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provide very strong material for statistical analysis. These two samples represent about one third (6.1–9.0°C) of the full temperature range in the study (from 6.1 to 15.4°C).

One odd parameter (DBT = distance beyond *tree-line* in km) is found in Table 1 (Olander *et al.*, 1999). Lakes 24 and 25 should be 81 and 84 km beyond the tree-line, but there are no large tundra areas in Finland which could be so far from the *forest limit*.

Olander *et al.* (1999) have also measured the pH values of the waters. We must remember that acidity varies in natural waters following the water temperature, and depends on the time of snowmelt, for example. The full range of annual pH variation should be known before we can determine whether it has any effect on the organisms and how this knowledge can be applied in palaeoclimatic reconstructions. A momentary pH measurement provides no indication of the year-round variations of lake acidity. Furthermore the organisms live in the water all year, but which conditions are the critical determinants?

Ice cover

The lakes on the high fells remain ice-covered often long into spring, but this does not necessarily mean that the air temperatures there are lower in winter. The ice cover on these lakes only becomes thicker because wind drifts insulating snow off the ice surface. In spring, more solar energy is needed to melt the thick lake ice. Ice thickness in this environment can be more than 1 m. This surely has an effect on the light requirements and living conditions of the aquatic organisms. Changes in lake-ice thickness need not reflect changes in air temperatures but may be controlled by snow depth and/or wind conditions. Some of the lakes do not become ice-free before the beginning of July. Therefore one may ask why should the occurrences of chironomid taxa be correlated with July mean temperatures if the most suitable living period might be August, even though the July air temperature is the highest. When modelling the living conditions of cladocera or chironomids, these types of factors should be considered. 'The primary climate effect on the aquatic biota of high-altitude lakes may be mediated by the timing of the ice cover' as Livingstone *et al.* (1999) warned.

The goal of Olander *et al.*'s (1999) study was really ambitious. 'Particular attention was paid to assessing the power of lakewater temperature in explaining the variance in the chironomid data, as the primary aim is to develop a chironomid-based calibration function for palaeotemperature reconstructions' (p. 284). It contains much new information on the chironomid taxa in subarctic waters in Lapland, but unfortunately the data used fail to provide a satisfactory basis for the statistical analyses. The conclusions drawn from these statistical evaluations are built on very weak foundations and are thus unreliable and probably misleading.

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Chironomids, temperature and numerical models: a reply to Seppälä

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Abstract: We reply to comments by Seppälä (2001) concerning the suitability of the surface-water temperature measurements and mean July air temperature estimates used by Olander *et al.* (1999) to derive quantitative chironomid-temperature transfer functions. We use new data for water temperatures based on two-hourly recordings from thermistors installed in 32 lakes and air-temperature data from an automatic weather station at one lake to refute Seppälä's accusations that our field data are unsatisfactory. We also respond to Seppälä's suggestions about factors influencing chironomid distribution and abundance and suggest that there is a serious confusion of temporal and spatial scales between Seppälä's ideas and the Olander *et al.* study. We attempt to explain the underlying logic behind empirical transfer functions that form a major part of Holocene quantitative environmental reconstructions and the major assumptions behind such transfer functions as Seppälä appears not to understand the basis or the assumptions of such widely used numerical models in palaeolimnology. We respond to Seppälä's comments that lakewater pH and distance beyond tree-line have been inadequately measured and answer his erroneous understanding that a helicopter was used to facilitate lake sampling. We briefly consider Seppälä's suggestion that a helicopter can totally mix the surface water of a lake for many hours.

Key words: Chironomidae, calibration modelling, transfer functions, summer temperature, palaeotemperatures, field measurements, northern Fennoscandia.

Introduction

Seppälä (2001) has raised several points with respect to our conclusions (Olander *et al.*, 1999) about the importance of temperature in controlling the distribution and abundance of chironomids in waters of northern Fennoscandia and hence about the use of fossil midges as indicators of climate change. He particularly criticizes the way in which water temperature and some other explanatory variables used in our study were measured and argues that the quality of these measurements or estimates is not good enough for numerical modelling. Our detailed responses follow.

Seppälä has correctly drawn attention to an extremely important aspect of all quantitative environmental reconstructions, namely the quality of the environmental data. It is well known that a great proportion of the unexplained variance ($1-r^2$) in calibration models results from errors related to the measurement of the modern environmental variable (Birks, 1998; Olander *et al.*, 1999). These errors set the upper limit of the variance that it is possible to model. Although there currently exist many robust numerical approaches and modelling techniques that can be applied to the difficult task of quantitative environmental reconstruction (Birks, 1995;

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1998; Vasko *et al*., 2000; Toivonen *et al.,* 2001), none will perform reliably if the original environmental and/or biological data are poor and heterogeneous. The limitations and constraints set by the quality of environmental data must therefore be considered seriously – and we are fully aware of this. For example, the review on numerical techniques in palaeolimnology by Birks (1998) strongly emphasizes the urgent need to improve the quality, reliability and representativeness of environmental data in calibration data sets.

Against this background we would have expected Seppälä to introduce some new aspects into the discussion and to provide comments and criticisms that might help palaeolimnologists improve their data in the future. Unfortunately, this is not the case. We and several colleagues are unable to find much sound scientific criticism or logical arguments in his comments, let alone suggestions as how to do things alternatively. Instead, he seems to shoot at almost everything that moves and does this by weak arguments, superficial reading of our and related papers, and out-of-context quotes, apparently with little knowledge or understanding of the numerical calibration procedures, regional limnology or biological indicators he is criticizing.

The comments by Seppälä, in our view, contain errors, unsubstantiated concerns, misunderstandings and a general mistrust of the numerical treatments we use. Most of the arguments he sets up are not relevant to the kind of analysis that we performed and seem to be based on a failure to understand the purpose of our study. We think that the most serious error of Seppälä's comments is his lack of appreciation of the importance of the different scales that operate in nature and that dictate our sampling strategies and numerical analyses. He repeatedly speaks about single cases and short-term variation, although these bear little relevance to our study, as we are dealing with large data sets, long environmental gradients and a clear concern for long-term changes.

In fact, many of his comments remind us of the debate that was held 10–15 years ago about the original use of chironomids to reconstruct water temperatures. The difference is that the opposing arguments in the original discussion were expressed in a clear and logical way (e.g., Warner and Hann, 1987; Walker and Mathewes, 1987; Hann *et al.,* 1992; Walker *et al.,* 1992). We recommend readers to read these references, as most of the issues raised by Seppälä have already been widely discussed in the international literature over 10 years ago. The methods and approaches we are using have since become standard in palaeolimnological studies involving chironomids. This does not mean that there is no need for improvement (Brooks and Birks, 2001). Nevertheless, since the initial debate in the 1980/90s the importance of temperature for the distribution, abundance, survival and composition of chironomid assemblages has now been widely accepted by palaeolimnologists (see Battarbee, 2000, and references therein). For example, Brooks and Birks (2000a) show the close parallelism between lateglacial chironomid-based July air-temperature reconstructions for a site in Scotland and the GRIP oxygen-isotope record. They argue that this close parallelism shows 'the potential of fossil chironomid assemblages and associated modern calibration functions to derive fine-resolution quantitative palaeoclimatic reconstructions'.

We structure our replies to Seppälä's comments and accusations of unsatisfactory field data and unsound practices in six parts: chironomid distributions and abundances; water-temperature measurements; air-temperature estimation; 'statistical evaluations'; model evaluations; and measurements of other environmental variables including pH and ice cover.

Chironomid distributions and abundances

Limiting factors

Seppälä criticizes us on the grounds that we do not take into account all possible environmental aspects that might affect chironomids in our study sites. Before going into detail, it is important to note that Olander *et al.* (1999) represents an extension to the study of Olander *et al.* (1997), in which the environmental control and temperature-dependence of chironomids in the lakes of northern Fennoscandia were established and discussed. The aim of our 1999 paper was to look for a statistical relationship with variables of palaeolimnological interest and not to discuss in detail the relationships of chironomids to other environmental factors. However, we are fully aware that there is a whole range of environmental factors – physical, chemical and biological – that influence chironomid composition and distribution patterns in addition to temperature (Olander *et al*., 1997; 1999; Korhola *et al.,* 2000a; Brooks and Birks, 2000b; 2001). Nowhere do we state that temperatures are 'the only limiting factors of life' as claimed by Seppälä, but, rather, we explicitly write that 'the current data set has large secondary gradients … presumably reflecting variation in the chironomid assemblages that is unrelated to the measured water or air temperatures' (p. 292). In Olander *et al.* (1997) we reported on the basis of statistical tests that: 'The total variance explained by the environmental variables selected for the current study is rather low, indicating that there must be some other unmeasured factors which affect the species distributions.'

We tried to consider as many critically considered explanatory variables as possible in our analysis in order to understand better the relationships between chironomid assemblages and their modern environments. This meant the inclusion of a total of 26 measured physical and chemical variables in our data set; all these variables can be recognized as potential direct or indirect determinants of chironomid distribution and abundance. In addition to the environmental variables considered in our study, it has been proposed that chironomid composition may depend on, among other things, phytoplankton biovolume, total P, total SO_4^{2-}, pH, hypolimnetic oxygen availability and water turbidity (e.g., Henrikson *et al.,* 1982; Warner and Hann, 1987; Johnson and Wiederholm, 1989; Quinlan *et al.,* 1998). Availability and quality of food are also unmeasured variables that may account for an additional proportion of the observed variance in the chironomid data. However, some of these variables are very difficult to determine for our waters due to very low concentrations (most nutrients) or are impossible to assess for a large number of sites (food availability). In any case, in Olander *et al.* (1999) there was an explicitly stated emphasis on temperature in order to see how effective it is in explaining, in a statistical sense, the distribution and abundance of modern chironomid head-capsule assemblages.

Seppälä also accuses us of not taking into account 'other climatic factors which are partly independent of temperature, including wind, precipitation, snow and ice conditions, etc.' By saying 'partly', he implies that these variables are related, in part, to temperature. In general, temperature is known to be a variable that is highly correlated with several climatic and climate-related factors such as annual degree-days, duration of ice cover, length of growing season, etc. (Shuter *et al.,* 1983). As Birks *et al.* (1990) and Birks (1995) state, one of the basic assumptions of all quantitative calibration work involving transfer functions is that: 'The environmental variable to be reconstructed is, or is linearly related to, an ecologically important variable in the system of interest.' Because direct gradient analyses demonstrate that chironomid distributions and abundances in our study lakes are strongly and significantly correlated with air and water temperatures, we conclude that it is statistically and ecologically reasonable to attempt to model and to quantify these relationships.

We emphasize that our study was on chironomids, not on algae, cladocerans, 'organisms' or the 'life' that Seppälä refers to in his comment. He lists some factors that might control 'the living conditions of organisms', such as acidity, precipitation and snow and ice conditions. We would be the first to admit that we do not know the factors that control life on Earth, but we have tried to find out what variables might determine the observed chironomid faunal patterns in our study area. Although the factors mentioned by Seppälä are certainly of importance for some groups, it is questionable whether they play any critical role for chironomids in our research area.

Seppälä does not know 'any organism which survives only within a certain limited temperature range with an accuracy of 0.1°C'. Neither do we. The estimated tolerances for the chironomid taxa are commonly several degrees C, yet the reporting to one decimal place is based on statistical modelling involving a large number of observations using either weighted averaging or maximum likelihood estimation of the tolerance ('one standard deviation' of a Gaussian species-environment response curve – see ter Braak and Looman, 1986, and Birks *et al*., 1990, for theoretical and mathematical details).

The role of extremes

According to Seppälä, 'for the survival of the living organisms, extremes are often much more important than the mean values'. We agree that extremes may be important in causing short-term local population changes; but the taxon will soon recolonize a site if suitable conditions return the following year, or even after a few years. However, we are interested in much more long-term changes, typically lasting decades or centuries, for which 'mean values' and climatic trends are more important in determining the distribution and abundance of populations than annual extremes. Because our ultimate aim is to apply our chironomid models to reconstruct Holocene climatic changes – which have involved shifts in atmospheric and oceanic circulation patterns over millennial or centennial scales – our focus is not on fine-scale processes.

Seppälä mentions a short period of coldness and drought as examples of extreme events. Although drought may be an important ecological factor to be considered in the case of small, shallow water bodies, it is difficult to imagine it playing a role in our study sites, which are all large, permanent lakes that do not dry up. Regarding coldness, it would be interesting if Seppälä could give examples of his findings about 'a short period of coldness' that has destroyed a whole chironomid population. Seppälä's comments about Holocene water-level fluctuations are largely irrelevant in the context of our study, as we were only dealing with modern surface-sediment chironomid assemblages in Olander *et al.* (1999).

Water-temperature measurements

We agree with Seppälä that spot measurements of water temperatures are not the optimal way of obtaining data on lake thermal environments. It is exactly because of this that we added air temperatures to our data set because air temperatures can be estimated with a higher reliability for our study area. We did not attempt to use surface-water temperature measurements to 'draw conclusions about past air temperatures' as suggested by Seppälä. Water and air temperature data represent two independent data sets in our analysis; we only demonstrated that there is a close correlation between our measured water and estimated air temperatures in our study region. This correlation is also evident from previous studies which are referred to in our paper (Kuusisto, 1981; *Atlas of Finland*, 1986).

We did not use a helicopter in Olander *et al.* (1999) to obtain water temperatures. Seppälä's comment that 'I understand that their lake-surface water-temperature measurements were determined at the same time as the bottom-sediment samples were collected using a helicopter' is amazing. First, bottom sediment samples were collected with a Limnos-type gravity corer, not with a helicopter, and the coring was done from an inflatable boat. Second, water samples were collected from the central part of each lake from 1 m depth using a Limnos-type water sampler operated from an inflatable boat. Third, water temperature, pH and conductivity were then measured on these water samples in the field. All these details are given in Olander *et al.* (1997), as referred to in Olander *et al.* (1999).

Even though all sampling was done from the side of a small inflatable boat, Seppälä proposes that 'the surface water of a lake is totally mixed for hours afterwards' by the turbulence and air currents created by a helicopter and that 'water temperature measured beneath the helicopter is unlikely therefore to correspond even with the natural surface-water temperature'. We wonder if Seppälä has calculated from physical limnological principles (Hutchinson, 1957), with assumptions about basin morphometry, water residence time and temperature profiles, how long a helicopter would have to hover above a lake of the size and depth sampled by us, so that 'the surface water is totally mixed for hours afterwards'? We are not physical limnologists but rough calculations suggest that the helicopter time required to disturb only *one* lake would certainly be beyond the fuel-carrying capacity of any modern helicopter, and way beyond the research budget of any environmental scientist. The helicopter time and cost for 53 lakes would be astronomic! Moreover, as most (79%) of our study lakes are isothermal and well mixed in any case (Korhola *et al*., 2001), any additional mechanical mixing of the water, even if it were physically possible to induce this by a helicopter in a reasonable time, would have no significant influence on the temperature readings.

In fact, determining lake surface-water temperatures (LSWTs) within a short time interval using a helicopter to visit each lake would seem to be an adequate means of obtaining data on lake thermal gradients for a large set of lakes. We measured LSWT from 38 lakes in northwestern Finnish Lapland within two days in mid-July 1998 using a helicopter (Korhola *et al.,* 2000b). We then installed, as part of the EU-funded project EMERGE, miniature thermistors with integrated data loggers in 32 of these lakes to record LSWTs and to measure water-temperature profiles across an altitudinal gradient and under different topographical conditions. The sampling interval for the mini-thermistors was set to two hours and the data were downloaded for the first time in autumn 2000, so that the entire open-water period in 2000 was covered by continuous measurements (note that four of the thermistors were lost). We found a very high positive correlation ($r = 0.98$, $p < 0.001$, $n = 28$; Figure 2A) between the LSWTs obtained by single measurements in 1998 and the mean July water temperature calculated on the basis of the continuous water-temperature measurements by the data loggers. In addition, a strong, statistically significant relationship ($r = 0.63$, $p < 0.05$, $n = 21$; Figure 2B) was also found between the thermistor data and the spot LSWT measurements that we used in Olander *et al.* (1999), although the latter represented a much longer sampling interval (2.5 weeks in 1995) than in the case of the measurements made on the helicopter visits in 1998. These results suggest that even single LSWT measurements may reflect the mean LSWT quite well in an area where the temperature gradient is relatively stable, as seems to be the case in this area of Finnish Lapland.

We do agree with Seppälä that single temperature measurements are not the mean temperature, *sensu stricto*. However, we do not call our measured water-temperature readings 'mean values' anywhere in the text ('water temperature' or 'measured water temperature' is mentioned over 70 times in the text), except in the abstract, where we discuss the overall water-temperature gradient of the study lakes. As our measured water temperature gradient closely agrees with the longer-term July water-temperature means (1961–75) provided by the *Atlas of Finland* (1986) for the study area, we feel that we are not guilty of Seppälä's accusation of regarding 'one temperature measurement as a monthly mean'.

Nowhere did we state that our field measurements of LSWTs represent mean July *air* temperatures, as claimed by Seppälä. The site-specific mean July air temperatures used in our study are not dependent at all on our water-temperature measurements, but were independently calculated from 30 years of recorded observations (see below). Seppälä continually mixes up these two independent data sets of water- and air-temperature data.

Seppälä shows data on water and air temperatures that he and his colleagues measured at a 'small seasonally dry pond' (60 m diameter) in the Kilpisjärvi region. These data are not a revelation. All limnologists are aware of the great daily and even hourly variation of LSWTs particularly in small-volume water bodies, and we do not dispute that a single water-temperature measurement is not ideal. Nevertheless, the fact that we have repeatedly found exactly the same ranking of lakes according to their water temperatures during different field samplings and that there is a significant correlation between our spot LSWT measurements and the interpolated site-specific air temperatures and long-term averages of epilimnetic water temperatures (our thermistor measurements and the mean values as indicated in *Atlas of Finland*, 1986) all suggest that the field spot measurements of LSWTs are not accidental but reflect the longer-term thermal gradient of lakes in our study area (see Weckström *et al.,* 1997a; 1997b). It is therefore not surprising that a quantitative relationship between midge composition and abundances and water temperature can be found and modelled.

Although interesting *per se*, the temperature record reported by Seppälä from his study pond has little to do with the data we have collected, as there is not a single 'seasonally dry' pond in our data set. Our study sites are all permanent water bodies and they are also much larger (median 8.4 ha; range 0.9–115.2 ha) than the pond studied by Seppälä. The lakes we are studying can, therefore, be expected to exhibit less variation in their thermal features than in a 60 m diameter, seasonally dry pond (Hutchinson, 1957), which is confirmed by the records of LSWTs from the thermistors (Figure 3). (In Seppälä's text, the mean July bottom-water temperature in his study pond is reported to vary between 9.7°C and 22.3°C, whereas in his Figure 1 a range from 8.9°C to 22.3°C is given.

According to Seppälä, the concept that 'air temperature is closely related to lakewater temperature, especially in the summer' provides the basis for our study. Where do we state anything like this? This quote from Livingstone and Lotter (1998) relates to our discussion (Olander *et al*., 1999: p. 291) about the potential importance of air versus water temperatures for chironomids during the different stages of their life cycle (see also Brooks and Birks, 2000b; 2001).

The fact that there were only few lakes with very cold waters in our data set is no secret; we show the frequency distributions of water and air temperature for the 53 sampled lakes in our paper (Figure 2 in Olander *et al.,* 1999) and clearly state that: 'There are few lakes with surface-water temperatures below 9°C and there is a gap between the interval 11–12°C, whereas the interval 12–13°C is overrepresented.' However, we also state that: 'The air temperatures are not significantly skewed, in contrast to the surface-water temperatures.' Finally, we conclude: 'It is therefore necessary to expand the geographical and temperature ranges of our data set, particularly at the low temperature end of the gradient, in an attempt to overcome these problems.' In response to this, we have expanded the data set further with 10 new sites from the colder end of the climate gradient (Vasko *et al.,* 2000).

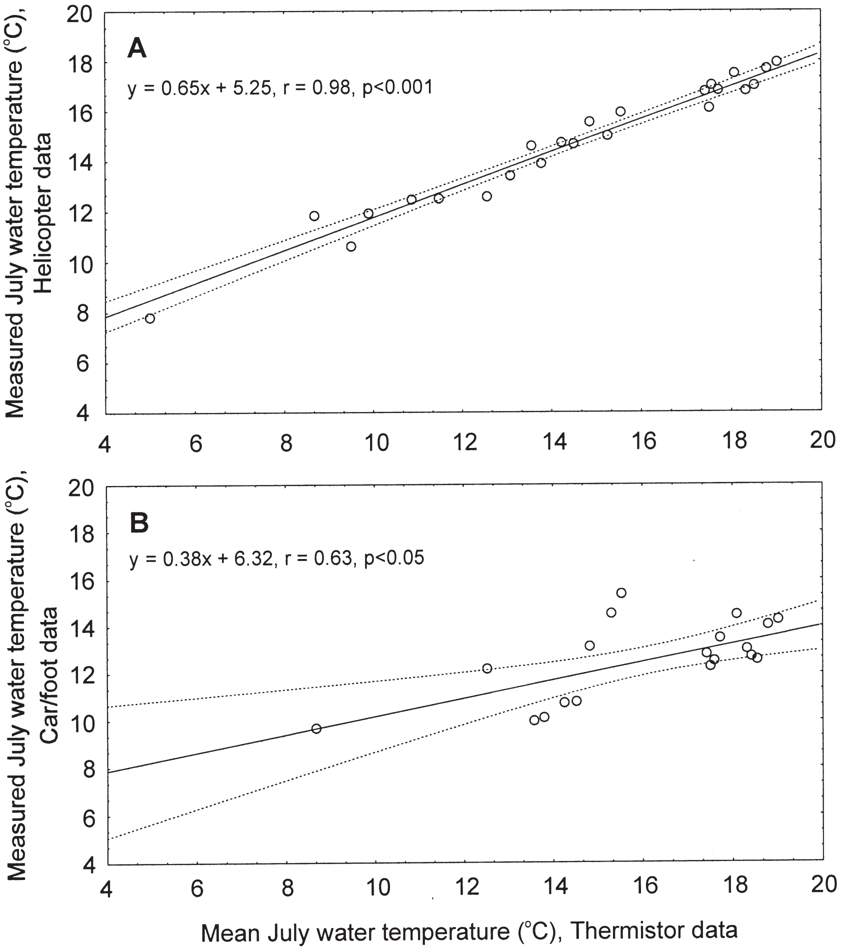

Figure 2 Relationship of single July lake-surface water-temperature readings to mean July water temperature in lakes in northern Fennoscandia. The spot water-temperature measurements refer to helicopter visits to the lakes in July 1998 (A) or car/foot visits to the sites in July 1996 (B). Mean July water temperatures were obtained from miniature thermistors with integrated data loggers in summer 2000. Twenty-one of the lakes with thermistors were the same as in Olander *et al.* (1999).

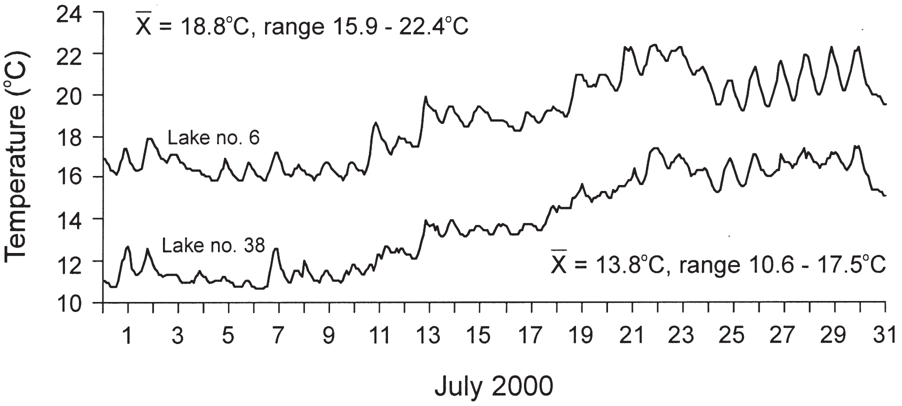

Figure 3 Surface-water temperatures of two lakes from Olander *et al.* (1999) in July 2000. Lake 6 has a surface area of 1.5 ha and is located at 252 m a.s.l.; lake 38 has an area of 45.3 at an altitude of 551 m a.s.l. Measurements were made at two-hour intervals using miniature thermistors with integrated data loggers.

Air-temperature estimation

Seppälä doubts our site-specific air-temperature estimates because the meteorological stations supplying the data on which the estimates are based are often located far from the lakes sampled and at different elevations. In addition, the meteorological stations are not necessarily exposed to the weather in the same way as the lakes. However, as shown by Livingstone and Lotter (1998) and Livingstone *et al.* (1999), even in the extremely mountainous Swiss Alpine region, air temperatures in summer are extremely highly correlated over large distances both horizontally and vertically, so that even in shaded locations air temperatures differ very little from values computed assuming a simple linear decrease with altitude. In addition, is it not exactly the differential location of the climate stations in the landscape and their altitudinal position that allow linear interpolations to be made and regional lapse rates to be estimated? If all stations were located at the same elevation and in the same environmental position, no conclusions about the effects of altitude on temperatures could be drawn.

Seppälä states that air temperature is not linearly correlated with altitude in mountainous regions. This is certainly true in winter, when temperature inversions are common. However, in summer, which is the period specifically dealt with by Olander *et al.* (1999), inversions in mountainous regions are rare, so that surface air temperature is in fact very highly correlated with altitude (e.g., Barry, 1992). This is known to be the case in general, but we also have data that show it to be the case specifically in our study area in Finnish Lapland (which can hardly be considered a 'mountainous region'). In August 1996 we installed an automatic weather station at 682.5 m a.s.l. on the shore of Saanajärvi (lake 24 in Olander *et al.,* 1999). A comparison of the air temperatures measured at our station with air temperatures measured at the nearby Mt Saana meteorological station, located 1.5 km southwest of the lake at 1050 m a.s.l., allowed the monthly frequency of inversions to be determined for 12 of the 15 months from August 1996 to October 1997 (Table 1). From December 1996 to April 1997, the computed lapse rates were substantially lower than the environmental lapse rate of 6 $K \cdot km^{-1}$ (Barry, 1992), suggesting that temperature inversions are common during the colder part of the year. During the warmer part of the year, however, inversions are much less common, and are completely absent in most summer months. Our data therefore suggest that temperature inversions in Finnish Lapland are typically a winter phenomenon and are likely to have little or no effect on the 30-year averaged July air-temperature data that we used to estimate site-specific mean July air temperatures in our study. The situation in the Swiss Alps is similar, with almost no inversions in the summer months and inversions only becoming a problem from September onwards (Livingstone *et al.*, 1999).

The suggestion by Seppälä that chironomid assemblages could have been correlated with the altitude of the lakes instead of with air or water temperatures is illogical within the context of our study, which was aimed specifically at the development of a chironomid-temperature calibration model for quantitative environmental reconstruction. By making this suggestion, Seppälä implies that he is either unable or unwilling to understand what we have actually done in our investigation, and what the purposes of transfer functions and calibration models are. Let us make it clear once again: the water temperatures in our study are based solely on field measurements and have nothing whatsoever to do with altitudinal corrections; our measured surface-water temperatures and our estimated air temperatures are two independent data sets derived in two totally different ways (see Figures 3, 7 and 8 in Olander *et al*., 1999). We did not use our surface-water temperature measurements to 'draw conclusions about past air temperatures'; and we did not 'transfer surface water temperatures to corresponding air temperatures'.

'Statistical evaluations'

It is unclear to us what Seppälä is trying to say with his demand that one should only include 'numbers representing quantitative characteristics of similar objects' in 'statistical evaluations'. He further seems to be saying that one cannot use data from different lakes to draw ecological conclusions about the organisms that inhabit them. One gets the impression that Seppälä is expecting an unbelievable conformity from nature that would make scientific research meaningless. What would be the need for measurement, statistical analyses, classification and overall scientific problem-solving if we could only consider systems that are alike?

Seppälä has found from our data an example of an 'anomaly' in which two neighbouring lakes (24 and 25) have different characteristics in terms of their water and air temperatures, but he fails to indicate the relevance of this observation to the questions under discussion. If his conclusion is that we should not try to 'transfer surface water temperatures to corresponding air temperatures' our response is easy: nobody is trying to do this. For us the example highlights the need of using both water and air temperatures as independent variables when examining chironomid distributions and abundances, as we did in Olander *et al.* (1999).

Table 1 Lapse rates of monthly mean surface air temperatures at Saanajärvi (1996–97), computed from the air temperatures measured at the Saanajärvi automatic weather station and those measured at the nearby Mt Saana meteorological station. The percentage of days with temperature inversions is also listed

Month	Lapse rate ($K \cdot km^{-1}$)	Percentage of days with inversions
August 1996	5.38	0
December 1996	0.91	23
January 1997	3.84	13
February 1997	3.48	21
March 1997	2.99	16
April 1997	2.82	20
May 1997	5.11	0
June 1997	3.07	17
July 1997	4.81	3
August 1997	6.73	0
September 1997	6.87	0
October 1997	6.56	0

Model evaluations

Despite Seppälä terming the quantitative analyses of Olander *et al*. (1999) 'statistical analyses', the analyses are not strictly statistical as no *a priori* hypothesis or probability values are being tested or assessed. Exceptions are the species-response modelling using generalized linear models (p. 284), the correlation between measured water temperature and calculated mean July air temperature (p. 281) and the variance partitioning and single variable canonical ordinations (p. 288). The bulk of the quantitative analyses (pp. 285, 289–92) concerns the derivation of chironomid-surface-water and chironomid-air-temperature calibration or transfer functions or inference models. This is numerical modelling and parameter estimation (e.g., taxon optima and tolerances) with no hypothesis testing or probability statements. The sole aim is to develop, by inverse regression, empirical predictive models for surface-water temperatures in relation to modern chironomid assemblages and for mean July air temperatures in relation to modern chironomid assemblages. The models should have a high predictive power as assessed by appropriate performance statistics, ideally estimated by some form of cross-validation (split sampling, leave-one-out, leave-*n*-out, etc.; see Birks, 1995; ter Braak, 1995).

Imbrie and Kipp (1971) presented the first organism-environment quantitative transfer function based on foraminifera and sea-surface temperatures, and this approach provided the basis for major international studies such as CLIMAP. Although there have been recent developments in the numerical procedures used (see reviews by Birks, 1995; 1998; ter Braak, 1995), general field methodology has remained very similar since Imbrie and Kipp's pioneering study. Many of Seppälä's comments about the quality of the environmental data used, about lack of ecological knowledge of the organisms considered and about ecological variables not considered can be applied to the other 900+ papers on quantitative transfer functions published in the last 30 years.

The estimation of transfer functions is primarily an empirical procedure with little rigorous underlying mathematical theory (except for the Gaussian and multinomial logit models; Birks, 1995; ter Braak, 1995). As it is not strictly statistical in terms of hypothesis testing, Seppälä's comment that 'I believe that statistical analyses require a reasonable number of observations that well represent the population' is not really relevant because we are not concerned with the concept of an underlying population of lakes and a representative subset or sample of lakes.

It has long been emphasized since Imbrie and Kipp (1971) that there are many mathematical and methodological problems in deriving empirical transfer functions. As Imbrie and Webb (1981) reiterated, 'if it were possible to derive transfer functions deductively from a process-orientated model based on ecological first principles, the predictive power of this model would be free of many of the problems encountered in its use. Given the current state of ecological theory, the empirical approach represents the only practical solution and we are, therefore, stuck with its limitations and have no choice but to confront the problems arising from its application.'

Ecological knowledge about the control of species distributions and abundances has not improved significantly in the 20 years since Imbrie and Webb (1981) commented on this deficiency. Of course, many ecological factors may be important, as Seppälä suggests, such as nutrients, acidity, competition, food availability, substrate and chance, but sadly we do not really know what determines the distribution and abundance of any organism, yet alone the 'limiting factors of life'. It is for this reason that the biological, environmental and mathematical assumptions behind empirical transfer functions have been clearly and repeatedly stated by, for example, Imbrie and Kipp (1971), Imbrie and Webb (1981), Birks *et al.* (1990) and Birks (1995).

Besides the obvious assumptions of any empirical linear or non-linear (inverse) regression model, the most critical assumption in this discussion is that the environmental variable being modelled (and subsequently reconstructed from fossil assemblages) is, or is linearly related to, an ecologically important determinant in the ecological system of interest. It therefore does not really matter if the inference model is based on mean July air temperature, mean August air temperature, mean summer temperature, annual 'growing' degree-days above 5°C, or duration of the ice-free period, because these are all linearly related to each other (e.g., Lotter *et al*., 1997; Livingstone, 1997) and, we assume, to the complex but unknown variable or set of interacting variables that actually determines the critical thermal budget for the life cycle and reproduction of chironomids.

Seppälä comments that unidentified Tanytarsini do 'not provide very strong material for statistical analysis'. This view contrasts with the findings of Walker *et al.* (1991) and Levesque *et al.* (1993) where the aggregate taxon Tanytarsini has been shown to carry considerable influence in inference models. All the evidence we have (Birks, 1994; Brooks and Birks, 2001) suggests that inference models will improve (as assessed by their performance statistics) as the taxonomy is better and better resolved. Ongoing work involving many chironomid palaeoecologists in Europe is continually improving the taxonomic resolution of chironomid head-capsules. The problem is that modern chironomid taxonomy is based on the adult phase whereas chironomid head-capsules preserved in lake sediments represent the larval stages of the life cycle. The taxonomic precision available for the adult stage is not always available for head-capsules.

Seppälä criticizes us for presenting the performance statistics of our 16 different inference models to three decimal places (Tables 8 and 9 in Olander *et al*., 1999), given the nature of the temperature data used in the models. This is a valid comment in relation to, for example, RMSE, RMSEP and r^2, but it is more difficult when considering the mean bias statistic (= systematic difference in the model predictions). Values for this statistic are usually very small, but as Vasko *et al*. (2000) have shown, it can be an important performance statistic in model evaluation. We believe it is always important to present mean and maximum bias as well as the widely presented RMSE(P) and r^2. For consistency in Tables 8 and 9 of Olander *et al.* (1999) we presented all the model performance statistics in the same way, namely with three decimal places. One decimal place is probably appropriate for RMSE(P), two for r^2 and maximum bias, and three for mean bias.

Seppälä proposes that 'it is much easier and quicker to make computer models without a real data base'. Although this is a commonly held view among non-quantitative scientists, it is not always true, as in this case. Soon after Olander *et al.* (1999) appeared, Steve Juggins discovered an error in the FORTRAN source code for subroutine CALIBB and the functions VARFUN and BERLIK called by CALIBB within the program WACALIB 3.3 (Line *et al*., 1994) used to implement the Gaussian logit models (GLM) in Olander *et al*. (1999). One of us (H.J.B.B.) immediately wrote a note (received 19 October 1999) to the *Journal of Paleolimnology* drawing attention to this error and presenting corrected values for all five sets of published results for GLM based on WACALIB, including the GLM results in Olander *et al*. (1999). The original incorrect and the later corrected GLM results are summarized in Table 2 (from Birks, 2001). Although WACALIB is 13 years old, the existence of a long-lived error in the source code for the maximization of the log-likelihood function summed for all taxa shows that it is not 'much easier and quicker to make computer models' when you also develop the mathematical methods and the relevant computer software yourself.

In his section on ice cover, Seppälä describes the goal of the Olander *et al.* (1999) study as 'really ambitious' and quotes us as saying that: 'Particular attention was paid to assessing the power of lakewater temperature.' This quote is from the middle of a paragraph on p. 284 of Olander *et al.* (1999) about the purposes of partitioning the variance in the chironomid data and how we implemented this variance decomposition. Seppälä's quote does not refer to the overall goal of Olander *et al.* (1999).

Measurements of other environmental variables including pH and ice cover

In contrast to what Seppälä states, the maximum lake depth in all our study sites was carefully located using a Humminbird LCR 400 ID portable echo sounder, as described in Olander *et al*. (1997). We do, however, agree with Seppälä that giving the lake depth to within 5 cm is too detailed; 0.5 m is probably more appropriate.

Seppälä calls our variable distance beyond tree-line (DBT) 'odd'. We are grateful to Seppälä for giving us an opportunity to provide a more detailed definition of this variable. With the term 'tree-line' we mean, in accordance with Seppä (1996: p. 9), 'the boundary between two major global biomes, namely the boreal coniferous forest and the arctic tundra'. Thus, DBT is measured as the closest straight-line distance of each lake to the continuous pine tree-limit, not mountain birch limit as presumably assumed by Seppälä. DBT was derived from 1:200 000 maps using the tree-line positions indicated in Hustich (1978). Distances measured north of the tree-line to tundra sites are recorded as positive values, whereas negative distance values are given to lakes situated south of the tree-line. The variable was included in our data set as a result of the study by Walker and MacDonald (1995), which demonstrated the potential importance of tree-line as an ecotonal boundary for aquatic insects.

Table 2 Root mean squared error (RMSE), coefficient of determination (r^2) between observed and estimated values of measured surface-water temperature (°C) and of mean July air temperature (°C), mean bias, and maximum bias and the related statistics (root mean squared error of prediction (RMSEP), r^2, mean bias, maximum bias) in leave-one-out cross-validation for the Olander *et al.* (1999) data set for Gaussian logit regression and maximum likelihood calibration

	Olander *et al.* (1999)	Corrected WACALIB 3.5
Surface-water temperature (°C)		
RMSE	1.5	1.2
r^2	0.40	0.63
Mean bias	0.000	0.001
Maximum bias	3.62	0.87
Leave-one-out cross-validation		
RMSEP	2.2	1.4
r^2	0.32	0.59
Mean bias	0.001	0.001
Maximum bias	3.94	1.28
Mean July air temperature (°C)		
RMSE	1.0	0.6
r^2	0.36	0.74
Mean bias	0.000	0.001
Maximum bias	1.88	0.49
Leave-one-out cross-validation		
RMSEP	1.4	1.1
r^2	0.34	0.69
Mean bias	–0.017	0.008
Maximum bias	2.90	1.02

Seppälä also casts doubts on our pH determinations, showing that he is not familiar with the chemical limnology of northern lakes. Our long-term monitoring records from several lakes in subarctic Fennoscandia clearly demonstrate that most water-chemistry variables, including pH, are extremely stable throughout the open-water period, except for the short-duration period during spring melt (Rautio, 1998; Blom *et al.,* 1998; 2000; MOLAR Water Chemistry Group, 1999; Sorvari *et al.,* 2000; Rautio *et al.,* 2000; Korhola *et al*., 2001; Catalan *et al.,* 2001). Based on results from the organisms most sensitive to pH, namely diatoms, the transient drop in pH during the spring melt does not affect the organisms (Korhola *et al.,* 1999).

The time of water-chemistry sampling is therefore not very critical in the case of northern clearwater lakes, which are well mixed throughout the open-water season, in contrast to boreal humic-water lakes that are characterized by a marked stagnation period. Each water sample we took consisted of four to six independent subsamples (volume of Limnos water sampler, 2.5 l). Such samples have been shown to represent well the mean water quality of the open-water area of a given lake (Ilmavirta, 1980).

We agree fully with Seppälä's suggestion (following Livingstone *et al*., 1999; Battarbee, 2000; and others) that the duration of lake ice cover or ice-free periods may be an important variable influencing aquatic biota in alpine and arctic lakes (see, for example, Birks *et al*., 2000; Lotter and Bigler, 2000). There are several projects currently under way attempting to estimate duration of ice cover for a large number of European lakes, to relate modern biotic assemblages to estimated duration of the ice-free period, to study modern limnological processes operative during ice cover and breakup, and to reconstruct past changes in ice cover from fossil assemblages. As with lakewater and site-specific air temperatures, a major problem is estimating lake ice-cover duration for lakes ranging from Svalbard to the Spanish Sierra Nevada, and east to the Alps and the Tatras.

Conclusions

We refute the accusations of Seppälä (2001) that the data Olander *et al.* (1999) used 'fail to provide a satisfactory basis for the statistical analyses' and that 'the conclusions drawn from these statistical evaluations are built on very weak foundations and are thus unreliable and probably misleading'. No field data are ever as satisfactory as one would like, just as 'all models are wrong; some, though, are more useful than others and we should seek these. At the same time we must recognize that eternal truth is not within our grasp' (McCullagh and Nelder, 1989). Olander *et al.* (1999) and other recent studies on chironomids in relation to air and/or water temperature in Scandinavia (e.g., Brooks and Birks, 2000a; 2000b; Birks *et al.*, 2000) have attempted to develop potentially useful models for the purpose for which they are designed, namely to reconstruct past temperatures from fossil chironomid assemblages. The results obtained speak for themselves.

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