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Daphnia resting eggs in the sediment of Bohemian Forest lakes: an evidence for sediment disturbance

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Abstract

We studied the vertical distribution of *Daphnia* ephippia in the sediment of four Bohemian Forest mountain lakes – Černé, Čertovo, Plešné and Prášilské. *Daphnia* cf. *rosea* (traditionally labelled as *D. longispina*) currently lives in Prášilské Lake only; *Daphnia* populations had become extinct in the remaining three lakes during the 20th century due to anthropogenic acidification. The distribution of ephippia (chitinous casings of the resting eggs) in the sediment can be used as a simple marker of sediment disturbance: we are comparing the ephippia profiles in the cores with the historical records of the *Daphnia* presence in the lakes. Vertical profiles of ephippia densities in several cores did not agree with the historical data. Ephippia were often present near the surface of the sediment, which confirms that the sediment must have been disturbed after the *Daphnia* extinction. This has been caused by the extensive human activity in the past: the previous limnological research as well as various other activities repeatedly affected the sediment record in all lakes. Therefore, any future paleolimnological studies in these valuable natural localities should be limited to deeper sediment layers.

Key words: ephippia, paleolimnology, acidification, *Daphnia longispina*, *Daphnia rosea*, Czech Republic

Introduction

The five lakes in the Bohemian Forest (Šumava Mts.) are the only relatively well-preserved natural lake habitats in the Czech Republic. They have therefore been the targets of many limnological studies since the last quarter of the 19th century. The history of almost 130 years of research as well as the recent status of the lakes is summarised in Veselý (1994) and Vrba et al. (2000). The lakes have been heavily affected by anthropogenic acidification (Fott et al. 1994, Vrba et al. 2000); the effects of acidification started to occur in the beginning of the 1960s or earlier (Procházková & Blažka 1999).

High levels of toxic aluminium, associated with acidification, were probably the reason for the extinction of most or all of planktonic cladocerans in most of the lakes (Fott et al. 1994). *Daphnia* gr. *longispina*, which had been originally recorded in seven out of eight lakes in the Bohemian Forest (Frič 1872, 1873), currently survives in two lakes only: Prášilské, and Laka (Vrba et al. 2003). A decrease in emissions since the second half of the 1980s has resulted in a rapid reversal in the hydrochemistry of the acidified Bohemian Forest lakes (Veselý 1996, Kopáček et al. 1998a, 2002). Both values of pH and concentration of toxic aluminium improved substantially (Veselý 1996, Kopáček et al. 2002). This is slowly reflected also in the biota of the lakes. The signs of recovery of planktonic populations can be observed in at least two still-acidified lakes (Kohout 2001, Kohout & Fott 2003, Vrba et al. 2003). The densities of rotifers substantially increased in Plešné Lake, and a planktonic crustacean returned to

Černé Lake. *Ceriodaphnia quadrangula*, the most abundant cladoceran of both the littoral and pelagic zones of Černé Lake in the 1930s (Šrámek-Hušek 1942), had apparently disappeared during the acidification period, the last specimen in the samples being found in 1979 (Pražáková & Fott 1994). Since the first subsequent finding in 1994, it has slowly become the dominant species in the littoral zone again; three years later it started to occur also in the pelagial of the lake, and its densities have been increasing (Kohout 2001, Kopáček et al. 2002, Kohout & Fott 2003). Although the further reversibility of lake water chemistry will be very slow, if any, due to washout from the catchments and the recent and expected future increase in nitrogen emissions (Kopáček et al. 1998a, 2002), there is a chance that other currently extinct planktonic taxa will re-appear in the lakes in the near future.

Hatching from resting eggs in the sediment, if they remain viable, is one of the possible mechanisms that might allow the return of some species. Cladocerans belong among the groups with this ability. They are well adapted to the variable conditions in the pelagic environment of temperate lakes. By producing the resting eggs, they can easily overcome the periods of low food availability, anoxic conditions below the ice or even the drying out of the habitat (e.g. Fryer 1996). Such eggs, in most cladoceran taxa produced in the sexual phase of their life cycle, are resistant to freezing and desiccation and serve both for survival of the population at a given locality, and as dispersal agents. The dispersal function of the resting eggs of some taxa is even more enhanced, as they are able to survive passage through the digestive tract of various vertebrate predators, including fish, amphibians and birds (e.g. Proctor 1964, Mellors 1975, Charalambidou & Santamaría 2002). The resting eggs of planktonic taxa are usually deposited in the sediment where so-called "egg bank" is formed – the reserve of dormant genotypes that might hatch in suitable conditions. The resting eggs of *Daphnia* can remain viable for a very long time – decades or even centuries. Cáceres (1998) and Kerfoot et al. (1999), for example, have hatched *Daphnia* eggs from the sediments 125 and 70 years old, respectively.

The resting eggs of most cladocerans are protected by part of the carapace that encloses the egg or eggs after the molt of the female. This protective cover – ephippium – is well chitinised in *Daphnia*, therefore the ephippia stay quite well preserved in the sediment. Ephippia therefore belong among the few parts of cladoceran bodies that can be used for the analysis of historical zooplankton structure. In one aspect, however, they differ from other cladoceran remains, such as the head shields of chydorids or *Daphnia* postabdominal claws: ephippia are relatively large (over 0.5 mm, and in some taxa much larger), and therefore they can be often easily separated from the fine sediment. This allows them to be used as a simple marker: given that the sediment stratification is preserved in original state, the ephippia presence of absence in various sediment layers can be used to check if the sediment was deposited before or after the extinction of crustacean zooplankton. On the other hand, the presence of *Daphnia* ephippia on the surface of the sediment on lakes where this cladoceran has not lived for several decades would clearly suggest that the sediment record had been disturbed.

The potential longevity of *Daphnia* resting eggs could help to restore the extinct populations. If the ephippial eggs remained viable in the acidified lakes, they would serve as a source of native genotypes for colonisation after amelioration of the chemical conditions. The return of *Daphnia* gr. *longispina* as the main planktonic filtrator in the Bohemian Forest lakes would be an important step toward the recovery of original planktonic community.

The nomenclature of these *Daphnia* populations deserves the following taxonomical note: the populations in all lakes have been traditionally labelled as *D. longispina* O.F. Müller, and this name is used also in the recent studies on the surviving population in Prášilské Lake (Kohout & Fott 2000, 2003). More accurate species assignment of at least this population should be, however, *Daphnia rosea* G.O. Sars. This is supported by the analysis of the sequence of mitochondrial gene for 16S rRNA (Faustová, Sacherová & Petrusek, unpubl.), which is congruent with the data of Schwenk et al. (2000). The morphology of Prášilské Lake *Daphnia* also agrees with the characteristics of *D. rosea* given by Flössner (2000). As the taxonomy of *D. longispina* complex in Europe remains still insufficiently resolved, the status of Bohemian Forest *Daphnia* gr. *longispina* should be yet confirmed, preferably by comparison with populations from the areas of type localities of respective species.

We have decided to examine the state of the *Daphnia* egg-banks in four Bohemian Forest lakes to assess the possibility of autochthonous recovery of local *Daphnia* populations. In this paper, we report the details of the sediment quality and the distribution of ephippia in the analysed cores. The results, showing that the state of the ephippial resting eggs in the sediment is very poor and that the recolonisation from the local sources is unlikely, are summarised elsewhere (Faustová et al., in press).

Site description

Four lakes in the Czech part of the Bohemian Forest were included in this study – Černé (German toponym: Schwarzer See; A=18.4 ha, Z_{max}=40 m), Čertovo (Teufelsee; A=10.3 ha, Z_{max}=36 m), Plešné (Plöckensteiner See; A=7.5 ha, Z_{max}=18 m), and Prášilské (Stubenbacher See; A=4.2 ha, Z_{max}=15 m) [depth and area data according to Kopáček et al. (2002)]. All of them are located at altitudes between 1000 and 1100 m a.s.l. in the nature protected areas. Their relatively small catchments with steep slopes are mostly covered with spruce forest. The fifth and smallest lake on the Czech side of the border, Laka, is unsuitable for paleolimnological studies, as the sediment had been repeatedly removed from the lake to prevent its filling (Veselý 1994).

Černé, Čertovo and Plešné lakes are currently regarded as highly acidified, and Prášilské Lake as moderately acidified (Vrba et al. 2000). Based on the data of nutrient concentration, DOM and oxygen profiles, Černé and Čertovo lakes can be characterised as oligotrophic and Plešné and Prášilské lakes as mesotrophic (Vrba et al. 1996). Plešné Lake is the most productive of the four because of a different catchment geology (Kopáček et al. 1998b).

All of the studied lakes are currently fishless. The crustacean zooplankton of the lakes is very poor, and most of the taxa found there belong to the littoral fauna. No typical planktonic crustaceans have been present in the plankton of Černé and Čertovo lakes during the acidification period; only *Acanthocyclops vernalis* has been found regularly but in low numbers in Čertovo Lake (Kohout 2001). The recent return of *Ceriodaphnia quadrangula* to Černé Lake has been mentioned above. Copepods *A. vernalis* and *Heterocope saliens* are present in plankton of Plešné Lake, *Daphnia* gr. *longispina* and *Cyclops abyssorum* are common in Prášilské Lake (Kohout 2001).

Material and methods

We collected two to five cores from each lake in 2000 (details of the cores are shown in Table 1). The coring sites were located on the bottom plateau of each lake; however, we avoided the places of maximum depth. Many samples were taken from these places during previous studies, so the sediment was more likely to be disturbed there. All cores were taken by a Kajak corer with a tube of 6.2 cm diameter. We retained only apparently undisturbed cores, and the upper undisturbed part of cores CT4 and CT5, whose lower parts separated from the top during sampling. Most of the cores were cut into segments as follows: the first 5 cm of the cores were sliced every 0.5 cm, the remainder every 1 cm. The longest core from Černé Lake (CN2) was sliced into 1.5 cm segments. The outer part of each slice was removed

Table 1. List of the analysed cores. The ephippia densities calculated from the whole core cannot be directly compared, as the core lengths differ. One core from Čertovo and one core from Prášilské lakes (CT1, PR1) are not listed, as they have been used for different purposes (FAUSTOVA et al., in press).

Lake	Maximal depth	Core code	Coring date	Coring depth	Core length	Ephippia density (m^{-2})	
						top 10 cm	whole core
Černé	40 m	CN1	Apr 13, 2000	23.5 m	20 cm	1.3×10^5	1.3×10^6
		CN2	Apr 13, 2000	21 m	30.5 cm	7.7×10^5	9.3×10^6
		CN3	Nov 9, 2000	31 m	15 cm	3.1×10^4	3.1×10^5
Čertovo	36 m	CT2	Apr 14, 2000	31.5 m	18 cm	4.2×10^4	6.9×10^5
		CT3	Apr 14, 2000	31.5 m	20 cm	3.9×10^4	7.1×10^5
		CT4	Nov 9, 2000	35 m	10 cm	4.9×10^4	4.9×10^4
		CT5	Nov 9, 2000	35 m	11 cm	3.6×10^4	4.4×10^4
Plešné	18 m	PL1	Nov 17, 2000	16.5 m	20 cm	3.6×10^4	8.7×10^5
		PL2	Nov 17, 2000	16.5 m	25 cm	0	5.9×10^5
		PL3	Nov 17, 2000	16 m	16 cm	1.5×10^5	2.6×10^5
Prášilské	15 m	PR2	Nov 10, 2000	16 m	20 cm	4.6×10^5	1.3×10^6

by a plastic ring of 5.8 cm diameter to prevent possible contamination from upper parts of the sediment while extruding the core. The surface area of the sediment samples in the analysis was therefore 26.4 cm^2.

Each sample was diluted in distilled water, passed through a sieve of 200 µm mesh size and washed with a large volume of water. The remaining matter (mineral particles, plant fragments, various chitinous remains etc.) was screened for *Daphnia* ephippia under a stereomicroscope; the ephippia were collected and counted. The number of ephippia in the deeper layers of the core CN2 from Černé Lake was exceptionally high (over 1000 ephippia per layer), so only half of the material from those layers was counted.

The ephippia density was expressed as a number of ephippia in the sediment layer of given thickness under 1 m^2 area. Although this actually represents a density in certain volume of the sediment (10 dm^3 per layer 1 cm thick), it is traditionally expressed in ecologically-oriented papers (e.g. CÁCERES 1998, BRENDONCK & RIDDOCH 2000) as a number of propagules per one square metre of the lake bottom. This allows to compare more readily the results with other works on resting egg banks, and stresses the main function of the resting eggs: if all the resting eggs were viable, their number per certain area unit would represent the recovery potential of the resting egg bank – i.e. the maximum number of individuals that could emerge from that area of the lake bottom.

RESULT

The vertical distribution of ephippia in the analysed cores, recalculated to the layer thickness of 1 cm, is shown on the Fig. 1. Both actual numbers per layer of the core and corresponding densities in the 10 dm^3 of the sediment (representing 1 cm thick sediment layer of the corresponding depth under 1 m^2 of the bottom) are shown.

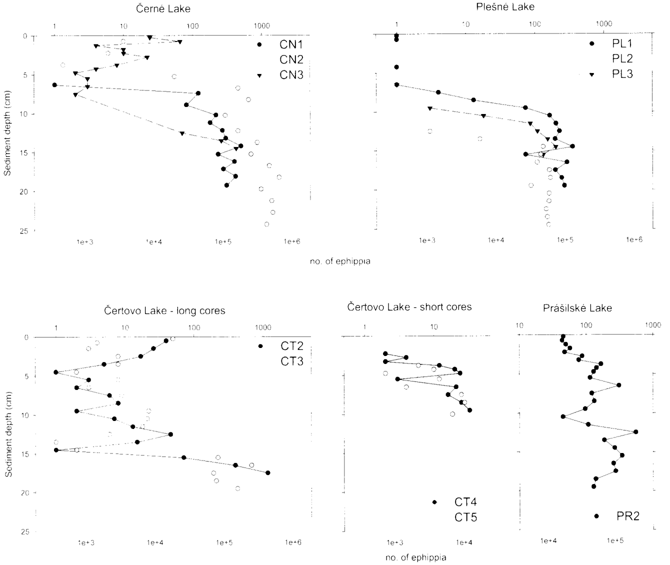

Fig. 1. The depth distribution of ephippia in the upper 25 cm of the cores. The upper x-axis shows the number of ephippia in the core, lower x-axis shows the corresponding density per square meter. The ephippia density in the layers was re-calculated to thickness of 1 cm, to allow comparison between layers in different depths without losing the resolution in the upper part. Logarithmic scale was chosen to cover both low densities in upper layers and high densities below. Note the scale shift in the graph from Prášilské Lake.

The upper 4 cm of all cores were semiliquid and contained a higher proportion of water. The remaining sediment was compact, without excessive water. The character of the sediment and of ephippia differed among lakes. Sediment from Černé Lake was mostly formed by fine organic particles, and no discernible layers could be seen on the core. Approximately 75% of ephippia in this core were transparent, with only very little pigment. Such ephippia could not be found in other lakes. The sediment of Plešné and Prášilské lakes was mostly formed by fine organic matter. Remains of chironomid tubes were often present in Plešné Lake; chitinous remains were common in Prášilské Lake. Only one core from Plešné Lake (PL1) contained also sand and small rubble in the 3–4 cm layer and clay at 13–14 cm.

The sediment from Čertovo Lake was mostly (~80%) formed by dark compact matter that could not be washed through the sieve. In addition, it contained many remains of organisms, especially plants (roots, wood, parts of cones and needles). There were several discernable layers in the two longer cores: CT2 contained high proportion of plant matter (roots, wood) at 7–8 cm, sand at 11–12 cm and clay between 14 and 17 cm. CT3 contained some sand at

10–11 cm and 16–20 cm, and clay between 13 and 17 cm. In addition to "standard" sized ephippia of approximately 0.85 mm, 25–30% larger ephippia could be found in deeper layers (below 12 cm) of the Čertovo Lake cores. Both size classes were identical in shape, and seemed to belong to *Daphnia longispina* group.

The ephippia density in the surface 10 cm of the sediment (see Table 1) varied both among the cores from the same lake and among lakes. The maximum total number of ephippia was found in the 30.5 cm long core from Černé Lake – the corresponding density per square metre was 9.3×10^6 ephippia m^{-2}. The densities in other cores longer than 10 cm varied between 2.6×10^5 m^{-2} (core PL3) and 1.3×10^6 m^{-2} (PR2). The densities in the near-surface layers (upper 2 cm) of the sediment were high in Prášilské Lake (core PR2) and some cores from Černé and Čertovo lakes (CN2, CN3, CT2, CT3) – over 5000 ephippia m^{-2}. If the eggs in the corresponding parts of the lake bottom were viable, they would have certainly the potential to revive the *Daphnia* population; unfortunately, this does not seem to be true (Faustová et al., in press). The ephippia in the surface layers of remaining cores were either rare or completely absent.

Discussion

The ephippia distribution in the core from Prášilské Lake, where a *Daphnia* population persists to the present, was in accord with our expectation: the ephippia were present in all layers and their density increased towards the deeper parts of the core where the sediment was more compact. The ephippia distribution in several cores from Černé, Čertovo and Plešné lakes (CN2, CN3, CT2, CT3, and to small extent PL1), where *Daphnia* is extinct, followed an unexpected pattern: some ephippia were present in the surface and subsurface layers. These layers should be void of ephippia in undisturbed sediment, as the *Daphnia* population has not been detected in the lakes for at least 40 years (Kohout 2001, Procházková & Blažka 1999). Although the possibility that small number of animals had survived undetected for longer time cannot be excluded, it is highly improbable because of high concentrations of toxic aluminium (Fott et al. 1994, Veselý 1996). However, even the hypothetical presence of surviving low-density *Daphnia* population would not explain the high numbers of the ephippia in the near-surface layers of the cores (hundreds to thousands per m^2): the production of ephippia could not have been in any case large enough.

It is certain that the lake sediment has been repeatedly disturbed in the past, with both anthropogenic and natural impacts possibly being the cause. The past limnological research included mechanical depth measuring, sediment and benthos sampling in the deep parts of the lakes, as well as various other activities requiring the boat anchoring. Several important sediment disturbances must have taken place during the research at the end of 19^{th} and the beginning of 20^{th} century [see Veselý (1994) for more details and references]: for example the detailed bathymetric measurements with suspended weight by Bayberger, Vávra, Frejlach and especially Švambera, or explosions of the dynamite charges during the ichthyological research by Frič. These activities, however, took place before the *Daphnia* extinctions in the lakes, therefore they could not have affected the distribution of ephippia in recent near-surface layers.

That unfortunately certainly happened during various activities of heavy-suit divers at the end of 1950s and 1960s, and the sediment could be resuspended also during later visits of scuba divers in the lakes. Another heavy disturbance (detonation of tritol explosives and damage of the shore) took place at Čertovo Lake in 1947 (Veselý 1947). The distribution of biomarkers in the surface sediment could have been also influenced by the intensive research activities in the last decades of 20^{th} century. Improperly closed benthos sampler or gravitational corer can release ephippia-containing sediment into water column, which would scatter ephippia on large areas of the bottom. Before the fixed buoys were placed in the areas of maximum depth of the lakes, the boat anchoring probably caused both extensive local damage of the sediment record and resuspension of smaller amount of material to larger areas. The presences of ephippia in the near-surface sediment layers in several cores suggest that some of the disturbances indeed happened in the recent past.

Natural causes of sediment disturbance would include mudslides from the steep parts of the lake bottom or bioturbation (KRANZBERG 1985). The latter is, however, less likely in a large scale, as large bottom organisms do not live in the lakes. The fish populations (trout *Salmo trutta* and later brook trout *Salvelinus fontinalis*) did not survive the acidification period (VRBA et al. 2000, 2003). Some vertical movement of the surface sediment layers (~2 cm) can be caused by chironomids and other small benthic invertebrates (KEARNS et al. 1996). This small-scale bioturbation, however, could not affect the ephippia distribution substantially. It affects the lake sediment continually, and if it had a large effect, it would virtually invalidate most of the paleolimnological research.

The cores from Černé, Čertovo and Plešné lakes where no ephippia were found in the surface layers (CN1, CT4, CT5, PL2, PL3) could reflect the situation in relatively undisturbed parts of the bottom. At least, we may expect that the surface layers of the sediment in these cores were deposited after the *Daphnia* extinction.

In Černé (core CN1) and Čertovo lakes (CT4, CT5), the depths of the sediment where more ephippia start to occur (7 cm and 3.5 cm, respectively) correspond with our knowledge of *Daphnia* presence. The ephippia profile in the core CN1 is comparable to the core taken in 1979 and processed by PRAŽÁKOVÁ & FOTT (1994), where they found the first *Daphnia* remains 3.5 cm below the surface. It is roughly equivalent to 5.5–6 cm of our core CN1 (where one single ephippium was found approximately 6 cm below the surface), if the difference in the year of sampling and the approximate sedimentation rate in the lake are taken into account. The peak and subsequent drop in ephippia density in the 14–16 cm depth of the core CN1 has also an equivalent in the 1979 core (12–14 cm).

The sedimentation rate in deep parts of Černé Lake in recent decades was estimated to be 1–1.2 mm.y^{-1} both directly by ^{210}Pb and ^{137}Cs dating (SCHMIDT et al. 1993) and indirectly by analysis of cladoceran remains (PRAŽÁKOVÁ & FOTT 1994). Although the sedimentation rate in the lakes varies both in time and in various parts of the lakes, this estimate seems to fit the cores from Černé Lake in comparison (as shown by the parallel distribution of cladoceran remains). The ephippia in the 7 cm depth would be approximately 60–70 years old, which is in agreement with ŠRÁMEK-HUŠEK (1942), who found only two *Daphnia* individuals during sampling of Černé Lake in 1935–1936.

A noteworthy fact is the extremely high ephippia density in the deeper layers of the core CN2, which does not correspond to any other core in our samples. Although differences in the cores collected from the same locality are quite common, the highest number of the resting eggs is usually found in the deepest part of lake (e.g. MORITZ 1987, NAESS 1996, CÁCERES 1998). This was not the case of the core CN2, as it was taken from a lesser depth than other two cores of Černé Lake and the lake is almost twice as deep as the sampling place of CN2 (see Table 1).

The "original" ephippia profile in Čertovo Lake cannot be well assessed. The short cores CT4 and CT5 have an apparently undisturbed surface, which might reflect the situation in recent decades. Other two cores (CT2 and CT3) have certainly a disturbed surface. Their lower layers (10 cm and below) showed similar profiles, sharing also distinct layers with a high proportion of sand or clay. These inorganic particles explain the sharp drop in ephippia density in 13–15 cm layers. It is not sure, however, whether the surface layers of the latter cores have been heavily mixed or are actually completely missing.

All three cores from Plešné Lake show a sharp increase in ephippia density from a certain depth and only very few ephippia above it (always single ephippium per layer, three such layers in PL1 and one in PL3). However, the depths where more ephippia occur differ among the cores, being 7, 12, and 9 cm. A drop of ephippia density can be seen in cores PL1 and PL3 (at 15–16 cm, and 19–20 cm, respectively). The difference in position of this local minimum is similar to the difference in position of the first ephippia density increase (7 and 12 cm). This suggests that part of the surface layer of the sediment might have been lost at the sampling site of PL1 for some reason. This is not uncommon in the studied lakes. For example, the comparison between cores collected from Černé Lake in 1979 and 1991 (SCHMIDT et al. 1993) led to similar conclusions: the core from 1991 lacked a surface layer of approximately 5 cm.

The overall ephippia densities calculated from the whole cores cannot be directly compared, as the lengths differ among the cores. They illustrate well, however, the variation of the density estimates caused by unequal core lengths. This factor, although very important, is sometimes neglected when the egg-banks in different habitats or localities are compared. Even then, the overall densities of ephippia in the analysed cores were in agreement with other published data on the cladoceran egg banks in ponds and lakes (HAIRSTON 1996, BRENDONCK & RIDDOCH 2000). The ephippia density estimates in the lakes range in the orders of magnitude 10^3 to 10^6 m^{-2}. The densities calculated from our cores fall into the same range.

Our data on ephippia distribution confirm quantitatively the conclusions of VESELÝ (e.g. 1994) that the surface layers of the sediment in Bohemian Forest lakes have been disturbed. This complicates the paleolimnological studies of recent processes in the lakes. Although the extent of the disturbance is highly variable, it is not possible to ensure that any cores taken from the Bohemian Forest lakes contain the original, undamaged sequence of the sediment layers near the surface. It can be presumed that only deep layers can be safely used to interpret the historical processes. Even then, the isotope dating of the core, and, if possible, use of independent markers, such as pollen analysis, is highly advisable.

These conclusions are probably valid for other lakes, not only those in the Bohemian Forest. Any locality where intensive research or other human activities took place in the last decades can be heavily affected by sediment disturbance. Care must therefore be taken when interpreting the results of paleolimnological studies dealing with recent, especially if core(s) analysed come from one sampling site only.

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