

## Quantitative and qualitative relationships between planktonic diatom communities and diatom assemblages in sedimenting material and surface sediments in Lake Baikal, Siberia

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### Abstract

Endemic planktonic diatoms are a major component of Lake Baikal sediments during interglacial periods. To investigate how these diatom assemblages are altered during sediment formation, quantitative plankton monitoring (1995–1998) was integrated with sediment trapping over 2 yr (1996–1997) in Baikal's southern basin (depth ~1,400 m). The traps consisted of both open (~6 monthly) and sequential (~2 weekly) collectors deployed throughout the water column. Sedimentation was seasonal, with diatom species composition, valve abundance, and total dry mass reflecting changes in the planktonic communities. Sedimented assemblages were transmitted largely intact to the deepest traps (~1,300–1,390 m); some compositional blurring occurred from differential sinking rates and dissolution of diatom valves. A rapid mass flux event of *Aulacoseira skvortzowii* and *A. baicalensis* was recorded in summer 1997 with particle sinking rates between 60 and 100 m d<sup>-1</sup> and dry mass fluxes >5 g m<sup>-2</sup> d<sup>-1</sup>. Although dissolution was evident for all species, more delicate taxa were preferentially affected (e.g., *A. skvortzowii* vegetative cells and fine *Synedra* species), whereas *Nitzschia acicularis* valves were almost entirely dissolved within the water column. Comparing trap and plankton diatom assemblages with those in nearby core tops demonstrated that a fundamental taphonomic change occurs in the surface sediment, with sedimentary diatom accumulation rates being only about 1% of trap deposition and plankton production rates. Dissolution was significant in explaining 5–30% of species variance between all taphonomic levels (plankton, trap samples, and surface sediments). Results indicate that diatom-based paleoclimatic records in Lake Baikal sediments could be improved and refined by taking taphonomic considerations into account.

The transmission of biogenic environmental signals from the upper water column of deep water bodies to the sediment

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anthropogenic and climate effects has been examined using high-resolution analysis of short cores (Flower et al. 1995a; Mackay et al. 1998). However, sediment transformation and sinking through Baikal's deep, oxic water column is complex, being affected by both transient current flows and gyre fields (Shimaraev et al. 1994). Major taphonomic problems in the upper sediment, such as turbidites, bioturbation, diagenesis (Lees et al. 1998), and microfossil preservation are also major issues confronting paleoenvironmental studies in Lake Baikal.

During nonglacial periods, planktonic diatom production is a major component of sediment formation (Colman et al. 1995; BDP-93 Baikal Drilling Project Members 1997). Sedimentary diatoms have the potential to permit quantitative reconstruction of climatic, or climatically related, parameters by developing and calibrating transfer functions from sedimentary species assemblages throughout the lake (Mackay et al. 2003) or from autecological models of species/environment relationships for individual taxa (Jewson et al. unpubl. data). Demonstrating connectivity between modern communities and sedimentary assemblages is an essential first step in applying environmental reconstruction techniques to Baikal's fossil record. Studies integrating plankton monitoring, sediment trapping, and analysis of surface sediments can establish the relative influence of different taphonomic processes (such as differential sinking rates and dissolution of diatom valves) on the preservation of environmental signals in the sediment stratigraphy.

Diatom dissolution indices have been developed to assess taxon and assemblage preservation that allow samples to be compared (Flower and Likhoshway 1993; Ryves et al. 2001). Where these indices have been applied to sedimentary diatom assemblages in Lake Baikal, dissolution has been found to be significant, with about half of all valves showing appreciable dissolution under light microscopy (Flower 1993a; Mackay et al. 1998). Dissolution adds error to environmental reconstructions, not only by increasing taxonomic uncertainty, but by the direct loss of valves, affecting measurements of total diatom abundance or biogenic silica (Ryves et al. 2001) and altering relative abundance of taxa by favoring more robust forms. Poor diatom preservation in sediments clearly compromises the quality of environmental inferences made using sedimentary assemblages.

In this paper, we report results from the international and interdisciplinary GEOPASS-NERC project (Flower et al. 1998) that has been monitoring contemporary diatom production in Baikal since 1994. Diatom abundance, composition, and dissolution state are compared throughout the water column and within nearby surface sediments. Multivariate techniques are used to explore the relationships between and within these three taphonomic units (plankton, traps, and surface sediments) and to quantify the role of dissolution on diatom assemblages. The implications that processes of sediment formation might have for paleoenvironmental inference are also addressed.

## Materials and methods

*Planktonic diatoms and biovolume estimates*—Water samples (1.5 liters) were collected from throughout the water

column at approximately monthly intervals in the region of the trap array (Fig. 1), beginning in December 1994 until June 1998. Diatom cells were concentrated and preserved in Lugol's iodine and analyzed under bright field microscopy at  $\times 400$ . Diatom results for plankton samples presented here are based on combined counts (cells  $m^{-2}$ ), both empty and with contents, integrated through the upper 500 m of the Baikal water column. Diatom biovolume was also estimated from mean cell dimensions for the main species for the upper 500 m and the whole-water column (1,400 m).

*Traps*—A vertical array of sediment traps, thermistor cables, and current meters was installed in the southern basin of Lake Baikal (Fig. 1) at a depth of  $\sim 1,390$  m on 12 December 1995 and was reset approximately every 6 months until 26 November 1997. This paper reports results from these four trap seasons: (1) 12 December 1995–26 June 1996; (2) 28 June 1996–10 December 1996; (3) 12 December 1996–7 July 1997; (4) 9 July 1997–26 November 1997.

Two types of sediment trap were employed: open-tube (or integrating) traps (Z traps) and sequencing traps (S traps; Table 1). Eight pairs of open, plastic tube traps (Z1–Z8), each with an effective sampling area of 65  $cm^2$  and aspect ratio (height : diameter) of 9, were deployed at various depths from 48 to 1,390 m on the same cable as three sequencing traps (S1, S2, and S3). The sequencing traps each consisted of a funnel (effective area 500  $cm^2$ , aspect ratio 4) above a carousel of 12 samplers (200  $cm^3$  each), which automatically rotates to open each collector in turn approximately every 2 weeks. S2 was a control for S1 for the first two seasons and is not discussed in detail here. S1 was set between 522 and 560 m, whereas S3 was a profundal trap operating between 1,283 and 1,384 m in all four seasons. The depths and times of trapping are summarized in Table 1.

For diatom analyses, all the material from one of each pair of the open Z traps and a 2-ml subsample of gently, but thoroughly, mixed S trap sediment were taken each time the trap array was exchanged. Material was stored in dark refrigeration both on board ship and on return to University College London (UCL) prior to preparation. Dry mass fluxes for Z and S traps were calculated from the remaining trap sediment.

*Surface sediments*—Short cores were collected during two campaigns in 1993–1994 (Mackay et al. 1998) and in 1996–1997 using both thin-bore (diameter 5.5 cm) gravity corers and a box corer (Flower et al. 1995b) from the vicinity of the trap site and elsewhere in the southern basin from measured depths. These cores were subsampled for diatom analysis using a Pasteur pipette to remove material from the top  $\sim 2$  mm of cores immediately after retrieval from the lake. Samples were kept in Whirlpac bags and stored in dark refrigeration until slide preparation.

*Diatom sample preparation and analysis*—Laboratory preparation techniques were developed for diatom analysis of Baikal material that minimized valve breakage, dissolution, and other processing losses. Procedures outlined in Mackay et al. (1998) were followed, which avoid the use of oxidizing agents or strong acids, using only distilled water

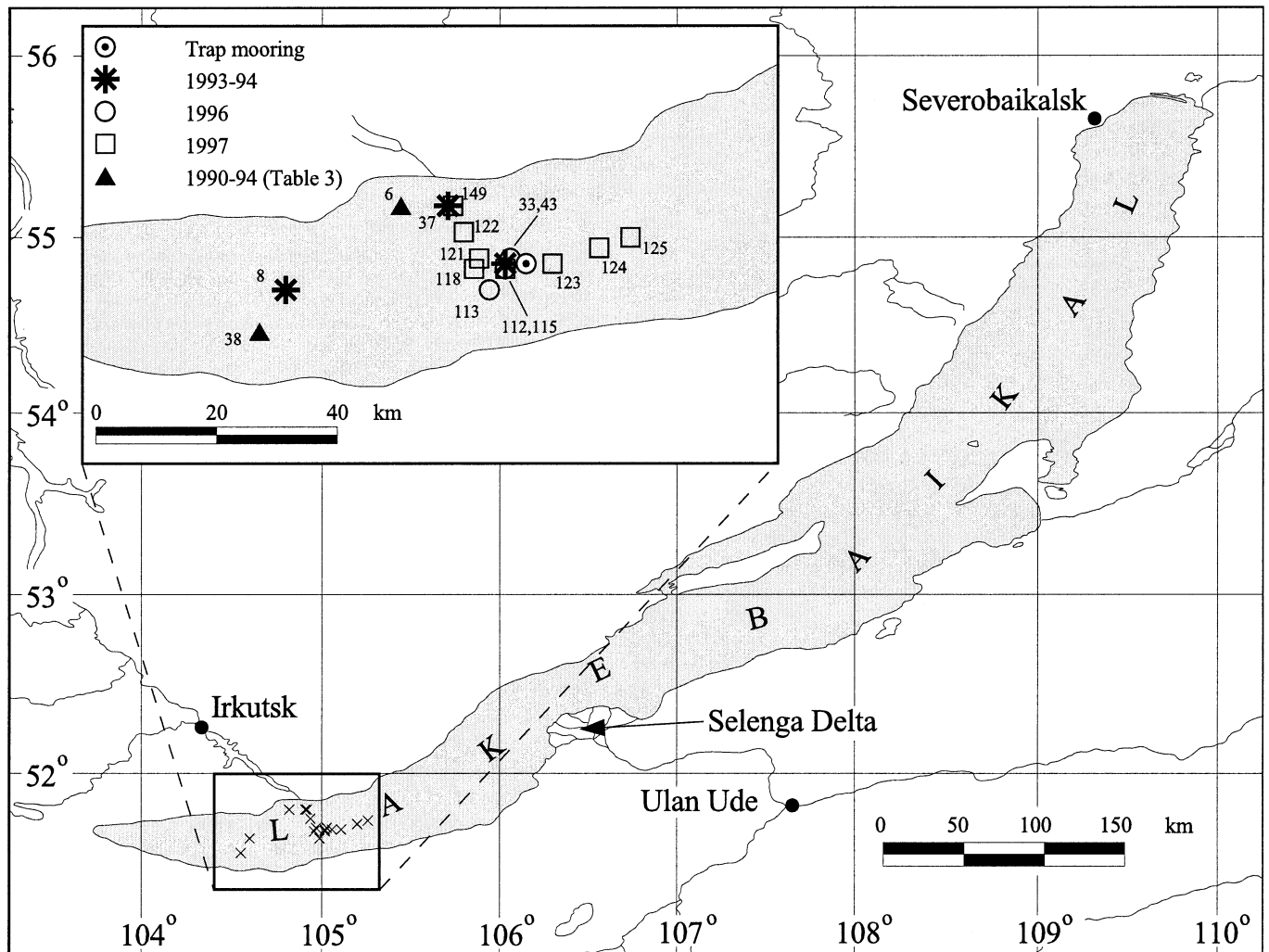


Fig. 1. Location map of the southern basin of Lake Baikal, showing position of trap mooring and surface sediments from cores used in this study (see Tables 1, 3).

to suspend sediment and minimal centrifugal washing. Cleaned suspensions were settled on glass coverslips, and permanent slides were made using Naphrax slide mountant.

Diatoms were enumerated using oil immersion phase contrast light microscopy at  $\times 1,000$  magnification using a variety of published and informal sources (e.g., Flower 1993b; Flower and Håkansson 1994; Edlund et al. 1996; Ryves and Flower 1998). Between 250 and 400 valves were counted, except where absolute abundance precluded this. Where  $< 100$  valves were found (in some S trap samples), reliable percentage calculations could not be made, but trace occurrence was recorded. For the open-tube traps, sufficient material was available to estimate diatom valve concentrations using microspheres (Battarbee and Kneen 1982).

**Diatom dissolution indices**—Sample preservation was estimated using a simple morphological diatom dissolution index (the F index). The F index for any sample is the proportion of pristine valves in an assemblage (see Flower and Likhoshway 1993; Mackay et al. 1998; Ryves et al. 2001). The index varies between 0 and 1; 1 indicates near perfect

preservation and 0 indicates that all valves are partly dissolved (implying considerable valve loss; Ryves et al. 2001). The index is a simple means of comparing the dissolution status of assemblages and can be related to differential valve destruction by taphonomic processes. A minimum count of 50 valves was used for assessing assemblage F index. Plankton samples were all assumed to be perfectly preserved ( $F = 1$ ).

**Numerical analysis**—Multivariate methods were used to explore the relationships within and between the various datasets (water column samples, trap contents, and surface sediments) and to identify factors that could explain variation in the diatom data as samples progressed from the living community (biocoenosis), to the sedimenting assemblage (seston taphocoenosis) and were finally incorporated into the sediment record (oryctocoenosis). Diatom identification protocols differed slightly between the plankton and other datasets. Original taxonomy was maintained for analysis of the plankton-only dataset, but harmonized for all other analyses

Table 1. Details of mooring site, traps and nearby cores in the southern basin of Lake Baikal (see Fig. 1 for locations) used in this study. Deployment periods and depths for the different trap types (sequencing traps = S1, S3; open traps = Z1–Z8) and core collection dates and depths are given.

Mooring site	Season			
	1	2	3	4
Water depth (m)	1,393	1,390	1,390	1,390
Longitude (N)	51°42'07"	51°42'04"	51°42'04"	51°41'00"
Latitude (E)	105°01'49"	105°02'12"	105°02'12"	105°02'31"
Date deployed	12 Dec 95	28 Jun 96	12 Dec 97	9 Jul 97
Date recovered	26 Jun 96	10 Dec 96	7 Jul 97	26 Nov 97
Traps	Trap depth (m)			
Sequencing trap				
S1	560	522	555	554
S3	1,287	1,384	1,384	1,283
Cup period (12, d)	16.42	14.25*	17.25	12†
Open trap				
Z1	70	48	157	254
Z2	560	144	555	554
Z3	764	522	574	660
Z4	964	754	774	780
Z5	1,164	954	974	980
Z6	1,264	1,154	1,174	1,180
Z7	1,287	1,254	1,278	1,283
Z8	1,390	1,287	1,384	1,386
Open trap period (d)	197	165	207	139
Cores‡				
Date collected	Number	Depth (m)	Reference	
1993–1994	3	1,390–1,478	Mackay et al. 1998	
1996	3	1,120–1,445	Mackay et al. 2003	
1997	8	955–1,445	Mackay et al. 2003	

\* Last cup collected after 8 d. † Last cup collected after 7.5 d. ‡ See Fig. 1.

along lines agreed on at a taxonomic workshop attended by all analysts (Ryves and Flower 1998).

Unconstrained analyses (detrended correspondence analysis [DCA] and principal components analysis [PCA], depending on whether linear or unimodal models were most appropriate; ter Braak 1995) were employed to summarize the main gradients of variation within the datasets as exploratory ordination biplots. Variables were superimposed upon such ordinations passively (C. J. F. ter Braak and P. Šmilauer, CANOCO for Windows v.4.0, Microcomputer Power). Constrained methods (canonical correspondence analysis [CCA] and redundancy analysis [RDA]) were used to test the significance of explanatory or “predictor” variables in explaining variance in the diatom data with Bonferroni adjusted forward selection and Monte Carlo testing of selected variables and axes ( $n = 499$  permutations). All such ordination techniques were carried out using CANOCO v.4.0. The significance of PCA or DCA axes was assessed using a broken stick model (Jolliffe 1986).

Biological count data from the water column (planktonic diatoms and biovolume) were log transformed to reduce bias from extreme values before PCA. Because absolute diatom abundance was not available for S traps and surface sediments, diatom data from all trap and surface sediment samples were transformed to relative abundance (%) prior to

analyses. For compatibility between datasets involving plankton, trap, and surface sediment data, plankton counts were also transformed to percentage data. To include the effects of season and year, dummy variables (0/1) were used to code for autumn (defined September–December), ice cover (January–April), and summer (May–August) for individual years from 1994 to 1998. Constrained analyses on all diatom samples (plankton, trap, and sediment) also included preservation as the F index or as a dissolution index ( $DI = 1 - F$ ), depending on dataset; depth (m, set at 250 m for all plankton samples); and an ordinal scale of time integration for each sample type ranging from 1 (plankton spot sample) to 4 (surface sediment covering ~1–3 yr accumulation; Mackay et al. 1998). Predictor variables were explored and transformed if necessary using the program CALIBRATE v.0.81 (S. Juggins and C. J. F. ter Braak, University of Newcastle).

Planktonic assemblage composition (analog) matching was performed on pooled samples (integrating 1–3 yr) of plankton and open-trap abundance data, converted to percent abundance for comparison with surface sediment samples. To ensure consistency between datasets in this analysis, trap and sedimentary assemblage percentage data were recalculated using only the 14 taxa found in plankton samples. A squared  $\chi^2$  dissimilarity index was used to compare samples

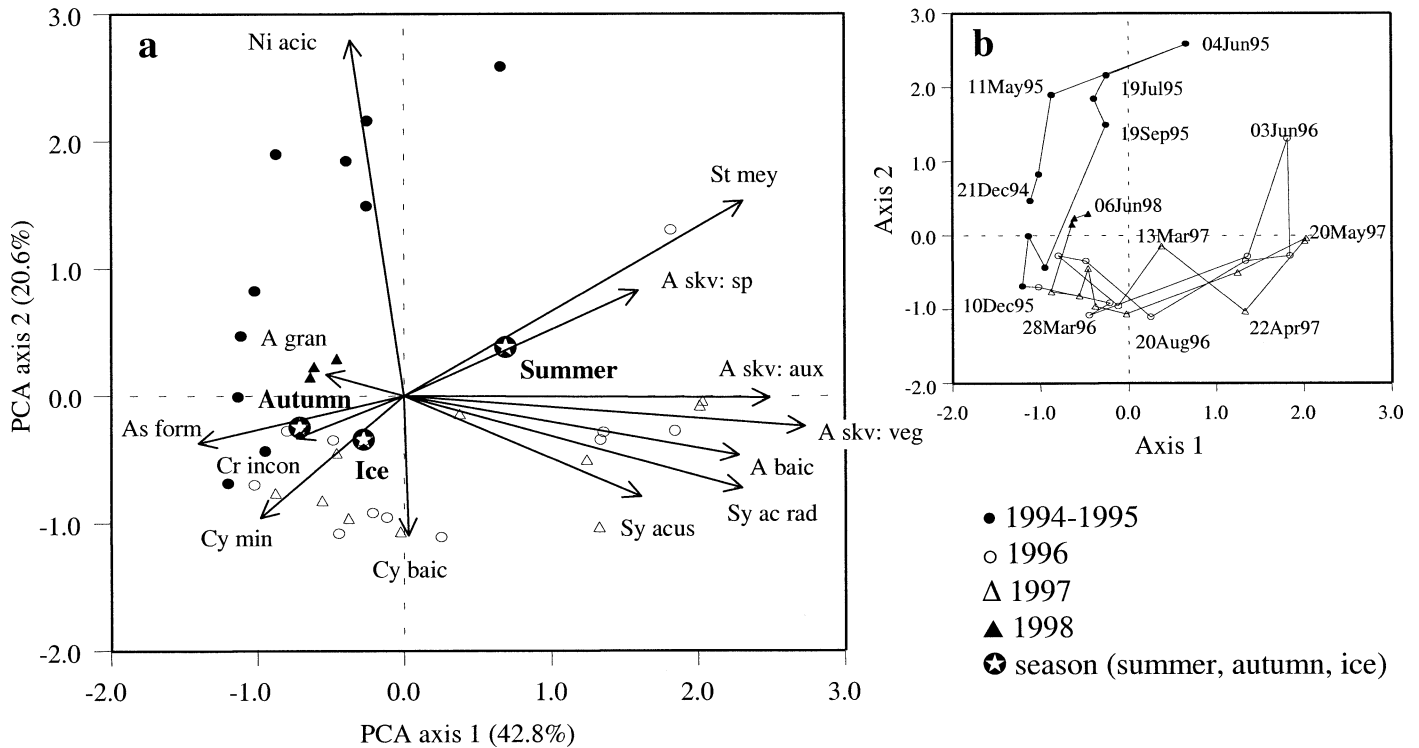


Fig. 2. Summary ordinations of 34 plankton samples (0–500 m, living + dead cell counts) from December 1994 to June 1998. (a) PCA axes 1 and 2 of plankton samples with species indicated by arrows: As form, *Asterionella formosa*; A baic, *Aulacoseira baicalensis*; A gran, *A. granulata*; A. skv, *A. skvortzowii*; sp, spores; veg, vegetative cells; aux, auxospores; Cr incon, *Crateriportula inconspicua*; Cy min, *Cyclotella minuta*; Cy baic, *C. baicalensis*; Ni acic, *Nitzschia acicularis*; St mey, *Stephanodiscus meyerii*; Sy acus, *Synedra acus*; Sy ac rad, *Synedra acus* var. *radians* (all forms). Seasons (as centroids) are: summer (May–August), autumn (September–December), and ice cover (January–April). (b) PCA of samples as in panel a, with samples linked in time sequence.

and was implemented by the program ANALOG 1.6 (H.J.B. Birks and J.M. Line unpubl.).

## Results

**Planktonic diatom communities**—Results from the plankton monitoring program are summarized here as a PCA ordination biplot (Fig. 2). Because the plankton diatom dataset is relatively small (34 samples and 14 species), a high proportion (>62%) of the variance is captured by the first two PCA axes, which are both significant (Fig. 2a). Large variations in total abundance and composition on both a seasonal (PCA axis 1) and yearly basis (PCA axis 2) were found in the planktonic diatom community from December 1994 to June 1998. Axis 2 might represent differences in hydrographic conditions from year to year.

Diatom communities in the autumn and ice seasons were fairly similar and characterized by maximum abundances of *Cyclotella minuta* (Skv.) Antip., *C. baicalensis* (Meyer) Skv., and *Crateriportula inconspicua* (Mak. and Pom.) Flower and Håkansson (Fig. 2a). Distinct summer communities developed, however, dominated by *Nitzschia acicularis* W. Smith in 1995 and *Aulacoseira baicalensis* (Meyer) Simonsen and *A. skvortzowii* Edlund, Stoermer and Taylor in 1997, with significant contributions by both *Stephanodiscus meyerii* Genkal and Popovskaya and *Synedra acus* Kütz. and vars. in 1996 and 1997 (Fig. 2a,b). The oscillation

in plankton communities along these different pathways represented by axes 1 and 2 is revealed more clearly if samples are plotted in time order (Fig. 2b). Under RDA (not shown), 40.4% ( $p = 0.002$ ) of the plankton dataset was explained by season (summer) and interannual effects.

**Diatom trap assemblages**—Open (Z) traps: Z1.a–Z8.a: 12 December 1995–26 June 1996 (Fig. 3a). Although not a numerically important component in the planktonic community after March 1996, *C. minuta* dominated the traps in terms of relative abundance (50–80%). *S. meyerii* was also found at all depths despite only appearing in significant abundance (>2%) on two occasions in the plankton during late May and early June (when it exceeded 20%). In contrast, the pulse of *S. acus* var. *radians* (Kütz.) Hust. fo. *pusilla* (described in fig. 22 in Ryves and Flower 1998) appeared only to have reached ~750 m by the end of June (despite being a significant component of the March plankton; cf. Fig. 2a).

Preservation was high for all samples ( $F > 0.85$ ). Mass flux values tended to increase with depth, whereas diatom fluxes tended to reflect the sequence of crops sinking through the water column (D. Jewson pers. comm.), with the upper trap collecting the summer 1996 *Synedra* bloom. The increase in *A. baicalensis* paralleled diatom and mass flux increases in the deepest trap (1390 m).

Z1.b–Z8.b: 28 June 1996–10 December 1996 (Fig.

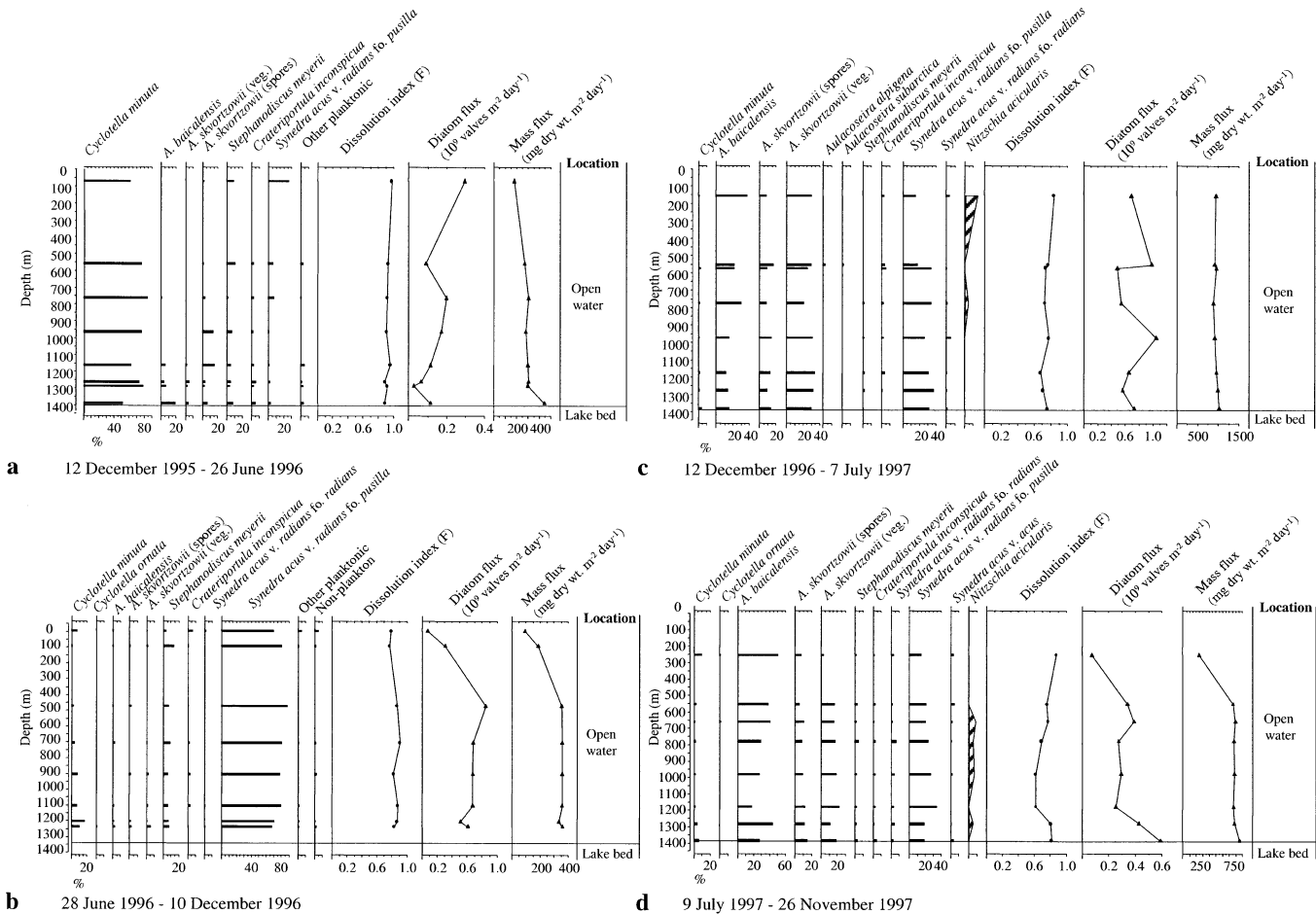


Fig. 3. Diatom analysis for open traps (Z traps) for each trap period. Data for individual taxa are presented as percent abundances for important taxa; stippling indicates  $\times 10$  exaggeration. Dissolution index (F), diatom flux, and mass flux are also shown for each sample. (a) Period 1: 12 December 1995–26 June 1996. (b) Period 2: 28 June 1996–10 December 1996. (c) Period 3: 12 December 1996–7 July 1997. (d) Period 4: 9 July–26 November 1997.

3b). All open traps reflected the bloom of *S. acus* var. *radians* fo. *pusilla*, which continued throughout summer 1996, with a minor component of *S. meyerii* continuing to enter traps, though disappearing from the plankton during July. *C. minuta* was present in low abundance in the lower and uppermost traps. The lower trap might record the final settling of the crop from spring 1996 and the upper the first deposition of fresh cells from autumn 1996, corroborated by observations from the water column (D. Jewson unpubl. data) and the sequential traps (see below). For this period, the correlation of mass and diatom flux is striking and both tend to increase with depth. Again sample preservation was good ( $F > 0.8$ ) at all depths, despite a small decrease in the bottom trap (1,287 m).

Z1.c-Z8.c: 12 December 1996–7 July 1997 (Fig. 3c). *A. baicalensis*, *A. skvortzowii* (both vegetative valves and spores), and *S. acus* var. *radians* fo. *pusilla* dominated open traps in the third period. The frequencies of *A. skvortzowii* vegetative valves and spores were stable at all depths (20–30% and 10–15%, respectively). In contrast, *A. baicalensis* had higher frequencies in the uppermost traps (up to 35%), whereas *Synedra* valves accounted for about 15% of the total

number above 500 m and around 30% below this. Other taxa, such as *C. inconspicua* and *N. acicularis* were occasionally found in upper traps, whereas *S. meyerii* only occurred in the deeper traps at very low abundance. The relatively poor crop of *C. minuta* in autumn 1996 was reflected in its low frequencies in open traps in this period.

Diatom preservation remained good with little change in depth, although dissolution was slightly greater than in the previous two periods ( $F = 0.7$ – $0.85$ ). Maximum fluxes for the entire 2-yr trapping period were recorded during this time for both total mass and diatom numbers, but while mass flux was high (around  $1 \text{ g m}^{-2} \text{ d}^{-1}$ ) and almost constant throughout the profile, diatom flux varied between 0.5 and  $1 \times 10^9 \text{ valves m}^{-2} \text{ d}^{-1}$ , with two peaks at around 550 and 950 m. Values change twofold between two traps only 25 m apart (Z2: 555 m and Z3: 574 m), with mass flux showing, if anything, a small increase in the opposite direction. Differences in species composition between these samples suggest that this flux event is real and is corroborated by bulk geochemical analyses, implying the upper sample is anomalous among open traps from this period (M. Sturm unpubl. data).

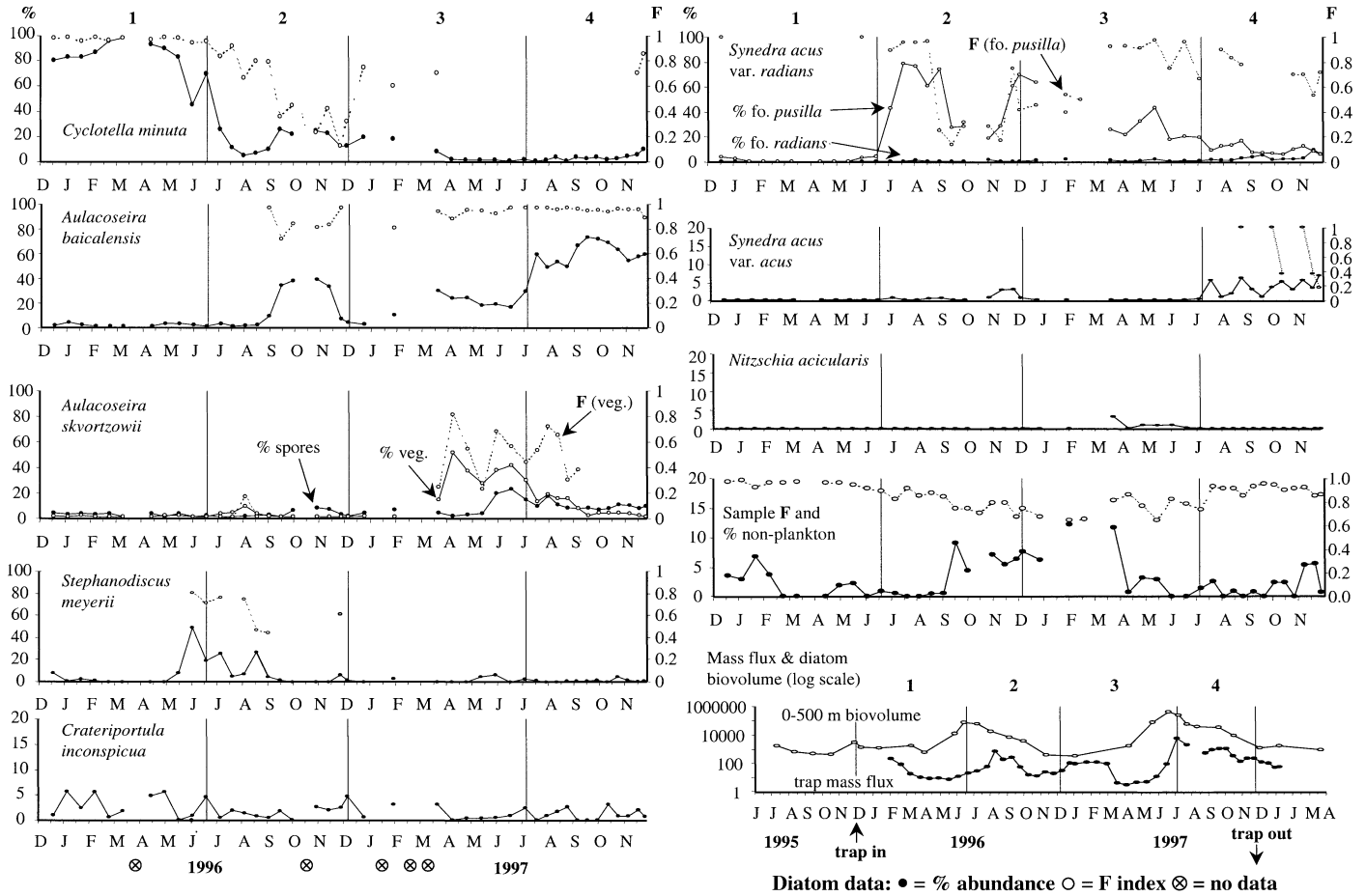


Fig. 4. Diatom analysis for upper (~550 m) sequencing (S) trap for all four trap seasons (indicated by 1–4; December 1995–November 1997) for selected taxa presented as percent abundances (left scale). Species dissolution index (F) is also shown for samples where enough valves were encountered to assess this (right scale). Sample F values and percent nonplankton over the trapping period are also shown. Diatom biovolume ( $\text{mm}^3 \text{m}^{-2}$ ) from plankton counts (0–500 m; June 1995–February 1998) and mass flux ( $\text{mg m}^{-2} \text{d}^{-1}$ ) are plotted on a logarithmic scale. Samples for which too few diatoms were found for abundance calculations of individual taxa are indicated below the lower left plot.

Z1.d-Z8.d: 9 July 1997–26 November 1997 (Fig. 3d). Diatom assemblages were similar to those of the previous 6 months, although *A. baicalensis* percentages were generally higher (between 20 and 50%), with decreases in *A. skvortzowii* (both vegetative valves and spores) and *S. acus* var. *radians* fo. *pusilla*. A larger *Synedra* species, *S. acus* var. *acus* Kütz., appeared in significant amounts for the first time in the traps, whereas *N. acicularis* was found in trace amounts below 250 m at depths up to 1,283 m, but not in the deepest trap (1,386 m). Diatom preservation reached the lowest values recorded in open traps throughout the 2-yr trapping period, with F values declining from about 0.9 in the uppermost trap (250 m) and approaching 0.6 at about 1,200 m. There was a sudden improvement in the lowest two traps to  $>0.8$ , largely inverse to the proportion of *S. acus* var. *radians* fo. *pusilla* throughout the profile. Mass and diatom fluxes were lower than the previous period and lowest in the uppermost trap. Mass fluxes were more or less constant below 500 m at about  $0.8 \text{ g m}^{-2} \text{ d}^{-1}$ , whereas there was more variability in diatom sedimentation rates with values up to  $0.6 \times 10^9 \text{ valves m}^{-2} \text{ d}^{-1}$  in the bottom trap.

Sequential traps S1 and S3: In the first trapping season (December 1995–June 1996), sample 1 from both S1 and S3 was exposed during trap recovery and might have included valves from the whole period collected in the main trap funnel. Over the 2-yr period, five samples from S1 and two samples from S3 contained too few diatoms for abundance calculations of individual taxa (Figs. 4, 5).

Upper sequencing trap: ~550 m (Fig. 4). For most of the trapping period, upper trap contents reflected relative abundance in the plankton, although this is complicated by differential settling rates for different taxa (and different colonial forms within taxa). Some taxa showed indistinct seasonal or annual signals in the upper trap (e.g., *C. inconspicua*), although this in part could be a function of the low frequencies encountered.

Samples from the first trap season were dominated by *C. minuta*, which bloomed in autumn 1995 and spring 1996 and persisted live in the upper plankton until May 1996. *C. minuta* valves were well preserved in all samples at this depth ( $F > 0.9$ ), but through July and August 1996, the relative abundance and preservation fell as residual valves sank out

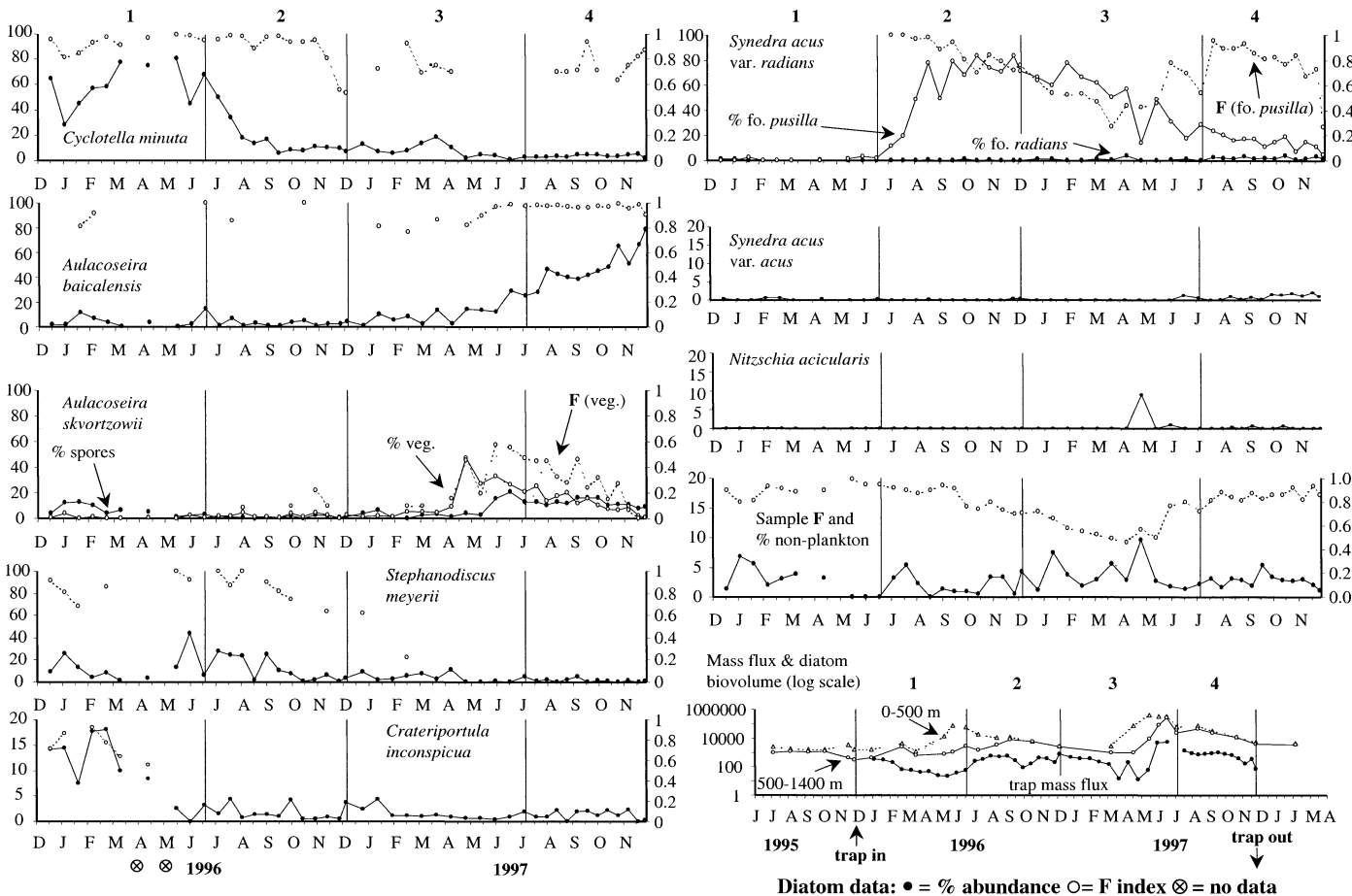


Fig. 5. Diatom analysis for lower (1,280–1,380 m) sequencing (S) trap for all four trap seasons (indicated by 1–4; December 1995–November 1997) for selected taxa presented as percent abundances (left scale). Species dissolution index (F) is also shown for samples where enough valves were encountered to assess this (right scale). Species dissolution index (F) is also shown for samples where enough valves were encountered to assess this (right scale). Sample F values and percent nonplankton over the trapping period are also shown. Diatom biovolume (mm<sup>3</sup> m<sup>-2</sup>) from plankton counts (0–500 m and 500–1,400 m) and mass flux (mg m<sup>-2</sup> d<sup>-1</sup>) are plotted on a logarithmic scale. Samples for which too few diatoms were found for abundance calculations of individual taxa are indicated below the lower left plot.

of the water column. During June 1996, well-preserved *S. meyerii* chains (F = 0.7–0.8) were recorded, although the appearance of the simultaneous spring blooms of *S. acus* var. *radians* fo. *pusilla* and *A. skvortzowii* was delayed until July and August, respectively, the latter poorly preserved (F ≈ 0.2).

During September 1996 until November or December, valve preservation of *Cyclotella*, *Stephanodiscus*, and *Synedra* taxa declined sharply. From September to November, *A. skvortzowii* spores were sedimented and *A. baicalensis* valves were relatively poorly preserved (F ≈ 0.75, the lowest value recorded for this taxon in the S1 traps over the 2-yr period). No plausible source for these changes can be seen in the plankton records, although this period coincided with elevated percentages of nonplanktonic taxa (up to 10% until April 1997) in the upper trap. Mass fluxes were also elevated over this time, despite low diatom biovolume measured in plankton samples. This might represent localized resuspension or other sediment transporting events, perhaps related to hydrographic turbulence. The sedimentation anomaly appeared to end during November 1996, when fluxes of well-

preserved *Synedra* entered the trap. *C. minuta* valves followed in January 1997 and both fluxes corresponded with observations in the plankton.

In the third trapping period, relative abundance changes in the plankton were largely reflected in the upper trap, with *S. acus* var. *radians* fo. *pusilla*, *A. skvortzowii* (first as vegetative valves, then spores), and *A. baicalensis* dominating in order. The only record of *N. acicularis* in the upper trap occurred during this time (between 1 and 3%), following a minor bloom in the plankton in March 1997. The largest diatom biovolume and mass flux for the trapping period were recorded in May and June (respectively), although values remained high throughout summer and autumn 1997.

The three spikes of good preservation (F ≈ 0.7) and greater frequencies of *A. skvortzowii* vegetative valves in April, June, and August 1997 (and perhaps *Synedra* in May, June, and August) suggest pulses of fresh material arriving in traps and progressive dissolution of the residual crops in intervening periods. Although important in the plankton throughout spring and summer 1997, *A. baicalensis* only dominated in the upper trap in the last period, reaching almost 80% in

September 1997. Preservation was then very high ( $F > 0.9$ ) and only fell to 0.9 in the final sample. Well-preserved *C. minuta* valves appeared in the final samples (coincident with an autumn bloom in the plankton), whereas the larger *S. acus* var. *acus*, recorded in significant numbers only in the early summer, was found sporadically up to 5% throughout the final period, with little dissolution.

Diatom biovolume was at a minimum when the lake was frozen and rapidly reached a peak in early summer, declining asymmetrically during the autumn. Dry weight mass flux tended to follow changes in water column diatom biovolume, with a yearly cycle peaking in summer between 1–2 weeks (1997) and 1–2 months (1996) after the diatom peak and a minimum during and just after ice cover. Sample preservation was generally good ( $F > 0.8$ ) for most of the period but declined over summer 1996–spring 1997, with a minimum of  $F \approx 0.7$  in May 1997.

*Lower sequencing trap: ~1,280–1,380 m (Fig. 5).* To a large extent, the lower trap reflected the upper trap, but with greater blurring of seasonal signals. The larger sedimentation distance exaggerates both taxon sedimentation rate differences and dissolution effects. Sample diatom dissolution, although generally good ( $F > 0.8$ ), was consistently lower than in the upper trap, especially during the third season, where it fell to the lowest values recorded in any trap ( $F < 0.5$ , and comparable with surface sediments; Mackay et al. 1998). There is, unsurprisingly, a greater offset between mass flux and diatom biovolume (0–500 m) than for the upper trap, but a clear correlation to the lower water column biovolume (500–1,400 m), except at the beginning of the first season (January–April 1996) and during winter 1996/1997. These periods might also be linked to fluctuations in the nonplankton proportions in the traps.

At the beginning of the trapping period, the trap collected remnants of crops of *C. inconspicua* (not recorded from the plankton), *S. meyerii*, *A. skvortzowii* (spores), and *C. minuta* from summer or autumn 1995. Valves gradually dissolved as they sunk out slowly under the ice (e.g., *C. inconspicua*:  $F \approx 0.9–0.55$ ; *S. meyerii*:  $F \approx 0.9–0.7$ ).

Sedimentation of *C. minuta* dominated the deep trap until June 1996, and after August 1996, it did not account for more than 20% of the assemblage. Valves, however, remained well preserved until November 1996, and subsequent influxes of fresh valves are implied by sudden increases in the  $F$  index in March, September, and November 1997, in general agreement with plankton records.

A sudden increase (to about 40% assemblage composition) of well-preserved *S. meyerii* chains in June 1996 was simultaneous with their appearance in the upper trap. Valves with little dissolution continued to enter the deep trap until September and declined thereafter in relative frequency and  $F$  index, only appearing occasionally afterwards. From July 1996, the major flux of *Synedra* valves from spring/summer 1996 began, contributing 50–80% of the assemblage from August 1996 until April 1997, although there was a steady decline in preservation from  $F > 0.9$  in July 1996 to  $F < 0.3$  in March 1997. There is little evidence of the unusual sedimentation seen in the upper trap from September to November 1996. Lower trap diatom assemblages were similar

to those in the lower water column (500–1,400 m; D. Jewson unpubl. data).

The flux of *A. skvortzowii* (valves preceding spores) reached the lower trap in May and June, with maximum values of 50 and 20%, respectively. Better preserved valves ( $F = 0.5–0.6$ ) appeared in late April and June, although percent contribution declined steadily until November 1997 in line with  $F$  values. Spore abundance remained between 10 and 20% throughout this period. In contrast, the proportion of *A. baicalensis* increased from ~10% in spring 1997 to 80% at the end of the period. Preservation rose from 0.8 to 0.9 by July and remained excellent (almost 1) until the final sample. A single occurrence of 8% *N. acicularis* ( $F = 0.71$ ) in May 1997 was followed by trace amounts (<1%) in four samples until October 1997.

Valves from the 1997 spring/summer bloom of *S. acus* var. *radians* fo. *pusilla* began to reach the lowest trap in late May, and although a relatively small proportion of the assemblage (10–30%), consisted of well-preserved valves. There is some evidence to suggest a second bloom in July as  $F$  values increase from ~0.5 to almost 1, but the dissolution index steadily declined as these valves slowly sank out. The final sample, with <5% of this taxon, was poorly preserved ( $F < 0.3$ ). Larger and more silicified forms of *Synedra* increased in relative abundance during the last period, although valves were too few to permit estimation of dissolution.

Comparison of diatom plankton, trap, and surface sediment assemblages: *Planktonic and sequencing trap data: seasonal signals.* The seasonal signal of the diatom plankton can be followed through the water column by comparing the planktonic and upper and lower S trap assemblages for the trapping period, here summarized by separate DCA axis 1 scores (Fig. 6). *N. acicularis* was infrequently found in trap samples, and excluding this taxon from the plankton dataset makes almost no difference to the axis 1 scores over the trapping period. Almost the same amount of species variance is accounted for by all datasets along axis 1 (between 36 and 38%).

The period of major change in the plankton community in trap period 1 (from *C. minuta* to *S. acus* and vars.) is found in the early part of trap period 2, with a delay of ~70–100 d as depth increases from 550 to 1,300 m. The transmission of the diatom plankton signal during trap periods 3 and 4 appeared to differ in nature as well as timing, as the axis 1 scores suggest. Taxa that appear together in plankton samples in period 3 (*A. skvortzowii* and *A. baicalensis*) appear to settle at different rates in the traps, the major pulse of *A. skvortzowii* appearing before that of *A. baicalensis*, which continued to settle into the lower traps in November 1997, some 5 months after its maximum abundance in the plankton (Figs. 2, 4).

Over the whole trapping period, there is more similarity between the trap scores and trends than with the plankton DCA scores. Once sedimentation begins in the water column, the signal is propagated down to the bottom waters (Fig. 6b,c), but its appearance is delayed and blurred to a greater or lesser extent.

*Plankton, trap, and surface sediments: taphonomic sig-*

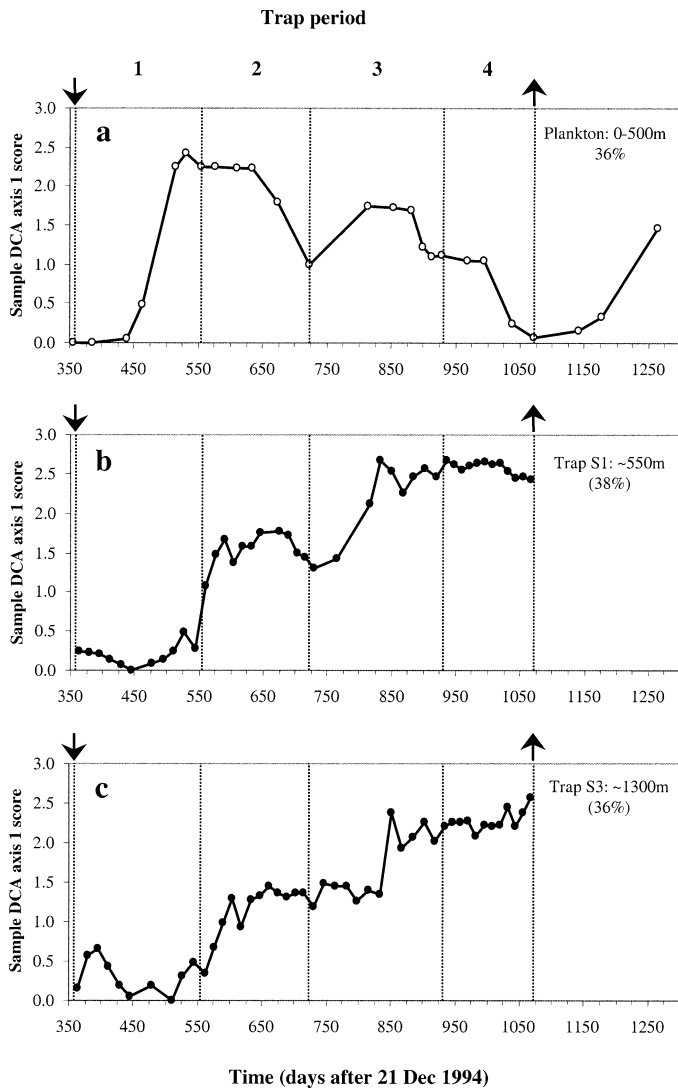


Fig. 6. Sample DCA axis scores (percentage data) for plankton (0–500 m) and sequencing trap samples from December 1995 to February 1998. Trap periods 1–4 are shown, with arrows indicating deployment period. Proportion of variance accounted for on axis 1 is given in each case. (a) Plankton DCA axis 1 scores. (b) Upper sequencing trap (~550 m) DCA axis 1 scores. (c) Lower sequencing trap (~1,300 m) DCA axis 1 scores.

nals. Plankton, and to a lesser extent sequencing trap samples, which undergo complete shifts in species composition, contrast with surface sediments, which are dominated by *C. minuta*, *A. baicalensis*, and *A. skvortzowii* around the trap site. This is a reflection of accumulation time, depth, and dissolution on diatom assemblages, and all are highly correlated. Samples represent longer accumulation periods along the progression from plankton (spot samples), to sequencing traps (~2 weeks) to open traps (~6 months), and finally to surface sediments (~1–3 yr), sedimenting over an increasing water column depth and with generally increasing dissolution. Diatom assemblages occupy smaller areas of taphonomic space along this progression.

Assemblage dissolution state varies widely within sample types, suggesting that dissolution is not a simple function of

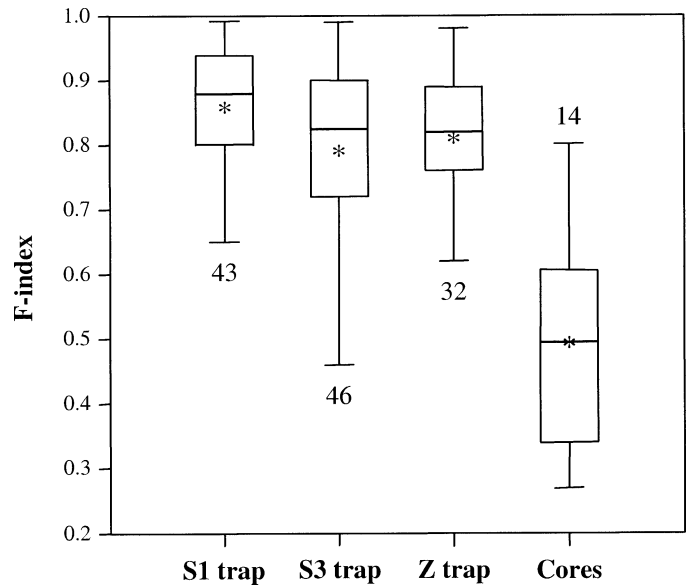


Fig. 7. Box plot of dissolution index (F) for four sample types, with number of cases in each group shown. Boxes contain interquartile range, with mean (asterisk) and median (horizontal line) F values indicated, and whiskers cover range. Comparing groups pairwise, F index values are significantly different between core tops and all other groups ( $p < 0.001$ ; Mann–Whitney *U*-test).

depth or sample integration time (Fig. 7), and might thus record the influence, and integrate the effects, of several taphonomic factors altering assemblages. There are subtle distinctions between trap sample types, but a major change occurs at the surface sediment, with core tops significantly more dissolved than all other sample types ( $p < 0.001$ ; Fig. 7). From an assumed initial F index of 1 (planktonic samples), the death assemblage becomes progressively more dissolved as it descends down the water column (S1 compared to S3). The integrated effect of this can be seen within the open (Z) traps, which are intermediate between the plankton samples and the surface sediments (mean  $F \approx 0.82$ ). At the sediment surface, however, dissolution state falls dramatically (mean  $F \approx 0.50$ ). At each taphonomic level, samples cover a considerable range of dissolution states, with good preservation possible in all types, although values of  $F < 0.45$  were only found in the surface sediments.

*Quantifying the role of taphonomic factors down the water column.* The role of dissolution, depth, and accumulation time in explaining the diatom data among the various sample types was examined using constrained ordination. The diatom datasets (plankton, trap, and surface sediments) were analyzed together and separately using CCA or RDA, depending on the underlying gradient length within the diatom data. Because there is strong time dependency within the various data types, which could effect the analysis, this was factored out in subsequent tests by including sample order, season, or year (as appropriate) in the different sample types. Results of these analyses are summarized in Table 2.

Although total numbers of samples and species are very different between sample types, assemblages become more similar (lower gradient lengths) in the progression from plankton to traps and surface sediments. Within the com-

Table 2. Results of constrained ordinations (CCA, RDA) for different combinations of sample types (percentage data). Predictor variables are dissolution indices (DI, F), time integration of samples (accumulation time), and sample depth. "All" includes plankton, open and sequencing traps, and surface sediments. Time-independent analyses (within the same sample type) factor out sample sequence as a proxy for directional changes over time (sample order used as covariable; either order or year). Significant variables are listed in order of importance, together with their unique contribution in explaining species variance [%]. The total species variance explained by all significant taphonomic parameters for the different sample types and the variance common to two or more significant variables is shown. Significance levels are given for dissolution effects only ( $n = 499$  Monte Carlo permutations).\*

Dataset	All	All†	Plankton	Trap			
				S1	S3	Open	Core tops
No. of samples	169	169	34	43	46	32	14
No. of species	69	68	12	39	42	33	44
Variance (DCA)	2.32	1.57	2.59	1.62	1.34	1.12	0.65
Gradient length	2.19	2.27	2.83	2.64	2.59	1.77	1.72
Method	CCA	CCA	CCA	CCA	CCA	CCA/RDA	RDA
Data type	%	%	%	%	%	%	log(% + 1)
Time dependent							
Significant variables	DI[5.3] Acc. time[1.9]	DI[7.3] Acc. time[2.9]		DI[13.6] Depth[7.5]	Depth[15.9] DI[10.6]	DI[31.4]	F index[19.2]
Total % explained	8.4	10.5	n/a	26.1	31.9	31.4	19.2
Common variance (%)	1.2	0.3	—	5.0	5.4	—	—
<i>p</i> Level (dissolution)	0.002	0.002	—	0.002	0.002	0.002	0.042
Time independent							
Significant variables			Year[34.6] Season[13.1]	Order[28.7] Depth[7.3] DI[6.6]	Order[26.3] Depth[11.7] DI[2.9]	Season [14.5] DI[6.4]	Year[43.4]
Total % explained	n/a	n/a	47.9	54.8	58.2	45.9	43.4
Common variance (%)	—	—	0.2	12.2	17.3	25.0	—
<i>p</i> Level (dissolution)	—	—	0.002	0.002	0.012	0.022	—

\* CCA, canonical correspondence analysis; DCA, detrended correspondence analysis; RDA, redundancy analysis. † Excludes *Nitzschia acicularis*.

bin dataset, accumulation time and dissolution state were both significant and explain about 8.4% of the variation among very heterogeneous diatom assemblages, with dissolution independently accounting for 5.3% (Table 2). Repeating the analysis without the highly dissolution-susceptible *N. acicularis* improved the explanation from these factors, with >7% of species variance uniquely explained by dissolution state. Adding time-dependent factors explained almost 50% of the change in plankton assemblages, showing the strength of seasonality on the diversity of planktonic diatom communities.

Dissolution was important for all other sample types, independently explaining between 10.6 and 31.4% of variance among trap and surface sediment samples (Table 2). Depth was important in the sequencing trap assemblages, having an effect independent of dissolution state, despite displaying little variation itself within the upper and lower traps. Even with time dependency factored within the S and Z traps, dissolution explains significant amounts of species variance (up to 6.6% for upper S traps). Interactions between significant factors were often limited. The results suggest that seasonal signals (i.e., time dependency) are transmitted down the water column, but that dissolution also has a significant effect on assemblages. Only for the core tops does dissolution state cease to be significant, independent of year the cores were taken, although this reflects the exact timing of core collection; good preservation was only found for cores collected in summer 1997. A dissolution gradient develops

within the water column and continues after sedimentation on the lake bed, blurring short-term signals from surface waters. As sediment samples become progressively more dissolved, they become increasingly similar in species composition, and dissolution itself cannot explain variance among assemblages.

*Planktonic, trap, and surface sediments: annual and interannual signals.* Using diatom abundance data for planktonic and open-tube trap samples, expected frequencies of the main planktonic taxa sinking through the water column can be calculated on an annual and multiannual basis and compared with the diatom composition found from core tops taken over the same period. This has been done for the three calendar years of plankton data (1995–1997) and for the 2 yr of trap data (1996–1997) for open traps at 500, 1,000, and 1,300 m and compared with core tops taken in 1996 ( $n = 3$ ) and 1997 ( $n = 8$ ) from the trap site (Fig. 1; Table 1). All combinations of year (1995–1997) and sample type were compared using a squared  $\chi^2$  dissimilarity index (SDI) on percentage data; results are shown in Fig. 8.

Within-group similarity was least among the planktonic community, as composite assemblages within the 1995 crop are biased by *N. acicularis*, which was rare in other samples (plankton SDI = 1.68 and 1.93, respectively, between 1995/1996 and 1995/1997). Variation between the 1996 and 1997 crops is still considerable, however (SDI = 1.26). Open-tube trap and core top samples are much more similar within each group, especially within the same year (1996 mean SDI:

		plankton mean															Z traps mean															core tops mean																																												
		annual (3): 1.62															1996 (3): 0.09															1996 (3): 0.31																																												
		all (15): 0.9															1997 (3): 0.06															1997 (28): 0.16																																												
																	all (36): 0.37															all (55): 0.45																																												
Plankton	P1996	<b>1.68</b>																																																																										
	P1997	<b>1.93</b>	1.26																																																																									
	P1995-6	0.55	0.56	1.39																																																																								
	P1996-7	<b>1.73</b>	<u>0.37</u>	<u>0.40</u>	0.78																																																																							
	P1995-7	0.83	0.67	0.73	<u>0.23</u>	<u>0.37</u>																																																																						
Z traps	Z550-96	<b>1.74</b>	<u>0.09</u>	1.28	0.65	0.46	0.76																																																																					
	Z1000-96	<b>1.75</b>	<u>0.25</u>	1.17	0.72	0.46	0.73	<b>0.11</b>																																																																				
	Z1300-96	<b>1.73</b>	<u>0.16</u>	1.01	0.67	<u>0.28</u>	0.58	<b>0.08</b>	<b>0.07</b>																																																																			
	Z550-97	<b>1.92</b>	1.18	<u>0.06</u>	1.34	<u>0.37</u>	0.70	1.17	1.04	0.91																																																																		
	Z1000-97	<b>1.89</b>	0.89	<u>0.11</u>	1.14	<u>0.20</u>	0.56	0.88	0.79	0.64	<b>0.07</b>																																																																	
	Z1300-97	<b>1.86</b>	0.83	<u>0.10</u>	1.09	<u>0.15</u>	0.51	0.83	0.76	0.60	<u>0.09</u>	<u>0.03</u>																																																																
	Z550:96-7	<b>1.81</b>	0.58	<u>0.30</u>	0.93	<u>0.08</u>	0.45	0.54	0.47	<u>0.34</u>	<u>0.20</u>	<u>0.09</u>	<u>0.08</u>																																																															
	Z1000:96-7	<b>1.80</b>	0.58	<u>0.35</u>	0.92	<u>0.11</u>	0.47	0.49	<u>0.38</u>	<u>0.28</u>	<u>0.27</u>	<u>0.12</u>	<u>0.12</u>	<u>0.12</u>	<u>0.03</u>																																																													
	Z1300:96-7	<b>1.79</b>	0.52	<u>0.32</u>	0.88	<u>0.06</u>	0.42	0.48	0.42	<u>0.27</u>	<u>0.28</u>	<u>0.13</u>	<u>0.09</u>	<u>0.03</u>	<u>0.03</u>																																																													
Core tops	1996	B43	<b>1.81</b>	<b>1.67</b>	0.68	<b>1.73</b>	1.01	1.20	<b>1.53</b>	1.26	1.26	0.72	0.89	0.75	0.86	0.87	0.84																																																											
		B112	<b>1.66</b>	1.40	1.09	<b>1.49</b>	1.01	1.13	<b>1.32</b>	0.95	1.02	1.05	1.11	1.04	0.97	0.91	0.93	0.45																																																										
		B113	<b>1.88</b>	<b>1.75</b>	1.00	<b>1.81</b>	1.25	1.39	<b>1.54</b>	1.17	1.29	0.97	1.13	1.04	1.05	1.02	1.05	<u>0.20</u>	<u>0.29</u>																																																									
	1997	B115	<b>1.83</b>	1.03	<u>0.11</u>	1.21	<u>0.29</u>	0.61	1.00	0.87	0.74	<u>0.11</u>	<u>0.15</u>	<u>0.08</u>	<u>0.18</u>	<u>0.23</u>	<u>0.19</u>	0.45	0.82	0.77																																																								
		B118	<b>1.88</b>	1.17	<u>0.07</u>	1.30	<u>0.38</u>	0.68	1.18	1.06	0.91	<u>0.09</u>	<u>0.06</u>	<u>0.11</u>	<u>0.26</u>	<u>0.26</u>	<u>0.29</u>	0.90	1.15	1.16	<u>0.21</u>																																																							
		B121	<b>1.81</b>	1.24	<u>0.14</u>	1.36	0.44	0.73	1.18	0.98	0.88	<u>0.13</u>	<u>0.15</u>	<u>0.18</u>	<u>0.28</u>	<u>0.25</u>	<u>0.31</u>	0.62	0.82	0.87	<u>0.16</u>	<u>0.09</u>																																																						
		B122	<b>1.82</b>	<b>1.62</b>	<u>0.23</u>	<b>1.68</b>	0.72	1.00	<b>1.70</b>	<b>1.57</b>	<b>1.41</b>	<u>0.32</u>	0.48	0.41	0.66	0.74	0.68	<u>0.40</u>	0.90	0.84	<u>0.27</u>	<u>0.41</u>	<u>0.33</u>																																																					
		B123	<b>1.85</b>	1.26	<u>0.04</u>	1.37	0.42	0.71	1.23	1.08	0.94	<u>0.08</u>	<u>0.13</u>	<u>0.11</u>	<u>0.28</u>	<u>0.29</u>	<u>0.29</u>	0.56	0.91	0.85	<u>0.07</u>	<u>0.08</u>	<u>0.07</u>	<u>0.24</u>																																																				
		B124	<b>1.91</b>	1.30	<u>0.02</u>	<b>1.42</b>	0.44	0.76	1.32	1.19	1.03	<u>0.07</u>	<u>0.12</u>	<u>0.13</u>	<u>0.32</u>	<u>0.35</u>	<u>0.35</u>	0.73	1.07	1.03	<u>0.15</u>	<u>0.04</u>	<u>0.09</u>	<u>0.26</u>	<u>0.03</u>																																																			
		B125	<b>1.87</b>	<b>1.43</b>	<u>0.09</u>	<b>1.50</b>	0.56	0.84	1.38	1.20	1.08	<u>0.13</u>	<u>0.21</u>	<u>0.21</u>	<u>0.39</u>	<u>0.39</u>	0.41	0.52	0.90	0.78	<u>0.15</u>	<u>0.11</u>	<u>0.07</u>	<u>0.24</u>	<u>0.03</u>	<u>0.07</u>																																																		
		B149	<b>1.75</b>	0.88	<u>0.20</u>	1.09	<u>0.22</u>	0.53	0.84	0.66	0.56	<u>0.16</u>	<u>0.13</u>	<u>0.11</u>	<u>0.13</u>	<u>0.11</u>	<u>0.13</u>	0.64	0.69	0.86	<u>0.10</u>	<u>0.17</u>	<u>0.08</u>	0.43	<u>0.12</u>	<u>0.18</u>	<u>0.19</u>																																																	
				P1995	P1996	P1997	P1995-6	P1996-7	P1995-7	Z550-96	Z1000-96	Z1300-96	Z550-97	Z1000-97	Z1300-97	Z550:96-7	Z1000:96-7	Z1300:96-7	B43	B112	B113	B115	B118	B121	B122	B123	B124	B125																																																
		Plankton						Z traps						1996			1997																																																											

Fig. 8. Squared  $\chi^2$  dissimilarity indices for different groups of samples covering similar timespan (percentage data on an annual or greater basis). Plankton samples are aggregated between 1 and 3 yr (1995–1997). Open-trap samples are aggregated for 1 or 2 yr (1996 and 1997) at three depths (550, 1,000, and 1,300 m). Core tops have been separated into those collected in 1996 and 1997. Values vary from 0 (identical samples) to 2 (maximum dissimilarity). Very similar samples (values  $\leq 0.4$ ) are underlined; very dissimilar samples (values  $\geq 1.4$ ) are boxed. Mean dissimilarity values are also given within selected groups, with numbers of pairwise comparisons in brackets.

open trap = 0.09, core tops = 0.31; 1997 mean SDI: open-tube traps = 0.06, core tops = 0.16).

There is also good agreement between expected assemblage composition from the plankton crop, open traps, and core tops for 1997 (mean SDI = 0.14, range 0.02–0.48 for  $n = 35$  pairwise comparisons) and for plankton and open traps in 1996 (mean SDI = 0.17,  $n = 3$ ), but not for core tops from that year (mean SDI = 1.35, range 0.95–1.75,  $n = 12$ ; Fig. 8). Over the 2-yr period 1996–1997, there is close correspondence between assemblages from open traps and plankton (mean SDI = 0.09,  $n = 3$ ) and open traps and core tops collected in 1997 (mean SDI = 0.32,  $n = 24$ ) but growing dissimilarity between plankton and core tops (mean SDI = 0.43,  $n = 8$ ). There does not appear to be any systematic variation in SDI values when comparing open-trap assemblages from the different depths.

Discussion

Lake Baikal as a taphonomic system—Diatom sedimentation from the photic zone is linked to the production of

extracellular polymeric substances (EPS) under the influence of nutrient limitation, which generally occurs toward the final stages of a diatom bloom (Thornton 2002). Such cells are likely to be senescent, moribund, or forming resting stages (morphological or cytological); at least, once out of the photic zone, cell growth will be arrested. Recent studies, however, have shown that sedimented diatom cells can survive, and be viable, for long periods in both freshwater and marine sediments (Sicko-Goad et al. 1986; McQuoid et al. 2002) and might even form an important seed bank for inoculating euphotic waters (Hansen and Josefson 2001). Although rarely addressed in diatom sedimentation studies, the extent to which sedimenting cells are actually alive or dead (or dying) has profound implications for diatom preservation, and indeed whether such sedimentation can be accurately described in taphonomic terms at all.

It was not possible to differentiate the living and dead cells within our methodology for analyzing the traps and the surface sediments. However, data on the proportion of intact cells with contents counted using light microscopy from plankton samples integrating the 0–500 m layer taken from

Table 3. Total plankton crop (estimated from plankton counts) in comparison with mass and diatom fluxes measured in open and sequential traps from 1996 and 1997. Reported mass and diatom accumulation rates (MAR and DAR) estimated from core tops in the southern basin are also given (*see Fig. 1* for core locations).

Type (depth, m)	Mass flux (mg dry weight cm <sup>-2</sup> yr <sup>-1</sup> )			Diatom flux (10 <sup>3</sup> valves cm <sup>-2</sup> yr <sup>-1</sup> )		
	1996	1997	Mean	1996	1997	Mean
Plankton	—	—	—	20,413	16,624	18,519
Z traps						
<70	5.31	—	5.31	6,726	—	6,726
150–250	—	23.48	23.48	—	15,440	15,440
~550	11.32	30.85	21.08	15,726	25,152	20,439
~750	11.99	30.34	21.17	14,868	15,674	15,271
~1,000	11.59	31.08	21.33	14,372	25,802	20,087
~1,200	11.91	31.70	21.81	13,267	17,569	15,418
~1,300	11.93	32.74	22.33	12,209	17,709	14,959
~1,400	—	34.53	34.53	—	23,425	23,425
Mean	10.68	30.68	20.68	12,861	20,110	16,486
S traps						
S1: ~550	3.04	21.46	12.25	—	—	—
S2: ~550	9.25	—	—	—	—	—
S3: ~1,300	7.95	32.29	20.12	—	—	—
Mean	6.75	26.87	16.18	—	—	—
Core	Year	Depth (m)	MAR	DAR		
BAIK38†	1990–1994	690	17	112.5		
BAIK6*	1990–1992	1,425	28	—		
South basin†	1990s	~1,400	—	~200		

\* Appleby et al. 1998. † Mackay et al. 1998.

July 1995 to February 1998 (and so including the mass flux event of 1997) are available. For the four main taxa (*A. baicalensis*, *A. skvortzowii*, *S. acus* var. *radians* fo. *pusilla*, and *C. minuta*, accounting for 87% of total cell numbers over this period), about 56% of cells had contents, although this varied according to species and year, and falls further at depth (D. Jewson unpubl. data). However, when compared with sample preservation from the upper sequencing trap (~550 m) over this period, good preservation is not linked solely, or simply, to periods of few empty cells. Furthermore, this method almost certainly overestimates the true proportion of viable cells (Sicko-Goad et al. 1986), perhaps by a factor of 5 (McQuoid et al. 2002). Most diatoms sedimenting below the photic zone are dead or moribund (even those with cell contents), and this proportion increases rapidly with water column depth. More cells will be alive after rapid transport from the photic zone in mass flux events (and intact cells, with contents were observed within green-brown, flocculent material after the flux event in July 1997; R. Flower pers. comm.), and the benthos can be expected to respond to this pulse rapidly (cf. Lampitt et al. 2001). Nonetheless, death assemblage taphonomy remains the dominant feature of deep-water sedimentation in the lake.

Several studies have reported long-term survival of diatoms (up to 60 yr) in sediments from shallow marine and coastal areas (e.g., Lewis et al. 1999; Hansen and Josefson 2001; McQuoid et al. 2002) and freshwaters (Sicko-Goad et al. 1986) in both oxic and anoxic conditions. Indeed, Hansen and Josefson (2001) found that in a shallow coastal system (depth <27 m), sediments were a major pool of viable di-

atoms and might be important seed banks, containing almost half (44%) the number of diatoms produced during the spring bloom. Rough calculations, however, suggest that this cannot be the situation in deep-water sediments of Lake Baikal. Even using a diatom accumulation rate of 100,000 cells cm<sup>-2</sup> yr<sup>-1</sup> for the southern basin (Table 3), and assuming 50% of cells in sediments are living and remain viable for 25 yr, the viable sedimentary inventory in the southern basin is calculated as  $1.25 \times 10^6$  cells cm<sup>-2</sup>, or about 14% of the average annual plankton count for 1996–1997 ( $9.25 \times 10^6$  cells cm<sup>-2</sup>; Table 3). If, more realistically, cells have a half-life of <5 yr in sediments, calculations suggest sediments contain not more than  $\sim 0.36 \times 10^6$  viable cells cm<sup>-2</sup>, around 4% of annual water column population; if the initial ratio of living cells is 25%, this drops to  $\sim 0.18 \times 10^6$  viable cells cm<sup>-2</sup>, or about 2% annual water column population. Such calculations almost certainly overestimate viable sedimentary population figures (*see above*). Also, any limited resuspension from the deep-water lake bed (*see below*) makes it extremely unlikely that cells, even if viable, can be returned to the photic zone. Yet although deep-water sediments in Lake Baikal today are unlikely to be seed banks for inoculating diatom blooms in the upper waters, significant sedimentary diatom populations probably do exist in shallower areas. Diatom blooms are often observed to begin in bays and along upper lake slopes, perhaps linked to thermal bar development, suggesting that these areas could indeed function as seed banks (D. Jewson pers. comm.).

*Taphonomic processes in the water column and at the sediment surface*—Results demonstrate that there is consid-

erable variation in the plankton community both seasonally and from year to year in the southern basin of Lake Baikal and that these signals are transmitted throughout the deep Baikal water column (Figs. 2–4). There are, however, taphonomic effects of both differential settling speeds and dissolution on the different diatom taxa that blur this signal with depth (Fig. 6). Although many studies have found surface productivity signals propagated over deep-water columns in the ocean (e.g., Billett et al. 1983; Abelmann and Gersonde 1991; Lampitt et al. 2001), several also report that factors such as zooplankton grazing in upper waters, selective dissolution of microfossils, and lateral advection/resuspension at depth can distort or decouple this signal entirely (e.g., Samtleben et al. 1995; von Bodungen et al. 1995; Kohly 1998). All these aspects are considered below.

The role of the faunal community: Zooplankton and other fauna can play an important role in diatom sedimentation as a control on the plankton community, by rapid transport of digested material to depth and by bioturbation in the uppermost, oxic layers of sediments. Data on zooplankton (numbers of individuals of copepods, rotifers, and total crustaceans) were enumerated from a subset of the same samples as water column diatom counts. In a multivariate analysis (RDA; not shown), zooplankton data (by group or in total) did not significantly explain any variation within contemporary diatom abundance data, although effects incorporating time lags were not tested. Zooplankton grazing under the ice might, however, have an important role in determining the development of the diatom inoculum in the following season in Lake Baikal (D. Jewson unpubl. data).

Diatoms transported within fecal pellets can suffer physical damage and the removal of protective organic coatings but reach the sediment surface quickly (Ragueneau et al. 2000; Gallinari et al. 2002). The role of fecal pellets (Buck and Newton 1995) as a transport mechanism cannot be determined from this study, but frustules of *Aulacoseira* spp. and *S. meyerii* were often unbroken in long chains of cells in both trap types after treatment, suggesting that the majority of valves in traps had not been digested. Furthermore, during summer 1997, although both *A. baicalensis* and *A. skvortzowii* were blooming in the plankton at the same time, sedimentation patterns were not simultaneous in S traps (Figs. 4, 5). If grazing is invoked as a major sedimentation mechanism at this time, it would have to be largely specific to *A. skvortzowii*. Grazing might nonetheless be important at certain times.

Because the zoobenthos is resource limited and feeds on deposited diatoms, invertebrate bioturbation of sediments could affect diatom preservation. This can exacerbate physical breakage, promoting release of dissolved silica to the overlying water and reducing silica saturation of pore waters. Alternatively, mixing might enhance preservation by transporting valves below the uppermost sediment, where most silica dissolution occurs (cf. Ragueneau et al. 2000). Sedimentary laminae of *Aulacoseira* (not identified to species level) do occur in thin sections of glacial and interglacial sediments collected from several depths in the (oxic) north basin, however (Francus and Karabanov 2000). These laminae, 0.6–2 mm thick, are interpreted as representing mass

flux events from *Aulacoseira* years because silt content and grain shape was similar within and outside laminae, suggesting that, in the north basin at least, bioturbation might not always blur mass flux events. The efficiency of bioturbation as a process mixing upper sediment might be overestimated in Lake Baikal, or at least variable in time, space, or both. Further work is needed to clarify the role that Lake Baikal's fauna play in diatom population dynamics, sedimentation through the water column, and preservation in sediments.

Diatom dissolution: Although biogenic silica produced in surface waters is partly remineralized in the water column of freshwater lakes (e.g., Schelske 1985), dissolution is not generally regarded as the dominant control on sedimentary diatom abundances in low alkalinity, oligosaline lakes (Colman et al. 1995) and is rarely assessed. Diatom dissolution in Baikal accounts for almost 20% of variation in surface sediment assemblages, between 11 and 31% among trap samples and 5 and 7% when all the diatom data are included (Table 2). This is comparable to that found within a natural and experimentally dissolved surface sediment dataset from the Southern Ocean (6.6%; Pichon et al. 1992a). Nonetheless, results might underestimate the effect of dissolution because, even within the biocoenosis, preservation might not be perfect (Ryves et al. 2001). This assumption could be even less secure for the plankton samples analyzed here, as these included live and dead cells from up to 500 m depth.

Previous studies have noted that tychoplanktonic *N. acicularis* is extremely poorly represented within the upper sediments, despite major blooms (Mackay et al. 1998; Bondarenko 1999; Popovskaya 2000). It was recorded in the plankton every year from 1994 to 1998 and was found growing in mass abundance on the upper surface of buoys of the trap array in June 1996 (R. Flower pers. comm.). Results here confirm that *N. acicularis* valves are almost entirely dissolved within the water column or soon after deposition at the sediment surface. No trace of the spring 1995 bloom of *N. acicularis* (Fig. 2) was found in the surface sediment of cores taken in 1996 from this area.

Dissolution affects all sedimenting planktonic taxa in Lake Baikal, however, albeit less severely, as F values from the sequencing traps indicate (Figs. 4, 5). This is particularly noticeable for the fine *Synedra* species and *A. skvortzowii* vegetative valves (Figs. 4, 5). Recent research in marine systems shows that colonization and utilization of aggregates by heterotrophs is important for biogenic remineralization in upper waters (Kiørboe et al. 1998; Kiørboe 2000; Azam and Long 2001). In particular, bacteria are associated with sinking biogenic matter in oceans (Kiørboe and Jackson 2001) and may have an important role on diatom dissolution (Bidle and Azam 1999). Bacterial removal of protective organic cell coatings and other EPSs is recognized with diatoms in both marine (Thornton 2002) and freshwater systems (Hoagland et al. 1993). EPSs are important in floc formation, which can accelerate diatom transport to the sediment surface. Both mechanisms promote diatom preservation, although the extent and nature of EPS in Lake Baikal diatoms is unknown. Bacteria are abundant throughout the Lake Baikal water column (Nagata et al. 1994).

Significant silica dissolution has been shown to occur within oceanic sediment traps themselves, especially when total biogenic silica flux is low (Gallinari et al. 2002). Over the whole trapping period, there was no correlation ( $r^2 < 0.03$ ) between mass flux and sample dissolution index for either S1 or S3 traps, but on a yearly basis, both S1 and S3 traps did show weak inverse relationships between (log) flux and sample F values in 1997, (significant for S3 trap:  $r^2 = 0.33$ ,  $n = 23$ ,  $p < 0.01$ ). However, if in-trap dissolution was the controlling factor, one might expect sample dissolution to vary in relation to the time between sedimentation in a trap cup and laboratory processing (within weeks after trap removal). Figures 4 and 5 show no consistent trend in dissolution index as a function of period within a trapping season, even within lower flux periods.

Low-flux, high-dissolution periods were dominated by *S. acus* and vars. in spring and early summer 1997 (Figs. 4, 5). High flux periods are associated with floc formation and rapid sinking speed, whereas low-flux periods are dominated by dispersed valves sinking more slowly, which might account for this observation. The tendency for diatom blooms to form flocs, then, might contribute to the poor preservation of taxa such as *S. acus* and *N. acicularis*, affecting sinking speed and the time that valves are exposed to bacterial or faunal activity in the water column, as well as the intrinsic susceptibility to dissolution of taxa with large apparent surface area to volume ratio. Average solubility of biogenic silica assemblages reaching the sediment surface has been shown to decrease with the speed with which particles sink within the water column (Ragueneau et al. 2000; Gallinari et al. 2002). Differential dissolution of the most soluble silica phases (species, valves within a population, and parts within a valve) can partly explain this observation, but other processes in the water column (e.g., interactions with metal ions, such as Al) also have important consequences for silica solubility and diatom preservation in the underlying sediments (Ragueneau et al. 2000). Changes in diatom assemblage composition during sedimentation are linked to changes in biogenic silica quality.

Diatom dissolution behaves asymptotically across the sediment–water interface, dropping from  $\sim 0.8$  (deepest open traps) to  $\sim 0.5$  (Fig. 7), with relatively little variation within uppermost sediments (Mackay et al. 1998). This is despite major fluxes of well-preserved *A. baicalensis* valves that follow the high-abundance “*Aulacoseira* years,” which occur approximately every 3–4 yr (Bondarenko et al. 1996). Valves of *A. baicalensis* sinking out during the last trapping period (Fig. 3) were very well preserved at all depths ( $F \approx 0.9$ ; Figs. 4, 5), yet in three nearby core tops taken from 1996, which should include the last *Aulacoseira* year (1994), *A. baicalensis* valves were badly dissolved ( $F = 0.31$ ). Good preservation in core tops collected in summer 1997, after a mass flux of *A. skvortzowii* and *A. baicalensis*, confirm the trap evidence that well-preserved valves reach the lake bed: average F values for surface sediment assemblages taken in 1993–1996 ( $F = 0.43$ ,  $n = 6$ ) are significantly lower than that for cores taken from 1997 ( $F = 0.58$ ,  $n = 8$ ;  $p < 0.05$ , Mann–Whitney *U*-test).

This implies that substantial dissolution occurs within the surface sediment, certainly within 3–4 yr and probably with-

in months after sedimentation. Given the low sedimentation rates ( $\sim 1 \text{ mm yr}^{-1}$  in cores from pelagic areas; Mackay et al. 1998) and bioturbation of uppermost sediments (*but see* Francus and Karabanov 2000), it is unlikely that a dissolution front will be seen by standard sampling techniques. Comparison of expected and observed fluxes (Mackay et al. 2000; R. Battarbee unpubl. data) show that poorly silicified taxa (e.g., fine *Synedra* spp., *A. skvortzowii* vegetative valves) are preferentially dissolved at the sediment–water interface, thus biasing assemblages in favor of more robust forms (e.g., *A. baicalensis*, *C. minuta*, and *A. skvortzowii* spores). The effect on reconstructions has generally not been addressed.

Horizontal transport: Sedimentary assemblages are not merely a mix of the seasonal diatom plankton but are qualitatively altered by taphonomic processes within the water column and at the sediment–water interface (Fig. 8), of which dissolution and accumulation time appear the most important (Table 2). Depth appears to have little effect in explaining diatom composition independent of dissolution itself (Table 2), although there is a suggestion from the sequencing traps that this is significant, at least over the short term. Movement of water masses and sedimentary material laterally into the trap site from areas beyond that monitored for plankton could explain this. For example, the flux of appreciably dissolved *A. baicalensis* (and *C. minuta* to some degree) into the upper trap in October–November 1996 (Fig. 4) cannot be convincingly explained by slow sedimentation from a planktonic crop, especially as it fails to appear in the lower trap later (Fig. 5). This pulse could, however, represent residual crops from another area of the southern basin, although this would invoke an advective current over several weeks. Storminess might have an influence on lateral advection and vertical mixing (and so particle sinking speed and signal blurring). Baikal’s southern basin is weakly stratified  $>250 \text{ m}$  depth, with surface winds in the open-water season providing much of the kinetic energy for bottom currents, although these averaged only  $3 \text{ cm s}^{-1}$  in 1996–1997 (Ravens et al. 2000). Because turbulence is at a maximum before ice cover, the event in autumn 1996 might record a middepth lateral current, although evidence of a similar event was not seen in traps in 1997, when winds speeds and turbulence were higher (Ravens et al. 2000).

Resuspension at depth: Resuspension of material from the lake floor of Baikal was not a major factor affecting profundal sedimentation over the period of this study. Although data from the open traps close (3–6 m) to the lake bed from the present study (trapping periods 1, 3, and 4; Fig. 3) suggest slight increases in diatom and mass flux, they also record increases in the preservation state of deposited diatom valves (Fig. 3). The reverse would be expected if diatom valves from adjacent surface sediments were resuspended into the traps. For example, *A. baicalensis* valves from 11 core tops collected nearby in 1996–1997 are appreciably dissolved ( $F_{A,baic} = 0.25\text{--}0.83$ , mean = 0.53). In contrast, *A. baicalensis* is well preserved in the near-bottom traps from these three periods ( $F_{A,baic} = 0.88\text{--}0.95$ ), suggesting little resuspension from adjacent sediments. This finding contradicts

some previous results reported from Lake Baikal from a deep trap (at 1,582 m, 28 m above the lake floor) in the middle basin (Kempe and Schaumburg 1995; Grachev et al. 1996) and is more reconcilable with the weak bottom currents (average  $3 \text{ cm s}^{-1}$ ) measured during the trap deployment (Ravens et al. 2000; *see above*). Poor diatom preservation (and higher proportions of benthic taxa) might be a useful marker for contamination by surface sediments in Lake Baikal.

*Diatom and bulk sedimentation, deposition, and accumulation*—Diatom-specific mean sinking velocities can be estimated from observed maximum abundance in the plankton and from the appearance at lower depths in the sequencing traps. Mean values of between  $7$  and  $9 \text{ m d}^{-1}$  were calculated for *C. minuta*, *S. acus* var. *radians* fo. *pusilla*, and *A. baicalensis*, whereas velocities for *A. skvortzowii* and *S. meyerii* are an order of magnitude greater, at  $\sim 70$ – $85 \text{ m d}^{-1}$ . Both *A. skvortzowii* (vegetative cells and spores) and *A. baicalensis* are implicated in the high and rapid flux recorded in the same single cup in upper and lower sequencing traps 830 m apart in early June 1997 (Figs. 4, 5), indicating sedimentation of at least  $60 \text{ m d}^{-1}$  during this period, and probably  $>100 \text{ m d}^{-1}$ . Rapid sinking speeds of  $>100 \text{ m d}^{-1}$  have been reported for diatom-rich flocs from marine systems (e.g., Scharek et al. 1999; Nodder and Northcote 2001; Gallinari et al. 2002), whereas values from  $<1$  to  $30 \text{ m d}^{-1}$  characterize sinking rates of individual cells or smaller aggregates (Waite and Nodder 2001; Gallinari et al. 2002). The open-trap data (Fig. 3c,d) suggest that early summer sedimentation, in terms of numbers of valves, is dominated by *A. skvortzowii*, although the larger and more heavily silicified valves of *A. baicalensis* will have a disproportionate effect on mass and biovolume fluxes.

Settling rates are highly variable within species (Figs. 4, 5) and between the plankton and upper trap and the upper and lower traps, suggesting that live diatoms sink more slowly than dead cells (Cushing 1992) and that factors affecting settling speed, such as coagulation and clumping (Kjørboe et al. 1994; Grimm et al. 1997), will vary over time. *S. meyerii*, *A. skvortzowii*, and *A. baicalensis* all produce long filaments of cells during summer blooms, but *A. baicalensis* appears more able to maintain buoyancy, or resist flocculation, than the other taxa (although aggregation by itself might not imply rapid sinking rates; Kjørboe et al. 1998). Even for dispersed valves, seasonal differences in sinking rates relating to valve morphology can be expected for *A. baicalensis*, because average valve length and width increase markedly during summer (D. Jewson unpubl. data). Trapping results suggest that if mass sedimentation events are associated with *A. skvortzowii* blooms, rather than *A. baicalensis*, such events should not necessarily characterize *Aulacoseira* years, although the two species generally co-occur (Edlund et al. 1996).

Trap fluxes can be compared to those estimated from cores from the southern basin (Table 3; Appleby et al. 1998; Mackay et al. 1998). Open-trap mass fluxes from 1996 and 1997 show remarkable consistency within a year at different depths, except for the traps  $<70 \text{ m}$  in 1996 (for which diatom abundance is also low), but increase threefold from 1996

to 1997 (from  $\sim 100$  to  $\sim 300 \text{ g dry weight m}^{-2} \text{ yr}^{-1}$ ). Sequential trap flux data, however, are very different between lower and upper depths: the trap at  $\sim 550 \text{ m}$  collected about half the amount in the open-tube trap at the same depth over the 2-yr period. Mass fluxes from both trap types averaged over the water column over both years show good agreement in quantity with estimated accumulation rates from two dated cores ( $\sim 200 \text{ g dry mass m}^{-2} \text{ yr}^{-1}$ ), although the quality of trap seston and lake sediment is very different, especially in terms of biogenic silica (cf. Ragueneau et al. 2000).

The anomaly in the upper sequencing trap might be due to poor collection efficiency, including removal of material from the funnel from resuspension effects, the action of animals, or both. Relatively little is known on the role of aquatic fauna in affecting trap content (e.g., swimming zooplankton) despite the likelihood that it does affect particle flux measurements (Lampitt et al. 2001). Counts of swimmers in sediment traps over several years in the north Atlantic have demonstrated their widespread distribution throughout the water column, even at  $>4,500 \text{ m}$  depth, broadly correlated with flux size, although numbers show a strong decrease with depth (Lampitt et al. 2001). Current speeds at the trap site might be even more critical for trapping efficiency; Lampitt et al. (2001) state that flux data should be discarded where current speeds  $>15 \text{ cm s}^{-1}$  are found. Based on concurrent measurements from the trap array at depth, which recorded a maximum current speed of  $3 \text{ cm s}^{-1}$  (Ravens et al. 2000; *see above*), this figure is unlikely to have been exceeded over much of the water column. Biological activity is thus mainly implicated at  $\sim 550 \text{ m}$  depth because the parallel S2 trap (deployed in 1996 and poisoned with formaldehyde) recorded three times the amount of material in 1996 as the untreated S1 trap, and only slightly less than the 550-m open-tube trap. Mean dry weight sedimentation in S1 over 1996–1997 rises to  $153.5 \text{ g m}^{-2} \text{ yr}^{-1}$  using the figures for S2 in 1996, though still lower than in the open traps at this depth. Despite such sediment scavenging from the upper S traps, assemblage composition is not noticeably affected (cf. Figs. 4–6). Differences between the deep S3 and the 1,300- and 1,400-m open-tube traps are smaller and suggest reduced in-trap processes at this depth. Low trap efficiency was inferred for a similar sequencing trap at 1,000 m in the North Atlantic, although composition was not thought to be affected, whereas at 3,000 m depth, sequencing traps were slightly less efficient during high flux periods (Lampitt et al. 2001).

Diatom flux rates (Table 3) from the open traps show considerable interannual variability through the water column (cf. Fig. 3). Consistent mass fluxes from the same traps could reflect errors in estimation of valve abundance; thus, valve abundances averaged down the water column might be a better guide to diatom deposition. Diatom fluxes are, on average, about 50% greater in 1997 than 1996 ( $\sim 13$  compared to  $\sim 20 \times 10^6 \text{ valves cm}^{-2} \text{ yr}^{-1}$ ), but they contribute disproportionately to the mass flux because larger more heavily silicified taxa are important (e.g., *A. baicalensis* valves and *A. skvortzowii* spores). However, contrary to the expectation from mass and diatom flux (Table 3) and biovolume estimates (Figs. 4, 5), diatom production (estimated from plankton monitoring) was larger in 1996 than 1997. This is ex-

plained by the delayed arrival of slowly sinking crops in traps at depth and the high numbers of more delicate valves produced in 1996 than 1997, some fraction of which is lost in the water column (e.g., *S. meyerii* and *S. acus* var. *radians* fo. *pusilla*). Average values over the period 1996–1997 are comparable between plankton production ( $\sim 18.5 \times 10^6$  valves  $\text{cm}^{-2} \text{yr}^{-1}$ ) and open-trap deposition ( $16.5 \times 10^6$  valves  $\text{cm}^{-2} \text{yr}^{-1}$ ), suggesting perhaps 10% loss of valves in the water column (in a non-*N. acicularis* year).

Diatom accumulation rates (DAR) reported from the southern basin (Table 3), especially from a shallower shoulder site (BAIK38; Fig. 1) are about two orders of magnitude smaller than open-trap deposition. This implies that perhaps only 1% of valves produced in the water column are preserved in sediments, although there are large differences between species in susceptibility to dissolution (*see below*), which compares to the global figure of 3% preservation efficiency (the ratio of biogenic silica buried to that produced in surface waters, on a mass basis) in the oceans (Tréguer et al. 1995). Results suggest most diatom dissolution occurs at the surface sediment in Lake Baikal (accounting for about 90% of valve losses). If valve flux could be equated to biogenic silica flux, it would be equivalent to a benthic preservation efficiency (ratio of biogenic silica buried to that reaching surface sediments) of  $\sim 1$ –2%, which is lower than reported from many deep-water marine systems (5–12%, rising to 30% at high flux sites; Ragueneau et al. 2000, 2001). A longer series of trap data from Lake Baikal, in terms of biogenic silica flux as well as valve number, is needed to establish a proper comparison, especially given the great interannual variability in biogenic silica production (if not valves; Table 3). Preliminary measurements from open-trap material from all depths in the third season (December 1996 to July 1997) suggest average silica content of 85% dry weight (SD = 3.3%,  $n = 8$ ; M. Sturm pers. comm.), whereas reported values of biogenic silica from upper sediments from the southern basin are  $\sim 20\%$  dry weight (Boyle et al. 1998). Even if a small fraction of trap silica is not biogenic, surface sediments clearly play a critical role in silica recycling in Lake Baikal.

Absolute flux rates from open traps in the present study are greater than those recorded from the middle basin (average values of 120.1 g and 198.8 g dry weight  $\text{m}^{-2} \text{yr}^{-1}$ , from upper and lower S traps respectively, compared to 11.5 g and 57.4 g  $\text{m}^{-2} \text{yr}^{-1}$  for traps at 396 and 1,582 m, respectively; Kempe and Schaumburg 1995). Differences in both organic and inorganic sedimentation are to be expected across Baikal because of the different hydrographic settings (such as the influence of major tributary inflows from the Selenga in the middle basin; Fig. 1) and phytoplankton communities (Kozhova 1987; Bondarenko et al. 1996). A strong regional signal in the diatom plankton is clearly shown by variations in surface sediment diatom assemblages across Lake Baikal (Mackay et al. 1998; Mackay et al. 2003).

*Taphonomic implications for limnology and paleolimnology*—An assessment of preservation is important not only for paleoenvironmental interpretation of assemblages, but it can shed light on limnological processes. Pulses of well-preserved diatoms in sediment traps can be traced to epi-

sodes of planktonic production, whereas anomalously poorly preserved valves can imply horizontal transport, resuspension of older material or variations in initial quality of biogenic silica (Gallinari et al. 2002). Although there is great interannual variability in planktonic species composition (Figs. 2, 8; Table 2), the character of sedimenting and sedimented assemblages is increasingly driven by taphonomic processes, especially dissolution. Taphonomic effects are highly dependent on species, which vary in their intrinsic resistance to dissolution (e.g., comparing *N. acicularis*, finer *Synedra* spp., and *A. skvortzowii* vegetative valves with *C. minuta*, *A. baicalensis*, and *A. skvortzowii* spores), their autecological behavior (e.g., floc formation or dispersed sinking), and their interactions with other organisms (e.g., zooplankton and zoobenthos).

Further Baikal studies are in progress to estimate absolute loss rates of diatom valve numbers for each of the major planktonic species during the sedimentation process. Preliminary data suggest that between 0.1 and 9% of valves (depending on species) produced in the water column become incorporated into sediments (Mackay et al. 2000; R. Battarbee unpubl. data). Although major glacial/interglacial diatom productivity changes do seem to be recorded by the biogenic silica content of sediments (Qiu et al. 1993; Colman et al. 1995; Karabanov et al. 2000), less extreme differences in paleoproductivity (e.g., over shorter timescales) might not be accurately estimated by biogenic silica content. Quantitative taphonomic studies might be needed to calibrate the relationship between dissolution state, diatom abundance, and biogenic silica loss (Ryves et al. 2001).

Differential diatom dissolution has major implications for inferences on the basis of species composition, although transfer functions developed from dissolved assemblages are still effective tools (Pichon et al. 1992b; Mackay et al. 2003). Developing loss rates for diatom species from taphonomic studies (Mackay et al. 2000; Ryves et al. 2001) could allow “correction factors” to be applied to species’ abundances in training sets and fossil samples and for the development of improved models for paleoenvironmental reconstruction.

Combining monitoring of seasonal and interannual variability of planktonic crops with sediment trapping and high-resolution studies of well-dated cores provides an integrated and powerful approach to complex issues of recent sedimentation of diatoms in Lake Baikal. Changes in the plankton crop are transmitted relatively quickly and coherently, even to the deep traps, although differential sinking rates and dissolution blur the signal. Differential dissolution of diatom valves in the water column, and especially at the sediment surface, partly destroys and certainly distorts the message during incorporation into the sedimentary archive, which could be further disrupted by episodic turbidite events. Rapid mass flux events are important short-term processes in sediment deposition to the lake floor, although dissolution and perhaps bioturbation soon mask their imprint in the sediment record. Because biogenic silica and sedimentary diatoms are used as climate proxies in Lake Baikal sediments, understanding biogenic silica deposition and dissolution dynamics in this system is essential for a better interpretation of long-term paleoclimate records and might also be relevant to silica cycling studies in the oceans and other large lakes.

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