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Influence of climate change on lake ecosystems – disentangling physical, chemical and biological interactions.

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Erklärung des Promovenden

Die Übereinstimmung dieses Exemplars mit dem Original der Dissertation zum Thema: "Influence of climate change on lake ecosystems – disentangling physical, chemical and biological interactions." wird hiermit bestätigt.

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1 Introduction and main results

1.1 Climate change

The world is “unequivocally” warming since the 19th century and the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) presents

> “evidence from multiple independent climate indicators, from high up in the atmosphere to the depths of the oceans. They include changes in surface, atmospheric and oceanic temperatures; glaciers; snow cover; sea ice; sea level and atmospheric water vapour” (IPCC 2013).

According to the IPCC (2013), air temperatures between 2003–2012 rose 0.78 °C compared to the average of 1850–1900 and the last three decades were the warmest 30-year period of the last 1400 years. Significant trends of warming in the oceans were found down to 2000 m depth and the cryospheric glaciers shrunk almost worldwide. Together with that, the rise of the sea level since 1900 was 0.2 m and acidification of oceans is ongoing due to elevated atmospheric carbon dioxide levels. The rate of sea level rise is higher than the mean rate during the previous two millenia. While it is partially discussed by the public if mankind is the prime driving force of all these current changes, the anthropogenic influence is a well established consensus in science and policy domains (Gerten 2008; Dokulil 2013). The United Nations Framework Convention on Climate Change (UNFCCC) tries to stabilise greenhouse gas concentrations in the atmosphere to mitigate climate change effects and to ensure sustainable provision of ecosystem services. Many mitigation strategies are also suggested by IPCC (2014b).

As a consequence of global warming, lake ecosystems are affected too (Dokulil et al. 2010). The impacts on internal processes and variables of aquatic ecosystems are manyfold and affect hydrology, the temperature regime, ice phenology, transparency, water chemistry, autecology and community and habitat structures (Adrian et al. 2009). The climate driven changes of the abiotic environment influence directly and – due to species specific preferences – indirectly the development, phenology and life histories of bacteria (Hoppe et al. 2008; Dziallas & Grossart 2011; Wohlers-Zoellner et al. 2011), phytoplankton (Adrian et al. 1999; Weyhenmeyer et al. 1999; Winder & Schindler 2004a), zooplankton (Adrian et al. 2006; Seebens et al. 2007; Wojtal-Frankiewicz 2012), invertebrate predators (Wagner et al. 2013) and fish (Jeppesen et al. 2012). Furthermore, the temporal and spatial match and mismatch of prey and predators can be uncoupled or altered (Cushing 1990; Winder & Schindler 2004b). For example, Wagner et al. (2013) found that due to the increase of spring water temperature larvae of perch hatch and develop faster and prefer earlier emerging chironomid pupae as main food while the usually ingested daphnids become temporally uncoupled from this predator. Due to large scale climatic patterns like the El Nino-Southern Oscillation or the North Atlantic Oscillation, the warming of lake ecosystems in Europe and North America can be highly synchronized (Straile et al. 2002; Gerten & Adrian 2002; Blenckner et al. 2007). Even if the lakes are not connected otherwise, by that, physical, chemical and biological processes can be synchronized over large distances (Gerten 2008). For example, Straile & Adrian (2000) and Straile (2002) showed that the algal supression by herbivores during early summer (clearwater phase), advanced on average by two weeks in central European lakes. This could be explained by faster zooplankton population growth rates in warmer water.

All these temperature interactions are complex on their own and interact with each other. Therefore, the identification of climate signals can be complicated and superimposed by other environmental changes which are caused by management or land use changes in the catchment areas leading to eutrophication, re-oligotrophication and acidification (Adrian et al. 2009). Thus, the analysis and quantification requires appropriate statistical methods and mathematical modelling (Adrian et al. 2009; Wojtal-Frankiewicz 2012). In addition to this, drinking water reservoirs are highly managed systems, where water levels, hydrological retention time, fish stocks and in confined limits also nutrient loadings can be regulated (Cooke et al. 2005; Kufeld et al. 2013). Because of the economic pressure to provide raw water of high quality, it is necessary to understand the climate related processes in reservoirs for optimal management decisions and to successfully counteract the mainly negative impacts of climate warming (IPCC 2014a). Hence, one purpose of this thesis was to seperate temperature effects from effects of management and other environmental influences.

For the recent study, long-term data of meteorological, hydrophysical and biological variables (phytoplankton, crustacean zooplankton, fish) of the German drinking water reservoir Saidenbach were analysed. Based on this long-term data set, strong indicators for climate induced changes have been identified. In particular, increasing water temperatures since 1975, earlier break up of ice covers and an altered hydrophysical structure could be detected (chapter 2). As further indicators of climate change, species shifts in the phytoplankton community in spring (chapter 4) and summer (chapter 2) had been observed. The finding of reduced and in its development delayed crustacean zooplankton in Saidenbach reservoir (chapter 3) was an unexpected finding because of the opposite expectation of better growth in warmer waters and elevated availability of phytoplankton as food resource. In this thesis, the underlying processes and the coupling to higher trophic levels within the food web (fish) could be revealed and explained by statistical and model aided analyses. Furthermore, it was possible to seperate the influence of single environmental impacts on the crustacean zooplankton, like temperature and nutrient effects.

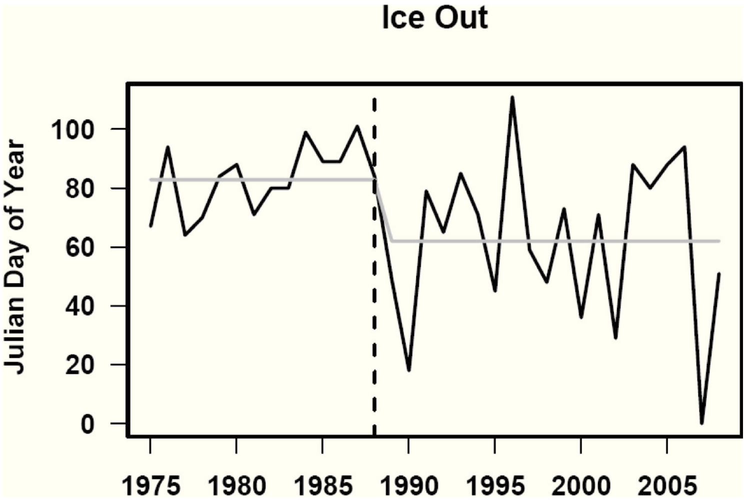

Figure 1.1: Time series of ice-out in Saidenbach reservoir since 1975. The gray line visualizes the mean value of the day of ice-out in each of the two identified phases by breakpoint analysis.

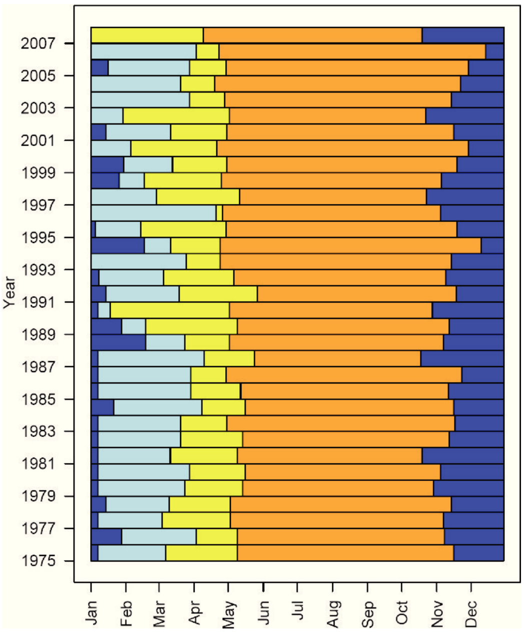

Figure 1.2: Patterns of mixing, ice-cover and stratification in Saidenbach reservoir since 1975. 🟦 autumnal overturn, 🟦 ice cover, 🟨 spring overturn, 🟧 summer stagnation

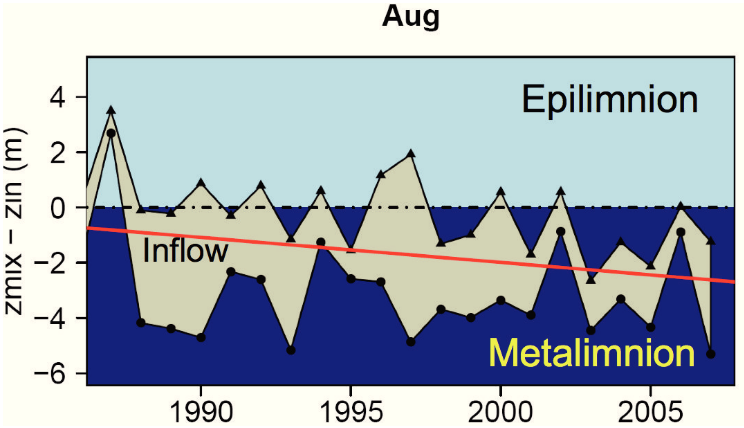

Figure 1.3: Estimated trend of the entrainment depth (zin) of the main tributary (Haselbach) to Saidenbach reservoir in August plotted relatively to mixing depth (zmix).

1.2 Hydrophysical consequences of climate change

Clear climate signals were found in Saidenbach reservoir in elevated surface water temperatures (chapter 2). The strongest significant temperature increase was found in May with 0.11 $\mathrm{K\,a^{-1}}$ since 1975 but also positive trends betweeen 0.06 and 0.09 $\mathrm{K\,a^{-1}}$ in summer and 0.03 $\mathrm{K\,a^{-1}}$ in winter were significant. In winter, warming of the surface water temperature resulted in earlier ice-out (Fig. 1.1, Rolinski et al. 2007). A break-point analysis revealed that the variability of ice-out increased after 1988 and on average, happened 20 days earlier after 1988 (Fig. 1.1, chapter 3). In 2008, the reservoir even stayed free of any ice-cover. As a consequence, spring overturn started earlier in years with early ice-out (Fig. 1.2) and its duration tended to be the longer the earlier the ice cover broke up (Fig. 1.2, 1.4).

Spring overturn might get extended by an earlier start of mixing, however, the onset of stratification also starts earlier due to stronger temperature gradients. Calculations of mixing depths and Brunt-Väisälä frequencies in chapter 2 revealed significant trends to more stable stratification and shallower mixing depths from April to October. This confirms the predictions for lake and reservoir mixing regimes of a 40-year climate simulation of Sahoo et al. (2011).

Estimates by empirical models, developed for this study, show that absolute warming of the inflows to the reservoir was lower than warming within the reservoir. Therefore, the tributaries entrained up to 0.08 $\mathrm{m\,a^{-1}}$ deeper related to the mixing depth during summer stagnation since 1986 (Fig. 1.3). Hence, nutrient supply to the epilimnion decreased unexpectedly (chapter 2).

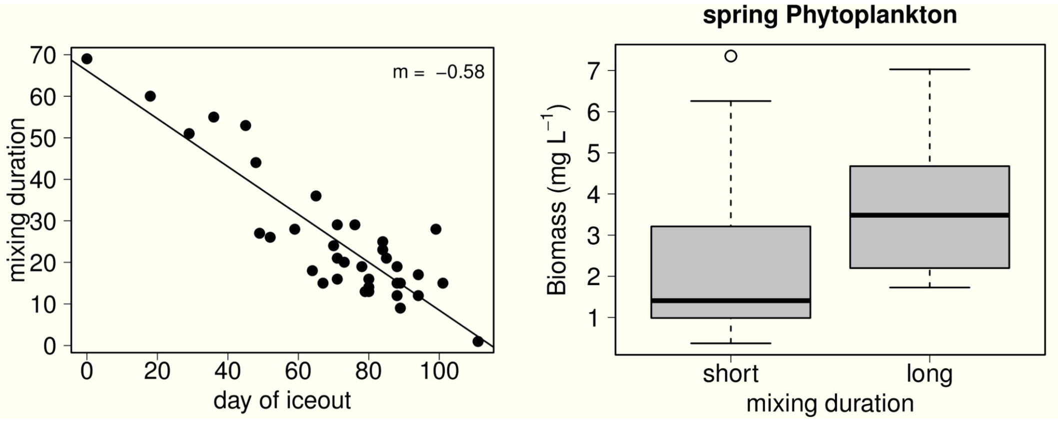

Figure 1.4: Circulation duration in dependency on day of ice-out (left). The slope (m) of the regression indicates that mixing duration is 0.58 days longer for each day of earlier ice-out. The plot on the right shows spring phytoplankton biomass in dependency on mixing duration (right). "Short" denotes to shorter than average and "long" to longer than average mixing durations.

1.3 Response of phytoplankton to climate change

In spring the phytoplankton biomass increased significantly since 1990 in Saidenbach reservoir (Fig. 1.5). This seemed counterintuitive related to a 50 % reduction of nutrient loadings after 1990. This phenomenon could be explained by the earlier light availability after earlier ice-out and longer mixing periods (Fig. 1.4) which maintain low sedimentation losses and nutrient availability from deeper water layers (Rolinski et al. 2007; Horn et al. 2011, see also chapter 3). An up to 4 weeks earlier onset of the spring phytoplankton bloom was also observed in other temperate lakes (Winder & Schindler 2004a; Adrian et al. 2006; Peeters et al. 2007; Huber et al. 2008).

To analyse reactions of phyto- and zooplankton to environmental changes more in detail and down to the species level, an automated peak detection algorithmn (Rolinski et al. 2007) was applied to the long term data. By fitting Weibull functions to the time series, the beginning, maximum and end of peaks could be determined in a consistent way (Fig. 1.6) and these cardinal dates of phytoplankton and zooplankton development could be made available for multivariate statistics (chapters 2 and 3).

Two remarkable phytoplankton species shifts were detected using this method (Fig. 1.7). The dominant spring diatom *Asterionella formosa* was replaced by *Aulacoseira subarctica* after warm winters (Horn et al. 2011, see also chapter 4); and in summer, the diatom *Fragilaria crotonensis* was displaced increasingly by cyanobacteria (chapter 2).

However, *Aulacoseira subarctica* showed an unusual annual spatial pattern with peaks in spring and autumn shortly above the lake bottom in aphotic depth (Fig. 1.8). This

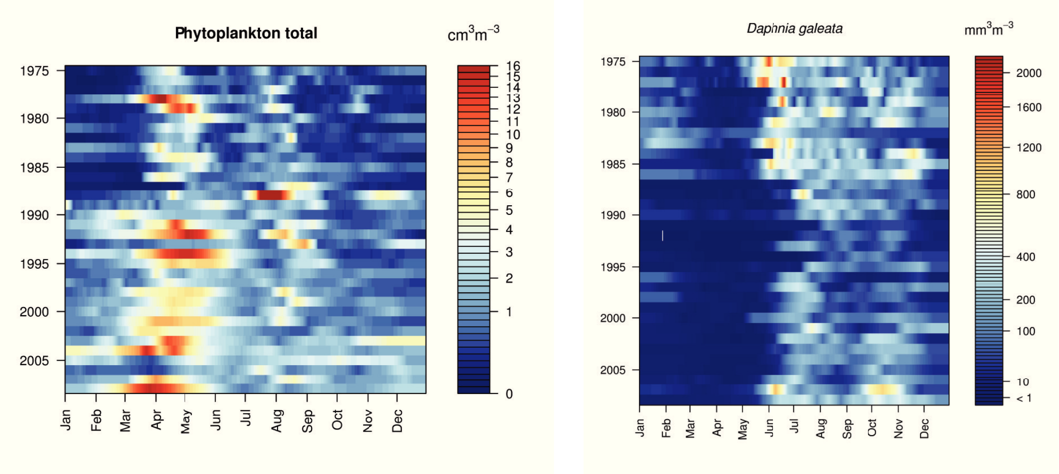

Figure 1.5: Annual patterns of total phytoplankton and *Daphnia galeata* in Saidenbach reservoir since 1975.

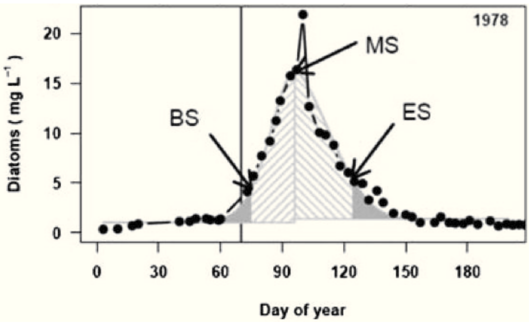

Figure 1.6: For automated peak detection, Weibull functions (gray) were fitted to planktonic time series according to Rolinski et al. (2007). Area below the curve before the peak maximum (MS) (upward shading) and after MS (downward shading). Beginning (BS) and end of the peaks (ES) were defined at 5 % quantiles (filled in gray). Diagram modified after Rolinski et al. (2007).

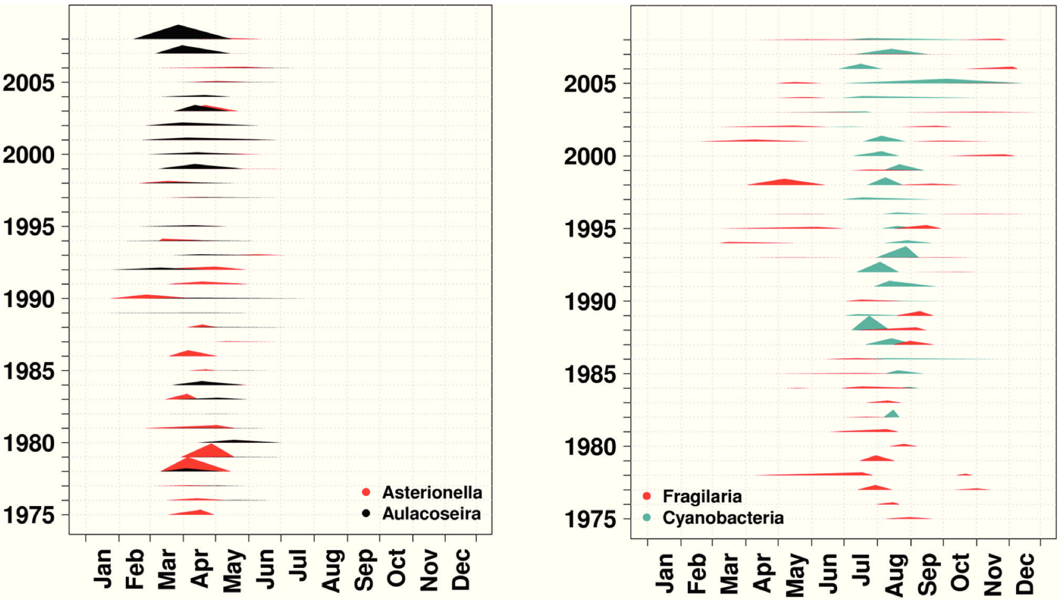

Figure 1.7: Species shifts of phytoplankton in the Saidenbach reservoir since 1975. In spring, the dominant diatom *Asterionella formosa* was replaced by *Aulacoseira subarctica*. In summer, the diatom *Fragilaria crotonensis* was displaced increasingly by cyanobacteria.

can have negative impacts on the quality of raw water for drinking water abstraction. To understand the mechanisms of its dominance under altered hydrophysical conditions and of its persistence in the hypolimnion, the species was observed intensively in the pelagic zone and in the sediments in 2009. In addition to this, growth, sedimentation and resuspension experiments were performed. *A. subarctica* did not show superior growth rates or heterotrophic capabilities compared to other diatoms but was resuspended at very low shear forces. So, during translocation by sediment refocussing to deeper depths it is resuspended and stays in the water column. A one-dimensional dynamic model assimilating information about growth, sedimentation and resuspension of diatoms was developed. The simulations reproduced the unusual field pattern (Fig. 1.8) and suggest that a high start biovolume due to early resuspension in spring is an advantage. Thus, as a low light adapted species, *A. subarctica* can outcompete other diatoms in spring in years with an early ice break up and early spring overturn.

In spite of the reduced nutrient loading to the epilimnion, summer phytoplankton composition gradually switched from the dominant diatom *Fragilaria crotonensis* to cyanobacterial species since the late 1980s (Fig. 1.7). This species shift could be explained well by the hydrophysical regime shift and was in line with observations from other lakes (Wagner & Adrian 2009; Mooij et al. 2005), predictions from experiments (Domis et al. 2007) and model simulations (Elliott 2012; Trolle et al. 2014) in which cyanobactria profited from higher temperatures directly and indirectly by reduced mixing and more stable stratification.

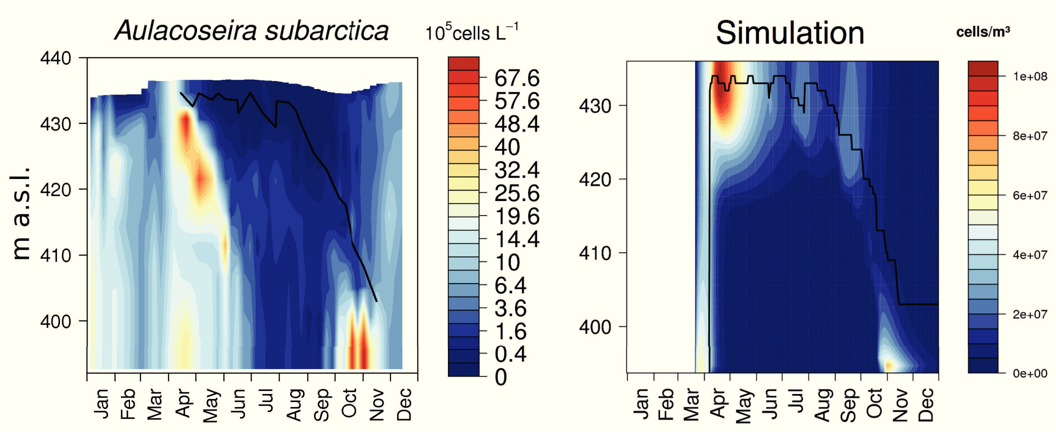

Figure 1.8: Observed (left) and simulated (right) annunal profiles of *Aulacoseira subarctica* in Saidenbach reservoir. The black line indicates the position of the thermocline.

1.4 Response of zooplankton to climate and environmental change

Although the annual total phytoplankton biomass increased since 1990, the crustacean zooplankton in Saidenbach reservoir did not seem to profit from improved food resources (chapter 3). To the contrary, *Daphnia* abundances reduced tremendously (Fig. 1.5). Their growth rates were not related to temperature since 1987 (Horn 2003), and the analysis of cardinal dates revealed that the biomass of all major crustacean species reduced by 50 % after 1990 and that *Daphnia* development was delayed by up to 4 weeks (chapter 3). It can be argued that zooplankton gets decoupled from its food resources when the phytoplankton peaks earlier in spring. But in Saidenbach reservoir, even after the spring peak, sufficient concentrations of edible phytoplankton were available. New molecular and physiological investigations from Saidenbach reservoir show, that genetically adapted *Daphnia*-clones stay in the water column during warm winters and could rapidly build up new populations in spring (Zeis et al. 2010). In chapter 3, the biomass of zooplanktivorous fish in the reservoir is estimated. It turned out that effects of silvercarp were previously underestimated. The species was stocked in 1987 and can not reproduce in the reservoir. However, the animals increased in individual body weight and may contribute up to 70 % of the total zooplanktivorous fish biomass. It could be shown that silvercarp has an temperature and density dependent effect and that the faster growth of *Daphnia* at higher temperatures can not compensate for the more actively grazing fish when stock of zooplankitvorous fish is too high. In recent years with only medium levels of zooplanktivorous fish biomass left in the reservoir, a faster *Daphnia*-development could be observed again. By means of multivariate statistics, temperature was identified as the most important factor that explained 29 % of the zooplankton phenology. The second most important predictors were zooplanktivorous fish biomass and nutrient loading which explained 18 % of the variance.

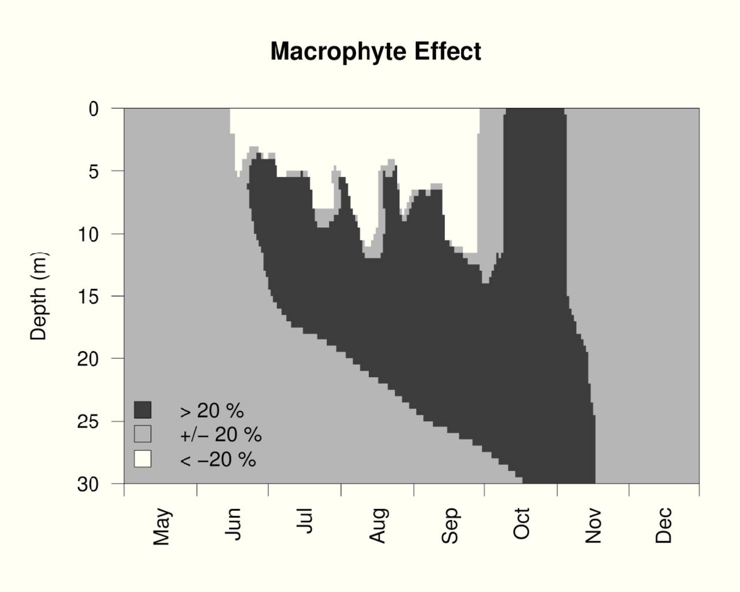

Figure 1.9: Simulated macrophyte effect on phytoplankton in a 30 m deep lake. During stagnation period, phytoplankton is suppressed by at least 20 % due to macrophytes in the epilimnion.

1.5 The importance of submerged macrophytes for stratified lakes

The observations so far were mainly related to one specific drinking water reservoir. However, lake managers are facing similar problems in their systems. Since lakes do not have such dramatic fluctuations of water level like reservoirs they often are populated by submerged macrophytes. Submerged macrophytes are important for the stabilisation of clear water-conditions in shallow lakes (Scheffer et al. 1993; Hilt et al. 2011). However, their impact in deep lakes and their role during climate change is not yet well understood. Furthermore, submerged macrophytes were neglected in most major models for deep lakes. To evaluate their potential also for the restoration of deep lakes under climate change, a model for stratified lakes that includes submerged macrophytes was developed (chapter 5). In the model, the macrophytes can act as nutrient sinks but also as nutrient source during respiration or when dead plants remineralise. The model enabled us to simulate competition for nutrients with phytoplankton, shadowing effects, the provision of shelter for zooplankton from fish predation and of reduced turbulence in macrophyte patches. The simulations showed that macrophyte effects were mainly positive for water quality (Fig. 1.9) and macrophytes in deep lakes were able to potentially reduce summer phytoplankton, especially cyanobacteria by 50 % in 11 m deep and still by 15 % in 100 m deep oligotrophic lakes. In a 30 m deep simulated lake, similar to Lake Scharmützelsee, the total phytoplankton biomass was suppressed at least by 20 % in the epilimnion during the whole stagnation period (Fig. 1.9). Only for a short period of time at the end of the stagnation period, when macrophytes were dying and its nutrients remineralised, an increase of phytoplankton was observed (Fig. 1.9). The extent of estimated macrophyte effects is remarkable, since macrophytes in deep lakes can only populate 10–20 % of the total area and infest less than 10 % of the total water volume. Nutrient competition with phytoplankton contributed most to this macrophyte effect (89 %), followed by light shadowing (8 %) and provision of zooplankton shelter (3 %). In conclusion, for deep lake restoration the re-establishment of submerged macrophytes might be as important as for shallow lakes (Hilt et al. 2006).

1.6 Dissemination of results

For dissemination of the analyses of the Saidenbach reservoir, a concept was developed collaboratively by Wagner et al. (2012) which divides the year into four temperature sensitive phases: into (i) inverse winter stratification, (ii) spring overturn, (iii) early thermal stratification and (iv) summer stagnation. These phases are not fixed to specific dates but are determined from sums of global irradiation. By that, the concept allows cross-site comparisons of the state of variables during these phases. The division of the year into phases was neccessary to distinguish years with cold winters and warm summers or vice versa. Years with exclusively warm phases througout the whole year are rare at the moment and so far only was observed in 2008 (Fig. 1.10A). Wagner et al. (2012) found an increasing frequency of warm phases and predict that 80 % of all temperature sensitive phases will be warm within the next 20 years (Fig. 1.10B). The phase-wise analyses enables more detailed investigations of impacts of water temperature on biotic ecosystem elements, e.g. on plankton during spring or during stable stratification. Similar to the synchronisation of spring conditions by the NAO (Gerten & Adrian 2002), several European lakes, the Baltic Sea and the North Sea (Wagner et al. 2012) as well as most German drinking water reservoirs (Jäschke et al. 2013), to which the concept was applied, showed a high coherence in the classification of their sensitive warm and cold phases also later in the year.

Cyanobacteria which are favoured by the more stable stratification regime and by reduced mixing are a problem for drinking water production, since they release organic toxins and their removal from the raw water is more cost intensive. In the future, it might be necessary to artificially alter the stratification regime to counteract this development. As an alternative, several reservoir administrations (e.g. Saidenbach and Klingenberg) technically updated their dams by the construction of an additional epilimnetic outlet as suggested by Prien et al. (2009). Instead of releasing and loosing the cold hypolimnetic water valuable for drinking water production by bottom outlets, in summer, water can be released from the warmed epilimnion instead. As a side effect, the warmest water and parts of the cyanobacteria bloom can be released from the reservoir. The full lake model which was developed for macrophyte investigations (chapter 5) includes hydrophysical and ecological submodules and thus

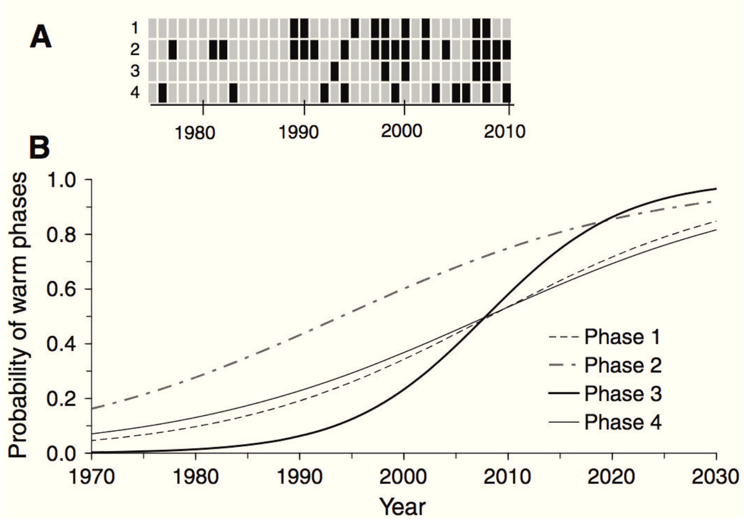

Figure 1.10: A) Pattern of warm (black) and cold (gray) sensitive phases in Saidenbach reservoir since 1975. The phase numbers 1–4 represent: 1 - inverse winter stratification, 2 - spring overturn, 3 - early thermal stratification, 4 - summer stagnation. B) Trend of probabilities of occurrence of warm phases predicted until 2030. Trends were described by logistic equations. See Wagner et al. (2012) from where the plot was taken for details.

allows comprehensive climate simulations and the evaluation of the effectivity of such adaptive strategies and scenarios for deep lakes and reservoirs.

In summary, using a broad range of methods covering field investigations, controlled experiments and statistical and model aided data analysis, it was possible to reveal direct temperature effects in lakes as well as indirect temperature effects on many hydrophysical conditions such as ice cover, stratification, timing of mixing periods, entrainment temperatures and entrainment depth as well as on turbulence. Finally, complex biological responses of phyto- and zooplankton on food web interactions, altered timing or non-trivial species shifts, as in the case of *A. subarctica*, could be explained. Additionally, the possible important role of submerged macrophytes in deep lakes for water quality was shown using complex, coupled hydrophysical and ecological models. The gained knowledge, the developed statistical tools and models already have been implemented in follow-up studies (Wagner et al. 2012; Jäschke et al. 2013) and will be helpful for further investigations of responses of lake ecosystems on climate change and can facilitate the evaluation of future management strategies e.g. for climate change mitigation and adaptation.

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2 Deeper entrainment of tributaries in a warmed up deep reservoir and consequences for summer phytoplankton

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Abstract

Global warming of air temperatures causes a highly synchronised warming of water in aquatic ecosystems. Hydrophysical and biological structure of the systems can change and cause alterations in hydrophysical conditions, biogeochemical cycles and species occurances. As a consequence of a warming trend of up to $0.1\,\mathrm{K\,a^{-1}}$ since 1975 we observed a phytoplanktonic species shift from diatoms to elevated biovolumes of cyanobacteria in a German drinking water reservoir despite a 50 % reduction of total nutrient loadings. We hypothesised that elevated temperatures of the tributaries caused shallower entrainment to the epilimnion and therefore a more frequent supply of nutrients to the photic zone supporting the growth of cyanobacteria. However, the estimation of entrainment depths revealed a trend to deeper entrainment by $0.08\,\mathrm{m\,a^{-1}}$ and a shallower mixing depth than 4.4 m in summer. This suggests that inflows warmed up slower than the reservoir itself and therefore entrain more meta- and hypolimnetic. As a consequence, no correlation was found between soluble reactive phosphorus (SRP) entrained to the epilimnion and cyanobacteria. Warmer water temperatures, shallow mixing depths and stratification stabilities higher than $0.026\,\mathrm{s^{-1}}$ seemed to favor cynaobacteria which in contrast to diatoms can possess physiological adaptations against fast sinking from poorly mixed water layers. Hence, in the future it might be increasingly necessary to artificially control hydrophysical structure of the reservoir.

2.1 Introduction

Climate change can have pronounced impacts on processes and on the internal structure of aquatic ecosystems (e.g. Geller 1998; McCarthy et al. 2001). The observed and expected responses are manyfold: (i) Warming and earlier end of ice covering has effects on timing and intensity of mixing and stratification, on the gas exchange with the atmosphere as well as on the solubility of oxygen in water, and on heat and matter exchange at the sediment-water-interface. (ii) Alterations of the flow regime affect the water residence time and the import of suspended matter and dissolved substances such as nutrients and DOM. (iii) Furthermore, lake volume variability with implications on sediment resuspension, transport and accumulation, matter exchange between sediment and water, and hypolimnetic oxygen depletion has to be taken into consideration. (iv) The planktonic ecosystems also might be affected by changes of irradiation and underwater light quality and intensity and possibly by growing effects of UV radiation on organisms.

Climate driven changes of the abiotic environment influence directly and - due to species specific preferences - indirectly the development of organisms (Blenckner et al. 2002; Blenckner & Hillebrand 2002). Alterations of phytoplankton abundance, seasonal succession and species composition have to be considered (e.g. Sommer et al. 1986; Adrian et al. 1995; Müller-Navarra et al. 1997; Adrian et al. 1999; Weyhenmeyer et al. 1999; Gerten & Adrian 2000; Anneville et al. 2004; Rolinski et al. 2007). Higher spring phytoplankton biomasses settle down earlier in the year and raise the supply of detritus at the lake bottom. This can affect food resources and, combined with elevated water temperatures, microbial matter turnover and the timing of the development of benthic organisms (Goedkoop & Tornblom 1996; Ahlgren et al. 1997). The impact of global warming on zooplankton is mediated directly by the strong dependency of its reproduction dynamics and growth rate on water temperature (Horn & Horn 1995; McKee et al. 2002; Horn 2003b). Indirectly zooplankton is affected by changing food quantity and quality (Rinke & Petzoldt 2003) as well as by shifts in the top-down control mechanisms (Mehner 2000; Benndorf et al. 2001; Scheffer et al. 2001; Hülsmann 2003; Wagner et al. 2004). Fish hatching, growth, feeding patterns (Dörner et al. 2001; Wagner et al. 2004), and inter-species competition are influenced by direct and indirect temperature effects as well.

Consequences of climate change are not only of ecological interest but imply serious socio-economic explosiveness as well. Schindler (2001) warned of adverse effects of global warming for water quality and quantity and their impacts on aquatic life, drinking water supply, waste water treatment and economy. Winkler (2002) studied impacts of climate change on the management of drinking water reservoirs and concluded that the average drinking water release from the reservoirs is likely to be reduced by about 30 % until 2050.

Climate change is a creeping and non-uniform process and the average rates of annual changes are relatively small. Considerable short term weather fluctuations generate significant inter-annual variability. Furthermore, the changes of the physical environment are superimposed by changing trophic conditions as consequence of modified structures and utilizations in the drainage area and alterations of the management practices. Therefore, long-term datasets of meteorological, hydrological, and limnological variables are imperative for ecosystem-scale studies on impacts of global warming on aquatic food webs (Tilzer & Bossard 1992; Bürgi 1994; Berman et al. 1995; ILTER 2000).

Evaluating a long-term dataset with daily values of meteorological and hydrological variables and observations of physical, chemical, and planktonic variables measured at a German drinking water reservoir since 1975, this study aims at the determination of trends of climate variables and alterations of the physical structure of the reservoir. In spite of a tremendous reduction of phosphorous loadings the summer phytoplankton composition changed from a dominance of diatoms (*Fragilaria crotonensis*) to cyanobacteria (Horn 2003a).

Cyanobacteria might be supported by warmer water temperatures (Reynolds & Walsby 1975; Paerl & Huisman 2009; Mehnert et al. 2010), by lower sedimentation during strong stratification periods (Whilhelm & Adrian 2008; Wagner & Adrian 2009; Salmaso 2010; Huisman et al. 2004) and by additional supply of nutrients (Salmaso 2010; Huber et al. 2011). In this study, we investigated whether a change of hydrophysical structure of the reservoir could explain the recent cyanobacteria domninance or whether warmed up tributaries entrain more regular to the epilimnion because of the smaller density of water at higher temperatures. Hence, we hypothesise that nutrient loadings to the epilimnion happen more often and provide favourable conditions for cyanobacteria growth. Alternatively we hypothesise that elevated temperatures and higher stratification stability are a more important contribution to cynabacteria dominance in the investigated reservoir.

2.2 Methods

2.2.1 Study site – the Saidenbach reservoir

The dimictic Saidenbach reservoir (volume: 22.4×10^6 m^3, surface: 146 ha, maximum depth: 45 m, mean depth: 15.3 m) became operational 1934. It is situated in low mountains (elevation: 438.8 m asl) of south-eastern Germany (E 13°14', N 50°44') and is used for drinking water supply and flood control. About 73% of the catchment (total area: 61 km^2) are agriculturally utilized, forests cover 19% and settlements ca. 8% (population density: 66 km^{-2}).

Four tributaries (Haselbach, Saidenbach, Lippersdorfer Bach, Hölzelbergbach) flow through seven pre-basins and three under water dams of different size before entering the reservoir (Paul 2003, Fig. 2.1). An additional and seasonally varying amount of water is transferred by a system of canals and galleries ("Revierwasserlaufanstalt" RWA) from Rauschenbach reservoir, located outside the watershed of the Saidenbach reservoir. Therefore, theoretical retention time varies between about 6 and 12 months.

Raw water is withdrawn through a depth-variable intake from the layer between about 15 m and 28 m above the ground but can also be taken from the bottom outlets. Compensation water is permanently released through the bottom outlets into the downstream river. Before a disastrous flood in August 2002, the reservoir was allowed

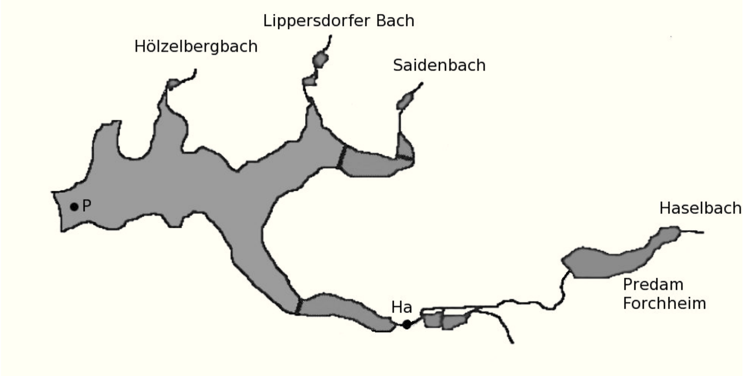

Figure 2.1: The Saidenbach reservoir and its four tributaries including pre-basins and under water dams (P -sampling point for profile measurements, Ha - sampling point for the Haselbach tributary).

to overspill. Thereafter, a regular flood storage of $3 \times 10^6\,\mathrm{m}^3$ was set and surface outflow was not observed ever since.

The reservoir changed from eutrophic to mesotrophic conditions after 1990 when detergents containing phosphorus were politically prohibited. Since nitrate and silicate depend at a higher degree on diffuse sources, their loadings remained almost constant (Horn 2003a).

2.2.2 Long term data

Regular weekly or biweekly measurements of physical, chemical, and biological variables are carried out approximately 100 m before the dam of SR since 1975 (Horn 2003a; Horn 2003b). The tributaries were measured in the same interval. Vertical profiles of water temperature (1 m intervals) and inflow temperatures were measured until 1990 with a thermistor probe and later on with pH-, oxygen- and conductivity-sensors (WTW Weilheim, Germany). A computer-controlled hydro-meteorological station registering air temperature T_A (°C), global radiation R_G ($\mathrm{W\,m^{-2}}$) wind speed and direction was installed in 2002. Further meteorological and hydrological variables are daily determined on-site by the Saxon State Reservoirs Administration (Landestalsperrenverwaltung, LTV): mean air temperature $T_{A,LTV} = (T_{7am} + T_{2pm} + 2T_{9pm})/4$ (with the temperatures T_{7am}, T_{2pm}, and T_{9pm} registered at 7 a.m., 2 p.m. and 9 p.m., respectively) using thermographs, precipitation P (Hellmann rain gauge), inflow Q_{in} and outflow Q_{out} (both in $\mathrm{m^3\,d^{-1}}$, recording gauges), surface altitude h_0 (in m, staff gauge; since 2000 water level data logger), surface temperature T_0 (in °C, 7 a.m. readings), ice thickness and ice coverage.

2.2.3 Estimation of air temperature at the sampling site

During the long period, some measuring devices had to be replaced and devices were regularly calibrated and homogeneity of the data series was checked. For the LTV air temperature dataset, a relative homogeneity test using meteorological observations of the neighbouring stations Dresden-Klotsche (DD) and Fichtelberg (FB) of the German Meteorological Service DWD was applied as recommended by Peterson et al. (1998). The test and showed varying deviations of $T_{A,LTV}$ in several years between 1985 and 1998. to overcome this shortcoming, multiple linear regression analyses between temperature data of LTV ($T_{A,LTV}$, $T_{A,DD}$) and the meteorological station on Fichtelberg ($T_{A,FB}$) were carried out for this data subset and resulted in the following equations for the daily mean $\overline{T}_{A,S}$, minmal $T_{A,S,min}$, and maximal $T_{A,S,max}$ air temperatures (°C) at SR:

$$\overline{T}_{A,S} = 0.910 + 0.044 \cdot \overline{T}_{A,FB} + 0.919 \cdot \overline{T}_{A,DD} \qquad r^2 = 0.99 \tag{2.1}$$

$$T_{A,S,min} = 0.258 - 0.026 \cdot T_{A,FB,min} + 1.012 \cdot T_{A,DD,min} \qquad r^2 = 0.96 \tag{2.2}$$

$$T_{A,S,max} = 2.136 + 0.198 \cdot T_{A,FB,max} + 0.755 \cdot T_{A,DD,max} \qquad r^2 = 0.99 \tag{2.3}$$

2.2.4 Estimation of mixing depth and thermoclines

According to Talling (1971) and Horn et al. (2006) the mixing depth z_{mix} was defined as the upper boundary of the metalimnion where the water density is $0.08\,\mathrm{kg\,m^{-3}}$ higher than in 2 m depth. Assuming only very small gradients in conductivity the temperature T_{zmix} in z_{mix} could be calculated using equation 2.4 (see Tab. 2.1 for parameters).

$$T_{zmix} = T_{2m} - \sum_{i=0}^{2} \left(a_i \exp\left(b_i\, T_{2m}\right)\right) \tag{2.4}$$

The equation is valid for a temperature range of $7.2\,°\mathrm{C} \leq T_{2m} \leq 30\,°\mathrm{C}$ and allowed to derive z_{mix}. The 10 °C isotherm in depth z_{10} was assumed as an approximate boundary between meta- and hypolimnion (Paul 1986). Stability of the water body was calculated as the mean of Brunt-Väisälä frequencies for the first 15 m of the water column to embrace the mixing depth for most of the times.

2.2.5 Estimation of tributary temperatures and entrainment horizon

In general, inflows to the reservoir will entrain into the horizon with the same density. Density depends on temperature, salinity and also high concentrations of suspended matter e.g. in case of high waters (Pharo & Carmack 1979; Paul & Pütz 2008). To some extent, inflowing water is also mixed with water of lower densities so that the resulting entrainment will not be as deep as expected.

Weekly or biweekly temperature measurements of the tributaries below the pre-dams were available since 1985 and conductivity measurments since 1994. During the period of stable stratification entrainment depths calculated with salinity according to Fofonoff & Millard (1983) differed only by a few centimeters from depths calculated only with temperature. Salinity was only important in winter and during full mixing conditions. Therefore, the influcence of salinity was omitted in all further estimations.

Water temperatures in the tributaries were always measured in the morning, near the temperature minimum. During the day, this temperature can increase by several degrees causing a shallower inflow depth. In order to estimate a daily minimal and maximal entrainment depth, temperature reanges of the tributaries were estimated from air temperatures. For the most important and warmest inflow, the Haselbach, detailed temperature logging in intervalls of 8 min was available in 1998, 2004, and 2005.

Following the assumption of Horn et al. (2006) that temperature variation in the streams is proportional to the variation of the air temperature integrated over the past m days, minimal ($T_{Ha,d,min}$) and maximal ($T_{Ha,d,max}$) daily temperatures of the tributary can be calculated according to equation 2.5(see Tab. 2.2 for parameters):

$$\begin{aligned} T_{Ha,d} &= p_1 + p_2\,X + p_3\,X^2 + T_{A,S}(m)\big(p_4 + p_5\,X\big) \\ \text{with } X &= \sin\big(2\pi(d+p_6)/365\big) \\ \text{and } T_{A,S}(m) &= \frac{1}{m}\sum_{d=0}^{m} T_{A,S,d} \end{aligned} \tag{2.5}$$

The horizon of entrainment into the reservoir was assumed to be situated between the depths matching this temperature range. The model is valid for the stratification period and the years after the construction of the pre-dams in 1985, since they considerably influence temperature.

Table 2.1: Parameters for calculation of T_{zmix}.

i	a_i	b_i
0	0.28	0
1	3031200	-2
2	5.2	-0.2

2.2.6 Estimation of SRP-loadings

Daily SRP concentrations were interpolated between fortnightly samples unsing the discharge class method of Harned et al. (1981) and data were binned into 10 logarithmic discharge classes according. To contribute for changes of waste water chemistry or acricultural land use, this procedure was applied separatley for periods of five to ten years years since 1985. Area- and volume loadings were calculated using hypsographic functions of area (A_{SR} in m^2) and volume of the reservoir (V_{SR} in m^3) in dependence of the water level (z in m asl.):

$$A_{SR}(z) = 146.194 \cdot 10^4 \Big(1 - \frac{438.8 - z}{45.95}\Big)^2 \tag{2.6}$$

$$V_{SR}(z) = 22.364 \cdot 10^6 \Big(1 - \frac{438.8 - z}{46.1833}\Big)^3 \tag{2.7}$$

and the epilimnetic volume with:

$$V_{Epi} = V(z) - V(z_{mix}) \tag{2.8}$$

If the estimated range of entrainment is completely within the epilimnion all loadings were referred to that volume for calculation of the epilimnetic nutrient load. In cases when the maximal entrainment was below the mixing depth and the minimal entrainment within the epilimnion, loadings were split equally between the different layers of entrainment.

2.2.7 Statistics and determination of phytoplankton peaks

All statistical analyses were performed using the R environment for statistical computing (R Development Core Team 2010). Peaks of *F. crotonensis* and cyanobacteria were detected using the add-on package `cardidates` by fitting six-parametric Weibull curves to the time series (Rolinski et al. 2007). Trend tests for meteorological and hydrophysical data were performed according to Zhang et al. (2000) and Wang &

Table 2.2: Parameters for the models of daily minimal and maximal water temperatures of the tributary Haselbach based on air temperatures (equation 2.5).

Model	p_1	p_2	p_3	p_4	p_5	p_6	r^2
$T_{Ha,d,min}$	6.107	6.256	-4.204	0.329	0.329	252.477	0.87
$T_{Ha,d,max}$	4.401	2.855	-2.730	0.364	0.272	259.147	0.92

Swail (2001) (add-on package `zyp`), which applies Mann-Kendall tests for the time series after correction for autocorrelation. The Theil-Sen approach then computes the slope of the trend. For comparison of variables with different units, relative trends based on long term means were used. Parameter fitting was done by the method of Nelder & Mead (1965). Relationships between phytoplankton biomass and nutrient loadings were analyesed using Spearman's rank correlation coefficient.

2.3 Results

2.3.1 Summer phytoplankton

Different phases of timing, coexistance or replacement of *F. crotonensis* and cyanobacteria were observed (Fig. 2.2). From 1975 – 1981 no prominent blooms of cyanobacteria existed and *F. crotonensis* dominated the summer phytoplankton. During that period only in 1977 and 1978 mentionable biomasses of *F. crotonensis* were found in autumn. In the following years until 1986 cyanobacteria occured after the peak of *F. crotonensis*. In the years thereafter, increasing abundances of cyanobacteria developed before the main peak of *F. crotonensis*, which was delayed until late August and September (1987 – 1989). With the begin of 1991 this coexistance in summer almost diminished and cyanobacteria fully replaced *F. crotonensis*. Interestingly, between 1994 and 2002 *F. crotonensis* occured regularly earlier in April and May. However, in recent years *F. crotonensis* decreased again in spring. Additionally, the second development in autumn was observed to be more distinct since 1996. Nevertheless, compared to earlier years, reached biomasses of *F. crotonensis* tremendously decreased throughout the whole year.

2.3.2 Estimation of entrainment depths

To estimate the horizon into which the main tributary of the reservoir entrains during stratification period, the daily minimum and maximum of the water temperature of the stream was modelled as a function of air temperature (Eq. 2.5). The model was successfully fitted to temperature data from 2004 and 2005 (Fig. 2.3, Tab. 2.2). Validation of the model for inflow-data from 1998 resulted in an acceptable R^2 of 0.625 for the temperature minima and 0.834 for the maxima, respectively (Fig. 2.3).

The minimal entrainment depth mostly was located within the epilimnion. But surprisingly, the entrainment depth decreased relative to the mixing depth in all investigated months for the Haselbach tributary (Fig. 2.4). As a consequence, increasing parts of the water entrains to deeper layers below the mixing depth. Since 2003 calculated entrainment depths in August always were situated underneath the epilimnion (Fig. 2.4).

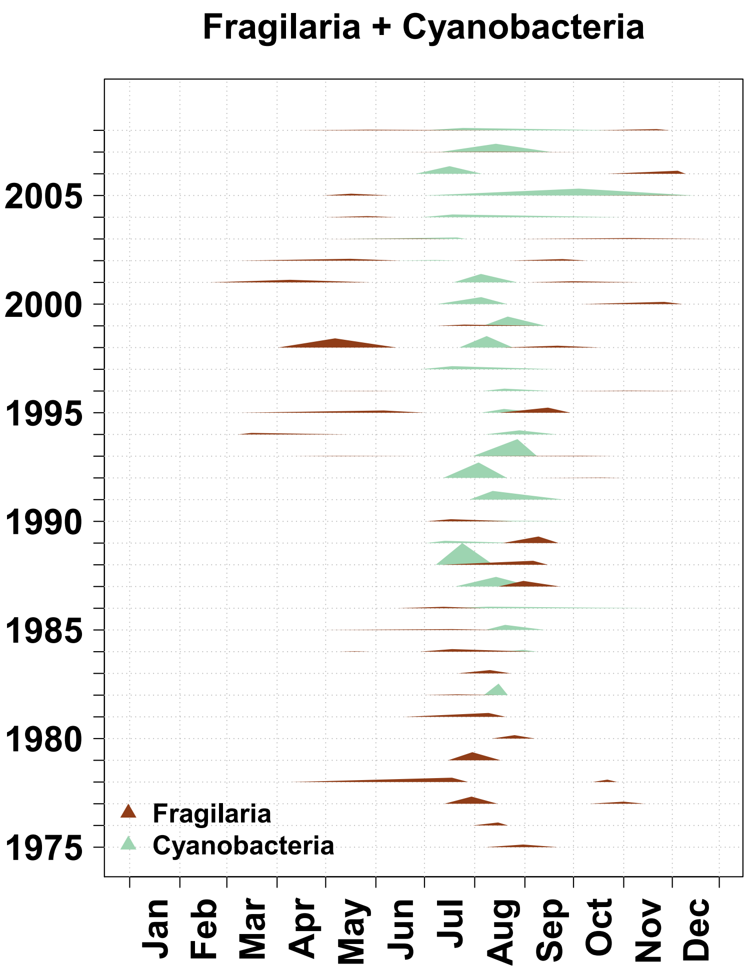

Figure 2.2: Main peaks of cyanobacteria and *F. crotonensis* occurances in the Saidenbach reservoir since 1975. Polygons indicate begin, maximum and end of the population development. The height of the polygons is scaled relatively to the most prominent occurance of each species since the start of the observations.

Table 2.3: Mean and standard deviation (SD) of annual discharge ($\overline{Q}$) and annual SRP loading ($\overline{SRP}$) of the four tributaries of the Saidenbach reservoir during the eutrophic (1975 – 1990) and mesotrophic (1991 – 2010) period.

Tributary	1975 – 1990		1991 – 2010	
	$\overline{Q} \pm SD$ ($\mathrm{m^3\,a^{-1}}$)	$\overline{SRP} \pm SD$ ($\mathrm{kg\,a^{-1}}$)	$\overline{Q} \pm SD$ ($\mathrm{m^3\,a^{-1}}$)	$\overline{SRP} \pm SD$ ($\mathrm{kg\,a^{-1}}$)
Haselbach	22793 ± 5631	425 ± 125	16314 ± 6208	98 ± 40
Saidenbach	10566 ± 5604	270 ± 106	8978 ± 3207	95 ± 36
Lippersdorfer Bach	2079 ± 800	259 ± 92	1807 ± 606	53 ± 28
Hölzelbergbach	283 ± 117	5 ± 3	284 ± 101	2 ± 1

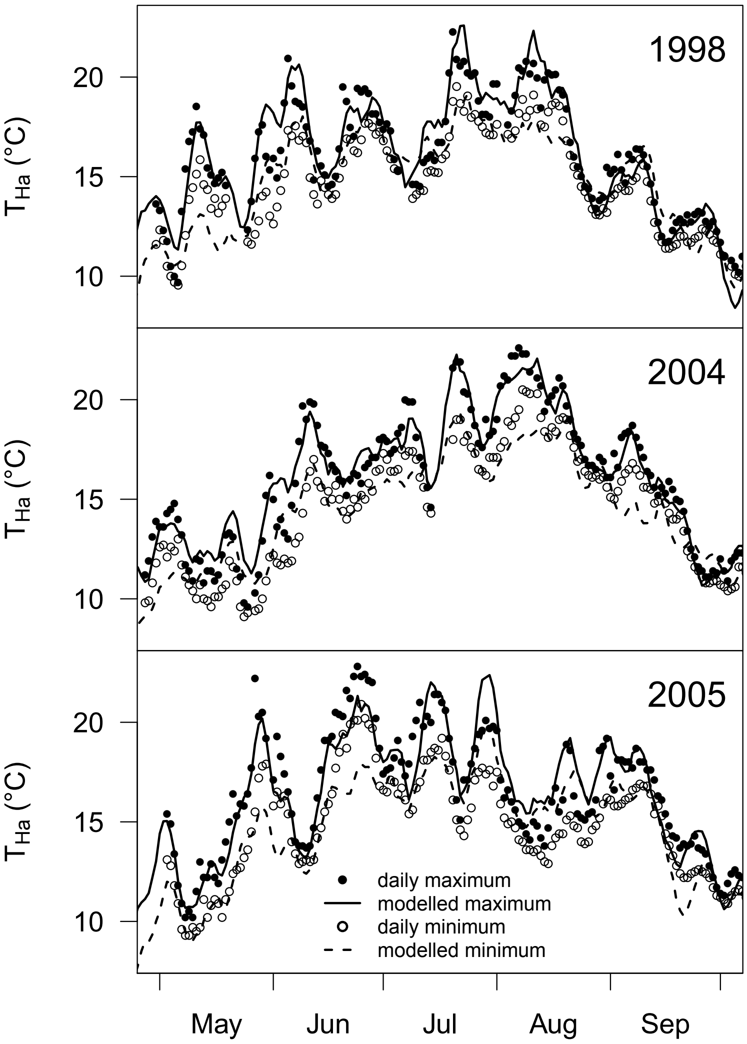

Figure 2.3: Measured and modelled daily minimal and maximal water temperatures of the Haselbach tributary. The models were calibrated in the years 2004 and 2005 and validated with data from 1998.

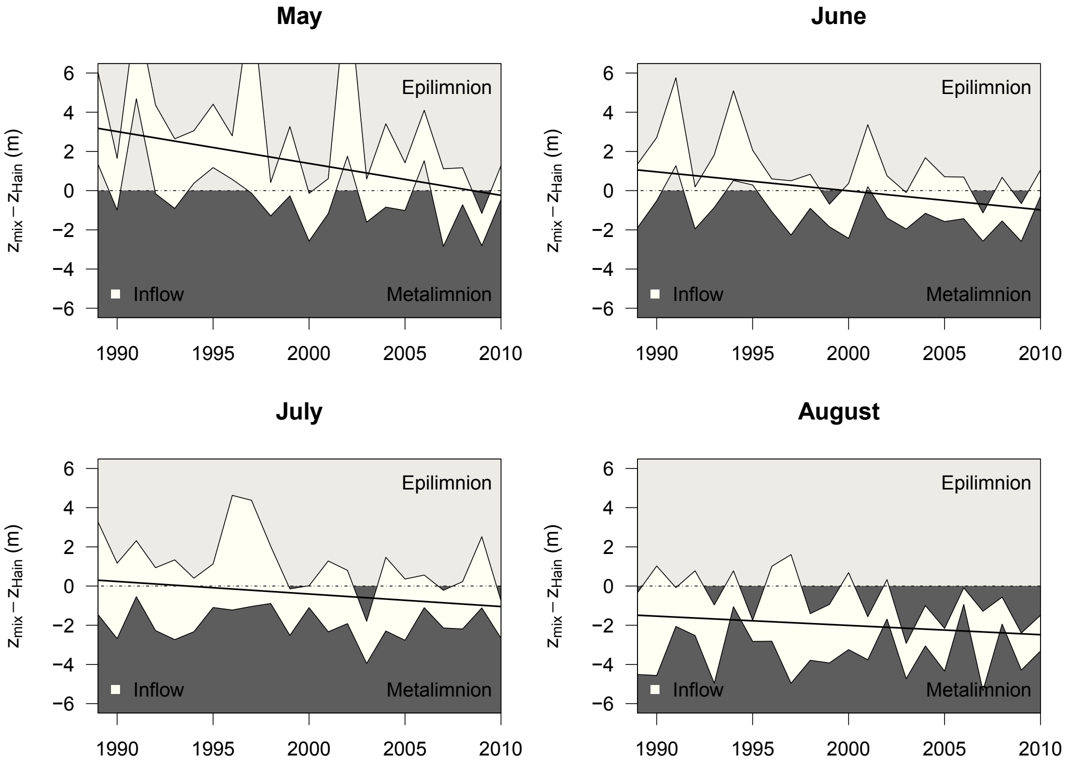

Figure 2.4: Estimated range of the entrainment depth of the Haselbach tributary into the Saidenbach reservoir. The entrainment depth is plotted relative to the mixing depth z_{mix}; black lines indicate the long term trend of the entrainment depth.

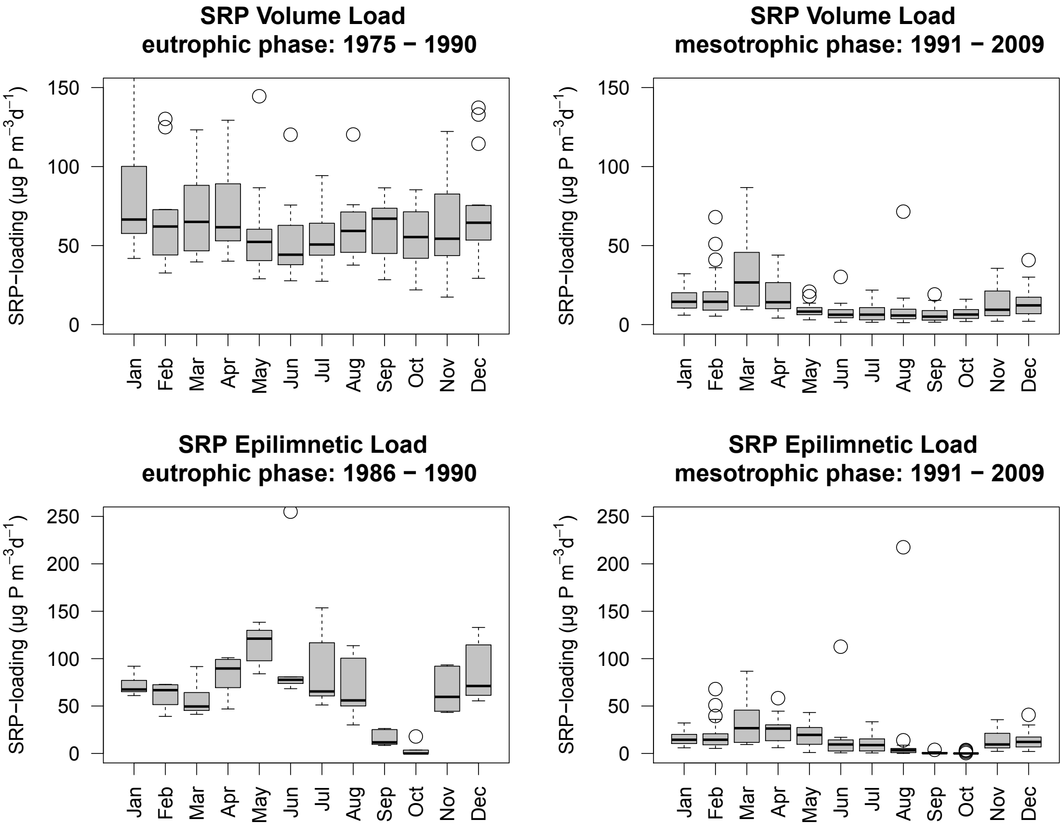

Figure 2.5: Volume loadings of SRP by the Haselbach tributary to the complete reservoir (upper row) or only fraction of the loading predicted to entrain to the epilimnion (lower row). Eutrophic and mesotrophic phase were seperated. Calculation of epilimnetic loadings was not possible before 1986 because the entrainment model is only valid for the period after the construction of the Forchheim prebasin.

2.3.3 Epilimnetic SRP-loadings

Highest loadings of SRP were entrained by the Haselbach tributary both during the eutrophic and the mesotrophic period (Tab. 2.3). The second most important inflow was the Saidenbach tributary. SRP loadings by Lippersdorfer Bach and Hölzelbergbach have been 1 – 2 magnitudes lower. Since temperatures of the Haselbach are the highest of all four tributaries it is likely that this stream entrains most shallow into the epilimnion.

SRP loadings to the entire water body decreased suddenly by approximately 50 % after 1990 due to introduction of P-free detergents and partly due to lower quantities of discharge (Fig. 2.5). Beside few exceptions caused by high waters, the epilimnetic SRP-loading decreased also by 50 %. In addition to this, SRP loadings dropped to very low values during the stratification period, which were lower than the values in winter and spring. This pattern could not be observed in the earlier years.

These findings do not support the hypothesis of increasing epilimnetic nutrient loadings. Furthermore, neither significant positive nor significant negative correlations of SRP surface loading, SRP volume loading or epilimnetic SRP loading 3 – 9 weeks before the maximum of cyanobacteria with the amount of cyanobacteria were detectable (Tab. 2.4). This suggests meteorological and hydrophysical factors being more causual for the recent cyanobacteria dominance rather than the trophic state of the epilimnion.

2.3.4 Meteorological and hydrophysical long-term trends

In the Saidenbach reservoir many hydro-physical trends since 1975 followed meteorological trends (Fig. 2.6). The decreasing discharge from April to October in spite of increasing precipitation seems to be a contradiction but this was caused by reduced surplus water from RWA in recent years.

Positive trends for air temperature were recorded in six months, with highest relative slopes in winter and spring. In April the highest absolute increasing trend with an temperature increase of $0.09\,\mathrm{K\,a^{-1}}$ was recorded (Tab. 2.5). Similiarly to the pattern of air temperature, increasing temperatures were found in all four tributaries. The trends for water temperatures were more pronounced, since water integrates the temperature over several days. During June and July water temperature of the inflows rose dramatically between $0.08\,\mathrm{K\,a^{-1}}$ to $0.21\,\mathrm{K\,a^{-1}}$ since 1986. Also the temperature in the epilimnion (T in 3 m depth) exposed positive trends throughout the whole year with highest relative trends in winter in spring. Particularly, epilimnetic temperature in May was affected most and shows an increasing trend of $0.11\,\mathrm{K\,a^{-1}}$.

As a consequence of altered temperatures other hydro-physical factors also changed over time. Increasing epilimnetic temperatures caused steeper vertical temperature gradients during summer and increased the stability of the water column. In contrast to this, higher winter temperatures weeken or prevent inverse stratification. Hence, observed Brunt-Väisälä frequencies of the top 15 m show a decreasing trend in winter. Interstingly, temperatures at deeper layers showed negatives trend in summer. This

Table 2.4: Spearman rank correlations of SRP loadings and cyanobacteria biomass. SRP loadings were summed up 3, 6, and 9 weeks prior to the cyanobacteria maximum.

weeks before maximum	Correlation of maximum cyanobacterio biomass with loadings of					
	SRP area		SRP volume		SRP epilimnion	
	ϱ	p	ϱ	p	ϱ	p
3	0.18	0.40	0.19	0.39	-0.01	0.96
6	0.22	0.31	0.22	0.32	0.18	0.42
9	0.21	0.34	0.21	0.34	0.15	0.49

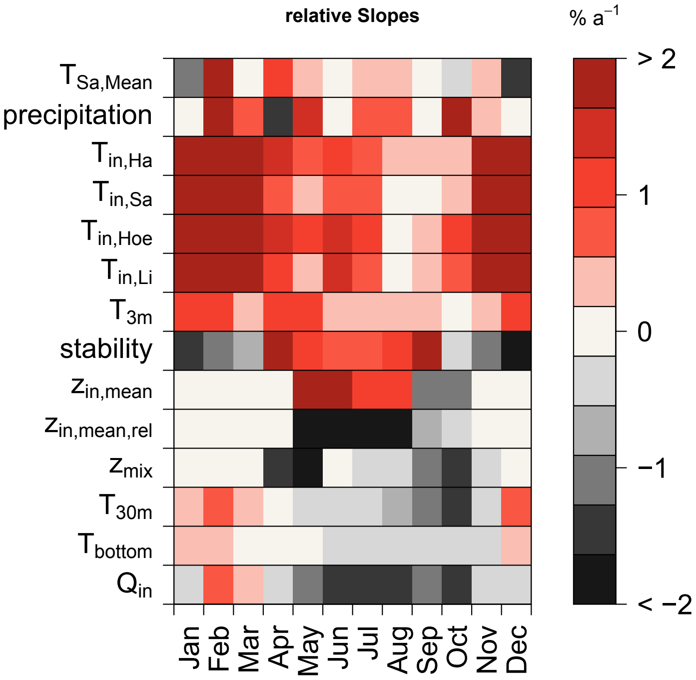

Figure 2.6: Increasing (red) and decreasing (black) long term trends of environmental variables influenced by climate and to a certain amount by management at Saidenbach reservoir from 1975 until 2010 (temperatures of tributaries T_{in} and entrainment depths z_{in} from 1986 until 2010). The monthly trend (Sen's Slope) is expressed as relative change per year compared to the long term monthly mean.

Table 2.5: Absolute long term trends (Sen's slopes) of important meteorological and hydro-physical variables in Saidenbach reservoir. Trends in bold font were significant with $p < 0.05$. Trends concerning temperatures of tributaries or entrainment depths start in 1986 and end in 2010. All other trend calculations started in 1975.

Month	$T_{Sa,Mean}$ ($\mathrm{K\,a^{-1}}$)	precipitation ($\mathrm{mm\,a^{-1}}$)	$T_{in,Ha}$ ($\mathrm{K\,a^{-1}}$)	$T_{in,Sa}$ ($\mathrm{K\,a^{-1}}$)	$T_{in,Hoe}$ ($\mathrm{K\,a^{-1}}$)	$T_{in,Li}$ ($\mathrm{K\,a^{-1}}$)	T_{3m} ($\mathrm{K\,a^{-1}}$)	stability ($\mathrm{s^{-1}\,a^{-1}}$)	$z_{in,mean}$ ($\mathrm{m\,a^{-1}}$)	$z_{in,mean,rel}$ ($\mathrm{m\,a^{-1}}$)	z_{mix} ($\mathrm{m\,a^{-1}}$)	T_{30m} ($\mathrm{K\,a^{-1}}$)	T_{bottom} ($\mathrm{K\,a^{-1}}$)	Q_{in} ($\mathrm{10^3m^3month^{-1}a^{-1}}$)
Jan	-0.01	-0.05	0.04	0.071	0.08	0.05	**0.03**	-0.000034				**0.02**	0.013	-6.93
Feb	0.04	**1.54**	**0.08**	0.063	**0.12**	**0.08**	**0.03**	-0.000035				**0.02**	0.010	16.83
Mar	-0.01	0.58	**0.09**	**0.075**	**0.16**	**0.15**	0.01	-0.000010				0.01	0.002	20.11
Apr	**0.09**	**-0.80**	0.11	0.037	0.09	0.08	**0.07**	**0.000126**			**-0.45**	0.0008	0.002	-17.91
May	0.04	**1.05**	0.09	0.055	**0.10**	0.04	**0.11**	**0.000193**	**0.06**	**-0.17**	**-0.12**	-0.01	-0.008	**-29.09**
Jun	0.03	-0.04	**0.16**	**0.080**	**0.18**	**0.21**	**0.07**	**0.000134**	**0.06**	**-0.07**	-0.01	-0.02	-0.015	**-26.50**
Jul	**0.06**	0.85	**0.15**	**0.110**	**0.15**	**0.15**	**0.08**	0.000157	**0.05**	**-0.08**	-0.03	-0.03	-0.020	**-31.52**
Aug	**0.04**	0.59	0.04	0.000	0.02	0.01	**0.09**	**0.000274**	**0.08**	**-0.08**	-0.02	**-0.04**	-0.030	**-29.72**
Sep	0.01	-0.03	0.06	0.000	0.05	0.03	**0.06**	**0.000243**	**-0.16**	-0.02	**-0.14**	**-0.09**	-0.034	-23.23
Oct	-0.02	**1.21**	0.02	0.036	0.09	0.05	0.02	-0.000006	**-0.31**	-0.01	**-0.34**	**-0.13**	-0.034	**-24.31**
Nov	0.02	0.21	**0.09**	**0.108**	**0.14**	**0.12**	0.02	**-0.000004**			**-0.21**	-0.03	-0.021	-6.94
Dec	-0.03	0.04	0.09	**0.100**	0.15	**0.09**	**0.04**	**-0.000013**				**0.03**	0.023	-8.12

was mainly caused by lower drinking water withdrawels from the hypolimnion in more recent years, so that the cold water remained in the reservoir. Then, after the autumn full circulation, positive temperature trends can be seen also for deep water layers until end of winter.

Due to steeper temperature gradients and higher stratification stabilities, mixing depth z_{mix} became shallower. Especially, in April z_{mix} moved $0.45\,\mathrm{m\,a^{-1}}$ nearer towards the surface and the onset of stratification started earlier. The consequence of warming epilimnetic water and warming tributaries at the same time was a negative relative trend of entrainment compared to z_{mix}. That implies that tributaries entrain more in the near of the metalimnioin or even more often below z_{mix}. Also in terms of absolute numbers entrainment of tributaries took place in heigher depths ($0.05\,\mathrm{m\,a^{-1}}$ to $0.08\,\mathrm{m\,a^{-1}}$), as indicated by positive trends for z_{in} from May to August. The absolute entrainment depth decreased only in September and October.

2.3.5 Influence of thermal structure on summer phytoplankton

In contrast to SRP-loadings thermal structure (epilimnetic temperature, stratification stability and z_{mix}) was clearly related to the occurence of cyanobacteria and *F. crotonensis* (Fig. 2.7). Especially in June and shortly before their main peaks, cyanobacteria biomass seemed to be regulated by thermal structure. High epilimnetic temperature lead to more stable stratification and a shallower epilimnion (smaller z_{mix}) and in effect higher cyanobacteria biovolumes already in June. Maximal cyanobacteria biomasses were found above 19 °C at BV-stabilities higher than $0.026\,\mathrm{s^{-1}}$ and z_{mix} smaller than 4.4 m.

F. crotonensis also can profit from thermal regime shifts. In May *F. crotonensis* exhibited highest biomasses at intermediate temperatures between 11 °C to 15 °C but seemed to be outcompeted outside this optimum range. In Summer this bacillariophyte prefered rather colder epilimnetic temperatures below 20 °C. Since temperature is correlated with z_{mix} and BV-stabiltiy frequencies this also means that deeper mixing and weeker stabilities were in favour for *F. crotonensis* in August. The occurences in autumn can be explained certainly by relatively shallow mixing depths below 33 m. Hence, growth of *F. crotonensis* late in the year required relatively high water temperatures above 8.5 °C which still supported the thermal stratification.

2.4 Discussion

The minimal entrainment depths during stratification period have been increasing since 1986 by up to $0.17\,\mathrm{m\,a^{-1}}$. However the estimated range of deeper entrainment depths for the warmest and with respect to external nutrient loadings most important tributary to the Saidenbach reservoir does not support the hypothesis of an increased frequency of epilimnetic entrainment events (Fig. 2.4). Both, epilimnetic

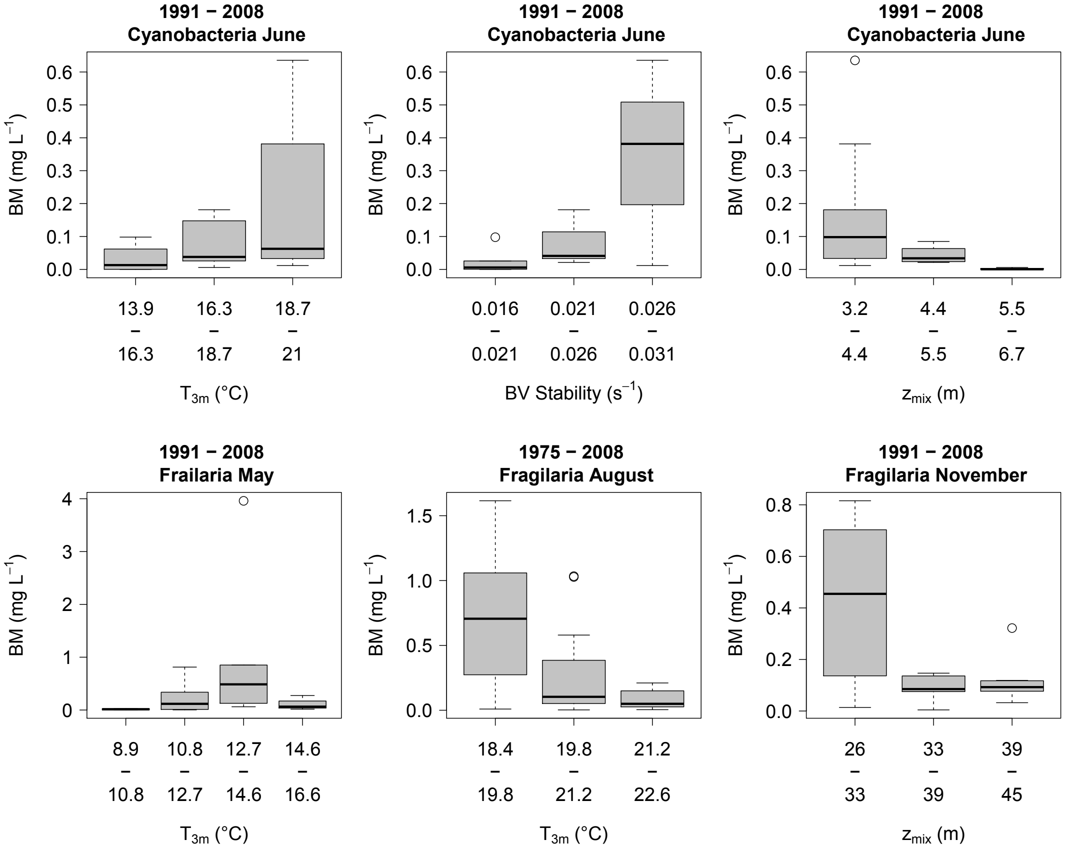

Figure 2.7: Biomass of cyanobacteria and *F. crotonensis* in dependence of thermal structure of the water column during the mesotrophic period from 1991 – 2008. *F. crotonensis* in August was plotted since 1975 because mean water temperatures colder than $19.8\,^{\circ}\mathrm{C}$ only occured before 1991.

as well as tributary temperatures revealed increasing trends. Temperature increase in the reservoir was higher compared to the temperature increase of the tributaries. This indicates, that the epilimnetic responds faster (missing shading by trees) and stronger to increasing air temperature than the inflows, which already entrain to the reservoir before having reached the maximal possible temperature. Furthermore decreasing mixing depths lead also to a relatively deeper entrainment below the thermocline. Therefore, nutrient loadings by the tributaries are lost in the meta- or hypolimnion during growth season and no correlations of external nutrient loadings and cyanobacteria could be found (Tab. 2.4, Fig. 2.5).

Among others, Salmaso (2010) and Huber et al. (2011) found that the amount of available nutrients is the most important factor for cyanobacteria blooms in summer. But, this can not be the reason in SR, so the found changes in water temperature and mixing regimes seem to be the most probable cause. Also Mooij et al. (2005), Blenckner et al. (2007), & Wagner & Adrian (2009) and Salmaso (2010) found long stratification periods, increased stability of the water column and higher water temperatures in favour of extended cyanobacteria developments in shallow as well as deep lakes. Huisman et al. (2004) pointed out that diatoms which occur in years with increased mixing regimes will be replaced by surface blooms of harmful cyanobacteria which have less sedimentation losses compared to other species in years with reduced epilimnetic turbulence. Ultimately, cyanobacteria are able to profit from hydrophysical changes without the need of increased nutrients so that eutrophication-like effects can be observed and even a reduction of nutrients can be counteracted (Mooij et al. 2005; Whilhelm & Adrian 2008). Beside these direct temperature effects also indirect effects like re-dissolution of internal phosphorus (Wagner & Adrian 2009) or modified food webs with increased abundances of copepods showing a high grazing pressure on edible algae (Blenckner et al. 2007), may promote cyanobacteria.

According to Ptacnik et al. (2003) *F. crotonensis* is most abundant at intermediate mixing depths. Increasing mixing depths lead to smaller sedimentation losses but lower growth rates due to decreasing light, while decreasing mixing depths will increase sedimentation losses. Taking the different preferences of cyanobacteria and *F. crotonensis* for temperature and turbulence into account, the pattern of their development in SR (Fig. 2.2) is highly plausible. In May this diatom started growing as soon as temperature and stratification was high enough, but probably diminished during this month when temperatures and stratification were too high again (Fig. 2.7). In summer a coexistence of *F. crotonensis* and cyanobacteria was observed around 19 °C, but at low mixing depths, high stratification stabilities and higher water temperatures *F. crotonensis* is outcompeted by cyanobacteria. In Autumn *F. crotonensis*only can develop when sedimentation losses are not too high, therefore longer durations of the stratification period will favour this species late in the year. In SR the longer maintenance of stratification in Autumn most probably is caused by decreased withdrawl of hypolimnetic water after 1990 (Fig. 2.6). This however, already may provide a picture of what might be even more realistic for natural lakes, since duration of stratification also is predicted to increase in other lakes.

As a consequence, increasing amounts of cyanobacteria are problematic for drinking water production. Especially, since increasing quantities and mass developments of potentially toxin producing species like *Plankthothrix sp.* have been observed during the last years. Adaptive strategies for water management are limited because of the external climate forcing, which also synchronises effects over different aquatic systems throughout Europe (Straile 2002; Wagner et al. 2012; Jäschke et al. 2013). A further reduction of nutrients from point sources is expensive and does not seem to be a sufficient measure to reduce cyanobacteria blooms in SR regarding the current results, that inflows entrain meta- or hypolimnetic and additional epilimnetic nutrient loading does not seem to be the controlling factor. Hence, in the future it might be increasingly necessary to artificially alter the hydrophysical structure of the reservoir, which was found to be the most prominent driver.

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3 Compensatory and amplifying effects of climate, oligotrophication and variable fish stocks on the plankton community in a deep reservoir

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Abstract

Changes in phenomenology of phyto- and zooplankton as consequence of global warming are hard to predict and not consistent througout model simulations, mesocosm studies and field observations. While in some lakes zooplankton gains from rising temperatures, in others such as in Saidenbach reservoir the opposite was found, although mean annual phytoplankton biomass increased along the temperature gradient. To disentangle temperature effects from nutrient effects and to seperate direct from indirect effects mediated by the food web, information gaps about the composition of the fish community needed to be filled. Thus, a growth model for the artificially stocked, non reproducing silver carps and other important fish species was applied. Thereafter, long term time series of temperature, nutrient loading, phytoplankton and zooplankton were analyzed by breakpoint analysis and multivariate statistics. The partial reduncancy analysis seperated temperature from nutrient effects and revealed that direct temperature contributed 29 % of the total variance. It can be shown that at low fish predation, population development of zooplanktonic organisms fasten and increase, but this relationship is lost at higher mortalities. Furthermore, epilimnetic temperature in summer seems to promote fish predation, so that an advancing effect of temperature on zooplankton timing turns into a delaying effect. Thus, compensatory mechanisms at low zooplanktivorous fish stocks can turn to amplification at high fish stocks. The example provided by the Saidenbach reservoir provides insights into contradictory results of former studies and demonstrates that for the prediction of plankton phenomenology, food web structures need to be considered.

3.1 Introduction

During the past decades significant global warming was observed (Trenberth et al. 2007). As a consequence, epilimnetic water temperatures also increased in many lakes (Blenckner et al. 2007; Adrian et al. 2009; Dokulil et al. 2010). It was shown that the warming of water affects the phenology of plankton species (Adrian et al. 2006) and that effects of meteorological forcings in the northern hemisphere are even synchronized between lakes by coupling to the North Atlantic Oscilliation (NAO, Straile & Adrian 2000).

As long as rising temperatures do not exceed the optimum of organisms, physiological rates increase and planktonic species prefering warm temperatures should benefit. But even in case of exceeding optimum thresholds, species composition might shift to better adapted and faster growing organims. Accordingly, model simulations predicted accelerated development of spring phytoplankton (Domis et al. 2007; Schalau et al. 2008) and as a consequence an earlier start of the zooplankton development up to more than one month (Scheffer et al. 2001; Schalau et al. 2008). However, Domis et al. (2007) pointed out that it would also be possible that hatching of zooplankton from resting stages, which often depends on photoperiod, might get uncoupled from temperature so that these species miss their prey, grow slower and approach lower population densities.

Indeed, mesocosm studies showed shallower stratification with increasing temperatures resulting in an accelerated phytoplankton spring bloom and of the subsequent *Daphnia* populations (Berger et al. 2010; Feuchtmayr et al. 2010). Beside the acceleration, phytoplankton biomass increased consistently throughout the studies, while *Daphnia* became more abundant only in the experiment of Berger et al. (2010).

The onset of the spring phytoplankton bloom up to 4 weeks earlier in temperate lakes is a common phenomenon related to climatic change. It is caused by earlier ice break up and/or earlier begining of the stratification period (Winder & Schindler 2004b; Adrian et al. 2006; Peeters et al. 2007; Huber et al. 2008). Accordingly, in the Saidenbach reservoir a significant correlation was found between the day of iceout and the start of the spring mass development of diatoms (Rolinski et al. 2007). Here, longer mixing after earlier ice breakups facilitates diatoms to persist longer in the water column. Therefore, higher diatom biomasses were reached in years after warm winters (Horn 2003a; Horn et al. 2011).

Similarly, cyclopoid (Gerten & Adrian 2002; Seebens et al. 2009; Huber et al. 2010) and calanoid copepods (Seebens et al. 2007) were found to benefit from higher spring temperatures. Some copepod species can even develop one maturing phase more per year (Blenckner et al. 2007). Other crustacean zooplankton like Cladocera react sensitively to temperature changes too, and climate variability during spring had strong impact on *Bosmina* dynamics (Huber et al. 2010; Straile & Muller 2010) and on *Daphnia*, for which a progressively earlier seasonal development was observed e.g. in lake Windermere (Thackeray et al. 2011) and Lake Constance (Straile 2000).

However, indirect effects turned out to influence zooplankton dynamics stronger than direct temperature effects in many lakes (Visconti et al. 2008). Zooplankton might benefit from lower mortality at higher temperatures due to longer predator free time periods and less stress when predators missmatch due to temperature shifts (Seebens et al. 2009; Wagner et al. 2012). On the other side, it also can be reduced considerably by invertebrate predators and fish (Sweetman et al. 2008) due to more active or more abundant predators when the predation windows still match. Invertebrate predators were found to occur two months earlier with higher abundances in warm years (Wagner & Benndorf 2007; Manca & Demott 2009; Anneville et al. 2010). Thus, they can superimpose direct temperature impacts in similar ways as fish (Benndorf et al. 2001; Mckee et al. 2003; Anneville et al. 2010). Winder et al. (2004) report that the keystone herbivore *Daphnia* can get decoupled from its food resources, when spring phytoplankton shifts further forward than *Daphnia*. A decline of Cladocerans might result from altered phytoplankton composition as well when Cyanobacteria getting dominant at higher temperatures, but are less edible and provide a lower food quality for *Daphnia* (Dupuis & Hann 2009).

In Saidenbach reservoir cladoceran biomass was reduced by over 50 %, and its development was delayed up to one month after the stocking of *Hypopthalmichtys molitrix* in 1986 and 1989 (Horn 2003b; Radke & Kahl 2002). Initially, copepods profited from reduced *Daphnia* biomasses shortly after the fish stocking. However, copepod biomass was significantly declining after 1990 (Horn 2003b) and the formerly significant temperature effects on the growth rate of *Daphnia* were not detectable after 1987 (Horn 2003b).

Simultanously with clear climate impacts (Rolinski et al. 2007) and changes of the fish composition, the trophic state of the reservoir altered from eutrophic to mesotrophic due to a remarkable and abrupt reduction of phoshorus loading in 1990 (Horn 2003a). All these changes occure simultaneously and hamper the disentanglement of temperature effectes but need to be considered when investigating climate impacts on planktonic food webs (Sweetman et al. 2008).

To reveal climate impacts and interactions with changing reservoir manangement (nutrients, fish stock) on the planktonic food web in Saidenbach reservoir, metrics describing plankton phenology were derived using multivariate statistics. For this purpose, the composition of the fish community needed to be estimated by modelling because of insufficient catch data. Contrary to the assumption that rising water tempertures accelerate the development of zooplankton and increase their biomass, for Saidenbach reservoir it was hypothesised that trophic effects at high planktivorous fish stocks operate antagonistically to climate change and ultimately result in lower zooplankton biomass and delayed population development.

3.2 Methods

3.2.1 Study site and long term data set

The Saidenbach reservoir, taken into operation in 1934, is situated in the low mountain range (Ore Mountains) at 439 m.a.s.l. in the south-east of Germany. At a maximum depth of 45 m during full storage it has a volume of 22.4 Mio m^3 and a mean depth of 15.3 m. The catchment area is mainly agriculturally utilized and only 19 % is forested (for further characteristics see Horn 2003b; Horn et al. 2006). The dimictic reservoir was subject to eutrophication and then changed from eutrophic to mesotrophic after the sudden drop of SRP-loading by 69 % (Fig. 3.1B) caused by land management alterations and the replacement of P-containing detergends by P-free ones after new legal reulations in 1990 (Paul et al. 2000; Horn 2003a). Due to its prominent importance for drinking water supply, the reservoir has been intensely investigated in at least forthnightly intervals since 1975. All relevant biological, chemical and physical criteria were investigated at several depths at the deepest point of the reservoir approximately 100 m in front of the dam. Chemical analyses were processed in the laboratory immediatly after sampling as described in Horn (2003a) and Horn (2003b). For calculation of nutrient loadings according to Harned et al. (1981), sampling and chemical analysis of the four tributaries took place in the same frequency.

3.2.2 Determination of cardinal dates for phyto- and zooplankton

To investigate long term trends of population development of the main planktonic species in Saidenbach reservoir, characteristic phenomenological points (cardinal dates), such as start, maximum, and end of the first development after ice-breakup as well as the maximum biomass were determined by an automated peak detection algorithm (Rolinski et al. 2007). Thereby, 6-parametric Weibull functions were fitted to the time series and a 5 % two-sided quantile (percentage of the integral) was used to define beginning and end of the peak.

3.2.3 Estimation of zooplanktivorous fish biomass

In order to evaluate the influence of zooplanktivorous fish on cardinal dates and biomass of zooplankton, the most probable composition of the fish community was estimated for every investigated year. Fish stock assessment of perch (*Perca fluviatilis*), common carp (*Cyprinus carpio*), pike (*Esox lucius*), roach (*Rutilus rutilus*), carp bream (*Abramis brama*), brown trout (*Salmo trutta forma lacustris*), and pike-perch (*Sander lucioperca*) was based on annual gill net catches and echolocation (Dorn 1964; Schultz 1983; Kahl 2003; Radke et al. 2003; Pitsch 2005; Horn et al. 2006; Hülsmann et al. 2006, and unpublished data).

Saidenbach reservoir was stocked several times with silver carp (*Hypopthalmichtys molitrix*) between 1986 and 1989 (Tab. 3.1). Due to the impossiblity to recapture this large species by the gill net method, a model approach was used to estimate development and growth of the silvercarp population. For that, a cohort based model consisting of three age-cohorts corresponding to the three years when stocking took place was used. Growth was described by a van Bertalanffy growth function based on body weights w (VBGF, Eq. 3.1, von Bertalanffy 1938):

$$w = \left(w_{max}^{\frac{1}{3}} - (w_{max}^{\frac{1}{3}} - w_0^{\frac{1}{3}}) \cdot \exp(-\frac{1}{3}\, b\, t)\right)^3 \tag{3.1}$$

with maximum body weight $w_{max} = 8\,\mathrm{kg}$, the initial weight w_0 in kg, time t in years (a), and growth rate $b = 0.45\,\mathrm{a}^{-1}$. VBGF was fitted to weight measurements taken from caught and found animals (see Tab. 3.1, Ruscher 2006; Radke 2000, Novack, water authority LTV Sachsen, pers. comm.). For the periods between 1986 – 2001 and 2006 – 2008 no counts or estimates for lost individuals exist. Because of that, losses were modeled by constant mortality rates m during these times (Eq. 3.2):

$$N = N_0\, e^{-m\,\Delta t} \tag{3.2}$$

with the number of individuals per cohort N, the initial number of individuals per cohort N_0 and the time duration Δt of the periods of interest.

To gain an estimate of the fish biomass contributing to zooplanktivorous feeding habits, each species i was assigned a mean proportion of zooplanktivory Z_i based on analyses of stomach contents (unpublished data, Tab. 3.2). Firstly, relative zooplanktivory was estimated for native species Z_{native} only (Eq. 3.3). Food of silvercarp was found to consist of 70 % of zooplankton (Z_{SC}). Since data for fish was gathered only in few years, total biomass (BM_{total}) and zooplanktivory without silver carp were linearly interpolated. Based on approximated total fish biomass and the modeled biomass of silvercarp, the relative proportion of silvercarp SC_{rel} was then calculated for each year. Further, total zooplanktivory was calculated as the sum of the zooplanktivory of silvercarp alone and the zooplanktivory of the native species. To allow adding proportions, both were related to silvercarp (Eq. 3.4). Finally, absolute zooplanktivorous fish biomass (BM_Z) was estimated by Eq. 3.5.

$$Z_{native} = \frac{\sum BM_i \cdot Z_i}{\sum BM_i} \tag{3.3}$$

$$Z_{total} = SC_{rel} \cdot Z_{SC} + (1 - SC_{rel}) \cdot Z_{native} \tag{3.4}$$

$$BM_Z = Z_{total} \cdot BM_{total} \tag{3.5}$$

Table 3.1: Stockings, weight measurements and estimated losses of *Hypopthalmichtys molitrix* in Saidenbach reservoir. Number of stocked individuals in 1986 is the number after an direct stocking loss of 20 % which was stated on the original stocking protocols. Calculation of mortality rate m for the period 1986 – 2001 was based on an estimated loss of the population of 40 % from 1986 – 1998. Mortality rate for the period 2006 – 2008 was based on the assumtion that 50 % of the remaining population died from 2000 – 2007 (Novack, LTV Sachsen, pers. comm.).

year	Stocking (Ind)	Weight (kg Ind^{-1})	Losses	Source
1986	12800	0.0125		Uhlig, LTV Sachsen, pers. comm.; Horn (2003b)
1988	400	1		Uhlig, LTV Sachsen, pers. comm.
1989	4400	0.7 – 1		Uhlig, LTV Sachsen, pers. comm.; Horn (2003b)
1986 – 2001			$m = 0.04\,\mathrm{a}^{-1}$	
2002		4.5	2000 Ind	Novack, LTV Sachsen
2003		5	50 Ind	Novack, LTV Sachsen
2004		7.2	500 Ind	Ruscher (2006)
2005		7.5	2000 Ind	Ruscher (2006)
2006 – 2008			$m = 0.1\,\mathrm{a}^{-1}$	

Table 3.2: Fish dietry composition; percentages are given for different feeding habits.

species	piscivorous	planktivorous (Z_i)	unknown
S. trutta f. lacustris	100	0	0
P. fluviatilis	20	50	30
A. brama	0	5	95
E. lucius	100	0	0
C. carpio	0	0	100
R. rutilus	0	50	50
H. molitrix	0	70	30
S. lucioperca	100	0	0
other	0	0	100

3.2.4 Statistical analyses

Statistical analyses and modeling were performed using the R environment for statistical computing (R Development Core Team 2010) and the specialized add-on packages “cardidates” for determination of cardinal dates (Rolinski et al. 2007), “strucchange” for discovering structural break points in time series (Zeileis et al. 2002), and “vegan” for multivariate statistics (Oksanen et al. 2011).

The analysis of the number of breaks and the optimum break points of the cardinal dates’ time series is based on the separation of segments with stable linear regression coefficients. The applied method described by Zeileis et al. (2003) uses a minimalization of residual sum of squares (RSS) to fit the linear regression model and a minimum BIC estimator to assess the number of breakpoints.

To identify typical patterns, nonmetric multidimensional scaling (NMDS, Kruskal 1964; Cox & Cox 1994) with Euclidean dissimilarities for cardinal dates of the first peak after iceout of *Daphnia*, *Cyclops*, *Eudiaptomus*, and spring phytoplankton was applied in a first step. Cardinal dates of *Bosmina* were not considered since this species was not sampled in all years. To make cardinal dates of different units comparable to each other, data were standardized into range 0..1 prior to analysis. Potential explanatory variables (Tab. 3.5) were projected to the NMDS by vector fitting (Oksanen 2010). In a second analysis, partial redundancy analysis (pRDA) with trophic conditions (SRP4_9) and amount of zooplanktivorous fish (*planktivores*) as covariates was applied to eliminate the effect of these variables and to reveal temperature caused effects. Only environmental variables identified to be significant in vector fitting were used as constraints for the pRDA (Tab. 3.5).

Since fish stock and temperature were identified as most influential predictors on cardinal dates of *Daphnia*, it was possible to investigate direct temperature relationships. Therefore, sampled years were sorted in ascending order according to zooplanktivorous fish biomass and then classified into 3 classes with equal number of years. Means of the zooplanktivorous fish biomasses of the 33.3, 66.6, and 100 % percentiles were rounded to 150 kg ha^{-1} (low), 200 kg ha^{-1} (medium), and 350 kg ha^{-1} (high). Cardinal dates were then investigated class-wise as a function of different mean and epilimnetic water temperatures (Fig. 3.8).

3.3 Results

3.3.1 The Saidenbach reservoir time series

Like in many other lakes of the northern hemisphere also in the Saidenbach reservoir measurable increases of water temperatures were found (Fig. 3.1A). Mann-Kendall-trend statistics showed significant positive trends for eplimnetic water temperatures in February, from April to September and in December. A breakpoint in the time

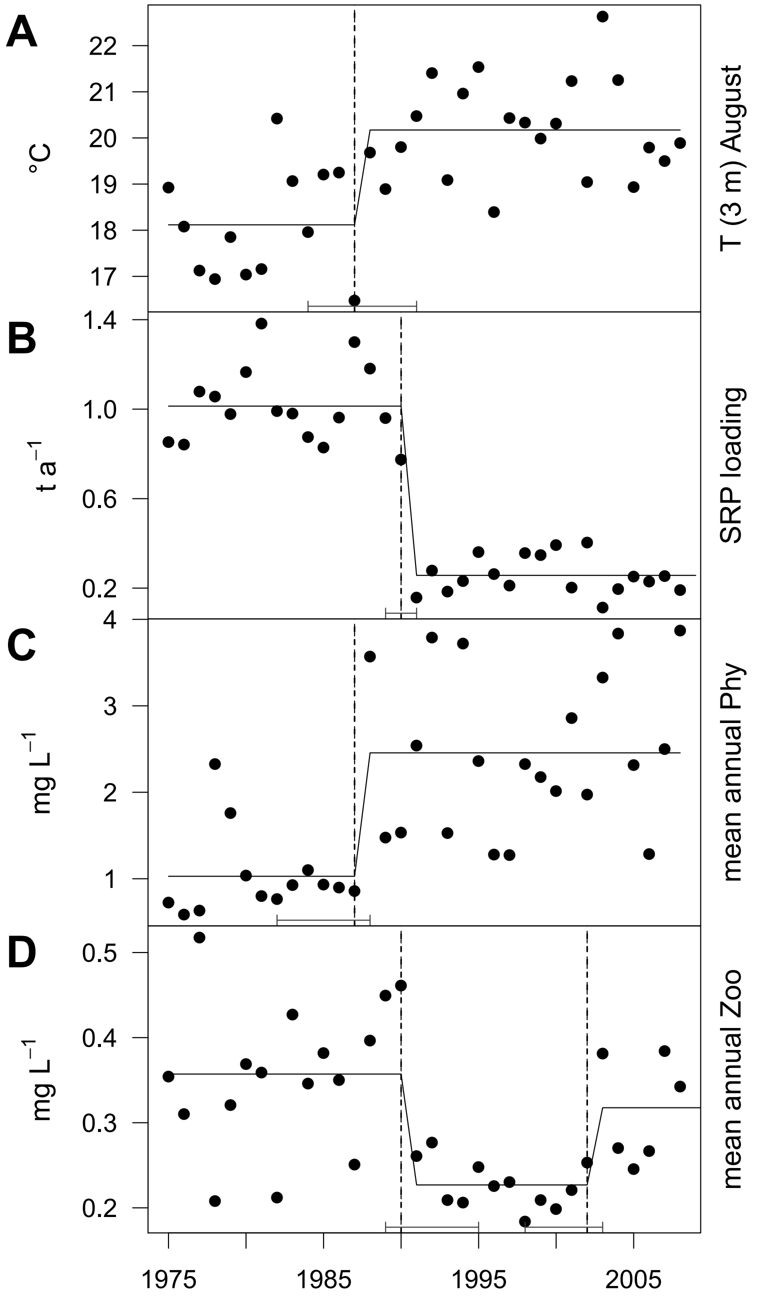

Figure 3.1: Structural breaks in time series of mean water temperatures in August, annual SRP loadings, mean annual phytoplankton, and zooplankton biomass since 1975. Breakpoints are indicated by dashed lines, their confidence intervall by grey lines and fitted models for the time intervalls are shown by solid lines.

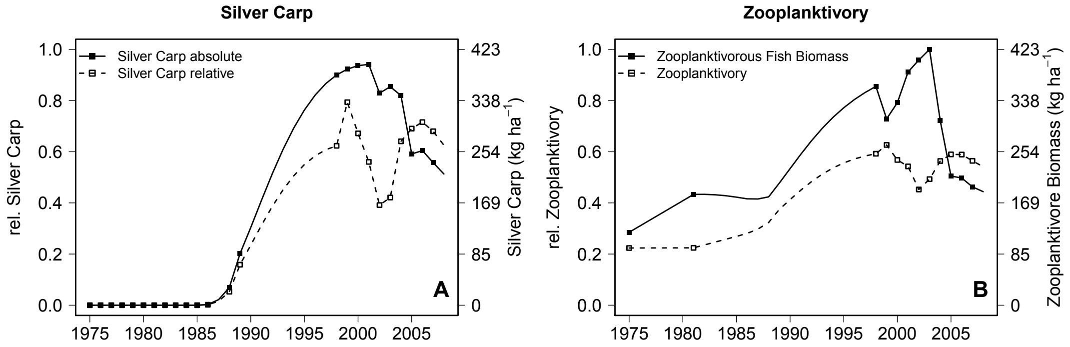

Figure 3.2: Devolopment of *H. molitrix* (A) and of the total zooplanktivory of the fish community (B) in the Saidenbach reservoir (points indicating dates with reliable data for the fish community, lines were modelled to fill data gaps).

series indicating a switch of temperature regimes from colder to 2 degrees warmer conditions in August could be determined in 1986/1987 (Fig. 3.1A).

The breakpoint when annual SRP loadings dropped by over 50 % could be determined precisely to 1990/1991 (Fig. 3.1B). In spite of notably reduced nutrient load, the mean annual phytoplankton biomass increased since 1987 and has remained at these elevated levels ever since (Fig. 3.1C). Inspite of higher water temperatures and phytoplankton abundances, the mean annual biomass of zooplankton decreased by almost 50 % after 1990 and recovered only partially during recent years (Fig. 3.1D).

3.3.2 Structure of the fish community

For explaining the mechanisms leading to the breakpoints of zooplankton patterns in the Saidenbach reservoir, it is neccessary to examine the structure of the food web including the fish community. Immediately after stocking with *H. molitrix* in 1986 and 1989, the relative importance of this species continuously increased. At its maximum in 1999 *H. molitrix* made up 79 % of the overall fish biomass (Fig. 3.2). Due to the general impossiblity of spawning in this lreservoir under the past and the current climatic conditions and due to mortality by age and a heavy flood event in 2002, the biomass dropped by 50 % but relative silvercarp proportion began rising afterwards again in consequence of somatic growth of silvercarp and decreasing stock of other planktivorous fish species. The zooplanktivorous fish biomass decreased since 2003 due to the loss of the high number of individuals of *H. molitrix* and reduced abundances of other species. Nonetheless, the amount of overall fish biomass contributing to zooplanktivorous feeding behaviour is highly correlated to the amount of *H. molitrix* ($r^2 = 0.91$, $p < 0.001$), indicating a high influence of this species for total zooplanktivory.

3.3.3 Development of mean annual crustacean biomasses

The spring mass development of Bacillariophytes (diatoms), the most abundant phytoplanktonic group in the reservoir, usually forms a unique peak shortly after ice-off. It was regularly followed in spring and early summer by developments of cyclopoid copepods with *Cyclops abyssorum* and *Cyclops vicinus* making up almost 100 % of this group, one single calanoid copepod *Eudiaptomus gracilis*, the cladocerans *Daphnia galeata*, and to a lesser amount *Bosmina longirostris*.

Mean annual biomass of the Cladocerans directly decreased after the strong rising of zooplanktivorous fish biomass in 1986 (Fig. 3.3). The proportion of *Daphnia* dropped from 50 % to below 20 % and recovered only slowly. *Daphnia* biomass has increased continuously again since 2000 and has almost reestablished its height from before 1986 in the latest years. The ratio between the zooplankton groups in the last two years of the data set is similiar to the state before (Fig. 3.3, 3.5).

Between the first and second stocking with *H. molitrix* the mean annual biomass of copepods increased with a more than proportional gain of *Cyclops*. However, after the second stocking event the mean annual biomass of *Cyclops* decreased too. The mean annual biomass of the calanoid copepod *Eudiaptomus* did not change over time (Tab. 3.3), but its maximal biomass at the peak was reduced after 1995 (Fig. 3.4B, Tab. 3.3).

3.3.4 Changing pattern of *Daphnia* population dynamics

Within the zooplankton community *Daphnia* showed the most conspicuous changes. Typical annual *Daphnia* population dynamics changed within three periods since 1975 (Fig. 3.5). Until 1985 the exponential growth phase started between the end of April and begin of May and biomass in autumn was rather high. With the beginning of

Table 3.3: Significant breakpoints for cardinal dates of zooplankton, phytoplankton and day of iceout. Breakpoints are given for the begin, maximum, and end of the peak, as well as for the maximum biomass ($\mathrm{BM}_{\mathrm{max}}$) and the annual mean of the biomass ($\overline{\mathrm{BM}}_{\mathrm{annual}}$).

	Breakpoints								
	begin		maximum		end		$\mathrm{BM}_{\mathrm{max}}$	$\overline{\mathrm{BM}}_{\mathrm{annual}}$	
Daphnia	1986	1995	1986	–	1988	1994	1985	1986	2000
Bosmina	–	–	–	–	–	–	1987	1983	1987
Eudiaptomus	1986	–	1986	–	1985	–	1995	–	–
Cyclops	–	–	1998	2003	1997	–	1992	1987	1992
Phytoplankton	–	–	–	–	1991	–	–	1987	
Diatoms	1989	–	–	–	1991	–	–	–	
Iceout					1988				

1986 the start of *Daphnia* development was delayed until June and maximal biomass decreased permantently to values less than 50 % of the previous phase. Furthermore, the population did not perform a second development in autumn after the first peak in summer. In recent years, starting with 2006, the exponential growth of the cladoceran started again earlier in May. A distinct autumnal population growth reoccured.

3.3.5 Cardinal dates and breakpoints of plankton time series

Charateristic points of population development of zooplanktonic species were determined to identify correlations with environmental factors. Cardinal dates of the first peak after iceout, except for *Bosmina*, showed clear changes in their pattern after 1986, or the years thereafter (Fig. 3.4) accompanied by significant positive trends (Tab. 3.4). Diatoms, which made up the main portion of the phytoplankton during spring mass development (Horn 2003a), showed a breakpoint for their timing around 1990 which coincided with a fundamental change in the sheduling of the date of ice-off (Tab. 3.3).

The whole timing of *Daphnia*- and *Eudiaptomus*-peaks shifted by more than one month to later dates. While the shift of the *Eudiaptomus* maximum was permanent, the beginning of the *Daphnia* peak returned to earlier dates again (no overall positive trend, Tab. 3.4), but maximum and end remained delayed (significant positive time trend, Tab. 3.4). The end of the *Daphnia*-peak occured very late during several years after 1986. Since 1997 also *Cyclops* exhibits such a late end of its peak.

The first breakpoints in the time series of the crustacean peaks date around 1986 (Tab. 3.3). A second breakpoint was identified in the mid 1990s. The maximum biomass of all zooplankton species showed one breakpoint; for Cladocerans around 1986 and for Copepods in the first half of the 1990s. The periods after these breakpoints are characterized by a 50 % decrease of the biomasses. This is consistent for all investigated zooplankton species (Fig. 3.4B).

Table 3.4: Linear trends of zooplankton cardinal dates for the complete range of the long term data set from 1975 – 2008 (slopes in $d\,a^{-1}$, significance: ** $p < 0.01$, * $p < 0.05$).

	Daphnia			*Bosmina*		*Eudiaptomus*			*Cyclops*		
	slope	p		slope	p	slope	p		slope	p	
begin	0.318	0.385		-0.774	0.433	0.998	0.040	*	-0.478	0.261	
maximum	1.448	0.018	*	-0.445	0.666	1.331	0.008	**	1.044	0.109	
end	1.640	0.042	*	-0.278	0.774	1.497	0.004	**	2.869	0.003	**

3.3.6 Disentanglement of climate and trophic effects

Nonmetric Multidimensional Scaling (NMDS) was performed to disentangle temperature effects from other substantial environmental influences (Fig. 3.6), such as nutrient loading and fish stock.

The NMDS showed a clustering of the different years along two main dimensions (Fig. 3.6). Vector fitting of potential explanatory variables revealed that mean water temperatures in spring and summer (March – August: T3 – T6), day of iceout, and epilimnetic water temperatures in May (TE5) and June (TE6) affected cardinal dates of plankton seperately from phosphorous loading (SRP), biomass of *H. molitrix* (BMsc), biomass of zooplanktivorous fish (BMz), and epilimnetic temperature in summer (TE7, TE8) (Tab. 3.5).

Timing and biomass (DIAbm) of the diatoms during spring mass development was explicitly determined by the day of iceout and mean water temperature in April. The later the day of iceout the later the beginning (DIAb), maximum (DIAm) and end (DIAe) of the phytoplankton peak was observed. A short duration of ice coverage correlated strongly with high diatom biomasses. Nutrients and fish biomass slightly influenced the beginning and end of the peak. In contrast to phytoplankton, the biomass of zooplankton (*Cyclops*: CYCbm, *Daphnia*: DAPbm, *Eudiaptomus*: EUDbm) was considerably influenced by the presence of zooplanktivorous fish, epilimnetic temperatures in summer, and nutrients. With decreasing zooplanktivorous fish biomass and increasing nutrient inflow the biomass of all three species increased. Remarkably, high epilimnetic temperatures in summer cause the same effect as high predation risks or low nutrients. Regarding the timing, *Daphnia* maximum (DAPm) and end (DAPe) were influenced most strongly by this first axis while beginning of *Daphnia* development (DAPb) seemed to be controlled equally by spring and early summer temperatures (second axis) with an earlier start in years with higher temperatures. The start of *Cyclops* (CYCb) and slightly of *Eudiaptomus*(EUDb) appear to be delayed by low temperatures too.

In RDA and partial RDA analyses, variables with no explanatory power (see Tab. 3.5) were ommitted. The RDA verified that the first two constrained ordination axes (Tab. 3.6, ordination not shown) reproduced the main results of the NMDS (Fig. 3.6). The first two RDA axes projected 62 % of the constrained variance which explained 47 % of total variance (Tab. 3.6). Partial RDA was performed with zooplanktivorous fish biomass and SRP loading as covariates to seperate temperature effects from trophic effects (Fig. 3.7). Co-variates were responsible for 18 % of total variance, whereas direct temperature effects contributed 29 % of total variation (Tab. 3.6). A clear effect of temperature and ice coverage was found and the orthogonal relationship between epilimnetic water temperatures in spring and August remained.

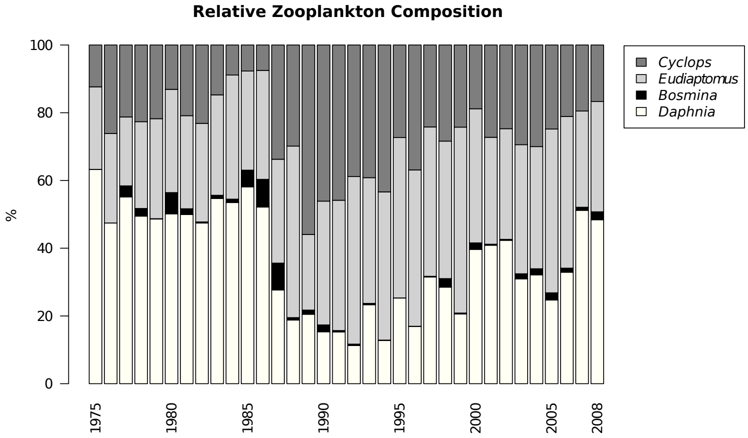

Figure 3.3: Relative biomass of zooplankton species compared to total zooplankton biomass. Modified after Horn (2003b).

Table 3.5: Variables used for environmental fitting to the NMDS. Significant variables are marked by stars (p > 0.5: no star, p < 0.1: ., p < 0.05: *, p < 0.01: **, p < 0.001 ***).

Variable	Symbol	Unit	NMDS1	NMDS2	r2	p	
Day of ice-out	*iceout*	Day	-0.488	-0.873	0.464	0.001	***
Epilimnetic temperature in 3 m depth							
in may	$TE5$	°C	0.712	0.702	0.298	0.004	**
in june	$TE6$	°C	0.780	0.626	0.249	0.008	**
in july	$TE7$	°C	0.958	-0.288	0.086	0.265	
in august	$TE8$	°C	0.999	-0.036	0.375	0.004	**
mean of water temperature over complete water column							
in march	$T3$	°C	0.455	0.890	0.157	0.061	.
in april	$T4$	°C	0.536	0.844	0.432	0.001	***
in may	$T5$	°C	0.273	0.962	0.300	0.004	**
in june	$T6$	°C	-0.031	1.000	0.210	0.023	*
in july	$T7$	°C	-0.541	0.841	0.120	0.124	
in august	$T8$	°C	-0.659	0.752	0.127	0.116	
Biomass of silvercarp	$BMsc$	$\mathrm{kg\,ha^{-1}}$	0.990	-0.138	0.505	0.001	***
Biomass of zooplanktivorous fish	BMz	$\mathrm{kg\,ha^{-1}}$	0.979	-0.203	0.493	0.001	***
Load of soluble reactive phosphorus (April – Septemper)	SRP	10^3 kg	-0.993	0.121	0.506	0.001	***

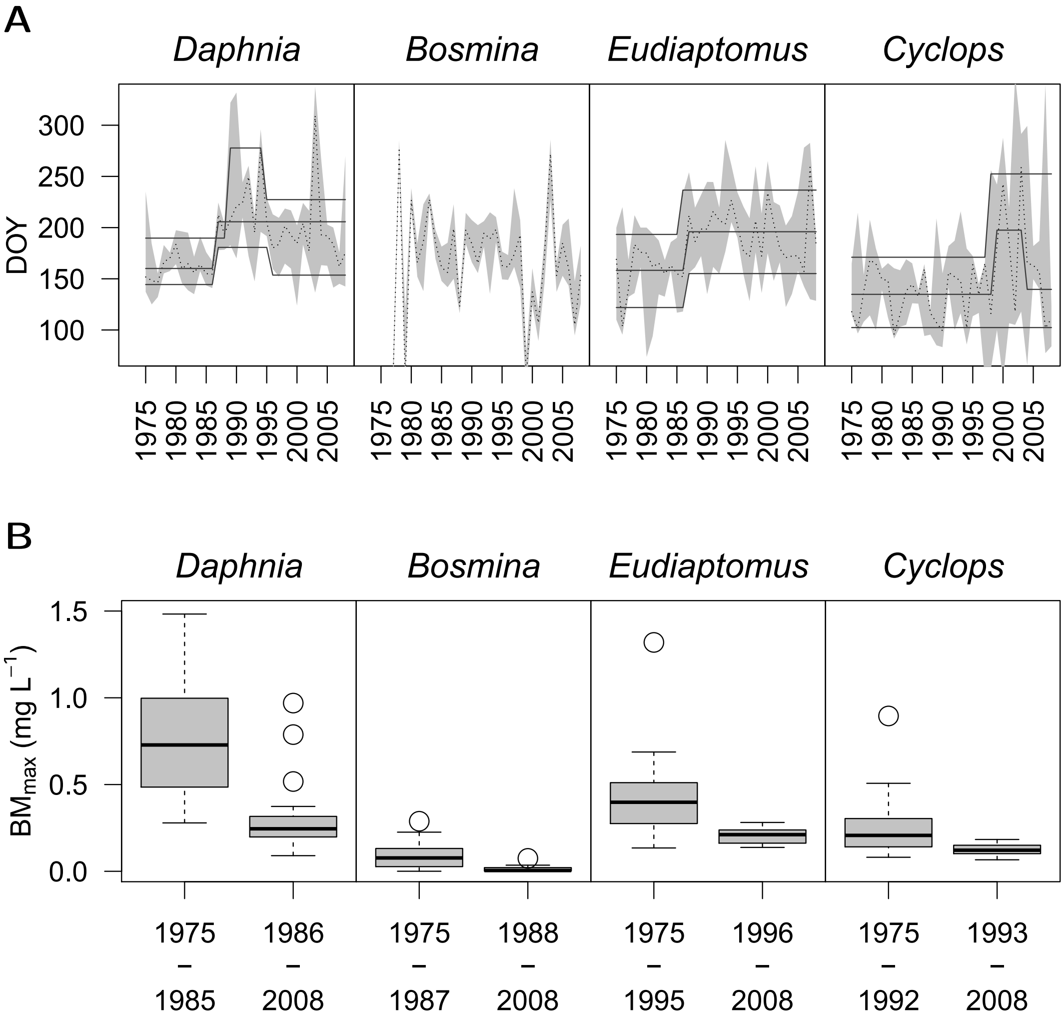

Figure 3.4: Cardinal dates of the main zooplankton species. A) begin, maximum (dotted line) and end of peaks are marked by gray band. Means of cardinal dates within the time intervalls between structural break points according to Tab. 3.3 are indicated by lines. B) Biomass at the peak maximum before and after al breakpoint of corresponding time series (Tab. 3.3). Whiskers indicate most extreme data point which is no more than 1.5 times the interquartile range from the box.

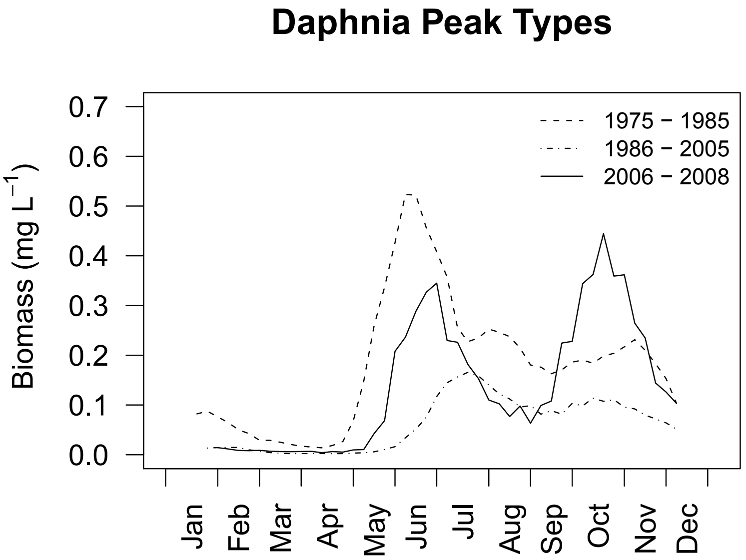

Figure 3.5: Annual dynamic of *Daphnia* showing different patterns within three periods since 1975 (weekly moving averages, modified after Horn 2003b).

Table 3.6: Explained and unexplained variance, determined by RDA and pRDA using only significant environmental variables from Tab. 3.5 as constraints. For pRDA zooplanktivorous fish biomass (BMz) and SRP were used as covariates.

	RDA			pRDA		
	Inertia (Variance)	Rank	relative	Inertia (Variance)	Rank	relative
Total	0.8516		100 %	0.8516		100 %
Conditional (BMz, SRP)				0.1512	2	18 %
Constrained axes	0.4015	10	47 %	0.2503	8	29 %
Unconstrained axes	0.4501	16	53 %	0.4501	16	53 %

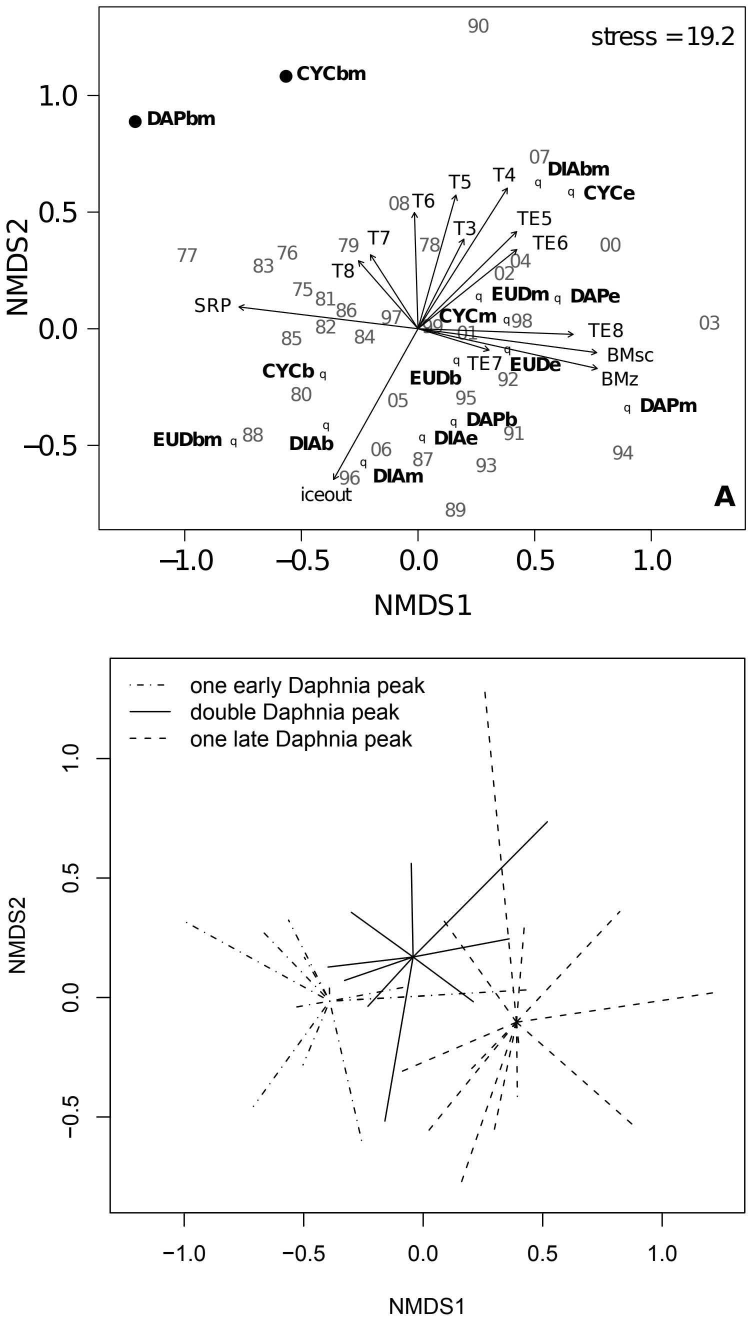

Figure 3.6: A) NMDS of cardinal dates of *Daphnia* (DAP), *Cyclops* (CYC), *Eudiaptomus* (EUD) and Diatoms (DIA) (b - begin, m - maximum, e - end, bm - biomass at peaks maximum, BMz - zooplanktivorous fish biomass, BMsc - biomass of silvercarp, other symbols see Tab. 3.5). B) Same ordination as before. Clusters of years with different kinds of *Daphnia* phenomenology are connected by spider plots and seperate well along the axis of nutrients, fish predation and summer epilimnion temperatures.

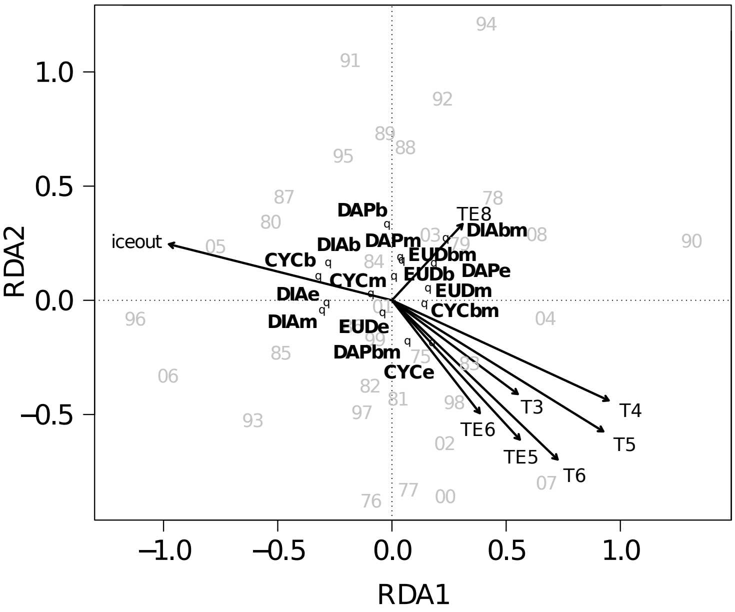

Figure 3.7: pRDA of cardinal dates of *Daphnia* (DAP), *Cyclops* (CYC), *Eudiaptomus* (EUD) and Diatoms (DIA) with SRP loadings and biomass of zooplanktivorous fish as conditioning covariates (b - begin, m - maximum, e - end, bm - biomass at peaks maximum, other symbols see Tab. 3.5)

3.3.7 Control of *Daphnia* peaks

Clusters of different *Daphnia* peak shapes can be connected to “spider”-diagrams to unveil their seperation along the environmental axes (Fig. 3.6B). Though, clusters partially overlap, years with one late peak could be seperatred along the axis of fish and nutrient effects from years showing one early *Daphnia* peak. Years which exhibited a late peak had a high predation by fish and years with an early peak corresponded to lower zooplanktivory. Years showing two peaks per year were located between these two groups at medium zooplanktivorous fish levels and at slightly higher temperatures in spring and early summer.

As zooplanktivorous fish and temperature were identified as major factors controlling planktonic organisms in Saidenbach reservoir, years can be grouped according to low, medium, and high zooplanktivorous fish biomass and then related to temperature (Fig. 3.8). In general, timing of *Daphnia* was delayed at medium and high fish levels (Fig. 3.8A–F). Lowest *Daphnia* biomasses were observed in years with maximum zooplanktivorous fish (Fig. 3.8G–H). At low fish predation *Daphnia* timing of the start and maximum of the peak was controlled by mean water temperatures (Fig. 3.8A, C), while the end of the peak remained uneffected at low fish levels from mean (Fig. 3.8E) and epilimnetic temperature (Fig. 3.8F). Since high predation can delay the peak for more than one month, later temperatures in the epilimnion during the period of

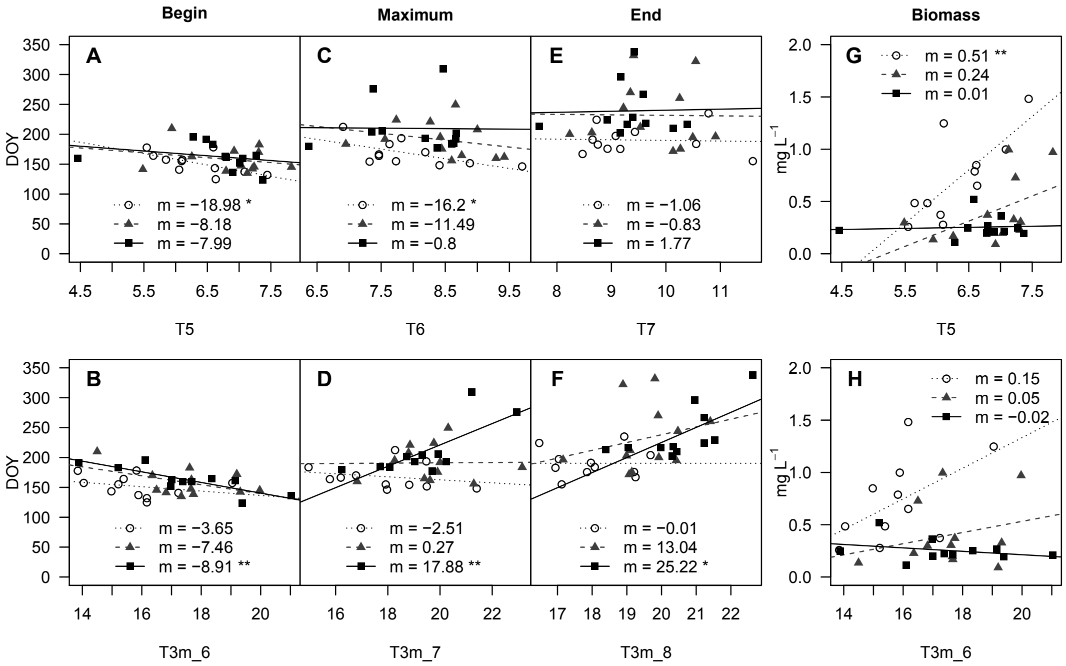

Figure 3.8: Cardinal dates of *Daphnia* in dependence of temperature and zooplanktivorous fish. Data was subdivided into 3 classes of zooplanktivorus fish biomass: class mids are shown by dotted line + circles: $150\,\mathrm{kg\,ha^{-1}}$, dashed line + gray triangles: $200\,\mathrm{kg\,ha^{-1}}$, solid line + rectangles: $350\,\mathrm{kg\,ha^{-1}}$. The slope m in Fig. A–F has unit $\mathrm{d\,K^{-1}}$, in Fig. G and H it is $\mathrm{mg\,L^{-1}\,K^{-1}}$. Significance of the slope is indicated by stars (no star: $p > 0.05$, *: $p < 0.05$, **: $p < 0.01$).

stratification were more meaningful for those years. A significant relationship between start and temperature was found even at high fish levels. While the start was delayed at cold temperatures, this effect was compensated at the highest temperatures, where the peak started as early as in years with lower fish stocks (Fig. 3.8B). However, the linear slope for the peak maximum gradually turned from negative to positive with increasing fish (Fig. 3.8E, F). The same phenomenon was observed for the end of the peak; while it was uninfluenced at lower fish levels, the peak ended considerably late at high fish levels and high epilimnetic summer temperatures (Fig. 3.8F). Water temperature relativly early during peak sucession (May – June) was already crucial for temperature control of *Daphnia* biomass (Fig. 3.8G, H). At lower predation, temperature had a strong positive effect on biomass, which decreased with rising predation. As a consequence, no influence of temperature on biomass was found at highest predation levels, indicating that temperature dependend predation rates might compensate the faster growth of *Daphnia* at higher temperatures.

3.4 Discussion

The purpose of this study was to identify climate related effects on phenological events of key planktonic organisms in Saidenbach reservoir and to discover mechanisms of observed trends and shifts in the long term time series. Therefore, effects of simultaneously changing environmental factors needed to be disentangled. Beside nutrient availability and fish predation, which were responsible for nearly 18 % of the variation, plankton phenology was equally or even more influenced by temperature that explained 29 % of the overall variability (Fig. 3.7, Tab. 3.6).

In contrast to this, a tremendous reduction nutrient loading did not affect timing of the phytoplankton spring bloom, which is similar to the findings in Lake Constance (Straile & Geller 1998; Peeters et al. 2007), indicating that nutrients were not limiting during spring overturn. Timing and spring biomass are strongly controlled by climate signals that determine start (ice-off) and duration of spring turnover. Long and intensive spring mixing reduces sedimentary phytoplankton and P-losses and, therefore, enables a maximum utilization of the available nutrient budget (Horn 2003a; Rolinski et al. 2007; Horn et al. 2011).

In spite of constantly rising water temperatures, advancing phytoplankton blooms potentially improved food resources for zooplankton in Saidenbach reservoir. Nevertheless, the development of *Daphnia* and *Eudiaptomus* became suddenly delayed for a long period directly after stockings with silver carp. Interestingly, breakpoints for the timing of both crustaceans occur immediately after fish stocking and several years before the reduction of phosphorus loading. Although nutrient loading and amount of zooplanktivorous fish were correlated (Fig. 3.6), the previously described circumstances indicate that zooplankton phenology changed independently from trophic state and likely was substantially top-down controlled (Horn 2003b; Radke & Kahl 2002; Wagner & Benndorf 2007).

Observations of concurrently occurring oligotrophication and warming suggest that warming affects zooplankton phenology in a compensatory way; e.g. zooplankton in shallow lakes showed no clear signal when reduced nutrients and increasing temperatures were combined (Jeppesen et al. 2005a; Jeppesen et al. 2005b). In deep lakes spring phenology of cladocerans such as *Daphnia* and *Bosmina* were not negativly affected by oligotrophication due to compensatory influcences of climate in the preceding winter (Straile & Geller 1998; Straile & Muller 2010). The same compensatory effect was observed for *Eudiaptomus graciles*, which displayed faster growth rates at increasing temperatures and compensated for reduced nutrients (Seebens et al. 2007).

Surprisingly, *Daphnia* and *Eudiaptomus* in Saidenbach reservoir were delayed, and all zooplankton species were reduced in biomass in spite of the warming, which should have compensated for possible effects of the nutrient reduction. Results suggest that this was primarily caused by predation by a high zooplanktivorous fish stock. While in the absence of fish, spring biomass of *Daphnia* depends on available nutrients (TP), this correlation is lost in the presence of fish (Mckee et al. 2003; Gyllstrom et al. 2005). Furthermore, temperature effects were also found elsewhere to be superimposed by fish (Anneville et al. 2010) and a reduction of herbivorous zooplankton by predation (Mckee et al. 2003). Additionally, Wagner & Benndorf (2007) showed that high May water temperatures raised the activity and growth of YOY perch resulting in higher predation pressure, but they also shortened the time frame for predation on zooplankton (Wagner et al. 2012). Therefore, positive and negative net effects on zooplankton phenology are possible depending on the trade-off between mortality caused by YOY fish and zooplankton growth rates. Due to suboptimal water temperatures in Saidenbach reservoir, silver carp does not reproduce and no offspring occurs. However, the adults are still high in number and biomass so that zooplanktivorous fish biomass was composed up to 80 % by silver carp. Copepod nauplii (Starling & Rocha 1990; Starling 1993) and other herbivorous zooplankton species compose up to 70 % of nutritional components of *H. molitrix* (Radke & Kahl 2002), necessitating relatively large amounts of prey. Thus, silver carp suppresses zooplankton when occuring in abundances as high as in Saidenbach reservoir (Radke & Kahl 2002).

Epilimnion summer temperature in July and August correlated to effects of silvercarp and zooplanktivorous fish (Fig. 3.6) indicating indirect effects of temperature, possibly mediated by fish causing an extra delay of the second half of zooplankton peaks (Fig. 3.6, 3.8). More active fish at higher temperature might surpress the zooplankton peak by reducing zooplankton biomasses and, consequentely, food resources are not overused. Therefore, no midsummer decline of *Daphnia* occurs (Benndorf et al. 2001) causing a stable population but with constantly low zooplankton biomasses (Fig. 3.5, 3.6B).

High water temperatures foster a high peak maximum of *Daphnia*. However, the presence of zooplanktivorous fish can moderate this effect until it completely diminishes

(Fig. 3.8). In general, higher predation causes delayed growth and a reduction of zooplankton biomass (Fig. 3.6, 3.8). However, a temperature interaction depending on the strength of the predation pressure was observed. At low and medium predation levels, zooplankton growth is accelerated with increasing temperature, while at higher mortality levels the temperature effects diminish or even turn negative. In the Saidenbach reservoir zooplanktivorous fish biomass was decreasing again since 2002 (Fig. 3.2) and dropped to medium and low levels but relative zooplanktivory of the fish community remained near its maximum. The recently almost restored pattern of *Daphnia* phenology to the status before silver carp stocking (Fig. 3.5), and the increasing annual *Daphnia* biomass after 2000 (Tab. 3.3), demonstrate the compensatory effect of temperature as soon as predatory loss of zooplankton drops below a critical level (Fig. 3.8).

Hatching from resting eggs contributed less than 1 % to the total abundance of *Daphnia* in Saidenbach reservoir (Rother et al. 2010). This is in contrast to Winder & Schindler (2004a) who found *Daphnia* recruitment from resting eggs in spring depending on photoperiod and a decoupling of *Daphnia* from spring phytoplankton, which was more controlled by temperature than by photoperiod. Zeis et al. (2010) observed increasing amounts of gentically adapted overwintering clones with increasing winter temperatures in Saidenbach reservoir. Hence, sufficient animals were always present in the water preventing mismatch between daphnid populations and their food. Hatched animals will only be relevant when the overwintering population is reduced to very low densities by predators (Rother et al. 2010). This might had been important during periods with high zooplanktivorous fish levels in the Saidenbach reservoir. Particularly, animals hatching from resting eggs and decoupling of *Daphnia* population from food resources in spring might have been relevant at elevated fish stocks. This would even increase the negative interaction of fish and temperature.

Differences in phenomenological effects between zooplankton species might result from different habitat choices. Copepods are often spatially separated from *Daphnia* by adjusting habitat preference below the thermocline, whereas, *Daphnia* usually have their center of gravity above the thermocline (Helland et al. 2007). Since the most abundant zooplanktivorous fish species in Saidenbach reservoir also use the epilimnion as feeding grounds, *Daphnia* will be affected by increasing fish stocks. The delayed reaction of copepods on fish stocking and the unchanged starting point of their spring development, as shown for *Cyclops*, can be explained by the spatially greater distance between their habitat and the fishes' preferred feeding grounds. Helland et al. (2007) also observed an up-movement of the gravity centers of zooplankton and fish nearer to the surface in warm months and thus, a spatial concentration of prey and predator. This is another possible explantion for the observed amplification of the negative fish and temperature interaction. Additionally, *Cyclops* is able to perform flexible modification to its life cycle and can adapt timing adaquately to changes in the environment to keep matching with occurrence of its food resources (Blenckner et al. 2007; Seebens et al. 2009). Also, different body sizes make *Daphnia* and *Eudiaptomus* more accesible prey items for silver carp than *Bosmina* whose phenomenology could not be correlated to any environmental factor. The type of movement of the different species also might influence success of predation by fish.

In addition to the modelling study of Schalau et al. (2008), who showed temperature as a key factor for variability in *Daphnia* phenology mainly enhancing *Daphnia*-timing, we presented data from a case study unfolding also nutrients and mortality by predators as second strongest predictor for plankton phenology in the field. Especially the positive effect of temperature on timing and peak biomass can change to a negative interaction at too high mortality levels, even amplifying the loss of zooplankton biomass and the delay in its timing. In conclusion, the study gave an insight into the reasons why results regarding plankton phenology and climate change at other lake sites were so inconsistent and outcomes of climate change were hard to predict or showed unexpected patterns e.g. warming destabilising plankton populations in one lake (Wagner & Benndorf 2007) or stabilising it in another (Wagner et al. 2012). As already proposed by Sweetman et al. (2008) not only direct temperature effects matter, but also trophic state and the structure of the food web.

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4 Mechanisms which favor the freshwater diatom *Aulacoseira subarctica* during climate change

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Abstract

Climate change induces alterations of the thermal structure in lakes. These alterations were shown to be responsible for shifts in the species composition of phytoplankton at many sites through a cascade of direct and indirect interactions. As an example, in the Saidenbach reservoir an increase of diatoms during the past three decades and a shift of the dominant diatom *Asterionella formosa* to *Aulacoseira subarctica* was observed in spring. However, compared to other diatoms in the reservoir, *A. subarctica* showed peaks in spring and autumn with very high abundances below the mixing depth. The hypolimnetic peak in autumn was located in the aphotic zone and can not had been resulted from sedimentation due to the lack of an epilimnetic population. This unusual pattern can not be explained by a common selection of species coping with stronger stratification stabilities and reduced mixing. We hypothesised that (i) *A. subarctica* can use lower light intensities than other diatoms shortly after ice break up or (ii) has heterotrophic capabilities or (iii) is favoured by easier resuspension. Besides field sampling, controlled experiments were conducted to estimate temperature and light dependend growth, sedimentation and resuspension traits. A one-dimensional model was developed to synthesise all findings. The experients revelead that *A. subarctica* does not perform higher growth rates compared to the diatoms *A. formosa* and *F. crotonensis* and most likely is not able to heterotrophic growth at light limiting conditions. However, the species was resuspended at aprox. 50 % lower shear forces compared to other diatoms. Sediment counts and simulation results which reproduced the pattern suggest that *A. subarctica* is translocated by sediment focussing. Sediment focussing also can explain the occurrences close above the lake bottom. Refocussing positions resting stages on top of the sediments or keeps cells resuspended in the hypolimnion. Ultimately, shortly after ice break up *A. subarctica* will be the first species with an high inoculum providing the neccessary advantage to outcompete other species in spring.

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4.1 Introduction

Diatoms are common and abundant in phytoplankton of freshwater lakes (Reynolds 2006). They have silicificated cell walls (Volcani 1981) which make the cells relatively heavy and cause fast sinking (Smol et al. 1984). Therefore, pelagic diatom species require sufficient turbulent mixing to stay suspended in the water column (Huisman et al. 2004) and often have their peaks in spring when these conditions are matched due to the spring overturn (Reynolds 1984a; Sommer et al. 1986). The thermal regime in lakes of the northern hemisphere is changing due to global warming, which can reduce spring mixing by stronger temperature gradients between upper and lower water layers. Winder et al. (2009) and Winder & Sommer (2012) found that at these conditions small, centric diatoms such as *Cyclotella* are positively selected.

In the German drinking water reservoir Saidenbach an increase of diatoms in spring could be observed since 1990. Thereby, the dominant species of the diatom community shifted from *Asterionella formosa* to the centric species *Aulacoseira subarctica* (Horn 2003b; Horn 2008; Horn et al. 2011). However, the species grows in filamentous colonies and does not seem to be especially adapted to stay in suspension near the water surface to gain maximum possible light intensities also at reduced mixing conditions, since it occurs mainly below the mixing depth. Causes for this species shift on the one hand are supposed to be a re-oligotrophication of the reservoir since 1990. The phosphorous optimum of *A. subarctica* is lower than for the more common species *A. formosa* and *Fragilaria crotonensis* which usally indicate meso- and eutrophic conditions (Anderson et al. 1997). On the other side, winters got milder with a shorter period of ice cover. As a consequence, spring full circulation elongated (Horn et al. 2011). These direct consequences of climate warming have also been found to support increases of *Aulacoseira* in Scandinavian lakes (Sorvari & Korhola 1998; Weyhenmeyer et al. 2008).

However, the unusual spatial pattern of *A. subarctica* in Saidenbach reservoir with high abundances in the aphotic zone of the hypolimnion in spring and autumn remain unexplained. In this study, three possible hypotheses were investigated: (i) *A. subarctica* is adapted to low light and might be able to use lower light intensitites in spring more efficiently than other species. (ii) The species might be able to outperform other species by mixo- or heterotrophic abilities. (iii) *A. subarctica* might profit from sediment focussing, explaining its occurance in deep water layers. Furthermore, if the cells reside on the top of the sediment, they would have the advantage of an higher inoculum shortly after onset of mixing.

For testing these hypotheses, two strains of *A. subarctica* were isolated from the reservoir. Experiments to measure growth rates in dependence of light and temperature and experiments to test heterotrophic and mixotrophic growth were performed. To investigate the sediment refocussing hypothesis, sedimenation and resuspension behaviour was measured under controlled conditions. Abundances of all relevant species were determined from water and sediment surface samples. For synthesis, a one-dimensional process modell using the parameters from the experiments for growth, loss and resuspension processes was developed.

4.2 Methods

4.2.1 Study site

The drinking water reservoir Saidenbach is located in the Erzgebirge mountain range in the southern part of Saxony, Germany (N 50.733°, E 13.223°, 438 m a.s.l.). The catchment has a size of 60.8 km^2, is densely settled and mainly used by agriculture. About 19 % of the catchment area is forested. The mean temperature and annual precipitation of the region are 7 °C and 830 mm, respectively. At its maximum water level the reservoir has an area of 1.46 km^2, a volume of 22.4×10^6 m^3, a maximum depth of 48 m and a mean depth of 15.3 m.

The artificial lake is dimictic and has been subject to limnological studies since 1975, now offering long run data sets with respect to hydrology, meteorology, chemistry, and biology (Horn et al. 2006). At the end of the 1970s the reservoir eutrophicated, due to an increasing external load of phosphorus, resulting in a reduction of the water quality with high phytoplankton abundances and summer blooms of cyanobacteria (Horn & Uhlmann 1995). After German reunification in 1990, the external P-loads were reduced to a mesotrophic level again. However, until now this did not have notable impacts on the mean annual phytoplankton concentration in the reservoir (Horn 2003b).

4.2.2 Sampling of phytoplankton and phytobenthos

In 2009 samples for phytoplankton and phytobenthos counting and identification were collected weekly or biweekly. At each sampling date, water samples were collected with a Ruttner-sampler from 9 to 10 representative depths at the deepest point of the reservoir (Fig. 4.1) and perserved with acidic iodine-potassium iodide solution (van Tümpling & Friedrich 1999). Sediments were sampled with a sediment corer (UVITEC) in 10 m, 20 m, and 30 m water depth along a transect in Reifland bay (Fig. 4.1). The first 5 mm of the sediment core surface were taken for phytobenthos analysis and fixated in 4 % formaldehyde. Adhesive sediments were treated with ten 1 s long impulses at 50 % power in a ultrasonic homogenizer (Sonoplus GM 70, BANDELIN electronic GmbH & Co. KG) prior to counting according to Thiel et al. (1975). Taxonomic phytoplankton identification and cell counts of species were analysed by using standard limnological methods according to Utermöhl (1958) & Höhn et al. (1998) and Krammer & Lange-Bertalot (2008). Means of phytoplankton cell concentrations were weighted by the sampling depths. Calculation of the mixing depth to divide the water column into epi- and hypolimnion followed Talling (1971)

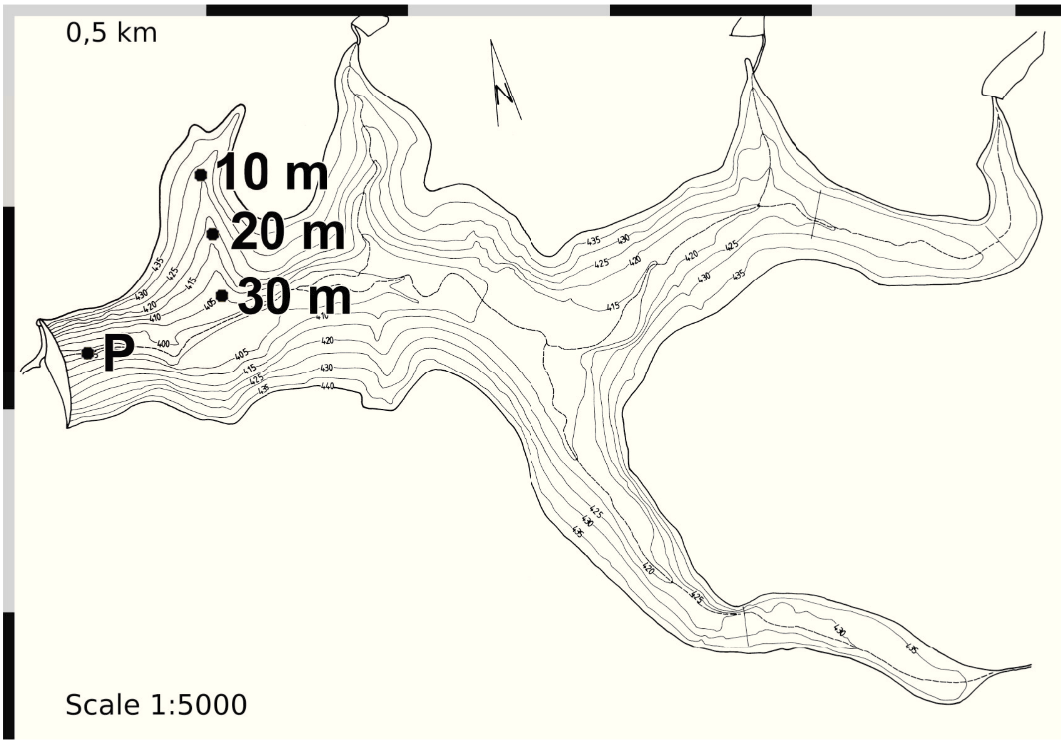


Figure 4.1: The Saidenbach Reservoir with the regular sampling point (P) at the deepest point close to the dam and the sampling points for sediment cores in 10 m, 20 m and 30 m depth.

and Horn et al. (2006). To analyse temporal and spatial anomalies, cell counts from sediments from different water depths were cross correlated with each other and with pelagic cell counts.

4.2.3 Phytoplankton strains

The laboratory experiments were carried out with non-axenic, monoclonal strains (Fig. 4.2). Two strains of *Aulacoseira subarctica* (P1B1 and P2A6) were isolated from the Saidenbach reservoir by microscopically picking single colonies with a glas pipette which was elongated using a Bunsen burner and washing them 5 times in sterile medium. A strain of *Asterionella formosa* was isolated previously from the Saxonian Klingenberg reservoir (Paetz 2009, SAG 2339) and a strain of *Fragilaria crotonensis* (SAG 28.96) was obtained from the SAG culture collection (`http://epsag.uni-goettingen.de`).

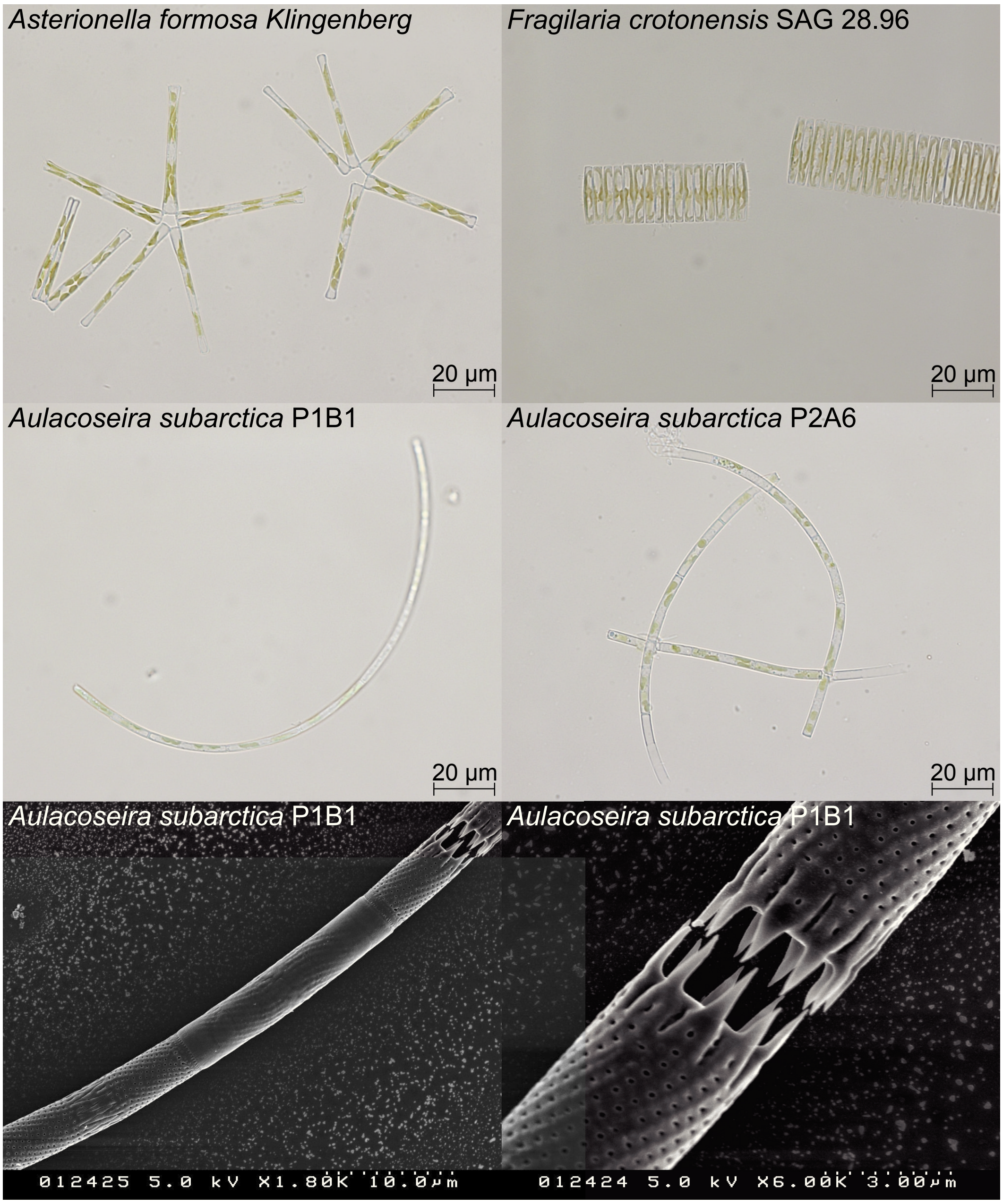


Figure 4.2: Light microscope (upper 4 pictures) and scanning electron microscope pictures (bottom) of the used diatom strains.

4.2.4 Photoautotrophic growth along temperature and light gradients

Light and temperature dependence of photoautotrophic growth was analyzed for the three diatom species simultaneously in the range of six light intensities from 5.9 µmol m^{-2} s^{-1} to 111.2 µmol m^{-2} s^{-1} at four temperatures from 3.0 °C to 18.3 °C. The experiments were carried out in batch-cultures with a volume of 40 mL on orbital shakers at 100 rpm and a light dark rhythm of 12 : 12 hours. The culture medium was BA50 (Fairburn et al. 1987) enriched with the vitamins biotin, cyanocobalamin and thiaminhydrochlorid according to Kilham et al. (1998). Cultures were adapted to the temperature of the experiments at an irradiation of 70 µmol m^{-2} s^{-1} for at least 5 days. The experiments were inoculated with 40 000 cells L^{-1}. For 10 days or until stationary growth phase was reached, 1 mL culture medium was removed every day from each batch. The algeal biomass was measured fluorometrically as the maximum fluorescence in the wavelength range between 625 nm to 725 nm at an excitation wavelength of 436 nm (Luminescens-Spectrometer LS 50B, Perkin-Elmer). Static quenching effects in dense cultures due to reduced fluorescence by self shadowing were corrected by means of Stern-Volmer-constants determined in dilution series (k_{vs} of *A. formosa* = 0.00218, *F. crotonensis* = 0.00318, *A. subarctica* = 0.00269, Stern & Volmer 1919). A linear model was fitted to the log transformed data from the exponential growth phase so that the slope of the model was equivalent to the specific growth rate at each temperature and light intensity. A multiplicative four parametric growth model with light and temperature as explanatory variables was fitted to the specific growth rates. The model described the relation between temperature and growth rate as linear what was sufficient for the investigated temperature range. The relation between light and growth rate was assumed to follow the non-linear Steele's-model (Steele 1962; Soetaert & Herman 2008) which included photoinhibition:

$$\mu = \mu_{max} \cdot \left(\frac{I}{I_{opt}} \cdot \exp\left(1 - \frac{I}{I_{opt}}\right) \right) \cdot (a \cdot T + b) \tag{4.1}$$

with the maximum specific growth rate μ_{max}, irradiation I, optimal irradiation I_{opt}, temperature T, and the parameters a, b for temperature dependence.

4.2.5 Heterotrophic growth

Potential heterotrophic or mixotrophic growth was investigated for the two strains of *A. subarctica* by enriching the culture medium with 10 g L^{-1} glucose (Tan & Johns 1996). The incubation was conducted as described before, but at a constant temperature of 18 °C under the three light intensities: no light, 4 and 70 µmol m^{-2} s^{-1}. Growth was measured by microscopic cell counts.

4.2.6 Measurement of settling velocities

Settling of the three diatom species was characterized using a sedimentation chamber (diameter: 15 cm; height above the sample outlet: 53 cm) according to Ripl & Uhl (2010). The chamber was filled with cultures from exponential growth phase, grown in BA50 medium in 0.3 L to 3 L Erlenmeyer flasks at $70\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$ and a light dark rhythm of 12 : 12 hours at 18 °C. The cultures were diluted 1:30 with ultrapure water according to the suspension method of DIN 66111 (1989) to a maximum of $10\,000\,\text{cells}\,\text{ml}^{-1}$ to keep particle-interactions neglectible (< 0.02 Vol. %, Stieß 1995). The sedimentation took place in a climatized room at 25 °C and in the dark to avoid cell proliferation.

Samples were taken from the chamber every 30 min (*F. crotonensis*) or every 50 min (*A. formosa*, *A. subarctica*) for a period of 2 d to 3 d by an automated particle counter (Abakus mobil fluid, Markus Klotz GmbH), which was calibrated to differenciate 32 logarithmic size classes from 3.2 µm to 139 µm. Sample volume for rinsing and measurement was 30 ml in total for each sampling time. Microscopic evaluation and viability tests for the cells were performed before and after the sedimentation experiment. No significant differences were found in viablity, length, width or biovolume of the cells between start and end of the experiments, indicating constant conditions and only negligible influence of the ultrapure water and darkness onto the cells during the experiment. The only effect was that a small amount of *A. subarctica* cells began transforming into resting stages. Sedimentation experiments were performed at least twice for each species and the particle size spectra for these replicates were confirmed to be comparable.

The particle counter records diameters equivalent to the projection area of particles. Phytoplankton cells pass the sensor in different states of rotation, hence, measured particle spectra differ considerably from microscopic assesment of particle sizes (Paetz 2009). Therefore, size spectra recorded by the particle counter were transformed using the cumulative distribution function of microscopic counts. After transformation, diameters represented equivalent diameters of spheres with the same volume of the original cells or colonies.

Mean settling velocities were calculated for each size class the counter captured. The velocity was determined on the basis of particle concentration changes over time. The calculations also accounted for the decreasing volume in the sedimenation chamber due to cyclical sampling of the counter. For each size class j, the relative particle concentration c_j (relative to the starting concentration) was fitted to a function of time t and the remaining sedimentation distance s. To account for different sedimentation patterns, a flexible three-step-function with 7 parameters ($p_1..p_7$) was fitted by non-linear regression (Fig. 4.3):

$$c_j(x) = p_1 \tanh\big(p_2(x - p_3)\big) + p_4 \tanh\big(p_5(x - p_6)\big) + p_7 \tag{4.2}$$

with $x = t$ or $x = s$. The barycenter of the functions $c_j(t)$ and $c_j(s)$ represent the mean settling velocities $\bar{t}_j$ and mean settling distances $\bar{s}_j$ weighted by particle concentration. For integration t_{end} and s_{end} were defined as times, when the a particle concentration of $c_j = 0.2$ was reached; that means when 80 % of the particles of a size class were settled:

$$\bar{t}_j = \frac{\int\limits_{t_0}^{t_{end}} t \cdot c_j(t)\,\mathrm{d}t}{\int\limits_{t_0}^{t_{end}} c_j(t)\,\mathrm{d}t} \tag{4.3}$$

$$\bar{s}_j = \frac{\int\limits_{s_{end}}^{s_0} s \cdot c_j(s)\,\mathrm{d}s}{\int\limits_{s_{end}}^{s_0} c_j(s)\,\mathrm{d}s} \tag{4.4}$$

Finally, the mean settling velocity $\bar{v}_{mean,j}$ for each particle size class j was calculated as:

$$\bar{v}_{mean,j} = \frac{\bar{s}_j}{\bar{t}_j} \tag{4.5}$$

4.2.7 Modelling settling velocities

Settling of diatom colonies due to gravity ($g = 9,8081\mathrm{m\,s^{-2}}$) was described similarly to the settling of inert particles in viscous liquids according to Stokes (1851). The velocity (w_s) of a sinking particle depends on diameter (d) and the density difference ρ_c of the particle related to the density of the surrounding medium ρ_w:

$$w_s = \frac{gd^2(\rho_c - \rho_w)}{18\eta} \tag{4.6}$$

This only is valid for very small particles with a Reynolds number of $Re < 0,1$ or with an error of 10 % for $Re < 0,5$ according to McNown & Malaika (1950). Phytoplanktonic organism also differ in shape from a spere. Because of that, Stoke's equation needed to be modified by introducing a shape factor φ_r:

$$w_s = \frac{gd^2(\rho_c - \rho_w)}{18\eta\varphi_r} \tag{4.7}$$

Reynolds (2006, S. 49ff) defined the shape factor as quotient of measured settling velocity w_s and of the calculated one $w_{s,calc}$:

$$\varphi_r = \frac{w_{s,calc}}{w_s} \tag{4.8}$$

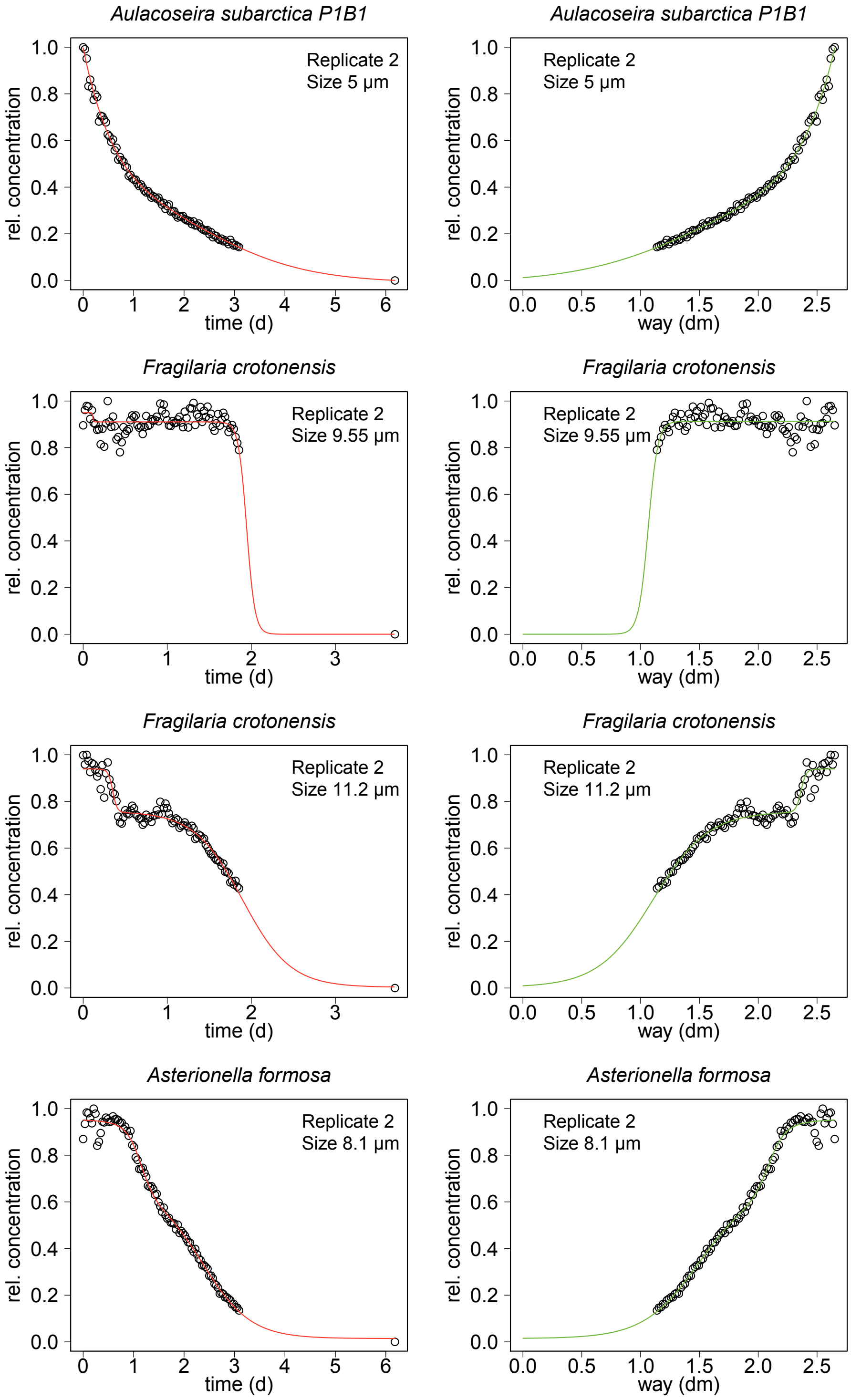


Figure 4.3: Examples for the fit of the three-step-function to raw sedimentation data.

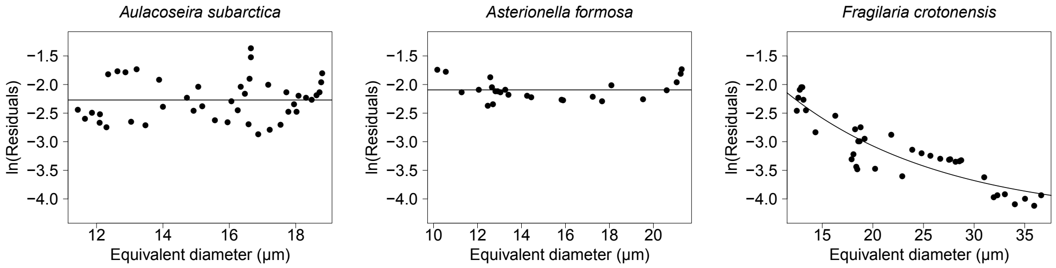


Figure 4.4: Residuals after substraction of calculated settling velocities according to Stoke's equation from measurements; lines show the model fit.

The shape factor in our study was estimated from the residuals $\ln r$ of the log-transformed settling rate:

$$\ln w_s = \ln r + \ln w_{s,calc} \tag{4.9}$$

To calculate the settling velocities $w_{s,calc}$ using Stoke's equation (Eq. 4.6) density values for the diatom species were retrieved from Reynolds (2006) (Tab. 4.1).

For *A. subarctica* and *A. formosa* it was sufficient to assume a constant form factor equal to the mean of the residuals (Fig. 4.4):

$$\ln r = p_1 \tag{4.10}$$

$$w_s = \frac{e^{p_1} \cdot gd^2(\rho_c - \rho_w)}{18\eta} \tag{4.11}$$

For *F. crotonensis* it was found that the form factor varied in dependence of colony size. Hence, a exponential equation was fitted to the residuals (Fig. 4.4):

$$\ln r = p_1 \cdot e^{(d-p_2)\cdot p_3} + p_4 \tag{4.12}$$

Table 4.1: Density of diatoms.

Species	Density	Source
A. subarctica	$1209.5\,\mathrm{kg\,m^{-3}}$	Reynolds (1984b)
A. formosa	$1183\,\mathrm{kg\,m^{-3}}$	Wiseman et al. (1983)
F. crotonensis	$1196\,\mathrm{kg\,m^{-3}}$	Reynolds (1984b)

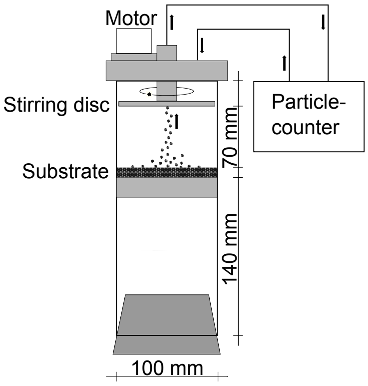


Figure 4.5: Experimental set up of the erosion chamber with connected particle counter.

In summary, settling velocity for *F. crotonensis* was calculated as:

$$\begin{aligned} w_s &= \frac{\hat{p}_4 \cdot \hat{p}_1^{\hat{p}_{2,3}} \cdot g d^2 (\rho_c - \rho_w)}{18\eta} \qquad (4.13) \\ \text{with } \hat{p}_4 &= e^{p_4} \\ \hat{p}_1 &= e^{p_1} \\ \hat{p}_{2,3} &= e^{(d-p_2)p_3} \end{aligned}$$

Settling velocities in the field were calculated based on these equations and the mean colony size per sampled depth at the date of sampling.

4.2.8 Resuspension

The resuspension behavior was analyzed by determining the critical shear velocity for resuspension of the diatoms from a fine sand surface (grain size: 80 µm to 250 µm). An erosion chamber according to Gust (1990) was used in which cultures of the diatom strains were given and sedimented within 48 hours. In order to use the calibration parameters from Gust (1990), the stirring disc had to be kept 7 cm above the sediment surface. The erosion chamber was driven as a closed system, i.e. culture medium was pumped through it at a flow of 16 ml min^{-1} (Kleeberg et al. 2008). The calibrated microcosm creates a spatially homogeneous bottom shear velocity ($u*$). The bottom shear velocity was increased every 6 min incrementally. The diatoms resuspension was measured with a Abakus mobil fluid particle counter (Markus Klotz GmbH). For data analysis the particle concentration before the start of the experiment and a blank value from a chamber without diatoms was substracted from the measurments of particle concentrations in the chambers. The critical shear velocity for resuspension was estimated by averaging the two forces surrounding the resuspension event.

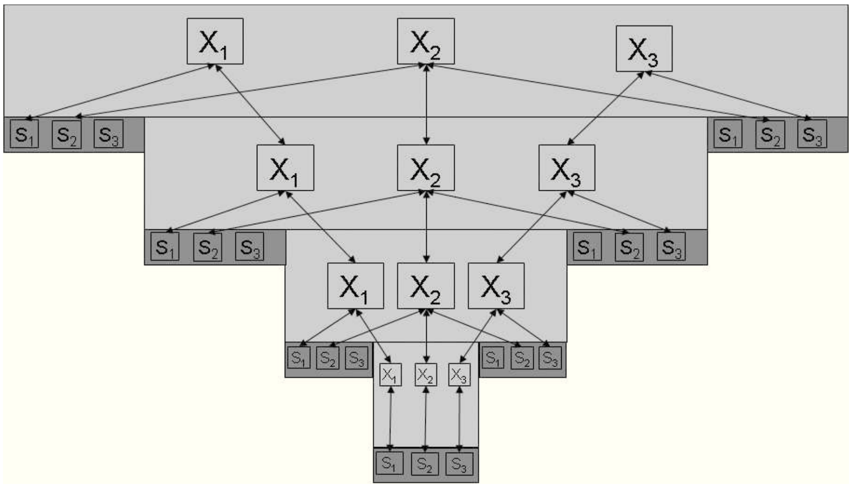


Figure 4.6: Schematic representation of the diatom process model and structuring in vertical layers. All state variables are simulated in each layer. There is an exchange of matter between the layers as well as between the water layer and the sediments.

4.2.9 One-dimensional model for diatoms

To summarize the findings of the experiments a one-dimensional model of Saidenbach reservoir was developed. The model enables to determine the impact of single processes on the pattern of occurance of the different diatom species so that the model can be used to test the hypothesis that *A. subarctica* profits from sediment focussing after warm winters.

The vertically one-dimensional resolved model includes six state variables: three states for different species of diatoms in the pelagial ($X_{1,2,3}$) and three states for corresponding concentrations stored in the sediment ($S_{1,2,3}$).

The water column was vertically divided in layers of 1 m height but with variable widths (Fig. 4.6). The difference of the areas from one layer to an other was defined as sediment area. The layer sizes followed the hypsographic curve of Saidenbach reservoir. All states were simulated in each layer and an exchange of matter between the layers as well as between the water layer and the sediments was allowed by turbulent diffusion, sedimentation or resuspension. Daily light intensities and temperature profiles of the year 2009 were used as abiotic forcing data. All model parameters are given in Tab. 4.2.

The partial differential equations for the mass balances of the three phytoplankton species in the pelagial X_i and in the sediment S_i were solved as ordinary differential equations by the method of lines approach (subdivision of the model in fixed layers). Integration was performed using the R-add on package deSolve (Soetaert et al. 2010) and the lsoda algorithm for stiff and non-stiff systems (Hindmarsh 1983).

$$\frac{\mathrm{d}X_i}{\mathrm{d}t} = growth_i + diffusion_i + resuspension_i - sedimentation_i - mort_i \tag{4.14}$$

$$\frac{\mathrm{d}S_i}{\mathrm{d}t} = sedimentation_i - resuspension_i \tag{4.15}$$

Logistic growth with a common carrying capacity K for all species was applied. The growth rates μ_i for each species was calculated according to equation 4.1 in dependence of light and temperature:

$$growth_i = \mu_i \, X_i \left(1 - \frac{\sum X_i}{K}\right) \tag{4.16}$$

To account for losses due to grazing and respiration mortality rates were calculated in dependency of the available photosynthecically active radiation (PAR_z) in euphotic $p_{mort,light}$ and under dark conditions $p_{mort,dark}$:

$$mort_i = \begin{cases} p_{mort,light,i} \cdot X_i & \text{if } PAR_z \geq 0.01 \, I_{opt} \\ p_{mort,dark,i} \cdot X_i & \text{if } PAR_z < 0.01 \, I_{opt} \end{cases} \tag{4.17}$$

Sedimentation from one layer in a lower one or into the sediment happened at the layer contact area according to the transport-reaction equation for lakes (cf. Soetaert & Herman 2008). Settling velocities were taken from section 4.2.7.

In the interest of simplicity, we assumed a constant eddy diffusion coefficient in the epilimnion $K_{v,epi}$ and in the hypolimnion $K_{v,hypo}$ for usage in the transport-reaction-equation.

$$K_v = \begin{cases} K_{v,epi} & \text{if } z \leq z_{mix} \\ K_{v,hypo} & \text{if } z > z_{mix} \end{cases} \tag{4.18}$$

Resuspension from the sediment was described by a constant import rate of $0.1\,\mathrm{d}^{-1}$, when the threshold for the critical shear velocity was exceeded. Shear velocity was modelled pragmatically in relation to mixing depth z_{mix}:

$$u* = \begin{cases} 0.5 & \text{if } z \leq z_{mix} \\ 0.25 & \text{if } z_{mix} < z < 1.8 \, z_{mix} \\ 0 & \text{if } z \geq 1.8 \, z_{mix} \end{cases} \tag{4.19}$$

Table 4.2: Parameters for the 1D-diatom process model.

Parameter				
Capacity K (cells/m^3)	7×10^9			
$K_{v,epi}$ (m^2 d^{-1})	20			
$K_{v,hype}$ (m^2 d^{-1})	0.2			
Extinktion coefficient ϵ (m^{-1})	0.35			
layer height dz (m)	1			
		X_1	X_2	X_3
μ_{max} (d^{-1})		0.25	0.76	0.8
I_{opt} (μE m^{-2} s^{-1})		50	64.35	71.37
a		0.4	0.31	0.2
b		0.035	0.04	0.043
settling velocity v_{sed} (mm h^{-1})		5	15	10
$p_{mort,light}$ (d^{-1})		0.05	0.05	0.05
$p_{mort,dark}$ (d^{-1})		0.12	0.12	0.12
$u{*}_{krit}$ (cm s^{-1})		0.2	0.4	0.4
entrainment rate $r_{entrain}$ (d^{-1})		-0.1	-0.1	-0.1

4.3 Results

4.3.1 Phytoplankton and phytobenthos abundance in the field

In 2009 the diatoms in Saidenbach reservoir showed a characteristic development, with a mass development in spring and autumn (Fig. 4.7). The most dominant species was *A. subarctica*, followed by *F. crotonensis*, *A. formosa* and by the group of centric diatom genera *Cyclotella* and *Stephanodiscus*. Other diatom species contributed only minor to total cell count and biomass.

The dominant diatom species differ in their pelagic and benthic pattern. The pelagic occurrence of *A. subarctica* (Fig. 4.7) started from low under-ice abundances. After breakup of the ice cover and onset of spring overturn on 18th May 2009 cell concentrations rose considerably. At the beginning of the spring peak, abundances of *A. subarctica* were highest directly above the bottom of the reservoir. The species diminished from the epilimnion shortly after onset of summer stratification but persisted with increasing abundances in the meta- and hypolimnion. The peak continuously translocated into higher depths until the species was not present in the water column any more during summer. With increasing mixing depth in autumn a strong occurrence in the meta- and hyplimnion developed with a maximum above the bottom. Continuously a mixing into the epilimnion was observed from October to November. At full circulation in December *A. subarctica* was homogenously distributed.

Related to the timing of its mass developments*A. formosa* showed a similar pattern like *A. subarctica* (Fig. 4.7). As an important difference, however, the increase of

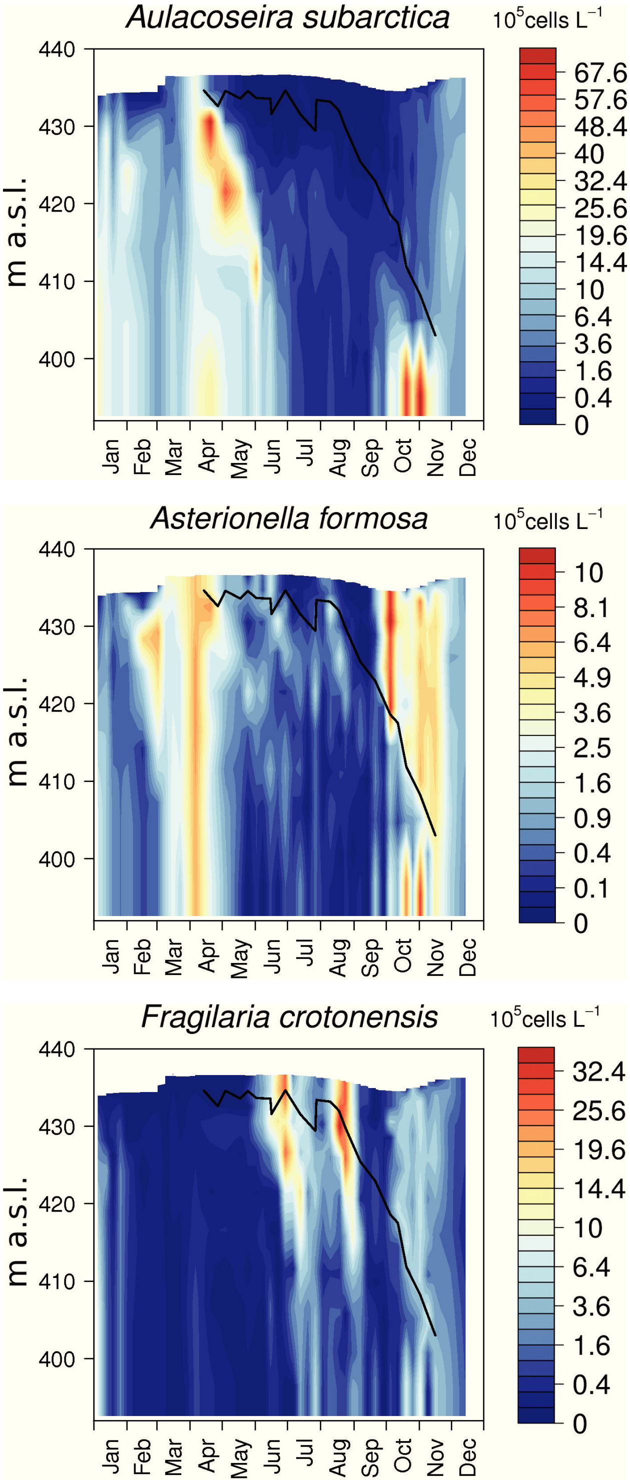


Figure 4.7: Pelagic pattern of the dominant diatom species in the field. Black lines show the position of the calculated mixing depth. Contour plots are based on 315 counted probes, that were smoothed in space and time for plotting.

abundance after ice-out did not start from the bottom of the lake but started in euphotic depths. *A. formosa* dissappeared much faster after the onset of summer stratification but showed several short term occurrences below the mixing depth during summer. In contrast to *A. subarctica*, *A. formosa* started growing in the epilimnion when mixing depths increased in autumn and occurred above the lake bottom only after that.

The pattern of *F. crotonensis* was different from the other two species (Fig. 4.7). The species was not observed in spring but in two epi- and metalimnetic time periods during sommer stagnation. Shortly before its development, a short term increase of mixing depth occurred. A translocation by sedimentation of cells to higher depths was observed. Abundance during autumn was low. On 6th July 2009 and 31st August 2009 a strong infection of the colonies of *F. crotonensis* with parasitic Chytridiomycetes was observed. This coincided with the end of the mass development.

The benthic emergence of the diatoms depended on mixing depth and pelagic appearance (Fig. 4.8, 4.9). *A. subarctica* decreased after the beginning of the summer stagnation. The decrease of the benthic cell abundance correlated with the pelagic decrease (Fig. 4.8 top). In autumn the benthic abundance increased together with increasing mixing depth. Maximums of the benthic peaks were observed 3 to 4 weeks before the mixing depths reached the corresponding depths. This observation is supported by the cross correlations, which show that the maximum in 10 m and 20 m depths was 42 or 28 days earlier than in 30 m depth (Tab. 4.3). In autumn, the pelagic abundances increased after the benthic increase in 10 m and 20 m water depth. Also in 30 m a significant increase of *A. subarctica* was observed 14 days before the pelagic increase (Fig. 4.9 bottom left).

In contrast to that, *A. formosa* did not show any time shift between benthic and pelagic emergence (Fig. 4.8). The correlation of benthic appearance at 10 m depth 28 days before the peak in autumn (Tab. 4.3), can be explained by lower sedimentation in 10 m compared to higher depths because of very high mixing depths and strong

Table 4.3: Cross correlations (CCF) between cell abundances of different watewr depths from where sediment was sampled and between benthic and pelagic cell abundances.

Sediment ~ Sediment			Sediment ~ Pelagial		
Correlation	Lag (d)	CCF	Correlation	Lag (d)	CCF
A. subarctica 10 m ~ 20 m	-14,00	0,55	*A. subarctica* 10 m ~ Pelagial	-70,00	0,38
A. subarctica 10 m ~ 30 m	-42,00	0,41	*A. subarctica* 20 m ~ Pelagial	-42,00	0,68
A. subarctica 20 m ~ 30 m	-28,00	0,67	*A. subarctica* 30 m ~ Pelagial	0,00	0,88
A. formosa 10 m ~ 20 m	0,00	0,88	*A. formosa* 10 m ~ Pelagial	-28,00	0.50
A. formosa 10 m ~ 30 m	0,00	0,71	*A. formosa* 20 m ~ Pelagial	0,00	0,66
A. formosa 20 m ~ 30 m	0,00	0,91	*A. formosa* 30 m ~ Pelagial	0,00	0,90
F. crotonensis 10 m ~ 20 m	14,00	0,80	*F. crotonensis* 10 m ~ Pelagial	14,00	0,65
F. crotonensis 10 m ~ 30 m	0,00	0,63	*F. crotonensis* 20 m ~ Pelagial	28,00	0,44
F. crotonensis 20 m ~ 30 m	0,00	0,83	*F. crotonensis* 30 m ~ Pelagial	28,00	0,69

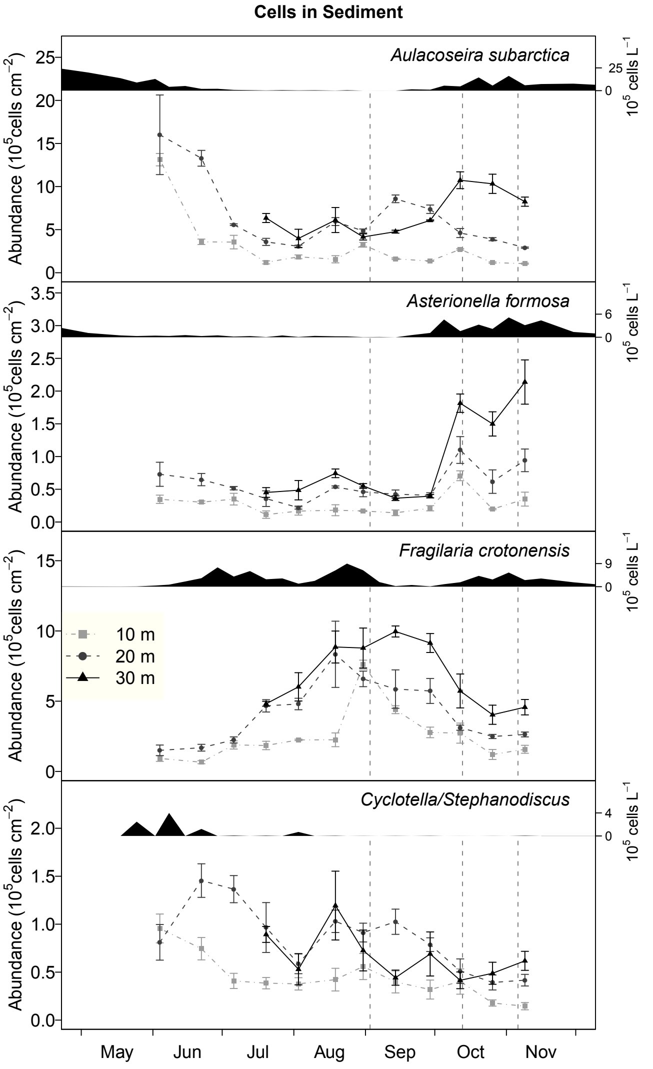
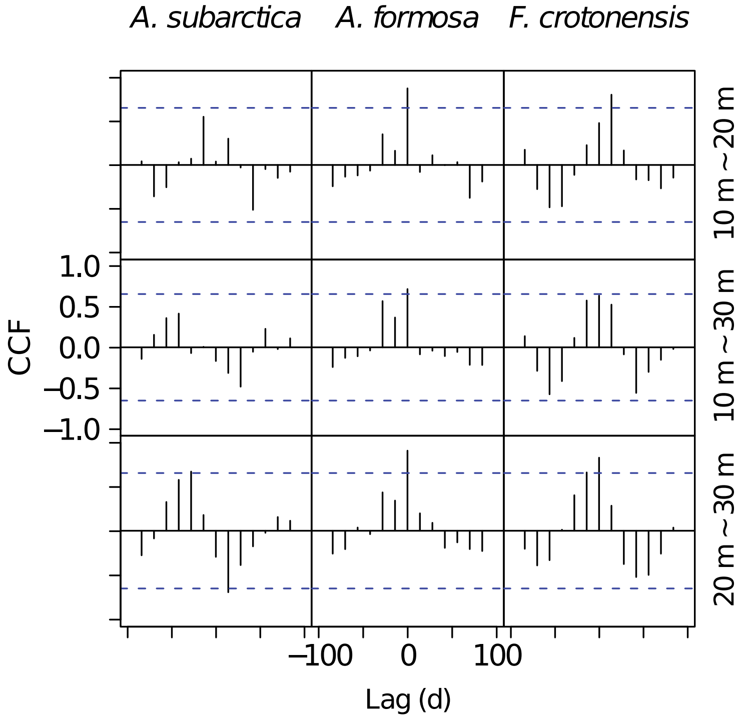


Figure 4.8: Benthic pattern of dominant diatoms in Saidenbach reservoir in 2009. For each of the three sampling depths of sediments the mean with sd (n=3) is shown. Polygons on the top show the mean of pelagic cell abundances. The encouters of the mixing depth in $10\,\mathrm{m}$, $20\,\mathrm{m}$ and $30\,\mathrm{m}$ is indicated by the vertical lines.



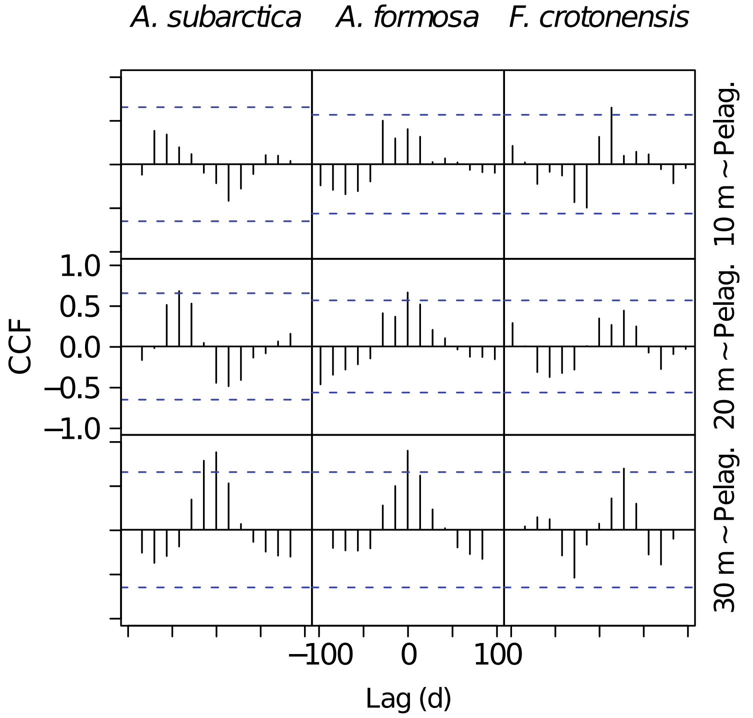


Figure 4.9: Cross correlaton coefficients (CCF) of cell abundances between different water depths from where sediment was sampled (top) and between abundances in sediment and pelagial (bottom). Blue dashed lines are the $95\,\%$ confidence intervall.

resuspension. The benthic abundance of *A. formosa* was higher in deeper depths as it was observed for *A. subarctica* too.

F. crotonensis occured in the benthic zone after its pelagic development with a time delay of 14 and 28 days, depending on depth (Tab. 4.3).

4.3.2 Light and temperature dependence of photoautotrophic growth

The photoautotrophic growth of the diatom strains showed a clear dependence on light and temperature (Fig. 4.10). A linear dependency of growth rates on temperature was found for all strains between 3 to 18 °C. The dependence on light could be described by Monod kinetics. However, *A. subarctica* showed an inhibition at high light intensities above 80 μmol m^{-2} s^{-1}. The light optimum of both *A. subarctica* strains was approximately 40 μmol m^{-2} s^{-1}. At 3 and 8 °C the light optimum for *A. formosa* (TS Klingenberg) and *F. crotonensis* (SAG 28.96) was also 40 μmol m^{-2} s^{-1}. However, at temperatures above 12 °C the light optimum was found to be higher than 80 μmol m^{-2} s^{-1}. The specific growth rates of the species differed considerably. The model fit estimates an advantage of *A. formosa* over a wide range of light intensity and temperature (Fig. 4.11 and Tab. 4.4). At high levels of light and temperature, *F. crotonensis* had higher specific growth rates. The specific growth rate of *A. subarctica* was lower than of *A. formosa* and *F. crotonensis* at most light-temperature combinations (Fig. 4.11). Only at the lowest light intensities and temperatures the growth of the *A. subarctica* strain P2A6 was higher than for *F. crotonensis.*

4.3.3 Heterotrophic growth with glucose as substrate

No heterotrophic or mixotrophic growth was observed for a mixed culture of the strains P1B1 and P2A6 of *A. subarctica.* Dark cultures developed chromatophore resting stages after 3 days. After 6 days a strong development of bacteria was observed.

Table 4.4: Parameters for the diatom growth model retrieved from experiments.

Species	Strain	μ_{max}	I_{opt}	b	a	r^2
A. subarctica	P1B1	0,223	45,346	0,590	0,030	0,352
A. subarctica	P2A6	0,297	48,733	0,254	0,047	0,836
A. formosa	Klingenberg reservoir	0,761	64,349	0,312	0,040	0,940
F. crotonensis	SAG 28.96	0,798	71,370	0,197	0,043	0,968

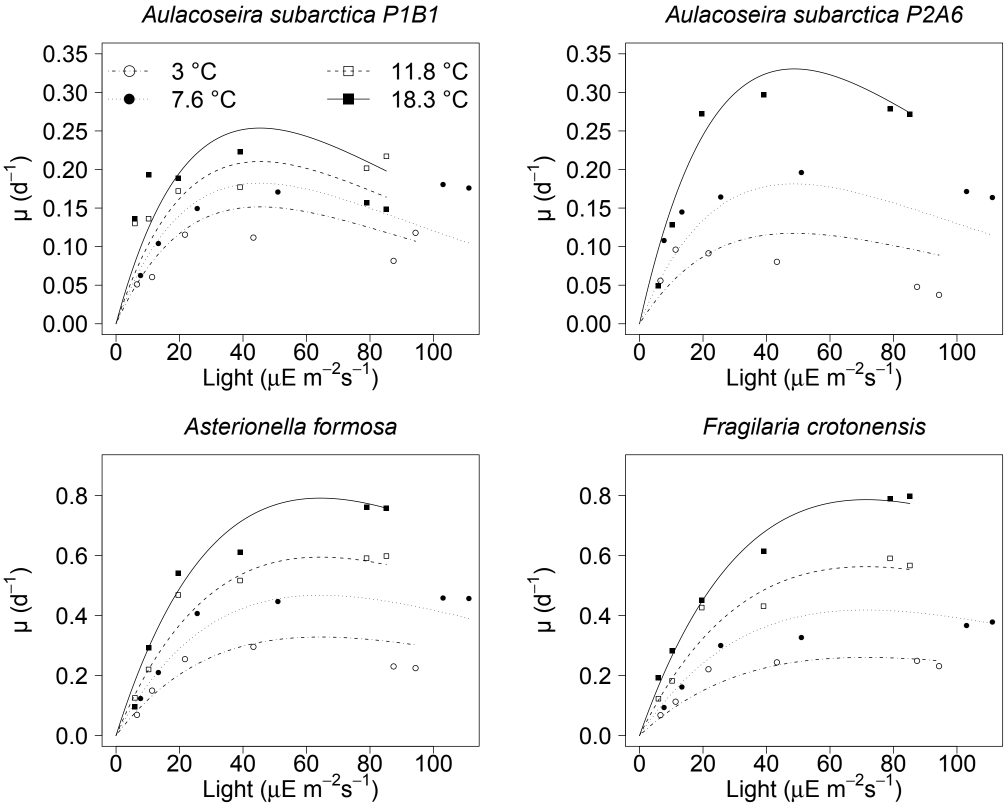


Figure 4.10: Measured and modelled growth of the diatom strains in dependence of light and temperature.

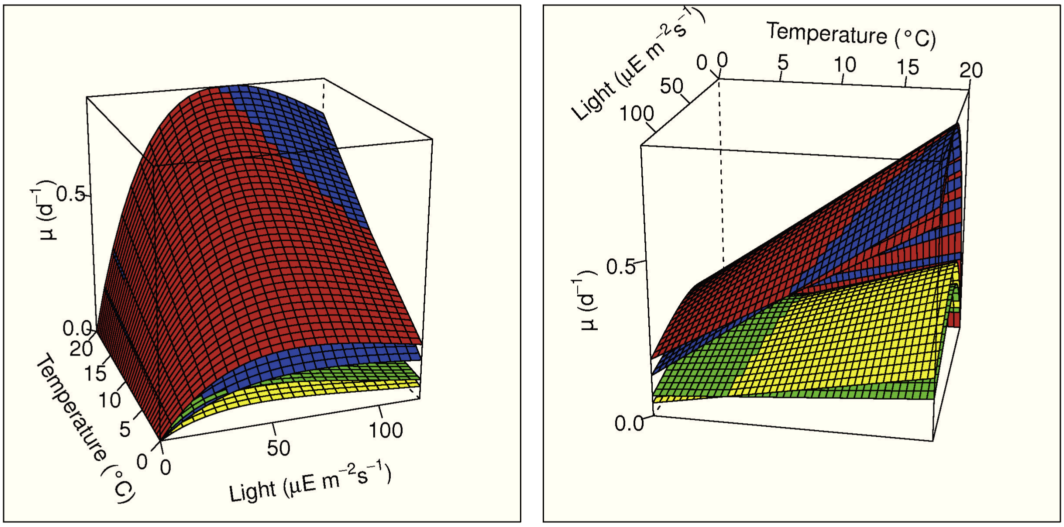


Figure 4.11: Growth differences of the diatom strains in dependency on light and temperature according to the growth model. The model is visualized from different viewing angels. 🟥 *A. formosa*, 🟦 *F. crotonensis*, 🟩 *A. subarctica* P1B1, 🟨 *A. subarctica* P2A6.

4.3.4 Differences in the sedimentation behavior

The two strains of *A. subarctica* and *A. formosa* revealed similar settling velocities with a constant form factor over the whole spectrum of size classes (Tab. 4.5, Fig. 4.12). The investigated strain of *F. crotonensis*, (SAG 28.96) however, had a variable form factor in dependence of colony size and a shallower slope of increasing settling velocities at increasing colony size (Fig. 4.12).

The application of the modified Stoke's equation to size spectra measured in the field showed that large and dividing colonies near to the water surface had large settling velocities, while the small colonies in larger depths had a slower settling speed. The highest velocities with $20\,\mathrm{mm\,h^{-1}}$ were reached by *A. formosa*. *A. subarctica* and *F. crotonensis* showed only half of these speeds, reaching $13\,\mathrm{mm\,h^{-1}}$ and $10\,\mathrm{mm\,h^{-1}}$, respectively.

4.3.5 Critical shear velocities for resuspension

The investigated diatom species showed different critical shear velocities which lead to resuspension from the substrate (Fig. 4.13). *A. subarctica* resuspended already at shear velocities of $0.2\,\mathrm{cm\,s^{-1}}$. To resuspend *A. formosa* and *F. crotonensis* shear velocity needed to be 75 % higher and to reach at least $0.35\,\mathrm{cm\,s^{-1}}$ (Fig. 4.13).

4.3.6 One-dimensional modelling results

To determine the influence of the resuspension and growth submodules of the diatom model, three scenarios were simulated: (i) no resuspension allowed, but growth, turbulence, sedimentation and mortality switched on; (ii) no growth but all other processes switched on; and (iii) a simulation including all processes. The model was initialised with mean cell counts from the field campaigns end of March 2009.

In the full scenarios, *A. subarctica* only grew in spring and was replaced afterwards by the other and faster growing species (Fig. 4.14 bottom). *F. crotonensis* and *A. formosa* peaked in summer and autumn. Summer maxima of *F. crotonensis* coincided wit maxima of water temperature (Fig. 4.14 bottom right). *A. formosa* showed its highest abundance in late spring (Fig. 4.14 bottom middle). In autumn the occurrence of *A. formosa* and *F. crotonensis* followed the sinking mixing depth.

Table 4.5: Parameters for the modified Stoke's equation.

Art	Stamm	p_1	p_2	p_3	p_4
A. subarctica	P1B1 and P2A6	-2,2704			
A. formosa	Klingenberg reservoir	-2,0933			
F. crotonensis	SAG 28.96	5,3699	-0,000002276	-64613,4	-4,3463

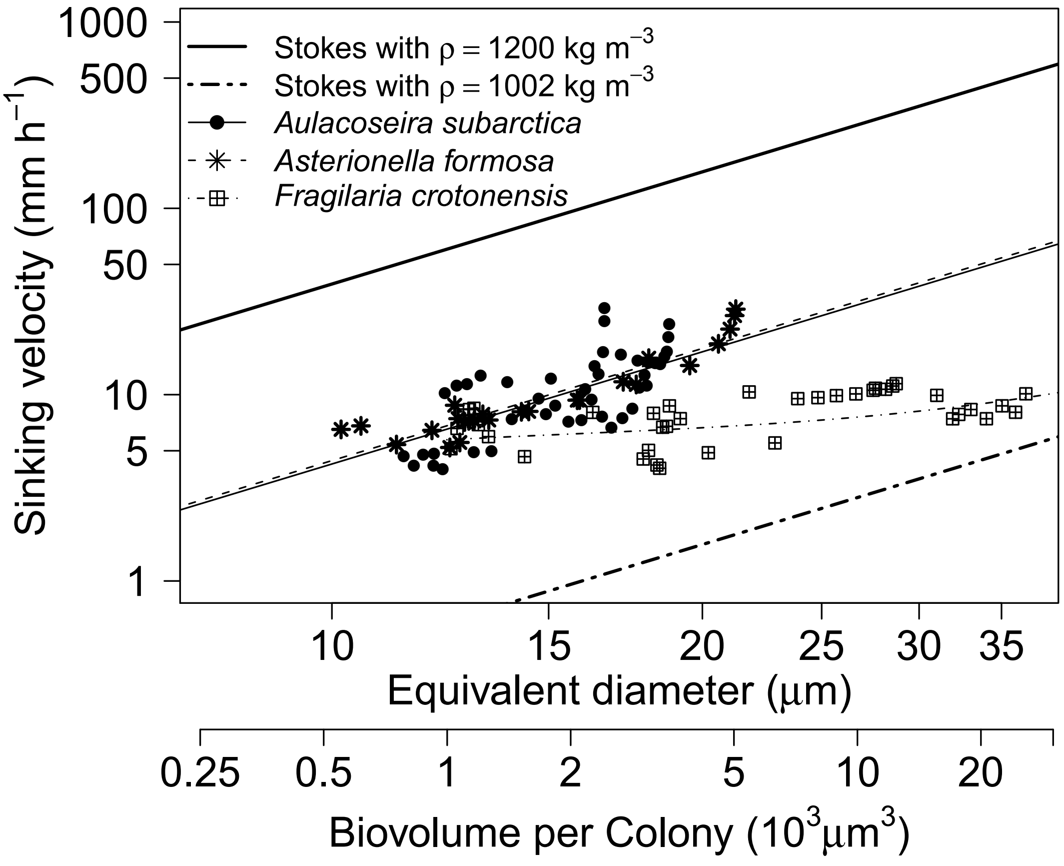


Figure 4.12: Settling velocities of the diatoms in comparison to predictions according to Stokes.

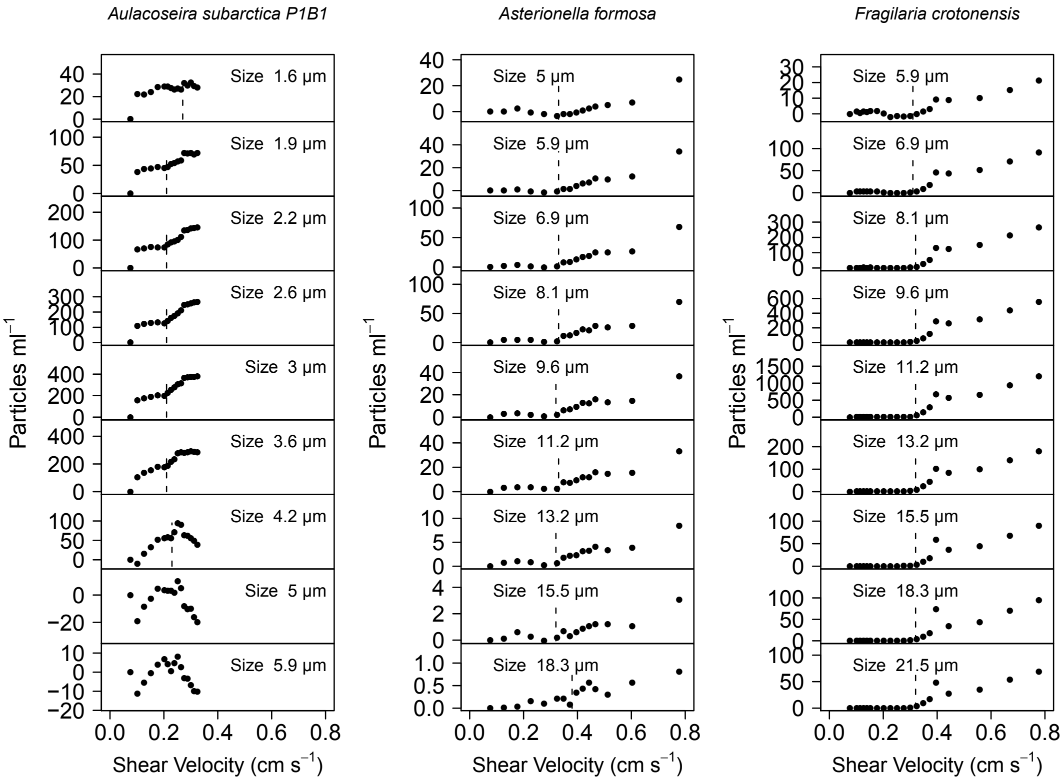


Figure 4.13: Crititcal resuspension velocities at the sediment for resuspension of the diatom strains.

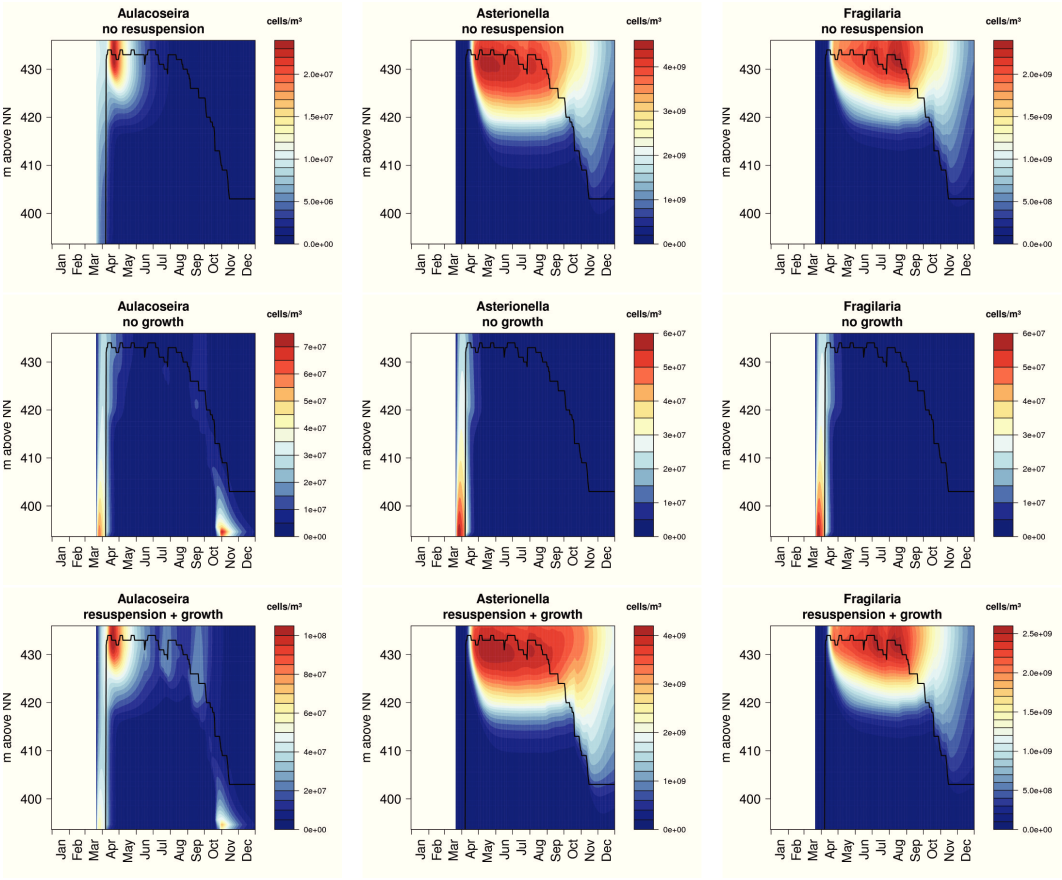


Figure 4.14: Simulation scenarios showing pattern of diatom occurrence. To disentangle effects of single processes, in the first row resuspension was switched off. In the middle row resuspension was allowed but growth was prohibited. The bottom row shows the full model with including all processes.

A resuspension of these two species was only simulated during full mixing events (Fig. 4.14 middle row). In contrast to that, resuspension of *A. subarctica* increased with increasing mixing (Fig. 4.14 middle row, left figure). The full scenario revealed that there is the possibility of slight *A. subarctica* growth in the euphotic zone in summer (e.g. July) after beeing resuspended during short term mixing events (Fig. 4.14 bottom left).

4.4 Discussion

4.4.1 Refocussing of sediment

A. subarctica, *A. formosa* and *F. crotonensis* were the dominant diatom species in Saidenbach reservoir in 2009. This is a typical composition for stratified, dimictic and mesotrophic lakes (Reynolds 2006, S. 332). The annual pattern of succession was in agreement with the PEG-model (Plankton Ecology Group of the SIL) (Sommer et al. 1986).

The basic life cycle of *A. subarctica* was already described by Lund (1954), Lund (1955), & Lund (1971) and are in agreement with the observations at Saidenbach reservoir. The species emergence is mainly influenced by turbidity and the species spents parts of its meroplanktic life cycle in the pelagic zone and partly as benthos in or on the surface of the sediment. Survival in aphotic depths is possible by resting stages which are produced below light intensities of $1.2\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ (Gibson & Fitzsimons 1990). These resting stages also had been found to persist several years in anoxic conditions in sediments up to a depth of 35 cm (Stockner & Lund 1970).

The time of survival as well as the number of resting stages of *A. subarctica* in sediments is higher than for *A. formosa* und *F. crotonensis* (Reynolds & Wiseman 1982; Reynolds et al. 1982). Both species often are recruted from individual cells with pelagic origin (Lund 1949). After the beginning of spring full circulation *A. subarctica* is transported into the whole water column by resuspension from the sediments. There the resting stages transform into the vegetative form. The abundance of resuspended cells is very high resulting in the observation of strong peaks. However, it seems that these peaks are not formed by high growth rates but merely by resuspension. The higher inocculum might give *A. subarctica* an advantage in spring against other diatom species such as *A. formosa* and species of the genera *Cyclotella* and *Stephanodiscus* what is supported by the findings of Horn et al. (2011).

Together with the onset of summer stagnation, epilimnetic temperatures rise and *A. subarctica* is outcompeted by other diatoms with higher growth rates. This was consistent with our measurements of growth rates and the modelling part. At this time, *A. subarctica* is settling and further growth might be possible in the photic zone of the pelagial and maybe also in the litoral. After reaching aphotic regions, resting stages are formed.

After that, *A. subarctica* is transported by sediment focussing into greater depths and is partly resuspended as was shown by cross-correlation analyses of the phytoplankton. Transport within the sediment to higher lake depths preceeds the arrival of mixing depth. Therefore, internal seiches can be assumed to be responsible for exceeding critical shear velocities as was shown for anorganic particles (Weyhenmeyer 1996). Refocussing of the sediments can be described as material which is sliding down a mountainside since cells do not originate from meta- or hyoplimnetic sedimentation (negative cross correlation lags), so they must orginate from higher sediments. Colonies during the observed hypolimnetic maximum of cell abundances at the bottom in autumn only originate from resuspension. During autumn full circulation, colonies are distributed homogenously in the lake and growth can be observed. In winter a proportion of *A. subarctica* will sink again under low turbulence conditions under ice while another part probably stays in suspension due to remaining convection as described by Kelley (1997) and Jewson et al. (2009) for the related species *Aulacoseira* *baikalensis*. Low settling velocities and the resuspension at relatively low shear forces due to the filamenteous form keeps *A. subarctica* at the top of the sediments or in suspension. This ability might support a high starting biomass after ice-out in the next year as discussed by Horn et al. (2011).

The different behaviour of the investigated diatom species can be explained by adaptations to different environmental conditions. *F. crotonensis* is often described to compete with cyanobacteria in summer (Horn 2003a). This is supported by our finding of high growth rates of *F. crotonensis* especially at high light intensities and high temperatures. According to Dauta et al. (1990) its optimum is 25 °C at high light availability, but *F. crotonensis* needs sufficiently high nutrient supplies with a high ratio of Si to P (Hartig 1987). We found unusually low sedimentation velocities for this species in respect to its colony sizes. This might be an indicator for adaption to epilimnetic summer conditions because not aggregating colonies will be able to persist longer in the upper water layers. This is supported by the observed mass developments shortly after mixing events. *A. formosa* generally is a species adapted to spring conditions, but it is outcompeted in years with early ice-out and long spring full circulation (Horn et al. 2011). Under this conditions *A. subarctica* is able to outcompete other diatoms by higher inoccula due to its resuspension behaviour. As a conclusion, the hypothesis that peaks of *A. subarctica* in aphotic depths in the hypolimnion can be explained by sediment focussing, is strongly supported.

4.4.2 Growth experiments

Maximal photoautotrophic growth rates were lower for *A. subarctica* ($0,223\,\mathrm{d}^{-1}$ for strain P1B1 and $0,297\,\mathrm{d}^{-1}$ for strain P2A6) than for *A. formosa* ($0,761\,\mathrm{d}^{-1}$) and *F. crotonensis* ($0,798\,\mathrm{d}^{-1}$). These estimates match well the growth rates reported by other studies (Tab. 4.6). Deviations from other reported rates can be explained by the usage of different culture media, different experimental set ups, individual differences of strains and fitted models.

In the range of low light intensities and low temperatures all investigated species

Table 4.6: Literature review of maximal diatom growth rates.

Species	μ_{max}	Source
A. subarctica	0,275	pers. comm. Shatwell, T., IGB Berlin; model parameterisation on basies of data from Foy & Gibson (1993) and Gibson & Foy (1988)
A. subarctica	0,321	Foy & Gibson (1993)
A. formosa	0,71	Wagner (2008)
A. formosa	0,79	Jaworski et al. (2003)
A. formosa	1,16	Hayakawa et al. (1994)
A. formosa	0,73	Tilman & Kilham (1976)
F. crotonensis	0,77	Dauta et al. (1990)

showed similarly low growth rates (see section 4.3.2). Hence, *A. subarctica* does not have an advantage at low light. This is consistent with findings of Foy & Gibson (1993), who showed that growth efficiency regarding to light availability of *A. subarctica* is relatively low compared to other species.

No strain of *A. subarctica* showed heterotrophic growth using glucose as substrate It might be neccessary to test further substrates (Tuchman et al. 2006). The ability of heterotrophy of *A. subarctica* was investigated already unsuccessfully in other studies (Amblard et al. 1992). However, it was shown that urea is taken up in dark conditions and is discussed to be used as nitrogen source for heterotrophic or mixotrophic growth (Cimbleris & Cáceres 1991). Hence, heterotrophy might play a role in sustaining resting stages in the sediments, but due low observed numbers of cell divisions of resting stages in the sediments (Lund 1954) it can be argued that survial of *A. subarctica* in the dark is rather based on the usage of reserve substances than on heterotrophy. Furthermore, hypolimnetic occurrences were already sufficiently explained by resuspension without the need of benthic growth. In summary, the hypotheses that hypolimnetic peaks are based on heterotrophic growth or special adaptions to low light have to be rejected at the current state of knowledge.

4.4.3 Sedimentation and resuspension

The investigated diatom strains can be differentiated by their settling velocities and shear velocities needed for resuspension. *A. subarctica* had the most advantageous properties with a settling velocity of $0.31\,\mathrm{m\,d^{-1-1}}$ and a critical shear velocity of $0.2\,\mathrm{cm\,s^{-1}}$; this was followed by *F. crotonensis* ($0.28\,\mathrm{m\,d^{-1-1}}$, $0.35\,\mathrm{cm\,s^{-1}}$) and *A. formosa* ($0.48\,\mathrm{m\,d^{-1-1}}$, $0.35\,\mathrm{cm\,s^{-1}}$).

The experimental results have still a considerable uncertainty because the estimation of settling velocities for the field was based on mean colony size. In reality, colony size varies spatially and temporaly in dependence on physical, chemical and biological factors. E.g. colony size of *A. formosa* depends on light intensity (Wagner 2008), on temperature (Hayakawa et al. 1994) and hydrodynamc conditions (Bertrand et al. 2003). Also nutrient limitation, especially of silicate and dead colonies have an influence on settling velocity (Gibson 1984). Reynolds (2006) could demonstrate a 2–4 times higher settling velocity of dead colonies compared to living ones.

Nevertheless, literature data showed general agreement with our experimental findings (Tab. 4.7). Reynolds (1984a) determined generally higher settling velocities in laboratory experiments due to killing the cells before the experiments. The settling velocities of *A. subarctica* and *A. formosa* show good agreement with the studies of Gibson (1984) and Jaworski et al. (1988). Sedimentation rates in the field seem to be higher than what would be expected by laboratory experiments (Horn & Horn 1993). Therefore, a simple application of lab-based settling velocities to the field is problematic. Reasons for faster settling in the field might be coaggulations (Kiorboe et al. 1996; Kiorboe et al. 1998) and aggregations (Grossart et al. 1997).

The resuspension experiments revealed that for resuspension of *A. subarctica* only half the shear forces were needed than for *A. formosa* and *F. crotonensis.* This strongly supports the sediment focussing hypothesis and was the most important factor to reproduce the field pattern in dynamic modelling since the scenario with resuspension but without growth could already fully reproduce the hypolimnetic occurrence of*A. subarctica.* Of course, our determined critical shear velocities are only valid for sandy substrates, however, lake sediments consist of an organic matrix with different properties (Haworth 1976; Reynolds 1996). Nonetheless, it seems plausible that resuspension of *A. subarctica* also is easier from other substrates.

The relation of settling and resuspensin can explain the field observations very well (see section 4.3.1). The easy resuspension and slow settling of *A. subarctica* might be the reason for its long hovering persistence under ice coverage and in autumn. The relatively low sedimentation of *F. crotonensis* is beneficial for its occurrence during summer stratification. *A. formosa* had the highest settling velocities what is in agreement with its occurrence only at times with sufficient mixing.

4.4.4 Impacts of climate change

Since 1990 the diatom biomass in Saidenbach reservoir increased. Thereby, the formerly dominant species *A. formosa* was replaced by *A. subarctica* (Horn 2003b; Horn 2008; Horn et al. 2011). One reason for the shift might be the reoligotrophication since than, which favours *A. subarctica* due to its lower optimum for phosphorous compared to the more meso- and eutrophic species *A. formosa* and *F. crotonensis* (Anderson et al. 1997). Furthermore, during the same period of time ice-outs became earlier resulting in longer spring full circulation. This favours the resuspension of *A. subarctica* compared to the other species. The trend to increasing abundances of *A. subarctica* however, reversed in years with cold winters and short mixing periods and might also be lost when spring temperatures experience further warming and the period of full circulation becomes shorter due to an earlier onset of temperature stratification. In accordance to that, Horn et al. (2011) found a strongly significant dependency on inoculum biomass and short winters by statistical analysis of long-term data and similiar climate caused changes were also reported from Scandinavian lakes (Sorvari & Korhola 1998; Weyhenmeyer et al. 2008).

Consequences of such climate induced changes for the anthropogenic usage of the affected aquatic systems often is unclear. Higher amounts of *Aulacoseira* in depths of typical withdrawal of raw water might be problematic and cause higher costs for drinking water production (Weyhenmeyer et al. 2008; König-Rinke 2008). Also positive effects are thinkable. Higher amounts of diatom biomasses in spring could cause a higher internal reduction of nutrients by bounding to phytoplankton and

Table 4.7: Literature review of diatom settling velocities.

Species	Method	Mean settling velocity (md^{-1})	Maximal settling velocity (md^{-1})	Source
A. subarctica (1-2 cells)	Lab	$0,64 \pm 0,24$	-	Reynolds (1984a)
A. subarctica (7-8 cells)	Lab	$0,98 \pm 0,35$	-	Reynolds (1984a)
A. subarctica	Lab	0,2 – 0,4	-	Gibson (1984)
A. subarctica	Field	1,4 – 2,0	2,0 – 4,0	Horn & Horn (1993)
A. subarctica	Field	0,86	-	Lund (1954)
A. subarctica	Field	0,86	-	Gibson (1984)
A. formosa (4 cells)	Lab	$0,51 \pm 0,02$	-	Reynolds (1984a)
A. formosa (8 cells)	Lab	$0,63 \pm 0,05$	-	Reynolds (2006)
A. formosa (16 cells)	Lab	$0,92 \pm 0,11$	-	Reynolds (1984a)
A. formosa (very short cells)	Lab	$0,35 \pm 0,05$	-	Jaworski et al. (1988)
A. formosa	Field	1,7 – 1,8	4,1 – 5,8	Horn & Horn (1993)
F. crotonensis (single cells)	Lab	$0,34 \pm 0,02$	-	Reynolds (1984a)
F. crotonensis (11-12 cells)	Lab	$0,97 \pm 0,04$	-	Reynolds (1984a)
F. crotonensis	Field	3,2 – 4,3	7,1 – 10,3	Horn & Horn (1993)

subsequent settling to the sediments (Grim 1967). Also benthic fauna might profit from increased food ressources.

The present study was able to reveal processes responsible for the unusual spatial annual pattern of *A. subarctica* in a deep and dimicitc reservoir. Especially, low settling velocities and a resuspension at low shear forces explain the persistence of *A. subarctica* in aphotic depths. The maximum of this species at the bottom of the reservoir in autumn is most likely caused by sediment refocussing processes, which is an important part of the meroplanktic life cycle of *A. subarctica*.

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5 Extending one-dimensional models for deep lakes to simulate the impact of submerged macrophytes on water quality

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Abstract

Submerged macrophytes can stabilise clear water conditions in shallow lakes. However, many existing models for deep lakes neglect their impact. Here, we tested the hypothesis that submerged macrophytes can affect the water clarity in deep lakes. A one-dimensional, vertically resolved macrophyte model was developed based on PCLake and coupled to to the water quality model SALMO-1D and GOTM hydrophysics and validated against field data. Validation showed good coherence in dynamic growth patterns and colonisation depths. In our simulations the presence of submerged macrophytes resulted in up to 50 % less phytoplankton biomass in the shallowest simulated lake (11 m) and still 15 % less phytoplankton was predicted in 100 m deep oligotrophic lakes. Nutrient loading, lake depth, and lake shape had a strong influence on macrophyte effects. Nutrient competition was found to be the strongest biological interaction. Despite a number of limitations, the derived dynamic lake model suggests significant effects of submerged macrophytes on deep lake water quality.

5.1 Introduction

Submerged macrophytes are key components of aquatic ecosystems and have major effects on productivity (Brothers et al. 2013) and biogeochemical cycles (Carpenter & Lodge 1986). In shallow temperate lakes and rivers, submerged macrophytes have been shown to contribute to the stabilisation of clear-water conditions (Scheffer et al. 1993; Hilt et al. 2011). This effect is based on a number of mechanisms by which submerged macrophytes can reduce the water turbidity caused by phytoplankton and suspended solids. Firstly, their physical presence may reduce mixing of the water column and resuspension of sediment particles (Barko & James 1998), increase sedimentation of particles (Vermaat et al. 2000) and reduce light availability for phytoplankton (Pokornỳ et al. 1984). Secondly, phytoplankton abundance may be reduced by competition for nutrients by macrophytes including their attached periphyton and bacterial biofilm (Kufel & Ozimek 1994; Weisner et al. 1994), excretion of inhibiting allelopathic substances (Hilt & Gross 2008) and increased grazing losses by zooplankton. Zooplankton is directly supported by provision of shelter against planktivorious fish predation (Timms & Moss 1984; Jeppesen et al. 1999), indirectly by provision of habitat for macroinvertebrates (Diehl 1992), as alternative food resources for omnivorous fish (Lewin et al. 2004) and piscivorous fish that control the abundance of planktivorous fish (Grimm & Backx 1990).

Based on this knowledge, submerged macrophytes became an integral part of shallow lake models. Using minimal models (Scheffer et al. 1993; Hilt et al. 2011), individual-based models with a more mechanistic representation of the interaction between macrophytes and turbidity (van Nes et al. 2002) and the integrated shallow lake model PCLake (Janse 1997; Janse 2005) it has been shown that above mentioned mechanisms can result in the occurrence of alternative stable regimes in shallow lakes and slow-flowing lowland rivers. At low nutrient loading, these systems are characterised by clear water and submerged vegetation covering large parts of the lake or river bottom. With increasing nutrient loading, turbidity remains low until a certain critical threshold level is reached at which submerged macrophytes collapse and the system abruptly shifts to a turbid and phytoplankton-dominated regime (Scheffer et al. 1993). Such regime shifts have often been recognised in shallow northern temperate lakes in response to eutrophication (e.g. Sand-Jensen et al. 2000; Hilt et al. 2013). Restoring the original state requires much lower nutrient loading thresholds resulting in a hysteresis (Scheffer et al. 1993). Re-colonisation with submerged macrophytes thus often fails to follow re-oligotrophication which is a major problem in shallow lake restoration (Jeppesen et al. 2005; Hilt et al. 2006; Hilt et al. 2013).

Most existing water quality models for deep lakes and reservoirs neglect the role of submerged macrophytes, probably because only a smaller part of the water body can be colonised and the vegetation response to changes in turbidity is not discontinuous as in shallow lakes (Scheffer et al. 1993). In a modelling study, Genkai-Kato & Carpenter (2005) indeed found no remarkable effect of macrophytes for lakes deeper than 10 m. However, the effect of submerged macrophytes on water clarity in their model was restricted to prevention of phosphorus recycling from the sediment not including other potential interactions of submerged macrophytes within the ecosystem. In contrast to these results, several empirical studies, suggest that submerged macrophytes may contribute to the stabilisation of the clear-water regime in deep lakes. Hilt et al. (2010) observed a sudden and stable shift to clear-water conditions in Lake Scharmützelsee (maximum depth 29.5 m) after a significant increase in submerged macrophyte coverage. Rooney & Kalff (2003) detected an inverse relationship between phytoplankton biomass and macrophyte coverage in nine lakes with maximum depths ranging from 2 to 20 m. In addition, Lauridsen et al. (1996) and Portielje & Van der

Molen (1999) showed that very low macrophyte coverages can significantly increase water clarity which indicates that low macrophyte coverage in deep lakes might have similar effects. Consequently, we hypothesise that the influence of submerged macrophytes on turbidity in deep lakes is underestimated.

In this study, we innovatively combined existing lake model components to test the hypotheses that 1) submerged macrophytes have a significant effect on water clarity in deep lakes and that 2) this effect is dependent on lake geometry, nutrient loading, and depth. We developed a 1D-macrophyte module based on equations used in the dynamic shallow lake model PCLake (Janse 2005). It includes several direct and indirect interactions between submerged macrophytes and phytoplankton such as shading, competition for nutrients, provision of shelter for zooplankton and reduced water turbulence. The macrophyte module was combined with the existing water quality model SALMO-1D (Benndorf & Recknagel 1982; Petzoldt et al. 2013) and a modified GOTM for hydrophysics (Burchard et al. 1999) and validated with field data on macrophyte biomass in the deep lake investigated by Hilt et al. (2010). Following the recommendations by Mooij et al. (2010) not to reinvent the wheel and to avoid tunnel vision in ecological modelling, we first scanned to what extend we could address our research questions with existing models. We concluded that creating a dedicated model by combining three well-documented, to-the-point and state-of-the-art models (PCLake, SALMO and GOTM) would be the best balance between minimising duplication of effort and maximising our scientific focus on macrophytes and our control over the model code.

5.2 Methods

5.2.1 Model development and coupling

We developed a vertically resolved lake model including submodels for hydrophysics, water quality, and macrophytes (Fig. 5.1). For hydrophysics, a version of the 1-dimensional GOTM (General Ocean Turbulence Model, Burchard et al. 1999; Umlauf et al. 2005) was used and specifically modified for use in lakes. Water quality state variables (biomass of three functional phytoplankton type groups representing large algae e.g. large cyanobacteria and colonies, medium sized, e.g. *Asterionella*, and small algae, e.g. diatoms and chlorophytes, zooplankton, concentrations of oxygen, dissolved inorganic phosphorus and dissolved inorganic nitrogen) were modelled using a 0-dimensional core of SALMO (Benndorf & Recknagel 1982; Petzoldt et al. 2005). This library allowed setting up of a 1-dimensional grid (Petzoldt et al. 2013) for the water column of a deep lake. Our macrophyte module was mainly based on equations from PCLake (Janse 2005). In contrast to other available macrophyte models, such as SAGA (Hootsmans 1999), CHARISMA (van Nes et al. 2002), and MILFO (Best & Boyd 1999) which track carbon, have fixed stoichiometry, and were developed for specific species only, PCLake offers a variable stoichiometry of carbon, phosphorus

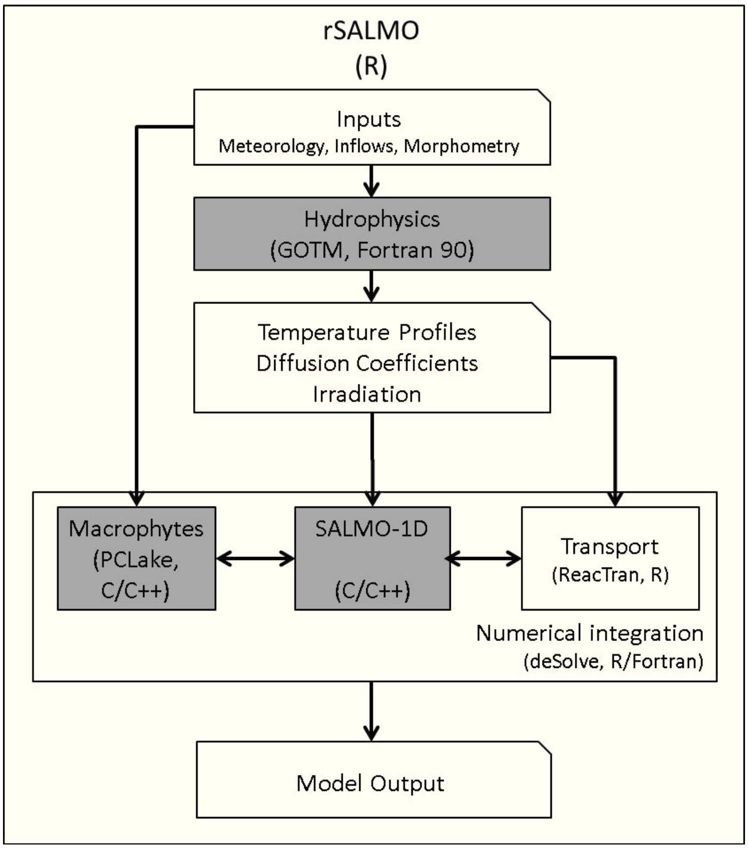

Figure 5.1: Linked models (grey boxes) and data flow to predict macrophyte influenced water quality. A modified stand-alone version of GOTM providing temperature profiles, diffusion coefficients and PAR on the lake surface is called from the R add-on package rSALMO. Temperature and light are than passed to the ecological submodels which are implemented in shared C-libraries and are coupled directly to the R-framework. Diffusion coefficients are used by the R add-on package ReacTran to calculate transport between layers of different depths.

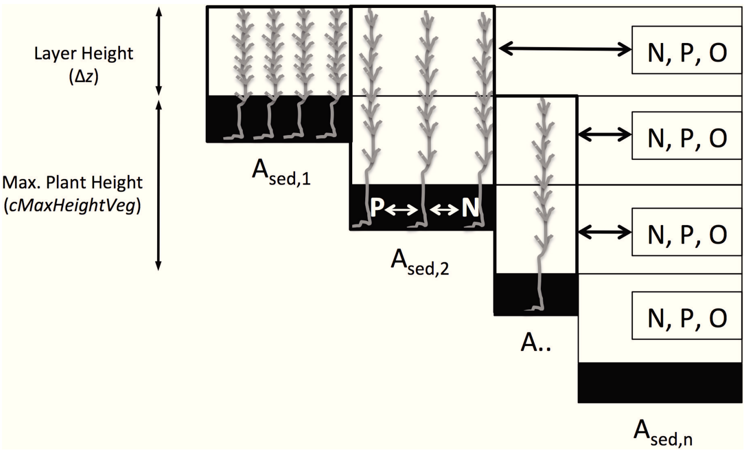

Figure 5.2: Layer structure of the model and chemical coupling (dissolved inorganic nitrogen - N, soluble reactive phosphorus - P, oxygen - O) of the macrophyte submodel. Plants grow across layers and exchange nutrients and oxygen in all layers they populate. They operate as zooplankton shelter and have shadowing effects on phytoplankton.

(P), and nitrogen (N) and has the possibility to parameterise functional type groups of submerged macrophytes rather than certain species. For the deep lake ecosystem, the 1D model SALMO was used, because it had been tested for several deep reservoirs and lakes but was missing the macrophyte parts. Both models, the hydrophysical and the ecological model had the same structure of vertically aligned water layers with constant layer heights (Fig. 5.2). The equations in all layers were the same, but macrophytes grew only where light, temperature, and nutrient conditions were sufficient and therefore colonised only the upper layers. This is an "emergent property" of the model. The hydrophysical model provided the temperature for each water layer and diffusion coefficients for the layer interfaces to calculate vertical matter exchange between these layers. For the horizontal dimension (within a layer) immediate mixing was assumed in the 1D model.

For rapid prototyping and testing of the newly developed macrophyte module, all submodels were coupled using the R environment for statistical computing (R Core Team 2012) and the add-on package rSALMO (Petzoldt et al. 2013). This setup allowed automated creation of input files, running and integration of several submodels as well as debugging and analyzing model results in a single programme. After generation of input files according to user specifications, a stand-alone GOTM was called which provided temperature profiles, profiles of turbulent diffusion coefficients and photosynthetically active radiation (PAR) at the water surface for the complete runtime of the scenario. These GOTM-outputs were further used to drive the ecological submodels and to calculate transport between the different water layers. Numerical integration was performed using the methods of line approach (Schiesser 1991) and a finite difference scheme from the package ReacTran (Soetaert & Meysman 2012) for the vertical transport (sedimentation, advection, and diffusion across layers).

Integration over time was performed with the package deSolve (Soetaert et al. 2010) and the BDF algorithm (backward differentiation formula, Hindmarsh 1983). The algorithm adjusted the step size automatically to keep the accuracy within user-defined absolute (atol) and relative (rtol) tolerances, that were set to atol = 1e-6 and rtol = 1e-6. More details can be found in Soetaert et al. (2012) and in the original description of the algorithm (Radhakrishnan & Hindmarsh 1993).

5.2.2 1D-Adaption of a macrophyte module

For the 0-dimensional macrophyte core, equations for one fully submerged functional type group were taken from PCLake (Janse 2005) and re-implemented in a shared C-library. This macrophyte type group did not have floating leaves or emergent plant parts, but could be rooted or non-rooted. The plants had four state variables: (i) $DVeg$ the total biomass in dry weight, (ii) $afRootVeg$ the fraction of the root of this total biomass, (iii) $PVeg$ the total P-content, and (iv) $NVeg$ the total N-content. In all simulations standard PCLake parameters were used from Janse (2005) (Tab. 5.1).

When water temperatures exceeded a specific threshold T_{m}, resources were allocated from the root into the shoot until the minimum root fraction ($fRootVegSum$) was reached, while after a specific day in autumn ($cDayWinVeg$) a fraction of the biomass was allocated from the shoot into the root up to the maximum possible root fraction ($fRootVegWin$) to prepare overwintering. A fraction of 25% of dead plant material was remineralised immediately, the other parts of plant-detritus were assigned to the sediments where nutrients were made available again for rooted plants. In PCLake allocation followed an analytical sinoidal equation and was always fixed to a specified period of time ($cLengAllo$) after T_{m} was exceeded for the first time. In our model, allocation of resources followed the same idea, but was described dynamically by a derivative ($\partial afRootVeg/\partial t$, Eq. 5.1) so that sprouting in spring could also be stalled several times in cases when temperatures dropped below Tm again and resumed later:

$$\frac{\partial afRootVeg}{\partial t} = \pm \frac{(fRootVegWin - fRootVegSum) \cdot \pi}{2 \cdot cLengAllo} \cdot sin\left(asin\left(\frac{2 \cdot afRootVeg - fRootVegWin - fRootVegSum}{fRootVegWin - fRootVegSum} \right) - \frac{\pi}{2} \right) \tag{5.1}$$

To keep the system dynamic the plants always allocated a minimum fraction of their biomass ($cAlloMin$) into the shoot or root as soon as $fRootVegSum$ or $fRootVegWin$ was reached. Implemented interactions of submerged macrophytes with the compartments of the other submodules included uptake and excretion of P and N in the pelagic zone and the sediment and production and consumption of

Table 5.1: Macrophyte parameters. For a full listing of parameters see Janse (2005). Wave mortality was implemented according to van Nes et al. (2002). Calibrated parameters were derived for Lake Scharmützelsee.

Parameter	Value	calibrated	Unit	Description
Δz	0.5		m	Layer height (grid size)
oPO_4S	2		$g\,m^{-3}$	SRP in sediment
oNS	5		$g\,m^{-3}$	DIN in sediment ($=oNH_4S + oNO_3S$)
fRootVegWin	0.6		$g\,root\,g^{-1}\,veg$	Root fraction outside of growing season
fRootVegSum	0.1		$g\,root\,g^{-1}\,veg$	Root fraction during growing season
cLengAllo	15		d	Duration of allocation phase, when biomass from root is allocated to the shoot
cLengMort	15	38	d	Duration of autumn mortality period
cAlloMin	1.00E-04		-	Min. root fraction allocated to shoot
cTmInitVeg	9	7	°C	Temperature for initial growth
fFloatVeg	0		$g\,floating\,g^{-1}\,shoot$	Floating fraction of shoot
fEmergVeg	0		$g\,floating\,g^{-1}\,shoot$	Emergent fraction of shoot
hLRefVeg	17	7	$W\,m^{-2}$	Half saturating light at 20 °C
cExtSpVeg	0.01		$m^2\,g\,DW^{-1}$	Specific extinction
fPAR	0.48		-	Fraction of photosynthetically active radiation (PAR)
fRefl	0.2		-	Fraction of radiation reflected at the water surface
kMigrVeg	1.00E-05		d^{-1}	Vegetation migration rate
cDVegIn	1		$g\,DW\,m^{-2}$	External vegetation density
cDCarrVeg	400		$g\,DW\,m^{-2}$	Max. vegetation standing crop
cDayWinVeg	259	222	day	End of growing season
fWinVeg	0.1	0.05	-	Fraction surviving in winter
kMortVegSum	0.005		d^{-1}	Background mortality in spring and summer
fDetWMortVeg	0		-	Fraction of shoot mortality becoming water detritus (original 0.1)
fDissMortVeg	0.25		-	Fraction dissolved nutrients from died plants
fDepth1Veg	0		-	Max. upper depth of submerged veget. layer, as fraction of layer height
fDepth2Veg	1		-	Max. lower depth of submerged veget. layer , as fraction of layer height
cMaxHeightVeg	3		m	Maximum macrophyte height
kVegResus	0.01		$m^2\,g^{-1}\,DW$	Rel. resuspension reduction per g vegetation
crelVegFiJv	0.01		-	Decrease of young fish feeding per % vegetation cover
pWaveMort	4	2	-	Exponent for steepness of sigmoidal curve of wave mortality
HWaveMort	0.15	1.25	m	Half saturation depth for wave mortality
MaxWaveMort	0	0.05	d^{-1}	Maximal wave induced mortality

oxygen. Further implemented interactions were shading, lowered predation pressure on zooplankton, and decreased turbulence within plant populated areas leading to increased phytoplankton sedimentation. Even though not having reached the full biomass, the plants were assumed to immediately have their parameterised maximum height which could be any fraction smaller than the simulated layer height (Δz, set at 0.5 m in this study) or a multiple of the layer heights for larger species (Fig. 5.2). Since macrophytes might grow over multiple layers (n_{Mac}, Eq. 5.2) in a 1D-model, adaptations to calculate weighted means of nutrients, light availability and other macrophyte influenced states were necessary. The weighted means approach enabled an approximation of macrophyte interactions with sediments, the pelagic zone, or planktonic organisms within a layer where patches of different macrophyte coverages occurred or even across layers (Fig. 5.2).

$$n_{Mac} = \mathrm{ceil}(cMaxHeightVeg/\Delta z) \tag{5.2}$$

In the latter case, plants rooted in one layer (i) were influenced by several layers atop (up to $i - n_{\mathrm{Mac}}$). Resources ($R_{\mathrm{Mac,i}}$) available for the plants (N, P) were averaged over all layers in which a plant grew (Eq. 5.3).

$$R_{Mac,i} = \Big(\sum_{n=i}^{i-n_{Mac}} R_n \Big) / n_{Mac} \tag{5.3}$$

To obtain a mean light attenuation for the whole plant the light extinction coefficients of phytoplankton, detritus and background extinction, were averaged in the same way prior to the calculation of further reduction of light by self-shading. The modelled plants could take up and excrete substances from and to the water and from and to the sediments according to the fraction of their biomass allocated to shoots and roots. After the calculation of nutrient and oxygen uptake ($aNutWup$) or release, released substances were split equally over all layers assigned to the macrophytes. To avoid overexploitation of substances from layers with very low concentrations, uptake of substances per layer ($\partial R_{Mac,i}/\partial t$) was weighted with the actual concentration of that resource in the layer (R_{i}, Eq. 5.4),

$$\frac{\partial R_{Mac,i}}{\partial t} = (R_i \cdot aNutWup)/(vol_i \sum_{n=i}^{i-n_{Mac}} R_n) \tag{5.4}$$

with the layer volume vol_{i}.

While the light intensity on top of the macrophytes was influenced by the specific extinction coefficients of the water and by phytoplankton in overlying layers, the light for phytoplankton in a specific layer was also influenced by patches with differing macrophyte coverages (Fig. 5.2). Therefore, an extinction coefficient was calculated for every patch and then weighted by the patch areas to average for the whole layer

(Eq. 5.5),

$$\epsilon_i = (\epsilon_{water,i} + \epsilon_{phyto,i}) \cdot \Big(\sum_{n=i}^{i+n_{Mac}} (\epsilon_{Mac,n} \cdot A_{sed,n}) + (A_i - \sum_{n=i}^{i+n_{Mac}} A_{sed,n}) \Big) / A_i \tag{5.5}$$

with the layers total area A_{i}, the contribution of the water $\epsilon_{\mathrm{water,i}}$, the phytoplankton $\epsilon_{\mathrm{phyto,i}}$, and of the macrophytes $\epsilon_{\mathrm{Mac,n}}$ of neighbouring layers to the overall light extinction in that layer (ϵ_{i}).

Increase of sedimentation velocities for particles and downregulation of the functional response of fish in dependence of macrophyte coverage was implemented according to Janse (2005) by means of simple density dependent relationships. Fish predation was altered by multiplying the SALMO parameters for minimal zooplankton mortality and slope of temperature dependent predation by fish (MOMIN, MOT, see Tab. 5.2) with this factor. Settling velocities and zooplankton mortalities again were weighted patchwise analogous to Eq. 5.5 for each layer.

To substitute increased predation by birds or macroinvertebrates in upper layers as well as competition with helophytes which were not part of this model or to represent mortality by waves we also added the possibility to use equations for wave mortality from van Nes et al. (2002). Increased mortality vanished quickly according to a sigmoidal relationship with depth, and therefore only occurred in the upper most layers.

The macrophyte module was designed for optimal data exchange with the ecological submodel SALMO-1D without the necessity to change the code of SALMO (Fig. 5.1). Therefore, it is possible to couple the macrophyte module to any other ecological submodel by providing appropriate interface functions.

5.2.3 The ecological submodel SALMO-1D

SALMO (Simulation by an Analytical Lake Model) is a dynamic ecological model that simulates the most important pelagic food-web compartments of lakes and reservoirs with a constant stoichiometry (Benndorf 1979b). It simulates the mass balance of soluble reactive P (SRP), dissolved inorganic N (DIN), three phytoplankton type groups (X_1 - large cyanobacteria-like and least grazable, X_2 - medium-sized diatom-like, X_3 - small and best grazable diatoms or small chlorophytes), one mixed zooplankton group (Z), allochthonous detritus (D) and oxygen (O). The original model parameters were validated over a broad range of lakes of all trophic states (Recknagel & Benndorf 1982; Recknagel 1989). Construction of a 1-dimensional grid for the water column of several SALMO-layers was done using the R add-on package rSALMO (Petzoldt et al. 2013). For this study, only a few changes to parameters (Tab. 5.2) and minor improvements to SALMO were made. In particular, to avoid negative oxygen concentrations, an oxygen-limiting term (*olim*) was introduced to all oxygen-consuming processes (Eq. 5.6),

$$olim = O/(K_O + O) \tag{5.6}$$

where O is the oxygen concentration ($\mathrm{mg\,L^{-1}}$) and K_O the half saturating oxygen concentration ($\mathrm{mg\,L^{-1}}$) at which respiration was half of maximum. Specific light attenuation coefficients for the three phytoplankton type groups were derived from the AEMON database (Aquatic Ecosystems MOdelling Network, `https://sites.google.com/site/aquaticmodelling/`) by converting chlorophyll *a* (mg Chl*a*) to wet weight based units (g WW) with a constant factor of 5 according to Kasprzak et al. (2008).

For the purpose of this study it was sufficient that inflows were homogeneously distributed across the top 10 m of layers and handled by SALMO directly. Thereby, no water level fluctuations were allowed, evaporation was neglected, and it was assumed that in- and outflow of each layer compensated exactly. The sediment in SALMO is modelled as infinite sink and source so that macrophytes did not change the initial nutrient concentrations of the sediment (Tab. 5.1).

5.2.4 The hydrophysical submodel GOTM

The hydrophysical part of the model system was done with a lake-adapted version of the one-dimensional water column model GOTM. It was originally published by Burchard et al. (1999) and regularly extended and applied to many case studies since then (Burchard 2002; Umlauf & Burchard 2003; Umlauf & Burchard 2005; Umlauf et al. 2005). For this study we used the two-equation k-ϵ turbulence model of Stips et al. (2002) who already applied it as an algebraic second-moment closure scheme to GOTM to simulate temperature profiles in Lake Maggiore. However, some modifications in the code were done to better simulate heat and substance transport within the water column in lakes, for calculation of more accurate temperature, salinity, and nutrient profiles. For that, we added bathymetry, and the effect of the layer volumes on the transport equations to the code. The effect of the bathymetry in the internal mixing was implemented using a shape factor f calculated as the volume ratio between two adjacent layers, $f = V_\mathrm{upper}/V_\mathrm{lower}$. This way the differences between the volumes of each upper (V_upper) and lower layer (V_lower) were considered in the heat and mass transfer processes. For further use of the hydrophysical results within the ecological models, the output of the modified GOTM version contained the hydrophysical description of the simulated lake, including temperature, turbulent diffusion, turbulent kinetic energy, dissipation, stratification, and availability of PAR. The numerical discretisation of the model is described in detail by Burchard et al. (1999) and Umlauf et al. (2005). To obtain numerically stable results for our strongly convective scenarios, a time step of $\Delta t = 600\,\mathrm{s}$ has been used. The vertical resolution was equidistant with $\Delta z = 0.5\,\mathrm{m}$. Because of the design of the overall lake model to initially run GOTM for the complete simulation period before the call of the ecological submodels, feedback of these submodules on hydrophysics was limited. The ecological models considered light penetration between macrophytes and phytoplankton in both directions but the influence of altered light penetration on temperature was not included. Increased phytoplankton settling velocities in dense macrophyte patches were calculated by the macrophyte module (see section 5.2.2) and used for calculating transport of phytoplankton. However, the altered turbulence in macrophyte covered areas was not passed back to GOTM where it could have influenced temperature stratification.

5.2.5 Model validation

The model was validated against macrophyte and phytoplankton field data obtained from Lake Scharmützelsee. In addition, profiles of temperature and dissolved oxygen measured at the deepest point of the lake and data on soluble reactive phosphorus (SRP) in the epilimnion (Grüneberg et al. 2011) were included in the validation.

We used a set of metrics to measure different aspects of agreement or disagreement between model and data (cf. Jachner et al. 2007; Bennett et al. 2013). The coefficient of determination R^2 showed the amount of variance explained by the model, but not the pattern, Spearman's rank correlation coefficient $\mathrm{r_S}$ measured the pattern, but is insensitive to systematic bias, and the the Nash Sutcliffe efficiency (EF, Nash & Sutcliffe 1970) measured both. The mean absolute percentage error (MAPE) represented an easily interpretable measure of the relative deviance.

The dimictic lake had a surface area of $12.1\,\mathrm{km}^2$, a maximum depth of 29.5 m and a hydraulic retention time of 10.7 years (Grüneberg et al. 2011). In 2010/2011 submerged macrophytes were sampled monthly along eight representative transects between 0 m and 5 m with a Van-Veen grabber ($0.06\,\mathrm{m}^2$). The plants were dried at 60 °C for 24 hours and the dry weight was determined with micro scales (Sartorius MC1, Analytic AC 210 S). Emergent species (helophytes) were excluded from the dataset and dry weights of all submerged species were then summed up, averaged over all transects and linearly approximated over depth to gain a regular 1-dimensional grid.

Phytoplankton was sampled bi- to four-weekly in 2005 with a 2.3 L-LIMNOS sampler (Turku, Finland) in 0.5 to 1 m steps at the deepest point of the lake. A single composite sample using weighted volumes from each depth (Tab. 5.3) was prepared for the uppermost mixed layer (i.e., the epilimnion during thermal stratification and down to 27 m depth during mixing periods), fixed with Lugol's solution and counted after Utermöhl (1958). The list of species was then classified into the three SALMO functional types. To allow comparisons, the modelled phytoplankton profiles were weighted in the same way.

Table 5.2: Changed or newly added SALMO parameters. For a full listing of parameters and equations see Petzoldt et al. (2013). Calibrated parameters (*) were derived for Lake Scharmützelsee and only used for simulating that specific lake.

Parameter	Value	Unit	Description
SEZMAX	0.2	$\mathrm{g\,O_2\,m^{-2}\,d^{-1}}$	Maximum rate of oxygen consumption of the sediment
K_O	0.5	$\mathrm{mg\,O_2\,L^{-1}}$	Half saturating oxygen concentration at which respiration is half maximal
EPSX	0.15, 0.1, 0.1	$\mathrm{m^2\,g^{-1}\,WW}$	Specific light attenuation coefficients for phytoplankton type groups 1, 2, 3
EPSMIN	0.2	$\mathrm{m^{-1}}$	Vertical light attenuation coefficient of phytoplankton-free water
MOMIN	0.015	$\mathrm{d^{-1}}$	Zooplankton mortality rate close to 0 °C
MOT	0.006	$\mathrm{K\,d^{-1}}$	Slope for temperature dependent zooplankton mortality rate
ANSFMIN*	0.001	$\mathrm{g\,N\,m^{-2}\,d^{-1}}$	Minimum re-dissolution of inorganic N from sediments at 0 °C
APSFMAX*	0.7	$\mathrm{mg\,P\,m^{-2}\,d^{-1}}$	Maximum re-dissolution of phosphate from sediment under anoxic conditions
APSFMIN*	0.1	$\mathrm{mg\,P\,m^{-2}\,d^{-1}}$	Minimum re-dissolution of phosphate from sediment under oxic conditions

Table 5.3: Volumes used from each sampling depth to prepare a single composite sample for phytoplankton quantification in Lake Scharmützelsee.

Depth (m)	Volume (L)
0, 1	2.0
2, 3	1.6
4, 5, 6, 7	1.4
8, 9, 10, 11	0.9
12, 13, 14, 15	0.6
16, 17, 18, 19	0.3
20, 21, 22, 23	0.04
24, 25, 26, 27	0.01

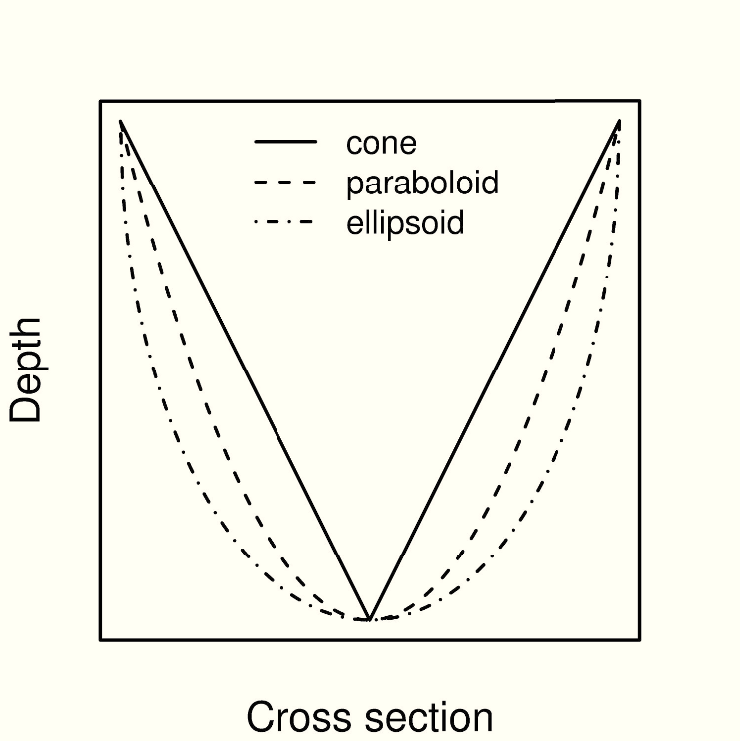

Figure 5.3: Basic basin geometries used for simulation. Cross section at the deepest point of a conic, a paraboloic, and an elliptic lake. While the cone shows most sediment area in its upper parts, the ellipsoid has steep shores and most of the sediment area is located in higher depths.

5.2.6 Tested scenarios

Macrophyte effects on lake water quality were tested in scenarios with different geometric lake basin morphometry, maximum depths, discharge regimes and nutrient loadings (Tab. 5.4). Since the calibrated parameters of Lake Scharmützelsee could not be generalised to other lakes, the standard parameter sets of the models, which already were validated against a large variety of different lakes, were used instead.

Carpenter (1983) found that a majority of lakes followed a basic conic, parabolic or elliptic geometric basin shape according to the morphometry model of Junge (1966). Also, the hypsographic curve of Lake Scharmützelsee could be described by the conic form. We limited our simulations to the same three geometries (Tab. 5.5, Fig. 5.3). The scenarios covered seven depths from 11 m to 100 m, five retention time regimes were varied from 0.25 years to 50 years, and nutrient loading was increased in six steps from $0.01\,\mathrm{g\,P\,m^{-2}\,yr^{-1}}$ to $3\,\mathrm{g\,P\,m^{-2}\,yr^{-1}}$ to induce oligotrophic to hypertrophic conditions according to the SRP modification of the Vollenweider Model (Benndorf 1979a). Every combination of basin shape, maximum depth, and discharge regime was run for the full series of subsequently increasing nutrient loadings. Thereby, each nutrient scenario was simulated for three years to allow the system to reach a stable

Table 5.4: Scenarios conducted in this study. All possible combinations of lake parameters were simulated. Nutrient scenarios were conducted as a subsequent series, where each run started with the results of the scenario with nutrient loading of the previous scenario with the same other lake parameters.

Scenario	Lake shape	Maximum depth (m)	Retention time (yr)	Nutrient loading ($\mathrm{g\,P\,m^{-2}\,yr^{-1}}$)	Simulation time for each scenario combination (yr)	Number of scenarios
Lake Scharmützelsee validation (calibrated parameters)	cone	30	15	0.015	1.1	2*
Sensitivity of macrophyte effect (standard parameters)	cone parabolic elliptic	11 20 30 40 50 70 100	0.25 1 5 15 50	0.01 0.1 0.3 0.5 1 3	3	1260*
Check for hysteresis (standard parameters)	cone	11 30 50 70 100	15	0.01 0.1 0.3 0.5 1 3 0.5 0.3 0.1 0.01	5	50
Evaluation of importance of the 4 macrophyte-plankton interactions(standard parameters)	cone	30	15	0.015	3	10*
Sensitivity of thermal structure from biological feedback on physics (standard parameters)	cone	30	15	0.1	1	2

*the number includes scenarios with and without macrophytes, therefore it is two times of all possible combinations state before increasing the nutrient load for the next scenario. To exclude initial stabilization effects, only results starting from the third year of each scenario were analysed further.

The occurrence of a hysteresis was tested by long-term simulations for five exemplary conic lakes with a medium retention time of 15 years. Each step of nutrient loading in these long term simulations was run for 5 years and after reaching hypertrophic conditions the nutrient loading was stepwise decreased.

In contrast to the validation run and in order to reduce complexity, potential nitrogen limitation was switched off by loading 100 times more nitrogen than phosphorus. As meteorological forcing, data for the region of Lake Scharmützelsee were obtained from Lindenberg Meteorological Observatory (DWD) for the year 2005. These data included: x- and y-component of wind at 10 m height, air pressure at 2 m height, air temperature at 2 m height, relative humidity, and relative cloud cover. To determine the influence of macrophytes, the same scenarios were calculated twice: first, without macrophytes and a second time with the macrophyte module switched on.

To evaluate the importance of each of the four implemented macrophyte-plankton interactions (shading, nutrient uptake, influence on sedimentation velocity, zooplankton refuge) single interaction terms were switched on and off individually for the Lake Scharmützelsee scenario. Importance was expressed as the proportion the individual process contributed to changes in summer phytoplankton biomass with macrophytes as compared to scenarios without macrophytes.

5.2.7 Estimation of sensitivity of the thermal structure to biological feedback

To determine the impact of the omitted biological feedback on the thermal structure we performed a sensitivity analysis by simulating a 30 m deep lake with 15 years retention time, an external phosphorus loading of $0.3\,\mathrm{g\,P\,m^{-2}\,yr^{-1}}$, with different light extinction scenarios. As reference scenario without biological feedback, the hydrophysical model GOTM was run with a constant light attenuation coefficient of $0.98\,\mathrm{m^{-1}}$. The scenario with biological feedback had the same boundary conditions, and GOTM was driven by variable light attenuation coefficients. This light extinction was derived as the sum of all specific light extinctions (phytoplankton, minimum

Table 5.5: Hypsographic curves for different basic geometric lake shapes (modified after Uhlmann et al. (2011)). The normalised depth x is defined as $x = z/z_{\mathsf{max}}$. See Fig. 5.3 for an illustration.

			Basic geometric lake type		
Parameter	Symbol	Unit	Cone	Paraboloid	Ellipsoid
Depth dependent area	A_z	m^2	$A_0\,(1-x)^2$	$A_0\,(1-x)$	$A_0\,(1-x^2)$
Depth dependent volume	V_z	m^3	$V_0\,(1-x)^3$	$V_0\,(1-x)^2$	$V_0\,(1-x(3-x^2)/2)$
Total volume	V_0	m^3	$A_0\,z_{\max}/3$	$A_0\,z_{\max}/2$	$2A_0\,z_{\max}/3$

light extinction of the water) from a previous simulation of the full model. As an indicator of impact on the thermal structure, the mixing depth (z_{mix}) was calculated from the simulated temperature profiles according to Talling (1971). The difference $\Delta z_{\mathrm{mix}} = z_{\mathrm{mix,ref}} - z_{\mathrm{mix,feedback}}$ of the mixing depths of the reference scenario ($z_{\mathrm{mix,ref}}$) and the mixing depths of the scenario with biological feedback ($z_{\mathrm{mix,feedback}}$) was used to quantify the potential impact.

5.2.8 Analysis of model results

Model results were analysed with the R environment for statistical computing (R Core Team 2012). For performing multivariate statistics, ecological state variables were aggregated spatially from 0 to 10 m to represent the epilimnion, and from 10 m to the lake bed as the hypolimnetic measure, and aggregated temporally to derive season means for winter (January–March), spring (April–May), summer (June–September) and autumn (October–December). Total macrophyte biomass of the lakes $DVeg_{\mathrm{lake}}$ was derived by multiplying sediment areas A_{n} and modelled macrophyte densities $DVeg_{\mathrm{n}}$ in all layers (Eq. 5.7).

$$DVeg_{\mathrm{lake}} = \sum (A_{\mathrm{n}} \cdot DVeg_{\mathrm{n}}) \tag{5.7}$$

Relative effects of submerged macrophytes ME were defined as the ratio of the difference of a state variable in the scenarios with (X_{Mac}) and without macrophytes (X) related to the value of the state without macrophyte influence (Eq. 5.8).

$$ME = (X - X_{\mathrm{Mac}})/X \tag{5.8}$$

Partial redundancy analyses (pRDA) with lake depth, retention time and nutrient loading as constraints were performed according to Oksanen et al. (2012) to disentangle the influences of these factors on macrophyte effects on seasonally and spatially aggregated water quality criteria.

To evaluate the tipping points between macrophyte- and phytoplankton dominated states, a threshold of $4\,\mathrm{mg\,L^{-1}}$ total phytoplankton in the epilimnion was set.

5.3 Results

5.3.1 Basic model behaviour and calibration for Lake Scharmützelsee

Field observations of temperature, dissolved oxygen, and SRP of Lake Scharmützelsee were reproduced well in our simulations using a few macrophyte-specific, calibrated parameters (Fig. 5.4, 5.5). Variance and pattern of epilimnetic und hypolimnetic temperature agreed well with simulated values (R^2 and $\mathrm{r_S} > 0.9$, Tab. 5.6, Fig. 5.4A) and the mean relative deviance from observations was relatively small (MAPE =

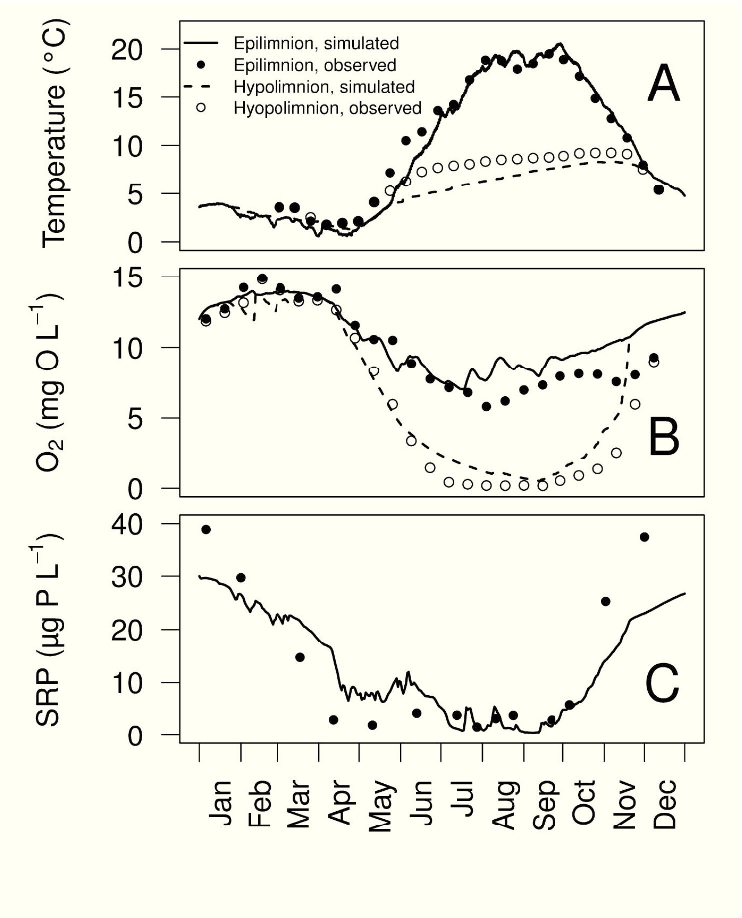

Figure 5.4: Validation of simulated temperature (A), dissolved oxygen (B) and soluble reactive phosphorus (C) against observations from Lake Scharmützelsee sampled in the year 2005.

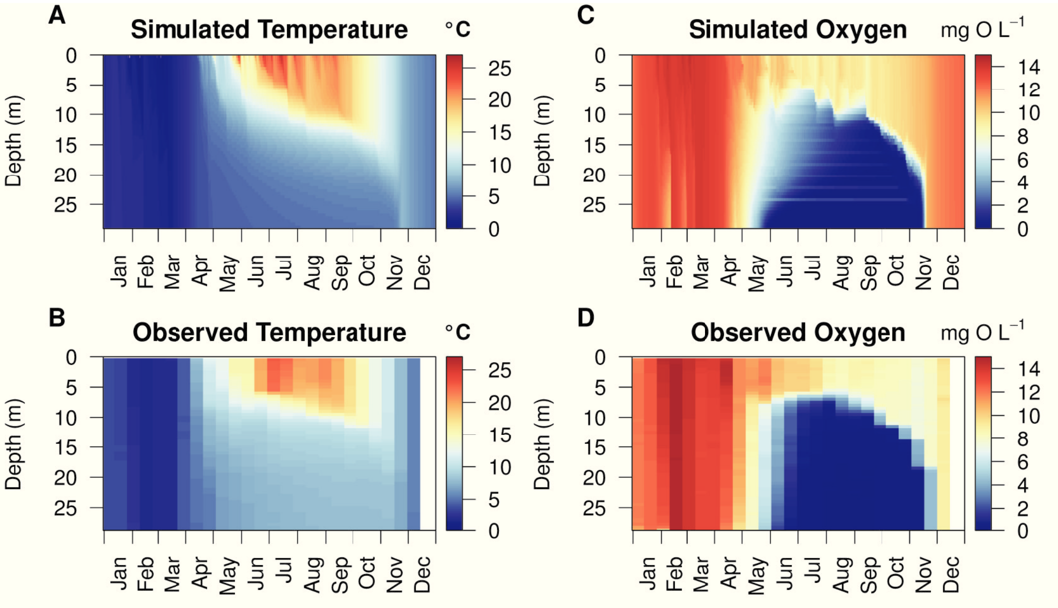

Figure 5.5: Comparison of simulated (A, C) and observed profiles (B, D) of temperature and dissolved oxygen sampled in Lake Scharmützelsee in the year 2005.

30%, Tab. 5.6). Epilimnetic temperatures at the beginning of the stagnation period were slightly underestimated, but fitted well to the overall time series ($EF = 0.96$, Tab. 5.6). The thermal pattern was reproduced, even if hypolimnetic temperatures were underestimated by 1 to 2 K during the stratification period (lower $EF = 0.63$, Tab. 5.6), possibly a result of missing feedback of phytoplankton on thermal structure. Dissolved oxygen fitted similarly well with low relative deviance from measurements ($MAPE < 35\%$, Fig. 5.4B). While the hypolimnetic oxygen concentration was predicted with an efficiency of 0.91, the epilimnetic concentration was overestimated in the second half of the year, probably because of an overestimated phytoplankton production. SRP was reproduced with less precision ($EF = 0.33$, Tab. 5.6), but the model still explained most of the dynamics (R^2 and $r_S > 0.7$, Tab. 5.6).

The pattern of simulated macrophytes was in good agreement with field measurements ($EF = 0.86$, Fig. 5.6A, C, D, Tab. 5.6) and was predicted with acceptable errors of 43% (Tab. 5.6). In agreement with the observations, simulated macrophyte biomass showed a strong population development during summer from June to August with a peak of 250 g DW m^{-2} at 2 m to 4 m depth (Fig. 5.6A). In the top 1 m submerged vegetation was missing or sparse. Submerged macrophytes only grew in the upper layers where roots could sprout and sufficient light was available (Fig. 5.6B). In autumn, vegetation died suddenly and re-allocated biomass into roots (Fig. 5.6A, B). At its maximum, up to 25% of the lake area was simulated to be covered by macrophytes.

Absence of macrophytes in very shallow areas was most probably caused by wave

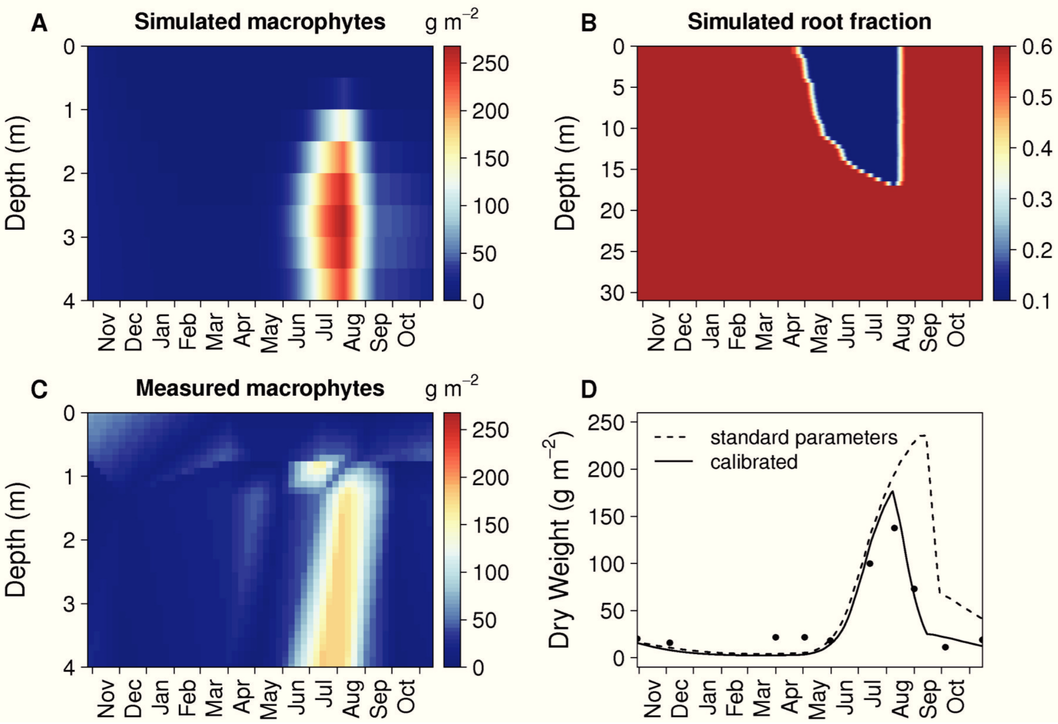

Figure 5.6: Example of two state variables of the macrophyte module in a 30 m deep lake (A: simulated biomass, B: simulated root fraction) and model validation for Lake Scharmützelse (C: measured biomass, D: comparison of mean measured and mean simulated biomass from 0 - 4 m depth).

Table 5.6: Coefficient of determination (R^2) from linear regression, Spearman's rank correlation coefficient (r_S), mean absolute percentage error (MAPE), and Nash-Sutcliffe efficiency factor (EF) for simulated macrophytes, phytoplankton, temperature, dissolved oxygen, and SRP using calibrated parameters and observed data from Lake Scharmützelsee.

State variable	Depth range (m)	Number of observations	R^2	r_S	MAPE	EF
Macrophyte dry weight	0–4	3879	0.79	0.44	67	0.60
Macrophyte dry weight	0–4 (aggregated)	72	0.97	0.49	43	0.86
Total phytoplankton	0–27	15	0.41	0.33	184	0.13
Temperature epilimnion	0–10 (aggregated)	25	0.99	0.97	29	0.96
Temperature hypolimnion	10–30 (aggregated)	25	0.90	0.94	30	0.63
Dissolved oxygen epilimnion	0–10 (aggregated)	25	0.83	0.90	12	0.53
Dissolved oxygen hypolimnion	10–30 (aggregated)	25	0.94	0.97	35	0.91
SRP epilimnion	0–10 (aggregated)	15	0.77	0.74	70	0.33

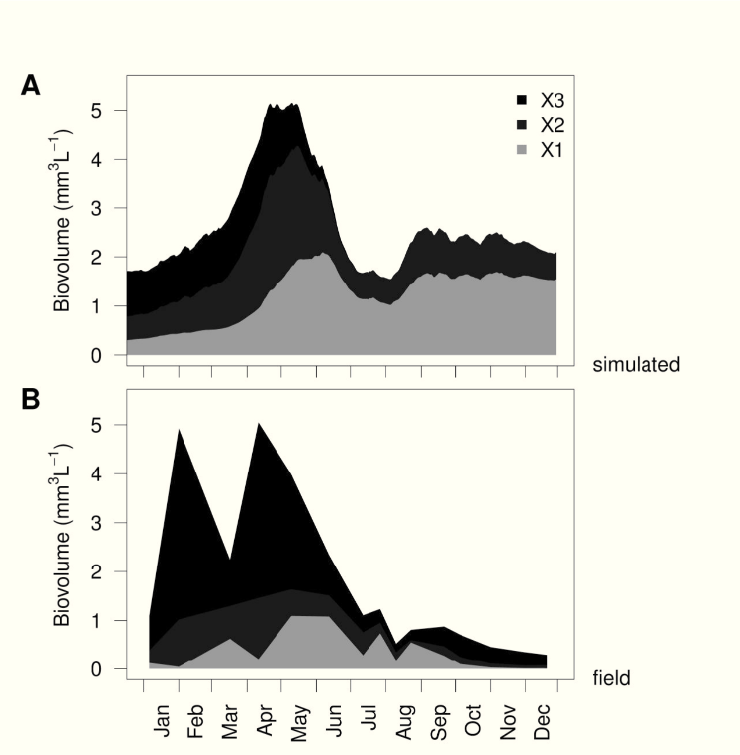

Figure 5.7: Simulated (A) and measured (B) biovolume of functional phytoplankton type groups in Lake Scharmützelse in the year 2005 (X1: large, X2: medium size, X3: small phytoplankton).

mortality and competition with helophytes. Simulations with standard parameters from the original models resulted already in good agreement of population development from May to July but lead to an over-prediction of total maximum biomass of submerged vegetation and a delayed initiation of the die-off phase (Fig. 5.6D). After calibration of several macrophyte and lake specific parameters (Tables 5.1, 5.2) the later development of macrophytes from August to September matched observations better (Fig. 5.6D, Tab. 5.6).

Simulated dynamics of phytoplankton qualitatively matched field measurements in Lake Scharmützelse in 2005 regarding biovolume and seasonal pattern, with a strong peak in spring and lower values in summer and autumn (Fig. 5.7). However, among phytoplankton type groups, there was too few small (X_3) and too much medium sized (X_2) phytoplankton. The biomass of phytoplankton in summer and autumn was overestimated almost by a factor of 2 (MAPE = 184%, Fig. 5.7) causing poorer R^2, correlation, MAPE, and EF compared to the other state variables (Tab. 5.6).

The lack of submerged macrophytes in the shallowest parts of Lake Scharmützelse was not typical and was different in other lakes (Chambers & Kaiff 1985). To also account for a possible coverage with submerged plants or for helophytes, which are not part of the model but might have similar effects in providing zooplankton shelter, in shading effects and in nutrient uptake by the plants or by attached periphyton, further simulations were done without wave mortality in the first (shallow) layers, allowing intense growth of submerged vegetation in the 0 m–1 m depth sections.

5.3.2 Comparing simulations of lake water quality with and without macrophytes

The influence of macrophytes on lake water quality (total phytoplankton, zooplankton/phytoplankton-ratio, SRP and dissolved oxygen concentrations) was assessed in time and space by comparing model results with and without the macrophyte module (Fig. 5.8). The strongest effects of submerged macrophytes occurred between June and November. The total phytoplankton biomass was reduced by at least 20% in the epilimnion throughout the whole summer (Fig. 5.8A). However, in the metalimnion an increase of total phytoplankton was observed, in some cases to more than 400% compared to scenarios without submerged macrophytes. After the death of shoots of submerged macrophytes in autumn, and increasing mixing depth, a more than 20% increase of total phytoplankton could be observed in the macrophyte scenarios.

The zooplankton/phytoplankton ratio only increased by more than 20% in June and July in the epilimnion in the presence of macrophytes (Fig. 5.8B). After the beginning of August the epilimnetic ratio stayed either unchanged or turned negative (-20%) because the reduced phytoplankton population could not sustain as much zooplankton as without macrophytes. The ratio also was at least 20% lower in the meta- and hypolimnion due to increased metalimnetic phytoplankton production.

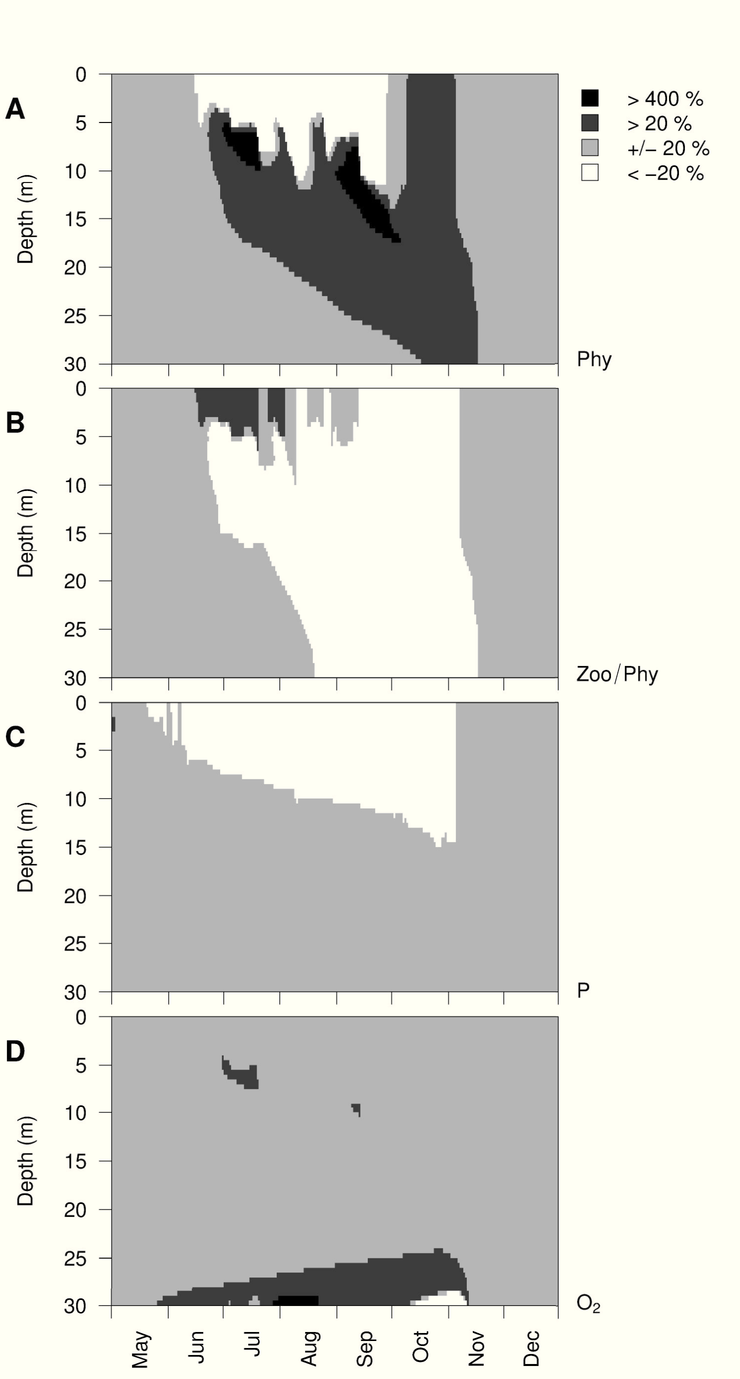

Figure 5.8: Relative differences of selected water quality criteria (Phy: phytoplankton, Zoo/Phy: ratio of zooplankton to phytoplankton, P: soluble reactive phosphorus, O2: oxygen) in a mesotrophic 30 m deep simulated conic lake ($t_R = 15\,\mathrm{a}$) with macrophytes related to a scenario without macrophytes. Extreme shadings indicate negative (white) or positive (black) macrophyte effects which exceeded a limit of $\pm 20\%$.

While the SRP concentration in the hypolimnion remained unchanged, a reduction of the SRP concentration by at least 20% was predicted in the epilimnion during the stratification period from May to October (Fig. 5.8C). Submerged vegetation had mainly positive effects on the lakes' oxygen storage in the meta- and hypolimnion (Fig. 5.8D). Surprisingly, strongest positive effects of submerged macrophytes occurred at the deepest points of the hypolimnion at 25 m–30 m depth (Fig. 5.8D). Here, oxygen concentrations were mostly more than 20% higher than in scenarios without macrophytes. The improved hypolimnetic oxygen demand could be explained by less available organic material sedimenting from the epilimnion. Only in late October and at the beginning of November, when the increased autumnal and metalimnetic phytoplankton biomass reached the lowest layers, hypolimnetic oxygen concentrations decreased by about 20% . However, improved hypolimnetic oxygen concentrations throughout most of the stratified period might have reduced nutrient release from the sediments and limited the available nutrient pool for phytoplankton after the next circulation period.

Analysis of the importance of the different macrophyte-plankton interactions showed that the strongest interaction in the simulated deep lakes was competition for nutrients in the open water which alone was responsible for 89% of the macrophyte effect. Light shadowing contributed by 8% and the provision of zooplankton shelter by 3% while reduced turbulence in macrophyte patches contributed only by 0.1% to the overall macrophyte effect.

5.3.3 Effects of lake geometry, depth and nutrient loading on macrophyte impacts

The pRDA performed for the model results of all scenarios of conic lake shapes identified the nutrient loading as the strongest influencing factor, explaining 22.2% of the variance between the scenarios. Lake depth was similarly important and explained 18.8% of the variance, while retention time had the weakest impact on model outcomes (1.2% explained variance). Therefore only the influence of lake depth and nutrient loading on the total biomass of epilimnetic phytoplankton was analysed further.

In conic lakes the phytoplankton in summer can be reduced by 50% by macrophytes in the 11 m shallow oligotrophic case (Fig. 5.9A). With increasing depth this reduction of phytoplankton is weakened, with an asymptotic relationship. Remarkably, the phytoplankton is still reduced by 15% in 100 m deep oligotrophic lakes. With increasing nutrient loads the macrophyte effect diminishes with a sigmoidal relationship, which is less steep than in shallow lakes. Nutrient loading can be increased from $0.01\,\mathrm{g\,P\,m^{-2}\,yr^{-1}}$ to $0.1\,\mathrm{g\,P\,m^{-2}\,yr^{-1}}$; within this range the phytoplankton reduction by macrophytes is fully maintained. When a load of $0.5\,\mathrm{g\,P\,m^{-2}\,yr^{-1}}$ is exceeded this influence of macrophytes on phytoplankton diminished rather fast. In 100 m deep and hypertrophic lakes no macrophyte effect is observed. In parabolic shaped lakes

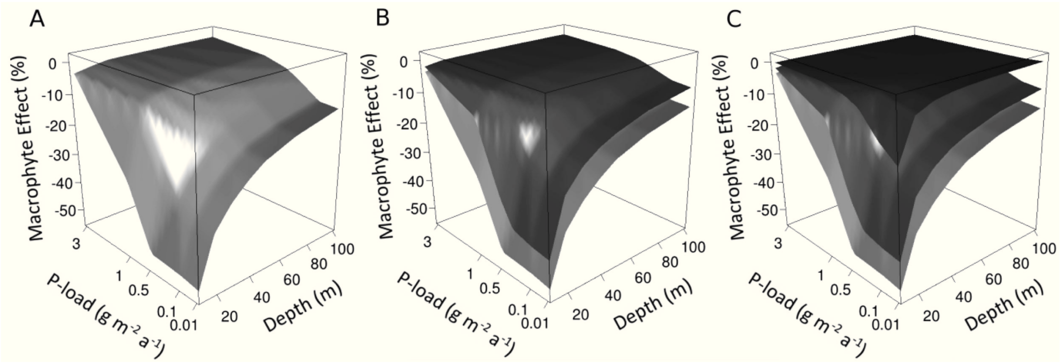

Figure 5.9: Macrophyte effects on epilimnetic summer phytoplankton (June–September) in dependence of lake depth and nutrient loading in A) a conic lake (light grey), B) a parabolic lake (grey) and C) an elliptic lake (dark grey).

the macrophyte effect is generally 17% to 63% weaker than in conic lakes (Fig. 5.9B). In elliptic shaped lakes the macrophyte effect is smallest (69% to 100% less than in conic lakes) and only observable in oligotrophic lakes shallower than 20 m where a reduction of summer phytoplankton of 20% can be achieved at most (Fig. 5.9C).

Lake area was also tested, but had no effect on the strength of the macrophyte effect. This was based on the fact that our model did not consider different wind fetches and macrophyte growth did not depend on the littoral slope. Because of that, all macrophyte covered area- and volume-relations stayed independent from the total lake area and followed the normalised form of the hypsographic curves (Tab. 5.5).

5.3.4 Occurrence of a hysteresis

Hysteresis effects of the model for restoration of the lakes after eutrophication were only small (Fig. 5.10A). The tipping point of critical nutrient loads after which the system switches into the turbid state (defined as phytoplankton WW levels $> 4\,\mathrm{mg\,L^{-1}}$) was always higher when the macrophyte module was switched on (Fig. 5.10B). No hysteresis occurred without the macrophyte module (Fig. 5.10B). The shallower lakes with 11 m to 30 m depth reacted most sensitively to increased nutrient loading when no macrophytes were present and switched to the turbid state very early. All macrophyte-free lakes deeper than 30 m showed the same critical nutrient load of $0.2\,\mathrm{g\,P\,m^{-2}\,yr^{-1}}$. When macrophytes were present, shallow lakes could buffer the highest amount of areal loading of $0.8\,\mathrm{g\,P\,m^{-2}\,yr^{-1}}$ before turning to the turbid state. This capability diminished with lake depth and might converge to the tipping point without macrophytes for lakes deeper than 100 m. The reason for diminishing macrophyte effects with lake depth was the decreasing macrophyte covered area and the sharper decrease in the total volume populated by macrophytes (PVI, Fig. 5.11). While the shallowest simulated oligotrophic and conic lake had 50% coverage and

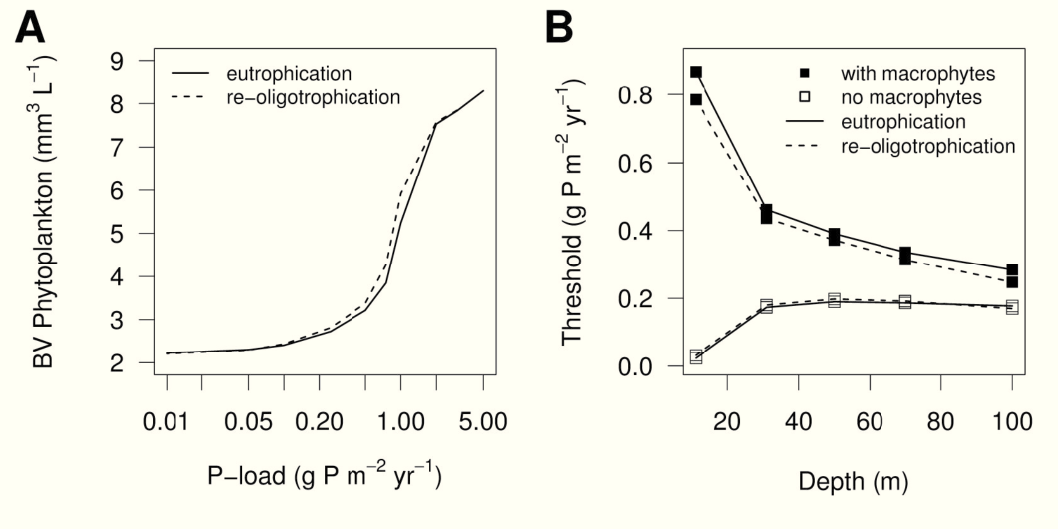

Figure 5.10: Hysteresis of summer phytoplankton biovolume (June–September) in A) the shallowest simulated lake (11 m) and B) nutrient thresholds at which a value of $4\,\mathrm{mm}^3\,\mathrm{L}^{-1}$ total phytoplankton was reached in dependence of lake depth and usage of the macrophyte module. While the system still reacted discontinuous around the phytoplankton threshold value, a pronounced hysteresis was missing in the model results.

almost 50% PVI, a lake of 60 m depth still had a coverage of 20% but only 2% of the total volume was filled by vegetation.

5.4 Discussion

5.4.1 Macrophyte effects in deep lakes

Our model simulations sugest that submerged macrophytes can significantly affect the water quality of deep lakes. Epilimnetic nutrients were exploited by macrophytes between May and October, leading to decreased phytoplankton development and less total abundance of zooplankton as a result of food limitation. In summer, macrophyte presence resulted in up to 50% less phytoplankton biomass (especially of the X_1 group which includes cyanobacteria) in the shallowest simulated conic lake (11 m maximum depth) and still 15% less phytoplankton was predicted in a 100 m deep oligotrophic lake with macrophytes as compared to a lake without macrophytes. The macrophyte effects on phytoplankton biomass decreased sigmoidally with increasing nutrient loading and asymptotically with increasing depth. In our study, weakest macrophyte effects were found in elliptic lakes, which have steep shores and therefore the least amount of littoral area colonisable by macrophytes. Furthermore, our simulations suggest that deep lakes with submerged macrophytes could resist two-

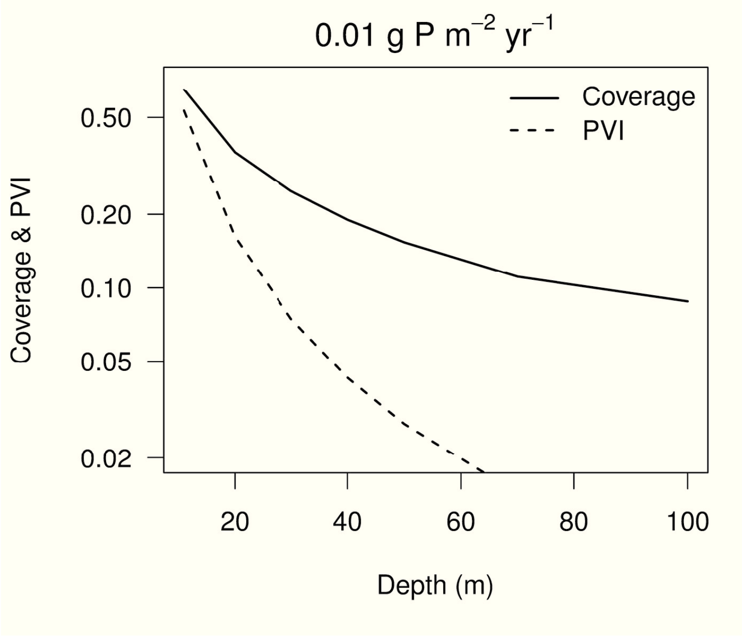

Figure 5.11: Dependence of macrophyte coverage and total volume infested with macrophytes (PVI) in an oligotrophic, 30 m deep, simulated, conic lake ($t_R = 5$ years) from depth.

to eightfold higher nutrient loading as compared to the lakes without macrophytes before switching from clear water to turbid conditions.

Due to clearer epilimnetic water under macrophyte presence, our model simulations predicted an increased metalimnetic planktonic production leading to deep chlorophyll maxima (DCM). This effect may look surprising at the first glance, but due to the observed high importance of nutrient competition with macrophytes, phytoplankton was outcompeted in the upper layer. This lead to deeper light penetration and thus supported phytoplankton development in deeper layers with higher nutrient concentrations, especially for low-light adapted species. DCM have been observed in deep lakes with abundant submerged macrophytes, e.g. in the oligotrophic, 70 m deep Lake Stechlin (Gervais et al. 1997; Padisák et al. 1997) or other lakes (Reynolds 1992) where sufficient light penetrates these depths and where the nutrient availability is higher than in the epilimnion (Padisák et al. 2003). Proving an effect of submerged macrophytes on DCM formation in real lakes, however, seems impossible.

In the sensitivity analysis of Janse et al. (2010) for PCLake, from which the macrophyte submodule was taken, lakes reacted most sensitive to alterations of external input factors. Thereby, water depth, P and N loading, retention time, and lake size were the most important factors followed by process parameters for zooplankton and phytoplankton growth rates, settling rates and macrophyte process parameters. In our combined model, lake area was of minor importance because wind fetch and resuspension of detritus were not implemented. Both processes would increase turbidity more easily in lakes with large areas. Nevertheless, the littoral area in deep lakes contributing to resuspension was only a fraction of the total area so that the contribution of resuspension to turbidity was expected to be lower than in shallow lakes. However, nearshore macrophytes may exert effects further offshore comparable to the effects described for dreissenid mussels in large lakes (e.g. Hecky et al. 2004). For SALMO, process parameters of photosynthetic production of the phytoplankton were most sensitive (Recknagel & Benndorf 1982) so that the specific light extinction of macrophytes strongly affected phytoplankton growth. However, in lakes deeper than 20 m shadowing by macrophytes only took place in less than 10% of the total lake volume (Fig. 5.11), and thereby reduced the shadowing impact of macrophytes on phytoplankton by a factor of 11 compared to the importance of nutrient competition.

The simulated effects of submerged macrophyte presence on phytoplankton abundance were mainly attributed to a competition for nutrients, resulting in lowered nutrient concentrations in the epilimnion. This seems a useful approach as nutrient constraints (bottom-up control) are comparatively strong in deep lakes as compared to shallow lakes (Jeppesen et al. 1997). A number of field studies confirm the potential importance of competition for nutrients between macrophytes and phytoplankton in both deep and shallow lakes. Hilt et al. (2010) noticed that the rapid spread of submerged macrophytes in Lake Scharmützelsee was paralleled by a sharp decrease in epilimnetic summer total P concentrations. They calculated that macrophytes, including epiphyton, may have stored P amounts comparable to those present in the epilimnion in summer. In another study, rapid colonisation with a rooted macrophyte (*Elodea species*) in a small shallow lake after biomanipulation was followed by low summer phytoplankton biomass due to nitrogen limitation (Ozimek et al. 1990; van Donk et al. 1993) and dense charophyte mats were able to keep phytoplankton biomass low by competition for phosphorus (Kufel & Ozimek 1994). In 231 lakes and ponds in The Netherlands, chlorophyll *a* and nutrient concentrations were lower in systems when areal macrophyte coverage exceeded 5% (Portielje & Van der Molen 1999). In general, nutrient competition is supposed to be highest for non-rooted macrophyte species (e.g., *Ceratophyllum* species, to a certain extend charophytes (Blindow et al. 2014), although their rhizoids are also able to take up sufficient nutrients for growth (Wuestenberg et al. 2011)) which cannot use the sediment nutrient pool, and thus take up nutrients from the water column (Barko et al. 1988; Barko et al. 1991). In contrast, rooted macrophytes mainly use nutrients from the sediment (Barko et al. 1988) and, depending on a number of factors, can act as a source or a sink for nutrients (Carignan & Kalff 1980; Pieczyńska 1993). Our simulated macrophytes were a sink as long as their internal nutrient storage did not reach their stoichiometric limit or they produced new biomass. Whenever respiration was higher than the uptake rate to fill the internal nutrient storages they were a net source. 25% of dying plant parts directly released their nutrients into the water column. For example in autumn when macrophytes were dying an enhanced phytoplankton development was simulated (Fig. 5.8A), which might have profited from remineralised nutrients. It is only the remaining detritus which was assigned completely to the sediments. A net source effect of macrophytes for longer periods has been found for very deep lakes (200 m) and extremely oligotrophic scenarios (data not shown), where macrophytes enriched the water with nutrients from sediments.

In our model, only 10% of the summer macrophyte biomass was allocated to the roots taking up nutrients from the sediment based on the data used in PCLake. A higher percentage would have resulted in a higher P uptake from the sediment. However, nutrients were also taken up from the water. Marl-encrustations occur on submerged macrophytes under certain conditions, especially on charophytes (Blindow 1987), favouring immobilisation of P (Kufel & Kufel 2002; Siong & Asaeda 2006). Reduced N availability may also occur due to increased nitrification (Körner 1999) and denitrification (Weisner et al. 1994) in the biofilm of plants. Macrophyte presence in our model also positively affected hypolimnetic oxygen concentrations, thus increasing P retention in the sediments. This mechanism further reduced P availability for phytoplankton during the next vegetation period.

The modelled macrophytes were assumed to equally populate available areas irrespective of littoral slopes or terrestrial shading so that their total influence might be overestimated and be considered as maximum predictions. Furthermore the macrophytes in this model version were assumed only to remineralise for 25%, which might have underestimated the nutrient release to the water column especially when the plants die. On the other side, the present model potentially underestimated the effect of zooplankton grazing on phytoplankton since active horizontal movements into protecting macrophyte stands were not modelled. Large zooplankton seeks refuge from fish predation either by vertical migration into the metalimnion and hypolimnion in deeper lakes (e.g., Gliwicz 1986) or by horizontal migration into macrophytes in shallow lakes (Timms & Moss 1984; Jeppesen et al. 1991; Jeppesen et al. 1997; Lauridsen & Lodge 1996). The importance of macrophytes as a refuge for pelagic cladocerans depends on plant density and type, and on the density and composition of the planktivorous fish in the vegetation (Jeppesen et al. 1997, and references therein). Blindow et al. (2000) concluded that in lakes with dense, well-established charophyte vegetation, zooplankton grazing was of minor importance as compared to nutrient competition due to predation, low food availability or a combination of both. In contrast, zooplankton to phytoplankton biomass ratios as a measure for grazing pressure were found to be positively related to submerged macrophyte cover in shallow lakes of Denmark, Belgium and The Netherlands (Muylaert et al. 2010). In general, however, top-down control is supposed to be less important in deep lakes as compared to shallow lakes (Jeppesen et al. 1997).

Our simulations based on a combination of existing model components are suggested to be a step forward towards a better mechanistic understanding of macrophyte effects in deep lakes. They showed that increased shading inside of macrophyte stands is of lesser importance in deep lakes as compared to the nutrient effect. Both effects were restricted to the lake volume filled with submerged macrophytes which was much smaller than in shallow lakes. The release of allelopathically active substances by macrophytes has not been considered in the model as this process has been suggested to require rather high macrophyte coverage (Hilt & Gross 2008). In deeper lakes, submerged macrophytes decline more gradually with increasing turbidity and the impact of submerged macrophytes on turbidity is smaller than in shallower lakes. The occurrence of a hysteresis is thus less likely with increasing water depth (Scheffer 1998). Collapse and recovery of macrophytes in response to gradual changes in water turbidity should thus be more predictable than in shallow lakes that often exhibit strong resilience. However, the response of deeper lakes to minor changes in nutrient loading can still be discontinuous when the lake is close to the critical threshold level, similar to findings made for rivers (Hilt et al. 2011). In practice, deep lakes that lost their submerged vegetation due to eutrophication may thus also show resilience to decreasing nutrient loading and the critical threshold level for macrophyte recovery may often be unknown. During deep lake restoration, re-establishment of submerged macrophytes may thus face some of the problems detected for shallow lakes (Hilt et al. 2006).

5.4.2 Model integration

Our results show that the integration of different existing model components can be a helpful approach to gain new insights into lake ecosystem functioning. This approach has been suggested as a future challenge for lake ecosystem modelling by Mooij et al. (2010).

Prototyping of the macrophyte model was relatively straightforward using the rSALMO framework and already allowed simulation of macrophyte impacts in deep lakes. It was essential that all employed model components and all numerical methods for transport modelling and numerical integration were either available as open source software or as published equation systems, allowing easy re-implementation. We strongly support Mooij et al. (2010) in their statement to keep equation systems in separate and easily accessible code. However, combining code from different programming languages still was challenging when not offered in linkable libraries. In spite of its capability to be coupled to other libraries via the FABM framework (Trolle et al. 2012), the hydrophysical model GOTM had to be run as a stand-alone version. Instead of a direct coupling, we used the GOTM output for forcing the ecological models, which prevented a complete ecological feedback on hydrophysics.

Nevertheless, the spatial agreement of temperature and dissolved oxygen profiles was acceptable (Fig. 5.5) considering the simplifications and assumptions of the model. The slight underestimation of temperature profiles might be due to the missing feedback of light extinction by phytoplankton on water temperature. The sensitivity analysis of this feedback mechanism revealed that the mixing depth would have been on average $0.8\,\mathrm{m} \pm 2.43\,\mathrm{m}$ (standard deviation) shallower (Fig. 5.12) when compared to the model without feedback. This indicates a significant, periodical

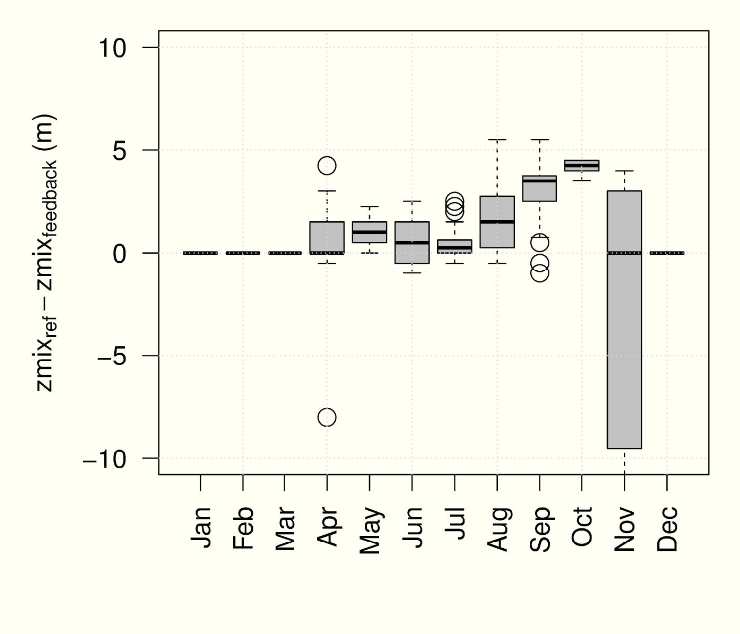

Figure 5.12: Impact of phytoplankton on thermal stratification compared to a scenario with fixed light attenuation. A positive difference of the mixing depth in the reference scenario ($z_{\text{mix,ref}}$) and the mixing depth in a scenario with variable light extinction ($z_{\text{mix,feedback}}$) indicates shallower stratification and warmer epilimnetic temperatures in the scenario with biological feedback.

warming of the epilimnion due to absorption of short wave radiation by phytoplankton. While in winter this feedback mechanism did not matter due to low phytoplankton quantities and low irradiation, this effect was most visible at the end of the stagnation period (Fig. 5.12). A similar impact of phytoplankton on water temperature was reported by Rinke et al. (2010) for Lake Constance. However, we most probably overestimated the impact of this feedback mechanism in September and October where degradation of the thermocline was postponed considerably by a warming because of the overestimated phytoplankton biomass. Smaller epilimnetic volumes might have increased the competition for nutrients between phytoplankton and macrophytes since the total amount of available nutrients for planktonic growth was limited.

In addition, macrophytes do not follow vertical transport and grow over several model layers, so they exceed the paradigm of the FABM framework (Trolle et al. 2012) to use a strictly 0-dimensional model within each layer. We addressed this problem by allowing the macrophyte submodule to access the state variables in all affected water layers.

The constant water level and neglected evaporation of the model is a simplification. Therefore, the quantity of outflow needed to be as high as the inflow. Furthermore, no influence of the inflowing water on turbidity and temperature was assumed. We distributed the inflows and outflows equally over the top 10 m which was representative for groundwater fed lakes with small water level fluctuations. Entraining all inflowing nutrients to the epilimnion resulted in a “worst case scenario” in terms of eutrophication and nutrient availability to algae and macrophytes. For the long hydraulic retention times of several years in the simulated deep lakes, inflows might not be the main driver for turbulence, temperature profiles and dilution thus keeping the error made by these simplifications low. Since this study was mainly focussed on a theoretical influence of submerged macrophytes on phytoplankton in deep lakes we considered this simplification necessary in order to reduce complexity and to be able to distinguish controlled factors (fixed effects) and random effects. The same holds for the weak correlation between simulated and measured phytoplankton biomass. It was considered to be sufficient for our purpose.

The low sensitivity of model outcomes to retention time of 1.2% indicated that the simulated retention times were still so high that biological processes were fast enough to make use of the loaded nutrients before plankton and water became diluted. The effect of retention time only becomes important at much shorter time scales (Hilt et al. 2011) which are unrealistic for most deep lakes. The 1D approach compared to 3D models has its strength in lower demands for computing power and fewer requirements for input data. In addition, simpler models allow more interactive use and therefore more flexibility for comparing alternative process formulations.

Due to the simplifications of the model and the assumptions of homogenous macrophyte colonisation and low sediment resuspension, the modelled macrophyte effect can be regarded as a maximum estimate for deep lakes. We thus conclude that our derived dynamic lake model suggests a significant impact of submerged macrophytes on water quality in deep lakes with comparable properties to the simulated ones. Our model might also be used to investigate the role of macrophytes during climate change in deep lakes similar to studies available for shallow lakes where more frequent transitions to turbid states were predicted (Mooij et al. 2007). Additions and extensions such as inclusion of further functional macrophyte type groups, reaction of macrophytes to changing water levels, or implementation of more interactions could be developed and tested within the rSALMO package prior to an incorporation of the macrophyte module in more complex frameworks such as FABM (Trolle et al. 2012) which even would allow coupling to 3D hydrophysical models.

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6 Summary

Climate change affects lake ecosystems in many ways by direct and indirect temperature impacts on hydrophysical structure, hydrology, chemical cycles and on biological interactions. The identification of these climate signals can be complicated and superimposed by other environmental changes, such as land use changes. The aim of this thesis was to seperate temperature effects from effects of management and other environmental influcences and to understand the underlying complex processes causing significant changes of ecosystem states. This understanding is important for decisions of lake and reservoir managers to counteract unfavorable consequences of climate change.

For the recent study, long-term data of meteorological, hydrophysical and biological variables (phytoplankton, crustacean zooplankton, fish) of the German drinking water reservoir Saidenbach were analysed. Based on this long-term data set, strong indicators for climate induced changes have been identified. In particular, increasing water temperatures since 1975, earlier break up of ice covers and an altered hydrophysical structure could be detected. Thereby, stratification stability increased and turbulent mixing decreased in summer. The water of the reservoir warmed more than the tributaries resulting in a trend to deeper entrainment of the inflows.

As further indicators of climate change, an increased annual biomass of phytoplankton and species shifts in the phytoplankton community in spring and summer had been observed. During the spring mass development, the diatom *Aulacoseira subarctica* became dominant in recent years with warm winters and early ice-out. Its unusual spatial pattern with occurrences in aphotic depths could be explained by easier resuspension compared to other diatoms. By being resuspended first and establishing a high inoculum, *A. subarctica* profits from an earlier ice-out and earlier full circulation. In spite of a reduced nutrient loading to the epilimnion, in summer, the diatom *Fragilaria crotonensis* was displaced increasingly by cyanobacteria. This species shift could be explained well by the hydrophysical regime shift.

Although, the annual total phytoplankton biomass increased since 1990, the crustacean zooplankton in Saidenbach reservoir did not seem to profit from improved food resources. To the contrary, *Daphnia* abundances reduced tremendously. We could show that the influcence of fish stocks were underestimated. The stocked silvercarp may have contributed up to 70 % of the total zooplanktivorous fish biomass which had a temperature and density dependent effect. The faster growth of *Daphnia* at higher temperatures could not compensate for the more actively grazing fish when stock of zooplankitvorous fish was too high. Still, temperature was identified as the most important factor that explained 29 % of the zooplankton phenology, while the second most important predictors were zooplanktivorous fish biomass and nutrient loading, explaining 18 % of the variance.

The importance of submerged macrophytes in shallow lakes is well investigated. To increase also the understanding of their impact and their role during climate change on water quality in deep lakes, a model for stratified lakes that includes submerged macrophytes was developed. The simulations showed that macrophyte effects were mainly positive for water quality and macrophytes in deep lakes were able to potentially reduce summer phytoplankton, especially cyanobacteria by 50 % in 11 m deep and still by 15 % in 100 m deep oligotrophic lakes. Nutrient competition with phytoplankton contributed most to this macrophyte effect. In conclusion, for deep lake restoration the re-establishment of submerged macrophytes might be as important as for shallow lakes. The full lake model includes hydrophysical and ecological submodules and thus will allow further comprehensive climate simulations and the evaluation of the effectivity of adaptive strategies and scenarios for deep lakes and reservoirs.

Peer-reviewed publications

1. **Sachse R**, Petzoldt T, Blumstock M, Moreira S, Pätzig M, Rücker J, Janse JH, Mooij WM, Hilt S. (2014). Extending one-dimensional models for deep lakes to simulate the impact of submerged macrophytes on water quality; Environmental Modelling & Software, `http://dx.doi.org/10.1016/j.envsoft.2014.05.023`, in press.
2. Kind B, Muster B, Staroske W, Rapp A, Herce H, **Sachse R**, Schmidt F, Koss S, Cardoso MC, Lee-Kirsch, MA (2014). Altered spatio-temporal dynamics of RNase H2 complex assembly at replication and repair sites in Aicardi-Goutières syndrome. Human Molecular Genetics, in press.
3. Dusi E, Krenek S, Schrallhammer M, **Sachse R**, Rauch G, Kaltz O, Berendonk TU (2014). Vertically transmitted symbiont reduces host fitness along temperature gradient. Journal of Evolutionary Biology. 27 (4); 796–800.
4. Jäschke, K, **Sachse, R**, Petzoldt, T, Wagner, A, Hegewald, T, Berendonk, TU, Paul L (2013). How do German Drinking Water Reservoirs Respond to Climate Change? Wasserwirtschaft, Volume 103 (5); 32–35.
5. Wagner A, Hülsmann S, Paul L, Paul RJ, Petzoldt T, **Sachse R**, Schiller T, Zeis B, Benndorf J, Berendonk TU (2012). A phenomenological approach shows a high coherence of warming patterns in dimictic aquatic systems across latitude. Marine Biology, Volume 159 (11); 2543–2559.
6. Röske K, **Sachse R**, Scheerer C, Röske I (2012). Microbial diversity and composition of the sediment in the drinking water reservoir Saidenbach (Saxonia, Germany). Applied and Environmental Microbiology. Volume 35 (1); 35–44.
7. Van Geest GJ, **Sachse R**, Brehm M, van Donk E, Hessen DO (2010). Maximizing growth rate at low temperatures: RNA:DNA allocation strategies and life history traits of Arctic and temperate Daphnia. Polar Biology, Volume 33; 1255–1262.

Erklärung

Hiermit versichere ich, dass ich die vorliegende Arbeit ohne unzulässige Hilfe Dritter und ohne Benutzung anderer als der angegebener Hilfsmittel angefertigt habe; die aus fremden Quellen direkt oder indirekt übernommenen Gedanken sind als diese kenntlich gemacht worden. Bei der Auswahl und Auswertung des Materials sowie bei der Herstellung des Manuskriptes habe ich Unterstützungsleistungen von folgenden Personen erhalten:

Deeper entrainment of tributaries in a warmed up deep reservoir and consequences for summer phytoplankton

- René Sachse (Erstautor):
  - Projektkonzeption
  - Datenanalyse und Interpretation der Ergebnisse
  - Verfassen des Manuskriptes
- Annekatrin Wagner
  - Hypothesenerstellung
- Sylvia Michel (Diplomandin):
  - vorläufige Berechnung von Einschichtungstiefen mit einem kleineren Datensatz
- Heidemarie Horn (Koautor)
  - Quantifizierung des Phytoplanktons
  - kritische Korrekturlesung
- Thomas Petzoldt (Koautor)
  - Projektantrag
  - Projektkonzeption
  - Interpretation der Ergebnisse
  - kritische Korrekturlesung
- Lothar Paul (Senior-Autor)
  - Projektantrag
  - Beteiligung an der Verfassung von Teilen der Einleitung und Teilen des Methodenteils ($< 50\%$)
  - Bereitstellung hydrophysikalischer und meteorologischer Daten
  - kritische Korrekturlesung

Compensatory and amplifying effects of climate, oligotrophication and variable fish stocks on the plankton community in a deep reservoir

- René Sachse (Erstautor):
  - Projektkonzeption

  - Datenanalyse und Interpretation der Ergebnisse
  - Verfassen des Manuskriptes
- Susanne Rolinski
  - Methodenentwicklung zur Quantifizierung von Fischbeständen
  - kritische Korrekturlesung
- Heidemarie Horn
  - Quantifizierung von Phytoplankton
  - Ergebnisinterpretation
  - kritische Korrekturlesung
- Wolfgang Horn
  - Quantifizierung von Zooplankton
  - Ergebnisinterpretation
  - kritische Korrekturlesung
- Annekatrin Wagner
  - Bereitstellung von Daten zu Fischbeständen
  - kritische Korrekturlesung
- Lothar Paul
  - Projektantrag
  - Bereitstellung hydrophysikalischer Daten
  - kritische Korrekturlesung
- Thomas Petzoldt
  - Projektantrag
  - Projektkonzeption
  - Ergebnisinterpretation
  - kritische Korrekturlesung

Mechanisms which favor the freshwater diatom *Aulacoseira subarctica* during climate change

- René Sachse (geteilte Erstautorschaft):
  - Projektkonzeption
  - Datenanalyse und Interpretation der Ergebnisse
  - Weiterentwicklung der Methode zur Berechnung von Sinkgeschwindigkeiten
  - Modellimplementation und Simulation
  - Assistenz bei der Durchführung von Laborversuchen und Freilandprobenahmen
  - Verfassen des englischen Manuskriptes
- Anselm Rossi (geteilte Erstautorschaft):
  - Durchführung von Laborversuchen und Freilandprobenahmen
  - Datenaufnahme und Datenanalyse
  - Interpretation der Ergebnisse
  - Verfassen einer deutschen Diplomarbeit zum Thema und von Teilen des englischen Methodenteils (50%)
- Andreas Kleeberg (Koautor)

    - Bereitstellung von Methoden und Laborgerät für die Resuspensionsexperimente
- Heidemarie Horn (Koautor)
    - Quantifikation von Phytoplankton
    - Ergebnisinterpretation
- Klaus Ripl (Koautor)
    - Bereitstellung von Methoden und Laborgerät für die Sedimentationsexperimente
- Thomas Petzoldt (Senior-Autor)
    - Projektantrag
    - Projektkonzeption
    - Interpretation der Ergebnisse

Extending one-dimensional models for deep lakes to simulate the impact of submerged macrophytes on water quality

- René Sachse (Erstautor):
    - Modellkonzeption, Modellimplementation und Simulationen
    - Datenanalyse und Ergebnisinterpretation
    - Verfassen des Manuskriptes
- Thomas Petzoldt (Koautor):
    - Projektantrag und Projektkonzeption
    - Modellkonzeption
    - kritische Korrekturlesung
- Maria Blumstock (Koautor):
    - Simulationen zur Untersuchung des Hysterese-Effekts im Rahmen einer Masterarbeit
- Santiago Moreira (Koautor):
    - Konzeption und Implementation des hydrophysikalischen Modells
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- Marlene Pätzig (Koautor):
    - Quantifizierung von submersen Makrophyten im Scharmützelsee
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- Jacqueline Rücker (Koautor):
    - Bereitstellung von Validationsdaten für den Scharmützelsee
    - kritische Korrekturlesung
- Jan. H. Janse (Koautor):
    - Bereitstellung von Computercode für PCLake
    - kritische Korrekturlesung
- Wolf M. Mooij (Koautor):
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- Sabine Hilt (Senior-Autor):
    - Projektantrag
    - Projektkonzeption

  - Hypothesen
  - Beteiligung am Verfassen von Teilen der Einleitung und Diskussion
  - kritische Korrektur des Manuskriptes

Weitere Personen waren an der geistigen Herstellung der vorliegenden Arbeit nicht beteiligt. Insbesondere habe ich nicht die Hilfe eines oder mehrerer Promotionsberater(s) in Anspruch genommen. Dritte haben von mir weder unmittelbar noch mittelbar geldwerte Leistungen für Arbeiten erhalten, die im Zusammenhang mit dem Inhalt der vorgelegten Dissertation stehen.

Die Arbeit wurde bisher weder im Inland noch im Ausland in gleicher oder ähnlicher Form einer anderen Prüfungsbehörde zum Zwecke der Promotion vorgelegt.

Ich bestätige, dass ich die Promotionsordnung der Fakultät Umweltwissenschaften der TU Dresden anerkenne.

Potsdam, 11.06.2014

René Sachse