Limnol. Oceanogr., 37(8), 1992, 1759–1769

The role of planktonic algae in the cycling of Zn and Cu in a productive soft-water lake

Abstract—Concentrations of dissolved Zn and Cu were measured alongside biomass (algal numbers, organic C, and Chl *a*) and dissolved micronutrients (P, Si) over an 8-week period, covering a pronounced bloom of the diatom, *Asterionella*. The distribution of dissolved Zn appears to be affected by algal cycling in two ways: in the period up to and including the diatom maximum, dissolved Zn correlates ($P < 0.01$) positively with phosphate and silicate, indicating atomic C : P : Zn ratios of 106 : 1 : 0.034, and negatively with Chl *a*; and following stratification, epilimnetic concentrations are significantly ($P < 0.01$) less than those in the hypolimnion. Dissolved Cu distributions are unaffected by the spring diatom bloom. The Zn and Cu contents of the diatom standing crop were also determined by elemental analysis of suspended particulate material in two consecutive years, providing independent estimates of metal stoichiometry. Mass budgets indicate a substantial removal and transfer to the sediments of Zn via phytoplankton, but a negligible effect on the cycling of Cu.

Increasingly, comparisons have been drawn between the geochemical cycling of metals in oceans and lakes, including consideration of the relative importance of planktonic algae in controlling metal concentrations and vertical fluxes through the water column (Sigg 1985; Murray 1987). Although a coherent pattern of behavior with regard to several metals has emerged in the oceans, the picture is less clear in lakes. In both environments, the trace metal composition of algae has been obtained from analyses of suspended particles and sediment trap material. However, in contrast to the oceans, there has been little or no supporting evidence in lakes from positive correlations between the concentrations of dissolved metals and those of micronutrients such as P and Si. The absence of such correlations may reflect a real difference between lakes and oceans, but may also in part reflect a lack of appropriate lacustrine data. The apparent absence of dissolved trace metal—micronutrient relations in lakes has been attributed to factors such as the lower sensitivity of lakes to metal uptake by algae (e.g. due to significant continuous metal inputs from runoff, atmospheric deposition and direct anthropogenic discharges, and to the depressed depth scale of lakes), blurring by other processes (e.g. redox cycling and scavenging by other categories of particles), and the highly dynamic nature of lake systems. Because of the interplay between these factors Murray (1987) has suggested that there may be a limited time window in lakes, during which dissolved metal-nutrient relations are apparent.

The present study was undertaken as part of a larger lake study (Reynolds 1986) with the aim of providing quantitative measures of Zn and Cu cycling by planktonic algae in Windermere (the English Lake District). Specific objectives were to investigate whether an algal-mediated relation between dissolved metal and micronutrient concentrations could be observed in Windermere and to quantify the importance of planktonic algae in trace metal budgets. The sampling strategy was based on Murray's concept of a suitable "time window" for such observations and on a previous report that particulate Cu deposition, determined by sediment trapping in 1980–1981, peaked in Windermere during March and April (Hamilton-Taylor et al. 1984). It was suggested that this may be related to the growth and sedimentation of the diatom *Asterionella formosa* Hassell during the spring bloom. The marked increase in biological activity and the associated decrease in micronutrient concentrations, together with gradual thermal stratification of the water column, are additional reasons why the

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Acknowledgments

Work supported by a Natural Environment Research Council studentship to G.L.R. (GT4/83/AAPS/24). We thank members of the Institute of Freshwater Ecology for cooperation and assistance throughout the study and the North West Water Authority for providing discharge data and access to its property.

Table 1. Measured detection limits and combined sampling and analytical precision for dissolved and particulate metal analysis.

	Dissolved metals			Particulate metals
	Detection limit (nmol liter^{-1})	Within-batch precision* (%)	Between-batch precision* (%)	within-batch precision* (%)
Zn	1.3	9.5	13	44
Cu	0.8	2.9	21	4.0

* Expressed as C.V.

March–May period is likely to be ideal for a detailed time-depth study of algal effects on trace metal distributions.

Windermere has a surface area of 14.8 km^2 and is a warm monomictic lake, naturally divided into two similar-sized basins. The north and south basins have maximal depths of 64 and 42 m. For most of this century, the lake has had a permanently oxygenated water column and oxidized surface sediment floc, but since 1979 there has been a tendency for hypolimnetic anoxia to develop late (September–October) in the stratified period in the south basin. The main sampling program was carried out weekly at the deepest point in the south basin (54°19′N, 2°56′W) over the period 2 April–4 June 1985. Samples of suspended matter were also collected at the peak of the bloom in 1984.

In the main program, the water was sampled at eight depths between 1 and 30 m by means of a peristaltic pump connected to 30 m of polyethylene tubing. All sampling and storage equipment coming in contact with trace metal samples was soaked in 4% Decon for 48 h, rinsed in double-distilled, deionized water (DDDW), soaked for at least 48 h in 10% HNO_3, and twice rinsed in DDDW before use. The sampling system additionally was flushed through with more than three times its own volume of lake water at each depth before collection of a sample. Samples for trace metal analysis were collected in duplicate in 250-ml polyethylene bottles and stored in resealable polyethylene bags. Each sample was filtered on the day of collection in the laboratory through an acid-washed borosilicate glass and PTFE filtration system fitted with a 0.45-μm Millipore membrane filter. The filters were prewashed, while in the filtration system, by passage of 100 ml of 0.5% Aristar HNO_3, followed by 200 ml of DDDW and 100 ml of sample. Two subsamples of each filtrate were retained in separate polyethylene bottles to eliminate further the chance of erroneous data. Each filtrate was acidified to pH 1.5 with Aristar HNO_3 and stored at 4°C. Thus, later analysis was carried out on four replicate solutions.

In 1985, the suspended matter samples from a depth of 2.5 m were kept for trace metal analysis. For most of the spring bloom, the highest density of Chl *a* was found at this depth (*see Fig. 1B*). Filters were digested at 80°C in two successive 10-ml aliquots of concentrated Aristar HNO_3 and the residues taken up in 0.5% HNO_3. The resulting solution was filtered through a Whatman 41 ashless filter, made up to volume (generally 25 ml) with 0.5% HNO_3, and stored in polyethylene bottles. The Whatman filter was prewashed with 50 ml of 0.5% Aristar HNO_3. All stages of sample preparation were carried out in a Microflow 21956 horizontal laminar flow cabinet.

Concentrations of Zn and Cu were determined by means of a Perkin-Elmer 2280 atomic absorption spectrophotometer fitted with a graphite furnace controlled by a Perkin-Elmer HGA 400 programmer. Matrix interferences were compensated for by the method of additions and instrumental background correction. Blanks were run through all procedures, including the entire sampling protocol under field conditions. The latter exercise was carried out at the beginning and toward the end of the sampling period in 1985. Measured limits of detection and combined sampling and analytical precision are given in Table 1.

Samples for the determination of Chl *a*, dissolved silicate, and orthophosphate were collected as for trace metals. Samples for determining particulate C and total suspended solids and algal species identification were similarly sampled but at 2.5 m only. Filtration through precombusted GFF filters and preservation of samples for analysis was carried out on the day of collection. Chl *a* was determined fluorometrically after extraction into 90% acetone following the procedure of the Standing Committee of

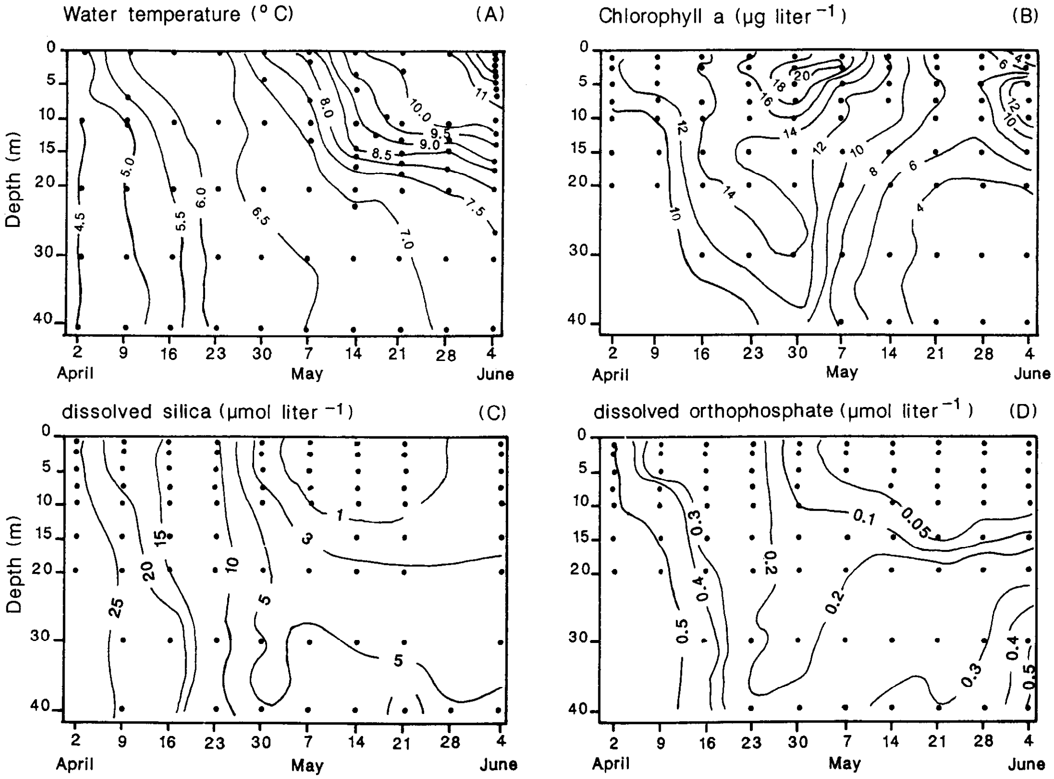

Fig. 1. Time-depth distributions at the deepest point in the south basin of Windermere, 2 April–4 June 1985. Samples—●.

Analysts (1980). Dissolved reactive silicate (C.V. ±4.5%, based on replicate analysis) and phosphate (±4%) were determined by standard colorimetric methods (Mackereth et al. 1978). *Asterionella* cells were counted by the sedimentation and inverted microscope method of Lund et al. (1958). The abundances of other major plankton species and the remaining material, including nonbiogenic detritus, were estimated volumetrically on a scale of 0–5 (Fritsch and Rich 1913), 5 being approximately equal to the volume of 5 × 10^6 *Asterionella* cells liter^{-1}. Total particulate C (±4%) was determined with a Carlo Erba Elemental Analyzer, following the procedure of Hilton et al. (1986).

Time-depth distributions of temperature and the concentrations of Chl *a*, dissolved silicate, and phosphate are shown in Fig. 1 for spring 1985. The numbers of *Asterionella* cells and equivalent volumes of other components at a depth of 2.5 m are shown in Fig. 2. The sequence of events portrayed in these figures is similar to that observed in previous years (e.g. Lund et al. 1963; George 1981). Gradual warming of well-mixed waters occurred throughout April. Stratification developed in May, being well advanced by the end of the month. The spring diatom bloom was dominated by *Melosira italica* in the early stages and later by *Asterionella*, which peaked around the end of April or beginning of May, after which there was a rapid decrease in cell numbers (Fig. 2). Significant degradation of *Asterionella* cells began before the peak, as evidenced by the number of empty frustules recorded. Chl *a* concentrations reflected diatom numbers throughout the spring period, with a maximum of ~20 μg liter^{-1} at 2.5 m in early May. The second, deeper (5–10 m) maximum in early June was due mainly to the blue-green *Oscillatoria bourrellyi* Lund, a species which in the 1980s

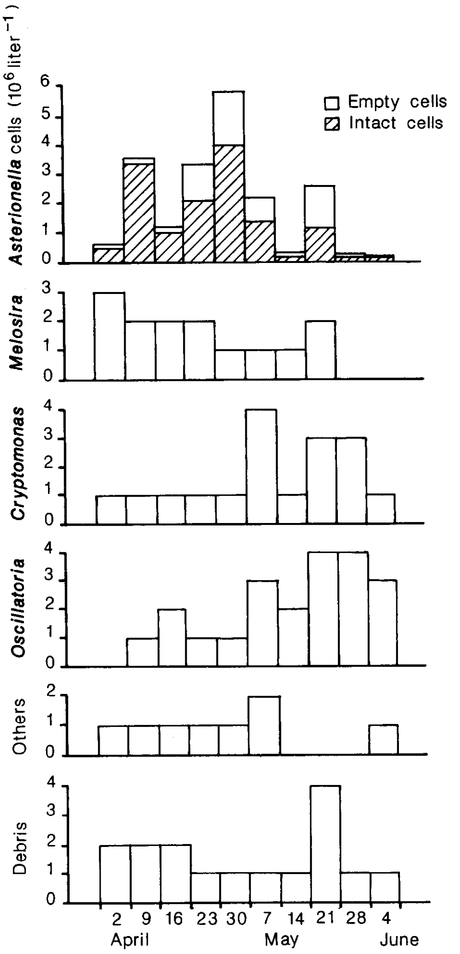

Fig. 2. Number of *Asterionella* cells (liter^{-1}) and relative volumes (dimensionless, where 5 is about equal in volume to 5 × 10^6 *Asterionella* cells liter^{-1}) of the other components of suspended particulate matter at a depth of 2.5 m at the deepest point in the south basin of Windermere, 2 April–4 June 1985.

has begun to dominate the algal succession in Windermere during summer months (Heaney 1986).

Distributions of phosphate and silicate followed the expected pattern, being depleted by algal growth and inversely related to Chl *a*. The distributions of phosphate, silicate, and chlorophyll demonstrate very well the combined effects of micronutrient cycling by algae and restricted vertical mixing associated with thermal stratification. Of particular note is that the growth of the *Asterionella* bloom in April was at a time when the lake waters were well mixed and the peak of the bloom coincided more or less with the onset of stratification. The increase in *Asterionella* numbers in April therefore occurred at all depths, as shown by the Chl *a* data (Fig. 1B).

Figure 3 shows time-depth distributions of the concentrations of dissolved Zn and Cu, each based on the mean of four subsamples (*see above*). At first appearance, the distribution of Zn appears to be unrelated to those of the micronutrients P and Si. If the period up to the peak of the *Asterionella* bloom (i.e. the whole of April) is considered in isolation, however, a comparable trend does emerge of a gradual depletion with time. Plots of dissolved Zn vs. silicate, phosphate, and Chl *a* over this period indicate significant linear relationships in all three cases (Fig. 4). Thereafter, the situation changes with the most striking feature being the high concentrations of dissolved Zn observed on 7 May (incidentally coinciding with the lowest concentrations of dissolved Cu). A less obvious but significant feature is that following stratification (i.e. after 30 April), epilimnetic Zn concentrations (29±5 nmol liter^{-1}; $n = 20$; at <7.5 m) are consistently lower than in the hypolimnion (40±6 nmol liter^{-1}; $n = 15$; at >15 m). A Student's *t*-test indicates that this difference is significant at a probability level <0.01.

In contrast, there is no apparent relation between dissolved Cu and the micronutrient elements within the time frame considered (Fig. 3B). The main feature is a week-to-week variation, which is largely attributable to the relatively poor between-batch precision since samples were initially analyzed for metals on the day after sample collection. Water samples from depths of 2.5 and 5 m were therefore reanalyzed in a single batch. Despite the greatly improved precision (*see Table 1*), no relation with the micronutrient elements could be found for the period leading up to the bloom (Fig. 5). Additionally, no significant difference in dissolved Cu concentrations exists between epilimnetic and hypolimnetic waters after stratification.

Analyses of suspended particulate material at the peak of the *Asterionella* bloom are presented in Table 2. In 1984, more than

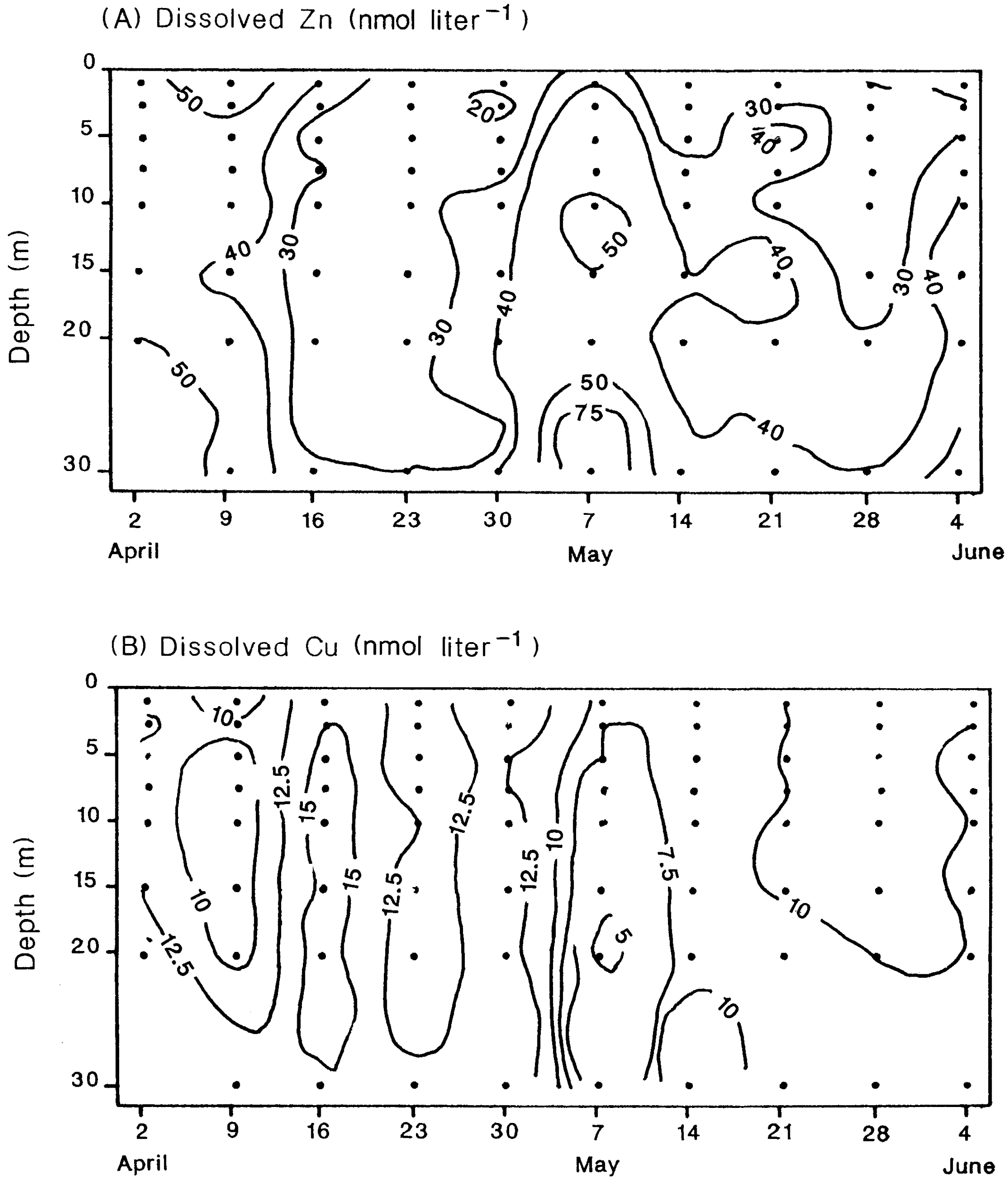

Fig. 3. Time-depth distributions at the deepest point in the south basin of Windermere, 2 April–4 June 1985. Samples—●.

90% of the material by volume comprised *Asterionella* cells. The proportion was lower (50–60%) in 1985, but >90% of the material comprised recognizable lake algae. The gravimetric analysis indicated patchiness in the distribution of algae in water from a single depth. The errors quoted in Table 2 represent the combined sampling and analytical precision. The metal precisions therefore include the effect of algal patchiness since the metal and gravimetric analyses, used to calculate the metal contents,

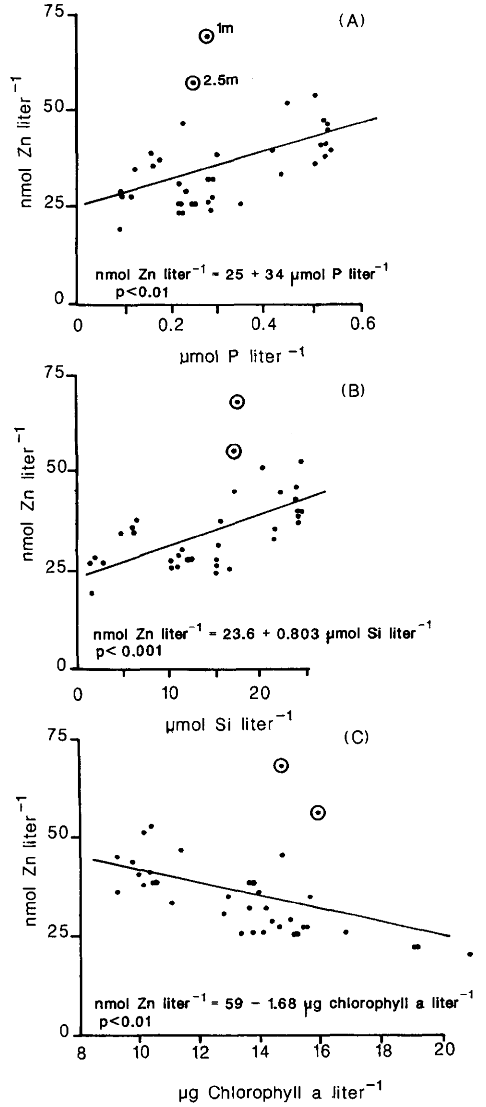

Fig. 4. Regression analysis of Windermere data, 2–30 April 1985, for all eight sample depths. Dissolved Zn vs. dissolved orthophosphate, dissolved silicate, and Chl *a*. Circled data points correspond to water depths of 1 and 2.5 m collected on 9 April 1985 following a period of heavy rainfall (included in the regression analysis).

were undertaken on separately filtered waters (i.e. through Millipore and GFF filters).

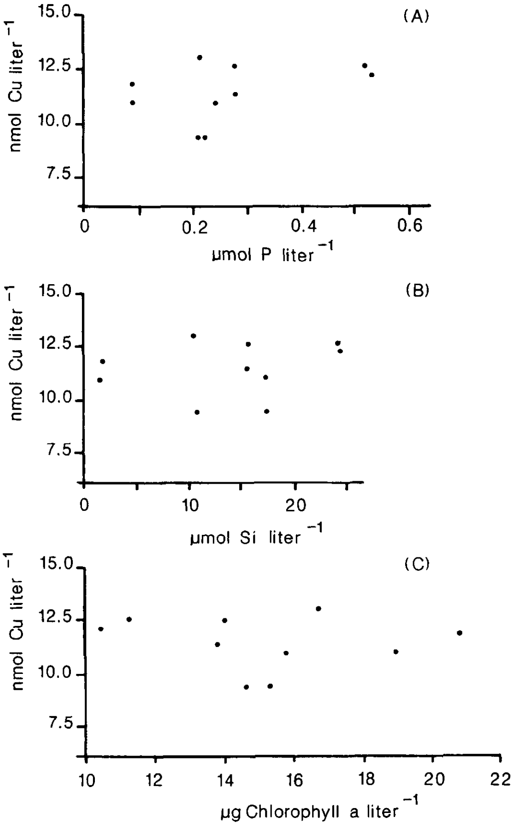

Fig. 5. Dissolved Cu vs. dissolved orthophosphate, dissolved silicate, and Chl *a* in Windermere samples collected at water depths of 2.5 and 5 m between 2 and 30 April 1985.

Estimates of the stoichiometric composition of algae in Windermere, derived from analysis of the standing crop and regression analysis of the dissolved element concentrations (Fig. 4), are shown in Table 3. The errors associated with the standing crop analysis are ±44% for Zn : C and ±6% for Cu : C (C.V.). The large Zn error derives from that for the Zn content of the suspended particulate matter (Table 2). The ratios determined by regression analysis assume a C : Si atomic ratio of 1 : 0.4, which is characteristic of the spring *Asterionella* bloom and is more consistent than the C : P ratio (Heaney et al. 1986). The remarkable agreement of the derived C : P ratio with the classic Redfield value of 106 : 1 must be regarded as somewhat fortuitous, given the rounding of the C : Si ratio and the presence of other algal species.

Dissolved Zn and Cu budgets were calculated for the 29-d period (i.e. 2–30 April 1985) leading up to the bloom in Windermere. The approach and assumptions were

Table 2. Algal C, Chl *a* (both % dry wt), and trace metal (μg g^{-1} dry wt) concentrations in near-surface suspended particulate matter in Windermere at the peak of the *Asterionella* bloom, together with combined sampling and analytical precision (SD).

	C	Chl *a*	Zn	Cu
1 May 1984	26±1	–	1,354±596	33±1
30 Apr 1985	48±2	1.7	1,032±454	56±2
Jan 1951*	–	–	1,240	–

* Lund 1957.

essentially the same as those detailed by Hamilton-Taylor and Willis (1990). Water budgets were based, for direct atmospheric deposition and river fluxes, on the rainfall measured 2 km west of the lake (data supplied by the Institute of Freshwater Ecology), and for direct sewage discharges on the discharge data for Windermere and Ambleside Sewage Treatment Works (data supplied by North West Water Authority). Mean dissolved metal concentrations in precipitation, effluents from the two Sewage Treatment Works, and the major inflowing rivers were assumed to be the same as those observed over the 2-yr period April 1981–April 1983 (Hamilton-Taylor and Willis 1990). Loss of dissolved Zn and Cu from the lake via river outflow was based on the mean surface (1- and 2.5-m depths) concentrations observed in the present study. The change in the dissolved metal content of Windermere between 2 and 30 April was estimated from the dissolved metal profiles and known volumes of different water depth layers (Ramsbottom 1976). Thus, it is assumed that lateral and vertical mixing is complete within each layer (between 2 m thick at the surface and 10 m at depth). Chl *a* correlates well with organic C in the surface waters of neighboring Esthwaite Water and provides a rough quantitative measure of the standing crop (Heaney et al. 1986); it is used here to estimate algal associated Zn and Cu based on the measured ratios shown in Table 2. Incorporation of dissolved Zn and Cu into the standing crop was estimated from the difference in algal-associated Zn and Cu on 2 and 30 April, based on depth profiles of Chl *a* (Fig. 1B) and known volumes of the different water depth layers. Washout of algal-associated Zn and Cu from the lake via river outflow was based on the mean surface (1- and 2.5-m depths) Chl *a* concentrations and rainfall. The results of the budget calculations, shown diagrammatically in Fig. 6, should be regarded as approximations because the associated errors are ill defined and may be substantial.

The C content (26% by wt, *see Table 2*) of the suspended particulate matter at the peak of the spring bloom in 1984 is close to that predicted from a C:Si atomic ratio of 1:0.4, which is characteristic of *Asterionella* at this time of year (Heaney et al. 1986). This fact is not surprising given the predominance of *Asterionella* in 1984. The mean metal contents of the suspended particulate matter in 1984 and 1985 are in reasonable agreement (Table 2), considering the differences in algal species and the relatively poor precision for Zn. It is probable that the metals are associated predominantly with the algae, given their overriding abundance and the similar metal contents in planktonic algae reported by other workers (e.g. Sigg

Table 3. Stoichiometric composition of freshwater planktonic algae. Windermere values are normalized to 106 C, with the regression data normalization being based on the C:Si atomic ratio of 1:0.40 in *Asterionella* (Heaney et al. 1986).

Location	Method	C	Si	P	Zn	Cu
Windermere (this study)	Standing crop composition					
	1984	106	–	–	0.10	0.003
	1985	106	–	–	0.04	0.002
	Regression analysis of dissolved concentrations (1985)	106	42.4	1.00	0.034	–
Lake Constance (Sigg 1985)	Sediment trap material	113	14	1	0.06	0.008
Lake Zurich (Sigg 1987)	Sediment trap material	97	–	1	0.03	0.006

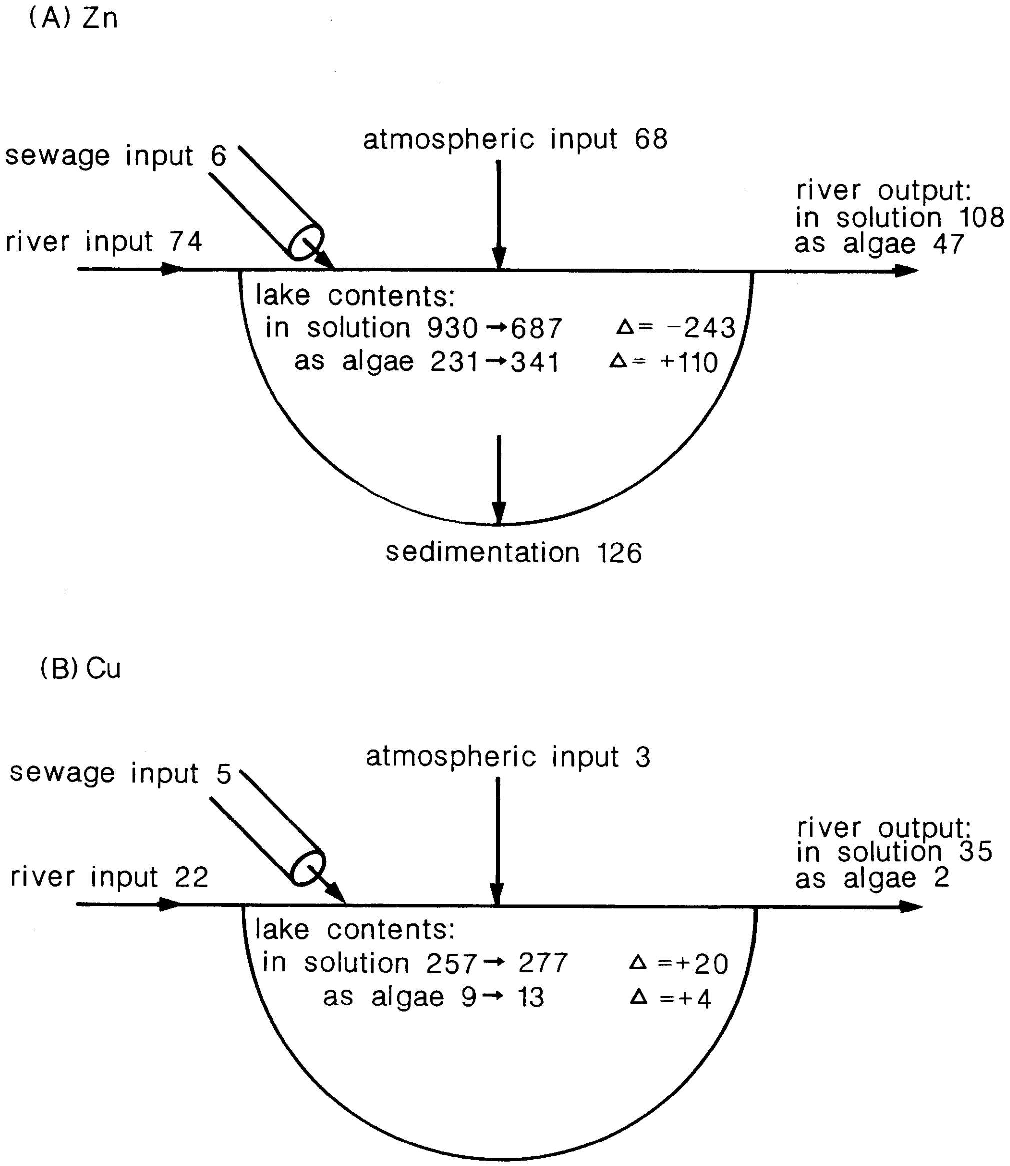

Fig. 6. Dissolved Zn and Cu budgets (in kg) in Windermere, 2–30 April 1985. The following terms are included: river inputs, direct atmospheric deposition, direct sewage discharges, dissolved metal contents of the lake on 2 and 30 April, the corresponding change in the dissolved metal contents, metal contents in the algal standing crop on 2 and 30 April, the corresponding change in the metal contents of the standing crop, river outputs, and algal outwash, and, for Zn, loss to bottom sediments estimated by difference.

1985; *see also Table 3*). Furthermore, the observed Zn concentrations are in good agreement with that reported for *Asterionella* in Windermere sampled during the spring bloom >30 yr earlier (Lund 1957). Thus the metal concentrations given in Table 2 are assumed to be representative of Windermere algae, dominated by *Asterionella,* during the spring bloom. It has been suggested that such an association can be passive, as a result of coordination reactions at the algal surface, or involve active uptake to fulfill nutritional requirements (Sigg 1985).

The "time window" suitable for observing metal-nutrient relations appears to be restricted to the growth phase of the spring diatom bloom. The C : Zn atomic ratio determined by regression analysis of the data for 2–30 April agrees well with that derived from analysis of the suspended particulate matter (Table 3). The fact that the linear relationships of dissolved Zn vs. Si, P, and Chl *a* do not hold after April may be associated with a change in relative element availability (i.e. supply) and in algal composition over the summer. A detailed study of chemical–biological interactions in neighboring Esthwaite Water showed that the C : N : P ratios of the standing crop were a dynamic characteristic of the algal species, availability of micronutrients (e.g. from the water column, river inflows, and recycling from bottom sediments), and linked to both these factors, the time of year (Heaney et al. 1986). The study found that the P content of the algae, relative to that predicted from the Redfield ratios, declined during the summer maximum (July–October, peaking in September), but evidence for such a depletion during the spring *Asterionella* maximum was less strong. In addition, the regression analysis approach, as used in the present study, treats the lake as a closed system, taking no account of the effect of the various inputs and outputs of Zn and other constituents to and from the lake, and this may not generally be the case.

Table 3 also shows the metal stoichiometry of planktonic algae in Lakes Constance and Zurich. There is good agreement with the metal stoichiometry observed in Windermere, despite the major differences in water chemistry. Constance and Zurich are hard-water lakes, with extensive biologically induced $CaCO_3$ precipitation, but have an algal succession that is not greatly different from that in Windermere, especially during the early part of the year (*see* Stabel 1988). The difference in Si stoichiometry is to be expected given the predominance of *Asterionella* in Windermere during April.

The metal budgets for April 1985 (Fig. 6) not only provide additional insight into the significance of metal cycling by algae in Windermere during the spring diatom bloom, but also a basis for understanding the observations made during the study. The most striking feature is the contrasting importance of algal cycling with respect to the two metals. The mass of Zn associated with the standing crop is ~50% of that in solution at the peak of the *Asterionella* bloom, whereas with Cu it is <5%. Additionally, the increase in Zn bound up with the standing crop, during the growth of the bloom, and the concomitant decrease in dissolved Zn are themselves both substantial compared to the total mass in solution. With Cu in contrast, the changes are minor, and probably not meaningful, compared to the large total mass in solution. The most probable chemical explanation for the lack of Cu uptake is that the Cu is biologically unavailable due to complexation by humic substances (Gachter et al. 1978; Wangersky 1986). The concentration of humic substances in Windermere is typically 1–2 mg liter^{-1} (E. Tipping pers. comm.). The application of a chemical equilibrium speciation model to a Welsh lake, comparable in composition to Windermere, indicated that >99.9% of the Cu is complexed by the humic material, whereas ~90% of the Zn occurs as the free ion (Mantoura et al. 1978).

Because of the lack of detailed trace metal studies in lakes (Murray 1987), it is illuminating to take the quantitative perspective one stage further by comparing the results with those obtained during earlier, complementary studies in Windermere. The deposition of Zn associated with planktonic algae in April 1985 is estimated from mass balance considerations (Fig. 6A). The difference between the measured inputs and river output corresponds to a net loss from the lake of 7 kg. Of the 243-kg decrease in dissolved Zn content, 110 kg can be accounted for by the growth of the algal bloom and 7 kg by the net river output. This gives 126 kg, by difference, as a tentative figure for algal sedimentation, although the calculation ignores Zn uptake and deposition by other sedimentary components. Depositional fluxes were previously measured directly at the same site in Windermere by means of sediment trapping (Hamilton-Taylor et al. 1984). In 1981, sedimentation of the main *Asterionella* bloom occurred in April and May.

An estimate of the associated organic matter deposition can be made, based on the number of *Asterionella* cells trapped and their known organic content (*see* Hamilton-Taylor et al. 1984). Reynolds et al. (1982) showed that there was considerable seasonal variability in the degree of preservation of the organic content of trapped *Asterionella* cells. Minimal preservation occurred in September, but in May reached a maximum of 95%. Assuming 100% preservation, that C comprises 50% of the total organic matter by weight, that the C : Zn atomic ratio is 106 : 0.04, and that the depositional flux occurs over an area of 12 km^2 (Hamilton-Taylor and Willis 1990), we estimate the deposition of Zn due to *Asterionella* in April and May 1981 to be 200–550 kg. The large range derives from the variable mass of individual *Asterionella* cells, determined by Lund (1965).

Given this degree of uncertainty and that the figures are for a different year and are overestimates due to the assumption of 100% preservation and a small effect from sediment focusing (*see* Hamilton-Taylor and Willis 1990), the agreement with the quantities shown in Fig. 6A are good (i.e. 126 kg deposited, 341 kg remaining in the water column associated with the algal standing crop). Comparisons with the independently derived data sets are, therefore, taken one stage further. To make the comparisons more representative, our estimates are based on the median mass of an *Asterionella* cell as well as the range. Thus by using a similar set of assumptions, we calculated that 375 (200–550) kg of Zn is equivalent to 10% (5–15%) and 44% (23–64%) of the annual depositional fluxes of total and 0.5 M HCl leachable Zn, respectively (based on trap data from Hamilton-Taylor et al. 1984), and 20% (10–30%) of the dissolved Zn retained annually in the lake by incorporation into bottom sediments (based on input–output budgets for dissolved Zn by Hamilton-Taylor and Willis 1990). In contrast, only 2% at most of the peak depositional flux of Cu, measured by trapping in March and April 1981, is attributable to the spring diatom bloom, as was previously suggested (Hamilton-Taylor et al. 1984).

The significantly lower epilimnetic concentrations of dissolved Zn observed in our study following stratification, compared to those in the hypolimnion, are explicable in terms of the interacting effects of algal cycling and reduced vertical mixing in the water column (i.e. continuing uptake in the epilimnion and net release in the hypolimnion). The fact that dissolved Zn is not depleted in the epilimnion to the same extent as P is not surprising, given the continuing significant inputs of Zn from external sources, particularly from direct atmospheric deposition. The elevated concentrations of dissolved Zn observed on 7 May are more difficult to explain. Examination of Figs. 3A and 6A indicates the scale of the increase and, together with Fig. 1B, suggests that it cannot be linked in any simple way to algal cycling. Normal rainfall-associated inputs (e.g. via rivers and direct deposition) can also be ruled out since cumulative rainfall was relatively low at this time. Sample contamination cannot be excluded, but none was apparent on other occasions, when sampling and handling procedures were identical.

The field data taken together provide a coherent picture of the role played by the spring diatom bloom in the biogeochemical cycling of Zn and Cu in Windermere. The results indicate that algal cycling is an important factor in the behavior of Zn, but has relatively little influence on the fate of Cu, both during the bloom and in terms of the annual metal budgets. The results also suggest that although the concept of Redfield ratios may be applicable to the metal content of algae in lakes, the dynamic nature of lakes limits the usefulness of the concept. It is only under severely restricted conditions that the stoichiometry is likely to be reflected in dissolved metal concentrations. The contrasting behavior that can arise between two biologically essential trace metals present in a lake at comparable concentrations is highlighted.

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References

FRITSCH, F. E., AND F. RICH. 1913. Studies on the occurrence and reproduction of British freshwater algae in nature. 3. A four year's observation of a freshwater pond. Ann. Biol. Lacustre **6:** 33–115.

GACHTER, R., J. S. DAVIS, AND A. MARES. 1978. Regulation of copper availability to phytoplankton by macromolecules in lake water. Environ. Sci. Technol. **12:** 1416–1421.

GEORGE, D. G. 1981. The spatial distribution of nutrients in the south basin of Windermere. Freshwater Biol. **11:** 405–424.

HAMILTON-TAYLOR, J., AND M. WILLIS. 1990. A quantitative assessment of the sources and general dynamics of trace metals in a soft-water lake. Limnol. Oceanogr. **35:** 840–851.

———, ———, AND C. S. REYNOLDS. 1984. Depositional fluxes of metals and phytoplankton in Windermere as measured by sediment traps. Limnol. Oceanogr. **29:** 695–710.

HEANEY, S. I. 1986. Unusual *Oscillatoria* populations in Windermere—is the lake changing? Br. Phycol. J. **21:** 330.

———, W. J. P. SMYLY, AND J. F. TALLING. 1986. Interactions of physical, chemical and biological processes in depth and time within a productive English lake during summer stratification. Int. Rev. Gesamten Hydrobiol. **71:** 441–494.

HILTON, J., J. P. LISHMAN, S. MACKNESS, AND S. I. HEANEY. 1986. An automated method for the analysis of 'particulate' carbon and nitrogen in natural waters. Hydrobiologia **141:** 269–271.

LUND, J. W. G. 1957. Chemical analysis in ecology illustrated from Lake District tarns and lakes. 2. Algal differences. Proc. Linn. Soc. Lond. **167:** 165–171.

———. 1965. The ecology of the freshwater phytoplankton. Biol. Rev. **40:** 231–293.

———, C. KIPLING, AND E. D. LECREN. 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiologia **11:** 143–170.

———, F. J. H. MACKERETH, AND C. H. MORTIMER. 1963. Changes in depth and time of certain chemical and physical conditions and of the standing crop of *Asterionella formosa* Hass. in the north basin of Windermere in 1947. Phil. Trans. R. Soc. Lond. Ser. B **246:** 255–290.

MACKERETH, F. J. H., J. HERON, AND J. F. TALLING. 1978. Water analysis: Some revised methods for limnologists. Sci. Publ. Freshwater Biol. Assoc. 36. 124 p.

MANTOURA, R. F. C., A. DICKSON, AND J. P. RILEY. 1978. The complexation of metals with humic materials in natural waters. Estuarine Coastal Mar. Sci. **6:** 387–408.

MURRAY, J. W. 1987. Mechanisms controlling the distributions of trace elements in oceans and lakes, p. 153–183. *In* Sources and fates of aquatic pollutants. Adv. Chem. Ser. 216. Am. Chem. Soc.

RAMSBOTTOM, A. E. 1976. Depth charts of the Cumbrian lakes. Sci. Publ. Freshwater Biol. Assoc. 33.

REYNOLDS, C. S., H. R. MORISON, AND C. BUTTERWICK. 1982. The sedimentary flux of phytoplankton in the south basin of Windermere. Limnol. Oceanogr. **27:** 1162–1175.

REYNOLDS, G. L. 1986. The role of phytoplankton in trace metal cycling in Lake Windermere. Ph.D. thesis, Lancaster Univ. 105 p.

SIGG, L. 1985. Metal transfer mechanisms in lakes; the role of settling particles, p. 283–310. *In* W. Stumm [ed.], Chemical processes in lakes. Wiley-Interscience.

———. 1987. Surface chemical aspects of the distribution and fate of metal ions in lakes, p. 319–349. *In* W. Stumm [ed.], Aquatic surface chemistry. Wiley-Interscience.

STABEL, H.-H. 1988. Algal control of elemental sedimentary fluxes in Lake Constance. Int. Ver. Theor. Angew. Limnol. Verh. **23:** 700–706.

STANDING COMMITTEE OF ANALYSTS. 1980. The determination of chlorophyll *a* in aquatic environments. HMSO, London.

WANGERSKY, P. J. 1986. Biological control of trace metal residence time and speciation: A review and synthesis. Mar. Chem. **18:** 269–297.

Submitted: 20 November 1991
Accepted: 7 May 1992
Revised: 16 July 1992