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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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-Tyrolian Alps differing in altitude, size and geology were examined for their diatom community response to climate warming. Subfossil data were related to ^{210}Pb and ^{137}Cs-dated sediment cores. Correspondence and regression analyses revealed five different assemblage developments depending on lake depth, altitude and origin. Planktic species, especially *Cyclotella*, dominated deeper and lower-altitude mountain lakes earlier and stronger. This depends on the stability and temperature of the epilimnion which in turn determines the tipping point. Instead, shallow lakes exhibit higher species reorganizations of diatom assemblages. Mountain lakes of lower altitudes or affected by water level fluctuations (WLF) establish complex substrata and *Achnanthidium* accompanied by epiphytic species or *Denticula tenuis* in WLF-lakes replace dominating *Staurosira*. Conversely, alpine shallow lakes lack directional shifts and *Staurosira* dominate, but approach the tipping point of macrophyte establishment. In a deep doline lake, *Diploneis* species replace *Nitzschia denticula* with negligible planktic proportions. In mountain lakes with direct anthropogenic influence, enhanced nutrient supply disguises diatom response to global warming. These findings revealed deep mountain lakes with low nutrient levels to be more resilient to climate change than shallow lakes with a higher trophic status as the onset of the response to rising temperatures is earlier and thus smoother. In conclusion, subfossil diatom analyses can provide a powerful tool for climate change assessment and other anthropogenic impacts on mountain lakes.

1. Introduction

Climate change impacts on mountain lakes are highly complex and still not completely understood since they are particularly vulnerable ecosystems that do not respond uniformly. Mountain lakes host unique and sensitive species that are highly adapted to harsh alpine conditions, making them ideal environmental sentinels (Catalan et al., 2013, Rogora et al., 2018; Moser et al., 2019). Recent studies point out that increasing air temperature results in earlier break-up and later onset of ice cover in the annual cycle, resulting in longer periods of strong stratification during summer (Karst-Riddoch et al., 2005; Rühland et al., 2008). Such well-stratified conditions culminate in marked shifts within the phytoplankton community towards motile, small cell or colony-

forming species (Winder et al., 2009; Daufrasne et al., 2009). Climate warming also alters the nutrient situation of the lakes mainly triggered by catchment modifications such as altitudinal tree-line shifts, uphill migration of plant species (Pauli et al., 2012) and increasing soil development (Rosbakh et al., 2014). As a consequence, the amount of organic matter entering the lakes can change markedly, especially in lakes that are located near climatically sensitive ecotonal boundaries such as tree line or timberline (Lotter et al., 1999; Sommaruga et al., 1999; Sommaruga and 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,

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extensive surface runoff and mudslides further changes light and nutrient conditions (Koinig et al., 1998). However, the climate-induced increase of erosion rates primarily affects the high-elevated lakes, while erosion in montane and subalpine catchments is mainly forced by human land use (deforestation, overgrazing), which strongly influences soil paedogenesis and vegetation dynamics (Arnaud et al., 2016). Longer growing seasons and enhanced nutrient supply culminate in higher algal productivity (Douglas and Smol, 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 et al., 2017), as past fluctuations of climate-mediated lake properties or catchment variations are well archived in lake sediment records (Smol et al., 2005). Diatoms are ideal biological indicators that mirror various types of long-term ecological perturbations such as acidification (Weckström et al., 1997; Koinig et al., 2002), eutrophication (Stoermer and Smol, 1999) and climate warming (Pienitz et al., 1995; Bigler and Hall, 2003; Smol et al., 2005; Karst-Riddoch et al., 2005; Rühland et al., 2008). Moreover, shifts in subfossil diatom assemblages are well preserved in lake sediments that can be used as environmental archives. Diatoms (Class Bacillariophyceaea) 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 et al., 2005).

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

2. Material and methods

2.1. Study area

The study is based on sedimentary records of 23 lakes located in the Bavarian and North-Tyrolian Alps. The area in which the lakes are located extends over a distance of about 220 km from west to east along the Bavarian-Austrian borderline (47°1$\acute{7}$ to 47°4$\acute{5}$N latitude, 10°1$\acute{5}$to 13°$\acute{1}$ E longitude, Fig. 1). The altitudinal gradient ranges from 955 to 2047 m a.s.l. (Table 1), representing eight montane (922 – 1207 m a.s.l.), nine subalpine (1458 – 1608 m a.s.l.) and six alpine (1809 – 2060 m a.s.l.) lakes. Catchment vegetation comprises conifer-dominated montane forests (*Picea abies* (L.) Karst and *Larix decidua* Mill., subordinate *Acer pseudoplatanus* L. and *Fagus sylvatica* L.) through subalpine grassland with patches of *Pinus mugo* ssp. *mugo* Turra and *Picea abies* as well as treeless alpine meadows (e.g. *Rhododendron hirsutum* L., *Carex sempervirens* Vill.) on poorly developed soils and rocky screes. Catchment geology is dominated by Triassic and Cretaceous carbonate rocks (limestone, dolomite, marlstone) and glacial deposits (lodgement till moraine deposits), partially covered by postglacial rock streams, talus slopes and alluvial cones. Most of the lakes are of glacial origin (cirque and moraine lakes), and two are postglacial (land slide lake, doline lake).

The lakes are limnologically diverse, ranging from shallow (1.3 m) to deep (20.7 m) lakes with ultra-oligotrophic to mesotrophic conditions and polymictic, dimictic or meromictic character. The substratum for benthic diatoms comprises sediments of different grain sizes, macrophytes and boulders. Some of the lakes are affected by strong water level fluctuations (WLF) up to 9.5 m within one season (Table 1, Hofmann et al., 2020; Kuefner et al., 2020a; Ossyssek 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 (arithmetic means and ranges): total phosphorous 8.5 µg L^{-1} (< 5 – 17.3 µg L^{-1}), nitrate-nitrogen 0.36 (0.03 – 0.93 mg L^{-1}) ammonium-nitrogen 35.8 µg L^{-1} (4 – 127 µg L^{-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 1).

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

2.2. 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.

2.3. 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 (Hofmann et al., 2020; Kuefner et al., 2020a; Ossyssek 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
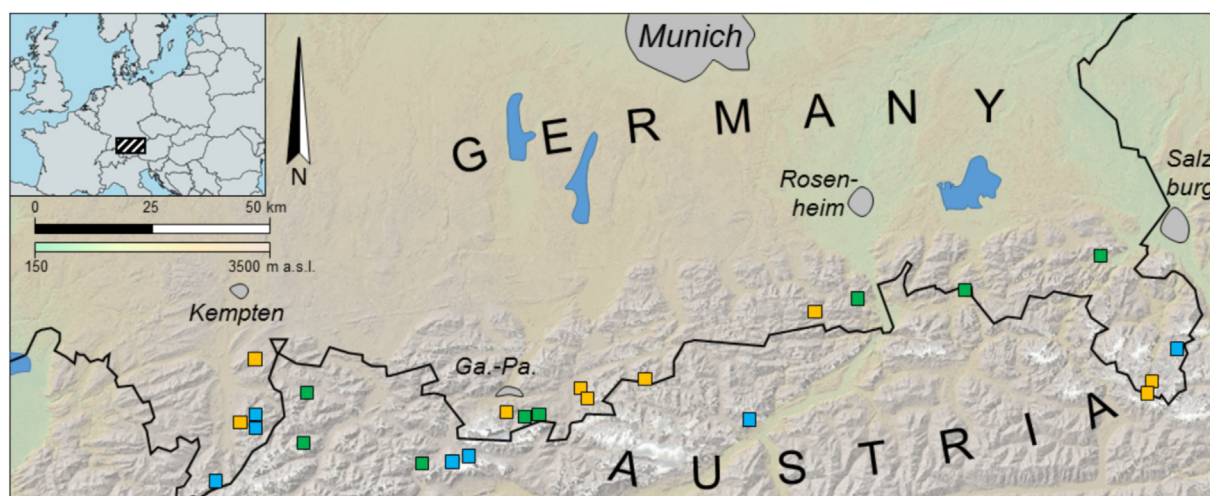
Fig. 1. Location of the 23 mountain lakes along the Bavarian-Tyrolian boarder. Blue squares: alpine, yellow: subalpine, green: montane lakes. Ga.-Pa.: Garmisch-Partenkirchen.

Table 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 (μgL^{-1})	NO_3^- (mgL^{-1})	NH_4^+ (μgL^{-1})	pH	Cond. (μScm^{-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
Engerats-gundsee	Eng	47°26′29″	10°23′30″	1876	3.6	17.3	15.5	< 5	0.04	27	8.2	236	dim.	MS	P
Ferchensee	Fe	47°26′18″	11°12′50″	1060	10.0	19.5	6.8	10.1	0.33	43	8.1	304	dim.	S	HP
Frillensee	Fri	47°45′57″	12°49′03″	973	1.2	5.5	4.6	7.2	0.93	84	8.6	224	dim.	M	–
Funtensee	Fun	47°29′37″	12°56′22″	1601	2.5	4.5	3.5	10.3	0.03	44	8.4	274	dim.	MS	hP
Gaisalpsee	Gais	47°45′56″	12°49′03″	1508	3.4	4.1	3.8	12.0	0.25	10	8.9	198	dim.	M	PD
Grubersee	Gru	47°27′13″	11°47′18″	2060	0.5	3.5	3.2	17.0	0.10	18	8.6	222	polym.	S	P
Grünsee	Grün	47°30′07″	12°57′11″	1474	3.5	6.9	5.0	8.3	0.20	61	8.5	194	dim.	MS	P
Höfersee	Höf	47°29′51″	10°29′25″	1192	0.6	1.9	1.9	< 5	0.47	5	8.9	221	polym.	M	P
Hörnlesee	Hörn	47°32′52″	10°23′29″	1601	0.5	1.8	1.8	17.3	0.34	20	7.9	225	polym.	M	DP
Lautersee	Lau	47°26′13″	11°14′08″	1013	12.0	18.0	6.0	13.5	0.21	51	8.6	310	dim.	S	H
Mittersee	Mit	47°22′07″	10°51′58″	1082	3.3	4.7	4.7	7.5	0.10	34	8.3	346	dim.	S	–
Rappensee	Rap	47°17′09″	10°15′10″	2047	2.3	7.8	5.0	9.2	0.04	16	8.6	205	dim.	MS	D
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

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.

2.4. 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).

2.5. Diatom analyses

Freeze-dried subsamples were prepared for diatom analyses according to Van der Werff (1953) and Kuefner et al. (2020a). Different dilutions of the cleaned material were embedded in the high-refractive medium Naphrax and fixed on microscopic slides to obtain permanent

Table 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 1.

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

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

2.6. Statistical analyses

Referring to local climate data, the strongest warming in the Bavarian Alps started in the 1970s (Kuefner et al., 2020b). To detect inter-lake variances of climate change response in diatoms within this period (~1975–2017), a principal component analysis (PCA) was computed for the subfossil assemblages of the upper compartment of each sediment core, which integrated the last ~45 years according to the ^{210}Pb and ^{137}Cs results. For a better comparability, inter-lake variances of the subfossil diatom assemblages were homogenized by summarizing diatom species abundances in groups on the genus level according to the three related proxies valve silicification, size and ecology (Kuefner et al., 2020a). An overview of species grouping is listed in the supplementary. Only groups with abundances of more than 2% were included in statistical analyses, so that the exclusion of underrepresented species eases inter-lake comparisons. Species abundances were Hellinger-transformed (Legendre and Gallagher, 2001) before analyses to stabilize variances and to avoid down-weighting of rare taxa (Smol et al., 2005). To determine the number of decisive components, a Scree plot was generated as well. Diatom species or groups, whose eigenvalues are lower than randomly modelled values of the broken-stick model are suggested to be insignificant for the distribution of the assemblages in the PCA (Jackson, 1993). Additionally, diatom compositional turnover (β-diversity) was quantified using Detrended Correspondence Analysis (DCA). This proxy refers to the length of the first DCA axis and scales values in SD units, which can also be referred to as turnover units of beta-diversity (ter Braak, 1987; ter Braak and Verdonschot, 1995). As a temporal constraint, the same 45-year core compartments as for the PCA were implemented into the DCA. This improves the comparability of beta diversities among the cores and compensates different sedimentation rates in different lakes as well as different core lengths. For the best estimation of diatom re-organization without distorting chance finds, only diatom species with relative abundances of more than 1% in at least one sample within a core were used and again square-root transformed (Legendre and Gallagher, 2001). To identify decisive parameters determining species turnover in mountain lakes, generalized linear models (GLM) with AIC-based stepwise backward model selection were calculated. Highly correlated parameters ($p < 0.001$), which can cause multiple comparison problems in the models and feign inverse relationships, were eliminated (Schröder and Reineking, 2004). According to Kuefner et al. (2020a), the parameters altitude and surface temperature as well as depth, volume and Secchi depth were implemented as dependent variables in the initial model formula, the remaining values bottom temperature, total phosphorous and lake surface are added separately. Comparisons among two factors were visualized as boxplots and statistically checked with a t-test in case of similar variances (F-test), otherwise with a Mann-Whitney U test and its distribution with a Kolmogorov-Smirnov test. Data preparation and transformations were conducted in Microsoft Excel 2016 ®, statistical analyses in PAST 3.20 (Ryan et al., 1995) and R version 3.4.1 with the package 'vegan' (Oksanen et al., 2018). To identify significantly different stratigraphical zones, broken-stick models were calculated (Bennet, 1996) with the R package 'rioja' (Juggins, 2017).

3. Results

3.1. Thermal stratification and light conditions

The analysis of the temperature logger data revealed 14 dimictic lakes and eight polymictic lakes (Tables 1 and 2). The special case of the doline lake 'Lake Sieglsee' was classified as meromictic. Although temperature data would allow its classification as polymictic lake, the electrical conductivity measurements suggested meromictic conditions.

In total, ten lakes were shallow and transparent enough to be completely euphotic, whereas 13 lakes contained an aphotic zone (Table 2).

3.2. 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.

3.3. 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 (Fig. 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* KÜTZING complex; (2) the planktic, colony-forming species *Asterionella formosa* HASSALL; (3) small-sized planktic centric taxa of the *Cyclotella* (KÜTZING) BRÉBISSON-complex; (4) the species *Cyclotella distinguenda* HUSTEDT; (5) medium-sized *Navicula* BORY species (*Navicula*-complex); (6) small benthic fragilarioid taxa (*Staurosira* EHRENBERG-complex); (7) small-sized, weakly silicified benthic fragilarioid taxa (*Staurosira* light-complex), and (8) the heavily silicified benthic fragilarioid *Staurosirella pinnata* (EHRENBERG) WILLIAMS & ROUND. The *Nitzschia* HASSALL and large-sized *Diploneis* EHRENBERG EX CLEVE complex were the 10th and 11th component and below significance, but were decisive particularly for the separation of the doline lake and additionally shown in Fig. 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* (EHRENBERG) CLEVE & MÖLLER) were plotted opposed of *Achnanthidium*- (especially *A. minutissimum* (KÜTZING) CZARNEKI, *A. rosenstockii* (LANGE-BERTALOT) LANGE-BERTALOT) and *Cyclotella*-dominated assemblages (especially *C. comensis* GRUNOW, *C. delicatula* HUSTEDT, *C. distinguenda*) (Fig. 2b).

3.4. 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. 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 1980 s and 2000 and subsequent increase of planktic taxa *(Cyclotella* species, *Fragilaria nanana* LANGE-BERTALOT) accompanied by an increase of periphytic diversity in the upper part of the core, while *Staurosira* species simultaneously decreased. Type 3 lakes (Lake Delpssee, Lake Funtensee, Lake Grubersee) merely showed composition changes within the

Staurosira-complex. Type 4 lakes were characterized by an equal replacement within periphytic diatom assemblages: type 4a (Lake Brendlsee, Lake Gaisalpsee, Lake Höfersee, Lake Hörnlesee, Lake Seeleinsee, Lake Unterer Soiernsee) gradually shifted from the *Staurosira*- to the *Achnanthidium*-complex, whereas type 4b (Lake Soinsee) shifted from the *Staurosira*-complex to *Diploneis oculata* (BRÉBISSON) CLEVE. Exclusively, the doline lake (Lake Sieglsee) was characterized by a change mainly from *Nitzschia denticula* GRUNOW to several *Diploneis* species (type 5). Two lakes (Lake Frillensee, Lake Mittersee) clustered in between the types 1 and 4 as they mainly showed oscillations between the *Cyclotella*-complex and the *Achnanthidium*-complex, but also properties of both lake types as defined above. The main lake types were equally distributed along the altitudinal gradient.
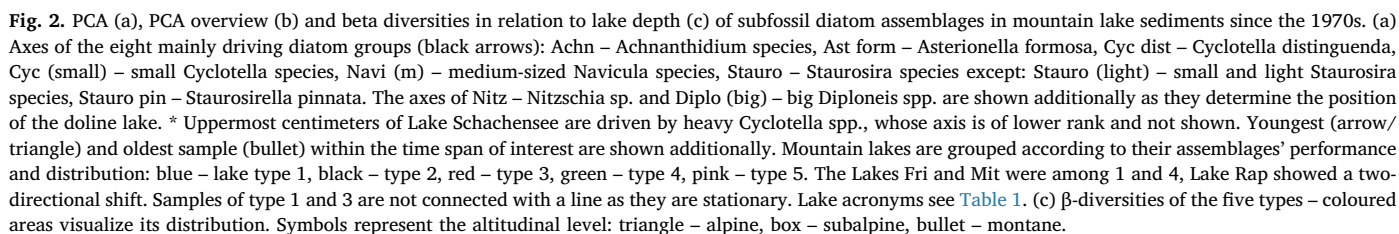
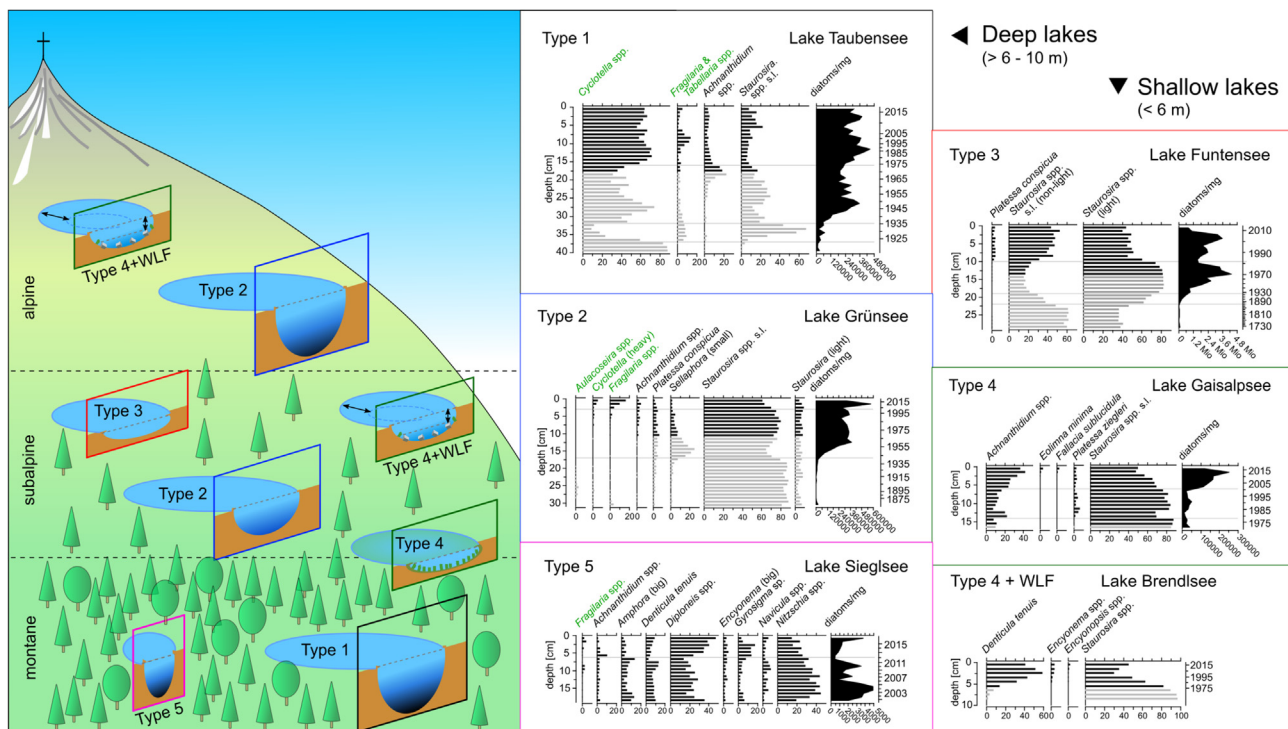### 3.5. Diatom response to changing environmental variables

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 2, Fig. 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 ($\rho_S = 0.569$, p = 0.037), which was in average higher than in type 2 lakes (p = 0.01; Fig. 4a). Within the shallow lakes, 'type 4' lakes were warmer and lower than 'type 3' lakes and/or impaired by water level fluctuations (WLF) (Fig. 4a & c). This allows a lake type identification by only three environmental variables (Fig. 4d): lake depth, summer surface temperature and lake origin.

4. 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-

Fig. 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 1. (c) β-diversities of the five types – coloured areas visualize its distribution. Symbols represent the altitudinal level: triangle – alpine, box – subalpine, bullet – montane.

Fig. 3. Diatom stratigraphies of the five mountain lakes types. Type colours correspond to Fig. 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. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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).

4.1. 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 (Kuefner et al., 2020a; Livingstone et al., 1999). Between the 23rd Aug and 1st Sep 2016, the lake surface of the warmest type 2 lake reached an average of 19.5 °C, at a mean ambient air temperature of 15.9 °C (summer average 2000–2010: 12.4 °C; extrapolated from regional weather data), whereas type 1 lakes were distinctly warmer (late-August: 19.7–21.7 °C, extrapolated ambient air temperature: ≥17.8 °C). Divergent lake and air temperatures may be the result of a strong topographic influence on mountain lake areas since they are mostly located in valley basins with effects of warmer southern slopes and wind protection (Dobrowski et al., 2009). Based on that, the sudden 'planktic appearance' probably represents a tipping point of the lake system as a consequence of increasing lake warming. *Cyclotella* species take advantage of increased thermal stability (Catalan et al., 2002; Winder et al., 2009) and a warmer epilimnion. For instance, the most frequent *C. comensis* describes an optimum at average summer air temperatures of 13.0 (± 3.8) °C (Hausmann and Lotter, 2001). Therefore, *Cyclotella* spp. could only leave detectable subfossil proportions when epilimnion temperatures reached the growth optimum of this genus, which probably happened in the 1970 s 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
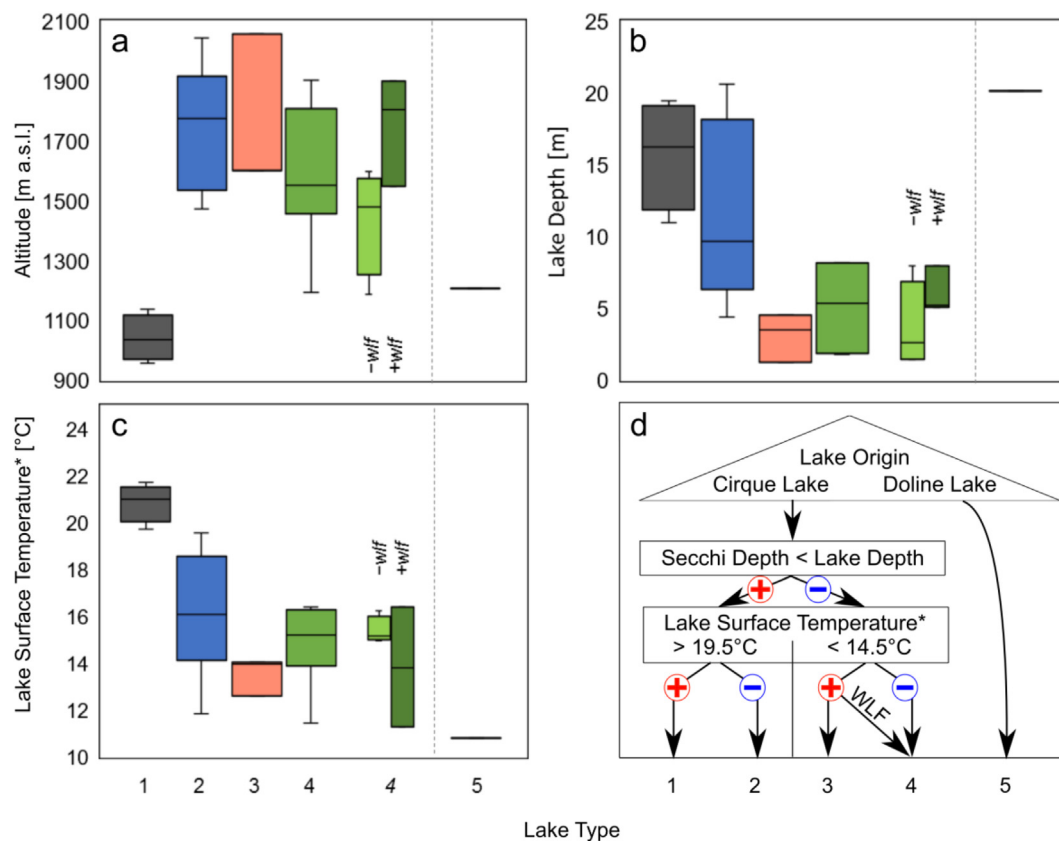
Fig. 4. Mountain lake types and their distributions along altitude (a), lake depth (b), lake August surface temperature (c). Differentiation scheme (d) according to the main factors lake origin, depth and temperature. Boxplot colours refer to Fig. 2. Type 4 is additionally split into lakes with (+wlf, 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.

epilimnion, an extended clear-water period and less turbid conditions (Fig. 5). Hence, the ability of small fragilarioids to cope with turbidity is no advantage anymore and this species can be outcompeted by increasing abundances of *Cyclotella* in the sedimented diatom assemblage (Kattel et al., 2015). Accompanying the small benthic fragilarioids, however, other planktic diatoms than *Cyclotella* are assumed to appear in turbid and turbulent water columns, such as strongly-silicified *Aulacoseira*, which are indicative of polymictic conditions (Rühland et al., 2015). There are indications that *Aulacoseira* spp. were present in such lakes before the 'planktic appearance', but they only appeared as fragments, which may be a methodical problem during diatom preparation.

In contrast to deeper lakes, mountain lakes that are less than 6 m deep are usually not stratified and therefore polymictic for most of the summer **(type 3 & 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 (Figs. 3 and 5) (Ossyssek et al., 2020; Hofmann et al., 2020). However, the plankton did not constitute much to the sediment's biomass, as shallowness limits planktic habitat and the lakes are less productive due to their oligotrophic conditions. Furthermore, the lake bottom in these shallow mountain lakes is completely illuminated, i.e. the entire bottom represents littoral zone, so that periphytic diatoms overgrow the low amounts of sedimented planktic diatoms. Consequently, the latter do not appear in any sediment sample in significant numbers. Therefore, global warming-driven shifts in diatom assemblages of shallow lakes occurred especially as shifts within the

periphytic diatom flora. The subfossil diatom assemblages of **type 3 lakes** were characterized by undirected shifts particularly within the small fragilarioid species. In contrast, **type 4 lakes** showed a general decrease of species of the *Staurosira* -complex, which can be interpreted as response to a warming environment (Lotter et al., 1999-2002). They were replaced by *Achnanthidium* spp. and in macrophyte-rich lakes additionally by epiphytic species, such as *Encyonopsis* spp. and some *Navicula* spp. (Stevenson et al., 1991; Wiklund et al., 2010). Making this a general development of benthic communities, type 2 lakes indicated a similar directional shift within the benthic proportion.

Comparable to the deep lakes, altitude is crucial for the separation of type 3 lakes and type 4 lakes. All lakes of the sample set that were assigned to type 3 lakes were located above 1600 m a.s.l., whereas this was the maximum altitude of type 4 lakes. In line with the altitude-temperature correlation, the average lake surface temperature in late-Aug 2016 was significantly lower in type 3 lakes with a maximum of 14.1 °C than in type 4 lakes where 15.0 °C was exceeded (Fig. 4c).

This further supports type 4 lakes with stable water levels to be rich in organic substratum and to be dominated by macrophytes of the genera *Potamogeton* L. and *Chara* L., whereas type 3 lakes are possibly still too cold to establish significant water plant populations. Only single macrophyte species can reproduce in cool conditions in alpine altitudes (Overton 1899; Dörr and Lippert, 2011; Bornette and Puijalon 2011). However, warming is supposed to increase macrophyte species richness in high altitudinal lakes (Rosset et al., 2010), evolving new habitats for epiphytic diatoms. Therefore, the replacement of *Staurosira* species by epiphytic species can be considered as a direct response to climate change (Rühland et al., 2010), whilst water plants in type 3 lakes of higher altitudes are still insignificant for epiphytic growth due to the cool water temperatures. Beside climate-induced changes in ice-
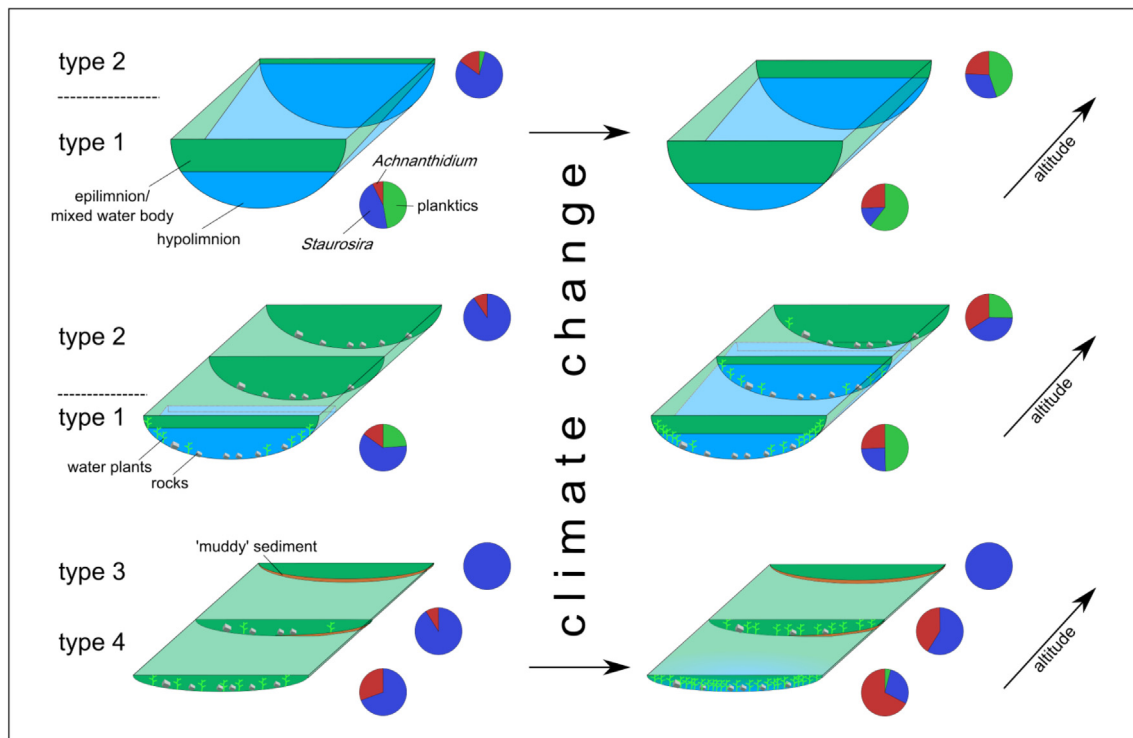
Fig. 5. Overview of the mountain lake developments in different lake types. The figures on the left represent the lakes before climate change influence, on the right with climate change impact. The z-axis is the altitude. The circles visualize the composition of the main diatom groups at the lake bottom: "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.

break up dates, these alpine lakes are impacted by changes of input of organic and inorganic material due to high alpine weathering. Additionally, these processes hamper macrophyte growth as it promotes lake turbidity and a muddy, gyttja-like, loose and dynamic sediment. Thus, conditions of type 3 lakes provide substrata especially for epipelic and epipsammic diatom species and robust pioneers such as *Staurosira* s.l., which can cope with turbidity and mechanical disturbances by turbulent benthos (Kattel et al., 2015). Other diatoms lack competitiveness under these harsh and unstable conditions. Therefore, no significant shifts in the composition of diatoms due to global change can be detected.

The development of initially epilithic and epipsammic diatoms like in type 3 up to finally epipelic and epiphytic species like in type 4 can be referred to as 'substratum succession' and results in the highest beta diversities within the mountain lake set. Crossing of ecological thresholds in terms of the evolution of new benthic habitats further supports the benthic diatom shift as the strongest climate change response among the mountain lake diatom flora (Michelutti et al., 2015; Antoniades et al., 2005). In the future, an altitudinal upward macrophyte distribution as decisive tipping point in mountain lakes can cause non-linear responses and turn the lowest type 3 into the highest type 4 lakes once new substrata for epiphytic diatoms are established. This process will likely be accompanied by a significant increase of organic matter both on and in the sediment, as measurements of water content and diatom densities have shown (Menounos, 1997; Avnimelech et al., 2001) (Figs. 3 & 4).

A special feature among the type 4 lakes are lakes that are exposed to marked WLF (**type 4 + WLF**). Different to the 'typical type 4 lakes, *Staurosira* species have been replaced by the desiccation tolerant *Denticula tenuis*, as also described by Cantonati et al. (2009) and Hofmann et al. (2020). WLF strongly affect phytoplankton structure and biomass (Adamczuk et al., 2020) as well as impede an intensive and species-rich development of macrophytes (Riis and Hawes, 2002; Bornette and Puijalon, 2011). Primarily, fast-growing small species

such as *Potamogeton filiformis* (PERS.) BÖRNER or *Ranunculus trichophyllus* CHAIX are able to cope with the short vegetation period and occasional desiccations. Additionally, *Chara*-species have a clear advantage over submerged vascular macrophytes in lakes with drastic fluctuations in hydrostatic pressure (Krause, 1997). Hence, substratum for epiphytic diatoms species is uncommon in lakes with distinct WLF, but may change with climate change (Rosett 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. 3). The geological origin of this doline lake causes special limnological features, including meromictic conditions, low water temperatures, high ion concentrations, and high lake transparency. The extraordinary conditions have caused the development of a special benthic diatom assemblage, so that a separate type 5 lake could be classified. A depth of 20.2 m would actually suggest planktic diatoms to appear in significant abundances in the lake sediments. In fact, phytoplankton analyses have shown that obligate plankton diatoms, such as *Fragilaria* and *Cyclotella*, grow in the water column in high numbers within the diatom community (Ossyssek et al., 2020). However, total plankton densities are supposed to be very low as the lake is ultraoligotrophic with phosphorous concentrations below 5 µg 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 (Kuefner et al., 2020a). Changes regarding groundwater inflow rate and lake conductivity may result in the observed special diatom shift. This in turn is possibly induced by climate warming as seasonal droughts and decreasing snow packs lead to a decreasing supply of ground water (Bard et al., 2012, Haslinger and Blöschl, 2017, Jenicek et al., 2018). Weakened pouring underwater sources (limnocrene) may reduce ion concentration, turbidity and sedimentation. These conditions formerly may have favoured *N. denticula* as a motile tychoplanktic diatom (Peterson, 1986, 1987). However, the reduced turbidity caused by climate change, i.e. the greater transparency of the water body, favours epipelic and epipsammic diatoms such as *Diploneis* and *Gyrosigma* (Douglas and Smol, 1995) in competition with *N. denticula*. Therefore, the decline of this species correlates with the development of alpine climate (Fig. 3).

4.2. 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 (Kuefner et al., 2020a; 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. 4). Based on these thresholds, temperature estimations allow to define tipping points and consequently assess lake types globally apart from ecotonal boundaries such as forest or timber lines.

These relationships can further be modulated by the **trophic level** of a lake as it controls algal production and water transparency, regulating the extension of the littoral zone**.** Accordingly, a mesotrophic shallow mountain lake may appear like a deep oligotrophic lake, e.g. Lake Schachensee. Although being polymictic and 4.4 m deep, a higher nutrient availability may have promoted stronger silicified plankton of the genus *Cyclotella,* which already dominate the sedimentary deposits after a few decades. Due to its high turbidity, benthic communities were displaced in the sediments. In contrast, *Asterionella formosa* can outcompete *Cyclotella* in deep mesotrophic lakes during earlier stratification phases as it is superior in competing for phosphorus (Tilmann, 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. 3). Hence, lake geology-dependent stability of lacustrine habitats makes doline lakes the most, and WLF-lakes the least resilient to global warming.

In line with hypothesis (3), local anthropogenic impacts were found to interact with warming environments. Some diatom developments within the dataset cannot be explained by climate change, as they show no directional (e.g. type 3 lakes) or even inverse trends (Lake Funtensee). There is evidence that these mountain lakes are affected by **local human activities**, which disguise their response to global warming. Again, lake depth and volume define the degree of resilience. In general, subfossil diatoms unearthed decades of enhanced nutrient availability in the concerning Bavarian mountain lakes. Down-core trends show that these diatom-inferred nutrient peaks coincide with hut construction, while gradual nutrient decrease is introduced by treatment plant constructions. The latter led to a reduction of bioavailable phosphorous within the last decades that counteracts the eutrophication caused by global change (Koinig et al., 1998; Rosbakh et al., 2014; Arnaud et al., 2016), especially observed in the deeper lakes, L. Ferchensee and L. Lautersee. Shallow lakes such as Lake Funtensee are less resilient to local human impact. Lake response to the nutrient decrease as inferred by shifts within the *Staurosira* complex (Kuefner et al., 2020a) is much stronger and contrary to the response to warming temperatures. In the medium-deep Lake Rappensee the construction of a little dam in 1948 resuls in an increase of nutrients and turbidity (Algarte et al., 2016) as eutraphentic species such as *Gyrosigma* spp. (Hofmann, 1999) or *Staurosira parasitoides* (Kuefner et al., 2020a) 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 palaeolimnological 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. 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.

CRediT authorship contribution statement

Wolfgang Kuefner: Writing - original draft, Conceptualization, Data curation, Investigation, Methodology, Validation. **Andrea Hofmann:** Writing - original draft, Conceptualization, Data curation, Investigation, Methodology, Validation. **Stefan Ossyssek:** Investigation, Methodology. **Nathalie Dubois:** Methodology. **Juergen Geist:** Supervision, Validation, Writing - review & editing. **Uta Raeder:** Funding acquisition, Project administration, Supervision, Validation, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgment

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.106590.

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