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Climate-induced changes in the trophic status of a Central European lake

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ABSTRACT

We present a case study of the development of Sacrower See, a stratified, eutrophic lake in northeastern Germany, over the past 13,000 years. Total epilimnetic phosphorus (TP) concentrations were reconstructed quantitatively using a diatom-TP transfer function. Fossil chironomid assemblages were used to support the trophic reconstruction and helped assessing past hypolimnetic oxygen availability. The results indicate eutrophic and anoxic conditions during the Younger Dryas cold period (~12,700-11,600 cal. BP) preceding the present interglacial. Throughout the early and mid-Holocene (~11,600-4000 cal. BP) stable oligo- to mesotrophic conditions with diatom-inferred TP values of ~20 µg L^{-1} prevailed. First evidence of increasing Holocene TP is recorded at ~3500 cal. BP associated with Bronze Age human impact and for the past 900 years diatoms indicate increasing TP values of 30-60 µg L^{-1}. During the early Holocene and the past two millennia chironomids indicated anoxic hypolimnetic conditions. The chironomid fauna is considered typical of oligo- to mesotrophic lakes. As a consequence of strongly increased primary production the hypolimnion of Sacrower See became anoxic again during the past 140 years. Our results indicate that highly productive eutrophic conditions can exist prior to cultural eutrophication. At Sacrower See the shift from eutrophic conditions in the Lateglacial to oligo-mesotrophic conditions in the early and mid-Holocene was associated with the climatic warming at the Younger Dryas/Holocene transition. The high productive state during the cold Younger Dryas is associated with changes in seasonality: the prolonged winters caused longer ice cover, stronger stratification, anoxia in the hypolimnion, and consequent internal phosphorus loading. During the warm Holocene, however, hypolimnetic anoxia and internal phosphorus loading decreased significantly, resulting in a substantially lower productivity.

Key words: palaeolimnology, total phosphorus, oxygen, diatoms, chironomids, climate change

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1. INTRODUCTION

Nutrient enrichment has become a major threat to freshwater ecosystems (e.g., Smol 2008) and has consequently received considerable attention on the political agenda. Climate change in combination with human induced eutrophication of lakes via nutrient loading through agriculture, industry, sewage release, and soil erosion can lead to adverse consequences for ecosystem functioning and services. As a consequence of such anthropogenic nutrient enrichment lakes may experience harmful algal blooms, oxygen depletion, decreased biodiversity, and/or massive fish kills (Moss 2008; Schindler 2001). Some lakes are, however, naturally nutrient-rich due to the local geological or morphological setting, whereas others can experience moderate nutrient enrichment throughout their history as a consequence of natural processes such as abiotic or plant-mediated weathering and transport of nutrients from the catchment to the lake (e.g., Engstrom *et al*. 2000). Nevertheless, it is widely accepted that most temperate European lakes would be oligo- to perhaps mesotrophic in a natural, undisturbed setting and in the absence of human impact.

When defining restoration targets for nutrient-enriched lakes, the lack of pristine reference sites coupled with limited availability of high-quality and long-term monitoring data are a major concern (Moss 2008). Where available, monitoring programs are usually initiated only after the signs of disturbance are evident. The lacustrine sediment record provides an alternative natural archive which allows the reconstruction of long-term ecosystem processes and the assessment of baseline conditions with regard to nutrients and ecosystem functioning which are essential for defining lake restoration aims (e.g., Bennion & Battarbee 2007). Indicator organisms, such as diatoms and chironomids (non-biting midges) that preserve as microfossils in the sedimentary record, are exceptionally useful for inferring past trophic conditions in lakes. Diatoms have been shown to be highly sensitive to changes in lake pH and nutrient concentrations (e.g., Stoermer & Smol 1999). The

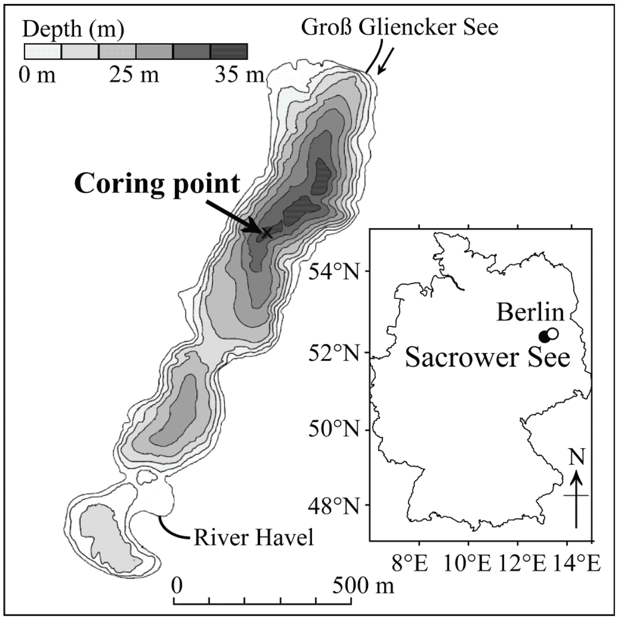

Fig. 1. Location of Sacrower See in an outline map of Germany and bathymetric map of the lake basin.

strong empirical relationship between nutrients and diatom assemblages (e.g., Bennion *et al.* 1996; Anderson 1997; Hall & Smol 1999) has been successfully used to infer past epilimnetic total phosphorus (TP) concentrations (e.g., Wunsman & Schmidt 1995; Lotter 1998; Bennion *et al.* 2000). Similarly, the analysis of chironomid assemblages can provide insights into the trophic state of lakes, especially in deep, stratified systems (e.g., Saether 1979). Since parts of these animals are well preserved as fossils in lake sediments, remains of chironomid larvae can be used for reconstructing TP and changes in hypolimnetic oxygen availability, both using qualitative (e.g., Itkonen *et al.* 1999; Heiri & Lotter 2003) and quantitative approaches (e.g., Lotter *et al.* 1998; Brooks *et al.* 2001; Little & Smol 2001).

Here, we present a palaeolimnological case-study on the long-term trophic development of Sacrower See, a lowland lake in Northeastern Germany. We report an unusual case of climate-induced trophic change under undisturbed, pre-anthropogenic conditions in a deep, stratified lake. Based on fossil diatoms from a continuous sediment record we reconstruct epilimnetic TP throughout the past 13,000 years and discuss factors affecting the lake's nutrient levels. Moreover, remains of chironomids are used as semi-quantitative indicators of hypolimnetic oxygen conditions and independent evidence for changes in trophic state as reconstructed by diatom assemblages.

2. STUDY AREA

Sacrower See is a eutrophic hardwater lake situated in Brandenburg, Germany (Fig. 1), at an elevation of 29.5 m a.s.l. (Tab. 1). The lake was formed during the Weichselian glaciation and presently has a maximum water depth of 38 m (Tab. 1). It is connected hydrologically (subsurface inflow) in the northeast with Groß Glienicker See and in the south with the River Havel *via* an artificial channel and subsurface in- and outflow (Fig. 1). The lake is dimictic and anoxic conditions often develop in the lake's hypolimnion during summer stagnation (Bluszcz *et al.* 2008) but also during winter and autumn.

Tab. 1. Basic morphometric, limnological, and climatic parameters characterizing Sacrower See (after Bluszcz *et al.* 2008).

Altitude	29.5 m a.s.l.
Catchment area	35.3 km^2
Surface area	1.07 km^2
Volume	19.3×10^6 m^3
Maximum depth	38 m
Mean depth	18 m
Mean water residence time	12-15 years
Stratification period	Apr-Nov
Mean annual precipitation	603 mm
Mean summer air temperature	17 °C
Mean annual air temperature	9.6 °C

3. MATERIAL AND METHODS

A 17 m long sediment sequence was retrieved in 2005 from the deepest part of Sacrower See at a water depth of 38 m (Fig. 1) using a modified Livingstone piston corer. The sediments consist of organic-rich calcareous gyttja with distinctly annually laminated sections in the top 40 cm and below 859 cm. The lowermost sediment unit consists of homogeneous, slightly graded sands with occasional lignite fragments interpreted as a slump deposit and consequently omitted

Tab. 2. Radiocarbon dates from the Sacrower See sediment core (Enters *et al*., accepted).

Composite depth (cm)	Lab. No.	Analyzed fraction	$\delta^{13}C$ (‰)	^{14}C Age	^{14}C Age (BP) ±SD	Cal. age range (2δ) (cal. BP)
0	-	Sediment surface	-	-	-	-55
39.5	-	Varves	-	-	-	74-86a
63-64	Poz-6086	Unidentified leaf remains	-26.5	220	±30	140-310
136-138	UtC 14516	*Quercus* leaf	-29.2	381	±32	310-510
272-273	UtC 14517	Unidentified leaf remains	-28.6	1215	±35	1050-1270
417-418	UtC 14518	Unidentified leaf remains	-27.3	2180	±37	2060-2330
512-513	UtC 14519	Unidentified leaf remains	-27.9	2840	±34	2860-3070
593-595	UtC 14520	Unidentified leaf remains	-28.0	3505	±39	3680-3890
671.5-672.5	UtC 14521	Unidentified leaf remains; *Alnus glutinosa* catkin scales	-28.6	4252	±37	4640-4880
784-786	UtC 14522	*Betula* fruit; c.f. *Pinus* cone axis and scale leaves	-29.3	5640	±90	6280-6660
892-893	UtC 14523	c.f. *Pinus* scale leaves and (charred) leaf remains	-28.6	7920	±50	8600-8980
1002-1003	UtC 14524	c.f. *Pinus* scale leaves	-23.1	10180	±130	(12150-12815)
1014-1015	Poz-21521	c.f. *Pinus* bark	-24.8	9500	±50	10580-11080
1107-1108	UtC 14525	*Betula* fruit, *Poytrichum* leaves, unidentified leaf remains	-27.5	10840	±60	(12875-12815)
1173-1176	-	Laacher See tephra	-	-	-	12790-12970b

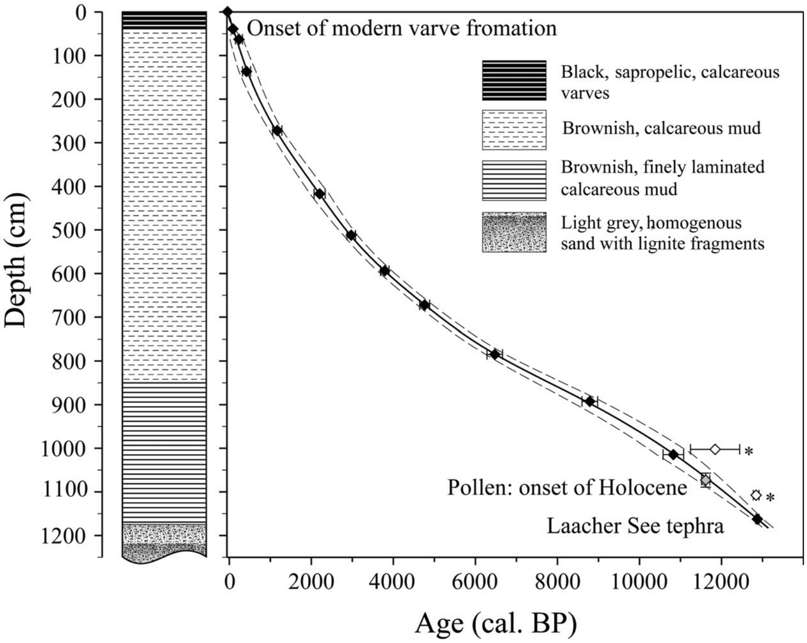

Fig. 2. Dating of the sediment core and age-depth relationship. Dashed lines mark the 95% confidence intervals. The two ^{14}C dates not included in the age-depth model are marked with stars.

from analysis together with an additional slump at 1130-1239 cm depth. This resulted in a final composite sediment profile with a total length of 1183 cm.

The chronology of the sediment record is based on 12 AMS ^{14}C dates measured on terrestrial plant remains (see Tab. 2), the Laacher See Tephra dated to 12,880±40 varve years BP (Brauer *et al*. 1999a), as well as ^{210}Pb and ^{137}Cs dating (Lüder *et al*. 2006). ^{14}C dates were transformed to calibrated ^{14}C years before present (cal. BP) using the program Calib 5.0.2 and the INTCAL04 calibration curve (Reimer *et al*. 2004). Age-depth modeling was performed using a generalized mixed-effect regression model (Heegaard *et al*. 2005; Fig. 2). Two radiocarbon dates in the lower part of the record were clearly too old and were therefore excluded. Preliminary pollen analysis located the onset of the Holocene (i.e., the past *ca* 11,600 years) between 1057 and 1089 cm sediment depth.

Titanium (Ti) was measured by X-ray fluorescence (XRF) analysis on split core surfaces as indicator of soil erosion. For diatom analysis 90 samples were digested with 30% H_2O_2 to remove organic matter. Further details regarding the age-depth model, geochemistry and pollen data are described in Enters *et al*. (accepted). Microscope slides were prepared using the sedimentation tray method (Battarbee 1973) and Naphrax® mounting medium. A minimum of 500 valves was counted on each slide under a light microscope at 1000× magnification using differential interference contrast optics. Taxonomy follows Krammer & Lange-Bertalot (1986, 1988, 1991a, 1991b), Håkansson (2002), and, for *Fragilaria*, Round *et al*. (1990) and Compère (2001).

A diatom TP transfer-function, based on a combined European diatom data-base (EDDI, http://craticula.ncl.ac.uk/Eddi/jsp/) and a Mecklenburg-Vorpommern (North-eastern Germany) calibration dataset (Adler & Hübener 2007; http://www.biologie.uni-rostock.de/abt/botanik/AG-Phykologie/), was used for quantitative TP reconstruction. The modern diatom training set consists of 429 samples and covers a range of 2-1189 µg TP L^{-1}. Diatom-based TP inference is based on weighted averaging partial least squares (WA-PLS) regression and calibration (Ter Braak & Juggins 1993) of square-root transformed diatom percentage data and log transformed TP and was calculated using the software C2 version 1.5 (Juggins 2007). The model features a root mean square error of prediction (RMSEP) of 0.28 log TP units and a coefficient of determination (r^2) of 0.73 as evaluated by leave-one-out cross-validation methods.

Chironomid assemblages from 44 sediment samples were analyzed and identified following Brooks *et al.* (2007). Samples were treated with 10% KOH and sieved with a 100 µm sieve. Chironomid head capsules (hc) and other arthropod remains were sorted from the sieve residue using a dissecting microscope.

Chironomid concentrations were very low in the record and adjacent samples had to be amalgamated to reach more reliable count sums. Since chironomid counts still remained well below the 45-50 hc per sample recommended for quantitative reconstruction (Heiri & Lotter 2001; Quinlan & Smol 2001), no further numerical analyses were attempted.

4. RESULTS

4.1. Diatom assemblage changes

In total 90 diatom assemblages were analyzed in the Sacrower See record. The diatom succession was subdivided into five significant zones as assessed using optimal zonation and the broken stick model (Fig. 3).

In the lowermost zone, Z1 (1184 – 1057 cm) diatom assemblages were dominated by *Fragilaria* spp. (including *Fragilaria*, *Ulnaria*, *Staurosira*, *Staurosirella*, *Synedra*, and *Pseudostaurosira*) and *Stephanodiscus* spp. The most abundant diatom species in this period were *Staurosira construens* f. *venter*, *Fragilaria tenera*, *Ulnaria ulna*, *Stephanodiscus neoastraea*, and *Stephanodiscus parvus*. Chrysophycean statocysts had a high abundance only in the lowermost part of this section.

During zone Z2 (1057-611 cm) *Cyclotella cyclopuncta* was the dominating diatom. Also, *Cyclotella ocellata*, *Puncticulata bodanica*, *Puncticulata radiosa*, *Fragilaria* spp., and *S. neoastraea* frequently occurred in this zone. In contrast, diatoms dominating the previous zone such as *S. costruens* f. *venter*, *Stephanodiscus minutulus* or *S. parvus* mostly disappeared from the record. Around 963 cm *S. parvus* briefly reappeared at low abundances. Chrysophycean statocysts increased in abundance and had a peak between 819 - 755 cm.

In Z3 (611-227 cm), the assemblages were dominated by *Cyclotella comensis* (5 - 80%) and *S. neoastraea* (10-40%). *P. bodanica* and *Stephanodiscus alpinus* also occurred in relatively high frequencies. *Fragilaria* spp. was present at low percentage values throughout the entire zone. *S. parvus* appeared at very low abundances at the beginning of this zone. In contrast with the transition between Z1 and Z2, which was fairly abrupt, the transition between Z2 and Z3 was more gradual in the diatom assemblages of Sacrower See. Chrysophycean statocysts showed low abundances in the entire zone Z3.

In Z4 (227-115 cm), *Aulacoseira islandica* and *Tabellaria flocculosa* increased their abundances and became the dominant species. *S. neoastraea* and *C. comensis* were subdominant species in this section. *C. comensis* and *P. bodanica*, two diatoms abundant in the previous zone, almost disappeared from the assemblages. Similarly, chrysophycean cysts, present at low abundances in the previous zone, are no longer present in Z4.

In Z5 (115-0 cm) diatom assemblages were dominated by *S. neoastraea*, *S. parvus*, and *S. alpinus*. *A. islandica*, *Fragilaria* spp. and *C. comensis* showed increased abundances at the onset of Z5, but were absent from the uppermost sediment layers. *Aulacoseira islandica* and *T. flocculosa* have strongly reduced abundances in Z5 compared with the previous diatom assemblage zone.

4.2. Chironomids

In the lowermost sediments of Sacrower See (>1080 cm) chironomid assemblages are dominated by taxa such as *Stictochironomus*, *Micropsectra radialis*-type, *Tanytarsus lugens*-type, *Paratanytarsus penicillatus*-type, and *Tanytarsus mendax*-type (Fig. 4). At the transition between zone C1 and C2 (1080 cm) a number of chironomids such as *M. radialis*-type and *Tanytarsus lugens*-type disappear from the sediments, whereas others, e.g., *Corynocera ambigua*, *Paratanytarsus penicillatus*-type and *Tanytarsus mendax*-type, show no major change in abundances. In zone C3 (1020-650 cm) assemblages are dominated by taxa such as *M. radialis*-type, *Heterotrissocladius grimshawi*-type, *Micropsectra insignilobus*-type, *T. mendax*-type and from *ca* 850 cm onwards *Sergentia coracina*-type. In zone C4 (650-380 cm) *S. coracina*-type is the dominating chironomid in Sacrower See. Furthermore, a number of taxa which were already present in C1 and C2 reappear in the assemblages, e.g. *Microtendipes* and *P. penicillatus*-type. In C5 (250-380 cm) *S. coracina*-type is still present, although in lower abundances than in the previous zone. Furthermore, taxa such as *Parakiefferiella bathophila*-type and *Tanytarsus pallidicornis*-type1 occur in the samples. In C6 (150-250 cm) *S. coracina*-type, *P. penicillatus*-type, and *P. bathophila*-type are still present in the sediments.

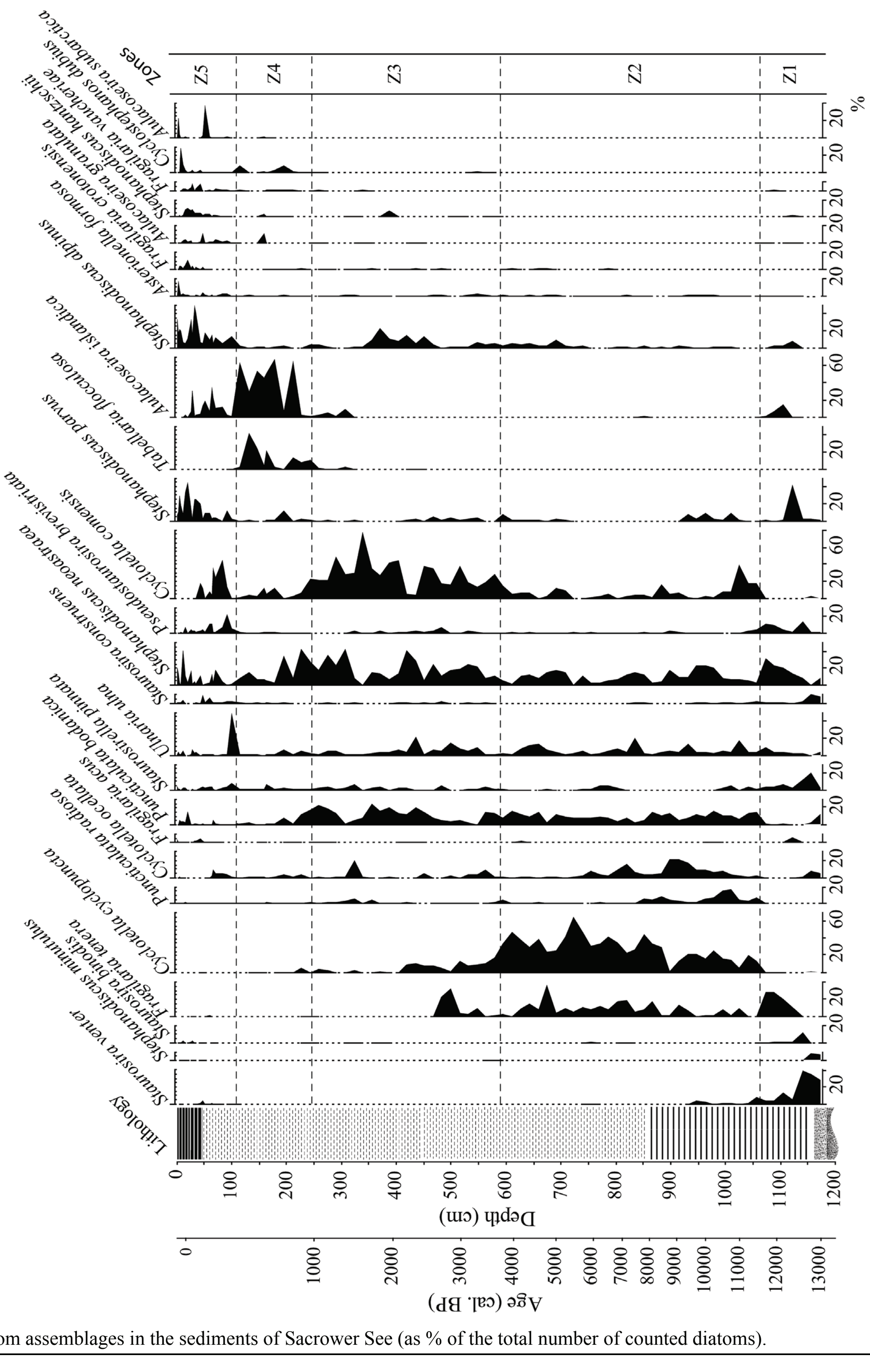

Fig. 3. Diatom assemblages in the sediments of Sacrower See (as % of the total number of counted diatoms).

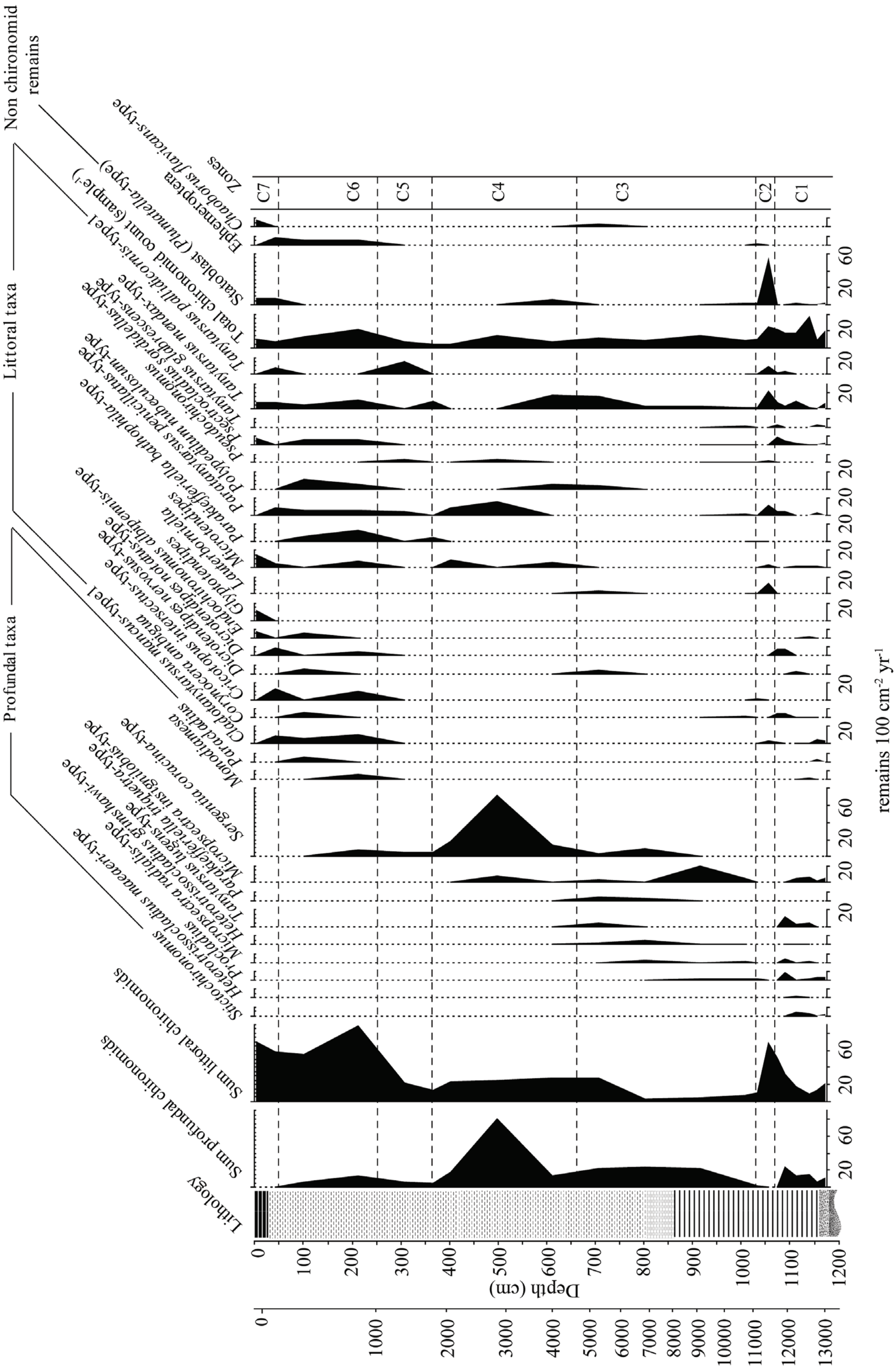

Fig. 4. Accumulation rates of fossil chironomids (as chironomid head capsules per 100 cm^2 per year) and some other invertebrate taxa (as remains per 100 cm^2 per year) in the sediments of Sacrower See.

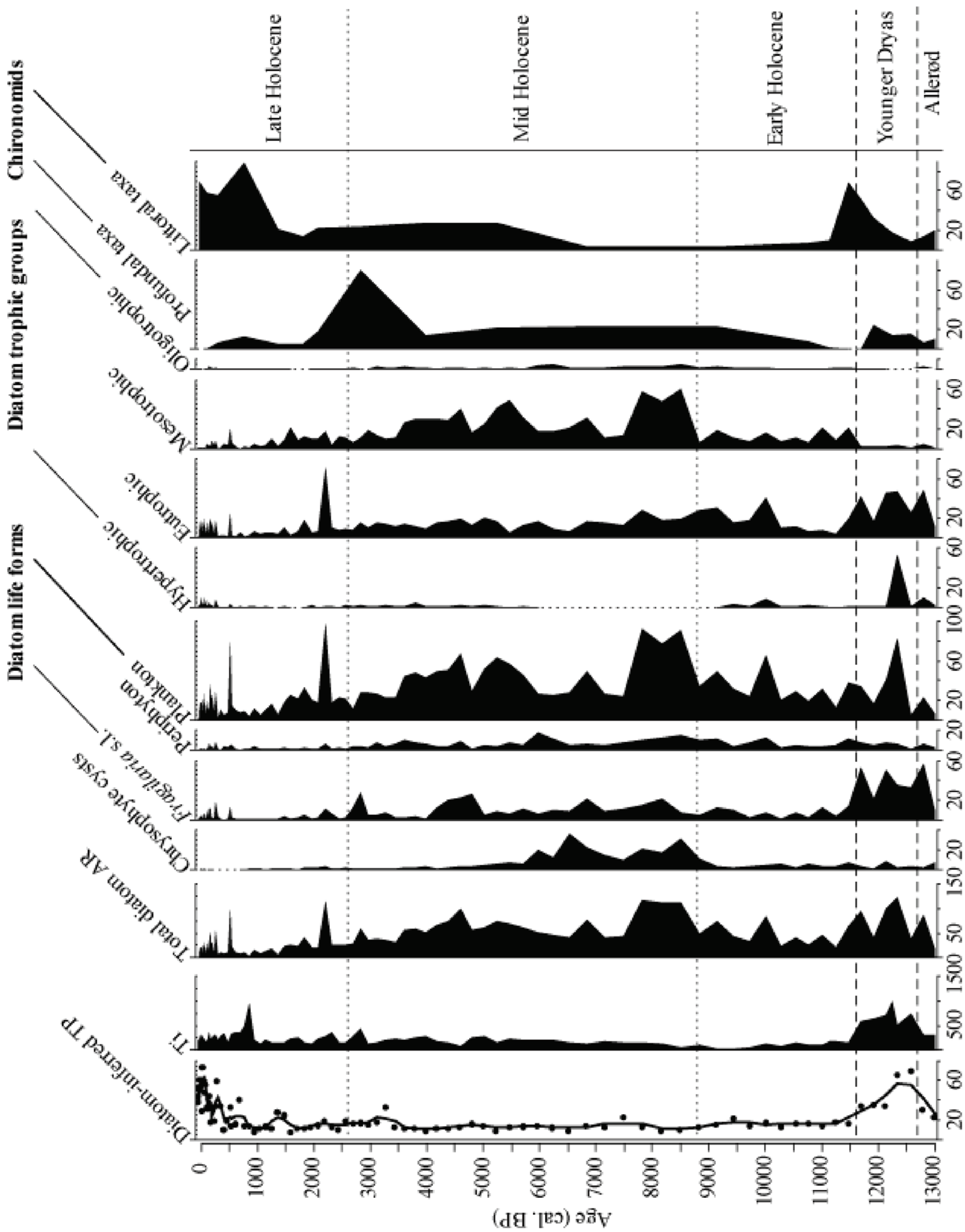

Fig. 5. Diatom-inferred total phosphorus concentration and accumulation rates (AR) for chrysophyte cysts, diatom valves grouped by life-form and trophic category (after Van Dam *et al*. 1994), and for chironomids grouped by habitat preference.

These taxa are joined by chironomids such as *Monodiamesa*, *Polypedilum nubeculosum*-type, *Dicrotendipes notatus*-type, *Cricotopus intersectus*-type and *Cladotanytarsus mancus*-type1. In the uppermost zone C7 (150-0 cm), finally, *S. coracina*-type is absent from the sediment samples, whereas many of the chironomid taxa present in C6 or C5 persevere in the lake.

4.3 Diatom-based TP reconstruction

Diatom-inferred TP (Fig. 5) indicates high nutrient availability in the lowermost part of the record (>1050 cm). Starting with values of 24-30 µg L^{-1}, TP rises to reach maximum values of ~50-70 µg L^{-1} at 1170-1130 cm sediment depth. Diatom assemblages indicate decreasing TP values thereafter and comparatively low TP of 10-20 µg L^{-1} is inferred 1050-220 cm. In Z4 (220-110 cm) reconstructed TP values are very variable and increase again to reach smoothed values around 20-30 µg L^{-1}. In the uppermost part of the sequence diatom-inferred TP continues to increase to reach maximum values of 60-70 µg L^{-1} at *ca* 30-50 cm below the sediment-water interface before decreasing again slightly in the in the surfical sediments.

5. DISCUSSION

Diatom (Fig. 3) and chironomid assemblages (Fig. 4) indicate that the trophic conditions in Sacrower See and the oxygen availability for the benthic fauna have varied distinctly throughout the past 13,000 years. Between ~13,000 and 11,550 cal. BP diatom-inferred TP (DI-TP) (Fig 5) is comparable to present-day epilimnetic TP concentrations (Fig 3). During this period of the Lateglacial diatoms typical of eutrophic to hypertrophic lakes, such as *Stephanodiscus parvus*, *S. minutulus*, *S. neoastraea*, *S. alpinus*, *S. hantzschii*, and of prolonged ice-cover (Douglas & Smol 1999; Lotter & Bigler 2000), such as *Fragilaria sensu lato* (s.l. e.g., *F. tenera*), were abundant. Fossil chironomid assemblages (Fig. 4) during this phase included taxa typical of both profundal and littoral environments. However, many of the chironomids typically restricted to the profundal in temperate lowland lakes can colonize littoral habitats under colder climatic conditions (e.g., Brundin 1949) such as during the Younger Dryas cold phase (~12,700-11,600 cal. BP). In this interval, which represents the last major cold phase of the last glaciation, *Stictochironomus* was present in Sacrower See. This chironomid is commonly found in inorganic sediments in lakes with elevated nutrient conditions (Saether 1979; Heiri & Lotter 2008) and its larvae feature relatively high hemoglobin concentrations (Int Panis *et al.* 1996). The presence of *Stictochironomus* suggests at least seasonally low oxygen concentrations in the lake's bottom water. However, the relatively high accumulation rate of chironomid fossils during the same interval (Fig. 5) indicates that oxygen levels were still sufficient to support larval chironomid populations at or close to the coring site.

Unexpectedly high DI-TP values (~70 µg L^{-1}) are inferred for Sacrower See during the Younger Dryas cold phase (~11,600-12,700 cal. BP, see Fig. 5). Intensified internal recycling of orthophosphate is a mechanism which could explain such high DI-TP values under pre-anthropogenic conditions. The Younger Dryas cold phase is characterized by a marked increase in seasonality (Renssen & Isarin 2001; Brauer *et al.* 2008). During periods of cooler climate and more severe winters, prolonged ice cover can lead to more stable and longer winter stratification. In deep lake basins this can cause prolonged phases of anoxia (e.g., Asikainen *et al.* 2007). Since redox conditions strongly influence the stability of phosphate in the sediments, this in turn may lead to a significant phosphorus release (e.g., Carignan & Flett 1981; Moosmann *et al.* 2006; Spears *et al.* 2008). Such internal loading may exceed the external phosphorus load (e.g., Søndergaard *et al.* 2001). At present, internal loading is at least partly responsible for maintaining high TP concentrations in Sacrower See. Owing to the low oxygen availability during summer stagnation, hypolimnetic phosphate concentrations in the lake may reach extremely high values (up to 4600 µg L^{-1}) due to remobilization of phosphorus from the sediments (Bluszcz *et al.* 2008). During autumn or spring circulation these nutrients are mixed into the photic zone thus enhancing the productivity of the lake substantially (Kirilova *et al.* 2008). Cooler temperatures and prolonged ice cover is likely to have triggered a similar response in the phosphorus cycle of Sacrower See during the Younger Dryas cold phase.

At Meerfelder Maar (Germany) Brauer *et al.* (1999) reported on increased productivity levels during the Younger Dryas. However, they attribute this to nutrient enrichment by soil erosion. Schmidt *et al.* (2002) observed a TP increase in an unlaminated sediments of Längsee (Austria) caused by allochthonous sources rather then reflecting internal phosphorus loading. Although high Ti counts were observed in the Younger Dryas sediments of Sacrower See, suggesting an increase in erosive input, it seems very unlikely that all allochthonous sources could lead to TP values as high as 60-70 µg L^{-1} in a pristine landscape.

A positive relationship between temperature and the nutrient availability in lakes has been reported in a number of limnological studies (e.g., Heiri & Lotter 2005; Lacoul & Freedman 2005). Especially in mountain regions this relationship may be partly explained by higher human activity in the catchment of warmer lowland sites. An increase in nutrient concentrations is also commonly reported as a likely response of temperate and arctic freshwater systems to climatic warming (e.g., Hauer *et al.* 1997; Rouse *et al.* 1997). In contrast, however, the climatic change at the Younger Dryas/Holocene transition (~11,600 cal. BP), in Europe associated with an abrupt summer temperature increase in the range of 2-4 °C (e.g., Lotter *et al.* 2000; Heiri *et al.* 2007) and a decrease in seasonality (Renssen & Isarin 2001), leading to shorter ice cover, less pronounced stratification and weaker anoxia, led to a rapid decrease in nutrient levels of Sarower See (Fig. 5).

After ~11,600 cal. BP DI-TP decreased to values of ~10-20 µg L^{-1} that persisted throughout most of the early and mid-Holocene. Diatoms with eutrophic affinities still were present in the assemblages, although the abundances of mesotrophic diatoms increased (Fig. 5). Laminations are present in the entire lowermost section of the Sacrower See core (Fig. 2), reflecting a perseverance of anoxic conditions and the absence of bioturbation during the Lateglacial and the early Holocene until *ca* 8000 cal. BP. However, chironomids typical of cold hypolimnetic waters were found in the record during most of the Lateglacial and again from *ca* 11,000 cal. BP onwards. This suggests that, with the exception of the short interval between *ca* 11,700 and 11,000 cal. BP, when profundal chironomids were absent from the record, the anoxia did not affect the entire hypolimnion. Most of these deep-water chironomids, such as *Micropsectra radialis*-type, *Heterotrissocladius grimshawi*-type, and *Micropsectra insignilobus*-type, are typical for oligo- to mesotrophic lakes (Saether 1979), which is in good agreement with the DI-TP reconstruction.

Reduced TP concentrations were also reconstructed in Längsee (Austria) during the Allerød period (*ca* 14,000-12, 700 cal. BP) which seemed to be caused by continental climatic conditions initiating a meromictic mixing regime in the lake (Schmidt *et al*. 2002). However, we believe that diatom and chironomid assemblages do not support a stable meromixis at Sacrower See. The main reasons for this conclusion are the presence of profundal chironomid taxa during a large part of the Holocene, suggesting at least seasonal oxygen availability in the lake's hypolimnion. Furthermore, high percentages of *Stephanodiscus* spp. were observed. These diatoms are spring bloomers which require relatively high phosphorus values. This suggests a significant transport of phosphorus from the hypolimnion to epilimnetic waters at least during spring overturn, contradicting a stable meromixis of Sacrower See. The formation of varved sediments can be explained by the temporary formation of an anoxic hypolimnion in the winter (e.g., Lüder *et al*. 2006; Bluszcz *et al*. 2008; Kirilova *et al*. 2008), and reduced oxygen availability and biological activity in the bottom waters in the deepest section of the lake basin.

After *ca* 8000 cal. BP laminations are absent indicating bioturbation by benthic organisms and consequently higher oxygen levels at the lake bottom. *Sergentia coracina*-type has its first occurrences in the lake around this time. *S. coracina*-type is a profundal-dwelling chironomid typical of mesotrophic lakes (Saether 1979) and known to tolerate low oxygen conditions. It is therefore likely that this chironomid colonized the deepest parts of Sacrower See and was at least partly responsible for the bioturbation of the sediments. The dominant diatom species found in this part of the record, *C. cyclopuncta* (Fig. 3), together with the high abundance of chrysophyte cysts (indicators of high Si:P, Fig. 5) are reflecting oligo- to mesotrophic conditions.

Most research shows elevated nutrient conditions during the Holocene due to increased temperatures and external nutrient input (e.g., Brauer *et al*. 1999; Lotter 2001; Baier *et al*. 2004; Brüchmann & Negendank 2004). In the case of Sacrower See, however, both diatom and chironomid assemblages show stable oligo- to mesotrophic conditions and at least seasonally oxygenated hypolimnion throughout the warm Holocene.

From the Bronze Age onwards (*ca* 4000 cal. BP) human influence on the landscape intensified in many parts of Europe and has been recorded in a number of sediment sequences (e.g., Fritz 1989; Wunsam & Schmidt 1995; Lotter 1999; Heiri & Lotter 2003; Zolitschka *et al*. 2003; Dreßler *et al*. 2006).

At Sacrower See an increase in DI-TP to values of ~ 30 µg L^{-1} is registered at ~3500 cal. BP and first minor peaks in Ti in the sediments are apparent from ~3000 cal. BP onwards, indicating increased soil erosion (Fig. 5) (Enters *et al*. accepted). This suggests that the first significant anthropogenic impact in the catchment area of Sacrower See began during the Bronze Age. There is archeological evidence for a local settlement of this time (Gramsch 2001). However, erosive input as recorded by sedimentary Ti remained relatively low until the Medieval Ages. Diatom assemblages were still dominated by mesotrophic diatoms, but *S. parvus*, a diatom typical of hypertrophic conditions reappeared at abundances of up to 10% in some samples. In addition, the decrease of the chrysophyte cysts also suggests a decrease of the Si:P ratio and increased nutrient levels in the lake. Around this time *C. cyclopuncta* decreased and was progressively replaced by *C. comensis* and *S. neoastraea*. Around ~4000 cal. BP chironomids typical for oligotrophic systems, such as *Heterotrissocladius grimshawi*-type and *Tanytarsus lugens*-type disappeared from the lake (Fig. 4). However, *Micropsectra insignilobus*-type, which is known to occur in oligo- to mesotrophic lakes (Saether 1979), persisted in Sacrower See until *ca* 2000 cal. BP and *Sergentia coracina*-type reached its highest abundances in this part of the sequence, suggesting at least seasonal oxygen availability in the deepest part of the lake basin.

Between ~800 and 300 cal. BP DI-TP increased to values between 30 and 40 µg L^{-1}. This rise in DI-TP coincides with a distinct increase in Ti concentrations in the sediments, suggesting enhanced soil erosion (Fig. 5). However, according to the diatom flora the lake was still meso- to eutrophic (DI-TP *ca* 40 µg L^{-1}) until the beginning of the 17th Century. From the 1870s onwards annually laminated sediments were formed again. Together with DI-TP values of *ca* 60 µg L^{-1} and the dominance of *Stephanodiscus* spp. this is strong evidence for an increase in nutrient loading. A geochemical study of Sacrower See varves provides additional evidence for the increase in the primary productivity during this period due to strong nutrient input from the catchment and the eutrophic River Havel, which led to subsequent anoxia (Lüder *et al*. 2006). Anoxic conditions in the lake's bottom waters are also supported by the absence of cold stenothermic profundal chironomids in the uppermost part of the sediment core. In contrast to the lowermost, Lateglacial sediments for which DI-TP also reached values of >60 µg L^{-1}, external nutrient loading is the major cause for the elevated trophic conditions in the lake's recent past.

5.1. Reference conditions

In a large part of Europe cultural eutrophication has affected lakes during the 20th Century and especially since the 1950s. In recent years nutrient concentrations in many of these lakes have started to decline, largely due to the successful reduction of external nutrient loading, or due to measures to decrease the internal remobilization of phosphorus (e.g., Søndergaard *et al*. 2007). However, in many cases the question remains whether these lakes are close to attaining their "natural" nutrient level or whether additional efforts are needed to further decrease P loading, especially where lake ecosystems need to be restored due to legislative actions. For example, the European Water Framework Directive (European Union 2000) aims at reverting European inland waters to a "good ecological quality". In order to achieve this aim, the directive requires reference states that represent ecological conditions in the absence of human impact other than very minor influence (e.g., Bennion & Battarbee 2007; Moss 2008). In this context the results from Sacrower See are noteworthy since they indicate two possible natural nutrient states for this lake depending on climatic conditions: one being meso-oligotrophic throughout several millennia of the temperate interglacial, whereas the other is in the meso- to eutrophic range during the cold phase of the Lateglacial. Furthermore, our results also indicate that deep, stratified lakes such as Sacrower See, can develop highly anoxic conditions in the absence of human impact and that internal nutrient loading can be strongly influenced by climatic conditions. This implies that effects of past and ongoing climate change must be taken into account when defining reference states. Lake ecosystems in different climatic settings, such as the more pristine lakes in mountain regions, do not necessarily provide suitable analogues or limnological reference conditions for lowland lakes.

In a number of palaeolimnological studies top and bottom samples of short sediment cores are used to assess ecological conditions in lakes before and after human impact (Smol 2008). The rationale behind this approach is that the lowermost sediment in a short core will generally predate the 19th Century industrial revolution and biotic assemblages in this sediment will therefore reflect ecosystem conditions before major eutrophication of the industrial period. However, our case study, as well as other examples (e.g., Fritz 1989; Heiri & Lotter 2003; Bradshaw *et al.* 2005), indicate that the eutrophication history of lakes can be complex. For Sacrower See, for example, the first evidence of nutrient enrichment due to human activity can be found as early as the Bronze Age (~3500 cal. BP). In this lake it would therefore be necessary to reach a sediment depth of at least 550 cm to reconstruct ecological conditions before major human influence. This suggests that in regions with a long history of human settlement, agriculture, and land use, e.g. most of central and southern Europe, the results obtained with the palaeolimnological top-bottom approach should be interpreted with caution when defining undisturbed reference conditions for lakes. Individual detailed palaeolimnological studies reconstructing the trophic history of lakes will be necessary to document the applicability of the top-bottom approach for a given region and to assess whether the pre-industrial sediments represent undisturbed reference conditions or simply the ecological state under more moderate human impact before peak eutrophication.

6. CONCLUSIONS

Many lake ecosystems have undergone dramatic changes in nutrient status since the onset of industrialization. The fact that lakes may have experienced distinct pre-industrial limnological changes due to human activity during prehistoric and historic times has been observed in a number of palaeolimnological studies. However, the present study provides a clear example of distinctly enhanced nutrient conditions in a lake during a period unaffected by human influence. At Sacrower See, these elevated nutrient conditions were most likely a consequence of the climatic conditions during the Younger Dryas cold phase and their effects on the duration of the lake's ice cover, leading to hypolimnetic oxygen depletion and internal phosphorus remobilization. We, therefore, conclude that the definition of (near) pristine, undisturbed reference conditions with regard to ecological status of a lake should take into account both the potential effects of climatic and human influences on a lake ecosystem. Pre-industrial ecosystem states may in many instances be appropriate analogues for defining lake quality standards. However, case-studies of long-term ecosystem development are important and necessary to define and evaluate such reference conditions, especially in regions with a long history of human activity. In Central Europe lake ecosystem conditions reconstructed for the early- to mid Holocene (*ca* 11,600-4000 cal. BP) provide examples of stable lacustrine system states in the absence of human activity and under climatic conditions comparable to today.

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