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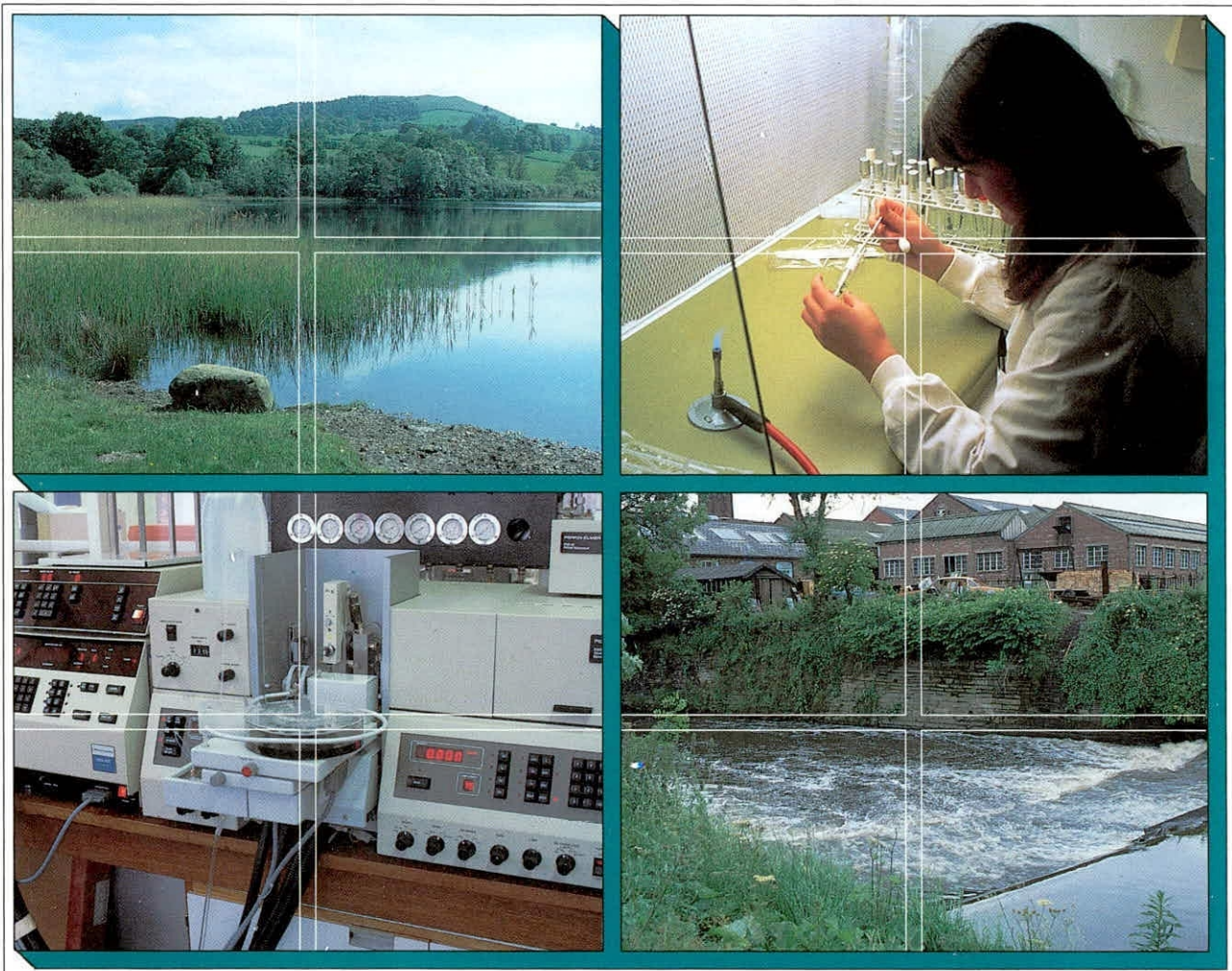
**Institute of
Freshwater
Ecology**

PHYTOPLANKTON DYNAMICS AND THE MAJOR ECOLOGICAL DETERMINANTS IN LOCH LEVEN NNR DURING 1994

Principal Investigators:

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A Kirika

Report to Scottish Natural Heritage and the Forth River Purification Board
(March 1995)



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Contract Completion Date:

31 March 1995

SNH Contract No.920/F4A/206/310

ED/T11055c1/4

The Institute of Freshwater Ecology contributed funds for this study

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The Institute of Freshwater Ecology is part of the Natural Environment Research Council's Centre for Ecology and Hydrology

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FIGURES

Summary

The 1994 studies on Loch Leven phytoplankton dynamics, and the ecological factors controlling changes in species composition and abundance in this year, have highlighted some very special developments. The findings are all the more remarkable bearing in mind intrinsically very capricious nature of this loch. Some of the interactions between the planktonic biota and their physical and chemical environment this year, have not been recorded for some 25 years, although there were some signs of change in 1993. Yet the possibility of their arising was forecast at least 18 months ago.

Existing knowledge stemming from the long-term research is sufficient to design strategies for improving the quality of water at Loch Leven. However, practical solutions that would meet reasonably quickly, the conflicting demands of the very diverse 'user community' (conservationists, fishery managers and industrialists), are unlikely to materialise even if financial resources were unlimited.

The supply to the loch, of the main nutrient limiting phytoplankton productivity here (phosphorus, P), has been reduced significantly over a number of years. Yet, quality standards were as low as ever in 1994. The factors that have consistently resulted in dense, and often troublesome phytoplankton populations in this loch are reviewed. These include (i) features of the light climate which ensure the efficient conversion of nutrients to phytoplankton, (ii) a continuing rich external supply, and frequent recycling from the sediments, of nutrients which enhance overall productivity, and (iii) a moderate flushing rate that facilitates the accumulation of phytoplankton biomass. The levels of algae recorded in 1994, however suggest that an additional factor - reduced grazing of the algae by zooplankton - is involved.

The annual (lakewide) mean and maximum chlorophyll_a levels for 1994 were 75 and 240 $\mu\text{g l}^{-1}$ respectively. At the highest crop densities only 5 algal species were encountered during the routine enumeration procedure, whereas considerably more diverse assemblages of 25 to 30 species, were recorded during periods when chlorophyll concentrations were more moderate. A total of nearly 90 species was recorded during the year. The list reflects the ongoing eutrophic nature of the loch, and the intermittent resuspension of organisms from the sediments. The population changes of the 7 species that contributed the greater proportions of the total chlorophyll measured during the year, are illustrated.

The influence of phytoplankton growth on water clarity and the concentrations of nutrients, and the feedback effects of the declining nutrient levels on the seasonal changes in species composition, are assessed. For example, while a maximum Secchi reading of 3.7m was recorded, values of 0.5 m to 1.0 m prevailed over long periods in the summer. Particular attention is paid to the factors controlling the abundance of the dominant organism - *Oscillatoria*. At its summer maximum of 230,000 filaments ml^{-1} , further production of cells was probably constrained in part by the low levels of nitrate and possibly, of phosphate in spite of evidence of earlier uptake of sediment-released P. The collapse of this population led to markedly reduced oxygen levels.

In addition to the extremely high pigment and turbidity values, there are other features indicating that the situation described for 1994, was last observed in 1968-1969. These are: (i) the spring prominence of the relatively large alga *Diatoma elongatum*, rather than the usual predominance of small centric diatoms, (ii) the occurrence of the overall phytoplankton biomass maximum in summer rather than early spring, (iii) the summer dominance by a small *Oscillatoria*, and (iv) the suggestion that the underwater light climate, rather than nutrients alone, checked algal growth in the summer. Of these features, the tendency towards a situation of light limitation, as opposed to mainly nutrient limitation, represents a shift of enormous magnitude in ecosystem functioning.

A hypothesis on why the loch exhibited these special features is presented. It rests on observational and experimental data, and attributes the changes primarily to the relatively low population densities achieved in 1994, by the planktonic crustacean - *Daphnia hyalina*. The mechanisms and factor interactions thought to have been involved are outlined. The importance attached to the *Daphnia* relates mainly to its feeding preferentially on the smaller phytoplankton elements. The relatively poor showing of this animal would thus be expected to lead to (i) a general elevation of phytoplankton abundance - towards 'self-shading' densities, nutrients permitting, and (ii) an increase in the relative abundance of small algal species which tend to be more efficient than the larger forms at taking up (potentially limiting) nutrients.

Albeit in the absence of fish population estimates and extensive, year-round analyses of the gut contents of fish and *Daphnia*, the decline in *Daphnia* is attributed primarily to the recent stocking of the loch with rainbow trout (*Onchorhynchus mykiss*). Whatever the prime cause, the loch plainly cannot sustain the effects.

1. GENERAL INTRODUCTION - RATIONALE, SCOPE AND AIMS OF THE STUDY

This report presents the results from the 1994 Loch Leven phytoplankton surveillance programme. It focuses primarily on the influence of selected physical, chemical and biotic factors on the observed changes in algal species composition and abundance. The work continues to provide further insights into the functioning of this shallow eutrophic waterbody, in spite of the fact that ecological studies on the planktonic algal assemblage here, have been maintained more or less uninterrupted since the late 1960s (Bailey-Watts 1978; Bailey-Watts *et al* 1990 - 4 authors). All those years ago, however, knowledge about the dynamics of lake phytoplankton and the controlling factors rested very largely on investigations of deep and regularly stratifying systems with which Leven contrasts considerably.

It is not only the continuing quest for limnological knowledge that has enabled the work on Leven to be sustained for such a long period. The loch is a Ramsar Site and National Nature Reserve, the location of a world-famous angling fishery, and the main water supply for the operation of downstream paper mills. Thus, concerns over continuing deterioration in water quality (see below) have been expressed at local, regional, national and international levels by the 'user community' of conservationists, naturalists, fishery managers and industrialists (LLAMAG 1993). Indeed, a growing literature on the application of the scientific results to the solving of these problems (Bailey-Watts, Gunn and Kirika 1993; Bailey-Watts and Maitland 1984; Bailey-Watts *et al* 1987 - 4 authors, 1994 - 5 authors), suggests that this, not the results themselves, is uppermost in the minds of many of the interested parties.

Deterioration in water quality affects all the users identified above. However, the problems for each of them stem primarily from the same factor - the clouding of the water due to what is viewed as an over-abundance of algae. Populations forming high densities lake-wide, or localised surface scums, occlude light and impair the growth of macrophytes and sediment microflora. This is likely to impact on the performance of a potentially very diverse community of associated invertebrates - and fish. Such algal-laden water is also more difficult than clear water to filter for certain industrial purposes, and high photosynthetic activity may lead to high pH levels which can also affect treatment processes.

The fact that such situations are commonplace at Loch Leven is well-known and reasonably well understood (see Bailey-Watts, May and Lyle 1992, for general principles): firstly, the efficient conversion of nutrients to phytoplankton is assured considering the shallow nature of the loch (see e.g. Talling 1971), and its intrinsically clear water i.e. devoid of significant peat staining (Bindloss 1974, 1976; Bailey-Watts

1988a); secondly, phytoplankton production is high as a result of the still abundant, supplies of nutrients from external sources (Bailey-Watts and Kirika 1987; Bailey-Watts, Smith and Kirika 1989) in addition to the sediments (Bailey-Watts 1976; Bailey-Watts *et al* 1990; Bailey-Watts, May and Kirika 1991; and see below); thirdly, large percentages of the algal biomass produced are often observed in the form of dense crops, because the theoretical hydraulic retention periods are seldom short enough to bring about major losses of the organisms *via* washout (Bailey-Watts *et al* 1990; Bailey-Watts, May and Kirika 1991).

This knowledge suggests that - given sufficient resources - the 'Leven Problem' could be solved relatively quickly i.e. over a period of 5 or 10 years. However, the strategies envisaged (e.g. water transfer and increased flushing, sediment dredging, or general deepening) would not satisfy all 'users'. Meanwhile, and largely in response to the scientific findings (LLAMAG 1993), local authorities and industry have brought about considerable cutbacks of what are perceived as the main point sources of phosphorus (P), which is almost certainly the main nutrient limiting phytoplankton production here - (Bailey-Watts 1988a; Bailey-Watts, Kirika and Hakansson 1994). An initial stemming of large amounts of total P (TP) from the lochside woollen mill was effected in the mid-1970s. An additional, estimated annual input of 6 tonnes from the same factory, was more or less completely eradicated in the late 1980s (Bailey-Watts, May and Kirika 1991), and even more TP has been prevented from entering the loch in line with upgradings of certain sewage treatment works (STWs; Forth River Purification Board and Scottish Natural Heritage - personal communication).

The present report attempts primarily to highlight and explain the causes of, and, by implication, identify ways of solving, the particular set of problems that arose during 1994. The incidence of e.g. water temperatures exceeding *ca* 17°C, heavy rainfall, and strong winds, can differ markedly from year to year, and this explains the extraordinary inter-seasonal and inter-annual variability that is the hallmark of algal succession here. Some early and recent examples of this are provided by Bailey-Watts (1974) and Bailey-Watts *et al* (1994). Even so, some of the features of the population dynamics in 1994, and the particular combination of factors to which they can be attributed, have not been observed at Loch Leven since 1969 (although 1993 data suggest the beginnings of a change - Bailey-Watts *et al* 1994). Yet, a number of the major developments were forecast (Bailey-Watts, Gunn and Kirika 1993) - albeit contingent on the stocking of the loch with trout - including *Onchorhynchus mykiss* (Walbaum) as well as the native *Salmo trutta* (L.) - with the view to re-vitalising an ailing sport fishery (Hutchinson and Walker 1994).

2. INVESTIGATIVE METHODS

Detailed accounts of various field and laboratory procedures followed for the plankton studies are given in a number of previous reports already referred to, and produced by this laboratory for SNH and FRPB. The spatial dispersion of the sampling sites, and the frequency of sampling are the only features differing to any significant extent. During 1994, the loch was visited weekly from March to October inclusive, and fortnightly in January, February, November and December. From near the outflow (where the total water depth is rarely more than 1.5m) water was collected by the immersion of a 10-l bucket or wide-mouthed aspirator. Integrated tube samples extending from the surface to 2m were collected - weather permitting - from 3 open water stations: (i) the centre of the west bay (3 m to 4 m water depth), (ii) at a point (4 m to 5 m deep) approximately halfway between Reed Bower and the southern shore of the loch, and (iii) at the South Deeps (21 m to 23 m). As will be illustrated, algae dominating even the very densest crops this year were not of the type that readily exhibit marked patchiness in their distribution. However, especially in summer when they can exhibit thermal stratification, the North and South 'Deeps' were sampled as above, and a closing bottle was also used to collect water from 15 m depth in each of these areas. Samples were always collected in duplicate.

The whole programme was designed by IFE, but the field sampling and recording was executed jointly by IFE, SNH and FRPB. Since the FRPB has a statutory obligation to monitor Loch Leven, it has also carried out all of the chemical analyses (including chlorophyll_a) since the beginning of March. This following a 3-month inter-calibration exercise with IFE. However, IFE has been responsible for the phytoplankton analyses throughout the year, and it remains in close contact with FRPB over all issues.

3. RESULTS

Many of the previous publications on the ecology of the phytoplankton of Loch Leven (e.g. reports quoted above) have described the factors that control algal biomass and species sequences first, rather than the nature of the algae themselves. By way of an alternative, this report focuses first on the phytoplankton *per se*. The manner in which the assemblage has responded to the environmental conditions is then discussed; the main emphasis is on the effects of the algae on certain physical and chemical aspects of water quality. The mechanisms whereby these and other factors ultimately controlled the phytoplankton are considered last.

3.1 Temporal fluctuations in total phytoplankton abundance (chlorophyll_a concentration)

Algal levels were very moderate at the beginning of the year but within two months most of the chlorophyll_a concentrations exceeded 75 µg l⁻¹ (Figure 1). The algae and small cyanobacteria that dominated the scene for much of 1994 are species not prone to forming patchy distributions. As a result these population densities (as well as the nutrient and other chemical concentrations, and the clarity values quoted below) are reasonably representative of the loch as a whole. The overall phytoplankton density remained at, or near 75 µg chlorophyll_a l⁻¹ for a further 3½ months. Nevertheless, by increasing at a more or less consistent weekly rate of 30 µg l⁻¹ for 6 weeks from the middle of May, the assemblage achieved a concentration of 240 µg l⁻¹ by the end of the first week in July. Thereafter some extraordinarily rapid fluctuations in chlorophyll level were recorded: first, within a week (or less), a decrease to approximately 75 µg l⁻¹ again; second, over a 2-week period, an increase equivalent to just over 1 doubling; and third, a decline to *ca* 90 µg l⁻¹ by late July. There followed a slight but significant increase of 20 µg l⁻¹ over the next week. For approximately 7 weeks thereafter, a more or less linear decrease in algal abundance brought chlorophyll_a levels down to some 20 µg l⁻¹. Values remained at, or below this for the rest of the year.

3.2 Overall species diversity and the population dynamics of the dominant forms

In early February and mid-August when the overall phytoplankton density was near the annual mean value (*ca* 75 µg l⁻¹), more than 30 phytoplankton species were recorded during the routine counting procedure. On most other occasions, between 10 and 30 species were encountered (Figure 1). Appendix I shows that approximately 90 algal types were recorded over the whole year. This list includes the authorities responsible for naming the species; these are important details, but they will not be repeated in the main text that follows.

The time and effort expended on algal enumeration varies from week to week according to two factors which affect the likelihood of an algal individual being recorded. These are as follows:

- *the composition of the crop in terms of size characteristics and size variation, rather than the 'mix' of species per se:* for example, small species that are relatively rare, are often 'missed'.

- *the composition of suspended particles as a whole:* detritus (whether washed in to the loch, or resuspended from the sediments) can occasionally constitute the major proportion of the total amount of particulate matter including plankton; in such

situations, it can prove difficult to assess the phytoplankton properly i.e. obtain statistically acceptable counts of the relatively sparse phytoplankton species.

[Note that total particle abundance itself is not a problem in this respect, as samples can be concentrated or diluted to facilitate convenient counting].

As a result of these considerations, the numbers of species indicated in **Figure 1** and **Appendix I** are undoubtedly underestimates. Also, since counting effort varies between the sampling dates, the different values in the Figure are not strictly comparable. Nevertheless, the general pattern of change in species diversity in the Figure is unlikely to deviate significantly from the true situation.

The rich nature of the loch is reflected in the species array as well as in the superabundance of phytoplankton. Of major significance here, is the prominence of species of cyanobacteria, green algae, and the 'eutrophic' diatom species. Even the Desmidiaceae - a group that would generally indicate a relative paucity of nutrients (Brook 1959) - are of the eutrophic type here. The preponderance of 'planktonic' *Scenedesmus* and *Aulacoseira* species which appear to be able to survive on the sediments as well as in the plankton ('tychobenthic' - Bailey-Watts 1973; see also Bailey-Watts 1990), also indicates the occasional re-suspension of such forms from the bottom deposits of this essentially shallow system.

One or more of just 7 species i.e. <10% of the total number recorded, accounted for the majority of the chlorophyll measured in 1994. In the order in which they achieved their annual population maxima, these are species of *Asterionella*, *Aulacoseira*, *Diatoma*, *Oscillatoria*, *Anabaena*, *Stephanodiscus* and *Rhodomonas*. The use of logarithmic scales for displaying the fluctuations in the densities of some of these populations (**Figure 2**) illustrates the orders-of-magnitude ranges in abundance over which they have been enumerated.

The colonial pennate diatom *Asterionella formosa* reached a very moderate peak of ca 1,200 cells ml⁻¹ in March. Lack of any further build-up of this species was probably effected in part by the growth of two other diatoms competing for similar light and nutrient resources. The main one of these was *Aulacoseira subarctica* whose filaments are considerably larger than *Asterionella* cells. It reached its maximum of 2,500 ml⁻¹ three weeks after the *Asterionella* peak. The population density of the other diatom, *Diatoma elongatum* (which is similar in size to *Asterionella*), was only some 600 cells ml⁻¹ at this time. However, a doubling of this concentration each week for the next three weeks was a significant factor enabling a peak concentration of 10,000 ml⁻¹ to be achieved by early May.

Throughout much of the first four of the 5 months of the year during which these three diatoms produced their maxima, unicellular centric forms were present in concentrations of around $10,000 \text{ ml}^{-1}$. These consisted primarily of *Stephanodiscus* species although *Cyclotella* was also present. It is only when these are considered in combination with the other other diatoms, that the relatively high concentrations of $50\text{-}100 \mu\text{g}$ chlorophyll l^{-1} that prevailed from the end of February can be accounted for. Still, this spring unicellular centric diatom population density is only one-tenth or one-fifth of many of those previously recorded in this loch. Indeed, their population maximum was not recorded until late July.

A population of the cyanobacterium *Anabaena flos-aquae* increased in numbers more or less continually for 8 weeks from late March (i.e. while diatoms were still abundant), albeit to a maximum of only a few hundred colonies per millilitre. A slightly denser assemblage of this species with *A. solitaria* was recorded in August, but this was due to a sudden increase rather than one sustained over a number of weeks.

Total algal biomass varied rather little during March, April and May. This is largely because each of the diatoms, and the *Anabaena*, succeeded each other very closely i.e. one species achieved a substantial biomass before the collapse of the previous species. The fact that the overall crop actually increased rather than decreased, as the *Diatoma* declined during May and June can be similarly attributed to the growth of the cyanobacterium *Oscillatoria subtilissima*. This was first recorded (at densities of a few tens of filaments per millilitre) in early March i.e. even earlier in the year than *Anabaena*. It sustained growth over the next 17 weeks. This period included an 11-week spell in which it doubled in biomass each week, in spite of the fact that diatoms were also growing very actively. The *Oscillatoria* finally attained a maximum density of $261,000 \text{ filaments ml}^{-1}$ (equivalent to $>24 \text{ km l}^{-1}$) on 28 June, and $236,000 \text{ filaments ml}^{-1}$ (equivalent to $>27 \text{ km l}^{-1}$) on 5 July.

The decline of the population was very protracted; filament densities of $<100 \text{ ml}^{-1}$ not being recorded until 11 October. As with the chlorophyll levels, the rate of decline in *Oscillatoria* biomass varied considerably. Spells of very rapid decreases in filament numbers alternated with periods during which the numbers changed little or even increased - due to week-on-week changes in filament length. However, three main phases can be distinguished. The first of these ran from 28 June to 26 July. During the first two weeks of the population density fell by approximately 50%, and in the third and fourth weeks the concentrations of filaments decreased to approximately 3% and 2% respectively of the peak level. During the second phase of net decline in this species - 26 July to 20 September - the numbers of filaments actually increased for a few weeks and then fluctuated about a mean concentration of approximately $5,000 \text{ ml}^{-1}$. It is possible that this temporary increase was due to a different species

of *Oscillatoria* i.e. another narrow species, *O. limnetica* Lemm. A further sharp - and final - decline in the population to <10 filaments ml^{-1} was the main feature of the third phase which ran from 20 September to 11 October.

The only other phytoplankton of any major note in terms of biomass, was what many workers still refer to as *Rhodomonas minuta* var. *nanoplanctica* Skuja (Lund 1962). It was recorded at various times throughout the year, but was prominent only in January and the last three months of the year when overall densities of other algae were low. At other times - even when it exceeded $2,000$ cells ml^{-1} - it was less noticeable among so many individuals of the other species.

3.3 Phytoplankton-environment interactions

3.3.1 Some effects of phytoplankton development on water quality

Water clarity

One of the most noticeable effects of the phytoplankton on the state of the water is that on clarity (**Figure 3**) and especially the impact of the dense concentrations of essentially small algae in the middle of the year. It is likely that Secchi Disc readings of less than 1m prevailed for more than 6 months. Moreover, the period when the loch was turbid was when it was under the maximum 'scrutiny' from the various user communities. Indeed, only in October did the water clear to a really desirable extent.

Dissolved oxygen

Another aspect of water quality affected by the very dense algal crops - albeit in combination with warm, still spells of summer weather - was the dissolved oxygen content. The routine sampling programme highlighted the de-oxygenation that can result from the collapse of such a crop (**Figure 3**); following a reduction in chlorophyll concentration from ca $240 \mu\text{g l}^{-1}$ on 5 July to $75 \mu\text{g l}^{-1}$ on 12 July, oxygen values as low as 50% saturation were recorded even in the surface waters (for the first time, as far as the first author is aware). Other reflections of reducing conditions and the breakdown of such a large algal crop, included elevated levels of SRP (see below), $\text{NH}_4\text{-N}$ and of dissolved organic P. Not surprisingly (since the situation has been recorded before - see e.g. Bailey-Watts 1973) values close to nil oxygen were also measured at 20-m depth in the two 'Deeps'. The FRPB's recording sonde, however, shows that the routine monitoring 'missed' a variety of physical and chemical changes over this, week and subsequent weeks (Armstrong, Sargent and Fozzard 1994). From its 30-minute interval recording capability, diurnal and even shorter timescale shifts were logged. Two examples are selected to illustrate this. First, over a 30-minute period in the early afternoon of 8 July, the temperature of the water (at 1 m depth) rose from 16.9°C to 18.8°C , the percentage dissolved oxygen from 48 to 158, and pH from 9.36 to 9.68.

Second, on 16 July, dissolved oxygen saturation values increased in line with assumed photosynthetic activity, from *ca* 10% at 0500h-0600h, to 47% by 1200h and on to 132% by 1600h. Over the period 1200h to 2000h the pH increased from 7.55 to 9.05 units.

Phytoplankton development impacts enormously on other chemical features of water quality. Of major importance are nitrate-nitrogen ($\text{NO}_3\text{-N}$), soluble reactive phosphorus (SRP) and dissolved silica (SRS) - see **Figure 4**. Increases in the concentrations of phytoplankton cells in the first few months of the year reduced SRP levels considerably. By contrast, but as observed in many previous years, the impact on $\text{NO}_3\text{-N}$ concentrations appears to be minor. As the early year assemblages consisted mainly of diatoms, large amounts of SRS were removed, and the concentrations of SRP and SRS were reduced to, and kept at, low levels for many weeks. As the cyanobacteria assumed dominance over diatoms, however, utilisation of SRS decreased. In addition, algae-generated pH values of >8.5 (even in mid-May), would favour SRS release from the sediments. Since at least some SRS would continue to enter the loch from the catchment, the concentrations of this nutrient increased. By early June the levels compared closely with those recorded at the beginning of the year.

It is possible that the net release of SRP from the sediments was later - albeit more marked - than that described for SRS. This is because reducing conditions consequent upon the main phase of collapse of the dense *Oscillatoria* bloom did not develop until early July. However, **Figure 5** shows that particulate P levels, were increasing in line with the rise in the cyanobacterial population, that is, well before the increase in the soluble reactive fraction was actually observed. This suggests that SRP was released from the sediments, but it remained undetected because it was so rapidly sequestered by the algal population. **Figure 5** shows that the PP-to-chlorophyll ratios in the filaments dominating the particulate matter in the column, also increased at this time, but remained well below 1:1 which suggests shortage. A subsequent increase in this ratio to *ca* 1.5:1 coincided with the temporary decrease in the abundance of the cyanobacterium. Other high values recorded later in the year do not reflect the P status of the phytoplankton, since they correspond to low phytoplankton densities and appreciable amounts of suspended detritus. That the cyanobacterial population appeared to take up the P is not surprising: around this time, the total surface area over which the *Oscillatoria* filaments could adsorb, or absorb the phosphate was approximately 6,000 km²! Data from previous years support the contention that SRP was released earlier than observed. Firstly, fluxes of phosphate from the sediments are commonly recorded as soon as nitrate levels are reduced to the limits of detectability (Bailey-Watts 1988a, and Bailey-Watts *et al* 1990). Secondly, pH values of >8.5 units which prevailed from as early as mid-May (Armstrong, Fozzard and Sargent (1994) would also enhance the mobilisation of phosphate. In 1994, $\text{NO}_3\text{-N}$ concentrations had fallen to very low values

even by early June. It is unlikely that much P entered the loch in runoff from the catchment, since rainfall was very low during May and June (**Figure 6**).

Later pulses of e.g. *Diatoma*, *Aulacoseira* and unicellular centric diatoms, along with *Anabaena* were not insubstantial. However, their impacts on nutrient levels were minor in comparison with those attributed to the later phases of growth and the subsequent wane of the *Oscillatoria*. The declining activity of the diatoms led to increases in the concentration of SRS in particular, and SRP to a lesser extent, from July or August onwards. In contrast, $\text{NO}_3\text{-N}$ levels did not increase significantly until early October. The main effect of the decline in algae was thus an increase in water clarity.

3.3.2 Factors ultimately controlling phytoplankton abundance and species composition, with especial reference to the annual maximum of Oscillatoria subtilissima

Plainly, some of the features of physical and chemical water quality attributed above to the activity of the phytoplankton, impact, in turn, on the algae. For example, algal growth may reduce the concentration of a nutrient to a level which permits little further growth. Certainly, at various times during 1994 (see earlier Figures), each of the three nutrients considered here is likely to have constrained the production of one or other algal species.

As an example of the complexities involved, let us consider a number of factors that are likely to have contributed to the peak biomass achieved by, and the subsequent collapse of, the *Oscillatoria* population. Firstly, there is the possible effect of N and P. Nitrate concentrations decreased by *ca* $2,250 \mu\text{g NO}_3\text{-N l}^{-1}$ from March to late June/early July. Over the same period PP levels rose to $160 \mu\text{g l}^{-1}$ i.e. by the time of the cyanobacterial maximum. It is reasonable to assume that virtually all of this P was in, or associated with the cyanobacteria. The weight ratio of N decrease to P incorporated by the population is thus 14:1. However, as mentioned above, the disappearance of nitrate from the column is almost certainly not due solely to *Oscillatoria*, and studies on other algal populations at Loch Leven support this view (Bailey-Watts 1988b). This suggests that (i) the cellular N-to-P weight ratio could have been considerably less than 14:1, and that N was limiting *relative to* P. The resurgence, later in the year, of *Anabaena* that has the potential to fix atmospheric N also tends to support this view. On the other hand, inorganic nitrogen, in the form of ammoniacal-N could have augmented some of the alga's N requirements at a critical time, or they may have inhibited growth. $\text{NH}_4\text{-N}$ concentrations increased very rapidly and thus, almost certainly from the sediments, to between 0.1 and 0.2 mg l^{-1} in open water (and to 2 mg l^{-1} in the deep zones) at the same time as the main flux of SRP from the deposits was observed. Even further qualification is necessary, however,

as ammonia values decreased to below detectable levels again within two weeks; this suggests that sediment-water interface processes, rather than algal uptake constituted the main mechanism.

Setting aside the possibility of factors that we have not even measured being responsible for the cessation of growth of the *Oscillatoria*, four further factors should be considered: (i) the underwater light climate, (ii) population washout, (iii) sinking, and (iv) parasitism/grazing/bacterial breakdown. The first of these could have impaired photosynthetic production of cells, while the other factors could effect losses of existing cells.

Bindloss (1976) and Bailey-Watts (1988b) have shown that the theoretical maximum possible concentration of chlorophyll_a in the euphotic zone (z_{eu} in metres) of Loch Leven lies between 350 and 430 mg m⁻². Bindloss *et al* (1972) and Bindloss (1974) showed that z_{eu} approximates to 3 times the Secchi Disc depth. z_{eu} was 1.41m on 5 July when *Oscillatoria* was at its peak biomass (237 mg chlorophyll_a m⁻³). At this time therefore, the concentration of chlorophyll_a in the euphotic zone was 1.41 x 237, or 334 mg chlorophyll_a m⁻². This does not differ significantly from the lower of the two values given above. It would thus appear that poor light conditions contributed to the lack of any further increase in the cyanobacterial population.

Rainfall and staff gauge readings (**Figure 6**) suggest that there was some water flowing out of the loch. However, bearing in mind the high evaporation rates at this time of the year, when temperatures were also quite high (also **Figure 6**), the rates of loss of water and algal individuals down the outflow (sluices) would have been very minor. Sinking losses also would not be expected to be high enough to explain the cessation of growth. Relatively calm conditions prevailed at this time, and 'healthy', 1.5µm-diameter filaments of *Oscillatoria subtilissima* are likely to sink very slowly. An unidentified protozoan ingesting filaments of this cyanobacterium was noticed, but at very low levels. So this too, is likely to have contributed very little to the decline in the cyanobacterium. However, numerous 'filaments' that were largely devoid of contents were noticed, so lysis of the cells, associated with reducing conditions that could have favoured bacterial activity, could have been a contributory factor.

4. DISCUSSION

This section considers firstly, some of the major quantitative and qualitative features of the 1994 phytoplankton that distinguish it from the last 24 years. Secondly, some thoughts are presented on why the loch has 'behaved' in such an unusual way. Finally, the gaps in knowledge highlighted by this year's work are outlined, along with proposals for new work on these problems.

4.1 The special features of 1994

The changes observed during 1994 in even the most basic quantitative and qualitative features of the Loch Leven phytoplankton render this year very special. These developments are all the more remarkable bearing in mind the traditionally innocuous nature of this loch (see e.g. Bailey-Watts *et al* 1994). Indeed, the database extends back - more or less uninterrupted - to January 1968, suggests that the situation prevailing in 1994 resembles a combination of conditions not recorded since 1969.

Similarities with the late 1960s and thus, contrasts with the intervening years in terms of total phytoplankton abundance (*chlorophyll_a concentration*) are as follows (see also Bailey-Watts 1982):

very high annual maximum value ($238 \mu\text{g l}^{-1}$); high annual mean value ($75 \mu\text{g l}^{-1}$); achievement of the maximum in summer (5 July); the high maximum-to-minimum ratio (238:8 or 29.8:1); the low number of times (3 or 4) the plot crosses the mean value.

Similarities to only those earlier years, in *species composition* include:

-the predominance of a generally small, in this case very narrow filamentous, alga in summer - although the small colonial cyanobacterium *Gomphosphaeria lacustris* and unicellular centric diatoms were prominent in summer and early autumn, respectively, in 1993 (Bailey-Watts *et al* 1994);

- the prominence of *Diatoma elongatum* in particular, and the increased importance of this and other non-unicellular centric diatoms, over the unicellular Centrales in much of the first half of the year. *D. elongatum* has not been recorded in any significant concentrations, if at all, since 1969. The same remarks apply to the small *Oscillatoria*, but in addition, the species to which this has been assigned (*O. subtilissima*) has never been recorded from Loch Leven. It is recognised, however, that such is the 'plasticity' of some of these small filamentous cyanobacteria, one has to accept that it could have been identified as another species in the past.

While the analysis has not allowed a definitive identification of the main factor limiting the phytoplankton maximum, *light limitation* was almost certainly a major issue. Sporadic instances of high chlorophyll concentrations have been recorded in Loch Leven over the years (e.g. 1981 - Bailey-Watts 1988a), but 'self-shading' (Talling 1960) to the extent suggested for 1994 has not been observed since the late 1960s (Bindloss 1976). The shift away from a situation in which limitation of primary photosynthetic production of the phytoplankton is due mainly to nutrient shortages,

towards one where light limitation is important, represents a change in ecosystem functioning of quite enormous proportions (see below). Still, 1994 could prove to be an isolated case, with the situation reverting back to that recorded over the last 25 years.

4.2 Why the 'special' features?

The relative scarcity, in 1994, of the planktonic cladoceran *Daphnia hyalina* Leydig is considered to be one of the main causes of significantly elevated concentrations of summer phytoplankton, and the prominence of small algal species in the assemblages. The animal is known to feed preferentially on the smaller planktonic algae, and various observational and experimental data have illustrated the association between increasing *Daphnia* abundances and declining numerical ratios of small algae to large algae (Bailey-Watts 1978, 1982 and 1986, and Bailey-Watts *et al* 1990). Gunn and May (1995, in prep.) explore the possible reasons for the sparse population of the cladoceran during 1994. Major attention is paid to the following view expressed nearly two years ago, by Bailey-Watts, Gunn and Kirika (1993), and now summarised in **Figure 7**: the increased predation of *Daphnia* consequent on recent introductions of *Onchorhynchus mykiss* to this loch (in addition to on-going stocking with the native *Salmo trutta*), could lead result in a decrease in grazing pressure on the phytoplankton, and the quantitative and qualitative shifts in the phytoplankton - as observed.

By highlighting the possibility of the loch reverting back to conditions documented for e.g. 1968 and 1969, the implication is that light limitation would, as now suspected, occur again. Nevertheless, the fact that the phytoplankton achieved concentrations of $>200 \mu\text{g chlorophyll}_a \text{ l}^{-1}$ as in 1968 and 1969, is somewhat puzzling. P loadings are considered, with some justification, to have been reduced significantly since the early 1970s. On the other hand, the first author has consistently expressed the view that the main cause of the major fall in overall pigment levels that occurred between the late 1960s and the early 1970s was the 're-appearance' of *Daphnia* (e.g. Bailey-Watts, Gunn and Kirika 1993). Reductions in P inputs from the mill were effected a little later, and some very dense crops of *Anabaena* developed in 1972 and 1974, for example.

If the nature of the nutrient and algal dynamics in 1994 is, as proposed here, linked to fish stocking, it illustrates well the potential 'top-down' control by fish on the ecosystem (see e.g. Northcote 1988). The Loch Leven observations also demonstrate the manner in which a lake can switch from this type of ecosystem functioning to that attributed mainly to 'bottom-up' influences i.e. nutrient inputs (see e.g. Carpenter, Cottingham and Schindler 1992).

4.3 The main gaps in knowledge highlighted by the events recorded in 1994, and future research requirements

Knowledge of the detailed light and nutrient requirements of the *Diatoma* is not sufficient to be able to explain why it 're-appeared' in abundance after such a long period of virtual absence. Experimental studies on this are warranted. There is also a need for the data on the environmental conditions corresponding to the earlier successes of this alga, to be compared with those relating to previous periods during which this diatom was growing vigorously. Similar investigations are merited for other species, but especially for the *Oscillatoria* - over which there are uncertainties concerning even its specific identity.

The recent resumption of work by FRPB, IFE and SNH aimed at measuring the current loadings of P to the loch are crucial for a number of reasons. In addition to estimating the present loadings, these studies could establish better than hitherto, the relative importance of the two main controls of phytoplankton abundance: nutrient supplies (in the production of the algae) and grazing zooplankton (in the removal of algal biomass).

It is suspected that a considerable amount of nutrient-rich material has been deposited over the existing sediments during 1994. Microscopic and chemical analyses of the upper layers could well identify contrasts between this recent deposition, and the deeper and older material.

Finally, far more detailed, year-round, information than exists at present, is urgently needed on trophic interactions i.e. the food and feeding of the two main trout species, and the suite of zooplankton species. Ideally, large-scale experiments should be mounted to assess these interrelationships.

4.4 Summary conclusions

Whatever the prime cause of the present, poor, state of the loch, this waterbody plainly cannot sustain its effects - assuming that the prolonged appearance of dense algal blooms is used as a yardstick of non-sustainability (Bailey-Watts, Gunn and Lyle, 1995, in press). Current strategies aimed at reducing the external burdens of P on the loch are focusing on the diffuse, runoff-related sources of P from land. These methods are undoubtedly more acceptable than those referred to above. However, they may take decades to achieve their goals. Progress may be even slower if (i) current fishery management practices are continued, and (ii) this report is correct in attributing the events described for 1994, primarily to these practices.

5. ACKNOWLEDGEMENTS

We thank Scottish Natural Heritage for funding the major programme on phytoplankton composition and abundance, and this ecological interpretation. We are especially indebted to Dr J W G Lund FRS for his painstaking review of the taxonomic literature which has allowed us to put a name to the *Oscillatoria*. A separate paper on these aspects is in preparation. The routine sampling (all aspects) and analytical programmes (chemistry and chlorophyll) were designed by IFE but, for most of 1994, executed by Gordon Wright and his staff based at the Loch Leven Office of Scottish Natural Heritage, and staff of the Forth River Purification Board under the direction of Dr Janet Armstrong. We are very grateful to all of the persons involved, and for the additional funds that FRPB provided for Miss Nicola Wiltshire (IFE and Sunderland University) to assist TB-W in all aspects of this work. We also thank Mrs Karen Sweetman (SNH) for commenting on an earlier draft of this report.

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Appendix I. Algae recorded from the water column of Loch Leven during the routine cell counting procedures in 1994.

In the following list, 'unidentified species' are those seen in very few numbers (just one specimen in many cases). The main algal grouping (Classes) is that of Bourrelly (1966, 1968, 1970), although retaining some features proposed by Christensen (1962). The following texts have also been consulted for most of the generic and specific identifications and nomenclature: Anagnostidis (1961), Anagnostidis and Komarek (1988), Ettl (1978), Hindak (1978), Hustedt (1930), Korshikov (1953), Krammer and Lange-Bertolot (1991), Lind and Brook (1980) and Starmach (1966). Additional papers are given below, with the view to reflecting as many as possible of the latest (continuing) taxonomic debates on certain species. For example, some of the organisms listed have been transferred to new, or other existing, taxa; examples are some of the *Pseudanabaena* species which are now classified under the subgenus *Ilyonema*, and many of the *Melosiras* to *Aulacoseira* (Haworth 1988). Many *Oscillatorias* have been transferred to *Planktothrix* (Anagnostidis and Komarek 1988) or *Limnothrix* (Meffert 1988) although Anagnostidis and Komarek (1988) consider that certain features of *O. subtilissima* (which was by far the most abundant and prominent phytoplankton in Loch Leven this year) merit its inclusion in a new genus - *Jaaginema* (see below).

Cyanobacteria (blue-green 'algae')

- Anabaena affinis* Lemm.
- Anabaena flos-aquae* (mainly forma *flos-aquae* Ralfs ex Born et Flah)
- Anabaena solitaria* Kleb., var. *planktonica* Brunth. (Kom.)
- Anabaena spiroides* Kleb.
- Aphanothece clathrata* W. et G.S. West
- Chroococcus limneticus* Lemm.
- Gomphosphaeria* near *G. lacustris* Chod.
- Merismopedia* species - near *M. tenuissima* Lemm.
- Microcystis aeruginosa* Kutz. emend Elenkin.
- Oscillatoria agardhii* Gom.
- Oscillatoria limnetica* Lemm.
- Oscillatoria subtilissima* Bocheri in Starmach (1966); *O. subtilissima* Kutz ex De Toni or *Jaaginema subtilissimum* Kutz ex De Toni, in Anagnostidis and Komarek (1988)
- Pseudanabaena* species near *P. catenata* Lauterb. See also *P.* (subgenus *Ilyonema*) *galeata* sensu Anagnostidis 1961).
- unidentified *Oscillatoria* species circa 1.5 µm diameter
- unidentified picocyanobacterium circa 0.5 µm diameter

Bacillariophyceae (diatoms):

- Asterionella formosa* Hassall
- Aulacoseira granulata* (Ehrenb.) Haworth
- Aulacoseira subarctica* (O. Mull.) Haworth
- Diatoma elongatum* (Lyngb.) Ag.
- Fragilaria crotonensis* Kitton
- Nitzschia* sp. (re-suspended from the sediment)
- unicellular Centrales assemblage yet to be checked for species composition, but mainly *Stephanodiscus* (discussed in Hakansson and Bailey-Watts 1993), with some *Cyclotella radiosia* (Grun.) Lemm.; see Bailey-Watts (1988b) for the range of species and morphotypes that can be found in a single sample at Loch Leven.
- Synedra acus* Kutz.
- Synedra ulna* (Nitzsch.) Ehrenb.
- unidentified *Synedra* species

Euchlorophyceae ('green' algae)

- Actinastrum hantzschii* Lagerh.
- Ankyra spatulifera* (Kors.) Fott, or *A. lanceolata* (Kors.) Fott
- Botryococcus braunii* Kutz.
- Chodatella ciliata* (Lagerh.) Chod.
- Chodatella genevensis* Lemm.

Coelastrum microporum Nag.
Coelastrum species near *C. pseudomicroporum* Kors.
Coenococcus planctonicus Kors.
Coenocystis planctonica Kors. (or *Eutetramorus planctonica* Kors. acc. to Anagnostidis and Komarek 1988).

Didymocystis inconspicua Kors.
Dictyosphaerium pulchellum Wood
Elakatothrix gelatinosa Wille
Heteromastix (Nephroselmis) angulata (Kors.) Skuja
Micractinium pusillum Fres.
Monoraphidium contortum (Thur.) Kom.-Legn.
Monoraphidium griffithii (Berk.) Kom.-Legn.
Monoraphidium minutum (Nag.) Kom.-Legn.
Nephrochlamys subsolitaria (G.S.West) Kors.
Oocystis lacustris Chod.
Other species of *Oocystis* A.Br.
Pediastrum boryanum (Turp.) Menegh.
Pseudosphaerocystis lacustris (Lemm.) Novakova
Raphidonema (Koliella) planctonica Hind.
Sphaerocystis schroeteri Chod., inc. single cell form near *Planktosphaeria gelatinosa* G.M.Smith
Scenedesmus abundans (Kirchn.) Chod.
Scenedesmus acuminatus (Lagerh.) Chod.
Scenedesmus alternans Reinsch.
Scenedesmus linearis Kom.
Scenedesmus quadricauda (Turp.) Breb.
Scenedesmus serratus (Corda) Bohl.
Tetraedron minimum (A.Br.) Hansg.
Tetraedron platyisthmum (Arch.) G.S.West
Tetrastrum staurogeniaeforme (Scrod.) Lemm.
Treubaria triappendiculata Bern.
unidentified chloromonad ('chlamydomonad?')
unidentified unicellular green algae (chlorelloid?)

***Chrysophyceae* ('yellow-green' algae)**

Species of *Chromulina* Cienk.
Species of *Mallomonas* Perty
Species of *Ochromonas* Wyss

Cryptophyceae

Mainly an assemblage of *Cryptomonas* with forms resembling *C. curvata* Ehrenb., *C. erosa* Ehrenb., *C. ovata* Ehrenb., *C. marssonii* Skuja, and *C. reflexa* Skuja, and of *Rhodomonas* Karsten including forms still known as *Rhodomonas lacustris* var *nanoplanktica* Skuja (see Lund 1962) and *R. pusilla* Bachm.

***Dinophyceae* ('dinoflagellates')**

Species of *Gymnodinium* Stein
Species of *Peridinium* Ehrenb.
Species of *Woloszynskia* Thompson

Haptophyceae (separated from the Chrysophyceae by Christensen 1962)

Chrysochromulina parva Lackey (see Parke, Lund and Manton 1962)

Xanthophyceae

Dichotomococcus curvatus Kors.

Zygophyceae ('desmids')- see Lind and Brook (1980), and Ruzicki (1977)

Closterium limneticum Lemm.

Closterium strigosum var *strigosum* Breb.

Closterium strigosum var *elegans* (G. S. West) W. Krieg

Cosmarium botrytis Menegh.

Cosmarium depressum var *planctonicum* Riverdin

Staurastrum lunatum (Ralfs) or var *planctonicum* (W. and G. S. West

Staurastrum muticum Breb.

Staurastrum planktonicum Teiling

7. FIGURES

Figure 1. Changes at Loch Leven during 1994 in the the overall abundance of phytoplankton measured as chlorophyll_a (**upper panel**) and in a measure of species diversity (**lower panel**).

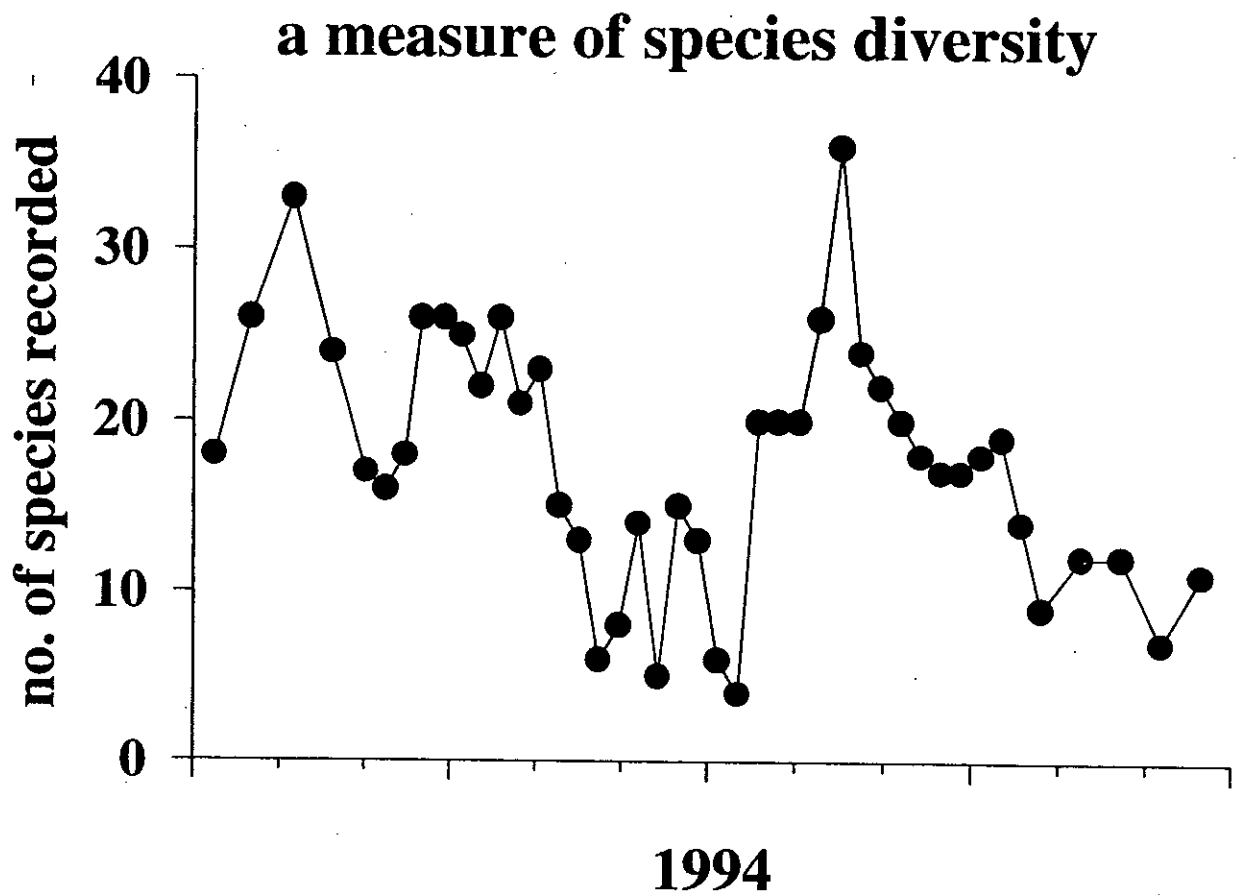
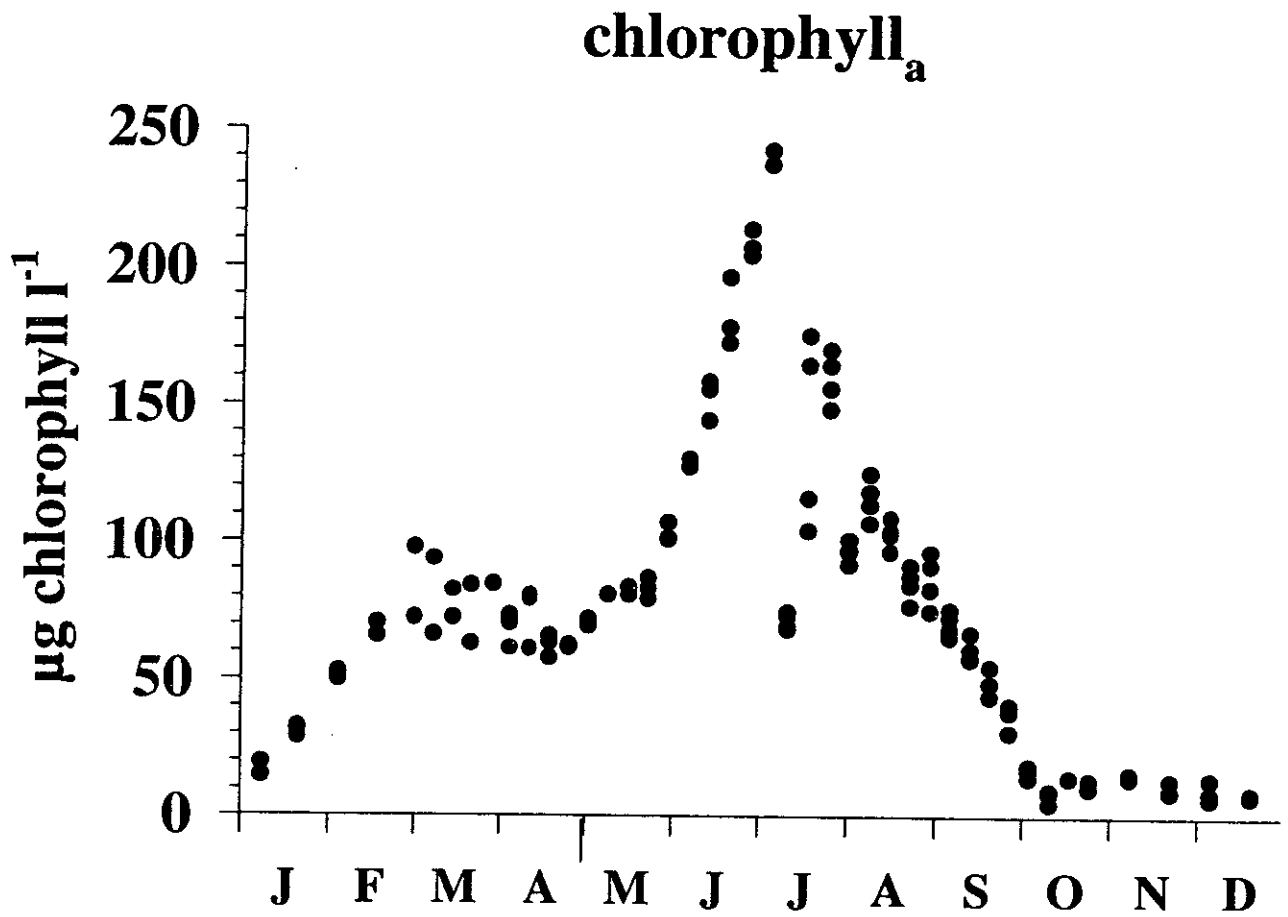
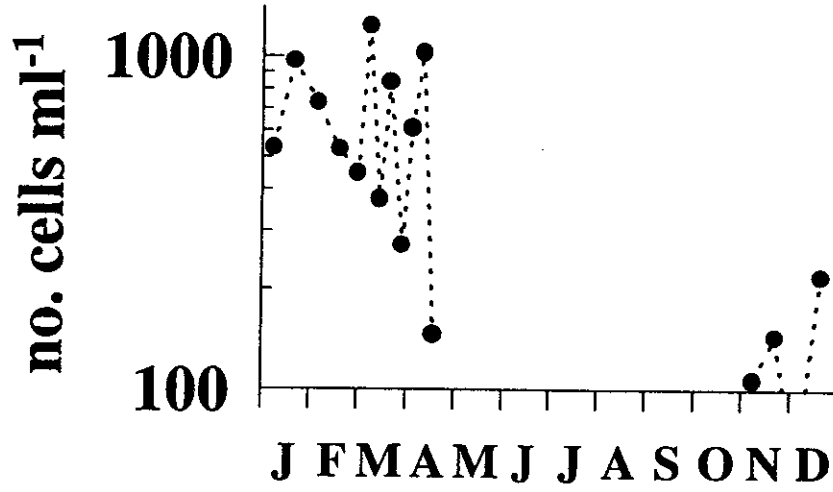
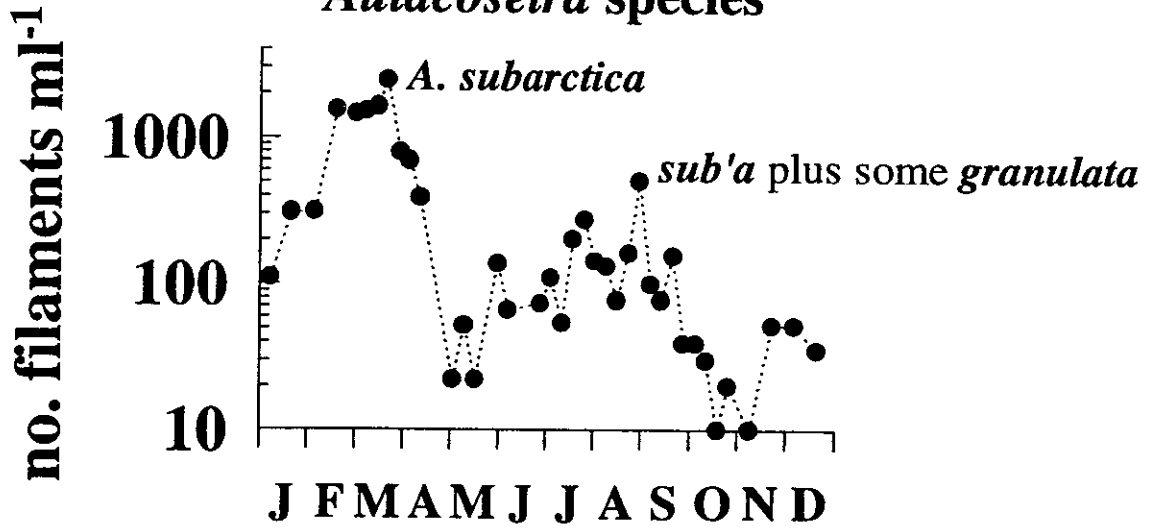


Figure 2. As Figure 1, for the population densities of *Asterionella formosa* (**upper panel**), two *Aulacoseira* species (**middle panel**), and *Diatoma elongatum* (**lower panel**). These abundance estimates refer to the open water site south of Reed Bower, or in the case of very stormy weather, the sluices (outflow) station.

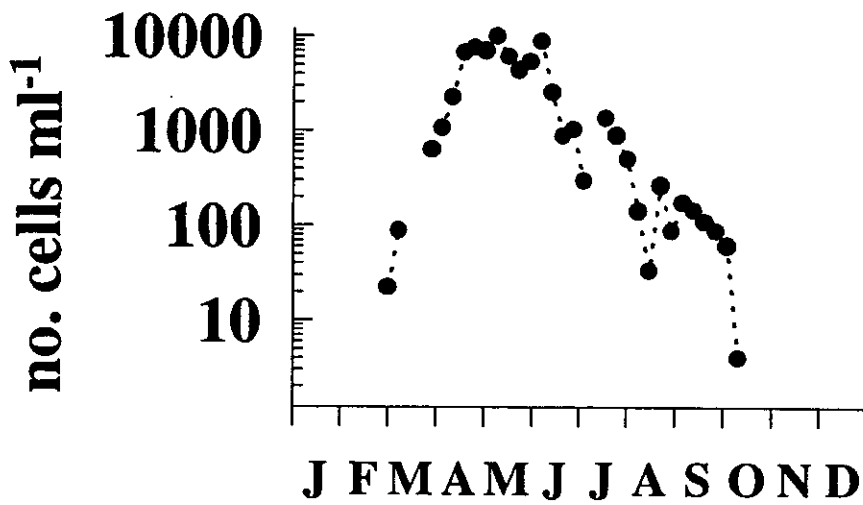
Asterionella formosa



Aulacoseira species



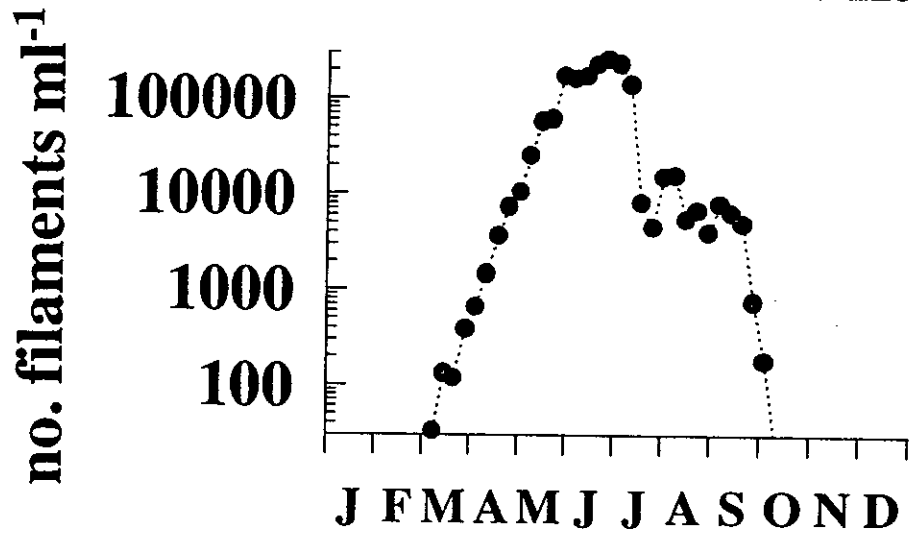
Diatoma elongatum



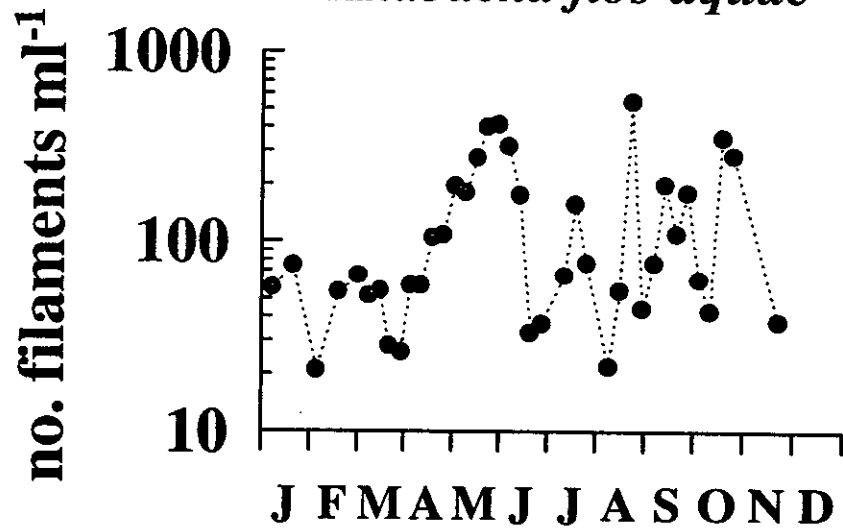
1994

Figure 2 continued. As Figure 1, for the population densities of *Oscillatoria subtilissima* (**upper panel**), *Anabaena flos-aquae* (**middle panel**) and unicellular centric diatoms (**lower panel**).

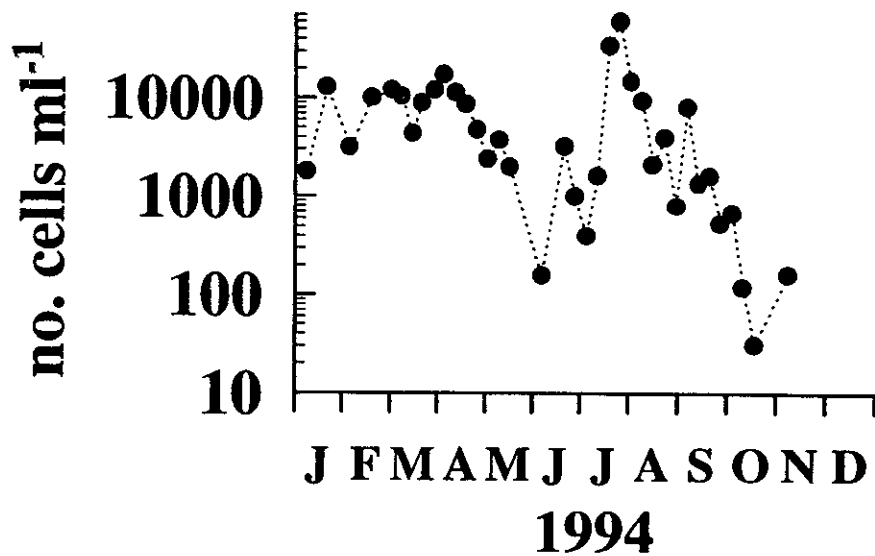
Oscillatoria subtilissima Kutz



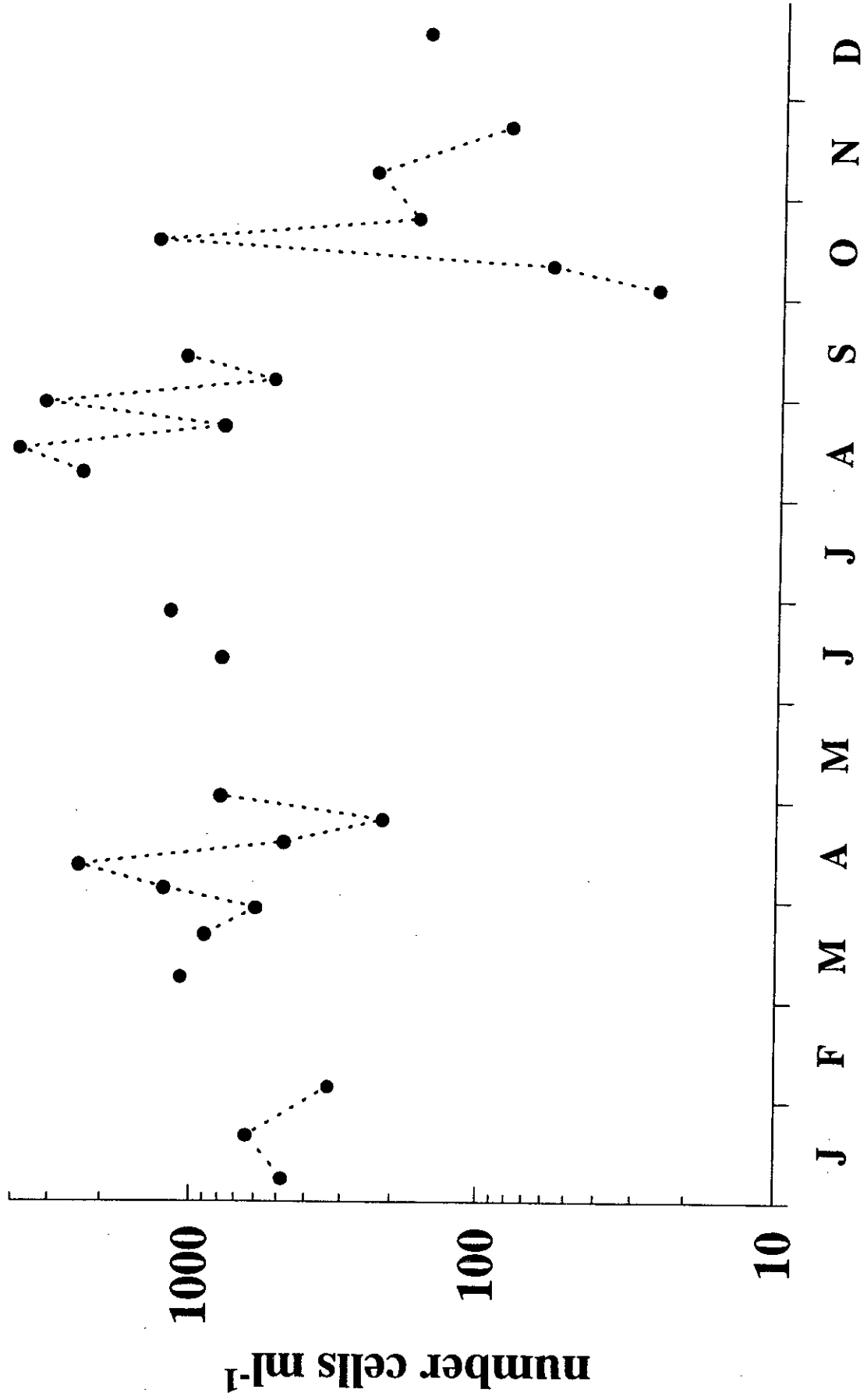
Anabaena flos-aquae



unicellular centric diatoms (mainly *Stephanodiscus*)



Rhodomonas



1994

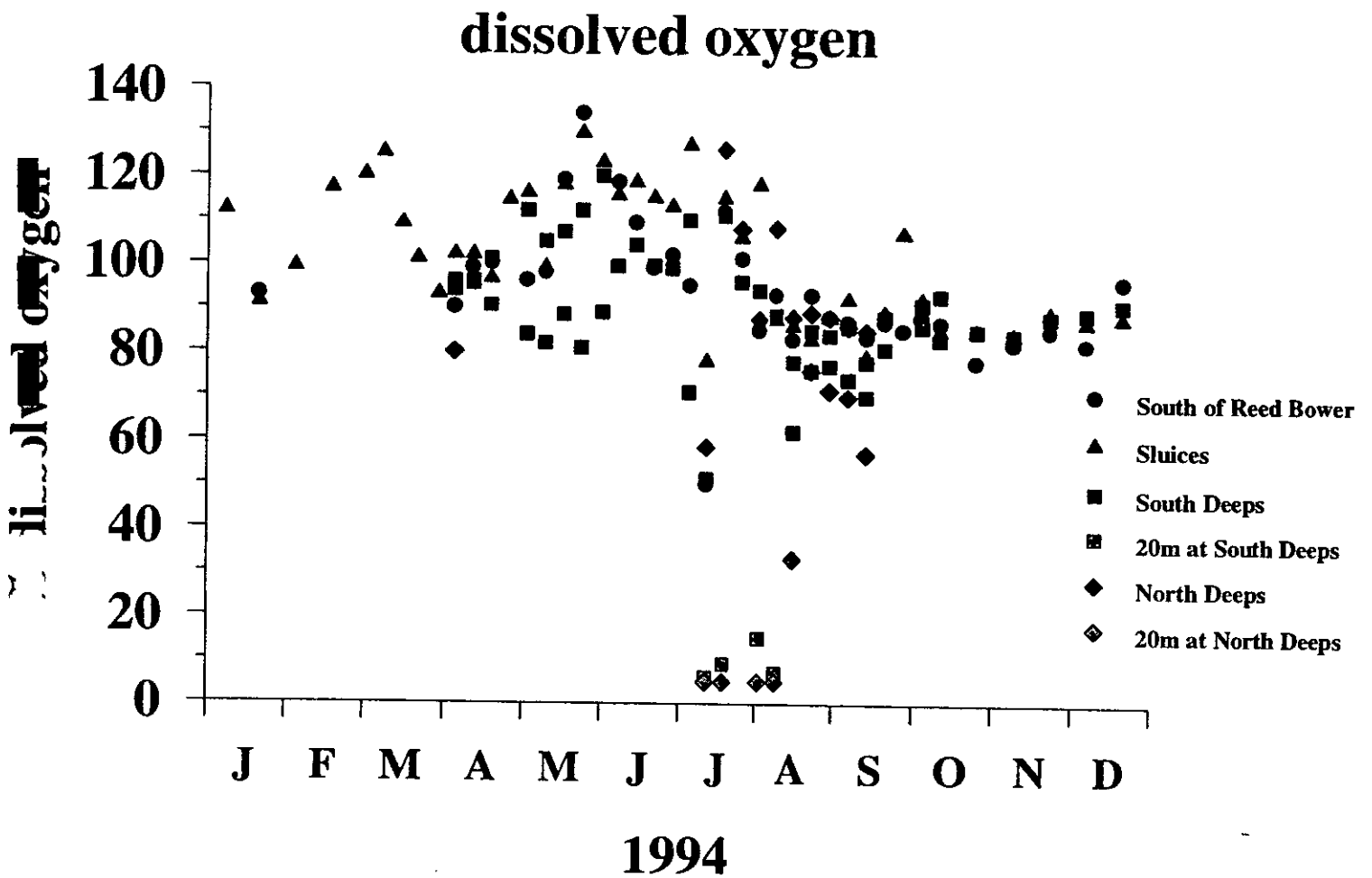
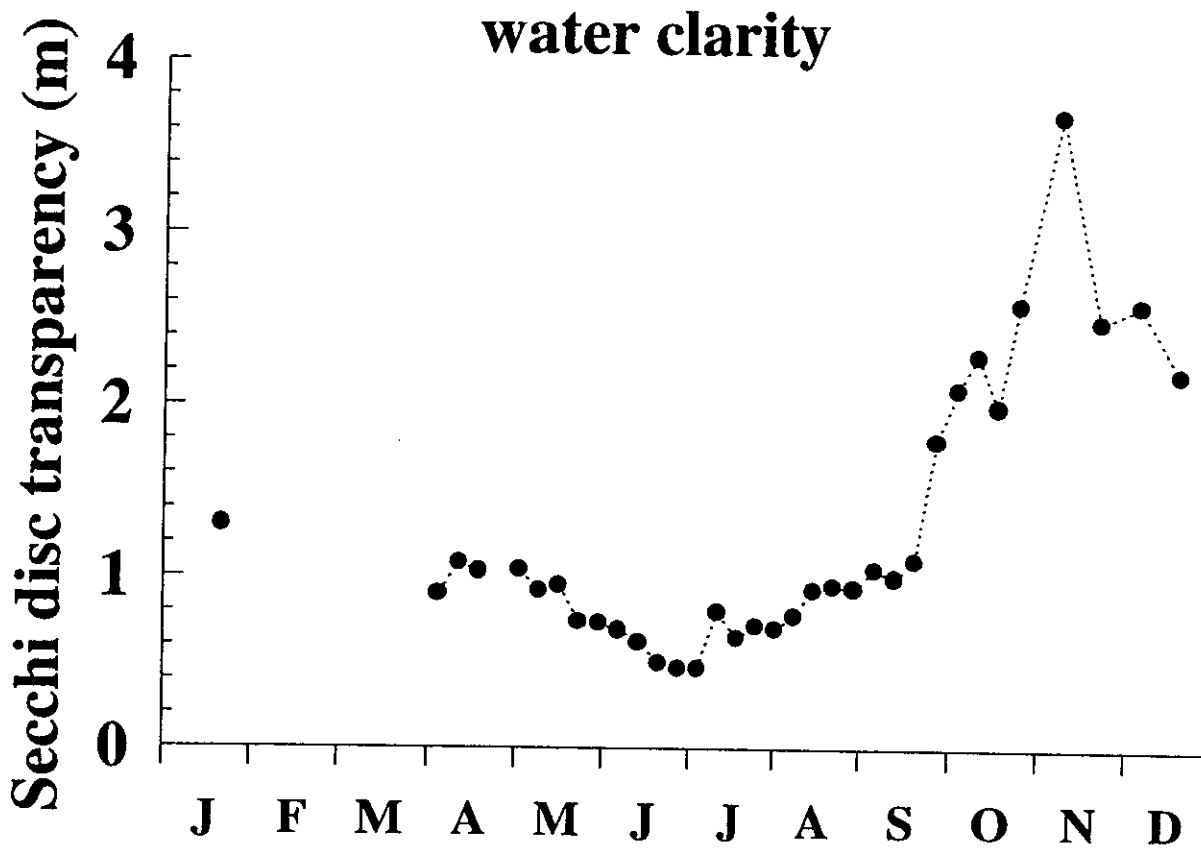
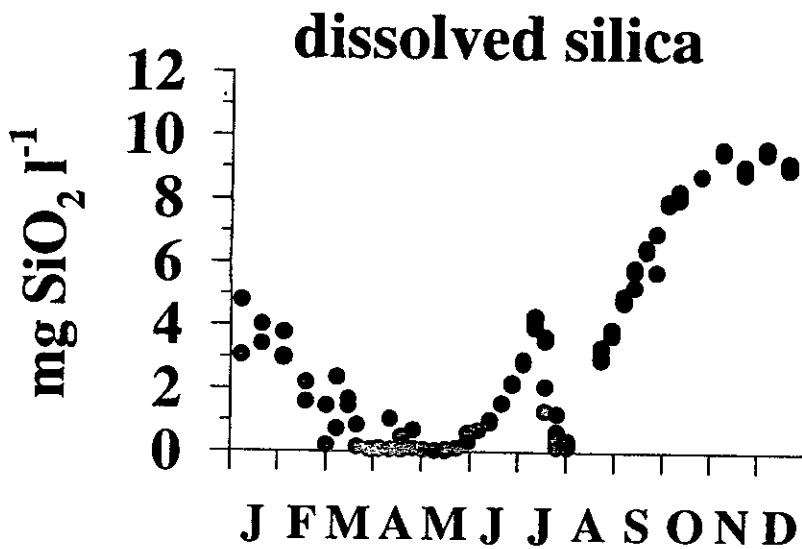
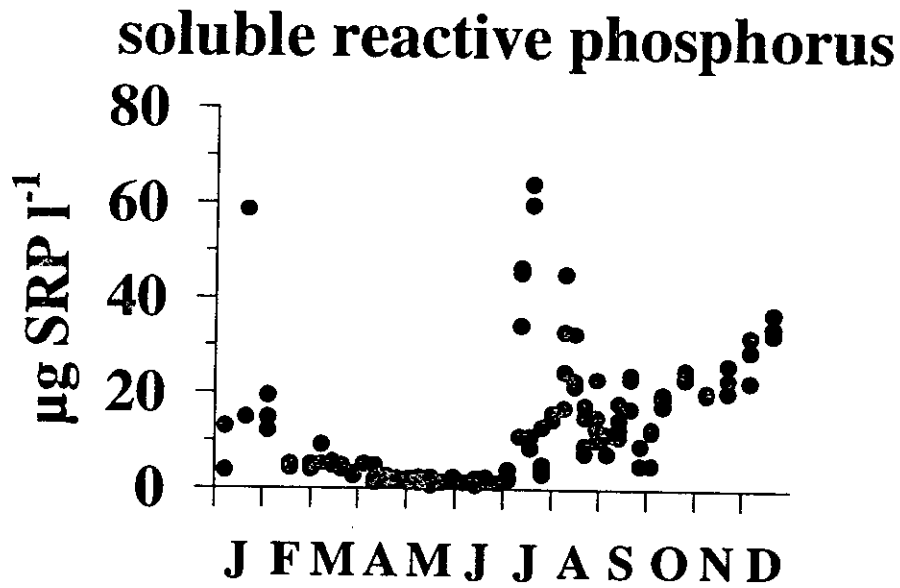
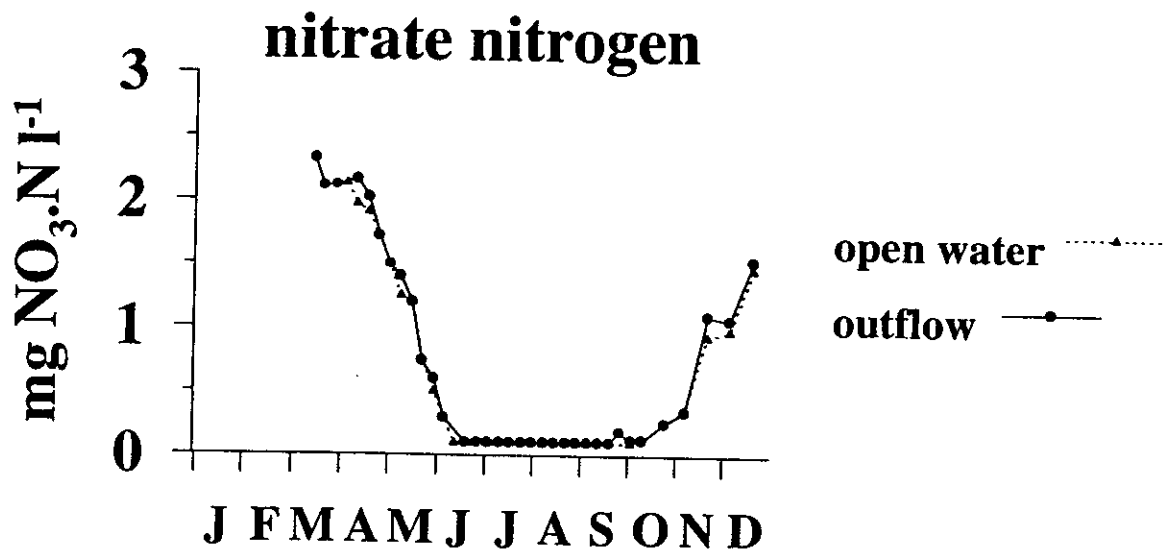


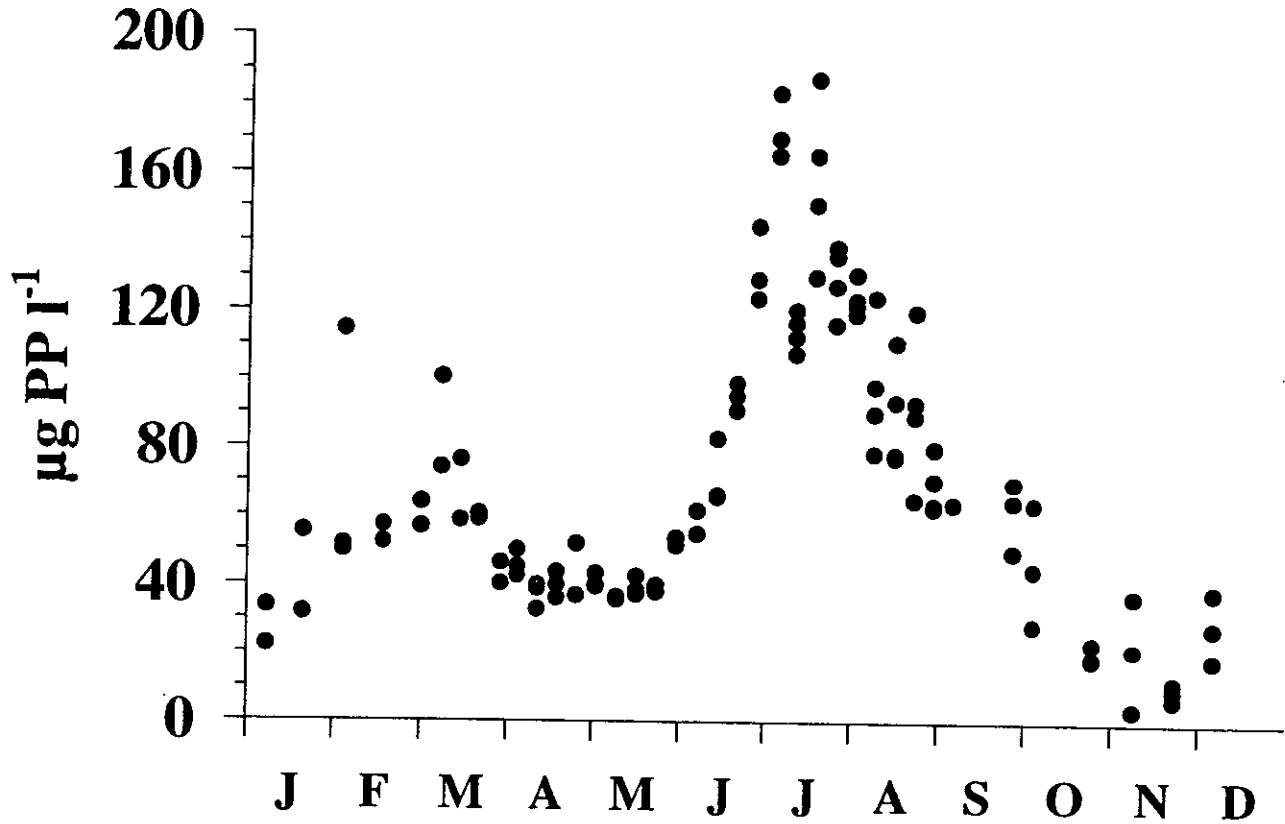
Figure 4. As Figure 3 for changes in the concentrations of nitrate nitrogen (**upper panel**), soluble reactive phosphorus (**middle panel**) and dissolved silica (**lower panel**).



1994

Figure 5. As Figure 3 for changes in the concentrations of particulate phosphorus (**upper panel**) and the particulate phosphorus-to-chlorophyll_a weight ratio (**lower panel**).

particulate phosphorus



particulate P-to-chlorophyll_a weight ratio

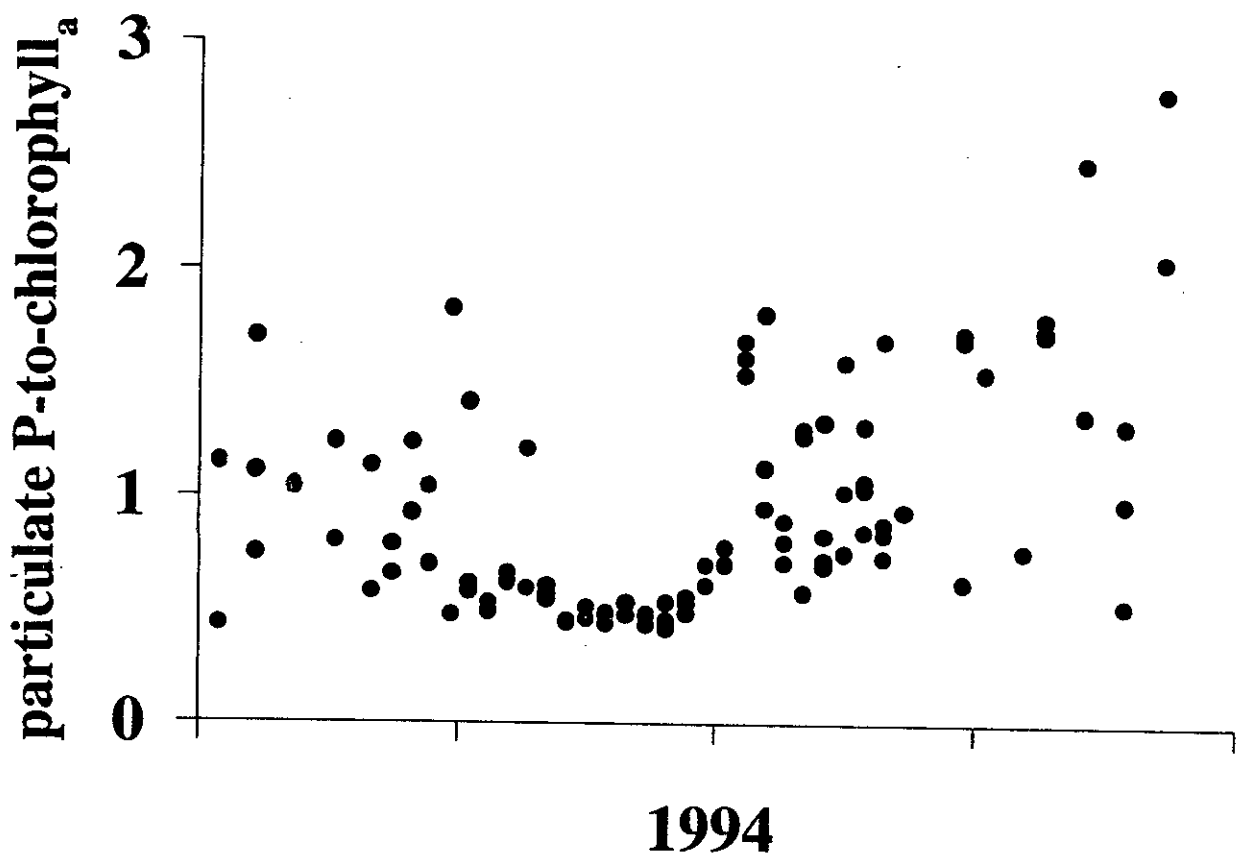
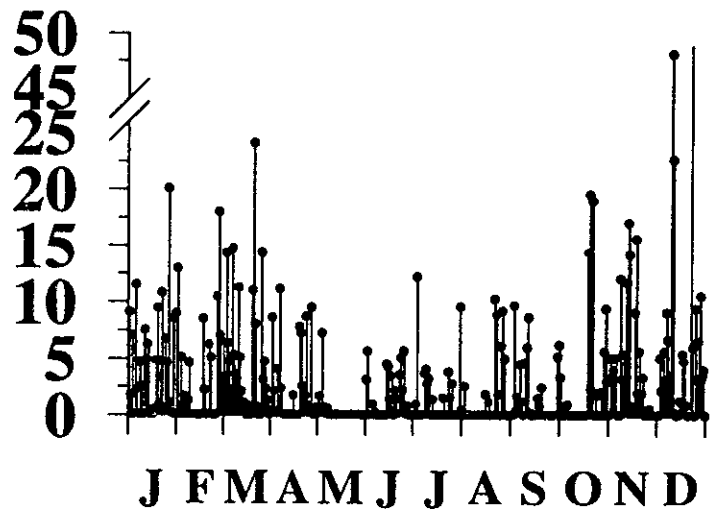
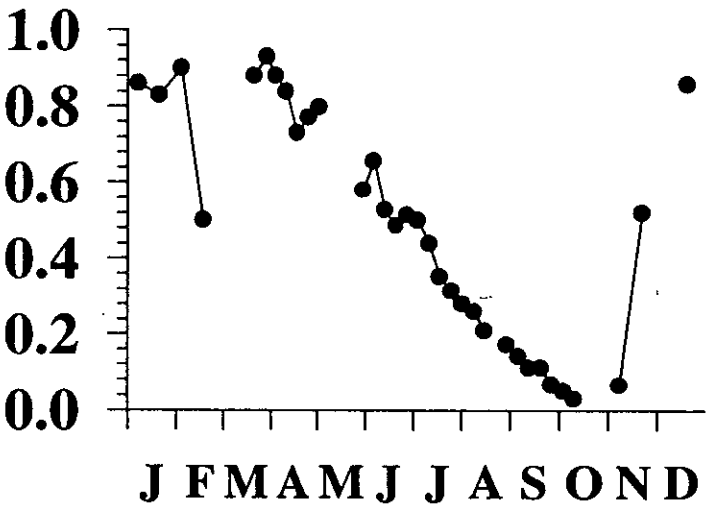


Figure 6. As Figure 3 for the changes in daily rainfall measured at Kinross (**upper panel**), loch level staff gauge readings (**middle panel**) and open water temperature (**lower panel**).

daily rainfall - mm



staff gauge reading - m



temperature @ 0.2m - °C

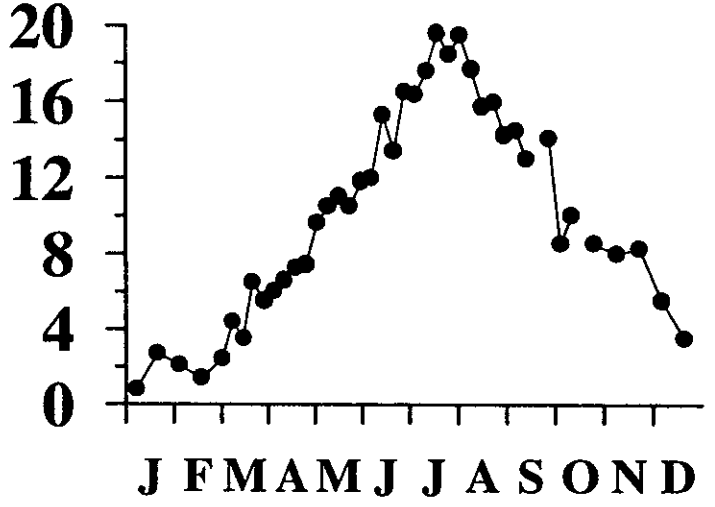


Figure 7. A scheme that attributes marked qualitative and quantitative changes in the plankton of Loch Leven in 1994, to the introduction of *Onchorhynchus mykiss* in late spring 1993; the shifts represent a return to a situation that last prevailed in the late 1960s.

stocking with *Onchorhynchus mykiss* - FACT

