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Long-term trends in the profundal chironomid-fauna in nitrogen-limited Lake Esrom, Denmark: a combined palaeolimnological/historical approach

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With 8 figures

Abstract: A 90-cm sediment core from Lake Esrom was analysed for subfossil diatoms and Chironomidae. Quantitative diatom-inferred reconstruction of total phosphorus showed an increase in TP levels from 84 µg P/l around 1600 AD (extrapolated ^{210}Pb chronology) to 200 µg P/l in 1975, followed by a decrease to 165 µg P/l at the present day. Chironomid-inferred chlorophyll-a concentration ranged from 5–15 µg chl-a/l throughout the core. Analysis of historical oxygen data and long-term zoobenthic population dynamics from the profundal zone of Lake Esrom suggested that the period of oxygen depletion in the hypolimnion increased during the 20th century. However, the chironomid record showed only minor variations in the subfossil assemblages over the last ~400 years and there was no chironomid indication of significant changes in the hypolimnetic (oxygen) conditions. Because primary production in Lake Esrom is nitrogen limited during the stratification period, the chlorophyll concentration is lower than commonly found for Danish lakes with comparable phosphorus concentrations. However, both the diatom-[TP] and chironomid-[chl-a] inferred values for recent periods agree well with monitored data. The two models work because the diatoms are reflecting the ([TP]) spring situation before nitrogen becomes the limiting factor whereas the chironomid fauna is reflecting the average summer (chlorophyll) situation both before and during the period of nitrogen limitation. This study illustrates the importance of multi-proxy analyses for quantitative palaeolimnological reconstruction of lake trophic state, particularly for lakes that behave differently from the more predictable responses to nutrient enrichment.

Key words: Subfossil diatoms, longterm zoobenthic population dynamics, hypolimnetic conditions, multi-proxy analyses.

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Introduction

Lake Esrom is one of a few Danish lakes that support a well-developed profundal fauna dominated by the non-biting midge *Chironomus anthracinus* ZETTERSTEDT and the oligochaete *Potamothrix hammoniensis* (MICHAELSEN). The lake has been subject to intensive macrobenthic research studies since the beginning of the 20th century (e.g. BERG 1938, WHITESIDE 1970, JÓNASSON 1972, HAMBURGER et al. 1994, LINDEGAARD et al. 1997). The monastery at the outlet in the northern end of the lake was founded in 1150, and the lake may have been influenced by human activity as early as the Early Middle Ages. It is reasonable to expect that an increased nutrient input from activity in the catchment area (see JÓNASSON 1977) has resulted in enhanced primary production followed by an increased decomposition and deteriorated oxygen conditions in the hypolimnion. Historical data suggest that during the 20th century the period of oxygen depletion in the profundal increased (JÓNASSON 1996). These data have lead to speculation that among Danish lakes, Lake Esrom if any, might have supported a more diverse and anoxia-intolerant benthic fauna in historic times before the development of modern agriculture and cultural influence in the catchment area (LINDEGAARD et al. 1997).

In this study we have used a palaeolimnological approach to address the following ecological questions. First, do changes in the subfossil chironomid assemblages indicate any deterioration in lake trophic state and profundal oxygen conditions over the last centuries? Second, can such changes, if any, be related to increased nutrient loading to the lake? The use of biological remains in lake monitoring, pollution assessment, trend detection and reconstruction of past-environmental conditions has several advantages (e.g. WALKER 1993, STOERMER & SMOL 1999). Analysis of subfossil assemblages (e.g. diatoms, chironomids) requires only small samples, few replicates and usually only one sampling point. Seasonal and intra-lake variation is low, time integration is good and the assemblage species richness is generally high (ANDERSON & BATTARBEE 1994, BRODERSEN & LINDEGAARD 1997). Quantitative models for inference of limnological parameters from subfossil remains have been developed for several taxonomic groups. In this study, we have used a diatom-based model for quantitative reconstruction of total phosphorus concentrations ([TP]) (BENNION et al. 1996), and a chironomid-based model for reconstruction of chlorophyll-a concentrations ([chl-a]) (BRODERSEN & LINDEGAARD 1999) in a 90-cm long sediment core from Lake Esrom, Denmark. We assess how the two models supplement each other with special reference to a lake where the primary production is **nitrogen limited**, as is the case with Lake Esrom (e.g. JÓNASSON 1996).

Study site

With a volume of 213×10^6 m^3, Lake Esrom is the largest freshwater lake in Denmark (Fig. 1). The lake area is 17.3 km^2 and the catchment area only 53 km^2. The lake is situated in a hilly landscape in North Zealand, glaciated during the Weichselian and is surrounded by forest and farmlands. The maximum and mean depth is 22 m and 12.3 m, respectively, and the area below 15 m covers 9 km^2 or 52 % of the lake area. The lake is eutrophic with mean summer total phosphorus and total nitrogen concentrations of 150 µg P/l and 650 µg N/l, respectively. Mean summer chlorophyll-a concentration is 8 µg chl-a/l and the mean Secchi depth is 3.5 m. Lake Esrom is thermally stratified for 3–6 months each year, during which there is almost anoxic conditions in the bottom water with oxygen concentrations <0.2 mg O_2/l for 2–3 months. Further comprehensive descriptions of the lake are given by BERG (1938) and JÓNASSON (1972, 1977, 1996).

Coring and dating

Five short profundal and littoral sediment cores were raised from a coring raft in August and September 1998. The sediment cores discussed in this study (BP 2 and BP 3) were taken using a 100 cm Mackereth corer (diameter 50 mm) at 22 m water depth (GPS coordinates: 56° 01′ 04.9″ N, 12° 23′ 16.5″ E; 56° 01′ 08.6″ N, 12° 23′ 16.5″ E) with an inter-site distance of 110 m. Both cores, showing visually uniform dark gyttja throughout, were extruded and cut into 1 cm (BP 2) or 2 cm (BP 3) slices in the laboratory. All samples were subjected to physical analysis of wet and dry density, loss-on-ignition and gravimetric $CaCO_3$. Stratigraphic profiles of physical variables matched closely between the cores and for inter-core correlation no correction of core depth was necessary. Samples from BP 2 were used for radionucleide dating and diatom analysis, while BP 3 samples were used for the analysis of chironomid remains. Analysis of ^{210}Pb, ^{226}Ra, ^{137}Cs and ^{241}Am was performed at the Environmental Radioactivity Research Centre, University of Liverpool, England using gamma ray techniques. The ^{210}Pb chronology, constrained by bomb / Chernobyl ^{137}Cs and ^{241}Am profiles, covers the upper 32 cm of core BP 2 and indicates a near constant accumulation rate between 1884 and the early 1960s after which it doubles over about a decade (Fig. 2). Assuming a constant accumulation rate below 24 cm the extrapolated chronology suggests a date of ~1600 for the bottom of core 2 (80 cm).

Methods

Diatom samples were analysed at 2-cm intervals over the length of the core and prepared using a standard H_2O_2 technique (RENBERG 1990). Mean annual epilimnetic TP concentrations were inferred from the diatom assemblages preserved in the sediment core using the NW European training set (BENNION et al. 1996). TP concentrations were inferred using a simple Weighted Averaging (WA) model as opposed to a 2-component WA-PLS model. The error statistics are slightly worse than that for the WA-

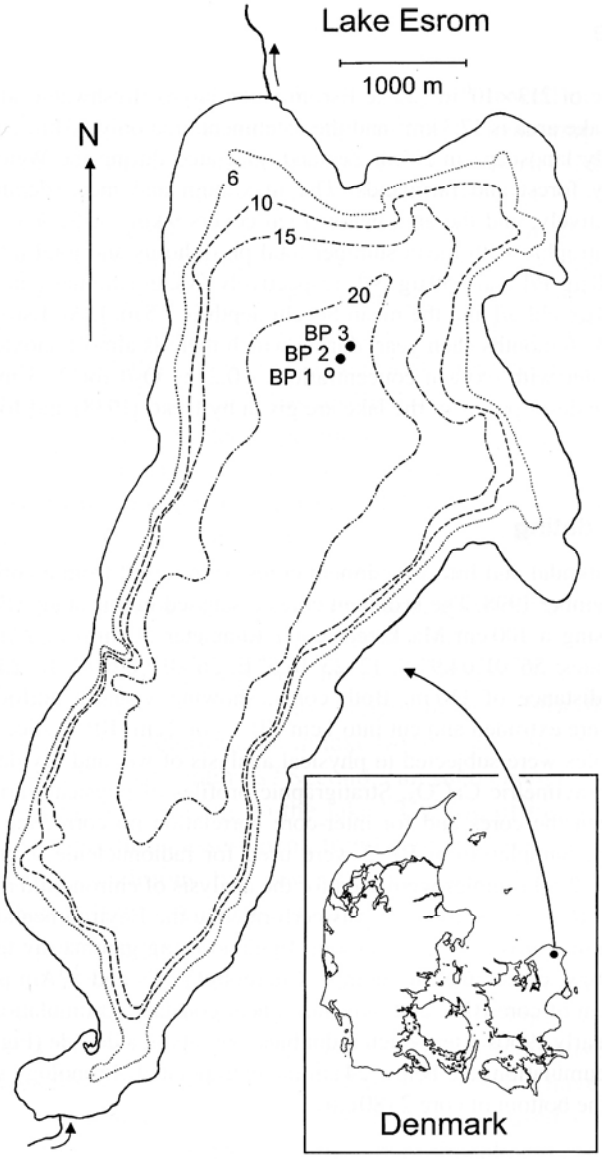

Fig. 1. Map of Lake Esrom showing the coring points BP 2 and BP 3 (GPS coordinates: 56° 01′ 04.9″ N, 12° 23′ 16.5″ E; 56° 01′ 08.6″ N, 12° 23′ 16.5″ E). The depth contours are in meters.

PLS model ($RMSE_{prediction} = 0.22$ compared to 0.21), but it is felt that there are fewer problems with "over-fitting" when the WA model is applied to sub-fossil assemblages. The NW European model works particularly well when applied to plankton-dominated systems, such as Lake Esrom, where the species present have well-defined TP optima.

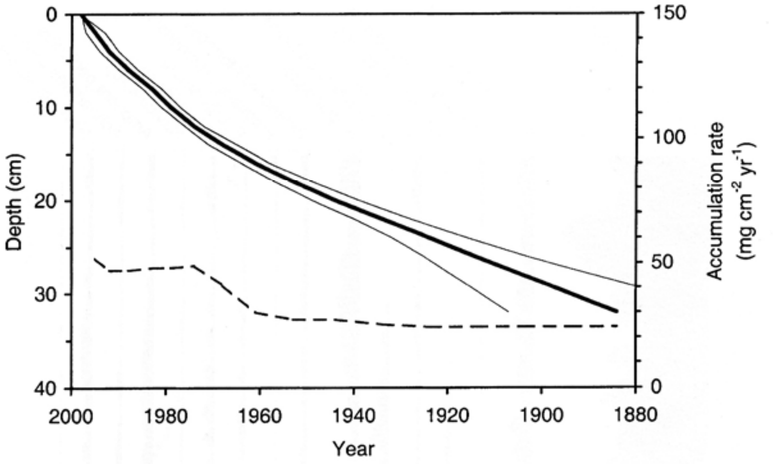

Fig. 2. Age–depth relationship (full line) and accumulation rate (broken line) of core BP 2 based on radionucleide chronology.

The sediment samples for chironomid analysis were treated in hot KOH and sieved through a 93 µm screen. The chironomid head capsules were sorted under a stereo microscope at 50× magnification. A minimum of 100 head capsules from each 5-cm level was sorted and mounted on microscope slides in Euparal®. The chironomid head capsules were identified mainly according to Hofmann (1971), Wiederholm (1983) and Moller Pillot (1984 a, 1984 b). The chaoborid mandibles were identified according to Sæther (1997). The results are given as the relative percentage species composition. Chironomid diversity parameters were calculated as the Shannon-diversity (*H′*) and evenness (Hill's *N2*). The application of diversity indices in palaeolimnology is somewhat problematical (Smol 1981), and the species richness (*S*) was calculated using rarefaction methods (*E*(*S*)) to adjust for differences in total chironomid count (Birks & Line 1992). Zonation of the chironomid stratigraphy using non-transformed and square root-transformed percentage data was performed using optimal splitting by information count in combination with a broken stick model (Bennett 1996) implemented in the software PSIMPOLL (Bennett 1994). Quantitative reconstruction of past [chl-a] was calculated using data from Brodersen & Lindegaard (1999).

Results

Diatoms

All diatom samples were dominated by centric, planktonic forms especially *Stephanodiscus parvus,* making up ~50 % of the total throughout the core but reaches a maximum (ca. 70 %) at 12 cm (Fig. 3). *Stephanodiscus neoastraea* is also present throughout while *Aulacoseira granulata* increases to >10 % above 35 cm depth. The diatom-inferred total phosphorus indicates an increase from

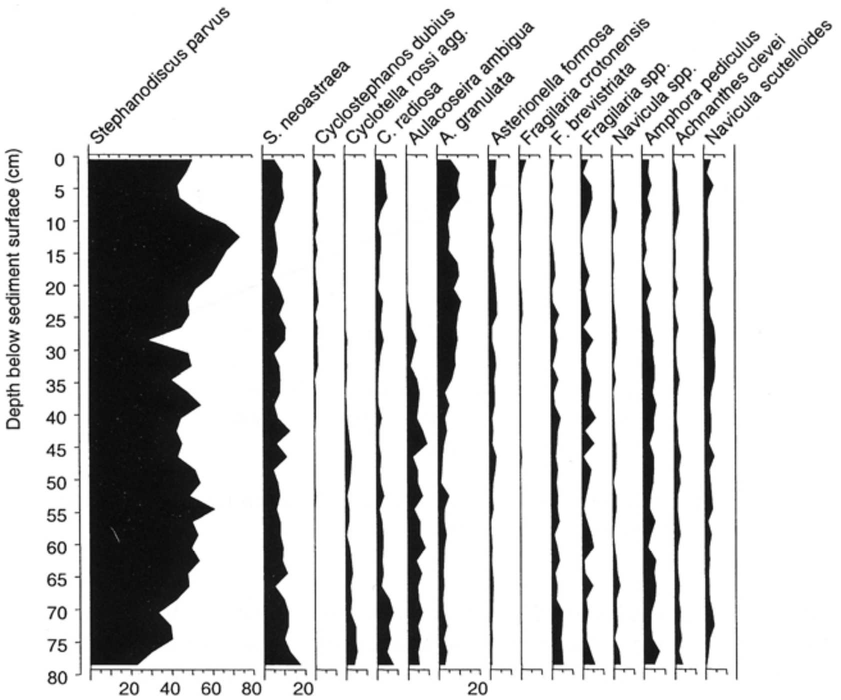

Fig. 3. Percentage diagram of the most common diatoms from the BP-2 core.

84 µg P/l at the bottom of the core to nearly 200 µg P/l around 10 cm (~1975), followed by a decrease to 165 µg P/l in the topmost sample (Fig. 4). Water chemistry analyses over recent years indicate a TP-concentration varying around 150 µg P/l which is comparable to the diatom-inferred values over the top 8 cm of the core.

Chironomids

A total of 3005 head capsules from 18 sediment samples (min. = 107; mean = 167; max. = 218) were examined. Thirty five taxa were identified including groups/types that could not be identified further. The chironomid stratigraphy in the sediment core represented as percentage values is shown in Fig. 5. The chironomid record showed little up-core variation, with a pronounced dominance of the profundal *Chironomus anthracinus* and sub-dominance of *Tanytarsus* spp. In the lower core section *C. anthracinus* made up 45–75 % of the subfossil assemblages. In the upper 15 cm (~1965–1998) the contribution of *C. anthracinus* was reduced to 30–35 % while remains of the Phantom midge (*Chaoborus flavicans*) and the littoral species *Microtendipes pedellus* increased. In the surface sample, *C. anthracinus* increased again to 45 % of the

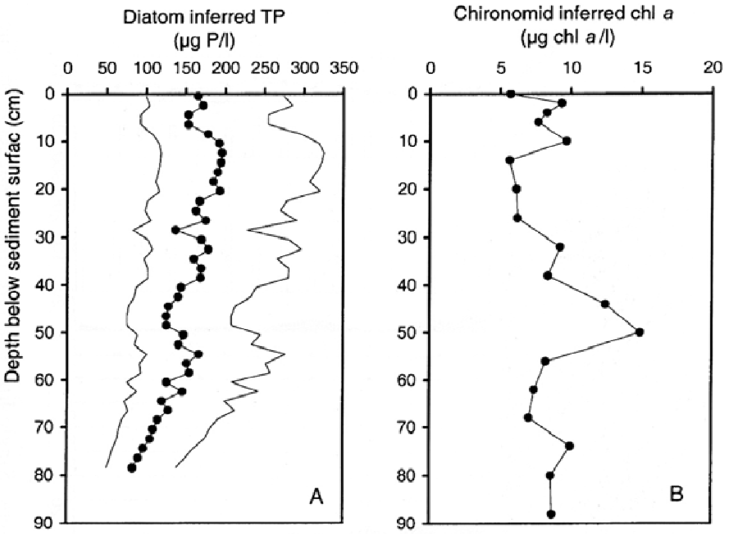

Fig. 4. Diatom-inferred [TP] (µg P/l, annual mean) from the BP-2 core assemblages. Errors are root mean squared errors of prediction (RMSEP) of the diatom TP-reconstruction model (**A**). Chironomid-inferred [chl-a] (µg chl-a/l, summer mean) from the BP-3 core assemblages (**B**).

assemblage. In the lower core section, three taxa from the Tanytarsini tribe were recorded: *Constempellina* sp., *Tanytarsus* type *chinyensis* and *Micropsectra* sp. A single headcapsule of *Micropsectra* sp. was also found in the 10–12 cm sample. Only two significant zones were identified. Zonation of non-transformed data suggested an optimal (significant) split between the 15 and the 20-cm samples, where *C. anthracinus* decreased rapidly. Square root transformed data gave more weight to the less abundant taxa and found a significant split between the 27 and 33 cm samples (Fig. 5).

There was an overall tendency of reduction in chironomid species richness (S) towards the core top (Fig. 6). The same tendency was found after correction for differences in sample size ($E(S)$) (Fig. 6). Among taxa not registered in the upper core section were *Chaetocladius* sp., *Paracladopelma* sp., *Polypedilum* type *pedestre/laetum, Constempellina* sp., and *T.* type *chinyensis*. The Shannon-Wiener diversity (H') showed a distinct decrease at the 20–25 cm interval partly due to decrease in richness (S) and partly due to reduced evenness ($N2$) with dominance of *C. anthracinus* (69 %) (Fig. 6).

The pronounced dominance of *C. anthracinus* in the core results in Lake Esrom being classified as a "B1"-lake throughout the time-period covered by the core, with the nearest faunal analogues being the mesotrophic and low-alkalinity Danish lakes (BRODERSEN & LINDEGAARD 1999). The quantitative reconstruction of [chl-a] showed little variation with values ranging around

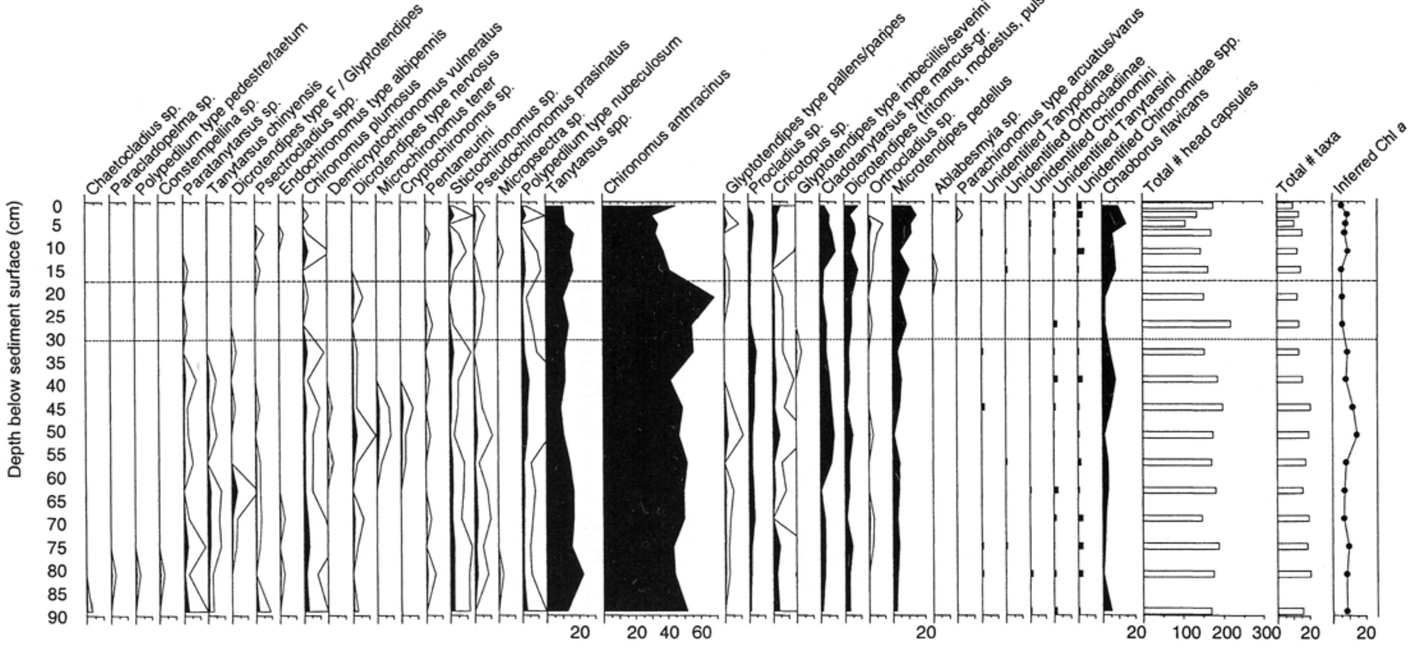

Fig. 5. Chironomid stratigraphy from the Lake Esrom BP-3 core. All data are percentages. Single line is a five-times exaggeration. The chironomid taxa are arranged according to their depth-weighted average in the stratigraphy.

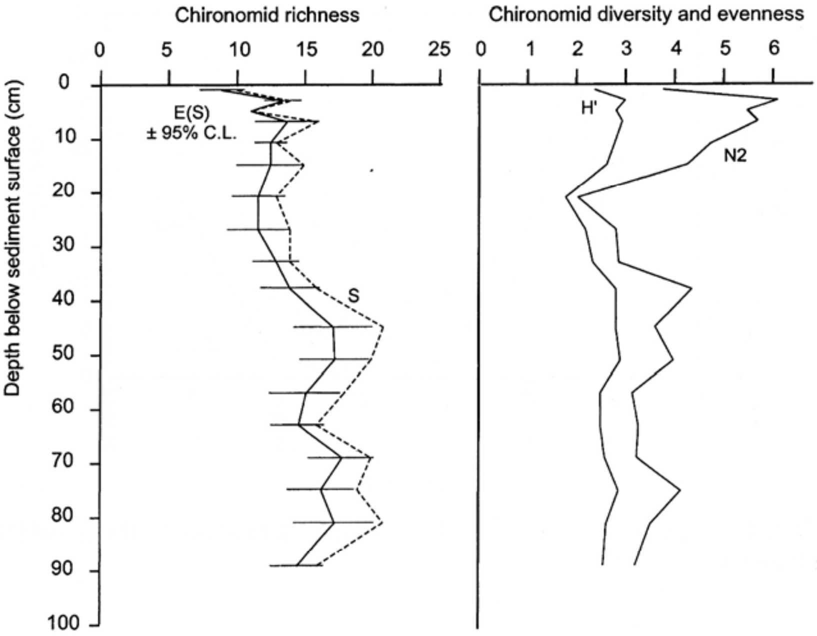

Fig. 6. Diversity measures of the chironomid assemblages in the BP-3 core. S, taxa richness; E(S) rarefaction estimated richness ± 95 % confidence limits; H′, Shannon diversity and N2, Hill's N2 diversity measure.

5–15 μg chl-a/l. A slight increase in estimated chlorophyll around 50 cm was caused by the presence of *Microchironomus tener* and *Cryptochironomus* sp., and an increased frequency of *Procladius* sp., *Cricotopus* sp. (type *sylvestris*) and *Cladotanytarsus mancus*-gr.

Modern chemistry and oxygen data

Water chemistry monitoring data for 1998 were available from the Frederiksborg County authorities. The development in the primary nutrients and the chlorophyll-a concentration in the surfacewater is shown in Fig. 7. A chlorophyll peak in early spring was primarily due to diatoms. Nitrate decreased rapidly from 0.40 mg/l in February to 0.02 mg/l in May. Phosphate was >0.17 mg/l throughout the season. The [chl-a] followed the decrease in [NO_3] and there was <10 μg chl-a/l after the onset of thermal stratification. The late-summer peaks in [chl-a] were primarily due to nitrogen fixing blue-green algae.

The 20th century bottom-water oxygen data from Lake Esrom are summarised in Fig. 8 and were compiled from data in BRØNDSTED & WESENBERG-LUND (1912), BERG (1938), JÓNASSON (1972), HOVEDSTADSRÅDET (1989) and from recent monitoring data kindly placed at our disposal by Frederiksborg

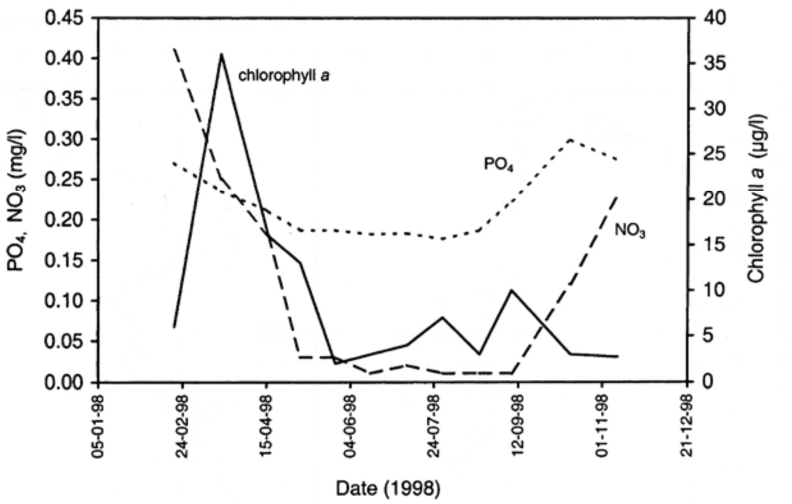

Fig. 7. Lake Esrom epilimnetic water chemistry data: [chl-a] (µg/l), [PO_4] and [NO_3] (mg/l) for the year of 1998.

County. The first indication of bottom water anoxia was measured on October 6th 1933 (0.24 mg O_2/l). At present, the level of <1.0 mg O_2/l is reached already in late June. One measurement from 1908 showed an oxygen concentration of 7.5 mg O_2/l at 18 meters depth on August 11th.

Discussion

The overall variation in the chironomid profile is low. Five aspects of the chironomid profile can be discussed in detail: (1) the fluctuations in the relative abundance of *C. anthracinus* remains in sediments deposited during the 20th century (0–25 cm), (2) the higher taxa richness in the older core sections, (3) the past bottom-water oxygen conditions reflected by the chironomid assemblages (4), the chironomid-inferred chlorophyll estimates compared to the diatom-inferred total phosphorus reconstruction and (5) the importance of nitrogen-limited primary production when reconstructing lake trophic state.

Considerable year-to-year variations in the profundal fauna of Lake Esrom are well known and historical data suggest that the population dynamics of *Pisidium* spp. changed dramatically in the mid-1950s and that also the densities of *C. anthracinus* were somewhat higher at that time compared to present day densities (JÓNASSON 1996, LINDEGAARD et al. 1997). These changes have been related to a possible increase in degree and duration of the hypolimnetic oxygen depletion in the summer season. The historical abundance data can be compared to the reduction in subfossil *C. anthracinus* abundance in the sedi-

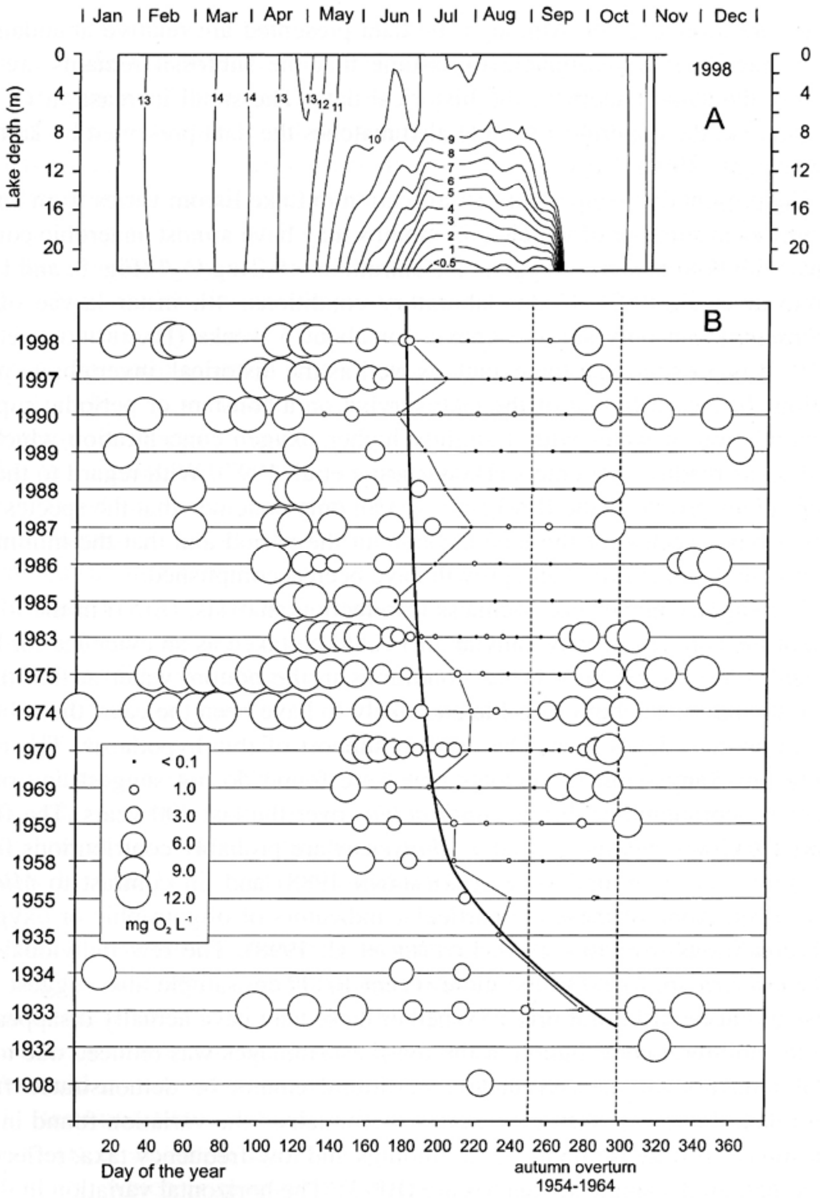

Fig. 8. Modern and historical oxygen data from Lake Esrom. (**A**) Oxygen stratification in 1998. The contours are mg O_2/l. (**B**) Bottom water oxygen data from 1908–1998. Thin line indicates the earliest **measured** oxygen concentration (<1.0 mg/l) for each year. The smoothed line indicates a hypothesised trend in development of the onset of the anoxic period. Data for the time of autumn overturn 1954–1964 (stippled lines) are from JÓNASSON (1972).

ment core around 1950. Although the data presented are relative abundances (percentages), it is reasonable to assume that the subfossil remains are reflecting the same pattern as the historical data. The small increase in *C. anthracinus* in the uppermost sample also matches the data presented by LINDEGAARD et al. (1997).

The present day temperature stratification in Lake Esrom varies from 3 to 6 months each summer of which 2–3 months may have almost anaerobic conditions, with bottom water oxygen concentrations $<0.2\,\mathrm{mg}\ O_2/\mathrm{l}$ (Fig. 8, and LINDEGAARD et al. 1997). Under laboratory conditions, 4th instar larvae of *C. anthracinus* can only survive anoxia for about 5 weeks (HAMBURGER et al. 1997). It is possible that the extant, as well as the historical, invertebrate populations in the profundal of the lake survive on a constant or periodic supply or circulation of water with a slightly higher oxygen concentration which is used up as readily as it enters (HAMBURGER et al. 1997). With regard to the *C. anthracinus* profile in the BP-3 core we can only conclude that the species has been a type-species for the lake throughout the period and that the minimum requirements for survival and growth have been accomplished.

The slightly higher taxa richness (rarefaction analysis, ($E(S)$)) in the lower part of the core (especially Tanytarsini) could be taken as an evidence for better and more favourable oxygen conditions in the bottom water at that time. Even though this is both possible and likely to have been the case, the subfossil chironomid data can not be used in support of this hypothesis. The relatively few Tanytarsini individuals that were found do not suggest any other character-communities than *C. anthracinus* over the last 400 years. The findings of *Constempellina* sp. and *T. chinyensis* are probably contributions from the littoral or sublittoral zones (HOFMANN 1988) and, in contrast to *Micropsectra* sp., none of these are particular indicators of oligotrophic or oxygen-rich conditions (SÆTHER 1979, LOTTER et al. 1998). The few individuals of *Micropsectra* sp. found in the more recent 10–12 cm sample also suggest that these might be of littoral origin. Whether these taxa have actually disappeared or the sublittoral contribution to the fossil assemblages was reduced due to an areal reduction of the oxygenated sublittoral cannot be demonstrated from these data. Further it should be noted, that much of the variation found in the chironomid profile is due to single findings and low-frequency taxa, reflecting the situation in a single sediment core (BP-3). The horizontal variation in these taxa among several cores might be important for diversity measures and quantitative [chl-a] reconstruction.

The chironomid-inferred [chl-a] suggest that the pelagic phytoplankton production in Lake Esrom throughout the period was relatively low according to Danish conditions (Fig. 4) (BRODERSEN & LINDEGAARD 1999). However, the diatom record suggests a variable but gradual increase in inferred [TP] and normally it would be expected that an increased nutrient loading should be reflected in an enhanced primary production. This coupling, however, is not found at Lake Esrom (JÓNASSON 1996) because the production in Lake Esrom is limited by availability of nitrogen and silica during the stratified summer season (JÓNASSON 1996), and not limited by the phosphorus availability as is the case in most other Danish lakes. In early spring, before the lake thermally stratifies and epilimnetic N is used up (Fig. 7), the growth of pelagic diatoms is responding to increased P-concentrations. The subfossil diatom assemblages, therefore, closely reflect the actual [TP] levels (~150 µg P/l) despite an overall N-limitation during the productive season. The zoological assemblages, however, are typical of Danish lakes with much more nutrient-poor conditions. Chironomid-inferred [chl-a] gave values between 5 and 15 µg chl-a/l (Fig. 4), which is in agreement with levels measured from water chemistry samples in recent years (8 µg chl-a/l). One explanation for this good agreement is that the chironomids respond to the integrated primary production over the season (food supply, degradation, oxygen demand), and the subfossil assemblages, therefore, reflect a mixture of the early spring situation and the long N-limited summer situation.

In Lake Esrom, the actual mean summer chlorophyll concentration (8 µg chl-a/l) is lower and the Secchi-depth (3.5 m) higher than commonly found at comparable [TP] concentrations, when Danish lakes are usually phosphorus limited. If nitrogen was not the limiting factor for the primary production in Lake Esrom, a chlorophyll concentration of 30–50 µg chl-a/l would be expected (JEPPESEN et al. 1997). It can be concluded, therefore, that both quantitative palaeo-proxies (diatoms and chironomids) correctly estimated the modern values despite the fact that these do not fit into the traditional ecological models (here the [TP]–[chl-a] correlations, e.g. summarised by JEPPESEN et al. 1997).

From a compilation of modern oxygen data by JÓNASSON (1996) and LINDEGAARD et al. (1997), it is tempting to conclude that no anoxia occurred in Lake Esrom before the summer of 1908 (Fig. 8). However, if considering oxygen as a controlling factor, such a development should have implied a shift in chironomid communities from anoxia-intolerant species (e.g. THIENEMANN 1921, BRUNDIN 1949, WIEDERHOLM & ERIKSSON 1979, WIEDERHOLM 1980, QUIANLAN et al. 1998, LOTTER et al. 1998) to the present *C. anthracinus* community, which is incompatible with the subfossil chironomid record. In contrast, the palaeolimnological proxies suggest that either some degree of hypoxia occurred frequently in Lake Esrom prior to 1908, or that the primary production in the lake never has been as low as required for supporting a chironomid community dominated by *Tanytarsus* with only few or no *C. anthracinus*. WESENBERG-LUND (1917, p. 166) reported that species of the *Tanytarsus*-group co-occurred with species of the *Chironomus*- (*Tendipes*) group in the profundal of Lake Esrom. This was not supported in the investigations by BERG

(1938), but it was reported that the *Tanytarsus gregarius*-group at that time occurred down to a level of 15 m. It seems evident from historical oxygen data that the hypolimnetic anoxia shows a development towards earlier onset in the season (Fig. 8). However, Fig. 8 also shows a considerable year-to-year variation in the timing of autumn overturn (30–50 days; JÓNASSON 1972). Thus, oxic hypolimnetic conditions in and before 1908 should not be concluded from the single measurement at 18 m depth on August 11th 1908.

The diatom-based TP-reconstruction suggests a minimum [TP] of 83 µg P/l in the oldest core-sections, which according to the models of NÜRNBERG (1995) corresponds to an anoxic factor (AF) of ~80 days in Canadian Shield lakes. These findings strongly support the chironomid-inferred description of the lake not as oligotrophic, but as a productive mesotrophic system where summer anoxia is likely to occur.

There is no evidence from this core study that within the last ~400 years Lake Esrom has supported a profundal fauna-community typical of more nutrient poor and oxygen rich conditions than found today. A trophic reconstruction of Lake Esrom solely based on diatom analysis could, therefore, have resulted in misleading speculations about long-term changes in the profundal zone of the lake. This study illustrates, therefore, the importance of multiproxy analyses for quantitative palaeolimnological reconstruction of lake trophic state, particularly where lakes behave differently from the more predictable responses to nutrient enrichment. The study also emphasises the importance of nitrogen as a controlling factor in the system, and even a small increase in the nitrogen loading to the lake might have profound effect on the dynamics of the profundal communities and for the trophic state of the lake in the future.

Conclusions

(1) Quantitative diatom-inferred reconstruction of total phosphorus showed an increase in TP levels from 84 at the base of the core to ~200 µg P/l around 1975, followed by a decrease to 165 µg P/l at the present day.

(2) Chironomid analysis showed only slight variation in the subfossil assemblages over the same period and there was no biological indication of significant changes in the hypolimnetic (oxygen) conditions over the last ~400 years. The chironomid inferred chlorophyll-a concentration ranged from 5–15 µg chl-a/l.

(3) The chlorophyll concentration in Lake Esrom is lower than commonly found at comparable phosphorus concentrations because the primary production in the lake is nitrogen limited. However, both the diatom-[TP] and the chironomid-[chl-a] reconstruction models estimated recent measurements accurately.

(4) The diatoms are reflecting the (TP) spring situation before the on-set of nitrogen limitation.

(5) The chironomids are reflecting the average summer (chlorophyll) situation both before and during the period of nitrogen limitation.

(6) This study illustrates the importance of multi-proxy analyses for quantitative palaeolimnological reconstruction of lake trophic state, particularly for lakes that behave differently from more predictable responses to nutrient enrichment.

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