TECHNISCHE UNIVERSITÄT MÜNCHEN

TUM School of Life Sciences
Lehrstuhl für Aquatische Systembiologie
Limnologische Station Iffeldorf

The response of Alpine aquatic ecosystems to climate change: a combined limnological and paleolimnological approach based on diatom, pigment and stable isotope analyses

Andrea Maria Hofmann

Vollständiger Abdruck der von der TUM School of Life Sciences der Technischen Universität München zur Erlangung des akademischen Grades eines

Doktors der Naturwissenschaften (Dr. rer. nat.)

genehmigten Dissertation

Vorsitzender: Prof. Dr. Johannes Kollmannn
Prüfende der Dissertation:
1. Prof. Dr. Jürgen Geist
2. Priv.-Doz. Dr. Christoph Mayr

Die Dissertation wurde am 24.02.2021 bei der Technischen Universität München eingereicht und durch die TUM School of Life Sciences am 28.07.2021 angenommen.

For Horst Hofmann and Magdalena Steger.

In memory.

Contents

List of tables

List of figures

Summary

The consequences of climate change are increasingly impacting the European Alps. The rising air temperatures lead to a rapidly thawing of glaciers, snowfields and permafrost resulting in rock-slope instabilities and downstream impacts on quality, quantity and seasonality of water resources. The upward shift of the treeline, increased vegetation cover and soil development significantly alter nutrient fluxes into streams and lakes. Furthermore, the rising frequency and intensity of extreme precipitation events result in enhanced erosion rates and debris flow activity strongly impacting the light and nutrient regime of aquatic systems. Climate warming also directly affect mountain lakes by changing lake levels, water chemistry, length of the growing seasons and the mixing regimes. Besides, the lakes are impacted by atmospheric deposition-fertilization and local disturbances, such as forestry, alpine pasture, and tourism.

The response of the algal communities to these multiple, concurrently occurring stresses is highly complex. As they form the base of the aquatic food web, the reorganisation within both, littoral and pelagic primary producers has cascading effects on the mountain lake ecosystem. Therefore, it is a great urgency to understand how far the changing environments impact the structure, the seasonal dynamics and the taxonomic composition of the phytoplankton and periphyton communities.

Morphological and biochemical remains of primary producers preserved in the lake sediments can be used to reconstruct past environmental conditions. Diatoms are among the most frequently used paleoindicators as they response sensitively and rapidly to changes of water temperature, lake alkalinity, salinity, nutrient regime, water transparency, lake mixing regime, habitat stability, and substrate availability. Sedimentary pigments are widely used to track past changes in lake production and shifts within the composition of primary producer communities. Additionally, records of carbon and nitrogen stable isotopes in bulk sediments provide information about sources of sedimentary organic matter, shifts within the lacustrine nutrient cycling and changes in lake trophic states.

The main goal of this thesis was to research the response and the resilience of mountain lakes located in the Bavarian and North-Tyrolean Alps to climate change. Three studies were carried out to (1) gather detailed knowledge about selected mountain lake ecosystems, (2) understand how local- and regional-scale processes interact with global climate change and (3) identify the factors that mainly control the lake responses to climate change. Therefore, contemporary investigations of the physical and chemical conditions and detailed analyses of the primary producers (diatoms, macrophytes, phytoplankton) were combined with paleolimnological analyses of subfossil diatoms, paleopigments and stable isotopes.

The findings of the first study indicate that depth significantly controls the composition of diatom assemblages and highlight the importance of considering lake depth and water transparency when developing diatom-based transfer-functions. The depth-distribution of the current diatom flora in two adjacent, but hydrologically distinct subalpine lakes was investigated by sampling stones and surficial sediments in one-meter depth increments along N-S transects. The results show that most periphytic diatoms preferred distinct depth areas within the littoral zone, mainly influenced by the type of substrate. Light availability controls the ratio between periphytic and planktic diatoms in the surficial sediments. Therefore, frustules of planktic diatoms dominated the assemblages of the aphotic profundal. The diatom–inferred depth models, developed by using weighted-averaging approaches were found to be highly appropriate to reconstruct past fluctuations of lake depth or water transparency. The significant influence of light availability suggests the creation of two different training-sets when developing diatom-based transfer-functions. One set, that includes both periphytic and planktonic diatoms, fits deep or low-transparency shallow lakes with an aphotic zone. Another training-set fits shallow, clear water lakes and uses periphytic diatoms exclusively.

The second study highlights the benefit of a multi-proxy approach to unravel climate change impacts from other anthropogenic disturbances via down-core analyses. Biological (subfossil diatoms), biochemical (paleopigments) and geochemical (nitrogen and carbon stable isotopes) paleoindicators were used to reconstruct the history of a small subalpine lake since the outgoing Little Ice Age (AD 1840–AD 2017). Shifts within the diatom assemblages were related to variations of light and nutrient availability, water temperature and thermal stratification. The organic carbon isotope ($\delta^{13}C_{org}$) records, the diatom valve density and the pigment concentrations documented the development of primary production. Total nitrogen isotope values ($\delta^{15}N$) are more likely to reflect the history of atmospheric nitrogen pollution than lake internal processes, also mirrored by the decoupling of $\delta^{15}N$ and $\delta^{13}C_{org}$ trends. The composition of sedimentary pigments allowed a differentiation between planktonic and benthic primary production. Concordant trends of all indicators suggested that the lake ecosystem passed a climatic threshold promoted by local and long-distance atmospheric nutrient loadings.

For the third study, the dataset was extended by inclusion of lakes located in the Berchtesgaden and Allgäu Alps to test the general validity of the findings presented in studies 1 and 2. Therefore, diatom assemblages of dated sediment records from 23 lakes, situated between 955 and 2060 m a.s.l. were analysed. The lakes differ widely in origin, hydrological features (depth, trophic state, habitat stability) and catchment characteristics (geology, morphology, soils, vegetation). The findings of this study show that especially altitude and lake depth control the response of lake diatom communities to climate change. Correspondence and regression analyses revealed five different developments of the diatom assemblages. Species reorganisation was highest in shallow montane and subalpine lakes, were the establishment of macrophytes offered new habitat for epiphytic species. In deeper lakes, the abrupt appearance of planktic diatoms (*Cyclotella* spp., *Fragilaria* spp.) defined tipping points of lake ecosystems, when the thermal stratification stabilized. Shallow alpine lakes, however, hardly showed any shift. Small, benthic pioneer species (*Staurosira* spp., *Staurosirella* spp., *Pseudostaurosira* spp.) dominated the diatom assemblages throughout the sedimentary records.

Together these results provide novel insights about global change impacts on mountain lakes located in the Northern Calcareous Alps. Down core studies revealed that eutrophication processes by local disturbances and atmospheric fertilization were amplified by climate warming particularly since ~ AD 1980. Several lakes already reached tipping points of lake ecosystem primarily determined by the establishment of stable stratification resulting in rising abundances of small centric diatoms and by the availability of macrophytes as habitat for epiphytic diatoms. Climate change was found to clearly modify the biomass and the structure of lake primary producers, whereby altitude and lake depth/transparency are the main drivers controlling their responses to global warming. As environmental change may impact different trophic levels in various ways, multi-trophic studies should be carried out to better understand the consequences of the rapidly changing climate on the whole aquatic system.

Zusammenfassung

Die Folgen des Klimawandels wirken sich in zunehmendem Maße auf die Europäischen Alpen aus. Die steigenden Lufttemperaturen führen zu einem raschen Abschmelzen von Gletschern, Schneefeldern und Permafrost. Die Folgen sind zum einen instabile Felshänge, zum anderen eine veränderte Qualität, Quantität und Saisonalität der alpinen Wasserreserven. Die Verschiebung der Baumgrenze in höhere Lagen und die zunehmende Vegetationsbedeckung und Bodenbildung verändert deutlich den Nährstoffeintrag in Flüsse und Seen. Die zunehmende Häufigkeit und Intensität von extremen Niederschlagsereignissen erhöhen die Erosionsraten und die Gefahr von Murenabgängen, was die Nährstoff- und Lichtverhältnisse der aquatischen Systeme stark beeinflussen kann. Der Klimawandel beeinträchtigt die Bergseen auch direkt indem er den Wasserstand der Seen, deren Wasserchemie, Vegetationsperiode und Schichtungsverhalten verändert. Zudem werden die Seen durch atmosphärische Deposition und lokale Störungen wie Forstwirtschaft, Weidewirtschaft und Tourismus beeinflusst.

Die Reaktion der Algengemeinschaften auf diese multiplen Belastungen ist sehr komplex. Da sie die Basis des aquatischen Nahrungsnetzes bilden, haben Veränderungen in der Zusammensetzung der litoralen und pelagischen Primärproduzenten kaskadenartige Auswirkungen auf das gesamte Ökosystem Bergsee. Daher ist es äußerst wichtig zu verstehen, inwieweit die verändernden Umweltbedingungen die Struktur, die saisonale Dynamik und die taxonomische Zusammensetzung der lakustrinen Algengesellschaften beeinflussen.

Mithilfe in Seesedimenten enthaltener fossiler Reste von Primärproduzenten ist es möglich vergangene Umweltbedingungen zu rekonstruieren. Kieselalgen gehören zu den am häufigsten verwendeten Paläoindikatoren, da sie empfindlich und schnell auf Veränderungen verschiedener Umweltbedingungen reagieren, wie zum Beispiel Veränderungen der Temperatur, der Alkalinität, des Salzgehalts, des Nährstoffregimes, der Wassertransparenz, des Durchmischungsregimes, der Stabilität des Lebensraums und der Substratverfügbarkeit. Subfossile Pigmente ermöglichen es, Veränderungen der Produktivität eines Sees und Verschiebungen in der Zusammensetzung der Primärproduzenten zu rekonstruieren. Zudem geben die Isotopenverhältnisse von Kohlenstoff- und Stickstoff-Isotope Auskunft über die Herkunft der sedimentären organischen Substanz und über Veränderungen des lakustrinen Nährstoffkreislauf und des trophischen Zustands eines Sees.

Das Hauptziel dieser Arbeit war die Erforschung der Reaktion und der Widerstandsfähigkeit von Bergseen der bayerischen und nordtiroler Alpen auf den Klimawandel. Drei Studien wurden durchgeführt, um (1) detailliertes Wissen über ausgewählte Bergsee-Ökosysteme zu sammeln, (2) zu verstehen, wie lokale und regionale Prozesse mit dem globalen Klimawandel interagieren und

(3) die Faktoren zu identifizieren, die hauptsächlich die Reaktionen der Seen auf den Klimawandel steuern. Dazu wurden physikalische, chemischen Untersuchungen der Seen und detaillierte Analysen der Primärproduzenten (Kieselalgen, Makrophyten, Phytoplankton) durchgeführt und die gewonnen Erkenntnisse mit paläolimnologischen Analysen subfossiler Kieselalgen, Paläopigmente und stabiler Isotope kombiniert.

Die Ergebnisse der ersten Studie zeigen, dass die Zusammensetzung der Diatomeen-Gesellschaften deutlich von der Wassertiefe beeinflusst wird und weisen darauf hin, dass bei der Entwicklung von auf Diatomeen basierten Transfer-Funktionen die Wassertiefe und die Wassertransparenz unbedingt berücksichtigt werden müssen. Die Tiefenverteilung der rezenten Kieselalgen-Flora in zwei benachbarten, aber hydrologisch unterschiedlichen subalpinen Seen wurde untersucht, indem Steine und Oberflächensedimente in 1-Meter-Tiefenschritten entlang zweier N-S-Transekte beprobt wurden. Die Ergebnisse zeigen, dass die meisten periphytischen Diatomeen bestimmte Tiefenbereiche innerhalb des Litorals bevorzugen, hauptsächlich beeinflusst von der Art des Substrats. Die Lichtverfügbarkeit hingegen steuert das Verhältnis von periphytischen zu planktischen Diatomeen in den Sedimenten. Daher dominieren die Schalen planktischer Arten die Diatomeen-Gesellschaften des aphotischen Profundals. Die mithilfe der DiatomeenVerteilung entwickelten Tiefenmodelle erwiesen sich als sehr geeignet, um vergangene Veränderungen der Wassertiefe oder -transparenz zu rekonstruieren. Der signifikante Einfluss der Lichtverhältnisse legt die Erstellung von zwei verschiedenen Trainings-Sets bei der Entwicklung von Diatomeen-basierten Transfer-Funktionen nahe. Ein Set, das sowohl periphytische als auch planktische Diatomeen enthält, eignet sich für tiefe oder wenig transparente, flachen Seen mit einer aphotischen Zone. Ein anderes Trainingsset passt zu flachen, klaren Seen und verwendet ausschließlich periphytische Diatomeen.

Die zweite Studie unterstreicht den Nutzen eines Multi-Proxy-Ansatzes, um die Auswirkungen des Klimawandels von anderen anthropogenen Störungen zu unterscheiden. Mithilfe biologischer (subfossile Kieselalgen), biochemischer (Paläopigmente) und geochemischer (stabile Stickstoff- und Kohlenstoffisotope) Paläoindikatoren wurde die Geschichte eines kleinen subalpinen Sees seit der ausgehenden Kleinen Eiszeit (AD 1840 bis AD 2017) rekonstruiert. Veränderungen in der Zusammensetzung der Diatomeengesellschaften konnten Veränderungen der Licht- und Nährstoffverfügbarkeit, der Wassertemperatur und der thermischen Schichtung in Verbindung aufzeigen. Der Verlauf des organischen Kohlenstoffs ($\delta^{13}C_{org}$), der Diatomeendichte und der Pigmentkonzentrationen dokumentierten die Entwicklung der Primärproduktion im See. Die Gesamt-Stickstoff-Isotopenwerte ($\delta^{15}N$) zeigen eher die Geschichte der atmosphärischen

Stickstoffverschmutzung als seeninterne Prozesse auf, was sich auch in der Entkopplung der δ^{15}N- und $\delta^{13}C_{org}$-Trends widerspiegelt. Die Zusammensetzung der Paläopigmente erlaubte eine Differenzierung zwischen planktonischer und benthischer Primärproduktion. Die übereinstimmenden Trends aller Indikatoren deuten darauf hin, dass das Ökosystem des Sees eine klimatische Schwelle überschritten hat, die durch langjährige lokale und atmosphärische Nährstoffeinträge verstärkt wurde.

Für die dritte Studie wurde der Datensatz um Seen in den Berchtesgadener und Allgäuer Alpen erweitert, um die Allgemeingültigkeit der in den Studien 1 und 2 präsentierten Ergebnisse zu testen. Dazu wurden Diatomeen-Gesellschaften datierter Sedimentkerne aus 23 Seen analysiert. Die Seen liegen zwischen 955 und 2060 m ü. NN und unterscheiden sich hinsichtlich ihrer Entstehung, ihrer hydrologischen Eigenschaften (Tiefe, trophischer Zustand, Habitatstabilität) und ihres Einzugsgebietes (Geologie, Morphologie, Böden, Vegetation). Die Ergebnisse dieser Studie zeigen, dass insbesondere die Höhenlage der Seen und die Wassertiefe die Reaktion der Diatomeengesellschaften auf den Klimawandel steuern. Korrespondenz- und Regressionsanalysen ergaben fünf verschiedene Entwicklungen der Diatomeengesellschaften. Die Veränderung der Artenzusammensetzung war am höchsten in flachen montanen und subalpinen Seen. Hier stellt die Etablierung von Makrophyten neuen Lebensraum für epiphytische Arten zur Verfügung. In tieferen Seen definierte das abrupte Auftreten von planktischen Kieselalgen (*Cyclotella* spp., *Fragilaria* spp.) tipping points der Seeökosysteme, als sich die thermische Schichtung stabilisierte. Flache alpine Seen zeigten dagegen kaum eine Veränderung der Artenzusammensetzung. Kleine, benthische Pionierarten (*Staurosira* spp., *Staurosirella* spp., *Pseudostaurosira* spp.) dominierten die Kieselalgen-Gesellschaften während der gesamten Sedimentaufzeichnungen.

Zusammen liefern diese Ergebnisse neue Erkenntnisse über die Auswirkungen des globalen Wandels auf Bergseen in den Nördlichen Kalkalpen. In beinahe allen untersuchten Seen konnten Folgen des Klimawandels nachgewiesen werden. Eutrophierungsprozesse, ausgelöst durch lokalen und atmosphärischen Nährstoffeintrag werden durch die Klimaerwärmung verstärkt, besonders seit ~ AD 1980. Mehrere Seen erreichten bereits tipping points, definiert durch (1) die Stabilisierung der thermischen Schichtung, die zu steigenden Abundanzen von kleinen zentrischen Kieselalgen führte, und (2) die Etablierung von Makrophyten als Lebensraum für epiphytische Kieselalgen. Es wurde festgestellt, dass der Klimawandel sowohl die Biomasse als auch die Struktur der Primärproduzenten deutlich verändert, wobei die Höhenlage und die Wassertiefe /Transparenz der Seen die Hauptfaktoren sind, die ihre Reaktionen auf die globale Erwärmung steuern. Da Umweltveränderungen verschiedene trophische Ebenen auf unterschiedliche Weise beeinflussen können, sollten in zukünftigen Studien multitrophische Analysen durchgeführt werden, um die Folgen des sich schnell ändernden Klimas auf das gesamte Ökosystem Bergsee besser zu verstehen.

1. Introduction

1.1 Climate warming in the European Alps

Mountain ecosystems are particularly sensitive to the impacts of a rapidly changing climate (IPPC 2014). Ohmura (2012) found that temperatur changes are more pronounced and occur distinctly faster at higher altitudes. In the European Alps, the recent warming has not been linear since the end of the Little Ice Age around AD 1850 (Ilyashuk et al. 2018). After the early 1980s, annual temperatures increased three-fold compared to global climate signal (Beniston 2005), primarily in response to water vapour-enhanced greenhouse warming caused by anthropogenic emissions (Philipona 2013). The increase of atmospheric humidity highly modifies the dry and cold atmosphere of higher altitudes resulting in a disproportionately high warming rate (Ruckstuhl et al. 2007). Both, regional atmospheric circulation dynamics and more local effects influence mountain surface temperature (Ceppi et al. 2012). Daytime cloud cover has a warming effect in the Alps, especially above 1500 m a.s.l. (Marty et al. 2002). Reduced snow cover alters the snow-albedo feedback mechanism resulting in distinctly increasing surface absorption of solar radiation (Winter et al. 2017).

Glaciers and mountain permafrost are highly affected by the global warming trend. About 45 % of the glaciers in the European Alps have been lost since AD 1900. The remaining glaciers have had increasingly negative mass balances since the mid-1980s (Huss 2012). Permafrost-ice and rock glaciers thawed especially since AD 2009 and accentuated since AD 2015 (Noetzli et al. 2016). The sharp decline of the snow cover since the late 1980s is unprecedented over the last ~ 150 years (Scherrer et al. 2013). Especially since the 1990s the dramatically fast glacier retreat and permafrost thawing resulted in enhanced slope instabilities and rising rates of rock falls and landslides in high-mountain areas (Stoffel and Huggel 2012; Fischer et al. 2012).

Additionally, an increased frequency and intensity of extreme precipitation events has been observed in the European Alps since the 1980s (Beniston et al. 1997; IPCC 2014). Mountain regions with steep, bare slopes are particularly sensitive to erosion and surface runoff during intense rainfall (Giguet-Covex et al. 2011) triggering debris flows and torrential floods.

The extraordinary rapid warming gradually transforms the plant communities of the European Alps resulting in losses of biodiversity (Schwager and Berg 2019), biotic homogenisation (Porro et al. 2019) and a distinct upward migration of plant species along elevational gradients (Frei et al. 2010). The mean vegetation cover has increased over the last 50 years, especially in subalpine and low alpine grassland (Rosback et al. 2014). Slow growing, cold adapted alpine plant species declined and even disappeared locally, especially high-altitude species (Pauli et al. 2012; Rumpf 2018), while thermophilic species significantly increased in their abundances (Gottfried et al. 2012).

Climate change endangers a series of essential ecosystem services provided by the mountainous areas of the European Alps and affect human livelihood, safeness and recreation. Weather extremes such as droughts and storms highly reduce mountain forest functioning as provider for timber and fuel wood and as regulator of natural hazards such as erosion, rock fall and avalanches (Theurillat and Guisan 2001; Timofeeva et al. 2012; Dupire et al. 2017). Furthermore, mountains play a key role in the water cycle by modulating the water run-off regime and mitigating the risks of extreme floods (Crouzat et al. 2015). In mountain regions freshwater is captured and stored in lakes, glaciers, permafrost and snowpack. These mountain water resources are highly relevant for freshwater supply, irrigation and hydroelectricity production (Viviroli et al. 2011). Heat waves, droughts and runoff extremes result in a reduced headwater discharge and an increased frequency and intensity of floods and debris flows (Zappa and Kan 2007) affecting water quality, aquatic life, hydropower supply, upland farming and mountain infrastructure (Huggel at al. 2012; Bätzing 2015; Schaefli et al. 2019).

1.2 Mountain lakes as sentinels for global change

Mountain lakes are particularly sensitive to global environmental change (Moser et al. 2019). Lakes of higher altitudes are characterised by long ice cover, short vegetation periods, low water temperatures, nutrient-poor conditions, rapid changes in chemical and physical conditions during snow melt, extreme changes in water transparency, and intensive ultraviolet radiation (Sommaruga 2001; Schmidt et al. 2004). They host organism that are well adapted to these harsh conditions. Even small climate variability represents serious impacts on biodiversity, food web dynamics and ecosystem function (Parker et al. 2008; Miller and McKnight 2012; Preston et al. 2016) resulting in significant shifts within species composition (Smol et al. 2005; Fjellheim et al. 2009; Williamson et al. 2010).

The influence of climate change on aquatic systems is highly complex. Climate affects fundamental aspects of lake ecosystem function and structure through both direct and indirect pathways (Fig. 1.1). Climate regulates the ice cover phenology (Preston et al. 2016), the mixing regimes (Butcher et al. 2015), the length of the growing season (Verdonschot et al. 2010) and the water chemistry (Adrian et al. 2009).

Water temperature controls metabolic rates, life cycle, growth, consumption, and enzyme activity of the individual organism and affect food web dynamics by regulating biomass, composition, diversity and phenology of aquatic communities (Yvon-Durocher et al. 2010; 2011). Warming of surface waters increases duration and intensity of thermal stratification resulting in reduced nutrient exchange and decreased hypolimnetic oxygen concentrations (Wilhelm and Adrian 2008). Beside the rising temperatures, the greater thermal variability (e.g., heat waves, cold waves), and the increased frequencies of extreme climatic events (e.g., droughts, torrential flood events) strongly impact lake ecosystems (Wilhelm 2012; Diffenbaugh et al. 2017).

The characteristically small surface of mountain lakes leads to a very close catchment-lake linkage. Changes in the catchment area, regarding run-offs and greening, but also land use and tourism activities significantly influence the mountain lakes, especially habitat stability, water transparency, nutrient concentrations, and finally substrate availability and heterogeneity. Climate-related upward shifts of the tree- and forest line, increasing vegetation cover and soil microbial biomass in alpine and subalpine altitudes significantly alter nutrient release into the lakes (Rogora et al. 2020) and result in enhanced DOC concentrations (Adrian et al. 2009). Frequency and intensity of heavy rainfall events, landslides and debris flows has increased significantly in the Alps over the last 30 years (Bogataj 2007; Wilhelm et al. 2012; Bätzing 2015). Runoff extremes such as high-intensity precipitation or rain-on-snow events play an important role in sediment mobilization and transport (Knapp et al. 2018) influencing nutrient availability and underwater light climate (Perga et al. 2018).

Dynamics within the cryosphere of mountain regions influence downstream aquatic ecosystems by regulating water runoff, erosion rates, sediment and nutrient transport (Huss et al. 2017). Changes in winter snowpack volume and timing and rate of spring snowmelt exercise bottom-up control of phytoplankton biomass and phenology by influencing nutrient loading rates (Sandro et al. 2018) and water temperatures (Roberts et al. 2017). Glacier-fed lakes lose their connection to the retreating glaciers (Tiberti et al. 2019) and a highly specific, cold and turbid habitat, which is hosting highly specialized communities disappears (Peter and Sommaruga 2016). Thawing of permafrost and rock glaciers not only lead to slope destabilization, flooding, and debris flows, but also influence the water chemistry (higher electrical conductivity, ion concentrations and heavy metal contents) and diatom composition and diversity of adjacent surface waters (Thies et al. 2013; Mair et al. 2015; Rotta et al. 2018).

The rising air temperatures and increased moisture trigger enhanced weathering rates in carbonate catchments and result in increasing pH-levels, ion concentrations (bicarbonate, calcium and magnesium) and conductivities of well buffered-lakes (Rogora et al. 2020; Adrian et al. 2009).

Warming-induced changes of lake properties and nutrient availability impact both littoral and pelagial habitats and shape the structure of macrophyte, periphyton and phytoplankton communities (McMaster and Schindler 2005). Figure 1.1 shows schematically the pathways of direct and indirect impacts of climate change on mountain lake primary producers. Changes in physical characteristics of the lakes, including surface temperature, ice cover phenology, stratification and mixing regime of the water column and the resulting alteration of oxygen concentration and nutrient cycling directly effect their phenology, species composition and biomass. The rising air temperatures indirectly impact the primary producers via alteration of the catchment area. Losses of glaciers, permafrost and snow pack, soil development and shifts in vegetation type and cover change water chemistry and DOC concentrations. Extreme precipitation events result in enhanced turbidity reducing light availability for algae and macrophytes. Prolonged droughts, on the other side result in falling lake levels and the alteration of the lake's biogeochemistry. Besides climate change, local disturbances and long-distance atmospheric fertilization seriously affect lake algae and macrophytes via altering the nutrient situation of the lakes.

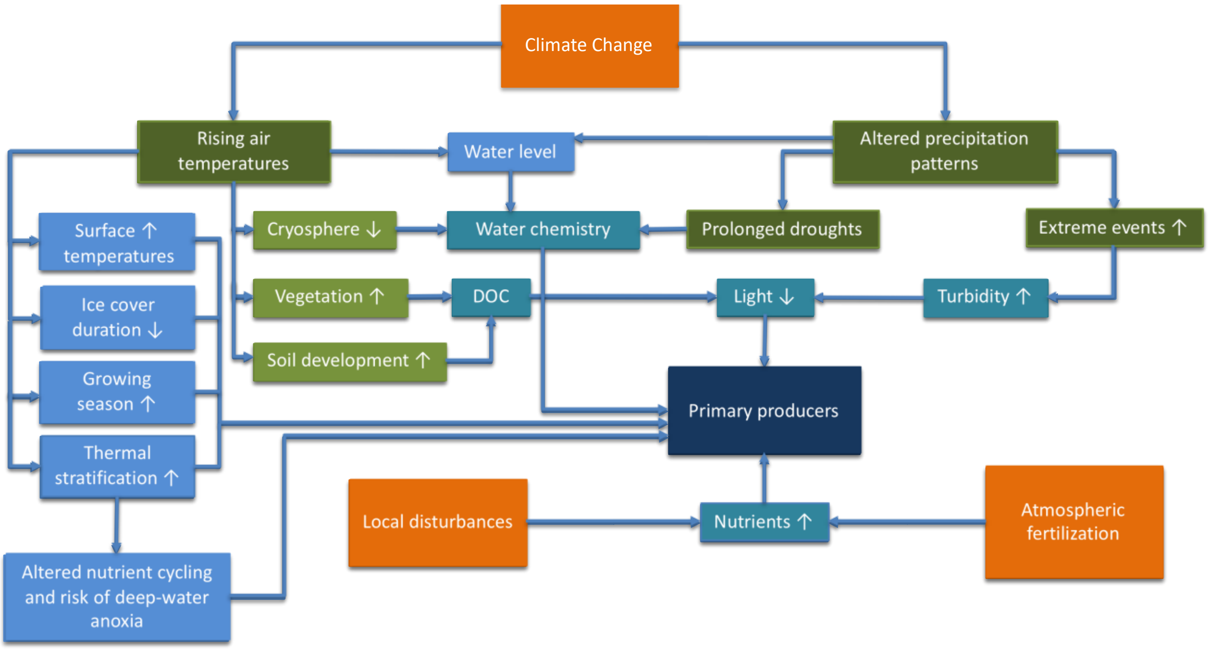


Figure 1.1 Schematic diagram showing the main stressors on mountain lake primary producers (PP): climate change, local disturbances and fertilization by long-distance atmospheric deposition (orange). The main impacts of climate change result from changes of air temperatures and alterd precipitation patterns including prolonged droughts and rising frequency of extreme events (dark green) and affect the PP directly via alteration of hydrological features (light blue) or indirectly via catchment modifications (light green). The resulting changes of water chemistry, DOC concentration and water turbidity influence PP directly or by alteration of the light climate (turquoise).

Macrophytes, providing habitat and refuge for epiphytic species, are expected to increase significantly in species richness in response to global warming, especially at high altitudes (Rosset et al. 2010). Low temperatures, the lacking of fine-grained sediment, and low nutrient concentrations or disturbances such as floods (resulting in turbidity) or marked water level fluctuations (resulting in desiccation, sediment resuspension, and light limitation at high lake levels) generally limit macrophyte growth in subalpine and alpine lakes (Bornette and Puijalon 2011; Fernández-Aláez 2018). Although macrophytes may occur at low temperatures (Boylen and Sheldon 1976; Olesen and Madsen 2000) and in lakes of higher altitudes (Overton 1899), macrophytes' temperature optima are usually > 20 °C (Bounette and Puijalon 2011). The rising temperatures enable macrophytes growth at higher altitudes. Additionally, the rising nutrient input triggered by the development of the vegetation cover in the catchment and the enhanced availability of fine-grained substrate facilitate the establishment of macrophytes (Garcia et al. 1994). The extended littoral heterogeneity and substrata availability culminate in more complex and diverse periphytic communities (Vadeboncoeur et al. 2006; Poulíčková et al. 2014; Cantonati and Lowe 2014).

The response of phytoplankton to climate change is complex owing to the interaction of temperature, UV radiation, light conditions, nutrient availability, and grazing pressure (Doyle et al. 2005). Rising temperatures directly affect phytoplankton metabolic processes (photosynthesis, growth, nutrient uptake) and impact phytoplankton sinking rates via altering water column viscosity and density (Zohary et al. 2020). Warming-induced changes in lake thermal and mixing regimes affect phytoplankton taxonomic composition and size structure and alter the competitive interactions for limiting resources among phytoplankton (Winder and Sommer 2012). Prolonged and intensified thermal stratification favours small-sized or motile (e.g. flagellate) organisms. Non-motile, passively floating algae cells usually require turbulent mixing of the water column. However, several phytoplankton species developed strategies to regulate their settling rate by forming protuberances, colonies or chains and Cyanobacteria use gas vacuoles as buoyancy-regulating mechanism (Diehl et al. 2002; Ptacnik et al. 2003; Reynolds 2006).

Milder winters lead to an earlier ice-off culminating in an earlier phytoplankton spring bloom (Adrian et al. 2006). However, temperatures generally have a greater impact on higher trophic levels, as the metabolic requirements of predators are more sensitive to warming environments (Murphy et al. 2019). Therefore, elevated temperatures may result in an inverse effect on phytoplankton biomass despite enhanced metabolism as a result of top-down control of enhanced grazing activity of overwintering zooplankton (Sommer and Lewandowska 2011; Sommer et al. 2012).

Total phytoplankton biomass in remote lakes is mainly indirectly controlled via climate-regulated nutrient release from the catchment (Jansson et al. 2010; Williamson et al. 2010) or via atmospheric nitrogen deposition (Jacquemin et al 2018). Additionally, local impacts such as tourism, alpine pasture, deforestation, mountain-hut-sewage, and fish-stocking modify nutrient availability and regulate algae biomass (Giguet-Covex et al. 2011; Moser et al. 2019). Reduced light availability triggered by climate-induced intensification of erosion processes and by shading due to the increase of phytoplankton biomass strongly impact both benthic and pelagic communities (Reynolds 2006).

Primary producers play an important role in lake ecosystems as they regulate nutrient cycles (C-fixation, N/P sequestration) and energy flow (Vadeboncoeur et al. 2014). The reorganisation within both, littoral and pelagic primary producers has cascading effects on the mountain lake ecosystem, as they form the base of the aquatic food web. Therefore, an improved understanding of the mechanism how climate affects the structure and dynamics of phytoplankton and periphytic communities is important for predicting climate change impacts on mountain lake ecosystems.

1.3 Paleolimnology

Paleolimnological records archived in lake sediments provide reliable insights into lake ecosystem responses to global, regional and local environmental changes such as climate warming, long distance atmospheric deposition, and lake eutrophication (Catalan et al. 2013). A series of biological, biochemical and geochemical paleoindicators are available to reconstruct climate-mediated changes in lake-properties, diffuse fertilizing processes and trophic state history. Analyses of subfossil diatom assemblages and pigments in lake sedimentary records are highly valuable to characterise community shifts in algal functional groups in relation to changing climate and environmental regimes. Stable isotope analyses of carbon and nitrogen provide information about origin of sedimentary organic matter and the trophic history of the lake.

Diatoms (Bacillariophyceae), unicellular, microscopic algae characterized by their aesthetic, siliceous cell walls (Battarbee et al. 2001), are among the most frequently used bioindicators in paleolimnological investigations revealing both direct and indirect consequences of global change (Stoermer and Smol 2010). They are highly abundant and ecologically diverse and exhibit planktonic, tychoplanktonic and periphytic life strategies colonizing a wide range of semiaquatic and aquatic habitats worldwide (Rühland et al. 2008). Their resistant siliceous frustules are typically well preserved in lake sediments (Smol 2008). Furthermore, specific ecological preferences and short life cycles enables them to respond sensitively and rapidly to a wide range of environmental changes including water temperature, lake alkalinity, salinity, nutrient regime, water transparency, lake mixing regime, habitat stability, and substrate availability (Rühland et al. 2015). Many species have well-defined optima and tolerances to a series of limnological variables (Douglas et al 2004).

Numerous paleolimnological studies observed unprecedented diatom assemblages shifts over the last 150 years in response to global warming (e.g., Douglas et al. 1994; Weckström et al. 1997; Michelutti et al. 2003; Smol et al. 2005; Karst-Riddoch et al. 2005; Rühland et al. 2002-2015). Species-poor periphytic diatom assemblages dominated by small, benthic taxa especially of the *Stauosira- Staurosirella- Pseudostaurosira-* complex shifted to more complex and diverse periphytic assemblages (Rühland et al. 2015). Several studies highlighted the sensitivity of diatoms to increasing water temperatures (Stoermer and Ladewski 1976; Kilham et al. 1996; Pienitz et al. 1995) or described distinct temperature optima of a series of diatom taxa (Wunsam et al. 1995; Cremer et al. 2001; Bouchard et al. 2004). Water temperature controls diatom growth, cell division and succession (Lotter et al. 2010) and influences the viscosity of raphe cytoplasm and thus the velocity of motile diatoms (Round et al. 1990). Already Hustedt´s (1930) classification of diatoms based on their thermal requirements. Besides warming temperatures, primarily changes regarding habitat stability and substrate variability control the dynamics of diatom communities. Planktonic and tychoplanktonic diatoms require turbulent mixing of water column due to their immobility and their high sinking rates owing to their heavy, siliceous valves (Reynolds 1984). Polymictic lakes, however, were predicted to stratify more permanently (Gerten and Adrian 2002). Small-celled cyclotelloid species, characterised by a high surface/volume ratio have significant competitive advantages during more stable and intense thermal stratification due to their low sinking velocity, high cell division rates and more effective nutrient uptake and light harvesting mechanism (Rühland et al. 2003). Besides small-sized centric diatoms (e.g. *Cyclotella* spp.), elongate, colony-forming pennate planktonic diatoms (e.g. *Fragilaria* spp.) increase significantly in their abundances, while heavily silicified tychoplanktonic diatoms (*e.g. Aulacoseira*) concurrently decline (Rühland et al. 2015).

Sedimentary pigments provide valuable insights into the impact of climate change and local anthropogenic activities on lake ecosystems (Zhang et al. 2019) by tracking historical changes in lake productivity (Guilizzoni et al. 2011) and taxonomic composition of past phototrophic communities (Leavitt and Hodgson 2001). Paleopigments are usually well archived in lake sediments, often representing the sole remains of non-siliceous algae (Lami et al. 2000). The main autochthonous sources of pigments are planktonic and periphytic algae, phototrophic bacteria and macrophytes (Leavitt and Hodgson 2001). However, their unstable character is a major problem when interpreting sedimentary pigment records (Leavitt 1993). After the death of an organism, its decomposition begins immediately. Already in the water column during the sinking process, more than 95% of the components are decomposed very intensively and rapidly by oxidation, cell lysis, and grazing. After deposition at the lake’s bottom, temperature, oxygen and light availability as well as the intensity of bioturbation determine the rate of pigment degradation in the surface sediment (Sun et al. 1993).

Analyses of carbon (C) and nitrogen (N) stable isotopes deposited in lake sediments are widespread used to get information about sources of sedimentary organic matter (OM) (Mayr et al. 2009), shifts within lacustrine nutrient cycling (Lehmann et al 2004) and variations of lake productivity (McKenzie 1985; Hollander and McKenzie 1991; Hollander and Smith 2001; Meyers and Teranes 2001). Climate change may alter lacustrine C and N dynamics mainly via catchment-related processes (altered precipitation and erosion patterns, changes in vegetation and soils development).

Especially the $\delta^{13}C_{org}$ records reflect changes in lacustrine paleoproductivity. Aquatic primary producers discriminate against ^{13}C during assimilation of aqueous CO_2. Hence, ^{13}C accumulates in the pool of epilimnetic dissolved inorganic carbon (DIC). With increasing productivity, phytoplankton and periphyton increasingly use $^{13}CO_2$ for biomass production (Farquar et al. 1989; Teranes and Bernasconi 2005) resulting in an increasing accumulation of ^{13}C in the organic material. Therefore, rising $\delta^{13}C_{org}$ values of OM deposited in the lake sediments indicate lake eutrophication (Teranes and Bernasconi 2005). However, the $\delta^{13}C_{org}$ record in the sediments is not exclusively determined by photosynthesis. Other biochemical processes such as respiration and methane oxidation also influence the isotope ratio (Finlay and Kendall 2007). For example, in nutrient-rich lakes with anoxic conditions in deep water, methanotrophic bacteria produce ^{12}C-rich DIC, resulting in decreasing $\delta^{13}C_{org}$ values despite increasing eutrophication (Hollander and Smith 2001).

The isotope fingerprints of nitrogen ($\delta^{15}N$) in the sediments also provide information about the former trophic situation of a lake. However, the interpretation of the N-isotope signal is much more difficult. The biochemical complexity of the nitrogen cycle and the multitude of fractionation effects lead to a high variability of the $\delta^{15}N$ values (Teranes and Bernasconi 2000). Phototrophic organisms discriminate against the heavier ^{15}N, therefore ^{15}N accumulates in the pool of dissolved inorganic nitrogen (DIN) in surface water (Lehmann et al. 2004). However, in lacustrine environments, where phosphorus rather than nitrogen is the limiting factor of primary productivity (Wetzel 2001), only a minor portion of the available nitrogen is consumed. Hence, the nitrogen isotopic composition of the DIN pool will remain largely unaltered. Rising primary production will not be reflected by increasing $\delta^{15}N$ as other factors than primary productivity more strongly influence the nitrogen isotopic composition of lacustrine OM (Teranes and Bernasconi 2000). Denitrification in anoxic basins and external nitrogen inputs from agricultural land use or livestock husbandry result in ^{15}N enrichment of the epilimnetic DIN pool (Kendall 1998; Gu 2009). Atmospheric nitrogen deposition leads to the decrease of $\delta^{15}N$ concentrations in the sediments (Hastings 2009). Shifts in phytoplankton species composition also may influence $\delta^{15}N$ signatures of sedimentary OM. N-fixing cyanobacteria result in ^{15}N-depleted OM (Fogel and Cifuentes 1993), while heterotrophic organisms elevate $\delta^{15}N$ as there is an increase of 3-4 ‰ for each trophic value (DeNiro and Epstein 1981). Records of nitrogen isotopes in OM therefore may reflect variations in epilimnetic nitrate utilization and enable the reconstruction of algal community structure and nutrient supply (Teranes and Bernasconi 2000).

Organic matter in lake sediments usually consists of a mixture of allochthonous and autochthonous sources. The ratio of total organic carbon to total nitrogen (TOC/TN) provides information about the origin of OM (Meyers and Teranes 2001). Values below 10 indicate autochthonous production by phytoplankton (Meyers 1994), while values above 25 indicate cellulose-rich vascular plants (Mayr et al. 2009). Sedimentary TOC/TN ratios above 10 therefore indicate allochthonous inputs of terrestrial plant material (Meyers 1994).

In summary, lake sediments can provide highly valuable insights to our understanding of environmental changes including global warming, long distance atmospheric deposition (industrialization, traffic, synthetic fertilizer from intensified agriculture) and local impacts (biological manipulation, deforestation, tourism, alpine pasture, agriculture).

1.4 Thesis objectives and outline

Climate change will be among the most serious stressors on freshwater ecosystems in the future. In the Alps an average temperature increase of 2.5°C by AD 2100 is predicted compared to the period from AD 1979 to AD 2000 (Kunstmann and Smiatek 2015). Chains of intertwined processes triggered by the rapidly rising temperatures and the altered precipitation patterns are interacting in complex ways with other anthropogenic influences such as local disturbances and atmospheric fertilitation. The resulting impacts on their ecosystem services highlight the importance of better understanding the hydrological, chemical and floral structure and function of mountain lake ecosystems.

The overall aim of this thesis was to understand response and resilience of mountain lakes located in the Bavarian and North-Tyrolian Alps to global change. The studied lakes are situated along an elevational gradient (1000-1900 m a.s.l), crossing the forest line and the tree line and differing in terms of remoteness, lake origin, catchment geology, surface area, basin depth and morphology, hydrological characteristics, and lake productivity.

I coupled contemporary and paleolimnological approaches by combining high-frequency monitoring data of physical lake parameters (temperature, conductivity, pH, oxygen, Secchi depth, and lake thermal structure), water chemistry (total phosphorus, silica, ammonia-nitrogen, and nitrate-nitrogen), and lake primary producers (phytoplankton, diatoms, macrophytes) with long-term paleolimnological data (subfossil diatoms, sedimentary pigments and stable isotopes) preserved in lake sediments.

In detail, the main objectives of this thesis were:

1. a better understanding of the linkages between climate forcing, lake thermodynamics, and diatom response by the detailed analyses of hydrochemical and hydrophysical paramenters, modern diatiom assemblages, phytoplankton succession and submerged macrophytes.

2. to disentangle the complex interactions between climate change and other human-induced impacts by analysing subfossil diatom assemblages, sedimentary pigments and stable isotope fingerprints in sedimentary records.

3. to evaluate how altitude affects the response of diatom assemblages to global change considering different lake origin, catchment characteristics (morphology, soil, vegetation cover, land-use) and hydrological features (depth, nutrient level, habitat stability).

This thesis is based on following hypotheses:

1. local anthropogenic disturbances such as touristic activities, forestry or agriculture may overprint the effects of global warming

2. lake altitude is the main driver controlling the response of primary producers to climate change

3. lake depth influences the structure of algal communites and the response of mountain lakes to rising temperatures

4. subalpine lakes are particularly appropriate to investigate climate-mediated changes of catchment-lake interactions

2. Material and Methods

2.1 Study sites

The studied lakes are located over a distance of about 220 km along the Bavarian-Austrian borderline (47°17´ to 47°45´N latitude, 10°15´to 13°1´E longitude). The altitudinal gradient ranges from 955 to 2047 m a.s.l. representing eight montane (922 – 1207 m a.s.l.), nine subalpine (1458 – 1680 m a.s.l.) and eight alpine (1809 – 2060 m a.s.l.) lakes (Table 2.1).

Table 2.1 Geographical position, altitude, depth and surface area of the mountain lakes included in this thesis.

	Lake	Latitude (N)	Longitude (E)	Altitude (m a.s.l.)	Lake area (ha)	Mean lake depth (m)	Presented in chapter			
							3	4	5	6
montane	Bichlersee	47°40‘34“	12°07‘21“	955	1.5	11.0			×	×
	Frillensee	47°45‘57“	12°49‘03“	973	1.2	5.5			×	×
	Lautersee	**47°26‘13“**	**11°14‘08“**	**1013**	**12**	**18.0**			×	×
	Ferchensee	**47°26‘18“**	**12°12‘50“**	**1060**	**10.8**	**19.5**			×	×
	Mittersee	47°22‘07“	10°51‘58“	1082	3.3	4.7			×	×
	Höfersee	47°29‘51“	10°29‘25“	1192	0.6	1.9			×	×
	Taubensee	47°41‘46“	12°25‘37“	1138	4.0	14.6			×	×
	Sieglsee	47°24‘30“	10°29‘46“	1207	0.8	20.2			×	×
subalpine	Soinsee	47°39‘01“	11°57‘20“	1458	4.0	8.2			×	×
	Grünsee	47°30‘07“	12°57‘11“	1474	3.5	6.9			×	×
	Gaisalpsee	47°45‘56“	12°49‘03“	1508	3.4	4.1			×	×
	Unterer Soiernsee	**47°29‘27“**	**11°21‘35“**	**1552**	**3.4**	**5.5-15.0**	×		×	×
	Oberer Soiernsee	**47°29‘77“**	**11°20‘44“**	**1558**	**3.5**	**13.1**	×	×	×	×
	Delpssee	**47°30‘19“**	**11°30‘36“**	**1600**	**0.6**	**1.3**			×	×
	Hörnlesee	47°32‘52“	10°23‘29“	1601	0.5	1.8			×	×
	Funtensee	47°29‘37“	12°56‘22“	1601	2.5	4.5			×	×
	Schachensee	**47°25‘27“**	**11°07‘12“**	**1680**	**0.8**	**4.4**			×	×
alpine	Seeleinsee	47°32‘16“	13°01‘47“	1809	0.4	5.4			×	×
	Soiernlache	**47°29‘05“**	**11°20‘47“**	**1843**	**0.7**	**1.0**				×
	Drachensee	**47°21‘31“**	**10°56‘05“**	**1874**	**5.3**	**20.7**			×	×
	Engeratsgundsee	47°26‘29“	10°23‘30“	1876	3.6	17.3			×	×
	Brendlsee	47°21‘58“	10°57‘30“	1903	1.5	6.2			×	×
	Stuibensee	**47°25‘39“**	**11°03‘41“**	**1921**	**0.8**	**5.1**				×
	Rappensee	47°17‘09“	10°15‘10“	2047	2.3	7.8			×	×
	Grubersee	47°27‘13“	11°47‘18“	2060	0.5	3.5			×	×

The sediments of all lakes, with the exception of Stuibensee and Soiernlache were analysed in terms of subfossil diatoms, sedimentary pigments and stable isotopes. Contemporary limnological studies were carried out on a set of lakes (Table 2.1, bold font) including hydrophysical measurements and analyses of hydrochemical parameters and primary producers (phytoplankton, diatom assemblages, macrophytes).

2.2 Catchment

2.2.1 Geology, vegetation and land-use

The geology of the lakes catchments was mapped, supported by geological maps 1: 25 000 (LfU Bayern). Catchment vegetation was documented using following rough classification: montane forest, dwarf shrub, subalpine grassland and alpine meadow. Land-use (agriculture, alpine pasture, forestry) and touristic impacts were recorded. Landowner, forestry offices, alp farmers and single sections of the Alpine association were interviewed regarding land-use history, mountain hut construction and sewage disposal.

2.2.2 Stable isotope analyses

Samples from soils and vegetation (herbs, leaves and pine needles) representing potential sources of terrestrial organic matter entering the lakes were collected. Disposable gloves were worn during sampling to avoid any contamination. In laboratory the samples were coarsely crushed with scissors, oven-dried (40 °C) and homogenized by sieving (soils) or grinded with a mortar. For the determination of total organic carbon content (TOC) and organic carbon isotope ratios ($\delta^{13}C$) ~ 2 mg material was weighted in silver capsules and decalcified first with 5 % and then with 20 % HCl at 70 °C. To analyse the nitrogen content (TN) and the nitrogen stable isotope ratio ($\delta^{15}N$) ~ 2.5 mg material was weighted in tin capsules. Both nitrogen and carbon isotope analyses follow Mayr et al. (2015), described more detailed in chapter 2.4.5.

2.2.3 Meteorological station

To estimate the divergence of a local microclimate from the regional meteorological conditions a weather station (Davis Vantage Pro 2^{TM}) was installed at the Lakes Soiernseen. Air temperature, wind direction and speed, solar radiation, rainfall and humidity data were collected half-hourly from June to November 2016. The data were downloaded every 28 days for detailed analyses using the software WeatherLink (Davis, Hayward, U.S.A.)

2.3 Limnological characterization of the lakes

2.3.1 Lake bathymetry

The sonar systems Biosonics MX and Lowrence HDS 8 were used to determine the basin morphology, lake maximum depth, and the distribution of macrophytes. The lakes were surveyed in a 10 m grid (Fig 2.1). The program Visual Habitat (Biosonics) and the software Reefmaster (Lowrence) were used to transform the data for designing the bathymetric maps with the program ArcView (ESRI).

Figure 2.1 Navigation grid of Lake Stuibensee

2.3.2 Lake mixing regimes

Temperature data loggers (Onset Hobo Pedant) were installed at depths of 0.2, 3, 5 and 8 m (subalpine and alpine lakes) and 0.2, 3, 5, 10 and 17 m (montane lakes) at buoys to obtain continuous temperature recordings. The buoys were positioned at the deepest areas of the lakes by fixing the rope at boulders on the lake bottoms. In lakes with minor lake level fluctuations the temperature data loggers were attached to the buoy with a second rope weighted with a bag of stones (Fig. 2.2 A). In lakes with marked lake level dynamics the following design was used (Fig 2.2 B): the rope with the buoy runs through carabiners fixed at two large boulders placed at the lakes bottom at a distance of about two meters. A second, smaller buoy was attached to the end of the rope holding the larger buoy at the water surface by its buoyancy. Here the data loggers were fixed directly at the rope.

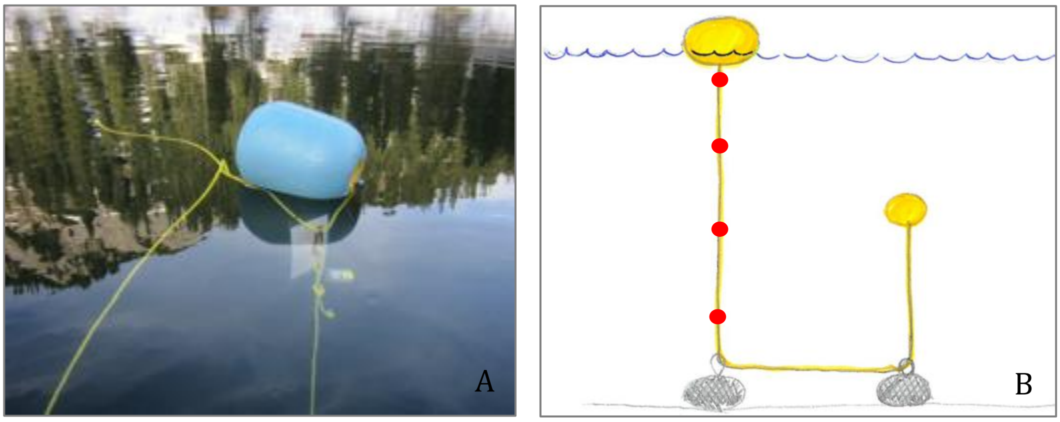


Figure 2.2 Installation of temperature data logger in lakes with minor (A) and marked (B) lake level fluctuations

2.3.3 Hydrophysical measurements and hydrochemical analyses

During ice-free periods, the hydrophysical parameters (temperature, conductivity, pH, oxygen) were measured monthly in vertical one-meter depth steps with a multiparameter probe (MPP 930 IDS WTW, Weilheim, Germany). At the same time water transparency was documented with a Secchi disk and water samples for hydrochemical analyses were taken in two-meter meter steps and 0.5 m above the sediment using a Ruttner sampler. The samples were transported cooled and light protected to the laboratory, where they were first filtered and then analysed for nitrate-nitrogen (DIN 38405-9:2011-09), ammonia-nitrogen (Navone 1964) and silica (Nanocolor silica test, Macherey-Nagel, Düren, Germany). Total phosphorus was analysed in unfiltered samples following DIN 171 EN ISO 6878. The concentrations were determined via spectrometric analyses (Hitachi 150-20, Japan).

2.3.4 Phytoplankton analyses

Phytoplankton analyses were carried out monthly during two vegetation periods in 2015 (May-September) and 2016 (May-November). Mixed water samples were taken from the euphotic zone using a hose sampler (DIN EN 16698:2015-12). Lake water was immediately filled in 100 ml brown glass bottles already containing 2 ml Lugol's solution. The phytoplankton samples were analysed according to Utermoehl (1958). Firstly, the fixed sample was filled into 50 ml sedimentation chambers. After 24 hours the organisms had sedimented on the bottom of the counting chamber (Furet and Benson-Evans 1982) and the plankton community could be classified under an inverted microscope (Leitz Labovert). For this purpose, phytoplankton species were counted in 10 squares evenly distributed over the chamber firstly at 100-fold, then at 200-fold and 400-fold magnification. In case of very small or difficult to identify species 1000 x magnification under oil immersion was applied. Taxonomy followed Huber-Pestalozzi (1938-1982). As phytoplankton cell size differ significantly among diverse genera, cell biovolume rather than quantity is more appropriate for phytoplankton analyses. The biovolumes of the different species were taken from Raeder (1990) or calculated by simplifying their shape to geometrical basic bodies (Sun and Liu 2003).

2.3.5 Analyses of current diatom communities

The current diatom assemblages were sampled from stones at four littoral sites evenly distributed along the lake’s shores. The topsides of five to eight stones from water depths of ~ 30 cm were brushed with a clean disposable toothbrush to remove the periphyton (Schaumburg et al. 2014). To consider seasonal and successional changes within littoral diatom assemblages the sampling was carried out three times a year in spring, summer and autumn. This approach avoided errors regarding diatom substrate specificity and the epilithic diatomic inventory of each lake was recorded considering spatial and seasonal heterogeneity. Thus, the water quality of each lake could be determined and variations among water-bodies of different altitudes could be detected.

In Lake Schachensee and both Lakes Soiernseen additionally depth-distribution of benthic diatom assemblages in relation to light and substrate was investigated. Therefore, samples were taken along depth-transects in one-meter depth increments and additionally at 0.3-0.5m depths. A team of scientific divers collected three fist-sized stones in closable, labeled polyethylene bags at each sample point. Additionally, they carefully pulled off the uppermost sediment layer (sand, silt, clay) at each site using a labeled 60 ml-syringe. The epilithon was removed from the stones with disposable toothbrushes and then mixed with 20 ml of sediment-water-suspension (epipsammon, epilpelon, epiphyton and sedimented planktonic organism) from the respective sampling depth in plastic bottles for subsequent analyses.

In laboratory, the sub-samples were prepared for diatom analyses according to van der Werff (1953). About 50 ml H_2O_2 (30 %) was added to each sample. After overnight incubation at room temperature, the samples were heated for at least four hours to oxidize organic material. Then a spatula tip of $K_2Cr_2O_7$ was added slowly and in portions to accelerate the oxidation process. Finally, about 10 drops of concentrate HCl was added to remove carbonates. Subsequently, the material was cleaned with distilled H_2O in four centrifugation steps (centrifugal acceleration 523 g). Permanent slides were prepared by embedding cleaned material in Naphrax (R.I. = 1.7). At least 550 pennate diatom valves per sample were identified under oil immersion at 1000x magnification using a Leitz Aristoplan microscope. Taxonomy followed Krammer and Lange-Bertalot (1986-1991), Lange-Bertalot (1993, 1996), Krammer (1997), Lange-Bertalot (2000-2003) and Hofmann et al. (2013), updated by current publications about individual species and different internet databases (Spaulding et al. 2018; Guiry and Guiry 2019). Water quality of each lake was calculated using the diatom Trophic Index (T_i, Formula 1) of Hofmann (1999).

$$Ti = \frac{T*G*H}{G*H} \qquad (1)$$

Ti = Trophic index H= abundance
T = trophic preferences G= sensitivity value

Diversity was calculated via Shannon-Index (H, Formula 2) and Evenness (E, Formula 3).

$$H = -\sum_{i=1}^{S} pi * \ln pi \qquad (2)$$

S = total numbers of species occurring in the community
i = taxon of community p = relative abundance of each taxon

$$E = \frac{H}{\ln S} \qquad (3)$$

H = Shannon-Index S = total number of species occurring in the community

2.3.6 Macrophyte mapping

The macrophyte mapping was carried out by a team of scientific divers once during the main vegetation period in August 2016 at Lake Schachensee and both lakes Soiernseen. The mapping method of Melzer and Schneider (2001) was slightly modified. Parallel to the slope the depths of 1-2 m, 2-3 m and > 3 m were snorkelled or scuba-dived. Beside the submerged and emerged macrophyte populations, the shore vegetation (reed beds, sedges) and the morphology, the structure of the lake bottom and the expansion of stony and muddy substrata were documented. The quantities of the occurring species were estimated on the basis of a five-step scale according to Kohler (1978). The species were determined already in the field. For verification, some individuals were additionally analysed under a stereomicroscope (Wiloscope, Hund Wetzlar). Taxonomy followed van de Weyer and Schmidt (2007). Macrophytes as well as stems of reeds and sedges were carefully sampled in plastic bags for stable isotope analyses. In laboratory the material was cleaned, oven-dried (40 °C) and subsequently crushed in a mortar.

2.4 Sediment analyses

2.4.1 Coring and sediment preparing

The sediment cores were obtained from the deepest part of each lake using a gravity corer (Uwitec, Mondsee, Austria) equipped with a 6-cm-diameter core tube. At Lake Ferchensee coring was carried out in February 2015 through a 40 cm thick ice cover. A 25 cm-diameter hole was drilled through the ice with a hand ice auger (Mora, Sweden). The sediment cores of the other lakes were retrieved in 2015 (Schachensee, C1 Oberer Soiernsee), in 2016 (Lautersee, Drachensee, Unterer Soiernsee, Delpssee, Brendlsee, Höfersee, Hörnlesee, Sieglsee, Mittersee, Rappensee, Engeratsgunsee), in 2017 (C2 Oberer Soiernsee, Bichlersee, Frillensee, Taubensee, Soinsee, Grünsee, Gaisalpsee, Funtensee, Seeleinsee, Grubersee) and in 2018 (C3 Oberer Soiernsee) using a rubber boat.

The sediment core surfaces were fixed with floristic foam (Mosy, Thedinghausen, Germany) and wrapped in an opaque foil. In the laboratory, the cores were split into two haves and subsampled in 1 cm intervals under subdued green light (Fig. 2.3). Subsequently, the subsamples were freeze-dried in plastic vials for diatom analyses, dating and stable isotope analyses (Christ 1-4 Loc; 48 h, -47 °C). For pigment analyses, subsamples were stored in aluminium foil at -24 °C until freeze-drying.

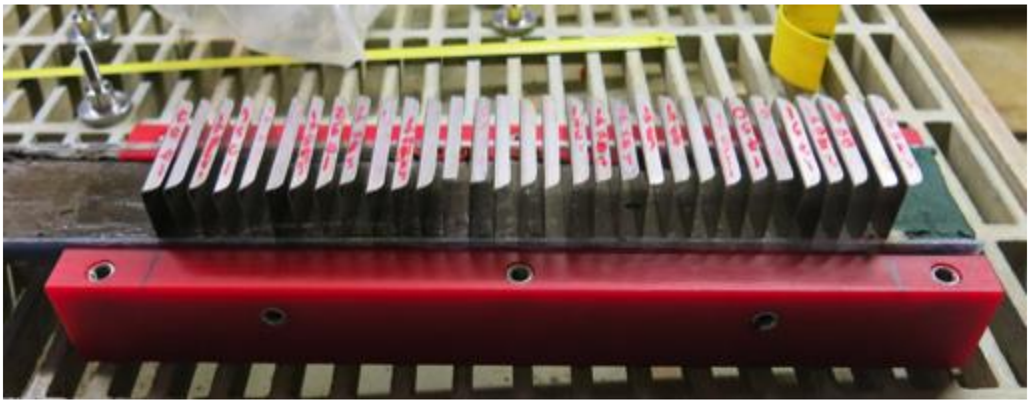


Figure 2.3 Subsampling the sediment cores

2.4.2 Sediment chronology

For sediment dating, 5 ml of the freeze-dried material was homogenized in a mortar, filled into labelled sampling tubes and weighed (R 160 P, Sartorius AG, Germany). The sediment cores were dated using ^{210}Pb (half-life 22.3 years) and ^{137}Cs (half-life 30.2 years) at EAWAG Dübendorf in Switzerland using a gamma spectrometer (High-purity Germanium Detector, Canberra). In paleolimnology, the ^{210}Pb method has become generally accepted for age determination of recent lake sediments deposited during the past 150 years (Robbins 1978). The constant rate of ^{210}Pb supply (CRS) model has proved to be an appropriate dating model even in lakes with non-uniform sedimentation rates (Appleby and Oldfield 1978). However, a perfect exponential decrease of ^{210}Pb activity concentration with increasing depth is extremely rare owing to disturbances of surficial sediments by bioturbation or increased sedimentation rates as a result of flood events or rising algae biomass (Rose et al. 2010, Sanchez-Cabeza and Riuz-Fernández 2012, Putyrskaya et al. 2015). The ^{210}Pb chronology has to be validated by independent chronostratigraphic dates, e.g. the sedimentary record of the artificial radionuclide ^{137}Cs (Appleby 2001, Kirchner 2011). Global fallout of ^{137}Cs began in 1954 and peaked in 1963 as a result of nuclear weapon tests. ^{137}Cs entered the atmosphere as an artificial, radioactive product of uranium nuclear fission, spread worldwide and was deposited by precipitation or dry deposition. During the Chernobyl reactor accident in 1986, an extremely high amount of radioactive nuclide activity was released and distributed irregularly across Europe. The sedimentation rates of the investigated lakes were calculated by combining the CRS ^{210}Pb dating model with^{137}Cs benchmarks (1954, 1963 and 1986). Supporting information was provided by photographical and lithological documentation of the sediment cores.

2.4.3 Subfossil diatom assemblages

For diatom analyses, 1.6 ml freeze-dried sediment was prepared following standard procedure (see section 2.3.5). At least 550 diatom valves per sample were identified under oil immersion at 1000x magnification using a Leitz Aristoplan microscope. Taxonomy followed the literature listed in section 2.3.5. The diversities of the subfossil assemblages were characterized by species richness and Shannon Index. The ratios between benthic+epiphytic and planktic species (B:P ratio) were used to identify alterations regarding the extension of the euphotic zone. The shift within the ratio between the most dominant fragilarioid species *Staurosirella pinnata* (Ehrenberg) Williams and Round and *Staurosira construens* var. *venter* (Ehrenberg) Hamilton (P:V ratio) was used to detect the onset of a warming trend (Cremer et al. 2001).

Past surface temperatures (Ø TSiVa) were inferred by using the novel silicification value (SiVa) developed by Kuefner et al. (2020 a).

$$\text{Ø}\, TSiVa\,[°C] = 25{,}956 - 4.7155 * SiVa \tag{4}$$

Past total phosphors (TP) concentrations were calculated by applying the TP interference model of Lotter et al. (1998).

Diatom concentrations were calculated by the number of microscope fields of view in relation to the amount of dry sediment (Formula 5).

$$diatoms/\mu l = \frac{N\,total}{Fv}/Vcs * Vt * D \tag{5}$$

N_{total} = amount of counted diatom valves in total
Fv = analysed fields of views
Vcs = volume of one counting square ((volume of dropped diatom dilution*area of one counting square)/area of the cover glass)
Vt = total volume of cleaned diatom solution
D = dilution of cleaned diatom material

2.4.4 Sedimentary pigments

Pigment analyses were performed following the method of Leavitt and Hodgson (2001). Under subdued green light ~ 0.3 g freeze-dried subsamples were filled into 4 ml amber glasses and extracted using 99 % Aceton (Rotisolv HPLC, Carl Roth, Germany). Subsequently the glasses were stored at -20°C for 24 h. After gently shaking 2 ml of the extract was filled into 2 ml Eppendorf tubes and centrifuged for 15 min at 2000 rpm and – 9 °C (Heraeus Fresco 17/21, Thermo Fisher Scientific, Schwerte, Germany). Using syringes with 0.2 µm PTFE filters, 1-1.5 ml supernatant was filtered into 1.5 ml HPLC glasses. Then the samples were stored deep-frozen (-80 °C) until analyzes. The individual pigments were identified and quantified by straight-phase high-performance liquid chromatography (HPLC, MD-2015 plus, Jasko, Pfungstadt, Germany) and measured by 436 nm and 450 nm detectors (Wright et al. 1991). The system was calibrated with standards from VWR (Darmstadt, Germany) and DHI (Hørsholm, Denmark). Chlorophyll a (chl a), its degradation derivate pheopythin a (phe a) and ß-carotene were used as marker pigments for total algal biomass and primary production (Leavitt and Hodgson 2001). The population dynamics of the green algae were tracked using chlorophyll b (chl b) and several carotenoids (lutein, neoxanthin, prasinoxanthin, zeaxanthin). Diatoms were detected by the pigments diatoxanthin, fucoxanthin and diadinochrome (degradation product of diadinoxanthin). Chrysophyta were represented by violaxanthin and fucoxanthin, Dinophyta by peridinin and diadinochrome/diadinoxanthin. Alloxanthin was selected to track abundances of Chryptophyta. The chl a/phe a ratio was used to estimate the pigment preservation in the sediments.

Table 2.2 Identified pigments, their abbreviations, stability (1= major stability, 4 = minor stability), functional groups of pigment molecular structure (stability declines with number of structure) and taxonomic affinity

Pigment	Pigment code	Stability (Leavitt and Hodgson, 2001)	Functional groups (Buchaca and Catalan 2008)	Taxonomic affinity
Chlorophyll a	Chl-a	3		Plantae, Algae
Chlorophyll b	Chl-b	2		Plantae, Chlorophyta, Euglenophyta
Alloxanthin	Allox	1	2	Cryptophyta
ß-carotene	ß-carot	1	0	Plantae, Algae
Diadinoxanthin	Diadin	3	3	Diatoms, Dinophyta
Diatoxanthin	Diato	2	2	Diatoms
Fucoxanthin	Fuco	2	5	Siliceous algae (Diatoms, Chrysophyta)
Lutein	Lut	1	2	Chlorophyta, Euglenophyta, Plantae
Neoxanthin	Neox	4	4	Chlorophyta, Euglenophyta, Plantae
Peridinin	Perid	4	6	Dinophyta
Prasinoxanthin	Prasi			Chlorophyta
Violaxanthin	Violax	4	4	Chrysophyta, Chlorophyta
Zeaxanthin	Zeax	1	2	Cyanobacteria, Chlorophyta
Diadinochrome	Diadinchr			diadinoxanthin degradation product
Ethyl-8´-beta-apocarotenoate	Ethyl			ß-carotene degradation product
Pheophytin a	Phe a	1		chl a degradation product (senescence)

2.4.5 Stable isotopes

Freeze-dried subsamples were sieved (250 µm mesh size) to homogenize and to remove organic macro-fossils (e.g., leaves, mosses, shells) and filled into 20 ml plastic vials using a brush. Sieve and brush were cleaned with oil-free compressed air after each sieving process. For the analysis of the total organic carbon content (TOC) and organic carbon isotope ratios ($\delta^{13}C$) ~ 2 mg of sieved material was weighted in silver capsules and decalcified first with 5 % and then with 20 % HCl at 70 °C. For the determination of the nitrogen content (TN) and the nitrogen stable isotope ratio ($\delta^{15}N$) ~ 2.5 mg of the homogenized material was weighted in tin capsules. Both nitrogen and carbon isotope analyses follow Mayr et al. (2015): The folded capsules were combusted at 1080 °C under constant helium flow (NC2500, Carlo Erba). The resulting gases first run through a reaction tube filled with silvered cobaltous and chromium oxides. Subsequently, the gas passed a reduction tube filled with copper wires (560°C), before running through a water trap filled with magnesium perchlorate and finally passing a gas chromatography column. $\delta^{15}N$ and $\delta^{13}C$ ratios were determined by analysing the isolated gases (N_2 and CO_2) in an isotopic-ratio mass spectrometer (DeltaPlus, Thermo-Finnigan, Germany). TOC and TN mass percentages were calculated from peak-areas using elemental standards (atropine, cyclohexanone-2.4-dinitrophenylhydrazone) and were presented as mass percentages (wt %). TOC/TN ratios were expressed as mass ratios. Isotope ratios were presented in δ–notation ($\delta^{15}N$ and $\delta^{13}C$) and given in ‰ (Formula 6).

$$\delta = \frac{RS}{RSt-1} \qquad (6)$$

RS = isotope ratio of the sample
RSt = isotope ratio of the international standards VPDB (carbon) and AIR (nitrogen)

Following Brand et al. 2014, several international standards (IAEA-N-1; IAEA-N-2; USGS41; IAEA-CH-7) as well as an internal laboratory standard (peptone) were used for isotope calibration.

2.4.6 Sediment pore water

Sediment pore water pH was measured in a sediment core retrieved in Lake Oberer Soiernsee. The pore water was directly sampled in the field using Rhizon SMS 10 cm (Eijkelkamp Soil and Water, Giesbeek, Netherlands) core solution samplers (2.5 mm diameter, 0.15 µm mean pore size). In total eight three-mm-diameter holes were drilled through the tube wall of the closed core using a gimlet. The

Figure 2.4 Pore water sampling (Lake Oberer Soiernsee)

saturated Rhizon samplers were inserted horizontally through the holes into the sediment. Then 10 ml syringes (Eijkelkamp Soil and Water, Giesbeek, Netherlands) were luer-lock connected with the Rhizon samplers. The pistons of the syringes were entirely pulled out to generate a vacuum and held open with a wooden retainer. The vacuum in the syringes is the driving force for pore-water extraction. Pore water passed from the sediment through the porous tubes and flexible hoses into the syringes. After three hours the Rhizons obtained sufficient pore water, and pH was directly measured (Multi 3630 IDS, WTW, Weilheim, Germany).

2.5 Statistical analyses

Statistical analyses were conducted in PAST 3.18 (Hammer and Harper 2006), PALSTAT 3.20 (Ryan et al. 1995), R version 3.4.1 with the package 'vegan' (Oksanen et al. 2018) and R version 3.4.3 with the package rioja (Juggins 2017).

Depth-constrained cluster analyses (Euclidean hierarchal clustering) were applied for defining the different assemblages-zones of the current diatom flora. To verify the dissimilarity of the defined assemblage-zones one-way analyses of similarity (ANOSIM, Clarke 1993) were run with 9999 permutations.

Redundancy analyses (RDA) were run with 999 permutations to determine the variance in diatom communities that can be explained by depth.

Diatom-inferred WA-PLS models were developed to reconstruct past fluctuations of lake-levels and TP concentrations.

Principal component analyses (PCA) were applied for graphical illustration of the current diatom-communities grouping in different depth zones and for detecting inter-lake variances of climate change response of the subfossil diatom floras.

Detrended correspondence analyses (DCA) were used to quantify diatom compositional turnover (β-diversity). To identify the decisive parameters determining species turnover, generalized linear models (GLM) with AIC-based stepwise backward model selection were calculated.

Broken-stick models (Bennet 1996) were calculated to detect the stratigraphic position of major changes within diatom assemblages, pigment compositions and stable isotopes in the sedimentary records.

Data preparation and transformations were conducted in Microsoft Excel 2016 ®. Down-core profiles of subfossil diatom assemblages, pigment concentrations and stable isotope records were illustrated by using C2 version 1.7.7 (Juggins 2007).

3. Depth-distribution of lake benthic diatom assemblages in relation to light availability and substrate: implications for paleolimnological studies

A similar version of this chapter was published: Hofmann AM, Geist J, Nowotny L, Raeder U (2020) Depth-distribution of lake benthic diatom assemblages in relation to light availability and substrate: implications for paleolimnological studies. Journal of Paleolimnology 64(3): 315-334.

Candidate´s contribution:
The candidate primarily conceived this study with critical revision of Jürgen Geist and Uta Raeder Hydrophysical and hydrochemical characterization of the lakes was carried out by the candidate and the graduate student Joachim Hilber. Diatom sampling strategy was designed by the candidate. Diatom analyses were realized by the candidate and Lena Nowotny. Phytoplankton analyses were carried out by Lena Nowotny and the graduate student Julia Mayr. The manuscript was drafted and finalized by the candidate with continuous input and revision by Jürgen Geist and Uta Raeder.

3.1 Abstract

We analyzed the depth-distributions of benthic diatoms in two adjacent, but hydrologically distinct subalpine lakes (Lakes Soiernseen, S-Germany). Lake Unterer Soiernsee is affected by marked water-level fluctuations and is light-penetrated to the bottom most of the year, while Lake Oberer Soiernsee provides more stable conditions and an extended aphotic zone. Mixed samples of epiphytic, epilithic, epipsammic and epipelic periphyton were taken in one-meter depth steps by scuba divers. Most of the common benthic diatoms occurred in distinct depth-areas. RDA analyses showed that depth was strongly correlated with species distribution in both lakes. Depth-constrained cluster analyses indicated three distinct diatom community zones in each lake. A shallow littoral zone hosting mainly epiphytic and epilithic species and a deeper littoral zone with mainly epipsammic and epipelic taxa existed in both lakes. Additionally, a highly disturbed near-shore littoral zone with diatoms adapted to unstable conditions (aerophilic taxa, pioneer species) was found in Lake Unterer Soiernsee, and a deep-water pelagic zone with mainly planktonic taxa in Lake Oberer Soiernsee. Light availability, substrate, physical stressors and nutrient concentrations were linked closely with water depth. While light availability affected the ratio of benthic and planktonic diatoms, substrate type influenced benthic diatom assemblage structures.

Diatoms occurring in surficial sediments of the aphotic zone represent an ideal cross-section of the recent diatom assemblage of the lake, including benthic and planktonic species. However, sediment samples taken in light-flooded depths are inappropriate for studies based on shifts between benthic and planktonic taxa, because *in-situ* benthic species dominate the surface-sediment assemblages, while settled tychoplanktonic and planktonic species occur less frequently. A diatom-inferred depth model was created for each lake to prove the usability for down-core studies using weighted-averaging approaches (WA-PLS). For both lakes these models are highly appropriate to reconstruct past fluctuations in water-transparency or lake-level. With regard to development of diatom-based TP-transfer-functions for Bavarian mountain lakes, we found it is highly important to consider lake depth and transparency. Based on the findings of this study we recommend the creation of two different training-sets, one for deep or low-transparency lakes with an aphotic zone including both benthic and planktonic diatoms, and another one for shallow, clear water lakes solely using benthic diatoms.

3.2 Introduction

Current global change is of multidimensional character (Catalan et al. 2013). Climate warming coupled with eutrophication is one of the most powerful drivers for the observed alarming alterations of aquatic ecosystems (Jacobson et al. 2017). Nutrient inputs into lakes, even into remote mountain lakes, have changed dramatically over many centuries due to human impacts such as deforestation, alpine pasture, fish stocking and mountain-hut-sewage (Kamenik et al. 2000) as well as changes in atmospheric deposition (Wolfe et al. 2001; Battarbee et al. 2010) and climate change (Dokulil 2013; Perga et al. 2015). Altered biogeochemical processes in the catchment triggered by regional climate warming may cause increased allochthonous nutrient loading, especially in combination with enhanced erosion as a result of increasing frequency and intensity of extreme rainfall events and storms (Dokulil 2013). Increasing air temperature may affect internal lake processes, mainly by enhanced algal productivity and altered thermal structure resulting in internal nutrient enrichment generated by nutrient release due to hypolimnetic oxygen stress (Anderson et al. 2012; Jeppesen et al. 2010). Direct impacts of climate warming, e.g. shortened ice cover duration, longer growing seasons, and increased water column stability, may alter the composition of primary producers. This is for instance evident from the increase of small-celled or colony-forming planktonic diatom taxa or benthic diatom assemblage complexity and species richness (Rühland et al. 2015). Due to their persistence, diversity and abundance in aquatic ecosystems, diatoms are widely used in paleolimnological studies. Their resistant and species-specific siliceous valves are well preserved in lake sediments (Batterbee et al. 2001; Smol 2008). Many diatom taxa have well-defined habitat requirements and substrate preferences as well as distinct optima and tolerances relating to pH-value, to salinity or to nutrient levels (Smol 2008; Battarbee et al. 2010) making them ideal indicators for the reconstruction of past environmental conditions. Diatoms respond rapidly to environmental and climate-driven changes in lake properties, thus they are highly suitable to reconstruct climate warming (Rühland et al. 2015) and lake eutrophication/recovery (Hall and Smol 2010). Past fluctuations of climate or trophic conditions are well preserved in lake sediment records (Smol 2008). Paleolimnological studies typically use shifts in ratios between planktonic and benthic diatom assemblages to reconstruct a series of climate-mediated water column properties, e.g. ice cover dynamic, mixing regime (Rühland and Smol 2005) and extension of the euphotic zone, as function of water level (Leira et al. 2015) or water transparency/nutrient status (Sayer and Roberts 2001; Laird et al. 2010; Althouse et al. 2014). In order to facilitate the reliable application of diatom-based predictions with respect to climate warming, eutrophication or water-level alterations, accurate knowledge of species-level diatom distribution in relation to lake ecosystems dynamics (habitat stability, substrate heterogeneity, light- and nutrient availability) is important.

Here we present data from high-resolution analyses of diatom depth-distribution patterns in two adjacent subalpine lakes characterized by similar catchment geology, climate conditions, conductivity, pH and TP concentrations, but significantly different hydrological features such as depth, mixis type, and water-level fluctuations.

Previous diatom depth-distribution studies are either less detailed regarding the spatial resolution (Stevenson and Stoermer 1981; Moos et al. 2005; Cantonati et al. 2009) or based on several lakes with a range of regional and local factors (Kingsbury et al. 2012). Comparable detailed studies (Laird et al. 2010; Kingsbury et al. 2012; Gushulak et al. 2017; Raposeiro et al. 2018) exclusively used samples from the sediment surface. All these studies did not consider either epilithic or epipsammic/epipelic diatoms. However, to reproduce depth-distribution patterns of lake diatom communities all substrates should be included. We chose our sampling strategy (mixed substrate, including dead and live frustules) with regard to the applicability to paleolimnological analyses of sedimentary records, as surficial sediments contain *in-situ* diatom taxa, dead valves from adjacent substrates, and sedimented frustules.

The objectives of our study were (1) to characterize the spatial variations in diatom assemblage composition with respect to depth, (2) to consider if these variations are significant enough to develop a diatom-inferred depth model for the studied lakes to reconstruct water-level dynamics via diatom assemblages preserved in lake sediments, (3) to identify potential differences between the diatom assemblages of the two adjacent but hydrologically different lakes, and (4) to validate if the studied lakes are appropriate calibration lakes for a surface sediment training set, in order to develop diatom-based TP (total phosphorus) transfer function for alkaline mountain lakes of the northern Alps.

With respect to spatial variations, we hypothesised (1) that the light availability controls the ratio between benthic and settled planktonic diatoms in surficial sediments and (2) that mainly the substrate influences the depth-distribution of benthic diatoms. Additional hypotheses were that in case of prevailing aphotic conditions the diatom assemblages in surficial sediments of the deepest part of the basin are appropriate for diatom-based training sets to infer (3) past fluctuations of lake-levels and (4) trophic conditions.

3.3 Materials and methods

3.3.1 Study site

Lakes Soiernseen (1552 m and 1558 m a.s.l.) are located in the Bavarian Alps 50 km south of Munich (Germany, Fig. 3.1) and are of glacial origin (März 1903).

Originally, they formed a linked cirque lake until an end moraine belt divided the upper lake from the lower lake (Schmidt-Thomé 1953). Lithology and geological setting of the catchment area are dominated by Triassic dolomite and carbonate rocks (Schmidt-Thomé 1953), which form the main karst aquifer. Quaternary glacial erosion caused the present shape of the caldron. Semipermeable

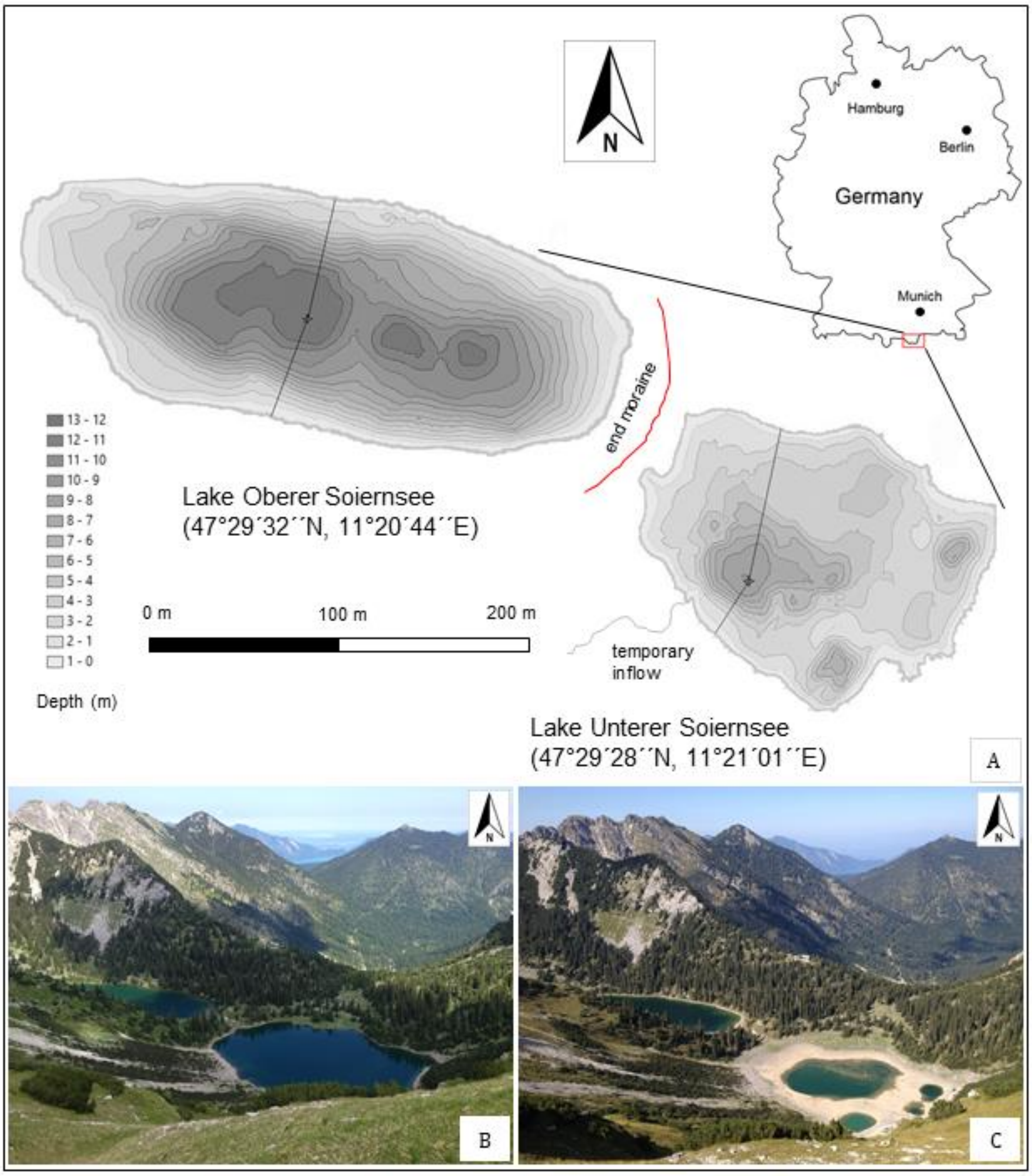


Figure 3.1 Lakes Soiernseen: geographical location (A), bathymetric chart (A) including the course of the sampling transects. Photos taken in June (B) and October (C) show the extreme water level fluctuations of Lake Unterer Soiernsee

moraine deposits seal the subsoil, forming the aquiclude (impermeable horizon) in the catchment area. Postglacial rock streams, talus slopes and alluvial cones have created another aquifer overlaying glacier deposits. Underground drainage dominates and underwater springs feed the lakes. Only Lake Unterer Soiernsee has a small surface inflow on the southwestern part of the lake. It constitutes the runoff from an artificial spring providing drinking water for two mountain huts. Lake Oberer Soiernsee drains through the permeable end moraine deposits into Lake Unterer Soiernsee (März 1903). Surface runoff from the upper to the lower lake occurs only after snowmelt, when water level is highest. Both lakes drain via groundwater into a small stream, springing up north of the cirque threshold. Anthropogenic pollution may occur from a small private mountain hut with a dry toilet, close to northern shore of Lake Oberer Soiernsee and from a nearby Alpine Association cottage, both highly frequented during summer months. The area surrounding the lakes is used for cattle grazing in July and August and the lakes are drinking water for the cattle. The high mountains (Schöttelkarspitze 2050 m, Soiernspitze 2257 m and Gumpenkarspitze 2019 m) forming the southern part of the surrounding caldron limit solar radiation during winter time (November-March).

3.3.2 Sampling and data collection

The lakes were studied from August 2014 to November 2016. In August 2014, the morphology of the two lake basins was mapped with a sonar device (Biosonics Mx, Seattle USA). Temperature data loggers (Onset Hobo Pendant) were placed at depths of 0.2, 3, 5 and 8 m at a buoy positioned at the deepest areas of the lakes to record water temperature continuously from June 2015 to November 2016. A weather station (Davis Vantage Pro 2^{TM}) collected wind velocity and precipitation data from June to November 2016. Data from the weather station and the temperature loggers were used to gain information about energetic dynamics of the littoral zone and stratification patterns, which govern nutrient exchange between the epilimnion and the hypolimnion. The sampling frequency for physical parameters and phytoplankton analysis was monthly during ice-free periods (May-October 2015 and June-November 2016). Physical parameters (temperature, conductivity, pH, oxygen) were documented in one-meter depth increments using a multi parameter probe (MPP 930 IDS WTW, Weilheim, Germany). Transparency was measured using a Secchi Disk. Mixed water samples for phytoplankton analysis were taken from the euphotic zone (Z_{eu}), calculated on basis of Tilzer (1988)

$$\mathrm{Z}_{eu} = 5 * \sqrt{Secchi - Depth}$$

using a hose sampler (DIN EN 16698:2015-12). Water samples for hydrochemical characterization were taken monthly (May-October 2015) at 0.2, 2, 4, 6, 8, and 10 m depth as well as 0.5 m above the sediment (depending on seasonal water levels) using a Ruttner sampler. Concentrations of total phosphorus (DIN EN ISO 6878), silica (Nanocolor silica test, Macherey-Nagel, Düren, Germany), nitrate-nitrogen (DIN 38405-9:2011-09) and ammonia-nitrogen (Navone 1964) were subsequently determined via spectrometric analyses (Hitachi, 150-20, Japan).

Diatom sampling for the depth profile took place in August 2016, at the same time as the macrophyte mapping of the lakes. Scuba divers recorded the structure of the lake bottom and the expansion of the different substrates (macrophytes, stones, sediment). They took the samples for diatom analyses in 0.3-0.5 m depths according to the European Water Framework Directive (Schaumburg et al. 2014) and in one-meter depth increments along N-S transects encompassing differences in degree of slope, wind and wave exposure, and seasonal light conditions. The locations of the depth-transects we used in this study are shown in Fig. 3.1. The scuba divers collected three fist-sized stones in closable, labeled polyethylene bags at each sample point. Additionally, they carefully pulled off the uppermost sediment layer (sand, silt, clay) using labeled 60 ml-syringes. Epilithon was removed from the stones using disposable toothbrushes. Epilithon and 20 ml of sediment-water-suspension (epipsammon, epilpelon, epiphyton and sedimented planktonic organism) from each sampling depth were mixed together in 200 ml-polyethylene bottles for subsequent analyses. The covering on the stones was documented descriptively and the estimation of the grain size was carried out by the finger test.

3.3.3 Diatom analysis

Mixed samples were prepared for diatom analysis using standard procedures: heating with 30 % hydrogen peroxide for at least four hours to oxidize organic material, then adding concentrate hydrochloride acid to remove carbonates and finally rinsing the processed material with distilled H_2O in four centrifugation steps (centrifugal acceleration 523 g). Cleaned material was embedded in Naphrax (R.I. = 1.7) to get permanent slides. At least 550 pennate diatom valves per sample were identified under oil immersion at 1000x magnification using a Leiz Aristoplan microscope. Centric diatoms were summarized to "*Centrales*". taxonomy followed Krammer and Lange-Bertalot (1986-1991), Lange-Bertalot (1993, 1996), Krammer (1997), Lange-Bertalot (2000-2003) and Hofmann et al. (2013), updated to recent taxonomic nomenclature using current publications about individual species and different internet databases (Spaulding et al. 2018; Guiry and Guiry 2019). We used Trophic Index TI (Hofmann1999) to evaluate trophic state of the lakes at the different depths along the two profiles. Planktonic diatoms were analyzed according to Utermöhl (DIN EN 15204) using an inverted microscope (Leitz Labovert).

3.3.4 Statistical analysis

Only species with relative abundances greater than 1 % in at least one sample were included in statistical analysis using PAST (version 3.18) statistical software package (Hammer and Harper 2006). Species abundances were Hellinger transformed (Legendre and Gallagher 2001) before analysis. Principal component analysis (PCA) was used for graphical illustration of diatom-community-grouping in different depth zones and enables identification of the species most responsible for defining these zones. A prior DCA test (first DCA Axis <3 units of standard division) indicated that a linear PCA approach was appropriate for our study (Lepŝ and Ŝmilauer 2003). Depth-constrained cluster analysis (Euclidean hierarchal clustering in PAST) was used to define the different diatom-assemblage zones. A one-way analysis of similarity (ANOSIM, Clarke 1993) was run with 9999 permutations in PAST to verify the similarity of the defined community-zones. Species richness and diversity (Shannon-Index, evenness) were calculated in PAST (Bootstrap N 9999). RDA was run with 999 permutations using R (version 3.4.3) and the package vegan (Oksanen et al. 2018) to determine the variance in diatom communities that can be explained by depth. Quantitative depth models were developed using R (version 3.4.3) and the package rioja (Juggins 2018). For both lakes the strongest model based on a weighted-averaging partial-least-square approach (WA-PLS) with 2 components (Lake Oberer Soiernsee) and 3 components (Lake Unterer Soiernsee) were selected, respectively. RMSE results were calculated under cross validation with bootstrapping.

3.4 Results

3.4.1 Bathymetry

Lake Unterer Soiernsee consists of one main basin (max. depth 15 m) and three smaller basins on the eastern part of the lake (max. depths 8-12 m, Fig. 3.1 A). During the study period (August 2014 - November 2016), marked seasonal water-level fluctuations were observed (9.5 m). The elongated basin of Lake Oberer Soiernsee has a maximum depth of 14.5 m (Fig. 3.1 A). Moraine material seals the lake's bottom; therefore, the lake-level fluctuations (1.8 m) are less than in Lake Unterer Soiernsee. Generally maximum lake-levels occur after snowmelt followed by continuous decrease of the lake water level during summer and a minimum during winter drought (Fig. 3.1 B, 3.1 C). However, after longer rainy periods, short-term lake-level rises were observed. In August 2016, during diatom sampling, maximum depths of 8.5 m (Lake Unterer Soiernsee) and 13.5 m (Lake Oberer Soiernsee) were measured.

3.4.2 Weather station data

During the ice-free period (June-November), a rainfall sum of 1348 mm was measured. Four heavy rainfall events (>20 mm h^{-1} precipitation) were recorded: June 12 (25.4 mm), June 24 (21.6 mm), July 7 (23.9 mm) and August 18 (22.3 mm). The July-event resulted in low water transparency during our sampling on August 2 (1.8 m Secchi depth). The predominant prevailing wind directions W (16 %), ESE (15 %), WSW (14 %) and E (13 %) and subsequent water action primarily affect the northern shores of both lakes.

3.4.3 Physical and chemical parameters

Average Secchi disk transparency was around 4 m in both lakes. Heavy rainfall events during the study period with massive surface runoff caused several short-term turbidities with Secchi-depths lower than 1 m in both lakes. However, Lake Unterer Soiernsee was light-flooded to the bottom during most of the study period. In contrast Lake Oberer Soiernsee is characterized by light-limited conditions in the deepest part of the lake, as its euphotic zone comprised about 10 m of water column. Temperature logger data as well as monthly measuring during ice-free periods point out the polymictic character of Lake Unterer Soiernsee, with a tendency towards short-term stratification during stable, warm periods. Due to polymixis no vertical gradients in chemical and physical parameters occurred. Only slight, seasonal variations in chemical and physical parameters were observed in Lake Unterer Soiernsee. In contrast, Lake Oberer Soiernsee showed longer periods of stable stratification. The pH values, as well as nitrate-nitrogen concentrations, decreased slightly with increasing depth whereas total phosphorus concentrations increased marginally with depth during summer months. Conductivity, as well as ammonia-nitrogen and silica concentrations were directly proportional to depth. The mean total phosphorus concentrations suggested an oligo-mesotrophic character of both lakes. A massive thunderstorm in July 2015, with intense rainfall and mudflows caused extreme turbidity of the lakes for nearly six weeks, resulting in a significant increase of total phosphorus concentrations in both lakes (approx. 30 $\mu g\ l^{-1}$). The karst catchment causes low conductivities in both lakes.

3.4.4 Phytoplankton

Phytoplankton biomass and species composition of the submerged vegetation indicate oligo- to mesotrophic conditions. In general, phytoplankton biomass was very low and consisted mainly of Dinophyceae and Diatomeae, dominated by the pennate, colony-forming *Fragilaria nanana*. Centric diatoms occur in very low proportions. Tychoplanktonic diatoms detached from their substrate reached abundances up to 35 % (Lake Unterer Soiernsee) and 7 % (Lake Oberer Soiernsee) of the bulk plankton biomass.

3.4.5 Substrate for benthic diatoms

The macroalga *Chara contraria* A. Braun ex Kützing dominated the submerged vegetation of both lakes. At the date of macrophyte mapping, *C. contraria* formed continuous meadows in the three smaller basins of Lake Unterer Soiernsee and occurred in patches of different sizes in its main basin (1-3 m). In Lake Oberer Soiernsee, light mixed stands of *C. contraria* and *C. tomentosa* L. occurred up to 6 m depths. *Ranunculus trychophyllus* Chaix ex Villard appeared along the entire shoreline of Lake Oberer Soiernsee but only in scattered patches in the northern part of Lake Unterer Soiernsee. *Potamogeton alpinus* Balb. was found in small patches at 0.5-1.5 m depths only in Lake Oberer Soiernsee.

Stones dominated as substrate in Lake Unterer Soiernsee, but with increasing depths they were more and more covered by sediment. At the deepest point of the lake stones lacked and exclusively fine sediment occurred. At the deepest area of Lake Oberer Soiernsee the sediment was rather solid covered only by a thin, loose layer. With decreasing depths, the sediment became more and more loose (billowing). In depths greater than 7-8 m, mainly sediment was availably as substrate for benthic diatoms and even the stones were covered by sediment. Between 7 m and 3 m stones, at the southern slope even boulders dominated and sedimentary sites were rare. Near the shore (0-3 m) stones and sediment were evenly distributed and the sediment was no longer billowing, but soft, with a flaky, loose coating. The finger test underlines the divers' observations that the sediment becomes denser and therefore finer with increasing depths.

3.4.6 Diatoms

A total of 229 pennate diatom taxa belonging to 51 genera were found in 46 samples taken from Lakes Soiernseen. The 31 most frequent taxa (contributing >1 % of the diatom community) are listed in Table 1. Additionally, five centric species could be identified in both lakes. Hierarchal clustering and PCA allowed the definition of different depth correlated community-zones with characteristic diatom species (Figs. 3.2, 3.3). Three benthic zones were identified in Lake Unterer Soiernsee, two benthic zones and a planktonic zone in the Lake Oberer Soiernsee. One-way ANOSIM tests running with 9999 permutations point out the significant differences between the community-zones.

Diatom assemblage zones

Results from the RDA showed that depth strongly correlated with diatom species distribution. RDA Axis 1 highly significantly ($p<0.001$) explained 23 % (Lake Unterer Soiernsee) and 35 % (Lake Oberer Soiernsee) of the variance according to the Monte Carlo Permutations Test. The developed WA-PLS models provide a robust reconstructive relationship between diatom-distribution and lake depth: r^2=0.95; RMSEP=0.59 m (Lake Unterer Soiernsee) and r^2=0.56; RMSEP=2.55 m (Lake Oberer Soiernsee).

Table 3.1 Most frequent pennate diatom taxa (> 1 %) of both lakes Soiernseen, their abbreviations, trophic and moisture preferences. ***T*** *(trophic preferences, Hofmann 1999): 1.0-1.8: oligotraphent; 1.9-3.0: oligo- to mesotraphent; 3.1-4.4: meso- to eutraphent; 4.5-5.0: eutraphent.* ***G*** *(sensivity value, Hofmann 1999): 1-3.* ***VDT*** *(trophic preferences, van Dam et al. 1994): 1: oligotraphent; 2: oligo- to mesotraphent; 3: mesotraphent; 4: meso- to eutraphent; 5: eutraphent; 7: oligo- to eutraphent.* ***VDM*** *(moisture preferences, van Dam et al. 1994): 1: almost never occuring outside water bodies; 2: mainly occurring in water bodies; 3: mainly occurring in water bodies and regulary in wet places; 4: mainly occurring in wet places; 5: nearly exclusively occurring outside water bodies.*

Taxa	Acronym	T	G	VDT	VDM
Achnanthes minutissimum var. "schmale Sippe" Krammer and Lange-Bertalot	Ach_sch				
Achnanthidium caledonicum Lange-Bertalot	A_cal	1.8	3		
Achnanthidium minutissimum var. *jackii* (Rabenhorst) Lange-Bertalot	A_jac				
Achnanthidium minutissimum var. *minutissimum* (Kützing) Czarnecky	A_min			7	3
Achnanthidium sp.	A_sp.			1	
Achnanthidium straubianum Lange-Bertalot	A_str				
Adlafia bryophila (Petersen) Lange-Bertalot	Adl_bry			3	5
Amphora pediculus (Kützing) Grunow	Amph_ped			5	3
Brachysira neoexilis Lange-Bertalot	Bra_neo	1.9	2		
Delicata delicatula (Kützing) Krammer	Del_del	1.5	3	1	3
Denticula tenuis Kützing	Det_ten	3	1	3	3
Diadesmis contenta (Grunow) DG Mann	Dia_con				
Encyonema minutum (Hilse) DG Mann	Enc_min	2	2		
Encyonopsis cesatii (Rabenhorst) Krammer	Encyo_ces	1.5	3	1	3
Encyonopsis krammeri Reichardt	Encyo_kra				
Encyonopsis microcephala (Grunow) Krammer	Encyo_mic			4	3
Encyonopsis minuta Krammer and Reichardt	Encyo_min				
Encyonopsis subminuta Krammer and Reichardt	Encyo_sub				
Fragilaria nanana Lange-Bertalot	Frag_nan	2.1	1	2	2
*Hippodonta neglecta (*Lange-Bertalot) Metzeltin and Witkowski	Hip_neg				
Navicula cryptotenella Lange-Bertalot	Nav_cry			7	2
Nitzschia dealpina Lange-Bertalot and G Hofmann	Nit_dea	2.5	1		
Nitzschia dissipata var. media (Hantzsch) Grunow	Nit_med				
Nitzschia fonticola Grunow	Nit_fon	4.5	3	4	1
Nitzschia lacuum Lange-Bertalot	Nit_lac			3	
Platessa conspicua (A Mayer) Lange-Bertalot	Plat_con			7	1
Pseudostaurosira robusta (Fusey) Williams and Round	Pseu_rob	2.5	1		
Sellaphora mutata (Krasske) Lange-Bertalot	Sel_mut			2	2
Simonsenia delognei (Grunow) Lange-Bertalot	Sim_del	4.5	3	4	4
Staurosira venter (Ehrenberg) Hamilton	Stau_ven			4	1
Staurosirella pinnata (Ehrenberg) Williams and Round	Stau_pin			7	3

The PCA scatterplots indicate discrete diatom communities along the depth gradients in both lakes and detect the taxa relevant for these arrangements. In Lake Unterer Soiernsee, separation of the diatom assemblages from the depths 0-4 m (LS_1) and the depths 5-8 m (LS_2) is clearly visible (Fig. 3.4 A). However, the separation of the 8.5 m-depth triggered by dominance of *Sellaphora mutata* (Krasske) Lange Bertalot is less obvious. The remarkable outside position of 0m_S is caused by dominance of *Diadesmis contenta* (Grunow) DG Mann. The scatterplot of Lake Oberer Soiernsee (Fig. 3.4 B) shows the clusters of the deepest samples (P: 12-13.5 m) differing from those of mid depth group (LD: 7-11 m) and the shallow water samples (LS: 0-6 m). The extraordinary position of the deep-water sample 11m_N within the near shore samples lead to the assumption that we sampled erratic stones at this depth (Fig. 3.4 B).

Depth-distribution of the diatoms in Lake Unterer Soiernsee

In Lake Unterer Soiernsee, 19 samples were taken and a total of 169 pennate diatom species representing 46 genera were identified, 21 of them occurred in abundances >1 % (Table 1). Pennate diatoms dominated the diatom assemblages by far. Centrales were only found sporadically (0.4 %) and were mainly represented by *Cyclotella praetermissa* and *Cyclotella comensis*. *Encyonopsis subminuta* Krammer and Reichardt (12 %), *Achnanthidium minutissimum* var. *minutissimum* (Kützing) Czarnecki (11 %), *Denticula tenuis* Kützing (9 %), *Brachysira neoexilis* Lange-Bertalot (7 %), and *Achnanthidium sp.* (5 %) were the most frequent diatoms. Depth-constrained cluster analysis and PCA separate three benthic community-zones, a near-shore littoral zone (LS_1), a shallow littoral zone (LS_2), and a deeper littoral zone (LD) (Figs. 3.2, 3.4 A).

With increasing depth, abundances of certain taxa changed gradually and there were differences between the gentle northern slope and the steeper southern slope. There was no clear, sharp boundary identified between the three zones, rather areas of higher abundances of certain taxa, gradually changing with depth. *Diadesmis contenta* only occurred in the near-shore samples of the southern transect (57 %), *Simonsenia delognei* (Grunow) Lange-Bertalot dominated the southern transect at a depth of 6 m (14 %). *Denticula tenuis* reached highest abundances between 3-6 m along the northern transect (LS_1, LS_2), but it was most abundant between 2-4 m along the southern transect (LS_1). The following dominant species preferred distinct depths: *Achnanthes minutissimum* var. "schmale Sippe" Krammer and Lange-Bertalot, *Achnanthidium caledonicum* Lange-Bertalot, *Brachysira neoexilis,* and *Encyonopsis subminuta* were most abundant in LS_1, whereas *Achnanthidium straubianum* Lange-Bertalot, *Achnanthidium sp., Hippodonta neglecta* (Lange-Bertalot) Metzelin and Witkowski, *Simonsenia delognei,* and *Staurosirella pinnata* (Ehrenberg) DM Williams and Round were the characteristic species of LS_2. The deeper littoral zone (LD) was dominated by *Sellaphora mutata.* Several subdominant species (*Diploneis oculata* (Brébisson) Cleve, *Amphora pediculus* (Kützing)

Grunow, *Gyrosigma acuminatum* (Kützing) Rabenhorst and *Fallacia lenzii* (Hustedt) Lange Bertalot) also showed marked preferences for LS_2. Some of the most common species (*A. minutissimun* var. *minutissimum*, *A. minutissimum* var. *jackii* (Rabenhorst) Lange-Bertalot, *Fragilaria nanana* Lange-Bertalot and *Navicula cryptotenella* Lange-Bertalot), however, were found throughout the depth profile. Statistical analysis points out the special character of 0m_S with its dominant appearance of *Diadesmis contenta*.

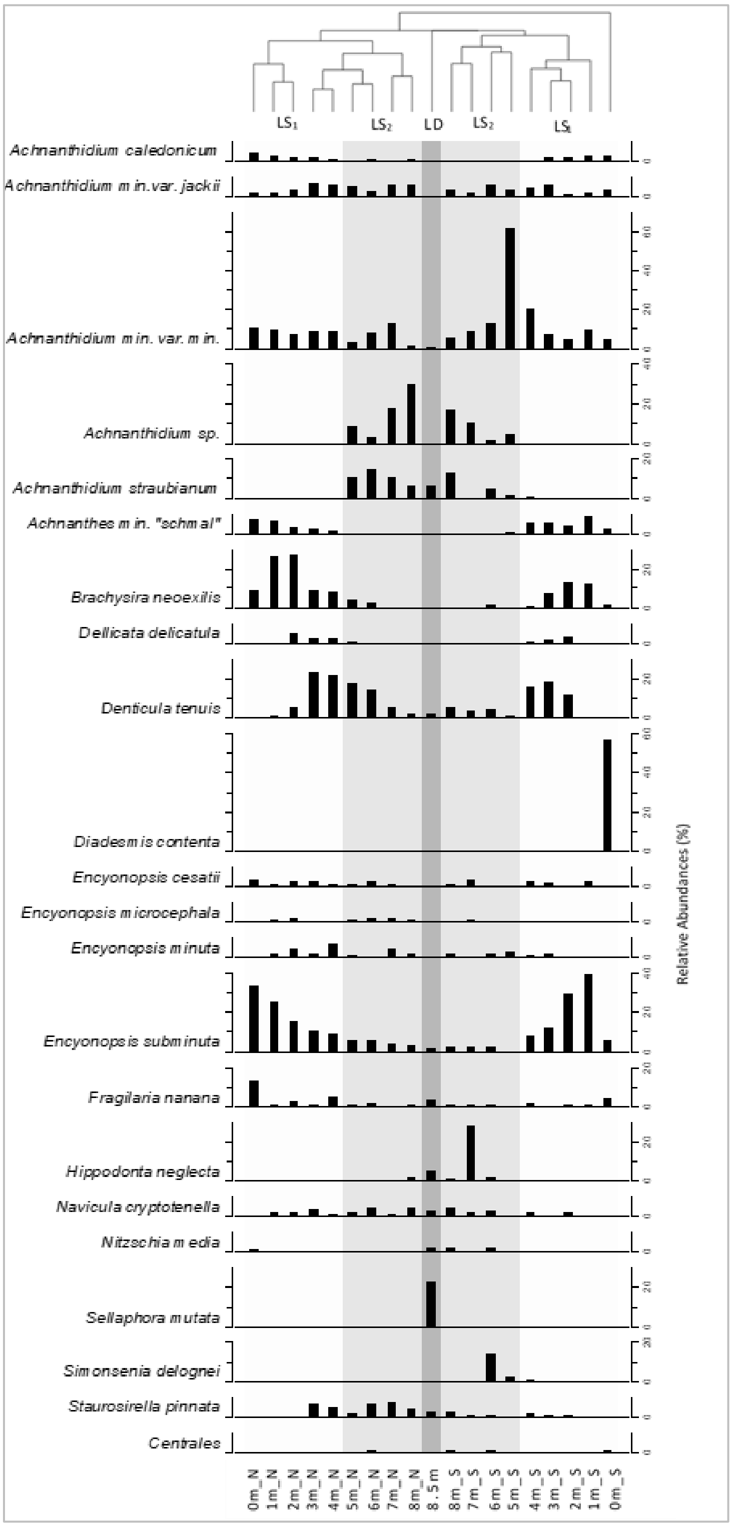


Figure 3.2 Depth-distribution and relative abundances of the most common (>1%) benthic and of total centric diatom taxa in Lake Unterer Soiernsee with depth constrained cluster analysis. Diatom community-zones: LS1 (near-shore littoral zone), LS2 (shallow littoral zone), LD (deeper littoral zone). The expansions of the zones are illustrated by different shades of grey

The ANOSIM test (*R*=0.30, *p*=0.001) shows that only the two shallow littoral community-zones LS_1 and LS_2 differ significantly, while the deeper littoral LD and LS_2 communities show clear similarities.

Depth-distribution of the diatoms in Lake Oberer Soiernsee

A total of 172 pennate diatom taxa representing 37 genera were identified in the 27 samples taken from Lake Oberer Soiernsee; 25 of them occurred in abundances >1 % (Table 3.1). Centric diatoms occurred in abundances between 0.6 % (1m_N) and 44 % (deepest area) and were mainly represented by *Cyclotella comensis* and *Cyclotella woltereckii*, subordinated by *Cyclotella costei*, *Cyclotella ocellata* and *Cyclotella praetermissa*. *Denticula tenuis* (12 %), *Fragilaria nanana* (10 %), *Amphora pediculus* (8 %), *Achnanthidium minutissimum* var. *minutissimum* (7 %), *Staurosirella pinnata* (7 %), *Achnanthidium minutissimum* var. *jackii* (5 %), and *Achnanthidium straubianum* (5 %) were common taxa in this lake (Fig. 3.3). Depth-constrained cluster analysis and PCA suggest there were three community-zones (Figs. 3.3, 3.4 B): two benthic zones (LS and LD) and a deep-water planktonic zone (P). Note that the LD zone differs between the two slopes.

Similar to Lake Unterer Soiernsee, the most frequent taxa showed clear depth-distribution patterns, but species changed gradually, especially across the two benthic zones. High abundances of planktonic diatoms, suggest a sharp boundary occurred between the benthic zones and the planktonic zone. *Achnanthes minutissima* var. "schmale Sippe", *Achnanthidium sp.*, *A. minutissimum* var. *minutissimum, A. minutissimum* var. *jackii, A. straubianum, Adlafia bryophila* (Petersen) Lange-Bertalot, *Brachysira neoexilis, Delicata delicatula* (Kützing) Krammer, *Denticula tenuis, Encyonopsis cesatii* (Rabenhorst) Krammer, *E. krammeri* Reichardt, *E. microcephala* (Grunow) Krammer, *E. minuta* Krammer and Reichardt, and *E. subminuta* appeared to prefer zone LS. *Amphora pediculus, Platessa conspicua* (A Mayer) Lange-Bertalot, *Pseudostaurosira robusta* (Fusey) Williams and Round, and *Staurosirella pinnata* favored the LD zone. The planktonic taxon *Fragilaria nanana* dominated the pennate diatom assemblages in P, where the centric diatoms reached highest percentages (16-44 %). *Encyonema minutum* (Hilse) DG Mann was only dominant in the uppermost sample of the northern transect (0m_N). PCA and hierarchal clustering point out the extraordinary positioning of the 11m_N sample with high abundances of typical LS epilithic taxa. It is possible that erratic stones from the shore were sampled. The ANOSIM test (*R*=0.78, *p*=0.0001) indicates that the three community zones are significantly different from each other.

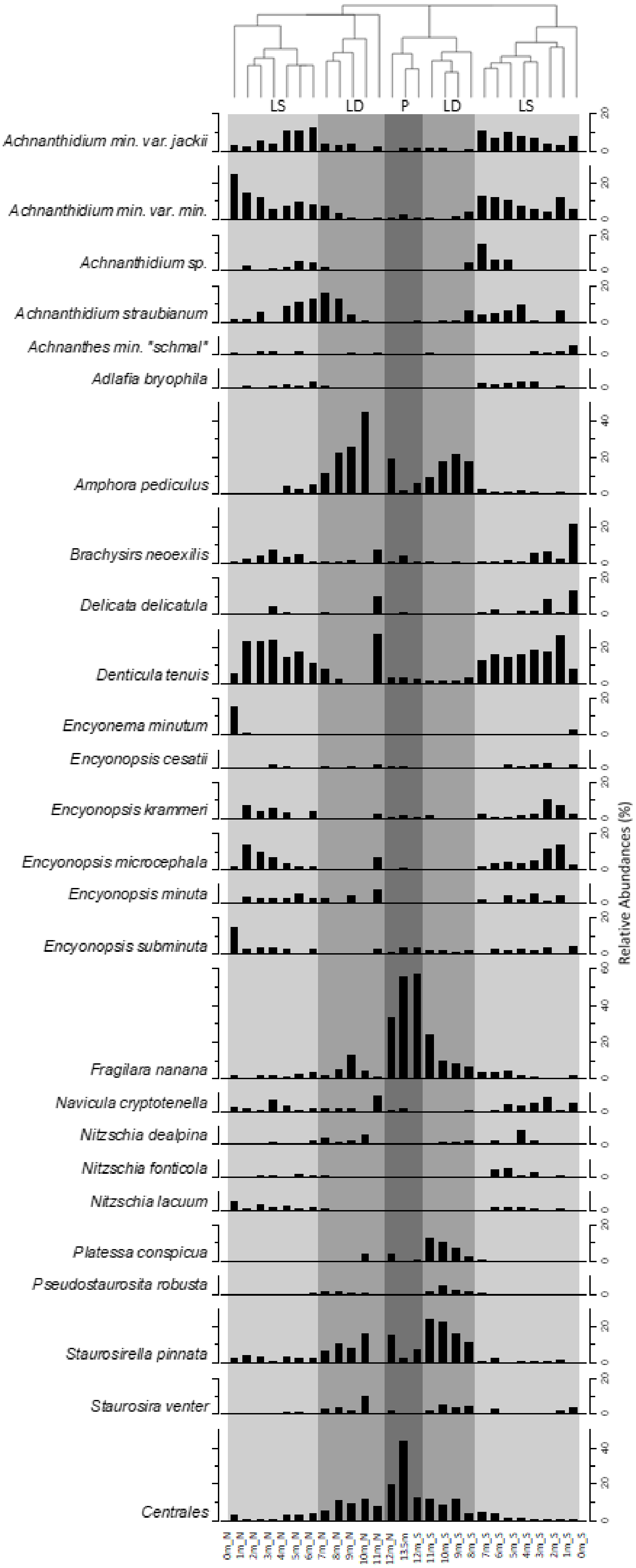


Figure 3.3 Depth-distribution and relative abundances of the most common (>1%) benthic and of total centric diatom taxa in Lake Oberer Soiernsee with depth constrained cluster analysis. Diatom community-zones: LS (shallow littoral zone), LD (deeper littoral zone), P (deep water planktonic zone). The expansions of the zones are illustrated by different shades of grey

Comparison of the diatom assemblages of the two lakes

The shallow-water diatom assemblages of Lake Unterer Soiernsee (0-2 m) differed clearly from all other assemblages (Fig. 3.4 C). The near-shore assemblages (0 m) of Lake Oberer Soiernsee were similar to the assemblages found in 3-4 m in Lake Unterer Soiernsee. Only the assemblages of the deepest sample of Lake Unterer Soiernsee (8.5 m) showed similarity to the deeper-water assemblages of Lake Oberer Soiernsee (8-13.5 m). The diatom assemblages of both lakes were most similar at medium depths (5-7 m).

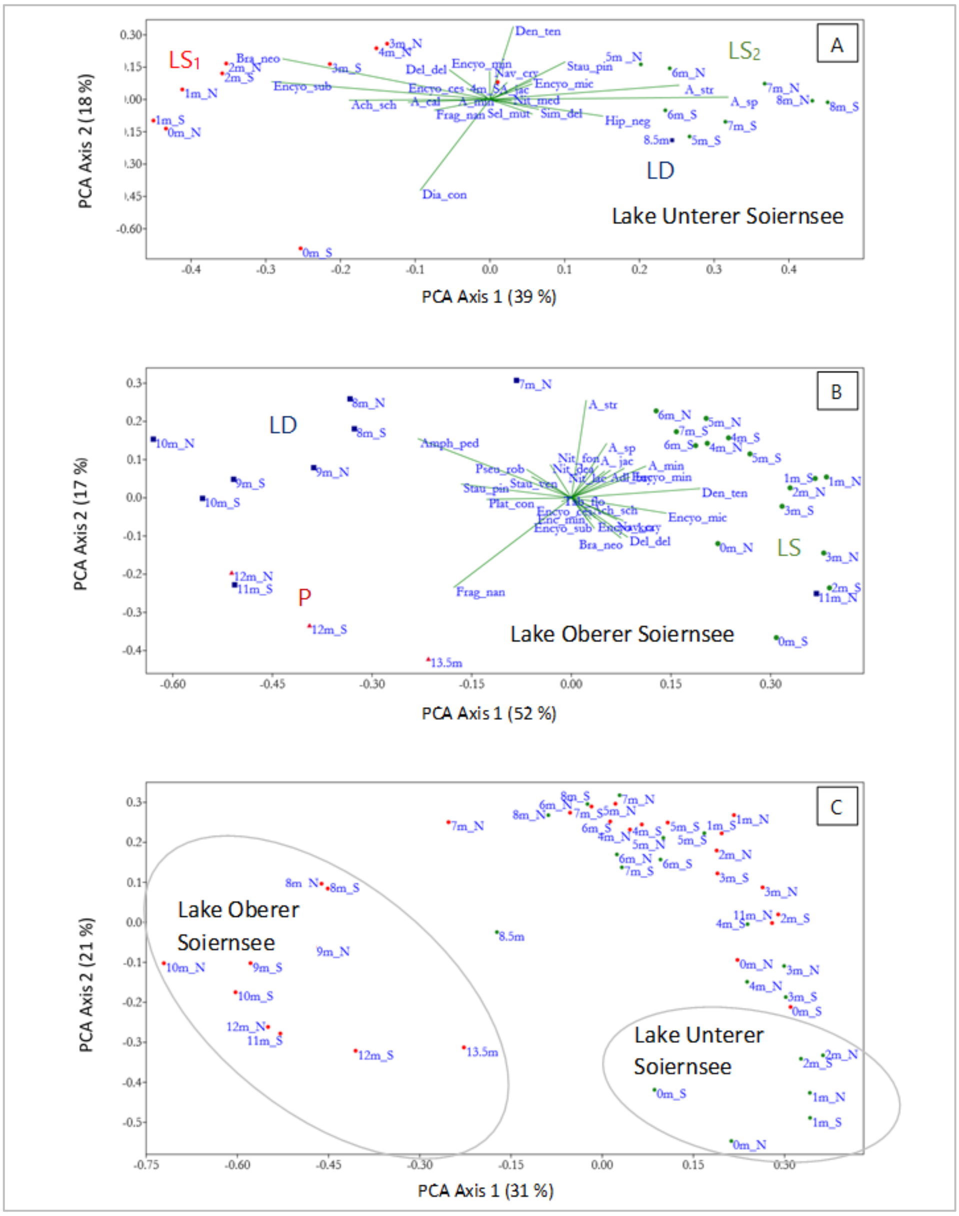


Figure 3.4 Scatterplot of Principal Component Analysis (PCA) showing the depth-distribution of the diatom communities and the dominant taxa in Lake Unterer Soiernsee (A) and Lake Oberer Soiernsee (B) from the northern (N) to the southern (S) near-shore samples (0m_N and 0m_S) to the deepest samples 8.5 m (Lake Unterer Soiernsee) and 13.5 m (Lake Oberer Soiernsee). LS_1 = near shore littoral zone (red dots), LS_2 and LS = shallow littoral (green dots), LD = deeper littoral zone (blue squares), P = pelagic zone (wine-red triangles). Acronyms see taxa list. C: Principal Component Analyses (PCA) comparing the diatom communities of both lakes. Differences are clearly visible by special position of the near shore samples of Lake Unterer Soiernsee (green dots) and the deeper-water samples of Lake Oberer Soiernsee (red dots)

Species richness and diversity of pennate diatoms, trophic states and B/P ratios

In both Lakes Soiernseen species richness and diversity indices were lowest in near-shore samples and highest in depths between 6-8.5 m (Fig. 3.5). In Lake Oberer Soiernsee indices increased from the near-shore to the mid-depths and declined clearly to the deep-water-zone (Fig. 3.5 B). Species richness per individual sample ranged from 33 to 74 taxa (Lake Unterer Soiernsee) and from 32 to 62 (Lake Oberer Soiernsee). Diversity was calculated as Shannon Index (Lake Unterer Soiernsee 1.83-3.42, Lake Oberer Soiernsee 1.95-3.27) and as evenness (Lake Unterer Soiernsee 0.16-0.46, Lake Oberer Soiernsee 0.17-0.48).

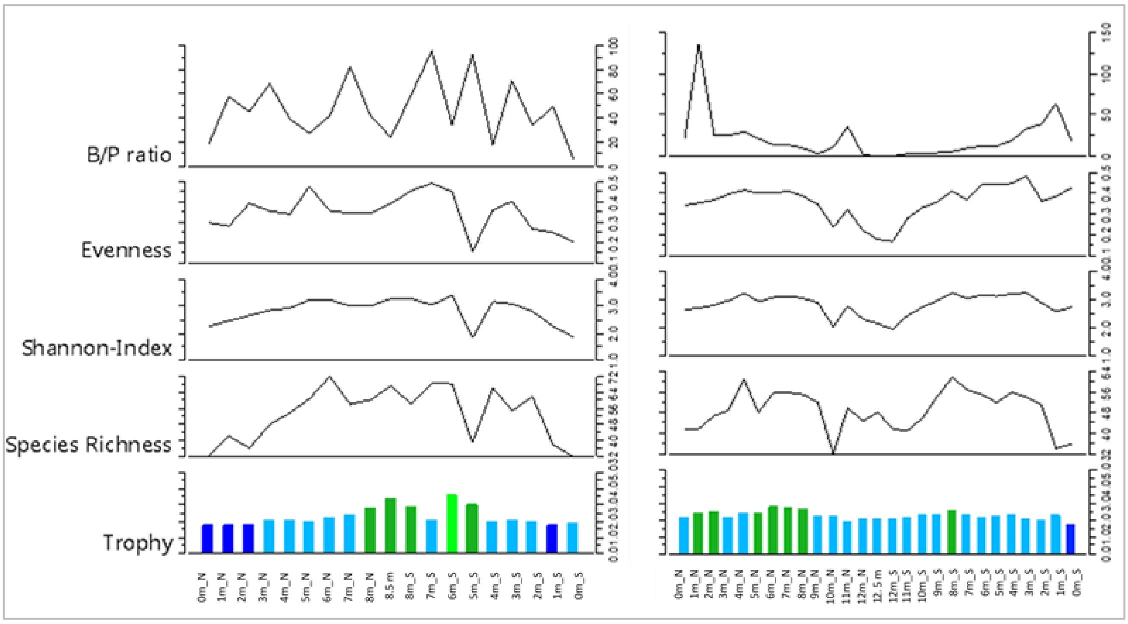


Figure 3.5 B/P ratios (ratios between benthic and planktic diatoms), diversity indices (Species richness, Evenness, Shannon-Index) and Trophic Indices (TI) by Hofmann (1999) of Lake Unterer Soiernsee (left) and Lake Oberer Soiernsee (right). Dark blue = oligotrophic, light blue = oligo- to mesotrophic, dark green = mesotrophic, light green=mesotrophic-eutrophic conditions

In Lake Unterer Soiernsee the trophic state expressed by TI tends to rise with increasing depth (Fig. 3.5), reaching highest values in the deepest area (except TI of 5m_S and 6m_S). TI analyses indicate oligotrophic conditions occurred in the shallow littoral (0-2m_N, 0-1m_S) whereas oligo- to mesotrophic conditions occurred from 3 to 7 m at the northern littoral zone and from 2 m to 4 m plus 7 m at the southern slope. TI values of the deepest area (8 m, 8.5 m) and of 5m_S signify mesotrophic conditions, TI analyses of 6m_S indicated meso- to eutrophic conditions. In Lake Oberer Soiernsee TI analyses indicated nearly constant oligo- to mesotrophic conditions occurred (Fig. 3.5). In the northern slope, TI values tend to be slightly higher characterizing mesotrophic states. At 8m_S, mesotrophic conditions prevail, whereas TI indicated oligotrophic state at 0m_S.

B/P ratios of the diatom assemblages occurring in Lake Unterer Soiernsee showed no tendencies, the values varied between 6.4 (0m_S) and 95.6 (7m_S) along the depth profile (Fig.

3.55). In Lake Oberer Soiernsee, however, the B/P ratios clearly declined with increasing depths comprising values between 0.3 (12.5 m) and 134.8 (1m_N).

3.5 Discussion

Our findings indicate that depth significantly controls diatom species composition and dynamics in both Lakes Soiernseen. Three diatom assemblage zones along in-lake depth gradients could be identified: a near-shore littoral zone, a shallow littoral and a deeper littoral zone in Lake Unterer Soiernsee and a shallow littoral zone, a deeper littoral and a deep-water planktonic zone in Lake Oberer Soiernsee. Comparable studies also indicate distinct depth-distribution patterns of benthic diatoms (Stevenson and Stoermer 1981; Moos et al. 2005; Cantonati et al. 2009; Laird et al. 2010; Kingsbury et al. 2012; Gushulak et al. 2017). Although we analysed diatom assemblages including live and dead frustules, the depth distribution of the *in-situ* benthic diatom communities should be well represented, as in the photic zone the majority of diatom valves are living cells (Yang and Flower 2012). Especially in Lake Unterer Soiernsee the light flooded conditions resulted in dominant abundance of *in-situ* taxa in the diatom assemblages, despite numerous planktonic and tychoplanktonic diatom species in the water column as a consequence of turbulent events and polymixis. Additionally, diatom distribution-patterns were found to be highly similar in both transects of each study lake. Consequently, mass slides or redistribution of dead diatom valves seem to be irrelevant in Lakes Soiernseen.

3.5.1 Characterization of spatial variations within the diatom communities with respect to depth

We found that the following environmental factors are linked to water depth: light availability, substrate, disturbances (water-level fluctuations, wave action), and nutrient concentrations. All these factors influence the composition of the diatom assemblages.

As we hypothesised (1) light availability mainly controls the benthic/planktonic diatom ratio in surficial sediments. Indeed, we found that in Lake Oberer Soiernsee an aphotic zone with lack of periphyic diatom growth exists (10-13.5 m) and the abundance of planktonic taxa significantly increase in samples taken deeper than 8 m. In Lake Unterer Soiernsee however, euphotic conditions exist most of the year and benthic diatoms dominate diatom community on the lake bottom by far. The light attenuation depends on depth, phytoplankton biomass and the concentration of other light-absorbing particles or substances (Vadeboncoeur et al. 2014). In Lakes Soiernseen, light availability is primarily a function of depth. Additionally, precipitation-triggered catchment erosion and surface-runoff may reduce the euphotic zone intermittently, but never phytoplankton shading. We found that epipsammic and epipelic diatoms were most abundant deeper than 7 m, where temporarily light limited conditions were detected. These taxa are proved to have a variety of strategies to cope with light limitation or temporary darkness, e.g., forming resting cells (Hill 1996), switching to facultative heterotrophic metabolism (Lewin 1953; Tuchman et al. 2006; Cantonati et al. 2009; Kingsbury et al. 2012), motility (Moss 1977; Hill 1996), and increasing production of the light-capturing accessory pigment fucoxanthin (Cantonati et al. 2009).

As we hypothesized (2), substrate type influences the composition of benthic diatom assemblages. Comparable with Lowe (1996) we found that benthic diatom assemblages changed along a littoral depth gradient from shallow littoral epilithic and epiphytic rheobionts, which are adapted to water movements, to deeper littoral epipsammic and epipelic limnobionts, which benefit from stable and undisturbed environment. Epilithic (*Denticula tenuis, Encyonopsis microcephala, E. minuta, E. subminuta*) and epiphytic (*Achnanthes minutissimum* var. “schmale Sippe", *Achnanthidium caledonicum, Brachysira neoexilis, Encyonopsis cesatii, E. krammeri, Encyonema minutum, Delicata delicatula*) diatoms dominate the upper benthic zones. Epipsammic and epipelic taxa are significantly more frequent in the deeper benthic zones. The epipsammic diatom community represents a unique assemblage of small species (*Staurosirella pinnata, Staurosira venter* (Ehrenberg) Hamilton, *Pseudostaurosira robusta, Platessa conspicua*) firmly attached on single sand grains, resistant to abrasion and physical damage by moving sand particles and even tolerating short terms of darkness and brief anaerobic conditions (Moss 1977). The epipelic assemblages on fine sediments like clay or silt rely on motility to avoid permanent burial (Moss 1977; Burckholder 1996). We found that highly (*Gyrosigma acuminatum*), moderately (*Navicula antonii* Lange-Bertalot, *Sellaphora pupula* (Kützing) Mereschkowsky, *Sellaphora mutata*) or slightly (*Amphora pediculus, Amphora ovalis* Kützing, *Diploneis oculata* (Brébisson) Cleve, *Platessa cospicua*) motile epipelic species (Krammer and Lange-Bertalot 1986-1991) are more frequently deeper than 5-7 m. The depth distribution patterns of small-celled stalked or slowly motile epiphytic diatoms, like *Brachysira neoexilis* and *Encyonopsis cesatii* (Letáková et al. 2016), reflect the presence of the stonewort stands in the shallow littoral zone of both lakes. The cell-to-cell linked, tube-forming *Encyonema minutum*, however, is associated with *Potamogeton alpinus* in Lake Oberer Soiernsee. Due to their harsh (carbonate encrusted) surface microstructure, *Characeae* represent a less appropriate substrate for high profile species (tall, tube-forming, chain-forming, filamentous or stalked diatoms), but small, adnate, short stalked or slow-moving diatoms are quite common (Messyasz and Kuczynska-Kippen 2006). Despite our mixed sampling strategy, we found a clear effect of substrate on the composition of diatom communities. Sampled substratum changed with depth, because grain size is generally proportional to the degree of physical disturbance (Forehead and Thompson 2010) and decreases naturally with distance from the shore (Hofmann et al. 2008; Yang and Flower 2012). Consequently, mud dominates the deeper parts of the lakes, while hard substrate is more frequent in the physically stressed upper littoral. We found stones throughout the depth profiles (with exception of the deepest area of Lake Unterer Soiernsee), but they were covered with sediment at greater depths. Consequently, real epilithic assemblages were unlikely in samples deeper than 6 m. The significant decrease of the epilithic diatom *Denticula tenuis* in depths greater than 5-6 m supports this hypothesis.

Physical stressors such as water-level fluctuations and wave action also effect the distribution of benthic diatoms (Passy 2007; Cantonati et al. 2009). We found high abundances of pioneer species in the physically disturbed shallow littoral of both lakes. The appearance of aerophilic taxa and the lack of macrophytes as substrate for epiphytic taxa can be correlated with the enormous water-level fluctuations observed in Lake Unterer Soiernsee. Large scale water-level alterations with significant shore line displacement impact lake ecosystems by changing light regime, habitat availability, plankton dynamics, nutrient concentration and especially the development of the near-shore littoral zone, e.g. sediment resuspension, desiccation, freezing (Hofmann et al. 2008; Cantonati and Lowe 2014). Extreme water-level fluctuations also lead to an extirpation of vascular macrophytes (Rørslett 1991). Consequently, exclusive *Characeae* are available host plants in habitats with significant fluctuations in hydrostatic pressure (Becker et al. 2016). We found a selection of diatom species in the highly disturbed near-shore zone of Lake Unterer Soiernsee adapted to drying out or changing moisture conditions, including *Diadesmis contenta*, *Luticola mutica* (Kützing) DG Mann, *L. pseudonivalis* (Bock) Levkov, *L. saxophila* (Bock ex Hustedt) DG Mann (van Dam et al. 1994; Poulíčková and Hašler 2007) and *Encyonopsis subminuta* (Novais et al. 2014).

Besides water-level fluctuations, short-term disturbances as wind and wave action impose physical stress on organisms living in the shallow littoral zone. The northern shores of both lakes are exposed to enhanced hydrodynamic energy due to the predominantly prevailing wind directions (WSW/ESE/SW/SE). The notably higher abundances of *Staurosirella pinnata* with its thick, solidly silicified cell wall and short, flexible mucilaginous stalk at the northern profile of both lakes may demonstrate that the northern shore is more exposed to wind and wave disturbance than the southern shore. Diatom growth forms and life strategies show adaptions to this highly dynamic habitat: strongly attached low-profile (prostrate, adnate, erect) taxa and r-selected taxa, e.g. small *Achnanthidium* and *Achnanthes* (Passy 2007; Kingsbury et al. 2012) are most abundant in the shallow littoral zones of both Lakes Soiernseen.

Nutrient availability was also found to influence the diatom distribution in both Lakes Soiernseen. Limiting nutrients for diatom growth are phosphorus and silica, as phosphorus is the main variable controlling diatom productivity and species composition (Battarbee et al. 2001) and silica regulates diatom metabolism and cell growth (Round et al. 1990). Concentrations of both nutrients vary with depth, especially in periodically stratified Lake Oberer Soiernsee. Dissolution, cell lysis and microbial degradation lead to enriched concentrations in deeper areas, while intensive biological consumption reduces nutrient availability in the shallow littoral (Wetzel 2001; Cantonati et al. 2009). High abundances of strongly silicified *Hippodonta neglecta* in the deeper part of Lake Unterer Soiernsee and the occurrence of large species with heavily silicified frustules (e.g. *Diploneis* species) in the deeper benthic zone of both lakes indicate higher silica concentration by dissolution of sedimented diatom frustules (Cantonati et al. 2009). We also found that several epipelic diatoms, which are adapted to slightly higher phosphorus nutrient concentration reach highest percentages in the deeper littoral zones of both lakes: *Amphora pediculus* and *Platessa conspicua* (Kingsbury et al. 2012; Kitner and Poulíčková 2003; van Dam et al. 1994) or subdominant *Gyrosigma acuminatum, Navicula antonii, N. associata* Lange-Bertalot, *N. hofmanniae* Lange-Bertalot*, N. trophicatrix* Lange-Bertalot*, and N. utermoehlii* Hustedt (Schaumburg et al. 2014; Hofmann et al. 2013). Sediment dwelling taxa intercept dissolved nutrients from sediment and its interstitial water (Burkholder 1996; Poulíĉková et al. 2008), particularly because microbial degradation of detrital organic matter mainly occurs in surficial sediments (Wetzel 2001; Dodds 2003).

3.5.2 Diversity and species richness

The littoral zone represents a hotspot of diatom productivity and biodiversity (Althouse et al. 2014). It comprises mesohabitats of high substrate diversity (boulders, stones, sand, silt, clay, submerged macrophytes and stoneworts) providing ideal conditions for highly diverse diatom communities. The upper littoral zone, however, is characterized by high-energy conditions, high UV irradiation, water-level fluctuations and seasonal shifts in temperature (Cantonati and Lowe 2014). This may account for the low diversity indices in the near-shore habitat of both lakes. Effects of wave disturbance, however, decrease rapidly with depth (Vadeboncoer et al. 2014). At mid-depth (4-8 m), high habitat stability and substrate heterogeneity provide favorable growth conditions resulting in the higher species richness, diversity and evenness, observed in both basins. The consequence of reduced substrate variability and light availability in the deeper benthic zone is decreasing species richness and diversity. This pattern has also been observed in other lakes (Cantonati et al. 2009; Laird et al. 2010; Kingsbury et al. 2012; Yang and Flower 2012).

3.5.3 Basic differences between the diatom assemblages of the two lakes

Species richness and diversity of the diatom assemblages as well as most of the dominant taxa were quite similar in both lakes. However, some significant differences in diatom composition occurred, primarily caused by the dramatic water-level fluctuations in Lake Unterer Soiernsee and the greater maximum depth of Lake Oberer Soiernsee. Feret et al. (2017) also found that water-level fluctuations and lake depth are important factors to explain variances in diatom species compositions. The extreme water-level fluctuations result in a highly disturbed near-shore littoral zone (LS_1), habitat for several aerophilic and subaerial species, which only appear in Lake Unterer Soiernsee. The instable habitat additionally leads to exclusive growth of *Characeae*, while the more stable environment of Lake Oberer Soiernsee offers a variety of host plants for epiphytic diatoms. The greater depth of Lake Oberer Soiernsee results in an extended deeper littoral, which host a more diverse epipelic community and in an aphotic, pelagic zone (P). We found that benthic diatom assemblages occur throughout the basin of Lake Unterer Soiernsee since it is light-flooded down to the bottom for most of the ice-free period. Short-term light-limited conditions exist only during high water levels after snowmelt or after heavy rainfall events with intense surface runoff causing excessive turbidities. Consequently, periphytic diatoms dominate the surface-sediment assemblages, while settled planktonic species occurred infrequently. In contrast, in Lake Oberer Soiernsee light-limiting conditions inhibit periphyton growth in the profundal zone, resulting in high abundances of planktonic diatoms.

3.5.4 Implications for paleolimnological studies

The developed diatom-inferred depth models provide powerful tools to reconstruct water column dynamics (water level, water transparency, thermal stratification) via ratio of benthic/planktonic taxa in Lake Oberer Soiernsee (aphotic conditions) and variations in periphytic diatom assemblages via substrate preferences in Lake Unterer Soiernsee (photic conditions). The spatial variability of the diatom assemblages from near-shore littoral to the deep-water area enables the interpretation of temporal assemblage shifts in sedimentary records (Rühland et al. 2015). If aphotic conditions prevail, diatom assemblages preserved in surface sediment samples comprise a mixture of the lakes diatom communities adapted to different habitats (littoral, pelagial), on distinct substrates (stones, plants, sediment) and in varied environmental conditions (disturbance regime, nutrient concentrations) (Pla-Rabés and Catalan 2018). Hence, in line with our hypothesis 3, lake level changes will be reflected in the ratio of benthic to planktonic species (B/P ratios) in down-core sediment samples of Lake Oberer Soiernsee, especially when the cores are taken near the littoral/pelagic transition zone. Despite similar biomass of planktonic diatoms in both studied lakes, we found that periphytic diatoms outnumber small-celled *Centrales* by far in the shallow, well-illuminated Lake Unterer Soiernsee. Consequently, we predict shifts in B/P ratios will not be documented in sedimentary records of this lake. Water-level alterations should be recorded via variations within the benthic diatom assemblages. However, interpretation of B/P ratio variations is very complex, as primarily changes in the lakes light regimes affect the ratio and lake transparency is influenced by nutrient enrichment (Hall and Smol 2010) as well as by higher erosion rates in the catchment. B/P ratios were also used to indicate climate warming. In deep lakes with an extended aphotic zone, stronger stratification patterns result in compositional shift of diatom assemblages from small benthic fragilarioid/heavy silicified tychoplanktonic taxa to small-celled cyclotelloid/elongate pennate planktonic taxa, while in shallow lakes climate warming forces more complex and diverse benthic communities associated with habitat expansion and substrate development, e.g. aquatic vegetation (Rühland et al. 2015).

As we hypothesized (4), the aphotic zone sample of Lake Oberer Soiernsee was appropriate for reconstruction of trophic status. The oligo- to mesotrophic state calculated by indicator species complies with the perennial average of the water column phosphorus concentrations. We choose the trophic index by Hofmann (1999), developed for lakes in southern Germany (inclusive lakes of the Alps) to calculate diatom-related trophic states along the depth-gradient. We concede the error susceptibility of this approach, as it relies on ecological preferences of single, partially rare indicator species. In contrast, the basis of a diatom-TP transfer function is the relation of whole contemporary diatom assemblage with corresponding TP concentrations (Juggins 2013). The purpose of our linear-relationship-method was providing a rough guide to evaluate the size of variance between the single sites and figure out the conformity with water column TP concentrations. Especially in Lake Unterer Soiernsee the calculated trophic indices are highly inconsistent and mainly mirror single point sources: underwater inflows indicated by high abundances of eutraphent *Simonsenia delognei*, a typical spring water species (Witkowski et al. 2014) lead to meso- to eutrophic conditions as consequence of weathering and erosion of phosphate-containing limestone (Valeton 1988). In contrast, the calculated indices of Lake Oberer Soiernsee were more constant. The higher indices on the northern slope probably reflect pollution by the small mountain hut.

Under aphotic conditions, a surface sediment sample from the deepest part of the basin represents an accumulation of diatom deposits from a variety of in-lake habitats and substrates (Hall and Smol 2010), including planktonic diatoms, which have closer relationship to water column nutrients than benthic diatoms (Althouse et al. 2014). The lack of phytoplanktonic taxa in the sediment constitutes a major problem of surface sediment training sets, as many periphytic diatoms are relatively insensitive to changes in epilimnetic nutrient concentrations (Sayer 2001). Especially epipsammic diatom communities, deriving the nutrients from the sediment as well as from the overlying water, would be less suitable to indicate an increase in phosphorus inputs (Bennion et al. 2010). However, epipelic taxa are particularly abundant in the deepest sample of Lake Unterer Soiernsee as a result of absence of stony substrate. Besides that, the *in-situ* benthic communities overprint the accumulation of planktonic and tychoplanktonic taxa in the diatom assemblages of the surface sediments.

Philibert and Prairie (2002) suggested the inclusion of both benthic and planktonic species as a requirement to obtain the most reliable transfer function. However, developing a training-set for shallow polymictic lakes, Werner and Smol (2005) found that distribution of benthic diatoms even of small fragilarioid taxa changes significantly with changing epilimnic TP concentrations. In order to develop a diatom-based TP-transfer-function for Bavarian mountain lakes, it is highly important to consider lake depth and transparency. Our findings highlighted the usefulness of creating two different training-sets, one for deep or low-transparency lakes with an aphotic zone including benthic and planktonic diatoms, and another one for shallow, clear water lakes solely based on benthic diatoms. Hence, our results are in line with Werner and Smol (2005) who also recommend separating shallow from deep lakes in their calibration set of Canadian alkaline lakes.

4. Unravelling climate change impacts from other anthropogenic influences in a small subalpine lake: a multi-proxy sediment study from Oberer Soiernsee (Northern Alps, Germany)

A similar version of this chapter was published: Hofmann AM, Kuefner W, Mayr C., Dubois N, Geist J, Raeder U (2021) Unravelling climate change impacts from other anthropogenic influences: a multi-proxy, down-core study of a small subalpine lake (Oberer Soiernsee, Northern Alps, Germany). Hydrobiologia, 848 (18), 4285-4309

Candidate´s contribution:
The study was primarily designed by the candidate with conceptual input of Christoph Mayr, Jürgen Geist and Uta Raeder. Sediment core sampling and sample preparation were carried out by the candidate. Sediment dating was done by Nathalie Dubois. Microscopic analyses were realized by the candidate. Pigment analyses were performed by the candidate and Wolfgang Kuefner. Stable isotope analyses were carried out by Christoph Mayr. The interpretation of the data was realized by the candidate in consultation with Nathalie Dubois (core chronology) and Christoph Mayr (stable isotopes). The manuscript was drafted and improved by the candidate, under continuous feedback of Christoph Mayr, Jürgen Geist und Uta Raeder.

4.1 Abstract

Mountain lakes are increasingly impacted by a series of both local and global disturbances. The present study reveals the eutrophication history of a remote subalpine lake (Oberer Soiernsee, Northern Alps, Germany), triggered by deforestation, alpine pasturing, hut construction, tourism and atmospheric deposition, and identifies the intertwined consequences of on-going global warming on the lake's ecosystem. The primary objective was to disentangle the various direct and indirect impacts of these multiple stressors via down-core analyses. Our multi-proxy approach included subfossil diatom assemblages, carbon and nitrogen stable isotope ratios and subfossil pigments from dated sediments. Shifts within the diatom assemblages were related to variations in trophic state, lake transparency, water temperature and thermal stratification. The organic carbon isotope ($\delta^{13}C_{org}$) records, the diatom valve density and the pigment concentrations documented the development of primary production and composition. Total nitrogen isotope values ($\delta^{15}N$) are more likely to reflect the history of atmospheric nitrogen pollution than lake internal processes, also mirrored by the decoupling of $\delta^{15}N$ and $\delta^{13}C_{org}$ trends. The composition of sedimentary

pigments allowed a differentiation between planktonic and benthic primary production. Concordant trends of all indicators suggested that the lake ecosystem passed a climatic threshold promoted by local and long-distance atmospheric nutrient loadings.

4.2 Introduction

Mountain regions are particularly sensitive to climate change. They are hotspots of biodiversity (Körner et al., 2016) and very valuable drinking water reservoirs (Beniston, 2006). The recent warming observed in the European Alps since the mid-1980s is roughly three times higher than the global average (Bogataj, 2007) and climate models predict even more severe changes in coming decades (IPCC, 2013; Stocker, 2020). Coupled with the intense warming, significant changes in the Alpine hydrological cycle were projected, with a tendency to more intense winter precipitation (increasingly as rain) and significantly reduced summer rainfall (Warscher et al., 2019). An upward shift of the snow line and heavy rainfall events notably increase the frequency and the magnitude of flash floods, landslides and debris-flows (Bätzing, 2015).

Recent global warming is affecting mountain lake ecosystems by a series of direct and indirect effects, altering the dynamics of these extremely sensitive habitats. External drivers such as climate-induced changes of catchment soil and vegetation cover may affect the chemical characteristics of the lakes (Fritz, 2008; Rosbakh et al., 2014). For instance, extreme precipitation events alternating with periods of drought will increase soil erosion and consequently nutrient input from the catchments into the lakes (Jeppesen et al., 2010). Warming thus has a direct effect on the lake ecosystem function and biodiversity by stimulating biological processes, resulting in higher internal phosphorus loadings, extension of the growing season (Magnuson et al., 2000; O´Reilly et al., 2015), and alteration of lake stratification patterns (Smol et al., 2005; Winder and Sommer, 2012). More stable and longer stratifications trigger compositional shifts within the phytoplankton communities to the benefit of mobile, small-sized or colony-forming species (Winder et al., 2009; Michelutti et al., 2015). Additionally, changes in precipitation patterns affect the water balance of lakes, especially in karstified catchment areas, leading to significant changes in water levels or enhanced seasonal water level fluctuations (Lauber and Goldscheider, 2014). All these complex impacts of climate change have been superimposed during the Anthropocene by simultaneous fertilization via a diffuse deposition of atmospheric nitrogen and by local anthropogenic disturbances, e.g. mountain huts, forestry or alpine pastures (McMaster and Schindler, 2005; Jeppesen et al., 2010).

Numerous proxies that are archived in lake sediments are valuable to track such impacts (Smol, 2010), thus allowing the study of various responses of the aquatic ecosystem to these environmental stressors. However, sedimentary records are often difficult to understand. Numerous drivers may trigger changes in sedimentary records by affecting the lake ecosystem in a series of direct and indirect ways. Lake sediments integrate sedimentary organic matter from both allochthonous and autochthonous sources and a number of internal lake processes complicate the interpretation of past climate or nutrient situations from sedimentary archives (Batterbee et al., 2012; Catalan et al., 2013; Rogora et al., 2018). Unravelling the combined effects of climate warming and eutrophication in down-core studies is indeed a great challenge, because the symptoms may be rather similar and both impacts have appeared synchronously (Jeppesen et al., 2010). Due to the complex interactions between biotic and abiotic components and between internal and external driving factors the analyses of several proxies should be carried out (Birks and Birks, 2006). Different proxies mirror different environmental factors and also have different strengths and weaknesses. By combining multiple proxies, their strengths can be exploited and their weaknesses identified (Mann, 2002 b).

For interpreting the long-term changes in lake ecosystem structure of the small subalpine Oberer Soiernsee a multi-proxy paleolimnological study was carried out based on sedimentological (event layers), biological (diatoms), biochemical (pigments) and geochemical (stable isotopes) paleoindicators, supported by data from a three-years sampling campaign (2014-2016; Hofmann et al., 2020). Additionally, historical information recorded in Alpine Club yearbooks and interviews with landowners and forest office were used to better interpret the results.

Diatoms are the most widely used bioindicators in paleolimnological studies inferring past environmental conditions (Stoermer and Smol, 2010). They are generally highly abundant and taxonomically diverse in any freshwater systems and, due to their siliceous cell walls, diatom valves are usually well preserved in the lake sediments (Smol and Cumming, 2000). Furthermore, many diatom taxa have well-defined optima and tolerances regarding water temperatures and nutrient concentrations or preferences for a given habitat. They response sensitively and due to their fast reproduction and migration rates also rapidly to a wide range of environmental changes of their aquatic environment (Smol, 2008). Climate-related changes of lake properties, such as length of the growing season, water-column mixing processes and light availability directly and indirectly alter diatom community composition, dynamics and size structure of both periphytic and planktonic diatom assemblages (e.g. Weckström et al., 1997; Rühland et al., 2015; Boeff et al., 2016; Griffiths et al., 2017). Especially the recent success of small-celled centric species related to increased thermal stability and associated changes in light and nutrient availability has been observed in alpine paleolimnological records around the world (Lotter and Bigler, 2000; Rühland et al., 2008; Catalan et al., 2013; Michelutti et al., 2015). Nutrient enrichment mediated by disturbances within the catchment area also may result in the reorganisation of diatom communities. Therefore, quantitative diatom-based inference models can be used to reconstruct past trophic states of lakes (Lotter et al., 1998; Stoermer and Smol 2010).

Sedimentary pigments are particularly valuable in multi-proxy studies. They are often the only fossil remains of non-siliceous algae and therefore provide a more complete picture of phototrophic communities (Lami, 2000). Records of paleopigments can be used to reconstruct taxonomic composition and biomass of past phytoplankton and periphyton communities (Leavitt and Hodgson, 2001). As nutrient supply and the lake´s thermal dynamics are important drivers that regulate algal composition and production (Reynolds, 2006), analyses of sedimentary pigments can be used to detect climate changes and past trophic conditions (Tõnno et al., 2019). However, in comparison to diatoms, pigments are labile compounds. Their degradation via chemical oxidation, photo-oxidation and herbivore grazing begins immediately after the death of the organism (Leavitt, 1993) and the decomposition continues after deposition in the surface sediments (Sanger, 1988). The rate of degradation depends on sinking rate, water temperature, pH, the availability of light and oxygen, the grazing pressure, turbulences and bioturbation. Additionally, the degree of chemical stability and preservation varies between the individual pigments (Leavitt andHodgson, 2001). Therefore, the pigments are deposited on surface sediments in various stages of decay, depending on the type of pigment and the degree photo- and chemical oxidation and biologically-mediated destruction (Leavitt, 1993), which considerably complicates the interpretation of paleopigment analyses. In shallow or highly transparent oligotrophic lakes the development of an active autotrophic biofilm on the surface sediment is another important source of sedimentary pigments. Hence, the paleopigment-composition in the surface sediments is dominated by the periphytic *in situ* production and the phytoplankton marker pigments are underrepresented (Buchaca and Catalan, 2008). Therefore, changes between planktic and benthic sources of the sedimentary pigments provide valuable information about changes in the extension of the euphotic zone.

The nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C_{org}$) isotope fingerprints as well as the TOC/TN (total organic carbon/total nitrogen) ratios of bulk sediment provide valuable information on the origin of sedimentary organic matter (OM) and help to distinguish between autochthonous or allochthonous sources (Meyers and Teranes, 2001). In cases where the sedimentary OM was predominantly autochthonous, testified by low TOC/TN ratios, the records of $\delta^{13}C_{org}$ and $\delta^{15}N$ were used to reconstruct past trophic conditions and changes in nutrient availability (Braig et al., 2013). The isotopic composition of the dissolved inorganic carbon (DIC) pool is controlled by the signature of atmospheric CO_2 permanently diffusing into the lake and by photosynthesis/respiration rates (Wetzel, 2001; Braig et al., 2013). $\delta^{13}C_{org}$ concentrations increase with enhanced photosynthetic productivity (McKenzie, 1985). Algae preferentially assimilate $^{12}CO_2$, while the heavier isotopologue containing ^{13}C gradually accumulates in the pool of dissolved inorganic carbon (Farquhar et al., 1989). Thus, primary producers will take up more and more accumulated $^{13}CO_2$ with an increasing assimilation. This fact is reflected by the increasing accumulation of ^{13}C in the biomass and finally in the sediments after the algae died and sunk. However, $\delta^{13}C_{org}$ values may initially decline during the first phase of eutrophication, when anaerobic microbial degradation dominates, which releases partly oxidized, ^{12}C-enriched methane into the water column (Hollander and Smith, 2001).

The interpretation of nitrogen isotope signals is complicated due to the biogeochemical complexity of the nitrogen cycle in lakes (Meyers and Teranes, 2001). Nitrogen is available to primary producers in various forms (ammonia, hydroxilamin, nitrate, nitrite), and the multitude of fractionation effects, transformation pathways and biochemical in-lake processes permanently alter the dissolved inorganic nitrogen (DIN) pool of a lake (Wetzel, 2001). Photosynthesis progressively enriches the DIN reservoir with ^{15}N as algae preferentially incorporate ^{14}N (Fogel and Cifuentes, 1993). Shifts in phytoplankton taxa composition are also known to trigger $\delta^{15}N$ variations in sedimentary OM due to the various ways in which DIN is used and fractionating effects among diverse algae groups (DeNiro and Epstein 1981; Gu, 2009; Lehmann et al., 2004). Sedimentary $\delta^{15}N$ variations also provide information about past hypolimnetic oxygen concentrations, as increased denitrification rates caused by anoxic bottom water lead to ^{15}N-enriched OM (Teranes and Bernasconi, 2000; Finlay and Kendall, 2007; Braig et al., 2013). Additionally, external nitrate loadings may increase (human and animal waste) or decrease (deposition of atmospheric nitrogen) $\delta^{15}N$ values (Kendall, 1998; Hastings et al., 2009).

The aim of our study was to reconstruct the environmental history of the remote Oberer Soiernsee since the outgoing Little Ice Age (AD 1840–1970), unravelling the multiple influences on the lake and their complex effects on its ecosystem. We hypothesized that (1) a series of human impacts (deforestation, alpine pasture, eutrophication, N-fertilisation, climate warming) are recorded in the lake sediments and (2) our multi-proxy approach will allow us to disentangle these various impacts. We expected that (3) shifts within the diatom flora in particular would reflect the effects of global warming.

4.3 Material and methods

4.3.1 Study site

Lake Oberer Soiernsee (47° 29' 30" N, 11° 20' 53" E) is located ~ 75 km south of Munich (Bavaria, Germany) in the Northern Calcareous Alps near the present tree-line ecotone (1558 m a.s.l.) (Fig. 4.1). The lake is of glacial origin (März 1903) and the catchment geology is dominated by Triassic limestone and dolomite, locally covered by moraine and post-glacial deposits (Schmidt-Thomé 1953). Due to karstification, underground drainage dominates, while surface runoff has been observed only during heavy rainfall events (Hofmann et al. 2020). The lake has no permanent surface inflow and drains exclusively through the permeable end moraine deposits into the adjacent lake Unterer Soiernsee (1553 m a.s.l.). Catchment vegetation ranges from subalpine grassland with patches of *Pinus mugo* Turra *ssp. mugo* and *Picea abies* L. Karst to treeless alpine meadows with shrubs (e.g. *Rhododendron hirsutum* L., *Carex sempervirens* Vill.) on poorly developed soils and fell-fields. Aquatic vegetation is characterized by mixed stands of *Chara contraria* A. Braun ex Kützing and *Chara tomentosa* L. and scattered populations of *Potamogeton alpinus* Balb. The elongated lake has a surface area of 3.46 ha and a maximum water depth of 14.5 m (Fig. 4.1). Lake Oberer Soiernsee is an oligo- to mesotrophic (mean TP = 13 µg l^{-1}), dimictic lake with mean NO_3^--N values of 330 µg l^{-1} and mean NH^{4+}-N values of 20 µg l^{-1}. The average lower limit of the euphotic zone is around 10 m, resulting in aphotic conditions at the deepest area of the basin (Hofmann et al. 2020). Seasonal lake-level fluctuations (1.8 m) were observed with a maximum water level after snowmelt and a minimum in autumn. The carstified, calcareous catchment causes a low conductivity (192 µS cm^{-1}) and a high pH (8.7). Phytoplankton biomass was consistently below 2 g m^{-3} throughout two successive growing periods. Detailed information regarding the lake's physical and chemical characteristics as well as phytoplankton analyses have already been published (Hofmann et al. 2020). The alpine meadows surrounding the lake were traditionally used for summer cattle grazing. A hut of the German Alpine Club (1616 m a.s.l.) and a small private mountain cabin (1560 m a.s.l.), both highly frequented during summer months, are situated within the lake catchment. The huts were built in AD 1866 on King Ludwig II's order. Since AD 1887, they have been put to increasing use, first as hunting lodges and later as Alpine Association cottages (Müller,

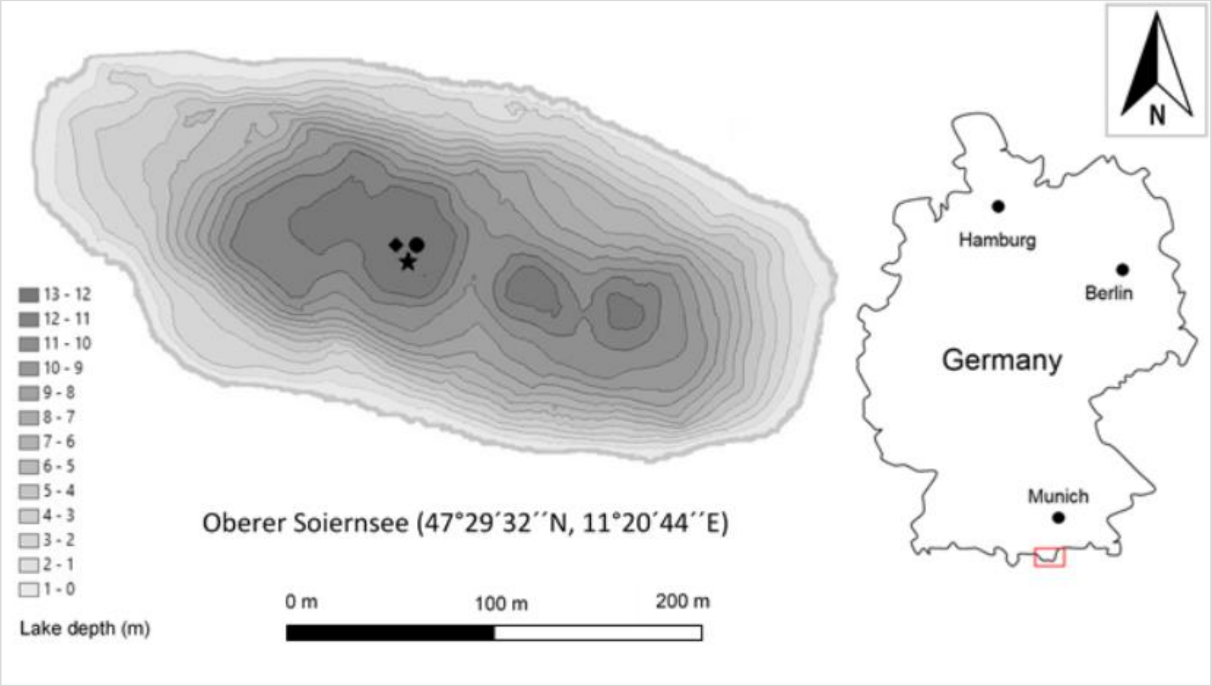


Figure 4.1 Geographical position of Oberer Soiernsee in southern Germany (right) and bathymetric map of the lake (left). Coring location of C1 (circle), C2 (star), and C3 (rhomb)

1922). In the small cabin situated directly at the lake, the number of overnight stays remained below 100 per year before AD 1960 and has risen sharply since then to 250-350 per year (Yearbooks of the Alpine Club Section Hochland 1920-2016). A dry toilet close to the northern shore in particular may be responsible for diffuse nutrient loadings, as indicated by higher trophic levels calculated at the northern littoral zone (Hofmann et al. 2020).

4.3.2 Sediment coring

A gravity corer (Uwitec, Mondsee, Austria) equipped with 6 cm-diameter core tubes was used to obtain three sediment cores from the deepest area of the lake basin, located by echo sounding (HDS8, Lowrance, Tulsa, USA). The master core (C1; length 29 cm) was sampled in June 2015 to carry out stable isotope analyses and core chronology. C2 (length 23 cm) was taken in June 2017 for geochemical, diatom and pigment analyses. The sediment cores were transported cooled and light-protected and split into two halves in the laboratory. The first halves of the cores were sliced at continuous 1 cm intervals under subdued green light. For pigment analyses, subsamples were stored in the dark at –24 °C until freeze-drying. The other halves of the cores were first described lithologically. They were then subsampled at 1 cm intervals too and freeze-dried in plastic vials for diatom analysis, dating and stable isotope analysis (Christ 1-4 Loc; 48 h, –47 °C). In October 2018, a third core (C3) was obtained to measure the pH values of the sediment-water interface and the sediment pore water at different sediment depths.

4.3.3 Core chronology

The age model is based primarily on ^{210}Pb dating, supported by peak signals of ^{137}Cs. Freeze-dried and fine-ground sediment subsamples were analysed by gamma spectrometry (High-purity Germanium Well Detector, HPGe, Canberra, USA) at Eawag (Dübendorf, Switzerland). Accumulation rates were determined using both ^{210}Pb and ^{137}Cs radionuclides. ^{210}Pb chronologies were calculated from unsupported isotopes using the CRS model (Constant Rate of Supply, Appleby 2001). The anthropogenic ^{137}C was used to confirm the ^{210}Pb dates. ^{137}Cs is a stable and clear time marker as it first appeared in 1951–1954 and peaked in 1963 as a result of atmospheric nuclear weapon testing fallout (Appleby 2001). A second peak of ^{137}Cs activity is related to the Chernobyl nuclear accident in 1986 (Kirchner 2011). The first recovered core (C1) was dated. The chronology was transferred to C2 via lithological (event layers) and $\delta^{13}C_{org}$ correlation (Mayr et al. 2005; Berthon et al. 2014).

4.3.4 Diatom analyses

For diatom preparation 1.6 ml of freeze-dried sediment of the C2 subsamples were treated using the hot H_2O_2 / $K_2Cr_2O_7$- method (DIN EN 13946:2014-07). The cleaned diatom material was filled into glass vials and was adjusted with detilled H_2O_2 to a fixed volume (5 ml). Permanent slides were prepared by first dropping 50 µl of several dilutions (1:10, 1:30, 1:50) of the cleaned diatom material on cover glasses (Ø 12 mm) and then embedding the dried material in Naphrax (Refractive Index = 1.7). At least 550 diatom valves per sample were identified under oil immersion at 1000 x magnification using a light microscope (Aristoplan and Labovert, Leitz, Wetzlar, Germany). Diatom taxonomy followed Krammer and Lange-Bertalot (1986-1991), Lange-Bertalot (1993), Lange-Bertalot et al. (1996), Krammer (1997), Lange-Bertalot (2000-2003), Houk et al. (2010), Houk et al. (2014) and Hofmann et al. (2013), updated to recent taxonomic nomenclature using current publications and databases. Thin, needle-shaped *Fragilaria nanana* was mainly preserved in fragments. Therefore, the lengths of the fragments were measured, summed and divided by the medium length of the intact valves.

Changes in the ratio between benthic+epiphytic and planktic diatom species (B:P ratio) were used to track past changes in the depth of the littoral/profundal boundary. This boundary is determined by lake level and water transparency both affecting light availability for benthic growth (Wetzel, 2001; Hofmann et al., 2020). For the quantitative reconstruction of past lake levels of Oberer Soiernsee Hofmann et al. (2020) developed a diatom-inferred depth-model based on the depth-distribution patterns of current diatom assemblages. The authors found that the strongest model is based on a weighted-averaging partial-least-square approach (WA-PLS) with two compounds that provides a robust reconstructive relationship between the distribution of diatoms and lake depth ($r^2 = 0.56$; RMSEP = 2.55 m).

Past surface temperatures (Ø TSiVa) were inferred by using the novel silicification value (SiVa) developed by Kuefner et al. (2020 a). The diatom-temperature transfer function is based on a training set of 43 mountain lakes located in the Northern Calcareous Alps and refers to the negative correlation between the summer surface temperature and the average degree of silicification of the diatom assemblages preserved in surface sediments (Kuefner et al. 2020 b).

$$\varnothing\, TSiVa\ [°C] = 25{,}956 - 4.7155 * SiVa$$

The ratio between *Staurosirella pinnata* (Ehrenberg) Williams and Round and *Staurosira construens* var. *venter* (Ehrenberg) Hamilton (P/V ratio) was used to indicate trends in lake temperatures. While

S. construens var. *venter* is reflecting cooler water temperatures, *S. pinnata* is more competitive under warmer growing conditions (Cremer et al., 2001).

Past total phosphors (TP) concentrations were calculated by applying the TP inference model of Lotter et al. (1998) that is based on 68 small lakes (300-2350 m a.s.l) located in the Swizz Alps. We chose this model as these lakes are also situated in catchments with calcareous lithology and 70 % of the fossil diatoms of Oberer Soiernsee are part of the modern diatom training set.

Diatom concentrations were calculated by the number of microscope fields of view in relation to the amount of dry sediment.

$$diatoms/\mu l = \frac{N\ total}{Fv} / Vcs * Vt * D$$

N_{total} = amount of counted diatom valves in total
Fv = analysed fields of views
Vcs = volume of one counting square ((volume of dropped diatom dilution*area of one counting square)/area of the cover glass)
Vt = total volume of cleaned diatom solution
D = dilution of cleaned diatom material

4.3.5 Pigment analyses

The sediments of C2 were analysed for sedimentary pigments following the method of Leavitt and Hodgson (2001). 0.3 ± 0.065 g freeze-dried subsamples were filled into 4 ml amber glasses under subdued green light, extracted using 99 % acetone (Rotisolv HPLC, Carl Roth, Germany) and stored at – 20 °C for 24 h. After gently shaking, 2 ml of the extract were filled into 2 ml Eppendorf tubes and centrifuged for 15 min at 2000 rpm and – 9 °C (Heraeus Fresco 17/21, Thermo Fisher Scientific, Schwerte, Germany). Subsequently, 1.0–1.5 ml of the supernatant was filtered through syringes equipped with 0.2 µm PTFE filters into 1.5 ml HPLC glasses. The samples were stored at – 80 °C until analysis. Pigments were identified and quantified by reverse-phase, high-performance liquid chromatography (HPLC, MD-2015 plus, Jasko, Pfungstadt, Germany) and measured by 436 nm and 450 nm detectors, based on Wright et al. (1991). Pigment concentrations were related to dry weight and translated to $\mu g\ g^{-1}$. Some pigments had to be identified by comparing peak time and spectra with data published in Wright et al. (1991) and then quantified by the peak area ($mV\ min^{-1}$). Following Leavitt and Hodgson (2001) and Buchaca and Catalan (2008), we used chlorophyll *a* (chl *a*), its derivate pheopythin-a (phe-a), *ß*-carotene and its degradation product ethyl-8´-beta-apocarotenoate as marker pigments for total algal biomass and primary production. Diatoms were identified by the pigments fucoxanthin, diatoxanthin, diadioxanthin and its degradation product diadinochrome. Chrysophyta were represented by violaxanthin, dinophyta by peridinin and diadinoxanthin/diadinochrome. The population dynamics of the chlorophyta were tracked by chlorophyll *b* and several carotenoids (lutein, neoxanthin, prasinoxanthin, zeaxanthin). Alloxanthin was selected to track abundances of chryptophyta. Pheophytin-a is a typical pigment for decaying communities (Buchaca and Catalan, 2008). Therefore, we used the chl *a*/phe-a ratio to estimate the degree of pigment preservation in the sediments (Tõnno et al., 2019). The ratio between alloxanthin and diatoxanthin was used to track past changes in water column transparency or lake level fluctuations (Buchaca and Catalan, 2007)

4.3.6 Stable isotope analyses

Freeze-dried subsamples were sieved (250-µm mesh size) to eliminate organic macro-remains and only the fine fraction was used for isotopic analysis. Additionally, potential in-lake OM sources (phytoplankton, *Chara* sp., *Potamogeton* sp.) and OM sources from the catchment (soil, leaves, pine needles, herbages) were collected, oven-dried (40°C) and homogenized by sieving (soil) or grinding with a mortar. For robust results, we extended the OM dataset and involved catchment OM samples from 23 mountain lakes situated in the northern Alps. For simultaneous organic carbon content (wt % TOC) and $\delta^{13}C_{org}$ analyses, ~ 2.0 mg material was filled into silver capsules and decalcified with first 5% and thereafter 20% hydrochloric acid at 70 °C on a heating plate. Droplets of the acid were successively added to the sediment in each capsule until no effervescence was observed anymore. After drying, the capsules were closed for subsequent isotope analysis (Mayr et al. 2017). In order to determine the total nitrogen content (wt % TN), $\delta^{15}N$, and total carbon (wt % TC), ~ 2.5 mg of bulk sediment was filled into tin capsules. Samples were combusted in an element analyser (NC 2500, Carlo Erba) coupled to a continuous-flow, isotope-ratio mass spectrometer (Delta Plus, Thermo-Finnigan, Germany) at Friedrich-Alexander-University of Erlangen. Isotope ratios are presented in δ–notation ($\delta^{15}N$, $\delta^{13}C_{org}$) as $\delta = (R_S/R_{St} - 1)$, with R_S and R_{St} as isotope ratios of the sample with the international standards VPDB (carbon) and AIR (nitrogen) and were quoted in ‰. An internal laboratory standard (peptone with $\delta^{15}N = 4.93$ ‰, $\delta^{13}C_{org} = -23.80$ ‰) and international standards (IAEA-N-1; IAEA-N-2; USGS41; IAEA-CH-7; Brand et al., 2014) were used for isotope calibration. Analytical precision (one standard deviation) was typically 0.1 ‰ for both $\delta^{15}N$ and $\delta^{13}C_{org}$. Elemental contents of total carbon (TC), total organic carbon (TOC), total inorganic carbon (TIC) and total nitrogen (TN) were calculated from the ratios of peak-area to sample weight using elemental standards (atropine, cyclohexanone-2.4-dinitrophenylhydrazone) for calibration and are shown as mass percentages (wt %). TOC/TN ratios are expressed as molar ratios.

4.3.7 Analyses of pore-water pH value

Sediment pore water was directly sampled from core C3 using Rhizon SMS 10 cm core solution samplers (2.5 mm diameter, 0.15 µm mean pore size; Eijkelkamp Soil and Water, Giesbeek, Netherlands). A total of eight 3-mm-diameter holes were drilled through the tube wall of the closed core using a gimlet. Saturated Rhizon samplers were inserted horizontally into the sediment through the holes. 10 ml syringes (Eijkelkamp Soil and Water, Giesbeek, Netherlands) were then luer-locked with the Rhizon samplers. The pistons of the syringes were fully withdrawn and held in position with a wooden retainer to generate a vacuum for pore-water extraction. Pore-water then passed from the sediment through the porous tubes and flexible hoses into the syringes. After three hours, the Rhizons obtained a sufficient amount of pore water and the pH could be measured (Multi 3630 IDS, WTW, Weilheim, Germany).

4.3.8 Statistical analyses

Broken-stick models (Bennet 1996) were calculated with the R package 'rioja' (Juggins 2018) to detect the stratigraphic position of major changes of diatom assemblages, pigment compositions and stable isotope records. PAST (version 3.18) statistical software package (Hammer and Harper 2006) was used for ecological analyses of life form and substrate preferences. Species abundances were Hellinger transformed (Legendre and Gallagher 2001) before analysis. Square-root transformed diatom data was imported in a diatom- inferred depth model (Hofmann et al. 2020) and diatom-inferred TP interference model (Lotter et al. 1998) using R (version 3.4.3) and the package rioja (Juggins 2018) for water depth reconstructions. Diversity was calculated by the Shannon-Index using ln (natural logarithm) of percentage of each taxon. Down-core profiles were illustrated using C2 version 1.7.7. (Juggins 2007), including only diatom species with relative abundances greater than 1 % in at least two subsamples. As diatoms were very scarce in core depths greater than 22 cm (< 50 valves per sample), the subsamples C2_22 and C2_23 were not included in diatom statistical studies and stratigraphic illustration.

4.4 Results

4.4.1 Sedimentology, core chronology, sedimentation rate and correlation of the cores

The sediment of Oberer Soiernsee mainly consisted of dark grey, partly organic-rich clay and silty clay, interrupted by clearly visible light grey silt layers (Fig. 4.2). Two ^{137}Cs peaks occurred in the sediments of core C1. Assuming that the ^{137}Cs peak at 1.5 cm corresponds to the Chernobyl disaster in AD 1986, the sedimentation rate has been very low during recent times (0.05 cm/y). Since this does not correlate with our results of a stable isotope and pigment analysis, that indicate enhanced in-lake productivity, we attributed this to the use of floaristic foam to seal the core after sampling, as it destroys the topmost core section. A sedimentation rate of 0.087 cm/y could be calculated from the distance between the first and the second peak at 3.5 cm (1963). A very similar mean sedimentation rate was estimated using the CRS-model (constant rate of supply) on ^{210}Pb activity (0.084 cm/y).

It is reasonable to interpret the light grey silt layers (C1: 11 cm, 13 cm, 16 cm and 20 cm) as flood layers resulting from fast deposition events such as debris flows and high surface runoffs, especially based on elevated TIC values. Hence, they were removed from the sedimentary record when developing the age-depth model.

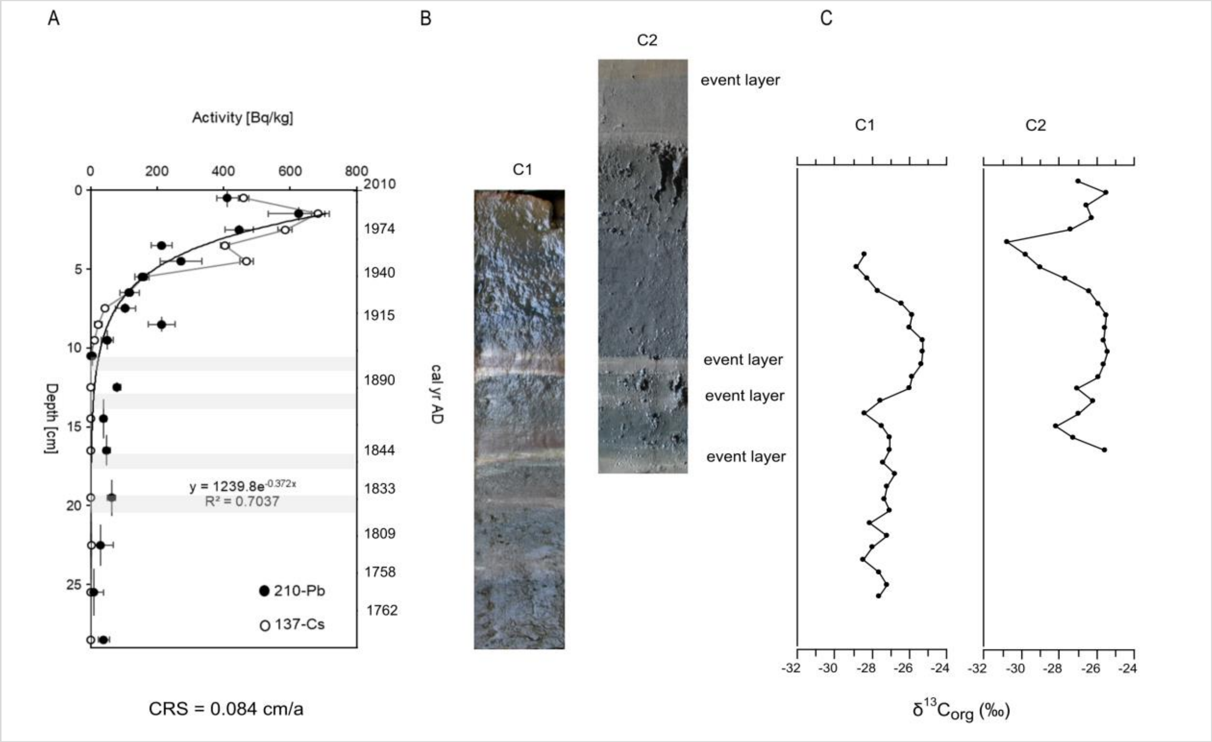


Figure 4.2 CRS depth-age model of core C1 using activity of unsupported ^{210}Pb (black dots) and ^{137}Cs (white dots) (A). Photos of both cores and position of event layers (B). Correlation of C1 and C2 via $\delta^{13}C_{org}$ records (C)

Core C2 was obtained two years after the master core. The core was complete and undisturbed (Fig. 4.2). The comparison of the $\delta^{13}C_{org}$ records of both cores reveals a high inter-core consistency. Three event layers of C1 (11 cm, 13 cm and 16 cm) were found to correspond exactly in their thickness and sequence with event layers of C2 (17 cm, 19 cm and 22 cm). Another time marker is represented by the ~ 3 cm thick event layer at the top of C2, which is the result of a strong thunderstorm in August 2015 with extreme rainfall and mud flows. By correlating the $\delta^{13}C_{org}$ records and event layers, the chronology of C2 was found to date back to ~ AD 1840.

4.4.2 Diatoms

Diatom biostratigraphy

A total of 125 diatom taxa representing 39 genera were identified in 21 subsamples, 21 of these occurred in relative abundances > 2 % in at least two samples (Fig 4.3 A). Benthic life forms dominated the diatom assemblages, especially fragilarioid species of the genera *Pseudostaurosira*, *Staurosira* and *Staurosirella*, which accounted for 41 % of the total subfossil assemblages. Centric diatoms reached a total abundance of 6 % and were mainly represented by *Cyclotella comensis* Grunow in van Heurck (3 %), *Cyclotella* cf. *woltereckii* Hustedt (3 %), and *Cyclotella praetermissa* Lund (1 %). Overall, the most frequent periphytic taxa were *Staurosirella pinnata* (28 %), *Amphora pediculus* (Kützing) Grunow (26 %), *Staurosira construens* var. *venter* (6 %), *Denticula tenuis* Kützing (4 %), *Achnanthidium straubianum* (Lange-Bertalot) Lange-Bertalot (3 %), *Achnanthidium minumtissimum* var. *minutissimum* (Kützing) Czarnecky (2 %), *Fragilaria nanana* Lange Bertalot (2%), *Platessa conspicua* (A. Mayer) Lange-Bertalot (2 %), *Pseudostaurosira elliptica* (Schumann) Edlund, E. Morales, S.A. Spauld (2 %), *Pseudostaurosira trainorii* E. Morales (2 %), and *Amphora inariensis* (Krammer) Lange-Bertalot (2 %). Species richness varied between 20 and 55, Shannon diversity between 1.8 and 2.8 (Fig. 4.3). The total diatom concentrations in the sediment samples ranged from $5 \cdot 10^2$ to $2 \cdot 10^4$ diatoms μl^{-1} (Fig. 4.3).

The broken-stick model (Bennet 1996) identified four different diatom assemblage zones (Figs. 4.3 A, B).

Zone D-A (21-18 cm; AD 1856–1880): *Amphora pediculus* and *Staurosirella pinnata* co-dominated the diatom assemblages of the deepest diatom zone. Fragments of *Aulacoseira* ssp. Occurred frequently in this zone.

Zone D-B (18–6cm; AD 1880–2010): The assemblages of this zone differ clearly from those of zone D-A, although *Amphora pediculus* and *Staurosirella pinnata* remained the dominant taxa. After a peak in AD 1960, *Staurosira construens* var. *venter* declined in frequency. *Pseudostaurosira elliptica* disappeared around AD 1960, when *Pseudostaurosira trainorii* clearly increased in its abundances.

Zone D-C (6–2 cm; AD 2010–2015): Beside *Amphora pediculus* and *Staurosirella pinnata, Platessa conspicua* dominated the diatom assemblages. Centric diatoms and the planktic taxa *Fragilaria nanana* started to increase distinctly in their abundances. The abundances of *Staurosira construens* var. *venter* clearly decreased towards the end of the zone, while *Staurosirella pinnata* increased slightly.

Zone D-D (2–0 cm; AD 2015–2017): Centric diatoms (31-65 %) and *Fragilaria nanana* (8-22 %) codominated the assemblages of this zone (39-87 %). Small *Cyclotella comensis* in particular is highly abundant (1-30 %). Simultaneously, all periphytic taxa clearly declined. All small fragilarioid taxa were absent with the exception of *Staurosirella pinnata*.

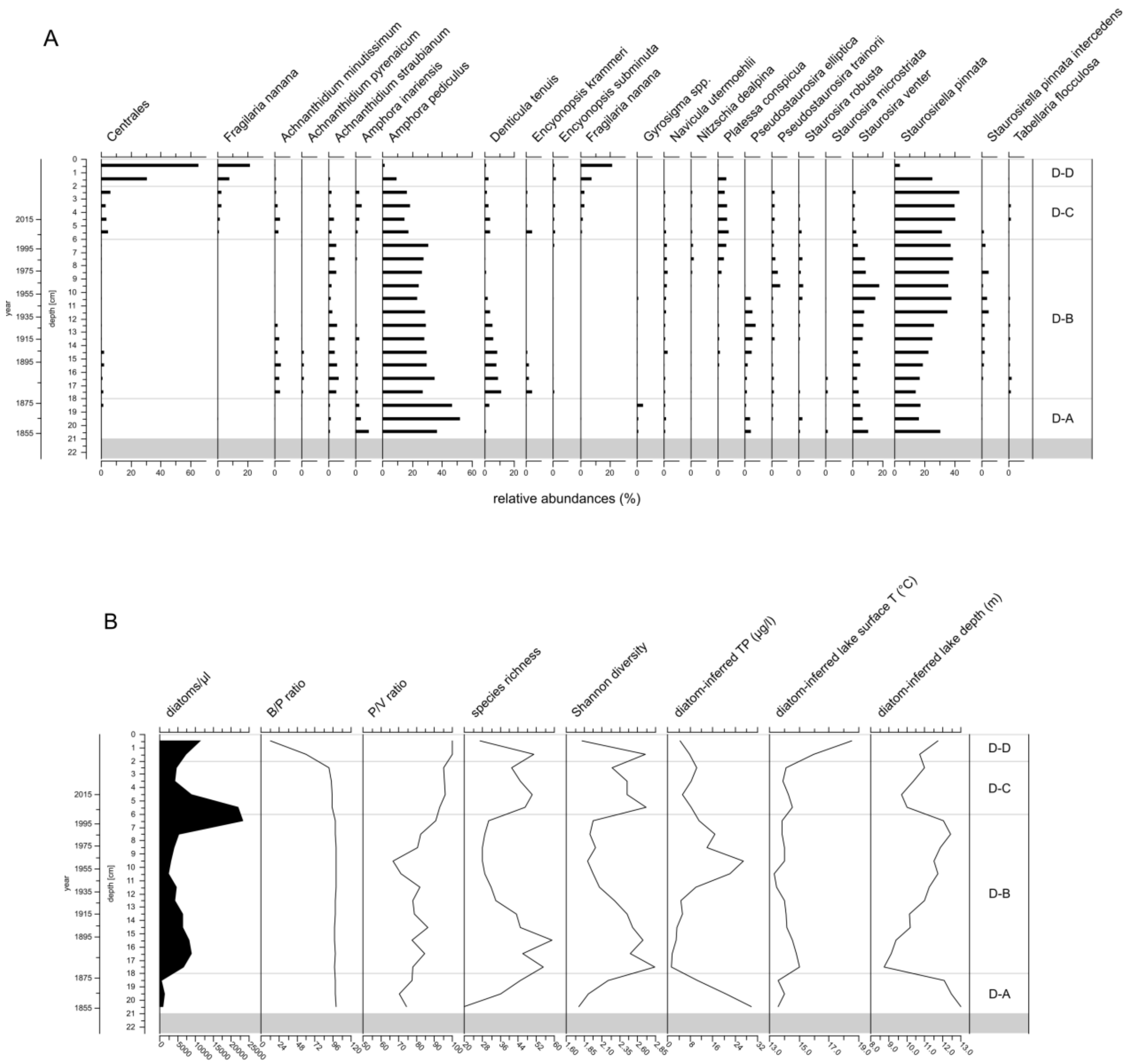


Figure 4.3 A) Diatom biostratigraphy of the most common taxa with relative abundances > 2 % in at least two samples. B) Variation in the ratios between benthic+epiphytic and planktic taxa (B/P ratio) and between Staurosirella pinnata and Staurosira construens var. venter (P/V ratio). Alteration of Shannon diversities and species richness. Reconstruction of lake temperature by using the silicification value (Kuefner et al. 2020) and of lake depth by applying the WA-PLS model (Hofmann et al. 2020). The four diatom zones (D-A to D-D) are separated by grey lines. The grey bar represents the two lowermost samples, where diatoms were too scare for including in statistical analyses

The valve density (Fig. 4.3 B) was very low in the deeper part of the core (zone D-A), but clearly increased after AD 1880. A distinct maximum was calculated in the transition between zones D-B and D-C (7.5–5.5 cm: AD 1986–2010). After this, the cell density declined visibly before it increased again in the younger sediments (2.5–0.5 cm: AD 2015–2017).

The ratio between benthic+epiphytic and planktic diatom species (B:P ratio; Fig. 4.3 B) showed only small variations before AD 2010, but declined markedly in zone D-D. After the distinct dominance of benthic diatoms in the deepest sample, planktic taxa gained importance between AD

1870 and AD 1900, which is also reflected in the increasing species richness and diversity. Between AD 1940 and AD 2000, epipsammic fragilarioid taxa clearly dominated the periphytic (benthic+epiphytic) diatom assemblages, while centric, epilithic and epiphytic species occurred in low percentages, resulting in low species richness and Shannon diversities (Fig. 4.3 B). Zone D-C is characterized by higher diversity indices and more diverse periphytic diatom assemblages. The B:P ratio decreased due to increasing abundances of centric diatoms. The distinct dominance of planktic species in zone D-D resulted in low B:P ratios and decreasing diversity indices.

The ratio between *Staurosirella pinnata* and *Staurosira construens* var. *venter* (P:V ratio; Fig 4.3 B) generally increased towards recent times. Whereas the ratio varied around a median of 78 between 21.5 and 7.5 cm, it clearly increased after ~ AD 1980 to a median of 95.6, implying the declining influence of *Staurosira construens* var. *venter* in zones D-C and D-D.

Diatom-based reconstruction of lake surface temperatures, lake levels and TP concentrations

By calculating the lake surface temperatures using the silicification value (Kuefner et al. 2020 a; Kuefner et al. 2020 b), there is clear evidence of a trend towards rising temperatures from 13.6 °C (~ AD 1856) to 18.5 °C (AD 2017) (Fig. 4.3 B). The diatom assemblages of the deepest diatom zone (D-A) indicated the lowest mean surface temperature (13.9 °C). Increasingly higher average surface temperatures were calculated for the diatom assemblages of the zones D-B (14.0 °C), D-C (14.2 °C), and D-D (17.2 °C).

By applying the diatom-inferred depth model designed by Hofmann et al. (2020), the WA-PLS (RMSE = 2.43 m; $r^2 = 0.63$) approach proved to be suitable. The reconstructed lake levels show a first maximum (12.5 ± 2.4 m) around AD 1868 and a second maximum (12.5 ± 2.4 m) around AD 1986 (Fig. 3). Inferred depth values steadily increased between AD 1880 and AD 1986. Subsequently the value declined to a second minimum (9.7 ± 2.4 m) in 2015, before the increased again up to 11.7 ± 2.4 m in AD 2017 (Fig. 4.3 B).

TP reconstructions (WA-PLS approach; RMSE = 0.27; $r^2 = 0{,}75$) by using the model of Lotter et al. (1998) revealed a maximum 29.9 ± 1.9 $\mu g\ l^{-1}$ around AD 1860. TP concentrations fist declined, and then started to rise after AD 1890. After a second maximum (27 ± 1.9 $\mu g\ l^{-1}$) around AD 1965 the values tended to decrease to 8.4 ± 1.9 $\mu g\ l^{-1}$ around AD 2015. Within the event layer mean TP concentrations ~ 8.0 ± 1.9 $\mu g\ l^{-1}$ were inferred. In the uppermost sample TP = 4.5 ± 1.9 $\mu g\ l^{-1}$ was reconstructed (Fig. 4.3 B).

4.4.3 Sedimentary pigments

Five different phases with regard to pigment concentration and preservation could be distinguished (Fig. 4.4):

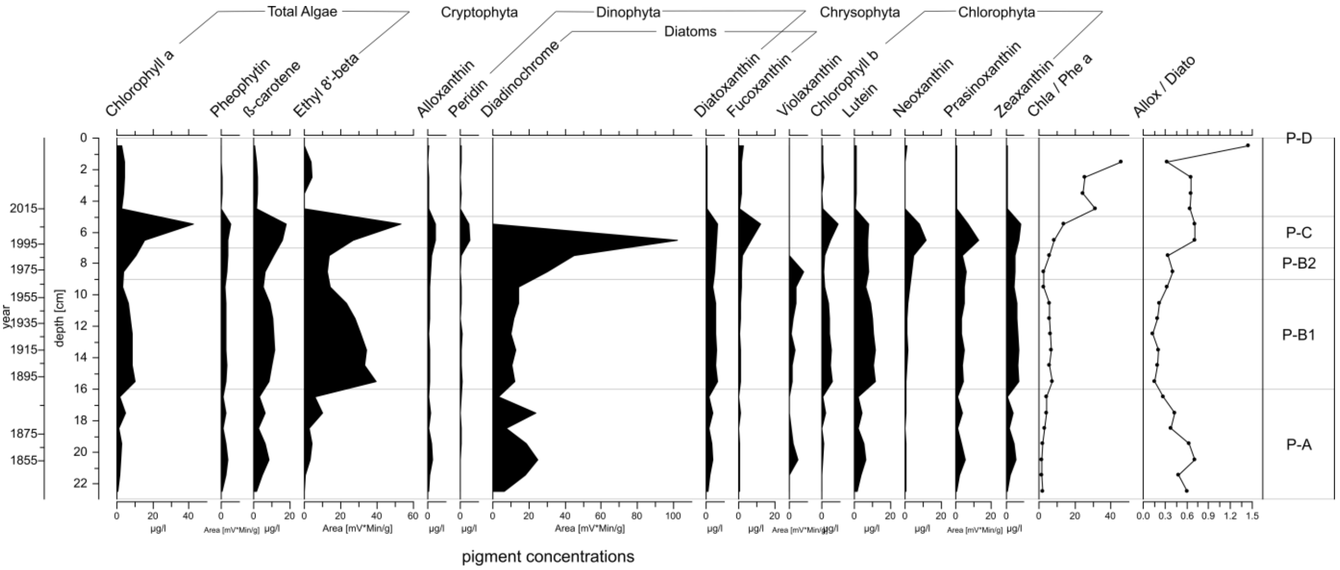


Figure 4.4 Sedimentary record of the marker pigments, of the pigment preservation (Chl a/Phe a) and of the ratio between alloxanthin and diatoxanthin (Allox/Diato). The five pigment zones (P-A to P-D) are separated by grey lines

Five different phases with regard to pigment concentration and preservation could be distinguished (Fig. 4):

Phase P-A (22.5–16.5 cm; before AD 1880) was characterized by low chl *a* and *ß*-carotene concentrations and low chl *a*/phe-a ratios, indicating low algal biomass and poor pigment preservation. Two clearly visible declines in all pigment concentrations at 16.5 cm and 18.5 cm are noticeable. The high concentrations of diadinchrome, a derivate of diadinoxanthin, suggest the dominance of periphytic diatoms in the outgoing 19th century.

Significantly higher concentrations of nearly all pigments and higher chl *a*/phe-a ratios were detected during phase P-B1 (15.5–9.5 cm; AD 1890–1960), suggesting an increasing total algae biomass and rising pigment preservation. However, a decrease in chl *a* and *ß*-carotene concentrations are evident towards the end of phase P-B1.

Phase P-B2 (8.5–7.5 cm; AD 1970–1986) started with low preservation ratios and a depression of total algal biomass marker concentration. However, the concentrations of most pigments began to increase within this phase. After a maximum around AD 1970, violaxanthin (Chrysophyta) disappeared abruptly.

Since ~ AD 1990 (phase P-C; 6.5–5.5 cm), there has been a dramatic increase in total algal biomass and a steady up to threefold, rise in preservation ratios. Peridin (Dinophyra), alloxanthin (Cryptophyta) and the marker pigments of green algae (chlorophyll *b*, neoxanthin, prasinoxanthin and zeaxanthin) appeared in their highest concentrations.

Between AD 2015 and 2017 (4.5–0.5 cm; phase P-D), the preservation ratios increased markedly by a factor of 10. Simultaneously, the concentrations of all pigments decreased abruptly.

4.4.4 Stable isotopes

Organic geochemistry and stable isotopes of the sediments

Four different phases could be separated in terms of organic geochemistry and stable isotope ratios (Fig. 4.5):

Phase SI-A (22.5–20.5 cm; before ~ AD 1868) began with high values of $\delta^{13}C_{org}$ (– 25.5 ‰) and TIC (9.4 wt %), followed by a marked decrease towards the end of the zone. TOC (3.1 wt %), TN (0.3) and $\delta^{15}N$ (1.9 ‰) exhibited low values at the base of the core and increased distinctly higher up. $\delta^{15}N$ showed the highest values (2.6 ‰) and TIC (4.9 wt %) the lowest values of the entire record at 20.5 cm (~ AD 1860). The highest TOC/TN ratio of the entire record (10.2) occurred at 22.5 cm.

$\delta^{13}C_{org}$, and TIC values initially rose during phase SI-B (19.5–8.5 cm; AD 1868–1980), accompanied by declining TOC and TN contents. Subsequently, between AD 1890 and AD 1950, hardly any changes were visible for the TN (median 0.4 wt %), $\delta^{13}C_{org}$ (median –26.6 ‰), TOC (median 3.8 wt %) and TIC (median 9.2 wt %) values. Only $\delta^{15}N$ (median 1.5 ‰) exhibits greater fluctuations, especially before AD 1890. $\delta^{15}N$ values began to decline after ~ AD 1960. From AD 1940 onwards, $\delta^{13}C_{org}$ and TIC decreased steadily, while TOC and TN increased towards the end of the phase.

Phase SI-C (7.5–5.5 cm; AD 1980–2015) is characterized by several prominent changes: there was a marked drop in $\delta^{13}C_{org}$ down to a minimum of –30.8 ‰ at 5.5 cm and a concurrent increase in TOC and TN up to a maximum of 6.1 wt % and 0.9 wt %, respectively. The TOC/TN ratio also reached a distinct minimum at 5.5 cm (6.9).

During phase SI-D (4.5–0.5 cm; AD 2015–2017), $\delta^{13}C_{org}$ shifted again to higher values (up to -25.5 ‰ at 1.5 cm). TOC showed the lowest contents during the entire investigation period (2.5-2.6 wt %). TIC increased markedly to the highest values (10.4–11.6 wt %). TN had the lowest values (0.3 wt %) comparable to values at the base of the core.

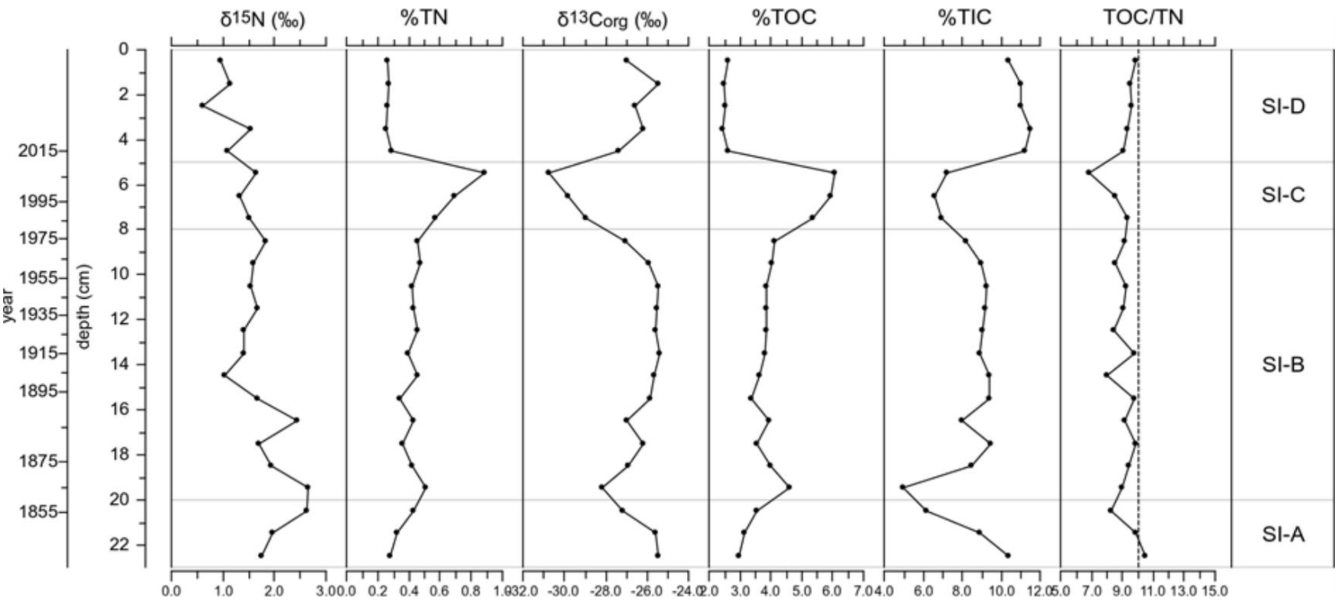


Figure 4.5 Stable isotope (δ13Corg, δ15N), geochemical (TN, TOC, TIC and TOC/TN data of sedimentary organic matter. The four phases (SI-A to SI-D) are separated by grey lines

Isotopic and geochemical signatures of OM sources and the origin of sedimentary OM

The isotopic signatures of modern OM (lake algae, herbaceous vegetation, terrestrial soils, trees and submerged macrophytes) collected in the lake and his catchment are shown in Table 4.1. .Based on modern isotopic fingerprints, algae appeared to be the main source of sedimentary OM (Fig. 4.6). Additionally, terrestrial soils contributed to sedimentary OM (Fig. 4.6). A proportion of sedimentary OM derived from macrophytes, herbaceous vegetation and trees, both coniferous and deciduous is very unlikely as their isotope signatures plot at a large distance to the sediment signatures (Fig. 4.6).

Table 4.1 Isotopic signatures of modern OM sources including macrophytes, lake algae and catchment saoil and vegetation

Modern OM source	$\delta^{13}C_{org}$	$\delta^{15}N$	TOC/TN
Lake algae	median – 28.4 ‰, (range between – 34.9 and – 19.8)	median 3.6 ‰ (range between 1.2 and 5.4	median 9.0 (range between 6.9 and 10.2
Herbaceous vegetation	median – 28.9 ‰, (range between – 30.5 and – 26.6 ‰)	median – 1.18 ‰, (range between – 3.6 and 0.8 ‰)	median 18.2, range (between 12.2 and 30.7)
Terrestrial soils	median – 26.9 ‰ (range between – 27.3 and –26.5)	median – 1.6 ‰ (range between – 3.5 and 0.6 ‰)	median 15.8 (range between 11.4 and 18.2).
Conifers	median – 28.8 ‰, (range between –30.8 and – 26.8 ‰)	median –4.4 ‰, (range between – 9.2 and – 1.0 ‰)	median 44.1, (range between 27.1 and 55.6)
Deciduous trees	median –29.4 ‰, (range between –32.7 and –26.4 ‰)	median 3.1 ‰, (range between – 5.4 and 0.31 ‰)	median 20.5, (range between 14.2 and 33.2)
Potamogeton alpinus	– 13.6 ‰	1.98 ‰	9.8
Chara spp.	– 17.8 ‰	– 7.9 ‰	9.0

Linkages between carbon and nitrogen cycles

Findlay and Kendall (2007) summarized the main geochemical processes controlling $\delta^{15}N$ and $\delta^{13}C_{org}$ of aquatic OM under the premise of a predominant algal origin of OM (Fig. 4.6). The TOC/TN ratios in the sediments of Oberer Soiernsee revealed that algae are the major sedimentary OM component, as pure algal matter typically ranges between 7 and 9 (Meyers and Teranes 2001). Accordingly, photosynthesis and eventually methane oxidation are the main factors that regulated changes in $\delta^{13}C_{org}$ records in Oberer Soiernsee (Fig 4.6). The variations in $\delta^{15}N$ are smaller than those in $\delta^{13}C_{org}$ record and may point to denitrification.

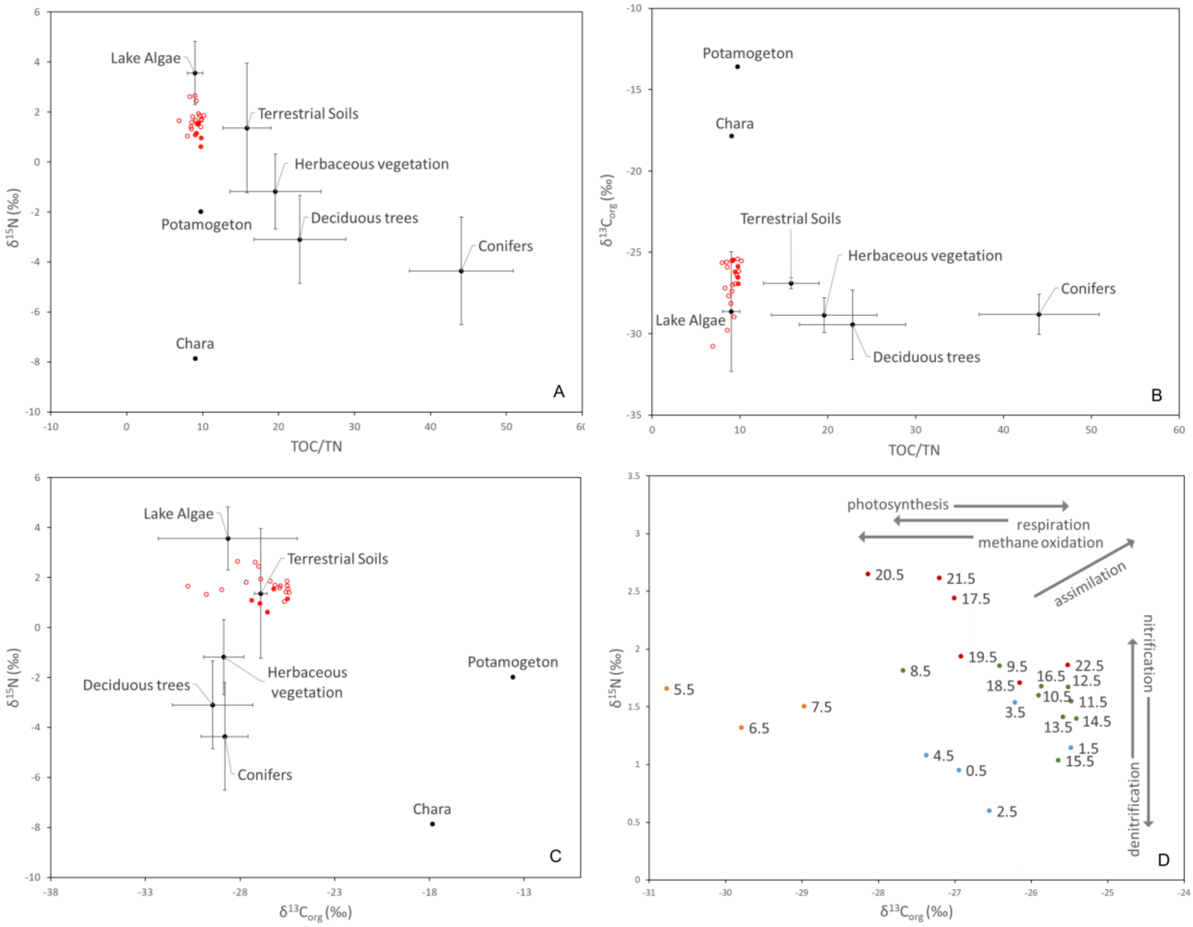


Figure 4.6 Isotopic and geochemical signatures of sediment record (red open circles) and potential sources of sedimentary OM. The red dots represent the most recent samples (AD 2015-2017) (A-C). $\delta^{15}N$ versus $\delta^{13}C_{org}$ based on Finlay and Kendall (2007) to evaluate main geochemical in-lake processes controlling $\delta^{15}N$ and $\delta^{13}C_{org}$ of aquatic OM (D)

Before the AD 1860s (red dots), an increasing $\delta^{15}N$ (positive shift of 0.8 ‰) and simultaneously decreasing $\delta^{13}C_{org}$ (negative shift of 2.6 ‰) indicated a combination of incipient denitrification and methane oxidation processes (Fig. 4.6). Between 1870 and 1980 (green dots), a marked shift towards 1.4 ‰ lower $\delta^{15}N$ values and 1.4 ‰ higher $\delta^{13}C_{org}$ values suggests elevated primary production. After AD 1970 the records of $\delta^{15}N$ and $\delta^{13}C_{org}$ are decoupled. Towards 1980, decreasing $\delta^{13}C_{org}$ indicates that respiration or, more likely, anoxic biochemical processes became increasingly important. Between AD 1980 and AD 2015, a marked negative shift (3.1 ‰) towards significantly lower $\delta^{13}C_{org}$ values indicates enhanced methane oxidation processes (orange dots). After AD 2015 the shift towards higher $\delta^{13}C_{org}$ values indicate enhanced photosynthesis and possibly nitrification as important processes (blue dots).

4.4.5 In-situ pore water pH (core C3)

The pH value at the sediment-water interface was 8.6 in October 2018. Down-core, the values declined continuously from 7.8 (2 cm) to 7.4 (20 cm) (Table 4.2).

Table 4.1 pH values of the sediment-water interface and of the sediment pore water in specific depths

Sediment depth (cm)	0	2	6	10	16	20
pH	8.6	7.8	7.7	7.5	7.5	7.4

4.5 Discussion

The combination of sedimentological, biological, biochemical and geochemical proxies, supported by historical information, proved as a powerful tool to reconstruct the ecological history of Oberer Soiernsee and to disentangle the effects of different environmental impacts on the lake evolution since ~ AD 1840. Diatom, pigment and $\delta^{13}C$ records provided valuable information on the effects of catchment-related changes on lake-internal biogeochemical processes. Chl *a* and $\delta^{13}C$ show very similar trends, facilitating the reconstruction of lake trophic history reliably. Diatom-inferred TP-concentrations, however, show partly distinct differences. Juggins (2013) warns against the uncritical use of quantitative reconstructions, as biotic communities respond sensitively and complexly to multiple environmental gradients. Lotter et al. (1998) conceded, that besides TP a series of other causal factors such as mean summer temperatures, mixing regimes, the availability of light and other nutrients (nitrogen, silica and carbon) and interspecific competition control the composition of the diatom assemblages. The application of transfer functions requires a negligible influence of these secondary environmental variables; furthermore, the effects of temporal change in the underlying causal relationships must be considered (Juggins, 2013).

However, several facets of global environmental changes have affected remote mountain lakes since the industrial revolution (Catalan et al. 2013). The effects these global changes on the lake ecology of Oberer Soiernsee were revealed by the $\delta^{15}N$ record (atmospheric deposition–fertilization) and by shifts in diatom species composition (changes of water temperature, thermal stratification and light availability).

4.5.1 Depth-age model

The applicability of the CRS model to date the sediments of Oberer Soiernsee may be debatable as the lake was exposed to a series of both catchment-mediated and lake-internal changes resulting in an increase of algae biomass (Figs. 4.3 and 4.4). However, after discarding the event layers (Fig. 4.2), our age-depth-model correlates well with historical records including land use, hut construction, overnight stays (Müller 1922; Cabin book Hans- Mertel-Cabin; Yearbooks of the Alpine Club Section Hochland 1920 – 2017).

4.5.2 Ecological history of Oberer Soiernsee

Period I (AD 1840 - AD 1880): Little Ice Age, alpine pasturing, hut construction

The high frequency of paleoflood layers in the deeper part of the core (Fig. 4.1) are indicators for heavy rainfall events (Giguet-Covex et al. 2012; Wilhelm et al. 2012; Wilhelm et al. 2013) and suggest the influence of the Little Ice Age (LIA), a period of low temperatures, high wind speeds and high precipitation that occurred from the 16th to the mid-19th century, particularly in the Northern Hemisphere (Bracht-Flyr and Fritz 2016; Ilyashuk et al. 2018). TOC/TN ratios > 10 indicate enhanced allochthonous OM sources (Meyers and Teranes 2001) in particular soils (Fig. 4.5), due to the enhanced erosion induced by higher precipitation rates in the LIA.

The high flood frequency and the harsh conditions including low temperatures and short growing seasons led to low diatom and pigment concentrations before ~ AD 1850 (Figs. 4.3 B, 4.5). Post-depositional dissolution of the siliceous diatom valves can be excluded as both heavily (e.g. *Diploneis* spp., *Gyrosigma* spp.) and slightly (e.g. *Staurosira microstriata*) silicified taxa were sporadically found. Furthermore, pore water analyses revealed pH = 7.4 (Tab. 4.2), suggesting favourable preservation conditions as diatom dissolution especially occurs at pH > 9.0 (Lewin 1961; Barker et al. 1994).

The large-celled, heavily silicified *Aulacoseira* species, occurring especially before ~ AD 1880 also indicate more turbulent conditions in context with the LIA, as this species requires turbulent mixing to remain in the photic zone and gain access to nutrient resources (Karst-Riddoch et al. 2005; Reynolds 2006; Saros and Anderson 2014; Weckström et al. 2016; Rühland et al. 2018).

The light availability for benthic growth depends on both water depth and light penetration. Hence, diatom-inferred high lake levels before ~ AD 1880 (Fig. 4.3 B) more likely indicate the high-turbid conditions with low water transparency that often prevailed during the windy periods towards the end of the LIA (Mann 2002 a). The high ratios between alloxanthin and diatoxanthin also indicate limited light availability for benthic algae (Fig 4.4). In contrast, high B/P ratios suggest extensive periphytic diatom growth, especially of small epipsammic fragilarioids and epipelic

Amphora spp. Figs 4.3 A, B), which are both indicative for the deeper littoral zone of Oberer Soiernsee today (Hofmann et al. 2020). The small epipsammic species are known to live firmly attached on sand grains, to be resistant to abrasion or damage due to a harsh and turbulent environment, and to even tolerate short terms of darkness and brief anaerobic conditions (Moss 1977; Hofmann et al. 2020). Epipelic taxa have a competitive advantage, as they are able to avoid permanent burial due to their mobility (Moss 1977; Burkholder 1996).

Diatom inferred TP reconstruction fits well with the $\delta^{13}C_{org}$ trend. TP ~ 30 ± 1.9 $\mu g\ l^{-1}$ revealed mesotrophic conditions around AD 1860 (Fig. 4.3) also reflected by rising pigment concentrations despite low preservation indices (Fig. 4.4). We assume that the high erosion rates related to the LIA may be responsible for the elevated TP concentrations, as the calcareous rocks in the catchment may contain considerable amounts of phosphorus-containing minerals (Valeton 1988). The high TIC values in the deepest part of the core (AD 1840-1860) support this assumption (Fig. 4.5).

The decline in $\delta^{13}C_{org}$ may have been triggered by the gradual ^{13}C depletion of atmospheric CO_2 since the industrial revolution. McCaroll and Loader (2004) found that the combustion of fossil fuels resulted in 1.5 ‰ more negative $\delta^{13}C_{org}$ values of atmospheric CO_2 as fossil fuels are relatively depleted in ^{13}C. The shift to 2.61 ‰ lower $\delta^{13}C_{org}$ values (Fig. 4.5) is, however, too large to be explained solely by a fossil fuel combustion effect. Enhanced external input by an increased flood frequency during the LIA and additionally alpine pasturing and forestry (Müller 1922) seems to be a more plausible cause for ^{13}C depletion of sedimentary OM as these activities are known to provide additional nutrient load to the lake and promote lake eutrophication (Schwoerbel and Brendelberger 2013). Enhanced primary productivity resulted in hypolimnetic anoxic conditions that promote chemoautotrophic organisms and methanotrophic bacteria with ^{13}C-depleted biomass (Braig et al. 2013). These microbes produce ^{13}C-depleted CO_2 and thus change the DIC reservoir of a lake (Hollander and Smith 2001). The resulting ^{13}C-depleted photoautotrophic biomass and the ^{13}C-depleted microbial biomass culminate in the negative trends in the $\delta^{13}C_{org}$ values of sedimentary OM (Fig. 4.5).

However, with progressing eutrophication since ~ AD 1870 the $\delta^{13}C_{org}$ values become more positive again (Fig. 4.5). Diatom-inferred TP (20.8 ± 1.9 $\mu g\ l^{-1}$) also reflects enhanced phosphorus input triggered by the massive deforestation related to the construction of the two mountain huts in AD 1866 (Müller 1922). The limitation of carbon availability in the course of the rise in algae biomass results in decreasing isotopic discrimination during photosynthesis, culminating in more ^{13}C-enriched OM (Fogel and Cifuentes 1993), and the rising flux of ^{13}C-enriched phytoplankton biomass started to overprint the microbially influenced isotopic signals after ~ AD 1870.

Plotting $\delta^{15}N$ versus $\delta^{13}C_{org}$ (Fig. 4.6) reveals a combination of methane oxidation processes and incipient denitrification in the deeper part of the core (Findlay and Kendall 2007). We assume that denitrification processes in context with the enhanced allochthonous input due to the high precipitation rates may have stimulated the weak rise in $\delta^{15}N$ values. This trend was additionally promoted by livestock, deforestation, and, after 1866, by the dry toilet as human and animal waste is enriched in ^{15}N (Kendall 1998).

Period II (AD 1880 – AD 1980): Rising temperatures, increasing eutrophication and atmospheric N fertilization

Rising temperatures towards the end of the LIA led to increasing photosynthesis rates (Hall and Smol 2010) documented by rising diatom densities and pigment concentrations after ~ AD 1880 (Figs. 4.3 A, 4). Within the benthic diatom assemblages, some structural shifts occurred especially within the small fragilarioids (Fig. 4.3 A). *Staurosira microstriata,* a taxon indicating low mean summer water temperatures (Schmidt et al. 2004), became absent after ~ AD 1880. *Pseudostaurosira elliptica* a species favouring low NO_3 concentrations (Morales 2011) abruptly disappeared after ~ AD 1960. The clear shift in the ratio between *Staurosira construens var. venter* and *Staurosirella pinnata* around AD 1970 may be indicative for gradually rising water temperatures, as *Staurosira construens* var. *venter* was described as being more competitive under cooler conditions, while *Staurosirella pinnata* is more frequent during warmer periods (Joynt and Wolfe 2001; Cremer et al. 2001; Bouchard et al. 2004). However, in line with Spaulding et al. (2015), we rather suppose the combined effect of rising temperatures and increasing nitrogen loadings may have triggered changes within the diatom assemblages.

Low alloxanthin/diatoxanthin and high B/P ratios indicate favourable light conditions for benthic production (Figs. 4.3, 4.4). However, diatom inferred lake-level increased since ~ AD 1880 inferred from decreasing frequency of epilithic species, such as *Achnanthidium minutissimum* and *Denticula tenuis.* Hofmann et al. (2020) found that the distribution of the benthic diatoms in Oberer Soiernsee mainly depends on substrate availability. Epilithic species primarily occurred in the upper littoral zone (0-7 m), while epipsammic and epipelic diatom prefer the deeper littoral (7-11 m). We assume that the diatom-inferred lake level changes are rather the consequence of enhanced availability of fine-grained substrate reflecting climate-mediated changes of the catchment. TOC/TN values revealed enhanced proportion of terrestrial sources on the sedimentary OM (Fig. 4.5). Between 1890 and the end of World War II, the small cabin situated at the northern shore of Oberer Soiernsee was rarely visited (Müller 1922; Alpine Yearbooks), as very well reflected by low diatom-inferred TP levels (mean 3.3 ± 1.9 $\mu g\ l^{-1}$). Diatom-inferred TP started to increase since ~

AD 1950 (Fig. 4.3 B). Concurrently declining $\delta^{13}C_{org}$ indicates that respiration or, more likely, anoxic biochemical processes releasing ^{13}C-depleted methane into the water column became increasingly important (Figs. 4.5 and 4.6). The mesotrophic conditions around AD 1960 (diatom-inferred TP = 27 ± 1.9 µg l^{-1}) may be due to the sharply increasing numbers of overnight stays in the small cabin since ~ 1960. Around the world the phosphorus loadings into water bodies markedly increased in the 1960s due to the development of phosphate detergents (Vollenweider 1969). We suppose that the sharply rising TP is the result of the discharge of the cabin's wastewater.

The short-term increase in $\delta^{15}N$ (Fig. 4.5) may also be related to the rising numbers in overnight guests and day-trippers resulting in enhanced nitrate-N loadings from the nearby dry toilet, as human excrements are enriched in ^{15}N (Kendal, 1998). A further positive correlation between $\delta^{15}N$ and $\delta^{13}C_{org}$ would be expected if variations in these parameters continued to be caused mainly by alterations of the algae productivity (Gu et al. 1996; Finlay and Kendall 2007). However, the decoupling of both records after ~ AD 1970 (Fig. 4.6) suggests the increasing influence of atmospheric nitrogen deposition from distant sources (fossil fuel combustion, industrial fertilizer and livestock) which is known to be a major external source of nitrogen in remote mountainous regions, especially since the 1950s (Catalan et al. 2013). Atmospheric nitrogen produced by agriculture and industry is ^{15}N depleted relative to preindustrial sources (Hastings et al. 2009). The clear and continuous depletion in sedimentary $\delta^{15}N$ after ~ AD 1970 (Fig. 4.5) likely reflects the increasing influence of atmospheric nitrogen loading, a trend that was widely observed in lake sediments of the Northern Hemisphere (Holtgrieve et al. 2011).

Period III AD (1980 – AD 2010): Rapid climate warming reinforced eutrophication

This period is characterized by the dramatic increase in both diatom productivity and pigment concentrations indicating that climate warming sharply reinforced the eutrophication processes impacting Oberer Soiensee. Algal responses were accelerated when lakes surpassed a climate-mediated ecological threshold associated with the establishment of a stronger thermal stratification (Smol et al. 2005).

Since 1980 a particularly pronounced warming (~ 0.5 °C per decade) has been observed in the European Alps (Gobiet et al., 2014). Also, at the Zugspitze, 30 km west of Oberer Soiernsee, a significant increase in annual mean temperatures was documented (data provided by DWD, Schneefernerhaus). In the sediments of Oberer Soiernsee a shift within the paleopigment composition around AD 1980 indicate the climate-induced stabilisation of the pelagic habitat. Violaxanthin, a proxy for cooler conditions (de Jong et al., 2013) suddenly disappeared and the indicators for a stronger thermal stabilisation (alloxanthin, peridinin and all green algae marker pigments) concurrently increased after ~ AD 1980 (Fig 4).

However, besides the rising air temperatures, changes in light transmission and heat transfer may also have contributed to the stabilization of the thermal stratification in Oberer Soiernsee. Climate-mediated changes in catchment vegetation cover, increased soil development and treeline migration (Vinebrooke and Leavitt, 1998; Sommaruga et al., 1999) may have led to an enhanced terrestrial input of light-aborting particles such as suspended inorganic and organic material and dissolved organic matter (DOC) (Saros and Anderson, 2014) resulting in an enhanced heat transfer to the lake.

Around AD 2000 the rapid increase in algal biomass (Figs. 3 and 4) indicates that an ecological threshold related to post-1980 warming has been surpassed. The intertwined stresses of rising temperatures and longstanding nutrient inputs from mountain hut tourism, atmospheric nitrogen fertilization and climate-related catchment changes culminate in a marked increase in paleopigment (up to 14-fold) and diatom (fourfold) concentrations. The success of labile pigments (fucoxanthin, neoxanthin, peridinin) and rising chl *a*/phe-a ratios point to reduced pigment degradation, which is also indicative for enhanced primary productivity as light and oxygen availability was reduced and dead OM was buried more rapidly. Therefore, the favourable preservation conditions possibly overestimate the rapid increase in pigment concentrations. Furthermore, it should be noted that the concentrations of sedimentary pigments are generally much higher in the topmost sediment layers than in the deeper part of the sediment core, because the degradation processes are still in progress (Tõnno, et al. 2019).

The marked negative shift (3.1 ‰) towards significantly lower $\delta^{13}C_{org}$ values after ~ AD 1980 (Fig. 5) indicates that enhanced lake productivity triggered methane oxidation processes. Additionally, methanogenesis and subsequent oxidation of the ^{13}C-depleted methane could occur also under oxic conditions in freshwater lakes (Bogard et al., 2014; Thottathil et al., 2018). The increase in total algae biomass suggests a progressive oxygen depletion at the bottom of the lake since ~ AD 1980, reinforced by the stronger thermal stability.

The continuously decreasing $\delta^{15}N$ values, however, did not reflect the denitrification processes. We assume that the continuous deposition of atmospheric nitrogen overrides the in-lake N-isotope dynamics, a process also described by Lehmann et al. (2004). As atmospheric nitrogen deposition in Europe declined after the peak in 1980 (Engardt et al., 2017) a reversal trend in $\delta^{15}N$ towards more positive values could have been expected after ~ AD 1980. However, $\delta^{15}N$ continues to decline (Fig. 5). Continuous atmospheric measurements since 1995 revealed no negative trend in the concentrations of atmospheric nitrogen oxides at the northern foothills of the Alps (DWD, Hohenpeißenberg). Measuring nitrogen deposition in a two-year monitoring of sites in the Northern Alps located ~ 20 km west of Oberer Soiernsee, Kirchner et al. (2014) observed that the region is even nowadays affected by marked deposition rates of nitrogen due to long-range atmospheric transport.

The broken-stick model revealed no significant diatom assemblage changes between AD 1980 and AD 2010. However, the ratio of benthic/epiphytic versus planktic frustules (B:P ratio) slightly decreased in this period (Fig. 3 B), while the allox/diatox ratio markedly increased and diatom-inferred lake levels reached a maximum (12.5 m; Fig. 4)). We assume, that the diatom-inferred lake level rise is rather the consequence of reduced light penetration due to phytoplankton shading limiting the light availability for benthic diatom species.

Period IV (AD 2010 – AD 2017): Rapid warming and an extreme precipitation event

Rapid warming appeared to be the main driver for surpassing an important ecological threshold resulting in the recent success of planktic diatom species. In the northern Alps the increase in air temperature was again markedly accelerated around 2010 (data provided by DWD, Schneefernerhaus) resulting in significantly rising surface water temperatures (Dokulil 2013), entailing a shorter ice-cover duration (Thompson et al. 2005; Weckström et al. 2014), longer growing seasons (Smol 1988), the alteration of the balance between thermal stratification and turbulent mixing (Luoto and Nevalainen 2013; Butcher et al. 2015), the development of more diverse littoral habitats (Lotter et al. 2010), and changes regarding the availability of light and nutrient resources (Douglas and Smol 2010).

The stabilisation of the pelagic habitat and the establishment of macrophytes as substrate for epiphytic taxa (e.g., *Encyonopsis* spp.) appeared to represent a tipping point in the ecosystem of lake Oberer Soiernsee indicated by a marked shift towards more complex, species rich diatom assemblages and distinctly rising abundances of planktic species (Figs. 4.3A, 4.3B). Especially small *Cyclotella* species and *Fragilaria nanana* occurred more frequently after ~ AD 2010 and their abundances abruptly increased after ~ AD 2015. Diatom-inferred temperature reconstructions by using the novel silicification value (Kuefner et al. 2020 a; Kuefner et al. 2020 b) revealed an abrupt warming of lake surface temperatures after ~ AD 2015 (Fig. 4.3 B). However, the direct effect of rising air temperatures is not likely alone the driver of diatom species shifts. Stratification patterns and mixing regimes were also regulated by the amount of light adsorbing particles. The marked increase in phytoplankton biomass and the extremely large amount of inorganic particles and soils released from the catchment after the extreme precipitation event in August 2015 reinforced the heat transfer into the lake by the enhanced adsorption of light energy. The complex interactions between the mechanism controlling the stratification patterns and the resulting effect of changing thermal regimes on the availability of light and nutrients greatly influence growth, structure and competition of both planktic and periphytic algae communities (Winder and Sommer 2012; Saros and Anderson 2014; Malik et al. 2017).

Sharply declining B:P ratios and increasing diatom-inferred lake levels after ~ AD 2015 (Fig. 4.3 B) indicated favourable conditions for planktic diatoms. *Cyclotella* spp. and *F. nanana* have competitive advantages during times of stronger stratification due to their low sinking rates, excellent light-harvesting skills and efficient nutrient uptake (small centrics) and their ability to reduce sinking velocity by forming ribbon-like colonies *(F. nanana)*. Numerous diatom paleo-records from sites across a wide geographic range highlighted the recent success of small, fast-growing cyclotelloid species with enhanced water column stability and reduced vertical mixing (e.g. Douglas et al. 2004: Smol et al. 2005; Karst Riddoch et al. 2005; Rühland et al. 2003; 2005; 2008; 2015; Kuefner and Hofmann et al. 2020). However, changes in nutrient concentrations also may have triggered shifts in the abundances of *Cyclotella* spp., as this species prefer oligo- to moderately mesotrophic waters. *Cyclotella comensis*, a taxon that is known to be a characteristic species in oligotrophic lakes (Marchetto et al. 1995; Marchetto et al. 2004; Reynolds 2006; Werner and Smol 2006; Saros and Anderson 2014; Berthon et al. 2014) occurred in low abundances (0.5-0.6 %) between AD 1880 and AD 1900, reappeared around AD 2015 (1 %) and subsequently sharply increased up to 30 %. Contemporary hydrochemical analyses revealed decreasing TP concentrations from 14.4 $\mu g\ l^{-1}$ to 4.5 $\mu g\ l^{-1}$ and increasing nitrate-N concentrations from 0.27 mg l^{-1} to 0.36 mg l^{-1} after the extreme precipitation event in August 2015 (Hofmann et al. 2020; Ossyssek et al. 2020). Analysing the distribution of *C. comensis* across oligotrophic mountain lakes in the northern European Alps, Ossyssek et al. (2020) additionally found that this taxon was positively correlated with the nitrate-N concentrations providing an indicator for rising water temperatures under elevated nitrate concentrations. Beside atmospheric fertilization, catchment soils are the main external nitrogen resource in remote lakes (Saros and Anderson 2014). Based on the TOC/TN ratios and the fingerprints of modern OM sources terrestrial soils were found to influence the composition of the sedimentary OM deposited after AD 2015 (Fig. 4.6). Rising TOC/TN ratios after AD 2015 also suggest enhanced autochthonous sources of sedimentary OM (Fig. 4.5).

The marked collapse of the diatom cell densities and pigment concentrations (Figs. 4.3 and 4.4) is related to the extensive catchment denudation triggered by the massive thunderstorm in August 2015. Highly turbid conditions existed for several weeks (Hofmann et al. 2020) and a 3cm thick flood layer was deposited. During the cold period of LIA an increased frequency of flood events have been observed (Fig. 1). The recent global warming, however, was found to increase the intensity of heavy rainfall events resulting in a significantly increasing activity of landslides and debris-flows in the Northern Calcareous Alps (Dietrich and Krautblatter 2016).

The AD 2015 flood event resulted in the reversal of the declining $\delta^{13}C_{org}$ trend. We presume that the flood layer sealed the lake bottom and inhibited the re-solution of TP. Contemporary hydrochemical analyses revealed steadily decreasing TP concentrations from 14.4 $\mu g\ l^{-1}$ (2015) to 11.8 $\mu g\ l^{-1}$ (2016) to 4.5 $\mu g\ l^{-1}$ (2017). Diatom-inferred TP concentrations show a similar trend from 8.4 ± 1.9 $\mu g\ l^{-1}$ (2015) to 4.5 ± 1.9 $\mu g\ l^{-1}$ (2017). Further investigations are needed to determine whether this is only a short-term phenomenon or whether the flood layer has the potential for a long-term influence over the lake's nutrient state.

4.6 Conclusions

The results of our study show that lake responses to climatic and human influences are complex, multidimensional, and often indirectly mediated through watershed processes.

The sedimentological, biological and biogeochemical information stored in it´s sediments revealed the eutrophication history of Oberer Soiernsee since the end of the Little Ice Age (AD 1840 - AD 2017). By combining the multiple proxies, we were able to disentangle external disturbances and lake internal processes and to unravel the complex responses of lake algae to local human activities, long distance atmospheric deposition and climate warming.

We could demonstrate that changes in catchment-lake interaction linked to climate warming are mirrored in the sediment archives, in particular by changes in the frequency and intensity of extreme rainfall events and in the release of nutrients and DOC into the lake.

Our findings confirm the benefit of combined analyses of $\delta^{13}C_{org}$ and $\delta^{15}N$ values as well as TOC and TN contents of sedimentary OM to reveal and explain changing trophic conditions. Comparing with isotopic values of modern OM, we were able to determine the origin of sedimentary OM as mainly autochthonous (algae), partly influenced by terrestrial soils. Diatom productivity and species composition and the concentrations of chlorophyll *a* and *ß*-carotene were found to share the analytical capability to reconstruct lake eutrophication.

Anthropogenic climate change and the linked chain of causal factors were found to be the main drivers influencing algal dynamics and species composition. The diatom record provided an important tool to reveal climate-warming signals and alterations regarding water column transparency, TP- and nitrate-N concentrations. The timing of the establishment of thermal stratification could be determined via the success of centric diatoms and via the marker pigments of Dinophyta and Cryptophyta.

Our study highlights the threat multiplier character of climate change on mountain lakes influenced by local human activities, resulting in amplified responses of algal communities. Based on the findings of this study, we assume that climatically-induced ecological thresholds have already been surpassed in most of the Alpine lakes. In view of the present and future challenges in effectively managing water resources our findings underline the urgency of a sharp reduction of local and atmospheric nutrient input to maintain valuable ecosystem services under future climate scenarios.

5. Composition of highly diverse diatom community shifts as response to climate change: a down-core study of 23 central European mountain lakes

A similar version of this paper was published: Kuefner W*, Hofmann AM*, Ossyssek S, Dubois N, Geist J, Raeder U (2020) Composition of highly diverse diatom community shifts as response to climate change: a down-core study of 23 central European mountain lakes. Ecological Indicators 117: 106590

*equal contributing authors

Candidate´s contribution:
The study was equally conceived by the candidate and Wolfgang Kuefner, in consultation with Uta Raeder and Jürgen Geist. Basic research and preliminary studies were carried out by the candidate. Hydrochemical and hydrophysical characterization of the lakes were performed by the candidate and Stefan Ossyssek. Sediment core sampling and preparation were realized by the candidate and Wolfgang Kuefner. Sediment dating was done and interpreted by Nathalie Dubois. Microscopic analyses were carried out by the candidate and Wolfgang Kuefner. Statistical analyses and graphics were performed by Wolfgang Kuefner. Data interpretation was equally done by the candidate and Wolfgang Kuefner. The manuscript was equally drafted and finalized by the candidate and Wolfgang Kuefner, continuously supervised and improved by Jürgen Geist and Uta Raeder.

5.1 Abstract

Alpine mountain lake biota is adapted to harsh conditions making them particularly vulnerable to global change. However, as each mountain lake has a different limnology, there are supposed to be differential responses and degrees of resilience to climate change. In this study, 23 lakes in the Bavarian-Tyrolian Alps differing in altitude, size and geology were examined for their diatom community response to climate warming. Subfossil data were related to ^{210}Pb and ^{137}Cs-dated sediment cores. Correspondence and regression analyses revealed five different assemblage developments depending on lake depth, altitude and origin. Planktic species, especially *Cyclotella*, dominated deeper and lower-altitude mountain lakes earlier and stronger. This depends on the stability and temperature of the epilimnion, which in turn determines the tipping point. Instead, shallow lakes exhibit higher species reorganizations of diatom assemblages. Mountain lakes of lower altitudes or affected by water level fluctuations (WLF) establish complex substrata and

Achnanthidium accompanied by epiphytic species or *Denticula tenuis* in WLF-lakes replace dominating *Staurosira*. Conversely, alpine shallow lakes lack directional shifts and *Staurosira* dominate, but approach the tipping point of macrophyte establishment. In a deep doline lake, *Diploneis* species replace *Nitzschia denticula* with negligible planktic proportions. In mountain lakes with direct anthropogenic influence, enhanced nutrient supply disguises diatom response to global warming. These findings revealed deep mountain lakes with low nutrient levels to be more resilient to climate change than shallow lakes with a higher trophic status as the onset of the response to rising temperatures is earlier and thus smoother. In conclusion, subfossil diatom analyses can provide a powerful tool for climate change assessment and other anthropogenic impacts on mountain lakes.

5.2 Introduction

Climate change impacts on mountain lakes are highly complex and still not completely understood since they are particularly vulnerable ecosystems that do not respond uniformly. Mountain lakes host unique and sensitive species that are highly adapted to harsh alpine conditions, making them ideal environmental sentinels (Catalan et al. 2013; Rogora et al. 2018; Moser et al. 2019). Recent studies point out that increasing air temperature results in earlier break-up and later onset of ice cover in the annual cycle, resulting in longer periods of strong stratification during summer (Karst-Riddoch et al. 2005; Rühland et al. 2008). Such well-stratified conditions culminate in marked shifts within the phytoplankton community towards motile, small cell or colony-forming species (Winder et al. 2009; Daufrasne et al. 2009). Climate warming also alters the nutrient situation of the lakes mainly triggered by catchment modifications such as altitudinal tree-line shifts, uphill migration of plant species (Pauli et al. 2012) and increasing soil development (Rosbakh et al. 2014). As a consequence, the amount of organic matter entering the lakes can change markedly, especially in lakes that are located near climatically sensitive ecotonal boundaries such as tree line or timberline (Sommaruga et al. 1999; Sommaruga and Augustin 2006; Lotter et al. 2010). Moreover, a significantly higher frequency of natural disasters, e.g. torrential floods, rockslides and extreme storms, has been observed in the Alps over the past 30 years (Bogataj 2007; Bätzing 2015). The increasing input of inorganic material due to intensified chemical weathering, greatly enhanced erosion, extensive surface runoff and mudslides further changes light and nutrient conditions (Koinig et al. 1998). However, the climate-induced increase of erosion rates primarily affects the high-elevated lakes, while erosion in montane and subalpine catchments is mainly forced by human land use (deforestation, overgrazing), which strongly influences soil paedogenesis and vegetation dynamics (Arnaud et al. 2016). Longer growing seasons and enhanced nutrient supply culminate in higher algal productivity (Douglas and Smol 2010) and increased substratum variability for benthic algae (Rühland et al. 2008). Additionally, local human activities (hut construction, alpine pasture, lake damming) and atmospheric deposition from distant sources significantly alter the trophic situation and the pH values even of remote mountain lakes (Kamenik et al., 2000; Wolfe et al., 2001; Koinig et al. 2002).

To reconstruct such a wide range of environmental changes, palaeolimnological analyses provide valuable approaches (Dubois et al. 2017), as past fluctuations of climate-mediated lake properties or catchment variations are well archived in lake sediment records (Smol et al. 2005). Diatoms are ideal biological indicators that mirror various types of long-term ecological perturbations such as acidification (Weckström et al. 1997; Koinig et al. 2002), eutrophication (Stoermer and Smol 2010) and climate warming (Pienitz et al., 1995; Bigler and Hall, 2003; Smol et al., 2005; Karst-Riddoch et al. 2005; Rühland et al. 2008). Moreover, shifts in subfossil diatom assemblages are well pre- served in lake sediments that can be used as environmental archives. Diatoms (Class Bacillariophycaea) are unicellular microscopic algae, ubiquitous, abundant and highly diverse. Their rapid growth and high immigration rates enable fast adaption to changing conditions. Several species have specific and well-known habitat requirements and sub- stratum preferences as well as a distinct optimum and tolerance in relation to pH, salinity or nutrient levels (phosphorus, nitrogen). Their highly resistant and species-specific siliceous valves are well preserved and abundant in lake sediments (Smol et al. 2005).

In limnological research, all the factors described above that cause the complex impact of climate change in the Alps have so far and to the best of our knowledge only been studied in high alpine lakes with crystalline bedrock in the catchments, e.g. Lake Gössenköllensee, Austria (Koinig et al., 2002; Kamenik et al., 2000) or at large pre- alpine lakes such as Lake Mondsee (Namiotko et al. 2015). However, effects of climate change on biological communities in mountain lakes from calcareous areas are poorly investigated, even though they comprise the majority of lakes in areas such as the Bavarian Alps. Therefore, we analysed the sediments of 23 montane, subalpine and alpine lakes (955–2060 m a.s.l.) located in the Bavarian and North-Tyrolian Calcareous Alps. The objective of our study was to detect the dimensions and varieties of climate-mediated changes in mountain lake properties using down-core studies of subfossil diatom assemblages. Our study is based on the following three hypotheses: (1) diatoms from mountain lake types that differ regarding lake depth, mixing regime and lake origin respond differently to climate change. (2) Diatom communities from high-elevated alpine lakes are most severally affected by global change due to the increase of catchment erosion and soil development triggered by the dramatic loss of snow cover especially in rocky alpine catchments. (3) Local anthropogenic impacts may overlap with climate- induced changes in all the lake types and at any altitudes.

5.3 Material and methods

5.3.1 Study area

The study is based on sedimentary records of 23 lakes located in the Bavarian and North-Tyrolian Alps. The area in which the lakes are located extends over a distance of about 220 km from west to east along the Bavarian-Austrian borderline (47°17´ to 47°45´N latitude, 10°15´to 13°1´ E longitude, Fig. 5.1). The altitudinal gradient ranges from 955 – 2047m a.s.l. (Table 5.1), representing eight montane (922 – 1207 m a.s.l.), nine subalpine (1458 – 1608 m a.s.l.) and six alpine (1809 – 2060 m a.s.l.) lakes. Catchment vegetation comprises conifer-dominated montane forests (*Picea abies* (L.) Karst and *Larix decidua* Mill., subordinate *Acer pseudoplatanus* L. and *Fagus sylvatica* L.) through subalpine grassland with patches of *Pinus mugo ssp. mugo* Turra and *Picea abies* as well as treeless alpine meadows (e.g. *Rhododendron hirsutum* L., *Carex sempervirens* Vill.) on poorly developed soils and rocky screes. Catchment geology is dominated by Triassic and Cretaceous carbonate rocks (limestone, dolomite, marlstone) and glacial deposits (lodgement till moraine deposits), partially covered by postglacial rock streams, talus slopes and alluvial cones. Most of the lakes are of glacial origin (cirque and moraine lakes), and two are postglacial (land slide lake, doline lake).

The lakes are limnologically diverse, ranging from shallow (1.3 m) to deep (20.7 m) lakes with ultra-oligotrophic to mesotrophic conditions and polymictic, dimictic or meromictic character. The substratum for benthic diatoms comprises sediments of different grain sizes, macrophytes and boulders. Some of the lakes are affected by strong water level fluctuations (WLF) up to 9.5 m within one season (Table 5.1, Kuefner et al. 2020 a, Ossyssek et al. 2020, Hofmann et al 2020). The lake surfaces range between 0.4 and 12 ha (mean 3 ha), lake depths between 1.3 and 20.7 m (mean 8.9) and Secchi depths between 1.3 and 15.5 m (mean 5.3 m). The average physical conditions are: pH 8.4 (7.9 – 8.8), electrical conductivity 240 µS cm^{-1} at 25°C (134 – 360 µS cm^{-1}) and August surface temperatures 16.3 °C (10.8 -22.6 °C). Hydrochemical parameters are on average (arithmetiric means and ranges): total phosphorous 8.5 µg L^{-1} (< 5 – 17.3 µg L^{-1}), nitrate-nitrogen 0.36 (0.03 – 0.93 mg L^{-1}) ammonium-nitrogen 35.8 µg L^{-1} (4 – 127 µgL^{-1}) and silica 0.23 mg L^{-1} (0.13–0.77 mg L^{-1}). Despite their prevailing remote location, the majority of the lakes is impacted by local human-induced disturbances such as tourism, alpine pasture or damming for water management (Table 5.1).

Climate and weather data derived from the observatories of Hohenpeißenberg (987 m a.s.l.), Munich (519 m a.s.l.), Wendelstein (1838 m a.s.l.) and Zugspitze (2962 m a.s.l.) of Germany's National Meteorological Service (DWD) and were provided by the European Climate Assessment and Dataset Project.

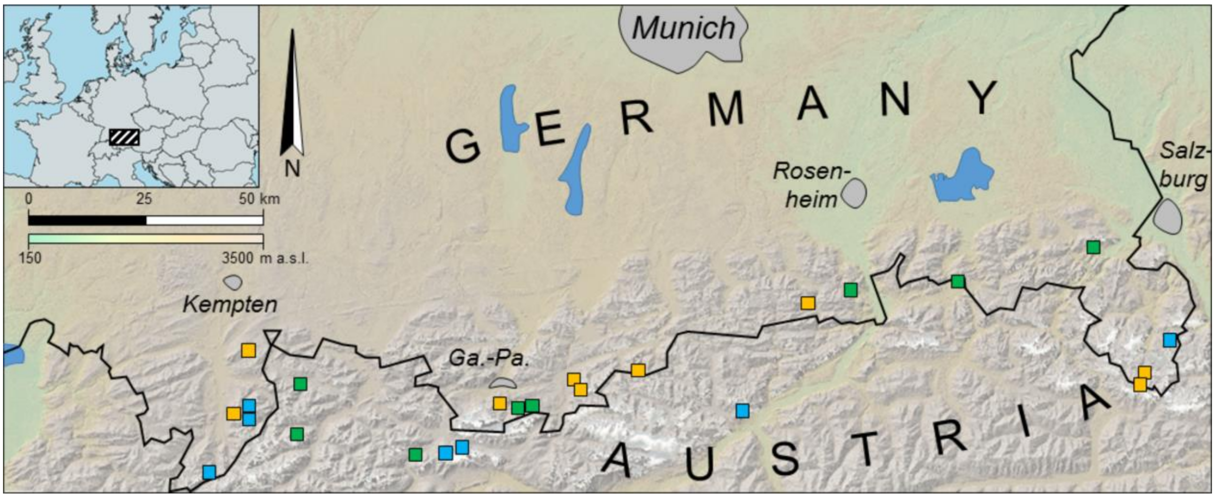


Figure 5.1 Location of the 23 mountain lakes along the Bavarian-Tyrolian boarder. Blue squares: alpine, yellow: subalpine, green: montane lakes. Ga.-Pa.: Garmisch-Partenkirchen

Table 5.1 Summary of main geographical, physical and chemical characteristics. TP = total phosphorous, NO_3^- = nitrate-nitrogen, NH_4^+ = ammonia-nitrogen, cond. = conductivity. Substratum types: M = macrophytes, R = rocks, S = sediment, += water level fluctuations. Anthropogenic influences: D = dam (< 1.5 m), h = alpine hut, H = hotel, P = grazing/alpine pasture

Lake	Code	Latitude (N)	Longitude (E)	Altitude (m a.s.l.)	Lake area (ha)	Max. depth (m)	Secchi depth (m)	TP (µgL-1)	NO_3^- (mgL-1)	NH_4^+ (µgL-1)	pH	Cond. (µScm-1)	Mixis	Littoral Sub-stratum	Anthro-pogenic influence
Bichlersee	Bich	47°40‘34“	12°07‘21“	955	1.5	11.0	4.4	< 5	0.76	32	7.9	360	dim.	MS	-
Brendlsee	Bre	47°21‘58“	10°57‘30“	1903	0.5	6.2	6.2	6.6	0.37	14	8.6	151	polym.	RS+	-
Delpssee	Delp	47°30‘19“	11°30‘36“	1600	0.6	1.3	1.3	5.7	0.45	15	8.2	223	polym.	S	P
Drachensee	Dra	47°21‘31“	10°56‘05“	1874	5.3	20.7	10.3	< 5	0.30	20	8.6	158	dim.	RS	h
Engerats-gundsee	Eng	47°26‘29“	10°23‘30“	1876	3.6	17.3	15.5	< 5	0.04	27	8.2	236	dim.	MS	P
Ferchensee	Fe	47°26‘18“	11°12‘50“	1060	10.0	19.5	6.8	10.1	0.33	43	8.1	304	dim.	S	HP
Frillensee	Fri	47°45‘57“	12°49‘03“	973	1.2	5.5	4.6	7.2	0.93	84	8.6	224	dim.	M	-
Funtensee	Fun	47°29‘37“	12°56‘22“	1601	2.5	4.5	3.5	10.3	0.03	44	8.4	274	dim.	MS	hP
Gaisalpsee	Gais	47°45‘56“	12°49‘03“	1508	3.4	4.1	3.8	12.0	0.25	10	8.9	198	dim.	M	PD
Grubersee	Gru	47°27‘13“	11°47‘18“	2060	0.5	3.5	3.2	17.0	0.10	18	8.6	222	polym.	S	P
Grünsee	Grün	47°30‘07“	12°57‘11“	1474	3.5	6.9	5.0	8.3	0.20	61	8.5	194	dim.	MS	P
Höfersee	Höf	47°29‘51“	10°29‘25“	1192	0.6	1.9	1.9	< 5	0.47	5	8.9	221	polym.	M	P
Hörnlesee	Hörn	47°32‘52“	10°23‘29“	1601	0.5	1.8	1.8	17.3	0.34	20	7.9	225	polym.	M	DP
Lautersee	Lau	47°26‘13“	11°14‘08“	1013	12.0	18.0	6.0	13.5	0.21	51	8.6	310	dim.	S	H
Mittersee	Mit	47°22‘07“	10°51‘58“	1082	3.3	4.7	4.7	7.5	0.10	34	8.3	346	dim.	S	-
Rappensee	Rap	47°17‘09“	10°15‘10“	2047	2.3	7.8	5.0	9.2	0.04	16	8.6	205	dim.	MS	D
Schachen-see	Sch	47°25‘27“	11°07‘12“	1680	2.0	4.4	3.8	7.2	0.49	20	8.7	167	polym.	S	P
Seeleinsee	See	47°32‘16“	13°01‘47“	1809	0.4	5.4	5.4	7.9	0.59	32	8.7	134	polym.	RMS+	-
Sieglsee	Sieg	47°24‘30“	10°29‘46“	1207	0.8	20.2	9.5	< 5	0.55	4	8.1	537	merom.	S	-
Unterer Soiernsee	SoE	47°29‘28“	11°21‘01“	1552	3.4	5.5	4.5	11.0	0.61	49	8.7	181	polym.	RS+	P
Oberer Soiernsee	SoW	47°29‘32“	11°20‘44“	1558	3.5	11.5	7.0	13.0	0.36	83	8.7	198	dim.	RMS	hP
Soinsee	Soi	47°39‘01“	11°57‘20“	1458	4.0	8.2	3.2	7.9	0.61	13	8.3	222	dim.	RMS	P
Taubensee	Tau	47°41‘46“	12°25‘37“	1138	4.0	14.6	4.3	< 5	0.66	127	8.0	247	dim.	RMS	P

5.3.2 Recording the mixing regime

Two temperature loggers (HOBO®, Onset, Bourne, USA) were installed below the surface and above the ground at the deepest spot of each lake to evaluate the mixing behaviour. The loggers simultaneously documented the temperature between 23rd Aug and 1st Sep 2016. Well-stratified lakes with autumnal holomixis were termed "dimictic", lakes with several mixing events during summer "polymictic". A mixing event was defined as a difference between lake surface and bottom temperature of $\leq 0.1°C$. Lake transparency was measured using a Secchi disc. Lakes were classified according to their depth$_{max}$/Secchi depth ratio. If the lake depth exceeded the Secchi depth, they were referred to as 'deep' or 'aphotic' since light did not reach the lake ground sufficiently. If lake depth limits the determination of the Secchi depth, the lakes were classified as 'shallow' or 'euphotic'. Their lake bottom is illuminated entirely, thus corresponding to the littoral zone.

5.3.3 Sediment coring

Lake sampling took place over a period of three years (2015-2018) as a part of a sampling campaign to investigate interactions between diatoms and environmental parameters (Kuefner et al. 2020 a, Ossyssek et al. 2020, Hofmann et al. 2020). Sediment cores were obtained from the deepest area of each lake basin (echo sounding with HDS8, Lowrance, Tulsa, USA) using a gravity corer (Uwitec, Mondsee, Austria) equipped with 6 cm-diameter core tubes. Sediment cores were hermetically sealed and stored at 4°C for a maximum of 90 days. The cores were subsampled at intervals of 1 cm and freeze-dried for diatom analyses and dating. Water content was determined by weight difference of the samples before and after freeze-drying.

5.3.3 Sediment Core Chronology

Freeze-dried and ground sediment subsamples were analysed by gamma spectrometry (High-purity Germanium Well Detector, HPGe, Canberra, USA) in the department of Surface Waters Research and Management of EAWAG (Dübendorf, Switzerland). Accumulation rates were determined using both ^{210}Pb and ^{137}Cs radionuclides. ^{210}Pb chronologies were calculated from unsupported isotopes using the CRS model (Constant Rate of Supply, Appleby 2001). The anthropogenic ^{137}Cs served to confirm the ^{210}Pb dates. ^{137}Cs represents a stable and clear time marker as it firstly appeared in 1951-1954 and peaked in 1963 in association with atmospheric nuclear weapons testing (Appleby 2001). In southern Germany, the ^{137}Cs activity shows a second peak in 1986 as a result of the Chernobyl disaster (Kirchner 2011).

5.3.4 Diatom Analyses

Freeze-dried subsamples were prepared for diatom analyses according to van der Werff (1953) and Kuefner et al. (2020a). Different dilutions of the cleaned material were embedded in the high-refractive medium Naphrax and fixed on microscopic slides to obtain permanent preparations. For SEM analyses, 50 µL of the most appropriate sample dilution were air-dried onto a glass cover slip (Ø 12 mm) and coated in gold using the Polaron SC502 Sputter Coater (Fisons Instruments, UK). At least 550 diatom valves per sample were identified under oil immersion at 1000x magnification using light microscopy (Aristoplan and Labovert, Leitz, Wetzlar, Germany). Additionally, SE microscopy (S-2300, Hitachi, Tokyo, Japan) at 5000-20000x magnification was used to improve determination of centric diatoms in planktic-rich samples. Diatom taxonomy followed Krammer and Lange-Bertalot (1986-1991), Lange-Bertalot et al. (1993-2003), Krammer (1997), Reichardt (1999), Houk et al. (2010 – 2014) and Hofmann et al. (2013) updated to recent taxonomic nomenclature using current publications and databases. The numbers of fields of view in the microscope to count 550 valves in combination with the used dry weight of sediment served to calculate diatom densities.

5.3.5 Statistical Analyses

Referring to local climate data, the strongest warming in the Bavarian Alps started in the 1970s (Kuefner et al. 2020 b). To detect inter-lake variances of climate change response in diatoms within this period (~1975–2017), a principal component analysis (PCA) was computed for the subfossil assemblages of the upper compartment of each sediment core, which integrated the last ~45 years according to the ^{210}Pb and ^{137}Cs results. For a better comparability, inter-lake variances of the subfossil diatom assemblages were homogenized by summarizing diatom species abundances in groups on the genus level according to the three related proxies valve silicification, size and ecology (Kuefner et al. 2020 a). An overview of species grouping is listed in the appendix. Only groups with abundances of more than 2 % were included in statistical analyses, so that the exclusion of underrepresented species eases inter-lake comparisons. Species abundances were Hellinger-transformed (Legendre and Gallagher 2001) before analyses to stabilize variances and to avoid down-weighting of rare taxa (Smol et al. 2005). To determine the number of decisive components, a Scree plot was generated as well. Diatom species or groups, whose eigenvalues are lower than randomly modelled values of the broken-stick model are suggested to be insignificant for the distribution of the assemblages in the PCA (Jackson 1993). Additionally, diatom compositional turnover (β-diversity) was quantified using Detrended Correspondence Analysis (DCA). This proxy refers to the length of the first DCA axis and scales values in SD units, which can also be referred to as turnover units of beta-diversity (ter Braak 1987; ter Braak and Verdonschot 1995).

As a temporal constraint, the same 45-year core compartments as for the PCA were implemented into the DCA. This improves the comparability of beta diversities among the cores and compensates different sedimentation rates in different lakes as well as different core lengths. For the best estimation of diatom reorganization without distorting chance finds, only diatom species with relative abundances of more than 1 % in at least one sample within a core were used and again square-root transformed (Legendre and Gallagher 2001). To identify decisive parameters determining species turnover in mountain lakes, generalized linear models (GLM) with AIC-based stepwise backward model selection were calculated. Highly correlated parameters ($p < 0.001$), which can cause multiple comparison problems in the models and feign inverse relationships, were eliminated (Schröder and Reineking 2004). According to Kuefner et al. (2020a), the parameters altitude and surface temperature as well as depth, volume and Secchi depth were implemented as dependent variables in the initial model formula, the remaining values bottom temperature, total phosphorous and lake surface are added separately. Comparisons among two factors were visualized as boxplots and statistically checked with a t-test in case of similar variances (F-test), otherwise with a Mann-Whitney U-test and its distribution with a Kolmogorov-Smirnov test. Data preparation and transformations were conducted in Microsoft Excel 2016 ®, statistical analyses in PAST 3.20 (Ryan et al. 1995) and R version 3.4.1 with the package 'vegan' (Oksanen et al. 2018). To identify significantly different stratigraphical zones, broken-stick models were calculated (Bennet 1996) with the R package 'rioja' (Juggins 2017).

5.4 Results

5.4.1 Thermal stratification and light conditions

The analysis of the temperature logger data revealed 14 dimictic lakes and eight polymictic lakes (Tables 5.1, 5.2). The special case of the doline lake 'Lake Sieglsee' was classified as meromictic. Although temperature data would allow its classification as polymictic lake, the electrical conductivity measurements suggested meromictic conditions. In total, ten lakes were shallow and transparent enough to be completely euphotic, whereas 13 lakes contained an aphotic zone (Table 5.2).

5.4.2 Sediment core chronology

The sediment cores were 9 to 55 cm long and comprised an average sedimentation rate of 0.27 cm a^{-1} (0.08 – 0.60 cm a^{-1}). Accordingly, the 23 sediment cores spanned on average 115 years with the shortest period (1971 – 2016) being archived in the core of Lake Höfersee and the longest in the core of Lake Drachensee, dating back to 1649. The doline lake Lake Sieglsee is again an exception with the highest sedimentation rate of 1.17 cm a^{-1} due to a high calcite fallout and its large water column; hence, the oldest part of this core only dated back to the year 2000.

5.4.3 Diatom analyses

In total, 593 species were identified in 555 sediment samples, but only 214 taxa were common with relative abundances of more than 1 % in at least one sediment sample. Diatom species clustering referring to valve silicification, size and ecology led to 24 diatom groups and 31 species with abundances of more than 2 %, which were included in the PCA (Figure 2a and b). The following eight dominant groups or species significantly determined the distribution and organisation of the diatom assemblages: (1) small-sized benthic species of the *Achnanthidium* Kützing complex; (2) the planktic, colony-forming species *Asterionella formosa* Hassall (3) small-sized planktic centric taxa of the *Cyclotella* (Kützing) Brébisson-complex; (4) the species *Cyclotella distinguenda* Hustedt; (5) medium-sized *Navicula* Bory species (*Navicula*-complex); (6) small benthic fragilarioid taxa (*Staurosira* Ehrenberg-complex); (7) small-sized, weakly silicified benthic fragilarioid taxa (*Staurosira* light-complex), and (8) the heavily silicified benthic fragilarioid *Staurosirella pinnata* (Ehrenberg) Williams and Round. The *Nitzschia* Hassall and large-sized *Diploneis* Ehrenberg ex cleve -complex were the 10th and 11th component and below significance, but were decisive particularly for the separation of the doline lake and additionally shown in Figure 5.2.

The first two axes of the PCA further explained 41.9% of the variation and dichotomously distributed the sediment samples corresponding to the stratification patterns into dimictic and polymictic mountain lakes. In general, the components of the main diatom species and groups indicated that *Staurosirella* Williams and Round/*Staurosira*-dominated assemblages (mainly *Staurosirella pinnata, Staurosira construens* Ehrenberg, *S. elliptica* (Schumann) Williams and Round, *S. microstriata* (Marciniak) Lange-Bertalot, *S. venter* (Ehrenberg) Cleve and Möller were plotted opposed of *Achnanthidium*- (especially *A. minutissimum* (Kützing) Czarneki, *A. rosenstockii* (Lange-Bertalot) Lange-Bertalot and *Cyclotella*-dominated assemblages (especially *C. comensis* Grunow, *C. delicatula* Hustedt, *C. distinguenda*) (Figure 5.2 b).

5.4.4 From diatom-assemblage shifts to lake types

With regard to the performance of the down-core diatom samples on the first two PCA axes, the analysis revealed five different developments of subfossil diatom assemblages (Fig. 5.2). Accordingly, five different lake types could be classified. Type 1 lakes (Lake Bichlersee, Lake Ferchensee, Lake Lautersee, Lake Taubensee) presented *Cyclotella* species throughout the entire five decades, whereby a weak increase of the planktic species (especially *Cyclotella* sp. and *A. formosa*) towards recent times could be observed. Type 2 lakes (Lake Drachensee, Lake Engeratsgundsee, Lake Grünsee, Lake Rappensee, Lake Schachensee, Lake Oberer Soiernsee) indicated an abrupt appearance between the 1980s and 2000 and subsequent increase of planktic taxa *(Cyclotella* species, *Fragilaria nanana* LANGE-BERTALOT) accompanied by an increase of periphytic diversity in the upper part of the core, while *Staurosira* species simultaneously decreased. Type 3 lakes (Lake Delpssee, Lake Funtensee, Lake Grubersee) merely showed composition changes within the *Staurosira*-complex. Type 4 lakes were characterized by an equal replacement within periphytic diatom assemblages: type 4a (Lake Brendlsee, Lake Gaisalpsee, Lake Höfersee, Lake Hörnlesee, Lake Seeleinsee, Lake Unterer Soiernsee) gradually shifted from the *Staurosira*- to the *Achnanthidium*-complex, whereas type 4b (Lake Soinsee) shifted from the *Staurosira*-complex to *Diploneis oculata* (BRÉBISSON) CLEVE. Exclusively, the doline lake (Lake Sieglsee) was characterized by a change mainly from *Nitzschia denticula* GRUNOW to several *Diploneis* species (type 5). Two lakes (Lake Frillensee, Lake Mittersee) clustered in between the types 1 and 4 as they mainly showed oscillations between the *Cyclotella*-complex and the *Achnanthidium*-complex, but also properties of both lake types as defined above. The main lake types were equally distributed along the altitudinal gradient.

5.4.5 Diatom response to changing environmental variables

The β-diversity of subfossil diatoms since 1975 calculated in standard deviation units averaged 2.44 SD in Bavarian mountain lakes, but was highly variable in different lake types (0.80 SD – 4.06 SD). However, two sediment cores did not comprise the required time span due to a high sedimentation rate (Lake Sieglsee) or infrequent appearance of diatoms in older sediments due to highly turbulent conditions as a result of extreme WLF (Lake Unterer Soiernsee). The average estimated β–diversity of shallow and completely euphotic lakes was not significantly higher than in deep lakes ($p = 0.07$), but considering distribution, this difference became significant ($p = 0.03$). It further suggested the weakest compositional change in the deeper 'type 1' lakes and the most significant in the shallow 'type 3 and 4' lakes (Table 5.2, Fig. 5.2c). Nevertheless, two 'type 2' lakes revealed highest values due to a change in the dominant diatom group from periphytic to planktic species. Stepwise linear regression analyses revealed that altitude ($p = 0.06$) in combination with lake August surface temperature ($p = 0.06$) and lake depth ($p = 0.11$) in combination with Secchi depth ($p = 0.10$) were the most significant environmental variables regarding diatom response. However, due to the shallow-deep lake dichotomy, the importance of the discovered variables differed. In 'type 1 and 2' lakes the β–diversity significantly correlated with altitude ($\varrho_S = 0.569$, $p = 0.037$), which was in average higher than in type 2 lakes ($p = 0.01$; Fig. 5.4a). Within the shallow lakes, 'type 4' lakes were warmer and lower than 'type 3' lakes and/or impaired by water level fluctuations (WLF) (Fig. 5.4a and c). This allows a lake type identification by only three environmental variables (Fig. 5.4d): lake depth, summer surface temperature and lake origin.

Table 5.2 Mountain lake classification according to their mixing behaviour and transparency, their beta diversities and lake type (1 = deep Cyclotella-dominated lakes, 2 = sudden appearance of planktics and decrease of Staurosira, 3 = shallow Staurosira-dominated lakes, 4a = classical replacement of Staurosira by Achanthidium, 4b = replacement of Staurosira by Diploneis oculata, 5 = replacement of Nitzschia denticula by Diploneis species). Green: montane, orange: subalpine, blue: alpine mountain lakes. For abbreviations see Table 5.1.

	Dimictic	**β**	**type**	**Poly-mictic**	**β**	**type**	**Mero-mictic**	**β**	**type**
euphotic				Höf	2.7816	4a			
	Fri	1.9162	1-4a	Delp	3.2199	3			
	Fun	2.1090	3	Hörn	3.5614	4a			
	Gais	1.9373	4a	Bre	0.8627	4a			
	Rap	2.4728	2	Gru	3.1599	3			
				See	3.3329	4a			
aphotic	Fe	1.4110	1						
	Lau	1.5847	1						
	Mit	2.9544	1-4						
	Bich	0.8034	1						
	Tau	1.2830	1	Scha	2.2471	2	Sieg	*2.4703**	5
	SoW	4.0649	2	SoE	*3.4063**	4a			
	Grün	1.4724	2						
	Soi	3.5198	4b						
	Dra	1.4133	2						
	Eng	4.0554	2						

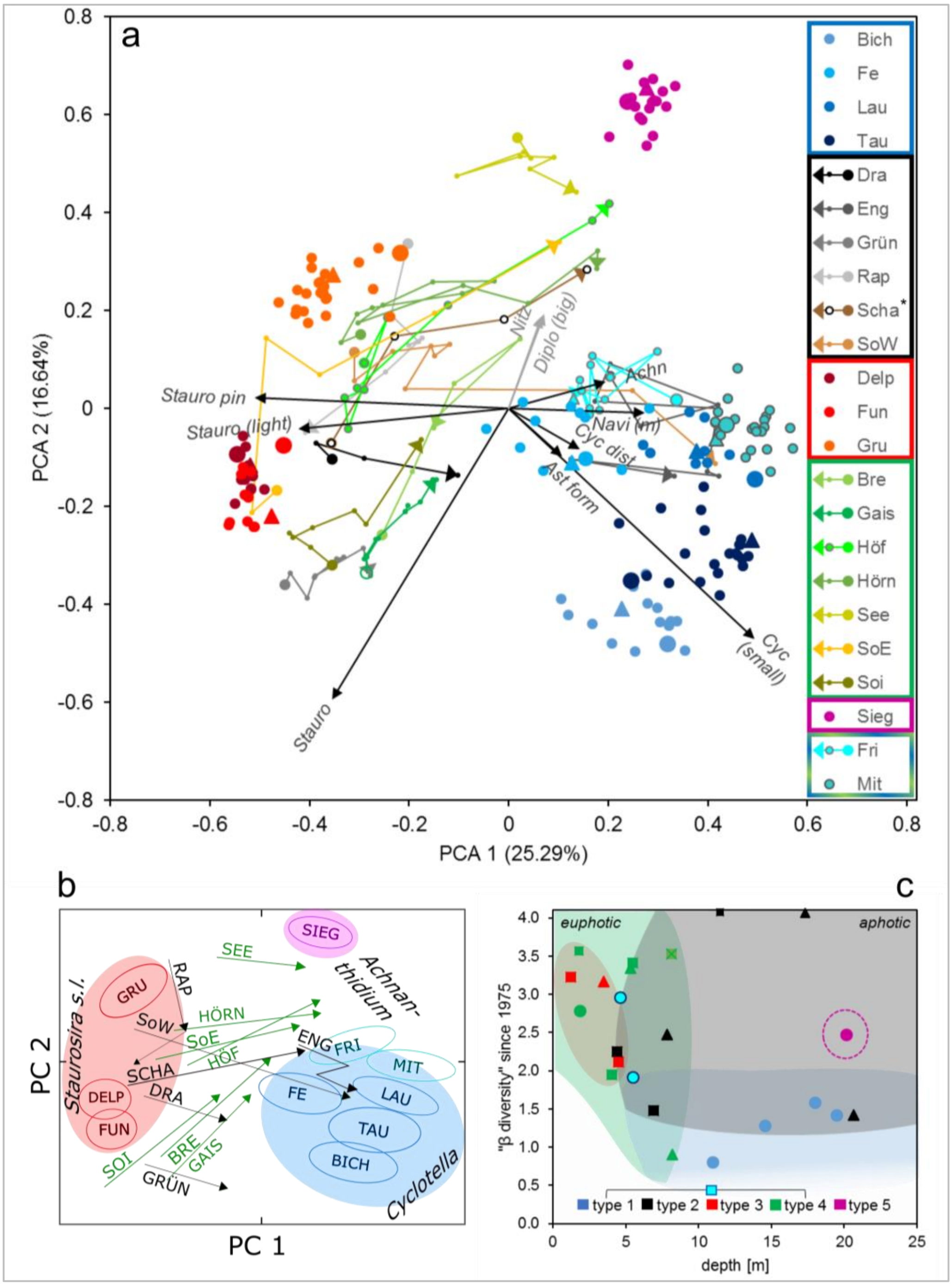


*Figure 5.2 PCA (a), PCA overview (b) and beta diversities in relation to lake depth (c) of subfossil diatom assemblages in mountain lake sediments since the 1970s. (a) Axes of the eight mainly driving diatom groups (black arrows): Achn – Achnanthidium species, Ast form – Asterionella formosa, Cyc dist – Cyclotella distinguenda, Cyc (small) – small Cyclotella species, Navi (m) – medium-sized Navicula species, Stauro – Staurosira species except: Stauro (light) – small and light Staurosira species, Stauro pin – Staurosirella pinnata. The axes of Nitz – Nitzschia sp. and Diplo (big) – big Diploneis spp. are shown additionally as they determine the position of the doline lake. * Uppermost centimeters of Lake Schachensee are driven by heavy Cyclotella spp., whose axis is of lower rank and not shown. Youngest (arrow/triangle) and oldest sample (bullet) within the time span of interest are shown additionally. Mountain lakes are grouped according to their assemblages' performance and distribution: blue – lake type 1, black – type 2, red – type 3, green – type 4, pink – type 5. The Lakes Fri and Mit were among 1 and 4, Lake Rap showed a two-directional shift. Samples of type 1 and 3 are not connected with a line as they are stationary. Lake acronyms see Table 5.1. (c) β-diversities of the five types – coloured areas visualize its distribution. Symbols represent the altitudinal level: triangle – alpine, box – subalpine, bullet – montane.*

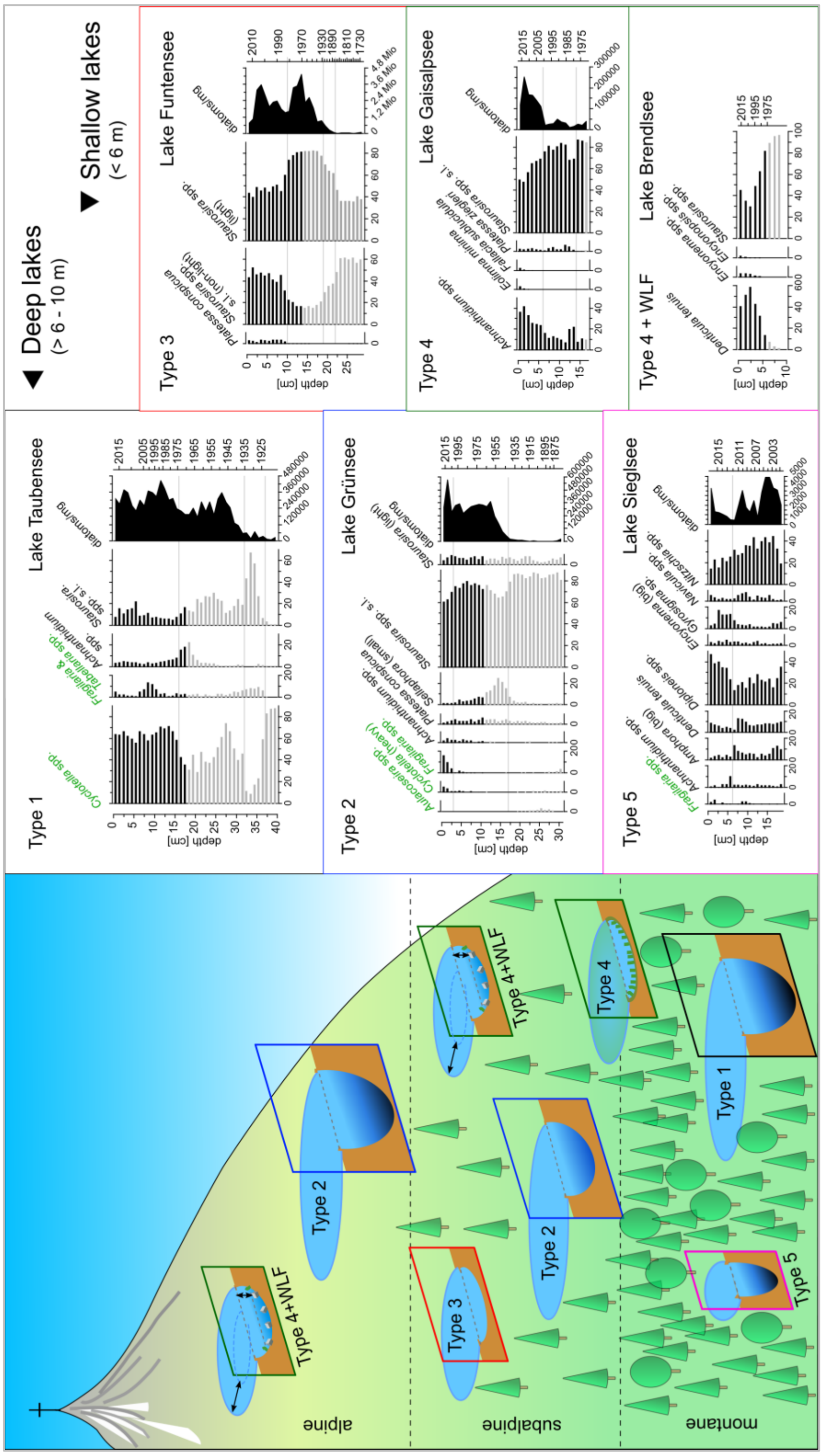


Figure 5.3 Diatom stratigraphies of the five mountain lakes types. Type colours correspond to Fig. 5.2 and arrangement on the left represents their altitudinal distribution. The two stratigraphy y-axes show age and depth of the sediment. Grey lines: significantly different stratigraphic zones as indicated by broken-stick model, grey bars: assemblages before 1970. Type 1 stratigraphy of L. Taubensee (black): planktic diatoms dominant throughout the sediment core, but increasing. Type 2 stratigraphy of L. Grünsee (blue): appearance and increase of planktic species, increase of diatom density and diversity. Type 3 stratigraphy of L. Funtensee (red): composition changes only within the genus Staurosira. Type 4 stratigraphy of L. Gaisalpsee (green): replacement of Staurosira by Achnanthidium. Type 4 + WLF stratigraphy of L. Brendlsee (green): replacement of S. by Denticula tenuis and diversity increase; Type 5 stratigraphy of L. Sieglsee (pink): replacement of Nitzschia denticula by Diploneis species

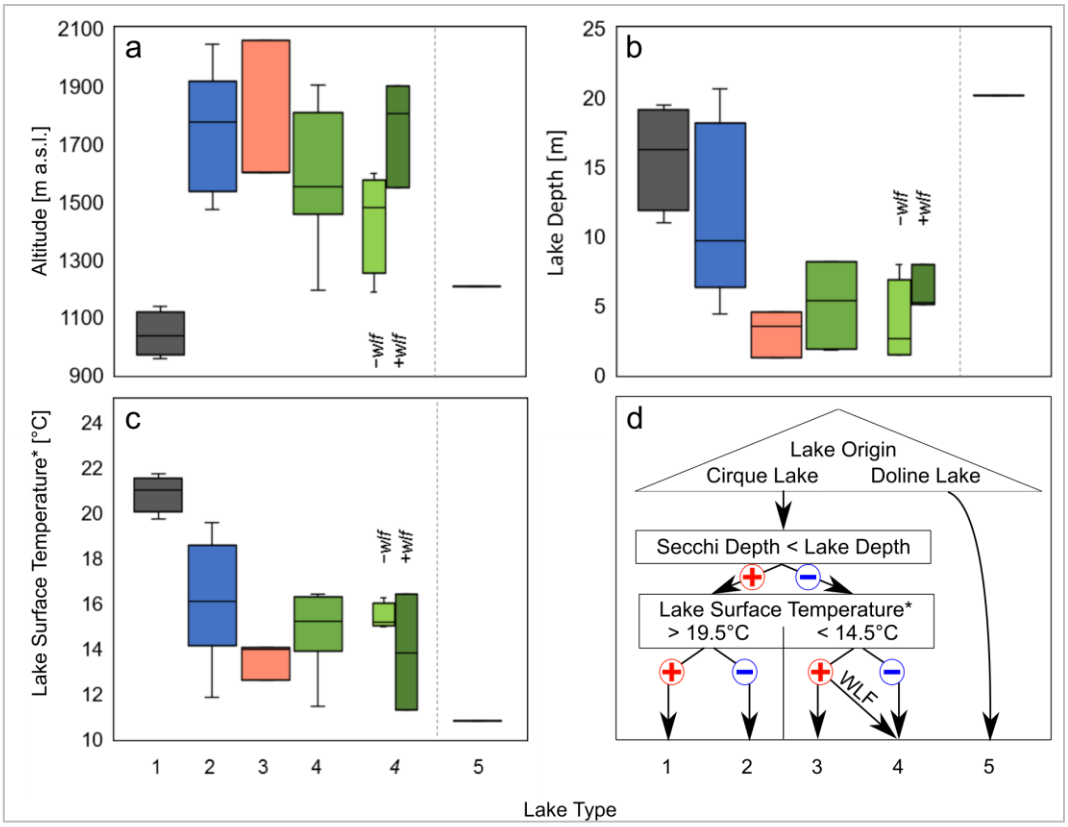


*Figure 5.4 Mountain lake types and their distributions along altitude (a), lake depth (b), lake August surface temperature (c). Differentiation scheme (d) according to the main factors lake origin, depth and temperature. Boxplot colours refer to Fig. 5.2. Type 4 is additionally split into lakes with (+wlf, dark green) and without (–wlf, bright green) water level fluctuations and special case type 5 is separated from the others by the dotted line. * Lake Surface Temperature refer to the period of simultaneous temperature documentation between 23rd Aug and 1st Sep 2016*

5.5 Discussion

Diatom community responses to recent climate warming were heterogeneous and strongly modulated by differences in lake depth, altitude, lake origin and anthropogenic pressure, which supports the initial hypotheses. In the Bavarian mountain lake set, PCA revealed that the development of subfossil diatom assemblages allowed a differentiation of five lake types according to their diatom community response. Over the entire time span of interest (1975–2017), two lake types showed a remarkable and directional shift from the *Staurosira*-complex either to the *Achnanthidium*- or to the *Cyclotella*-complex, whereas three of them remained stable within the *Staurosira*, *Cyclotella* and *Nitzschia denticula*/*Denticula tenuis* complexes, respectively.

In line with the hypotheses 1 and 2, regression analyses identified lake depth and altitude as the main drivers for the extent of diatom species reorganization. Accordingly, diatom species turnover was strongest in shallow mountain lakes. They show significant diversification of the periphytic diatom community, regardless of their altitude, due to enhanced substratum availability. On the other hand, deep alpine lakes reveal a distinct regime shift through the abrupt appearance of centric diatoms due to the establishment of a stable stratification, representing favourable conditions for small cyclotelloid or colony-forming species. In contrast, deep mountain lakes of montane altitudes were found to be most resilient to climate warming. They underwent the subtlest species changes, just as originally expected (hypothesis 2). Concluding, two shallow lake types (type 3 and 4) could be differentiated in regard to their diatom assemblage composition. The bottoms of these lakes are completely illuminated, allowing benthic diatoms to thrive well and to overgrow settled planktic species. These shallow lakes are contrasted by two deep lake types (types 1 and 2) where planktic diatoms dominate because light does not reach the lake bottom and benthic diatoms can hardly develop at the deepest area where the sediment cores were obtained.

Depending on the altitude, the different composition of planktic diatom assemblages defines two deep lake types, just as the different structure of benthic assemblages does in shallow lakes (Fig. 5.5).

5.5.1 The Lake types

In detail, the montane type 1 lakes are deeper than 10 m and planktic diatom species appeared already more than 100 years ago in high abundances. However, the planktic proportion – mainly *Cyclotella*-complex – shows an increase over the entire sediment core indicating prolonged summer stratification and increased temperatures in the epilimnion caused by global warming (Winder et al. 2009; Daufrasne et al. 2009; Rühland et al. 2008 – 2015). The least prominent species change is evident in these lakes, as the diatom shift is limited to a mere increase of small *Cyclotella* species evoked by thermal stabilisation of their habitat, the epilimnion. According to Rühland et al. (2008, 2015) and Chen et al. (2014), the changes induced by global warming in deeper lakes could have started much earlier than 1970, and the responses of these lakes are more gradual processes compared to sudden changes in shallow lakes that do not start before 1970, as our results indicate for the Bavarian mountain lakes as well.

In contrast, type 2 lakes are characterized by a sudden appearance of planktic species within the last ~ 30 years, accompanied by a decrease of *Staurosira* species as a response to climate change (Lotter et al. 1999-2010; Rühland et al. 2015). Type 2 lakes are four to ten meters deep or even deeper in case of cooler alpine lakes.

As regression analyses and literature have shown, the decisive variable in an ecosystem is not the altitude per se but its influence on lake surface temperature, which separates type 2 lakes from type 1 lakes (Livingstone et al. 1999, Kuefner et al. 2020a). Between the 23rd Aug and 1st Sep 2016, the lake surface of the warmest type 2 lake reached an average of 19.5°C, at a mean ambient air temperature of 15.9°C (summer average 2000-2010: 12.4°C; extrapolated from regional weather data), whereas type 1 lakes were distinctly warmer (late-August: 19.7 – 21.7°C, extrapolated ambient air temperature: ≥ 17.8°C). Divergent lake and air temperatures may be the result of a strong topographic influence on mountain lake areas since they are mostly located in valley basins with effects of warmer southern slopes and wind protection (Dobrowski et al. 2009). Based on that, the sudden 'planktic appearance' probably represents a tipping point of the lake system as a consequence of increasing lake warming. *Cyclotella* species take advantage of increased thermal stability (Catalan et al. 2002, Winder et al. 2009) and a warmer epilimnion. For instance, the most frequent *C. comensis* describes an optimum at average summer air temperatures of 13.0 (±3.8) °C (Hausmann and Lotter 2001). Therefore, *Cyclotella* spp. could only leave detectable subfossil proportions when epilimnion temperatures reached the growth optimum of this genus, which probably happened in the 1970s for the first time in (sub)alpine lakes. In accordance, this warming-induced stabilization of mostly 'medium-deep' lakes supported a shift from polymictic to dimictic mixing regimes in recent decades with an increasingly stable epilimnion, an extended clear-water period and less turbid conditions (Fig. 5.5). Hence, the ability of small fragilarioids to cope with turbidity is no advantage anymore and this species can be outcompeted by increasing abundances of *Cyclotella* in the sedimented diatom assemblage (Kattel et al. 2015). Accompanying the small benthic fragilarioids, however, other planktic diatoms than *Cyclotella* are assumed to appear in turbid and turbulent water columns, such as strongly-silicified *Aulacoseira*, which are indicative of polymictic conditions (Rühland et al. 2015). There are indications that *Aulacoseira* spp. were present in such lakes before the 'planktic appearance', but they only appeared as fragments, which may be a methodical problem during diatom preparation.

In contrast to deeper lakes, mountain lakes that are less than 6 m deep are usually not stratified and therefore polymictic for most of the summer (type 3 and 4). Nevertheless, temperature logger data showed that even such shallow lakes could develop a warmed surface and a short-term stratification for a few weeks during summer. These conditions allowed the growth of planktic diatoms, e.g. elongate *Fragilaria* spp. and *Cyclotella* spp., in some shallow mountain lakes, as shown by analyses of samples from the water column and from the sediment surface (Fig. 5.3 and 5.5) (Ossyssek et al. 2020, Hofmann et al. 2020). However, the plankton did not constitute much to the sediment's biomass, as shallowness limits planktic habitat and the lakes are less productive due to their oligotrophic conditions. Furthermore, the lake bottom in these shallow mountain lakes is completely illuminated, i.e. the entire bottom represents littoral zone, so that periphytic diatoms overgrow the low amounts of sedimented planktic diatoms. Consequently, the latter do not appear in any sediment sample in significant numbers. Therefore, global warming-driven shifts in diatom assemblages of shallow lakes occurred especially as shifts within the periphytic diatom flora. The subfossil diatom assemblages of type 3 lakes were characterized by undirected shifts particularly within the small fragilarioid species. In contrast, type 4 lakes showed a general decrease of species of the *Staurosira* -complex, which can be interpreted as response to a warming environment (Lotter et al. 1999-2002). They were replaced by *Achnanthidium* spp. and in macrophyte-rich lakes additionally by epiphytic species, such as *Encyonopsis* spp. and some *Navicula* spp. (Stevenson et al. 1991, Wiklund et al. 2010). Making this a general development of benthic communities, type 2 lakes indicated a similar directional shift within the benthic proportion.

Comparable to the deep lakes, altitude is crucial for the separation of type 3 lakes and type 4 lakes. All lakes of the sample set that were assigned to type 3 lakes were located above 1600 m a.s.l., whereas this was the maximum altitude of type 4 lakes. In line with the altitude-temperature correlation, the average lake surface temperature in late-Aug 2016 was significantly lower in type 3 lakes with a maximum of 14.1°C than in type 4 lakes where 15.0 °C was exceeded (Fig. 5.4c).
This further supports type 4 lakes with stable water levels to be rich in organic substratum and to be dominated by macrophytes of the genera *Potamogeton* L. and *Chara* L., whereas type 3 lakes are possibly still too cold to establish significant water plant populations. Only single macrophyte species can reproduce in cool conditions in alpine altitudes (Overton 1899, Dörr and Lippert 2001, Bornette and Puijalon 2011). However, warming is supposed to increase macrophyte species richness in high altitudinal lakes (Rosset et al. 2010), evolving new habitats for epiphytic diatoms. Therefore, the replacement of *Staurosira* species by epiphytic species can be considered as a direct response to climate change (Rühland et al. 2010), whilst water plants in type 3 lakes of higher altitudes are still insignificant for epiphytic growth due to the cool water temperatures. Beside climate-induced changes in ice-break up dates, these alpine lakes are impacted by changes of input of organic and inorganic material due to high alpine weathering. Additionally, these processes hamper macrophyte growth as it promotes lake turbidity and a muddy, gyttja-like, loose and dynamic sediment. Thus, conditions of type 3 lakes provide substrata especially for epipelic and epipsammic diatom species and robust pioneers such as *Staurosira* s.l., which can cope with turbidity and mechanical disturbances by turbulent benthos (Kattel et al. 2015). Other diatoms lack competitiveness under these harsh and unstable conditions. Therefore, no significant shifts in the composition of diatoms due to global change can be detected.

The development of initially epilithic and epipsammic diatoms like in type 3 up to finally epipelic and epiphytic species like in type 4 can be referred to as 'substratum succession' and results in the highest beta diversities within the mountain lake set. Crossing of ecological thresholds in terms of the evolution of new benthic habitats further supports the benthic diatom shift as the strongest climate change response among the mountain lake diatom flora (Michelutti et al. 2002; Antoniades et al. 2005). In the future, an altitudinal upward macrophyte distribution as decisive tipping point in mountain lakes can cause non-linear responses and turn the lowest type 3 into the highest type 4 lakes once new substrata for epiphytic diatoms are established. This process will likely be accompanied by a significant increase of organic matter both on and in the sediment, as measurements of water content and diatom densities have shown (Menounos 1997, Avnimelech et al. 2001) (Fig. 5.3 and 5.4).

A special feature among the type 4 lakes are lakes that are exposed to marked WLF (type 4+WLF). Different to the 'typical type 4 lakes, *Staurosira* species have been replaced by the desiccation tolerant *Denticula tenuis*, as also described by Cantonati et al. (2009) and Hofmann et al. (2020). WLF strongly affect phytoplankton structure and biomass (Adamczuk et al. 2020) as well as impede an intensive and species-rich development of macrophytes (Riis and Hawes 2002, Bornette and Puijalon 2011). Primarily, fast-growing small species such as *Potamogeton filiformis* (PERS.) BÖRNER or *Ranunculus trichophyllus* CHAIX are able to cope with the short vegetation period and occasional desiccations. Additionally, *Chara*-species have a clear advantage over submerged vascular macrophytes in lakes with drastic fluctuations in hydrostatic pressure (Krause 1997). Hence, substratum for epiphytic diatoms species is uncommon in lakes with distinct WLF, but may change with climate change (Rosset et al. 2010) as indicated by the subfossil diatoms. Stones and rocks dominate the bottom of these lakes providing substrates for epilihic diatoms such as *D. tenuis*. Conversely to 'normal' type 4 lakes, this distinct diatom shifts can occur independently of altitude and temperature. Summarizing, the replacement of *Staurosira* by *D. tenuis* is likely to be a direct response to global change, as the extent and frequency of WLF in mountain lakes increase with enhanced drought as predicted by IPCC (2014).

Type 5 lake also show shifts only within the periphytic diatom community, despite beeing a deep lake. However, the shift occurred within completely different genera, i.e. from *Nitzschia denticula* to several *Diploneis* species and to *Gyrosigma acuminatum* (KÜTZING) RABENHORST (Fig. 5.3). The geological origin of this doline lake causes special limnological features, including meromictic conditions, low water temperatures, high ion concentrations, and high lake transparency. The extraordinary conditions have caused the development of a special benthic diatom assemblage, so that a separate type 5 lake could be classified. A depth of 20.2 m would actually suggest planktic diatoms to appear in significant abundances in the lake sediments. In fact, phytoplankton analyses have shown that obligate plankton diatoms, such as *Fragilaria* and *Cyclotella*, grow in the water column in high numbers within the diatom community (Ossyssek et al. 2020). However, total plankton densities are supposed to be very low as the lake is ultraoligotrophic with phosphorous concentrations below 5 $\mu g\ L^{-1}$. Furthermore, the deep extension of the trophogenic zone allows periphytic diatom growth even in deeper parts of the lake outcompeting settled planktic valves in the sediments. High ion concentrations, especially within the monimolimnion, may favor strongly silicified diatom species which dominate the diatom assemblages of Lake Sieglsee (Kuefner et al. 2020 a). Changes regarding groundwater inflow rate and lake conductivity may result in the observed special diatom shift. This in turn is possibly induced by climate warming as seasonal droughts and decreasing snow packs lead to a decreasing supply of ground water (Bard et al. 2012, Haslinger and Blöschl 2017, Jenicek et al. 2018). Weakened pouring underwater sources (limnocrene) may reduce ion concentration, turbidity and sedimentation. These conditions formerly may have favoured *N. denticula* as a motile tychoplanktic diatom (Peterson 1986, 1987). However, the reduced turbidity caused by climate change, i.e. the greater transparency of the water body, favours epipelic and epipsammic diatoms such as *Diploneis* and *Gyrosigma* (Douglas and Smol 1995) in competition with *N. denticula*. Therefore, the decline of this species correlates with the development of alpine climate (Fig. 5.3).

5.5.2 Factors controlling response of mountain lakes to climate change

The results of this study show that lake depth is the most important variable determining the response of diatom communities from mountain lakes to climate change. This can be explained by strong influences of climate change on limnological parameters such as expansion of euphotic zone or mixing behaviour, thus extent and structure of pelagic habitats and thus the composition and diversity of the plankton (Huisman et al. 1999). Accordingly, deep lakes seem to be more resilient to climate change as regime shifts are concentrated on the epilimnion. In contrast, climate warming in shallow ponds and lakes affects both the water body and the entire littoral habitat facilitating tipping points to cross, e.g. the establishment water plants as substrate for epiphytic flora. This increases species richness, but at its one, it is subordinate since the ecological resilience appears to be most pronounced in lake systems with various, highly dynamic and adaptable communities (Roberts et al. 2019).

The hypothesized role of the altitude is the second most important variable in terms of a global change climaxing in alpine regions. Altitude influences lake surface temperature and substratum availability, as well as catchment vegetation. As summer surface temperature considerably influences the extent and stability of the epilimnion (Livingstone et al. 1999, Kuefner et al. 2020 a, Ossyssek et al. 2020), lake altitude determines the timing of tipping points, e.g. favouring the 'planktic diatom appearance'. Therefore, the most resilient lakes are currently the deep plankton-rich montane lakes (type 1), where temperature thresholds, which are shaping the structure of the plankton communities were already exceeded in the decades of the oldest sediment layers. In shallow montane lakes, warming also allows low abundances of *Cyclotella* in recent years possibly due to longer ice-free periods that even promotes stratification of shallow lakes. Nevertheless, their short water column will keep the plankton underrepresented. In deeper alpine lakes, however, temperatures nowadays apparently exceed certain thresholds leading to the appearance and subsequently to an increase of planktics (Fig. 5.4). Based on these thresholds, temperature estimations allow to define tipping points and consequently assess lake types globally apart from ecotonal boundaries such as forest or timber lines.

These relationships can further be modulated by the trophic level of a lake as it controls algal production and water transparency, regulating the extension of the littoral zone**.** Accordingly, a mesotrophic shallow mountain lake may appear like a deep oligotrophic lake, e.g. Lake Schachensee. Although being polymictic and 4.4 m deep, a higher nutrient availability may have promoted stronger silicified plankton of the genus *Cyclotella,* which already dominate the sedimentary deposits after a few decades. Due to its high turbidity, benthic communities were displaced in the sediments. In contrast, *Asterionella formosa* can outcompete *Cyclotella* in deep mesotrophic lakes during earlier stratification phases as it is superior in competing for phosphorus (Tilman 1982). In two deep montane lakes (L. Ferchensee, L. Lautersee), for instance, the sudden appearance of *A. formosa* seems to define a tipping point, when climate warming promotes the consequences of rising trophic levels (Berthon et al. 2014, Sivarajah et al. 2016). Concluding, the trophic level not only affects the algal community composition, it also decreases the resilience to climate change especially in shallow lakes with amplified responses compared to lakes of lower nutrient levels.

As a fourth factor, the geological genesis of a lake further influences planktic communities, confirming the hypothesis (1) as it determines lake morphometry, water supply and habitat stability (WLF). Firstly, a special geological shape such as the one of doline lakes with a permanent supply of ‘soil-filtered’ ground water keeps the lake extremely low in nutrients, cold, unstratified, but elevated in ion concentrations. This results in unfavourable conditions for planktic species and limits its diatom assemblages to a completely different species composition compared to the periphytic flora of cirque lakes. Secondly, lakes that lack ground moraines sealing the lake bottom in contrast to cirque lakes are characterized by unstable water levels, resulting in unfavourable conditions for littoral diatom flora and macrophytes. Consequently, sedimentary assemblages of such ‘WLF’-lakes are increasingly restricted to desiccation tolerant species in response to climate warming (Fig. 5.3). Hence, lake geology-dependent stability of lacustrine habitats makes doline lakes the most, and WLF-lakes the least resilient to global warming.

In line with hypothesis (3), local anthropogenic impacts were found to interact with warming environments. Some diatom developments within the dataset cannot be explained by climate change, as they show no directional (e.g. type 3 lakes) or even inverse trends (Lake Funtensee). There is evidence that these mountain lakes are affected by local human activities, which disguise their response to global warming. Again, lake depth and volume define the degree of resilience. In general, subfossil diatoms unearthed decades of enhanced nutrient availability in the concerning Bavarian mountain lakes. Down-core trends show that these diatom-inferred nutrient peaks coincide with hut construction, while gradual nutrient decrease is introduced by treatment plant constructions. The latter led to a reduction of bioavailable phosphorous within the last decades that counteracts the eutrophication caused by global change (Koinig et al. 1998; Rosbakh et al. 2014; Arnaud et al. 2016), especially observed in the deeper lakes, L. Ferchensee and L. Lautersee. Shallow lakes such as Lake Funtensee are less resilient to local human impact. Lake response to the nutrient decrease as inferred by shifts within the *Staurosira* complex (Kuefner et al. 2020 a) is much stronger and contrary to the response to warming temperatures. In the medium-deep Lake Rappensee the construction of a little dam in 1948 resuls in an increase of nutrients and turbidity (Algarte et al. 2016) as eutraphentic species such as *Gyrosigma* spp. (Hofmann 1999) or *Staurosira parasitoides* (Kuefner et al. 2020 a) also indicated. However, the lake could recover again with typical signs of global change such as the appearance of planktic species. Nevertheless, the combination of lake warming and nutrient decline only reached the threshold for *Cyclotella* species, but did not cross it. They therefore disappeared again when the lake re-oligotrophicated despite an ongoing warming. This allows the definition of ecological thresholds e.g. for certain *Cyclotella* species which is highly important in paleolimnological studies as it facilitates the explanation of certain shifts within diatom community structures (Grenier et al. 2010). Concluding, the hypothesis (3) can be confirmed that anthropogenic influence may smother the impact of climate change, but also decreases the resilience of mountain lakes to climate change as the response of the biota is amplified due to enhanced nutrient levels.

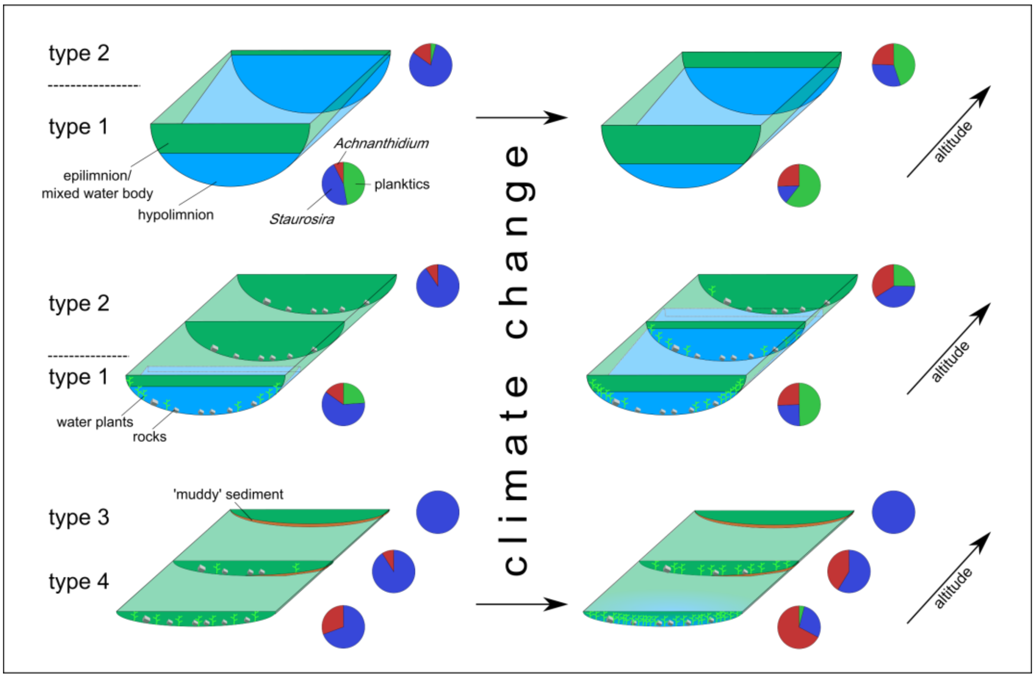


Figure 5.5 Overview oft he mountain lake developements in different lake types. The figures on the left represent the lakes before climate change influence, on the right with climate change inpact. The z-axis is the altitude. The circles visualize the composition of the main diatom groups at the lake bottom. "Achnanthidium" group includes all epiphytic diatoms. In deeper lakes, benthic substratum like rocks and water plants is negligible for the sediment assemblages at the deepest spot of the lake. Doline lakes and mountain lakes with marked water level fluctuations and/or direct anthropogenic influence are not shown

5.6 Conclusion

Subfossil diatom analyses revealed deep mountain lakes to be more resilient to climate change than shallow lakes as the onset of the response to rising temperatures is earlier and thus smoother. Global change in deep lakes only extends the epilimnion as indicated by increases of planktic diatoms. However, benthic communities – in shallow areas of both deep and shallow lakes – can completely reorganize. Benthic, completely illuminated habitats comprise the entire lake bottom in shallow lakes, hence enhances warming by reflection and absorption of long-wave radiation additionally. In accordance, a small and shallow water body warms faster than bigger volumes with a dark and cool hypolimnion. Moreover, the altitude and the stability of water levels is supposed to affect the response to lake warming. On the one hand, diatom-inferred species turnover peaks in deep lakes of higher altitudes and shallow lakes of lower altitudes. This is the result of certain tipping points such as established summer stratification and macrophytes with a benthos succession from epilithic to epipsammic or epiphytic substrata, respectively. On the other hand, shallow lakes of higher altitudes still lack a sufficient number of macrophytes and subsequently substratum heterogeneity. Hence, *Staurosira* species as robust pioneers are the only species which can cope with the muddy demanding i.e. epipelic benthos of such lakes. which dramatic diurnal and seasonal variations in lake temperature may further support. It is likely that these lakes will experience the aforementioned tipping points within the next decades as a consequence of global warming. In shallow lakes with great WLF, however, changing conditions hamper macrophyte growth and a great sedimentation, but increasingly select for epilithic and desiccation tolerant species. The ongoing warming will enhance the importance of epiphytic diatoms.

It is evident that the benthic diatom reorganization, in particular the replacement of *Staurosira* species by *Achnanthidium* and other epiphytic diatom species, matches the development towards a higher autochthonous production that coincides with a significant increase of water plant pigments. Future work is about to focus on making a comprehensive model out of all proxies to predict the future development of hard-water mountain lakes in the temperate mountain region and to observe the mountain lakes that are suggested to be close to important tipping points. However, subfossil diatom analyses already allow to indicate the extent of current and future climate change impacts as well as its variety of responses in several central European mountain lakes.

6. General discussion

The studies presented in this thesis provide novel insights about global climate change impacts on Bavarian and North Tyrolean mountain lakes. The results promote a better understanding of (1) the linkages between climate drivers, lake thermodynamics and primary producers, (2) the interactions of local and regional impacts with global warming and (3) the role of altitude regarding the response of the lakes to climate change. The results of this thesis evidence the increasing pressures on the mountain lakes. Climate change impacts were found to be detectable in most of the studied lakes. Several lakes have already reached a tipping point of lake ecosystem, mainly triggered by reinforcement of eutrophication processes by climate warming. The findings show the essential necessity for policy and stakeholders to protect Alpine aquatic systems assuring the supply of freshwater under changing environmental conditions and to present sustainable local recreational and tourism-related concepts including visitor guidance and measures to reduce motorised individual transport through mobility management.

6.1 The interaction of climate change with other anthropogenic impacts

Local disturbances were hypothesised (1) to overprint the effects of global warming, especially in montane lakes influenced by tourism and agriculture. The findings presented in this thesis rather show that global climate change amplified the impacts of local human activities, as the processes involved in mountain lake responses to eutrophication and climate change were often intertwined.

Climate and the hydrological cycle are closely coupled (Michalak 2016). Climate change affects precipitation, air temperatures and wind patterns and all these factors influence the lakes' physical characteristics, water quality and aquatic life. Changes in precipitation patterns were found to alter the lakes' trophic situations. Furthermore, a prolonged drought led to declining lake levels and to rising nutrient concentration in the remaining water body (chapter 3). Enhanced thermal stratification of the water column hampers the exchange of nutrients and oxygen resulting in oxygen-depleted and nutrient enriched deep-water zones. All these climate-induced eutrophication processes were exacerbated by nutrient releases from mountain huts or grazing cattle and by atmospheric nitrogen fertilization (chapter 4).

The availability of epilimnetic nutrients, especially nitrogen and phosphorus controls phytoplankton productivity. Additionally, water temperature regulates a series of biological processes including organism growth and respiration. Rising temperatures modify phenology and life history towards shorter lifespans and earlier reproduction, resulting in altered trophic dynamics and a mismatch between prey and consumer (Straile 2000; Adrian et al. 2006). Both, rising nutrient concentrations and a warming environment were found to stimulate primary production in the studied lakes, indicated by increasing concentrations of sedimentary pigments and shifts within stable isotope and diatom records. Decomposition of enhanced phytoplankton biomass impaired hypolimnetic oxygen conditions and promoted anaerobic microbial processes, indicated by sharply declining $\delta^{13}C_{org}$ values (chapter 4).

Unravelling the complex chains of tangled factors affecting lake ecosystems represents an important challenge in times of climate change and increasing human population. The multi-proxy approach of biological, biochemical and geochemical indicators applied in the study presented in chapter 4 enabled to disentangle the diverse impacts on a small subalpine lake. The correlation between TOC, $\delta^{13}C_{org}$ and paleopigment concentrations indicated progressive lake eutrophication and rising algae biomass. Simultaneously increasing amounts of centric diatoms and rising concentrations of paleopigments restricted to planktic algae suggest the thermal stabilisation of the water column and the extension of the pelagic habitat. Lake eutrophication and climate-induced intensified stratification culminated in an “explosion” of phytoplankton biomass highlighting that a tipping point of lake ecosystem is crossed by the interaction of human activities on local, regional and global scale (chapter 4).

6.2 Humans and Alps: a long history of settlement and touristic activities

The results presented in chapter 4 and 5 indicated that Alpine ecosystems have already been modified by a series of local disturbances. Continuous settlement of the Alpine region began around 13,000 BC at the end of the Würm glacial and intensified since the Bronce Age (2200 BC) (Mathieu 2015). Since then the Alps are under steadily increasing pressure including agriculture, alpine pasture, forestry and tourism. Additionally, fossil fuel combustion, mineral fertilizers and livestock manures have caused the emissions of greenhouse gases and air pollutants such as nitrogen compounds into the atmosphere (Unger et al. 2016; Engardt et al. 2017). Especially the fringe of the Northern Alps is affected by high atmospheric nitrogen deposition owing to the steep slopes and the prevailing wind direction (Kirchner et al. 2014). Indeed, the results of this thesis show that these multidimensional and entangled stressors seriously affected mountain lake ecosystems and bequeathed a range of footprints on the lakes sediments.

6.2.1 Local disturbances: tourism and alpine pasture

Local anthropogenic impacts, primarily due to tourism or alpine pasture appeared even in the remote subalpine and alpine lakes (chapters 4 and 5). The Alps are the world’s second most important tourist region (Flury et al. 2013). The impressing landscapes, the options for various outdoor activities and the access to wilderness and wildlife make the Alps an attractive destination for nature-based recreation. The montane lakes Ferchensee and Lautersee have already been popular destinations since the beginning of the 20th century due to their easy accessibility and the gastronomic options (Hasdenteufel and Streifinger 2012). Especially during the summer month both lakes are highly frequented. The geochemical proxies recorded in the sediments of both lakes excellently disclosed the progressive eutrophication due to the increasing influence of touristic activities since ~ AD 1940. The sharply increasing tourism, documented in the Alpine Club Yearbooks by rising overnight stays in the Hans-Mertel-Hütte since the mid-20th century is reflected in the sediments of subalpine Oberer Soiernsee by rising chlorophyll a concentrations, markedly decreasing $\delta^{13}C_{org}$ values and shifts within diatom assemblage composition (chapter 4). Same trends coincided with hut construction and increasing numbers of visitors are recorded in the sediments of subalpine Funtensee (Kärlinger Haus) and alpine Drachensee (Coburger Hütte). Hut construction projects additionally promote slope instabilities by deforestation, destruction of the vegetation cover and earth-movements, evidenced by flood layers or marked shifts from in-lake to terrestrial source of sedimentary organic matter (chapters 4 and 5). Analysing the current littoral diatom assemblages, clearly higher Trophic Indices were calculated near guesthouses (Ferchensee, Lautersee) or a small mountain hut (Oberer Soiernsee) indicating enhanced nutrient inputs especially during the warm seasons (Appendix; chapter 4).

Humans shaped the present cultural landscape of the Alps since ancient times (Flury 2012). In the humid and cooler northern part of the Alps, the steep slopes and meadows of high alpine regions are primarily used for summer grazing pasture and hay production (Tasser et al. 2011). The areas around the montane lakes Lautersee and Ferchensee were additionally used for agriculture and forestry (Hasdenteufel and Streifinger 2012). On the subalpine grassland and alpine meadows of the study area mainly young cattle, but also horses, sheep and goats traditionally graze during the summer months. The lakes serve as drinking water source for the animals. Their excrements were widely found at the shorelines of the lakes. Additionally, severe soil erosion caused by livestock was observed. In line with Apollo et al (2018), the degree of anthropo-zoogenic erosion varied depending on slope gradient and intensity of usage, especially on time of grazing, animal species and number. Furthermore, geology, vegetation and soil development were found to play an important role. The areas surrounding the lakes Schachensee and Delpssee were intensively used as summer pasture by a great number of cattle. Furthermore, deeply weathered marls and clays of the Raibler Formation outcrop at the eastern part of Lake Schachensee. Erosion by cattle treading formed an extended alluvial fan at the north-eastern shore and appeared to be jointly responsible for loads of organic material into the lake resulting in mesotrophic conditions (chapter 5). Intensive pasturing and anthropo-zoogenetic erosion led to a high sedimentation rate (0.29 cm/y) in Lake Delpssee, surrounded by deeply weathered local ground moraine (chapter 5). Around both lakes Soiernseen and the studied alpine lakes, however, the erosion caused by cattle treating was found to be significantly less pronounced due to poor soil development on talus deposits or karstified limestones.

Local impacts, such as tourism and pasturing were hypothesised (1) to may mask the signals of global warming. However, the findings of this thesis showed that climate change and local stressors rather interact resulting in the reinforcement of eutrophication processes and amplified responses of lake algae (chapters 4 and 5). However, the multi-proxy approach applied in this thesis enabled to disentangle climate change impacts from local disturbances. Especially shifts in diatom assemblages were found to be highly appropriate to detect climate change impacts. Even in the highly anthropogenically influenced lakes Ferchensee and Lautersee changes in diatom community composition revealed the climate-induced modification of the mixing regimes. While the abrupt appearance of *Asterionella formosa* around AD 1960 initially indicated the fertilization by atmospheric nitrogen deposition, the rising abundances of these colony-forming diatoms around AD 1980, appeared to be in context with a markedly enhanced thermal stratification.

6.2.2 Regional and global influences: industrialization and agricultural intensification

The findings of chapter 4 revealed long-distance atmospheric depositions as a driving force of lake eutrophication. The fringe of the Northern Alps is affected by particularly high rates of atmospheric nitrogen deposition (Lorenz et al. 2008; Kaiser 2009; Kirchner et al. 2014). Especially since the 1950s, atmospheric transport of anthropogenic nitrogen has increasingly led to the acidification and eutrophication of soils and water bodies (Galloway et al. 2008; Fowler et al. 2013). Fossil fuel combustion (coal-fired power plant, traffic), intensification of agriculture (Haber-Bosch process) and animal husbandry provide the major sources for reactive nitrogen (Engardt et al 2017). Additionally, increasing temperatures due to global warming especially amplify NH_4 emissions from soil to atmosphere (Skjøth and Geels 2013). In the lake sediments, the increasing deposition of atmospheric nitrogen is documented by the depletion of sedimentary $\delta^{15}N$ and the decoupling of $\delta^{15}N$ and $\delta^{13}C_{org}$ signatures since ~ AD 1970 (chapter 4).

Industrialization and intensification of agriculture also controls the isotopic composition of the lakes' DIC pool and consequently $\delta^{13}C_{org}$ signatures of sedimentary organic matter. Acid rain enhances carbonate weathering and lead to rising pH-levels in lakes with catchment areas dominated by limestone formations (Smol 2010). Bicarbonate (HCO_3^-) then represents the predominant DIC source for photosynthesis (Wetzel 2001), resulting in ^{13}C enriched primary producers (Keeley and Sandquist 1992). In Lake Oberer Soiernsee (pH = 8.7) submerged macrophytes were found to be enriched by 5.3‰ (*Potamogeton* sp.) and 9.8‰ (*Chara* sp) in their $\delta^{13}C_{org}$ signatures (chapter 4).

Furthermore, the combustion of coal and oil changed the $^{13}C/^{12}C$ ratio of atmospheric CO_2

(Keeling et al. 1979) and led to a gradual depletion of atmospheric CO_2 especially since ~ AD 1850 (McCarroll and Loader 2004). Via permanent exchange of CO_2 by diffusion at the water/air interface ^{13}C-depeted CO_2 accumulates in the DIC pool of a lake. This "fossil fuel effect" (Mayr et al. 2005) is excellently recorded in the lake sediments especially of the oligotrophic subalpine and alpine lakes (Drachensee, Brendlsee, Rappensee, Soinsee, Seeleinsee).

However, with the onset of eutrophication, other processes superimposed the effect of atmospheric CO_2 depletion (chapter 4). During photosynthesis ^{12}C is energetically more favourable in the assimilation of CO_2. With rising photosynthesis rates, $^{13}CO_2$ gradually accumulates in the epilimnetic DIC pool (Farquar et al. 1989). Consequently, primary producers increasingly incorporate $^{13}CO_2$. When algae died and sunk, the ^{13}C-enriched biomass is finally stored in the sediments. This trend is documented in the sedimentary records of all studied lakes, especially in context of touristic activities, amplified by climate warming since the 1980s (e.g., chapter 4). In the first phase of eutrophication, however, when anaerobic microbial processes produce ^{12}C-enriched methane, a shift to more negative $\delta^{13}C_{org}$ signatures may occur (Hollander and Smith 2001), evidenced in the sediments of the lakes Drachensee and Oberer Soiernsee (e.g., chapter 4).

6.3 Response and resilience of mountain lakes to climate change

In line with hypothesis 2, altitude turned out to be the main driver controlling diatom responses to climate change. Additionally, lake depth, lake origin and trophic state modulated the timing of regime shifts within diatom communities (chapter 5).

Ecological resilience appeared to be more distinctive in lakes with a stable water column, a structurally more complex habitat and a greater substrate heterogeneity resulting in a more diverse and dynamic diatom population. Thermal stratification created cold deep-water refuges for planktic species and undisturbed mid-depth zones provided stable conditions with constant temperature and attenuated but sufficient light for benthic diatoms (chapters 3 and 5).

Deep, montane lakes that host species-rich and highly diverse diatom communities have proven to be most resilient to climate warming. In contrast, deep lakes of higher altitudes and shallow lakes of lower altitudes appeared to be most vulnerable to climatically induced environmental changes as tipping points of lake ecosystems were crossed. The stabilisation of thermal stratification led to an abrupt appearance of small centric diatoms and increased success of *Dinophyta* and *Cryptophyta* (chapters 4 and 5). The establishment of macrophytes provided new habitat and substrate for epiphytic diatoms and resulted in reorganization of periphytic diatom communities (chapter 5).

6.3.1 Environmental parameters changing along the altitudinal gradient

As hypothesized (2), altitude markedly controlled mountain lake response to climate warming.

However, the results of this thesis also showed that more local effects associated with land use, catchment geomorphology, and basin morphology often superimpose the large-scale influences of altitude (chapters 4 and 5).

The findings of this thesis revealed altitude to markedly influence the structure of mountain lake primary producers. Biomass and diversity of both phytoplankton communities and littoral diatoms were significantly lower in alpine lakes. Diatom assemblages show a clear zonation along the altitudinal gradient (Fig. 6.1). Planktic diatoms were highly abundant in deep, montane lakes, whereas small periphytic species dominated the highly transparent, polymictic alpine lakes. Especially robust pioneer species (*Staurosira* ssp., *Staurosirella* ssp., *Pseudostaurosira* ssp.) which cope well with environmental instabilities (e.g., dramatic diurnal and seasonal variation of lake temperatures and lake chemistry) and small mobile epipelic taxa, which are able to actively seek out low UVR refuges were highly abundant in alpine lakes. As the low temperatures limited macrophyte growth at high altitudes, they are not available as habitat and refuge for epiphytic diatoms, which in turn reached high percentages in the diatom assemblages of montane lakes.

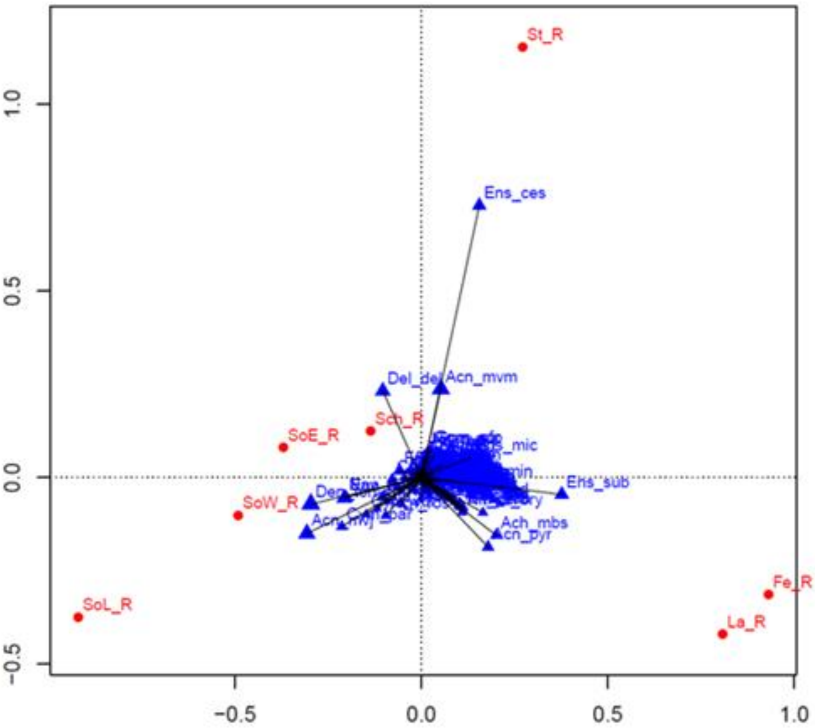


Figure 6.1 Scatterplot of CA showing the zonation of recent diatom assemblages along an altitudinal gradient. The selected lakes are located near Garmisch-Patenkirchen: montane lakes Ferchensee (Fe_R) and Lautersee (La_R), subalpine lakes Unterer Soiernsee (SoE_R), Oberer Soiernsee (SoW_R) and Schachensee (Sch_R), alpine lakes Soiernlache (SoL_R) and Stuibensee (St_R)

Generally, altitude influences climate-related impacts on mountain lake ecosystems, as it controls solar ultraviolet radiation (UVR, 290-400 nm), air temperature and catchment vegetation. In the Alps, the global UVR (direct and diffuse) increases by about 11 % per 1.000 m (Schmucki and Philipona 2002). In contrast, the heat capacity of the atmosphere is lower at higher altitudes (Beniston 2005). Kirchner et al. (2009) found that in the Alps, the mean decline of air temperatures ranges between 0.41 and 0.59 °C per 100 m. Furthermore, alpine lakes are generally characterized by low nutrient and DOC concentrations, as a result of reduced terrestrial vegetation cover and soil development in catchments above the tree line (Sommaruga et al. 1999). Hence, high-elevation aquatic ecosystems are harsh habitats hosting highly adapted floral and faunal communities, that tolerate high UVR, low temperatures, short growing seasons and low nutrient concentrations (Loria et al. 2019).

However, differences regarding the lakes trophic state and origin were found to superimpose the influence on altitude on lake algae. Within the set of limnologically analysed alpine lakes, phytoplankton communities clearly differed in their composition owing to significant differences in their terrestrial environment. In Lake Stuibensee, surrounded by alpine meadows pastured during summer months, the green algae *Chlorella* sp. Beyerinck, *Scenedesmus* sp. Meyen and *Chlamydomonas* sp. Ehrenberg were highly abundant in summer phytoplankton communities. These species, indicating phosphorus and nitrate enrichment (Gardner et al. 2008), were absent in alpine Lake Soiernlache, a small lake surrounded by rocky catchment area and sparse vegetation. Subalpine Lake Schachensee showed a 12-fold higher summer phytoplankton production than the other subalpine lakes due to the enhanced nutrient inputs related to pasturing, tourism and the outcropped geological formation (Fig. 6.2).

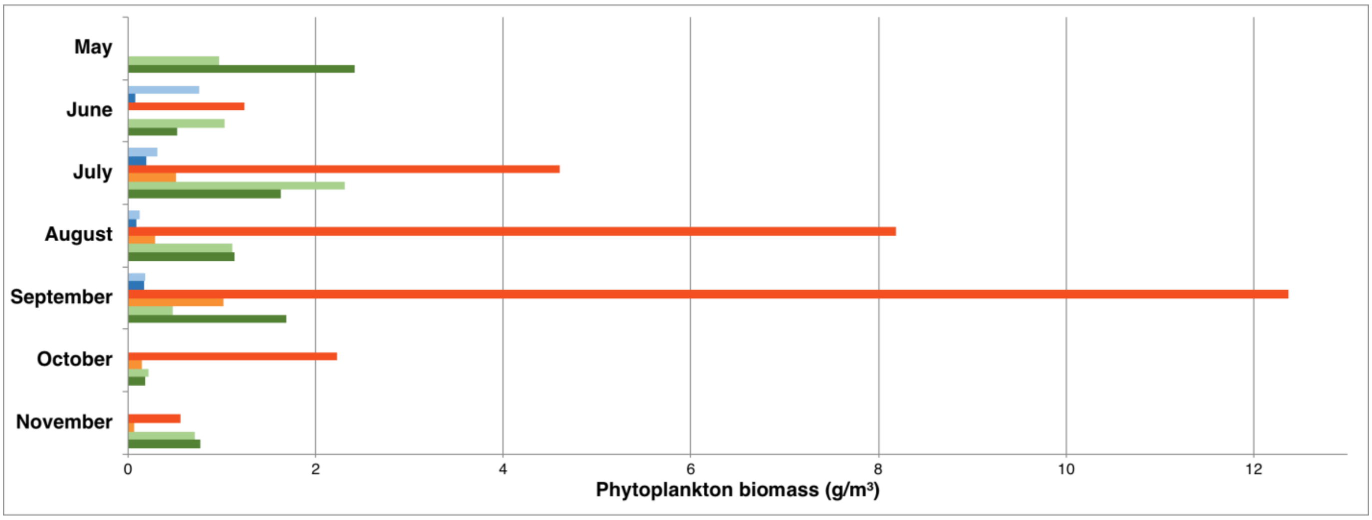


Figure 6.2 Phytoplankton biomass along an altitudinal gradient in May to November 2016. In May only the montane lakes (green) were ice-fee. In October and November, only phytoplankton from the montane and subalpine (red/orange) lakes could be analysed, while the alpine lakes (blue) already were ice covered. The analysed lakes are lacated near Garmisch-Patenkirchen: montane lakes Lautersee (dark green) and Ferchensee (light green), subalpine lakes Schachensee (red) and Unterer Soiernseee (orange), alpine lakes Stuibensee (light blue) and Soiernlache (dark blue). The markedly higher phytoplankton biomass in Lake Schochensee clearly demonstrate the influence of local impacts on the lake's trophic state

Lake origin also appeared to shape the structure of diatom communities and influence diatom response to changing environmental conditions (chapters 3 and 5). Despite their adjacent position, the marked water level fluctuations (up to 9.5 m) of Lake Unterer Soiernsee resulted in a highly disturbed near- shore zone hosting aerophilic and subaerial diatom taxa. These taxa did not occur in the adjacent Lake Oberer Soiernsee, a lake with more stable conditions due to the sealing effect of the groud moraine. The meromictic doline Lake Sieglsee hosted diatom taxa which are adapted to the special conditions of the monimolimnion and exhibited a reorganisation of diatom assemblages significantly different from the other lakes (chapter 5).

In effect, altitude influences the lakes response to climate change. However, the high degree in heterogeneity (topography, geology, land use) of mountain regions, lead to the effect that large-scale climate processes are mediated at local scales, creating a mosaic of possible lake responses. The evaluation of the data from the local weather station positioned at lakes Soiernseen showed that the local weather differed in part clearly from metereological data from weather stations of Germanys National Meteorological Service (DWD), especially in terms of solar radiation, rainfall, wind direction and wind speed (chapter 3). This fact may be due to the special location in a caldron surrounded by high summits shielding the lakes from westerlies. The impact of UVR depends on solar zenith angle, albedo values and atmospheric conditions (ozone, aerosols, and cloud cover). The complexity of Alpine topography and the resultant different microclimates influence lake temperatures and stability of thermal stratification. Location at a northern slope and shading by summits left snow patches in the catchment and enabled cold-water input even in summertime (e.g., Lake Soiernlache). Despite their adjacent location in a deep cirque, the non-uniform shading by surrounding summits resulted in highly dissimilar intensity of solar radiation on lakes Soiernseen, especially between October and April and in significant differences regarding duration of ice cover and timing of ice break (chapter 3).

Additionally, catchment-geology affects lake origin, soil development and type of vegetation causing a variety of different hydromorphological features and supply of organic carbon and nutrients (chapter 5). Additionally, atmospheric N deposition, alpine pasturing, forestry and tourism lead to enhanced nutrient release to the lakes and influence the response of mountain lakes to climate warming independent from their altitude (chapters 4 and 5).

6.3.2 Influence of lake depth on the response to climate warming

In line with hypothesis (3) lake depth was found to have a crucial impact on lake's respone to rising temperatures by contolling heat transfer and mixing regime. Shallow lakes warmed up faster than deeper lakes. Besides warming by solar radiation, there is additionally a heat transfer from the sediments to the water (Wetzel 2001). On the other hand, in deeper lakes the thermal stratification tended to stabilize as surface waters warmed up and deep-water temperatures decreased because greater depths receive reduced solar radiation.

However, the decisive factor for warming trends is dependent on the range of solar radiation and hence the water transparency. Water clarity trends may amplify or suppress climate-induced warming rates by influencing the depth range where the energy of solar radiation is absorbed. Especially lakes of intermediate depths (4-8 m) are particularly sensitive to changes in underwater light climate (Rose et al. 2016; Shatwell et al. 2016). Climate-induced catchment greening and alterations in precipitation patterns regulate the light transmission by altering DOC concentrations and the amounts of light-absorbing organic and inorganic particulate matter. A heavy rainfall event in August 2015 associated with extremely high terrestrial input from the watershed strongly modified the light conditions for the rest of the open-water season and reinforced the heat transfer into both lakes Soiernseen (Chapter 4). Increasing phytoplankton biomass as a result of land use changes, touristic activities, and atmospheric fertilization were also found to alter the lakes's light regime and the heat transfer into the lake. Increased solar absorption by both, the rising phytoplankton biomass and the suspended terrestrial particles appeared to be a puzzle piece reinforcing the warming trend of Lake Oberer Soiernsee (chapter 4).

Lake depth and transparency markedly controlled the mixing regimes of the studied lakes (chapter 5). Most shallow lakes were found to be polymictic. Lake Schachensee, however, appeared to be stratified owing to the wind-protected position and the high phytoplankton biomass resulting in an enhanced absorbance of solar energy in surface waters. The stabilisation of the thermal stratification was recorded in the lake sediments by rising abundances of small centric diatoms especially in oligo- to mesotrophic lakes of intermediate depths (chapters 4 and 5). In contrast, the appearance of heavy silicified *Aulcaoseira* sp. signified turbid, high-turbulent and shallow-water conditions prevailing during cold and windy periods (chapter 4).

The light conditions markedly influenced composition of diatom assemblages in the surficial sediments. In transparent lakes, periphytic *in-situ* growing diatoms outnumber the planktic taxa, while light-limited conditions result in high abundances of planktic diatoms (chapter 3). Especially in lakes of intermediate depths, the range of light transmission controlled the existence and extension of an aphotic zone (chapters 3 and 5). In Lake Schachensee, phytoplankton shading resulted in light limited conditions in depths greater than 2 m inhibiting periphytic diatom growth. Despite shallowness (max. depth 5.4 m), planktic taxa were found be highly abundant in the diatom assemblages sampled between 3 and 5.4 m.

The results presented in chapter 3 highlighted the importance of considering lake depth and transparency by developing diatom-based transfer functions. With regard to reconstruct trophic state or lake level changes it was found to be highly useful to create two different training sets, one for deep or low-transparency lakes including periphytic and planktic diatoms and another one for shallow clear-water lakes solely based on periphytic diatom species. Aphotic conditions are essential for paleolimnological studies researching changes of lake mixing regimes and phytoplankton dynamics. In aphotic depths, diatom assemblages on surface sediments were found to comprise a cross-section of diatoms from the pelagial habitat and from the littoral zone including different substrates (e.g., macrophytes, sediments, stones). Light-flooded lake bottoms, however, lead to favoured conditions for benthic diatoms outnumbering settled planktic taxa, especially small-celled *Centrales* (chapter 3).

If aphotic conditions prevail, shifts within the ratio between periphytic and planktic diatom frustules enable the reconstruction of dynamics in water column transparency. In well-illuminated lakes, the preference of periphytic diatoms for distinct depth areas can be used to track lake level changes in down-core studies (chapters 3 and 4). Epilithic and epiphytic low-profile (primarily prostate) diatoms were found to colonize the upper littoral zone. Epipsammic low-profile taxa, firmly attached on sand grains mainly occured in the deeper littoral. Motile diatoms were found to have a competitive advantage on finer sediments of physically less disturbed deeper water areas. High-profile tube-forming species indicated the development of a three-dimensional biofilm and therefore physically more stable conditions (chapter 3).

6.3.3 Lake and catchment characteristics influencing the response of subalpine lakes to climate change

A closer view on four selected subalpine lakes clearly demonstrates the multiplicity of hydrological features (Table 6.1) and catchments characteristics despite a narrow range of altitude and reveals the role of lake transparency rather than lake depth influencing lake response to climate change.

Table 6.1 Hydrological parameters of selected subalpine lakes

Lake	Altitude (m a.s.l.)	Max. depth (m)	Aphotic conditions	Trophic state	Stratified	Water level fluctuations	Inflow/ outflow
Oberer Soiernsee	1558	14.5	✓	oligo-meso	Longer periods	1.8	×
Unterer Soiernsee	1552	15	×	oligo-meso	✓	9.5	×
Delpsee	1600	1.3	×	oligo	×	×	✓
Schachensee	1680	5.4	✓	meso	✓	0.8	✓

All these differences modulate the lake's response to climate change and the archiving of diatom remains in the lake sediments. Despite shallowness of Lake Schachensee aphotic conditions prevailed owing to the mesotrophic conditions and high phytoplankton biomass. Additionally, wind sheltered location prevented wind-induced mixing and promote thermal stratification. The response to climate warming was similar to significantly deeper Lake Oberer Soiernsee. Since AD

1980, rising abundances of centric diatoms indicated the stabilization of the water column of both lakes. Concurrently rising concentrations of chlorophyll a and markedly decreasing $\delta^{13}C$ values signified the amplifying effect of global change and local eutrophication.

The dramatic lake level changes of Lake Unterer Soiernsee, however, resulted in a highly disturbed upper littoral zone and light-flooded conditions during most time of the vegetation period. Despite similar amounts of planktic diatoms as in adjacent Lake Oberer Soiernsee, benthic species significantly dominated diatom assemblages of the surficial sediments. Lake level was found to be more stable in Lake Oberer Soiernsee as moraine material has served as aquiclude and sealed the lake bottom. The fluctuating water levels of Lake Unterer Soiernsee led to frequently resuspension and redistribution of lake sediments. Sediment dating was found to be complicated and densities of diatom frustules were too low for diatom analyses. However, the lake response to a changing environment was documented by rising chlorophyll a concentration and declining $\delta^{13}C$ values since AD 2000.

Shallow Lake Delpssee is characterized by oligotrophic conditions, a surface in- and outflow and numerous underwater springs. Due to the high water transparency and a maximal depth of 1.3 m planktic species occurred very rarely within the diatom assemblages archived in the lake sediments. However, a shift within the benthic, fragilarioid diatoms around AD 1980 evidenced the lake response to climate warming. Additionally, increasing concentrations of total algae biomass markers and decreasing $\delta^{13}C$ values documented changes in the catchment area.

As hypothesised (4) the location at the tree line ecotone make subalpine lakes particularly appropriate for detecting climate-mediated changes of catchment-lake interaction.

Climate-induced tree line upshift, catchment greening, and soil development lead to gradually increasing DOC and nutrient influx from the terrestrial environment into lakes (Vinebrooke and Leavitt 1998). The rising DOC concentrations appeared to decrease the UVR supress on algae growth, evidenced by sharply increasing concentrations of phytoplankton-indicating pigments in recent decades (e.g., chapter 4). Additionally, climate warming promoted the establishment of macrophytes especially in lakes of subalpine altitudes, resulting in the abrupt appearance of epiphytic diatoms (chapter 5).

However, it is highly advisable to request information on land use changes from landowners and forestry offices to better interpret the complex interactions of climate warming with changes in terrestrial vegetation and erosional processes. For centuries, the alpine farming and forest pasturing artificially lowered the climatic positions of tree line in the Alps (Holtmeier 2003). Nowadays, land abandonment is the most dominant driver for the losses of woodland clearings in subalpine altitudes (Gehrig-Fasel et al. 2007; Kyriazopoulos et al. 2017).

7. Conclusions and outlook

In summary, this thesis demonstrates that climate change is markedly impacting Alpine aquatic ecosystems. Several lakes have already passed climate-related thresholds associated with changes in habitat availability and thermal stratification. Furthermore, the response of the mountain lakes to global warming was amplified by local nutrient inputs and atmospheric fertilization resulting in sharply increasing total algae biomass.

The rising water temperatures clearly modified the structure of the primary producer communities. Within the phytoplankton the stronger stratification resulted in competitive advantage of small centric, needle-shaped and colony-forming diatom species, dinoflagllates and *Crytophyta*. Within the periphyton fragilarioid diatoms shifts from cold adapted to more thermophile species have been observed. Furthermore, the establishment of macrophytes offered new habitat for epiphytic diatom species.

Both, phytoplankton and periphytic algae play a crucial role in mountain lake systems by forming the basis of the aquatic food web and transferring biomass to higher trophic levels. Further research on primary producer-herbivore interactions and on the cascade effects on predators is urgently needed to predict the consequences of the rapidly changing environments on the aquatic systems and their ecosystem services. Multi-trophic studies should be carried out to understand (1) how shifts within the phytoplankton communities and the periphytic algae bottom-up control the zooplankton communities and the benthic fauna (e.g. macroinvertebrates, molluscs), (2) the role of altered consumer activities (e.g., overwintering zooplankton, fish stocking) by top-down controlling primary producers and (3) how altered trophic interaction impact community responses to climate change.

Furthermore, the role of climate-induced catchment modification in the response of the mountain lakes to climate change should be studied more closely. Therefore, (4) remote sensing data about glacier retreat, rock slope failures, debris flows, land-use changes, climate-related upward shifts of the treeline, catchment greening and hydromorphological alterations of the lakes should be evaluated for better interpreting the history of the lakes archieved in the lake sediments.

8. Publication List

8.1 Peer-reviewed publications included in this thesis

Hofmann AM, Geist J, Nowotny L, Raeder U (2020) Depth-distribution of lake benthic diatom assemblages in relation to light availability and substrate: implications for paleolimnological studies. Journal of Paleolimnology 64 (3): 315-334.

Kuefner K, Hofmann AM, Ossyssek S, Dubois N, Geist J, Raeder U (2020) Composition of highly diverse diatom community shifts as response to climate change: A down-core study of 23 central European mountain lakes. Ecological Indicators 117: 106590.

Hofmann AM, Kuefner W, Mayr C, Dubois N, Geist J, Raeder U (2021) Unravelling climate change impacts from other anthropogenic influences: a multi-proxy down-core study of a small subalpine lake (Oberer Soiernsee, Northern Alps, Germany). Hydrobiologia, 848 (18), 4285-4309.

8.2 Selected oral contribution to this thesis

Hofmann AH, Ossyssek S, Kuefner W (2019): Verschiebung der Primärproduzenten in Bergseen als Indikator des Klimawandels. Workshop Bergseen im Klimawandel, June 27 2019. Technical University Munich, Iffeldof, Germany.

Hofmann AH, Raeder U (2018): Diatoms in subalpine lake sediments - Indicators for climate induced lake level changes? IPA-IAL 2018 Joint Meeting. June 18-21. Stockholm University, Sweden.

Hofmann AH, Geist J, Raeder U (2017): Tiefenverteilungsmuster benthischer Diatomeen in den subalpinen Soiernseen (Karwendel). 33. Annual Meeting of the German Society for Limnology (DGL) und oft the Societas Internationalis Limnologiae (SIL). September 25-29 2015. Brandenburg University of Technology Cottbus-Senftenberg, Germany.

8.3 Selected poster presentations related to this thesis

Hofmann AH, Geist J, Raeder U (2018): Subfossil diatom–assemblages in subalpine lake sediments as an indicator of climate-driven water-level changes. 34. Annual Meeting of the German Society for Limnology (DGL) und of the Societas Internationalis Limnologiae (SIL). September 10-24 2018. Hochschule Rhein-Waal, Kamp-Lintfort, Germany.

Hofmann AH, Ossyssek S, Kuefner W, Raeder U (2017): Mountain Lakes and Climate Change. Central European Diatom Meeting. March 22-25 2017. Prague, Czech Republic.

Hofmann AH, Ossyssek S, Kuefner W, Raeder U (2017): Bergseen im Klimawandel. 32. Annual Meeting of the German Society for Limnology (DGL) und of the Societas Internationalis Limnologiae (SIL). September 26-30 2017. BOKU Wien, Austria.

9. Authors contribution

Chapter 3: Depth-distribution of lake benthic diatom assemblages in relation to light availability and substrate: implications for paleolimnological studies

Andrea M. Hofmann (AH) primarily conceived this study with critical revision of Jürgen Geist (JG) and Uta Raeder (UR). Hydrophysical and hydrochemical characterization of the lakes was carried out by AH and the graduate student Joachim Hilber. Diatom sampling strategy was designed by AH. Sample preparation was done by AH and Lena Nowotny (LN). Diatom analyses were realized by AH and LN under supervision of AH. Phytoplankton analyses were carried out by LN and the graduate student Julia Mayr under supervision of UR and AH. The manuscript was drafted and finalized by AH with continuous input and revision by JG and UR.

Chapter 4: Unravelling climate change impacts from other anthropogenic influences: a multi-proxy down-core study of a small subalpine lake (Oberer Soiernsee, Northern Alps, Germany)

The study was primarily designed by AH with conceptual input of Christoph Mayr, JG and UR. Sediment core sampling and sample preparation were carried out by AH. Sediment dating was done by Nathalie Dubois (ND) at the Swiss Federal Institute of Aquatic Science and Technology, Departement Surface Waters EAWAG in Dübendorf, CH. Microscopic analyses were realized by AH. Pigment analyses were performed by AH and Wolfgang Kuefner (WK). Stable isotope analyses were carried out by CM at the FAU Erlangen. The interpretation of the data was realized by AH in consultation with ND (core chronology) and CM (stable isotopes). The manuscript was drafted and improved by AH, under continuous feedback of CM, JG and UR.

Chapter 5: Composition of highly diverse diatom community shifts as response to climate change: A down-core study of 23 central European mountain lakes

The study was equally conceived by AH and WK, in consultation with UR and JG. Basic research and preliminary studies were carried out by AH. Hydrochemical and hydrophysical characterization of the lakes were performed by AH and Stefan Ossyssek. Sediment core sampling and preparation were realized by AH and WK. Sediment dating was done and interpreted by ND. Microscopic analyses were carried out by AH and WK. Statistical analyses and graphics were performed by WK. Data interpretation was equally done by AH and WK. The manuscript was equally drafted and finalized by AH and WK, continuously supervised and improved by JG and UR.

10. Acknowledgements

I would like to thank the Bavarian State Ministry of the Environment and Consumer Protection for funding the project “Impact of Climate Change on Bavarian mountain lakes” (Grant number TKP01KPB-70807), especially Prof. Tanja Gschlößl for her continuous appreciative feedback.

There are many to whom I owe thanks for their support with the finalization of my PhD thesis. I would like to thank my supervisor Prof. Dr. Jürgen Geist for his constructive feedback, his organizing support and his immediate help when questions arose. My special gratitude to my advisor Dr. Uta Raeder for her constant support troughout my time at the Limnological Station, for her tireless supervision and her persistent encouragement. My sincerely thanks go to my mentor Dr. Christoph Mayr for his valuable advice, for his assistance with the more complex core samplings and for his guidance during stable isotope data analyses.

Throughout the course of my research, I had a lot of support from colleagues and students. Special thanks are due to Stefan Ossyssek for sharing the journey of this project from the beginning, for the scientific exchange, and for his assistance in R. Thanks a lot, Stefan! Furthermore, I would like to thank Wolfgang Kuefner for the shared time in laboratory, for the constructive collaboration on manuscript three, and his open ear for questions regarding C2 and “the other computer”. Thanks, Wolfi! Sincere thanks go to Joachim Hilber, Lena Novotny, and Julia Mayr for providing valuable raw data for this thesis. I would like to thank Markus Heinrichs for his helpful comments on the first manuscript. I thank Pia Scherer and Josua Sellmaier for proofreading parts of this thesis and Samuel Sellmaier for formatting support. Furthermore, I am thankful to Petra Werner, Marco Cantonati and Horst Lange-Bertalot for help identifying single diatom taxa. I am grateful to Pascal Rüenzi and Alfred Lück for dating the sediments, to Nadja Schlieder for assistance in the isotope laboratory and to Schteffi Rüegg, Severin Sebald and Karin Kronseder for scientific diving. I would like to thank Pierre Manthe, Bettina Heigl, Christina Aulehner and Emanuel Karl for assistance in the field and data acquisition. Finally, I would like to express my special thanks to my colleagues and friends Simon Baier, Dr. Franzi Bauer, Dr. Tine Fritz, Dr. Nico Cortis, Dr. Markus Hoffmann, Dr. Basti Lenz, Dr. Pia Scherer, Dr. Schteffi Rüegg, and Joachim Ruber for the good time at the Limnological Field Station, for the motivation and for the respectful working atmosphere.

My deepest thanks are addressed to my sons Josua, Samuel and Benjamin for their patience and their love and to my mother for her tireless and unwavering support and for always believing in me.

11. Cited literature

Adamczuk M, Pawlik-Skowrońska B, Solis M (2020) Do anthropogenic hydrological alterations in shallow lakes affect the dynamics of phytoplankton? Ecological Indicators 114: 106312

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

Adrian R, O'Reilly CM, Zagarese H, Baines SB, Hessen DO, Keller W, Livingstone DM, Sommaruga R, Straile D, Van Donk E, Weyhenmeyer GA, Winder M (2009) Lakes as sentinels of climate change. Limnology and Oceanography 54: 2283–2297

Algarte VM, Dunck B, Leandrini JA, Rodrigues L (2016) Periphytic diatom ecological guilds in floodplain: Ten years after dam. Ecological Indicators 69: 407–414

Althouse B, Higgins S, Zanden MJV (2014) Benthic and planktonic primary production along a nutrient gradient in Green Bay, Lake Michigan, USA. Freshwater Science 33: 487-498

Anderson NJ, Foy RH, Engstrom DR, Rippey B, Alamgir F (2012) Climate forcing of diatom productivity in a lowland, eutrophic lake: White Lough revisited. Freshwater Biology 57: 2030–2043

Antoniades D, Douglas MSV, Smol JP (2005) Quantitative estimates of recent environmental changes in the Canadian High Arctic inferred diatoms in lake and pond sediments. Journal of Palaeolimnology 33: 349 – 360

Apollo M, Andreychouk V, Bhattarai SS (2018) Short-Term Impacts of Livestock Grazing on Vegetation and Track Formation in a High Mountain Environment: A Case Study from the Himalayan Miyar Valley (India). Sustainability 10: 1-17

Appleby PG (2001) Chronostratigraphic techniques in recent sediments. In: Last WM, Smol JP (eds) Tracking environmental change using lake sediments. Kluwer Academic Publisher, Dordrecht, Netherlands, pp. 171-203

Appleby PG, Oldfield F (1978) The calculation of ^{210}Pb dates assuming a constant rate of unsupported ^{210}Pb to the sediment. Catena 5: 1-8

Arnaud F, Pulenard J, Giguet-Covex C, Wilhelm B, Révillon S, Jenny J-P, Revel M, Enters D, Bajard M, Fouinat L, Doyen E, Simonneau A, Pignol C, Chapron E, Vannière B, Sabatier P (2016) Erosion under climate and human pressures: An alpine lake sediment perspective. Quaternary Science Reviews 152: 1–18

Avnimelech Y, Ritvo G, Meijer LE, Kochba M (2001) Water content, organic carbon and dry bulk density in flooded sediments. Aquacultural Engineering 25: 25-33

Bätzing W (2015) Die Alpen Geschichte und Zukunft einer europäischen Kulturlandschaft. C.H. Beck Verlag, Munich, Germany

Bard A, Renard B, Lang M (2012) Observed Trends in the hydrologic regime of Alpine catchments. Houille Blanche-Revue Internationale De L Eau 1: 38-43

Barker P, Fontes JC, Gasse F, Druart J-C (1994) Experimental dissolution of diatom silica in concentrated salt solutions and implications for paleoenvironmental reconstruction. Limnology and Oceanography 39: 99-110

Battarbee RW, Jones VJ, Flower RJ, Cameron NG, Bennion H, Carvalho L, Juggins S (2001) Diatoms. In: Smol JP, Birks HJB, Last WM (eds) Tracking environmental change using lake sediments. Volume 3: Terrestrial, algal and siliceous indicators. Kluwer Academic Publishers, Netherlands, pp 155-202

Battarbee RW, Charles DF, Bigler C, Cumming BF, Renberg I (2010) Diatoms as indicators of lake-water acidity. In: Smol JP, Stoermer EF (eds) The diatoms: applications for the environmental and earth sciences. Cambridge University Press, Cambridge, pp 98–121

Bayerisches Landesamt für Statistik: https://www.statistik.bayern.de/statistik/wirtschaft_handel/tourismus/index.html (aufgerufen am 28.6.20)

Becker R, Blindow I, Doege A, Franke T, Gregor T, Hamann U, Jäger D, Jorda C, Kabus T, Korsch H, Korte E, Kusber W-H, Pätzold F, Raabe U, Schubert H, Teppke M, van de Weyer K, Wolff P (2016) Beschreibung der Characeea-Arten Deutschlands. In: Arbeitsgruppe Characeen Deutschlands (eds) Armleuchteralgen Die Characeen Deutschlands. Springer-Verlag, Berlin Heidelberg

Beniston M, Diaz HF, Bradley RS (1997) Climatic change at high elevation sites; a review. Climatic Change **36**: 233–251

Beniston M (2005) Mountain climates and climatic change: an overview of processes focusing on the European Alps. Pure and Applied Geophysics 162: 1587-1606

Beniston M (2006) Mountain weather and climate: A general overview and a focus on climatic change in the Alps. Hydrobiologia 562: 3–16

Beniston M, Farinotti D, Stoffel M, Andreassen LM, Coppola E, Eckert N, Fantini A, Giacona F, Hauck C, Huss M, Huwald H, Lehning M, López-Moreno J-I, Magnusson J, Marty C, Morán-Tejéda E, Morin S, Naaim M, Provenzale A, Rabatel A, Six D, Stötter J, Strasser U, Terzago S, Vincent C (2018) The European mountain cryosphere: A review of past, current and future issues. The Cryosphere 12: 759-794

Bennet KD (1996) Determination of the number of zones in a biostratigraphical sequence. New Phytologist 132: 155-170

Bennion H, Sayer C, Tibby T, Carrick H (2010) Diatoms as indicators of environmental change in shallow lakes. In: Smol JP, Stoermer EF (eds) The diatoms: applications for the environmental and earth sciences. Cambridge University Press, Cambridge, pp 152–173

Bergstrom A-K, Jansson M (2006) Atmospheric nitrogen deposition has caused nitrogen enrichment and eutrophication of lakes in the northern hemisphere. Global Change Biology 12: 635–643

Berthon V, Alric B, Rimet F, Perga M-E (2014) Sensitivity and responses of diatoms to climate warming in lakes heavily influenced by humans. Freshwater Biology 59: 1755–1767

Bigler C, Hall RI (2003) Diatoms as quantitative indicators of July temperature: a validation attempt at century-scale with meteorological data from northern Sweden. Palaeogeography Palaeoclimatology Palaeoecology 189: 147-160

Birks HH, Birks HJB (2006) Multi-proxy studies in paleolimnology. Vegetation History and Archaeobotany 15: 235-251

Boeff KA, Strock KE, Saros JE (2016) Evaluating planktonic diatom response to climate change across three lakes with differing morphometry. Journal of Paleolimology 56: 33–47

Bogard MJ, del Giorgio PA, Boutet L, Garcia Chaves MC, Prairie YT, Merante A, Derry AM (2014) Oxic water column methanogenesis as a major component of aquatic CH_4 fluxes. Nature Communication 5, 5350

Bogataj LK (2007) How will the Alps Respond to Climate Change? Scenarios for the Future of Alpine Water. Alpine Space - Man and Environment 3: 43–51

Bornette G, Puijalon S (2011) Response of aquatic plants to abiotic factors: a review. Aquatic Science 73: 1-14

Bouchard G, Gajewski K, Hamilton PB (2004) Freshwater diatom biogeography in the Canadian Arctic Archipelago. Journal of Biogeography 31: 1955–1973

Boylen CW, Sheldon RB (1976) Submerged macrophytes: growth under winter ice cover. Science 194: 841-842

Bracht-Flyr B, Fritz SC (2016) Combining lake core records with the limnologic model DYRESM-CAEDYM to evaluate lake response during the Little Ice Age and Medieval Climate Anomaly. Journal of Paleolimology 56: 79–92

Braig E, Mayr C, Kirchner G, Hofmann A, Raeder U, Melzer A (2013) Fifty years of eutrophication and lake restoration reflected in sedimentary carbon and nitrogen isotopes of a small, hardwater lake (South Germany). Journal of Limnology 72: 262–279

Brand WA, Coplen TB, Vogl J, Rosner M, Prohaska T (2014) Assessment of international reference materials for isotope-ratio analysis (IUPAC Technical Report). IUPA Technical Report. Pure and Applied Chemistry 86: 425–467

Buchaca T, Catalan J (2007) Factors influencing the variability of pigments in the surface sediments of mountain lakes. Freshwater Biology 52: 1365–1379

Buchaca T, Catalan J (2008) On the contribution of phytoplankton and benthic biofilms to the sediment record of marker pigments in high mountain lakes. Journal of Paleolimology 40: 369–383

Burkholder JM (1996) Interactions of benthic algae with their substrata. In: Stevenson RJ, Bothwell ML, Lowe RL (eds): Algal ecology, freshwater benthic ecosystems. Academic Press San Diego, California, pp 253-297

Butcher JB, Nover D, Johnson TE, Clark CM (2015) Sensitivity of lake thermal and mixing dynamics to climate change. Climate Change 129: 295–305

Cantonati M, Lowe RL (2014) Lake benthic algae: toward an understanding of their ecology. Freshwater Science 33: 475-486

Cantonati M, Scola S, Angeli N, Guella G, Frassanito R (2009) Environmental controls of epilithic diatom depth-distribution in an oligotrophic lake characterized by marked water-level fluctuations. European Journal of Phycology

44(1): 15-29

Catalan J, Pla S, Rieradevall M, Felip M, Ventura M, Buchaca T, Camarero L, Brancelj A, Appleby PG, Lami A, Grytnes JA, Agustí-Panareda A, Thompson R (2002) Lake Redó ecosystem response to an increasing warming in the Pyrenees during the twentieth century. Journal of Paleolimnology 28: 129-145

Catalan J, Pla-Rabés S, Wolfe AP, Smol JP, Rühland KM, Anderson NJ, Kopácek J, Stuchlík E, Schmidt R, Koinig KA, Camarero L, Flower R., Heiri O, Kamenik C, Korhola A, Laevitt PR, Psenner R, Renberg I (2013) Global change revealed by palaeolimnological records from remote lakes: a review. Journal of Paleolimology 49: 513-535

Ceppi P, Scherrer SC, Fischer AM, Appenzeller C (2012) Revisiting Swiss temperature trends 1959–2008. International Journal of Climatology 32: 203-213

Chen G, Selbie DT, Griffiths K, Sweetman JN, Botrel M, Taranu ZE, Knops S, Bondy J, Michelutti N, Smol JP, Gregory-Eaves I (2014) Proximity to ice fields and lake depth as modulators of paleoclimate records: a regional study from southwest Yukon, Canada. Journal of Paleolimnology 52: 185-200

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18: 117-143

Cremer H, Melles M, Wagner B (2001) Holocene climate changes reflected in a diatom succession from Basaltsø, East Greenland. Canadian Journal of Botany 79: 649–656

Crouzat E, Mouchet M, Turkelboom F, Byczek C, Meersmann J, Berger F, Verkerk PJ, Lavorel S (2015) Assessing bundles of ecosystem services from regional to landscape scale: insights from the French Alps. Journal of Applied Ecology 52: 1145-1155

Daufrasne M, Lengfellner K, Sommer U (2009) Global warming benefits the small in aquatic ecosystems. PNAS 106: 12788-12793

de Jong R, Kamenik C, Westover K, Grosjean M (2013) A chrysophyte stomatocyst-based reconstruction of cold-season air temperature from Alpine Lake Silvaplana (AD 1500–2003); methods and concepts for quantitative inferences. Journal of Paleolimology 50: 519-533

DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. Geochimica et Cosmochimica Acta 42: 495-506

Diehl S, Berger S, Ptacnik R, Wild A (2002) Phytoplankton, light, and nutrients in a gradient of mixing depths: field experiments. Ecology 83: 399–411

Dietrich A, Krautblatter M (2016) Evidence for enhanced debris-flow activity in the Northern Calcareous Alps since the 1980s (Plansee, Austria). Geomorphology 287: 144-158

Diffenbaugh NS, Singh D, Mankin JS, Horton DE, Swain DL, Touma D, Charland A, Liu Y, Haugen M, Tsiang M, Rajaratnam B (2017) Quantifying the influence of global warming on unprecedented extreme climate events. PNAS 114: 4881–4886

Dobrowski SZ, Abatzoglou JT, Greenberg JA, Schladow SG (2009) How much influence does landscape-scale physiography have on air temperature in a mountain environment. Agricultural and Forest Meteorology 149: 1751-1758

Dörr E, Lippert W (2011) Flora des Allgäus und seiner Umgebung. IHW-Verlag, Eching, Germany, 680 pp.

Dokulil MT (2013) Impact of climate warming on European inland waters. Inland Waters 4: 27-40

Dodds WK (2003) The role of periphyton in phosphorus retention in shallow freshwater aquatic systems. Journal of Phycology 39: 840–849

Douglas MSV, Smol JP, Blake W Jr. (1994) Marked post-18th century environmental change in high-arctic ecosystems. Science 266: 416-419

Douglas MSV, Smol JP (1995) Periphytic diatom assemblages from high arctic ponds. Journal of Phycology 31: 60-69

Douglas MSV, Smol JP (2010) Freshwater diatoms as indicators of environmental change in the High Arctic. In: Stoermer EF, Smol JP (eds) The Diatoms: Applications for the Environmental and Earth Sciences. Cambridge University Press, Cambridge, pp. 249-266

Douglas MSV, Hamilton PB, Pienitz R (2004) Algal indicators of environmental change in Arctic and Antarctic lakes and ponds. In: Pienitz R., Douglas MSV, J.P. Smol (eds) Long-term environmental change in Arctic and Antarctic Lakes. Kluwer Academic Publishers, Dordrecht, The Netherlands: 117-147

Doyle SA, Saros JE, Williamson CE (2005) Interactive effects of temperature and nutrient limitation on the response of alpine phytoplankton growth to ultraviolet radiation. Limnology and Oceanography 50: 1362–1367

Dubois N, Saulner-Talbot E, Mills K, Gell P, Battarbee RW, Bennion H, Chawchai S, Dong X, Francus P, Flower R, Gomes DF, Gregory-Eaves I, Humane S, Kattel G, Jenny JP, Langdon P, Massaferro J, McGowan S, Mikomägi A, Thi Minh Ngoc N, Sandaruwan Ratnayake A, Reid M, Rose N, Saros J, Schillereff D, Tolotti M, Valero-Garcés B (2017) First human impacts and responses of aquatic systems: A review of palaeolimnological records from around the world. The Anthropocene Review 5: 28-68

DWD (Deutscher Wetterdienst), Schneefernerhaus: meteorological data accessed on 20.01.2021 https://schneefernerhaus.de/daten/monatsrueckblicke/archiv/

DWD (Deutscher Wetterdienst), Hohenpeißenberg: time series of nitrogen oxide concentrations, data accessed on 20.01.2021 https://www.dwd.de/DE/forschung/atmosphaerenbeob/zusammensetzung_atmosphaere/spurengase/inh_nav/nox.html?nn=19216

Dupire S, Curt T, Bigot S (2017) Spatio-temporal trends in fire weather in the French Alps. Science of the Total Environment 595: 801-817

Elkin C, Gutiérrez AG, Leuzinger S, Manusch C, Temperli C, Rasche L, Bugmann H (2013) A 2 °C warmer world is not safe for ecosystem services in the European Alps. Global Change Biology 19: 1827-1840

Engardt M, Simpson D, Schwikowski M, Granat L (2017) Deposition of sulphur and nitrogen in Europe 1900–2050. Model calculations and comparison to historical observations. Tellus B: Chemical and Physical Meteorology 69: 1

Farquar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. Annual Review of Physiology and Plant Molecular Biology 40: 503-537

Feret LE, Bouchez A, Rimet F (2017) Benthic diatom communities in high altitude lakes: a large scale study in the French Alps. Annales de Limnologie –International Journal of Limnology 53: 411-423

Fernández-Aláez C, Fernández-Aláez M, García-Criado F, García-Girón J (2016) Environmental drivers of aquatic macrophyte assemblages in ponds along an altitudinal gradient. Hydrobiologia 812: 79-98

Finlay JC, Kendall C (2007) Stable isotope tracing of temporal and spatial variability in organic matter sources to freshwater ecosystems. In: Michener R, Lajtha K (eds) Stable isotopes in ecology and environmental science. Blackwell, Oxford, pp 283–333

Fischer L, Purves RS, Huggel C, Noetzli J, Haeberli W (2012) On the influence of topographic, geological and cryospheric factors on rock avalanches and rockfalls in high-mountain areas. Natural Hazards Earth System Science 12: 241-254

Fjellheim A, Raddum GG, Vandvik V, Lniceanu C, Boggero A, Brancelj A, Stuchlik E et al. (2009) Diversity and distribution patterns of benthic invertebrates along alpine gradients. A study of remote European freshwater lakes. Advances in Limnology 62: 167–190

Flury C, Huber R, Tasser E (2013) Future of mountain agriculture in the Alps. In: Mann S (ed) The future of mountain agriculture. Springer-Verlag Berlin Heidelberg

Fogel ML, Cifuentes LA (1993) Isotope fractionation during primary production. In: Engel MH, Macko SA (eds) Organic geochemistry. Plenum Press, NY, pp 73–98

Forehead HI, Thompson PA (2010) Microbial communities of subtidal shallow sandy sediments change with depth and wave disturbance, but nutrient exchanges remain similar. Marine Ecology Progress Series 414: 11–26

Fowler D, Coyle M, Skiba U et al. (2013): The global nitrogen cycle in the tenty-first century. Philosophical Transactions of the Royal Society B 368: 20130164

Frei E, Bodin J, Walther G-R (2010) Plant species' range shifts in mountainous areas-all uphill from here? Botanica Helvetica 120: 117-128

Fritz SC (2008) Deciphering climatic history from lake sediments. Journal of Paleolimnology 39: 5–16

Furet JE, Benson-Evans K (1982) An evaluation of the time required to obtain complete sedimentation of fixed algae particles prior to enumeration. British Phycological Journal 17: 253-258

Garcia E, Ballesteros E, Camarero L, Delgado O, Palau A, Riera JL, Catalan J (1994) Macrophytes from lakes in the eastern Pyrenees: community composition and ordination in relation to environmental factors. Freshwater Biology 32: 73-81

Galloway JN, Dentener FJ, Capone DG et al. (2008) Nitrogen Cycles: Past, Present, and Future. Boegeochemistry 70: 153-226

Gardner EM, McKnight DM, Lewis Jr WM, Miller MP (2008) Effects of Nutrient Enrichment on Phytoplankton in an Alpine Lake, Colorado, U.S.A. Arctic, Antarctic, and Alpine Research 40: 55-64

Gehrig-Fasel J, Guisan A, Zimmermann NE (2007) Tree line shifts in the Swiss Alps: Climate change or land abandonment? Journal of Vegetation Science 18: 571-582

Gerten D, Adrian R (2002) Effects of Climate Warming, North Atlantic Oscillation, and El NiÒo-Southern Oscillation on Thermal Conditions and Plankton Dynamics in Northern Hemispheric Lakes. The Scientific World Journal 2: 586-606

Giguet-Covex C, Arnaud F, Enters D, Poulenard J, Millet L, Francus P, David F, Pierre-Jérôme R, Wilhelm B, Delannoy J-J (2012) Frequency and intensity of high-altitude floods over the last 3.5 ka in northwestern French Alps (Lake Anterne). Quaternary Research 77: 12–22

Giguet-Covex C, Arnauld F, Poulenard J, Disnar J-R, Delhon C, Francus P, David F, Enters D, Rey P-J, Delannoy J-J (2011) Changes in erosion patterns during the Holocene in a cur- rently treeless subalpine catchment inferred from Lake sediment geochemistry (lake Anterne, 2063 m a.s.l., NW French Alps): the role of climate and human activities. Holocene 21: 651–665

Gottfried M, Pauli H, Futschik A, Akhalkatsi M, Barančok P, Alonso JLB, Coldea G, Dick J, Erschbamer B, Fernández Calzado MR, Kazakis G et al. (2012) Continent-wide response of mountain vegetation to climate change. Nature Climate Change 2: 111–115

Grace J, Berninger F, Nagy L (2002) Impacts of climate change on the tree line. Annals of Botany 90: 537-544

Grenier M, Lavoie I, Rousseau A, Campeau S (2010) Defining ecological thresholds to determine class boundaries in a bioassessment tool: The case of the Eastern Canadian Diatom Index (IDEC). Ecological Indicators 10: 980-989

Griffiths K, Michelutti N, Sugar M, Douglas MSV, Smol JP (2017) Ice-cover is the principal driver of ecological change in High Arctic lakes and ponds. PLoS ONE 12: e0172989

Guiry MD, Guiry GM (2019) AlgaeBase. World-wide electronic publication, National University of Ireland, Galway

Gu B (2009) Variations and controls of nitrogen stable isotopes in particulate organic matter of lakes. Oecologia 160: 421–431

Gu B, Schelske CL, Brenner M (1996) Relationship between sediment and plankton isotope ratios (δ^{13}C and δ^{15}N) and primary productivity in Florida lakes. Canadian Journal of Fisheries and Aquatic Science 53: 875–883

Guilizzoni P, Marchetto A, Lami A, Gerli S, Musazzi S (2011) Use of sedimentary pigments to infer past phosphorus concentration in lakes. Journal of Paleolimnology 45: 433–445

Gushulak CAC, Laird KR, Bennett JR, Cumming BF (2017) Water depth is a strong driver of intra-lake diatom distributions in a small boreal lake. Journal of Paleolimnology 58: 231–241

Hall RI, Smol JP (2010) Diatoms as indicators of lake eutrophication. In Stoermer EF, Smol JP (eds) The Diatoms: Applications for the Environmental and Earth Sciences. Cambridge University Press, Cambridge: 122-151

Hammer Ø, Harper DAT (2006) Paleontological data analysis. Blackwell, Malden

Hasdenteufel P, Streifinger M W (2012) Wasserweg Lautersee.Geolehrpfad mit fünf Stelltafeln. Mittenwald

Haslinger K, Blöschl G (2017) Space-time pattern of meteorological drought events in the European Greater Alpine Region over the past 210 years. Water Resources Research 53: 9807-9823

Hastings MG, Jarvis JC, Steig EJ (2009) Anthropogenic impacts on nitrogen isotopes of ice-core nitrate. Science 324, 1288

Hausmann S, Lotter AF (2001) Morphological variation within the diatom taxon *Cyclotella comensis* and its importance for quantitative temperature reconstructions. Freshwater Biology 46: 1323-1333

Hill WR (1996) Effects of light. In: Stevenson RJ, Bothwell ML, Lowe RL (eds) Algal ecology, Freshwater benthic ecosystems. Academic Press, San Diego California, pp 121-148

Hofmann G (1999) Trophiebewertung von Seen anhand von Aufwuchsditomeen. In: v Tümpling W, Friedrich G, (eds) Biologische Gewässeruntersuchung, Gustav Fischer Verlag, Jena, pp 319- 333

Hofmann G, Werum M, Lange-Bertalot H (2013) Diatomeen im Süßwasser-Benthos von Mitteleuropa. 2. Auflage. Koeltz Scientific Books, Königstein

Hofmann H, Lorke A, Peeters F (2008) Temporal scales of water-level fluctuations in lakes and their ecological implications. Hydrobiologia 613: 85–96

Hock R, Rasul G, Adler C, Cáceres B, Gruber S et al. (2019) High Mountain Areas. In: IPCC Special Report on the Ocean and Cryosphere in a Changing Climate. The Intergovernmental Panel on Climate Change (IPCC)

Hollander DJ, McKenzie JA (1991) CO_2 control on carbon- isotope fractionation during aqueous photosynthesis: a paleo-pCO_2 barometer. Geology 19: 929–932

Hollander DJ, Smith MA (2001) Microbially mediated carbon cycling as a control on the $\delta^{13}C$ of sedimentary carbon in eutrophic Lake Mendota (USA): new models for interpreting isotopic excursions in the sedimentary record. Geochimica et Cosmochimica Acta 65: 4321–4337

Holtgrieve GW, Schindler DE, Hobbs WO, Leavitt PR, Ward EJ, Bunting L, Chen G, Finney BP, Gregory-Eaves I, Holmgren S, Lisac MJ, Lisi PJ, Nydick K, Rogers LA, Saros JE, Selbie DT, Shapley MD, Walsh PB, Wolfe AP (2011) A coherent signature of anthropogenic nitrogen deposition to watersheds of the Northern Hemisphere. Science 334: 1545–1548

Holtmeier F-K (2003) Mountain timberlines: Ecology, patchiness, and dynamics. Kluwer Academic Publishers, Dordrecht, NL

Houk, V, Klee R, Tanaka H (2010). Atlas of freshwater centric diatoms with a brief key and descriptions. Part III. Stephanodiscaceae A. Cyclotella, Tertiarius, Discostella. Fottea. Praha: Czech Phycological Society

Houk V, Klee R, Tanaka H (2014) Atlas of Freshwater centric diatoms with a brief key and descriptions. Part IV. Stephanodiscaceae B. Stephanodisus, Cyclostephanus, Pliocaenicus, Hemistephanos, Stephanocistis, Mesodictyon, Spicaticribia. Fottea. Praha: Czech Phycological Society

Huber-Pestalozzi G (1938-1982) Das Phytoplankton des Süßwassers. Schweizbart´sche Verlagsbuchhandlung Stuttgart

Huisman J, van Oostveen P, Weissing FJ (1999) Species dynamics in phytoplankton blooms: incomplete mixing and competition for light. The American Naturalist 154: 46-68

Huggel C, Allen S, Deline P, Fischer L, Noetzli J, Ravanel L (2012) Ice thawing, mountains falling–are alpine rock slope failures increasing? Geology Today 28: 98-104

Huss M (2012) Extrapolating glacier mass balance to the mountain-range scale: the European Alps 1900–2100. The Cryosphere 6: 713-727

Huss M, Bookhagen B, Huggel C, Jacobsen D, Bradley RS, Clague JJ, Vuille M, Buytaert W, Cayan DR, Greenwood G, Mark BG, Milner MW, Weingartner R, Winder M (2017) Toward mountains without permanent snow and ice. Earth's Future 5: 418–435

Hustedt F (1930) Bacillariophyta (Diatomeae). In: Pascher A (ed) Die Subwasser Flora Mitteleuropas 10. Gustav Fischer, Jena

Ilyashuk EA, Heiri O, Ilyashuk BP, Koinig KA, Psenner R (2018) The Little Ice Age signature in a 700-year high-resolution chironomid record of summer temperatures in the Central Eastern Alps. Climate dynamics 52: 6953-6967

IPCC (2014) Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Core Writing Team Pachauri RK and Meyer LS (eds). IPCC, Geneva, Switzerland, 151 pp

Jackson DA (1993) Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. Ecology 74: 2204-2214

Jacobson PC, Hansen GJA, Bethke BJ, Cross TK (2017) Disentangling the effects of a century of eutrophication and climate warming on freshwater lake fish assemblages. PLoS ONE 12: e0182667

Jacquemin C, Bertrand C, Oursel B, Thorel M, Franquet E, Cavalli L (2018) Growth rate of alpine phytoplankton assemblages from contrasting watersheds and N-deposition regimes exposed to nitrogen and phosphorus enrichments. Freshwater Biology 63: 1326–1339

Jansson M, Jonsson A, Andersson A, Karlsson J (2010) Biomass and structure of planktonic communities along an air temperature gradient in subarctic Sweden. Freshwater Biology 55: 691-700

Jenicek M, Seibert J, Staudinger M (2018) Modeling of Future Changes in Seasonal Snowpack and Impacts on Summer Low Flows in Alpine Catchments. Water Resources Research 54: 538-556

Jeppesen E, Moss B, Bennion H, Carvalho L, DeMeester L, Feuchtmayr H, Friberg N, Gessner MO, Hefting M, Lauridsen TL, Liboriussen L, Malmquist HJ, May L, Meerhoff M, Olafsson JS, Soons MB, Verhoeven JTA (2010) Interaction of Climate Change and Eutrophication. In: Kernan M, Battarbee R, Moss B (eds) Climate Change Impacts on Freshwater Ecosystems. Blackwell Publishing Ltd.

Joynt EH III, Wolfe AP (2001) Paleoenvironmental inference models from sediment diatom assemblages in Baffin Island lakes (Nunavut, Canada) and reconstruction of summer water temperature. Canadian Journal of Fisheries and Aquatic Science 58: 1222–1243

Juggins S (2007) C2 User Guide. Software for Ecological and Paleoecological Data Analysis and Visualisation. University of Newcastle, Newcastle upon Tyne, UK

Juggins S, Anderson NJ, Hobbs JMR, Heathcote AJ (2013) Reconstructing epilimnetic total phosphorus using diatoms: statistical and ecological constraints. Journal of Paleolimnology 49: 373–390

Juggins S (2018) Package 'rioja'. CRAN R-Project, 1-58

Kaiser A (2009) Origin of polluted air masses in the Alps. An overview and first results for MONARPOP. Environmental Pollution 157: 3232-3237

Kamenik C, Koinig KA, Schmidt R, Appleby PG, Dearing J, Lami A, Thompson R, Psenner R. (2000) Eight hundred years of environmental changes in a high alpine lake (Gossenköllesee, Tyrol) inferred from sediment records. Journal of Limnology 59: 43–52

Karst-Riddoch TL, Pisaric MFJ, Smol JP (2005) Diatom responses to 20th century climate-related environmental changes in high-elevation mountain lakes of the northern Canadian Cordillera. Journal of Paleolimnology 33: 265–282

Kattel G, Gell P, Perga M-E, Jeppesen E, Grundell R, Weller S, Zawadzki A, Barry L (2015) Tracking a century of change in trophic structure and dynamics in a floodplain wetland: integrating palaeoecological and palaeoisotopic evidence. Freshwater Biology 60: 711-723

Keeley JE, Sandquist DR (1992) Carbon: freshwater plants. Plant Cell Environ 15:1021–1035

Keeling CD, Mook WG, Tans PP (1979) Recent trends in the $^{13}C/^{12}C$ ratio of atmospheric carbon dioxide. Nature 277: 121-122

Kendall C (1998) Tracing Nitrogen Sources and Cycling in Catchments. In: Kendall C, McDonnell JJ (eds) Isotope Tracers in Catchment Hydrology. Elsevier Science, Amsterdam, pp 519–576

Kilham SS, Theriot EC, Fritz SC (1996) Linking planktonic diatoms and climate change in the large lakes of the Yellowstone ecosystem using resource theory. Limnology and Oceanography 41: 1052–1062

Kingsbury MV, Laird KR, Cumming BF (2012) Consistent patterns in diatom assemblages and diversity measures across water-depth gradients from eight Boreal lakes from North-Western Ontario (Canada). Freshwater Biology 57: 1151–1165

Kirchner G (2011) ^{210}Pb as a tool for establishing sediment chronologies: examples of potentials and limitations of conventional dating models. Journal of Environmental Radioactivity 102: 490-494

Kirchner M, Faus-Kessler T, Jakobi G, Levy W et al. (2009) Vertical distribution of organochlorine pesticides in humus along Alpine altitudinal profiles in relation to ambiental parameters. Environmental Pollution 157: 3238-3247

Kirchner M, Faus-Kesseler T, Jakobi G, Leuchner M, Ries L, Scheel H-E, Suppan P (2012) Altitudinal temperature lapse rates in an Alpine valley: trends and the influence of season and weather patterns. Intentional Journal of Climatology 33: 539-555

Kirchner M, Fegg W, Römmelt H, Leuchner M, Ries L, Zimmermann R, Michalke B, Wallasch M, Maguhn J, Faus-Kessler T, Jakobi G (2014) Nitrogen deposition along differently exposed slopes in the Bavarian Alps. Science of the Total Environment. 470–471: 895-906

Kitner M, Poulíčková A (2003) Littoral diatoms as indicators for the eutrophication of shallow lakes. Hydrobiologia 506: 519–524

Knapp S, Gilli A, Anselmetti FS, Krautblatter M, Hajdas I (2018) Multistage Rock-Slope Failures Revealed in Lake Sediments in a Seismically Active Alpine Region (Lake Oeschinen, Switzerland). Journal of Geophysical Research: Earth Surface 123: 658-677

Körner C, Jetz W, Paulsen J, Payne D, Rudmann-Maurer K, Spehn EM (2016) A global inventory of mountains for bio-geographical applications. Alpine Botany 127: 1-15

Kohler A (1978) Methoden der Kartierung von Flora und Vegetation von Süßwasserbiotopen. Landschaft und Stadt 10: 73-85

Koinig KA, Schmidt R, Sommaruga-Wögrath S, Tessadri R, Psenner R (1998) Climate Change as the primary cause for pH shifts in a high alpine lake. Water, Air, and Soil Pollution 104: 167–180

Koinig KA, Kamenik C, Schmidt R, Agustí-Panareda A, Appleby PG, Lami A, Prazakova M, Rose N, Schnell ØA, Tessadri R, Thompson R, Psenner R (2002) Environmental changes in an alpine lake (Gossenköllesee, Austria) over the last two centuries–the influence of air temperature on biological parameters. Journal of Paleolimnology 28: 147-160

Krammer K, Lange-Bertalot H (1986-1991) Bacillariophyciae 1-4. In: Ettl H, Gerloff J, Heynig H, Mollenhauer D (eds) Süßwasserflora von Mitteleuropa. Gustav Fischer Verlag, Stuttgart

Krammer K (1997) Die cymbelloiden Diatomeen. Eine Monographie der weltweit bekannten Taxa, 1-2. Bibliotheca Diatomologica. Cramer, Berlin

Krause W (1997) Charales (Charophyceae). In: Ettl H, Gärtner G, Heying H, Mollenhauer D (eds) Süßewasserflora von Mitteleuropa 18, Gustav Fischer Verlag, Jena

Kuefner W, Hofmann AM, Geist J, Raeder U (2020 b) Evaluating climate change impacts on mountain lakes by applying the new silicification value to paleolimnological samples. Science of the Total Environment 715: 136913

Kuefner W, Ossyssek S, Geist J, Raeder U (2020 a) The silicification value: a novel diatom-based indicator to assess climate change in freshwater habitats. Diatom research 35: 1-16

Kunstmann H, Smiatek G (2015) Wie gut sind regionale Klimamodelle für den Alpenraum und welches zukünftige Klima erwarten wir? Klima-Report Bayern 2015-Klimawandel, Auswirkungen, Anpassungs- und Forschungsaktivitäten. München: Bayerisches Staatsministerium für Umwelt und Verbraucherschutz. pp. 28-29

Kyriazopoulos AP, Skre O, Sarkki S, Wielgolaski FE, Abraham EM, Ficko A (2017) Human-environment dynamics in European treeline ecosystems: a synthesis based on the DPSIR framework. Climate Research 73: 17-29

Laird KR, Kingsbury MV, Cumming BF (2010) Diatom habitats, species diversity and water-depth inference models across surface-sediment transects in Worth Lake, northwest Ontario, Canada. Journal of Paleolimnology 44: 1009–1024

Lami A, Guilizzoni P, Marchetto A (2000) High resolution analysis of fossil pigments, carbon, nitrogen and sulfur in the sediment of eight European Alpine lakes: the MOLAR project. In Lami A, Cameron N, Korhola A (eds) 2000 Paleolimnology and ecosystem dynamics at remote European Alpine lakes. Journal of Limnology 59: 15-28

Lange-Bertalot H (1993) 85 Neue Taxa und über 100 weitere neu definierte Taxa ergänzend zur Süßwasserflora von Mitteleuropa. Vol. 2. Bibliotheca Diatomologica 27, J. Cramer, Berlin/Stuttgart, Germany

Lange-Bertalot H, Krammer K (2000-2003) Diatoms of Europe Vol. 1-4, A.R.G. Ganter Verlag K.G., Rugell

Lange-Bertalot H, Külbs K, Lauser T, Nörpel-Schempp M, Willmann M (1996) Annotated diatom monographs. Iconographia Diatomologica 3, Koeltz Scientific Books, Königstein, Germany

Lange-Bertalot H, Metzelin D (1996) Indicators of Oligotrophy. Iconographia Diatomologica 2, Koeltz Scientific Books, Germany, Germany

Lange-Bertalot H, Moser G (1994) *Brachysira* - Monographie der Gattung. J. Cramer Berlin/Stuttgart, Germany

Lauber U, Goldscheider N (2014) Use of artificial and natural tracers to assess groundwater transit-time distribution and flow systems in a high-alpine karst system (Wetterstein Mountains, Germany). Hydrogeology Journal 22: 1807–1824

Leavitt PR (1993) A review of factors that regulate carotenoid and chlorophyll deposition and fossil pigment abundance. Journal of Paleolimnology 9: 109–127

Leavitt PR, Findlay DL (1994) Comparison of fossil pigments with 20 years of phytoplankton data from eutrophic Lake 227, Experimental Lakes Area, Ontario. Canadian Journal of Fisheries and Aquatic Sciences 51: 2286–2299

Leavitt PR, Hodgson DA (2001) Sedimentary pigments. In: Smol JP, Birks HJB, Last WM (eds) (2001) Tracking Environmental Change Using Lake Sediments. Volume 3: Terrestrial. Algal and Siliceous Indicators. Kluwer Academic Publishers, Dordrecht Boston London, pp. 295-325

Legendre P, Gallagher ED (2001): Ecologically meaningful transformations for ordination of species data. Oecologia 129: 271–280

Lepš J, Šmilauer P (2003) Multivariate Analysis of Ecological Data using CANOCO. Cambridge University Press, Cambridge

Letáková M, Cantonati M, Hašler P, Angeli N, Poulíčková A (2016) Substrate specificity and fine-scale distribution of epiphytic diatoms in a shallow tarn in the Brenta Dolomites (south-eastern Alps). Plant Ecology and Evolution 149: 144–156

Leira M, Filippi ML, Cantonati M (2015) Diatom community response to extreme water-level fluctuations in two

Alpine lakes: a core case study. Journal of Paleolimnology 53: 289-307

Lehmann MF, Bernasconi SM, McKenzie JA, Barbieri A, Simona M, Veronesi M (2004) Seasonal variation of the $\delta^{13}C$ and $\delta^{15}N$ of particulate and dissolved carbon and nitrogen in Lake Lugano: constraints on biogeochemical cycling in a eutrophic lake. Limnology and Oceanography 49: 415–429

Lewin JC (1953) Heterotrophy in diatoms. Journal of General Microbiology 9: 305-313

Lewin JC (1961) The dissolution of silica from diatom walls. Geochimica et Cosmochimica Acta 21: 182–198

Livingstone DM, Lotter AF, Walker IR (1999) The Decrease in Summer surface Water Temperature with Altitude in Swiss Alpine Lakes: A Comparison with Air Temperature Lapse Rates. Arctic, Antarctic, and Alpine Research 31: 341-352

Lotter AF, Pienitz R, Schmidt R (2010) Diatoms as indicators of environmental change near arctic and alpine treeline. In: Stoermer EF, Smol JP (eds) The Diatoms. Applications for the environmental and earth siences. Cambridge Universtiy Press, pp. 231-248

Lotter AF, Birks JB, Hofmann W, Marchetto A (1998) Modern diatom, cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for reconstruction of past environmental changes in the Alps. II. Nutrients. Journal of Paleolimnology 19: 443-463

Lotter AF, Bigler C (2000) Do diatoms in the Swiss Alps reflect the length of ice cover? Aquatic Sciences 62: 125-141

Lotter AF, Hofmann W, Kamenik C, Lami A, Ohlendorf C, Sturm M, van der Knaap WO, van Leeuwen JFN (2000) Sedimentological and biostratigraphical analyses of short sediment cores from Hagelseewli (2339 m a.s.l.) in the Swiss Alps. Journal of Limnology 59: 53-64

Lotter AF, Appleby PG, Bindler R, Dearing JA, Grytnes JA, Hofmann W, Kamenik C, Lami A, Livingstone DM, Ohlendorf C, Rose N, Sturm M (2002) The sediment record of the past 200 years in a Swiss high-alpine lake: Hagelseewli (2339 m a.s.l.). Journal of Paleolimnology 28: 111-127

Lorenz M, Nagel H-D, Granke O, Kraft P (2008) Critical loads and their exceedances at intensive forest monitoring sites in Europe. Environmental Pollution 155: 426-435

Loria KA, McKnight D, Ragar DM, Johnson PTJ (2019) The life aquatic in high relief: shifts in the physical and biological characteristics of alpine lakes along an elevation gradient in the Rocky Mountains, USA. Aquatic Sciences 82: 11

Lowe RL (1996) Periphyton patterns in lakes. In: Stevenson R.J., Bothwell M.L., Lowe R.L. (eds) Algal ecology, Freshwater benthic ecosystems. Academic Press, San Diego California, pp 57-76

Luoto TP, Nevalainen L (2013) Long-term water temperature reconstructions from mountain lakes with different catchment and morphometric features. Scientific Report 3: 2488

Mann ME (2002 a) The Little Ice Age. In MacCracken M.C. and J.S. Perry (eds), Encyclopedia of global environmental change. Volume 1. The earth system: physical and chemical dimensions of global environmental change. Wiley, Chichester: 504–509

Mann ME (2002 b) The value of multiple proxies. Science 297:1481– 1482

März C (1903) Der Seenkessel der Soiern - Ein Karwendelkar. Duncker und Humblot, Leipzig

Magnuson JJ, Robertson DM, Benson BJ, Wynne RH, Livingstone DM, Arai T, Assel RA, Barry RG, Card V, Kuusisto E, Granin NG, Prowse TD, Stewart KM, Vuglinski VS (2000) Historical trends in lake and river ice cover in the Northern Hemisphere. Science 289: 1743 – 1746

Mair V, Lang K, Tonidandel D, Thaler B, Alber R, Lösch B, Tait D, Nickus U, Krainer K, Thies H, Hirnsprenger M, Sapelza A, Talotti M (2015) Projekt Permaqua. Permafrost und seine Auswirkungen auf Wasserhaushalt und Gewässerökologie im Hochgebirge. www. Permaqua.eu

Malik HI, Northington RM, Saros JE (2017) Nutrient limitation status of Arctic lakes affects the responses of *Cyclotella* sensu lato diatom species to light: implications for distribution patterns. Polar Biology 40: 2445-2456

Mann ME (2002) The Little Ice Age. In: MacCracken MC, Perry JS (eds) Encyclopedia of global environmental change. Volume 1, The earth system: physical and chemical dimensions of global environmental change. Wiley, Chichester, pp 504–509

Marchetto A, Bettinetti R (1995) Reconstruction of the phosphorus history of two deep, subalpine Italian lakes from sedimentary diatoms, compared with long-term chemical measurements. Mem. Ist.Ital. Idorbiol., 53: 27-38

Marchetto A, Lami A, Musazzi S, Massaferro J, Langone L, Guilizzoni P (2004) Lake Maggiore (N. Italy) trophic history: fossil diatom, plant, pigment, and chironomids, and comparison with long-term limnological data. Quaternary International 113: 97-110

Marty C, Philipona R, Fröhlich C, Ohmura A (2002) Altitude dependence of surface radiation fluxes and cloud forcing in the Alps: Results from the alpine surface radiation budget network. Theoretical and Applied Climatology 72: 137–155

Mathieu J (2015) Die Alpen. Raum-Kultur-Geschichte. Phillip Reclam jun. GmbH and Co.KG, Stuttgart, Germany

Mayr C, Fey M, Haberzettl T, Janssen S, Lücke A, Maidana NI, Ohlendorf C, Schäbitz F, Schleser GH, Struck U, Wille M, Zolitschka B (2005) Palaeoenvironmental changes in southern Patagonia during the last millennium recorded in lake sediments from Laguna Azul (Argentina). Palaeogeography Palaeoclimatology Palaeoecology 228: 203–227

Mayr C, Lücke A, Maidana NI, Wille M, Haberzettel T, Corbella H, Ohlendorf C, Schäbitz F, Fey M, Janssen S, Zolitschka B (2009) Isotopic fingerprints on lacustrine organic matter from Laguna Potrok Aike (southern Patagonia, Argentina) reflect environmental changes during the last 16,000 years. Journal of Paleolimnology 42: 81-102

McKenzie JA (1985) Carbon isotopes and productivity in the lacustrine and marine environment. In: Stumm W (ed) Chemical processes in lakes. Wiley, New York, pp 99–118

McCarroll D, Loader NJ (2004) Stable isotopes in tree rings. Quaternary Science Reviews 23: 771–801

McMaster NL, Schindler DW (2005) Planktonic and epipelic algal communities and their relationship to physical and chemical variables in alpine ponds in Banff National Park, Canada. Arctic, Antarctic, and Alpine Research 37: 337–347

Melzer A, Schneider S (2001) Submerse Macrophyten als Indikatoren der Nährstoffbelastung von Seen. In: Handbuch Angewandte Limnologie: Grundlagen–Gewässerbelastung–Restaurierung–Aquatische Ökotoxikologie – Bewertung – Gewässerschutz

Messyasz B, Kuczyńska-Kippen N (2006) Periphytic algal communities: a comparison of *Typha angustifolia* L. and *Chara tomentosa* L. beds in three shallow lakes (West Poland). Polish Journal of Ecology 54: 15-27

Meyers PA (1994) Preservation of elemental and isotopic source identification of sedimentary organic matter. Chemical Geology 144: 289-302

Meyers PA, Teranes JL (2001) Sediment organic matter. In: Last WM, Smol J (eds) Tracking Environmental Change Using Lake Sediments. Volume 2. Physical und Geochemical Methods. Kluwer Academic Publishers, Dordrecht Boston London, pp 339-269

Michalak AM (2016) Study role of climate change in extreme threats to water quality. Nature 535: 349-350

Michelutti N, Douglas MSV, Smol JP (2003) Diatom response to recent climatic change in a high arctic lake (Char Lake, Cornwallis Island, Nunavut). Global and Planetary Change 38: 257-271

Michelutti N, Cooke CA, Hobbs WO, Smol JP (2015) Climate driven changes in lakes from the Peruvian Andes. Journal of Paleolimnology 54: 153–160

Miller MP, McKnight DM (2012) Limnology of the Green Lakes valley: phytoplankton ecology and dissolved organic matter biogeochemistry at a long-term ecological research site. Plant Ecology and Diversity 8: 698-702

Moos MT, Laird KR, Cumming BF (2005) Diatom assemblages and water depth in Lake 239 (Experimental Lakes Area, Ontario): implications for paleoclimatic studies. Journal of Paleolimnology 34: 217–227

Morales E (2011) *Pseudostauroseira elliptica*. In Diatoms of North America. Retrieved January 24, 2021, from https://diatoms.org/species/pseudostaurosira_elliptica

Moser KA, Baron JS, Brahney J, Oleksy IA, Saros JE, Hundey EJ, Sadro SA, Kopáček J, Sommaruga R, Kainz MJ, Strecker AL, Chandra S, Walters DM, Preston DL, Michelutti N, Lepori F, Spaulding SA, Christianton KR, Melack JM, Smol JP (2019) Mountain lakes: eyes on global environmental change. Global Planet Change 178: 77–95

Moss B (1977) Adaptations of epipelic and epipsammic freshwater algae. Oecologia 28: 103-108

Müller EM (1922) Die Soiernhäuser. In: Yearbook of the Alpine Club Section 1922, pp. 105-110

Navone R (1964) Proposed method for nitrate in potable waters. Journal of the American Water Works Association 56: 781-783

Murphy GEP, Romanuk TN, Worm B (2019) Cascading effects of climate change on plankton community structure. Ecology and Evolution 10: 2170-2181

Namiotko T, Danielopol DL, von Grafenstein U, Lauterbach S, Brauer A, Andersen N, Hüls M, Milecka K, Baltanás A, Geiger W (2015) Palaeoecology of Late Glacial and Holocene profundal Ostracoda of pre-Alpine lake Mondsee (Austria) – A base for further (palaeo) biological research. Palaeogeography Palaeoclimatology Palaeoecology 419: 23-36

Noetzli J, Christiansen HH, Gugliemin M, Romanovski VE, Shiklomanov NI, Smith SL, Zhao L (2016) Permafrost thermal state. Bullein of the American Metereological Society 98: 13-14

Novais MH, Morais MM, Rosado J, Dias LS, Hoffmann L, Ector L (2014) Diatoms of temporary and permanent watercourses in Southern Europe (Portugal). River Research and Applications 30: 1216–1232

Ohmura A (2012) Enhanced temperature variability in high-altitude climate change. Theoretical and Applied Climatology 110: 499-508

Oksanen J, Blanchet FG, Friendly M, Kindt R, Lengendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2018) Package 'vegan'. CRAN R-Project, 1-297

Olesen B, Madsen TV (2000) Growth and physiological acclimation to temperature and inorganic carbon availability by two submerged aquatic macrophyte species, *Callitriche cophocarpa* and *Elodea canadensis*. Functional Ecology 14: 252-260

O´Reilly CM, Sharma S, Derek KG, Hampton SE, Read JS et al. (2015) Rapid and highly variable warming of lake surfacewaters around the globe, Geophysical Research Letters 42: 10,773–10,781

Ossyssek S, Geist J, Werner P, Raeder U (2020) Identification of the ecological preferences of *Cyclotella comensis* in mountain lakes of the northern European Alps. Arctic, Antarctic and Alpine Research 51: 512-523

Overton E (1899) Notitzen über die Wassergewächse des Oberengadins. Vierteljahrschrift der Naturforschenden Gesellschaft Zürich 44: 211-228

Parker BR, Vinebrooke RD, Schindler DW (2008) Recent climate extremes alter alpine lake ecosystems. PNAS 105: 12927-12931

Passy SI (2007) Diatom ecological guilds display distinct and predictable behavior along nutrient and disturbance gradients in running waters. Aquatic Botany 86: 171–178

Pauli H, Gottfried M, Dullinger S, Abdaladze O, Akhalkatsi M, Alonso JLB, Coldea G, Dick J, Erschbamer B, Calzado RF, Ghosn D, Holten JI, Kanka R, Kazakis G, Kollár J, Larsson P, Moiseev P, Moiseev D, Molau U, Mesa JM, Nagy L, Pelino G, Puşcaş M, Rossi G, Stanisci A, Syverhuset AO, Theurillat J-P, Tomaselli M, Unterluggauer P, Villar L, Vittoz P, Grabherr G (2012) Recent plant diversity changes on Europe's mountain summits. Science 336: 353–355

Perga ME, Frossard V, Jenny JP, Alric B, Arnaud F, Berthon V, Black J, Domaizon I, et al. (2015) High-resolution paleolimnology opens new management perspectives for lakes adaptation to climate warming. Frontiers in Ecology and Evolution 3: 72

Perga ME, Bruel M, Rodriguez L, Guénand Y, Bouffard D (2018) Storm impacts on alpine lakes: Antecedent weather conditions matter more than the event intensity. Global Change Biology 24: 5004–5016

Peter H, Sommaruga R (2016) Shifts in diversity and function of lake bacterial communities upon glacier retreat. International Journal of Microbial Ecology 1-10

Peterson CG (1986) Effects of discharge reduction on diatom colonization below a large hydroelectric dam. Journal of the North American Benthological Society 5: 278-289

Peterson CG (1987) Influences of flow regime on development and desiccation response of lotic diatom communities. Ecology 68: 946-954

Philibert A, Prairie YT (2002) Is the introduction of benthic species necessary for open-water chemical reconstruction in diatom-based transfer functions? Canadian Journal of Fisheries and Aquatic Science 59: 938–951

Philipona R (2013) Greenhouse warming and solar brightening in and around the Alps. International Journal of Climatology 33: 1530-1537

Pienitz R, Smol JP, Birks HJB (1995) Assessment of freshwater diatoms as quantitative indicators of past climate change in the Yukon and Northwest Territories, Canada. Journal of Paleolimnology 13: 21-49

Pla-Rabés S, Catalan J (2018) Diatom species variation between lake habitats: implications for interpretation of paleolimnological records. Journal of Paleolimnology 60: 169-187

Porro F, Tomaselli M, Abeli T, Gandini M, Gualmini M, Orsenigo S, Petraglia A, Rossi G, Carbognani M (2019) Could plant diversity metrics explain climate-driven vegetation changes on mountain summits of the GLORIA network? Biodiversity and Conservation 28: 3575-3596

Poulíčková A, Hašler P (2007) Aerophytic diatoms from caves in central Moravia (Czech Republic). Preslia 79: 185–204

Poulíčková A, Hašler P, Lysáková M, Spears B (2008) The ecology of freshwater epipelic algae: an update. Phycologia 47: 437–450

Poulíčková A, Dvořák P, Mazalová P, Hašler P (2014) Epipelic microphototrophs: an overlooked assemblage in lake ecosystems. Freshwater Science 33: 513-523

Preston DL, Caine N, McKnight DM, Williams MW, Hell K, Miller MP, Hart SJ, Johnson PTJ (2016) Climate regulates alpine lake ice cover phenology and aquatic ecosystem structure. Geophysical Research Letters 43: 5353-5360

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

Putyrska V, Klemt E, Röllin S, Astner M, Sahli H (2015) Dating of sediments from four Swiss prealpine lakes with ^{210}Pb determined by gamma-spectrometry: progress and problems. Journal of Environmental Radioactivity 145: 78-95

R Core Team (2013) R: A language and environment for statistical computing (Version 3.4.3). Vienna: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org/

Raeder U (1990) Vergleichende Untersuchungen der Phytoplanktonsukzessionen in 15 Seen des Osterseengebietes. Dissertation. Technical University Munich.

Raposeiro PM, Saez A, Giralt S, Costa AC, Gonçalves V (2018) Causes of spatial distribution of subfossil diatom and chironomid assemblages in surface sediments of a remote deep island lake. Hydrobiologia 815: 141-163

Reichardt E (1999) Zur Revision der Gattung *Gomphonema*. In: Lange-Bertalot H. (ed) Iconographia Diatomologica 8. A.R.G. Gantner Verlag K.G., Rugell, Liechtenstein

Reynolds CS (1984) The Ecology of Freshwater Phytoplankton. Cambridge University Press, Cambridge: 384 pp.

Reynolds CS (2006) The Ecology of Phytoplankton (Ecology, Biodiversity and Conservation). Cambridge University Press

Riis T, Hawes I (2002) Relationships between water level fluctuations and vegetation diversity in shallow water of New Zealand lakes. Aquatic Botany 74: 133-148

Rørslett B (1991) Principal determinants of aquatic macrophyte richness in northern European lakes. Aquatic Botany 39: 173-193

Robbins JA (1978) Geochemical and geophysical applications of radioactive lead isotopes. In: Nriagu JO (ed) Biochemistry of lead. Elsevier, Amsterdam, pp 85-393

Roberts CP, Twidwell D, Angeler DG, Allen CR (2019) How do ecological resilience metrics relate to community stability and collapse. Ecological Indicators 107: 105552

Rogora M, Frate L, Carranza ML, Freppaz M, Stanisci A, Bertani I, Bottarin R, Brambilla A, Canullo R, Carbognani M, Cerrato C, Chelli S, Cremonese E, Cutini M, Di Musciano M, Erschbamer B, Godone D, Iocchi M, Isabellon M, Magnani A, Mazzola L, Morra di Cella U, Pauli H, Petey M, Petriccione B, Porro F, Psenner R, Rossetti G, Scotti A, Sommaruga R, Tapperiner U, Theurillat J-P, Tomaselli M, Viglietti D, Viterbi R, Vittoz P, Winkler M, Matteucci G (2018) Assessment of climate change effects on mountain ecosystems through a cross-site analysis in the Alps and Apennines. Science of the Total Environment 624: 1429-1442

Rogora M, Somaschini L, Marchetto A, Mosello R, Tartari GA, Paro L (2020) Decadal trends in water chemistry of Alpine lakes in calcareous catchments driven by climate change. Science of the Total Environment 708: 135180

Roberts JJ, Fausch KD, Schmidt TS, Walters DM (2017) Thermal regimes of Rocky Mountain lakes warm with climate change. PLoS One 12, e0179498

Rosbakh S, Bernhardt-Roemermann M, Poschlod P (2014) Elevation matters: contrasting effects of climate change on the vegetation development at different elevations in the Bavarian Alps. Alpine Botany 124: 143–154

Rose NL, Morley D, Appleby PG, Battarbee RW, Alliksaar T, Guilizzoni P, Jeppesen E, Korhola A, Punning J-M (2010) Sediment accumulation rates in European lakes since AD 1850: trend, reference conditions and exeedence. Journal of Paleolimnology 45: 447-468

Rose KC, Winslow LA, Read JS, Hansen GJA (2016) Climate-induced warming of lakes can be either amplified or suppressed by trends in water clarity. Limnology and Oceanography Letters 1: 44-53

Rosset V, Lehmann A, Oertli B (2010) Warmer and richer? Predicting the impact of climate warming on species richness in small temperate waterbodies. Global Change Biology 16: 2376-2387

Round FE, Crawford RM, Mann DG (1990) The diatoms, biology and morphology of the genera. Cambridge University Press

Ruckstuhl C, Philipona R, Morland J, Ohmura A (2007) Observed relationship between surface specific humidity, integrated water vapor, and longwave downward radiation at different altitudes. Journal of Geophysical Research 112: D03302

Rühland KM, Priesnitz A, Smol JP (2003) Paleolimnological Evidence from Diatoms for Recent Environmental Changes in 50 Lakes across Canadian Arctic Treeline. Arctic, Antarctic, and Alpine Research 35: 110–123

Rühland KM, Smol JP (2005) Diatom shifts as evidence for recent Subarctic warming in a remote tundra lake, NWT, Canada. Palaeogeography Palaeoclimatology Palaeoecology 226: 1–16

Rühland KM, Paterson AM, Smol JP (2008) Hemispheric-scale patterns of climate-related shifts in planktonic diatoms from North American and European lakes. Global Change Biology 14: 2740–2754

Rühland KM, Paterson AM, Smol JP (2015) Lake diatom responses to warming: reviewing the evidence. Journal of Paleolimnology 54: 1–35

Rühland KM, Rentz K, Paterson AM, Teller JT, Smol JP (2018) The post-glacial history of northern Lake of the Woods: A multi-proxy perspective on climate variability and lake ontogeny. Journal of Great Lakes Research 44: 367–376

Rumpf SB, Hülber K, Klonner G, Moser D, Schütz M, Wessely J, Willner W, Zimmermann NE, Dullinger S (2018) Range dynamics of mountain plants decrease with elevation. PNAS 115: 1848-1853

Ryan PD, Harper DAT, Whalley JS (1995) PALSTAT: user's manual and case histories: statistics for palaeontologists and palaeobiologists. Chapman and Hall, London, 1-136

Sadro S, Sickman JO, Melack JM, Skeen K (2018) Effects of climate variability on snowmelt and implications for organic matter in a high elevation lake. Water Resources Research 54: 4563–4578

Sanchez-Cabeza JA, Riuz-Fernández AC (2015) ^{210}Pb sediment radiochronology: an integrated formulation and classification of dating models. Geochimica et Cosmochimica Acta 82: 183-200

Sanger JE (1988) Fossil pigments in paleoecology and paleolimnology. Palaeogeography Palaeoclimatology Palaeoecology 62: 343– 359

Saros JE, Anderson NJ (2014) The ecology of the planktonic diatom *Cyclotella* and its implications for global environmental change studies. Biological reviews 90: 522-541

Sayer CD (2001) Problems with the application of diatom- total phosphorus transfer functions: examples from a shallow English lake. Freshwater Biology 46: 743–757

Sayer CD, Roberts N (2001) Establishing realistic restoration targets for nutrient-enriched shallow lakes: linking diatom ecology and palaeoecology at the Attenborough Ponds, U.K. Hydrobiologia 448: 117–142

Schaefli B, Manso P, Fischer M, Huss M, Farinotti D (2019) The role of glacier retreat for Swiss hydropower production. Renewable Energy 132: 615-627

Schaumburg J, Schranz C, Stelzer D, Vogel A (2014) Verfahrensanleitung für die ökologische Bewertung von Seen zur Umsetzung der EG-Wasserrahmenrichtlinie: Makrophyten and Phytobenthos. Bayerisches Landesamt für Umwelt, München

Schermer M, Kirchengast C (2006) Perspektiven der Berglandwirtschaft. Alpine space-man and environment 1: Die Alpen im Jahr 2020

Scherrer SC, Wüthrich C, Croci-Maspoli M, Weingartner R, Appenzeller C (2013) Snow variability in the Swiss Alps 1864–2009. International Journal of Climatology 33: 3162-3173

Schmidt R, Lange-Bertalot H, Klee R (2004) *Staurosira parasitoides* sp. nova and *Staurosira microstriata* (Marciniak) Lange-Bertalot from surface sediment samples of Austrian alpine lakes. Algological Studies 114: 1-9

Schmidt R, Kamenik C, Lange-Bertalot H, Klee R (2004) Fragilaria and Staurosira (Bacillariophyceae) from sediment surfaces of 40 lakes in the Austrian Alps in relation to environmental variables, and their potential for palaeoclimatology. Journal of Limnology 63: 171-189

Schmidt-Thome P (1953) Beobachtungen an Karen im Vorkarwendel. Geologica Bavarica. Bayerisches Geologisches Landesamt, München

Schmucki DA, Phiipona R (2002) Ultraviolet radiation in the Alps: the altitude effect. Optical Engineering 41: 3090-3095

Schröder B, Reineking B (2004) Modellierung der Art-Habitat-Beziehung – ein Überblick über die Verfahren der Habitatmodellierung. UFZ-Bericht 9/2004 Habitatmodelle – Methodik, Anwendung, Nutzen, 6-26

Schwager P, Berg C (2019) Global warming threatens conservation status of alpine EU habitat types in the European Eastern Alps. Regional Environmental Change 19: 2411-2421

Schwoerbel J, Brendelberger H (2005) Einführung in die Limnologie. 9. Auflage. Spektrum Akademischer Verlag, Heidelberg.

Shatwell T, Adrian R, Kirillin G (2016) Planktonic events may cause polymictic-dimictic regime shifts in temperate lakes. Scientific reports 6: 24361

Sivarajah B, Rühland KM, Labaj AL, Paterson AM, Smol JP (2016) Why is the relative abundance of *Asterionella formosa* increasing in a Boreal Shield lake as nutrient levels decline? Journal of Paleolimnology 55: 357–367

Skjøth CA, Geels C (2013) The effect of climate and climate change on ammonia emissions in Europe. Atmospheric Chemistry and Physics 13: 117–128

Smol JP, Cumming BF (2000) Tracking long-term changes in climate using algal indicators in lake sediments. Journal of Phycology 36: 986-1011

Smol JP, Wolfe AP, Birks HJB, Douglas MSV, Jones VJ, Korhola A, Pienitz R, Rühland KM, Sorvari S, Antoniades D, Brooks SJ, Fallu M-A, Hughes M, Keatley BE, Laing TE, Michelutti N, Nazarova L, Nyman M, Paterson AP, Perren B, Quinlan R, Rautio M, Saulnier-Talbot E, Siitonen S, Solovieva N, Weckström J (2005) Climate-driven regime shifts in the biological communities of arctic lakes. PNAS 102: 4397–4402

Smol JP (1988) Paleoclimate proxy data from freshwater arctic diatoms. Verhandlungen des Internationalen Verein Limnologie 23: 837–44

Smol JP (2008) Pollution of Lakes and Rivers: A Paleoenvironmental Perspective, 2nd edn. Blackwell Publishing, Oxford

Smol JP (2010) The power of the past: using sediments to track the effects of multiple stressors on lake ecosystems. Freshwater Biology 55: 43–59

Sommaruga R, Psenner R, Schaffner E, Koinig K, Sommaruga-Wögrath S (1999) Dissolved organic carbon concentration and phytoplankton biomass in high-mountain lakes of the Austrian Alps: Potential effect of climatic warming on UV underwater attenuation. Arctic, Antarctic, and Alpine Research 31: 247-253

Sommaruga R (2001) The role of solar UV radiation in the ecology of alpine lakes. Journal of Photochemistry and Photobiology B. Biology 62: 35-42

Sommaruga R, Augustin G (2006) Seasonality in UV transparency of an alpine lake is associated to changes in phytoplankton biomass. Aquatic Sciences 68: 129-141

Sommer U, Lewandowska A (2011) Climate change and the phytoplankton spring bloom: warming and overwintering zoo- plankton have similar effects on phytoplankton. Global Change Biology 17: 154–162

Sommer U, Adrian R, de Senerpont Domis L, Elser JJ, Gaedke U, Ibelings B, Jeppesen E, Lürling M, Molinero JC, Mooij WM, van Donk E, Winder M (2012) Beyond the Plankton Ecology Group (PEG) model: mechanisms driving plankton succession. Annual Reviews of Ecology, Evolution and Systematics 43: 429–48

Spaudling SA, Bishop IW, Edlund MB, Potapova M (2018) Diatoms of North America. https://diatoms.org/

Spaulding SA, Otu MK, Wolfe AP, Baron JS (2015) Paleolimnological Records of Nitrogen Deposition in Shallow, High-Elevation Lakes of Grand Teton National Park, Wyoming, U.S.A. Arctic, Antarctic, and Alpine Research 47: 703-717

Stevenson RJ, Stoermer EF (1981) Quantitative differences between benthic algal communities along a depth gradient in Lake Michigan. Journal of Phycology 17: 29-36

Stevenson RJ, Peterson CG, Kirschtel DB, King CC, Tuchman NC (1991) Densitiy-dependent growth, ecological strategies, and effects of nutrients and shading on benthic diatom succession in streams. Journal of Phycology 27: 59-69

Stevenson RJ, Smol JP (2015) Use of algae in ecological assessment. In: Wehr J, Sheath R, Kociolek JP (eds) Freshwater algae of North America, Ecology and Classification. Academic Press Elsevier, London pp 921-952

Stocker TF (2020) Surprises for climate stability. Science 367 (6485): 1425-1426

Stoermer EF, Ladewski TB (1976) Apparent optimal temperatures for the occurrence of some common phytoplankton species in southern Lake Michigan. Great Lakes Research Division, Publication 18

Stoermer EF, Smol JP (2010): Applications and use of diatoms: prologue. In: Stoermer EF, Smol JP (eds): The Diatoms: Applications for the Environmental and earth Sciences. Cambridge University press, pp. 3-7

Stoffel M, Huggel C (2012) Effects of climate change on mass movements in mountain environments. Progress in Physical Geography 36: 421–39

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

Sun J, Liu D (2003) geometric models for calculating cell biovolume and surface area for phytoplankton. Journal of Plankton research 25: 1331-1346

Sun M-Y, Lee C, Aller RC (1993) Laboratory studies of oxic and anoxic degradation of chlorophyll-a in Long Island Sound sediments. Geochimica et Cosmochimica Acta 57: 147-157

Tolotti M, Thies H, Cantonati M, Hansen CME, Thaler B (2003) Flagellate algae (Chrysophyceae, Dino- phyceae, Cryptophyceae) in 48 high mountain lakes of the Northern and Southern slope of the Eastern Alps: biodiversity, taxa distribution and their driving variables. Hydrobiologia 502: 331–348

Tasser E, Ruffini FV, Tappeiner U (2009) An integrative approach for analysing landscape dynamics in diverse cultivated and natural mountain areas. Landscape Ecology 24: 611–628

Tasser E, Leitinger G, Pecher C, Tappeiner U (2011) Agricultural changes in the European Alpine Bow and their impact on other policies. In: Pötsch EM, Krautzer B, Hopkins A (eds) Grassland Farming and Land Management Systems in Mountainous Regions. Grasland Science in Europe Vol 16

Teranes JL, Bernasconi SM (2000) The record of nitrate utilization and productivity limitation provided by $\delta^{15}N$ values in lake organic matter - a study of sediment trap and core sediments from Baldeggersee, Switzerland. Limnology and Oceanography 45: 801–813

Teranes JL, Bernasconi SM (2005) Factors controlling $\delta^{13}C$ values of sedimentary carbon in hypertrophic Baldeggersee, Switzerland, and implications for interpreting isotope excursions in lake sedimentary records. Limnology and Oceanography 50: 914-922

ter Braak CFJ (1987) Ordination. In: Jongman RHG, ter Braak CFJ, van Tongeren OFR. (eds) Data analysis in community and landscape ecology. Pudoc, Wageningen (reprinted by Cambridge University Press, Cambridge, 1995), pp. 91-173

ter Braak CFJ, Verdonschot PFM (1995) Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquatic Sciences 57: 255-289

Theurillat J, Guisan A (2001) Potential impact of climate change on vegetation in the European Alps: a review. Climatic Change 50: 77-109

Thies H, Nickus U, Tolotti M, Tessadri R, Krainer K (2013) Evidence of rock glacier melt impacts on water chemistry and diatoms in high mountain streams. Cold Regions Science and Technology 96: 77–85

Thompson R, Price D, Cameron N, Jones V, Bigler C, Rosén P, Hall RI, Catalan J, García J, Weckström J, Korhola A (2005) Quantitative Calibration of Remote Mountain-Lake Sediments as Climatic Recorders of Air Temperature and Ice-Cover Duration, Arctic, Antarctic, and Alpine Research, 37: 626-635

Thottathil SD, Reis PCJ, del Giorgio PA, Prairie YT (2018) The extent and regulation of summer menthane oxidation in northern lakes. Journal of Geophysical Research: Biogeosciences 123: 3216-3230

Tiberti R, Nelli L, Marchetto A, Tartari G, Wienckowski E, Rogora M (2019) Multi-year trends and determinants of the hydrochemistry of high mountain lakes in the Western Italian Alps. Aquatic Science 81: 54

Tilmann D (1982) Response competition and community structure. Princeton University Press. Princeton, N.Y.

Tilzer MM (1988) Secchi disk-chlorophyll relationships in a lake with highly variable phytoplankton biomass. Hydrobiologia 162: 163-171

Timofeeva G, Treydte K, Bugmann H, Rigling A, Schaub M, Siegwolf R, Saurer M (2012) Long-term effects of drought on tree-ring growth and carbon isotope variability in Scots pine in a dry environment. Tree Physiology 37: 1028-1041

Tõnno I, Nauts K, Belle S, Nõmm M, Freiberg R, Kõiv T, Alliksaar T (2019) Holocene shifts in the primary producer community of large, shallow European Lake Peipsi, inferred from sediment pigment analysis. Journal of Paleolimnology 61: 403–417

Tuchman NC, Schollett MA, Rier ST, Geddes P (2006) Differential heterotrophic utilization of organic compounds by diatoms and bacteria under light and dark conditions. Hydrobiologia 561: 167–177

Unger R, Abegg B, Mailer M, Stampfl P (2016) Energy consumption and greenhouse gas emissions resulting from tourism travel in an Alpine setting. Mountain Research and Developement 36: 475-483

Vadeboncoeur Y, Kalff J, Christoffersen K, Jeppesen E (2006) Substratum as a driver of variation in periphyton chlorophyll and productivity in lakes. Journal of the North American Benthological Society 25: 379-392

Vadeboncoeur Y, Devlin S, McIntyre PB, Zanden MJV (2014) Is there light after depth? Distribution of periphyton chlorophyll and productivity in lake littoral zones. Freshwater Science 33: 524-536

Valeton I (1988) Sedimentäre Phosphatgesteine. In: Füchtbauer N (ed) Sedimente und Sedimentgesteine. E. Schweizbart, Stuttgart, pp 543-567

van Dam H, Mertens A, Sinkeldam J (1994) A coded checklist and ecological indicator values of freshwater diatoms from the Netherlands. Netherlands Journal of Aquatic Ecology 28: 117–133

van de Weyer K, Schmidt C (2007) Bestimmungsschlüssel für aquatische Makrophyten (gefäßpflanzen, Armleuchteralgen, Moose) in Deutschland: LUGV

van der Werff A (1953) A new method of concentrating and cleaning diatoms and other organisms. Internationale Vereinigung für Theoretische und Angewandte Limnologie Verhandlungen 12: 276-277

Verdonschot PFM, Hering D, Murphy J, Jähnig SC, Rose NL, Graf W, Brabec K, Sandin L (2010) Climate change and the hydrology and morphology of freshwater ecosystems. IIn: Kernan M, Battarbee R, Moss B (eds) Climate Change Impacts on Freshwater Ecosystems. Blackwell Publishing Ltd.

Vinebrooke RD, Leavitt PR (1996) Effects of ultraviolet radiation on periphyton in an alpine lake. Limnology and Oceanography 41: 1035-1040

Vinebrooke RD, Leavitt PJ (1998) Direct and interactive effects of allochthonous dissolved organic matter, inorganic nutrients, and ultraviolet radiation on an alpine littoral food web. Limnology and Oceanography 43: 1065-1081

Viviroli D, Archer DR, Buytaert W, Fowler HJ, Greenwood G, Hamlet AF, Huang Y, Koboltschnig G, Litaor I, López-Moreno JI (2011) Climate change and mountain water resources: Overview and recommendations for research, management and policy. Hydrology and Earth System Sciences 15: 471–504

Vollenweider RA (1968) Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors in eutrophication. Paris, Rep. Organization for Economic Cooperation and Development

Warscher M, Wagner S. Marke T, Laux P, Smiatek G, Strasser U, Kunstmann H (2019): A 5 km resolution regional climate simulation for Central Europe: Performance in high mountain areas and sesonal, regional and elevation-dependent variations. Atmosphere 10: 682

Weckström J, Korhola A and Blom T (1997) The relationship between diatoms and water temperature in thirty subarctic Fennoscandian lakes. Arctic and Alpine research 29: 75-92

Weckström J, Hanhijärvi S, Forsström L, Kuusisto E, Korhola A (2014) Reconstructing lake ice cover in subarctic lakes using a diatom-based inference model. Geophysical Research Letters 41: 2026– 2032

Weckström K, Weckström J, Huber K, Kamenik C, Schmidt R, Salvenmoser W, Rieradevall M, Weisse T, Psenner R, Kurmayer R (2016) Impacts of Climate Warming on Alpine Lake Biota Over the Past Decade. Arctic, Antarctic, and Alpine Research 48: 361–376

Werner P, Smol JP (2005) Diatom–environmental relationships and nutrient transfer functions from contrasting shallow and deep limestone lakes in Ontario, Canada. Hydrobiologia 533: 145-173

Werner P, Smol JP (2006) The distribution of the diatom *Cyclotella comensis* in Ontario (Canada) lakes. Nova Hedwigia, Beiheft 130, pp 373–392

Wetzel RG (2001) Limnology Lake and River. Academic Press, San Diego California

Wiklund JA, Bozinovski N, Hall RI, Wolfe BB (2010) Epiphytic diatoms as flood indicators. Journal of Paleolimnology 44: 25-42

Wilhelm B, Arnaud F, Sabatier P, Crouzet C, Brisset E, Chaumillon E, Disnar J-R, Guiter F, Malet E, Reyss J-L, Tachikawa K, Bard E, Delannoy J-J (2012) 1400 years of extreme precipitation patterns over the Mediterranean French Alps and possible forcing mechanisms. Quaternary Research 78: 1–12

Wilhelm B, Arnaud F, Enters D, Allignol F, Legaz A, Magand O, Revillon S, Giguet-Covex C, Malet E (2012) Does global warming favour the occurrence of extreme floods in European Alps? First evidences from a NW Alps proglacial lake sediment record. Climatic Change 113: 563-581

Wilhelm B, Arnaud F, Sabatier P, Magand O, Chapron E, Courp T, Tachikawa K, Fanget B, Malet E, Pignol C, Bard E, Delannoy JJ (2013) Palaeoflood activity and climate change over the last 1400 years recorded by lake sediments in the north-west European Alps. Journal of Quaternary Science 28 (2): 189-199

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

Williamson CE, Salm C, Cooke SL, Saros JE (2010) How do UV radiation, temperature, and zooplankton influence the dynamics of alpine phytoplankton communities? Hydrobiologia 648: 73– 81

Winder M, Reuter JE and Schladow SG (2009) Lake warming favours small-sized planktonic diatom species. Proceedings of the Royal Society B 27: 427–435

Winder M, Sommer U (2012) Phytoplankton response to a changing climate. Hydrobiologia 698: 5–16

Winter KJ-PM, Kotlarski S, Scherrer SC, Schär C (2017) The Alpine snow albedo feedback in regional climate models. Climate Dynamics 48: 1109-1124

Witkowski A, Żelazna-Wieczorek J, Solak CN, Kulikovskiy M (2014) Morphology, ecology and distribution of the diatom (Bacillariophyceae) species Simonsenia delognei (Grunow) Lange-Bertalot. Oceanological and Hydrological Studies 43: 393-401

Wolfe AP, Baron JS, Cornett RJ (2001) Anthropogenic nitrogen deposition induces rapid ecological changes in alpine lakes of the Colorado Front Range (USA). Journal of Paleolimnology 25: 1-7

Wright SW, Jeffrey SW, Mantoura RFC, Llewellyn CA, Bjornland T, Repeta D, Weelschmeyer N (1991) Improved HPLC methods for the analysis of chlorophylls and carotenoids from marine phytoplankton. Marine Ecologic Progress Series 77: 183-196

Wunsam S, Schmidt R, Klee R (1995) *Cyclotella*-taxa (Bacillariaphyceae) in lakes of the Alpine regions and their relationships to environmental variables. Aquatic Sciences 57: 360-386

Yang H, Flower RJ (2012) Effects of light and substrate on the benthic diatoms in an oligotrophic lake: a comparison between natural and artificial substrates. Journal of Phycology 48: 1166–1177

Yvon-Durocher G, Jones JI, Trimmer M, Woodward G, Montoya JM (2010) Warming alters the metabolic balance of ecosystems. Philosophical Transactions of the Royal Society B 365: 2117–2126

Yvon-Durocher G, Montoya JM, Trimmer M, Woodward G (2011) Warming alters the size spectrum and shifts the distribution of biomass in freshwater ecosystems. Global change biology 17: 16811694

Zappa M, Kan C (2007) Extreme heat and runoff extremes in the Swiss Alps. Natural Hazards and Earth Sysems Sciences 7: 375–389

Zhang H, Huo S, Yeager KM, He Z, Xi B, Li X, Ma C, Wu F (2019) Phytoplankton response to climate changes and anthropogenic activities recorded by sedimentary pigments in a shallow eutrophied lake. Science of the Total Environment 647: 1398–140

Zohary T, Flaim G, Sommer U (2020) Temperature and the size of freshwater phytoplankton. Hydrobioligia. doi: 10.1007/s10750-020-04246-6

Appendix

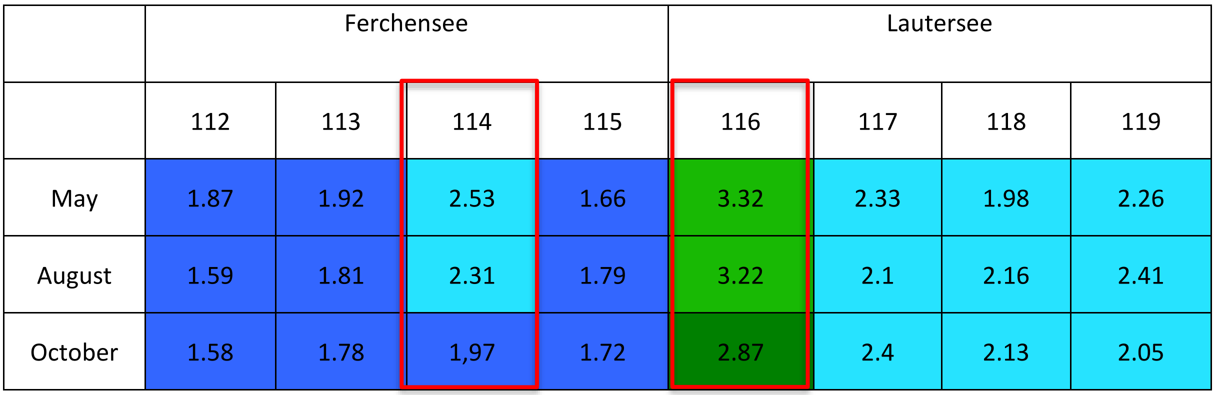
Chapter 5: Grouping of the diatom species

Diatom group	**Diatom species**
Achnanthidium	*Achnanthidium macrocephalum* *Achnanthidium caledonicum* *Achnanthidium linearioides* *Achnanthidium minutissimum* *Achnanthidium neomicrocephalum* *Achnanthidium rosenstockii* *Achnanthidium straubianum*
Amphora pediculus	*Amphora pediculus*
Amphora (big)	*Amphora aequalis* *Amphora alpestris* *Amphora copulata* *Amphora lange-bertalotii* *Amphora ovalis*
Aneumastus tusculus	*Aneumastus tusculus*
Asterionella formosa	*Asterionella formosa*
Brachysira	*Brachysira neglectissima* *Brachysira neoexilis* *Brachysira vitrea*
Caloneis silicula	*Caloneis silicula*
Cocconeis placentula	*Cocconeis placentula var. euglypta* *Cocconeis placentula var. placentula*
Cyclotella (small)	*Cyclotella comensis* *Cyclotella delicatula* *Cyclotella ocellata* *Cyclotella wuethrichiana*
Cyclotella distinguenda	*Cyclotella distinguenda*
Cyclotella (heavy)	*Cyclotella bodanica* *Cyclotella praetermissa* *Cyclotella radiosa*
Cymbella (small)	*Cymbella affinis* *Cymbella laevis*
Cymbopleura diminuta	*Cymbopleura diminuta*
Cymbopleura inaequalis	*Cymbopleura inaequalis*
Delicata delicatula	*Delicata delicatula*
Denticula tenuis	*Denticula tenuis*
Diploneis (small)	*Diploneis oculata* *Diploneis parma* *Diploneis petersenii*
Diploneis separanda	*Diploneis separanda*
Diploneis (big and heavy)	*Diploneis elliptica* *Diploneis krammeri*
Discostella	*Discostella pseudostelligera* *Discostella stelligera*
Encyonema (small)	*Encyonema minutum* *Encyonema ventricosum*
Encyonema (big)	*Encyonema obscurum* *Encyonema silesiacum*

Encyonopsis (small)	*Encyonopsis krammeri* *Encyonopsis minuta* *Encyonopsis subminuta*
Encyonopsis cesatii	*Encyonopsis cesatii*
Eolimna minima	*Eolimna minima*
Eucocconeis flexella	*Eucocconeis flexella*
Eunotia arcubus	*Eunotia arcubus*
Fallacia sublucidula	*Fallacia sublucidula*
Fragilaria	*Fragilaria acus* *Fragilaria delicatissima* *Fragilaria nanana* *Fragilaria tenera*
Staurosira	*Staurosira binodis* *Staurosira construens* *Staurosira lapponica* *Staurosira pseudoconstruens* *Staurosira venter*
Staurosira (light)	*Staurosira elliptica* *Staurosira microstriata* *Staurosira parasitoides*
Pseudostaurosira	*Pseudostaurosira brevistriata* *Pseudostaurosira parasitica*
Staurosirella pinnata	*Staurosirella pinnata*
Gomphonema lateripunctatum	*Gomphonema lateripunctatum*
Gyrosigma acuminatum	*Gyrosigma acuminatum*
Gyrosigma attenuatum	*Gyrosigma attenuatum*
Halamphora thumensis	*Halamphora thumensis*
Hippodonta neglecta	*Hippodonta neglecta*
Navicula (small)	*Navicula antonii* *Navicula cryptotenella* *Navicula utermoehlii*
Navicula (medium)	*Cymbellafalsa diluviana* *Navicula dealpina* *Navicula hofmanniae* *Navicula krammerae* *Navicula subalpine* *Navicula trophicatrix* *Navicula wildii*
Navicula concentrica	*Navicula concentrica*
Naviculadicta	*Naviculadicta geissleriae* *Naviculadicta raederae*
Neidium ampliatum	*Neidium ampliatum*
Nitzschia (small)	*Nitzschia alpinobacillum* *Nitzschia dealpina* *Nitzschia fonticola* *Nitzschia lacuum*
Nitzschia denticula	*Nitzschia denticula*
Pinnularia borealis	*Pinnularia borealis*
Placoneis clementis	*Placoneis clementis*
Planothidium frequentissimum	*Planothidium frequentissimum*
Platessa conspicua	*Platessa conspicua*

Platessa ziegleri	*Platessa ziegleri*
Reimeria sinuata	*Reimeria sinuata*
Sellaphora (big)	*Sellaphora calcicola* *Sellaphora laevissima* *Sellaphora mutata* *Sellaphora pupula*
Sellaphora (small)	*Sellaphora pseudoventralis* *Sellaphora joubaudii* *Sellaphora verecundiae*
Stephanodiscus	*Stephanodiscus cf. alpinus* *Stephanodiscus cf. minutulus*
Surirella helvetica	*Surirella helvetica*
Tabellaria flocculosa	*Tabellaria flocculosa*

Table A.1 Trophic Indices ($TI_{süd}$) calculated from littoral diatom assemblages indicating oligotrophic (blue), oligo- to mesotrophic (turquoise), mesotrophic 1 (dark green) and mesotrophic 2 (light green) conditions in montane lakes Ferchensee (littoral sites 112-115) and Lautersee (littoral sites 116-119) in May, August and October. Sites 114 and 116 are located next to guesthouses (red frame) and show distinctly higher $TI_{süd}$ values



	Ferchensee				Lautersee			
	112	113	114	115	116	117	118	119
May	1.87	1.92	2.53	1.66	3.32	2.33	1.98	2.26
August	1.59	1.81	2.31	1.79	3.22	2.1	2.16	2.41
October	1.58	1.78	1,97	1.72	2.87	2.4	2.13	2.05