Response of plankton dynamics to inter-annual climatic variations and trends

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Abstract

The aim of our research was to investigate long-term effects of inter-annual climatic variations and trends on hydrological conditions and processes of Lake Plußsee and to examine their influence on the zooplankton community since the beginning of measurements in 1969. Therefore, we analyzed the impact of large-scale and regional forcing parameters on the trends and the variability of the stratification pattern and of water temperatures, oxygen, and nutrients prior and during the stratification period. Next, we examined the influence of these parameters on the zooplankton community in October, whereas we also analyzed if changes in the zooplankton composition could also be explained by interspecific competition or by effects of a biomanipulation experiment, which was performed in Lake Plußsee from 1991 to 1994.

Regional air temperatures and wind speeds in winter and early spring, which were closely linked to the North Atlantic Oscillation, affected the lake's heat content and the vertical mixing intensity at that time of the year and determined, therefore, the timing of the onset of stratification and the phenological dynamics of the phytoplankton and the zooplankton. The trend towards an earlier onset of stratification, which shifted from mid-April to beginning of April, resulted in earlier water-column stability in spring and entailed, thus, the extent of the epilimnetic warming trends and the hypolimnetic cooling trends in April and May. Large increases of epilimnetic temperatures and water-column stability in summer and autumn resulted in a later breakdown of stratification, which shifted from beginning of November to mid-November. Due to the prolonged stratification period deep-water oxygen concentrations were lower during the last weeks of stratification.

Despite these large changes prior and during the stratification period, we ascribed the largest variability within the cladoceran and copepod communities in October to alterations of the predation pressure by zooplanktivorous fish, whereas large-bodied species benefited from reduced predation pressure during the biomanipulation experiment. In contrast, rotifers were influenced by interspecific competition with cladocerans and copepods and by water temperature, O_2, pH, and nutrient concentrations as well. Species diversity of rotifers was negatively associated with these parameters, which can serve as proxies for primary production. Hence, our results highlight the importance of considering also food-web interactions when the aim is to analyze long-term effects of climate change on zooplankton communities, because effects of changing species interactions may superimpose the effects of abiotic environmental changes.

Zusammenfassung

Das Ziel unserer Forschung war die Untersuchung langfristiger klimatischer Veränderungen und deren Trends auf hydrologische Bedingungen und Prozesse im Plußsee und deren Einfluss auf die Zooplanktongemeinschaft seit dem Beginn der Messungen im Jahr 1969. Dafür haben wir die Auswirkungen großräumiger und regionaler meteorologischer Bedingungen auf die Trends und die Schwankungen des Schichtungsverhaltens und der Wassertemperaturen, Sauerstoffverhältnisse und Nährstoffe vor und während der Schichtungsperiode erforscht. Im nächsten Schritt haben wir den Einfluss dieser Parameter auf die Zooplanktongemeinschaft im Oktober untersucht, wobei wir ebenfalls überprüft haben, ob Veränderungen in der Zooplanktonzusammensetzung auch auf interspezifische Konkurrenz oder auf Effekte eines Biomanipulationsexperiments, welches von 1991 bis 1994 im Plußsee durchgeführt wurde, zurückgeführt werden konnten.

Die regionalen Lufttemperaturen und Windgeschwindigkeiten im Winter und Frühjahr, welche stark mit der Nordatlantischen Oszillation verbunden waren, wirkten sich zu dieser Zeit auf den Wärmegehalt und die Durchmischungsintensität aus und beeinflussten dadurch den Zeitpunkt des Schichtungsbeginns und die phänologischen Dynamiken des Phytoplanktons und des Zooplanktons. Die Berechnungen zeigten, dass die Schichtung im Frühjahr zunehmend früher eintrat; sie verschob sich von Mitte April auf Anfang April. Die zunehmend frühere Ausbildung einer stabilen Wassersäule hatte zur Folge, dass sich die Epilimniontemperaturen im April und im Mai stärker erwärmen konnten, im Vergleich dazu kühlten sich die Hypolimniontemperaturen zunehmend ab. Die starke Erwärmung der Epilimniontemperaturen und die zunehmende Wassersäulenstabilität im Sommer und im Herbst führten schließlich zu einer zunehmend späteren Schichtungsauflösung; sie verschob sich von Anfang November auf Mitte November. Die verlängerte Schichtungsphase wirkte

sich dabei negativ auf die Sauerstoffkonzentrationen in tieferen Wasserschichten während der letzten Wochen der Schichtung aus.

Trotz dieser großen Veränderungen vor und während der Schichtungsperiode konnten wir die größte Variabilität innerhalb der Cladoceren- und Copepoden-Gemeinschaften im Oktober auf Veränderungen im Prädationsdruck zooplanktivorer Fische zurückführen - in erster Linie profitierten große Arten vom verringerten Prädationsdruck während des Biomanipulationsexperiments. Rotatorien wurden hingegen sowohl durch interspezifische Konkurrenz mit Cladoceren und Copepoden, als auch durch Wassertemperaturen, Sauerstoff, pH, und Nährstoffe beeinflusst. Die Speziesdiversität der Rotatorien war negativ mit diesen Parametern verbunden, die auf eine Verbindung mit der Primärproduktion schließen lassen. Unsere Ergebnisse verdeutlichen, wie wichtig es ist bei Langzeituntersuchungen zum Einfluss von Klimaveränderungen auf Zooplanktongemeinschaften auch Veränderungen innerhalb des Nahrungsnetzes zu berücksichtigen, denn die Einflüsse veränderter Speziesinteraktionen können die Effekte abiotischer Umweltveränderungen überlagern.

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Zusammenfassung

1 Introduction

1.1. State of the art

Measurements of global near-surface temperatures displayed a warming trend that was most pronounced during the last decades of the 20th century (Trenberth et al. 2007). By comparison, land and ocean surface temperature trends were larger in the northern hemisphere than in the southern hemisphere (Brohan et al. 2006; Rayner et al. 2006). According to simulations with climate models driven by increasing concentrations of carbon dioxide and methane in the atmosphere, these trends are also predicted to continue in the future (Meehl et al. 2007). Although mean surface temperatures will increase globally in the 21st century, some regions will experience larger warming than the global mean. These are, for instance, Europe, North America, Africa, and Central Asia (Christensen et al. 2007).

The heat balance of lakes is determined by meteorological forcing that acts across the air–water interface (Edinger et al. 1968; Sweers 1976). Thereby, several meteorological parameters contribute to the thermal conditions of a lake; above all, solar radiation, air temperature, and wind speed (Wetzel 2001). A change in meteorological forcing parameters will, therefore, influence the physical conditions of the lake. However, due to the interdependency of meteorological variables, it is quite difficult to estimate and predict the consequences of each single forcing parameter on a lake ecosystem and its most important processes. Although other factors also contribute to the heat balance of lakes, many studies have shown that air temperatures and lake surface temperatures are closely connected and that increasing air temperatures will substantially affect lake water temperatures (Robertson and Ragotzkie 1990; Hondzo and Stefan 1993; Livingstone and Dokulil 2001; Peeters et al. 2002).

Large-scale meteorological phenomena can also exert great influence on the regional climate and are, therefore, able to affect the dynamics of biotic ecosystems. The North Atlantic Oscillation (NAO), for example, is a major pattern encapsulating the interannual climate variability in the northern hemisphere during wintertime (Hurrell 1995). The changes in the NAO-index are determined from differences in sea-level pressure between the sub-tropic Azores high and the sub-polar Icelandic low. A positive NAO-index is characterized by a remarkably high sea-level pressure across the Atlantic in combination with a remarkably low sea-level pressure across the Arctic, whereas a negative NAO-index is represented by relatively low levels of both pressures systems (Hurrell 1995). The largest amplitude anomalies in sea-level pressures occur during the winter months, when atmosphere dynamics are most pronounced (Hurrell and Deser 2009). This is why the largest effects of the NAO-index on meteorological conditions can be detected in winter. In years with a positive NAO-index northern Europe and eastern United States experience warmer air temperatures, increased precipitation, and higher wind speeds than average, while the northwestern Atlantic and Mediterranean regions experience colder and drier conditions. The opposite applies to years with a negative NAO-index (Visbeck et al. 2001). Especially during the late 1980s and early 1990s, the NAO-index was associated with a strong positive phase of the NAO-index (Hurrell 1995).

Due to its strongest signal on regional meteorological conditions in winter, the NAO-index was often used to asses its influence on freshwater ecosystems in winter and spring. With its strong influence on air temperatures, the winter NAO-index was found to be associated with lake surface temperatures in winter and early spring (George et al. 2000; Gerten and Adrian 2001; Livingstone and Dokulil 2001; Scheffer et al. 2001). Ice cover also plays an important role determining water temperatures and lake dynamics at that time. Ice-off dates occurred earlier in years with milder winters (Robertson et al. 1992; Livingstone 1997; Adrian and Hintze 2000; Weyhenmeyer et al. 2004). Many lakes experienced a shorter duration (Palecki and Barry 1986; Magnuson et al. 2000; Assel et al. 2003), a reduced frequency (Hendricks Franssen and Scherrer 2008), or even the absence (Assel and Robertson 1995; DeStasio et al. 1996; Adrian and Hintze 2000) of ice coverage as a result of increasingly warm winter temperatures within the last decades. Austin and Colman (2007) also found a decline in winter ice cover during the last decades and they even detected that the extent of surface temperature increase in summer was related to ice cover duration during the previous winter.

The effect of climatic conditions on the thermal conditions of various lakes becomes especially noticeable in the changes of the stratification and mixing pattern of a lake. Numerous lakes experienced an earlier onset of the summer stratification period in consequence of increasingly warm air temperatures and an earlier ice-off in winter and earlier spring (Adrian et al. 1995; King et al. 1997; Winder and Schindler 2004; Austin and Colman 2007). A shift in the timing of the onset of stratification implied consequences for vertical mixing and the temperatures of the epilimnion and the hypolimnion. Various lakes experienced long-term warming trends of surface water temperatures, which reflected increasingly warm air temperatures within the last decades (Livingstone 2003; Arhonditsis et al. 2004; Coats et al. 2006; Schneider and Hook 2010). In contrast, deep-water temperatures displayed large differences between lakes in response to warmer winter temperatures: Some lakes experienced warmer (Livingstone 2003; Arhonditsis et al. 2004; Vollmer et al. 2005), unchanged (Robertson and Ragotzkie 1990), or even colder (Hondzo and Stefan 1991; Gerten and Adrian 2001) temperatures. Hondzo and Stefan (1993) showed in their modeling study that the response of these temperatures to future global warming depends on lake morphology.

Observations and model studies showed that the depth of vertical mixing in large and deep lakes will decrease after warmer winters (DeStasio et al. 1996; Livingstone 1997; Straile et al. 2003a; Verburg et al. 2003). These perturbations of vertical mixing will also interfere with a downward mixing of oxygen to deeper strata of the lake (DeStasio et al. 1996; Livingstone and Imboden 1996; Straile et al. 2003a). A trend towards a later breakdown of stratification (Livingstone 2003) can even intensify low oxygen concentration conditions or even produce anoxic conditions in deeper strata of a lake (DeStasio et al. 1996; Jankowski et al. 2006;

Rempfer et al. 2010). Furthermore, Straile et al. (2003b) found reduced cooling of the upper water layers in warm winters to account for a reduced upward mixing of nutrients compared to colder winters.

In addition to its effect on vertical mixing and, hence, on nutrient redistribution, meteorological conditions associated with the NAO-index also influence the intensity of nutrient release from the catchment area into a lake. Warmer air temperatures and increased precipitation, which are associated with a positive NAO-index in Northern Europe, can accelerate the thawing of frozen ground in the catchment area and enhance the release of essential and limiting nutrients from the soil into rivers and lakes (Monteith et al. 2000; George et al. 2004; Weyhenmeyer 2004).

In consequence of milder winters and springs, the phytoplankton spring maximum was observed to shift towards an earlier date in many lakes (Adrian et al. 1995; Weyhenmeyer et al. 1999; Winder and Schindler 2004; Peeters et al. 2007). There are also indications for an earlier (Müller-Navarra et al. 1997) and more intense (Güss et al. 2000) phytoplankton spring maximum in Lake Plußsee in response to warmer winter and spring temperatures. The observed shifts of the phytoplankton maximum can primarily be ascribed to changes in the light and nutrient availability whereas the duration of snow and ice cover have an important effect on light availability and vertical mixing intensity. These are key parameters for the development and growth of phytoplankton species and primary production, but they also set the starting conditions that modulate the species composition (Diehl 2002; Huisman et al. 2004; Winder and Hunter 2008; Berger et al. 2010).

Zooplankton populations also reached their spring maximum earlier after mild winters and springs. In spring, zooplankton species development is predominantly influenced by water temperature (Adrian and Deneke 1996; Gaedke et al. 1998; Straile 2000; Benndorf et al. 2001). Müller-Navarra and Lampert (1996) demonstrated that both food quality and food quantity are high during the phytoplankton maximum in spring. High food availability and warm water temperatures enable a rapid increase of the zooplankton community at that time. Thus, in response to warmer water temperatures and an earlier phytoplankton spring maximum, which both occurred in response to warmer winter and spring temperatures, zooplankton species were able to reach higher abundances at an earlier date. Above all, rotifers (Adrian et al. 1999; Gerten and Adrian 2000; Winder and Schindler 2004; Tirok and Gaedke 2006), cladocerans (Gaedke et al. 1998; Gerten and Adrian 2000; Straile 2000; Benndorf et al. 2001), and copepods (George 2000; Gerten and Adrian 2002; Adrian et al. 2006; Seebens et al. 2007) benefited from warmer water temperatures in spring.

Although growth and development rates of rotifers, cladocerans, and copepods are positively related to water temperature (Bottrell et al. 1976; Vijverberg 1977; Vijverberg 1980; Stemberger and Gilbert 1985), warmer water temperatures at the beginning of the seasonal succession of the zooplankton (Sommer et al. 1986) had a different influence on these groups. Rotifers and cladocerans reproduce parthenogenetically and their populations can grow rapidly in spring within a short period (Gerten and Adrian 2000; Straile 2000). In contrast, sexually reproducing copepods undergo a complex life cycle development of six embryonic and six juvenile stages; the last stage representing the adult stage (see references in Vijverberg 1980). Thus, although warmer temperatures accelerate ontogenetic development of copepods, the effects of winter and spring warming will, however, be apparent at a later stage (Gerten and Adrian 2002). In Müggelsee, the earlier start of the pelagic phase and the magnitude of the summer abundance of the copepod *Thermocyclops oithonoides* were related to winter and spring warming. Seebens et al. (2007) also related summer/autumn abundances of *Eudiaptomus gracilis* to spring variability.

Only few studies focused on the effect of climate variability on zooplankton in late summer and autumn so far (but see Adrian et al. 2006; Seebens et al. 2007; Huber et al. 2010; Sommer and Lewandowska 2011). However, increasingly growing attention on these seasons has arisen within the previous years, especially regarding the impacts of summer heat waves and their effects on freshwater ecosystems (Jankowski et al. 2006; Jöhnk et al. 2008; Wilhelm and Adrian 2008; Rempfer et al. 2010). Ecosystem dynamics in winter and spring are not only influenced by conditions in these respective seasons, but they are also influenced by conditions during the preceding seasons (memory effect; see Güss et al. [2000]). In addition, Gaedke et al. (2010) found initial phytoplankton biomass in spring to be influenced by processes during the previous year, whereby these conditions were memorized through concentrations of overwintering plankton species. Wiltshire and Manly (2004) demonstrated for the North Sea that warmer water temperatures in autumn (October-December) delayed the diatom phytoplankton bloom in the following winter (January-March). Wiltshire et al. (2008) hypothesized that overwintering copepods can retard the spring phytoplankton bloom after warm winters due to higher grazing rates. These findings are based on marine systems. However, George and Hewitt (1999) observed higher numbers of overwintering *Eudiaptomus gracilis* in Eastwaite Water feeding effectively on diatom *Asterionella* spp. during warm winters.

The development and the phenology of species are, however, also controlled by interactions between species. Rotifers, for example, interfere with cladocerans and copepods via exploitative competition of shared, limiting food resources and via mechanical interference (see reviews by Walz 1995 and Brandl 2005). In contrast, larger cladocerans and copepods interfere primarily with invertebrate predators as *Chaoborus* spp. (Hanazato and Yasuno 1989; Neill 1990; Stibor 1992; Mumm 1997) or with vertebrate predators as fish (Brooks and Dodson 1965; Hall et al. 1976; O'Brien 1979; Christoffersen et al. 1993). While vertebrate predators selectively feed on larger-sized zooplankton species, invertebrates prefer small or medium-sized prey (Brooks and Dodson 1965; Hall et al. 1976; Black and Hairston 1988). Since the development of invertebrates and vertebrates also depend on water temperature, these groups will also be affected by climate warming and will, therefore, produce perturbations in the food-web structure.

1.2. Aim of this thesis

The aim of this PhD thesis was to assess the effects of climate warming on Lake Plußsee since the beginning of measurements in 1969 to 2011. Therefore, we studied the long-term effects of inter-annual climatic variations and trends on hydrological conditions and processes of Lake Plußsee and examined their influences on the lake's zooplankton community.

The purpose of the first part of this thesis was to assess the influence of meteorological forcing conditions on physical, chemical, and nutrient parameters of Lake Plußsee from 1969 to 2006. Therefore, we studied the long-term variability of the North Atlantic Oscillation on the weekly trends of regional air temperatures and wind speeds. Next, we examined the impact of meteorological forcing on the stratification pattern and analyzed the trends of the onset and the breakdown of stratification. Furthermore, we analyzed the trends of water temperatures, oxygen concentrations, and pH in the epilimnion, metalimnion, and hypolimnion for each calendar week. We also considered the monthly trends of nutrient concentrations in each layer to assess how they were affected by vertical mixing in spring and by water column stability throughout the stratification period. Furthermore, we related nitrogen, phosphorus, and silicate concentrations to pH, and oxygen concentrations, which can serve as proxies for photosynthetic activity.

Most long-term studies analyzed the trends of parameters, which are based on data with a time-resolution of seasons or months. In Lake Plußsee, several limnological parameters were measured on at least a monthly basis from 1969 to 1980 and on a weekly basis from 1981 to 2006. Thus, it was possible to identify possible long-term temperature changes that would possibly remain undetected if we had only analyzed monthly trends. Furthermore, our analysis also takes the vertical structure of the lake into account and considers an often neglected part of the stratified system: The metalimnion.

The first part of this thesis – except for the analysis of nutrients – is based on the paper "Trend analysis of weekly temperatures and oxygen concentrations during summer stratification in Lake Plußsee: A long-term study" published by R. Rösner, D. C. Müller-Navarra, and E. Zorita in the journal "Limnology and Oceanography" in 2012 (Rösner et al. 2012). These are the chapters 1, 2.1, 2.2.1-2.2.3, 3.1, and 4.1. In the course of this thesis, new ideas developed which elaborated on the original text of the published paper without changing the fundamental statements of it.

The purpose of the second part of this thesis was to investigate how biomasses, species diversities, and species abundances of the three major zooplankton groups (rotifer, cladocerans, and copepods) of Lake Plußsee in October from 1969 to 2011 were affected by changing abiotic environmental conditions which we analyzed in the first part of this thesis. For this purpose, we performed a Principal Component Analysis (PCA) on each zooplankton group in October as well as on physical, chemical, and nutrient parameters of each month from February to October. Next, we correlated the principal components derived from abiotic environmental parameters with the principal components derived from each zooplankton group. We also used the principal components of the abiotic environmental parameters to correlate them with the biomasses and the species diversities of each zooplankton group. In this way, we could examine how and at which time of the year physical, chemical, and nutrient parameters affected the rotifer, cladoceran, and copepod species in October. Furthermore, we performed a Canonical Correlation Analysis (CCA) to assess possible effects of interspecific competition between rotifers, cladocerans and copepods. In addition, we investigated if the zooplankton community was affected by the biomanipulation experiment, which was performed from 1991 to 1994 in Lake Plußsee.

Numerous studies researched the effects of climate change on zooplankton community dynamics in response to changing winter and spring conditions; however, only few studies focused on the effects of climate warming on zooplankton communities in summer and autumn. Therefore, our analysis covers a time period, which has not yet received that much attention. Furthermore, we considered all zooplankton species on a species level. Several studies focused either only on specific species of the food-web or they considered several zooplankton groups only on the genus level. This way, we could identify possible alterations in the zooplankton species compositions or in the species interactions that would have probably remained unclear if we had only considered the zooplankton on a genus level.

2 Materials and Methods

2.1. Characteristic features of Lake Plußsee

Lake Plußsee is situated in Schleswig-Holstein in northern Germany (54°10’ N, 10°23’ E). Lake Plußsee was formed as a kettle lake about 12000 years ago during the last glacial period (Overbeck and Chróst 1993). The lake has an area of 142900 m², a volume of 1345000 m³, a maximum depth of about 29.2 m, a mean depth of 9.4 m, and is situated about 24.5 m above sea level (Krambeck 1974). Fig. 1 shows an aerial view and the vertical profile with isopleths for every meter of depth of Lake Plußsee.

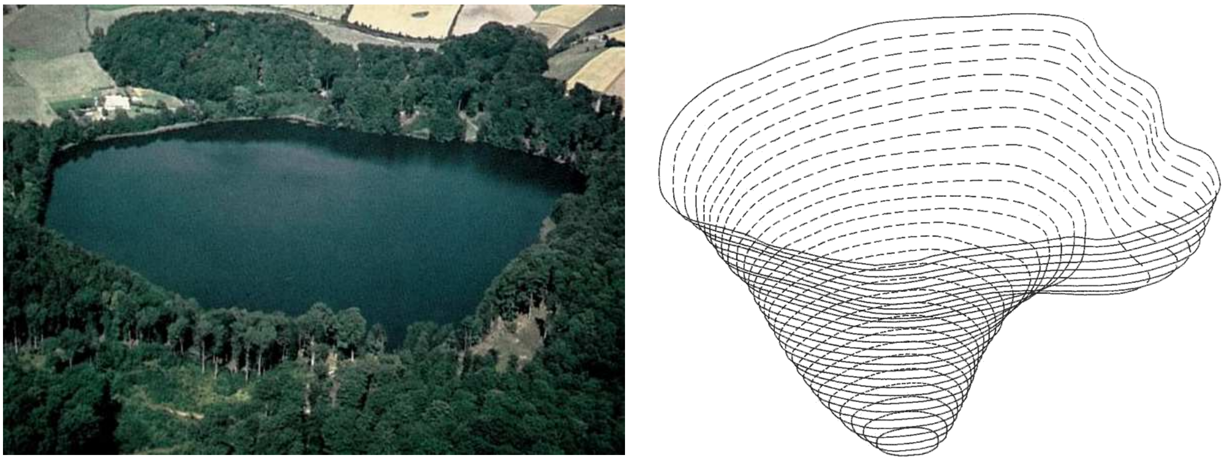

Fig. 1. Left: Aerial view of Lake Plußsee (photo taken by Waldemar Ohle; Overbeck and Chróst 1993); Right: Vertical profile of Lake Plußsee with isopleths for every meter of depth (Krambeck 1974)

The lake is situated in a valley and is surrounded by woodland, which creates an effective wind shelter. Lake Plußsee possesses no direct inflow and only a minor outflow; therefore, the flushing rates are small (Güss et al. 2000).

Lake Plußsee is a dimictic lake. It circulates twice a year in spring and autumn and stratifies in summer and winter. The lake is inversely stratified during periods of ice cover in winter and the summer stratification period lasts approximately from mid-April to mid-November. Between both stratification periods, the lake is more or less completely mixed.

Lake Plußsee is a eutrophic lake. It is characterized by a high production due to high phosphorus concentrations and high nitrogen concentrations in spring. During spring circulation, the content of soluble reactive phosphorus (SRP) is about 200 µg P L^{-1}. During the phytoplankton maximum in spring and the stratification period, the amount of SRP decreases rapidly in the euphotic zone due to the activity bacteria and algae, which are the most important planktonic organisms responsible for the depletion of this nutrient in the epilimnion (Overbeck and Chróst 1993). Inorganic nitrogen is the second most important nutrient for phytoplankton growth in Lake Plußsee. Its most important fractions are nitrate (NO_3^-), nitrite (NO_2^-), and ammonium (NH_4^+). During phytoplankton development in spring, nitrate concentrations decrease from 100-250 µg N L^{-1} to below 25 µg N L^{-1} in the euphotic zone and remained at similar concentrations until December. The highest ammonium concentrations (500-700 µg N L^{-1}) occur after autumn turnover and decrease continuously during winter due to nitrification. Highest ammonium concentrations (500-1000 µg N L^{-1}) are observed in the hypolimnion during the summer stratification (Overbeck and Chróst 1993). Nitrite concentrations are generally low at all times in Lake Plußsee, because nitrite is an intermediate product of (de-)nitrification.

2.2. Analysis of abiotic environmental parameters

2.2.1. Measurements of abiotic lake parameters

Lake Plußsee had been previously monitored by the Max-Planck-Institute for Limnology in Plön for several years (reviewed by Overbeck and Chróst 1993). Measurements of the hydrological parameters date back to 1969, with irregular temporal coverage. For instance, measurements do not cover the whole calendar year, because no measurements were performed during periods of ice cover in winter. In most years from 1969 to 1980 lake parameters were measured more irregularly, but at least on a monthly basis. From 1981 to 2006 weekly measurements were carried out. Measurements were recommenced in 2009 and were also performed on a weekly basis. However, measurements performed from 2009 to 2011, which covered the period of the PhD project, were not included in this analysis due to an inaccurately measuring water analyzing probe.

Measurements were taken at the point of largest depth of the lake with a vertical resolution of one meter over the water column at depths 0-15, 20, and 25 m. Physical and chemical lake parameters were measured in situ with a WTW-probe. Water temperatures were measured with a water thermometer, dissolved oxygen was determined with the use of an oxygen electrode, a glass electrode was used for pH measurement, and electrical conductivity was determined with platinum electrodes placed 1 cm apart at 20°C (Overbeck and Chróst 1993). Nutrients were measured in the laboratory. Therefore, water samples were taken with the use of a 2-L Ruttner sampler and collected in 500-ml polyethylene bottles. Dissolved components were filtered over ash-free filters. These compounds were analyzed by a Technicon continuous-flow system (Overbeck and Chróst 1993).

In the following, we used the term “abiotic environmental parameters” to comprise physical, chemical, and nutrient parameters. Thus, we excluded the biological component from this term, which is also included in “environmental parameters” or “hydrological parameters”.

2.2.2. Meteorological parameters and NAO-index

For the analysis of the influence of meteorological forcing parameters on Lake Plußsee, we used air temperature and wind speed data from the nearest meteorological station in Schleswig (54°32’ N, 9°33’ E) obtained by the German Weather Service (Deutscher Wetterdienst DWD). Schleswig is approximately 80 km away from Lake Plußsee; however, it is the closest meteorological station where data of all parameters and over the whole analysis period could be obtained.

In addition to regional meteorological forcing parameters, we used the winter NAO-index ($NAO_{Dec\text{-}Mar}$, annual mean of monthly NAO-indices from December to March), which is based on the normalized sea-level pressure differences between Ponta Delgada, Azores, and Stykkisholmur, Iceland (Hurrel 1995). The data were provided by the National Center of Atmospheric Research in Boulder, Colorado (available online at: http://www.cgd.ucar.edu/cas/jhurrell/indices.data.html#naostatmon).

2.2.3. Long-term trend analysis of physical and chemical parameters

For the analysis of long-term trends of physical and chemical parameters during the stratification period, we selected parameters which were measured most continuously and which are directly linked to meteorological forcing, above all, water temperature and dissolved oxygen (O_2) concentration. Furthermore, two more parameters were also taken into account: pH and electrical conductivity.

Since these lake parameters were not measured at the same calendar day every year throughout the analysis period, we had to create a homogenous data set first. Therefore, we linearly interpolated the available data at daily intervals and calculated the weekly means at one-meter intervals down the water column of the lake and for every year. A few years were completely removed from the analysis for the following reasons: In 1978, there were too few measurements, and in 1985 and 1986, a pump was installed which inhibited stratification. Furthermore, some years were excluded only for specific parameters due to the lack of data: These years were 1974 and 1975 for O_2 concentration and 1975 and 1976 for pH and electrical conductivity.

In the next step we identified the boundaries of the three layers (epilimnion, metalimnion, and hypolimnion) using the weekly temperature profiles. We considered the lake stratified when the temperature gradient exceeded 1°C m^{-1}, because we wanted to make sure that the lake established a stable stratification and not a transient stage of stratification that could be easily disrupted by wind again. We defined the boundaries epilimnion-metalimnion and metalimnion-hypolimnion to be situated at depths where the temperature gradients exceeded 1°C m^{-1}. Having identified the layer boundaries, we calculated the means of weekly parameters within the three layers. We, furthermore, defined the thermocline depth to be situated at depths with the maximum temperature gradient. The thermocline denotes a plane that separates the upper mixed layer from the calm deep water below and corresponds, therefore, to the depth of vertical mixing.

Electrical conductivity was used to estimate salinity, which was then used to calculate the in situ pressure (ρ) for every meter of depth (Chen and Millero 1986; Boehrer and Schultze 2008). The in situ pressure was then used to calculate Schmidt's Stability Index (SSI, Schmidt 1928; Hutchinson 1957; Idso 1973) and heat content (HC, Hutchinson 1957).

SSI is a measure of the thermal stability, which is defined as the amount of work needed to transform temperature-dependent density differences of a lake into a vertically uniform temperature distribution by mixing without addition or subtraction of heat (Schmidt 1928; Hutchinson 1957; Idso 1973).

$$\mathrm{SSI} = \frac{g}{\mathrm{A}_0} \int_{z_0}^{z_m} (z - z_g)\, \mathrm{A}_z\, (\rho_z - \rho_m)\, dz \qquad (1)$$

$$z_g = \frac{1}{\mathrm{V}} \int_{z_0}^{z_m} z\ \mathrm{A}_z\, dz \qquad (2)$$

$$\rho_m = \frac{1}{\mathrm{V}} \int_{z_0}^{z_m} \rho_z\ \mathrm{A}_z\, dz \qquad (3)$$

where SSI is the stability of the lake per unit of surface area, g is the acceleration of gravity, A_0 is the surface area of the lake, z is the depth of the lake, z_0 is the depth of the water surface, z_m is the maximum depth, z_g is the depth of the center of gravity of a lake, A_z is the area at depth z, ρ_z is the density at depth z, ρ_m is the density at complete mixing (unstratified lake), and V is the volume of the lake.

The heat content of a water body is defined as the amount of heat needed to raise the lake's water from minimum winter temperature to the maximum summer temperature (Hutchinson 1957). Since water temperatures were recorded irregularly in Lake Plußsee in winter and spring, we had to focus on the summer heat content. The total heat content (HC) of the water in each week was determined from

$$\mathrm{HC} = \frac{1}{A_0} \int_{z_0}^{z_m} A_z \ \rho_z \ T_z \ c_p \, dz \qquad (4)$$

where HC is the heat content of the lake per unit of surface area, A_0 is the surface area of the lake, z is the depth of the lake, z_0 is the depth of the water surface, z_m is the maximum depth, A_z is the volume of a lake at depth z, ρ_z is the density at depth z, T_z is the water temperature at depth z, and c_p is the water heat capacity.

We calculated the weekly linear trends of each meteorological and lake parameter using an ordinary linear regression analysis. We performed a *t*-test to test for the significance of the regression coefficients. Additionally, we calculated Pearson's correlation coefficients (*r*) to test for correlations between the time series of various parameters. For instance, the correlation between air temperature and water temperature in week 26 indicates the strength of the linear link between the values of these time series in week 26 through the analysis period.

Furthermore, we analyzed how large-scale ($NAO_{Dec\text{-}Mar}$) and regional (air temperatures and wind speeds) meteorological forcing in winter and early spring affected the timing of the onset of stratification. We also assessed the influence of an earlier and a later onset of stratification on epilimnetic, metalimnetic, and hypolimnetic temperatures during the first week of stratification. Therefore, we usually applied a Welch two-sample *t*-test, which requires normally distributed data. When a Kolmogorov-Smirnov test detected deviations from normal distribution, we applied a Mann-Whitney-*U*-test.

2.2.4. Long-term trend analysis of nutrient parameters

For the analysis of long-term trends of nutrients during the stratification period, we selected fractions of nutrient parameters which were measured most continuously and which considerably affect the nutrient cycle of lakes. We selected nitrate (NO_3^-), nitrite (NO_2^-), and ammonium (NH_4^+) as components of the nitrogen cycle, inorganic phosphate (PO_4^{3-}) and total dissolved phosphorus (TDP) as components of the phosphorus cycle, and silicate (SiO_2) as the most important component of the silicate cycle. Other fractions, e.g., total nitrogen (TN) or total phosphorus (TP), were only measured in particular years and were not included in this study.

As for physical and chemical lake parameters, we had to create a homogenous dataset first because nutrient parameters were not measured at the same calendar day every year. We linearly interpolated the available data at daily intervals and calculated the monthly means at one-meter intervals down the water column of the lake and for every year. In contrast to physical lake parameters, we analyzed the monthly means of chemical parameters instead of weekly means. Comparisons between weekly and monthly trends of nutrient parameters showed strong week-to-week fluctuation of the weekly trends probably caused by biological activity; however, the patterns of weekly and monthly trends were very similar. Some years were completely removed from the analysis for the following reasons: In 1978, there were too few measurements, and in 1985 and 1986, a pump was installed which inhibited stratification. Furthermore, some years were excluded only for specific parameters due to the lack of data: These years were 1975 for NO_3^-, 1975 and 1976 for NO_2^-, 1975 for NH_4^+, 1975 for PO_4^{3-}, 1977, 1981, 1982, and 1983 for TDP, and 1975 and 1976 for SiO_2. In addition, these parameters were not measured below a depth of 20 m from 1971 to 1976. Hence, we excluded the hypolimnetic parameters for these years from further analyses.

In the next step we calculated the monthly means of each parameter in each layer (epilimnion, metalimnion, and hypolimnion) using the layer boundaries where the temperature gradient exceeded 1°C m^{-1} and of the 0-10 m water column as well.

Finally, we calculated the monthly linear trends of each parameter from May to October using an ordinary linear regression analysis and performed a *t*-test to test for the significance of the regression coefficients. We excluded April and November from our analysis since we could not calculate the monthly means of the complete months because of the onset of stratification in mid-April and the breakdown of stratification in mid-November. We would have calculated untrustworthy monthly means for April and November if we had used values of parameters that were calculated over different time periods. Additionally, we calculated Pearson's correlation coefficients (r) to test for correlations between the time series of various parameters. We also linked physical and chemical parameters with nutrients by correlating monthly means of water temperatures, O_2 concentrations, oxygen saturations, pH, and Secchi disc transparencies with monthly mean concentrations of NO_3^-, NO_2^-, NH_4^+, PO_4^{3-}, TDP, and SiO_2 of the monthly means of the 0-10 m water column from February to October.

2.2.5. Principal Component Analysis of abiotic environmental parameters

The Principal Component Analysis (PCA) is a statistical method to define new variables as linear combinations of the original variables that fulfill certain properties, namely, that they describe a large part of the total variance. We calculated two series of independent PCAs of abiotic environmental variables for each month from February to October: One for physical and chemical parameters, and one for nutrient parameters. The purpose of this procedure was, on the one hand, to identify the most important underlying gradients in a set of collinear variables, which can already explain a large proportion of total variance of a dataset, and, on the other hand, to understand how these variables were related to each other. The PCA terminology in the literature is sometimes confusing, as different disciplines apply different definitions. In our case, *factor scores* are the time series of the new variables. The advantage of using factor scores instead of the original variables is that factor scores are independent (uncorrelated) from each other. Hence, the problem of interpreting a large number of collinear variables is reduced. Reducing the number of variables reduces also the probability of committing a Type I error in a statistical test. Type I errors denote the probability of erroneously claiming statistical significance. The risk of committing a Type I error increases when too many statistical tests are performed on the same variables in a dataset. Factor scores can also be used to calculate the *factor loadings*. Factor loadings are Pearson’s correlation coefficients between the factor scores and the original variables. They describe how much information the factor scores and the original variables share on a given principal component. Hence, they can be used to interpret the underlying gradient of a principal component.

Table 1 shows all abiotic environmental variables we used to perform the PCAs for each group of parameters and for each month from February to October. In addition to dissolved oxygen concentrations, we calculated the percentage saturation of oxygen using the method of Mortimer (1981). Oxygen saturation is the percentage of dissolved oxygen concentration relative to the equilibrium concentration of oxygen of the atmosphere and depends on the atmospheric partial pressure of oxygen, the water temperature and pressure at a given depth of a lake. Secchi disc readings were included as a generalized way to estimate the approximate density of phytoplankton populations (Wetzel 2001). In Lake Plußsee, seasonal variation in Secchi disk transparencies was closely related to chlorophyll concentrations (Overbeck and Chróst 1993). Most parameters included were the epilimnetic, metalimnetic, and hypolimnetic means of a parameter, but we also calculated the means of the upper ten meter water column of the most important parameters. We decided to include these means because they reflect the sampling technique of the zooplankton, which were taken with a single vertical tow from a depth of 10 m of the lake to the surface.

Since stratification was not yet established in February, March, and April (at least not for the entire month to consider reliable monthly means of epilimnetic, metalimnetic, and hypolimnetic variables), we performed PCAs on a reduced number of variables for these months. Therefore, we only used parameters that are independent of stratification. As physical and chemical parameters, we considered air temperature, wind speed, $\text{NAO}_{\text{Dec-Mar}}$, Secchi disc transparency, Schmidt’s Stability Index, heat content, lake surface temperature, mean lake temperature, and the means of water temperature, dissolved oxygen concentration, oxygen saturation, and pH calculated for the upper ten meter water column. As nutrient parameters, we only considered the means of nitrate, nitrite, ammonium, phosphate, total dissolved phosphate, and silicate calculated for the upper ten meter water column. Since variables are expressed in different measurement scales, we standardized all variables before the PCAs.

For all PCAs, we only used a reduced number of years instead of all years where parameters were available. Since we wanted to use the factor scores of the PCAs of abiotic environmental variables for further analyses, e.g., for correlation with the factor scores of the PCAs of the zooplankton data, we only used abiotic environmental variables of years where zooplankton samples were available. Since no physical, chemical, and nutrient variables were available for

Table 1. Physical, chemical, and nutrient parameters used for the Principal Component Analysis of abiotic environmental variables. The abbreviations used for each parameter are written in parentheses.

Abiotic environmental parameters	
Physical and chemical parameters	**Nutrient parameters**
Air temperature (AT)	Epilimnetic nitrate concentrations (ENO_3^-)
Wind speeds (WS)	Metalimnetic nitrate concentrations (MNO_3^-)
Epilimnetic water temperatures (ET)	Hypolimnetic nitrate concentrations (HNO_3^-)
Metalimnetic water temperatures (MT)	Epilimnetic nitrite concentrations (ENO_2^-)
Hypolimnetic water temperatures (HT)	Metalimnetic nitrite concentrations (MNO_2^-)
Epilimnetic oxygen concentrations (EO)	Hypolimnetic nitrite concentrations (HNO_2^-)
Metalimnetic oxygen concentrations (MO)	Epilimnetic ammonium concentrations (ENH_4^+)
Hypolimnetic oxygen concentrations (HO)	Metalimnetic ammonium concentrations (MNH_4^+)
Epilimnetic oxygen saturations (EOS)	Hypolimnetic ammonium concentrations (HNH_4^+)
Metalimnetic oxygen saturations (MOS)	Epilimnetic phosphate concentrations (EPO_4^{3-})
Hypolimnetic oxygen saturations (HOS)	Metalimnetic phosphate concentrations (MPO_4^{3-})
Epilimnetic pH (EPH)	Hypolimnetic phosphate concentrations (HPO_4^{3-})
Metalimnetic pH (MPH)	Epilimnetic total dissolved phosphorus concentrations (ETDP)
Hypolimnetic pH (HPH)	Metalimnetic total dissolved phosphorus concentrations (MTDP)
Secchi disc transparencies (SD)	Hypolimnetic total dissolved phosphorus concentrations (HTDP)
Thermocline depths (TD)	Epilimnetic silicate concentrations ($ESiO_2$)
Epilimnetic layer thickness (ED)	Metalimnetic silicate concentrations ($MSiO_2$)
Metalimnetic layer thickness (MD)	Hypolimnetic silicate concentrations ($HSiO_2$)
Hypolimnetic layer thickness (HD)	Mean nitrate concentrations 0-10 m (NO_3^- 0-10 m)
Schmidt's Stability Index (SSI)	Mean nitrite concentrations 0-10 m (NO_2^- 0-10 m)
Heat content (HC)	Mean ammonium concentrations 0-10 m (NH_4^+ 0-10 m)
Lake surface temperature (LST)	Mean phosphate concentrations 0-10 m (PO_4^{3-} 0-10 m)
Mean lake temperature 0-25 m (MLT)	Mean total dissolved phosphorus concentrations 0-10 m (TDP 0-10 m)
Mean water temperature 0-10 m (T 0-10 m)	Mean silicate concentrations 0-10 m (SiO_2 0-10 m)
Mean oxygen concentration 0-10 m (O_2 0-10 m)	
Mean oxygen saturation 0-10 m (OS 0-10 m)	
Mean pH 0-10 m (pH 0-10 m)	

the current period (2009-2011) and not all nutrients were measured for most of the 1970s and 1982, we restricted the PCA of abiotic environmental variables to the years 1969, 1970, 1984, 1988-1996 to guarantee an optimal fit of these variables with the zooplankton data. To ensure that the factor scores of the first principal components did not differ significantly, we correlated the eigenvectors calculated for the reduced number of years with the eigenvectors calculated for all available years. This analysis showed that the eigenvectors of the first three principal components of the period May to October and the first two eigenvectors of the period February to April were significantly correlated with each other and for each month, even if the eigenvectors of a certain principal component was associated with another principal component of the other dataset.

2.3. Zooplankton community analysis

2.3.1. Zooplankton samples

Zooplankton samples, which were taken by employees of the former Max-Planck-Institute for Limnology in Plön from 1969 to 1996, were made available by the museum in Kiel. These zooplankton samples were conserved in 4% formaldehyde (CH_2O) in small polyethylene bottles. Zooplankton was sampled with irregular temporal coverage within that time period. Besides 1977, samples were taken only for certain months or seasons from 1971 to 1980; consecutive weekly sampling covering longer periods of a year were not available for that time period. Also the methods of sampling and conservation varied from year to year. In 1969, 1970, 1977, and from 1981 to 1996, zooplankton was sampled on a weekly or biweekly scale and the methods can be assumed to be homogenous over this period. From 1997 to 2008 no zooplankton samples were available. From 2009 to 2011 zooplankton was sampled by Dr. Müller-Navarra on a weekly or biweekly scale and the methods were comparable to the methods from 1981 to 1996. As for abiotic environmental parameters, sampling of zooplankton was not performed during periods of ice cover. Zooplankton samples were taken at the point of largest depth of the lake with a single vertical tow taken from a depth of 10 m of the lake to the surface. Therefore, a cone plankton-net with a 56 µm mesh sieve being attached to a funnel with a 10 cm diameter was used. These samples were immediately transferred to polyethylene bottles and conserved in 4% formaldehyde.

Zooplankton samples were identified and counted by Prof. Dr. Gerhard Maier of the “Büro für Gewässerökologie”. For the identification and counting, zooplankton samples were subsampled due to the high density of organisms. Dependent on the species density, zooplankton samples were suspended in 100-1000 ml flasks with water. Subsamples were taken from the homogenously mixed suspension, transferred to 10 cm high sedimentation chambers, and counted after a sedimentation time of half an hour with an inverted microscope (Zeiss IM35). At least two aliquots per sample were counted. Furthermore, at least 100 individuals of the dominant species were counted and at least 400 individuals (apart from naupliar stages) per sample were counted. Finally, species abundances of the aliquots were extrapolated to species abundances per liter (Ind L^{-1}).

Zooplankton samples were identified and counted for the following groups only: rotifers, cladocerans, and copepods. Other zooplankton groups were not taken into account; hence, species like *Chaoborus* were excluded from the analysis. The identification was performed on the species level. In addition, the identification of cladocerans and copepods was also differentiated between the single juvenile and adult stages of each species. If identification was not possible due to poor fixation or if it was too time-consuming, identification was performed on the genus level. For instance, the identification of the species of the genus *Asplanchna* spp. would be too time-consuming since a trustworthy identification of the species requires the preparation and the analysis of the mastax of the individuals. For zooplankton identification, the following literature was used: For rotifers: Ruttner-Kolisko (1972) and Voigt and Koste (1978); for cladocerans: Flössner (1993, 2000) and Lieder (1999); for copepods: Kiefer (1973), Kiefer and Fryer (1978), and Einsle (1993). The dataset of the considered zooplankton samples comprised 56 species: 38 rotifers, 11 cladocerans, and 7 copepods (Appendix table A1).

For the analysis of the zooplankton community, we only took years into account with a homogenous sampling technique and for which samples were available that were sampled consecutively in autumn. These were the following 17 years: 1969, 1970, 1977, 1982, 1984, 1988-1996, and 2009-2011. As already mentioned, some years had to be removed from the analysis due to irregular sampling, different methods of sampling and conservation, and not available samples. Furthermore, some years had to be removed from the analysis because of to the following reasons: In 1981 and 1983, zooplankton samples could not be identified and counted due to poor fixation. The years 1985 and 1986 were removed because of the installation of a pump which inhibited stratification. Also samples of 1987 were not taken into account because of possible aftereffects of increased nutrients due to the artificial mixing caused by the pump. Furthermore, there were too few samples available for this year.

For the analysis of the zooplankton community in October, we used the species abundances (individuals per liter) of the weeks 40-43 to calculate the monthly means of each species in each of the seventeen years. Hence, the analysis comprised 68 samples in total. However, 25 samples were not available due to non-sampling. Missing dates were linearly interpolated.

2.3.2. Zooplankton biomass

The most commonly adopted method to determine the biomass of zooplankton is to calculate the dry weights by using length to weight-regression-analysis or biovolume estimations and multiply these weights with the number of individuals. Due to the small size and weights of rotifers it is more applicable to determine the dry weights indirectly by calculating the biovolumes of the different rotifer genera. Ruttner-Kolisko (1977) presented a method how to derive the biovolumes of the most common rotifer genera from rotifer body measurements. We decided to adapt the simplified formula provided by Ruttner-Kolisko (1977) where body lengths already suffice to approximate the body volume of the most common rotifer genera. If a certain genus was not described by Ruttner-Kolisko (1977), we used the formula of a genus with a similar body shape (e.g., for the genera *Lecane*, *Monostyla*, *Lepadella*, *Platyias*, and *Trichotria*, we used the formula of *Brachionus*). Biovolumes can be transformed to fresh weight assuming a specific density of 1 (10^6 µm^3 = 1 µg). Dry weights can, then, be calculated from fresh weights by considering a conversion factor. Pauli (1989) showed that large, soft-bodied genera like *Asplanchna* and *Synchaeta* have dry weight contents lower than 10%, while smaller genera like *Keratella* and *Kellicottia* with thick loricas have higher dry weight contents. In consultation with Prof. Dr. Gerhard Maier, we used a conversion factor of 2.8 for *Asplanchna*, a conversion factor of 9.1 for rotifers without loricas, a conversion factor of 32.3 for *Keratella cochlearis* and *Kellicottia longispina*, which are small and have thick loricas or very long spines, and a conversion factor of 16.1 for all other rotifers, which have soft to strong loricas. A more detailed description is shown in the Appendix table A2.

Dry weights of cladocerans and copepods can be obtained by using length to weight-regression-analysis. For daphnids and bosminids, we used the regressions derived from many different species of the respective genus (reviewed by Bottrell et al. 1976). For all other cladoceran species, we used the respective regressions derived from each species (reviewed by Dumont et al. 1975). For calanoid and cyclopoid nauplii, we used the respective regressions by Culver et al. (1985). For *Eudiaptomus gracilis*, we used the respective regression reviewed by McCauley (1984). For cyclopoid copepods, we distinguished between large (*Cyclops* spp.) and small (*Mesocyclops* spp., *Thermocyclops* spp., and *Diacyclops* spp.) species. For large cyclopoid copepods, we used the regression of *Cyclops abyssorum*, whereas for small cyclopoid copepods, we used the regression of *Mesocyclops leuckarti* (reviewed by Bottrell et al. 1976).

Unfortunately, no body measurements were available for the zooplankton species of Lake Plußsee. Body lengths of most rotifers were obtained from Ruttner-Kolisko (1972) and Voigt and Koste (1978); only the body lengths of the different *Trichocerca* species were provided by Prof. Dr. Gerhard Maier. Body lengths of the different stages of the cladoceran and copepod species were also provided by Prof. Dr. Gerhard Maier. A more detailed description is shown in Table (Appendix tables A2-A4).

In the next step, we calculated the biomasses for the entire zooplankton, rotifer, cladoceran, and copepod communities and also derived the percentage shares of the different groups in respect to entire zooplankton biomass. Finally, we correlated the biomasses and the percentage biomasses with the factor scores derived from abiotic environmental variables from February to October to analyze which variables affected the biomasses of different zooplankton groups in October.

2.3.3. Zooplankton species diversity

We used two diversity indices to estimate if the species diversity has changed in Lake Plußsee within the last decades. The Shannon-index (*H*) describes the biodiversity of a habitat and considers, thereby, the relative abundances of the different categories of variables (Shannon and Weaver 1949). It was determined from

$$H = -\sum_i p_i \cdot \ln p_i \text{, whereas } p_i = \frac{n_i}{N} \qquad (5)$$

where p_i denotes the percentage of a species i, which is the number of species n_i in respect to the total number of species N.

The Simpson-index (*D*) describes the probability that two randomly and independently chosen individuals of a habitat belong to the same species (Simpson 1949). It was determined from

$$D = 1 - \sum_i p_i^2 \qquad (6)$$

where p_i denotes the relative abundance of a species.

We calculated the Shannon- and Simpson-index for the entire zooplankton, rotifer, cladoceran, and copepod communities and correlated the indices with the factor scores derived from the abiotic environmental variables from February to October to analyze which variables affected species diversity of different zooplankton groups in October.

2.3.4. Principal Component Analysis of zooplankton groups

To estimate possible differences between the three zooplankton groups, we formed four groups, which we analyzed separately: the entire zooplankton community, rotifers, cladocerans, and copepods. Additionally, we split up the cladoceran and copepod datasets to analyze possible differences between the juvenile and adult stages of these two groups. Throughout the analysis we used the following abbreviations: Entire zooplankton community (*Zoo*), entire rotifer community (*Rot*), entire cladoceran community (*Clad*), juveniles stages of cladocerans (*Clad J*), adult stages of cladocerans (*Clad A*), entire copepod community (*Cop*), copepodite stages of copepods (*Cop C*), and adult stages of copepods (*Cop A*). We also used the abbreviation “PC” for principal components and we used Roman numerals to numerate the principal components.

Since it is more convenient to use normally distributed data for a PCA, we pre-transformed each zooplankton dataset prior to the different PCAs. We used a logarithmic transformation, where all values apart from “zero” were logarithmized (zeros were left as zeros), to approximate normal distribution of the datasets. Furthermore, logarithmic transformation has also the advantage of reducing the importance of very high values (Leyer and Wesche 2007; Borcard et al. 2011). We used a Scree-plot analysis and the Kaiser-Guttman-Criterion to help deciding upon a reasonable number of principal components for a closer interpretation of the zooplankton groups. A Scree-plot shows the eigenvalues plotted along the x-axis and, according to this method, only those principal components whose eigenvalues located left of the knee of the curve should be interpreted. According to the Kaiser-Guttman-Criterion, only principal components whose eigenvalues are larger than the mean of all eigenvalues should be taken into account (Leyer and Wesche 2007; Borcard et al. 2011).

We performed a PCA on each of the 8 datasets. The purpose of this procedure was, on the one hand, to identify species with a similar behavior and similar ecological requirements by finding the most important underlying gradients in a set of collinear variables, which can already explain a large proportion of total variance of a zooplankton community. On the other hand, we derived the factor scores from the relevant principal components of each PCA to use them as new variables for further analyses and, furthermore, to calculate the *contributions*. Since the eigenvalue of a principal component is equal to the sum of squared factor scores for this principal component, it can be used to calculate the contribution of an observation to a component. Therefore, the importance of an observation for a component can be obtained by the ratio of the squared factor score f of an observation i by the eigenvalue λ associated with this component l. Multiplying the contribution (ctr) with the factor 100 equals the percentage share of a factor score on a principal component (Abdi and Williams 2010).

$$\mathrm{ctr}_{i,l} = \frac{f_{i,l}^2}{\sum_i f_{i,l}^2} = \frac{f_{i,l}^2}{\lambda_l} \qquad (7)$$

In the next step, we used the factor scores derived from the zooplankton groups to correlate them with the factor scores we derived from physical and chemical parameters and from nutrient parameters to identify which abiotic environmental conditions were related to certain zooplankton species. Therefore, we calculated Pearson’s correlation coefficient (r) to test for correlations between the respective zooplankton community in October and the abiotic environmental variables for each month from February to October.

2.3.5. Canonical Correlation Analysis of zooplankton groups

We used the factor scores derived from the zooplankton groups as new variables to perform a Canonical Correlation Analysis (CCA) and to investigate if a large proportion of variance in the zooplankton datasets could also be explained by interspecific competition.

The purpose of a CCA is to examine the relationship between two multivariate sets of variables. Thereby, the CCA extracts linear combinations (*canonical factors*) of the original variables from the two datasets so that the correlation between the new canonical factors is maximized on the first canonical function. Mathematically, the canonical factors are found as eigenvectors of a matrix that is the product of some co-variance and cross-covariance matrices, in some sense similarly as in the PCA. The correlation between the two canonical factors of the two datasets in CCA is called *canonical correlation* (R_c). R_c denotes Pearson's correlation coefficient r between the canonical variables, whereas R_c^2 represents their shared variance. R_c^2 is the eigenvalue corresponding to the canonical factors (eigenvectors). The CCA is a symmetrical method. This means that both sets of variables are treated equally. However, for the sake of clarity, in the following we named the dataset with the smaller number of PCs the "predictor dataset" and the dataset with the larger number of PCs "criterion dataset".

CCA requires the calculation of the inverse of the co-variance matrices of both datasets. When the number of variables is large and the variables are not totally independent (collinear variables), these matrices are often numerically singular, i.e., at least one eigenvalue is close to zero. Their inverse does not exist. In these cases, a regularization method has to be used to reduce the number of variables and/or their collinearity before. A usual way is to apply a PCA prior to the CCA. Thus, the original datasets were first subject to a PCA to reduce their dimensionality and to obtain new uncorrelated variables, and then a CCA is applied to these variables to obtain the final canonical variables.

Significant correlations between principal components of the compared datasets were tested with a multivariate test. Thereby, the canonical functions were tested hierarchically. First, the full model was tested (with all canonical functions); next, all canonical functions apart from the first canonical function were tested. This procedure continued until only the last canonical function was tested by itself. Wilks' λ was obtained by calculating 1 minus the *squared canonical correlation* (R_c^2) of each canonical function. Canonical functions that only explained a small proportion of shared variance were discarded from further analysis.

For the interpretation of the CCA results, we also used the *canonical loadings* (*load*), the *structure coefficients* (r_s), and the *squared structure coefficients* (r_s^2). They can give information about the interpretation of the relationship between the criterion and predictor variables. Canonical loadings represent the correlation of the canonical variables and the values of the original variables. The structure coefficients represent the correlation of the canonical factor scores of the criterion dataset with the values of the predictor variables (in our case: the factor scores of the PCA performed on the criterion dataset), and vice versa. Hence, structure coefficients can help to identify which principal components of each dataset contributed largely to the structure of a respective canonical function. The squared structure coefficients represent the shared percentage (r_s^2 multiplied by 100) of variance between both datasets (Bortz 2005; Sherry and Henson 2005).

2.3.6. Analysis of the biomanipulation experiment period

From 1991 to 1994, a biomanipulation experiment was performed in Lake Plußsee (Kremser 1995). The aim of this experiment was to reduce predation pressure of planktivorous fish on the zooplankton community. Therefore, piscivorous pikeperches (*Stizostedion lucioperca*), eels (*Anguilla anguilla*), pikes (*Esox lucius*), and trouts (*Salmo trutta*) were added, while planktivorous breams (*Abramis brama*), roaches (*Rutilus rutilus*), and perches (*Perca fluviatilis*) were removed in the course of each year in October. To assess if the zooplankton community was significantly affected in the course of the biomanipulation experiment, we performed Mann-Whitney-*U*-tests, comparing species abundances from 1991 to 1994 with all other years considered in this analysis.

We did not exclude the years in which the biomanipulation experiment was performed for two reasons: Firstly, before and after the experiment, fish stocking was only randomly evaluated in Lake Plußsee. Hence, it is difficult to quantitatively assess the influence of fish on the zooplankton community before, during, and after the experiment. Especially due to possible aftereffects, it is impossible to detect years which should be excluded from the analysis to reduce the effect of the biomanipulation experiment. Secondly, including years with a biomanipulation effect on the zooplankton community enabled me to investigate if the abiotic or the biotic effect played a more important role regulating the different groups of the zooplankton community.

All calculations were performed using the software package R (R Development Core Team 2009). For species diversity analysis and for data standardization we used the add-on package ‘vegan’ (Oksanen et al. 2010). Furthermore, for Canonical Correlation Analysis we used the add-on package ‘CCA’ (González and Déjean 2009).

3 Results

3.1. Long-term trend analysis of physical and chemical parameters

3.1.1. Meteorological parameters, NAO, and the linkage to lake surface temperatures

Over the period of 1969-2006, annual mean air temperatures (AT) increased significantly by 0.04°C yr^{-1} ($p<0.001$), which resulted in an increase of 1.4°C over the whole period (Fig. 2a). Largest temperature trends occurred in the last week of April with 0.14°C yr^{-1} ($p<0.001$, overall increase: 5.2°C) and in the first week of May with 0.10°C yr^{-1} ($p<0.001$, overall increase: 4.0°C). However, monthly trends for April (0.07°C yr^{-1}, $p<0.001$, overall increase: 2.7°C) and May (0.03°C yr^{-1}, $p<0.05$, overall increase: 1.3°C) were much lower. Largest long-term AT warming trends were from July to September (0.06-0.08°C, $p<0.05$, overall increases: 2.1-2.9°C), but the trends showed large week-to-week fluctuations. Positive temperature trends were also apparent during the first months of the year before the onset of stratification, but due to high interannual variability those trends were mostly non-significant. Although air temperatures were measured 80 km away from the lake, air and lake surface temperatures correlated significantly in each week (Fig. 3, $0.38<r<0.80$, $0.001<p<0.05$).

Wind speeds (WS) showed large interannual variability within the analysis period (Fig. 2b). We found significant negative trends of WS in the last week of April (-0.02 m s^{-1} yr^{-1}, $p<0.05$) and in the last week of November (-0.02 m s^{-1} yr^{-1}, $p<0.01$). On a monthly scale, however, long-term trends were only significant for November (-0.01 m s^{-1} yr^{-1}, $p<0.01$), but not for April (0.00 m s^{-1} yr^{-1}, $p>0.1$). WS and lake surface temperatures were negatively correlated in spring and in summer (Fig. 3), but due to high week-to-week fluctuations correlations were only significant for a few weeks, e.g., mid-March ($r=-0.58$, $p<0.001$) and end of June ($r=-0.50$, $p<0.01$).

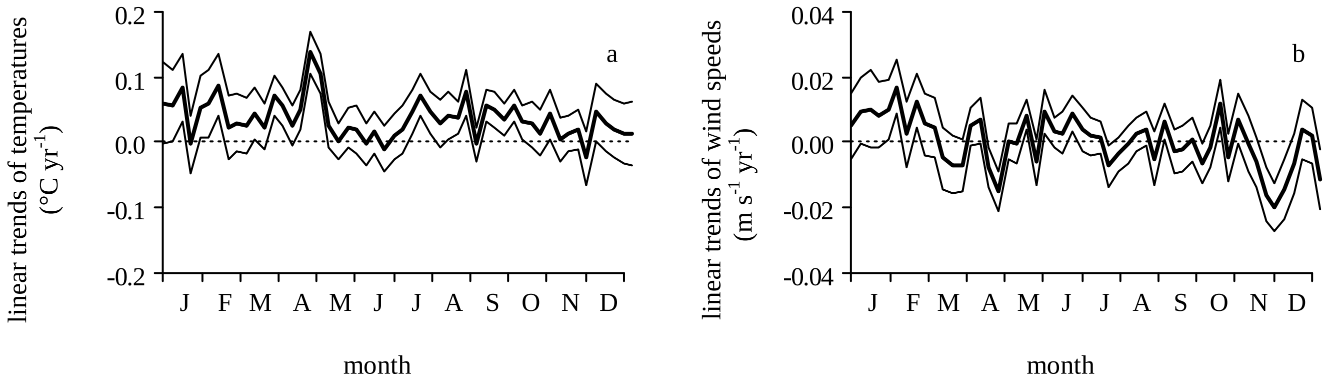

Fig. 2. Linear trends of (a) air temperatures and (b) wind speeds in Schleswig within the period from 1969-2006. Trends were calculated for each calendar week, but for a better comprehensibility, we used a monthly, instead of a weekly, labeling of the x-axis. The thick lines show the slopes of the linear trends and the thin lines show the standard errors of the trends.

The winter NAO-index ($NAO_{Dec\text{-}Mar}$) correlated significantly with mean air temperatures ($AT_{Dec\text{-}Mar}$, r=0.74, p<0.001) and mean wind speeds ($WS_{Dec\text{-}Mar}$, r=0.41, p<0.01) from December to March. To assess the influence of positive and negative $NAO_{Dec\text{-}Mar}$ on air temperatures and wind speeds in winter and early spring and the week of onset of stratification, we defined years with positive and negative $NAO_{Dec\text{-}Mar}$ as years that were above and below the 38 years mean (=0.68). $AT_{Dec\text{-}Mar}$ (Welch two-sample *t*-test, p<0.001) and

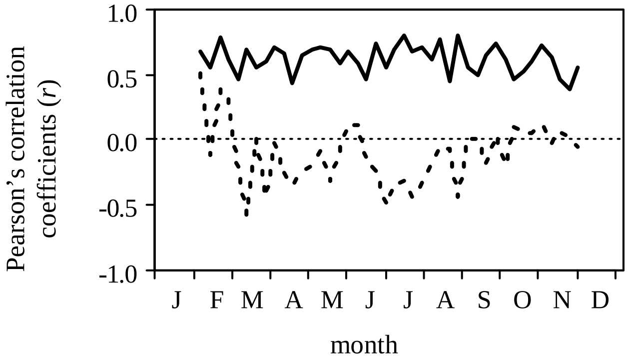

Fig. 3. Pearson's correlation coefficients (r) between the lake's surface temperatures and air temperatures (solid line) and wind speeds (dotted line) within the period 1969-2006. Correlation coefficients were calculated for each calendar week, but for a better comprehensibility, we used a monthly, instead of a weekly, labeling of the x-axis.

Table 2. Welch two-sample *t*-tests of air temperatures ($AT_{Dec\text{-}Mar}$) and wind speeds ($WS_{Dec\text{-}Mar}$) differentiated between years with negative (neg.) and positive (pos.) $NAO_{Dec\text{-}Mar}$-indices (years with $NAO_{Dec\text{-}Mar}$-indices below and above their 38-years mean). * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

	years with neg. $NAO_{Dec\text{-}Mar}$	years with pos. $NAO_{Dec\text{-}Mar}$	*t*-value	df	*p*-value
$AT_{Dec\text{-}Mar}$ (°C)	0.61	2.84	-5.07	33.51	<0.001 ***
$WS_{Dec\text{-}Mar}$ (m s^{-1})	2.92	3.11	-2.72	35.95	0.010 *

$WS_{Dec\text{-}Mar}$ (Welch two-sample *t*-test, $p<0.05$) were significantly higher in years with a positive $NAO_{Dec\text{-}Mar}$ than for years with a negative $NAO_{Dec\text{-}Mar}$ (Table 2).

3.1.2. Stratification

From 1969 to 2006 Lake Plußsee stratified about 1.4 weeks earlier in spring (-0.04 weeks yr^{-1}, $p=0.13$) and the onset of stratification advanced by about 10 days from mid-April to beginning of April (Fig. 4a). The timing of the onset of stratification differed significantly between years with a positive $NAO_{Dec\text{-}Mar}$ and years with a negative $NAO_{Dec\text{-}Mar}$ (Mann-Whitney *U*-test, $p<0.05$). Lake Plußsee stratified earlier in years with a positive $NAO_{Dec\text{-}Mar}$ (mean of weeks with an earlier onset of stratification = week 14.8) than in years with a negative $NAO_{Dec\text{-}Mar}$ (mean of weeks with a later onset of stratification = week 15.9).

The $NAO_{Dec\text{-}Mar}$ can have an effect on the timing of the onset of stratification by affecting lake conditions (e.g., ice-cover) in early spring; however, the index is not adequate to describe processes establishing a stable stratification within a short timeframe. In this context, regional meteorological parameters, above all prevalent local wind speed conditions, play a more important role. Monthly wind speeds in March ($r=0.47$, $p<0.01$) and April ($r=0.15$, $p>0.1$) correlated positively with the week of the onset of stratification. We found highest correlations with weekly wind speeds in the last week of March ($r=0.43$, $p<0.05$). Monthly air temperatures correlated negatively with the week of the onset of stratification in March ($r=-0.27$, $p>0.1$) and in April ($r=-0.42$, $p<0.05$). We found the highest correlation with weekly air temperatures in the first week of April ($r=-0.54$, $p<0.01$).

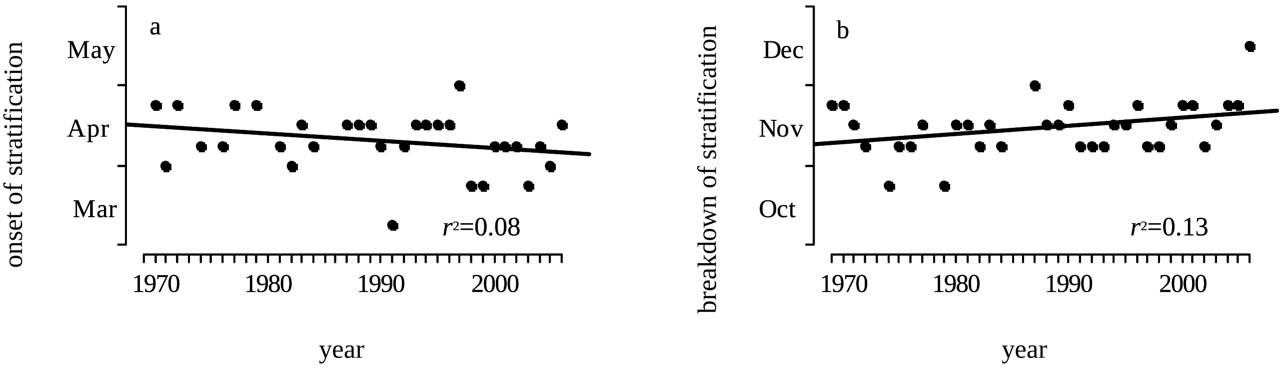

Fig. 4. Weeks of (a) onset and (b) breakdown of stratification within the period 1969-2006. The dots mark the weeks of the stratification event and the lines show the regression lines. For a better comprehensibility, we used a monthly, instead of a weekly, labeling of the y-axis.

However, the timing of the onset of stratification varies in each year. Calculating the monthly or weekly long-term trends may only give approximate information on a timeframe when changes occurred. However, influencing parameters, which also vary from year to year, are difficult to detect with this method. Therefore, we calculated a Welch two-sample *t*-test to find out whether wind speeds and air temperatures during the week of the onset of stratification differed from wind speeds and air temperatures in weeks within a timeframe of about two months before the onset of stratification. Air temperatures were significantly higher during the week of the onset of stratification than in the previous seven weeks (Welch two-sample *t*-test, $p<0.001$). Apart from two weeks before the onset of stratification (Welch two-sample *t*-test, $p>0.1$), wind speeds were significantly lower than in the previous seven weeks (Welch two-sample *t*-test, $p<0.05$). These findings indicate that the process of initiating a stable stratification must have been started within this timeframe of about 2-3 weeks before the onset of stratification. Before this timeframe, wind speeds were not low enough and air temperatures were not high enough to initiate a stable stratification. Thereby, increasing air temperatures warmed the lake water faster than the lower wind speeds were able to distribute the heat within the water column. Hence, an earlier onset of stratification was associated with larger air temperatures and weaker wind speeds in March and April.

Table 3. Welch two-sample *t*-tests of epilimnetic temperatures (ET), metalimnetic temperatures (MT), and hypolimnetic temperatures (HT) during the first week of stratification differentiated between years with an earlier and a later onset of stratification (years with weeks of the onset of stratification below and above their 38-years mean). * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

	years with an earlier onset of stratification	years with a later onset of stratification	*t*-value	df	*p*-value
ET (°C)	8.39	10.45	-3.05	22.51	0.006 **
MT (°C)	6.92	8.63	-3.50	21.70	0.002 **
HT (°C)	4.47	4.80	-2.37	21.57	0.027 *

The stratification period ended about 1.6 weeks later (0.04 weeks yr^{-1}, $p<0.05$) and the breakdown of stratification was delayed by about 11 days from the beginning of November to mid-November (Fig. 4b). As a result of the earlier onset and the later breakdown of stratification, we observed a significant prolonged duration of stratification of about 3.4 weeks, i.e., about 24 days (0.09 weeks yr^{-1}, $p<0.01$). However, adding up the number of weeks (or days) of the earlier onset and the later breakdown of stratification to calculate the duration of the stratification period, we found an extension of 3.0 weeks (or 21 days). This mismatch to estimate the trend of the duration of the stratification period can be explained by different numbers of years we used to calculate the trends of the onset (n=29), the breakdown (n=32), and the duration (n=29) of stratification.

3.1.3. Water temperatures and thermocline depths

To find out whether epi-, meta-, and hypolimnetic temperatures during the first week of stratification differed between years with an earlier onset and a later onset of stratification, we calculated a Welch two-sample *t*-test on the differences of means. Therefore, we calculated the 38 years mean of the week of the onset of stratification (= week 15.2, i.e., mid-April) and compared the layer temperatures of years below the 38 years mean with the layer temperatures of years above the 38 years mean. Initial epi-, meta-, and hypolimnetic temperatures were significantly lower in years with an earlier onset than in years with a later

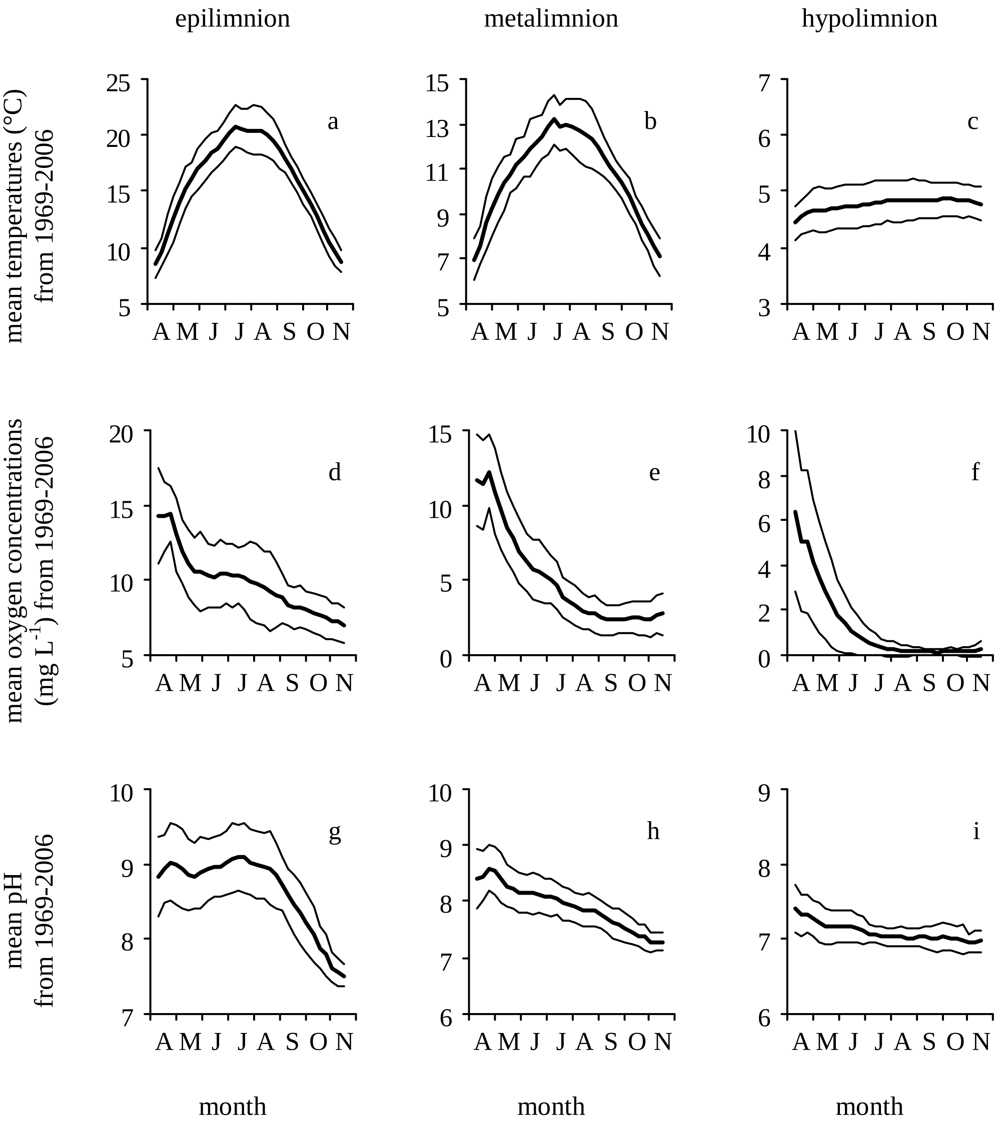

Fig. 5. Annual cycles of (a-c) water temperatures, (d-f) dissolved oxygen concentrations, and (g-i) pH in each layer within the period 1969-2006. The thick lines show the means and the thin lines show the standard deviations. Note the different scales of the y-axes.

onset of stratification (Table 3). Initial layer temperatures are determined by the prevalent water temperatures at times when the corresponding layers are detached from vertical mixing. If stratification were solely triggered by the atmospheric heat flux when a certain temperature threshold was attained, the water temperature at the onset of stratification would always lie within a narrow range. The results suggest that wind also influences water temperatures at that time by affecting the duration and depth of vertical mixing. Lower deep-water temperatures

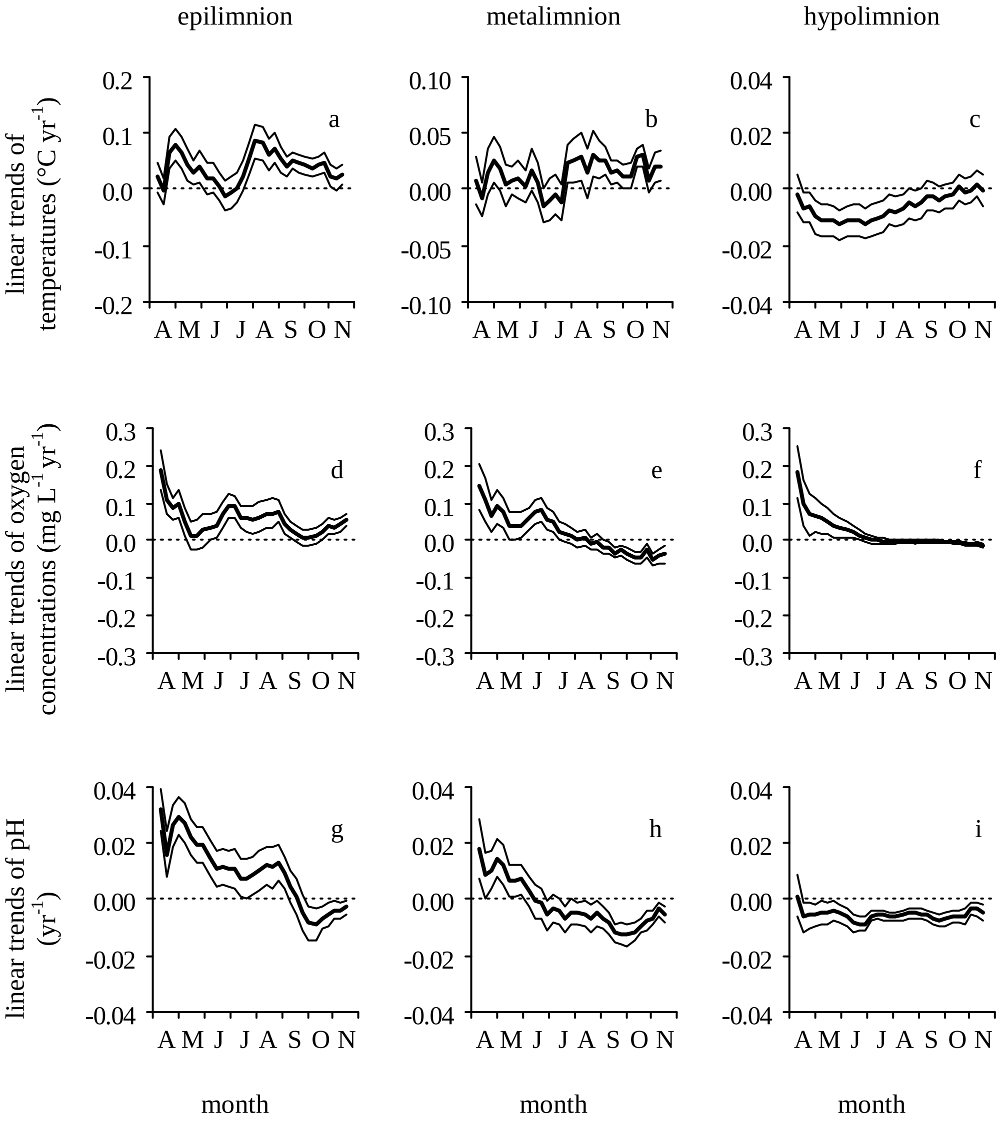

Fig. 6. Linear trends of (a-c) water temperatures, (d-f) dissolved oxygen concentrations, and (g-i) pH within the period 1969-2006. The thick lines show the slopes of the linear trends and the thin lines show the standard errors of the trends. Note the different scales of the y-axis of the temperature trends.

were detached from vertical mixing at an earlier date when water temperatures were generally low. Higher deep-water temperatures, in contrast, were detached from vertical mixing at a later date when water temperatures were comparably warmer.

The annual cycles of mean epi-, meta-, and hypolimnetic temperatures (1969-2006) are depicted in Fig. 5a-c. Highest mean epilimnetic temperatures (20.8 ± 1.8°C) and metalimnetic temperatures (13.2 ± 1.1°C) were recorded in mid-July. Lowest mean hypolimnetic temperatures (4.5 ± 0.3°C) were recorded in mid-April.

Table 4. Linear trends of annual air temperature maxima (AT_{Max}), epilimnetic temperature maxima (ET_{Max}), Schmidt's Stability Index maxima (SSI_{Max}), and of weeks, in which these maxima occurred. * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

	r^2	SE	df	F-value	p-value
AT_{Max} (°C yr^{-1})	0.03	0.03	36	1.15	0.291
week AT_{Max}	0.06	0.05	36	1.25	0.271
ET_{Max} (°C yr^{-1})	0.04	0.02	32	2.79	0.105
week ET_{Max}	0.09	0.04	32	4.72	0.037 *
SSI_{Max} (J m^{-2} yr^{-1})	3.16	1.12	31	7.92	0.008 **
week SSI_{Max}	0.14	0.04	31	15.14	<0.001 ***

Positive trends of epilimnetic temperatures (ET) were apparent throughout the stratification season except for two weeks at the end of June, but mainly from April to May and from August to November (Fig. 6a). Especially the first week of May (0.08°C yr^{-1}, $p<0.01$, overall increase: 3.0°C) and the first week of August (0.09°C yr^{-1}, $p<0.01$, overall increase: 3.2°C) showed the most pronounced temperature increases. Table 4 shows that the extent of the large positive ET trends in summer and autumn can also be explained by a shift of the timing of the epilimnetic temperature maximum (ET_{Max}), which was delayed by about 3.5 weeks from start of July to start of August ($p<0.05$), and by an ET_{Max} increase of about 1.5°C ($p>0.1$).

Epilimnetic and metalimnetic temperature trends exhibited a similar annual warming pattern, but metalimnetic temperature (MT) trends were less pronounced than ET trends (Fig. 6b). Except for negative temperature trends at the end of June and at the beginning of July (-0.01°C yr^{-1}, $p>0.1$), we found positive MT trends for the rest of the stratification period, especially during mid-November (0.03°C yr^{-1}, $p<0.01$, overall increase: 1.1°C).

In contrast to predominantly positive ET and MT trends, we found negative hypolimnetic temperature (HT) trends from the onset of stratification to autumn (Fig. 6c). Those were most pronounced from May to June (e.g., last week of May: -0.01°C yr^{-1}, $p<0.05$, overall decrease: -0.5°C). From that point on, HT trends became continuously lower towards the end of the stratification period.

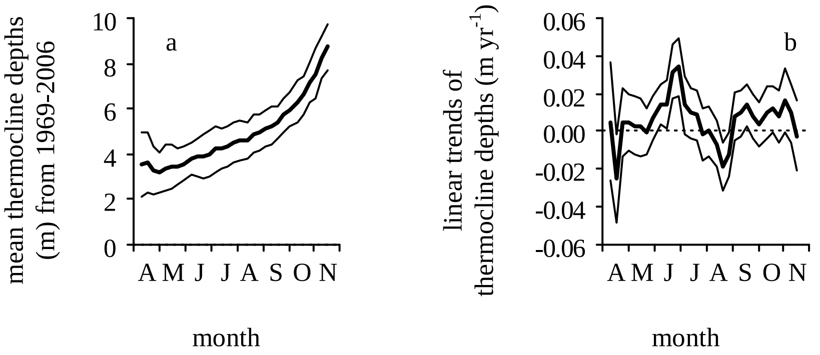

Fig. 7. (a) Annual cycle and (b) linear trends of thermocline depths within the period 1969-2006. (a) The thick lines show the means and the thin lines show the standard deviations. (b) The thick lines show the slopes of the linear trends and the thin lines show the standard errors of the trends.

From the onset of stratification in April to the breakdown of stratification in November, the mean thermocline depth deepened from about 3.1 m to about 8.5 m (Fig. 7a). The mean thermocline depths during the first week of stratification were only slightly deeper in years with an earlier onset of stratification (about 3.2 m) than in years with a later onset of stratification (about 3.0 m; Mann-Whitney *U*-test, $p>0.05$). As shown in Fig. 7b, significant trends of the thermocline depths were only apparent in two weeks end of June, when the thermocline deepened by 0.03 m yr^{-1}, ($p<0.05$, overall increase: 1.3 m).

3.1.4. Heat content and lake stability

The annual cycle of mean heat content (HC) is shown in Fig. 8a. Maximum mean heat contents were calculated for summer, especially for August ($5.2 \times 10^8 \pm 4.2 \times 10^7$ J m^{-2}). Except for negative trends from mid-May to mid-July (Fig. 8b), with the largest negative trends being end of June (-4.2×10^5 J m^{-2} yr^{-1}, $p>0.1$), we found positive HC trends for the rest of the stratification period, especially in the first week of August (1.4×10^6 J m^{-2} yr^{-1}, $p<0.05$, overall increase: 5.1×10^7 J m^{-2}). We found significant positive trends from August to mid-October ($p<0.05$); however, positive trends in spring were not significant ($p>0.05$).

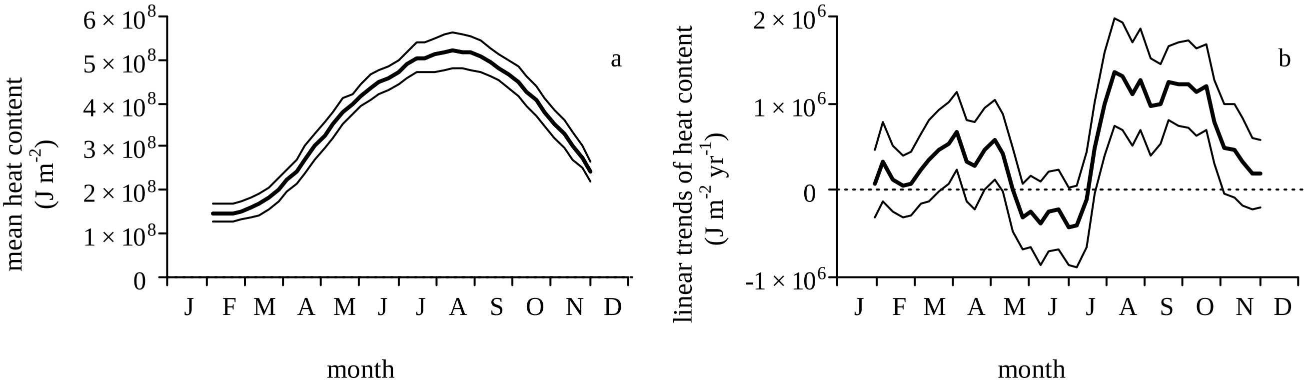

Fig. 8. (a) Annual cycle and (b) linear trends of lake heat content (HC) within the period 1969-2006. (a) The thick lines show the means and the thin lines show the standard deviations. (b) The thick lines show the slopes of the linear trends and the thin lines show the standard errors of the trends.

The annual cycle of mean lake stability (Schmidt's Stability Index, SSI) is depicted in Fig. 9a. Highest mean SSI values were calculated for summer, especially, for the beginning of August (400.2 ± 87.0 J m^{-2}). SSI trends were positive throughout the stratification period (Fig. 9b). In accordance with ET trends, we found the largest increases of SSI in May and from August to November, with a maximum increase of 3.5 J m^{-2} yr^{-1} ($p<0.01$, overall increase: 96.6 J m^{-2}) in the first week of August. Table 4 shows, that the SSI maximum (SSI_{Max}) increased significantly by about 122.0 J m^{-2} ($p<0.01$), which was an increase of about 30%, and the timing of SSI_{Max} shifted significantly by about 5.5 weeks ($p<0.001$) from early July to mid-August.

Table 5 shows that SSI_{Aug} was significantly correlated with SSI_{Max} ($p<0.001$) and with the week of SSI_{Max} ($p<0.01$). SSI was only significantly correlated with SSI of the following month, but not with other months. The weeks of the breakdown of stratification were significantly correlated with SSI_{Oct} ($p<0.001$).

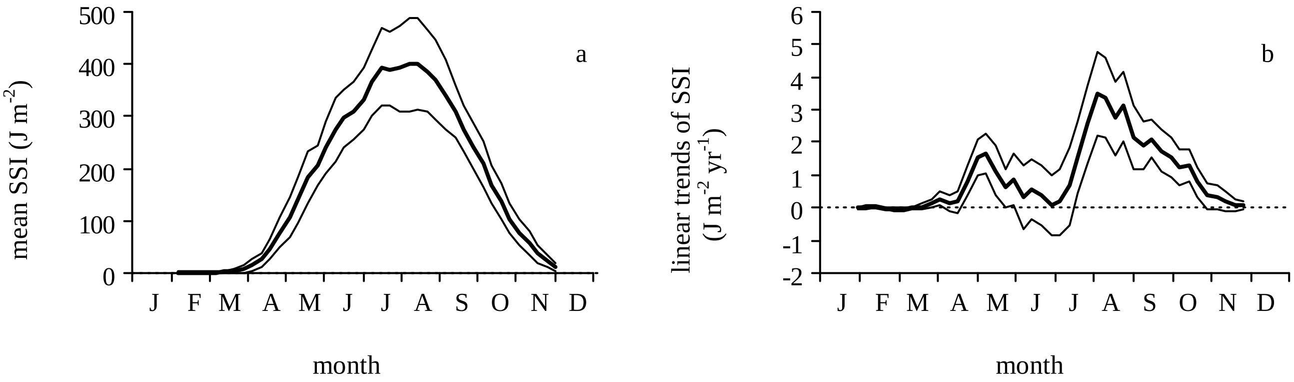

Fig. 9. (a) Annual cycle and (b) linear trends of Schmidt's Stability Index (SSI) within the period 1969-2006. (a) The thick lines show the means and the thin lines show the standard deviations. (b) The thick lines show the slopes of the linear trends and the thin lines show the standard errors of the trends.

3.1.5. Oxygen concentrations and pH

The annual cycles of mean epi-, meta-, and hypolimnetic O_2 concentrations (1969-2006) are depicted in Fig. 5d-f. In April, we recorded highest mean O_2 concentrations within the epilimnion (14.4 ± 1.9 mg L^{-1}), the metalimnion (12.3 ± 12.4 mg L^{-1}), and the hypolimnion (5.1 ± 3.1 mg L^{-1}), which decreased continuously in all layers from then onwards. From June on, mean hypolimnetic O_2 concentrations were below 1 mg L^{-1}.

Epilimnetic O_2 concentrations increased for all weeks of the stratification period (Fig. 6d) with the largest positive trends from April to May (e.g., last week of April with 0.1 mg L^{-1} yr^{-1}, $p<0.01$, overall increase: 3.7 mg L^{-1}), from June to September (e.g., last week of June with 0.09 mg L^{-1} yr^{-1}, $p<0.01$, overall increase: 3.5 mg L^{-1}) and during the last weeks of stratification (e.g., second week of November with 0.06 mg L^{-1} yr^{-1}, $p<0.01$, overall increase: 2.2 mg L^{-1}). Although metalimnetic O_2 concentrations increased from the start of stratification to August, they decreased continuously from that point onwards until the breakdown of stratification (Fig. 6e). The trends were significantly negative from mid-September onwards, with the largest O_2 decreases in the last week of October (-0.05 mg L^{-1} yr^{-1}, $p<0.01$, overall decrease: 1.9 mg L^{-1}). A similar change of behavior of O_2 concentrations was also apparent in

Table 5. Pearson's correlation coefficients (*r*) between different SSI in summer and autumn and their influence on the breakdown of stratification. * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

correlations	*r*	*t*-value	df	*p*-value
week SSI_{Max} – SSI_{Aug}	0.49	3.17	31	0.003 **
SSI_{Max} – SSI_{Aug}	0.90	11.80	31	<0.001 ***
SSI_{Aug} – SSI_{Sep}	0.60	4.13	31	<0.001 ***
SSI_{Sep} – SSI_{Oct}	0.67	4.97	31	<0.001 ***
SSI_{Oct} – week of stratification breakdown	0.69	5.24	30	<0.001 ***

the hypolimnion (Fig. 6f), although the transition from positive to negative O_2 concentration trends already started about one month earlier (July) and was less pronounced than in the metalimnion. Hypolimnetic O_2 concentration trends were negative from August onwards and the trends were significantly negative in the last weeks of October (-0.01 mg L^{-1} yr^{-1}, $p<0.01$, overall decrease: 0.3 mg L^{-1}).

The annual cycles of mean epi-, meta-, and hypolimnetic pH (1969-2006) are depicted in Fig. 5g-i. We recorded highest mean pH within the epilimnion (9.0 ± 0.5), the metalimnion (8.6 ± 0.4), and the hypolimnion (7.3 ± 0.3) in April. Metalimnetic and hypolimnetic pH decreased continuously from then on, whereas there was a second epilimnetic pH peak in July (9.1 ± 0.4).

Epilimnetic pH trends were positive from the beginning of stratification to mid-September and negative for the rest of the stratification period (Fig. 6g). Positive trends of epilimnetic pH were most pronounced during the first two weeks of May (0.03 yr^{-1}, $p<0.001$, overall increase: 1.3). In accordance to the metalimnetic O_2 concentration pattern, metalimnetic pH trends showed a similar change in trends from positive to negative, with largest positive trends in the first week of May and negative trends starting mid-June (Fig. 6h). Significant positive trends of pH were largest during the first week of May (0.01 yr^{-1}, $p<0.05$, overall increase: 0.6). From mid-September to the end of October pH trends were significantly negative (e.g., first week of October with -0.01 yr^{-1}, $p<0.001$, overall decrease: 0.5). We only found negative trends of pH in the hypolimnion (Fig. 6i). We observed significant negative trends from the mid-June onwards (e.g., last week of September with -0.01 yr^{-1}, $p<0.001$, overall decrease: 0.3).

3.2. Long-term trend analysis of nutrient parameters

3.2.1. Nitrate, nitrite, and ammonium concentrations

Fig. 10 shows the annual cycles and the linear trends of the most important nitrogen fractions within the 0-10 m water column from February to November. Mean NO_3^- concentrations were highest in March (about 370 ± 180 µg L^{-1}) and decreased from that point on. The opposite was true for NH_4^+ concentrations: They were lowest in April (about 65 ± 46 µg L^{-1}) and increased from that point on. Highest NO_2^- concentrations were measured in August (about 16 ± 12 µg L^{-1}). The linear trends of these nitrogen fractions revealed mostly negative trends: NO_3^- concentration trends were significantly negative from April to June and from September to November ($p<0.05$) and the largest negative trend was calculated for April (6.4 µg L^{-1} yr^{-1}, $p<0.01$, overall decrease: about 240 µg L^{-1}). NH_4^+ concentration trends were significantly negative from April to November ($p<0.01$), whereas the largest negative trend was calculated for October (5.6 µg L^{-1} yr^{-1}, $p<0.001$, overall decrease: about 214 µg L^{-1}). Apart from August, NO_2^- concentrations trends were negative and the largest negative trend was calculated for June (0.35 µg L^{-1} yr^{-1}, $p<0.05$, overall decrease: about 13 µg L^{-1}).

Annual cycles of epilimnetic, metalimnetic, and hypolimnetic nitrogen fractions agree with the annual cycles calculated over the 0-10 m water column (Fig. 11). However, epilimnetic concentrations were generally lower and hypolimnetic concentrations were generally higher.

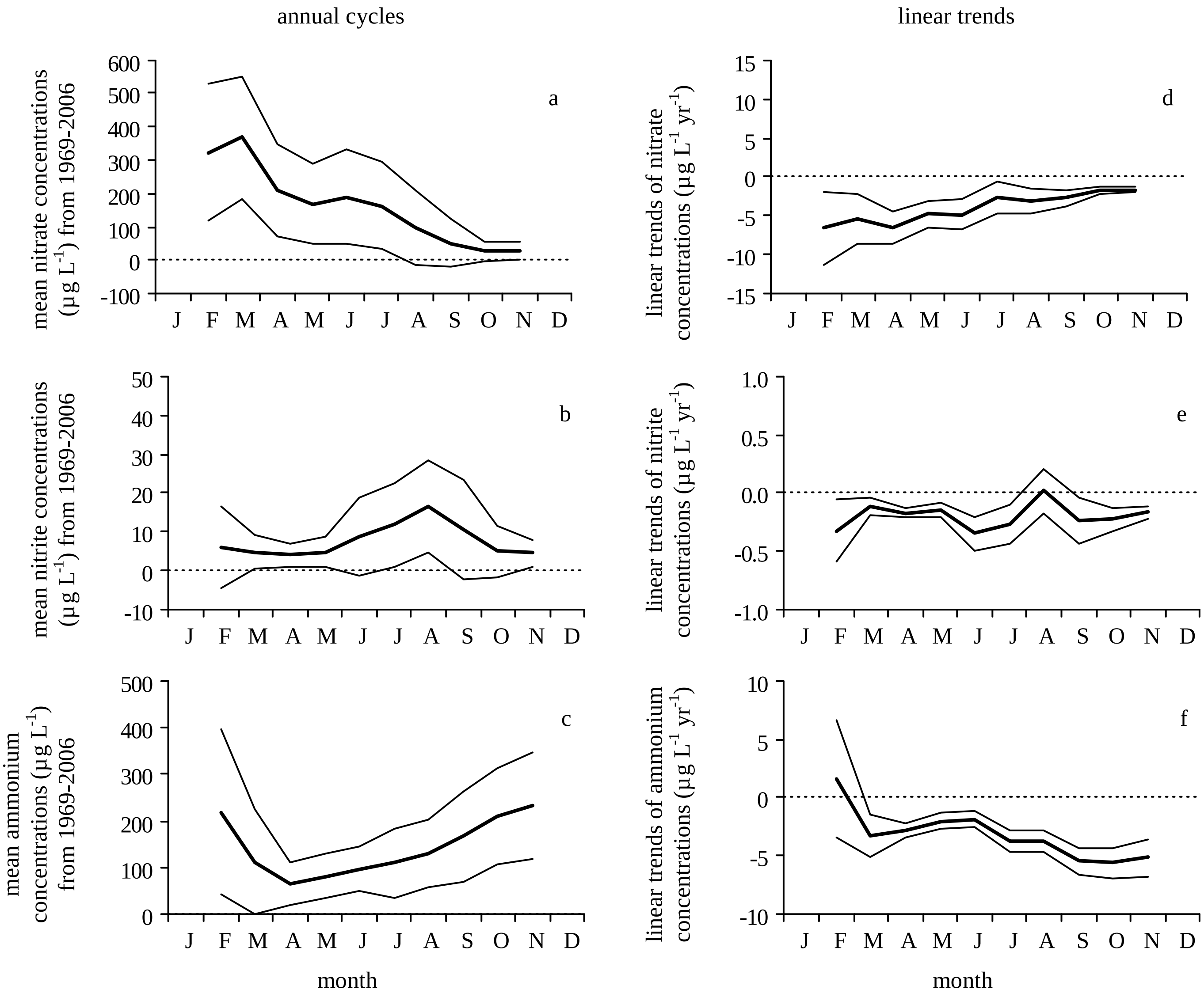

Fig. 10. Annual cycles (a-c) and linear trends (d-f) of monthly nitrate, nitrite, and ammonium concentrations in the 0-10 m water column from February to November within the period from 1969-2006. The thick lines of the annual cycles show the means and the thin lines show the standard deviations, whereas the thick lines of the linear trends show the slopes of the linear trends and the thin lines show the standard errors of the trends.

Epilimnetic NO_3^- concentrations (about 20-60 µg L^{-1}), epilimnetic NO_2^- concentrations (about 3-5 µg L^{-1}), and epilimnetic NH_4^+ concentrations (about 60-80 µg L^{-1}) remained almost at the same low level throughout the stratification period. Hypolimnetic NO_3^- concentrations were largest in May (about 320 ± 220 µg L^{-1}) and lowest in October (about 30 ± 40 µg L^{-1}). In contrast, hypolimnetic NH_4^+ concentrations were lowest in May (about 280 ± 250 µg L^{-1}) and largest in October (about 1200 ± 450 µg L^{-1}). Hypolimnetic NO_2^- concentrations were largest

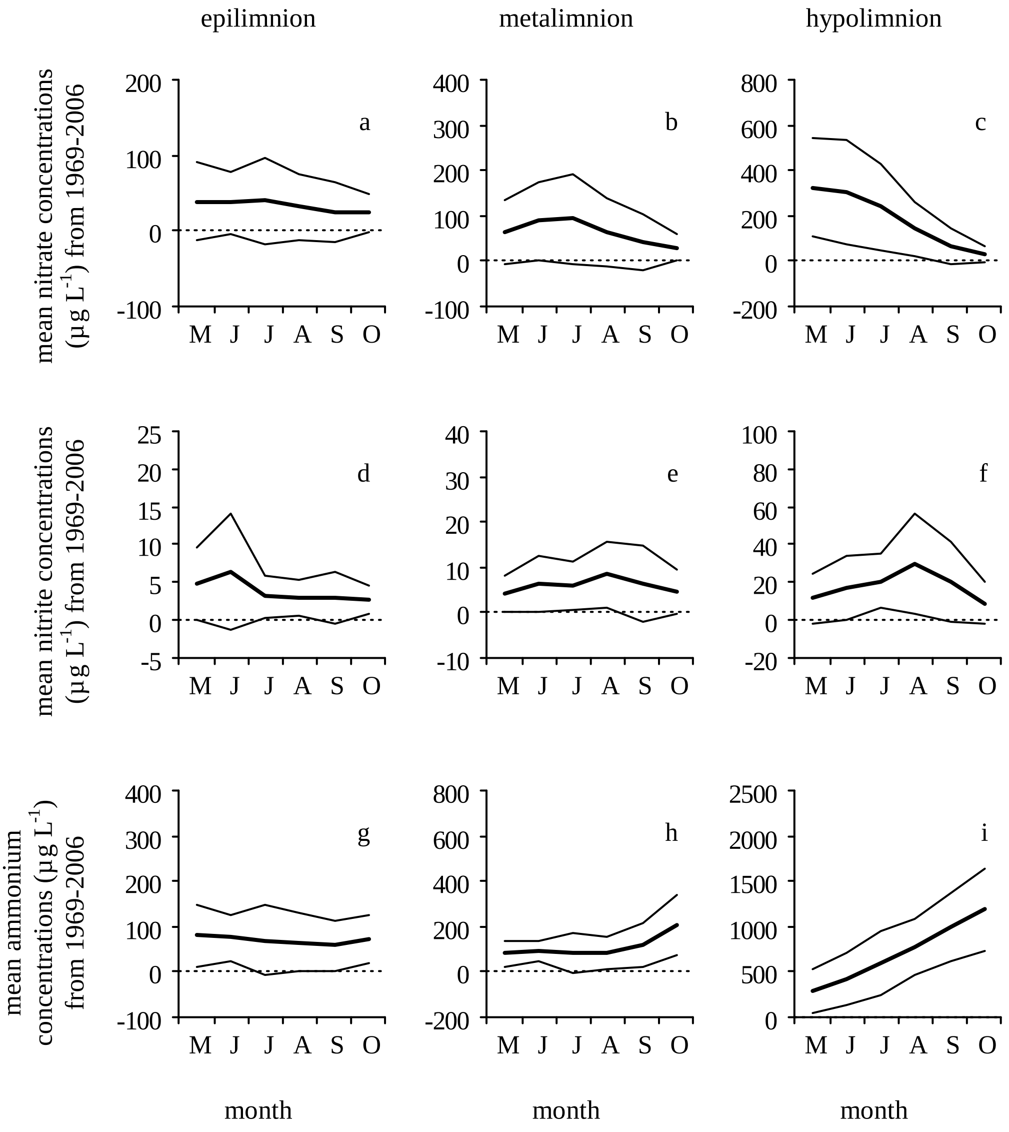

Fig. 11. Annual cycles of monthly (a-c) nitrate concentrations, (d-f) nitrite concentrations, and (g-i) ammonium concentrations in the epilimnion, metalimnion, and hypolimnion from May to October within the period from 1969-2006. The thick lines show the means and the thin lines show the standard deviations. Note the different scale of the y-axis.

in August (30 ± 28 µg L^{-1}). Metalimnetic NO_3^-, NO_2^-, and NH_4^+ concentrations corresponded quite well to the mean NO_3^- and NH_4^+ concentrations calculated over the 0-10 m water column.

Trends of epilimnetic, metalimnetic, and hypolimnetic NO_3^-, NO_2^-, and NH_4^+ concentrations were negative from May to October (Fig. 12). Largest negative epilimnetic NO_3^- concentrations trends were calculated for May (2.2 µg L^{-1} yr^{-1}, $p<0.01$, overall decrease: about

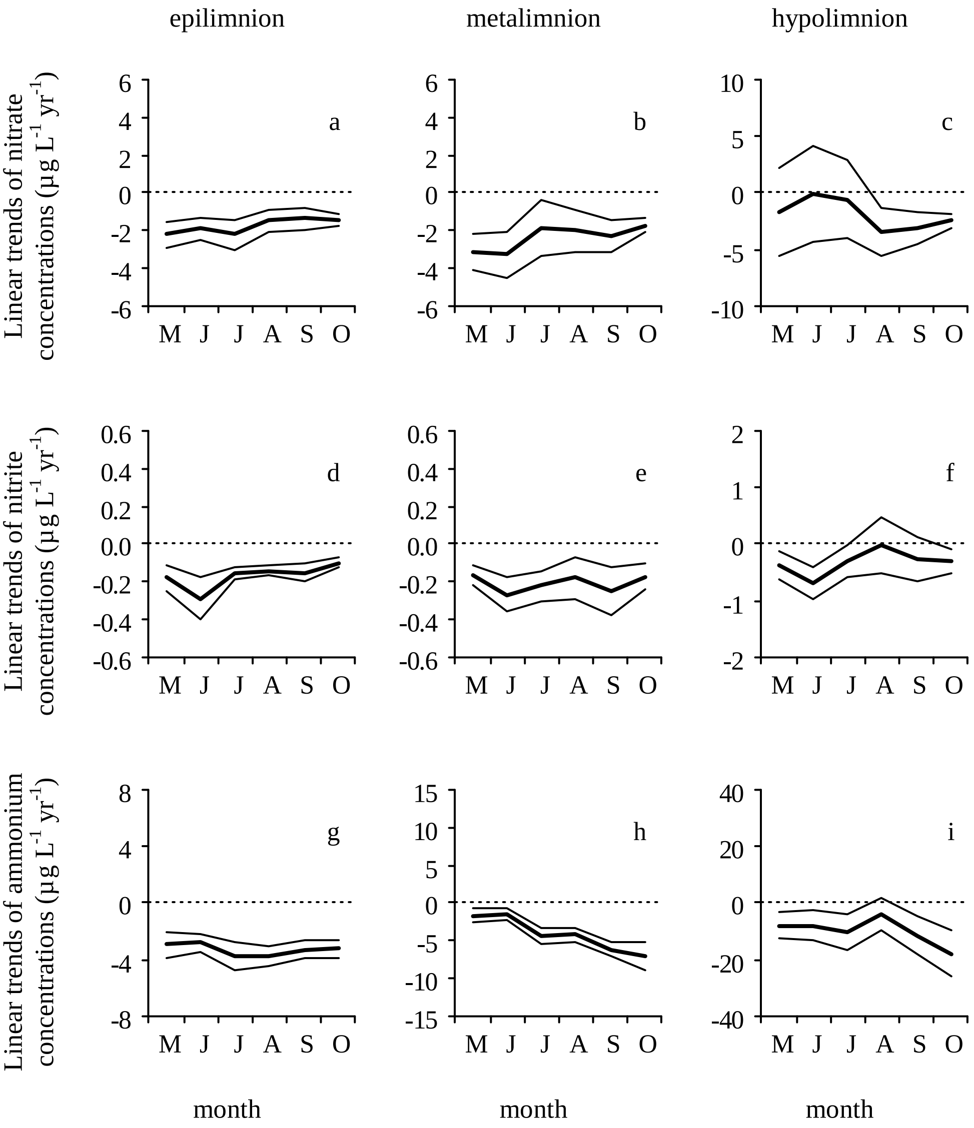

Fig. 12. Linear trends of monthly (a-c) nitrate concentrations, (d-f) nitrite concentrations, and (g-i) ammonium concentrations in the epilimnion, metalimnion, and hypolimnion from May to October within the period from 1969-2006. The thick lines show the slopes of the linear trends and the thin lines show the standard errors of the trends. Note the different scale of the y-axis.

85 µg L^{-1}) and the trends remained significantly negative ($p<0.05$) until October. Metalimnetic NO_3^- concentrations decreased most pronounced in May and June (3.1-3.3 µg L^{-1} yr^{-1}, $p<0.01$, overall decrease: about 120 µg L^{-1}). The trends became less pronounced, but remained negative towards the end of the stratification period. Hypolimnetic NO_3^- concentration trends were significantly negative in September (3.1 µg L^{-1} yr^{-1}, $p<0.05$, overall

decrease: about 120 µg L^{-1}) and in October (2.5 µg L^{-1} yr^{-1}, $p<0.01$, overall decrease: about 95 µg L^{-1}). Trends were not significantly lower from May to August ($p>0.05$).

Largest negative NO_2^- concentration trends were calculated in the epilimnion (0.3 µg L^{-1} yr^{-1}, $p<0.05$, overall decrease: about 11 µg L^{-1}), metalimnion (0.3 µg L^{-1} yr^{-1}, $p<0.01$, overall decrease: about 10 µg L^{-1}), hypolimnion (0.7 µg L^{-1} yr^{-1}, $p<0.05$, overall decrease: about 26 µg L^{-1}) in June. From that point on, trends became lower. In contrast to the hypolimnion, however, epilimnetic and metalimnetic trends remained significantly negative in each month from July to October.

Largest negative epilimnetic NH_4^+ concentration trends were calculated in July (3.8 µg L^{-1} yr^{-1}, $p<0.001$, overall decrease: about 145 µg L^{-1}); however, these trends were quite similar in each month ($p<0.01$). Metalimnetic NH_4^+ concentrations became more pronounced from May to October and the largest negative trend was calculated for October (7.1 µg L^{-1} yr^{-1}, $p<0.001$, overall decrease: about 270 µg L^{-1}). Although hypolimnetic NH_4^+ concentration trends were negative from May to October, the only significant hypolimnetic trend was observed in October (18.1 µg L^{-1} yr^{-1}, $p<0.05$, overall decrease: about 690 µg L^{-1}).

3.2.2. Inorganic phosphate and total dissolved phosphorus concentrations

Fig. 13 displays the annual cycles and the linear trends of the two phosphorus fractions within the 0-10 m water column from February to November. Mean PO_4^{3-} (about 150 ± 44 µg L^{-1}) and TDP concentrations (about 180 ± 38 µg L^{-1}) were highest in February and decreased continuously from that point on. Linear trends of both phosphorus fractions were mostly not significant, with the only exception being PO_4^{3-} in March (1.5 µg L^{-1} yr^{-1}, $p<0.05$, overall decrease: about 57 µg L^{-1}).

Annual cycles of epilimnetic PO_4^{3-} and TDP concentrations agree with the annual cycles calculated over the 0-10 m water column (Fig. 14); however, there was an increase of

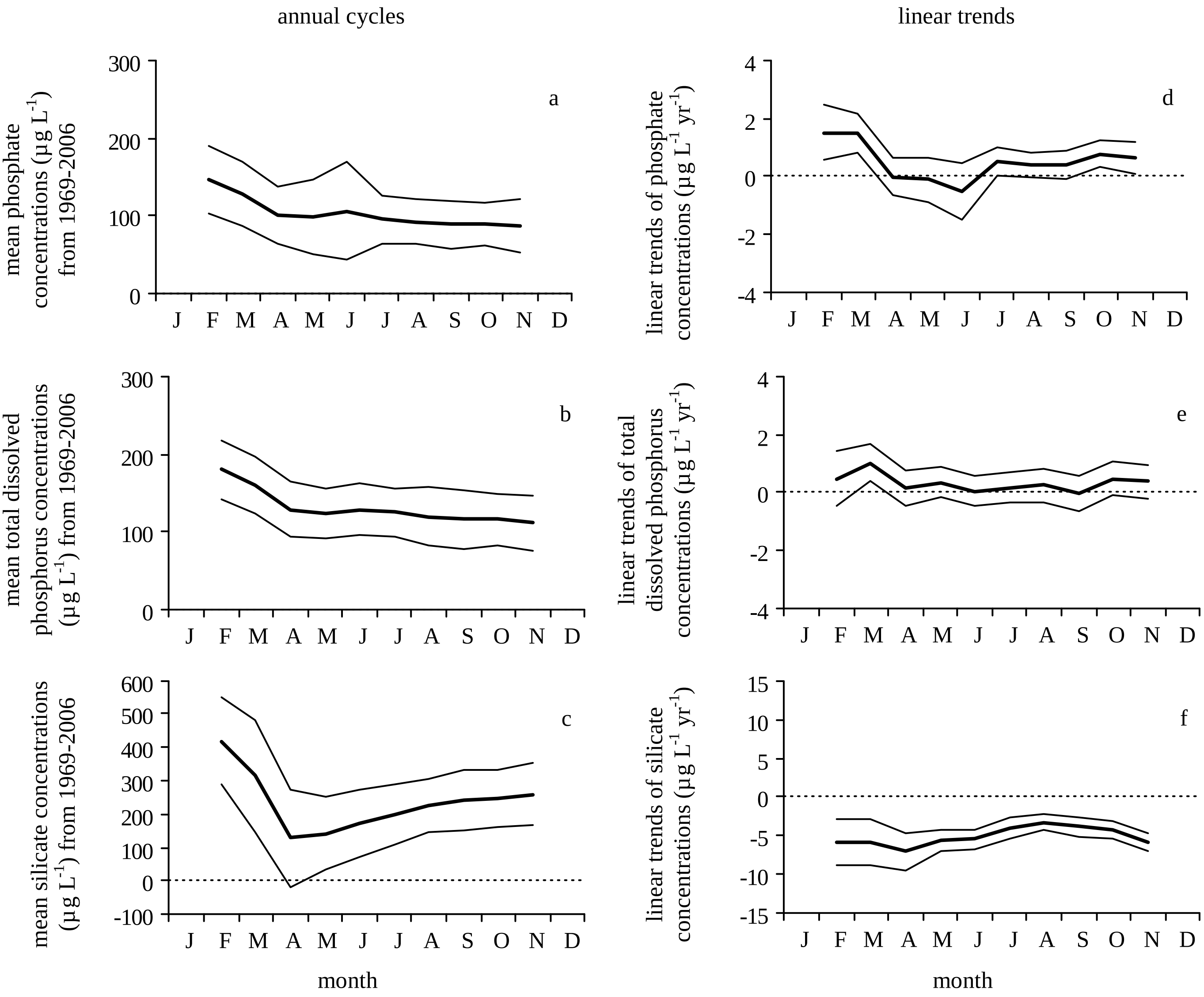

Fig. 13. Annual cycles (a-c) and linear trends (d-f) of monthly phosphate, total dissolved phosphorus, and silicate concentrations in the 0-10 m water column from February to November within the period from 1969-2006. The thick lines of the annual cycles show the means and the thin lines show the standard deviations, whereas the thick lines of the linear trends show the slopes of the linear trends and the thin lines show the standard errors of the trends.

epilimnetic PO_4^{3-} and TDP concentrations in October. Furthermore, the annual cycles of PO_4^{3-} and TDP concentrations in each layer resembled each other quite well. Concentrations of epilimnetic PO_4^{3-} decreased from May (about 35 ± 26 µg L^{-1}) to a minimum in August (about 5.0 ± 4.2 µg L^{-1}) and then increased up to about 22.1 ± 19.2 µg L^{-1} in October. Epilimnetic TDP concentrations decreased from May (about 69 ± 31 µg L^{-1}) to a minimum in September (about 25 ± 17 µg L^{-1}) and then increased up to about 43 ± 27 µg L^{-1} in October.

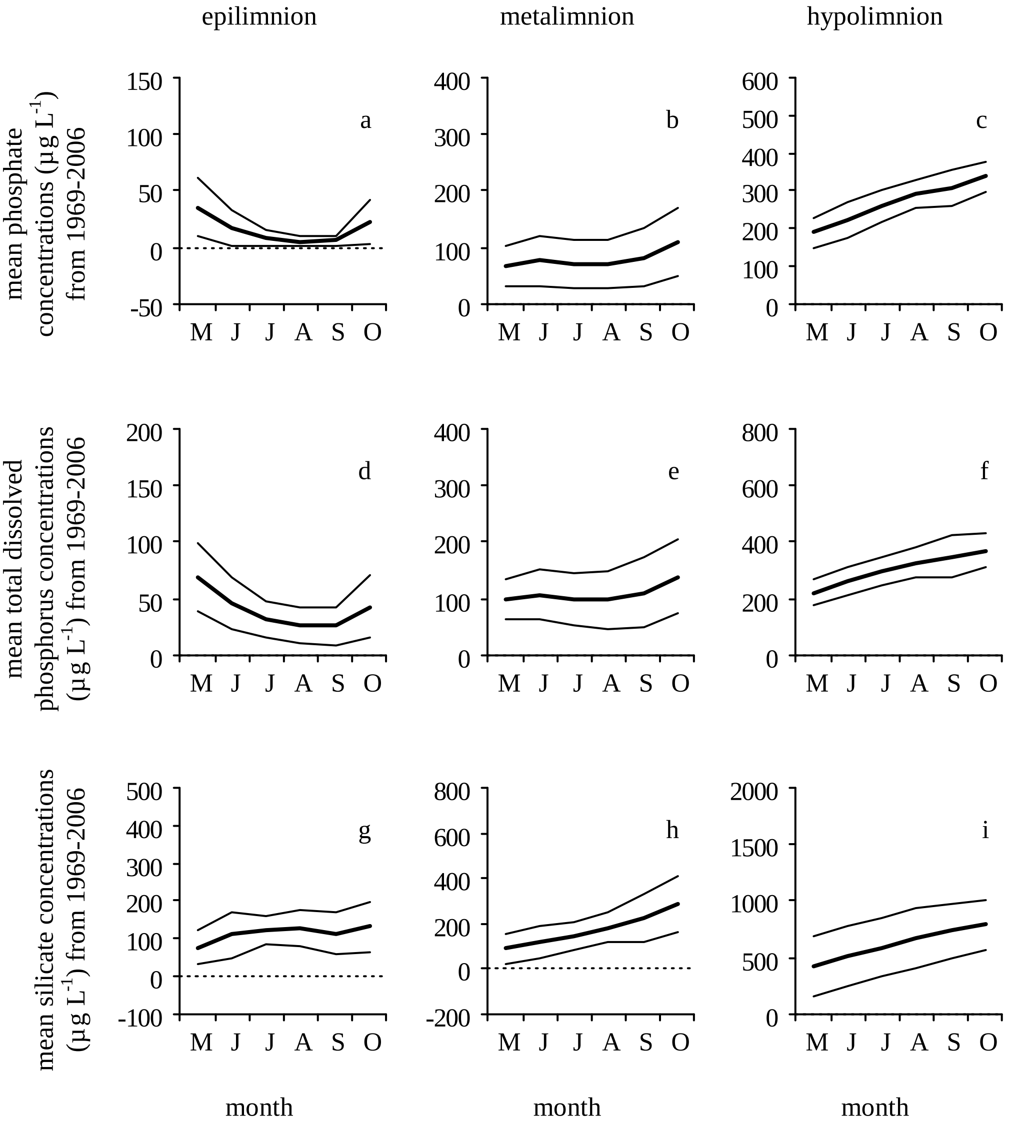

Fig. 14. Annual cycles of monthly (a-c) phosphate concentrations, (d-f) total dissolved phosphorus concentrations, and (g-i) silicate concentrations in the epilimnion, metalimnion, and hypolimnion from May to October within the period from 1969-2006. The thick lines show the means and the thin lines show the standard deviations. Note the different scale of the y-axis.

Metalimnetic PO_4^{3-} concentrations increased from May (about 66 ± 36 µg L^{-1}) to a maximum in October (about 109 ± 60 µg L^{-1}) and metalimnetic TDP concentrations increased from May (about 99 ± 36 µg L^{-1}) to a maximum in October (about 140 ± 50 µg L^{-1}).

Hypolimnetic PO_4^{3-} concentrations increased continuously from May (about 190 ± 41 µg L^{-1}) to a maximum in October (about 340 ± 40 µg L^{-1}) and hypolimnetic TDP concentrations increased also from May (about 220 ± 47 µg L^{-1}) to October (about 370 ± 63 µg L^{-1}).

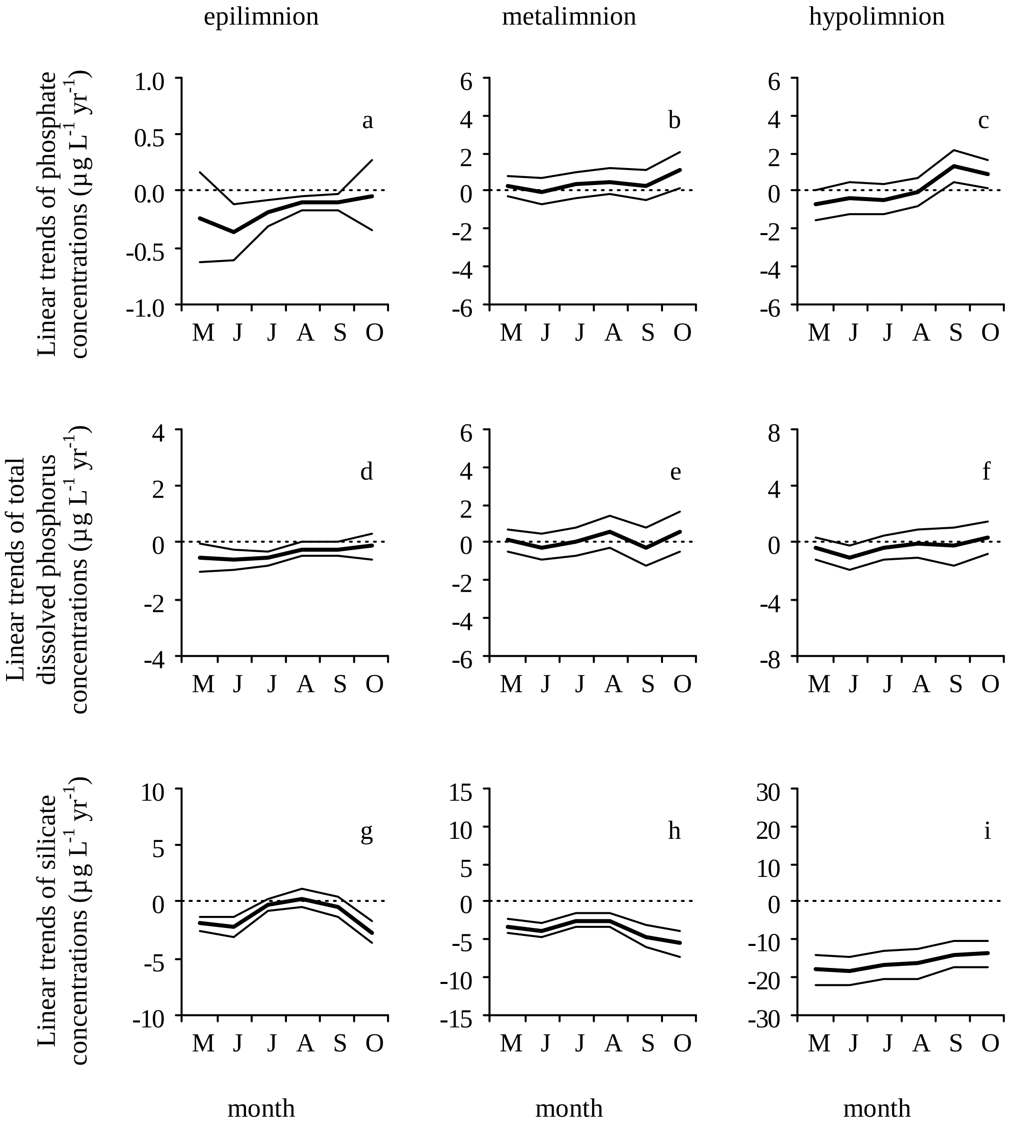

Fig. 15. Linear trends of monthly (a-c) phosphate concentrations, (d-f) total dissolved phosphorus concentrations, and (g-i) silicate concentrations in the epilimnion, metalimnion, and hypolimnion from May to October within the period from 1969-2006. The thick lines show the slopes of the linear trends and the thin lines show the standard errors of the trends. Note the different scale of the y-axis.

Fig. 15 depicts the linear trends of PO_4^{3-} and TDP concentrations in each layer from May to October. Epilimnetic PO_4^{3-} and TDP concentration trends were negative throughout the stratification period. Hypolimnetic PO_4^{3-} and TDP concentration trends were negative from May to August (PO_4^{3-}) or September (TDP) and became positive afterwards. Metalimnetic PO_4^{3-} and TDP concentration trends fluctuated from month to month from positive trends to negative trends. All these trends were not significant (*p*>0.05).

3.2.3. Silicate concentrations

Fig. 13 shows the annual cycles and the linear trends of silicate within the 0-10 m water column from February to November. Mean SiO_2 concentrations were highest in February (about 420 ± 130 $\mu g\ L^{-1}$) and decreased to a minimum in April (about 130 ± 150 $\mu g\ L^{-1}$) and increased continuously from that point on (about 260 ± 95 $\mu g\ L^{-1}$ in November). Linear trends were negative for all months with a negative trend maximum in April (7.0 $\mu g\ L^{-1}\ yr^{-1}$, $p<0.01$, overall decrease: about 266 $\mu g\ L^{-1}$).

Annual cycles of epilimnetic, metalimnetic, and hypolimnetic SiO_2 concentrations agree with the annual cycles calculated for the 0-10 m water column (Fig. 14). Epilimnetic SiO_2 concentrations increased from May (about 76 ± 44 $\mu g\ L^{-1}$) to October (about 130 ± 68 $\mu g\ L^{-1}$), metalimnetic SiO_2 concentrations increased from May (about 87 ± 66 $\mu g\ L^{-1}$) to October (about 287 ± 124 $\mu g\ L^{-1}$), and hypolimnetic SiO_2 concentrations increased from May (about 427 ± 268 $\mu g\ L^{-1}$) to October (about 787 ± 225 $\mu g\ L^{-1}$).

Fig. 15 displays the linear trends of SiO_2 concentrations in each layer from May to October. Metalimnetic and hypolimnetic SiO_2 concentration trends were significantly negative throughout the stratification period. Hypolimnetic SiO_2 concentration trends were most pronounced in May (18.0 $\mu g\ L^{-1}\ yr^{-1}$, $p<0.001$, overall decrease: about 683 $\mu g\ L^{-1}$); from that point on these trends became continuously lower (October: 13.8 $\mu g\ L^{-1}\ yr^{-1}$, $p<0.001$, overall decrease: about 524 $\mu g\ L^{-1}$). Following a metalimnetic SiO_2 concentration trend of 3.8 $\mu g\ L^{-1}\ yr^{-1}$ ($p<0.001$, overall decrease: about 145 $\mu g\ L^{-1}$) in June, there was a trend minimum in July and August (2.5 $\mu g\ L^{-1}\ yr^{-1}$, $p<0.05$, overall decrease: about 95 $\mu g\ L^{-1}$) followed by negative trends towards October (5.6 $\mu g\ L^{-1}\ yr^{-1}$, $p<0.05$, overall decrease: about 212 $\mu g\ L^{-1}$). Epilimnetic SiO_2 trends were only significantly negative in May (2.0 $\mu g\ L^{-1}\ yr^{-1}$, $p<0.05$, overall decrease: about 74 $\mu g\ L^{-1}$), June (2.2 $\mu g\ L^{-1}\ yr^{-1}$, $p<0.05$, overall decrease: about 85 $\mu g\ L^{-1}$), and October (2.7 $\mu g\ L^{-1}\ yr^{-1}$, $p<0.05$, overall decrease: about 104 $\mu g\ L^{-1}$).

3.2.4. Linkage of abiotic environmental parameters

Annual cycles of mean Secchi disc transparencies, dissolved oxygen concentrations, oxygen saturations, and pH calculated for the 0-10 m water column are shown in Fig. 16. All four figures indicate that the phytoplankton spring maximum occurred in April: Secchi disc transparencies displayed a minimum in April (about 1.5 ± 0.5 m), whereas oxygen concentrations (about 10.2 ± 2.8 mg L^{-1}), oxygen saturations (about 60 ± 15 %), and pH (about 8.0 ± 0.3) displayed maxima in April. Linear trends of oxygen concentration (0.1 mg L^{-1} yr^{-1}, $p<0.01$, overall increase: about 5.1 µg L^{-1}), oxygen saturation (0.8 % yr^{-1}, $p<0.001$, overall increase: about 31.1 µg L^{-1}), and pH (0.01 yr^{-1}, $p=0.05$, overall increase: about 0.4) were significantly positive in April, whereas Secchi disc transparencies did not change significantly ($p>0.05$) from 1969 to 2006. In April, mean Secchi disk transparencies were significantly negative correlated with mean oxygen concentrations ($r=-0.54$, $p<0.01$), mean oxygen saturations ($r=-0.51$, $p<0.01$), and mean pH ($r=-0.49$, $p<0.01$); however, from June to November, Secchi disc transparencies were only significantly correlated with mean pH ($-0.53<r<-0.64$, $0.01<p<0.001$) and did not correlate significantly with mean oxygen concentration and mean oxygen saturation ($p>0.05$). From September to November, Secchi disc transparencies increased significantly (0.05-0.07 m yr^{-1}, $0.01<p<0.001$, overall increase: about 1.8-2.7 m) and pH decreased (0.01 yr^{-1}, $p<0.05$, overall decrease: about 0.22-0.28) correspondingly.

Fig. 17 shows correlations of mean pH of the 0-10 m water column with mean NO_3^-, PO_4^{3-}, and SiO_2 of the 0-10 m water column from February to November, which revealed that pH correlated significantly negative with SiO_2 in March ($r=-0.52$, $p<0.01$) and April ($r=-0.60$, $p<0.001$), but not with NO_3^- or PO_4^{3-} ($p>0.05$). In the further course of the stratification period, the correlations of SiO_2 with pH decreased, whereas the correlation of NO_3^- with pH increased: NO_3^- was significantly positive correlated with pH from June to July ($0.36<r<0.37$,

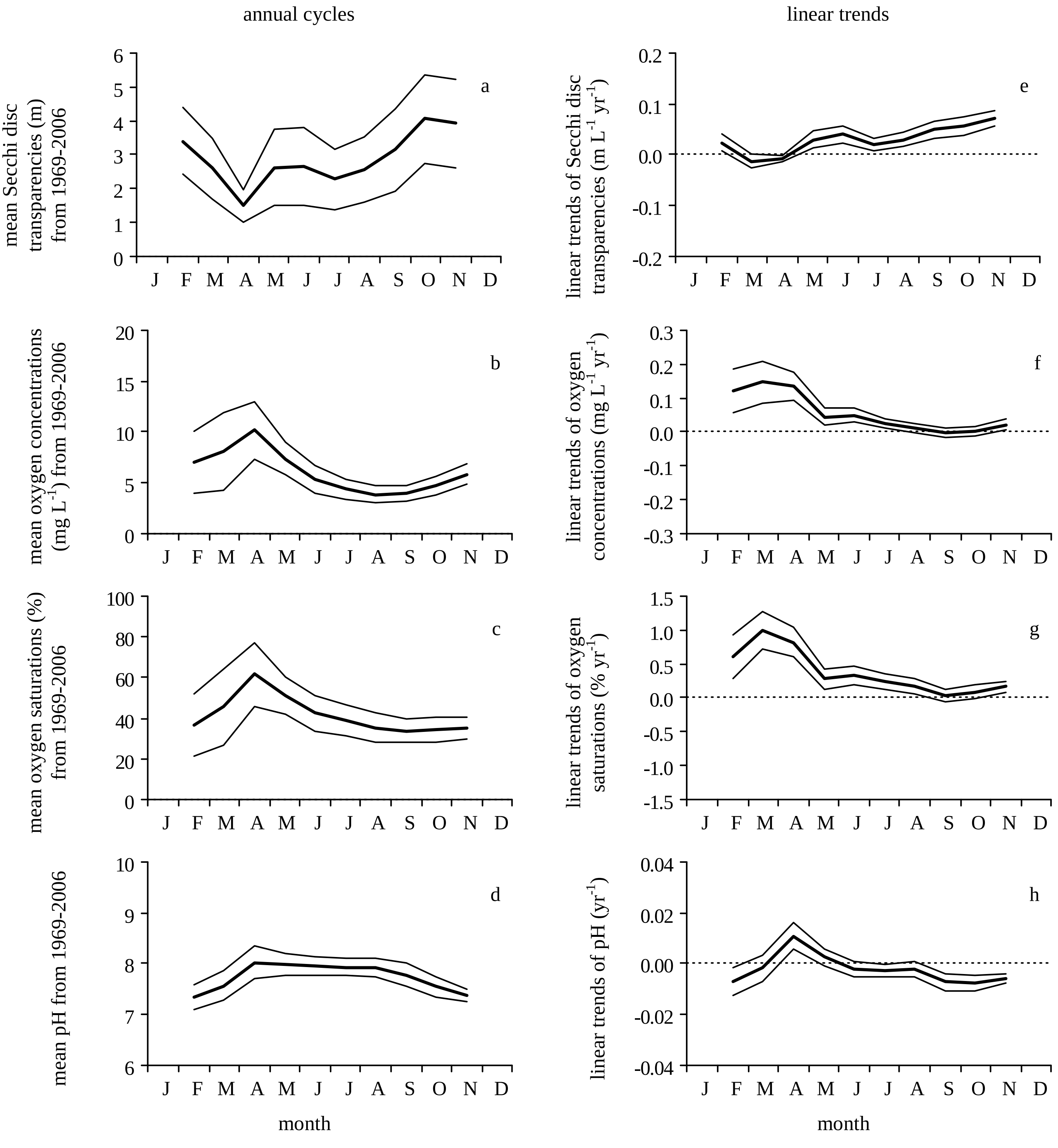

Fig. 16. Annual cycles (a-d) and linear trends (e-h) of monthly Secchi disc transparencies, oxygen concentrations, oxygen saturations, and pH in the 0-10 m water column from February to November within the period from 1969-2006. The thick lines of the annual cycles show the means and the thin lines show the standard deviations, whereas the thick lines of the linear trends show the slopes of the linear trends and the thin lines show the standard errors of the trends.

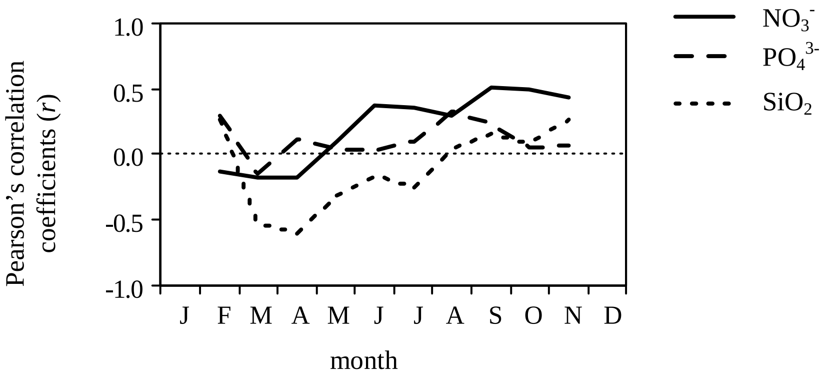

Fig. 17. Pearson's correlation coefficients (*r*) between the mean pH and mean NO_3^- (solid line), PO_4^{3-} (dashed line), and SiO_2 (dotted line) within the period 1969-2006. All parameters were calculated as means of the 0-10 m water column.

$p<0.05$) and from September to November ($0.43<r<0.51$, $0.05<p<0.01$). PO_4^{3-}, however, never correlated significantly with pH ($p<0.05$).

To assess the influence of positive and negative $NAO_{Dec\text{-}Mar}$ on lake parameters before the onset of stratification, we applied a Welch two-sample *t*-tests of parameters that were associated with years with a positive or negative $NAO_{Dec\text{-}Mar}$, i.e., above and below the 38 years mean (=0.68). Table 6 shows that mean water temperature, mean oxygen concentration, mean oxygen saturation, and mean pH of the 0-10 m water column were significantly higher in April in years with a positive $NAO_{Dec\text{-}Mar}$ than in years with a negative $NAO_{Dec\text{-}Mar}$. Furthermore, PO_4^{3-} concentrations in February and March were significantly higher in years with a positive $NAO_{Dec\text{-}Mar}$ than in years with a negative $NAO_{Dec\text{-}Mar}$. In addition, TDP concentrations were significantly higher in March and NH_4^+ concentrations were significantly lower in March and April in years with a positive $NAO_{Dec\text{-}Mar}$ than in years with a negative $NAO_{Dec\text{-}Mar}$. There was no significant difference in SiO_2, NO_3^-, and NO_2^- concentrations in years with positive or negative $NAO_{Dec\text{-}Mar}$.

Further analyses of PO_4^{3-} concentration revealed that PO_4^{3-} concentrations were associated with the mixing depth. Epilimnetic PO_4^{3-} concentrations correlated significantly positive with the thermocline depths in May, June, August, and October ($p<0.05$) and the thickness of the

Table 6. Welch two-sample *t*-tests of monthly mean water temperature, dissolved O_2 concentration, oxygen saturation, and pH in April and NO_3^-, NO_2^-, NH_4^+, PO_4^{3-}, TDP, and SiO_2 from February to April differentiated between years with negative and positive $NAO_{Dec\text{-}Mar}$-indices. All parameters were calculated for the 0-10 m water column. * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

		means (neg. $NAO_{Dec\text{-}Mar}$)	means (pos. $NAO_{Dec\text{-}Mar}$)	*t*-value	df	*p*-value
T (0-10 m)$_{Apr}$	(°C)	5.90	6.41	-2.25	17	0.038 *
O_2 (0-10 m)$_{Apr}$	(µg L^{-1})	8.11	11.97	-4.75	19	<0.001 ***
OS (0-10 m)$_{Apr}$	(%)	50.21	71.17	-4.66	19	<0.001 ***
pH (0-10 m)$_{Apr}$		7.77	8.17	-4.03	19	<0.001 ***
NO_3^- (0-10 m)$_{Feb}$	(µg L^{-1})	312.10	328.22	-0.16	11	0.877
NO_3^- (0-10 m)$_{Mar}$	(µg L^{-1})	335.19	388.47	-0.68	17	0.504
NO_3^- (0-10 m)$_{Apr}$	(µg L^{-1})	194.45	217.49	-0.44	25	0.667
NO_2^- (0-10 m)$_{Feb}$	(µg L^{-1})	4.72	6.73	-0.54	17	0.595
NO_2^- (0-10 m)$_{Mar}$	(µg L^{-1})	5.70	4.16	0.88	19	0.392
NO_2^- (0-10 m)$_{Apr}$	(µg L^{-1})	4.57	3.66	0.70	14	0.497
NH_4^+ (0-10 m)$_{Feb}$	(µg L^{-1})	269.44	194.42	0.75	8	0.475
NH_4^+ (0-10 m)$_{Mar}$	(µg L^{-1})	183.72	63.01	2.84	12	0.014 *
NH_4^+ (0-10 m)$_{Apr}$	(µg L^{-1})	85.36	48.41	2.14	17	0.047 *
PO_4^{3-} (0-10 m)$_{Feb}$	(µg L^{-1})	109.01	167.42	-3.42	11	0.006 **
PO_4^{3-} (0-10 m)$_{Mar}$	(µg L^{-1})	99.70	147.77	-3.48	20	0.002 **
PO_4^{3-} (0-10 m)$_{Apr}$	(µg L^{-1})	88.58	109.64	-1.46	18	0.163
TDP (0-10 m)$_{Feb}$	(µg L^{-1})	161.40	188.73	-1.50	10	0.163
TDP (0-10 m)$_{Mar}$	(µg L^{-1})	141.62	172.51	-2.23	19	0.038 *
TDP (0-10 m)$_{Apr}$	(µg L^{-1})	114.38	139.03	-1.89	22	0.073
SiO_2 (0-10 m)$_{Feb}$	(µg L^{-1})	372.45	441.76	-1.30	15	0.213
SiO_2 (0-10 m)$_{Mar}$	(µg L^{-1})	362.35	289.33	0.90	11	0.386
SiO_2 (0-10 m)$_{Apr}$	(µg L^{-1})	192.59	89.98	1.47	10	0.170

epilimnion from May to July ($p<0.05$). Metalimnetic PO_4^{3-} concentrations correlated significantly with thermocline depths throughout the stratification period ($p<0.05$).

To assess if the mixing depth in spring differed significantly between years with positive or negative $NAO_{Dec\text{-}Mar}$ and if higher mean PO_4^{3-} concentrations in the 0-10 m water column could, therefore, be explained by deep mixing, we applied a Welch two-sample *t*-tests of hypolimnetic oxygen parameters, because larger concentrations of oxygen in the deeper strata of the water column can be explained by a deeper vertical mixing in spring. Table 7 shows that hypolimnetic O_2 concentrations from May to July and oxygen saturations from May to August were significantly higher in years with a positive $NAO_{Dec\text{-}Mar}$ than in years with a

Table 7. Welch two-sample *t*-tests of monthly mean hypolimnetic dissolved oxygen concentrations (HO), oxygen saturations (HOS), nitrate concentrations (HNO_3^-) and ammonium concentrations (HNH_4^+) from May to October differentiated between years with negative and positive $NAO_{Dec\text{-}Mar}$-indices. * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

		means (neg. $NAO_{Dec\text{-}Mar}$)	means (pos. $NAO_{Dec\text{-}Mar}$)	*t*-value	df	*p*-value
HO May	($\mu g\ L^{-1}$)	1.26	4.22	-5.48	28	<0.001 ***
HO June	($\mu g\ L^{-1}$)	0.29	1.55	-5.09	24	<0.001 ***
HO July	($\mu g\ L^{-1}$)	0.16	0.56	-3.48	25	0.002 **
HO August	($\mu g\ L^{-1}$)	0.08	0.21	-2.02	24	0.055
HO September	($\mu g\ L^{-1}$)	0.08	0.13	-1.32	26	0.199
HO October	($\mu g\ L^{-1}$)	0.12	0.13	-0.28	30	0.782
HOS May	(%)	5.18	15.26	-5.28	28	<0.001 ***
HOS June	(%)	1.17	5.90	-5.07	25	<0.001 ***
HOS July	(%)	0.63	2.09	-3.46	26	0.002 **
HOS August	(%)	0.29	0.77	-2.08	24	0.048 *
HOS September	(%)	0.33	0.51	-1.13	24	0.271
HOS October	(%)	0.47	0.51	-0.19	29	0.851
HNO_3^- May	($\mu g\ L^{-1}$)	177.54	444.55	-4.20	27	<0.001 ***
HNO_3^- June	($\mu g\ L^{-1}$)	130.32	439.12	-5.07	28	<0.001 ***
HNO_3^- July	($\mu g\ L^{-1}$)	79.97	341.82	-5.47	27	<0.001 ***
HNO_3^- August	($\mu g\ L^{-1}$)	45.87	202.16	-4.95	25	<0.001 ***
HNO_3^- September	($\mu g\ L^{-1}$)	25.81	86.58	-2.49	21	0.021 *
HNO_3^- October	($\mu g\ L^{-1}$)	30.92	25.63	0.31	15	0.764
HNH_4^+ May	($\mu g\ L^{-1}$)	509.22	102.63	6.38	12	<0.001 ***
HNH_4^+ June	($\mu g\ L^{-1}$)	665.02	225.71	5.31	14	<0.001 ***
HNH_4^+ July	($\mu g\ L^{-1}$)	882.28	396.44	4.36	15	<0.001 ***
HNH_4^+ August	($\mu g\ L^{-1}$)	1030.64	571.32	5.31	17	<0.001 ***
HNH_4^+ September	($\mu g\ L^{-1}$)	1302.43	767.43	4.79	16	<0.001 ***
HNH_4^+ October	($\mu g\ L^{-1}$)	1524.50	969.65	3.73	18	0.002 **

negative $NAO_{Dec\text{-}Mar}$. Furthermore, hypolimnetic NO_3^- and NH_4^+ displayed the opposite pattern: Oxygenated NO_3^- concentrations were significantly higher in the hypolimnion from May to September in years with a positive $NAO_{Dec\text{-}Mar}$ than in years with a negative $NAO_{Dec\text{-}Mar}$. Oxygen-reduced NH_4^+ concentrations in the hypolimnion were significantly lower from May to October in years with a positive $NAO_{Dec\text{-}Mar}$ than in years with a negative $NAO_{Dec\text{-}Mar}$.

In the 0-10 m water column, NH_4^+ concentrations displayed a significant negative correlation with O_2 concentrations and oxygen saturations from April to August ($-0.43 < r < -0.71$, $0.05 < p < 0.001$); however, NO_3^- concentrations displayed a significantly

Table 8. Pearson's correlation coefficients (*r*) between SSI in August (SSI$_{Aug}$) and different nutrient parameters of the 0-10 m water column from August to November. * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

correlations	*r*	*t*-value	df	*p*-value
SSI$_{Aug}$ – NO_3^- (0-10 m)$_{Oct}$	-0.34	-2.03	31	0.051
SSI$_{Aug}$ – NO_3^- (0-10 m)$_{Sep}$	-0.32	-1.91	31	0.066
SSI$_{Aug}$ – NO_3^- (0-10 m)$_{Oct}$	-0.42	-2.54	30	0.017 **
SSI$_{Aug}$ – NO_3^- (0-10 m)$_{Nov}$	-0.58	-3.83	29	0.001 **
SSI$_{Aug}$ – NO_2^- (0-10 m)$_{Aug}$	0.08	0.46	31	0.648
SSI$_{Aug}$ – NO_2^- (0-10 m)$_{Sep}$	-0.18	-1.02	31	0.314
SSI$_{Aug}$ – NO_2^- (0-10 m)$_{Oct}$	-0.30	-1.74	30	0.093
SSI$_{Aug}$ – NO_2^- (0-10 m)$_{Nov}$	-0.22	-1.23	30	0.229
SSI$_{Aug}$ – NH_4^+ (0-10 m)$_{Aug}$	-0.35	-2.11	31	0.043 *
SSI$_{Aug}$ – NH_4^+ (0-10 m)$_{Sep}$	-0.35	-2.07	31	0.047 *
SSI$_{Aug}$ – NH_4^+ (0-10 m)$_{Oct}$	-0.23	-1.27	30	0.212
SSI$_{Aug}$ – NH_4^+ (0-10 m)$_{Nov}$	-0.07	-0.36	29	0.720
SSI$_{Aug}$ – PO_4^{3-} (0-10 m)$_{Aug}$	0.09	0.53	31	0.600
SSI$_{Aug}$ – PO_4^{3-} (0-10 m)$_{Sep}$	0.02	0.13	31	0.895
SSI$_{Aug}$ – PO_4^{3-} (0-10 m)$_{Oct}$	-0.01	-0.07	30	0.942
SSI$_{Aug}$ – PO_4^{3-} (0-10 m)$_{Nov}$	0.16	0.87	29	0.390
SSI$_{Aug}$ – TDP (0-10 m)$_{Aug}$	-0.14	-0.74	27	0.466
SSI$_{Aug}$ – TDP (0-10 m)$_{Sep}$	-0.06	-0.33	27	0.747
SSI$_{Aug}$ – TDP (0-10 m)$_{Oct}$	-0.07	-0.33	26	0.742
SSI$_{Aug}$ – TDP (0-10 m)$_{Nov}$	0.02	0.12	25	0.905
SSI$_{Aug}$ – SiO_2 (0-10 m)$_{Aug}$	-0.40	-2.43	31	0.021 *
SSI$_{Aug}$ – SiO_2 (0-10 m)$_{Sep}$	-0.42	-2.61	31	0.014 *
SSI$_{Aug}$ – SiO_2 (0-10 m)$_{Oct}$	-0.52	-3.34	30	0.002 **
SSI$_{Aug}$ – SiO_2 (0-10 m)$_{Nov}$	-0.49	-3.01	28	0.006 **

positive correlation only with O_2 concentrations (r=0.41, p<0.05) and oxygen saturations (r=0.39, p<0.05) in September.

The SSI in August correlated significantly negative with mean NH_4^+ and SiO_2 concentrations within the 0-10 m water column, but not with NO_3^-, NO_2^-, PO_4^{3-}, and TDP (Table 8). However, SSI in August affected not only nutrient concentration in August, but also in the following months. More importantly, SiO_2 concentrations were particularly inversely associated with water column stability.

3.3. Principal component analysis of abiotic environmental parameters

We performed a PCA on a set of abiotic environmental parameters for each month of the annual cycle separately. We implemented PCAs, on the one hand, on physical and chemical parameters and, on the other hand, on nutrient parameters (Table 1). Furthermore, we performed two different sets of PCAs, one for the months before the onset of stratification from February to April, and one for the months during the stratification period from May to October. This can be explained by the reduced number of considered variables in the datasets of the period before to the onset of stratification.

3.3.1. Principal Component Analysis of physical and chemical parameters

According to a Scree-plot analysis and the Kaiser-Guttman-Criterion, two principal components (PCs) sufficed to describe a large proportion of variance of the included variables from February to April. From May to October, however, we decided to interpret three PCs. Table 9 shows, for each month, the ratio of explained variances of each component relative to the total variance and the ratio of the cumulative variance of the considered PCs relative to the total variance.

Table 9. Explained and cumulative variances of the relevant principal components (PCs) derived from PCAs performed on physical and chemical parameters for each month from February to October. The Roman numerals indicate the respective PC.

	physical and chemical parameters			
	PC I	PC II	PC III	cum. variance
February	0.54	0.26		0.80
March	0.59	0.23		0.82
April	0.69	0.19		0.88
May	0.50	0.26	0.08	0.84
June	0.32	0.26	0.19	0.77
July	0.32	0.27	0.14	0.73
August	0.38	0.28	0.12	0.78
September	0.34	0.19	0.19	0.72
October	0.28	0.27	0.15	0.70

Table 10 shows the factor loadings of each PC. Factor loadings are the Pearson's correlation coefficients between each factor score and the original variables and describe how much information each factor score shares with the original variables.

The first PCs of the PCAs performed on the February, March, and April datasets were linked to temperature: All PCs were associated with air temperature, $\text{NAO}_{\text{Dec-Mar}}$, water temperature, and O_2. However, SSI was negatively connected with these variables in February, but positively connected in April. The second PCs described less variance. In February, the second PC was, again, associated with mean water temperature. In March, PC II described the relationship of water temperature and lake stability, whereas in April, PC II described the negative relationship of wind speed and lake stability.

In May, PC I represented a gradient of water temperature and pH in all layers and of O_2 in rather deeper strata of the lake. PC II was, again, associated with oxygen availability; however, this time, this principal component was connected with O_2 and pH in the upper strata of the lake and it was negatively connected with mean lake temperature. PC III was represented by mixing depth.

Table 10. Factor loadings of the relevant principal components (PCs) derived from PCAs performed on physical and chemical parameters for each month from February to October. Significant loadings (p<0.05) are written bald. The Roman numerals indicate the respective PC.

	loadings February			loadings March			loadings April		
	PC I	PC II	PC III	PC I	PC II	PC III	PC I	PC II	PC III
AT	**0.92**	0.11		**0.94**	-0.06		**0.85**	0.21	
WS	**0.65**	0.47		-0.38	-0.08		-0.35	**-0.77**	
$\text{NAO}_{\text{Dec-Mar}}$	**0.86**	-0.38		**0.86**	-0.41		**0.71**	-0.59	
SD	-0.18	0.60		**-0.65**	0.56		**-0.82**	0.06	
SSI	**-0.87**	0.31		0.17	**0.81**		**0.68**	**0.66**	
HC	**0.78**	0.58		**0.81**	0.57		**0.96**	0.19	
LST	**0.93**	0.03		**0.95**	0.19		**0.88**	0.44	
MLT	**0.59**	**0.77**		**0.62**	**0.70**		**0.93**	0.02	
T (0-10 m)	**0.77**	0.59		**0.80**	**0.58**		**0.98**	0.11	
O_2 (0-10 m)	**0.77**	-0.58		**0.86**	-0.48		**0.86**	-0.43	
OS (0-10 m)	**0.77**	-0.56		**0.89**	-0.42		**0.90**	-0.36	
pH (0-10 m)	0.35	-0.61		**0.85**	-0.18		**0.84**	-0.50	

Table continued from previous page

	loadings May			loadings June			loadings July		
	PC I	PC II	PC III	PC I	PC II	PC III	PC I	PC II	PC III
AT	**0.87**	0.15	0.23	0.56	0.18	**-0.65**	**0.91**	-0.17	0.20
WS	-0.34	**-0.59**	0.21	-0.54	-0.11	0.01	**-0.60**	-0.08	-0.10
ET	**0.93**	0.17	0.20	**0.67**	0.05	**-0.71**	**0.84**	-0.33	0.33
MT	**0.93**	-0.02	0.15	0.52	0.27	-0.37	**0.70**	-0.02	0.30
HT	**0.78**	0.38	0.16	**0.70**	0.26	0.46	0.20	**0.81**	-0.17
EO	-0.35	**-0.73**	-0.31	-0.57	0.26	0.30	0.26	0.28	**-0.90**
MO	**0.59**	-0.53	0.13	-0.11	**0.87**	-0.06	**0.74**	-0.27	-0.04
HO	**0.87**	-0.20	-0.29	0.29	**0.85**	0.23	**0.60**	0.46	0.07
EOS	0.01	**-0.81**	-0.05	-0.53	0.33	0.00	0.45	0.16	**-0.85**
MOS	0.57	**-0.62**	0.26	-0.22	**0.84**	-0.28	**0.75**	-0.43	-0.08
HOS	**0.89**	-0.23	-0.25	0.29	**0.87**	0.22	**0.66**	0.42	0.08
EPH	**0.67**	-0.38	-0.34	**-0.66**	0.45	-0.02	0.47	0.00	**-0.72**
MPH	**0.74**	-0.55	0.23	-0.43	**0.61**	**-0.60**	0.52	**-0.71**	-0.08
HPH	**0.84**	-0.18	-0.15	**0.69**	0.55	0.04	0.28	0.48	0.44
SD	-0.05	**0.83**	0.33	0.57	0.02	0.08	-0.11	0.03	0.40
TD	-0.25	0.48	**-0.60**	0.14	-0.04	**0.91**	-0.57	**0.69**	0.18
ED	-0.02	0.44	**-0.80**	0.39	-0.16	**0.86**	-0.43	**0.85**	0.01
MD	-0.31	**0.80**	0.36	0.18	**-0.58**	-0.47	0.02	0.19	0.26
HD	0.23	**-0.88**	0.31	-0.48	**0.63**	-0.33	0.35	-0.83	-0.15
SSI	**0.91**	0.35	0.08	**0.81**	0.06	-0.55	**0.85**	-0.12	0.44
HC	**0.76**	**0.62**	-0.01	**0.99**	-0.05	0.06	0.46	**0.75**	0.38
LST	**0.93**	0.17	0.18	**0.68**	0.07	**-0.71**	**0.86**	-0.26	0.35
MLT	**0.72**	**0.66**	0.05	**0.94**	-0.04	0.28	0.28	**0.89**	0.17
T (0-10 m)	**0.75**	**0.64**	-0.02	**0.97**	-0.09	0.18	0.31	**0.87**	0.31
O_2 (0-10 m)	**0.92**	-0.14	-0.27	0.24	**0.85**	0.39	0.55	**0.61**	-0.34
OS (0-10 m)	**0.92**	-0.14	-0.27	0.25	**0.82**	0.43	0.54	**0.59**	-0.49
pH (0-10 m)	**0.92**	-0.21	-0.13	-0.11	**0.81**	-0.18	0.51	0.29	-0.33

	loadings August			loadings September			loadings October		
	PC I	PC II	PC III	PC I	PC II	PC III	PC I	PC II	PC III
AT	-0.03	**0.85**	0.18	0.46	-0.18	**0.68**	**0.79**	-0.22	-0.10
WS	-0.33	-0.40	0.00	**-0.64**	0.22	0.19	0.30	-0.17	0.33
ET	0.19	**0.91**	0.22	0.08	0.09	**0.95**	**0.78**	-0.22	-0.38
MT	**0.75**	**0.58**	-0.07	0.30	**0.60**	0.36	**0.68**	0.22	-0.47
HT	**0.81**	-0.23	0.30	**0.78**	0.25	-0.20	0.46	**0.64**	-0.29
EO	**0.94**	-0.04	-0.16	0.38	**0.88**	-0.06	-0.42	**0.65**	0.01
MO	0.11	**0.80**	-0.31	**-0.59**	**0.58**	0.04	-0.45	0.37	0.17
HO	0.49	-0.07	**-0.69**	**0.68**	-0.20	0.30	0.43	0.14	**0.71**
EOS	**0.94**	0.09	-0.14	0.38	**0.87**	0.15	-0.38	0.53	-0.08
MOS	0.14	**0.86**	-0.31	**-0.63**	**0.62**	0.11	-0.51	0.14	0.02
HOS	0.49	-0.07	**-0.68**	**0.69**	-0.17	0.30	0.46	0.16	**0.72**
EPH	**0.86**	-0.03	-0.26	0.53	0.44	-0.11	-0.22	0.53	**-0.68**
MPH	0.11	**0.63**	-0.53	-0.34	0.47	-0.38	-0.27	0.52	-0.55
HPH	0.14	-0.48	0.04	0.21	0.42	-0.02	0.22	**0.93**	-0.10
SD	**-0.90**	0.07	-0.01	-0.39	**-0.70**	-0.24	0.32	-0.52	0.39
TD	0.43	**-0.75**	-0.10	**0.68**	-0.15	**-0.62**	0.47	0.55	**0.61**
ED	-0.10	**-0.88**	0.04	0.53	-0.33	**-0.66**	0.24	**0.75**	0.34
MD	**0.60**	0.23	0.36	0.53	-0.40	0.27	0.37	-0.32	0.33
HD	-0.55	0.56	-0.42	**-0.68**	0.48	0.17	-0.47	-0.50	-0.53
SSI	0.18	**0.84**	0.36	0.17	-0.02	**0.95**	**0.64**	-0.39	-0.38
HC	**0.78**	0.12	0.56	**0.88**	-0.17	0.27	**0.93**	0.25	-0.18
LST	0.16	**0.89**	0.26	0.13	0.07	**0.96**	**0.71**	-0.28	-0.42
MLT	**0.83**	-0.14	0.49	**0.90**	-0.09	-0.04	**0.82**	0.50	-0.16
T (0-10 m)	**0.81**	-0.08	0.53	**0.91**	-0.22	0.10	**0.92**	0.33	-0.10
O_2 (0-10 m)	**0.85**	-0.16	-0.29	**0.68**	0.49	-0.35	-0.16	**0.89**	0.29
OS (0-10 m)	**0.90**	-0.08	-0.22	**0.71**	**0.59**	-0.21	-0.14	**0.87**	0.19
pH (0-10 m)	**0.77**	-0.29	-0.33	0.53	0.37	-0.33	-0.06	**0.78**	-0.44

In June, PC I was related to water temperature in all layers of the lake, but it was not related to O_2. In addition, PC III was also linked to water temperature; however, this principal component was exclusively associated with lake surface temperature. PC II was correlated with O_2 in rather deeper strata of the lake.

In July, PC I represented a gradient of water temperature in the upper strata and of O_2 in deeper strata of the lake. PC II described a gradient of mean water temperature and mean O_2 concentration in association with mixing depth. PC III was exclusively associated with epilimnetic O_2 and pH.

In August, PC I was positively associated with mean lake water temperature and with O_2 and pH, but it was also negatively associated with Secchi disc transparencies. In contrast to PC I, PC II was exclusively associated with lake surface temperature, whereas PC III was associated with hypolimnetic O_2.

In September, PC I was correlated with mixing depth and displayed its effect on mean lake temperature and deep water O_2, whereas PC II was connected with O_2 in the upper strata of the lake. PC III described the relationship of mixing depth and lake surface temperature.

In October, PC I was associated with mean water temperature, whereas PC II was associated with mean O_2 and pH. PC III was represented by mixing depth and it expressed its effect on epilimnetic pH and hypolimnetic O_2.

The first two principal components from February to April and the first three principal components from May to October were in most cases represented by temperature or by oxygen conditions. Apart from February to April, where we only considered the means of the 0-10 m water column, the loadings of the respective principal components can be interpreted as an indication of the interplay between temperature and oxygen and of the layers primarily associated with these two parameters. Some principal components also describe the influence of mixing depth or lake stability on temperature and oxygen.

3.3.2. Principal Component Analysis of nutrient parameters

In contrast to the PCAs of physical and chemical parameter datasets, we decided to interpret only two principal components of the nutrient datasets from February to October, since they already explained a large proportion of variance of the original datasets (Table 11). PC III only explained a minor proportion of variance. Table 12 shows the factor loadings of each PC.

In February, PC I was associated with mean NH_4^+, PO_4^{3-}, TDP, and SiO_2, whereas PC II was associated with mean NO_3^-.

In March, PC I described a negative relationship of NH_4^+ and PO_4^{3-} and TDP. NO_3^- and SiO_2 were connected with PC II.

In April, PC I was positively linked to PO_4^{3-} and TDP and negatively linked to NO_2^-, NH_4^+, and SiO_2, whereas PC II was correlated with NO_3^-.

In contrast to the first PCs of the PCAs performed on physical and chemical parameters from May to October, the first PCs of the PCAs performed on nutrient parameters from May to October were quite robust: Besides some additional single parameters in each month, the first principal components were always positively connected with NO_3^-, PO_4^{3-}, and TDP in each month. To describe the degree to which the structure of the factor loadings obtained from the analysis of each month were similar throughout the year, the correlations of the loadings of PC I in May (Table 12) with the loadings of the first principal components of each month from June to October (also shown in Table 12) revealed that PC I in May was significantly associated with the first principal components in June (r=0.88, p<0.001), July (r=0.88, p<0.001), August (r=0.85, p<0.001), September (r=0.83, p<0.001), and October (r=0.82, p<0.001). From June to September, the first principal components were also (negatively) associated with NH_4^+. The factor loadings obtained from the PCA of May retains the same structure of variables in the subsequent months.

Table 11. Explained and cumulative variances of the relevant principal components (PCs) derived from PCAs performed on nutrient parameters for each month from February to October. The Roman numerals indicate the respective PC.

	nutrient parameters		
	PC I	PC II	cum. variance
February	0.55	0.28	0.83
March	0.46	0.25	0.71
April	0.58	0.25	0.83
May	0.39	0.21	0.60
June	0.43	0.17	0.60
July	0.42	0.20	0.62
August	0.47	0.24	0.71
September	0.47	0.24	0.71
October	0.41	0.30	0.71

In September and October NO_3^- and NH_4^+ were positively associated with the second principal components, in contrast to the previous months, where NO_3^- and NH_4^+ were negatively related to the first principal components. Apart from June, NO_2^- and SiO_2 were positively associated with each other in respect to the second PC in each month.

In contrast to the PCAs of physical and chemical parameters, two principal components sufficed to describe a large proportion of variance in the nutrient parameter dataset. The first principal components of nutrient parameters were quite robust from May to October: They were all positively represented by NO_3^-, PO_4^{3-}, and TDP and there was also little variation in the association between these parameters and the respective layers of the lake. The second PCs were mostly associated with SiO_2 concentrations. In September and October, PCs II were also positively related to NO_3^- and NH_4^+, which was not apparent in the previous months. This

Table 12. Factor loadings of the relevant principal components (PCs) derived from PCAs performed on nutrient parameters for each month from February to October. Significant loadings (p<0.05) are written bald. The Roman numerals indicate the respective PC.

	loadings February		loadings March		loadings April	
	PC I	PC II	PC I	PC II	PC I	PC II
NO_3^- (0-10 m)	-0.31	**0.93**	0.30	**0.80**	0.00	**0.97**
NO_2^- (0-10 m)	-0.42	0.03	-0.38	0.33	**-0.80**	0.41
NH_4^+ (0-10 m)	**0.77**	-0.60	**-0.78**	0.25	**-0.73**	-0.01
PO_4^{3-} (0-10 m)	**0.91**	0.36	**0.93**	0.21	**0.92**	0.32
TDP (0-10 m)	**0.82**	0.55	**0.88**	0.29	**0.86**	0.41
SiO_2 (0-10 m)	**0.97**	-0.02	-0.51	**0.73**	**-0.85**	0.38

Table continued from previous page

	loadings May		loadings June		loadings July	
	PC I	PC II	PC I	PC II	PC I	PC II
ENO_3^-	0.56	0.53	0.33	0.29	**0.61**	0.33
MNO_3^-	**0.74**	**0.59**	**0.75**	0.19	**0.77**	-0.02
HNO_3^-	**0.84**	-0.05	**0.79**	0.51	**0.87**	0.02
ENO_2^-	0.49	**0.61**	-0.55	**0.58**	**-0.66**	0.22
MNO_2^-	0.31	**0.66**	-0.45	**0.67**	0.04	0.57
HNO_2^-	0.11	0.51	-0.05	0.42	-0.01	0.43
ENH_4^+	-0.13	0.41	**-0.74**	0.32	**-0.73**	0.28
MNH_4^+	0.27	0.03	-0.46	0.55	**-0.63**	0.37
HNH_4^+	**-0.73**	0.15	**-0.76**	-0.49	**-0.78**	0.08
EPO_4^{3-}	**0.93**	-0.06	**0.84**	0.05	**0.83**	0.12
MPO_4^{3-}	**0.94**	-0.17	**0.92**	0.07	**0.89**	0.32
HPO_4^{3-}	0.49	-0.39	**0.74**	-0.21	-0.03	**0.83**
ETDP	**0.88**	0.13	**0.74**	-0.18	**0.66**	0.40
MTDP	**0.95**	-0.08	**0.91**	-0.17	**0.85**	0.43
HTDP	0.26	0.07	0.05	**-0.83**	-0.17	**0.76**
$ESiO_2$	0.20	**0.67**	0.51	**-0.59**	0.26	0.27
$MSiO_2$	-0.06	**0.82**	-0.16	-0.41	-0.35	**0.75**
$HSiO_2$	-0.55	0.47	**-0.64**	-0.52	**-0.71**	0.42
NO_3^- (0-10 m)	**0.84**	0.29	**0.76**	0.43	**0.88**	0.04
NO_2^- (0-10 m)	-0.09	**0.89**	-0.31	0.18	-0.15	0.54
NH_4^+ (0-10 m)	-0.27	0.12	**-0.78**	0.09	**-0.84**	0.35
PO_4^{3-} (0-10 m)	**0.92**	-0.31	**0.87**	0.13	**0.70**	0.50
TDP (0-10 m)	**0.93**	-0.11	**0.83**	-0.17	**0.71**	**0.64**
SiO_2 (0-10 m)	-0.48	**0.69**	-0.52	-0.45	**-0.66**	**0.62**

	loadings August		loadings September		loadings October	
	PC I	PC II	PC I	PC II	PC I	PC II
ENO_3^-	**0.66**	0.54	**0.63**	0.54	0.53	**0.65**
MNO_3^-	**0.85**	0.44	**0.73**	0.57	**0.65**	**0.67**
HNO_3^-	**0.80**	0.41	**0.61**	**0.58**	0.07	**0.84**
ENO_2^-	-0.21	**0.74**	0.22	0.52	**0.64**	0.45
MNO_2^-	0.50	0.56	**0.59**	0.33	**0.59**	0.26
HNO_2^-	0.30	0.38	0.44	-0.08	0.49	0.08
ENH_4^+	**-0.62**	**0.72**	**-0.67**	**0.58**	-0.43	**0.73**
MNH_4^+	-0.45	**0.78**	-0.45	**0.87**	-0.42	**0.83**
HNH_4^+	**-0.69**	0.35	**-0.67**	**0.59**	**-0.64**	**0.62**
EPO_4^{3-}	**0.78**	0.23	**0.79**	0.42	**0.81**	0.02
MPO_4^{3-}	**0.85**	-0.05	**0.91**	0.14	**0.90**	-0.03
HPO_4^{3-}	**0.84**	-0.01	**0.82**	-0.37	**0.77**	-0.14
ETDP	**0.80**	0.37	**0.92**	0.24	**0.88**	0.09
MTDP	**0.88**	0.17	**0.92**	0.20	**0.89**	0.25
HTDP	**0.85**	0.16	**0.86**	0.05	0.51	**0.62**
$ESiO_2$	0.42	0.31	0.47	0.30	0.14	0.53
$MSiO_2$	-0.28	**0.88**	-0.21	**0.71**	-0.38	**0.72**
$HSiO_2$	-0.56	**0.64**	-0.43	**0.70**	-0.56	**0.65**
NO_3^- (0-10 m)	**0.89**	0.36	**0.79**	0.54	**0.60**	**0.71**
NO_2^- (0-10 m)	0.44	0.20	**0.65**	0.12	**0.76**	0.26
NH_4^+ (0-10 m)	**-0.60**	**0.74**	**-0.64**	**0.70**	-0.54	**0.78**
PO_4^{3-} (0-10 m)	**0.91**	-0.21	**0.89**	-0.29	**0.87**	-0.21
TDP (0-10 m)	**0.95**	0.04	**0.94**	-0.07	**0.91**	0.12
SiO_2 (0-10 m)	-0.40	**0.80**	-0.27	**0.82**	-0.41	**0.82**

could be an indication that these PCs were associated with nitrogen and that these PCs did not represent an interplay of oxygenated and reduced nitrogen anymore. Prior to the stratification period, PCs I were mostly connected with PO_4^{3-}, TDP, NH_4^+, and SiO_2, whereas PC II was linked to NO_3^- from February to April.

3.4. Zooplankton community analysis

3.4.1. Zooplankton species abundances

In the samples retrieved from the October months, 56 species were identified in the pelagial in Lake Plußsee. The majority of species (38) belonged to the zooplankton group of rotifers, 11 species belonged to the cladoceran group, and 7 species belonged to the copepod group. Table 13 shows all zooplankton species classified into the three major zooplankton groups. It also shows the abbreviations we used in tables and figures throughout the zooplankton analysis.

Fig. 18 shows that highest zooplankton abundances (number of individuals) were reached in 1989 (about 600 Ind L^{-1}), 1970, 2010, and 2011 (>200 Ind L^{-1}), whereas the lowest abundances were established in 1969 (about 30 Ind L^{-1}), 1984, 1991, 1992, and 1996 (<100 Ind L^{-1}). Years with high zooplankton abundances were related to high abundances of rotifers, whereas years with low zooplankton abundances were related to low abundances of rotifers ($r=0.99$, $p<0.001$).

The relationship of high zooplankton and high rotifer abundances can also be seen in Fig. 19, which depicts the relative abundances of rotifers, cladocerans, and copepods relative to the total number of zooplankton individuals. In years with low rotifer abundances, rotifers still contributed to at least 40% (1984) of the zooplankton community, whereas in years with high

Table 13. Rotifer, cladoceran, and copepod species found in Lake Plußsee in October. The right column contains the abbreviations we used for figures and tables.

rotifers			
species	abbreviations	species	abbreviations
Anuraeopsis fissa	Anu.fis	*Lecane* spp.	Lec.spp
Ascomorpha ecaudis	Asc.eca	*Monostyla* spp.	Mon.spp
Ascomorpha ovalis	Asc.ova	*Lepadella* spp.	Lep.spp
Ascomorpha saltans	Asc.sal	*Platyias quadricornis*	Pla.qua
Asplanchna spp.	Asp.spp	*Polyarthra dolichoptera*	Pol.dol
Brachionus angularis	Bra.ang	*Polyarthra euryptera*	Pol.eur
Brachionus calyciflorus	Bra.cal	*Polyarthra major*	Pol.maj
Brachionus falcatus	Bra.fal	*Polyarthra remata*	Pol.rem
Collotheca spp.	Col.spp	*Polyarthra vulgaris*	Pol.vul
Conochilus unicornis	Con.hip	*Pompholyx sulcata*	Pom.sul
Conochilus hippocrepis	Con.uni	*Synchaeta pectinata*	Syn.pec
Euchlanis dilatata	Euc.dil	*Synchaeta oblonga*	Syn.obl
Filinia longiseta	Fil.lon	*Testudinella patina*	Tes.pat
Filinia terminalis	Fil.ter	*Trichocerca capucina*	Tri.cap
Gastropus stylifer	Gas.sty	*Trichocerca cylindrica*	Tri.cyl
Kellicottia longispina	Kel.lon	*Trichocerca pusilla*	Tri.pus
Keratella cochlearis cochlearis	Ker.coc	*Trichocerca similis*	Tri.sim
Keratella hiemalis	Ker.hie	*Trichotria pocillum*	Tri.poc
Keratella quadrata	Ker.qua		
Keratella cochlearis tecta	Ker.tec		

cladoceran species	
species	abbreviations
Bosmina coregoni	Bos.cor
Bosmina longirostris	Bos.lon
Ceriodaphnia quadrangula	Cer.qua
Chydorus sphaericus	Chy.sph
Daphnia cucullata	Dap.cuc
Daphnia galeata	Dap.gal
Daphnia hyalina	Dap.hya
D. galeata × *D. cucullata*	Dap.G×C
D. hyalina × *D. galeata*	Dap.H×G
D. cucullata × *D. hyalina*	Dap.C×H
Diaphanosoma brachyurum	Dia.bra

copepod species	
species	abbreviations
Eudiaptomus gracilis	Eud.gra
Cyclops abyssorum	Cyc.aby
Cyclops kolensis	Cyc.kol
Cyclops vicinus	Cyc.vic
Diacyclops bicuspidatus	Dia.bic
Mesocyclops leuckarti	Mes.leu
Thermocyclops oithonoides	The.oit

abundances, this group contributed to even more than 90% (1993 and 2010) of the zooplankton community. Apart from 1969-1984, 1989, and 1996, the relative abundances of copepods were higher than the relative abundances of cladocerans. However, there was not a distinct trend of any one of these two groups dominating the other group throughout the period of analysis.

Fig. 20 shows the medians of species abundances and of relative species abundances of the rotifers, cladocerans, and copepods in October. *Keratella* was the most abundant rotifer genus in Lake Plußsee. This genus was represented by the three species *Keratella cochlearis*,

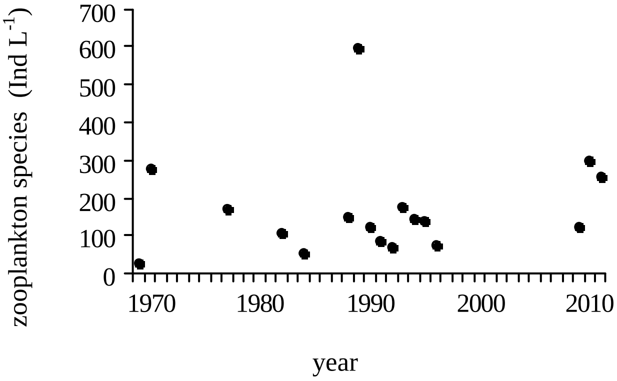

Fig. 18. Zooplankton abundance (Ind L^{-1}) in October

Keratella quadrata, and *Keratella hiemalis*, whereas there were two subspecies of *K. cochlearis*: *Keratella cochlearis cochlearis* (*typica*) and *Keratella cochlearis tecta*. In most years, the rotifer *K. cochlearis cochlearis* was the most abundant species in Lake Plußsee reaching maximum abundances of >100 Ind L^{-1} in 1988, 1989, 2010, and 2011. *K. cochlearis cochlearis* even reached an exceptionally high mean abundance in 1989 with more than 400 Ind L^{-1}. The median of *K. cochlearis cochlearis* abundances calculated over all considered years was about 30 Ind L^{-1}. The median of relative abundance of this species was about 25% of the entire zooplankton community and about 48% of the rotifer community. *K. cochlearis tecta* was abundant only in some years. It reached high mean abundances from 1993 to 1995 (9-14 Ind L^{-1}), in 1989 (20 Ind L^{-1}), and in 2010 (65 Ind L^{-1}). The median of relative species abundance was, however, only 1.4% of the rotifer community. *K. quadrata* was the second most abundant rotifer species in Lake Plußsee. The median of relative species abundance was about 2.8% of the entire zooplankton community and about 4.5% of the rotifer community. Highest species abundances (>10 Ind L^{-1}) were observed in 1970, 1977, 1989, 1996, and 2011 and the median of species abundance was 3.5 Ind L^{-1}. *K. hiemalis* was almost exclusively observed from 1993 to 1995, when *K. hiemalis* reached abundances of about 15 Ind L^{-1} in 1993, 41 Ind L^{-1} in 1994, and 9 Ind L^{-1}in 1995. The median species abundance was only 0.1 Ind L^{-1}.

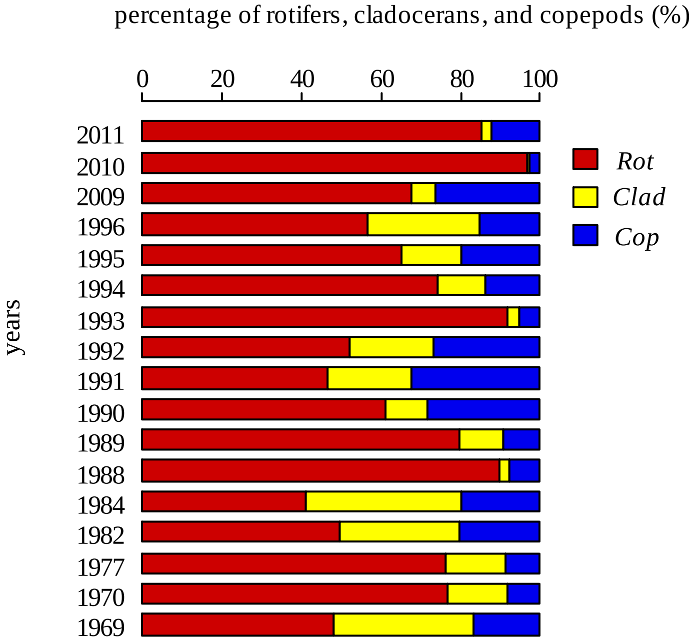

Fig. 19. Relative abundances of rotifers (*Rot*), cladocerans (*Clad*), and copepods (*Cop*) in October.

Besides the genus *Keratella*, other rotifer genera were also abundant in October in Lake Plußsee. The genus *Filinia*, for example, was represented by *Filinia longiseta* and *Filinia terminalis*. Both species established maximum abundances from 1993 to 1995 with 13-83 Ind L^{-1} (*F. longiseta*) and 0.8-5.7 Ind L^{-1} (*F. terminalis*). However, the medians of relative species abundances of *F. longiseta* and *F. terminalis* were about 1.7% and 0.4% of the entire zooplankton community and about 3.5% and 0.5% of the rotifer community. Apart from 1970 and 1993, when *Asplanchna* spp. was not part of the zooplankton community in October, this species had abundances of 0.2-3 Ind L^{-1} and reached maximum abundances of 19 Ind L^{-1} in 1989 and 9 Ind L^{-1} in 1990. *Kellicottia longispina* was part of the zooplankton community in each year. Although it reached abundances of 0.2-5 Ind L^{-1} in most years, it reached abundances of >10 Ind L^{-1} in 1991, 2010, and 2011, and even a maximum abundance of 71 Ind L^{-1} in 1970.

Fig. 20. Medians of zooplankton abundances (left column), relative zooplankton species abundances (center column) and relative abundances of rotifers, cladocerans, and copepods within their groups (right column).

Other species were also quite abundant in October; however, they only occurred in some years. For example, *Synchaeta pectinata* reached a maximum abundance in 2010 with 12 Ind L^{-1}, but this species was only present in 7 of the considered 17 years. Similarly, *Ascomorpha ecaudis* attained maximum abundances of 10-11 Ind L^{-1} in 1970, 1982, and 2009, but it was not part of the rotifer community in October in 9 out of 17 years. Most rotifer species or genera, however, were only present in just a few years and reached only very low abundances. These were, for example, *Brachionus* spp., *Lecane* spp., and most of the *Trichocerca* species (all species of this genus apart from *T. similis,* which was part of the rotifer community in each year).

The second most abundant zooplankton species and the most abundant copepod species in October was *Thermocyclops oithonoides*. It was part of the copepod community in each year and reached maximum abundances of about 25 Ind L^{-1} in 1989. The median of species abundance was about 9 Ind L^{-1}. The median of relative species abundance was about 7% of the entire zooplankton community and about 47% of the copepod community.

The copepod species *Eudiaptomus gracilis* and *Mesocyclops leuckarti* were also part of the zooplankton community in each year: They established maximum abundances of about 12-15 Ind L^{-1}. The medians of relative species abundances were about 3.5% of the entire zooplankton community and about 20% of the copepod community.

Diaphanosoma brachyurum was the most abundant cladoceran species in October. It reached maximum abundances of about 4 Ind L^{-1}. The median of relative species abundance was about 0.8% of the entire zooplankton community and about 9% of the cladoceran community. Although the medians of species abundances and of relative abundances of *D. brachyurum* were generally higher, many other cladoceran species were even more abundant in October in certain years. *Ceriodaphnia quadrangula*, for example, reached species abundances of about 26 individuals per liter in 1982 and 1989.

The genus with the most cladoceran taxa in Lake Plußsee was *Daphnia*. The *Daphnia* community comprised the three species *D. hyalina*, *D. galeata*, *D. cucullata*, and the hybrids of these three species: *D. galeata* × *D. cucullata*, *D. hyalina* × *D. galeata*, and *D. cucullata* × *D. hyalina*. The most abundant daphnid species was *D. cucullata* with highest abundances in 1977 (16 Ind L^{-1}), 1989 (21 Ind L^{-1}), and 1994 (13 Ind L^{-1}). Median species abundance was 0.3 Ind L^{-1}, median relative species abundance was 0.4% of the entire zooplankton community and 5.7% of the cladoceran community. Species abundances of *D. galeata* were generally very small with highest species abundances of 0.5-1 Ind L^{-1} from 1990-1994. *D. hyalina* was observed only occasionally from 1969 to 1996, however, this species was quite abundant from 2009 to 2011, with a maximum species abundance in 2011 (4.6 Ind L^{-1}).

Considering the percentage occurrence of daphnids in Lake Plußsee, *D. cucullata* was the most common daphnid species in 1969, 1970, 1977, 1984, 1989, 1994, and 1995 (Fig. 21). In 1992 and 1993, *D. galeata* was the most common daphnid species and in 2011, *D. hyalina* was the most common daphnid. In 1982, 1988, 1990, 1991, 2009, and 2010, hybrids of *Daphnia* were also quite abundant. From 1969 to 1996, *D. galeata* × *D. cucullata* was the most common hybrid species in Lake Plußsee, whereas *D. cucullata* × *D. hyalina* and *D. hyalina* × *D. galeata* were only occasionally found in small numbers within that time period. However, *D. cucullata* × *D. hyalina* and *D. hyalina* × *D. galeata* were more frequently observed in 2009 and 2010. *D. galeata* × *D. cucullata* established maximum abundances in 1990 and 1991 with 9-10 Ind L^{-1}, maximum abundance of *D. hyalina* × *D. galeata* was detected in 2009 with (5 Ind L^{-1}), and in 2010 *D. cucullata* × *D. hyalina* and *D. galeata* × *D. cucullata* were quite equally common (0.3 Ind L^{-1}).

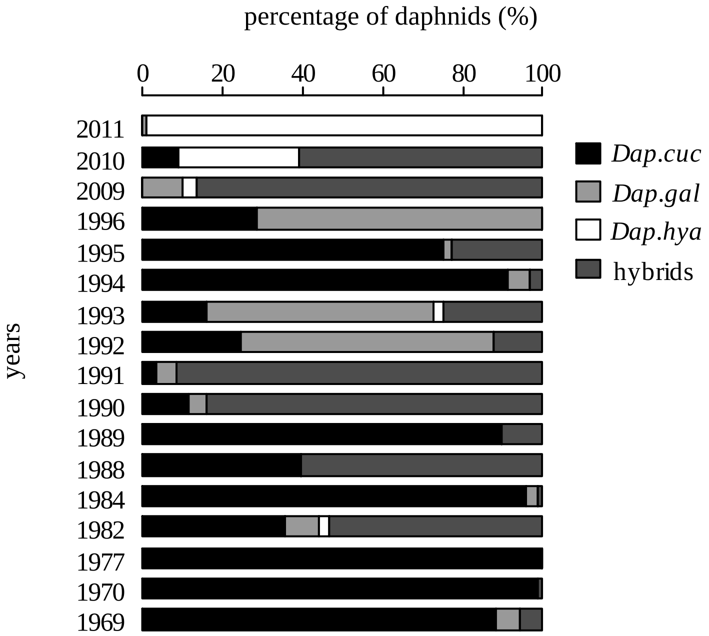

Fig. 21. Percentage of *D. cucullata* (Dap.cuc), *D. galeata* (Dap.gal), *D. hyalina* (Dap.hya) and their hybrids in respect to total daphnid occurrence in October.

3.4.2. Zooplankton biomass

Largest zooplankton biomass was calculated for 1989 with almost 260 µg L^{-1} (Fig. 22), whereas smallest biomass values (<50 µg L^{-1}) were calculated for 1969 and 2010. In most years zooplankton biomass values were larger than 100 µg L^{-1}. In 1988, 1990, 1991, 1993, and 2009-2011, copepods contributed predominantly to zooplankton biomass; in most years, however, largest percentage contribution to zooplankton biomass was made by cladocerans (Fig. 23).

Eudiaptomus gracilis and *Thermocyclops oithonoides* together contributed predominantly (37-81%) to copepod biomass in each year. *Mesocyclops leuckarti* and *Diacyclops bicuspidatus* contributed only in some years to a large extent to copepod biomass. Large cyclopoid copepod *Cyclops vicinus* contributed about 11-14% to copepod biomass from 1992-1995, however only little in other years. Other copepod species were less important. Considering also the copepod stages, copepodite stages IV and V contributed predominantly to copepod biomass at that time of the year.

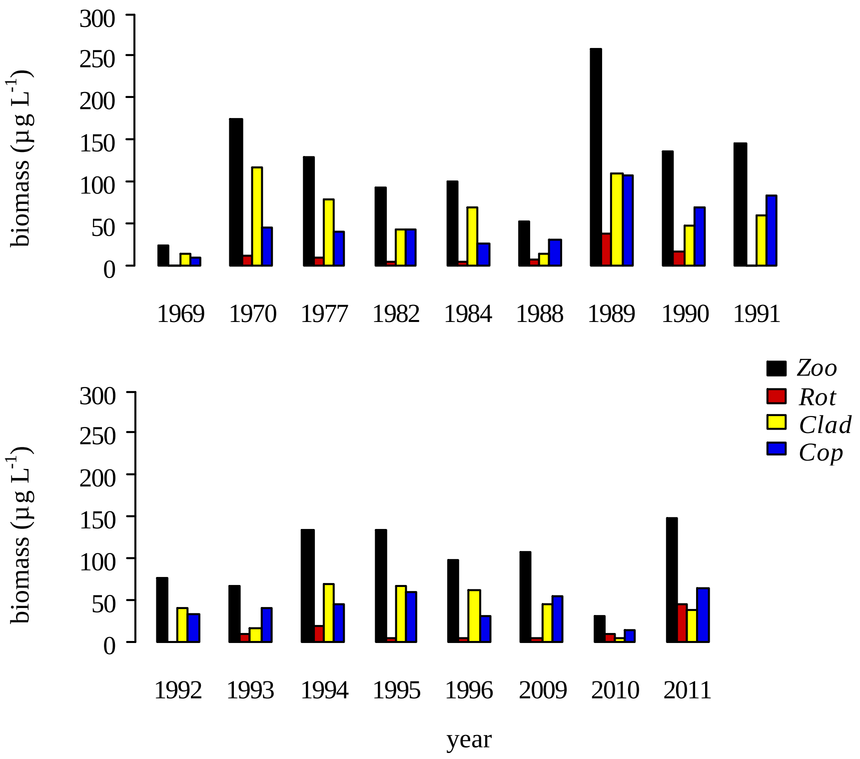

Fig. 22. Biomass (µg L^{-1}) of the zooplankton community (*Zoo*), rotifers (*Rot*), cladocerans (*Clad*), and copepods (*Cop*).

Regarding cladoceran biomass, *Bosmina*, *Ceriodaphnia*, *Daphnia*, and *Diaphanosoma* contributed predominantly to cladoceran biomass and, hence, also to zooplankton biomass. Since the relations of species dominance varied from year to year within the cladoceran community, contributions of certain species to biomass changed accordingly. This was especially noticeable in the contribution of certain daphnid species to cladoceran biomass: In 1977, 1989, 1994, and 1995, *D. cucullata* contributed about 53-80% to cladoceran biomass, whereas in 2011, *D. hyalina* contributed about 86%, *D. galeata* contributed about 30% in 1993, *D. galeata* × *D. cucullata* contributed 50-60% in 1990 and 1991, *D. hyalina* × *D. galeata* contributed about 84% in 2009, and *D. cucullata* × *D. hyalina* contributed about 28% in 2010 to cladoceran biomass. *Bosmina* and *Diaphanosoma* made a contribution to cladoceran biomass in almost every year. For instance, *B. coregoni* contributed about 74-78% to cladoceran biomass in 1988, 1992, and 1996 and *D. brachyurum* contributed about 10-20%

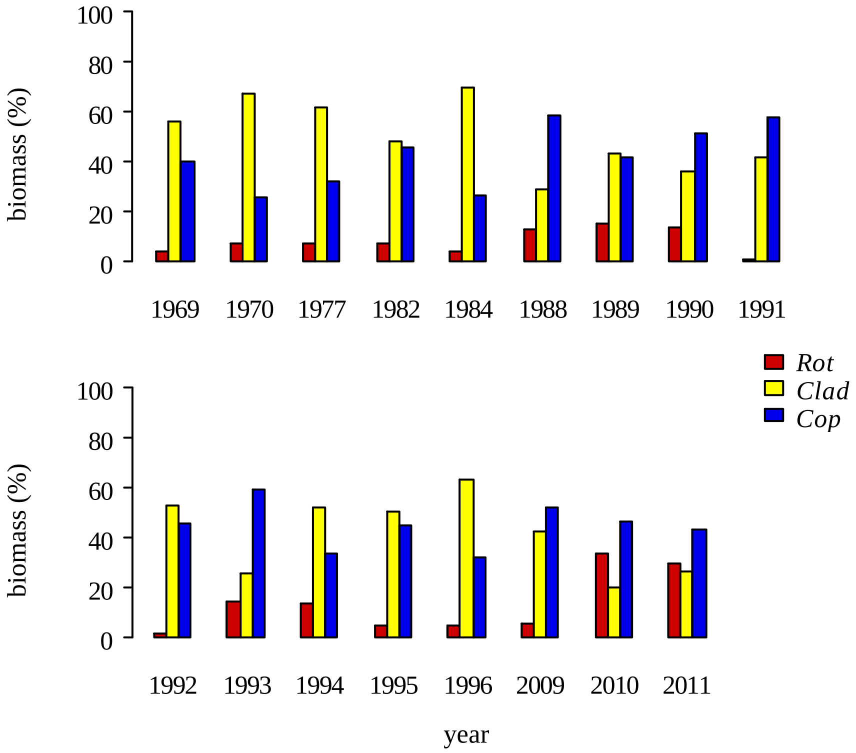

Fig. 23. Percentages of rotifer (*Rot*), cladoceran (*Clad*), and copepod (*Cop*) biomass in respect to total zooplankton biomass

to cladoceran biomass in almost every year. Considering the stages of the cladocerans, adult stages contributed predominantly to cladoceran biomass.

Although *Keratella cochlearis* was the most abundant rotifer species in terms of number of individuals in Lake Plußsee in October, its contribution to rotifer biomass was rather small due to its small body size. Two other *Keratella* species contributed predominantly to rotifer biomass. *K. quadrata* contributed in almost every year on average about 20% and even up to 79% in 1996 to rotifer biomass. *K. hiemalis* contributed only from 1992 to 1994 notably to rotifer biomass; especially in 1994, its contribution to rotifer biomass was about 62%. Some species only contributed notably to rotifer biomass in particular years. For example, *Filinia longiseta* contributed only in 1969 (14%), 1992 (12%), 1993 (41%), and 1995 (24%) to rotifer biomass, whereas *Synchaeta pectinata* contributed only in 1977 (15%), 1982 (25%), and 2010 (64%) to rotifer biomass.

Correlating the biomasses of the zooplankton, rotifer, cladoceran, and copepod community with the factor scores of abiotic environmental parameters (Chapter 3.3) revealed that biomasses were predominantly associated with lake conditions in the time period prior to stratification in the previous spring: PC II of nutrient parameters was significantly negative correlated with *Zoo* (r=-0.85, p<0.01), *Rot* (r=-0.77, p<0.05), *Clad* (r=-0.71, p<0.05), and *Cop* (r=-0.79, p<0.05) in February. This factor was negatively correlated with mean NO_3^- concentrations and positively correlated with NH_4^+ concentrations in the 0-10 m water column in February. Thus, higher NO_3^- and lower NH_4 concentrations tended to promote higher biomasses in October. Since both nitrogen fractions were negatively correlated with this principal component, and this principal component reflected, thus, an interplay of oxygenated and reduced nitrogen, it is possible that PC II reflected an oxygen concentration or a vertical mixing gradient. Biomasses of copepods, but not the biomasses of rotifers and cladocerans, were also correlated with the first principal components of February and March derived from the PCAs of physical and chemical parameters. Both PCs indicated an association of higher copepod biomasses in October with higher oxygen concentrations and water temperatures in February and March; however, only March PC I was significantly associated with copepod biomass (r=0.70, p<0.05); February PC I was not (r=-0.59, p=0.07).

3.4.3. Zooplankton species diversity

Comparing the species diversity indices calculated for *Zoo*, *Rot*, *Clad*, and *Cop*, the Shannon-index (H) and the Simpson-index (D) showed similar time series patterns for each zooplankton group (Fig. 24 and Fig. 25). Furthermore, correlations of *Zoo* and *Rot* of the Shannon-index (r=0.85, p<0.001) and the Simpson-index (r=0.84, p<0.001) revealed a strong resemblance, which can be ascribed to the large number of different species (i.e., species richness) of rotifers predominantly influencing the zooplankton species richness and, hence, species diversity. In contrast, cladocerans and copepods were represented by less species and their relative abundances were lower too.

Correlations of the Shannon- and Simpson-indices of *Zoo*, *Rot*, *Clad*, and *Cop* with factor scores derived from abiotic environmental variables (Chapter 3.3) revealed that *Zoo* and *Rot* were negatively correlated with the first PCs of nutrient parameters from February to October; however, only February and May to October were significantly ($p<0.05$) linked to H and D (Fig. 26 and 27). Thus, high rotifer species diversity in October was associated with low concentrations of NO_3^-, PO_4^{3-}, and TDP. H and D of *Zoo* and *Rot* were also negatively correlated with the first principal components of physical and chemical parameters from February to October, whereas only March and September were significant ($p<0.05$). These principal components were predominantly associated with O_2 concentrations and pH.

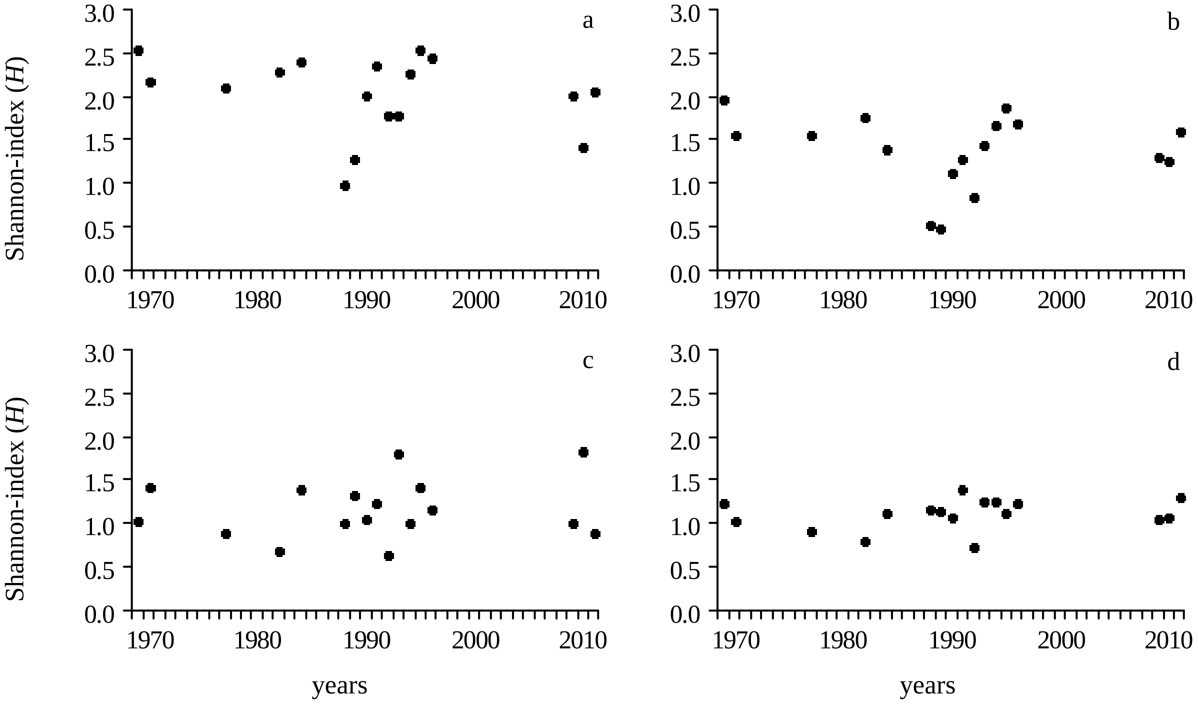

Fig. 24. Shannon-indices of a) the entire zooplankton community (*Zoo*), b) rotifer community (*Rot*), c) cladoceran community (*Clad*), and d) copepod community (*Cop*).

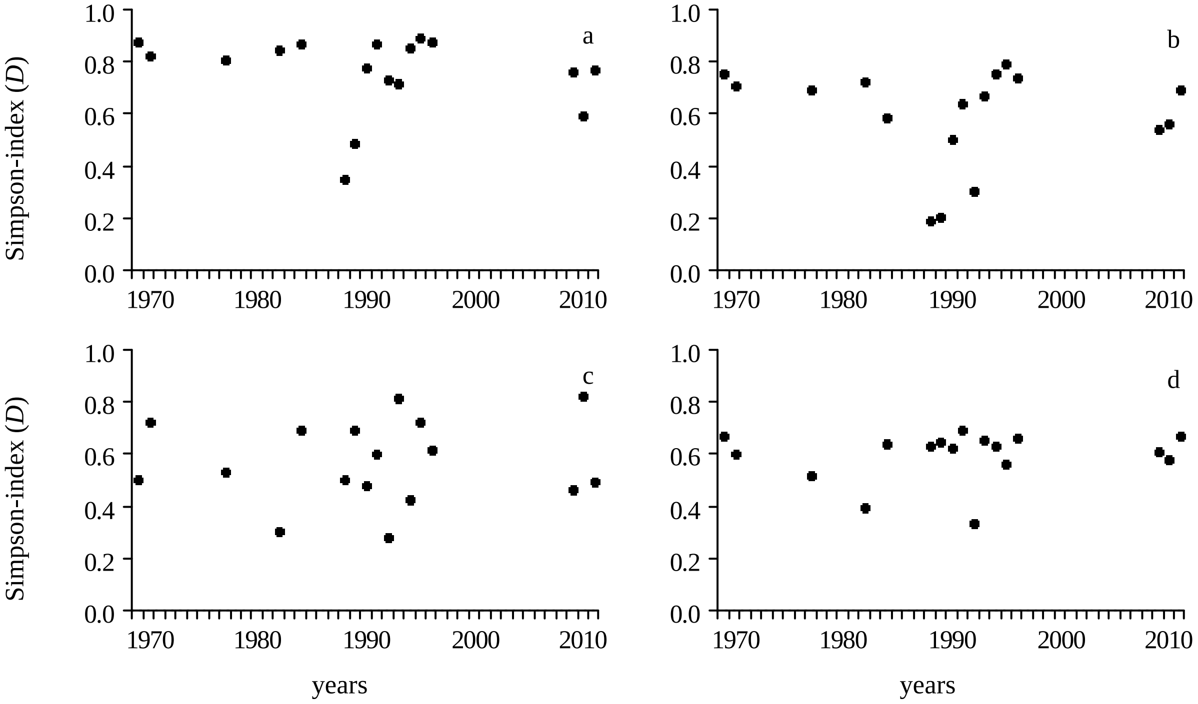

Fig. 25. Simpson-indices of a) the entire zooplankton community (*Zoo*), b) rotifer community (*Rot*), c) cladoceran community (*Clad*), and d) copepod community (*Cop*).

Cladoceran and copepod species diversity displayed a similar time series pattern. *H* and *D* of both groups were, however, not significantly correlated with principal components derived from physical and chemical parameters as well as with principal components derived from nutrient parameters from February to October ($p>0.05$), which suggests that probably a different factor affected the species richness and diversity of both zooplankton groups (e.g., fish abundance).

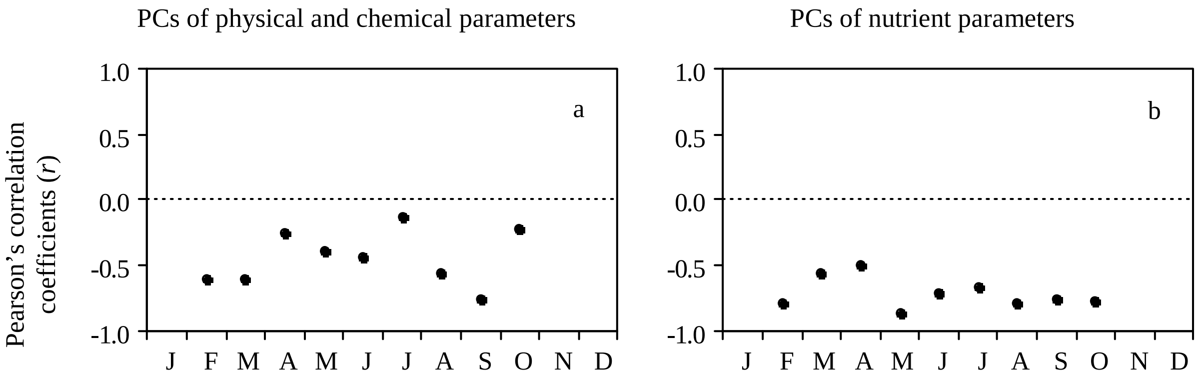

Figure 26. Correlations of the Shannon-index of *Rot* with the first principal components of a) physical and chemical and b) nutrient parameters.

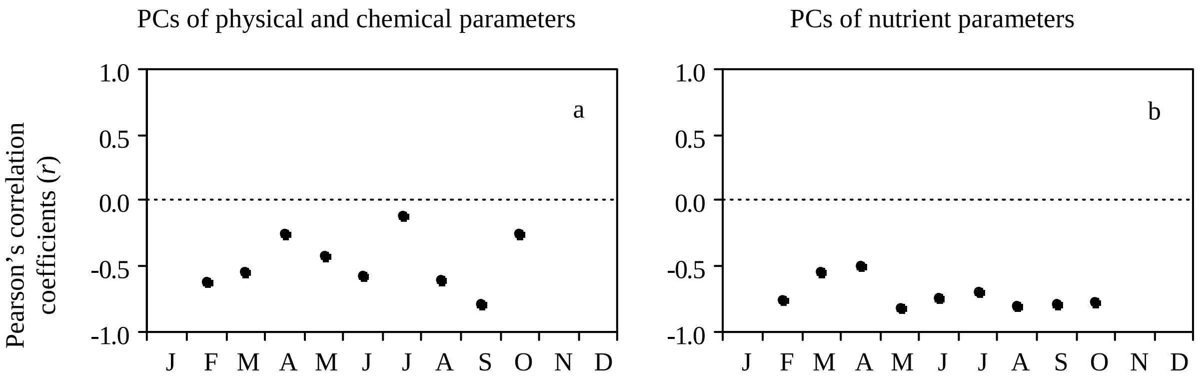

Figure 27. Correlations of the Simpson-index of *Rot* with the first principal components of a) physical and chemical and b) nutrient parameters.

3.4.4. Principal Component Analysis of zooplankton groups

We performed PCAs on the entire zooplankton community (*Zoo*), the entire rotifer community (*Rot*), the entire cladoceran community (*Clad*), and the entire copepod community (*Cop*). Additionally, we implemented PCAs on the juvenile and adult stages of cladocerans (*Clad J* and *Clad A*) and on the copepodite and adult stages of copepods (*Cop C* and *Cop A*). Prior to the different PCAs we performed a logarithmic pre-transformation of the datasets containing the species abundances.

According to a Scree-plot analysis and the Kaiser-Guttman-Criterion performed on the PCA results of each dataset, we decided to consider only a certain number of PCs that can already explain a large proportion of variance (Table 14); hence, interpreting 2-4 PCs already sufficed to explain 59-72% of total variance of the datasets. We used the factor loadings (Table 15) and the contributions (Table 16) of each principal component for the interpretation of the PCA results.

Table 15 displays only a summary of the significant ($p<0.05$) factor loadings of each principal component. A more detailed illustration is provided in the Appendix figures A1-A8, which illustrate all species and their association with the different PCs. Species with a similar or opposing ecological requirements are positioned along gradients which are represented by principal components. To determine the character of those underlying gradients, we correlated the zooplankton factor scores with the factor scores, which we derived from PCAs of physical and chemical parameters as well as of nutrient parameters (Chapter 3.3). In this respect, the signs of the factor scores play an important role, because they give information on the relationship between the species and the abiotic environmental parameters.

Table 14. Explained and cumulative variances of the relevant principal components (PCs) derived from PCAs performed on different zooplankton groups in October. The Roman numerals indicate the respective PC.

	zooplankton				
	PC I	PC II	PC III	PC IV	cum. variance
Zoo	21.4	17.5	11.0	9.5	59.4
Rot	24.9	15.5	11.1	10.5	62.0
Clad	31.0	22.3	18.8		72.1
Cop	53.3	17.5			70.8
Clad J	29.1	22.3	18.9		70.3
Clad A	33.3	23.0	15.8		72.1
Cop C	50.4	18.4			68.8
Cop A	41.1	28.2			69.3

Table 15. Summary of significant ($p<0.05$) factor loadings (r) of the relevant principal components derived from PCAs performed on *Zoo*, *Rot*, *Clad*, *Cop*, *Clad J*, *Clad A*, *Cop C*, and *Cop A*. A positive or negative sign indicates whether a certain species was significantly positive or negative associated with a principal component (PC). The Roman numerals indicate the respective PC.

Zoo I		*Zoo* II		*Zoo* III		*Zoo* IV	
-	+	-	+	-	+	-	+
Asc.eca *r*=-0.57	Asc.sal *r*=0.58	Asc.ova *r*=-0.69	Con.uni *r*=0.57	Pol.dol *r*=-0.51	Bra.cal *r*=0.61	Fil.ter *r*=-0.67	Lep.spp *r*=0.58
Asc.ova *r*=-0.54	Fil.lon *r*=0.49	Fil.lon *r*=-0.62	Mon.spp *r*=0.48	Bos.cor *r*=-0.49	Ker.tec *r*=0.52	Ker.hie *r*=-0.51	Dap.G×C *r*=0.67
Pol.maj *r*=-0.55	Ker.hie *r*=0.70	Ker.tec *r*=-0.55	Pol.eur *r*=0.64	Cer.qua *r*=-0.51	Syn.obl *r*=0.65	Dia.bra *r*=-0.59	Eud.gra *r*=0.50
Pol.rem *r*=-0.84	Bos.cor *r*=0.49	Pol.dol *r*=-0.51	Pom.sul *r*=0.71		Tri.pus *r*=0.51		
Syn.pec *r*=-0.76	Chy.sph *r*=0.59	Dap.hya *r*=-0.80	Tri.cyl *r*=0.55		Tri.sim *r*=0.49		
	Dap.gal *r*=0.60	Dap.H×G *r*=-0.57	Bos.cor *r*=0.60		Bos.lon *r*=0.49		
	Cyc.aby *r*=0.53	Cyc.aby *r*=-0.63	Dap.cuc *r*=0.54		Dap.cuc *r*=0.68		
	Cyc.vic *r*=0.64	Dia.bic *r*=-0.49	Dia.bra *r*=0.51		Cyc.kol *r*=0.64		
	Dia.bic *r*=0.63						

Rot I		*Rot* II		*Rot* III		*Rot* IV	
-	+	-	+	-	+	-	+
Asc.eca *r*=-0.63	Asc.sal *r*=0.53	Asc.ova *r*=-0.70	Con.uni *r*=0.73	Fil.ter *r*=-0.80	Asp.spp *r*=0.69	Col.spp *r*=-0.51	Bra.cal *r*=0.53
Pol.maj *r*=-0.61	Fil.lon *r*=0.63	Ker.tec *r*=-0.67	Pol.eur *r*=0.64		Syn.obl *r*=0.49	Con.hip *r*=-0.52	Mon.spp *r*=0.54
Pol.rem *r*=-0.78	Ker.hie *r*=0.80	Pol.dol *r*=-0.51	Pom.sul *r*=0.68			Pol.dol *r*=-0.62	Tri.cap *r*=0.53
Syn.pec *r*=-0.77		Tri.sim *r*=-0.56	Tri.cyl *r*=0.60				Tri.pus *r*=0.51

Clad I		*Clad* II		*Clad* III	
-	+	-	+	-	+
Bos.cor *r*=-0.68	Dap.hya *r*=0.82	Bos.cor *r*=-0.60	Bos.lon *r*=0.89		Dap.cuc *r*=0.54
Chy.sph *r*=-0.77	Dap.H×G *r*=0.57	Dap.gal *r*=-0.68			Dap.G×C *r*=0.76
Dap.cuc *r*=-0.65	Dap.C×H *r*=0.56				Dap.H×G *r*=0.56
Dia.bra *r*=-0.59					

Cop I		*Cop* II	
-	+	-	+
Cyc.aby *r*=-0.88	Cyc.kol *r*=0.50	Eud.gra *r*=-0.66	
Cyc.vic *r*=-0.87		Cyc.kol *r*=-0.59	
Dia.bic *r*=-0.85		Mes.leu *r*=-0.73	
		The.oit *r*=-0.54	

Table continued from previous page

Clad J I		*Clad J* II		*Clad J* III	
-	+	-	+	-	+
Bos.cor *r*=-0.52	Dap.hya *r*=0.71	Dap.gal *r*=-0.83	Bos.lon *r*=0.66	Bos.cor *r*=-0.66	Bos.lon *r*=0.48
Chy.sph *r*=-0.81	Dap.H×G *r*=0.62	Dap.G×C *r*=-0.71			Dap.cuc *r*=0.57
Dap.cuc *r*=-0.73		Dap.H×G *r*=-0.53			Dap.G×C *r*=0.49
Dia.bra *r*=-0.63					

Clad A I		*Clad A* II		*Clad A* III	
-	+	-	+	-	+
Bos.cor *r*=-0.62	Dap.hya *r*=0.79	Bos.cor *r*=-0.72	Bos.lon *r*=0.82	Dia.bra *r*=-0.62	Dap.gal *r*=0.72
Chy.sph *r*=-0.80	Dap.H×G *r*=0.53		Dap.cuc *r*=0.62		Dap.G×C *r*=0.68
Dap.cuc *r*=-0.70	Dap.C×H *r*=0.64				Dap.H×G *r*=0.68
Dap.G×C *r*=-0.53					
Dia.bra *r*=-0.57					

Cop C I		*Cop C* II	
-	+	-	+
Cyc.aby *r*=-0.84		Eud.gra *r*=-0.70	
Cyc.vic *r*=-0.78		Cyc.kol *r*=-0.62	
Dia.bic *r*=-0.91		Mes.leu *r*=-0.68	
		The.oit *r*=-0.57	

Cop A I		*Cop A* II	
-	+	-	+
Cyc.aby *r*=-0.69	The.oit *r*=0.72	Cyc.vic *r*=-0.53	
Cyc.vic *r*=-0.73		Dia.bic *r*=-0.53	
Dia.bic *r*=-0.62		The.oit *r*=-0.69	

Table 16. Contributions of relevant principal components derived from PCAs performed on *Zoo*, *Rot*, *Clad*, *Cop*, *Clad J*, *Clad A*, *Cop C*, and *Cop A*. A positive or negative sign indicates whether a certain observation was positively or negatively associated with a certain factor score of a PC. The Roman numerals indicate the respective PC.

	Zoo				*Rot*				*Clad*			*Cop*	
	PC I	PC II	PC III	PC IV	PC I	PC II	PC III	PC IV	PC I	PC II	PC III	PC I	PC II
1969	-1	3	-4	-1	-3	0	-6	-1	-4	1	-2	-1	-3
1970	-5	25	-3	-3	-26	2	-18	3	-14	0	-1	-2	-7
1977	-13	1	41	-14	-17	-5	-2	31	-3	27	5	0	-7
1982	0	0	0	0	-3	-6	-4	5	-7	-2	0	-4	-4
1984	0	4	2	1	-2	-1	0	1	-12	-2	1	-2	-6
1988	1	1	0	0	0	0	0	4	-5	-1	-1	-5	-7
1989	0	0	20	6	0	-4	0	0	-9	19	6	-6	-11
1990	0	-4	2	20	-1	-7	0	0	-1	-10	25	-5	-8
1991	7	-1	-1	3	0	-2	-5	0	-6	-17	12	-14	-7
1992	3	0	0	-1	0	-3	-2	9	-7	-10	0	-7	-4
1993	16	3	1	-6	10	-4	-10	12	-5	-5	1	-9	-3
1994	14	4	15	-5	9	-9	-5	9	-8	0	16	-10	-5
1995	14	0	6	-9	5	-1	-11	8	-11	1	9	-11	-5
1996	5	0	-4	-11	1	-1	-8	0	-8	-2	-11	-5	-4
2009	-6	-15	0	1	-7	-13	-5	0	0	-2	5	-3	-7
2010	-13	-12	0	-9	-14	-22	-8	11	0	1	0	-4	-5
2011	-1	-25	-2	-9	-1	-21	-14	-6	0	1	-4	-12	-6

	Clad J			*Clad A*			*Cop C*		*Cop A*	
	PC I	PC II	PC III	PC I	PC II	PC III	PC I	PC II	PC I	PC II
1969	-3	4	-1	-3	0	-4	-2	-2	0	-3
1970	-14	0	-2	-14	0	-4	-2	-7	13	-7
1977	-4	7	21	-3	28	-1	0	-7	12	-4
1982	-6	-1	-2	-7	-5	-1	-4	-4	-1	-5
1984	-11	-5	-3	-13	-2	0	-1	-6	4	-8
1988	-4	0	-3	-3	-9	-2	-4	-7	0	-3
1989	-13	3	17	-10	15	-1	-6	-11	2	-7
1990	-1	-18	10	-1	-2	34	-4	-8	-1	-3
1991	-4	-34	1	-6	-8	14	-14	-8	-26	-6
1992	-6	-6	-8	-6	-12	0	-7	-5	-3	-3
1993	-4	-5	0	-5	-5	1	-9	-3	-4	-5
1994	-10	-3	4	-8	3	12	-9	-5	-6	-14
1995	-12	-2	5	-13	1	3	-11	-5	0	-18
1996	-7	0	-21	-7	-10	-12	-6	-4	7	-8
2009	0	-7	2	0	0	3	-5	-7	0	0
2010	0	1	0	0	0	-1	-4	-4	-1	-1
2011	0	4	-1	0	0	-6	-12	-6	-18	-5

The following figures (Fig. 28-35) display the correlations of factor scores derived from physical and chemical parameters, on the one hand, and from nutrient parameters, on the other hand, from February to October with factor scores derived from each zooplankton community (*Zoo*, *Rot*, *Clad*, *Clad J*, *Clad A*, *Cop*, *Cop C*, and *Cop A*) in October. We depicted, however, only correlations with the first two PCs of abiotic environmental parameters. Correlations with the third PC of physical and chemical parameters from May to October were in most cases non-significant. A more detailed illustration of the correlation coefficients is provided in the Appendix Tables A5-A8.

The first principal component of the zooplankton community, *Zoo* I, which already explained a variance of about 21% of the total variance of this dataset, was linked to *Ascomorpha ecaudis*, *Ascomorpha ovalis*, *Polyarthra major*, *Polyarthra remata*, and *Synchaeta pectinata*. This principal component attained large amplitude in 1970, 1977, 2009, and 2010. Fig. 28 shows that this species composition was significantly associated with warmer lake temperature in February (r=0.66, p<0.05) and higher concentrations of NO_3^- and SiO_2 concentrations from March to May (0.64<r<0.83, p<0.05) and from August to October (0.74<r<0.90, p<0.01). In contrast, *Ascomorpha saltans, Filinia longiseta, Keratella hiemalis, Bosmina coregoni*, *Chydorus sphaericus*, *Daphnia galeata*, *Cyclops abyssorum*, *Cyclops vicinus*, and *Diacyclops bicuspidatus*, which were, above all, abundant from 1991 to 1996, were associated with colder lake temperature in February and with lower concentrations of mean NO_3^- and SiO_2 concentrations from March to May and from August to October.

Zoo II, which explained a variance of 17.5%, was negatively associated with *Conochilus unicornis, Monostyla* spp., *Polyarthra euryptera, Pompholyx sulcata*, *Trichocerca cylindrica*, *Bosmina coregoni*, *Daphnia cucullata*, and *Diaphanosoma brachyurum*. This principal component was particularly strong in 1970, 1984, 1993, and 1994. These species were more abundant in those October months with a negative $NAO_{Dec\text{-}Mar}$, colder lake temperatures, lower O_2 concentrations and pH, and higher Secchi disc transparencies from March to April (0.63<r<0.84, p<0.01). Furthermore, these species were significantly related to lower concentrations of NH_4^+ and SiO_2 from March to May (0.68<r<0.75, p<0.05) and from August to September (0.66<r<0.77, p<0.05). *Ascomorpha ovalis, Filinia longiseta*, *Keratella*

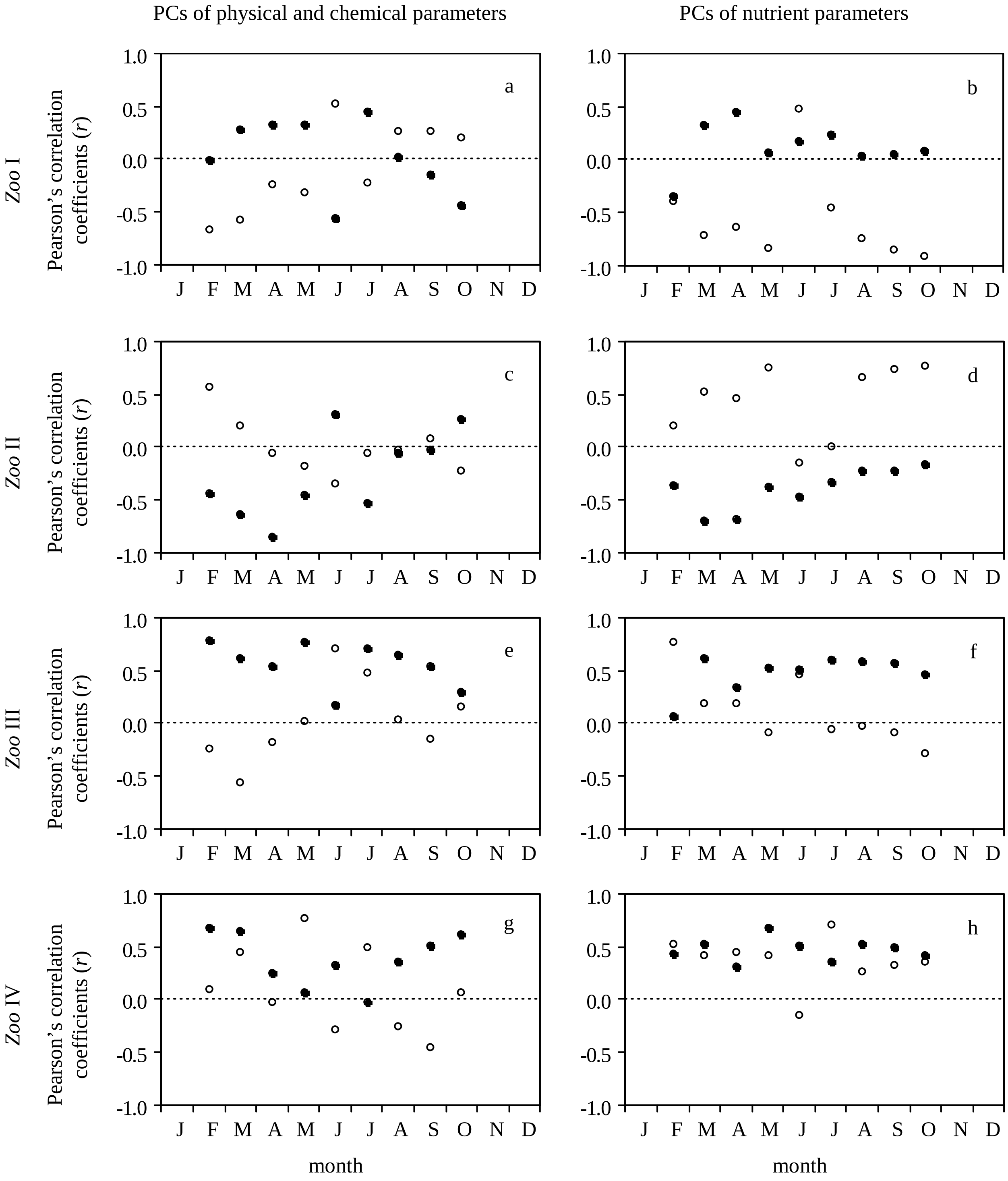

Figure 28. Pearson's correlation coefficients (*r*) between factor scores of *Zoo* I-IV in October and factor scores of physical and chemical (left) and nutrient (right) parameters from February to October. The black dots represent the first PC and the white dots represent the second PC of abiotic environmental parameters.

cochlearis tecta, Polyarthra dolichoptera, Daphnia hyalina, Daphnia hyalina × *Daphnia galeata, Cyclops abyssorum*, and *Diacyclops bicuspidatus,* which were most abundant from

2009 to 2011, were negatively correlated with the previously mentioned species and were, therefore, associated with the opposite range of the abiotic environmental parameters.

Zoo III, which accounted for a proportion of 11% of variance, was, on the one hand, connected with *Brachionus calyciflorus*, *Keratella cochlearis tecta*, *Synchaeta oblonga*, *Trichocerca pusilla*, *Trichocerca similis*, *Bosmina longirostris*, *Daphnia cucullata*, and *Cyclops kolensis*, and attained high amplitudes in 1969, 1970, and 1996. This group of species was, apart from April (r=0.54, p>0.05), associated with warmer water temperatures and higher O_2 concentrations and pH from February to August (0.61<r<0.79, p<0.05). In spring, these species were also positively affected by the $NAO_{Dec\text{-}Mar}$. Furthermore, these species were more abundant in years with higher NO_3^-, PO_4^{3-}, and TDP, but lower NH_4^+ and SiO_2 concentrations from February to October; however, the factor scores were only significantly correlated in February, March, July, and August (0.58<r<0.76, p<0.05). *Polyarthra dolichoptera*, *Bosmina coregoni*, and *Ceriodaphnia quadrangula*, which were also associated with *Zoo* III, above all, in 1977, 1989, 1994, and 1995, were connected with the opposite range of physical, chemical, and nutrient parameters.

Zoo IV explained a variance of 9.5% and was correlated with *Filinia terminalis*, *Keratella hiemalis*, and *Diaphanosoma brachyurum*, which were particularly abundant in 1977 and 1991-1996. These species were predominantly related to colder water temperatures in February, March, May, and October (p<0.05) and to lower concentrations of NO_3^-, PO_4^{3-}, and TDP from February to October, but especially in May (r=0.68, p<0.05) and in July (r=0.71, p<0.01). *Lepadella* spp., *Daphnia galeata* × *Daphnia cucullata*, and *Eudiaptomus gracilis*, which were especially abundant from 1989 to 1991, were, however, connected with warmer lake temperatures and higher NO_3^-, PO_4^{3-}, and TDP concentrations.

The first principal component of the rotifer community, *Rot* I, explained a variance of 24.9% and displayed the same variable structure as *Zoo* I and was associated with the same rotifer species: *Ascomorpha saltans*, *Filinia longiseta*, and *Keratella hiemalis* were related to

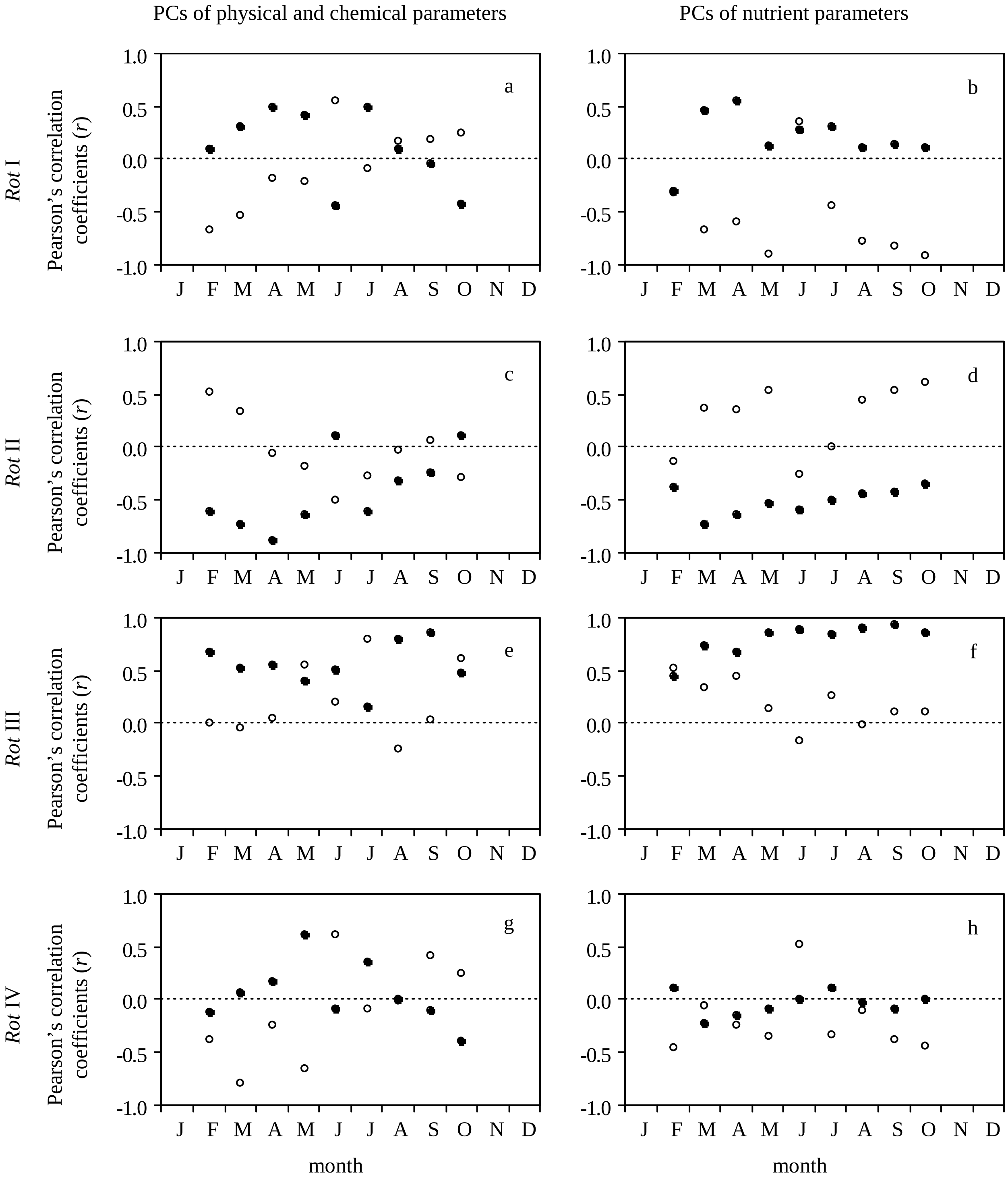

Figure 29. Pearson's correlation coefficients (*r*) between factor scores of *Rot* I-IV in October and factor scores of physical and chemical (left) and nutrient (right) parameters from February to October. The black dots represent the first PC and the white dots represent the second PC of abiotic environmental parameters.

colder mean lake temperature in February ($p<0.05$), lower concentrations of mean NO_3^- and SiO_2 from March to May ($0.59<r<0.89$, $p<0.05$) and from August to October ($0.74<r<0.90$,

$p<0.01$). *Ascomorpha ecaudis*, *Polyarthra major*, *Polyarthra remata*, and *Synchaeta pectinata* were oppositely affected by these conditions in the respective months (Fig. 29).

Rot II explained a variance of 15.5% and was connected with *Ascomorpha ovalis*, *Keratella cochlearis tecta*, *Polyarthra dolichoptera*, and *Trichocerca similis,* above all, in 1993, 1994, and from 2009 to 2011. These species were correlated with a positive $NAO_{Dec-Mar}$, warmer lake temperatures, higher O_2 concentrations and pH predominantly from February to May and in July ($0.61<r<0.87$, $p<0.05$). Furthermore, this species composition were positively correlated with PO_4^{3-} and TDP concentrations from March to October, but mainly in March, April and June ($0.61<r<0.87$, $p<0.05$) and they were related to lower NH_4^+ concentrations from August to October (October: $r=0.62$, $p<0.05$). *Conochilus unicornis*, *Polyarthra euryptera*, *Pompholyx sulcata, and Trichocerca cylindrica* were most abundant 1969, 1970, and 1988 and they were oppositely influenced by these parameters.

Rot III accounted for a variance of 11.1% and was, on the one hand, associated with *Filinia terminalis* in 1970, 1993-1996, and 2009-2011 and was, on the other hand, associated with *Asplanchna* spp., and *Synchaeta oblonga* in 1984 and from 1988 to 1990. *Asplanchna* spp. and *Synchaeta oblonga* were related to warmer water temperatures, higher oxygen concentrations, and higher pH from July to October ($0.62<r<0.80$, $p<0.05$). Furthermore, these species were related to higher concentrations of NO_3^-, PO_4^{3-}, and TDP and lower NH_4^+ concentrations from March to October ($0.67<r<0.93$, $p<0.05$). In contrast, *Filinia terminalis* was linked to colder water temperatures, lower pH, and lower concentrations of O_2, NO_3^-, PO_4^{3-}, and TDP.

Brachionus calyciflorus, *Monostyla* spp., *Trichocerca capucina*, and *Trichocerca pusilla* were linked to *Rot* IV, which explained a proportion of 10.5% of variance. This species composition was most abundant in 1977, 1993-1995 and in 2010. These species were associated with deeper vertical mixing in March, May, and June ($0.61<r<0.78$, $p<0.05$), which had a positive influence on deep water temperatures, O_2 concentrations, and pH. In

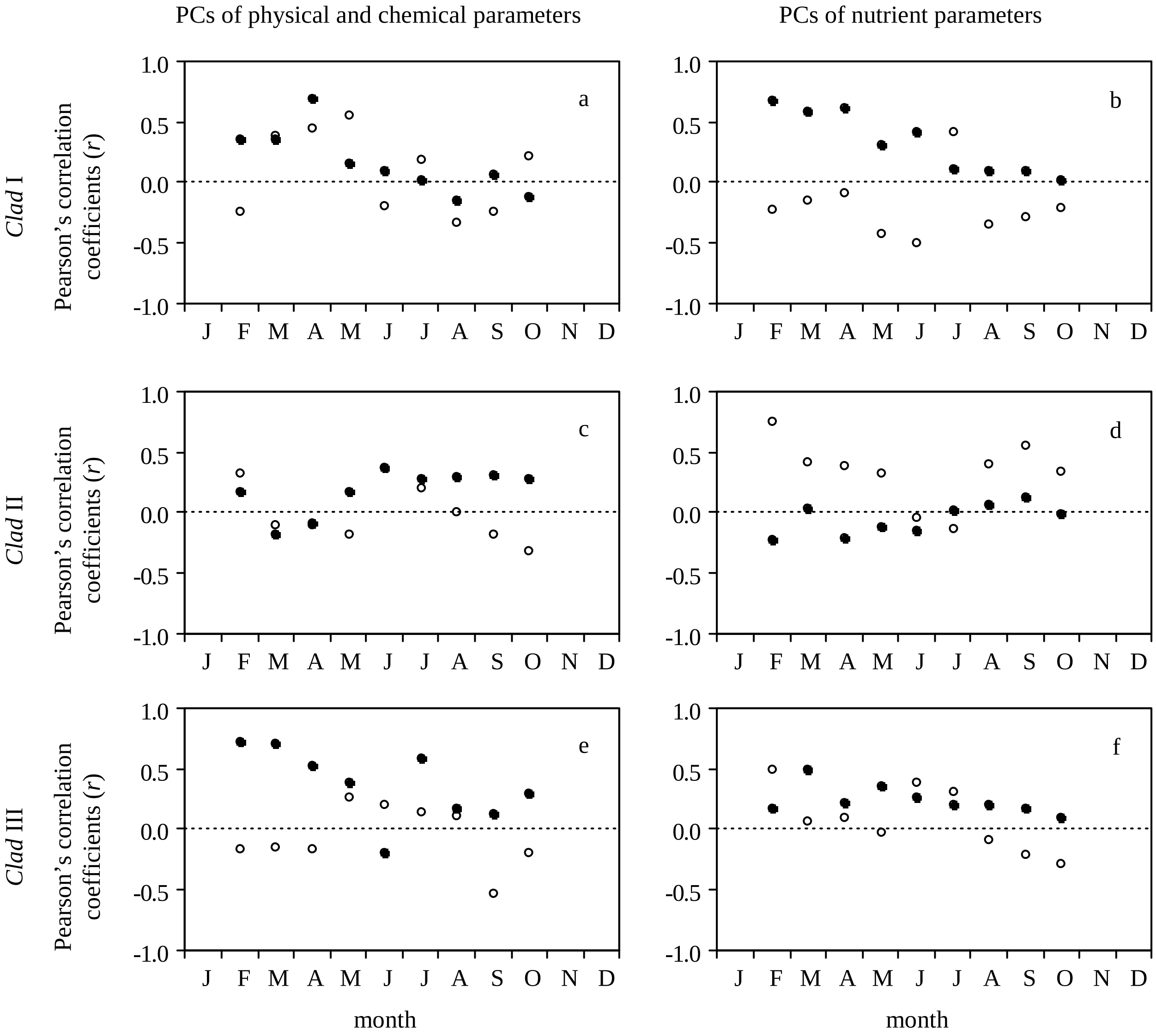

Figure 30. Pearson's correlation coefficients (*r*) between factor scores of *Clad* I-III in October and factor scores of physical and chemical (left) and nutrient (right) parameters from February to October. The black dots represent the first PC and the white dots represent the second PC of abiotic environmental parameters.

contrast, *Collotheca* spp., *Conochilus hippocrepis*, *Polyarthra dolichoptera*, which were also connected with *Rot* IV and which were most abundant in 1969 and 2011, were oppositely affected.

Despite small differences, associations between the principal components of *Clad*, *Clad J*, and *Clad A* and PCs of physical, chemical, and nutrient parameters were very similar (Fig. 30-32). The first principal components of *Clad*, *Clad J*, and *Clad A*, which explained about 30%

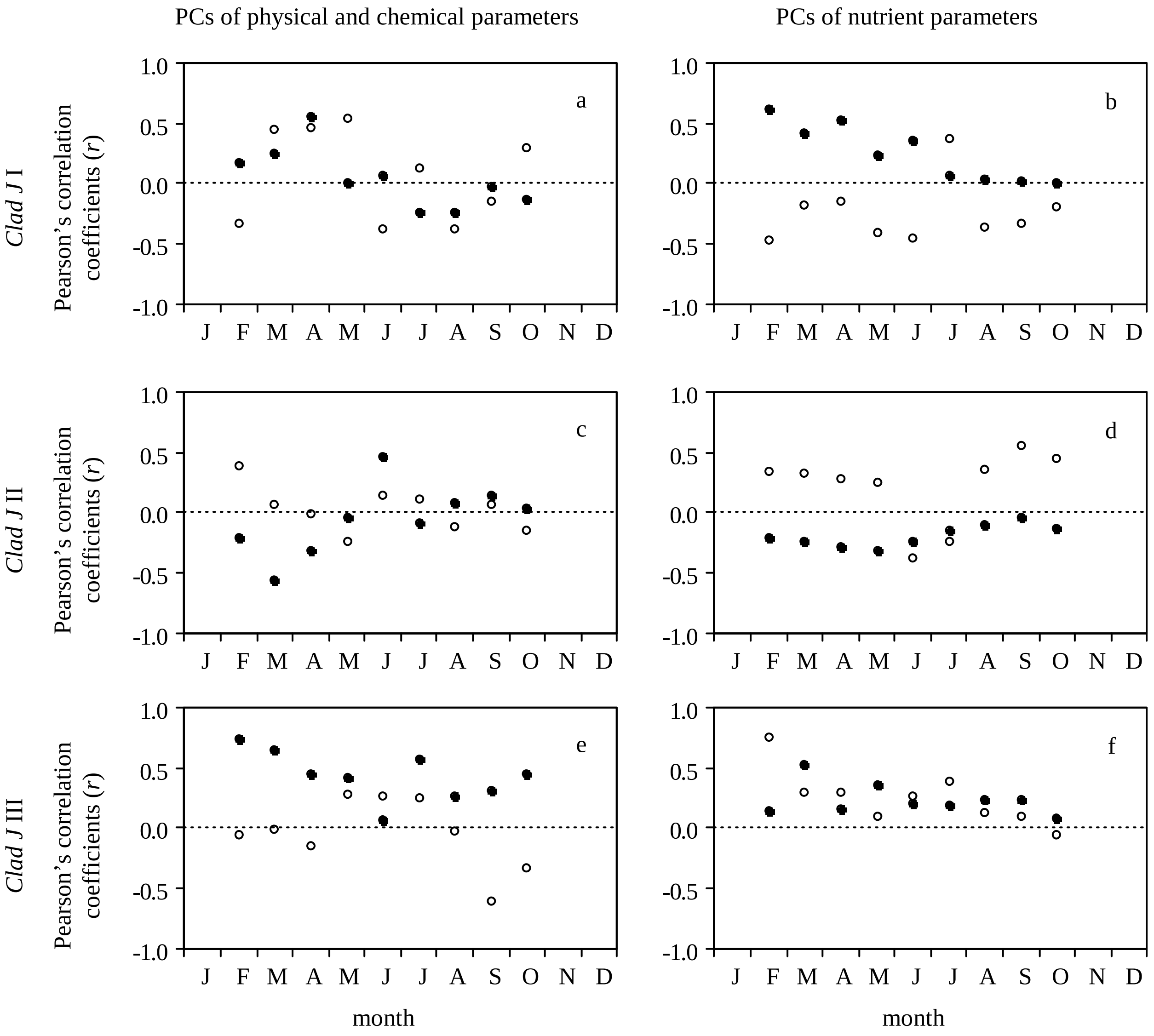

Figure 31. Pearson's correlation coefficients (*r*) between factor scores of *Clad J* I-III in October and factor scores of physical and chemical (left) and nutrient (right) parameters from February to October. The black dots represent the first PC and the white dots represent the second PC of abiotic environmental parameters.

of variance, were, on the one hand, associated with *Bosmina coregoni*, *Chydorus sphaericus*, *Daphnia cucullata*, and *Diaphanosoma brachyurum* from 1969 to 1996, and were, on the other hand, correlated with *Daphnia hyalina*, *Daphnia hyalina* × *Daphnia galeata*, and *Daphnia cucullata* × *Daphnia hyalina* from 2009 to 2011. *Bosmina coregoni*, *Chydorus sphaericus*, *Daphnia cucullata*, and *Diaphanosoma brachyurum* were related to lower concentrations of PO_4^{3-} and TDP from February to April ($0.59<r<0.67$, $p<0.05$) and with colder water temperature, with decreased lake stability, and with lower oxygen concentration

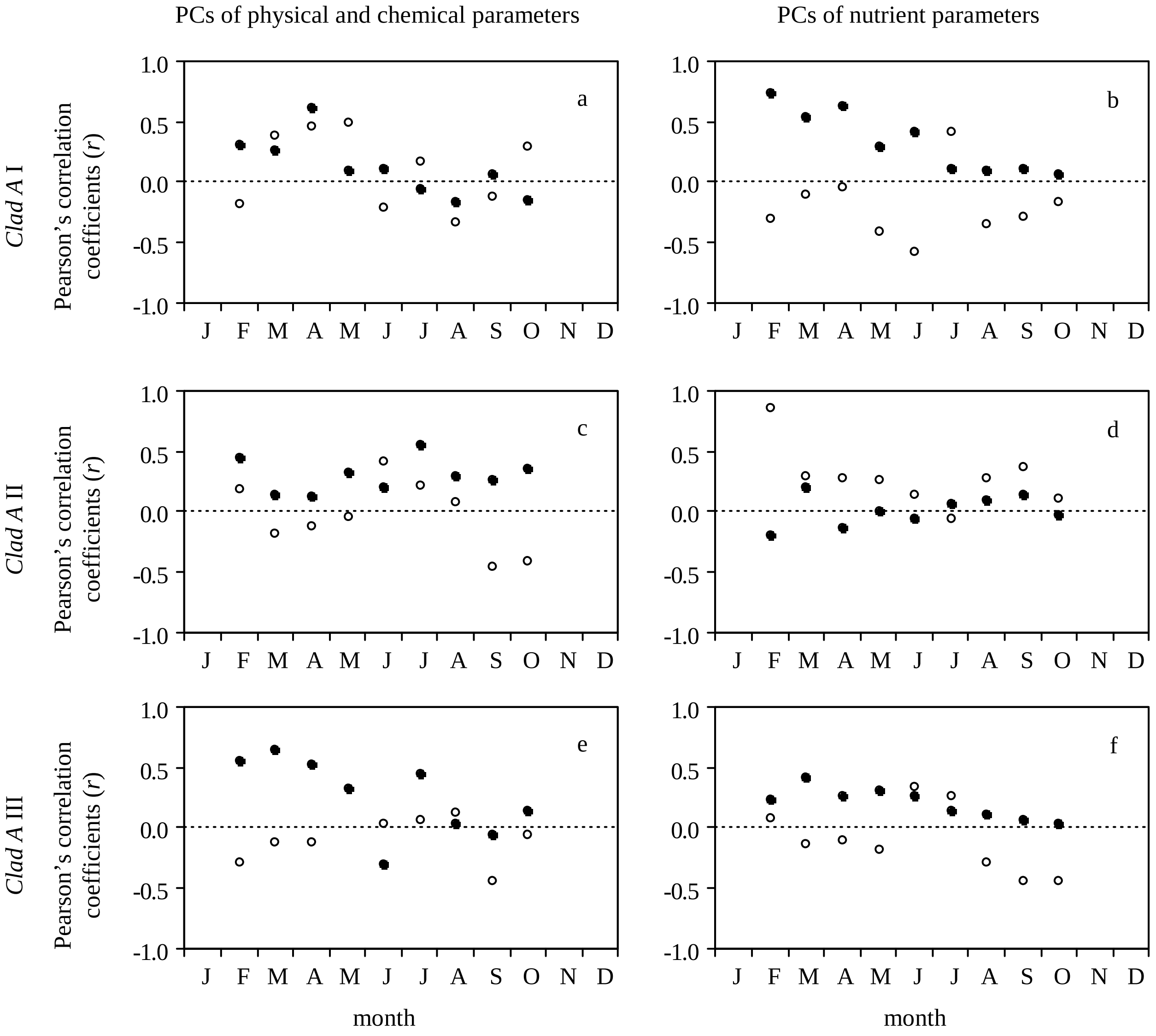

Figure 32. Pearson's correlation coefficients (*r*) between factor scores of *Clad A* I-III in October and factor scores of physical and chemical (left) and nutrient (right) parameters from February to October. The black dots represent the first PC and the white dots represent the second PC of abiotic environmental parameters.

in April (r=0.69, $p<0.05$). However, abiotic environmental parameters were not measured from 2009 to 2011; thus, reliable statements cannot be made, if *Daphnia hyalina*, *Daphnia hyalina* × *Daphnia galeata*, and *Daphnia cucullata* × *Daphnia hyalina* were oppositely affected by these parameters.

Although the second and third principal components of *Clad*, *Clad J*, and *Clad A* were interchanged, they shared similar information and they explained about 20% of variance.

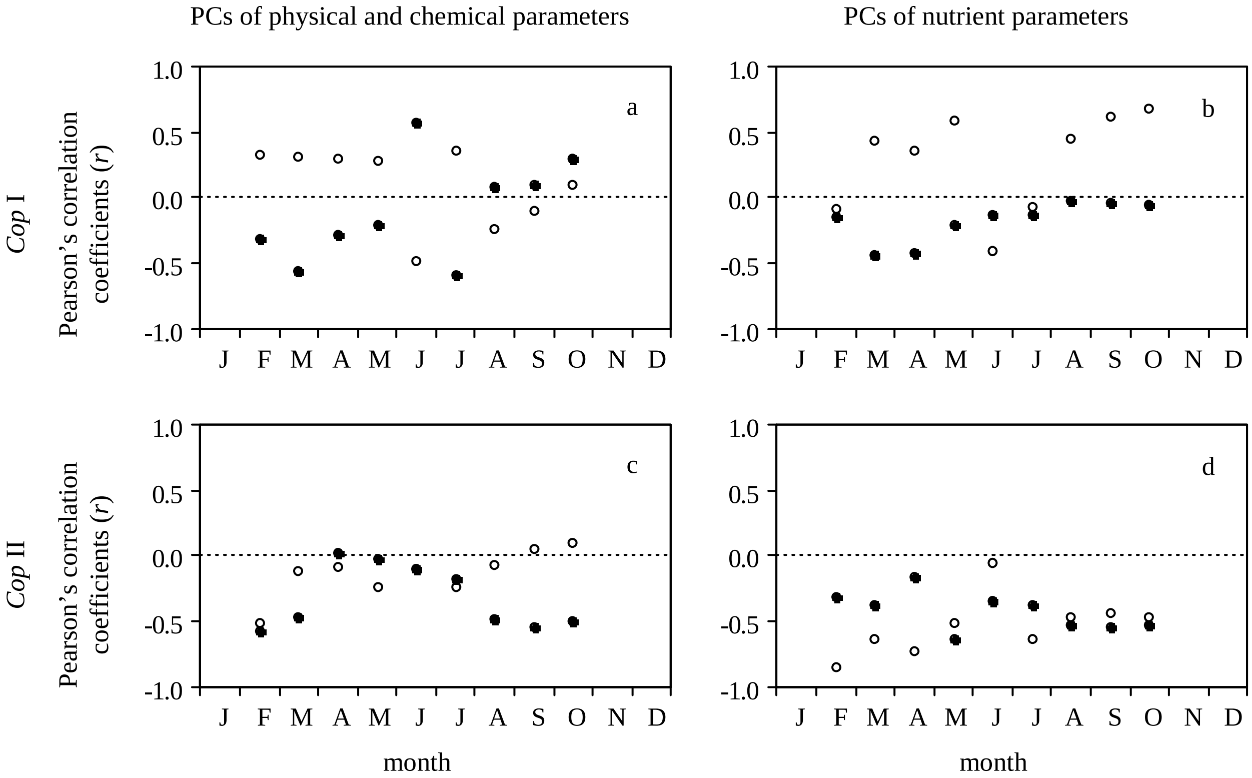

Figure 33. Pearson's correlation coefficients (*r*) between factor scores of *Cop* I-II in October and factor scores of physical and chemical (left) and nutrient (right) parameters from February to October. The black dots represent the first PC and the white dots represent the second PC of abiotic environmental parameters.

Clad II, *Clad J* III, and *Clad A* II were, on the one hand, represented by *Bosmina coregoni* and *Daphnia galeata* mainly from 1990 to 1993, and were, on the other hand, represented by *Bosmina longirostris* and *Daphnia cucullata* mainly in 1977 and 1989. The latter species were positively correlated with NO_3^- concentrations in February (r=0.75, p<0.01), whereas the former species were negatively correlated with NO_3^- concentrations in February.

Clad III, *Clad J* II, and *Clad A* III were, above all, associated with *D. galeata*, *D. galeata* × *D. cucullata* and *D. hyalina* × *D. galeata* from 1990 to 1995. These species were related to a positive $NAO_{Dec\text{-}Mar}$, warmer water temperature and higher concentrations of O_2 and pH from February to April. However, these principal components were also correlated with other species (e.g., *D. cucullata* and *D. galeata*), which is why the significance levels differ between the respective months and principal components.

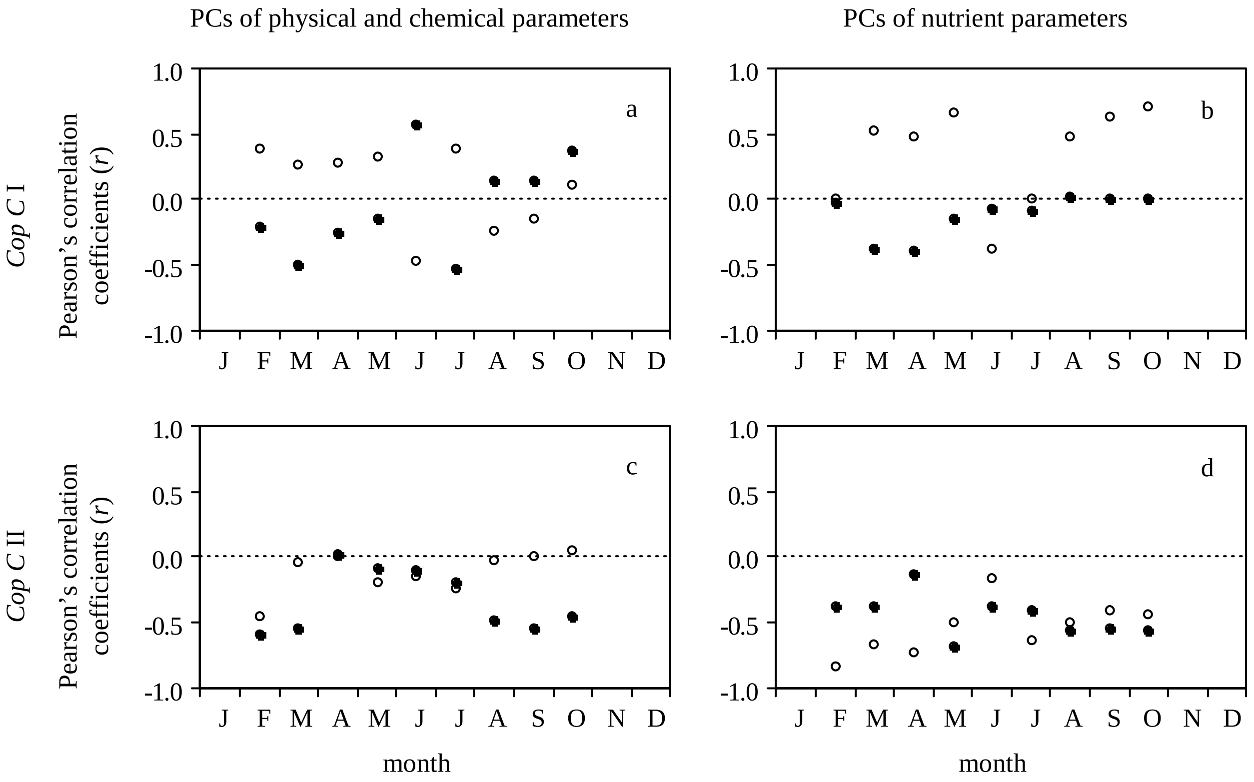

Figure 34. Pearson’s correlation coefficients (*r*) between factor scores of *Cop C* I-II in October and factor scores of physical and chemical (left) and nutrient (right) parameters from February to October. The black dots represent the first PC and the white dots represent the second PC of abiotic environmental parameters.

Similar to principal components of the cladoceran datasets, the principal components derived from the entire copepod community (*Cop*), the copepodite stages (*Cop C*), and the adult copepod stages (*Cop A*) resembled each other in respect of the species compositions and their correlations with abiotic environmental variables (Fig. 33-35). For instance, the first principal components of *Cop*, *Cop C,* and *Cop A* accounted for a variance of about 41-53% and they were linked with *Cyclops abyssorum*, *Cyclops vicinus*, and *Diacyclops bicuspidatus*. These species established largest abundances from 1991 to 1994, and in 2011, when concentrations of NH_4^+ and SiO_2 were low in September and October ($0.61<r<0.67$, $p<0.05$).

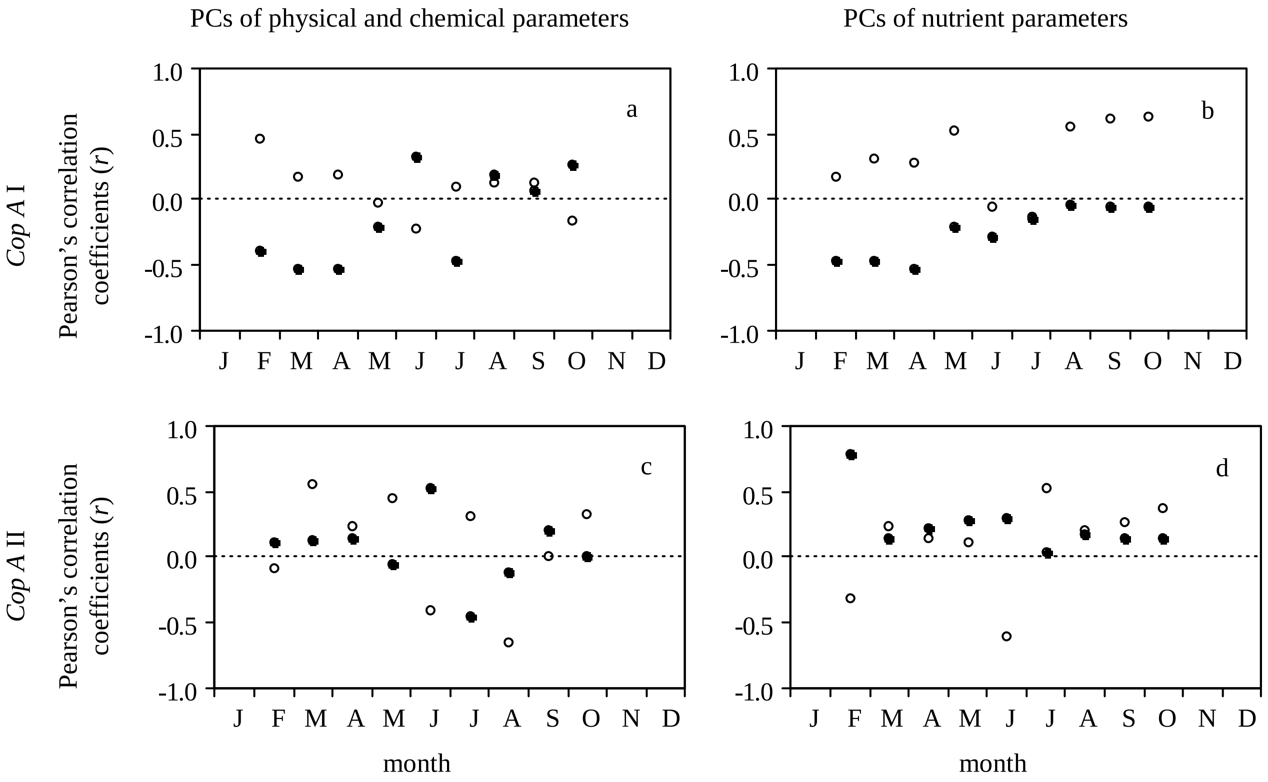

Figure 35. Pearson's correlation coefficients (*r*) between factor scores of *Cop A* I-II in October and factor scores of physical and chemical (left) and nutrient (right) parameters from February to October. The black dots represent the first PC and the white dots represent the second PC of environmental parameters.

Cop II and *Cop C* II were connected with *Eudiaptomus gracilis*, *Cyclops kolensis*, *Mesocyclops leuckarti*, and *Thermocyclops oithonoides* and both principal components explained about 18% of variance. Apart from *Cyclops kolensis*, these species dominated the copepod community in each year. These copepodite species were linked to high concentrations of NO_3^-, PO_4^{3-}, TDP, and SiO_2 from February to October, but predominantly with NO_3^- concentrations from February to May ($0.63<r<0.85$, $p<0.05$). Furthermore, *Cop C* II was correlated with warmer water temperatures, higher O_2 concentrations and pH in February and March ($0.54<r<0.59$, $p>0.05$) and from August to October ($0.45<r<0.54$, $p>0.05$).

Cyclops vicinus, *Diacyclops bicuspidatus*, and *Thermocyclops oithonoides* were most abundant in 1988, from 1991 to 1993, and in 1996 and were correlated with *Cop A* II. These species were associated with abiotic environmental parameters only in distinct months.

3.4.5 Canonical Correlation Analysis of zooplankton groups

We performed a Canonical Correlation Analysis to analyze if the zooplankton pattern in October could also be explained by the interaction of several zooplankton groups.

Table 17. Summary of CCA results calculated for several zooplankton group comparisons. The number in parentheses represents the number of factor scores of a zooplankton group included in this analysis. R_c represents the *canonical correlation* and R_c^2 represents the *squared canonical correlation*. This table includes only the first canonical functions because further canonical functions were not significant ($p>0.05$).

Comparison		Statistics					R_c	R_c^2
Criterion variable	Predictor variable	Wilks' λ	*F*-value	df1	df2	*p*-value		
Rot (4)	*Clad* (3)	0.14	2.46	12.00	26.75	0.026	0.88	0.78
Rot (4)	*Clad J* (3)	0.20	1.91	12.00	26.75	0.081	0.84	0.71
Rot (4)	*Clad A* (3)	0.16	2.24	12.00	26.75	0.040	0.87	0.76
Rot (4)	*Cop* (2)	0.11	5.48	8.00	22.00	<0.001	0.92	0.84
Rot (4)	*Cop C* (2)	0.10	5.90	8.00	22.00	<0.001	0.93	0.86
Rot (4)	*Cop A* (2)	0.24	2.88	8.00	22.0	0.023	0.79	0.62

a) CCA of rotifers and cladocerans

Table 17 shows that the rotifer community (*Rot*) and the cladoceran community (*Clad*) were significantly correlated (R_c=0.88, $p<0.05$) at the first canonical function, which explained a large proportion of shared variance (R_c^2=78%). The multivariate test for significance revealed that juvenile stages of cladocerans (*Clad J*) were not significantly correlated with *Rot* (R_c=0.84, p=0.08) and the first canonical function explained a proportion of 71% of shared variance between both groups. In contrast, *Rot* and adult cladoceran stages (*Clad A*) shared a large proportion of shared variance (R_c^2=76%) and were significantly correlated (R_c=0.87, $p<0.05$) at the first canonical function. These results show that adult cladoceran stages interacted predominantly with the rotifer community. In contrast, the influence of juvenile cladocerans on the rotifer community was less pronounced.

Table 18. Canonical loadings (*load*), structure coefficients (r_s), and squared structure coefficients (r_s^2) of the first canonical function a) between *Rot* and *Clad* and b) between *Rot* and *Clad A.* The Roman numerals denote for the respective principal components of both datasets.

a)	***Rot - Clad (first canonical function)***		
Variable	***load***	r_s	r_s^2 **(%)**
Rot **I**	-0.354	-0.313	9.81
Rot **II**	-0.908	-0.803	64.47
Rot **III**	-0.107	-0.094	0.89
Rot **IV**	-0.198	-0.175	3.06
Clad **I**	0.982	0.869	75.51
Clad **II**	0.161	0.143	2.04
Clad **III**	0.093	0.083	0.68

b)	***Rot - Clad A (first canonical function)***		
Variable	***load***	r_s	r_s^2 **(%)**
Rot **I**	-0.389	-0.339	11.47
Rot **II**	-0.903	-0.787	61.87
Rot **III**	-0.068	-0.059	0.35
Rot **IV**	-0.169	-0.147	2.17
Clad A **I**	0.954	0.831	68.98
Clad A **II**	0.299	0.261	6.79
Clad A **III**	0.034	0.030	0.09

Table 18 a) and b) display a similar pattern of relationship between *Rot* and the two cladoceran groups *Clad* and *Clad A*: The second principal component of the rotifer community (*Rot* II) was the relevant criterion variable that contributed mainly to the variance of the first canonical criterion factor, while *Rot* I, *Rot* II, and *Rot* IV contributed less to that factor. *Clad* I was the relevant predictor variable that contributed predominantly to the variance of the first canonical predictor factor, while *Clad* II and *Clad* III contributed less to that factor. The same pattern applied also to *Clad A* I (relevant predictor variable) and *Clad A* II and *Clad A* III (less important predictor variables). *Rot* II was negatively associated with *Ascomorpha ovalis*, *Keratella cochlearis tecta*, *Polyarthra dolichoptera*, and *Trichocerca similis* and it was positively associated with *Conochilus unicornis*, *Polyarthra euryptera*, *Pompholyx sulcata*, and *Trichocerca cylindrica*. *Clad* I and *Clad A* I were negatively associated with *Bosmina coregoni*, *Chydorus sphaericus*, *Daphnia cucullata*, and *Diaphanosoma brachyurum* and both principal components were positively associated with *Daphnia hyalina*, *Daphnia hyalina* × *Daphnia galeata*, and *Daphnia cucullata* × *Daphnia* *hyalina*. Due to the different signs of the canonical loadings and structure coefficients of *Rot* II and *Clad* I (and *Clad A* I), the canonical correlation between these two canonical factors was negative. Hence, the rotifer species *Ascomorpha ovalis*, *Keratella cochlearis tecta*, *Polyarthra dolichoptera*, and *Trichocerca similis* were, on the one hand, positively related to the cladoceran species *Daphnia hyalina*, *Daphnia hyalina* × *Daphnia galeata*, and *Daphnia cucullata* × *Daphnia hyalina*, but, on the other hand, negatively linked to *Bosmina coregoni*, *Chydorus sphaericus*, *Daphnia cucullata*, and *Diaphanosoma brachyurum*. These species were positively connected with *Conochilus unicornis*, *Polyarthra euryptera*, *Pompholyx sulcata*, and *Trichocerca cylindrica*.

b) CCA of rotifers and copepods

Table 17 shows that *Rot* and the entire copepod community (*Cop*) were significantly correlated at the first canonical function (R_c=0.92, p<0.001) and shared a large proportion of variance (R_c^2=84%). *Rot* and copepodite stages of copepods (*Cop C*) were significantly correlated at the first canonical function (R_c=0.93, p<0.001), which explained a proportion of 86% of shared variance between both groups. The multivariate test for significance revealed that adult stages of copepods (*Cop A*) were significantly correlated with *Rot* (R_c=0.79, p<0.05) and both groups shared a variance of 62% at the first canonical function. These results reveal that copepodite stages as well as adult stages of copepods interacted significantly with the rotifer community.

Table 19 a) and b) depict a similar pattern of association between *Rot* and *Cop* and *Cop C*: *Rot* I and *Rot* III were the relevant criterion variables that contributed mainly to the variance of the first canonical criterion factor, while *Rot* II and *Rot* IV contributed less to that factor.

Table 19. Canonical loadings (*load*), structure coefficients (r_s), and squared structure coefficients (r_s^2) of the first canonical function a) between *Rot* and *Cop* and b) between *Rot* and *Cop C*, and c) between *Rot* and *Cop A*. The Roman numerals denote for the respective principal components of both datasets.

a) **Variable**	***Rot - Cop (first canonical function)*** ***load***	 r_s	 r_s^2 **(%)**
Rot **I**	-0.830	-0.762	58.09
Rot **II**	0.188	0.173	3.00
Rot **III**	0.510	0.468	21.89
Rot **IV**	0.126	0.116	1.34
Cop **I**	0.870	0.799	63.87
Cop **II**	-0.492	-0.452	20.44

b) **Variable**	***Rot - Cop C (first canonical function)*** ***load***	 r_s	 r_s^2 **(%)**
Rot **I**	-0.802	-0.745	55.49
Rot **II**	0.220	0.204	4.16
Rot **III**	0.510	0.474	22.42
Rot **IV**	0.222	0.206	4.25
Cop C **I**	0.916	0.851	72.45
Cop C **II**	-0.401	-0.372	13.88

c) **Variable**	***Rot - Cop A (first canonical function)*** ***load***	 r_s	 r_s^2 **(%)**
Rot **I**	-0.922	-0.723	52.29
Rot **II**	0.209	0.163	2.68
Rot **III**	0.283	0.222	4.92
Rot **IV**	0.161	0.126	1.60
Cop A **I**	0.828	0.649	42.13
Cop A **II**	0.561	0.440	19.36

Cop I and *Cop* II were the relevant predictor variables that contributed mainly to the variance of the first canonical predictor factor. The same pattern applied also to *Cop C* I and to *Cop C* II (relevant predictor factors). *Rot* I was negatively connected with *Ascomorpha ecaudis*, *Polyarthra major*, *Polyarthra remata*, and *Synchaeta pectinata* and positively connected with *Ascomorpha saltans*, *Filinia longiseta*, and *Keratella hiemalis*. *Rot* III was negatively linked to *Filinia terminalis* and positively associated with *Asplanchna* spp. and *Synchaeta oblonga*. *Cop* I was negatively related to *Cyclops abyssorum*, *Cyclops vicinus*, and *Diacyclops bicuspidatus* and positively related to *Cyclops kolensis*. *Cop* II was negatively correlated with *Eudiaptomus gracilis*, *Cyclops kolensis*, *Mesocyclops leuckarti*, and *Thermocyclops oithonoides*. According to the different signs of the canonical loadings and structure coefficients, *Ascomorpha ecaudis*, *Asplanchna* spp., *Polyarthra major*, *Polyarthra remata*, *Synchaeta oblonga*, and *Synchaeta pectinata* were positively associated with the copepodite stages of *Eudiaptomus gracilis*, *Cyclops kolensis*, *Mesocyclops leuckarti*, and *Thermocyclops oithonoides*. These rotifer species were, however, negatively associated with copepodite stages of *Cyclops abyssorum*, *Cyclops vicinus*, and *Diacyclops bicuspidatus*. The latter copepods were positively correlated with *Ascomorpha saltans*, *Filinia longiseta*, *Filinia terminalis*, and *Keratella hiemalis*.

Table 19 c) shows a different pattern of association between *Rot* and *Cop A*: Again, *Cop A* I and *Cop A* II were the relevant predictor variables that contributed mainly to the variance of the first canonical predictor factor. *Cop A* I and *Cop A* II were negatively associated with *Cyclops abyssorum*, *Cyclops vicinus*, and *Diacyclops bicuspidatus*. Due to the same signs of the canonical loadings and structure coefficients of *Cop A* I and *Cop A* II, adult stages of *Cyclops abyssorum*, *Cyclops vicinus*, and *Diacyclops bicuspidatus* were positively connected with *Ascomorpha saltans*, *Filinia longiseta*, *Filinia terminalis*, and *Keratella hiemalis*, but negatively connected with *Ascomorpha ecaudis*, *Asplanchna* spp., *Polyarthra major*, *Polyarthra remata*, *Synchaeta oblonga*, and *Synchaeta pectinata*.

3.4.6. Analysis of the biomanipulation experiment period

We performed Mann-Whitney-*U*-tests to assess if species abundances during the biomanipulation experiment (1991-1994) differed significantly from other years considered in this analysis (Fig. 36). Abundances of rotifer *Keratella hiemalis* were significantly higher (7.5 Ind L^{-1}) during the biomanipulation period compared to other years (0.0 Ind L^{-1}; Mann-Whitney *U*-test, $p<0.05$), whereas the opposite was true for *Keratella quadrata*, which was less abundant during the biomanipulation experiment (1.4 Ind L^{-1}), than in other years (4.6 Ind L^{-1}; Mann-Whitney *U*-test, $p<0.05$). *Daphnia galeata* exhibited the only significant difference within the cladoceran community in response to the biomanipulation experiment:

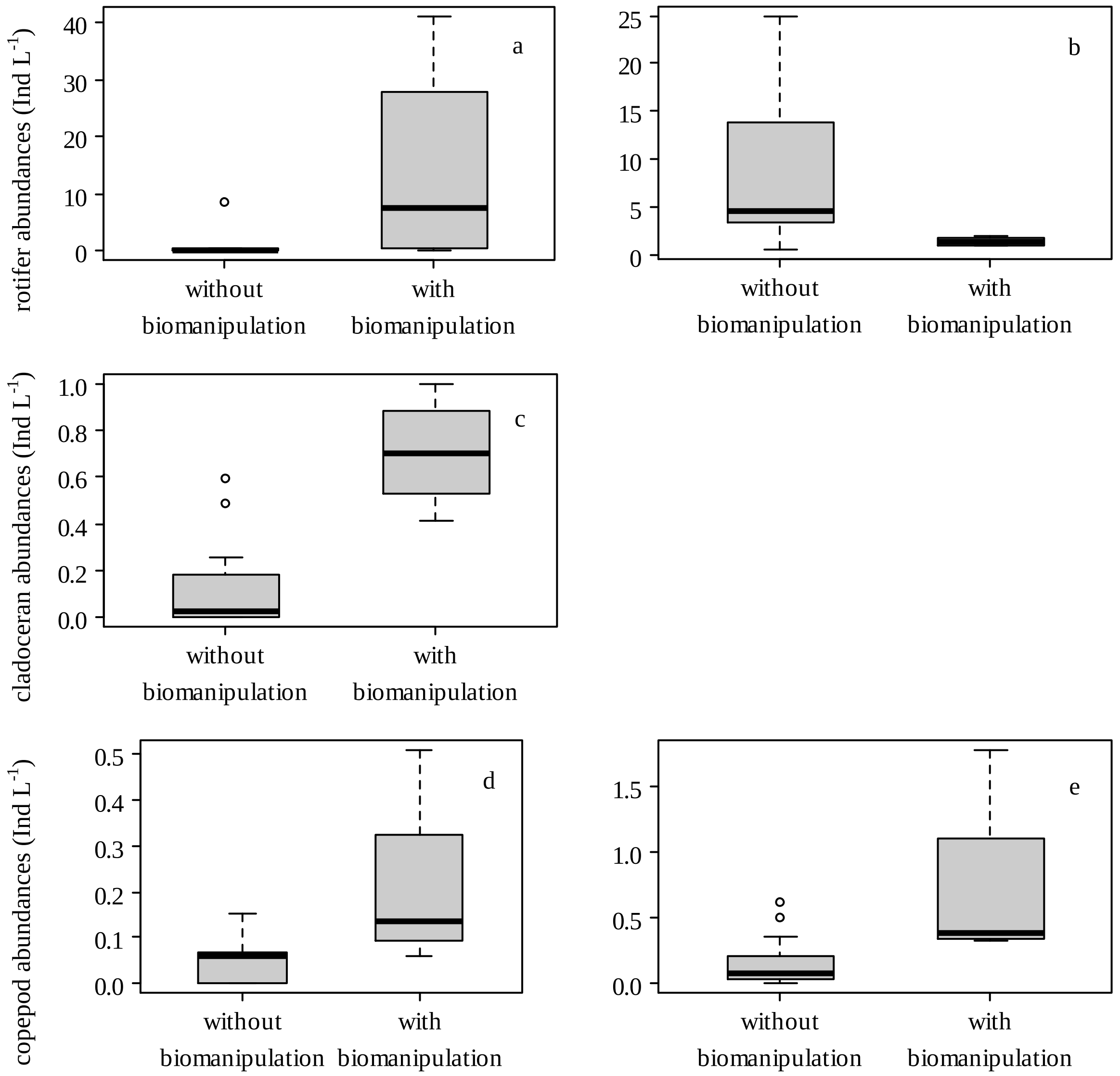

Fig. 36. Boxplots of species abundances (Ind L^{-1}) that differed significantly (p<0.05) between years with and without a biomanipulation effect: a) *Keratella hiemalis*, b) *Keratella quadrata*, c) *Daphnia galeata*, d) *Cyclops abyssorum*, and e) *Cyclops vicinus*.

Daphnia galeata was significantly more abundant from 1991 to 1994 (0.7 Ind L^{-1}) than in other years (0.03 Ind L^{-1}; Mann-Whitney *U*-test, p<0.01). Large-bodied copepods *Cyclops abyssorum* and *Cyclops vicinus* were more abundant during the biomanipulation experiment (0.14 Ind L^{-1} and 0.4 Ind L^{-1}, respectively) than in other years (0.06 Ind L^{-1} and 0.08 Ind L^{-1}, respectively; Mann-Whitney *U*-test, p<0.05). Abundances of other species did not differ significantly between both periods (Mann-Whitney *U*-test, p>0.05).

4 Discussion

4.1. Long-term trend analysis of abiotic environmental parameters

Our study differs from other studies that analyzed the effects of climate change in that we could analyze long time-series of weekly measured lake data, instead of monthly observations. This enabled us to analyze weekly trends instead of monthly trends of meteorological, physical, and chemical lake parameters, which was commonly done in previous studies. In some cases, the resolution of monthly measurements is too coarse if the aim is to determine the timing of certain events from interpolated data, such as, for example, the onset of stratification (Gerten and Adrian 2001). We found an earlier onset of stratification shifting from mid-April to the beginning of April, but this trend was not statistically significant. The stratified phase started significantly earlier in years with a positive winter NAO-index ($NAO_{Dec–Mar}$) than in years with a negative winter NAO-index. Furthermore, positive $NAO_{Dec–Mar}$ were associated with warmer AT and higher WS in winter and early spring, which is in line with the findings of Hurrell and van Loon (1997). The $NAO_{Dec–Mar}$ seemed to be a reasonable proxy to roughly describe the timing of the stratification period in Lake Plußsee, probably because of the accumulating effect of atmospheric heat fluxes on lake-water heat content. However, the index was not adequate to describe the fine tuning during the initiation of stratification and could, for example, not predict the lake-water temperatures at that time, because average wind conditions prevailing from December to March, which were associated with the $NAO_{Dec–Mar}$, did not mirror wind conditions at the timing of stratification in April. In contrast, the timing of the onset of stratification was associated with lower monthly mean WS in March and April. Especially low WS in the last week of March were closely related to the week of the onset of stratification. This indicates that short-duration meteorological conditions, with emphasis on wind conditions, are important for the initiation of stratification, which occurs within a short timeframe. Therefore, by assessing whether WS and AT differed among weeks around the onset of stratification, we could show that WS were significantly lower and AT were significantly higher during the weeks at the onset of stratification than in the preceding weeks. Our findings indicate that the initiation of a stable stratification started within a timeframe of about 2–3 weeks prior to the onset of stratification. Prior to this timeframe WS were not low enough at increasing AT to initiate a stable stratification. Due to increasing air temperatures in spring, the critical timeframe shifted toward an earlier date and promoted an earlier onset of stratification. Thus, within the time window of possible stratification, there is a negative effect of WS on the timing of stratification (i.e., lower WS promote stratification). In contrast, there should be a positive effect during ice-free periods in winter and early spring as higher WS enable a better distribution of heat within the water column. The later can well be approximated by the $NAO_{Dec–Mar}$. The timing of freezing and break-up dates of lake ice cover is also known to have an influence on the timing of the onset of stratification (Magnuson et al. 2000). Austin and Allen (2011) even found lake-surface temperatures in summer to increase with increased air temperatures, decreased wind speeds, and decreased ice cover during the previous winter. Unfortunately, we cannot access data on ice-out for Lake Plußsee and can, therefore, not estimate the influence of ice cover on the onset of stratification and lake temperatures of the following summer.

Large-scale and regional meteorological parameters in spring affected the timing of the onset of stratification and, therefore, also the layer temperatures at the beginning of the stratification period. Initial ET, MT, and HT were significantly colder in years with an earlier onset of stratification than in years with a later onset of stratification (Table 2). Initial layer temperatures reflected the prevalent water temperatures at times when the corresponding layers were detached from vertical mixing and, therefore, from heat exchange with warmer strata above. Thus, lower deep-water temperatures were detached from vertical mixing at an earlier date when water temperatures were generally low. Higher deep-water temperatures, in contrast, were detached from vertical mixing at a later date when water temperatures were comparably warmer. As a result of increasing AT and decreasing WS in spring, the height of the mixed water column decreases and increasing air temperatures can warm the smaller mixed lake volume faster; this also occurs because less thermal energy is lost to deeper strata of the lake. Due to generally lower water temperatures in years with an earlier onset of stratification, comparably low water temperatures suffice to form a temperature gradient, which induces a stable stratification.

The depth of vertical mixing (i.e., the mean thermocline depth) during the first week of stratification was only slightly deeper in years with an earlier onset of stratification (about 3.2 m) than in years with a later onset of stratification (about 3.0 m). Stable stratification was usually initiated at similar depths; therefore, lower initial layer temperatures cannot be explained by the fact that the gradient inducing a stable stratification was established at lower depths of the lake. Hence, initial ET, MT, and HT were determined by the prevalent meteorological conditions in spring that affected the duration of vertical mixing and, therefore, the timing of the establishment of the gradient inducing a stable stratification. Adrian et al. (1995) named the period before the establishment of a stable stratification a 'prestagnation period,' which was characterized by temperature gradients <1°C m^{-1}. This period started generally in mid-April in Lake Heiligensee and lasted for about 2 weeks until a stable stratification, which was characterized by a stable thermocline (with temperature gradients >1°C m^{-1}), was established. This is in line with our findings in Lake Plußsee where the 'prestagnation period' started about 2-3 weeks before the onset of stratification.

Large ET and MT trends in April and May resulted, on the one hand, from an earlier establishment of a stable water column, whereas the epilimnion and the metalimnion warmed earlier and faster because less thermal energy was lost by mixing to the hypolimnion. On the other hand, those large trends were caused by a cumulative effect. We calculated the trends for each calendar week, so we calculated the trends irrespective of the date of the onset of stratification. Therefore, we calculated the trends (e.g., for the first week of May) using warmer ET and MT of years with an earlier onset of stratification and not so warm ET and MT of years with a later onset of stratification.

In contrast to positive ET and MT trends in April and May, we observed largest negative HT trends for these months. The earlier establishment of a stable water column resulted in an earlier detachment of deeper strata from vertical heat exchange, with the warmer strata above resulting in lower initial HT. Large negative HT trends, therefore, resulted, on the one hand, from an earlier onset of stratification and the earlier conservation of lower HT. On the other hand, largest negative HT trends (e.g., in the first week of May) were caused, again, by a cumulative effect: due to the different timing of the onset of stratification, we calculated trends using warmer HT of years with a later onset of stratification and colder HT of years with an earlier onset of stratification.

Negative HT trends were most pronounced during April and May. From that point onward, the extent of HT trends became continuously smaller toward the end of the stratification period. In the course of the stratification period, the hypolimnion constantly gains thermal energy from the metalimnion above (Imberger and Patterson 1990). However, we assume that HT trends, which became continuously smaller in extent from June to November, can also be explained by a cumulative effect: cooler HT, which resulted from an earlier onset of stratification, were conserved longer than were less cold HT, which resulted from a later onset of stratification. When calculating the HT trends for, for example, the first week of August, HT determined by an earlier onset of stratification were still colder than HT determined by a later onset of stratification at that time. Long-term HT trends show large variations among different lakes. In some lakes, hypolimnetic temperatures increased (Livingstone 2003; Arhonditsis et al. 2004) or remained unchanged (Robertson and Ragotzkie 1990; Rempfer et al. 2010). In other lakes, for instance in dimictic Lake Holland (Hondzo and Stefan 1991) and in dimictic Lake Heiligensee (Gerten and Adrian 2001), decreasing hypolimnetic temperatures were recorded. Hondzo and Stefan (1993) showed in a modeling study that the response of hypolimnetic temperatures to future global warming depends on lake morphology and predicted lowest hypolimnetic temperatures for small, deep, and eutrophic lakes, which are also the characteristic features of Lake Plußsee.

In addition to ET and MT increases in April and May, we observed another warming period in both layers from August to October, with a relative trend minimum at the end of June. Again, our results agree with the findings of the modeling study of Hondzo and Stefan (1993), who also predicted two epilimnetic warming periods and a minimum temperature change in between. Hondzo and Stefan (1993) prescribed the expected annual pattern of air temperature change caused by anthropogenic greenhouse gases, which is rather homogenous throughout the year, and simulated with a lake model how weekly epilimnetic and hypolimnetic temperatures of different lake types will change after a doubling of CO_2. Simulated epilimnetic and hypolimnetic temperature changes for small, deep, and eutrophic lakes show a strong resemblance to our ET and HT trend estimations of Lake Plußsee. In particular, the spring and summer/autumn maxima of epilimnetic temperatures would have been difficult to detect in our observations using only monthly data. The model results suggest that although the observed large air temperature trends in April may have an effect on the ET in April, they are not necessarily required to explain the observed ET trends in April, because a general increase of air temperatures produces the observed pattern of ET trends in the model. This agreement between observations and model results also supports our definition of the layer boundaries based on a vertical temperature gradient of 1°C m^{-1}. Although this threshold seems quite coarse, its adoption is still accepted in limnological studies (Wetzel 2001). We decided to choose a gradient with which we could be sure to define a stable stratification and not a transient stage shortly after the phase of thermal homogeneity where density differences are apparent, but not large enough to induce a stable stratification. Given the narrow range of temperatures under consideration, we presented our data on temperature gradients as it is often done in literature (Adrian et al. 1995; Stefan et al. 1996; Gerten and Adrian 2001). However, because density gradients are preferred and our chosen method considers density differences only implicitly through the effect of temperature, we also calculated SSI to back up this method and the discussion of our results. SSI reflects temperature-dependent density differences between the layers of a lake, but also takes layer volumes into account. The pattern of SSI trends corresponded to the pattern of ET trends quite well. Although we observed similar warming trends within the epilimnion in spring, summer, and autumn, we found the largest increases of SSI in summer and autumn. In spring, we detected positive ET and negative HT trends; however, temperature differences were quite small at that time. Therefore, positive SSI trends were also relatively small. In summer and autumn, increasing ET and constantly low HT resulted in enhancing temperature differences. The moderately warming metalimnion acted as an additional barrier between the epilimnion and the hypolimnion. As a result, ET and MT increases resulted in large increases of SSI at that time.

We also included heat content analysis in our study to determine the strength and the effect of water temperature trends, because this analysis is less susceptible to bias from apparently strong changes at specific depths or certain weeks. The amount of heat stored in the lake changes throughout the year and represents changes in the water temperatures at all depths of a lake. Hence, this analysis also takes the lake volumes at all depths into account, which are represented by the characteristic temperatures of the epi-, meta-, and hypolimnion during the stratification period.

Trends of HC corresponded to the pattern of ET, MT, and SSI trends throughout the year. However, in contrast to significantly positive trends of ET, MT, and SSI in April and May, positive trends of HC were not significant at that time. In spring, the lake heat content is still quite small, because of the relatively small heat income by air temperature warming. Positive ET and MT trends and negative HT trends at that time resulted in small HC trends. From August to mid-October, HC trends were significantly positive, which corresponded with the also significant ET, MT, and SSI trends. In summer and autumn, increased heat income by air temperature resulted in higher ET and MT, whereas HT remained unchanged since spring. In accordance with large positive ET and MT trends, we also observed large positive HC trends. Furthermore, heat content calculations also consider lake volume changes with depth. Deeper strata contain smaller volumes of water, so they contribute less to total heat content than do upper strata of a lake. As the year progresses, the thicknesses of the epilimnion and metalimnion expand at the expense of the hypolimnion. In April and May, the hypolimnion contributed to about 50% of the lake volume, whereas from August to October the hypolimnion contributed to about 25–30% of the lake volume. The remaining lake volumes were shared by the epilimnion and the metalimnion. Hence, due to the increasing volumes of the epilimnion and the metalimnion in summer and autumn, increasing ET and MT at that time carried even more weight to the calculation of the heat content than in spring, which resulted in the large positive trends of HC.

In addition to positive ET and SSI trends within each week, large trends also resulted from temperature and stability shifts between successive weeks. The yearly maxima of air temperature (AT_{Max}), epilimnetic temperature (ET_{Max}), and SSI (SSI_{Max}) increased within the analysis period, and the weeks in which the maxima occurred shifted forward in the season. For example, ET_{Max} increased by 1.5°C and was delayed from the beginning of July to beginning of August. SSI_{Max} increased by about 30% and the timing of SSI_{Max} was delayed from the beginning of July to mid-August.

From May to July, we observed a period of smaller ET and SSI trends with a trend minimum at the end of June. At the same time, we detected trends toward deeper thermocline depths with a trend maximum end of June. These trends corresponded with decreasing heat content trends. In their simulations of climate change effects on lakes, Hondzo and Stefan (1993) found smallest increases in epilimnetic temperatures in July and explained them with increased evaporative losses. Long-term energy-budget studies of north temperate lakes found evaporation being negatively correlated with lake heat storage, whereas evaporation rates were low in spring and in autumn and high in summer (Winter et al. 2003; Lenters et al. 2005). These studies also pointed out that evaporation rates varied considerable over the open-water season from year to year. Because ET_{Max} and SSI_{Max} shifted significantly toward autumn, we assume that the timing of the maximum evaporation rate probably also shifted toward a later date in Lake Plußsee.

Warmer ET and increased SSI at a later time of the year resulted in warmer ET and increased SSI in the following months. These changed water column conditions, finally, resulted in a later breakdown of stratification, which shifted from the beginning of November to mid-November. The whole stratification period was extended due to the earlier onset and the later breakdown of stratification by about 3 weeks. Many other studies also found extended periods of stratification in several lakes. Most of them observed that the extension was mainly associated with an earlier onset of stratification in spring (Adrian et al. 1995; Winder and Schindler 2004), rather than to a later breakdown of stratification in autumn (Livingstone 2003). Our results indicate that the early stratification in spring was much more variable than the later date of stratification breakdown in autumn, indicated by a non-significant trend in spring in contrast to a highly significant trend in the shift during autumn.

The prolonged duration of stratification considerably affected conditions of dissolved oxygen concentrations in the hypolimnion and the metalimnion within the last weeks of stratification. The negative O_2 concentration trends in both layers were consistent with negative pH trends, because pH can serve as a proxy for photosynthetic and respiratory processes in a lake. Lower pH values reflect higher CO_2 concentrations as a result of enhanced respiratory processes or enhanced decomposition of organic matter. Higher CO_2 concentrations accumulate within the hypolimnion at higher water column stability and these conditions are even enhanced during the last weeks of stratification.

Lower O_2 concentrations during the last weeks of the stratification period can either be due to shallower mixing at the end of spring turnover (Livingstone and Imboden 1996) or be associated with an extension of the summer stratification period. However, our results point to the later reason because we found positive epilimnetic, metalimnetic, and hypolimnetic O_2 concentration trends at the beginning of the stratification period. Consequently, positive epilimnetic and metalimnetic pH trends, which indicate an enhanced uptake of CO_2 due to higher photosynthesis rates exceeding respiration processes, support our findings of increased O_2 production. These findings indicate that the vertical mixing was deeper before the establishment of a stratified water column in winter and early spring.

These findings were also supported by significantly higher hypolimnetic O_2 concentrations and saturations from the start of the stratification period to July in years with positive $NAO_{Dec\text{-}Mar}$ compared to years with negative $NAO_{Dec\text{-}Mar}$. Higher concentrations of NO_3^- and lower concentrations of NH_4^+ in the hypolimnion almost throughout the stratification period also indicate that vertical mixing was deeper in years with positive $NAO_{Dec\text{-}Mar}$ than in years with negative $NAO_{Dec\text{-}Mar}$. This agrees with findings of Güss et al. (2000), who explained a better ventilation and higher concentrations of NO_3^- concentrations in the hypolimnion with short or no ice coverage in warm winters which accelerated remineralization and nitrification, whereas under aerobic conditions bacteria oxidize ammonium to nitrite (as an intermediate stage) and to nitrate (nitrification), whereas the reverse process (denitrification) is performed under anaerobic conditions.

Besides the downward mixing of oxygen, upward mixing of nutrients can also be used as a tracer to assess the impact of NAO-index on vertical mixing intensity. In the upper strata of the lake (0-10 m), higher concentrations of NO_3^-, NO_2^-, PO_4^{3-}, TDP and lower concentrations of NH_4^+ and SiO_2 were measured in years with positive $NAO_{Dec\text{-}Mar}$ before the onset of stratification, whereas only PO_4^{3-} (February-March) and NH_4^+ (March-April) concentrations differed significantly between years with a positive and a negative NAO-index. George et al.

(2004) and Weyhenmeyer (2004) provided an additional explanation for higher nutrient concentrations in association with a positive NAO-index. George et al. (2004) found positive correlations of dissolved reactive phosphorus and negative correlations of nitrate concentrations with the NAO-index in two small English lakes, whereas Weyhenmeyer (2004) found positive correlations of PO_4^{3-} and NO_3^- concentrations with the NAO-index in Swedish lakes. George et al. (2004) explained higher concentrations of dissolved reactive phosphorus with heavier rainfall in mild winters in positive NAO-index years, which transported increased phosphorus concentrations from the soil of the catchment area into the lakes. Weyhenmeyer (2004) connected higher PO_4^{3-} concentrations in the Swedish lakes with higher nutrient loadings of inflow waters during warm winters. Weyhenmeyer (2004) explained the differences of nitrate concentrations between both studies with the different times of assimilation and leaching of nitrate in the surrounding catchment in mild winters, which depended on the timing of thawing of the soil of the catchment areas and the lakes' ice sheets. Blenckner et al. (2007) also highlighted that site-specific differences can produce different climate-driven responses of nutrient dynamics. Thereby, the influence of nutrient loadings from the catchment area or the timing of the nutrient uptake by the phytoplankton can vary among lake ecosystems. Although Lake Plußsee possesses no direct inflow, it is still possible that the lake was enriched with higher phosphorus concentrations from the catchment area during warm and wet winters; however, data on the effect of nutrient discharge from the catchment area, which could support or refute this hypothesis, are not available.

Weyhenmeyer (2004) also found a negative relationship of SiO_2 concentrations and the NAO-index during the diatom-dominated spring phytoplankton maximum. In addition, SiO_2 depletion was accompanied with pH increases. Although we could not detect a significant relationship of SiO_2 and the $NAO_{Dec\text{-}Mar}$ in Lake Plußsee, we found a significantly negative relationship of SiO_2 and pH in March and in April. The phytoplankton spring maximum in Lake Plußsee is also dominated by diatoms; especially *Stephanodiscus, Cyclotella*, and

Asterionella contributed essentially to the phytoplankton biomass during that time period (Makulla and Sommer 1993; Overbeck and Chróst 1993). Lower Secchi disc transparencies and SiO_2 concentrations as well as higher pH and higher oxygen concentrations and saturations also indicated that the phytoplankton spring maximum occurred in April. Since we only considered monthly means of these parameters, it was not possible to determine if the timing of the phytoplankton maximum shifted to an earlier date. However, Müller-Navarra et al. (1997) found that the spring algal maximum occurred earlier with increasing winter and early spring temperatures. Additionally, Güss et al. (2000) found indications for a more intense algal maximum in spring in response to mild winters in Lake Plußsee. Trends towards increased epilimnetic O_2 concentrations and pH in April and May also suggest that the phytoplankton maximum became more intense during the last decades. These findings can also explain the negative trends of NO_3^-, NO_2^-, NH_4^+, and SiO_2 concentrations from spring to autumn, because an earlier onset and a more intense phytoplankton maximum depleted nutrient concentrations earlier and to a greater extent. Hence, trends were calculated using years with a later and probably less intense phytoplankton maximum, which were associated with negative $NAO_{Dec\text{-}Mar}$ years, and years with an earlier and probably more intense phytoplankton maximum, which were associated with positive $NAO_{Dec\text{-}Mar}$ years. Consequently, negative nutrient concentration trends probably also resulted from a shift and different intensities of the phytoplankton spring maximum as an effect of the winter and spring conditions, which also affected the nutrient concentrations in the following months until the next mixing period in autumn. Earlier phytoplankton maxima after mild winters were also detected in many other lakes (e.g., Heiligensee [Adrian et al. 1995], Lake Erken [Weyhenmeyer et al. 1999], Müggelsee [Gerten and Adrian 2000], and Lake Washington [Winder and Schindler 2004]) and seem, therefore, to be a general phenomenon. These changes can be attributed to shorter ice cover periods in mild winters, since the timing of ice break-up is essential for the development of the phytoplankton due to changes of a lake's mixing conditions and the underwater light conditions (Weyhenmeyer et al. 1999; Straile and Adrian 2000; Peeters et al. 2007; Berger et al. 2010). Thackeray et al. (2008) also pointed out species-specific differences in the advancement of the timing of peak abundances of two diatom species: Whereas *Cyclotella* advanced as a result of an earlier thermal stratification, *Asterionella* was more related to nutrient enrichment and lake warming.

Concentrations of SiO_2 were only significantly negative associated with pH in March and April; afterwards this signal diminished. The annual cycle of SiO_2 concentrations corresponded to the typical seasonal succession of phytoplankton and zooplankton in temperate lakes, which was described by the PEG-model (Sommer et al. 1986): In spring, diatoms dominate the phytoplankton maximum, which is associated with a depletion of SiO_2 concentrations. After the clear-water phase, which is a characterized by a minimum of the phytoplankton biomass and which is caused by increased zooplankton grazing, other phytoplankton species develop and become more important; these are, for example, cyanophytes, cryptophytes, and dinoflagellates (Overbeck and Chróst 1993). Accordingly, SiO_2, which is predominantly used by diatoms, does not play a comparably important role for the phytoplankton growth anymore, and other nutrients, as phosphorus and nitrogen become more important in summer and autumn. After the clear-water phase and the re-cycling of nutrients, which occurs as a consequence of the grazing process, a second phytoplankton maximum develops in summer (Sommer et al. 1986). Trends towards higher O_2 concentrations and pH in the epilimnion and lower Secchi disc transparencies in June and July indicate a more intense summer phytoplankton maximum in Lake Plußsee. From June to October, NO_3^- concentrations became positively associated with pH. Although, phosphorus is the limiting element in most freshwater ecosystems, Sommer (1991) and Makulla and Sommer (1993) found indications that nitrogen and not phosphorus could be the phytoplankton growth limiting nutrient in Lake Plußsee, at least for some species. However, Makulla and Sommer (1993) could exclude phosphorus as a limiting nutrient. We could not prove these findings since we could not access measurements of SRP (soluble reactive phosphorus), total phosphorus, or total nitrogen concentrations. But we found that pH correlated significantly with NO_3^- concentrations from June to October, whereas pH and PO_4^{3-} concentrations were at no time significantly correlated, which could also be an indication that phosphorus is not the growth limiting nutrient in Lake Plußsee.

Increased primary production in summer could also explain trends towards decreasing nutrient concentrations in summer and autumn. Additionally, lake stability also affected nutrient concentrations throughout the stratification period, but especially during the period of maximum lake stability in summer. Apart from PO_4^{3-} concentrations, SSI in August had a negative effect on the concentrations of NO_3^-, NO_2^-, NH_4^+, and, above all, of SiO_2 in August and the following months until the end of the stratification period. However, the negative relationship of lake stability and nutrient concentrations was probably an indirect effect. Lake stability rather affected phytoplankton species negatively due to increased sedimentation rates. Increasing temperatures, which affect lake stability, decrease the viscosity of a liquid, whereas lower viscosities increase the sinking velocities of particles within that liquid. Hence, the sedimentation rates of nutrients, phytoplankton, and organic material are higher when they sink down the stable water column (Wetzel 2001). Winder and Hunter (2008) confirmed that lake stability altered the structure, dynamics, and the composition of the phytoplankton due to the effects of nutrient availability and sinking velocities. In accordance with the availability of certain nutrients and with altered stratified conditions, certain phytoplankton species expanded and outcompeted other species. For example, Winder and Hunter (2008) found that low nitrogen:phosphorus ratios, i.e., nitrogen limitation, favored large-sized flagellates (e.g., *Chlamydomonas*), whereas Makulla and Sommer (1993) found that high nitrogen:phosphorus ratios, i.e., phosphorus limitation, favored chlorophytes (e.g., *Chlorella*). Furthermore, Winder and Hunter (2008) demonstrated that increased water column stability favored species that are less susceptible to sinking. These are, above all, small-sized species and species that are able to regulate their buoyancy within the water column. The latter group of species consists mainly of flagellates and cyanophytes. Tilman (1986) also observed a different outcome of nutrient competition due to temperature-optima differences of the phytoplankton species. Thereby, cyanobacteria and green algae dominated at temperatures larger than 20°C, while diatoms dominated at temperatures lower than 14°C.

Especially, blooms of cyanophytes in eutrophic lakes during warm summers became of increasing interest within the last years, because of their impact on recreation and the health of ecosystems, animals, and humans. Cyanophyte dominance in freshwater ecosystems is promoted by increased lake stability due their ability to decrease their density due to their gas vesicles, which allow them to float in the water column during increased water column stability and decreased mixing conditions (Walsby 1994). Hence, buoyant cyanophytes have a competition advantage for access to light to other species that sink out faster of the euphotic zone (Huisman et al. 2004; Jöhnk et al. 2008). Furthermore, cyanophytes have a higher tolerance to warmer water temperatures, are less grazed by herbivores due to their toxins, and are potent competitors for resources, above all, nitrogen and phosphorus (Hyenstrand 1998; Downing et al. 2001; Jöhnk et al. 2008). In Lake Plußsee, Hickel (1988) observed a sudden change of the algae population from cyanophytes (*Limnothrix redekei*) 1972-1978 to dinoflagellates (*Ceratium hirundinella*) 1979-1990. These changes were attributed to climatic conditions in winter affecting the timing of ice break-up. Similar findings were observed by Weyhenmeyer et al. (2002) who observed higher cyanophyte biomasses after mild winters in association with the NAO-index. Adrian and Deneke (1996) observed a change in the phytoplankton species composition during the phytoplankton spring maximum shifting from diatoms and cryptopytes to cyanophytes in response to mild winters.

Interannual phytoplankton variability was quite large in Lake Plußsee. Unfortunately, we could not access phytoplankton data for Lake Plußsee to make clear and reliable statements on the phytoplankton community, its relationship to nutrient concentrations, and its trends.

However, trends towards earlier and more intense phytoplankton maxima due to warmer winter and spring conditions, extended durations of the stratification periods, and increased water column stability due to increased water temperatures could drastically affect nutrient concentrations and lake productivity if the so far observed changes will continue in the future. Moreover, these changes will be passed onto higher trophic levels.

4.2. Zooplankton community analysis

Although many studies investigated the effects of climate change on zooplankton dynamics in freshwater ecosystems, the majority of these studies concentrated on zooplankton communities in spring and early summer and analyzed how they were affected by warmer winter and spring conditions. So far, only few studies focused on the effects of climate variability on zooplankton in summer and autumn (e.g., Adrian et al. 2006; Seebens et al. 2007; Huber et al. 2010; Sommer and Lewandowska 2011). We decided to focus on the zooplankton community in October, because we found most pronounced changes of lake conditions in summer and autumn. These changes included, among others, trends towards warmer water temperatures, increased lake stability, lower deep-water oxygen concentrations, lower nutrient concentrations, and a later breakdown of stratification. Besides only considering summer and autumn conditions to affect the zooplankton community at the end of the stratification period, we extended the timeframe of possible effects to spring. Thus, we could display the effects of physical, chemical, and nutrient parameters in the respective seasons on the zooplankton community in October. In the following, we used the term “abiotic environmental parameters” to comprise physical, chemical, and nutrient parameters.

However, this method has its limitations: Since we only considered the zooplankton community in October, we have no information on the composition and the dynamics of species from the beginning of the zooplankton’s growing season in winter and spring to September. Therefore, we cannot make reliable statements on this time period. Nevertheless, prevailing lake conditions prior to October can be linked to the zooplankton population in October. A change in environmental conditions at the beginning of the seasonal succession of the plankton (Sommer et al. 1986) can produce alterations in the population dynamics that can propagate further into the season. For instance, the timing and the magnitude of the peak maximum of certain copepod species could be attributed to spring warming (Gerten and Adrian 2002; Adrian et al. 2006; Seebens et al. 2007). At that time, prevalent conditions determine the timing of the emergence of copepods from their resting stages (Gerten and Adrian 2002; Adrian et al. 2006) or they have an effect on the number of overwintering species (George 2000; Seebens et al. 2007). In respect of the different starting conditions at the beginning of the seasonal succession, the population dynamics in the later season can, thus, be traced back to prior winter and spring conditions.

In Lake Plußsee, zooplankton biomass in October was predominantly associated with lake conditions before the onset of stratification: Rotifer, cladoceran, and copepod biomasses were associated with higher mean NO_3^- concentrations and lower NH_4^+ concentrations in February. This negative interplay of oxygenated and reduced nitrogen fractions probably reflected an oxygen gradient or vertical mixing conditions at that time. The copepod biomass in October was also significantly positive correlated with the $NAO_{Dec\text{-}Mar}$, water temperatures, O_2 concentrations, and vertical mixing in February and March. Although rotifer and cladoceran biomasses were not significantly correlated with these parameters, these findings indicate a positive relationship between the zooplankton biomass in autumn and the lake conditions in the prior winter and spring. Güss et al. (2000) also found higher zooplankton biomass in autumn in response to warmer winter conditions in Lake Plußsee. They explained their findings with higher decomposition of organic matter which was probably caused by a more intense phytoplankton maximum in summer. Larger densities of decomposing bacteria, protozoa, and organisms were then consumed by the zooplankton.

Güss et al. (2000) only considered an indicator for zooplankton biomass which included all zooplankton groups. However, changes in the zooplankton community in response to abiotic environmental changes are sometimes difficult to detect when functional groups are considered only. Therefore, we considered rotifers, cladocerans, and copepods on a species level. In contrast to physical, chemical, and nutrient parameters, however, we did not calculate the linear trends of the zooplankton species. Due to the large gaps between the years with available zooplankton samples, these trend calculations would produce untrustworthy results about long-term developments of species in Lake Plußsee. Therefore, we adapted another method for the zooplankton analysis in Lake Plußsee. With a Principal Component Analysis, which calculates linear combinations of the original variables (species) so that they describe the largest proportion of variance of zooplankton datasets, we synthesized species that had a similar pattern of species occurrence along the time series in new groups (principal components of *Zoo*, *Rot*, *Clad*, and *Cop*). In the next step, we correlated them with principal components of nutrients and of physical and chemical lake parameters to detect the nature of the principal components' underlying gradients. Apart from one exception (*Cop* I), all principal components of all zooplankton groups were predominantly associated with lake conditions before the onset of stratification in spring of the same year. These findings emphasize the importance of this period and the involved processes which lay the foundation for the seasonal succession of the phytoplankton and zooplankton throughout the stratification period.

The second principal components of the entire copepod community and the copepodite community were represented by *Eudiaptomus gracilis*, *Mesocyclops leuckarti,* and *Thermocyclops oithonoides*. Both principal components explained a proportion of variance of about 18% and showed a strong resemblance, whereas the principal components derived from the adult copepod community represented a different pattern. These findings reveal that the copepodite stages of *E. gracilis, M. leuckarti,* and *T. oithonoides* predominated in October.

These three copepods were the most abundant copepod species in October in Lake Plußsee and they were part of the copepod community in each year. In agreement with copepod biomasses, these species were significantly correlated with higher nitrate concentrations from February to May. Furthermore, they were highly correlated with warmer water temperatures, higher O_2 concentrations, and higher pH in February and March and from August to October; however, these correlations were not significant. Hence, these findings indicate that *E. gracilis*, *M. leuckarti*, and *T. oithonoides* were more abundant in those October months when water temperatures were warmer and O_2 concentrations and pH were higher in winter and early spring and in late summer and autumn. Thereby, winter and spring conditions already influenced the development of these species at an early stage and these effects propagated further into the season by population dynamics.

Seebens et al. (2007) found an increase of the *Eudiaptomus gracilis* population in Lake Constance in late summer/autumn and related their abundances to spring climate variability and to the resulting shifts in seasonal succession dynamics: Higher spring water temperatures resulted in faster ontogenetic development and in higher abundances in April/May, which resulted in an earlier population minimum in June/July probably due to predation, and in an earlier increase of *Eudiaptomus* abundances in August/September. Eurytherm calanoid copepod *E. gracilis* is able to reproduce throughout the year (Herzig 1983; Santer 1990; Einsle 1993). Due to their low food threshold level for reproduction they are also active in winter and do not perform winter diapause (Einsle 1993; Santer 1994). George (2000) observed higher abundances of overwintering *E. gracilis* in response to mild winters in years with a positive NAO-index. In accordance with the population dynamics of *E. gracilis* in Lake Constance (Seebens et al. 2007), *E. gracilis* probably also established higher spring abundances after milder winters and springs in Lake Plußsee. It is also possible that winter and early spring conditions had a positive effect on the summer and autumn abundances of this species. Furthermore, it probably also benefited from warmer water temperatures in late summer and autumn.

Cyclopoid copepods *T. oithonoides* and *M. leuckarti* are warm-water species and perform winter diapause, whereas their active phases last from early spring to autumn (Frenzel 1977; Vijverberg 1980; Herzig 1983; Maier 1990). Winter diapause enables these species to withstand conditions of low temperatures and reduced food availability during winter (Elgmork et al. 1990; Santer 1990). Nilssen and Wærvågen (2000) reviewed for a variety of European lakes that the duration of the pelagic phase and the number of generations of *T. oithonoides* and *M. leuckarti* depend on the temperature regime of the lake. In Müggelsee, the pelagic phase and summer peak abundance of *T. oithonoides* were synchronized with the timing of spring warming (Gerten and Adrian 2002; Adrian et al. 2006). In this respect, Gerten and Adrian (2002) assumed that warmer spring temperatures favored the earlier emergence from resting stages, which enabled this species to mature earlier and to build-up its peak abundance earlier in summer. Peak abundance, but not the timing of the pelagic phases, of *M. leuckarti* was also related to spring warming.

In Müggelsee, *T. oithonoides* and *M. leuckarti* probably also developed an additional generation (three instead of two generations) in response to warm spring temperatures (Gerten and Adrian 2002; Adrian et al. 2006). Egg, naupliar, copepodite, and adult copepod development are strongly related to ambient water temperatures (Vijverberg 1980; Herzig 1983; Maier 1989). Therefore, trends towards an earlier onset and a later breakdown of stratification within the last decades as a result of increasingly warm water temperatures could enable warm-water species *T. oithonoides* and *M. leuckarti* to emerge earlier in spring and to enter winter diapause at a later date in autumn in Lake Plußsee. *Thermocyclops* and *Mesocyclops* enter winter diapause as fourth and fifth copepodite stages (Vijverberg 1980; Herzig 1983; Maier 1989). In Lake Plußsee, these copepodite stages of *Thermocyclops* and *Mesocyclops* species predominated in October in Lake Plußsee which indicates that both species entered diapause at that time. Therefore, it was not possible to determine if the diapause of these species shifted towards a later date by analyzing the October zooplankton. Notwithstanding the possibility of an additional generation, *T. oithonoides* and *M. leuckarti* benefited from warmer water temperatures throughout their growing phase, but predominantly in winter and early spring and in late summer and autumn. These conditions probably enabled them to develop higher abundances before the start of the diapause phase before they sink to the bottom of the lake in autumn compared to years with colder water temperatures and an earlier breakdown of stratification.

Diacyclops bicuspidatus, *Cyclops abyssorum*, and *Cyclops vicinus* were associated with the first principal components of the entire copepod community, the copepodite community, and the adult copepod community, which explained the largest proportions of variance within these datasets (41-53%). Hence, in contrast to *E. gracilis, M. leuckarti,* and *T. oithonoides*, copepodite and adult stages of *D. bicuspidatus*, *C. abyssorum*, and *C. vicinus* were part of the copepod community in October. However, these species only established high abundances from 1991 to 1994 and in 2011. Probably due to low abundances and irregular appearances in autumn, *Cyclops kolensis* was not associated with these principal components, although *D. bicuspidatus* and all three cyclopoid *Cyclops* species have similar life histories and perform summer diapause (Elgmork 1967; George 1973; Santer and Lampert 1995). *D. bicuspidatus, C. vicinus,* and *C. kolensis* are cold-water species (Vijverberg 1980; Herzig 1983; Maier 1989), whereas *C. abyssorum* is an eurytherm species (Herzig 1983). The onset, termination, and duration of the diapause of *C. abyssorum* can vary among habitats: Santer and Lampert (1995) observed summer diapause of *C. abyssorum*, whereas Nilssen and Elgmork (1977) observed winter diapause of this species. *D. bicuspidatus* performs summer diapause and its active phase lasts from autumn to the end of spring (Vijverberg 1977; Lacroix and Lescher-Moutoué 1984; Maier 1989; Maier 1998). However, Santer and Lampert (1995) and Adrian et al. (2006) reported that *D. bicuspidatus* also occurred in summer at low densities. This indicates that, in some lakes, *D. bicuspidatus* performs summer diapause, whereas in other lakes the active pelagic phase of this species is only reduced.

Besides avoiding food competition with highly efficient filter-feeders (Maier 1994; Santer and Lampert 1995; Hansen and Santer 1995; Hopp and Maier 2005), fish predation is considered to be the ultimate reason for summer diapause of *Cyclops* spp. and *D. bicuspidatus* (Hansen and Santer 1995; Santer and Lampert 1995; Maier 1998; Santer 1998). Thereby, size-selective fish predation leads to the elimination of larger individuals, which are more conspicuous and, thus, more susceptible to predation than smaller ones (Brooks and Dodson 1965; Hall et al. 1976; Vijverberg 1977; O'Brien 1979). Small *D. bicuspidatus*, which produces large egg sacs in relation to body size (Maier 1998), and large *Cyclops* spp. have their population maximum in spring when fish predation is low, whereas the active phase of small *M. leuckarti* coincides with high predation pressure in summer (Hansen and Santer 1995).

From 1991 to 1994 *Cyclops* and *Diacyclops* reached highest abundances within the period of analysis. Before that time period, their abundances were generally low or they were virtually absent. This time period coincided with a biomanipulation experiment, which was conducted in Lake Plußsee from 1991 to 1994 (Kremser 1995). The aim of a biomanipulation experiment is to increase water transparency by reducing the nutrient loading and, hence, to get rid of noxious algae blooms. Thereby, this goal is achieved by interfering into the food chain of an ecosystem. The biomanipulation experiment in Lake Plußsee was performed to reduce the predation pressure of planktivorous fish on zooplankton. In the course of the experiment, piscivorous pikeperches (*Stizostedion lucioperca*), eels (*Anguilla anguilla*), pikes (*Esox lucius*), and trouts (*Salmo trutta*) were added, while planktivorous breams (*Abramis brama*), roaches (*Rutilus rutilus*), and perches (*Perca fluviatilis*) were removed in each year in autumn (Kremser 1995). As a result of this biomanipulation, piscivorous fish depressed planktivorous fish, which had a positive effect on large-bodied zooplankton species, which would in turn result in low phytoplankton biomasses by increased grazing (Post et al. 1997). Results of the biomanipulation experiment in Lake Plußsee indicate that the influence of the introduced species on the zooplankton community was rather small, because the morphometry of Lake Plußsee was not adequate for all introduced species (Kremser 1995). The small and steep littoral zone only enables the development of few macrophytes near the shore (Overbeck and Chróst 1993). This part of the lake is predominantly used as home range of young and small fish that live concealed between the macrophytes and it also serves as hunting ground for predators such as pike. Due to the limited habitat space, introduced species probably did not accustom well in Lake Plußsee (Kremser 1995; Mumm 1996). Although the biomanipulation was rather moderate, zooplanktivorous fish densities decreased within the course of the experiment. Furthermore, largest copepods in Lake Plußsee (*Cyclops* spp.) benefited from the introduction of piscivorous fish and from the removal of zooplanktivorous fish. Small-bodied *Mesocylops* and *Thermocyclops* were probably influenced to a lesser extent by the biomanipulation experiment. Before the biomanipulation experiment, *Mesocylops* and *Thermocyclops* were predominantly associated with perch and roach, which amounted to approximately 70% of the fish standing stock of Lake Plußsee prior to the food web manipulation (Overbeck and Chróst 1993). *Thermocyclops* is negligibly colored and pigmented. Therefore, it is probably outside the prey range of most fish species. *Mesocyclops* is more conspicuous, especially when female carry large egg sacs, which also reduce their maneuverability (Winfield and Townsend 1983). However, this species is able to survive in the littoral area (reviewed by Nilssen and Wærvågen 2000). A similar biomanipulation experiment was conducted in Lake Væng, Denmark (Hansen and Jeppesen 1992): In the course of the experiment, reduction of bream and roach enabled *C. vicinus* to establish high abundances. After the experiment, however, their abundances declined again due to higher fish predation which favored smaller *M. leuckarti*.

Cyclops spp. and *D. bicuspidatus* were also abundant from 2009 to 2011. Copepod countings of the year 2004, which were provided by Barbara Santer, also indicate that *Cyclops* spp. and *D. bicuspidatus* established high abundances in October of that year. Apart from these countings, however, zooplankton data were unavailable from 1997 to 2008. Furthermore, fish data was also unavailable since the completion of the biomanipulation experiment. Therefore, we cannot draw reliable conclusions on whether the fish community changed sustainably in response to the biomanipulation experiment and whether the copepod community was sustainably affected by an altered fish community. In addition, physical, chemical, and nutrient parameters are also unavailable from 2009 to 2011 due to an inaccurately measuring water probe which could give some indication on changing physical, chemical, and nutrient conditions favoring *Cyclops* spp. and *D. bicuspidatus*.

Our results indicate that the largest variability in the copepod community can be attributed to alterations of the fish predation pressure. During the biomanipulation experiment from 1991 to 1994, large-bodied *Cyclops* spp. and *Diacyclops bicuspidatus* established high abundances, whereas in most other years they reached only low abundances or they were virtually absent. Hence, they benefited from reduced predation pressure by zooplanktivorous fish. In contrast, *Eudiaptomus gracilis* and small-bodied *Mesocyclops leuckarti* and *Thermocyclops oithonoides* were probably influenced to a lesser extent by alterations of the fish predation pressure. These species were the most abundant copepod species in October in Lake Plußsee and they established high abundances in those October months when water temperatures were warmer and O_2 concentrations and pH were higher in winter and early spring and in late summer and autumn.

Changes in the species composition within the cladoceran community can probably also be ascribed to the biomanipulation experiment and possible aftereffects. Particularly noticeable were changes in the daphnid community: During the biomanipulation experiment, the daphnid community was associated with higher abundances of large *Daphnia galeata* and comparably low abundances of small *Daphnia cucullata*; however, only *D. galeata* abundances were significantly higher during that period. Spaak and Hoekstra (1997) also observed higher predation risk on *D. galeata* than on *D. cucullata*: *D. galeata* was replaced by *D. cucullata* in the year with highest fish predation pressure, whereas *D. galeata* was abundant in absence of strong fish predation. Furthermore, from 2009 to 2011, the daphnid community in Lake Plußsee was predominantly associated with large-bodied *Daphnia hyalina*, whereas *D. cucullata* was virtually absent. However, due to the reasons mentioned above, it is impossible to state with certainty that the observed changes were mediated by a sustainable effect of the biomanipulation experiment. However, Spaak et al. (2004) demonstrated that *D. hyalina* was the dominant daphnid species in Lake Plußsee in autumn of 1997, which could be an indication that the transition to *D. hyalina* was probably already initiated at that time.

Taking only the years into account that were considered in this analysis, two periods can be distinguished: From 1969 to 1996, *Daphnia cucullata*, *Daphnia galeata*, their hybrid *D. galeata* × *D. cucullata*, and small cladocerans (e.g., *Bosmina* spp. and *Diaphanosoma brachyurum*) dominated the cladoceran community in October, and from 2009 to 2011, *Daphnia hyalina*, and its hybrids *D. hyalina* × *D. galeata* and *D. cucullata* × *D. hyalina* were most abundant and small cladocerans were rare. These two periods were probably also represented by the first principal components of *Clad*, *Clad J*, and *Clad A*, which explained variance proportions of about 30% within these datasets. Correlations with abiotic environmental parameters indicate that *Daphnia cucullata*, *Bosmina coregoni*, *Chydorus sphaericus*, and *Diaphanosoma brachyurum* were associated with lower concentrations of PO_4^{3-} and TDP in spring and with colder water temperatures, decreased lake stability, and lower oxygen concentrations in April. Thus, these species were associated with a later onset of stratification, but also with lower phosphorus concentrations. *D. hyalina*, *D. hyalina* × *D. galeata*, and *D. cucullata* × *D. hyalina* were associated with the opposite range of these parameters. However, missing measurements from 2009 to 2011 do not allow reliable conclusions on the relation of physical, chemical, and nutrient parameters with the first principal components derived from the cladoceran communities.

During the period of the biomanipulation experiment and probably also in the recent period, large species benefited from a decrease of zooplanktivorous fish, whereas small species became less abundant. Basically, our results, especially those considering small cladoceran species, agree with the findings of Mumm (1996). *Bosmina* and *Ceriodaphnia* decreased during that time period (Mumm 1996). However, due to contradicting results of biomanipulation experiments on *Bosmina* (e.g., Søndergaard et al. 1990; McQueen et al. 1992), Mumm (1996) concluded that this genus was probably affected by competitors or by different predators rather than by planktivorous fish.

In contrast to our findings, Mumm (1996) found *Diaphanosoma brachyurum* to increase in response to the biomanipulation experiment. However, this discrepancy can be explained by the different periods considered in both studies: Mumm (1996) considered a period from 1982 to 1995, whereas we also considered years before and after that period. In October, *D. brachyurum* reached higher abundances in earlier and later years than during the experiment. Furthermore, Mumm (1996) found the invertebrate predator *Chaoborus* to increase in summer in absence of planktivorous fish, which could have had a positive effect on *Diaphanosoma*. However, considering available counts of *Chaoborus* of Mumm (1996) and our data, we cannot verify this assumption, because *Chaoborus* densities did not change significantly in October. Nevertheless, it is possible that *D. brachyurum* was affected by *Chaoborus* in summer, because *D. brachyurum* is a warm-water species (Herzig 1984), which has its peak abundances in summer. Hofmann and Krambeck (1991) observed *D. brachyurum* to be present in the upper epilimnion in Lake Plußsee in summer.

Also in contrast to our findings, Mumm (1996) could not detect effects on *Daphnia*, which can probably be explained by the fact that her study only considered daphnids as a species complex without distinguishing between the single *Daphnia* species and their hybrids.

However, zooplanktivorous fish reduction favoring large-bodied *Daphnia*, either due to natural environmental changes or due to biomanipulation experiments, was demonstrated in many studies (e.g., Søndergaard et al. 1990; Vanni et al. 1990; McQueen et al. 1992; Benndorf et al. 2001). Basically, our results agree with the size-efficiency hypothesis (Brooks and Dodson 1965; Hall et al. 1976). According to the size-efficiency hypothesis, intense size-dependent predation will predominantly eliminate large forms enabling small zooplankter to become dominant, whereas reduced predation intensity will competitively eliminate small herbivorous zooplankter and favor larges pecies. The competitive advantage of *Daphnia* in comparison to other (smaller) herbivorous species is that they are highly efficient filter-feeders: On the one hand, their filtering apparatus enables them to use a broader size range of algae particles than smaller species (Geller and Müller 1981). On the other hand, their food threshold is lower than those of smaller species (Lampert and Schober 1978; Porter et al. 1983; Gliwicz 1990).

Water temperatures in winter and spring are considered to be an important factor influencing zooplankton dynamics because warmer water temperatures speed up egg development and increase somatic growth rates at unlimited food conditions (Allen 1976; Bottrell et al. 1976; Vijverberg 1980). Due to the direct response of zooplankton species to water temperatures, the timing and dynamics of phenological processes (e.g., the clear-water phase) can be attributed to prevalent water temperatures. Thereby, Schalau et al. (2008) highlighted in their modeling study that the spring development of *Daphnia* is primarily governed by water temperature and not by food availability. Berger et al. (2007, 2010) achieved similar results with mesocosm experiments by disentangling the governing factors of the phytoplankton maximum in spring and the zooplankton development. Hence, a critical zooplankton biomass to suppress the phytoplankton biomass can be established at an earlier date in warmer years compared to colder years (e.g., Gerten and Adrian 2000; Straile 2000;

Benndorf et al. 2001). In Lake Plußsee, Müller-Navarra et al. (1997) also observed an earlier onset of the clear-water phase mediated by warmer water temperatures.

Although climatic effects on the species being associated with *Clad* III, *Clad J* II, and *Clad A* III were probably influenced by fish predation effects, there is some indication that positive $NAO_{Dec\text{-}Mar}$, warmer water temperatures, and higher O_2 concentrations and pH in winter and early spring had a positive effect on *D. galeata*, *D. galeata* × *D. cucullata*, and *D. hyalina* × *D. galeata* densities in October. Probably, *D. galeata* and its hybrids already benefited from these conditions in spring, whereas these conditions were transferred later into the season by their population dynamics. *D. galeata* is predominantly abundant from spring to early summer (e.g., Wolf 1987; Spaak et al. 2004; Wagner and Benndorf 2007), but it can also have higher abundances in autumn (e.g., Weider and Stich 1992; Adrian and Deneke 1996; Jankowski and Straile 2004). Jankowski and Straile (2004) showed that *D. galeata* performs best at high food availability and low predation pressure. Furthermore, *D. galeata* is characterized by high growth rates (Spaak and Hoekstra 1995; Spaak et al. 2000; Löffler et al. 2004). This is why *D. galeata* rapidly reaches high abundances during the spring algae maximum when fish predation pressure is still low (Mehner and Thiel 1999). During the later season, *D. galeata* and its hybrids probably benefited from the reduction of planktivorous fish and they were able to establish higher abundances during the biomanipulation experiment period in Lake Plußsee. In contrast, years with high zooplanktivorous fish activity probably exerted great influence on *D. galeata* and other large crustaceans in summer and autumn.

Mehner and Thiel (1999) reviewed that fish larvae of zooplanktivorous fish exert only little influence on small zooplankton (e.g., rotifer, small cladocerans, and copepodites) in spring. However, juvenile fish can control large cladocerans and copepods in summer and autumn, because of their larger mouth size enabling them to feed on large zooplankton and because of their better developed hunting abilities.

However, due to the short generation times of daphnids, it is difficult to deduce their population dynamics in autumn from winter and spring conditions. Nevertheless, our results indicate that winter and spring conditions and fish predation pressure played an important role in determining the daphnid composition in autumn. Further studies should, therefore, consider shorter time intervals of sample identification and counting to recognize how precisely abiotic and biotic environmental conditions influenced the daphnid community.

In contrast to *D. galeata*, *D. hyalina* has a competitive advantage at lower food concentrations (e.g., Stich and Lampert 1984; Jankowski and Straile 2004; Zeis et al. 2010), and has, therefore, its highest abundances in autumn (e.g., Seitz 1980; Jankowski and Straile 2004). Spaak et al. (2004) observed *D. hyalina* to be the dominant daphnid species in Lake Plußsee in autumn of 1997. *D. hyalina* was also found in summer (Adrian and Deneke 1996) or it was abundant throughout the year in deeper strata of the lake (Weider and Stich 1992). In contrast to *D. galeata*, *D. hyalina* is known to perform diel vertical migration to reduce the risk of fish predation in Lake Constance (Seitz 1980; Stich and Lampert 1981, 1984). Spaak et al. (2004) also found indications for vertical migration of *D. hyalina* in Lake Plußsee. Kruse (1988) did not find differences in the vertical migration behavior between *D. galeata* and *D. hyalina* in the Schöhsee; in the Schierensee, however, *D. hyalina* performed vertical migration, while *D. galeata* did not. These differences between neighboring lakes of Lake Plußsee can probably be ascribed to differing predation pressures by planktivorous fish.

Small *D. cucullata* is less affected by visually hunting fish compared to larger *D. galeata* and *D. hyalina*. Therefore, it has its peak abundances in summer and it does not perform vertical migration (Seitz 1980; Adrian and Deneke 1996). Wolf (1987) reported that *D. cucullata* dominated the daphnid population throughout the year in 1984 in Lake Plußsee, while Spaak et al. (2004) showed that *D. cucullata* only reached low abundances throughout the year in 1997. In accordance with Wolf (1987), we found *D. cucullata* to be the most abundant daphnid species in autumn of 1984. However, we could not access zooplankton samples of the year 1997 to examine, if *D. hyalina* was the dominant daphnid species or if *D. cucullata* only reached low abundances in autumn in this year. These observations support our hypothesis of possible aftereffects of the biomanipulation experiment and they show that the predation pressure by fish probably differed between these years.

Daphnia performs cyclical parthenogenesis, which means that asexual reproduction alternates with sexual reproduction. For many generations reproduction is solely performed through parthenogenesis, but unfavorable or stressful conditions induce sexual reproduction. Interspecific reproduction and hybridization is possible, if co-occurring different taxa produce males and sexual females at the same time. Often hybrids co-occur with their parental species or they can even dominate the daphnid population due to comparable or even higher fitness values (e.g., Wolf 1987; Weider and Stich 1992; Weider 1993; Spaak and Hoekstra 1995). Life history studies on *Daphnia* hybrids demonstrated that they often show an intermediate pattern of their parental taxa (Weider 1993; Boersma and Vijverberg 1994; Spaak et al. 2000).

Hybrids of *D. hyalina* and *D. galeata* have an intermediate body size compared to the parental taxa, but their intrinsic growth rate is similar to the faster growing *D. galeata* than to *D. hyalina* (Weider 1993; Löffler et al. 2004). Furthermore, vertical distribution of *D. hyalina* × *D. galeata* was more similar to *D. hyalina* than to *D. galeata* (Wolf 1987; Weider and Stich 1992; Kessler 2004). De Meester et al. (1995) also found differences in the vertical distribution of *D. hyalina* × *D. galeata* clones, with the largest clones dwelling in deeper strata of the water column than smaller clones. Hence, *D. hyalina* × *D. galeata* has a selective advantage under moderate fish predation compared to both parental species (Spaak and Hoekstra 1995).

A similar pattern can also be observed in hybrids of *D. cucullata* and *D. galeata*, where the combination of life history traits (small body size of *D. cucullata* and high growth rates of *D. galeata*) probably lowers the fish predation pressure on this hybrid species (Spaak and Hoekstra 1995; Spaak et al. 2000). In Lake Plußsee, *D. galeata* × *D. cucullata* was the second most abundant daphnid species (following *D. cucullata*) in autumn in the period 1969-1996, but it established largest abundances during the biomanipulation experiment. These observations suggest that this hybrid species performed well under increased fish predation and reduced fish predation. High fish predation selectively favors smaller *D. cucullata*, but the slightly larger *D. galeata* × *D. cucullata* also benefited from higher growth rates. On the contrary, lower fish predation selectively favors larger *D. galeata*, but slightly smaller *D. galeata* × *D. cucullata* also benefited from a smaller body size. High abundances of *D. galeata* × *D. cucullata* during the biomanipulation experiment indicate that predation by planktivorous fish was reduced, but was not absent, which supports the statement of Kremser (1995) and Mumm (1996) in behalf of a moderate biomanipulation experiment.

In 2009 and 2010, *D. cucullata* × *D. hyalina* only established low abundances, whereas this hybrid species was virtually absent in all other years. In addition, Spaak et al. (2004) also found only small numbers of this hybrid in Lake Plußsee throughout the year in 1997.

These results clearly demonstrate that the members of the daphnid community in Lake Plußsee were indeed affected by the biomanipulation experiment, which contradicts the findings of Mumm (1996), who did not detect any changes in the daphnid species complex. This is in agreement with Adrian and Deneke (1996), who could not detect any substantial changes in total abundances or in species richness of *Daphnia* as a functional group, but they found marked changes at the species level. The genus *Daphnia* was represented by three species and their hybrids in Lake Plußsee. They are characterized by different life history traits and patterns of temporal and spatial occurrence. Furthermore, they are differently adapted to fish predation pressure, which also explains and reflects their occurrence in Lake Plußsee. This highlights the importance of investigating species instead of functional groups if the aim is to identify changes in ecosystem processes.

In contrast to copepods and cladocerans, rotifers were probably not directly affected by the biomanipulation experiment. Due to their small size, rotifers are less conspicuous than large cladocerans and copepods (Brooks and Dodson 1965; Hall et al. 1976). Therefore, the impact of fish predation on rotifers can be assumed to be small. Rotifers were rather indirectly influenced during the biomanipulation experiment period as fish preyed on cladocerans and copepods, which act as competitors of rotifers (Walz 1995). Principal components derived from the cladoceran and copepod communities were predominantly correlated with physical, chemical, and nutrient variables in winter and spring. In summer and autumn, fish influence probably increased and dominated the effect on the formation of the composition of both communities (Mehner and Thiel 1999) and superimposed, thereby, the influence of abiotic environmental variables. In addition to a less intense and probably more indirect influence of fish predation, rotifers were more strongly related to abiotic environmental conditions than cladocerans and copepods because of their higher reproduction and development rates. Due to these life history characteristics, rotifers are able to respond faster and more sensitively to changes of ambient temperatures and food availability (Edmondson 1965; Allen 1976; Herzig 1987; Stemberger and Gilbert 1985).

Asplanchna spp. and *Synchaeta oblonga* were significantly correlated with warmer water temperatures, higher pH, and higher concentrations of O_2, NO_3^-, PO_4^{3-}, and TDP from February to October, while *Filinia terminalis* was associated with the opposite range of parameters. *Asplanchna* spp. and *Synchaeta oblonga* benefited from higher pH, and higher concentrations of O_2, NO_3^-, PO_4^{3-}, and TDP, whereas these parameters can serve as proxies for photosynthetic activity and primary production. In contrast, *Filinia terminalis* was related to lower pH, and lower concentrations of O_2, NO_3^-, PO_4^{3-}, and TDP. Lower pH values probably reflected higher CO_2 concentrations as a result of enhanced respiratory processes or enhanced decomposition of organic matter. *Filinia terminalis* probably benefited from larger densities of decomposing bacteria, because this species is capable of feeding on bacteria and detritus in deeper strata of the lake (Herzig 1987; Walz 1995). *Synchaeta* spp. and *Asplanchna* spp., however, have high food requirements (Stemberger and Gilbert 1985). Furthermore, eurytherm *Asplanchna* spp. and warm-water species *S. oblonga* benefited from warmer water temperatures, while cold-stenotherm *F. terminalis* benefited from colder water temperatures (Herzig 1987; Bērzinš and Pejler 1989). Elliott (1977) reported that *Asplanchna priodonta* needs higher oxygen concentrations, whereas *Filinia terminalis* reaches high abundances at low oxygen concentrations. *Synchaeta* spp., however, develops high densities over a wide range of temperatures, but it depends on high oxygen concentrations (Elliott 1977).

Ascomorpha ecaudis, *Polyarthra major*, *Polyarthra remata*, and *Synchaeta pectinata* developed high densities in autumn when high concentrations of NO_3^- and SiO_2 concentrations in spring, late summer, and autumn predominated. Thereby, increased SiO_2 seems to enable the build-up of higher abundances of available food algae, especially of diatoms, which favored these rotifer species. *Ascomorpha saltans*, *Filinia longiseta*, and *Keratella hiemalis*, however, established higher densities at lower NO_3^- and SiO_2 concentrations. Apart from *K. hiemalis*, which is a cold-water species, all other species are warm-water species (Herzig 1987; Bērzinš and Pejler 1989). Hence, the positive and negative association of these species with this principal component can rather be ascribed to differences in food resource preference than to temperature preferences. *A. ecaudis* prefers unicellular green algae, whereas *A. saltans* and *A. ovalis* prefer dinoflagellates (Voigt and Koste 1978; Walz 1995). *Polyarthra* spp. and *Synchaeta* spp. prefer large algae particles such as cryptomonads (Voigt and Koste 1978; Herzig 1987; Walz 1995). In contrast, *Filinia* spp. and *Keratella hiemalis* are also able to feed on bacteria and detritus from deeper strata of the lake (Sanders et al. 1989; Herzig 1987). *Keratella hiemalis* and *Filinia terminalis* were predominantly observed in the deeper strata of Lake Plußsee (Hofmann 1985; Hofmann and Krambeck 1991) and *Filinia longiseta* also moved down the water column to escape the rapid temperature increase in spring (Hofmann 1972). Hofmann (1972) observed that *F. longiseta* rather behaved like a cold-stenotherm species than a warm-water species in response to increasing water temperatures in Lake Plußsee.

Hence, all mentioned rotifer species positioned themselves along ecological gradients (represented by *Rot* I and *Rot* III), which met their preference of water temperatures, oxygen concentrations, and food resources. However, according to the Canonical Correlation Analysis, the rotifer species, which were associated with *Rot* I and *Rot* III, were also significantly associated with the copepod community in Lake Plußsee. Copepods *Cyclops vicinus*, *Cyclops abyssorum*, and *Diacyclops bicuspidatus* were predominantly associated with the rotifers *Ascomorpha saltans*, *Filinia terminalis*, *Filinia longiseta*, and *Keratella hiemalis* during the biomanipulation experiment period from 1991 to 1994. In contrast, copepods *Eudiaptomus gracilis*, *Mesocyclops leuckarti*, and *Thermocyclops oithonoides* were predominantly associated with the rotifers *Ascomorpha ecaudis, Polyarthra major, Polyarthra remata*, *Synchaeta pectinata*, *Synchaeta oblonga*, and *Asplanchna* spp. in other years. *Cyclops vicinus*, *Cyclops abyssorum*, and *Diacyclops bicuspidatus* are known to prey on a variety of rotifer species (reviewed by Brandl 2005). In accordance with our results, Devetter (1998) reported that predation pressure of *Cyclops* spp. was the main factor reducing rotifer abundance: *Cyclops vicinus* was, for example, positively associated with *Keratella hiemalis* and negatively associated with *Polyarthra major*. Brandl and Fernando (1978) observed that *C. vicinus* preferentially selected *Asplanchna* spp., *Polyarthra* spp., and *Synchaeta* spp. as prey. Walz et al. (1987) observed that populations of *Asplanchna* spp., *Polyarthra* spp., and *Keratella* spp. increased markedly after *C. vicinus* initiated summer diapause in Lake Constance. Plaßmann et al. (1997) found *C. vicinus* to feed selectively on *Synchaeta* spp. and to be responsible for its decline in spring in Lake Constance. Stemberger (1985) found *Diacyclops* spp. to select soft-bodied *Synchaeta pectinata*, *Polyarthra major,* and *Polyarthra remata*, while it did not select for *Ascomorpha ecaudis*, *Asplanchna* spp., and *Keratella* spp. *Diacyclops bicuspidatus* was observed to co-occur together with *Keratella hiemalis* and *Filinia terminalis* in the deeper strata of Lake Plußsee (Hofmann and Krambeck

1991). These rotifers probably avoided predation by *Cyclops vicinus* through vertical segregation.

Mesocyclops leuckarti also feeds on a variety of rotifer species (reviewed in Williamson 1983). *M. leuckarti* preyed, for example, on *Asplanchna* spp., *Synchaeta pectinata* (Gophen 1977) and *Synchaeta oblonga* (Karabin 1978). In contrast to *M. leuckarti*, which needs prey for successful development (Hansen and Santer 1995; Hopp et al. 1997), *Eudiaptomus gracilis* and *Thermocyclops oithonoides* have been reported to do well on algae food alone, although both species were also found to feed on rotifers (Santer 1994; Hopp et al. 1997; Berger and Maier 2001).

Our findings indicate that the differences in the rotifer assemblage can primarily be attributed to the biomanipulation experiment: The reduced impact of zooplanktivorous fish enabled *Cyclops vicinus*, *Cyclops abyssorum*, and *Diacyclops bicuspidatus* to become dominant and to exert an altered predation pressure on the rotifer community. During that time period these copepods exerted great influence on *Ascomorpha ecaudis*, *Polyarthra major*, *Polyarthra remata*, *Synchaeta pectinata*, *Synchaeta oblonga*, and *Asplanchna* spp, which enabled *Filinia terminalis*, *Filinia longiseta* and *Keratella hiemalis* to become more abundant. In other years, however, the former group of rotifers benefited from low numbers of *Cyclops vicinus*, *Cyclops abyssorum*, and *Diacyclops bicuspidatus* and co-occurred together with *Eudiaptomus gracilis*, *Mesocyclops leuckarti*, and *Thermocyclops oithonoides*, which probably exerted less pressure on these species.

Copepods *Cyclops vicinus*, *Diacyclops bicuspidatus* co-occurred with rotifers *Filinia terminalis* and *Keratella hiemalis*. These species can be considered as cold-water species. In contrast, co-occurring copepods *Mesocyclops leuckarti* and *Thermocyclops oithonoides* and rotifers *Ascomorpha ecaudis*, *Polyarthra major*, *Polyarthra remata*, *Synchaeta pectinata*, and *Synchaeta oblonga* prefer warm water temperatures. However, our results do not clearly indicate that the underlying gradients of the respective principal components represent a temperature gradient. Firstly, not all species being associated with these principal components have the same temperature preferences. For example, warm-water species *Ascomorpha saltans* and *Filinia longiseta* and cold-water species *Keratella hiemalis* were associated with the same principal component. Secondly, the occurrence of cold- or warm-water species in particular years cannot be clearly attributed to cold or warm years, but their occurrence can rather be ascribed to the period of the biomanipulation experiment. For that reason, we can assume that the altered copepod community during the biomanipulation experiment period primarily affected the rotifer assemblage and that the altered predation pressure superimposed the effect of abiotic environmental changes.

Furthermore, eurytherm *Keratella quadrata* (Herzig 1987; Bērzinš and Pejler 1989) showed the inverse pattern of occurrence compared to *Keratella hiemalis*. *K. quadrata* occurred in significantly smaller numbers during the biomanipulation experiment than in other years. The temporary dominance of *K. hiemalis* in the presence of *C. vicinus* spp. can probably be explained with the ability of *K. hiemalis* to dwell in deeper strata of the lake. In contrast, *K. quadrata* predominated in the epilimnion in Lake Plußsee (Hofmann 1985) and was, therefore, more susceptible to copepod predation.

According to correlations of the second principal component of the rotifer dataset with physical, chemical, and nutrient parameters, higher abundances of *Ascomorpha ovalis, Keratella cochlearis tecta*, *Polyarthra dolichoptera,* and *Trichocerca similis* in October were significantly associated with positive $NAO_{Dec\text{-}Mar}$, warmer water temperatures, higher pH, and higher O_2 concentrations from February to May. Furthermore, these species were related to higher concentrations of NO_3^-, PO_4^{3-}, and TDP and to lower NH_4^+ concentrations from March to June and in October. Hence, these species benefited from warmer water temperatures, higher oxygen concentrations, and higher nutrient concentrations. *Conochilus unicornis, Polyarthra euryptera, Pompholyx sulcata,* and *Trichocerca cylindrica* were linked to the opposite range of parameters. The former group of species predominantly developed high abundances from 2009 to 2011, while they were virtually absent during the earlier period from 1969 to 1996. The opposite pattern applies to the latter group of species. However as already mentioned before, missing measurements from 2009 to 2011 do not allow reliable conclusions of the relationship between abiotic environmental parameters and ecological preferences of rotifers, which were associated with this principal component. Furthermore, the nature of this gradient is difficult to deduce due to the specific composition of species being associated with this principal component. For example, indicators for eutrophy as *Keratella cochlearis tecta* (Ruttner-Kolisko 1972) and *Trichocerca similis* (Pejler and Bērzinš 1993) are positioned on different sides of the gradient. Furthermore, warm-water species *Ascomorpha ovalis* (Herzig 1987) was, on the one hand, negatively associated with warm-water species *Polyarthra euryptera* (Ruttner-Kolisko 1972) and *Conochilus unicornis* (Elliott 1977), but, on the other hand, positively associated with cold-stenotherm *Polyarthra dolichoptera* (Herzig 1987; Bērzinš and Pejler 1989).

According to the Canonical Correlation Analysis, rotifer species *Ascomorpha ovalis*, *Keratella cochlearis tecta*, *Polyarthra dolichoptera*, and *Trichocerca similis* were positively correlated with cladoceran species *Daphnia hyalina*, *Daphnia hyalina* × *Daphnia galeata*, and *Daphnia cucullata* × *Daphnia hyalina*, which were also predominantly abundant from 2009 to 2011. Accordingly, rotifer species *Conochilus unicornis*, *Polyarthra euryptera*, *Pompholyx sulcata*, and *Trichocerca cylindrica* were associated with cladoceran species *Bosmina coregoni*, *Chydorus sphaericus*, *Daphnia cucullata*, and *Diaphanosoma brachyurum* during the period 1969 to 1996. Many studies demonstrated that *Daphnia* are able to suppress rotifers from “bottom-up” through exploitative competition of limiting food resources, because threshold food levels of rotifers are higher than those of cladocerans (e.g., Stemberger and Gilbert 1985, Duncan 1989; Gliwicz 1990). In addition, *Daphnia* are able to interfere mechanically with rotifers from “top-down” (e.g., Gilbert and Stemberger 1985; Burns and Gilbert 1986; MacIsaac and Gilbert 1989). Small cladocerans (e.g., *Bosmina* *coregoni*, *Chydorus sphaericus*) often co-exist with rotifers in absence of large cladocerans (e.g., *Daphnia*), because smaller species are less able to mechanically interfere with rotifers and because they are less able to deplete food resources as effectively as large cladocerans (Gilbert 1988).

Rotifers, however, developed various strategies to reduce the probability of being harmed by cladocerans and copepods (Williamson 1983; Walz 1995; Brandl 2005): For example, *Ascomorpha* spp. and *Conochilus unicornis* have gelatinous sheaths which increase the size of the species. Furthermore, *Conochilus unicornis* forms large colonies with many species, which make it more difficult for predators to prey on them effectively. By contrast, species of the genus *Polyarthra* developed efficient escape responses. However, *Polyarthra dolichoptera* and *Polyarthra euryptera*, which have similar defence mechanism, were positioned on opposite sides of the same principal component. Hence, this rotifer species composition makes it difficult to draw reliable conclusions from the interaction between cladocerans and both *Polyarthra* species.

The fourth principal component of the rotifer dataset was, apart from *Polyarthra dolichoptera*, predominantly associated with species as *Collotheca* spp., *Conochilus hippocrepis*, *Brachionus calyciflorus*, *Monostyla* spp., *Trichocerca capucina*, and *Trichocerca pusilla*, which only established low abundances or which were virtually absent in most years in October.

The rotifer species diversity indices by Shannon (Shannon and Weaver 1949) and Simpson (Simpson 1949) were negatively correlated with O_2, NO_3^-, PO_4^{3-}, and TDP concentrations and with pH from May to October. Overbeck and Chróst (1993) showed that nitrogen and phosphorus, which are the two most important nutrients for phytoplankton growth in Lake Plußsee, as well as O_2 concentrations and pH, can serve as proxies for photosynthetic activity and primary production in Lake Plußsee. Hence, high species diversity was probably associated with low primary production. However, lower pH values can also be an indication for enhanced decomposition of organic material by bacteria after a more intense summer phytoplankton bloom (Güss et al. 2000). Hence, larger densities of decomposing bacteria, which are consumed by rotifers, enable higher species diversity.

Jeppesen et al. (2000) found zooplankton species richness, which represents the number of different species in an ecosystem, to decline significantly with increasing TP (total phosphorus) concentrations. Furthermore, they found a unimodal response of the Shannon-index, which also takes the relative abundances of the present species into account, to TP concentrations. Dodson et al. (2000) found a unimodal response of species richness and species diversity to trophic state. Thereby, only few species dominated the community at extremely low or extremely high resource concentrations, while species richness in lakes was high at intermediate resource concentrations. For example, Tilman (1987) observed a decline in species richness in response to an experimental increase of productivity: Only few species responded strongly to an increase of the limiting resource and were able to outcompete other species of the community which, finally, resulted in a decline of species richness. Another explanation for high species richness at intermediate productivity levels is that species are often not adapted to extreme environmental gradients (e.g., extremely low or extremely high pH values or O_2 concentrations). Again, only few species are able to withstand these extreme conditions which is why highest species richness or species diversity can be observed at intermediate productivity levels (Dodson 1992).

However, a unimodal response of species richness or of species diversity to primary production is often difficult to detect since the environmental gradients (represented, e.g., by total phosphorus concentrations) are not always reproduced from extremely low to extremely high values in one ecosystem. Studies finding an unimodal response often analyzed a large number of lakes ranging from oligotrophic to highly eutrophic lakes (e.g., Dodson 1992) or differing in their TP concentrations (Jeppesen et al. 2000).

The Shannon-index and the Simpson-index of the entire zooplankton community, which included the species of all three zooplankton groups, showed the same pattern of correlations with nutrient parameters as the rotifer community. This similarity can be explained with species richness. Rotifers contributed primarily to the entire zooplankton community because of their large number of different species. Furthermore, rotifers displayed a strong variability in the species occurrence in different years. In contrast, cladocerans and copepods were only represented by comparably few species and the variability of their species occurrence was also comparably smaller in relation to rotifers. Unfortunately, we could not detect significant correlations between the species diversity indices of the cladoceran and copepod communities and abiotic environmental parameters. This agrees to a large degree with our findings of correlations between principal components derived from both communities and physical, chemical, and nutrient parameters. Dodson et al. (2000) showed in their survey that cladocerans and copepods also responded unimodally to lake productivity. Since cladocerans and copepods are expected to respond similarly to differences in lake productivity as rotifers, changes in the time series pattern of species diversity indices by Shannon and Simpson of the cladoceran and copepod communities cannot be explained by changes of the abiotic environment. Species diversity changes within the cladoceran and copepod community can probably also be ascribed to changes in the fish community in Lake Plußsee.

Generally, rotifers responded more directly to changes of physical, chemical, and nutrient parameters than cladocerans and copepods. On the one hand, rotifers have higher reproduction rates and shorter generation due to faster development times. Due to these life history characteristics, species abundances, species composition, and species diversity of rotifers were more strongly related to changes of the abiotic environmental conditions. On the other hand, rotifers are smaller and less conspicuous than large cladocerans and copepods and they were, therefore, probably only indirectly influenced by the biomanipulation experiment through its effect on cladocerans and copepods. In this respect, we could demonstrate that cladocerans and copepods exerted great influence on the rotifer community in October.

5 Conclusion

The aim of this PhD thesis was to examine the effects of inter-annual climatic variations and trends on Lake Plußsee, a small eutrophic lake in Schleswig-Holstein. Thereby, long-term variability and trends of large-scale and regional meteorological forcing parameters were analyzed and related to abiotic and biotic environmental changes of the lake. In the first part of our research, we investigated, therefore, the influence of the winter-index of the North Atlantic Oscillation ($NAO_{Dec-Mar}$) on regional air temperatures and wind speeds. Next, we examined their influence on the trends and the variability of water temperatures, oxygen and nutrient concentrations, and pH prior and during the stratification period from the beginning of measurements in 1969 to 2006. In the second part, we analyzed the influence of these parameters on the zooplankton community with its three major zooplankton groups (rotifers, cladocerans, and copepods) in October in particular years from 1969 to 2011. Furthermore, we examined whether changes in the species composition could also be ascribed to interspecific competition between these groups or to food-web alterations during the biomanipulation experiment (1991-1994).

Our results show that Lake Plußsee experienced major long-term changes of water temperatures, pH, and concentrations of oxygen and nutrients from 1969 to 2006, which reflected long-term changes of meteorological forcing. Years with a positive $NAO_{Dec-Mar}$ probably affected the duration of the ice coverage period of the lake due to warmer air temperatures whereas higher wind speeds enabled a better distribution of heat within the water column in winter and early spring, and vice versa. The index was also a reasonable proxy to describe the timing of the onset of stratification, which shifted from mid-April to beginning of April within the period of analysis. However, we could reveal that meteorological conditions, which occurred within a short timeframe of about 2-3 weeks (i.e., warmer air temperatures and lower wind speeds), were important for the initiation of a stable water column. Hence, in some cases, the resolution of monthly measurements is too coarse, if the aim is to determine certain events with interpolated data, because the crucial processes involved for initiating a stable stratification take place within a short timeframe.

The timing of the onset of stratification determined the epilimnetic, metalimnetic, and hypolimnetic temperatures and their long-term trends during the initial weeks of stratification. Large epilimnetic warming trends (about 3°C throughout the period of analysis) resulted from large air temperature trends at that time and from reduced thermal energy being lost to deeper strata in years with an earlier onset of stratification. The opposite was true for hypolimnetic temperature trends, because colder deep water temperatures were conserved at an earlier date in years with an earlier onset of stratification. Thereby, we demonstrated that the hypolimnetic temperature trends decreased significantly (by about 0.5°C throughout the period of analysis) during the first weeks of the stratification period in association with the trends towards an earlier onset of stratification. The extent of epilimnetic and hypolimnetic temperatures in spring can also be explained by a cumulative effect, because these trends were calculated irrespective of the timing of the onset of stratification. Again, the resolution of monthly measurements would have been too coarse to identify the reason for these large temperature trends.

In the further course of the stratification period, air temperatures were strongly related to epilimnetic temperatures, while the influence of wind became less important. Although epilimnetic temperature trends in August were similar to those in spring, lake stability and lake heat content increased more strongly in summer than in spring. In summer, temperature-differences between the epilimnion and the hypolimnion are larger than in spring and also the lake volume encompassed by the warm epilimnion is larger than in spring. As a result of the positive trends of epilimnetic temperatures, of lake stability, and of heat content in summer and autumn, the breakdown of stratification shifted from beginning of November to mid-November during the period of analysis.

Large trends of oxygen concentrations, pH, and nutrient concentrations in spring and in summer indicate more intense spring and summer phytoplankton maxima. However due to time constraints, we could not consider the phytoplankton community in our research. We only used Secchi disc transparencies, oxygen concentrations, pH, and nutrient concentrations as proxies for the phytoplankton densities or for the primary production. However, future studies on Lake Plußsee should investigate the composition of the phytoplankton community. This will help comprehending our findings of the annual cycles and the long-term trends of oxygen, pH, and nutrient concentrations better. Certain phytoplankton species might benefit from the observed long-term changes in Lake Plußsee. For example, increased water column stability and lower nutrient concentrations in summer could favor cyanophyte blooms in Lake Plußsee. Furthermore, an accurate identification of the phytoplankton community will help to assess the influence of different food resources on the occurrence of certain zooplankton species. For example, cyanophytes are known to affect most herbivore species because they avoid cyanophytes as food resource due to their toxins.

Despite large changes of water temperatures, pH, and concentrations of oxygen and nutrients prior and during summer stratification, we could ascribe the largest variability of species occurrence within the cladoceran and copepod datasets in October to predation pressure alterations during the biomanipulation experiment. In the course of this biomanipulation experiment, which was performed from 1991 to 1994 in Lake Plußsee, piscivorous fish were added and zooplanktivorous fish were removed to reduce the predation pressure on the zooplankton. The Principal Component Analysis performed on the copepod and cladoceran communities revealed that large-bodied copepods *Cyclops vicinus*, *Cyclops abyssorum*, and *Diacyclops bicuspidatus* and large-bodied cladocerans *Daphnia galeata* and its hybrid species *Daphnia galeata* × *Daphnia cucullata* and *Daphnia hyalina* × *Daphnia galeata* probably benefited from reduced predation pressure by zooplanktivorous fish during the biomanipulation experiment. Before the biomanipulation experiment, however, the cladoceran community was predominantly associated with smaller species (e.g., *Daphnia cucullata* and *Bosmina*). There are also indications of a sustainable effect of the biomanipulation experiment, because large-bodied copepods (e.g., *Cyclops vicinus*) and cladocerans (*Daphnia hyalina* and its hybrid species) also reached high abundances in October in recent years (2009-2011). However, unavailable zooplankton samples from 1997 to 2008 do not allow reliable conclusions on possible sustainable effects of the biomanipulation experiment on the zooplankton community. Furthermore, fish stocking was only randomly evaluated in Lake Plußsee before and after the biomanipulation experiment. Hence, it is difficult to quantitatively assess the influence of fish on the zooplankton community before, during, and after the experiment.

Principal components derived from the cladoceran and copepod communities were predominantly correlated with physical, chemical, and nutrient parameters during the previous winter and early spring. At this time, fish predation on both zooplankton communities was probably small. In summer and autumn, however, the influence of an altered fish predation pressure probably dominated the effect on the formation of the composition of both communities and superimposed, thereby, the influence of abiotic environmental variables. For example, abundances of *D. galeata*, *D. galeata* × *D. cucullata*, and *D. hyalina* × *D. galeata* in October were predominantly affected by warmer water temperatures and higher oxygen concentrations and pH during the prior winter and early spring. Copepods *Eudiaptomus gracilis*, *Mesocyclops leuckarti*, and *Thermocyclops oithonoides* were also positively linked to warmer water temperatures and higher oxygen concentrations and pH during the prior winter and early spring, but they were also linked to these parameters in late summer and autumn. In contrast to large-bodied copepods *Cyclops vicinus*, *Cyclops abyssorum*, and *Diacyclops bicuspidatus*, *Eudiaptomus gracilis*, *Mesocyclops leuckarti*, and *Thermocyclops oithonoides* were probably influenced to a lesser extent by alterations in the fish predation pressure due to their smaller body size.

In contrast, rotifers were indirectly affected by the biomanipulation experiment because alterations in the fish population primarily influenced the competitors of the rotifers: With a Canonical Correlation Analysis, we demonstrated that rotifers were influenced by cladocerans and copepods. However, due to the probably less intense and more indirect effect of fish predation and probably also due to their higher reproduction and development rates, rotifers were significantly correlated with water temperatures, pH, and concentrations of oxygen and nutrients throughout the stratification period.

The species diversity of the rotifer community was negatively related to pH and to oxygen and nutrient concentrations from May to October, whereas NO_3^-, PO_4^{3-}, and TDP concentrations were particularly important. The negative association of rotifer species diversity and these parameters, which can serve as proxies for primary production, indicate that species diversity probably declined in response to increasing primary production. In contrast to the large year-to-year variability in the species richness of the rotifer community, the variability of the smaller species richness of the cladoceran and the copepod communities did not yield any significant correlations to abiotic environmental variables.

Due to the strong impact of the biomanipulation experiment on the long-term variability of the zooplankton community datasets, we could not clearly demonstrate the impact of environmental changes mediated by climate variations within the last decades on the three zooplankton groups of Lake Plußsee. Further studies on the impact of climate warming on zooplankton species, groups, or communities should, therefore, try to disentangle the influences of changing environmental parameters from species-specific interactions. For example, mesocosm experiments allow the simulation of realistic environmental conditions in an isolated system under controlled conditions, whereas single key factors can be changed to analyze their impact on certain zooplankton species, groups, or communities.

The main conclusion of our study on the long-term effects of climatic variations on Lake Plußsee is that the lake experienced pronounced changes of water temperatures, pH, and concentrations of oxygen and nutrients since the beginning of measurements in 1969. Especially noticeable was the increasingly prolonged stratification period, which was caused, on the one hand, by milder winters and springs, and, on the other hand, by increasingly warm air temperatures in summer and autumn in recent years. In this respect, we could demonstrate the effects of an earlier onset of stratification on water temperatures in spring and we could also show that deeper strata of the lake experienced increasingly oxygen-reduced or even anoxic conditions during the last weeks of stratification in autumn as a result of a later breakdown of stratification.

Although we detected major changes of the abiotic environment within the last decades in Lake Plußsee, we ascribed the largest variability within the zooplankton community in October to changes of the fish predation pressure caused by a biomanipulation experiment that was performed in Lake Plußsee from 1991 to 1994. In this respect we could demonstrate that rotifers, cladocerans, and copepods were differently affected. Due to the strong effect of the biomanipulation experiment we were not able to clearly demonstrate the long-term effects of changing abiotic environmental conditions on the zooplankton community of Lake Plußsee; however, our results highlight the importance of considering also food-web interactions when the aim is to analyze long-term effects of climate change on zooplankton communities, because effects of changing species interactions may superimpose the effects of abiotic environmental changes.

Bibliography

Abdi, H., and L. J. Williams. 2010. Principal component analysis. WIREs Comp. Stat. **2**: 433-459.

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

Adrian, R., and R. Deneke. 1996. Possible impact of mild winters on zooplankton succession in eutrophic lakes of the Atlantic European area. Freshwater Biol. **36**: 757-770.

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

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

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

Allan, J. D. 1976. Life history patterns in zooplankton. The American Naturalist **110**: 165-180.

Arhonditsis, G. B., M. T. Brett, C. L. DeGasperi, and D. E. Schindler. 2004. Effects of climatic variability on the thermal properties of Lake Washington. Limnol. Oceanogr. **49**: 256-270.

Assel, R., K. Cronk, and D. Norton. 2003. Recent trends in Laurentian Great Lakes ice cover. Clim. Change **57**: 185-204.

Assel, R. A., and D. M. Robertson. 1995. Changes in winter air temperatures near Lake Michigan, 1851-1993, as determined from regional lake-ice records. Limnol. Oceanogr. **40**: 165-176.

Austin, J. A., and J. Allen. 2011. Sensitivity of summer Lake Superior thermal structure to meteorological forcing. Limnol. Oceanogr. **56**: 1141-1154.

Austin, J. A., and S. M. Colman. 2007. Lake Superior summer water temperatures are increasing more rapidly than regional air temperatures: A positive ice-albedo feedback. Geophys. Res. Lett. **34**: L06604.

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

Berger, I., and G. Maier. 2001. The mating and reproductive biology of the freshwater planktonic calanoid copepod *Eudiaptomus gracilis*. Freshwater Biol. **46**: 787-794.

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

Berger, S. A., S. Diehl, H. Stibor, G. Trommer, and M. Ruhenstroth. 2010. Water temperature and stratification depth independently shift cardinal events during plankton spring succession. Glob. Chang. Biol. **16**: 1954-1965.

Bērzinš, B., and B. Pejler. 1989. Rotifer occurrence in relation to temperature. Hydrobiologia **175**: 223-231.

Black, R. W. II., and N. G. Jr. Hairston. 1988. Predator driven changes in community structure. Oecologia **77**: 468-479.

Blenckner, T., R. Adrian, D. M. Livingstone, E. Jennings, G. A. Weyhenmeyer, D. G. George, T. Jankowski, M. Järvinen, C. N. Aonghusa, T. Nõges, D. Straile, and K. Teubner. 2007. Large-scale climatic signatures in lakes across Europe: a meta-analysis. Glob. Chang. Biol. **13**: 1314-1326.

Boehrer, B., and M. Schultze. 2008. Stratification of lakes. Rev. Geophys. **46**: RG2005

Boersma, M., and J. Vijverberg. 1994. Resource depression in *Daphnia galeata, Daphnia cucullata* and their interspecific hybrid: life history consequences. J. Plankton Res. **16**: 1741-1758.

Borcard, D., F. Gillet, and P. Legendre. 2011. Numerical ecology with R. Springer.

Bortz, J. 2005. Statistik: Für Human- und Sozialwissenschaftler. 6th ed. Springer.

Bottrell, H. H., A. Duncan, Z. M. Gliwicz, E. Grygierek, A. Herzig, A. Hillbricht-Ilkowska, H. Kurasawa, P. Larsson, and T. Weglenska. 1976. A review of some problems in zooplankton production studies. Norw. J. Zool. **24**: 419-456.

Brandl, Z. 2005. Freshwater copepods and rotifers: predators and their prey. Hydrobiologia **546**: 475-489.

Brandl, Z., and C. H. Fernando. 1978. Prey selection by the cyclopoid copepods *Mesocyclops edax* and *Cyclops vicinus*. Verh. Int. Ver. Theoret. Angew. Limnol. **20**: 2505-2510.

Brohan, P., J. J. Kennedy, I. Harris, S. F. B. Tett, and P. D. Jones. 2005. Uncertainty estimates in regional and global observed temperature changes: A new dataset from 1850. J. Geophys. Res. **111**: D12106.

Brooks, J. L., and S. I. Dodson. 1965. Predation, body size, and composition of plankton. Science **150**: 28-35.

Burns, C. W., and J. J. Gilbert. 1986. Direct observations of the mechanisms of interference between *Daphnia* and *Keratella cochlearis*. Limnol. Oceanogr. **31**: 859-866.

Chen, C.-T. A., and F. J. Millero. 1986. Precise thermodynamic properties for natural waters covering only limnological range. Limnol. Oceanogr. **31**: 657-662.

Christensen, J. H., B. Hewitson, A. Busuioc, A. Chen, X. Gao, I. Held, R. Jones, R. K. Kolli, W.-T. Kwon, R. Laprise, V. Magaña Rueda, L. Mearns, C. G. Menéndez, J. Räisänen, A. Rinke, A. Sarr, and P. Whetton. 2007. Regional Climate Projections. p. 847-940, *In* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor and H. L. Miller, [eds.], Climate Change 2007: The Physical Science Basis - Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge Univ. Press.

Christoffersen, K., B. Riemann, A. Klysner, and M. Søndergaard. 1993. Potential role of fish predation and natural populations of zooplankton in structuring a plankton community in eutrophic lake water. Limnol. Oceanogr. **38**: 561-573.

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

Culver, D. A., M. M. Boucherle, D. J. Bean, and J. W. Fletcher. 1985. Biomass of freshwater crustacean zooplankton from length-weight regressions. Can. J. Fish. Aquat. Sci. **42**: 1380-1390.

De Meester, L., L. J. Weider, and R. Tollrian. 1995. Alternative antipredator defences and genetic polymorphism in a pelagic predator – prey system. Nature **378**: 483-485.

DeStasio, B. T. Jr., D. K. Hill, J. M. Kleinhans, N. P. Nibbelink, and J. J. Magnuson. 1996. Potential effects of global climate change on small north-temperate lakes: Physics, fish, and plankton. Limnol. Oceanogr. **41**: 1136-1149.

Devetter, M. 1998. Influence of environmental factors on the rotifer assemblage in an artificial lake. Hydrobiologia **387/388**: 171-178.

Diehl, S. 2002. Phytoplankton, light, and nutrients in a gradient of mixing depths: Theory. Ecology **83**: 386-398.

Dodson, S. 1992. Predicting crustacean zooplankton species richness. Limnol. Oceanogr. **37**: 848-856.

Dodson, S. I., S. E. Arnott, and K. L. Cottingham. 2000. The relationship in lake communities between primary productivity and species richness. Ecology **81**: 2662-2679.

Downing, J. A., S. B. Watson, and E. McCauley. 2001. Predicting cyanobacteria dominance in lakes. Can. J. Fish. Aquat. Sci. **58**: 1905-1908.

Dumont, H. J., I. van de Velde, and S. Dumont. 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. Oecologia **19**: 75-97.

Duncan, A. 1989. Food limitation and body size in the life cycles of planktonic rotifers and cladocerans. Hydrobiologia **186/187**: 11-28.

Edinger, J. E., D. W. Duttweiler, and J. C. Geyer. 1968. The response of water temperatures to meteorological conditions. Water Resour. Res. **4**: 1137-1143.

Edmondson, W. T. 1965. Reproductive rate of planktonic rotifers as related to food and temperature in nature. Ecol. Monogr. **35**: 61-111.

Einsle, U. 1993. Crustacea: Copepoda: Calanoida und Cyclopoida. *In* J. Schwoerbel, and P. Zwick [eds.], Süßwasserfauna von Mitteleuropa, **8**, Fischer.

Elgmork, K. 1967. Ecological aspects of diapause in copepods. Proc. Symp. Crust. **3**: 947-954.

Elgmork, K., G. Halvorsen, J. A. Eie, and A. Langeland. 1990. Coexistence with similar life cycles in two species of freshwater copepods (Crustacea). Hydrobiologia **208**: 187-199.

Elliott, J. I. 1977. Seasonal changes in the abundance of and distribution of planktonic rotifers in Grasmere (English Lake District). Freshwater Biol. **7**: 147-166.

Flössner, D. 1993. Zur Kenntnis einiger Daphnien-Hybriden (Crustacea: Cladocera). Limnologica **23**: 71-79. [On the knowledge of some hybrids of Daphnia]

Flössner, D. 2000. Die Haplopoda und Cladocera (ohne Bosminidae) Mitteleuropas. Backhuys Publishers.

Frenzel, P. 1977. Zur Bionomie von *Thermocyclops oithonoides* (G. O. SARS). Arch. Hydrobiol. **80**: 108-130.

Gaedke, U., D. Ollinger, E. Bäuerle, and D. Straile. 1998. The impact of the interannual variability in hydrodynamic conditions on the plankton development in Lake Constance in spring and summer. Adv. Limnol. **53**: 565-585.

Gaedke, U., M. Ruhenstroth-Bauer, I. Wiegand, K. Tirok, N. Aberle, P. Breithaupt, K. Lengfellner, J. Wohlers, and U. Sommer. 2010. Biotic interactions may overrule direct climate effects on spring phytoplankton dynamics. Glob. Chang. Biol. **16**: 1122-1136.

Geller, W., and H. Müller. 1981. The filtration apparatus of cladocera: filter mesh size and their implications on food selectivity. Oecologia **49**: 316-321.

George, D. G. 1973. Diapause in *Cyclops vicinus*. Oikos **24**: 136-142.

George, D. G. 2000. The impact of regional-scale changes in the weather on the long-term dynamics of *Eudiaptomus* and *Daphnia* in Eastwaite Water, Cumbria. Freshwater Biol. **45**: 111-121.

George, D. G., and D. P. Hewitt. 1999. The influence of year-to-year variations in winter weather on the dynamics of *Daphnia* and *Eudiaptomus* in Eastwaite, Cumbria. Funct. Ecol. **13**: 45-54.

George, D. G., J. F. Talling, and E. Rigg. 2000. Factors influencing the temporal coherence of five lakes in the English Lake District. Freshwater Biol. **43**: 449-461.

George, D. G., S. C. Maberly, and D. P. Hewitt. 2004. The influence of the North Atlantic Oscillation on the physical, chemical and biological characteristics of four lakes in the English Lake District. Freshwater Biol. **49**: 760-774.

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

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

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

Gilbert, J. J. 1988. Suppression of rotifer populations by *Daphnia*: A review of the evidence, the mechanisms, and the effects on zooplankton community structure. Limnol. Oceanogr. **33**: 1286-1303.

Gliwicz, Z. M. 1990. Food thresholds and body size in cladocerans. Nature **343**: 638-640.

González, I., and S. Déjean. 2009. CCA: Canonical correlation analysis. R package version 1.2. Available from http://CRAN.R-project.org/package=CCA

Gophen, M. 1977. Food and feeding habits of *Mesocyclops leuckarti* (Claus) in Lake Kinneret (Israel). Freshwater Biol. **7**: 513-518.

Güss, S., D. Albrecht, H.-J. Krambeck, D. C. Müller-Navarra, and H. Mumm. 2000. Impact of weather on a lake ecosystem, assessed by cyclo-stationary MCCA of long-term observations. Ecology **81**: 1720-1735.

Hall, D. J., S. T. Threlkeld, C. W. Burns, and P. H. Crowley. 1976. The Size-Efficiency Hypothesis and the size structure of zooplankton communities. Ann. Rev. Ecol. Syst. **7**: 177-208.

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

Hansen, A.-M., and E. Jeppesen. 1992. Changes in the abundance and composition of cyclopoid copepods following fish manipulation in eutrophic Lake Væng, Denmark. Freshwater Biol. **28**: 183-193.

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

Hendricks Franssen, H. J., and S. C. Scherrer. 2008. Freezing of lakes on the Swiss plateau in the period 1901-2006. Int. J. Climatol. **28**: 421-433.

Herzig, A. 1983. The ecological significance of the relationship between temperature and duration of embryonic development in planktonic freshwater copepods. Hydrobiologia **100**: 65-91.

Herzig, A. 1984. Temperature and life cycle strategies of *Diaphanosoma brachyurum*: an experimental study on development, growth and survival. Arch. Hydrobiol. **101**: 143-178.

Herzig, A. 1987. The analysis of planktonic rotifer populations: A plea for long-term investigations. Hydrobiologia **147**: 163-180.

Hickel, B. 1988. Unexpected disappearance of cyanophyte blooms in Plußsee (North Germany). Arch. Hydrobiol. Suppl. **80**: 545-554.

Hofmann, W. 1972. Zur Populationsökologie des Zooplanktons im Plußsee. Verh. Internat. Verein. Limnol. **18**: 410-418.

Hofmann, W. 1985. Dynamics of vertical zooplankton community structure in the Plußsee: Cluster analysis. Verh. Internat. Verein. Limnol. **22**: 2983-2986.

Hofmann, W., and H.-J. Krambeck. 1991. Manipulation of the thermocline in a eutrophic lake: The response of the zooplankton. Verh. Internat. Verein. Limnol. **24**: 786-790.

Hondzo, M., and H. G. Stefan. 1991. Three case studies of lake temperature and stratification response to warmer climate. Water Resour. Res. **27**: 1837-1846.

Hondzo, M., and H. G. Stefan. 1993. Regional water temperature characteristics of lakes subjected to climate change. Clim. Change **24**: 187-211.

Hopp, U., G. Maier, and R. Bleher. 1997. Reproduction and adult longevity of five species of planktonic cyclopoid copepods reared on different diets: a comparative study. Freshwater Biol. **38**: 289-300.

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

Huber, V., R. Adrian, and D. Gerten. 2010. A matter of timing: heat wave impact on crustacean zooplankton. Freshwater Biol. **55**: 1769-1779.

Huisman, J., J. Sharples, J. M. Stroom, P. M. Visser, W. E. A. Kardinaal, J. M. H. Verspagen, and B. Sommejer. 2004. Changes in turbulent mixing shift competition for light between phytoplankton species. Ecology **85**: 2960-2970.

Hurrell, J. W. 1995. Decadal trends in the North Atlantic Oscillation: Regional temperatures and precipitation. Science **269**: 676-679.

Hurrell, J. W., and H. van Loon. 1997. Decadal variations in climate associated with the North Atlantic Oscillation. Clim. Change **36**: 301-326.

Hurrell, J. W., and C. Deser. 2009. North Atlantic climate variability: The role of the North Atlantic Oscillation. J. Mar. Syst. **78**: 28-41.

Hutchinson, G. E. 1957. A treatise on limnology, v. 1. Geography, physics, and chemistry. Wiley.

Hyenstrand, P., P. Blomqvist, and A. Petterson. 1998. Factors determining cyanobacterial success in aquatic systems – a literature review. Arch. Hydrobiol. Spec. Issues Adv. Limnol. **15**: 41-62.

Idso, S. B. 1973. On the concept of lake stability. Limnol. Oceanogr. **18**: 681-683.

Imberger, J., and J. C. Patterson. 1990. Physical limnology. Adv. Appl. Mechanics **27**: 303-475.

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

Jankowski, T., and D. Straile. 2004. Allochronic differentiation among *Daphnia* species, hybrids and backcrosses: the importance of sexual reproduction for population dynamics and genetic architecture. J. Evolution. Biol. **17**: 312-321.

Jeppesen, E., J. P. Jensen, M. Søndergaard, T. Lauridsen, and F. Landkildehus. 2000. Trophic structure, species richness and diversity in Danish lakes: changes along a phosphorus gradient. Freshwater Biol. **45**: 201-218.

Jöhnk, K. D., J. Huisman, J. Sharples, B. Sommejer, P. M. Visser, and J. M. Stroom. 2008. Summer heatwaves promote blooms of harmful cyanobacteria. Glob. Chang. Biol. **14**: 495-512.

Karabin, A. 1978. The pressure of pelagic predators of the genus *Mesocyclops* (Copepoda, Crustacea) on small zooplankton. Ekol. Pol. **26**: 241-257.

Kessler, K. 2004. Distribution of *Daphnia* in a trade-off between food and temperature: individual habitat choice and time allocation. Freshwater Biol. **49**: 1220-1229.

Kiefer, F. 1973. Ruderfußkrebse. *In* Einführung in die Kleinlebewelt. Kosmos Verlag.

Kiefer, F., and G. Fryer. 1978. Copepoda. *In* Das Zooplankton der Binnengewässer, v. 2. Schweizerbart'sche Verlagsbuchhandlung.

King, J. R., B. J. Shuter, and A. P. Zimmerman. 1997. The response of the thermal stratification of South Bay (Lake Huron) to climatic variability. Can. J. Fish. Aquat. Sci. **54**: 1873-1882.

Krambeck, H.-J. 1974. Energiehaushalt und Stofftransport eines Sees: Beispiel einer mathematischen Analyse limnologischer Prozesse. Arch. Hydrobiol. **73**: 137-192. [Energy balance and exchange in a lake: Example of a mathematical analysis of limnological processes]

Kremser, A. 1995. Nahrungskettenmanipulation im Plußsee: Die Regulation der planktivoren Fische (*Perca fluviatilis* L. und *Rutilus rutilus* L.) durch Ressourcen und Konsumenten. PhD thesis. University of Kiel, Germany.

Kruse, S. 1988. Tagesperiodische Vertikalwanderung von *Daphnia* (Cladocera). Diploma thesis. University of Kiel, Germany.

Lacroix, G., and F. Lescher-Moutoué. 1984. Diapause in cyclopoids of a limnetic shallow ecosystem (Lake of Créteil, France). Ann. Limnol. **20**: 183-192.

Lampert, W., and U. Schober. 1978. Climatic conditions and planktonic interactions as factors controlling the regular succession of spring algal bloom and extremely clear water in Lake Constance. Verh. Int. Ver. Limnol. **20**: 969-974.

Lenters, J. D., T. K. Kratz, and C. J. Browser. 2005. Effects of climate variability on lake evaporation: Results from a long-term study of Sparkling Lake, northern Wisconsin (USA). J. Hydrol. **308**: 168-195.

Leyer, I., and K. Wesche. 2007. Multivariate Statistik in der Ökologie. Springer.

Lieder, U. 1996. Crustacea. Cladocera/Bosminidae. *In* J. Schwoerbel and P. Zwick. Süßwasserfauna von Mitteleuropa. v. 8/2-3. Fischer Verlag.

Livingstone, D. M. 1997. Break-up dates of Alpine lakes as proxy data for local and regional mean surface air temperatures. Clim. Change **37**: 407-439.

Livingstone, D. M. 2003. Impact of secular climate change on the thermal structure of a large temperate central European lake. Clim. Change **57**: 205-225.

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

Livingstone, D. M., and D. M. Imboden. 1996. The prediction of hypolimnetic oxygen profiles: A plea for a deductive approach. Can. J. Fish. Aquat. Sci. **53**: 924-932.

Löffler, A., J. Wolinska, B. Keller, K.-O. Rothhaupt, and P. Spaak. 2004. Life history patterns of parental and hybrid *Daphnia* differ between lakes. Freshwater Biol. **49**: 1372-1380.

MacIsaac, H. J., and J. J. Gilbert. 1989. Competition between rotifers and cladocerans of different body sizes. Oecologia **81**: 295-301.

Magnuson, J. J., D. M. Robertson, B. J. Benson, R. H. Wynne, D. M. Livingstone, T. Arai, R. A. Assel, R. G. Barry, V. Card, E. Kuusisto, N. G. Granin, T. D. Prowse, K. M. Stewart, and V. S. Vuglinski. 2000. Historical trends in lake and river ice cover in the Northern Hemisphere. Science **289**: 1743-1746.

Maier, G. 1989. The effects of temperature on the development times of egg, naupliar and copepodite stages of five species of cyclopoid species. Hydrobiologia **184**: 79-88.

Maier, G. 1990. Coexistence of the predatory cyclopoids *Acanthocyclops robustus* (Sars) and *Mesocyclops leuckarti* (Claus) in a small eutrophic lake. Hydrobiologia **198**: 185-203.

Maier, G. 1994. Patterns of life history among cyclopoid copepods of central Europe. Freshwater Biol. **31**: 77-86.

Maier, G. 1998. Differential success of cyclopoid copepods in the pelagic zone of eutrophic lakes. J. Mar. Syst. **15**: 135-138.

Makulla, A., and U. Sommer. 1993. Relationships between resource ratios and phytoplankton species composition during spring in five north German lakes. Limnol. Oceanogr. **38**: 846-856.

McCauley, E. 1984. The estimation of abundance and biomass of zooplankton samples, p. 228-265. *In* J. A. Downing, and F. H. Rigler: A manual on methods for the assessment of secondary productivity in fresh waters. Blackwell Scientific Publications, Oxford.

McQueen, D. J., R. France, and C. Kraft. 1992. Confounded impacts of planktivorous fish on freshwater biomanipulations. Arch. Hydrobiol. **125**: 1-24.

Meehl, G. A., T. F. Stocker, W. D. Collins, P. Friedlingstein, A. T. Gaye, J. M. Gregory, A. Kitoh, R. Knutti, J. M. Murphy, A. Noda, S. C. B. Raper, I. G. Watterson, A. J. Weaver, and Z.-C. Zhao. 2007. Global climate projections, p. 747-846. *In* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller [eds.], Climate change 2007: The physical science basis - Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge Univ. Press.

Mehner, T., and R. Thiel. 1999. A review of predation impact by 0+ fish on zooplankton in fresh and brackish waters of the temperate northern hemisphere. Environ. Biol. Fishes **56**: 169-181.

Monteith, D. T., C. D. Evans, and B. Reynolds. 2000. Are temporal variations in the nitrate content of UK upland freshwaters linked to the North Atlantic Oscillation? Hydrol. Processes **14**: 1745-1749.

Mortimer, C. H. 1981. The oxygen content of air-saturated fresh waters over ranges of temperature and atmospheric pressure of limnological interest. Mitt. Internat. Verein. Limnol. **22**: 1-23.

Mumm, H. 1996. Zooplanktonentwicklung im Plußsee: Invertebrate Räuber, die Wirkung der Biomanipulation und Langzeittrends. PhD thesis. University of Kiel, Germany.

Mumm, H. 1997. Effects of competitors and *Chaoborus* predation on the cladocerans of a eutrophic lake: an enclosure study. Hydrobiologia **360**: 253-264.

Müller-Navarra, D. C., S. Güss, and H. von Storch. 1997. Interannual variability of seasonal succession events in a temperate lake and its relation to temperature variability. Glob. Chang. Biol. **3**: 429-438.

Müller-Navarra, D., and W. Lampert. 1996. Seasonal patterns of food limitation in *Daphnia galeata*: separating food quantity and food quality effects. J. Plankton Res. **18**: 1137-1157.

Neill, W. E. 1990. Induced vertical migration in copepods as a defense against invertebrate predation. Nature **345**: 524-526.

Nilssen, J. P., and K. Elgmork. 1977. *Cyclops abyssorum* – life cycle dynamics and habitat selection. Mem. Ist. Ital. Idrobiol. **34**: 197-238.

Nilssen, J. P., and S. B. Wærvågen. 2000. Superficial ecosystem similarities *vs* autecological stripping: the ‘twin species’ *Mesocyclops leuckarti* (Claus) and *Thermocyclops oithonoides* (Sars) – seasonal habitat utilisation and life history traits. J. Limnol. **59**: 79-102.

O’Brien, W. J. 1979. The predator-prey interaction of planktivorous fish and zooplankton. Recent research with planktivorous fish and their zooplankton prey shows the evolutionary thrust and parry of the predator-prey relationship. Am. Scientist **67**: 572-568.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, R. G. O'Hara, G. L. Simpson, P. Solymos, M. Henry, H. Stevens, and H. Wagner. 2010. vegan: Community Ecology Package. R package version 1.17-0. Available from http://CRAN.R-project.org/package=vegan

Overbeck, J., and R. Chróst. 1993. Ecological studies, v. 105. Microbial ecology of Lake Plußsee. Springer.

Palecki, M. A., and R. G. Barry. 1986. Freeze-up and break-up of lakes as an index of temperature changes during the transition seasons: a case study for Finland. J. Appl. Climatol. **25**: 893-902.

Pauli, H.-R. 1989. A new method to estimate individual dry weights of rotifers. Hydrobiologia **186**: 355-361.

Peeters, F., D. M. Livingstone, G.-H. Goudsmit, R. Kipfer, R. Forster. 2002. Modeling 50 years of historical temperature profiles in a large central European lake. Limnol. Oceanogr. **47**: 186-197.

Peeters, F., D. Straile, A. Lorke, and D. M. Livingstone. 2007. Earlier onset of the spring phytoplankton bloom in lakes of the temperate zone in a warmer climate. Glob. Chang. Biol. **13**: 1898-1909.

Pejler, B., and B. Bērzinš. 1993. On the ecology of Trichocercidae (Rotifera). Hydrobiologia **263**: 55-59.

Plaßmann, T., G. Maier, and H. B. Stich. 1997. Predation impact of *Cyclops vicinus* on the rotifer community in Lake Constance in spring. J. Plankton Res. **19**: 1069-1079.

Porter, K. G., Y. S. Feig, and E. F. Vetter. 1983. Morphology, flow regimes, and filtering rates of *Daphnia, Ceriodaphnia,* and *Bosmina* fed natural bacteria. Oecologia **58**: 156-163.

Post, D. M., S. R. Carpenter, D. L. Christensen, K. L. Cottingham, J. F. Kitchell, D. E. Schindler, and J. R. Hodgson. 1997. Seasonal effects of variable recruitment of a dominant piscivore on pelagic food web structure. Limnol. Oceanogr. **42**: 722-729.

R Development Core Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Available from http://cran.r-prject.org/

Rayner, N. A., P. Brohan, D. E. Parker, C. K. Folland, J. J. Kennedy, M. Vanicek, T. J. Ansell, and S. F. B. Tett. 2006. Improved analyses of changes and uncertainties in sea surface temperature measured in situ since the mid-nineteenth century: The HadSST2 dataset. J. Climate **19**: 446-469.

Rempfer, J., D. M. Livingstone, C. Blodau, R. Forster, P. Niederhauser, and R. Kipfer. 2010. The effect of the exceptionally mild European winter of 2006-2007 on temperature and oxygen profiles in lakes in Switzerland: A foretaste of the future? Limnol. Oceanogr. **55**: 2170-2180.

Robertson, D. M., and R. A. Ragotzkie. 1990. Changes in the thermal structure of moderate to large sized lakes in response to changes in air temperature. Aquat. Sci. **52**: 360-380.

Robertson, D. M., R. A. Ragotzkie, and J. J. Magnuson. 1992. Lake ice records used to detect historical and future climatic changes. Clim. Change **21**: 407-427.

Ruttner-Kolisko, A. 1972. Rotatoria. *In* H. Bick, G. Breitig, T. Grospietsch, C. Holmquist, H. Löffler, E. Reisinger, A. Ruttner-Kolisko, O. A. Sæther & J. Schwoerbel. Das Zooplankton der Binnengewässer, v. 1. *In* H.-J. Elster & W. Ohle, Die Binnengewässer. v. 26/1. Schweizerbart'sche Buchhandlung.

Ruttner-Kolisko, A. 1977. Suggestions for biomass calculation of plankton rotifers. Ergeb. Limnol. **8**: 71-76.

Rösner, R., D. C. Müller-Navarra, and E. Zorita. 2012. Trend analysis of weekly temperatures and oxygen concentrations during summer stratification in Lake Plußsee: A long-term study. Limnology and Oceanography **57**: 1479-1491.

Sanders, R. W., K. G. Porter, S. J. Bennett, and A. E. DeBiase. 1989. Seasonal patterns of bacterivory by flagellates, ciliates, rotifers, and cladocerans in a freshwater planktonic community. Limnol. Oceanogr. **34**: 673-687.

Santer, B. 1990. Lebenszyklusstrategien cyclopoider Copepoden. PhD thesis. University of Kiel, Germany.

Santer, B. 1994. Influences of food type and concentration on the development of *Eudiaptomus gracilis* and implications for interactions between calanoid and cyclopoid copepods. Arch. Hydrobiol. **131**: 141-159.

Santer, B. 1998. Life cycle strategies of free-living copepods in fresh waters. J. Mar. Syst. **15**: 327-336.

Santer, B., and W. Lampert. 1995. Summer diapause in cyclopoid copepods: adaptive response to a food bottleneck? J. Anim. Ecol. **64**: 600-613.

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

Scheffer, M., D. Straile, E. H. van Nes, and H. Hosper. 2001. Climatic warming causes regime shifts in lake food webs. Limnol. Oceanogr. **46**: 1280-1283.

Schmidt, W. 1928. Über die Temperatur- und Stabilitätsverhältnisse von Seen. Geogr. Ann. **10**: 145-177. [Conditions of lake temperature and stability]

Schneider, P., and S. J. Hook. 2010. Space observations of inland water bodies show rapid surface warming since 1985. Geophys. Res. Lett. **37**: L22405.

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

Seitz, A. 1980. The coexistence of three species of *Daphnia* in the Klostersee. Oecologia **45**: 117-130.

Shannon, C. E., and W. Weaver. 1949. The mathematical theory of communication. The University of Illinois Press, Urbana, 117 pp.

Sherry, A., and R. K. Henson. 2005. Conducting and interpreting Canonical Correlation Analysis in Personality Research: A user-friendly primer. Journal of Personality Assessment **84**: 37-48.

Simpson, E. H. 1949. Measurement of diversity. Nature **163**: 688.

Sommer, U. 1991. A comparison of the Droop and the Monod models of nutrient limited growth applied to natural populations of phytoplankton. Funct. Ecol. **5**: 535-544.

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

Sommer, U., and A. Lewandowska. 2011. Climate change and the phytoplankton spring bloom: warming and overwintering zooplankton have similar effects on phytoplankton. Glob. Chang. Biol. **17**: 154-162.

Spaak, P., and J. R. Hoekstra. 1995. Life history variation and the coexistence of a *Daphnia* hybrid with its parental species. Ecology **76**: 553-564.

Spaak, P., and J. R. Hoekstra. 1997. Fish predation on a *Daphnia* hybrid species complex: A factor explaining coexistence? Limnol. Oceanogr. **42**: 753-762.

Spaak, P., J. Vanoverbeke, and M. Boersma. 2000. Predator-induced life history changes and the coexistence of five taxa in a *Daphnia* species complex. Oikos **89**: 164-174.

Spaak, P., A. Denk, M. Boersma, and L. J. Weider. 2004. Spatial and temporal patterns of sexual reproduction in a hybrid *Daphnia* species complex. J. Plankton Res. **26**: 625-635.

Stefan, H. G., M. Hondzo, X. Fang, J. G. Eaton, and J. H. McCormick. 1996. Simulated long-term temperature and dissolved oxygen characteristics of lakes in the north-central United States and associated fish habitat limits. Limnol. Oceaonogr. **41**: 1124-1135.

Stemberger, R. S. 1985. Prey selection by the copepod *Diacyclops thomasi*. Oecologia **65**: 492-497.

Stemberger, R. S., and J. J. Gilbert. 1985. Body size, food concentration, and population growth in planktonic rotifers. Ecology **66**: 1151-1159.

Stibor, H. 1992. Predator induced life-history shifts in a freshwater cladoceran. Oecologia **92**: 162-165.

Stich, H.-B., and W. Lampert. 1981. Predator evasion as an explanation of diurnal vertical migration by zooplankton. Nature **293**: 396-398.

Stich, H.-B., and W. Lampert. 1984. Growth and reproduction of migrating and non-migrating *Daphnia* species under simulated food and temperature conditions of diurnal vertical migration. Oecologia **61**: 192-196.

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

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

Straile, D., D. M. Livingstone, G. A. Weyhenmeyer, and D. G. George. 2003a. The response of freshwater ecosystems to climate variability associated with the North Atlantic Oscillation, p. 263-279. *In* J. W. Hurrell, Y. Kushnir, G. Ottersen, and M. Visbeck [eds.], The North Atlantic Oscillation: Climatic significance and environmental impact. AGU Geophys. Monogr. Ser. 134.

Straile, D., K. Jöhnk, and H. Rossknecht. 2003b. Complex effects of winter warming on the physicochemical characteristics of a deep lake. Limnol. Oceanogr. **48**: 1432-1438.

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

Søndergaard, M., E. Jeppesen, E. Mortensen, E. Dall, P. Kristensen, and O. Sortkjær. 1990. Phytoplankton biomass reduction after planktivorous fish reduction in a shallow, eutrophic lake: a combined effect of reduced internal P-loading and increased zooplankton grazing. Hydrobiologia **200/201**: 229-240.

Thackeray, S. J., I. D. Jones, and S. C. Maberly. 2008. Long-term change in the phenology of spring phytoplankton: species-specific responses to nutrient enrichment and climatic change. Journal of Ecology **96**: 523-535.

Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecol. Monograph **57**: 189-214.

Tilman, D., R. Kiesling, R. Sterner, S. S. Kilham, and F. A. Johnson. 1986. Green, bluegreen and diatom algae: Taxonomic differences in competitive ability for phosphorus, silicon and nitrogen. Arch. Hydrobiol. **106**: 473-485.

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

Trenberth, K. E., P. D. Jones, P. Ambenje, R. Bojariu, D. Easterling, A. Klein Tank, D. Parker, F. Rahimzadeh, J. A. Renwick, M. Rusticucci, B. Soden, and P. Zhai. 2007. Observations: Surface and atmospheric climate change, p. 235-336. *In* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller [eds.], Climate change 2007: The physical science basis - Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge Univ. Press.

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

Verburg, P., R. E. Hecky, and H. Kling. 2003. Ecological consequences of a century of warming in Lake Tanganyika. Science **301**: 505-507.

Vijverberg, J. 1977. Population structure, life histories and abundance of copepods in Tjeukemeer, the Netherlands. Freshwater Biol. **7**: 579-597.

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

Visbeck, M. H., J. W. Hurrell, L. Polvani, and H. M. Cullen. 2001. The North Atlantic Oscillation: Past, present, and future. PNAS **98**: 12876-12877.

Voigt, M., and W. Koste. 1978. Rotatoria. Die Rädertiere Mitteleuropas. Überordnung Monogononta. 2nd ed. Gebrüder Borntraeger

Vollmer, M. K., H. A. Bootsma, R. E. Hecky, G. Patterson, J. D. Halfman, J. M. Edmond, D. H. Eccles, and R. F. Weiss. 2005. Deep-water warming trend in Lake Malawi, East Africa. Limnol. Oceanogr. **50**: 727-732.

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

Walsby, A. E. 1994. Gas vesicles. Microbiological Reviews **58**: 94-144.

Walz, N. 1995. Rotifer populations in plankton communities: Energetics and life history strategies. Experientia **51**: 437-453.

Walz, N., H.-J. Elster, and M. Mezger. 1987. The development of the rotifer community structure in Lake Constance during its eutrophication. Arch. Hydrobiol. Suppl. (Monogr. Beitr.) **74**: 452-487

Weider, L. J. 1993. Niche breadth and life history variation in a hybrid *Daphnia* complex. Ecology **74**: 935-943.

Weider, L. J., and H. B. Stich. 1992. Spatial and temporal heterogeneity of *Daphnia* in Lake Constance: Intra- and interspecific comparisons. Limnol. Oceanogr. **37**: 1327-1334.

Wetzel, R. G. 2001. Limnology: Lake and river ecosystems, 3rd ed. Academic Press.

Weyhenmeyer, G. A. 2004. Synchrony in relationships between the North Atlantic Oscillation and water chemistry among Sweden’s largest lakes. Limnol. Oceaonogr. **49**: 1191-1201.

Weyhenmeyer, G. A., T. Blenckner, and K. Pettersson. 1999. Changes of the plankton spring outburst related to the North Atlantic Oscillation. Limnol. Oceaonogr. **44**: 1788-1792.

Weyhenmeyer, G. A., R. Adrian, U. Gaedke, D. M. Livingstone, and S. C. Maberly. 2002. Response of phytoplankton in European lakes to a change in the North Atlantic Oscillation. Verh. Internat. Verein. Limnol. **28**: 1436-1439.

Weyhenmeyer, G. A., M. Meili, and D. M. Livingstone. 2004. Nonlinear temperature response of lake ice breakup. Geophys. Res. Lett. **31**: L07203.

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

Williamson, C. E. 1983. invertebrate predation on planktonic rotifers. Hydrobiologia **104**: 385-396.

Wiltshire, K. H., and B. F. J. Manly. 2004. The warming trend at Helgoland Roads, North Sea: phytoplankton response. Helgol. Mar. Res. **58**: 269-273.

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

Winder, M., and D. E. Schindler. 2004. Climatic effects on the phenology of lake processes. Glob. Chang. Biol. **10**: 1844-1856.

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

Winfield, I. J., and C. R. Townsend. 1983. The cost of copepod reproduction: increased susceptibility to fish predation. Oecologia **59**: 406-411.

Winter, T. C., D. C. Buso, D. O. Rosenberry, G. E. Likens, A. M. Jr. Sturrock, and D. P. Mau. 2003. Evaporation determined by the energy-budget method for Mirror Lake, New Hampshire. Limnol. Oceanogr. **48**: 995-1009.

Wolf, H. G. 1987. Interspecific hybridization between *Daphnia hyalina*, *D. galeata*, and *D. cucullata* and seasonal abundances of these species and their hybrids. Hydrobiologia **145**: 213-217.

Zeis, B., W. Horn, U. Gigengack, M. Koch, and R. J. Paul. 2010. A major shift in *Daphnia* genetic structure after the first ice-free-winter in a German reservoir. Freshwater Biol. **55**: 2296-2304.

Appendix

Table A1. Rotifer, cladoceran, and copepod species found in Lake Plußsee in October. The right column contains the abbreviations we used for figures and tables.

	rotifer species	originial description	abbreviations
rotifers	*Anuraeopsis fissa*	GOSSE 1851	Anu.fis
	Ascomorpha ecaudis	PERTY 1850	Asc.eca
	Ascomorpha ovalis	CARLIN 1943	Asc.ova
	Ascomorpha saltans	BARTSCH 1850	Asc.sal
	Asplanchna spp.	GOSSE 1850	Asp.spp
	Brachionus angularis	GOSSE 1851	Bra.ang
	Brachionus calyciflorus	PALLAS 1766	Bra.cal
	Brachionus falcatus	ZACHARIAS 1898	Bra.fal
	Collotheca spp.	HARRING 1913	Col.spp
	Conochilus unicornis	ROUSSELET 1892	Con.hip
	Conochilus hippocrepis	SCHRANK 1830	Con.uni
	Euchlanis dilatata	EHRENBERG 1832	Euc.dil
	Filinia longiseta	EHRENBERG 1832	Fil.lon
	Filinia terminalis	PLATE 1886	Fil.ter
	Gastropus stylifer	IMHOF 1891	Gas.sty
	Kellicottia longispina	KELLICOTT 1879	Kel.lon
	Keratella cochlearis cochlearis	GOSSE 1851	Ker.coc
	Keratella hiemalis	CARLIN 1943	Ker.hie
	Keratella quadrata	MÜLLER 1786	Ker.qua
	Keratella cochlearis tecta	GOSSE 1851	Ker.tec
	Lecane spp.	NITZSCH 1827	Lec.spp
	Monostyla spp.	EHRENBERG 1830	Mon.spp
	Lepadella spp.	BORY DE ST. VINCENT 1826	Lep.spp
	Platyias quadricornis	EHRENBERG 1832	Pla.qua
	Polyarthra dolichoptera	IDELSON 1925	Pol.dol
	Polyarthra euryptera	WIERZEJSKI 1893	Pol.eur
	Polyarthra major	BURCKHARDT 1900	Pol.maj
	Polyarthra remata	SKORIKOW 1896	Pol.rem
	Polyarthra vulgaris	CARLIN 1943	Pol.vul
	Pompholyx sulcata	HUDSON 1885	Pom.sul
	Synchaeta pectinata	EHRENBERG 1832	Syn.pec
	Synchaeta oblonga	EHRENBERG 1832	Syn.obl
	Testudinella patina	HERMANN 1783	Tes.pat
	Trichocerca capucina	WIERZEJSKI 1893	Tri.cap
	Trichocerca cylindrica	IMHOF 1891	Tri.cyl
	Trichocerca pusilla	JENNINGS 1903	Tri.pus
	Trichocerca similis	WIERZEJSKI 1893	Tri.sim
	Trichotria pocillum	MÜLLER 1776	Tri.poc

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cladocerans	*Bosmina coregoni*	BAIRD 1857	Bos.cor
	Bosmina longirostris	MÜLLER 1776	Bos.lon
	Ceriodaphnia quadrangula	MÜLLER 1785	Cer.qua
	Chydorus sphaericus	MÜLLER 1785	Chy.sph
	Daphnia cucullata	LEYDIG 1860	Dap.cuc
	Daphnia galeata	SARS 1863	Dap.gal
	Daphnia hyalina	SARS 1862	Dap.hya
	D. galeata × *D. cucullata*	WOLF AND MORT 1986	Dap.G×C
	D. hyalina × *D. galeata*	WOLF AND MORT 1986	Dap.H×G
	D. cucullata × *D. hyalina*	WOLF AND MORT 1986	Dap.C×H
	Diaphanosoma brachyurum	LIEVEN 1848	Dia.bra

copepods	*Eudiaptomus gracilis*	SARS 1863	Eud.gra
	Cyclops abyssorum	SARS 1863	Cyc.aby
	Cyclops kolensis	LILLJEBORG 1901	Cyc.kol
	Cyclops vicinus	ULJANIN 1875	Cyc.vic
	Diacyclops bicuspidatus	CLAUS 1857	Dia.bic
	Mesocyclops leuckarti	CLAUS 1857	Mes.leu
	Thermocyclops oithonoides	SARS 1863	The.oit

Table A2: Body length ranges of rotifer species and their means used to calculate the dry weights. Reference denotes the source of information: 1: Ruttner-Kolisko (1974), 2: Voigt and Koste (1978), 3: G. Maier. The conversion factor denotes the factor used to transform fresh weight of rotifers to dry weights.

Rotifer species	range of species length (µm)	reference	mean species length (µm)	fresh weight (µg Ind^{1})	Conversion factor	dry weight (µg Ind^{-1})
Anuraeopsis fissa	80-100	1	90	0.022	16.1	0.004
Ascomorpha ecaudis	130-200	1	165	0.539	9.1	0.049
Ascomorpha ovalis	100-200	1	150	0.405	9.1	0.037
Ascomorpha saltans	100-150	1	125	0.234	9.1	0.021
Asplanchna spp.	600-700	2	650	63.164	2.8	1.769
Brachionus angularis	100-200	1	150	0.405	16.1	0.065
Brachionus calyciflorus	200-500	1	350	5.145	9.1	0.468
Brachionus falcatus	200-400	1	300	3.240	9.1	0.295
Collotheca spp.	100-500	1	300	0.142	9.1	0.013
Conochilus unicornis	250-1300	2	775	2.015	9.1	0.183
Conochilus hippocrepis	410-800	2	605	1.573	9.1	0.143
Euchlanis dilatata	100-200	2	150	0.338	16.1	0.054
Filinia longiseta	70-250	1	160	0.532	9.1	0.048
Filinia terminalis	70-250	1	160	0.532	9.1	0.048
Gastropus stylifer	100-250	1	175	1.072	16.1	0.173
Kellicottia longispina	400-800	1	126	0.060	32.3	0.019
Keratella cochlearis cochlearis	126	3	100	0.020	32.3	0.006
Keratella hiemalis	200	1	200	1.760	16.1	0.283
Keratella quadrata	100-300	1	200	1.760	16.1	0.283
Keratella cochlearis tecta	82-120	2	101	0.021	32.3	0.007

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Lecane spp.	100	2	100	0.120	16.1	0.019
Monostyla spp.	100	2	100	0.120	16.1	0.019
Lepadella spp.	100	2	100	0.120	9.1	0.011
Platyias quadricornis	200-350	1	275	2.496	16.1	0.402
Polyarthra dolichoptera	90-120	1	105	0.324	9.1	0.029
Polyarthra euryptera	180-200	1	190	1.921	9.1	0.175
Polyarthra major	150-170	1	160	1.147	9.1	0.104
Polyarthra remata	50	1	50	0.035	9.1	0.003
Polyarthra vulgaris	100-150	1	125	0.547	9.1	0.050
Pompholyx sulcata	100	1	100	0.150	16.1	0.024
Synchaeta pectinata	300-500	1	400	6.400	9.1	0.582
Synchaeta oblonga	250	1	250	1.563	9.1	0.142
Testudinella patina	100-250	1	175	0.429	16.1	0.069
Trichocerca capucina	197	3	197	0.502	16.1	0.081
Trichocerca cylindrica	214	3	214	0.500	16.1	0.080
Trichocerca pusilla	82	3	82	0.079	16.1	0.013
Trichocerca similis	160	3	160	0.216	16.1	0.035
Trichotria pocillum	200-350	1	275	2.496	16.1	0.402

Table A3: Body length ranges of cladoceran species and their means used to calculate the dry weights. Body lengths were obtained by G. Maier. Reference denotes the source of information from which we obtained the regression formula: 1: Bottrell et al. (1976), 2: Dumont et al. (1975).

Cladoceran species	range of species length (µm)	reference	mean species length (µm)	dry weight (µg Ind^{-1})
Bosmina coregoni (juveniles)	200-420	1	310	0.625
Bosmina coregoni (females without eggs)	280-970	1	625	5.265
Bosmina coregoni (females with eggs)	280-970	1	625	5.265
Bosmina coregoni (males)	200-420	1	310	0.625
Bosmina coregoni (females with ephippia)	280-970	1	625	5.265
Bosmina longirostris (juveniles)	290-360	1	325	0.721
Bosmina longirostris (females without eggs)	320-450	1	385	1.207
Bosmina longirostris (females with eggs)	320-450	1	385	1.207
Bosmina longirostris (males)	290-360	1	325	0.721
Bosmina longirostris (females with ephippia)	320-450	1	385	1.207
Ceriodaphnia quadrangula (juveniles)	270-460	2	365	0.448
Ceriodaphnia quadrangula (females without eggs)	340-650	2	495	1.240
Ceriodaphnia quadrangula (females with eggs)	340-650	2	495	1.240
Ceriodaphnia quadrangula (males)	270-460	2	365	0.448
Ceriodaphnia quadrangula (females with ephippia)	340-650	2	495	1.240
Chydorus spaericus (juveniles)	160-340	2	250	0.385
Chydorus spaericus (females without eggs)	160-340	2	250	0.385
Chydorus spaericus (females with eggs)	160-340	2	250	0.385
Chydorus spaericus (males)	160-340	2	250	0.385
Chydorus spaericus (females with ephippia)	160-340	2	250	0.385

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Daphnia cucullata (juvenile stage 1)	400-700	1	550	0.800
Daphnia cucullata (juvenile stage 2)	700-1000	1	850	2.741
Daphnia cucullata (adult stage 1)	100-1300	1	1150	6.446
Daphnia cucullata (adult stage 2)	1300-1600	1	1450	12.420
Daphnia cucullata (adult stage 3)	1600-1900	1	1750	21.144
Daphnia cucullata (males)	700-1000	1	850	2.741
Daphnia cucullata (females with ephippia)	1600-1900	1	1750	21.144
Daphnia galeata (juvenile stage 1)	400-700	1	550	0.800
Daphnia galeata (juvenile stage 2)	700-1000	1	850	2.741
Daphnia galeata (adult stage 1)	100-1300	1	1150	6.446
Daphnia galeata (adult stage 2)	1300-1600	1	1450	12.420
Daphnia galeata (adult stage 3)	1600-1900	1	1750	21.144
Daphnia galeata (males)	700-1000	1	850	2.741
Daphnia galeata (females with ephippia)	1600-1900	1	1750	21.144
Daphnia hyalina (juvenile stage 1)	400-700	1	550	0.800
Daphnia hyalina (juvenile stage 2)	700-1000	1	850	2.741
Daphnia hyalina (adult stage 1)	100-1300	1	1150	6.446
Daphnia hyalina (adult stage 2)	1300-1600	1	1450	12.420
Daphnia hyalina (adult stage 3)	1600-1900	1	1750	21.144
Daphnia hyalina (males)	700-1000	1	850	2.741
Daphnia hyalina (females with ephippia)	1600-1900	1	1750	21.144
D. galeata × *D. cucullata* (juvenile stage 1)	400-700	1	550	0.800
D. galeata × *D. cucullata* (juvenile stage 2)	700-1000	1	850	2.741
D. galeata × *D. cucullata* (adult stage 1)	100-1300	1	1150	6.446
D. galeata × *D. cucullata* (adult stage 2)	1300-1600	1	1450	12.420
D. galeata × *D. cucullata* (adult stage 3)	1600-1900	1	1750	21.144
D. galeata × *D. cucullata* (males)	700-1000	1	850	2.741
D. galeata × *D. cucullata* (females with ephippia)	1600-1900	1	1750	21.144
D. hyalina × *D. galeata (juvenile stage 1)*	400-700	1	550	0.800
D. hyalina × *D. galeata (juvenile stage 2)*	700-1000	1	850	2.741
D. hyalina × *D. galeata (adult stage 1)*	100-1300	1	1150	6.446
D. hyalina × *D. galeata (adult stage 2)*	1300-1600	1	1450	12.420
D. hyalina × *D. galeata (adult stage 3)*	1600-1900	1	1750	21.144
D. hyalina × *D. galeata (males)*	700-1000	1	850	2.741
D. hyalina × *D. galeata (females with ephippia)*	1600-1900	1	1750	21.144
D. cucullata × *D. hyalina (juvenile stage 1)*	400-700	1	550	0.800
D. cucullata × *D. hyalina (juvenile stage 2)*	700-1000	1	850	2.741
D. cucullata × *D. hyalina (adult stage 1)*	100-1300	1	1150	6.446
D. cucullata × *D. hyalina (adult stage 2)*	1300-1600	1	1450	12.420
D. cucullata × *D. hyalina (adult stage 3)*	1600-1900	1	1750	21.144
D. cucullata × *D. hyalina (males)*	700-1000	1	850	2.741
D. cucullata × *D. hyalina (females with ephippia)*	1600-1900	1	1750	21.144
Diaphanosoma brachyurum (juveniles)	370-610	2	490	0.577
Diaphanosoma brachyurum (females without eggs)	640-1200	2	920	3.936
Diaphanosoma brachyurum (females with eggs)	640-1200	2	920	3.936
Diaphanosoma brachyurum (males)	370-610	2	490	0.577
Diaphanosoma brachyurum (females with ephippia)	640-1200	2	920	3.936

Table A4: Body length ranges of copepod species and their means used to calculate the dry weights. Body lengths were obtained by G. Maier. “C” refers to the copepodite stage, whereas the Roman numerals denote the respective stage. Reference denotes the source of information from which we obtained the regression formula: 1: Culver et al. (1985), 2: McCauley (1984), 3: Bottrell et al. (1976).

Copepod species	range of species length (µm)	reference	mean species length (µm)	dry weight (µg Ind^{1})
calanoid nauplia	140-480	1	310	0.405
cyclopoid nauplia	110-420	1	265	0.297
Eudiaptomus gracilis (C I)	420-630	2	525	0.806
Eudiaptomus gracilis (C II)	510-830	2	670	1.400
Eudiaptomus gracilis (C III)	690-990	2	840	2.336
Eudiaptomus gracilis (C IV)	830-1170	2	1000	3.466
Eudiaptomus gracilis (C V)	870-1230	2	1050	3.871
Eudiaptomus gracilis (females without eggs)	1070-1580	2	1325	6.554
Eudiaptomus gracilis (females with eggs)	1070-1580	2	1325	6.554
Eudiaptomus gracilis (males)	1010-1510	2	1260	5.849
Cyclops abyssorum (C I)	420-660	3	540	2.223
Cyclops abyssorum (C II)	540-920	3	730	4.440
Cyclops abyssorum (C III)	640-1030	3	835	6.044
Cyclops abyssorum (C IV)	750-1340	3	1045	10.113
Cyclops abyssorum (C V)	870-1770	3	1320	17.286
Cyclops abyssorum (females without eggs)	1060-1900	3	1480	22.475
Cyclops abyssorum (females with eggs)	1060-1900	3	1480	22.475
Cyclops abyssorum (males)	770-1450	3	1110	11.615
Cyclops kolensis (C I)	420-660	3	540	2.223
Cyclops kolensis (C II)	540-920	3	730	4.440
Cyclops kolensis (C III)	640-1030	3	835	6.044
Cyclops kolensis (C IV)	750-1340	3	1045	10.113
Cyclops kolensis (C V)	870-1770	3	1320	17.286
Cyclops kolensis (females without eggs)	1060-1900	3	1480	22.475
Cyclops kolensis (females with eggs)	1060-1900	3	1480	22.475
Cyclops kolensis (males)	770-1450	3	1110	11.615
Cyclops vicinus (C I)	420-660	3	540	2.223
Cyclops vicinus (C II)	540-920	3	730	4.440
Cyclops vicinus (C III)	640-1030	3	835	6.044
Cyclops vicinus (C IV)	750-1340	3	1045	10.113
Cyclops vicinus (C V)	870-1770	3	1320	17.286
Cyclops vicinus (females without eggs)	1060-1900	3	1480	22.475
Cyclops vicinus (females with eggs)	1060-1900	3	1480	22.475
Cyclops vicinus (males)	770-1450	3	1110	11.615
Diacyclops bicuspidatus (C I)	300-460	3	380	0.401
Diacyclops bicuspidatus (C II)	360-510	3	435	0.544
Diacyclops bicuspidatus (C III)	380-680	3	530	0.850
Diacyclops bicuspidatus (C IV)	480-910	3	695	1.566
Diacyclops bicuspidatus (C V)	510-110	3	805	2.182
Diacyclops bicuspidatus (females without eggs)	660-1390	3	1025	3.765
Diacyclops bicuspidatus (females with eggs)	660-1390	3	1025	3.765
Diacyclops bicuspidatus (males)	510-1070	3	790	2.092

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Mesocyclops leuckarti (C I)	300-460	3	380	0.401
Mesocyclops leuckarti (C II)	360-510	3	435	0.544
Mesocyclops leuckarti (C III)	380-680	3	530	0.850
Mesocyclops leuckarti (C IV)	480-910	3	695	1.566
Mesocyclops leuckarti (C V)	510-110	3	805	2.182
Mesocyclops leuckarti (females without eggs)	660-1390	3	1025	3.765
Mesocyclops leuckarti (females with eggs)	660-1390	3	1025	3.765
Mesocyclops leuckarti (males)	510-1070	3	790	2.092
Thermocyclops oithonoides (C I)	300-460	3	380	0.401
Thermocyclops oithonoides (C II)	360-510	3	435	0.544
Thermocyclops oithonoides (C III)	380-680	3	530	0.850
Thermocyclops oithonoides (C IV)	480-910	3	695	1.566
Thermocyclops oithonoides (C V)	510-110	3	805	2.182
Thermocyclops oithonoides (females without eggs)	660-1390	3	1025	3.765
Thermocyclops oithonoides (females with eggs)	660-1390	3	1025	3.765
Thermocyclops oithonoides (males)	510-1070	3	790	2.092

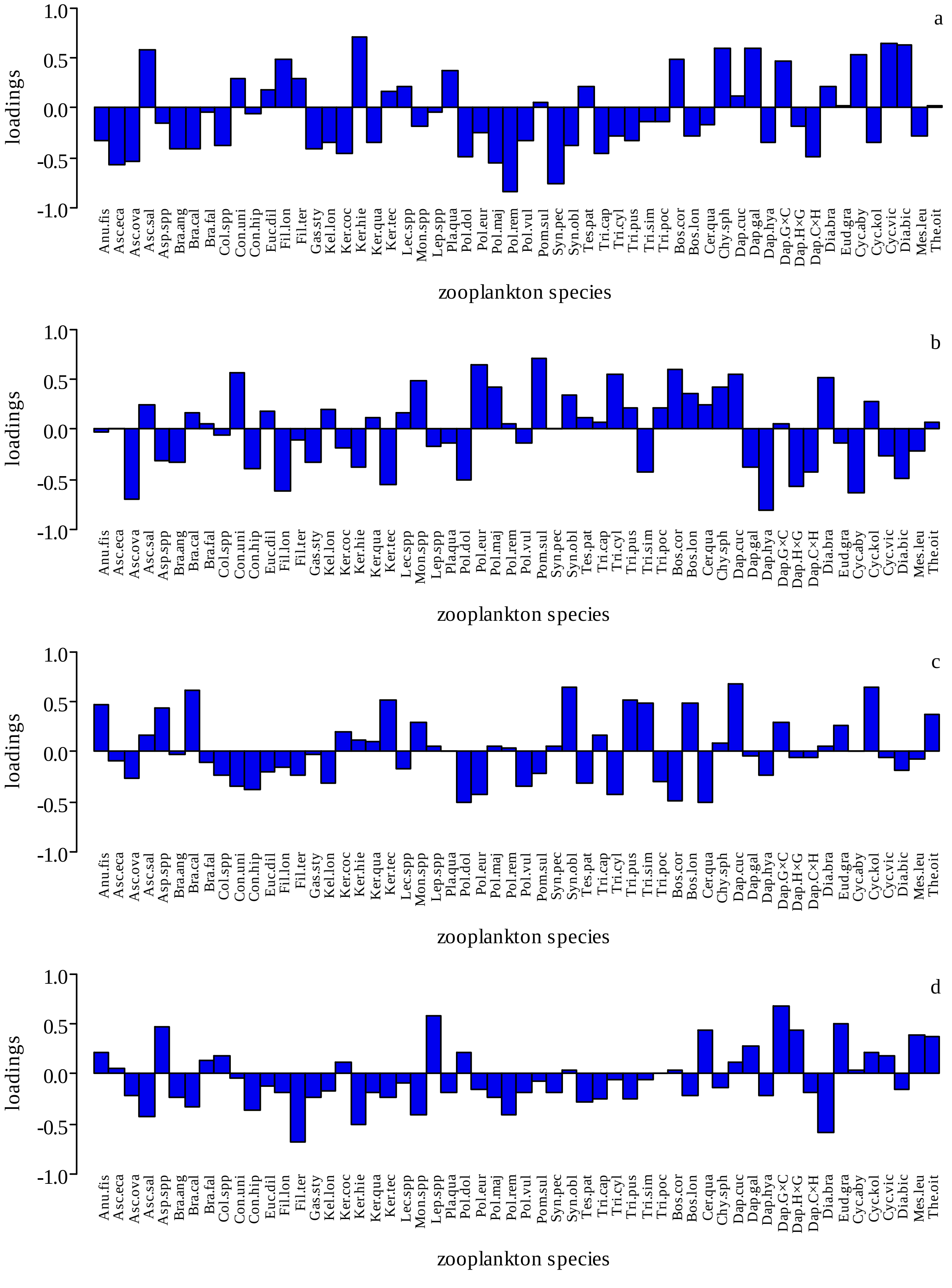

Fig. A1: Factor loadings of a) the first, b) the second, c) the third, and d) the fourth principal component derived from PCA performed on *Zoo*.

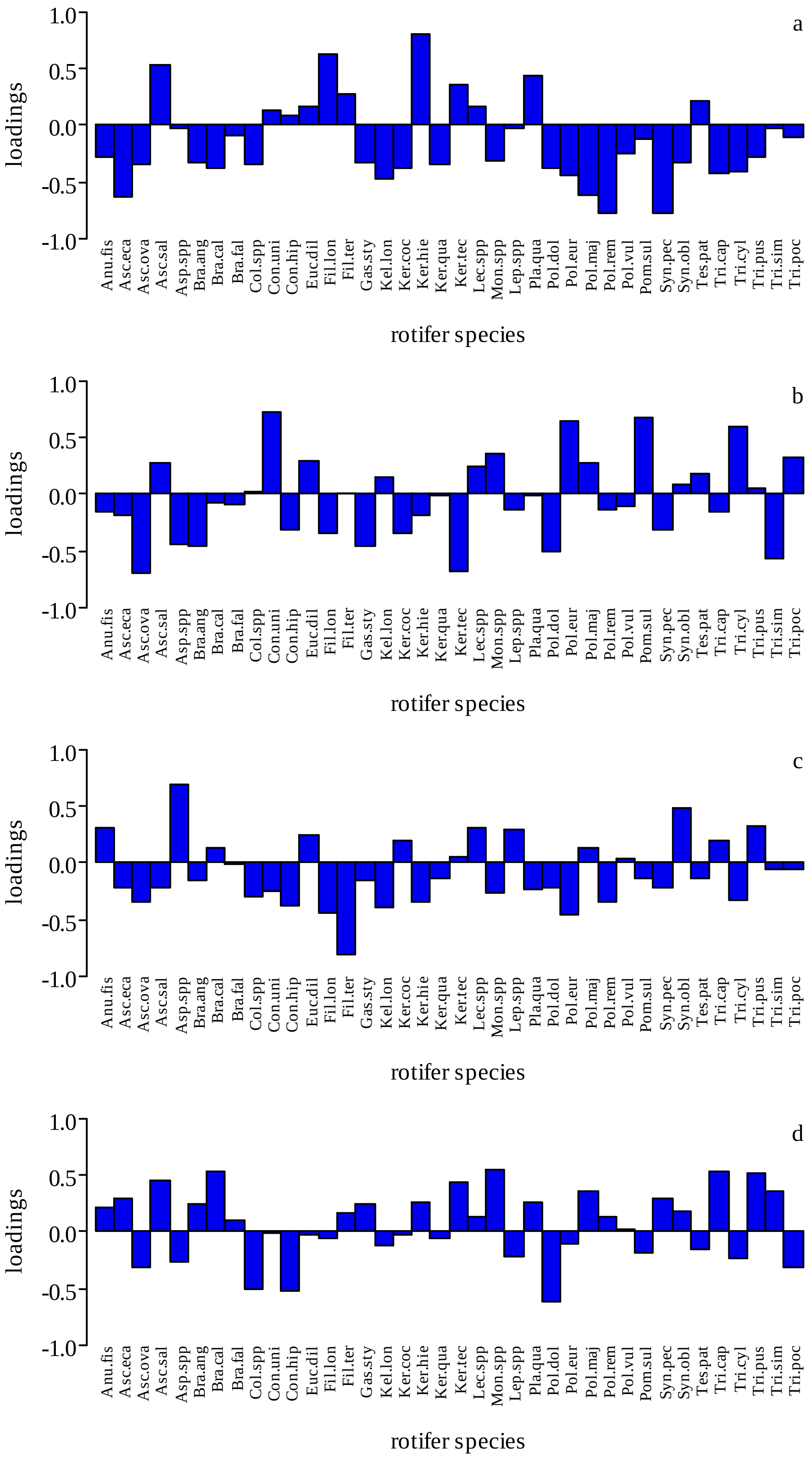

Fig. A2: Factor loadings of a) the first, b) the second, c) the third, and d) the fourth principal component derived from PCA performed on *Rot*.

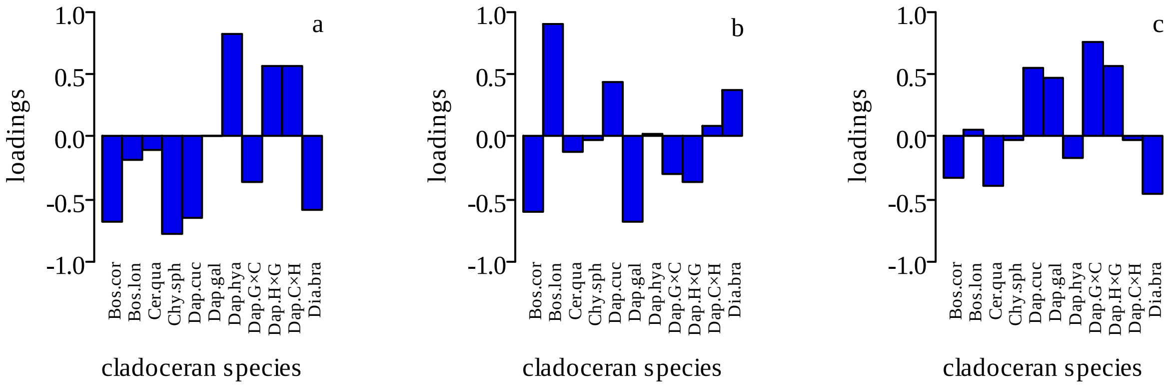

Fig. A3: Factor loadings of a) the first, b) the second, and c) the third principal component derived from PCA performed on *Clad*.

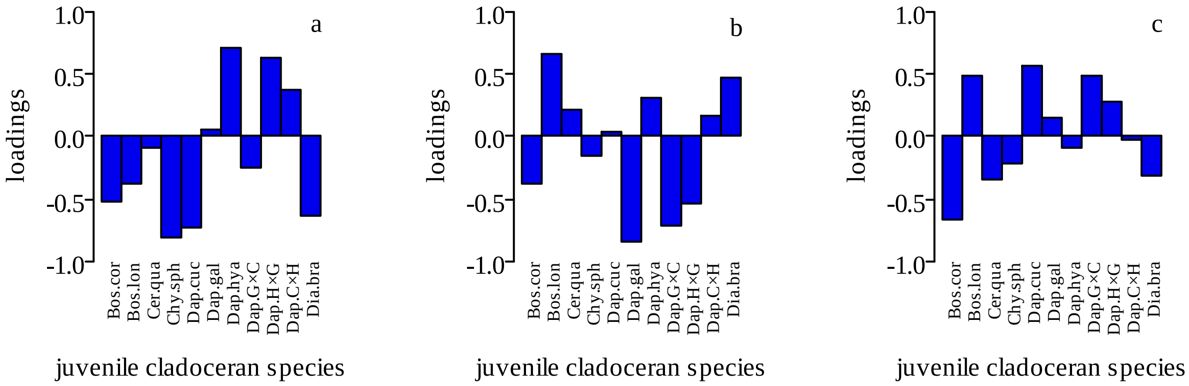

Fig. A4: Factor loadings of a) the first, b) the second, and c) the third principal component derived from PCA performed on *Clad J*.

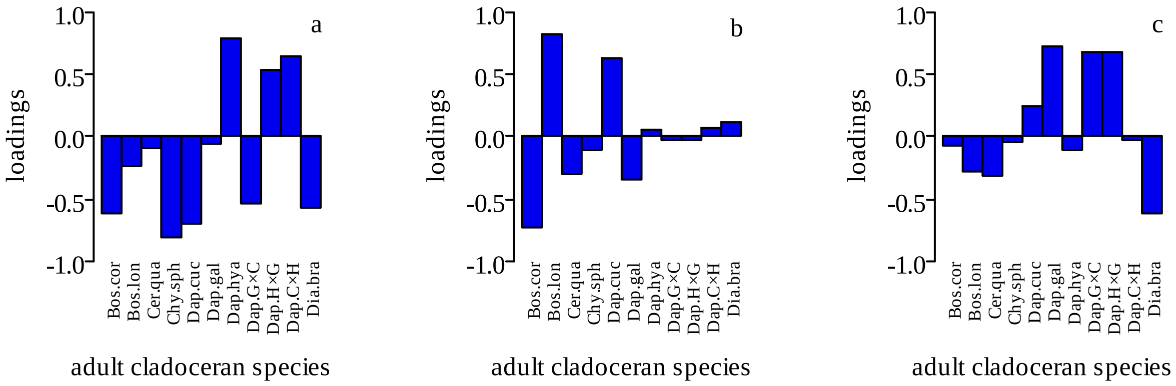

Fig. A5: Factor loadings of a) the first, b) the second, and c) the third principal component derived from PCA performed on *Clad A*.

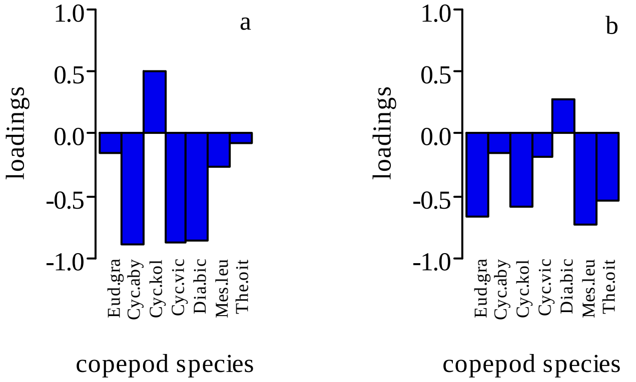

Fig. A6: Factor loadings of a) the first and b) the second principal component derived from PCA performed on *Cop*.

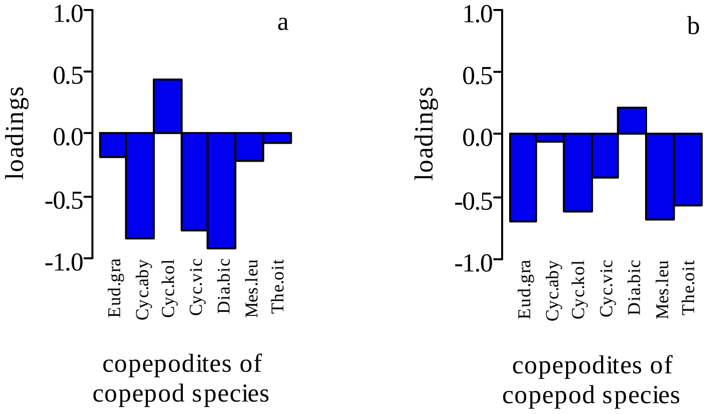

Fig. A7: Factor loadings of a) the first and b) the second principal component derived from PCA performed on *Cop C*.

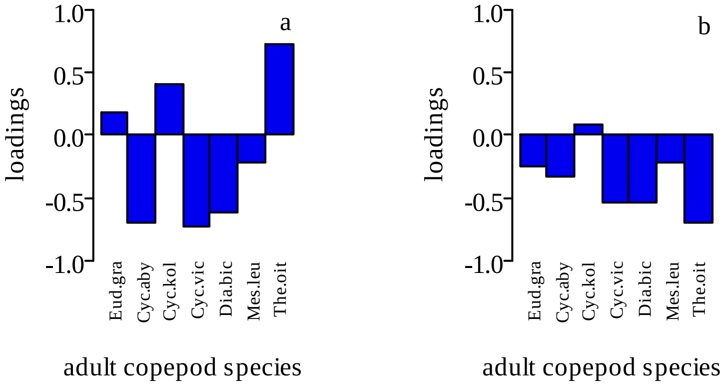

Fig. A8: Factor loadings of a) the first and b) the second principal component derived from PCA performed on *Cop A*.

Table A5. Correlations of factor scores of the zooplankton community (*Zoo*) in October with factor scores of the physical and chemical (left) and of nutrient parameters (right) from February to October. * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$. The Roman numerals indicate the respective PC.

			Zoo I	*Zoo* II	*Zoo* III	*Zoo* IV
PCs of physical and chemical parameters	Feb	PC I	-0.01	-0.44	0.79 ***	0.67 *
		PC II	-0.66 *	0.57	-0.23	0.09
	Mar	PC I	0.28	-0.63 **	0.61 *	0.64 *
		PC II	-0.57	0.21	-0.55	0.45
	Apr	PC I	0.33	-0.84 ***	0.54	0.25
		PC II	-0.23	-0.06	-0.17	-0.02
	May	PC I	0.32	-0.45	0.77 **	0.07
		PC II	-0.32	-0.18	0.02	0.77 **
	Jun	PC I	-0.55	0.31	0.17	0.32
		PC II	0.52	-0.35	0.70 *	-0.29
	Jul	PC I	0.45	-0.52	0.71 **	-0.02
		PC II	-0.22	-0.06	0.48	0.50
	Aug	PC I	0.02	-0.06	0.65 *	0.36
		PC II	0.26	-0.03	0.03	-0.25
	Sep	PC I	-0.14	-0.03	0.54	0.51
		PC II	0.26	0.08	-0.14	-0.45
	Oct	PC I	-0.44	0.26	0.29	0.61 *
		PC II	0.20	-0.22	0.16	0.06

			Zoo I	*Zoo* II	*Zoo* III	*Zoo* IV
PCs of nutrient parameters	Feb	PC I	-0.35	-0.36	0.07	0.43
		PC II	-0.39	0.20	0.76 **	0.52
	Mar	PC I	0.33	-0.69 *	0.61 *	0.52
		PC II	-0.71 **	0.52	0.19	0.41
	Apr	PC I	0.44	-0.68 *	0.34	0.31
		PC II	-0.64 *	0.46	0.19	0.45
	May	PC I	0.06	-0.38	0.52	0.68 *
		PC II	-0.83 ***	0.75 **	-0.08	0.42
	Jun	PC I	0.17	-0.47	0.51	0.51
		PC II	0.48	-0.15	0.46	-0.14
	Jul	PC I	0.24	-0.33	0.60 *	0.35
		PC II	-0.45	0.00	-0.05	0.71 **
	Aug	PC I	0.04	-0.22	0.58 *	0.52
		PC II	-0.74 **	0.66 *	-0.03	0.27
	Sep	PC I	0.05	-0.22	0.57	0.50
		PC II	-0.85 ***	0.74 **	-0.09	0.32
	Oct	PC I	0.08	-0.16	0.47	0.42
		PC II	-0.90 ***	0.77 **	-0.28	0.35

Table A6. Correlations of factor scores of the rotifer community (*Rot*) in October with factor scores of the physical and chemical (left) and of nutrient parameters (right) from February to October. * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$. The Roman numerals indicate the respective PC.

			Rot I	*Rot* II	*Rot* III	*Rot* IV
PCs of physical and chemical parameters	Feb	PC I	0.10	-0.61 *	0.68 *	-0.12
		PC II	-0.67 *	0.52	0.00	-0.37
	Mar	PC I	0.31	-0.72 **	0.53	0.06
		PC II	-0.52	0.34	-0.04	-0.78 **
	Apr	PC I	0.50	-0.87 ***	0.56	0.18
		PC II	-0.17	-0.05	0.05	-0.23
	May	PC I	0.41	-0.63 *	0.40	0.61 *
		PC II	-0.21	-0.18	0.56	-0.65 *
	Jun	PC I	-0.43	0.12	0.51	-0.09
		PC II	0.56	-0.50	0.20	0.61 *
	Jul	PC I	0.49	-0.61 *	0.16	0.36
		PC II	-0.09	-0.27	0.80 **	-0.08
	Aug	PC I	0.09	-0.31	0.80 **	0.01
		PC II	0.17	-0.02	-0.23	-0.01
	Sep	PC I	-0.04	-0.23	0.86 ***	-0.10
		PC II	0.19	0.06	0.03	0.42
	Oct	PC I	-0.42	0.12	0.48	-0.39
		PC II	0.25	-0.28	0.62 *	0.25

			Rot I	*Rot* II	*Rot* III	*Rot* IV
PCs of nutrient parameters	Feb	PC I	-0.30	-0.38	0.44	0.11
		PC II	-0.31	-0.13	0.53	-0.45
	Mar	PC I	0.47	-0.73 **	0.74 **	-0.22
		PC II	-0.66 *	0.37	0.34	-0.06
	Apr	PC I	0.55	-0.64 *	0.67 *	-0.14
		PC II	-0.59 *	0.35	0.44	-0.23
	May	PC I	0.13	-0.53	0.86 ***	-0.08
		PC II	-0.89 ***	0.54	0.14	-0.35
	Jun	PC I	0.28	-0.59 *	0.89 ***	0.01
		PC II	0.35	-0.25	-0.16	0.53
	Jul	PC I	0.31	-0.49	0.84 ***	0.11
		PC II	-0.44	0.01	0.26	-0.33
	Aug	PC I	0.12	-0.44	0.91 ***	-0.02
		PC II	-0.77 **	0.45	-0.01	-0.10
	Sep	PC I	0.15	-0.42	0.93 ***	-0.09
		PC II	-0.82 **	0.54	0.11	-0.38
	Oct	PC I	0.12	-0.34	0.86 ***	0.01
		PC II	-0.90 ***	0.62 *	0.12	-0.44

Table A7. Correlations of factor scores of the a) entire cladoceran community (*Clad*), b) juvenile stages of cladocerans (*Clad J*), and c) adult stages of cladocerans (*Clad A*) in October with factor scores of the physical and chemical (left) and of nutrient parameters (right) from February to October. * *p*≤0.05, ** *p*≤0.01, *** *p*≤0.001. The Roman numerals indicate the respective PC.

a)			*Clad* I	*Clad* II	*Clad* III
PCs of physical and chemical parameters	Feb	PC I	0.36	0.17	0.72 **
		PC II	-0.24	0.33	-0.16
	Mar	PC I	0.36	-0.18	0.70 *
		PC II	0.39	-0.10	-0.14
	Apr	PC I	0.69 *	-0.09	0.53
		PC II	0.44	-0.10	-0.16
	May	PC I	0.16	0.17	0.38
		PC II	0.55	-0.18	0.27
	Jun	PC I	0.10	0.37	-0.19
		PC II	-0.19	0.37	0.20
	Jul	PC I	0.02	0.28	0.58 *
		PC II	0.19	0.20	0.14
	Aug	PC I	-0.15	0.29	0.18
		PC II	-0.33	0.00	0.12
	Sep	PC I	0.06	0.31	0.13
		PC II	-0.24	-0.18	-0.52
	Oct	PC I	-0.11	0.28	0.30
		PC II	0.22	-0.31	-0.19

			Clad I	*Clad* II	*Clad* III
PCs of nutrient parameters	Feb	PC I	0.67 *	-0.22	0.17
		PC II	-0.22	0.75 **	0.49
	Mar	PC I	0.59 *	0.03	0.49
		PC II	-0.14	0.41	0.07
	Apr	PC I	0.61 *	-0.21	0.22
		PC II	-0.09	0.38	0.10
	May	PC I	0.31	-0.11	0.36
		PC II	-0.42	0.33	-0.02
	Jun	PC I	0.41	-0.14	0.26
		PC II	-0.50	-0.04	0.39
	Jul	PC I	0.11	0.02	0.20
		PC II	0.41	-0.13	0.31
	Aug	PC I	0.10	0.07	0.20
		PC II	-0.35	0.40	-0.09
	Sep	PC I	0.10	0.13	0.17
		PC II	-0.29	0.56	-0.21
	Oct	PC I	0.02	-0.01	0.10
		PC II	-0.21	0.34	-0.28

b)			*Clad J* I	*Clad J* II	*Clad J* III
PCs of physical and chemical parameters	Feb	PC I	0.18	-0.21	0.74 **
		PC II	-0.33	0.38	-0.05
	Mar	PC I	0.25	-0.55	0.64 *
		PC II	0.44	0.06	-0.01
	Apr	PC I	0.56	-0.31	0.45
		PC II	0.46	-0.01	-0.14
	May	PC I	0.01	-0.04	0.42
		PC II	0.54	-0.23	0.28
	Jun	PC I	0.07	0.46	0.06
		PC II	-0.37	0.15	0.26
	Jul	PC I	-0.23	-0.09	0.57
		PC II	0.13	0.12	0.25
	Aug	PC I	-0.23	0.08	0.26
		PC II	-0.37	-0.12	-0.02
	Sep	PC I	-0.02	0.14	0.31
		PC II	-0.14	0.06	-0.61 *
	Oct	PC I	-0.13	0.04	0.44
		PC II	0.30	-0.14	-0.33

			Clad J I	*Clad J* II	*Clad J* III
PCs of nutrient parameters	Feb	PC I	0.61 *	-0.20	0.15
		PC II	-0.47	0.34	0.75 **
	Mar	PC I	0.41	-0.23	0.52
		PC II	-0.18	0.33	0.29
	Apr	PC I	0.53	-0.29	0.16
		PC II	-0.14	0.28	0.30
	May	PC I	0.24	-0.32	0.35
		PC II	-0.40	0.25	0.10
	Jun	PC I	0.35	-0.24	0.21
		PC II	-0.45	-0.37	0.27
	Jul	PC I	0.06	-0.14	0.19
		PC II	0.37	-0.23	0.38
	Aug	PC I	0.04	-0.10	0.24
		PC II	-0.36	0.36	0.13
	Sep	PC I	0.02	-0.04	0.23
		PC II	-0.33	0.56	0.10
	Oct	PC I	0.01	-0.13	0.08
		PC II	-0.19	0.44	-0.06

Table continued from previous page

c)			*Clad A* I	*Clad A* II	*Clad A* III
PCs of physical and chemical parameters	Feb	PC I	0.31	0.45	0.55
		PC II	-0.17	0.19	-0.29
	Mar	PC I	0.27	0.15	0.65 *
		PC II	0.39	-0.17	-0.11
	Apr	PC I	0.61 *	0.13	0.53
		PC II	0.47	-0.12	-0.12
	May	PC I	0.09	0.33	0.32
		PC II	0.50	-0.04	0.32
	Jun	PC I	0.11	0.20	-0.30
		PC II	-0.21	0.42	0.04
	Jul	PC I	-0.05	0.55	0.45
		PC II	0.17	0.22	0.06
	Aug	PC I	-0.16	0.29	0.03
		PC II	-0.33	0.08	0.13
	Sep	PC I	0.06	0.26	-0.05
		PC II	-0.12	-0.45	-0.43
	Oct	PC I	-0.15	0.35	0.14
		PC II	0.30	-0.40	-0.05

			Clad A I	*Clad A* II	*Clad A* III
PCs of nutrient parameters	Feb	PC I	0.73 **	-0.19	0.23
		PC II	-0.30	0.86 ***	0.08
	Mar	PC I	0.54	0.21	0.41
		PC II	-0.10	0.30	-0.13
	Apr	PC I	0.63 *	-0.13	0.27
		PC II	-0.04	0.28	-0.10
	May	PC I	0.30	0.01	0.31
		PC II	-0.40	0.27	-0.18
	Jun	PC I	0.42	-0.05	0.27
		PC II	-0.58 *	0.15	0.34
	Jul	PC I	0.12	0.06	0.15
		PC II	0.41	-0.05	0.26
	Aug	PC I	0.10	0.10	0.11
		PC II	-0.34	0.28	-0.28
	Sep	PC I	0.11	0.14	0.06
		PC II	-0.28	0.37	-0.43
	Oct	PC I	0.06	-0.03	0.04
		PC II	-0.16	0.12	-0.43

Table A8. Correlations of factor scores of the a) entire copepod community (*Cop*), b) copepodite stages (*Cop C*), and c) adult stages of copepods (*Cop A*) in October with factor scores of the physical and chemical (left) and of nutrient parameters (right) from February to October. * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$. The Roman numerals indicate the respective PC.

a)			*Cop* I	*Cop* II
PCs of physical and chemical parameters	Feb	PC I	-0.32	-0.57
		PC II	0.33	-0.51
	Mar	PC I	-0.55	-0.47
		PC II	0.31	-0.11
	Apr	PC I	-0.29	0.02
		PC II	0.30	-0.08
	May	PC I	-0.20	-0.02
		PC II	0.28	-0.24
	Jun	PC I	0.57	-0.10
		PC II	-0.48	-0.10
	Jul	PC I	-0.59 *	-0.18
		PC II	0.35	-0.24
	Aug	PC I	0.08	-0.48
		PC II	-0.24	-0.07
	Sep	PC I	0.10	-0.54
		PC II	-0.10	0.05
	Oct	PC I	0.30	-0.49
		PC II	0.10	0.09

			Cop I	*Cop* II
PCs of nutrient parameters	Feb	PC I	-0.14	-0.31
		PC II	-0.08	-0.85 ***
	Mar	PC I	-0.44	-0.38
		PC II	0.43	-0.63 *
	Apr	PC I	-0.42	-0.16
		PC II	0.36	-0.72 **
	May	PC I	-0.21	-0.64 *
		PC II	0.59 *	-0.51
	Jun	PC I	-0.13	-0.35
		PC II	-0.40	-0.06
	Jul	PC I	-0.13	-0.38
		PC II	-0.07	-0.63 *
	Aug	PC I	-0.03	-0.53
		PC II	0.44	-0.47
	Sep	PC I	-0.04	-0.54
		PC II	0.61 *	-0.43
	Oct	PC I	-0.05	-0.53
		PC II	0.67 *	-0.46

Table continued from previous page

b)			*Cop C* I	*Cop C* II
PCs of physical and chemical parameters	Feb	PC I	-0.20	-0.59
		PC II	0.38	-0.45
	Mar	PC I	-0.49	-0.54
		PC II	0.27	-0.04
	Apr	PC I	-0.26	0.02
		PC II	0.28	0.01
	May	PC I	-0.15	-0.09
		PC II	0.33	-0.19
	Jun	PC I	0.57	-0.10
		PC II	-0.47	-0.14
	Jul	PC I	-0.53	-0.19
		PC II	0.39	-0.24
	Aug	PC I	0.14	-0.48
		PC II	-0.23	-0.02
	Sep	PC I	0.15	-0.54
		PC II	-0.14	0.00
	Oct	PC I	0.37	-0.45
		PC II	0.12	0.05

			Cop C I	*Cop C* II
PCs of nutrient parameters	Feb	PC I	-0.03	-0.38
		PC II	0.01	-0.83 ***
	Mar	PC I	-0.38	-0.37
		PC II	0.53	-0.67 *
	Apr	PC I	-0.39	-0.13
		PC II	0.48	-0.72 **
	May	PC I	-0.14	-0.68 *
		PC II	0.66 *	-0.50
	Jun	PC I	-0.07	-0.37
		PC II	-0.38	-0.16
	Jul	PC I	-0.08	-0.40
		PC II	0.01	-0.64 *
	Aug	PC I	0.02	-0.55
		PC II	0.48	-0.49
	Sep	PC I	0.01	-0.54
		PC II	0.63 *	-0.40
	Oct	PC I	0.01	-0.55
		PC II	0.71 **	-0.43

c)			*Cop A* I	*Cop A* II
PCs of physical and chemical parameters	Feb	PC I	-0.39	0.11
		PC II	0.47	-0.08
	Mar	PC I	-0.53	0.13
		PC II	0.18	0.56
	Apr	PC I	-0.52	0.15
		PC II	0.19	0.23
	May	PC I	-0.21	-0.05
		PC II	-0.03	0.44
	Jun	PC I	0.32	0.53
		PC II	-0.22	-0.40
	Jul	PC I	-0.46	-0.45
		PC II	0.09	0.31
	Aug	PC I	0.19	-0.12
		PC II	0.13	-0.65 *
	Sep	PC I	0.06	0.21
		PC II	0.13	0.00
	Oct	PC I	0.27	0.00
		PC II	-0.16	0.32

			Cop A I	*Cop A* II
PCs of nutrient parameters	Feb	PC I	-0.47	0.78 **
		PC II	0.17	-0.31
	Mar	PC I	-0.46	0.15
		PC II	0.31	0.24
	Apr	PC I	-0.52	0.22
		PC II	0.28	0.15
	May	PC I	-0.21	0.28
		PC II	0.53	0.11
	Jun	PC I	-0.29	0.29
		PC II	-0.06	-0.60 *
	Jul	PC I	-0.14	0.04
		PC II	-0.13	0.52
	Aug	PC I	-0.04	0.18
		PC II	0.55	0.21
	Sep	PC I	-0.05	0.14
		PC II	0.61 *	0.27
	Oct	PC I	-0.06	0.14
		PC II	0.63 *	0.37

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Eidesstattliche Versicherung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Hamburg, den 14.05.2013