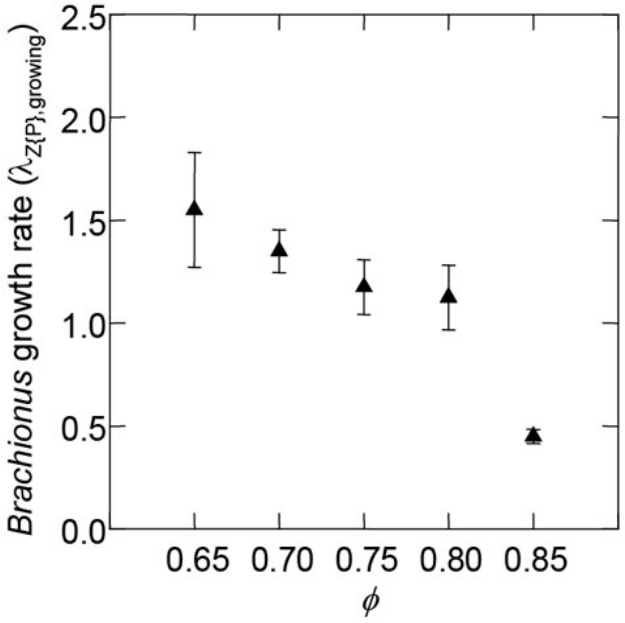
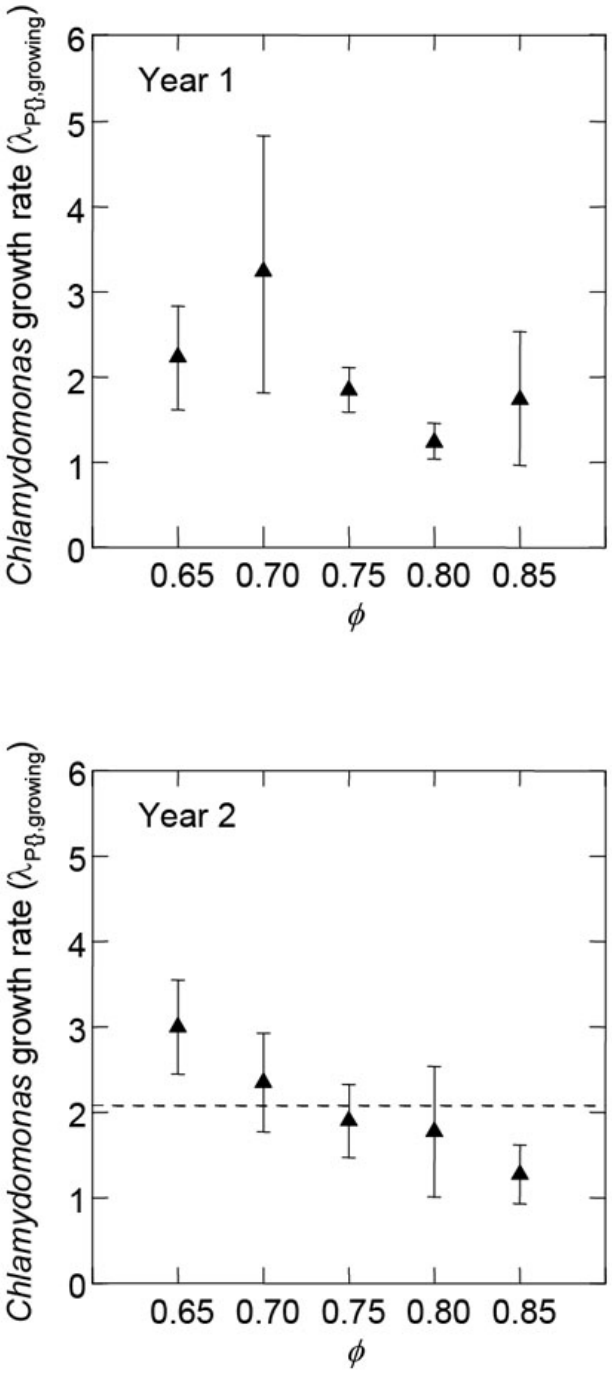


Fig. A2.6. Variation in *Chlamydomonas* growth rates across ϕ treatments in year 1 and 2. Shown are means and standard errors. The dashed line in the year 2 panel represents the mean growth rate generated from year 1 (averaged across ϕ treatments). There was no effect of ϕ in year 1 (P=0.32, one-way ANOVA). Although a trend for decreasing growth rate with increasing ϕ was evident in year 2, the effect was weak (P=0.19, one-way ANOVA).



2.9 Appendix B – description of the genetic algorithm

The genetic algorithm was based on a procedure used by Tietjen and Huth (2006) and Huber *et al*. (2008). For a more general introduction to genetic algorithms see Haupt and Haupt (1998). It was initialized by creating a suite of 64 parameter sets. Each set consisted of 7 parameters (the growth rates $\lambda_{P,\{\},growing}$, $\lambda_{Z,\{\},growing}$, $\lambda_{Z,\{P\},growing}$, the density thresholds K_p, K_z, and the initial densities P_0, Z_0). The parameters were drawn randomly from intervals defined by visually inspecting the data. The genetic algorithm was run for each replicate of the five period length treatments (ϕ = 0.65, 0.7, 0.75, 0.8 and 0.85) separately. Once initiated, each generation of the genetic algorithm was composed of the following steps:

a) Selection of the best parameter set: For each parameter set the trajectories of the SSD model (Fig. 2.1A) were established by numerically determining timing and densities at transitions t_p and t_z (for details see Klausmeier unpublished manuscript). After interpolation of trajectories, fitness F of each parameter set was evaluated by assessing the inverse of the sum of squared differences in observed and predicted densities $F = \frac{1}{\sum(observed - predicted)^2}$. Then, a total of 8 parameter sets were selected: the two sets that produced the highest fitness and six other parameter sets chosen randomly with a probability proportional to their fitness.

b) Crossover: A new suite of parameter sets was constructed by recombining all possible pairs of the selected parameter sets. The recombination consisted of cutting the parameter string of two sets at a random position and creating two new sets by combining the corresponding parts of the parameter strings.

c) Mutation: After recombination, random changes were imposed on parameters with a mutation rate of 0.1 (except for the parameter set that had produced the best performance). The magnitude of mutation, added to the current parameter value, was drawn from a normal distribution $N(0,\sigma_m)$ where σ_m was 1 for thresholds and initial densities and 0.5 for growth rates. If growth rates underwent a sign change during the

mutation procedure, the magnitude of mutation was alternatively drawn from a uniform distribution between zero and the current parameter value.

These steps were repeated for 300 000 generations. Last, the parameter set with the highest fitness in the final selection procedure provided the default parameter estimates. We applied several test runs of the genetic algorithm to make sure that the chosen number of generations was sufficient for convergence. The convergence criterion applied was that the parameter estimates for three independent initializations of the genetic algorithm did not differ more than by 0.1 in the first decimal place. Example plots showing that parameters converged quickly to their default values can be found in Appendix A.

Chapter 3

To bloom or not to bloom: contrasting development of cyanobacteria during the European heat waves of 2003 and 2006 in a shallow lake

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In revision for *Global Change Biology* as Huber V., C. Wagner, D. Gerten and R. Adrian. To bloom or not to bloom: contrasting development of cyanobacteria during the European heat waves of 2003 and 2006 in a shallow lake.

3.1 Abstract

Heat wave events might give us a glance of the climate to come and therefore allow investigating how ecosystems could evolve in the future. In nutrient-rich freshwater systems, harmful blooms of cyanobacteria are considered to be promoted under heat wave conditions, posing a threat to water quality. Here the effects of the Central European summer heat waves in 2003 and 2006 on cyanobacteria of a eutrophic, shallow lake were evaluated. While a bloom of cyanobacteria developed in 2006 according to expectations, cyanobacteria surprisingly remained at a record-low during the entire summer of 2003. Results of classification tree analysis based on a long-term (1993-2007) data set of physical, chemical and biological variables suggested that differences in air temperature and wind speed and related differences in the timing, intensity and duration of thermal stratification were the main reasons for the contrasting development of cyanobacteria. In addition to seasonal patterns of heat wave conditions, which were less favourable for blooms in 2003 than in 2006, differences in grazer (daphnid) abundance might have also contributed to the suppression of a cyanobacteria bloom in 2003. Our findings point to the importance of local weather patterns and caution against conclusions on climate change as a catalyst of cyanobacteria blooms that are drawn from single extreme events and that consider meteorological conditions averaged over large temporal scales only.

3.2 Introduction

Central Europe has recently experienced several extreme heat waves, most prominently the summer heat wave of 2003. Mean air temperature in the summer of that year exceeded the long-term average by around 3°C over a large area (Schär et al. 2004). Similarly, mean air temperatures in July 2006 locally were up to 5°C higher than on average (Struzewska and Kaminski 2008). Assessing the impacts of such extreme weather conditions on ecosystems is important, especially because summer heat waves are expected to occur more frequently under future climate warming (Meehl and Tebaldi 2004; Schär and Jendritzky 2004). Aquatic ecosystems have been shown to be strongly affected by the summer heat wave of 2003 (Jankowski *et al.* 2006; Daufresne *et al.* 2007; Wilhelm and Adrian 2007); in particular, the occurrence of harmful cyanobacteria blooms was promoted in some nutrient-rich water bodies (Paerl and Huisman 2008; Jöhnk *et al.* 2008).

Cyanobacteria pose a threat to water quality in many aquatic ecosystems (Huisman *et al.* 2005). Therefore, the factors that induce blooms of harmful cyanobacteria have been the subject of intensive research in the past decades. It is well established knowledge that nutrient enrichment of water bodies (eutrophication) enhances the risk of cyanobacteria blooms (Huisman and Hulot 2005). Considering that cyanobacteria species can differ quite substantially in functional attributes (e.g., nitrogen fixing, buoyancy), generalization of processes promoting blooms is difficult (Hyenstrand *et al.* 1998; Dokulil and Teubner 2000). However, high concentrations of total phosphorus and total nitrogen (Downing *et al.* 2001) and also low supply ratios of nitrogen to phosphorus (Smith 1983) have been shown to correlate with high biomass of cyanobacteria in many systems.

More recently, scientists have turned their attention to the question of climate change as a potential catalyst for the extension and intensification of cyanobacteria blooms (de Senerpont Domis *et al.* 2007b; Paerl and Huisman 2008). Besides possible indirect effects such as climate-induced nutrient enrichment, cyanobacteria are thought to be directly favoured by rising water temperatures, as their high temperature optima for growth (e.g., around 28 °C

for the cyanobacteria species *Microcystis* sp.) give them a competitive advantage over other algae in warm water (Butterwick *et al.* 2005; Jöhnk *et al.* 2008). In eutrophic water bodies, buoyant cyanobacteria species are also known to benefit from intensified and prolonged thermal stratification that often co-occurs with high water temperatures (Huisman *et al.* 2005). When the stability of the water column is high, their buoyancy enables them to float to the surface and out-compete other algae for light (Huisman *et al.* 2004).

Cyanobacteria blooms have been observed in the nutrient-rich shallow lake studied here (Müggelsee) during most summers since the start of a monitoring program in 1979. The lake, located in north-eastern Germany, was under the influence of the European summer heat waves of 2003 and 2006. Despite similarly favourable physical conditions (high water temperatures and relatively strong thermal stratification) at times of anomalously hot weather cyanobacteria bloomed strongly in the summer of 2006, but remained at a record low during all of 2003.

Recently, Wagner and Adrian (2009) used classification tree analysis to identify the main environmental factors that determine the contribution of cyanobacteria to total phytoplankton biovolume in Müggelsee. They showed that while high total phosphorus concentration was the best indicator of elevated cyanobacteria contribution, intensified and prolonged thermal stratification also promoted cyanobacterial dominance in this polymictic lake. Here, we used the critical thresholds of environmental factors determined by Wagner and Adrian (2009) to investigate the reasons for the surprisingly contrasting development of cyanobacteria during the heat wave summers of 2003 and 2006. Classification tree analysis was also applied to characterize meteorological conditions that favour thermal stratification in the lake.

3.3 Methods

Study sites and data basis—Müggelsee (52°26’ N, 13°39’ E) is a polymictic, shallow lake (mean depth 4.9 m, maximum depth 7.9 m) with a surface area of 7.3 km^2. An ongoing sampling program has collected data on plankton, physical and chemical variables, with biweekly sampling in winter and weekly sampling

in summer, beginning in 1979 (Driescher *et al*. 1993). Since the start of this sampling program the lake has experienced an increase in water temperature (around 0.5 °C per decade in summer) and quasi-simultaneously a decrease in nutrient loading (Köhler *et al*. 2005; Huber *et al*. 2008). To restrict confounding effects of a change in trophic state (Köhler *et al*. 2005) and also due to missing data for total nitrogen prior to 1993, analyses were restricted to 1993-2007, the eutrophic phase of the lake. Intermittent thermal stratification during summer is common in this shallow lake (exposed to prevailing south-westerly winds), with consequent effects on water temperature, oxygen, internal nutrient load, and phytoplankton development (Wilhelm and Adrian 2008).

Weekly profile measurements (0-5 m depth at 0.5 m intervals) of water temperature (°C) were used to calculate the Schmidt stability index (g cm cm^{-2}) according to Soranno (1997), which assesses the intensity of thermal stratification of the water column:

$$S_i = A_0^{-1} \sum_{s=0}^{z_{\max}} (s - z^*)(\rho_s - \rho^*) A_s \Delta z \qquad (1)$$

where A_0 the surface area of the lake, A_s lake area at depth s; p_s density calculated from water temperature at depth s, ρ^* mean density; z^* depth where mean density occurs, z_{max} maximum depth, and Δz depth interval of 1 m.

We considered the lake to be thermally stratified when the difference in water temperature between the surface and at 5 m depth was > 1°C (Wilhelm and Adrian 2008; Wagner and Adrian 2009). High frequency data (available from an automatic measurement station on the lake since 2003) revealed that the weekly data of water temperature used here is a good indicator of the timing and duration of thermal stratification events that last longer than 1 week (Wagner and Adrian 2009). Only one of six thermal stratification events > 1 week observed between 2003 and 2006 was misclassified in duration (Wagner and Adrian 2009). All nutrient concentrations (total nitrogen (TN, mg L^{-1}), total phosphorus (TP, μg L^{-1}), and soluble reactive phosphorus (SRP, μg L^{-1})) and plankton abundance used in this study (see below) were determined from volumetrically weighted mixed samples in the absence of thermal stratification, while only the upper 3.5 m of the water column, corresponding to the average

epilimnetic depth, were taken into account when the lake was stratified (Wilhelm and Adrian 2008).

Algal biovolumes (mm^3 L^{-1}) were determined using standard limnological techniques, based on microscope counts and individually measured cell volumes (Driescher *et al.* 1993). However, data on individual cell and filament volumes (μm^3 ind^{-1}) were not accessible prior to 1999. Data resolved to phytoplankton species level was summed to yield time-series of total phytoplankton, cyanobacteria, cryptophytes, and the cyanobacteria genus *Anabaena*, which was dominant during the summer of 2006. Since individual body size of zooplankton was not directly measured we used the available abundance data (ind. L^{-1}) to construct time-series of the main zooplankton groups, daphnids and cyclopoid copepods. Given that grazing pressure on phytoplankton is closely linked to zooplankton body size (Sterner 1989; Adrian and Frost 1992) we cannot exclude that the lack of individual body-size measurements introduced a certain bias. However, daphnid and cyclopoid copepod species composition was similar in the heat wave summers of 2003 and 2006 (dominating species were *Daphnia cucullata,* and *Mesocyclops* sp. and *Thermocyclops* sp., respectively, in both years). This similarity made us confident that differences in abundance also translated into differences in grazing pressure, at least in these two years.

Mean weekly measurements of meteorological variables were provided by the nearby weather station Schöneiche (~ 4 km to the northeast of Müggelsee) for 1993-2006. In addition to Müggelsee, data of mean cyanobacteria biovolume during the summers of 2003 and 2006 in eight other mesotrophic to hypertrophic lakes of north-eastern Germany was available from the German national lake phytoplankton data base compiled by Mischke (2008; LAWA-project O9.08; unpublished data). Summer was defined as the period from June to August.

Classification tree analysis—Classification tree analysis is a nonparametric, recursive data-mining technique that produces a collection of rules, involving thresholds of key predictor variables, to best explain variability in a categorical response variable (for further details see Wagner and Adrian 2009; Breiman *et al*. 1993). When applying this method to cyanobacteria data, Wagner and Adrian

(2009) constructed categorical response variables indicating whether the cyanobacteria contribution to total phytoplankton biovolume exceeded (value 1) or fell below (0) a predefined percentage. They found that three of the computed classification trees (namely cyanobacteria contribution cut-offs 30%, 50%, and 70%) best separated the main environmental drivers of cyanobacteria dominance in Müggelsee. Here, we adopted the authors' three contribution classes 30%, 50%, and 70% and used the identified classification rules, including as key predictor variables concentrations of TN and TP, duration and intensity of thermal stratification, and log-transformed daphnid abundance (Table 3.1), to explore the reasons for the contrasting development of cyanobacteria in 2003 and 2006.

Table 3.1. Rules derived from classification tree analysis of Wagner and Adrian (2009) to predict ranges of cyanobacteria contribution to total phytoplankton biovolume (< or >= 30%, < or >= 50%, < or >= 70%) using thresholds for total nitrogen (TN), total phosphorus (TP), log-transformed daphnid abundance (Daph), duration of thermal stratification (S_d), and intensity of stratification (Schmidt stability, S_i) (for units of these variables see Fig. 3.2). Percentages of misclassified cases were calculated based on weekly data of 1993-2007, considering summer thermal stratification events (30% class) and the entire summer (50% and 70% classes), respectively. Rules classifying cyanobacteria contribution >= 70% were not used in the analysis of 2003 and 2006 because misclassification occurred in > 60% of these cases. Symbols as in Fig. 3.3.

Cyanobact. contribution	Time period	Symbol	Rule	# cases	# errors	% errors	% errors (< / >)	% errors total
< 30%	Summer thermal stratification	▽	TN<=1.01 & TP<=70	12	0	0	24	21
		▼	TN<=1.01 & TP>70 & Daph>1.6	22	8	36		
>=30%		△	TN>1.01	27	5	19	18	
		▲	TN<=1.01 & TP>70 & Daph<=1.6	6	1	17		
< 50%	All summer	▽	TP<70	23	0	0	19	23
		▼	70<=TP<=215 & S_d<=3	127	29	23		
>=50%		△	TP>215	30	12	40	37	
		▲	70<=TP<=215 & S_d>3	16	5	31		
< 70%	All summer	▽	TP<70	23	0	0	11	
		▼	70<=TP<=215 & S_i<=44	127	17	13		
>=70%		△	TP>215	30	19	63	(61)	
		▲	70<=TP<=215 & S_i>44	11	6	55		

While Wagner and Adrian (2009) analysed thermal stratification events only, we additionally assessed the predictive power of these rules for the whole summer, with the aim of increasing the number of data points in the analysis. Predictive power was estimated by computing the proportion of cases, in which cyanobacteria contribution was wrongly classified to lie below or above the respective limits (30%, 50% or 70%). Due to considerably higher frequency of misclassification when the lake was non-stratified, we decided to limit the analysis of contribution class 30% to times of thermal stratification (Table 3.1). For contribution classes 50% and 70% the entire summer was considered (Table 3.1). Since cyanobacteria contribution to total phytoplankton biovolume was strongly positively correlated to absolute cyanobacteria biovolume in summer (Spearman's $\rho = 0.94$, $p < 0.001$, $n = 190$), factors identified as influential for cyanobacteria contribution were also assumed to affect absolute biovolume.

To identify the meteorological factors that determine the occurrence of thermal stratification in Müggelsee we also applied classification tree analysis. We used a categorical response variable indicating stratified (value 1) or non-stratified (value 0) conditions and included as predictor variables air temperature (°C), cloudiness (1/8), incident global radiation (W m^{-2}), wind speed (m s^{-1}), and relative humidity (%), which were found to influence the thermal regime in Müggelsee (Wilhelm *et al.* 2006). Weekly data of the entire time period 1993-2006 were considered, and the frequency of misclassification was assessed as for cyanobacteria classification rules (Table 3.2). All computations were done using Matlab 7.6.0 (The MathWorks 2008).

Table 3.2. Rules resulting from classification tree analysis to predict the occurrence of thermal stratification using thresholds for incident radiation (IR), wind speed (WS), and air temperature (AT) (for units of these variables see Fig. 3.4). Percentages of misclassified cases were calculated based on mean weekly data of 1993-2006.

Thermal stratification	Rule	# cases	# errors	% errors	% errors	% errors total
No	IR<=173.9	536	19	4		
No	IR > 173.9 & WS > 3	44	6	14	10	11
No	IR >173.9 & WS <= 3 & AT <= 20.5	99	42	42		
Yes	IR >173.9 & WS <= 3 & AT > 20.5	49	12	24	24	

3.4 Results

Physical water conditions and contrasting development of cyanobacteria—Mean summer water temperature in 2003 and 2006 exceeded that in all other years (1993-2007), being around 1.6 °C (2003) and 1.5 °C (2006) higher than the long-term mean (μ) (Fig. 3.1). Mean thermal stratification intensity (Schmidt stability) was especially strong in the summer of 2006 (2.7 standard deviations (σ) above μ), but was also relatively strong in 2003 (0.8 σ above μ).

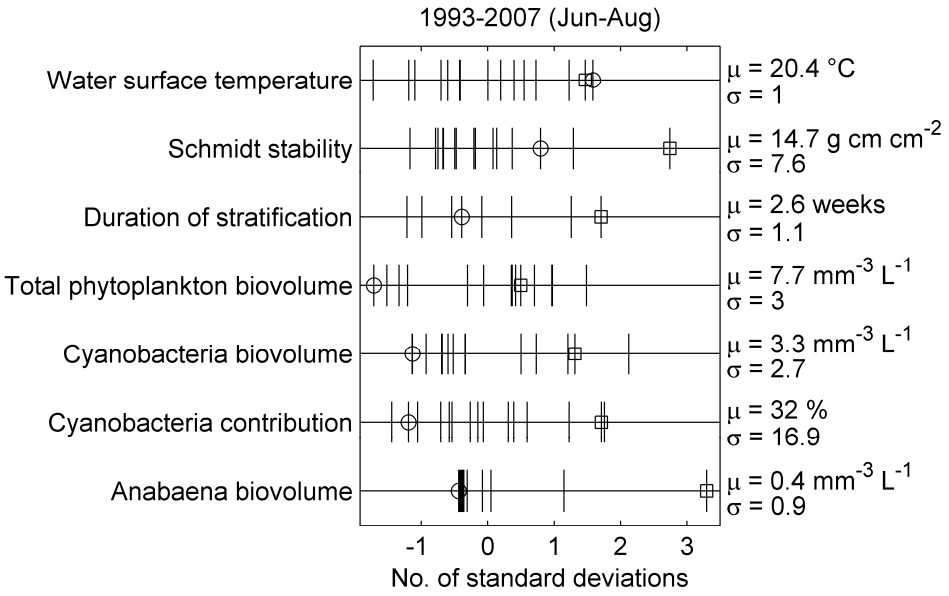

Fig. 3.1. Comparison of heat wave summers 2003 (open circles) and 2006 (open squares) in terms of summer averages of selected physical and biological variables in Müggelsee. The summer averages were standardized by removing the long-term means μ (1993-2007) and dividing by the long-term standard deviations σ, as given on the right-hand side.

Although average water temperature was similarly favourable for cyanobacteria in 2003 and 2006, their development was strikingly different between years. In accordance with expectations, a bloom of cyanobacteria developed in the summer of 2006: Mean cyanobacteria biovolume as well as mean contribution to total phytoplankton bivolume was at the high end of values observed during the eutrophic phase of the lake (Fig. 3.1; Fig. 3.2A). In particular, biovolume of the genus *Anabaena* reached more than 3 σ above μ (Fig. 3.1). In strong contrast, cyanobacteria biovolume, just like total phytoplankton biovolume, reached an all-record low in the summer of 2003 and average cyanobacteria contribution was the second lowest on the 1993-2007 record (Fig 3.1; Fig. 3.2A).

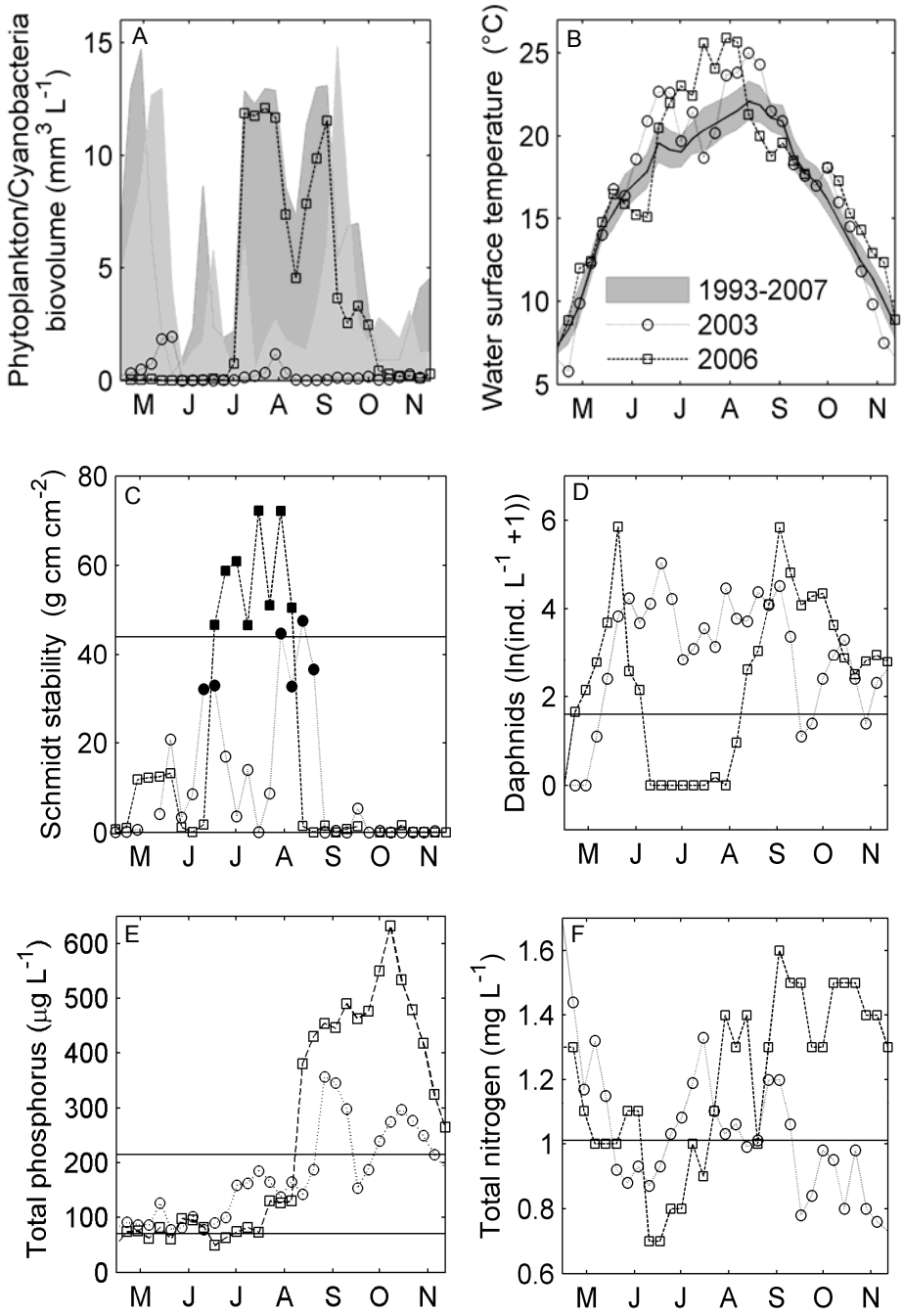

Fig. 3.2. Seasonal dynamics of A) phytoplankton biovolume (shaded areas) and cyanobacteria biovolume (markers and lines), B) water surface temperature, C) thermal stratification intensity (Schmidt stability), D) log-transformed daphnid abundance, E) concentration of total nitrogen, and F) concentration of total phosphorus; during 2003 (open circles with dotted lines) and 2006 (open squares with dashed lines). In panel B the weekly long-term mean (1993-2007) ± 1 SE is indicated by the shaded area. The lake is considered thermally stratified during weeks marked with filled symbols in panel C. Horizontal lines in panels C-F mark thresholds used in classification rules of Table 3.1 and Fig. 3.3.

Seasonal patterns of water temperature and thermal stratification—As a first step to better understand the striking contrast in cyanobacteria development, we considered the seasonal patterns of water temperature and thermal stratification. While the water temperature was continuously above the long-term average from mid-June to mid-August in 2006, two separated periods of relatively warm water were observed in June and August of 2003 (Fig. 3.2B). The mixing regime of the lake followed the same pattern: an 8-week period of continuous thermal stratification in 2006, and by contrast two shorter stratification periods (of 2 and 4 weeks) in 2003 (Fig. 3.2C). Due to the intermittent mixing event in July of 2003 the mean duration of stratification was around average in this summer, despite a relatively strong intensity of stratification (Fig. 3.1). As follows, we investigated whether this mixing event was a sufficient explanation for the surprisingly low biovolume of cyanobacteria in 2003 or whether other environmental factors were also influential.

Rule-based predictions of cyanobacteria contribution to total phytoplankton biovolume—Mean frequencies of misclassification of cyanobacteria contribution to total phytoplankton biovolume (calculated based on 1993-2007) were ~21%, ~23% and ~11% for contribution classes 30%, 50%, and 70%, respectively (Table 3.1). These values gave us confidence that the selected classification rules derived from Wagner and Adrian (2009) provide insight into the environmental factors that caused the outstanding difference in cyanobacteria development in 2003 and 2006.

Classification rules suggested that for much of the summer 2003 the insufficient *duration* of thermal stratification (<= 3 weeks) was the determinant factor that kept cyanobacteria contribution below 50% (Fig. 3.3C). Except for one week in early July, observed cyanobacteria contribution indeed remained below 50% during this time. The duration of stratification reached the critical threshold of 4 weeks, allowing for cyanobacteria dominance according to the classification rules, only once in August 2003. By contrast, in 2006 missing or insufficiently long stratification (<= 3 weeks) was predicted to prevent the dominance of cyanobacteria early in the summer only (Fig. 3.3D). During all of July 2006,

cyanobacteria contribution was correctly classified to lie above 50% due to an extended period of stratification (> 3 weeks).

Comparing 2003 and 2006 in terms of *intensity* of thermal stratification gave a similar picture: while insufficiently strong stratification (Schmidt stability <= 44 g cm cm^{-2}) prevented a pronounced dominance (>= 70%) of cyanobacteria once in early summer of 2006 only, the intensity of stratification fell below the critical threshold several times during the summer of 2003 (Fig. 3.2C; Fig. 3.3E,F). In all of these cases, predictions well matched observations. Thus, it appears from this analysis that differences in thermal stratification pattern were indeed at least one of the reasons why cyanobacteria contribution to total phytoplankton biovolume stayed low in 2003 while it reached high values in 2006.

After the breakdown of thermal stratification in August of both years (Fig. 3.2C), high TP concentrations (> 215 μg L^{-1}; Fig. 3.2E) apparently favoured cyanobacteria dominance. However, while in 2006 cyanobacteria contribution exceeded 50% during much of this period (Fig. 3.3D), it stayed extremely low in 2003 despite high TP concentrations (Fig. 3.3C). Very unfavourable TP concentrations, below the lower critical threshold (< 70 μg L^{-1}), occurred in early summer of 2006 (Fig. 3.2E; Fig. 3.3B,D,F), but were never prevailing in 2003.

During the two weeks that preceded that breakdown of thermal stratification in August 2003 (Fig. 3.2C) cyanobacteria contribution was predicted to lie below 30% because concentrations of TN and log-transformed daphnid abundance had crossed their critical thresholds (<= 1.1 mg L^{-1} and >1.6 ind. L^{-1}, respectively) (Fig. 3.2D,F and Fig. 3.3A). In contrast, cyanobacteria contribution was classified to be above 30% for six of the eight weeks of stratification in 2006, due to low daphnid abundance (<=1.6 ind. L^{-1}) and high TN concentrations (> 1.1 mg L^{-1}) (Fig. 3.3B). In accordance with these predictions, cyanobacteria contribution was observed below and above 30%, respectively (Fig. 3.3A,B).

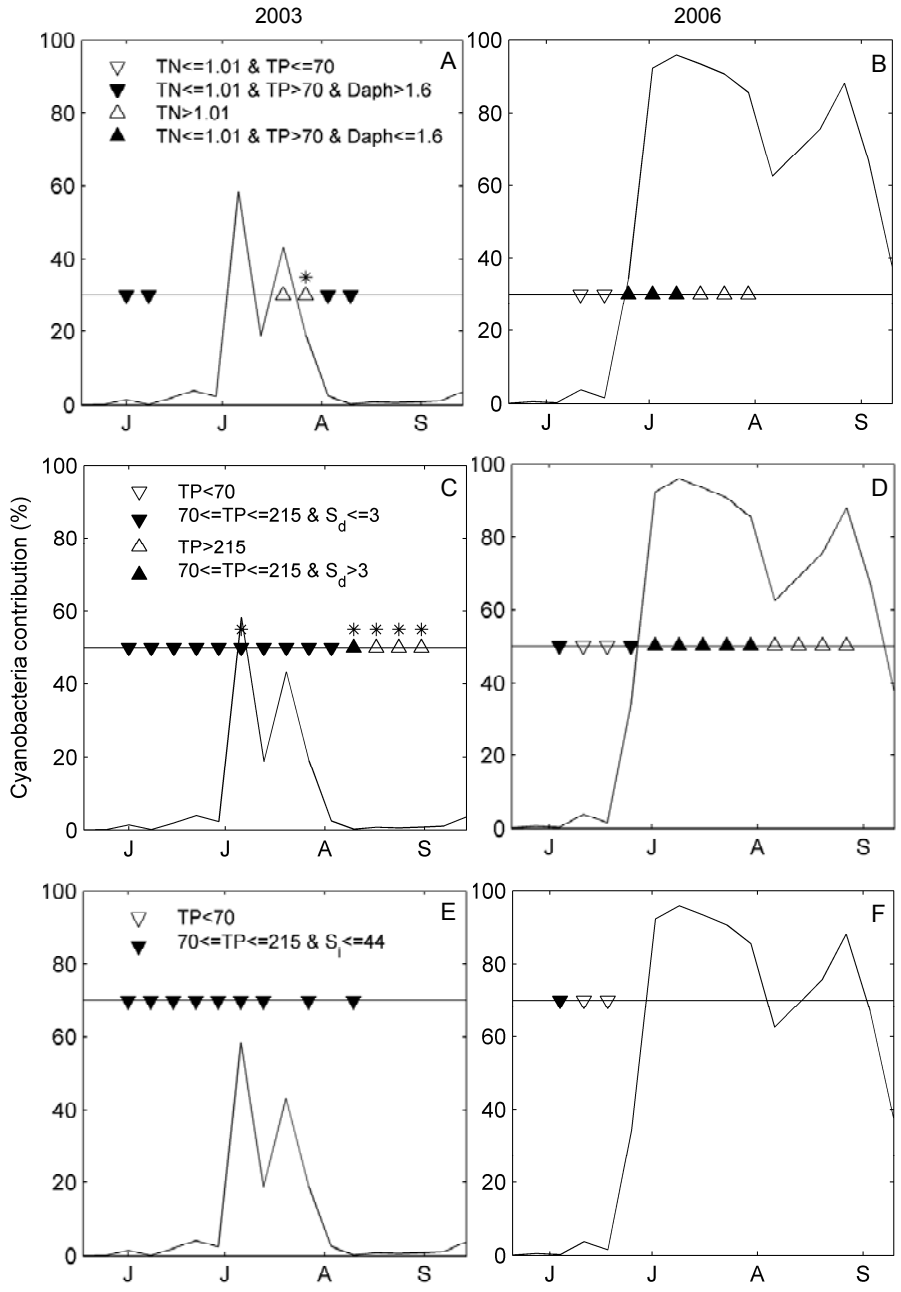

Fig. 3.3. Observed cyanobacteria contribution to total phytoplankton biovolume (solid lines) and rule-based predictions of contribution ranges (triangles) for 2003 and 2006 (see Table 3.1). Upward (downward) facing triangles indicate that rules predict cyanobacteria contribution to be above (below) 30% (panels A and B), 50% (panels C and D) and 70% (panels E and F), respectively. Predictions were restricted to stratification events (see Fig. 3.2C) in panels A and B, while the whole summer was considered in panels C to F (Table 3.1). For thresholds of total nitrogen concentration (TN), total phosphorus concentration (TP), log-transformed daphnid abundance (Daph) and stratification intensity (S_i) applied here (and their units) see Fig. 3.2 C-F. Misclassifications are marked with asterisks. Predictions of cyanobacteria contribution >= 70% are not shown since average (1993-2007) misclassification frequency was extremely high in these cases (Table 3.1).

Meteorological conditions influencing thermal stratification—Since the intensity and duration of thermal stratification were important in explaining the differences in cyanobacteria contribution, we next identified the meteorological variables that caused the differences in temporal patterns of stratification. Classification tree analysis suggested that incident radiation, wind speed and air temperature were the main determinants of thermal stratification in Müggelsee (Table 3.2). The lake was correctly classified as being stratified in ~75% and non-stratified in ~90% of all cases (Table 3.2). Incident radiation <= 173.9 W m^{-2} was generally a good indicator of non-stratified conditions, but did not explain the mixing event in 2003 since it fell below this threshold not before early fall (Fig. 3.4A). Furthermore, mean wind speed of > 3 m s^{-1} was associated with times of mixing when incident radiation was above its critical threshold. Interestingly, while wind speed remained below the identified critical threshold during the entire summer of 2006, wind speeds above this threshold were observed in mid-summer of 2003, exactly during the time period when intermittent mixing took place in the lake (Fig. 3.2C; Fig. 3.4B). At about the same time, air temperature also dropped below the critical threshold of 20.5°C, indicative of conditions that favoured mixing (Fig. 3.4C).

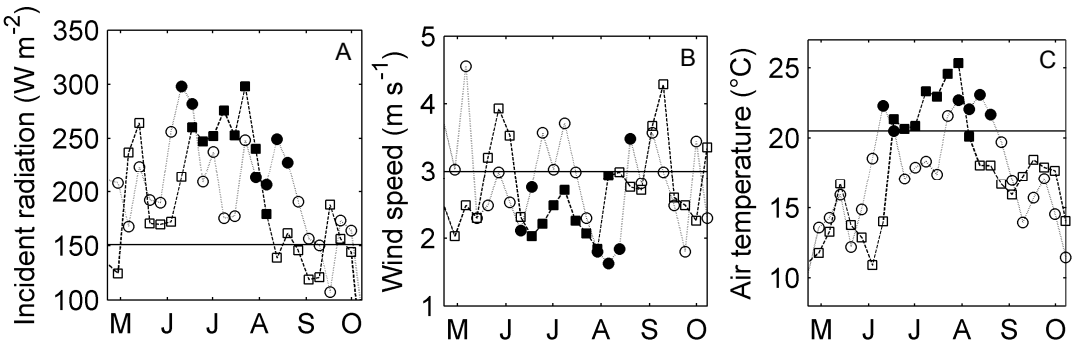

Fig. 3.4. Seasonal dynamics of A) incident radiation, B) wind speed, and C) air temperature during 2003 and 2006. Horizontal lines mark thresholds from classification tree analysis (Table 3.2). Circles: 2003; squares: 2006; filled symbols: weeks of thermal stratification (Fig. 3.2C).

3.5 Discussion

In this study, we asked why during the European heat waves of 2003 and 2006 cyanobacteria in Müggelsee showed a strikingly different development, although high water temperature and intense thermal stratification in the lake during times of hot weather should have favoured cyanobacteria in both years. Rules extracted from classification tree analysis of Wagner and Adrian (2009) indicated that insufficiently long-lasting and strong thermal stratification could explain part of the surprisingly low cyanobacteria biovolume in 2003. While 2006 experienced continuous intense thermal stratification for eight weeks between June and August, 2003 was marked by two shorter, less intense stratification events separated by intermittent mixing in July, which was probably induced by comparatively strong wind and low air temperature during this time. Classification rules also suggested that when the thermal regime became favourable in late summer of 2003 daphnids might have played a role in suppressing cyanobacteria.

Classically, cyanobacteria are considered to be relatively resistant against grazing by herbivorous zooplankton due to large filament and colony sizes. Despite this relative grazing resistance found in many short-term experiments (Burns 1968), there is considerable evidence, mostly from whole-lake or large enclosure studies, that daphnids sometimes have large negative effects on cyanobacteria (Vanni *et al.* 1990; Sarnelle 2007). One explanation for this apparent discrepancy is that daphnids are able to graze on cyanobacteria species in the initial stage of the bloom when colonies or filaments are still small (Davidowicz *et al.* 1988). In fact, e.g., Chan *et al.* (2004) showed in microcosm experiments that herbivorous zooplankton was able to graze on nitrogen fixing cyanobacteria, reducing their mean filament size and as a result their growth rate. Interestingly, mean cell/filament size of the cyanobacteria community in July and August of 2003 was extremely small compared to the long-term mean of 1999-2007, while it was exceptionally large in 2006 (Fig. 3.5A). This observation supports the findings from classification rules, indicating that daphnids might have indeed contributed to low cyanobacteria biovolume in 2003.

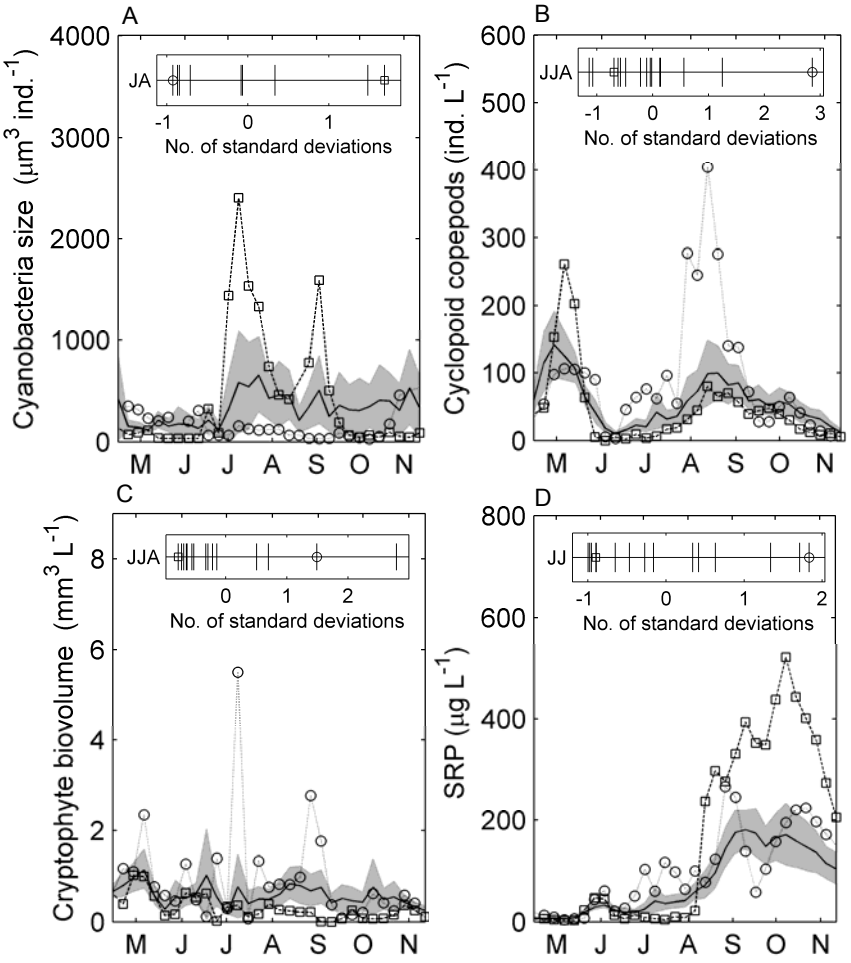

Fig. 3.5. Seasonal dynamics of A) filament/cell size of cyanobacteria B) abundance of cyclopoid copepods, C) cryptophyte biovolume, and D) soluble reactive phosphorus concentrations in 2003 and 2006, compared to weekly long-term means ± 1 SE (1999-2007 for panel A; 1993-2007 for panels B-D). Inlays show standardized averages of summer months calculated as for Fig. 3.1 (panel A: July-August; panel B-C: June-August; panel D: June-July). For symbols and line codes see Figs. 3.1 and 3.2.

The interesting question then is why daphnid populations were thriving during all of summer 2003 but collapsed in June and July 2006 (Fig. 3.2D). When studying daphnid population dynamics in a dimictic reservoir, Wagner and Benndorf (2006) found that significant reductions of daphnid abundance in midsummer occurred only in years in which mean water temperature in May exceeded 14°C. In Müggelsee, mean May water temperature (0-5 m depths) was 16.2°C in 2003 and 14.7 °C in 2006, while daphnid abundance was high in midsummer of 2003 and extremely low in 2006. Hence, the results of Wagner

and Benndorf (2006) did not provide an explanation for the contrasting observations. However, it would be an interesting avenue for further research to explore whether the sharp drop of water temperature in June of 2006 (Fig. 3.2B) might have caused the daphnid population collapse observed at about the same time of this year (Fig. 3.2D).

Additional environmental factors, not included in the classification rules, might explain why cyanobacteria contribution remained low despite high TP concentrations after the breakdown of thermal stratification in August of 2003 (Fig. 3.3C). When screening a large number of abiotic and biotic variables, we found that cyclopoid copepods reached extremely high abundance in the summer of 2003 (summer mean was 2.9 σ above μ) (Fig. 3.5B). Unfortunately, we were not able to discern whether this high abundance was the cause or rather the consequence of low cyanobacteria biovolume. There is evidence that cyclopoid copepods were independently favoured by elevated water temperature in early summer 2003 (chapter 4), interestingly during a time period when water was exceptionally cool in 2006 (Fig. 3.2B). Concurrently, cyclopoid copepods were also promoted by high biovolume of cryptophytes in 2003 (chapter 4), which most likely occurred because these algae out-competed cyanobacteria during the midsummer mixing event (Fig. 3.5C). In any case, a strong overall grazing pressure on cyanobacteria and other phytoplankton species during the summer of 2003 is in accordance with the particularly high SRP concentrations observed (Fig. 3.5D), indicating that some factor must have prevented phytoplankton from exploiting this resource.

We presented data from one shallow, polymictic lake of the temperate zone only. At least one other study of a moderately deep (mean depth 18 m), hypertrophic lake, Lake Nieuwe Meer in the Netherlands, found that cyanobacteria were strongly promoted by the heat wave of 2003 (Jöhnk *et al.* 2008). Contrary to our findings, artificially induced intermittent mixing with a 1-2 week periodicity was not sufficient in Lake Nieuwe Meer to suppress a bloom of cyanobacteria that occurred when the heat wave hit the lake in August. Interestingly, model predictions show that buoyant cyanobacteria out-compete other phytoplankton at much lower intensity of thermal stratification in deep than in shallow lakes (Huisman *et al*. 2004). Thus, differences in lake depth might explain the

contrasting observations. In addition, the different trophic states of the two lakes might play a role. Jöhnk *et al*. (2008) report extremely high mean summer concentrations of TP and TN in Lake Nieuwe Meer in the range of ~400 μgL^{-1} and ~3.6 mg L^{-1}, respectively. These concentrations largely exceed the thresholds of 215 μgL^{-1} TP and ~1 mg L^{-1} TN found by Wagner and Adrian (2009), above which cyanobacteria contribution to total phytoplankton biovolume tend to be high in Müggelsee, independent of the thermal regime and daphnid abundance (Table 3.1).

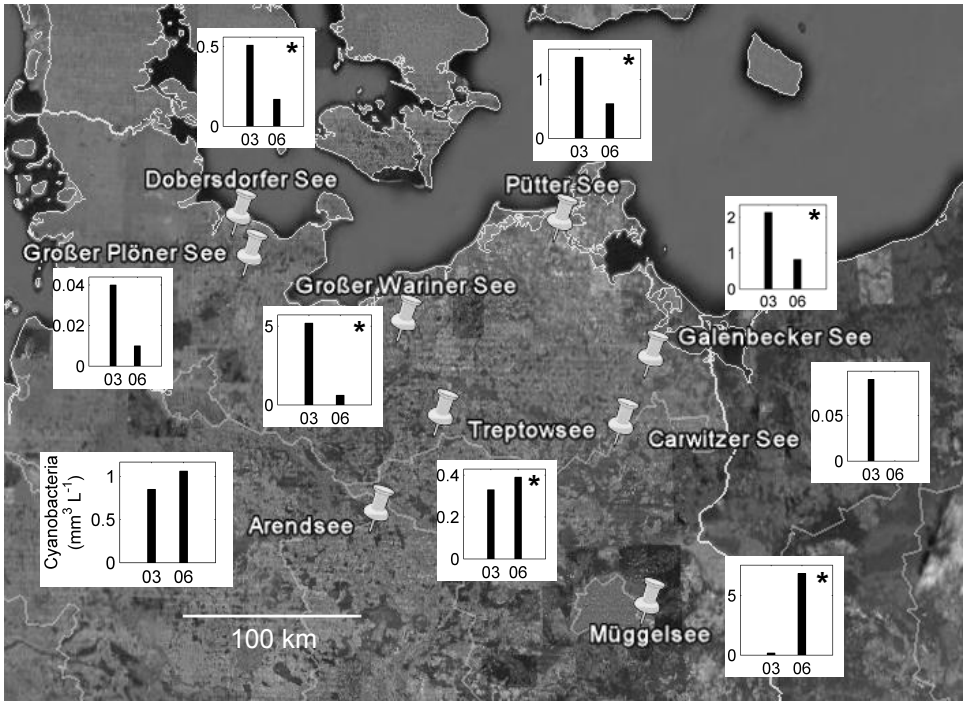

Fig. 3.6. Comparison of cyanobacteria summer biovolume in 2003 and 2006 in Müggelsee and eight geographically relatively close mesotrophic to hypertrophic lakes in north-eastern Germany. Asterisks mark data from polymictic lakes. Note different scales on y-axes. Map source: Google Earth 2009.

A survey of eight lakes of different depths and trophic states, which are relatively close to our lake, revealed that the observation of low cyanobacteria biovolume in 2003 and high biovolume in 2006 could neither be generalized to geographically more neighbouring lakes (Fig. 3.6). In six of the nine lakes, summer biovolume of cyanobacteria in 2003 exceeded the 2006 magnitude, in contrast to the observation in Müggelsee. As for Lake Nieuwe Meer, differences in lake depth and trophic state might be decisive, but differences in local

weather patterns could have also been influential. Presumably, the thermal stratification regime remained more favourable for cyanobacteria in some of these lakes throughout the summer of 2003, because the meteorological conditions that induced intermittent mixing in mid-summer 2003 in Müggelsee (Fig. 3.4) did not extend to the entire region or did not impact the thermal regimes of these lakes similarly, e.g., due to less wind-exposed sites or more stable thermal regimes (the latter especially applicable to dimictic Arendsee, Carwitzer See and Plöner See; Fig. 3.6). Overall, the comparisons with other lakes re-emphasize the complexity of processes involved in the formation of cyanobacteria blooms, making it a challenging task to project their evolution under future climate warming.

3.6 Conclusions

Many studies have pointed to the increasing risk of cyanobacterial blooms with climate warming. There are a number of studies indicating that many of the lake features that are thought to change in the future, indeed, favour cyanobacteria (Paerl and Huisman 2008). However, here we show that heat waves do not necessarily promote cyanobacteria blooms, even not in the same lake and when similarly high water temperatures occur. Our findings point to the importance of seasonal weather patterns that critically determine the thermal regime of shallow, polymictic lakes and thereby the occurrence of cyanobacteria blooms. Albeit of secondary importance, our study also suggests that zooplankton, which is known to be strongly sensitive to temperature and therefore likely to be affected by heat wave events (Blenckner *et al.* 2007), can at least contribute to the suppression of cyanobacteria blooms. Our results caution against conclusions on climate change as a catalyst of cyanobacteria blooms that are drawn from single extreme events and that consider summer averages of meteorological conditions only. Anticipating the effects of climate change on cyanobacteria requires a still better understanding of the complexity underlying cyanobacteria bloom formation in lakes of different depth and trophic state.

3.7 Acknowledgements

We thank all scientists and technicians who have been involved in the collection and compilation of the long-term data set of Müggelsee. We are especially grateful to Thomas Hintze and Helgard Täuscher who helped during the preparation of the raw data. We also acknowledge Ute Mischke who provided data on cyanobacteria in neighbouring lakes. Katrin Tirok and three anonymous reviewers gave extremely useful advice on earlier versions of the manuscript. The German Research Foundation (DFG) supported Veronika Huber within the priority program AQUASHIFT (SPP 1162).

Chapter 4

A matter of timing: heat wave impact on crustacean zooplankton

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In revision for *Freshwater Biology* as Huber V., D. Gerten and R. Adrian. A matter of timing: heat wave impact on crustacean zooplankton.

4.1 Abstract

1. Climate change has affected zooplankton phenology and abundance in many freshwater ecosystems. The strong temperature anomalies that characterize summer heat waves make these events particularly suitable to study the effects of different seasonal warming patterns on zooplankton. Since heat waves are expected to occur more frequently under further ongoing climate change they also allow us to investigate how freshwater systems may be affected in the future.
2. Using a long-term data set (1991-2007) from a shallow, eutrophic lake in Germany, we identify time periods in spring and summer during which cyclopoid copepods and bosminids are particularly sensitive to changes in water temperature. Based on this knowledge, we consider why summer populations responded differently to recent heat wave events that occurred at different times in the season.
3. Linear regressions of moving averages suggested that water temperatures shortly before and shortly after the clear-water phase were crucial for summer development of bosminids and cyclopoid copepods, respectively. Algal food availability (diatoms and cryptophytes) in the first weeks after the clear-water phase also strongly influenced the summer populations of the two zooplankton groups.
4. Inter-annual differences in water temperature during the critical time periods at least partly explained the contrasting responses of cyclopoid copepods and bosminids to heat wave events.
5. Our findings indicate that the zooplankton response to climate warming, particularly to heat wave events, is critically dependent on the temporal patterns of elevated water temperatures. Beyond that, we show that zooplankton populations react to periods of warming in relation to events in the plankton annual cycle (such as the clear-water phase in eutrophic lakes) rather than to warming at a fixed time in the season.

4.2 Introduction

Due to their sensitivity to temperature, zooplankton species are particularly prone to climate-induced changes in their physical environment (e.g., Moore *et al.* 1996), and changes in their phenology and abundance have been attributed to altered climatic conditions in a variety of freshwater ecosystems (Blenckner *et al.* 2007). Most prominently, spring dynamics of cladoceran species in temperate lakes are strongly driven by water temperature (Gerten and Adrian 2000; Straile and Adrian 2000; Schalau *et al.* 2008). By contrast, far fewer studies have investigated the impact of climate variability on zooplankton in the summer (but see Adrian *et al.* 2006). Moreover, understanding of the impact of extreme events such as summer heat waves on freshwater ecosystems is just beginning to emerge (Jankowski *et al.* 2006; Daufresne *et al.* 2007).

The response of crustacean zooplankton to temperature change does not only depend on the magnitude of change but also on its seasonal timing (Adrian *et al.* 2006). This is because crustacean life-cycle events such as emergence from resting stages, egg development and the early pre-adult growth are particularly, and differentially, sensitive to temperature and day length (Vijverberg 1980; Cáceres 1998; Gyllström and Hansson 2004). Also, direct temperature effects are more likely to be manifested in population dynamics when no other factors, such as food availability or predation, limit growth (Moore *et al.* 1996; Giebelhausen and Lampert 2001).

Food limitation of crustacean zooplankton in eutrophic lakes of the temperate zone is most prominent during the clear-water phase (CWP) (Sommer *et al.* 1986). This stage of low phytoplankton concentrations and high water transparency usually occurs in May/June, but its precise timing depends on winter and spring meteorological conditions across the Northern hemisphere, as synchronized by the North Atlantic Oscillation (Straile 2002; Blenckner *et al.* 2007).

Several summer heat waves have occurred over Central Europe in recent years, most prominently in 2003. The strong temperature anomalies prevailing during heat waves make these extreme events particularly suitable to study the effects of the seasonal patterns of warming on lakes. The assessment of their impacts is

also important because heat waves are expected to occur more frequently under future climate warming (Meehl and Tebaldi 2004; Schär and Jendritzky 2004). Heat wave conditions can be expected to favour rather than inhibit thermophilic species in many lakes of the temperate zone because water temperatures – even during these extreme events – so far remain below thresholds (~ 25 °C) that are considered detrimental (Moore *et al.* 1996; Chen and Folt 2002).

Investigating the temperature impact on crustacean population dynamics may be complicated by delayed responses. While cladoceran populations are thought to respond within days to temperature changes, effects may propagate through the different life-cycle stages of copepods until they manifest themselves (Gerten and Adrian 2002; Adrian *et al*. 2006). Cyclopoid copepods encompass a number of pre-adult stages (nauplii and copepodids) – a development that can last up to several weeks. These life-cycle effects have been proposed to explain why the impact of meteorological conditions in the spring can be transferred to later in the season (Gerten and Adrian 2002; Seebens *et al.* 2007). Other studies that found lagged responses to temperature changes identified indirect predator-prey effects and attributed the delay to food web interactions (Wagner and Benndorf 2006).

The objective of this study, which is based on a long-term data set (1991-2007) of physical and biological variables in a shallow lake (Müggelsee, Germany), was to identify seasonal periods during which water temperature changes are crucial for the summer development of cyclopoid copepods and bosminids – two prominent groups of the crustacean zooplankton. With this, we aimed at better understanding the observed differing impact of recent heat wave events (2003, 2006 and 2007) on these two zooplankton groups. In fact, although previous studies have indicated that high water temperatures are accompanied by high biomass of cyclopoid copepods (Blenckner *et al.* 2007; Wagner and Adrian *in prep.*) and bosminids (Straile and Adrian 2000), hot spells did not always favour these groups in Müggelsee. Our hypothesis was that the heat wave impact on cyclopoid copepods and bosminids is determined by the specific seasonal timing of the event. Linear regressions of moving averages were used to screen the seasonal dynamics of zooplankton, water temperature and other environmental

factors (phytoplankton and other crustacean subgroups) for periods of highest correlations while accounting for their specific temporal patterning.

4.3 Methods

Study site and data—Müggelsee (52°26' N, 13°39' E) is a polymictic shallow lake (mean depth 4.9 m, maximum depth 7.9 m) with a surface area of 7.3 km^2. Since 1980 an ongoing sampling program has collected data on plankton, physical and chemical variables (with a weekly data resolution except for biweekly sampling during winter months). Standard limnological techniques were used that are described in Driescher *et al.* (1993) and Gerten and Adrian (2000). Mean near-surface water temperatures in the summer have shown an increasing trend rising by ~ 0.5 °C per decade since 1980 in the studied lake (Adrian *et al.* 2006). In parallel, the lake has undergone a change in trophic state from hypertrophic in the 1980s to eutrophic in more recent years (Köhler *et al.* 2005; Huber *et al.* 2008). To limit the confounding effects of this trophic shift the analysis was based on the eutrophic period (1991-2007) if not otherwise stated.

Weekly water temperature measurements (°C) were averaged between the surface and the mean depth of the lake (~5 m) to yield a time-series of mean water column temperature (T). As a measure of light availability in the water column we used the light index (dimensionless) combining day length and water transparency (Sommer 1993) $LI = 2z_s \frac{D}{D_{\max}} \frac{1}{z_m}$, where z_s is the Secchi depth (m), D the day length (h), D_{max} is 24 hours, and z_m the mixing depth; z_m was set to the mean depth of the lake, which has proven to be a good approximation for the polymictic lake considered here (Wilhelm and Adrian 2008). Zooplankton abundances were converted into biomass (mg FW L^{-1}) using species-specific individual body weights (Bottrell *et al.* 1976) and measured biovolume (mm^3 L^{-1}) of phytoplankton was considered. A conversion factor of 0.12 mg C mm^{-3} (Rocha and Duncan 1985) was used to calculate the carbon content of phytoplankton biovolume. Variables taken into account and abbreviations used are listed in Table 4.1a. If not otherwise indicated mean summer biomass (MSB) was the June-August average.

Table 4.1. a) Variable abbreviations and b) parameters that define temporal integration periods used in regression analysis.

	Symbol	Explanation
a)	CRUST	Total crustacean zooplankton
	BOSM	Bosminids
	CALCOP	Calanoid copepods (adults and copepodids)
	CYCCOP	Cyclopoid copepods (adults and copepodids)
	DAPH	Daphnids
	PHYTO	Total phytoplankton
	CHLORO	Chlorophytes
	CRYPTO	Chryptophytes
	CYANO	Cyanobacteria
	DIATO	Diatoms
	LI	Light index
	T	Water column temperature
b)	W	Upper bound of integration period (calendar week; 17<=W<=35)
	N	Length of integration period (weeks; 2<=N<=5)
	W_{CWP}	Timing of clear-water phase (calendar week)
	M	Upper bound of integration period with respect to W_{CWP} (week; -4<=M<=16)
	W_c	Centre of integration period

Statistical analysis—To assess whether specific seasonal warming patterns influenced summer populations of cyclopoid copepods and bosminids we calculated linear regressions of moving averages (cf. fixed-period regression method; Livingstone 1999). For this purpose all variables were log-transformed. Regression models applied are summarized in Table 4.2.

In a first step, we assumed that mean summer biomass of cyclopoid copepods and bosminids respectively ($\overline{Z}_{MSB}$) was influenced by T integrated over some fixed period between spring (April) and the end of summer (August). Specifically, T was averaged according to

$$\overline{X}_{W,N} = \frac{1}{N} \sum_{i=W-N+1}^{W} X_i \qquad (1)$$

where X_i is the integration variable in week i, and N and W define the length and location of the integration period (cf. Table 4.1b and 4.2). Pearson correlation coefficients between $\overline{Z}_{MSB}$ and T averaged according to Eq. 1 were calculated and depicted as a function of W_c, the week on which the averaging is centred.

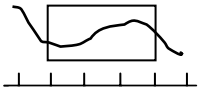
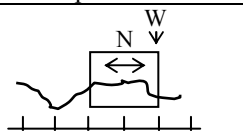
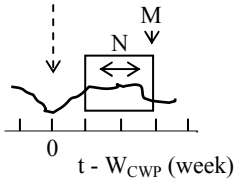
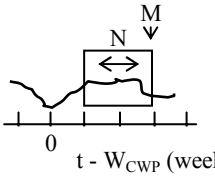
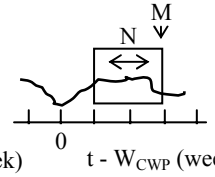
The CWP is known to strongly influence the structure of plankton communities in the summer (Sommer *et al.* 1986). Therefore, in a second step, we assumed

that $\overline{Z}_{MSB}$ was influenced by T integrated over some fixed period related to the timing of the CWP. For this purpose W was set to

$$W = W_{CWP} + M \quad (2)$$

where W_{CWP} is the week when the CWP occurred and M marks the upper bound of the integration period (cf. Table 4.1b and 4.2). W_{CWP} was set to the week when maximum of Secchi depth (transparency) occurred in spring for each year. (In 2007, when no distinct increase in Secchi depth was observed, the definition was based on the timing of the diatom minimum after the spring peak, which typically coincides with maximum Secchi depth in Müggelsee.) To avoid bias resulting from potential covariance between W_{CWP} and T averaged according to Eqs. 1 and 2 ($\overline{T}_{W_{CWP}+M,N}$) partial correlation coefficients controlling for the timing of the CWP were calculated.

Table 4.2. Outline of fixed-period regression analysis applied in this study. Additional symbols and abbreviations are explained in Table 4.1.

Dependent variable		Independent variable(s)		Illustration of integration time-periods depend. var.	independent var.	Fig./ Table
$\overline{Z}_{MSB}$	Mean summer biomass of CYCCOP and BOSM	$\overline{T}_{W,N}$	T averaged over fixed period based on calendar season			Fig. 4.3 a,b
		$\overline{T}_{W_{CWP}+M,N}$	T averaged over fixed period with respect to W_{CWP}			Fig. 4.3 c,d
$\overline{Z}_{W_{CWP}+M,N}$	Biomass of CYCCOP and BOSM averaged over fixed period with respect to W_{CWP}	$\overline{T}_{W_{CWP}+M,N}$	(see above)			Fig. 4.4
		$\overline{U}_{W_{CWP}+M,N}$ $\overline{V}_{W_{CWP}+M,N}$	Environ-mental factors (cf. methods) averaged over fixed periods with respect to W_{CWP}			Table 4.3

In a third step, we did no longer consider $\overline{Z}_{MSB}$ but integrated zooplankton biomass over a period fixed relative to the timing of the CWP using eq. 1 and 2 as for T ($\overline{Z}_{W_{CWP}+M,N}$). For each combination of different integration period lengths *N*, a matrix of partial correlation coefficients R(*i*,*j*) was determined running *M* over its full range for both $\overline{T}_{W_{CWP}+M,N}$ and $\overline{Z}_{W_{CWP}+M,N}$. Correlation coefficients from the matrix that yielded the highest mean of adjacent entries *R*(*i*-1:*i*+1,*j*-1:*j*+1) were depicted with contour plots.

Fourth, we assessed the impact of environmental factors other than T known to influence zooplankton summer biomass. While the potential effects of food availability and competition could be assessed, we unfortunately had to neglect fish predation due to the lack of respective time series data. Binary linear regressions were calculated according to

$$\overline{Z}_{W_{CWP}+M,N} = \beta_0 + \beta_U \overline{U}_{W_{CWP}+M,N} + \beta_V \overline{V}_{W_{CWP}+M,N} \quad (3)$$

where β_0,β_U,β_V are regression coefficient and U and V are environmental factors integrated using eqs. 1 and 2. Environmental factors considered were T, LI, CHLORO, CRYPTO, DIATO, CYANO, DAPH, CALCOP and either BOSM or CYCCOP (cf. Table 4.1). Integration period locations and lengths (*M* and *N*) were varied over their full ranges (as indicated above) and all combinations of U and V (2 taken out of 9; n = 36) were considered. We excluded models with non-significant regression coefficients ($p>0.05$) and linearly dependent $\overline{U}_{W_{CWP}+M,N}$ and $\overline{V}_{W_{CWP}+M,N}$. Models were ranked according to the amount of explained inter-annual variability (R^2). The model with largest R^2 was selected given that models with the same variables and adjacent integration periods were similarly ranked. For all analysis, we only considered combinations of *M* and *N* that assured that the integration period for $\overline{T}_{W_{CWP}+M,N}$ ($\overline{U}_{W_{CWP}+M,N}$, $\overline{V}_{W_{CWP}+M,N}$) lay before or within the integration period for $\overline{Z}_{W_{CWP}+M,N}$. This accounted for the assumed causal link between temperature (environmental covariates) and zooplankton development.

4.4 Results

Heat waves and crustacean mean summer biomass—Recent heat waves occurred in 2003, 2006 and 2007 at the studied lake, with monthly means of water temperature exceeding 1.5 standard deviations above the long-term (1991-2007) mean in spring and summer (Fig. 4.1). The seasonal patterns of these heat wave events, however, differed substantially between years: While 2003 was marked by exceptionally high water temperatures in June and August, 2006 experienced anomalous temperatures in July, and in 2007 water temperatures were exceptionally elevated in April to June.

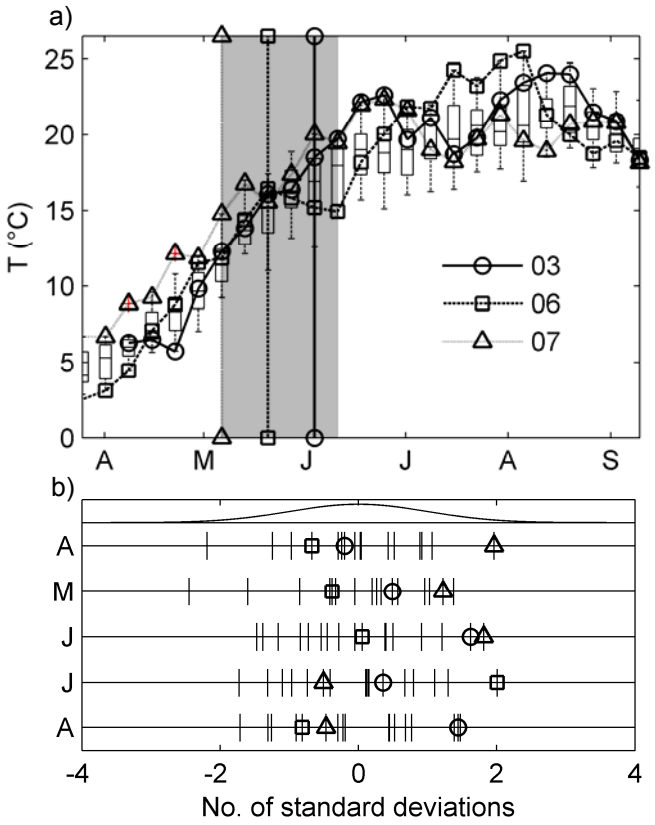


Fig. 4.1. Seasonal warming patterns of water temperature (T) a) Weekly data of T for 2003 (open circles), 2006 (open squares), and 2007 (open triangles) in comparison to complete data of 1991-2007 (boxplots; whiskers cover 1.5 times the interquartile range); the gray area marks the range of the timing of the clear-water phase (W_{CWP}) in 1991-2007; vertical lines and symbols (as for T) indicate W_{CWP} for 2003, 2006 and 2007. Note the especially early timing of the clear-water phase in 2007. b) Monthly averages of T during spring and summer standardized by removing the long-term means and dividing by the standard deviations (1991-2007).

Despite heat waves of similar average strength, mean summer biomass of total crustacean zooplankton was exceptionally high in 2003 only (Fig. 4.2). It did not show any outstanding development during the summer of 2006 and 2007. By contrast, in 2003 a magnitude was reached that was last observed during the hypertrophic phase of the lake, which was characterized by high phytoplankton biovolume. The exceptional development of crustaceans in 2003 was largely due to cyclopoid copepods and bosminids, which attained mean summer biomasses ($\overline{Z}_{MSB}$) that lay 2.8 and 2.2 standard deviations above their long-term means, respectively (Fig. 4.2).

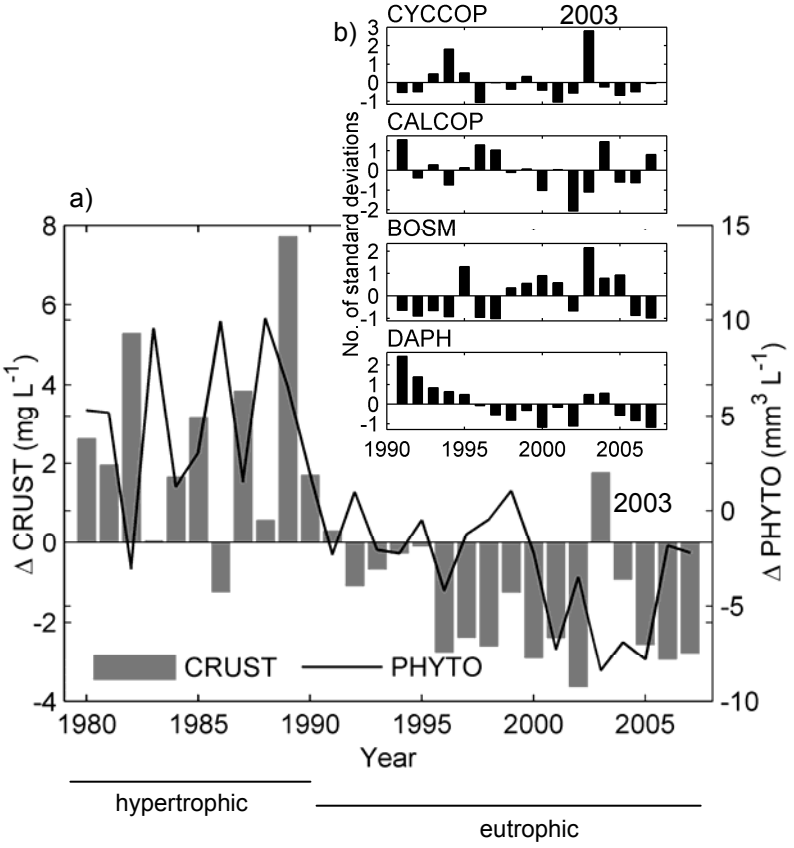


Fig. 4.2. Inter-annual variability of crustacean summer biomass during the hypertrophic (1980-1990) and eutrophic period (1991-2007) in Müggelsee: a) Deviations of crustacean mean summer biomass and phytoplankton mean summer biovolume from their long-term means (1980-2007); b) Mean summer biomass of main crustacean subgroups standardized by removing the long-term means and dividing by the standard deviations of the eutrophic period. Note the exceptionally high biomass of cyclopoid copepods and bosminids in 2003. Abbreviations as listed in Table 4.1.

Next, we aimed to identify crucial time periods of elevated temperatures in the long-term data (1991-2007) to examine our hypothesis that the heat wave impact on cyclopoid copepods and bosminids was dependent on the temporal patterning of its occurrence.

Temporal correlations between $\overline{Z}_{MSB}$ *and T*—Interestingly, the crucial time periods identified by correlation analysis (Table 4.2) were not fixed relative to the calendar season but rather fixed relative to the timing of the CWP. Correlation coefficients between water temperature integrated over a fixed period between April and August ($\overline{T}_{W,N}$) and mean summer biomass ($\overline{Z}_{MSB}$) of cyclopoid copepods and bosminids were relatively low (Fig. 4.3a,b). Marginally significant ($p<0.05$) correlations were only found for cyclopoid copepods (Fig. 4.3a). In contrast, integrating T over a fixed period relative to the timing of the CWP ($\overline{T}_{W_{CWP}+M,N}$) resulted in significant ($p<0.01$) partial correlation coefficients for both crustacean subgroups (Fig. 4.3c,d). Correlation coefficients suggested that crucial time periods of elevated water temperature lay shortly after and before the CWP for cyclopoid copepods and bosminids respectively.

Temporal correlations between $\overline{Z}_{W_{CWP}+M,N}$ *and* $\overline{T}_{W_{CWP}+M,N}$ —When accounting for the seasonal dynamics of crustaceans with respect to the timing of the CWP (i.e. basing correlation analysis on $\overline{Z}_{W_{CWP}+M,N}$; Table 4.2), instead of considering mean summer biomass, similar crucial time periods were identified. Mean start-up population biomasses of cyclopoid copepods ($\overline{Z}_{W_{CWP}+7,5}$) and bosminids ($\overline{Z}_{W_{CWP}+6,3}$), developing after the food bottleneck of the CWP, were most strongly correlated with mean water temperature shortly after ($\overline{T}_{W_{CWP}+3,2}$) and before ($\overline{T}_{W_{CWP}-2,2}$) the CWP, respectively (Fig. 4.4a,b; Fig. 4.5 gray areas I). These start-up populations determined the success of cyclopoid copepods and bosminids throughout the summer, as suggested by positive correlations with mean summer biomass ($r = 0.62$, $p<0.01$ for cyclopoid copepods and $r = 0.78$, $p<0.001$ for bosminids).

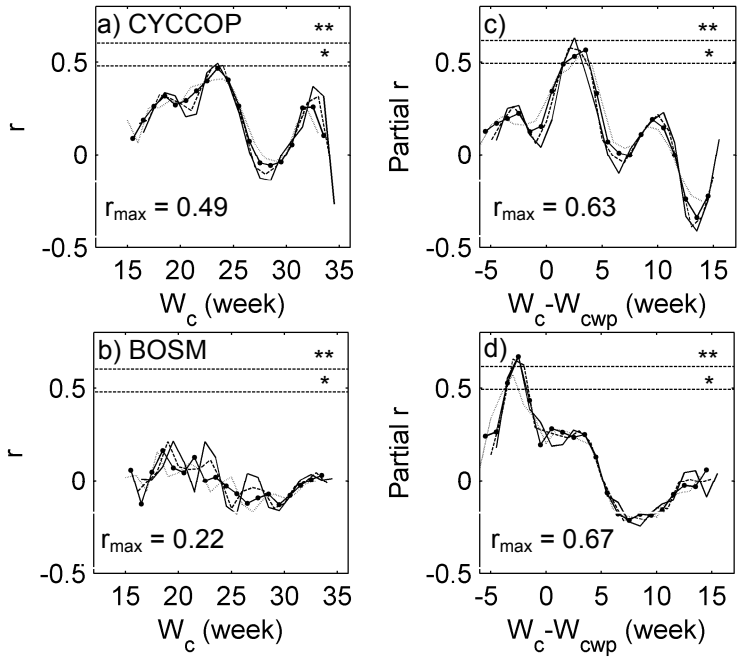


Fig. 4.3. (Partial) correlation coefficients between mean summer biomass of cyclopoid copepods and bosminids and (a-b) $T_{W,N}$, i.e. water temperature integrated over a fixed period between April and August ($17<=W<=35$) and (c-d) $T_{Wcwp+M,N}$, i.e. water temperature integrated over a period fixed relative to the timing of the clear-water phase (W_{CWP}) (Table 4.2). The x-axis shows the week (W_C) on which the integration period is centred (in panels c-d relative to W_{CWP}). Different line codes correspond to different integration period lengths (N=2 solid; N=3 dashed; N=4 dotted; N = 5 hatched). Horizontal lines marked * and ** indicate the threshold for 95% and 99% significance of correlation coefficients, respectively. For abbreviations see Table 4.1.

While water temperature was especially high during the identified crucial time periods in 2003, it was at or below average in 2006 and 2007 (Fig. 4.4c,d; Fig. 4.5 gray areas I). Thus, correlations suggested that different timing of heat wave events with regard to the CWP could at least partly explain the contrasting development of cyclopoid copepods and bosminids during these years.

Temporal correlations between $\overline{Z}_{W_{CWP}+M,N}$ *and further environmental factors*—As expected, extended regression models indicated that environmental factors other than water temperature also influenced summer biomass of these crustacean subgroups. For biomass of cyclopoid copepods, highest R^2 was achieved when regressing against the light index (~6%) and biovolume of cryptophytes (~85%) (Table 4.3). Biomass of cyclopoid copepods observed approximately two months

after the occurrence of the CWP (Fig. 4.5 b gray area II) appeared to be influenced by light and cryptophyte availability in the weeks following the clear-water phase (Fig. 4.5 b; black bars). For bosminids, the best model suggested that biovolume of diatoms in addition to water temperature influenced start-up population biomass after the CWP (Table 4.3, Fig. 4.5c black bars and area II). Biovolume of diatoms contributed ~23% while water temperature contributed ~65% to the total explained variability. The crucial time period identified for diatoms lay in the five weeks directly succeeding the CWP (Fig. 4.5c, black bar).

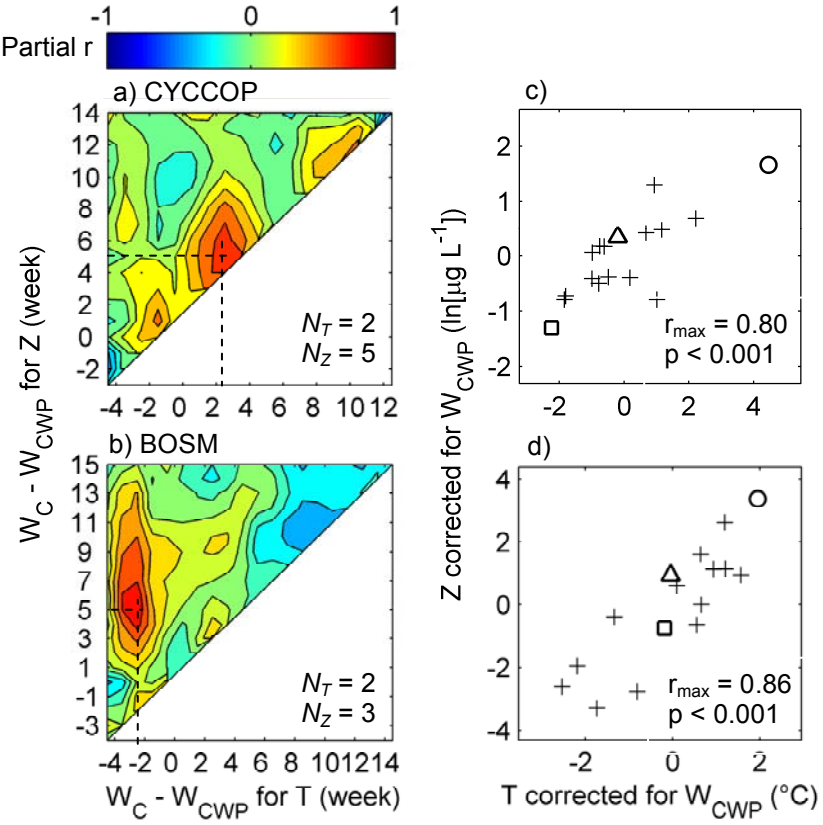


Fig. 4.4. Partial correlation coefficients between water temperature and a) cyclopoid copepod and b) bosminid biomass, both integrated over fixed periods relative to the timing of the clear-water phase ($T_{Wcwp+M,N}$ and $Z_{Wcwp+M,N}$; Table 4.2). Integration period lengths used for water temperature (N_T) and zooplankton (N_Z) are indicated. Dashed lines point to the location of the integration periods that resulted in maximal partial correlation coefficients (r_{max}). The corresponding data of $T_{Wcwp+M,N}$ and $Z_{Wcwp+M,N}$ corrected for the timing of the clear-water phase (W_{CWP}) are shown in panels c-d. r_{max} remained significant when taking out data from 2003 (r_{max} = 0.60, p< 0.05 in panel c; r_{max} = 0.74, p< 0.01 in panel d). For abbreviations see Table 4.1; symbols as in Fig. 4.1.

Table 4.3. Selected linear regression models (cf. Table 4.2) explaining highest amount of observed variability (R^2_{tot}) of cyclopoid copepod and bosminid biomass during specific time periods in the summer. For variables, square brackets contain M and N, i.e. parameters that define integration periods with respect to the timing of the clear-water phase (W_{CWP}) (time periods are illustrated in Fig. 4.5 b,c as gray areas II and black bars); for correlation coefficients, brackets contain the significance level p, and for regression coefficients, the 95% confidence intervals are given. Further variables, parameters and abbreviations are as in Tables 4.1 and 4.2.

Dependent variable	Independent variables		Correlation coefficient between U and V	Standardized regression coefficients		Coefficients of multiple determination		Explained variability
$\overline{Z}_{W_{CWP}+M,N}$ [M,N]	$\overline{U}_{W_{CWP}+M,N}$ [M,N]	$\overline{V}_{W_{CWP}+M,N}$ [M,N]	r [p]	β_U [95% CI]	β_V [95% CI]	R^2_U	R^2_V	R^2_{tot}
CYCCOP [9,2]	CRYPTO [7,4]	LI [3,4]	0.08 [0.77]	0.93 [0.77 1.10]	-0.28 [-0.44 -0.11]	0.85	0.06	0.91
BOSM [6,4]	DIATO [4,5]	T [-2,3]	0.16 [0.57]	-0.55 [-0.75 -0.35]	0.85 [0.65 1.05]	0.23	0.65	0.88

4.5 Discussion

This study suggests that the success of cyclopoid copepod and bosminid summer populations is influenced by water temperature at specific times during the annual plankton cycle. Crucial time windows identified in our correlation analysis lay shortly before and after the clear-water phase for bosminids and cyclopoid copepods, respectively. This result could at least partly explain the contrasting responses of these zooplankton groups to recent heat wave events, which showed different temporal patterns of temperature anomalies. Other environmental factors of importance for summer populations were cryptophyte and diatom biovolumes, presumably reflecting the tightness of the food bottlenecks that these zooplankton groups need to overcome in early summer.

Clearly, correlations do not necessarily point to causal relationships. Where causal relationships exist, they may be based on indirect rather than direct effects; e.g., a positive effect of elevated temperatures on crustacean plankton may arise from a direct effect of increased fecundity, however indirect effects such as a thermally induced improvement of food conditions or reduction of predation are also conceivable (Moore *et al.* 1996). We considered direct effects of

temperature on cyclopoid copepod and bosminid species documented in the literature to assess plausible causal links underlying the correlations found here.

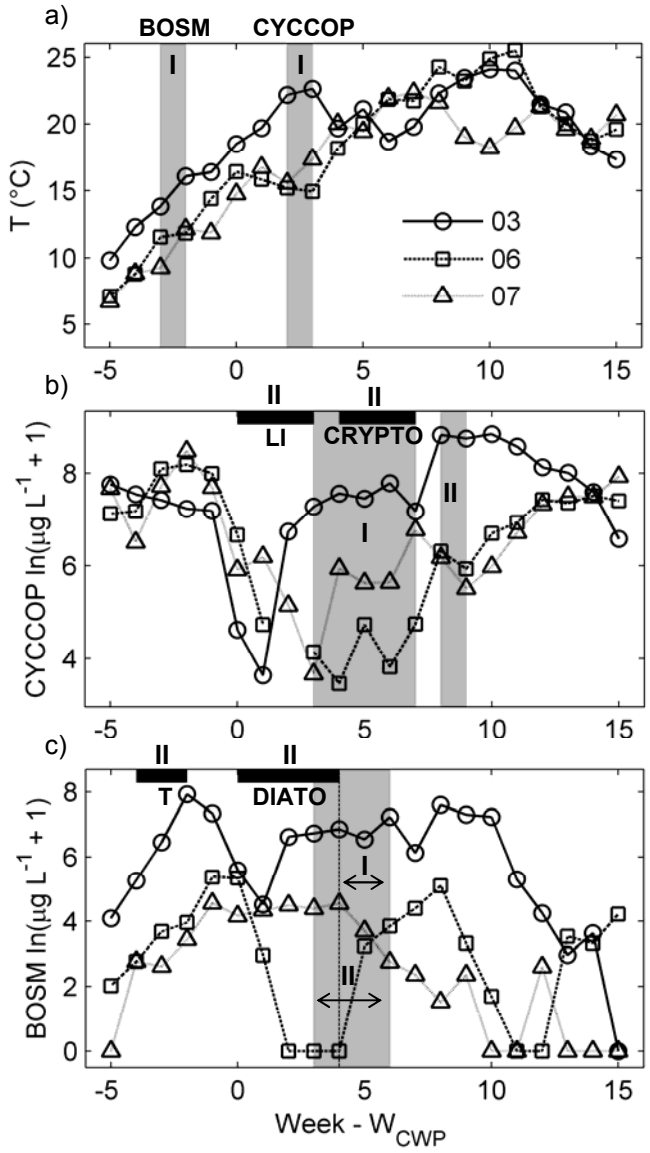


Fig. 4.5. Seasonal dynamics of a) water temperature, b) cyclopoid copepods and c) bosminids relative to the timing of the clear-water phase (W_{CWP}) in 2003, 2006, and 2007; symbols as in Fig. 4.1. Gray areas labelled I show time periods of maximum correlation between water temperature and cyclopoid copepods and bosminids, respectively (as identified in Fig. 4.4). Black horizontal bars and gray areas labelled II in panels b) and c) mark crucial time periods identified in the extended regression models (Table 4.3): light index and cryptophytes best explain mean cyclopoid copepod biomass of gray area II in panel b); likewise, water temperature and diatoms best explain mean bosminid biomass of area II in panel c). Abbreviations as in Table 4.1.

Potential mechanisms for the effect of water temperature on cyclopoid copepods— A large number of laboratory studies have documented that increasing temperatures accelerate the development times of eggs and larval stages (nauplii and copepodids) of cyclopoid copepods (e.g., Vijverberg 1980; Maier 1989). The rate of emergence from diapause has also been shown to rise with higher temperatures (Maier 1990). The question is a) how are these known effects of temperature on demographic rates translated to elevated population abundance and b) why is the timing shortly after the CWP crucial for this putative process. Unfortunately, detailed data on eggs and larval stages of cyclopoid copepods and emergence patterns are missing for the studied lake. Nonetheless, we can deduce possible mechanisms from the literature and supportive own investigations as follows:

The species that dominate cyclopoid copepod summer abundance in our lake (*Thermocyclops* sp., *Mesocyclops* sp. and *Acanthocyclops* sp.) overwinter as late copepodid stages in the sediment. Individuals are usually detected in the pelagial zone for the first time in spring or early summer – in most cases before the occurrence of the CWP (Gerten and Adrian 2002). The time when water temperature surpasses 5-8°C (which usually takes place in April in Müggelsee) has been shown to be a good predictor of the start of the pelagial phase of *T. oithonoides* (Adrian *et al.* 2006). Interestingly, Hairston *et al.* (2000) have suggested that cyclopoid copepods in contrast to cladocerans emerge from resting stages at various times during the year. The species they investigated (*Mesocyclops edax* and *Acanthocyclops vernalis*) showed patterns of emergence with two peak times, in spring and in summer. We hypothesize that water temperatures in the time period identified in this study (2-3 weeks after the CWP; gray area I in Fig. 4.5a) could strongly influence the success of the summer emergence from diapause, which presumably is initiated after the CWP. The range of water temperature during this period encompasses between below 15 °C to well above 20 °C in the three heat wave years (Fig. 4.5a). Maier (1990) found different emergence rates of cyclopoid copepods (*Mesocyclops leuckarti* and *Thermocyclops crassus*) for this temperature range: While at 20 °C half of the individuals had emerged after a maximum of only 4 days, at 15°C it took up to 25 days for 50% to leave diapause. A pulsed emergence of resting

individuals during conditions that are favourable could increase survival probabilities and ultimately translate to higher summer abundance of copepodids and adults.

Besides temperature, light is discussed as an important cue for the termination of diapause (e.g., Gyllström and Hansson 2004). It is conceivable that the period of high water transparency during the CWP, allowing elevated light intensities to reach the sediment of the lake, therefore plays a role in activating the diapausing copepodids. Yet, our extended regression models contained a negative coefficient for the light index suggesting a detrimental effect of high light intensity shortly after the CWP on cyclopoid copepod abundance later in the summer (Table 4.3; Fig. 4.5b). Since variability in water transparency is mainly determined by phytoplankton abundance and composition in the lake studied (Huber *et al.* 2008) we assume that this regression result does not reflect a direct effect of light but rather an effect of food quantity and quality on vulnerable stages of cyclopoid copepod development.

Nauplii are generally considered the bottleneck of cyclopoid copepod development because they are particularly sensitive to poor food conditions (Hopp and Maier 2005). Preferred food consists of small phytoplankton such as cryptophytes and chlorophytes (Hansen and Santer 1995). In eutrophic lakes such as Müggelsee these small algae are often the first to develop after the CWP before they are replaced by larger algal species, which are less apt for nauplii (Sommer *et al.* 1986). It has been suggested that faster development through the vulnerable naupliar stage might reduce mortality (Seebens *et al.* 2007). This phenomenon could represent another mechanism contributing to the positive correlations between water temperature and summer biomass of cyclopoid copepods found in this study. Naupliar development times have been shown to strongly differ within the temperature range identified as crucial here: e.g., while *M. leuckarti* required ~26 days at 15°C to develop from the first naupliar stage to the first copepodid stage, the time was approximately halved at 20°C (Maier, 1989).

Additional evidence for the importance of nauplii food conditions stems from the extended regression model (Table 4.3). Cryptophyte biomass was identified as a

variable with surprisingly high explanatory force. Compatibly, the time-lag between the centres of integration period for cryptophytes and cyclopoid copepods was three weeks (Fig. 4.5b black bar and area II) which falls within the range of naupliar development times identified by Maier (1989). Mean cryptophyte biomass varied between 0.01 and 0.18 mg C L^{-1} in the identified integration period. Since these values fall below typical food limitation thresholds for cyclopoid copepod nauplii (such as 0.2 mg C L^{-1} for *M. leuckarti* determined by Hansen and Santer 1995) cryptophyte availability might indeed largely determine inter-annual differences in nauplii survival.

Potential mechanisms for the effect of water temperature on bosminids—Similar to copepods, laboratory and field studies have shown that demographic rates and emergence of bosminids directly depend on temperature (Allan 1977; Vijverberg 1980; Vandekerkhove *et al.* 2005). These findings have been drawn on to explain why elevated spring temperature commonly coincide with an earlier growth onset and sometimes also an increased spring abundance of bosminids in some lakes (Gerten and Adrian 2000; Straile and Adrian 2000). However, considering the lagged response of bosminids to water temperature found here (centres of integration periods with respect to the CWP (W_C - W_{CWP}) were –2.5 weeks for water temperature and +5 weeks for bosminid biomass; thus they lie > 7 weeks apart; Fig. 4.4 and 4.5) we assume that the correlations observed most likely stem from indirect temperature effects possibly mediated by changes in (i) food availability, (ii) competition among zooplankton or (iii) predation pressure.

(i) The extended regression model included diatoms as the second most important variable after water temperature to explain bosminids biomass shortly after the CWP. At the same time, water temperature and diatoms as included in the model were independent (Table 4.3), a finding that excludes any indirect temperature effect mediated by diatoms. Bosminids are known to prefer small phytoplankton for prey (DeMott and Kerfoot 1982) whereas the summer diatom assemblage in Müggelsee consists of rather large species. Thus, the negative effect of high diatom densities shortly after the CWP, as suggested by the model, probably reflects unfavourable food conditions for bosminids under

situations of high diatom abundance. (In fact, during the identified crucial time period (weeks 0-4 after the CWP; cf. Table 4.3 and black bar DIATO in Fig. 4.5c) average diatom biomass and the average contribution of cryptophytes and chlorophytes to total phytoplankton biomass are negatively correlated $r = -0.65$, $p<0.01$.)

(ii) Some studies have suggested that small bodied zooplankton such as bosminids gain competitive advantage over larger bodied zooplankton at higher temperatures (Moore *et al.* 1996). Thus, temperature driven changes in competition among zooplankton might have contributed to the correlations between spring water temperature and bosminid summer start-up populations. Yet, all of the extended regression models that included negative coefficients for daphnids, calanoid copepods or cyclopoid copepods (suggesting competition) yielded lower explanatory power than the selected model (not shown).

(iii) Indirect temperature effects mediated by changes in predation have also been documented for several cladoceran species, most prominently for fish predation on daphnids (Moore *et al.* 1996; Wagner and Benndorf 2006). Due to their smaller size bosminids are considered less vulnerable to fish predation than daphnids (Hanazato and Yasuno 1989). However, accounting for the possible effects of temperature driven changes in invertebrate predation on bosminids would certainly be interesting to pursue in the future and could yield a more direct explanation for the correlations with water temperature found here.

Delayed responses of cladocerans and copepods to warming— Parthenogenetically reproducing cladocerans have often been observed to respond with shorter time-lags to warming than sexually reproducing copepods undergoing more complex life cycles (Straile and Adrian 2000; Gerten and Adrian 2002; Seebens *et al*. 2007) . By contrast, our results suggested that copepods were influenced more promptly by periods of exceptionally elevated water temperatures than bosminids. As discussed above it is most likely that indirect effects of temperature on bosminids dominated over direct effects explaining why we found longer time-lags than expected. Response time of copepods on the other hand was probably determined by direct temperature

effects here. In a recent study Wagner (2009) showed a direct effect of higher water temperatures especially on thermophilic cyclopoid copepod species abundances during extended periods of thermal stratification in Müggelsee.

Accounting for the clear-water phase to normalize phenology shifts—Normalizing seasonal trajectories of variables by the timing of the CWP resulted in significantly higher correlations than taking the more conventional approach of sticking to the calendar season. The CWP has been shown to structure crustacean seasonal dynamics, representing a period of extremely low food availability for many species (Sommer *et al*. 1986). Slight changes in its timing are often accompanied by synchronous phenology shifts of crustacean populations. Therefore, by correcting for the timing of the CWP these phenology shifts no longer blur strong links to typical patterns of plankton succession. Accounting for important events in the annual cycle of lake ecosystems rather than relating strictly to the calendar seasons has been successfully applied in various other analyses of plankton time-series (Tirok and Gaedke, 2006; Shatwell *et al*. 2008; Wagner and Adrian, 2009).

In our study, this change in perspective (Fig. 4.6) provided some explanation for the contrasting responses of cyclopoid copepods and bosminid summer populations to recent heat wave events. As an illustrative example, considering the calendar season only (Fig. 4.3a; Fig. 4.6a) one might have expected a positive effect of elevated water temperatures in June of 2003 and 2007 on the summer abundance of cyclopoid copepods in both years. Accounting for the timing of the CWP (Fig. 4.3c; Fig. 4.6b) yielded a considerably better explanation for the differences in abundance observed (Fig. 4.2): while in 2003 water temperatures were high shortly after the CWP, the period identified as crucial for cyclopoid copepods, no such anomalies were observed in 2007. The temporal patterns of warming with respect to the timing of the CWP (Fig. 4.6b) differed strongly between 2003 and 2007 mainly because the CWP occurred exceptionally early in 2007 (Fig. 4.6a). This in turn can be related to an extremely warm spring (Fig. 4.1; Fig. 4.6a) that – as has been shown for Müggelsee and many freshwater systems (Gerten and Adrian, 2000; Straile, 2002) – generally results in a seasonal forward shift of the CWP.

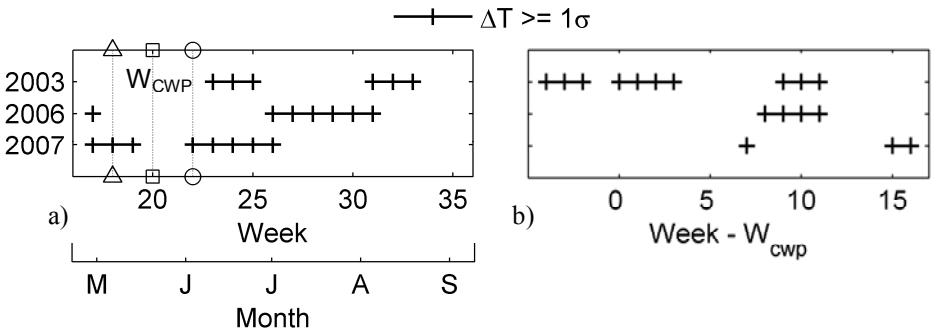


Fig. 4.6. Temporal patterns of exceptionally elevated water temperatures during heat wave years 2003, 2006 and 2007 with respect to a) the calendar season and b) the timing of the clear-water phase. Crosses indicate weeks, in which the deviation of water temperature from the long-term (1991-2007) mean (ΔT) is greater than one long-term standard deviation (σ). In panel a) the week of the clear-water phase (W_{CWP}) of 2003, 2006 and 2007 is indicated by open circles, squares and triangles, respectively.

4.6 Conclusions

Several recent studies have found that aquatic communities are at least as strongly affected by the seasonal timing as by the magnitude of climate warming (Gerten and Adrian, 2002; Wagner and Benndorf, 2006). Here, we went beyond this finding by showing that the crustacean responses to warming were dependent on temperature conditions at times close to a specific phenological event, the clear-water phase, rather than at a fixed time during the season. Thus, accounting for phenological events in the typical seasonal cycle of plankton appears crucial when assessing the effect of temporal patterns of warming on crustaceans.

This finding furthermore suggests that since the timing of clear-water phase is itself determined by winter and spring weather, the effect of a summer heat wave will depend on meteorological conditions earlier in the year. Thus, any climate change projection that does not provide estimates on patterns of warming during the *entire* course of the season will not be sufficient to anticipate its impact on aquatic communities.

4.7 Acknowledgements

We thank all scientists and technicians who have been involved in the collection and compilation of the long-term data set of Müggelsee. The study profited from continuous discussions with Carola Wagner. The German Research Foundation (DFG) supported Veronika Huber within the priority program AQUASHIFT (Ad91/12-1).

General discussion

The results presented in this thesis add to the growing body of evidence that aquatic ecosystems have strongly responded to climatic changes of recent decades. Given that past temperature rise has been small in comparison to increases projected for the future (IPCC 2007) aquatic ecosystems will certainly continue to be affected. What do the main findings of this thesis contribute to better anticipate the changes in plankton growth patterns to be expected? How could some of the analyses be carried on to further improve the required understanding?

5.1 Modelling phytoplankton spring phenology

Models presented in chapters 1 and 2 both indicated that an earlier onset of the growing period due to climate change advances the spring phenology of phytoplankton, in accordance with a large number of previous, mostly observational studies (e.g., Weyhenmeyer *et al*. 1999; Gerten and Adrian 2000; Adrian *et al*. 2006). The modeling approaches allowed gaining some insights into the mechanisms that drive the observed forward shifts, albeit they suggested differing mechanisms.

The detailed process-based model applied in chapter 1 indicated that high winter and spring temperatures induced an earlier onset of diatom growth because early ice-off provided sufficient light to reach the water column. Silicate limitation then triggered the seasonal advancement of the bloom collapse because silicate concentration was earlier drawn to its limitation threshold (a mechanism also proposed recently by Meis *et al*. 2009). The bloom collapse also occurred earlier in years in which it was caused by grazing because *Daphnia* generally advanced their onset of growth similarly to diatoms after a warm winter and spring.

The general and more simplified model approach applied in chapter 2 on the other hand predicted an advancement of spring phenology through increased

growing-season length and reduced winter mortality. Populations of phytoplankton and zooplankton started from elevated densities when conditions turned favourable and therefore reached bloom densities earlier. However, it needs to be emphasized that this latter mechanism occurred in a simplified experimental system, in which the effect of climate warming was mimicked by artificially lowering winter mortality. Whether it is also important in the field and how it relates to the mechanisms revealed in chapter 1 would be an interesting question to explore further.

In fact, a previous study at Müggelsee has shown that winter densities of diatoms are affected by ice duration and suggested that the timing of the spring bloom is related to the magnitude of the inoculum at the beginning of the growing season (Adrian *et al*. 1999). Due to low frequencies of sampling during winter at most temperate lake study sites and the generally high measurement errors close to detection limits, such effects are difficult to assess using statistical data analysis only. It is one of the great advantages of models such as presented in chapter 1 and 2 that they would allow gaining a better understanding of the role of inocula for plankton spring phenology. The model of chapter 2 could easily be parameterized using field data (such as of Müggelsee, see Fig. 5.1).

In addition to providing insights into mechanisms the obvious advantage of models in the context of climate impact research are their ability to be used for simulating future development. While forecasts have been undertaken by numerous studies concerned with terrestrial plant phenology (Cleland *et al*. 2007), examples from aquatic ecosystems are rare (but see, e.g., Peeters *et al*. 2007b; Braune *et al*. 2008). For this purpose the advantages of strongly simplified approaches (chapter 2) over detailed process-based models (chapter 1) are that they require a lower number of parameters and are easily applicable to different lake types. At the same time, the results of chapter 1 point to the advantage of choosing a process-based approach: Accurate simulations of phenology in this case required knowing the exact underlying mechanisms that even within one lake differed depending on trophic state.

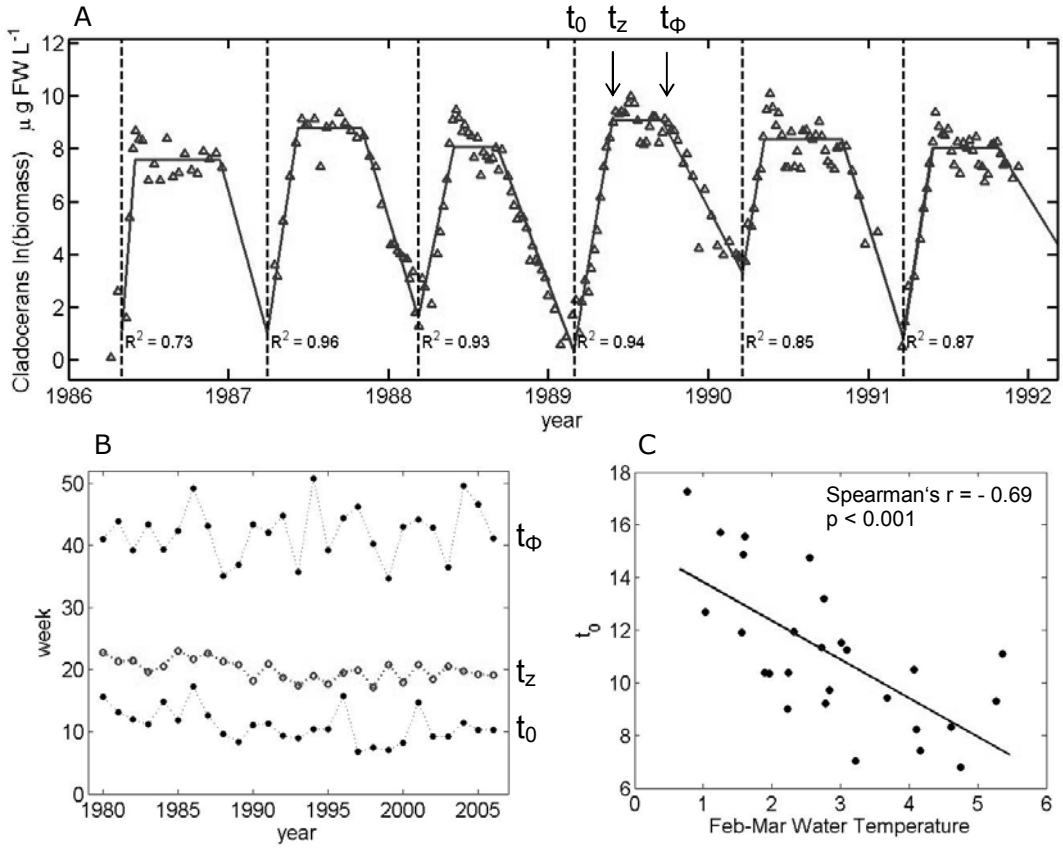


Fig. 5.1. Applying the SSD approach (chapter 2) to model cladoceran phenology in Müggelsee. A) Observed log-transformed cladoceran biomass (open triangles) and fitted SSD trajectories (solid lines) for selected years. Model fit (R^2) is given for each year; overall (1980 – 2006) fit was excellent: R^2 = 0.79. Transition times t_0 (onset of spring growth), t_z (spring peak) and t_ϕ (onset of winter decline) are marked as an example for the year 1989. B) Inter-annual variability in estimated transition times (showing temporal forward shifts in t_0 and t_z). C) Negative correlation between mean water temperatures in February and March and the onset of spring cladoceran growth (t_0). These results re-confirm the dependence of cladoceran spring phenology on winter and early spring temperatures as shown by, e.g., Straile (2002) and Gerten and Adrian (2000) and indicate that SSD models are a promising approach to assess and possibly project warming induced phenology shifts based on field data.

5.2 Phenology shifts and mismatch of species interactions

While many studies of both terrestrial and aquatic ecosystems have focused on species or group of species only, it becomes increasingly clear that the phenology of entire communities needs to be monitored (Harrington *et al*. 1999; Cleland *et al*. 2007). Cascading effects with severe impacts on entire food webs might occur, if climate change de-synchronizes predator-prey dynamics. Temporal mismatches of predator and prey have already been observed in a number of

systems, ranging from freshwater (Winder and Schindler 2004a; de Senerpont Domis *et al*. 2007a) and marine (Edwards and Richardson 2004; Hays *et al*. 2005) to terrestrial ecosystems (Both *et al*. 2006; Visser *et al*. 2006), but it is far from clear yet whether they are a general phenomena to be expected under climate change (Cleland *et al*. 2007).

As discussed in chapter 1 and emphasized in Fig. 5.2 a decline of *Daphnia* due to temporal mismatch was not observed in Müggelsee, despite a decoupling of these grazers from the dominant phytoplankton (diatoms) in years of extremely mild winters during the hypertrophic period of the lake (see chapter 1, Fig. 1.5 A, p. 35).

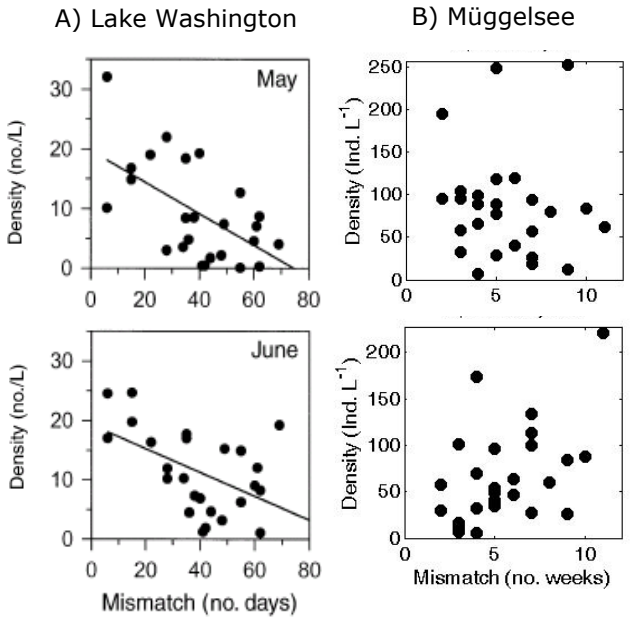


Fig. 5.2. Temporal mismatch between *Daphnia* and phytoplankton in spring, and *Daphnia* densities in May (upper panels) and June (lower panels) for A) Lake Washington (figure taken from Winder and Schindler 2004a) and B) Müggelsee. Mismatch is calculated as the number of days (weeks) elapsed between the phytoplankton peak and the *Daphnia* maximum in spring. While a decline of *Daphnia* after spring mismatch was observed in Lake Washington, no such relationship exist in Müggelsee. The contrast might be due to differences in lake depth (phytoplankton bloom collapse is induced by the onset of thermal stratification in monomictic Lake Washington, while it is brought about by silicate limitation or *Daphnia* grazing in polymictic Müggelsee) or differences in trophic state (in hypertrophic Müggelsee phytoplankton biomass remained above the food limitation threshold for *Daphnia* even after the collapse of the bloom, see chapter 1).

Shatwell *et al*. (2008), however, recently showed that cyanobacteria profited from this decoupling: annual cyanobacteria biovolume was higher the greater the time-lag between the spring diatom and cladoceran peak (Fig. 5.3). Thus, the consequence of climate-induced temporal mismatch of predator and prey may not always be the direct decline of the predator, but the increase of competitors at the level of the prey. A reshuffling of competitive forces at one trophic level may ultimately produce as severe impacts on the entire food web as the decline of the predator (e.g., nuisance blooms of cyanobacteria). It would be certainly a promising avenue for further research to use an extended version of the model of chapter 1 to explore the critical conditions for such competitive release triggered by warming-induced predator-prey mismatch.

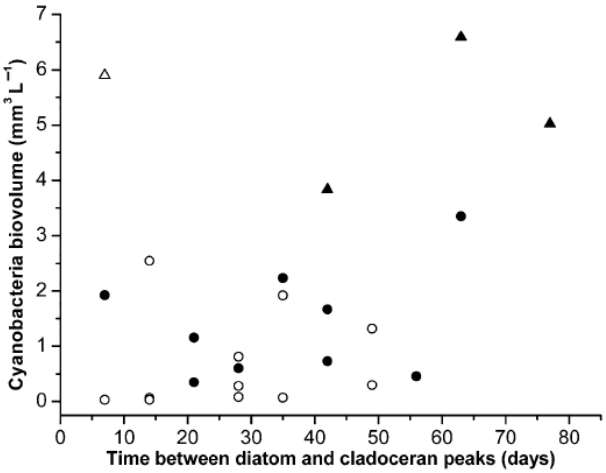


Fig. 5.3. Temporal mismatch between diatoms and cladoceran in spring and mean annual cyanobacteria biovolume in Müggelsee; (since diatoms strongly dominate phytoplankton and *Daphnia* cladoceran biomass in Müggelsee mismatch shown on x-axis can be directly compared to Fig. 5.2) Solid symbols: years with likely silicate limitation; open symbols: years with likely phosphorus limitation of diatoms; circles: years with clear-water phase; triangles: years without clear-water phase. Figure taken from Shatwell *et al*. (2008).

5.3 Seasonal warming patterns

Chapters 3 and 4 of this thesis indicate that the seasonal patterns of warming strongly determine the climate impact on lake plankton communities. Taylor *et*

al. (2002) have reported that plankton food webs may amplify weak climatic signals due to non-linear dynamics. This is certainly one of the reasons that comparatively small temporal differences in lake warming may induce strongly diverging ecosystem responses, as documented in this thesis. This finding is of particular importance when scaling from the local to the regional or global level since small-scale local variability in weather pattern might trigger small, but crucial differences in the seasonal course of warming in different lakes. The need to incorporate local processes has also been highlighted by studies of terrestrial ecosystems, e.g., Fisher *et al*. (2006) achieved to explain differences in tree phenology only when taking micro-gradients created by cold-air drainage into account. Overall, the results of this thesis re-emphasize that projections of meteorological conditions averaged over large temporal and spatial scales will not be sufficient to anticipate the response of lake ecosystems to future climate change.

5.4 Climate change and eutrophication

An important question is whether climate change bears the risk of counteracting efforts to curtail lake eutrophication, which were undertaken by reducing anthropogenic nutrient loading of catchment areas in the recent past (Jeppesen *et al*. 2005). Crucial items of concern are the frequency and intensity of phytoplankton blooms, which are suspected to increase during anomalously warm weather (Schindler 2006). It is useful to differentiate between two main pathways by which climate change may promote phytoplankton productivity in lakes.

First, climate change has been suggested to affect nutrient load and thus phytoplankton biomass by altering precipitation patterns and nutrient run-off in catchment areas (Schindler 2006) or by influencing the lake mixing regime, facilitating internal nutrient release from the sediments (e.g., Wilhelm and Adrian 2008). However, while climate-induced changes in nutrient load may be influential on short time-scales, some recent studies have indicated that trophic state is ultimately determined by local watershed characteristics, such as soil type and human land-use, which are primarily independent of climate change (Nõges 2009, Kosten *et al*. 2009).

Second, climate-induced change in water temperature, incident radiation, ice cover, and thermal stratification exert *direct* effects on phytoplankton growth and may thereby impact on the magnitude of phytoplankton blooms. For example, a recent study on re-oligotrophication of Lake Geneva suggested an increase in primary production and phytoplankton biomass despite falling nutrient concentrations due to higher availability of light and strengthened thermal stratification (Tadonleke *et al*. 2009). However, other studies have found that warming may exacerbate some symptoms of eutrophication such as de-oxygenation and reduced fish biomass (Feuchtmayr *et al*. 2009) or may influence the temporal organization and vertical positioning of the phytoplankton community (Winder and Hunter 2009), but did not affect total phytoplankton biomass. Sommer and Lengfellner (2008) have even reported that in their mesocosm experiments temperature elevation decreased phytoplankton peak biomass in spring. They speculated that in warmer mesocosms higher grazer activity lowered accumulation of phytoplankton biomass during the spring bloom.

In the light of these findings, which conclusions can be drawn from the results of this thesis? In chapter 1, I modelled trophic state independently of climate change by imposing a maximum amount of available phosphorus regardless of meteorological conditions. Making the phosphorus recycling rate (see chapter 1, eq. 3) dependent on temperature would be an interesting extension to the model, allowing for better differentiating between direct climate impacts on phytoplankton via water temperature and ice-cover and more indirect effects via potentially accelerated phosphorus recycling. In the simulation experiments applied, climatic conditions (water temperature and ice cover) only slightly modified the magnitude of the diatom spring bloom, which was predetermined by the lake's trophic state (phosphorus availability) (see chapter 1, Fig. 1.3, p. 33). Thus, with the mentioned caveats, the findings of chapter 1 suggest that, regarding the magnitude of the phytoplankton blooms in spring, climate change is unlikely to fully counteract successfully implemented nutrient reduction measures of recent decades.

In contrast, results of chapter 3 suggest that extreme meteorological conditions in the summer can principally work against past containment of eutrophication

by favouring cyanobacteria, which profit from intensified thermal stratification. However, whether increased cyanobacteria dominance during heat waves will remain an exception or will become a general rule in the future, will not only depend on the frequency of heat waves but also on their seasonal timing and duration, and food web interactions, as I have also shown in chapter 3. Yet, it is important to note that these conclusions apply only to moderately eutrophic, polymictic lakes: Wagner and Adrian (2009) found that under hypertrophic conditions, characterized by extremely high total phosphorus concentrations, dominance of cyanobacteria is promoted independently of the thermal regime.

Overall, the findings of this thesis suggest that nutrients remain the primary agents determining the magnitude of phytoplankton blooms, but that future climate change may exacerbate symptoms of eutrophication, such as the occurrence of cyanobacteria blooms. My results also indicate that the impacts of climate change (concerning timing and magnitude of phytoplankton blooms) in nutrient-rich lakes are more severe than in nutrient-poor lakes. Consequently, lake management that aims at containing eutrophication by reducing the anthropogenic supply of phosphorus and nitrogen to watersheds remains essential and might under future global warming prove even more important than in the past.

5.5 Conclusions

This thesis contributes to a better mechanistic understanding of the climate impacts on the timing and magnitude of phytoplankton blooms in shallow lakes. Key conclusions regarding the overarching research questions (see section 0.2, Fig. 0.4, p. 11) are:

(1) Trophic state determines the mechanisms that drive phytoplankton spring phenology in shallow lakes. Eutrophication amplifies the temporal advancement of the phytoplankton spring bloom triggered by climate warming.

(2) Future climate change is likely to further advance phytoplankton spring blooming in the season. However, accurately projecting spring phenology of phytoplankton may prove more demanding than of terrestrial plants,

since in addition to meteorological conditions food web interactions and especially nutrient availability and will need to be accounted for.

(3) The risk of decoupling the phytoplankton from the zooplankton spring peak due to de-synchronized phenology shifts is more elevated in nutrient-rich than in nutrient-poor shallow lakes. The consequence of predator-prey mismatch in nutrient-rich systems is not necessarily a decline of the predator.

(4) Summer heat waves do not generally promote cyanobacteria in eutrophic, polymictic lakes. Their seasonal timing and duration determine whether critical thresholds of thermal stratification, decisive for cyanobacteria bloom formation, are crossed.

(5) The temporal patterns of heat wave events critically influence the summer abundance of some zooplankton species, which may serve as a buffer by suppressing phytoplankton bloom formation.

(6) Nutrients are the primary drivers of phytoplankton bloom magnitudes. However, future climate warming has the potential to exacerbate some symptoms of eutrophication, such as the occurrence of cyanobacteria blooms.

References

Adrian R. & Frost T.M. (1992). Comparative feeding ecology of Tropocyclops-prasinus-mexicanus (Copepoda, Cyclopoida). *Journal of Plankton Research*, **14**, 1369-1382.

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

Adrian R. & Hintze T. (2000). Effects of winter air temperature on the ice phenology of the Müggelsee (Berlin, Germany). *Verh. Internat. Verein. Limnol.*, **27**, 2808-2811.

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

Adrian R., O'Reilly C.M., Zagarese H., *et al.* (2009) Lakes as sentinels of climate change. *Limnology and Oceanography,* **54**, in press.

Allan J.D. (1977). Analysis of seasonal dynamics of a mixed population of *Daphnia*, and associated cladoceran community. *Freshwater Biology*, **7**, 505-512.

Allen J.I., Howland R.M.H., Bloomer N. & Uncles R.J. (1998). Simulating the spring phytoplankton bloom in the Humber plume, UK. *Marine Pollution Bulletin*, **37**, 295-305.

Andersen T. (1997). *Pelagic nutrient cycles: herbivores as sources and sinks*. Springer Verlag, Heidelberg.

Arhonditsis G.B. & Brett M.T. (2005). Eutrophication model for Lake Washington (USA) Part I. Model description and sensitivity analysis. *Ecological Modelling*, **187**, 140-178.

Battisti D.S. & Naylor R.L. (2009). Historical Warnings of Future Food Insecurity with Unprecedented Seasonal Heat. *Science*, **323**, 240-244.

Benndorf J., Kranich J., 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). *Freshwater Biology*, **46**, 199-211.

Berger S.A., Diehl S., Stibor H., Trommer G., Ruhenstroth M., Wild A., Weigert A., Jäger C.G. & Striebel M. (2007). Water temperature and mixing depth affect timing and magnitude of events during spring succession of the plankton. *Oecologia*, **150**, 643-654.

Blenckner T., Adrian R., Livingstone D.M., Jennings E., Weyhenmeyer G.A., George D.G., Jankowski T., Jarvinen M., Aonghusa C.N., Noges T., Straile D. & Teubner K. (2007). Large-scale climatic signatures in lakes across Europe: a meta-analysis. *Global Change Biology*, **13**, 1314-1326.

Both C., Bouwhuis S., Lessells C.M. & Visser M.E. (2006). Climate change and population declines in a long-distance migratory bird. *Nature*, **441**, 81-83.

Bottrell H.H., Duncan A., Gliwicz Z.M., Grygierek E., Herzig A., Hillbrichtilkowska A., Kurasawa H., Larsson P. & Weglenska T. (1976). Review of some problems in zooplankton production studies. *Norwegian Journal of Zoology*, **24**, 419-456.

Bowie, G.L., W.B. Mills, D.B. Porcella, C.L. Campbell, J.R. Pagenkopf, G.L. Rupp, K.M. Johnson, P.W.H. Chan, and S.A. Gherini. 1985. *Rates, constants, and kinetics formulations in surface water quality modelling*. EPA/600/3-85/040, 2nd ed., U.S. Environmental Protection Agency.

Braune E., Richter O., Sondgerath D. & Suhling F. (2008). Voltinism flexibility of a riverine dragonfly along thermal gradients. *Global Change Biology*, **14**, 470-482.

Breiman L., Friedman J., Stone C.J. & Olshen R.A. (1993). *Classification and regression trees*. Chapman & Hall, Boca Raton.

Burns C.W. (1968). Relationship between body size of filter-feeding cladocera and maximum size of particle ingested. *Limnology and Oceanography*, **13**, 675-678.

Butterwick C., Heaney S.I. & Talling J.F. (2005). Diversity in the influence of temperature on the growth rates of freshwater algae, and its ecological relevance. *Freshwater Biology*, **50**, 291-300.

Caceres C.E. (1998). Interspecific variation in the abundance, production, and emergence of Daphnia diapausing eggs. *Ecology*, **79**, 1699-1710.

Chan F., Pace M.L., Howarth R.W. & Marino R.M. (2004). Bloom formation in heterocystic nitrogen-fixing cyanobacteria: The dependence on colony size and zooplankton grazing. *Limnology and Oceanography*, **49**, 2171-2178.

Chen C.Y. & Folt C.L. (2002). Ecophysiological responses to warming events by two sympatric zooplankton species. *Journal of Plankton Research*, **24**, 579-589.

Chorus I. & Bartram J. (1999). *Toxic Cyanobacteria in Water: A Guide to their Public Health Consequences, Monitoring and Management*. Spon, London.

Cleland E.E., Chuine I., Menzel A., Mooney H.A. & Schwartz M.D. (2007). Shifting plant phenology in response to global change. *Trends in Ecology & Evolution*, **22**, 357-365.

Conley D.J., Schelske C.L. & Stoermer E.F. (1993). Modification of the biogeochemical cycle of silica with eutrophication. *Marine Ecology-Progress Series*, **101**, 179-192.

Daufresne M., Bady P. & Fruget J.F. (2007). Impacts of global changes and extreme hydroclimatic events on macroinvertebrate community structures in the French Rhone River. *Oecologia*, **151**, 544-559.

Davidowicz P.Z., Gliwicz M. & Gulati R.D. (1988). Can Daphnia prevent a blue-green algae bloom in hypertrophic lakes? *Limnologica*, **19**, 21-26.

De Senerpont Domis L.N.D., Mooij W.M. & Huisman J. (2007a). Climate-induced shifts in an experimental phytoplankton community: a mechanistic approach. *Hydrobiologia*, **584**, 403-413.

De Senerpont Domis L.N.D., Mooij W.M., Hulsmann S., van Nes E.H. & Scheffer M. (2007b). Can overwintering versus diapausing strategy in Daphnia determine match-mismatch events in zooplankton-algae interactions? *Oecologia*, **150**, 682-698.

Demott W.R. & Kerfoot W.C. (1982). Competition among cladocerans – nature of interaction between *Bosmina* and *Daphnia*. *Ecology*, **63**, 1949-1966.

Diehl S., Berger S. & Wöhrl R. (2005). Flexible nutrient stoichiometry mediates environmental influences, on phytoplankton and its resources. *Ecology*, **86**, 2931-2945.

Dokulil M.T. & Teubner K. (2000). Cyanobacterial dominance in lakes.

Hydrobiologia, **438**, 1-12.

Downing J.A., Watson S.B. & McCauley E. (2001). Predicting Cyanobacteria dominance in lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 1905-1908.

Driescher E., Behrendt H., Schellenberger G. & Stellmacher R. (1993). Lake Müggelsee and ist environment – natural conditions and anthropogenic impacts. *Internationale Revue der Gesamten Hydrobiologie*, **78**, 327-343.

Droop M.R. (1983). 25 years of algal growth kinetics – a personal view. *Botanica Marina*, **26**, 99-112.

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

Elliott J.A., Jones I.D. & Thackeray S.J. (2006). Testing the sensitivity of phytoplankton communities to changes in water temperature and nutrient load, in a temperate lake. *Hydrobiologia*, **559**, 401-411.

Feuchtmayr H., Moran R., Hatton K., Connor L., Heyes T., Moss B., Harvey I. & Atkinson D. (2009). Global warming and eutrophication: effects on water chemistry and autotrophic communities in experimental hypertrophic shallow lake mesocosms. *Journal of Applied Ecology*, **46**, 713-723.

Fisher J.I., Mustard J.F. & Vadeboncoeur M.A. (2006). Green leaf phenology at Landsat resolution: Scaling from the field to the satellite. *Remote Sensing of Environment*, **100**, 265-279.

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

Gerten D. & Adrian R. (2002). Species-specific changes in the phenology and peak abundance of freshwater copepods in response to warm summers. *Freshwater Biology*, **47**, 2163-2173.

Giebelhausen B. & Lampert W. (2001). Temperature reaction norms of Daphnia magna: the effect of food concentration. *Freshwater Biology*, **46**, 281-289.

Gleick P.H. (1996). Water resources. In: *Encyclopedia of Climate and Weather*, (ed.) Schneider S.H., Oxford University Press, New York.

Gyllstrom M. & Hansson L.A. (2004). Dormancy in freshwater zooplankton: Induction, termination and the importance of benthic-pelagic coupling.

Aquatic Sciences, **66**, 274-295.

Hairston N.G., Hansen A.M. & Schaffner W.R. (2000). The effect of diapause emergence on the seasonal dynamics of a zooplankton assemblage. *Freshwater Biology*, **45**, 133-145.

Hanazato T. & Yasuno M. (1989). Zooplankton community structure driven by vertebrate and invertebrate predators. *Oecologia*, **81**, 450-458.

Hansen A.M. & Santer B. (1995). The influence of food resources on the development, survival and reproduction of the 2 cyclopoid copepods *Cyclops vicinus* and *Mesocyclops leuckarti*. *Journal of Plankton Research*, **17**, 631-646.

Harrington R., Woiwod I. & Sparks T. (1999). Climate change and trophic interactions. *Trends in Ecology & Evolution*, **14**, 146-150.

Harris E. (1989). *The Chlamydomonas sourcebook: a comprehensive guide to biology and laboratory use*. Academic Press, New York.

Hastings A. (2001). Transient dynamics and persistence of ecological systems. *Ecology Letters*, **4**, 215-220.

Hastings A. (2004). Transients: the key to long-term ecological understanding? *Trends in Ecology & Evolution*, **19**, 39-45.

Haupt R.L. & Haupt S.E. (1998). *Practical genetic algorithms*. Wiley, New York.

Hays G.C., Richardson A.J. & Robinson C. (2005). Climate change and marine plankton. *Trends in Ecology & Evolution*, **20**, 337-344.

Hopp U. & Maier G. (2005). Survival and development of five species of cyclopoid copepods in relation to food supply: experiments with algal food in a flow-through system. *Freshwater Biology*, **50**, 1454-1463.

Horn H. (2003). The relative importance of climate and nutrients in controlling phytoplankton growth in Saidenbach Reservoir. *Hydrobiologia*, **504**, 159-166.

Huber V., Adrian R. & Gerten D. (2008). Phytoplankton response to climate warming modified by trophic state. *Limnology and Oceanography*, **53**, 1-13.

Huber V. & Gaedke U. (2006). The role of predation for seasonal variability patterns among phytoplankton and ciliates. *Oikos*, **114**, 265-276.

Huisman J., Sharples J., Stroom J.M., Visser P.M., Kardinaal W.E.A.,

Verspagen J.M.H. & Sommeijer B. (2004). Changes in turbulent mixing shift competition for light between phytoplankton species. *Ecology*, **85**, 2960-2970.

Huisman J. & Hulot F.D. (2005). Population dynamics of harmful cyanobacteria. In: *Harmful Cyanobacteria,* (eds.) Huisman J., Matthijs P.M. & Visser P.M., Springer, Heidelberg.

Huisman J., Matthijs P.M. & Visser P.M. (eds.) (2005). *Harmful Cyanobacteria.* Springer, Heidelberg.

Hyenstrand P., Blomquist P. & Pettersson A. (1998). Factors determining cyanobacterial success in aquatic systems - a literature review. *Archiv Fuer Hydrobiologie Special Issues for Advancement of Limnology*, **51**, 41-62.

Ibelings B.W., Vonk M., Los H.F.J., van der Molen D.T. & Mooij W.M. (2003). Fuzzy modeling of cyanobacterial surface waterblooms: Validation with NOAA-AVHRR satellite images. *Ecological Applications*, **13**, 1456-1472.

IPCC (2007). *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, (eds.) Parry M.L., Canziani O.F., Palutikof J.P., van der Linden P.J. & Hanson C.E., Cambridge University Press, Cambridge.

Ives A.R., Gross K. & Jansen V.A.A. (2000). Periodic mortality events in predator-prey systems. *Ecology*, **81**, 3330-3340.

Jäger C.G., Diehl S., Matauschek C., Klausmeier C.A. & Stibor H. (2008). Transient dynamics of pelagic producer grazer systems in a gradient of nutrients and mixing depths. *Ecology*, **89**, 1272-1286.

Jankowski T., Livingstone D.M., Buhrer 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. *Limnology and Oceanography*, **51**, 815-819.

Jeppesen E., Sondergaard M. & Jensen J.P. (2003). Climatic warming and regime shifts in lake food webs - some comments. *Limnology and Oceanography*, **48**, 1346-1349.

Jeppesen E., Sondergaard M., Jensen J.P., Havens K.E., Anneville O., Carvalho L., Coveney M.F., Deneke R., Dokulil M.T., Foy B., Gerdeaux D., Hampton S.E., Hilt S., Kangur K., Kohler J., Lammens E., Lauridsen T.L., Manca M., Miracle M.R., Moss B., Noges P., Persson G., Phillips G., Portielje R., Schelske C.L., 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. *Freshwater Biology* **50**, 1747-1771.

Johnk K.D., Huisman J., Sharples J., Sommeijer B., Visser P.M. & Stroom J.M. (2008). Summer heatwaves promote blooms of harmful cyanobacteria. *Global Change Biology*, **14**, 495-512.

Kilham S.S., Kreeger D.A., Lynn S.G., Goulden C.E. & Herrera L. (1998). COMBO: a defined freshwater culture medium for algae and zooplankton. *Hydrobiologia*, **377**, 147-159.

Kirchner A. (1997). *Untersuchung der Bindungsformen und der Mobilität von Phosphor im Sediment des Grossen Müggelsees*. Diploma thesis, University of Braunschweig/Wolfenbüttel.

Klausmeier C.A., Litchman E. & Levin S.A. (2004). Phytoplankton growth and stoichiometry under multiple nutrient limitation. *Limnology and Oceanography*, **49**, 1463-1470.

Köhler J., Behrendt H. & Hoeg S. (2000). Long-term response of phytoplankton to reduced nutrient load in the flushed Lake Müggelsee (Spree system, Germany). *Archiv für Hydrobiologie*, **148**, 209-229.

Köhler J., Hilt S., Adrian R., Nicklisch A., Kozerski H.P. & Walz N. (2005). Long-term response of a shallow, moderately flushed lake to reduced external phosphorus and nitrogen loading. *Freshwater Biology*, **50**, 1639-1650.

Kosten S., Huszar V.L.M., Mazzeo N., Scheffer M., Sternberg L.D.L. & Jeppesen E. (2009). Lake and watershed characteristics rather than climate influence nutrient limitation in shallow lakes. *Ecological Applications*, **19**, 1791-1804.

Lampert W., Fleckner W., Rai H. & Taylor B.E. (1986). Phytoplankton control by grazing zooplankton – a study on the spring clear-water phase.

Limnology and Oceanography, **31**, 478-490.

Lampert W. & Sommer U. (1999). *Limnoökologie*. Thieme, Stuttgart.

Law T., Zhang W.T., Zhao J.Y. & Arhonditsis G.B. (2009). Structural changes in lake functioning induced from nutrient loading and climate variability. *Ecological Modelling*, **220**, 979-997.

Litchman E. & Klausmeier C.A. (2001). Competition of phytoplankton under fluctuating light. *American Naturalist*, **157**, 170-187.

Livingstone D.M. (1999). Ice break-up on southern Lake Baikal and its relationship to local and regional air temperatures in Siberia and to the North Atlantic Oscillation. *Limnology and Oceanography*, **44**, 1486-1497.

Lund J.W.G. (1950). Studies on *Asterionella formosa* Hass. 2. Nutrient depletion and the spring maximum. *Journal of Ecology*, **38**, 15-35.

Maier G. (1989). The effect of temperature on the development times of eggs, naupliar and copepodite stages of 5 species of cyclopoid copepods. *Hydrobiologia*, **184**, 79-88.

Maier G. (1990). Spatial distribution of resting stages, rate of emergence from diapause and times to adulthood and to the appearance of the 1st clutch in 3 species of cyclopoid copepods. *Hydrobiologia*, **206**, 11-18.

Malmaeus J.M., Blenckner T., Markensten H. & Persson I. (2006). Lake phosphorus dynamics and climate warming: A mechanistic model approach. *Ecological Modelling*, **190**, 1-14.

Meehl G.A. & Tebaldi C. (2004). More intense, more frequent, and longer lasting heat waves in the 21st century. *Science*, **305**, 994-997.

Meis S., Thackeray S.J. & Jones I.D. (2009). Effects of recent climate change on phytoplankton phenology in a temperate lake. *Freshwater Biology*, **54**, 1888-1898.

Menzel A., Sparks T.H., Estrella N., Koch E., Aasa A., Ahas R., Alm-Kubler K., Bissolli P., Braslavska O., Briede A., Chmielewski F.M., Crepinsek Z., Curnel Y., Dahl A., Defila C., Donnelly A., Filella Y., Jatcza K., Mage F., Mestre A., Nordli O., Penuelas J., Pirinen P., Remisova V., Scheifinger H., Striz M., Susnik A., Van Vliet A.J.H., Wielgolaski F.E., Zach S. & Zust A. (2006). European phenological response to climate change matches the warming pattern. *Global Change Biology*, **12**, 1969-1976.

Mooij W.M., Hulsmann S., Domis L.N.D., Nolet B.A., Bodelier P.L.E., Boers P.C.M., Pires L.M.D., Gons H.J., Ibelings B.W., Noordhuis R., Portielje R., Wolfstein K. & Lammens E. (2005). The impact of climate change on lakes in the Netherlands: a review. *Aquatic Ecology*, **39**, 381-400.

Moore M.V., Folt C.L. & Stemberger R.S. (1996). Consequences of elevated temperatures for zooplankton assemblages in temperate lakes. *Archiv für Hydrobiologie*, **135**, 289-319.

Morel F.M.M. (1987). Kinetics of nutrient uptake and growth in phytoplankton. *Journal of Phycology*, **23**, 137-150.

Nicklisch A. & Kohl J.-G. (1989). The influence of light on primary production of two planktic blue-green algae. *Arch. Hydrobiol., Beih. Ergebn. Limnol.* **33**,451-455.

Nicklisch A., Shatwell T. & Köhler J. (2008). Analysis and modelling of the interactive effects of temperature and light on phytoplankton growth and relevance for the spring bloom. *Journal of Plankton Research*, **30**, 75-91.

Nõges T. (2009) Relationships between morphometry, geographic location and water quality parameters of European lakes. *Hydrobiologia*, **633**,33-43.

Norberg J. & DeAngelis D. (1997). Temperature effects on stocks and stability of a phytoplankton-zooplankton model and the dependence on light and nutrients. *Ecological Modelling*, **95**, 75-86.

Omlin M., Brun R. & Reichert P. (2001). Biogeochemical model of Lake Zurich: sensitivity, identifiability and uncertainty analysis. *Ecological Modelling*, **141**, 105-123.

Paerl H.W. & Huisman J. (2008). Climate - Blooms like it hot. *Science*, **320**, 57-58.

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

Peeters F., Straile D., Lorke A. & Ollinger D. (2007a). Turbulent mixing and phytoplankton spring bloom development in a deep lake. *Limnology and Oceanography*, **52**, 286-298.

Peeters F., Straile D., Lorke A. & Livingstone D.M. (2007b). Earlier onset of the spring phytoplankton bloom in lakes of the temperate zone in a warmer climate. *Global Change Biology*, **13**, 1898-1909.

Post A.F., Dewit R. & Mur L.R. (1985). Interactions between temperature and light-intensity on growth and photosynthesis of the cyanobacterium *Oscillatoria agardhii*. *Journal of Plankton Research*, **7**, 487-495.

Rhee G.Y. & Gotham I.J. (1981). The effect of environmental factors on phytoplankton growth: light and the interactions of light with nitrate limitation. *Limnology and Oceanography*, **26**, 649-659.

Rocha O. & Duncan A. (1985). The relationship between cell carbon and cell-volume in freshwater algal species used in zooplanctonic studies. *Journal of Plankton Research*, **7**, 279-294.

Sarnelle O. (2007). Initial conditions mediate the interaction between Daphnia and bloom-forming cyanobacteria. *Limnology and Oceanography*, **52**, 2120-2127.

Schalau K., Rinke K., Straile D. & Peeters F. (2008). Temperature is the key factor explaining interannual variability of Daphnia development in spring: a modelling study. *Oecologia*, **157**, 531-543.

Schär C. & Jendritzky G. (2004). Climate change: Hot news from summer 2003. *Nature*, **432**, 559-560.

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

Scheffer M., Rinaldi S., Kuznetsov Y.A. & vanNes E.H. (1997). Seasonal dynamics of Daphnia and algae explained as a periodically forced predator-prey system. *Oikos*, **80**, 519-532.

Scheffer M., Straile D., van Nes E.H. & Hosper H. (2001). Climatic warming causes regime shifts in lake food webs. *Limnology and Oceanography*, **46**, 1780-1783.

Scheffer M., Straile D., van Nes E.H. & Hosper H. (2003). Climatic effects on regime shifts in lakes: A reply. *Limnology and Oceanography*, **48**, 1353-1356

Schellenberger G.H., Behrendt H., Kozerski H.-P., & Mohaupt V. (1983). Ein mathematisches Ökosystemmodell für eutrophe Flachgewässer. *Acta Hydrophysica***, 28**, 109-172..

Schelske C.L. & Stoermer E.F. (1971). Eutrophication, Silica Depletion, and

Predicted Changes in Algal Quality in Lake Michigan. *Science*, **173**, 423-424.

Schindler D.W. (1974). Eutrophication and recovery in experimental lakes – implications for lake management. *Science*, **184**, 897-899.

Schindler D.W. (2006). Recent advances in the understanding and management of eutrophication. *Limnology and Oceanography*, **51**, 356-363.

Seebens H., Straile D., Hoegg R., Stich H.B. & Einsle U. (2007). Population dynamics of a freshwater calanoid copepod: Complex responses to changes in trophic status and climate variability. *Limnology and Oceanography*, **52**, 2364-2372.

Shatwell T., Köhler J. & Nicklisch A. (2008). Warming promotes cold-adapted phytoplankton in temperate lakes and opens a loophole for Oscillatoriales in spring. *Global Change Biology*, **14**, 2194-2200.

Smayda T.J. (1971). Normal and accelerated sinking of phytoplankton in the sea. *Marine Geology*, **11**, 105-&.

Smith V.H. (1983). Low nitrogen to phosphorus ratios favor dominance of blue-green-algae in lake phytoplankton. *Science*, **221**, 669-671.

Sommer U. (1989). *Plankton ecology: succession in plankton communities*. Springer Verlag, New York.

Sommer U. (1991). A comparison of the Droop and the Monod models of nutrient limited growth applied to natural populations of phytoplankton. *Functional Ecology*, **5**, 535-544.

Sommer U. (1993). Phytoplankton competition in Plusssee – a field-test of the resource-ratio hypothesis. *Limnology and Oceanography*, **38**, 838-845.

Sommer U. (1994). *Planktologie*. Springer Verlag, Heidelberg.

Sommer U., Gliwicz Z.M., Lampert W. & Duncan A. (1986). The PEG-model of seasonal succession of planktonic events in fresh waters. *Archiv für Hydrobiologie*, **106**, 433-471.

Sommer U., Aberle N., Engel A., Hansen T., Lengfellner K., Sandow M., Wohlers J., Zollner E. & Riebesell U. (2007). An indoor mesocosm system to study the effect of climate change on the late winter and spring succession of Baltic Sea phyto- and zooplankton. *Oecologia*, **150**, 655-667.

Sommer U. & Lengfellner K. (2008). Climate change and the timing, magnitude,

and composition of the phytoplankton spring bloom. *Global Change Biology*, **14**, 1199-1208.

Soranno P.A. (1997). Factors affecting the timing of surface scums and epilimnetic blooms of blue-green algae in a eutrophic lake. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 1965-1975.

Sterner R.W. (1989) The role of grazers in phytoplankton succession. In: *Plankton ecology. eucession in plankton communities*, (ed.) Sommer U., Springer, Heidelberg.

Straile D. (2002). North Atlantic Oscillation synchronizes food-web interactions in central European lakes. *Proceedings of the Royal Society B-Biological Sciences*, **269**, 391-395.

Straile D. & Adrian R. (2000). The North Atlantic Oscillation and plankton dynamics in two European lakes - two variations on a general theme. *Global Change Biology*, **6**, 663-670.

Struzewska J. & Kaminski J.W. (2008). Formation and transport of photooxidants over Europe during the July 2006 heat wave - observations and GEM-AQ model simulations. *Atmospheric Chemistry and Physics*, **8**, 721-736.

Tadonleke R.D., Lazzarotto J., Anneville O. & Druart J.C. (2009). Phytoplankton productivity increased in Lake Geneva despite phosphorus loading reduction. *Journal of Plankton Research*, **31**, 1179-1194.

Taylor A.H., Allen J.I. & Clark P.A. (2002). Extraction of a weak climatic signal by an ecosystem. *Nature*, **416**, 629-632.

Tietjen B. & Huth A. (2006). Modelling dynamics of managed tropical rainforests - An aggregated approach. *Ecological Modelling*, **199**: 421-432.

Tilman D. (1982). *Resource Competition and Community Structure*. Princeton University Press, Princeton and Oxford.

Tirok K. & Gaedke U. (2006). Spring weather determines the relative importance of ciliates, rotifers and crustaceans for the initiation of the clear-water phase in a large, deep lake. *Journal of Plankton Research*, **28**, 361-373.

Tirok K. & Gaedke U. (2007). The effect of irradiance, vertical mixing and temperature on spring phytoplankton dynamics under climate change: long-term observations and model analysis. *Oecologia*, **150**, 625-642.

Van Donk E., Lurling M., Hessen D.O. & Lokhorst G.M. (1997). Altered cell wall morphology in nutrient-deficient phytoplankton and its impact on grazers. *Limnology and Oceanography* **42**: 357-364.

Van Donk E., Santamaria L. & Mooij W.M. (2003). Climate warming causes regime shifts in lake food webs: A reassessment. *Limnology and Oceanography*, **48**, 1350-1353.

Vandekerkhove J., Declerck S., Brendonck L., Conde-Porcuna J.M., Jeppesen E. & De Meester L. (2005). Hatching of cladoceran resting eggs: temperature and photoperiod. *Freshwater Biology***, 50**, 96-104.

VanDonk E., Lurling M., Hessen D.O. & Lokhorst G.M. (1997). Altered cell wall morphology in nutrient-deficient phytoplankton and its impact on grazers. *Limnology and Oceanography*, **42**, 357-364.

Vanni M.J., Luecke C., Kitchell J.F., Allen Y., Temte J. & Magnuson J.J. (1990). Effects on lower trophic levels of massive fish mortality. *Nature*, **344**, 333-335.

Vanni M.J. & Temte J. (1990). Seasonal patterns of grazing and nutrient limitation of phytoplankton in a eutrophic lake. *Limnology and Oceanography*, **35**, 697-709.

Vijverberg J. (1980). Effect of temperature in laboratory studies on development and growth of Cladocera and Copepoda from Tjeukemeer, The Netherlands. *Freshwater Biology*, **10**, 317-340.

Visser M.E., Holleman L.J.M. & Gienapp P. (2006). Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia*, **147**, 164-172.

Vollenweider R.A. & Kerekes J. (1982). *Eutrophication of waters – monitoring, assessment and control*. OECD, Paris.

Wagner A. & Benndorf J. (2007). Climate-driven warming during spring destabilises a Daphnia population: a mechanistic food web approach. *Oecologia*, **151**, 351-364.

Wagner C. (2009). *Lake ecosystem responses to climate warming*. Dissertation thesis, Free University Berlin.

Wagner C, Adrian R (2009) Cyanobacteria dominance: Quantifying the effect of climate change. *Limnology and Oceanography*, **54**, 2460-2468.

Walther G.R., Post E., Convey P., Menzel A., Parmesan C., Beebee T.J.C., Fromentin J.M., Hoegh-Guldberg O. & Bairlein F. (2002). Ecological responses to recent climate change. *Nature*, **416**, 389-395.

Wernicke P. & Nicklisch A. (1986). Light/dark cycle and temperature - their impact on phosphate-limited growth of *Oscillatoria redekei* VAN GOOR in semicontinuous culture. *Internationale Revue der gesamten Hydrobiologie*, **71**, 297-313.

Wetzel R.G. (2001). *Limnology - Lake and River Ecosystems*. Academic Press, San Diego.

Weyhenmeyer G.A., Blenckner T. & Pettersson K. (1999). Changes of the plankton spring outburst related to the North Atlantic Oscillation. *Limnology and Oceanography***, 44**, 1788-1792.

Wilhelm S., Hintze T., Livingstone D.M, & Adrian R. (2006). Long-term response of daily epilimnetic temperature extrema to climate forcing. *Canadian Journal of Fisheries and Aquatic Sciences,* **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.

Wilhelm S. & Adrian R. (2008). Impact of summer warming on the thermal characteristics of a polymictic lake and consequences for oxygen, nutrients and phytoplankton. *Freshwater Biology*, **53**, 226-237.

Williamson C.E., Saros J.E. & Schindler D.W. (2009). Sentinels of Change. *Science*, **323**, 887-888.

Willmott C.J. (1982). Some comments on the evaluation of model performance. *Bulletin of the American Meteorological Society*, **63**, 1309-1313.

Wiltshire K.H., Malzahn A.M., Wirtz K., Greve W., Janisch S., Mangelsdorf P., Manly B.F.J. & Boersma M. (2008). Resilience of North Sea phytoplankton spring bloom dynamics: An analysis of long-term data at Helgoland Roads. *Limnology and Oceanography*, **53**, 1294-1302.

Winder M. & Hunter D.A. (2008). Temporal organization of phytoplankton communities linked to physical forcing. *Oecologia*, **156**, 179-192.

Winder M. & Schindler D.E. (2004a). Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology*, **85**, 2100-2106.

Winder M. & Schindler D.E. (2004b). Climatic effects on the phenology of lake processes. *Global Change Biology*, **10**, 1844-1856.

Declaration on contributions to manuscripts

This thesis comprises four independent studies that are either published or have been submitted to international scientific journals. All of the studies were undertaken together with co-authors. Author contributions were as follows:

Chapter 1: Dieter Gerten suggested the initial research question. Ideas for addressing the question were mine. Construction of the model, analysis of the results and writing of the manuscript were also entirely done by myself. Dieter Gerten and Rita Adrian gave advice on methodological issues and made suggestions for manuscript improvement.

Chapter 2 (see chapter acknowledgement section; p. 65): My co-authors developed the model approach, designed and performed the experiment. I was involved in analysing the data and writing the manuscript. My part in analysing the data was developing a concept of how to parameterize the model, and programming and implementing the genetic algorithm. I also constructed part of the figures (namely Fig. 2.2, p.58, and Figs. A2.1—3, p.66—73) or suggested ideas for visualisation (namely Fig. 2.3, p. 60). While the first author Christopher F. Steiner wrote most of the manuscript, I contributed substantially to the method section, the discussion and the appendix on the genetic algorithm.

Chapter 3: I independently decided to work on the research question and to use the methods (classification tree analysis) of Wagner and Adrian (2009) to address it. Data analyses were partly based on results of Wagner and Adrian (2009), but were exclusively undertaken by myself. Writing of the manuscripts profited from continuous discussions with Carola Wagner, Rita Adrian and Dieter Gerten.

Chapter 4: Research questions addressed and methods used were my own idea. Rita Adrian and Dieter Gerten gave advice on data analysis and writing of the manuscripts, but left the implementation entirely to me.

Zusammenfassung

Weltweit haben Seeökosysteme auf den Klimawandel der letzten Jahrzehnte reagiert. Beobachtete Veränderungen eindeutig dem Klimawandel zuzuordnen, wird jedoch häufig dadurch erschwert, dass Seen gleichzeitig vielfachen anthropogenen Einflüssen ausgesetzt sind. Mit dieser Arbeit trage ich zu einem besseren Verständnis des Klimaeinflusses auf Algen bei, die am Anfang der Nahrungskette stehen und maßgeblich die Wasserqualität eines Sees beeinflussen können.

Zum größten Teil stützt sich die Arbeit auf eine dreißigjährige Datenreihe eines unregelmäßig geschichteten Flachsees im Nordosten von Deutschland (Müggelsee), in dem sowohl steigende Wassertemperaturen als auch sinkende Nährstoffeinträge zu verzeichnen waren. Bei der Datenanalyse nutzte ich ein neu erstelltes dynamisches Simulationsmodell, genetische Algorithmen zur Parametrisierung von Modellen, und statistische Methoden der Klassifizierung und Zeitreihenanalyse.

Ergebnisse dieser Arbeit zeigen, dass nicht nur klimatische Faktoren sondern auch die Nährstoffverfügbarkeit im See den Zeitpunkt der Algenfrühjahrsblüte (Phänologie) beeinflussen. Durch eine Veränderung der Mechanismen, die zum Kollaps der Blüte führen, trat diese trotz ähnlich milder Winterbedingungen bei hoher Nährstoffverfügbarkeit früher auf als bei niedriger. Ein neuentwickelter Ansatz zur Modellierung von Phänologie erwies sich als geeignet, um vorherzusagen, wann Algen und ihre Räuber in einem künstlich periodisch angetriebenen Laborsystem ihre Populationshöhepunkte erreichten. Eine Verlängerung der Wachstumsperiode führte dazu, dass diese früher auftraten.

Die Untersuchung, warum sich Blaualgen im betrachteten See während jüngster Hitzewellenereignisse überraschend unterschiedlich entwickelt hatten, ergab, dass ungewöhnlich warmes Wetter nicht wie häufig vermutet generell förderlich für ihre Entwicklung ist. Der Zeitpunkt und die Dauer der Hitzewellen waren entscheidend dafür, ob für Blaualgen kritische Schwellenwerte der thermischen Schichtung im See überschritten wurden.

Zudem zeigte sich, dass saisonale Erwärmungsmuster einen bedeutenden Einfluss auf Räuber nahmen, die das Auftreten von Algenblüten verhindern können.

Diese Arbeit reiht sich in eine wachsende Anzahl von Studien ein, die zeigen, dass Seeökosysteme bereits stark auf die Klimaveränderungen der letzen Jahrzehnte reagiert haben. Mit ihrem Fokus auf Mechanismen und der expliziten Berücksichtigung simultaner anthropogener Einflüsse geht diese Arbeit gleichzeitig über viele bisherige Studien hinaus, die sich auf reine Beobachtung und die Betrachtung klimatischer Faktoren beschränkten.

Kernergebnisse deuten daraufhin, dass Klimafolgen in nährstoffreichen Seen stärker ausfallen als in nährstoffarmen Seen. Nur mit einem umfassenden, mechanistischen Verständnis des vielfältigen anthropogenen Einflusses wird eine hohe Wasserqualität in Seen auch in Zukunft aufrechtzuerhalten sein.

General acknowledgements

The present thesis was carried out at the Leibniz-Institute for Freshwater Ecology and Inland Fisheries (IGB) in Berlin, with the exception of chapter 2, which for the largest part evolved at W.K. Kellogg Biological Station (KBS) of Michigan State University.

I am grateful to the German Research Foundation who supported the thesis within the priority program AQUASHIFT "The effect of climate variability on aquatic ecosystems" (SPP 1162). The German Academic Exchange Service provided funds for the research undertaken at KBS.

Most people who scientifically contributed to the accomplishment of this thesis are gratefully acknowledged at the end of each chapter.

I am particularly thankful to Rita Adrian and Dieter Gerten who supervised most of the research that has been incorporated into this thesis. Rita Adrian besides giving good scientific advice taught me to look beyond the Müggelsee horizon by for example initiating fruitful discussion on Thomas Kuhn's paradigm shifts. Comments by Dieter Gerten were always straight to the point and helped structuring the work when I risked not seeing the woods for the trees.

Ursula Gaedke inspired my interest for limnology. I am grateful for her continuous support and advice.

The "Adrian Working Group" Carola Wagner and Susann Wilhelm are acknowledged for valuable comments on work in progress. I am grateful to them, and to Nadine Bauer and Friederike Gabel, for sharing times of long office hours, sometimes frustration, but also excitement and laughter.

Elena Litchman and Christopher Klausmeier are gratefully acknowledged for hosting me in their lab and integrating me into their research activities.

My time at IGB would not have been half as nice without Sheku Kamara and Alaa Osman, who made me grasp — more than anything else — the privilege of being part of an international scientific community.

Many thanks also go to John Schellnhuber and my colleagues in the Director's Office at the Potsdam Institute for Climate Impact Research for their understanding and encouragement during times of double challenge.

Nicht zuletzt möchte ich mich bei den Menschen bedanken, die mich auf meinem Lebensweg bis zu diesem Punkt begleitet und im entscheidenden Moment angeleitet und inspiriert haben. Ein ganz besonderer Dank gilt meinen Eltern und meiner Schwester für ihre Unterstützung und Ermutigung in allen Lebenslagen, in guten wie in schlechten Zeiten. Auch bei Robert möchte ich mich herzlich bedanken für seinen Humor, seine Neugier und sein Verständnis.