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Phacotus lenticularis content in carbonate sediments and epilimnion in four German hard-water lakes

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ABSTRACT

Autochthonous calcite precipitation is an important process for C-fixation in hard-water lakes, which is mainly induced by the photosynthesis of planktonic microorganisms. Among these, the widespread calcifying green alga *Phacotus lenticularis* (Ehrenberg) Diesing contributes to biogenic calcite precipitation in temperate regions. Its role in carbonate precipitation needs to be investigated, because there are no studies dedicated to the quantitative contribution of *Phacotus* shells to long term carbonate sequestration in hard-water lake sediments. In order to fill this gap, the *Phacotus* shell content in the sediments of four German hard-water lakes was determined and compared to the fraction of *Phacotus* shells in the total suspended autochthonous calcite of the euphotic zone. It was found that the *Phacotus* shells contributed at least 10% to the autochthonous carbonate precipitation in the upper water column in three investigated lakes. During a *Phacotus* mass occurrence with a cell density of 1.8×10^6 Ind L^{-1} in Lake Hopfensee, even 59% of the 3.6 mg L^{-1} total carbonate concentration consisted of *Phacotus* shells. In contrast to this high amount, the topmost basinal sediment contained a *Phacotus* shell content between 80 and 36,252 individuals per mg dry sediment, representing only 0.02% to 2.28% of the total carbonate sediment content. In a gravity core from Lake Grosser Ostersee, dating back ~ 150 years, the *Phacotus* shell content was continuously below 0.24% whereas the shell diameters remained equal to those of living individuals found in the water column proving that *Phacotus* shells are capable to persist in the sediment after deposition. A main reason for the large discrepancy between *Phacotus* shell abundance in the euphotic zone and in sediment was found to be the gross authigenic carbonate precipitation, which dilutes the sedimenting *Phacotus* shells that accumulate exclusively during short and intensive population peaks in summer. Additionally, dissolution of the carbonate shells during sedimentation was proven to be a relevant factor in Lake Igelsbachsee by means of reducing the number of *Phacotus* shells reaching the lake bottom. These facts explain that short-term high *Phacotus* carbonate contents of the total suspended carbonate in the water column do not mirror the contribution of *Phacotus* shells in the sedimentary record.

INTRODUCTION

Autochthonous calcite precipitation induced by primary production is a common process in alkaline hard-water lakes (Dittrich *et al.,* 2004; Müller *et al.,* 2006; Stabel, 1986). Similarly, calcite precipitation occurs in surface waters as a result of the warming effects. This phenomenon is also well understood and has been applied in

quantitative approaches determining fine sediment deposition (Auerswald and Geist, 2018). Biological calcite precipitation involves formation of carbonate shells by the planktonic calcifying phytoflagellate *Phacotus lenticularis* (Ehrenberg) Diesing (1866) (Guiry 2019). *Phacotus lenticularis*, hereinafter abbreviated *Phacotus,* is a widespread alga that lives in temperate, subtropical and tropical regions and occurs worldwide in lime-rich alkaline stagnant inland waters (Schlegel *et al.,* 1998).

The epilimnion *Phacotus* substantially contributes to the total suspended epilimnetic calcite precipitation, particularly during mass developments, due to its two lens-like calcite shells. The normal contributions ranges from 5-10% and can sometimes reach 100% (Koschel and Raidt, 1988; Krienitz *et al.,* 1993; Gruenert and Raeder, 2014; Lenz *et al.,* 2018). *Phacotus* is also supposed to be a significant source of carbonate in lake sediments as suggested by Kelts and Hsü (1978). Sedimentary records prove that *Phacotus* shells can be preserved and form dominating sediment fractions. The oldest reported occurrences of the calcareous shells were found in an early Miocene (126-138 ka BP) fresh water deposit in Öhningen in southwest Germany and in a middle Miocene (115–126 ka BP) limestone deposit, which had a 'particularly high occurrence' of *Phacotus* shells that it was referred to as '*Phacotus*-Kalk', in Jutland, Denmark (Lagerheim,

1902). In addition, a sediment core from the early Dryas (13-11 ka BP) found in south Argentina contained sediments, in which the calcite fraction almost exclusively consisted of *Phacotus* shells (Haberzettl *et al.,* 2007; Jouve *et al.,* 2013). Müller and Oti (1981) introduced a summary and a detailed description of the documented fossil *Phacotus* occurrences in Eurasia, including a fossil *Phacotus* occurrence in brackish sediments from the Miocene Ries crater (72-116 ka BP) in south Germany. However, all these findings offer only qualitative descriptions of the *Phacotus* records.

This study aimed to quantitatively evaluate the role of *Phacotus* in lacustrine calcite precipitation based on the quantitative assessment of the *Phacotus* shell fraction in the sediment and the water body of four German lakes. The percentage of suspended *Phacotus* shells in the total suspended autochthonous calcite in the epilimnion was determined and compared to the *Phacotus* shell amount in the corresponding sediment deposits. It was hypothesised that *Phacotus* shells significantly contribute to the lacustrine 'carbonate sequestration', because carbon is mineralised as carbonate and sequestered over long geologic timescales.

Study site

Four Bavarian lakes (Tab. 1) with documented occurrences of *Phacotus* in the last ten years (2005-2015) were investigated: Lake Grosser Ostersee (GOS), Lake Abtsdorfer See (ABS), Lake Igelsbachsee (IGS), and Lake Hopfensee (HOP) (Fig. 1). They are all stratified natural hard-water lakes located in the pre-alpine basin in south Bavaria, Germany, except IGS, which is a Ca-rich artificial reservoir lying in a basin of late Triassic quartz sandstones surrounded by Jurassic carbonates. All other lakes have carbonate dominated catchments, are fed with alkaline water from the Northern Limestone Alps, and are a part of an open quaternary aquifer of predominantly fluvioglacial sediments with intercalated basal moraine tills that overlay a Tertiary sandstone aquitard.

METHODS

Water samples for *Phacotus* abundance and total epilimnetic particulate calcite analysis (Fig. 2) were collected on a weekly basis from the surface water (0-7 m depth) at the deepest point of each lake following the method described by Lenz *et al.* (2018). Depth profiles of water temperature and pH were measured *in situ* with a WTW MPP 930 mulitprobe. The concentrations of Ca^{2+} in solution were determined following the method described in Gruenert and Raeder (2014). Particulate $CaCO_3$ concentration was measured using infrared CO_2 analysis on a Saxon Junkalor Infralyt 50 gas analyser (Lenz *et al.,* 2018), and the plankton abundance was determined with an inverted microscope Leitz Labovert at 200× based on the method mentioned in Utermöhl (1958).

A scientific diver used a tube from a PVC Uwitec gravity corer to collect samples from the surface sediment, *i.e.* the topmost material from the deepest point of each lake. The upper 4 cm of the composite samples were examined, in order to obtain a representative mean value over several years to diminish the effects of annual variance of *Phacotus* populations and to include carbonate dissolution in the oxic part of the sediment. An aliquot of each sample was suspended in 10 mL buffered suspension liquid ($NH_3 + H_2O$) with a pH of ≥ 8.5 (Bollmann *et al.,* 1999). The sediment was mildly dried and carefully homogenised in a mortar. A 0.50 mg homogenised sample mixed with 2 mL of the suspension liquid was transferred into an Eppendorf tube. Next, 0.50 mg of borosilicate microspheres (ThermoFisher Scientific #9015; Waltham, MA, USA) were used as calibration standard, and the disaggregation of the carbonate aggregates was conducted using a BAndelin Sonorex TK52 (Berlin, Germany) ultrasound bath (one minute, 150 W, 35 kHz) following the method used by Bordiga *et al.* (2015). Finally, the sample was mixed using a CHS Vortex homogeniser (Praha, Czech Republic). A 50-µL sample of the suspension was obtained during the mixing and placed into the centre of a circular coverslip using a laboratory pipette according to the 'drop' method (Bordiga *et al.,* 2015; Koch and

Tab. 1. Limnologic characteristics and sampling locations at the deepest point of the examined hard-water lakes.

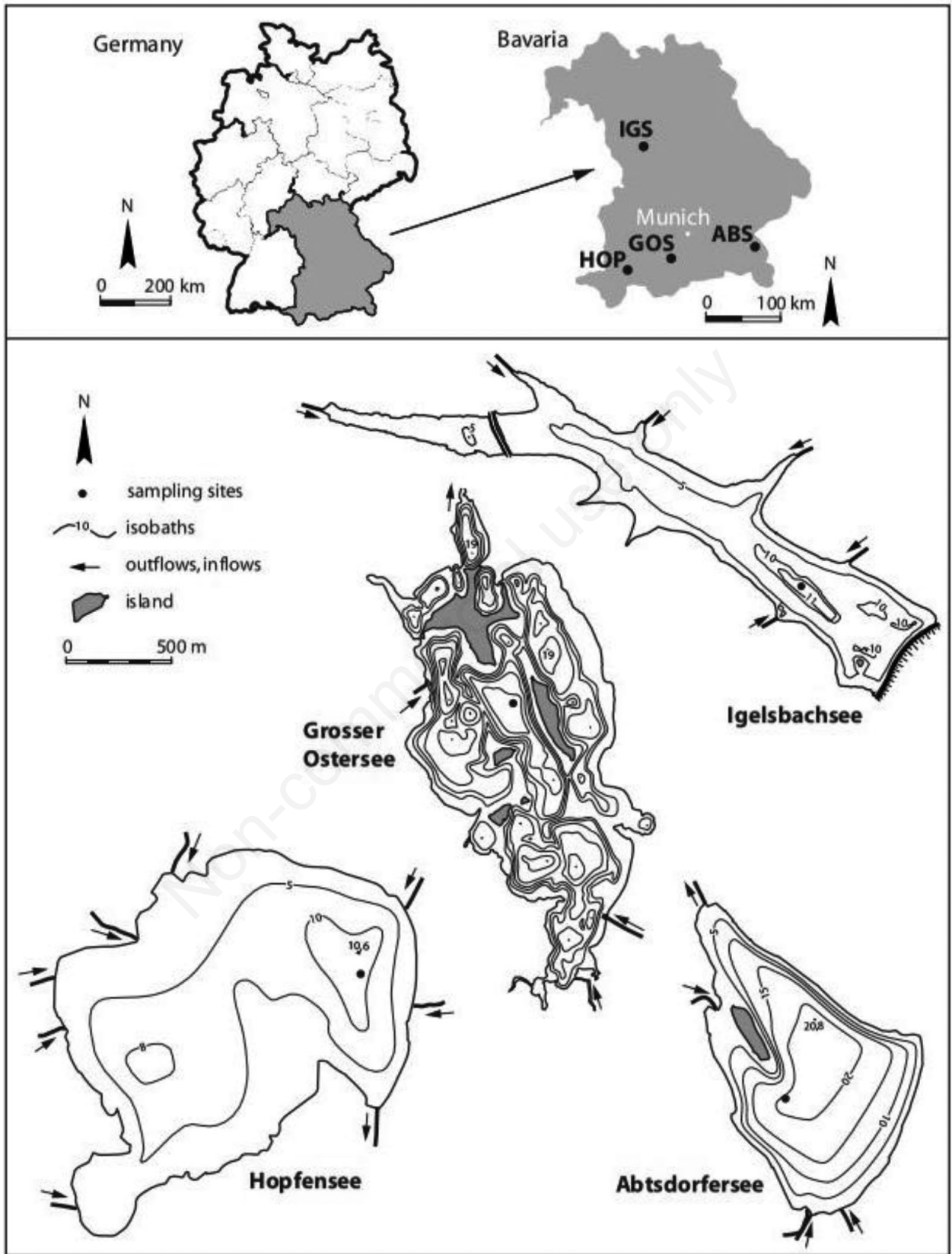|	Gr. Ostersee	Abtsdorfersee	Igelsbachsee	Hopfensee
Trophic state	Oligotrophic	Mesotrophic	Mesotrophic	Eutrophic
Circulation type	Dimictic	Dimictic	Polymictic	Dimictic
Surface area [ha]	118	78	72	186
Max. depth [m]	29.7	20.0	11.5	10.4
Volume [100 m³]	14.0	9.4	3.9	8.9
Calc. residence time [d]	247	252	-/-	128
Coordinates (WGS 84)	47°47'25" 011°18'07"	47°54'35" 012°54'22"	49°08'45" 010°54'13"	47°36'06" 010°40'46"

Fig. 1. Locations of the study sites in Bavaria, Germany: bathymetry and sampling points at Lake Igelsbachsee (IGS), Lake Grosser Ostersee (GOS), Lake Hopfensee (HOP), and Lake Abtsdorfersee (ABS).

Young, 2007). This process was replicated five times for each sample. The exact mass of sediment ($m_{sed\_DG\_soll}$) on the coverslips was calculated from the total amount of microspheres on them. Shell number was visually determined for each coverslip using light-microscopy with polarised light at 200× magnification. Intact *Phacotus* individuals were counted as two shells whereas single shells were counted as half individuals. Rare broken shells were counted as an entire shell, if the fragment was more than half of a shell to avoid overestimation of the *Phacotus* shell abundance. The *Phacotus* shell fraction in the sediment $w_{Phacotus}$ [%] was calculated using the product of shell number and lake specific mean shell mass relative to the total sediment and carbonate mass on the entire coverslip, respectively, according to the method described by Lenz *et al.* (2018).

A sediment core from GOS (GOS-07) was selected for further analysis and dating. The core samples were collected using a UWITEC gravity corer (Mondsee, Austria) at the deepest point of the lake in 2017. The core was split lengthwise, lithologically described, and subsequently sub-sampled at 1 cm resolution. One half of the core was used for dating, elemental analysis, and sediment size distribution at Eawag in Dübendorf, Switzerland. The freeze-dried samples were carefully homogenised and dated through ^{137}Cs and ^{210}Pb activity measurements using a Canberra Ge well detector (San Ramon, CA, USA) ac-

cording to the methods described in Appleby (2001) and McGowan *et al.* (2015). The sedimentation rate of ^{210}Pb was determined after subtracting the ^{226}Ra activity using a constant flux sedimentation rate model. The elemental analysis of total carbon (TC) and total nitrogen (TN) was conducted using a Hekatech Euro EA 300 elemental analyser (Wegberg, Germany). Total inorganic carbon (TIC) was determined using a UIC Coulometer CM 5015 (Joliet, IL, USA). Total organic carbon (TOC) was calculated by subtraction of TIC from TC. The carbonate content ($CaCO_3$) was calculated from TIC through multiplication by the ratio of the molecular weights of $CaCO_3$ and C (100.09 g mol^{-1} and 12.01 g mol^{-1}, respectively). Total carbon accumulation rate $R_{acc\ TC}$ [g cm^{-2} a^{-1}] was derived from the total carbon fraction TC [wt%] of the sediment mass accumulation rate $R_{acc\ sm}$ [g cm^{-2} a^{-1}] (eq. 1). $R_{acc\ sm}$ of each sample was individually calculated through the multiplication of sediment density ρ_{sed} [g cm^{-3}] by the sedimentation rate R_{sed} [cm a^{-1}] (eq. 2).

$$R_{acc\ TC} = R_{acc\ sm} * (TC) \qquad \text{(eq. 1)}$$
$$R_{acc\ sm} = \rho_{sed} * R_{sed} \qquad \text{(eq. 2)}$$

The particle size analysis was performed on wet unprocessed sediment from the sediment core (GOS-06) that was obtained at the same location and date as GOS-07. It was also stored and divided in the exact same manner. To
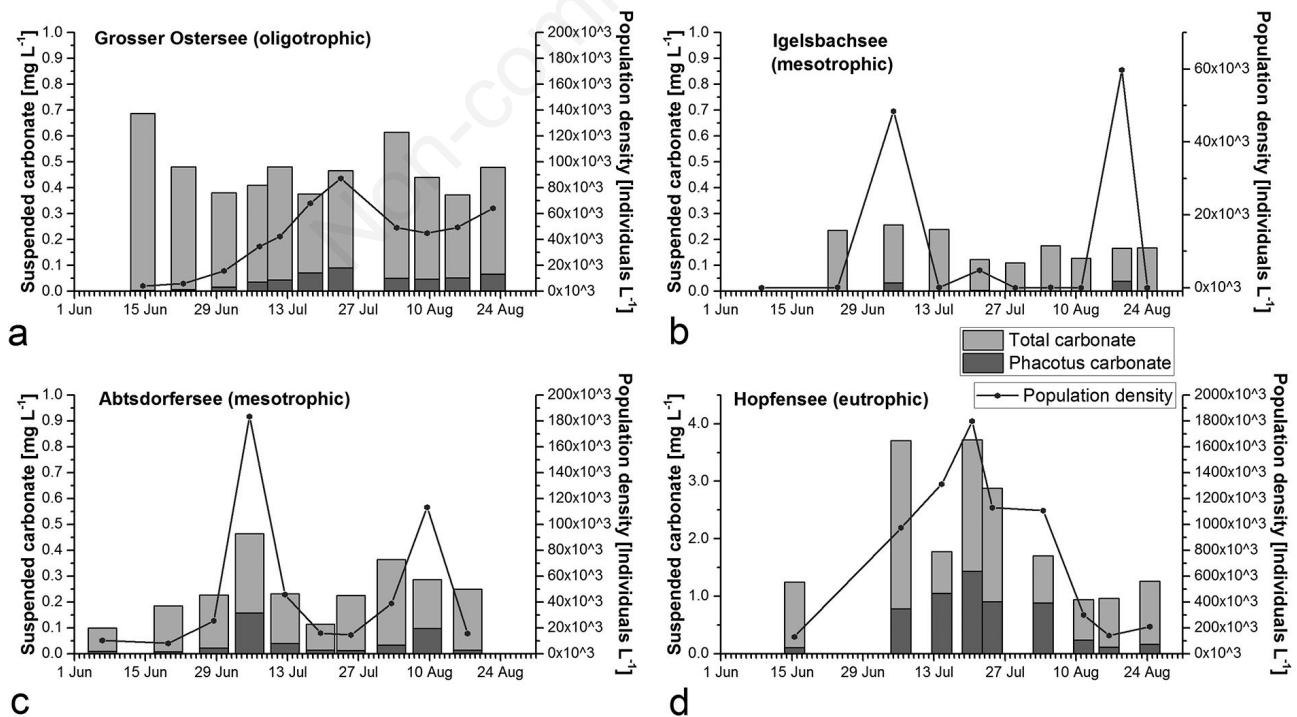

Fig. 2. Total suspended epilimnetic carbonate (white bars) and *Phacotus* carbonate fraction (grey bars) with the corresponding *Phacotus* population density (data points) during the growth period in the summer of 2016.

ensure comparability, both cores were lithologically described and cross-correlated based on their lithological description. Samples were disaggregated using Na-Pyrophosphate and ultra sound, and then particle size analysis was conducted with a Malvern Mastersizer 2000 (Malvern, UK).

The second half of GOS-07 was used to determine the *Phacotus* shell content using the previously described method for surface sediment samples. Additionally, *Phacotus* shell diameter measurements were performed on 136 evenly distributed shells over the complete sediment core using Kappa Opto-Electronics & AccuSoft (Gleichen, Germany) camera software Kappa ImageBase (2007). Micrographs were analysed with FiJi ImageJ image analysis software (Rasband, 2016) using two perpendicular diameter measurements, and the selected shells were examined under scanning electron microscope (SEM) at the Limnological Research Station of TU Munich, Germany, in order to detect potential dissolution features.

RESULTS

Suspended carbonate in lake water and *Phacotus* fraction

The amount and temporal variation of total suspended carbonate in the lake water and the contributing *Phacotus* fraction measured during the period of the strongest *Phacotus* growth, which took place between June and August 2016, were found to be different in the four investigated lakes (Fig. 2). In the eutrophic HOP, the total carbonate concentration reached its highest level at 3.5 mg L^{-1}. In the other three lakes, the values were always below 0.7 mg L^{-1}. Furthermore, in HOP during a *Phacotus* bloom, the cell density was 1.8×10^6 Ind L^{-1}. The *Phacotus* carbonate temporal contribution to the total suspended carbonate in the epilimnion was measured during this period to be 59%. In ABS, two *Phacotus* growth peaks were observed with a maximum cell density of 183,400 Ind L^{-1} during the first peak when *Phacotus* represented 34% of the total suspended carbonate. In GOS, the first population peak had a lower maximum cell density of 84,200 *Phacotus* L^{-1} at the end of June, during which the *Phacotus* shells contributed 19% to the total suspended carbonate in the epilimnion.

In HOP, ABS, and GOS, the pH values and conductivities of the lake water indicated permanent carbonate oversaturation throughout the entire depth of the water column (Tab. 2). These conditions did not prevail in IGS, where the actual amount of *Phacotus* could not be accurately recorded, due to the dissolution of *Phacotus* shells caused by the low Ca^{2+} concentrations. This was observed by counting *Phacotus* shells of two identical plankton samples at different times. Cell densities measured immediately after the fieldwork were found to be around 5×10^4 Ind L^{-1}, while *Phacotus* shells disappeared after one month. Therefore, IGS represents a lake with *Phacotus* population in the water column, but with almost no sedimentary *Phacotus* records, because the shells dissolve before being preserved in the sediment.

Surface sediment analysis

Surface sediment analysis revealed that the four lakes had significantly different total carbonate contents (Tab. 2).

Tab. 2. *Phacotus lenticularis* (*P.l.*) fraction in surface sediment (0-4 cm) and surface water (0-7 m) with the corresponding epilimnetic physical chemical water conditions (standard deviation indicated between brackets).

	Gr. Ostersee	Abtsdorfersee	Igelsbachsee	Hopfensee
Sediment from deepest point of the lake (0–4 cm):				
P.l. shells [Individuals mg^{-1}]	3.255 (1.074)	24.401 (603)	80 (22)	36.252 (1.539)
P.l. fraction sediment [%]*	0.15 (0.06)	1.05 (0.03)	0.00 (0.00)	1.45 (0.06)
$CaCO_3$ fraction sediment [%]	88.8	42.8	12.5	63.6
P.l.* fraction in total carbonate sediment [%]	**0.16 (0.06)**	**2.45 (0.06)**	**0.02 (0.01)**	**2.28 (0.10)**
Suspended carbonate from water column (0–7 m): average values of water, June-August 2016				
Mean *P.l.* fraction in suspended carbonate in water [%]*	**9.9 (6.1)**	**13.9 (10.6)**	**4.3 (7.9)**	**29.0 (16.9)**
Water temp. (°C)	17.4 (4.7)	15.5 (5.2)	20.9 (2.7)	17.3 (2.8)
pH value	8.2 (0.2)	7.9 (0.4)	8.6 (0.5)	8.2 (0.4)
Ca^{2+}conc. (mg L^{-1})	69.2	78.2	37.6	69.3
TP (µg L^{-1})	> 8.2	> 17.4	> 25	> 35
Secci depth (m)	3.3 (0.6)	1.1 (0.2)	3.0 (0.6)	1.1 (0.3)

*TP data from Bavarian Environmental Agency, Ca^{2+} concentration from last sampling in August 2016; *the lake specific* P.l. *shell mass according to Lenz* et al. *(2018) was used for mass calculation.*

This strongly affected the *Phacotus* fraction of the total carbonate sediment with *Phacotus* shell content ranging from 80 (IGS) to 36,252 (HOP) individuals per mg dry sediment [Ind mg^{-1}] in the topmost 4 cm of basinal sediment. This represents total *Phacotus* carbonate content of 0.02% and 2.28% in IGS and HOP, respectively. The other two lakes (GOS and ABS) had intermediate *Phacotus* shell contents of 3255 and 24,401 shells per mg dry sediment, respectively, and the *Phacotus* fraction contributed 0.16% and 2.45%, respectively, to the total carbonate in the sediment.

Sediment core from Lake Grosser Ostersee

The age model (Fig. 3) is based on ^{137}Cs-activity measurements and confirmed by the sedimentation rate derived from the ^{210}Pb-activity measurements. In the topmost section, R_{sed} was determined through the interpolation between the surface (2016), the ^{137}Cs peaks (1963 and 1986), and the first signal of ^{137}Cs activity (1954). The time determination for 1963 was set at the depth of 11.5 cm below the actual ^{137}Cs-activity peak, because the coherent lamination and varve thickness were better fitted with the rest of the sediment core, suggesting that Cs probably has been remobilised in the sediment. In the section from 1954 (13.5 cm) to 1925 (19.5 cm), the age of the samples was determined by counting the biochemical varves downwards. In the non-laminated section above 19.5 cm, the ^{210}Pb a 0.21 cm a^{-1} sedimentation rate was used, resulting in a basal age of ~150 a. As sampling was conducted in 1.0 cm steps, every sample represented four to five years.

The core was subdivided into three lithological units: A (0-10 cm), B (10-19 cm), and C (19-31.5 cm) (Fig. 4).
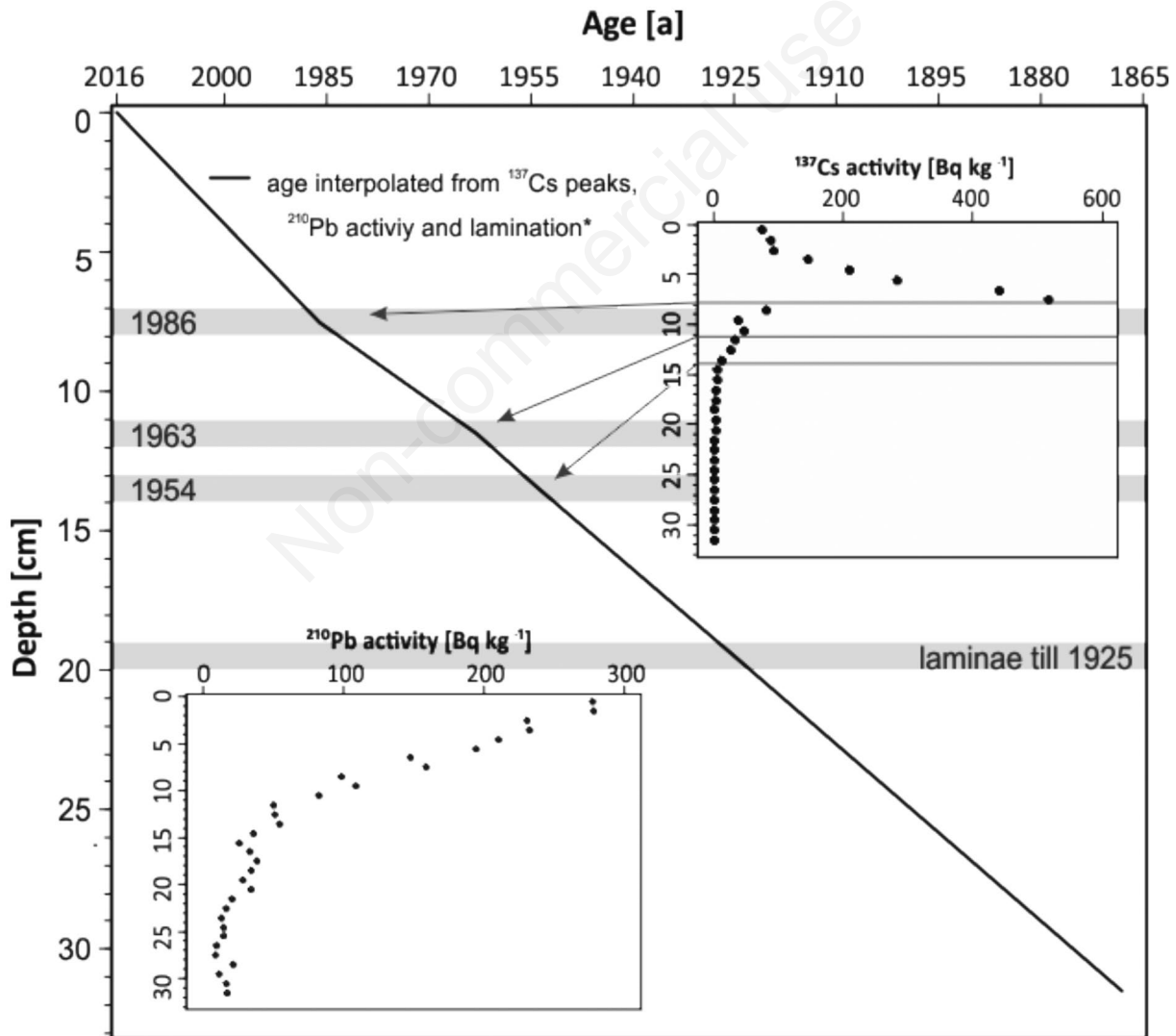

Fig. 3. Age-depth model for the GOS-07 sediment core with activity depth profiles for ^{137}Cs and ^{210}Pb.

The sedimentologic characteristics of the three main core units are listed in Tab. 3. The sediment of unit C appeared dark grey with few dark streaks and no lamination. At the transition from the unstratified unit C to layered unit B, a steady decline of the mean TOC/TN ratio from the maximum value of 14.6 (20.5 cm) to 9.4 (17.5 cm) indicated a loss in the input of external organic carbon from vascular plants (Fig. 5). Unit B was laminated with approx. 40 varve cycles of decreasing thickness. At the transition from unit B (10.5) to unit A (9.5) cm, several proxies changed. Below 10.5 cm, approximately 16 varve cycles showed regular undisturbed sedimentation. From this point upward, the sediment got darker accompanied by a steady rise in the TOC from 1.8 wt% (11.5 cm) to reach its maximum value of 3.1 wt% (9.5 cm). Simultaneously, the $CaCO_3$ content declined to its minimum of 81 wt% (9.5 cm). The well preserved core section terminated at this point with a dark 2 mm thick autumn-winter layer (10.2–10.0 cm). From
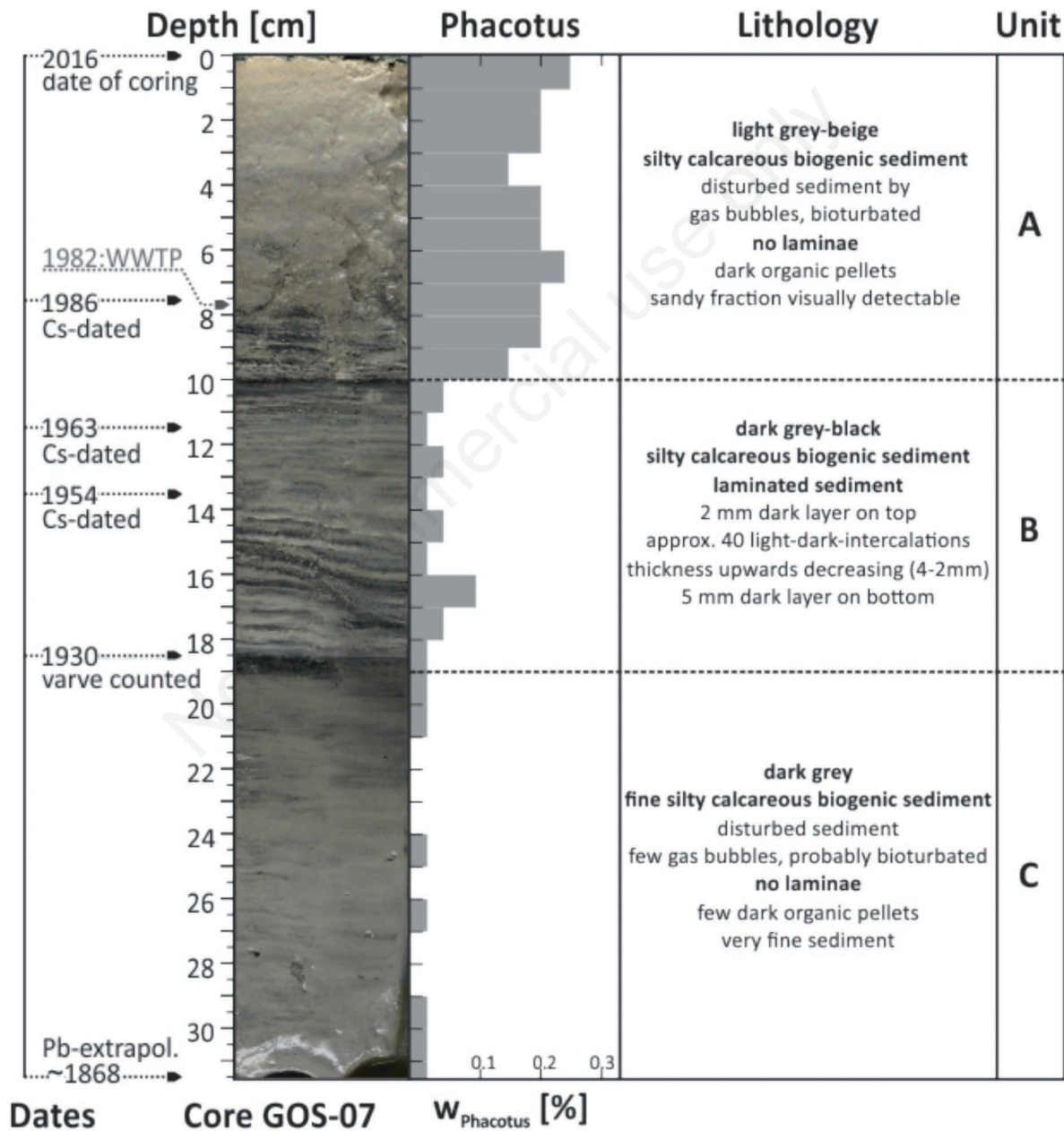

Fig. 4. Photograph of the GOS-07 core with lithology and radioisotopic dates from Lake Grosser Ostersee, and the maximum *Phacotus* shell abundance w*Phacotus* [wt%] is given as weight per cent of dry sediment. The arrow pointing at 1982 indicates the operation start of a wastewater treatment plant (WWTP).

10.2 cm upward, there were four duplets of diffuse and unclear preserved laminations. The grey-beige unit A was found to be sandier. In the section from 10 to 8 cm, the sand fraction increased (+ 7 wt%) at the expense of the silt fraction. In this section, endobenthic bottom dwellers and plant macro remains were occasionally found in other cores from the same location. Additionally, cavities from gas bubbles were found at 6.0 to 7.5 cm depths.

The GOS-07 sediment core was 31.5 cm long (Fig. 4) and showed a continuous record of biogenic silty pelagic sediment with a high carbonate content of more than 87 wt% $CaCO_3$ and a low TOC content of less than 3 wt%. The SEM sediment examination confirmed that the laminations were biochemical non-glacial varves. No allochthonous input was assumed at the deepest point of GOS, because the lake has no natural superficial inflow and the central basin is surrounded by several smaller basins (Fig. 1). This assumption was confirmed by the low mean TOC/TN ratio of 10.2 (standard deviation SD = 1.8) (Fig. 5).

Tab. 3. Summary of the analysis of the sediment from the GOS-07 core divided into three lithological units: A, B and C.

| Unit (depth)	A (0–10 cm)	B (10–19 cm)	C (19–31.5 cm)
Year	2016–1970 (46 a)	1970–1927 (43 a)	1927–1868 (59 a)
Trophic state of the lake*	Meso-/Oligotrophic	Mesotrophic	Oligotrophic
Sand fraction [%]	15.5 ± 2.7	7.6 ± 1.8	6.1 ± 1.2
Silt fraction [%]	79.2 ± 2.2	85.3 ± 0.8	86.7 ± 0.8
Clay fraction [%]	5.3 ± 2.2	7.1 ± 1.1	7.2 ± 0.6
Total organic carbon [%]	2.5 ± 0.3	2.0 ± 0.2	1.8 ± 0.4
Carbonate content [%]	87.7 ± 3.3	89.7 ± 1.6	90.0 ± 2.9
Phacotus shells [Individuals mg^{-1}]	3286 ± 903	327 ± 292	34 ± 77

Gruenert and Raeder, 2014; Melzer, 1976.
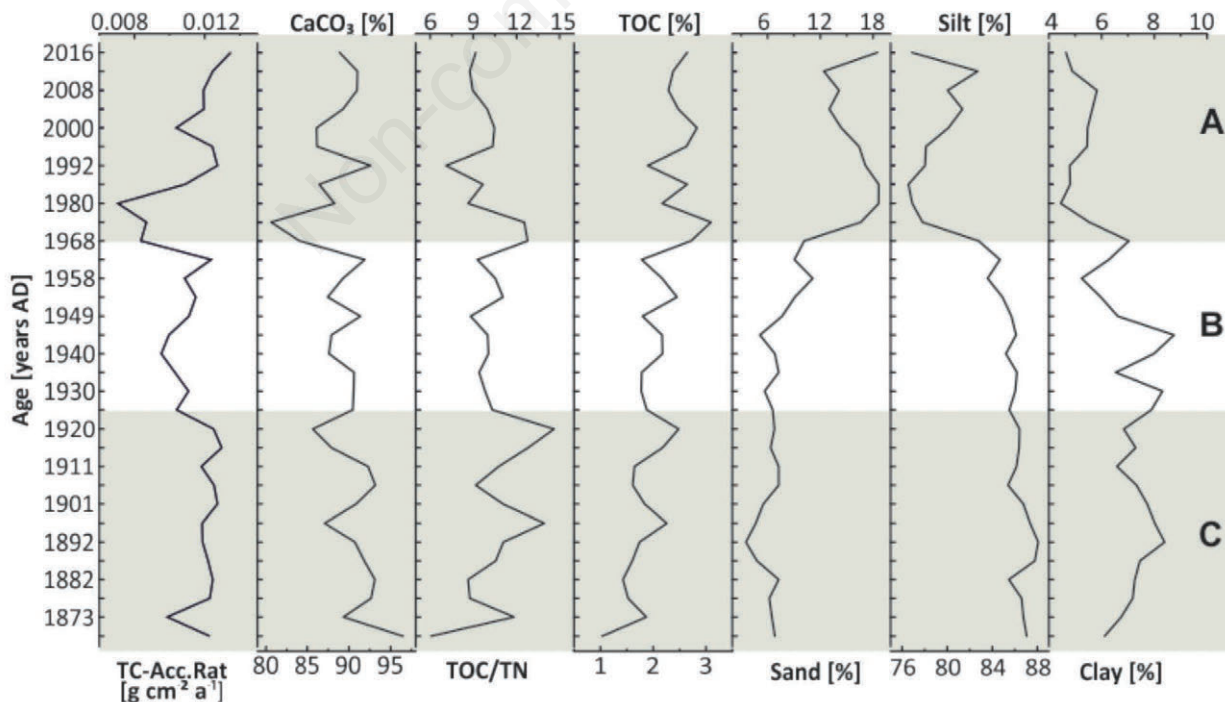
Fig. 5. Geochemical and grain size distribution profiles of the GOS-07 core from Lake Grosser Ostersee: all element content [wt-%] is given as weigh per cent of dry sediment, and the Total Carbon Accumulation rate (TC-Acc.Rate) is given in [g C m^{-2} a^{-1}].

The $w_{Phacotus}$ was determined relative to the total dry sediment mass, which ranged from 0.00 to 0.24 wt% (Fig. 4). The threefold division of the sediment core units was also reflected in terms of the *Phacotus* shell content. The units C and B contained very low amounts of *Phacotus* shells ranging between 34 and 327 Ind mg^{-1} (Tab. 3). In contrast, in unit A the *Phacotus* shell fraction was ten times higher and accounted for 3286 Ind/mg. This represented a $w_{Phacotus}$ of 0.24 wt% of the total dry sediment mass.

Fig. 6 shows a micrograph of the counted *Phacotus* shells during microscopic analysis. These micrographs were used for diameter measurements and to check the shells for indications of carbonate dissolution. The mean diameter of 136 *Phacotus* shells from evenly distributed core depths was 13.7 μm (SD=1.7). This value was slightly higher than the mean diameter that was determined for living *Phacotus* shells in GOS (13.6 μm, SD=0.9) (Lenz *et al.,* 2018).

DISCUSSION

The hypothesis that *Phacotus* shells represent a considerable part of carbonate sequestration in lakes was confirmed in part of the samples, in which the calcite shells represented over 10% of the autochthonous calcite precipitation during the summer season in the investigated hard-water lakes.

Several aspects influence the *Phacotus* shell abundance in the water column and in the sediments, including (1) the difference in the specific timeframes of reference between water and sediment samples; (2) the dilution of *Phacotus* shell carbonate by the overall carbonate sedimentation; (3) the dissolution of *Phacotus* shells during sedimentation, which played a subordinate role with the exception of IGS (Fig. 2); (4) the reduction of *Phacotus* shell abundance in the lakes sediment, which may be caused by dissolution after deposition, such as in IGS.

For the first aspect (1), Tab. 2 shows the large discrepancy between *Phacotus* shell abundance in water and in sediment. This difference lies in the timeframe of reference. For example, water samples from HOP, which represent a single sampling day, contained a *Phacotus* shell fraction of 29% of the mean suspended calcite, whereas in the sediment samples representing approximately 15 years of carbonate sedimentation, *Phacotus* shells represented only 2.28% of the total carbonate sediment.

The second aspect (2) indicates that the low *Phacotus* fractions in lake sediments were caused by 'dilution'. The *Phacotus* populations showed strong growth and high abundances in midsummer (Fig. 2), but these periods were generally short (Koschel *et al.,* 1987; Krienitz *et al.,* 1993; Gruenert and Raeder, 2014; Lenz *et al.,* 2017). Therefore, the contribution of *Phacotus* shells to the carbonate sediment remains low in comparison to the overall autochthonous biogenic calcite. In spring and late summer, the autochthonous carbonate precipitation induced by diatoms and cyanobacteria blooms (Dittrich and Obst, 2004) is the source of most sedimented carbonate in lakes (Kelts and Hsü, 1978). However, charaphyceans, their crushed stem casts, and oogonia can also be transported as suspended particles from the littoral zone as a result of wind induced wave activity (Emi, 2001), and they can contribute to the carbonate sequestration in the deepest lake sectors. This was especially the case in GOS, where the GOS-07 sediment core contained a low *Phacotus* shell content of not more than 0.24% which equals an amount of 4593 shells per mg. These low *Phacotus* contents at this location might have resulted from a combination of several factors. The oligotrophic lake with limited primary production showed a high abundance of the picocyanobacterium Synechococcus (Ruber *et al.,* 2018), which contributed to intense autochthonous carbonate precipitation (Dittrich *et*
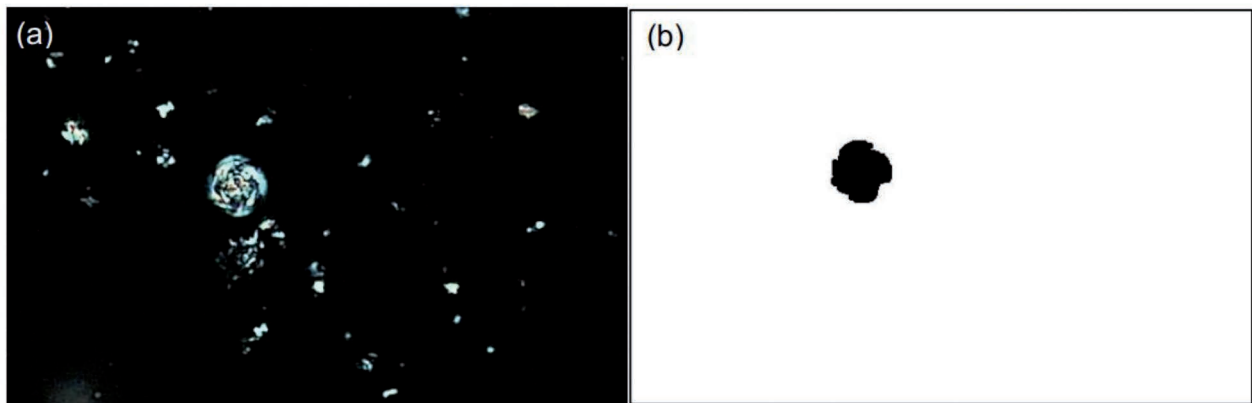

Fig. 6. Micrograph of sediment sample from 0.5 cm of the GOS-07 core under crossed nicols (a) and the corresponding picture for diameter measurements after processing with ImageJ Fiji software.

al., 2003; Dittrich *et al.*, 2004), resulting in an extraordinary high total carbonate content in the sediment (>89%). In addition to the generally moderate *Phacotus* population, the sediment had a very low *Phacotus* content. Nevertheless, *Phacotus* shells were always present over the complete depth of the sediment core. From 1970, the *Phacotus* shell abundance rose to the maximum value of 0.24% in the topmost sediment layer. The lowest *Phacotus* shell contents were found in the deepest core in unit C, not exceeding 0.02% which equals an amount of less than 290 shells per mg. From this point upward, the *Phacotus* shell content gradually increased (Fig. 4).

Aspect (3) indicates that *Phacotus* shells dissolve in the water column during sedimentation. This aspect was not confirmed and seemed unlikely in the majority of the investigated lakes. For example the groundwater-fed and relatively cold pre-alpine GOS is characterised by constant high alkalinity with permanent carbonate super saturated conditions. In contrast, in IGS, practically no shells were detected in the sediment, although in the epilimnion, numerous *Phacotus* shells had been observed (Fig. 2b). Shells from sediment trap experiments at the bottom of IGS (Lenz *et al.*, 2020) showed partly dissolved *Phacotus* shells, which was interpreted as an evidence of the carbonate dissolution conditions in the water.

However, aspect (4), which is related to the dissolution of carbonate particles, has to be considered in the sediment. Under oxic conditions, which were indicated by living bottom dwellers found in the bioturbated sediment core sections, carbonates are likely to dissolve, because the decomposition of organic matter provides free protons that lead to the dissolution of carbonate particles (Müller *et al.*, 2006). For example, based on a sedimentation rate of 0.2 mm a^{-1}, the residence time for sedimented carbonates in the oxic sediment zone of GOS-07 sediment core was found to be approximately two to three years. Therefore, carbonate dissolution was likely to occur in the topmost sediment of GOS. However, the embedded *Phacotus* shells were not altered. The value of their diameter over the complete depth of the sediment core remained constant at 13.7 μm (SD=1.7), which was also within the same range as the living *Phacotus* shells that were analysed from the water column (Lenz *et al.*, 2018). Furthermore, light microscopic images showed that, in the epilimnion of GOS, small calcite particles (<2μm) were present in abundance, which were not observed during microscopic examination of the lakes' sediment. This result is in accordance with the findings of Müller *et al.* (2006), which proposed that dissolution in aerated hardwater lake sediments preferentially take place at the expense of smaller calcite crystals, due to their elevated weight-specific surface area, instead of reducing the amount of *Phacotus* shells.

CONCLUSIONS

The abundance of *Phacotus* shell in lacustrine sediments is mainly affected by total carbonate sedimentation. Although the dynamic population development of *Phacotus* in the water column temporally provides the *Phacotus* carbonate contents with 59% of the total suspended carbonate, in the sedimentary record, only low total sediment carbonate contents could be observed. Dissolution can reduce the number of *Phacotus* shells present in the water column before they reach the ground. However, once embedded in the anoxic section of the basinal sediment, shells were found to be preserved in the investigated sediment cores with shell diameters in the same range of recent living *Phacotus* individuals.

Quantitative data are necessary to accurately define the '*Phacotus*-rich' sediments as described by (Haberzettl *et al.*, 2007; Jouve *et al.*, 2013; Lagerheim, 1902) and their formation mechanisms. The two most probable mechanisms are supposed to be formation as a result of primary concentration in the water column due to wind action in littoral zones and formation resulting from the secondary concentration caused by the dissolution of smaller carbonate particles around the *Phacotus* shells.

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