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Response of diatoms to climate change in mountain lakes in the Northern calcareous Alps with indications for the future development of the lake biota

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Preface

This dissertation aims to investigate the responses of the montane, subalpine and alpine mountain lake biota to climate warming by reconstructing the past development using sediment cores. The beginning of the thesis gives a fundamental definition of mountain lakes and introduces into their special features and enhanced vulnerabilities in times of climate change. The next two sections of the introduction further review the palaeolimnological methods for environmental reconstructions and lead to the diatoms as ideal bioindicators for the aims of this study. After the introduction closes with the main goals and objectives of this dissertation, chapter 2 presents an overview of investigated study sites and applied methods from on-site-measurements to sediment core separation until microscopical analyses.

The subsequent chapters 3 to 5 base on published and autonomous research papers. Thereof, the chapters 3 and 4 elaborate a new method to reconstruct individual lake warming as a basis to better understand biotic developments in the lakes. Therefore, chapter 3 detected the significant correlation of a morphological trait of diatoms with lake temperatures. In chapter 4, this relationship was then set into a palaeolimnological context in terms of establishing a transfer-function, which can be applied to subfossil diatom assemblages of time series from sediment cores. With this method, individual lake warming could be calculated and contrasted to regional atmospheric warming. Based on this, chapter 5 then expands the scope to the entire diatom assemblage of all retrieved sediment cores to study the biotic lake developments. In this context, this chapter identifies the main lake characteristics and tipping points that modulate and determine the lake responses to global warming.

The final chapter 6 provides the general discussion and focuses on three different topics. The first section evaluates the temporal development of the studied mountain lakes including predictions for future climate warming. The second section transfers the dissertation's results derived from primary producers to a broader context in the food web of mountain lakes and generally discusses the developments of the aquatic fauna. The third section of the general discussion illustrates the global transferability of the findings of this dissertation and highlights their limits considering different climates and continents. Finally, this chapter closes with an outlook targeting a global understanding of biotic responses in mountain lakes to warming and their regional role for terrestrial wildlife to improve management and conservations strategies with future global change.

Marginal note: In consideration of Emiliani (1952), this dissertation uses the term "planktic", which is etymologically the actual adjective of "plankton".

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Summary

Climate change is globally causing a warming environment but with locally different effects. Areas at high altitudes and latitudes particularly experience extremer warming due to factors such as the most significant decreases in snowfall and snow cover versus prolonged vegetation periods and establishing vegetation. These substantial changes culminate in mountain lakes with additional cascading effects but their biota is highly adapted to those specific and harsh conditions. Thus, already little changes in atmosphere and landscape can cause significant changes in the highly sensitive aquatic community structures. This makes the biota mountain lakes to bellwethers for environmental changes due to climate warming, which they archive in sediments. Previous studies already indicated lake responses to warming that increase with altitude, as siliceous high-alpine lakes revealed massive biotic changes. However, mountain lake developments at lower altitudes, in calcareous catchments, and modulatory effects of ecotones such as the treeline are still rarely understood. Therefore, this PhD thesis studies diatoms as ubiquitous bioindicators and derives past warming in montane, subalpine and alpine calcareous mountain lakes. Including shifts in subfossil diatom communities, the study eventually classifies the variety of mountain lake responses to climate change.

On the basis of recent samples from 43 mountain lakes, it could be shown that diatom community shifts are accompanied by variances in average valve silicification. The novel approach of the 'Silicification Value' (SiVa) classifies species-specific silicification and averages it over a diatom assemblage. In the studied lakes, these mean SiVas were negatively correlated with summerly lake temperature, i.e. warmer waters seem to select for weaker silicified species. Transferring this finding to subfossil samples, this approach was able to fill the gap of hitherto existing temperature transfer-functions that failed in low-diversity hard-water mountain lakes. After establishing the palaeolimnological application, lake warming in Bavarian and North-Tyrolean mountain lakes was estimated to average 0.087 °C a^{-1}. Moreover, lakes deeper than 8–10 m heated up significantly weaker than shallow lakes and revealed an epilimnetic warming of August water temperatures of 0.013 °C a^{-1} since the 1970s. This threshold value in lake depth also appeared in species shifts in Bavarian and North-Tyrolean subfossil diatom assemblages. In total, five different lake types of climate change response could be defined, whereby lakes deeper than 8 m clearly revealed other tipping points than shallow lakes. The former is dominated by the timing of appearing plankton, whereas the timing of macrophyte establishment is crucial in the latter. Both, however, coincided with specific lake temperatures. Steepest compositional changes could be observed in shallow lakes that averaged > 14.5 °C in late-August and < 19.5 °C in deep lakes. Beyond common cirque lakes, doline lakes appeared to be the most resilient and showed the weakest changes in their specific diatom assemblages.

With future warming, recently resilient alpine shallow lakes are predicted to experience drastic changes soon, whereas steep changes in alpine deep lakes may slow down within the next decades. However, warming-driven catchment developments, e.g. uphill shifting treeline, affects especially the subalpine and alpine lakes and particularly results in an increase in nutrients. Simultaneously, future warming may enable new species of aquatic plants and algae to invade montane lakes. In addition, processes such as ongoing decreases in lake icing and increasing frequency of droughts, which cause heavier water level fluctuations, may result in further significant changes in the mountain lake biota. Consequently, these developments will also have significant effects for higher trophic levels of the food web such as invertebrates and 'higher' animals. Inferring from species shifts of the primary producers, faunal community structures in and around the lakes are likely to describe similar substantial changes. Eventually, these findings may serve as a comprehensive basis to evaluate and to predict globally the evolution of temperate to boreo-alpine mountain lakes.

Zusammenfassung

Die Klimaerwärmung ist mittlerweile weltweit spürbar, aber regional verschieden ausgeprägt. Gerade Habitate größerer Höhen und Breitengrade verzeichnen eine stärkere Erwärmung wegen rückläufiger Schneefälle und –bedeckungen sowie sich verlängernden Vegetationsperioden, wodurch sich dort zunehmend Pflanzen etablieren können. Solch massive Entwicklungen summieren sich gerade in Bergseen mit weiteren Folgeeffekten auf. Dessen Biozönosen sind aber an die harten Bedingungen im Gebirge hochadaptiert, sodass bereits geringste Veränderungen von Atmosphäre und Einzugsgebiet zu erheblichen Umstrukturierungen der aquatischen Lebensgemeinschaften führen. Somit sind Bergseen durch hochsensiblen Organismen charakterisiert und können daher als Gradmesser von Umweltveränderungen in Folge des Klimawandels fungieren, die zudem in den Sedimenten archiviert werden. Bisherige Studien deuten bereits an, dass die Reaktionen der Bergseen-Biozönosen mit der Höhe zunehmen, wie massive Veränderungen in silikatischen Hochalpenseen zeigten. Wie aber niedriger gelegene kalkreiche Bergseen reagieren und wie dies von den dortigen Ökotonen wie der Baumgrenze beeinflusst wird, ist noch wenig bekannt. Deshalb werden in dieser Doktorarbeit Gesellschaften von Diatomeen als allgegenwärtige biologische Indikatoren untersucht und daraus die bisherige Erwärmung von Bergseen hergeleitet. Zusammen mit Veränderungen in sedimentären Diatomeengemeinschaften werden schließlich die verschiedenen Reaktionen klassifiziert, die die unterschiedlichen montanen, subalpinen und alpinen Hartwasser-Bergseen mit dem Klimawandel beschreiben.

Anhand von Oberflächensedimentproben aus 43 Bergseen konnte gezeigt werden, dass Veränderungen der Diatomeengemeinschaften mit Veränderungen der durchschnittlichen Silifizierung

einhergeht. Der neue Ansatz des Silifizierungs-Werts (englisch: kurz „SiVa“) klassifiziert die verschiedenen Silifizierungsstärken der jeweiligen Diatomeenarten und wird letztlich über die gesamte Gesellschaft einer Probe gemittelt. In den untersuchten Seen war dieser gemittelte SiVa negativ mit der Seetemperatur im Sommer korreliert, d.h. wärmere Temperaturen begünstigen vor allem schwächer silifizierte Arten. Wird dies dann auf subfossile Proben übertragen, kann damit die Lücke bisher existierender Temperatur-Transferfunktionen füllen, deren Anwendung in artenarmen Hartwasserseen scheitert. Nach Etablierung der paläolimnologischen Anwendung konnte anhand der Diatomeen die mittlere Erwärmung der bayerischen und nord-tiroler Bergseen auf 0.087 °C a^{-1} beziffert werden. Zudem zeigten Seen, die tiefer als 8–10 m waren, mit einer Erwärmung des Oberflächenwassers von 0.013 °C a^{-1} eine signifikant schwächere Ausprägung als flache Seen. Dieser Schwellenwert der Seetiefe konnte auch bei Untersuchungen der Artenverschiebungen in den subfossilen Diatomeengemeinschaften der bayerischen und nordtiroler Bergseen gefunden werden. Insgesamt wurde hierbei fünf verschiedene Seetypen der Klimawandelreaktion definiert, wobei die tieferen Seen klar andere Kipppunkte aufzeigten als flache Seen. Bei ersteren war ist es entscheidend, wann Phytoplankton auftrat, während es bei letzteren das Auftauchen von Makrophyten ist. Beides lässt sich aber mit bestimmten Seetemperaturen in Einklang bringen. Die stärksten Veränderungen der Artenzusammensetzung ereigneten sich in flachen Seen, wenn sie Ende August 2016 wärmer als 14,5 °C, und in tiefen Seen, wenn sie kälter als 19,5 °C waren. Neben den üblichen Karseen waren aber auch Dolinenseen unter den untersuchten Bergseen. Diese erschienen am widerstandsfähigsten gegenüber dem Klimawandel und zeigten die geringsten Veränderungen ihrer vergleichsweise andersartigen Diatomeengemeinschaften.

Mit der fortschreitenden künftigen Klimaerwärmung werden gerade alpine flache Seen, die bislang noch relativ resilient erschienen, bald massive Veränderungen erfahren, während sich die massiven Entwicklungen in alpinen tiefen Seen in den nächsten Jahrzehnten abschwächen wird. Allerdings werden die durch den Klimawandel angetriebenen Sukzessionsprozesse der Einzugsgebiete wie etwa dem Anstieg der Baumgrenze vor allem subalpine und alpine Seen betreffen, wodurch insbesondere die Nährstoffverfügbarkeit ansteigen wird. Zugleich werden steigende Temperaturen es ermöglichen, dass neue Algen- und Wasserpflanzenarten in die montanen Seen einwandern können. Darüber hinaus kommen Prozesse wie sich verkürzende Eisbedeckungen und häufende Dürren hinzu, die stärkere Wasserspiegelschwankungen nach sich ziehen und die Biozönosen der Bergseen weiter signifikant verändern werden. Demzufolge sind auch Lebensgemeinschaften höherer Ebenen der Nahrungsketten bzw. –netze wie beispielsweise Wirbellose und ‚höhere‘ Tiere betroffen. Diese werden ähnlich den Artenverschiebungen der Autotrophen deutliche Veränderungen beschreiben. Diese Ergebnisse können letztlich dazu dienen, die Entwicklung von Bergseen gemäßigter bis boreo-alpiner Klimate weltweit zu bewerten und vorherzusagen.

1 Introduction

1.1 Mountain Lakes and Their Vulnerability in Times of Climate Warming

Figure 1.1: Waterfalls of the Gaisalpbach shortly after draining the Lake Gaisalpsee

Mountain lakes are a certain set of lakes, which is defined by the topography of their catchments. However, the main characteristic of the proximity to mountains or steep catchments (Moser et al. 2019) leads to great divergences of assignments to that specific lake group. In limnology, big lakes at the foothill of the Alps such as the Lake Chiemsee as well as small ponds – in England also called 'tarns' – were sometimes both called mountain lakes. In fact, the former are actually 'pre-alpine lakes' since true mountain lakes have to be defined as lentic systems 'on' a mountain. Defining true mountain lakes, their lake surface does not represent the deepest point in the immediate surrounding, i.e. they are not situated at the bottom of the (supra-)regionally dominating valley (Fig. 1.2). This implies that mountain lakes are embedded in a superordinate slope or mountain with summits above parts of the shoreline and the main valley usually on the opposite side. If any small mountain river drains the lake at the surface, it consequently falls towards the valley overcoming many meters of altitude and regularly forming a V-shaped lateral valley (Fig. 1.1). Geologically, true mountain lakes are cirque lakes in most cases, but also dammed by small end moraines or landslides, whereas the 'pre-alpine lakes' are glacier basin lakes.

According to this definition, true mountain lakes are distinctly smaller measuring a few hectares instead of some square kilometres in the case of pre-alpine lakes. Additionally, they are usually remote from direct anthropogenic influences such as intensive agriculture and tourism that can

Figure 1.2: Lake Taubensee located in a small cirque on top of a little mountain range and above the main valley of the Tiroler Ache near Schleching in the Chiemgau Alps.

disguise environmental impacts (Adrian et al. 2009). Apart from these preconditions, the biota of mountain lakes has to be highly adapted to harsh conditions of high elevations such as long winters with early freezing and late ice break-up, short vegetation periods, low temperatures and high UV radiation (Schmidt et al. 2004, Catalan et al. 2013, Rogora et al. 2018). Species communities in such habitats are therefore unique and very sensitive to environmental variances so that little changes in the limnology cause big changes in the specialised lake communities (Sala et al. 2000, Smol et al. 2005, Fjellheim et al. 2009, Williamson et al. 2010). This makes mountain lakes vulnerable, but also ideal sentinels and 'early warning systems' for global warming as it is supposed to be the only 'stressor' causing changes in the lake (Catalan et al. 2013, Rogora et al. 2018, Moser et al. 2019).

Global warming rises the temperatures all over the world. As warmer air can absorb more vapour from the oceans, there is plenty of cascading meteorological effects such as increasing precipitation and frequency of hurricanes and thunderstorms (IPCC 2014). This leads to changing global wind systems in the atmosphere, which equally support the contrasting extremes of droughts and wild fires in different places (IPCC 2014). However, many studies have shown that climate warming-driven changes in the environment climax in areas at high altitudes and latitudes (Smol et al. 2005, Mueller et al. 2009, Michelutti et al. 2015, Rühland et al. 2015, Weckström et al. 2016). As one of the currently most widespread explanations, this phenomenon is mediated by the most

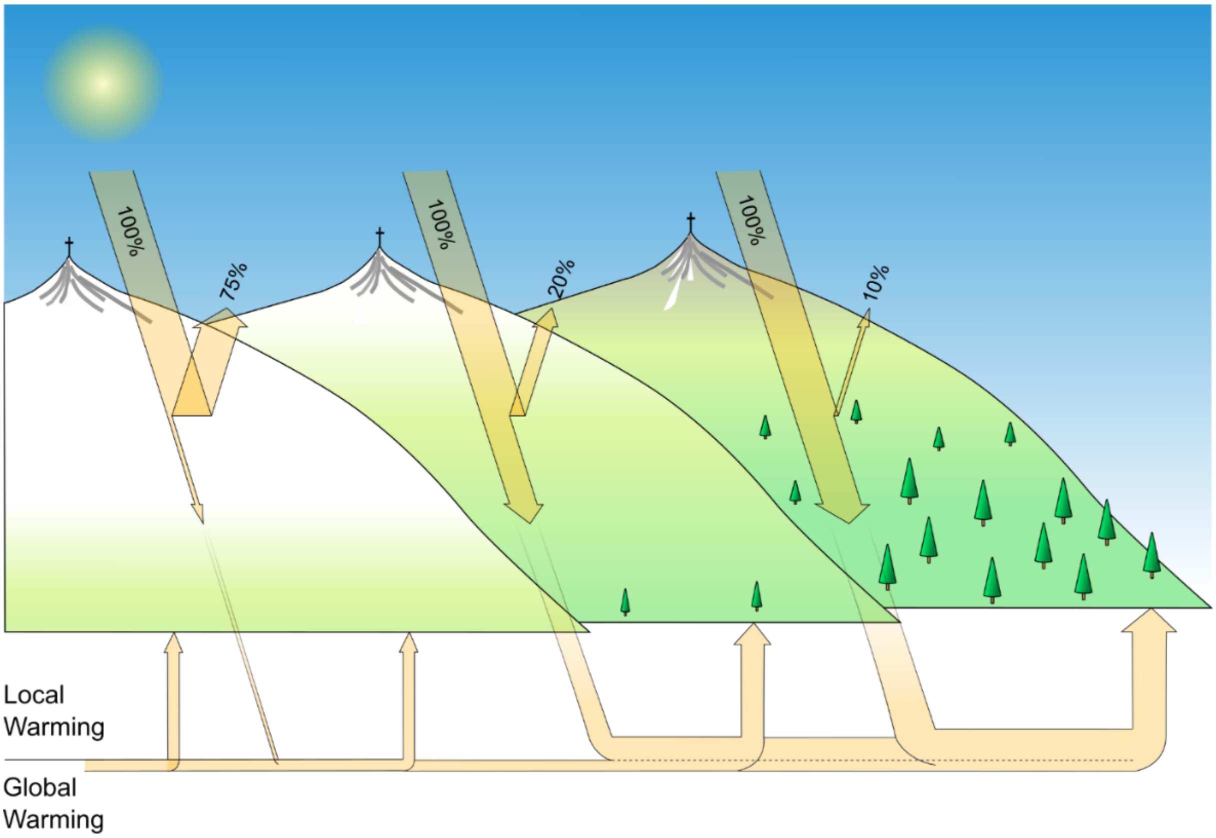

Figure 1.3: Positive feed-back loop of climate warming in alpine areas. The external effector of global warming leads to the decrease of snow versus the increase of vegetation that in sum decreases the albedo and multiplies the local warming.

significant decreases in snow cover at these areas. These are then supposed to be succeeded by the uphill migration of plant species and related ecotonal boundaries such as the treeline (Gehrig-Fasel et al. 2007, Pauli et al. 2012) as well as vegetation, soil development and enhanced weathering (Rosbakh et al. 2014, Rogora et al. 2020). Altogether, it sets off a positive feed-back loop as warming decreases the average annual albedo in such areas due to decreasing periods of snow cover versus upcoming dark vegetation that in turn absorbs an increasing amount of the long wave radiation (Fig. 1.3). Therefore, effects of global warming can be multiplied at higher altitudes and latitudes so that arctic and high alpine areas already warmed approximately 2–3 °C compared to pre-industrial times, whereas the global trend moves around +0,9 °C (EEA 2009, Allen et al. 2018).

Particularly in mountain lakes, another cascade of effects follows these rising temperatures and its consequences in alpine areas (Fig. 1.4). Primarily, shorter alpine winters lead to an earlier ice break-up in spring and later onset of ice cover that results in longer periods of open water with the ability to absorb thermal radiation (Lotter & Bigler 2000, Koinig et al. 2002, Karst-Riddoch et al. 2005, Rühland et al. 2008). As a consequence, mountain lakes can not only stratify earlier, but also

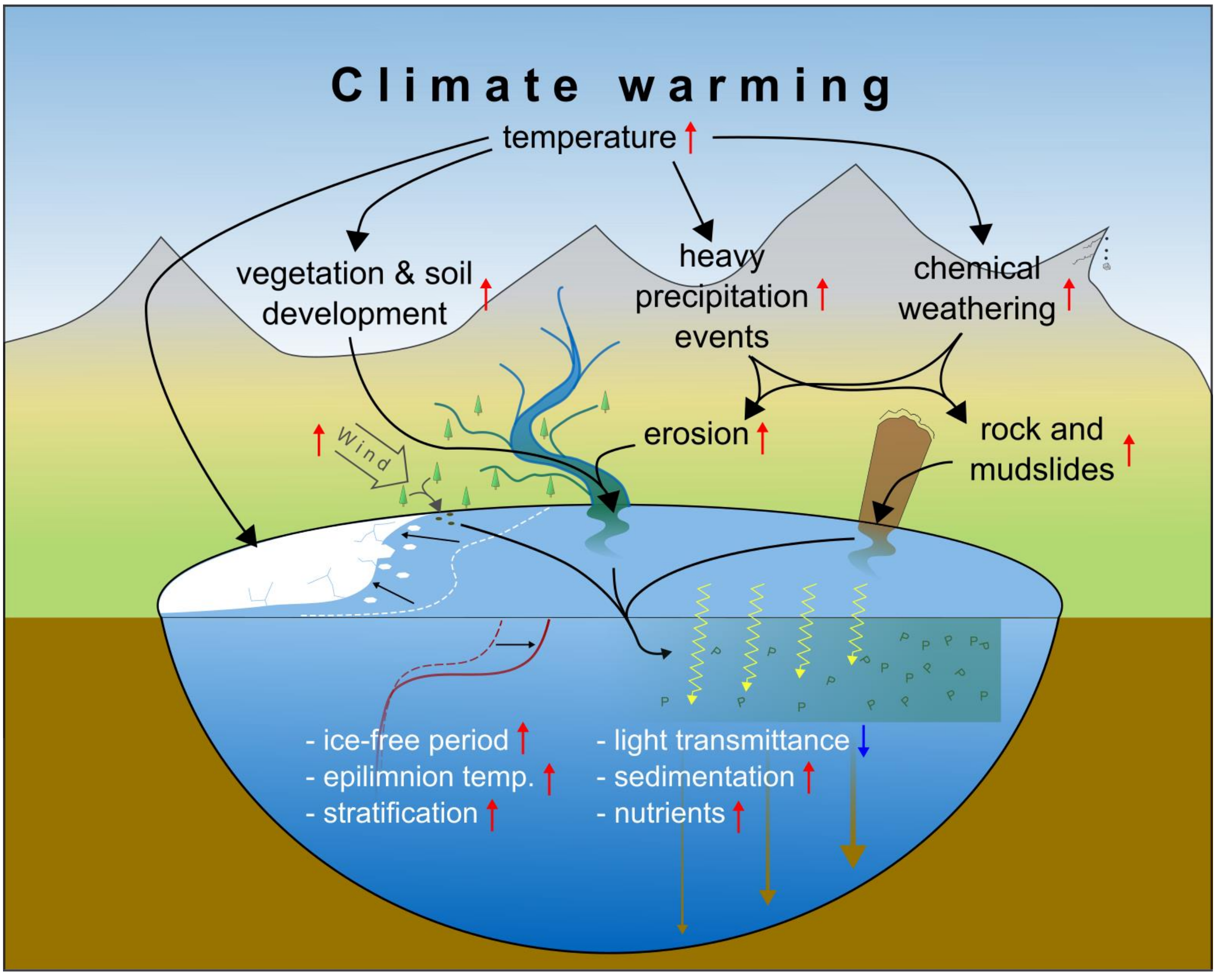

Figure 1.4: Cascading effects of climate warming on mountain lakes. Climate change and the increase in temperatures is also accompanied by vegetation and soil development in alpine areas and an increase in heavy precipitation events, storms, weathering and erosion. As a consequence, vegetation period and nutrient supply increases in mountain lakes versus decreasing transparency.

longer and stronger because the surface water layer, the so-called epilimnion, is able to reach higher temperatures and thermally stabilises the lamination. This in turn postpones the autumnal holomixis and therefore lake freezing. Such developments are crucial especially for the mountain lake plankton. An increase in thermal stability is supposed to cause shifts from robust species, which depend on frequent lake mixing, towards motile, small cell or colony-forming species (Winder et al. 2009, Daufrasne et al. 2009, Rühland et al. 2015). Nevertheless, global warming-driven changes in lake conditions also influence the lake benthos. In line with the soil development in alpine areas, increasing lake temperatures are supposed to increase substratum complexity in the littoral area and therefore species richness (Antoniades et al. 2005, Michelutti et al. 2015, Rühland et al. 2015). Apart from these 'direct' consequences of warming, there is also plenty of secondary effects in alpine catchments, which are sudden and dramatic rather than gradual as the aforementioned effects. Due to the higher temperatures and thus increasing amount of energy in the atmosphere, heavy precipitation events and extreme storms accompanied by torrential floods and rockslides have been observed to occur more often in the Alps within the past decades (Beniston 2006, Bogataj 2007, IPCC 2014, Bätzing 2015). Contrasting this fast erosion processes, warming also results in melting permafrost as well as intensified chemical weathering and erosion, which further promote rock- and mudslides. Accordingly, the input of organic, if the catchment characteristics allow, and inorganic material into mountain lakes increases as well and changes light and nutrient conditions (Koinig et al. 1998, Lotter et al. 1999). Eventually, this in combination with the longer growing seasons lead to an increasing algal productivity in mountain lakes and constitutes dramatic changes of the vulnerable and highly sensitive alpine lake biota (Douglas & Smol 1999).

1.2 Overview of Applied Palaeolimnology in Climate Change Research

The reconstruction of variable lake characteristics based on analyses of sediments is a special scientific discipline, the palaeolimnology. It was already a theme almost two centuries ago for the first time (Last & Smol 2001). Comparable to evaluate the impacts of lake pollution (Davidson & Jeppesen 2013), there is an increasing interest in its application in climate change

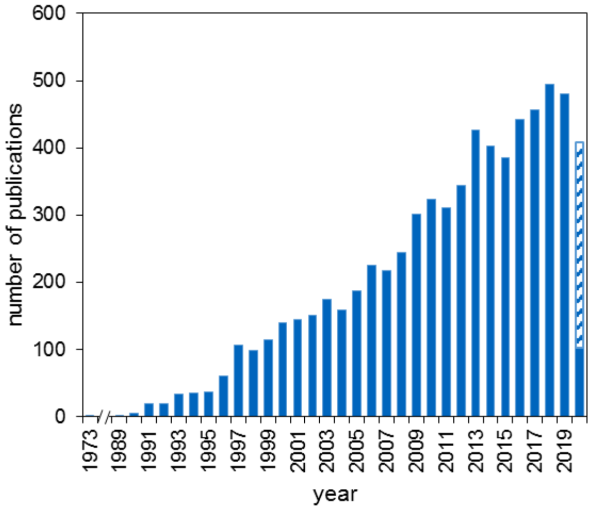

Figure 1.5: Number of climate change-related publications with applied palaeolimnological techniques. Bar of 2020 is extrapolated and refers to the 1st calendar quarter. Results base on the number of results in the Web of Science searching for the words „lake“, „climate change“ and „pal*“ including all related spellings.


Figure 1.6: Section of the varved sediment core from the Lake Enge-ratsgundsee. Dark organic layers form during summer, bright inorganic in winter or after heavy precipitation events.

research as it crucially affects aquatic habitats (Fig. 1.5). To extract useful information from sediment cores, robust legacies from the lake are needed that can persist several decades and centuries and respond to changes in lake conditions (Battarbee et al. 2001). Such indicative remnants can then be perfectly archived and concentrated in the lake sediments (Smol 2008). Given that there are low turbation activities in the sediment such as burrowing macroinvertebrates (bioturbation) or physical processes such e.g. limnocrenes, they are laminated in a chronological order allowing sediments to read like a book – ideally, the sediment is 'varved' (Fig. 1.6). The pattern of such varves can already indicate conditions of the main seasons. Dark organic matter emerges in summer for example due to algal productivity. In contrast, bright inorganic layers develop during or after winter because of snowmelt or heavy precipitation events that result in enhanced erosion and increased inflow of water as well as fine sediments (Zolitschka et al. 2015). Accordingly, for instance thick dark layers would imply a warmer summer with higher lake productivity. In addition to such basic observations, numerous techniques were elaborated in the field of palaeolimnology to study the past of lakes and their catchments in more detail.

1.2.1 Physico- and Geochemical Methods in Palaeolimnology

Based on the colour differences of sediment laminae, upcoming imaging techniques try to infer climate proxies just by analysing sediment cores optically (Nederbragt & Thurow 2004). Sediment colour is no longer a mere descriptive characteristic, but a quantitatively measured value with possibilities for statistical calculations and environmental reconstructions. Moreover, **optical analyses** of sediment cores is a non-destructive way to infer data from the past. Such techniques can also deliver a precision from years down to individual seasons depending on the methodological and stratigraphic resolution of imaging, e.g. digital resolution of the used camera, and lamination quality of the sediment cores (Nederbragt & Thurow 2004). The sophisticated nature of these methods spans over a wide scale from easy digital cameras with grey scale or RGB colour data up to highly complex X-ray fluorescence (XRF) scanners, which refer to characteristic fluorescence patterns that are indicative of certain metals or other sedimentary compounds (Nederbragt & Thurow 2004, Ojala 2004, Croudace et al. 2006). Despite its possibilities of a high throughput and non-destructive methodology, inferred environmental proxies are usually limited to a physico-chemical level such as wind speeds inferred by grain sizes and shapes or changes in trace element compositions. Hence, the palaeolimnologist can only indirectly draw consequences for historic biota and their development. Additionally, imaging analysis depend on undisturbed varved sediments, which is only the case in a certain type of lakes.

A more destructive method but with less preconditions of the studied core, a broader environmental and better biological context is the application of **geochemical methods**. As a sediment core needs to be subsampled for further analysis – usually into uniform layers –, it is independent of any lamination quality. Equivalent to sophisticated imaging analysis, a basic application in this field is the extraction of trace elements from sediment samples and corresponding detection techniques. As an advantage, however, this allows to precisely determine the individual element concentrations and their accumulation rates in the sediment (Boyle 2001). Additionally, geochemical extractions are able to detect a greater set of elements, whereas imaging analyses may oversee rare trace elements or compounds that are unfortunately not located on the visual surface of the dissected sediment core. Although needing a longer and more complex procedure than e.g. XRF scanning, such precise geochemical data that are extracted directly from the sediments are needed to calibrate the fluorescence patterns of newly developed and non-destructive imaging methods.

A higher geochemical level than extracting trace elements are **minerals**, which cover a wider interest in climate change issues. Mineralogical sediment analyses focus on inorganic geochemical compounds that can immediately hint on certain lake conditions (Last 2001). As an example, increasing amounts of the mineral calcite can be indicative of warming lake temperatures and carbonate concentrations. As a reason, physicochemical carbonate precipitation due to the lime-carbonic acid equilibrium and/or biogenic condensation caused by algae growth increase with higher water temperatures, so that the sedimentation of calcite minerals increases (Lenz et al. 2018). Instead, the presence of pyrite can be the result of anoxic conditions and consequent bacterial activities, which naturally appear in lakes of higher trophy or in case of meromixis (Berner 1984). Last (2001) lists hundreds of minerals that can be found in lake sediments after diffraction, e.g. using X-ray, and geochemical analytical procedures.

In contrast to the analyses of inorganic proportions of the sediment, geochemical studies on the organic content, e.g. TOC (total organic carbon), is an immediate remnant of lake and catchment biota. This can be inferred from the so-called loss-on-ignition, i.e. quantifying the 'burnable' amount of a sediment sample. TOC is not only directly indicative of the autochthonous primary production. It also integrates the degree of degradation of the sedimented biomass, its preservation after sedimentation and can also deliver information about autochthonous input (Meyers & Teranes 2001). In order to estimate the origin of the organic matter, **stable isotopes** are widely used proxies. Carbon and nitrogen isotopes are typical tracers of the material's origin (Wolfe et al. 2001, Talbot 2001). This can be obtained by comparing the sediment isotopic signature with the original matter, e.g. sediment samples with living beech leaves, or using ratios of these elements. Autochthonous material such as algae or macrophytes reveal significantly lower C/N ratios than terrestrial vascular plants due to different isotopic signatures of the nutrients and physiological preferences (Meyers & Teranes 2001, Heyng et al. 2012). Furthermore, these signatures can also hint on bacterial activities, e.g. methane production because of anoxia (Hollander & Smith 2001, Finlay & Kendall 2007).

Apart from carbon and nitrogen, water and oxygen isotopes are popular in geochemical and palaeoecological studies. The relation between heavy and light oxygen atoms is one of the main methods, which were used to reconstruct atmospheric conditions such as air temperature over thousands to millions of years, for example using Antarctic ice cores (Ito 2001). This relies on the fact that the isotopic signature of oxygen is significantly dependent on air temperature and evaporation rates.

A very specific palaeolimnological discipline is the investigation of **fluid inclusions** in sediments (Lowenstein & Brennan 2001). This relies on microscopic water samples that were encapped and preserved, so that the isotopic signature and trace elements of the historic water can now still be analysed. Another possibility are minerals such as salts or calcite crystals that emerged from fluid intrusions. However, this only works when the inclusions and their remnants are isolated from the current lake and ground water.

1.2.2 Palaeobiological Methods in Palaeolimnology

In contrast to the physicochemical applications and mainly analytical methods in palaeolimnology that studies sediment properties itself and its elementary composition, certain organic sedimentary compounds can be extracted. Instead of indirectly transferring the conditions of a lake and its biota from the composition of atoms and inorganic minerals, the biota itself can left its marks in the sediments. Depending on the environmental sensitivity of these organisms, the subfossil composition can be indicative of lake conditions and reveal bioenvironmentally relevant tipping points of the lentic ecosystem. However, the survival of such indicative deposits can be challenged by the pore water chemistry, which often deviates from the lake conditions (Maassen et al. 2005). Due to degradation processes, sediments are usually anoxic and can therefore differ significantly from neutral pH values. Moreover, mechanical 'stressors' like sediment weight can appear. Therefore, it is difficult to detect and extract instable molecules or unprotected and fragile remnants of sedimented organisms. Nevertheless, with the progress of analytical techniques in palaeolimnological research, an increasing spectrum of molecules and their degraded derivates are able to serve for the reconstruction of lake histories. For example, the comparably soft matter of plants, especially water plants, or algae can be degraded quickly by destruents such as bacteria and invertebrates just like on a compost heap, but in a decelerated or mitigated speed because of the anoxic conditions in sediments. Despite this, the organic matter of primary producers can still leave molecules such as **pigments** or the **DNA**, which can still be detected by extraction and chromatographic or molecular-genetic methods (Leavitt & Hodgson 2001). The composition of the pigments or the groups of detected DNA can then mirror the past composition of the algae, bacteria or other organisms and indicate corresponding lake conditions (Appleby 2001, Jørgensen et al. 2012, Pansu et al. 2015). Accordingly, the increase in pigments of obligate planktic algae would either imply an increase in water temperature or lake depth (Lami et al. 2000, Buchaca & Catalan 2008).

Furthermore, the legacy of historical aquatic biocoenosis can leave more than just molecules for complex analytical methods. Accordingly, not only certain animals and higher plants are able to form stabile micro- and macroscopic structures that were buried in the sediments such as popular archaeological finds of bones and splinters, but also pristine organisms such as **protozoa**. Within the Amoebae, the big order of the Acellinida is able to build robust microscopic proteinaceous or agglutinate shells. Such remnants have even been found in Carboniferous deposits, i.e. older than ca. 300 million years (Wightman et al. 1994, Beyens & Meisterfeld 2001). The composition and abundance of species-specific shells, the so-called tests, can in turn be indicative of aquatic conditions but reach highest abundances in wetlands and bogs (Heal 1962). For example, subfossil testate amoebae allowed reconstructing the depth of water tables in habitats that appear as peat lands nowadays (Charman et al. 1999).

Other leftovers of pristine life forms are siliceous spicules from the skeletons of **sponges** that also appear in freshwater habitats (Frost et al. 2001a). As these sponges require certain chemical conditions that are accompanied by a good water quality (Frost et al. 2001b), the abundance and shape composition of such freshwater sponge spicules serve as a palaeolimnoligcal tool (Harrison 1974).

In addition, signs of higher sensitive animals can be found in lacustrine sediments for climate change issues as well. Two of the most widely used taxa belong to the arthropods: **Cladocera** and **Chironomidae**. The former group of the 'water fleas' such as the famous genera *Daphnia* O.F. MÜLLER and *Bosmina* BAIRD are ubiquitous zooplankton. They build up a chitinous exoskeleton, which can withstand demanding sediment conditions at least in parts, but these parts, e.g. head shields or postabdomen with claws, are specific to individual species (Korhola & Rautio 2001). Making it a powerful tool for palaeolimnology, several genera and species are sensitive to certain lake conditions (Kamenik et al. 2007). For instance, in contrast to *Daphnia*, *Bosmina* can dominate during warm and eutrophic situations that are accompanied by cyanobacterial blooms (Korhola & Rautio 2001). Therefore, they can be used for reconstructing climate change impacts (e.g. Labaj et al. 2017). Due to this sensitivity, there are already several established transfer-functions to reconstruct past lake conditions (e.g. Lotter et al. 1998, Kattel et al. 2008, Davidson et al. 2011) – similar to Chironomidae (e.g. Brooks 2006, Luoto 2009, Medeiros et al. 2019). This family is one of the most common within the Diptera in lake sediments. Its composition significantly reacts on changes in lakes and thus sediment conditions such as oxygen saturation. Different to planktic Cladocera, only the larvae of the midges are in the palaeoecological focus as they leave chitinous and robust head capsules allowing to identify the species composition (Walker 2001).

Extending the zoological possibilities in palaeolimnology, there are much more animals that inhabit lentic habitats, leave remnants in the sediments and whose species composition is indicative of certain lake conditions. Even within the arthropods, there are more groups than the aforementioned such as **oribatid mites** (Solhøy 2001) and **ostracoda** (Holmes 2001), but also beyond them, there are **freshwater molluscs** (Miller & Tevesz 2001) and **fish** (Patterson & Smith 2001) worth to mention. However, these zoological groups are less popular and more distinctive in its distribution and abundance, particularly concerning the useful amount of leftovers in the sediment.

Apart from zoological remains, representatives of a nutritional order below, the primary producers such as plants and algae are present in any aquatic habitat and in a greater numerical order. In freshwater habitats, high abundances of algae can blur the water and significantly mitigate the transparency down to some centimetres. This does not remain traceless for the lake sediment, so that primary producers constitute the majority of sedimentary organic matter. Making this the crucial advantage, this thesis focuses on the primary producers in mountain lakes as they are supposed to appear in the studied lake sediments reliably in sufficient amounts. On the one hand, some palaeolimnological investigations use **plant macrofossils** or – with greater popularity – **pollen** (Fig. 1.7). However, the probability to find plant macrofossils in the sediments not only depends on the catchment vegetation, but also on the effectivity to function as a good macrofossil trap (Birks 2001). Therefore, this is strongly affected by the topography of the direct surrounding, degree of wind protection and the amount of direct inflows. These biasing effects, however, constitute a disadvantage of this discipline when studying widely ranged and dozens of lakes. Instead, pollen appear everywhere where vegetation covers the catchment. Stratigraphical pollen analyses become popular especially to evaluate the 're-greening' of landscapes during deglaciation after the last Ice Age (e.g. Liu et al. 1998, Bennett & Willis 2001, Pederson et al. 2005). Nevertheless, pollen analyses are beyond the scope of this Ph.D. thesis as they are a terrestrial signal with a focus on developments of the catchment and not of the lake itself.

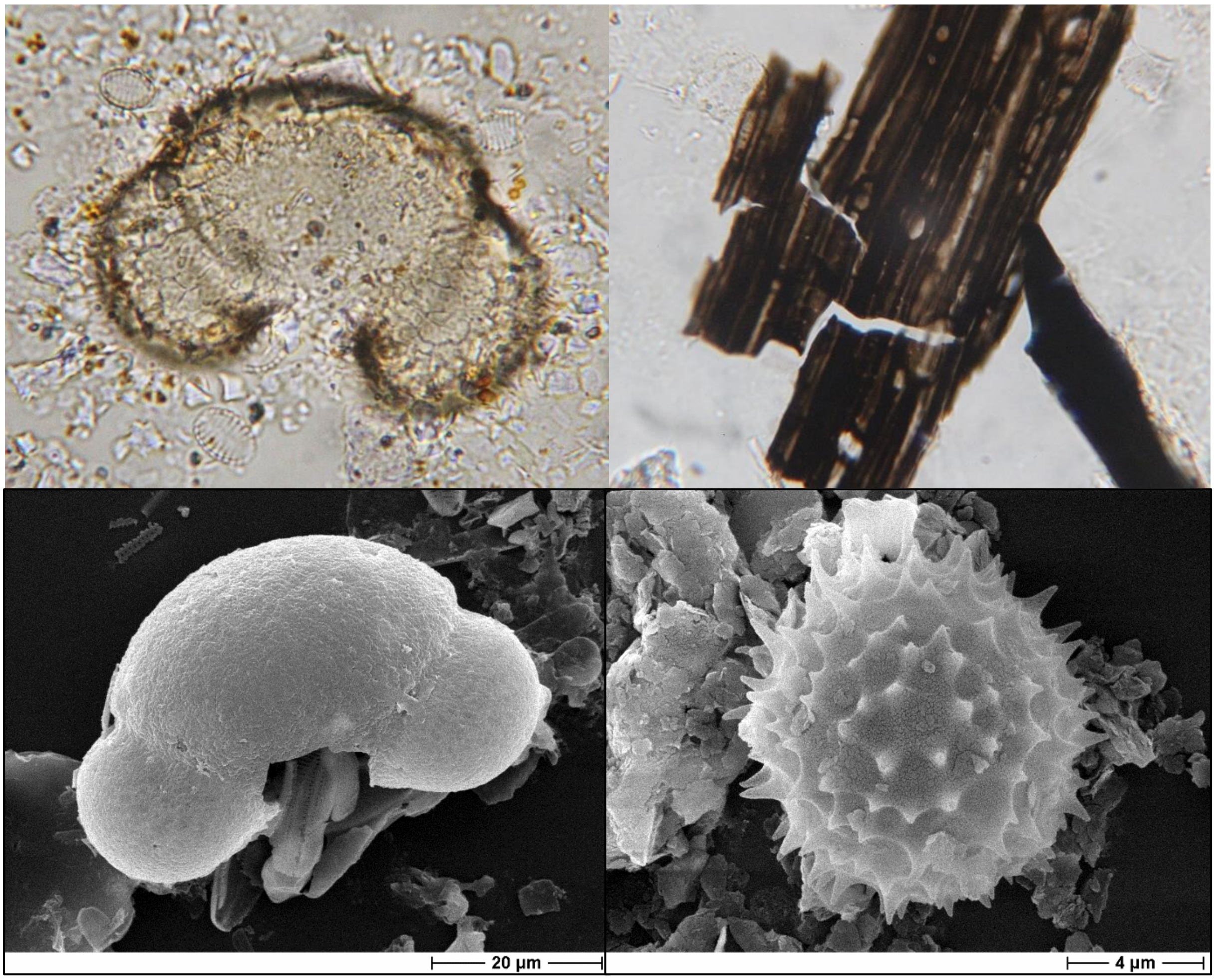

Figure 1.7: Microscopic leftovers of plants and algae in lake sediments. Left: picture Coniferous pollen in the sediments of Lake Gaisalpsee (top) and of Lake Mittersee (bottom). Top right: Peace of reed in the sediments of Lake Mittersee. Bottom right: Chrysophyte cyst in the sediments of Lake Engeratsgundsee. Top pictures are taken by light microscopy, bottom pictures by REM. For lake information, see chapter 2 & 3. Picture credit: W. Küfner.

Within lacustrine habitats, **chrysophyte cysts** and diatoms are the main contributors to the subfossil composition in sediments. Both form microscopic siliceous structures and contain highly sensitive species, so that they serve as a basis for numerous transfer-functions in palaeolimnology (Smol 1988, Lotter et al. 1997, Battarbee et al. 2001). Chrysophytes comprise hundreds of species, which form individual cysts with and without complex structures (Fig. 1.7)(Zeeb & Smol 2001). These structures can fall off the cyst and remain as scales within the sediment, so that they can also serve as a proxy to evaluate preservation of the siliceous indicators. However, most of the species are euplanktic implying very low abundances in shallow lakes.

Consequently, **diatoms** remain as one the most abundant life form in any lake with a ubiquitous distribution from periphytic to planktic species making them to appear in any lake sediment usually in high abundances (Smol 2008). Furthermore, diatoms form structures that can withstand the demanding sediment conditions as a whole, so that they can be found even in several hundred-year-old sediments (Battarbee et al. 2001). Therefore, diatoms are the best bioindicators for the scope of this thesis. The next chapter focuses on the biology, characteristics and advantages of diatoms for palaeolimnological studies.

1.3 Biology and Bioindicator Characteristics of Diatoms

Diatoms are unicellular eukaryotic organisms that contain yellow-brownish chloroplasts. They allow diatoms to photosynthesise and give them the typical colour of brownish diatomaceous biofilms like on rocks in rivers. The taxonomic placement of this algae group is still not finally clarified; the current status is shown in Fig. 1.8. Two of the three main important features of diatoms making them ideal bioindicators in palaeolimnology are their ubiquitous and abundant distribution in aquatic ecosystems and the formation of two 'shells' out of silicate around the actual cell body, the so-called 'valves' conferring their robustness. These structures survive the actual living cell and are the 'immortal' remnants that are well preserved in lake sediments (Battarbee et al. 2001, Smol 2008). Valves can be full of nanostructures like nodes, spines, furrows ('raphe') and

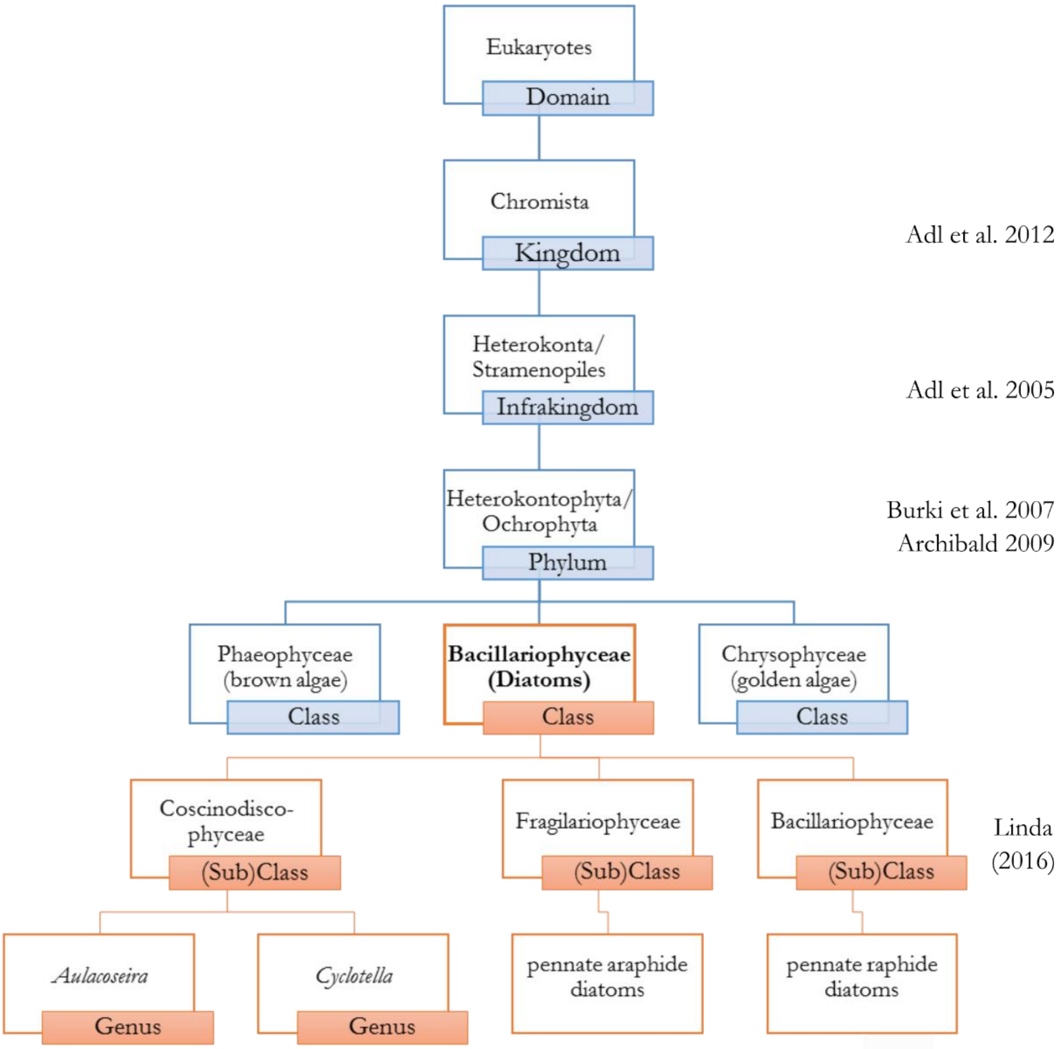

Figure 1.8: Current status of taxonomy of the diatoms (orange) with classification of two common centric genera.

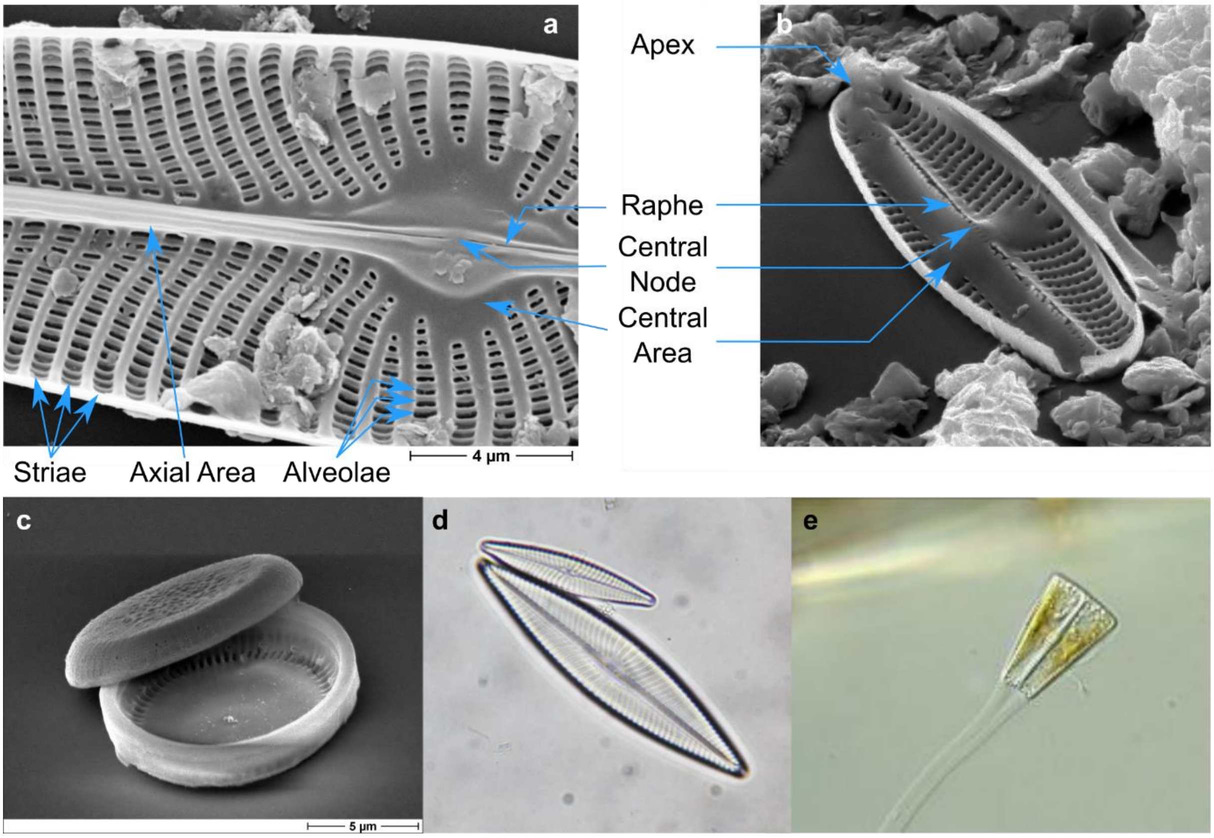

Figure 1.9: Structure of diatoms. a) Main species-specific structures in the central section of a valve of *Navicula radiosa* and b) of a *Sellaphora joubaudii* at the same magnification. c) REM picture of the epi- and hypotheka of a *Cyclotella delicatula*, d) LM picture of a *Navicula concentrica* and *N. krammerae* and e) living mini-colony of a *Gomphonema*, which is attached to a substratum with a viscous stalk. Picture credit: W. Küfner.

pores or ‘alveolae’ that can be arranged in stripes or ‘striae’ (Fig. 1.9). Each species has its own set and variety of those nanostructures, so that valves from over a hundred year old sediment sample can easily be identified under the microscope as they range from 5 to 300 µm (pers. obs.). With these prerequisites, diatoms are well suited to evaluate the development of subfossil assemblages along a sediment core and its integrated time span.

The third main advantage of diatoms is that a big percentage of the thousands of different species described in literature is specialistic and more or less strictly dependent on definite ranges of different lake proxies (Battarbee et al. 2001). Accordingly, each diatom community with its species composition is indicative of certain lake conditions. In combination with the short regeneration times of diatoms, they are able to mirror changes in lakes and their catchments within days (Morin et al. 2008). As an example for morphological adaptations and specialisations of diatoms to distinct ecological niches, some species are able to move actively. Such species are mainly periphytic as they need substrates to move on. Different to typical locomotion apparatuses such as cilia, raphid diatoms can secret adhesive mucilage through the raphe making them capable of gliding on surfaces (Edgar & Pickett-Heaps 1984, Poulsen et al. 1999). Araphid and centric diatoms lack a raphe and can only be moved passively. The latter group exclusively contains planktic species that live in the open water. They either rely on recurrent mixing and are therefore stronger silicified to increase their robustness to survive turbulences in the water column such as *Aulacoseira* THWAITES (Rühland et al. 2015) or need different adaptations to avoid sinking to the dark unviable hypolimnion. Planktic species, which are adapted to calm and stratified lake conditions form light valves, colonies or spines, so that they can 'hover' in the water column and promote buoyancy for staying in the euphotic area of a lake (Padisák et al. 2003, Winder et al. 2009, Berthon et al. 2014). Accordingly, these species are indicative of stratified conditions or simply warmer temperatures in case of areas, where non-polymictic lakes are typical. Combining such bioindicative information with subfossil assemblages from sediments, precise reconstructions are possible when ecological preferences, optima and tolerances are known. Based on this, several transfer-functions already exist to calculate for instance past eutrophication (Stoermer & Smol 1999), changes of pH such as acidification (Weckström 1997, Koinig et al. 2002), air temperature (Anderson 2000, Larocque & Bigler 2004) or – with increasing popularity – to evaluate climate warming in lakes (Pienitz et al. 1995, Bigler & Hall 2003, Smol et al. 2005, Karst-Riddoch et al. 2005, Rühland et al. 2008).

Consequently, diatoms serve as ideal bioindicators to evaluate environmental changes in aquatic systems. However, transfer-functions are challenged by dominances of generalistic species since they need a minimum amount of indicative and specialistic species to be statistically valid. Moreover, known preferences and tolerances, which transfer-functions rely on, are only limitedly transferrable to other areas of different conditions such as bedrock geology. Therefore, species ecologies usually have to be re-evaluated in the so-called 'training sets' before applying such functions in 'foreign' biomes.

1.4 Objectives

Previous studies on high-alpine mountain lakes revealed a strong vulnerability to climate warming, which triggers changes in autotrophic aquatic community structures as the very first responsive organisms. This indicates a correlating link between lake altitude and climate change impact. However, it is still not fully understood how the forest and treeline ecotones as well as differential lake geologies may modulate this relationship in mountain lakes at lower altitudes. As a contribution to that, this work investigates the recent development of the mountain lake biota from below the forest line until above the treeline in the calcareous Bavarian Alps.

The basic objective of this work was to assess the diversity of ecological responses of primary producers in the Bavarian and North-Tyrolean mountain lakes to recent climate warming. For that purpose, a broad spectrum of montane, subalpine and alpine mountain lakes was selected including the documentation of a variety of lake characteristics. As a second step, the autotrophic assemblages of the entire mountain lake set were evaluated using diatoms as representative bioindicators. These assemblages then served as a training set to better understand past in-lake processes and to infer certain lake proxies such as the individual lake warming. In order to finally study the past biotic development, time series of subfossil assemblages from sediment cores were analysed and compared with the training set.

Based on this, the following general hypotheses could be tested:

1. The composition of the highly adapted diatom communities depends on the altitude, thus the lake temperature and is therefore susceptible for climate warming.
2. Physical warming of the mountain lakes inferred from shifts in subfossil diatom assemblages both increase from montane to alpine lakes.
3. Lake and catchment characteristics within the study area, particularly ecotonal boundaries such as the treeline, crucially modify the responses of the mountain lake biota.

The results should clarify how vulnerable montane, subalpine and alpine mountain lakes are to global warming and which lakes appear to be the most resilient in the climates of the Alps in central Europe. Furthermore, conclusions for the future susceptibility and development of the mountain flora and fauna were aimed to draw.

2 Materials and Methods

2.1 Study Sites

The study is based on a total of 43 hard water mountain lakes situated in the Northern calcareous Alps along the Bavarian-Tyrolean boarder (Table 2.1). The complete study area extends over 220 km in east-west direction and comprises three altitudinal levels from 955 to 2469 m a.s.l. (47°11' to 47°45' N latitude, 10°15' to 13°01' E longitude, Fig. 2.1). The classification of the altitudinal levels mainly followed the catchment characteristics of the direct vicinity of each lake. Montane lakes were embedded within conifer-dominated forests (*Picea abies* (L.) KARST, *Larix decidua* MILL. with some *Acer pseudoplatanus* L. and *Fagus sylvatica* L.) and are all located below 1250 m above sea level. In catchments of subalpine lakes, the forests become lighter and increasingly mix with patches of grassland and *Pinus mugo* TURRA. In the Bavarian Alps, these lakes can usually be found between 1250 and 1700 m a.s.l., except one the southernmost subalpine lakes of the study area in Tyrol that is situated at 1799 m. The surroundings of alpine lakes lack any forests apart from patches of dwarf

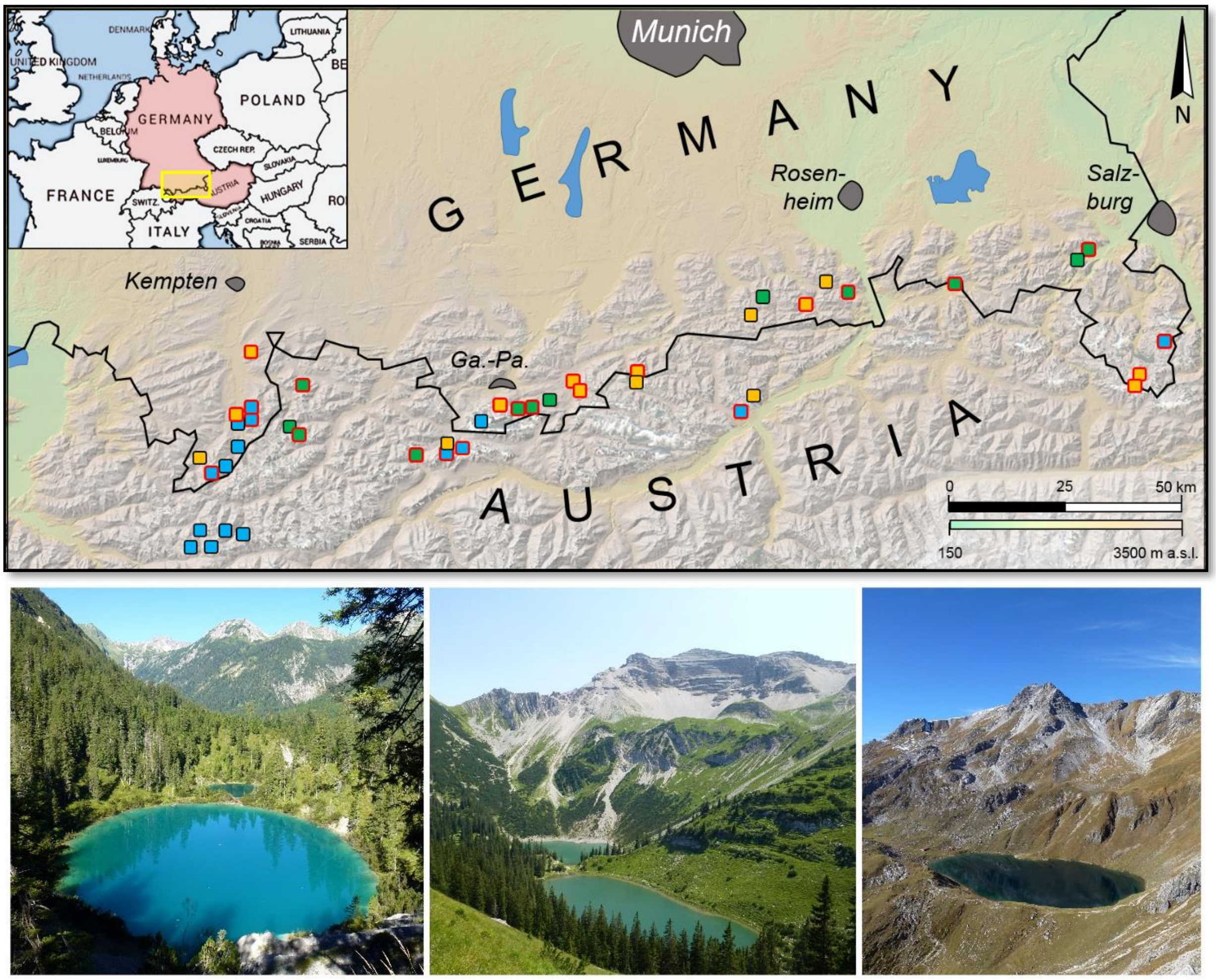

Figure 2.1: Map of the 43 investigated mountain lakes along the Bavarian-Tyrolean boarder (top) and altitudinal levels of the exemplary Bavarian mountain lakes (bottom). Colours represent the altitudinal level: blue – alpine, orange – subalpine, green – montane mountain lakes. Boxes with red frame: sediment cores were taken and analysed additionally. Montane (bottom left) with dense coniferous forests, subalpine (b. middle) with a mix of light forests and grasslands, and alpine lakes (b. right) with meadows and rocky screes.

Table 2.1: Overview of all considered lakes. The individual lake codes, altitudes, areas and depths are given in the centre columns. The two columns on the right visualise, if a surface sediment sample (S.S.S.) and a sediment core was taken. The former were used for the chapter 3 study, the latter for the studies in chapter 4 and 5.

Alt. Level	Lake	Code	Altitude [m a.s.l.]	Area [ha]	Depth [m]	S.S.S.	Sed. Core
Montane	Bichlersee	Bic	955	1.50	11.00	•	•
	Falkensee	Fal	760	1.00	15.00	•	
	Ferchensee	Fer	1060	10.00	19.50	•	•
	Frillensee	Fri	973	1.20	5.53	•	•
	Höfersee	Höf	1192	0.60	1.85	•	•
	Lautersee	Laut	1013	12.00	18.00	•	•
	Mittersee	Mit	1082	3.30	4.65	•	•
	Suttensee	Sut	995	1.50	1.50	•	
	Großer Sieglsee	SieG	1207	0.80	20.18	•	•
	Kleiner Sieglsee	SieK	1205	0.10	11.25	•	
	Taubensee	Tau	1138	4.00	14.57	•	•
	Wildensee	Wild	1136	2.30	2.35	•	
Subalpine	Nördlicher Delpsee	DelN	1600	0.60	1.25	•	•
	Südlicher Delpsee	DelS	1600	0.20	4.15	•	
	Funtensee	Fun	1601	2.50	4.53	•	•
	Oberer Gaisalpsee	GaiO	1769	0.70	2.90	•	
	Unterer Gaisalpsee	Gais	1508	3.40	4.07	•	•
	Grünsee (Berchtesgaden)	Grün	1474	3.45	6.93	•	•
	Grünsee (Spitzing)	GruW	1393	2.30	5.75	•	
	Guggersee	Gug	1725	0.10	1.93	•	
	Hörnlesee	Hörn	1601	0.45	1.80	•	•
	Röthensteiner See	Roe	1450	1.20	7.55	•	
	Schachensee	Scha	1680	2.00	4.40	•	•
	Seebensee	Seeb	1657	6.40	18.35	•	
	Unterer Soiernsee	SoE	1552	2.00	5.50	•	•
	Oberer Soiernsee	SoW	1558	3.00	11.50	•	•
	Soinsee (Wendelstein)	SoiN	1520	0.33	4.65	•	
	Soinsee (Rotwand)	Soi	1458	4.00	8.17	•	•
	Ziereinersee	Zie	1799	3.00	15.10	•	
Alpine	Auf der Lacke	Adl	2294	1.90	1.65	•	
	Brendlsee	Bre	1903	0.50	6.15	•	•
	Drachensee	Dra	1874	5.30	20.65	•	•
	Eissee	Eis	1827	0.67	3.85	•	
	Engeratsgundsee	Eng	1876	3.60	17.32	•	•
	Grubersee	Grub	2060	0.50	3.50	•	•
	Laufbichlsee	Lauf	2012	0.80	5.55	•	*
	Rappensee	Rap	2047	2.30	7.83	•	•
	Schiefersee	Schi	2300	2.00	5.50	•	
	Seeleinsee	Seel	1809	0.40	5.35	•	•
	Mittlerer Seewisee	SeeM	2424	0.50	4.05	•	
	Oberer Seewisee	SeeO	2469	1.60	13.10	•	
	Unterer Seewisee	SeeU	2224	2.40	1.73	•	
	Stuibensee	Stu	1921	2.00	5.08	•	

pine (*Pinus mugo*) and are dominated by alpine meadows (e.g. *Rhododendron hirsutum* L., *Carex sempervirens* VILL.) on poorly developed soils and rocky areas (Fig. 2.1). These lakes are among the highest lakes of the entire Northern calcareous Alps and range from 1700 to almost 2500 m a.s.l. As the exception of one subalpine lake indicates, the ranges of the three levels as well as the forest and treeline as their ecotonal boundaries in between are dynamic, which has already been observed by Alexander von Humboldt almost 200 years ago. On a global perspective, these characteristic lines depend on climate and latitude and increase in altitude towards the equator (Charrier 2011, Paulsen & Körner 2014).

The geology of all catchments is dominated by carbonaceous rocks such as Triassic and Cretaceous limestones, dolomites and marlstones as bedrocks or glacial deposits, e.g. lodgements and moraine deposits. With the exception of two doline lakes and one landslide lake, all studied mountain lakes are of glacial origin and mostly cirque lakes, some are moraine lakes.

In the field, each lake was visited at least two times, i.e. in early summer and in autumn. During the first visit, a mountain lake was measured bathymetrically using the sonar system HDS 8 (Lowrance, Tulsa, USA) to find its deepest area. At this place, a buoy with a rock as an anchor was installed with two temperature loggers close to the lake bottom and ca. 0.5 m beneath the surface (Fig. 2.2). They documented the water temperature throughout the summer until they were removed again at the second visit. Subsequently, the buoy was used to continuously keep the boat above the deepest

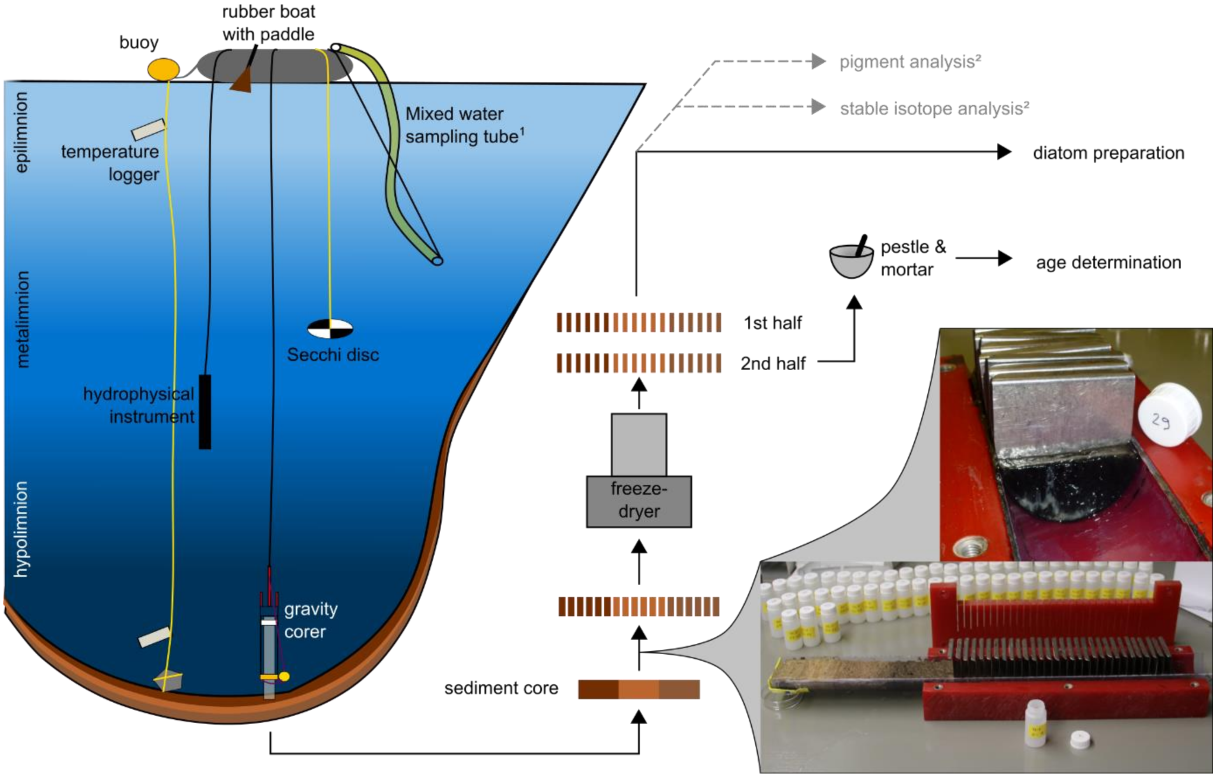

Figure 2.2: Overview of a mountain lake sampling and sediment core processing. Except the littoral sampling, the entire lake sampling took place while being anchored at the buoy. 1) Mix-water sampling technique collecting the entire upper water column with the diameter of the used hose as described in Lenz et al. (2020). 2) Two third of the first core half were used for the analysis of other substances.

area to measure the hydrophysical parameters in 1 m-steps along the greatest depth gradient using the Multisonde 350i (WTW, Weilheim, Germany), water transparency using a Secchi disc and to take a mixed water sample from the epilimnion for the hydrochemical analyses (Fig. 2.2). For the mixed water sampling, the entire water column of the epilimnion was retrieved using a hose as described in Lenz et al. (2020). An overview of the parameters of the studied lakes is shown in Table 2.2, a detailed presentation is given in the supplementary (Table S 2 & 3). Eventually, all the lakes were evaluated for indications of water level fluctuations and the presence of water plants such as *Potamogeton* L., *Chara* L. or the yellow water-lily (*Nuphar lutea* (L.) SM.).

Table 2.2: Averages and extrema of the main lake parameters in the 43 Bavarian and Tyrolean mountain lakes. * Bottom and surface temperature values refer to late-August 2016.

Lake parameters	Unit	Mean	Minimum	Maximum
Altitude	m a.s.l.	1597	760	2469
Area	ha	2,29	0,10	12,00
Depth	m	7,79	1,25	20,65
Secchi depth	m	4,58	1,25	15,50
pH	–	8,44	7,90	8,99
O_2 saturation	%	93,44	5,12	129,75
Electrical conductivity	$\mu S\ cm^{-1}$	225,95	121,44	536,70
Bottom temperature August*	°C	9,51	4,56	20,89
Surface temperature August*	°C	15,54	8,82	21,71
NO_3^--N	$mg\ L^{-1}$	0,44	0,00	2,86
NH_4^+-N	$\mu g\ L^{-1}$	36,45	3,84	126,85
Total phosphorous	$\mu g\ L^{-1}$	6,86	0,10	20,41
Silicate	$mg\ L^{-1}$	0,22	0,12	0,77
Na^+	$mg\ L^{-1}$	0,37	0,00	2,11
Ca^{2+}	$mg\ L^{-1}$	28,87	12,44	49,24
Mg^{2+}	$mg\ L^{-1}$	7,12	0,98	19,47

2.2 Diatom Sampling and Sediment Coring

In all the lakes, diatom samples were collected from the littoral area at the Northern and Southern shore as well as from the sediment surface at the deepest area of the lake. For the littoral samples, four to seven small rocks – or other surfaces if rocks were absent – were taken from approximately 20 to 30 cm depth close to the shore (Fig. 2.3). Using a new tooth brush for each sample and distilled or tab water, the diatomaceous biofilm was scrubbed and rinsed from the rocks and eventually filled in vials. The sediment samples were collected from the deepest area of a lake using a gravity corer (Uwitech, Mondsee, Austria) and extracting the uppermost layer of the core in the laboratory. However, the sediment cores of 24 mountain lakes (Fig. 2.1) were hermetically sealed immediately after retrieving and kept as a whole at 4°C for a maximum of 3 months until further preparation. These cores served as a basis for the palaeolimnological studies on the Bavarian mountain lakes.

Figure 2.3: Mountain lake sampling in autumn 2016 at the alpine Lake Mittlerer Seewisee. Stefan Ossyssek and Ben Horsman on the boat at the left-hand side are measuring and sampling over the deepest area of the lake and Lena Hofmeister taking littoral diatom samples at the right-hand side

2.3 Sample Processing

The littoral and surface sediment samples, which were taken from every lake (Table 2.1), served as a direct basis for diatom preparation without intermediate steps. Instead, diatom samples from the sediment cores, which were retrieved from nearly every second lake, needed special processing before diatom preparation. Sediment cores were cut into two halves and each of them sliced into 1 cm layers (Fig. 2.2). Subsequently, each sediment sample was filled in small polyvials (Zinsser

NA, Northridge/CA, USA), frozen at –20°C and freeze-dried for at least 48 h in a Christ 1-4 Loc 1m freeze-dryer (Martin Christ, Osterode am Harz, Germany). The samples were weighed before and after drying to determine the water content of the sediment layers, which is an indicator of organic content (Menounos 1997, Avnimelech et al. 2001).

Afterwards, the samples of the first core half, which were used for the age determination, were ground with a pestle and filled into glass tubes, adjusted to a certain amount and analysed by gamma spectrometry (High-purity Germanium Well Detector, HPGe, Canberra, USA). Accumulation rates and age interpretation based on the natural nuclear radiation of ^{210}Pb and ^{137}Cs radionuclides. The measurements were carried out by the department of Surface Waters Research and Management of EAWAG (Dübendorf, Switzerland).

For diatom preparation, a part of the dried sediment samples of the other core half was adjusted to a certain amount that depended on the organic content of a sediment core and remained constant throughout a core. For inorganic-rich samples, more material was used to gain enough diatom valve for microscopic analysis. Parallel to the littoral and surface sediment samples, the core samples were processed according to Van der Werff (1953). Firstly, ca. 50 mL H_2O_2 (30 % v/v) were added to the samples and incubated overnight at 20 °C. The samples were then heated for 4 h at an almost boiling temperature. Finally, a spatula tip of $K_2Cr_2O_7$ and ten drops of HCl (17 % v/v) from a Pasteur pipette were added to oxidize any remaining organic matter and to decalcify the sample. After cooling, the samples were washed four times by centrifugation at 532 g for 15 min. The supernatant was replaced by double-distilled water. The precipitate containing diatom valves was placed in glass vials and adjusted to a fixed volume. The vials' content served as a stock solution (slurry). Finally, different dilutions optimal for diatom counting were mounted on slides in Naphrax® (Morphisto, Frankfurt a.M., Germany).

2.4 Diatom Counting

The diatom valves were counted and identified at 1000× magnification (Leitz light microscope Labovert, Wetzlar, Germany) under oil immersion. To ensure representability, at least 550 valves per sample were counted. If the samples were rich in different centric diatoms, SEM pictures of at least 30 individuals were taken to improve their identification. For SEM, 50 µL of the most appropriate sample dilution were air-dried onto a glass cover slip (Ø 12 mm), then coated in gold using the Polaron SC502 Sputter Coater (Fisons Instruments, UK) and examined in a Hitachi S-2300 (Hitachi, Tokyo, Japan) at 5000–20,000× magnification. The identification was carried out according to Hofmann et al. (2013), Houk et al. (2010, 2014), Krammer & Lange-Bertalot (1986, 1988, 1991a, 1991b), Lange-Bertalot (2011), Lange-Bertalot & Moser (1994). The number of fields of view (N_{FoV}) in the light microscope needed for a complete count was noted. In combination with the sample dry weight that was used for the diatom preparation, this served as a diatom-density proxy and was calculated with the formula 2.1.

$$Diatom\ Density\ [mg^{-1}] = \frac{N_{Diatoms}}{N_{FoV}} \cdot \frac{Dilution\ \cdot V_{Stock\ Sol.}\ [\mu L]}{dry\ weight\ [mg] \cdot \frac{50\ \mu L\ \cdot 0.01\ mm^2}{36\ mm^2 \cdot \pi}}$$

Formula 2.1: $V_{Stock\ Sol.}$= Volume of the stock solution; N_{FoV} = Amount of fields of view

The first term of formula 2.1 calculates the relative amount of diatom valves per field of view and the fraction in the denominator of the second term defines the amount of the sample solution per field of view.

3 The Silicification Value: A Novel Diatom-Based Indicator to Assess Climate Change in Freshwater Habitats

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Author contributions: This study was conceived by Wolfgang Küfner (WK) in consultation with Uta Raeder (UR) and Jürgen Geist (JG). On-site-measurements and laboratory analyses were mainly carried out by WK and Stefan Ossyssek (SO). Diatom preparation and microscopic analyses was done by WK and SO. Statistical analysis, visualisation, and data interpretation was mainly conducted by WK. The manuscript was drafted by WK and continuously refined, improved and edited by UR and JG.

3.1 Abstract

Formation of diatom frustules depends on the process of silicification. In many planktic species of algae, ambient temperature and nutrients are already known to affect growth and morphology, making them suitable bioindicators. In this study, a similar indicator function of benthic diatoms is proposed based on the principle that cell wall thickness is inversely proportional to temperature and nutrients. Therefore, higher turnover rates at warmer temperatures are hypothesized to favour smaller and lighter diatoms due to their shorter regeneration time. Accordingly, benthic diatom species were classified into seven categories according to their intensity of silicification, referred to as “Silicification Value”. For each diatom assemblage an abundance-weighted average silicification value was calculated and tested for its applicability to assess global change impact on mountain lakes in the northern calcareous Alps of Europe. Surface sediment diatom samples and morphometric and ecological parameters of 41 lakes from a wide altitudinal range in the Bavarian and Tyrolean Alps were collected and analysed. Statistical tests revealed that temperature conditions in a lake and its altitude were the most decisive proxies related to the “Silicification Value”. Moreover, trophic status and the presence of macrophytes had some influence. This supported the hypothesis that lakes, which are warmer and richer in nutrients, show a weaker average silicification in diatom assemblages. A dependence of silicification on valve size could be shown, but appears to be negligible in climatological issues. In particular, the correlation with temperature makes the Silicification Value an applicable palaeoecological proxy to assess climate change impact in freshwater lakes.

3.2 Introduction

Diatoms (Bacillariophyta) are characterized by their silicified cell walls which increase their persistence, e.g. in lake sediments (Stoermer & Smol 1999, Battarbee et al. 2001), marine sediments (Kennett 1983, Renaudie et al. 2018) and even preserved fish guts (Sellmann et al. 2002, Lavoie & Campeau 2010). This persistence, combined with their ubiquitous distribution and numerous species traits, facilitates the use of diatoms as an ‘early warning system’ for anthropogenic climate change, which causes substantial changes in freshwater habitats (Smol et al. 2005, Solomon et al. 2015, Rantala et al. 2017). Cell wall silicification occurs after cell formation, but the exact timing depends on whether vegetative (mitosis) or sexual reproduction (meiosis) occurs. It either happens immediately after cell division or after forming an auxospore, respectively, which grows to a maximum size and contains the subsequently silicifying initial cell (Geitler 1969, Drebes 1977, Krammer & Lange-Bertalot 1986, Round et al. 1990, Mann 1993, Kaczmarska et al. 2018).

The amount of silicate incorporated in the cell wall is primarily genetically determined and species-specific (Sullivan 1986, Falasco et al. 2009). However, there are many environmental drivers that can affect silicification including light conditions and bioavailability of nitrogen, phosphorous and iron. Iron, for example, ‘makes thinner diatoms’ (Boyle 1998) because it limits diatom growth and silica uptake, as reported for the Laurentian Great Lakes (Twiss et al. 2000, Sterner et al. 2004), oligotrophic soft water lakes (Vrede & Tranvik 2006) and especially in oceans (Hutchins & Bruland 1998, Takeda 1998). However, in oceans iron is either co-limiting with nitrogen and phosphorous (North et al. 2007) or primarily limiting (Blomqvist et al. 2004), unlike in freshwater lakes. Nevertheless, it is generally accepted that the lower the diatom growth rates, the higher the silica content in their cells (Davis 1976, Furnas 1978, Brzezinski 1985, Taylor 1985, Theriot et al. 1988, Takeda 1998, Claquin et al. 2002). Slow growth rates lead to a longer exposure time to available silica, therefore higher amounts of silica in the cell wall and vice versa (Taylor 1985, Pančić et al. 2019). Moreover, predation on phytoplankton can also enhance cell wall silicification (Pondaven et al. 2006). Planktic diatoms can further adapt its degree of silicification to nutritional and hydrophysical conditions (Reynolds 1973, Titman & Kilham 1976, Sommer & Stabel 1983, Scavia & Fahnenstiel 1987, Raven et al. 2004, Thackeray et al. 2008). In accordance, freshwater species are on average more strongly silicified than marine species (Conley et al. 1989, Svensson et al. 2014) since sinking to the hypolimnion may not be terminal due to lake mixing.

In freshwater habitats, the research focus on silicification has traditionally focused on planktic species and eutrophic conditions (e.g. Znachor et al. 2013). A well-studied genus is *Stephanodiscus* EHRENBERG (Theriot 1987, Edlund & Stoermer 1991). A positive correlation was observed between silicification and cell size, which was also found in marine species (Conley et al. 1989). In contrast to their planktic counterparts, benthic diatoms in freshwater habitats have been poorly studied with respect to their silicification, cell size and variation in relation to ambient environmental conditions. Passy (2007) suggested that size variations (biovolume and length-width ratio) are significantly lower in benthic diatoms. Furthermore, variations in silicate accumulation, which can alter sinking speeds in planktic species (Raven et al. 2004), is not necessary for benthic species. Thus, as long as the freshwater habitat is not eutrophic and therefore likely to become silicate-limited, temperature may be the only abiotic factor affecting silicate content (per biovolume) in benthic diatoms. Therefore, the degree of silicification within species and communities makes it a potentially powerful indicator for monitoring climate change. This may only be compromised by biotic factors like grazing pressure (Pondaven et al. 2006) or competing silica consumers, e.g. chrysophytes or freshwater sponges (Street-Perrot & Barker 2008).

Benthic diatom species are one of the main groups used to assess the quality of surface water bodies (e.g. Schaumburg et al. 2012) or to reconstruct past conditions (e.g. Karst-Riddoch et al. 2004, Nogués-Bravo et al. 2006, Beniston 2006, Thackeray et al. 2008, Parker et al. 2008, Catalan et al. 2013). Nevertheless, subfossil diatom assemblages in lacustrine sediments often lack sufficient indicator species, hampering palaeolimnological assessments. In such cases, only diatom assemblage evaluation remains, including assessment of functional or ecological guilds, correspondence analysis scores or diversity indices (e.g. Antoniades et al. 2005, Michelutti et al. 2015). However, species diversity in palaeoecological studies is greatly affected by variable sedimentation rates and preservation (Smol 1981). Additionally, equal species replacements in diatom assemblages may not be reflected in the Shannon-Index.

Other studies refer to cell size proxies like biovolume or length-width ratios (Margalef 1969, Klee & Schmidt 1987, Roessler 1988, Kling 1993, Finkel et al. 2009, Svensson et al. 2014). Apart from a focus of those studies on planktic diatoms, there are divergent observations, which interfere with interpretations. Whereas many species-specific studies report cell size decreases with temperature and nutrient availability in planktics, brackish benthics and local communities increase in cell size although smaller species are supposed to live in warmer areas (Svensson et al. 2014). They further highlighted effects of nutrients on cell size rather than summer warming. All these divergences impair cell size proxies to indicate climate change. Instead, Bahls (1993) proposed the percentage of motile diatom species to evaluate sediment pressure, which supposed to increase with climate change (Lotter et al. 1999, Bogataj 2007, Brookshire et al. 2011, Rosbakh et al. 2014, Bätzing 2015). However, this proxy appears to be a weak indicator for fine sediment stress (Jones et al. 2016), is unaffected by seasonal temperature variations (Svensson et al. 2014) and was applied for rivers (Bahls 1993).

Another applicable proxy is the silicification of diatoms in freshwater habitats, which is mainly affected by variable preservation due to pore water conditions (Lewin 1961, Coradin & Lopez

2003, Zgrundo et al. 2017) and biotic stressors such as grazing and competitive silicate consumers. The latter may only impair inter-lake comparisons as different lakes may contain different grazer communities, but intra-lake analyses remain possible, assuming that the grazing pressure remains constant in an ecologically balanced system. On palaeolimnological scales, limiting the incorporated time range as well as describing the diatoms’ silicification development relatively is presumed to overcome the main stressors. In conclusion, a single proxy such as silicification in benthic freshwater diatoms appears to remain as a usable variable that would be applicable to any species, wheterh a generalist or a specialist.

Silicification in diatom assemblages is presumed to be indicative of environmental conditions linked to climate change. Accordingly, increasing lake temperatures cause higher productivity and individual turnover rates of individuals (Montagnes & Franklin 2001, Montagnes et al. 2003, Weckström et al. 2016), which leads to shorter time spans for valve silicification. Therefore, a changing environment may support a shift in diatom assemblages towards species that produce lighter valves. Depending on the benthic substratum, heavily silicified diatoms will still be apparent in warm freshwater lakes. Climate change, however, may reduce their importance in relative abundance analyses because the comparably longer regeneration time of ‘heavy diatoms’ will not be able to keep up with opportunistic light species (Morin et al. 2008). Thus, average silicification pattern in diatom assemblages can potentially serve as a powerful indicator of lake warming.

In this study, (1) low intraspecific variability of silicification in benthic freshwater diatoms was assumed. Based on this, (2) a silicification value integrating abundance and degree of silicification of each diatom species was proposed. Subsequently, (3) the applicability and usefulness of this value was validated in the context of climate change-related research assuming lighter silicification in warmer habitats with higher turnover. This hypothesis was finally (4) checked for possible coincidences with valve size. For that, diatom assemblages from surface samples of sediment cores were used, sampled in almost every mountain lake over a wide range in the northern calcareous Alps in Bavaria and Tyrol (Europe).

3.3 Methods

3.3.1 Study Site

The sampling sites comprised 41 mountain lakes located in the Bavarian and Tyrolean Alps between Salzburg, Austria and Lake Constance, at three different altitudinal levels (montane, subalpine, alpine), between 900 and 2500 m above sea level (Fig. 3.1, Table 3.1, Table S 2–3). The main criterion for the selection of lakes was low anthropogenic influence from roads, huts or other touristic facilities, which could bias or disguise climate change-related effects (Adrian et al. 2009).

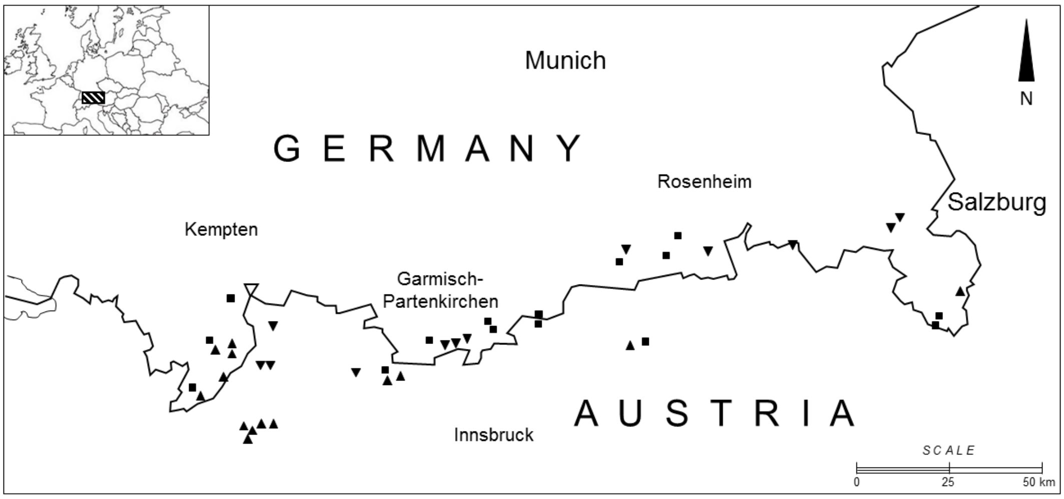


Figure 3.1: Map showing the 41 studied mountain lakes along the German-Austrian (Bavarian-Tyrolean) boarder. Upright triangles: alpine, squares: subalpine, upside down triangles: montaneous mountain lakes.

The bedrock of the entire area is dominated by calcareous formations (Hauptdolomit, Wetterstein- and Dachsteinkalk). All sites are cirque lakes except for two, which are doline lakes. The vegetation varies across the three altitudinal levels. The montane level (1000 – ca. 1300 m) is mainly characterized by mixed forests (dominated by *Fagus sylvatica*, *Picea abies*) below the forest line, the subalpine (ca. 1300 – 1700 m) by light pine forests (dominated by *Picea abies*, *Pinus mugo*) with meadows and mountain pasture between forest and treeline, and the alpine stage (> ca. 1700 m) by rocky and grassy catchments above the treeline (cf. Rosbakh et al. 2014) (Table 2.1).

3.3.2 Measurements and Analysis

The morphology of each lake was characterized using the sonar system HDS 8 (Lowrance, Tulsa, USA). Depth profiles of hydrophysical and -chemical variables (temperature, pH-value, O_2, and electrical conductivity corrected to 25°C) were measured in 1 m steps over the deepest point of the lake using a Multisonde 350i (WTW, Weilheim, Germany). Additionally, two temperature loggers (HOBO®, Onset, Bourne, USA) were installed above the ground and below the surface of each lake, in summer 2016. In most lakes the loggers were exposed not later than July, except for seven in which logger installation occurred in August. The data collection from 17 loggers ended in September, 14 loggers in October, and three loggers after an entire year. Consequently, average temperatures were calculated for August only, when all the lakes were monitored. To evaluate lake mixing behaviour, the temperature data from each pair of loggers per lake were compared. Lake mixing events were defined as times when surface and bottom temperature deviated by less than 0.11°C.

A mixed water sample from the euphotic zone was collected above the deepest point for hydrochemical analysis in the laboratory. The concentrations of total phosphorus (TP), nitrate- and ammonium-nitrogen, silicate and water hardness were determined by ion chromatography

(DIONEX ICS-1100, Thermo Fisher Scientific, Waltham, USA) and cross-validated by established methods: TP: molybdenum blue (cf. Murphey & Riley 1962, Koroleff 1983); nitrate-nitrogen: UV photometry (Navone 1964), ammonium-nitrogen: indophenol blue (cf. Koroleff 1969), silicate: NANOCOLOR test kit (Macherey-Nagel GmbH & Co KG, Düren, Germany), water hardness: EDTA titration. Four structural (altitude, area, depth, volume), seven hydrochemical (concentration of NO_3^--N, NH_4^+-N, TP, silicate, Na^+, Ca^{2+}, Mg^{2+}) and four hydrophysical variables (pH-value, electric conductivity, O2, Secchi depth) were available from 40 mountain lakes for further analyses (Table 2.1).

Freshwater lakes were classified according to their primary production. Accordingly, the mountain lakes were subdivided into two different trophic categories of approximately equal sample size using 7 µg L^{-1} TP as the threshold. These groups can be referred to as "ultraoligotrophic" (< 7 µg L-1) and "oligo-mesotrophic" (≥ 7 µg L-1) (cf. LAWA 1998, Melzer & Schneider 2014).

Additionally, the presence of aquatic plants was assessed. Therefore, the sample set was separated into two categories: "1" if the surface sediment was dominated by macrophytes – mostly of *Potamogeton* and/or *Chara* – and "0" if there were no aquatic plants.

3.3.3 Diatom Sampling

For palaeolimnological studies, one sediment core was taken at the deepest point of each mountain lake using the gravity corer (Uwitec, Mondsee, Austria). Sediment cores were hermetically sealed and cooled to 4°C for a maximum of 90 days. After separating into 1 cm layers, the samples were frozen at – 20°C and freeze-dried for at least 48 h. Moreover, the weight was determined before and after drying to determine the water content of a sample, a proxy for the percentage of organic matter in the sediment (Menounos 1997, Avnimelech et al. 2001). Cores were also dated by Pb210 and Cs137 at the EAWAG in Dübendorf, Switzerland. Using the CRS model, the sedimentation rate of each lake could be evaluated, and hence the time frame represented by 1 cm layer.

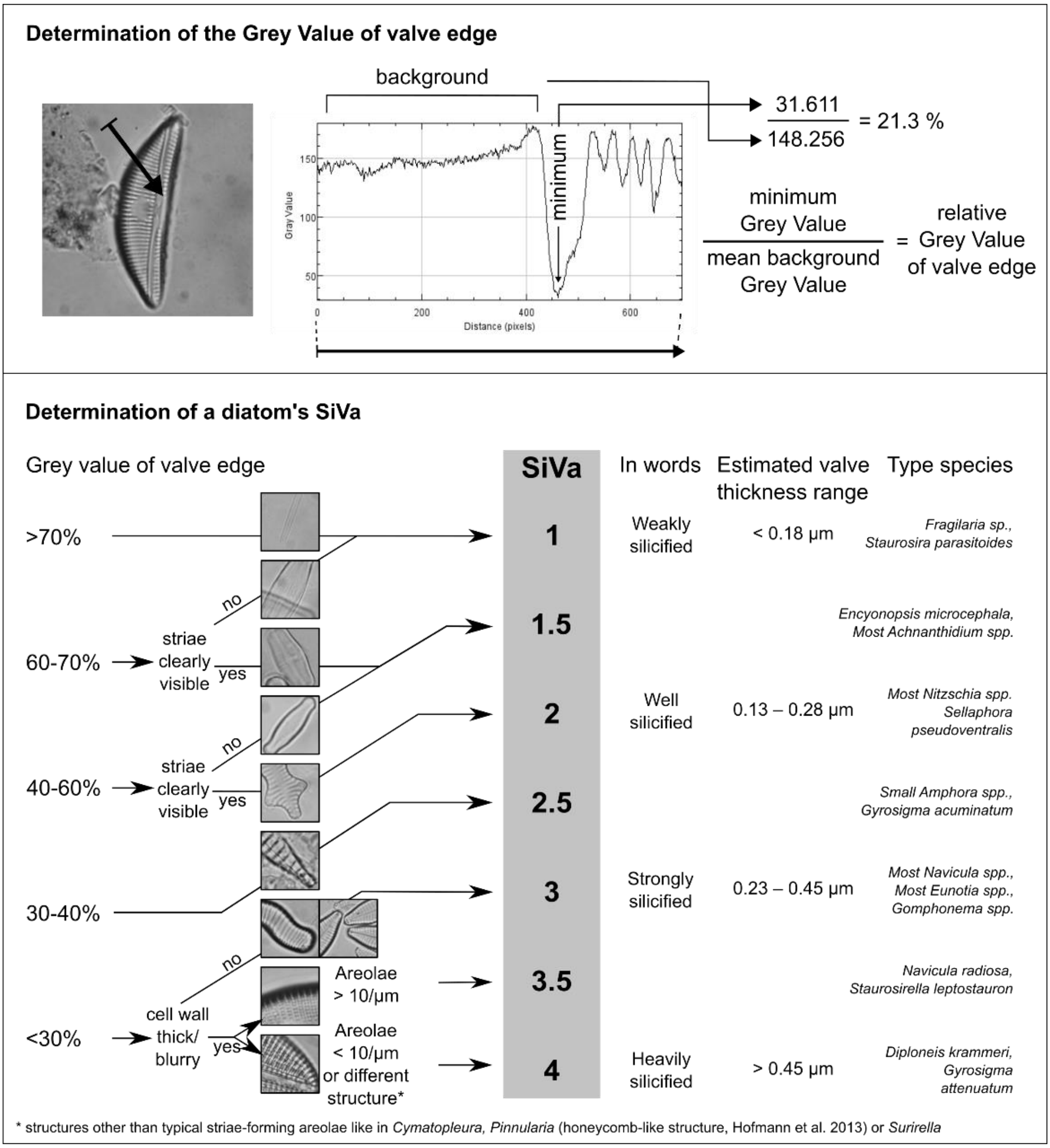
The diatom samples were processed according to van der Werff (1953). Each dried surface sediment sample was weighed to the nearest milligram before diatom preparation. About 50mL H2O2 (30% v/v) were added and samples were incubated at 20°C overnight. The sample was then heated for 4 h and finally a spatula tip of $K_2Cr_2O_7$ and a ten drops of a Pasteur pipette of HCl (17% v/v) were added to oxidize any remaining organic matter and to decalcify the sample. After cooling the samples were washed four times by centrifugation at 532 g for 15 min. The supernatant was replaced by double-distilled water. The precipitate containing the diatom valves was placed in glass vials and adjusted to a fixed volume. The vials' content served as stock solution (slurry). Finally, different dilutions were mounted on slides Naphrax ®.

3.3.4 Diatom Analysis

The diatom valves were counted and identified at 1000x magnification (Leitz light microscope Labovert, Wetzlar, Germany) under oil immersion. To ensure representativity, at least 550 valves per sample were counted. If the samples were rich in different centric diatoms, SEM pictures of at least 30 individuals were taken to improve their identification. For SEM, 50 µl of the most appropriate sample dilution were air-dried onto a glass cover slip (Ø 12 mm), then coated in gold using the Polaron SC502 Sputter Coater (Fisons Instruments, UK) and examined in a Hitachi S-2300 (Hitachi, Tokyo, Japan) at 5000-20000x magnification. The identification was carried out according to Hofmann et al. (2013), Houk et al. (2010 – 2014), Krammer & Lange-Bertalot (1986 – 1991), Lange-Bertalot (2011), Lange-Bertalot & Moser (1994). The number of fields of view in the light microscope needed for a complete count was noted. In combination with the sample weight, this served as a diatom-density proxy.

3.3.5 The Silicification Value

Diatom species and varieties that contributed less than 1% to a diatom assemblage of surface sediment samples were excluded from further analysis. This avoids distortion of the results by random appearances and unsafe identifications. The remaining species were targeted to evaluate and quantify the extent of their silicification by the introduction of a new parameter referred to as “Silicification Value” (SiVa) distinguishing four different and discrete classes of silicification (Fig. 3.2). Value assignment was based on visual assessment of diatom valves under the light microscope. The minimum Grey Value, in terms of the ‘darkness of the valves’ edges’, was measured. Grey Value was then adjusted against the average Grey Value or ‘mean brightness of the background’ since pictures from different light microscopes and cameras might vary in brightness. The images were taken with a Canon 600D (Canon, Tokyo, Japan), converted into a black-white image and the Grey Values estimated using ImageJ version 1.50e (Abramoff et al. 2004) (Fig. 3.2). This system already applies intermediate levels since some species did not fit into the four main SiVa classes (Fig. 3.2, cf. Table S 1 in supplementary). The lowest SiVa 1 includes lightly silicified diatoms with very bright valve edges of Grey Value >70% and >60% if striae are barely visible. SiVa 1.5 contains light species with Grey Values of >60% if striae are visible and between 40 and 60% without visible striae. If species in the latter range appeared with visible striae, they were assigned to SiVa 2. SiVa 2.5 is then characterized by species, whose valve edges show relative Grey Values between 30 and 40 %. Species below 30% are strongly silicified, but can be split into the highest three SiVas. SiVa 3 contains diatoms with focusable valve edges, whose striae do not appear as strong and black as the edge. Conversely, species of SiVa 3.5 and 4 form thick valves, so that the inner valve edge is usually blurry in the light microscope. In addition, the former describes species with finer structure, i.e. the areoladensity within striae is at least 10 per micron, the latter 'coarser' species whose striae either have 10 or fewer areolae per micron. This group also includes Surirella and the honeycomb-like areola patterns within the striae of Pinnularia. The striae of '3.5 species' appear brighter than the edges and of '4 species' as strong as the edges. For this SiVa system, only benthic diatom species (as categorised by Krammer & Lange-Bertalot 1986-1991, and Schaumburg et al. 2012) because variation in planktonic species have been reported (Theriot 1987). The main SiVa groups, which express the degree of silicification, are approximately supported by and interpreted as valve thickness, which allows the initial separation using Grey Values. Therefore, valve thickness ranges



* structures other than typical striae-forming areolae like in *Cymatopleura*, *Pinnularia* (honeycomb-like structure, Hofmann et al. 2013) or *Surirella*

Figure 3.2: Estimation of the Grey Value of the valve edge (top) and the Grey Value-based determination of a diatom species' SiVa and description of its levels (bottom). The SiVa classification follows the optical 'darkness' of the valve edge and integrates striae appearance.

measured under SEM, are added in the description of the different following values (Fig. 3.2). Afterwards, the mean SiVa of a diatom assemblage was calculated (formula 3.1). Here, the species’ values were weighted according to their abundance in the assemblage.

$$\emptyset\ SiVa = \sum SiVa_i \cdot \frac{N_i}{N_{total}}$$

Formula 3.1: Ø SiVa = diatom assemblages’ mean silicification value; $SiVa_i$ = silicification value of diatom species i; N_i = amount of counted valves of diatom species i; N_{total} = amount of counted valves of the diatom sample in total (Ni/Ntotal = abundance of species i).

3.3.6 Valve Sizes

More strongly silicified diatoms often appeared to be bigger. To evaluate this relationship, diatom valves were also measured in µm (±10-3). Pictures of the abundant species (≥ 1%) were taken with a Canon 600D (Canon, Tokyo, Japan) and the average valve size of each species estimated with the program ImageJ version 1.50e (Abramoff et al. 2004). Since cell wall thickness remains unknown in light micrographs, only the surface area of the valve as μm^2 was calculated as a proxy for valve size. Some research estimates average valve volume in diatom populations (e.g. Jakobsen & Carstensen 2011), but others use valve lengths only as a size estimate (Finkel et al. 2009, Spaulding et al. 2012).

3.3.7 Statistical analyses

Statistical analyses were run on the programs Microsoft Excel 2016 ®, PAST 3.20 (Hammer et al. 2001) and R version 3.4.1. Canonical correspondence analysis was used to examine the relationship between surface sediment diatom samples and environmental parameters. To test dependencies among parameters of different units, e.g. the dependence of the SiVa on environmental parameters, Spearman rank correlation coefficients were calculated. This facilitated comparisons without prior transformation, by using ranks instead of the actual values whose differential units can bias the coefficient. Following the correlation analyses, which were calculated pairwise and separately for each variable, a Bonferroni correction was conducted to correct for multiple testings. The Bonferroni-corrected p-values are referred to as “p_{BC}” and were most important when testing dependences of the SiVa. In the case of factorial parameters, visualized as box plots, the F-test was calculated to check the similarity of variances. In the case of similarity, a t-test was used, otherwise the Mann Whitney U-test. A correlation was considered significant at $p \leq 0.05$.

Temperature data for mountain lakes, where no logger data were available (no logger installation, logger damaged) were calculated using a generalized linear model (GLM) and a backward stepwise linear regression starting with all environmental variables.

3.4 Results

3.4.1 Diatom Analyses

In 41 different lakes, 360 different diatom species and varieties were identified. 153 of them were sufficiently abundant (≥1%) to assign silicification values. The most abundant species were *Staurosirella pinnata* (EHRENBERG) WILLIAMS & ROUND, which on average contributed 18.6 % of all valves, followed by *Denticula tenuis* KÜTZING (9.3%) and *Staurosira venter* (EHRENBERG) CLEVE & MÖLLER) (9.0%). According to the CCA (Fig. 3.3), the most important drivers determining the benthic diatom surface sediment assemblages were TP, lake area and depth, and therefore volume and temperature conditions, at the lake bottom in particular. Additionally, the electrical conductivity, which is primarily determined by concentrations of Na^+, Mg^{2+} and Ca^{2+}, was an important factor, especially for the Sieglsee. This is one of the two doline lakes and the only one in the sampling set which is entirely fed by ground water. Furthermore, this lake showed the highest conductivity values (> 800 µS/cm).

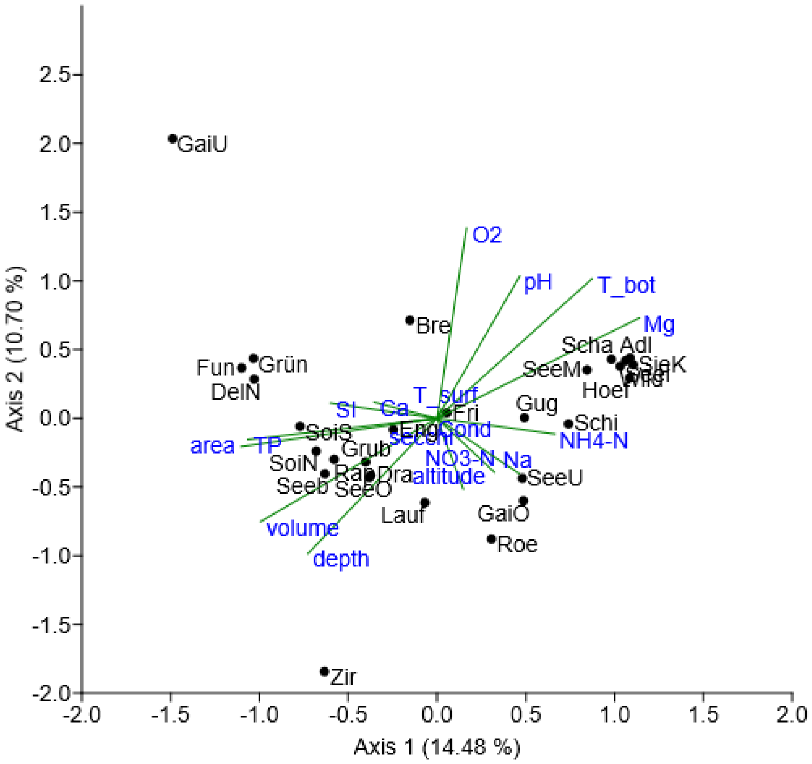


Figure 3.3: CCA of the diatom assemblages of surface sediments of mountain lakes and environmental variables. Only the 28 mountain lakes with a complete environmental data set were used. The triplot of variables is 2.5x amplified for a better visibility. The deep lakes Bichlersee, Ferchensee, Lautersee, Soiernsee (W) and Taubensee are excluded as outliers due to their dominance of planktic diatom species, which strongly biased the CCA plot. The bigger doline lake Großer Sieglsee was excluded additionally, which was mainly conductivity-driven. Environmental parameters explained 25% of assemblage variation

3.4.2 Environmental Variables

Continuous temperature logger data were available for 34 mountain lakes. For the remaining seven lakes, average August temperatures were obtained from GLM calculations. The main predictor for surface temperature was altitude, for bottom temperature lake depth (cf. Fig. 3.3/Table S 4 in supplementary).

Electrical conductivity of water depends on the concentration of dissolved ions such as Na^{+}, Ca^{2+}, and Mg^{2+}. Logically, conductivity and ion concentrations showed a significant positive relationship (Fig. 3.3/Table S 4 in supplementary). Another clear series of significant correlations appears among summer Secchi depth and volume/depth and temperature. However, these two proxies are not independent because lake depth limits Secchi depth especially in shallow lakes. In many cases, the Secchi depth matched lake depth. Conversely, Secchi depth affects temperatures negatively, whereas surface temperature is not significantly influenced by lake depth.

The sedimentation rates in the Bavaria mountain lakes averaged 4.5 ± 2.4 a cm^{-1} with two outliers far above (18 and 30 a cm^{-1}), and the doline lake below average (~ 1 a cm^{-1}). Therefore, every surface sediment assemblage comprised at least two entire vegetation periods.

3.4.3 Silicification Value

Individual SiVa assignment resulted in low intraspecific variation. Although not all individuals in a species fell in a SiVa level, the deviation of a species' SiVa average from different mountain lake

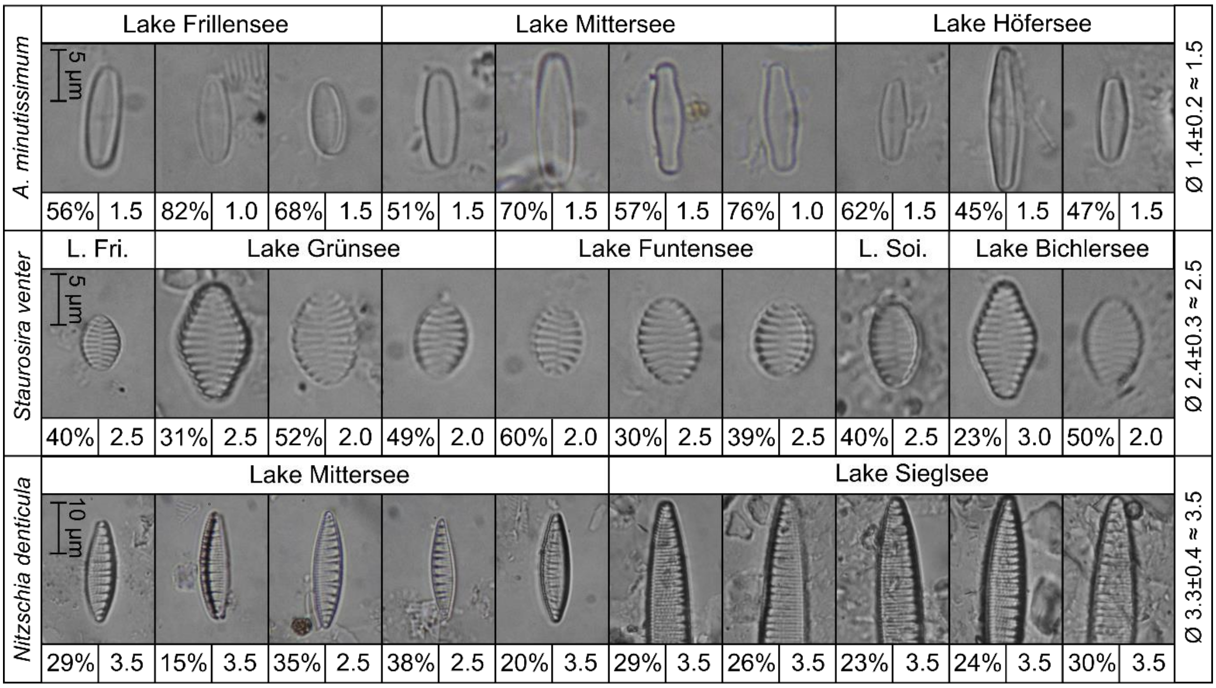


Figure 3.4: Silicification of three abundant benthic diatom species of surface sediments of different mountain lakes. For each picture relative Grey Values (bottom left) and SiVa (bottom right) are displayed. The right column shows the average SiVas. Irrespective of most lake characteristics, diatom silicification within species exhibit narrow deviations and so do the SiVas

assemblages did not exceed 0.4 (Fig. 3.4). Transferring species SiVas to the assemblage scale, the mean SiVa of the surface sediment samples averaged 2.3, ranging from 1.6 to 2.9. Within this range, different SiVas were equally distributed (Fig. 3.6e). The correlation test between the environmental variables and the mean SiVa of the diatom assemblages identified temperature as the most important variable (Fig. 3.5/Table S 4 in supplementary); surface and bottom temperature of the mountain lakes were both negatively correlated (Temp (surf): $\varrho_S = -0.560$; $p_{BC} = 0.036$, Temp (bot): $\varrho_S = -0.336$; $p_{BC} = 1/p = 0.036$). Apart from altitude as the third decisive proxy ($\varrho_S = 0.503$; $p_{BC} = 1/p = 0.187$), no other parameter significantly affected the SiVa of the diatom assemblages.

TP as a proxy for lake trophic status appeared to be decisive when the mountain lakes are grouped into two categories (cf. LAWA 1998, Melzer & Schneider 2014). Mean SiVas in mountain lakes with less than 7 $\mu g\ L^{-1}$ TP are significantly higher in the lakes $\geq 7\ \mu g\ L^{-1}$ ($p < 0.001$, Fig. 3.6c). The presence of macrophytes indicated lower SiVas ($p = 0.08$, Fig. 3.6a), whereas the frequency of lake mixing did not seem to be a decisive parameter for the diatom valve silicification ($p = 0.62$, Fig. 3.6b). In addition to ecological influences on SiVa, the importance of valve size was tested. Species' valve size range mainly varies between ≤ 3 and ≥ 3.5. (Fig. 3.6d). SiVa 4 species were on average approximately 20 times larger than SiVa 1 species. However, size variances within those two groups were larger than the size influence on diatom silicification.

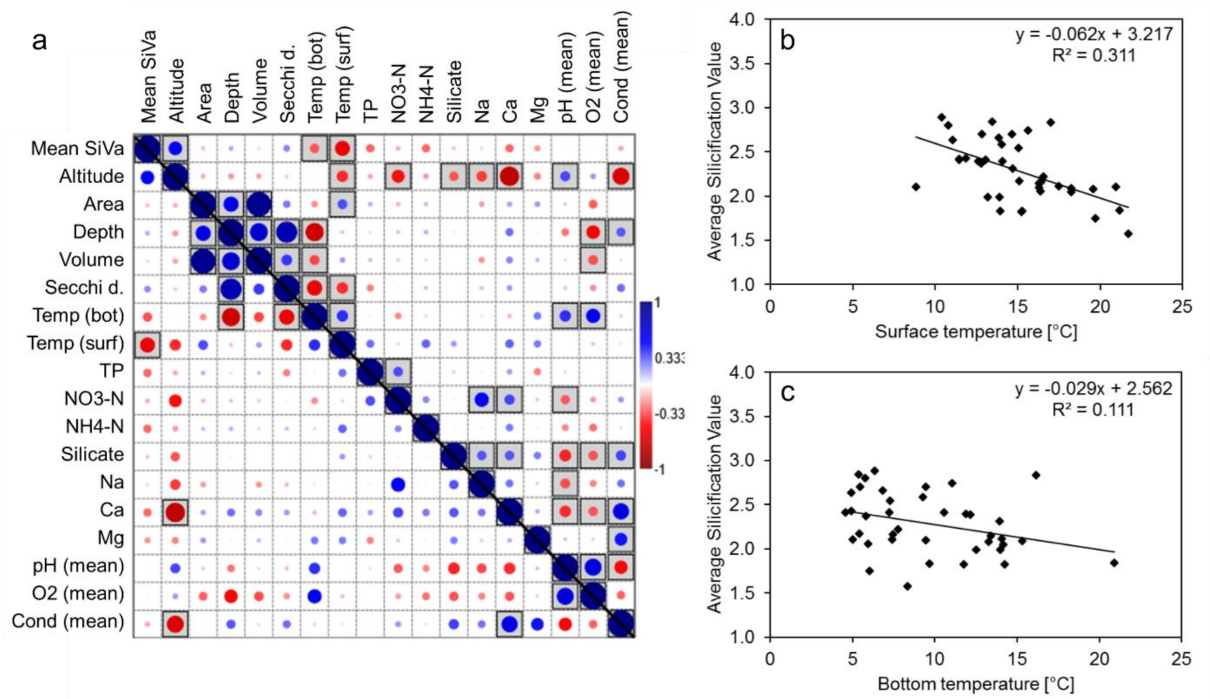


Figure 3.5: Spearman rank correlation matrix of the Mean SiVas in surface sediments and lake proxies (a), mean SiVa in relation to surface (b) and bottom August temperatures (c). The upper right triangle of the correlation plot shows the results of the mere Spearman correlation, the bottom left triangle the results with Bonferroni correction. Circle size indicates the significance of the relationship, if boxed $p < 0.05$ (significant). Red: negative, blue: positive relationship. Altitude and August temperatures were the only significant parameters, which influence the silicification pattern in diatom communities in surface sediments of mountain lakes. The scatter plots show that the surface temperatures in mountain lakes were closer related to average SiVa in the surface sediment assemblages than bottom temperatures.

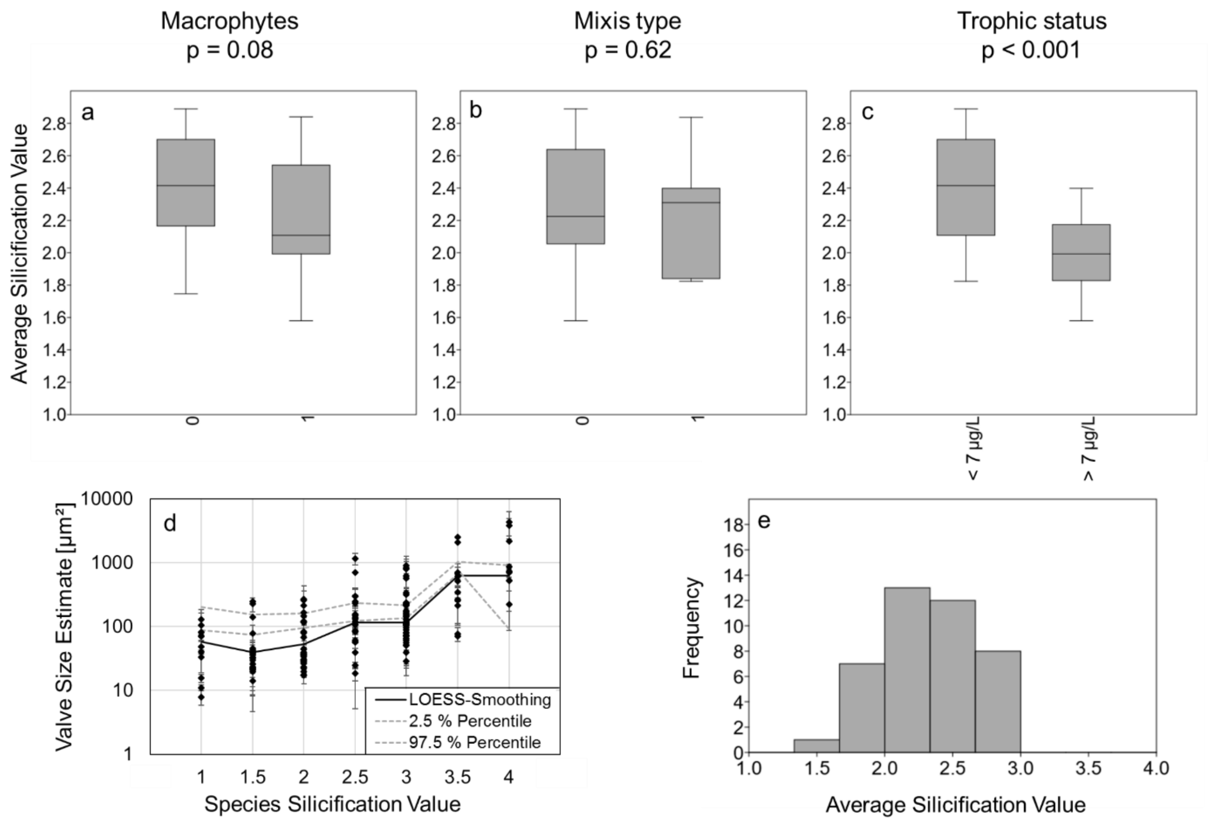


Figure 3.6: Presence of macrophytes (a), the mountain lake's mixis type (b) and trophic status (c) in relation to the mean SiVa of the diatom community in surface sediments. Left: 0 absence, 1 presence of macrophytes, right: 0 dimictic, 1 polymictic (observed holomixis events during summer). The trophic status was divided into two groups below and above 7 µg L^{-1} TP. (d) Relationship of the SiVas and the mean valve size estimates. The calculations comprised the 153 diatom species with abundances >1% in at least one sample. LOESS-Smoothing (Factor 0.2), 2.5% and 97.5% Percentile show that size mainly differed between SiVas below 3 and above 3,5, but did not matter within these two groups. (e) Histogram of observed average SiVas in surface sediments in Bavarian and Tyrolean mountain lakes. Apart from two lakes with least values, the numbers were equally distributed between 1.8 and 3.

3.5 Discussion

Based on diatom community analyses of 41 mountain lakes, the initial hypothesis (1) that cell wall silicification within a benthic diatom species hardly varies was confirmed. As deduced from visual perception, the results of the photographic measurements of a species' frustules differed only as much as the SiVa levels and, when measured, their valve thickness ranged according to the 'identification key' (Fig. 3.2 & 3.4). This (2) allowed calculation of the proposed average SiVa, which then (3) supported the hypothesized response to climate change-induced variables. On the community scale, silicification pattern was inversely related to temperature. The likely explanation is that the warmer the lakes are in summer, the higher is their productivity and biomass turnover. This leads to the proposed shortening in possible growth time of benthic diatoms. Accordingly, this results in diatom species with shorter regeneration time and weaker silicification. The mean SiVa of a diatom assemblage of surface sediments can thus become a powerful proxy to assess temperature changes in lakes over time, e.g. in the context of global change. In particular, it may expand the ways of assessing the impact of climate change in palaeolimnological, based on a bioecological scale rather than of mere statistical or diversity scores.

The linear relationship of mean SiVa with surface temperature is fairly weak ($R^2 = 0.311$, Fig. 3.5c) because it integrates several other ecologically relevant factors, as a surface sample reflects various biotic and abiotic parameters of large parts of the water body. Apart from surface temperature, influences of bottom temperature ($\varrho_S = -0.336$; $p_{BC} = 1/p = 0.036$) and Secchi depth ($\varrho_S = 0.233$; $p_{BC} = 1/p = 0.154$) on diatom silicification also were apparent. On the one hand, the surface is the lake area where exchange with the atmosphere takes place, so that surface temperatures show a negative relationship with lake altitude ($\varrho_S = -0.414$; $p = 0.009$, Livingstone et al. 1999). SiVa reacts in the same manner ($\varrho_S = 0.503$; $p_{BC} = 0.187$): the higher and the cooler the lake, the heavier the frustules. On the other hand, Secchi depth and bottom temperature are more related to lake depth and volume (Fig. 3.5/Table S 4 in supplementary). Over a third of all lakes in the sample set consists entirely of littoral zone, where Secchi depth was equal to lake depth and which can be referred to as 'shallow'. Most of these mountain lakes are usually polymictic and the bottom temperature differs from the surface by only a few degrees and shows the same diurnal variation. Conversely, in deeper lakes with a clear stratification the extent of the hypolimnion and the strength of ground water inflow is more decisive for the local temperature than the frequency of water exchange with the surface. As a result, bottom temperature, lake depth and Secchi transparency affect the SiVa only weakly. Although benthic diatoms grow on the lake bottom, surface temperatures are more important than bottom temperatures, probably because the latter are biased by lake depth and hypolimnion conditions. Surface sediment samples of deep lakes tend to be dominated by planktic and benthic assemblages, which originate from the illuminated littoral zone, where surface temperatures are crucial (Hilton 1985, Stone & Fritz 2004, Gushulak et al. 2017). Nevertheless, the way in which bottom temperature, lake depth and Secchi depth are correlated with SiVa matches the general statement, the deeper and cooler the lakes, the heavier the frustules. This is explained by the fact that great Secchi depths occur in clear and well-stratified water bodies with low productivity and turnover rates. Thus, in accordance with hypothesis (3), heavier diatom species are able to grow because they live in cool, stable low productivity conditions in deep-water zones without water plants. Supporting this finding, SiVas in lakes with macrophytes were slightly lower ($p = 0.08$), because aquatic plant growth leads to higher organic material content and result in higher turnover at the lake bottom. Additionally, a lake bottom covered by aquatic plants provides an annually rapidly changing substratum for periphytic species and promotes small opportunistic diatoms, like typical pioneer species with lower SiVas (e.g. *Achnanthidium minutissimum* (KÜTZING) CZARNEKI). Hence, after the main driver, 'surface temperature', substratum conditions may also be able to explain some of the variance of the average SiVa of surface sediment assemblages, weakening its linear relationship with temperature (Fig. 3.5c).

All the above-mentioned proxies are presumed to be the main factors influencing lake mixing behaviour (Green et al. 1987, Lewis 1996), and consequently also spatio-temporal nutrient availability and diatom assemblages. The presence of frequent summer lake mixing indicates weaker silicification in polymictic lakes ($p = 0.62$, Fig. 3.6b). Therefore, they may favour smaller, lighter diatoms (e.g. pioneer species) that grow under unstable conditions, although this seems to be negligible. However, polymictic lakes are equally distributed along the altitudinal gradient in the sample set and therefore the altitudinal range of polymictic and dimictic mountain lakes is statistically the same ($p = 0.77$). Thus, in this data set, lake morphometry (area, depth, volume), may modify the response of lake temperature and silicification to mixing behaviour.

The SiVa is weakly negatively correlated with TP concentration in the mountain lake set ($\varrho_S = -0.299$, $p_{BC} = 1/p = 0.06$), although when the mountain lakes are divided into "ultraoligotrophic" and "oligotrophic" (cf. LAWA 1998, Melzer & Schneider 2014), the latter show significantly lower mean silicification. Spurious trophic level relationships due to altitude ($p = 0.28$), surface temperature ($p = 0.05$) and bottom temperature ($p = 0.09$) can be excluded. Although the higher trophic status mountain lakes tended to be warmer, ANCOVA revealed independent responses of SiVa to both temperature and trophy. This is supported by Theriot (1987), who observed weaker silicification in several species of Stephanodiscus under higher trophy and decreased silicification under low Si : P ratios, whereas Si concentrations alone correlated weakly with silicification, like SiVa in the mountain lakes (Fig. 3.5/Table S 4 in supplementary). Whereas Finkel et al. (2010) showed differences in cell wall silicification in *S. pinnata*, which also occurs frequently in freshwater habitats, Schelske & Stoermer (1971) suggested that diatom growth was independent of silica concentration, as long as that did not fall below 0.1 mg L^{-1}. However, Finkel et al. (2010) used a marine-brackish strain, which showed pronounced intraspecific differences in silicification pattern (Conley et al. 1989). On the other hand, variation in freshwater strains would probably be lower and hardly vary, as shown above for freshwater benthics and by Passy (2007). With respect to the Schelske & Stoermer (1971) work, silica availability in the Bavarian mountain lakes was never below the limit; the lowest silica concentration was 0.13 mg L^{-1}. Furthermore, no remains of other competing silica consumers could be found, apart from some chrysophyte cysts, and other siliceous organisms, such as freshwater sponges, probably do not impair diatom silica uptake. Iron availability, which can also affect silicification (Boyle 1998, Twiss et al. 2000, Sterner et al. 2004, Vrede & Tranvik 2006), is unlikely to be limited in small freshwater lakes like the studied mountain lakes, which are strongly influenced by big catchments and erosion although climate warming is presumed to intensify potential silicate limitation. Warmer temperatures, decreasing extent and duration of snow cover, increased soil formation in the catchment and frequency of heavy precipitation events lead to an increase of erosion and material input into mountain lakes (Lotter et al. 1999, Bogataj 2007, Brookshire et al. 2011, Rosbakh et al. 2014, Bätzing 2015). Accordingly, there are predicted increasing loads of bioavailable phosphorous. As long as the inorganic input balances an increasing silica need also in non-siliceous bedrock like in the sampled lakes, the phosphorous response of the diatom silicification can further contribute to its indicator function for climate warming as initially hypothesized (3).

3.5.1 The Silicification Value and Size Effect

Apart from a climate warming-driven shift from heavily towards lightly silicified diatom, silicification pattern may also be the result of a mere size effect, that (4) bigger diatoms tend to have heavier valves. However, an evaluation of SiVa levels and the valve size estimate did not confirm a direct positive relationship (Fig. 3.6d). Additionally, none of the environmental parameters correlated significantly with average valve sizes. In planktic diatoms, warming or eutrophication is presumed to result in changes in average valve size (Finkel et al. 2009, Margalef 1969), particularly in *Asterionella formosa* HASSALL (Kling 1993), *Tabellaria flocculosa* (ROTH) KÜTZING (Klee & Schmidt 1987), and some *Fragilaria* s.l. LYNGBYE (Roessler 1988, Kling 1993). Intraspecific size reductions can be a response to higher reproduction rates since good nutrient availability enhances algal blooms and many vegetative generations that lead to a decrease in cell size in most species (Krammer & Lange-Bertalot 1986, Round et al. 1990). Diatoms can also possibly take advantage of good conditions to increase the frequency of auxosporulation and to ensure long-term survival in a habitat (Kling 1993, Kaczmarska et al. 2018). In contrast to planktic diatoms, size variation in benthic diatom species is significantly lower, although underlain by similar ecological constraints by temperature and nutrients (Passy 2007), and benthic communities can even increase in average cell size as a response to warming (Svensson et al. 2014). Nevertheless, those small variations seem to be directional, as bigger cells appear in cold seasons (winter and spring) and as smaller cells in the warm seasons (summer and autumn) (Sun et al. 2018). This may be the result of many vegetative generations during growth period or an adaptation to clear-water stages in summer since smaller cells have higher nutrient uptake rates relative to larger cells (Biggs et al. 1998, Passy 2007, Lange et al. 2015). Such seasonal benthic size variation may affect relationships between environmental parameters and valve size, as the studied surface sediment assemblages integrate several seasons, 1 cm represents approximately 5 years. Accordingly, both size extrema could be observed in Bavarian mountain lakes. On the one hand, there many large individuals of *Gyrosigma attenuatum* (KÜTZING) RABENHORST of around 280 µm long (largest was 306 µm) in a cold alpine lake exceeding the proposed size range (Hofmann et al. 2013) by far. On the other hand, a similar habitat contained also small sized *Diploneis oculata* (BRÉBISSON) CLEVE, which fitted better in the smaller size range as described in high Arctic regions (Antoniades et al. 2008) than in temperate Central Europe (Hofmann et al. 2013) contrasting the size-temperature relation as observed by Svensson et al. 2014. Here, it is discussable whether small sized individuals with shorter regeneration time appear because of a short vegetation period in summer in alpine altitudes rather than temperature or nutrient effects.

All these divergences lead to the suggestion that any valve size's effect on the SiVa can be ignored and its use for any environmental interpretations is more complex than the SiVa.

3.5.2 The Silicification Value and Alternatives

Focusing on the ecologically-driven silicification of diatoms, another way to evaluate this in subfossil diatom assemblages would be to measure the thickness of valves to estimate a population's average, or the silica content in sediment layers. However, subfossil assemblages are often affected by taphonomic processes, shown by broken or partially dissolved valves suggesting weaker silicifications. These processes make it difficult to measure only silica content or valves, further complicated by pore water chemistry and temperature, which affect silica dissolution rates (Lewin 1961, Coradin & Lopez 2003, Zgrundo et al. 2017) and diatom community composition and structure (Ryves et al. 2001). There are also other sources of silica, e.g. chrysophyte cysts, which are often abundant in lacustrine sediments (e.g. Stoermer et al. 1995). The SiVa can avoid such problems as it uses fixed values based on existing assemblages and can be applied as long as the valves are identifiable. SiVa can therefore overcome the aforementioned problems as long as taphonomic processes do not distort the assemblage composition due to variable preservation and identification problems. Accordingly, evaluating taphonomy by estimating the percentage of dissolved valves, e.g. 'diatom dissolution index' (Ryves et al. 2006), diatom densities or counting broken scales and spines of chrysophyte cysts may still be necessary in down-core studies (Battarbee et al. 2001, Dong et al. 2008).

Alternative calculations for climate change and lake quality assessment use species tolerance ranges. However, mountain lake communities are often dominated by a few generalistic species. Thus, calculating diatom-inferred trophic status, pH-value, etc. is not possible in many cases because of the lack of indicative species.

In contrast to using valve size changes to assess diatom assemblages, it is more appropriate and also easier to apply the more robust SiVa. Calculating size ranges of diatom frustules in each population, which can also differ among habitats, is labour intensive and dependent on accurate identifications. As the SiVa can bypass this and also eliminates the effect of valve size in climatological issues. Although correlations between SiVa and valve size were initially assumed and valve size was thought to correlate with temperature, no significant relationship was found. Size effect on diatom silicification is limited to distinguishing between ‘heavily’ and ‘not heavily’ silicified diatom, rather than being positively correlated with the SiVa.

3.6 Conclusions

Small lakes in extreme habitats often lack specialised indicator species for diatom-related proxies (e.g. transfer-functions) and are dominated by generalists. Therefore, it is often problematic to assess lake quality and calculate past conditions. One way to overcome this lack of specialists is to consider the species-dependent silicification of diatom frustules. Except for some planktics, this appears to be a consistent process within a species, as long as silica is not limited. The newly introduced SiVa categorizes these silicate shell morphologies and can be averaged over an entire diatom assemblage. Mean SiVas of surface sediment communities were strongly determined by temperature, and can therefore be used as indicators and quantifiers of climate change, where traditional transfer-functions fail. Another important driver for local turnover as well as the SiVa is the bioavailable phosphorous in a lake which increases with climate change. This makes the SiVa a powerful indicator for climate change in freshwater habitats as it integrates all its main response variables. Apart from this indicative function, there are more advantages to the SiVa: (1) robustness against taphonomic processes in the sediment, or other organisms providing silica in the sediment, (2) robustness against identification discrepancies between diatom counters, and (3) applicability to any diatom species.

The SiVa can also serve as a palaeolimnological proxy. Within the scope of the ongoing Bavarian “Mountain Lake Project”, the application of SiVa onto a time series is currently being tested. The implementation of the SiVa to subfossil diatom assemblages may be useful to detect and quantify climate change impact in lakes (cf. Küfner & Raeder 2018).

Future work needs to evaluate the possibility of iron limitation in freshwater habitats, which may affect diatom silicification, and the transferability of using 1 cm layers to assess surface sediment assemblages. As an improvement, surface scrapes could be used in lakes with extremely low sedimentation to assess assemblages of recent years, or to evaluate silicification pattern with seasonal precision. Another need is to include planktic diatom species, which dominate in deep lake sediments. For this purpose, their silicification pattern has to be evaluated carefully. A possibility is to split heterogeneous taxa into different morphological groups according to different silicification patterns or to introduce silicification ranges instead of values. In combination with diatom densities, other possible applications of the SiVa are evaluations of subfossil biomass, trophic status or silica concentrations. The latter can take advantage of the finding that it increases with biovolume, can be calculated from each other and does not differ among pennates and centrics (Conley et al. 1989).

In contrast, the palaeolimnological application is challenged by sediments with unusual pore water conditions (e.g. extreme pH values)(Lewin 1961, Coradin & Lopez 2003, Zgrundo et al. 2017) and, especially in older sediments, a diatom valve's preservation. The 'half-life' of a strong and large *Navicula oblonga* KÜTZING under defined experimental conditions is almost as ten times longer than those of a little *Nitzschia fonticola* GRUNOW (Ryves et al. 2001). Lakes in high altitudes and latitudes are also affected by high amounts of clastics in sediments. Clastics can cover small diatoms and lead to believe in lower diatom densities and a higher abundance of bigger and stronger species, which can still be well observed. Altogether, these problems can increase the SiVa throughout a sediment core towards older sediments and thus mislead or exaggerate the interpretation of former cooler conditions. Whereas various cleaning techniques are able to overcome the clastic problem, subfossil diatom assemblages have to be carefully evaluated for the preservation of diatom valves like implementing diatom densities, percentages of broken or partially dissolved valves or chrysophytes and their scales if apparent. These methods can indicate the degree of preservation of subfossil assemblages. Sediment layers affected by temporarily higher sedimentation rates, and/or poor in diatoms in general, have to be taken with caution as well. Altogether, when preservation and density of sub-fossil diatoms is doubtful impairing a diatom analysis, the application of the SiVa is questionable. Nevertheless, it is always better to exclude such samples from palaeoecological studies.

4 Evaluating Climate Change Impacts on Mountain Lakes by Applying the New Silicification Value to Paleolimnological Samples

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Author contributions: WK conceptualised this study and carried out data collection. Sampling, preparation and analyses of the sediment cores as well as microscopic analyses was mainly perfomed by WK and Andrea Hofmann (AH). Statistical analyses, visualisation and data interpretation was the main work of WK in consultation with AH. The manuscript was drafted and finalised by WK and continuously reviewed and improved by JG and UR.

4.1 Abstract

The evaluation of climate change impact on lakes typically relies on statistical methods like the reorganisation of organism communities (beta diversity) or transfer functions. A new method uses the silicification of diatoms that correlates with temperature and nutrients. The so-called silicification value (SiVa) overcomes problems of descriptive statistics or absent indicator species. Averaged over diatom communities, it related inversely to lake surface temperatures in mountain lakes. Hence, its change over time (δ SiVa) in a lake was hypothesised to reflect global change-driven lake warming quantitatively, which supposedly climaxes in shallow lakes. Sixteen different δ SiVa calculation approaches were tested. They (1) included or excluded planktic diatoms, (2) integrated fixed or variable time series referring to climate data or changes in diatom assemblages, (3) employed a top-bottom or regression approach and (4) expressed the δ SiVa as relative or absolute values. Subfossil diatom assemblages from 24 sediment cores from Bavarian and north Tyrolean mountain lakes served as sample set. All possible approaches were evaluated for their explanatory power for lake characteristics using GLMs. The top-bottom benthic approach with fixed climate data-based time series appeared to be the best model based on AIC and the extent of variable integration. In line with the hypothesis, the strongest decrease of δ SiVa was evident in most shallow lakes. Segmented regression further highlighted a positive correlation with depth if shallower than 10 m. By referring to the negative SiVa-summer temperature relation, δ SiVa also enabled the quantification of lake warming within the last decades, which ranged mainly between 0.1 °C and 1.1 °C per decade, consistent with existing literature. Additionally, a 100 year temperature reconstruction from a varved sediment core successfully validated the approach. Further studies may focus and extend its application to deeper lakes, but it can already serve as a powerful tool in palaeolimnological studies of shallow lakes like hard-water mountain lakes.

4.2 Introduction

The evaluation of climate change impacts on lakes is one of the most important goals in palaeolimnology (Last & Smol 2001). Such lake sediment studies can be based on a broad spectrum of organisms (e.g. diatoms) (Smol 1988, Pienitz et al. 1995, Michelutti et al. 2015, Rühland et al. 2015) and molecules (e.g. pigments, DNA) (Appleby 2001, Jørgensen et al. 2012, Pansu et al. 2015) as well as diverse analytical (e.g. XRF scanning) (Croudace et al. 2006, Francus et al. 2009) and statistical techniques (ter Braak 1987, ter Braak and Verdonschot 1995, Smol et al. 2005). Diatoms are one of the most widely used groups of organisms in these studies since they are ubiquitous in limnic habitats, usually well-preserved and easy to extract from sediments. The development of the mere species composition of subfossil assemblages can already provide first indications of changes within a lake. For instance, alpha diversity indices like the Shannon index are indicative of the complexity of the substrate (Antoniades et al. 2005, Michelutti et al. 2015). Climate change has been shown to cause a succession of the benthos from epipelic or epilithic to epiphytic substrates because the warming favours the growth of aquatic plants (Heino & Toivonen 2008, Heino et al. 2009). Such an increase in substrate heterogeneity leads to an increase of the Shannon index in benthic species, as a more diverse benthos is colonised by a more species-rich diatom community. Furthermore, the mere species composition of all samples of a sediment core is often used for descriptive statistical calculations like the beta diversity (ter Braak 1987, ter Braak & Verdonschot 1995). This technique quantifies the extent of an assemblages' reorganisation, which may be driven by external effects like climate change. In case of a directional shift of the assemblages in the diatom stratigraphy that are in line with the literature in terms of climate warming response (Lotter et al. 1999, Lotter & Bigler 2000, Rühland et al. 2015), such values can serve as an indicator of the extent of global change impact on a lake (Smol et al. 2005). Apart from species compositions, many studies also take advantage of the indicator function of many diatom species. For example, transfer functions can be used to extrapolate various parameters like pH (e.g. Weckström 1997, Koinig et al. 2002), nutrient concentrations (e.g. Stoermer & Smol 1999, Schaumburg et al. 2011) or temperature (e.g. Anderson 2000, Larocque & Bigler 2004) from diatom species composition. However, most of those temperature transfer functions are based on soft-water lakes, which host significantly differing diatom communities than in calcareous lakes (Weckström et al. 1997, 2006, Joynt III et al. 2001, Thompson et al. 2005a) and are strongly affected by pH and bedrock chemistry (Pienitz et al. 1995, 1997, Lotter et al. 1997). Available functions from Swiss hard-water lakes are further strongly impaired by nutrient conditions (Lotter et al. 1997, 1998). Additionally, especially shallow lakes often lack indicator species and are dominated by a few generalistic diatoms, challenging the applicability of common diatom-inferred proxies (Rühland et al. 2015, Miettinen 2018). To overcome this problem, the silicification value (SiVa) can be used to classify any diatom species into seven groups according to the intensity of valve silicification (see Chapter 3). Additionally, this value mirrors and integrates lake temperature and phosphorous concentration, both of which are affected by climate change (see Chapter 3). Thus, the SiVa refers to the diatom’s individual ecology in contrast to the beta diversity as a mere statistical technique.

In Chapter 3, it could be observed that the average SiVa of diatom communities on surface sediment samples decreases with temperature and nutrient availability. A likely explanation for this phenomenon is that warmer temperatures and an increased trophic state cause higher biomass turnover in the diatom communities. Therefore, conditions of higher productivity support smaller and slightly more silicified species because their regeneration time is shorter, as has already been observed in planktic diatoms (Theriot 1987). Conversely, larger diatom species that require more time to construct heavily silicified valves decrease in their relative abundance as small and rapidly growing pioneers overgrow them. Influencing this relation, climate change likely results in increased warming of lakes and enhanced soil formation in the alpine region as well as increased erosion due to an increase in extreme precipitation events and decreasing snow cover. This in turn leads to an increased influx of organic and inorganic material into lakes, thereby increasing the phosphorous concentration (Koinig et al. 1998, Bogataj 2007, Bätzing 2015, Arnaud et al. 2016). As a result, the number of diatom species with high SiVas, which are adapted to cooler conditions, is hypothesised to decrease. The extent of the δ SiVa, or the speed of the decrease in average silicification, may further allow quantifying this climate change impact based on the composition of the subfossil diatom assemblages.

Accordingly, δ SiVa should also detect a varied response of deep and shallow lakes. Lake depth (Chen et al. 2014, Rühland et al. 2015), as well as the altitude in the case of mountain lakes (Chapter 3, Livingstone et al. 1999), can decisively determine the temperature and warming of a lake and the nature of diatom reorganisation. Whereas deep lakes are stratified during summer and buffer warming with a cool hypolimnion, shallow lakes lack stratification, and, if completely illuminated, the lake bottom further absorbs and reflects long-wave radiation. Consequently, shallow lakes can be expected to express a strong response to climate change in terms of an extreme species turnover in the benthic communities. Transferring this to diatom silicification, δ SiVa values are expected to become strongly negative in shallow lakes, i.e. average silicification rapidly decreases, and should exhibit a positive relationship with lake depth until a certain depth threshold is reached: the shallower a lake, the stronger the decrease of the average silicification in the diatom community. This threshold is assumed to split into shallow polymictic or completely illuminated lakes and deep dimictic lakes with an aphotic zone, which can be influenced by lake altitude. Apart from altitudinal effects especially on mountain lakes, such limnic systems are well suited for climatological studies. Their remoteness and the absence of direct anthropogenic influences, which might otherwise mask signals of global warming, makes mountain lakes sentinels of climate change (Rogora et al. 2018, Moser et al. 2019). Therefore, mountain lakes are perfect to test the applicability of the SiVa.

(1) Assuming that the SiVa can be used to detect climate change-driven changes in subfossil diatom assemblages, this study initially tests which approach is the best to apply this indicator on a palaeolimnological scale in terms of goodness of fit, model simplicity and parameter integration. (2) Further, the inclusion of planktic diatom species into the SiVa calculations, which was first modelled for benthic species, is evaluated. (3) Once the best method has been established, the development of the silicification value (δ SiVa) on a defined time scale is compared with the beta diversity as a classic statistical method and hypothesised to differ between shallow and deep lakes. (4) Lastly, the plausibility of δ SiVa-referred lake warming is validated with literature and weather station data, which is comparable to classic transfer functions. For these goals, subfossil diatom assemblages from several sediment cores from many different mountain lakes in the Bavarian and Tyrolean calcareous Alps were analysed.

4.3 Methods

4.3.1 Study Site

The sediment coring campaign comprised 24 mountain lakes in the Bavarian and Tyrolean calcareous Alps (47°17’ to 47°45’ N, 10°15’ to 13°1’ E, Fig. 4.1), where annual precipitation ranges from 1179 (Hohenpeißenberg, 987 m a.s.l.) to 2071 mm (Zugspitze, 2962 m a.s.l.) and in summer from 470 to 560 mm (DWD). The lakes are distributed over a wide altitudinal range (922–2060 m a.s.l.). The lakes can be classed into three distinct levels. The catchment of (1) mountainous lakes is characterised by mixed forests (*Picea abies*, *Fagus sylvatica*), the catchment of (2) subalpine lakes ranges from alpine pasture to sparse coniferous forests (*Picea abies*, *Larix decidua*) and the catchment of (3) alpine lakes lacks forests and consists of alpine meadows (e.g. *Rhododendron hirsutum*, *Carex sempervirens*), patches of dwarf pine (*Pinus mugo*) and poorly developed soils or rocky areas. Carbonate rocks (dolomite, limestone) and glacial deposits (lodgement, moraine deposits) dominate the geology of the area. Except two postglacial (doline and landslide) lakes, all the others are of glacial origin (cirque and moraine lakes). Due to their altitude, it can be assumed with high probability that the catchment areas of all investigated mountain lakes have been glacier-free for more than 100 years. The 24 hard-water mountain lakes average in size around 3 ha (0.4–12 ha), maximum water depth 8.9 m (1.3–20.7 m), pH 8.4 (7.9–8.8), conductivity at 25 °C of 240 µS cm^{-1} (134–360 µS cm^{-1}), and ultra-oligotrophic to mesotrophic nutrient conditions (TP around 7.7 µg L^{-1}, 0.1–20.4 µg L^{-1}). A detailed description of the lake morphometries along with their hydrophysical and hydrochemical parameters is presented in Chapter 3 and Table 2.1. Lake mixing behaviour was defined according to temperature logger data (HOBO®, Onset, Bourne, USA); the data loggers were installed above the lake bottom and below the surface in each lake mainly from June until October 2016 as the summer temperature is predominantly affecting aquatic communities (Luoto & Nevalainen 2016). An observed difference between the surface and bottom temperature of <1 °C was defined as a mixing event. If mixing events occurred in a lake during summer, the lake was classified as polymictic; otherwise, the events were considered dimictic if there was evidence for a proper stratification throughout the summer.

Climatological data derived from the Hohenpeißenberg pre-alpine weather station (987 m a.s.l.) of Germany's National Meteorological Service (DWD) were used to validate SiVa-related temperature reconstructions. This weather station recorded the longest available dataset for the area starting in 1781. The data were delivered by the European Climate Assessment & Dataset Project.

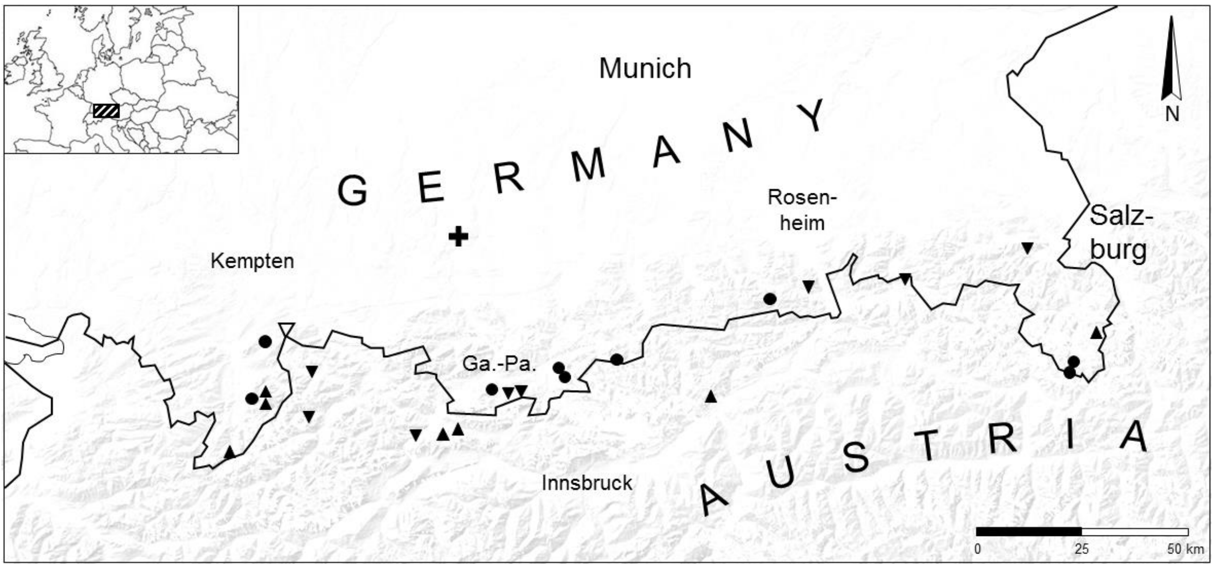

Figure 4.1: Map of the Bavarian–Tyrolean Alps along the German–Austrian border with the location of the 24 mountain lakes. Triangles: alpine, circles: montane, upside down triangles: montane mountain lakes, cross: Hohenpeißenberg DWD-weather observatory. Ga.–Pa.: Garmisch–Partenkirchen.

4.3.2 Sediment Coring and Dating

The sediment coring took place from 2015 until 2017 at the deepest spot of each mountain lake, which was identified by sonar screening (HDS8, Lowrance, Tulsa, USA). The sediment cores were taken with a gravity corer (Uwitech, Mondsee, Austria), hermetically sealed and stored at 4 °C for not longer than 90 days until they were subsampled in intervals of 1 cm. Then, the sediment samples were freeze-dried and additionally ground for the dating. The core dating samples were analysed by gamma spectrometry (High-purity Germanium Well Detector, HPGe, Canberra, USA) at the EAWAG in Dübendorf, Switzerland. To determine accumulation rates, the radionuclides ^{210}Pb and ^{137}Cs were used. The latter isotope provides two markers as it firstly peaked in 1963 because of atmospheric nuclear weapon testing (Appleby 2001) and secondly in 1986 after the Chernobyl disaster. The ^{137}Cs data were used to support the ^{210}Pb chronology calculations, which were based on the CRS model (Constant Rate of Supply, Appleby 2001). In varved sediment cores, varve counting adjusted by ^{137}Cs and ^{210}Pb data was used instead of the CRS model for core dating. Resulting age-depth models are supplied in the supplementary (Fig. S 1–3).

4.3.3 Diatom Analyses

Depending on the organic content, 0.2–1 g of the freeze-dried sediment samples were used to prepare permanent slides according to the method of Van der Werff (1953) with certain adaptions as described in Chapter 3. Different dilutions of the cleaned diatom material were embedded in the high-refractive index medium Naphrax. In the case of samples that were rich in Centrales, SEM slides were prepared additionally by air-drying 50 µL of the most appropriate sample dilution onto a glass cover slip (Ø 12 mm) and coating in gold using the Polaron SC502 Sputter Coater (Fisons Instruments, UK). In each sample, at least 550 diatom valves were counted under oil immersion at 1000x magnification using light microscopy (Aristoplan and Labovert, Leitz, Wetzlar, Germany), additional SEM pictures were taken at 5000–20000x magnification using an S-2300 (Hitachi, Tokyo, Japan). Diatom identification followed Krammer & Lange-Bertalot (1986–1991), Lange-Bertalot et al. (1993–2003), Krammer (1997), Reichardt (1999), Houk et al. (2010–2014) and Hofmann et al. (2013) with current updates in literature. For further calculations, only species that contributed at least 1% in a count of at least one sample were taken into account.

The diatom stratigraphies of the 24 mountain lake sediment cores can be distinguished into four groups (see Chapter 5): type 1 lakes (increase in planktics in deep lake assemblages), type 2 lakes (recent appearance of planktics accompanied by decreasing *Staurosira* EHRENBERG), type 3 lakes (dominated by *Staurosira* species without directional species shifts), type 4 lakes (replacement of *Staurosira* by *Achnanthidium* KÜTZING) and type 5 lakes (replacement of *Nitzschia denticula* by *Diploneis* spp. EHRENBERG EX CLEVE).

4.3.4 Statistical Analyses

According to the formula 4.1, an average SiVa was calculated for every subfossil diatom assemblage of each sediment sample. The values of the SiVa downcore development (δ SiVa) can be negative (decrease) or positive (increase in average diatom silicification). To obtain the best method of estimating δ SiVa for the palaeolimnological approach, 16 different modelling approaches were tested (Table 4.1), evaluated for their explanatory power and compared with lake data and beta diversity. Lake data refer to Chapter 2.1 & 3, whereas beta diversity refers to the length of the first axis of a detrended correspondence analysis with an implementation of 45 year-core compartments as the temporal constraint. This technique scales values in SD units, which can also be referred to as turnover units of beta diversity (ter Braak 1987, ter Braak & Verdonschot 1995). Firstly, there were two different temporal approaches assuming that climate change started to affect different mountain lakes at different times. Hence, either a qualitatively chosen or a fixed time series served as the basis. The former referred to the development of the diatom assemblage determining the onset of climate change, i.e. when diatom assemblages started to shift (hereinafter referred to as the 'qualitative approach'); the latter relied instead on climate data, which indicated that the onset of the strongest warming in the study area occurred in the 1970s (Gehrig-Fasel et al. 2007), leading to the implementation only of those core compartments for further analyses that integrated the last ~45 years (hereinafter referred to as the 'quantitative approach'). Secondly, the δ SiVa was computed for the entirety of the chosen core compartment versus a top–bottom approach. The whole compartment value expresses a regression of the SiVa over time. In contrast, the top–bottom value averages the youngest 3 cm and compares them with 3 cm of the decade of the climate change onset (1975–1985). This method avoids the introduction of a user-dependent choice effect in sample comparison. Thirdly, the inclusion of planktic diatoms of the subfossil assemblages was contrasted with its exclusion as in Chapter 3; for that comparison, SiVas were assigned to the planktic diatom species as it occurred for the benthics in the preliminary study. Lastly, the quality of absolute δ SiVas versus relative δ SiVas was checked. The latter was related to the mean SiVa of the corresponding core as a reference value, i.e. scaled without a unit in percent. The values of the regression and qualitative time approaches are typically relativised by year and represent the silicification value development per year (δ SiVa/a). Instead, the quantitative top–bottom approach estimates the mere difference of the SiVas since the approach continuously integrates the same period of ~45 years, which avoids unnecessary downsizing of the value.

Table 4.1: Different approaches used to calculate the δ SiVa. There were two approaches in each of the four categories resulting in 16 different tests.

Implemented core compartment	Mathematical approach	Implemented diatoms	Data type
Qualitative, diatom-based	Regression approach	With planktics (all)	Absolute data
Quantitative (fixed time series), climate data-based	Top–bottom approach	Benthics only	Relative data

Multiple reports have already indicated the importance of lake depth and the separation of the mountain lakes into 'shallow' and 'deep' lakes referring to the Secchi depth, which is equal to lake depth in 'shallow' mountain lakes (Pienitz et al. 1997, Chen et al. 2014, Rühland et al. 2015). To evaluate whether the δ SiVa expresses such a dichotomy as well, a break point analysis and segmented regression were computed. For the shallow mountain lakes, which are supposed to be directly dependent on lake depth, generalised linear models were calculated for each approach to evaluate the explanatory power and response to morphometric and hydrophysical data. The application of an AIC-based stepwise backward selection unearthed decisive proxies in the models. If parameters were highly correlated ($\varrho > 0.7$), only one of them was used for the model (Schröder & Reineking 2004). Eventually, the proxy 'lake surface' was implemented as the independent factor and the 'depth' and 'bottom temperature' as well as 'altitude' and 'surface temperature' as dependent factors in the model. The interpretation of the models was further supported by Spearman correlation analyses based on ranks. In case of categorical data (e.g. mixing behaviour), t- or Mann–Whitney U-tests were calculated depending on the results of the F-test checking for variance similarities; p-values ≤ 0.05 were considered significant.

The estimation of the lake warming based on the δ SiVa refers to the negative linear relationship between the average silicification of diatom communities of surface sediment samples and the August surface temperature ($\varrho_{\text{Spearman}} = -0.560$; $p_{\text{Bonferroni}} = 0.036$; Chapter 3.4). August temperature is one of main drivers in mountain lakes (Luoto & Nevalainen 2016) and the first month of the year that is significantly warming due to climate change (Niederist et al. 2018). Accordingly, the surface temperature in summer (August) can be calculated from the SiVa (formula 4.1) and the warming per year from the δ SiVa (formula 4.2). To evaluate the predictive ability of those formulas, forecast skills (Lorenz 1956, Thompson et al. 2005a) and prediction errors like root mean squared error (RMSE) (Wallach & Goffinet 1989) and RMSE of prediction (RMSEP) with jack-knifing are supplied (ter Braak & Juggins 1993). As the calibration set included a variety of nutrient concentrations and geological origins, the forecast skill of formula 4.1 was only 44%, RMSE = 2.51 °C and RMSEP = 2.66°C. For instance, the exclusion of a special small doline lake, which is completely filled by the adjacent cold Lake Sieglsee, led to an improvement of predicting power (56%). The formulas only implement absolute values to ease the calculation without back-transformation of relative values.

(Formula 4.1) $$\text{temperature (surface) [°C]} = 25.956 - 4.7155 \times \text{SiVa}$$

(Formula 4.2) $$\delta\ \text{temperature (surface) [°C a}^{-1}] = -4.7155 \times \delta\ \text{SiVa}$$

Depending on the approach evaluation results, the best δ SiVa was implemented in the temperature functions. For reconstructing the temperature development, formula 4.1 was calculated for each sediment sample of a suitable core, compared with weather station data, which is a probate way in case of missing historical water temperature data (Livingstone & Lotter 1998), and evaluated for its predictive power. To infer annual temperatures from the sediments and to expand the comparable data set, Loess-smoothers were applied to both SiVa-inferred temperature and weather station data.

The initial data preparation occurred in Microsoft Excel 2016 ® and the statistical analyses were performed in PAST 3.20 (Hammer et al. 2001) and R version 3.4.1 with the packages 'PerformanceAnalytics' (Peterson et al. 2018) and 'segmented' (Muggeo 2017).

4.4 Results

4.4.1 δ SiVa

The silicification value development per year (δ SiVa a^{-1}) of the regression and 'qualitative' approaches averaged a decrease of 0.011 units per year (−0.186 to 0.004), the relative values 0.317 % a^{-1} (−1.754 to 0.207 % a^{-1}) and the top–bottom values decreased by 0.159 (−0.925 to 0.129), a relative change of 6.069 % (−38.672 to 6.019 %) considering the entire dataset from all 20 lakes. Four lakes had to be excluded because of insufficient diatoms densities or core dating data.

The segmented regression of all δ SiVa in relation to lake depth revealed two break points (Fig. 4.2a). They are located at depths of approximately 4.5 and 10 m. Except in the deeper lakes (>10 m), the δ SiVa of the 'shallower' mountain lakes was positively related to lake depth, i.e. the most negative δ SiVas were observed in the shallowest lakes. Furthermore, the inclusion of planktic diatoms only resulted in deviated δ SiVas in deep lakes compared with their benthic δ SiVas. In shallow lakes (<10 m), the δ SiVas with planktics equalled the δ SiVas without.

4.4.2 Model testing

Based on the segmented regression analysis results, GLMs were only calculated for the mountain lakes <10 m depth. The models showed that the top–bottom approaches are able to include more variables in a significant way than the regression approaches; the latter either lacked significances or their backward selection resulted in a single explanatory proxy only (Table 4.2). The AIC as an estimate to evaluate the quality of the model as well as the amount and value of significances highlights the 'relative qualitative benthic top–bottom approach' as the most appropriate model. This model as well as all the others indicated positive correlations of the δ SiVa with lake surface ($p = 0.009$) and depth ($p = 0.004$). The surface and bottom temperatures showed the same correlation trend; however, their dependence on altitude and lake depth, respectively, may mask their actual influence on δ SiVa. Correlation analyses support a negligible influence of the sole surface temperature (Table 4.2).

The comparison between the δ SiVa of the relative top–bottom approaches and the beta diversity reveals a dichotomous distribution of the mountain lakes: one branch represents a negative relationship, the inverse branch outliers consisting of a group of four lakes (Fig. 4.2c). This inverse

Table 4.2: GLM results of all 16 possible approaches of the δ SiVa application. The approach columns are ordered according to Table 4.1. 'Math': mathematical approach; 'Benth.': only benthic diatoms are implemented in the model; 'all': benthics and planktics are implemented; 'abs': absolute; '%': relative values. Upper value: regression coefficient (estimate); bottom value: p-value. (Highly**) significant* connections are highlighted in (red) orange.

Approach				Surface	Depth	Altitude	Temperature (surface)	Temperature (bottom)	Altitude: Temp. (surf)	Depth: Temp. (bot)	Intercept	AIC
Time	Math	Diatoms	Data									
Qualitative	Regression	Benth.	abs	6.898e-03 (0.038)*	5.560e-03 (0.106)	1.094e-04 (0.084)	3.566e-03 (0.516)	4.839e-03 (0.096)	−6.129e-06 (0.094)	−2.431e-04 (0.321)	−0.1770 (0.092)	−83.61
			%	2.838e-03 (0.045)*	2.436e-03 (0.105)	4.647e-05 (0.090)	1.639e-03 (0.495)	2.058e-03 (0.102)	−2.584e-06 (0.102)	−1.103e-04 (0.304)	−0.0773 (0.091)	−103.51
		all	abs	5.437e-03 (0.092)	5.124e-03 (0.153)	9.014e-05 (0.159)	3.434e-03 (0.563)	3.922e-03 (0.182)	−4.984e-06 (0.177)	−2.050e-04 (0.430)	−0.1575 (0.145)	−81.57
			%	2.197e-03 (0.107)	2.243e-03 (0.148)	3.819e-05 (0.165)	1.621e-03 (0.529)	1.642e-03 (0.192)	−2.088e-06 (0.187)	−9.467e-05 (0.401)	−0.0693 (0.139)	−101.74
	Top-bottom	Benth.	abs	6.685e-03 (0.007)**	9.162e-03 (0.004)**	8.677e-05 (0.036)*	1.395e-03 (0.659)	7.183e-03 (0.005)**	−4.930e-06 (0.039)*	−5.048e-04 (0.016)	−0.1669 (0.024)*	−96.45
			%	2.770e-03 (0.009)**	4.079e-03 (0.004)**	3.704e-05 (0.039)*	6.669e-04 (0.630)	3.124e-03 (0.005)**	−2.073e-06 (0.044)*	−2.314e-04 (0.013)	−0.0734 (0.023)	−116.35
		all	abs	3.748e-03 (0.098)	8.115e-03 (0.017)*	6.768e-05 (0.141)	3.781e-03 (0.384)	5.072e-03 (0.042)*	−3.687e-06 (0.163)	−4.885e-04 (0.042)*	−0.1664 (0.055)	−89.794
			%	1.625e-03 (0.107)	3.575e-03 (0.018)*	3.063e-05 (0.139)	1.681e-03 (0.389)	2.260e-03 (0.043)*	−1.618e-06 (0.171)	−2.169e-04 (0.044)*	−0.0749 (0.054)	−109.01
Quantitative	Regression	Benth.	abs	3.782e-03 (0.160)	6.178e-03 (0.076)	5.168e-05 (0.328)	2.780e-04 (0.957)	4.449e-03 (0.109)	−2.820e-06 (0.358)	−2.926e-04 (0.233)	−0.1021 (0.259)	−84.32
			%	1.517e-03 (0.175)	2.590e-03 (0.076)	2.091e-05 (0.344)	9.810e-05 (0.964)	1.844e-03 (0.113)	−1.130e-06 (0.378)	−1.236e-04 (0.231)	−0.0421 (0.267)	−105.14
		all	abs		2.852e-03 (0.001)**						−0.0230 (0.000)**	−87.24
			%		1.179e-03 (0.001)**						−0.0095 (0.000)**	−108.54
	Top-bottom	Benth.	abs	0.1449 (0.076)	0.2538 (0.024)*	1.346e-03 (0.355)	−0.0636 (0.662)	0.1893 (0.034)*	−7.458e-05 (0.378)	−0.0185 (0.109)	−2.8060 (0.263)	−4.60
			%	0.0651 (0.057)	0.1089 (0.020)*	5.914e-04 (0.319)	−0.0314 (0.595)	0.0835 (0.026)*	−3.270e-05 (0.343)	−5.094e-03 (0.094)	−1.1760 (0.248)	−26.33
		all	abs		0.2089 (0.011)*			0.0848 (0.054)		−0.0098 (0.114)	−1.7708 (0.005)**	−4.44
			%		0.0881 (0.010)*			0.0358 (0.050)*		−0.0042 (0.104)	−0.7433 (0.004)**	−25.69

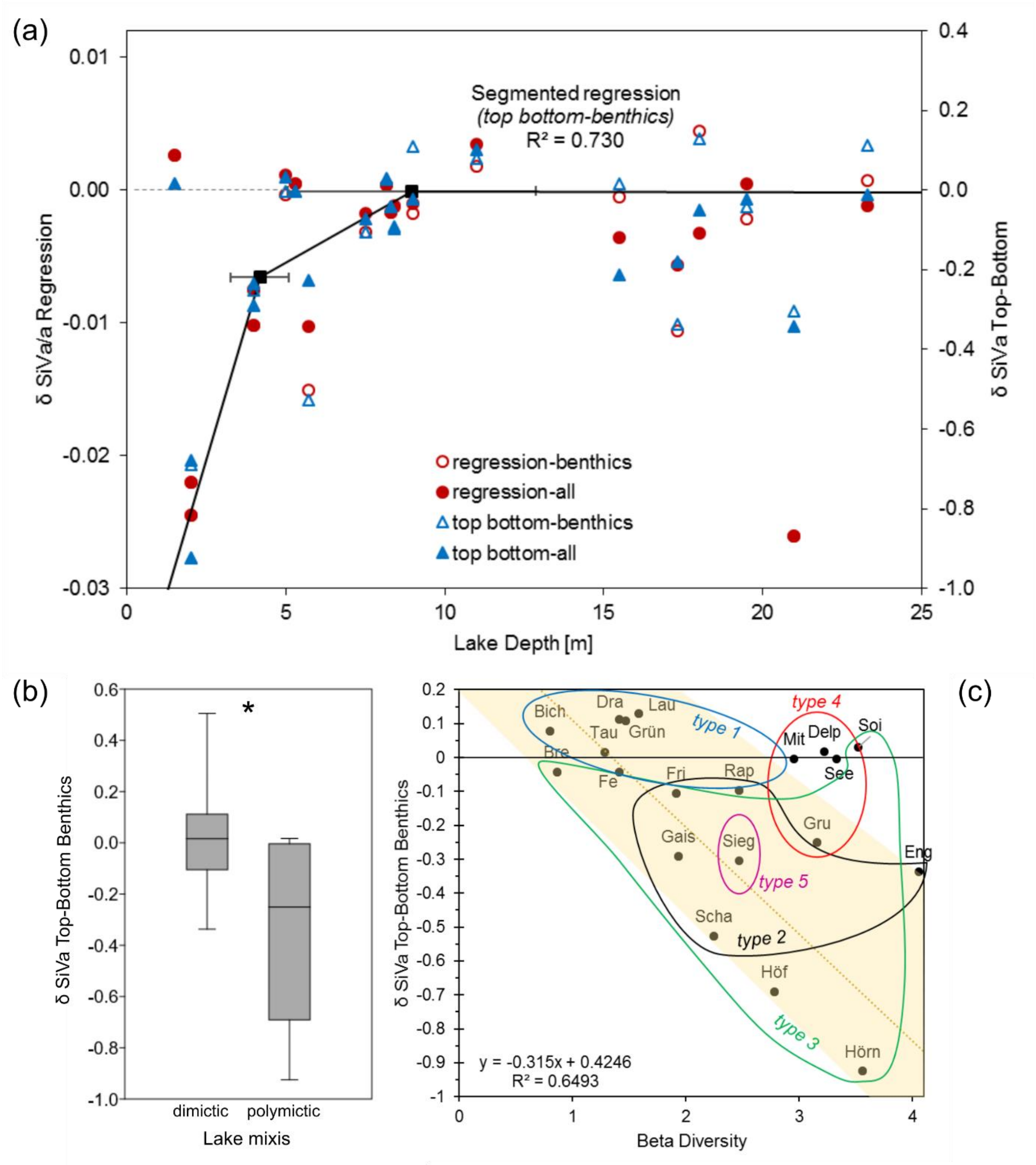

Figure 4.2: δ SiVa in relation to lake depth (a), mixing behaviour (b) and beta diversity (c). a) Quantitative regression and top–bottom approaches (absolute values) with the exemplary segmented regression of the top–bottom benthics values with two break points (black line). The shallow outlier of Lake Delpssee (top left) and the deep outlier of Lake Sieglsee (doline lake, bottom right) are excluded in the segmented regression. b) Dimictic lakes have significantly lower δ SiVa compared with polymictic lakes (1) – p = 0.019 (t-test). c) Quantitative top–bottom benthics approach with the visualised distribution of the five lake types in diatom stratigraphies of Bavarian mountain lakes: blue = type 1, black = type 2, red = type 3, green = type 4 and pink = type 5. The strongly positive outlier Lake Funtensee (0.5; 2.1) is not shown. The yellow corridor represents the area with the assumed correlation (‘Corridor of Classic Climate Change response’) with the linear regression (yellow line). This corridor is not calculated statistically.

branch mainly contained type 3 mountain lakes, the main branch shifted from deep type 1 via medium-deep type 2 to shallow type 4 lakes. As diatom assemblages of deeper mountain lakes appear to exhibit weaker δ SiVas, the decrease of the SiVa in dimictic lakes is also significantly weaker than that in polymictic lakes (t-test: p = 0.019, Fig. 4.2c).

The estimation of the mountain lake warming will now refer to the absolute top–bottom approaches only (Table 4.3). The qualitative δ SiVa indicated an average warming of Bavarian and Tyrolean mountain lakes of 0.087 °C per year (−0.015–0.877 °C a^{-1}) and the quantitative approach indicated an average of 0.028 °C a^{-1} (−0.019–0.122 °C a^{-1}) within the past 45 years, i.e. a total of 0.739 °C over this time period. In the group of shallow lakes, the mean warming was 0.104 °C a^{-1} in the qualitative approach and 0.034 °C a^{-1} in the quantitative approach, the latter adding up to 1.011 °C since the onset of the main warming. Except for the doline Lake Sieglsee, which shows the typical warming, all of the deep lakes in contrast appear to cool down slowly (by an average of 0.013°C a^{-1}). Regardless of the lake depth, polymictic lakes showed a significantly stronger warming than dimictic lakes (Mann–Whitney U-test: $p = 0.009$).

Table 4.3: δ SiVa, δ SiVa-inferred lake warming and beta diversity in the Bavarian and Tyrolean mountain lakes. The lakes are ordered according to their depth. Warming of the lake surface refers to the benthic top–bottom approaches (tbb). Qual.: qualitative, Quant.: quantitative. The temperature increase is shown in degrees per year and degrees per 45 years for the quantitative approach. The upper part of the table represents the 'shallow' lakes, the bottom part the 'deep' lakes. There are no qualitative approach data for the Lakes 'Lau' and 'Fe' because of lacking diatom shifts. Lake Sieglsee's warming in 45 years is extrapolated since the sediment core only comprises 15 years and is marked with an asterisk (*).

	Depth [m]	Altitude [m a.s.l.]	Beta diversity	δ SiVa Quant. tbb	δ SiVa [a^{-1}] Qual. tbb	δ T/t [°C a^{-1}] Qual-tbb	δ T/t [°C a^{-1}] Quant-tbb	δ T [°C] Quant-tbb
Delp	1.5	1600	3.22	0.017	−0.186	0.877	0.013	−0.079
Höf	2.0	1192	2.78	−0.691	−0.023	0.109	0.109	3.257
Hörn	2.0	1601	3.56	−0.925	−0.034	0.162	0.122	4.362
Gru	4.0	2060	3.16	−0.251	−0.007	0.032	0.030	1.185
Gais	4.0	1508	1.94	−0.291	−0.008	0.038	0.038	1.372
Mit	5.0	1082	2.95	−0.004	0.000	0.001	0.001	0.021
See	5.3	1809	3.33	−0.005	−0.006	0.030	0.001	0.023
Scha	5.7	1670	2.25	−0.528	−0.023	0.107	0.117	2.488
Fri	7.5	973	1.92	−0.105	0.001	−0.003	0.014	0.495
Soi	8.2	1458	3.52	0.030	0.000	0.000	−0.004	−0.125
Bre	8.3	1903	0.86	−0.043	−0.001	0.005	0.008	0.203
Rap	8.4	2047	2.47	−0.098	−0.003	0.014	0.014	0.461
Grün	9.0	1474	1.47	0.108	0.003	−0.015	−0.017	−0.510
Bich	11.0	995	0.80	0.079	0.000	0.000	−0.010	−0.371
Tau	15.5	1138	1.28	0.016	−0.006	0.029	−0.002	−0.075
Eng	17.3	1876	4.06	−0.337	−0.018	0.083	0.057	1.590
Lau	18.0	1013	1.58	0.129	–	–	−0.019	−0.609
Fe	19.5	1060	1.41	−0.043	–	–	0.007	0.203
Sieg	21.0	1207	2.47	−0.305	−0.022	0.104	0.104	4.696*
Dra	23.3	1874	1.41	0.112	0.000	0.002	−0.017	−0.528

4.4.3 δ SiVa-based Temperature Reconstruction

The temperature reconstruction test based on benthic SiVas was calculated for each layer of the sediment core of the alpine Lake Engeratsgundsee (Fig. 4.3). Its heterogeneous and well-varved sediment comprised between 1 and 10 years per centimetre. Since a water body physically smoothens air temperature variations, the daily lake surface temperature resembles the 0.1- and weekly data the 0.15-Loess smoothed Hohenpeißenberg weather data with a delay of 3 days during the measuring campaign in summer 2016 (cf. supplementary, Fig. S 4). Accordingly, smoothing factors 0.1 and 0.15 were used for further analysis. A comparison of SiVa-related lake August surface water temperatures (LASWT) with 0.15 Loess-smoothed annual average temperatures (AAT) of the Hohenpeißenberg weather observatory revealed the best predictive ability (RMSEP = 0.678°C) and a strong correlation of values ($\varrho = 0.391$, $p < 0.001$), but with low $R^2 = 0.153$ (Table 4.4). For the 0.15 Loess-smoothed Late-August data, when lake temperature documentation occurred simultaneously in the entire calibration set (cf. Chapter 3), the best regression quality ($R^2 = 0.302$) with strongest correlation ($\varrho = 0.549$; $p < 0.001$) was obtained, but with greater prediction errors (RMSEP = 0.976°C). Apart from the first decades and two more layers, the two temperature series describe similar developments, especially since the 1980s with a comparable warming (Fig. 4.3).

Table 4.4: Pearson correlation (ϱ), its significance (p) and Prediction errors of the applied 0.1-Loess-smoothed δ SiVa-inferred temperature model in comparison with weather data from Hohenpeißenberg observatory. Implemented temperature data were AAT: annual average, SAT: summer average, Aug: August average, Late-Aug: average between 23rd Aug – 1st Sep.

Climate data	AAT		SAT		Aug		Late-Aug	
Smoothing factor	0.1	0.15	0.1	0.15	0.1	0.15	0.1	0.15
ϱ	0.381	0.391	0.301	0.327	0.277	0.295	0.505	0.549
p	0.000	0.000	0.002	0.001	0.004	0.002	0.000	0.000
R^2	0.145	0.153	0.091	0.107	0.077	0.088	0.255	0.302
RMSEP [°C]	0.694	0.678	0.829	0.809	0.942	0.900	1.129	0.976

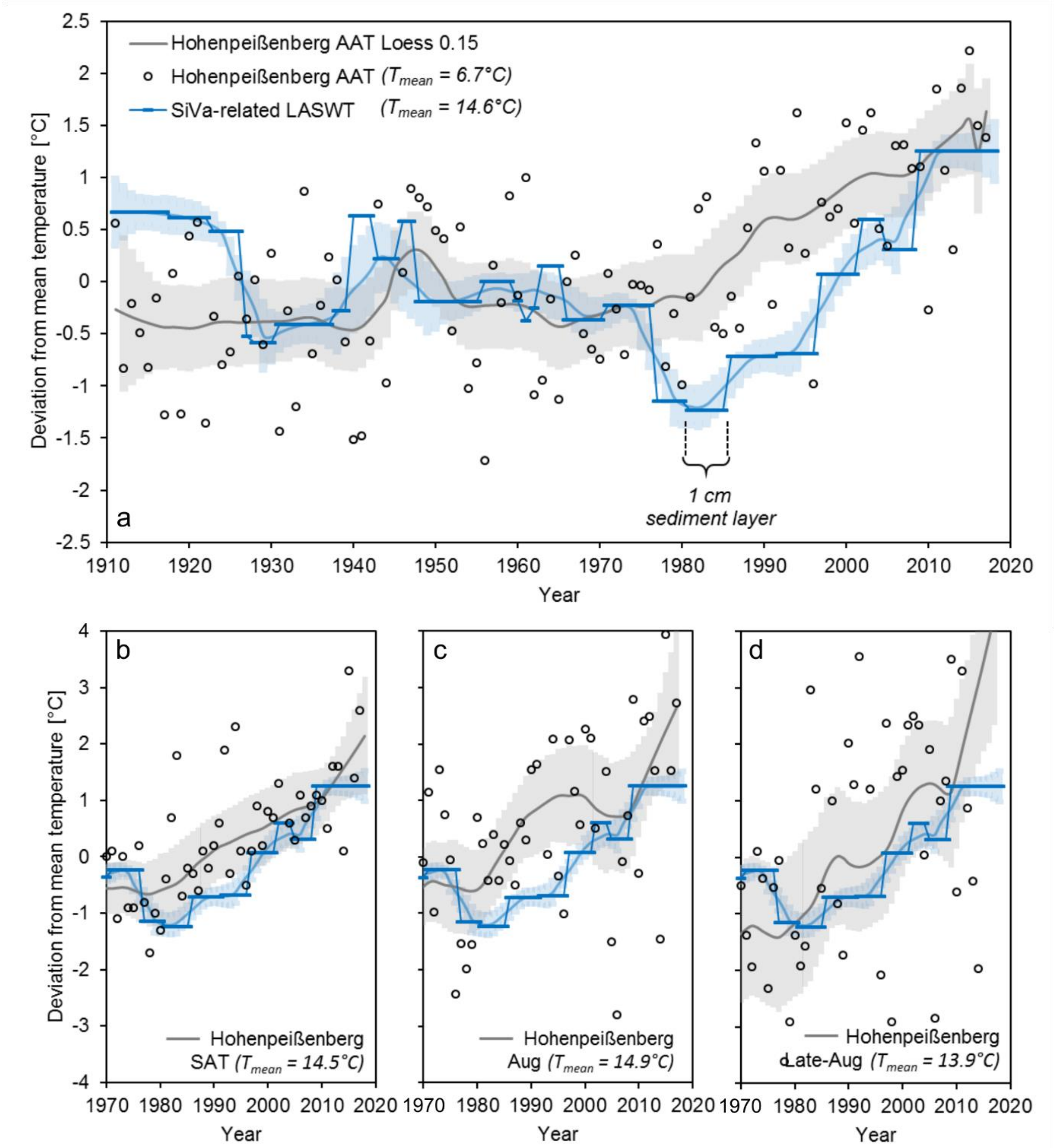

Figure 4.3: SiVa-related temperature (blue) of alpine Lake Engeratsgundsee in comparison with (a) annual, (b) summer, (c) August and (d) Late-August average temperatures of the Hohenpeißenberg weather station, Germany (black). 'LASWT': Lake August Surface Water Temperature; 'AAT': Annual, 'SAT': Summer, 'Aug': August and 'Late-August': 23rd Aug – 1st Sep average air temperature. SiVa-temperatures were calculated for the number of years recorded within a 1 cm sediment layer according to varve counting and Cs–Pb data. Black circles represent single annual means of Hohenpeißenberg data; bright curves represent Loess-smoothed temperature data with 2.5th and 97.5th percentile values. Smoothing factors: 0.15 for Hohenpeißenberg (grey), 0.1 for SiVa-related data (bright blue).

4.5 Discussion

The silicification of diatoms provides an important tool to monitor global change in mountain lakes; furthermore, mountain lakes can be sentinels for global change largely because of the remoteness of direct anthropogenic influences (Rogora et al. 2018, Moser et al. 2019). In this study, the usefulness of the silicification value in palaeolimnological approaches to assess and reconstruct climate change impacts on mountain lakes has been demonstrated. The segmented regression analysis suggested that the model is valid for lakes shallower than 10 m and the model evaluation identified the top–bottom approach as the most suitable method. In contrast to the top–bottom approaches, the regression models either were not able to identify significant correlations with the implemented variables or they reduced the set of explanatory proxies to lake depth only. However, the main decisive parameters for lake communities are lake depth, altitude and therefore lake temperature (cf. Chapter 3, Livingstone et al. 1999, Lotter & Bigler 2000, Rühland et al. 2015). It is possible that the explanatory power of regression approaches is weaker because it includes every annual weather fluctuation. Extraordinary layers whose diatom species composition may contradict an overall directional shift is likely to attenuate the slope of the regression and limit the ability to evaluate that shift. Instead, the top–bottom approach only compares the global change onset with its current state, thus overcoming the aforementioned regression problems and promoting significant correlations. Nonetheless, this approach is strongly dependent on the 'bottom' conditions. This can be biased especially when the bottom samples are somewhat disturbed or the diatom shift started much later. Therefore, sediment cores need to be evaluated for their onset of climate change response first considering its trajectory (Smol 2002) such as the qualitative approaches of this study. The GLM calculations further recommend that qualitative approach, which takes the entire shift in the subfossil assemblages into account, unlike the quantitative approach. Nevertheless, its disadvantages are that the chosen reference core compartments are user-biased and mountain lakes without a notable trend in the diatom stratigraphy cannot be evaluated. Therefore, the quantitative climate data-based approach with a fixed period as the calculation basis was used in parallel to the diatom-based technique. Moreover, the relative values expressed more significant connections with the explanatory variables than the absolute values, but the difference is negligible since all of the lakes were within the same range of silicification values. The model evaluation as well as the segmented regression indicated that it may be unnecessary to include planktic silicification. Since shallow lakes vary the most in depth in response to climate change, deep planktic-rich lakes were not taken into account for the main calculations. The inclusion of planktic silicification, however, indicated overall negative values in lakes larger than the 10 m break point despite approaching zero values around that point. This may be caused by increasing abundances of lightly silicified *Cyclotella* (KÜTZING) DE BRÉBISSON. There is evidence that planktic diatoms reduce average cell size in the community with higher temperatures (Margalef 1969, Klee & Schmidt 1987, Kling 1993, Winder et al. 2008, Finkel et al. 2009). Accordingly, they can reveal faster growth that leads to shorter exposure time to silica, causing not only smaller but also lighter silicified cells (Taylor 1985). Possibly, planktic diatoms contribute so much biomass in deeper lakes, which preferably appear in warmer lower altitudes because of geology and orography, that this effect becomes visible in terms of a negative δ SiVa. However, the silicification value, which correlates negatively with temperature, initially referred to benthic diatom species (Chapter 3). Therefore, the trend in such planktic-rich deeper lakes cannot be interpreted and transferred to temperature in the same way. In deeper and/or plankton-dominated lakes, lighter silicified *Cyclotella* species usually replace heavily silicified *Aulacoseira* species (Rühland et al. 2015). Consequently, the SiVa in such lakes is supposed to decrease like the benthic SiVa does in shallow lakes. However, the sedimentary assemblages of Bavarian mountain lakes lacked *Aulacoseira* spp., so that this shift could neither be studied nor transferred to the SiVa model. Summarising, the application of benthic SiVa on deep and/or plankton-rich lakes is doubtful. Its application in such lakes is probably misleading since the benthic minority in such sediments cannot catch environmental responses sufficiently. Accordingly, the observed seemingly uncoupled relation of benthic δ SiVa and lake depth > 10 m is likely to only be the result of the low abundance of benthics in deeper lake sediments. Despite being underrepresented in the deep lakes over 10 m, most of the benthic δ SiVa approaches there scattered into positive values indicating a cooling. Although contradicting climate warming, this can be realistic as Niederist et al. (2018) observed a cooling of the hypolimnion in mountain lakes because of an increased thermal stability and decreased energy exchange among water layers. As a consequence, benthic assemblages may derive from the uppermost benthic area within the hypolimnion, which may still be euphotic, so that benthic diatoms describe developments of the hypolimnion.

However, in most mountain lakes, the top–bottom benthic δ SiVa correlated negatively with the beta diversity as initially hypothesised, which further supported the power of this approach. Species reorganisation of diatom assemblages in shallow lakes is greater because of 'benthic succession' that overcomes ecological thresholds and establishes new habitats (Smol et al. 2005). Therefore, these lakes express a stronger decrease in average silicification because lightly silicified diatom species have a competitive advantage in an increasingly heterogeneous habitat with higher substrate diversity. In contrast, deep lake assemblages only increase in planktics corresponding to the growing epilimnion and reveal a low variability in average silicification in subfossil diatoms (Rühland et al. 2015). Such deep lakes with low species turnover that are herein classified as type 1 lakes seem to show slightly positive δ SiVa, but this has to be taken with caution as the value only refers to a minority of the diatom assemblage. The negative beta diversity–δ SiVa relation then continues with moderate negative values in type 2 lakes (recent appearance of planktics accompanied by decreasing *Staurosira*) and partly strong negative values in type 4 lakes (recent appearance of macrophytes and replacement of *Staurosira* by *Achnanthidium*). Nevertheless, there appeared a group that contradicts the negative relation among δ SiVa and beta diversities, which is referred to as the ‘inverse branch’. This inverse branch mainly contained type 3 lakes, which are dominated by *Staurosira* species without directional species shifts. Such lakes lack significant climate change response, and thus, lack changes in average silicification. In addition to type 3 lakes, some type 4 lakes appear there as well. The δ SiVa in these lakes is probably hampered by water-level fluctuations or a missing sudden increase of macrophytes that occurred in many of the shallow lakes as a consequence of warming and ‘upwelling’ water plants (Rosset et al. 2010). If a mountain lake is vulnerable to water-level fluctuations due geological preconditions like lacking sealing material, climate change can increase evaporation and the danger of desiccation; hence, former pioneer species are replaced by other pioneers that exist in the same habitat but exhibit greater tolerance to dry conditions (Cantonati et al. 2009). Therefore, diatom reorganisation as indicated by high beta diversities is driven by additional effects than the mere warming of the water body. It may further be covered by other external effects such as increased turbidity due to heavy precipitation events or anthropogenic impacts like a recent nutrient decrease, which causes an increasing SiVa conversely to the hypothesised reaction (see Chapter 3). Anthropogenic acidification and nitrogen deposition effects are not supposed to carry weight in the studied lakes because they are well-buffered hard-water lakes (Lajewski et al. 2003, Garbe-Schöneberg et al. 2013) and limited by phosphorous as freshwater lakes usually are (Crouzet et al. 1999). The exclusion of this extraordinary group intensifies the δ SiVa–beta diversity relation and is to be proposed as the corridor of classic climate change response of mountain lakes, abbreviated as corridor of classic climate change (CCCC) (Fig. 4.2c, yellow area), which are unaffected by other covering effects.

Based on the correlation of 41 surface sediment samples in the same study area, the δ SiVa is able to describe and to quantify climate change impact very well and its transfer to August surface temperatures resulted in realistic values. SiVa-inferred lake warming ranged in most mountain lakes between 0.1 °C and 1.1 °C per decade, which is comparable with lakes around the Alps with an average warming of 0.32 °C decade^{-1} peaking to approximately 0.75 °C decade^{-1} (O’Reilly et al. 2015). However, this was again limited to shallow or polymictic mountain lakes since the function calculated a warming in the non-dimictic deep doline lake but predicted even a weak cooling of the lake surface in many deeper lakes. This corresponds to the above-mentioned planktic problem for the δ SiVa with underrepresented benthic species, but the indicated trend may be the reason of cooling hypolimnia (Niederist et al. 2018). Furthermore, the qualitative approach seems to overestimate the warming in some lakes, e.g. the almost 9 °C decade^{-1} warming trend in Lake Delpssee. The integration of the entire diatom shift possibly extrapolates the warming towards extreme values, but it may still be useful as a proxy with which to generally assess changes in ecological processes on the basis of the food web. Since warming is only one of many aspects driving species compositions, this value can be interpreted differently than just an estimation of temperature. Accordingly, the ecosystem of 'Lake Delpssee' has changed to the extent, as it would have experienced a 9 °C warming. Nevertheless, the quantitative method appears to better quantify lake warming than the user-dependent qualitative approach. This 'quantitative' way further implements an 'independent' time period since the referred time range is irrespective of users and equal to all lakes. Apart from some deep lakes seeming to cool, it is significant that polymictic lakes warm faster or more strongly than deeper dimictic mountain lakes, whose reaction is smoother (Chen et al. 2014, Rühland et al. 2015). The role of altitude is the second most important. Accordingly, deep lakes warm to a different extent than shallow lakes, but the highest among them indicated the strongest warming. Whereas mountainous shallow and polymictic lakes seemed not to warm more than 1 °C since the 1970s, subalpine lakes lie between 2.5 – 4.4 °C except the type 3 lakes with no trends (Table 4.3). In deep and dimictic lakes, the SiVa-inferred warming of the highest lake is 1.5°C, while the others move around zero, which, however, has to be taken with caution due to benthic minorities especially in mountainous deep lakes. This supports the altitude as an amplifier of climate warming response (EEA 2009, Rühland et al. 2015, Warscher et al. 2019).

Besides the applicability of the SiVa to estimate absolute lake warming, it is also possible to reconstruct lake temperatures. The sediment core of the alpine Lake Engeratsgundsee is particularly suitable to test temperature reconstructions using the SiVa. This lake is among the deepest in the sample set but characterised by high benthic diversity and low plankton abundances in the sediment. Additionally, its varved sediments allow to assign years precisely. The development of SiVa-inferred lake temperatures correlated well with data from the weather station and resembled the Hohenpeißenberg data particularly in the middle of the 20th century. Nevertheless, the first decades of the comparison (24–26 cm, 1910–1920s), two more layers (19 cm/early 1940s, 11 cm/early 1960s) and especially the main climate change-driven warming of the recent three decades exhibit deviations; the latter indicating a stronger warming than that observed in the pre-alpine location of the weather station. This also worsens the prediction errors. Whereas the deviation of the 1940s can be the result of incorrect dating, so that the SiVa-inferred temperature peak appears a few years too early, it is likely that the temperature-modulating topography hampers a comparison among a pre-alpine exposed, i.e. non-shaded, weather station versus an alpine cirque lake (Dombrowski et al. 2009). Moreover, meteorological differences between the two locations like extent and duration of snow cover, amount of thunderstorms and heavy precipitation events may have caused deviations before 1970 (Thompson et al. 2005a, Napoli et al. 2019). This can in turn cause worse conditions during the vegetative period than expected under pre-alpine conditions. Such deteriorations that lead to enhanced influx of inorganic material and turbid lake conditions may also have selected for more robust diatom species with higher silicification in the mid-1970s. Coinciding with δ SiVa-inferred temperatures, summer and August means of the weather station in the 1970s were ca. 1 °C and 2 °C colder than average, respectively, whereas the annual values lack such a minimum (Fig. 4.3). Hence, the SiVa-temperatures matches summer conditions better than annual averages. Apparently, that cooling event induced a lasting shift within the diatom community towards 'heavier' diatoms, so that it may exaggerate the consequent warming. However, the seemingly stronger warming of 0.6 °C decade^{-1} in the last four decades in the alpine lake is realistic for mountain lakes (Niederist et al. 2018) and alpine regions (Warscher et al. 2019). They warmed 0.5 °C decade^{-1} since the 1980s, which is predicted to proceed until the end of the 21st century with a cumulated warming scenario of 4.2 °C in alpine regions > 1500 m a.s.l. (EEA 2009). The main factor for more rapid warming at alpine altitudes is the greater impact of decreasing snow covers and fewer snow days, hence lower albedo and its cascading effects (Bradley et al. 2006, Mueller et al. 2009, Williamson et al. 2009, Rogora et al. 2018).

To summarise, the modelling of past in-lake conditions is complex, but the SiVa has been shown to be applicable to quantify lake warming as well as to reconstruct temperature developments. Because of the formula 4.1, however, the reconstruction of absolute temperatures may be limited to lakes of subpolar and temperate climates. A theoretical diatom community of only SiVa 1 species would lead to the maximum possible LASWT of 21.2 °C, whereas a community of SiVa 4 would lead to the theoretical minimum of 7.1 °C. Thus, cold-monomictic lakes of the polar regions as well as warmer lakes of Mediterranean to tropical climates exceed the conditions required by formula 4.1. However, formula 4.2 may still be applicable in those lakes for an estimation of lake warming referring to changes and reductions of average silicification in the diatom assemblages.

4.6 Conclusion

In conclusion, the SiVa, which refers to the degree of valve silicification and correlates with lake surface temperature, can be used to detect and reconstruct the extent and development of climate change-driven lake warming in mountain lakes in summer. However, this palaeolimnological approach relies mainly on benthic diatoms, resulting in a restricted validity of the method to lakes without dominating planktics, mainly shallow mountain lakes with a maximum depth of 10 m. To increase the number of implementable lakes, the combination with the beta diversity as a proxy of species turnover can be proposed to evaluate the response of lakes to climate change. As the δ SiVa is inversely congruent to beta diversity, a CCCC may be applied. Lakes that are located within this corridor in the δ SiVa–beta diversity graph may respond to global change as proposed in the literature like directional diatom community shifts. In contrast, diatom reorganisation in lakes that exist outside this corridor may be impaired by other factors like anthropogenic influences or extreme water-level fluctuations altering the climate change impact. Anthropogenic acidification and nitrogen deposition effects were negligible in the study area, but may further restrict the approach validity to hard-water and phosphorous-limited ecosystems. Since warming-driven changes in plankton composition in deep lakes may also result in SiVa decreases, it can be hypothesised that they also fit in this CCCC-model. However, a precise statistical definition of the boarder of this corridor or an extension with a floating boarder will be necessary. The latter might then be used to estimate quantitatively the role of climate change as a driver of diatom species turnover. Moreover, it remains to be seen whether lakes deeper than those in the sample set, i.e. >25 m, fit in this model. Those lakes will need to be evaluated in more detail in order to implement their planktic diatom assemblages in the future instead of a partial exclusion like in this study. Such an extension of the method may also extend its applicability to bigger lakes than mountain lakes, which rarely exceed 4 ha in surface area or 25 m in depth. Furthermore, deeper lake sediments are more often perfectly varved. Therefore, they are particularly suitable for a precise reconstruction of the entire past temperature development, which has been shown in this study. Apart from lake size, the validity of the approach in ice-dominated and ice-free lakes of polar and tropical climates needs to be checked. Nevertheless, the SiVa is already a powerful tool that can be applied for palaeolimnological research in mountain lakes or even similar shallow lakes of lower elevation and contains possibilities for further extensions in future studies.

5 Composition of Highly Diverse Diatom Community Shifts As Response to Climate Change: A Down-Core Study of 23 Central European Mountain Lakes

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Author contributions: This study was an equal-authorship publication of WK and AH with continuous advice from JG and UR. Preliminary studies were performed by AH. Hydrochemical and hydrophysical analyses were carried out by SO, AH and WK. Sampling and preparation of the sediment cores was the equivalent work of WK and AH. Sediment dating was realised and interpreted by Nathalie Dubois at the Swiss Federal Institute of Aquatic Science and Technology, Department Surface Waters EAWAG in Dübendorf. Preparation of diatom samples and microscopic analyses was equally performed by WK and AH. Statistical analyses and visualisation was mainly done by WK. Data interpretation, drafting and finalisation of the manuscript was equally carried out by WK and AH. JG and UR continuously supervised, improved and edited the manuscript.

5.1 Abstract

Alpine mountain lake biota are 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-Tyrolean 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 treeline or timberline (Lotter et al. 1999; Sommaruga et al. 1999; Sommaruga & Augustin 2006). 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 & Smol 1999) 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 2017), as past fluctuations of climate-mediated lake properties or catchment variations are well archived in lake sediment records (Smol 2008). Diatoms are ideal biological indicators that mirror various types of long-term ecological perturbations such as acidification (Weckström 1997; Koinig et al. 2002), eutrophication (Stoermer & Smol 1999) and climate warming (Pienitz et al. 1995; Bigler & Hall 2003; Smol et al. 2005; Karst-Riddoch et al. 2005; Rühland et al. 2008). Moreover, shifts in subfossil diatom assemblages are well preserved 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 substratum 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 2008).

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 Gössenköllesee, Austria (Koinig et al. 2002; Kamenik et al. 2000) or Hagelseewli, CH (Lotter et al. 2000–2002) – 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-Tyrolean 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-Tyrolean 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 – 2047 m 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* and *Larix decidua*, subordinate *Acer pseudoplatanus* and *Fagus sylvatica*) through subalpine grassland with patches of *Pinus mugo ssp. mugo* and *Picea abies* as well as treeless alpine meadows (e.g. *Rhododendron hirsutum*, *Carex sempervirens*) 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).

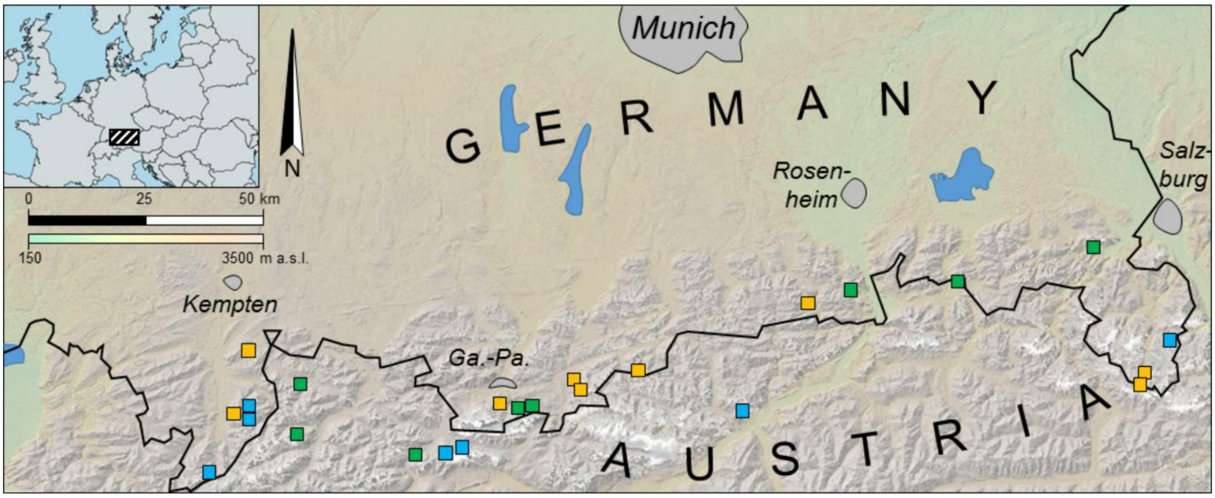

Figure 5.1: Location of the 23 mountain lakes along the Bavarian-Tyrolean boarder. Blue squares: alpine, yellow: subalpine, green: montane lakes. Ga.-Pa.: Garmisch-Partenkirchen.

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, Chapter 3, 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 ranges and means): TP 8.5 µg L^{-1} (< 5 – 17.3 µg L^{-1}), nitrate- 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) provided by the European Climate Assessment & Dataset Project.

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, S+ = Sediment and 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 [µg · L^{-1}]	NO_3^- [mg · L^{-1}]	NH_4^+ [µg · L^{-1}]	pH	Cond. [µS · cm^{-1}]	Mixis	Littoral Substratum	Anthropogenic 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
Engeratsgundsee	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
Schachensee	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	< 5/ 11.0	0.61/ 0.35	49/ 20	8.8/ 8.6	178/ 184	polym.	RS+	P
Oberer Soiernsee	SoW	47°29‘32“	11°20‘44“	1558	3.5	11.5	7.0	< 5/ 13.0	0.36/ 0.24	83/ 53	8.3/ 8.7	204/ 192	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 ≤ 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 (see Chapter 3, 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.

5.3.4 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).

5.3.5 Diatom Analyses

Freeze-dried subsamples were prepared for diatom analyses according to van der Werff (1953) and are described in Chapter 3 in detail. 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 plankton-rich samples. Diatom taxonomy followed Krammer & 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.

5.3.6 Statistical Analyses

Referring to local climate data, the strongest warming in the Bavarian Alps started in the 1970s (cf. Chapter 4.4.3). 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 (Chapter 3). An overview of species grouping is listed in the supplementary (Table S 5). 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 & 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 & 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 & 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 & Reineking 2004). According to the findings in Chapter 3, 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, TP 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 (Hammer et al. 2001) 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 (Table 5.1 & 5.2). The special case of the doline 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 lake Höfersee core and the longest in the Lake Drachensee core, 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.

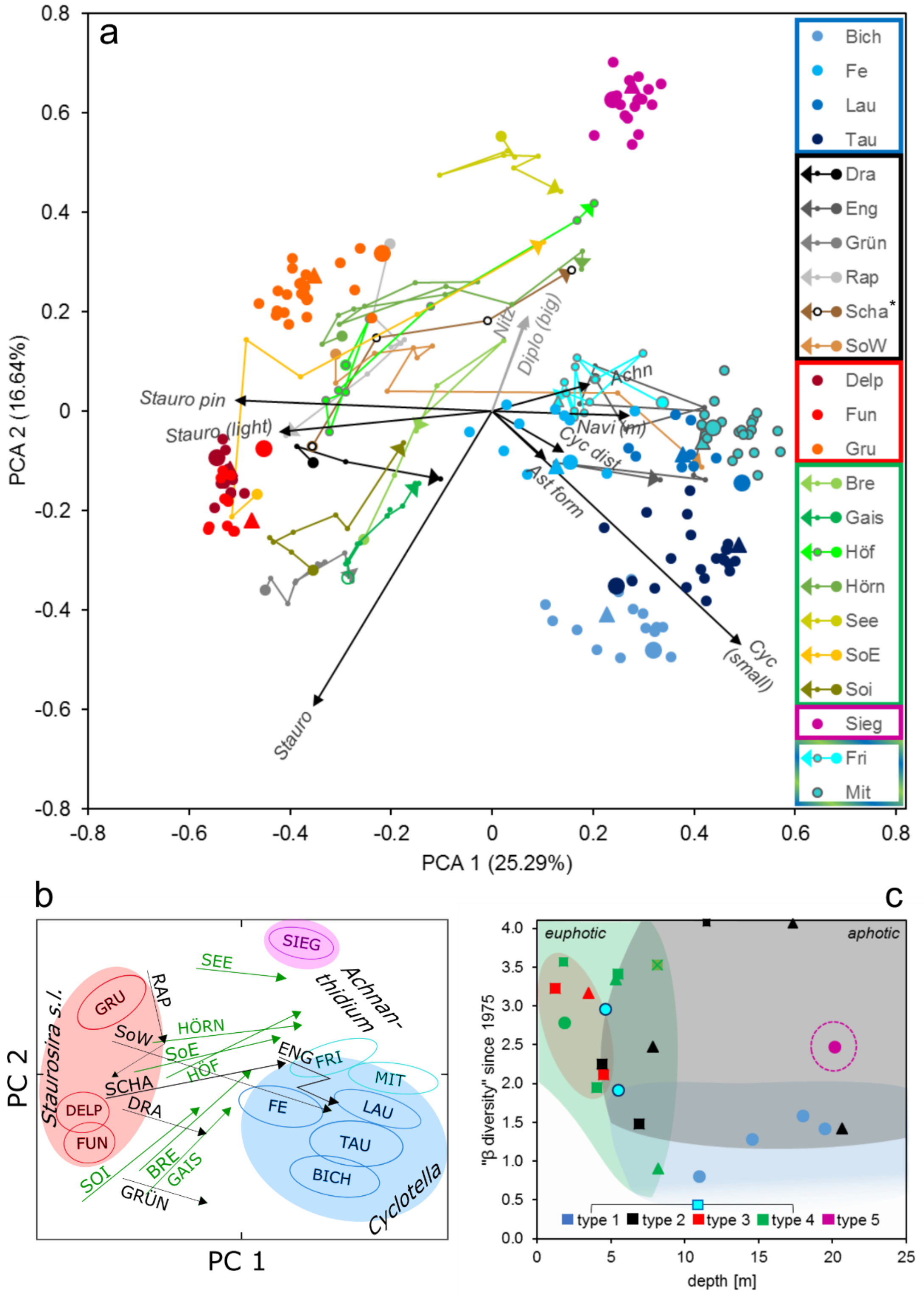

Figure 5.2: PCA (a), PCA overview (b) and beta diversities in relation to lake depth (c) of subfossil diatom assemblages in mountain lake sediments since the 1970s. (a) Axes of the eight mainly driving diatom groups (black arrows): Achn – *Achnanthidium* species, Ast form – *Asterionella formosa*, Cyc 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 the altitudinal level: triangle – alpine, box – subalpine, bullet – montane.

Table 5.2: Mountain lake classification according to their mixing behaviour and extent of the euphotic zone, their beta diversities and stratigraphy type of the subfossil diatom assemblages. Green: montane, orange: subalpine, blue: alpine mountain lakes. "Aphotic lakes": lake depth exceeds Secchi depth. Lake types: 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. Lakes with two values can be assigned to two different types. Subfossil diatom analyses with an insufficient time span are marked with an asterisk (*). For abbreviations see Table 5.1.

	Dimictic	β	type	Polymictic	β	type	Meromictic	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						

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 5.2a & 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* complex; (2) the planktic, colony-forming species *Asterionella formosa*; (3) small-sized planktic centric taxa of the *Cyclotella*-complex; (4) the species *Cyclotella distinguenda* HUSTEDT; (5) medium-sized *Navicula* BORY species (*Navicula*-complex); (6) small benthic fragilarioid taxa (*Staurosira*-complex); (7) small-sized, weakly silicified benthic fragilarioid taxa (*Staurosira* light-complex), and (8) the heavily silicified benthic fragilarioid *Staurosirella pinnata*. The *Nitzschia* HASSALL and large-sized *Diploneis* 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 & ROUND/*Staurosira*-dominated assemblages (mainly *Staurosirella pinnata*, *Staurosira construens* EHRENBERG, *S. elliptica* (SCHUMANN) WILLIAMS & ROUND, *S. microstriata* (MARCINIAK) LANGE-BERTALOT, *S. venter* were plotted opposed of *Achnanthidium*- (especially *A. minutissimum*, *A. rosenstockii* (LANGE-BERTALOT) LANGE-BERTALOT) and *Cyclotella*-dominated assemblages (especially *C. comensis* GRUNOW, *C. delicatula* HUSTEDT, *C. distinguenda*) (Figure 5.2b).

5.4.4 From Diatom Assemblages 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*. Exclusively, the doline lake (Lake Sieglsee) was characterized by a change mainly from *Nitzschia denticula* 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 (Fig. 5.4). 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. 5.3a). Within the shallow lakes, 'type 4' lakes were warmer and lower than 'type 3' lakes and/or impaired by water level fluctuations (WLF)(Fig. 5.3a & c). This allows a lake type identification by only three environmental variables (Fig. 5.3d): lake depth, summer surface temperature and lake origin.

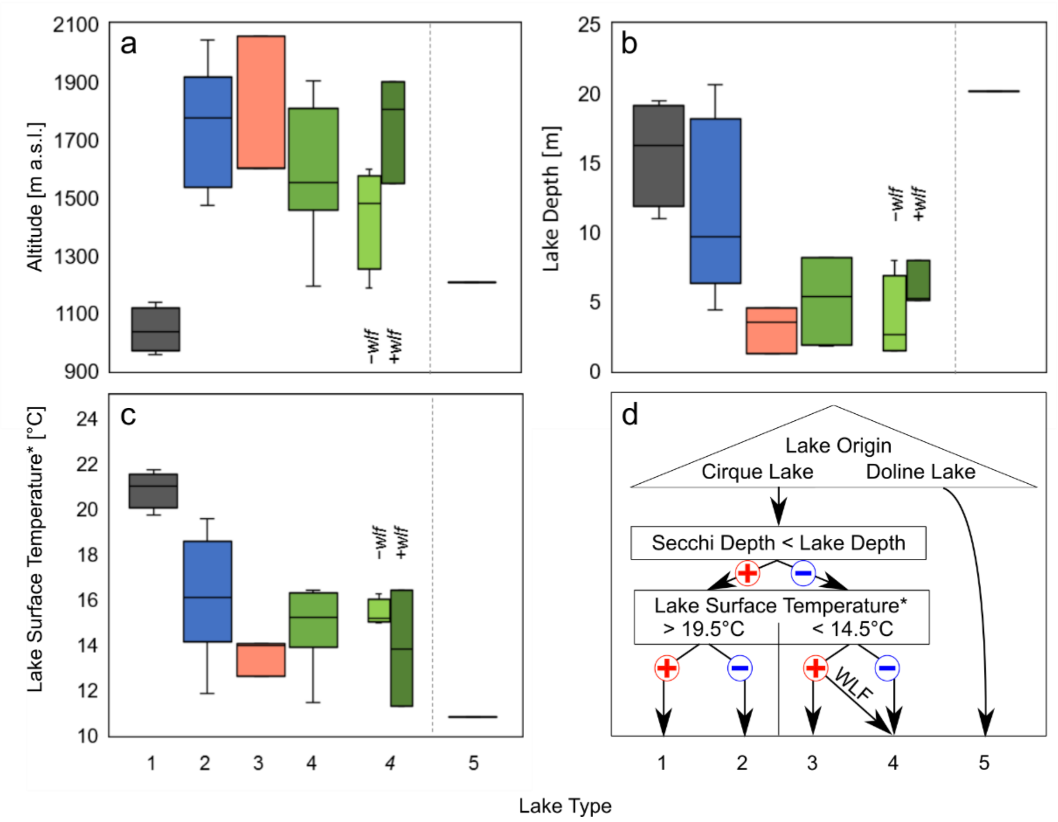

Figure 5.3: Mountain lake types and their distributions along altitude (a), lake depth (b), lake August surface temperature (c). Differentiation scheme (d) according to the main factors lake origin, depth and temperature. Boxplot colours refer to Fig. 5.2. Type 4 is additionally split into lakes with (+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.

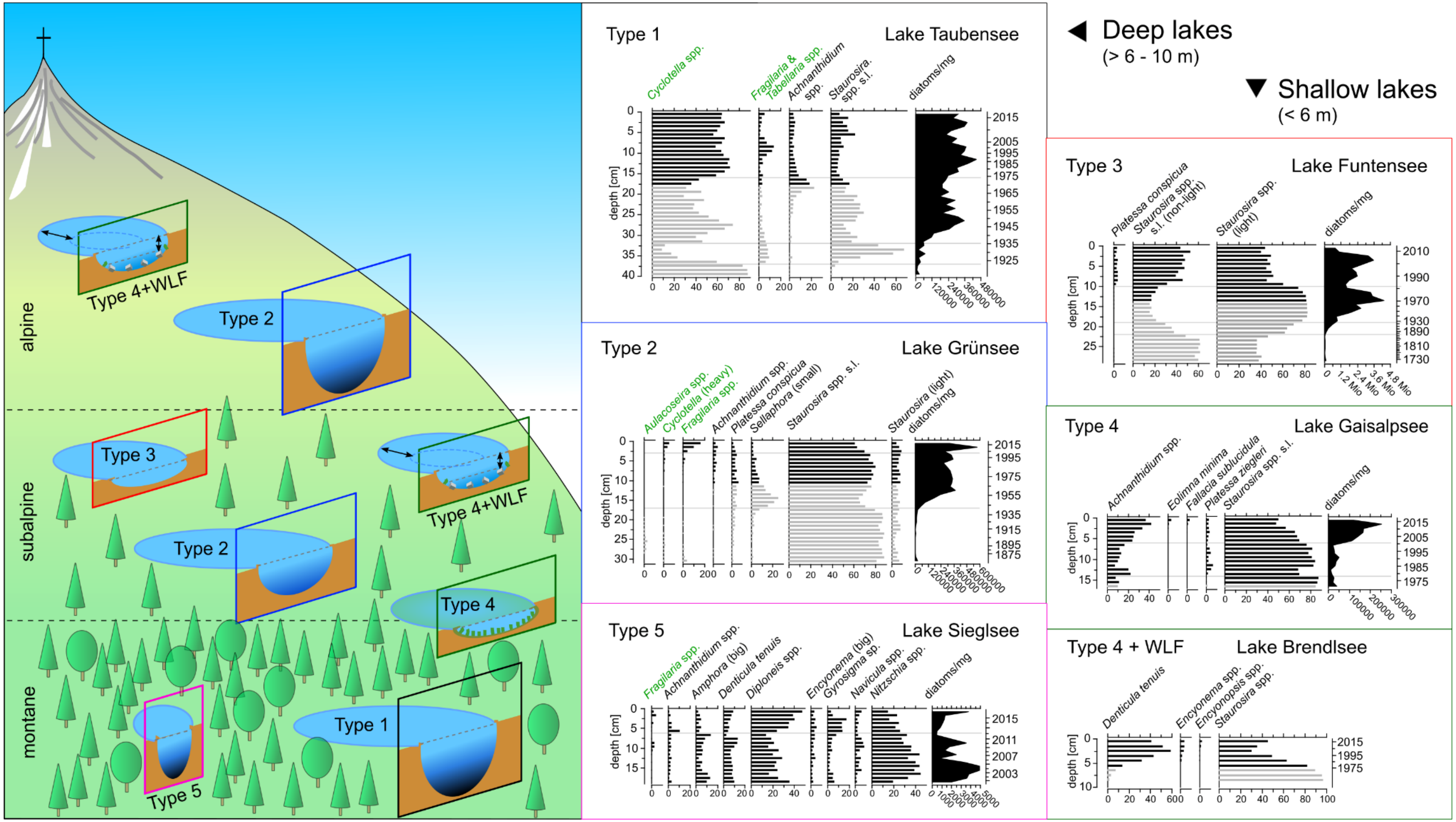

Figure 5.4: Diatom stratigraphies of the five mountain lakes types. Type colours correspond to Fig. 5.2 and arrangement on the left represents their altitudinal distribution. The two stratigraphy y-axes show age and depth of the sediment. Grey lines: significantly different stratigraphic zones as indicated 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.

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 most subtle species changes, just as originally expected (hypothesis 2). Concluding, two shallow lake types (type 3 & 4) could be differentiated in regard to their diatom assemblage composition. The bottom 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 & 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. 1999-2002; 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, cf. Chapter 3). 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 & 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.

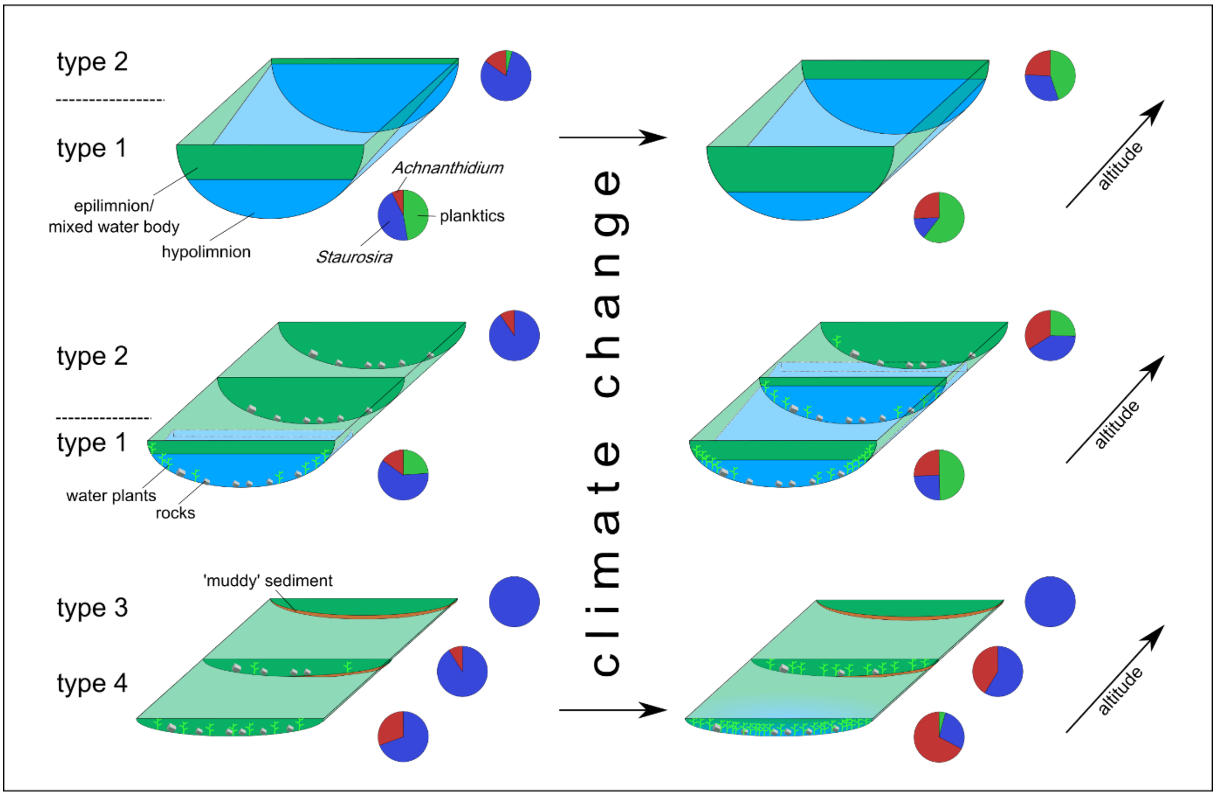

Figure 5.5: Overview of the mountain lake developments in different lake types. The figures on the left represent the lakes before climate change influence, on the right with climate change impact. The z-axis is the altitude. The circles visualize the composition of the main diatom groups at the lake 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 big water level fluctuations and/or direct anthropogenic influence are not shown.

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 & 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. 5.4 & 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. KRAMMER 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. 5.3c).

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* and *Chara*, 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 & Lippert 2001, Bornette & 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 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 significant increases in organic matter on and in the sediment, as water content measurements and diatom densities have shown (Menounos 1997, Avnimelech et al. 2001) (Fig. 5.3 & 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 & Hawes 2002, Bornette & 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 epilithic 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 being 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. 5.4). 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 favour strongly silicified diatom species which dominate the diatom assemblages of Lake Sieglsee (cf. Chapter 3). 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 &

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* HASALL (Douglas & Smol 1995) in competition with *N. denticula*. Therefore, the decline of this species correlates with the development of alpine climate (Fig. 5.4).

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 (cf. Chapter 3, Livingstone et al. 1999, 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. 5.3). 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 timberlines.

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 (cf. Chapter 3) 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 results in an increase of nutrients and turbidity (Algarte et al. 2016) as eutraphentic species such as *Gyrosigma* spp. (Hofmann 1999) or *Staurosira parasitoides* (MARCINIAK) LANGE-BERTALOT (cf. Chapter 3 & 6.1.1) 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.

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

This work addressed warming in mountain lakes below the high-alpine altitude with calcareous catchments and the biological responses to a changing climate. In order to understand the developments of the aquatic biota, it was necessary to evaluate the individual lake warming first, which can express differential patterns than the atmosphere. Therefore, this work initially correlated lake temperatures with assemblages of diatoms, which are generally known as valuable and ubiquitous environmental indicators. As a basic finding, it could be extracted that the average silicification of a diatom assemblage indicates lake warming. In the chapters 3 and 4, this was then established as a new diatom index to reconstruct and to quantify the differential warming of the highly divers mountain lakes. Eventually, the impact of climate change on the primary producers of the mountain lakes could be characterised and categorised from montane to alpine altitudes in chapter 5. In the history of Bavarian mountain lakes, five distinct types of lake response could be defined that depended on lake depth, altitude, and therefore lake temperatures. These are one of the most important 'adjusting screws' of climate change impact, which determine the environmental reaction and the location of ecological tipping points separating the lake types. Although these results hitherto focused on the developments of primary producers within the period of strongest warming, they can help to fully understand the processes in the entire studied freshwater system. This includes the complete lake food web and its ecologically relevant higher trophic levels as well as the ability to predict its future development. In this context, this section discusses and extrapolates the findings of the previous chapters in time and space as well as the lake fauna.

6.1 Susceptibility and Evolution of Bavarian Mountain Lakes with Time

6.1.1 Temporal Development of the Current Mountain Lake Types

The response of the studied mountain lake biota to recent global warming could be separated into four main types (Chapter 5). Their current location is defined by ecotonal boundaries and altitudinal isotherms. In that context, key temperatures could be found that determine the performance of the biota of deep and shallow lakes. In detail, deep lakes of a LASWT colder than 19.5 °C revealed a different development than warmer lakes. The colder deep lakes at higher altitudes were mainly located above the forest line and were characterised by recently appearing and increasing plankton algae (type 2), whereas the warmer lakes at montane elevations already hosted an established plankton flora (type 1). Similarly, the LASWT threshold of 14.5 °C resulted in dichotomous histories in shallow lakes. Biotic developments in colder shallow lakes at higher altitudes were restricted to undirected shifts within robust pioneer species (type 3). In contrast, the warmer lakes at lower altitudes revealed strong directional shifts towards lightly silicified and epiphytic species, which indicated the recent invasion of aquatic plants (type 4). However, these findings only represent a snapshot of the Bavarian and North-Tyrolean mountain lakes. Ongoing climate warming will further lift the altitude of the ecotones and isotherms so that their vertical distribution will keep on changing the next decades. Therefore, this section sets the results of chapter 5 into a temporal context and evaluates the velocity of recent developments to extrapolate and to predict the future evolution of the studied mountain lakes. Specifically, the question arises when the type 2 lakes at higher altitudes will turn into type 1 lakes, and type 3 become type 4 lakes, respectively.

6.1.1.1 Deep Lake Types

Deep lakes at lower altitudes are characterised by established phytoplankton assemblages that reached the carrying capacity and define the type 1, whereas they are still increasing at higher elevations defining type 2. Hence, the subfossil assemblages of these types experience a differential contribution of planktic diatoms. They either provide constant and significant amounts in type 1 lakes or suddenly appearing and increasing quantities in type 2 lakes within the considered period, i.e. after the 1970s when the onset of steepest warming in the Alps was documented as a consequence of climate change (see Chapter 5, Gehrig-Fasel et al. 2007, EEA 2009). However, defining the transition of a type 2 into a type 1 lake after a certain time period of presence of a significant plankton proportion would exclude any ecological influences. Moreover, reaching the crucial temperature of 18–19.5 °C in late-August may only define the possible existence instead of an established and balanced plankton (Chapter 5, Ossyssek et al. 2020). Ecologically, the question would be at which level the planktic community reaches the carrying capacity of the mountain lake, so that the phytoplankton succession merges into a stable level. One of the main drivers of this level is the nutrient availability, which can even be more important than the temperature (Vadeboncoeur et al. 2003, De Senerpont Domis et al. 2013). As an example, the alpine Lake Rappensee already described higher

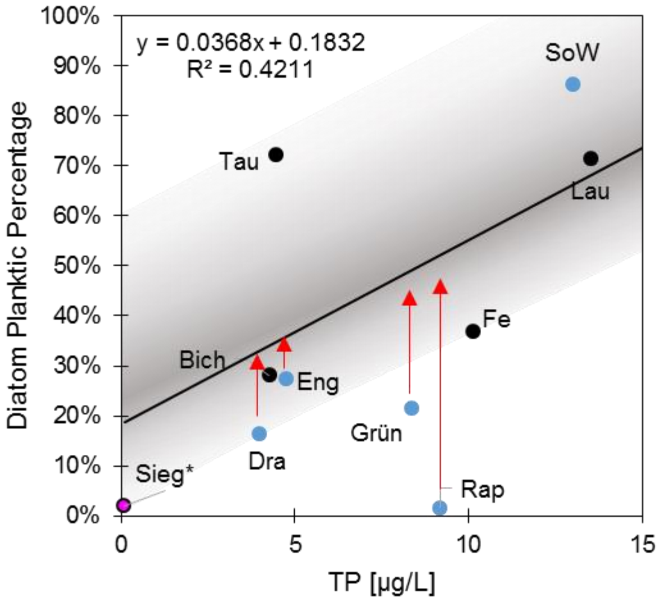

Figure 6.1: Proportion of planktic diatoms in the current community in relation to the TP concentration. Black dots: type 1 lakes with established and 'saturated' plankton communities; blue dots: type 2 lakes with recently appearing and still increasing plankton proportions. Black line: trend line with formula and R^2. The greyish area visualises a non-statistically estimated deviation. Red arrows: Remaining achievable plankton percentage. *Lake Sieglsee was included representing lowest plankton values due to lowest nutrient levels.

plankton abundances in the 1990s although being 'cold' but as a consequence of a still increased trophic level after the dam construction 42 years earlier in combination with accelerated warming (see Chapter 5.4.2). Nevertheless, it is complex to precisely estimate the carrying capacities of planktic diatom species as it depends on various limnological factors (Ossyssek et al. 2020) but the separate consideration of the mere TP in relation to the planktic proportions of type 1 lakes allows an approximation. Within the studied mountain lakes, the maximum possible planktic percentage seems to increase about 3.7 % per microgram phosphorous (Fig. 6.1). Extrapolating, the phytoplankton may become the dominating primary producer at around 10–20 µg L^{-1} as also indicated by Vadeboncoeur et al. (2003). Assuming constant phosphorous concentrations, this correlation makes it possible to quantify the remaining planktic proportions, which can be achieved by each type 2 mountain lake. Based on the recent increase in planktic percentages in these lakes, the time frame can be estimated when type 2 lakes are 'planklicly saturated' and supposed to switch into type 1 lakes. Accordingly, the Bavarian and North-Tyrolean mountain lakes currently classified as type 2 may perform this switch already within the next 20–30 years and will then be characterised by established and balanced planktic communities (Table 6.1). As an exception, the lake Soiernsee (W) may already have reached its maximal potential in present times possibly also due to other limnological factors such as elevated nutrient levels.

Table 6.1: Extrapolation of the current increase of planktic diatom species in type 2 lakes towards the TP-based saturation level and estimation of the year reaching this level. The current plankton percentage is based on and related to the uppermost sediment assemblage. [1] The plankton appearance refers to the date, when the proportion exceeded 2 %. [2] Year of saturation refers to the date, when TP values reach 15±5 µg L^{-1}, which is accompanied by plankton saturation.

Lake	Current plankton percentage	Year of Plankton Appearance[1]	Rate of Plankton Increase [y^{-1}]	Estimated Saturation Level (TP = const.)	Estimated Plankton Saturation	
					with TP = const.	with TP increase
Dra	16.5 %	1982	0.38	33 %	2059	*2166±48* [2]
Eng	27.4 %	1930	0.32	36 %	2045	*2160±57* [2]
Grün	21.6 %	1999	1.20	49 %	2040	2048
Rap	1.4 %	–	1.71	52 %	2047	2054
SoW	86.4 %	1996	4.32	35 %	2016?	–

However, the nutrient loads especially in subalpine and alpine lakes are supposed to increase due to increasing establishing vegetation, heavy precipitation events and erosion along with global warming. Therefore, the maximum possible percentage of planktic diatoms in relation to the entire diatom assemblage may further increase within the next decades. Analyses on subfossil pigments of Bavarian mountain lake sediments estimated an increase of TP concentrations of 1 µg L^{-1} per decade further elevating the planktic carrying capacity (Kuefner et al. 2020). This may postpone the year of saturation, hence the type 2–1 transition. In the lakes Grünsee and Rappensee, the plankton increase may overtake the TP increase, so that the predicted transition may occur only a few years later than forecasted with constant TP values (Table 6.1). In contrast, the alpine (ultra)oligotrophic lakes Drachensee and Engeratsgundsee may experience a run-away of the potential saturation against the plankton increase, unless it reaches dominating percentages along with predicted TP values of 10–20 μg L^{-1} (cf. Fig. 6.1). Nevertheless, it is likely that warming will amplify the plankton increase and saturation may take place at an earlier date than predicted.

6.1.1.2 Shallow Lakes Types

In contrast to the deep lake types, where global warming causes a transition from changing towards stable balanced communities, the shallow types describe the opposite development. The type 3 as a balanced 'shift-less' lake at higher altitudes is clearly separated from low-elevational type 4 that is defined by the invasion of macrophytes (see Chapter 5.4). Their altitudinal distribution appears to be limited by the water temperature as it has also been indicated by Carr et al. (1997) as well as in Pyrenean mountain lakes (Gacia et al. 1994). Accordingly, the climate change-driven uphill migration of plant species is also valid for macrophytes in lentic habitats.

An extrapolation of the diatom proportion that increases with the macrophytes such as epiphytic species and *Achnanthidium* spp. to determine the 'macrophyte front' is complex. Due to the unknown relationship between the developing aquatic plant population and the corresponding diatom proportion, it remains unclear whether they correlate exponentially, linearly or in a different pattern. As a solution, the crucial temperature splitting the two lake types can be used. Based on the diatom-inferred warming of shallow mountain lakes (see Chapter 4.3.2), the threshold of 14.5 °C will already be reached in the year 2034 in the Lake Grubersee and in 2036 in the Lake Funtensee, whereas the Lake Delpssee may not turn into a type 4 lake before 2084 as it is the coldest lake among the studied shallow mountain lakes.

Besides temperature, altitude-dependent UV irradiance may further vertically limit aquatic plants (Vinebrooke & Leavitt 1996, 1999) but its impact may change with global warming as well. Increasing air temperatures are able to contain more vapour and to cause more absorbing matter in lakes along with the climate warming-driven lake and catchment developments, which has been shown in Canadian mountain lakes (Leavitt et al. 2003). Eventually, this can increasingly attenuate UV irradiance (Vincent et al. 1998, Laurion et al. 2000, Sommaruga 2001, Rose et al. 2009, Shutov et al. 2019) and support the uphill shift of plants.

In conclusion, the lower limit of the altitudinal range of shallow lakes with negligible aquatic plant flora may already exceed the Bavarian Alps within the next decades. Additionally, diatoms of the genera *Staurosira* may become rare as they will be replaced by other pioneers and epiphytic species as observed in type 4 lakes.

6.1.1.3 Lakes of Special Geology

Type 4 lakes with water level fluctuations may increasingly be challenged by the consequences of snow-poor winters and droughts during the vegetation period (see Chapter 5.4.2). Therefore, water level fluctuations will further increase and suppress possible macrophyte establishments (Gacia et al. 1994). As observed in Lake Brendlsee and Lake Seeleinsee, aquatic plants may increasingly be limited to small and fast-growing species in the future such as *Potamogeton pectinatus* (L.) BÖRNER. This in turn limits the proportion of epiphytic diatom species to low amounts as in L. Brendlsee. Summarising, the future development of this mountain lake type may mainly consist of an ongoing replacement of the diatom community by desiccation tolerant species such as *Denticula tenuis*. However, an increasing frequency of water level fluctuations may promote the gradual invasion of herbaceous vegetation in the waterfront areas. There is evidence from alpine lakes in the Spanish Sierra Nevada that regular floodings of that areas may then dissolve nutrients from newly developing organic soil matter and increase lake trophy (de Vicente et al. 2010). This may be able to counteract the replacement by *D. tenuis* and promote other species that indicate higher nutrient levels.

Type 5 lakes, i.e. doline lakes, are possibly among the most resilient mountain lakes. Nevertheless, only a vague prediction can be stated as there was only one representative in the study set. This single lake, the Lake Sieglsee, indicated changes from turbidity tolerant diatoms towards a more diverse assemblage but mainly within heavily silicified species such as *Diploneis* spp. due to altered groundwater inflow characteristics (see Chapter 5.4.1). Moreover, the lake temperature of 6–8 °C is likely to be linked to the average annual air temperature of that altitude as it can be observed in the water temperature of steadily pouring springs in Sweden and Finland (Glazier 2009, Jyväsjärvi et al. 2015). Accordingly, and in combination with the extremely low nutrient level, immigrations of aquatic plants seem to be improbable even with the currently ongoing most drastic warming scenario of +4.5 °C until the end of this century (Schwalm et al. 2020). Based on these results, the observed development of the sedimentary assemblages may keep going with the gradual warming due to climate change unless unforeseeable changes of the doline's limnology appear.

6.1.2 Upcoming Tipping Points New to Bavarian Mountain Lakes

The investigations of this Ph.D. thesis revealed two major tipping points in Bavarian mountain lakes: the appearance and consequent establishment of macrophytes in shallow lakes and planktic diatoms in deep lakes, which is indicative of a stable thermal stratification in summer for a minimum amount of days (see Chapter 5). These two events are coupled with lake temperature, allow the differentiation among lake types, and are therefore affected by climate warming.

However, the lentic systems are still challenged by climate warming and other anthropogenic impacts such as the abandonment of alpine pastures. Consequently, when the uphill moving lake types 1 and 4 reached the highest Bavarian and North-Tyrolean mountain lakes, more ecologically relevant events can be expected. Further changing environmental parameters in mountain lakes may collectively exceed certain thresholds and trigger unprecedented changes in the lake biota again, which are then indicative of more tipping points that are new to the studied lakes.

6.1.2.1 Lack of Lake Icing

Ice phenology in lakes is an important driver as it determines when first sunlight can penetrate the water body and benthos (Pechlaner 1970, Lotter & Bigler 2000, Adrian et al. 2006, Thackeray et al. 2013, Hampton et al. 2015). Additionally, it restricts lake holomixis as the ice cover protects the lake from turbulences by wind and keeps the lake stratified with cooler water approaching 0 °C floating above the denser 4 °C water (Schwoerbel & Brendelberger 2013). With climate change, the ice cover thaws gradually earlier and freezes later (Magnuson et al. 2000, Livingstone et al. 2010, Benson et al. 2011, Peng et al. 2013) as this process is correlated with air temperature (Weyhenmeyer et al. 2004). However, the timing of ice-out and spring holomixis is crucial as light availability within the lake increases in spring with the increasing angle of the sun. Therefore, plankton algae and bacteria can take advantage of an early ice-out because they are able to cope with weaker light conditions, whereas macrophytes are dependent on a minimum temperature and amount of light (Asaeda & Bon 1997, Laugaste et al. 2010, Winder & Sommer 2012, Ejankowski & Lenard 2016). Consequently, phytoplankton can assimilate and increasingly compete for nutrients and light with aquatic plants before they are able to grow. This is further promoted by the warming-triggered mismatch between phyto- and zooplankton, which would usually induce the clear water period in late spring and summer (Winder & Schindler 2004, Winder & Sommer 2012). Hence, an earlier ice-out or even a total lack of icing supports phytoplankton to 'conquer' the new temporal niche of ice-free waters in (late) winter and early spring (Fig. 6.2), whereas later ice-out promotes macrophytes (Ejankowski & Lenard 2016).

In (optically) shallow lakes, lake type 4 with established aquatic plant communities may then be followed by a combination of type 4 and 2. Thus, even shallow mountain lakes may experience a growing importance of phytoplankton with ongoing climate warming in the future. This may be referred to as new 'type 6', which may become more divers with a significant planktic proportion (Fig. 6.8). Probably, this can be predicted for most of the studied mountain lakes as they are characterised by low nutritional levels. However, climate change is supposed to increase the nutrient availability up to a possible doubling in the first half of the 21st century (Kuefner et al. 2020). In lakes of higher trophy, in turn, plankton may become dominating and make even shallow

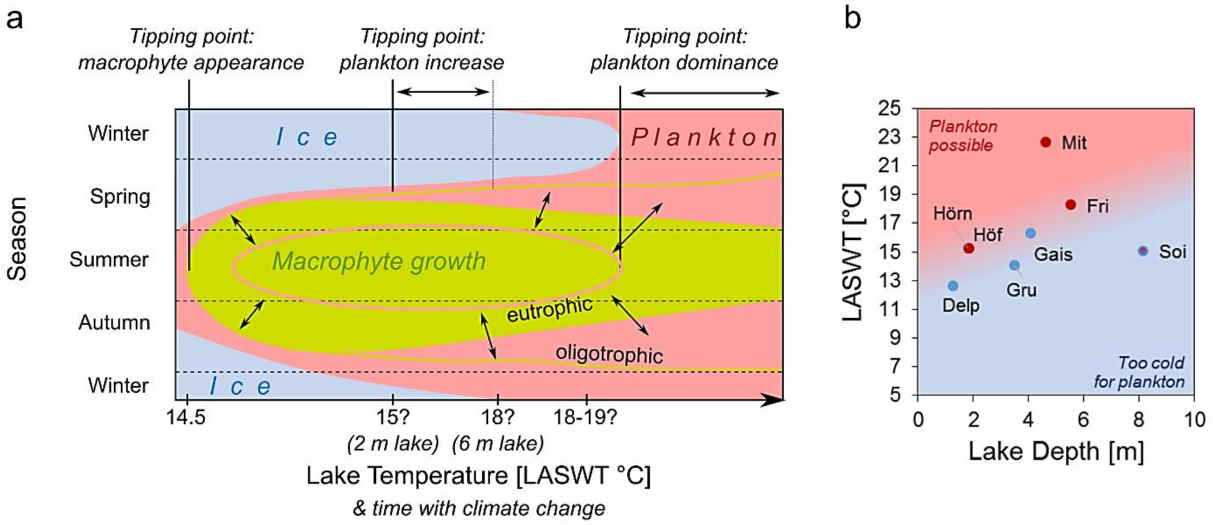

Figure 6.2: Icing and temperature-dependent tipping points in shallow mountain lakes (a) and relation of lake depth with the necessary minimum surface temperature to allow significant proportions of planktic diatoms of the *Cyclotella* complex (b). Arrows in the left graph represent the variances of the tipping points depending on lake temperature and trophic status. The tipping point triggering plankton dominance not necessarily follows the ice disappearance as in a.

lakes optically deep throughout the entire vegetation period. Increasing plankton turbidity may then repress macrophytes and cause a shift from epiphytic towards a plankton-dominated lake biota, hence from type 4 to type 2 (Fig. 6.2 & 6.7). Nevertheless, only mountain lakes of already elevated trophic levels in present times may exceed that tipping point triggering a shift from benthos dominated flora, such as a macrophyte vegetation, towards plankton dominated flora. In deep lakes, which are already (type 1) or increasingly dominated by plankton (type 2), a new niche will emerge during the future winter holomixis of mountain lakes. After recently shifting from polymictic to dimictic as also evidenced in alpine lakes in the Ecuadorian Andes (Labaj et al. 2018), the mixis type of deep lakes may continue shifting towards warm-monomictic lakes. Then, the niche for tychoplanktic algae such as *Aulacoseira* will re-appear. They probably existed already in earlier times before being dominated by summer stratification plankton, e.g. *Cyclotella*. Therefore, such lakes did already reveal higher abundances of mixing and turbulence tolerant tychoplankton (Winder et al. 2009, Rühland et al. 2015). With increasingly ice-free lakes in winter, this niche can recur again and may allow e.g. *Aulacoseira* to re-gain importance (Fig. 6.8). The resulting stage was already observed in large lakes in North America with dominating tychoplanktic diatoms in winter (Twiss et al. 2012). This may lead to a new type 7 with significant proportions of both algae of the ecology of *Cyclotella* and *Aulacoseira* in sedimented assemblages.

In present times, the uppermost layers of some montane lake sediments, e.g. shallow Lake Höfersee and deep Lake Taubensee, already reveal first planktic and tychoplanktic proportions, respectively. Possibly, they are the first type 6 and 7 lakes among the studied where the hypothesised shift has already begun, and the decisive water temperature is reached. This is most significant in L. Höfersee and would approximately be 15 °C in late August in a 2 m deep oligotrophic lake. However, the necessary temperature for the growth of significant plankton proportions seems to increase with depth. As a reason, the polymictic character of lakes, which decreases with depth in central-European mountain climates, improves the distribution of phytoplankton-supporting nutrients in the water body (Fig. 5.2b, Winder & Sommer 2012). Increasing concentrations of nutrients in turn promotes physically shallow lakes to become optically deep, i.e. lake depth > Secchi depth. This already occurred in the mesotrophic Lake Schachensee, which is a plankton-turbid lake in summer. Hence, such a transition from type 3 or 4 to a plankton-dominated type 2 lake can only appear under at least mesotrophic conditions. In conclusion, diatom analyses show that cryptic tipping points along with the gradual decrease of lake icing can already trigger and support (tycho)plankton, so that the total lack of icing by itself is subordinate.

6.1.2.2 Appearance of Algal Blooms

Mountain lakes can be dominated by phytoplankton if they have a higher trophic level, e.g. meso- or – unobserved in the study site – eutrophic. These lakes can experience another tipping point with ongoing climate warming. If average epilimnion temperatures exceed 20 °C in summer, bloom-forming cyanobacteria can gain importance in the phytoplankton (Paerl & Otten 2013, Scherer et al. 2016). Especially warmer cirque lakes at lower altitudes and with anthropogenic pollution, e.g. from huts in the direct vicinity, could in the future become increasingly vulnerable to be colonized by potentially toxic cyanobacteria such as *Microcystis*. Toxic cyanobacterial blooms are favoured by mesotrophic conditions of at least 15–20 $\mu g\ L^{-1}$ (Leigh et al. 2010) and long retention times (Elliott 2010, Carvalho et al. 2011), which are likely to occur in mountain lakes with frequently missing surface in- and outflows. In addition, cyanobacterial blooms are promoted if a previous decrease in lake icing has already led to the suppression of macrophytes, which would compete for nutrients (Peretyatko et al. 2012). Moreover, studies on Austrian and Californian mountain lakes revealed that decreasing snow packs or even a lack of meltwater from snow can cause unprecedented lake warming and therefore ease the water to reach cyanobacterial optimum temperatures (Thompson et al. 2005b, Sadro et al. 2019). The appearance of toxic blooms can have drastic consequences on the aquatic life, e.g. death of fish and waterfowl as the top predators, which can in turn change the entire food web and therefore also macrophytes and algae (Anderson et al. 2002, Paerl & Otten 2013, Scherer et al. 2017).

Within the study area, these risk factors are most likely to occur for the two montane lakes Ferchensee and Lautersee. Both lakes already reach temperatures of over 20 °C in August. Additionally, they are mesotrophic and their phosphor content approaches the estimated threshold of 15 $\mu g\ L^{-1}$ TP. It may further increase with global warming-driven developments in the catchment such as increased erosion (Kuefner et al. 2020). However, it is doubtful, whether the cyanotoxin concentrations under the expected conditions can already reach critical levels that affect mountain lake biota as described above. The current data (Table 3.1 and 5.1) indicate that no cyanobacterial blooms will occur in most of the mountain lakes in the near future. The plankton monitoring on some Bavarian mountain lakes further revealed that the proportion of cyanobacteria is still negligible even in montane lakes of elevated trophy (Hofmann & Raeder 2014, Mayr 2018).

6.1.2.3 Diversification of Macrophyte Communities

Another effect of warming water is that more macrophyte species may thrive in the Bavarian and Tyrolean mountain lakes. This process could lead to a diversification of their aquatic flora (Rosett et al. 2010), which has also been detected in Pyrenean mountain lakes with decreasing altitude (Gacia et al. 1994). Charophytes tolerate colder waters as they can also grow in the hypolimnion (Becker et al. 2016). However, they are only limitedly colonised by epiphytic diatom species, mainly by *Encyonopsis* spp. and *Brachysira* spp. KÜTZING (Raeder et al. 1997, Messyasz & Kuczynska-Kippen 2006, Letáková et al. 2016). As a result of warming, the *Characeae* can be partially replaced by less cold-tolerant macrophytes such as *Potamogeton*. This improves substratum availability for the entire mountain lake diatom community and significantly increases its diversity. Additionally, such higher plants among the macrophytes may be favoured by the competition for nutrients with the upcoming plankton. As a reason, they form proper roots to absorb nutrients from the sediment, whereas the rhizoids of *Characeae* only serve for anchoring. However, in deeper areas of transparent mountain lakes, the charophytes will still prevail, as they are the only macrophytes that can persist the higher water pressure.

With increasing temperatures, the warmest mountain lakes of the montane altitude may even become a habitat for thermophile macrophyte species. The annual *Najas marina* L., for instance, needs at least 15 °C to germinate in spring and a period of about 2 months in summer with at least 20 °C water temperature to develop mature seeds (Hoffmann & Raeder 2016). All of the deep montane lakes may already be a possible habitat for *Najas* as Lake Bichlersee already averaged 20.2 °C in July and August 2016 as well as Lake Lautersee 21.8 °C in the same months 2015. The montane lakes Ferchensee, Taubensee and Wildensee have current averages of about 19.5 °C in July and August. These lakes are therefore candidates for a *Najas* occurrence, as the critical temperature thresholds could be exceeded within the next years. However, current distribution boarders of *Najas* may hamper the colonisation of the remote mountain lakes.

In conclusion, specific temperature scenarios can be predicted and thresholds defined, which may result in a systematic diversification of macrophytes. This process finally leads to an unprecedented diversification of the diatoms, as additional substrata are provided. Thus it is expected that epiphytic diatom species will appear, which did not occur or were barely detected in the lakes in the current study. This diversification process may then be passed on in the entire food web and enable new species of other organism groups to exist in mountain lakes comparable to the changes triggered by the macrophyte appearance (see Chapter 5 & 6.2). Accordingly, the increase in biodiversity in these systems follows and can be indicative of climate change.

6.1.2.4 Change of the Calcite Deposition Regime

The available benthic substrata in Bavarian and North-Tyrolean mountain lakes are principally expressed by a combination of organic and inorganic deposits in the sediments. Its composition depends on lake depth, productivity and the type of dominant primary producers, i.e. plankton, periphyton or aquatic plants (Yang & Flower 2012, Cantonati & Lowe 2014, Hofmann et al. 2020). The organic proportion increases with lake depth and trophy due to increasingly accumulating algal material. Therefore, the sediments of the deep Lake Taubensee are completely organic and dark due to sedimented algae, those of the shallow L. Hörnlesee are brownish due to the remnants of decomposing macrophytes and in the ultraoligotrophic doline lake Sieglsee light grey-brown and totally inorganic (Fig. 6.3). Consequently, cold unproductive lakes, e.g. alpine or doline lakes, select for epipsammic and epilithic diatoms. In contrast, increasing temperature and productivity promotes substrata for epiphytic and epipelic species, which is comparable to the 'substratum succession' process along with climate change (see Chapter 5). However, also sediments of warmer oligotrophic deep lowland lakes can be dominated by lacustrine chalk and support epipsammic and -pelic periphyton as in Lake Großer Ostersee (Hüttner 2020). In such hard-water lakes, this is the result of so-called 'whiting events'. By assimilating carbonate for photosynthesis, planktic blooms trigger calcite precipitation in well-buffered lakes due to the lime-carbonic acid balance (Noges et al. 2016). Additionally, the green alga *Phacotus* PERTY produces a calcite shell and further promotes in-lake calcite precipitation (Lenz et al. 2018). Nevertheless, these calcifying algae need average water temperatures over 15 °C in the epilimnion from May to October (Gruenert & Raeder 2014).

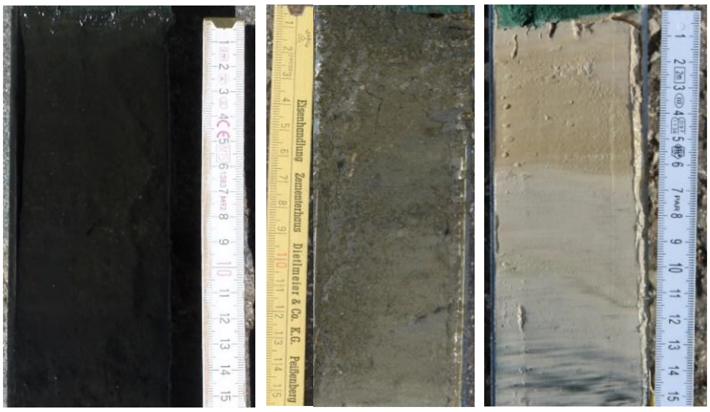

Figure 6.3: Sediments of different organic contents. Left: deep, black and totally organic sediment of L. Taubensee. Centre: Brownish organic sediment of shallow L. Hörnlesee. Right: Bright totally inorganic sediment of L. Sieglsee.

The actual triggers and tipping points of such changing calcite deposition regimes are very complex but mainly driven by temperature as it defines both physicochemical (PCP) and biogenic calcite production (BCP) especially by phytoplankton (Noges et al. 2016). The main representatives of phytoplankton in temperate hard-water lakes are picocyanobacteria such as

Synechococcus (Thompson et al. 1997, Dittrich et al. 2004). In ultraoligotrophic lakes, plankton is negligible (Ossyssek et al. 2020), so that calcite precipitation is limited to PCP and appears to significantly increase over approximately 15–18 °C (Homa & Chapra 2011); conditions as observed in the ultraoligotrophic L. Sieglsee. Despite being a cold polymictic doline lake, surface temperatures regularly exceeded 15 °C in August 2016 during a 2-week-period of stratification with maximum values of 18.7 °C. Hence, significant calcite precipitation can be observed causing the turquoise lake colour and light brownish 'calcite-sediment' (Fig. 2.1, 6.3). Climate change may promote these conditions and calcite formation, so that changes in subfossil diatom assemblages as described in Chapter 5 may also be the response to increased calcite fallout.

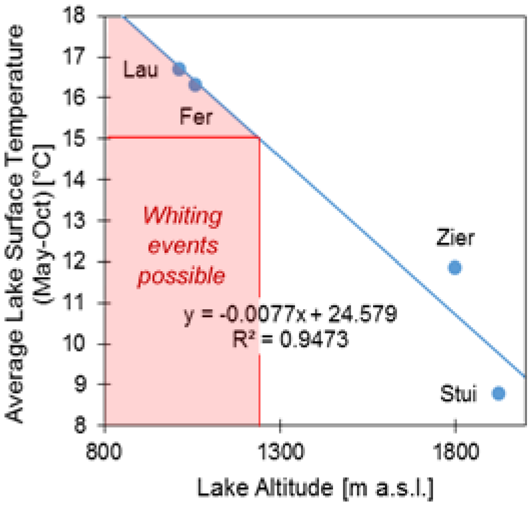

Figure 6.4: Relation of lake altitude and average surface water temperatures from May to October 2016 in Bavarian cirque mountain lakes and regression formula. Mountain lakes of altitudes within the red area can theoretically perform biologically-driven whiting events. Logger data over such a long period were only available for four lakes. Temperature averages were corrected for yearly variances.

Altogether, an epilimnetic lake water temperature of 15 °C may approximately describe the threshold enhancing calcite fallout potential in deep lakes. In plankton-less ultraoligotrophic mountain lakes, exceeding this threshold is necessary for several days triggering PCP, whereas in (meso-)oligotrophic lakes, at least 6 months in average are needed for increased BCP assuming enhanced 'blooming conditions' for both *Phacotus* and *Synechococcus* NÄGELI (cf. Gruenert & Raeder 2014). Evaluating and extrapolating available temperature data of the studied mountain lakes, whiting events are already possible in montane altitudes nowadays and can promote diatom species as they appear in the doline lake (Fig. 6.4). However, the densities of the main algal and bacterial drivers of BCP may still be too low for significant calcite precipitation (Hofmann & Raeder 2014, Mayr 2018). Possibly, the increased UV radiation at higher altitudes suppresses green algae and picocyanobacteria (Vinebrooke & Leavitt 1996, 1999, Sommaruga 2001, Chen et al. 2015). Additionally, the mountain lakes that are already within the 'whiting range', namely L. Ferchensee and L. Lautersee, may be too rich in nutrients, i.e. mesotrophic, so that picocyanobacteria in general do not reach necessary abundances and have to compete with heterotrophic species (Ruber et al. 2018). This indicates that in lakes of a trophic level higher than meso-oligotrophic, algal organic matter may dominate the sediments resulting in inorganic precipitated calcite to become unimportant.

6.1.2.5 Towards a Balanced Catchment Vegetation

Comparing the mountain lakes during the strongest climate warming occurring in the past five decades, the weakest changes can be seen in lakes of montane sites, while alpine lakes have partly experienced steep and sudden developments. Many of these alterations are triggered by changes in the catchment such as uphill migration of the treeline, soil paedogenesis and enhanced weathering (see Chapter 5), which has also been shown in Italian alpine mountain lakes (Rogora et al. 2020). This led to the exceeding of several tipping points and thus to sudden changes in nutrient, plankton and benthic regimes of (sub)alpine mountain lakes. However, the mostly slight changes in montane lakes indicated that the sudden developments at higher elevations may fade away one day. Accordingly, there may be a cryptic tipping point leading to the transition from a changing towards a 'stable' habitat of a completed succession. Establishing dense mountain forests increasingly protect the soil from erosion, so that the natural increase in nutrients and optically active particles affecting the transparency may stop. Autochthonous biomass production may then remain at a stable level except still responding to temperature variations. The corresponding tipping point is supposed to simply coincide with the forest or also known as 'timberline', which splits established dense mountain forests from light forest at higher altitudes. LASWT at this ecotonal boundary ranged between 17–18 °C in 2016 (Fig. 6.5). With climate change, the forest line will further move uphill and so will do the corresponding lake temperatures. The extrapolation of average diatom-inferred warming of 0.087 °C per year (see Chapter 4) would suggest subalpine lakes to experience this tipping point within the next ca. 25 years (Fig. 6.5b), but pioneer-like mountain forests cannot grow and densify that fast. In contrast to the forest line, data are available for the treeline. When extrapolating current vegetation period air temperatures at the treeline altitude from local weather stations over the past twelve decades (Körner 1998, Körner & Paulsen 2004), the potential alpine treeline only moved ca. 200 m uphill (Fig. 6.5a). In fact, only shifts of about 100 m, i.e. the half of

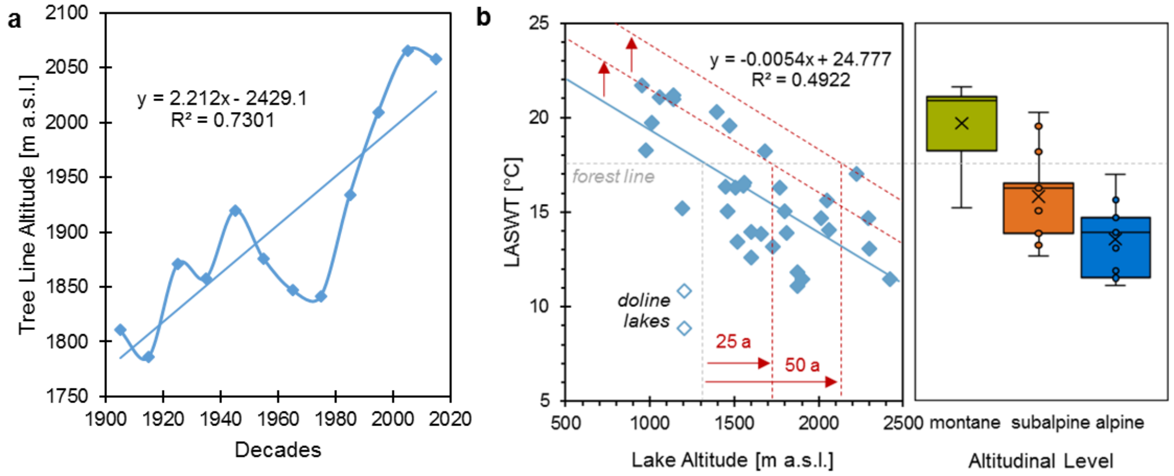

Figure 6.5a: Development of the alpine treeline inferred from extrapolated local temperatures. B: Current Lake August Surface Water Temperatures (LASWT) of Bavarian mountain lakes in relation to the lake altitude. In cirque lakes, the forest line coincides with water temperatures of 17–18°C. With constant lake warming, the 'forest line temperature' may be able to rise about 400 m in 25 years.

the theoretical values, were observed in the Alps, which are additionally strongly influenced by geomorphological and anthropogenic processes such as abandoned mountain pastures (Gehrig-Fasel et al. 2007, Leonelli et al. 2011, Mietkiewicz et al. 2017). Consequently, the exaggerated development inferred by summer water temperatures in mountain lakes are probably the result of changing stratification and icing that cascade into disproportional lake warming behaviour.

Table 6.2: Year of the forest line reaching the subalpine altitudes, i.e. completed mountain forest densification, based on extrapolated tree and forest line temperatures ("theoretical") and halved values based on observed treeline shifts.

Altitude [m a.s.l.]	Completed mountain forest densification	
	Theoretical	„Practical“
1300	Current timberline	
1400	2065	2043
1500	2110	2065
1600	2156	2088
1700	2201	2110
1800	2246	2133

Accordingly, assuming that the forest or timberline describes the same temperature-driven development as the (potential) treeline, it may theoretically rise about 2.2 m per year and practically 1.1 m a^{-1} leaving finally densified mountain forests behind. Concluding, the highest subalpine catchments and the mountain lakes situated within may experience the tipping point towards a balanced catchment vegetation within the next 110–220 years unless unpredictable changes in mountain pasture or climate warming occur (Table 6.2).

Such unpredictable changes include e.g. storm catastrophes and wind-fall, which will appear more often with climate change (Bogataj 2007, Bätzing 2015). Similar effects would be caused by cutting activities, especially if they were unfortunately followed by thunderstorms and/or heavy

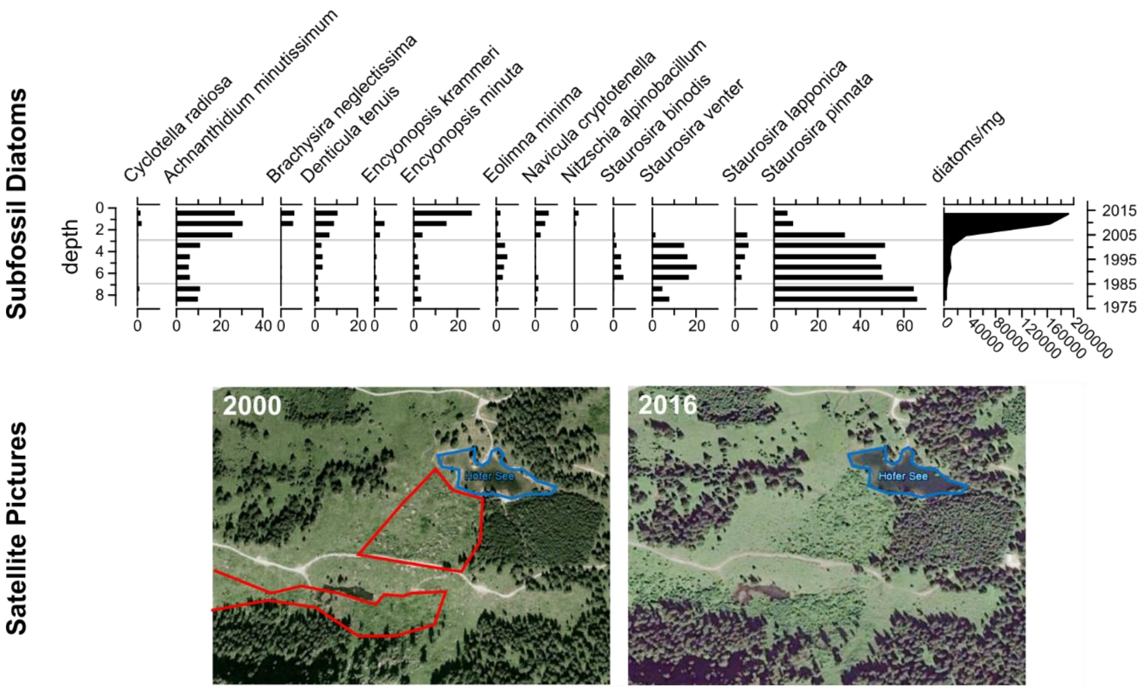

Figure 6.6: Indications for drastic changes of the lake biota in the montane Lake Höfersee after great forest losses, which may be the result of Lothar hurricane in December 1999. Red line: Disappeared forest areas, blue line: Lake Höfersee. The picture of 2016 shows growing young forest. Satellite pictures derive from Google Earth.

precipitation. Contrasting the hypothesised transition to stability, such events would suddenly increase material input again as it was indicated by the montane Lake Höfersee. Its sediments revealed a suddenly initiated replacement of small staurosiroid species by *Achnanthidium* spp. along with an explosion of organic matter and diatom density. Using satellite pictures, this could be explained by losses of forest areas in the direct vicinity of the lake, possibly as a consequence of the Lothar hurricane in 1999 (Fig. 6.6). As this is also supposed to increase nutrients, this may have eased the appearance of Cyclotelloids as an indication for the hypothetical type 6 lake.

6.1.2.6 The First 'Total Desiccation Event'

Along with increasingly challenging hydrological conditions due to summer droughts and decreasing snowmelt after winter, climate change may increasingly cause fluctuating water levels especially in shallow lakes located in small cirques (see Chapter 5.4). Therefore, in particular lakes with weak sealing of the lake bottom such as Lake Soiernsee (E) already experience dramatically decreasing water levels that already appear in early summer (Hofmann et al. 2020). Eventually, increasing WLFs can peak into a first Total Desiccation Event (TDE). Such a TDE can be dramatic for planktic and periphytic organisms and promote desiccation tolerant species such as *D. tenuis*. For instance, mountain lakes near treeline in Utah, USA with increased WLFs described a break-down of the plankton versus favoured pioneer species such as *Staurosira*, which resembled consequences of landslides (Hundey et al. 2014). Consequently, lakes that already perform pronounced WLF are in risk to lose their algal diversity, which makes them more vulnerable to environmental changes and invading species.

The alpine Lake Seeleinsee is one of the WLF-lakes, where an 'almost' TDE has been documented in 2015 (Fig. 6.7). When analysing the weather data from the stations listed in Chapter 5.3.1 plus Innsbruck, Salzburg and Hoher Sonnblick, the year 2015 revealed the second highest average temperature within the vegetation period from May till September as well as especially in summer months only (Jun–Aug) since the beginning of weather recordings. In the high-alpine altitude, the average was 2.4 °C above the average of 1960–1990, the highest positive anomaly was measured in 2003 with +3.0 °C. Additionally, in 2015 has been the third driest summer since 1970 (368 mm, relative: –92 mm), the fifth 'warm-driest' summer[1] (38 d, relative: +16 d), which followed the fourth worst high-alpine winter

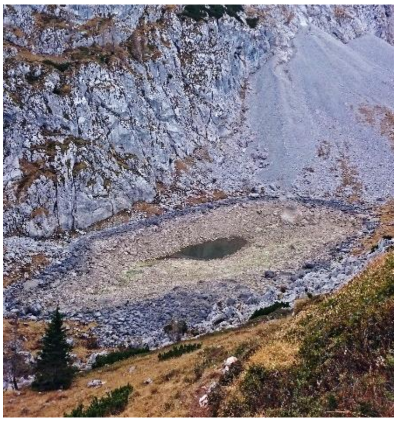

Figure 6.7: Extreme low water level in the Lake Seeleinsee in autumn 2015. Photo credit: Toni Wegscheider.

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[1] Amount of days of daily average temperature > 75th percentile and precipitation < 25th percentile compared to the period 1961–1990 (https://www.ecad.eu/indicesextremes/indicesdictionary.php)

related to the amount of snow days (227 d, relative: –10.6 d). It is likely that the Lake Seeleinsee already experienced a first TDE in 2003, which is still the driest and warmest summer in history in the Bavarian Alps. This may be the reason why fast-growing pioneers such as *Achnanthidium minutissimum* subsequently appeared, while planktic *Cyclotella* disappeared and the sedimentation rates increased. The hypothesis is that, increasingly smaller water bodies warm faster and allow more periphyton to grow on the coring spots, whereas in earlier times, periphytic growth only focused on shallow epilimnetic areas in a constantly filled lake. This supporting, decreasing snow packs not only increase summerly WLF, but also promote lake warming significantly as shown in Californian mountain lakes due to the lack of cool meltwater (Sadro et al. 2019).

However, completely documented observations of the WLF do not exist and available transfer-functions to reconstruct water levels are not reliable in such lakes, where diatom concentrations and biodiversities are extremely low. Therefore, it needs still to be investigated, which climatic parameters and tipping points lead to TDEs in the individual vulnerable mountain lakes. Based on the evidence at Lake Seeleinsee, the tipping point for TDEs in Bavarian-Tyrolean mountain lakes may be exceeded in years such as 2015 fulfilling following criteria: summer anomalies of > +2.5 °C and < –100 mm referred to 1960–1990, probably combined with preceding dry snowless winters.

6.1.2.7 Synthesis

Based on extrapolations and assumptions of the previous chapters, Fig. 6.8 summarizes all possible future developments in the studied Bavarian and North-Tyrolean mountain lakes except for lakes of special geology (type 4+WLF, type 5). Moreover, these hypothesised developments refer to a constant warming as it appeared in the previous decades. Extrapolating this warming, it currently coincides with a global warming of 4.5 °C until 2100 following the modelled RCP8.5 "worst-case" scenario (Schwalm et al. 2020). To easier understand the figure, the altitudinal classification in montane, subalpine and alpine lakes was fixed at certain altitudes although these ranges logically move uphill following the timber- and treeline. For an improved transferability to other regions, the LASWTs of the year 2016 are given additionally for the altitudinal range limits and absolute limits in the study site. Similar to the altitudinal classification, the location of these temperatures is supposed to climb with future warming, so that the tipping point lines can be interpreted as isotherms.

The currently optically shallow lakes undergo a transition from type 3 to 4 to a predicted type 6. Type 3 lakes can currently be found mainly in alpine lakes and will be replaced by type 4 even in the highest locations of North Tyrolean and Bavarian Alps, i.e. shortly below 2500 m a.s.l. until the year 2080. This transition is triggered by the macrophyte establishment. With warming water temperatures and the new niche of ice-free waters in the winter half year, planktic algae will appear

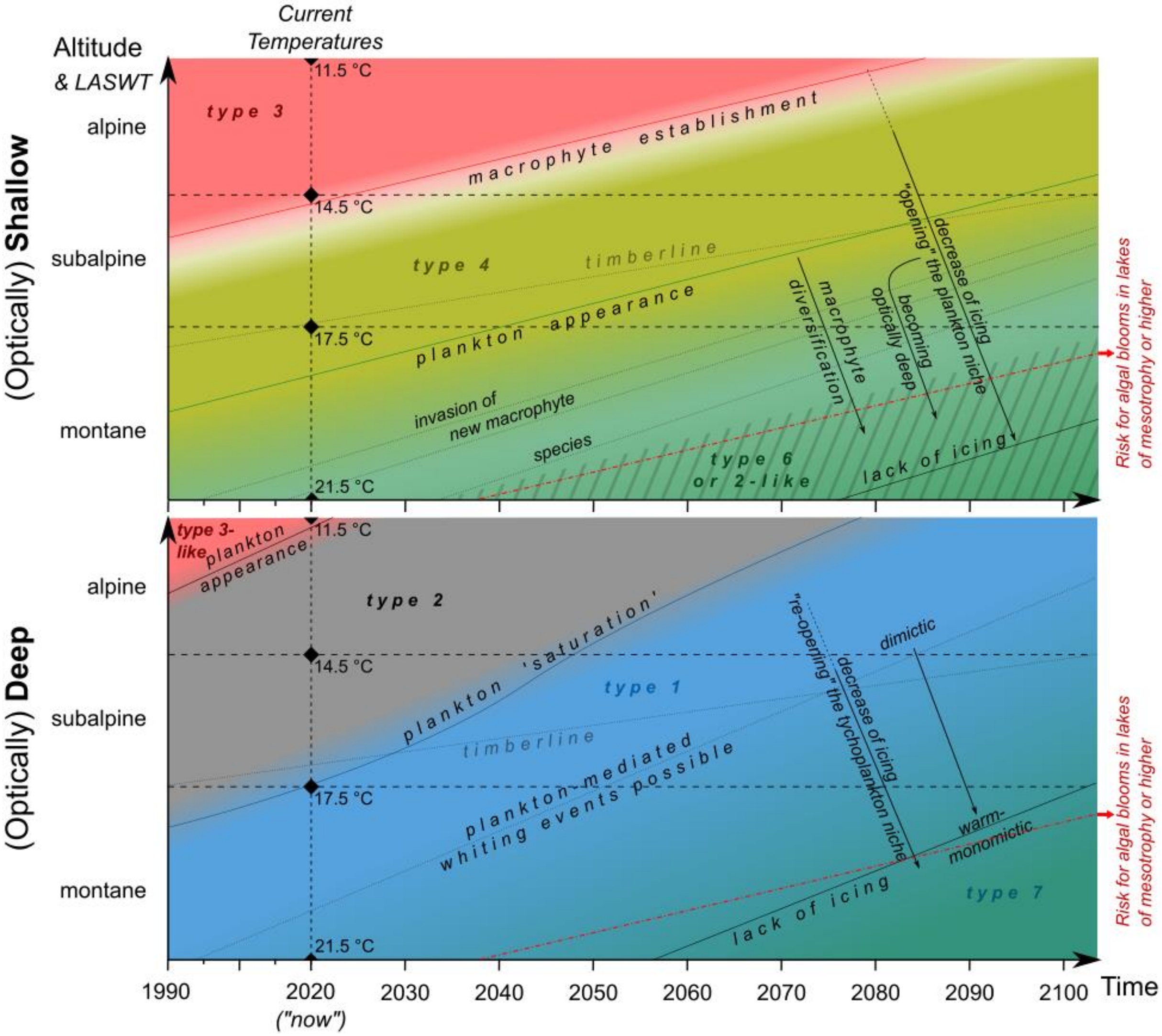

Figure 6.8: Summarized overview of the future development of Bavarian mountain lakes. Optically shallow and deep lakes are shown separately. The future development relies on a constant warming comparable to recent decades. The altitudinal levels are set on fixed altitudes based on the current timber- and treeline. Current late-August surface water temperatures (LASWT) are shown for the current altitudinal boarders as well as extrema in the study site. Lines: Evidenced and predicted tipping points; they rise in elevation with ongoing lake warming. Arrows: Processes triggered by passing tipping points. Current lake types are coloured as in Chapter 5 plus the two new possible types 6 and 7. The main overview is valid for (ultra-or meso-)oligotrophic mountain lakes, developments in higher trophic states are mentioned separately such as the risk for algal blooms and shallow lakes becoming optically deep (grey hatching).

and increase until total lack of icing occurs. This would result in the hypothetical type 6 lake, with significant proportions of periphytic and planktic species. Additionally, the periphytic and the epiphytic communities in particular will become more divers with the invasion of new macrophyte species. In lakes whose trophic level is mesotrophic or higher, plankton algae will become the dominating primary producers, minimizing lake transparency and suppressing the aquatic plants. These lakes will become optically deep and shift towards a type 2 lake.

Among the optically deep lakes, the 'cold and nutrient-poor' type with negligible plankton except for some tychoplankton, which is referred to as 'type 3-like' in Fig. 6.8, possibly already disappeared in the study area. They are replaced by type 2 after plankton appearance. When the subsequent increase of the plankton proportion reaches the carrying capacities, i.e. plankton 'saturation', type

2 switches into type 1. This transition is likely to occur until the 2070s in the highest locations. With further warming and decrease of icing, the niche for mixing-tolerant algae, i.e. the tychoplankton, re-appears. This is accompanied by a change in the mixing regime from dimictic towards warm-monomictic lakes, which will perform holomixis in the winter months. With both, plankton from summer and tychoplankton from winter, this would constitute the new hypothetical lake type 7.

Irrespective of the lake depth, especially montane lakes of already elevated trophy may be vulnerable to further warming within the next decades and experience algal and toxic blooms, the lack of icing, and increase in nutrients due to increased erosion with more frequent heavy precipitation events.

6.1.3 Future Challenges for the Newly Established 'Silicification Value'

The temperature reconstruction based on diatoms using the SiVa was established in hard-water mountain lakes that are comparably low in nutrients and temperature (see Chapter 2 and 3). However, lake warming and consequent surpassing of several tipping points may change some lake characteristics and possibly bias the transfer-function in the future.

6.1.3.1 Predation on Diatoms

With increasing water temperatures and nutrient concentrations, the conditions for herbivorous fauna such as zooplankton may increasingly be favourable, enabling them to occur in higher abundances (Obertegger et al. 2007, De Senerpont Domis et al. 2013). Predation on phytoplankton is one of the possible drivers that can alter cell wall silicification in diatoms (Pondaven et al. 2006). Accordingly, a possible alteration of the silicification behaviour may counteract the observed average decreases with climate warming. Consequently, a biased application of the SiVa in lakes that are richer in zooplankton, e.g. especially lowland and montane lakes, would falsely indicate cooler temperatures in the future. Nevertheless, it remains doubtful, whether such alterations may appear that drastic unless nutritional conditions undergo sudden unpredictable and unprecedented changes.

6.1.3.2 Iron Limitation

Another possible factor challenging the SiVa comes along with the gradual eutrophication and lake warming with climate change: iron limitation. There is evidence that the concentration of bioavailable iron in aquatic habitats can affect diatom silicification with a limitation causing thinner cell walls (Boyle 1998, Twiss et al. 2000, Sterner et al. 2004, Vrede & Tranvik 2006). However, this was classified as ‘negligible’ in the studied small mountain lakes (see Chapter 3.1 and 3.4). Stating that small-sized mountain lakes are highly influenced by catchment and strong mountainous erosion, the influxes are suggested to be rich (enough) in iron compounds. In combination with predominantly low trophic states, environmentally-driven community changes are probably more serious than changes in silicification due to iron concentrations. Despite this, little is known about iron limitation in the freshwater systems of mountain lakes and neither concentrations were measured nor can consequences for limitations be drawn in the studied lakes. Possibly, lakes with higher primary production are closer to the proposed limitation than assumed due to longer vegetation periods, warmer temperatures and higher trophy such as some montane mountain lakes. Iron deficiency may be further exacerbated by long water retention times because of poor water inflow and resulting nutrient depletion (Verburg et al. 2013, Tong et al. 2019) but also with climate change, i.e. further gradual eutrophication, warmer waters and drier summers. Furthermore, increases in erosion and inorganic inputs are much lower at montane altitudes unlike subalpine and alpine lakes (Lotter et al. 1999, Sommaruga et al. 1999, Sommaruga & Augustin 2006). Thus, direct consequences of lake warming at lower altitudes may overweigh the developments in the catchments and therefore unbalance the lakes’ iron budget. Accordingly, the decreasing availability of iron may lead to feigned warmer temperatures inferred from the SiVa. Concluding, future studies should consider possible iron limitation regarding diatoms especially in warmer lakes of higher trophy.

6.1.3.3 Synthesis

On the one hand, increased predation on diatoms may increase cell wall silicification. On the other hand, lakes where this may happen may become limited in iron, which in turn decreases cell wall silicification. As a result, future developments due to climate change may even compensate for aforementioned alterations of silicification, so that the SiVas of the individual diatom species remain constant. Further supporting the robustness of this newly established transfer-function, using the same SiVas once being evaluated can overcome such biases (see Chapter 3.5). Finally, the SiVas of all diatom species were averaged over diatom assemblages from several mountain lakes of different lake temperatures and include possible morphological variances at different sites. Therefore, the assigned values are already averaged over a wide range of accompanying proxies such as possible iron deficiencies at montane altitudes and varying zooplankton densities.

6.2 Consequences of the Indicated Changes for the Mountain Lake Fauna

Diatom assemblages are indicative of nutrients, temperature and substratum developments in lakes, so that also substantial changes in other groups of the mountain lake flora could be identified such as the establishment of macrophytes. Similar to diatoms, more organisms of the food web depend on certain environmental proxies as well, e.g. sufficient substratum for macroscopic algae to grow on. However, this work hitherto focused on the producing level in the food web but left out higher trophic levels, i.e. consumers, to which changes in community structure were passed on. Hence, shifts in diatom assemblages may also serve to indicate shifts in the consumer communities, in particular the fauna. This chapter therefore extrapolates the possible consequences of flora developments to animals that either live in the habitats of mountain lakes or crucially depend on them. Accordingly, the following discussion focuses on invertebrates, such as zooplankton or macrozoobenthos, and vertebrates such as fish, amphibians or birds.

6.2.1 Cladocera, Chironomids and Other Invertebrates

Macroinvertebrate diversity significantly decreases with the altitude in Central European mountain lakes (Hamerlik et al. 2017). Hence, there are species, which can take advantage of warmer lake temperatures and are supposed to be profiteers of climate warming. In the following, different groups of invertebrates are discussed in the context of this Ph.D. thesis.

6.2.1.1 Cladoceras

In boreo-alpine climates, *Cladocera* abundances increase with nutrients and temperature, so that they can therefore even be absent in cold ultraoligotrophic lakes (Kamenik et al. 2007). This makes Cladoceran communities vulnerable for climate change in Bavarian and North-Tyrolean mountain lakes. In Austrian mountain lakes, littoral species appear at a minimum amount of periphyton, whereas larger amounts of Cladocera are reached in lakes with phytobenthos and -plankton allowing benthic and planktic *Cladocera* species (Kamenik et al. 2007). The corresponding threshold values were (1) a mean LASWT of 8.9 °C, which differentiated between presence and absence of *Cladocera* and (2) mean October air temperature of 5.1 °C, which separated planktic from non-planktic assemblages in the surface sediments. The latter was also related to the date of autumn mixing. Accordingly, established and diverse *Cladocera* communities can be expected in mountain lake type 1 already since a long time and in the type 2 since a few decades. Moreover, type 4 may already reveal higher Cladoceran densities, whose communities may become more diverse with increasing amounts of phytoplankton, i.e. becoming the hypothetical type 6. Based on local weather stations, however, lakes above ca. 1625 m a.s.l., i.e. mostly alpine lakes, may still lack planktic Cladoceras according to the second threshold value. Thus, the alpine type 2 lakes such as L.

Engeratsgundsee and L. Drachensee may still be too phytoplankton-poor for *Daphnia* and other water fleas as well as all the type 3 lakes regardless their shallowness. In contrast, all the mountain lakes of the study area lie above the first threshold, so that in all of them probably exists a benthic Cladoceran community unless they are doline lakes. Temperature logger data indicated that the two doline lakes Großer and Kleiner Sieglsee are colder than 8.9 °C in August in average. Supporting these thresholds, they seem to be valid globally, as planktic Bosminidae have also been observed in extremely high abundances in tropical lakes in the Andes with temperatures higher than 8.9 °C (Michelutti et al. 2016, Labaj et al. 2017). Apart from temperature-dependent communities, however, the compositions and densities of such Crustacean communities can also be linked to UV exposure (Siebeck 1994), which additionally causes significant changes at the treeline ecotone. There, UV radiation can be attenuated by allochthonous inputs such as organic matter from establishing forests (Leavitt et al. 2003, Nevalainen et al. 2018).

On the genus and species level, Bosminidae were indicative of warm and nutrient-rich lakes, so that planktic species such as *Bosmina longirostris* O.F. MÜLLER mainly appear in warmer lakes at lower altitudes with forested catchments (Nevalainen et al. 2018). Consequently, *Bosmina* can dominate during warm and eutrophic conditions that are accompanied by cyanobacterial blooms (Korhola & Rautio 2001) and take advantage of climate change in the mountain lakes. Instead, littoral *Alona affinis* LEYDIG and *Chydorus sphaericus* O.F. MÜLLER seem to be indicative of cold and nutrient-poor lakes (Korhola & Rautio 2001, Kamenik et al. 2007), so that alpine lakes are dominated by benthic genera such as *Acroperus* BAIRD, *Alona* BAIRD and *Chydorus* LEACH (Lotter et al. 1997, Kamenik et al. 2007). These genera may lose importance with warming, but most of such benthic species are only cold-tolerant (Meijering 1983, Lotter et al. 1997) rather than cold-stenotherm species in the climates at higher latitudes (Harmsworth 1968). Among that two extrema, *Daphnia* spp. reach highest abundances around the tree and forest line, i.e. subalpine level, where most of the compositional change could be observed (Lotter et al. 1997).

6.2.1.2 Chironomids

Chironomids are a key stone in the food web of freshwater ecosystems (Brooks et al. 2007), so that their development can be important for the future evolution of the mountain lake biota. Making them particularly vulnerable for global warming, the diversity of Chironomids strongly depends on temperature conditions (Heiri et al. 2014). Species numbers increase with July air temperatures until 14 °C and seem to balance or even to decline again at warmer conditions in lakes of the Northern Hemisphere (Engels et al. 2020). Based on regional weather stations, this average temperature is currently located around 1300 m a.s.l., so that especially subalpine and alpine lakes are likely to experience an increase in Chironomid diversity with future climate change. Additionally, water depth and TP in combination with warming positively effected the diversity (Engels & Cwynar 2011, Engels et al. 2020). However, midge communities may be insensitive to temperature alterations of less than 2 °C (Engels et al. 2020) making them to appear less responsive to climate change than diatoms in Austrian mountain lakes (Weckström et al. 2016). Additionally, they are more tolerant to oxygen-depleted sedimentary conditions compared to other benthic invertebrates such as oligochaets (Brodersen et al. 2008) (Chapter 6.2.1.3). In mountain lakes, anthropogenic impacts or climate-triggered processes such as the lack of icing (Chapter 6.1.2.1), catchment succession (Chapter 5) and a prolonged summer stratification (Chapter 5) can together make lakes optically deep, i.e. plankton-turbid, and lead to hypoxia or even anoxia in the deeper benthos (Chapter 6.1.2.7). This can in turn be a factor causing the decline of Chironomid diversity in some lakes, when July exceeds the threshold of 14 °C plus rising the trophic level above (oligo)mesotrophic (Engels et al. 2020). Consequently, enhanced nutrient levels can select for Chironomids that are tolerant to lower oxygen levels and reduce diversity. Apart from temperature and nutrients, DOC is a decisive proxy determining the composition of non-biting midge communities. Accordingly, higher concentrations of DOC with higher benthic productivity significantly revealed other midge communities than of lower values without microbial mats, but higher planktic productivity in Finnish lakes (Luoto et al. 2016). This also depended on catchment vegetation and stage of Taiga forest, i.e. more forest, more nutrients and benthic mats (Luoto et al. 2016).

Concluding, non-montane mountain lakes will witness greatest increases in Chironomid diversity, whereas in lake type 1 a balanced high-diversity community can be assumed. This stage will be reached in type 2 lakes simultaneously with the future transition to type 1. In subalpine lakes, the compositional reorganisation will be the greatest in the near future with global warming, as warm-stenothermic species increasingly invade the cold-stenothermic-dominated communities. Additionally, this process is accompanied by the increase in DOC and therefore in nutrients and benthic food sources. Mesotrophic lakes such as L. Ferchensee and L. Lautersee are in turn among the most vulnerable to nutrient-driven declines of diversity. In the sediments of Bavarian and North-Tyrolean mountain lakes, however, marks from Chironomids were rarely found. Surprisingly, they were only apparent in the sediment core of the alpine Lake Brendlsee (Fig. 6.9). It is remarkable that this lake constituted the coldest lake bottom temperature of all studied mountain lakes and

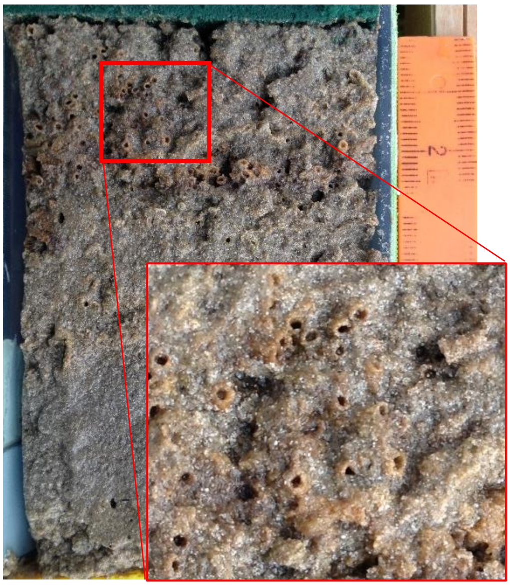

Figure 6.9: Openings of Chironomid tubes in the sediment core of Lake Brendlsee (Photo credit: Andrea Hofmann).

averaged only 4.56 °C in late-August 2016, which has been the warmest period of that year. Possibly, highly transparent waters combined with fluctuating water levels allowed comparably much sunlight to reach the ground at least periodically and microbial and periphytic mats to grow. Because of high oxygen concentrations in the cold water, certain probably cold-stenothermic Chironomids could reach significant abundances in the stable sediment habitat of Lake Brendlsee.

Within the communities, cold-stenothermic genera such as *Smittia* HOLMGREN, *Diamesa* MEIGEN in GISTL and *Pseudokiefferiella* ZAVREL reach highest abundances in alpine lakes (Hamerlik et al. 2017). With climate warming, they may go extinct in the montane lakes the soonest (Armitage et al. 1995, Hamerlik et al. 2017). Instead, *Ablabesmyia monilis* L., *Synendotendipes* GRODHAUS and *Procladius* SKUSE, which revealed the strongest negative correlation with the altitude in Tatran mountain lakes, and warm-stenothermic species such as *Micropsectra* KIEFFER are supposed to be profiteers of warming (Lang 2016, Hamerlik et al. 2017).

6.2.1.3 Oligochaets

Figure 6.10: *Tubifex* found in the alpine sediments of Lake Seeleinsee.

Benthic invertebrate communities such as Oligochaets respond to the amount and quality of the organic matter settling on the bottom (Lang & Hutter 1981, Fuentes et al. 2013). For instance, *Tubifex tubifex* MÜLLER can tolerate higher temperatures, longer periods of anoxia and more organic pollution, whereas e.g. *Stylodrilus heringianus* CLAPARÈDE is a species of cold oligotrophic lakes such as most of the mountain lakes (Chapman et al. 1982, Lang 2016). With climate change, hypoxia in deep waters due to enhanced autochthonous productivity and prolonged summer stratification can increasingly be a stressor for the Oligochaets (Jenny et al. 2014, Lang 2016). Correspondingly changing conditions in the sediment may thus favour insensitive species such as *T. tubifex*, whereas most sensitive taxa are disadvantaged. In contrast, e.g. Chironomids are less affected as they feed on a broader spectrum of algae, bacteria, detritus, and on sediment surfaces (Lang 2016). With warmer waters, invertebrates such as the oligochaete *Limnodrilus* increase, as such 'thermophile' species are rather limited by cold conditions (Lang 2016).

In the investigated sediments of this study, Oligochaets such as *Tubifex* in the alpine Lake Seeleinsee were sporadically found but were rare chance finds (Fig. 6.10). However, this shows that such insensitive species are already well-distributed and appear in alpine lakes already in present times. In the future, the communities are probably mostly challenged by decreasing oxygen levels in deeper lakes particularly of type 1 and hypothetical type 7 as well as type 4 and hypothetical type 6 with high in-lake production. For instance, Lake Hörnlesee already performed pronounced hypoxia at the lake bottom underneath the *Potamogeton* 'forest' (cf. Kuefner et al. 2020).

6.2.1.4 Molluscs

In the sediments of the Bavarian mountain lakes, only two taxa of Molluscs could be identified: the pea clam *Pisidium* PFEIFFER among the Bivalvia and an equally small snail, which is probably *Valvata piscinalis* O.F. MÜLLER. Regarding the pea clam, *Pisidium casertanum* POLI, which reaches even high-alpine altitudes in the Central Alps can dominate mollusc communities in mountain lakes (Boggero 2018). A rarer species is *P. hibernicum* WESTERLUND. Pea clams can also be found in Arctic lakes with an ice-free period of only three months in summer and can widely vary their life-history traits as an adaption to different climates (Bailey & Mackie 1986, Guralnick 2004, Bespalaya et al. 2018). In lakes at higher altitudes, relative brood production decreases with colder water temperatures, possibly due to lower DOM and ions as well (Guralnick 2004). Accordingly, *P. casertanum* is a cosmopolitan species (Kuiper et al. 1989). Abundances and life-histories of pea clams are also dependent on several hydrochemical proxies (Bespalaya et al. 2018), but this is less important in the studied well-buffered hard-water lakes with comparably small variances of such proxies except e.g. phosphorous concentrations. *Pisidium* is also typical of soft substrata with highest proportions of inorganic and detritus particles (Rieradevall et al. 1999), so that they can co-dominate the invertebrate communities with oligochaets in lakes of the Central Alps (Boggero et al. 2005).

In this study in particular, pea clams appeared in the deeper sediments of montane Lake Mittersee (cm 50 downwards, < 1915) and throughout the core of montane L. Frillensee, where it reached highest densities in cm 9 – 12 and cm 25 – 26 representing early 1920s and 1980s. Other sporadic finds came from subalpine L. Soinsee and even the alpine L. Grubersee. *Pisidium* seemed to be concentrated in sediments with coarse-grained brown lithology (Fig. 6.11). Comparing the pea clam peaks of L. Frillensee with the diatom analyses, they coincided with peaks of *Denticula tenuis* and minima of *Staurosira venter* and *Pseudostaurosira brevistriata*. This may indicate slightly lower water levels and higher amounts of DOM after the water level rose again, so that the mussels could take advantage of an increased food supply. Accordingly, *Pisidium* may reach its highest abundances in medium-deep lake depths and around the metalimnion, respectively. Therefore, the density of pea clam finds in the sediment cores also depended on the lake depth at which

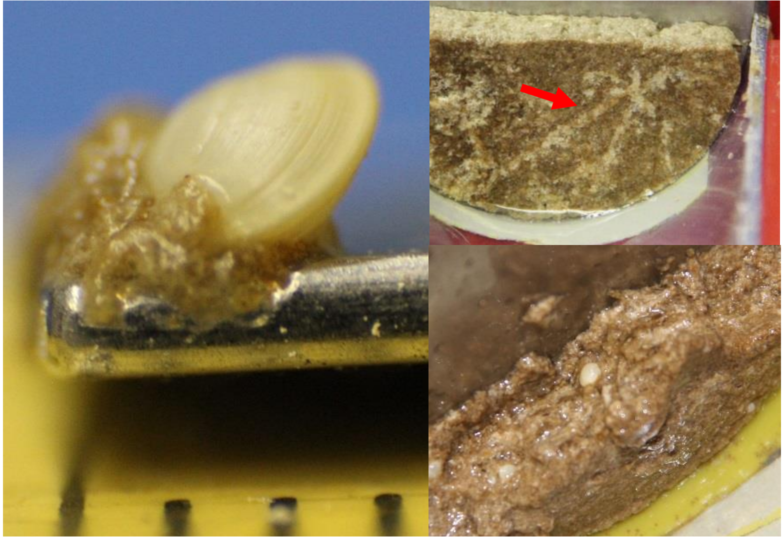

Figure 6.11: *Pisidium* found in the sediments of the montane lake Frillensee. Left: magnified shells on a spatula above a metre rule (short lines are the millimetres). Right top: sedimentary structures probably made by *Pisidium* like former feeding tunnels. Right bottom: *Pisidium* find in a sediment layer.

cores were taken. At the depth of the herein so-called 'Pisidium belt', the benthos is deep enough to sufficiently accumulate DOM at the lake bottoms and coring spots, as also indicated by Rieradevall et al. (1999). In contrast, the coring spots in deeper lakes are beyond the depth of that belt and shallow lakes are too poor in nutrients and DOM (Fig. 6.12). Consequently, the highest densities appeared in warm montane and medium-deep lakes, sporadically in shallow lakes and finds in deep lake cores are restricted to drifted exemplars.

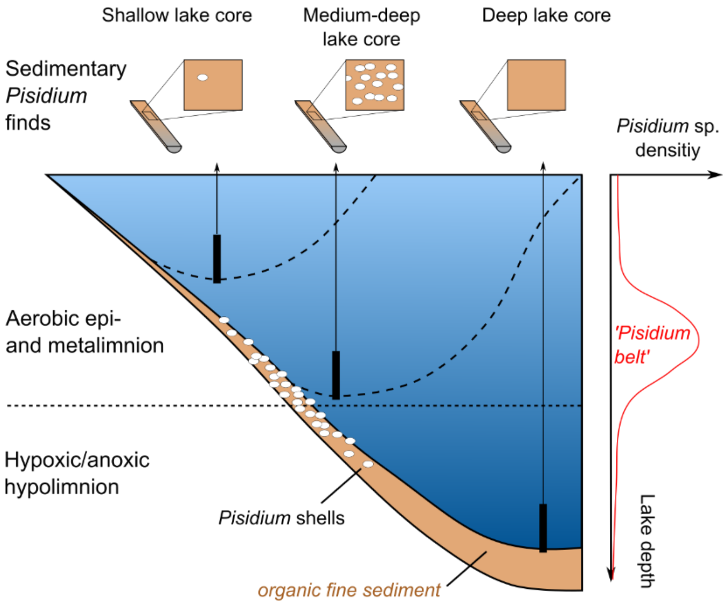

Figure 6.12: Dependence of *Pisidium* finds in sediment cores from coring site and lake depth. *Pisidium* densities in drilled cores are visualised on the top line and their distribution related to lake depth on the right. At medium-deep sediments around the metalimnion a peak is assumed and referred to as 'Pisidium belt'.

Concluding, the future development of pea clams in Bavarian mountain lakes is difficult to predict and probably determined by changes in the depth location of the 'Pisidium belt'. Furthermore, increases of DOM concentrations due to global warming-triggered eutrophication may support pea clam populations in shallow lakes and increase brood sizes in general.

Comparable to pea clams, the distribution of **snails** depends on available organic matter as food source and the oxygen concentrations as observed in Austrian mountain lakes (Sturm 2007). Accompanying the densest *Pisidium* populations, the snail shells of *Valvata piscinalis* appeared in higher abundances only throughout the core of L. Frillensee and sporadically in L. Mittersee (Fig. 6.13). This may support either similar habitat preferences with the abundant Bivalvia or the dependence on landscape position and regional dispersal processes (Heino & Muotka 2006), so that these two lakes are the best reachable for molluscs among the studied mountain lakes. Furthermore, *V. piscinalis* is closely related to charophytes (van den Berg et al. 1997), which explains the highest abundance to occur in L. Frillensee, as it is covered by *Chara*. Generally, snails may be profiteers of climate change in mountain lakes, as increased erosion and catchment succession will provide more organic matter and therefore improve the nutritional conditions. Additionally, warming-triggered uphill moving distribution of macrophytes can also promote snail species feeding on aquatic plants. Such advantaged species are for instance *Galba truncatula* O.F. MÜLLER and *Radix labiata* ROSSMAESSLER, which can already be found in alpine mountain lakes for instance in the Hohe Tauern in Austria (Sturm 2007, Schniebs et al. 2013).

Figure 6.13: Probably *Valvata piscinalis* (left) and pea clam shell (top right) collected from the sediments of the montane Lake Frillensee. One square on the sheet represents 5x5 mm.

6.2.1.5 Other Invertebrates

Less is known about other invertebrates in lakes and particularly mountain lakes such as amphipods, water mites and beetles (Boggero 2018). In general, such species are probably favoured by the overall diversity increases with climate warming and benthic succession (see Chapter 5). However, genera such as Trichoptera are supported by hard substrata (Rieradevall et al. 1999). They may be limited to alpine (ultra)oligotrophic lakes with great WLF such as Lake Seeleinsee or Lake Brendlsee. There, autochthonous production will stay at low levels and hard substrata such as stones will prevail. Boggero et al. (2005) also found evidence for positive effects of permanent surface outflows in mountain lakes for the macrozoobenthos possibly by promoting invasions. Nevertheless, only a low percentage of lakes in the study area possess such outlets, so that this factor is likely to be negligible.

6.2.2 Fish and Amphibians

Mountain lakes are originally not inhabited by fish (Ventura et al. 2017). They are mostly isolated from streams by physical barriers such as lacking surface outflows that prevent the lakes from being invaded by upstream migrating fish (Pechlaner 1984, Knapp et al. 2001, Miró & Ventura 2013). Among the studied mountain lakes, only the montane lakes Ferchensee, Frillensee and Lautersee are naturally reachable for fish, but the runoffs of the first two lakes are interrupted by several lateral buildings and affect fish migration. Within the last centuries, however, humans have introduced cold-stenothermic or -tolerant fish species especially in deeper mountain lakes, therefore particularly Salmonids but also Stone Loach (*Barbatula barbatula* L.) was found (Müller

Figure 6.14: Stone Loach (*Barbatula barbatula*) in the subalpine Lake Soiernsee (W). Photo credit: Severin Sebald.

1967, de Mendoza et al. 2012) (Fig. 6.14). The predatory pressure of fish has a direct impact on the composition of the zooplankton community, as the fish very selectively consume larger food animals. On average, it takes 19 years for a zooplankton population to recover after fish removal (Donald et al. 2001, de Mendoza et al. 2012). Conversely, the density and composition of the zooplankton also has a long-term effect on the fish. Changes in fish populations caused by climate warming are therefore actually mediated by the zooplankton (Labaj et al. 2017). Accordingly, conditions for fish will improve especially at subalpine altitudes, where planktic species of Cladocera will increase the most in the near future (see Chapter 6.2.1.1). The uphill migration of macrophytes will be less important as mainly Salmonids have been introduced into the mountain lakes that are not dependent on aquatic plants. However, they may even have negative effects on the Salmonids as macrophytes provide refuges for zooplankton and support their diversity (de Mendoza et al. 2012). If other fish species have been introduced, a change in underwater vegetation could be of greater relevance. Climate warming-driven effects such as eutrophication of mountain lakes up to eu- and hypertrophic level is not expected, so that the fish should not be affected by deteriorating oxygen conditions. Finally, the introduction of new fish species must be viewed very critically. Apart from the effects on water plants and zooplankton, some organic pollutants can accumulate with altitude in slowly growing fish of cold mountain lakes, so that it may even reach toxic levels for piscivorous consumers (Battarbee et al. 2009).

Amphibians can mostly be seen as profiteers of climate warming in the Central European mountain lakes (Araújo et al. 2006). Being ectotherms, their life cycle crucially depends on the ambient temperature. Warming therefore shifts spawning to earlier dates (Corn 2005, Araújo et al. 2006) and the tadpoles have a longer vegetation period increasing the chances for a greater percentage to complete metamorphosis. Additionally, species such as the Common Toad (*Bufo bufo* L.), Common Frog (*Rana temporaria* L.) and Newts prefer positioning their spawn onto macrophytes, which provide sufficient oxygen supply for the larvae. Macrophytes in turn are predicted to further disperse to higher altitudes (see Chapter 5), so that frogs can follow them into higher mountain lakes.

During the study, Toads and Frogs were regularly found in montane and subalpine mountain lakes, particularly when aquatic plants were present. At higher altitudes such as alpine lakes, the amphibian communities seemed to be limited mainly to Alpine Newts (*Ichthyosaura alpestris* LAURENTI). Until the end of this century, however, also Anura species are supposed to reach the alpine altitudes. Simultaneously, more amphibian species may invade the lowest mountain lakes, which still avoid mountainous areas in present times such as Smooth Newt (*Lissotriton vulgaris* L.), Edible Frog (*Pelophylax esculentus* L.) and European Tree Frog (*Hyla arborea* L.) (LfU 2016). Despite this, the positive effects of climate change on amphibian diversity in mountain lakes can be mitigated anthropogenically by a further introduction of fish. Mountain lakes with fish reveal lower Amphibian diversity than fishless lakes due to feeding of the amphibian spawn and predation on the tadpoles (Braña et al. 1996, McGeoch et al. 2010, Ventura et al. 2017, Miró et al. 2018). As a way out, Alpine Newts can then evade into peripheric or nearby ponds (Denoë et al. 2016). In line with this, the actual role of small ponds as depicted in Figure 6.15 for the diversity of this taxa is unclear. They can be numerous in the Bavarian and North-Tyrolean mountains and are regularly inhabited by Amphibians. Accordingly, it remains to be investigated to what extent the presence of such pools can alter the predicted developments in mountain lakes and its consequences for Amphibian diversity in the Bavarian Alps.

Different to Frogs and Newts, mountain lakes are less important for Salamanders. The two main species in the study area spawn into alpine creeks and springs in case of the Fire Salamander (*Salamandra salamandra* L.) or are even widely independent of running waters in case of the Alpine Salamander (*Salamandra atra* LAURENTI). The latter is even especially adapted to the harsh mountainous climate by being ovoviviparous and solely distributed from montane to alpine altitudes in Bavaria (LfU 2016). Similarly, the Yellow-bellied Toad (*Bombina variegate* L.), which is also distributed until subalpine altitudes, mainly live in small puddles and ponds rather than proper mountain lakes. Such small and sometimes only temporal aquatic habitats provide warmer temperatures and better larval growth due to its size.

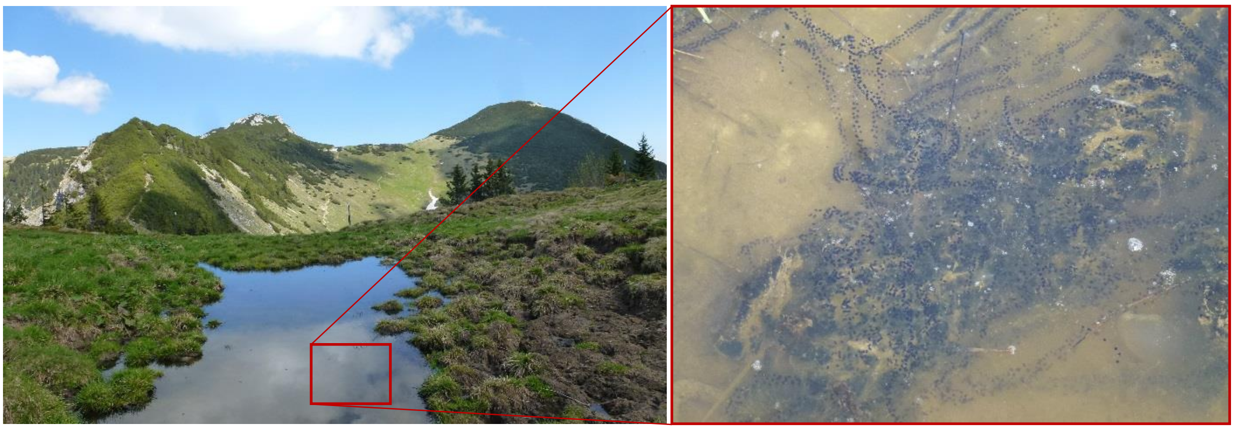

Figure 6.15: Egg strings (right) of toads (*Bufo bufo*) in an alpine pool close to the Geigelstein (left; right summit in the background).

6.2.3 Birds

Figure 6.16: Water Pipit (*Anthus spinoletta*) at the alpine lake Oberer Seewisee (top) and White-throated Dipper (*Cinclus cinclus*) feeding on a ’worm‘ in the alpine lake Mittlerer Seewisee (bottom).

Decreasing temperatures with increasing altitudes result in different habitats and similarly cause changes in bird diversity from montane to alpine levels (Kuefner & Utschick 2016). Because birds in the mountain area are almost exclusively no waterfowl, they thus primarily respond to catchment changes and use lakes only as an additional food source but do not depend on aquatic habitats. Despite this, there are indications in the Rocky Mountains that the presence of mountain lakes positively influences the surrounding bird populations, so that the abundance of some American songbird species increase with the presence of aquatic insects such as Trichoptera (Garwood et al. 2009, Epanchin et al. 2010). Nevertheless, there is still poorly known if mountain lake proxies correlate with bird population densities and diversities, e.g. in the Alps. In the study area, mountain lakes seemed to attract Water Pipits (*Anthus spinoletta* L.), White-throated Dipper (*Cinclus cinclus* L.), White (*Motacilla alba* L.) and Grey Wagtail (*M. cinerea* TUNSTALL). The lakes apparently contain a rich invertebrate fauna in the benthos, so that these insectivorous songbird species preferably forage at the littoral zones even at alpine altitudes (Fig. 6.16). Climate warming-driven changes in songbird population may therefore be mediated by changes in the invertebrate fauna as discussed in Chapter 6.2.1. Generally, the insectivorous birds will profit of increasing invertebrate densities and diversities in the near future especially in subalpine lakes. Nevertheless, it remains unclear if this would cause changes in bird diversity or only change the foraging behaviour, i.e. changing feeding preferences, which may slightly support the population densities. In contrast, it may be certain that artificial fish stocking of mountain lakes negatively affect passerine populations due to the impact on the invertebrates (Epanchin et al. 2010).

Accordingly, waterfowl may be more affected by the predicted environmental changes in mountain lakes. One of most distributed species of this group is the Mallard (*Anas platyrhynchos* L.). In the study area, this duck was already observed in subalpine waters (own observation, Bezzel et al. 2005). In Bavaria, there is evidence for high altitude broods of Mallards to infrequently occur at the montane Lakes Ferchensee and Lautersee, whereas in Austria even high altitude broods up to almost alpine altitudes were reported (Bezzel 1996). As a predominantly herbivorous duck, it will be a direct profiteer of climate warming-triggered eutrophication or increased primary production.

Following macroscopic algae and aquatic plants, it will probably expand its breeding area towards higher altitudes. According to Chapter 6.1.2.7, Mallards may possibly even breed in alpine lakes until the end of the 21st century in Bavaria as well. A similar development can be predicted for other widespread waterfowl species such as Eurasian Coot (*Fulica atra* L.) and Great-crested Grebe (*Podiceps cristatus* L.), whose breeding areas in Bavaria already ranges up to 1150 and 1040 m a.s.l., respectively (Bezzel et al. 2005). Additionally, a few more species of rails, grebes and ducks are shortly before extending the breeding range to the montane level (Bezzel et al. 2005).

In return, ducks and rails may promote algae and macrophytes to invade the highest lakes in the Bavarian Alps by transporting seeds and cells in the plumage (Coughlan et al. 2017). Additionally, waterfowl are important vectors for the dispersal of zooplankton (Hessen et al. 2019) and can further support the warming-driven increases of nutrients and facilitate mountain lakes to reach new trophic levels (Manny et al. 1994).

6.3 Global Transferability

The final results of this Ph.D. thesis are mainly based on ecotonal boundaries, in particular the tree and the forest line. Theoretically, this directly allows a worldwide transferability within the altitudinal levels montane, subalpine and alpine (Fig. 6.17). This is further supported by corresponding references from mountain lakes all over the world, which underpinned the discussion of this Ph.D. thesis and were similarly oriented towards these ecotones. On a global perspective, they are gradually situated at higher altitudes towards the equator due to the increasing angle of the sun and increasing radiative power with the decreasing latitude (Charrier 2011, Paulsen & Körner 2014). Accordingly, for instance shallow type 3 lakes may be found in the lowlands close to the ocean in Northern Scandinavia and in the highlands of Scotland and Southern Scandinavia, which are still at lower altitudes than the study area. In contrast, this type may reach altitudes of 3000 and 4000 m a.s.l. at lower latitudes such as mountain lakes in the Himalayan, Rocky Mountains or equally at same latitudes in the Andes in the Southern Hemisphere. Furthermore, the hypothesised future lake types such as type 6 in shallow lakes and type 7 in deep lakes, may extend the transferability to lakes at lower altitudes that follow the montane level downhill such as the colline level. Comparably, type 2 lakes were assumed that they have been 'type 3-like' before the planktic appearance (see Chapter 6.1.2.7). As this stage is already supposed to be extirpated in the study area in the climate warming-driven succession of the mountain lakes, they may still exist at higher altitudes such as high-alpine lakes. Therefore, this may further promote an extrapolation of the findings towards higher lakes than the studied and lift the 'validity range' until the alpine-nival transition. Therefore, developments in subpolar areas may simultaneously be explained based on the results of this thesis. Nevertheless, these 'type 3-like' deep lakes are not totally plankton-free but, similarly to studies on Lake Tahoe in the USA, they may already be inhabited by tychoplankton such as *Aulacoseira* (Winder et al. 2009, Rühland et al. 2015). However, such diatoms were barely found in the studied lakes possibly because of methodological issues.

In lakes above the alpine-nival ecotone, mountain lake catchments are usually characterised by glaciers and 'glacial climates'. Firstly, ice break-up in such lakes is limited to summer months, so that they can contain patches of ice throughout the year. Secondly, there is a higher risk for freezing and snow fall even during summer as well as elevated cloudiness (Livingstone et al. 2005). Thirdly, glacier-fed inflow greatly enhances inorganic sedimentation, so that such lakes often appear very turbid and turquoise. Additionally, retreating glaciers may mainly challenge the lakes by increasing WLFs as observed in the Himalayas (Nie et al. 2013). Algal communities in such lakes are thus often restricted to low amounts of robust diatoms, *Staurosira* in particular (Koinig et al. 2002, Lotter et al. 2002, Michelutti et al. 2003). Altogether, this results in totally different sedimentation, temperature and mixing regimes with a weaker correlation of lake temperatures with altitude compared to lower altitudes. Mountain lakes of such altitudes therefore reveal a weaker response to and forcing by climate change as postulated on Swiss high-alpine lakes (Livingstone et al. 2005). Their lake developments are not covered by this study and can barely extrapolated from the highest practical and hypothetical lake types. Furthermore, the presence of glaciers in the catchment can also hamper the validity of the thesis' results in alpine altitudes, where a direct transferability was stated.

Apart from ecotones, climate and mixing conditions similar to those in the Bavarian and Tyrolean Alps are preconditions of the transferability and validity. In the study area, the climate consists of four seasons with winters usually rich in snow and humid conditions throughout the year.

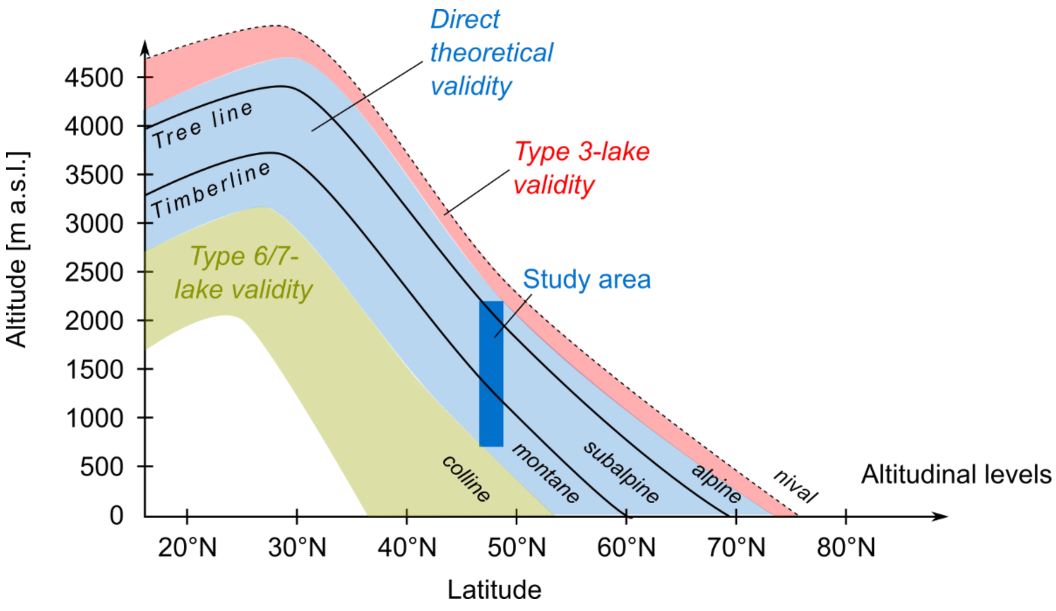

Figure 6.17: The study's validity on a global scale. Following tree and timberline according to Paulsen & Körner (2014), the findings can be extrapolated directly along the corresponding altitudinal levels (blue area). The assumptions for type 3(-like) lakes and hypothesised type 6 and 7 lakes allow an extension of the validity until the alpine-nival transition (blue area) and into the colline level (green area).

Accordingly, different climates already in Europe such as maritime conditions with comparably weak annual amplitudes, e.g. in Scotland, may reveal different relations of seasonal proxies with climate change (Thompson et al. 2009). As an extreme case, arid climates within the range of the direct theoretical validity may lead to other developments in mountain lakes than in the study area. Due to bare soil and sparse vegetation in dry areas, the lakes may reveal lower nutritional levels for instance in central Asia or the southern Rocky Mountains. Additionally, if such climates allow lakes to exist at all, they are strongly affected by pronounced water-level fluctuations up to periodic desiccations and are frequently subject to enhanced salinity (Vallet-Coulomb et al. 2001, Timms 2010). This in turn may resemble the type 4+WLF category especially with the predicted future changes with warming and an increasing risk for desiccations (see Chapter 6.1.1, 5.1.2.6). However, lakes in arid climates may experience stronger changes in temperature from freezing to > 25 °C with unprecedented consequences for the lake biota, as they probably cannot be extrapolated from type 4+WLF lakes.

Total non-transferability can be stated for mountain lakes in the most extreme climates of the earth. Warm-polymictic (or even amictic) mountain lakes of the tropics as well as cold-poly- or –mono-mictic lakes (or even amictic) of the nival and polar areas are beyond any comparability due to different temperature, nutrient and mixing regimes. The former reveals average annual temperatures, which were only reached during the warmest periods in the study area, and can prevail throughout the entire water column (Umana 2014). Additionally, extreme precipitation cause enormous loads of inorganic and organic material making the lakes brownish turbid throughout the year (Bozelli 1994). This can in turn result in totally different diatom communities in tropic lakes than in the mountain lakes of the study area (Finney & Johnson 1991, Haberyan et al. 1997, Tibby & Haberle 2007). In contrast, polar lakes may experience only single and short ice break-ups in summer, so that the dominating temperatures are close to freezing. Water is mostly ultra-oligotrophic and can completely be melt water from the glaciers (Cremer et al. 2004). Apart from inorganic sandy and stony substrata, small 'ice bergs' may be one of the most important surfaces for periphytic algae due to permanently apparent ice (Yallop & Anesio 2010). Such habitats can only be inhabited by low abundances of robust and partly even endemic species with different ecology than apparent in the studied lakes (Cremer et al. 2004, Ohtsuka et al. 2006). All these factors cause different algal communities, strongly deviating developments and responses to climate warming, which can barely extrapolated from this thesis.

However, studies of (mountain) lakes in these extreme areas of the Earth from tropics to polar areas as well as arid and hotter regions may extend the mountain lake model as inferred by the Ph.D. thesis' results. Finally, appropriate investigations may allow to elaborate a 'global mountain lake model' with a worldwide validity and evaluation of climate change consequences in any lake.

6.4 Outlook

Based on the new method to reconstruct lake warming inferred by diatoms and the evaluation of the impact of increasing temperatures on mountain lakes, valid indications for the development of mountain lakes in regions similar to the study site can be drawn. The study area represents an ideal model area that globally covers freshwater habitats from subpolar to temperate climates (Chapter 6.3), but brings along open questions in regions beyond.

The correlation of the indicative diatom trait of valve silicification with lake temperature was observed in calcareous lakes, which may be more limited to silicate than soft-water lakes in siliceous catchments. Such habitats host significantly different species compositions and a greater supply of silica that may alter the relationship of the average valve silicification with water temperatures. This highlights the need for further research to expand the applicability of the newly established index.

Similarly, further investigations in different climates may be considered to improve global validity of both the diatom index and the evaluation of mountain lake responses to climate change. As already discussed in Chapter 6.3, the lake biota of polar, tropic or (semi)arid areas may be forced by different factors than in the study area, e.g. WLF and subsequent strong annual variances in light transmittance, dissolved substances, and nutrient concentrations. Extracting more major tipping points in these systems may allow to reconstruct and to predict the responses of such lakes to global warming. This may further help to expand the results of this Ph.D. thesis spatially and to formulate a global mountain lake model.

Apart from different climates, specific lake geologies can crucially affect lake response as well. In the study area, doline lakes appeared to be the most stable and resilient systems to a warming climate. However, there were only two twin lakes of this type within the study area. Accordingly, the question arises if the assumptions drawn from the Sieglsee lakes is valid for other doline lakes in the Alps or in other climates as well. In addition, it is still not fully understood, how the lakes of volcanic geology may respond to global change and how this may fit or expand the results from the studied lakes in this thesis.

Once all the responses of mountain lakes to the changing climate are known and predictable, it remains open, how their developments may influence the surrounding catchment. As indicated in Chapter 6.2.3, mountain lakes can have positive effects on mountain bird populations by increasing the food diversity. Future studies may test, whether these freshwater habitats are able to enrich faunal diversity in mountainous catchments either by factors of food supply, indirectly via modulating local microclimates or even more complex processes. Suitable areas for such studies are adjacent alpine cirques, so that the main environmental difference is the presence or absence of mountain lakes as existing in the Allgäu Alps. This can then help to improve and to adjust management and conservation strategies in the face of future climate warming in mountainous landscapes.

7 Author contributions

Chapter 3: The Silicification Value: A novel Diatom based Indicator to Assess Climate Change in Freshwater Habitats

This chapter was conceived by Wolfgang Küfner (WK) in consultation with Uta Raeder (UR) and Jürgen Geist (JG). On-site-measurements and laboratory analyses were mainly carried out by WK and Stefan Ossyssek (SO). Diatom preparation and microscopic analyses was done by WK and SO. Statistical analysis, visualisation, and data interpretation was mainly conducted by WK. The manuscript was drafted by WK and continuously refined, improved and edited by UR and JG.

Chapter 4: Evaluating Climate Change Impacts on Lakes by Applying the New Silicification Value to Paleolimnological Samples

WK conceptualised this chapter and carried out data collection. Sampling, preparation and analyses of the sediment cores as well as microscopic analyses was mainly performed by WK and Andrea Hofmann (AH). Statistical analyses, visualisation and data interpretation was the main work of WK in consultation with AH. The manuscript was drafted and finalised by WK and continuously reviewed and improved by 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

This chapter was an equal-authorship publication of WK and AH with continuous advice from JG and UR. Preliminary studies were performed by AH. Hydrochemical and hydrophysical analyses were carried out by SO, AH and WK. Sampling and preparation of the sediment cores was the equivalent work of WK and AH. Sediment dating was realised and interpreted by Nathalie Dubois at the Swiss Federal Institute of Aquatic Science and Technology, Department Surface Waters EAWAG in Dübendorf. Preparation of diatom samples and microscopic analyses was equally performed by WK and AH. Statistical analyses and visualisation was mainly done by WK. Data interpretation, drafting and finalisation of the manuscript was equally carried out by WK and AH. JG and UR continuously supervised, improved and edited the manuscript.

8 Publication list

Publications being included in this thesis:

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Kuefner W, Hofmann AM, Geist J, Raeder U (2020) Evaluating climate change impacts on mountain lakes by applying the new silicification value to paleolimnological samples. Science of the Total Environment 715, 136913. https://doi.org/10.1016/j.scitotenv.2020.136913

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Oral presentations referred to this thesis:

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Kuefner W (2018) Climate Change in Mountain Lakes – Stable Isotopes as an Important Proxy in Sediments. Guest Talk in „Methodenkurs: Stabile Isotope in der Hydrogeologie und in den Umweltwissenschaften“, 5 March 2018, Friedrich-Alexander-Universität Nürnberg-Erlangen, Germany.

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Kuefner W (2018) Mountain lakes in Bavaria, Germany – High diversity in lakes, high diversity in climate change effects? Limnology Seminar, 7 November 2018, Queen's University, Kingston, Canada.

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11 Supplementary

List of Tables in the Supplementary

List of Figures in the Supplementary

Table S 1: 153 most abundant diatom species and varieties (> 1%) in surface sediment samples in the mountain lakes and its silicification values. The list contains three planktonic species since they were even found in higher abundances in littoral samples and are marked with an asterisk (*).

Species	Silicification Value
Achnanthes minuscula Hustedt	2
Achnanthidium caledonicum Lange-Bertalot	1.5
Achnanthidium linearioides Lange-Bertalot	1.5
Achnanthidium macrocephalum (Hustedt) Round & Bukhtiyarova	1.5
Achnanthidium minutissimum (Kützing) Czarneki	1.5
Achnanthidium neomicrocephalum Lange-Bertalot & Staab	1
Achnanthidium pyrenaicum (Hustedt) Kobayasi	1.5
Achnanthidium rosenstockii Lange-Bertalot	1.5
Achnanthidium straubianum Lange-Bertalot	1.5
Adlafia bryophila (Petersen) Lange-Bertalot	1
Adlafia minuscula var. minuscula (Grunow) Lange-Bertalot	1
Amphora aequalis Krammer	3
Amphora alpestris Levkov	3.5
Amphora eximia Carter	3
Amphora inariensis Krammer	2.5
Amphora lange-bertalotii Levkov & Metzelin	3
Amphora ovalis Kützing	4
Amphora pediculus (Kützing) Grunow	2.5
Aneumastus stroesei (Østrup) Mann & Stickle	3.5
Aneumastus tusculus (Ehrenberg) Mann & Stickle	4
Brachysira liliana Lange-Bertalot	1
Brachysira neglectissima Lange-Bertalot	1
Brachysira neoexilis Lange-Bertalot	1
Brachysira vitrea (Grunow) Ross	1
Caloneis obtusa (Smith) Cleve	3
Caloneis silicula (Ehrenberg) Cleve	3
Caloneis tenuis (Gregory) Krammer	2.5
Cavinula pseudoscutiformis (Hustedt) Mann & Stickle	1.5
Cocconeis placentula var. euglypta Ehrenberg	2
Cocconeis placentula var. placentula Ehrenberg	2
Craticula cuspidata (Kützing) Mann	3.5
Cymatopleura elliptica (Brébisson) Smith	4
Cymbella cymbiformis Agardh	3.5
Cymbella excisiformis Krammer	3
Cymbella laevis var. laevis Nägeli ex Kützing	3
Cymbella neocistula Krammer	3.5
Cymbella parva (Smith) Kirchner	3
Cymbellafalsa diluviana Krasske	3
Cymbopleura amphicephala (Nägeli) Krammer	2.5
Cymbopleura diminuta (Grunow) Krammer	2.5
Cymbopleura florentina var. brevis Krammer	2.5
Cymbopleura inaequalis (Ehrenberg) Krammer	3.5
Delicata delicatula (Kützing) Krammer	1.5
Denticula tenuis Kützing	2.5
Diatoma mesodon (Ehrenberg) Kützing	2.5
Diploneis elliptica (Kützing) Cleve	4
Diploneis krammeri Lange-Bertalot & Reichardt	4
Diploneis oculata (Brébisson) Cleve	2.5

Diploneis parma Cleve	3
Diploneis separanda Lange-Bertalot	3
Encyonema caespitosum Kützing	3.5
Encyonema minutum (Hilse) Mann	2
Encyonema obscurum (Krasske) Mann	2.5
Encyonema reichardtii (Krammer) Mann	2
Encyonema silesiacum (Bleisch) Mann	3
Encyonema ventricosum (Agardh) Grunow	2
Encyonopsis cesatii (Rabenhorst) Krammer	2
Encyonopsis krammeri Reichardt	1.5
Encyonopsis microcephala (Grunow) Krammer	1.5
Encyonopsis minuta Krammer & Reichardt	1.5
Encyonopsis subminuta Krammer & Reichardt	1.5
Encyonopsis vandamii Krammer & Lange-Bertalot	1.5
Eolimna minima (Grunow) Lange-Bertalot	1.5
Epithemia adnata (Kützing) Brébisson	4
Epithemia sorex Kützing	4
Eucocconeis flexella (Kützing) Meister	2
Eunotia arcubus Nörpel & Lange-Bertalot	3
Fallacia sublucidula (Hustedt) Mann	1.5
*Fragilaria delicatissima** (Smith) Lange-Bertalot	1.5
*Fragilaria nanana** Lange-Bertalot	1
*Fragilaria tenera** (Smith) Lange-Bertalot	1
Geissleria cummerowi (Kalbe) Lange-Bertalot	2
Geissleria decussis (Hustedt) Lange-Bertalot & Metzelin	3
Geissleria similis (Krasske) Lange-Bertalot & Metzelin	3
Gomphonema angustum Agardh	3
Gomphonema auritum Braun & Kützing	3
Gomphonema capitatum Ehrenberg	3
Gomphonema lateripunctatum Reichardt & Lange-Bertalot	3
Gomphonema micropus Kützing	3
Gomphonema minusculum Krasske	3
Gomphonema parvulum Kützing	3
Gomphonema procerum Reichardt & Lange-Bertalot	3
Gomphonema pumilum var. rigidum (Grunow) Reichardt & Lange-Bertalot	3
Gyrosigma acuminatum (Kützing) Rabenhorst	2.5
Gyrosigma attenuatum (Kützing) Rabenhorst	4
Halamphora thumensis (Mayer) Levkov	2
Hippodonta neglecta Lange-Bertalot, Metzelin & Wikowski	3
Kobayasiella jaagii (Meister) Lange-Bertalot	1
Mastogloia lacustris (Grunow) Van Heurck	3.5
Meridion circulare var. circulare (Gréville) Agardh	2.5
Navicula antonii Lange-Bertalot	3
Navicula concentrica Carter	3.5
Navicula cryptocephala Kützing	2.5
Navicula cryptotenella Lange-Bertalot	2.5
Navicula densilineolata Lange-Bertalot	3
Navicula krammerae Lange-Bertalot	3
Navicula radiosa Kützing	3.5
Navicula trivialis Lange-Bertalot	2.5
Navicula trophicatrix Lange-Bertalot	3
Navicula upsaliensis (Grunow) Peragallo	3
Navicula utermoehlii Hustedt	1.5

Navicula wildii Lange-Bertalot	3
Naviculadicta geissleriae Jahn	2.5
Naviculadicta raederae Lange-Bertalot	1.5
Neidium ampliatum (Ehrenberg) Krammer	3.5
Nitzschia alpine Hustedt	2
Nitzschia alpinobacillum Lange-Bertalot	2
Nitzschia dealpina Lange-Bertalot & Hofmann	2
Nitzschia denticula Grunow	3.5
Nitzschia dissipata (Kützing) Grunow	2
Nitzschia fonticola Grunow	2
Nitzschia hantzschiana Rabenhorst	2
Nitzschia lacuum Lange-Bertalot	2
Nitzschia palea (Kützing) Smith	2
Nitzschia perminuta (Grunow) Peragallo	2
Nitzschia pura Hustedt	1.5
Nitzschia recta Hantzsch	2.5
Nitzschia tabellaria Grunow	2.5
Pinnularia borealis var. borealis Ehrenberg	4
Pinnularia microstauron (Ehrenberg) Cleve	4
Pinnularia obscura Krasske	3
Pinnularia obscuriformis Krammer	3
Placoneis clementis (Grunow) Cox	3
Placoneis pseudanglica (Lange-Bertalot) Cox	3
Planothidium frequentissimum Lange-Bertalot	2
Planothidium rostratum (Østrup) Lange-Bertalot	2
Platessa conspicua (Mayer) Lange-Bertalot	2
Platessa holsatica (Hustedt) Lange-Bertalot	2
Platessa ziegleri Lange-Bertalot	2
Psammothidium subatomoides (Hustedt) Bukhtiyarova & Round	1.5
Pseudostaurosira brevistriata Grunow	2
Pseudostaurosira p. var. parasitica (Smith) Grunow	1.5
Pseudostaurosira robusta (Fusey) Manguin	2
Reimeria sinuata (Gregory) Kociolek & Stoermer	3
Sellaphora bacillum (Ehrenberg) Mann	2.5
Sellaphora joubaudii (Germain) Aboal	2
Sellaphora laevissima (Kützing) Mann	3
Sellaphora pseudoventralis Hustedt	2
Sellaphora pupula (Kützing) Mereschkowsky	2
Sellaphora verecundiae Lange-Bertalot	2
Stauroneis gracilis Ehrenberg	3
Stauroneis smithii Grunow	2
Staurosira binodis (Ehrenberg) Hustedt	2
Staurosira construens (Ehrenberg) Grunow	2
Staurosira venter (Ehrenberg) Hustedt	2.5
Staurosira elliptica (Schumann) Williams & Round	1
Staurosira lapponica (Grunow) Lange-Bertalot	3
Staurosira microstriata (Marciniak) Lange-Bertalot	1
Staurosira parasitoides Lange-Bertalot, Schmidt & Klee	1
Staurosira pseudoconstruens Marciniak	2
Staurosirella leptostauron var. dubia (Grunow) Hustedt	3.5
Staurosirella pinnata Ehrenberg	3
Surirella helvetica Brun	4

Table S 2: The 41 mountain lakes of the sample set of the Bavarian and Tyrolean Alps. The columns show its coordinates, geology, volume and hydrophysical data. Temperature data refer to LASWT. The last four columns are values averaged over the water column at the two sampling dates.

Lake	Latitude	Longitude	Geology	Vol.ume [100 m³]	T_{bottom}	$T_{surface}$	Secchi Depth	Mean pH	Mean Conductivity	Mean O_2
Auf der Lacke	47°12‘47“N	10°32‘15“E	Cirque	162	13.96	14.70	1.65	8.53	159.6	96.11
Bichlersee	47°40‘34“N	12°07‘21“E	Cirque	975	8.37	21.71	4.37	7.90	360.2	60.92
Brendlsee	47°21‘58“N	10°57‘30“E	Cirque	170	4.56	11.44	6.15	8.60	150.6	109.60
Nördl. Delpssee	47°30‘19“N	11°30‘36“E	Cirque	54	11.90	12.61	1.25	8.22	223.3	81.68
Südl. Delpssee	47°30‘16“N	11°30‘37“E	Cirque	39	9.28	14.05	4.15	8.85	177.2	102.19
Drachensee	47°21‘31“N	10°56‘05“E	Cirque	6332	4.94	11.85	10.25	8.59	157.7	102.36
Eissee	47°21‘12“N	10°22‘07“E	Cirque	140	6.35	10.41	3.85	8.24	192.7	100.63
Engeratsgundsee	47°26‘29“N	10°23‘30“E	Cirque	3807	4.93	14.89	15.50	8.22	235.6	77.05
Falkensee	47°44‘53“N	12°45‘59“E	Cirque	665	5.83	12.80	7.00	8.00	266.3	64.38
Ferchensee	47°26‘18“N	11°12‘50“E	Cirque	14461	7.13	21.06	6.75	8.10	304.0	5.12
Frillensee	47°45‘57“N	12°49‘03“E	Cirque	1650	14.16	18.25	4.60	8.60	224.3	129.7
Funtensee	47°29‘37“N	12°56‘22“E	Cirque	860	9.66	13.96	3.50	8.44	274.4	118.45
Oberer Gaisalpsee	47°25‘22“N	10°19‘45“E	Cirque	125	9.47	16.31	2.65	8.55	201.0	99.05
Unterer Gaisalpsee	47°45‘56“N	12°49‘03“E	Cirque	975	13.39	16.28	3.83	8.93	198.3	120.26
Grubersee	47°27‘13“N	11°47‘18“E	Cirque	231	12.16	14.06	3.15	8.57	222.4	112.03
Grünsee	47°30‘07“N	12°57‘11“E	Cirque	2040	13.28	19.57	5.00	8.53	194.5	112.01
Guggersee	47°19‘01“N	10°14‘57“E	Cirque	10	14.00	13.20	1.93	8.99	207.3	114.65
Höfersee	47°29‘51“N	10°29‘25“E	Cirque	86	14.26	15.22	1.85	8.85	220.6	122.58
Hörnlesee	47°32‘52“N	10°23‘29“E	Cirque	68	11.76	15.26	1.80	7.92	225.2	90.83
Laufbichelsee	47°26‘06“N	10°22‘35“E	Cirque	274	9.44	14.67	3.70	8.33	168.2	81.24
Lautersee	47°26‘13“N	11°14‘08“E	Cirque	14492	6.06	19.73	6.00	8.60	310.0	48.75
Mittersee	47°22‘07“N	10°51‘58“E	Cirque	1013	18.42	22.64	4.65	8.25	345.8	91.10
Rappensee	47°17‘09“N	10°15‘10“E	Cirque	1493	11.04	15.61	5.03	8.58	205.1	89.90
Röthensteiner See	47°38‘22“N	11°47‘33“E	Cirque	137	5.96	16.37	1.45	8.22	248.1	81.79
Schachensee	47°25‘27“N	11°07‘12“E	Cirque	235	15.30	18.23	3.80	8.65	167.1	113.95
Schiefersee	47°12‘55“N	10°30‘59“E	Cirque	572	7.23	13.06	3.25	8.34	164.7	100.07
Seebensee	47°22‘07“N	10°56‘05“E	Cirque	8346	6.81	13.84	6.90	8.76	165.9	114.09
Seeleinsee	47°32‘16“N	13°01‘47“E	Cirque	242	12.53	13.88	5.35	8.71	134.2	107.42
Mittlerer Seewisee	47°11‘42“N	10°29‘26“E	Cirque	130	10.55	11.48	4.05	8.67	137.8	92.50
Oberer Seewisee	47°11‘30“N	10°29‘09“E	Cirque	1111	5.46	12.85	5.75	8.59	121.4	96.17
Unt. Seewisee	47°11‘53“N	10°28‘54“E	Cirque	228	16.14	17.01	1.35	8.82	208.6	96.91
Großer Sieglsee	47°24‘30“N	10°29‘46“E	Doline	1023	5.76	10.80	9.50	8.12	536.7	89.39
Kleiner Sieglsee	47°24‘31“N	10°29‘41“E	Doline	94	7.41	8.82	11.25	8.22	382.4	90.49
Östl. Soiernsee	47°29‘27“N	11°21‘01“E	Cirque	1298	7.46	16.42	4.50	8.77	177.7	112.00
Westl. Soiernsee	47°29‘32“N	11°20‘44“E	Cirque	2068	5.35	13.44	4.15	8.15	251.8	98.67
Soinsee (Nord)	47°42‘11“N	12°01‘42“E	Cirque	96	7.28	15.04	3.17	8.29	222.1	101.06
Soinsee (Süd)	47°39‘01“N	11°57‘20“E	Cirque	2980	7.77	16.54	7.00	8.34	204.2	73.40
Suttersee	47°38‘50“N	11°50‘19“E	Cirque	93	14.06	17.47	1.50	8.03	280.7	93.83
Taubensee	47°41‘46“N	12°25‘37“E	Cirque	3066	5.02	20.97	4.33	7.96	246.8	47.28
Wildensee	47°27‘26“N	11°14‘18“E	Cirque	433	20.89	21.18	2.35	8.57	296.8	122.22
Ziereiner See	47°27’52“N	11°48’45“E	Cirque	3842	5.41	15.08	5.00	8.20	219.8	70.81

Table S 3: Hydrochemical data of the 41 mountain lakes of the sample set of the Bavarian and Tyrolean Alps.

Lake	**NO_3–N** [mg L^{-1}]	**NH_4–N** [µg L^{-1}]	**TP** [µg L^{-1}]	**SiO_2** [mg L^{-1}]	**Na^+** [mg L^{-1}]	**Ca^{2+}** [mg L^{-1}]	**Mg^{2+}** [mg L^{-1}]
Auf der Lacke	0.15	30.32	0.83	0.13	0.32	19.36	9.16
Bichlersee	0.76	32.27	4.26	0.77	0.30	49.24	14.70
Brendlsee	0.37	13.95	6.62	0.12	0.10	26.67	2.82
Nördlicher Delpssee	0.37	15.12	5.68	0.38	0.39	35.14	2.78
Südlicher Delpssee	0.45	16.65	4.61	0.23	0.22	40.55	5.02
Drachensee	0.30	19.57	3.96	0.19	0.10	26.75	3.12
Eissee	0.24	23.30	1.06	0.21	0.36	16.02	3.57
Engeratsgundsee	0.04	27.02	4.73	0.59	0.31	19.82	7.23
Falkensee	1.84	16.98	9.05	0.18	2.11	42.29	6.66
Ferchensee	0.33	43.00	10.12	0.21	0.10	47.22	18.09
Frillensee	0.93	83.68	7.22	0.15	0.48	39.62	5.38
Funtensee	0.03	44.26	10.32	0.13	0.00	31.30	4.31
Oberer Gaisalpsee	0.15	25.29	3.73	0.24	0.18	14.59	6.98
Unterer Gaisalpsee	0.25	9.60	12.01	0.29	0.18	16.42	10.14
Grubersee	0.00	17.79	17.03	0.15	0.18	37.93	2.64
Grünsee	0.20	60.84	8.34	0.13	0.10	26.47	1.42
Guggersee	0.29	10.59	4.61	0.23	0.86	14.97	10.30
Höfersee	0.47	5.26	3.08	0.14	0.14	20.74	10.06
Hörnlesee	0.34	20.36	17.30	0.21	0.37	24.72	1.01
Laufbichelsee	0.13	24.86	3.84	0.22	0.19	12.44	6.30
Lautersee	0.21	50.80	13.50	0.25	0.10	46.06	15.95
Mittersee	0.10	33.96	7.45	0.13	1.23	38.46	18.40
Rappensee	0.04	15.88	9.17	0.17	0.23	21.24	9.31
Röthensteiner See	2.86	78.15	20.41	0.18	0.86	28.92	3.17
Schachensee	0.49	19.81	7.22	0.17	0.00	27.06	4.89
Schiefersee	0.34	45.68	0.10	0.14	0.29	19.78	10.06
Seebensee	0.52	23.26	4.47	0.14	0.14	26.95	4.35
Seeleinsee	0.59	31.53	7.87	0.12	0.00	23.83	0.98
Mittlerer Seewisee	0.20	67.81	1.54	0.13	0.14	17.63	9.92
Oberer Seewisee	0.11	67.91	7.28	0.18	0.23	15.40	5.54
Unterer Seewisee	0.07	21.42	2.48	0.25	0.99	19.83	9.14
Großer Sieglsee	0.55	3.84	0.10	0.24	0.51	39.14	11.81
Kleiner Sieglsee	0.56	99.44	0.47	0.23	0.36	38.63	10.77
Östlicher Soiernsee	0.61	49.32	3.90	0.18	0.00	31.09	6.62
Westllicher Soiernsee	0.77	13.94	10.82	0.24	0.37	36.31	6.79
Soinsee (Nord)	0.61	13.40	7.93	0.27	0.33	29.76	3.92
Soinsee (Süd)	0.36	82.87	4.50	0.16	0.10	30.24	6.34
Suttersee	0.67	60.85	4.79	0.76	1.62	41.17	6.67
Taubensee	0.66	126.85	4.44	0.20	0.49	40.40	4.12
Wildensee	0.22	53.59	8.64	0.19	0.35	31.55	19.47
Ziereiner See	0.14	26.68	7.63	0.15	0.00	22.49	1.62

Table S 4: Spearman rank correlation matrix between the mean silicification values, mean diatom sizes of surface sediment samples and environmental variables. The upper right triangle shows the p-values with (bottom line) and without (upper line) Bonferroni corre

	Mean SiVa	Valve Size	Altitude	Area	Depth	Volume	Secchi depth	Temp (bot) ^{1}	Temp (surf) ^{1}	TP	NO3-N	NH4-N	Silicate	Na	Ca	Mg	pH*	O2*	Cond*
Mean SiVa		0.331 1	0.001 0.187	0.437 1	0.321 1	0.614 1	0.154 1	0.036 1	0.000 0.036	0.064 1	0.346 1	0.067 1	0.456 1	0.649 1	0.069 1	0.199 1	0.894 1	0.951 1	0.286 1
Valve Size	0.160		0.313 1	0.682 1	0.861 1	0.898 1	0.460 1	0.541 1	0.473 1	0.950 1	0.911 1	0.964 1	0.796 1	0.374 1	0.693 1	0.426 1	0.514 1	0.480 1	0.276 1
Altitude	0.503	0.166		0.325 1	0.220 1	0.264 1	0.**503** 1	0.893 1	0.009 1	0.299 1	0.002 0.403	0.231 1	0.038 1	0.017 1	0.000 0.000	0.137 1	0.025 1	0.240 1	0.000 0.002
Area	-0.128	0.068	-0.162		0.000 0.033	0.000 0.000	0.113 1	0.179 1	0.029 1	0.367 1	0.382 1	0.428 1	0.930 1	0.237 1	0.275 1	0.233 1	0.530 1	0.054 1	0.860 1
Depth	0.163	-0.029	-0.201	0.562		0.000 0	0.000 0.000	0.000 0	0.442 1	0.631 1	0.482 1	0.379 1	0.784 1	0.861 1	0.084 1	0.827 1	0.102 1	0.001 0.206	0.044 1
Volume	-0.083	0.021	-0.183	0.945	0.674		0.014 1	0.025 1	0.248 1	0.450 1	0.498 1	0.612 1	0.975 1	0.201 1	0.154 1	0.413 1	0.650 1	0.031 1	0.684 1
Secchi depth	0.233	-0.122	-0.111	0.258	0.804	0.390		0.000 0.026	0.009 1	0.128 1	0.764 1	0.453 1	0.971 1	0.399 1	0.235 1	0.866 1	0.434 1	0.186 1	0.082 1
Temp (bot)	-0.336	0.101	-0.022	-0.220	-0.687	-0.359	-0.570		0.009 1	0.787 1	0.163 1	0.557 1	0.977 1	0.708 1	0.379 1	0.104 1	0.010 1	0.001 0.106	0.549 1
Temp (surf)	-0.560	0.118	-0.414	0.350	-0.127	0.190	-0.414	0.411		0.084 1	0.592 1	0.062 1	0.231 1	0.973 1	0.059 1	0.115 1	0.933 1	0.427 1	0.703 1
TP	-0.299	-0.010	-0.171	0.149	-0.079	0.125	-0.248	0.045	0.280		0.029 1	0.868 1	0.522 1	0.812 1	0.256 1	0.128 1	0.624 1	0.929 1	0.921 1
NO3-N	-0.155	-0.018	-0.473	-0.144	0.116	-0.112	-0.050	-0.228	0.088	0.349		0.160 1	0.818 1	0.001 0.094	0.021 1	0.477 1	0.044 1	0.228 1	0.216 1
NH4-N	-0.296	-0.007	-0.196	0.131	0.145	0.084	0.124	-0.097	0.302	-0.028	0.229		0.807 1	0.837 1	0.112 1	0.824 1	0.149 1	0.089 1	0.675 1
Silicate	-0.123	0.043	-0.334	0.015	0.045	-0.005	-0.006	-0.005	0.196	-0.106	0.038	-0.040		0.037 1	0.039 1	0.120 1	0.006 1	0.036 1	0.021 1
Na	0.075	0.146	-0.380	-0.194	-0.029	-0.209	-0.139	0.062	-0.006	0.039	0.528	0.034	0.335		0.098 1	0.571 1	0.028 1	0.139 1	0.094 1
Ca	-0.295	-0.065	-0.734	0.179	0.280	0.233	0.195	-0.145	0.305	0.186	0.368	0.259	0.332	0.269		0.353 1	0.008 1	0.038 1	0.000 0.008
Mg	-0.210	0.131	-0.243	0.195	0.036	0.135	0.028	0.264	0.256	-0.248	-0.117	0.037	0.253	0.093	0.153		0.487 1	0.543 1	0.003 0.498
pH*	0.022	0.108	0.359	0.104	-0.266	0.075	-0.129	0.409	-0.014	-0.081	-0.325	-0.236	-0.431	-0.352	-0.418	0.115		0.000 0.002	0.002 0.266
O2*	0.010	-0.117	0.193	-0.311	-0.500	-0.347	-0.216	0.524	-0.131	-0.015	-0.198	-0.276	-0.336	-0.241	-0.334	-0.100	0.636		0.061 1
Cond*	-0.175	0.179	-0.636	0.029	0.324	0.067	0.282	-0.099	0.063	-0.016	0.203	0.069	0.369	0.272	0.603	0.464	-0.490	-0.302	

Table S 5: Diatom group assignments.

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 copulate* *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 & 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	*G. 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	*P. 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*

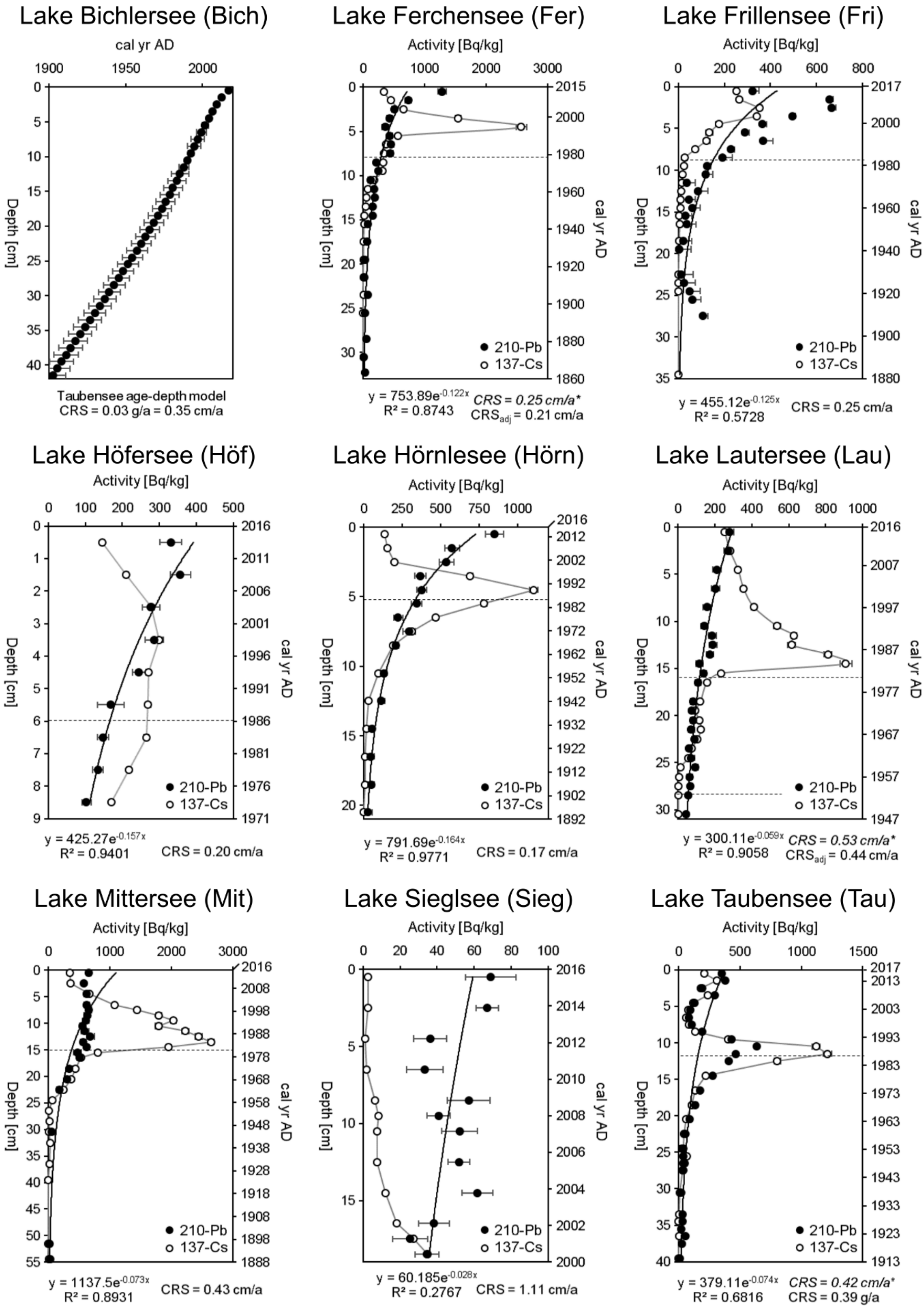

Figure S 1: Age-depth models of montane Bavarian mountain lakes. Pb210 (black) and Cs137 activities (black circles, grey line) are given with sediment depth (left axis) and assigned calibrated year AD (right axis). Dotted line: 1986 (Chernobyl disaster) as inferred by Pb210 decay curve (formula at bottom left), a 2nd dotted line represents 1962 (nuclear weapon testing) if necessary. Bottom right: sedimentation rate (CRS model). A second adjusted sedimentation rate is shown if lead model was doubtful as indicated by an asterisk (*). 'Cumulative dry weight model' (g a–1) of L. Taubensee was better than 'cm a–1 model' and applied to L. Bichlersee.

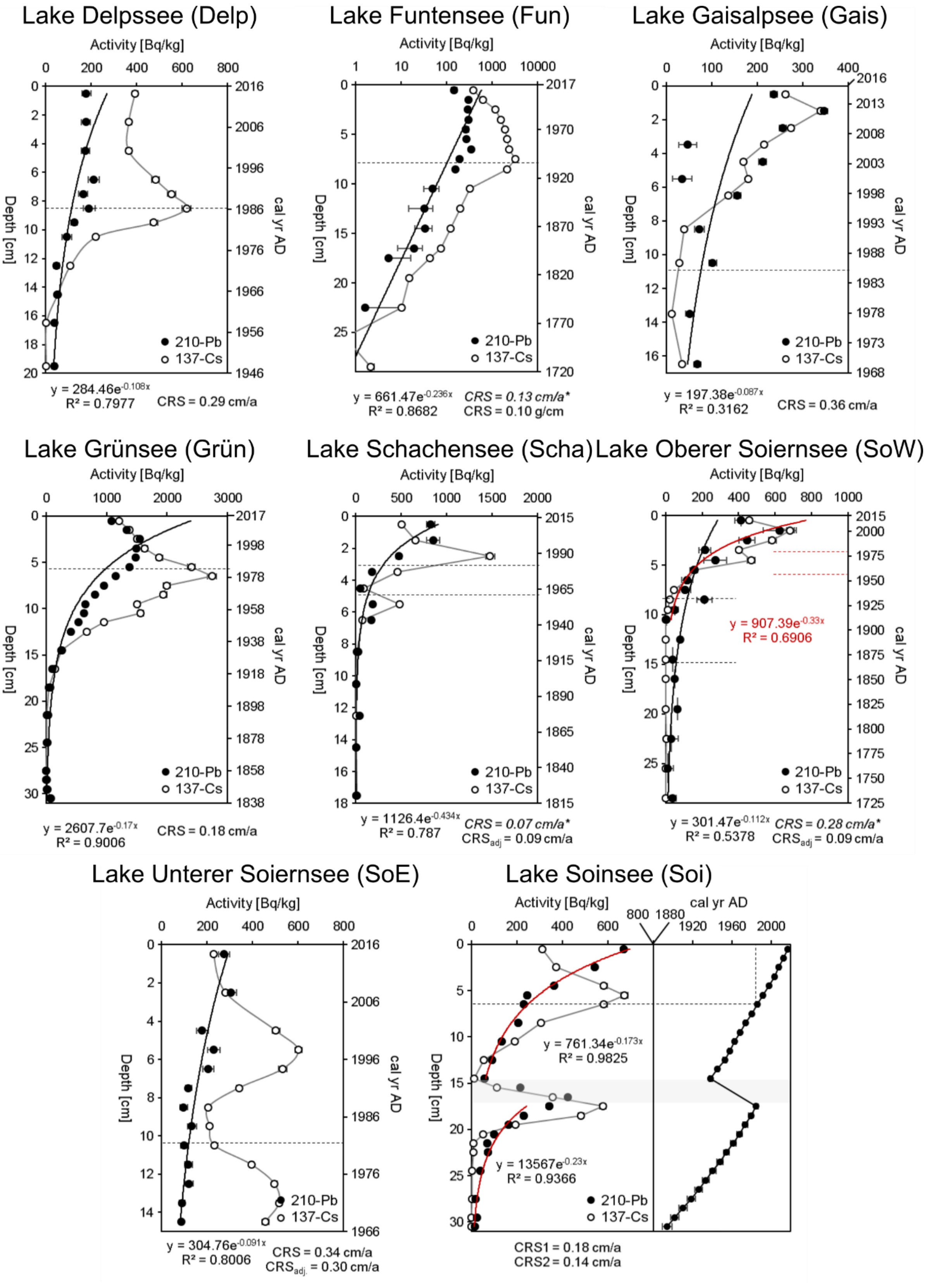

Figure S 2: Age-depth models of subalpine Bavarian mountain lakes. Pb210 (black) and Cs137 activities (black circles, grey line) are given with sediment depth (left axis) and assigned calibrated year AD (right axis). For a detailed description, see Fig. 1. 'Cumulative dry weight model' (g a–1) of L. Funtensee was better than 'cm a–1 model'. For L. Oberer Soiernsee two lead models were calculated. L. Soinsee revealed a repetition with a slumping layer (grey area): two separate sedimentation rates are shown for the two core halves with an extra age model (right graph).

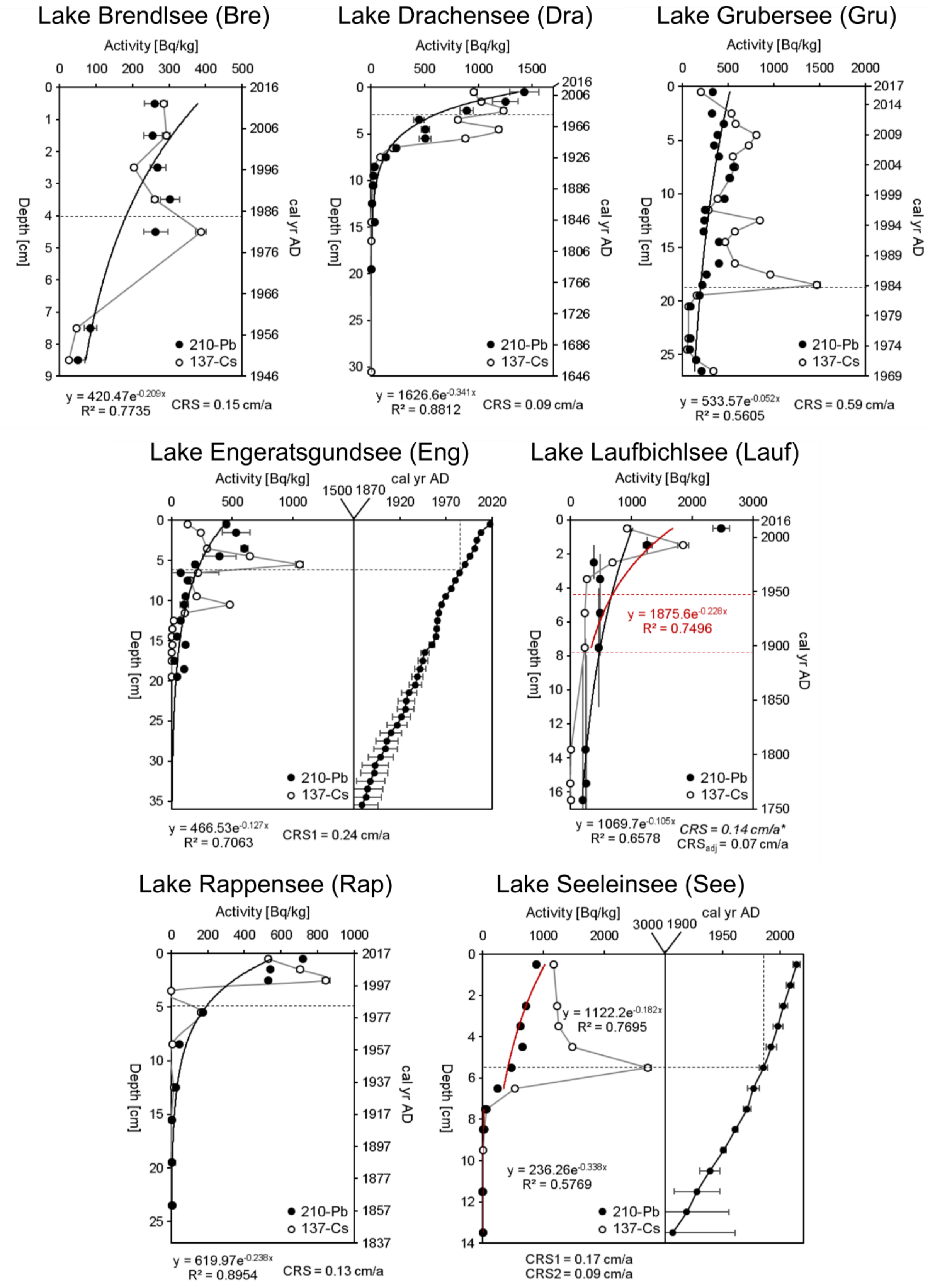

Figure S 3: Age-depth models of alpine Bavarian mountain lakes. Pb210 (black) and Cs137 activities (black circles, grey line) are given with sediment depth (left axis) and assigned calibrated year AD (right axis). For a detailed description, see Fig. 1. For L. Laufbichlsee two lead models were calculated (black and red), but the more reliable adjusted CRS model referred to Cs137 data. In L. Seeleinsee, sedimentation rate changed and two models were applied. An extra age model was added for L. Engeratsgundsee and L. Seeleinsee (right graph).

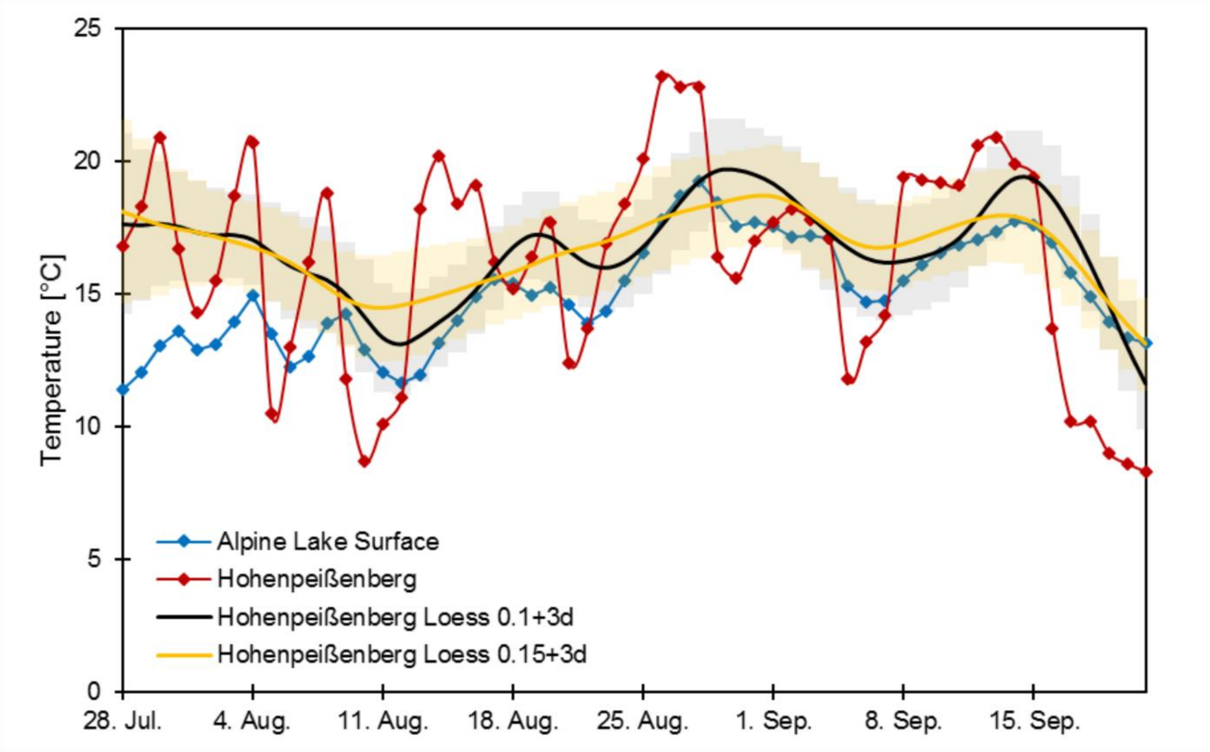

Figure S 4: Comparison between LASWT of L. Engeratsgundsee (blue) and air temperatures of Hohenpeißenberg weather observatory (daily averages, red line). The black and yellow line represent the Loess smoothed Hohenpeißenberg data with a delay of 3 days with smoothing factor 0.1 and 0.15, respectively. The latter resembles alpine lake conditions the most.

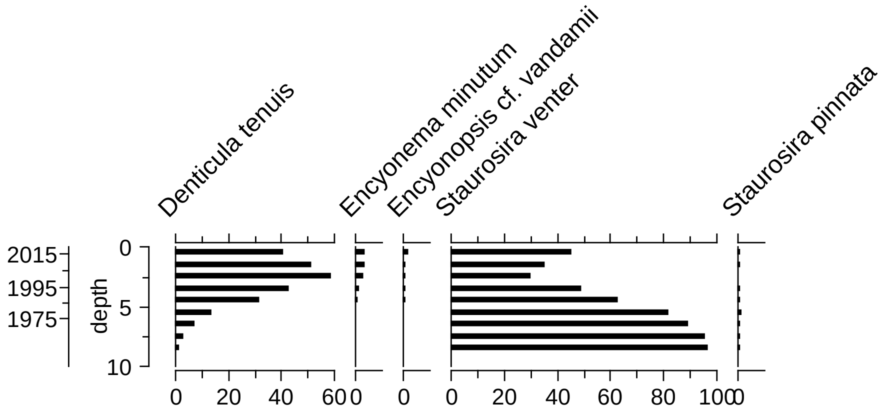

Figure S 5: Stratigraphy of the subfossil diatom assemblages in the alpine lake Brendlsee (1903 m). The left axis represents the age of the sediment layers, the second y axis the sediment depth. Black bars illustrate percentages of the diatom assemblages. Diatoms are ordered from planktic (if apparent) to non-planktic, each in alphabetical order. The sum axis on the right (if apparent) shows the sum of counted diatoms in this sample.

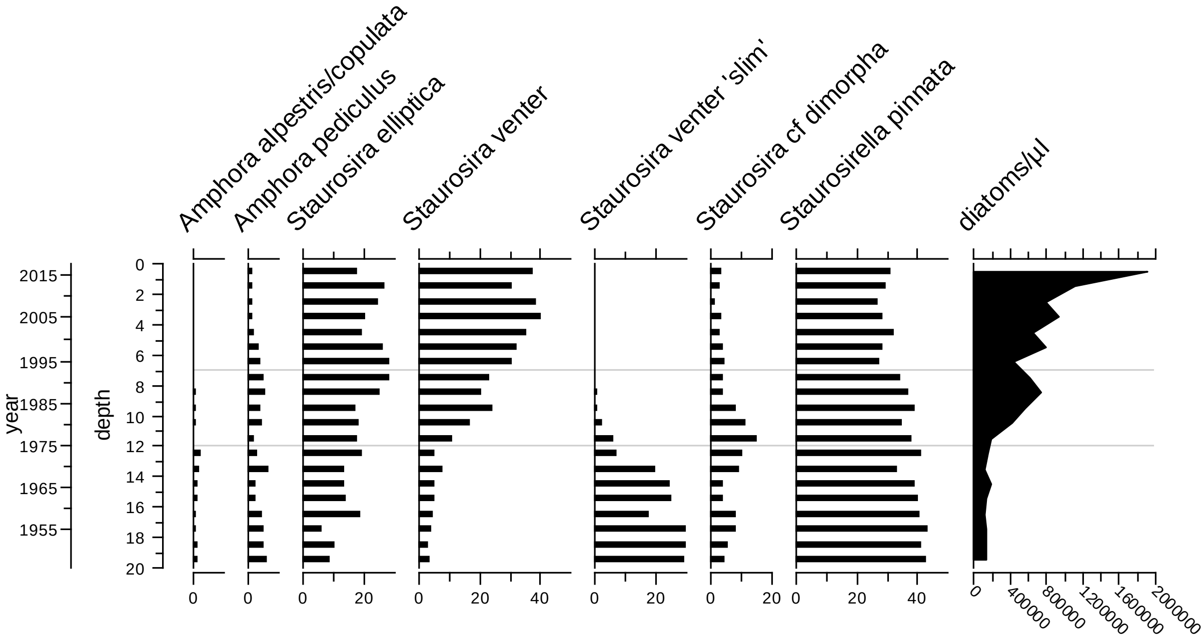

Figure S 6: Stratigraphy of the diatom assemblages in the subalpine lake Delpssee (N) (1600 m). For further explanation, see Fig. S 5.

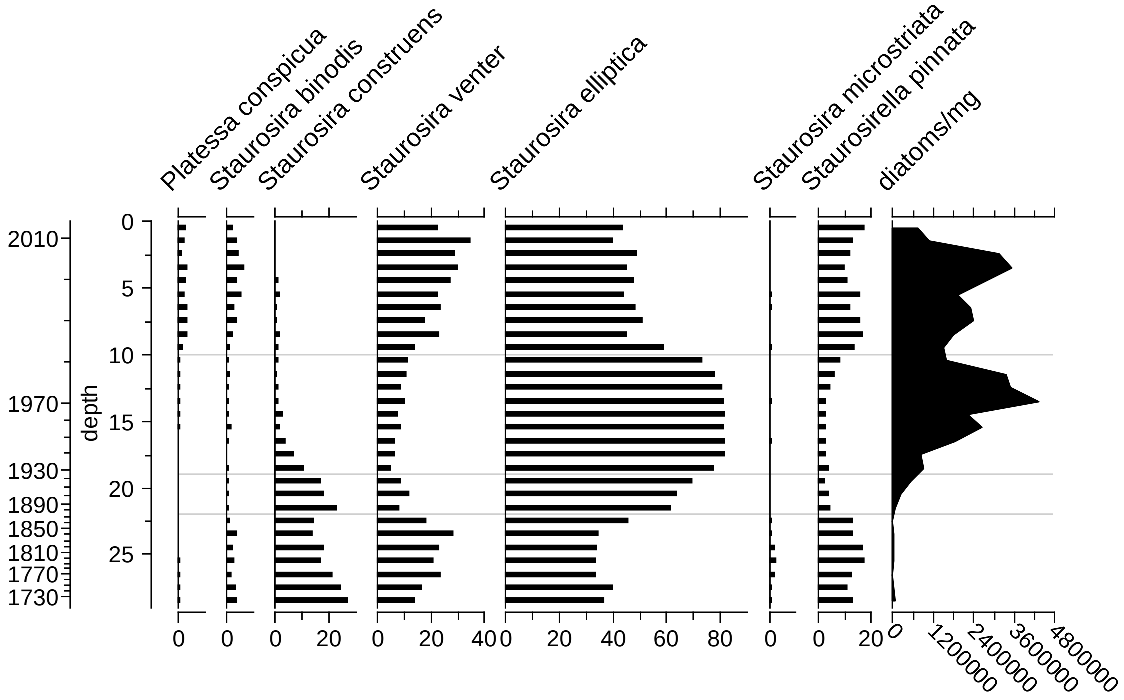

Figure S 7: Stratigraphy of the diatom assemblages in the subalpine lake Funtensee (1601 m). For further explanation, see Fig. S 5.

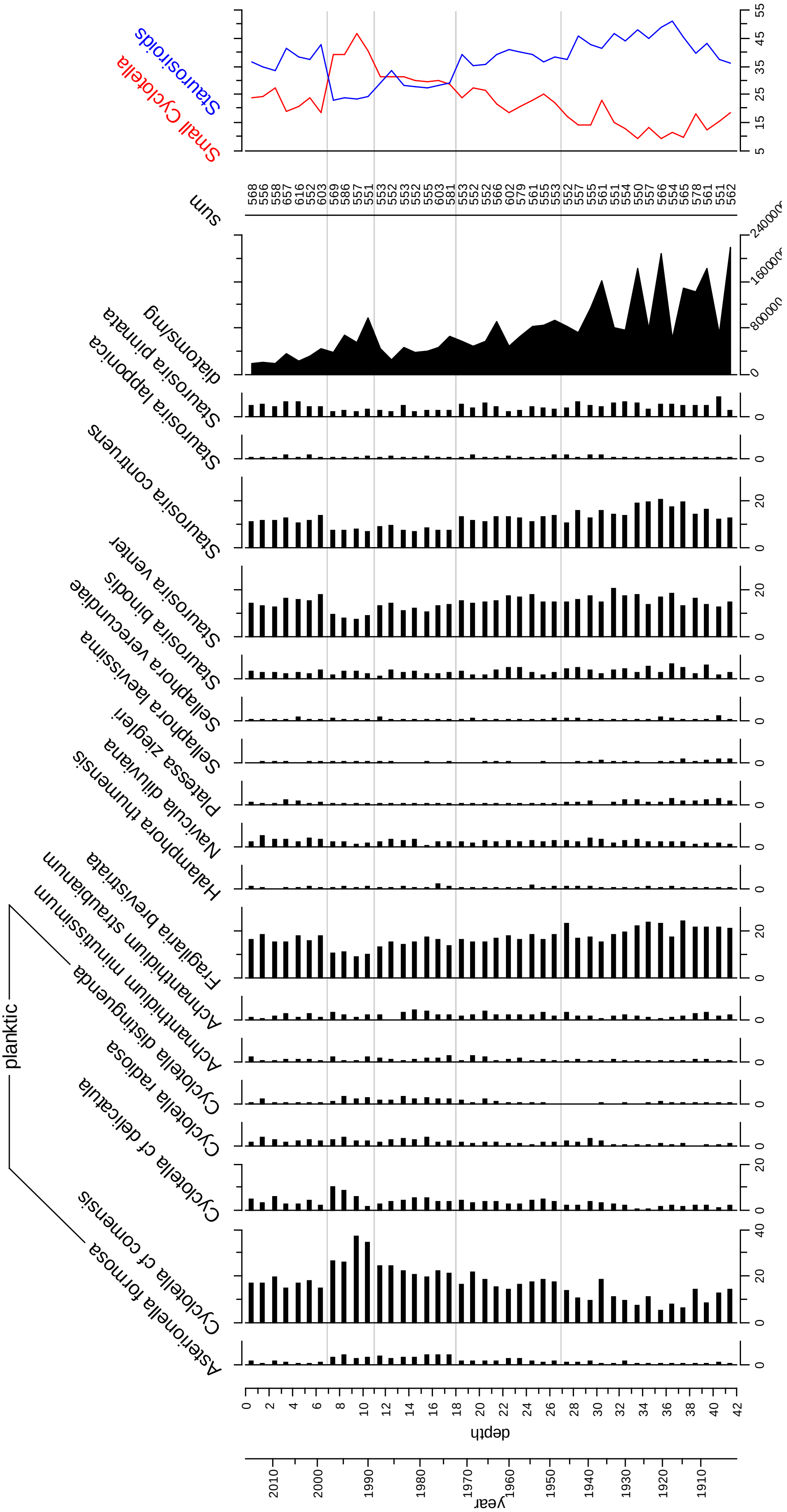

Figure S 8: Stratigraphy of the diatom assemblages in the montane lake Bichlersee (955 m). For further explanation, see Fig. S 5.

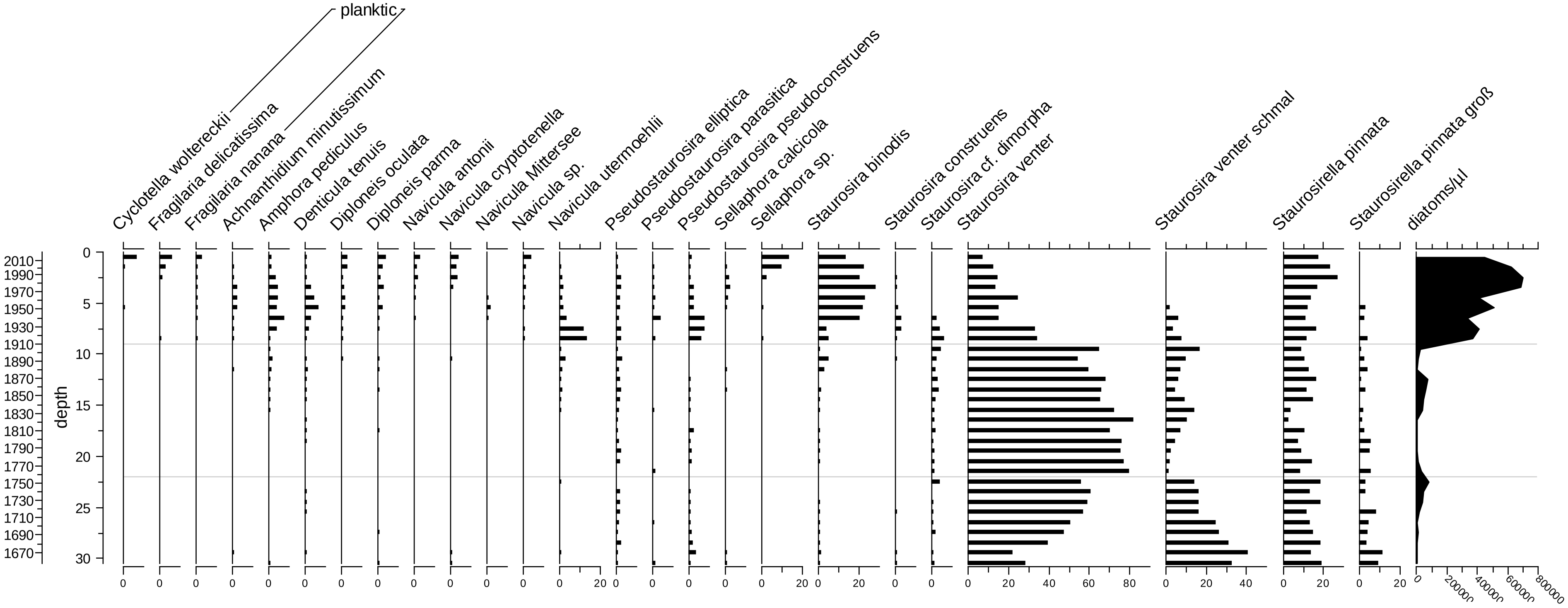

Figure S 9: Stratigraphy of the diatom assemblages in the alpine lake Drachensee (1874 m). For further explanation, see Fig. S 5.

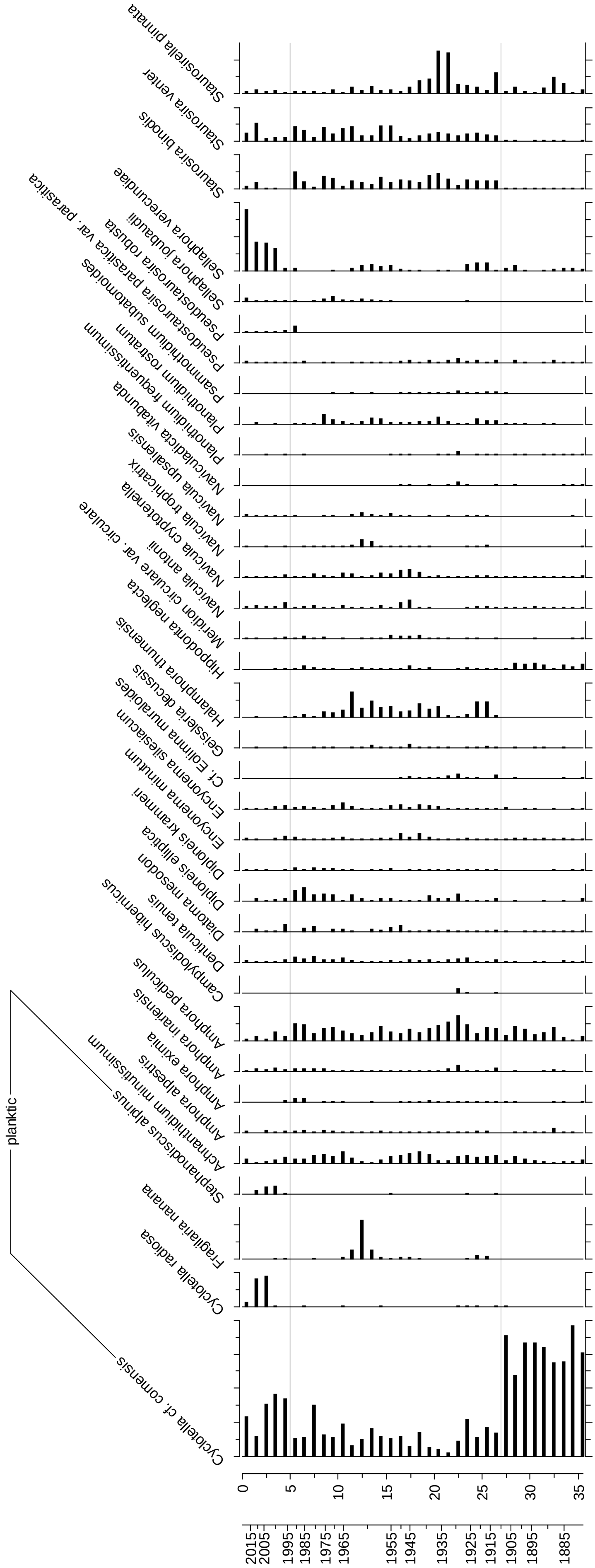

Figure S 10: Stratigraphy of the diatom assemblages in the alpine lake Engeratsgundsee (1876 m). For further explanation, see Fig. S 5.

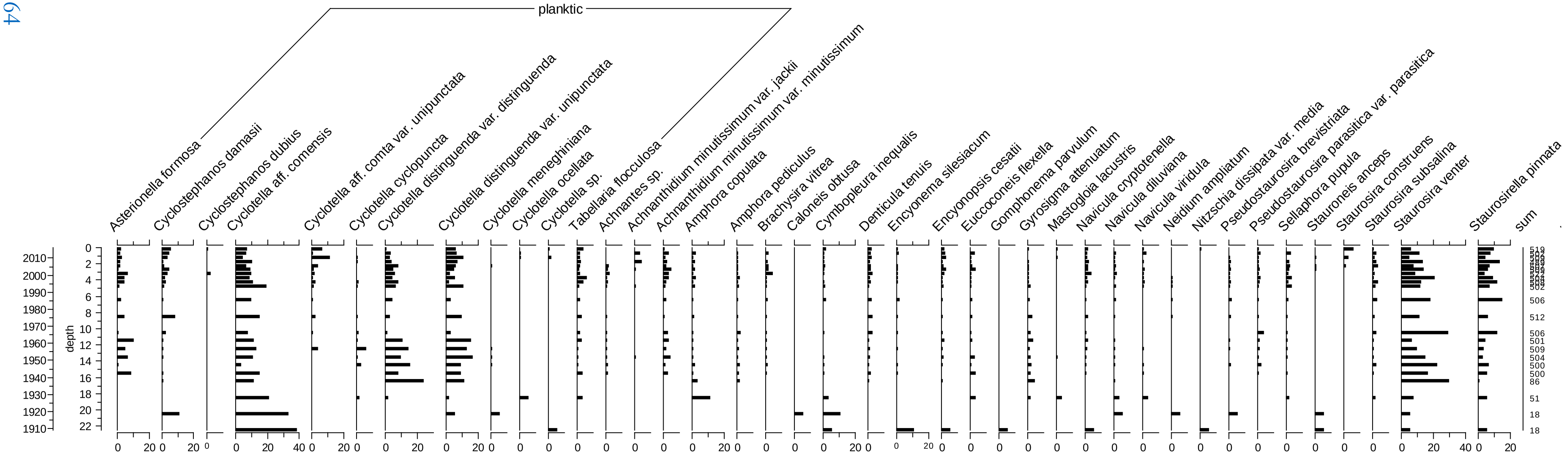

Figure S 12: Stratigraphy of the diatom assemblages in the montane lake Ferchensee (1060 m). For further explanation, see Fig. S 5.

Figure S 11: Stratigraphy of the diatom assemblages in the subalpine lake Hörnlesee (1601 m). For further explanation, see Fig. S 5.

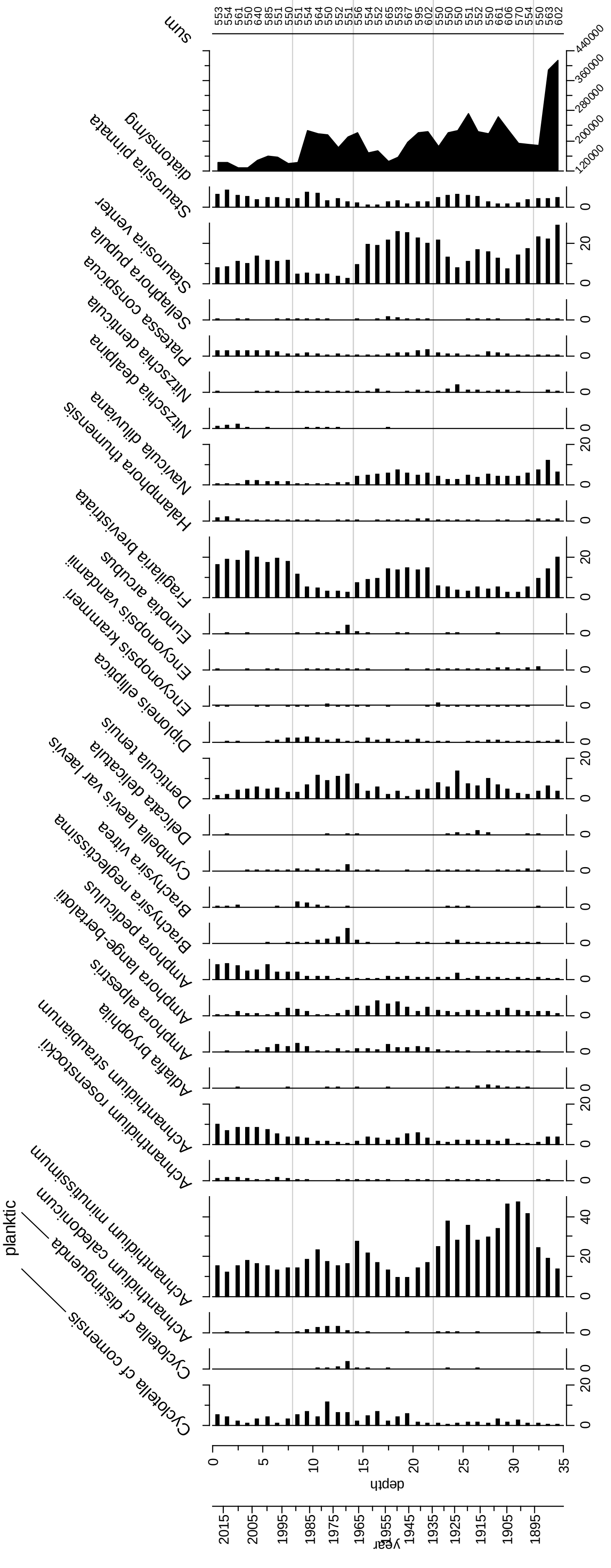

Figure S 13: Stratigraphy of the diatom assemblages in the montane lake Frillensee (973 m). For further explanation, see Fig. S 5.

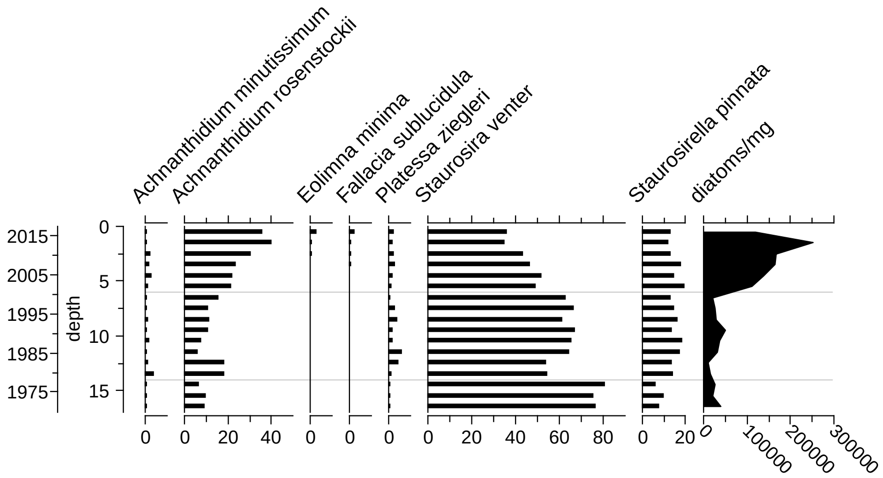

Figure S 14: Stratigraphy of the diatom assemblages in the subalpine lake Gaisalpsee (1508 m). For further explanation, see Fig. S 5.

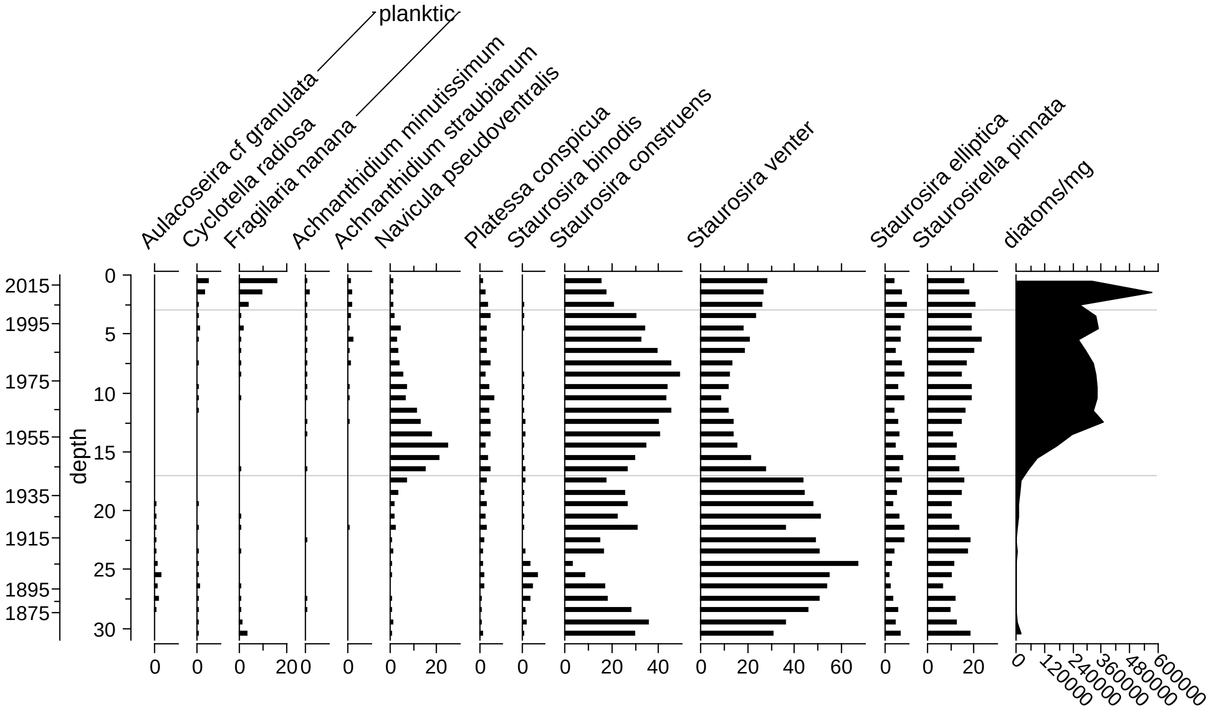

Figure S 15: Stratigraphy of the diatom assemblages in the subalpine lake Grünsee (1474 m). For further explanation, see Fig. S 5.

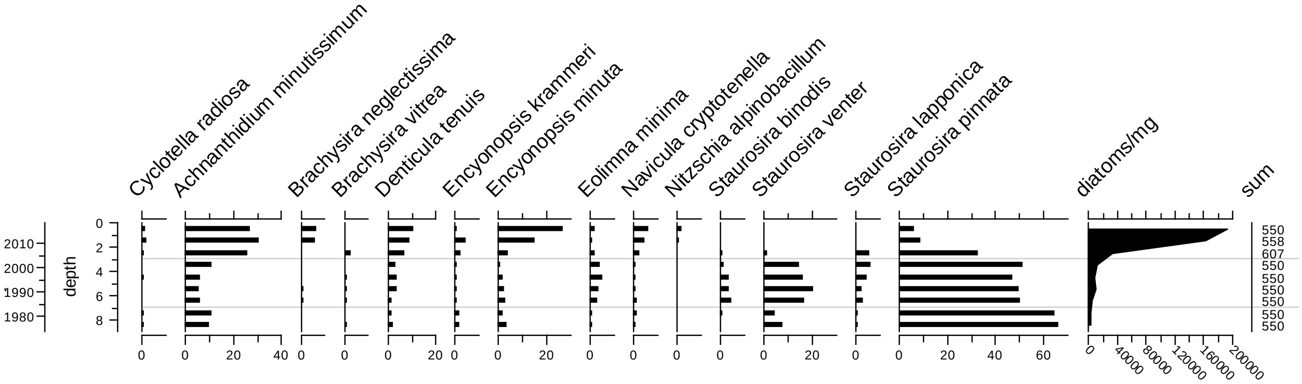

Figure S 16: Stratigraphy of the diatom assemblages in the montane lake Höfersee (1192 m). For further explanation, see Fig. S 5.

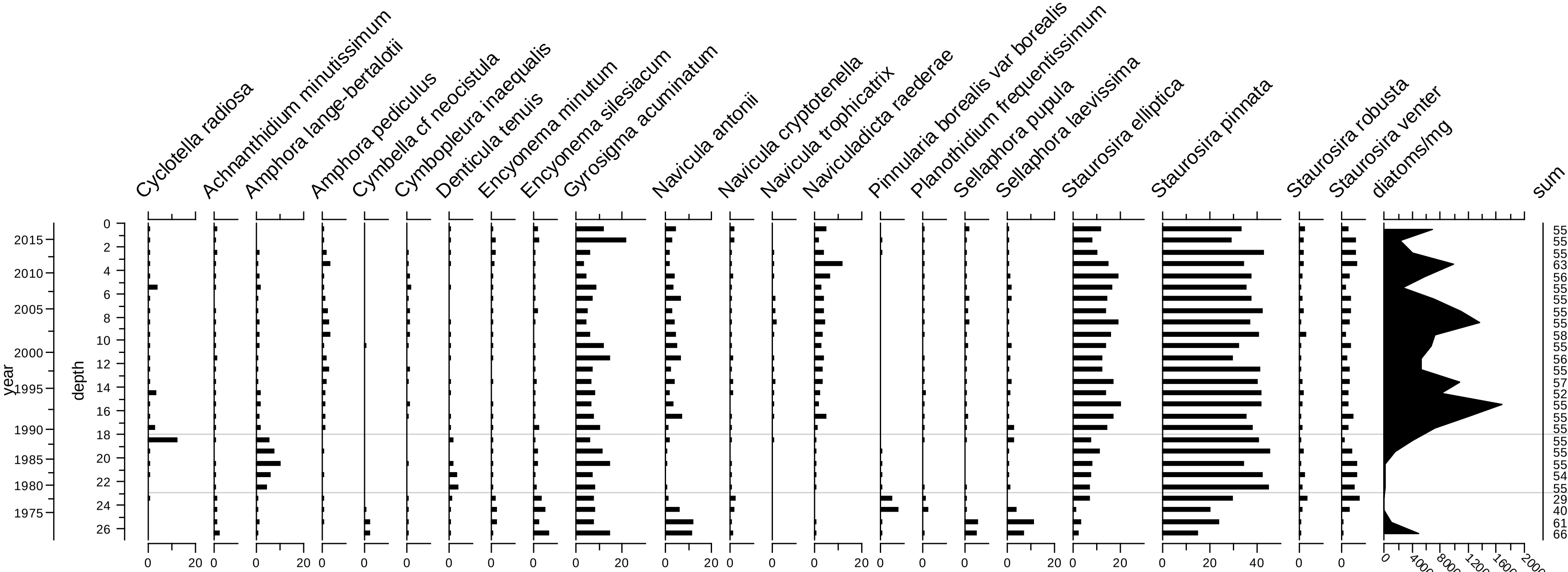

Figure S 18: Stratigraphy of the diatom assemblages in the alpine lake Grubersee (2060 m). For further explanation, see Fig. S 5.

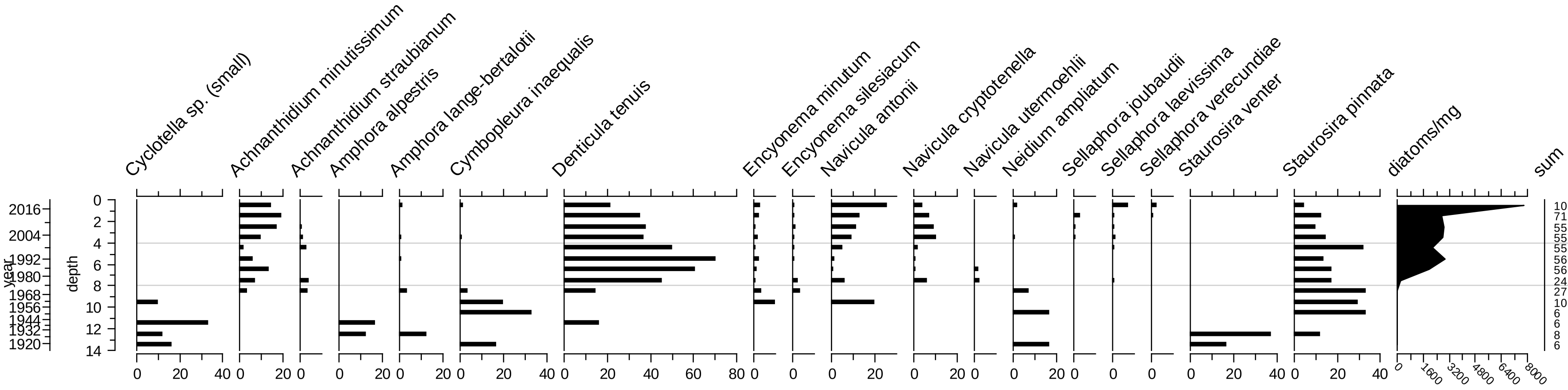

Figure S 17: Stratigraphy of the diatom assemblages in the alpine lake Seeleinsee (1809 m). For further explanation, see Fig. S 5.

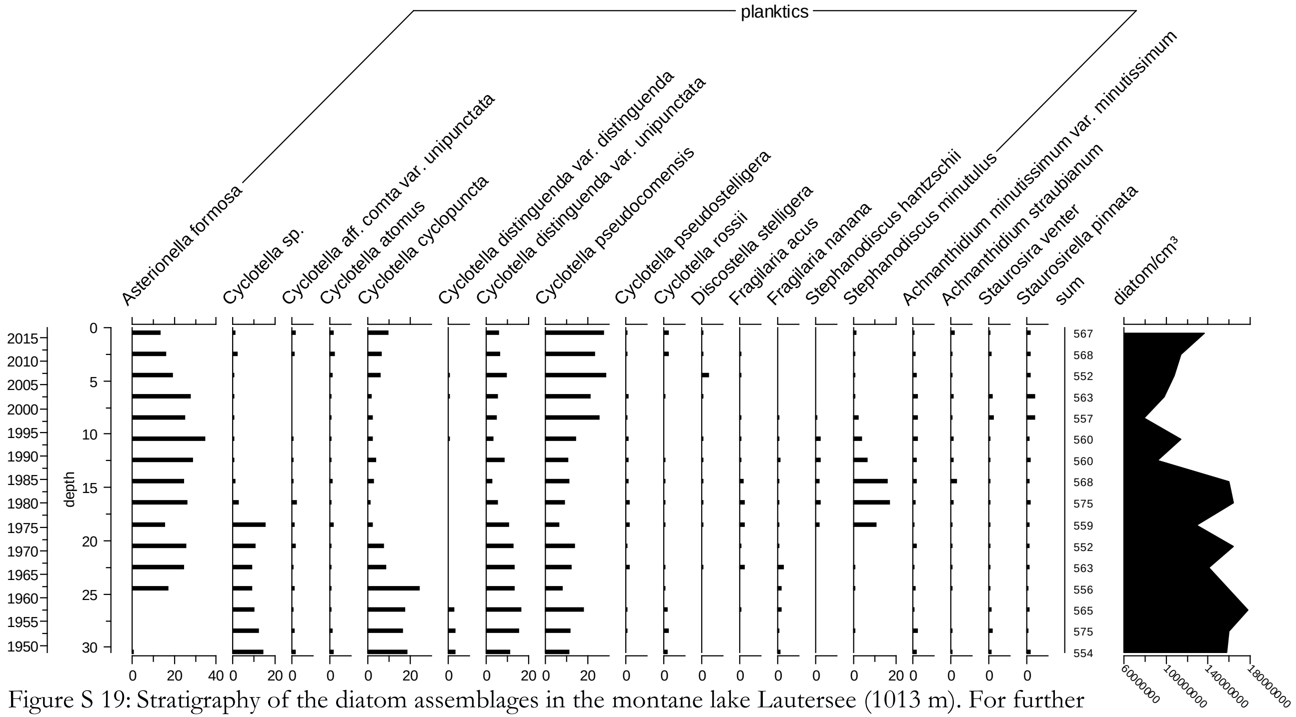

Figure S 19: Stratigraphy of the diatom assemblages in the montane lake Lautersee (1013 m). For further explanation, see Fig. S 5.

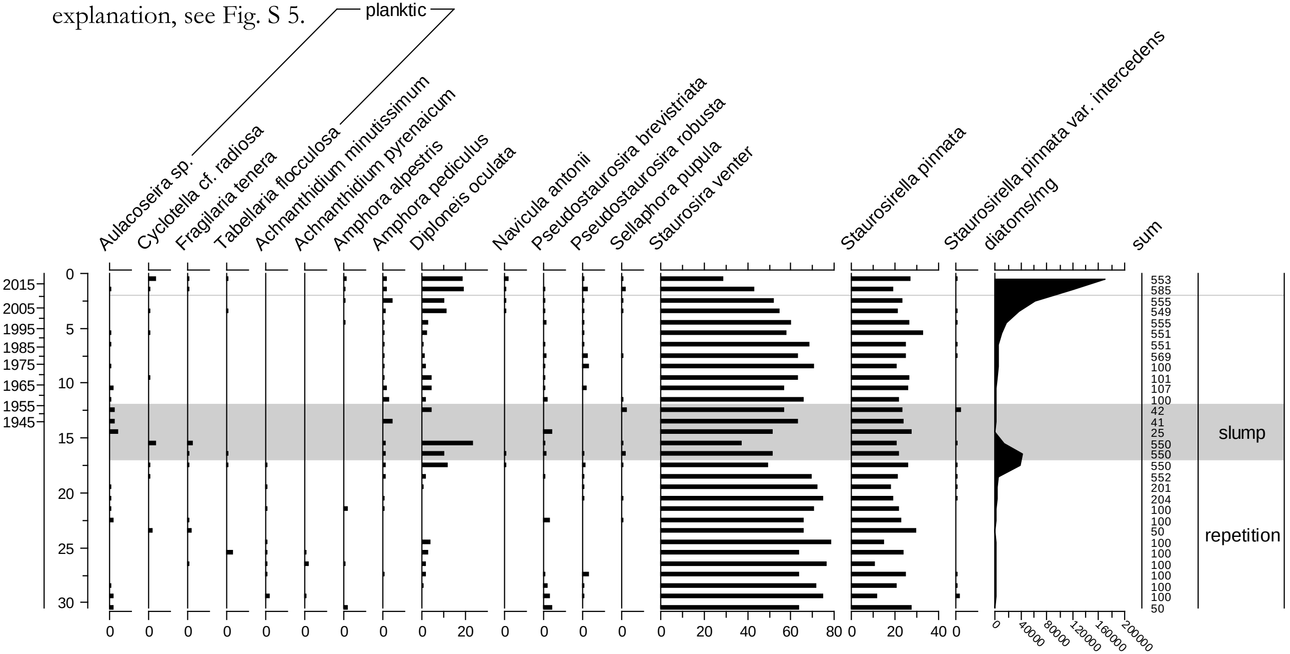

Figure S 20: Stratigraphy of the diatom assemblages in the subalpine lake Soinsee (1458 m). For further explanation, see Fig. S 5.

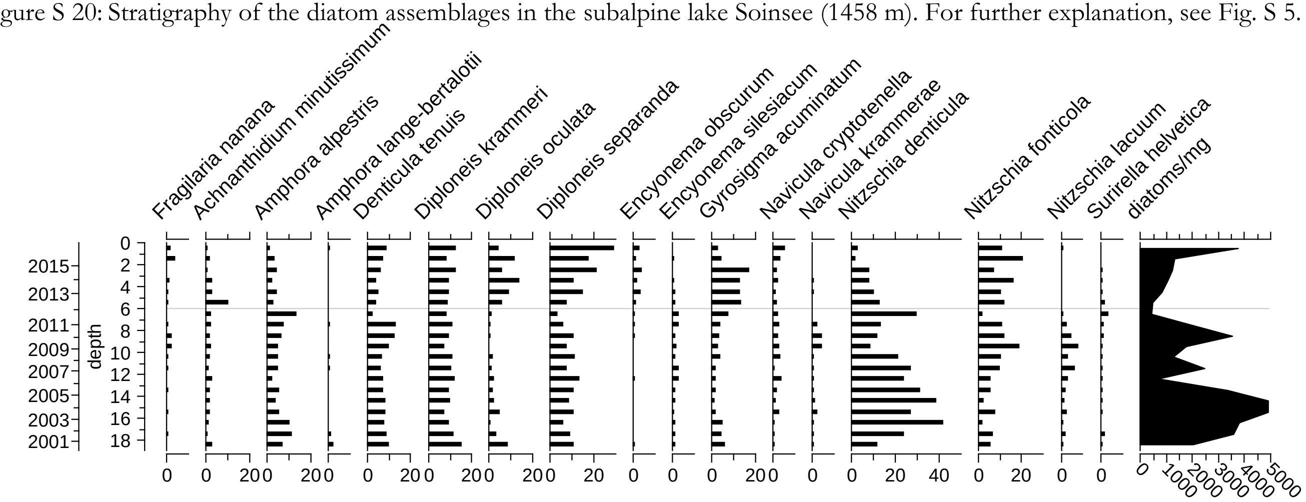

Figure S 21: Diatom stratigraphy in the montane lake Sieglsee (1207 m). For further explanation, see Fig. S 5.

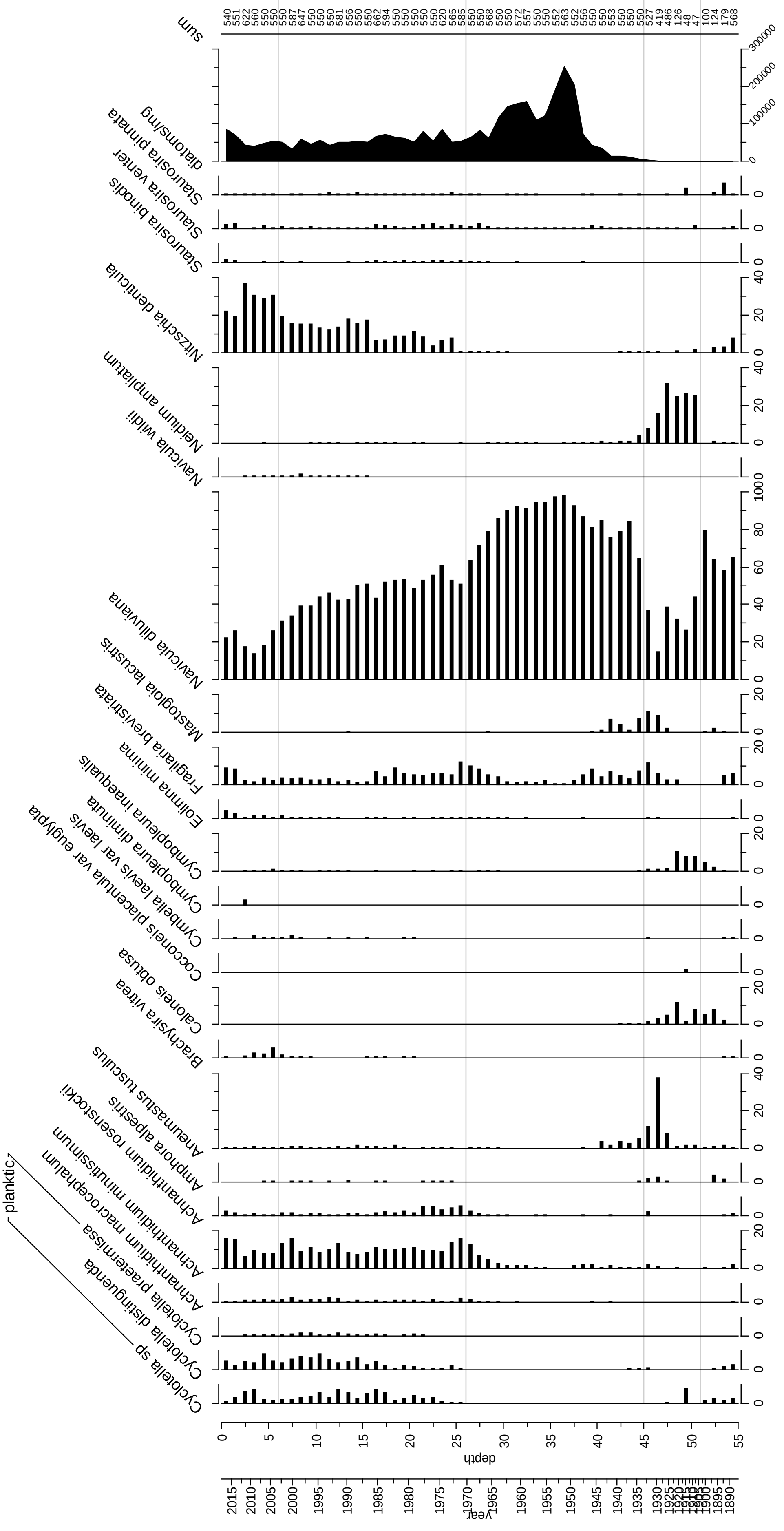

Figure S 22: Stratigraphy of the diatom assemblages in the montane lake Mittersee (1082 m). For further explanation, see Fig. S 5.

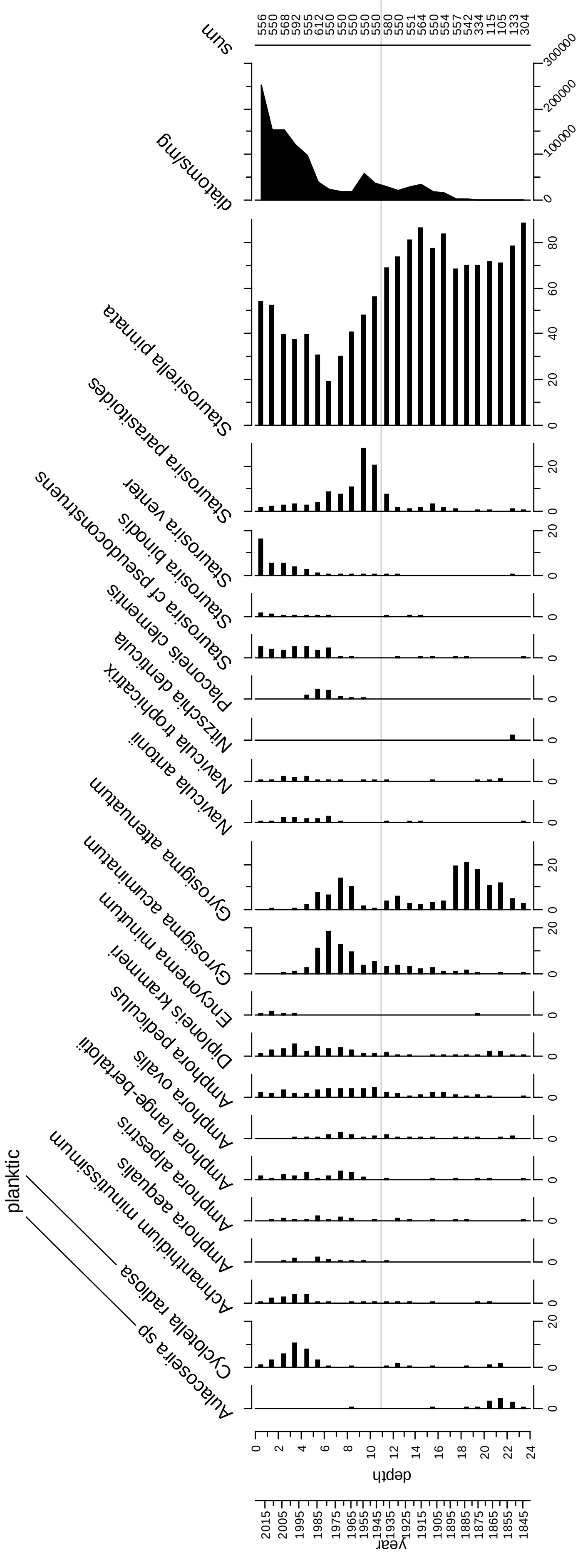

Figure S 23: Stratigraphy of the diatom assemblages in the alpine lake Rappensee (2047 m). For further explanation, see Fig. S 5.

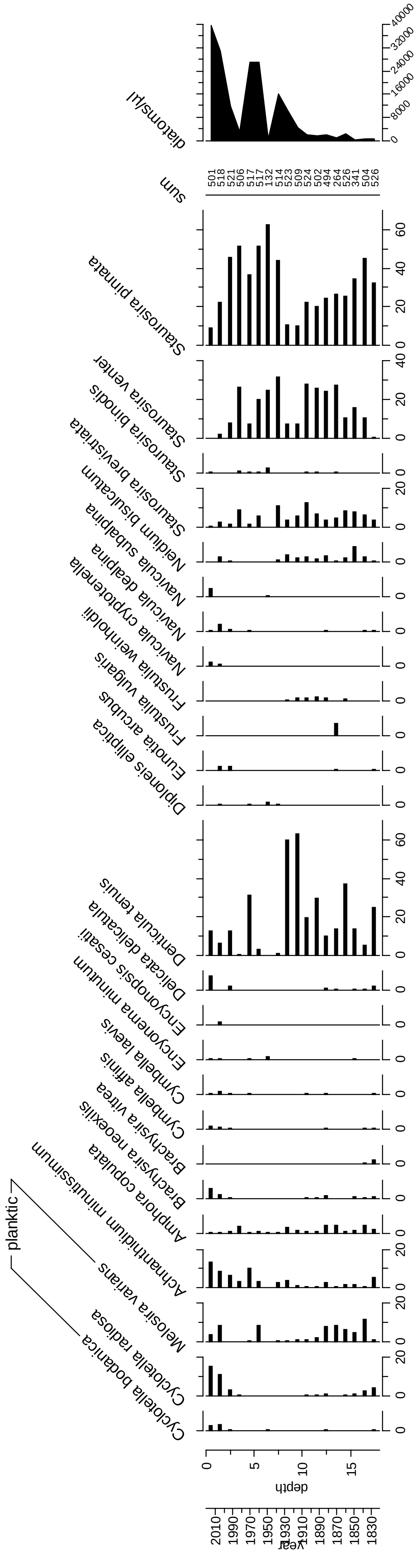

Figure S 24: Stratigraphy of the diatom assemblages in the subalpine lake Schachensee (1680 m). For further explanation, see Fig. S 5.

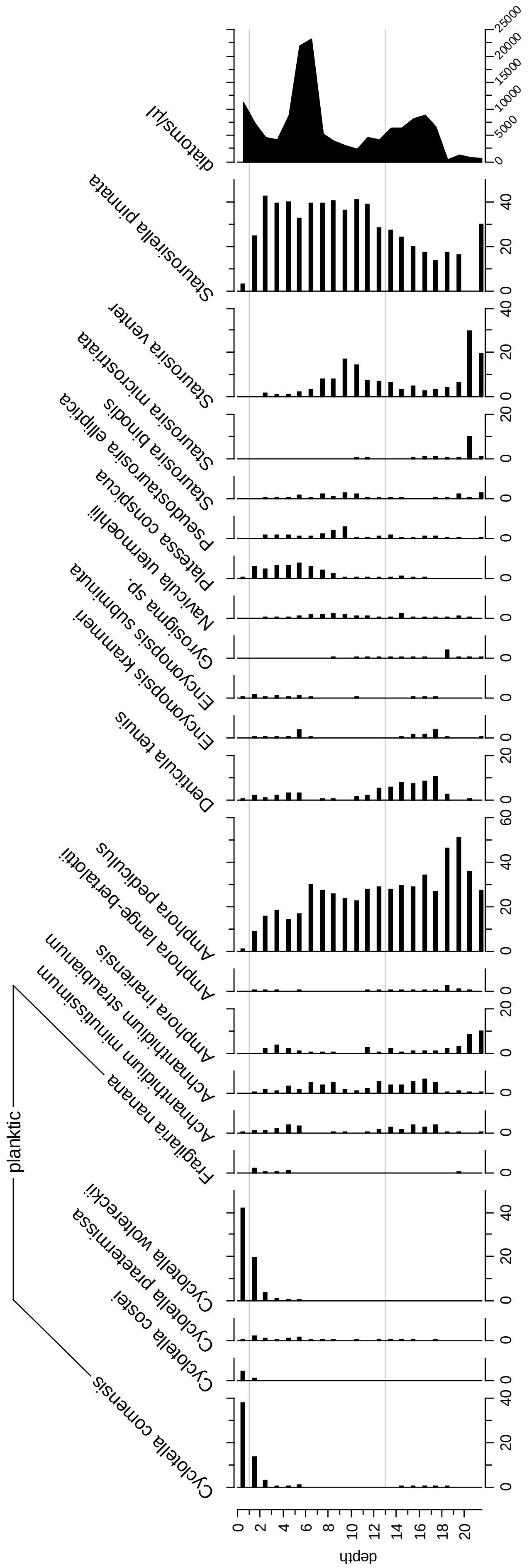

Figure S 26: Stratigraphy of the diatom assemblages in the subalpine lake Soiernsee (W) (1558 m). For further explanation, see Fig. S 5.

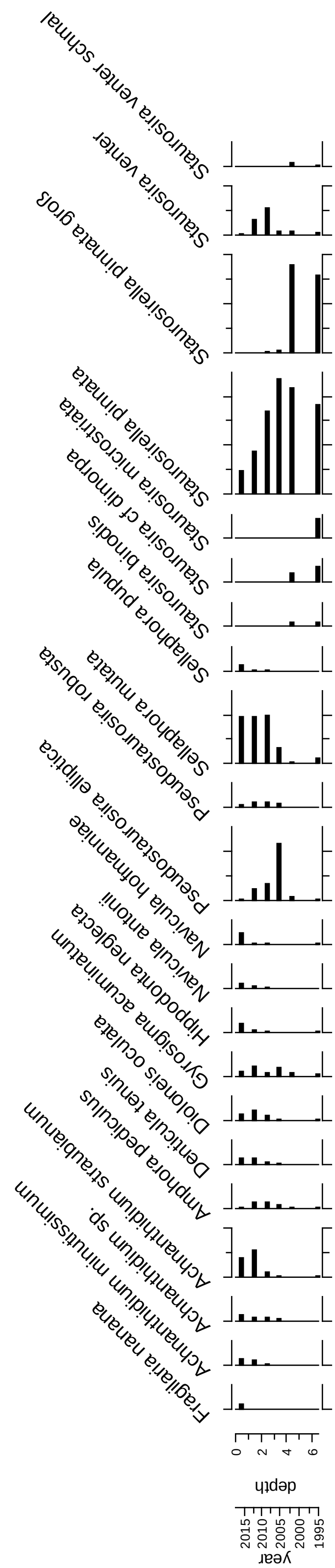

Figure S 25: Stratigraphy of the diatom assemblages in the subalpine lake Soiernsee (E) (1552 m). For further explanation, see Fig. S 5.

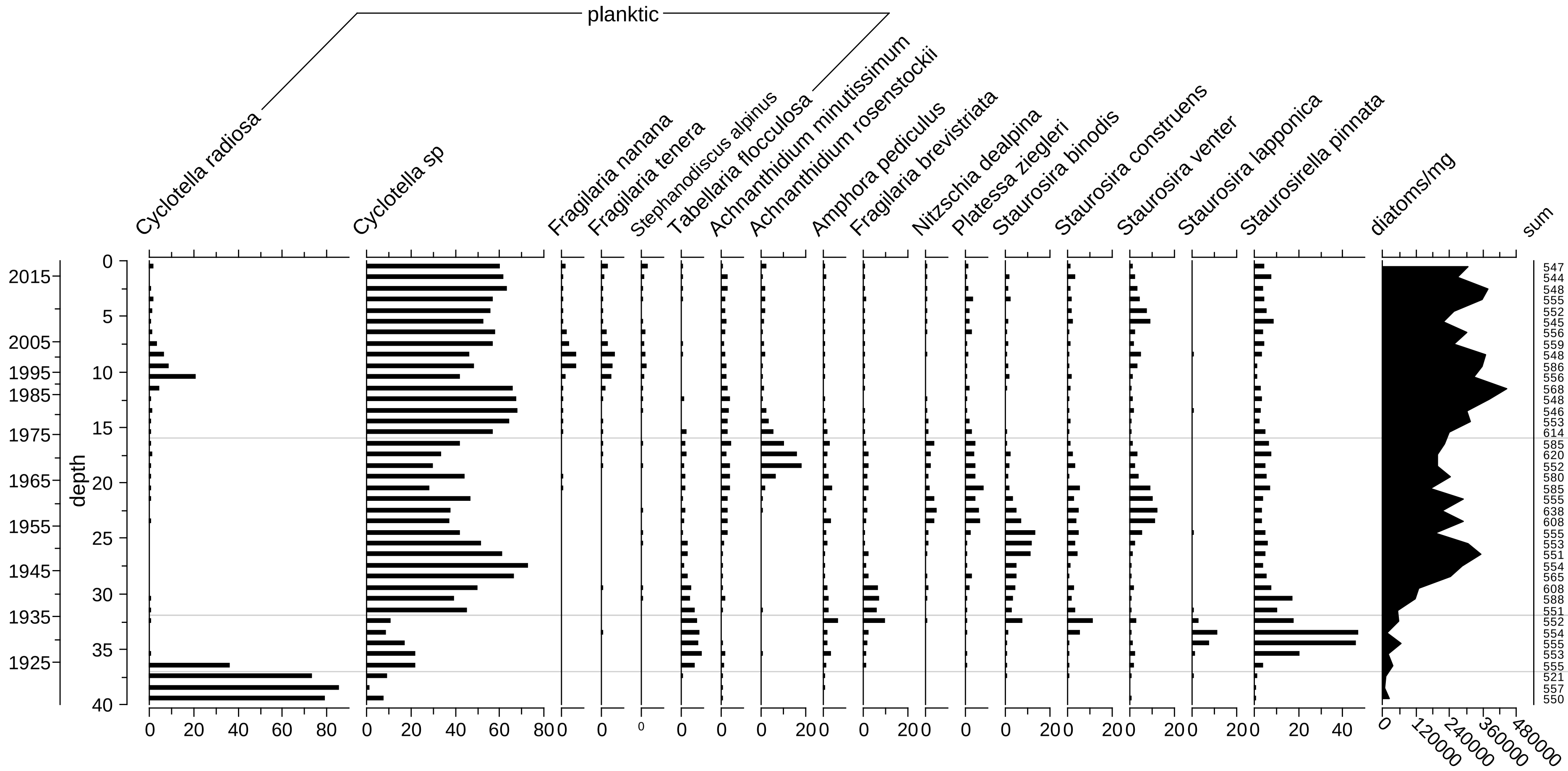

Figure S 27: Stratigraphy of the diatom assemblages in the montane lake Taubensee (1138 m). For further explanation, see Fig. S 5.


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