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Impacts of climate warming on Alpine lake biota over the past decade

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ABSTRACT

Alpine temperatures have risen at twice the rate compared to the northern-hemispheric average during the past century. This can be expected to affect Alpine lake ecosystems via, for example, intensified thermal stratification, shorter ice cover periods, and altered catchment processes. Our study assesses changes in some main constituents of the planktic and benthic communities of five mid-Alpine lakes in the Niedere Tauern region in Austria in relation to climatic warming, by comparing community and environmental data from 1998–1999 to data from 2010–2011. Although lake chemistry remained relatively stable between the study periods, we observed an increase in lake water temperatures and a decrease in ice cover durations. Several of the dominant diatom species and chrysophyte cyst types show relatively clear changes; the responses of the whole communities, however, are less evident. Yet, in particular, diatoms show distinct assemblage changes along the climatic gradients in the two lakes with the largest decrease in ice-cover duration. Chironomid communities appear to be less sensitive compared to diatoms and chrysophyte cysts, which are known for reacting quickly to changes in their environment. Finally, Alpine lakes, which are moderately nutrient-enriched because of human activities in the catchment area, are likely to experience increases in their productivity with climate warming.

INTRODUCTION

The ongoing global warming is amplified in high-elevation regions such as the European Alps compared to the global average (Wang et al., 2014). During the past century, Alpine temperatures have risen at twice the rate compared to the northern-hemispheric average, amounting to a total annual mean temperature increase of about 2 °C (Auer et al., 2007). This observed warming was particularly pronounced from the 1980s onward, with annual mean warming rates of about 0.5 °C per decade (European Environment Agency, 2009). Mountain lake ecosystems, due to their simple structures, are inherently sensitive to both direct (lake temperature, stratification, ice cover duration) and indirect (changes in their catchment areas) effects of rising surface air temperatures. At the same time, compared to lowland lakes, they are generally less affected by anthropogenic activities (especially eutrophication), which can confound the climatic signal (Battarbee et al., 2002; Leavitt et al., 2009; Catalan et al., 2013). As climate models project further warming in the 21st century (e.g., Gobiet et al., 2014), Alpine lakes can be considered important sentinels of climate change.

The altitude of an Alpine lake is critical in determining its climatic sensitivity: both low and high Alpine lakes are relatively insensitive, whereas lakes at intermediate altitudes (1500–2000 m a.s.l.) have the potential to be highly sensitive due to the strongest impact of air temperature changes on ice cover duration at these altitudes (Thompson et al., 2005). Here we aim to assess changes in some main constituents of the planktic and benthic communities (diatoms, chrysophytes, chironomids) of a set of mid-Alpine lakes in the Niedere Tauern region in Austria in relation to climatic warming by comparing community and environmental data from 1998–1999 to data from 2010–2011. Although many paleolimnological studies on Alpine climate change over centennial to millennial timescales exist (e.g., Lotter et al., 1997; Heiri et al., 2003; Huber et al., 2010; Larocque-Tobler et al., 2010; Ilyashuk et al., 2011; Nevalainen et al., 2014), data on recent community changes in Alpine lakes are rare, despite their indisputable value for environmental quality and conservation programs, and for better understanding the effects of global climate change on lake ecosystems.

STUDY AREA

Our five lakes are part of a calibration data set of 44 oligo- to ultra-oligotrophic, circumneutral to slightly alkaline lakes located in the Niedere (Schladminger) Tauern, Eastern Central Alps (47°13′15″N–47°21′31″N, 13°36′06″E–14°04′12″E, Fig. 1). This data set was first described by Kamenik et al. (2001a). The lakes, which all are characterized by small catchment areas (<9 km^2), span an altitudinal gradient of 1502 to 2309 m a.s.l. Crystalline bedrock, schists, and diagenetic or metamorphic carbonates dominate the catchment areas. Despite the high altitudes, no glaciers are found in the study area. The present treeline ranges between 2000 and 2100 m a.s.l. and is formed mainly by Cembra pine (*Pinus cembra*).

MATERIAL AND METHODS

The 44 lake calibration data set (Kamenik et al., 2001a, 2001b; Schmidt et al., 2004; Kamenik and Schmidt, 2005), which was collected in 1998–1999, consists of environmental measurements and modern diatom, chrysophyte cyst, and chironomid data from surface sediments (diatoms and chironomids) and sediment traps (chrysophyte cysts). In 2009, we chose a subset of these lakes located in the mid-Alpine zone to resample them for the same organism groups and physical and chemical lake variables. The chosen lakes cover the main bedrock types and the variability in the water temperature-altitude relationship. This variability is caused by, for example, topographic shading (or the lack of it) and local snow fields, and it can affect the sensitivity of lakes to the warming climate (Thompson et al., 2005). Lakes Moaralmsee (MOA, 1825 m a.s.l.) and Oberer Landschitzsee (OLA, 2067 m a.s.l.) are both located in a catchment dominated by crystalline bedrock. While MOA is unusually cold in the summer compared to what would be expected from altitude alone in the 44-lake data set, OLA is unusually warm (Thompson et al., 2005). Unterer Giglachsee (GIG, 1922 m a.s.l.) and Twenger Almsee (TWA, 2118 m a.s.l.) are located in a catchment area dominated by carbonaceous bedrock. While the summer epilimnetic temperatures in the former correspond to what would be expected by its altitude, the latter is unusually warm in the summer (Thompson et al., 2005). Unterer Wirpitschsee (WIR, 1700 m a.s.l.) is located at the transition from crystalline to metamorphic carbonates in the study area, and was classified by Thompson et al. (2005) as a lake with lower (but not unusually low like in MOA) temperatures in the summer. For the major limnological and morphological characteristics of these lakes, see Table 1.

For the sampling details of the 44 lake data set, see Kamenik et al. (2001a, 2001b), Schmidt

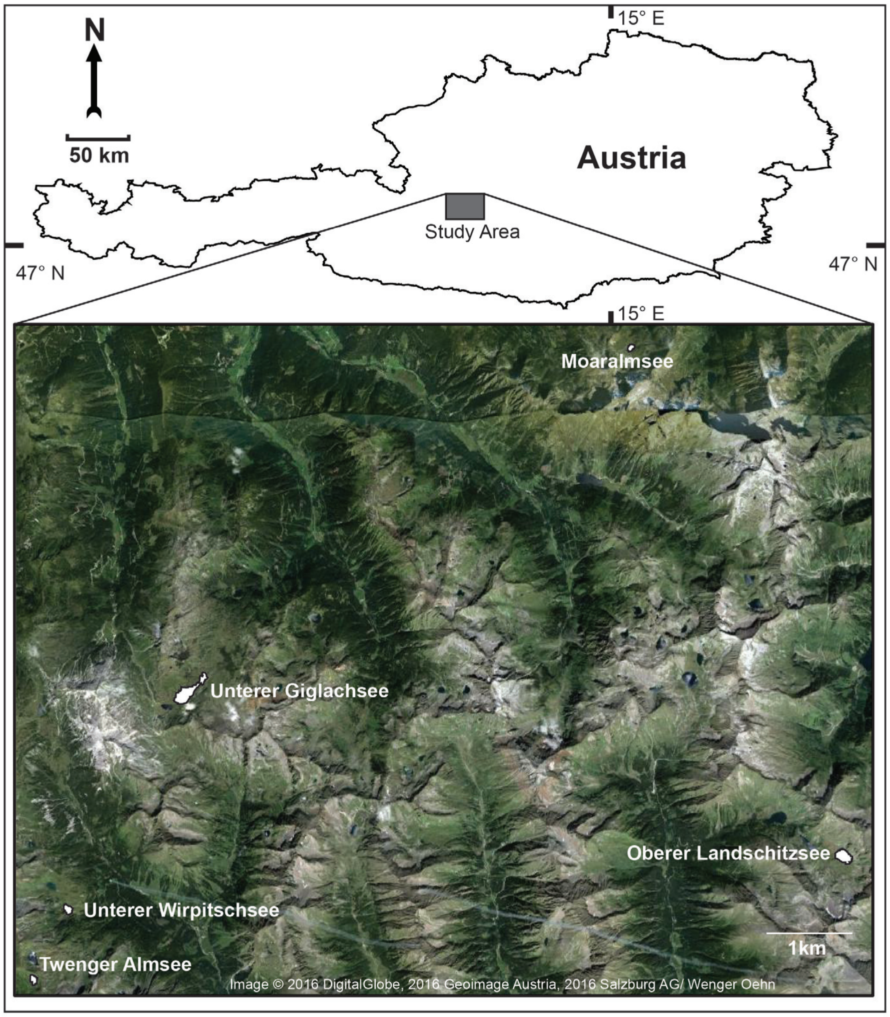

FIGURE 1. Map of study area in the Niedere (Schladminger) Tauern, Eastern Central Alps (47°13′15″–47°21′31″N, 13°36′06″–14°04′12″E).

et al. (2004), and Kamenik and Schmidt (2005). The chosen subset of five lakes was sampled four to five times for physical and chemical variables during the summer and early autumn months in 2010 and 2011 (except epilimnetic water temperature, which was measured at 2–4 hour intervals). The sampling included (1) physical and chemical parameters, (2) surface sediment samples for chironomids (0–2 cm and 2–4 cm), and (3) trap samples for chrysophyte cyst assemblages and diatoms. Surface sediment samples from the deepest part of the lakes were taken in 2011 using a Kajak gravity corer (UWITEC; Mondsee). The sediment traps were exposed from July/August 2010 to July/August 2011. The traps were built of four plastic tubes (length 58 cm and diameter 6 cm) on a fixture. They were exposed in the profundal of the five lakes close to the bottom.

Physical and Chemical Parameters

The sampling strategy of the lakes was based on the notion that overall, seasonal changes of chemical and morphological features of mountain lakes are clearly less variable than the seasonal changes of their physical characteristics (Catalan et al., 2002). Epilimnetic temperature was measured using thermistors (MINILOG, Vemco Ltd.) left in the lakes over the study periods 1998–1999 and 2010–2011 (two thermistors in each lake recording at 2–4 hour intervals at 2.5 m depth). Ice cover durations (days) were estimated from the number of days between the first day in autumn with water temperature <4 °C (date of autumn mixing) and the last day in spring when temperature increased to >4 °C (date of spring mixing). Given the remote location of the lakes, it was most feasible to

TABLE 1

Physical and morphological summary of the study lakes. July temp = mean July water temperature 2010–2011 (°C).

Environmental variable	Oberer Landschitzsee (OLA)	Moaralmsee (MOA)	Unterer Giglachsee (GIG)	Twenger Almsee (TWA)	Unterer Wirpitschsee (WIR)
Altitude (m a.s.l.)	2067	1825	1922	2118	1700
Lake area (ha)	8.8	2.1	16.8	3.1	2.7
Max depth (m)	13.6	5.9	18.0	33.6	8.0
July temp (°C)	12.0	8.3	13.8	9.9	11.2

use the thermistor data to estimate ice cover duration, even if this method slightly overestimates the number of days. Conductivity and pH were analyzed in the field, while the samples for chemical analyses were kept cooled and analyzed within two days. These variables included alkalinity, HCO_3, NO_3-N, SO_4, Cl^-, NH_4-N, Na^+, K^+, Mg_2^+, Ca_2^+, total phosphorus (TP), dissolved phosphorus (Pdis), dissolved organic carbon (DOC), and dissolved reactive silica (DRSi). A detailed description of the analytical methods used can be found in Kamenik et al. (2001a) and in Schmidt et al. (2004).

Diatoms

The wet sediment was chemically treated using standard procedures (Battarbee, 1986). Subsamples were evaporated on slides and mounted in Naphrax. At least 400 valves were counted using a Leitz microscope with a 100× oil immersion and phase contrast objective (PL APO 1.32). The percentage abundance of each species is based on the total diatom sum. Identification followed mainly Krammer and Lange-Bertalot (1999a, 1999b, 2000, 2004), Schmidt et al. (2004) (Fragilariaceae), and Wunsam et al. (1995) (*Cyclotella*).

Chrysophyte Cysts

The chemical pretreatment for chrysophyte cyst samples is the same as for diatoms. A minimum of 200 chrysophyte cysts was counted from the 2010–2011 trap samples, while >500 cysts per sample were counted to establish the chrysophyte cysts–environmental variables calibration data set collected in 1998–1999. A lower total count for the 2010–2011 samples was considered adequate to detect the major changes in the assemblages over the decade. Samples were screened by SEM (DSM 950, Zeiss West Germany), and all cysts found along transects were photographed and counted. Cysts were morphologically assigned using Duff et al. (1995) and Wilkinson et al. (2001) as well as the image collection on morphotypes from the 1998 Niedere Tauern data set (Kamenik et al., 2001b; Kamenik and Schmidt, 2005).

Chironomids

The sediment samples were analyzed following the standard methodology for subfossil chironomid remains (Walker, 2001). After being kept cold for conservation purposes, a variable quantity of wet sediment was deflocculated in hot KOH 10%, sieved through 90 μm mesh size, and the chironomid head capsules picked out by hand under a binocular stereoscope. The chironomid remains were mounted on slides under Euparal® as a permanent mounting media. At least 50 head capsules were counted per sample. Wiederholm (1983) and Brooks et al. (2007) were used for identification, and the taxonomic coding followed Schnell et al. (1999).

Statistical Analyses

Water Temperature

The sample sizes of monthly average values of the five lakes were too small to allow for meaningful statistical comparison of water temperature in 1998–1999 and in 2010–2011. Consequently, weekly median values were used to compare the potential temperature changes during the summer (June–September) within each sampling period. A two-factorial univariate analysis of variance design (SPSS 20.0) was used to test for significant differences between lakes and within the decade of observation and the potential interaction.

Ordination Analysis of Species-Environment Data

We first analyzed the species-environment data of the larger 1998–1999 data set in order to assess the main environmental gradients that influence the biota. The final size of the three species-environment data sets is 42 lakes for diatoms, 32 lakes for chrysophyte cysts, and 44 lakes for chironomids (due to loss of sediment traps for cysts and low concentrations of diatoms in some samples). All environmental variables were tested for skewness and, if necessary, $\log_{10}(x + 1)$ transformed prior to data analyses, whereas the species data were square-root transformed. Detrended correspondence analysis (DCA) with detrending-by-segments and nonlinear rescaling of axes was used to estimate the gradient length of the diatom, chrysophyte cyst, and chironomid data in terms of standard deviation (SD) units of biological turnover. The gradient lengths (3.9, 2.3, and 2.4 for diatoms, chironomids, and chrysophyte cysts, respectively) indicated that unimodal methods were appropriate for further ordination analyses (Birks, 1995). A series of constrained CCAs (canonical correspondence analyses) with associated Monte Carlo permutation tests (999 unrestricted permutations, $P \leq 0.01$) were run to identify a subset of the environmental variables described in Kamenik et al. (2001a) that would statistically significantly explain the variation in the species data. To reduce the amount of redundancy in our data, we then divided the resulting environmental variables into three groups representing (1) catchment/lake morphometry, (2) water chemistry, and (3) temperature. We assigned altitude to the catchment/lake morphometry variables instead of the group representing temperature. Due to, for example, topographic shading, local snow fields, and differences in lake volume, lake water temperature can not always be inferred from altitude alone: Thompson et al. (2005) found a rather poor relationship between water temperature and altitude in the Niedere Tauern 44-lake set used in this study.

Within each group we used variance partitioning to assess the relative explanatory power of the environmental variables. This was done using CCA and partial CCA to estimate the marginal effects of each gradient and to partition the total variance in the data into components related to (1) the unique or independent contributions of each variable, (2) the conditional effects or covariances between the variables, and (3) the unexplained variance (Borcard et al., 1992). Finally, to assess the change in the biota along the environmental gradients, we performed a CCA of the 1998–1999 and 2010–2011 samples including the final subsets of our statistically significant environmental variables for the 1998–1999 data. The 2010–2011 samples of the biota were added as supplementary (passive) samples to the analysis. DCA and CCA were performed with the computer program CANOCO for Windows, version 5.01 (ter Braak and Šmilauer, 1997–2012).

Species Diversity

The widely used diversity index Shannon H was calculated using the PAST 3.07 statistical software (Hammer et al., 2001). The formula for the Shannon H is $-\sum P_i(\ln P_i)$ where P_i is the proportion of each species in the sample.

RESULTS AND DISCUSSION

Summer Temperature and Ice Cover

Water temperature was highly variable but differed consistently between the five lakes during the summer due to lake specific characteristics ($p < 0.01$). Within the decade of observation, the water temperature increased significantly in July (TWA: 0.1 °C; WIR: 0.6 °C; MOA: 0.8 °C; OLA: 1.0 °C; and GIG: 1.3 °C; decadal effect $p < 0.05$) and in September (OLA: 1.3 °C; MOA: 1.4 °C; GIG: 1.6 °C; TWA: 1.6 °C; and WIR: 1.7 °C; decadal effect $p < 0.001$). No interaction between lake and decadal warming effect was observed, suggesting that all lakes showed a relatively similar response. The four ZAMG weather stations located in the study area (Sonnblick [3109 m a.s.l.], Rudolfshütte [2317 m a.s.l.], Schmittenhöhe [1956 m a.s.l.], Obertauern [1772 m a.s.l.]) showed higher July temperatures ($p = 0.025$) in 2010–2011 compared to 1998–1999.

The ice cover duration in all lakes was clearly shorter during the winter 2010–2011 when com-

TABLE 2

Duration of ice cover (in days) for the study lakes as estimated between date of autumn mixing (first day in autumn when water temperature decreases to <4 °C) and spring mixing (last day in spring when water temperature increases to >4 °C) at the end of the 1990s and during 2010–2011. See Table 1 for study lakes abbreviations.

Year	OLA	MOA	GIG	TWA	WIR
1998–1999	224	223	221	240	209
2010–2011	211	187	212	221	172
Difference	*−5.8%*	*−16.1%*	*−4.1%*	*−7.9%*	*−17.7%*

pared to the winter 1998–1999. The largest decrease in the ice cover duration was observed in WIR and MOA (37 and 36 days, respectively), while the smallest was reported for GIG (9 days) (Table 2). The shorter ice cover duration times correlated significantly with earlier spring mixing ($R^2 = 0.85$) but not with the date of autumn mixing ($R^2 = 0.12$). Consequently, the shorter ice coverage could rather be explained by earlier ice breakup in spring than by later ice formation during autumn.

Water Chemistry

Overall the chemical variables recorded during 1998–1999 and 2010–2011 revealed little change compared to the physical variables (above). The only clear change was a DOC decrease in OLA (Table 3). Some variables showed a systematic change: Mg and Cl values were higher in all lakes in 2010–2011, while Na and pH values were lower. The differences in the first three variables were, however, extremely small. The observed decreases in pH contradict earlier findings from the Alps, which report a strong positive relationship between lake temperature and pH (Sommaruga-Wögrath et al., 1997) linked to the length of the ice cover period (gas exchange, productivity) and catchment weathering. In our data set pH is strongly correlated with alkalinity ($\rho = 0.92$), conductivity ($\rho = 0.85$), calcium ($\rho = 0.91$), and magnesium ($\rho = 0.64$), $P > 0.00042$ (Kamenik et al., 2001a). As none of these variables shows any clear change between the study periods, the most plausible explanation for the systematically lower pH is an effect of CO_2 oversaturation (which depends on, for example, the period since ice out, primary production vs. respiration, and stratification vs. mixing), as the sampling in 1998–1999 occurred slightly later in the season than in 2010–2011 and was based on a single sample.

Diatoms

The most distinct changes observed in the diatom assemblages of our five lakes between the two studied time periods (Fig. 2, part a) are (1) the clear increase in *Achnanthidium minutissimum* (and varieties) in three of the lakes at the expense of either *Staurosira* (MOA and WIR) or *Aulacoseira* taxa (OLA), (2) the appearance of new *Cyclotella* taxa in TWA and GIG (*C. stelligeroides* and *Cyclotella* aff. *gordonensis* at the expense of *C. comensis* and the *Fragilaria delicatissima/tenera/nanoides* group (TWA) and *Staurosira* taxa (GIG), and (3) the increase in the abundance of the planktic *Fragilaria delicatissima/tenera/nanoides* group in OLA. In addition, *Asterionella formosa*, which was not present in any of the studied 41 lakes of the 1998–1999 data set, was found at low abundances in MOA in 2010–2011 (not shown in Fig. 2). The enumeration of phytoplankton showed a stable occurrence of *A. formosa* during these years (S. Blank, R. Kurmayer, unpublished data).

In polar and alpine regions, *Achnanthidium minutissimum* typically grows attached on various substrates such as stones and aquatic mosses (Keatley et al., 2006; Lotter et al., 2010). The significant expansion of *A. minutissimum* could potentially be explained by increased habitat availability with a longer ice-free season. Wunsam et al. (2002) observed in a study on Traunsee, an Alpine hardwater lake, that the species is opportunistic and takes advantage when rapid environmental changes take place. The simultaneous decline in epipelic and -psammic *Staurosira* species (*S. pseudoconstruens, S. aff. venter*, and *S. robusta*), which have been found to dominate alpine and arctic lakes with extensive ice cover (Schmidt et al., 2004; Smol et al., 2005; Rühland et al., 2008, and references therein) supports this interpretation. In Canadian High Arctic lakes,

TABLE 3

Water chemistry of the studied lakes. Average early autumn values are shown for 2010–2011 and are comparable with the 1998–1999 sampling times. Abbreviations for studied lakes are explained in Table 1.

	Cond (μS cm^{-1} at 25 °C)	pH (units)	Alk (μeq L^{-1})	DOC (μg L^{-1})	NO_3-N (μg L^{-1})	NH_4-N (μg L^{-1})	Ptot (μg L^{-1})	Pdis (μg L^{-1})	DRSi (μg L^{-1})	SO_4 (mg L^{-1})	Cl (mg L^{-1})	Na (mg L^{-1})	K (mg L^{-1})	Mg (mg L^{-})	Ca (mg L^{-1})
MOA															
1998–1999	32.5	7.3	197	598	223	1	2.9	1.3	1327	3.5	0.09	0.58	0.3	0.27	5.3
2010–2011	30.2	6.5	196	478	193	5	3.7	1.8	1175	2.9	0.16	0.51	0.3	0.29	4.6
OLA															
1998–1999	13.8	7	61	1007	62	4	2.2	1.4	705	2.2	0.08	0.32	0.27	0.13	2.1
2010–2011	14.4	6.3	71	635	64	2.5	2.6	1.1	650	2.1	0.1	0.29	0.28	0.14	1.9
TWA															
1998–1999	74.9	7.9	558	667	0	1	3.2	2.1	419	8.4	0.1	0.48	0.18	2.5	9.5
2010–2011	72.2	7.4	550	583	0	2.5	3.5	1	669	7.2	0.14	0.44	0.18	2.9	8.9
GIG															
1998–1999	73.5	7.8	579	801	43	3	5.6	3.3	644	5.6	0.16	0.48	0.15	1.8	10.7
2010–2011	74.3	7.7	604	814	11	3	4.2	2.1	530	5.8	0.19	0.44	0.15	2.2	10.9
WIR															
1998–1999	86	7.7	738	490	141	6	3.2	1.8	1072	4.9	0.13	0.6	0.23	1.4	14.2
2010–2011	88	7.4	749	522	157	6.5	2.6	1	1037	5.1	0.16	0.57	0.23	1.7	14.2

Notes: Cond = conductivity, Alk = alkalinity, DOC = dissolved organic carbon, Ptot = total phosphorus, Pdis = dissolved phosphorus, and DSRi = dissolved reactive silica.

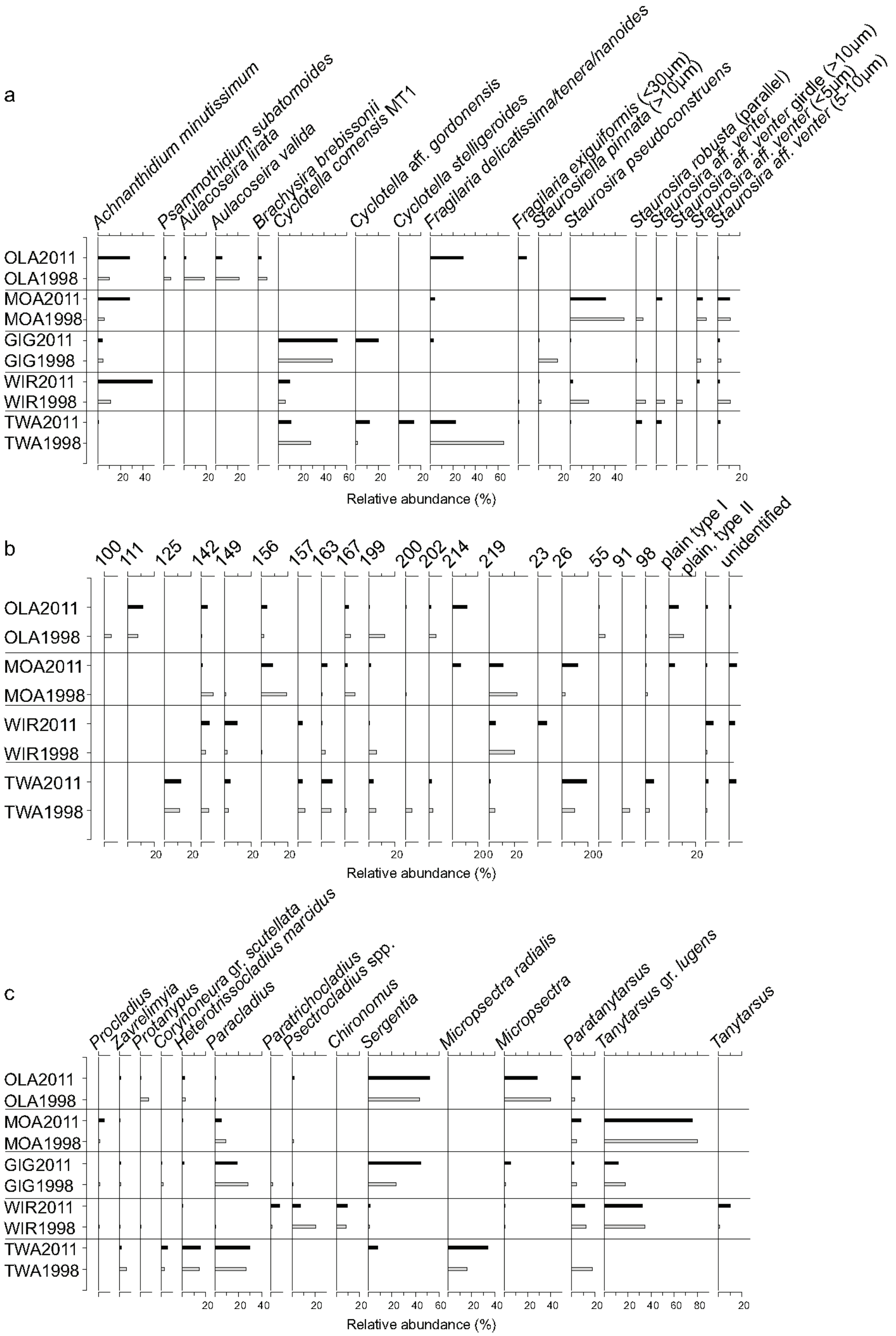

FIGURE 2. Relative abundances of the most common taxa (>5% in at least one sample): (a) diatoms, (b) chrysophyte cysts, and (c) chironomids. Data from 1998–1999 are shown in gray, while data from 2010–2011 are shown in black.

increases in *A. minutissimum* during the early 20th century have been linked to climate warming (Antoniades et al., 2005; Keatley et al., 2006). In TWA and GIG, similar changes were not observed as *A. minutissimum* is either nonexistent or occurs at very low abundances due to their depth (33.6 and 18 m, respectively), which lowers the light availability for benthic algal and macrophyte growth.

In the three deepest lakes—TWA, GIG, and OLA—the main changes have happened within the planktic community. The decrease in *Aulacoseira* species (*A. valida*, *A. lirata*, and other less abundant *Aulacoseira* taxa) in OLA is what would be expected with a longer open-water season and increased temperatures. These species are heavily silicified and need turbulent conditions to stay in the epilimnion (Reynolds, 1994; Rühland et al., 2015). Stronger temperature stratification in the summer would provide less favorable conditions for them to thrive. On the contrary, the long needle-like (high surface area to volume ratio) and less-silificied planktic *Fragilaria* taxa (the *Fragilaria delicatissima/tenera/nanoides* group), which increased in abundance in OLA, would thrive well under such conditions (Rühland et al., 2015).

The increase in *Cyclotella* aff. *gordonensis* (MT2) and *C. stelligeroides* in GIG and TWA are somewhat difficult to explain, as little information exists on their ecology. However, both species are very small (generally < 5 μm), even smaller than *C. comensis* (Kling and Håkansson, 1988; Wunsam et al., 1995), which may be why they are favored during a stronger/longer-lasting summer stratification (slower sinking rates [although depending on physiological state] and more efficient nutrient uptake dynamics/blooming in deeper subsurface habitats where nutrient concentrations are somewhat elevated within the nutrient-poor/depleted epilimnion). Several studies have reported that during a longer growing season and periods of high stability small centric diatoms (e.g., small *Cyclotella*) are able to out-compete larger-sized cells under intensified stratification (Rühland et al., 2008; Catalan et al., 2013; Rühland et al., 2015, and references therein). These changes in the thermal regime are related to decreased ice cover duration in arctic and alpine lakes (Smol and Douglas, 2007; Rühland et al., 2008; Prowse et al., 2011). Saros and Anderson (2014) provide a detailed discussion on *Cyclotella* abundance in lakes in relation to thermal stratification and the interaction of water column stability, light, and nutrients.

Finally, the appearance of *A. formosa* in Lake MOA only is noteworthy. *A. formosa* is an opportunistic diatom species that responds rapidly to disturbance and nutrient enrichment (Saros et al., 2005). It is generally classified as a mesotrophic species (Spaulding et al., 2010). McKnight et al. (1990) found its growth was accelerated by in-lake nitrogen additions, which was confirmed by culturing experiments (Interlandi and Kilham, 1998). More recently, Saros et al. (2005) reported that although *A. formosa* is indicative of P enrichment in temperate lakes, its recent increase in Canadian oligotrophic alpine lakes is in fact driven by N enrichment. MOA had clearly the highest NO_3-N concentrations of our lakes during both observational periods (mean values for 1998: 223 μg L^{-1} and 2010–2011: 193 μg L^{-1}). The high NO_3-N possibly originates from regular fish feeding by an automatic vessel and/or pasturing (personal observations by R. Kurmayer). Also WIR had relatively high NO_3-N values, whereas the concentrations in the other three lakes were much lower. In Unterer Landschitzsee, Schmidt et al. (2002) found that *A. formosa* appeared when air temperatures began to increase after cold climate periods during preanthropogenic times. It is possible that the higher nitrogen concentrations of MOA only stimulated the growth of *A. formosa* when the lake became warmer. The likely importance of both sufficient nutrients and a stronger thermal stratification for *A. formosa* were also postulated by Rühland et al. (2015).

The overall changes observed in the diatom communities agree well with a large survey on arctic and subarctic lakes by Smol et al. (2005), who found recent (post-1850) increased abundances of small planktic *Cyclotella* taxa at the expense of *Fragilaria* spp. and tychoplanktic taxa such as *Aulacoseira* spp. in the deeper lakes, linking these changes to reduced ice cover and/or enhanced thermal stratification. This has been supported by later studies, including another comprehensive survey by Rühland et al. (2008), who found similar changes in diatom communities not only in arctic, but also in alpine and temperate lakes. Rühland et al. (2015) provided an in-depth review on this phenomenon.

Chrysophyte Cysts

Although information on the responses of total chrysophyte cyst assemblages to several environmental variables exist via work with inference models (transfer functions: e.g., Facher and Schmidt, 1996; Kamenik and Schmidt, 2005; Pla and Anderson, 2005; Pla and Catalan, 2005; Hernández-Almeida et al., 2015), there is relatively little known about the autecology of individual cysts (Duff et al., 1995, 1997; Wilkinson et al., 2001; Betts-Piper et al., 2004). For the majority of the cyst morphotypes, it is still not known which species is forming them (Zeeb and Smol, 2001; Huber et al., 2009). This poses a challenge for the interpretation of the changes in the chrysophyte cyst assemblages that have taken place between 1998–1999 and 2010–2011 (Fig. 2, part b). Most cyst morphotypes with known ecological preferences occurring in our lakes are described in literature as oligotrophic, Arctic/alpine species. Several species present in 1998–1999 are not present in 2010–2011 and vice versa.

For cysts with known ecological preferences, we observed several distinct changes: Cyst 26 (described as #26 in Facher and Schmidt, 1996, and as PEARL #161 in Duff et al., 1995) increased in abundance in two of the lakes in 2010–2011 compared to 1998–1999 (MOA and TWA). This cyst has been assigned to the chrysophyte species *Dinobryon divergens* (Duff et al., 1995), which is a typical constituent of the early spring-summer blooming. Cyst 199 (described as PEARL #113 in Duff et al., 1995) is an oligotrophic, cool-water taxon. It occurred in three lakes in 1998–1999 (WIR, TWA, and OLA), but decreased clearly in 2010–2011 in OLA and WIR. Cyst 214 (described as #112 in Facher and Schmidt, 1996), an acidic species showing a preference for lower altitudes, and hence longer open-water seasons (Facher and Schmidt, 1996), was present only in 2010–2011 at moderate abundances in MOA and OLA. These changes could be caused by the observed earlier ice breakup and the longer open-water season. We can also see clear changes in cysts 219 (described as PEARL #219 in Duff et al., 1995) and 156 (described as #59 in Facher and Schmidt, 1996, and as PEARL #210 in Duff et al., 1995), unfortunately the autecological information on these taxa is either very general (156) or not known (219).

Chironomids

The chironomid assemblages recorded during both time periods consisted mainly of cold stenothermal taxa known from oligotrophic waters. Among the most abundant taxa in these lakes are the profundal *Tanytarsus* group *lugens*, *Micropsectra radialis* and the common and abundant Chironomini genus *Sergentia*, all inhabitants of mountain lakes in Alpine Central Europe (e.g., Lotter et al., 1997; Luoto and Nevalainen, 2013). The high abundance of *Paracladius* in two of the lakes (TWA and GIG) is noteworthy, as it has rarely been recorded (and usually at low abundances) in European mountain lakes.

In our five lakes, the chironomid assemblage composition is different for each lake in terms of taxa dominance, however, in general the same chironomid taxa which dominated in each lake during 1998 also dominated in 2011 (Fig. 2, part c). Some taxa, albeit few, showed changes: In TWA, *Paratanytarsus* spp. (Partind) was dominant in 1998, but was not present in 2011, while *Micropsectra radialis* (Micr rad) became more abundant. In WIR, *Psectrocladius* spp. (Psecind) decreased from 1998 to 2011. And finally, in GIG, *Sergentia* (Sergind) became more abundant in 2010–2011 (Fig. 2, part c). In addition to changes in individual taxa abundance, the number of head capsules counted in 2011 was higher than in 1998. In 2011, most lakes had values around 20–30 head capsules (HC) per gram wet weight of sediment, except lake TWA, which is located at the highest altitude and is the least productive of the lakes (HC: 3.5–6 HC g^{-1} WW).

The high decadal stability of chironomid genus/species composition was confirmed by the high similarity in taxa dominance between 0–2 cm and 2–4 cm taken in 2011 (latter data not shown here). In contrast to algal communities (diatoms and chrysophytes), chironomids did not show a clear response to the observed temperature increase and longer open-water season. Temperature-related variables, trophic status, conductivity (ions), and depth exert a strong influence on Alpine chironomid communities (Catalan et al., 2009). Of these, only temperature-related variables showed a significant change between 1998–1999 and 2010–2011. As our lakes stratify in the summer—the deeper lakes displaying a larger temperature difference between surface and bottom waters—hypolimnetic temperatures were likely not strongly affected by the epilimnetic temperature increase, mainly because this increase would further strengthen lake stratification. The stable lake chemistry between the observed periods and the permanently colder hypolimnion may explain why little change was observed in the chironomid communities.

Ordination Analyses

The subset of environmental variables identified by a series of constrained CCAs was divided into three groups representing (1) catchment/lake morphometry, (2) water chemistry, and (3) temperature. By using variance partitioning within each group to assess the relative explanatory power of the environmental variables (Table 4), we identified the two strongest variables in each group shown in the ordination diagram of Figure 3 (in some cases less than two variables were statistically significant in the constrained CCAs). For diatoms, these variables included ice cover duration, July temperature, pH, DOC, and lake depth; for chrysophyte cysts, June temperature, date of spring mixing, chloride, dissolved phosphorus, and the % of grass/dwarf shrubs in the catchment; and for chironomids, May temperature, altitude, maximum depth, the % of shrubs in the catchment area, DOC, and chloride (Fig. 3). The amount of chloride in alpine lakes correlates strongly with catchment vegetation, as thicker soils allow more chemical weathering (Kamenik et al., 2001a). These variables relating to the altitudinal gradient, tropho-dynamic status, acid-base balance, and lake size have been found in other studies to define the distribution of alpine lake biota (e.g., Lotter et al., 1997; Kamenik and Schmidt, 2005; Catalan et al., 2009).

In the CCA, the 2010–2011 data were added as passive samples to the ordination. The position of the 2010–2011 samples in the ordination biplot in Figure 3 is defined by their species assemblages only, and samples with a similar species composition to the 1998–1999 assemblages will be located close to these. Their environmental setting can be read from their species-based position in the biplot along the environmental gradients. The greatest change in the diatom assemblages can be observed in lakes MOA and WIR. A large part of this change occurs along the lake temperature/ice cover duration gradients. These were the lakes that witnessed the largest decrease in ice cover between the two study periods. In MOA, the change in diatom assemblages along the pH gradient could be explained by higher productivity during summer months in 2010–2011 (as indicated by the appearance of the mesotrophic *Asterionella formosa*). The chrysophyte cyst assemblages show the largest change in OLA, along the gradient of catchment vegetation (grass/dwarf shrubs and Cl^-). This change suggests a more vegetated catchment in 2010–2011, which binds the soil more effectively and could decrease the load of DOC to the lake (as observed by measurements between the study periods) (Wetzel, 2001).

TABLE 4

Marginal and unique effects of environmental variables, which were statistically significant at $p \leq 0.01$ in the constrained canonical correspondence analyses (CCAs). Marginal effects denote percentage variance explained by each environmental variable as the sole predictor (constrained CCAs); unique effects in this exercise denote percentage variance explained by each environmental variable within their own group ([1] catchment/lake morphometry, [2] water chemistry, and [3] temperature) with the remaining group variables treated as covariables. Max depth (diatoms) and % grass ds^{-1} (chrysophytes) were the only significant variables in their group.

Diatoms			Chrysophytes			Chironomids		
Variable	Marginal	Unique	Variable	Marginal	Unique	Variable	Marginal	Unique
pH	9.2	3.0	Spring mix	7.1	3.7	Altitude	11.2	3.4
DOC	5.4	3.2	June temp	6.9	4.0	May temp	9.8	3.4
July temp	5.2	2.1	Cl	5.6	3.3	% shrubs	7.9	3.2
Ice cover	4.4	2.2	% grass ds^{-1}	5.1	—	Max depth	6.5	2.3
Max depth	4.2	—	Pdis	4.6	3.2	Cl	6.0	3.5
						DOC	5.2	3.2

Notes: DOC = dissolved organic carbon, Pdis = dissolved phosphorus, Grass ds^{-1} = grass/dwarf shrubs, temp = temperature, mix = mixing.

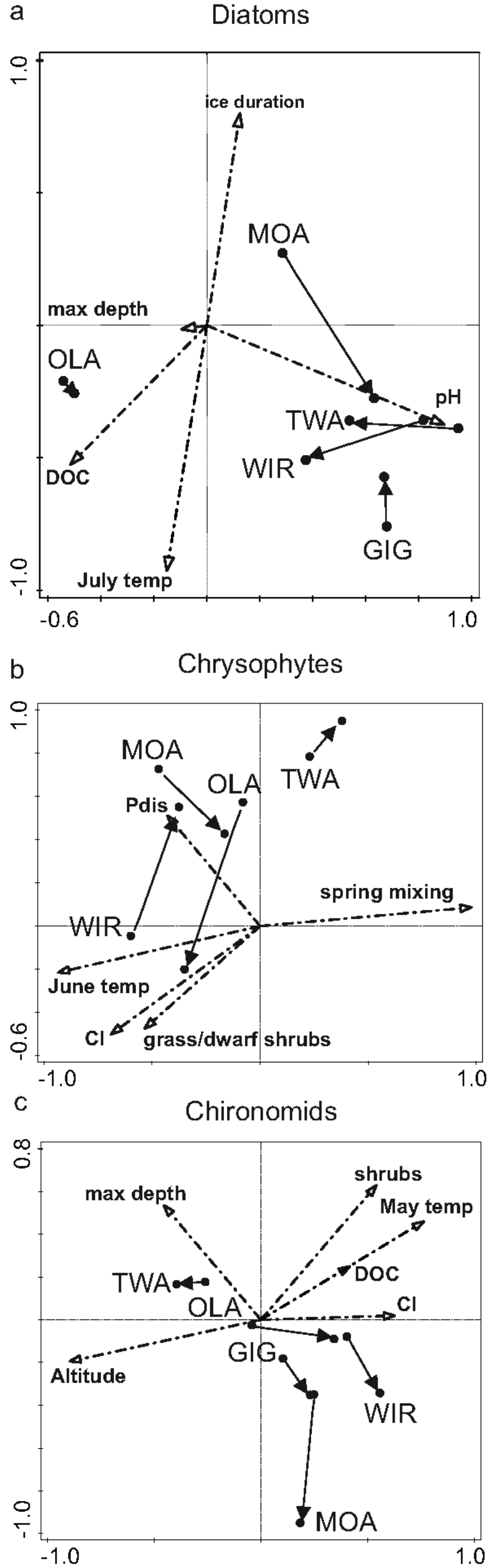

FIGURE 3. A canonical correspondence analysis biplot showing the difference between the 1998–1999 and 2010–2011 samples for diatoms, chrysophyte cysts, and chironomids. Arrows indicate the direction of change. The 2010–2011 data were added as supplementary (passive) samples.

The chironomid assemblages show little change, apart from MOA. This change happens largely along environmental gradients not included in the ordination diagram (Fig. 3). The abundance of the dominant chironomid species in MOA, however, is the same during both study periods (Fig. 2).

It appears that diatom communities show the clearest response to the observed water temperature increase and decrease in ice cover duration, whereas chrysophyte and chironomid communities change along other gradients (in lakes where change can be observed). Interestingly, both for diatoms and chrysophyte cysts, individual (indicator) species show responses to the measured decrease in ice cover duration/increased water temperature, whereas the overall community change along these gradients is less clear. The relevant question (e.g., for environmental monitoring or conservation biology) then is whether one should rely more on the indicator species (with known ecological preferences) or the whole community response. While the former is more important for conservation biology, monitoring may reveal little change at the ecosystem level as long as there is functional redundancy (Lawton and Brown, 1994; Rosenfeld, 2002). This is because some species (such as diatom species in this study) perform similar roles in communities and ecosystems (e.g., lakes), and may therefore be substitutable with little impact on ecosystem processes.

Diversity

Although diversities may have changed within the entire phytoplankton and benthic communities due to the observed lake water temperature increase and increase in the open-water season (e.g., see Schabhüttl et al., 2013), the diversity of our organism groups shows relatively little variability between the two study periods; only in TWA a clear increase in diversity was observed for diatoms (Table 5). However, this is rather based on the exceptionally low diatom diversity in 1998 than on an unusually high diversity in 2010–2011.

CONCLUSIONS

The aim of this study was to assess changes in diatom, chrysophyte, and chironomid communities of a set of climate-sensitive mid-Alpine lakes in Austria in relation to climatic warming by comparing commu-

TABLE 5

Diversities of the three organism groups in 1998–1999 and in 2010–2011 (Shannon H). Lake abbreviations are explained in Table 1.

	Diatoms		Chrysophytes		Chironomids	
	1998–1999	2010–2011	1998–1999	2010–2011	1998–1999	2010–2011
MOA	1.93	2.23	2.80	3.16	1.07	0.91
OLA	2.91	2.60	3.31	3.17	1.31	1.25
TWA	0.94	2.60	3.08	2.89	1.69	1.64
GIG	2.17	1.85	—	—	1.75	1.83
WIR	3.12	2.97	3.63	3.36	1.75	2.00

nity and environmental data from 1998–1999 to data from 2010–2011. While lake chemistry was generally stable between the study periods, we observed an increase in lake water temperature and a decrease in ice cover duration. Several of the dominant diatom species and chrysophyte cyst types show relatively clear changes, which can be interpreted as a response to increased temperature stratification and a shorter ice cover period/longer growing season. The changes observed in the diatom communities of these Alpine lakes are similar to changes reported from arctic and subarctic lakes linked to climate warming. The responses of the whole communities are less clear, although in particular diatom assemblages show a distinct change along the climatic gradients in the lakes with the largest decrease in ice cover duration (MOA and WIR). Chironomid communities appear to be less sensitive compared to diatoms and chrysophyte cysts, which are known for reacting quickly to changes in their environment. The stable lake chemistry between the observed periods and the permanently colder hypolimnion may explain why little change was observed in the chironomid communities. Regarding chrysophyte cysts, more information on their ecological preferences are clearly needed to increase their value as an environmental proxy. The biota of the five study lakes responded to the observed change in climatic parameters rather individually, which is probably caused by local habitat-specific influences (hydrology, topographic shading, catchment characteristics etc.). No real change in diversities was detected in any of the organism groups.

Undercooled lakes (like MOA), which are nutrient-rich due to human activities in the catchment area will possibly experience increased algal growth in the near future as the ice-free period increases with climate change. Such shifts in productivity would have significant consequences on the ecosystem level, for example, high algal biomass production during summer and increased oxygen consumption in the sediments due to sinking algal biomass leading to bottom water hypoxia/anoxia. Accordingly, in MOA the effects of increasing temperatures were more pronounced because of the high nitrate concentrations and resulting eutrophication. Such conditions may also create favorable niches for opportunistic Cladocera species affecting higher levels of the food web. In the future, efforts to preserve the pristine nature of these remote alpine lakes should be intensified, which is of relevance not only and most importantly from the perspective of lake conservation, but also as the use of these lakes for various recreational activities is expected to increase during summer heat waves like in Europe in 2003 (e.g. Chase et al., 2006).

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