# Spatial heterogeneity of diatom stratigraphy in varved and non-varved sediments of a small, boreal-forest lake

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ABSTRACT

Spatial and temporal heterogeneity of recent diatom stratigraphy were assessed for a small (23 ha) dimictic lake in Northern Sweden (Kassjön). Varves are confined to water depths > 10 m. Six freeze cores were taken along a transect covering a range of water depths (3–12 m) and both varved and non-varved sediments. Core profiles were compared for dry mass accumulation, loss-on-ignition (LOI), and diatom relative frequency stratigraphy and accumulation rate. Excluding the 3.2 m water depth, non-varved core, all parameters showed good repeatability between cores, apart from diatom accumulation rates which were more variable. The 3.2 m core was atypical and had lower LOI values, low planktonic diatom percentages and high values of benthic taxa that were not abundant in the deep-water sediments. Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA) ordinations were compared; both methods clearly differentiated the shallow water core, and showed the general similar ecological trends of the deeper-water cores. CCA axes constrained by "environmental" (i.e. core location) data resulted in slightly lower eigenvalues than that obtained by Correspondence Analysis (CA), but the axes were significantly non-random. A Partial-CCA of the four varved cores alone (with effects of sediment depth, i.e. age, partialled out), indicated that there was no significant difference between their diatom assemblages.

## Introduction

Varved or annually laminated sediments offer a number of advantages over visually or stratigraphically homogenous lake sediments, and are increasingly being used as the basis for palaeolimnological and palaeoecological study (Renberg 1978; Simola 1977). Varves potentially offer high resolution (associated with low mixing rates required for their formation), an implicit chronology, and hence the ability to calculate accumulation rates of parameters being studied (Renberg 1981a; Segerström et al. 1984).

Diatom stratigraphy in lake sediments varies due to variable diatom productivity, spatially heterogenous sources, transport, and depositional processes (Anderson 1990a). While most palaeolimnological studies have to assume that one core is a representative sample of the whole lake, many workers choose to ignore the implications of qualitative

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and quantatitive variability in biostratigraphical data (cf. Battarbee 1978; Anderson 1989, 1990a).

Any attempt to assess spatial variability and/or heterogeneity in diatom stratigraphy requires correlation of the different cores. For financial reasons it is unusual to date multiple cores, and where it has been done variable deposition of $^{210}$Pb requires some matching of cores to obtain a reliable chronology (Murchie 1985). Cores are, therefore, usually matched biostratigraphically (Battarbee 1978; Anderson 1986; 1990a, b), with correlation facilitated by numerical sequence slotting of microfossils (Anderson 1986), and ordination techniques (Birks 1987). All these approaches inevitably involve some subjectivity, and a degree of circularity if the correlations are then used to construct a chronology and diatom accumulation rates, although correlations can be substantiated by other parameters (Dearing 1986; Anderson 1986). Varves provide an accurate way of correlating cores and avoid this circularity (the correlation and chronology are independent of the biostratigraphy).

Varves are, however, normally confined to deep areas of lakes where bioturbation and resuspension processes are limited (Nipkow 1928; Renberg 1981b; Leavitt & Carpenter 1989), or areas of the lake where the epilimnion and hypolimnion are chemically differentiated (Anthony 1978). As such, lakes with varves also offer the possibility of assessing the effect of spatially variable processes on the stratigraphical record (Leavitt & Carpenter, 1989). Varved cores can be compared to mixed cores outside the area of varves, although correlation may again be problematical. In this study, as with that of Leavitt & Carpenter (1989) a clay inwash horizon provides a baseline for correlation between varved and non-varved cores.

This study presents diatom stratigraphy from a transect of cores covering a range of water depths in a varved lake in northern Sweden. It compares quantitative and qualitative biostratigraphy between cores, and assesses the implications for diatom stratigraphical interpretation and process studies.

## Study site

Kassjön is a small (23 ha) dimictic lake in Northern Sweden (63° 55′N, 20°01′E). Maximum water depth is 12.5 m and varved sediments are confined to water depths >10 m (Fig. 1). The lake was formed ~6300 yr ago by land uplift, and the sediment record in Kassjön is continously varved (Segerström 1990). The catchment area is 1300 ha with 75% boreal forest (mixed *Picea abies, Pinus sylvestris* and *Betula* spp.), and 25% cultivated land. Drains were cut in the catchment to the north of the lake in 1900–1902, the resulting erosion deposited a clear clay marker horizon across the whole-lake (Segerström et al. 1984). The varves have a thin dark winter layer of fine organic material, usually a thin spring mineral grain layer and a thicker summer-autumn layer of organic matter and biogenic silica (Renberg 1981a).

## Methods

Six cores were taken in March 1979 using a freeze corer (Renberg 1981b), along a transect from the deep-water sediments in the centre of the lake towards shallow water, close to the
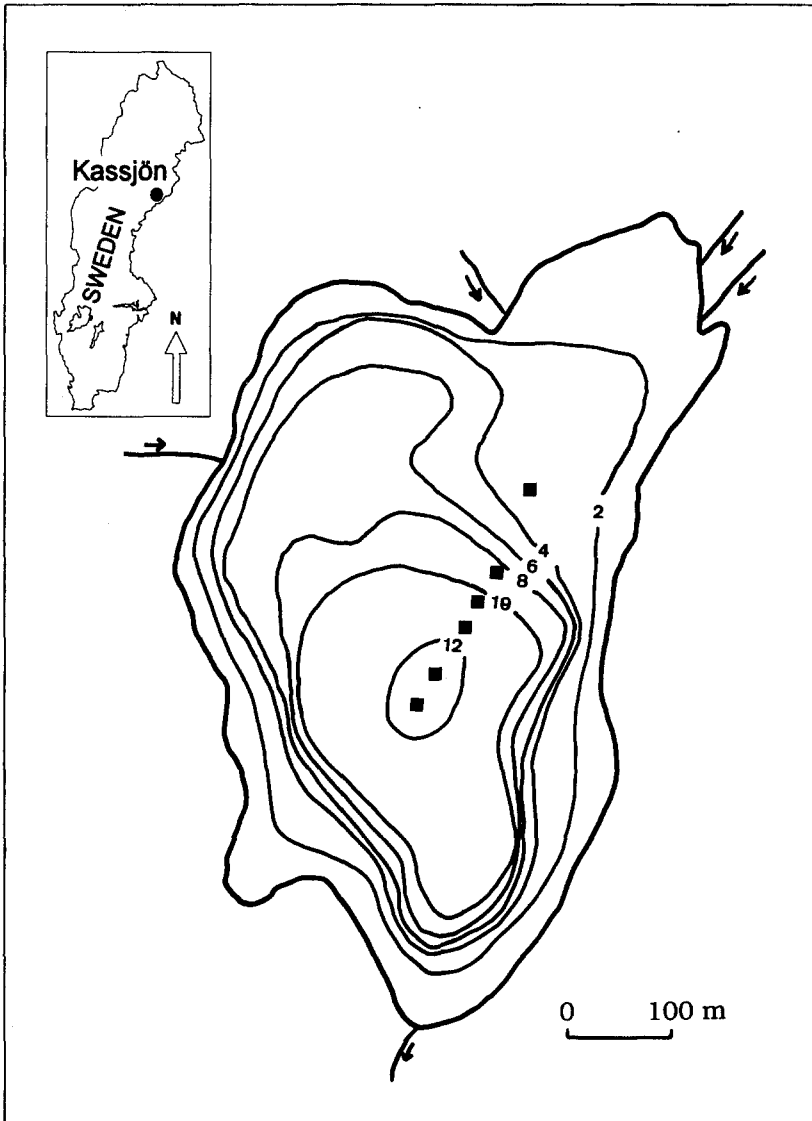
**Fig. 1.** Bathymetry (water depths in m) of Kassjön with locations of freeze-cores (■)

inflow channels in the north-east (Fig. 1). The different water-depths have varves of varying quality, with varves uncountable by 9.0 m, and the sediments extensively mixed at 3 m water depth. Core sub-sampling followed standard methods with sections of known mass and varve number cut from sediment slabs cleaned previously by planing (Renberg 1981b). After determination of dry weight (drying overnight at 105 °C) these data were then used to calculate dry mass accumulation rates (DMAR). Following homogenization the samples were sub-sampled again for loss-on-ignition (LOI) at 550 °C and diatom analyses.
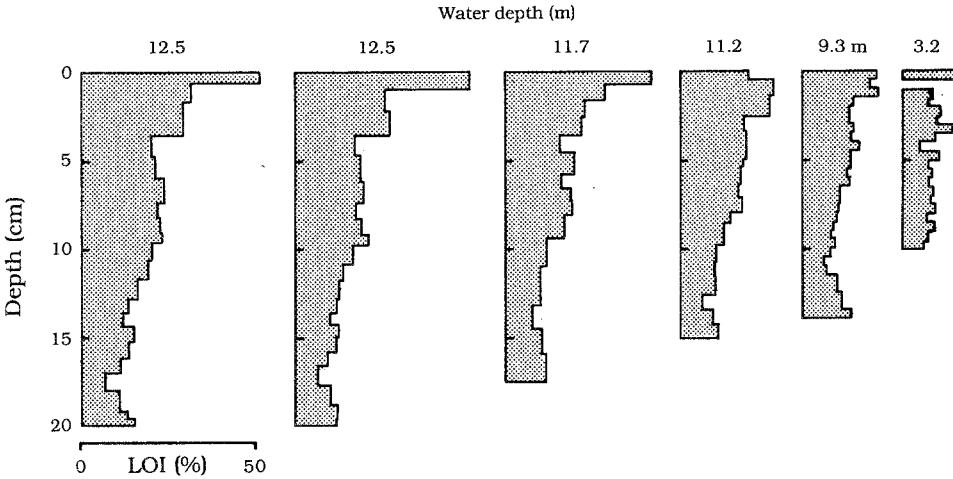
LOSS-ON-IGNITION PROFILES



Fig. 2. Loss-on-ignition profiles plotted versus sediment depth (cm)

Subsamples for diatom analysis were taken contiguously with sample intervals determined by distinct marker varves, so individual samples represent a varying time interval, but for the two 12.5 m cores the repeatability of the varves was so good that samples of an identical number of years could be cut. As the 11.7 m and 11.2 m cores were cut at varying time-intervals the mean calculated for the 4 cores (i.e. that integrates between-core variability) was based on the best temporal resolution obtainable in all four varved cores (cf. Dearing 1986; Anderson 1989). Eight time-periods were identified, primarily on the basis of distinct varves identifiable in all four varved cores, and are not necessarily the
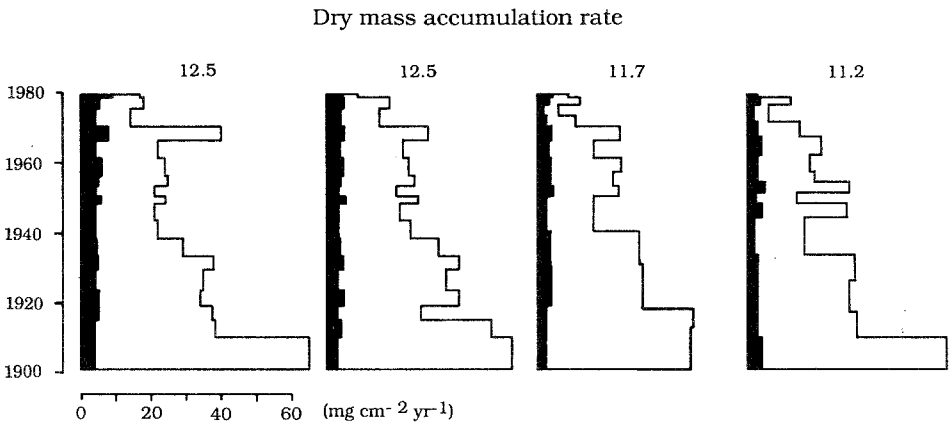
Dry mass accumulation rate



Fig. 3. Dry mass accumulation rates (mg cm$^{-2}$ yr$^{-1}$) plotted against sediment age; the black part is the organic matter accumulation rate. The high values at the base of the cores result from the digging of drainage ditches

same as the biostratigrahical zones. The intervals chosen were used to calculate the mean Correspondence Analysis (CA) scores and accumulation rates used for the between-core comparisons (Figs. 5 & 8). The surface and basal periods consisted of only one sample (representing 1 and 9 years, respectively) and were not used in the inter-core comparisons (i.e. Fig. 8). The 9.0 m and 3.2 m cores were sampled at contiguous 0.5 cm intervals.

Diatom methodology followed standard procedures (Battarbee 1986). Relative frequency stratigraphy was zoned subjectively to assist with stratigraphical description and allow comparison between varved and non-varved cores. Diatom concentrations were determined by the microsphere method (Battarbee & Kneen 1982) which has a good repeatability (Anderson 1990a), and diatom accumulation rates (DAR) calculated by multiplying the diatom concentration $(g[DW]^{-1})$ by the dry mass accumulation rate (g $cm^{-2} yr^{-1}$) for that particular interval. Concentrations were not determined for the 9.0 m core. Ages are given as calendar years.

Multivariate ordination methods (Correspondence Analysis [CA], Detrended Correspondence Analysis [DCA], and Canonical Correspondence Analysis [CCA]; ter Braak 1986) were used on a combined (percentage) data set of all cores using all species with an abundance greater than 3% in any sample. CA permits the rapid and simultaneous relationship of species and samples to be assessed by means of a joint plot, with similar cores lying close together in the ordination plot. DCA was used to assess the length of the first axis (in standard deviation units) to determine whether linear (e.g. Redundancy Analysis [RDA]) or non-linear (e.g. CCA) methods should be used. ter Braak and Prentice (1988) have suggested that data with first axis gradient lengths greater than 2 standard deviation (SD) units should be analysed using non-linear methods.

However, it is possible that the extracted ordination axes may represent random variabilty as well as ecological trends and depositional-induced variability, together with sampling and analytical error. With CCA, however, it is possible to constrain the sample scores to be linear functions of supplied "environmental" (external) variables which are assumed (*a priori*) to be potentially important explanatory or predictor variables for the observed stratigraphical patterns within and between cores. When the axes have been extracted their significance can be tested statistically by comparing the observed result (of both the first eigenvalue and the trace [the sum of all the eigenvalues]) with that obtained from Monte Carlo permutations of the data (ter Braak, 1987). The environmental variables used are listed in Table 2. All ordination analyses were made using options in the program CANOCO 3.1 (ter Braak 1987).

## Results

*Loss-on-ignition (Fig. 2)*

All cores, apart from the 3.2 m core, have broadly similar profiles (although mean values vary; Table 1), with a minimum value associated with the minerogenic inwash towards the base of the core. The depth of this minimum decreases with decreasing water depth. Values increase up core, with a zone of higher values (> 30%) between 4 cm depth and the core surface in the deeper water cores (> 9 m). The two 12.5 cores and the 11.7 m core have a distinct surface peak and repeatability of trends in these three cores is very good (Fig. 2). Similar profiles, apart from surface peaks, are evident in the 11.2 and 9 m cores, but LOI
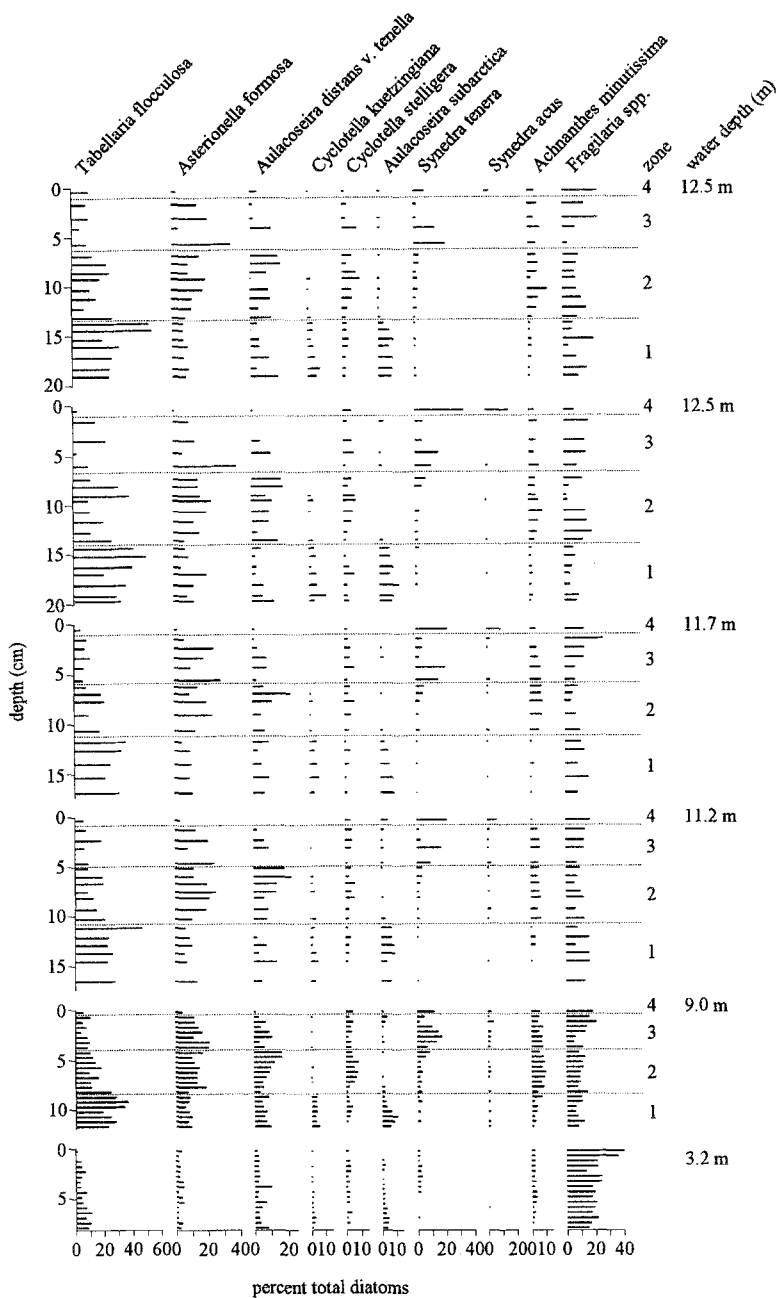
**Fig. 4.** Diatoms relative frequency stratigraphy with associated biostratigraphical zones for the four-varved and 9.0 m cores. The biostratigraphic zones represent the following time-periods: Zone 1, 1900–1934; Zone 2, 1934–1960; Zone 3, 1960–1980; and Zone 4, a single varve at the core surface, 1981
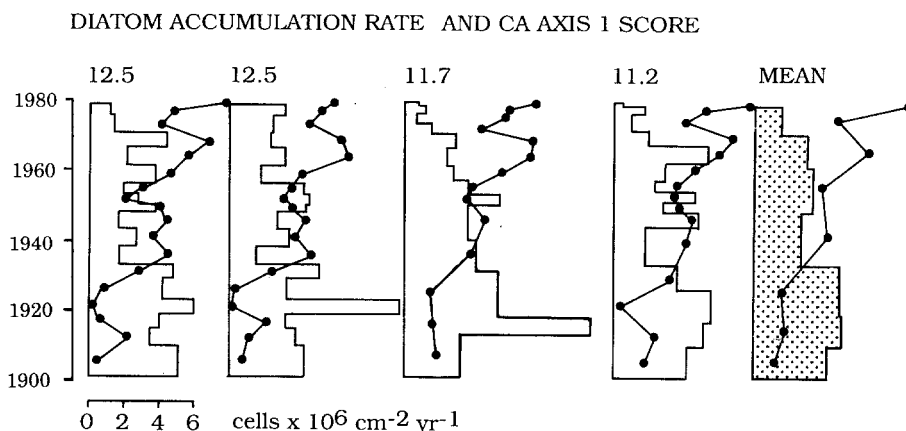
DIATOM ACCUMULATION RATE   AND CA AXIS 1 SCORE



**Fig. 5.** Diatom accumulation rates (frustules $\times 10^6$ cm$^{-2}$ yr$^{-1}$) plotted against sediment age and the mean of the four varved cores. CA axis 1 scores (•—•; on a relative scale) have been superimposed as a summary of ecological change in the relative frequency diatom stratigraphy

values throughout the length of the cores are reduced (mean 15% vs 22%; Table 1), while in the 3.2 m core there is no clearly discernible trend and all values are <10%, apart from 3.0–3.5 cm (14%) and the slightly higher surface value (15%).

## Dry mass accumulation rates (Fig. 3)

Profiles are similar for the varved cores, although detail varies between cores. All varved cores have maximum accumulation rates (40–60 mg cm$^{-2}$ yr$^{-1}$) associated with the inwash period (~1900–1915), after which values decline steadily upcore, apart from a distinct peak between 1971 and 1968 in the 12.5 m and 11.7 m cores. The 11.7 m core also has a period of increased DMAR (~25 mg cm$^{-2}$ yr$^{-1}$) between 1963 and 1953, which is also apparent, albeit to a lesser extent, in the other varved cores. The two 12.5 m cores show very good repeatability apart from small differences for four periods: 1968–1971 (above), 1917–1919, 1919–1921, and the DMAR increase associated with the clay inwash, at the base of the cores. All cores have low and relatively uniform organic matter accumulation rates, ~5 mg cm$^{-2}$ yr$^{-1}$.

## Relative frequency diatom stratigraphy (Fig. 4)

For the deep-water cores (including the 9.0 m core) 4 biostratigraphical zones are identifiable. A basal assemblage (Zone 1; 1900–1934) is dominated by *Tabellaria flocculosa* (ca. 30%), with *Asterionella formosa, Aulacoseira distans* var. *tenella, Cyclotella kuetzingiana* and *Aulacoseira subarctica* as sub-dominants. The latter two species decline steadily up-core.

Zone 2 (1934–1960) is characterized by increased *Asterionella, A. distans* var. *tenella* and *C. stelligera* and correspondingly reduced *T. flocculosa* (<20%). Zone 3
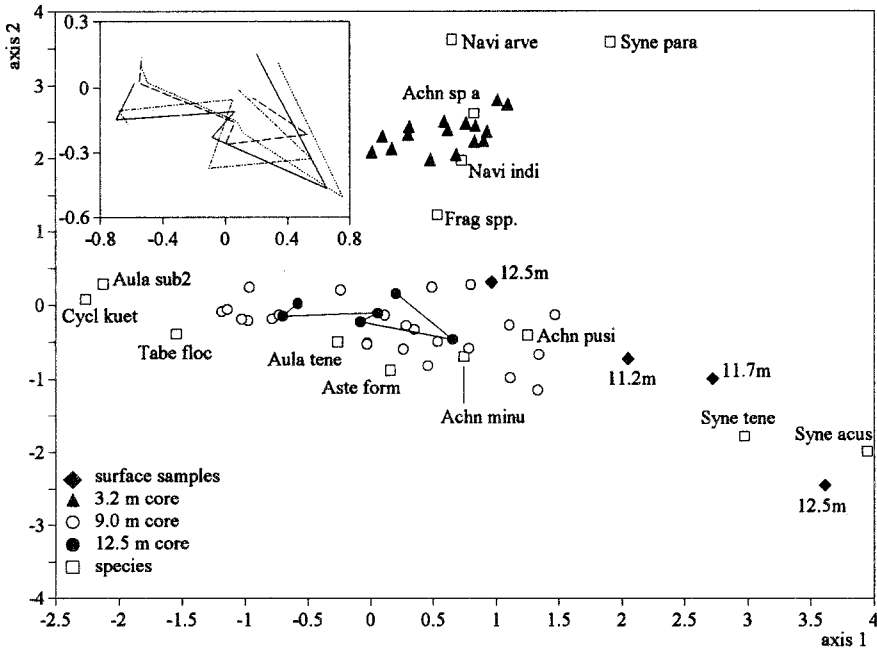
**Fig. 6a & 6b.** CA ordination, joint-plot of species (●), a deep-water (12.5 m) varved core (mean sample scores [axes 1 & 2] for the biostratigraphic zones – see fig. 4), sample scores of the 9.0 m core (○) and the shallow water, 3.2 m core (▲). The surface samples of the four varved-cores shown separately together with selected species scores. Species abbreviations Aula sub2: *Aulacoseira subarctica;* Cycl kuet: *Cyclotella kuetzingiana;* Tabe floc: *Tabellaria flocculosa;* Aula tene: *Aulacoseira tenella;* Aste form: *Asterionella formosa;* Achn minu: *Achnanthes miutissima;* Achn pusi: *Achnanthes pusilla;* Frag spp.: *total Fragilaria;* Navi indi: *Navicula indifferens;* Achn sp A: *Achnanthes cf. impexa;* Navi arve: *Navicula arvensis;* Syne para: *Synedra parasitica;* Syne tene: *Synedra tenera;* Syne acus: *Synedra acus*

**Fig. 6b.** Inset, CA ordination of the varved cores; mean sample scores for axes 1 & 2 for the biostratigraphic zones (see Fig. 4)

(1960–1980) has high *Synedra tenera* values, and maximum *Asterionella* and minimum *T. flocculosa* values. The surface (zone 4; 1981) has peaks of *S. tenera* and *S. acus*. *Achnanthes minutissima* and *Fragilaria* spp. form an important subsidary component throughout. Both *A. minutissima* and *A. pusilla* have higher percentages in the deep-water cores (>9 m) than in the 3.2 m core.

The shallow water core (3.2 m), however, is quite different, with significantly lower percentages of the dominant planktonic taxa. *Fragilaria* spp. and a variety of small *Achnanthes* and *Navicula* spp. (e.g. *Navicula arvensis, N. indifferens, N.* cf. *phylepta;* profiles not shown) dominate the 3.2 m core assemblages. There are a number of taxa (e.g. *Nitzschia* spp., *Achnanthes* sp. A., *Aulacoseira lirata, A. perglabra* var. *floriniae*) which have significant percentages in the 3.2 m core and occur only very infrequently in the deep-water cores.

All varved cores and the 9.0 m core have similar planktonic taxa trends and the repeatability of the signal of individual taxa is very good. An exception to these generalisations
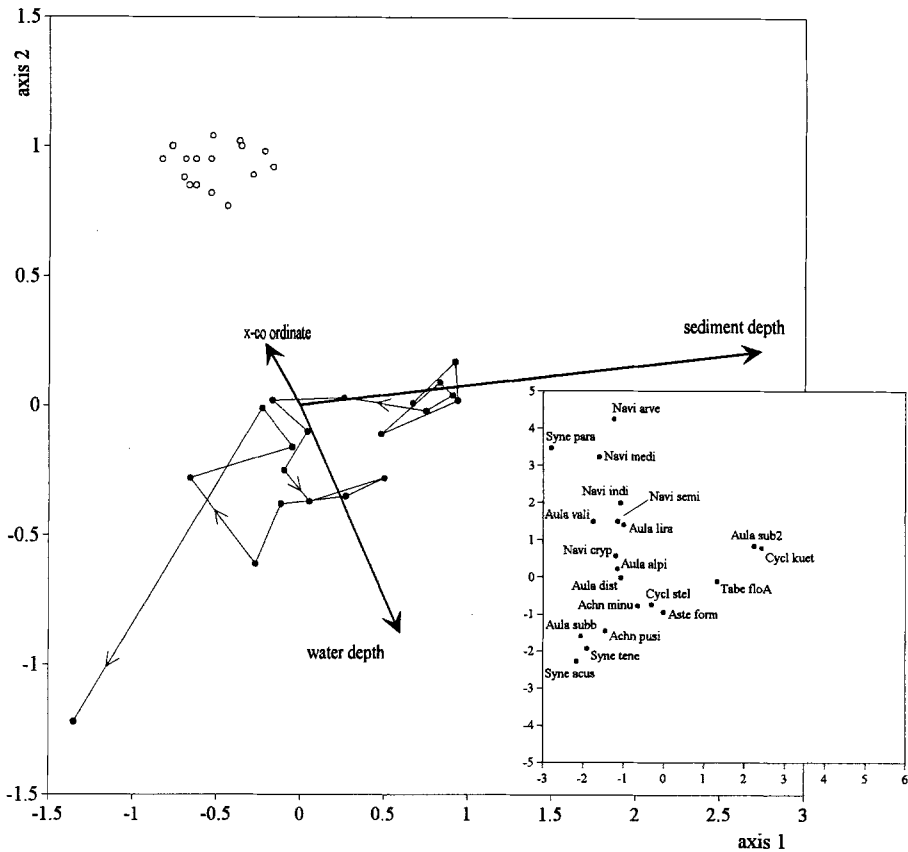
**Fig. 7.** CCA ordination; sample scores from a 12.5 m varved core joined as a time trajectory, and individual sample scores (○) from the 3.2 m core. The vectors for the significant environmental vectors are also shown; the length of the vector indicates its relative influence on the ordination. The location of the 3.2 m is negatively associated with the water-depth vector. Species scores of some important taxa have been indicated. Abbreviations as Fig. 6, additional species: Aula vali: *Aulacoseira valida;* Navi medi: *Navicula mediocris;* Navi semi *Navicula seminulum;* Aula subb *Aulacoseira subborealis;* Aula dist *Aulacoseira distans;* Aula alpi *Aulacoseira alpigena*

is the variable percentages of *Synedra tenera* and *S. acus*, particularly in the surface sample. Compared to the variability of the surface levels, however, the high values (15–20%) of *S. tenera* between 1960 and 1970 are reasonably consistent between cores.

## Diatom concentrations and accumulation rates

Diatom concentrations (Table 1) have similar ranges ($11 - 18 \times 10^7$ frustules g[DW]$^{-1}$), and there is an inverse relationship between mean values (for all levels analysed within a core) and water depth. The 3.2 m core has slightly higher concentrations, ca. $18 \times 10^7$ frustules g[DW]$^{-1}$.

**A.** CA Axis 1

**B.** DIATOM ACCUMULATION RATE
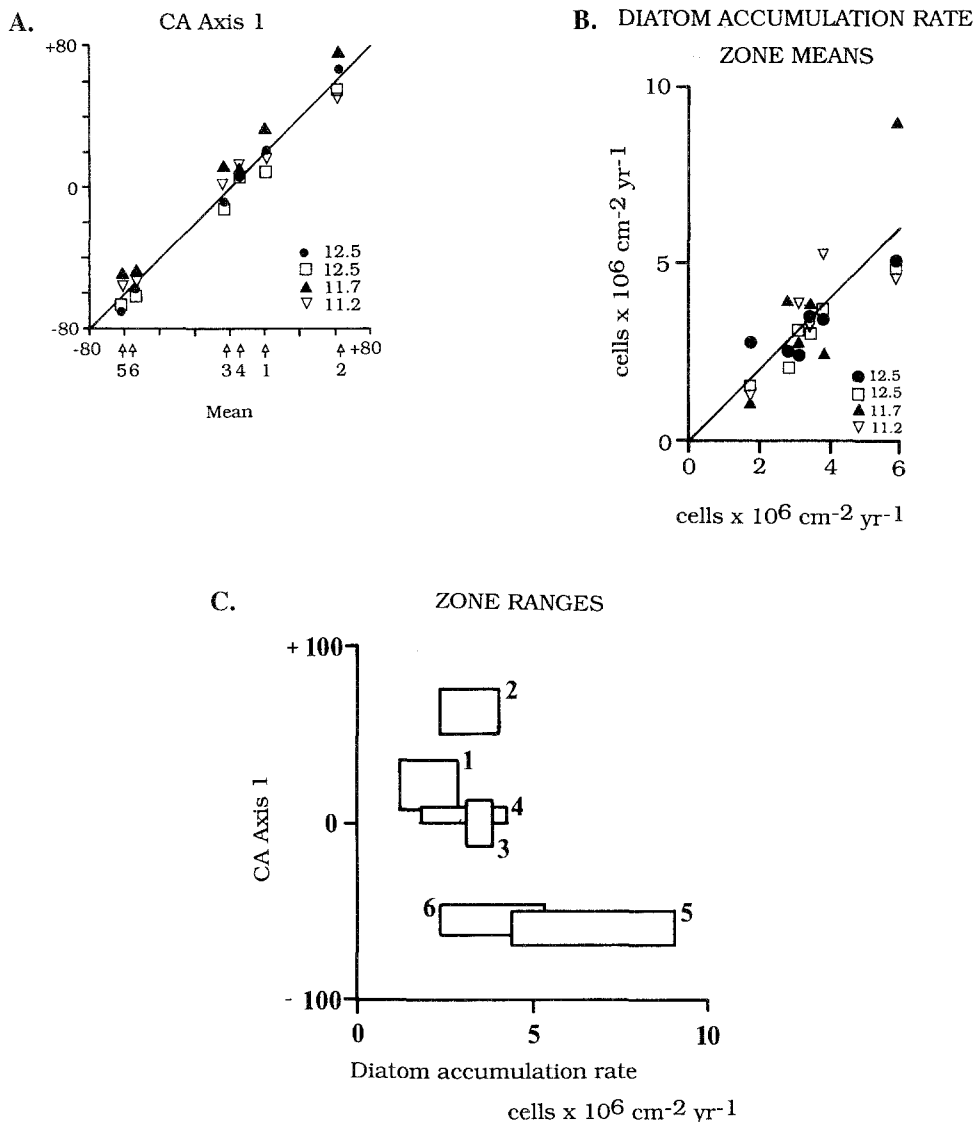ZONE MEANS

**C.** ZONE RANGES

**Fig. 8 a–c.**

**8 a.** Summary of the mean CA axis 1 sample scores for individual cores vs the mean of the four varved cores. The closer a point from an individual core plots to the 1:1 line the more similar it is to the average of the varved cores. The numbers along the x-axis indicate the time periods, 1 being the youngest and 6 the oldest. Of the 8 time-periods used to calculate these means, the surface, single varve and the basal, oldest zone were excluded

**8 b.** As for 8 a but for diatom accumulation rates

**8 c.** A summary of parts 8 a & b to illustrate the greater variability of the accumulation rate data compared to the relative frequency data, and the changes in the degree of variability between different time-periods: sediment accumulation is not constant in space and time. The numbers (1–6) again refer to the time-periods (cf part a). The boxes encompass the maxima and minima found in any of the four varved cores

**Table 1.** Mean loss-on-ignition and diatom concentrations for the six freeze-cores analysed in this study

| Core/Water depth (m) | LOI (%) | Diatom concentration ($10^7$ gDW$^{-1}$) | |
|---|---|---|---|
| | | mean | range |
| 12.5$\oplus$ | 15.1 | 11.0 | 5.7–24.4 |
| 12.5$\oplus$ | 17.6 | 13.1 | 4.8–26.1 |
| 11.7$\oplus$ | 16.0 | 14.8 | 7.5–23.8 |
| 11.2$\oplus$ | 16.5 | 15.6 | 7.4–25.4 |
| 9.0 | 13.0 | nd | nd |
| 3.2 | 8.2 | 17.76 | 10.8–36.13 |

$\oplus$ varved cores
nd: Not determined

Diatom accumulation rates vary between cores, but there are some similarities of trends (Fig. 5). All cores, apart from the 11.7 m core, have maximum rates between 1920 and 1940, although in the 11.2 m core there is a secondary maximum ca. 1966. At the 11.7 m site, there is a clear peak around 1921–26 that reflects significantly higher than average diatom concentrations ($\sim 24 \times 10^7$ frustules g[DW]$^{-1}$). In the 12.5 m cores there is a trend of decreasing accumulation rates upcore, with a number of oscillations, and a similar trend is identifiable in the 11.7 core. In the 11.2 core between 1967 and 1946 accumulation rates are comparable to those after 1920. Although values are different (6 vs $\sim 10 \times 10^6$ frustules cm$^{-2}$ yr$^{-1}$), the 12.5 m cores have synchronous DAR maxima between 1925 and 1921.

Averaging these data from the four cores gives maximum diatom accumulation rates between 1935 and 1921 (Fig. 5), with reduced rates after this, reaching a minumum in the surface period; (DAR were not calculated for the topmost – single varve – samples [1981]). Mean accumulation rates prior to 1935 are higher ($\sim 5 \times 10^6$ frustules cm$^{-2}$ yr$^{-1}$) than those after this date ($3 \times 10^6$ frustules cm$^{-2}$ yr$^{-1}$).

## Ordination

Ordination methods reduce multidimensional data to a few, more manageable dimensions (Birks 1987). Given the number of cores analysed and taxa encountered, for reasons of clarity of presentation a full joint-plot of all cores and taxa was not considered feasible. Therefore, CA axis 1 and 2 sample score zone means (as used for calculation of the 4 core accumulation rate averages; see methods) of the varved cores are presented separately in the joint-plot of dominant species and non-varved cores (Fig. 6a & b). All varved cores have similar trends (Fig. 6b) as one would expect given the relative frequency data (Fig. 4), although sample score means for individual cores vary, altering the ecological trajectory of the cores slightly (Fig. 6b). Axis 1 CA scores (cf. Fig. 5) are clearly repeatable, but there is greater variability on axis 2, reflecting the influence of *Synedra* spp and benthic species on that axis (Fig. 6a). The first and second CA axes account for 70% of the variability in the data.

**Table 2.** Eigenvalues for selected runs of CA, DCA and CCA. Sum of all unconstrained eigenvalues is 0.847; this is reduced after fitting of covariables. The trace is the sum of all constrained eigenvalues

| | | | All cores | | 3.2 m omitted. Sum of unconstrained eigenvalues 0.687 | | CCA with covariables⊕ Varved cores only | |
|---|---|---|---|---|---|---|---|---|
| Axis | DCA | CA | Full CCA⁺ | CCA* | CCA** | CCA*** | CCA sed depth⊕ | CCA water depth⊕ |
| 1 | 0.22 | 0.22 | 0.171 | 0.17 | 0.17 | 0.17 | 0.126 | 0.175 |
| 2 | 0.14 | 0.15 | 0.124 | 0.12 | 0.076 | 0.014 | 0.006 | 0.006 |
| 3 | 0.04 | 0.09 | 0.009 | 0.01 | 0.005 | 0.005 | 0.005 | 0.139 |
| 4 | 0.03 | 0.05 | 0.004 | 0.11 | 0.004 | 0.113 | 0.107 | 0.08 |
| Trace | | | 0.309 | 0.30 | 0.198 | 0.188 | 0.137 | 0.18 |
| Sum of unconstrained eigenvalues after fitting covariables | | | | | | 0.578 | 0.730 | |

+ Variables 5 and 6 omitted as non-significant after forward selection
* Environmental variables omitted 3,5,6
** 3.2 m core omitted; variable 6 – deleted because of collinearity
*** 3.2 m core omitted; 3,5,6 variables omitted

Environmental variables:
1 sediment depth
2 x-coordinate of cores
3 y-coordinate of cores
4 water depth
5 distance from inflow
6 distance from shre (omitted in all analyses because it is a collinear variable)

*Achnanthes minutissima* and *A. pusilla* have species scores (Fig. 6 a) comparable to most of the planktonic species, reflecting their more repeatable occurrence in the deep-water cores. The samples scores of the 9 m core are similar to the four varved cores (Fig. 6 a), but the 3.2 m core samples have high positive axis 2 scores reflecting the different species composition, with increased benthic taxa.

The surface samples (which consist of a single varve) have greater variability than the rest of the cores, although they are not directly comparable with the older time periods because of differential time-averaging (see below). This variability reflects different proportions of *Synedra* spp. in the samples, as indicated by their increasing proximity to the species points on the joint-plot (Fig. 6 a & b).

DCA indicated a first axis gradient length of 2.37 SD, therefore a non-linear method (CCA) was used. Constrained ordination using CCA gave broadly similar results to that of CA (Table 2, Fig. 7), although the eigenvalues are naturally lower than in CA (Table 2; ter Braak 1986). The eigenvalues for CCA axes 1 (0.17) and 2 (0.13) are similar to those for unconstrained CA and DCA (0.22, 0.14–0.15; Table 2), indicating that the external variables account for the major gradients in the diatom data. Of the "environmental" variables sediment depth (age) is strongly correlated with the first axis (Table 3), but water

depth and the x-coordinate less so. The latter variables are, however, more strongly and negatively correlated with axis 2, reflecting the localised nature of the 3.2 m core, with its assemblage of benthic and attached diatoms (Fig. 4).

Removing the shallow-water core to reduce its influence on the ordination did not substantially alter the results, although water depth was slightly less correlated with the second axis (Table 3). Removing those environmental variables that exhibited collinearity or were not significant (ter Braak 1986) resulted in an unconstrained 4th axis (eigenvalue = 0.113), indicating that some of the variation in the data set remained unexplained by the available environmental variables. The extracted axes of all CCA runs are significantly differently from random expectation at the $P < 0.01$ level.

The relationships between the stratigraphical profiles and the "environmental" variables were further explored by use of partial-CCA, where in separate analyses 'water depth' and then 'sediment depth' were used as covariables. In partial-CCA overly strong or "uninteresting" environmental signals are removed prior to further constrained ordination using the remaining "environmental" variables. In attempt to clarify whether there were significant differences between the varved cores (i.e. those cores from that part of the lake normally chosen for palaeoecological study) the 3.2 and 9 m cores were excluded from the partial-CCA analyses. When sediment-depth (i.e. age) is partialled out the resultant ordination is non-significant $(P > 0.05)$, indicating that there are no significant differences between the varved cores in relation to either water-depth or core location (the two remaining "environmental" variables; Table 2). With water-depth partialled out there is, however, still a significant relationship between the diatom changes and sediment age.

## Discussion

### *Heterogeneity versus variability in biostratigraphical data*

Prior to a discussion of the implications of the results presented here, it is perhaps important to distinguish between variability and heterogeneity in sediment studies. This study,

**Table 3.** Correlation of environmental variables with axes 1 and 2 for selected runs of DCA and CCA

| Environmental variables | | DCA | | CCA all cores | | CCA 3.2 m core omitted | |
|---|---|---|---|---|---|---|---|
| | | Axis 1 | Axis 2 | Axis 1 | Axis 2 | Axis 1 | Axis 2 |
| Sed depth | 1 | −0.86 | 0.0 | −0.87 | 0.18 | 0.85 | 0.12 |
| x-co ord | 2 | 0.32 | 0.5 | 0.41 | 0.46 | −0.17 | −0.68 |
| y-co ord | 3 | 0.32 | 0.5 | 0.42 | 0.47 | − | − |
| water depth | 4 | −0.34 | −0.7 | −0.48 | −0.67 | 0.15 | 0.55 |
| distance from inflow | 5 | −0.33 | −0.5 | − | − | − | − |
| distance from shore | 6 | 0.33 | −0.6 | − | − | − | − |

as with other comparable surveys (e.g. Anderson 1989; 1990 a) was largely concerned with differences in stratigraphical records at a whole-lake scale. Such differences are important if ecologically meaningful estimates of, for example, diatom accumulation rates, are to be made. Taking cores from a variety of core-locations and water depths clearly must accentuate between-core differences and should, therefore, be termed spatial hetereogeneity. Anderson (1990a), for example, took no replicate cores at a single site, but compared stratigraphies from extreme, littoral locations with profundal cores. However, the use of constrained ordination and comparison of real data with Monte-carlo permutations is useful in determining whether there are statistically significant differences between-cores in these types of study (see below).

Replication at different core-locations, however, has been undertaken by Downing & Rath (1989), Charles et al. (1991), and Cumming et al. (1992). Such studies are primarily concerned with repeatability (i.e. variability) of an ecological signal (often diatom-inferred pH) at a given location; i.e. deep-water sites normally used for palaeoecological study. These two approaches (whole-lake multicoring and single-site replication) are not, therefore, mutually exclusive and in fact, reinforce each other. Comparisons of replicated diatom-inferred pH values as a measure of spatial heterogeneity within palaeolimnological sampling strategies, however, can be misleading because the resultant pH value disguises variability within individual taxa (cf. Anderson 1990b). Two different taxa may have similar pH preference categories or weighted-averaging optima, and hence contribute equally to the calculated pH value.

However, replication of diatom accumulation rate data within a small area has not been undertaken. The results from this study, of variation of diatom accumulation rates within the area of the lake depositing varved sediments, suggests that even at such a restrictive scale accumulation rates are quite variable (the area of the lake with varved sediments is only 20% of the total area). Importantly, the coefficient of variation of a given technique is important in defining statistically significant variability at these more spatially restricted scales (cf Downing & Rath 1989).

## Quantitative vs. qualitative data and ecological trends

At Kassjön percentage data are more repeatable than accumulation rate data, and confirm the results of other, comparable studies (Battarbee 1978; Anderson 1989, 1990a). Importantly, the ecological trends of the four varved cores and the 9 m core are the same, and in qualitative terms would provide the same record of the changes in the planktonic diatoms (Figs 4 & 6). The deep-water cores do not, however, provide a complete floristic history of the lake: the 3.2 m core is dominated by species which occur only seldomly in the deep-water sediments. The profiles of those benthic species which do occur in the deep-water (varved) cores (e.g. *Fragilaria* spp.) are more variable than the planktonic taxa. These differences presumably reflect the life-form differences, with most of the planktonic taxa production being deposited directly onto the sediment from the water column at the end of the growing season, while benthic and attached taxa are subject to variable resuspension processes in the littoral zone and transfer to the deeper sediments (Anderson 1990a). However, the profiles and species scores (from the ordination analyses) of *Achnanthes pusilla* and *A. minutissima* suggest that these taxa have more ubquitous sources around the lake periphery, or are more readily transferred into the deeper-water. However, *Fragila-*

*ria,* as a loosely attached and benthic genus would be expected to be more readily transported than attached species.

There must be localised diatom sources on the broad 2–3 m shelf towards the northeast of the basin, as represented by the 3.2 m core, and these assemblages are not being transferred into the centre of the lake (cf. Bradbury & Winter 1976). These unique sediment assemblages may reflect inflow inputs and/or *in situ* growth of benthic species. Unfortunately, light climate data are unavailable to delimit the area of possible *in situ* production by littoral species, such as benthic *Aulacoseira* spp. Other studies have illustrated how localised diatom sources can influence diatom stratigraphy (Bradbury & Winter 1976), and it is clear that homogenization of all diatom communities within a lake is unlikely, except perhaps in well-mixed systems.

The differences between the varved cores – i.e. those cores from the area which would normally be sampled for palaeoecological study – can be illustrated by comparing zone means in individual cores against the mean of all four cores. The CA axis 1 (i.e. relative frequency data) period means show minimal variation compared to the variability in the diatom accumulation means for the same period (Fig. 8 a, b). The use of the first CA axis has been proposed as a good summary indicator of change in palaeoecological data (Birks 1987). Here much of the variation in the ordination is on the second axis, reflecting spatial variation and differences in abundance of *Synedra* spp. The first axis summary (Fig. 5) is a reasonable indication of the change (over time) and uniformity of the diatom assemblages. Importantly, when considered together (Fig. 8 c) it is clear that there is variation in both space (i.e. between cores) and time (between period means).

Furthermore, the results of the partial-CCA, where the effects of sediment-age are removed, indicate that the varved cores are not significantly different in their relative frequency composition. Subjective visual inspection of these cores, where stratigraphic features can be matched easily between cores, also supports the conclusion that the varved-cores are identical in terms of their relative frequency stratigraphy (Fig. 4).

While the repeatability of the percentage record is good (Fig. 8 a), the accumulation rate variability makes it more difficult to identify a single, representative, core. However, as an ecological summary, in all varved cores there is a general upcore decrease in accumulation rate together with repeatable structural change in the assemblages of planktonic diatoms (Fig. 5).

## Comparisons of CA and CCA ordination analyses

Both the CA and CCA results clearly differentiate between the deep-water cores and the 3.2 m core. The use of "environmental" (locational) variables indicated that there were significant differences between the cores across the whole basin (Table 2). However, deepwater varved cores considered in isolation were not significantly different. The alignment of the first CCA axis with sediment depth (i.e. time) (Fig. 7) is significant, with and without the removal of covariable effects. At Kassjön, although the diatom assemblages change with time (Fig. 4), the degree of replacement of one species by another is not unidirectional, as indicated by the reversal of sample scores in the most recent time zone (Figs 6 & 7).

Removing the collinear environmental variables left an unconstrained 4th axis (Table 2) and illustrated the problem of defining suitable variables to analyse spatial

variability of biostratigraphy via CCA. However, the size of the unconstrained fourth axis (0.11), is not greater than the sum of the first three axes (0.30, Table 2), suggesting that the environmental variables are reasonably appropriate. Use of more cores would permit a fuller exploration of spatial variablity. Environmental variables more closely reflecting depositional process (e.g. measures of resuspension and bioturbation variability with changing water depth) may also assist in clarifying the observed differences between the deep-water cores.

Importantly, the surface samples from the four-varved cores are quite different (Fig. 6), and exhibit large ranges on both CA axis 1 and 2. While the degree of variation in the single-varve surface sediments cannot be compared directly to the samples at greater depth (the latter represent different time integrated periods) they do represent the extreme in intrasample variability. This variability in surface sediments has a important implications for calibration data sets, and supports the need to take a number of samples from the pro-fundal area of the lake and to integrate them prior to analysis. In non-varved sediments, however, combining a number of surface-sediment samples to create a composite sample, integrates over time as well as spatially, because sediment accumulation rates will vary between the samples (Anderson 1990a). For training sets this homogenisation may, how-ever, help to reduce the error in the relationship between the microfossil assemblages and the water chemistry.

Smoothing of biostratigraphy, whether it is the result of analytical methods (i.e. tem-porally-coarse sampling strategies) or sedimentation processes (i.e. interface mixing; Leavitt & Carpenter 1989) reduces temporal variability (i.e. noise); but can also destroy the ecological signal. Even in varved lakes the surface, flocculent sediments will be liable to some resuspension and turbulent mixing at overturn, but this will not, presumably, be as great as that in isothermal lakes (Kristensen et al. 1992). Moreover, resuspension from the littoral zone can result in inputs of older sediment and microfossils to the deep-water sediments.

## Process implications

Varved sediments are usually restricted to deep or sheltered anoxic sediments, and, as such, permit comparisons to be made between cores from areas which are spatially distinct and characterised by different processes. It is clear from both the lack of varves in the shallower-water cores and the declining LOI values, that depositonal processes in this lake are non-uniform. Diatom stratigraphy largely reflects these differences, although trends in the 9.0 m core, clearly match those of the deep-water cores despite disruption of the varves (Fig. 3). The mixing at the 9 m core location was not sufficient to destroy the ecological signal recorded in the sediment at that water depth.

The atypical diatom composition of the shallow water (3.2 m) core is clear indication of variable inputs and reduced plankton deposition, as well as enhanced bioturbation and/or physical mixing as shown by the absence of varves. However, processes controlling deposition and post-depositional re-working in profundal sediments in small lakes have still not been critically evaluated.

That DAR variation is greater than DMAR (Fig. 8) suggests that concentration vari-ability is an important factor affecting DAR; this may be due to analytical error or signifi-cant natural variation in concentrations (cf. Downing and Rath 1988; Anderson 1990a).

However, both LOI and DMAR estimates show some variation between profiles (Figs 3 & 4) and as these parameters are analytically more robust (coefficient of variation of LOI and bulk density estimates are <5%, compared to ~15% for diatoms; Anderson 1990a) it suggests strongly that inherent depositional variabilty is influencing the stratigraphy. Similarly, the deterioration in the varve quality between 12 and 9 m demonstrates non-uniform processes (see below).

Factors that may result in process variabiliy in dimictic lakes are largely related to the oxic-anoxic dichotomy that results in lower animal densities in deeper-water (reduced bioturbation), and thermal stratification reducing physical resuspension of sediments deposited below the metalimnion. The period between ice-out and onset of thermal stratification in dimictic lakes in northern Sweden, such as Kassjön, is quick (~3 weeks). The main period of physical disturbance in N.E. Sweden probably comes with autumn overturn, in the period before the lake freezes, and associated exposure to autumn storms. Importantly, the latter are perhaps not that important in eastern Sweden, which has only minor influences from the north-westerly depression belt.

Water depth influences biostratigraphical resolution (Fig. 4) and accumulation rates (in Kassjön planktonic taxa are highly focused into deep-water) but it does not appear to be that important *per se* in controlling varve formation; anoxia, stratification, shelter, overturn periods may be more important. Kassjön is, relatively, quite a shallow lake (mean depth 5 m), compared to many deep-lakes with varves in North America and Finland (e.g. Simola 1977; Anderson *et al.* 1985), implying that these other factors (above) are as at least important as water depth in determining varve formation and distribution.


## Conclusion

Varves undoubtedly offer a reliable basis for palaeoecological study, in terms of reduced mixing, chronology and accumulation rate data (Simola 1977; Renberg 1981a; Anderson *et al.* 1985, Leavitt & Carpenter 1989). Varved deep-water cores from Kassjön provide a clear and repeatable qualitative history of the planktonic diatom communities, and support sampling strategies based on cores taken from the deepest-part of the lake. There are no significant differences between the varved cores (i.e. >10 m water depth) in terms of percentage composition of the diatom assemblages. The variety of benthic taxa in the lake and their history cannot, however, be evaluated fully from deep-water cores. As with other comparable studies, diatom accumulation rate data are more variable than percentage data (Battarbee 1978; Anderson 1990a, b). Importantly, apart from the greater between-core variability of accumulation rates, deep-water cores would overestimate the total planktonic production and underestimate the contribution of the littoral zone.

REFERENCES

Anderson, N.J. 1986. Diatom biostratigraphy and comparative core correlation within a small lake basin. Hydrobiologia 143:105–112.

Anderson, N.J. 1989. A whole-basin diatom accumulation rate for a small eutrophic lake in Northern Ireland and its palaeoecological implications. J. Ecol. 77:926–946.

Anderson, N.J. 1990a. Variability of diatom concentrations and accumulation rates in sediments of a small lake basin. Limnol. Oceanogr. 35:497–508.

Anderson, N.J. 1990b. Variability of sediment diatom assemblages in an upland, windstressed lake (Loch Fleet, Galloway, S.W. Scotland). J. Paleolimnol. 4:43–59.

Anderson, R.Y., W.E. Dean, J.P. Bradbury, and D. Love. 1985. Meromictic lakes and varved lake sediments in Nort America. U.S. Geological Survey Bulletin 1607.

Anthony, R.S. 1977. Iron-rich rhythmically laminated sediments in Lake of the Clouds, northeastern Minnesota. Limnol. Oceanogr. 22, 45–54.

Battarbee, R.W. 1978. Biostratigraphical evidence for variations in the recent pattern of sediment accumulation in Lough Neagh, Northern Ireland. Verh. Internat. Verein. Limnol. 20:625–629.

Battarbee, R.W. 1986. Diatom analysis, in Berglund, B.E. (ed.) Handbook of Holocene Palaeoecology and Palaeohydrology. Chichester, J. Wiley, pp: 527–570.

Battarbee; R.W. and M.J. Kneen. 1982. The use of electronically counted microspheres in absolut diatom analysis. Limnol. Oceanogr. 27:184–188.

Birks, H.J.B. 1987. Multivariate analysis of stratigraphic data in geology: a review. Chemometrics 2:109–126.

Bradbury, J.P., and T.C. Winter. 1976. Areal distribution and stratigraphy of diatoms in the sediments of Lake Sallie, Minnesota. Ecology 57:1005–1014.

Charles, D.F., S.S. Dixit, B.F. Cumming and J.P. Smol. 1991. Variability in diatom and chrysophyte assemblages and inferred pH: paleolimnological studies of Big Moose L., (N.Y., U.S.A.) J. Paleolimnol. 5:267–284.

Cumming, B.F. (and others) 1992). How much acidification has occurred in Adirondack region lakes (New York, USA) since preindustrial times? Can. J. Fish. Aquat. Sci. 49:128–141.

Dearing, J.A. 1986. Core correlation and total sediment influx. In. B.E. Berglund (ed.) Handbook of Holocene Palaeoecology and Palaeohydrology. Chichester, J. Wiley pp: 247–270.

Downing, J.A. and Rath, L.C. 1988. Spatial patchiness in the lacustrine sedimentary environment. Limnol. Oceanogr. 27:137–150.

Kristensen, P., Søndergaard, M. and Jeppesen, E. 1992. Resuspension in a shallow eutrophic lake. Hydrobiologia 228:101–109.

Leavitt, P.R., and Carpenter, S.R. 1989. Effects of sediment mixing and benthic algal production on fossil algal stratigraphies. J. Paleolimnol. 2:147–158.

Murchie, S.L. 1985. 210Pb dating and the recent geologic history of Crystal Bay, Lake Minnetonka, Minnesota. Limnol. Oceanogr. 30:1154–1170.

Nipkow, H.F. 1928. Über das Verhalten der Skelette planktischer Kieselalgen im geschichteten Tiefenschlamm des Zürich- und Baldeggersees. Zeits für Hydrologie IV, 71–120.

Renberg, I. 1978. Palaeolimnology and varve counts of the annually laminated sediment of Lake Rudetjärn, Northern Sweden. Early Norrland 11:63–92.

Renberg, I. 1981a. Formation, structure and visual appearance of iron-rich, varved lake sediments. Verh. Internat. Verein. Limnol. 21:94–101.

Renberg, I. 1981b. Improved methods for sampling, photographing and varve-counting of varved lake sediments. Boreas 10:255–258.

Segerström, U. 1990. The natural Holocene vegetation development and the introduction of agriculture in Northern Norrland, Sweden. Studies of soil, peat, and especially varved lake sediments. Ph.D thesis University of Umeå.

Segerström, U., Renberg, I. and Wallin, J.-E. 1984. Annual sediment accumulation and landuse history; investigations of varved lake sediments. Verh. Internat. Verein. Limnol. 22:1396–1403.

Simola, H. 1977. Diatom succession in the formation of annually laminated sediments in Lovojarvi, a small eutrophic lake. Ann. Bot. Fenn. 14:143–148.

ter Braak, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for mulitvariate direct gradient analysis. Ecology 67:1167–1179.

ter Braak, C.J.F. 1987. CANOCO – a FORTRAN program for canonical community ordination by (partial) (detrended) (canonical) correspondence analysis, principal components analysis and redundancy analysis (version 2.1). TNO Institute of Applied Computer Science, Wageningen.
ter Braak, C.J. F. and Prentice, I. C. 1988. A theory for gradient analysis. Adv. Ecol Res. 18:271–317.