

Pronounced early human impact on lakeshore environments documented by aquatic invertebrate remains in waterlogged Neolithic settlement deposits

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23 Highlights

- 24 ○ Subfossil invertebrates were analysed from Neolithic settlement deposits at Lake
25 Zürich.
- 26 ○ Invertebrates indicated permanent presence of standing water under pile dwellings.
- 27 ○ Aquatic invertebrate assemblages changed periodically related to human activity.
- 28 ○ Invertebrates indicate organic matter load and anoxia during settlement phases.
- 29 ○ Rapid ecosystem recovery was observed after settlement phases.
- 30 ○ Chironomids showed stronger response to environmental changes than cladocerans.
- 31

Abstract

At waterlogged archaeological sites paleolimnological approaches can provide important supporting information about conditions and processes of past human life and human impact on environments around former settlements. In this study, subfossil Cladocera and Chironomidae assemblages were analysed from Neolithic lakeside sediments uncovered at Zürich-Parkhaus Opéra (OP), Switzerland. Our main objectives were to assess how periodic settlement phases altered lakeshore environments and aquatic invertebrate communities during the Neolithic. Aquatic invertebrates occurred in considerable number throughout the investigated sediment sections, supporting that Neolithic settlements at site OP were established above the lake surface and sedimentation occurred mostly under water. Two separate aquatic invertebrate communities were distinguished: an impacted community within cultural layers and a pre- and post-impacted community in sediments between cultural layers. Aquatic invertebrates indicated that human impact likely manifested in surplus organic material load and nutrient input into the water during the cultural periods. This substantially increased biological oxygen demand of the sediments and overall nutrient concentrations of the near-shore water and thereby led to hypoxic conditions. Chironomids showed generally higher amplitude assemblage changes than cladocerans. This could be explained by the very local influence of humans and higher susceptibility of the less mobile chironomids to local hypoxia in and above the sediment. After settlements were abandoned invertebrate assemblages rapidly recovered to pre-impacted states, suggesting their considerable resilience to local human impact. Our results confirm that cladoceran and chironomid remains can trace localised environmental changes associated with human presence and provide important information for the interpretation of prehistoric human activities.

Keywords

Cladocera, Chironomidae, trophic state changes, biological oxygen demand, saprobity, anoxia, wetland archaeology, Neolithic, paleolimnology

1. Introduction

Lakeside settlements provide a special and important type of archaeological site. Due to their location (i.e. at the lakeshore or even on the lake) a wide range of organic remains can be preserved under waterlogged conditions (Menotti, 2012; Ismail-Meyer et al., 2013). Paleolimnological methods applied to archaeological sites of former lakeshore settlements can provide valuable information about the conditions and processes of past human life (an archaeological perspective) and about human impact on the environment around ancient settlements (an ecological perspective). Various plant remains (pollen, macrofossils, etc.) occur generally in high numbers at waterlogged sites, and therefore, palaeobotanical (or archaeobotanical) studies have become an integral part of many archaeological projects (e.g. Jacomet, 2004; Antolín et al., 2016, 2017a, b). Remains of animals, such as vertebrate bones or exoskeleton remains of terrestrial insects (e.g. beetles) are also regularly analysed in archaeological studies (O'Brien et al., 2005). However, more recently “death assemblages” of aquatic invertebrate groups such as cladocerans or aquatic insects have also received increasing attention, especially in waterlogged deposits (e.g. Kenward, 1976; Szeroczyńska, 2002; Ruiz et al., 2006; Whitehouse et al., 2008).

Subfossil remains of Cladocera (water fleas), a group of microscopic branchiopod crustaceans, preserve in remarkable number in sediments. They provide excellent proxy data; since the various cladoceran species and assemblages can indicate climatic changes (e.g. Lotter et al., 1997; Duigan and Birks, 2000), changes in trophic status of lakes (e.g. Lotter et al., 1998; Jeppesen et al., 2001; Szeroczyńska, 2002) and lake level (e.g. Korhola et al., 2005; Nevalainen et al., 2011) or even biological interactions (such as predator-prey relationships; see Korhola and Rautio, 2001). Additionally, cladocerans are widely used to describe human-environment

relationships, mainly from the ecological perspective (e.g. Jeppesen et al., 2001; Szeroczyńska, 2002). Further macroscopic aquatic invertebrate taxa are considered more sporadically in archaeological studies. For instance, subfossil remains of adult aquatic and terrestrial beetles (Coleoptera) and larvae of caddisflies (Trichoptera) were successfully included in some archaeological studies to indicate climatic and environmental changes, and to provide general information on past human activity and living conditions (e.g. Kenward, 1976; Carrott and Kenward, 2001; Greenwood et al., 2006; Whitehouse et al., 2008; Schäfer, 2017). However, subfossil remains of other aquatic insect groups, such as the head capsules of larvae of the Chironomidae (“non-biting midges”, Diptera), are also abundant in lake sediments and probably in several waterlogged deposits. Nevertheless their potential in archaeological studies has been recognized only recently (O’Brien et al., 2005; Ruiz et al., 2006; Whitehouse et al., 2008; Taylor et al., 2013, 2017). In undisturbed small lakes, chironomids are excellent and sensitive indicators of air and water temperature changes (e.g. Eggermont and Heiri, 2012). However, the group also strongly responds to changes in lake trophic state (e.g. Saether, 1979; Brooks et al., 2001; Luoto, 2011), water depth (e.g. Engels and Cwynar, 2011; Velle et al., 2012), dissolved oxygen concentration (e.g. Luoto and Salonen, 2010; Stewart et al., 2013), and availability of different substrates and aquatic macrophytes for colonization (e.g. Brodersen et al., 2001; Langdon et al., 2010). Their ecological sensitivity with the short generation times and relatively good dispersal ability of the winged adults provides the basis for the broad application of larval assemblages of chironomids in recent ecological and paleoecological studies as environmental indicators (e.g. Brodersen and Quinlan, 2006; Langdon et al., 2010).

In 2010, detailed excavations of the remains of Neolithic lakeside settlements were conducted, at a site discovered at the shore of Lake Zürich in the city of Zürich, Switzerland (site Zürich-Parkhaus Opéra, hereafter OP, Fig. 1). An area of approximately 3000 m² was excavated and six layers of settlement deposits (cultural layers) with varying degrees of organic preservation were documented. The oldest settlement on the site had produced a relatively indistinct cultural

layer (Layer 12) with no organic preservation except for some pieces of wood. Two cultural layers (Layers 13 and 14) showed a high degree of organic preservation in the whole or a large part of the excavation area respectively, and contained large quantities of waterlogged organic material. The three youngest layers (Layers 15–17) showed little or partial organic preservation (Bleicher et al., 2018; Fig. 2). During the excavation, rich assemblages of more than ten thousand finds of different materials (ceramics, silex, wooden artefacts, bone and antler objects, textiles, etc.) were recovered (see Harb and Bleicher, 2016; Bleicher et al., 2018).

Due to the high abundance of timber, dating of the cultural layers concentrated on dendrochronology, as this method gives the most precise dates. A detailed dendrochronological study of the pile field and stratified timber allowed not only dating of the cultural layers (see below) but also the identification of settlement phases and individual buildings within these along with their actual building dates and times of use (Bleicher and Harb, 2018).

During the excavation numerous sediment samples were obtained, both as large volume bulk samples (Antolín et al., 2016) and as monoliths. Archaeobotanical analysis of sediments from such waterlogged prehistoric lakeside sites has a long tradition in Zürich and so detailed information was available on the Neolithic economy and ecology from the surrounding sites of Zürich-Mozartstrasse, Kleiner Hafner, Pressehaus and KanSan (Schibler et al., 1997; Fig. 1). However, the aquatic environment and its mutual relation with local human settlements was only examined marginally in prior excavations (Jacomet and Ruoff, 1985).

In the context of an interdisciplinary project (including archaeological, sedimentological, micromorphological and palaeoecological analyses; Bleicher and Harb, 2015; Harb and Bleicher, 2016; Bleicher and Harb, 2017) sediment samples from OP were analysed. Detailed results of this study, including the invertebrate identifications and some initial ecological interpretations and numerical analyses, are provided in the published report of the OP project (Bleicher and Harb, 2017, Heiri et al., 2017, in German). Here we summarize the results of the analyses of chitinous aquatic invertebrate remains from these sediments, including remains of

cladocerans, chironomids and other macroinvertebrates, provide a detailed ecological and numerical analyses of the results and discuss the broader palaeoecological and archaeological implications of these analyses. We aim to assess the extent to which these invertebrate assemblages allow the reconstruction of the environment at the Neolithic settlements, particularly whether the settlement was built on dry land or above open water, which has been a subject of debate in archaeology for decades (e.g. Bleicher and Schubert, 2015; Dieckmann et al., 2006). Furthermore, we assess whether invertebrate assemblages allow the reconstruction of past changes in the local lacustrine environment at the shore of Lake Zürich during the settlement phases (between 3234 and 2727 BC in the Neolithic; Bleicher and Harb, 2015; Bleicher and Harb, 2018). From the ecological perspective, an important characteristic of our study is that the settlement phases were not persistent but were periodically interrupted by periods without evidence for on-site activities within the settlement area. This in turn provides the opportunity to assess the repeated impact of Neolithic human activity (defined by archaeological finds, sediment lithology and human indicator pollen; see Bleicher et al., 2018) on the aquatic environment and its recovery from these influences at the same site. The dendrochronologically dated settlement phases provided precise chronological constraints for phases of human impact and recovery. The repetitive responses of the biota to human presence can also provide information about the life of Neolithic lake-side civilization as detected by aquatic indicator groups. In this paper our main objectives were (1) to assess periodic anthropogenic alterations of the lakeshore environment and the aquatic ecosystem during the Neolithic, utilizing the indicator value of aquatic invertebrates; (2) to compare the response of various aquatic invertebrate groups (mainly cladocerans and chironomids) at the studied near-shore environments to prehistoric human activity; and (3) to constrain the extent and the rate at which invertebrate assemblages recovered from settlement phases.

2. Methods

2.1. Study site and sampling design

From various places within the excavated area of OP several sediment monoliths were obtained (henceforth referred to as sediment columns). These sediment columns were used for high-resolution analyses of fossil assemblages of cladocerans, and chironomids (and other aquatic invertebrates). Pollen were analysed in these records as well (Gobet et al. 2017). Moreover, a 13.6 m long sediment core ("lake core"; OP 11) was obtained directly outside of the former settlement area using an UWITEC coring platform. The location of the lake core is on dry land at present. On the lake core chironomid (and other aquatic invertebrates) remains were analysed and pollen were analysed as well by Gobet et al. (2017). In this paper, we present data from five cultural layers from the Neolithic (dated between 3234 and 2727 BC) situated in the sediment columns and in the lake core (Fig. 2 and 3). The cultural layers (defined by archaeological finds, sediment lithology and human indicator pollen; see Bleicher et al., 2018) showed various degrees of organic preservation and their distribution varied also within the excavating area (Bleicher and Harb, 2015; Bleicher et al., 2018). The cultural layers were clearly identifiable in the studied sediment cores (Fig. 2): visually, they were mainly made up of brown peat-like coarse material and they were much darker than the neighbouring fine-grained pale lake marl deposits (or non-cultural layers). Lithologically, the cultural layers consisted mostly of organic detritus regularly containing loam structures, stones, sand, ash and a large number of archaeological finds (for more details see Bleicher and Harb, 2015; Bleicher et al., 2018). Cultural layers could also be clearly separated based on the elevated abundance of pollen types indicative for human activity (e.g. *Allium*, *Ranunculus*, *Cerealia*, *Papaver rhoeas* and *Plantago lanceolata* pollen) compared with under- and overlying non-cultural layers (see Gobet et al., 2017). Sediment composition, preservation of organic structures, spatial extent and thickness of the cultural layers varied in the studied area.

For analyses of chitinous invertebrate remains, particularly of Cladocera and Chironomidae, five sediment columns were sampled and investigated within the area of the former Neolithic

187 settlement (OP 5060; OP 8584; OP 9624; OP 10432; OP 13184; Fig. 3). Additionally, the lake
188 core (OP 11) was examined for chironomids and other macroinvertebrate remains, whereas it
189 was not investigated for cladocerans.

190 The excavation site was extensively studied by means of dendrochronology which provided a
191 chronological framework for the present study. In total, more than 2800 wood samples were
192 measured and finally 2121 samples were dated. This revealed eight Late and Final Neolithic
193 settlement phases between 3234 and 2727 BC (Bleicher and Burger, 2015; Bleicher and Harb,
194 2018). The layers were dated mainly dendrochronologically based on the stratigraphic position
195 of horizontal pieces of timber and to a lesser extent by find typology and radiocarbon
196 measurements of clearly stratified material (Bleicher and Harb 2018). Therefore, the settlement
197 deposits are precisely dated whereas the age of the lake sediments between them is constrained
198 based on the age of the cultural layers (Fig. 2 and 3).

199 In contrast, the chronological framework of the lake core (OP 11) was based on 10 AMS
200 radiocarbon dates on terrestrial plant macrofossils, providing an independent chronology
201 (Gobet et al., 2017). The radiocarbon ages were calibrated into calendar years before Christ
202 (BC) using CALIB 6.1.0 and the age-depth relationship was assessed using a linear model that
203 excludes the two youngest radiocarbon dates because they seemed to be too young (Gobet et
204 al., 2017).

205

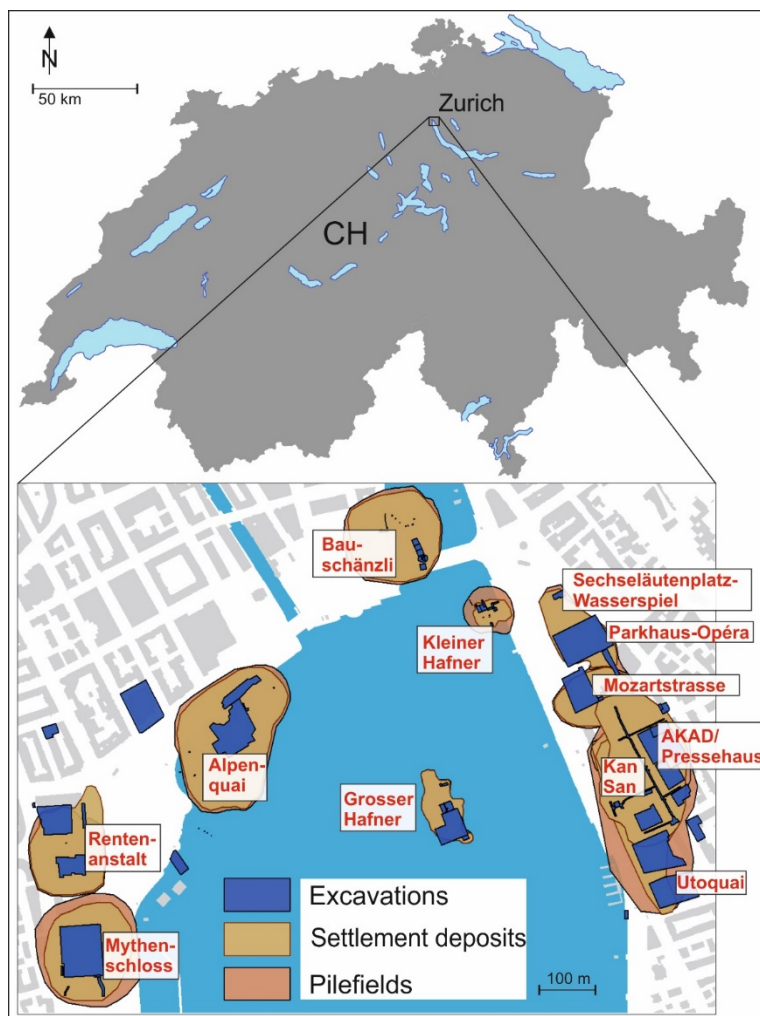


Figure 1. Location of Zürich within Switzerland and location of the Zürich-Parkhaus Opéra excavation area among other prehistoric lakeside settlements within Zürich.

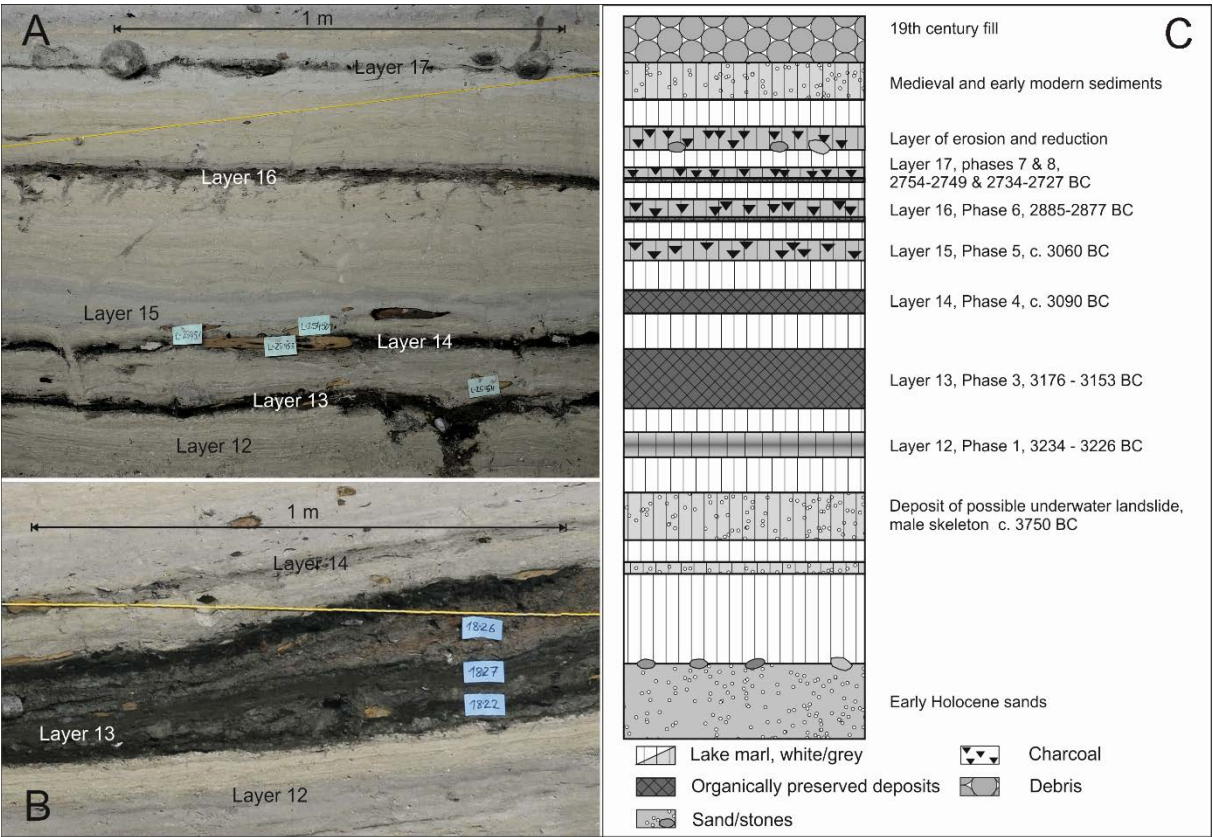


Figure 2. Two examples of profile views of the cultural layers and the variability of their appearance and thickness (A-B); and the idealised sediment stratigraphy of Zürich-Parkhaus Opéra (C).

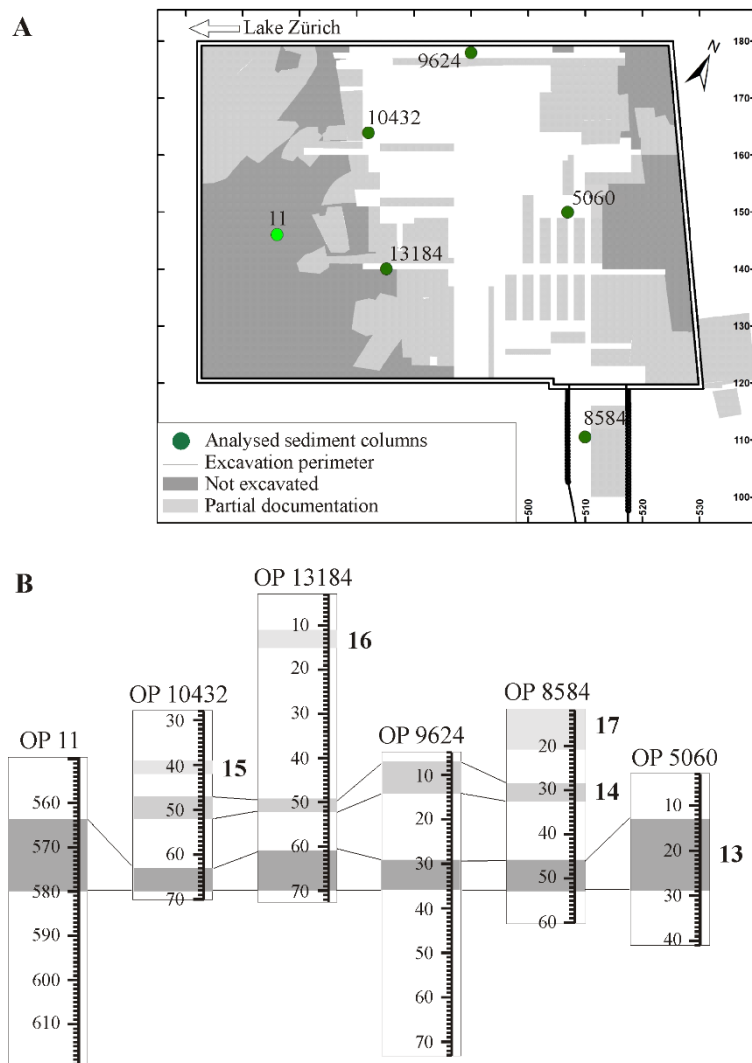


Figure 3. Location of the investigated sediment columns (OP 5060, OP 8584, OP 9624, OP 10432, OP 13184) within the settlement area of Zürich-Parkhaus Opéra and of the lake core (OP 11) (A); and position of the cultural layers (13: 3176–3153 BC; 14: 3090 BC; 15: 3060 BC; 16: 2885–2877 BC; 17: 2754–2749 and 2734–2727 BC) within the sediment columns (B).

The oldest cultural layer, Layer 12, was associated with the first settlement phase from the Late Neolithic (dendrochronologically dated to 3234–3226 BC; Bleicher and Harb, 2015) and apparently did not produce any preserved organic remains except for dispersed timber so it was not visible in our studied sediment columns. Layer 13, dendrochronologically dated between 3176 and 3153 BC (associated with the third settlement phase), showed the best organic preservation and was documented throughout the entire excavated area (Fig. 2 and 3). Therefore, several studies had already been performed concentrating mainly on this layer (e.g.

Antolín et al., 2016, 2017a, b; Heiss et al., 2017 on archaeobotanical remains). Layer 14, dendrochronologically dated to 3090 BC, was most likely associated with the fourth settlement phase and showed good organic preservation (similar to Layer 13) in large parts of the site. It appeared in most of our studied sediment columns (OP 8584, OP 9624, OP 10432 and OP 13184; Fig. 3). Layer 15, dendrochronologically dated to 3060 BC, was associated with the fifth settlement phase. It showed poor organic preservation of the anthropogenic material and was apparent only in one of the investigated sediment cores (in OP 10432; Fig. 3). The two youngest cultural layers associated with settlement phase six (Layer 16; dendrochronologically dated to 2885–2877 BC) and settlement phases seven and eight (Layer 17; dendrochronologically dated to 2754–2749 and 2734–2727 BC) showed similarly poor preservation of anthropogenic remains. These layers were also present in only some sediment columns in this study. Layer 16 was only visible in sediment core OP 13184, while layer 17 was only documented in OP 8584 (Fig. 3). More detailed information on the cultural layers in the site Zürich-Parkhaus Opéra is available in Bleicher et al. (2018).

2.2. Cladocera analysis

For Cladocera altogether 80 sediment sub-samples of 2 cm³ volume each were investigated from the five sediment columns located within the area of the Neolithic settlement (OP 5060; OP 8584; OP 9624; OP 10432; OP 13184).

Sub-samples were treated with 10% KOH for 30 minutes at 70°C in a water bath and sieved through a 45 µm mesh. Samples containing significant amounts of (mainly plant) debris were first sieved through 1 mm mesh, and the large particle fractions were checked for Cladocera remains. Sieved samples were then treated with 5% HCl for 15 minutes at room temperature, sieved through 45 µm mesh again and transferred to test tubes containing 1 *Lycopodium* tablet, centrifuged for 5 minutes and the supernatant was then decanted. Before use the *Lycopodium*

tablets were dissolved in 10% HCl, the samples were then centrifuged and the fluid above the *Lycopodium* spores was decanted.

After the chemical treatment 15–30 drops of glycerol-safranin dye were added, the samples were mixed well and glycerol was added. Next, samples were warmed to 70°C in a water bath, centrifuged for 5 minutes and the supernatant was then decanted. The samples were mixed and used to produce semi-permanent microscope slides in glycerol, sealed with wax or nail varnish. Identification of Cladocera remains followed Frey (1958, 1959, 1960, 1993), Flössner (2000) and Szeroczyńska and Sarmaja-Korjonen (2007).

2.3. Analysis of chironomids and other macroinvertebrate remains

For chironomid analysis altogether 103 sub-samples of 3–5 cm³ volume each from the sediment columns in the area of the Neolithic settlement (the same samples as for the cladoceran analysis) as well as of 1.5–2 cm³ volume each from the lake core were investigated.

Sub-samples were treated with 10% KOH at room temperature for 2 hours. Afterwards the sediment was sieved with a 100 µm mesh. Some of the samples were also shortly treated with 10% HCl (until no gas bubbles formed anymore) and sieved again with a 100 µm mesh sieve.

Chironomid larval head capsules were picked from a Bogorov-counting tray (Gannon, 1971) under stereomicroscope at 40x magnification. Larval head capsules were mounted on microscope slides in Euparal® mounting medium for microscopic identification. Identification of chironomid head capsules followed Wiederholm (1983), Rieradevall and Brooks (2001), and Brooks et al. (2007). Generally, 26–33 chironomid head capsules were identified per cm³ with an overall count of 135–140 head capsules per sample.

We qualitatively evaluated the preservation state of the subfossil chironomid remains in each sample based on three different categories: brittleness, evidence for microbial degradation and folding, respectively. Each sample was assigned scores between 0 and 5 for these categories, with 5 indicating the poorest preservation state. Our aim with this description was to determine

possible differences in the preservation conditions of the chironomid remains between the cultural and non-cultural layers.

Remains of other macroscopic invertebrates such as mandibles of Ephemeroptera (mayflies), Coleoptera (beetles), *Sialis* (Sialidae, alderflies), Trichoptera (caddisflies) and *Chaoborus* (Chaoboridae, phantom midges); resting stages of Bryozoa (moss animals) and larval fragments of *Sialis*, Trichoptera (caddisflies) and *Dashyelea* (Ceratopogonidae, biting midges) were also sorted from the sediment sub-samples used for chironomid analysis, and identified generally to coarser taxonomic level (ranging from genus to order).

2.4. Numerical analysis

Stratigraphic patterns of cladoceran, chironomid and other macroinvertebrate remains with the preservation scores of chironomid remains were plotted for each sediment record separately using the program psimpoll 4.27 (Bennett, 2007; see Supplementary material and Heiri et al., 2017).

Other invertebrate remains occurred in relatively small numbers in every sediment column (relative to cladoceran and chironomid remains) and they were identified at coarser taxonomic resolution than the chironomid and cladoceran remains. Therefore, other invertebrates were not included in the statistical analyses, however, they provide important supplementary information about past ecosystem changes at the study site.

To investigate whether cultural and non-cultural layers (defined by archaeological finds, sediment lithology and human indicator pollen; Bleicher and Harb, 2015; Gobet et al., 2017; Bleicher et al., 2018) could be separated based on cladoceran and chironomid remains, one-way ANOSIM (analysis of similarities) was applied by using the PAST software (Hammer et al., 2001). One-way ANOSIM is based on comparing distances (using Euclidean distances) between *a priori* defined groups and significance is calculated by permutation of group membership (9999 permutations). All pairs of groups (i.e. cultural versus non-cultural layers

and between individual cultural layers) were compared to detect significant ($p < 0.05$) differences using a post hoc test (Table 1A–B).

To summarize major changes in assemblages of Cladocera and Chironomidae, detrended correspondence analysis (DCA) was performed for the individual sediment cores using CANOCO version 4.5 (ter Braak and Šmilauer, 1998). Before the ordinations, percentage data were square root transformed and rare taxa were down-weighted. DCA axes were rescaled where it was necessary by multiplying by -1 and subtracting the minimum value of the transformed axis scores to ensure high DCA axes scores represented impacted conditions in all DCAs. Apart from the ordinations for each individual sediment column, two further DCAs were calculated including all data (all sediment columns combined) of Cladocera and Chironomidae assemblages, respectively.

Significant indicator taxa of Cladocera and Chironomidae for cultural and non-cultural layers were identified with the indicator value method using IndVal 2.0 software (Dufrêne and Legendre, 1997). This method calculates an indicator value (IV) that may range between 0 and 100 for each taxon for pre-defined groups of samples and tests the significance by Monte Carlo permutations (9999 permutations). The indicator taxa are described as the most characteristic taxa of *a priori* defined groups of samples, which are mainly found in a certain group (specificity) and usually or even always present in all samples belonging to that group (fidelity). IV index values can reach the maximum value of 100 when a taxon is found only in a certain group of samples and occurs in all samples of that group. The *a priori* defined groups of samples in our analyses were the cultural and non-cultural samples within the sediment columns. Two IndVal analyses were run including all five sediment columns situated within the settlement area: one for the cladoceran and one for the chironomid data.

Finally, in order to assess possible water quality changes, saprobity index values were calculated based on the chironomid data. Based on the saprobic values of taxa occurring in a sample, we calculated the saprobity index (SI) based on tabulated values in Moog (2002). These

saprobic values are defined for individual chironomid species, whereas identification of fossil chironomids is typically possible only to morphotype or genus level. To account for this we worked with mean saprobic index scores for higher order taxa based on the index values for all species belonging to this morphotype (Moog 2002; see Suppl. table 1). We excluded strictly rheophilic taxa presented in Moog (2002) from these calculations, since our samples originated from lentic environment and the role of flowing water was clearly minor. Saprobic index values for individual samples were calculated as mean values of the chironomid taxa in this sample, weighted by their abundance (for more details about the method and the calculation see Moog, 2002).

3. Results

3.1. Cladocera assemblages

Altogether more than 8600 Cladocera remains belonging to 36 taxa were identified from the five sediment columns located within the Neolithic settlement. Half of the identified cladoceran taxa (19) reached at least 1% relative abundance in the assemblage. The cladoceran assemblages were mainly characterized by the dominance of the Chydoridae family. However, taxa belonging to the families of Bosminidae, Daphniidae, Sididae and Macrothricidae were also present at low numbers. Accordingly, most of the identified cladoceran taxa are typically associated with benthic habitats, while planktonic taxa occurred in small proportion and reached only 0–13% in the assemblage.

3.2. Assemblages of Chironomidae and other macroinvertebrate remains

Altogether more than 14,800 chironomid head capsules belonging to 66 Chironomidae taxa and three subfamilies (Tanypodinae, Orthoclaadiinae and Chironominae) were identified from six sediment columns. Most of the chironomid taxa occurred in all sediment records, although only 21 taxa reached at least 1% relative abundance in the assemblages. In general, the subfamily

Chironominae occurred at the highest overall abundance, while Orthoclaadiinae and Tanypodinae occurred at lower abundance. Subfossil chironomid head capsules showed evidence of fragmentation, decay and folding, probably due to the littoral position of the sediment columns. However, their overall preservation state was still generally good (index scores 0 to 2 units) and allowed reliable identification of the head capsules. Preservation state was noticeably weaker in the cultural layers, possibly due to compaction of these more organic-rich layers which promoted fragmentation and folding.

Remains of other macroinvertebrate groups occurred consistently in all the sediment cores and altogether more than 1700 such remains were identified. The most abundant ones were mouthparts of larvae of mayflies (Ephemeroptera) and caddisflies (Trichoptera), but remains of several other invertebrate groups (e.g. Rhabdocoela, Bryozoa, Ceratopogonidae, Chaoboridae) also occurred regularly in the samples.

3.3. Differences between cultural and non-cultural layers

Both in the cladoceran and chironomid assemblages no significant differences were found between the individual cultural layers in most of the sediment columns, while most of the cultural layers differed significantly from non-cultural sediment sections (Table 1A–B). However, there are some exceptions: Layer 17 (in column OP 8584) differed significantly from Layers 13 and 14 but did not differ from non-cultural layers based on cladoceran and chironomid data; Layer 16 (in column OP 13184) significantly differed from Layer 13 based on chironomid data. In the lake core (OP 11) we did not find any significant difference between cultural and non-cultural layers (Table 1A–B).

Table 1A. Results of dissimilarity analyses between cultural and non-cultural layers and between the individual cultural layers identified based on one-way ANOSIM (R = rate of dissimilarity between groups, p = significance level, NS = non-significant) using Cladocera

data, respectively, in the individual sediment columns of Zürich-Parkhaus Opéra (OP 5060, OP 8584, OP 9624, OP 10432, OP 13184).

Sediment columns	Dissimilarity	<i>p</i>	R
OP 5060	cultural layer (13) vs. non-cultural layers	<0.005	0.61
OP 8584	all cultural layers vs. non-cultural layers	NS	–
	Layer 17 vs. non-cultural layers	NS	–
	Layer 13 and 14 vs. non-cultural layers	<0.05	0.21
	Layer 17 vs. Layers 13 and 14	<0.05	0.65
	Layer 14 vs. Layer 13	NS	–
OP 9624	all cultural layers vs. non-cultural layers	NS	–
	Layer 14 vs. non-cultural layers	NS	–
	Layer 13 vs. non-cultural layers	NS	–
OP 10432	all cultural layers vs. non-cultural layers	<0.05	0.33
	Layer 15 vs. non-cultural layers	NS	–
	Layer 14 vs. non-cultural layers	NS	–
	Layer 13 vs. non-cultural layers	<0.01	0.54
	Layer 15 vs. Layer 14	NS	–
	Layer 15 vs. Layer 13	NS	–
	Layer 14 vs. Layer 13	NS	–
OP 13184	all cultural layers vs. non-cultural layers	<0.001	0.47
	Layer 16 vs. non-cultural layers	NS	–
	Layer 14 vs. non-cultural layers	NS	–
	Layer 13 vs. non-cultural layers	NS	–
	Layer 16 vs. Layer 14	NS	–
	Layer 16 vs. Layer 13	NS	–
	Layer 14 vs. Layer 13	NS	–

Table 1B. Results of dissimilarity analyses between cultural and non-cultural layers and between the individual cultural layers identified based on one-way ANOSIM (R = rate of dissimilarity between groups, *p* = significance level, NS = non-significant) using Chironomidae data, respectively, in the individual sediment columns of Zürich-Parkhaus Opéra (OP 5060, OP 8584, OP 9624, OP 10432, OP 13184) and in the lake core (OP 11).

Sediment columns	Dissimilarity	<i>p</i>	R
OP 5060	cultural layer (13) vs. non-cultural layers	<0.001	0.86
OP 8584	all cultural layers vs. non-cultural layers	NS	–
	Layer 17 vs. non-cultural layers	NS	–
	Layer 13 and 14 vs. non-cultural layers	<0.05	0.30
	Layer 17 vs. Layers 13 and 14	<0.05	0.42

	Layer 14 vs. Layer 13	NS	–
OP 9624	all cultural layers vs. non-cultural layers	<0.001	0.56
	Layer 14 vs. non-cultural layers	<0.05	0.51
	Layer 13 vs. non-cultural layers	<0.001	0.72
	Layer 14 vs Layer 13	NS	–
OP 10432	all cultural layers vs. non-cultural layers	<0.05	0.31
	Layer 15 vs. non-cultural layers	NS	–
	Layer 14 vs. non-cultural layers	<0.01	0.74
	Layer 13 vs. non-cultural layers	<0.01	0.81
	Layer 15 vs. Layer 14	NS	–
	Layer 15 vs. Layer 13	NS	–
	Layer 14 vs. Layer 13	NS	–
OP 13184	all cultural layers vs. non-cultural layers	<0.001	0.52
	Layer 16 vs. non-cultural layers	<0.01	0.82
	Layer 14 vs. non-cultural layers	<0.05	0.56
	Layer 13 vs. non-cultural layers	<0.001	0.84
	Layer 16 vs. Layer 14	NS	–
	Layer 16 vs. Layer 13	<0.05	0.46
	Layer 14 vs. Layer 13	NS	–
OP 11	cultural layer (13) vs. non-cultural layers	NS	–

3.4. Compositional changes associated with the cultural layers

Cladoceran assemblages showed distinct changes in the cultural layers. Layer 13 and 16 were marked by increased relative abundance of *Alona rectangularis*, *Pleuroxus trigonellus*, *Pleuroxus unicatus* and *Graptoleberis testudinaria* (reaching 24–37% and 34% of total cladoceran abundance in Layer 13 and 16, respectively; Suppl. figures 1–5A). In Layer 14, *A. rectangularis*, *Alona quadrangularis* and *Paralona pigra* increased in relative abundance with *Chydorus sphaericus* and *P. trigonellus* (reaching 20–41% of total cladoceran abundance; Suppl. figures 2–5A). Finally, in Layers 15 and 17 *Alona affinis* and *Paralona pigra* reached high relative abundance with *A. quadrangularis*, *Disparalona rostrata* and *Pleuroxus truncatus* reaching 24% relative abundances in both layers (Suppl. figures 2A and 4A). Based on IndVal analysis, four cladoceran taxa can be considered significant indicators for the cultural layers: *P.*

trigonellus, *G. testudinaria*, *P. unicatus* and *D. rostrata*. Additionally, *A. rectangula* and *A. quadrangularis* also characterized cultural layers with high IV, although they were not identified as significant indicators (Table 2).

Table 2. Indicator values (IndVal) and significance level (p; NS= non-significant result) for Cladocera and Chironomidae taxa, respectively, in cultural and non-cultural layers of the sediment columns of Zürich-Parkhaus Opéra (OP 5060, OP 8584, OP 9624, OP 10432, OP 13184).

Cladocera					
Cultural layers			Non-cultural layers		
	IndVal	p		IndVal	p
<i>Pleuroxus trigonellus</i>	69.28	<0.01	<i>Alonella excisa</i>	68.95	<0.01
<i>Graptoleberis testudinaria</i>	68.16	<0.01	<i>Eurycercus</i>	67.40	<0.01
<i>Pleuroxus unicatus</i>	56.33	<0.01	<i>Alona intermedia</i>	67.28	<0.01
<i>Alona rectangula</i>	50.03	NS	<i>Alona affinis</i>	66.41	<0.01
<i>Alona quadrangularis</i>	46.25	NS	<i>Acroperus harpae</i>	60.04	NS
<i>Campocercus rectirostris</i>	43.75	NS	<i>Chydorus sphaericus</i>	59.91	NS
<i>Disparalona rostrata</i>	24.96	<0.01	<i>Bosmina</i>	56.92	NS
<i>Alonella exigua</i>	20.51	NS	<i>Paralona pigra</i>	56.43	NS
			<i>Alonella nana</i>	44.06	NS
			<i>Sida crystallina</i>	40.22	NS
			<i>Pleuroxus truncatus</i>	38.82	NS
			<i>Alona costata</i>	32.53	NS
			<i>Alonopsis elongata</i>	32.39	NS
			<i>Monospilus dispar</i>	30.22	NS

Chironomidae					
Cultural layers			Non-cultural layers		
	IndVal	p		IndVal	p
<i>Phaenopsectra flavipes</i> -type	75.34	<0.01	<i>Tanytarsus glabrescens</i> -type	73.03	<0.01
<i>Polypedilum nubeculosum</i> -type	69.94	<0.01	<i>Pentaneurini</i>	69.92	<0.01
<i>Microtendipes pedellus</i> -type	65.57	<0.01	<i>Procladius</i>	69.87	<0.01
<i>Chironomus plumosus</i> -type	61.01	<0.01	<i>Cricotopus cylindraceus</i> -type	68.29	<0.01
<i>Dicrotendipes notatus</i> -type	51.65	<0.01	<i>Tanytarsus</i> indet.	63.47	<0.01
<i>Polypedilum sordens</i> -type	49.71	<0.01	<i>Dicrotendipes nervosus</i> -type	60.90	<0.01
<i>Cricotopus intersectus</i> -type	48.04	NS	<i>Paratanytarsus penicillatus</i> -type	59.56	<0.01
<i>Chironomus anthracinus</i> -type	22.48	NS	<i>Tanytarsus pallidicornis</i> -type	58.20	<0.01
			<i>Tanytarsus mendax</i> -type	53.02	NS
			<i>Cladotanytarsus mancus</i> -type	49.03	<0.01
			<i>Paratanytarsus austriacus</i> -type	39.40	NS
			<i>Glyptotendipes pallens</i> -type	38.28	NS
			<i>Cladopelma lateralis</i> -type	29.55	NS

At subfamily/tribe level, chironomid assemblages were dominated by the tribe Chironomini (belonging to the subfamily Chironominae) in all cultural layers and this group reached distinctly higher relative abundances (e.g. in Layers 13 and 14) than in the lake marl deposits (non-cultural layers) within the Neolithic settlement area. Contrarily, in the non-cultural layers overlying the cultural layers, relative abundance of Chironomini mostly dropped to lower values, while Tanytarsini, and subfamilies of Orthoclaadiinae and Tanypodinae increased (Fig. 4).

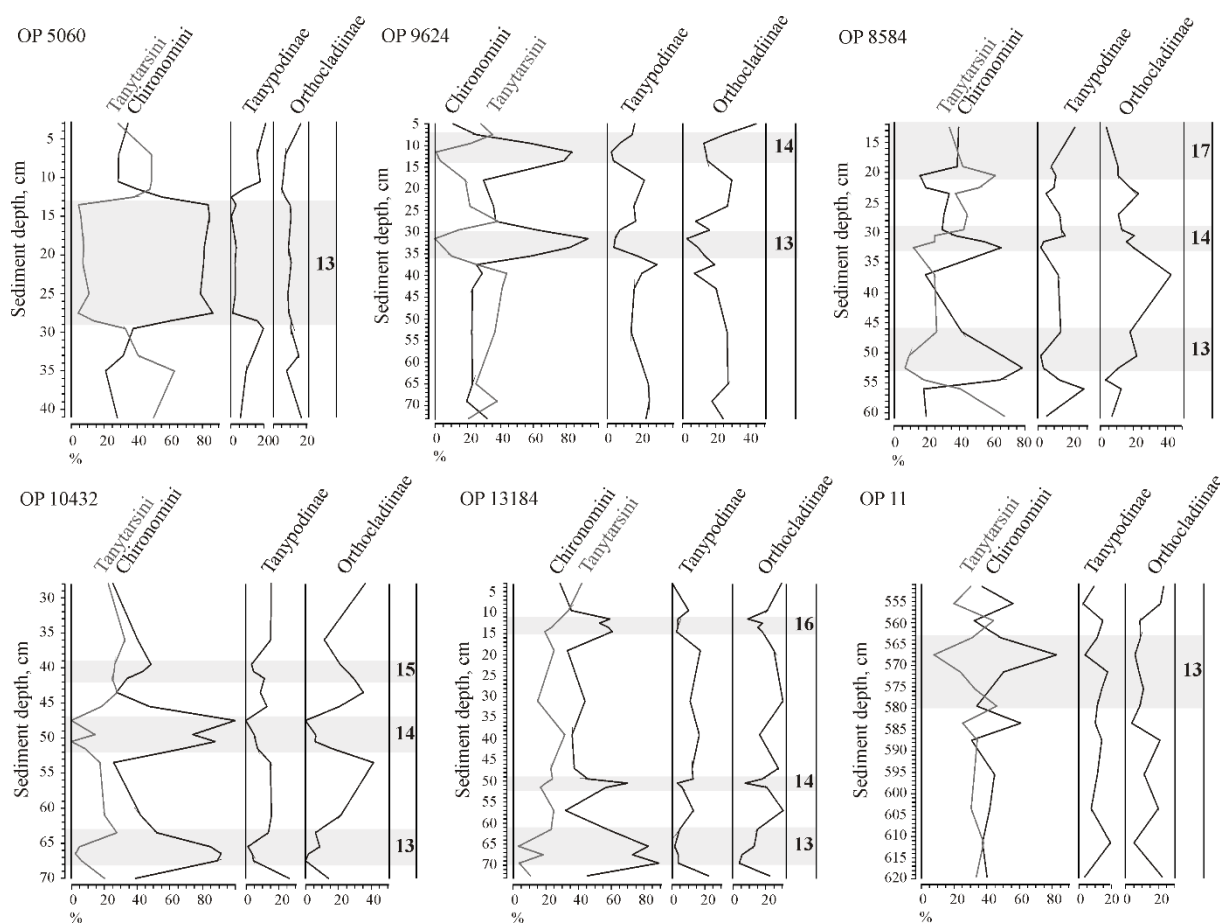


Figure 4. Relative abundance changes of chironomid subfamilies (Chironominae (including Tanytarsini and Chironomini tribes), Tanypodinae and Orthoclaadiinae) in cultural layers (13: 3176–3153 BC; 14: 3090 BC; 15: 3060 BC; 16: 2885–2877 BC; 17: 2754–2749 and 2734–2727 BC) in the individual sediment columns located in the settlement area of Zürich-Parkhaus Opéra (OP 5060, OP 8584, OP 9624, OP 10432, OP 13184) and in the lake core (OP 11).

At species group and genus level, minor differences in dominant chironomid taxa among the individual cultural layers were apparent. In Layers 13, 14 and 15 *Chironomus plumosus*-, *Phaenopsectra flavipes*-, *Microtendipes pedellus*- and *Polypedilum nubeculosum*-type dominated. Moreover, *Dicortendipes notatus*-, *Polypedilum sordens*- and *Cricotopus intersectus*-type reached high relative abundance within the settlement area (reaching 50–62%, 29–54% and 40% of total chironomid abundance in Layers 13, 14 and 15, respectively; Suppl. figures 1–6B). In Layer 16 *P. nubeculosum*-, *M. pedellus*- and *P. flavipes*-type dominated (reaching 25% of the total chironomid abundance; Suppl. figure. 5B). Finally, in Layer 17 next to *C. plumosus*- and *P. sordens*-type, only *C. anthracinus*- and *C. intersectus*-type dominated and these taxa reached 17–24% of the total chironomid abundance (Suppl. figure 3B). Indicator value analysis showed a very consistent picture in the Neolithic settlement area, where *P. flavipes*-, *P. nubeculosum*-, *M. pedellus*-, *C. plumosus*-, *D. notatus*- and *P. sordens*-type were significant indicators for the cultural layers, while *C. intersectus*- and *C. anthracinus*-type also had high IV for the cultural layers but were not identified as significant indicators. In the lake core, however, no significant indicator taxa were identified for the cultural layers (Table 2). Finally, remains of other macroinvertebrates showed a similar pattern in most cultural layers and sediment columns with highest absolute numbers of caddisfly remains (Trichoptera). Exceptions are lake core and Layer 17 in OP 8584, where remains of turbellarian flatworms (Rhabdocoela) became dominant (Suppl. figures 1–6B). Next to caddisfly larvae, mandibles of phantom midge larvae (*Chaoborus* spp.) reached relatively high number in Layer 16 in OP 10432 (Suppl. figure 5B).

3.5. Assemblage changes associated with the cultural layers

In general, cladoceran and chironomid assemblage changes were clearly visible on the first DCA axes for most cultural layers in most sediment columns. The amplitude of these changes

(based on mean DCA axis 1 scores changes), however, varied between invertebrate groups, between sediment columns and between the cultural layers as well (Fig. 5).

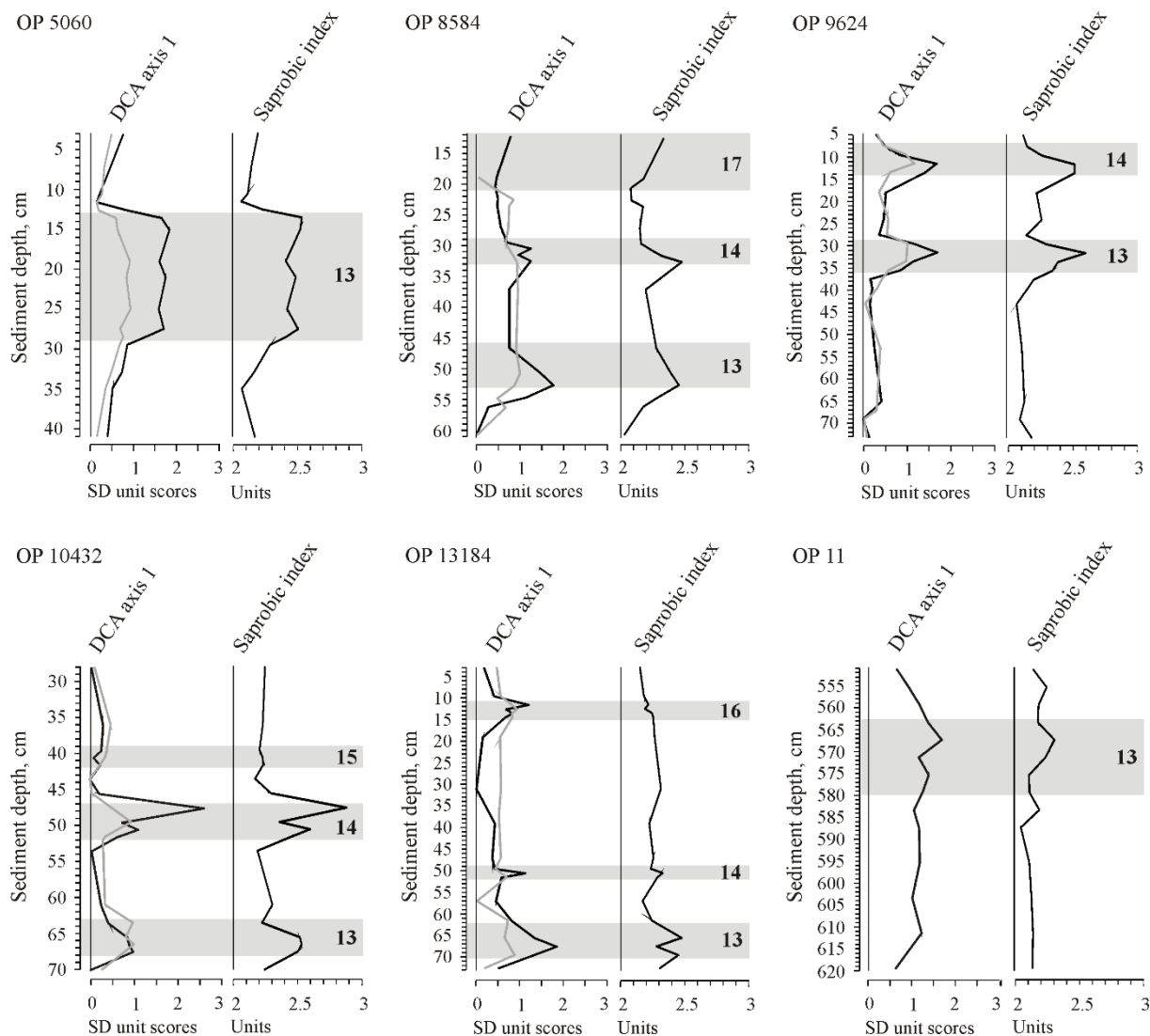


Figure 5. DCA axis 1 score changes of cladocerans (grey line) and chironomids (black line) and chironomid-inferred saprobic index changes in cultural layers (13: 3176–3153 BC; 14: 3090 BC; 15: 3060 BC; 16: 2885–2877 BC; 17: 2754–2749 and 2734–2727 BC) in the individual sediment columns located in the settlement area of Zürich-Parkhaus Opéra (OP 5060, OP 8584, OP 9624, OP 10432, OP 13184) and in the lake core (OP 11).

Generally, cladoceran and chironomid assemblage changes were most pronounced in Layers 13 and 14. However, chironomids always showed higher amplitude change than cladocerans (Fig. 5).

The comparison of assemblage changes between sediment columns was possible only for Layers 13 and 14, because only these two layers were present in most sediment records. For cladocerans, differences between the records were not remarkable for Layer 13 (varied between *ca.* 0.46–0.64 SD units; Fig. 5). For Layer 14 the strongest cladoceran assemblage changes were noted in OP 13184 (by *ca.* 0.54 SD units), followed by OP 9624 (by *ca.* 0.33 SD units) and OP 10432 (by *ca.* 0.31 SD units) and finally by OP 8584 (by *ca.* 0.14 SD units; Fig. 5). Based on chironomids, changes in Layer 13 were strongest in the most landward positioned OP 5060 (by *ca.* 1.29 SD units) and OP 9624 (by *ca.* 1.05 SD units), followed by OP 8584 (by *ca.* 0.85 SD units), OP 13184 (by *ca.* 0.81 SD units) and OP 10432 (by *ca.* 0.77 SD units), and finally by the lake core (OP 11; by *ca.* 0.33 SD units) (Fig. 5).

Overall DCA analyses including all cladoceran and chironomid assemblages from all columns together showed a gradient length <3 SD units (1.06 SD units for cladoceran and 2.26 SD units for chironomid data, respectively). The first two DCA axes explained 27.3% and 24.1% of total variance based on cladoceran and chironomid data, respectively. Overall DCAs showed clear division of assemblages from cultural and non-cultural (or lake marl) samples for both cladoceran and chironomid taxa (Fig. 6). However, for chironomids this division was along the strongest, first DCA axis, whereas for cladocerans cultural and non-cultural samples were divided along DCA axis 2. This suggests that this separation was stronger and more pronounced for the chironomids samples.

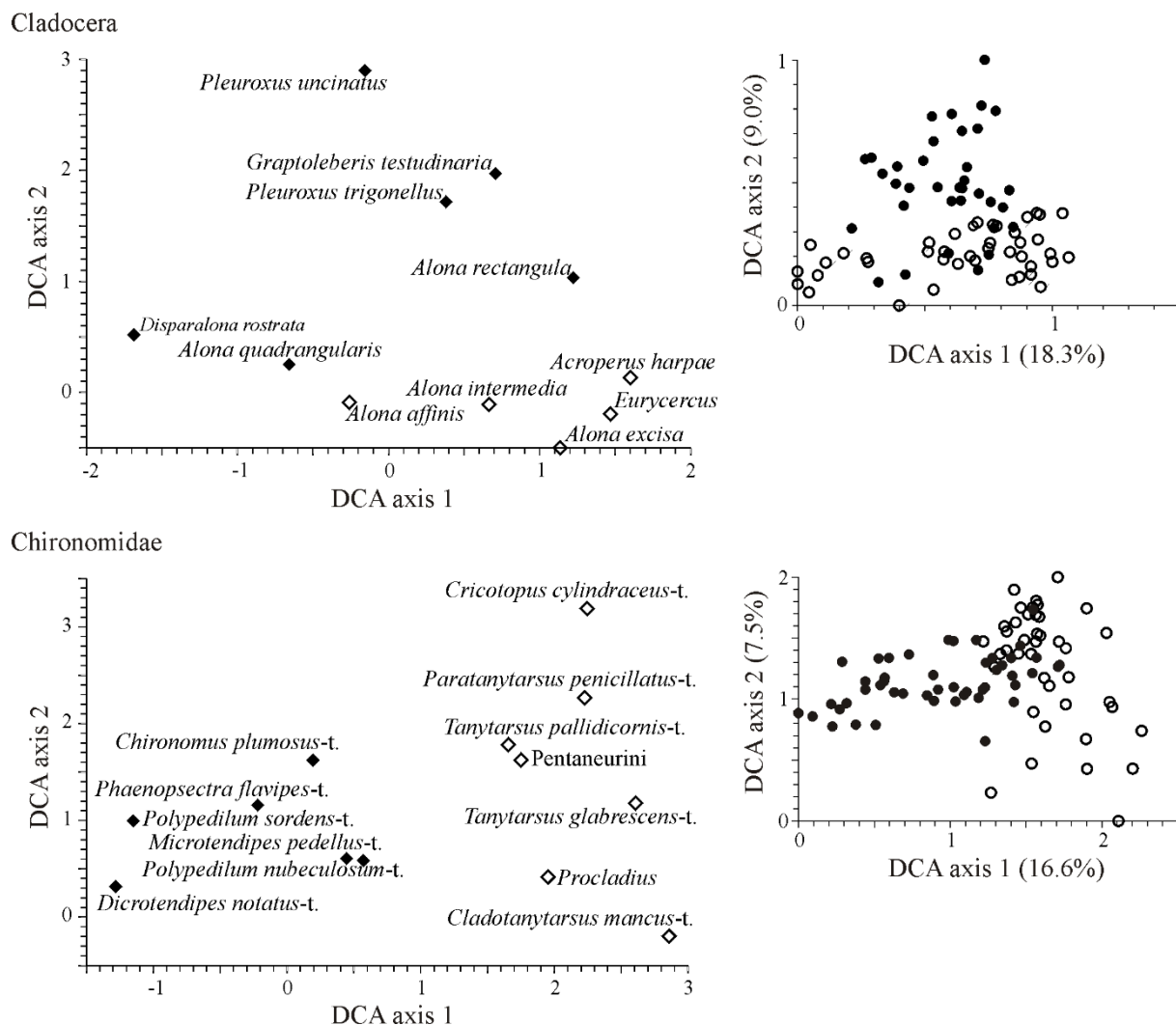


Figure 6. Results of overall DCA analyses. Left: species scores for Cladocera and Chironomidae taxa (open diamond: taxa indicating non-cultural layer samples; black diamond: taxa indicating cultural layer samples). Right: Site scores indicating the division of samples from lake marl (i.e. from non-cultural layer; open circles) and from cultural layers (black circles) along the first two DCA axes (variance explained by the axes in brackets). The analyses were based on all Cladocera and Chironomidae data from the sediment columns located within the settlement area of Zürich-Parkhaus Opéra.

3.6. Saprobity changes associated with the cultural layers

Chironomid-based SI values indicated increasing saprobity (i.e. increasing abundances of taxa indicative of high rates of organic matter degradation and oxygen demand) in cultural layers. The strongest increase in SI values was detected in OP 5060, OP8584, OP 9624 and OP 10432,

whereas SI values were less elevated in OP 13184 and OP 11 (Fig. 5). Similarly, SI index values showed a clear tendency to higher values in Layers 13 and 14, with the exception in OP 13184, where only a slight increase was apparent (Fig. 5). In the younger sediment layers, however, SI did not change or even decreased slightly compared to the preceding non-cultural layer, except in Layer 17 of OP 8584, where increasing saprobity values were noted again (Fig. 5).

4. Discussion

Embedded in an interdisciplinary project, we investigated near-shore Neolithic sediment sequences at Lake Zürich (Switzerland) with the aim of describing the aquatic environmental conditions at the ancient settlement and to assess periodic environmental alterations induced by human presence and activity by utilizing the indicator value of aquatic invertebrates. Our observations indicate that aquatic invertebrates occurred in considerable number throughout all the investigated sediment sections, both in cultural and non-cultural layers. Therefore, our data support the interpretation that the Neolithic settlements in the OP excavation area were established above the lake surface and sedimentation happened mostly under water. This agrees with other findings such as the lack of evidence of trampling and bioturbation by livestock, the presence of aquatic plant remains in the cultural layers and the results of palaeotopographical investigations (Schneider et al., 2015; Bleicher et al., 2018). Only the area in the most landward part of the settlement showed some evidence that it may have temporarily fallen dry for short periods (e.g. evidence for currents and wave action, see Bleicher and Harb, 2015; Schneider et al., 2015; Bleicher et al., 2017). The results and analyses described in this study furthermore demonstrate consistent and clear responses of aquatic invertebrate assemblages during periods of human presence (i.e. in the cultural layers), indicating a major and systematic effect of Neolithic human activity on the near-shore environments and habitats at this lake.

4.1. Human-induced alterations of the aquatic environment

Typically, the assessment of human impact on ecosystems and environments is based on comparisons of pre-impacted and impacted states (e.g. European Union, 2000; Bennion and Battarbee, 2007). In our study, we are in a situation where we can compare several consecutive phases of human impact with aquatic invertebrate assemblages before and after the phases of human occupancy of the lakeside settlements. We found essentially two types of aquatic invertebrate communities: impacted communities within the cultural layers differing in several aspects from pre- and post-impact communities in the non-cultural layers. Indicative cladoceran taxa in non-cultural sediment sections are *Alona excisa*, *Eurycercus*, *Alona intermedia*, *Alona affinis* and *Acroperus harpae*. All of these taxa typically occur in low productivity lake environments (e.g., Whiteside, 1970; Lotter et al., 1998; Bjerring et al., 2009). Similarly, chironomid taxa associated with non-cultural layers belonged mainly to the tribe Tanytarsini (e.g. *Tanytarsus* spp., *Paratanytarsus penicillatus*- and *Cladotanytarsus mancus*-type) as well as the subfamilies of Tanypodinae (*Procladius* and *Pentaneurini*) and Orthocladiinae (*Cricotopus cylindraceus*-type). Such assemblages dominated by Tanytarsini and Orthocladiinae are typically found in relatively unimpacted environments with low to moderate productivity and high oxygen availability (e.g., Saether, 1979; Moog, 2002; Langdon et al., 2006). Moreover, *P. penicillatus*-, *C. mancus*-, *Dicrotendipes nervosus*- and *Cladopelma lateralis*-type larvae often indicate macrophyte coverage and moderately productive waters (Brodersen et al., 2001; Brooks et al., 2007; Moller Pillot, 2009). An important common feature of this chironomid assemblage is that its members do not tolerate anoxia (e.g., Brodersen and Quinlan, 2006; Luoto and Salonen, 2010; Luoto, 2011). Moreover, amongst other macroinvertebrate remains those of Ephemeroptera (mayflies) and *Plumatella* (bryozoans) dominated. Although *Plumatella* statoblasts can be widely transported in lakes, Ephemeroptera remains are less mobile and this group occurs mainly in well-oxygenated waters.

In contrast, cladoceran assemblages in the cultural or human-impacted sediment layers were dominated by species often associated with eutrophic lake conditions, such as *Pleuroxus trigonellus*, *Pleuroxus unicatus*, *Alona rectangula*, *Alona quadrangularis* and *Disparalona rostrata* (Fig. 7A) (e.g., Whitehouse, 1970; Lotter et al., 1998; Sarmaja-Korjonen, 2003; Bjerring et al., 2009). Most of these species have been identified in earlier studies as indicators of human impact, probably due to their preference for higher lake productivity (Whitehouse, 1970; Szeroczynska, 2002). Similarly, the chironomid assemblages of cultural layers were dominated by taxa that can tolerate high lake productivity and low oxygen concentrations, such as *Phaenopsectra flavipes*-, *Polypedilum nubeculosum*-, *Polypedilum sordens*-, *Microtendipes pedellus*-, *Dicortendipen notatus*-, *Cricotopus intersectus*- and *Chironomus anthracinus*-type (Fig. 7B) (e.g., Langdon et al., 2006; Moller Pillot, 2009; Luoto and Salonen, 2010; Luoto, 2011; Potito et al., 2014). Periodic anoxia might have occurred, as indicated particularly by the high abundances of *Chironomus* in the samples, a taxon that is able to survive in hypoxic environments (Brooks et al., 2007; Moller Pillot, 2009; Luoto and Salonen, 2010). In addition, amongst the other macroinvertebrates, Trichoptera (caddisflies) and sometimes Rhabdocoela (turbelarian flatworms) remains dominated, whereas Ephemeroptera (mayflies) remains disappeared or were found only at lower abundances. This also agrees with increased organic matter loading and lower oxygen concentration compared to the non-cultural conditions. Alterations of aquatic invertebrate communities at OP, therefore, indicate periodic phases of significant human impact on the shallow water ecosystem of Lake Zürich.

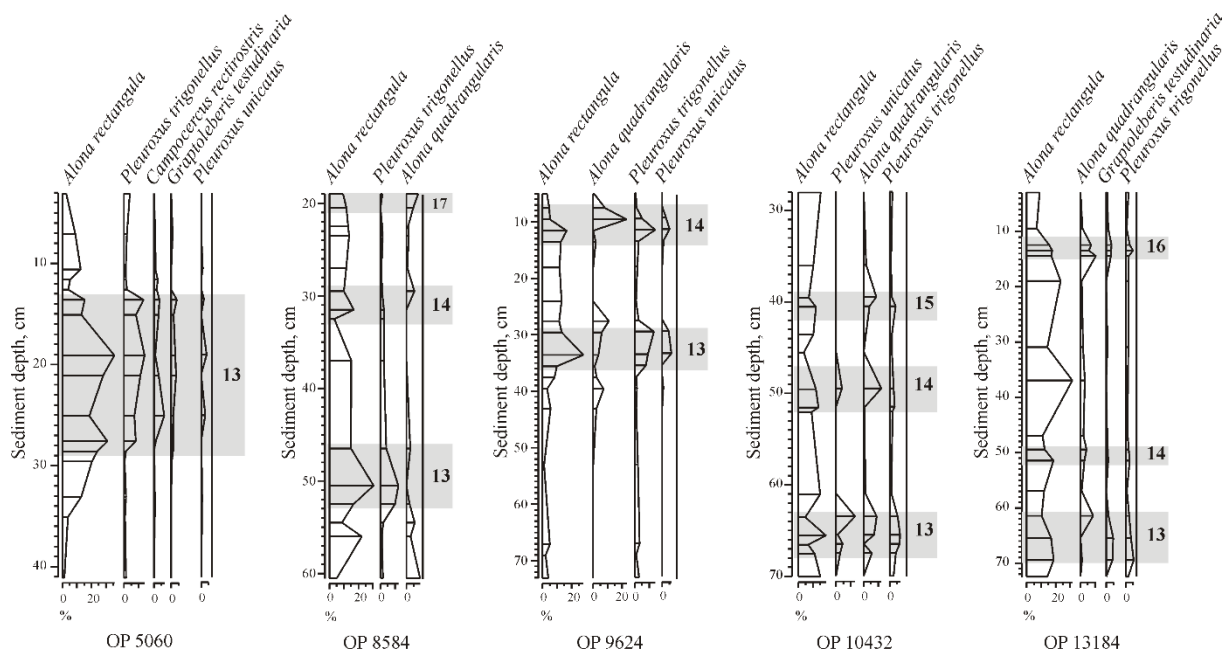


Figure 7A. Relative abundance of the most important cladoceran species associated with cultural or human-impacted sediment layers (13: 3176–3153 BC; 14: 3090 BC; 15: 3060 BC; 16: 2885–2877 BC; 17: 2754–2749 and 2734–2727 BC) in the individual sediment columns located in the settlement area of Zürich-Parkhaus Opéra (OP 5060, OP 8584, OP 9624, OP 10432, OP 13184).

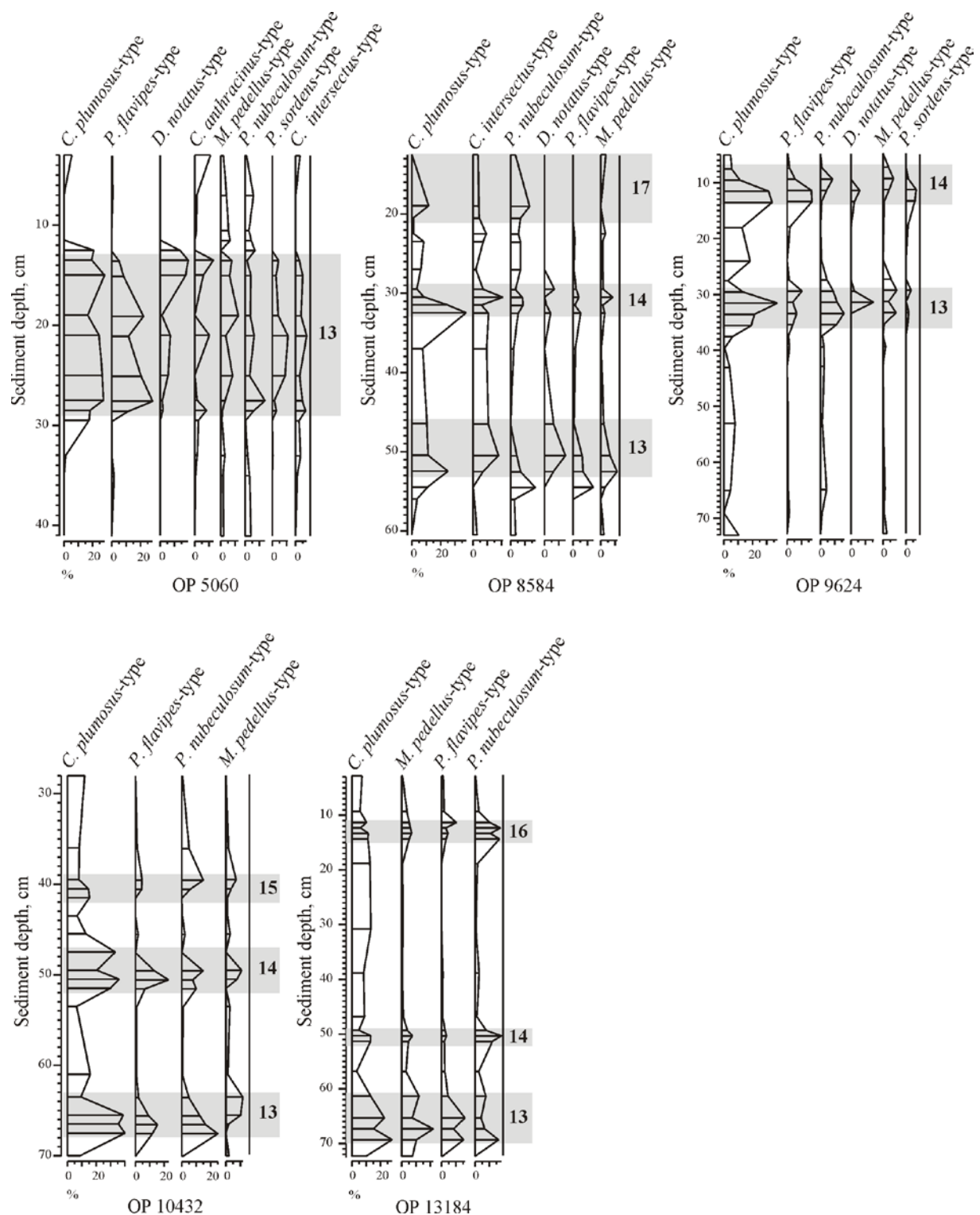


Figure 7B. Relative abundance of the most important chironomid morphotypes (*C. anthracinus*-type=*Chironomus anthracinus*-type; *C. plumosus*-type=*Chironomus plumosus*-type; *C. intersectus*-type=*Cricotopus intersectus*-type; *D. notatus*-type=*Dicrotendipes notatus*-type; *M. pedellus*-type=*Microtendipes pedellus*-type; *P. flavipes* -type=*Phaenopsectra flavipes*-type; *P. nubeculosum*-type=*Polypedilum nubeculosum*-type; *P. sordens*-

type=*Polypedilum sordens*-type) associated with cultural or human-impacted sediment layers (13: 3176–3153 BC; 14: 3090 BC; 15: 3060 BC; 16: 2885–2877 BC; 17: 2754–2749 and 2734–2727 BC) in the individual sediment columns located in the settlement area of Zürich-Parkhaus Opéra (OP 5060, OP 8584, OP 9624, OP 10432, OP 13184).

Available evidence (e.g. concentrations of bones, ash, plant remains and dung within the settlement layers) indicates a massive organic material load into the water during the cultural periods (see Bleicher et al., 2018). This is also confirmed by the high overall organic matter contents of the cultural layers relative to the under- and overlying sediments. The origin of the surplus organic matter during the settlement phases is probably the household waste, which was deposited directly into the lake from the houses within the settlement area. Such input will have substantially increased the biological oxygen demand of the sediment and increased the overall nutrient concentrations and productivity of the near-shore waters. Anoxic or at least hypoxic conditions during deposition of the cultural layers is supported also by excellent preservation of biological remains (e.g. leaf remains which were still green at excavation; Bleicher et al., 2018). Since chironomid assemblages in the sediment core taken outside the settlement area (i.e. from the lake core; OP 11) showed less pronounced changes, this implies that human impact and the influence of the elevated organic matter load were very local and mainly restricted to the vicinity of the settlement. In addition, the archaeological analyses noted that elevated accumulations of waste material or middens were located around the centres of buildings (see Bleicher et al., 2018), which indicates that secondary movement by water currents and erosion was very limited. Accordingly, organic matter stayed mostly where it was deposited. Therefore, nutrient input, the bulk of organic matter decomposition and the related oxygen depletion probably occurred locally within the settlement area.

A clear decrease in water quality during the deposition of the cultural layers is supported by the saprobic index (SI) scores calculated based on the chironomid data (Fig. 5). During these phases SI consistently moved to higher values and indicated poorer water quality than before. The changes in SI values are relatively minor in this study (from 1.7 to 2.9 units, with maximum values for the taxon *Chironomus*; Suppl. table 1). However, this is a consequence of applying this approach at the genus and species group level, which results in a smaller range of SI values for fossil chironomid taxa than possible for the individual chironomid species belonging to the chironomid morphotypes we identified (e.g. the species *Chironomus riparius* and *C. plumosus*, belonging to our fossil taxon *Chironomus*, could reach SI values of 3.5 and 3.6, respectively; see Moog, 2002).

Our data also clearly show that when humans abandoned the settlement, lake conditions recovered rapidly and aquatic invertebrate assemblages were very similar to the pre-impact state. Taylor et al. (2013, 2017) assessed the effects of Neolithic and Bronze Age farming activity on chironomid assemblages in Ireland and found that Neolithic farming increased notably the productivity of the studied lake but this effect was not persistent, and with the decrease of farming activity, the lake ecosystem rapidly reverted back to its pre-impact state (unlike the response to later Bronze Age farming). According to the results from some of our sediment columns from OP the ecological recovery process was likely rapid, based on the well-constrained chronology of the cultural layers and evidence from cladoceran and chironomid assemblages (see Suppl. figures 1–6). For example, the time between Layer 13 and 14 is estimated at ca. 60 years based on dendrochronology (Bleicher and Burger, 2015), represented by 5–15 cm of lake marl (1–2 mm lake marl per year). The recovery from high DCA scores and SI values in cultural layers to low values in non-cultural layers never took more than a third of the time in between cultural layers, suggesting recovery took at most 20 years. 2 mm of lake marl is enough to effectively seal off oxygen (Maerki et al., 2009). This would mean that after at most 5 years there was no or only very reduced organic degradation, and decomposition of

material from cultural layers was no longer decreasing available oxygen and thereby impacting aquatic invertebrate communities at the study site.

Kenward (1976) provided an early summary about the problems associated with utilizing “death assemblages” (in this case subfossils of Coleoptera or beetles) in archaeological studies in terms of the possible existence of transported elements in the locally reconstructed fauna. These transported elements represent the subfossil remains of insects that moved into the study site (during their life) from the nearby surroundings which may seriously affect and bias ecological reconstructions. However, by using chironomid larvae as biotic indicators this problem can be circumvented. Due to their flying adults and short generation time, these insects are good dispersers and can respond rapidly to environmental changes. On the other hand, the larvae of chironomids have very limited ability to move independently, and they usually remain within a few metre range until pupation. The role of local environmental processes in determining the distribution of chironomid larvae assemblages, due to their limited dispersal capacity and their strong taxa–environment relationships, has been described even at small spatial scales (within a lake; Árvai et al., 2015). In contrast, since cladocerans may be transported by water flow, their remains could provide a less strict assessment of local lake ecosystem conditions. This agrees with weaker responses of cladocerans to the above described environmental alterations compared with chironomids. The deposition of cladoceran remains, however, must have taken place in standing water, leaving little doubt that the settlement was built above the lake surface. Some chironomids, mainly belonging to the tribe Chironomini, are able to burrow to several cm below the sediment surface (Int Panis et al., 1996; Moller Pillot, 2009) in unconsolidated sediments and some of these taxa (e.g. *Chironomus*) occurred in large numbers in the sediment columns of OP, particularly in the cultural layers. At the same time, other chironomids, which are not able to burrow far into the sediment (e.g. *Cricotopus* or *Tanytarsus* taxa; see Moller Pillot, 2013; Epler et al., 2013), were present regularly in both cultural and non-cultural layers. Similarly, remains of cladocerans occurred continuously in the sediment columns. Of the

identified cladoceran taxa it is known that they usually crawl on the sediment but cannot burrow significantly below the sediment surface (e.g. Fryer, 1974). These results confirm that the invertebrate remains in the cultural sediment layers were not deposited during secondary colonization but represent the invertebrate fauna that existed at the sites when the cultural layers were formed.

4.2. Amplitude of biotic responses to human presence and activity at the settlement

In most parts of the excavated area, a sharp stratigraphic transition is visible from the lake marl deposits to the organic-rich anthropogenic cultural layers (Bleicher et al., 2018). This sharp transition is supported also by pollen types indicating local human activity (e.g. *Allium*, *Ranunculus*, *Cerealia*, *Papaver rhoeas* and *Plantago lanceolata*; see Gobet et al. 2017), which also clearly change in abundance at the boundaries of the cultural layers. Similarly, our results indicate that assemblages of cladocerans, chironomids and other macroinvertebrates altered rapidly and consistently between deposition of the non-cultural and cultural layers.

Comparing the individual cultural layers, Layers 13 and 14 showed very similar results regarding all investigated invertebrate assemblages. For the younger layers (Layers 15, 16 and 17) aquatic invertebrate assemblages exhibited weaker but also consistent biological responses. This could at least partly be due to differences in the deposition rate and degree of organic preservation of the individual cultural layers. Layers 13 and 14 are organically well preserved, possibly because of quick burial and oxygen depletion (Bleicher and Schubert, 2015), while in younger cultural layers the generally poorer preservation of the archaeological deposits indicate that biological oxygen demand probably did not reach a level supporting similarly good organic preservation (see Bleicher et al., 2018).

Moreover, the younger cultural layers do not appear in every sediment core, complicating their interpretation in our data set. Absence of certain cultural layers in certain parts of the area might be explained by the results of topographical analysis, which showed that the excavated area was

located on a slope to the lake (up to 10%; Schneider et al., 2015). It is possible, therefore, that younger layers (situated above Layer 13) were not preserved at particular parts of the excavated area located close to the land (i.e. at higher elevation) because of mechanical erosion and/or lack of flooding at that time (Schneider et al., 2015; Bleicher and Ruckstuhl, 2015; Bleicher et al., 2018).

Comparison of the response of invertebrate assemblages across different profiles is only possible for Layers 13 and 14, as these layers are present in multiple cores. Generally, chironomids showed higher amplitude assemblage changes from non-cultural to cultural layers than cladocerans (Fig. 5). At the same time, both cladoceran and chironomid assemblages showed differences in the amplitude of their response to human presence within various parts of the settlement area that likely confirm the role of local environmental conditions. In Layer 13, cladoceran assemblages showed very similar responses in all sediment columns, while in Layer 14 the strongest cladoceran assemblage change was noted in the most lakeward OP 13184 column, followed by the landward OP 9624 and by the intermediate positioned OP 10432 and OP 8584 columns (Fig. 5). In contrast, the amplitude of chironomid assemblage changes in Layer 13 tended to decrease from the most landward sediment column (OP 5060, followed by the landward OP 9624 and OP 8584) to the most lakeward columns (OP 13184 and OP 10432), and finally to the lake core (OP 11; Fig. 5). In Layer 14, chironomids showed the strongest assemblage change in the intermediately positioned OP 10432, followed by the landward OP 9624 and then by close-to-land positioned OP 8584 and the most lakeward OP 13184 (Fig. 4). Accordingly, we could assume, based on chironomids, that Neolithic human activity affected mainly the close vicinity of the settlement with a generally decreasing impact from the most landward to the most lakeward sites; and that this influence rapidly weakened beyond the settlement area (i.e. at location of the lake core). At the same time, cladocerans showed a less consequent picture that could likely correspond with their mobility (i.e. they can temporarily move away from sites that are not favourable) while chironomid larvae have only limited

718 dispersal capacity. Therefore, the less mobile chironomids had higher susceptibility to local
719 hypoxia in and just above the sediment than the more mobile cladocerans. Another possible
720 explanation for weaker cladoceran assemblage responses could be that cladocerans probably
721 have a wider tolerance range against nutrient level changes than chironomids (e.g. Lotter et al.,
722 1998).

723 It would be logical to assume that sediment columns located at the most frequently populated
724 (and likely most impacted) areas would record the strongest assemblage responses in the
725 cultural layers, since these areas would receive the highest amount organic material causing
726 increased nutrient concentration and biological productivity, and would have the highest
727 increased oxygen demand in the sediment. However, there is no evidence for substantial
728 differences in density and duration of the human presence within the excavated settlement area
729 (Bleicher et al., 2018). At the same time, clear differences are visible when comparing the
730 thickness of the individual cultural layers. Layer 13, for instance, is around 16 cm thick in OP
731 5060 (with the strongest assemblage response), while only 5 cm thick in OP 10432 (with some
732 of the weakest assemblage response based on chironomids). Results indicate that the organic
733 deposits in the cultural layer consist to a considerable extent of refuse such as animal bones,
734 dung, plant remains and ashes deposited in the sediments (Bleicher et al., 2018). Differential
735 deposition of such refuse across the study site may therefore explain the stronger response of
736 chironomids in some sediment profiles (e.g. OP 5060) compared with others. This indicates
737 that possibly layer thickness and probably related sedimentation and preservation rate may have
738 affected the observed spatial pattern of invertebrate assemblages to some extent.

739 Nevertheless, cladoceran and chironomid assemblages showed clear and consequent responses
740 both in their taxonomic composition and relative abundances of the dominant taxa (e.g. results
741 of ANOSIM and DCA analyses) to the periodic human presence within the excavated area
742 during the Neolithic. Our results and previous studies confirm that Neolithic human impacts on
743 aquatic ecosystems may have been locally substantial and caused major changes in species

assemblages of aquatic organism groups (e.g. Taylor et al., 2013, 2017). These results therefore are in contrast with views that major human ecosystem impacts in Central Europe predominantly occurred during the Bronze or Iron Ages or even later in the Medieval or Industrial periods (e.g. Dotterweich, 2008).

5. Conclusions

As part of an interdisciplinary project we investigated subfossil Cladocera and Chironomidae remains from the excavation area of Neolithic lakeside settlements (Zürich-Parkhaus Opéra; OP) discovered at the shore of Lake Zürich (Switzerland). Our aims were to assess the surrounding environmental conditions at the ancient settlements and to assess periodic anthropogenic environmental alterations by utilizing the indicator value of aquatic invertebrates.

Concluding, our results show that the Neolithic settlements in the OP excavation area were established on the lake and sedimentation happened mainly under water. Moreover, human activity in settlements at OP resulted in severe degradation of water quality within the settlement area. This confirms that Neolithic human impacts on aquatic ecosystems, though generally considered to have been moderate, may have been locally substantial and caused major changes in species assemblages of aquatic organism groups. These results therefore show that major human ecosystem impacts on aquatic ecosystems in Central Europe might have started earlier than the Bronze or Iron Ages, as has also been shown for terrestrial ecosystems (e.g. Rey et al., 2017). At the same time, we are able to show that the effects of human activity were very local, implying that in the case of Lake Zürich this impact did not lead to system level responses of the lake ecosystem. This also explains why conditions rapidly reverted to pre-impact state after the ending of the settlement activities. Nevertheless, our analyses, together with previous studies on lake ecosystem response to Neolithic activities (e.g. Taylor et al., 2013; Rey et al., 2017) imply that a long-term perspective is essential when reconstructing

the history of anthropogenic influence on aquatic ecosystems, e.g. in the context of defining pre-impact reference states for modern ecosystem assessments. Clearly human alteration of lakeside environments and ecosystem components at OP started the latest at *ca* 3234 cal BC. During this early phase, human impact on lakeside environments at Lake Zürich appears to have been characterized by repeated phases of locally strong, human-induced alterations of biotic communities and environmental conditions followed by phases of recovery. Such sequences of impact phases followed by recovery have also been reported based on palynological analyses from sediment records from small lakes in Northern Switzerland that were characterized by distinct phases of local Neolithic human impact (e.g. Akeret et al., 1999; Rey et al., 2017), also believed to have been associated with the establishment of activities in Neolithic lakeside settlements.

Finally, our study emphasises the potential of analyses of cladocerans, chironomids and other aquatic insect remains for archaeological studies of waterlogged archaeological deposits. Our analyses provide particularly evidence for shallow water habitats expanding over most of the Neolithic settlements and clear indications on the environment within the ancient settlement at OP. Future analyses of aquatic invertebrate remains (e.g. cladocerans and chironomids) in similar lakeside deposits, therefore have the potential to supplement existing commonly applied palaeoecological approaches and to provide detailed assessments of lake level changes and variations in subaquatic environments within past lake-side settlements as well as for the periods between settlement phases.

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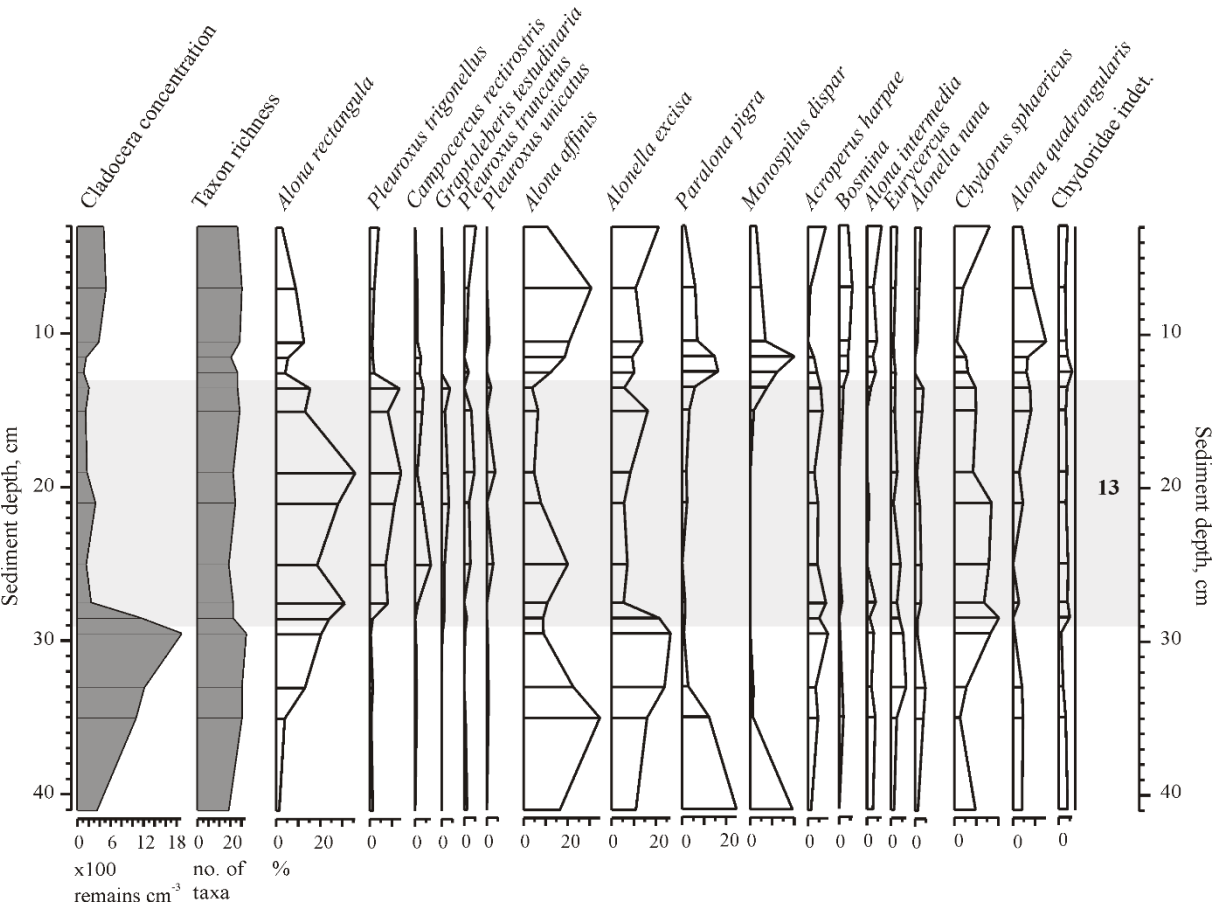
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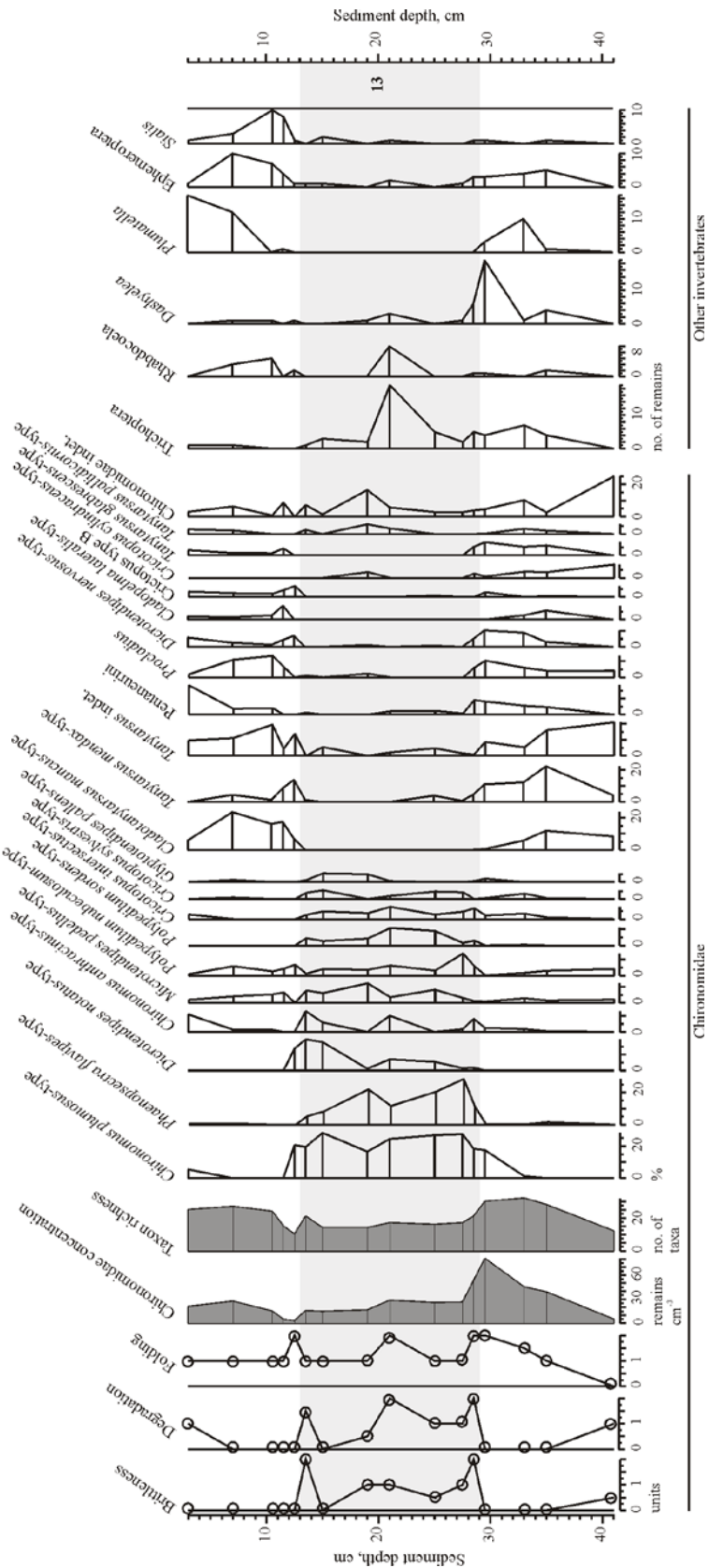
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Supplementary figures

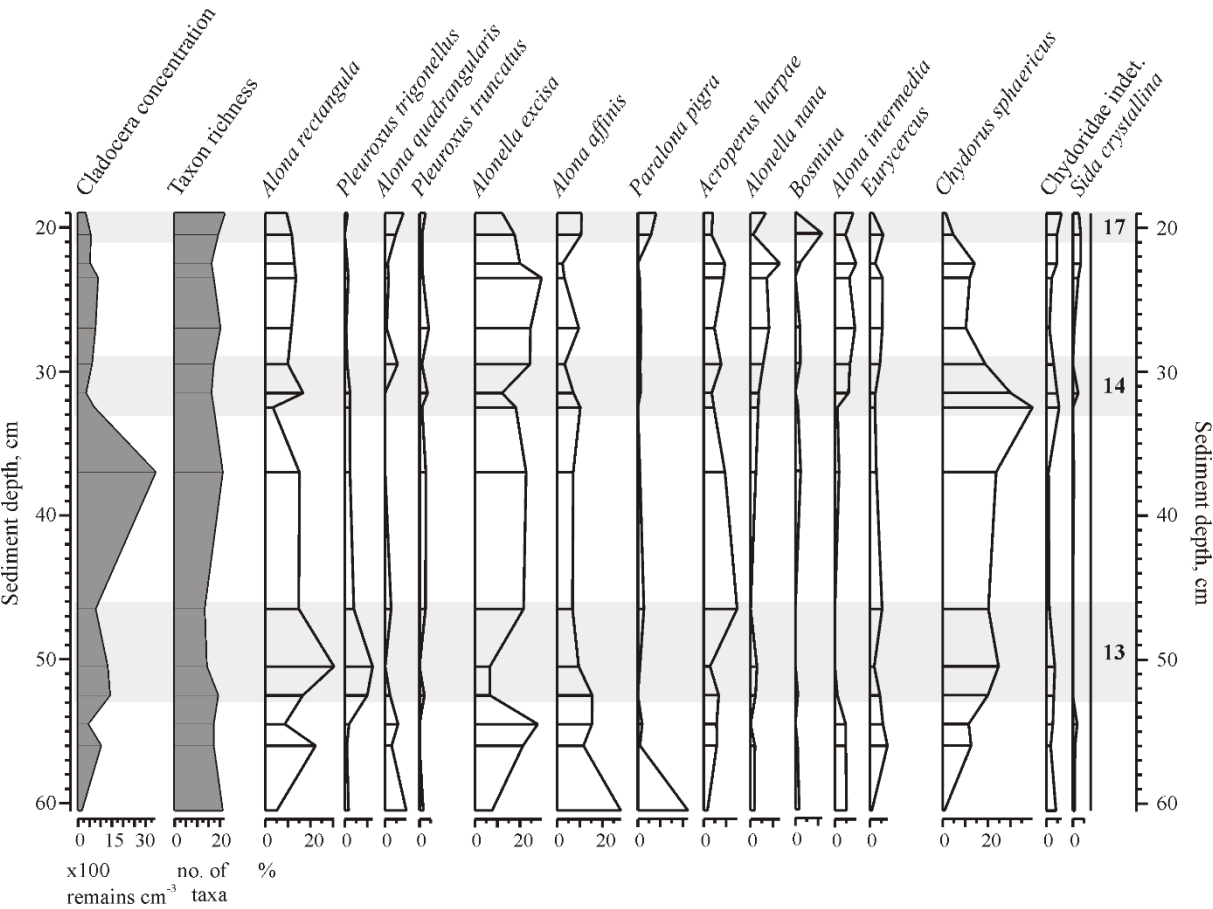
Raw data for the aquatic invertebrate data from the Zurich Opéra project are available in the published project report (Heiri et al., 2017, in German). Here we provide summary diagrams for chironomid and cladoceran analyses of the different sediment columns and cores.



Supplementary figure 1A. Changes in the concentration, taxon richness and relative abundance of selected Cladocera species (>1% relative abundance) in the OP 5060 sediment column. The grey band indicates cultural Layer 13 (3176–3153 cal BC).



Supplementary figure 1B. Changes in the preservation (brittleness, degradation and folding), concentration, taxon richness and relative abundance of selected Chironomidae (>1% relative abundance) and other invertebrate taxa in the OP 5060 sediment column. The grey band indicates cultural Layer 13 (3176–3153 cal BC).



Supplementary figure 2A. Changes in the concentration, taxon richness and relative abundance of the selected Cladocera species (>1% relative abundance) in the OP 8584 sediment column. Grey bands indicate cultural Layer 13 (3176–3153 cal BC), 14 (~3090 cal BC) and 17 (2754–2749 and 2734–2727 cal BC).

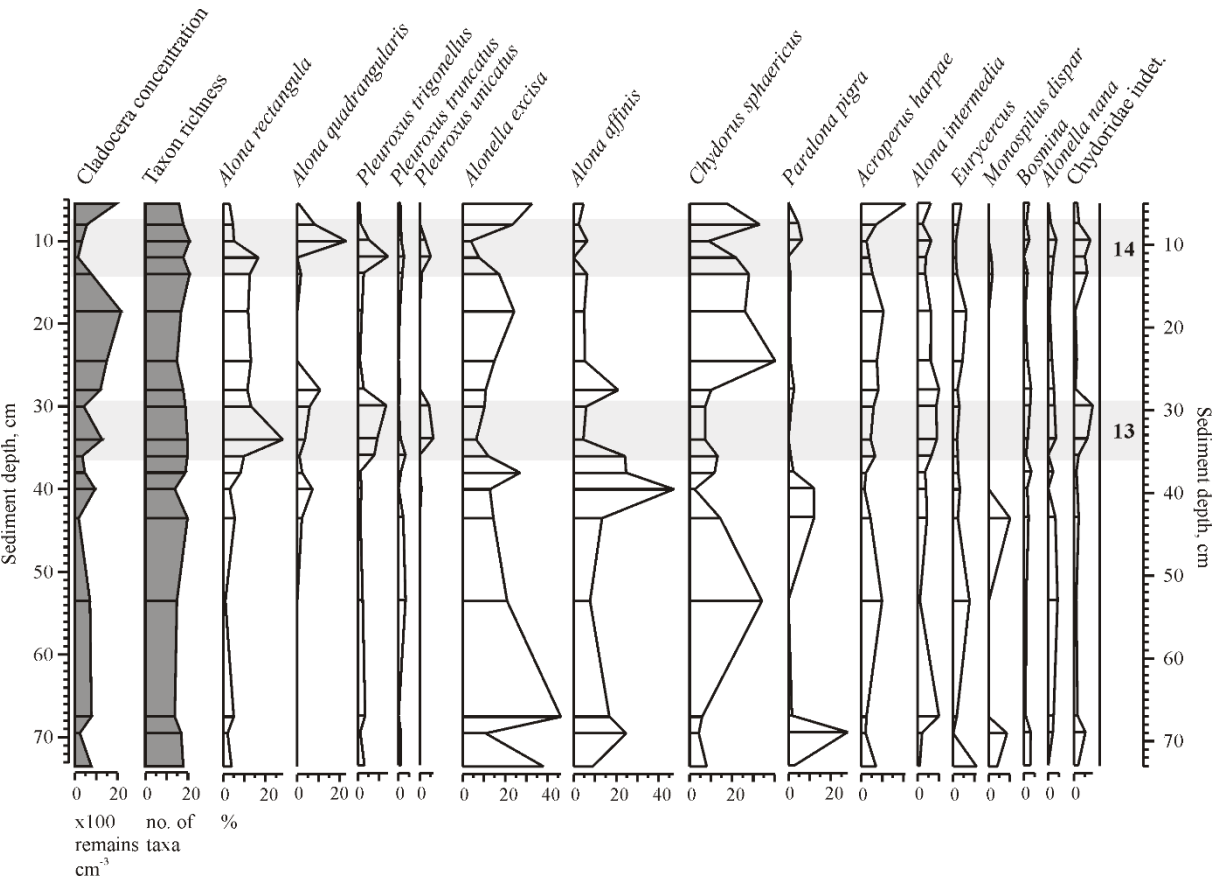
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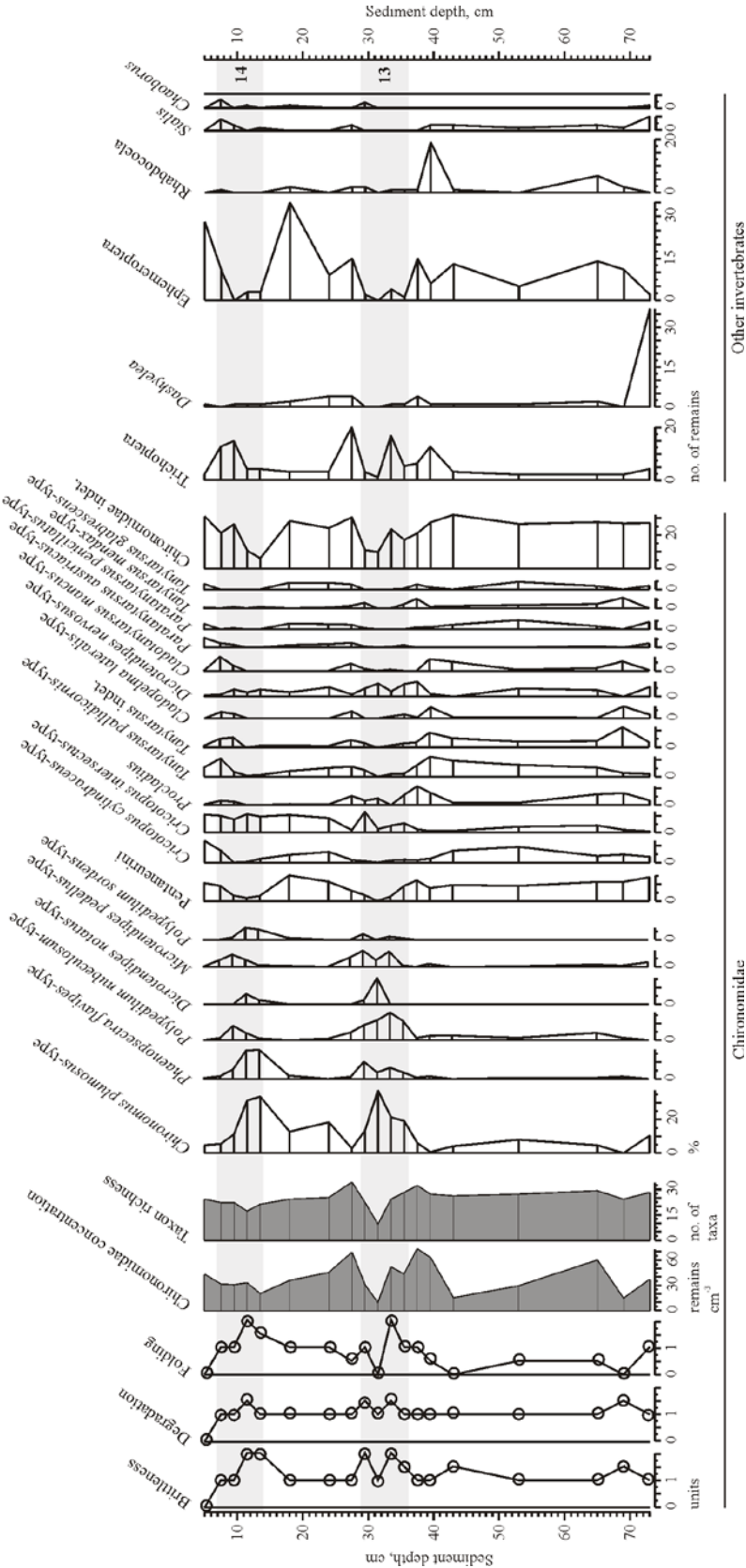
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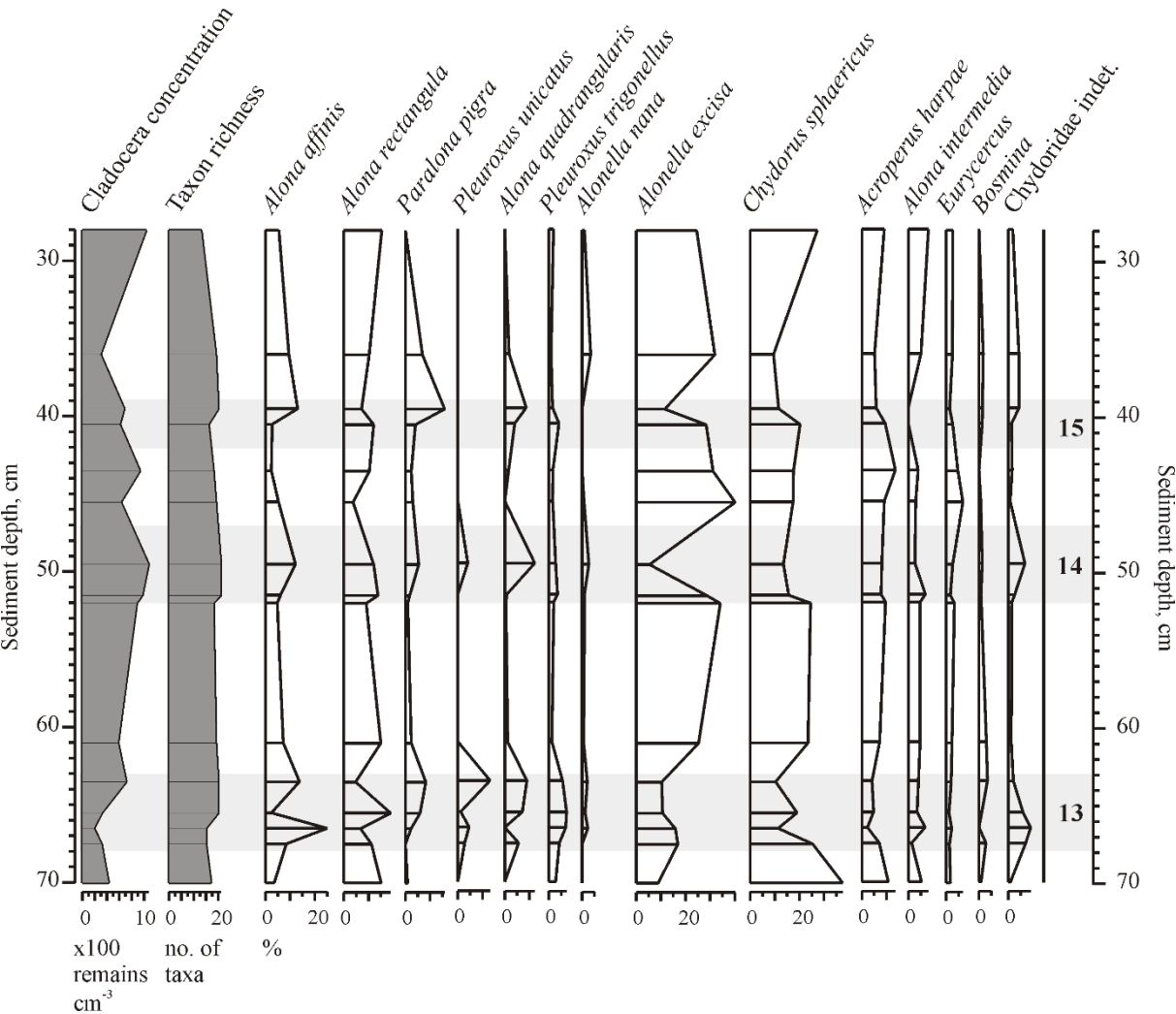




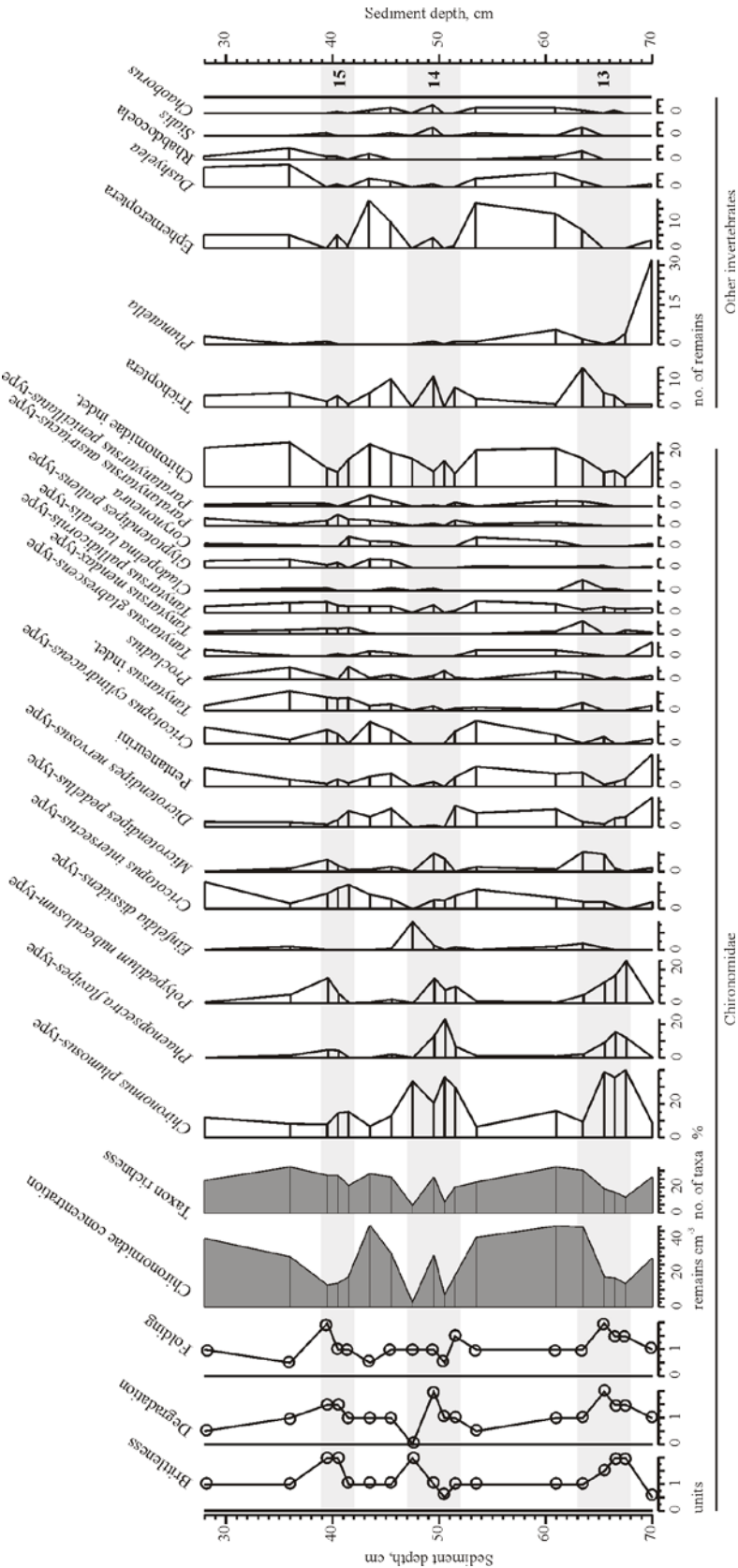
Supplementary figure 3A. Changes in the concentration, taxon richness and relative abundance of selected Cladocera species (>1% relative abundance) in the OP 9624 sediment column. Grey bands indicate cultural Layer 13 (3176–3153 cal BC) and 14 (~3090 cal BC).



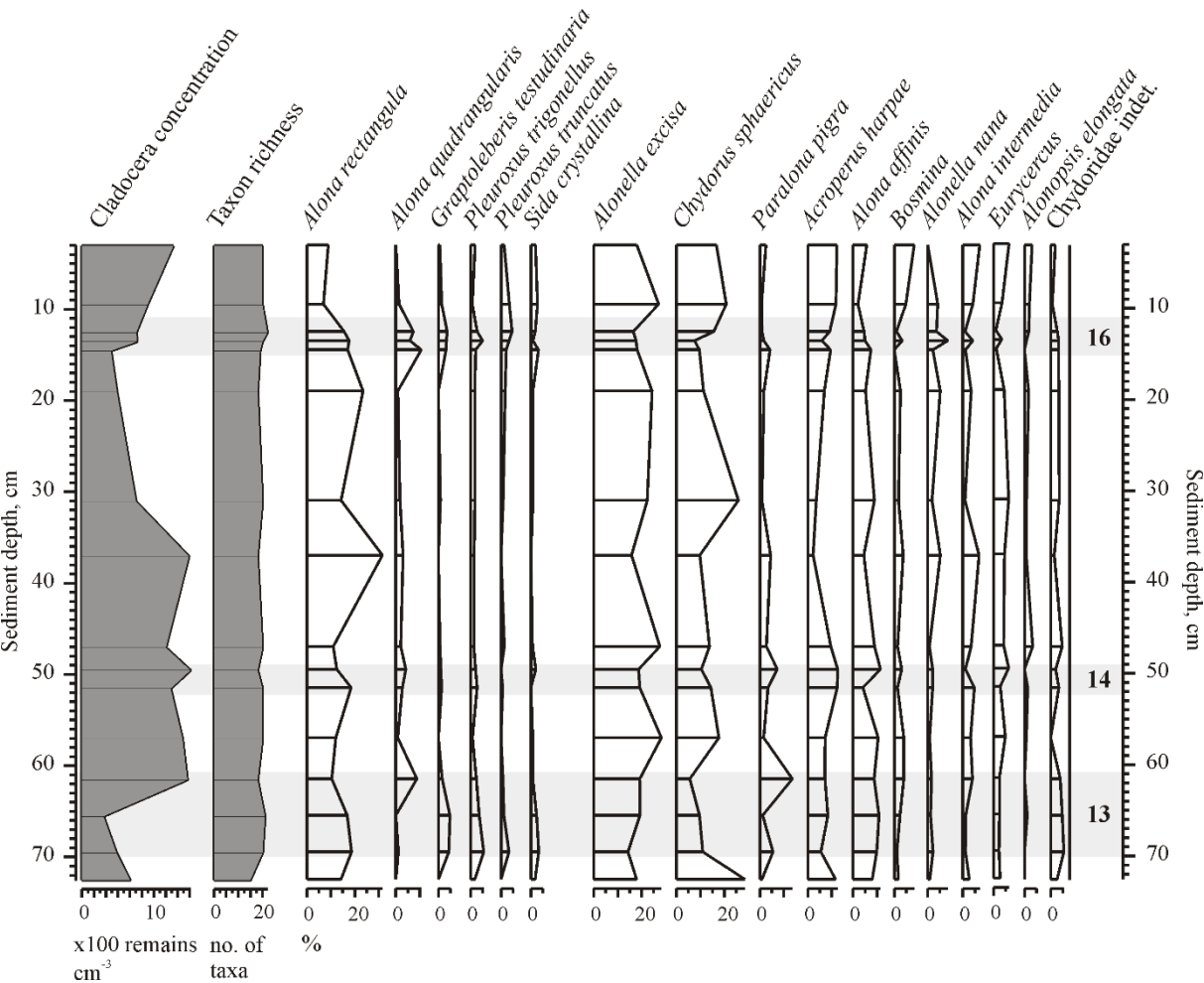
Supplementary figure 3B. Changes in the preservation (brittleness, degradation and folding), concentration, taxon richness and relative abundance of selected Chironomidae (>1% relative abundance) and other invertebrate taxa in the OP 9624 sediment column. Grey bands indicate cultural Layer 13 (3176–3153 cal BC) and 14 (~3090 cal BC).

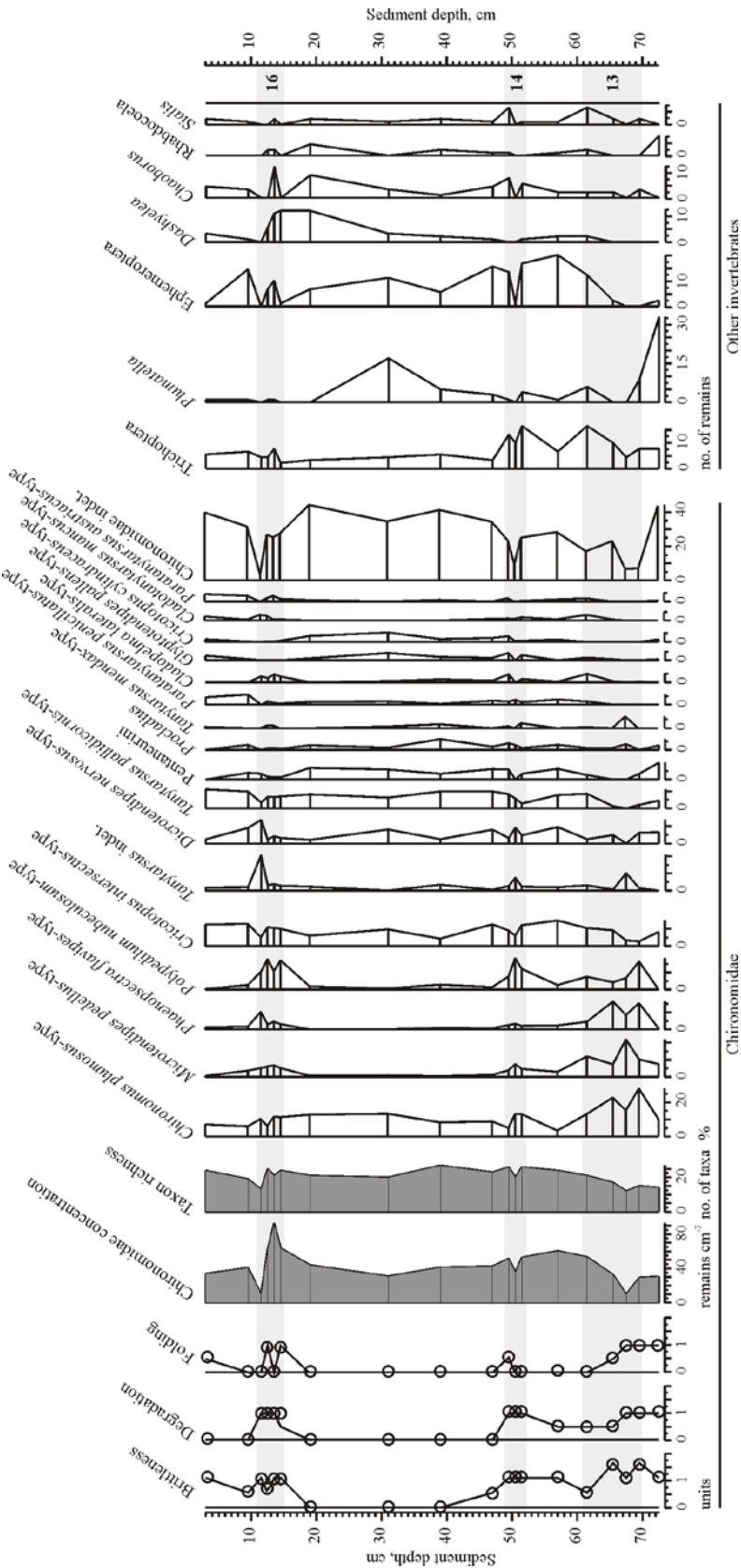


Supplementary figure 4A. Changes in the concentration, taxon richness and relative abundance of selected (>1% relative abundance) Cladocera species (>1% relative abundance) in the OP 10432 sediment column. Grey bands indicate cultural Layer 13 (3176–3153 cal BC), 14 (~3090 cal BC) and 15 (~3063 cal BC).

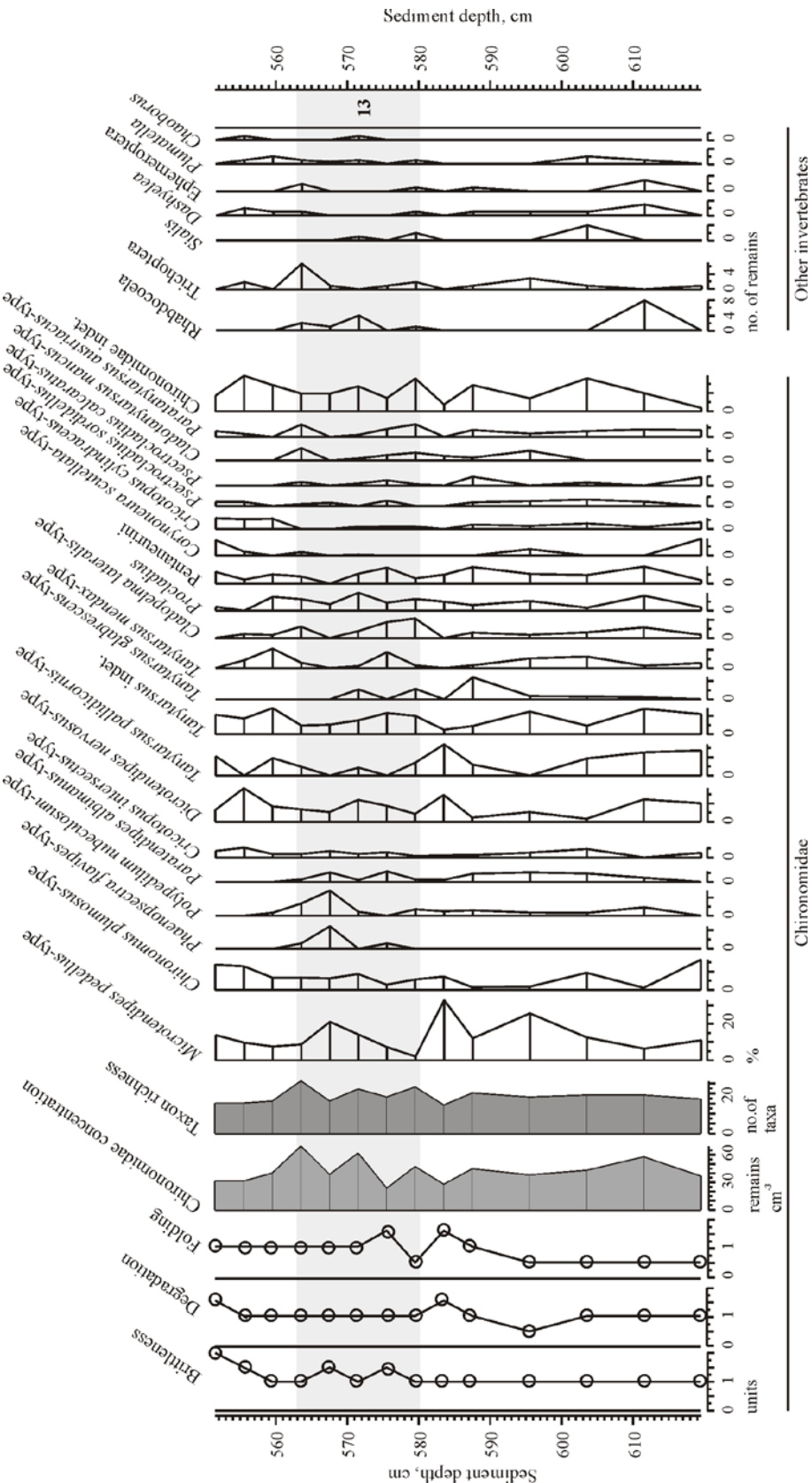


Supplementary figure 4B. Changes in the preservation (brittleness, degradation and folding), concentration, taxon richness and relative abundance of selected Chironomidae (>1% relative abundance) and other invertebrate taxa in the OP 10432 sediment column. Grey bands indicate cultural Layer 13 (3176–3153 cal BC), 14 (~3090 cal BC) and 15 (~3063 cal BC).





Supplementary figure 5B. Changes in the preservation (brittleness, degradation and folding), concentration, taxon richness and relative abundance of selected Chironomidae (>1% relative abundance) and other invertebrate taxa in the OP 10432 sediment column. Grey bands indicate cultural Layer 13 (3176–3153 cal BC), 14 (~3090 cal BC) and 16 (2885–2882 cal BC).



Supplementary figure 6. Changes in the preservation (brittleness, degradation and folding), concentration, taxon richness and relative abundance of selected Chironomidae (>1% relative abundance) and other invertebrate taxa in the OP 11 sediment core. Grey band indicates cultural Layer 13 (3176–3153 cal BC).

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1115 Supplementary table

1116 Supplementary table 1. Mean saprobic values of the subfossil chironomid genera following
 1117 Moog (2002). x = Xenosaprobic, o = Oligosaprobic, β = Beta-mesosaprobic, α = Alpha-
 1118 mesosaprobic, p = Polysaprobic, G = indicator value, SI = Saprobic Index.

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	x	o	β	α	p	G	SI
<i>Chironomus</i>	0	0.75	2.25	3.63	3.38	1.63	2.96
<i>Cladopelma</i>	0	2	4	4	0	2	2.2
<i>Cryptochironomus</i>	0	1	4	4	1	1	2.5
<i>Demicryptochironomus</i>	0	1	4	5	0	2	2.3
<i>Dicrotendipes</i>	0	0.67	4.67	4	0.67	1.67	2.47
<i>Einfeldia</i>	0	0	3	5	2	2	2.9
<i>Endochironomus</i>	0	1	4	4	1	1	2.5
<i>Glyptotendipes</i>	0	0.5	4.25	4.25	1	1.5	2.58
<i>Microtendipes</i>	0	2	4.67	3.33	0	2	2.13
<i>Parachironomus</i>	0	1	4	4	1	1	2.5
<i>Phaenopsectra</i>	0	1	4	4	1	1	2.5
<i>Paratendipes</i>	0	1	5	4	0	2	2.3
<i>Polypedilum</i>	0	1.57	4.86	3.14	0.43	2.14	2.24
<i>Sergentia</i>	0	3	6	1	0	3	1.8
<i>Corynoneura</i>	0	4	5	1	0	2	1.7
<i>Cricotopus</i>	0.22	1	4.78	3.78	0.22	2.11	2.28
<i>Heterotrissocladius</i>	1	5	4	0	0	3	2.3
<i>Orthocladius</i>	2	2	3	2	1	1	1.8
<i>Paracladius</i>	0	1	6	3	0	3	2.2
<i>Parakiefferiella</i>	0	2	6	2	0	3	2
<i>Psectrocladius</i>	0	3	6	1	0	3	1.8
<i>Procladius</i>	0	0	5	5	0	3	2.5
Pentaneurini	0	1.33	5.33	3.33	0	2.33	2.2
<i>Cladotanytarsus</i>	0	1	7.5	1.5	0	3.5	2.05
<i>Paratanytarsus</i>	0.33	3.67	4	2	0	2.33	1.77
<i>Stempellina</i>	4	5	1	0	0	2	1.7
<i>Tanytarsus</i>	0.25	2.25	5.5	2	0	2.25	1.93

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