

9000 years of chironomid assemblage dynamics in an Alpine lake: long-term trends, sensitivity to disturbance, and resilience of the fauna

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Abstract

Subfossil chironomid analysis was applied to a sediment core from Sägistalsee, a small lake at present-day tree-line elevation in the Swiss Alps. During the whole 9000-year stratigraphy the chironomid fauna was dominated by taxa typical of alpine lakes. Major faunistic trends were caused by changes in accumulation rates of three taxa, namely *Procladius*, *Stictochironomus*, and *Tanytarsus lugens*-type. In the early Holocene *Procladius* was the dominant taxon. In younger samples, *Stictochironomus* tended to have as high or higher abundances and both taxa showed an increase in accumulation rates. A possible cause of this succession is the decrease of lake-water depth due to infilling of the lake basin and changes in associated limnological parameters. The immigration of *Picea* (spruce) at ca. 6500 cal. ¹⁴C yrs BP and the resulting denser woodlands in the lake's catchment may have promoted this trend. During three phases, from ca. 70–1450, 1900–2350, and 3500–3950 cal. BP, remains of *Procladius*, *Stictochironomus*, and *Tanytarsus lugens*-type are absent from the lake sediment, whereas other typical lake taxa and stream chironomids show no change in accumulation rate. Together with sediment chemistry data, this suggests that increased oxygen deficits in the lake's bottom water during these intervals caused the elimination of chironomids living in the deepest part of the lake. All three periods coincide with increased human activity in the catchment, as deduced from palaeobotanical evidence. Therefore, enhanced nutrient loading of the lake due to the presence of humans and their livestock in the catchment is the most likely cause of the increased anoxia. The chironomid fauna reacted the same way to intensive pasturing during the last ca. 1500 years as to Bronze Age clear-cutting and more moderate pasturing during the Bronze, Iron, and Roman Ages, suggesting that alpine lake ecosystems can be extremely sensitive to human activity in the catchment. On the other hand, the chironomid assemblages show a considerable amount of resilience to human disturbance, as the chironomid fauna reverted to the pre-impact stage after the first two periods of human activity. In recent years, even though pasturing decreased again, the chironomid fauna has only partly recovered. This is possibly due to other human-induced changes in the lake ecosystem, e.g., the stocking of the lake with fish. The chironomid stratigraphy is difficult to interpret climatologically as the strongest changes in chironomid-inferred temperatures coincide with periods of intensive human activity in the catchment.

This is the third in a series of eight papers published in this issue dedicated to the palaeolimnology of Sägistalsee. Drs. André F. Lotter and H. John B. Birks were the guest editors of this issue.

Introduction

Larvae of Chironomidae (Insecta: Diptera) form one of the dominant and most diverse components in the macrozoobenthos of lakes. The survival of chironomid larvae depends on a number of different environmental parameters, including water temperature, habitat and food availability, and the chemical characteristics of the lake water, such as oxygen content or pH (Oliver, 1971; Pinder, 1986). Therefore, chironomids have been widely used in biomonitoring, e.g., to classify lakes in relation to trophic state (Sæther, 1979; Wiederholm, 1984) or to assess the impact of acidification on lake benthos (Raddum and Sæther, 1981; Buskens, 1987). Furthermore, remains of chironomid larvae are common in lake sediments and can generally be identified to genus or, more rarely, to species-group level. This offers the possibility of using the fossil chironomid record to infer past environmental conditions in lakes. Subfossil chironomid analysis has been used to address questions such as the natural, undisturbed development of lakes (Walker, 1987), the effects of human-induced eutrophication or acidification on lake benthos (e.g., Brodin, 1982; Henrikson et al., 1982; Kansanen, 1985; Brodin, 1990), and, more recently, the reconstruction of past climate (e.g., Walker et al., 1991a; Levesque et al., 1993).

Many of these studies have focused on lowland lakes. In contrast few studies on alpine lakes are available (Walker, 1995). A few authors have addressed the effects of acid precipitation on the chironomid fauna of European alpine and mountain lakes (e.g., Wathne et al., 1995; Guilizzoni et al., 1996), although all of them concentrate on changes during the past few decades or centuries only. To our knowledge only two chironomid stratigraphies covering a large part of the Holocene from lakes in alpine or subalpine settings are available (Smith et al., 1998; Pellatt et al., 2000). Alpine ecosystems in general and alpine lakes in particular are regarded as being exceptionally susceptible to the adverse effects of human activities (Chapin and Körner, 1995; Grabherr et al., 1995; Skjelkvale and Wright, 1998; Gross, 1999). Though alpine lakes are often considered to be a pristine habitat, they have, at least in Europe, been subject to strong human influence in the past few millennia and increasingly so in recent centuries. The presence of Mesolithic hunters in alpine localities in Central Europe as early as 8200 cal. BP has been reported (Fedele and Wick, 1996). First vegetation changes possibly associated with human activity have been inferred from a number of sites from as far back as ca. 5400–

6800 cal. BP (Tinner et al., 1996; Wick and Tinner, 1997). A strong and continuing increase in deposition of airborne pollutants has been recorded from Alpine lake sediments and glaciers (Lami et al., 1994; Döscher et al., 1995). Other recent human influences on Alpine lake ecosystems include increasing winter and summer tourism, damming of lakes for hydroelectric power generation, and the stocking of lakes with fish (Grimås and Nilsson, 1962; Bretschko, 1995; Guthruf et al., 1999). In contrast to the effects of acid precipitation on Alpine lakes for example (e.g., Psenner and Schmidt, 1992; Wathne et al., 1995), little is known about how these systems react to human activity in the lake catchment, and if human-induced changes in alpine lakes are reversible.

In the following we describe the chironomid stratigraphy of Sägistalsee, a lake in the Bernese Alps, Switzerland, with particular focus on the long-term dynamics of the chironomid fauna. The sediment core is well dated and includes approximately the last 9000 calibrated ^{14}C years as a continuous sequence (Lotter and Birks, 2003). Analyses of proxies for terrestrial vegetation (Wick et al., 2003) reveal a series of possibly climate-associated vegetation changes and three distinct periods of human activity in the lake's catchment. As chironomids are considered to be good climate indicators (Walker et al., 1991b; Lotter et al., 1997), this therefore offers the possibility of comparing the chironomid stratigraphy with vegetational changes in the catchment and with known or proposed periods of climatic change in the Swiss Alps (e.g., Wick and Tinner, 1997; Haas et al., 1998). Furthermore, chironomids can be used to infer past temperatures directly (Walker et al., 1991b; Lotter et al., 1997) and we present a chironomid-based July air temperature reconstruction from Sägistalsee. Finally, the repeated phases of human activity allow the study of the response and recovery of the lake ecosystem to human disturbance in relation to the natural long-term dynamics of the fauna.

Study site

Sägistalsee is a small alpine lake situated 8 km east of Interlaken at the present day tree-line in the calcareous bedrock of the Northern Swiss Alps (see Lotter and Birks, 2003 for more details). It lies at 1935 m asl in a small valley running roughly south-west to north-east, with major tributaries entering the lake from both the western and eastern side. Water leaves the lake through

a number of sink holes on the northern shore and runs underground to empty partly into Giessbach, a minor tributary of the Lake of Brienz, and partly into the river Lütschine (Spengler, 1973; Guthruf et al., 1999). The maximum lake depth measured on July 7, 1993 was 9.7 m, but, as the amount of water leaving the lake is limited by the size of the sink holes, yearly water-level fluctuations of up to 1.3 m have been observed (Spengler, 1973). The present-day vegetation in the lake's catchment consists mainly of alpine meadows with a few scattered spruce (*Picea abies*) growing on the slope above the northwestern shoreline. In summer the pastures around the lake are used for cattle grazing (Spengler, 1973).

The lake's present-day phosphorus loading suggests mesotrophic conditions, though only very low values of dissolved organic carbon have been measured (Lotter et al., 1998; Müller et al., 1998). Available water-temperature profiles suggest that the lake reaches a stable stratification in summer (surface temperatures 11.5–13 °C, bottom temperatures 4.4–6.0 °C; unpublished data and Spengler, 1973).

Methods

In 1996 two parallel cores were taken from the deepest part of the lake using a Livingstone piston corer (Lotter and Birks, 2003). The cores were correlated using lithological features to produce a continuous sediment record of 13.5 m length. Radiocarbon dating and pollen analysis indicate that continuous sedimentation took place for approximately 9000 calibrated ¹⁴C years (see Lotter and Birks, 2003). The sedimentation rate was high during the first 1500 years of the sequence (maximum 0.33 cm/yr) but remained near 0.11 cm/yr for much of the Holocene to increase again slightly during the last 1500 years (maximum 0.18 cm/yr; Lotter and Birks, 2003).

Two centimetre slices of sediment were prepared for chironomid analysis (between 20 and 60 cm³). Sampling intervals were chosen to give a time resolution of approximately one sample every 100 yrs using the age-depth model described by Lotter and Birks (2003) (average sample interval = 71 years, maximum sample interval = 130 yrs). After measuring the sample volume by water displacement the sediment was deflocculated for 2 h at room temperature in a 5% KOH solution and subsequently washed through a 100 µm sieve. Due to

the minerogenic nature of the sediment and very low head-capsule concentrations, chemical treatment of the residue with HF was necessary to remove inorganic detritus (Walker and Mathewes, 1989a). After 15 min of exposure in 10% HCl to dissolve carbonates, the samples were immersed in 40% HF for twelve hours. Following rinsing with distilled water the residue was again treated with 10% HCl to eliminate any traces of fluoride and rinsed again.

As head-capsule concentrations showed large fluctuations, it was sometimes necessary to use a modified two-chamber subsampler (Meyer, 1990) to reduce sample size before sorting the material. Head-capsules were picked with fine forceps using a stereomicroscope (35× magnification) and mounted in Euparal® mounting medium after dehydration. Identification was accomplished at 100 and 400× magnification with a compound microscope. Head-capsule accumulation rates were calculated following Walker and Mathewes (1989b). Some of the samples yielded less than the 45 head-capsules recommended for subfossil chironomid analysis (Hofmann, 1986; Heiri and Lotter, 2001) even when the whole sediment slice was analysed. In order to reach a more reliable count, adjacent samples were pooled to produce a minimum head-capsule count of 50 specimens per sample for zonation, ordination, and temperature reconstruction. Zonation of the stratigraphy was accomplished by optimal sum-of-squares zonation (Birks and Gordon, 1985) and the number of statistically significant zones was estimated using the broken stick model proposed by Bennett (1996). Due to the large amount of noise in the data, a log (x+1) transformation was applied to head-capsule accumulation rates before zonation. Detrended Correspondence Analysis (DCA) applied to the square-root transformed percentages revealed a gradient length of 1.6 standard deviation units in the chironomid dataset, therefore warranting the use of linear ordination methods (ter Braak and Prentice, 1988). Principal components analysis (PCA; following ter Braak, 1987; Legendre and Legendre, 1998) calculated on a covariance matrix was used to summarise major faunistic trends in the square-root transformed percentage data. All ordinations were carried out using the program CANOCO version 4.0 (ter Braak and Smilauer, 1998). Quantitative temperature reconstruction was performed using the program CALIBRATE (S. Juggins and C.J.F. ter Braak, unpublished software), based on a chironomid-July air temperature model described in more detail in Heiri (2001).

Results

Taxonomy

Of the 27 taxa identified, *Chaetocladius*, *Diamesa*, *Helieniella*, *Limnophyes*, *Paracladius*, *Parakiefferiella*, *Paratanytarsus*, *Protanypus*, *Pseudosmittia*, *Rheocricotopus*, and *Stictochironomus* were assigned to genera using mentum characteristics (mentum and ventromental plate shape, number of mentum teeth, position of setae submenti) and generally showed good agreement with descriptions in Hofmann (1971a), Wiederholm (1983), and Schmid (1993). Where available the premandibles and the pecten epipharyngis were used to confirm the diagnosis of *Paratanytarsus* (Wiederholm, 1983). *Procladius* and *Zavreliomyia* were identified using the descriptions in Wiederholm (1983) and Rieradevall and Brooks (2001). A number of taxa possibly include two or more genera due to poor preservation of the material or to inadequate generic diagnoses for subfossil head-capsules (i.e., *Eukiefferiella/Tvetenia*, *Parametriocnemus/Paraphaenocladius*, *Smittia/Parasmittia* and *Cricotopus/Orthocladius/Paratrithocladius*). Similarly, *Metriocnemus*-type head capsules include all Orthoclaadiinae with a bifid, short median tooth on the mentum. Infrageneric identification was possible for a number of taxa. Identification of *Brillia modesta* follows Cranston (1982) and *Chironomus anthracinus*-type the mentum description in Hofmann (1971a). Head capsules of *Corynoneura scutellata*-type were separated from other *Corynoneura* by the combination of a mentum with all lateral teeth subequal (Cranston, 1982) and the distinct patterning on the head-capsule surface as described in Hirvenoja and Hirvenoja (1988; note that *Corynoneura arctica* has the same characteristics). *Psectrocladius* (*s.str.*) includes all *Psectrocladius* head-capsules with the mentum not of an *Allopsectrocladius*-, *Mesopsectrocladius*-, or *Monopsectrocladius*-type as described in Wiederholm (1983). Remains of *Micropsectra* were split into two categories. Fourth instars of *Micropsectra radialis*-type are characterised by short, squarish antennal pedestals with a short sharp spur and a roundish ventral post-occipital margin with the postoccipital plate strongly reduced. Other *Micropsectra* found had longer antennal pedestals, a more incised ventral postoccipital margin, and a distinct postoccipital plate in the fourth instar (henceforth abbreviated as *Micropsectra* spp.). *Tanytarsus lugens*-type includes *Tanytarsus* head-capsules with mandibles with three inner teeth, two outer teeth, and one surface tooth. The mouthparts were often worn

and it was generally not possible to determine if the surface tooth was of the same size as the apical mandible tooth, as described for *Tanytarsus lugens* (Hofmann, 1971a; Wiederholm, 1983), or if the surface tooth had the shape of a large plate as described for *Corynocera oliveri* (Wiederholm, 1983) or for head capsules similar to *Tanytarsus lugens* in Alm and Willassen (1993). The category Orthoclaadiinae includes all damaged orthocladine specimens that were not identifiable further than subfamily level and rare Orthoclaadiinae (i.e., with less than 5 occurrences or less than 10 head capsules in the whole stratigraphy). Larval remains of Chaoboridae, Simuliidae, and Thaumaleidae were identified following descriptions in Uutala (1990), Currie and Walker (1992), and Peterson et al. (1989).

Stratigraphy and zonation

Down-core concentrations of chironomid head-capsules showed large fluctuations in the Sägistalsee sediment, ranging from 0.2 to almost 11 head capsules per cm³. These variations were mainly caused by changes in abundance of *Procladius*, *Stictochironomus*, and *Tanytarsus lugens*-type. In order to avoid problems due to the effect of closure in percentage data (see Kovach, 1995) and as the Sägistalsee core is well dated with a reasonable age-depth relationship (Lotter and Birks, 2003), head-capsule accumulation rates (HCAR) were used for the presentation of the results and for zonation procedures (Fig. 1).

The minimal number of statistically significant zones in a stratigraphy can be estimated using a broken stick model (Bennett, 1996). The successive reduction of variance for each additional zone is compared with the reduction of variance as predicted for an unstructured stratigraphy. At some point the reduction of variance by the divisive zonation will intercept values calculated by the broken stick model and the last zonal boundary before the intercept gives the minimal number of statistically significant zones. For the Sägistalsee chironomid stratigraphy this procedure led to three interceptions between the reduction of variance by zonation and the broken stick model and, therefore, to three possible zonation schemes (3, 5, or 7 zones). In the absence of independent evidence, the zonation scheme with 7 zones was accepted as it agrees most closely with our interpretation of the stratigraphy (see Table 1, Fig. 1). Furthermore, one zone boundary (at 488 cm depth) was readjusted one sample downcore (to 500 cm), thus providing zones more consistent with respect to the dominant chironomid taxa (see discussion of individual

Table 1. Zonation of the Sägistalsee chironomid stratigraphy

Chironomid assemblage zone	Depth (cm)	Age (cal. ¹⁴ C yrs BP)	Total HCAR (hc/100 cm ² /yr)	Dominant taxon	Subdominant taxa
CAZ-7 B	0–20	–43–70	17.2–51.3	<i>Stictochironomus</i>	<i>Micropsectra radialis</i> -type
CAZ-7 A	20–254	70–1470	3.9–35.1	<i>Micropsectra radialis</i> -type	<i>Paracladius</i> <i>Smittia</i> Orthoclaadiinae <i>Eukiefferiella</i> <i>Diamesa</i> unident. Tanytarsini
CAZ-6	254–312	1470–1890	50.6–146	<i>Procladius</i>	<i>Stictochironomus</i> (<i>Tanytarsus lugens</i> -type)
CAZ-5	312–373	1890–2370	3.5–18.3	<i>Micropsectra radialis</i> -type	Orthoclaadiinae <i>Paracladius</i>
CAZ-4	373–500	2370–3480	7.0–120	<i>Procladius</i> <i>Stictochironomus</i>	<i>Micropsectra radialis</i> -type <i>Paracladius</i>
CAZ-3	500–550	3480–3940	4.2–8.3	<i>Micropsectra radialis</i> -type	<i>Paracladius</i> Orthoclaadiinae
CAZ-2	550–805	3940–6360	10.1–102	<i>Procladius</i>	<i>Stictochironomus</i>
CAZ-1	805–1348	6360–9060	7.6–56.5	<i>Procladius</i>	<i>Zavrelimyia</i> <i>Tanytarsus lugens</i> -type <i>Micropsectra radialis</i> -type <i>Stictochironomus</i>

zones below). In order to better discuss recent changes in the chironomid assemblages the uppermost zone was additionally divided into two subzones.

Chironomid assemblage zone 1 (CAZ-1)

From the core bottom to 805 cm *Procladius* is the dominant chironomid taxon in the Sägistalsee sediment (Fig. 1, Table 1), although the head-capsule accumulation rate (HCAR) is variable. Other taxa, e.g., *Micropsectra radialis*-type, *Paracladius*, *Limnophyes*, Orthoclaadiinae, *Parametriocnemus/Paraphaenocladus*, and *Smittia/Parasmittia* are present in the whole zone in more or less constant HCARS. *Stictochironomus* is absent or occurs only sporadically in the lowermost part of the core (below 1040 cm) but shows a variable and increasing HCAR during the rest of the zone. *Tanytarsus lugens*-type is present during three distinct maxima (805–842, 954–1012, 1200–1278 cm). However, the taxon is almost absent in intermediate sequences. *Zavrelimyia* is present both at the top and the bottom of the zone, but disappears from 1013–1200 cm. *Protanypus* shows a low but constant HCAR starting at 1142 cm, later followed by *Corynoneura scutellata*-type. Other

chironomid taxa are present only sporadically (e.g., *Corynoneura* spp., *Brillia modesta*, and *Chaetocladus*).

Chironomid assemblage zone 2 (CAZ-2)

Procladius still remains the dominant chironomid at the bottom of CAZ-2, but contrary to CAZ-1, *Stictochironomus* is consistently the second most abundant taxon and towards the top of the zone replaces *Procladius* as the most abundant. The HCAR of both *Procladius* and *Stictochironomus* reach higher values than in CAZ-1. *Tanytarsus lugens*-type shows two distinct peaks at the beginning of the zone, but the HCAR is low for the rest of CAZ-2. *Micropsectra radialis*-type, *Micropsectra* spp., *Paracladius*, and *Protanypus* all show a tendency to slightly higher HCARS towards the top of the zone. Other taxa remain at the same low HCAR as previously. Total HCAR, being generally higher than in CAZ-1, tracks the changes of *Procladius* and *Stictochironomus*.

Chironomid assemblage zone 3 (CAZ-3)

A complete change in the chironomid fauna marks the beginning of CAZ-3. *Procladius*, *Stictochironomus*,

and *Tanytarsus lugens*-type head-capsules all but disappear, leaving *Micropsectra radialis*-type as the dominant taxon. Most of the other chironomids are also present only in low abundances. Still, a number of taxa persist throughout the whole zone, e.g., *Procladius*, *Paratanytarsus*, and *Corynoneura scutellata*-type. Others, such as *Limnophyes* and *Zavreliomyia*, occur sporadically. Total HCAR is strongly reduced, reaching some of the lowest values in the whole sequence (Table 1).

Chironomid assemblage zone 4 (CAZ-4)

Procladius resumes its position as the dominant chironomid taxon in CAZ-4. Similarly, *Stictochironomus* reaches high HCARS and even replaces *Procladius* as the most abundant taxon for a short sequence. *Micropsectra radialis*-type and *Procladius* are the most common subdominant chironomids, although like *Procladius* and *Stictochironomus*, their HCARS show strong fluctuations. Other taxa have low but more constant HCARS (e.g., *Protanypus*, *Eukiefferiella/Tvetenia*) or only sporadic occurrences (e.g., *Paratanytarsus*, *Chironomus anthracinus*-type). Total chironomid HCAR is generally high but very variable (Table 1). A single sample (410–412 cm) shows extremely low head-capsule abundances with an almost total disappearance of *Procladius* and *Stictochironomus* (Fig. 1).

Chironomid assemblage zone 5 (CAZ-5)

As in CAZ-3, the accumulation rates of both *Procladius* and *Stictochironomus* decrease drastically in CAZ-5. *Micropsectra radialis*-type, *Micropsectra* spp., and *Procladius* also show slightly lower values but persist during the whole zone. Other taxa do not show any noticeable change in accumulation or only appear infrequently. Again, total chironomid accumulation is low.

Chironomid assemblage zone 6 (CAZ-6)

Higher chironomid HCARS again characterise CAZ-6. In the first sample of the zone *Stictochironomus* dominates but is subsequently replaced by *Procladius*. *Stictochironomus* remains abundant during the whole zone, though in the upper part *Tanytarsus lugens*-type head-capsules become more dominant. *Micropsectra radialis*-type also increases towards the top of the zone, whereas other taxa remain unchanged (e.g., *Procladius*, *Corynoneura scutellata*-type, *Zavreliomyia*) or occur

infrequently (e.g., *Parakiefferiella*, *Chaetocladius*-type). At the end of CAZ-6, the total HCAR reaches the highest values in the whole stratigraphy.

Chironomid assemblage zone 7 (CAZ-7)

Subzone A: As in CAZ-3 and CAZ-5, both *Procladius* and *Stictochironomus* show a strong decrease in their HCAR in CAZ-7. Similarly, *Tanytarsus lugens*-type occurs in strongly reduced numbers only. Other taxa show slightly lower HCARS (e.g., *Micropsectra radialis*-type, *Micropsectra* spp.) or remain unchanged (e.g., *Eukiefferiella/Tvetenia*, *Smittia/Parasmittia*). Total chironomid HCAR is again low throughout the whole subzone A (Table 1).

Subzone B: In the two uppermost samples of the core the HCAR of *Stictochironomus* rises again. Also, accumulation rates of *Procladius* and *Micropsectra radialis*-type and total HCAR increase at the end of CAZ-7. Whereas high accumulation rates in the whole core are generally characterised by the dominance of *Procladius* head-capsules, this taxon is missing in the most recent sediment of Sägistalsee (Fig. 1).

Non-chironomid remains

In addition to chironomid remains, the larval mandibles and head-capsules of other dipteran families such as Chaoboridae, Simuliidae and Thaumaleidae were also isolated from the Sägistalsee sediments. Fragments of all three families were sparse compared to the abundance of chironomid head-capsules. *Chaoborus flavicans*-type mandibles were most abundant in CAZ-1 and persisted at lower accumulation rates until CAZ-4. Thaumaleid and simuliid remains occurred irregularly during the whole stratigraphy, although Simuliidae are missing for a large part of CAZ-7.

Discussion

Faunistic trends in the stratigraphy

The composition of the Holocene chironomid fauna of Sägistalsee (Fig. 1) can be considered to be typical of a high-altitude lake in the Swiss Alps: *Procladius*, *Tanytarsus lugens*-type, *Stictochironomus*, *Micropsectra*, *Corynoneura*, *Psectrocladius*, *Paratanytarsus*, and *Zavreliomyia* (as Pentaneurini A) are common components of the zoobenthos of Swiss lakes above 1500 m asl (Lotter et al., 1997). A further typical feature of

Sägistalsee is the high abundance of rheophilous taxa in the lake sediment. Even though larvae of *Chaetocladius*, *Diamesa*, *Eukiefferiella*, *Tvetenia*, *Heleniella*, *Limnophyes*, *Orthocladius*, *Parametriocnemus*, *Paraphaenocladius*, *Paratrichocladius*, *Pseudosmittia*, and *Rheocricotopus* have been reported from littoral habitats of lakes (see e.g., Reiss, 1968; Raddum and Sæther, 1981; Moog, 1995), they are generally considered to be typical of running waters or, in the case of *Limnophyes* and *Pseudosmittia*, even semi-terrestrial habitats (Wiederholm, 1983; Moog, 1995). The strong influence of head capsules from running waters in the Sägistalsee sediment is further supported by the simuliid and thumaleid fragments that were isolated from the core (Fig. 1). Simuliid larvae are dependent on a unidirectional current for feeding and can therefore - with very few exceptions - only survive in running waters (Currie and Walker, 1992) and thumaleid larvae typically live in the hygropetric zone of alpine streams and springs (Wagner, 1997).

The down-core changes in the Sägistalsee chironomid stratigraphy on the other hand are very pronounced and unexpected in their magnitude. Changes in the chironomid assemblage are dominated by the dynamics of three taxa, namely *Procladius*, *Stictochironomus*, and *Tanytarsus lugens*-type. *Procladius* and *Stictochironomus* are reported as being common inhabitants of lake zoobenthos (Wiederholm, 1983). Larvae of *Procladius* live in soft sediment in the littoral and profundal of lakes over a range of trophic conditions and altitude (Wiederholm, 1981, 1989; Lotter et al., 1997, 1998). *Stictochironomus* typically inhabits profundal soft sediments or littoral sandy sediments in mesotrophic and oligotrophic lakes (Wiederholm, 1989). *Tanytarsus lugens*-type head-capsules feature a very distinct mandible. Hofmann (1971a) describes the larva of *Tanytarsus lugens* and *T. bathophilus* as having this mandible morphology, but other chironomid species may well be included in the taxon. Therefore, little can be said about the ecology of *Tanytarsus lugens*-type larvae except that they can form a major component of the subfossil chironomid assemblage in Swiss Northern Alpine lakes above 1500 m asl (Lotter et al., 1997).

Other taxa known to occur commonly in lakes show little or no changes in the Sägistalsee stratigraphy. In small Swiss lakes, *Micropsectra* and *Paracladius* are restricted to alpine and subalpine habitats (Lotter et al., 1997). *Corynoneura*, *Paratanytarsus*, *Psectrocladius*, and *Zavrelimyia* are more eurythermic and occur over a wide temperature range (Lotter et al., 1997). Similarly, the rheophilous taxa found in Sägistalsee show

little change in accumulation rate during the last 9000 years (e.g., *Diamesa*, *Eukiefferiella/Tvetenia*, or *Smittia/Parasmittia*) or only occur sporadically (e.g., *Pseudosmittia* or *Rheocricotopus*).

In order to summarise major faunistic trends in the chironomid stratigraphy Principal Components Analysis (PCA) was applied to the square-root transformed percentage data (Fig. 2). As Euclidean distance scaling is used, the distance between samples in a scatter plot of the first two PCA axes can be interpreted as a dissimilarity measure (Legendre and Legendre, 1998). The first two PCA axes explain 54% of the total variance in the data set and clearly separate CAZ-3, 5, and 7 from all other samples. Changes in the first PCA axis scores are largely responsible for this separation, with high axis scores during phases of low head-capsule accumulation and low values during periods of abundant sedimentation of chironomid remains (Fig. 2). The second PCA axis spreads the high head-capsule accumulation samples, with samples of CAZ-1 tending to negative scores, whereas younger samples (CAZ-2, 4, 6) have higher second PCA axis scores (Fig. 2). The topmost sample in the stratigraphy with high first and second PCA axis scores is clearly separated from all other samples. Taking into account the species scores (Fig. 2), the major faunistic changes in the Sägistalsee chironomid fauna during the last 9000 years can be summarised as a general succession from an assemblage dominated by *Procladius*, *Tanytarsus lugens*-type, and *Zavrelimyia* (low second PCA axis scores), with moderate HCARs, to an assemblage with an increasing importance of *Stictochironomus* with high HCARs (Figs. 1 and 2). This general succession has been abruptly interrupted three times (CAZ-3, 5, 7) by a steep decline of total head-capsule accumulation. This is caused by the elimination of the dominant chironomids (*Procladius*, *Stictochironomus*, *Tanytarsus lugens*-type) from the assemblage, leaving *Micropsectra radialis*-type, *Paracladius*, and *Micropsectra* spp. as the main taxa.

Possible causes of major faunistic patterns

(a) *Declining lake depth and immigration of spruce*
Sägistalsee's bathymetry has changed significantly during the last 9000 years. Assuming a constant water-surface level during the Holocene, the maximum depth of Sägistalsee has decreased from 23 m in the early Holocene to ca. 10 m at present due to sediment infilling. Water depth is a key factor affecting the limnology of lakes and the habitats available for chironomid larvae.

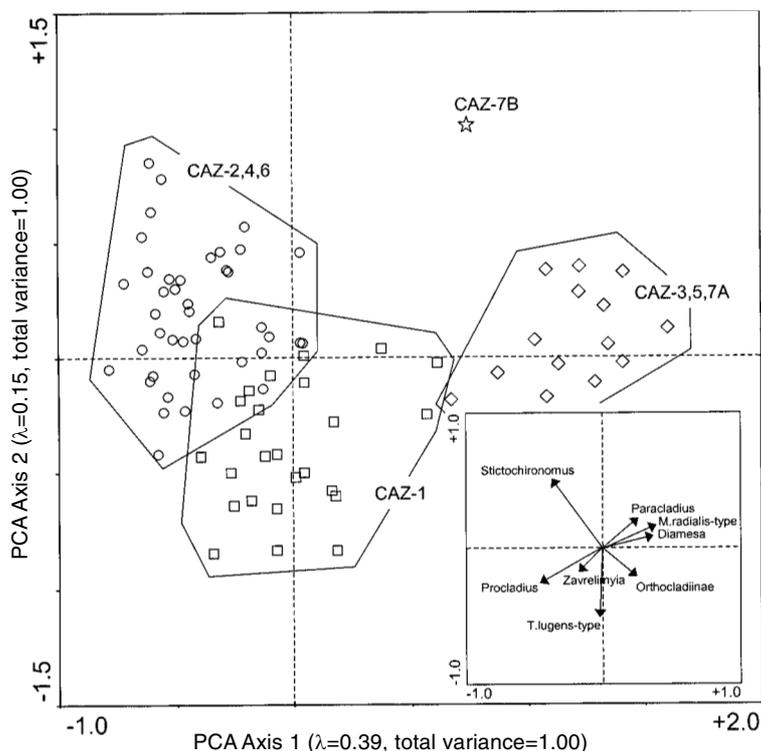


Fig. 2. Euclidean distance scatter plot of a Principal Components Analysis (PCA) of the Sägistalsee stratigraphy (squares indicate samples from CAZ-1, circles CAZ-2, 4, 6, diamonds CAZ-3, 5, 7A and the star CAZ-7B). The inset shows a scatter plot of the species scores of selected chironomid taxa.

Amongst other parameters, it influences the extent of thermal stratification and stratification stability, and, thereby, water temperature, length of ice cover, and nutrient cycling (Hutchinson, 1975). In dimictic lakes water depth directly affects the size of the hypolimnion, which influences the oxygen supply available during stratification for decompositional processes at the lake bottom (Hutchinson, 1975; Frey, 1988). Finally, water depth influences the amount of light available for photosynthesis and, thus, the quality and quantity of benthic algae, a possible source of food for chironomid larvae (Berg, 1995). During the phases of high total head-capsule accumulation (CAZ-1, 2, 4, 6) the chironomid fauna of Sägistalsee parallels the decreasing lake depth by an increase in the accumulation rates of both *Procladius* and *Stictochironomus* and the succession from a *Procladius* to a *Procladius-Stictochironomus*-dominated assemblage (Figs. 1 and 2). Also, major long-term trends in geochemistry and sedimentation are registered in the sediment, e.g., an increase of the organic matter content and a decrease in calcite concentration (Koinig et al., 2003; Ohlendorf et al., 2003). At ca. 6500 cal. BP, synchronous to the strongest change

in many of these trends, spruce (*Picea*) immigrates into the previously pine- and fir-dominated woodlands in the lake's catchment, leading to a denser forest in the watershed (Wick et al., 2003). The boundary between CAZ-1 and 2 coincides with the first occurrences of *Picea* macrofossils in the sediment. However, the general successional trend in CAZ-1, 2, 4, and 6 begins before the immigration of *Picea* and continues on afterwards (see e.g., the successive importance of *Stictochironomus* in the chironomid fauna; Fig. 1). Therefore, a possible cause for the succession from an assemblage dominated by *Procladius* to one dominated by *Procladius* and *Stictochironomus* is the lake's decreasing depth and changes in associated limnological parameters. The immigration of *Picea* into Sägistalsee's catchment had a modifying effect on many of the sediment chemistry variables (see discussions in Koinig et al., 2003; Ohlendorf et al., 2003) and thus may have favoured this trend.

(b) Human impact

A phase of high abundance of macroscopic charcoal particles in the lake sediment from ca. 4400–3600 cal.

BP accompanied by a reduction of tree macrofossils is registered in the Sägistalsee sediment record (Wick et al., 2003). Together with a strong decrease in the ratio of tree to herb pollen during ca. 4200–3500 cal. BP (Wick et al., 2003), this suggests human presence and clear-cutting in the catchment as early as the Bronze Age. Later, two additional phases of reduced tree pollen and increased grazing indicator pollen (mainly *Plantago alpina*) point to further periods of high human activity near Sägistalsee during the Iron Age/Roman period and from the Mediaeval Age onwards (Wick et al., 2003). The three periods are synchronous with CAZ-3, 5, and 7, respectively, when the dominant chironomid taxa disappear from the sediment record and total chironomid accumulation is strongly reduced (Fig. 3). In periods with lower human impact, during which the catchment vegetation recovers, the chironomid fauna reverts to the pre-impact state with a high total chironomid accumulation and a dominance of *Procladius* and *Stictochironomus*.

The results of Iovino (1975) suggest that most chironomid remains are deposited close to the habitat of the living larvae. The fact that only the most dominant lake-living taxa are affected by abrupt fluctuations of accumulation rates therefore suggests that chironomid populations close to the coring site, i.e., near the centre of the lake, were strongly reduced or absent during the low chironomid accumulation phases, whereas others, living on the slopes of the lake basin, remained unaffected. A major factor affecting the abundance and survival of chironomid populations in the deepest part of a lake is the oxygen content of the hypolimnetic water (Hofmann, 1971b; Frey, 1988; Lindegaard, 1995; Dinsmore and Prepas, 1997). Dimictic lakes can experience seasonal anoxia in the bottom waters during summer and autumn, which are caused by decompositional processes in the profundal (Hutchinson, 1975). Furthermore, lakes with prolonged ice-cover may also experience oxygen deficiencies during the winter, as the lake is decoupled from the atmospheric oxygen supply (Pechlaner, 1966; Welch, 1991). Small lakes near the treeline in the northern Swiss Alps can freeze as early as October and thaw out as late as May (personal observations) resulting in an up to 7 month long period between spring and autumn circulation. Even though the Sägistalsee sediments have a very low content of organic carbon (ca. 5–20 g/kg; Ohlendorf et al., 2003), recent water-chemistry measurements reveal that the lake experiences moderate oxygen depletion of bottom waters during early summer (25% absolute oxygen deficit measured above bottom on July 7, 1993,

corrected for altitude and following Hutchinson, 1975). Due to Sägistalsee's bathymetry (e.g., more than 40% of the lake bottom is deeper than 9 m; see Lotter and Birks, 2003), oxygen depletion of a relatively thin water layer can affect a disproportionately large area of the lake bottom. Therefore, changes in seasonal oxygen availability to the zoobenthos either during summer stratification, during the long winter ice-cover, or both, are a possible explanation for the strong reduction of *Procladius*, *Stictochironomus* and *Tanytarsus lugens*-type remains during CAZ-3, 5, and 7. This hypothesis is further supported by geochemistry measurements on the Sägistalsee core. Koinig et al. (2003) record a reduction of calcite content and of the ratio between manganese and iron (Mn/Fe) during all three phases of low chironomid accumulation. They interpret this signal as reflecting an increase of decompositional processes at the lake bottom with an associated reduction in bottom-water oxygen content and pH, and hypothesise that the lake may even have become meromictic during CAZ-3, 5, and 7.

A possible mechanism linking anoxia in the lake with human activity in the catchment is an increase in nutrient loading of the lake caused by inwash of manure and faeces of livestock. Modern water-chemistry measurements suggest that Sägistalsee is mesotrophic (Lotter et al., 1998; Müller et al., 1998). The lake's pollen stratigraphy suggests that during parts of the Iron Age, the Roman period, and the Mediaeval period grazing near Sägistalsee was even more intensive than today (Wick et al., 2003). Hence, the lake may have been more productive in the past, leading to higher oxygen demand in the hypolimnion.

(c) Climate

A number of Holocene climate oscillations have been proposed for the Swiss Alps (Wick and Tinner, 1997). Furthermore, Wick et al. (2003) suggest that a reduction of *Abies* macrofossils in the sediment sequence between 1050 and 1120 cm may be a consequence of cooler climate around 8200 cal. BP. Subfossil chironomid remains are useful climate proxies and have been used to reconstruct major climatic oscillations during the Late Glacial (Walker et al., 1991a; Levesque et al., 1993) or long-term climate trends during the Holocene (Pellatt et al., 2000). When using chironomids as climate indicators the underlying assumption is that the chironomid assemblage of a lake is affected by air and/or water temperature, or by associated limnological parameters (see e.g., Lotter et al., 1997; Walker et al., 1997). Therefore, as the temperature changes, the

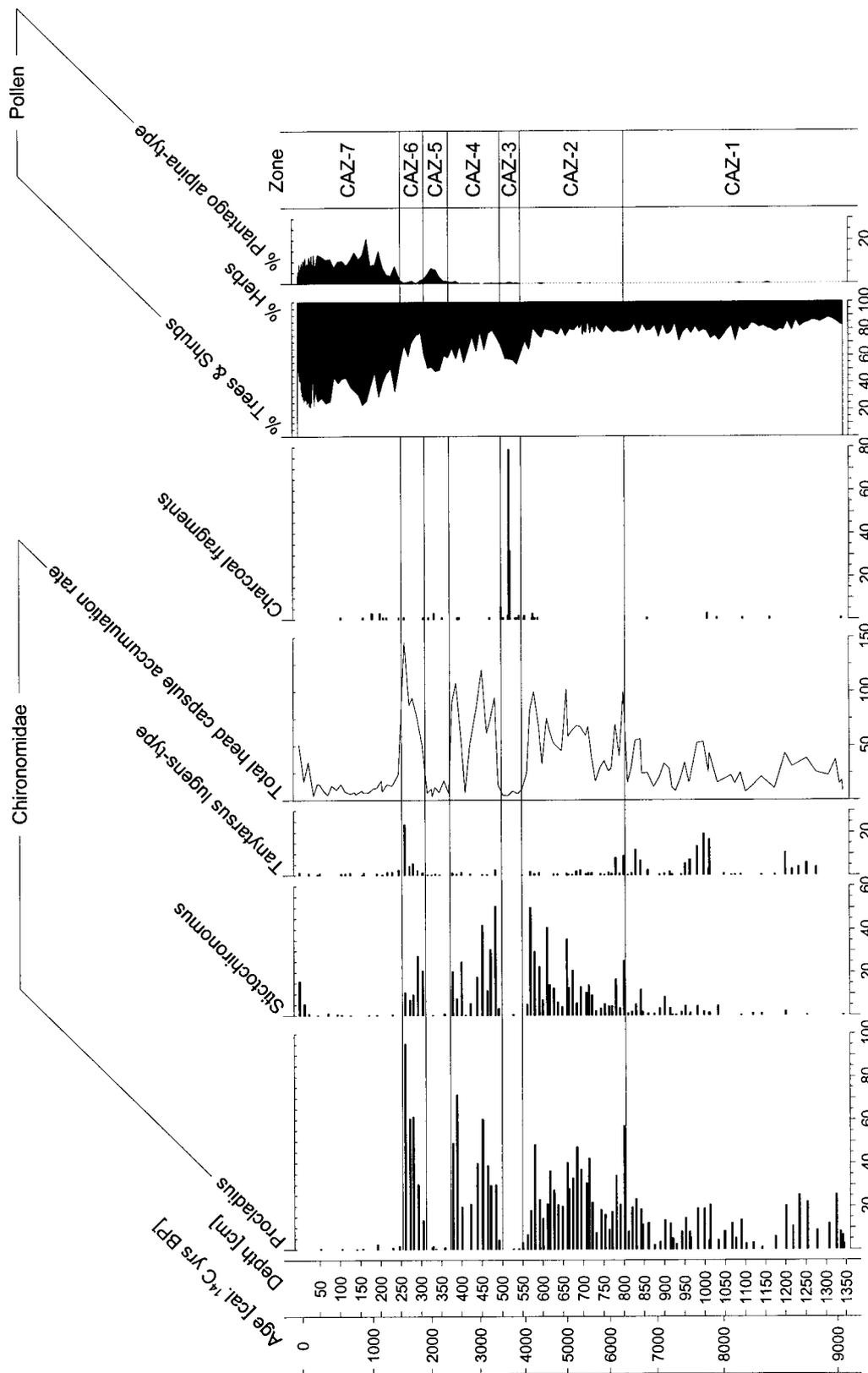


Fig. 3. Summary diagram of the chironomid stratigraphy compared with palaeobotanical proxies analysed in the Sigistalsee core (Wick et al., 2003). Chironomid taxa (*Procladius*, *Sicochironomus*, *Tanytarsus lugens-type*), and total head capsule accumulation rate (HCAR) are in $hc/100\text{ cm}^2/\text{yr}$. Macroscopic charcoal is plotted as particles per sample. All pollen curves are in percentages of total pollen.

chironomid fauna of a lake should undergo a succession to an assemblage with a higher dominance of taxa better adapted to the new climate. In the early Holocene, around 8200 cal. BP, no clear signal is visible in the chironomid stratigraphy. The only chironomid taxon that parallels the reduction in *Abies* macrofossils is *Zavreliomyia*. The Pentaneurini have sometimes been used at tribe level as indicators of 'temperate' climate conditions (Walker et al., 1991a). This, therefore, might suggest cooler conditions during the absence of *Zavreliomyia* from the sediment. However, remains of *Zavreliomyia* have been found in surface sediments of lakes above 2000 m asl in the Swiss Alps (as Pentaneurini A in Lotter et al., 1997). Also, the decrease in *Zavreliomyia* begins before and ends later than the period with no *Abies* remains in the plant macrofossil diagram.

Of the major faunistic trends in the stratigraphy, the succession from an assemblage dominated by *Procladius* to one dominated by *Procladius* and *Stictochironomus* is difficult to interpret climatically. Whereas *Stictochironomus* is a cold indicator in small lakes in the northern Swiss Alps, *Procladius* seems to be a eurythermic genus with no clear temperature preferences (Lotter et al., 1997). Also, no subdominant chironomid taxa with clear temperature preferences track the changing abundances of *Procladius* or *Stictochironomus* (Fig. 1).

CAZ-3, 5, and 7 are numerically dominated by *Micropsectra radialis*-type, a cold-indicating taxon that is largely restricted to lakes above 2000 m asl in the lake data-set of Lotter et al. (1997; slides reexamined by the authors). Therefore, the change from a *Stictochironomus*- and *Procladius*-dominated assemblage to a *Micropsectra radialis*-type dominated assemblage could possibly be interpreted as a climate signal. On the other hand, our results suggest that the faunistic changes between CAZ-2, 4, and 6 and CAZ-3, 5, and 7 are a consequence of human disturbance and that the dominance of *Micropsectra radialis*-type is an artefact of the elimination of the formerly dominant chironomid taxa from the lake rather than a succession (Figs. 1 and 3).

Finally, *Chaoborus* has been reported as being an indicator of warm-water temperatures in a surface-sediment transect from eastern Canada (Walker et al., 1997). Larvae of *Chaoborus* were present in Sägistalsee from the early Holocene until ca. 3000 cal. BP. However, in the Swiss Alps no detailed information on the distribution of *Chaoborus* with respect to temperature or altitude is available. Furthermore, *Chaoborus* mandibles have been collected by the authors from the surface

sediments of Gouillé Rion, a lake at ca. 2343 m asl in the Central Swiss Alps. Therefore, *Chaoborus* is clearly not restricted to warm lakes in Switzerland.

Figure 4 presents the results of a quantitative chironomid-July air temperature inference model applied to the Sägistalsee chironomid stratigraphy. The two-component weighted averaging-partial least squares regression (WA-PLS) model includes 76 taxa and 81 lakes and is presented in more detail in Heiri (2001). After harmonising the taxonomy to the level of the Sägistalsee stratigraphy (causing a reduction of the number of taxa to 74), the model has an r^2 of 0.82 and a root mean square error of prediction (RMSEP) of 1.48 °C estimated by leave-one-out cross-validation. Temperatures around 10.5–11.5 °C are inferred during the presence of *Procladius* and *Stictochironomus*. The strongest Holocene temperature decreases are reconstructed during the periods of low chironomid accumulation and a numerical dominance of *Micropsectra radialis*-type with temperatures around 10–10.5 °C. A period of slightly lower temperatures is apparent between ca. 8000 and 7600 cal. BP. However, this decrease in temperatures is difficult to separate from the between-sample variability of the inferred temperatures and does not approach the magnitude of temperature changes inferred during the periods of human presence near Sägistalsee.

A comparison of these results to other Holocene reconstructions of summer temperature is difficult. Many periods of cooler climate have been described from the Swiss Alps, but presumably due to dating problems these are not always synchronous and, given the inherent error of radiocarbon dating, it is possible to find a reference to a cold period for almost any time span of ca. 500 years (Wick and Tinner, 1997; Haas et al., 1998). Therefore, the chironomid-based July air temperatures inferred from Sägistalsee should be treated with caution, as human impact seems to be the driving force affecting chironomid-assemblage composition. Anoxia in Sägistalsee may have been favoured by prolonged winter ice-cover associated with cooler climate. However, even if this was the case, the abrupt fluctuations between two different states of chironomid assemblages (*Procladius-Stictochironomus*-dominated vs. *Micropsectra radialis*-type-dominated) suggest that the climate signal may have been overamplified by changes in the lake's oxygen regime. More palaeolimnological and palaeobotanical work on well-dated sediment sequences in the region is clearly necessary to resolve the question if the land-use changes during CAZ-3, 5, and 7 were associated with periods of cooler climate.

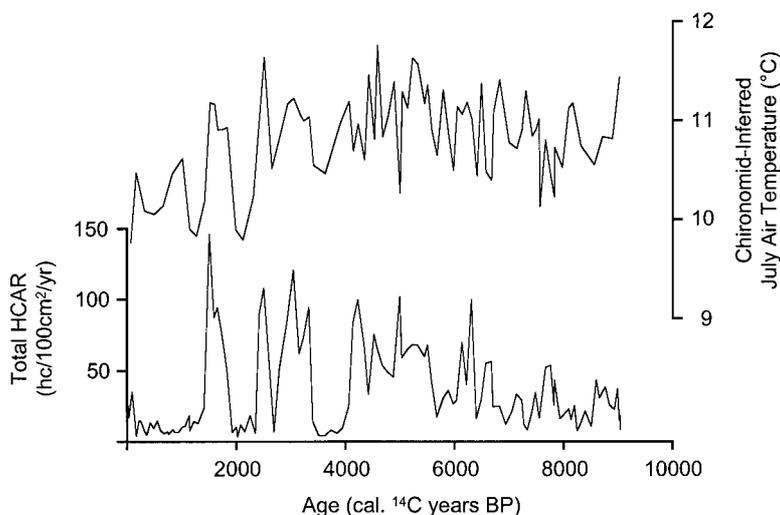


Fig. 4. Chironomid-inferred July air temperatures from Sägistalsee reconstructed using a two-component WAPLS model (r^2 0.82; RMSEP 1.48 °C) compared to the total head-capsule accumulation rate (HCAR) in the sediment core (as hc/100 cm²/yr). Samples with less than 50 counts were amalgamated to reach a more reliable count sum for temperature reconstruction, reducing the stratigraphy from 118 samples (used to illustrate the accumulation rates) to 82.

Sensitivity to disturbance and resilience of the lake ecosystem

The Sägistalsee chironomid stratigraphy is unusual in having abrupt fluctuations between two states of assemblage composition as described in this study (Figs. 1 and 2). Other published Holocene chironomid stratigraphies either show less change in chironomid composition during large parts of the Holocene (Brooks, 1996; Massaferro and Corley, 1998; Rück et al., 1998; Itkonen et al., 1999), or long-term Holocene trends are attributed to Holocene climate changes (Smith et al., 1998; Pellatt et al., 2000) or natural lake ontogeny (Hofmann, 1971b, 1999). An exception is a 6000-year chironomid stratigraphy from a mountain lake on the South Island of New Zealand, which also shows strong fluctuations in the Holocene chironomid fauna (Schakau, 1990). However, these changes were interpreted as being a consequence of changing hydrology, lake inflow, and sedimentation type. Prehistoric human impact on lakes has been registered a number of times using palaeolimnological techniques (e.g., Warwick, 1980; Haworth, 1985; Fritz, 1989). Nevertheless, a record of strong human influence on a remote alpine lake ecosystem as early as 4000 years cal. BP is, to our knowledge, unprecedented. The fact that Sägistalsee's catchment experienced three distinct phases of human activity, interrupted by periods with significantly reduced human impact, offers the possibility of studying

the chironomid fauna's response to disturbance and its recovery over a time scale of millennia. Chironomid larvae form an abundant and diverse component of the lake benthos and have repeatedly been used as bio-monitoring organisms to assess the effects of human activity on lakes (Lindegaard, 1995; Wiederholm, 1984). Thus, they can provide insights on the response of Sägistalsee's ecosystem to human disturbance.

Although pollen and plant macrofossil analysis suggests that human impact in the catchment was progressively more intensive from CAZ-3 onwards to CAZ-5 and 7 (e.g., see the ratio of tree to herb pollen and the pollen percentages of *Plantago alpina* in Fig. 3), the chironomid assemblages responded to all three phases of 'anthropogenic forcing' in the same way (Figs. 2 and 3). It therefore seems that Sägistalsee's aquatic ecosystem responded extremely sensitively to human activity in the catchment in the sense that minor disturbances of the lake ecosystem had the same effect as more pronounced ones. Even though human-induced vegetation changes linger for a few centuries after the end of CAZ-3 (e.g., the lowering of the treeline as suggested by plant macrofossil analysis; Wick et al., 2003), this does not seem to affect the chironomid fauna as strongly as the presence of humans and their livestock in the lake's surroundings.

The chironomid assemblage also shows considerable resilience, the chironomid fauna reverts to the pre-impact state at least after the first two phases of human

disturbance. This suggests that, contrary to other lakes where the ecosystems are substantially affected by negative feedback mechanisms (e.g., Niessen and Sturm, 1987; Sandman et al., 1990; Scheffer, 1998; Little and Smol, 2000), the 'low chironomid accumulation state' in Sägistalsee is highly dependent on external nutrient loading. This is not surprising given the high proportion of allochthonous detritus and low content of organic carbon in the lake's sediment and the high sedimentation rate. Organic material deposited at the lake bottom is rapidly diluted and covered and therefore decoupled from the water column. In addition the lake possesses a low water-residence time (Müller et al., 1998) and nutrients are rapidly flushed from the lake if external loading is reduced. A detailed assessment of the rate of change from an assemblage dominated by *Micropectra radialis*-type (i.e., the low chironomid accumulation state) to one dominated by *Procladius* and/or *Stictochironomus* is hindered by the resolution of the chironomid stratigraphy available, but the transition was generally completed within one sample interval (70–110 years).

Pollen analysis indicates that pasturing in the vicinity of Sägistalsee has declined again since ca. 20–30 cal. BP (see herb pollen and *Plantago alpina* in Fig. 3; Wick et al., 2003). Correspondingly, chironomid accumulation increased at the end of CAZ-7. High chironomid concentrations in the sediment were accompanied by the dominance of *Procladius* throughout the whole stratigraphy. However, *Procladius* is entirely absent from the topmost samples (Fig. 1). This suggests that the lake's chironomid fauna has only partially recovered. In the last few centuries, human activities have influenced alpine lake ecosystems as never before. Atmospheric deposition of pollutants and human non-agricultural activities have increased significantly. In addition many lakes that do not have a natural fish population have been heavily stocked. Different salmonids have been introduced to Sägistalsee since at least 40 cal. BP (Steiner, 1911; Guthruf et al., 1999). *Procladius* has been reported as being a preferred prey of salmonids in another alpine lake (Serra-Tosio, 1978) and this may be the reason for the absence of remains of the large and free-living *Procladius* larvae from the most recent sediment.

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References

- Alm T. and Willassen E. 1993. Late Weichselian Chironomidae (Diptera) stratigraphy of lake Nedre Æråsvatn, Andøya, Northern Norway. *Hydrobiologia* 264: 21–32.
- Bennett K.D. 1996. Determination of the number of zones in a biostratigraphical sequence. *New Phytol.* 132: 155–170.
- Berg M.B. 1995. Larval food and feeding behaviour. In: Armitage P.D., Cranston P.S. and Pinder L.C.V. (eds), *The Chironomidae*. Chapman and Hall, London, pp. 136–168.
- Birks H.J.B. and Gordon A.D. 1985. *Numerical Methods in Quaternary Pollen Analysis*. Academic Press, London, 317 pp.
- Bretschko G. 1995. Opportunities of high alpine research, the lake 'Vorderer Finstertaler See' as an example (Kühtai, Tirol, 2237 m a.s.l.). *Limnologia* 25: 105–108.
- Brodin Y. 1982. Palaeoecological studies of the recent development of the lake Väjösjön IV. Interpretation of the eutrophication process through the analysis of subfossil chironomids. *Arch. Hydrobiol.* 93: 313–326.
- Brodin Y.W. 1990. Midge fauna development in acidified lakes in northern Europe. *Phil. Trans. r. Soc. Lond. B* 327: 295–298.
- Brooks S.J. 1996. Three thousand years of environmental history in a Cairngorms Lochan revealed by analysis of non-biting midges (Insecta: Diptera: Chironomidae). *Bot. J. Scotl.* 48: 89–98.
- Buskens R.F.M. 1987. The chironomid assemblages in shallow lentic waters differing in acidity, buffering capacity and trophic level in the Netherlands. *Ent. scand. Suppl.* 29: 217–224.
- Chapin F.S. III and Körner C. 1995. Patterns, causes, changes, and consequences of biodiversity in arctic and alpine ecosystems. *Ecol. Stud.* 113: 313–320.
- Cranston P.S. 1982. A key to the larvae of the British Orthocladinae (Chironomidae). *Freshwat. biol. Assoc. sci. Publ.* 45: 1–152.
- Currie D.C. and Walker I.R. 1992. Recognition and paleohydrologic

- significance of fossil black fly larvae, with a key to the Nearctic genera (Diptera: Simuliidae). *J. Paleolim.* 7: 37–54.
- Dinsmore W.P. and Prepas E.E. 1997. Impact of hypolimnetic oxygenation on profundal invertebrates in a eutrophic lake in central Alberta. II. Changes in *Chironomus* spp. abundance and biomass. *Can. J. Fish. Aquat. Sci.* 54: 2170–2181.
- Döscher A., Gäggeler H.W., Schotterer U. and Schwikowski M. 1995. A 130 year deposition record of sulfate, nitrate and chloride from a high-alpine glacier. *Wat. Air Soil Pollut.* 85: 603–609.
- Fedele F.G. and Wick L. 1996. Glacial/postglacial transition south of Splügen pass: environment and human activity. II *Quaternario* 9: 541–550.
- Frey D.G. 1988. Littoral and offshore communities of diatoms, cladocerans, and dipterous larvae, and their interpretation in paleolimnology. *J. Paleolim.* 1: 179–191.
- Fritz S.C. 1989. Lake development and limnological response to prehistoric and historic land use in Diss, Norfolk, U.K. *J. Ecol.* 77: 182–202.
- Grabherr G., Gottfried M., Gruber A. and Pauli H. 1995. Patterns and current changes in Alpine plant diversity. *Ecol. Stud.* 113: 167–181.
- Grimås U. and Nilsson N.-A. 1962. Nahrungsauna und kanadische Seeforelle in Berner Gebirgsseen. *Schweiz. Z. Hydrol.* 24: 49–75.
- Gross T. 1999. Biodiversity and sustainable development in mountains. In: Price M.F. (ed.), *Global Change in the Mountains*. Parthenon Publishing, New York: 4–6.
- Guilizzoni P., Marchetto A., Lami A., Cameron N.G., Appleby P.G., Rose N.L., Schnell Ø.A., Belis C.A., Giorgis A. and Guzzi L. 1996. The environmental history of a mountain lake (Lago Paione Superiore, Central Alps, Italy) for the last c. 100 years: a multidisciplinary palaeolimnological study. *J. Paleolim.* 15: 245–264.
- Guthruf J., Guthruf-Seiler K. and Zeh M. 1999. Kleinseen im Kanton Bern. *Gewässer und Bodenschutzlabor des Kantons Bern (GBL)*, Bern, 229 pp.
- Haas J.N., Richoz I., Tinner W. and Wick L. 1998. Synchronous Holocene climate oscillations recorded on the Swiss Plateau and at timberline in the Alps. *Holocene* 8: 301–309.
- Haworth E.Y. 1985. 'The highly nervous system of the English lakes': Aquatic ecosystem sensitivity to external changes, as demonstrated by diatoms. *Freshwat. Biol. Assoc. Ann. Report* 53: 60–79.
- Heiri O. 2001. *Holocene Palaeolimnology of Swiss Mountain Lakes Reconstructed Using Subfossil Chironomid Remains: Past Climate and Prehistoric Human Impact on Lake Ecosystems*. PhD Diss., University of Bern, Bern, 113 pp.
- Heiri O. and Lotter A.F. 2001. Effect of low count sums on quantitative environmental reconstructions: an example using subfossil chironomids. *J. Paleolim.* 26: 343–350.
- Henrikson L., Olofson J.B. and Oscarson H.G. 1982. The impact of acidification on Chironomidae (Diptera) as indicated by subfossil stratification. *Hydrobiologia* 86: 223–229.
- Hirvenoja M. and Hirvenoja E. 1988. *Corynoneura brundini* spec. nov. Ein Beitrag zur Systematik der Gattung *Corynoneura* (Diptera, Chironomidae). *Spixiana/Suppl.* 14: 213–238.
- Hofmann W. 1971a. Zur Taxonomie und Palökologie subfossiler Chironomiden (Dipt.) in Seesedimenten. *Arch. Hydrobiol. Beih.* 6: 1–50.
- Hofmann W. 1971b. Die postglaziale Entwicklung der Chironomiden- und Chaoboriden-Fauna (Dipt.) des Schöhsees. *Arch. Hydrobiol./Suppl.* 40: 1–74.
- Hofmann W. 1986. Chironomid analysis. In: Berglund B.E. (ed.), *Handbook of Holocene Palaeoecology and Palaeohydrology*. J. Wiley and Sons, Chichester, pp. 715–727.
- Hofmann W. 1999. Holocene succession and morphological variation of the *Bosmina* (*Eubosmina*) taxa of Plussee (northern Germany). *Arch. Hydrobiol. spec. Issues Advanc. Limnol.* 54: 359–372.
- Hutchinson G.E. 1975. *A Treatise on Limnology. Volume I: Geography, Physics, and Chemistry*. J. Wiley and Sons, New York, 137 pp.
- Iovino A.J. 1975. *Extant Chironomid Populations and the Representativeness and Nature of Their Remains in Lake Sediments*. PhD Diss., Indiana University, 54 pp.
- Itkonen A., Marttila V., Meriläinen J.J. and Salonen V.-P. 1999. 8000-year history of palaeoproductivity in a large boreal lake. *J. Paleolim.* 21: 271–294.
- Kansanen P.H. 1985. Assessment of pollution history from recent sediments in Lake Vanajavesi, southern Finland. II. Changes in the Chironomidae, Chaoboridae and Ceratopogonidae (Diptera) fauna. *Ann. zool. fennici* 22: 57–90.
- Koinig K., Shotyk W., Lotter A.F., Ohlendorf C. and Sturm M. 2003. 9000 years of geochemical evolution of lithogenic major and trace elements in the sediment of an alpine lake – the role of climate, vegetation and land-use history. *J. Paleolim.* 30: 307–320.
- Kovach J.S. 1995. Multivariate data analysis. In: Maddy D. and Brew J.S. (eds), *Statistical Modelling of Quaternary Science Data. Technical Guide 5*, Quaternary Science Association, Cambridge, pp. 1–38.
- Lami A., Marchetto A., Guilizzoni P., Giorgis A. and Massaferrò J. 1994. Paleolimnological records of carotenoids and carbonaceous particles in sediments of some lakes in the Southern Alps. *Hydrobiologia* 274: 57–64.
- Legendre P. and Legendre L. 1998. *Numerical Ecology*. Elsevier Science B.V., Amsterdam, 853 pp.
- Levesque A.J., Mayle F.E., Walker I.R. and Cwynar L.C. 1993. A previously unrecognized late-glacial cold event in eastern North America. *Nature* 361: 623–626.
- Lindgaard C. 1995. Classification of water-bodies and pollution. In: Armitage P.D., Cranston P.S. and Pinder L.C.V. (eds), *The Chironomidae*. Chapman and Hall, London, pp. 385–404.
- Little J.L. and Smol J.P. 2000. Changes in fossil midge (Chironomidae) assemblages in response to cultural activities in a shallow, polymictic lake. *J. Paleolim.* 23: 207–212.
- Lotter A.F. and Birks H.J.B. 2003. Holocene sediments of Sägistalsee, a small lake at the present-day tree-line in the Swiss Alps. *J. Paleolim.* 30: 253–260.
- Lotter A.F., Birks H.J.B., Hofmann W. and Marchetto A. 1997. Modern diatom, cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. I. Climate. *J. Paleolim.* 18: 395–420.
- Lotter A.F., Birks H.J.B., Hofmann W. and Marchetto A. 1998. Modern diatom, cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. II. Nutrients. *J. Paleolim.* 19: 443–463.
- Massaferrò J. and Corley J. 1998. Environmental disturbance and chironomid palaeodiversity: 15 kyr BP of history at Lake Mascardi, Patagonia, Argentina. *Aquat. Conserv.* 8: 315–323.

- Meyer E. 1990. A simple subsampling device for macroinvertebrates with general remarks on the processing of stream benthos samples. *Arch. Hydrobiol.* 117: 309–318.
- Moog O. 1995. Fauna Aquatica Austriaca. Abteilung für Hydrobiologie, Fischereiwirtschaft und Aquakultur der Universität für Bodenkultur, Wien.
- Müller B., Lotter A.F., Sturm M. and Ammann A. 1998. Influence of catchment quality and altitude on the water and sediment composition of 68 small lakes in Central Europe. *Aquat. Sci.* 60: 316–337.
- Niessen F. and Sturm M. 1987. Die Sedimente des Baldeggersees (Schweiz) – Ablagerungsraum und Eutrophierungsentwicklung während der letzten 100 Jahre. *Arch. Hydrobiol.* 108: 365–383.
- Ohlendorf C., Sturm M. and Hausmann S. 2003. Natural environmental changes and human impact reflected in sediments of a high alpine lake in Switzerland. *J. Paleolim.* 30: 297–306.
- Oliver D.R. 1971. Life history of Chironomidae. *Ann. Rev. Ent.* 16: 211–230.
- Pechlaner R. 1966. Die Finstertaler Seen (Kühtai, Österreich) I. Morphometrie, Hydrographie, Limnophysik und Limnochemie. *Arch. Hydrobiol.* 62: 165–230.
- Pellatt M.G., Smith M.J., Mathewes R.W., Walker I.R. and Palmer S.L. 2000. Holocene treeline and climate change in the subalpine zone near Stoyoma Mountain, Cascade Mountains, southwestern British Columbia, Canada. *Arct. antarct. alp. Res.* 32: 73–83.
- Peterson B.V., Baez M. and Sinclair B.J. 1989. A redescription of the adults and larva of *Thaumalea subafricana* (Diptera: Thaumaleidae), and first description of the pupa. *Ent. News* 100: 49–58.
- Pinder L.C.V. 1986. Biology of freshwater Chironomidae. *Ann. Rev. Ent.* 31: 1–23.
- Psenner R. and Schmidt R. 1992. Climate-driven pH control of remote alpine lakes and effects of acid deposition. *Nature* 356: 781–783.
- Raddum G.G. and Sæther O.A. 1981. Chironomid communities in Norwegian lakes with different degrees of acidification. *Verh. internat. Verein. Limnol.* 21: 399–405.
- Reiss F. 1968. Verbreitung lakustrischer Chironomiden (Diptera) des Alpengebietes. *Ann. zool. fenn.* 5: 119–125.
- Rieradevall M. and Brooks S.J. 2001. An identification guide to subfossil Tanytopodinae larvae (Insecta: Diptera: Chironomidae) based on cephalic setation. *J. Paleolim.* 25: 81–99.
- Rück A., Walker I.R. and Hebda R. 1998. A paleolimnological study of Tugulnuit Lake, British Columbia, Canada, with special emphasis on river influence as recorded by chironomids in the lake's sediment. *J. Paleolim.* 19: 63–75.
- Sæther O.A. 1979. Chironomid communities as water quality indicators. *Holarct. Ecol.* 2: 65–74.
- Sandman O., Eskonen K. and Liehu A. 1990. The eutrophication history of Lake Särkinen, Finland and the effects of lake aeration. *Hydrobiologia* 214: 191–199.
- Schakau B. 1990. Stratigraphy of the fossil Chironomidae (Diptera) from Lake Grasmere, South Island, New Zealand, during the last 6000 years. *Hydrobiologia* 214: 213–221.
- Scheffer M. 1998. *The Ecology of Shallow Lakes*. Chapman and Hall, London, 357 pp.
- Schmid P.E. 1993. A key to the larval Chironomidae and their instars from Austrian Danube region streams and rivers with particular reference to a numerical taxonomic approach. Part I. Diamesinae, Prodiamesinae and Orthoclaudiinae, Wasser und Abwasser Suppl. 3/93: 1–514.
- Serra-Tosio B. 1978. Les Diptères chironomidés du Lac de Mont Coua (Parc National de la Vanoise). *Travaux Scientifiques du Parc National de la Vanoise* 9: 141–145.
- Skjelkvale B.L. and Wright R.F. 1998. Mountain lakes; Sensitivity to acid deposition and global change. *Ambio* 27: 280–286.
- Smith M.J., Pellatt M.G., Walker I.R. and Mathewes R.W. 1998. Postglacial changes in chironomid communities and inferred climate near treeline at Mount Stoyoma, Cascade mountains, southwestern British Columbia, Canada. *J. Paleolim.* 20: 277–293.
- Spengler D. 1973. *Limnologische, hydrologische und morphologische Untersuchungen im Faulhorngebiet (Berner Oberland)*. PhD Diss., University of Bern, Bern, 155 pp.
- Steiner G. 1911. *Biologische Studien an Seen der Faulhornkette im Berner Oberland*. PhD Diss., University of Bern, Bern.
- ter Braak C.J.F. 1987. Ordination. In: Jongman R.H., ter Braak C.J.F. and van Tongeren O.F.R. (eds), *Data Analysis in Community and Landscape Ecology*. Pudoc, Wageningen, pp. 91–173.
- ter Braak C.J.F. and Prentice I.C. 1988. A theory of gradient analysis. *Adv. ecol. Res.* 18: 271–317.
- ter Braak C.J.F. and Smilauer P. 1998. *CANOCO Reference Manual and User's Guide to CANOCO for Windows*. Centre for Biometry Wageningen, Wageningen, 352 pp.
- Tinner W., Ammann B. and Germann P. 1996. Treeline fluctuations recorded for 12,500 years by soil profiles, pollen, and plant macrofossils in the Central Swiss Alps. *Arct. alp. Res.* 28: 131–147.
- Uutala A.J. 1990. *Chaoborus* (Diptera: Chaoboridae) mandibles – paleolimnological indicators of the historical status of fish populations of acid sensitive lakes. *J. Paleolim.* 4: 139–152.
- Wagner R. 1997. Diptera, Thaumaleidae. In: Nilsson A.N. (ed.), *Aquatic Insects of Northern Europe, Volume 2*. Apollo Books, Stenstrup DK, pp. 187–191.
- Walker I.R. 1987. Chironomidae (Diptera) in paleolimnology. *Quat. Sci. Rev.* 6: 29–40.
- Walker I.R. 1995. Chironomids as indicators of past environmental change. In: Armitage P.D., Cranston P.S. and Pinder L.C.V. (eds), *The Chironomidae*. Chapman and Hall, London, pp. 405–422.
- Walker I.R. and Mathewes R.W. 1989a. Chironomidae (Diptera) remains in surficial lake sediments from the Canadian Cordillera: analysis of the fauna across an altitudinal gradient. *J. Paleolim.* 2: 61–80.
- Walker I.R. and Mathewes R.W. 1989b. Early postglacial chironomid succession in southwestern British Columbia, Canada, and its paleoenvironmental significance. *J. Paleolim.* 2: 1–14.
- Walker I.R., Mott R.J. and Smol J.P. 1991a. Allerød-Younger Dryas lake temperatures from midge fossils in Atlantic Canada. *Science* 253: 1010–1012.
- Walker I.R., Levesque A.J., Cwynar L.C. and Lotter A.F. 1997. An expanded surface-water paleotemperature inference model for use with fossil midges from eastern Canada. *J. Paleolim.* 18: 165–178.
- Walker I.R., Smol J.P., Engstrom D.R. and Birks H.J.B. 1991b. An assessment of Chironomidae as quantitative indicators of past climatic change. *Can. J. Fish. aquat. Sci.* 48: 975–987.
- Warwick W.F. 1980. Paleolimnology of the Bay of Quinte, Lake Ontario: 2800 years of cultural influence. *Can. Bull. Fish. aquat. Sci.* 206: 1–117.

- Wathne B.M., Patrick S.T., Monteith D. and Barth H. 1995. AL:PE – Acidification of Mountain Lakes: Palaeolimnology and Ecology. AL:PE 1 report for the period April 1991–April 1993. Ecosystem Research Report, Volume 9, European Commission, Directorate-General for Science, Research and Development, Luxembourg, 296 pp.
- Welch H. 1991. Comparison between lakes and seas during the Arctic winter. *Arct. alp. Res.* 23: 11–23.
- Wick L. and Tinner W. 1997. Vegetation changes and timberline fluctuations in the Central Alps as indicators of Holocene climate fluctuations. *Arct. alp. Res.* 29: 445–458.
- Wick L., van Leeuwen J.F.N., van der Knaap W.O. and Lotter A.F. 2003. Holocene vegetation development in the catchment of Sägistalsee (1935 m asl), a small lake in the Swiss Alps. *J. Paleolim.* 30: 261–272.
- Wiederholm T. 1981. Associations of lake-living Chironomidae. *Schweiz. Z. Hydrol.* 43: 140–150.
- Wiederholm T. (ed.) 1983. Chironomidae of the Holarctic region. Keys and diagnoses. Part I. Larvae. *Ent. scand. Suppl.* 19: 1–457.
- Wiederholm T. 1984. Responses of aquatic insects to environmental pollution. In: Resh V.H. and Rosenberg D.M. (eds), *The Ecology of Aquatic Insects*. Praeger Publishers, New York, pp. 508–557.
- Wiederholm T. (ed.) 1989. Chironomidae of the Holarctic region. Keys and diagnoses. Part III. Adult males. *Ent. scand. Suppl.* 34: 1–532.

