Institute of Freshwater Ecology
Edinburgh Laboratory, Bush Estate, Penicuik
Midlothian EH26 OQB, Scotland
Telephone 0131 445 4343; Fax 0131 445 3943

THE ECOLOGY OF THE PHYTOPLANKTON OF LOCH LEVEN DURING 1995 - A PERSONAL ASSESSMENT

Project Manager: A E Bailey-Watts

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Principal Investigators:

A E Bailey-Watts, BSc, PhD, DSc, CBiol, FIBiol, MIWEM
N J Wiltshire BSc

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Summary

The report details many aspects of the ecology of the phytoplankton of Loch Leven over 1995 as a whole, but pays major attention to the summer, particularly August when an enormous crop of large gas-vacuolate, blue-green algae developed and constituted the annual chlorophyll maximum; this combination of features has not been recorded before.

The development is attributed to spells of very warm, calm weather and associated releases of soluble reactive phosphorus and ammonia from the sediments which supported the prominent cyanobacteria as well as a less noticeable but diverse assemblage of smaller algae remaining in low population densities; this was on account of grazing by *Daphnia* which itself produced one of the densest populations ever recorded.

Phytoplankton developments outside the main period if interest were generally moderate, due to seasonal shortages of mainly phosphorus, but also, for some algal types, nitrate-nitrogen and silica. As a consequence, water clarity was relatively high with Secchi Disc readings of 2m or more for a total of 6 months.

The collapse of the summer (mainly *Anabaena*) population in August corresponded to a resumption of cooler, windier and wetter weather than had prevailed over the previous few weeks; however, cellular phosphorus-to-chlorophyll weight ratios at this time were among the lowest recorded over the year. Although the lowest Secchi Disc readings - *ca* 0.5 m - were measured at this time, light is not thought to have been the main cause of the wane in the *Anabaena* population.

Factor interactions of the type that culminated in the success of the large blue-green algae in 1995 are undoubtedly masking improvements in water quality e.g. decreases in mean concentrations of phosphorus and chlorophyll, that might be reasonably expected as a result of efforts to reduce phosphorus loadings to the loch - and cut back the inputs of bio-available, P-rich, point-sources in particular. However, a preliminary comparison of the 1995 findings with the preceding long run of data, indicates that currently, the loch is not noticeably deteriorating; indeed, some algal species and abundance changes (in winter, early spring and late autumn) suggest that conditions are improving. Certainly, a number of pigment and phosphorus values calculated from the 1995 data, are generally much lower than those obtained from the work carried out in the period 1985-1990 for example.

On the basis of the 1995 analyses, previous ideas on the significance to the ecology of the algae of (i) ‘cascade’ effects of fish stocking, and (ii) recycling of nutrients from the sediments, may have to be revised. In any event, however, considerable more work is necessary to establish for example, the food preferences and feeding rates of fish and zooplankton. These and other field, laboratory and desk projects are proposed. Some suggestions are also made for improving on the sampling programme; of particular importance are those areas relating to the lakewide estimation of organisms and nutrients when these are very patchily distributed.

CONTENTS

1. GENERAL INTRODUCTION - RATIONALE AND SCOPE OF THE STUDY

This report presents the results from the surveillance of Loch Leven phytoplankton and the factors thought to be most important in controlling the observed changes in the species composition and abundance of the assemblage during 1995. Like a number of previous reports and scientific publications on this loch (e.g. Bailey-Watts and Kirika 1995) it focuses on the influence of selected physical, chemical and biotic factors. Even after nearly 30 years of almost continuous surveillance, the studies continue to provide further insights into the functioning of the system. Marked inter-annual differences in the weather impact considerably on this loch because it is both broad and shallow; erratic changes thus result in the rates of (i) the input of water and dissolved and particulate components, and (ii) mixing of the water column. These in turn affect the availability of light and nutrients which are the two major sources of energy fuelling the production of phytoplankton and thus, of most of the other organisms including fish and many waterfowl at the higher trophic levels.

One of the main events during 1995 corresponds to a truly extraordinary summer in which Europe's temperatures exceeded values not recorded for some 400 years. At Leven this resulted in a situation that has features common to both the 'pre- or low-*Daphnia*' years 1968, 1969 and 1994 (Bailey-Watts and Kirika 1995), and the other years i.e. those in which the cladoceran has been reasonably prominent. Much of the report concentrates on this event, although a start is also made towards establishing to what extent the loch is responding to a range of strategies proposed by Bailey-Watts *et al* (1987) and, more recently, Bailey-Watts, Gunn and Kirika (1993) for reducing phosphorus (P) inputs to the loch.

The report presents and discusses first the descriptors of overall phytoplankton biomass, and its effects on water clarity; many view this as one of the most important issues, although, due to the complex relationship between algal abundance and water transparency, 'clear' water may not necessarily imply good water quality (e.g Bailey-Watts, Gunn and Kirika 1993). Secondly, it comments on the seasonal changes in the abundance of the most prominent species. Thirdly, more attention than in recent years, is paid to the relatively sparse, or at least less noticeable, small components of the total phytoplankton assemblage. The latter are rare because they are continually grazed down by *Daphnia* - this very activity (among a suite of other conditions) contributing to the development of dense blooms of large blue-green algae[1]. The influence on the observed 'performance' of the phytoplankton, of these

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[1] As they are prokaryotic like bacteria, 'blue-green algae' have been viewed by many over the last 25 years as 'cyanobacteria'; this report uses both terms; the term 'phytoplankton' encompasses all essentially microscopic plants (fungi, algae and cyanobacteria) that spend the majority of their existence in the water column.

interactions, and the situations regarding the weather and nutrients, are discussed next.. A separate section attempts to place the 1995 findings in the long-term context and highlight briefly, features that might signal effects of P control strategies. A concluding section identifies new projects as well as modifications to existing activities, that would enhance our understanding of the system and our ability to reverse eutrophication trends and improve water quality.

2. INVESTIGATIVE METHODS

The spatial dispersion of the sampling sites, and the frequency of sampling, along with the various field and laboratory procedures adopted for the plankton studies during 1995, are as referred by Bailey-Watts and Kirika (1995). Also, as before, the programme was designed by IFE, but the field sampling and recording was executed mainly by SNH and FRPB. Since the FRPB has a statutory obligation to monitor Loch Leven, it has also carried out the greater majority of chemical and chlorophyll$_a$ analyses. However, both authors were involved in the identification and enumeration of the phytoplankton. TBW is ultimately responsible for the views expressed on the basis of all of the data presented.

3. RESULTS AND DISCUSSION ON THE ECOLOGY OF THE PHYTOPLANKTON IN 1995

3.1 The phytoplankton

3.1.1 Temporal fluctuations in total abundance

The concentrations of chlorophyll$_a$ and particulate phosphorus (PP) are used here as indices of total algal abundance (**Figure 1**). The following events characterise the changes in pigment:

- a more or less linear rise from <10 μg l^{-1} at the start of the year, to approximately 70 μg l^{-1} in mid-March.
- a rapid decrease to *ca* 12 μg l^{-1} by mid-April and little net change over the next 8 weeks (i.e. to mid-June).
- from mid-June to mid-September, rises to, and decreases following each of three, increasingly large peaks i.e. of 40, 70 and 230 μg l^{-1}.
- minor fluctuations around a mean value of approximately 35 μg l^{-1} until late October, and others generally around 10 μg l^{-1} (as recorded at the beginning of the year) throughout the rest of 1995.

Figure 1 also indicates that diatoms dominated the phytoplankton over the first 4 months of the year, while cyanobacteria characterised the second 4-month period.

The PP values describe a somewhat similar pattern to that exhibited by chlorophyll. The plots differ in detail, however, for two main reasons. Firstly, the PP includes phosphorus not only in phytoplankton and detritus, but - especially in August - in Crustacean zooplankton too, while chlorophyll is more specifically associated with the algae. Secondly, even in the unlikely event of the algae representing all of the suspended particulate matter, cellular P-to-pigment ratios vary between species, and even between cells of the same species at different stages in the population cycle. It follows that the values that are most likely to represent the actual situation as regards PP: chlorophyll ratios, are those corresponding to the densest crops as indicated by chlorophyll; these were recorded in mid-August, and they are referred to later, in relation to considerations about nutrient limitation of algal production and growth.

3.1.2 Effects on water clarity

Reduction in water clarity is one of the most visible effects of dense developments of algae. The correspondence in mid-August between low Secchi Disc readings of approximately 0.75 m (**Figure 2**) and the chlorophyll maximum in Figure 1 illustrates this point. Note however, that only slightly higher Secchi Disc values were obtained in mid-March, when considerably lower chlorophyll concentrations were measured. Previous analyses that this is likely to be due to the presence of detritus, and the fact that a given concentration of large algae such as those predominating in August (see below), attenuates light to a lesser degree than that of a similar crop (biomass, concentration) of small species. Figure 2 also illustrates how much clearer on average the water was in 1995 than 1994. Indeed, apart from the two periods referred to above, Secchi Disc readings were manifestly higher in 1995 than 1994. However, because of the contrast between the two years in terms of algal species (particularly as regards the development in August), many observers may well have viewed the loch as being of poorer quality in 1995 than in 1994.

3.1.3 The dynamics of the most prominent species

Seasonal changes in the most abundant phytoplankton species (diatoms and cyanobacteria) recorded in 1995 are shown in **Figure 3**. The colonial diatom *Asterionella formosa* and the unicellular centric *Stephanodiscus* (dominating an assemblage of these small diatoms) attained maxima of approximately 8 000 and 3 000 cells ml^{-1} respectively, before the end of February, while a third diatom, *Aulacoseira subarctica* peaked at a concentration of 3 000 filaments ml^{-1} before the end of March. This last maximum coincides with the chlorophyll peak of *ca* 70 μg

l^{-1} in Figure 1. *Asterionella* achieved another, somewhat smaller, maximum in late July, and *Aulacoseira* did much the same in early August. Contrastingly, *Stephanodiscus* achieved a second peak in late April which was very similar to the first. Other diatoms feature in **Appendix I** but they contributed little in terms of biomass; for example, *Diatoma elongatum* was recorded more or less consistently from mid-April to early August, but achieved a maximum density of only 190 cells ml^{-1}. This is in sharp contrast to its maximum of *ca* 10 000 cells ml in 1994 (Bailey-Watts and Kirika 1995).

Anabaena spiroides especially, but also *Microcystis aeruginosa*, *A. solitaria* and *A. flos-aquae* dominated the summer scene. Indeed, although limited largely to a period of less than one month, the dynamics of the *A. spiroides* population constitute the main 'event' for 1995. Some of the reasons for this are as follows:

- it is a very large cyanobacterium (**Figure 4**), but it achieved on occasions albeit patchy, densities of 1000s of filaments ml^{-1} (note in Figure 1 some wide ranges of chlorophyll and particulate P values corresponding to this period).
- as a large and gas-vacuolate species, its population can - under calm conditions - migrate up to, and concentrate at the water surface ('bloom') extremely rapidly.
- the conditions enhancing the success of such species usually prevail in the summer when anglers and other visitors to the loch are most numerous; the blooms are thus firmly in the public eye; the population in question achieved its peak concentrations in August.

The considerable contrast between 1994 and 1995 in the performance of *Diatoma*, is parallelled by the cyanobacterium *Oscillatoria subtilissima*. This 2-µm diameter species hardly featured at all in 1995, although it attained a maximum density of 261,000 filaments ml^{-1} in 1994.

The only other algae worthy of note are cryptomomonads. However, these were prominent in terms of their characteristic morphology rather than abundance. Indeed, while species of *Cryptomonas* can reach 30 µm, cells of the other main genus - *Rhodomonas* - are commonly only 10 µm in length. These organisms have achieved population densities of many thousands per millilitre in Loch Leven in the past. However, in 1995 *Cryptomonas* remained at less than 100 ml^{-1} apart from a brief increases to 300 ml^{-1} in late June and late September, while *Rhodomonas* exceeded 1,000 ml^{-1} only once - in May.

3.1.4 Overall diversity and the 'rare' species

Appendix I lists the approximately 90 phytoplankters which were recorded during the routine counting procedures during 1995. The term 'approximately' is used, because a number of forms could not be ascertained to species level. Indeed, further examination of some of the centric diatoms (including unicellular *Stephanodiscus* and filamentous *Aulacoseira*) may well reveal more species, and a number of algae presently recorded to Genus are likely to include more than one species.

Even taking account of these shortcomings with identification, the overall diversity of forms is not insignificant. More than 20 'species' were recorded on each sampling occasion in the second quarter of the year, although much fewer types were encountered in e.g. early February and August-September (**Figure 5**). As a result of the effects of the relative abundance and size distributions of algae and detrital material on counting efficiency (Bailey-Watts 1996), the numbers of species indicated are undoubtedly underestimates. A particularly striking example of this relates to July and August corresponding to high chlorophyll values associated with the major development of the large blue-green alga *Anabaena spiroides* (see below).

Occasionally, the population was so dense that the water sample had to be diluted before reasonable counts could be achieved. In so doing, however, the already relatively rare or inconspicuous algae were rendered even more sparse - and thus, more likely to be overlooked. Also (as pointed out in the 1995 report), since counting effort varies between the sampling dates, the different values in Figure 5 are not strictly comparable. Nevertheless, the general trends in diversity illustrated are unlikely to deviate significantly from the true situation.

Extra attention to the rare and other less readily detected forms revealed some 20 other species even at the height of the major blue-green algal development in August (Table 1). Occasionally during that month, there were also some 10-100 colonies of the fungus *Planctomyces bekefii* (Skuja 1956) and >100,000 pico planktonic cells (fragmented *Aphanocapsa, Aphanothece* and the like). These observations are discussed further in relation to the *Daphnia* population maximum that coincided with the *Anabaena spiroides* peak.

3.2 Factors controlling phytoplankton performance

This section discusses factors controlling the types of algae present as well as the overall abundance, bearing in mind that the significance of a particular alga may be just as much a function of the 'type' of organism as the numbers/biomass it

Table 1. Rare, and other less readily detected species recorded at the time of *Anabaena* dominance during August 1995.

species achieving a maximum of >1.0 - 10.0 ml^{-1}
Ceratium hirundinella
Merismopedia tenuissima
Monoraphidium contortum
species achieving a maximum of >10.0 - 100 ml^{-1}
Coelastrum microporum
Cosmarium botrytis
Cyclotella sp.
Oocystis lacustris
Oscillatoria (5µm diameter)
Pediastrum boryanum
Pandorina sp.
Pseudosphaerocystis lacustris
Scenedesmus quadricauda
Sphaerocystis schroeteri
Staurastrum planctonicum
Tetraedron minimum
Trachelomonas sp.
Unidentified 'benthic', pennate diatom
species achieving a maximum of >100 - 1000 ml^{-1}
Aphanocapsa sp.
Gomphosphaeria lacustris
species achieving a maximum of >1000 - 10000 ml^{-1}
Aphanothece sp.

achieves. As a consequence of the somewhat unprecedented development in August 1995, some views are expressed on the factors controlling the relatively sparse forms as well as the dominant species.

3.2.1 Controls over the general balance between abundant and sparse forms - the distinction between production and biomass

The prominent and most abundant species (in terms of biomass) discussed above are important in that they affect gross features of the system such as water clarity and colour. This does not mean to suggest, however, that the relatively inconspicuous and less abundant forms are unimportant; indeed, while an abundant alga may represent a largely un-tapped resource - in the short-term at least - the forms that are sparse at any instant (and they include the vast majority of the species listed in Appendix I) may be playing an extremely important role. What may appear to be an anomaly can be explained by highlighting the difference between production and biomass of these organisms, and the factors controlling these features.

A species that is observed to increase in numbers over a period and assume a degree of 'dominance' does so by maintaining gains by means of growth, over (i) reductions by senescence and failure to produce more individuals (due to nutrient or light limitation, for example), and (ii) losses due to sinking (on to the sediments), fungal parasitism, grazing (by various planktonic and benthic invertebrates) and washout (flushing out of the lake). Contrastingly, the presence of species at a relatively low population density over a particular period, can be due to one or both of the following reasons:

- because light conditions and the concentrations of nutrients, and perhaps the prevailing nutrient ratios, prevent the organism producing more cells.
- because conditions favour cell replication, but not at a rate sufficient to outstrip the losses due to grazing etc.

In this connection, it is worth stressing that the observed changes in the abundance and species composition of the phytoplankton in any system, is in large part, a reflection of the availability of light and nutrients, and the relative abilities of the different organisms to capitalise on, or contend with, the (changing) conditions as regards nutrient and light availability, and the factors determining the losses cited above, that is, wind regimes, the abundance and type of parasitic fungi and grazing animals, and the situations regarding rainfall and the water level.

Such considerations start to clarify why the following (as examples from the past) may occur:

- silica may disappear at a greater rate and to a greater extent than the observed growth rates and numbers of diatoms would suggest (Bailey-Watts 1988a, 1990).
- algal biomass can accumulate in the apparent absence of e.g. SRP (Bailey-Watts and Kirika 1995).
- *Daphnia* may burgeon in the apparent absence of what we perceive to be its favoured food items i.e. the smaller phytoplankton elements (Bailey-Watts and Kirika 1981; Bailey-Watts 1986 - and see below in relation to the situation obtaining in 1995).

3.2.2 Conditions (other than those thought to be due to a reduction in phosphorus loading) controlling the major features of the phytoplankton during 1995

The major features of the phytoplankton during 1995 can be attributed to temporal changes in the combination of weather conditions, nutrient levels and *Daphnia* abundance. The changes observed in the most noticeable phytoplankton species, suggest that the controlling factors are best highlighted by examining the regimes prevailing in each of the three, 4-month periods of the year. Features that may reflect an effect of phosphorus loading reduction are dealt with separately in the General Discussion.

January to April

This period was characterised by the following conditions:

- generally low air and water temperatures (**Figure 6**); it was initially very cold (although ice formation was restricted to the loch edge and then only for periods of days), and even by the end of April the loch had 'heated up' to only 8°C.
- moderately high winds and rainfall, and the highest water levels for the year (**Figure 7**).
- initially at least, all of the three nutrients of major importance i.e. nitrate-nitrogen (NO_3-N), soluble reactive phosphorus (SRP) and dissolved silica (SiO_2) were at their winter maxima (**Figure 8**), and the values for NO_3-N and SRP also turned out to be the annual maxima; the concentrations of firstly, SRP and secondly, SiO_2 were reduced to near-undetectable values, while the decrease in NO_3-N concentration was relatively insignificant; this depletion sequence i.e. SRP → SiO_2 → NO_3-N, reflects the early growth of phytoplankton dominated by diatoms, and i) the ability of some of these algae to store P in excess of immediate needs, (ii) their inability to store SiO_2 in this way, and (iii) the superabundance of NO_3-N (see also Bailey-Watts 1988a).
- planktonic rotifers and micro-Crustacea - and *Daphnia* in particular, were present at very low levels i.e.$<200\ l^{-1}$ and $<5\ l^{-1}$ respectively.

This environmental profile is consistent with the success of diatoms during this 4-month period. Without the reasonably turbulent conditions, much of the production of these 'heavy-weights' of the algal plankton would be lost to the deposits; due almost certainly to sinking losses, the overall growth of diatoms is not fully reflected in the depletion of some 9 mg $SiO_2\ l^{-1}$. On the other hand, the somewhat erratic shifts in diatom numbers in January and February, are likely to be a result of re-suspension of cells from the sediments, as in the 1988-89 winter (Bailey-Watts 1990). The dominance by diatoms over the period, is in keeping with their ability to produce cells as soon as daylengths increase from the winter minima, regardless of low temperatures (Bailey-Watts 1988a). The overall success of these particular algae was also enhanced by the cold conditions limiting the metabolism including grazing potential (Jones, Lack and Jones 1979) of the major zooplankters; in addition these animals were very sparse i.e. <5 individuals l^{-1} throughout this period (see later).

May to August

The weather regime and conditions regarding nutrients and grazing zooplankton during the second 4-month period were quite different to those prevailing upto the end of April. The main features are as follows:

- using Smith's (1974) terminology, the loch exited its 'cold' phase, passed through a period of 'heating' to the 'warm' period, with the latter including some spells of extraordinarily warm weather resulting in water temperatures of 17°C to 21°C (Figure 6); it is not surprising that daily maximum air temperatures often exceeded 25°C at certain times, but the recording of daily minimum values of a few degrees above zero (e.g. on the apparently very calm 1 August) is noteworthy.
- the period is characterised by more or less consistently drier weather than that prevailing in the first four months (Figure 7) and this is reflected in the continuing fall in water level.
- the weather during the May-to-August period was generally much calmer than that of the first four months.
- **Figure 9** shows that the very warm, calm conditions at the end of June resulted in anoxia - at least near the sediment - and releases of ammonia (NH_4-N); during the next two weeks, SiO_2 first, and SRP second were also released from the sediments, while in contrast, NO_3-N finally 'disappeared' (Figure 8)[2]; over most of the loch oxygen levels rarely exceeded 100% saturation, but they also only fell below 80% saturation after the collapse of the main blue-green algal populations.
- by the beginning of August, the major blue-green algal populations had increased markedly, and reached their maxima just two weeks later in the cases of *A. spiroides* and *A. solitaria*
- the rapid, though marked blue-green development in August was accompanied by a massive and equally short-lived increase in the *Daphnia* population - which had not exceeded 10 individuals.l^{-1} until mid-July (**Figure 10**).

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[2] This decrease brings to an end a 3-month period in which the nitrate levels fell by 2.0 mg N l^{-1} - equivalent to 100 tonnes over the loch as a whole; the observed increases in chlorophyll and the depletion of SRP over the same period suggest that the phytoplankton utilised only 0.6 mg N l^{-1}, with the rest almost certainly being reduced by denitrifying bacteria (Johnston, Holding and McCluskie 1974); the strikingly linear decrease in nitrate once temperatures had reached 10°C supports this view (e.g. Bailey-Watts *et al* 1990).

The blue-green algal development constitutes the main feature of this second 4-month period of the year, and of 1995 as a whole. This can be attributed to a suite of conditions favouring both the production and biomass accumulation of these particular organisms. Ample light supply, and largely internally re-cycled P resources fuelled vigorous production. Although nitrate was at near-undetectable levels, ammonia was abundant, and this is very significant for a number of reasons. Firstly, while, the major *Anabaena* species are capable of augmenting their nitrogen requirements by fixing N from the dissolved atmospheric N_2 , the release of ammonia into the water (from the bacterial breakdown of organic matter in the sediments) represents the 'best' source of N in that it is in the form that can be taken up directly by the phytoplankton; nitrate for example, has to be reduced by energy-consuming, enzyme-mediated reactions prior to assimilation (Brezonik 1972).

The ammonia data are of additional interest in manifesting (i) the earliest (mid- to late June), and most marked accumulations in the North Deeps, (ii) later (mid- to late July) and less marked increases in the South Deeps, and (iii) the latest (August) and evidence of a build-up at other (shallower) sites.

The dominant cyanobacteria were also able to accumulate biomass to a considerable extent, because the rates of loss or removal of cells/filaments produced would be relatively minor. Firstly, the dry weather coupled with controls on the loch sluice gates assured very low percentage losses *via* washout. Secondly, the gas-vacuolate nature of these species enabled them to maintain station in the calmest of water columns, while many diatoms under such conditions will sink rapidly on to the deposits; pulses of diatom development in mid-July were at the very least also hampered by a lack of dissolved SiO_2 (compare the changes in *Aulacoseira* and *Asterionella* population densities in Figure 3a, with the silica data in Figure 8c). A third factor in the success of the large blue-green forms was the very rapid and marked increase in *Daphnia* abundance. Numerous field and laboratory data (Bailey-Watts 1978, 1986; Bailey-Watts and Kirika 1981; May and Jones 1989) point to the efficiency with which these animals can graze down particularly, the smaller algal species. At the high temperatures that prevailed, overall metabolism including feeding rates of these micro-Crustacea would also have been very high. It is suggested that *Daphnia* subsisted on the numerous species such as the cryptomonads referred to above, each present at moderate numbers, but adding upto thousands and tens of thousands of cells per millilitre - this situation 'opening the window' for the large cyanobacteria. The scarcity of Unlike the N-fixing cyanobacteria, other algae and cyanobacteria have an absolute requirement for nitrate or ammonia; the provision of inorganic N especially as ammonia (along with SRP released from the sediments) would thus appear to have been of considerable importance in supporting the other phytoplankton species on which the *Daphnia* fed.

With a mounting body of data pointing to the success of the phytoplankton in August - which constituted by a considerable margin, the annual maximum - it seems sensible important to explore the factors that determined this maximum and thus, the (rapid) decrease in the main populations. The cessation of the whole gamut of physical, chemical and biotic conditions that culminated in the main blooms are potential candidates here. The following changes in the weather (Figures 6 and 7) must have contributed:

- the onset of rain, and a slight rise in loch level following a period of 10 weeks during which the water level fell continuously).
- a decrease in temperature of some 5 degrees Celsius.
- an increase in wind.

At the very least, these changes brought about a more thorough mixing of the loch than had been the case in the preceding few weeks. Indeed, what is viewed as a 'collapse' in blue-green algal biomass lakewide, could be attributed in part at least, to wind-induced mixing. In this connection, it should be borne in mind that the population densities of the large blue-green algae derived from samples taken in calm weather (i.e. under surface 'bloom' conditions) have almost certainly over-estimated the lakewide densities. The problem arises because the standard 2-m integrated tube samples accounted for the upper 50% of the column at most (i.e. at points where the total depth is say, 4m); in this situation, and assuming that all of the gas-vacuolate forms are in the upper 2 m, the concentration of these organisms, that is, the numbers per unit volume of water, would be over-estimated by 100%. By the same reasoning, and assuming surface bloom conditions, where the 2-m tube represents an even smaller fraction of the water column (e.g. at the 20- to 25-m 'deeps'), the overestimation will be correspondingly greater.

Setting aside the reservations stemming from possible flaws in sampling[3], there is a possibility that the peak phytoplankton populations were constrained by light availability. Bindloss (1976) showed 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 0.75m at the time of the peak biomass of 230 mg chlorophyll$_a$ m^{-3} in mid-August. At this time therefore, the concentration of chlorophyll$_a$ in the euphotic zone was 0.75 x 230, or 173 mg

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[3] Somewhat similar uncertainties exist over the 'lakewide' estimates of *Daphnia* which is often very patchily distributed on account of its shoaling behaviour.

chlorophyll$_a$ m^{-2}. In contrast to the situation in 1994 (Bailey-Watts and Kirika 1995), this is well below the lower of the two values given above. The 'collapse' of the annual maximum phytoplankton level in 1995, thus appears not to be due to light limitation. Light conditions could still have played a significant role, however. It is reasonably well-established that algae concentrated at the water surface for appreciable lengths of time, are susceptible to stress due to the very high light intensities. Temperatures exceeding 20°C, and (albeit largely algae-generated) pH values above 9 units (**Figure 11**) - could compound these stresses.

Shortage of nutrients could constitute a major resource-limiting factor. However, the dominant algae can be considered to have been unaffected by the very low nitrate levels that prevailed, because (i) they could fix atmospheric N - and the presence of heterocysts suggested that the population was capitalising on this ability (but see below) - and (ii) ammonia (and probably dissolved organic N compounds) were also present in plenty; indeed ammonia reached a concentration of 0.5 **mg** l^{-1}. Meanwhile, SRP derived from the sediments was maintaining water column concentrations of at least 40 µg l^{-1} (Figure 8b); a comparison between the SRP plot and that of particulate P (Figure 1) suggests that, as in 1994, even more SRP was coming out of the sediments than was observed, but it was rapidly sequestered by the algae and manifested as PP. It is likely too, that phosphate recycling was enhanced by the vigorous feeding (Lehman 1980; see also Carpenter, Cottingham and Schindler (1992) that was presumably necessary to support even the observed increase in *Daphnia* numbers (let alone any individuals eaten by fish, for example). SiO_2 concentrations had started to rise again by mid-August, but the main blue-green algae would have been little affected by whatever minor production was possible from such a low baseline 'inoculum' of diatoms at the time.

In spite of all these data suggesting nutrient sufficiency, the PP-to-chlorophyll$_a$ weight ratios at, and around the time of the *Anabaena* maxima, were some of the lowest recorded during the year (**Figure 12**). At approximately 0.6:1 these ratios suggest a somewhat low P content; as a consequence P-dependant processes including N-fixation may also have been limited (Paerl 1988).

September to December

The last of the three 4-month periods saw first, a considerable decrease in water temperature (Figure 6) on resumption of somewhat cooler, windier and wetter weather (Figure 7). These changes led to what may be loosely defined as a combination of (i) the reversal of a number of the physical, chemical and biochemical processes controlling the fluxes of nutrients between the sediments and the overlying water (ii) the influence of reduced biological activity and (iii) the increased impact of external loadings of nutrients. SRP levels thus fell, while the concentrations of NO_3-N and SiO_2 increased, to their respective background (autumn and winter) values. This period also saw the return to turn-of-the-year conditions regarding dissolved oxygen, ammonia, and pH. Concomitant increases in water clarity parallel considerable decreases in the abundance of phytoplankton - and of *Daphnia* - although the number of species recorded during the routine counting procedure remained at values near the year's average of *ca* 15.

4. GENERAL DISCUSSION - 1995 IN THE LONG-TERM CONTEXT

This section considers two aspects of the ecology of the phytoplankton of the loch in the long-term context. These are:

- the main features such as the timing of the annual chlorophyll maximum, and the correspondence between *Daphnia* performance and the relative abundance of large and small algal species.
- features that might be expected to reflect the effects of cutbacks in the external P loading to the loch; considerable reductions are now fairly well-substantiated (Bailey-Watts and Kirika, in prep).

4.1 Phytoplankton ecology

The acutely capricious nature of phytoplankton development in Loch Leven was first highlighted more than 20 years ago (e.g. Bailey-Watts 1974) and referred to as a major hallmark of this loch on many occasions since then (e.g. Bailey-Watts 1978, 1982; Bailey-Watts *et al* 1990, 1994; Bailey-Watts and Kirika 1994). Still however, the annual 'performance' has been viewed as being of just two main types. The first of these is exemplified by the years 1968, 1969 and 1994 while the second is characterised by all of the other years excluding 1995 (Table 2). These two situations appear to be largely determined by the population densities achieved by filter-feeding *Daphnia*. Type I developments correspond to low numbers of this cladoceran, while the Type II sequence of events takes place when *Daphnia* numbers are high (see also Bailey-Watts 1978, 1986).

1995 however, exhibited features of Type I and Type II algal developments. The Type I characteristics are a high annual chlorophyll maximum the mid-year achievement of this maximum, while the main Type II features are a moderate annual mean pigment level, and the predominance of a (very) large alga at the summer chlorophyll maximum. Why this is the case, is not yet known, but it is significant that the very large *Anabaena spiroides* has not been recorded in such abundance in Loch Leven before, and it was accompanied by extraordinarily dense swarms of the daphnid e.g. 250 individuals l^{-1} in one sample. Whether these two developments are linked to what has been hailed as the warmest summer for more than 400 years, is also not known.

Table 2. The two main types of phytoplankton development in Loch Leven prior to 1995.

Type I (1968, 1969 and 1994)	Type II (all other years excl. 1995)
annual mean and maximum chlorophyll concentrations of e.g. >80 and >200 μg l^{-1}	annual mean and usually, maximum, chlorophyll levels of e.g. 20 and 80 μg l^{-1}, although maxima can be much higher
the occurrence of the annual maximum in the middle of the year	maxima can occur at any time of the year, although the high ones usually develop in late-winter to early spring
predominance of small phytoplankton species at the (summer) maximum	large algae dominate the summer scene; small algae are limited to the winter, early spring and late autumn

Over the period mid-July to mid-August, SRP concentrations increased (due almost certainly to release from the sediments, and possibly some re-cycling by *Daphnia*) by approximately 50 μg P l^{-1}. As particulate P levels (in the form of *Anabaena* at this time) increased by 55 μg P l^{-1} over the same period, it is likely that the actual release of P from the deposits was approximately double that observed, and that some other factor prevented the cyanobacterium from capitalising on more SRP. This situation is somewhat similar to that of 1994 (Bailey-Watts and Kirika 1995) when some 100 μg SRP l^{-1} is thought to have been released from the sediments, but was rendered 'unseen' because it was rapidly sequestered by a dense population of *Oscillatoria*. In 1995, both algal particulate P and dissolved P exhibit a net decline, so it is probable that the disappearance of SRP was due primarily to a reversal of the physical and chemical mechanisms that brought it out of the sediments in the first place. Certainly, SRP levels started to decline with changes in the weather - including the sharp drop in temperature in mid-August - which would contribute to this reversal, and there were no major increases in any other algae around this time.

The hot spell in 1995 follows a long series of warm summers allowing the loch to stratify on occasions, and release key nutrients from the sediments. Such conditions favour the 'bloom' forming algae in any event, but the success of the cyanobacteria was all the more apparent in 1995 with *Daphnia* numbers increasing so markedly over a few weeks - apparently subsisting on the (smaller) phytoplankton species whose production was fuelled by the nutrients. The very low NO_3.N-to-SRP weight ratio - in addition to the virtual absence of nitrate-N - would also have contributed to the success of the N_2-fixing cyanobacteria[4]. However, they may not have needed to draw on this capability, bearing in mind the enormous concentrations of ammonia prevailing at the time.

The phytoplankton-*Daphnia* interactions observed, are in keeping with the conclusions of Bailey-Watts (e.g. 1986) that the cladoceran feeds primarily on the smaller algal elements (although no gut analyses have been carried out - see below). Indeed, it is on this basis that the character of the phytoplankton in 1994 (Bailey-Watts and Kirika 1995), appeared to agree with that forecast by Bailey-Watts (in Bailey-Watts, Gunn and Kirika 1993). However, whereas a 'cascade effect' (see e.g. Northcote 1988; Neill 1994) involving the introduction of rainbow trout was implicated in this aspect of the work, recent investigations on the crustacean zooplankton (Gunn and May 1996), suggest that the fish were not involved in the case of Loch Leven. Equally, these authors (pers. comm.) readily accept that new work is sorely needed in this area (see below). Considerable confusion exists over the significance of the overall size of *Daphnia* and the length of the 'helmet'; are these controlled mainly by fish predation or water temperature, for example?

While the situation described for 1995 is 'different' even in the context of the highly variable Loch Leven, it complies with that most commonly recorded in that nutrients rather than light constitute the major limiting factor on the phytoplankton. Phosphorus thus reamains the key nutrient in this context, although seasonal shortages of nitrate may have enhanced the success of some of the cyanobacteria, while SiO_2 levels have controlled the performance of diatoms (see also Bailey-Watts, Kirika and Hakansson 1994), and as a consequence the outcome of any competition with other algae. In a number of years too, major inputs of SRP from the sediments in summer, have resulted in the annual maximum for this nutrient occuring at this time of the year. Such pulses are very significant. For example, a mean annual TP concentration of 64 $\mu g\ l^{-1}$ is calculated (by planimetry of the area under the curve) using all of the values in **Figure 13**. If the values attributed to internal recycling are ignored - as indicated in the Figure, a mean value of only 50 $\mu g\ l^{-1}$ is calculated. The same exercise on the chlorophyll data (Figure 1) gives concentrations of 34 $\mu g\ l^{-1}$ for the whole array, and 27 $\mu g\ l^{-1}$ excluding the values relating to the *Anabaena spiroides* development.

4.2 Effects of phosphorus cutbacks

The long-term database has yet to be fully explored with the express purpose of assessing whether step-wise cutbacks in P loading are affecting in-loch P levels. In

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[4] Summer ratios were <1:1, in contrast to those approximating to1000:1 in early Spring.

other words, a separate desk study on this needs to be initiated (see below). The present section is thus based on a more or less general familiarity with the data and literature accrued.

As far as we can ascertain at present, the current P loading is as indicated and contrasted with the 1985 situation in Table 3. Plainly, some considerable cutbacks have been achieved - and especially those relating to SRP-rich effluents from point-sources such as the woollen mill, and sewage treatment works (STWs).

Table 3. Contrasts in the P loading situation at Loch Leven, between 1985 (before point-source P reduction) and 1995 (after P reduction).

1985		**1995***
20.5t	**total P loading**	12.6t
12.3t	**SRP loading**	6.6t
56%	**point-source TP load/total TP load**	29%
68%	**point-source SRP load/total SRP load**	41%

* The findings of the 1995 P loading assessment are not yet available; the figures in this column are thus estimated from Forth River Purification Board data on e.g. P *concentrations* in sewage effluent.

In spite of the apparent (obvious) logic of concentrating on STWs and the like at Loch Leven and elsewhere, it has to be accepted that the approach has been adopted primarily because these well-defined outfalls and pipes are usually much more easily defined and targetted, than diffuse inputs from land, for example. Although not the main focus of this report, it is worth considering some of the likely impacts on the P dynamics of the loch, before concnetrating on the phytoplankton. Table 4 thus highlights a number of changes associated with the reduction of P loads, the lowering of the point-source to diffuse-source ratio, and the decreases in the percentage of bio-available P.

Where diffuse, runoff-derived P dominates the loading to a system, increased rainfall will lead to increased loadings and, to some extent at least, increased phytoplankton productivity. As flushing rates will increase at the same time however, the potential for algal biomass to accumulate is reduced.

The weather and associated nutrient re-cycling (along with elements such as *Daphnia*) plainly 'conspired' to mask at least some of the reduction in algal biomass that might be reasonably expected; meaningful analyses of the data will thus take these factors into account. Still, however, the annual mean TP level quoted above

Table 4. Some ecologically relevant features arising as a result of reductions in point-source P loadings.

Pre- point-source P reduction	Post- point-source P reduction
major inputs of (bio-available) P enter the system at a relatively constant rate throughout the year[a]	major inputs of P tied to rainfall events i.e. could be very erratic
large percentage of P enters the system in relatively highly concentrated form - with little flushing	most of the P supplies accompanied by considerable volumes of water
potential for high productivity AND biomass accumulation	reduced potential for both production and biomass accumulation
relatively low P retention coefficient	with increased proportion of particulate P, an increase in overall P retention coefficient (sedimentationl)

[a] depends on industrial production schedules, and tourist areas may experience seasonal increases in sewage disposal.

(64 µg l^{-1}) is to all intents and purposes no different to the 63 µg l^{-1} measured in 1985 (Bailey-Watts *et al* 1987) when low P levels were attributed in large part to rapid flushing in summer and autumn. In contrast, the annual mean chlorophyll concentration in 1995 (34 µg l^{-1}) is just over 50% higher than that recorded in the 'low algae year' of 1985 i.e. 21 µg l^{-1} - and thus nearer to the value of 27 µg l^{-1} estimated assuming no major *Anabaena* development[5].

The foregoing still suggests, however, that the first few months of the year, and the late autumn-early winter periods are the most likely to reflect P loading reduction. The following observations are interesting in this connection:

- the build-up of algae to a peak of 70 µg l^{-1} by the middle of March; the maximum ranks 17th out of 24 sets of data, but the 3-month mean value is one of the lowest recorded so far - with 1976, 1985 and 1993 exhibiting even lower values; this points to the lack of any consistent trend.
- the performance of unicellular Centric diatoms in 1995 and at least 1994, has been poorer than in many years, bearing in mind that the early spring bloom consisting of these forms, has been described as one of the more regular features of this loch (Bailey-Watts 1988a, b); meanwhile, filamentous centric forms (*Aulacoseira*) and pennate diatoms have become relatively more common, and although the

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[5] It must be remembered however, that the cyanobacteria populations have probably been over-estimated.

literature needs to be more fully explored than hitherto, there is a suggestion that this switch represents a down-turn in trophic status.

- an equally cursory examination of the data for the 3-month periods beginning with April, suggests that 1995 manifested one of the lowest mean crop densities at 25 μg l^{-1}; somewhat similar levels were recorded in 1982, 1988, 1989 and 1993, and even lower values are suggested for 1985, 1990.
- as described above, the third quarter of the year in 1995 saw very high (but possibly over-estimated) biomass; indeed, the mean values for this period exceed those for the corresponding quarter in 22 out of the 24 sets of data available; only 1972 and 1994 saw higher values.
- as far as the final quarter of the year is concerned the mean value of *ca* 10 μg l^{-1}in 1995 is probably the lowest but for 1980 and 1994.

There has been a random occurrence of similar chlorophyll values over the years, rather than any consistent trends. Nevertheless, there is a suggestion of some decreases rather than noticeable increases in phytoplankton biomass in those periods of the year not susceptable to releases of nutrients from the sediments - which we now know to fuel algae in some years at least. Otherwise, the main reduction in phytoplankton biomass is still that of the earlt 1970's as a consequence of the 'return' of *Daphnia* in 1971, and the first major reduction in the discharge of P from theb woollen mill in 1972. The chlorophyll and TP values measured in 1995 are also generally much lower than those recorded during the period 1985-1990 (Bailey-Watts, May and Kirika 1991). It is stressed again, however, that a more definitive conclusion awaits a more thorough inspection of the data (see below).

5. CONCLUDING REMARKS WITH SPECIAL REFERENCE TO PRIORITY RESEARCH AREAS

This report has furthered our knowledge on, and extended our experience of variability in the Leven system, and the major factors determining the chnages in the abundance and species composition of the phytoplankton over a variety of timescales. It has also led us to question further our views on e.g. the influence of fish on the system, and the significance of sediment-released P on algal biomass. As with previous reports and scientific publications, the present work has also highlighted a number of issues on which we can only speculate at this time, and it is these with which this section is primarily concerned. In identifying some of the major gaps in knowledge, a number of field, laboratory and desk studies that are worthy of attention can be proposed. **Table 5** lists those areas that we consider especially important in view of their relevance to the management of the loch and the on-going programme of P reduction in particular. The choice of subjects for further attention reflects two types of concern. The first of these is with areas of work that are plainly of considerable importance, but have been attended to somewhat cursorily. A prime example concerns fish-zooplankton-phytoplankton interactions. *Daphnia* is almost certainly a 'fulcrum' organism on which the performance of fish on the one hand and algae (and thus many aspects of water quality) on the other, are largely controlled. Many more analyses of the gut contents of the animals involved need to be done, moreover on fresh material, taking account of 'all' food items including the smallest organisms, and embracing the likelihood of seasonal changes in food and feeding preferences. Only in this way, will present and future investigators generate the comparable data crucial to establishing with confidence (i) the main determinants of water quality, (ii) the changes in quality, and (iii) the significance in all this of the P reduction strategies on the one hand, and the fishery management practices on the other.

Table 5. Priority research areas relating to the management of Loch Leven.

field and laboratory studies	desk-studies
food and feeding rates of fish and zooplankton - especially *Daphnia*	identifying signals in the long-term database that have a bearing on the impacts of P reduction strategies
the effects of sampling strategies on the estimation of cyanobacteria under 'bloom' conditions	application of the IFE 'PROTECH' model to the Leven data
the impacts of benthic algae on water column nutrient dynamics	verification of the predictions regarding the impacts of reducing primarily the point-source
a review of sampling frequency	

Other items in Table 5 reflect worries over the tendency (by all involved at one time or another) to reduce the sampling frequency. The following comments stem from discussions initiated by Dr Armstrong (FRPB, now SEPA). Reduction in sampling effort is attractive in relieving some of the very real pressures on both field and and associated laboratory work. However, plenty is known about Loch Leven to emphasise the need for the shortest sampling intervals possible here. This would usually need to be done no more frequently than weekly - and it could be limited to those determinands that relate to the really key aspects of water. Gaps in data can hamper analyses (such as those referred to in this report) aiming to compare e.g. current annual and quarterly mean values of a particular feature, with past results. Such problems can also be compounded if for some unavoidable reason a sampling visit has to be curtailed; then gaps of perhaps a month could arise. In this connection, a pair of dip samples taken weekly from the sluices end of the loch i.e. without involving boats, between 1 November and 1 March - and possibly longer - should be seriously considered. Outwith these periods, excursions would involve gradually more boatwork - basically as a consequence of the increased likelihood of spatial patchiness in organisms and water chemistry. Decisions on this might be settled primarily on information on water temperature which could be relayed/telemetred daily to the laboratories involved.

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Appendix I. Algae recorded from the water column of Loch Leven during the routine counting

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, 1988, 1990), Hustedt (1930), Korshikov (1953), Krammer and Lange-Bertalot (1991), Lind and Brook (1980), Skuja (1956) 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 phytoplankter in Loch Leven during 1994, but very rare in 1995) merit its inclusion in a new genus - *Jaaginema*.

CHLOROPHYTA (true 'green' algae, with starch stored in the chloroplasts)

Euchlorophyceae ('green' algae; motile stages have 2, rarely 4, flagella of equal length - whereas many Chrysophyta and Pyrrophyta bear flagella of unequal length and often structure too)

Botryococcus braunii Kutz.
Chodatella ciliata (Lagerh.) Chod.
Chodatella longiseta (Lemm) Wille
unidentified *Chodatella* species
Coelastrum microporum Nag.
unidentified *Crucigenia* species
Dictyosphaerium pulchellum Wood
Didymocystis inconspicua Kors.
unidentified *Eudorina* species
unidentified *Elakatothrix* species - but near *gelatinosa* Wille
unidentified *Franceia* species
Micractinium pusillum Fres.
Monoraphidium contortum (Thur.) Kom.-Legn.
Monoraphidium griffithii (Berk.) Kom.-Legn.
Monoraphidium minutum (Nag.) Kom.-Legn.
Oocystis lacustris Chod.
unidentified *Pandorina* species
Pediastrum boryanum (Turp.) Menegh.
unidentified *Planktosphaeria* species
Pseudosphaerocystis lacustris (Lemm.) Novakova
Raphidonema (Koliella) planctonica Hind.
Sphaerocystis schroeteri Chod., inc. single cell form near *Planktosphaeria gelatinosa* G.M.Smith

Scenedesmus acuminatus (Lagerh.) Chod.
Scenedesmus near *bijuga* (see Hindak 1990).
Scenedesmus brasiliensis Bohl
Scenedesmus dimorphus Turp.) Kutz.
Scenedesmus quadricauda (Turp.) Breb.
'2-cell' *Scenedesmus*
Other species of *Scenedesmus* Meyen
Tetraedron minimum (A.Br.) Hansg.

***Zygophyceae* including the *Desmidiaceae* ('desmids' - see Lind and Brook 1980, and Ruzicki 1977) and the *Zygnemataceae* (see Bourrelly 1966).**

Closterium limneticum Lemm.
Closterium strigosum var *elegans* (G. S. West) W. Krieg
Cosmarium depressum (Nag) Lund
Cosmarium depressum var *planctonicum* Riverdin
Cosmarium turpinii Breb.
Staurastrum lunatum (Ralfs) or var *planktonicum* (W. and G. S. West)
Staurastrum planktonicum Teiling

CYANOPHYTA

***Cyanobacteria* (rather than blue-green 'algae' because they - in common with bacteria - have no true membrane-bound nucleus or chloroplasts; instead, the nuclear and pigment materials are distributed throughout the cells; this group of 'algae' never possess flagella)**

Anabaena flos-aquae (mainly forma *flos-aquae* Ralfs *ex* Born *et* Flah)
Anabaena spiroides Kleb.
Aphanothece clathrata W. *et* G.S. West
Chroococcus limneticus Lemm.
Gomphosphaeria near *G. lacustris* Chod.
unidentified *Gomphosphaeria* species
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 Anognostidis and Komarek (1988)
unidentified *Oscillatoria* species
unidentified picocyanobacterium *circa* 0.5 µm diameter

CHRYSOPHYTA (brown, yellow or yellow-green chloroplasts; no starch)

***Bacillariophyceae* (diatoms, characterised by siliceous 'valves')**

Asterionella formosa Hassall
Aulacoseira subarctica (O. Mull.) Haworth
unidentified *Aulacoseira* species
Cyclotella comta (Ehrenb.) Kutz.

unidentified *Cymbella* species
Diatoma elongatum (Lyngb.) Ag.
unidentified *Diatoma* species
Fragilaria crotonensis Kitton
Nitzschia sp. (re-suspended from the sediment)
unidentified *Navicula* species

unicellular Centrales assemblage - mainly *Stephanodiscus* (discussed in Hakansson and Bailey-Watts 1993), with some *Cyclotella radiosa* (Grun.) Lemm.; see Bailey-Watts (1988b) for the range of species and morphotypes that can be found in a single sample at Loch Leven.

unidentified pennate diatom species
unidentified *Surirella* species
Synedra ulna (Nitzsch.) Ehrenb.
Synedra ulna var *danica* (Kutz) Grun.
unidentified *Synedra* species
Tabellaria fenestrata (Lyng.) Kutz.
Tabellaria flocculosa (Roth) Kutz.

***Chrysophyceae* (often forming siliceous, and more or less spherical cysts)**

Species of *Chrysococcus* Klebs.
Species of *Dinobryon* Ehrenb.
Species of *Mallomonas* Perty
unidentified colonial chrysophyte

***Haptophyceae* (characterised by a very long haptonema which can coil or attach to a surface; on the basis of this structure, Christensen (1962) separated the group from the Chrysophyceae)**

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

PYRROPHYTA (predominantly motile algae - unequal flagella - with brown or sometimes red or blue-green chromatophores; these organisms also store starch but - in contrast to the green algae - outside the plastids.

***Cryptophyceae* (cells characterised by a 'bean' shape, and groove-like cytopharynx)**

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'; cells with transverse and longitudinal furrows containing the very different flagella)**

Ceratium hirundinella (Muller) Schrank
Other species of *Gymnodinium* Stein
Species of *Peridinium* Ehrenb.

Euglenophyceae **(euglenoid forms with one long and one very short flagellum; storage products such as paramylum, and certain pigments in some species at least, are characteristic of both plants and animals)**

Unidentified species of *Euglena*
Trachelomonas sp. (near *T. oblonga* Lemm.).

8. FIGURES

Figure 1. Changes in the the overall abundance of phytoplankton as indicated by the concentrations of chlorophyll$_a$ and particulate phosphorus.

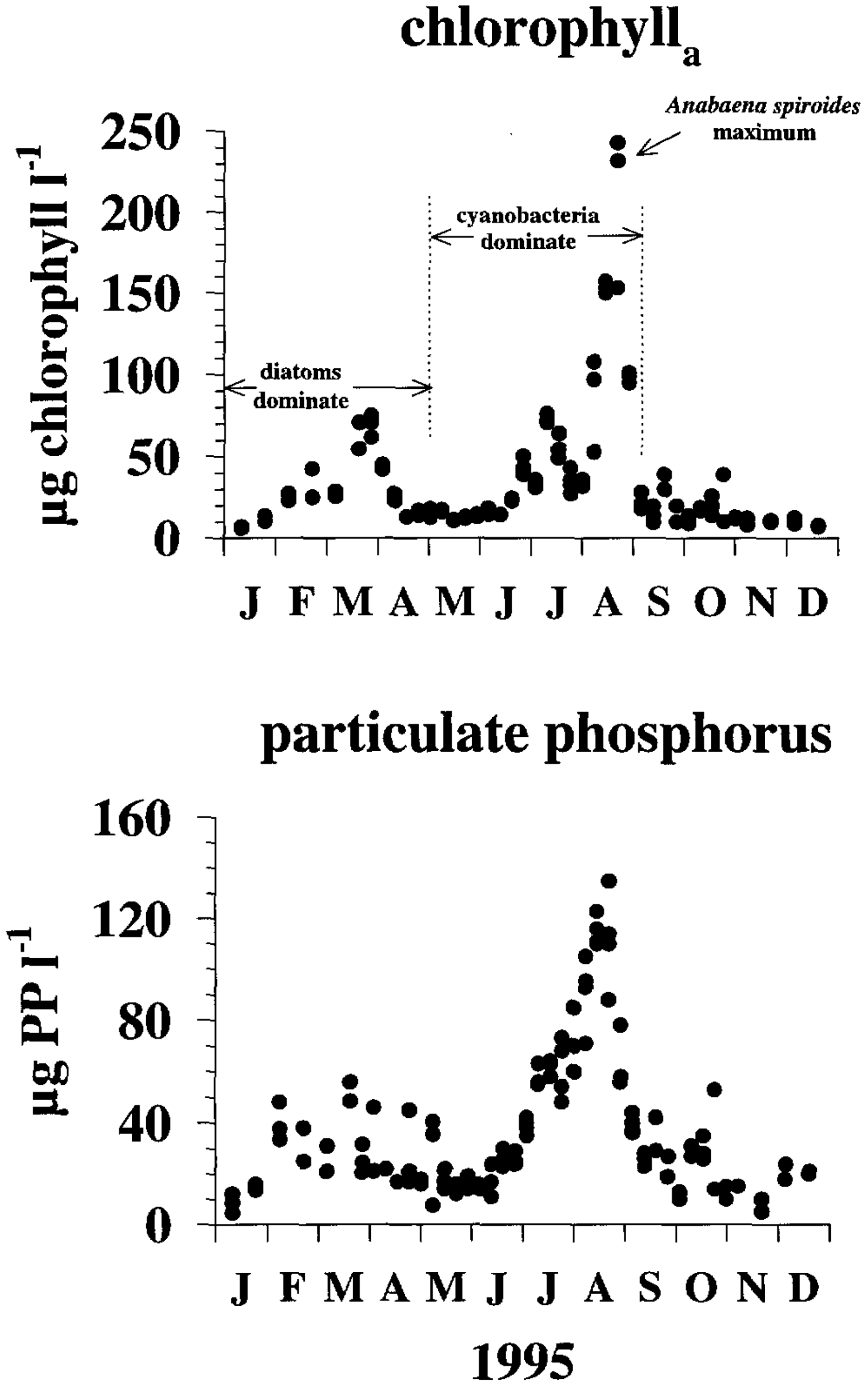

chlorophyll a
µg chlorophyll l⁻¹
250
200
150
100
50
0
Anabaena spiroides maximum
cyanobacteria dominate
diatoms dominate
J F M A M J J A S O N D
particulate phosphorus
µg PP l⁻¹
160
120
80
40
0
J F M A M J J A S O N D
1995

Figure 2. Water clarity as measured by Secchi Disc: 1994 and 1995 compared.

water clarity

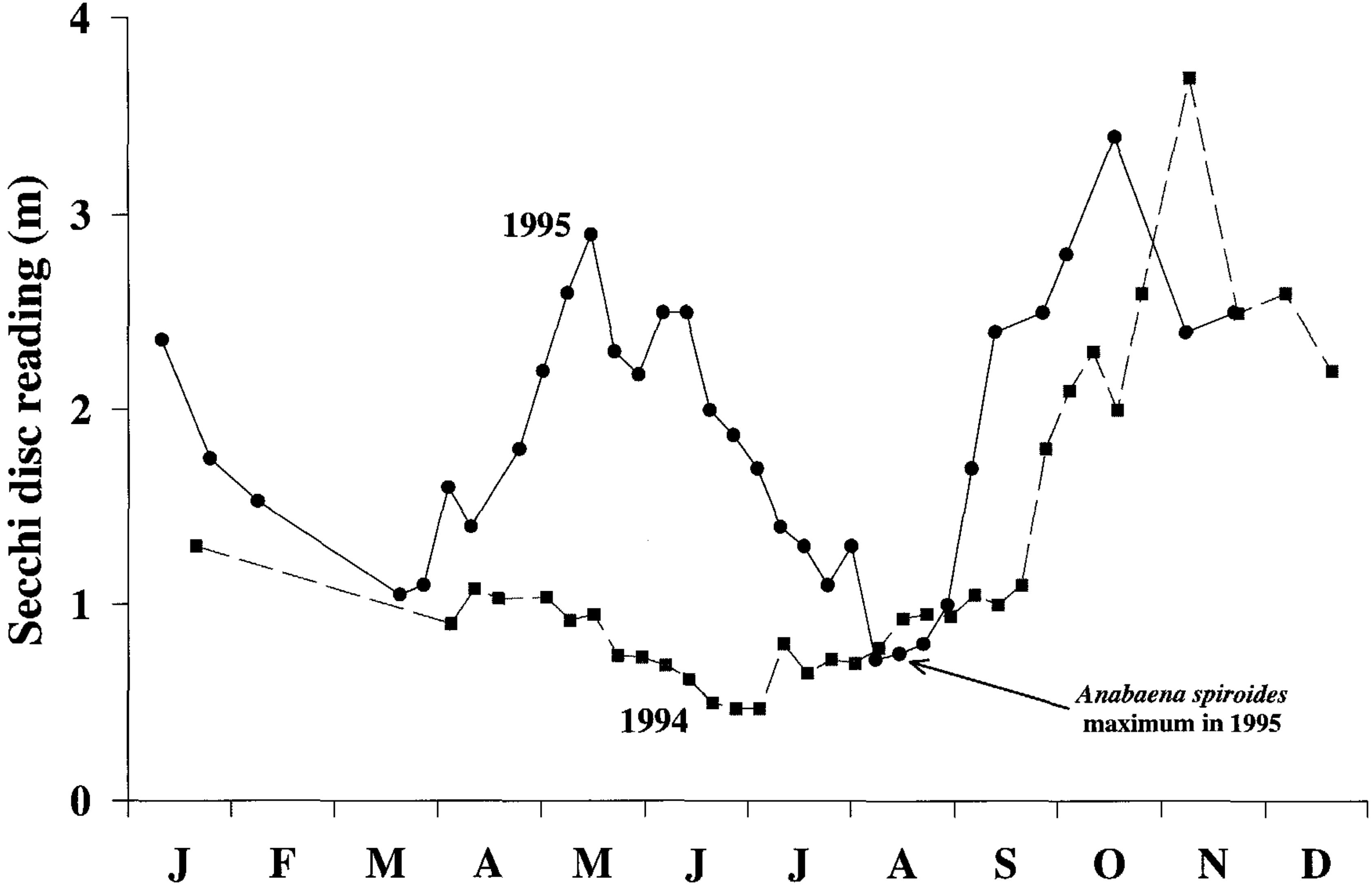


Figure 3a. Changes in the population densities of the major diatoms: *Asterionella formosa, Aulacoseira subarctica* and *Stephanodiscus* species. These abundance estimates refer to the open water site south of Reed Bower, or in the case of very stormy weather, the sluices (outflow) station.

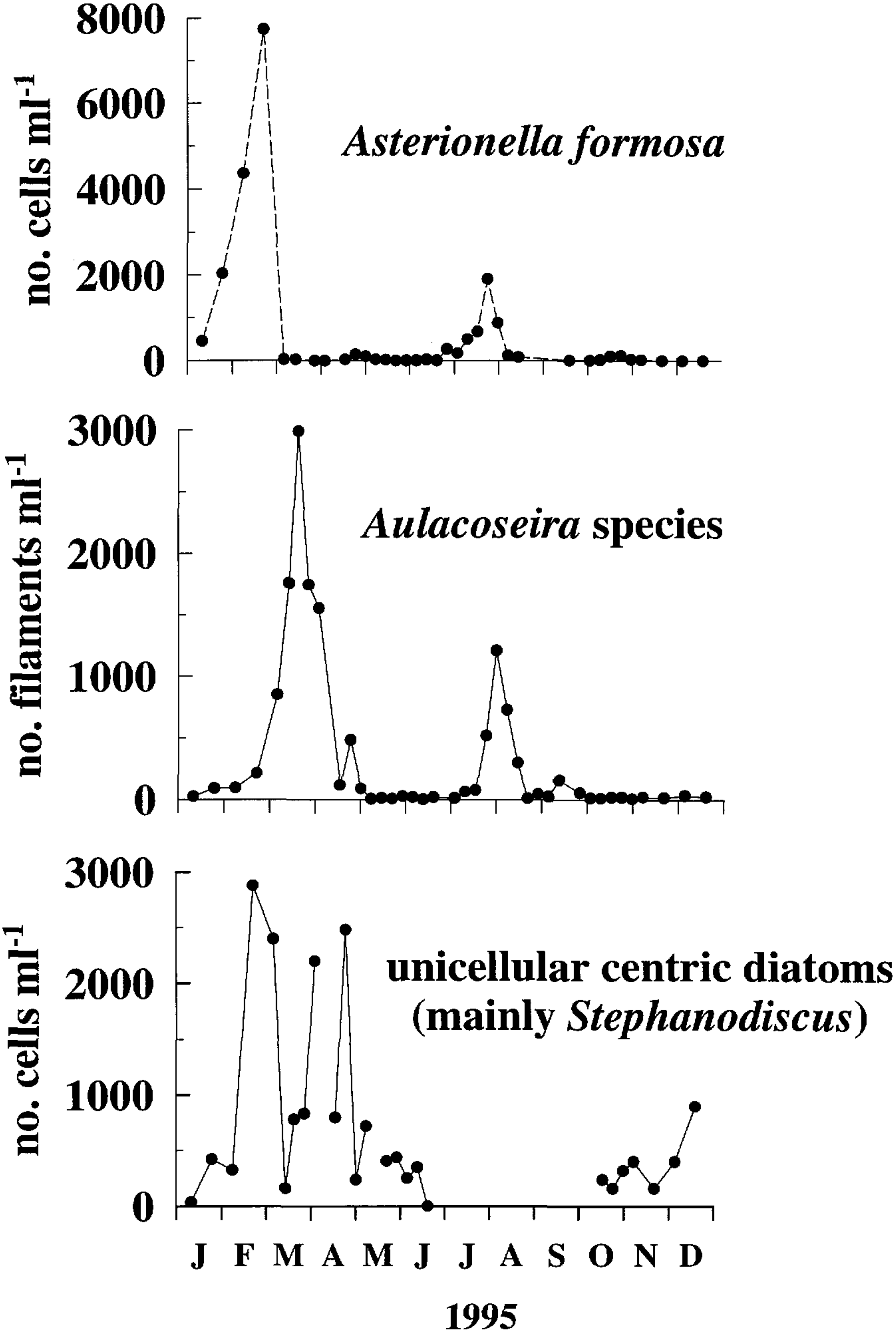

8000
6000
4000
2000
0
no. cells ml-1
Asterionella formosa
3000
2000
1000
0
no. filaments ml-1
Aulacoseira species
3000
2000
1000
0
no. cells ml-1
unicellular centric diatoms
(mainly Stephanodiscus)
J F M A M J J A S O N D
1995

Figure 3b. As Figure 3a, for the population densities of the major cyanobacteria: *Microcystis* and *Anabaena*.

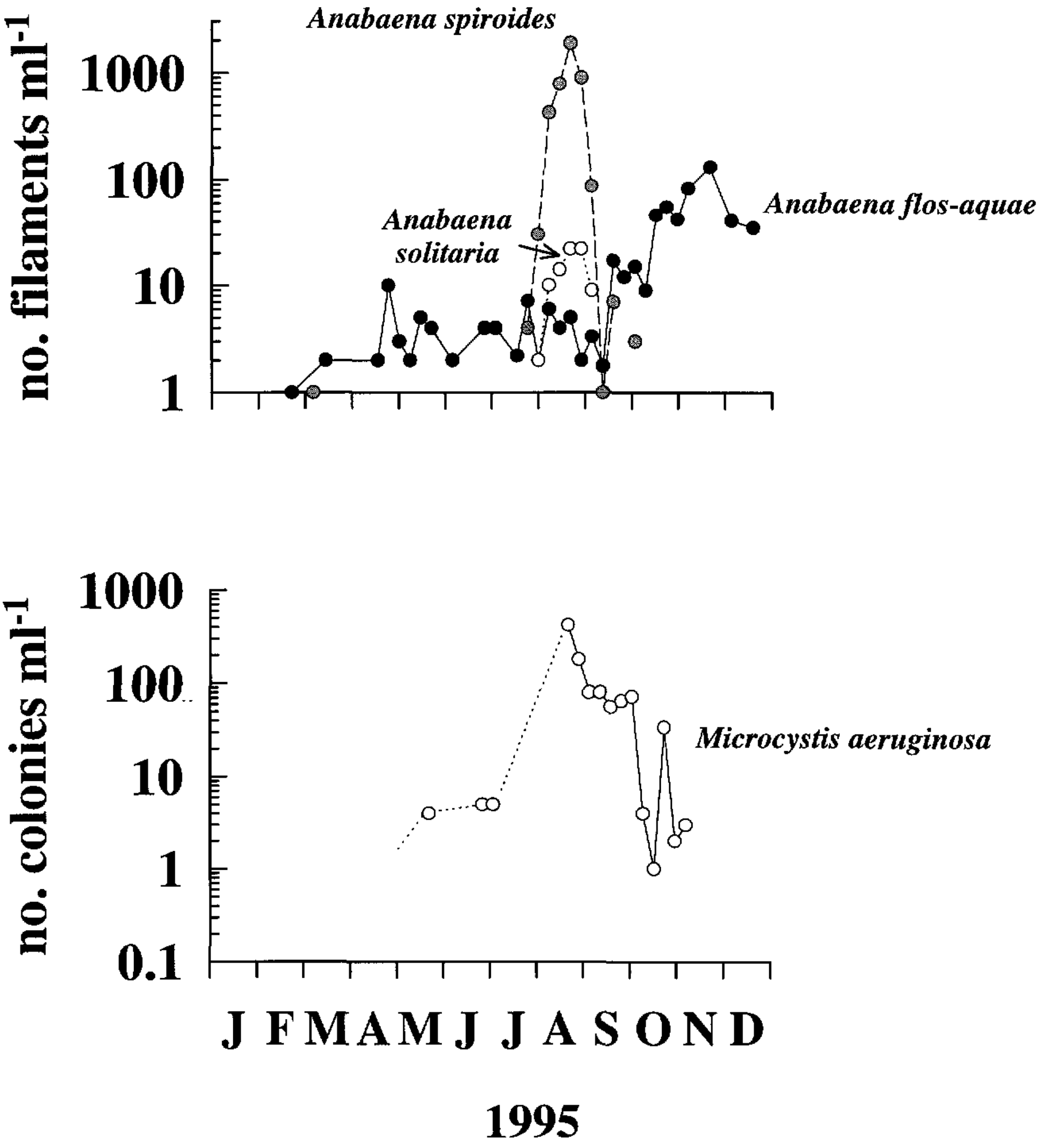

Anabaena spiroides
no. filaments ml^{-1}
1000
100
10
1
Anabaena flos-aquae
Anabaena solitaria
no. colonies ml^{-1}
1000
100
10
1
0.1
Microcystis aeruginosa
J F M A M J J A S O N D
1995

Figure 4. *Anabaena spiroides:* the Loch Leven population consisted largely of the form *crassa* (drawings 5-7) although the form *spiroides* was also present. Drawings copied from Komarek and Ettl (1958). Heterocysts (H, the sites of nitrogen-fixation), spores (S) and vegetative cells (V) are indicated.

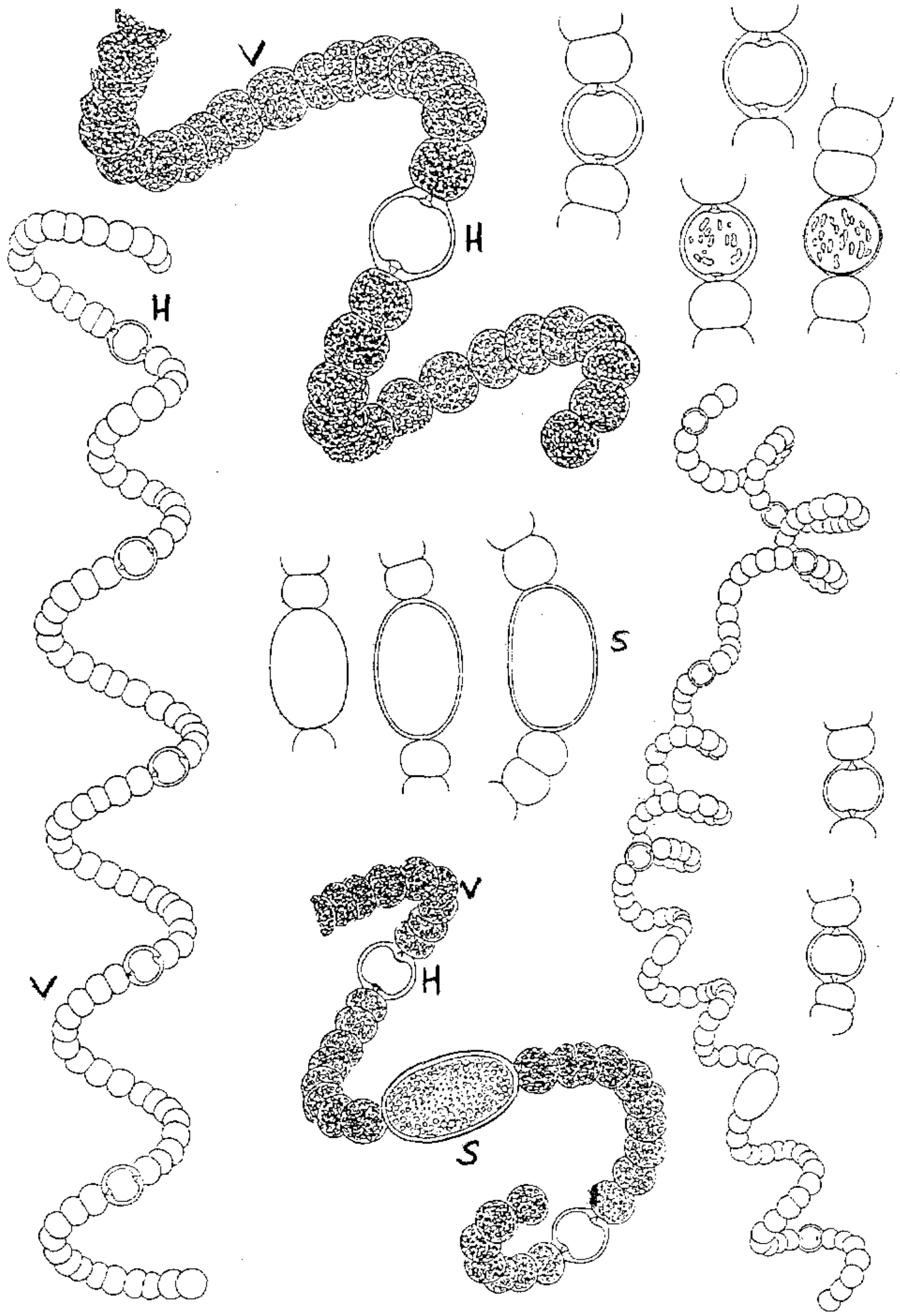

V
H
H
S
V
H
S
V

Figure 5. A measure of phytoplankton species diversity and its variation through the year.

a measure of species diversity

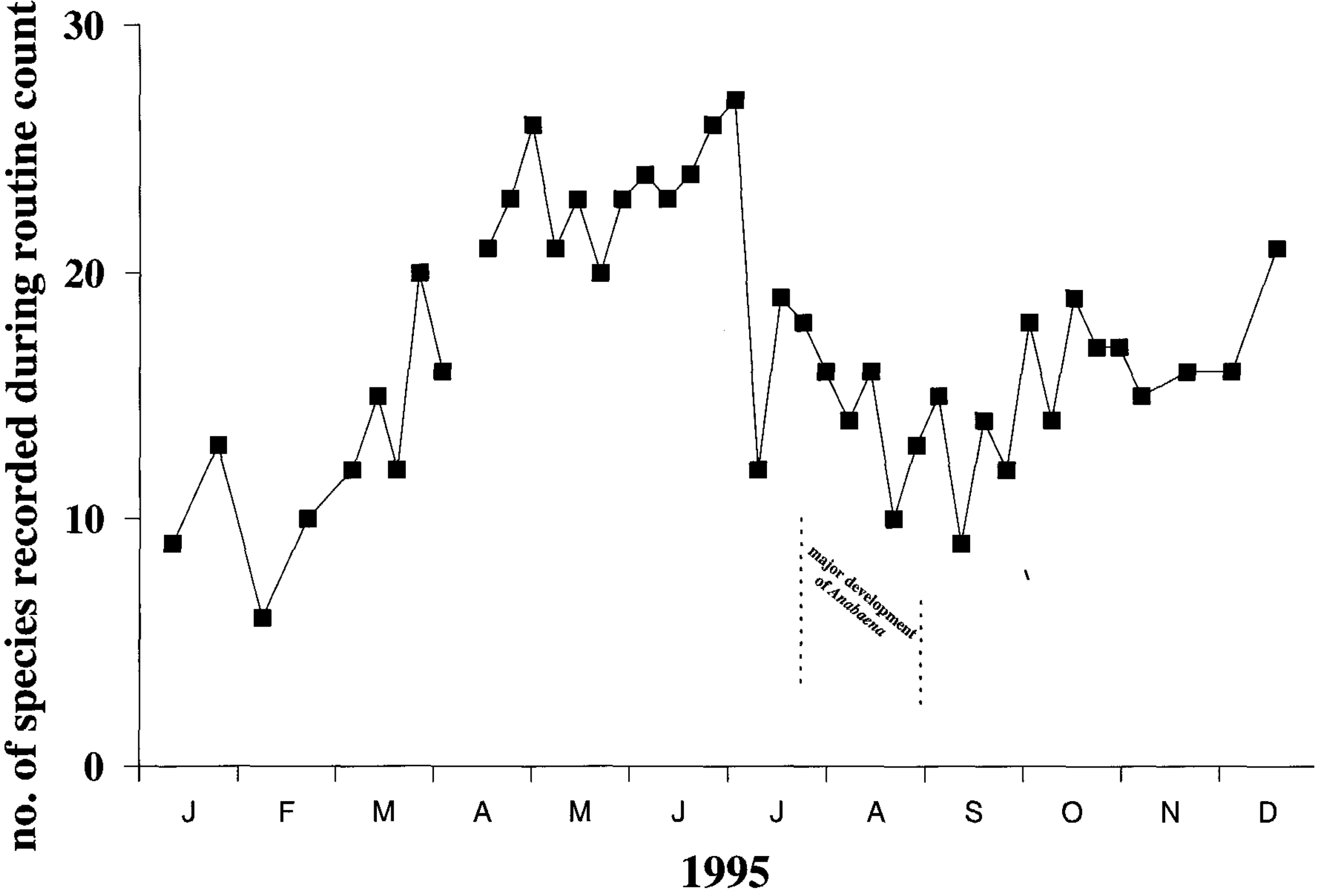
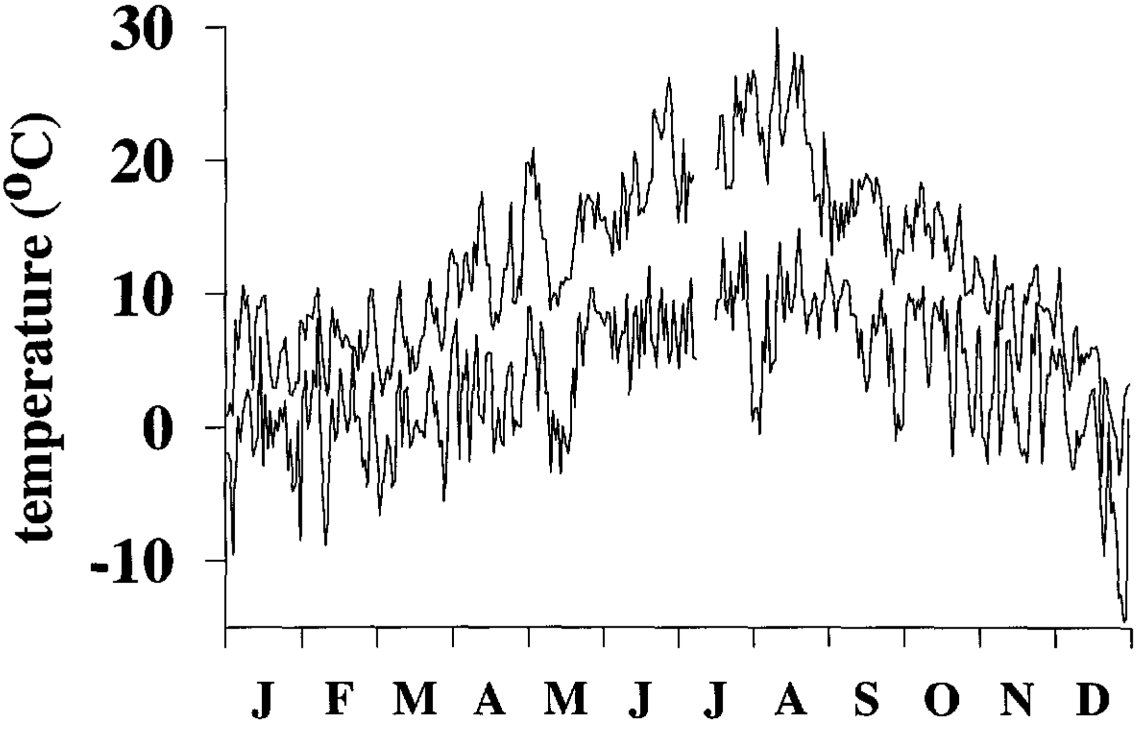


Figure 6. Changes in the daily maximum and minimum air temperatures, and in water temperature measured at the times of phytoplankton sampling.

daily maximum and minimum air temperatures



open water temperature

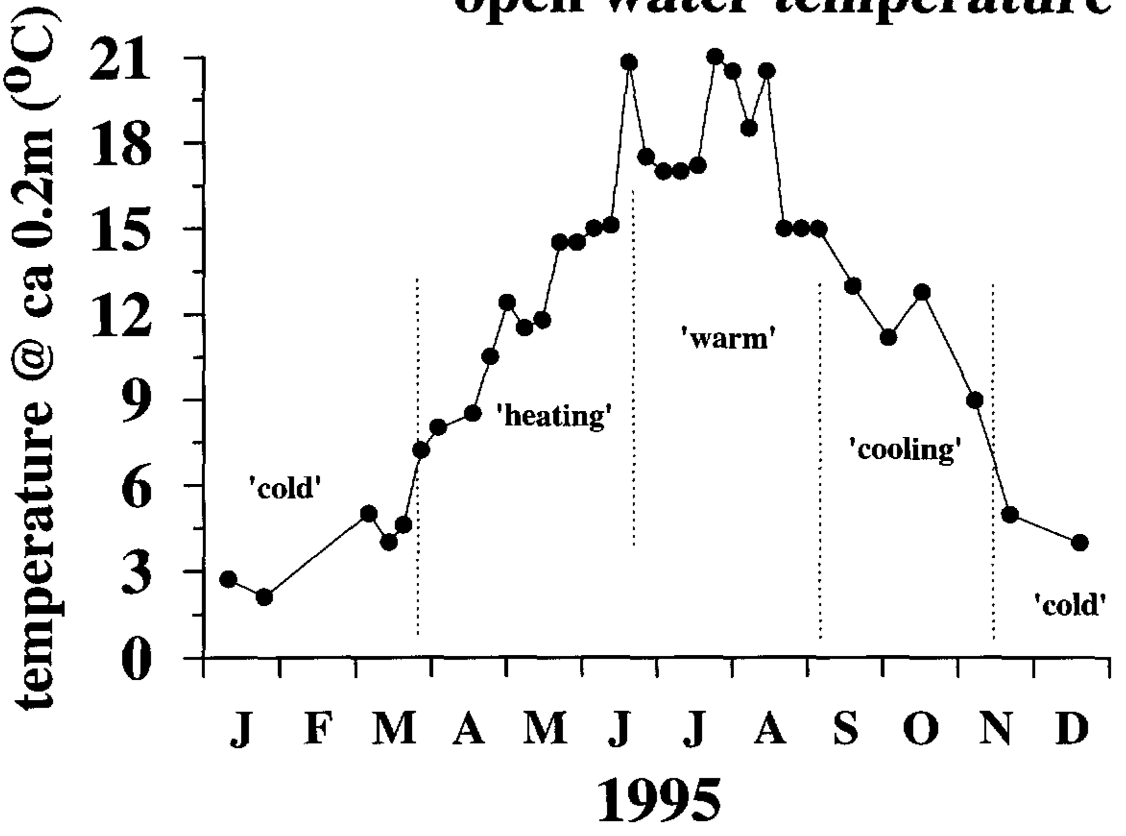


Figure 7. Variation in the weather as indicated by wind, rain and water level records.

Figure 8a. Fluctuations in the concentrations of nitrate-nitogen.

nitrate nitrogen

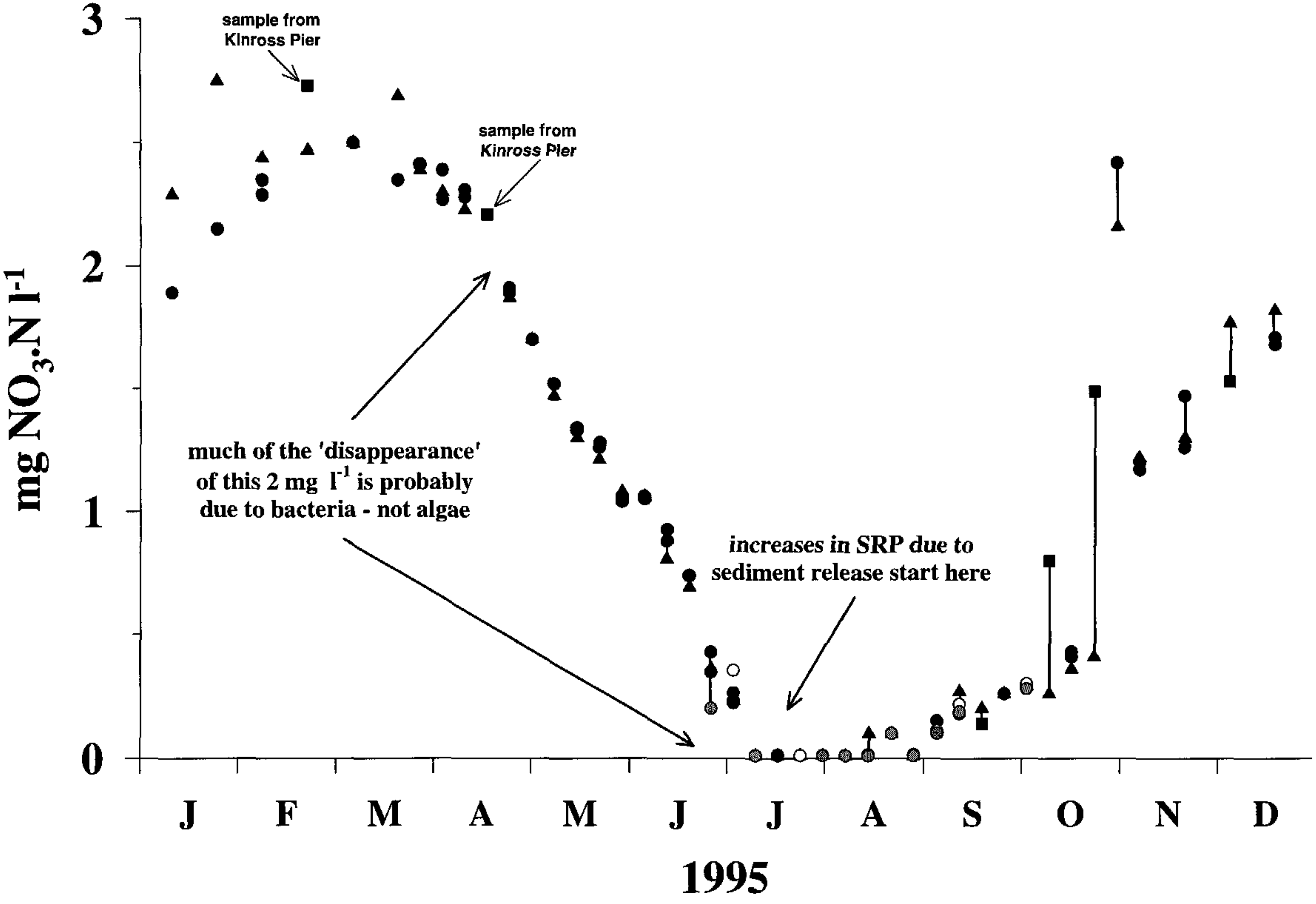
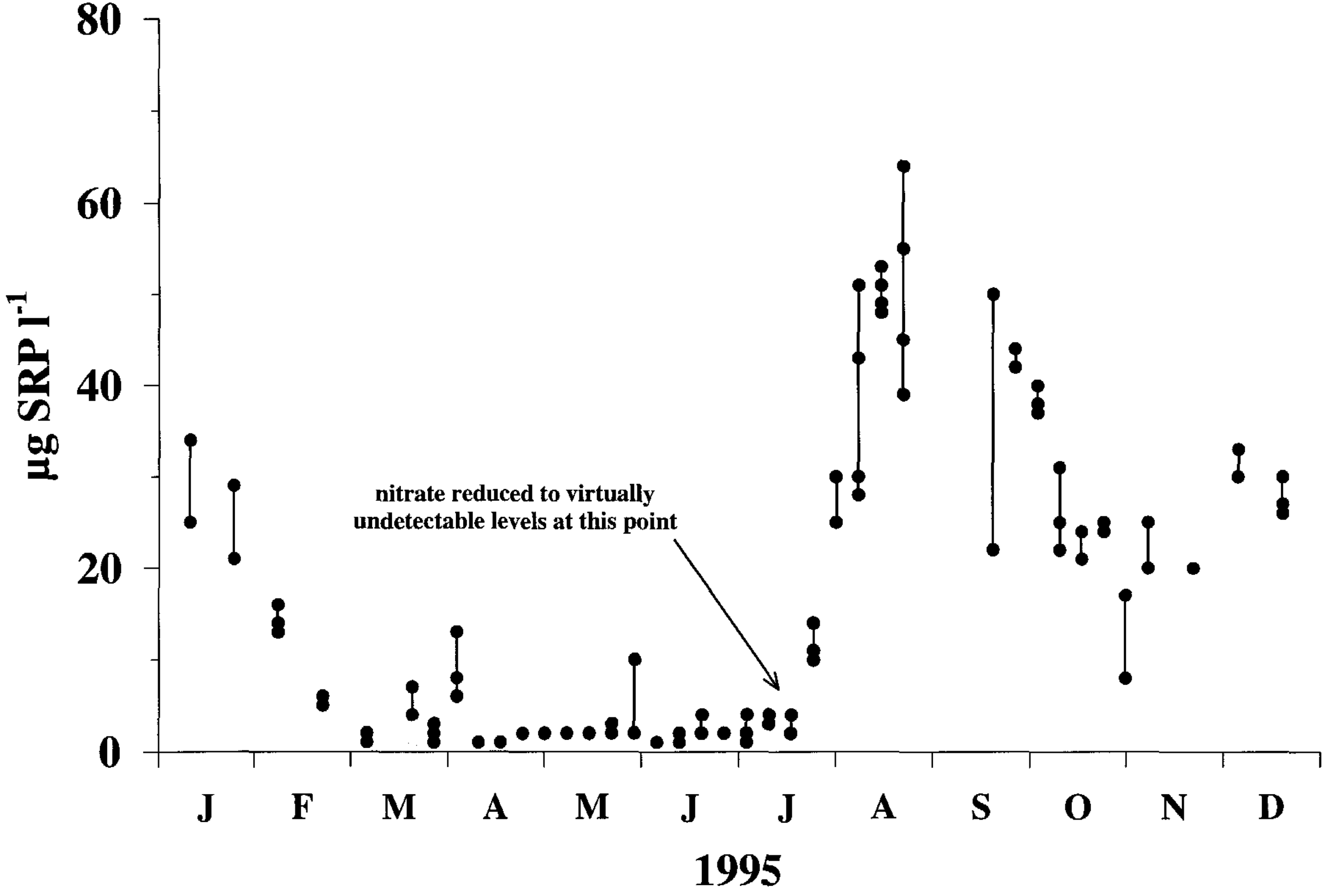


Figure 8b. Fluctuations in the concentrations of soluble reactive phosphorus.



soluble reactive phosphorus

Figure 8c. Fluctuations in the concentrations of dissolved silica.

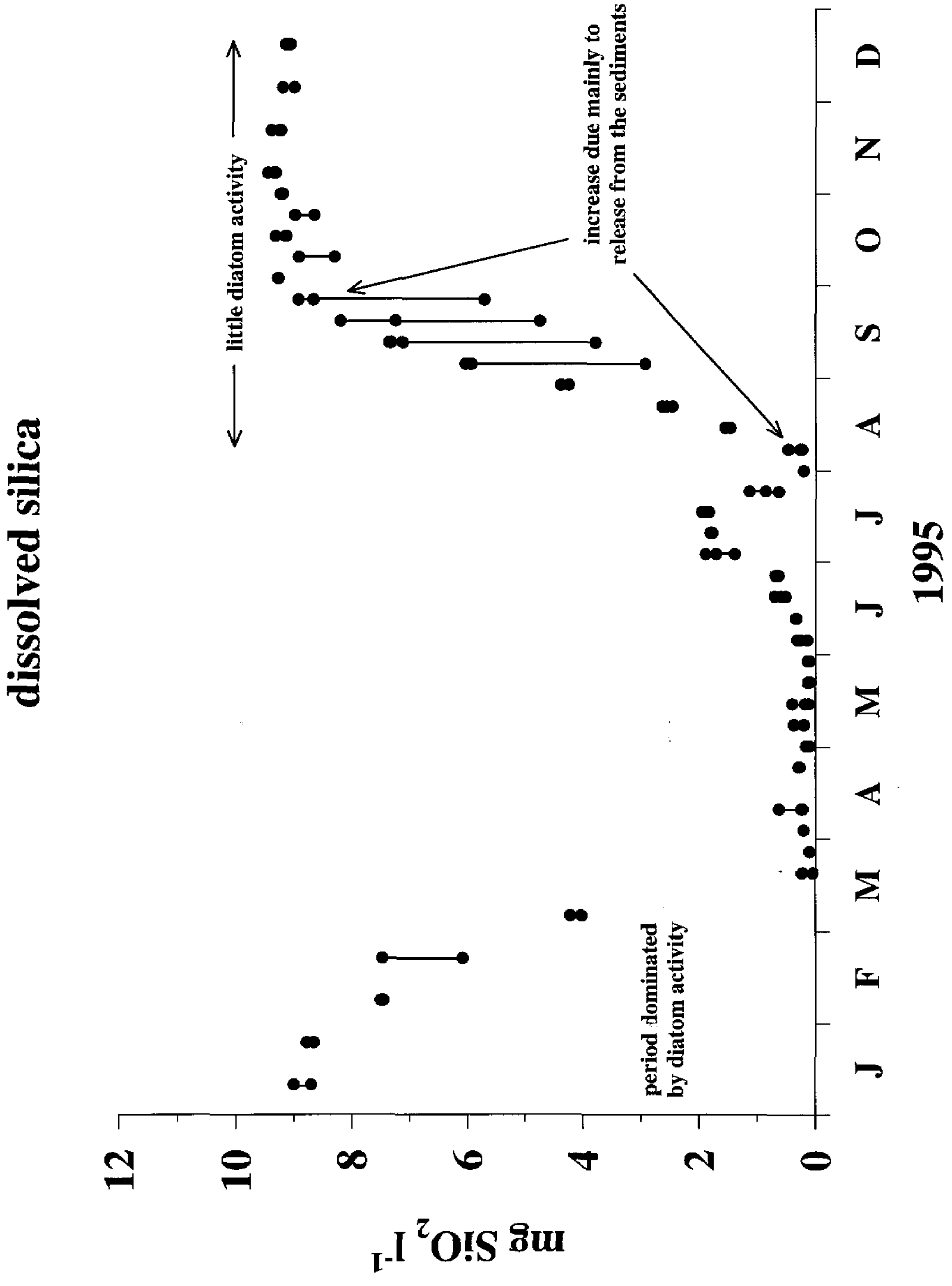

dissolved silica
mg SiO$_2$ l^{-1}
0
2
4
6
8
10
12
J
F
M
A
M
J
J
A
S
O
N
D
1995
period dominated by diatom activity
little diatom activity
increase due mainly to release from the sediments

Figure 9a. Dissolved oxygen levels.

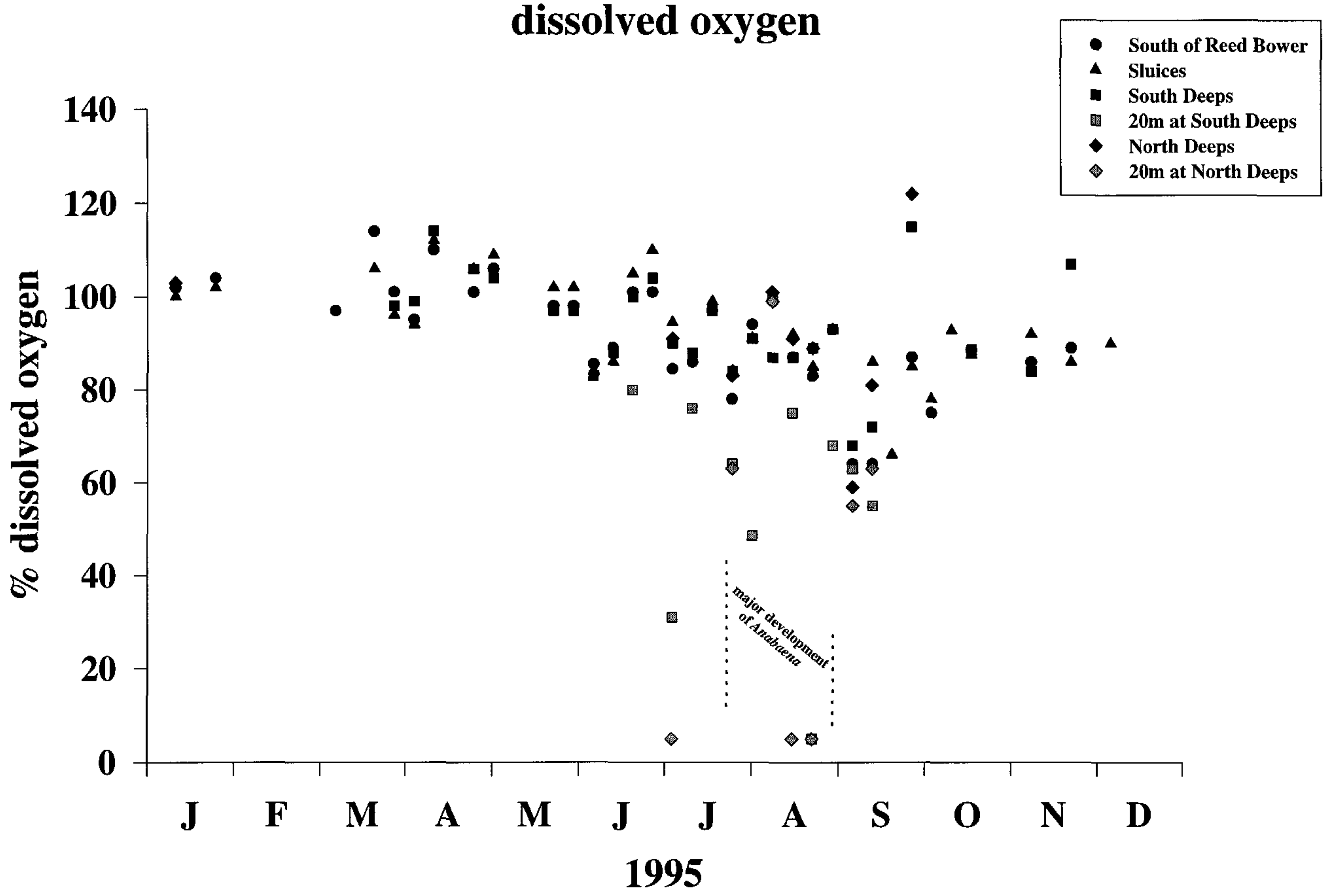

dissolved oxygen
● South of Reed Bower
▲ Sluices
■ South Deeps
▨ 20m at South Deeps
◆ North Deeps
◈ 20m at North Deeps
% dissolved oxygen
140
120
100
80
60
40
20
0
J
F
M
A
M
J
J
A
S
O
N
D
1995
major development of *Anabaena*

Figure 9b. Ammonia levels.

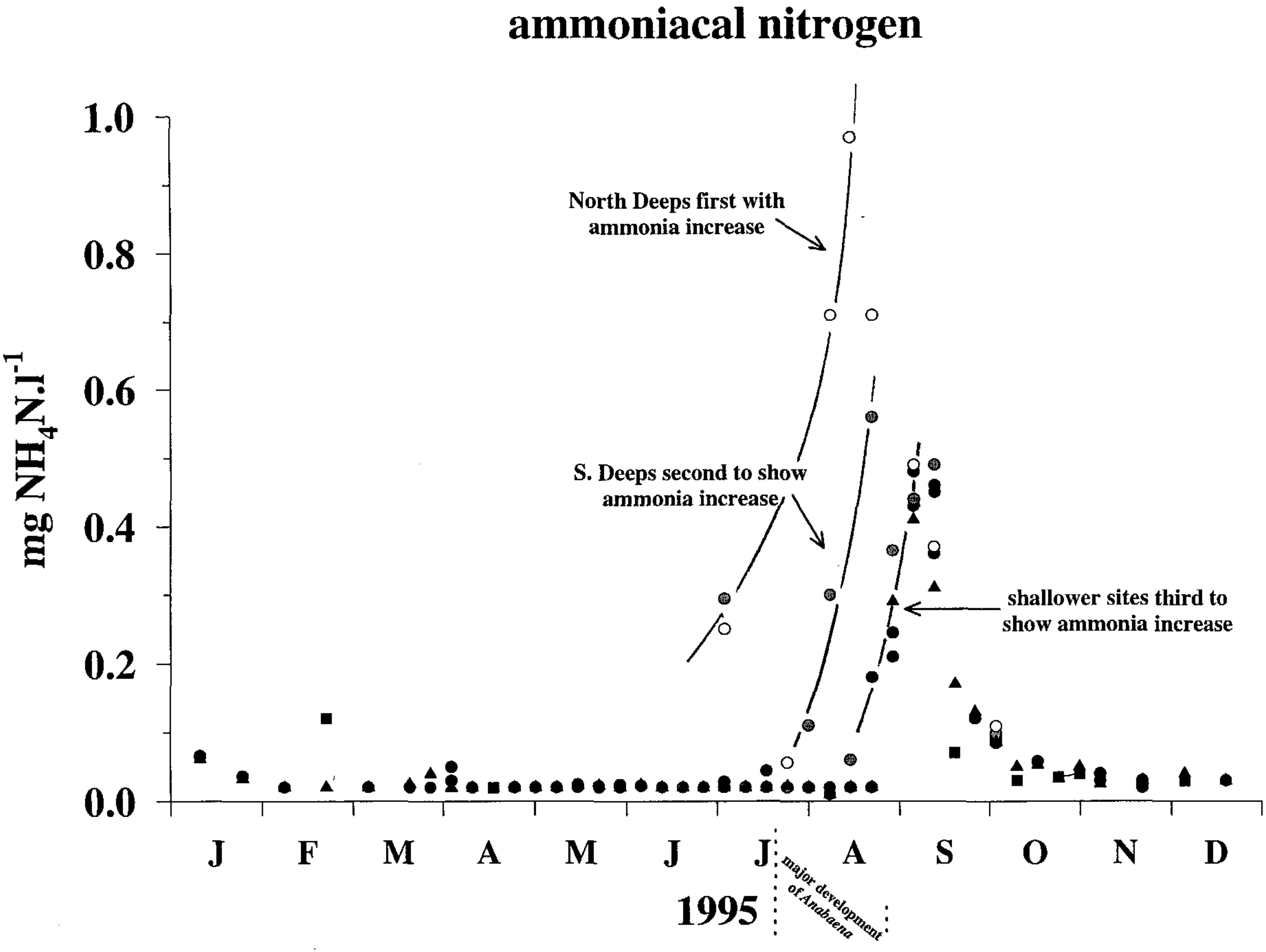

ammoniacal nitrogen
mg $NH_4N.l^{-1}$
1.0
0.8
0.6
0.4
0.2
0.0
North Deeps first with ammonia increase
S. Deeps second to show ammonia increase
shallower sites third to show ammonia increase
J
F
M
A
M
J
J
A
S
O
N
D
1995
major development of *Anabaena*

Figure 10. Fluctuations in overall phytoplankton biomass (measured as chlorophyll$_a$) and the abundance of *Daphnia*.

chlorophyll$_a$ and *Daphnia*

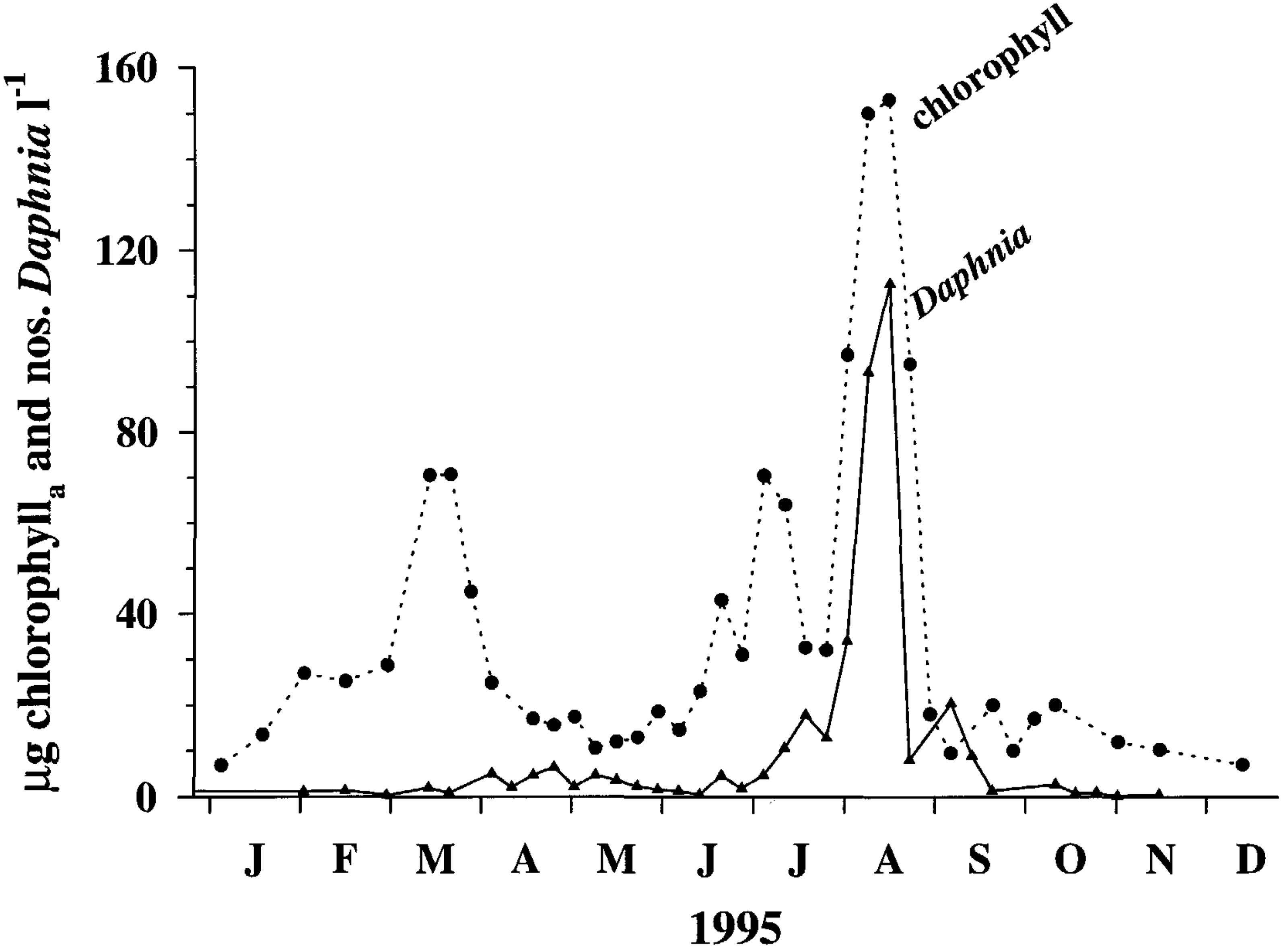
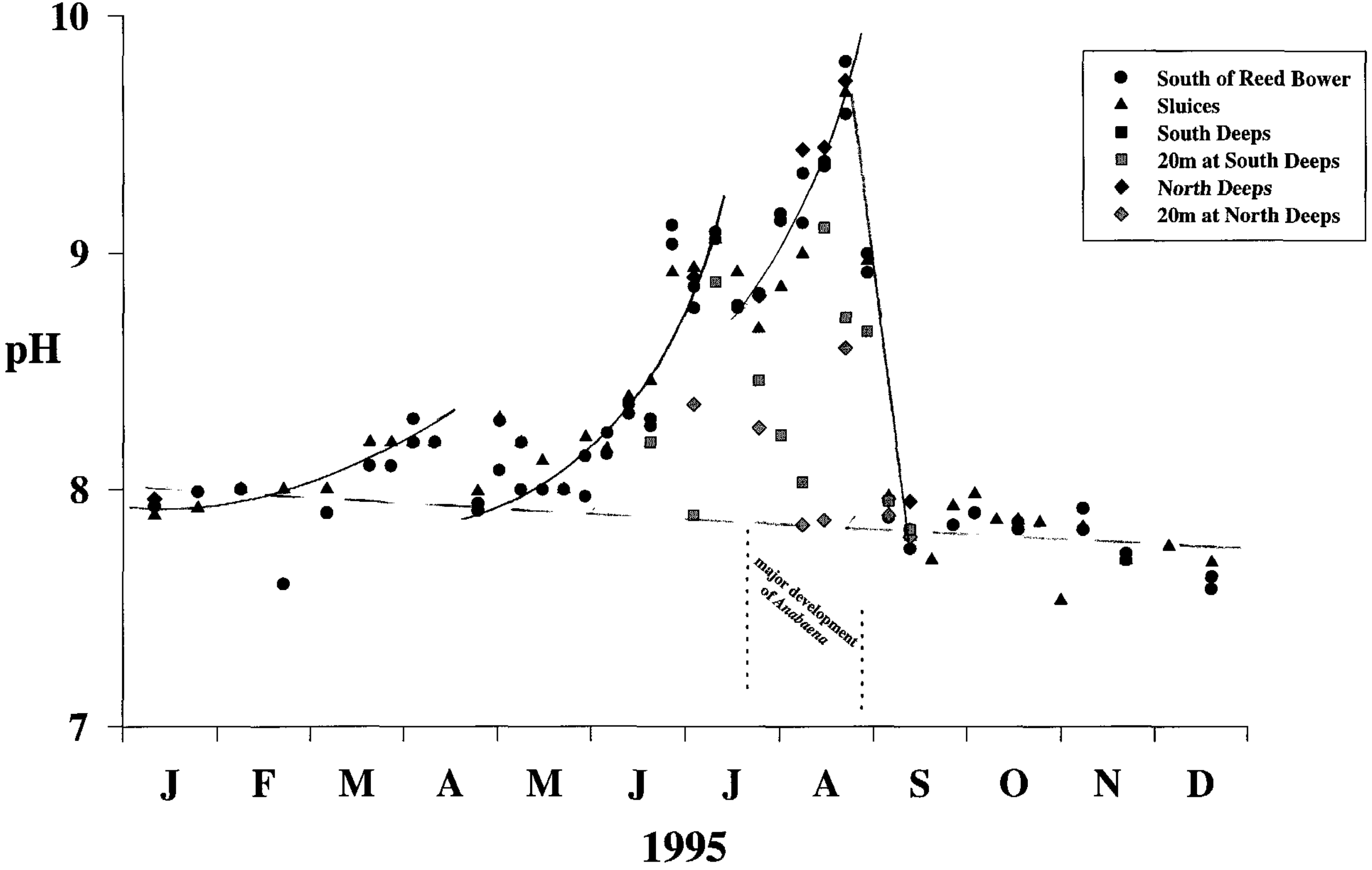


Figure11. Changes in pH.



pH

10
9
8
7
pH
J
F
M
A
M
J
J
A
S
O
N
D
1995
South of Reed Bower
Sluices
South Deeps
20m at South Deeps
North Deeps
20m at North Deeps
major development of *Anabaena*

Figure 12. Variation over the year in the particulate phosphorus-to-chlorophyll$_a$ weight ratio.

particulate P-to-chlorophyll$_a$ weight ratio

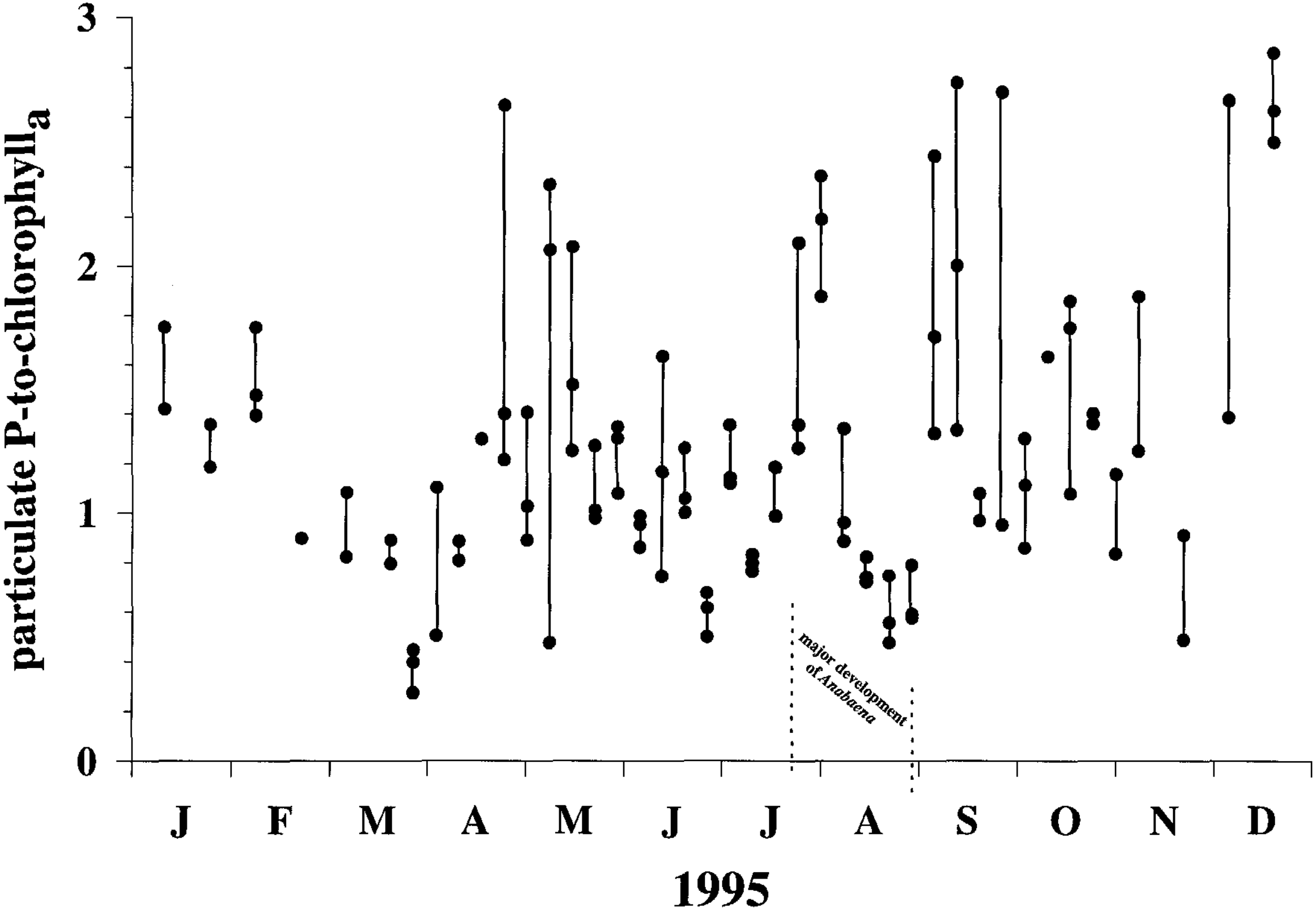


Figure 13. Changes in total phosphorus levels, and an indication of the effect of the release of soluble reactive phosphorus from the sediments.