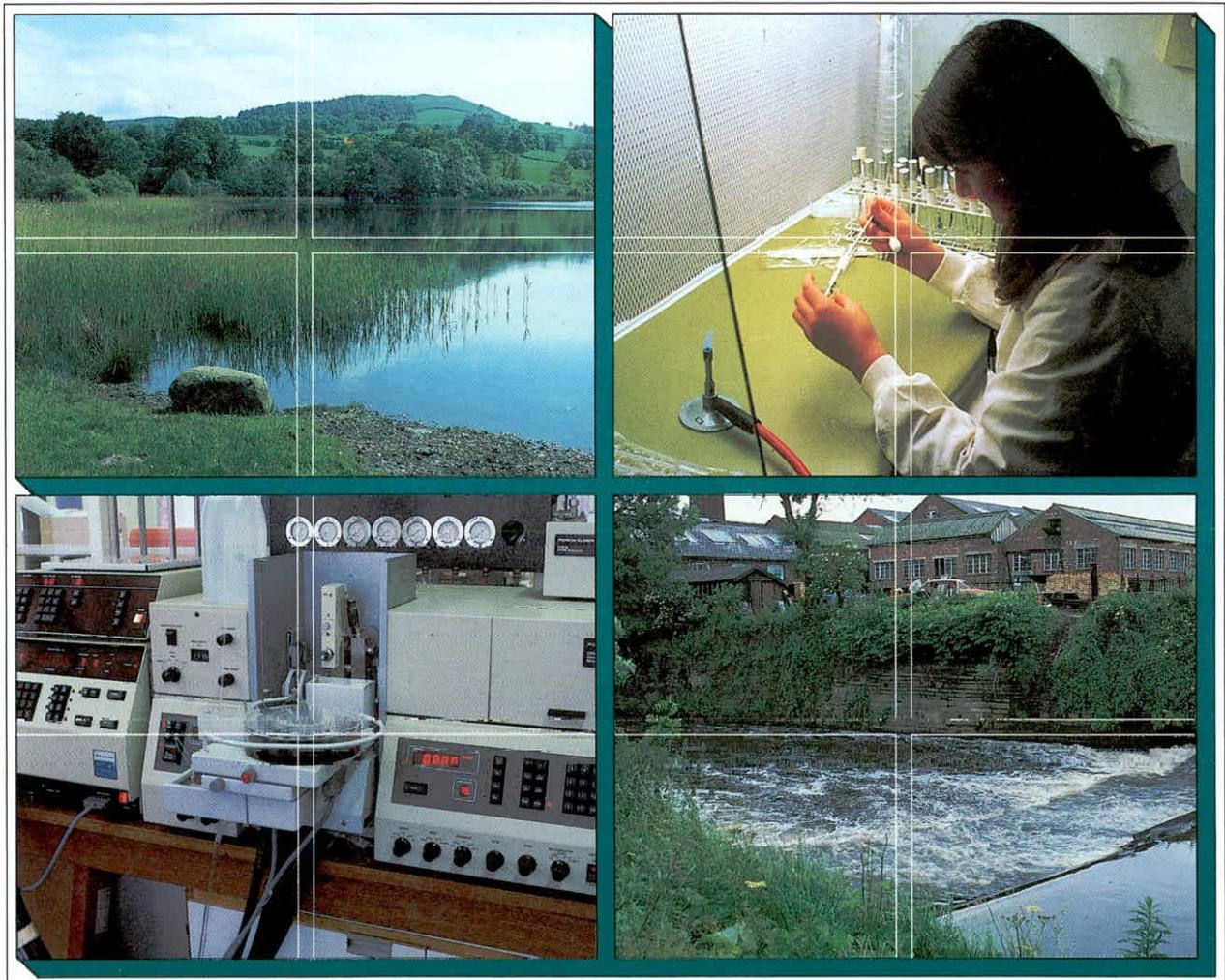


A basic surveillance of the phytoplankton of a rapidly flushed, upland lake (Loch Dee, Galloway, Scotland), and thoughts on the ecological determinants of the main features of the algal assemblages.

Project Manager : A E Bailey-Watts

Report to the Scottish Office,
Department of Agriculture and Fisheries, 1991



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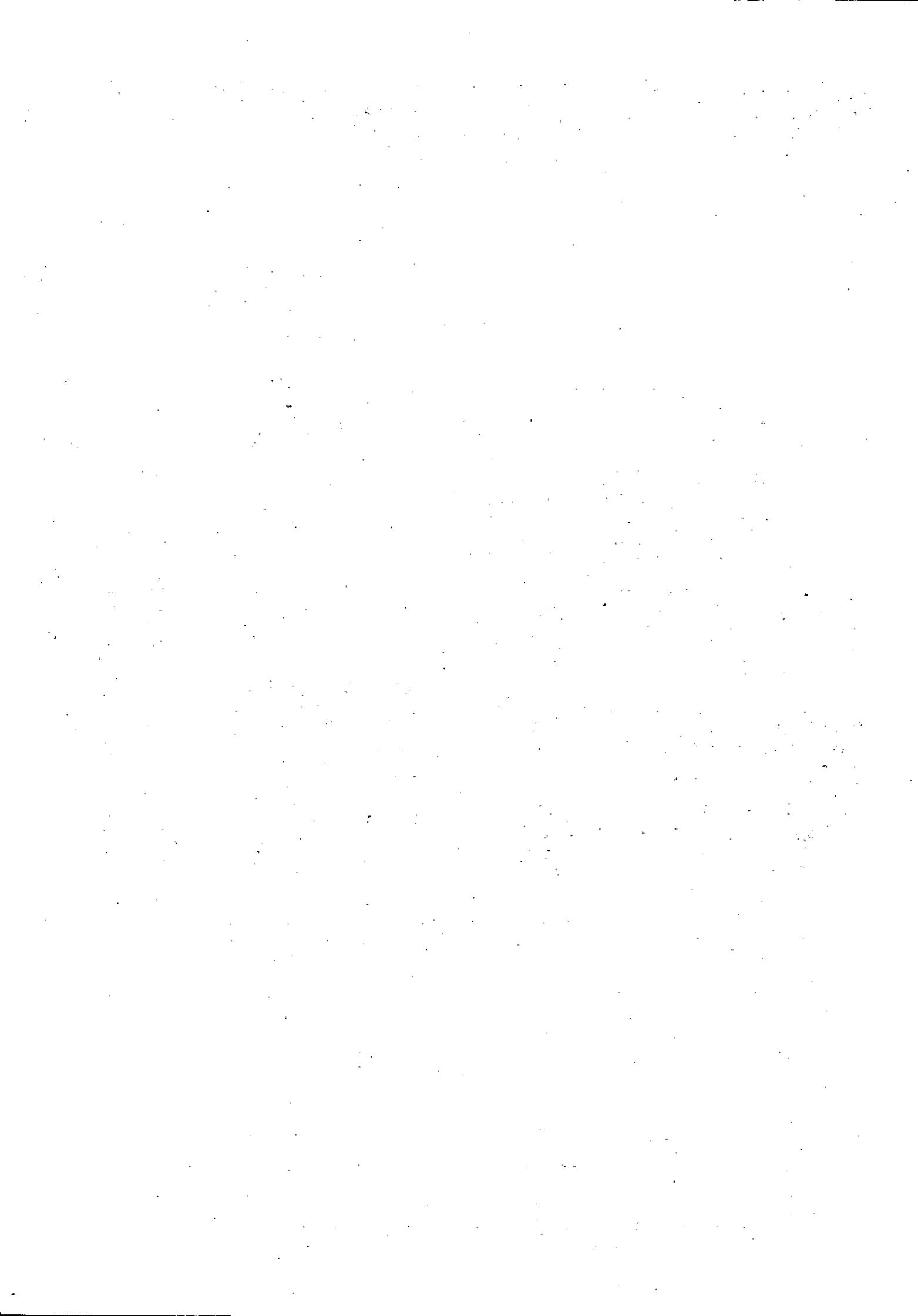
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Summary

The basic surveillance of the phytoplankton of Loch Dee was started (in 1988) to fill a gap in an otherwise comprehensive investigation aimed primarily at assessing the effects of liming of the catchment on this upland, acid water, and restoring the brown trout fishery.

The following features of the catchment, the loch, and aspects of the relationship between the two are considered to be of major importance in governing general features of the phytoplankton assemblage; in this report, they are discussed before examining the phytoplankton (and nutrient) results *per se*.

1. In terms of nutrient status, the wet catchment (receiving > 2000 mm rainfall annually), lying mostly above 305 m a.s.l., can be considered 'pristine'; the runoff is not likely to lead to high phytoplankton biomass or productivity.
2. The reasonably high ratio of the area of the catchment (15.6 km²) to that of the loch (1.0 km²) i.e. 15.6:1, suggests that the drainage area will affect the loch considerably. Firstly, it will be raising the nutrient status of the loch, albeit slowly in view of the impoverished status of the land. Secondly, however, because the volume of water running off the catchment is so large - estimated at $29 \times 10^6 \text{ m}^3 \text{ y}^{-1}$ - particles and solutes will be generally dilute; moreover, as this volume is equivalent to 7 times the median volume of the loch itself, it will effect a high flushing rate.
3. The limitations on planktonic algal biomass accumulation, of the flushing regime - equivalent to a theoretical average hydraulic retention period of only 52 days - are discussed. The likely effect on the trap efficiency of the loch is also explored. From the water balance figures, a high areal water loading value (q_s of Kirchner and Dillon) of 29.0 m y^{-1} is calculated for Loch Dee; as a consequence, the retention coefficient of phosphorus, for example, is low ~ *ca* 44%.

In spite of an environment with physical and chemical features likely to mediate against the building up of high population densities of organisms, the records indicate that certain species do achieve comparatively high densities, including zooplankters, e.g. 160 *Holopedium* l⁻¹ and 20 *Daphnia* l⁻¹.

Nutrient analyses carried out in parallel with the phytoplankton assessments, confirm the oligo-trophic nature of the system. Nitrate levels rarely exceed a few tenths of 1 mg N l⁻¹, phosphate levels normally lie below 3 µg P l⁻¹, and silica remains at less than 2 mg SiO₂ l⁻¹. Seasonal patterns exhibited by nitrate and silica (both with winter peaks and summer minima) contrast with the erratic fluctuations of phosphate.

Relative to N, P is likely to be the nutrient most commonly limiting phytoplankton biomass, but the possible effects of seasonal shortages of N and SiO₂ are noted. Assuming a requirement by diatoms, for nutrients in the ratio of *ca* 190 SiO₂:11 NO₃:N:1 SRP, the amounts of phosphate needed to support growth that effected observed decreases of 1 mg SiO₂ l⁻¹, would appear to be greater than the amounts of P available. It is also borne in mind that epiphytic and other attached communities of algae, and rooted

macrophytes as well as phytoplankton are likely to be competing for this resource. The possibility that dissolved forms of P other than SRP are being utilised, is mentioned.

Phytoplankton is indeed, sparse; chlorophyll *a* concentrations rarely exceed $4 \mu\text{g l}^{-1}$. In contrast to the situation with nutrients, which seem to be present in approximately similar concentrations over the loch as a whole, chlorophyll levels are often significantly different (but neither consistently higher nor lower) in the NE Bay, from those recorded in the centre of the loch and near the fish cage.

In spite of a low biomass, the concentrations of algal plankton are often considerable e.g. $> 10^4 \text{ ml}^{-1}$. This is explained by the fact that the assemblages are dominated by extremely small forms, i.e. 'picoplankton' of $< 2 \mu\text{m}$. Many of these have not yet been identified to Family, let alone genus or species.

The ecology of the phytoplankton is briefly discussed in relation to possibly mixotrophy, and the influence of zooplankton on algal size.

The observed net increase of a population of an *Ochromonas* sp., over the period 17 August to 7 September 1988 - *ca* $12 \times 10^3 \text{ cells ml}^{-1}$ - would have required a very high, mean rate of increase i.e. by doubling every 2 days - and this, at the theoretical mean hydraulic residence time of the loch.

This is puzzling.

In terms of analysing existing data further, and identifying new work, the most pressing issues are (i) the better assessment of flushing rate, and (ii) the identification and better understanding of the biology and ecology of the picophytoplankton. A major 'unknown' appears to be whether, for example, inflowing water from the Green Burn is short-circuited rapidly to the nearby outflow, such that water stays in other areas of the loch for longer than the calculated mean retention time suggests. As to the plankton, the role of the 'pico' forms in energy chains possibly involving organic phosphate (*cf.* SRP), and the planktonic ciliates and rotifers observed (*cf.* the more prominent Crustacea), are exciting areas worthy of considerable attention.

1. INTRODUCTION

1.1 Background to, and rationale of the study

The basic, descriptive work on the phytoplankton of Loch Dee reported here, was started in May 1988 in response to a request from The Loch Dee Project group. That group had been investigating various aspects of the ecology of this upland, rapidly flushed waterbody since 1980, focusing on acidification processes and a large-scale liming experiment, and the restoration of a brown trout (*Salmo trutta* L.) fishery (Burns *et al* 1984; Tervet and Harriman 1988). The first reason for contributing to the study, relates to the fact that, in spite of valuable information being gathered on benthic and planktonic fauna in parallel with studies on land-use, hydrology and water balances (see e.g. Lees 1988, 1990), and comprehensive analyses of inflow, loch, sediment and outflow chemistry, the plant plankton had been neglected. However, information on other algae, especially epilithic forms, exists - as a result of the contribution of the project to the United Kingdom Acid Waters Monitoring Network (see e.g. UKAWMN 1989, 1991); indeed, planktonic algal remains - especially the opaline frustules of diatoms - feature prominently in paleolimnological studies (sediment stratigraphy) carried out on Loch Dee and elsewhere (see e.g. Battarbee 1984; Flower, Battarbee and Appleby 1987; Battarbee *et al* 1988). The second reason prompting the phytoplankton work related to a plan by the Forestry Commission to apply fertiliser to an area of *Sitka* woodland in the catchment of Loch Dee. This would have formed the basis of a valuable, field-scale, eutrophication experiment - there being concern over the potential effects of such action on water quality (Bailey-Watts, Kirika and Howell 1988). The aim was to monitor changes in phytoplankton (species) composition and abundance, for approximately 1 year prior to the

intended fertilisation programme (set for 1989), as well as during, and for a number of years following it. However, the FC programme was eventually cancelled - in early 1989 - on economic grounds. Nevertheless, virtually 12 months' phytoplankton data had been collected by then, and these suggested that the (monthly) surveillance should be maintained, because of the intrinsic scientific value of following such events in a rapidly flushed, upland water; this type of lake is rarely studied from this viewpoint. In any event, there was the added interest of the possible long-term effects of liming, and in this regard, the phytoplankton work should be considered alongside the annual reports on other aspects of Loch Dee Ecology.

1.2 Layout of the report

The report summarises firstly, some physical, chemical and selected biotic features of the catchment that are likely to have a bearing on the Loch Dee phytoplankton. In considering these features before examining the nature of the phytoplankton itself, some views on what might be expected as regards the general characteristics of the planktonic flora, are presented. A section on investigative field and laboratory methods precedes the phytoplankton results and discussion in relation to data on nutrients - nitrate-nitrogen (N), soluble reactive phosphorus (SRP) and dissolved silica (SiO₂). A concluding discussion is limited mainly to proposals for future work. Figures (graphs) are bound together at the back of the report.

2. FEATURES OF LOCH DEE LIKELY TO HAVE A SPECIAL BEARING ON ITS PHYTOPLANKTON

To a greater or lesser extent, every feature of the waterbody will affect the 'performance' of its phytoplankton. Indeed, the inexorable links between different biota within and between trophic levels ensure that a change in one, will directly or indirectly, affect all the others; for example, a shift such as that in the population density of trout apparently in response to acidification at Loch Dee, will probably result in changes in the zooplankton, for example, and thence the phytoplankton. Equally important, are (i) changes in pH and major ion ratios, (ii) variation over different time scales in the loadings and concentrations of nutrients, and (iii) the altering situation regarding the underwater light climate. This section, however, focuses on factors that are likely to have an especially marked influence on even the basic features of the phytoplankton, such as general abundance, and the major types and size characteristics of this algal assemblage. For present purposes, the possible influences are discussed with reference primarily to issues affecting nutrient availability.

2.1 The catchment

In the context of nutrient status, the Loch Dee catchment (as described by Burns *et al* 1984) can be considered reasonably pristine. It ranges from 225 to 716 m a.s.l. (with ca 66% of the area lying above 305 m). While the impact of Man involving nutrient enrichment (ie N, P and SiO₂) has been identified in relation to afforestation, the ploughing involved, and use of fertilisers, this is probably of minor consequence so far. The greater

concern is over Man's influence on the acid status, particularly as the loch is of a base- and nutrient-poor nature - a situation to be expected at this altitude and in an area where the annual rainfall commonly exceeds 2000 mm.

A loch in such a wet, oligotrophic landscape, would not be expected to be very productive in terms of phytoplankton, neither would large accumulations (high biomass) of these unattached algae be considered likely.

2.2 Catchment-loch relationships

The ratio of the area of catchment (A_c) to that of the loch (A_l), indicates what impact the catchment - through its influence on loadings of nutrients, and on the inputs of water itself, (flushing, see below) - is likely to have on the physical and chemical nature of the water mass, and on the dynamics (and, indeed, composition) of its biota. The values for A_c and A_l are 15.6 km² and 1.0 km² respectively, so the ratio $A_c:A_l$ is 15.6:1. To place it in a Scottish context, this value is higher than the figures of 10.9:1 for Loch Leven (Smith 1974) and 3.9:1 for Coldingham Loch (Bailey-Watts *et al* 1987a), but lower than the ratio of *ca* 22:1 calculated for the Loch of Cliff, Unst, Shetland (Bailey-Watts 1990), and an insignificant figure compared to the value of *ca* 820:1 obtained for Loch Insh - a widening of the River Spey (Watson 1991). On the basis of the ratio for Loch Dee, the catchment is likely to be a significant source of dissolved and particulate material. At the same time, however, this drainage area releases comparatively large amounts of water to the loch, and so effects a potentially high flushing rate (p - in units of loch volumes). Bailey-

Watts *et al* (1990) have illustrated for another shallow Scottish loch, the marked influence of p on (i) water temperature, (ii) changes in nutrient concentrations (including those associated with the sediment-water interface), and (iii) above all, the time that processes, such as warming and cooling of the water, releases of P from sediments, shifts in numbers of phytoplankton, and the feeding of zooplankton, can proceed i.e. before water (and the released nutrients and accumulated organisms that it contains), flows out of the system. Up to a point, the higher the flushing rate, the greater the likelihood of the more rapidly growing species being prominent. Beyond this point, and providing favourably lit substrates are available, attached, rather than free-living, plants will dominate. The actual flushing rate of Loch Dee is calculated in the following section, and is considered along with other physical attributes of the loch itself.

2.3 Physical features of the loch

An indication of how Loch Dee might be categorised in terms of p can be obtained from the values shown in Table 1. From these figures it is estimated that $29.0 \times 10^6 \text{ m}^3$ of water enters Loch Dee in an 'average' year.

Table 1. Data* used to calculate the annual average flushing rate of Loch Dee.

Catchment area	15.6 km ²
Loch surface area	1.0 km ²
Annual rainfall	2200 mm
Potential evaporation:	
(i) from the catchment	450 mm
(ii) from the loch surface	540 mm

* from Burns *et al* (1984) and Meteorological Office maps of average annual rainfall (1941-1970, published in 1977) and potential evaporation (provisional map Met. O./CARTO/D.00/3111).

It is this volume (rather than the volume of the loch) in which all wind- and water-borne materials entering in one year, are dissolved or suspended. It is *ca* 7 times the median volume of the loch, i.e. $4.2 \times 10^6 \text{ m}^3$ (calculated from the maximum and minimum volumes given by Burns *et al*, 1984). In other words, the mean hydraulic retention time ($1/p$) is *ca* 52 days. Given unlimited supplies of nutrients, light and other growth requirements, many phytoplankton species are capable of at least doubling in number every 3 days (see e.g. Bailey-Watts 1974, 1988). If this doubling rate was sustained over 52 days, and assuming no losses of cells *via* e.g. sinking, flushing out, grazing or fungal parasitism, an algal population could increase some 130000-fold. This means that an alga present initially at a low population density of say, 1 l^{-1} would achieve a (significant) concentration of *ca* 130 individuals ml^{-1} ; by the same reckoning, a species present at an initial level of just 1 ml^{-1} would achieve a high density of *ca* 130 000 ml^{-1} .

As, by definition, high hydraulic flushing suggests a rapid throughput of water, Loch Dee would be considered by geomorphologists to have a low 'trap efficiency'. This means that the retention coefficients of many materials entering the loch will be low. It is worth considering on the basis of the data discussed so far, the likely P retention coefficient (R) of Loch Dee. The empirical model of Kirchner and Dillon (1975) provides the basis of the calculations that follow. Certainly, data based on extensive, close-time interval sampling and P loading estimations at Loch Leven, fitted this model very closely (Bailey-Watts *et al* 1987b). Its central term is q_s , the 'areal water loading', in units of m y^{-1} ; this is the volume of water entering a lake, V_{in} ($\text{m}^3 \text{ y}^{-1}$) divided by the surface area of the lake, A_1 (in units of m^2). V_{in} has already been assessed in relation

to the calculation of p , and equates to an annual exchange of 29.0×10^6 m^3 , and A_1 is 1×10^6 m^2 . q_s is thus 29.0 m y^{-1} . The model then predicts R from q_s according to:

$$R = 0.426e^{(-0.271q_s)} + 0.574e^{(-0.00949q_s)}$$

so, where q_s is 29.0 , R is 0.44 .

Thus, the amounts of P passing out of Loch Dee in one year are likely to be equivalent to *ca* 56% of the external loading in the same period. Although the errors involved in arriving at this value are likely to be high, the equation supports the original notion that Loch Dee retains a comparatively small proportion of its external, stream-borne supply of P. The R value for Loch Leven, for example, is 0.8 (Bailey-Watts *et al* 1987b).

The theoretically possible increases in phytoplankton numbers discussed above would require, as stipulated already, availability of all growth requirements. This would include a favourable light climate. It is notable that with a mean depth of 4.5 m (Tervet and Harriman 1988), Loch Dee is likely to favour such growth. A number of studies starting with the work of Sakamoto (1966) indicate that this is an optimum depth in the context of phytoplankton photosynthesis. Primary productivity of these organisms is often limited by vertical mixing into 'dark' zones of deeper columns, and by wind-induced suspension of light-attenuating, sedimentary material in much shallower waters. Bindloss (1974, 1976) showed that much of the success of phytoplankton in Loch Leven could be attributed to its mean depth of 3.9 m ~ somewhat similar to the Loch Dee value - although an added advantage at Leven stems from the intrinsic clarity of the water

itself. Loch Dee water is somewhat more coloured with dissolved humic matter - a factor mediating against the most efficient conversion of nutrients to phytoplankton.

2.4 Chemical water quality

Chemical analyses of Loch Dee water over many years (Lees 1988, who gives flow-weighted figures for the outlet from loch) reveal a soft water (mean annual conductivity values near $30 \mu\text{S cm}^{-1}$) with correspondingly low concentrations of Na^+ (ca $2.6 - 4.8 \text{ mg l}^{-1}$), K^+ ($0.3 - 0.4 \text{ mg l}^{-1}$), Ca^{++} ($0.9 - 1.2 \text{ mg l}^{-1}$), Mg ($0.6 - 0.9 \text{ mg l}^{-1}$), Cl^- ($5 - 9 \text{ mg l}^{-1}$) and SO_4^{--} ($3.5 - 4.0 \text{ mg l}^{-1}$). Nutrient levels are also low with, for example, $100 - 140 \mu\text{g NO}_3\text{-N l}^{-1}$, and $3-8 \mu\text{g SRP l}^{-1}$. This would suggest that the fish cage (installed in 1986) is having but a minor effect on the nutrient economy of the loch, (*cf* its significant though localised effect on the composition and abundance of the benthic fauna). The sequestration of nutrient ions by complexation with humic compounds should not be discounted. This could be viewed as a form of competition with phytoplankton and other plants, for already limited resources of phosphate in particular (e.g. Jones, Salonen and de Haan 1988) but also silica (Tessanow 1972). Under this regime, sparse, an oligotrophic flora can be expected.

2.5 Biota other than phytoplankton

A considerable amount of work has been done on the benthic fauna of Loch Dee - revealing, for example, the sparse, thin-shelled, molluscan assemblage in 1981 (Burns *et al* 1984). However, results on the crustacean

zooplankton are of more immediate relevance to a consideration of the phytoplankton on which many of them feed. Of especial significance is the contrast between 1982 and subsequent years associated with the liming programme. In 1982, the assemblage was typical of acid systems in being apparently devoid of *Daphnia* - although other cladocerans, especially *Bosmina* and *Holopedium* were prominent (Burns *et al* 1984); in 1988 (September) *D. hyalina* Sars appeared, and subsequently increased to population maxima of *ca* 20 individuals l^{-1} in the 1989-1990 winter (Mr B R S Morrison - personal communication). In most years, however, *Holopedium gibberum* Zaddach, produced the densest crustacean populations e.g. 28 l^{-1} in early 1988, and 160 l^{-1} in spring 1987. Plainly therefore, certain planktonic animals can build up appreciable populations in this theoretically highly flushed system; but it is not known if this is due to their ability to avoid outflow losses, or reflects periods of longer hydraulic retention than the theoretical value of 52 days suggests.

3. INVESTIGATIVE METHODS

3.1 Field methods

With the view to assessing the impact of the fish cage, and taking account of the not very simple shape of the loch, monthly, duplicate dip samples for nutrient and phytoplankton analysis were taken by SOAFD staff from 3 sites:

- (i) the N.E. bay between the sediment sampling points 12 and 14 indicated in Figure 2 of Tervet and Harriman (1988); the water depth there is *ca* 1.5 m.
- (ii) the main S.W. basin approximately half-way along the loch - near Tervet and Harriman's site 10, where the water depth is *ca* 10 m; this is referred to as 'open water' or 'mid-loch' in the rest of this report.
- (iii) near the centre of the S.W. bay - corresponding to Tervet and Harriman's site 6 - where the depth is also *ca* 10 m, and the fish cage is normally positioned; in winter the cage is moved inshore towards Tervet and Harriman's site 2 near the White Laggan Burn inlet.

The samples were kept cool and transported to a cold store (*ca* 4°C) at the Edinburgh Laboratory of IFE.

3.2 Laboratory analyses

nutrients: the concentrations of nitrate-N, soluble reactive P (SRP) and

soluble reactive silica (SRS as SiO_2) were determined usually on the day after collection on Whatman GF/C-filtered water; the results differ little from those using $0.45 \mu\text{m}$ Millipore filters (Casey and Walker 1983) but the GF/C discs are cheaper and more convenient to use. For SRP - the fraction of P most immediately available for algal growth - the spectrophotometric method described by Murphy and Riley (1962) was used; while it was suspected that the concentrations of SRP in Loch Dee would be around a few microgrammes per litre, no prior concentration of the phosphate (in e.g. hexanol) was done. Instead, on triplicate subsamples from each bottle of water, the aliquots and proportions of molybdate reagent were modified, and 4-cm path length cuvettes were used, to obtain absorbance readings such that trends involving changes of 1 or $2 \mu\text{g P l}^{-1}$ could be considered significant. SRS - an important nutrient for diatoms and many chrysophycean algae - was determined using the method of Mullin and Riley (1955) and adopting the procedures outlined by Golterman, Clymo and Ohnstad (1978); the limit of detection is $50 \mu\text{g SiO}_2 \text{ l}^{-1}$. Filtered sub-samples used for nitrate determinations were freezer stored until analysis as nitrite, by the modified hydrazine-copper reduction method proposed by Hilton and Rigg (1983).

Determinations of the levels of total P (TP) and the total soluble fraction (TSP) was also carried out, in triplicate, on each sample. TP concentrations constitute a useful index of trophic status, while a measure of TSP provides information on the levels of soluble un-reactive P (SURP or dissolved 'organic' P) from:

$$\text{SURP} = \text{TSP} - \text{SRP}$$

Similarly, the difference between TP and TSP gives the concentration of particulate P (PP). TP and TSP were analysed on unfiltered and GF/C-

filtered subsamples of water respectively. In each case the P was measured as SRP following acid digestion to first convert all of the P present to the soluble reactive form.

chlorophyll a: concentrations of this pigment were determined on methanolic extracts of the algal material concentrated from known volumes of water on the GF/C filters referred to above. The spectrophometric equation of Talling and Driver (1963) was used to convert absorbance readings at 665 nm (corrected for turbidity at 750 nm) to concentrations of chlorophyll *a*.

phytoplankton counts and species determinations: 250 ml of water from each of the 2 bottles filled at each site were transferred to a glass measuring cylinder and fixed with Lugol's Iodine at a concentration of *ca* 0.4%, i.e. 1 ml of iodine in 250 ml of sample; Lugol's Iodine is a saturated solution of iodine in a saturated aqueous solution of potassium iodide, which preserves the algae effectively, stains e.g. starch contents, and also increases the weight of the cells such that they sediment reasonably quickly in the cylinder. Over a period of 24-48 hours, the samples were thus concentrated by this sedimentation technique, and the overlying water siphoned off to leave a volume of *ca* 30 ml. This was transferred to a plastic, screw-top centrifuge tube, for further concentration by centrifugation and siphoning off of the clear supernatant, down to 10 ml or 5 ml, i.e. to achieve a final concentration of 25- to 50-fold.

In essence, this procedure brings the specimens closer together, such that they can be readily found, even under the often high power magnifications,

e.g. 600x, needed to examine these small organisms. As highlighted below, many of the forms observed, have not been determined to species level. This is primarily because the present authors (and a number of truly world 'experts' consulted by them) do not know what the species are; indeed, it is likely that some will prove to be new to science. In a number of cases, difficulties with identification stem from the fact that very few specimens were seen. In addition, the Loch Dee phytoplankton is characterised very much by a preponderance of very tiny organisms. Counting was done using a Lund nanoplankton chamber as modified by Youngman (1971); Bailey-Watts (1978) describes in full the procedures adopted; to obtain as comprehensive an assessment of this assemblage as possible, the material was examined at a range of magnifications from *ca* 40x (for relatively large, often numerically rare forms) to 600x (for the smaller, often numerous 'species').

phytoplankton size characteristics: the sizes of the organisms present give clues to the physical, chemical and biotic nature of the environment in which they exist (Bailey-Watts and Kirika 1981; Bailey-Watts 1986). Not least of importance at Loch Dee in this connection, are the possible interactions between the phytoplankton and size-selective grazing of zooplankton, and the influences of a potentially nutrient-poor water on cell size through the effect on surface area-to-volume ratios. The phytoplankton assemblage size spectrum ('PASS' of Bailey-Watts 1986) was assessed on a number of sampling occasions using a Vickers Image Shearing Module; the greatest axial linear dimension ('GALD' of Lewis 1976 of each of 30 or 50 randomly chosen phytoplankton individuals (regardless of species identity) were measured to the nearest 0.14 - 0.21 μm . The measurements were then plotted against normalised scores (see Sokal and

Rohlf 1969) to illustrate the nature of the size frequency distributions of the arrays. Bailey-Watts (1986) and Bailey-Watts, Kirika and Howell (1988) give fuller accounts of the procedures used, and Bailey-Watts (1974, 1978, 1987) quotes a range of taxonomic texts consulted.

4. RESULTS AND DISCUSSION

4.1 Open water nutrient concentrations

Nutrients can be considered as a resource of major importance, as each of them at one time or another can be reduced to potentially growth-limiting levels. Other factors especially light, can limit the growth and population maxima of phytoplankton, and indeed physical factors such as flushing rate and light determine to what extent the organisms capitalise on the nutrients. Nevertheless, in many waters in Scotland and other temperate parts of the world, phosphorus is particularly important in controlling phytoplankton growth generally; however, nitrate, in often becoming scarce in summer, and silica in being commonly reduced by diatom growth, are each significant in affecting specific groups of algae.

nitrate, soluble reactive phosphorus and silica

Fluctuations in the concentrations of these 3 nutrients are illustrated for the mid-loch site in Figure 1. Similar patterns were recorded for the other 2 sites; thus while, for example, marginally higher peaks in SRP in the last half of 1988 were observed at the cage site, the trends are the same. The latest peak recorded - in early July 1990 - was also echoed at the other sites. As predicted from general information on the Loch Dee catchment, and knowledge that nutrient inputs are heavily diluted by the flushed water volume, the nutrient concentrations are low. In summary, nitrate levels rarely exceed a few tenths of 1 mg N l^{-1} , phosphate levels usually lie below 3 P l^{-1} , and silica remains at less than $2 \text{ mg SiO}_2 \text{ l}^{-1}$. Nitrate and silica exhibit similar seasonal patterns, with late winter to

early spring maxima, and summer to early autumn minima. Contrastingly, inorganic phosphate levels show few trends, with continual fluctuations between *ca* $0.5 \mu\text{g l}^{-1}$ and $2.0 \mu\text{g l}^{-1}$. These concentrations are very low, and while they represent the stock of P unused by e.g. phytoplankton, they also indicate what little amounts of this nutrient is apparently available for the growth of all of the aquatic plants, i.e. epiphytic algae and rooted vegetation in addition to the plankton.

On the basis of the data on the standing stocks of the nutrients, and in the absence of information on the rates at which the substances are being supplied, *relative to N*, P is more likely to be limiting phytoplankton growth. However, since the actual concentrations of nitrate are often low, all but a fairly mild level of phosphorus enrichment would probably see N limiting. Under current conditions, silica would appear to be present in excess all the time - since the concentrations rarely fall below $1 \text{ mg SiO}_2 \text{ l}^{-1}$. Indeed, while the causes of the seasonal declines of *ca* 1 mg l^{-1} in SiO_2 are not known, it is worth considering how much N and P would have needed to accompany these shifts in SiO_2 if they can be attributed to diatom and chrysophycean growth. A spring unicellular diatom population in Loch Leven in 1981, utilised the 3 nutrients in the following ratios (by weight): 190 SiO_2 :11 $\text{NO}_3\text{.N}$:1 SRP (Bailey-Watts 1988). Therefore, for each milligramme of SiO_2 utilised, *ca* $55 \mu\text{g N}$ and $5 \mu\text{g P}$ was also taken up. If these figures are applied to the Loch Dee situation, it can be seen that during most of the period over which the decrease in SiO_2 occurred, N was in excess, while P was present at concentrations somewhat smaller than the net amount 'required'. Nevertheless, and ignoring the fact that the fluxes of P into the system, rather than the standing stocks are important, other dissolved forms of P are present, and these may be

utilised by some organisms. In Figure 2 the differences between the levels of TSP and SRP represent the soluble un-reactive/dissolved 'organic' fraction.

4.2 The phytoplankton

4.2.1 General abundance (chlorophyll α concentrations and total numbers)

From the above considerations, a sparse phytoplankton would be predicted. Figure 3 shows that this is the case, with total biomass expressed as chlorophyll α concentration rarely exceeding $4 \mu\text{g l}^{-1}$. The data in this Figure also suggest that:

- the cage site does not seem to effect a consistently higher algal crop in its vicinity, compared to the levels recorded at the other 2 stations
- levels of phytoplankton in the N.E. Bay are often significantly different from those measured at the other 2 sites (but neither consistently higher nor lower).

The pigment levels are generally in keeping with the measurements of particulate P (Figure 4), assuming a ratio of approximately 1:1, but bearing in mind that (i) the PP fraction includes all suspended matter e.g. detritus and animal plankton, in addition to phytoplankton, and (ii) that the chlorophyll analysis used here, is likely to overestimate algal biomass, as no correction has been made for the presence of phaeo-pigments (chlorophyll breakdown products) that also have an absorbance peak at 665 nm.

The biomass levels described above are indeed, low; they are similar to those recorded in Scotland's 'classic' oligotrophic waters such as Morar and Shiel (Bailey-Watts and Duncan 1981), and thus contrast with the values of $10\text{-}10^2$ μg chlorophyll *a* l^{-1} reported for e.g. Leven (Bailey-Watts *et al* 1990) and Coldingham (Bailey-Watts *et al* 1987). Nevertheless, the number of phytoplankton organisms in Loch Dee usually exceed 5×10^3 ml^{-1} and, occasionally, 20×10^3 ml^{-1} (Figure 5).

4.2.2 Types of organism recorded

One of the major features of the Dee phytoplankton is the predominance of very small species. This is illustrated by the 3 plots in Figure 6. If the size classificatory scheme introduced by Sieburth, Smetacek and Lenz (1978) is followed, Loch Dee is primarily characterised by a mixture of 'picoplankton' ie of organisms 0.2 to 2.0 μm width. Small size is in keeping with the high numbers-low chlorophyll situation described above. Comparatively large species are encountered, but these are rare e.g. the desmid *Staurodesmus triangularis* (Lagerheim) Teiling var. *parallelus* (Smith) Thom; and *Euastrum oblongum* (Grev.) Ralfs, the cryptoflagellate *Cryptomonas* (consisting of at least 3 forms here) and even the colonial green algae *Botryococcus* and *Sphaerocystis*, and cyanobacteria such as *Gomphosphaeria* and *Aphanothece*. The large forms are also usually less significant than the assemblages of small species in terms of biomass, although important pulses of the colonial diatom *Tabellaria flocculosa* (Roth) Kütz., perhaps associated with the surfaces of the fish-cage framework in open water, do occur. Generally a little more numerous are comparatively 'large' chryso-flagellates - but these are due to the large overall dimensions of their loricas; for example a single cell of *Dinobryon*

suecicum var. *longispinum* Lemm. is ca 8 μ m, *Chrysolikos planktonicus* Mack is ca 15 μ m and *Diceras* species are ca 35 μ m. These last 3 types are depicted in Figure 7 to illustrate how such forms extend the range of size and skew the frequency distribution it to the right. The most numerous organisms forming the main body of the distribution in Figure 7, are small Chrysophyceae. These are mainly flagellated forms as depicted, and virtually pure stands of *Ochromonas* species (bi-flagellate with both flagella visible) and *Chromulina* (bi-flagellate but in which normally only 1 flagellum is visible) have been recorded.

The specific identify of many of these organisms has not yet been checked. The authors' preliminary consultation with far better taxonomists than themselves, suggest that definitive identifications are going to be very difficult to achieve.

4.2.3 Ecological considerations

Of numerous factors of relevance to an understanding of the ecology of phytoplankton in L. Dee, the following would appear to be of major importance: low nutrient levels, the reported shift in *Daphnia* abundance, and the flushing regime.

It is plain that the Loch Dee phytoplankton is a complex assemblage. Many of the 'pico-flagellates' are likely to be mixo-trophic, i.e. capable of augmenting their growth requirements by phagotrophy; this means that they are not solely dependant on photosynthesis and thus the light and nutrient resources supporting that process.

While enumerating the phytoplankton the abundances of other small organisms such as ciliates (e.g. *Strombidium/Halteria* types), and rotifers have been recorded. It is possible that energy pathways deriving from inputs of dissolved and particulate organic matter, and involving microbes and mixotrophic organisms, are as important in the nutrient-poor Loch Dee as the more 'traditional' primary photosynthetic algae and consumer species.

If the maximum population densities of *Daphnia* reported by Morrison (Mr B Morrison - *pers. comm.* see section 2.5) can be considered as representative of the loch as a whole at these times, the impact of this animal on phytoplankton abundance is likely to be considerable. Firstly, the abundance is of the same order as the maxima recorded in some years in much richer waters, where the impact of selective grazing (removal) of smaller algae, on the size distribution of the phytoplankton, and on the succession of species classified in size terms, is very marked (Bailey-Watts 1986; Bailey-Watts *et al* 1990). Bear in mind, too, that another fairly large, herbivorous cladoceran - *Holopedium* - attains concentrations of many tens of individuals l^{-1} on occasions. Most of its peaks are followed closely by a pulse of the carnivorous, raptorial cladoceran *Leptodora kindtii* Focke, which may be preying on *Holopedium*. It appears that, after *Leptodora* declines, *Daphnia* increases. In this connection, the densest population of *Daphnia* recorded by Morrison - ca $20 l^{-1}$ in mid-winter 1989/90 - corresponds to one of the lowest phytoplankton densities measured (see Figure 5), but a crop still consisting mainly of small phytoplankters, and picoplankton rather than nanoplankton. The feeding mechanism of Daphniidae is extremely complex (Fryer 1991), but a preference for 'small' algae is probably generally true for many species of *Daphnia*. It would be of interest to know whether the 'pico' forms prevalent in Loch Dee

represent a size category not preyed on so intensively by such animals, as these cells are so small.

However important the issues on nutrient status of the water, and the composition of the zooplankton. The rapid flushing can be considered as being of overriding significance in the ecology of Loch Dee. Indeed, the title of the paper by Tervet and Harriman (1988) draws attention to this factor. While it reflects a large runoff of water from the drainage area, this brings about a fairly dilute medium of particles and of solutes in the feeder streams; flow-weighted phosphate and nitrate concentrations, for example, range from around 3 to 10 $\mu\text{g P l}^{-1}$ and 170 to 290 $\mu\text{g N l}^{-1}$. Moreover, considered in relation to other well-studied lochs, the water is apparently passing through Loch Dee at a high rate. How then, are prodigious concentrations of some of the planktonic organisms achieved? For example, a pure stand of *Ochromonas* was recorded on 7 September 1988, when a population of some 12.5×10^3 cells ml^{-1} was estimated. On the previous sampling date - 17 August - the population density of this organism was *ca* 0.5×10^3 ml^{-1} . A net increase of approximately 12×10^3 cells ml^{-1} occurred in the intervening 21 days; this increase alone requires a doubling time of only 4.5 days. But, over this period, assuming an average hydraulic retention time of *ca* 52 days, some 40% of the water, including algae, will have passed out of the loch. As a consequence, the actual growth rate of such organisms would need to have been $2\frac{1}{2}$ times greater than observed, i.e. 4.5/2.5 or 1.8 days. Such rapid growth would seem unlikely, since it exceeds values obtained for similar species in batch culture i.e. where there are no outflow or grazing losses, or shortages of nutrient and/or light resources. Over the period in

question, it would therefore appear that the water resided in Loch Dee for longer than the mean retention time suggests.

5. CONCLUDING DISCUSSION WITH SPECIAL REFERENCE TO FUTURE STUDIES.

This investigation of the ecology of Loch Dee, albeit preliminary, and using phytoplankton as a central focus, has identified a number of issues worthy of further consideration. This section deals firstly with aspects that should be addressed with reference to existing data, and secondly, with new projects to fill other gaps in knowledge.

5.1 Further analysis of existing data

The water balance data obtained by the Solway RPB (see e.g. Lees 1988, 1990) should be further examined, with the view to resolving p values on a monthly basis; then, the records of nutrient and major ion levels, and of phyto- and zoo-plankton abundances, may be better interpreted. Certainly, the recent work on Loch Leven, focusing on p after many years neglecting this factor, has proved vital to a fuller understanding of how that complex system functions (Bailey-Watts *et al* 1990).

The preserved phytoplankton samples on which this report is based, should be further examined in order to improve on the identification of many of the organisms observed. There are even types that have formed comparatively dense populations, which have not been properly assigned to the 'correct' algal Family, let alone genus or species.

5.2 Proposals for new studies

New work at Loch Dee, which would nevertheless, enhance our understanding of the dynamics and interrelationships of plankton components generally,

include studies of the nutrient requirements, and feeding interactions of the picoplankton, protozoal organisms, rotifers and micro-Crustacea.

However, new approaches within the 2 main areas identified in section 5.1 are perhaps the most urgently required - flushing and picoplankton.

Flushing rate studies should address the question as to the representativeness of the p values calculated so far to the water mass of L. Dee as a whole. For example, does water flowing in from the Green Burn, come more or less immediately within the influence of the nearby outflow, and so 'short-circuit' out of the loch? And, as a consequence of this, does water in the main, deeper, western bay of the loch, reside there for a correspondingly longer period than the theoretical average retention value suggests?

The other area of work which is much needed concerns the basic taxonomy, biology and autecology of the picoplankton. Using cultures, the identity, major environmental requirements and features of the growth of these organisms would be attempted.

6. ACKNOWLEDGEMENTS

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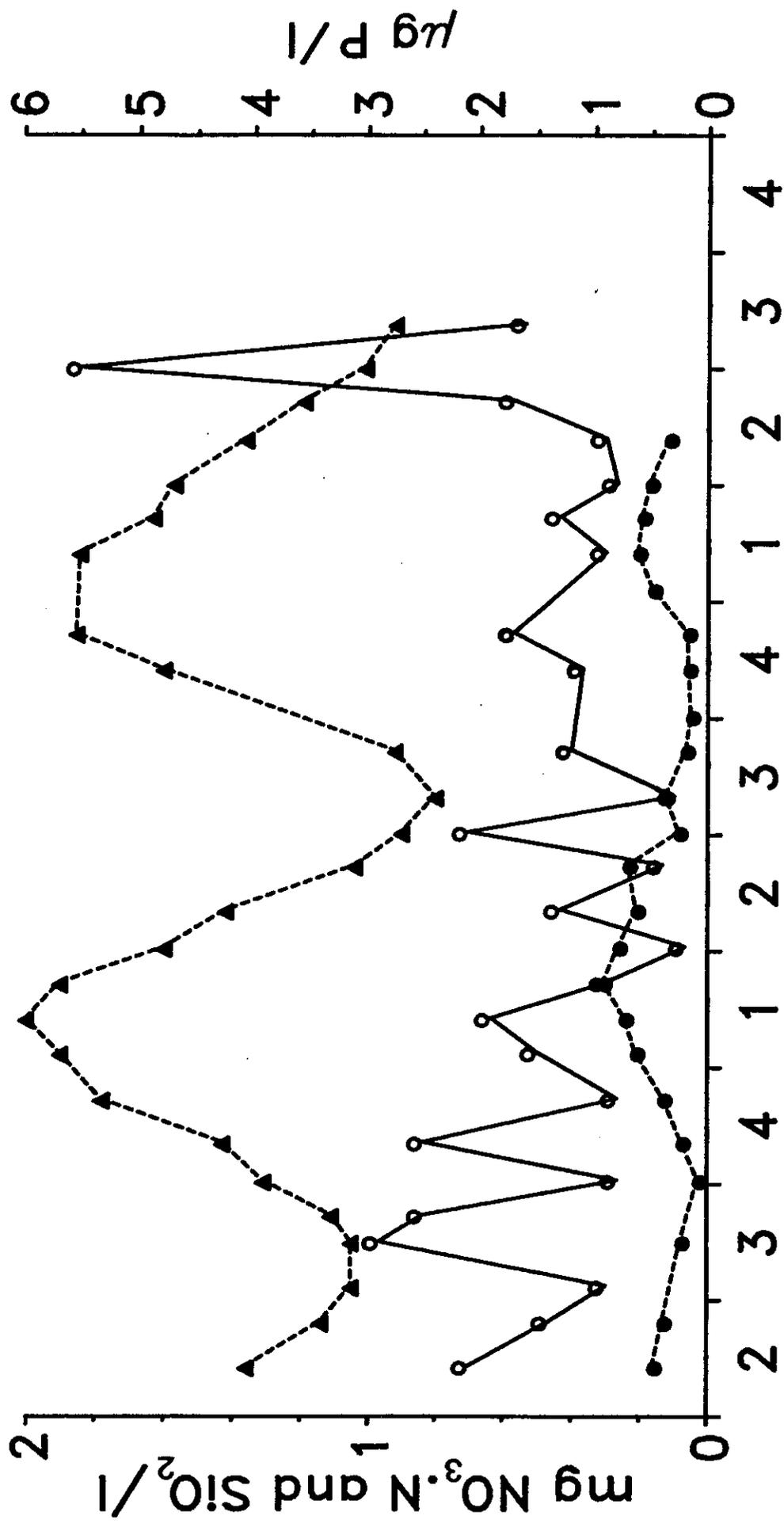
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8. FIGURES

Figure 1. Fluctuations in the concentrations of
3 main phytoplankton nutrients in Loch
Dee, May 1988 to August 1990.

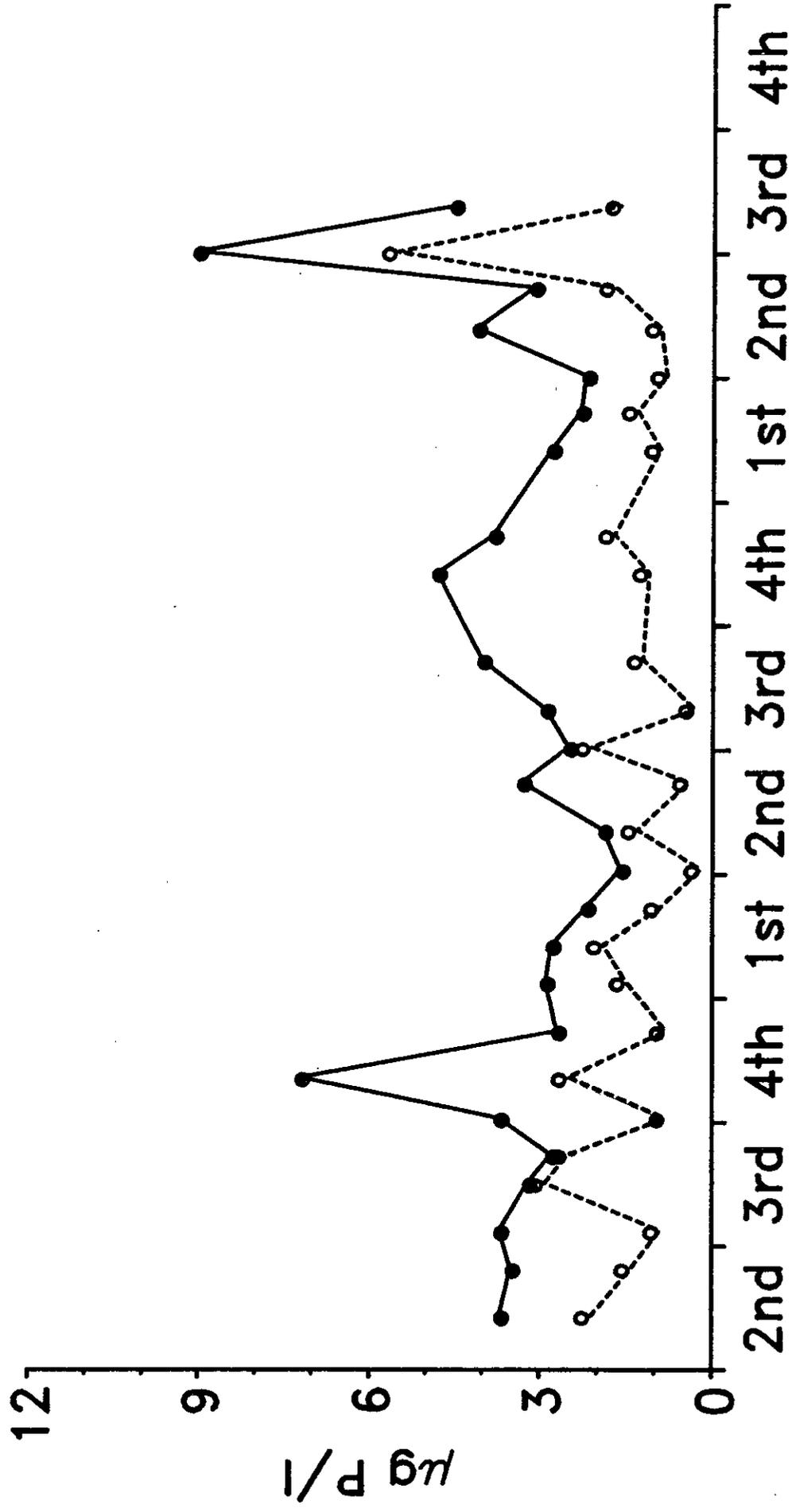
Nutrients in Loch Dee open water:
 nitrate-N (●), sol.react. P (○) and silicate-SiO₂ (▲)



quarters of the years 1988-1990

Figure 2. Changes in the concentrations of total soluble phosphorus and the soluble reactive component, in Loch Dee, May 1988 to August 1990; the 'space' between the 2 plots represents the soluble un-reactive/dissolved organic phosphorus.

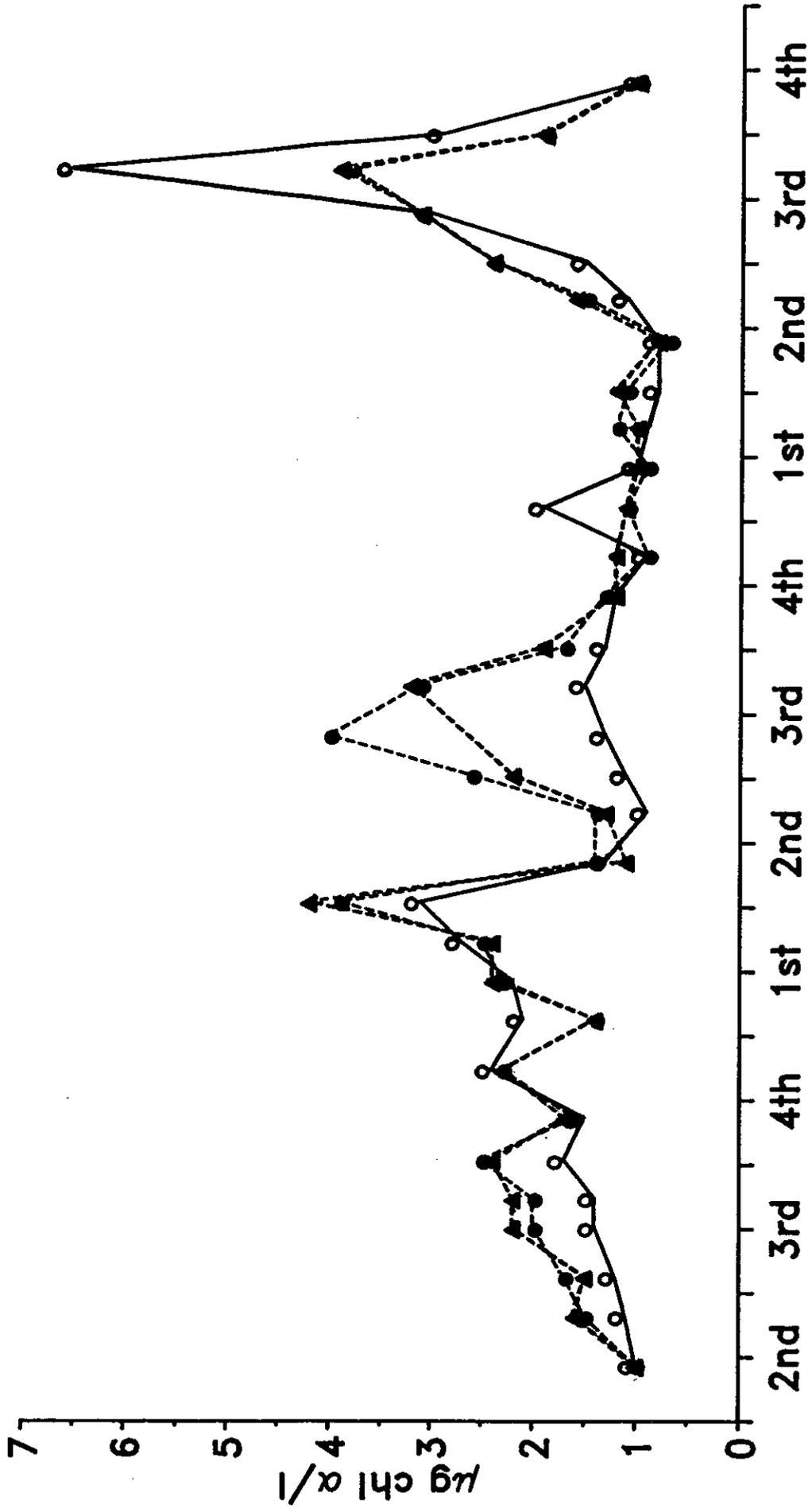
Nutrients in Loch Dee – open water:
total sol. P (●) and sol. react. P (○).



quarters of the years 1988–1990

Figure 3. Chlorophyll *a* levels as an index of total phytoplankton biomass in samples taken from 3 sites in Loch Dee (see text), May 1988 to October 1990.

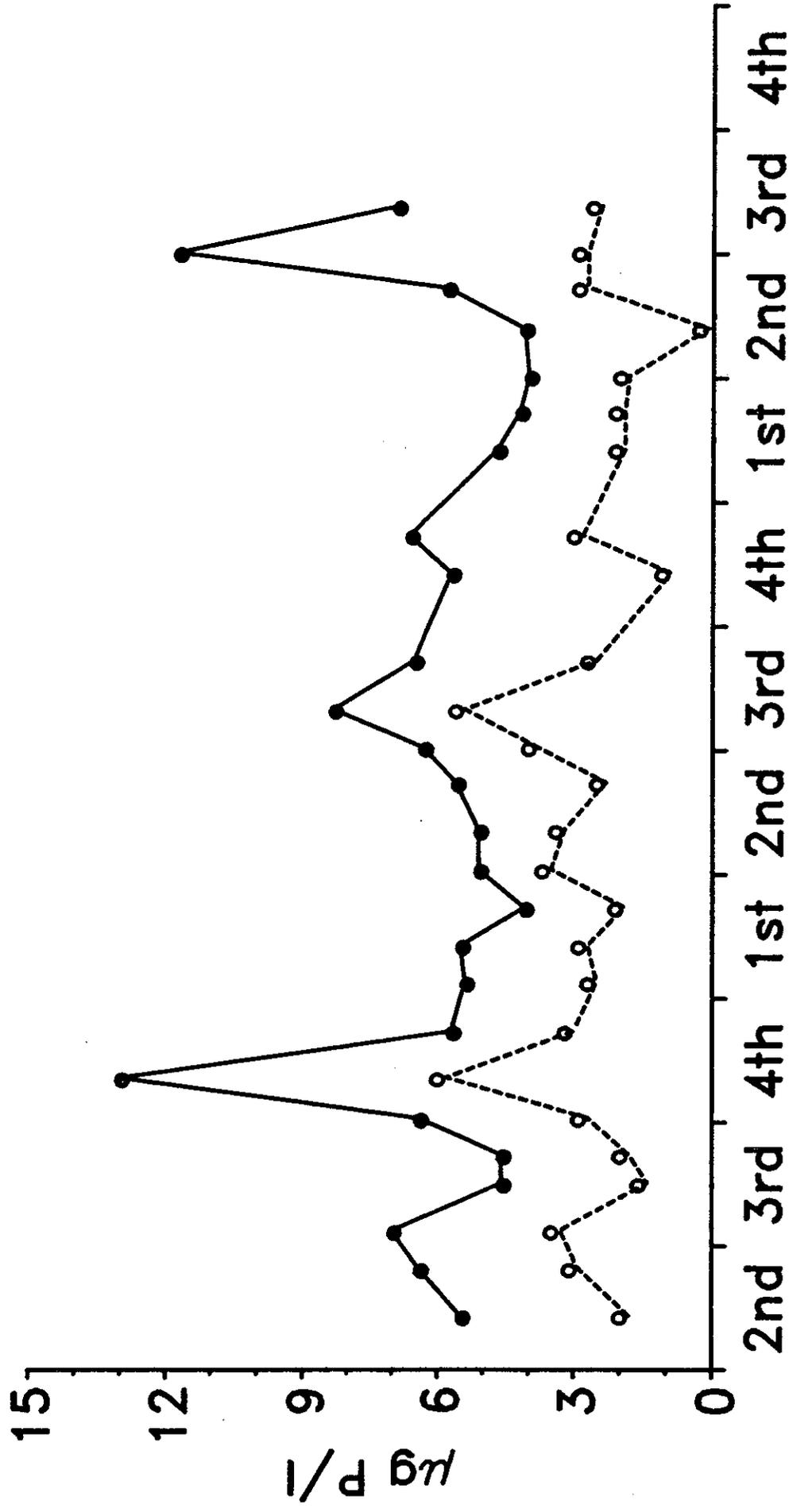
Chlorophyll α in Loch Dee
open water (\circ), N.E. bay (\bullet) and cage site (\blacktriangle)



quarters of the years 1988-1990

Figure 4. The levels of total phosphorus and the particulate component in dip samples of Loch Dee water May 1988 to August 1990; the 'space' between the 2 plots represents the soluble phosphorus (*cf* Figure 2):

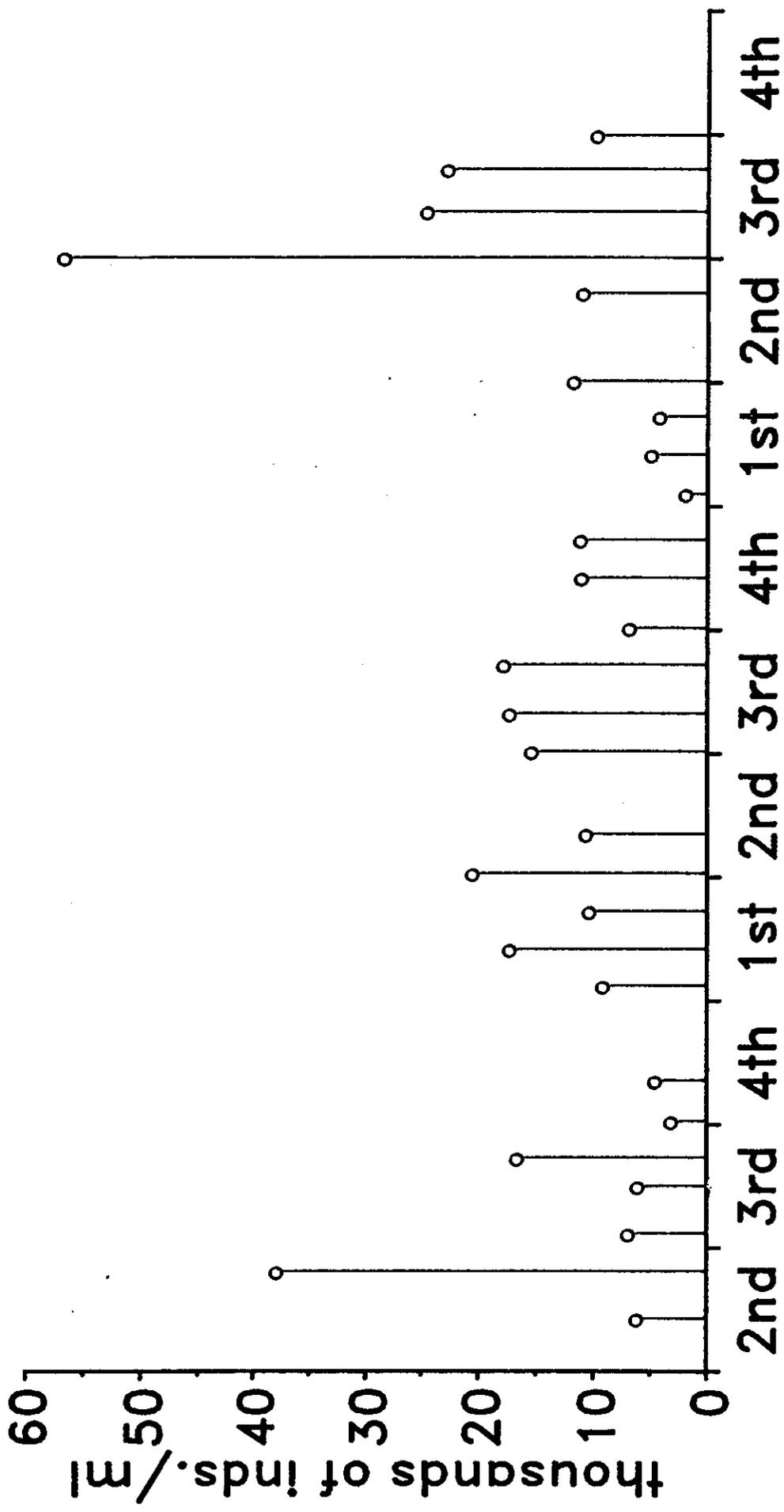
Nutrients in Loch Dee – open water:
total P (●) and particulate P (○).



quarters of the years 1988–1990

Figure 5. The total numbers of phytoplankton organisms per millilitre of surface water in Loch Dee, May 1988 to August 1990.

**Total phytoplankton densities in Loch Dee
open water**



quarters of the years 1988-1990

Figure 6. The size frequency distributions of Loch Dee phytoplankton assemblages sampled in April and August 1989, and in August 1990; the graphs use the procedure of normalised scores (rankits) of Sokal and Rohlf (1969), and, in each of these plots the size values show a distribution skewed markedly to the right..

Size distributions of L. Dee phytoplankton
Apr. 89 (●), Aug. 89 (○) and Aug. 90 (▲)

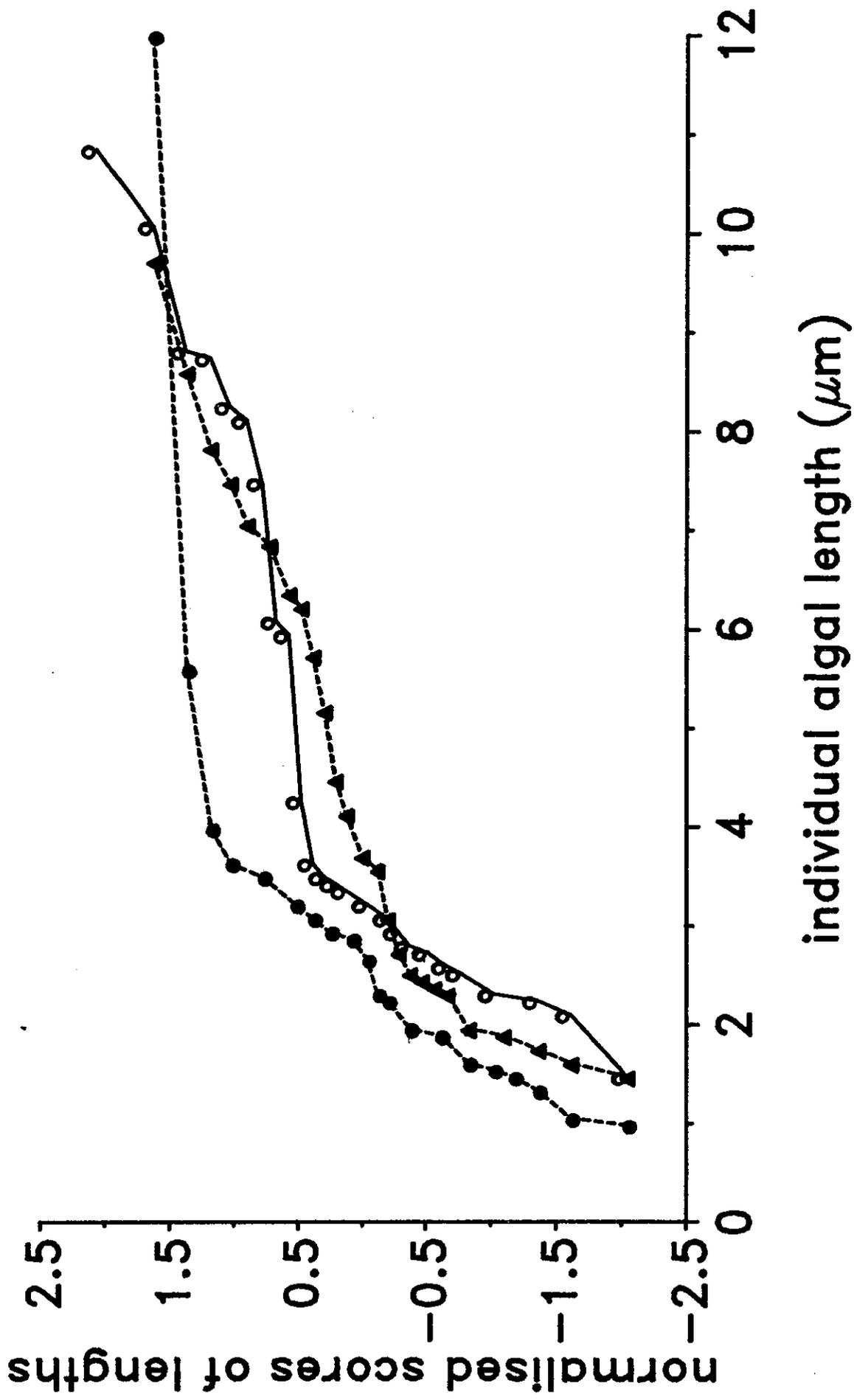


Figure 7. As Figure 6, for the assemblage present in September 1988, and depicting some of the main types of organism present.

