Experimental limnology on four Cheshire Meres

Thesis submitted in accordance with the requirements of the University of Liverpool for the degree of Doctor in Philosophy by Laurence Ravinder Carvalho.

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Abstract

There has been much debate about the relative importance of determination of phytoplankton biomass by nutrients (bottom-up control), usually phosphorus, or by zooplankton grazing (top-down control). In shallow lakes, a major role for grazing has been shown, but as depth increases, nutrients appear to be of greater importance. The importance of grazing also appears to be reduced in eutrophic lakes, as cyanobacteria become more dominant.

Through regular monitoring of water chemistry and plankton populations, this study examined limitation of phytoplankton biomass in four Cheshire Meres: Rostherne Mere, Mere Mere, Little Mere, and Oak Mere. To investigate limiting factors further, experimental manipulations of the lake communities were carried out in enclosures in Rostherne Mere and Oak Mere.

At the start of the study, Little Mere and Rostherne Mere received sewage effluent, which provided quantities of phosphorus far in excess of phytoplankton growth requirements. In these two lakes phosphorus was clearly not important in limiting phytoplankton biomass. Little Mere was seriously affected by the sewage effluent; fish-kills occurred during the summer, allowing huge populations of large, efficient grazers to develop. The large phytoplankton crops that Little Mere could potentially have supported were, therefore, prevented from developing. Following diversion of the sewage effluent in 1991, fish populations may recover, resulting in a reduced zooplankton population and increased phytoplankton crops. However, the well-developed aquatic plant community present in Little Mere may provide a refuge for grazers, allowing them to maintain a large population. Grazing did not appear to be a significant limiting factor in Rostherne Mere. Because of the abundance of nutrients, phytoplankton biomass appeared to be limited by light, although nitrogen may have been of importance during late-summer. Following the sewage diversion, nutrient concentrations may become more important. No clear limiting factor could be identified in Mere Mere or Oak Mere, although

nitrogen appeared to be of greater importance than phosphorus. In Oak Mere, pH appeared to be of importance in combination with nutrients.

There was no evidence to suggest that the high phosphorus concentrations of these lakes were naturally derived; the phosphorus concentrations of Oak Mere and Mere Mere were not exceptionally high, and a detailed nutrient budget for Rostherne Mere revealed that only 2 % of its external phosphorus load could be attributable to groundwater. Consideration of data from other lakes in the region, and comparisons with other lake regions, provide further evidence that the high phosphorus concentrations present in these meres are the result of the effects of long-standing settlements and intensive agriculture on small, relatively shallow lake basins.

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Chapter 1: Introduction

1.1 Introduction

Lakes have long been appreciated for their beauty and amenity value. However, during the latter half of this century, there have been worries over the increasing nutrient status, or eutrophication, of many lakes, and the associated increase in phytoplankton populations, stimulating research into factors that may limit phytoplankton populations. Since the work of Pearsall (1932), when silicate limitation was connected with dramatic declines in diatom populations, a large number of factors have been proposed as limiting phytoplankton biomass in lakes. Initially, with most intensive limnological studies focussed on large, deep lakes, such as those of the English Lake District in Cumbria, the importance of light and nutrients was recognised. However, more recently, a great deal of research has been carried out in shallow lakes, where the significance of zooplankton grazing has become apparent.

There has been much debate about the relative importance of determination of phytoplankton crops by nutrients (bottom-up control) or by zooplankton grazing (top-down control) (De Melo *et al.*, 1992; Carpenter & Kitchell, 1992). Despite the fact that it has become generally accepted that both influences may operate, little information on the relative importance of the coupling between zooplankton, phytoplankton, and nutrients exists.

In shallow lakes, dominated by macrophytes, a major role for grazing has been shown throughout the summer; plants provide refuges for containment of a very large cladoceran

population, despite an abundance of zooplanktivorous fish (Timms & Moss, 1984). Fortuitous, or experimental, removal of fish may also lead to increases in zooplankton and dramatic declines in phytoplankton (Van Donk *et al.*, 1989), and this may be exploited as a restoration technique for improving the clarity of lakewater (biomanipulation) (Shapiro *et al.*, 1975).

As depth increases, zooplankton grazing often appears to be less important than nutrient or mixing mechanisms in the determination of phytoplankton crop-size (McQueen, 1990). Grazing has been shown to be important, in spring, in deep lakes (Luecke *et al.*, 1990), but it plays an uncertain role later in the year after the young-of-the-year fish have become large enough to feed on crustacean zooplankters.

The importance of grazing by zooplankton may also be reduced in eutrophic lakes. In these lakes cyanobacteria frequently dominate, and because of their size (Burns, 1968), toxicity (Lampert, 1981), poor nutritional value (Arnold, 1971), or combination of these factors, they are often considered an unsuitable food for zooplankton. In very eutrophic lakes light may limit the size of the summer phytoplankton crop (Talling *et al.*, 1973).

One group of lakes in the north-west midlands of England, may help shed some light on these issues, as they cover a range of depths, nutrient status, and importance of plant dominance.

1.2 The study area

The North-West Midland Meres are a large association of lakes that lie over the Shropshire-Cheshire plain (Fig. 1.1). There are over sixty lakes exceeding 1 ha in area in this lowland drift

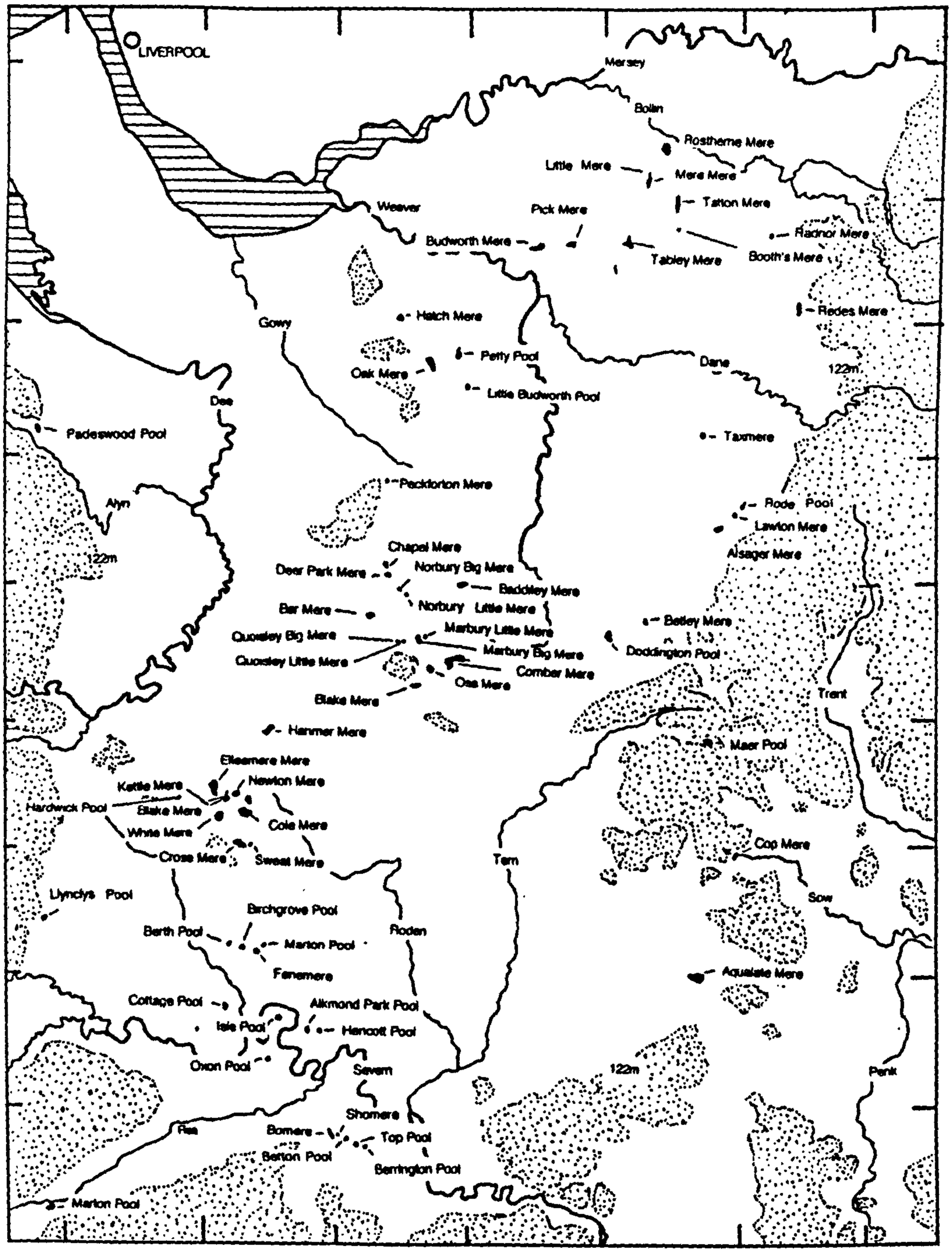


Fig. 1.1. The North-West Midland Meres.

plain, which was mostly laid down on the retreat of the last phase of the Devensian, about 13000 years ago. Most of the meres were probably formed in kettle holes, when ice-blocks, buried in the drift, melted. Others are moraine dammed, and some may have arisen from subsidence of the land, following dissolution of underlying salt deposits (Tallis, 1973). Some of the basins have completely filled in with vegetation and have succeeded to raised bog.

The meres have been described as Britain's naturally eutrophic lakes (Reynolds & Sinker, 1976) in contrast to the more oligotrophic lakes of the Cumbrian Lake District, and some of them are reported to have supported cyanobacterial blooms at least since the nineteenth century (Phillips, 1884). However, records from the nineteenth century (Leighton, 1841) also reveal that plants, such as *Lobelia dortmanna*, a species characteristic of waters with low nutrient concentrations (Palmer *et al.*, 1992), have disappeared from several of the meres. It, therefore, appears likely that further eutrophication has occurred in the region.

The limnology of the meres was reviewed in detail by Reynolds (1979) who suggested that, relative to algal growth requirements, nitrogen appeared to be scarcer than phosphorus, but, because of the meres', apparently, naturally-occurring, nutrient-rich water, the phytoplankton biomass may be light-limited, and only rarely nutrient-limited. There have been studies of the seasonal periodicity of the water chemistry (Reynolds & Allen, 1968; Grimshaw & Hudson, 1970; Reynolds, 1971), phytoplankton populations, (Pearsall, 1923; Lind, 1944; Belcher & Storey, 1968; Swale, 1968; Reynolds, 1973; 1978a;

Reynolds & Allen, 1968; Reynolds & Bellinger, 1992), and zooplankton populations (Galliford, 1954; Reynolds, 1978b) in a few of the meres, but, no intensive study of these three aspects has been carried out simultaneously.

1.3 Limitation of phytoplankton

A number of factors can control the distribution, size, and species composition of phytoplankton populations. The persistence of a population can be explained in terms of differences in growth rates, affected by light, nutrients, and temperature, and loss rates, influenced by factors such as, flushing, parasitism, sedimentation, physiological death, and grazing

1.3.1 Nutrients limiting algal growth

The concept of growth-limiting factors was first described by Liebig (1840), with his "Law of the Minimum", which essentially stated that the development of a population is regulated by the substance occurring in minimal quantity relative to the requirement of the population. It was graphically represented by O'Brien (1972), who termed it Type I growth, where growth proceeds at a constant rate independent of nutrient concentration, but the final yield increases with increasing availability of the limiting nutrient (Fig. 1.2a). He distinguished this from Type II growth, where the growth rate increases with increasing concentration of the limiting factor (Fig. 1.2b). The difference between Type I and Type II growth was demonstrated by Schindler (1971), who compared the effects of nutrient enrichment on production rates and on

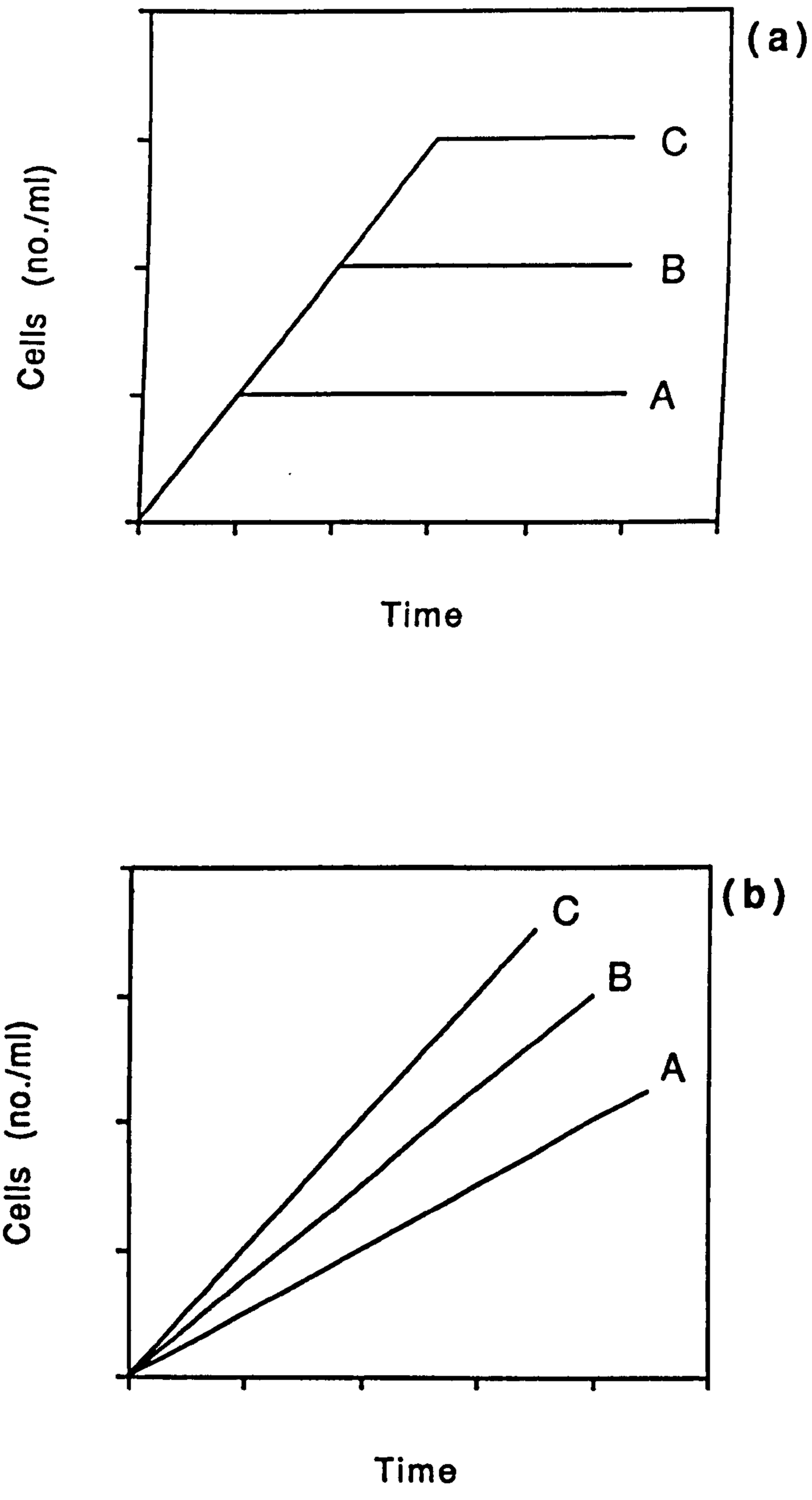


Fig. 1.2. (a) Type I growth, and (b) Type II growth. The ordinate is a logarithmic scale. Increasing concentrations of the limiting factor are represented by A, B, and C. Taken from O'Brien (1972).

phytoplankton standing crops. In laboratory bioassays, lasting four hours, he found that the greatest increase in primary productivity (i.e. growth rate) resulted from addition of carbon. Phosphorus and nitrogen additions caused little and no response respectively. However, in experiments lasting several weeks, in isolated, *in situ* water columns, phosphorus enrichment led to increased standing crops, whereas additions of carbon and nitrogen had no effect.

O'Brien (1972) believes that in many laboratory experiments, one rate-limiting factor is in such a low concentration that it obscures the effects which a change in concentration of other potentially limiting factors could have on the algal growth rate. In the experiments carried out by Schindler (1971) the concentration, or form, of carbon in the culture medium could have had such an effect. Another possibility is that the duration of the experiment affected the results; despite the possibility of carbon limitation of growth rates in the short-term, over several weeks the biomass may be limited by another factor that is not replenished so quickly, such as phosphorus. This would mean that only resource-addition experiments followed by relatively long-term observations of the dynamics of the major species would unequivocally demonstrate which, if any, resources were limiting phytoplankton biomass in lakes.

Many nutrients have been shown experimentally to limit phytoplankton growth in natural waters, including phosphorus (Schelske & Stoermer, 1972; Schindler, 1974), nitrogen (Talling

& Talling, 1965; Moss, 1969), carbon (Allen, 1972; Kerr *et al.*, 1972), silicon (Lund, 1954), and trace metals (Goldman, 1960).

Phosphorus is the element most likely to limit algal growth in freshwaters because of its scarcity relative to the requirements of algae and the availability of other nutrients (Hutchinson, 1957). Phosphorus supply is commonly considered to be the major cause of eutrophication, and that it is a factor limiting phytoplankton biomass in lakes has been shown by laboratory enrichment experiments (Moss, 1972), algal bioassays (Lund *et al.*, 1975), *in situ* experiments (Schindler, 1971), and whole-lake enrichment experiments (Schindler & Fee, 1974), not to mention significant correlations between total phosphorus and chlorophyll *a* concentrations for large sets of lakes (Dillon & Rigler, 1974).

The role of carbon in limiting phytoplankton biomass in a lake has been the subject of much discussion (King, 1970; Schindler, 1971). It is now generally agreed that it is only in extremely enriched lakes that carbon may limit the standing crop of phytoplankton (Lehman *et al.*, 1975). However, it has been shown to be an important factor in determining phytoplankton community composition (Talling, 1976; Shapiro, 1984; Williams & Turpin, 1987).

Nitrogen has been shown to limit phytoplankton biomass in areas where rocks particularly rich in phosphate occur, such as in East and Central Africa (Talling & Talling, 1965; Moss, 1969), and potentially in areas where the water has become enriched with sewage effluent, which has a low N:P ratio. Reynolds (1979) suggests that, unlike most other British waters, phytoplankton production in the North-West Midland Meres is

more likely to be controlled by the availability of nitrogen, rather than phosphorus. He suggests that the relative richness of phosphorus seems natural, and may be due to deposits of apatite, a phosphate-rich mineral, in the drift. Schindler (1977) suggests that even where nitrogen is scarce, the growth of nitrogen-fixing cyanobacteria will quickly reverse the situation bringing phosphorus back into prime importance.

Although all phytoplankton have a requirement for silicon, it is only chrysophytes, and diatoms in particular with their silicate cell walls, that the requirement is potentially limiting. There are many examples in the literature of the restriction of diatom population growth associated with declining concentrations of dissolved silicate (Lund, 1950; Bailey-Watts, 1976, Gibson, 1981). Silicon-limitation is usually followed by a decline in diatom biomass, either through mortality (Lund, 1950), or through an increased sedimentation rate (Gibson, 1981).

There are also many micro nutrients, required only in low amounts, including several 'trace metals', such as iron, manganese, molybdenum, copper, and zinc, which may be toxic if present at higher concentrations. Their role in limiting phytoplankton biomass is uncertain because of their speciation and chemical transformations in natural waters. Their supply to algae is regulated by organic chelating agents which maintain the metals in solution. Their solubility increases in acid conditions, making them potentially toxic in very acid environments.

All these nutrients will affect different species in different amounts; diatom crops may be limited by silicate, nitrogen-fixing cyanobacteria by phosphorus, or a trace element essential to N-fixation, such as molybdenum, whilst other species may be limited by phosphorus. However, potential upper limits of growth may never be reached because of loss processes, which again affect different species by different amounts, and may in fact be the dominant factors limiting the phytoplankton population.

Because of the complexity of the phytoplankton community, it will show an average response, based on the responses of each individual cell to all these factors. The community response will, therefore, be most affected by the species dominating. It is often practical, therefore, to define a factor as not limiting if an increase in that factor produces no significant stimulation in population growth (Gibson, 1971), or where factors affecting loss rates are important, the opposite will be true.

1.3.2 Approaches to examining limitation

Three basic approaches have been used in studying limiting factors:

(1) Measurement of the nutrient concentrations in the lake

The nutrient content of the water is measured and limitation by the nutrient in shortest supply, relative to its requirements, is inferred. However, chemical methods may be too insensitive to measure the low concentrations of nutrients which are available to growth. There is doubt also as to whether the chemical methods are really measuring nutrients available

to growth; this is particularly true for phosphorus (Lean & White, 1983). It has also been shown that algae take up nutrients in excess of their requirements (luxury uptake), so measures of dissolved nutrients may underestimate the algal growth potential (Mackereth, 1953). Despite these doubts, nutrient concentrations in a lake can still suggest which nutrient is most likely to become limiting first. This is based on the fact that algal cells require elements in relatively fixed proportions, in a atomic ratio of C:N:P of approximately 106:16:1 (about 42:7:1 by weight) (Redfield, 1958). However, the fact that the ratio varies between algae (Rhee & Gotham, 1980) has led to various N:P ratios being used to suggest nitrogen or phosphorus limitation. The critical ratio used generally ranges from 10-16:1 (by weight) (Golterman & Kouwe, 1980). For this reason, in this particular study phosphorus-limitation will be considered more likely than nitrogen-limitation if the ratio is greater than 16:1, and nitrogen-limitation will be considered more likely than phosphorus-limitation if the ratio is less than 10:1.

(2) Measurement of cell contents or nutrient uptake kinetics

A lowered cellular content of the limiting nutrient (Droop, 1974) is a general response to nutrient limitation, however, other factors, such as temperature, light, and luxury uptake, can also affect the cell composition. Carotenoid to chlorophyll *a* pigment ratios, have been linked to nitrogen supply (Watson & Osborne, 1979), as nitrogen-limited green algae produce large quantities of the carotenoid astaxanthin (Dersch, 1960), whilst, in common with other algae limited by nutrients, they also lose chlorophyll (Healey, 1978). A high ratio is, therefore, indicative

of nitrogen deficiency, except in the presence of nitrogen-fixing cyanobacteria.

Nutrient limitation may also induce the potential for a high uptake rate of the nutrient concerned. High alkaline phosphatase activity indicates phosphorus deficiency and nitrogen-deprived phytoplankton have higher dark uptake rates of nitrogen than nitrogen-sufficient phytoplankton (Fitzgerald, 1969). These latter two indicators of nutrient-limitation are less affected by environmental factors than the cellular content of nutrients (Zevenboom *et al.*, 1982). However, they are only useful if one species is predominant, and not if the phytoplankton community is composed of several abundant species.

(3) Bioassays

Two types of bioassay techniques are used to assess nutrient shortage to phytoplankton: primary production methods (^{14}C) (Gerhart & Likens, 1975) and batch bioassay. In the primary production method, the additional amount of ^{14}C incorporated in a culture with added nutrient, or combination of nutrients, is compared with a control culture. In the batch bioassay, the additional amount of chlorophyll *a* in a culture with added nutrient is compared with a control culture.

There are two major variants of bioassay:

i) nutrients are added to filtered lake water in which laboratory cultured species are inoculated (Lund *et al.*, 1975).

ii) nutrients are added to lake water containing the natural phytoplankton community (Reynolds & Butterwick, 1979).

The first variant allows the results from different lakes to be easily compared. However, it cannot be used to evaluate the *effects of limiting factors on species* composition and succession in a lake as it is based on the response of only one species.

The second variant has been carried out over time scales varying from a few hours (Goldman, 1960) to several months (Reynolds & Butterwick, 1979) and on a scale varying from enrichment of lake water contained in flasks (Moss, 1969), enclosures (Vanni, 1987), up to the experimental enrichment of whole lakes (Schindler & Fee, 1974).

1.4 Aims of the study

Through regular monitoring of water chemistry and plankton populations, and surveys of the aquatic plant populations, the study aimed to identify the reasons for the seasonality of the phytoplankton populations, and, what factors were of importance in limiting phytoplankton biomass in four Cheshire meres: Rostherne Mere, Mere Mere, Little Mere, and Oak Mere. The four sites were chosen largely on their proximity to Liverpool and the relatively good background information available on their past phytoplankton populations, enabling comparisons to be made with the present study. The four lakes also covered a range of depths and nutrient status.

Even closely timed observations, however, are often insufficient to identify which factors are limiting the phytoplankton species composition and biomass, as any observed net change in population abundance results from a balance of gains and losses. Therefore, experimental manipulations of the lake communities, in enclosures, were

carried out, to attempt to clarify which limiting factors were of greatest importance.

The study also covered a period of change in the management of the catchment of two of the lakes: Little Mere and Rostherne Mere. Detailed water and nutrient budgets were made for Rostherne Mere, to examine the major sources of nutrients to the lake, and to predict the future water quality following the changes in the catchment.

Chapter 2: Rostherne Mere

2.1 Introduction

Rostherne Mere has long been considered eutrophic, algal blooms being referred to as far back as the sixteenth century (see Griffiths, 1925). Brinkhurst & Walsh (1967) suggested that faecal inputs from the large, resident bird population may be responsible for the eutrophic state (guanotrophy), although, Reynolds & Sinker (1976) believe that it may be the natural state of many of the North-West Midland Meres.

Rostherne Mere is part of a series of three lakes, Mere Mere, Little Mere, and Rostherne Mere, in the north of the Cheshire Plain, which are connected by Rostherne Brook. The latter two lakes received treated sewage from Mere Sewage Treatment Works (STW). Rostherne Mere also received a small flow of effluent from the village of Rostherne. Little Mere has been severely affected by the sewage effluent and is discussed in Chapter 4, along with Mere Mere. This chapter makes an assessment of the impact of the sewage effluent on Rostherne Mere and examines what factors may limit the phytoplankton biomass. Future changes in the lake are discussed following closure of the STWs.

2.1.1 Site description

The Rostherne Brook catchment is shown in Figure 2.1. Rostherne Brook rises on Tabley Moss, and drains into the southern end of Mere Mere. Water enters Little Mere, from Mere Mere, over a concrete sluice at its southern end, and flows out at the northern end. Rostherne Brook then continues for about 2

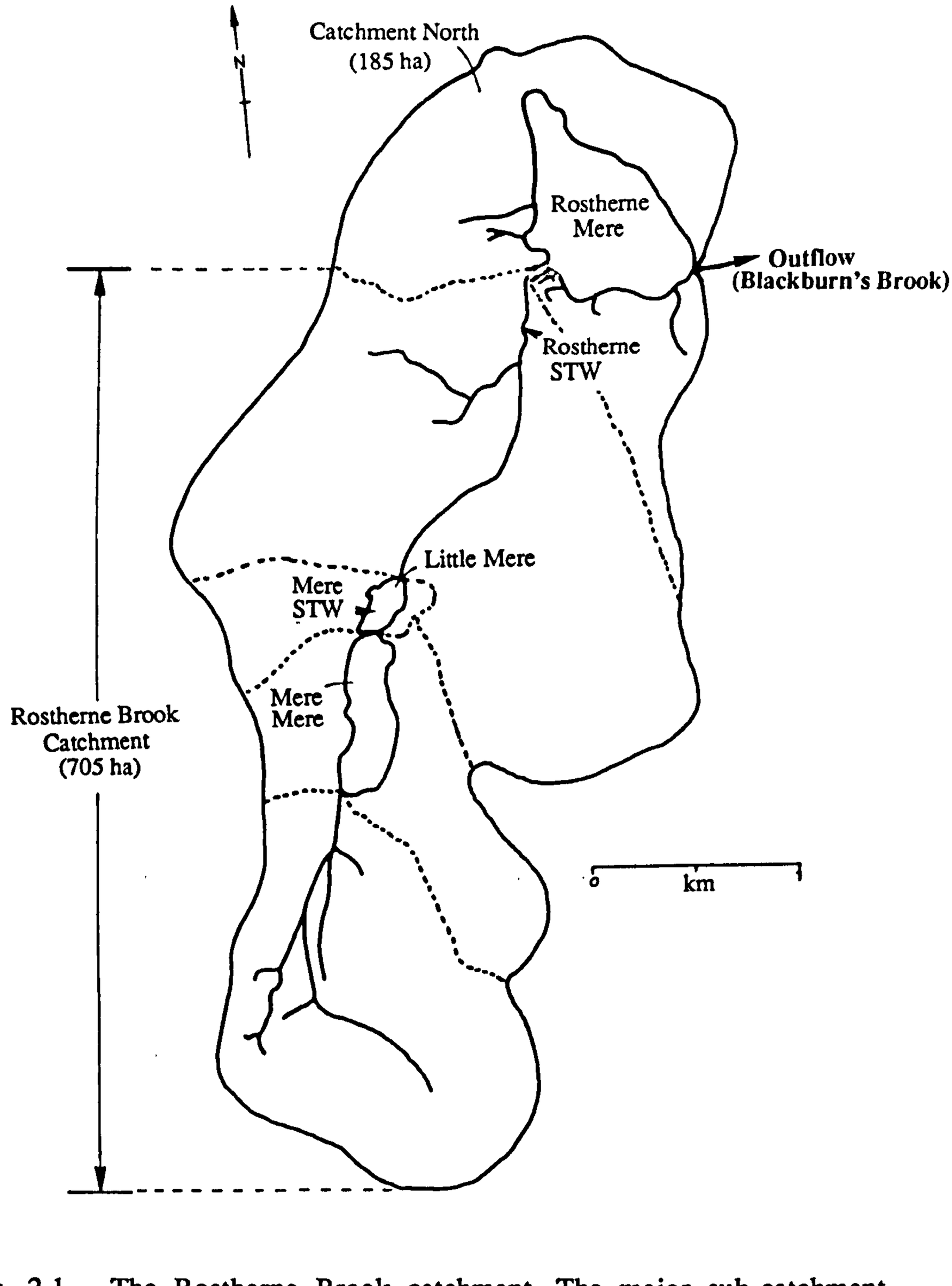


Fig. 2.1 The Rostherne Brook catchment. The major sub-catchment divisions (Rostherne Brook and Catchment North) are shown by dotted lines. Inputs of sewage effluent are also indicated.

km before entering Rostherne Mere. As Fig. 2.1 shows, the brook drains about 7 km^2 of the 9 km^2 catchment of Rostherne Mere. There are several other short streams, springs, and transitory drainage ditches that flow into the lake, draining small areas of the catchment. The most significant of which is a spring in Harper's Bank Wood, on the west side of the lake (Fig. 2.2). This appeared to be groundwater fed, from a confined region of an aquifer, as iron and manganese salts were deposited where the spring emerged, suggesting low dissolved oxygen concentrations (Stumm & Morgan, 1981).

The outflow of Rostherne Mere, Blackburn's Brook, flows east from the south-east corner of the Mere, and joins Birkin Brook 1.3 km further on. Birkin Brook flows into the River Bollin which eventually discharges into the River Mersey and Manchester Ship Canal near Warrington. The gradient in the Birkin is very low, and when there is heavy rain the level of the Birkin rises much faster than the level in Blackburn's Brook, as the latter is stabilised by Rostherne Mere. The flow in Blackburn's Brook may then be reversed, the outflow becoming an inflow. This may raise the level of the water in the lake by as much as 30 cm.

Fig. 2.1 also shows the two STWs that, until July 1991, discharged effluent into the system. Mere STW discharged directly into Little Mere, and Rostherne STW, which treated a very small flow from the village of Rostherne, discharged into Rostherne Brook, just before the brook enters Rostherne Mere.

Rostherne Mere (National Grid reference SJ 745 843) (Plate 2.1) is the deepest and one of the largest of the North-West Midland Meres. It is a grade 1 SSSI and became a National

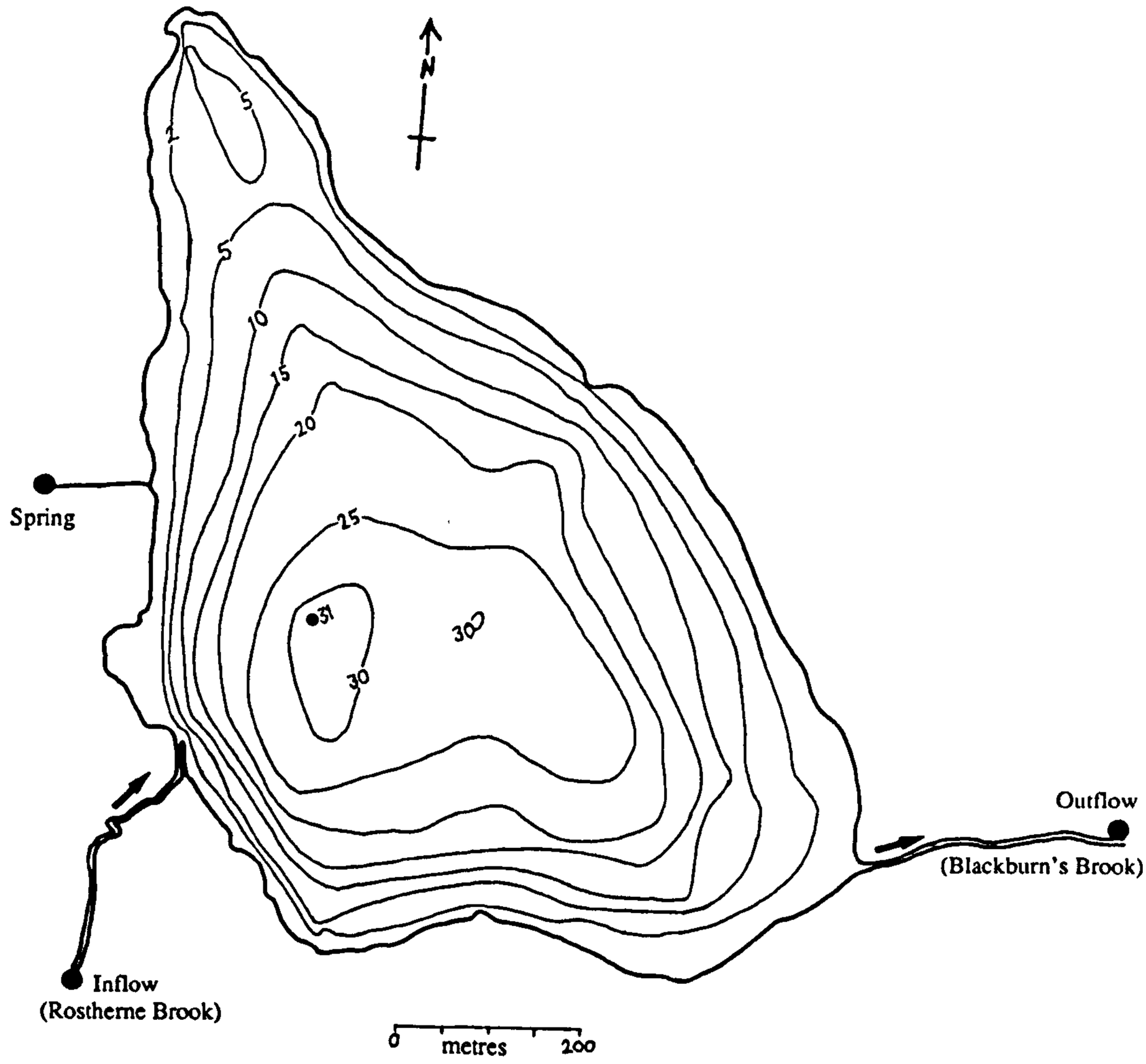


Fig. 2.2 Bathymetric map of Rostherne Mere (taken from Woof & Wall, 1984). Depths shown are in metres. Solid round symbols (•) indicate the sampling points in this study.

Plate 2.1: Aerial view of Rostherne Mere, with Rostherne village in the foreground. (photographed by Bryan Lewis, May 1992)

Nature Reserve in 1961. It is listed under the Ramsar convention as a wetland of international importance as it is an important site for many kinds of wintering wildfowl. It is also an important site for research in freshwater biology, water chemistry, and sediments. There is no public access to the lake to prevent disturbance of the bird populations. The lake is surrounded by pasture, arable fields, and woodland. There are also extensive reed beds around large parts of the margin of the mere and there is a peat bog at its northern end. The lake is situated in a deep hollow in the glacial drift deposits, composed mainly of boulder clay, sands and gravels. The bedrock under most of the lake consists of Lower Keuper Saliferous Beds, with Lower Keuper Red Marl in the northern end (Wall, 1985). The soils surrounding the lake are mainly a mixture of clay and sandy loams (Rogers & Ball, 1974).

Details of the lake are shown in Table 2.1. A bathymetric map is shown in Figure 2.2.

2.1.2 Background to the study

Descriptive accounts of the phytoplankton assemblages for 1912 (Pearsall, 1923), 1922 (Griffiths, 1925), 1941-43 (Lind, 1944), 1962-63 (David, 1963), 1963-66 (Belcher & Storey, 1968), and 1967-89 (Booth, 1988; Reynolds, 1978a; Reynolds & Bellinger, 1992) have been recognised as a most important long-term phytoplankton data set (Elliott, 1990). These data not only provide evidence for the long-standing eutrophic character of the lake, but also appear to show a change in the seasonal succession of the dominant phytoplankton, with a reduction in the importance of the dinoflagellate *Ceratium hirundinella* and a

Table 2.1 Details of Rostherne Mere and its catchment.

	Rostherne Mere
Geographical co-ordinates	53° 20′ N; 2° 23′ W
Altitude (m a.s.l.)	21
Surface Area (ha) [1]	48.7
Maximum Depth (m) [1]	31
Mean Depth (m) [1]	13.6
Volume (m^3) [1]	6.6×10^6
Catchment area (ha)	940
Retention time (year)	1.6

[1] Taken from Woof & Wall (1984).

recent dominance by the cyanobacterium *Microcystis aeruginosa*.

Livingstone's (1979) investigation of the stratigraphic records of the sediment confirmed that the recent shift to increased *Microcystis* occurred around 1958. Nelms (1984) confirmed, through diatom stratigraphy, that there was a shift in the phytoplankton community around this time, and, like Reynolds (1979), believes that the change was due to further enrichment of the mere's nutrient supply, through increased use of synthetic fertilisers. Fertiliser use has particularly increased since the 1950s (Hood, 1982), which could have shifted Rostherne Mere from a state where nitrogen was the limiting factor, to a state where the populations are limited by light, rather than by nutrients (Reynolds & Bellinger, 1992). Brinkhurst and Walsh (1967) hypothesised that the high nutrient concentrations in the lake, (particularly phosphorus) were the result of the large populations of birds that roosted on the lake, contributing large quantities of faecal matter. Loadings from the bird roosts were roughly estimated by Livingstone (1979) to contribute about 10 % of the yearly input of phosphorus. Further enrichment of Rostherne Mere has also occurred through increased loading from the two STW's.

There is obvious concern for the consequences of this further eutrophication on the bird communities utilising the lake, through its effects on the fish and aquatic plant communities. Trout and smelt (*Osmerus eperlanus* L.), recorded in early fish surveys by Tattersall *et al.* in 1912 and Coward in 1922 (see Ellison & Chubb, 1968), have not been caught in more recent surveys (Banks, 1968). The extinction of smelt (Rostherne

Mere was the only site in Britain where there was a landlocked population) has been attributed to eutrophication (Maitland & Lyle, 1992). Several aquatic plant species, including the yellow and white water-lilies, have also disappeared over the last century (Wall, 1985).

Chemical analyses of the water of Rostherne Mere have previously been carried out by Tattersall & Coward (1914), Gorham (1957), Grimshaw & Hudson (1970), and the NWWA. (1983). Unfortunately, there are no accurate pre-1960 data available on the concentrations of nitrogen and phosphorus. Gorham's (1957) figures are based on samples taken in October 1954 which he himself admits "are not highly reliable" as the analyses were not carried out until some weeks after the samples had been collected and filtered. In this time nitrates could be denitrified and phosphates may be absorbed into the container or released from suspended particles. Reynolds (1978a; 1978b; 1979), Livingstone (1979), and Wall (1985) all compared the changes in nitrate concentration between Gorham's (1957) "unreliable" value, measured in October 1954, at the end of the main growth phase of phytoplankton, to the maximum concentration recorded by Grimshaw & Hudson (1970), in April. The comparison, they state, is evidence for the further enrichment of Rostherne Mere. The comparison is, however, unacceptable. The first reliable figures are from the study by Grimshaw and Hudson (1970) in which phosphate was never undetectable, the minimum concentration recorded being 100 $\mu g\ l^{-1}$; nitrate concentrations, however, were undetectable near the end of the summer. Nitrogen, therefore, may have been limiting the growth of certain phytoplankton species.

Nitrogen has been suggested as being an important limiting nutrient in Rostherne Mere pre-1960 (Reynolds, 1978b), and it is still considered to be the limiting nutrient in many other North-West Midland meres (Moss *et al.*, 1992).

Unlike nitrogen, which usually enters lakes from diffuse sources, such as run-off from agricultural land, phosphorus inputs are usually from point sources, such as sewage works. One of the main reasons for the closure of the two STWs in the catchment of Rostherne Mere, was to reduce the loading of phosphorus to the lake, in order to reduce the phytoplankton crop-size (N.W.W.A., 1983).

There may also be internal sources of nutrients, such as nitrogen-fixation by cyanobacteria and the release of phosphate and ammonium from the sediment during anoxic conditions (Mortimer, 1941; 1942). This final source may be important in Rostherne Mere as it is a deep, stratifying lake which, in summer, results in a deoxygenated hypolimnion; the sediments in the deepest parts of the lake have been shown to be permanently deoxygenated (Brinkhurst &Walsh, 1967).

Clearly a detailed monitoring programme of the water chemistry and plankton populations was needed to investigate any claims of further nutrient enrichment and to assess the present state of the mere. To make any reasonable predictions of the impact of the sewage diversion or other management proposals, detailed water and nutrient budgets were also required.

2.2 Methods

2.2.1 Physical factors and water chemistry

Water samples were collected at approximately fortnightly intervals from January 1990 to March 1992. Lake samples were taken from the upper 4 m, using a weighted length of polyethylene hose at a buoy moored at the deepest part of the lake, and were transferred into an acid-washed 1-litre Pyrex bottle. Water temperature and dissolved oxygen concentrations were measured, in the afternoon, using a WTW oxygen meter. Water samples were also taken for analysis from Rostherne Brook, Harper's Bank spring inflow, and the outflow of Rostherne Mere, at the sites shown in Figure 2.2.

Chemical analyses were carried out on return to the laboratory and on the following day. Table 2.2 gives a list of the chemical analyses carried out, the methods used, and their precision. For appropriate analyses water was filtered through glass-fibre filters (Whatman GF/C).

The pH and conductivity were measured on return to the laboratory using a Corning 250 ion analyser and a Jenway 4010 conductivity meter.

2.2.2 Chlorophyll *a*, carotenoids, and pigment ratios

A measured volume of water was filtered through a 4.5 cm diameter GF/C filter. The filter was then ground with sand (AnalaR), 1 ml of 1% magnesium carbonate suspension and 4 ml of acetone. This was then made up to a total volume of 10 ml, with acetone, in a centrifuge tube, and then left in the dark surrounded by ice for 3-4 hours. The mixture was then

Table 2.2 Chemical analyses, methods, and precisions.

Chemical Analysis	Method	Precision
pH	pH electrode	± 0.1 pH units
Conductivity	Conductivity meter	± 0.5 %
Phenolphthalein Alkalinity	Golterman *et al.* (1978)	± 5 %
Total Alkalinity	Mackereth *et al.* (1978)	± 5 %
Nitrate-nitrogen	Mackereth *et al.* (1978)	± 8 %
Ammonium-nitrogen	Chaney and Morbach (1962)	± 4 %
Soluble reactive phosphorus	Mackereth *et al.* (1978)	± 3 %
Total soluble and total phosphorus	Mackereth *et al.* (1978)	± 3 %
Dissolved silicate-silicon	Golterman *et al.* (1978)	± 1-2 %
Chloride	Mohr method (see Mackereth *et al.*, 1978)	± 6 %
Chlorophyll *a* and carotenoids	see 2.2.2	± 5 %

centrifuged at 3630 g for 10 minutes. The absorbance of the supernatant was measured at 750 nm, 663 nm, 480 nm, 430 nm, and 410 nm against an acetone blank in 1-cm cells using a Philips PU 8675 VIS spectrophotometer. The value at 750 nm corrects for any fine colloidal matter (Moss,1967), and was subtracted from each of the other values.

Chlorophyll *a* concentration was calculated from the absorbance reading at 663 nm (Talling & Driver, 1961), as in equation 1:

Chlorophyll *a* (ug l^{-1}) = 110 . Absorbance (663) . $(V)^{-1}$

(Equation 1)

where V = volume of water filtered in litres.

Carotenoid concentrations were calculated from the absorbance at 480 nm (Richards and Thompson, 1952), as in equation 2.

Carotenoids (µspu l^{-1}) = 100 . Absorbance (480) . $(V)^{-1}$

(Equation 2)

The ratio of absorbances at 480 nm : 663 nm potentially gives an indication of the nitrogen status of the phytoplankton. A ratio value >1.3 may indicate nitrogen deficiency (Watson and Osborne,1979). However, the ratio may just be an indication of decomposition products of chlorophyll *a* (by grazing or resuspension of mud), therefore, the ratio of absorbance values at 430 nm : 410 nm was also calculated. For undecomposed chlorophyll *a* (even in nitrogen-deficient conditions) the A430:410 ratio has a value of 1.2 or more. For partly or completely degraded chlorophyll *a*, the A430:410 ratio often falls below 1.0 (Moss, 1967), this therefore enables the reason

for a high A480:663 ratio to be assessed. The exception to the use of these ratios is when nitrogen-fixing species are dominant as nitrogen-limitation does not affect them in this way.

2.2.3 Phytoplankton and zooplankton

Phytoplankton and zooplankton samples were collected at the same time and place as the lake water sample. Integrated samples from the upper 4 m of the water column were taken for phytoplankton, from the mixed water samples. Samples were preserved within 1 hour by the addition of Lugol's solution (Vollenweider, 1969a). Phytoplankton was counted under an inverted microscope (Wild M40 and Zeiss Sedival) at a magnification of 400 x. The most common species was counted to a precision of ±20%; the other dominant species were counted to a precision of at least ±50% (Lund, Kipling, and Le Cren, 1958). Identification was carried out to genus level, or species level, where possible, with the aid of standard works (Bourrelly, 1966; 1968; 1970; Hustedt, 1942; Prescot, 1962). Diatom identification was also carried out by preparing and examining slides of cleaned frustules. Centrifuged cells were digested in nitric acid and then repeatedly centrifuged and washed with distilled water until neutral to pH paper. They were then dried on coverslips (Thickness 0), mounted in Naphrax, and examined under an oil immersion lens (x1000).

Integrated zooplankton samples were collected to a depth of 7.5 m using a 300 μm mesh-size, nylon, plankton net. The zooplankters were promptly narcotized with chloroform water (Gannon & Gannon, 1975) and preserved in a solution of formaldehyde to give a final formaldehyde concentration of

about 4%. Samples were normally sub-sampled, using a wide-bore pipette, and counted under a Kyowa stereo-microscope. When samples were sub-sampled at least 100 of the commonest species were counted (Bottrell *et al.*, 1976). Animals were identified to species whenever possible using standard works (Scourfield and Harding, 1966; Harding and Smith, 1974). Most of the zooplankton in freshwaters are members of three main phyla: Protozoa, Rotifera, and Crustacea. Species in the former two taxa are less than 500 μm in length, and could, therefore, pass through the zooplankton net used for sampling. The adult crustacea are large enough to be caught in the net. All quantitative data are therfore based on this group.

2.2.4 Aquatic plants

Aquatic plants were surveyed in August 1990. Sampling was carried out from a boat using a grapnell and a Petersen grab. Aquatic plants were identified using Haslam, Sinker & Wolseley (1975). Percentage cover of the submerged and floating-leaved communities was estimated from a weighed, photocopied image of the vegetation map.

2.2.5 Water budget

There are several sources and sinks of water to a lake: direct precipitation, surface run-off and drainage from the catchment, sub-surface loss and seepage to and from the groundwater, and evaporation. A water budget can be constructed to balance these processes:

outflow = inputs - evaporation - ∂lake volume (Equation 2.1)

Figure 2.1 shows the two sub-catchment divisions used to calculate the budget: the Rostherne Brook catchment and Catchment North. The catchment areas were measured from the 1:25000 Ordnance Survey map.

A water budget was calculated for four periods of the year: winter to spring, unstratified; early summer, stratified; late summer, stratified; and autumn to winter, unstratified. The start and end of these periods varied according to the timing of stratification, and the sampling programme. Annual budgets and a total budget for the whole study period were also calculated.

There were four inputs calculated:

1. Rostherne Brook catchment, calculated from the flow rate of the Brook just before it enters Rostherne Mere.

2. Catchment North drainage, calculated from the rainfall over this area, corrected for evapotranspiration.

3. Catchment North groundwater, calculated from the minimum flow of the Spring in Harper's Bank Wood, when (2) above was calculated as being non-existent. This prevented any additions to the flow, from run-off, from being included. Assuming the flow to be constant throughout the year, the minimum flow was used to calculate groundwater flow for the remaining part of the year

4. Direct rainfall on the lake surface.

The flow rates (Q) of the inflow and outflow of Rostherne Mere were initially calculated, using equation 2.2, from measurements using a float (Wetzel & Likens, 1991):

$Q = wdla/t$ (Equation 2.2)

where w is width in m, d is mean depth in m, l is distance in m over which a float travels in time, t , in sec, and a is a coefficient which varies with the nature of the sediment (0.8 if rough and 0.9 if smooth)

Later in the study, flow measurements were taken using an OTT current meter and measurements of the cross-sectional area of the stream. Both methods were checked for conformity. Measurements were also taken from the spring in Harper's Bank Wood.

Mean monthly rainfall and temperature data (Monthly Weather Report, 1990; 1991; 1992) were recorded by the Meteorological Office at Manchester Ringway Airport, 4 miles south of Rostherne Mere. Potential evaporation, used to calculate direct evaporation over the lake surface, and actual evapotranspiration, used to calculate evapotranspiration over the land surfaces, were calculated using the Thornthwaite equation, as described in Appendix 1.

Water level measurements were taken every two weeks from a fixed gauge in the boathouse. Changes in lake volume were calculated by multiplying the change in lake level by the surface area of the lake. This assumes, validly in the case of Rostherne Mere, that the change in lake level caused an insignificant change in surface area of the lake.

From the volume of water flowing out of Rostherne Mere (V_{out}) per unit time (t), and the volume of the lake (V_{lake}), a theoretical flushing rate (p) can be calculated:

$$p = \frac{V_{out}}{V_{lake}} \cdot t^{-1}$$ (Equation 2.3) (Vollenweider, 1975)

2.2.6 Nutrient budgets

There are various sources of both phosphorus and nitrogen to Rostherne Mere. These include effluent from the STWs, field drainage and groundwater inputs, stock and silage effluent from farm yards, direct rainfall, excreta from the bird roosts, and internal loading in the lake from various sources. Budgets for total phosphorus and dissolved inorganic nitrogen (DIN) were calculated. As in the water budget an equation can be constructed to balance the processes for a given time period:

$$\text{Output} = \text{External inputs} \pm \text{internal sources/sinks} - \frac{\partial \text{Lake}}{}$$ (equation 2.4)

where, Output = (concentration x volume) of the outflow

∂Lake = the change in nutrient quantity in the whole lake, or, epilimnion in stratified conditions.

Four categories of external inputs were quantified:

Rostherne Brook (includes effluent from both STWs)

Catchment North via run-off and drainage

Catchment North via groundwater

Direct rainfall

Bird roosts

Loadings from Catchment North via run-off and drainage were estimated by multiplying the estimated volume of water entering from this source by the monthly-mean nutrient concentration of the inflow of Mere Mere. This stream, which was monitored on a two week period throughout the study, drains an area of land with very similar land usage to that of Catchment North and so gives a reasonable estimate of loadings from woodland and agricultural land unaffected by sewage inputs. This may be an overestimate of loadings as the run-off from Catchment North has to drain through a lowland marsh area, and in some places, a reed bed, which are likely to absorb some of the nutrients.

Loadings from Catchment North via groundwater were estimated by multiplying the estimated volume of water entering from the spring in Harper's Bank Wood by the mean nutrient concentration of the spring water when Catchment North drainage was calculated as being non-existent.

Nutrient concentrations in rainfall were not measured, but Williams (1976) found a mean PO_4-P concentration of rainfall, collected at Rothamsted, of 0.06 mg l^{-1}. Sutcliffe *et al.* (1982) reported DIN inputs in rainfall in the Lake District of about 0.05 mg l^{-1}, which appear in agreement with NO_3-N figures from Aldergrove, Northern England (Soderlund *et al.*, 1985) of 0.035 mg l^{-1}. These figures for PO_4-P and DIN could then be used to calculate the rainfall loadings.

The winter bird roosts on Rostherne are typically dominated by gulls, in particular the black-headed gull (*Larus ridibundus*) and the common gull (*L. canus*). Counts of monthly

roost numbers are made at Rostherne (Appendix 2), although figures are approximate, as most of the gulls enter the reserve at dusk, making counting of large numbers difficult (Martin Davey, warden, Rostherne Mere, pers. comm.). Gould & Fletcher (1978) studied daily loads of phosphorus from captive gulls. The estimated 24 hour nutrient loads for PO_4-P were 30 mg for the black-headed gull and 42 mg for the common gull. If it is assumed that only half of this is excreted during the roosting period, loadings can be calculated from the monthly averages of birds/night. A similar calculation for DIN is not possible as Gould & Fletcher (1978) were unable to measure the oxidised forms of nitrogen in gull droppings.

The number of resident birds is small in comparison to the gull numbers and they feed from the lake, bringing little external nutrients to the water. They may, however, convert organic forms of phosphorus and nitrogen to soluble inorganic forms.

The change in nutrient quantity in the lake (∂Lake) was calculated for the whole lake volume during unstratified periods, and for the epilimnion (taken as the top five metres (1.38×10^6 m^3)) during stratified periods. This volume was then multiplied by the change in concentration of the nutrient between the start and end of the period.

The internal sources include release of nutrients from the sediment/hypolimnion and nitrogen fixation by cyanobacteria. The sinks include sedimentation of particulate matter and denitrification by bacteria.

As total nitrogen was not measured a budget for DIN (nitrate, nitrite, and ammonium) could only be calculated. Particulate and dissolved organic nitrogen loadings were not accounted for, which could severely underestimate the total nitrogen load to the lake. Johnes & Burt (1991) have shown that in the Windrush catchment, a lowland agricultural area, nitrate was the single largest constituent of the total nitrogen load, although organic nitrogen contributed about 40 % of the load in one year. Holden & Caines (1974) found that on average about 32 % of nitrogen in sewage effluent was in an organic form. DIN therefore probably only accounts for, at the most, two thirds of the total nitrogen load to the lake.

2.3 Results

2.3.1 Physical factors and water chemistry

Detailed physical and chemical data recorded for Rostherne Mere can be found in Appendix 3.

Figure 2.3 shows the temperature and oxygen stratification over the period of study. Stratification set in during May and lasted until about the end of October. There were a few short periods of intense stratification, with surface temperatures reaching up to 22°C (July 1990). The development of stratification coincided with the development of a deoxygenated hypolimnion. For the rest of the year the lake was well mixed, with the possible exception of the early part of 1991, when the lake almost completely froze over, which almost certainly resulted in an inverse stratification.

Soluble reactive phosphorus (SRP) showed a very similar pattern to that of dissolved inorganic nitrogen (DIN) (r^2=0.48, p$^-$0.0001) (Fig. 2.4a). Concentration maxima were recorded in the winter (610 µg l^{-1} and 1.89 mg l^{-1} respectively) and minima during the summer. The depletions of DIN and SRP in the epilimnion were correlated with the summer increase in chlorophyll *a* concentration (r^2=0.51, p$^-$0.0001, r^2=0.59, p$^-$0.0001, respectively). SRP never reached low concentrations (relative to the concentrations in most natural waters); the minimum recorded was 98 µg l^{-1}, in September 1990. DIN, on the other hand, in both years, declined rapidly from July, to reach very low concentrations at the start of September (0.02 mg l^{-1} 1990, 0.05 mg l^{-1} 1991)

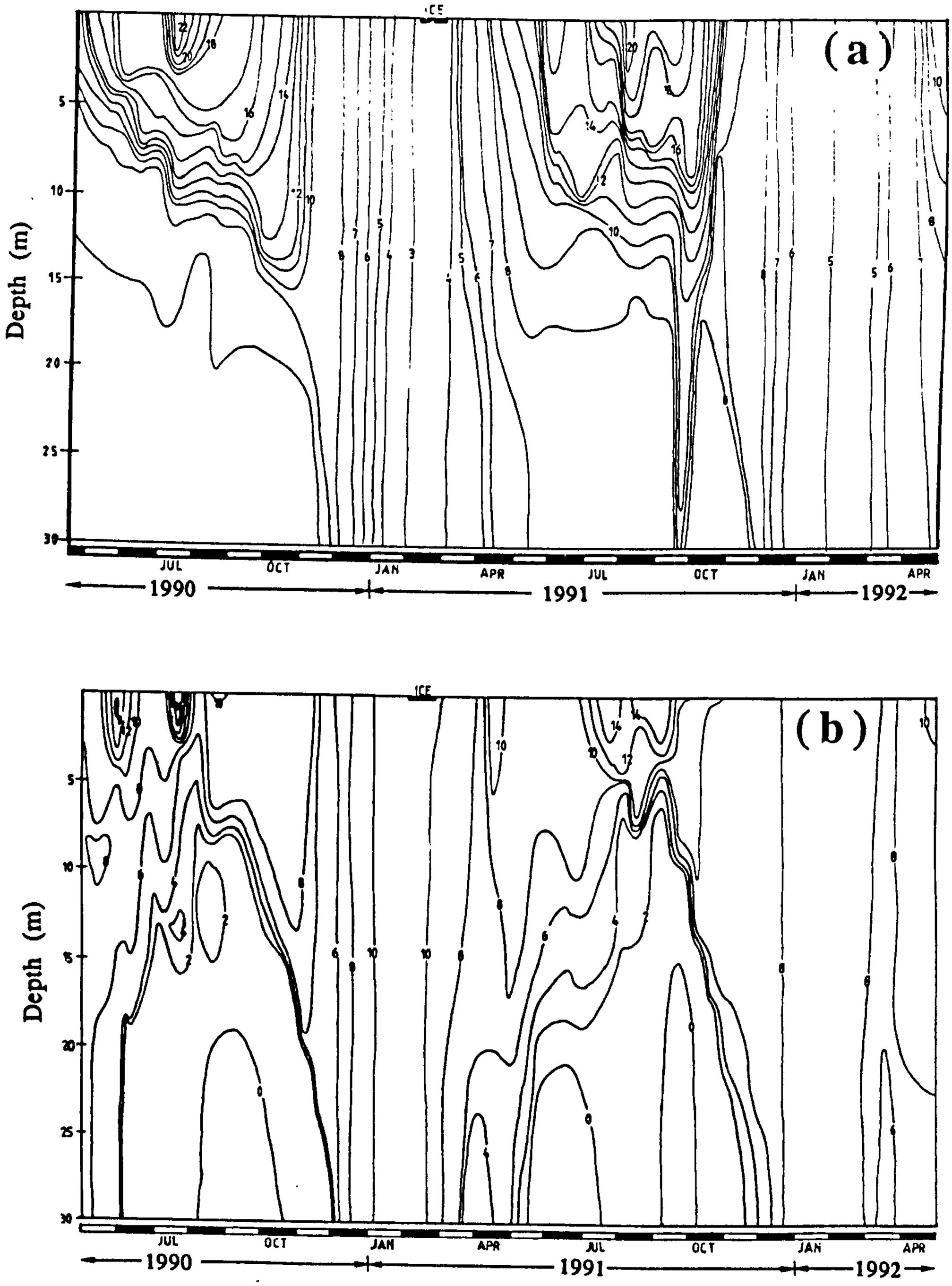


Fig. 2.3 Depth-time diagrams for (a) temperature (°C), and (b) dissolved oxygen (mg l^{-1}), in Rostherne Mere, from May 1990 to April 1992.

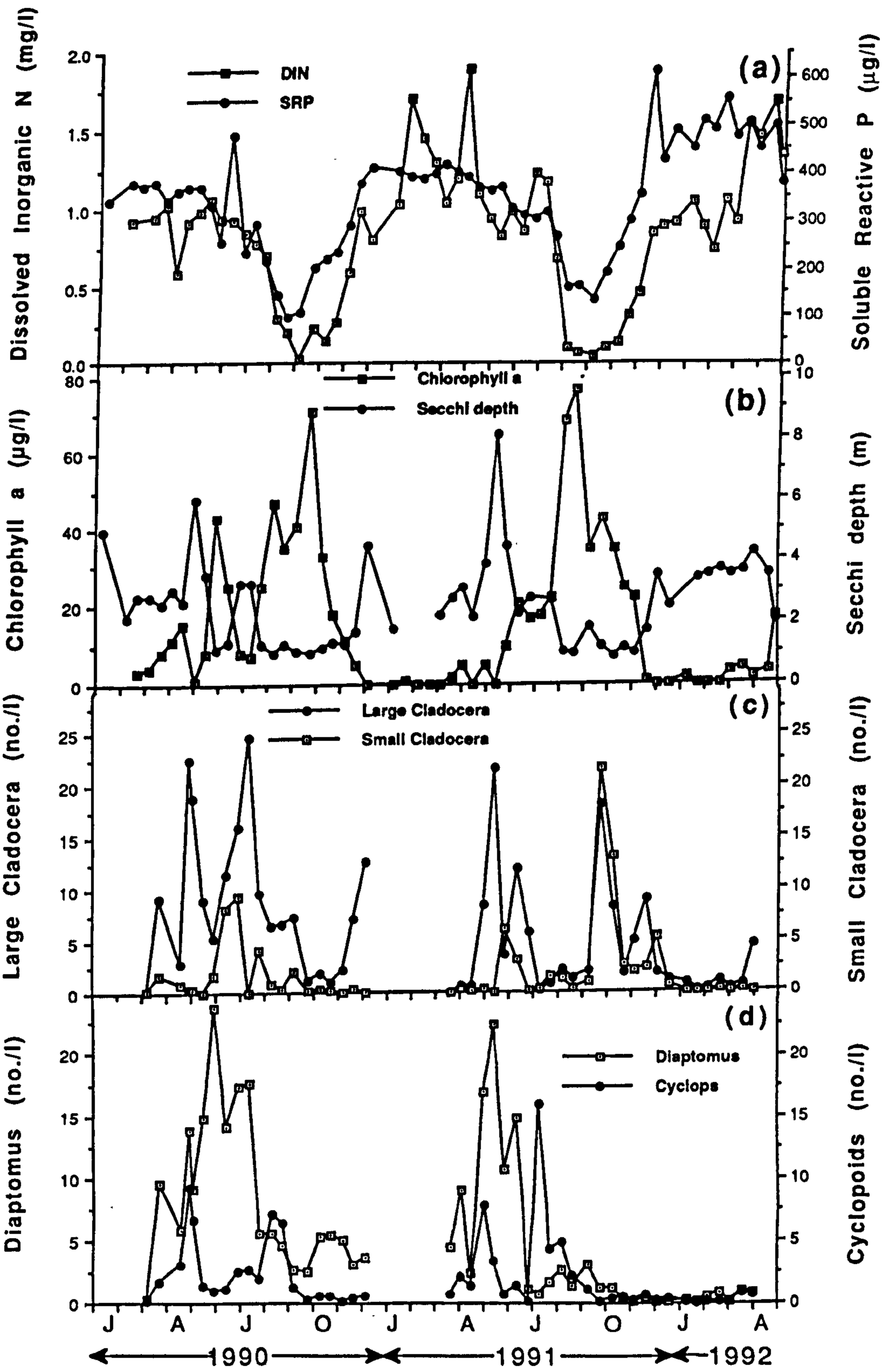


Fig. 2.4 Seasonality of (a) dissolved inorganic nitrogen and soluble reactive phosphorus, (b) chlorophyll *a* and secchi depth, (c) small and large Cladocera, and (d) *Diaptomus* and cyclopoids, in Rostherne Mere, from January 1990 to April 1992.

Of the two forms of nitrogen analysed (Fig. 2.5a), nitrate-nitrogen was dominant. Ammonium-nitrogen concentrations, on the other hand, were low for much of the year but increased sharply at the end of October, when stratification broke down.

Reactive silicate-silicon concentrations (Fig. 2.5b) showed a marked seasonality with late spring/early summer minima (0.3 mg l^{-1} 1990; 0.46 mg l^{-1} 1991) and winter maxima (≥ 2.0 mg l^{-1})

pH (Fig. 2.5b) also showed a marked seasonality, with summer maxima (9.5, 1990; 9.7, 1991) and winter minima (7.8, Jan 1991; 7.5, Jan 1992).

2.3.2 Phytoplankton and zooplankton

Chlorophyll *a* concentrations (Fig. 2.4b) increased in spring, early summer, and mid-late summer. The maxima for 1990 and 1991 were 71 µg l^{-1}, and 77 µg l^{-1} respectively; it was often undetectable over the winter period. Chlorophyll *a* was closely correlated with pH (r^2=0.72, p<0.0001), and inversely correlated with secchi depth (r^2=0.39, p<0.0001) (Fig. 2.4b).

Detailed plankton data can be found in Appendix 4, along with a full list of taxa observed in this study, with their authorities. The seasonal periodicity of the phytoplankton phyla is shown in Figure 2.6. Algal numbers were either cells, filaments, or colonies, as appropriate to the normal morphology of the organism. The spring increase in chlorophyll *a* was largely due to diatoms (*Stephanodiscus hantzschii* and *Asterionella formosa*) and *Rhodomonas* sp. and other small flagellates. It coincided with the spring decline in silicate concentrations. The

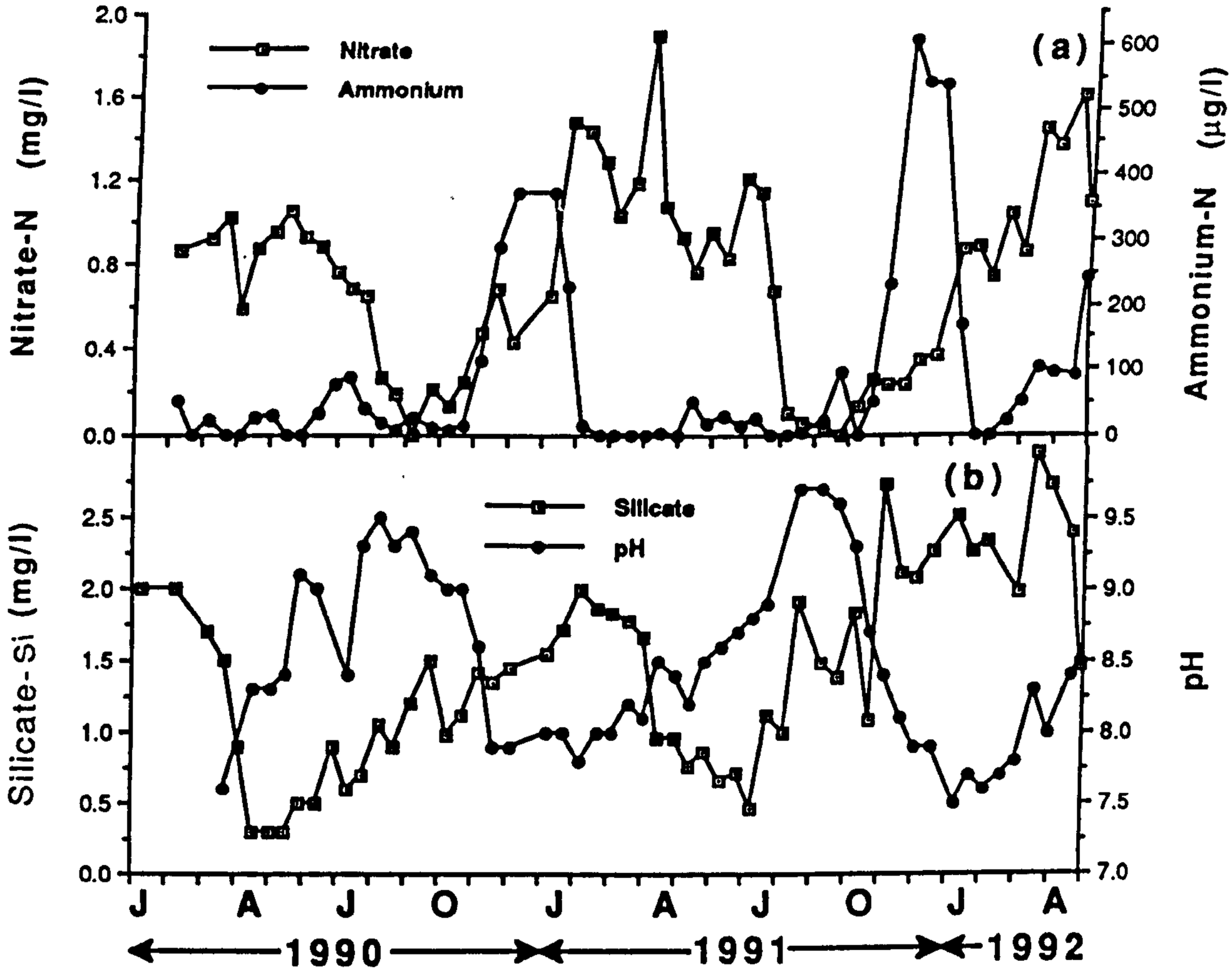


Fig. 2.5. Seasonality of (a) nitrate-nitrogen and ammonium-nitrogen, and (b) silicate-silicon and pH, in Rostherne Mere, from January 1990 to April 1992.

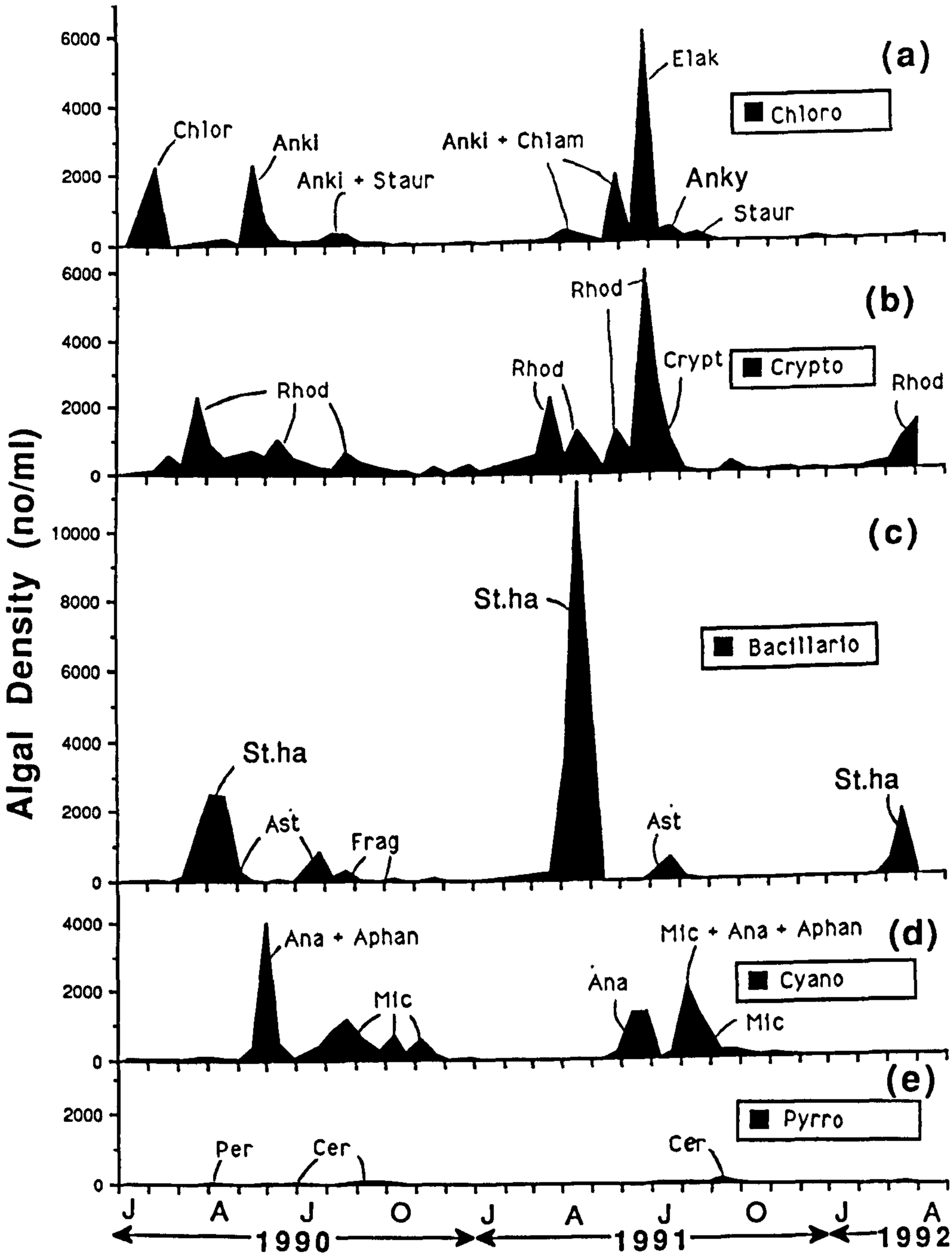


Fig. 2.6 Changes in density of (a) Chlorophyta, (b) Cryptomonads and Euglenophyta, (c) Bacillariophyceae,(d)Cyanobacteria, and (e) Pyrrophyta, in Rostherne Mere, from January 1990 to April 1992. Main algal taxa responsible for the peaks are indicated.

early summer increase was principally due to the filamentous cyanobacteria, *Anabaena* sp., and the mid-late summer increase due to the colonial cyanobacteria, *Microcystis aeruginosa*. The dinoflagellate, *Ceratium hirundinella*, showed its population maxima during September in both years. Although its numbers were relatively low (95/ml in 1990, 142/ml in 1991), a few hundred cells of *Ceratium* per ml may yield the same concentration of chlorophyll *a* as tens of thousands of cells of the diatom *Asterionella*. There were also small peaks in numbers of chlorophytes and flagellates in summer. When chlorophyll *a* and species data are compared, the two principal cyanobacteria *Anabaena* and *Microcystis* clearly dominated the phytoplankton biomass, owing to the large size of their individual filaments or colonies.

The zooplankton results are based on adult Crustacea. The cladoceran grazers (Fig. 2.4c) are separated into two groups: the large-bodied species, including *Daphnia longispina* agg., *Daphnia pulex*, and *Diaphanosoma brachyurum*, and the small-bodied species, dominated by *Daphnia cucullata*, with small numbers of *Bosmina longirostris* and *Chydorus* sp. occasionally observed. Both groups of Cladocera showed a very similar seasonality, although, the large-bodied species were generally more abundant. Densities were greatest in the spring and early summer, and declined during mid to late summer. In autumn 1991 densities briefly increased again.

Diaptomus gracilis (Fig. 2.4d) showed a similar seasonality to that of the Cladocera, with peak densities in the spring and early summer. Cyclopoids were not so abundant exhibiting two

peaks in density each year, in April/May and in July/August. For the rest of the year densities were very low.

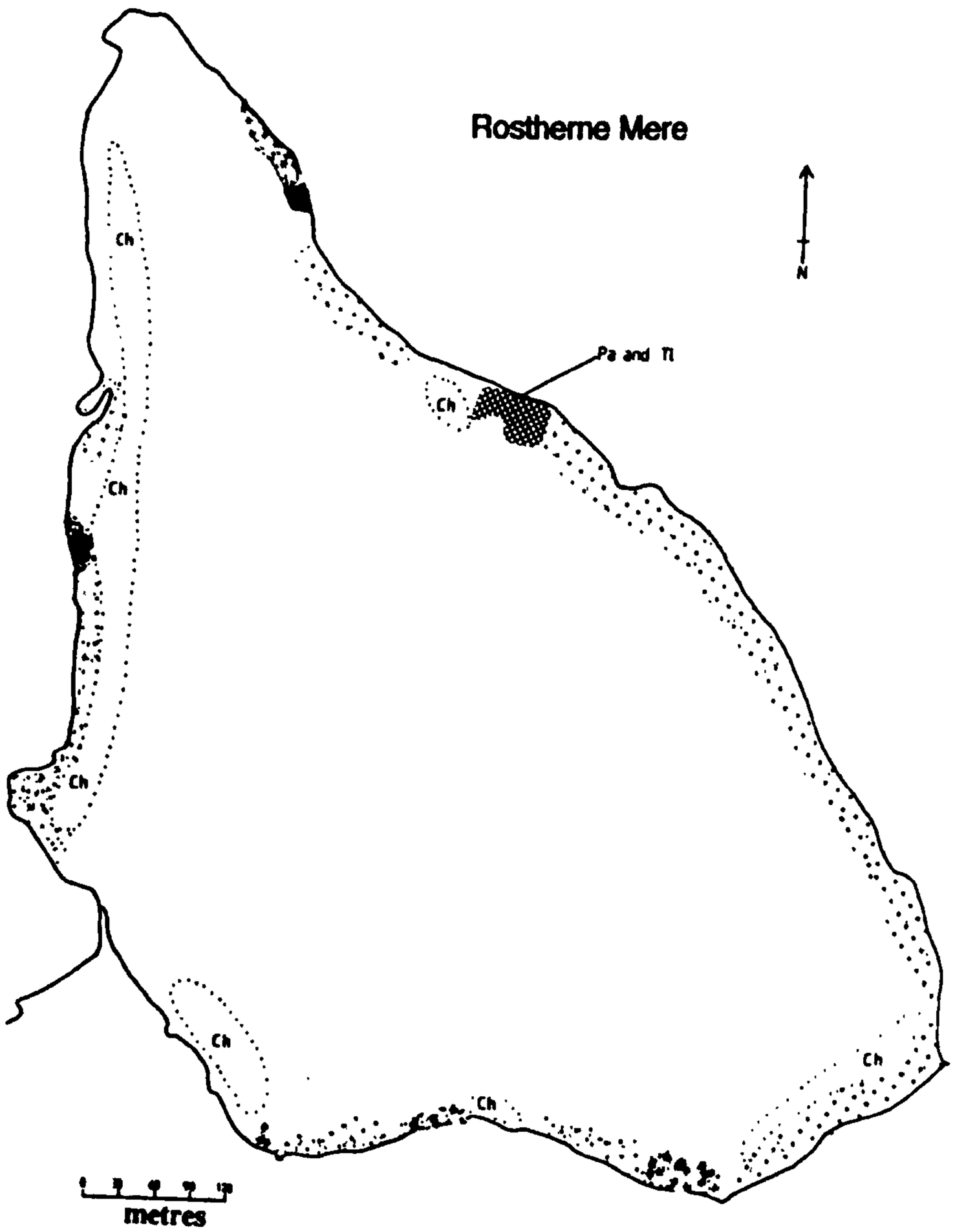
2.3.3 Aquatic plants

The results of the aquatic plant survey carried out on 1990 are shown in Fig. 2.7. Species diversity was very low with *Callitriche hermaphroditica* L. the only submerged plant recorded. There was, however, an extensive reed bed (*Phragmites australis* (Cav.) Steudel) along many stretches of the shore, and small patches of *Polygonum amphibium* L., *Typha latifolia* L., and *Acorus calamus* L. The submerged and floating-leaved species covered less than 5 % of the lake area.

2.3.4 Water budget

Table 2.3 shows the results of the water budget. The percentage contribution of the four inputs in terms of the total input volume are shown in brackets. To aid comparison of the data, the volume lost from the lake surface through evaporation and volume required to balance equation 2.1 are also shown as percentages of the total inputs.

Rostherne Brook was clearly the most important of the measured inputs, contributing between 67 to 83 % of the total. There were no inputs from surface run-off and drainage from Catchment North during the summer months, when evaporation was greater than rainfall, but during the autumn to winter period 1990 they contributed 22 % of the total inputs. Direct rainfall accounted for 7 to 17 % and Catchment North groundwater only 2 to 9 % of total inputs.



Ch = *Callitriche hermaphroditica*

= *Phragmites australis*

Pa = *Polygonum amphibium*

= *Typha angustifolia*

Tl = *Typha latifolia*

= *Acorus calamus*

Fig. 2.7 Aquatic plant survey of Rostherne Mere (carried out in August 1990).

Evaporation over the lake surface was a significant sink during the summer periods, causing a loss of between 18 to 38 % of the total inputs, whereas during the winter budget periods it only accounted for a loss of between 3 to 9 % of the total inputs.

For all but one, (12 Jul '90-24 Sep '90), budget periods the outflow volume exceeded the total inputs. Taking into account the evaporation and the change in lake volume the volume of water required to balance the budget equation (equation 2.1) was calculated. This varied to a huge extent, with no apparent seasonal pattern. For the period 12 Jul '90-24 Sep '90 the volume of water required to balance the budget was actually slightly negative, whereas during the period 15 May '91 to 22 Jul '91 it had as large a value as the total measured inputs.

The flushing rate fluctuated throughout the year, from 0.29 yr^{-1} recorded during the early summer 1992, up to 0.90 yr^{-1} recorded during the autumn and winter 1990/1991. The mean flushing rate recorded over a two year period was 0.63 yr^{-1}. This is equivalent to a retention time of 1.6 years.

The period from 3 May '90 to 14 May '91 was a much wetter period than from 23 Jul '91 to 21 Jul '92, having slightly more rainfall and lower evapotranspiration. Total inputs, adjusting for evapotranspiration, in the 90/91 budget were 34.6 x 10^5 m^3 compared to 25.9 x 10^5 m^3 during the 91/92 budget period.

Table 2.3 also gives figures for the whole period of study, showing that the four inputs, Rostherne Brook, Catchment North drainage, Catchment North groundwater, and direct rainfall contributed, on average, 73 %, 13 %, 4 %, and 10 % respectively. It also shows that direct evaporation was responsible for the loss

Table 2.3 Water Budget of Rostherne Mere from 22.2.90 to 1.4.92. Values given are 10^5 m^3. Values in brackets indicate the percentage contribution in relation to the total input volume for the corresponding period.

Budget Period	Days	Rostherne Brook	Catchment North Drainage	Catchment North Groundwater	Direct Rainfall	Total Input	Direct Evaporation	Outflow	∂ Lake Volume	Balance	Flushing Rate (yr^{-1})
22.2.90-2.5.90	70	3.93 (81)	0.22 (5)	0.27 (6)	0.42 (9)	4.84	0.43 (9)	8.79	-0.53	3.85 (80)	0.69
3.5.90-11.7.90	70	2.76 (77)	0	0.27 (8)	0.56 (16)	3.59	0.98 (27)	4.07	+0.24	1.70 (47)	0.32
12.7.90-24.9.90	75	5.25 (83)	0.07 (1)	0.29 (5)	0.69 (11)	6.30	1.11 (18)	4.36	+0.34	-0.49 (-8)	0.32
25.9.90-7.1.91	105	11.33 (67)	3.68 (22)	0.41 (2)	1.41 (8)	16.83	0.46 (3)	17.05	+1.60	2.28 (14)	0.90
8.1.91-14.5.91	127	8.46 (76)	1.34 (12)	0.49 (4)	0.77 (7)	11.06	0.63 (6)	20.35	-1.94	7.98 (72)	0.89
15.5.91-22.7.91	69	2.97 (79)	0	0.27 (7)	0.52 (14)	3.76	1.05 (28)	6.13	+0.34	3.76 (100)	0.49
23.7.91-23.9.91	63	2.07 (76)	0	0.24 (9)	0.40 (15)	2.71	1.02 (38)	4.26	-0.58	1.99 (73)	0.37
24.9.91-18.12.91	86	4.89 (70)	0.88 (13)	0.33 (5)	0.92 (13)	7.02	0.48 (7)	7.37	+1.02	1.85 (26)	0.47
19.12.91-12.5.92	146	12.00 (72)	2.63 (16)	0.56 (3)	1.37 (8)	16.56	0.75 (5)	21.14	-0.68	4.65 (28)	0.80
13.5.92-21.7.92	70	2.26 (74)	0	0.27 (9)	0.53 (17)	3.06	1.16 (38)	3.66	-0.58	1.18 (39)	0.29
3.5.90-14.5.91	377	27.80 (74)	5.09 (13)	1.46 (4)	3.43 (9)	37.78	3.18 (8)	45.83	+0.24	11.47 (30)	0.67
23.7.91-21.7.92	365	21.22 (72)	3.51 (12)	1.40 (5)	3.22 (11)	29.35	3.41 (12)	36.43	-0.82	9.67 (33)	0.55
3.5.90-12.5.92	742	49.73 (73)	8.60 (13)	2.86 (4)	6.64 (10)	67.83	6.48 (10)	84.73	+0.34	23.72 (35)	0.63

of about 10 % of these total inputs and the extra volume of water required to balance the budget was equivalent to 35 % of the total inputs.

2.3.5 Total phosphorus budget

Table 2.4 shows the results of the total phosphorus budget. Annual budgets for before (3 May '90-14 May '91) and after (23 Jul '91-21 Jul '92) sewage diversion are shown.

The inputs, in terms of percentage of the total external (catchment-derived) inputs, from Rostherne Brook, Catchment North drainage, Catchment North groundwater, direct rainfall, and the bird roost were 96 %, 2 %, 0 %, 1 %, and 1 % respectively before diversion, and 85 %, 7 %, 1 %, 3 %, and 3 % respectively after diversion.

Rostherne Brook was clearly the major source of phosphorus from these inputs, although, since sewage diversion its contribution has reduced. The actual annual input has decreased dramatically from 2250 kg (6.0 kg day^{-1}) to 504 kg (1.4 kg day^{-1}). The highest loading rates of 15.6 kg day^{-1} in the pre-diversion period were found during late summer (12.7.90-24.9.90),which coincided with the return of flow of extremely nutrient-rich water (5370 µg l^{-1} PO_4-P) over the outflow of Little Mere. During the post-diversion period the highest loading rate, 2.1 kg day^{-1}, was found during early winter. Again this coincided with the return of flow of nutrient-rich water (1320 µg l^{-1} PO_4-P) over the outflow of Little Mere.

Catchment North drainage (including surface run-off) was the next largest of these sources of phosphorus, on average 48 kg annually, although this entered mainly during the winter

periods. Negligible amounts entered during the summer periods, when evaporation was greater than rainfall. Summer inputs were probably an underestimate due to exaggeration of evaporation. Winter inputs may be an overestimate, as a lot of the run-off from this area had to drain through soil which may have led to a lot of sedimentation of particulate phosphorus, and binding of reactive phosphorus. Catchment North groundwater provided the smallest contribution to the phosphorus budget, on average 6 kg annually.

Direct rainfall added about 20 kg annually, which was only a small contribution to the total external inputs (1 % pre-diversion, 3 % post-diversion). Its greatest % contribution was 7 % during the early summer period 1992.

The bird roost was also a small source of phosphorus, about 21 kg annually, although, like the other sources its percentage contribution to the budget has increased (up to 4 % of total external inputs) as that of Rostherne Brook has decreased.

Total annual inputs from the catchment decreased dramatically in the year following the sewage diversion from 2281 kg to 590 kg, i.e. about a 75 % reduction.

Phosphorus concentration in the lake (epilimnion during the summer periods) can be seen to decrease throughout the year, except for the early winter periods, when there was always a large increase.

Despite a large reduction in the total external inputs to the lake, the output slightly increased, from 1770 kg annually to 1994 kg annually.

Table 2.4 Total phosphorus budget of Rostherne Mere from 22.2.90 to 1.4.92. Values given are kg (except Rostherne Brook and Outflow loads). Figures in brackets represent % contribution of total inputs for the given period.

Period	Days	Rostherne Brook	Rostherne Brook Load (kg day^{-1})	Catchment North Drainage	Catchment North Groundwater	Direct Rainfall	Bird roost	Total Inputs	∂ Plake	Outflow	Outflow Load (kg day^{-1})	Balance
22.2.90-2.5.90	70	141 (92)	2.0	5 (3)	1 (1)	2 (1)	4 (3)	153	-119	370	5.3	+98
3.5.90-11.7.90	70	135 (96)	1.9	0	2 (1)	3 (2)	0	140	-52	186	2.7	-6
12.7.90-24.9.90	75	1170 (99)	15.6	2 (0)	1 (0)	4 (0)	2 (0)	1179	-6	158	2.1	-1027
25.9.90-7.1.91	105	609 (91)	5.8	35 (5)	2 (0)	9 (1)	12 (2)	667	+504	713	6.8	+550
8.1.91-14.5.91	127	336 (91)	2.6	18 (5)	2 (1)	5 (1)	9 (2)	370	-311	771	6.1	+90
15.5.91-22.7.91	69	149 (97)	2.2	0	1 (1)	3 (2)	0	153	-54	236	3.4	+29
23.7.91-23.9.91	63	50 (93)	0.8	0	1 (2)	2 (4)	1 (2)	54	-109	113	1.8	-50
24.9.91-18.12.91	86	181 (86)	2.1	15 (7)	1 (0)	6 (3)	8 (4)	211	+2936	457	5.3	+3182
19.12.91-12.5.92	146	234 (83)	1.6	27 (10)	2 (1)	8 (3)	11 (4)	282	-1430	1280	8.8	-432
13.5.92-21.7.92	70	39 (91)	0.6	0	1 (2)	3 (7)	0	43	+99	144	2.1	+200
3.5.90-14.5.91	377	2250 (96)	6.0	55 (2)	7 (0)	21 (1)	23 (1)	2356	-100	1828	4.8	-628
23.7.91-21.7.92	365	504 (85)	1.4	42 (7)	5 (1)	19 (3)	20 (3)	590	-345	1994	5.5	+1059

A negative result of the balance indicates sedimentation > sediment release. This was of most significance during the late summer period in 1990, when there was net sedimentation of 1027 kg, and in the winter/spring period of 91/92 when there was a net sedimentation of 432 kg. The opposite, a net gain of phosphorus to the water body, occurs when phosphorus-rich hypolimnion water mixes with the epilimnion water. This was of greatest significance during the autumn/winter period in both 1990/1 and 1991/2 (550 kg and 3182 kg respectively). In terms of % of the amount of phosphorus entering from Rostherne Brook for the corresponding period, these amounts were 90 % and 1758 %. The pre-diversion "annual" budget showed a net loss of phosphorus to the sediment of 628 kg. The post-diversion annual budget showed a net gain of phosphorus from the sediment of 1059 kg.

2.3.6 Dissolved inorganic nitrogen budget

Table 2.5 shows the results of the DIN budget. Annual budgets for before (3.5.90-14.5.90) and after (23.7.91-21.7.92) sewage diversion are shown.

The inputs, in terms of % of the total external inputs, from Rostherne Brook and Catchment North drainage were 86 % and 14%, respectively, before diversion, and 84 % and 16%, respectively, after diversion. Catchment North groundwater and direct rainfall inputs were negligible in both periods.

Rostherne Brook was clearly the most important source of DIN from these inputs. The actual annual input decreased dramatically in the post-diversion budget compared to the pre-diversion budget, from 10910 kg (28.9 kg day^{-1}) to 6282 kg

(17.2 kg day^{-1}). The highest loading rates (up to 52.6 kg day^{-1}) were found over the wet winter periods, although there was also a high loading rate during the period 12 Jul '90 to 24 Sep '90, which coincided with the return of flow of extremely nutrient-rich water (9.68 mg l^{-1} DIN) over the outflow of Little Mere.

Catchment North drainage (including surface run-off) was the next largest external source of DIN, 1759 kg during pre-diversion year, 1163 kg in post-diversion year. Inputs varied according to the amount of rain, virtually all DIN entered during the winter periods. Negligible amounts entered during the summer periods, when evaporation was greater than rainfall. Summer inputs were probably an underestimate due to exaggeration of evaporation. Winter inputs may be an overestimate, as a lot of the run-off from this area had to drain through waterlogged soils, and in some places a reed bed, which may have reduced the DIN concentration through denitrification. Catchment North groundwater added on average 24 kg annually (<1 % of total external inputs before and after diversion), suggesting that groundwater over the whole catchment was an unimportant source of DIN.

Direct rainfall provided the smallest contribution to the DIN budget, on average 17 kg annually.

Total inputs from the catchment decreased from about 12306 kg annually to 7486 kg annually, i.e. about a 40 % reduction of the pre-diversion budget.

DIN concentration in the lake (epilimnion during the summer periods) can be seen, in general, to decrease during the summer periods and increase during winter periods, particularly

early winter when there was always a large increase in concentration in the lake.

The output slightly decreased, from 6375 kg annually to 4604 kg annually (a 28 % reduction). The DIN load in the outflow declined from 17.5 kg day^{-1} to 12.6 kg day^{-1} respectively).

Balancing the DIN budget does not provide much information on sedimentation/internal release as there are more sources and sinks to take into account. Sources include nitrogen-fixing bacteria, ammonium release due to bacteria on the sediment surface, and conversion of organic nitrogen to DIN by other members of the biota. Sinks include denitrification by bacteria and conversion of DIN to an organic form of nitrogen. To get a more accurate picture of the internal sources and sinks of DIN a total nitrogen budget would have to be calculated.

Table 2.5 DIN budget of Rostherne Mere from 22.2.90 to 1.4.92. Values given are kg (except Rostherne Brook and Outflow loads). Figures in brackets represent % contribution of total external inputs for the given period.

Period	Days	Rostherne Brook	Rostherne Brook Load (kg day^{-1})	Catchment North Drainage	Catchment North Groundwater	Direct Rainfall	Total External Inputs	∂ DIN_{lake}	Outflow	Outflow Load (kg day^{-1})
22.2.90-2.5.90	70	708 (93)	10.1	45 (6)	5 (1)	2 (0)	760	+246	792	11.3
3.5.90-11.7.90	70	531 (99)	7.6	0	5 (1)	3 (1)	539	-282	423	6.0
12.7.9-24.9.90	75	1608 (99)	21.4	8 (0)	5 (0)	3 (0)	1624	-765	388	5.2
25.9.90-7.1.91	105	5523 (81)	52.6	1280 (19)	7 (0)	7 (0)	6817	+5319	3068	29.2
8.1.91-14.5.91	127	3248 (87)	25.6	471 (13)	8 (0)	4 (0)	3731	-1355	2706	21.3
15.5.91-22.7.91	69	543 (99)	7.9	0	5 (1)	3 (1)	551	-192	614	8.9
23.7.9-23.9.91	63	408 (99)	6.5	0	4 (1)	2 (0)	414	-809	64	1.0
24.9.91-18.12.91	86	1360 (90)	15.8	147 (10)	6 (0)	5 (0)	1518	+5398	1220	14.2
19.12.91-12.5.92	146	4201 (80)	28.8	1016 (19)	9 (0)	7 (0)	5233	+1642	3147	21.6
13.5.92-21.7.92	70	313 (98)	4.5	0	5 (2)	3 (1)	321	-1397	173	2.5
3.5.90-14.5.91	377	10910 (86)	28.9	1759 (14)	25 (0)	17 (0)	12711	+1071	6585	17.5
23.7.91-21.7.92	365	6282 (84)	17.2	1163 (16)	24 (0)	17 (0)	7486	-3524	4604	12.6

2.4 Discussion

With maximum chlorophyll *a* concentrations of 60-70 µg l^{-1} and growing season SRP concentrations of 100-200 µg l^{-1} it is clear that Rostherne Mere was very eutrophic. Results of an international survey (Vollenweider & Kerekes, 1982) suggest values of 43 µg l^{-1} peak chlorophyll *a* concentration and 84 µg l^{-1} annual mean total phosphorus concentration for eutrophic lakes. DIN, however, reached very low concentrations during summer. The summer phytoplankton community was dominated by algae that could either tap sources of nutrients in the hypolimnion, or fix nitrogen.

The following discussion examines the seasonal changes in detail, discusses the possibility of nitrogen-limitation of the phytoplankton, and compares the present study to that of previous work. A discussion of the water, total phosphorus and DIN budgets is then followed by a conclusion of whether the diversion of the sewage effluent will bring about an improvement in the water quality.

2.4.1 Seasonality of water chemistry, physical factors, and plankton

The spring increase in chlorophyll *a* concentration, which was mainly due to the diatom *S. hantzschii*, correlated closely with a marked decline in silicate concentrations, as is common in many temperate lakes (Hutchinson, 1967). The only difference between Rostherne Mere and many other of the North-West Midland Meres was in the timing; diatoms did not develop in Rostherne Mere until mid-March, later than in most of the other meres. Reynolds (1978b) has attributed this to the shorter

photoperiod available to the algae in Rostherne Mere, as it is the deepest mere. The lake then began to stratify in May, so that conditions favouring diatom growth (Lund, Mackereth & Mortimer, 1963) were short-lived, although the rise of the diatom *Asterionella* during July in both years, suggests that there were short periods of mixing at these times.

The increase in grazer density during the late spring appeared to be the reason for the high water clarity (increased secchi depth) that followed the spring growth of diatoms. Reynolds & Bellinger (1992), however, believe it to be at least as likely due to the settlement of inert suspended particulates following the onset of stratification.

The onset of thermal stratification in May provided higher water temperatures and reduced circulation (i.e. effectively increased the photoperiod), which appeared to be the stimulus for the development of the summer and autumn peaks of phytoplankton biomass (measured as chlorophyll *a*). Associated with the peaks in phytoplankton biomass were the peaks in pH, due to CO_2 uptake by the phytoplankton. As photosynthesis removes CO_2 from solution, bicarbonate ions react with water to yield more CO_2 and carbonate ions (Equation 2.5). The carbonate ions react with water to yield hydroxyl ions (OH^-) (Equation 2.6), and therefore pH rises.

$$2HCO_3^- + H_2O = CO_2 + CO_3^{2-} + 2H_2O \quad \text{(Equation 2.5)}$$

$$CO_3^{2-} + H_2O = OH^- + HCO_3^- \quad \text{(Equation 2.6)}$$

The summer of 1990 was initially dominated by *Anabaena* and *Aphanizomenon*. The brief decline in the grazer population in late May/early June in 1990 coincided with this increase in the density of *Anabaena*. The major collapse in the grazer population however did not occur until July in 1990 and June in 1991. During the rest of the summer grazing pressure appeared to be of little importance in limiting the phytoplankton biomass. Whether the decrease in grazer densities was due to interference in feeding due to the colony size (Arnold, 1971) or toxicity (Lampert, 1981) of cyanobacteria, or due to predation by zooplanktivorous fish (Andersson *et al.*, 1978), was not clear. This question was examined further in an enclosure experiment carried out in Rostherne Mere during July/August 1991 (see Chapter 3). In both years, *Microcystis* dominated the phytoplankton for the rest of the summer and the autumn, until stratification broke down.

Why *Anabaena* (and *Aphanizomenon*), whose population developed earlier than *Microcystis*, failed to dominate over the summer periods was not clear. The decline in *Anabaena* in 1990 and June 1991 may have been due to a breakdown in stratification - which was evident from a rise in numbers of the diatom *Asterionella*. The decline of *Anabaena* and *Aphanizomenon* in August 1991 is, however, more difficult to explain. Reynolds & Bellinger (1992) suggest that both *Anabaena* and *Aphanizomenon* grow and develop well at temperatures marginally below those preferred by *Microcystis*, and dominate only in years when the development of *Microcystis* (and *Ceratium*) is delayed due to cooler conditions. This, however, did

not appear to be the case in August 1991 as *Anabaena* and *Aphanizomenon* developed at the same time as *Microcystis*.

2.4.2 Limitation of phytoplankton crop-size

Reynolds (1978b) suggests that light most likely limits the spring phytoplankton crop. Rostherne Mere is a deep lake, and when the water column is isothermally mixed, phytoplankton must spend large parts of the day in low-light conditions. The seasonal data showed that grazing pressure may also be important in limiting the size of the spring phytoplankton crop, and may be responsible for the spring clear-water phase. Multiple regression analysis of spring chlorophyll *a* concentrations (April to May) against DIN, SRP, and silicate concentrations and herbivore densities (Cladocera and *Diaptomus*) showed no significant relationship (Table 2.6), although silicate and herbivores appeared to be of greatest importance. The role of silicate and the zooplankton community during spring was examined further in an enclosure experiment carried out in Rostherne Mere during April/May 1991 (see Chapter 3).

Multiple regression analysis of summer chlorophyll *a* concentrations (June to September) against DIN and SRP concentrations and herbivore densities showed a highly significant relationship (Table 2.7); DIN appeared to be of greatest importance. However, linear regression analysis of DIN concentrations against chlorophyll *a* concentrations (Fig. 2.8) showed that this was a negative relationship, chlorophyll *a* concentration increasing as DIN concentrations decreased. This does not show limitation by DIN, but instead shows the

Table 2.6 Results of multiple regression analysis on spring (April to Mid-May) chlorophyll *a* concentrations.

Chlorophyll *a*		Partial F	r^2	probability
Versus:	DIN	0.105		
	SRP	0.007		
	Silicate	0.394		
	Herbivores	0.385		
	Total		0.356	p>0.25

Table 2.7 Results of multiple regression analysis on summer (Late-May to September) chlorophyll *a* concentrations.

Chlorophyll *a*		Partial F	r^2	probability
Versus:	DIN	10.06		
	SRP	1.02		
	Herbivores	3.45		
	Total		0.634	0.0001<p≤0.005

dependence of DIN concentrations on chlorophyll *a*. However, DIN did decline to very low concentrations during August and September in both years, so if any nutrient was limiting the summer phytoplankton crop it appeared most likely to be nitrogen. Herbivores were the next most important factor in the multiple regression analysis. Linear regression analysis of herbivore density against chlorophyll *a* concentrations (Fig. 2.9) showed that it was not quite significant at the 5 % level. However, chlorophyll *a* concentrations decreased as herbivore density increased suggesting that grazers were having some limiting influence. Although, it is also possible that the relationship could be the result of an inhibition of grazer-feeding by large, inedible algae. The relationship between the phytoplankton and zooplankton communities during summer was examined further in an enclosure experiment carried out in Rostherne Mere during July and August. The lack of a significant relationship between SRP concentrations and chlorophyll *a* concentrations, and the fact that the minimum SRP concentration recorded was 98 $\mu g\ l^{-1}$, indicates that phosphorus concentrations were not important in limiting phytoplankton biomass during summer.

The ratio of carotenoid pigments to chlorophyll *a* pigment (A480:663) was > 1.3 throughout most of the study period (Fig. 2.10), indicating that the phytoplankton community may have been nitrogen deficient. However, for long periods the ratio of A430:410 was < 1.2 which suggests that the high A480:663 ratio may be due to grazing effects or resuspended sediment. The ratio was > 1.2, though, during June, August, and September, which suggests that the high A480:663 ratio during these

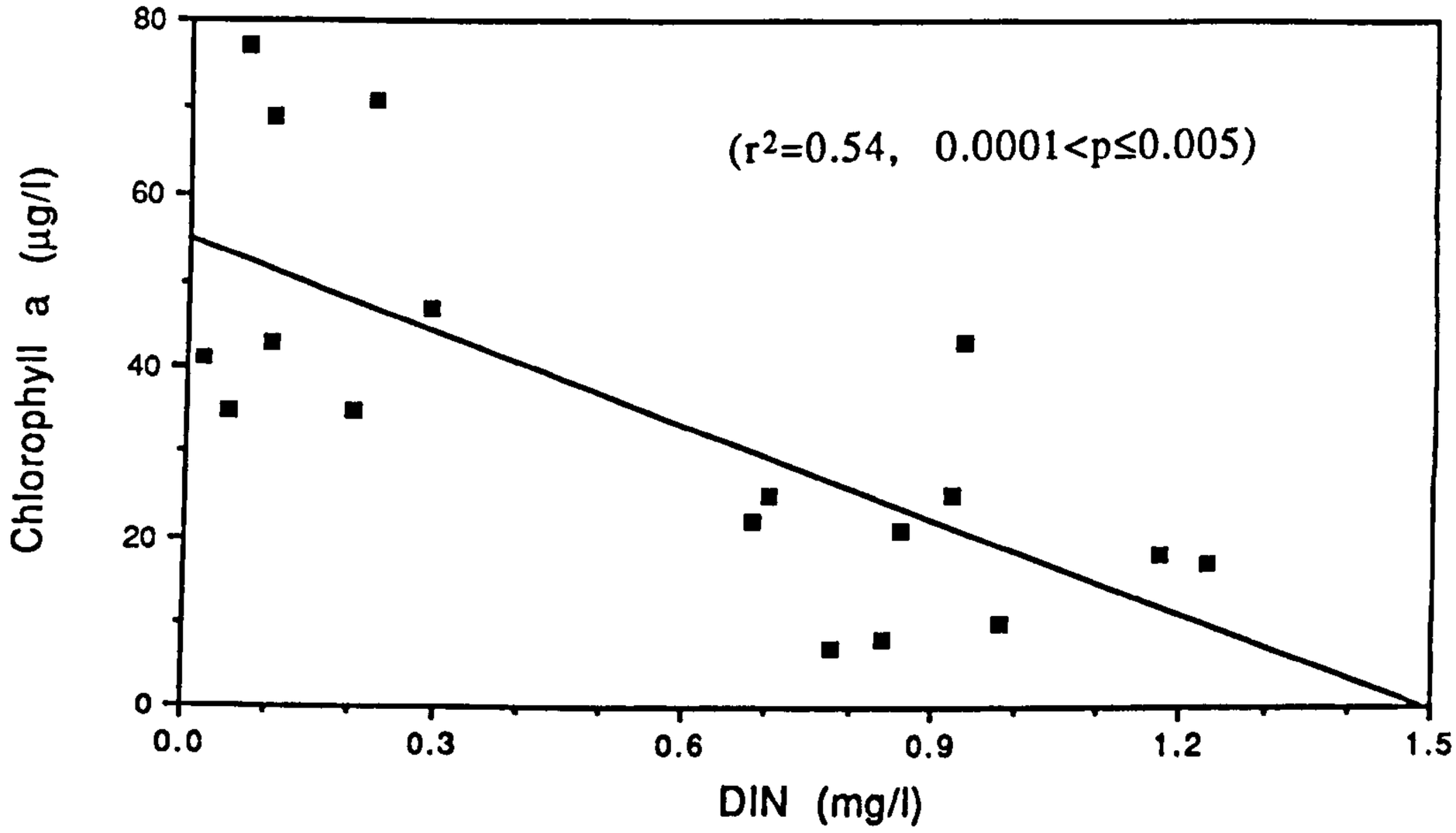


Fig. 2.8 Relationship between chlorophyll *a* and dissolved inorganic nitrogen concentrations in Rostherne Mere, during summer (Late-May to September).

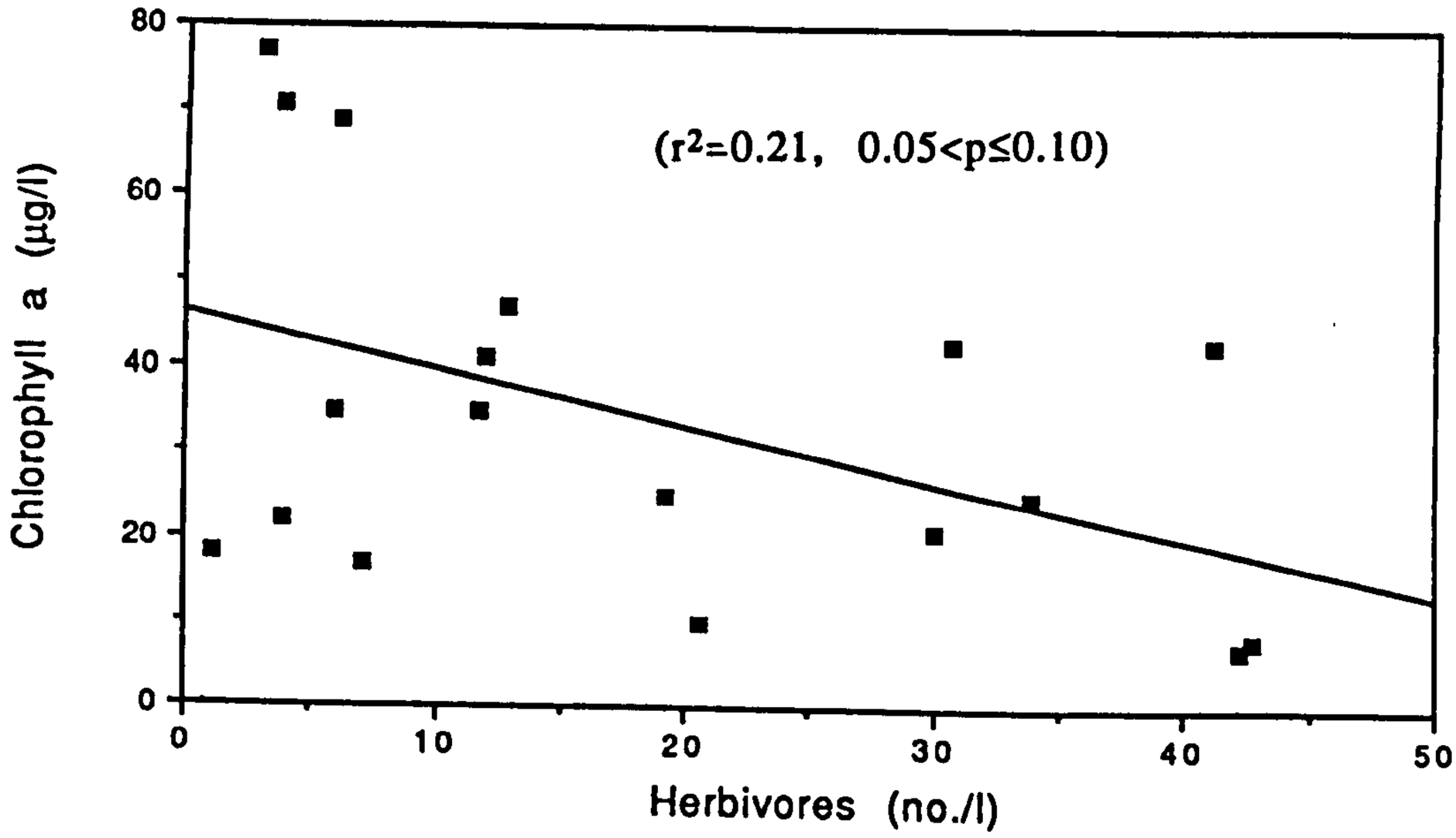


Fig. 2.9 Relationship between chlorophyll *a* concentration and herbivore (Cladocera and *Diaptomus*) density in Rostherne Mere, during summer (Late-May to September).

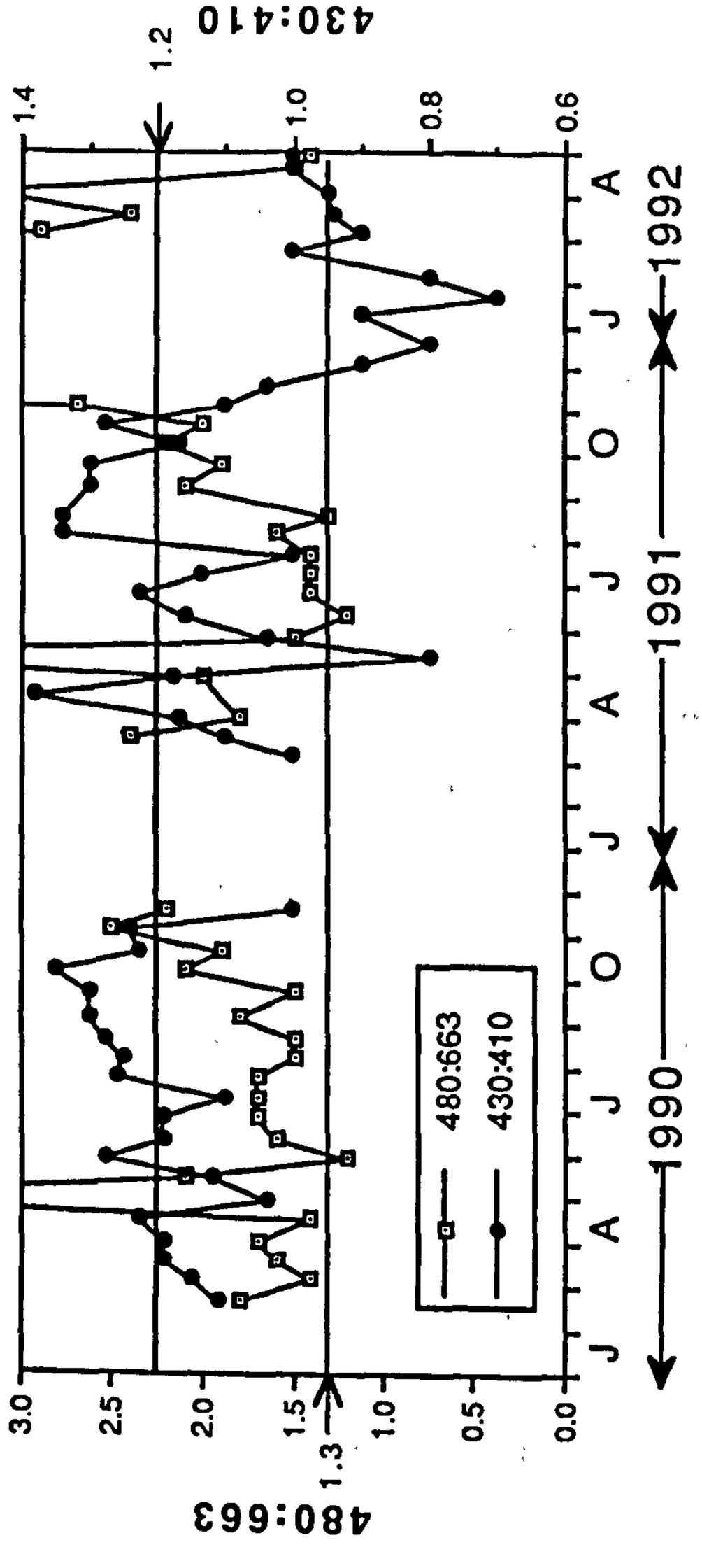


Fig. 2.10 Seasonality of the ratio of carotenoid pigments to chlorophyll *a* (ratio of absorbances at 480 nm:663 nm) and the ratio of the absorbances at 430 nm:410 nm.

months was due to nitrogen deficiency, however, the presence of N-fixing cyanobacteria during these months invalidates the ratios. The presence of large populations of nitrogen-fixing algae is, on the other hand, an indication of nitrogen deficiency in itself (Schindler, 1977). In Rostherne Mere, in 1990, *Anabaena* and *Aphanizomenon*, the two nitrogen-fixing algae observed, dominated in early summer from May to June, before major depletion of DIN had occurred. In 1991, *Anabaena* was again abundant in June, pre-DIN depletion, but also increased, along with *Aphanizomenon*, during the period of DIN depletion in August.

Microcystis was the phytoplankter most dominant during August, September, and October, along with the dinoflagellate *Ceratium*. These algae have both been shown to undergo strong diel vertical migrations (Heaney & Eppley, 1981; Ganf, 1975) and most likely were able to tap the nitrogen (and phosphorus) source in the hypolimnion, which has been shown to build up in Rostherne Mere over the summer period, during times of thermal stratification (Grimshaw & Hudson, 1970).

Reynolds *et al.* (1981) have shown with bioassays of fertilised water from Blelham Tarn, that the nutrient concentrations in the surface waters of Rostherne Mere are adequate to saturate maximal growth rate requirements of *Microcystis*. Reynolds and Bellinger (1992), therefore, hypothesized that the phytoplankton population was light-limited, rather than nutrient-limited.

It is likely that the nitrogen concentration limited the crop-size of some species, but not the community as a whole. The low epilimnetic concentrations of DIN were probably

important in favouring species that were able to utilise other sources of nitrogen; *Microcystis* and *Ceratium* are able to utilise hypolimnetic sources of nitrogen, and *Anabaena* and *Aphanizomenon* are able to fix nitrogen.

2.4.3 Current status of the lake: water chemistry and phytoplankton in comparison to previous work

Changes in land usage in the parishes containing the catchment of Rostherne Mere between 1931 and 1987 are shown in Table 2.8. Stock keeping has increased in the catchment quite considerably, but field usage has remained relatively stable, with a little loss of land to non-agricultural purposes. The use of synthetic fertilisers over this period has also increased, paricularly since the 1950s (Hood, 1982). There has also been an increase in the nutrient loading to Rostherne Brook, from Mere STW. Built in the 1930s to deal with the effluent from 550 people, by the date of its closure it was working over-capacity, treating effluent from 3315 people (M. Walker, NWWA, pers. comm.).

Paleolimnological studies of Rostherne Mere (Livingstone, 1979; Nelms, 1984) provided evidence for there having been an enrichment of the lake, that led to a shift in the phytoplankton composition, around the late 1950s. This was thought to be due to the increased use of synthetic fertilisers. To assess whether there has been any further enrichment of the lake in recent years, comparisons can be made with earlier records of water chemistry and phytoplankton composition.

Table 2.8. Land usage in the parishes containing the catchment of Rostherne Mere in 1931 and 1987. Based on data taken from the Agricultural Census returns, held at the Public Records Office at Kew. For stock headage, an index of potential relative nutrient supply from excreta has been derived from the annual average amounts of nitrogen and phosphorus excreted per head. The amounts of nitrogen and phosphorus excreted by each stock type have been summed and then normalised relative to a value of 1 for humans. The index has then been multiplied by the headage to give an indication of change in nutrient load (see Moss *et al.* (1992) for further details).

	1931	1987
Cattle (head)	828	1351
nutrient units	10102	16482
Pigs (head)	311	641
nutrient units	1973	3077
Sheep (head)	298	1565
nutrient units	449	2320
Poultry (head)	7042	38530
nutrient units	986	5394
Total nutrient units	13510	27273
Permanent grass (ha)	431	324
Temporary grass (ha)	243	276
Arable (ha)	522	580
Woodland (ha)	4	1
Rough grazing (ha)	35	4
Total hectarage	1235	1185

Water Chemistry

The first reliable data on water chemistry are those of Grimshaw & Hudson (1970). Their SRP and nitrate-nitrogen data are shown, in comparison with those recorded by the present study, in Figure 2.11. Nitrate-nitrogen exhibits a very similar pattern in both studies, suggesting that there has been little change in nitrate loading since 1965-1967. The situation regarding phosphorus, on the other hand, is not so clear. Grimshaw and Hudson's data are very erratic and show little seasonality. This may due to their method, using a stannous chloride reducing solution, the reliability of which is questionable (B. Moss, pers. comm.). It does appear though, that the winter concentrations of phosphorus have increased since the 1960s. This may just be an artefact due to the method used by Grimshaw and Hudson or it may be due to an increased phosphorus loading to the lake.

Phytoplankton

Phytoplankton records for Rostherne Mere date from net collections made in 1912 (Pearsall, 1923), with further descriptions by Griffiths (1925) and Lind (1944). Since 1963 there has been frequent sampling, using a plastic hosepipe, to depths no greater than 4.5 m (Belcher & Storey, 1968; Reynolds & Bellinger, 1992).

Recent publications (Reynolds, 1978a; Reynolds & Bellinger, 1992) have detailed a "striking change" in the phytoplankton community from the early surveys of Pearsall and Lind, who observed a diatom - *Ceratium* - *Aphanizomenon* or *Coelosphaerium* sequence, which has given way to a cycle

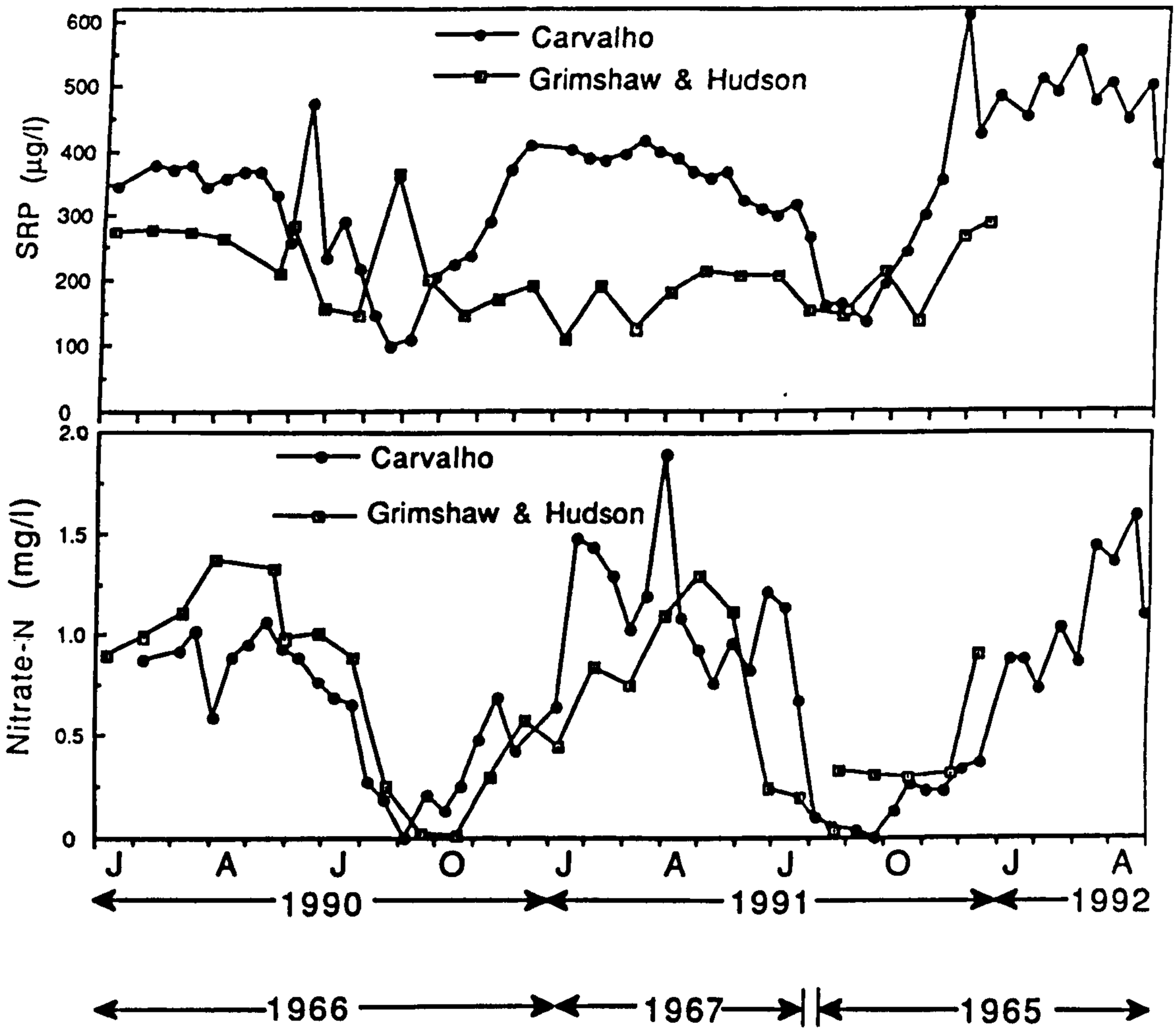


Fig. 2.11. Comparison of the nitrate-nitrogen and soluble reactive phosphorus data between that of Grimshaw & Hudson (1970) and that of the present study (Carvalho). Data from Grimshaw & Hudson was calculated as the mean epilimnion concentration (0-6 m).

where there is usually a brief spring diatom phase, followed by a major summer growth of either *Microcystis* or *Ceratium* (Belcher & Storey, 1968; Reynolds & Bellinger, 1992). If a more detailed examination of the data is made it is clear that the change is less "striking". The only clear difference is the rise in dominance of *Microcystis* (never common in the five years covered by the early surveys, and abundant in 14 out of 23 of the summers of the more recent surveys (1962-1989). This increase in abundance of *Microcystis* was confirmed in a study of algal remains in the sediments (Livingstone, 1979).

Changes in the other summer dominants are less obvious. *Ceratium* was very abundant in four out of five years covered by the early surveys, but has only been abundant in seven out of 23 years studied between 1962 and 1989; *Anabaena* was sparse in the early studies, but has been abundant in six out of 23 of the later years; *Coelosphaerium* was common in three out of five of the earlier surveys, but has been sparse in all the later surveys; and *Aphanizomenon* has been erratic throughout.

My results confirm the abundance of *Microcystis* over the summer, and the rise of *Anabaena* and decline of *Coelosphaerium* and*Ceratium.*

Reynolds (1979), Nelms (1984), and Reynolds & Bellinger (1992) have all described the changes as supporting evidence for the theory that the lake has changed from a state where the populations are light-limited, rather than nitrogen-limited. The increase in abundance of the non-nitrogen fixing cyanophyte *Microcystis* would support this theory, although this species has been shown to migrate with vertical speeds in excess of 3 m h^{-1} (Ganf, 1975), and so is able to tap hypolimnetic sources of

nitrogen. However, the decline of *Coelosphaerium* (non-N_2 fixer) and rise of *Anabaena* (N_2 fixer) would suggest that nitrogen depletion is still important, so it is difficult to conclude that the changes suggest nitrogen-limitation no longer applies.

Reynolds & Bellinger (1992) provide some evidence which suggests that the largest standing crops of *Ceratium* were achieved when there was a poor production of *Microcystis*, although they state that this was not always the case. Another explanation of the apparent decline of *Ceratium* in recent years could be that it is just an artefact of the different sampling techniques used. Belcher and Storey (1968), who used both methods, demonstrated the "great tendency to concentration of the larger forms (of phytoplankton) in the tow-net samples". It is known that *Ceratium* populations may form deep aggregations (Heaney and Talling, 1980), which may be below the top four metres sampled in this study and those since 1963, particularly in Rostherne Mere where the thermocline was around 6-7 m depth from July to September.

The increase in *Microcystis* may be a response to increased loadings of phosphorus and nitrogen. The nutrient concentrations may now be sufficient to allow phytoplankton to increase until they become light-limited (Reynolds, 1978b; Reynolds & Bellinger, 1992); *Microcystis* may then outcompete the other cyanobacteria. In some years when, for some reason, biomass does not increase as much, nitrogen-limitation may be more important, and the nitrogen-fixing cyanobacteria may dominate.

2.4.4 Water and nutrient budgets: implications for future management

2.4.4.1 Water budget

The results of the water budget showed that, over about two years, the four inputs: Rostherne Brook, Catchment North drainage, Catchment North groundwater, and direct rainfall, contributed on average, 73 %, 13 %, 4 %, and 10 % respectively. Despite the percentage contribution of the different sources remaining roughly the same over the two annual budgets (before and after sewage diversion), the period from 3 May '90 to 14 May '91 was a much wetter period than from 23 Jul '91 to 21 Jul '92.

The budget also showed that direct evaporation was responsible for the loss of about 10 % of these total inputs and the extra volume of water required to balance the budget was equivalent to 35 % of the total inputs.

Possible contributors to the balance include:-

1. Groundwater flow not accounted for. Groundwater inputs were not accounted for the whole of Catchment North, just for the spring in Harper's Bank Wood. There may have been additional groundwater inputs in other areas of Catchment North.

2. Errors created by extrapolation of the spot flow measurements to cover a two week period. This is particularly important after periods of heavy rain, when for a short period, flows can exceed the base flow by many times. The backflow of Blackburn's Brook produced errors in this way.

3. Errors produced in estimating potential evaporation and actual evapotranspiration. During the summer months the Thornthwaite equation exaggerates evaporation (Shaw, 1988), over-estimating losses from the catchment and the lake surface.

Blackburn's Brook did flow backwards at the end of January/start of February 1990 which led to a big rise in the water level of the lake. When the level of the River Bollin subsided the flow was able to revert back to its usual direction, with very high outflow rates during February and the start of March.

From examination of the flow measurements (Appendix 3) it is apparent that the large variations in the amount of water required to balance the budget for some of the quarterly periods may have been due to extrapolating unusual spot flow measurements, although these errors ought to balance out over the study period as a whole.

As Rostherne Brook is the major source of water, the nutrients contributed by it must be of prime importance. Water entering from this source will be a mixture of run-off and drainage from the catchment and inputs from the groundwater, and in previous years effluent from the two STWs. Flow measurements of Mere STW, from dilution gauging, have given a dry weather flow of 0.3 Ml day^{-1} (0.0035 $m^3 s^{-1}$) (NWWA, 1983), however, this does not enter Rostherne Brook over the summer months as the water level in Little Mere drops below the level of the sluice at its outflow. Flow from Rostherne STW is insignificant in the water budget (0.02 Ml day^{-1}, Mike Walker (NWWA), pers. comm.).

From the estimations of rainfall and evaporation over the catchment, if run-off and drainage were the only sources, there ought to be no flow in Rostherne Brook from March to August (inclusive) in 1990 and April to September in 1991. As the Thornthwaite equation exaggerates evaporation over the summer months, these periods would have been shorter. However, flows recorded during the driest months of the year ought to represent the contribution of groundwater only. Figure 2.12 shows the seasonality of total alkalinity in Rostherne Brook and in the spring. Typical of groundwater (Stumm & Morgan, 1981), the spring had a relatively high alkalinity, of about 4.1 mequiv. l^{-1}, which remained fairly constant throughout the year, whereas the total alkalinity of Rostherne Brook fluctuated seasonally, around 2.4 mequiv. l^{-1} in winter and over 4 mequiv. l^{-1} in summer. This suggests that at times, in the summer, the flow in Rostherne Brook is more or less solely due to groundwater seepage. The minimum flows recorded over the three years were 0.028 m^3s^{-1} (1990), 0.030 m^3s^{-1} (1991), 0.031 m^3s^{-1} (1992). Whether these figures can be extrapolated for the rest of the year depends upon whether groundwater inputs are constant. Assuming they are, the relative contributions from groundwater and from run-off/drainage can be estimated (Table 2.9). These estimates suggest that for the two year budget period, of the water entering Rostherne Mere from the catchment, about 36 % was from groundwater, and 64 % was surface run-off and drainage (and during winter and spring a small contribution from the sewage works). The study was, however, carried out during two very dry years, particularly

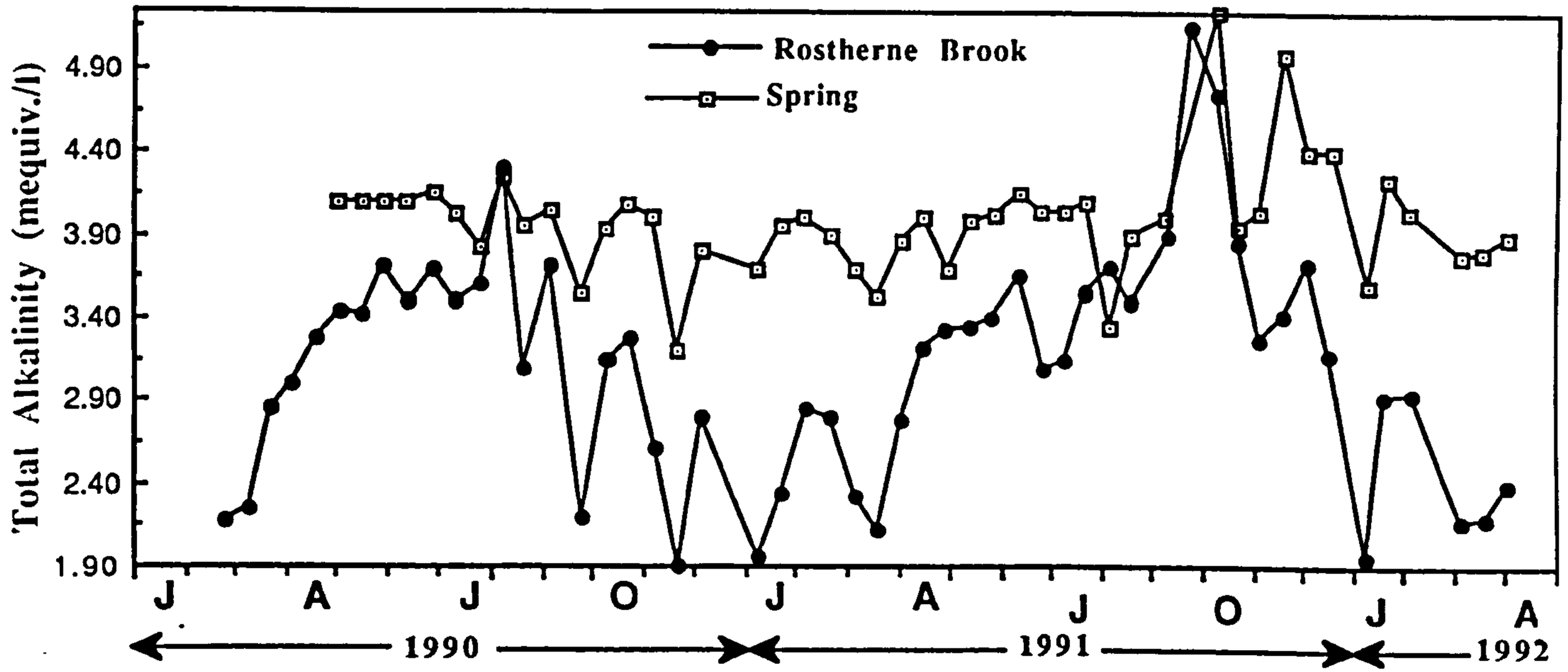


Fig. 2.12. Seasonality of total alkalinity in Rostherne Brook and Harper's Bank Spring

Table 2.9. Estimated volumes of groundwater (V_{gr}) and other sources of water (V_r) for the Rostherne Brook catchment, Catchment North, and the catchment as a whole. Values given are $m^3 \times 10^{-5}$ of the volume calculated. Values in brackets indicate % of the total input for the given period.

	Rostherne Brook Catchment		Catchment North		Total Catchment	
Period	V_{gr}	V_r	V_{gr}	V_r	V_{gr}	V_r
22.2.90-2.5.90	1.69	2.24	0.27	0.22	1.96	2.46
3.5.90-11.7.90	1.69	1.07	0.27	0	1.96	1.07
12.7.90-24.9.90	1.81	3.44	0.29	0.07	2.10	3.51
25.9.90-7.1.91	2.54	8.79	0.41	3.68	2.95	12.47
8.1.91-14.5.91	3.29	5.17	0.49	1.34	3.78	6.51
15.5.91-22.7.91	1.79	1.18	0.27	0	2.06	1.18
23.7.91-23.9.91	1.63	0.44	0.24	0	1.87	0.44
24.9.91-18.12.91	2.23	2.66	0.33	0.88	2.56	3.54
19.12.91-12.5.92	3.92	8.08	0.56	2.27	4.48	10.35
13.5.92-21.7.92	1.88	0.38	0.27	0	2.15	0.38
3.5.90-14.5.91	9.33	18.47	1.46	5.09	10.79 (31)	23.56 (69)
23.7.91-21.7.92	9.66	11.56	1.40	3.15	11.06 (43)	14.71 (57)
3.5.90-12.5.92	18.9	30.83	2.86	8.24	21.76 (36)	39.07 (64)

1991, so the percentage contribution from groundwater is probably, on average, less than 36 %.

As 64 % of the inputs to Rostherne Mere were due to surface run-off and drainage, the flushing rate will show a seasonality corresponding to these inputs, hence the lower flushing rates over the summer months due to greater evapotranspiration rates over these months.

2.4.4.2 Phosphorus budget

Rostherne Brook was by far the most significant of the external sources of phosphorus to the lake. The budget shows that, in the "annual" period prior to sewage diversion, it accounted for 2250 kg, or 96 %, of the external phosphorus load to the lake; the year following diversion it accounted for 504 kg, or 86 %, of the external phosphorus load to the lake.

To deduce the change due to the sewage diversion the 90/91 figure must be adjusted to represent 365 days:

2250 kg x (365/377) = 2178 kg,

change in loading due to sewage diversion = 2178 kg - 504 kg

= 1674 kg

This figure assumes the amount from other sources remained the same over the two budget periods. The water budget showed that the 91/92 budget period was a much drier year than the 90/91 budget period; in the latter year, Catchment North drainage inputs, were 71 % of the previous years inputs. Groundwater inputs, on the other hand, appeared to be greater in the 91/92 budget period. The change in loading must, therefore, be adjusted to take into account changes in loading from these two sources:

Annual phosphorus loads from Catchment North drainage for 90/91 and 91/92 were 53 kg and 42 kg respectively.

Rostherne Brook catchment = 705 ha

Catchment North = 187 ha

therefore, assuming the catchment land-use was similar,

loading from Rostherne Brook drainage 90/91 = 53 x (705/187)

= 200 kg

loading from Rostherne Brook drainage 91/92 = 42 x (705/187)

= 158 kg

200 kg -158 kg = 42 kg

i.e. a reduction of about 42 kg was due to a reduction in loading from drainage.

The load from groundwater to Rostherne Brook can be roughly estimated using the load from groundwater in Catchment North and the estimation of groundwater entering the Rostherne Brook catchment (Table 2.9):

Rostherne Brook groundwater inputs before diversion:

(Rostherne Brook groundwater/Catchment North groundwater)

x Catchment North groundwater load

= (9.33/1.46) x 7 kg

= 45 kg

Rostherne Brook groundwater inputs after diversion:

= (9.66/1.40) x 5 kg

= 35 kg

45 kg -35 kg = 10 kg

i.e. a reduction of about 10 kg was due to a reduction in loading from groundwater.

Therefore,

Sewage effluent load = total change in loading - change from sources other than sewage effluent

= 1674 kg - 42 kg - 10 kg

= 1622 kg

The NWWA (1983) calculated an annual load of 832 kg of soluble reactive phosphorus. This is lower than my estimate but this is as expected as it excludes particulate and soluble, unreactive phosphorus. It is also based on the mean concentration of SRP in the sewage effluent and a single measurement of dry weather flow. There is a large source of error associated with this measurement as most flow is pumped to the works (NWWA, 1983).

From the data on people served by the STW (3315 people), assuming 1 person contributes 0.77 kg of total phosphorus per year (Moss *et al.*, 1988), the annual load into Little Mere ought to be 2553 kg. This figure is greater than my loading figure, which suggests that some phosphorus is lost from the water as it flows down Rostherne Brook from Little Mere. This was shown to be the case by the NWWA (1983). Possible reasons include sedimentation of particulate phosphorus, precipitation on the stream bed in calcium and iron complexes, and uptake by aquatic plants.

Even taking into account the load from the STW, drainage, and groundwater, this leaves a remaining load of 311 kg unaccounted for. Possible sources of this are additional phosphorus-rich catchment inputs, such as slurry from intensive stock units, in the Rostherne Brook catchment that are not present in Catchment North, and internal release from Little

Mere. The latter source was probably quite important in both years but should start to decrease in the future with an improvement in the dissolved oxygen concentration in Little Mere.

All the other external sources: Catchment North groundwater, Catchment North drainage, direct rainfall, and the bird roost were relatively insignificant in their contributions compared to Rostherne Brook. Table 2.10 gives a summary of the external phosphorus inputs to Rostherne Mere before and after diversion.

The hypothesis that the high nutrient concentrations in the lake are the result of the bird roost (Brinkhurst & Walsh, 1967) is clearly false, even after sewage diversion it only accounted for 3 % of the total external phosphorus load. Neither is there any evidence of high phosphorus concentrations in the groundwater. This indicates that the high phosphorus concentration of the lake water is not derived from minerals in the drift, but appears to be anthropogenic, from sewage and run-off from agricultural land.

Despite a large reduction in the total external inputs to the lake, the phosphorus output of Rostherne Mere increased slightly, which suggests that either the internal source of phosphorus (sediment release) was greater, or there was less sedimentation, in the year after diversion, compared to before diversion. The latter reason appears unlikely as the flushing rate for the year after diversion was lower than for the year before diversion, therefore, there ought to be greater loss of phosphorus through sedimentation. The possibility that internal

Table 2.10. Total phosphorus (kg) contribution from external sources to Rostherne Mere. Values in brackets indicate the % contribution to the total, for the corresponding period.

	1990/91	1991/92
Mere STW	1622 (72)	-
Rostherne Brook: drainage	200 (9)	158 (27)
Rostherne Brook: groundwater	45 (2)	35 (6)
Rostherne Brook: other	311 (14)	311 (53)
Catchment North: drainage	53 (2)	42 (7)
Catchment North: groundwater	7 (0)	5 (1)
Direct rainfall	20 (1)	19 (3)
Bird roost	22 (1)	20 (3)
Total External Inputs	2280	590

sources of phosphorus were greater in the budget period after diversion is supported by the values calculated to balance the budget. The pre-diversion budget shows a net loss to the sediment of 628 kg, the post-diversion budget shows a net gain from the sediment of 1059 kg. This observation of a large net annual release in the first year after reduction in phosphorus loading was also made in a study of 18 lakes undergoing restoration, although only in shallow lakes (Sas, 1989).

2.4.4.3 Dissolved inorganic nitrogen

As with phosphorus, Rostherne Brook was by far the most significant of the external sources of DIN to the lake. The budget shows that, in the "annual" period prior to sewage diversion, it accounted for 10910 kg, or 86 %, of the external DIN load to the lake; the year following diversion it accounted for 6282 kg, or 84 %, of the external DIN load to the lake.

To deduce the change due to the sewage diversion the 90/91 figure must first be adjusted to represent 365 days:

10910 kg x (365/377) = 10563 kg,

change in loading = 10563 kg - 6282 kg

= 4283 kg

as with the phosphorus loading, this figure must be adjusted to take into account changes in loading from drainage and groundwater:

Annual DIN loads from Catchment North drainage for 90/91 and 91/92 were 1703 kg and 1163 kg respectively. therefore, assuming the catchment land-use was similar,

loading from Rostherne Brook drainage 90/91

= 1703 x (705/187)

= 6420 kg

loading from Rostherne Brook drainage 91/92

= 1163 x (705/187)

= 4385 kg

6420 kg -4385 kg = 2035 kg

i.e. a reduction of about 2035 kg was due to a reduction in loading from drainage.

Rostherne Brook groundwater inputs before diversion:

= (9.33/1.46) x 24 kg

= 153 kg

Rostherne Brook groundwater inputs after diversion:

= (9.66/1.40) x 24 kg

= 166 kg

166 kg -153 kg = 13 kg

i.e. a gain of about 13 kg was due to a change in loading from groundwater.

Therefore,

Sewage effluent load = total change in loading - change from sources other than sewage effluent

= 4281 kg - 2035 kg + 13 kg

= 2259 kg

This figure corresponds closely to a rough estimate provided by the NWWA (1983) of an annual load of 2190 kg.

Even taking into account the load from the STW, drainage, and groundwater this leaves a remaining load of 1731 kg unaccounted for. This could be due to an underestimation of the

load from drainage in the Rostherne Brook catchment compared to Catchment North. Another possible source was the internal release of ammonium from Little Mere.

Of the other known external sources only Catchment North drainage was of any significance, before and after diversion respectively providing 14 % and 16 % of the total external inputs of the annual budgets. Catchment North groundwater, and direct rainfall were insignificant in their contributions. Table 2.11 gives a summary of the external DIN inputs to Rostherne Brook before and after diversion.

2.5 Impact of sewage diversion on Rostherne Mere

The response of lakes to a decrease in nutrient loading varies. It is often the case that a reduction in nutrient loading does not immediately lead to a reduction in the concentration of the nutrient in the lake, and, therefore, a reduction in phytoplankton biomass. The resilience of the lake to change may depend on factors such as flushing rate, internal release from the sediments, and the biological community (Jeppesen *et al.*, 1991).

Two questions must first be answered in order to predict what change in phytoplankton biomass ought to occur, following the reduction in loading:

1) Are the algae nutrient limited, and if so, by what ?

2) What is the relationship between the external load of the limiting nutrient and the phytoplankton biomass ?

As discussed earlier, it does not appear at present that the phytoplankton biomass in Rostherne Mere is phosphorus-

Table 2.11. Dissolved inorganic nitrogen (kg) contribution from external sources to Rostherne Mere. Values in brackets indicate the % contribution to the total, for the corresponding period.

	1990/91	1991/92
Mere STW	2259 (18)	-
Rostherne Brook: drainage	6420 (52)	4385 (59)
Rostherne Brook: groundwater	153 (1)	166 (2)
Rostherne Brook: other	1731 (14)	1731 (23)
Catchment North: drainage	1703 (14)	1163 (16)
Catchment North: groundwater	24 (0)	24 (0)
Direct rainfall	17 (0)	17 (0)
Total External Inputs	12307	7486

limited, but nitrogen may be limiting. However, following the big reduction in phosphorus loading to the lake this may change. The N:P ratio after diversion can be calculated using estimates of lake nutrient concentrations calculated from the nutrient loads after diversion.

The relationship between loading and lake nutrient concentration cannot be established without consideration of sedimentation and flushing (Vollenweider, 1969b; Dillon, 1975). This led to the development of the prediction of mean lake total phosphorus concentration from load by equation 2.7 (Vollenweider & Kerekes, 1982). Assuming that similar factors are important in the relationship between DIN loading and mean DIN concentration, this equation can be used to predict future mean lake concentrations of DIN and total phosphorus:

$$[Nu]_{lake} = [Nu]_i / (1 + \sqrt{R}) \quad \text{(equation 2.7)}$$

where,

$[Nu]_{lake}$ = mean lake concentration of the nutrient

$[Nu]_i$ = mean inflow concentration of the nutrient

R = mean residence time of water

For Rostherne Mere, after diversion:

$[P]_i$ = mean inflow concentration of total phosphorus

$$= \frac{\text{annual load of total phosphorus}}{\text{annual inflow volume of water}}$$

$$= \frac{590 \text{ kg yr}^{-1}}{2.94 \times 10^6 \text{ m}^3 \text{ yr}^{-1}}$$

$$= 0.20 \text{ mg l}^{-1}$$

$[DIN]_i$ = mean inflow concentration of DIN

$$= \frac{\text{annual load of DIN}}{\text{annual inflow volume of water}}$$

$$= \frac{7486 \text{ kg yr}^{-1}}{2.94 \times 10^6 \text{ m}^3 \text{ yr}^{-1}}$$

$$= 2.55 \text{ mg l}^{-1}$$

$$R = \frac{\text{volume of Rostherne Mere}}{\text{annual volume of outflow}}$$

$$= \frac{6.6 \times 10^6 \text{ m}^3}{3.6 \times 10^6 \text{ m}^3 \text{ yr}^{-1}}$$

$$= 1.83 \text{ yr}$$

therefore, using equation 2.5:

$$[P]_{lake} = [P]_i / (1 + \sqrt{R})$$

$$= 0.20 / (1 + \sqrt{1.83})$$

$$= 0.085 \text{ mg l}^{-1}$$

$$= 85 \text{ µg l}^{-1}$$

$$[DIN]_{lake} = [DIN]_i / (1 + \sqrt{R})$$

$$= 2.55 / (1 + \sqrt{1.83})$$

$$= 1.08 \text{ mg l}^{-1}$$

$$N:P = 1.08:0.085$$

$$\approx 13:1$$

This ratio above uses the predicted value of total P, and not orthophosphate-P, and so the real ratio ought to be even higher than this. This ratio suggests that in the future, assuming the predicted lake concentrations are attained, phosphorus may become important in limiting the phytoplankton biomass, although, even with this estimate of phosphorus concentration, it is still not certain. This may be even more likely if phosphorus loading is reduced further following a reduction in internal release of phosphorus from Little Mere.

Most previous research has concentrated on phosphorus as the key limiting nutrient. This has shown that the relationship between phosphorus loading and lake concentration slightly underestimates concentrations at low levels, and overestimates concentrations at higher levels. Actual $[P]_{lake}$ can be estimated from the loading using the OECD standard regression equation (Vollenweieder & Kerekes, 1982):

Actual $[P]_{lake} = 1.55\ (\text{Predicted } [P]_{lake})^{0.82}$ (equation 2.8)

for Rostherne Mere, predicted $[P]_{lake} = 85\ \mu g\ l^{-1}$

therefore, substituting this in equation 2.8,

Actual $[P]_{lake} = 59\ \mu g\ l^{-1}$

Unfortunately, no such regression equation is available for the relationship between DIN loading and lake concentration.

These relationships assume that lakes can be treated as mixed reactors in steady state ("repetitive state over time" for which the sum of the changes in concentration of the nutrient over a given period of time are equal to zero ($\sum \pm d[Nu]/dt = 0$)). This assumption, however, is not true for most lakes. The relationship described in equation 2.8 is the average statistical relationship between phosphorus load and phosphorus concentration. Variation from the relationships may be caused by error in estimating the load. This could be true for Rostherne Mere: the load from run-off and drainage may have been lower than on average because of the dry year, or it may actually have been higher than in future years, due to large amounts of phosphorus still being released from Little Mere. Variation from the relationships may also be due to the fact that the lake is functionally different; sedimentation rate may be above or below normal, there may be additional sinks of nutrients, such

as denitrification, or there may be some form of internal release of phosphorus and ammonium.

The relationship between phytoplankton biomass and nutrient concentration has not been developed for nitrogen, as nitrogen-fixing cyanobacteria often become established in conditions of nitrogen-limitation. The relationship between phytoplankton biomass (usually in terms of chlorophyll *a*) and lake phosphorus concentration, however, has been examined on many occasions (Sakamoto, 1966; Lund, 1970; Dillon & Rigler, 1974). In phosphorus-limited lakes, the annual mean chlorophyll *a* concentration and the maximum chlorophyll *a* concentration can be estimated from the predicted annual lake phosphorus concentration using the OECD standard regression equations (Vollenweieder & Kerekes, 1982):

$$\text{annual mean [Chl a]} = 0.37\ ([P]_{lake})^{0.82} \quad \text{(equation 2.9)}$$

$$\text{maximum [Chl a]} = 0.74\ ([P]_{lake})^{0.89} \quad \text{(equation 2.10)}$$

Using the corrected figure of 59 $\mu g\ l^{-1}$, and assuming phosphorus-limitation, the future chlorophyll *a* concentration of Rostherne Mere can be predicted using equations 2.9 and 2.10:

annual mean [Chl a] = 10 $\mu g\ l^{-1}$

maximum [Chl a] = 28 $\mu g\ l^{-1}$

This analysis clearly gives an indication of what is probably one of the best scenarios that could be hoped for in Rostherne Mere. This state would certainly not be achieved immediately; assuming that the lake can be treated as a homogeneous system without any nutrient exchange between sediment and water, then the time required to reduce the surplus pool of phosphorus in the lake water by 95 %, by simple flushing, will be three

times the hydraulic retention time (Sas, 1989). Applying this to Rostherne Mere means that it would take about five years to get a 95 % reduction. It would be wrong, however, to blindly apply all these relationships for predictive purposes, regardless of known false assumptions made, specifically, the fact that there is a large amount of phosphorus released internally from the sediment over the summer growth phase. This is clearly apparent when the predicted annual mean phosphorus concentration was 59 μg l^{-1}, but that observed after diversion was 492 μg l^{-1}. In a study of 27 Danish lakes undergoing recovery, following a loading reduction, Jeppesen *et al.* (1991) observed that, mainly because of internal release of phosphorus, lakes with a retention time similar to that of Rostherne Mere showed delays up to ten times longer than could be explained by dilution (i.e. up to 50 years for Rostherne Mere). Seasonal variation in retention time may contribute to resilience. If the retention time is even higher in summer than the annual mean retention time, as is the case in Rostherne Mere, phosphorus released is more likely to return to the sediment than be flushed out, prolonging the recovery phase. Planktivorous and benthivorous fish may also contribute to the resilience of the lake. This is partly by enhancement of phosphorus release from the sediment due to feeding activity (Andersson *et al.*, 1978) and partly because a high density of fish may prevent occurrence of large cladocerans, decreasing the grazing pressure on phytoplankton. This may allow higher biomass algae to dominate the system.

2.6 Summary

Rostherne Mere has been eutrophic for many years. Cyanobacteria have dominated the phytoplankton community throughout this century, although it is most probable that the phytoplankton crop-size has increased throughout this period due to increases in loading of both nitrogen and phosphorus. Grazing pressure did not appear to have any significant effect on the phytoplankton-crop size, although it may have had a slight limiting effect. It appears that the large, summer phytoplankton crops are restricted to periods when the lake is thermally stratified and are either nitrogen-limited, or light-limited.

Rostherne Brook was the major external source of nutrients for both total phosphorus and DIN. The bird roosts were not an important source of phosphorus, and neither was there any evidence to suggest that the eutrophic state was naturally derived from phosphorus-rich minerals in the drift. Phosphorus loadings from Rostherne Brook have been reduced dramatically following a recent diversion of sewage effluent that entered the lake. External inputs may decrease even further with a reduction in the amount of phosphorus released from the sediment in Little Mere. It is, therefore, possible that in the future the phytoplankton crop-size will become phosphorus-limited. This, however, depends greatly on internal sources of phosphorus in Rostherne Mere. This source of nutrients may delay recovery of the lake for up to 50 years, and even then phosphorus-limitation is uncertain.

DIN inputs have also been reduced with the sewage diversion, so it may be that nitrogen-limitation will become more severe. Reduction any further in DIN loadings will be

difficult to achieve as the remaining nitrogen is generally from diffuse sources, such as run-off from agricultural land. Changes in ploughing practice, amount of land left fallow, and timing of fertiliser/slurry applications are likely to be much more beneficial than straight reductions in applications (Harris & Skinner, 1992). A reduction in phytoplankton crop-size may come about with a decline in nitrogen concentrations, although Schindler (1977) has hypothesized that attempts to control eutrophication by nitrogen removal may just promote nitrogen-fixing cyanobacteria, which are still objectionable from a water quality standpoint. The usefulness of further nutrient control in the catchment is therefore questionable.

Chapter 3: Rostherne Mere enclosure experiments

3.1 Introduction

The monitoring of Rostherne Mere highlighted two areas of controversy about the role of grazing zooplankton: firstly, their importance in producing the spring, clear-water phase, and secondly, their role in limiting the summer phytoplankton biomass, in particular their relationship with cyanobacteria. To comprehend more fully the role of the zooplankton community it was necessary to conduct experimental studies.

Laboratory experiments were considered inappropriate as zooplankton generally do not survive for long in small culture flasks; larger-scale enclosure experiments are also more suitable in that the enclosed community has a greater chance of being representative of that of the lake, and edge effects are reduced. Carrying out the experiments *in situ* also allows factors not taken into account in the experiment, such as light intensity, daylength, and temperature, to resemble the situation in the lake, as close as possible. However, as a result of the size and cost of enclosures, and the time involved in sampling and analysing results, replication has to be limited.

Enclosures are not perfect replicas of a lake environment. Circulation within them is inhibited, edge effects are greater than in the lake, and nutrient loading from the catchment, and from the sediment, may be excluded in closed enclosures. Very large-scale enclosure studies, or whole-lake studies, may remove problems of spatial scale and heterogeneity, but lack reference or adequate control treatments. It was, therefore, decided to carry out relatively small-scale, *in situ*, enclosure studies.

Freshwater plankton communities are ideal for such experiments as populations large enough to be sampled repeatedly can be enclosed. Factors (predation and resources) can easily be manipulated and species have relatively short life-spans, allowing experiments to include several generations. Replication of treatments is easily possible.

Factorial experiments enable effects of more than one factor to be analysed simultaneously, saving time, effort, and money. Also, factorial analysis can test for interaction among factors. Despite this, there have been few experimental studies in which both zooplankton grazers and chemical factors have been manipulated simultaneously.

In the present study, two factorial experiments were carried out in Rostherne Mere, to investigate the role of the zooplankton community in shaping the seasonal patterns observed in the phytoplankton community. Details of the experiments are described separately.

3.2 Methods

3.2.1 Design and apparatus

There are differing opinions about the optimal size and structure of an enclosure and these will depend to a large extent on the aims and duration of the experiment (de Noyelles *et al.*, 1980; Lund & Reynolds, 1982). In the present study, clear, colourless polyethylene bags (2 m deep, 1 m diameter, 125 μm wall thickness) were used. The thickness was chosen as a compromise between strength, flexibility, and brittleness. Enclosures were sealed at the bottom and open to the

atmosphere at the top. Lake water was pumped from a depth of 1 m into the polyethylene bags, which were suspended from a wooden frame, anchored to the lake bottom. The bags were filled with about 1200 litres of water. The frame was buoyed up with large, air-filled plastic bottles, which kept the open ends of the bags about 0.3 m above the lake surface (Plate 3.1). Details of the design and timing of each experiment are described separately.

3.2.2 Sampling methods

Sampling was carried out at 3-6 day intervals from the upper 1 m of the enclosures and upper 1 m of the lake. Before sampling, the water in the enclosures was stirred using a wooden oar. Samples for chemical analysis and phytoplankton were collected using a bucket. Water for chemical analysis was stored in acid-washed 1-litre Pyrex bottles. Alkalinity, pH, soluble reactive phosphorus, nitrate-nitrogen, ammonium-nitrogen, silicate-silicon, and chlorophyll *a* were determined in the laboratory, as described in Chapter 2. Samples for phytoplankton analysis were preserved with Lugol's solution immediately after sampling. To make interspecific comparisons of performance it was necessary to convert the populations into biovolumes. Bio-volumes (Table 3.1) were determined from measurements of the linear dimensions of ten preserved specimens of each taxon, using the formula for the appropriate geometric shape (Wetzel & Likens, 1991). Values were taken from the literature (Blomqvist *et al.*, 1989; Reynolds & Bellinger, 1992) for those taxa which were rare in the counts, and which had a fairly uniform size. Bio-volume density ($mm^3\ l^{-1}$) was

Plate 3.1: Experimental enclosures used on Rostherne Mere and Oak Mere.

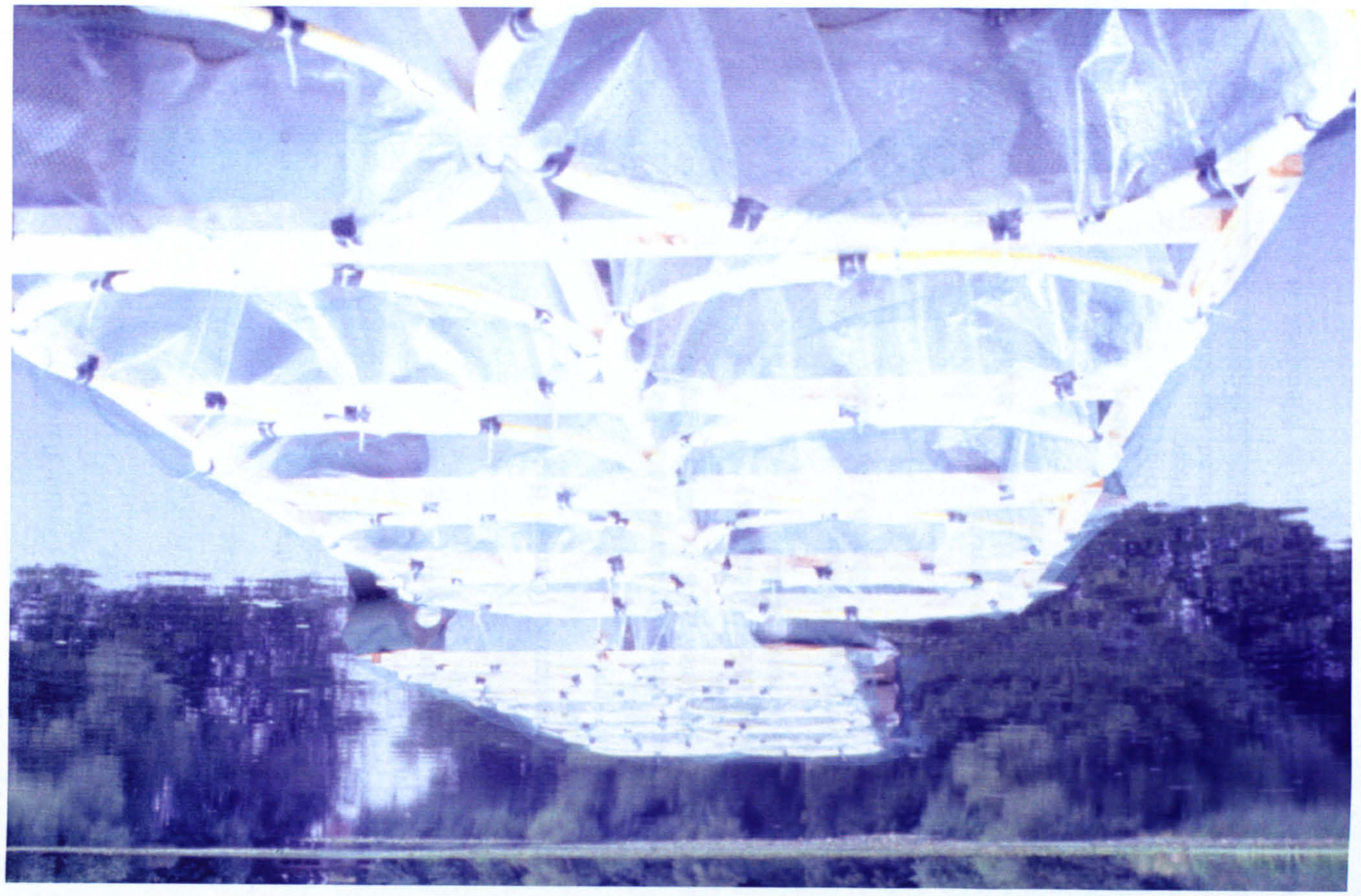


Table 3.1 Volumes of taxa recorded in enclosure experiments.

		Volume (μm^3)	
Chlorophyta			
Actinastrum sp.	cell	300	
Ankistrodesmus falcatus (Corda) Ralfs	cell	25	
Ankyra judayi (G. M. Sm.) Fott	cell	24	(a)
Botryococcus braunni Kütz.	mean colony	4215	(b)
Chlamydomonas sp.	cell	345	
Chlorella sp.	cell	33	(a)
Closterium sp.	cell	2000	(a)
Coelastrum microporum Nag.	cell	145	
Dictyosphaerium sp.	cell	45	
Elakatothrix gelatinosa Wille	cell	80	
Eudorina unicocca G. M. Sm.	cell	380	(a)
Gleocystis sp.	cell	80	
Oocystis sp.	cell	150	
Pandorina sp.	cell	325	
Pediastrum duplex Meyen	cell	250	(a)
Scenedesmus spp.	cell	50	
Selenastrum sp.	cell	35	
Staurastrum sp.	cell	5800	
Tetraedron caudatum (Corda) Hansgirg	mean colony	315	
Cryptophyta			
Cryptomonas spp.	cell	2610	
Rhodomonas sp.	cell	215	
Pyrrophyta: Dinophyceae (dinoflagellates)			
Ceratium hirundinella (O. F. Müll.) Schrank	cell	43740	(a)
Gymnodinium sp.	cell	1480	
Bacillariophyceae (diatoms)			
Asterionella formosa Hass.	cell	950	
Cyclotella sp.	cell	910	
Fragillaria crotonensis Kitton	cell	623	(a)
Aulacoseira granulata (Ehrenb.) Simonsen	cell	847	(a)
Navicula sp.	cell	910	
Nitzschia sp.	cell	515	
Synedra acus Kütz.	cell	420	
Synedra ulna (Nitzsch) Ehrenb.	cell	10260	
Stephanodiscus neoastrea Hackansson & Hickel	cell	11120	
Stephanodiscus hantzschii Grun.	cell	400	
Cyanobacteria			
Anabaena circinalis Rabenh. *ex* Born. *et* Flah.	mean filament	3970	
Aphanizomenon flos-aquae Ralfs *ex* Born. *et* Flah.	mean filament	4170	
Coelosphaerium kuetzingianum Nag.	cell	80	(a)
Coelosphaerium naegelianum Unger	cell	45	(a)
Microcystis aeruginosa Kütz. emend. Elenkin	mean colony	4960	
Planktothrix agardhi (Gom.) Anagn. et Kom.	/mm length	39369	(a)

(a) Reynolds & Bellinger (1992); (b) Blomqvist *et al.* (1989).

determined for each taxon by multiplying mean taxon volume by taxon density.

Zooplankton samples were collected by 1 m vertical hauls, using a 300 µm mesh-size net. Samples were preserved and analysed as described in Chapter 2.

3.2.3 Statistical analysis

Data were analysed over the time series using two-way ANOVA with repeated measures (Gurevitch & Chester, 1986). This analysis tests for the main effects of the treatments separately over time, and their interaction. Sample date was considered a repeated measure, the analysis not assuming that successive dates are independent of each other. All analyses were run using the Statistical Analysis System General Linear Models (GLM) routine (SAS Institute Inc.). All dates except the initial sampling date were used in the analyses. Repeated measures ANOVA discards all values from a replicate if one or more sampling dates have missing values. To check for normality in the data, plots of fitted values in the ANOVA model against error terms were examined; when there was noticeable heterogeneity of error variance, ($\log_{10}$+1) transformations were performed.

To assess whether initial conditions were similar amongst the treatments, one-way ANOVA on the chlorophyll *a* concentrations and densities of dominant phytoplankton taxa were performed.

ANOVA could not be used when there was a complete absence of a species from certain treatments. In these cases effects were clear and treatment means were compared.

3.3 Experiment one

3.3.1 Introduction

In temperate lakes, a spring development of diatoms is often followed by a clear-water phase (Hutchinson, 1967). In some lakes the reason for the decline has been reported as being due to low silica concentrations (Lund, 1950), whilst in other studies top-down control by grazing zooplankton has been implicated (Luecke *et al.*, 1990). In Rostherne Mere, both explanations appear plausible. The increase in grazer density during the late spring appeared to be the reason for the high water clarity that followed the spring growth of diatoms, however, in both 1990 and 1991, silicate-silicon concentrations declined to less than 0.5 mg l^{-1}, a concentration that may limit growth of natural populations of some diatom species (Kilham, 1971). This experiment, therefore, aimed to investigate whether zooplankton density, or silicate concentration, or both, were important in limiting diatom numbers in the spring, in Rostherne Mere, and in producing the spring clear-water phase.

3.3.2 Methods

The experiment was carried out from 19 April 1991 to 3 May 1991

Four treatments were set up:

(1) Control. Enclosures filled with lake water with lake densities of phytoplankton and zooplankton.

(2) Reduced zooplankton. During the filling of these bags water was pumped through a 300 µm mesh-size net to remove cladoceran and copepod zooplankton.

(3) Added silicate-silicon. Silcate-silicon was added to the enclosures during filling to ensure good-mixing. It was added as $Na_2SiO_3.5H_2O$, made up as a stock solution in distilled water, to produce enclosure concentrations of 4 mg l^{-1}. This concentration was considered ample to prevent limitation of diatoms by silicon.

(4) Reduced zooplankton and added silicate-silicon. A combination of treatments two and three.

The four treatments will from hereafter be referred to as control, reduced zooplankton, silicate, and interaction respectively.

Treatments were run in triplicate, making a total of twelve enclosures. The placement of the treatments was randomized within the wooden frame.

3.3.3 Results

Standard error bars are omitted from the graphs of treatment means as there was great overlap between treatments. Because of the overlap, the reasons for the significant responses have to be viewed with caution.

3.3.3.1 Initial conditions and water chemistry

At the start of the experiment, the lake was just beginning to stratify. Concentrations of silicate-silicon, DIN, SRP, and chlorophyll *a* were 1.05 mg l^{-1}, 0.89 mg l^{-1}, 370 µg l^{-1}, and 8.4 µg l^{-1} respectively. The pH of the lake water was 8.4, however, addition of silicate stock-solution caused the pH to rise to 9.0 in half the enclosures. The phytoplankton community was

dominated by *Stephanodiscus hantzschii*. The zooplankton community was dominated by *Diaptomus gracilis* and cyclopoid copepods. *Daphnia cucullata* was also present.

One-way ANOVA performed on the initial chlorophyll *a* concentrations and densities of the dominant phytoplankton species revealed no significant differences between the treatments.

During the experiment the pH rose from 8.3 to 9.3 in the control and reduced zooplankton enclosures, and from 9.0 to 9.4 in the silicate and interaction enclosures, whilst it remained stable, around 8.3, in the lake (Fig. 3.1.1). By day 15, silicate-silicon concentrations had declined to less than 0.5 mg l^{-1} in the control and reduced zooplankton enclosures. In the enclosures enriched with silicate, the minimum concentration reached was 1.6 mg l^{-1}; lake concentrations declined from 1.1 mg l^{-1} to 0.8 mg l^{-1} (Fig. 3.1.1). Throughout the experiment DIN and SRP concentrations in the enclosures remained above 0.55 mg l^{-1} and 175 µg l^{-1} respectively; lake concentrations were even higher.

3.3.3.2 Response of the zooplankton community

Repeated measures ANOVA performed on *Diaptomus* densities (the dominant zooplankton), showed that, during the experiment, densities were significantly lower in the reduced zooplankton and interaction enclosures compared with the control and silicate enclosures (Table 3.2, Fig. 3.1.2). Densities in all four treatments collapsed during the first five days of the experiment, and then gradually recovered, although less so in the interaction and reduced zooplankton treatments. However, Cladocera densities were not significantly different between

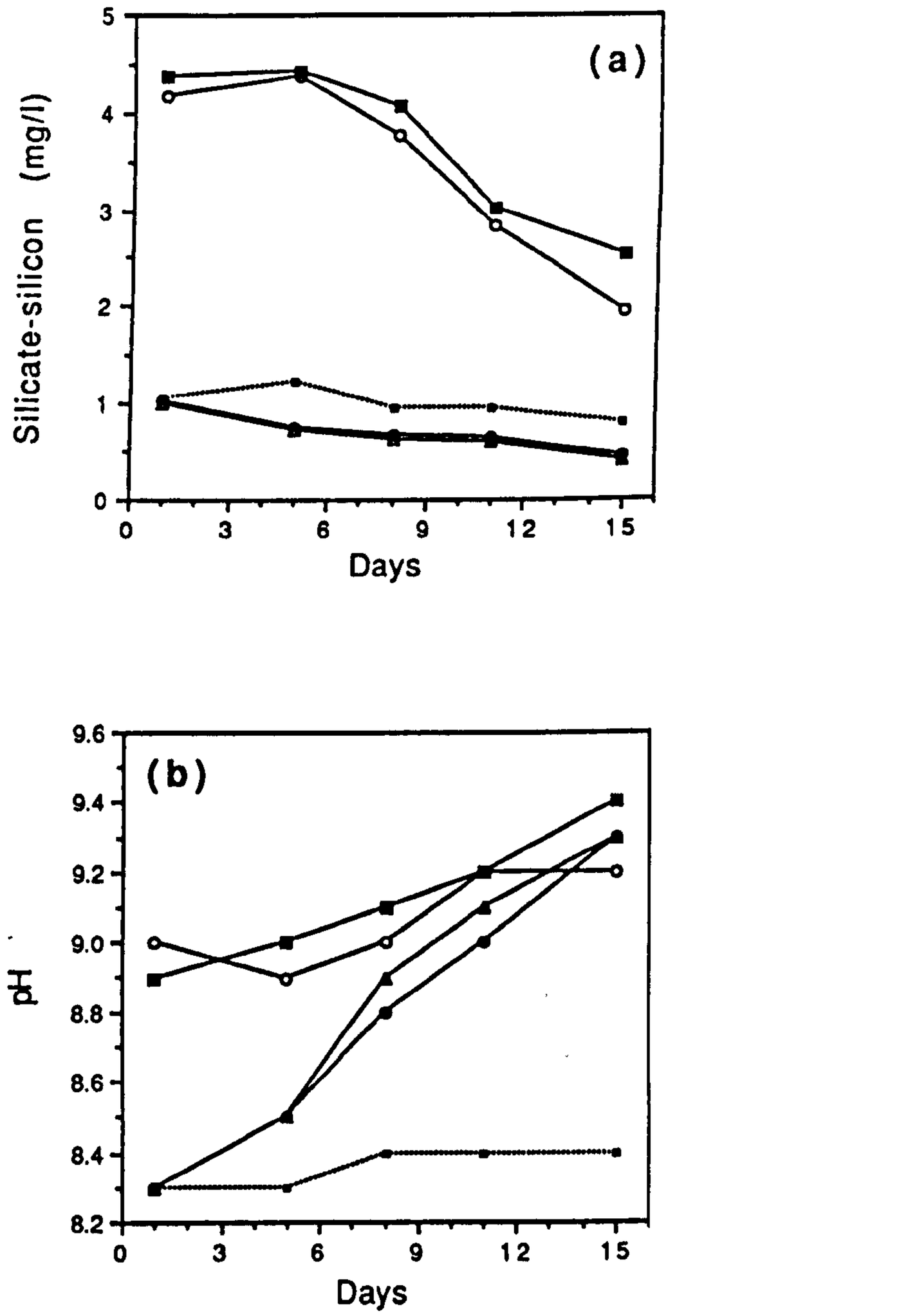


Fig. 3.1.1. Two variables monitored from day 1 to day 15: (a) mean silicate-silicon concentrations, and (b) mean pH, in lake (-▪-), control (-●-), added silicate (-○-), reduced zooplankton (-▲-), and interaction (-■-) treatments.

Table 3.2 Summary of the repeated measures ANOVA results on the effects of zooplankton and silicate on chlorophyll *a* concentrations, phytoplankton biovolumes, and zooplankton densities. F statistic and degree of significance are indicated. NS indicates no significance, * = $p<0.05$, ** = $p<0.01$, and *** = $p<0.001$.

Subject	Zooplankton effect	Silicate effect	Interaction effect
Chlorophyll *a*	0.92 NS	0.72 NS	1.81 NS
Bacillariophceae	0.02 NS	3.73 NS	0.18 NS
Asterionella	0.11 NS	0.30 NS	0.56 NS
S.neoastrea	0.71 NS	7.94 *	0.41 NS
S. hantzschii	0.39 NS	8.65 *	0.12 NS
Chlamydomonas	1.87 NS	0.02 NS	0.97 NS
Cryptomonas	64.46 ***	9.59 *	3.58 NS
Rhodomonas	0.61 NS	0.21 NS	0.00 NS
Gymnodinium	11.97 *	15.12 **	2.06 NS
Diaptomus	12.17 **	1.60 NS	0.01 NS
Cladocera	3.79 NS	0.11 NS	4.66 NS

treatments (Table 3.2, Fig. 3.1.2). Despite this, the reduced zooplankton treatment can be considered effective, as, in terms of numbers, Cladocera were of minor importance compared with *Diaptomus*.

3.3.3.3 Response of chlorophyll *a* concentrations and phytoplankton biovolumes

Chlorophyll *a* concentrations showed no significant response to any of the treatments (Table 3.2). Concentrations steadily increased in all four treatments, from about 11 μg l^{-1} up to about 27 μg l^{-1} by day 12, and then by day 15 had increased sharply to about 63 μg l^{-1} in the silicate treatment and about 93 μg l^{-1} in the other treatments (Fig. 3.1.2). Lake concentrations declined from 8.4 μg l^{-1} to 4.0 μg l^{-1}.

The diatoms dominated the phytoplankton at the start of the experiment. Both *Stephanodiscus* species showed a significant response to silicate (Table 3.2). *S.neoastrea* showed a general increase in density in the silicate and interaction treatments, compared with their decline and eventual disappearance from the control and reduced zooplankton treatments (Fig. 3.1.3). *S.hantzschii*, in general, declined in all four treatments, although the decline was less marked in the silicate and interaction treatments (Fig. 3.1.3). *Asterionella* increased throughout the experiment, showing no significant response to any of the treatments (Table 3.2, Fig. 3.1.3). Overall, the diatoms showed a substantial (but not significant at the 5 % level) response to silicate. Comparison of their overall treatment means, reveals the effect of silicate; control, reduced zooplankton, silicate, and interaction treatment mean

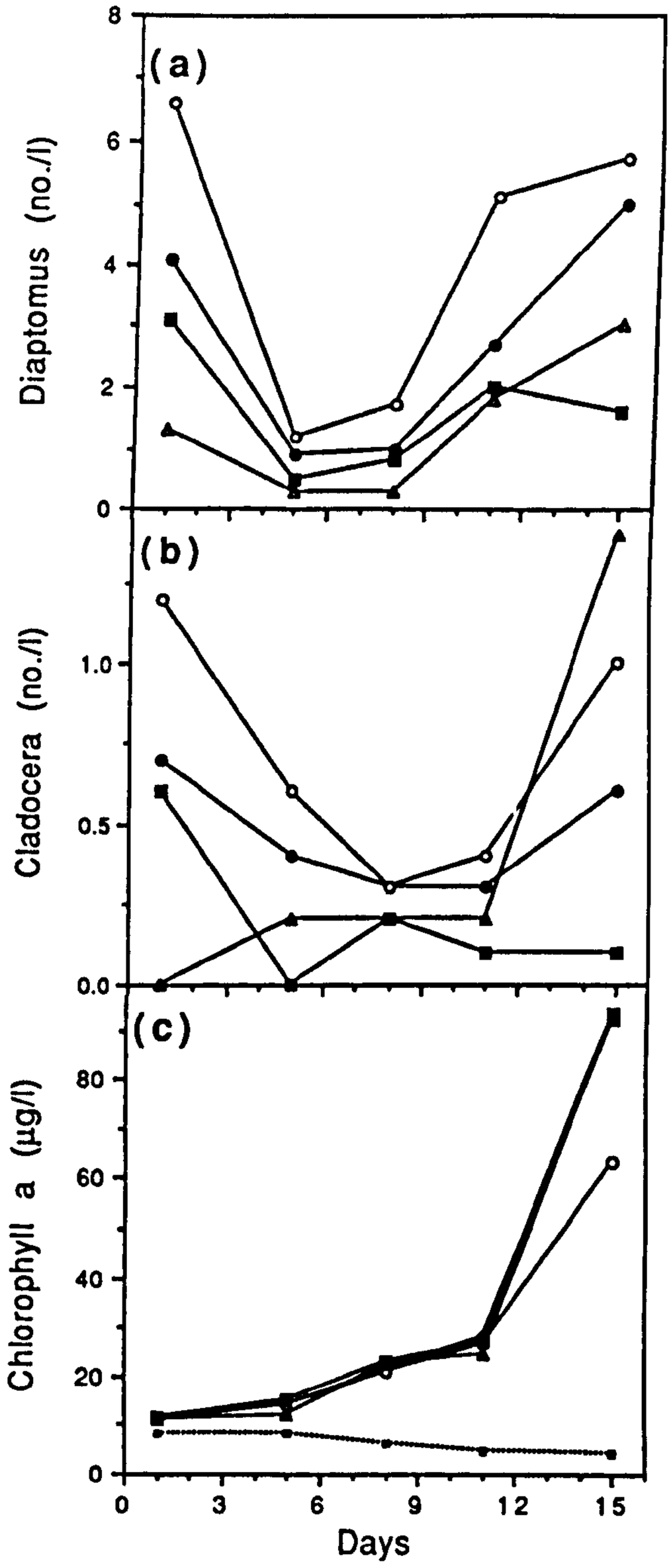


Fig. 3.1.2. Three variables monitored from day 1 to day 15: (a) mean *Diaptomus* density, (b) mean Cladocera density, and (c) mean chlorophyll *a* concentration, in lake (-▪-) (chlorophyll *a* only), and control (-●-), added silicate (-○-), reduced zooplankton (-▲-), and interaction (-■-) treatments.

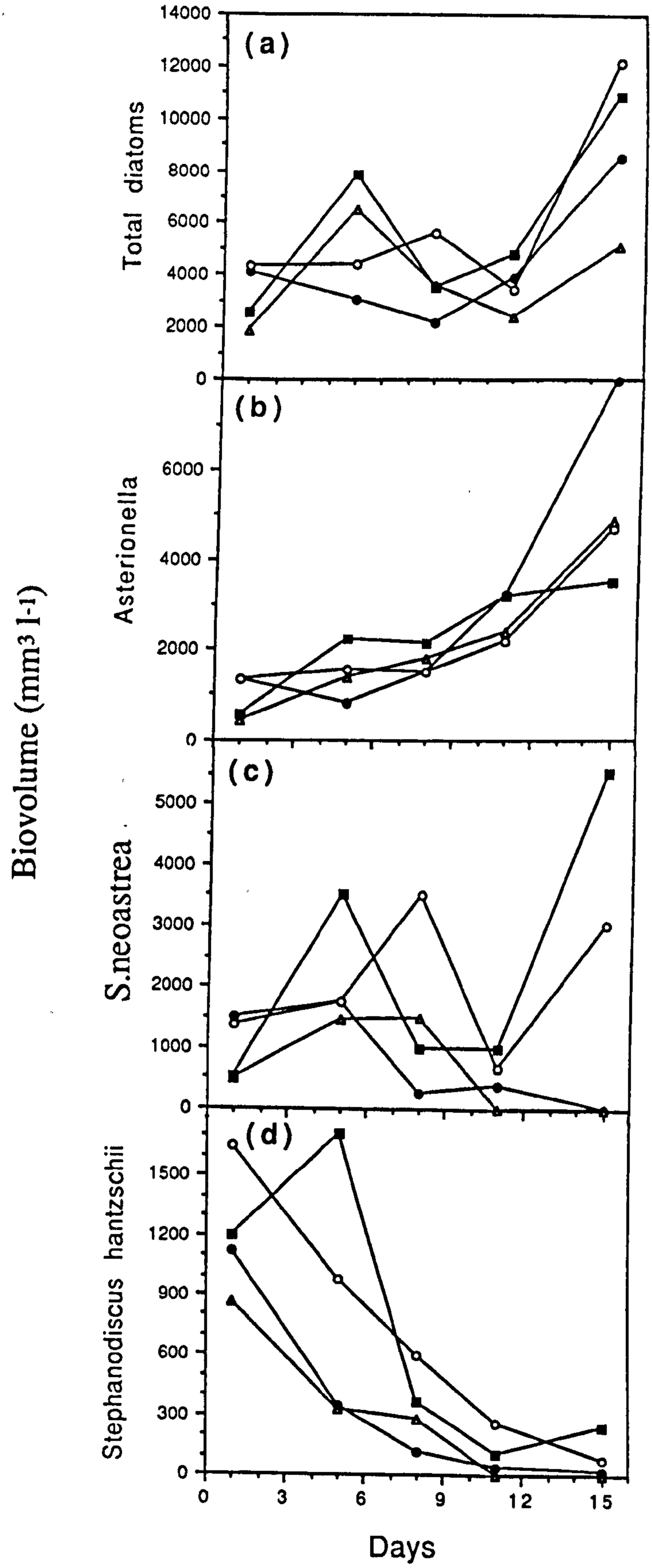


Fig. 3.1.3. Mean population densities of phytoplankton from day 1 to day 15: (a) total diatoms, (b) *Asterionella*, (c) *Stephanodiscus neoastrea*, and (d) *Stephanodiscus hantzschii*, in control (-●-), added silicate (-○-), reduced zooplankton (-▲-), and interaction (-■-) treatments.

biovolumes were 4.34 x 10^6 μm^3 ml^{-1}, 3.41 x 10^6 μm^3 ml^{-1}, 5.80 x 10^6 μm^3 ml^{-1}, and 5.90 x 10^6 μm^3 ml^{-1} respectively.

The chlorophyte, *Chlamydomonas*, undetected at the start of the experiment, increased to become the dominant phytoplankton in all four treatments. It showed no significant responses to any of the treatments (Table 3.2, Fig. 3.1.4).

Densities of the dinoflagellate, *Gymnodinium*, showed a highly significant response to silicate and a significant response to zooplankton (Table 3.2). The silicate treatment produced a clear increase in *Gymnodinium* density (Fig. 3.1.4). The reduced zooplankton treatment caused initial increases, greater than those produced in the control treatment, but then densities declined to levels lower than those found in the control treatment. As the initial *Gymnodinium* densities were similar in all four treatments the overall treatment means can be compared. These were 2.23 x 10^6 μm^3 ml^{-1}, 2.64 x 10^6 μm^3 ml^{-1}, 2.92 x 10^6 μm^3 ml^{-1}, and 3.88 x 10^6 μm^3 ml^{-1} in the control, reduced zooplankton, silicate, and interaction treatments respectively. The overall stimulatory effect of both silicate and reduced zooplankton density is, therefore, apparent.

The only other species of importance, in terms of biovolume, were *Cryptomonas* sp. and *Rhodomonas* sp. Repeated measures ANOVA performed on *Cryptomonas* densities revealed a highly significant response to zooplankton and a significant response to silicate (Table 3.2). Densities increased throughout the experiment in all four treatments (Fig. 3.1.4), but increases were greatest in the interaction and reduced zooplankton treatments. Densities were also greater in the silicate treatment compared with the control treatment. There

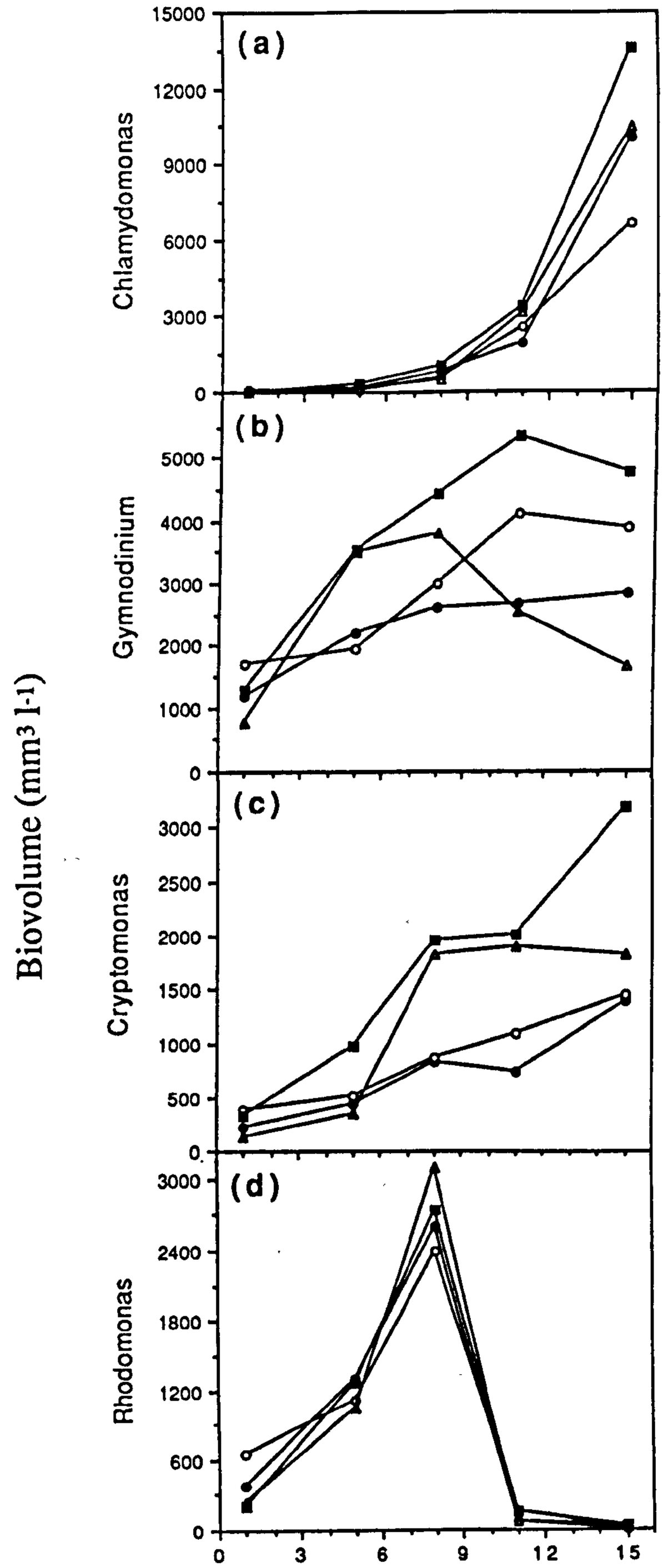


Fig. 3.1.4. Mean population densities of phytoplankton from day 1 to day 15: (a) *Chlamydomonas*, (b) *Gymnodinium*, (c) *Cryptomonas*, and (d) *Rhodomonas*, in control (●), added silicate (○), reduced zooplankton (▲), and interaction (△) treatments.

was no significant response of *Rhodomonas* to any of the treatments (Table 3.2). All four treatments showed a very similar response; densities increased up to day 9, then declined to very low densities by day 11, remaining low up to day 15 (Fig. 3.1.4).

3.3.4 Discussion

3.3.4.1 The effect of zooplankton

The only species to be significantly affected by zooplankton were *Cryptomonas* and *Gymnodinium*. Smaller algae, such as *Rhodomonas*, *Chlamydomonas*, and *Stephanodiscus hantzschii*, and diatoms in general, appeared unaffected. The dominant grazer, *Diaptomus* has been shown to be able to feed selectively on particles > 12 μm in diameter (Richman *et al.*, 1980) and so may have selected *Cryptomonas* and *Gymnodinium* because of their larger size and lack of silica wall.

An increase in chlorophyll *a* concentration was observed in all four treatments. The increases cannot be explained by reduced grazing pressure, as they were almost identical between treatments, despite the differences in zooplankton density. However, increases in the silicate treatment, which had the highest *Diaptomus* densities, were slightly smaller than in the other treatments.

The potential importance of the grazing zooplankton in producing the spring clear water phase was indicated by the seasonal monitoring data. During the experiment, lake *Diaptomus* and *Daphnia* densities increased up to 34.1 l^{-1} and 17.6 l^{-1} respectively, much higher than enclosure densities. Grazing

pressure may, therefore, have been more important in the lake, than in the experiment, and may have been responsible for the observed decline in lake chlorophyll *a* concentrations.

3.3.4.2 The effect of silicate

Silicate concentrations also appeared to have little effect on chlorophyll *a* concentrations. This was not surprising as, in terms of biomass, diatoms became less important during the experiment due to the large increase in *Chlamydomonas* density. It is, therefore, more appropriate to examine the response of the diatoms alone. Three species were of importance: *Asterionella formosa*, *Stephanodiscus neoastrea*, and *S. hantzschii*.

Asterionella biovolumes were not significantly greater in the treatments with added silicate. Silicate-silicon concentrations in the control and reduced zooplankton treatments declined to a mean of 0.44 mg l^{-1} and 0.40 mg l^{-1} respectively, which are higher than those shown to cause a decline in *Asterionella* in Windermere (0.23 mg l^{-1}) (Lund, 1950). It is possible that, if the experiment had been allowed to continue for a few more days, a decline in *Asterionella* would have been observed.

Both *S.neoastrea*, and *S.hantzschii* showed significant positive responses to the treatments with added silicate, which suggests that *Stephanodiscus* species may be less suited to low silicate concentrations than *Asterionella*. Kilham (1971), however, in a review of the literature suggests that the opposite appears to be true; *S.neoastrea* frequently replaces *Asterionella* as silicate concentrations decline. The Si:P ratio has also been shown to be important in explaining seasonal successions of diatoms, high Si:P ratios favouring *Asterionella* and low Si:P

ratios favouring *S.neoastrea* and *S.hantzschii* (Van Donk, 1984). Again, this does not explain the results as *Asterionella* responded the same in all four treatments, despite different Si:P ratios, which in fact were very low, suggesting dominance of the two *Stephanodiscus* species. It is possible that the *Stephanodiscus* species were affected to a greater extent by losses from sedimentation, compared with *Asterionella*, but survived for longer in the treatments with added silicate due to greater growth rates than in the other two treatments.

The fact that the *Stephanodiscus* populations in the enclosures may have been stimulated by increased silicate, does not mean that silicon-limitation is the cause of their decline in the lake. Silicate is most likely replenished in the lake at a much greater rate than in the enclosures. In fact lake concentrations were only observed less than 0.5 mg l^{-1} for a short period in the spring, so if silicon-limitation of diatoms was to occur, it would most likely be short-lived. It, therefore seems unlikely that it is the major factor accounting for diatom population declines in Rostherne Mere.

The importance of mixing in limiting diatom growth has been shown previously in Rostherne Mere (Reynolds, 1978b). A delay in the onset of stratification, in 1972, allowed a much greater population of *Asterionella* to develop, indicating that it is the physical, rather than chemical, characteristics of the lake that limit their spring growth.

The reasons why *Gymnodinium* showed a highly significant, and *Cryptomonas* showed a significant, positive response to the silicate treatment is unclear. From the plot of the treatment means (Fig. 3.1.4) it appears that *Cryptomonas*

responded to differences in grazing pressure rather than silicate concentration. It is possible that these two species were actually significantly affected by the higher pH present in the treatments with added silicate, compared with the lower pH in the other treatments.

3.3.4.3 Interaction of reduced zooplankton and added silicate

There were no significant response to the interaction of zooplankton and silicate, which suggests that there was no effect in addition to those that can be ascribed to silicate addition or reduced zooplanton.

3.3.5 Conclusions to experiment one

What the results of the experiment have shown is that chlorophyll *a* concentrations in the enclosures did not appear to be limited by silicate concentrations or grazing pressure. Individual species, though, did show responses: *Stephanodiscus* spp. appeared to be limited by silicon, and *Cryptomonas* and *Gymnodinium* appeared to be limited by grazing pressure. The latter two also appeared to be limited by silicon, although this was more likely to have been a response to the pH change associated with addition of the silicate-stock solution.

What was more striking about the experiment though was the almost identical increase in chlorophyll *a* concentration in all four treatments, largely due to increases in *Chlamydomonas* and *Asterionella*. What made this even more interesting was the fact that over this same period, there was a reduction in chlorophyll *a* concentration in the lake. Clearly the enclosures were not reflecting the lake situation.

The difference between the lake and the enclosures could not be explained by silicate-silicon concentrations, as concentrations in the control and reduced zooplankton treatments were lower than in the lake. Nitrogen and phosphorus concentrations were, similarly, lower in the enclosures compared with the lake. Grazer densities, on the other hand, increased considerably in the lake, compared with the enclosures, and so may have been the factor responsible for the low chlorophyll *a* concentrations, and clear water, present in the lake.

Grazing pressure, nonetheless, clearly did not have a major impact in the enclosures. The almost identical increases in chlorophyll *a* concentration in all four treatments suggest that some other factor, common to all, must have been of greater importance in limiting the phytoplankton populations. Reynolds (1978b) suggests that light-limitation may be important in the lake. As long as the phytoplankton are able to remain in the water column, this would not be the case in the enclosures. *Chlamydomonas*, *Cryptomonas*, and *Gymnodinium* are all motile and would, therefore, be able to maintain their positions in the water column. *Asterionella* is not motile, but may have been able to remain in the water column through the limited mixing by the wind and the artificial mixing of the enclosures every sampling day. An increase in light availability would explain the similar response in all four treatments, and the major difference to the lake.

Clear water conditions were present when the water column was just beginning to stratify. It therefore seems

plausible that a combination of light-limitation and grazing pressure are responsible for the spring clear-water phase.

3.4 Experiment two

3.4.1 Introduction

In the summer of 1991, in Rostherne Mere, the phytoplankton community was dominated by cyanobacteria. Despite this being the peak period of algal biomass, the zooplankton community declined from its spring peak, to very low densities. Controversy surrounds the reason for this pattern, commonly seen in eutrophic lakes. Predation by fish has long been considered the main reason for the decline in zooplankton numbers (Hrbáček *et al.*, 1961), but the unsuitability of cyanobacteria as a food for zooplankton (Arnold, 1971; Lampert, 1981) may be an additional reason. This experiment aimed to investigate the relationship between the zooplankton and phytoplankton communities of Rostherne Mere, during the summer, in the absence of fish predation. It aimed to manipulate, not only the zooplankton density, but also the pH, by which it was hoped that cyanobacteria density would be reduced. Chlorophyta appear to be favoured over cyanobacteria at low pH/high free-CO_2 concentrations (Shapiro, 1984).

3.4.1.1 The inorganic carbon system and pH

In aqueous solution dissolved inorganic carbon (DIC) exists in a number of forms: CO_2 may be hydrated to form carbonic acid (H_2CO_3) (Equation 3.1), which then dissociates to form bicarbonate (HCO_3^-) (Equation 3.2) and carbonate (CO_3^{2-}) (Equation 3.3) ions.

$$CO_2 + H_2O \rightleftharpoons H_2CO_3 \qquad \text{(Equation 3.1)}$$

$$H_2CO_3 \rightleftharpoons H^+ + HCO_3^- \qquad \text{(Equation 3.2)}$$

$$HCO_3^- \rightleftharpoons H^+ + CO_3^{2-} \qquad \text{(Equation 3.3)}$$

For convenience dissolved CO_2 and H_2CO_3 added together is termed "free-CO_2". The effect of pH on the proportions of free-CO_2, bicarbonate, and carbonate is illustrated in Figure 3.2.1: free-CO_2 is present in significant proportions between pH 4 and 7, decreases rapidly by pH 8, and only accounts for 0.003 % by pH 9; between pH 7 and 10 bicarbonate predominates; above pH 9.5 carbonate is significant.

3.4.2 Methods

The experiment was carried out from 25 July 1991 to 8 August 1991, in Rostherne Mere. Four treatments were set up:

(1) Control. Enclosures filled with lake water with lake densities of phytoplankton and zooplankton.

(2) Increased zooplankton. After filling these bags, zooplankton, obtained from a 3 m vertical haul of a 300 µm mesh-size net, was added.

(3) Lowered pH. 10 M hydrochloric acid was added, during filling, to give a pH of about 7.5. The amount of acid required was determined from titrations of 100 ml of lake water carried out one week previously.

(4) Increased zooplankton and lowered pH. A combination of treatments two and three.

The four treatments will from hereafter be referred to as control, low pH, increased zooplankton, and interaction respectively.

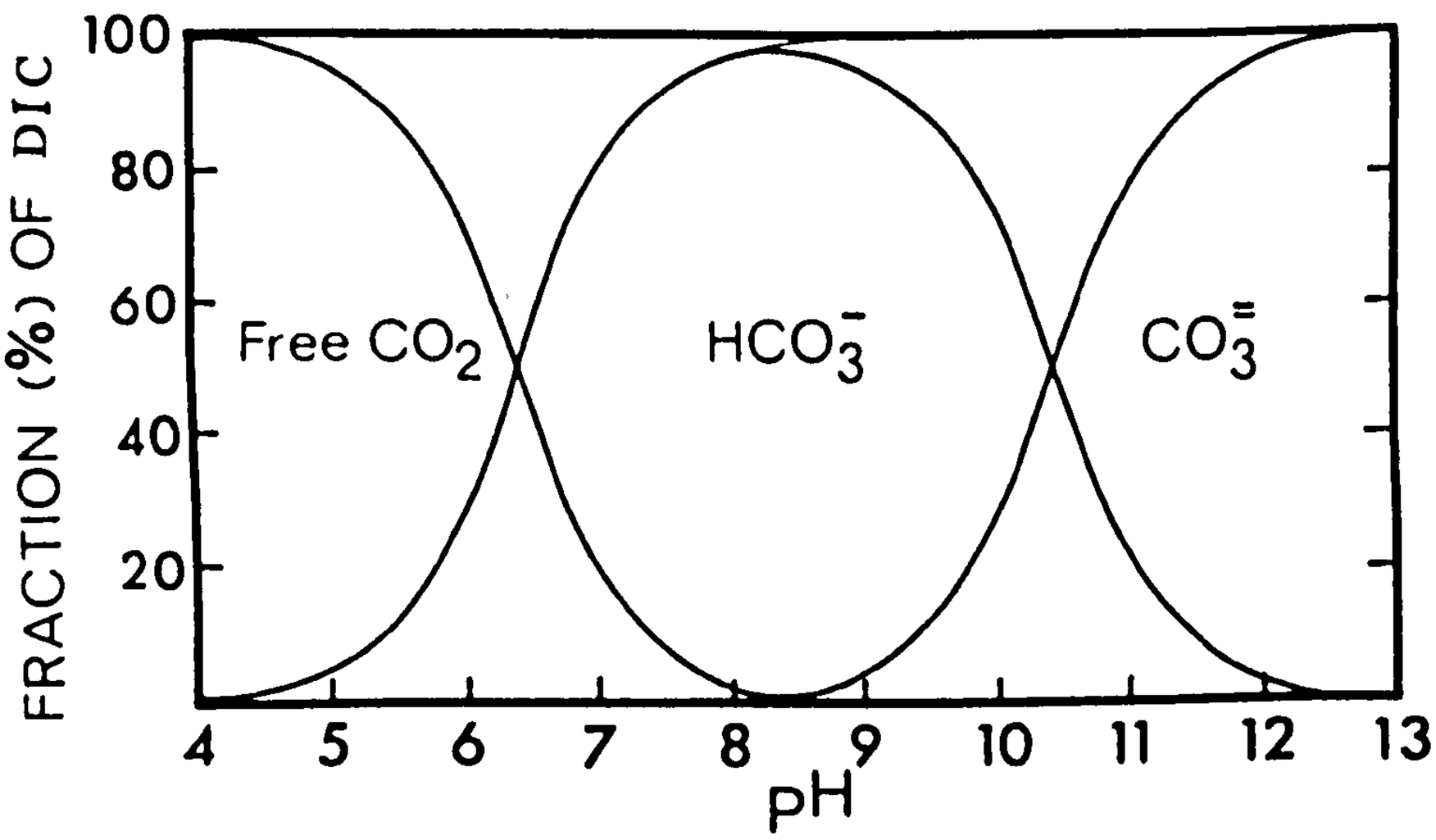


Fig. 3.2.1Relationship between pH and relative proportions of inorganic carbon species in solution. (taken from Wetzel (1975)).

Treatments were run in triplicate, making a total of twelve enclosures. The placement of the treatments was randomized within the wooden frame.

3.4.3 Results

Standard error bars are omitted from the graphs of treatment means as there was great overlap between treatments. Because of the overlap, the reasons for the significant responses have to be viewed with caution.

3.4.3.1 Initial conditions and water chemistry

At the start of the experiment the lake was well stratified. Concentrations of DIN, SRP, silicate-silicon, and chlorophyll *a* were 0.74 mg l^{-1}, 250 µg l^{-1}, 2.2 mg l^{-1}, and 31 µg l^{-1} respectively. The pH of the lake water was 9.1. The phytoplankton community was dominated, in terms of biovolume, by *Anabaena*, *Aphanizomenon*, and *Ceratium*, although *Microcystis*, *Cryptomonas*, *Rhodomonas*, and *Staurastrum* were also important. The zooplankton community collapsed during June and densities remained low up to the start of the experiment. Cyclopoids (4.3 l^{-1}), *Diaptomus* (1.7 l^{-1}), *Daphnia cucculata* (1.5 l^{-1}), and *Daphnia longispina* agg. (0.6 l^{-1}) were present.

One-way ANOVA performed on the initial chlorophyll *a* concentrations revealed significantly lower concentrations in the interaction enclosures compared with the other treatments. No significant differences were observed, at the start of the

experiment, in the densities of the dominant phytoplankton species between the treatments.

During the experiment DIN concentrations in the enclosures declined to levels below the detection limit of the analysis, SRP concentrations were also reduced dramatically to 18 $\mu g\ l^{-1}$ in the control and interaction treatments, 11 $\mu g\ l^{-1}$ in the increased zooplankton treatment, and < 5 $\mu g\ l^{-1}$ in the low pH treatment.

Because of holes formed in the polyethylene bags, during the experiment, one of the control and increased zooplankton replicates, and two of the interaction replicates were omitted from the repeated measures ANOVA. Results must, therefore, be viewed with caution, particularly with respect to the interaction effect.

3.4.3.2 Response of pH and the zooplankton community

Addition of hydrochloric acid to half the enclosures caused their pH to reduce to 7.5. Repeated measures ANOVA performed on the pH of the enclosures showed that there was a significant effect of adding acid, the acid treated enclosures having a significantly lower pH (Table 3.3, Fig. 3.2.2). The treatment can, therefore, be considered effective. However, the actual pH of the low pH and interaction enclosures did not remain at 7.5; by day 9 it had risen to 9.8. Acid was then added again to lower the pH back to 7.5, but by day 15 it had risen to 9.5 in the low pH treatment and 9.1 in the interaction treatment. In the control and increased zooplankton treatments pH rose steadily from 9.1

Table 3.3 Summary of the repeated measures ANOVA results on the effects of pH and zooplankton on chlorophyll *a* concentrations, phytoplankton biovolumes, zooplankton densities, and pH. F statistic and degree of significance are indicated. NS indicates no significance, * = $p<0.05$, ** = $p<0.01$, and *** = $p<0.001$.

Subject	pH effect	Zooplankton effect	Interaction effect
Chlorophyll *a*	107.36 ***	0.78 NS	4.16 NS
Cyanobacteria	5.13 NS	3.98 NS	2.73 NS
Anabaena	49.80 **	4.04 NS	0.00 NS
Aphanizomenon	27.65 **	6.52 NS	9.72 *
Microcystis	0.33 NS	0.94 NS	0.16 NS
Cryptomonas	3.91 NS	6.88 NS	0.47 NS
Rhodomonas	0.19 NS	0.41 NS	0.50 NS
Staurastrum	43.94 **	8.76 *	7.44 NS
Cyclotella	11.24 *	2.59 NS	3.22 NS
Nitzschia	4.33 NS	0.15 NS	0.00 NS
Cladocera	2.55 NS	7.02 NS	0.04 NS
Cyclopoids	9.45 *	1.07 NS	0.16 NS
Diaptomus	15.56 *	7.95 *	4.32 NS
pH	71.95 **	4.36 NS	3.76 NS

to 10.3. Changes in the lake pH were intermediate between the treatments with or without added acid (Fig. 3.2.2).

Repeated measures ANOVA revealed that *Diaptomus* densities responded to the pH and increased zooplankton treatment (Table 3.3). In the low pH and interaction treatments, densities increased dramatically between day 9 and 12 (Fig. 3.2.2). Mean densities in the control, low pH, increased zooplankton, and interaction treatments were 1.9 l^{-1}, 4.7 l^{-1}, 3.0 l^{-1}, and 12.0 l^{-1}, respectively, which shows that increases were greatest in the treatments where acid had been added, although densities in the increased zooplankton treatment were still greater than those in the control treatment.

Cyclopoids may be carnivores, omnivores, or detrital feeders (Fryer, 1957), and so may not have been feeding on the phytoplankton community. However, in terms of numbers, they were of greater importance than *Diaptomus*. Cyclopoid densities also showed a significant, positive response to the low pH treatment (Table 3.3, Fig. 3.2.2). Mean densities in the control, low pH, increased zooplankton, and interaction treatments were 11.1 l^{-1}, 18.9 l^{-1}, 14.3 l^{-1}, and 20.4 l^{-1}, respectively.

Cladocera were the most abundant zooplankters, and so were probably of greatest importance with respect to grazing pressure. Densities up to day nine remained less than 8 l^{-1}, but then increased dramatically in all four treatments. Repeated measures ANOVA revealed no significant differences between the treatments (Table 3.3), although, comparison of the treatment means (Fig. 3.2.2) again shows the positive effect of the pH treatment, although the increased zooplankton and interaction treatments had the greatest densities. Mean densities

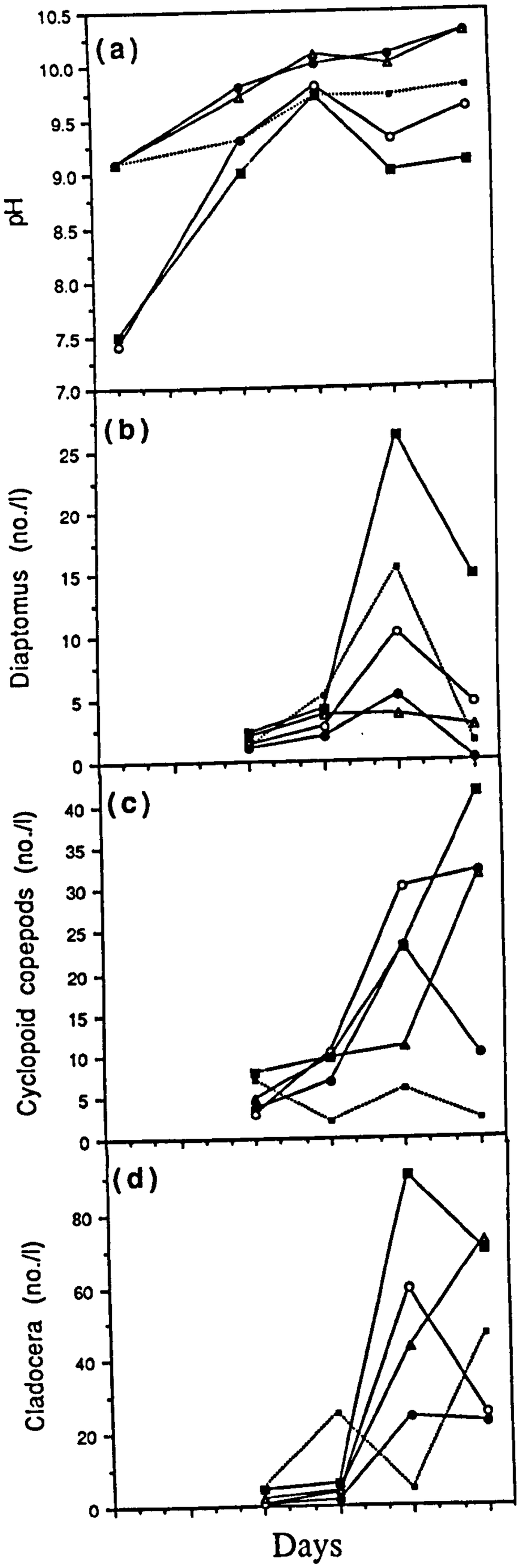


Fig. 3.2.2. (a) mean pH, (b) mean *Diaptomus* density, (c) mean cyclopoid copepod density, and (d) mean Cladocera density, in lake (-•-), and control (-•-), low pH (-○-), increased zooplankton (-▲-), and interaction (-■-) treatments.

in the control, low pH, increased zooplankton, and interaction treatments were 14.3 l^{-1}, 22.2 l^{-1}, 30.5 l^{-1}, and 42.6 l^{-1}, respectively.

Due to the large increases in zooplankton densities that occurred during the experiment, largely between day 9 and day 12, initial starting densities were relatively unimportant. During the experiment, in general, densities were lowest in the control treatment and highest in the interaction treatment. The addition of acid, in particular, appeared to stimulate the zooplankton, in particular the copepods. Despite this, the treatments can be considered reasonably effective, in that, in terms of numbers, zooplankton (dominated by Cladocera) were greater in the increased zooplankton and interaction treatments compared with the control treatment. Zooplankton densities also increased in the lake (Fig. 3.2.2). Increases in *Diaptomus* density followed a similar pattern to those observed in the enclosures, Cladocera increased, but in an erratic manner, and *Cyclops* remained at a low density in the lake.

3.4.3.3 Response of chlorophyll *a* concentrations and phytoplankton biovolumes

The repeated measures ANOVA, performed on chlorophyll *a* concentrations, revealed a highly significant effect of pH (Table 3.3). Concentrations increased in all four treatments, but the low pH and interaction treatments had significantly greater increases compared with the control and increased zooplankton treatments, particularly after day 12 (Fig. 3.2.3). Mean concentrations for control, low pH, increased zooplankton, and interaction treatments were 94 µg l^{-1}, 111 µg l^{-1}, 78 µg l^{-1}, and

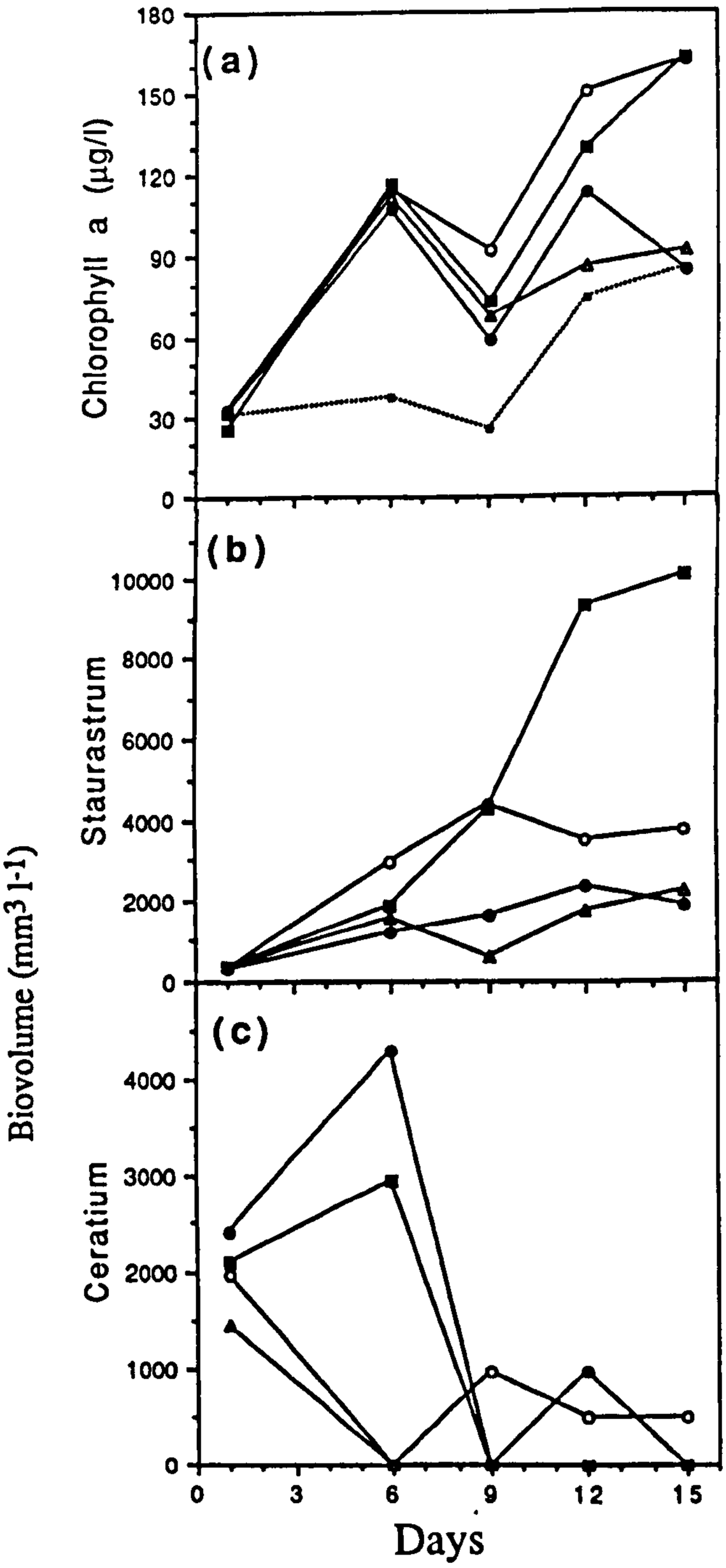


Fig. 3.2.3. (a) mean chlorophyll *a* concentrations, (b) mean *Staurastrum* densities, and (c) mean *Ceratium* densities, in lake (-▪-) (chlorophyll *a* only), and control (-●-), low pH (-○-), increased zooplankton (-▲-), and interaction (-■-) treatments.

101 µg l^{-1} respectively. The significantly lower starting concentration in the interaction treatment was clearly insignificant compared with the changes that occurred during the experiment. Chlorophyll *a* concentrations also increased in the lake, but to a lesser extent than in the enclosures (Fig. 3.2.3).

The cyanobacteria dominanted the phytoplankton community at the start and during the experiment. Excepting the low pH treatment, densities decreased dramatically between day 9 and day 12. Densities were not significantly affected by the treatments, but a plot of the treatment means revealed the positive effect of the low pH (Table 3.3, Fig. 3.2.4). Mean biovolume densities for control, low pH, increased zooplankton, and interaction treatments were 9.6 x 10^6 μm^3 ml^{-1}, 15.9 x 10^6 μm^3 ml^{-1}, 9.5 x 10^6 μm^3 ml^{-1}, and 5.2 x 10^6 μm^3 ml^{-1} respectively.

Anabaena sp. and *Aphanizomenon flos-aquae* were, at least initially, the dominant cyanobacteria. Repeated measures ANOVA revealed highly significant responses to the lowering of the pH (Table 3.3). Comparisons among the treatment means revealed the positive effect of the low pH (Fig. 3.2.4). An abrupt decline in *Anabaena* densities occurred in the control and increased zooplankton treatments, between day 9 and day 12, whereas densities remained high in the low pH treatment, and to a lesser extent in the interaction treatment. *Aphanizomenon* showed a very similar response to *Anabaena*, although the decline in the control and increased zooplankton treatments was less abrupt. *Aphanizomenon* was also affected significantly by the interaction. From the plot of the treatment means it appears that densities exhibited a pattern intermediate to the reduction

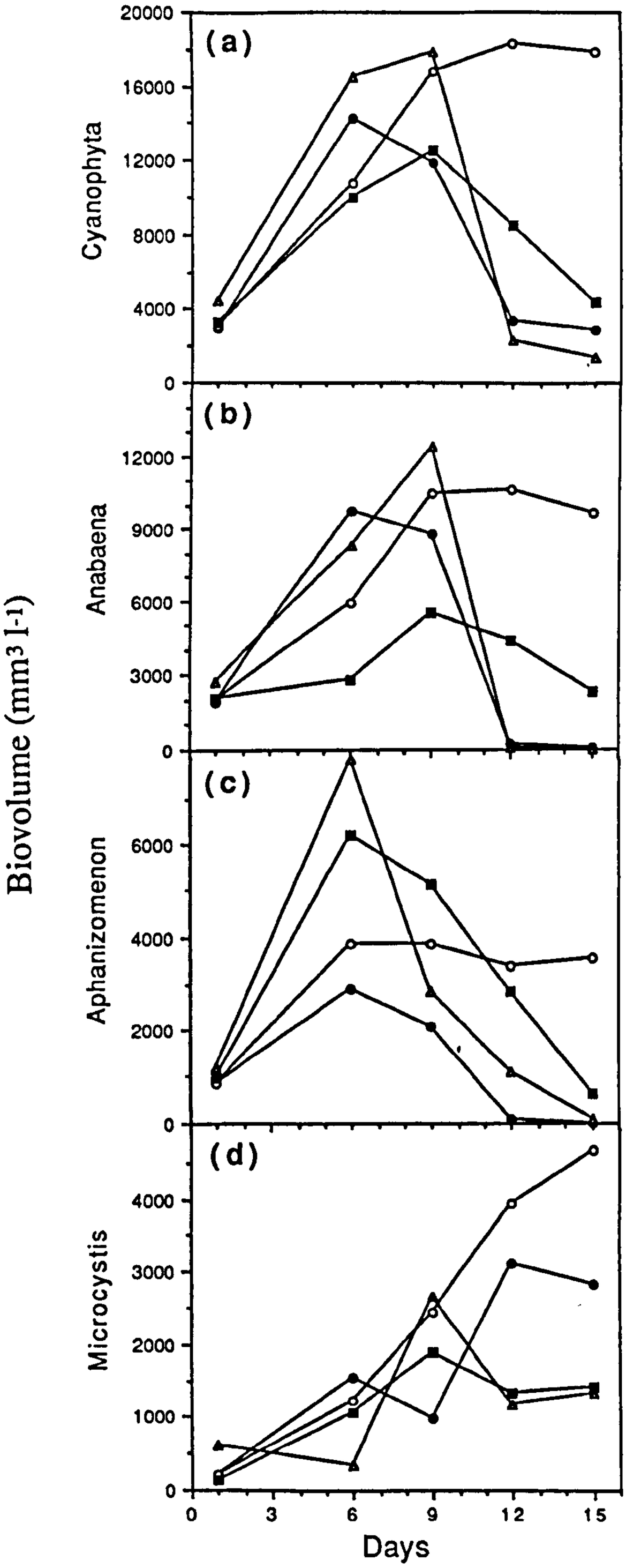


Fig. 3.2.4. Mean population densities of phytoplankton: (a) total cyanobacteria, (b) *Anabaena*, (c) *Aphanizomenon*, and (d) *Microcystis*, in control (-●-), low pH (-○-), increased zooplankton (-▲-), and interaction (-■-) treatments.

seen in the increased zooplankton treatment and the increase seen in the low pH treatment.

Repeated measures ANOVA performed on *Microcystis aeruginosa* density revealed no significant responses to the treatments (Table 3.3); densities increased in all four treatments (Fig. 3.2.4). However, there was a greater increase in the low pH and control treatments compared with the increased zooplankton and the interaction treatments. Mean biovolume densities for control, low pH, increased zooplankton, and interaction treatments were 2.0 x 10^6 μm^3 ml^{-1}, 2.5 x 10^6 μm^3 ml^{-1}, 1.2 x 10^6 μm^3 ml^{-1}, and 1.2 x 10^6 μm^3 ml^{-1} respectively.

In terms of biovolume, at the start of the experiment *Ceratium hirundinella* was also very important. However, populations collapsed in all four treatments, although there was an initial increase in density in the control and interaction treatments (Fig. 3.2.3). From day 6 onwards, *Ceratium* was frequently undetected, preventing repeated measures ANOVA from being performed.

The Chlorophyta were represented largely by *Staurastrum* sp., which showed a highly significant response to pH, and a significant response to increased zooplankton (Table 3.3). Populations increased in all four treatments, but increases were significantly greater in the low pH and interaction treatments, indicating the positive effect of the acid additions (Fig. 3.2.3). The significant response to increased zooplankton was not clear from the plot of treatment means, as the increased zooplankton treatment produced little change, like the control treatment. Although, the very large increase seen in the interaction

treatment, which actually had the greatest density of grazers, suggests that it was a positive effect.

Cryptomonas sp. and *Rhodomonas* sp. showed no significant responses to any of the treatments (Table 3.3). In terms of biovolume, *Cryptomonas* was of greater importance. The responses of both cryptophytes were, however, similar (Fig. 3.2.5). Densities increased during the first six days of the experiment, and then declined to very low values. An exception to this pattern was *Cryptomonas* in the control enclosures which remained at high densities.

The last two species of importance were the diatoms, *Cyclotella* sp. and *Nitzschia* sp. Low pH had a significant effect on *Cyclotella* (Table 3.3), allowing much greater densities to develop (Fig.3.2.5). Increases in density were observed in all four treatments, during the first six days, although, substantially larger increases were observed in the interaction and low pH treatments compared with the control and increased zooplankton treatments. The increases were followed by a complete collapse in populations, although this was delayed in the low pH and interaction treatments.

Nitzschia showed almost the opposite pattern of response. Although no significant responses were revealed by the repeated measures ANOVA (Table 3.3), densities were greatest in the control and increased zooplankton treatments (Fig. 3.2.5). During the first six days, *Nitzschia* increased in density, similarly, in all four treatments. Populations then declined dramatically in the low pH and interaction treatments, whilst increasing further in the other two treatments.

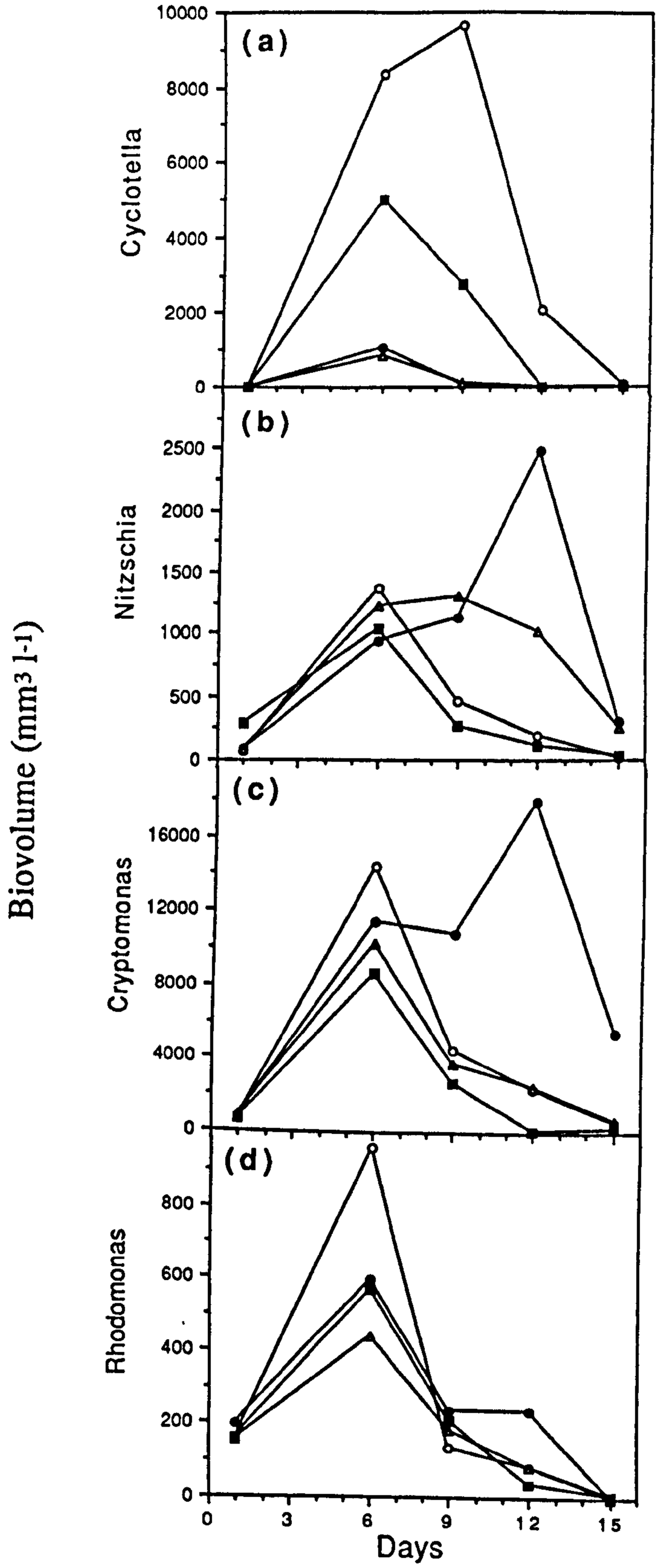


Fig. 3.2.5. Mean population densities of phytoplankton: (a) *Cyclotella*, (b) *Nitzschia*, (c) *Cryptomonas*, and (d) *Rhodomonas*, in control (-●-), low pH (-○-), increased zooplankton (-▲-), and interaction (-■-) treatments.

3.4.4 Discussion

3.4.4.1 The effect of pH

It has previously been shown in enclosure experiments (Shapiro, 1990a) that a lowering of pH to below 7.5 will shift a phytoplankton community from cyanobacteria to Chlorophyta dominance. It was for this reason the low pH treatment was set up. Unfortunately in Rostherne Mere, the pH did not remain at 7.5 for any length of time, so such a shift was unlikely. In fact, the opposite was true; greater growth of cyanobacteria was observed in treatments with added acid compared with the control and increased zooplankton treatments. The only exception to this was *Microcystis*, which increased least of all in the interaction treatment. A positive response to the low pH and interaction treatments was also observed in the chlorophyte, *Staurastrum* and the diatom *Cyclotella*.

None of the algae analysed showed a significant, negative response to the low pH and interaction treatments. The diatom, *Nitzschia*, appeared to grow less well, but, this may just have been a response to the high zooplankton densities that were present in these two treatments.

The difference in pH between the low pH and interaction treatments, compared with the control and increased zooplankton treatment, was in the scale of the increase. By day nine, pH had risen to 10.0 in the latter two treatments, and continued to rise. In the former two treatments pH was never observed to rise above 9.8. The highly significant, positive, effect of the lower pH on the chlorophyll *a* concentrations, and

phytoplankton biovolumes in general, suggests that phytoplankton growth was restricted above pH 10.0. Reynolds (1986) analysed the relation between cessation of growth and pH in enclosures in Blelham Tarn and found that only *Anabaena flos-aquae*, *Microcystis aeruginosa*, and *Staurastrum pingue* continued growth at pH values exceeding 10. This value may be slightly greater in lakes of higher alkalinity (Talling, 1976), but it does indicate that algal growth is restricted about this pH level. Goldman *et al.*. (1974) hypothesized that high pH affects the rate of photosynthesis by directly influencing the activity of certain Calvin cycle enzymes.

The ambiguous responses of *Nitzschia* and *Microcystis* suggests that their growth rate was not affected in this pH range. The ability of *Nitzschia palea* to grow at pH levels greater than 10 has been shown previously by Moss (1973).

The addition of acid not only affected the phytoplankton community, but also had repercussions on the zooplankton community. Because of the huge increases observed in zooplankton density, the initial starting densities were of little relevance. Zooplankton densities were greatest in the interaction treatment, and to a lesser extent, in the low pH treatment. It is possible that the increases were a response to the greater phytoplankton biomass present in these two treatments, although the fact that the interaction treatment, with substantially greater zooplankton densities, had slightly lower chlorophyll *a* concentrations, compared with the low pH treatment, suggests that it was more of a direct response to pH, the interaction treatment having a lower pH than the low pH

treatment. Although, the slightly lower chlorophyll *a* concentrations may have actually resulted from the higher zooplankton densities in the interaction treatment, compared with the low pH treatment.

3.4.4.2 The effect of the zooplankton community

Because of the large increases in zooplankton density that occurred during the experiment, the treatments did not turn out as expected. Highest zooplankton densities were present in the interaction treatment, and lowest in the control treatment. The other two treatments had intermediate densities.

The only alga to show a significant response to "increased zooplankton" was *Staurastrum*, which appeared to increase with increasing zooplankton density. The *Staurastrum* species was greater than 50 µm in diameter, which probably made it inedible to Cladocera (Burns, 1968; Nadin-Hurley & Duncan, 1976). Increased zooplankton may have had a positive effect on *Staurastrum* by reducing competition from other algae (Lynch, 1980) and increasing nutrient remineralization (Lehman, 1980).

Despite the lack of significant evidence for the limitation of phytoplankton growth by zooplankton, many species did appear to decline alongside increased zooplankton densities. The decline, from day nine, of the cyanobacteria, *Anabaena* and *Aphanizomenon*, and the diatom *Cyclotella*, coincided with increases observed in the zooplankton densities. Further evidence that grazing was affecting these three species comes from comparing the low pH and interaction treatments. Both these treatments showed greater growth than the other two treatments, apparently due to the lower pH, but the interaction

treatment, with its substantially greater zooplankton densities, was markedly less productive than the low pH treatment. Controversy surrounds the suitability of *Anabaena* and *Aphanizomenon* as a food for zooplankton. Results from laboratory (Lampert, 1987) and enclosure (Burns, 1987) studies suggest that, generally, they are not eaten, or are a poor food. However, in field studies, *Daphnia* has been shown to limit development of *Anabaena* (Arnold, 1971), and, *Aphanizomenon*, unless "grass-blade" colonies are able to form, in which case *Aphanizomenon* may be promoted (Lynch & Shapiro, 1981). Lynch & Shapiro (1981) reported that "grass-blade" colonies did not form when the bottom waters were anoxic, or in enclosures. It is also significant that in studies following fish-kills, or fish removals, the subsequent increase in both size and numbers of filter-feeding zooplankton was often associated with a simultaneous decline in cyanobacteria density (de Bernardi & Giussani, 1990; Shapiro & Wright, 1984; Jepessen *et al.*, 1990b).

Another possible reason for the reduced growth of these three algae in the interaction treatment compared with the low pH treatment was the lower pH present in the interaction treatment; their optimum pH for growth may have been slightly higher.

The effect of grazing on the cyanobacterium, *Microcystis*, was unclear. *Microcystis* has been shown to affect growth and mortality of grazers in the laboratory by producing toxic chemicals (Lampert, 1981). This may not necessarily occur in field situations, as the strain present may not be toxic, or may be avoided by the grazers. Reductions in *Microcystis* densities, from day 9, in the increased zooplankton and interaction treatments,

compared with an increase in the control treatment, suggests that the higher zooplankton densities in the former two treatments were responsible. However, *Microcystis* densities continued to increase in the low pH treatment, which also had high zooplankton densities. The pH in the low pH treatment may have been optimal for growth, so production could possibly have outstripped losses from grazing.

Cryptomonas and *Nitzschia* may also have been limited by zooplankton, as increases observed in all four treatments at the start of the experiment were only sustained in the control treatment, which had the lowest density of zooplankton. *Rhodomonas* showed a similar pattern except that populations collapsed in all four treatments, possibly suggesting it was even more susceptible to grazing pressure.

3.4.4.3 Interaction of increased zooplankton and low pH

A significant interactive response was revealed in *Aphanizomenon*, but, from the plot of treatment means, the response appeared to be just a combination of an increase in density due to the low pH treatment and a decrease in density due to the increased zooplankton treatment.

3.4.5 Conclusions to experiment two

Zooplankton densities in the enclosures increased, despite cyanobacteria representing a large proportion of the phytoplankton population. Increased zooplankton densities, in fact, appeared to cause a decrease in *Aphanizomenon* and *Anabaena* densities. This suggests that fish predation was of greater significance than cyanobacteria to the decline in

zooplankton during summer. Zooplankton densities in the upper 1 m of the lake, sampled during the experiment were up to four times as great as those recorded in the same period in the upper 7.5 m (see 2.3.2), which suggests that even during the day, zooplankton were most abundant near the surface. Predation from zooplanktivorous fish, which were abundant in Rostherne Mere during the summer (C. Goldspink, pers. comm.), ought to be greater near the surface, but may have been restricted by the large cyanobacteria colonies acting as an interference refuge for the zooplankton (Shapiro, 1990b).

The fact that increases in chlorophyll *a* concentration were greater in all the enclosures compared with the lake, despite the lower nitrogen and phosphorus concentrations and higher zooplankton densities in the enclosures, suggests that something other than these nutrients or grazers was limiting the phytoplankton in the lake. pH also does not appear important as changes in the lake pH were intermediate between the treatments with, or without, added acid. Reynolds & Bellinger (1992) suggest that, following recent eutrophication of Rostherne Mere, light may now limit summer phytoplankton biomass. The reason for the higher chlorophyll *a* concentrations in the enclosures compared with the lake may, therefore, be because the lake populations experience greater circulation into deeper, darker water. The shallow depth of the enclosures precluded this.

Chapter 4: Mere Mere and Little Mere

4.1 Introduction

An understanding of the factors affecting the structure and dynamics of phytoplankton communities has frequently been achieved through experimental work on whole lake systems (Schindler, 1977) or large enclosed areas of a lake (Lund & Reynolds, 1982). Despite the problems of no two lakes (or areas of a lake) being identical, these situations provide the complexity of a lake ecosystem, impossible to create in artificial laboratory surroundings, or small enclosures. However, the lack of resources (lakes and money) in Britain has meant that only a limited number of such studies have been undertaken. The opportunity of observing a "natural" whole-lake experiment on "top-down" versus "bottom-up" control of phytoplankton was provided in two adjacent lake basins in Cheshire.

Mere Mere and Little Mere (Fig. 4.1) constitute a system of two lake basins separated from each other by a sluice. Despite their largely equivalent catchment areas, their phytoplankton populations were vastly different. The apparent reason for this was that Little Mere received sewage effluent which led to a major fish reduction in this lake.

This chapter discusses the effects of the fish reduction in Little Mere compared to Mere Mere (the control situation) and, following the diversion of the effluent in June 1991, discusses the potential for future cyanobacteria dominance in Little Mere, and the prospect for long-term improvement.

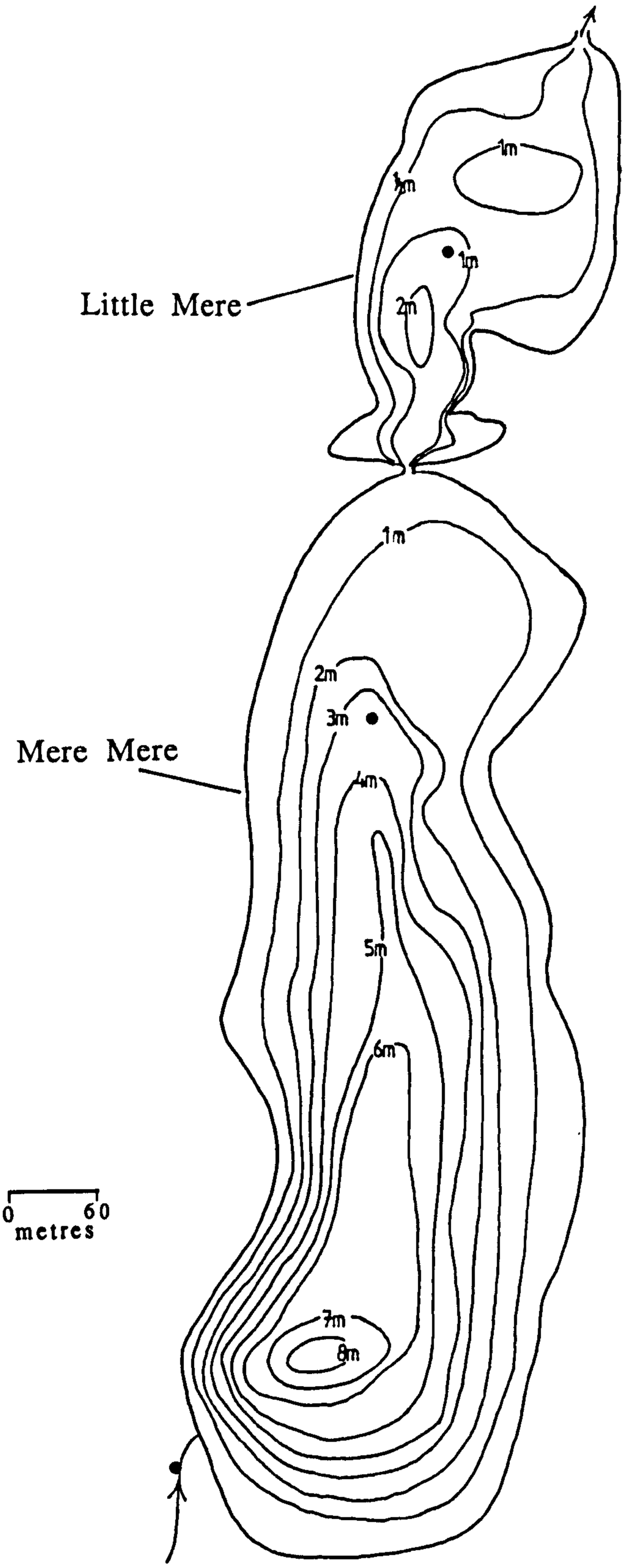


Fig. 4.1 Bathymetric map of Mere Mere (surveyed June 1992) and Little Mere (surveyed April 1992). Depths shown are in metres. Solid round symbols (●) indicate the sampling points in this study.

Plate 4.1: View across Mere Mere, looking towards private housing on the eastern bank (photographed July 1992).

Plate 4.2: Aerial view of Little Mere showing coverage of water lilies, with Mere Golf and Country Club golf-course in the background. (photographed May 1992).

4.1.1 Site descriptions

Mere Mere and Little Mere form part of a series of lakes connected by Rostherne Brook (see figure 2.1). Water enters Mere Mere from a stream in its south-west end. It enters Little Mere, from Mere Mere, over a sluice, and flows out over another sluice at the north end of Little Mere. For much of the summer, when the water level in both lakes drops, water stops flowing over both sluices.

In terms of aquatic plants Mere Mere (National grid reference SJ 733 828) (Plate 4.1) is one of the most diverse of the North-West Midland Meres. It was because of this that it was notified as an SSSI in 1985. The golf course of Mere Golf and Country Club borders the southern and western sides of the lake, although there is a thin strip of mixed woodland immediately adjacent to the lake here. Private housing lines the eastern side of the lake, and here the margin of the mere has been greatly altered by artificial banks, jetties, and gardens. There is little recreational use of the lake, just a limited amount of angling and rowing. There is also a golf driving range into the lake (for which floating golf balls are wisely used) that has very little impact on the lake. The catchment area is mainly mixed farmland and woodland. The phytoplankton of Mere Mere has been studied on three occasions (Griffiths, 1925; David, 1963; Belcher & Storey, 1968) and has been shown to be dominated in summer by *Ceratium hirundinella* and a variety of chlorophytes and cyanobacteria.

Little Mere (National grid reference SJ 73 82) (Plate 4.2) is a shallow lake, with an abundant aquatic plant community, but of low diversity. From sediment cores it appears to be a

relatively new lake, and most likely man-made (Meryem Beklioglu, Liverpool University, unpublished data). The lake is surrounded partly by a narrow fringe of established, mixed woodland, and partly by private housing. The catchment area consists largely of a golf-course, agricultural land, and woodland. Upto July 1991 there was also a sewage treatment works (Mere S.T.W.) situated on its bank (Fig. 2.1). It has received very little limnological attention in the past, but it is included in the SSSI created in 1985 for the diverse aquatic plant flora in Mere Mere. There have been three aquatic plant surveys of both lakes carried out in recent years (Wiggington,1980; 1989; Cox, 1989)

The lake basins overly boulder clay, and have patches of glacial sands and gravels, and alluvium in their catchments (Geological Survey of Great Britain (England and Wales) Drift Sheet 98). The soil is a freely-draining brown earth of sandy loam texture (Rogers and Ball,1974).

Details of the lakes are given in Table 4.1. Bathymetric maps (Figure 4.1) reveal that the two lakes are not similar in terms of morphometry. Mere Mere is much deeper than Little Mere, with consequently a less significant littoral area.

4.1.2 Mere sewage treatment works

The sewage treatment works (S.T.W.) were built in 1935 to serve a domestic population of about 550 people. The treatment process comprised a coarse screen, three small primary sedimentation tanks, two circular percolating filters, and two holding tanks to remove solids at times of peak flow.

Its closure on June 25 1991 was largely because of the fact that it had been overloaded for many years,serving 3350 people,

and appeared to be the cause of nutrient enrichment in Little Mere, and more importantly, the National Nature Reserve, Rostherne Mere, further downstream (NWWA,1983). Flow from the S.T.W., measured by dilution gauging, gave a dry weather flow of 0.3 Ml d^{-1}, although this is subject to a large source of error as most of the flow was pumped to the works (NWWA,1983). Estimates of loading to Little Mere of phosphate, nitrate, and ammonium were 2 kg d^{-1}, 3 kg d^{-1}, and 3 kg d^{-1} respectively. Little Mere acted as an oxidation pond for the effluent although phosphate and ammonium were in such excess that considerable quantities passed through the outlet into Rostherne Brook (NWWA,1983).

Table 4.1. Details of Mere Mere and Little Mere. The time taken to displace the lake volume was calculated from the annual rainfall and actual evaporation figures of the Rostherne Brook catchment,for 1990 and 1991 (see Appendix 1).

	Mere Mere	Little Mere
Geographical co-ordinates	53° 20′ N 2° 24′ W	53° 20′ N 2° 24′ W
Altitude (m a.s.l.)	51	50
Surface area (ha)	15.5	2.8
Maximum depth (m)	8.0	2.6
Mean depth (m)	2.8	0.7
Volume (m^3)	4.4×10^5	2.1×10^4
Catchment area (ha)	310	351
Time taken to displace the lake volume (year)	0.8-9.5	0.03-0.4

4.2 Methods

Methods were as described in Chapter 2, except where detailed below.

4.2.1 Bathymetric survey

A bathymetric survey of Mere Mere was carried out in June 1992, using a Lowrance LRG-1510B echosounder. Due to the shallow nature of Little Mere, an echosounder could not be used; depth was measured using a plumb line, every 10 m along a series of transects across the lake.

4.2.2 Water chemistry, physical factors, phytoplankton, and zooplankton

Samples from Mere Mere were collected from the top 3 m using a plastic hosepipe. In Little Mere, samples were taken from the surface water in the middle of the lake, using a bucket. Water chemistry samples were also taken from the inflow of Mere Mere (see Fig. 4.1). Flow measurements of the inflow of Mere Mere were also taken.

Free-carbon dioxide concentrations were calculated according to Mackereth *et al.* (1978).

4.2.3 Fish

Fishing was carried out on December 6 1991 using a micro-mesh seine net (25 m long, 2 m deep, 2.5 mm mesh-size) and a gang of four gill-nets (each 25 m long, 2 m deep, mesh sizes: 23 mm, 27 mm, 29 mm, and 32 mm) left overnight. As there was no inflow over the summer period no fish had been able to enter via the inflow since June 1991. Following a rise in

the level of Mere Mere in November 1991, a fine mesh was placed over the sluice to prevent any fish from entering. No fish are able to enter via the outflow as there is a 1 m stepped drop from the lake.

Fish caught in the gill-nets were brought back to the laboratory for sexing, ageing, weighing, length measurements, and gut analysis.

4.2.4 Aquatic plants

Aquatic plants were surveyed in July 1992. The percentage cover of water-lilies in Little Mere was estimated from aerial photographs taken in early June 1992 (see Plate 4.2).

4.3 Results and discussion

4.3.1 Mere Mere

4.3.1.1 Physical factors and water chemistry

Temperature (Fig. 4.2a) increased in spring and summer, from the winter minimum (0°C Jan & Feb 1991), reaching a maximum of 21°C during August 1991. There was no evidence of stratification in the top 2 m, although, it almost certainly occurred at greater depths, during calm periods in summer. Percentage saturation of dissolved oxygen (Fig. 4.2b) did not show such a marked seasonality. During winter, about 75 % saturation was recorded. Peaks upto 100 % in spring and autumn, and 125 % in summer were associated with the high phytoplankton biomass (March-September: r^2=0.77, p<0.0001). Over the summer period there was also a decrease in % saturation with depth, although this was rarely well developed in the top 2 m.

Soluble reactive phosphorus (SRP) concentrations (Fig. 4.3a) were relatively low for the North-West Midland Meres (Moss *et al.*, 1992), never exceeding 25 µg l^{-1}. The highest concentrations were found in the winter months, whilst from February to August/September concentrations were almost always less than 5 µg l^{-1}, the detection limit of the analysis.

Total phosphorus concentrations (Fig. 4.5a) ranged from about 20 to 160 µg l^{-1}, although there was no apparent seasonality. The total phosphorus load in the inflow to Mere Mere (Fig.4.5a), generally increased during the winter and decreased during spring and summer. There was no correlation

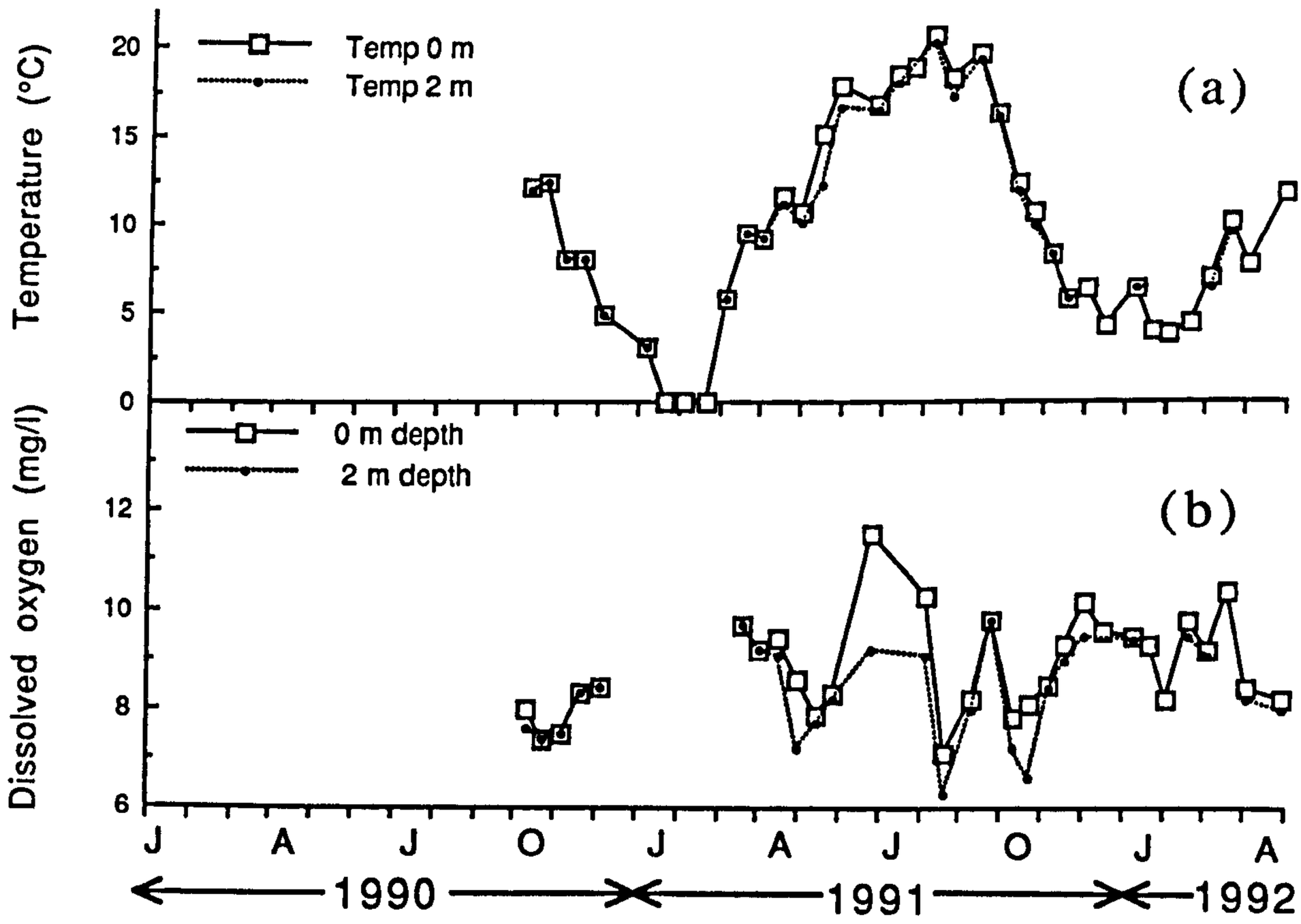


Fig. 4.2 Seasonality of (a) temperature at the surface (0m) and at 2 m depth, and (b) dissolved oxygen at the surface (0m) and at 2 m depth, in Mere Mere.

($p>0.25$) between total phosphorus load and lake total phosphorus concentration.

Dissolved inorganic nitrogen (DIN) (Fig. 4.3a) showed a marked seasonal pattern. Concentration maxima were recorded in March 1991 and February 1992 (2.45 mg l^{-1} and 2.35 mg l^{-1} respectively). Concentrations declined to undetectable levels by July in both 1990 and 1991. The DIN load in the inflow of Mere Mere showed a similar seasonality to the DIN concentration of Mere Mere (Fig. 4.5b), increasing during winter and decreasing in spring and summer, although the relationship was not statistically significant ($0.05<p^{-}0.10$).

Nitrate-nitrogen (Fig. 4.4a) had a similar seasonal pattern, with winter maxima (2.45 mg l^{-1} 1991; 2.13 mg l^{-1} 1992) and summer minima (0 mg l^{-1} 1990; 0 mg l^{-1} 1991). Ammonium-nitrogen concentrations (Fig. 4.4a) exhibited a slightly different seasonality with minima in spring and summer (0 µg l^{-1} 1990 and 1991). Concentrations increased sharply in autumn and remained high during winter. Maximum concentrations recorded were 266 µg l^{-1} in Sep 1990 and 232 µg l^{-1} in Oct 1991.

SRP and ammonium-nitrogen concentrations were directly related to each other ($r^2=0.67$, $p^{-}0.001$). Their increase in the autumn of both years was most probably due to mixing of nutrient-rich hypolimnion water, and suggests that stratification did occur during the summer.

Silicate-silicon concentrations (fig. 4.3b) showed minima in spring and autumn, declining to undetectable levels during May 1990 and October 1991.

pH showed a clear seasonal pattern with minima in winter (7.3 in Jan 1991, 7.0 in Feb 1992) and maxima in summer (9.4 in

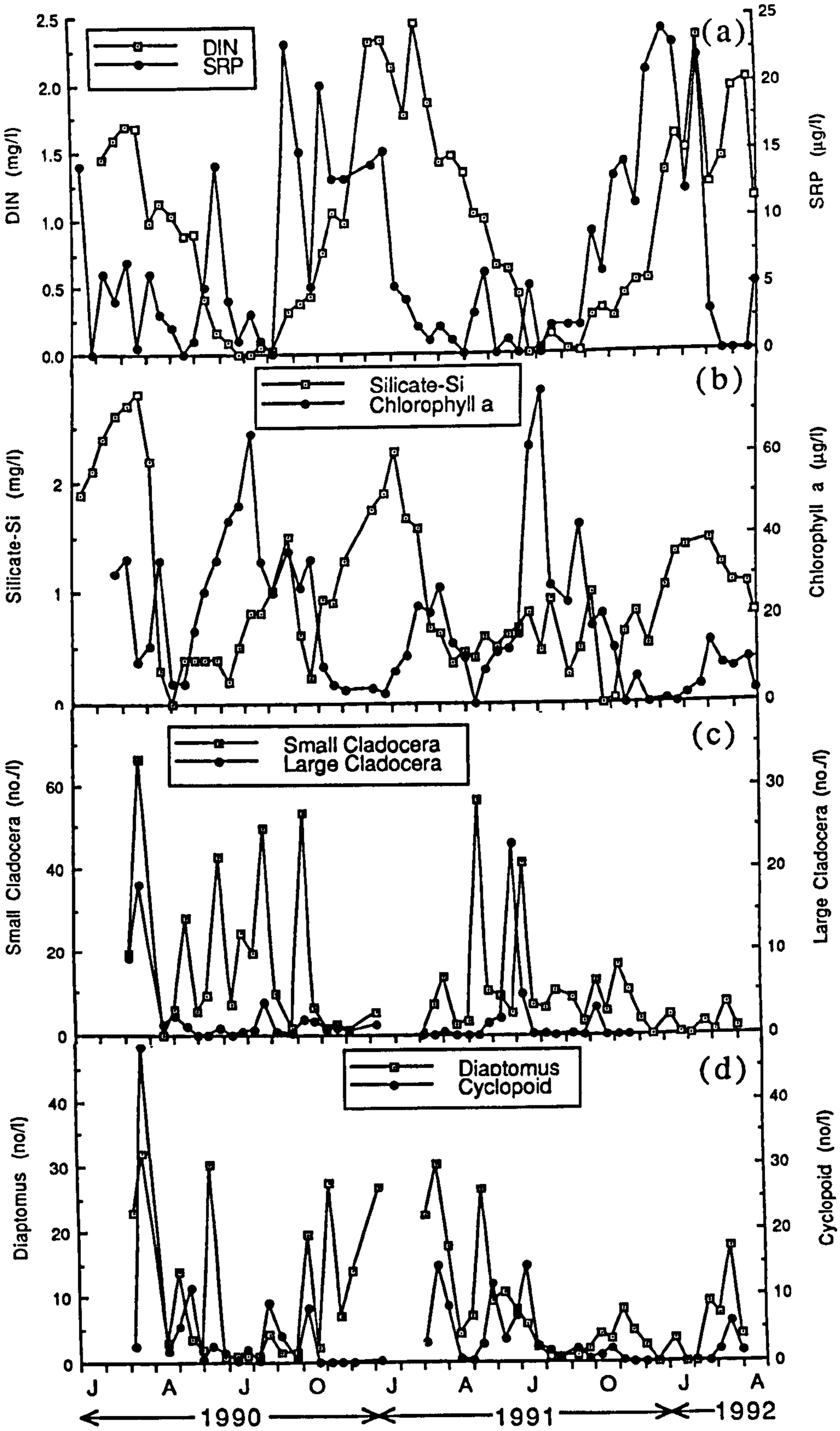


Fig. 4.3 Seasonality of (a) dissolved inorganic nitrogen and soluble reactive phosphorus, (b) silicate-silicon and chlorophyll *a*, (c) small cladocera and large cladocera, and (d) *Diaptomus gracilis* and cyclopoids, in Mere Mere, from January 1990 to April 1992.

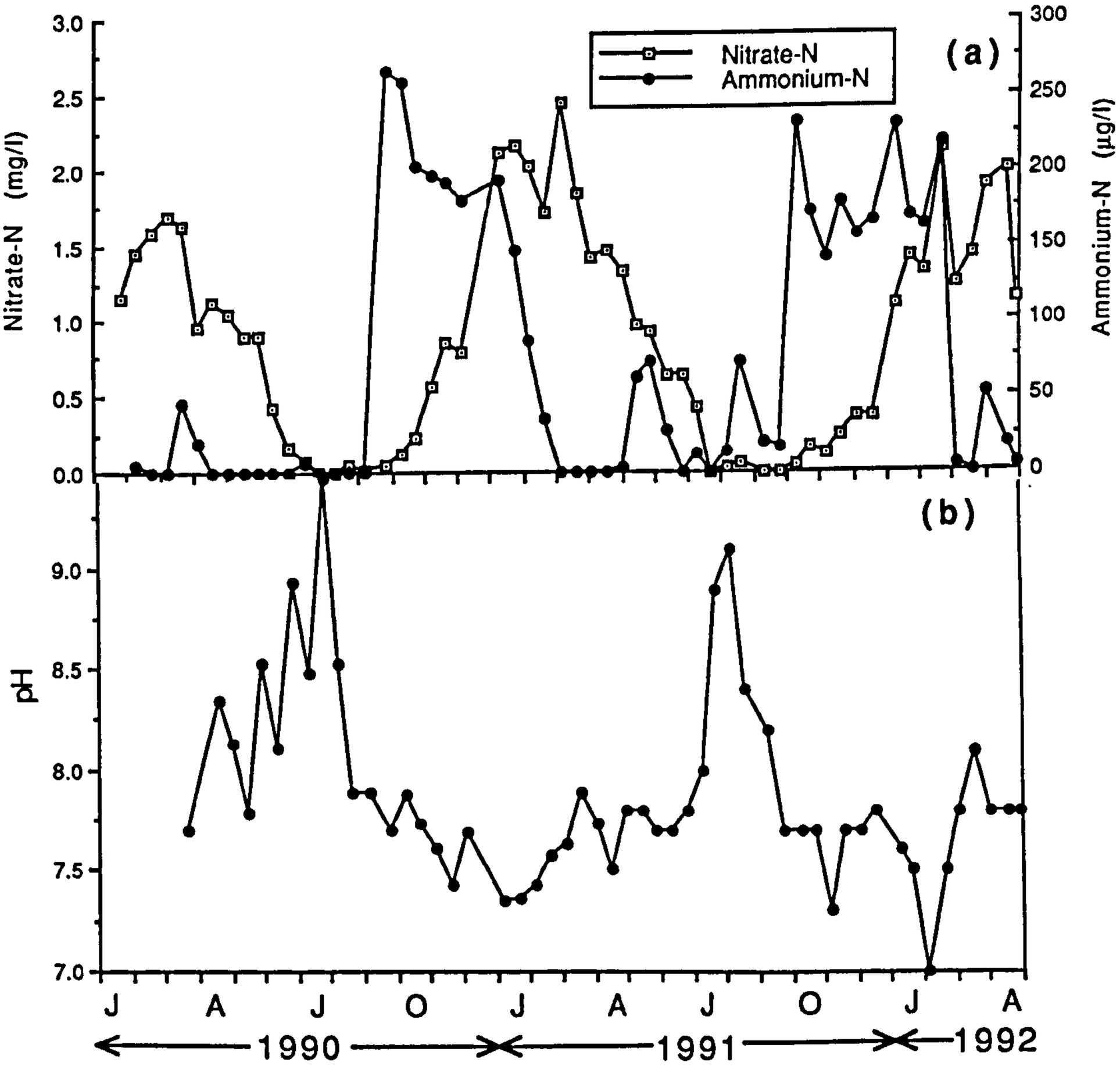


Fig. 4.4 Seasonality of (a) nitrate-nitrogen and ammonium-nitrogen, and (b) pH, in Mere Mere, from January 1990 to April 1992.

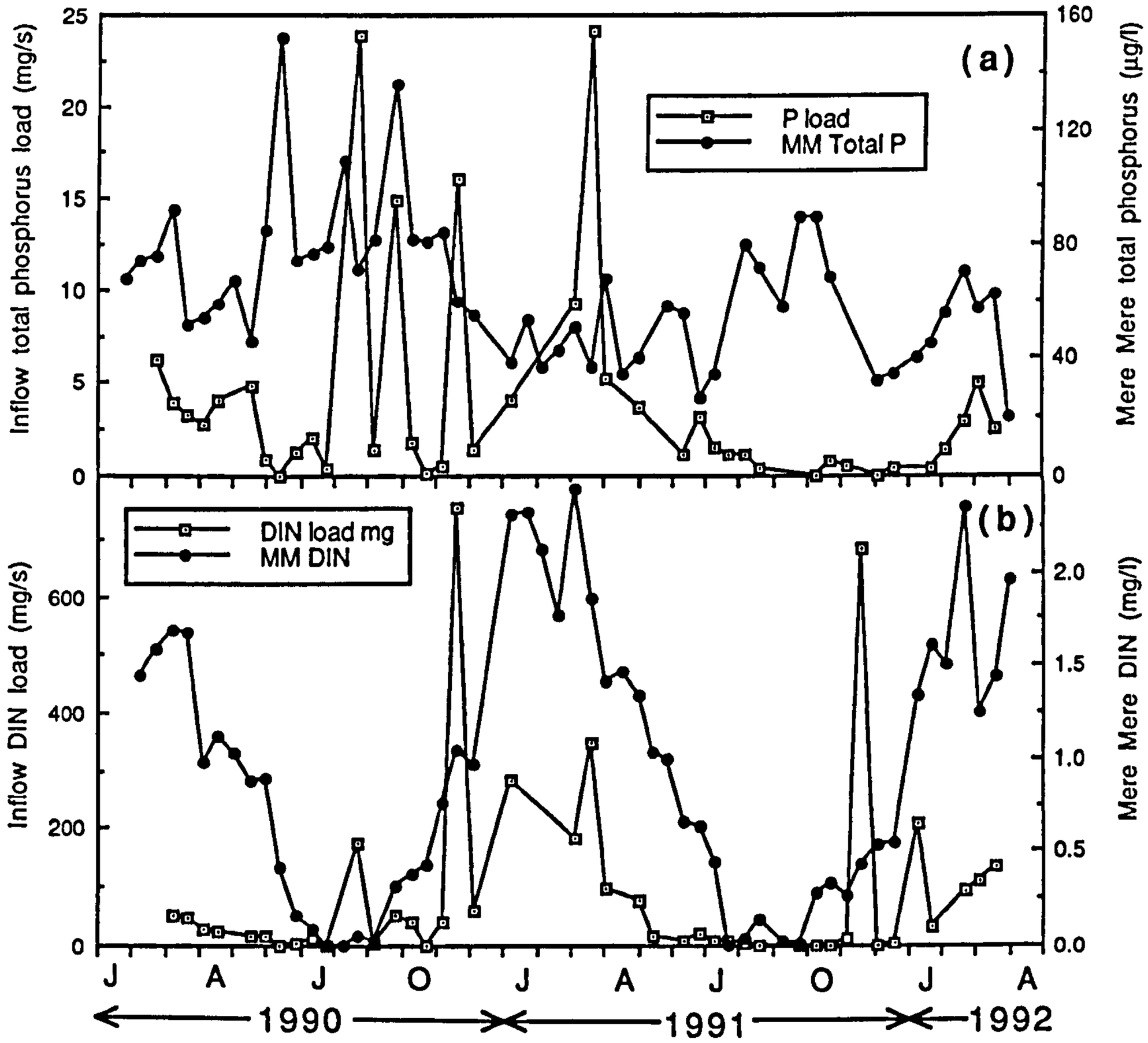


Fig. 4.5 Seasonality of (a) lake total phosphorus and inflow total phosphorus loading, and (b) lake dissolved inorganic nitrogen and inflow dissolved inorganic nitrogen loading, from January 1990 to April 1992.

Jul 1990, 9.1 in Aug 1991) (Fig. 4.3b). pH was very closely correlated with chlorophyll *a* concentration ($r^2=0.53$, $p^{-}0.0001$).

Detailed physical and chemical data recorded for Mere Mere, and the inflow, can be found in Appendix 3.

4.3.1.2 Phytoplankton and zooplankton

Chlorophyll *a* concentrations (Fig. 4.3b) increased in spring, summer and autumn. The maxima for 1990 and 1991 were 71 µg l^{-1}, and 77 µg l^{-1} respectively, during August. Mean chlorophyll *a* concentrations over the phytoplankton growing season (Feb-Oct) were 29 µg l^{-1} (1990) and 24 µg l^{-1} (1991).

Detailed plankton data can be found in Appendix 4. The seasonal periodicity of the phytoplankton taxa is shown in Figure 4.6. Algal numbers are expressed either as cells, filaments, or colonies, as appropriate to the normal morphology of the organism (see Appendix 4 for further details).

The spring increase in chlorophyll *a* was largely due to the diatom *Asterionella formosa*, but there were also high densities of*Rhodomonas* sp. other small flagellates, and the large, filamentous cyanobacterium *Planktothrix agardhii*.

The summer increase in phytoplankton biomass, from June to September, was principally due to the cyanobacteria *Anabaena* spp., *Coelosphaerium naegelianum*, *Aphanizomenon flos-aquae*, and *P. agardhii* in the latter part of summer. The dinoflagellates, *Ceratium hirundinella* and *Peridinium* sp., also showed their population maxima during summer. Although their numbers were relatively low (379/ml in 1990, 285/ml in 1991), a few hundred cells of *Ceratium* per ml may yield the same

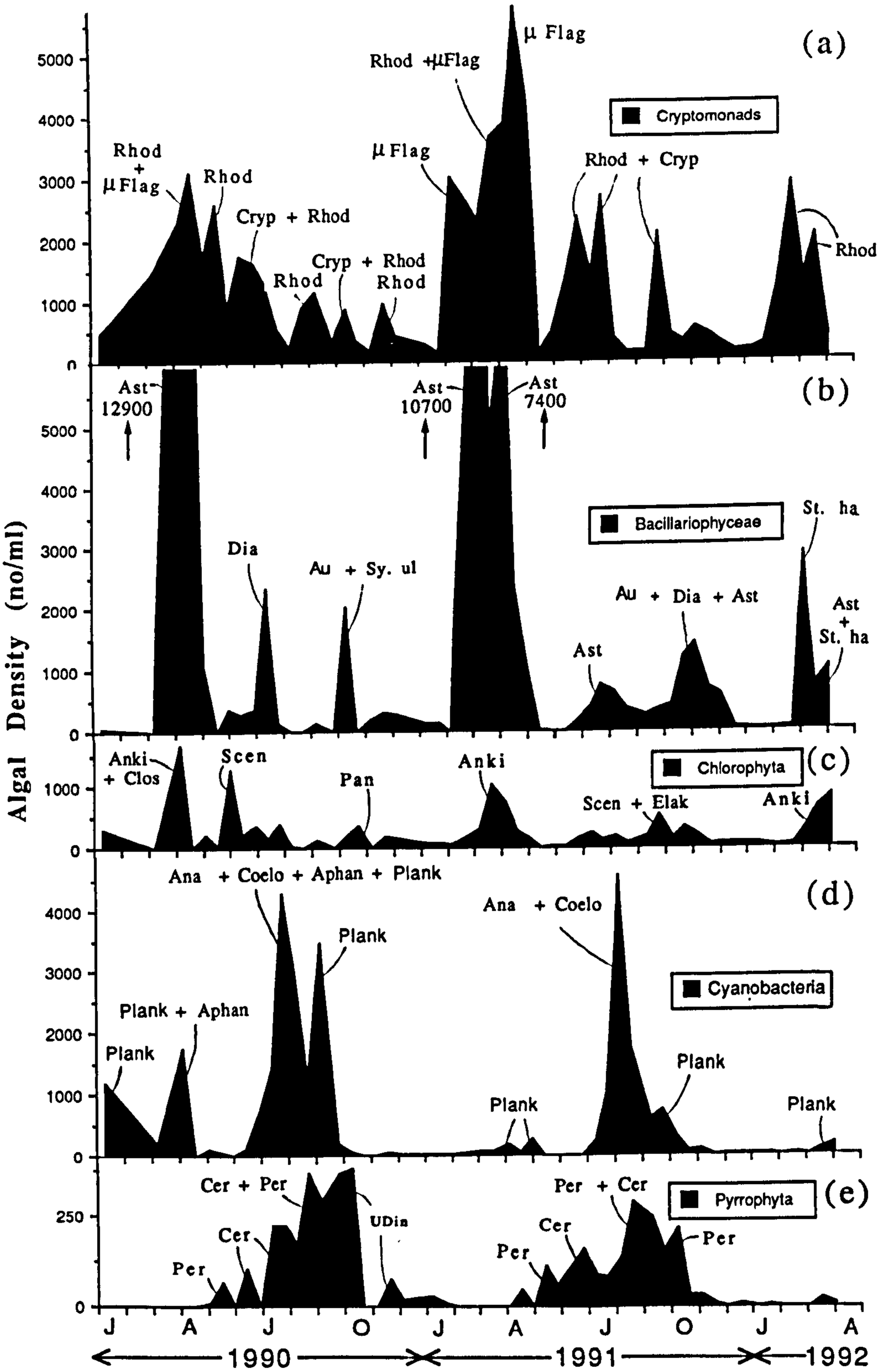


Fig. 4.6 Changes in density of (a) Cryptomonads, Euglenophyta, and small, unidentified flagellates, (b) Baccillariophyceae, (c) Chlorophyta, (d) Cyanobacteria and (e) Pyrrophyta, in Mere Mere, from January 1990 to April 1992. Main algal taxa responsible for the peaks are indicated.

concentration of chlorophyll *a* as tens of thousands of cells of the diatom *Asterionella* (Heaney & Talling, 1980).

There was a small peak in diatom densities in July of both years (*Diatoma elongatum* in 1990 and *Asterionella* in 1991). The autumn peak in chlorophyll *a* was also principally due to diatoms, in particular, *Aulacoseira* spp.

There were small peaks in numbers of cryptomonads and chlorophytes throughout the year, particularly *Rhodomonas*, *Cryptomonas* spp., and *Ankistrodesmus falcatus*..

The zooplankton results are shown in figure 4.3c and 4.3d. The cladoceran grazers (Fig. 4.3c) are separated into two groups: the large-bodied species *Daphnia pulex*, *Daphnia longispina* (agg.) and *Diaphanosoma brachyurum*; and the small-bodied species *Daphnia cucullata*, *Bosmina longirostris*, and *Ceriodaphnia dubia*. *Daphnia longispina* (agg.) was the only taxon of the former group to become abundant, in March 1990 and May 1991. For the rest of the year, large Cladocera densities were very low.

The small Cladocera were much more abundant, although their population did not remain at a stable density, showing a series of peaks throughout the spring and summer. Early spring peaks were principally due to *Bosmina* and those in summer to *D. cucullata*.

The copepods (Fig. 4.3d) were most abundant in spring and autumn. *Diaptomus gracilis* reached a peak in March and November in both years (maximum densities: 32 l^{-1} in March 1990 and 30 l^{-1} in March 1991), but from July to September numbers remained low (< 5 l^{-1}). Cyclopoids also showed spring

peaks in density (48 l^{-1} in March 1990 and 15 l^{-1} in March 1991), but increased in August 1990 (9 l^{-1}) and July 1991 (15 l^{-1}) also.

4.3.1.3 Seasonality of water chemistry, physical factors, and plankton

The spring increase in chlorophyll *a* concentration was largely due to the diatom *Asterionella*, and hence was closely correlated with a depletion of silicate to undetectable concentrations. This depletion of silicate is likely to have caused a decline in the diatom populations, although losses would have been increased by the high density of grazers present during spring.

The depletion of DIN and SRP, along with silicate, may have favoured the growth of the nitrogen-fixing cyanobacterium *Anabaena* and the dinoflagellates *Ceratium* and *Peridinium*, which have low nutrient requirements, due to their lower growth rates (Pollingher, 1988). During summer, the zooplankton community was dominated by the small cladoceran *Daphnia cucullata*. Small cladocera are believed to have little impact on net phytoplankton and may even promote them through feeding solely on smaller phytoplankton species (Haney, 1987).

Multiple regression analyses were carried out to examine which factors may have been responsible for changes in chlorophyll *a* concentration. Multiple regression analysis of spring (March to April) chlorophyll *a* concentrations against DIN, SRP, and silicate concentrations and Cladocera densities (Table 4.2) showed no significant relationships. However, analysis of summer (June to September) chlorophyll *a* concentrations

against DIN and SRP concentrations and Cladocera densities (Table 4.3) showed a significant relationship ($r^2=0.51$, $0.025<p^{-}0.05$). DIN appeared to be of greatest importance. However, DIN concentrations decreased as chlorophyll *a* concentrations increased (Fig. 4.7), which shows the dependence of DIN concentrations on chlorophyll *a*. It does not indicate limitation of phytoplankton biomass by DIN. Although, DIN did decline to undetectable, or very low, concentrations during July and August in 1990 and June, July, and August 1991, so the phytoplankton biomass may have been limited by nitrogen. SRP concentrations appeared to be of little importance in explaining the variation in summer chlorophyll *a* concentrations, although, during summer SRP concentrations were also very low, or below the detection limit of the analysis, and so may also have been important in limiting biomass. Grazing pressure did not appear to be of great importance.

The ratio of carotenoid pigments to chlorophyll *a* (A480:663) was >1.3 throughout most of the study period (Fig. 4.8), indicating that the phytoplankton community may have been nitrogen deficient. During winter the A430:410 ratio was <1.2 which suggests that the high A480:663 ratio was due to resuspended sediment or grazing effects, though during the spring and summer months the A430:410 ratio was >1.2 which suggests that the phytoplankton were nitrogen deficient, although, the presence of N-fixing cyanobacteria during these months invalidates the use of the ratios. The presence of large populations of nitrogen-fixing cyanobacteria is, however, an indication of nitrogen deficiency in itself (Schindler, 1977).

Table 4.2 Results of multiple regression analysis on spring (March to April) chlorophyll *a* concentrations.

Chlorophyll *a*		Partial F	r^2	probability
Versus:	DIN	1.16		p>0.25
	SRP	4.16		0.05<p≤0.10
	Silicate	0.37		p>0.25
	Herbivores	0.16		p>0.25
	Total		0.47	p>0.25

Table 4.3 Results of multiple regression analysis on summer (June to September) chlorophyll *a* concentrations.

Chlorophyll *a*		Partial F	r^2	probability
Versus:	DIN	10.83		0.0005<p≤0.001
	SRP	0.20		p>0.25
	Herbivores	0.61		p>0.25
Total			0.51	0.025<p≤0.05

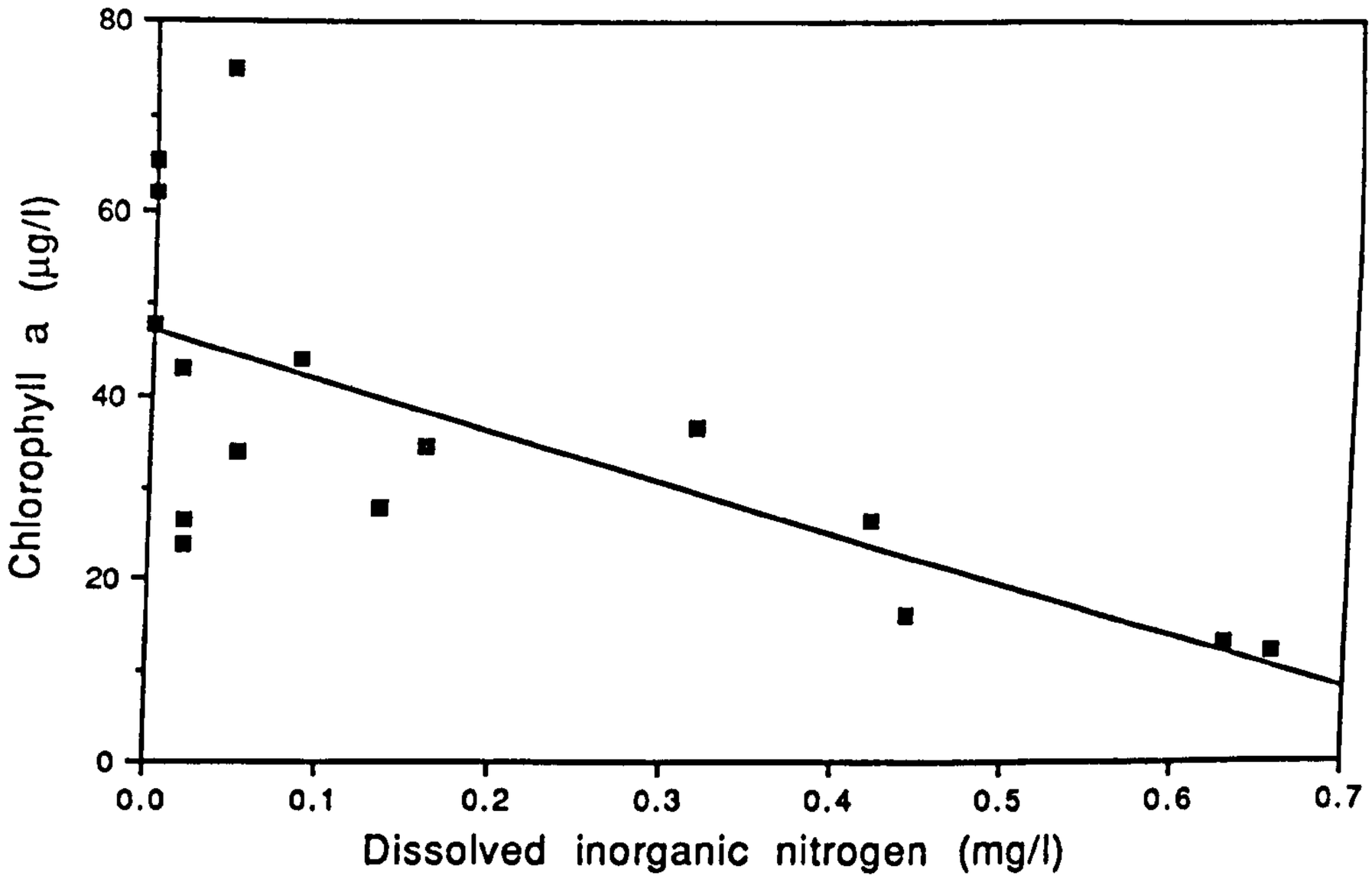


Fig. 4.7 Relationship between chlorophyll *a* and dissolved inorganic nitrogen concentrations, in Mere Mere, during summer (June to September).

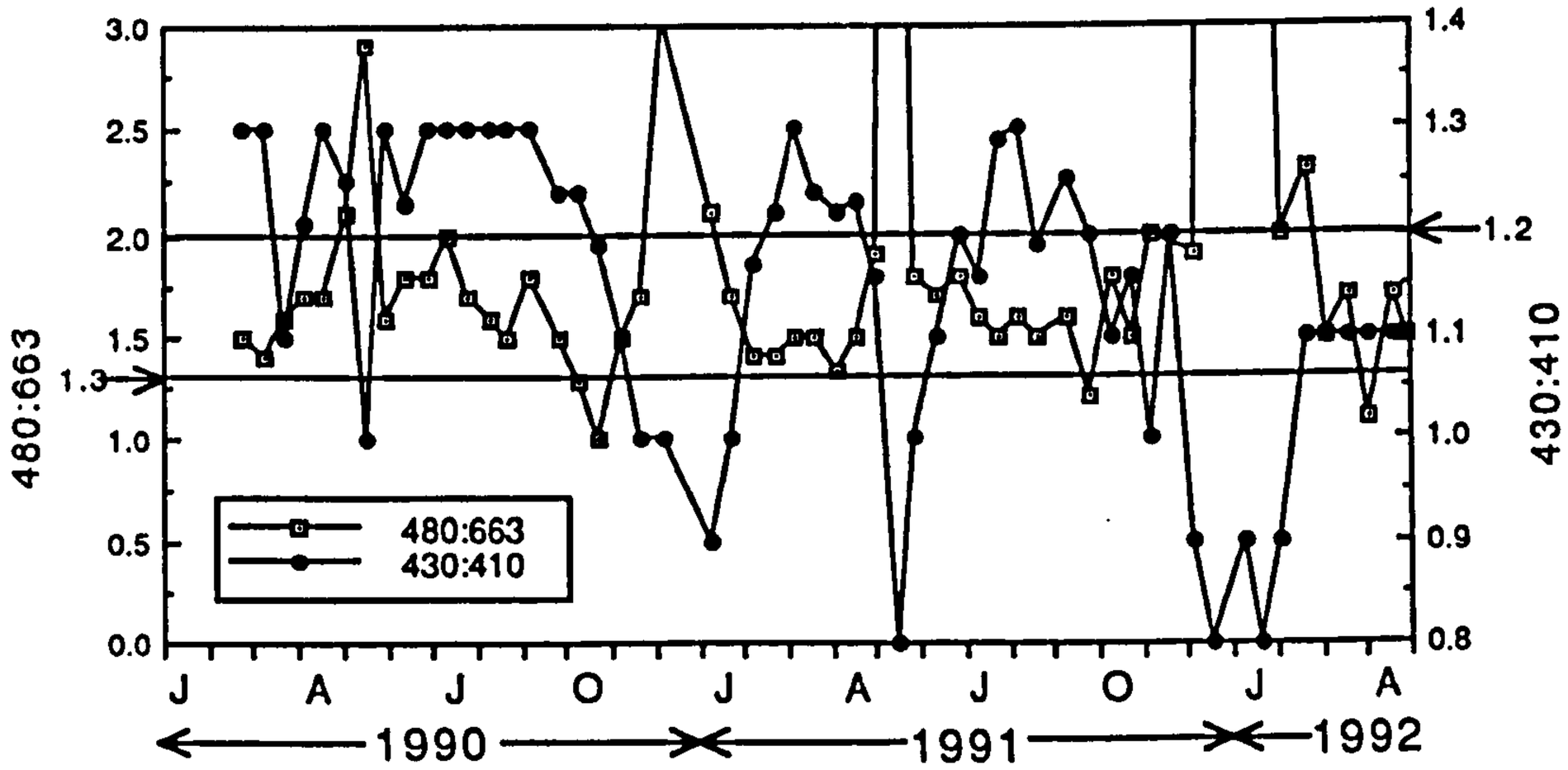


Fig. 4.8 Seasonality of the ratio of carotenoid pigments to chlorophyll *a* (ratio of absorbances at 480 nm:663 nm) and the ratio of the absorbances at 430 nm:410 nm.

4.3.1.4 Aquatic Plants

The aquatic plant community of Mere Mere (Fig. 4.9) remains diverse and abundant. Nine submerged, four floating-leaved, and seven emergent species were recorded. Little has changed since the first survey carried out (Wiggington, 1980). The submerged and floating-leaved species covered about 30 % of the lake area.

4.3.1.5 Summary of the limnology of Mere Mere

During summer, nitrogen appeared to be the factor most likely to be limiting the phytoplankton biomass, phosphorus may have been important at times too. The phytoplankton periodicity has changed a little from previous studies (Griffiths, 1925; David, 1963; Belcher & Storey, 1968). *Ceratium* and *Coelosphaerium* are still abundant during summer. However, *Microcystis*, which was recorded in the two earliest studies, was not observed in the present study, or the previous one (Belcher & Storey, 1968), whereas the nitrogen-fixing cyanobacteria *Anabaena* (and *Aphanizomenon* to a lesser extent) has become much more abundant. These changes support the hypothesis that nitrogen concentrations are important in limiting the phytoplankton crop. Moss *et al.* (1992) have shown a highly significant relationship (r^2=0.81, p<0.0001) between winter DIN and chlorophyll *a* concentrations in the deep (maximum depth >3 m) North-West Midland Meres, which suggests that nitrogen may be the limiting factor of phytoplankton crop-size in many lakes of this area.

Phytoplankton crops were high, averaging 27 µg l^{-1} over the two growing seasons (Feb-Oct), reaching higher peaks in late

Key to Vegetation Maps

Ec	*Elodea canadensis*
Lt	*Lemna trisulca*
Ch	*Callitriche hermaphroditica*
Lu	*Littorella uniflora*
Se	*Sparganium emersum*
Pn	*Potamogeton natans*
Ppf	*Potamogeton perfoliatus*
Pb	*Potamogeton berchtoldii*
Ea	*Eleocharis acicularis*
Ms	*Myriophyllum spicatum*
Eh	*Elatine hexandra*
Cs	*Callitriche stagnalis*
Chi	*Crassula helmsii*
Nt	*Nitella* spp
Cv	*Chara vulgaris*
Ep	*Eleocharis palustris*
Df	*Drepanocladius fluitans*
Nl	*Nuphar lutea*
Na	*Nymphaea alba*
Nx	Cultivated Nymphaeid
Pa	*Polygonum amphibium*
Pc	*Phragmites communis*
Ta	*Typha angustifolia*
Tl	*Typha latifolia*
Ser	*Sparganium erectum*
Ip	*Iris pseudacorus*
J	*Juncus* spp
Ac	*Acorus calamus*
C	*Carex* spp
Ef	*Equisetum fluviatile*
	Mixed emergent vegetation

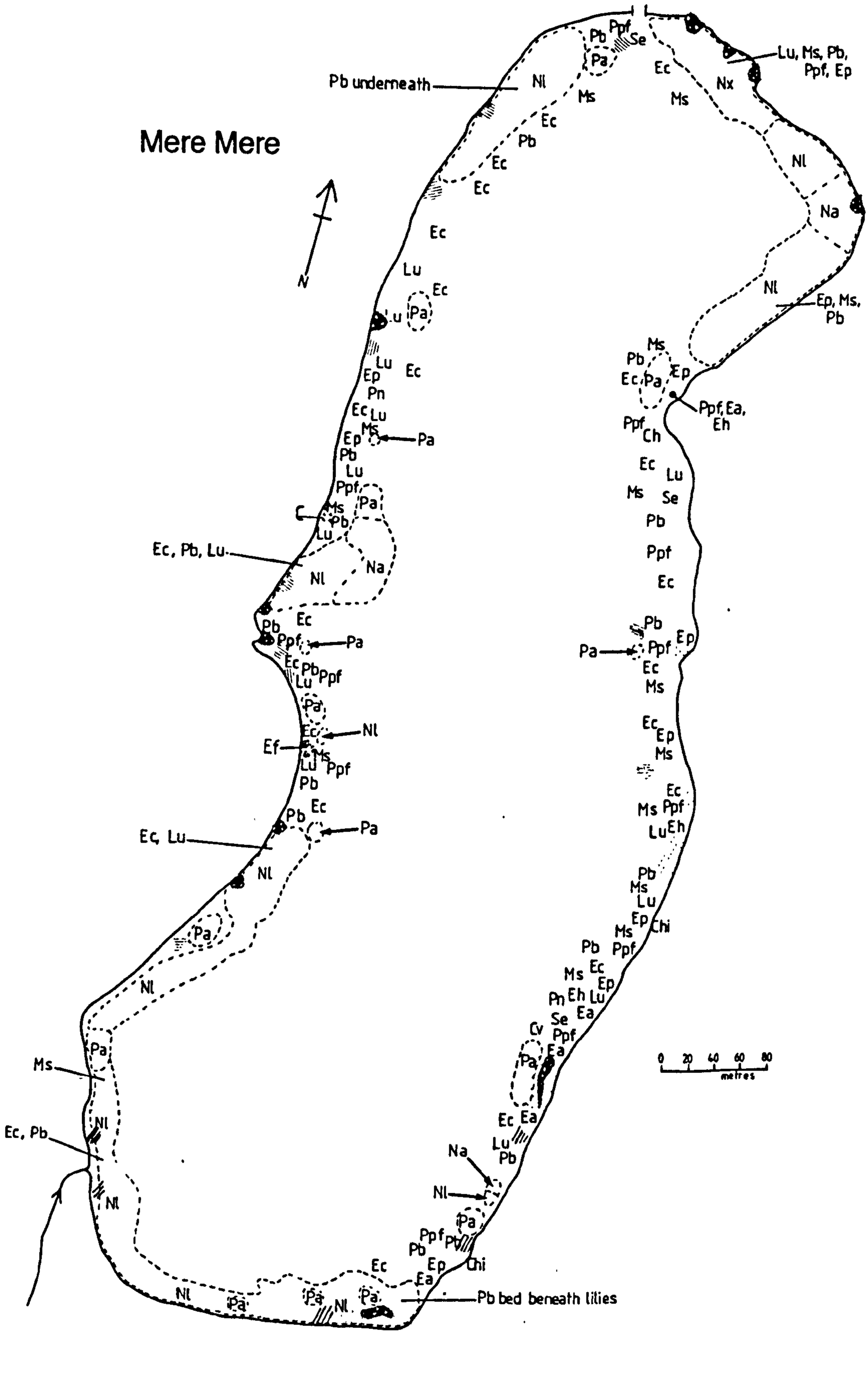


Fig. 4.9 Aquatic plant survey of Mere Mere (carried out in July 1992).

summer associated with the populations of cyanobacteria and dinoflagellates. Despite these populations, the aquatic plant community remains well developed, with one of the highest diversities of submerged species in the North-West Midland Meres.

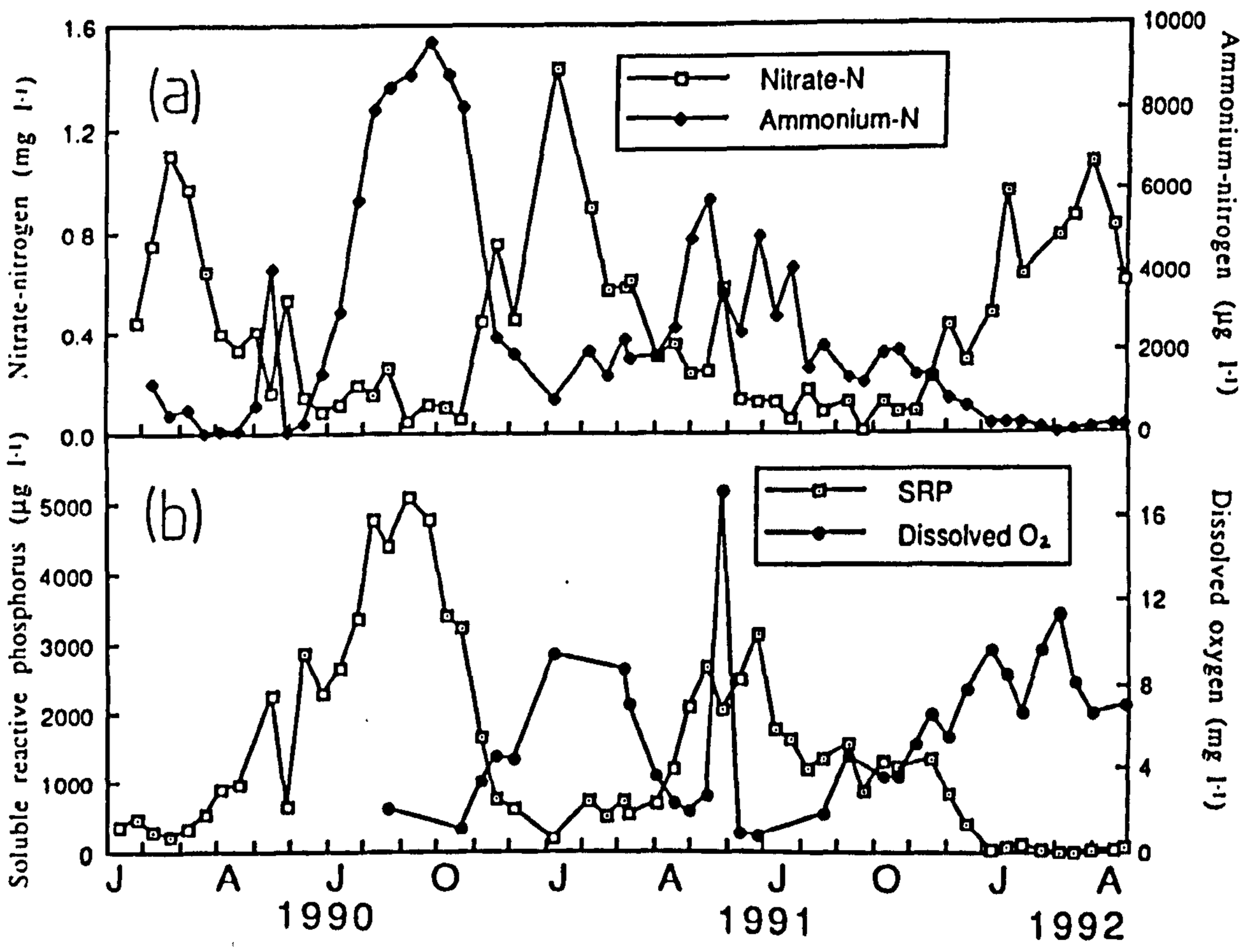
4.3.2 Little Mere

4.3.2.1 Physical factors and water chemistry

There were two striking differences in the water chemistry of Little Mere compared to Mere Mere: during summer, Little Mere exhibited extremely low dissolved oxygen concentrations and very high nutrient concentrations compared to Mere Mere.

Dissolved oxygen concentrations (Fig. 4.10b) appeared to vary seasonally. Concentrations were greater than 6 mg l^{-1} over the winter months, less than 4 mg l^{-1} over the summer months. The minimum recorded was 0.7 mg l^{-1} in June 1991. There was a brief exception to this in May 1991 when dissolved oxygen concentrations were very high, up to 18 mg l^{-1}; this was closely correlated with a sharp increase in chlorophyll *a* (May-August 1991: r^2=0.99, 0.0001<p~0.005). Since September 1991 the concentrations have been higher than for similar dates from the previous year.

Soluble reactive phosphorus (SRP) showed a very similar pattern to that of dissolved inorganic nitrogen (DIN) (r^2=0.68, p~0.0001) (Fig. 4.11a). Both nutrients showed extremely high concentration maxima (5.1 mg l^{-1} and 9.7 mg l^{-1} respectively)



4.10 Seasonality of (a) nitrate-nitrogen and ammonium-nitrogen, and (b) soluble reactive phosphorus and dissolved oxygen, in Little Mere, from January 1990 to April 1992.

during summer 1990. Concentrations have steadily declined from early summer 1991.

Nitrate-nitrogen concentrations (Fig. 4.10a) were significantly correlated with those of dissolved oxygen (r^2=0.39, 0.0001<p⁻0.005), with winter maxima (1.10 mg l^{-1} 1990; 1.43 mg l^{-1} 1991; 1.07 mg l^{-1} 1992) and summer minima (0.05 mg l^{-1} 1990; 0.01 mg l^{-1} 1991). Ammonium-nitrogen concentrations (Fig. 4.10a) were slightly more variable than those of nitrate-nitrogen. In 1990 and early 1991 there was still a seasonality with minima in late winter/early spring (0 mg l^{-1} 1990; 0.82 mg l^{-1} 1991) and a maximum in summer 1990 (9.58 mg l^{-1}). Ammonium concentrations have steadily declined from May 1991, from the maximum then of 5.80 mg l^{-1} to 0.01 mg l^{-1} in March 1992. Nitrate-nitrogen and ammonium-nitrogen concentrations showed an inverse relationship (r^2=0.25, 0.0001< $p < 0.005$).

Both SRP and ammonium-nitrogen concentrations were directly related to each other (r^2=0.81, $p \leq 0.001$) and there was an inverse relationship for both of them with dissolved oxygen concentration (SRP, r^2=0.64, $p \leq 0.0001$; NH_4-N, r^2=0.53, $p \leq 0.0001$).

pH, which was generally in the range 7-8, showing increases in the spring, was closely correlated with chlorophyll *a* (r^2=0.55, $p \leq 0.0001$) (Fig. 4.11b).

Detailed physical and chemical data recorded for Little Mere can be found in Appendix 3.

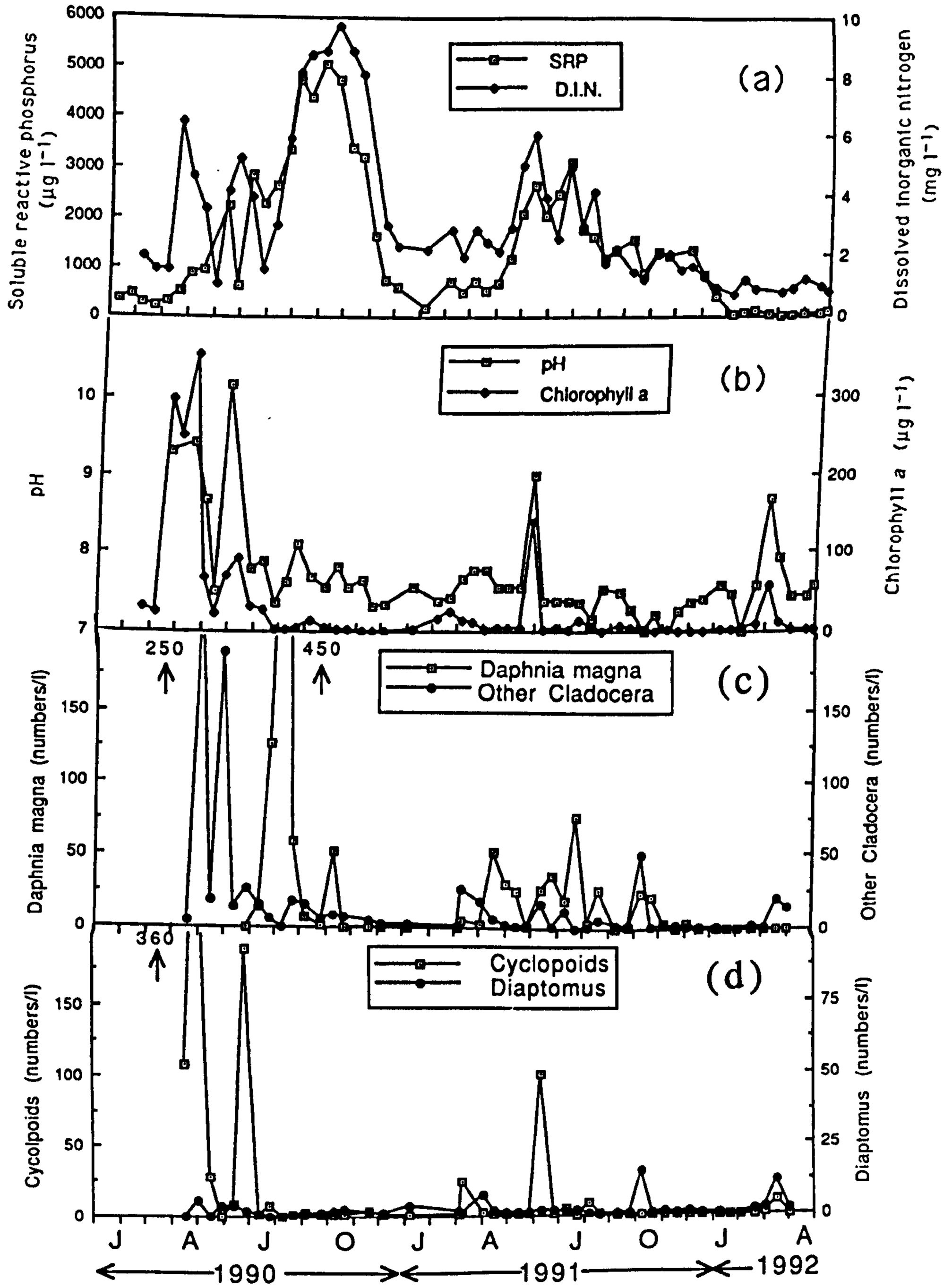


Fig. 4.11 Seasonality of (a) dissolved inorganic nitrogen and soluble reactive phosphorus, (b) pH and chlorophyll *a*, (c) *Daphnia magna* and other cladocera, and (d) *Diaptomus gracilis* and cyclopoids, in Little Mere, from January 1990 to April 1992.

4.3.2.2 Effects of the sewage effluent on the water chemistry

The huge influence of the sewage effluent is apparent from comparisons between the nutrient concentrations in Little Mere before diversion, and those in Mere Mere (Table 4.4). In particular, the dissolved oxygen concentration was much lower, and concentrations of ammonium and soluble, reactive phosphorus were much higher in Little Mere. Nutrient maxima were found during winter in Mere Mere and summer in Little Mere. The unusual nature of Little Mere was brought about by the low dissolved oxygen concentrations. These were extremely low for surface waters, and were probably caused by the respiration of large populations of bacteria feeding on organic matter in the effluent, and on the sediment surface. Anaerobic conditions promote the release of phosphate from the sediment and allow anaerobic bacteria to convert nitrate to ammonium (Mortimer, 1941; 1942). Following diversion of the effluent, ammonium and phosphate concentrations were still high in Little Mere, compared with those in Mere Mere (Table 4.4), but concentrations of these two nutrients are decreasing as dissolved oxygen concentrations increase (Fig.4.10).

4.3.2.3 Phytoplankton, zooplankton, and fish

There were sharp increases in chlorophyll *a* concentration (Fig. 4.11b) during spring. The maxima for 1990 and 1991 were 355 $\mu g\ l^{-1}$, and 140 $\mu g\ l^{-1}$ respectively. However, for the rest of the summer concentrations were less than 10 $\mu g\ l^{-1}$. The spring increase in phytoplankton biomass developed later, and to a lesser extent, in 1991 compared with 1990, although the summers were much the same, with a very low biomass.

Table 4.4 Concentration of nutrients in Mere Mere; Little Mere before diversion; and Little Mere after diversion of sewage effluent.

	Mere Mere July '90-Apr'91 & July '91-Apr'92		Little Mere Before diversion July '90-Apr '91		Little Mere After diversion July '91-Apr '92	
	Mean	Range	Mean	Range	Mean	Range
S.R.P. ($\mu g\ l^{-1}$)	8	0-25	2174	195-5070	686	10-1755
Total P ($\mu g\ l^{-1}$)	62	20-135	2484	310-5340	745	40-1910
NH_4-N ($mg\ l^{-1}$)	0.10	0-0.27	4.58	0.82-9.58	1.10	0.01-4.12
NO_3-N ($mg\ l^{-1}$)	0.84	0-2.45	0.41	0.05-1.43	0.40	0.01-1.07
D.I.N. ($mg\ l^{-1}$)	0.92	0-2.45	4.69	0.45-9.69	1.48	0.09-4.18
O_2 ($mg\ l^{-1}$)	9.2	7.1-13.6	4.6	1.1-9.4	6.6	1.8-11.3
pH	7.9	7.0-9.4	7.7	7.3-9.0	7.4	6.9-8.7
Chl. *a* ($\mu g\ l^{-1}$)	20	0-75	6	0-23	6	0-58

Figure 4.12 shows the seasonal pattern of phytoplankton species. Algal numbers were either cells, filaments, or colonies, as appropriate to the normal morphology of the organism. From both the chlorophyll *a* and phytoplankton results it is clear that, in the spring, huge populations developed, in particular, the diatom *Stephanodiscus hantzschii* and species of *Rhodomonas*, *Cryptomonas* , and other small flagellates. In the early summer of 1990 there was an increase in the gelatinous green alga *Coelastrum* sp. For the rest of the year phytoplankton populations remained very low. The only alga of any importance during either of the summers was the large, grazer-resistant*Volvox* sp. which was visibly present in late summer in 1990 and 1991, but had little impact on chlorophyll *a* concentrations or algal numbers.

Cyanobacteria also showed a peak in numbers in spring, which was greater in 1990 than in 1991. The peaks were due to the large filamentous cyanobacteria *Planktothrix agardhii* and *Aphanizomenon flos-aquae* and the colonial cyanobacterium *Coelosphaerium naegelianum*. Their numbers were very low relative to the diatoms and small flagellates, although in terms of biomass they may have been just as abundant.

The zooplankton results (Fig. 4.11c & 4.11d) are solely based on numbers of adult Crustacea as rotifers and nauplii were not retained by the zooplankton net used.

The cladoceran grazers (Fig. 4.11c) are separated into two groups, the large-bodied *Daphnia magna* and other Cladocera. The latter group, dominated by *Daphnia longispina* (agg.), reached a peak in density in the spring of 1990, coinciding with

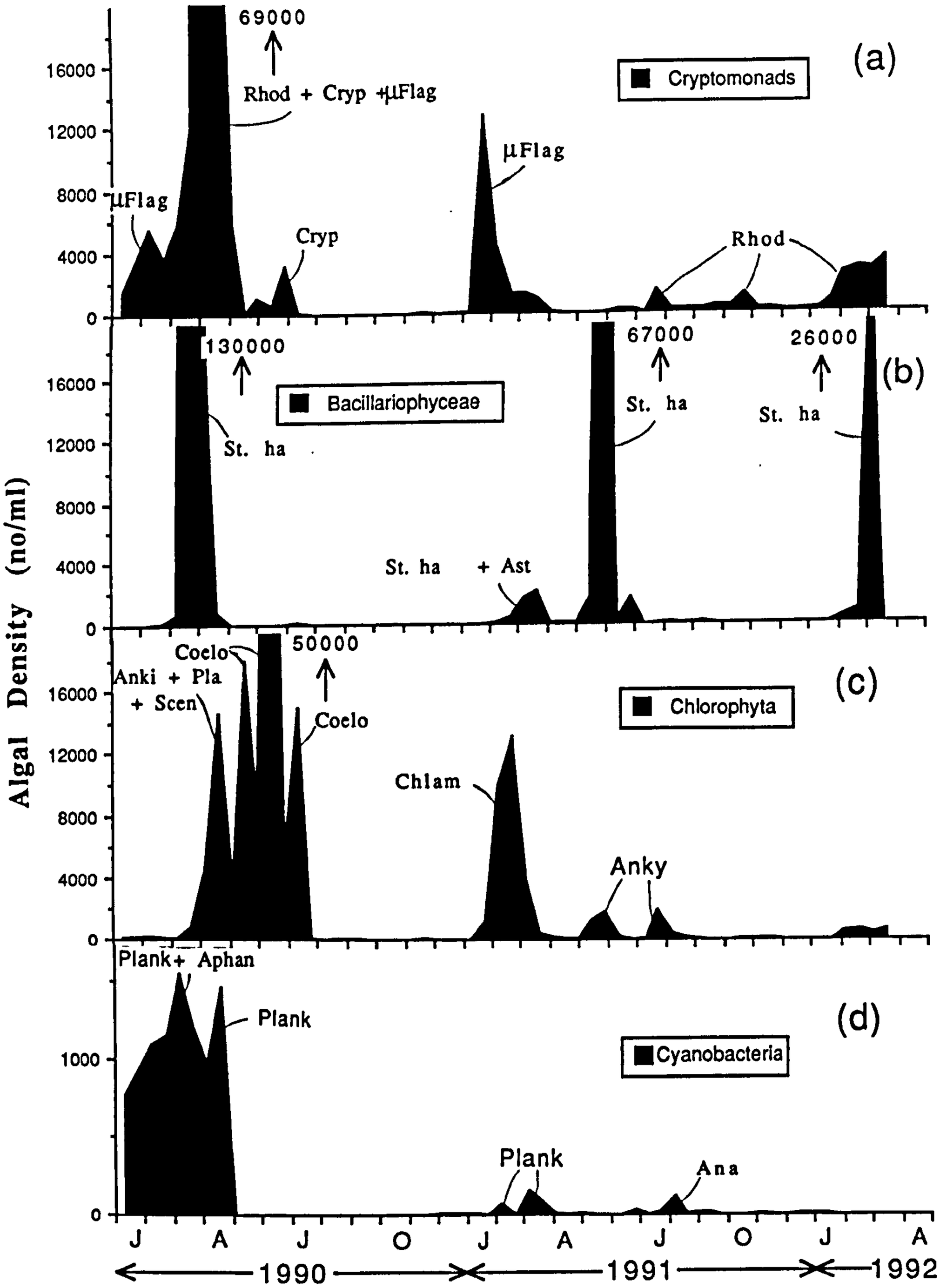
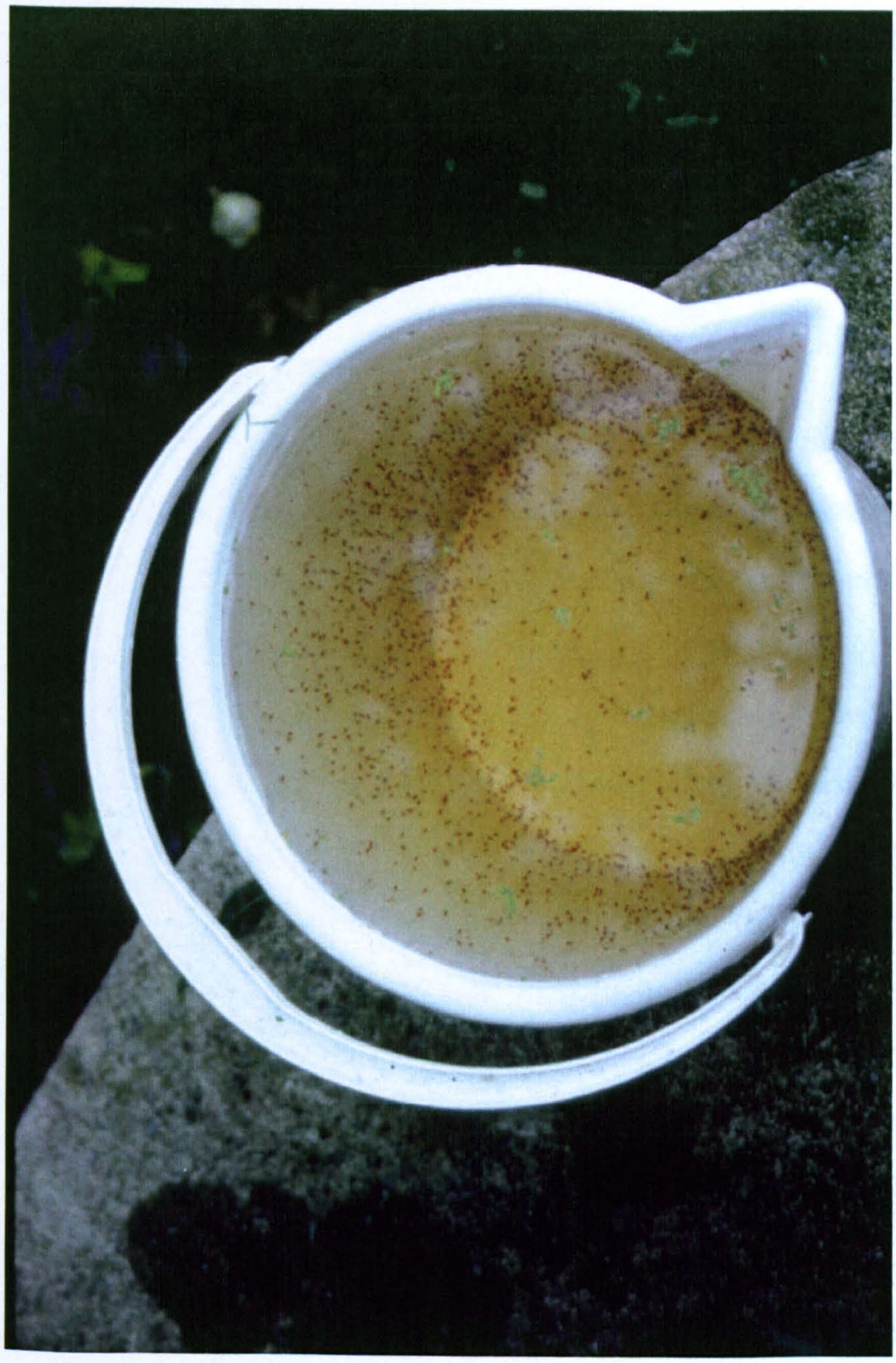


Fig. 4.12 Changes in density of (a) Cryptomonads, Euglenophyta, and small, unidentified flagellates, (b) Baccillariophyceae, (c) Chlorophyta, and (d) Cyanobacteria, in Little Mere, from January 1990 to April 1992. Main algal taxa responsible for the peaks are indicated.

Plate 4.3: Bucket containing water sample from Little Mere, showing unconcentrated *Daphnia magna*.
(photographed by Brian Moss, July 1991)



the increase in phytoplankton biomass. This large spring population did not develop in 1991, either because of the late start to the phytoplankton growing season, or because of an increase in predation pressure. The *D. magna* population appeared in early summer and reached extremely high densities even when algal biomass was very low between July and October. This was particularly marked in August 1990. In both years, these animals were unusually bright red, and because of their large size (growing up to 5 mm) they were clearly visible in the water (Plate 4.3).

Of the copepods (Fig. 4.11d) only cyclopoids were of any significance; their numbers reached a peak in spring and early summer, and then declined rapidly; numbers remained low for the rest of the year.

There was a clear decrease in density of the zooplankton populations from 1990 to 1991. This was possibly due to a decreased amount of food available (lower phytoplankton biomass in the spring, and perhaps much reduced bacteria and detritus inputs in the summer), although it could also be due to an increase in predation pressure throughout the year. The highly fluctuating densities may also be a result of sampling error, the zooplankton were visibly clumped in distribution and tended to aggregate amongst the plant beds.

Detailed plankton data can be found in Appendix 4.

No fish were caught in three sweeps of the micromesh seine net. Gill-netting caught ten fish: six roach (*Rutilis rutilis* L.) and four pike (*Esox lucius* L.) (see Table 4.5 for details).

Species	Sex	Age	Total Length (cm)	Fresh Weight (kg)	Gut Contents
Pike	Female	4+	53	1.10	Empty
Pike	Female	4+	51	1.00	> 30 *Asellus*
Pike	Male	4+	45	0.60	> 30 *Asellus*
Pike	Male	4+	44	0.62	> 30 *Asellus*
Roach	Female	4+	22	0.18	Corixidae wing covers
Roach	Female	5+	27	0.25	Empty
Roach	Female	4+	22	0.18	Empty
Roach	Female	5+	23	0.20	Empty
Roach	Male	4+	21	0.15	Empty
Roach	Male	5+	21	0.10	Empty

Table 4.5 Details of fish caught in Little Mere, on 6 December 1991.

4.3.2.4 Aquatic plants

The aquatic plant community (Fig 4.13 & Plate 4.2) was well developed in the clear water and included extensive beds of water-lilies (*Nuphar lutea* (L.) Smith and *Nymphaea alba* L.), which covered about 45 % of the lake area. The dominant submerged species included *Potamogeton berchtoldii* Fieber, *Elodea canadensis* Michaux, and *Nitella* sp.

4.3.2.5 Seasonality of phytoplankton and zooplankton

According to observed relationships between lake phosphorus and chlorophyll *a* concentrations (Dillon & Rigler, 1974), Little Mere shows a huge potential for phytoplankton growth. Each year the lake had a spring increase in diatoms and small flagellates, as is common in many temperate lakes (Hutchinson, 1967). This is often followed by a spring 'clear water' phase, when grazing by zooplankton causes a collapse in the phytoplankton population, and a summer phytoplankton dominated by grazer-resistant cyanobacteria (de Bernardi & Giussani, 1990). In Little Mere, apart from a brief phase in early summer 1990 when the gelatinous green alga *Coelastrum* sp. became abundant, the clear-water phase extended throughout both summers. Clearly nitrogen or phosphorus were not limiting the phytoplankton biomass. *Coelastrum*, and other gelatinous greens are often considered resistant to grazing, as they have been shown to pass intact through the guts of grazers (Porter, 1973). The disappearance of *Coelastrum*, and the summer clear-water phase, however, did appear to be due to high levels of zooplankton grazers, in particular, the large-bodied grazer *Daphnia magna*. This species maintained a high density despite a

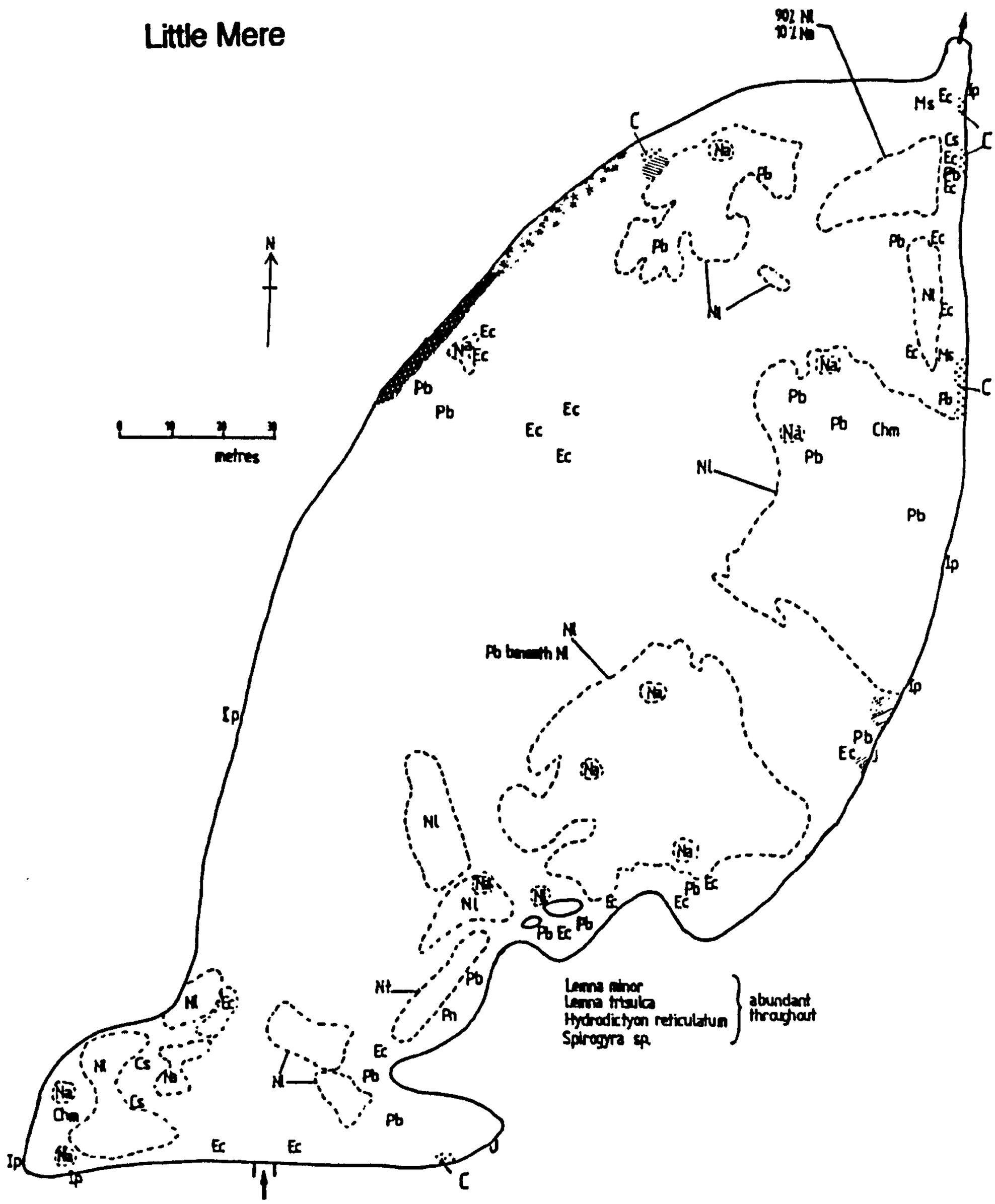


Fig. 4.13 Aquatic plant survey of Little Mere (carried out in July 1992)

low phytoplankton population. *D. magna* was most likely also feeding on the bacteria and detritus in the lake. It has been shown to have a fine-mesh filter size, and is capable of utilizing bacteria as a food source (Geller & Muller, 1981; Brendelberger, 1991).

Individuals of *D. magna* were bright red, probably due to the presence of haemoglobin, which is produced in response to low levels of dissolved oxygen (Fox *et al.*, 1951). This pigmentation increases their vulnerability to visual predation by fish (Kerfoot, 1980); together with their large size and the clear water conditions, *D. magna* ought to have been very susceptible to fish predation.

Evidently, there was little predation pressure on the zooplankton community. This was supported by the results of the fish survey (Table 4.5). The fish population in Little Mere was very low, and comprised a high proportion of pike, a piscivorous fish, which appeared to have been forced to feed benthically on the invertebrate *Asellus* sp. The low fish population in Little Mere occurred despite a rich coarse fishery in the upstream, and immediately adjacent, Mere Mere, and the stocking of fish by residents whose houses border the lake. It appears that, during summer, the quality of the sewage effluent was such as to deoxygenate the water. The low concentrations of dissolved oxygen are likely to have resulted in a fish-kill. Large, efficient grazers were then able to develop huge populations. The large phytoplankton crops that Little Mere could potentially have supported, during summer, were, therefore, prevented from developing due to grazing pressure.

4.4 Future changes to the phytoplankton of Little Mere

The clear-water condition, found throughout summer in Little Mere, may not necessarily persist in the future, as, following the effluent diversion, oxygen concentrations have been increasing (Fig 4.10). The increased oxygen concentrations may allow fish populations to recover, either through colonisation from Mere Mere, or through illegal stocking by the public. Increased numbers of fish may result in increasing summer phytoplankton biomass, through reductions in grazer numbers, or through bioturbation of the sediments (Lammens, 1988) and nutrient regeneration (McQueen, 1990). How might these changes affect the prospects for future phytoplankton dominance?

The first possible scenario is that it will not change. Little Mere has large stands of water-lilies, and submerged aquatic plants, which cover about 45 % of the lake area. Aquatic plant communities are resilient to change as they help maintain low phytoplankton standing crops through the provision of refuges for grazers. Similar situations occur elsewhere in the North-West Midland Meres (Moss *et al.*, 1992), and in the Norfolk Broads (Timms & Moss, 1984) in which clear-water is maintained at high nutrient concentrations by grazers co-existing with zooplanktivorous fish. Other mechanisms which may preserve plant beds are direct shading, consumption of nutrients and denitrification (van Donk *et al.*, 1989; Ozimek *et al.*, 1990), provision of suitable habitat for piscivores (Grimm, 1989), and allelopathy (van Vierssen & Prins, 1985).

The changing conditions in the lake may, however, favour different phytoplankton communities from before. Despite

inocula present in Mere Mere, cyanobacteria were relatively unimportant in Little Mere, disappearing in the spring at the same time as the increase in zooplankton density. Controversy surrounds the suitability of cyanobacteria as a food for zooplankton. They have been shown to affect growth and mortality of grazers: (1) by producing toxic chemicals (Lampert, 1981), (2) by being poorly assimilated (Arnold, 1971), and (3) by inhibiting feeding on co-occurring nutritious foods (Fulton & Paerl, 1987). Despite this, some studies (Van Donk *et al.*, 1989; Jeppesen *et al.*, 1990a) have shown a disappearance of cyanobacteria, due to grazing pressure, following fish removal, although in some cases fish removal may actually stimulate cyanobacteria, such as the development of grazer-resistant flakes of *Aphanizomenon flos-aquae* (Lynch, 1980; Jeppesen *et al.*, 1990b). Another explanation for the absence of cyanobacteria in Little Mere during the summer is that conditions did not favour them, so that their numbers remained low.

In respect of its very low flushing rate in summer, Little Mere would be expected to favour the large, slow-growing cyanobacteria over small species with high growth rates. However, shallow lakes and ponds, particularly those that are organically-rich, like Little Mere, tend to favour green algae (King, 1970). This is possibly because there is a reduced chance of CO_2-depletion, due to a large contact area of organic sediments, in relation to water volume. Bacterial respiration at this sediment surface, or on organic matter in the sewage effluent may establish an abundance of free-CO_2. A CO_2-depleted epilimnion is also less likely to develop in a shallow lake than in

a deep lake (Talling, 1976), as thermal stratification is usually very short-lived. Cyanobacteria tend to be favoured over other algal types by low free-CO_2 concentrations (Shapiro, 1990b), due to their greater affinity for carbon at low concentration (Long, 1975) and their ability to utilise bicarbonate (Beardall, 1985). During the summer free-CO_2 concentrations (Fig. 4.14) in Little Mere remained above 2 $\mu g\ l^{-1}$, whereas in Mere Mere, where large populations of cyanobacteria were present, they were reduced to negligible amounts.

Now that the sewage effluent has been diverted, free-CO_2 concentrations may be expected to fall. Concentrations of nutrients will also fall, but are likely to remain abundant for several years due to release from the sediments in summer. For these reasons there may, therefore, be a change towards cyanobacteria in the phytoplankton.

4.5 Prospects for long-term improvement

Re-development of the fish community in Little Mere will increase the predation pressure on *D. magna* even in the presence of the aquatic plant refuges. A grazer cladoceran community should persist, although, it may be of animals too small to cope with cyanobacteria (Dawidowicz, 1990), if they become established. The phytoplankton community of Little Mere may therefore change from being grazer-limited to nutrient-limited, as it appears to be in Mere Mere. If this should occur, increasing summer phytoplankton biomass may be sufficient to compete with the aquatic plants and destabilize the system (Moss, 1990). On the other hand, Mere Mere retains its rich and diverse aquatic plant community alongside a summer

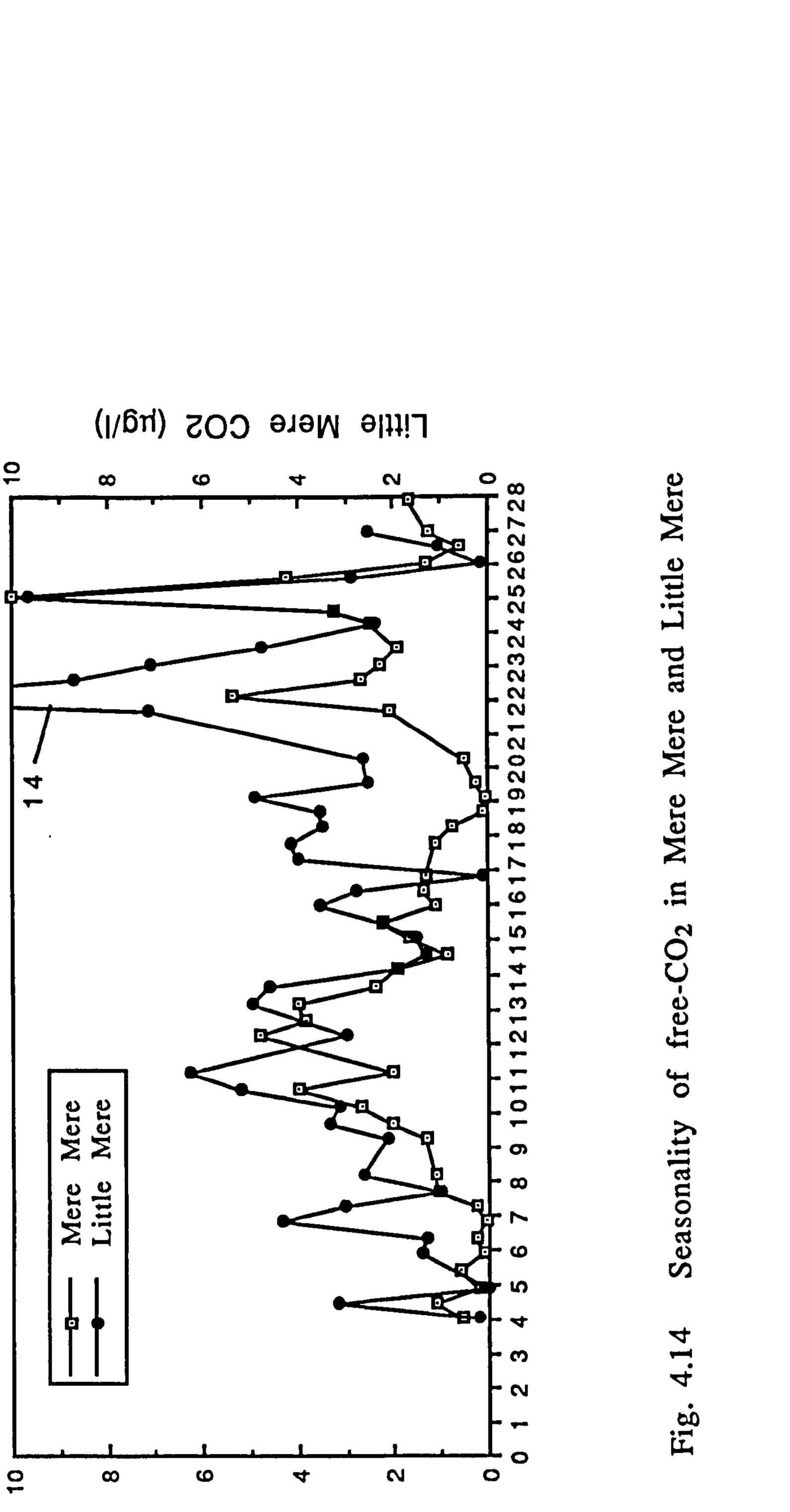


Fig. 4.14 Seasonality of free-CO_2 in Mere Mere and Little Mere

plankton community in which *D. magna* is absent and cyanobacteria are common, so, Little Mere with its more significant aquatic plant community (in terms of relative area), and decreased likelihood of CO_2-depletion (due to its greater sediment-area:volume ratio) should be even more resilient to change.

Chapter 5: Oak Mere geology and hydrology

5.1 Introduction

Many of the North-West Midland Meres have no visible inflow or outflow and are thought to be largely fed by groundwater. Due to the complexity of measuring groundwater inputs, particularly given the heterogeneous nature of the surface drift geology in this region (Land, 1965), there has been very little work on the hydrology of the meres. Only one detailed water budget of the lakes of this region has been made for Crose Mere by Reynolds (1975), and this had an outflow. Oak Mere is one of the 'isolated' meres with no inflow or outflow, and one which in recent years has experienced a fall in lake level with a consequent dramatic reduction in surface area. Reduced rainfall in the area was the most obvious explanation for the drop in lake level, but, it was not certain that this was the sole reason, as Oak Mere appeared to be affected to a much greater extent than other lakes in the region.

There have been two recent studies (Seymour, 1992; Savage *et al.*, 1992) of the hydrology of Oak Mere which aimed to understand and explain the changes in water level. The former was a study based on groundwater data from nearby boreholes, which provided detailed information on the geology and hydrology of the area. It concluded that Oak Mere is in hydraulic continuum with the groundwater and the lack of effective rainfall over recent years was the primary reason for the observed fall in water level. The latter study (Savage *et al.*, 1992) describes a hydrological model for Oak Mere based on very limited water level measurements and chemical data. It

Plate 5.1: View across Oak Mere, looking north. Foreground shows the southern sandy shore and the dominant submerged plant, *Littorella uniflora*. (photographed by Bryan Lewis July 1990).

suggests that the lower part of the mere basin is sealed from the groundwater by lake sediment and at times the lake lies "perched" above the water table; water moving between Oak Mere and the groundwater by "inspilling" or "outspilling" through or above the impermeable layer.

Regular monitoring of the water level of Oak Mere during this study has enabled a detailed water budget to be constructed, which may allow a greater understanding of the importance of climate on the lake level of Oak Mere.

5.1.1 Site description

Oak Mere (National Grid Reference SJ 576 676) (Plate 5.1) is a relatively shallow lake with a mean depth ranging from 1.5-1.7m (depending on the fluctuating lake volume). Land use around the lake (Table 5.1) is principally improved agriculture. In recent years, some agricultural land has been lost to sand and gravel extraction, resulting in large, flooded sandpits to the north-east of the mere. There is a small area of woodland around the northern end of the mere, although a thin strip of woodland extends around the whole of its border. Details of the lake are shown in Table 5.2.

5.1.2 Geology and hydrology

The underlying geological strata (Fig. 5.1) comprise the Lower Keuper Saliferous Beds beneath the mere, with the mudstones and gravels of the Lower Keuper Marl to the east and Keuper Sandstone to the west. The East Delamere fault runs approximately north-south about 200 m west of Oak Mere, and separates the Keuper Sandstone from the Lower Keuper Marl

Table 5.1. Land usage in Oak Mere parish in 1931 and 1987. Based on data taken from the Agricultural Census returns, held at the Public Records Office at Kew. For stock headage, an index of potential relative nutrient supply from excreta has been derived from the annual average amounts of nitrogen and phosphorus excreted per head. The amounts of nitrogen and phosphorus excreted by each stock type have been summed and then normalised relative to a value of 1 for humans. The index has then been multiplied by the headage to give an indication of change in nutrient load (see Moss *et al.* (1992) for further details).

	1931	1987
Cattle (head)	623	462
nutrient units	7601	5636
Pigs (head)	119	3452
nutrient units	571	16570
Sheep (head)	96	72
nutrient units	144	108
Poultry (head)	4717	168
nutrient units	660	24
Total nutrient units	8976	22338
Permanent grass (ha)	342	192
Temporary grass (ha)	216	63
Arable (ha)	230	215
Woodland (ha)	1	4
Rough grazing (ha)	17	9
Total hectarage	806	483

Table 5.2 Lake and catchment details of Oak Mere.

	Oak Mere
Geographical co-ordinates	53° 12′ N; 2° 38′ W
Altitude (m a.s.l.)	73
Surface Area (ha) [1]	18-22
Maximum Depth (m) [1]	7-8
Mean Depth (m) [1]	1.5-1.7
Volume (m^3) [1]	(3.1-3.3) x 10^5
Catchment area (ha) [2]	20-90

[1] range covering the changes in water level observed during this study.

[2] range is given due to the difficulties in defining the catchment area to the South of Oak Mere (see sections 5.3.1 and 5.3.3 for further details on the estimation of the catchment area).

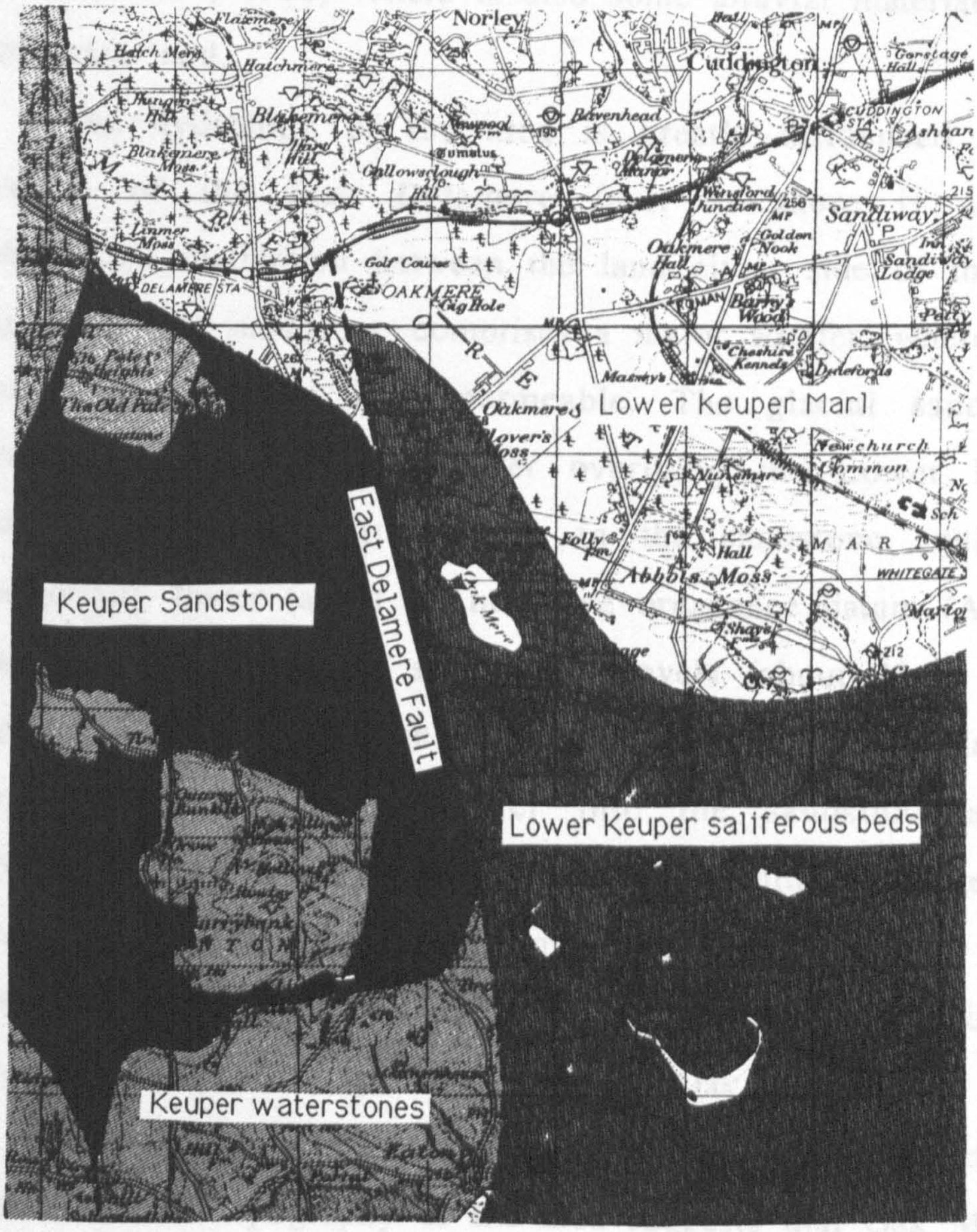


Fig. 5.1 Solid geology of the Delamere area.
(Geological Survey of Great Britain, Solid Sheet 109).
Scale: 1 cm = 0.63 km

and Lower Keuper Saliferous beds. The drift geology of the area (Fig. 5.2) comprises largely glacial sands and gravels. The actual lake basin lies in a sandy area with peat underlying its northern end (Beresford, 1960). There is also some alluvial material at the south-east end.

The hydrology of the area is greatly influenced by the location of the East Delamere fault as there is a clear hydrological distinction between the land either side of the fault (Fig. 5.3). The sandstone comprises a major aquifer, whereas the Lower Keuper Marl is impermeable. The glacial sands and gravels form a permeable layer overlying the Lower Keuper Marl. The level of groundwater in the sandstone aquifer is substantially lower (about 35 m above ordanance datum (AOD)) than those in the glacial sands and gravels (about 70 m AOD) (Fig. 5.3). The NRA believe that water moves by gravity drainage from the glacial sands aquifer into the sandstone aquifer (Seymour, 1992). The NRA also holds confidential borehole data, provided by Alfred McAlpine, owners of a sand and gravel quarry north of Oak Mere, which suggests that there is a distinct hydraulic gradient towards the north of Oak Mere, with which the glacial sands to the East of the fault are in hydraulic continuum. The topography of the area suggests that Oak Mere is near the upper end of this gradient and groundwater moves away from the north end of Oak Mere, emerging at a stream system 3 km further north.

5.1.3 Historical changes in water level

Water was abstracted from Oak Mere from 1926 until 1948. Records from 1948 (Mid and South East Cheshire Water

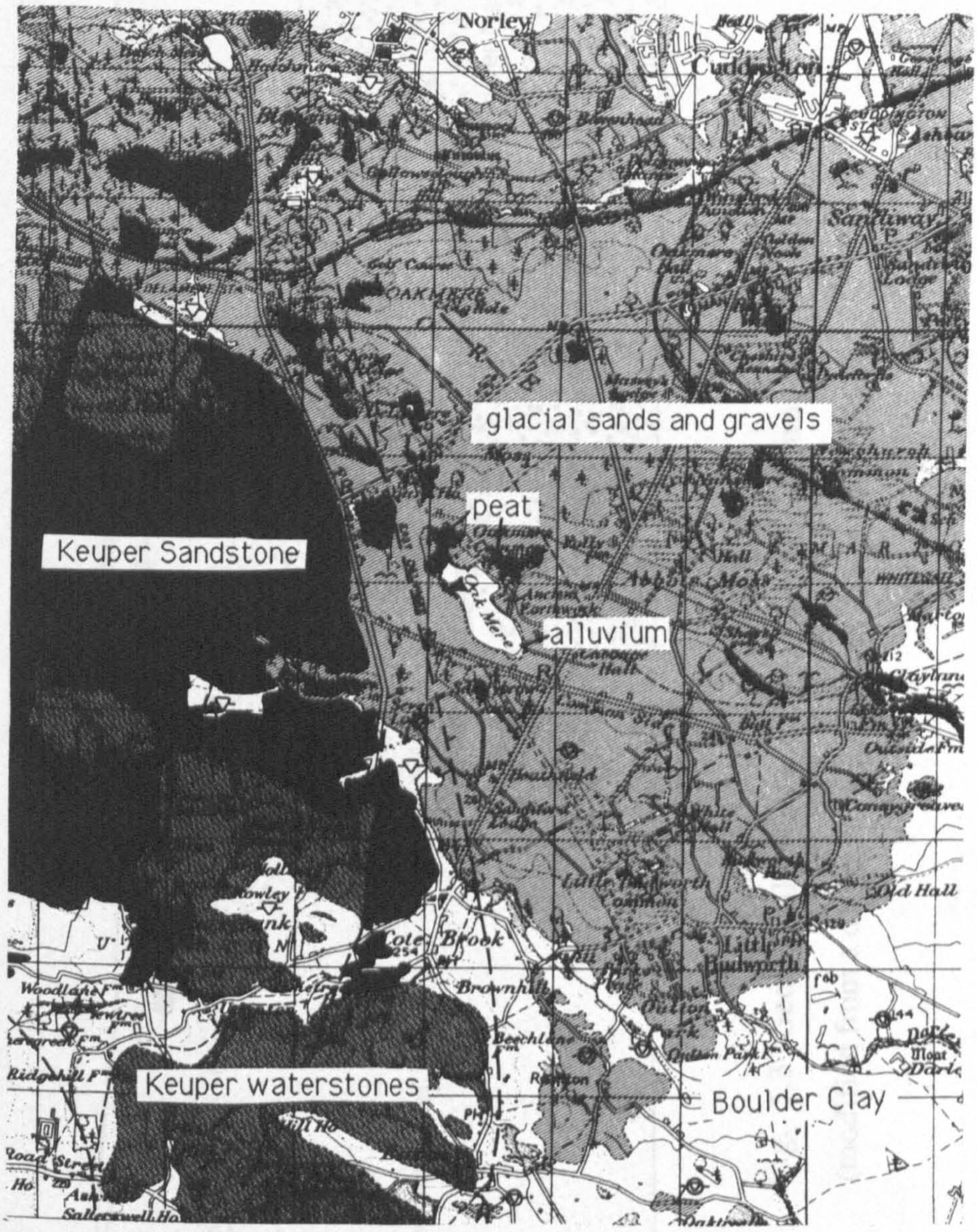


Fig. 5.2 Drift geology of Delamere area.

(Geological Survey of Great Britain, Drift Sheet 109).

Scale: 1 cm = 0.63 km

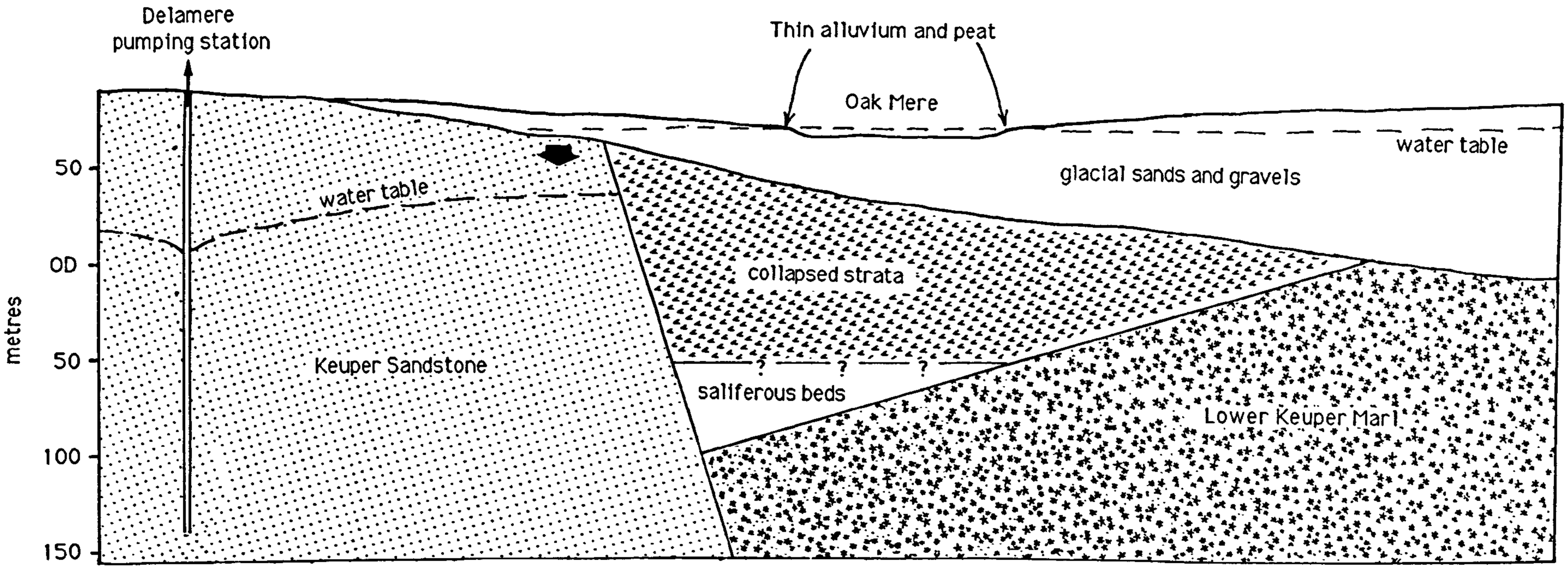


Fig. 5.3 Geological cross-section (East-West) through Oak Mere (modified from a diagram by R. Ireland, North West Water).

Board, pers. comm. to English Nature (former NCC)) show that the lake level rose during January by about 15 cm despite abstraction of over 12500 m^3, and levels remained constant during February and March despite abstraction of over 13000 m^3 each month. The first detailed observations of water level changes were made by Lind (1951) which included a period in July 1951 when over a period of two weeks 136400 m^3 of borehole water was added to Oak Mere, and the water level rose by 0.35 m. If the lake basin was impermeable the lake would be expected to have risen by about 1 m (see Fig. 5.6a). By about November the lake had almost returned to the level at the start of July, without any visible outflow.

5.2 Water budget methods

As Oak Mere has no surface inflow or outflow there were only three identifiable components to the water budget:

(1) Catchment drainage, calculated from the rainfall over the area, corrected for evapotranspiration.

(2) Direct rainfall on the lake surface.

(3) Evaporation from the lake surface.

The catchment area was estimated from contour lines using the 1:25000 Ordnance Survey.

Mean monthly rainfall and temperature data (Monthly Weather Report, 1990; 1991; 1992) were recorded by the Delamere Forest Outdoor Education Centre (National Grid Reference SJ 529713). Missing rainfall data points were estimated by calculating a regression equation relating the rainfall at the Delamere Forest station to the rainfall recorded at

the Meteorological Office at Manchester Ringway Airport. This relationship was highly significant (r^2=0.89, p<0.0001). Potential and actual evaporation were calculated as described in Appendix 1.

A bathymetric survey of the lake was carried out in June 1990, using a Lowrance LRG-1510B echosounder. Water level measurements were taken every two weeks from an old pier extending out into the lake. The surface area of the lake was estimated from the relationship between surface area and depth, calculated from the bathymetric survey. (Fig. 5.6b). Changes in lake volume were calculated by multiplying the change in lake level by the surface area of the lake.

5.3 Results and discussion

5.3.1 Catchment area and bathymetric survey

The catchment area (Fig. 5.4) is difficult to define because of the relatively flat area to the south of the lake. For this reason maximum (360 ha) and minimum (270 ha) limits to the catchment area were estimated.

The bathymetric survey (Fig. 5.5) showed that Oak Mere was shallow over much of its area. Based on this survey the relationships between depth and surface area and lake volume can be estimated (Fig. 5.6). These suggest that a small reduction in water level will lead to relatively large reductions in surface area.

5.3.2 Water level changes and water budget

Monitoring of the water level (Fig. 5.7) showed a fall of 32 cm during the summer of 1990, and a fall of 44 cm during 1991. There was very little recharge during the intervening winter, or in the following winter, resulting in a net fall of 54 cm over the period covered in this study.

Details of potential evaporation and effective rainfall for the Oak Mere catchment are given in Appendix 1. The results of the water budget for the minimum estimated catchment area (Table 5.3) reveal a major problem with the water budget model. The total inputs to the lake (1.03×10^6 m^3 1990; 0.53×10^6 m^3 1991), of which catchment drainage appeared to be responsible for a large proportion (86 % 1990, 80 % 1991), were much greater than the total outputs (evaporation) (0.13×10^6 m^3 1990; 0.12×10^6 m^3 1991). Correcting for lake volume change,

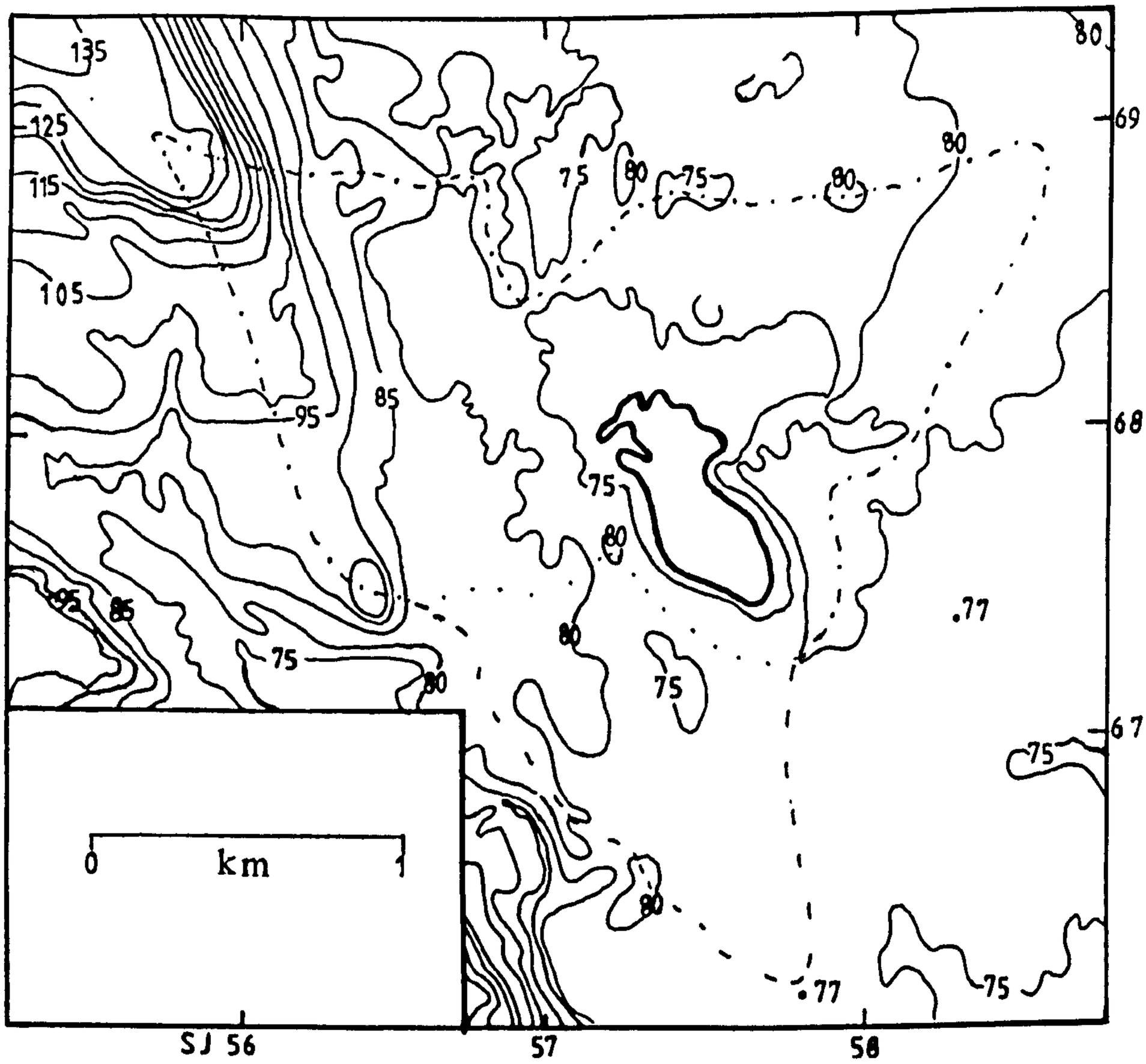


Fig. 5.4 Catchment area of Oak Mere. The dotted line indicates the minimum catchment, the dashed line indicates the maximum catchment.

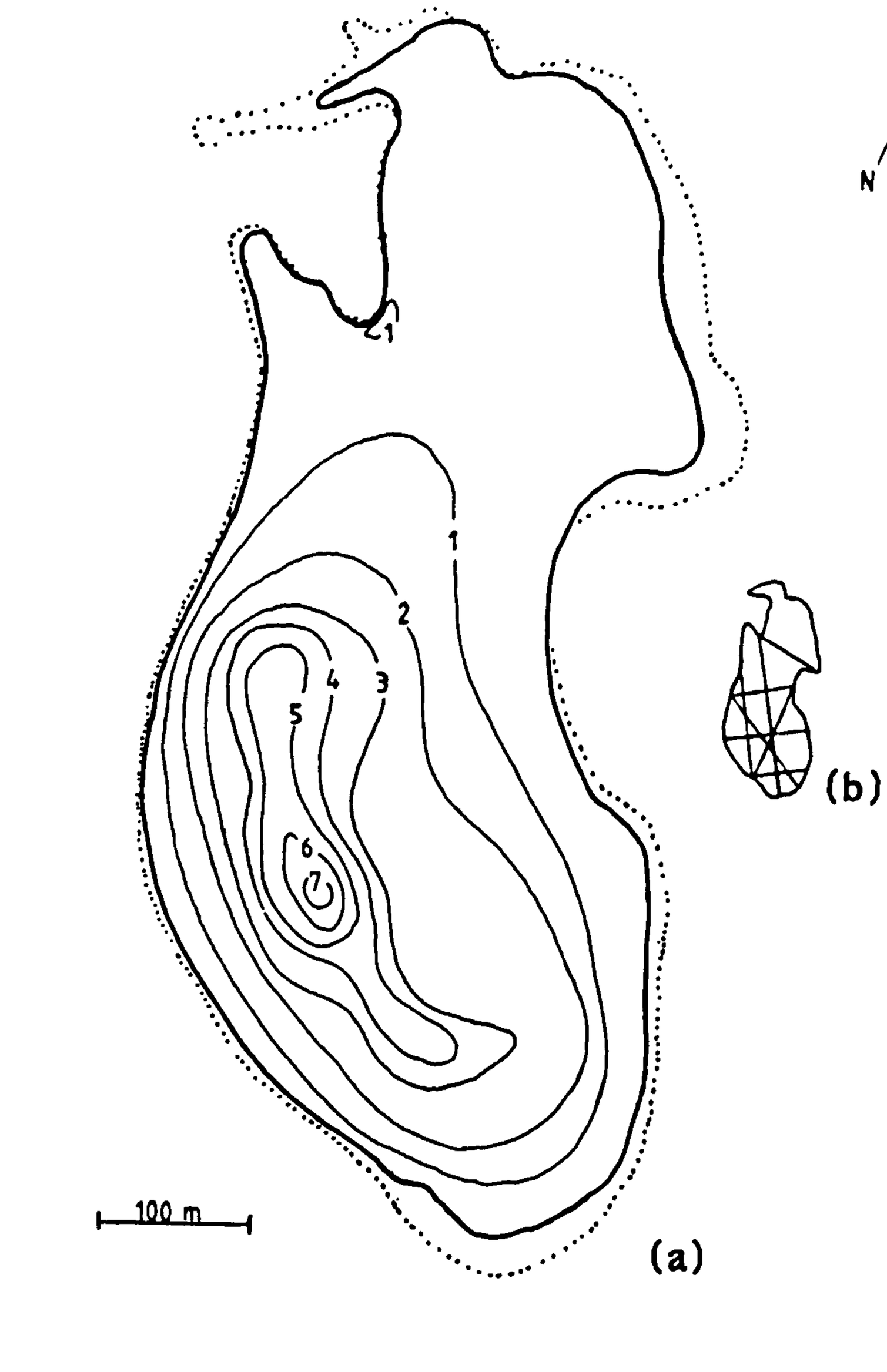


Fig. 5.5 (a) Bathymetric map of Oak Mere (surveyed 19 August 1990). Depths shown are in metres. The dotted line indicates the recent past limit of the lake, and (b) map showing the echo-sounding runs.

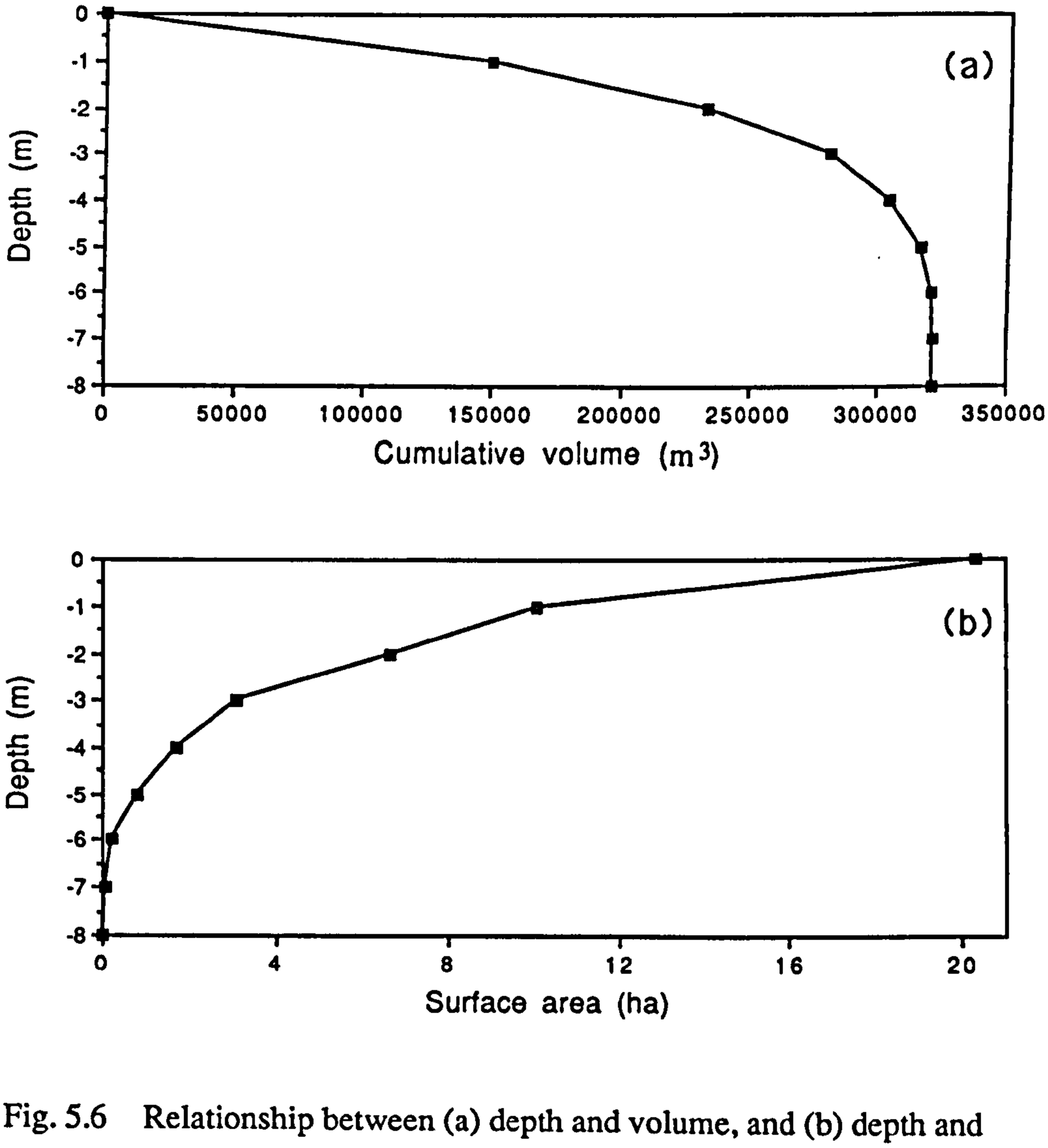


Fig. 5.6 Relationship between (a) depth and volume, and (b) depth and surface area, in Oak Mere.

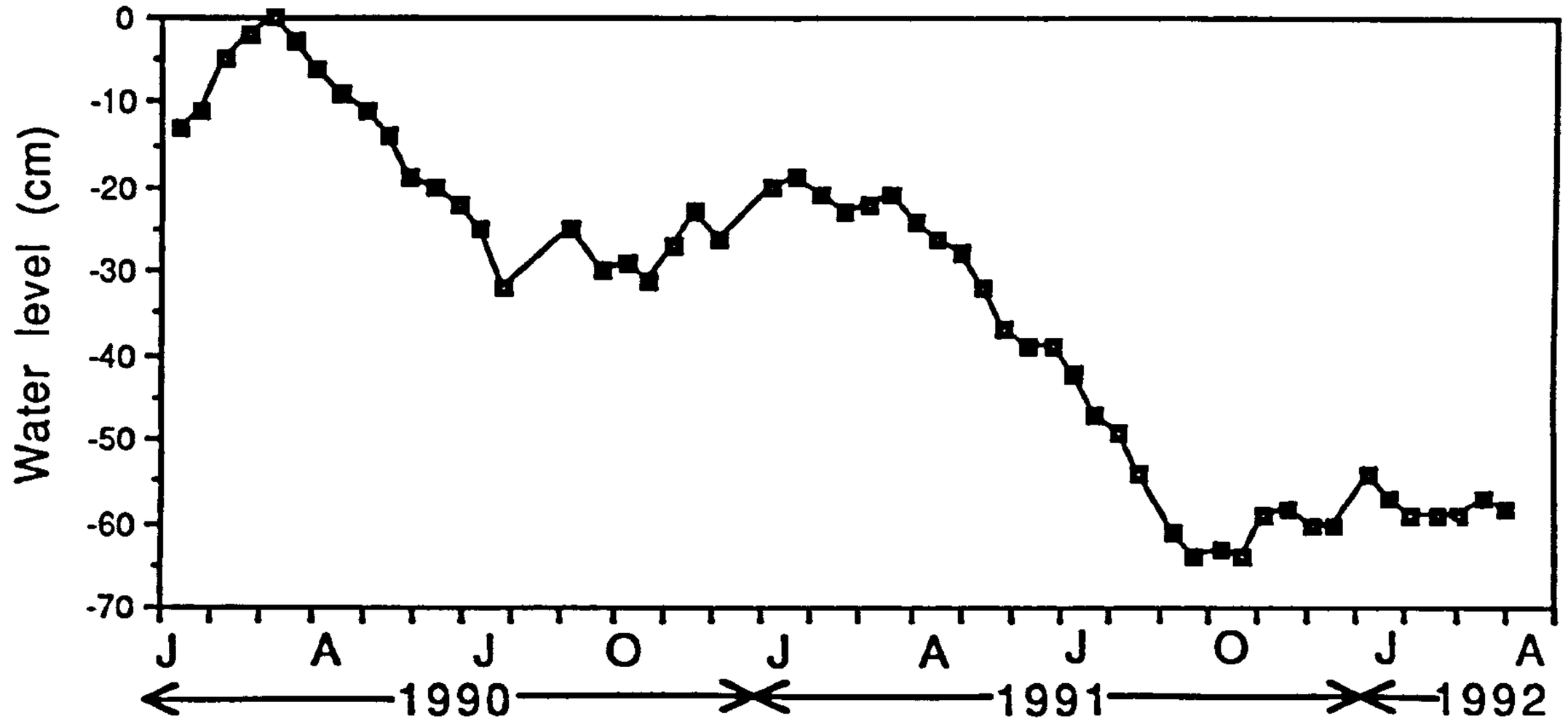


Fig. 5.7 Seasonality of water level of Oak Mere.

Table 5.3 Water budget of Oak Mere from January 1990 to March 1992. Values given are 10^2 m^3.

Budget period	Catchment drainage	Direct rainfall	Total input	Direct evaporation	∂ lake volume	Balance
Jan '90	2064	192	2256	38	+147	-2071
Feb	2037	168	2205	56	+147	-2002
Mar	0	32	32	76	-84	-40
Apr	0	60	60	84	-126	-102
May	0	50	50	156	-160	-54
Jun	0	162	162	186	-80	-56
Jul	0	56	56	228	-160	+12
Aug	0	134	134	220	+120	+206
Sep	54	128	182	124	-100	-158
Oct	1715	226	1941	98	+40	-1803
Nov	938	108	1046	38	+60	-948
Dec	1983	170	2153	22	+80	-2051
1990	8790	1486	10276	1326	-116	-9066
Jan '91	1152	98	1250	12	0	-1238
Feb	750	70	820	14	-20	-826
Mar	241	90	331	72	-40	-299
Apr	0	54	54	94	-80	-40
May	0	14	14	140	-190	-64
Jun	0	134	134	154	-38	-18
Jul	0	106	106	226	-152	-32
Aug	0	64	64	192	-180	-52
Sep	0	96	96	142	-90	-44
Oct	590	130	720	86	+36	-598
Nov	1233	132	1365	40	+36	-1289
Dec	322	52	374	28	+36	-310
1991	4288	1040	5328	1200	-898	-5026
Jan '92	750	78	828	22	-18	-824
Feb	402	74	476	44	-18	-450
Mar	1233	162	1395	70	+18	-1307

reveals that, particularly during the winter months, the budget is extremely unbalanced, with 0.90×10^6 m^3 unaccounted for in1990 and 0.50×10^6 m^3 unaccounted for in1991.

5.3.3 Explanations for the unbalanced water budget model

There are three possible explanations for the unbalanced budget:

(1) Only a limited amount of water from the catchment flows into Oak Mere due to an impermeable seal completely surrounding the lake.

(2) The actual catchment area is significantly smaller than the contours of the land suggest.

(3) Oak Mere is a surface manifestation of the groundwater which exhibits a hydraulic gradient; the water output emerging elsewhere.

The first possibility that Oak Mere is somehow sealed from the water table prompts the question: where in the catchment does the water go ? There is also no evidence for a complete impermeable seal. Borings taken to determine the geology of the basin (Beresford, 1960) revealed only humus-stained sand, with peat deposits at the northern end. The report clearly points out that no clay layers were found. Finally, an impermeable seal would make it difficult to explain the limited (and short-term) effects of the pumping and water abstraction to and from the lake. This hypothesis, therefore, seems very unlikely.

Considering that rain falling to the west of the East Delamere Fault enters the sandstone aquifer, which is not in continuum with the glacial sand aquifer, the second hypothesis

appears plausible. In addition to this, the NRA hold confidential borehole data which suggests that the water table appears to have a hydraulic gradient (hypothesis three), flowing south to north; water emerging at a stream system 3 km to the north of Oak Mere (Seymour, 1992). This movement of water would mean that the catchment area was further restricted (hypothesis two) to the south of Oak Mere. The catchment area may, therefore, be only 20-90 ha (Fig. 5.8).

The hypothesis that Oak Mere is perched above the water table has often been suggested (Lind, 1951; Tallis, 1973; Savage *et al.*, 1992). This would also significantly reduce the catchment area to, more or less, the surface area of the lake. However, groundwater measurements from boreholes to the north of Oak Mere show that the water table fluctuates around 70 m AOD (Seymour, 1992). The surface of Oak Mere is around 73 m AOD. There would therefore have to be an impermeable seal around the lake basin for Oak Mere to remain perched above the water table, and as previously discussed this is highly unlikely.

Both the idea of a perched water table and a reduced catchment would also mean that Oak Mere was similar to an endorheic lake, i.e. with no outflow. Oak Mere would, therefore, be expected to become more saline over time, particularly considering its relatively small volume. The chloride concentration of Oak Mere (Fig. 5.9) was however low for freshwater and remained relatively stable, except for short-lived peaks in the winter, which were most likely associated with salting of the roads during cold weather. This further supports the hypothesis that Oak Mere is part of a hydraulic gradient with an output elsewhere. Furthermore, high

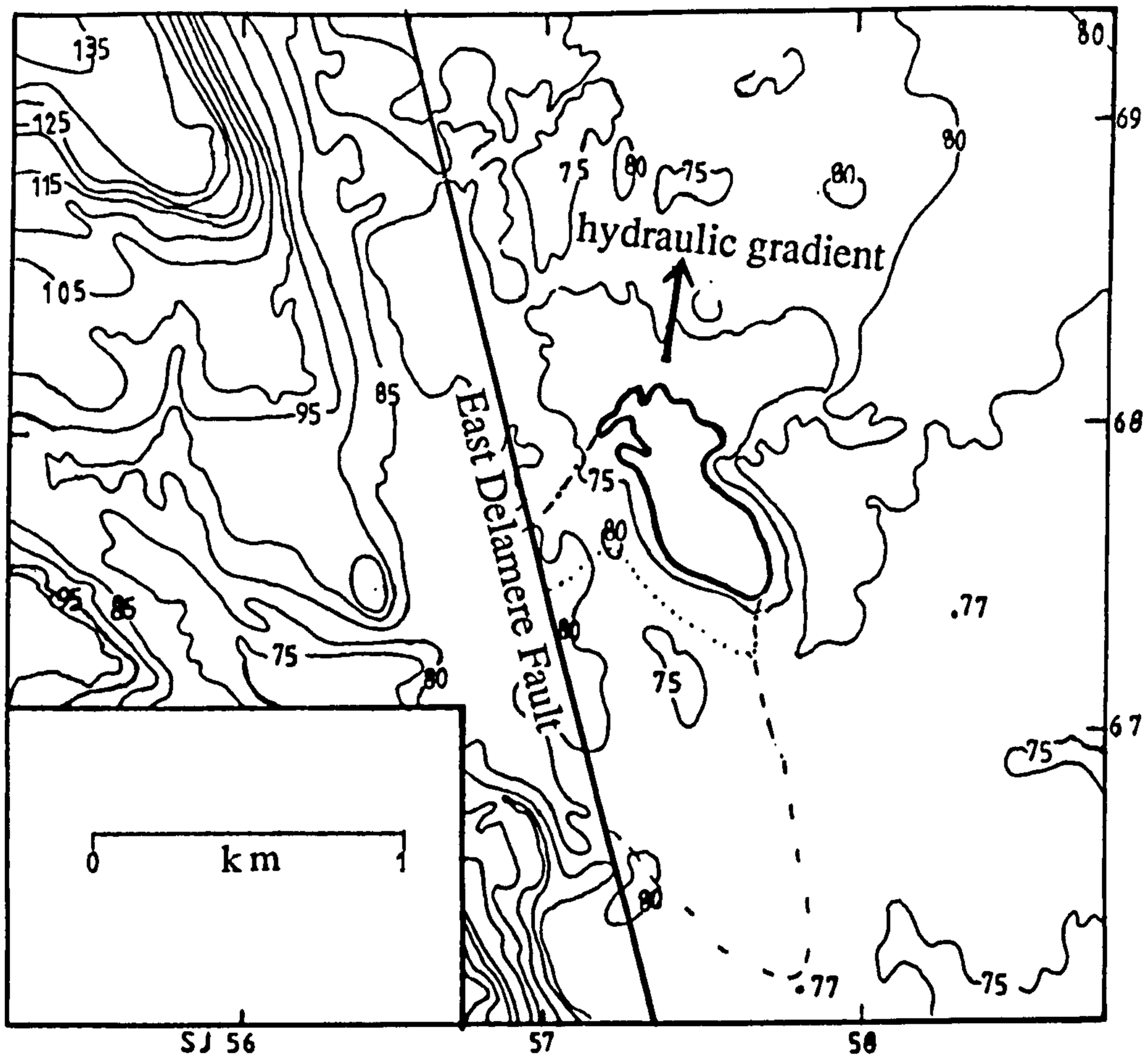


Fig. 5.8 Revised catchment area of Oak Mere. The dotted line indicates the minimum catchment, the dashed line indicates the maximum catchment.

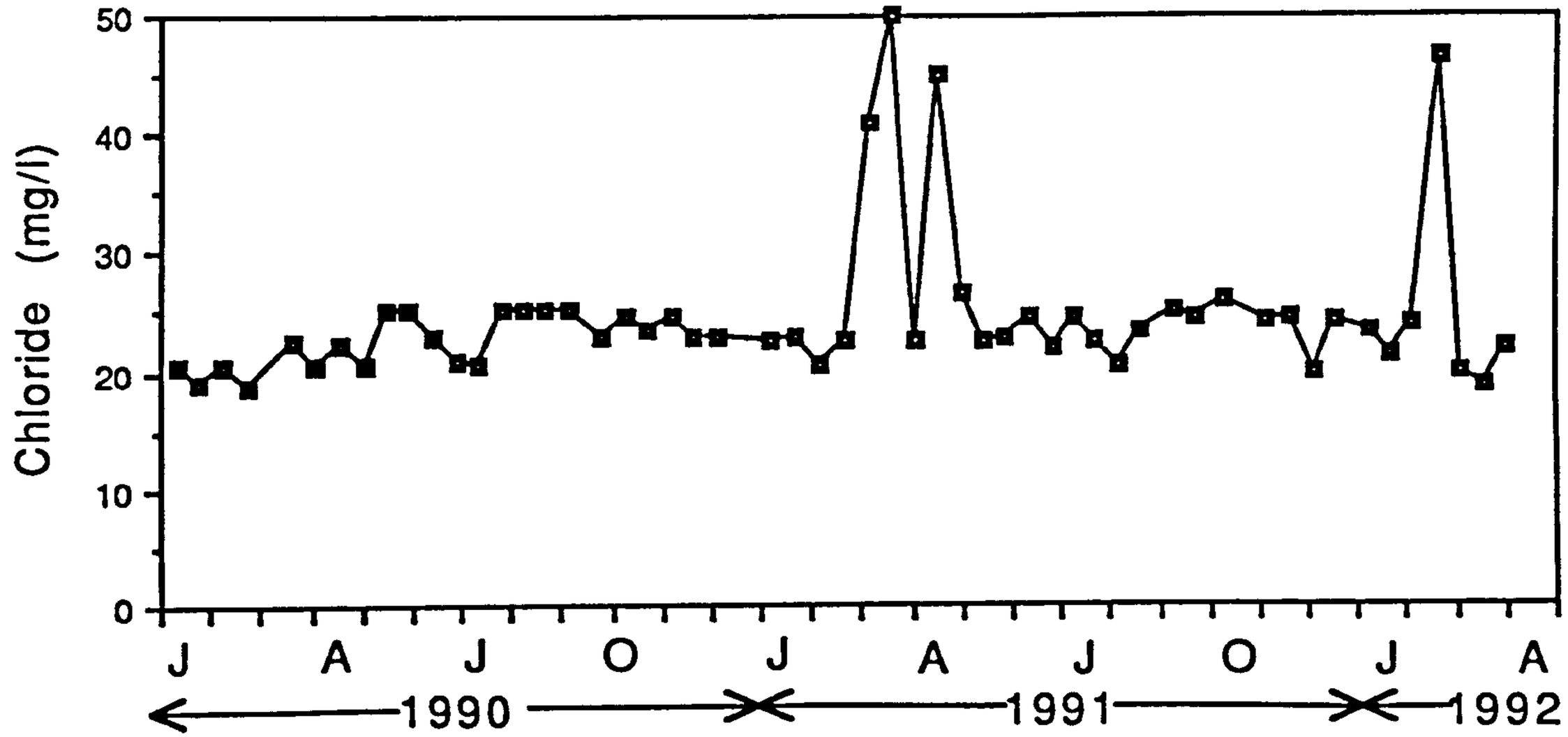


Fig. 5.9 Seasonality of chloride ion concentration in Oak Mere.

evaporation rates during summer would be expected to result in increased chloride concentrations; the lack of any seasonality in chloride concentrations, therefore, suggests that the retention time is short.

5.3.4 Possible causes for the water level changes

Clearly the hydrology of Oak Mere is complicated, preventing construction of a detailed water budget. However, this does not prevent an investigation of the causes for the water level changes.

There has undoubtedly been a significant fall in the water levels of Oak Mere, and confidential data held by the NRA also show that since 1985 there has been a fall of about 1 m in groundwater levels in the glacial sands aquifer (Seymour, 1992). There are several factors that may have influenced the water balance of Oak Mere, or the glacial sands aquifer:

1) Changes in land use in the catchment
2) Direct abstraction
3) Abstraction from the aquifer
4) Changes in rainfall

(1) Changes in land use may alter the amount of water lost by evapotranspiration. The only major change in the area has been the increase in sand and gravel extraction, resulting in two large, flooded sand pits to the north and west of Oak Mere. In these areas potential evaporation rates would then have been realised, resulting in an increased water loss. Water is also abstracted for washing quarried material, but is returned to the aquifer. However, these are both likely to have a negligible effect on the

water level in the glacial sands aquifer. There has been no major intensification of extraction since the operation began in the 1970's (Seymour, NRA North West Region, pers. comm.), so there is no reason why the impact should have increased dramatically in recent years.

(2) There has been no direct abstraction from Oak Mere since 1948 when the Oak Mere pumping station was closed down.

(3) There are four licences for abstraction in the glacial sands aquifer. The major one (maximum abstraction limit 3.82 x 10^6 m^3yr^{-1}), issued to the quarry owners, Alfred McAlpine, states that the water is to be returned to the ground. The other licences, two for spray irrigation and one for agricultural uses, are likely to lead to a more significant water loss from the aquifer. The licences, however, only grant a maximum abstraction of 1.28 x 10^5 m^3yr^{-1} in total, and so are unlikely to significantly affect the water level in the aquifer. The licence for 1.03 x 10^5 m^3yr^{-1} of this was, however, only issued in May 1989, and so could possibly be considered a contributory factor in the reduction in water level of the aquifer in recent years.

Abstraction from the sandstone aquifer has been ongoing for many years, and has been in excess of recharge (Seymour, 1992). Groundwater levels fell about 6 m between 1978 and 1988. Because of this, abstraction was restricted, resulting in a slight increase in groundwater levels since 1988. Any reduction in the level of the sandstone aquifer ought not to lead to increased groundwater flow from the glacial sands aquifer, as water moves between the two by gravity drainage (Seymour, 1992). In addition to this, it could not account for the drop in the

water level of Oak Mere since 1990 as the water level in the sandstone aquifer has been rising since 1988.

(4) The estimated annual average rainfall for the Delamere region for the thirty year period between 1941-1970 was 850 mm (Seymour, 1992). Since 1989 the annual totals have consistently been lower than this; 1991 was a particularly dry year with only 520 mm rain falling. The amount of rainfall entering the aquifer is altered by evapotranspiration, and is termed the 'effective rainfall'. Figure 5.10 shows the relationship between the monthly effective rainfall for the region around Oak Mere against monthly changes in water level. The relationship is highly significant (r^2=0.86, p~0.0001) which strongly suggests that this is the primary reason for the changes seen in the water level. Furthermore, the relationship weakens considerably if any lag is considered between rainfall and water level changes (1 month lag: r^2=0.26, 0.01<p~0.025) i.e. Oak Mere rapidly responds to changes in the effective rainfall. This final point may help explain why Oak Mere has shown a greater response to the recent dry years compared with many other of the North-West Midland Meres. A rapidly draining lake, such as Oak Mere, would be expected to show a greater range in water level than a poorly drained lake.

5.3.5 Summary

Oak mere has a very complex hydrology owing to its proximity to the boundary between two hydrologically distinct areas. It appears to be a surface manifestation of the water table of the underlying glacial sands. This water table appears to have a hydraulic gradient, flowing south to north and emerging at a

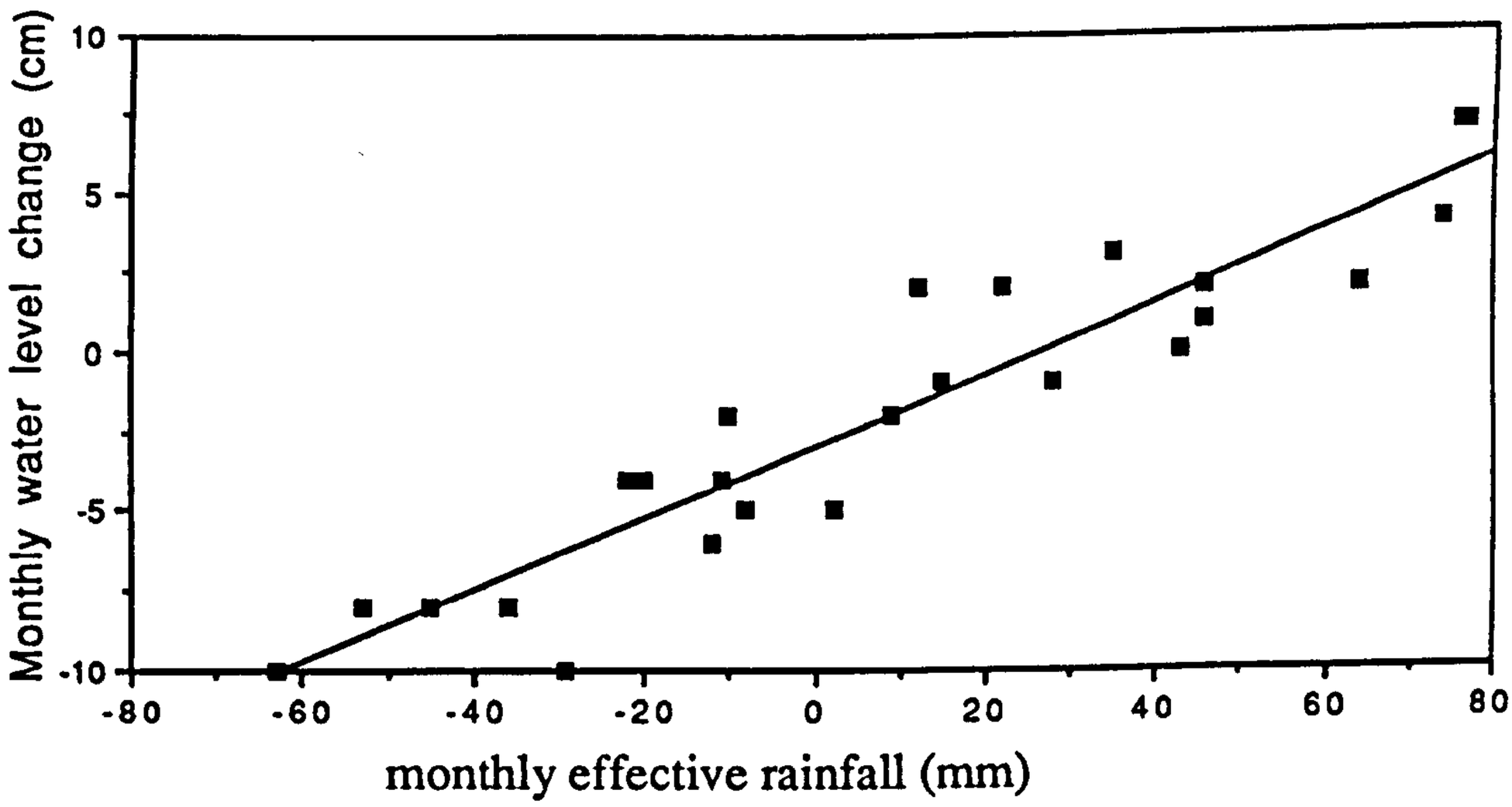


Fig. 5.10 Relationship between monthly effective rainfall and monthly water level change in Oak Mere, from January 1990 to April 1992.

stream system 3 km to the north of Oak Mere. Because of the very permeable nature of its sandy basin, Oak Mere responds rapidly to changes in the effective rainfall of the region. Also because of the gently sloping shape of the basin, the surface area is greatly modified by any changes in water level. For these two reasons Oak Mere appears to have been more affected by the recent dry spell compared to many other of the North-West Midland Meres.

Recovery of the level of Oak Mere is only likely to occur with an increase in water level in the glacial sand aquifer. In this respect, the effects of abstraction of water from the glacial sands aquifer should be taken into consideration, although long-term climate patterns are likely to be of much greater importance; the water level of Oak Mere is unlikely to recover until a long period of above average rainfall.

Further information on the extent of the catchment area to the south of the lake, and the direction of movement of groundwater in the glacial sands aquifer, would aid in understanding the consequences of human impacts in the area. This is of particular importance in understanding where land-use changes are most likely to affect the water quality of Oak Mere. The direction of movement of the groundwater could be estimated by measuring the heights of the water table, on the same day, in the boreholes, Oak Mere, and other surface waters in the area. A contour map of the height of the water table could then be plotted, and the direction of movement estimated.

Chapter 6: Oak Mere water chemistry and biology

6.1 Introduction

Oak Mere is unusual among the North-West Midland Meres in that it is acidic and of extremely low alkalinity. The pH and alkalinity of Oak Mere are more typical of an upland tarn in the English Lake District, or rain water (Sutcliffe *et al.*, 1982) than a lowland lake in Cheshire (Moss *et al.*,1992). SRP and DIN concentrations although low compared with many of the other North-West Midland Meres, are higher than might be expected from a water of comparable alkalinity.

As a result of its water chemistry, Oak Mere has a distinctive phytoplankton community, differing considerably from that of the more typical, alkaline meres, which are characterised by large numbers of diatoms, cyanobacteria, and dinoflagellates. The phytoplankton biomass is low relative to many other of the North-West Midland Meres. The phytoplankton community is often dominated by the colonial chlorophyte *Botryococcus braunii* Kutz., a species frequently found in lakes of low productivity, though of varying pH (Wake & Hillen, 1981).

6.1.1 Previous work

Records of the water chemistry of Oak Mere date back to 1943. From these various accounts (Table 6.1) it can be seen that there have been marked fluctuations in pH and nitrate concentrations. These fluctuations in water chemistry were partly the reason the lake has been considered sealed off from groundwater. Savage *et al.* (1992) thought that base-rich

Table 6.1 pH and nitrate concentration data on Oak Mere, given as single analyses, means ±95% confidence limits, or ranges, as appropriate.

Date	pH	Nitrate-N (mg/l)	Reference
Apr '32	6.6	<0.05	Cheshire County Council Record
Mar '43	4.0	<0.05	Lind (1944)
Aug '43	-	0.20	Lind (1944)
Dec '48	4.7	<0.05	Lind & Galliford (1952)
May '51	4.6	1.00	Lind & Galliford (1952)
Oct '54	4.7	-	Gorham (1957)
Aug '65-Jun '66	4.7-5.2	0.06-0.41	Reynolds & Allen (1968)
Jul '66-Sep '67	5.5-6.6	<0.05-0.48	Reynolds & Allen (1968)
Aug '68	5.5	-	Reynolds (1978b)
'74	6.5	-	Savage & Pratt (1976)
Aug '74	4.9	-	Beales (1976)
May '77	7.2	-	Savage *et al.* (1992)
Aug/Sep '85	5.0	0.40	Slade (1988)
Mar '86-Dec '86	6.0-7.8	0.01-1.26	Savage *et al.* (1992)
Apr '86-Sep '86	6.5-7.0	<0.05-0.25	NWWA (1986)
Jun '88-May '89	6.1±0.2	0.29±0.05	Savage *et al.* (1992)
Nov '89-May '90	5.5-7.2	1.00-3.78	Savage *et al.* (1992)
Jun '90-Sep '90	4.5-5.1	0.19-0.40	Savage *et al.* (1992)

groundwater occasionally broke through the seal, raising the pH and nitrate concentrations. Such a change in water chemistry occurred in 1966, following the artificial pumping-in of groundwater from the sandstone aquifer to the west of Oak Mere. As the previous chapter has shown, however, Oak Mere appears highly permeable, rapidly responding to rainfall. The acidity and low nutrient concentrations found in Oak Mere most likely represent rain water that has been only slightly modified through brief contact with the sandy soils of the area. The latter hypothesis, however, leaves unanswered the question of why there are large fluctuations in the pH and nitrate concentration.

The atypical nature of the phytoplankton community of Oak Mere became apparent from the first early accounts from 1942-43 (Lind, 1944) and 1949-51 (Lind & Galliford, 1952). *Botryococcus* dominated the community throughout; diatoms and cyanobacteria were relatively insignificant. Swale's (1968) investigation of the phytoplankton from August 1963 to November 1966 showed a slightly different picture. At the start of the study *Botryococcus* was absent; a succession of other Chlorophyta was observed in the first year. *Botryococcus*, however, developed a large population in June 1965 which persisted until September 1966; cyanobacteria were again noticeably insignificant.

Records for 1963 (David, 1963) and July 1966 - September 1967 (Reynolds & Allen, 1968) showed a completely different picture, cyanobacteria and diatoms being much more significant. These changes though were due to pumping in of large quantities of base-rich groundwater from the sandstone aquifer

to the west of Oak Mere. Since 1967, there have been no further studies of the phytoplankton community.

Detailed descriptive accounts of the zooplankton community have been published by Lind & Galliford (1952) and Galliford (1954), who found it dominated by large populations of the small cladoceran *Bosmina obtusirostris* Sars (now *B. coregoni* var. *obtusirostris* (Sars), a species characteristic of northern, oligotrophic lakes. *Diaptomus gracilis* and *Diaphanosoma brachyurum* were also numerous.

Studies have also been made of the Corixidae (water boatmen) (Savage, 1986; 1990; Savage & Pratt, 1976) and aquatic plant communities (Wiggington, 1980; 1989).

A detailed monitoring programme of water chemistry and plankton populations was undertaken to understand the fluctuations in pH and nutrients, and to examine what factors controlled the phytoplankton composition and biomass.

6.2 Methods

Methods were as described in Chapter 2, except where detailed below.

6.2.1 Water chemistry, physical factors, phytoplankton, and zooplankton

Water and phytoplankton samples were collected, in the morning, from the top 5 m, at a buoy moored at the deepest part of the lake. Integrated zooplankton samples were also collected from a depth of 5 m upwards.

Small Chroococcaceae cells (< 1μm) were only distinct when their population was abundant. At this stage they were so numerous that counting was impossible under the inverted microscope. Chroococcaceae cells were, therefore, counted under a binocular microscope, using a haemocytometer, from a minimum of 240 small grid squares. All other phytoplankta were counted using an inverted microscope, as described in Chapter 2.

6.2.2 Aquatic plants

Aquatic plants were surveyed in July 1990.

6.3 Results

6.3.1 Physical factors and water chemistry

Figure 6.1a shows that temperature stratification occurred between April and September 1991, although stratification was never strongly developed, and there were intermittent periods of mixing in May and June. The maximum temperature (20 °C) was recorded in August 1991. For the rest of the year the lake was well mixed, with the exception of the early part of 1991, when more than 10 cm of ice formed over parts of the lake, almost certainly resulting from inverse stratification. The development of thermal stratification in summer coincided with the development of a deoxygenated hypolimnion (Fig. 6.1b). Deoxygenation was particularly strong in August and September 1991, when dissolved oxygen levels were less than 20 % saturation below 6 m. At the same time, in the top 2 m, dissolved oxygen was greater than 100 % saturation.

Soluble reactive phosphorus (SRP) concentrations had a clear seasonality (Fig. 6.2a). Peaks in concentration occurred in the winter months (58 $\mu g\ l^{-1}$ Jan 1990; 28 $\mu g\ l^{-1}$ Dec 1990; 23 $\mu g\ l^{-1}$ Nov 1991). These concentrations were low relative to many other of the North-West Midland Meres (Moss *et al.*, 1992). Concentrations declined to the limits of detection (< 5 $\mu g\ l^{-1}$) during the summer periods. Concentrations exhibited a highly significant declining trend with time ($r^2=0.28$, $p \leqslant 0.0001$) (Fig. 6.4a) and a highly significant relationship with water level ($r^2=0.23$, $0.0001 < p \leqslant 0.005$) (Fig. 6.5a). Total phosphorus concentrations had no clear seasonal pattern, but, exhibited a highly significant declining trend over time ($r^2=0.41$,

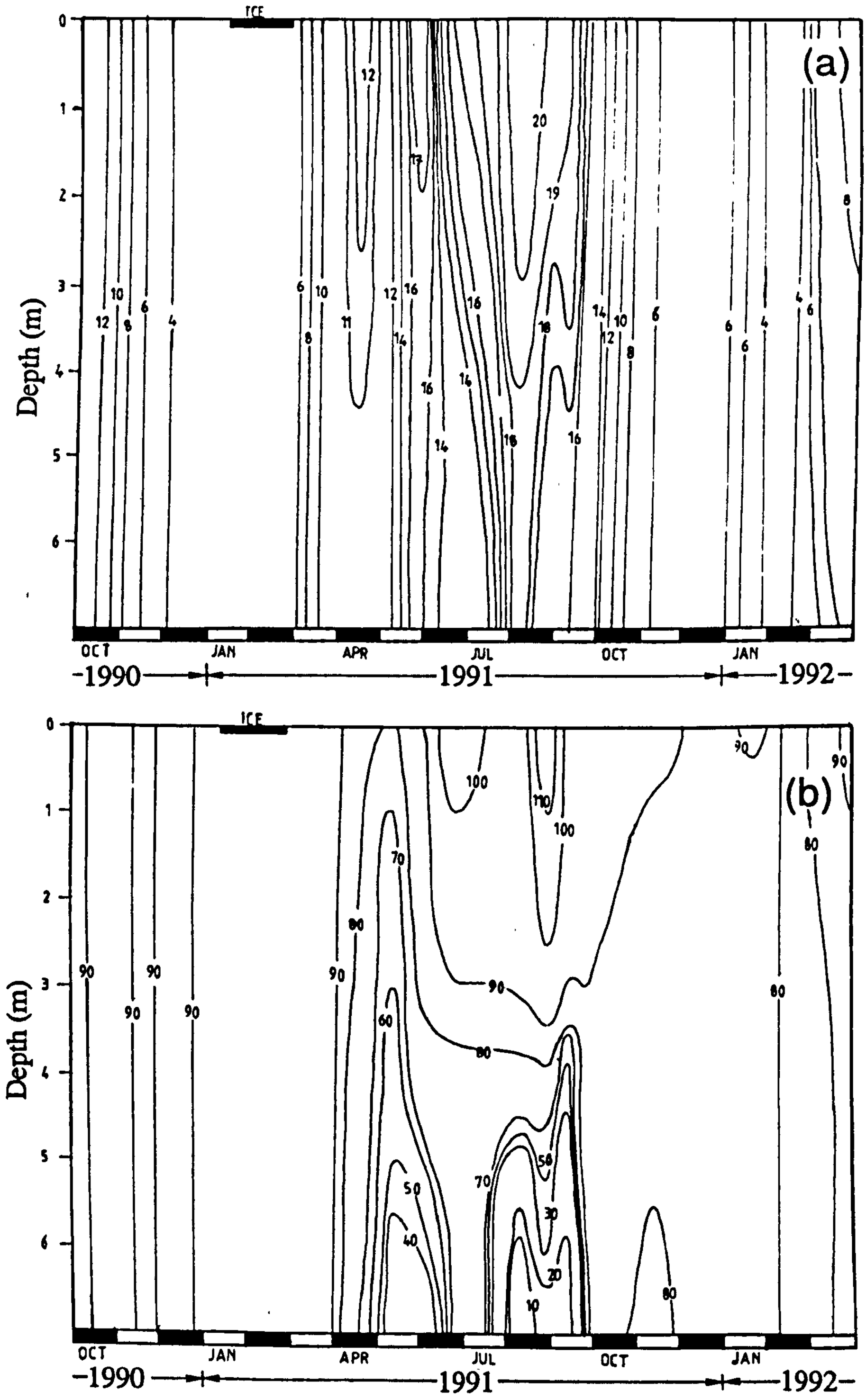


Fig. 6.1 Depth-time diagrams for (a) temperature (°C), and (b) dissolved oxygen (% saturation), in Oak Mere.

$0.0001<p^{-}0.005$) (Fig. 6.4b) and a highly significant relationship with water level ($r^2=0.16$, $0.0001<p^{-}0.005$) (Fig. 6.5b).

SRP concentrations were also signifcantly correlated with dissolved inorganic nitrogen (DIN) concentrations ($r^2=0.34$, $p^{-}0.0001$), which showed a seasonality of winter maxima (0.46 mg l^{-1} Mar 1990; 0.52 mg l^{-1} Feb 1991; 0.39 mg l^{-1} Feb 1992) and summer minima (< 5 µg l^{-1}) (Fig. 6.2a). Winter DIN concentrations were also low relative to many other of the North-West Midland Meres (Moss *et al.*, 1992). Concentrations showed no significant declining trend with time ($r^2=0.002$, $p>0.25$) or with water level ($r^2=0.02$, $p>0.25$).

Both forms of nitrogen analysed exhibited the seasonality of winter maxima and summer minima, although ammonium-nitrogen increased more rapidly in the autumn than nitrate-nitrogen (Fig. 6.3a). Nitrate-nitrogen concentrations were positively correlated with water level ($r^2=0.08$, $0.025<p^{-}0.05$) (Fig. 6.5c), but showed no significant trend over time ($r^2=0.01$, $p>0.25$) (Fig. 6.4c), whilst ammonium-nitrogen concentrations were inversely correlated with water level ($r^2=0.09$, $0.025<p^{-}0.05$) (Fig. 6.5d) and showed a significant increasing trend over time ($r^2=0.10$, $0.01<p^{-}0.025$) (Fig. 6.4d).

Silicate-silicon concentrations did not exhibit any clear seasonality (Fig. 6.3b), but showed a highly significant declining trend with time ($r^2=0.37$, $p^{-}0.0001$) (Fig. 6.4e) and a highly significant relationship with water level ($r^2=0.45$, $0.0001<p^{-}0.005$) (Fig. 6.5e). Concentrations declined from the maximum (1.80 mg l^{-1}) recorded in February 1990 to the minimum (0.06 mg l^{-1}) recorded in June 1991.

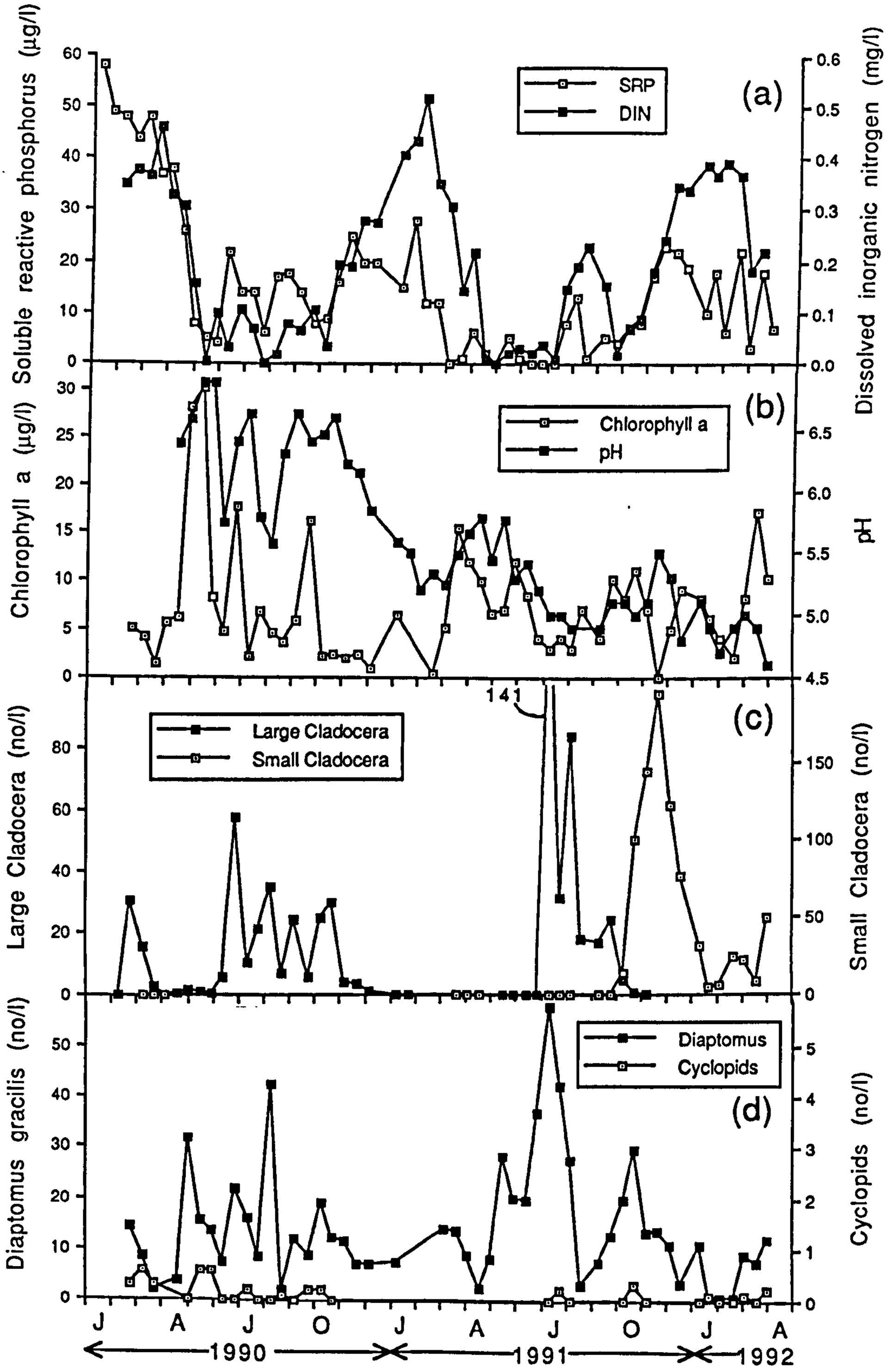


Fig. 6.2 Seasonality of (a) dissolved inorganic nitrogen and soluble reactive phosphorus, (b) pH and chlorophyll *a*, (c) small Cladocera and large Cladocera, and (d) *Diaptomus gracilis* and Cyclopoids, in Oak Mere.

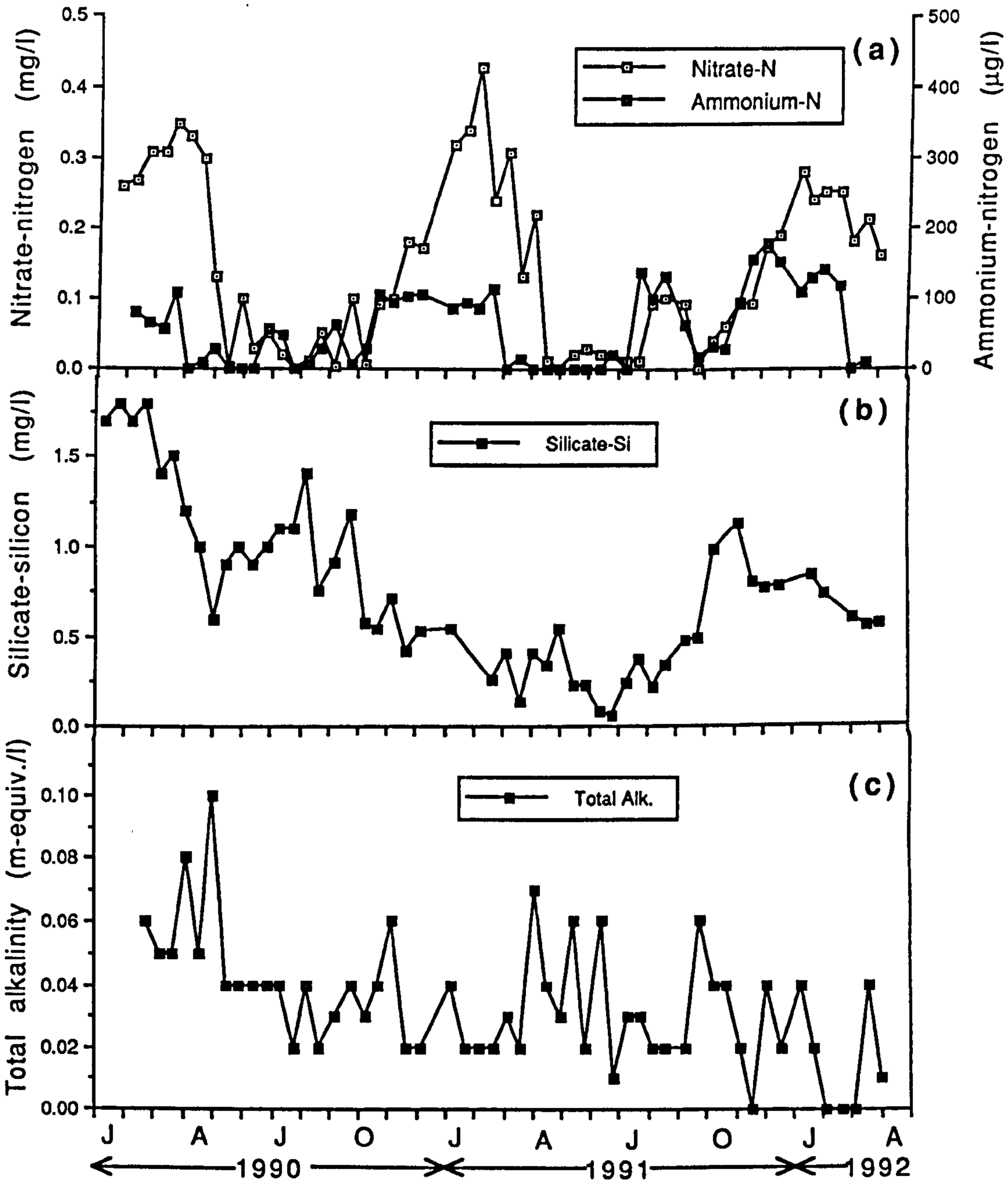


Fig. 6.3 Seasonality of (a) nitrate-nitrogen and ammonium-nitrogen, (b) silicate-silicon, and (c) total alkalinity, in Oak Mere.

Total alkalinities were extremely low, fluctuating around 0.03 mequiv. l^{-1} (range: 0-0.10) (Fig. 6.3c). They had a highly significant declining trend with time (r^2=0.26, 0.0001<p~0.005) (Fig. 6.4f) and a highly significant positive relationship with chlorophyll *a* concentrations (r^2=0.14, 0.005<p~0.01) and water level (r^2=0.22, 0.0001<p~0.005) (Fig. 6.5f).

pH fluctuated erratically (Fig. 6.2b), although it showed a highly significant declining trend over the study period (r^2=0.76, p~0.0001) (Fig. 6.4g) , and a highly significant relationship with water level (r^2=0.56, p~0.0001) (fig. 6.5g). During the phytoplankton growth season, there was a significant positive relationship between pH and chlorophyll *a* concentrations (r^2=0.25, 0.01<p~0.025).

Conductivity was 195 µS in December 1991 and 178 µS in April 1992.

Detailed water chemistry data can be found in Appendix 3.

6.3.2 Phytoplankton and zooplankton

There was no clear seasonality to the chlorophyll *a* concentrations, although the maximum concentration occurred each year in the spring (30 µg l^{-1} May 1990, 15 µg l^{-1} March 1991, 17 µg l^{-1} March 1992) (Fig. 6.2b). The mean growth-season chlorophyll *a* concentrations (March to September) were low (10 µg l^{-1} in 1990, 7 µg l^{-1} in 1991). Concentrations showed no significant relationship with time (r^2=0.01, p>0.25) (Fig. 6.4h) or water level (r^2=0.01, p>0.25) (Fig. 6.5h).

The seasonal periodicity of the phytoplankton taxa is shown in Figure 6.6. The 1990 spring increase in chlorophyll *a*

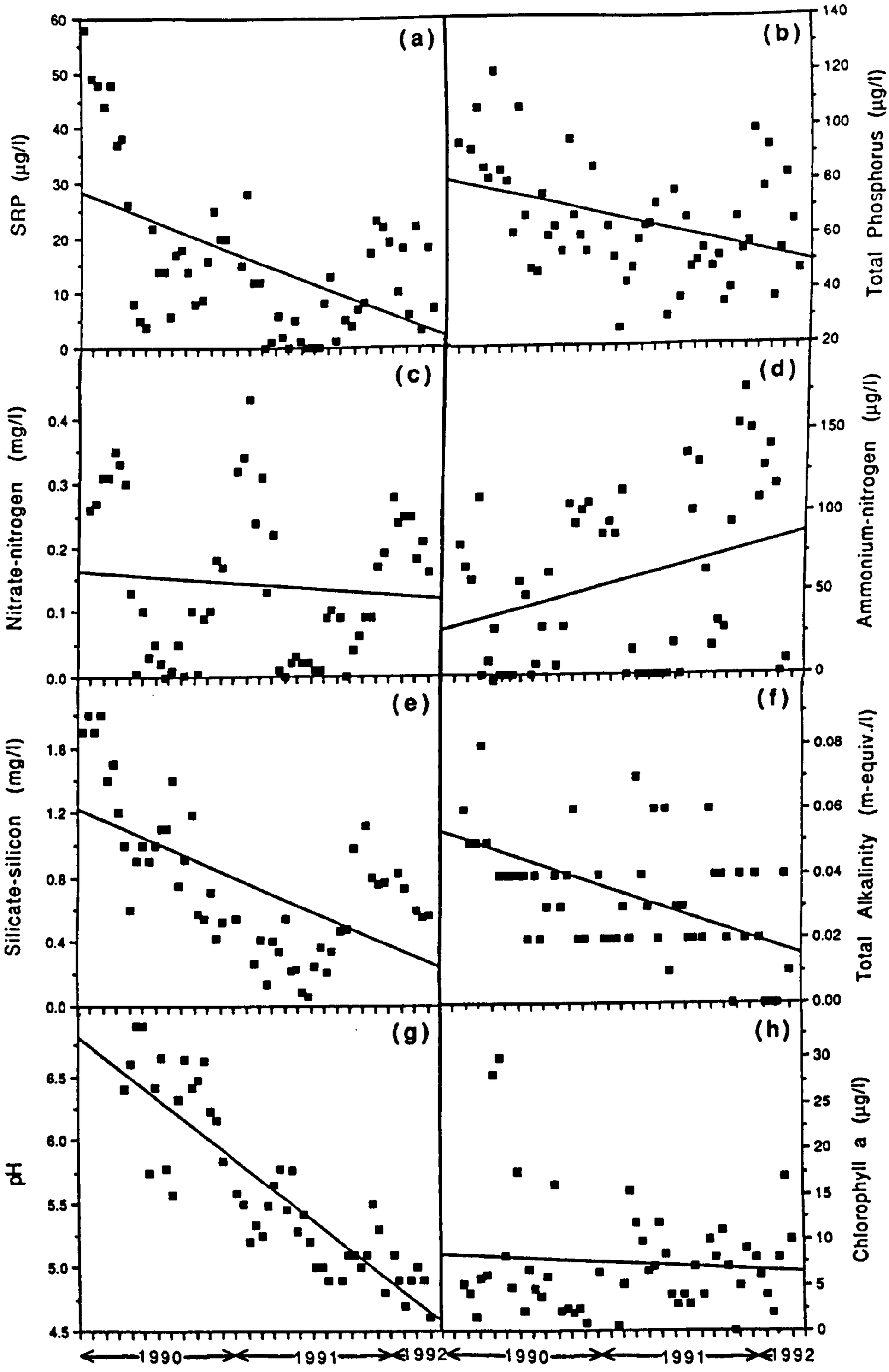


Fig. 6.4 Scatter diagrams showing the relationship in Oak Mere between time (from January 1990 to April 1992) and (a) soluble reactive phosphorus, (b) total phosphorus, (c) nitrate-nitrogen, (d) ammonium-nitrogen, (e) silicate-silicon, (f) total alkalinity, (g) pH, and (h) chlorophyll *a*.

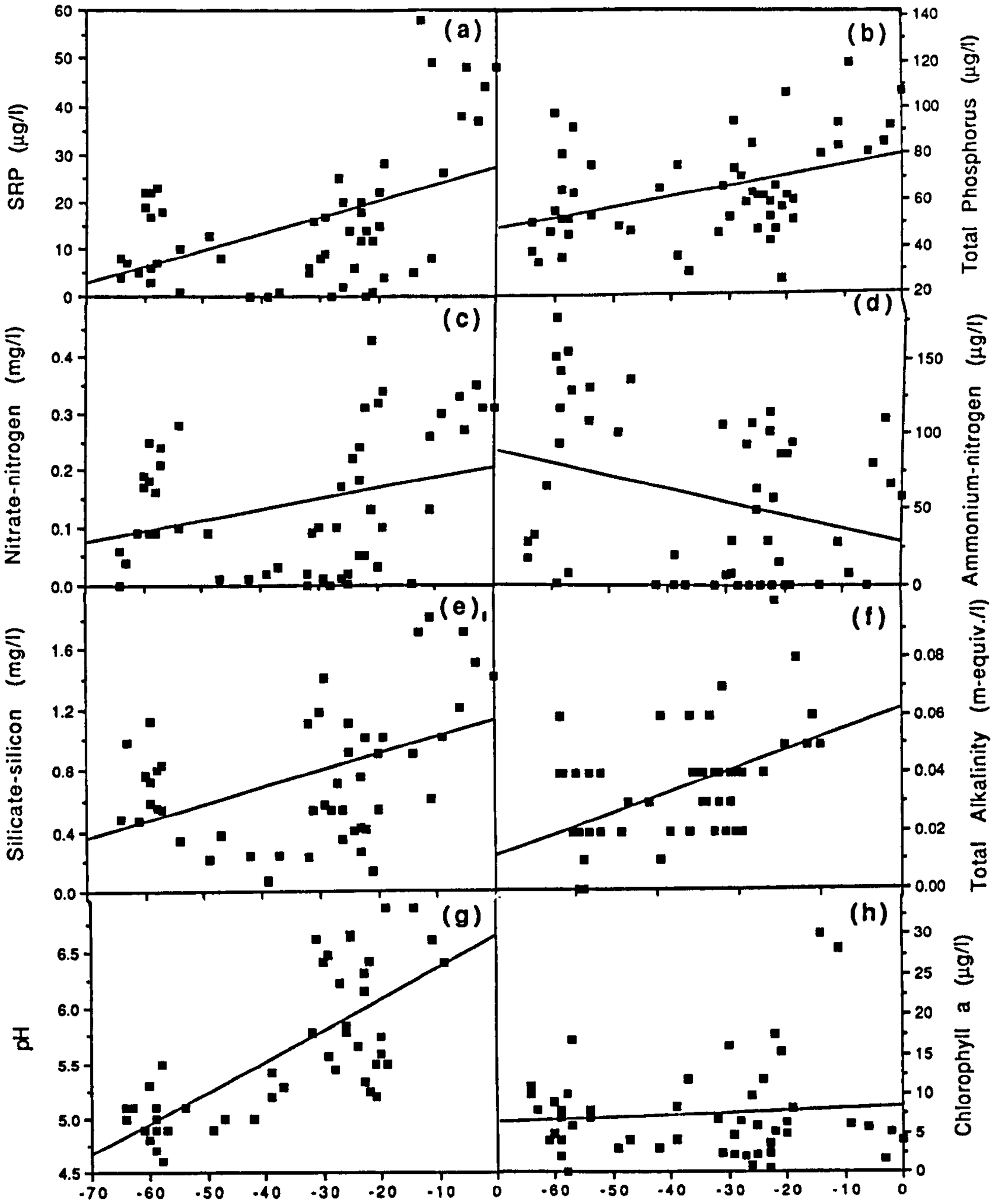


Fig. 6.5 Scatter diagrams showing the relationship in Oak Mere between water level (from January 1990 to April 1992) and (a) soluble reactive phosphorus, (b) total phosphorus, (c) nitrate-nitrogen, (d) ammonium-nitrogen, (e) silicate-silicon, (f) total alkalinity, (g) pH, and (h) chlorophyll *a*.

concentration was more or less solely due to a huge population of the chlorophyte *Ankistrodesmus falcatus* (402000 cells/ml). Following the decline of *Ankistrodesmus*, there was a brief increase in small, unidentified flagellates in June. Low phytoplankton numbers were then present until late-September, when, for a short period, *Rhodomonas* sp. developed a large population.

The chlorophyll *a* peaks of spring and early summer 1991 were due to the development of large populations of small cyanobacterial cells (Chroococcaceae) (1 μm in diameter), and to a lesser extent, unidentified flagellates and dinoflagellates. For the rest of the year, the Chlorophyta, *Gloeocystis* sp., *Elakatothrix gelatinosa*, *Ankyra judaii*, and *Botryococcus braunii* were the only algae to show significant increases. The *Botryococcus* population persisted throughout the winter, although by April 1992 numbers had declined to low densities, and Chroococcales were becoming abundant again.

The zooplankton results are shown in Figure 6.2c and 6.2d. The large-bodied Cladocera included *Diaphanosoma brachyurum*, *Daphnia pulex*, and *Daphnia longispina* (agg.). The latter was the dominant species in the spring of 1990. Populations of the former two species developed during June 1990, and showed a series of peaks throughout the summer; *D. pulex* persisted into the autumn. In 1991, *D. brachyurum* was the only large cladoceran to develop any significant numbers, reaching high densities (up to 140 l^{-1}) in July and August. During the autumn of 1991, the small-bodied Cladocera, dominated exclusively by *Bosmina coregoni* var. *obtusirostris* (formerly *B. obtusirostris*)

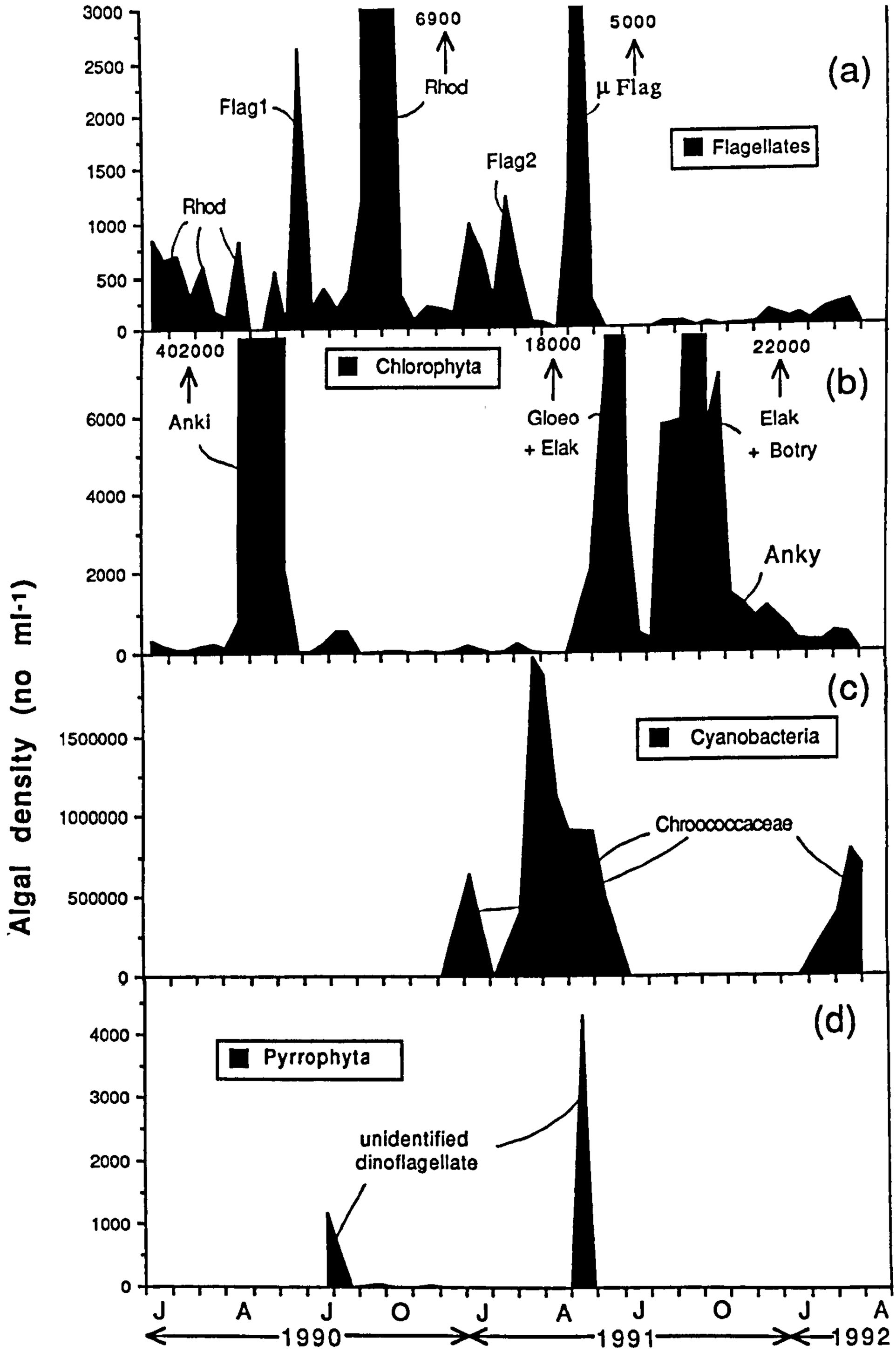


Fig. 6.6 Changes in density of (a) Cryptomonads and unidentified flagellates, (b) Chlorophyta, (c) cyanobacteria, and (d) Pyrrophyta, in Oak Mere. Main algal taxa responsible for the peaks are indicated

developed a large population, and remained at high densities into January 1992.

Of the copepods (Fig. 6.2d), *Diaptomus gracilis* was present throughout most of the study period, with peak densities in August 1990 (43 l^{-1}) and July 1991 (58 l^{-1}). Cyclopopoid copepods were never abundant.

Daphnia species were completely absent below pH 5.5 (Fig. 6.7a), whereas *Bosmina* was completely absent above pH 5.5 (Fig. 6.7b). *D. brachyurum* was also more abundant in the lower pH range, particularly at pH values around 5.0 (fig. 6.7c). The presence of *D. gracilis* did not appear to be affected by pH (Fig. 6.7d).

6.3.3 Aquatic plants

The aquatic plant community was of low diversity (Fig. 6.8) and had changed little since the previous study (Wiggington, 1989). The submerged vegetation consisted of *Littorella uniflora* (L.) Aschers. and the moss *Drepanocladus fluitans*. A small patch of *Nuphar lutea* (L.) Sm. was the only floating-leaved species found, although by 1992 this was found above the water level, and was dormant. The submerged and floating-leaved species covered about 10 % of the lake area.

The emergent vegetation consisted of *Littorella uniflora*, *Typha latifolia* L., and *Typha angustifolia* L. By 1992, stands of the latter two species were in a poor condition, probably because of the drop in water level.

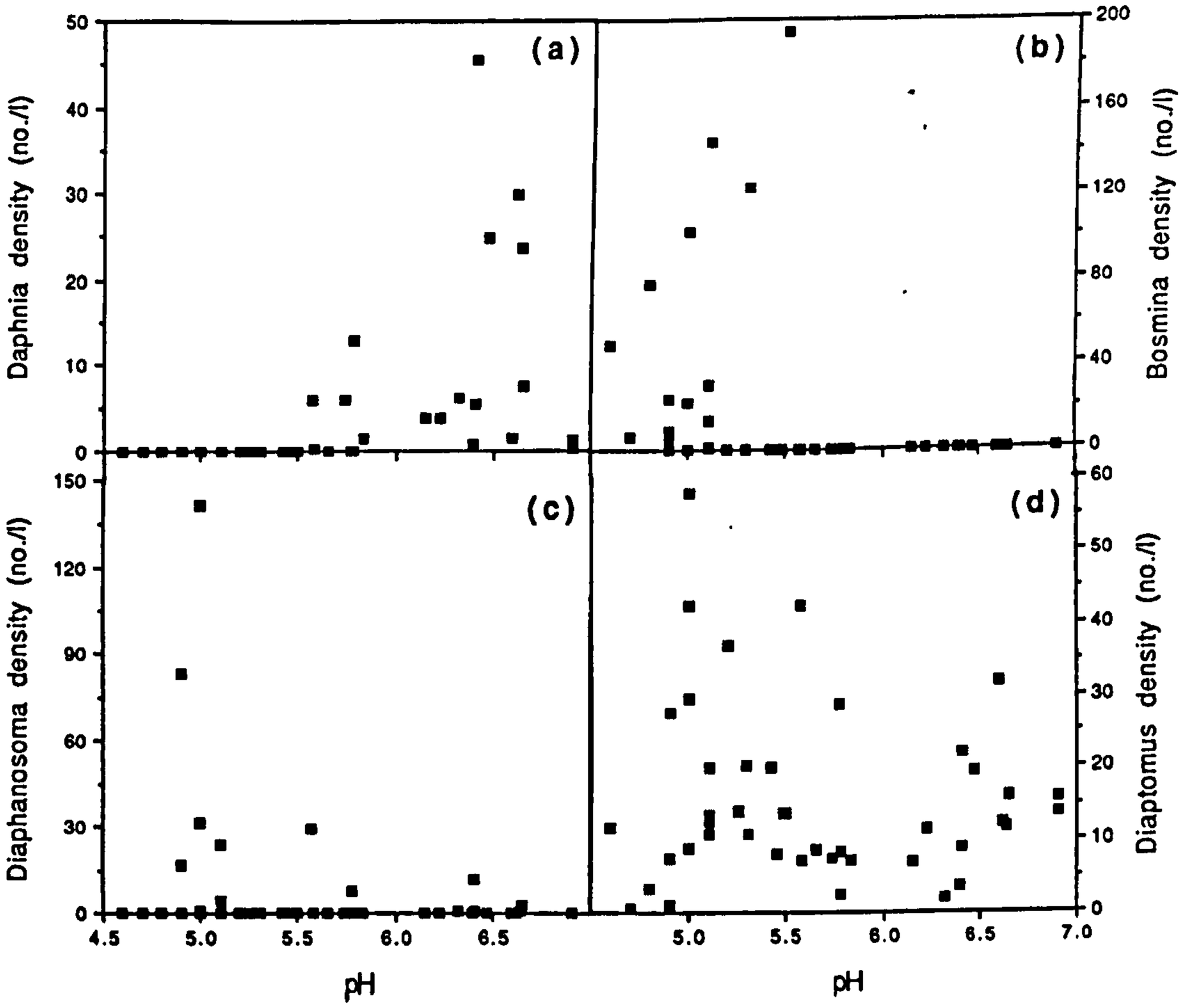


Fig. 6.7 Scatter diagrams showing the relationship, in Oak Mere, between pH and (a) *Daphnia*, (b) *Bosmina*, (c) *Diaphanosoma*, and (d) *Diaptomus*.

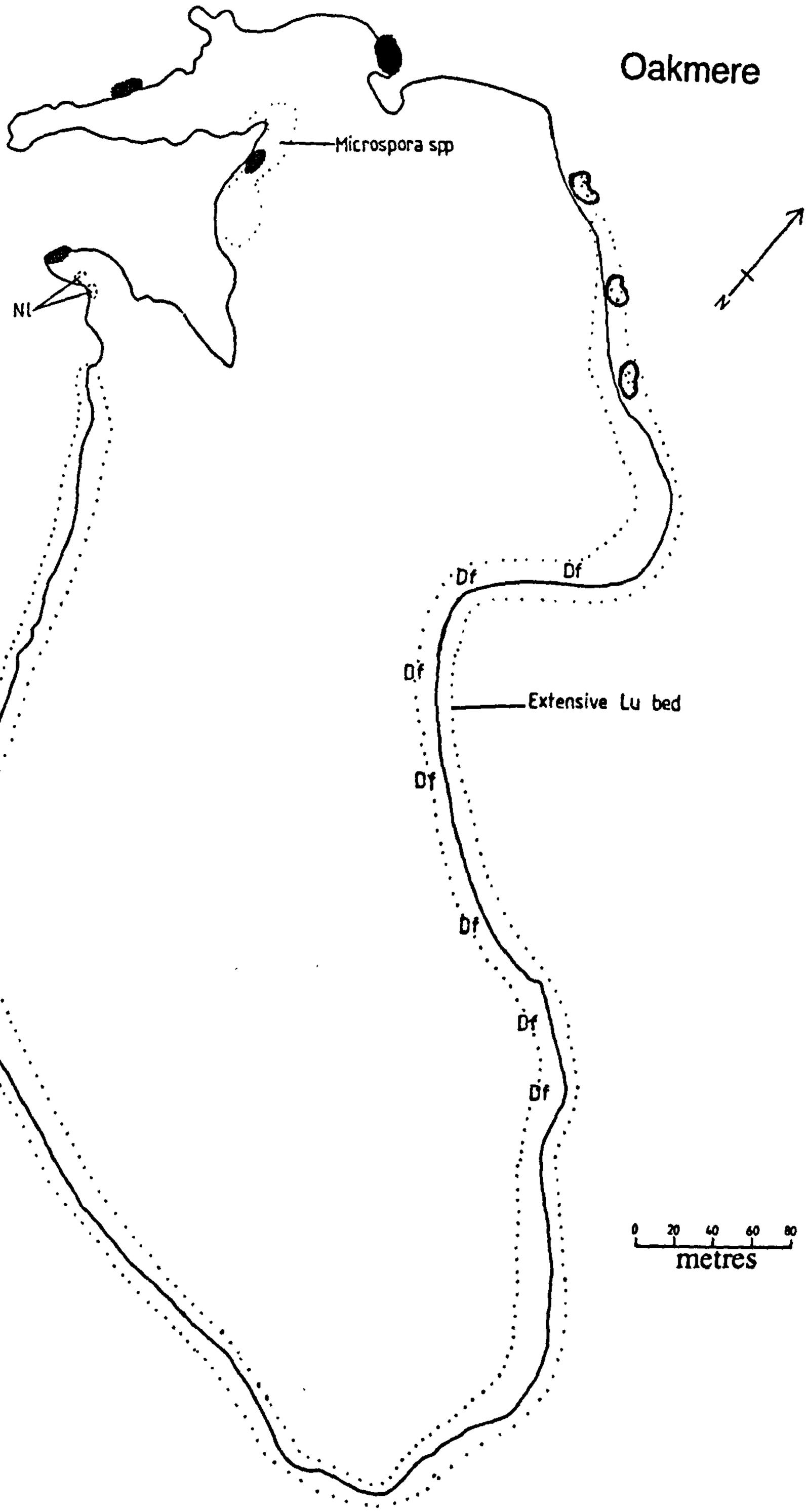


Fig. 6.8 Aquatic plant survey of Oak Mere (carried out in July 1990).

6.4 Discussion

6.4.1 Trends in water chemistry

The most striking pattern in the water chemistry was the declining trends over the study period in pH, alkalinity, SRP, total phosphorus and silicate-silicon. The fact that the trends were highly significant irrespective of seasonal effects, stresses the strong relationship. The trends were also significantly related to the declining water level. One possible explanation could be that there was an increase in retention time in the lake, so nutrient concentrations declined, leading to reduced phytoplankton growth and a reduced pH. There was, however, no clear reduction in chlorophyll *a* concentrations to support this. Also, reduced water inputs do not neccessarily mean outputs would have been reduced, and retention time would increase. A more likely explanation is that there was a change in the quality of the water entering the lake. The previous chapter has shown that there are two sources of water to Oak Mere, drainage from land, predominantly from a small area to the south of the lake, and direct rainfall. During drier years, the soil moisture deficit will rise and direct rainfall will contribute an increasing proportion of the input; the water quality would therefore resemble rainwater quality more closely, hence the lower pH, alkalinity and nutrient concentrations.

Nitrate-nitrogen did not, however, show a significant trend over time, just a slight declining trend. Large seasonal effects may have obscured any trend present. To overcome this, monthly data were compared between years (Fig. 6.9). This showed that the decline in nitrate was insignificant. Possible

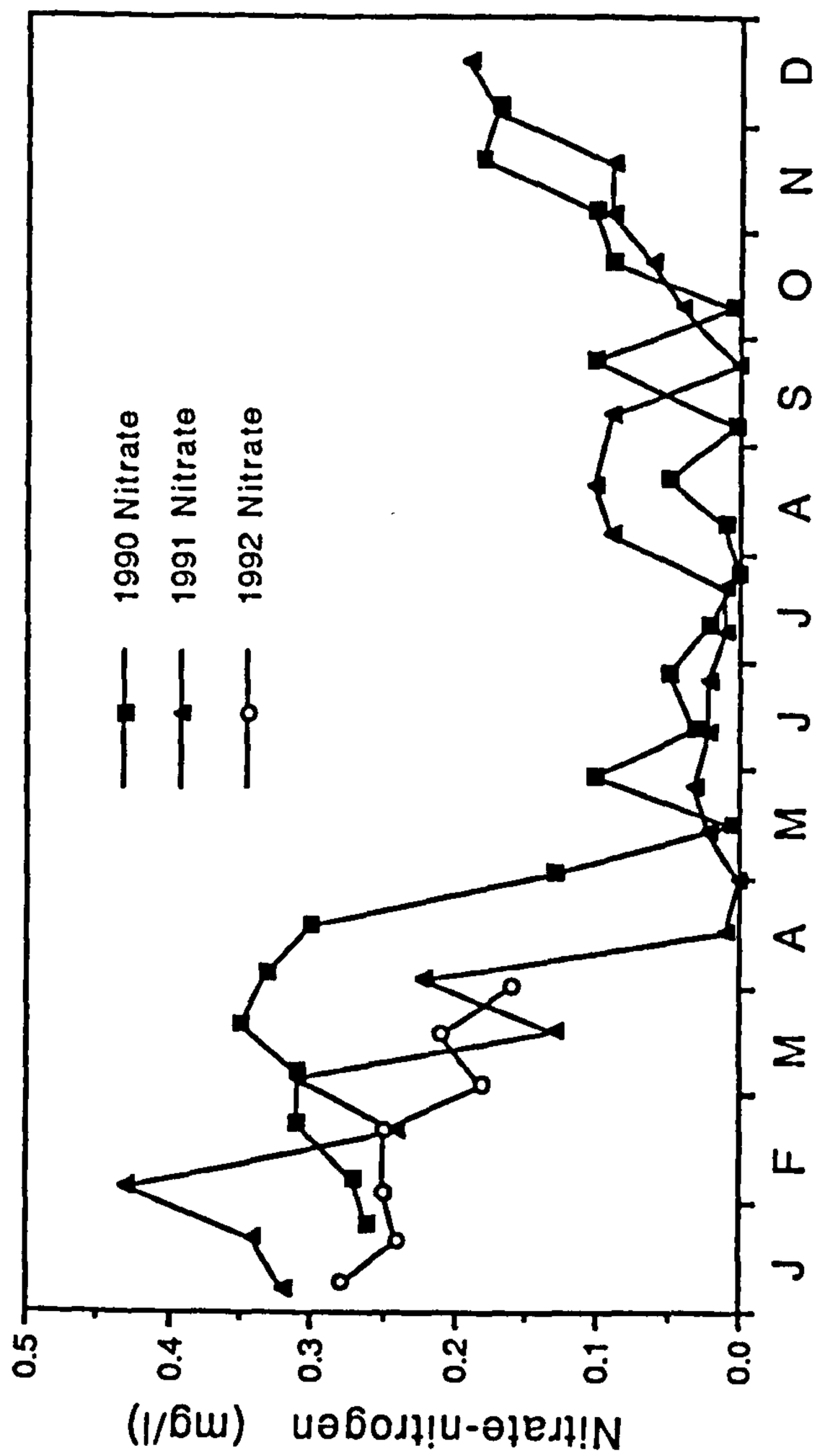


Fig. 6.9 Seasonality of nitrate concentration in Oak Mere.

explanations for this are that the nitrate concentration of rainfall was similar to that of the water entering from drainage, or, nitrate loading may not have been so much a response to the amount of rainfall, but the timing of rainfall; rainfall coinciding with a period of slurry application may cause large quantities of nitrate to be washed in.

Ammonium concentrations actually showed a significant increase with declining water level. Ammonium is largely derived from internal sources (sediment), during deoxygenated conditions, and so would be expected to be independent of changes in rainfall. However, assuming release from the sediments in 1990 was similar to that of 1991, lake concentrations would increase with a declining lake volume, as there would be less dilution of the ammonium released. Another possible explanation is that if stratification was more intense during 1991, deoxygenation would have been more severe, resulting in an increased release of ammonium. Unfortunately no dissolved oxygen data are available for the summer of 1990 for a comparison to be made.

Apart from the long-term trends in water chemistry there were also seasonal patterns, particularly in SRP, DIN, and the two forms of nitrogen analysed. Depletion of nitrogen and phosphorus accompanied the spring increase in phytoplankton, which resulted in low nutrient concentrations that remained throughout summer. Concentrations increased in the autumn and winter, most probably due to mixing of more nutrient-rich hypolimnion water and increased drainage from the catchment.

6.4.2 Limitation of phytoplankton biomass

Phytoplankton densities were greatest in the spring, and appeared to cause depletion of SRP and DIN. The spring and summer biomass may, therefore, have been limited by low nutrient concentrations. Spring chlorophyll *a* concentrations were higher in 1990 than 1991, and this may have been related to the higher winter SRP concentrations found in 1990 compared with those in 1991. Winter DIN concentrations were similar during the two years, and so appear less likely to have been limiting the spring phytoplankton biomass.

High densities of zooplankton grazers may occasionally have had a significant limiting effect, as when grazer populations were high, decreases in chlorophyll *a* concentration were observed. In oligotrophic lakes, however, small grazers can actually have a stimulatory effect on phytoplankton biomass, due to increased nutrient recycling (Carrillo *et al.*, 1990).

Multiple regression analyses were carried out to give an indication of which factors may have been responsible for limiting the chlorophyll *a* concentration. There were, however, no significant inverse relationships between chlorophyll *a* and any factor tested (SRP, total phosphorus, DIN, silicate-silicon, and total herbivores), or combination of factors, during the spring (March to May), summer (June to September), autumn (October to November), or phytoplankton growth-season (March to November). There were, however, significant relationships between chlorophyll *a* and SRP (r^2=0.09, 0.025<p~0.05) and chlorophyll *a* and DIN (r^2=0.08, 0.025<p~0.05) for the whole study period.

The lack of any significant relationships during the spring, summer, autumn, and growth-season periods does not rule out limitation by any of these factors. It is possible that phosphorus was important in determining the peak spring biomass, but not for the whole spring period. The same may be true for nitrogen and phosphorus during summer, and herbivores at various times. The importance of nutrients in limiting phytoplankton biomass in Oak Mere was investigated further in an enclosure experiment in the lake during August and September 1991 (see Chapter 7).

The DIN:SRP ratio (Fig. 6.10) suggests that during the summer of 1990 nitrogen was likely to have been more important in limiting phytoplankton biomass than phosphorus, although during the summer of 1991 phosphorus appeared to be more important. The ratio of carotenoid pigments to chlorophyll *a* pigments (A480:663) (Fig. 6.11) indicate that the phytoplankton may have been nitrogen deficient, although the high ratio of A430:410 (Fig. 6.11) suggests that the high A480:663 ratio may be due to grazing effects or resuspended sediment.

Gibson (1971) suggests that a nutrient factor is not limiting if an increase in the concentration of that factor produces no significant stimulation in algal growth, although a substance that limits growth rates does not necessarily limit the biomass (O' Brien, 1972). The only factors to show a significant positive relationship with chlorophyll *a* were alkalinity (all year round, growth-season) and pH (growth-season only). Increasing pH was almost certainly a response to carbon dioxide removal from the water for photosynthesis, which would explain the

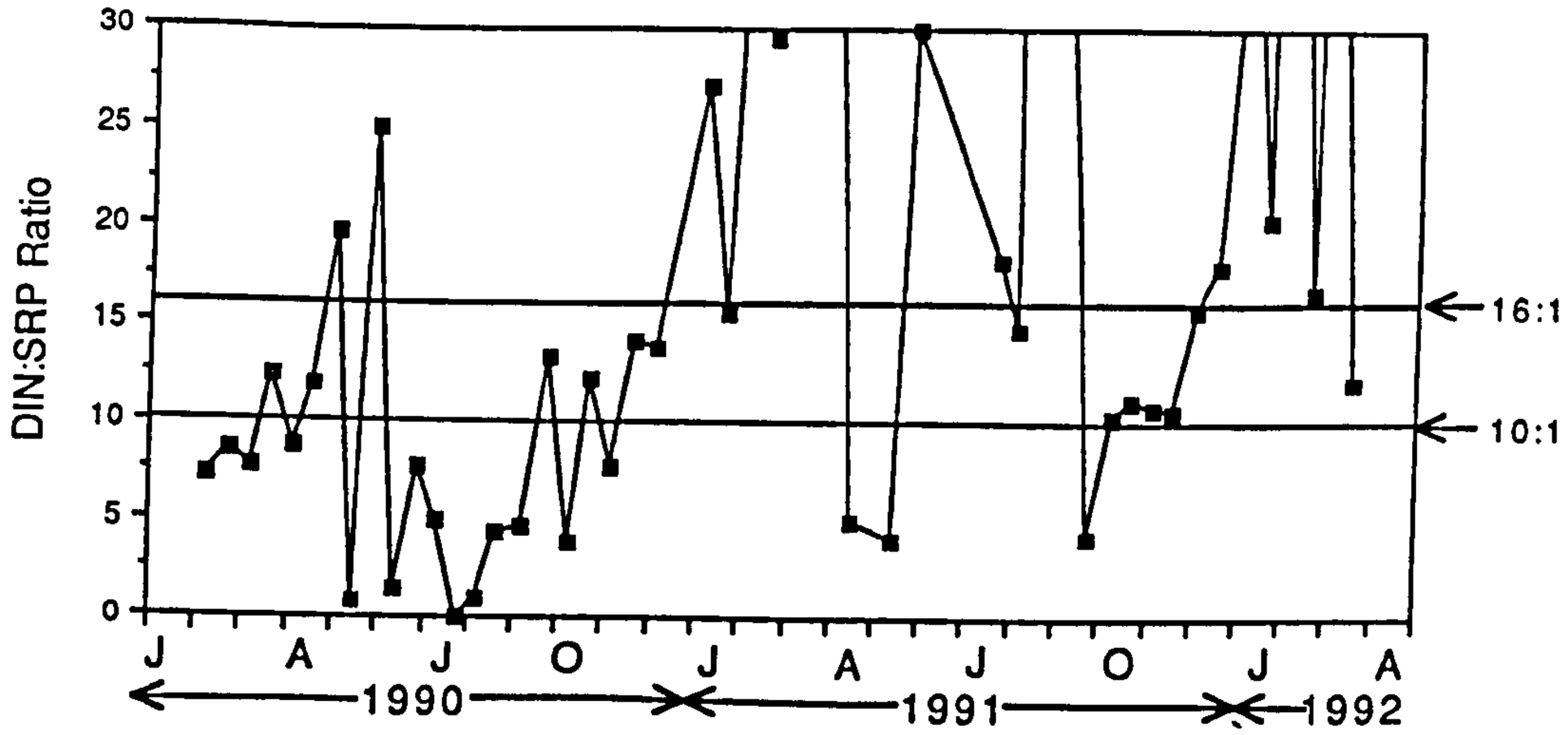


Fig. 6.10 Seasonality of the DIN:SRP ratio in Oak Mere.

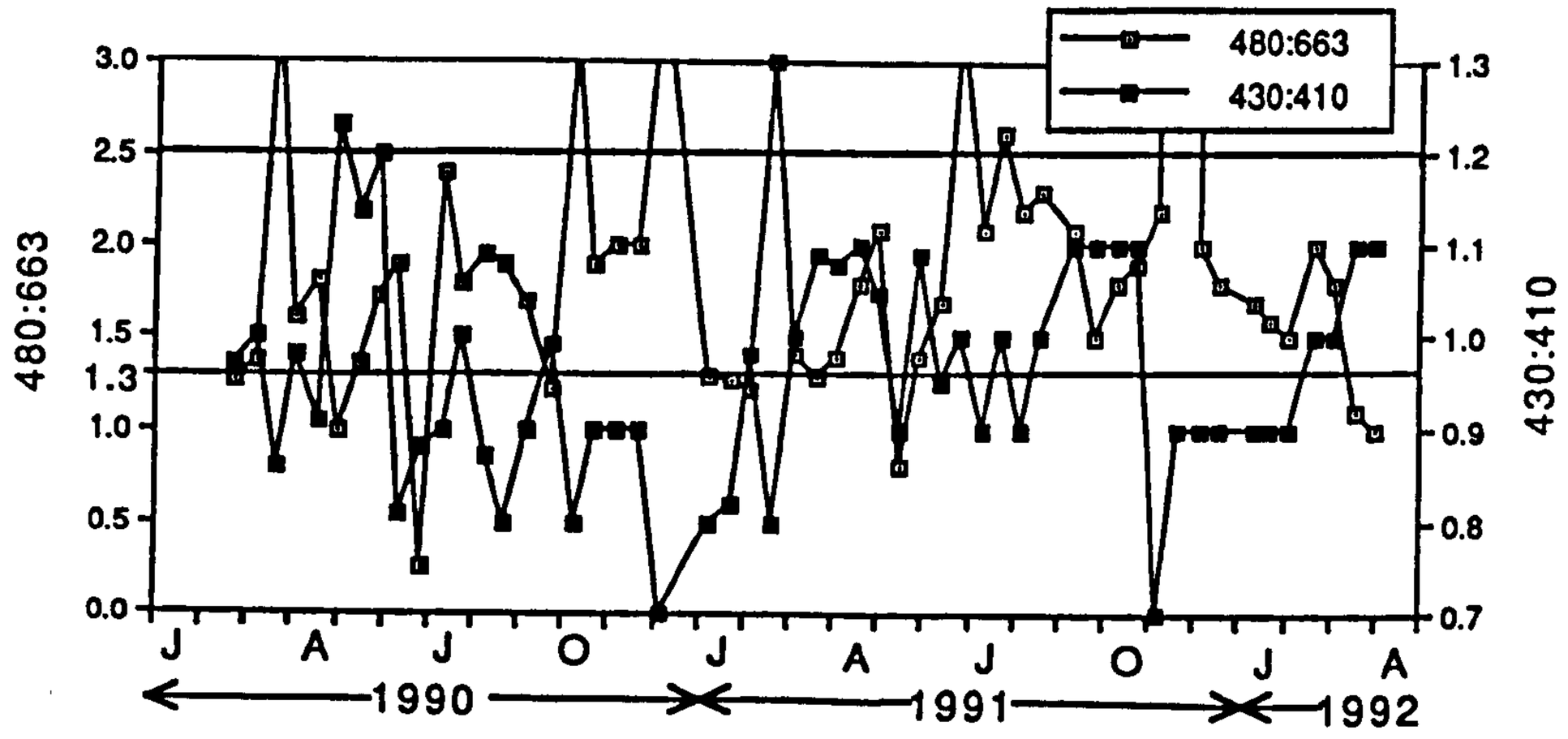


Fig. 6.11 Seasonality of the ratio of carotenoid pigments to chlorophyll *a* (ratio of absorbances at 480 nm:663 nm) and the ratio of the absorbances at 430 nm:410 nm.

significant relationship between pH and chlorophyll *a* concentrations during the phytoplankton growth season.

The changes in the bicarbonate equilibrium system that occur with removal of carbon dioxide do not, however, lead to changes in alkalinity (Stumm & Morgan, 1981). The significant relationship between alkalinity and chlorophyll *a*, therfore, means that either photosynthesis in some other way affected alkalinity, or photosynthesis itself must have been limited by alkalinity. Alkalinity can be defined as the capacity to neutralize strong acids (Stumm & Morgan, 1981), and is due to any dissolved species that can accept and neutralize protons. Alkalinity in freshwaters is largely due to bicarbonate ions, although organic acids and silicates can be important, and carbonate ions are important at high pH (>9).

The assimilation processes that accompany photosynthesis have been shown to affect alkalinity (Brewer & Goldman, 1976); alkalinity increases as a result of photosynthetic nitrate assimilation (Equation 6.1) and decreases as a result of photosynthetic ammonium assimilation (Equation 6.2) (Stumm & Morgan, 1981).

$$106CO_2 + 16NO_3^- + HPO_4^{2-} + 122H_2O + 18H^+ = \{C_{106}H_{263}O_{110}N_{16}P_1\} + 138O_2$$

"algae" (Equation 6.1)

$$106CO_2 + 16NH_4^+ + HPO_4^{2-} + 108H_2O = \{C_{106}H_{263}O_{110}N_{16}P_1\} + 107O_2 + 14H^+$$

"algae" (Equation 6.2)

From 18 April to 2 May 1990 an increase in chlorophyll *a* coincided with an increase in alkalinity, ammonium was negligible, therefore, if photosynthetic nitrate assimilation was responsible,

change in alkalinity = (18/16*[change in NO_3^-])

= (18/16*[0.75 mg l^{-1}])

= 0.84 mg l^{-1}

= 0.014 m-equiv. l^{-1}

alkalinity change seen was 0.05 mequiv. l^{-1}, which suggests that photosynthetic nitrate assimilation could only partly explain the alkalinity increase.

When it is available, algae derive most of their nitrogen from ammonium, even if high nitrate concentrations exist (Brezonik, 1972). In Oak Mere when ammonium concentrations increase, photosynthetic ammonium assimilation should occur in preference to photosynthetic nitrate assimilation, and, therefore, a decrease should be observed in alkalinity. Regression analysis between ammonium concentration and alkalinity shows a highly significant negative relationship (r^2=0.14, 0.005<p~0.01) which suggests that photosynthetic ammonium assimilation was the cause for some of the decreases in total alkalinity.

Chlorophyll *a* concentrations, however, showed no declining trend over the study period, which suggets that the general declining trend in alkalinity was most likely due to the drier years, and not due to a decline in net photosynthesis.

It is possible that changes in dissolved inorganic carbon (DIC) concentration, associated with changes in alkalinity, were at times important in limiting the phytoplankton biomass. Carbon-limitation of phytoplankton biomass in the field has

been rejected, except in extremely nutrient-rich waters (Kerr *et al.*, 1972; Lehman *et al.*, 1975), though, laboratory experiments on the photosynthetic kinetics for DIC (Williams & Turpin, 1987) suggest that in acid lakes it may be an important rate-limiting resource. DIC concentrations can be calculated from relationships between temperature, alkalinity, conductivity, and pH (Mackereth *et al.*, 1978). However, at a pH < 5.5, slight errors in pH measurement can lead to huge differences in the estimated DIC concentration (Fig. 6.12). Estimates for Oak Mere showed that small changes in alkalinity at pH values less than 5.5 led to changes in DIC concentration ranging from 0 to 1000 $\mu M\ l^{-1}$ (Fig. 6.13). However, in this study, the method used to determine alkalinity was extremely inaccurate at very low alkalinites (Stumm & Morgan, 1981); more accurate Gran titrations (Mackereth *et al.*, 1978) ought to have been carried out. In addition to these inaccuracies in pH and alkalinity measurements, the calculation of DIC concentrations assumes that the alkalinity changes were due to changes in the bicarbonate equilibrium system. As discussed previously, this may not always be the case. Figure 6.12 does, however, show that in low alkalinity lakes, such as Oak Mere, increases in pH are likely to lead to complete depletion of DIC. A value of 10 $\mu M\ l^{-1}$ of DIC has been shown to limit growth rate in all species examined (Goldman *et al.*, 1974; Goldman & Graham, 1981; Miller *et al.*, 1984; Williams & Turpin, 1987). There is, therefore, a strong possibility of carbon-limitation of the phytoplankton growth-rate of Oak Mere during intense periods of photosynthesis. That this then limits biomass is, however, unlikely, as during the night, when photosynthesis is not

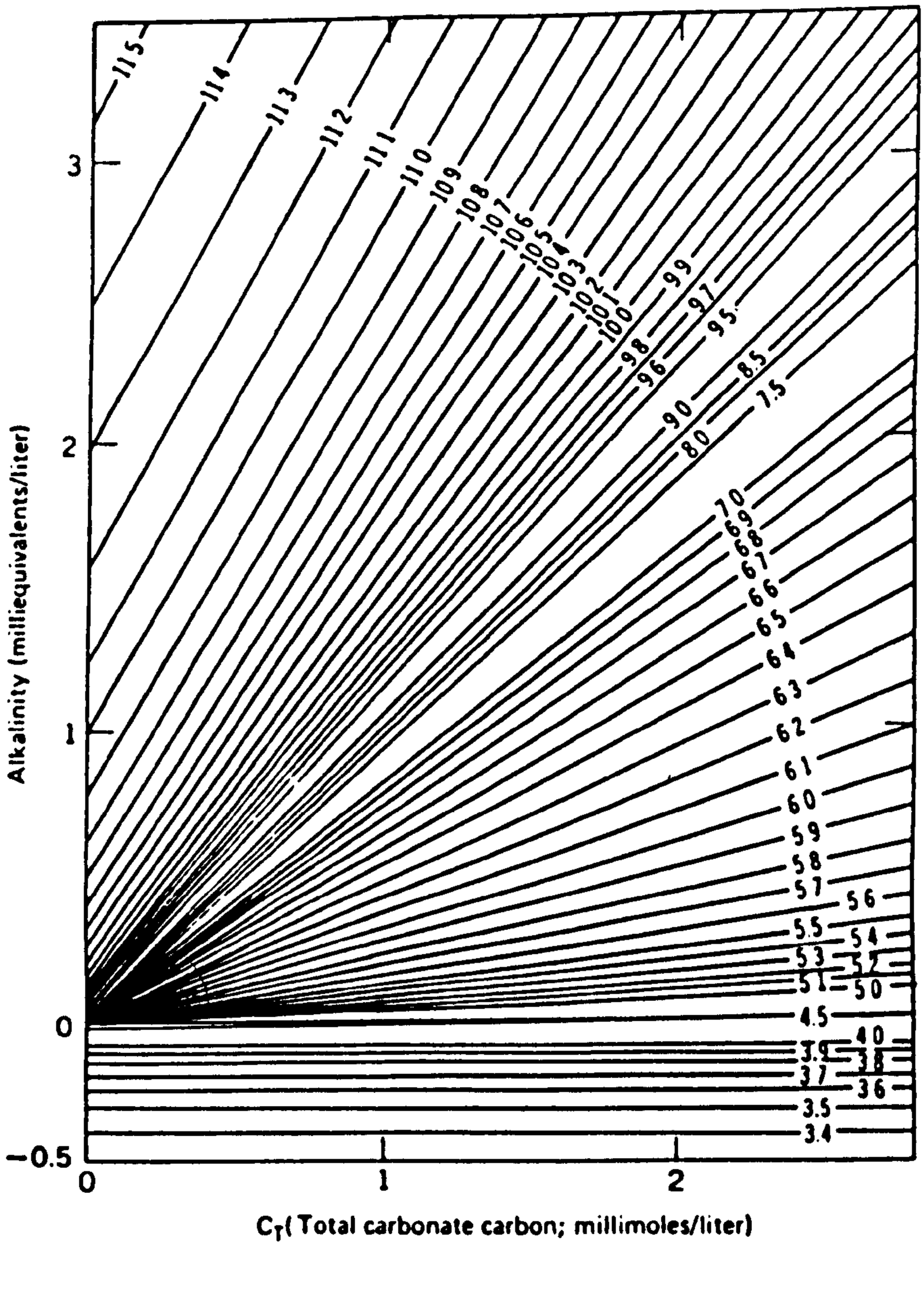


Fig. 6.12 pH contours in the relationship between alkalinity and total carbonate carbon (taken from Stumm & Morgan (1981)).

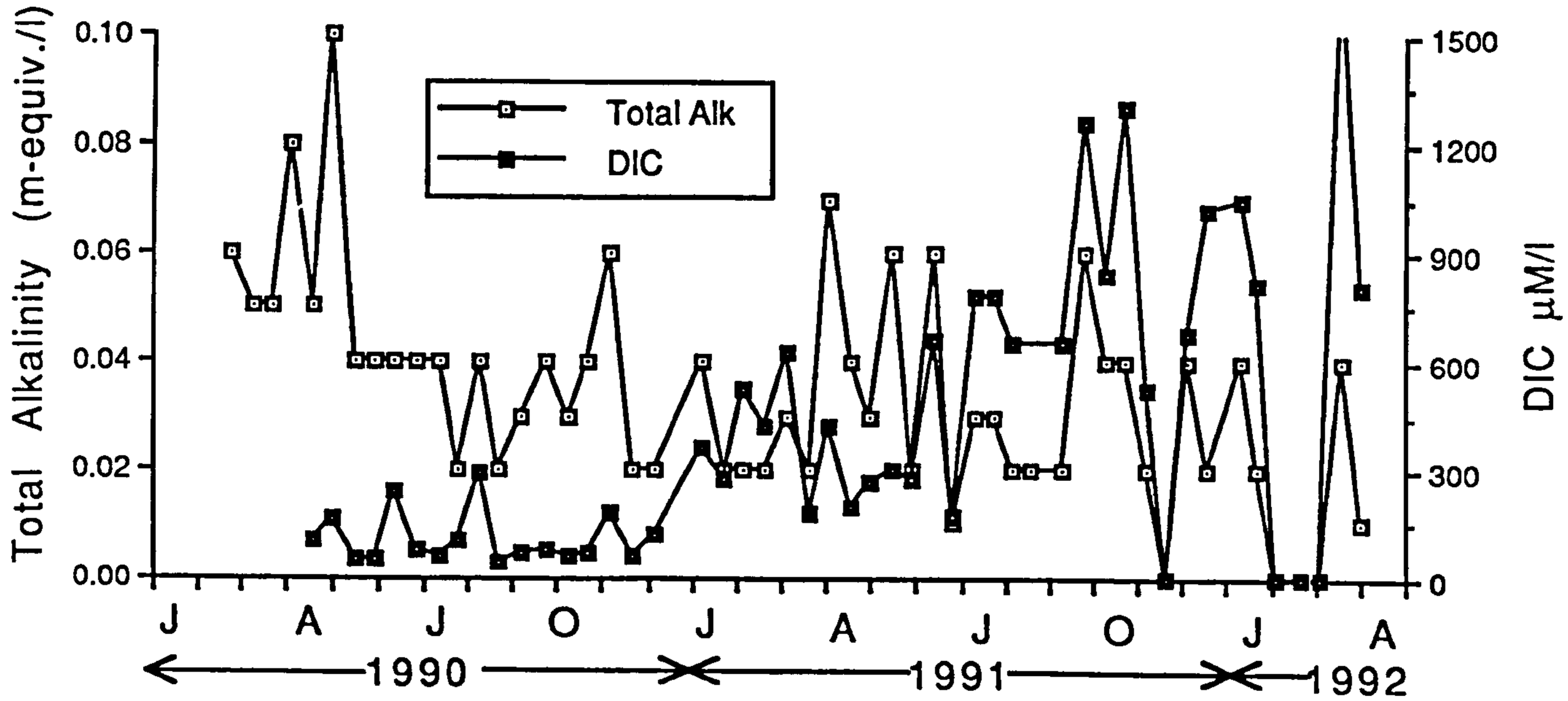


Fig. 6.13 Seasonality of total alkalinity and DIC.

occurring, DIC concentrations are likely to return to equilibrium concentrations. Phosphorus and nitrogen are, therefore, more likely to limit the summer phytoplankton biomass.

6.4.3 Factors controlling the species composition of the plankton and aquatic plant communities

The low DIC concentrations may not have limited biomass, they may, however, have excluded some species of algae. In a study of the phytoplankton and water chemistry of Oak Mere following pumping-in of base-rich groundwater, Reynolds & Allen (1968) found that the composition of the phytoplankton responded to an increase in pH, rather than nitrogen or phosphorus concentrations. In particular, large forms of cyanobacteria and Chlorophyta, and diatoms became important. This pH change was associated with a rise in calcium concentration, and so most likely also reflected an increase in carbonate or bicarbonate ions (i.e. DIC concentration) rather than being solely due to increased photosynthesis. There is, therefore, a possibility that the changes were a direct result of changes in DIC concentration.

The phytoplankton species recorded in Oak Mere, with the exception of *Botryococcus*, were small in size. This is metabolically advantageous in freshwaters of low nutrient concentrations (Wetzel, 1975), as small size increases the ratio of absorptive surface area to cell volume. This supports the idea that nutrient limitation was affecting the species composition. *Botryococcus* blooms have been observed in alkaline water bodies (Wake & Hillen, 1981); pH, therefore, does not appear to be critical to this species. Its very low growth rate (Belcher,

1968) and its ability to float at the surface may be the reason it can withstand the low DIC concentrations.

Diatoms and cyanobacteria have often been shown to be reduced in density with acidification (Brock, 1973; Delisle *et al.*, 1984; Findlay & Kaisan, 1986), whilst the dinoflagellate genera *Peridinium* and *Gymnodinium* dominate acid lakes (Almer *et al.*, 1974; Stokes, 1986; Blomqvist *et al.*, 1989). In the study by Blomqvist *et al.* (1989), the cyanobacteria genera *Merismopedia* and *Chroococcus* dominated when the pH ranged from 5.5-6.5, although they disappeared at pH values around 5.0. In the present study, Chroococcaceae, to which the latter two genera belong, dominated when the pH ranged from 5.2-5.8 in 1991 and 4.6-5.0 in 1992. Lind & Galliford (1952) recorded *Merismopedia glauca* Nag. in Oak Mere, although they state it was never abundant. Their results, however, would have been biased towards large forms of algae as they sampled using a plankton net with a mesh aperture probably about 70 μm. This would have allowed many smaller species to pass through. Galliford (1954) noted that "the poverty of the phytoplankton of Oak Mere raised problems as to the nourishment of the large zooplankton population.....one can only assume either there is a vast nannoplankton which has escaped detection by net sampling or that these species are able to utilize suspended organic matter derived from the peaty bed of the mere". The phytoplankton species observed in this study suggest that the former reason is likely. The importance of pH in determining phytoplankton species composition was investigated further in an enclosure experiment, in Oak Mere, during August and September 1991.

As Reynolds & Allen (1968) point out, diatoms may be restricted from Oak Mere by the low silicate concentrations. In this study, *Asterionella formosa* was the only species to show any sizeable population (470 ml^{-1}) in spring 1990 when silicate-silicon concentrations were generally greater than 1 mg l^{-1}, higher than those shown to cause a decline in *Asterionella* in Windermere (0.23 mg l^{-1}) (Lund, 1950). However, from mid-May to mid-August 1991, concentrations were generally less than 0.25 mg l^{-1}, and therefore, may have inhibited growth of *Asterionella*, and diatoms in general (Pearsall, 1932).

pH appeared very important in Oak Mere in determining the zooplankton species composition. A review of zooplankton changes associated with acidification (Brett, 1989) shows that *Daphnia* and *Cyclops* are commonly absent, or reduced, in acidic lakes, whereas *Diaphanosoma* and *Bosmina longirostris* are a common dominants. The changes that occurred in Oak Mere fit closely with this pattern, although, in this study *B. longirostris* was replaced by *B. obtusirostris* a species common to the upland lakes of Scotland, the English Lake District, and North Wales (Lind & Galliford, 1952). The exclusion of *Bosmina* at pH values greater than 5.5 was most likely not a direct response to the pH change but a response to competition from *Daphnia*, which may feed more efficiently than the smaller *Bosmina* species (Brooks & Dodson, 1965).

Information on the rotifer populations would have been useful, as they are sometimes found in significant numbers in acid lakes (Brett, 1989). Unfortunately, the net used for collection of zooplankton had a mesh-size too large to retain all rotifers. Lind & Galliford (1952), however, state that during the

period of their study rotifers were rarely an appreciable proportion of the zooplankton.

Low carbon concentrations may be the reason for the low diversity of the aquatic plant community. In general, phytoplankton species have been shown to be more efficient at removing DIC than aquatic plants (Maberley & Spence, 1983). Carbon depletion during the day in low alkalinity waters may, therefore, exclude many submerged species. The dominant species in Oak Mere, *LIttorella uniflora*, has, however, been shown to use free-CO_2 directly from the sediments (Søndergaard & Sand-Jensen, 1979) and can, therefore, tolerate carbon depletion in the water column.

6.4.4 Fluctuations in pH and nutrient concentrations

Changes in the chemistry (and phytoplankton) of Oak Mere were examined in detail in 1966, following the artificial pumping-in of base-rich groundwater from the sandstone aquifer to the west of Oak Mere (Reynolds & Allen, 1968). This showed that, immediately after pumping, simultaneous increases occurred in pH, conductivity, calcium concentration, and nitrate concentration.

This study has shown that pH increases also occur as a response to carbon dioxide uptake for photosynthesis. Allen (1972) recorded shifts in pH between 10 am and midday from 6.0 to 9.8, in Star Lake which had an alkalinity of about 0.1 m-equiv. l^{-1}. Because of the very low buffering capacity of Oak Mere water, the season and time of day the water samples are taken are critical. On a sunny day, pH measurements recorded in the field at midday are likely to be much higher than those

taken in the early morning. Savage *et al.* (1992) suggest that the single pH measurements taken in 1974 (pH 6.5) and May 1977 (pH 7.2) were in response to inputs of base-rich groundwater, however, they could simply be increases associated with photosynthesis. As discussed in the previous section (6.3.5), the observed increases in 1986 of pH (6.0-7.8) and bicarbonate ions ("i.e. alkalinity" ?) (0.1-0.2 m-equiv. l^{-1}) could also be explained in this way.

The extremely high nitrate concentration recorded during February 1986 by Savage *et al.* (1992) appears to be more difficult to explain than the changes in pH. However, there are two reasons why the high concentration was unlikely to have been due to a breach in an impermeable seal lining the lake. First, the increases in nitrate concentration occurred two months prior to the changes in pH and alkalinity, and secondly, the nitrate concentration was extremely high for Oak Mere (1.26 mg l^{-1}), over twice the highest concentration previously reliably recorded (0.48 mg l^{-1}), during the pumping-in of base-rich groundwater in July 1966. As the groundwater then had a nitrate-nitrogen concentration of 6.5 mg l^{-1} (Reynolds & Allen, 1968), it is difficult to imagine a source of water enriched enough to increase Oak Mere concentrations up to 1.26 mg l^{-1}. Further analyses of nitrate concentrations from November 1989 to May 1990 (Savage *et al.*, 1992) show even higher concentrations (1.00 - 3.78 mg l^{-1}); Oak Mere appeared seriously polluted. The timing of these analyses, however, overlapped with that of analyses made for this study, which showed concentrations an order of magnitude lower (0.00 - 0.35 mg l^{-1}), and in a similar range to previous records. The former analyses

(Savage *et al.*, 1992) appear unreliable and not evidence for breaching of an impermeable seal lining the lake.

6.5 Summary of the limnology of Oak Mere

With pH as low as 4.6, it was clear that Oak Mere was at times very acidic. It also had an extremely low alkalinity. SRP and DIN concentrations during winter were low, compared with many of the other North-West Midland Meres, though concentrations were higher than might be expected from a water of comparable conductivity and alkalinity. The chemical composition of the lake water suggests that Oak Mere is largely rain-fed, influenced slightly by a small amount of drainage water from the well leached sandy sub-soil to the south of the lake. The declining trends in pH, alkalinity, phosphorus, and silicate-silicon appear to be a response to the drier years; direct rainfall forming an increasing proportion of the water input.

Phytoplankton populations were low, particularly over the summer months. Phosphorus and nitrogen concentrations may have been important in limiting the biomass, particularly phosphorus during spring. Herbivores may also have limited the biomass for short periods of time. The growth-rate may have been limited by DIC, which can be fully depleted in lakes of low alkalinity.

Apart from *Botryococcus*, the phytoplankton community was dominated by small species of Chlorophyta, Chroococcaceae (cyanobacteria), and unidentified flagellates. There appeared to be little change in composition from earlier studies. pH, or possibly DIC concentration, may be important in determining the

phytoplankton species composition. The zooplankton species composition did appear to be determined largely by pH.

Short-term fluctuations in alkalinity and pH were most probably in response to changes in photosynthetic activity. Increases in nitrate concentrations in recent years appear to be errors produced in analysis rather than evidence of groundwater inputs. The fluctuations in water chemistry do not provide evidence for the hypothesis that Oak Mere is an impermeable basin, occassionally breached by groundwater.

Even though water appears to have little contact with the soil before entering Oak Mere, land-use changes in the catchment should not be ignored. In particular, the area to the south of the lake should be carefully managed, particularly with respect to nitrogen and phosphorus inputs.

6.6 Future work

Further work could be carried out to investigate carbon-limitation and what effects it may be having on the phytoplankton (and submerged macrophyte) species composition. More accurate alkalinity measurements using the Gran titration method (Mackereth *et al.*, 1978) and observations of pH in the field on an hourly basis would provide valuable information on pH fluctuations and DIC-limitation of growth-rates.

As the water chemistry of Oak Mere is a close reflection of rainwater quality, it would be of interest to reconstruct the past water quality and phytoplankton community and examine how they have changed following the increase in acidity of rainwater over the last two centuries.

Chapter 7: Oak Mere enclosure experiment

7.1 Introduction

In Oak Mere, the seasonal monitoring data revealed clear declining trends in pH, phosphorus, and phytoplankton chlorophyll *a* concentration, associated with low effective rainfall. However, which factor limited chlorophyll *a* concentrations was not clear. Positive responses to phosphorus fertilization have been reported previously for other acid lakes (Dillon *et al.*, 1979; DeCosta & Preston, 1980), although in Oak Mere nitrogen appears at least as likely to be significant.

Evidence for the importance of pH in Oak Mere was documented by Swale (1968) and Reynolds & Allen (1968). From 1963-66 the phytoplankton of Oak Mere was dominated by various chlorophytes (*Ankistrodesmus*, *Lagerheima*, *Closterium*, and *Botryococcus*). During the summer of 1966, pumping of base-rich bore-hole water raised the pH from 5 to about 6.5, resulting in *Asterionella*, *Scenedesmius*, *Anabaena*, and *Microcystis* becoming the dominant species. The most striking change being the appearance of cyanobacteria which in all previous studies (Lind, 1944; Lind & Galliford, 1952; Swale, 1965) had rarely been seen.

This experiment aimed to investigate whether pH or nutrients (nitrogen and phosphorus), or both, were important in determining phytoplankton species composition and biomass, in particular cyanobacteria.

7.2 Methods

Methods were as described in Chapter 3, except were indicated below. The experiment was carried out in Oak Mere, from 19 August 1991 to 5 September 1991. Four treatments were set up:

(1) Control. Enclosures filled with lake water with lake densities of phytoplankton and zooplankton.

(2) Increased nutrients. Nitrate-nitrogen and phosphate-phosphorus were added to the enclosures, during filling. Nitrogen was added as KNO_3, made up as a stock solution in distilled water, to produce an enclosure concentration of about 1.5 mg l^{-1} nitrate-nitrogen. Phosphate-phosphorus was added as $NaH_2PO_4.2H_2O$, to produce an enclosure concentration of about 100 µg l^{-1} phosphate-phosphorus.

These concentrations were considered ample to prevent limitation of phytoplankton by these nutrients.

(3) Higher pH. 1 M sodium hydroxide solution was added, during filling, to give a pH of about 9. The amount of alkali required was determined from titrations of 100 ml of lake water carried out one week previously.

(4) Increased nutrients and higher pH. A combination of treatments two and three.

The four treatments will from hereafter be referred to as control, nutrients, high pH, and interaction respectively.

Treatments were run in triplicate, making a total of twelve enclosures. The placement of the treatments was randomized within the wooden frame.

7.3 Results

Standard error bars are omitted from the graphs of treatment means as there was great overlap between treatments. Because of the overlap, the reasons for the significant responses have to be viewed with caution.

7.3.1 Initial conditions and water chemistry

At the start of the experiment pH, alkalinity, and nutrient concentrations in the lake were low (pH 4.9, alkalinity 0.02 m-equiv. l^{-1}, SRP < 5 µg l^{-1}, and DIN 0.23 mg l^{-1}). During the experiment pH declined from 4.9 to 4.6 in the control and nutrient enclosures and from 9.3 to 9.0 in the high pH and interaction enclosures; SRP concentrations were below the analysis detection limit in the control enclosures, throughout the experiment, and from day 11 onwards in the high pH enclosures. DIN concentrations ranged from 0.1-0.25 mg l^{-1} in the control enclosures and from 0.03-0.23 mg l^{-1} in the high pH enclosures. The minimum SRP and DIN concentrations recorded in the enclosures with added nutrients were 65 µg l^{-1} and 0.4 mg l^{-1} respectively.

At the start of the experiment, the lake phytoplankton community was dominated by the Chlorophyta, in particular *Botryococcus* and *Elakatothrix*; and the zooplankton community by *Diaphanosoma* and to a lesser extent *Diaptomus gracilis*. One-way ANOVA on the initial chlorophyll *a* concentrations and densities of Chlorophyta and the dominant phytoplankton species, revealed no significant differences between the treatments.

7.3.2 Response of chlorophyll *a* concentrations and phytoplankton biovolumes

Chlorophyll *a* concentrations in the enclosures were significantly affected by pH, nutrient concentrations, and their interaction (Table 7.1). After the initial decline in all four treatments, the chlorophyll *a* concentrations in the high pH and interaction treatments increased up to day 15 (up to about 8 μg l^{-1} and 17 μg l^{-1} respectively) (Fig. 7.1). During the final three days of the experiment there was a further slight increase in mean chlorophyll *a* concentration in the interaction treatment, whilst the high pH treatment declined to about 1 μg l^{-1}. The control and nutrient treatments showed a general decline throughout the experiment to about 1 μg l^{-1}. The significant effect of nutrients is difficult to assess from Fig. 7.1, although, nutrient addition alone did not appear to stimulate phytoplankton growth (in terms of chlorophyll *a* concentration).

Despite lower initial concentrations, chlorophyll *a* in the lake fluctuated in a similar manner to that in the control treatment (Fig. 7.1).

As nearly all the phytoplankton species observed belonged to the Chlorophyta, there should have been a similarity between Chlorophyta results and those of chlorophyll *a*. However, Chlorophyta were only significantly affected by pH (Table 7.1), although the effects of nutrients, and the interaction effect, were almost significant at the 5 % level. There were increased volumes of Chlorophyta in the high pH treatment compared with the control treatment; the interaction treatment appears to fluctuate but generally seem to be greater than the control

Table 7.1 Summary of the repeated measures ANOVA results on the effects of pH and nutrients on chlorophyll *a* concentrations, phytoplankton biovolumes, and zooplankton densities. F statistic and degree of significance are indicated. NS indicates no significance, * = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$.

Subject	pH effect	Nutrient effect	pH x nutrient interaction
Chlorophyll *a*	27.47 **	22.06 **	47.14 ***
Chlorophyta	13.69 **	5.33 NS	3.97 NS
Botryococcus	12.15 *	6.20 *	3.52 NS
Chlamydomonas	1.24 NS	10.72 *	2.49 NS
Elakatothrix	60.80 ***	36.60 **	10.00 *
Diaphanosoma	21.91 **	2.75 NS	1.86 NS
Diaptomus	0.03 NS	0.94 NS	1.51 NS

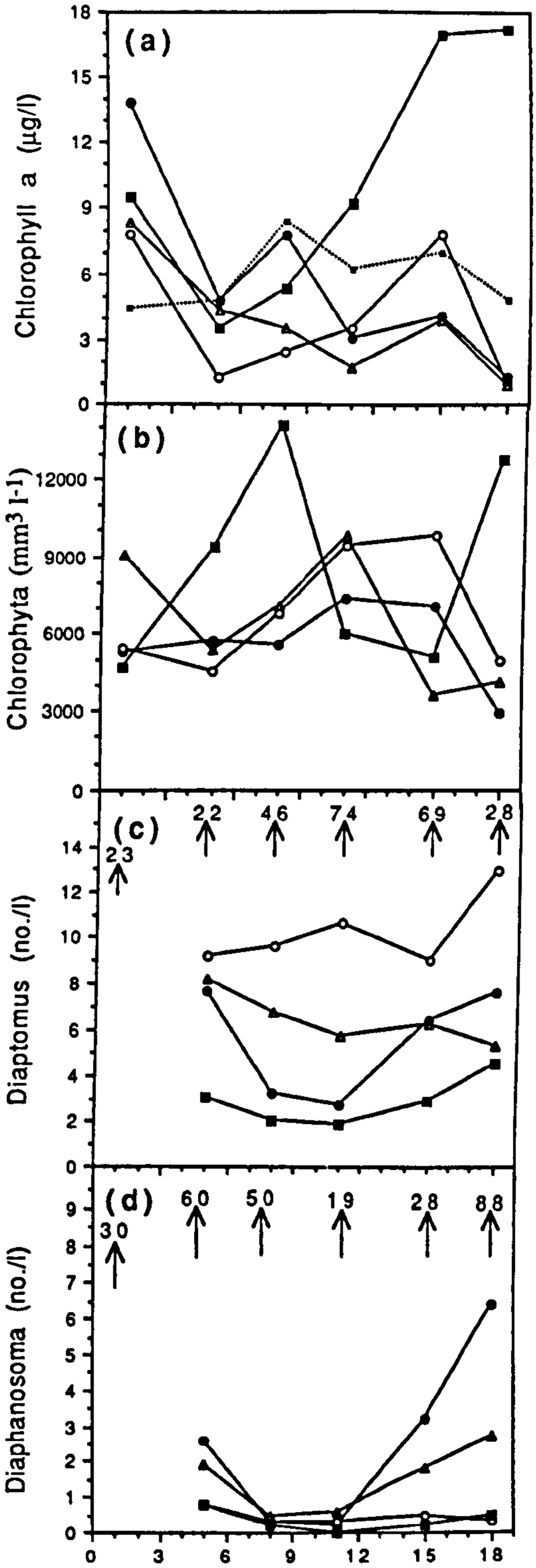


Fig. 7.1 (a) mean chlorophyll *a* concentration, (b) mean Chlorophyta biovolume, (c) mean *Diaptomus* density, and (d) mean *Diaphanosoma* density, in lake (-•-) (Chlorophyll *a* only), and control (-●-), nutrient (-▲-), high pH (-○-), and interaction (-■-) treatments. As lake zooplankton densities are off the scale of the graphs, they are indicated by arrows for the six sampling dates.

treatment; and again there appears to be no clear stimulation of growth in the nutrient treatment (Fig. 7.1). As the initial biovolumes were more or less the same in the control treatment as in the pH and interaction treatments, their mean biovolumes over the whole experiment can be compared. The pH and interaction treatments had mean biovolumes of 6.8 x 10^6 μm^3 ml^{-1} and 9.5 x 10^6 μm^3 ml^{-1} respectively, compared with 5.7 x 10^6 μm^3 ml^{-1} in the control treatment. This highlights the positive effect of increased pH and, in particular, its interaction with increased nutrients (N & P). Increased nutrients alone did not appear to stimulate chlorophyte growth.

Botryococcus (Fig. 7.2) showed an almost identical pattern of response as that of the Chlorophyta. This was because it was largely responsible for the total biovolume; most other phytoplankton species present were of much smaller size.

In terms of biovolume, the next most important species was *Elakatothrix*, which was significantly affected particularly by pH and nutrients, but also by their interaction. There was a clear reduction in *Elakatothrix* densities in the high pH, nutrient, and interaction treatments, compared with increased densities (at least up to day 15) in the control treatment (Fig. 7.2).

Only nutrients significantly affected *Chlamydomonas* densities (Table 7.1), although comparison of the treatment means does not clearly reveal how they were affected. Little response, in terms of increased or reduced biovolume, was seen in the control, high pH, and nutrient treatments, compared with the interaction treatment, which increased dramatically after day 15 (Fig. 7.2). However, this was solely due to a huge increase in *Chlamydomonas* density in only one of the three replicates.

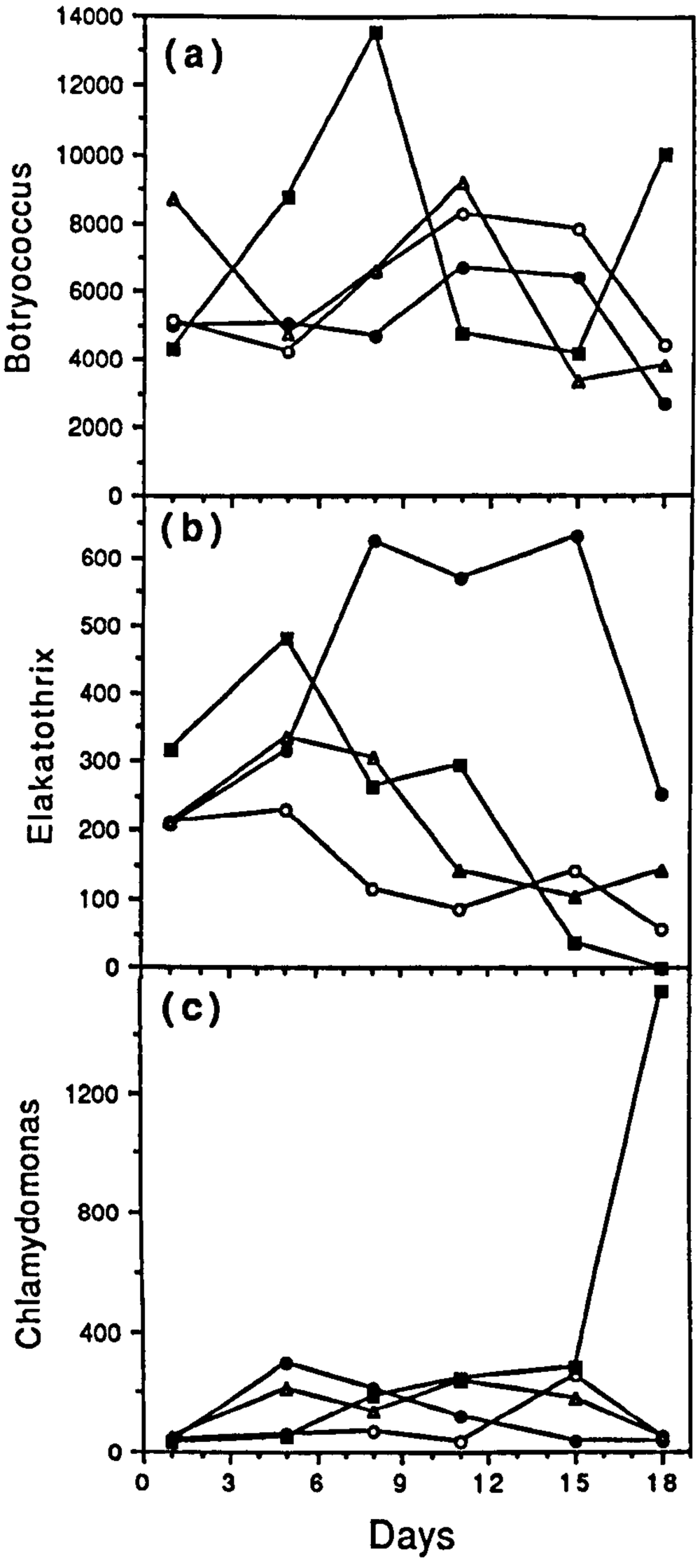


Fig. 7.2 Mean population densities of phytoplankton: (a) *Botryococcus*, (b) *Elakatothrix*, and (c) *Chlamydomonas*, in control (-●-), nutrient (-■-), high pH (-○-), and interaction (-▲-) treatments.

The only other important species in terms of biovolume were *Ankistrodesmus*, *Dictyosphaerium* and *Scenedesmus*. Their virtual absence from the control and nutrient treatments (Fig. 7.3), prevented ANOVA being performed on their densities, but emphasised the importance of high pH. Further stimulation of *Ankistrodesmus* and *Scenedesmus* appeared to occur from day 15, if nutrients were added in addition to the high pH.

7.3.3 Response of the zooplankton community

The only significant response of the zooplankton community was the response of *Diaphanosoma* to pH (Table 7.1). Densities decreased in the first week of the experiment, in all four treatments. Densities remained low in the high pH and interaction treatment, but recovered in the control and nutrient treatments (Fig. 7.1). By the end of the experiment, mean densities in the control treatment were ten times as much as those in the high pH and interaction treatments. This suggests that, after day 11, grazing pressure from *Diaphanosoma* was greater in the control and nutrient treatments than in the high pH and interaction treatments.

Diaptomus densities showed no significant response to any of the treatments, although, differences were observed in the mean densities between the four treatments (Fig. 6.3). Mean densities were 10.3 l^{-1}, 6.4 l^{-1}, 5.5 l^{-1}, and 2.8 l^{-1} in the high pH, nutrient, control, and interaction treatments respectively.

Clearly there were differences in grazing pressure between the four treatment types: the interaction treatment had the lowest densities of both grazer species; the high pH treatment had low *Diaphanosoma* densities, but high *Diaptomus* densities;

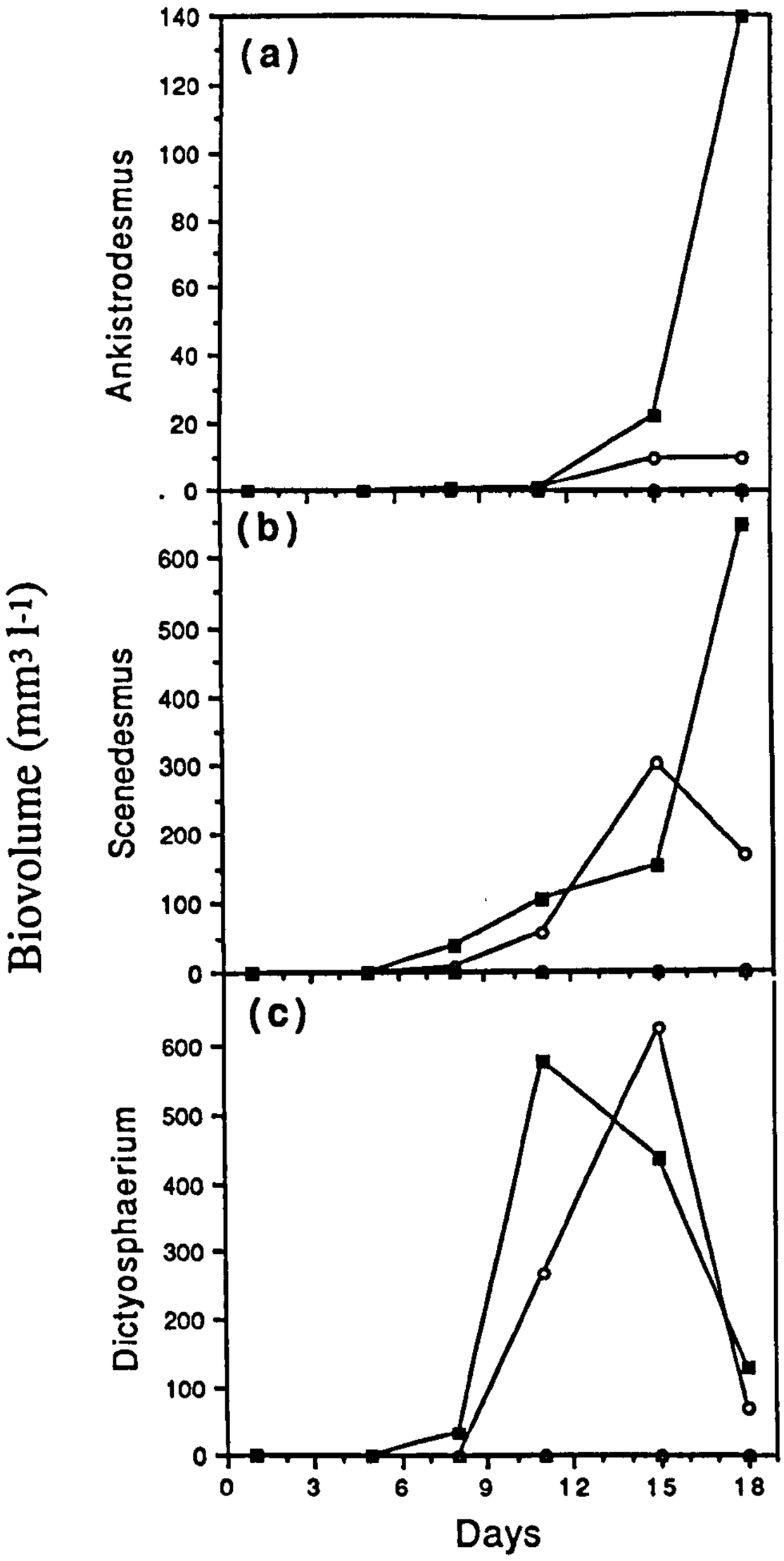


Fig. 7.3 Mean population densities of phytoplankton: (a) *Ankistrodesmus*, (b) *Scenedesmus*, and (c) *Dictyosphaerium*, in control (-●-), nutrient (-■-), high pH (-○-), and interaction (-□-) treatments.

the nutrient treatment had intermediate densities of both grazer types; and the control treatment had high *Diaphanosoma* densities and intermediate *Diaptomus* densities.

Zooplankton densities in the top metre of the lake were much higher than those in the enclosures (Fig. 7.1). Densities appeared to be dramatically reduced by pumping. Either zooplankton were able to avoid the pump, or were killed as they passed through it.

7.4 Discussion

7.4.1 The effect of nutrients

Because of the low nutrient concentrations present in Oak Mere during summer, nutrient limitation of the phytoplankton community appeared plausible. However, in the nutrient treatment no stimulation of phytoplankton growth was observed, and in fact chlorophyll *a* concentration and Chlorophyta biovolume declined. This suggests that neither nitrogen or phosphorus were limiting the growth rate or phytoplankton biomass. The decline observed in chlorophyll *a* concentrations in the nutrient treatment was similar to that observed in the control treatment, and could be explained by grazing pressure by *Diaphanosoma*, which increased in density in both these treatments from day 11 onwards; phytoplankton biomass may, therefore, have been grazer-limited in these treatments.

7.4.2 The effect of pH

Raising the pH appeared to have a much more significant positive effect than nutrient addition; chlorophyll *a* concentrations and Chlorophyta biovolumes did not decline, as in the control and nutrient treatments. One possible reason for the observed effect is that carbon limited the phytoplankton growth rate at low pH, and losses exceeded population growth. The addition of alkali to half of the enclosures would have increased their DIC concentration, as more CO_2 would have come into solution from the atmosphere. Increased DIC concentrations may then have allowed greater growth; population growth may then have balanced losses.

The effect of pH may be explained simply by differences in grazer density between treatments. In the high pH and interaction treatments *Diaphanosoma* densities remained low throughout the experiment, and, therefore, grazing pressure would have been lower. *Diaptomus* densities, however, were greatest in the high pH treatment, suggesting that the results were not just due to differences in grazing pressure.

7.4.3 Interaction of nutrients and pH

Peak chlorophyll *a* concentrations and Chlorophyta biovolumes were greatest in the interaction treatment, which suggests that nitrogen and phosphorus concentrations, in combination with pH, may have limited the phytoplankton biomass. However, the fact that the interaction treatment had the lowest densities of both zooplankton species suggests that

reduced grazing pressure may have been the underlying reason for the observed results.

Despite the peaks in both chlorophyll *a* concentrations and Chlorophyta biovolumes in the interaction treatment, the repeated measures ANOVA only revealed a significant effect on chlorophyll *a* concentrations. Non-chlorophytes were not of any importance throughout the experiment, so could not account for this discrepancy. The difference may be because Chlorophyta biovolumes were mainly due to the large, colonial alga, *Botryococcus*, which because of its large size, was probably inedible, and little affected by differences in grazing pressure. As an extracellular matrix makes up most of the *Botryococcus* biovolume, chlorophyll *a* concentration may not shadow changes in *Botryococcus* so closely. Increased chlorophyll *a* concentration in the interaction treatment may have resulted from increases in smaller Chlorophyta, which affected chlorophyll *a* concentrations, but not Chlorophyta biovolumes. In fact, *Ankistrodesmus*, and *Scenedesmus* appeared to be largely responsible for the significant increase in chlorophyll *a* concentration in this treatment, as none of the other species tested by the ANOVA showed a significant positive response. This further supports the idea that a reduced grazing pressure was responsible for the significant effect of the interaction treatment.

7.4.4 Treatment effects on species composition

No conclusions can be drawn from species that appear very rarely, so this discussion relates to the species already

mentioned. The only phytoplankton species to show a clear reduction with all treatments, compared with the control treatment, was *Elakatothrix*; increased nutrients and a high pH both appeared to have been detrimental. The opposite was true for *Ankistrodesmus*, *Scenedesmus* and *Dictyosphaerium*, the low pH of Oak Mere clearly restricted their development, which in the case of the former two taxa was further stimulated by increased nutrients.

The importance of the low pH in restricting cyanobacteria was not apparent from this experiment. Despite these species being rarely observed, an inoculum existed from which a population could have developed: two cyanobacteria species were observed in the enclosures, *Aphanizomenon flos-aquae* on day 1 in a nutrient enclosure and day 11 in an interaction enclosure, and *Coelosphaerium* sp. on day 1 in an interaction enclosure. Either some other condition prevented them developing, or, their development time was too slow for any increases to be seen during the course of the experiment. Shapiro (1984) carried out an enclosure experiment that, following lowering of the pH, more or less, eliminated cyanobacteria. After restoring the pH back to 9.5, it took 29 days for cyanobacteria to once again become rich. Despite this, some observable changes would be expected in the Oak Mere enclosures within 18 days. The fact that none were seen suggests that some other factor, other than pH and nutrients, was restricting their development. It is unlikely that DIC concentrations limited them, as, if this was true, they ought to have increased in the high pH and interaction treatments.

The experiment did, however, support the observations of the seasonal monitoring on the sensitivities of the zooplankton species to pH change; changes in the enclosures appeared to be unimportant to *Diaptomus*, whilst *Diaphanosoma* densities never recovered from their initial decline in the enclosures with increased pH.

7.5 Conclusions to experiment three

Fortunately in Oak Mere, because of its low buffering capacity, the experimental manipulation of the pH was effective. However, because of the rapid nature of the pH change, the results may not be relevant, as pH changes observed in Oak Mere have occurred more gradually. However, the results may indicate the response, particularly of the zooplankton community, to rapid pH changes, which may occur during periods of intense photosynthesis. These changes may affect zooplankton species sensitive to pH change, such as *Diaphanosoma*, although as photosynthetic pH changes are short-lived, they are unlikely to affect phytoplankton species composition.

Even though the experiment aimed to examine the effects of pH and nutrients, grazer effects appeared important. McCauley & Briand (1979), showed in enclosure experiments, that grazing can cause an increase in the relative abundance of inedible phytoplankton species. An increase in smaller, edible phytoplankton species was seen in the interaction treatment, which had the lowest density of both zooplankton species, although, increases in these algae also occurred in the high pH treatment, which suggests that differences in grazing pressure

cannot fully explain the observed changes. Cyanobacteria, which are commonly considered inedible, did not develop in the enclosures with the greatest grazing pressure, although this may simply have been because the experiment was too short for their response to be seen, or some other factor was limiting their population.

As grazer densities were very different between treatments no definite conclusions can be made about the effects of pH and nutrients in Oak Mere. However, tentatively it could be concluded that increased pH was important in stimulating growth, and that biomass may have been limited by pH in combination with nitrogen and/or phosphorus concentrations. If grazers had been excluded from all four treatments, the effects of nutrients and pH would probably have been clearer. The lack of grazers would, however, make extrapolation of the results to the lake situation more difficult. Grazer densities in the lake were actually much higher than in the enclosures, which suggests that grazing may be of even more importance than the experiment indicated.

Chapter 8: Conclusions

8.1 Introduction

Problems associated with interpreting results from the enclosure experiments are initially discussed, along with brief conclusions from the experiments. The chapter then summarises what factors appear to be of greatest importance in limiting phytoplankton biomass in the four Cheshire Meres studied, and the North-West Midland Meres as a whole, and the reasons for this. Finally, to assess whether the phosphorus concentrations are naturally high, the lakes of this study are compared with other North-West Midland Meres, and with other lake regions.

8.2 The use of enclosures for research

Small-scale, *in-situ*, enclosure experiments were carried out as they were a compromise between whole-lake experiments, where replication is impossible, and the more artificial conditions of the laboratory. However, the effect of container size on the results of nutrient limitation (Gerhart & Likens, 1975), or predation (Carpenter & Kitchell, 1988) studies has been demonstrated. The three enclosure experiments, performed in this study, highlighted many of the problems of enclosure studies, which prevented conclusive results from being obtained:

1) Treatments may be difficult to maintain.

One of the major problems with all three experiments was in maintaining suitable zooplankton densities. In experiment one the reduced zooplankton treatment was not greatly different

from the other treatments due to reductions in all enclosures; in experiment two the increased zooplankton treatment was not significantly different from the other treatments, because of increased densities of Cladocera in all the enclosures; and in experiment three, significant differences existed in zooplankton densities between treatments, making it difficult to interpret results in terms of the pH and nutrient treatment effects. The experiments may have been more effective if stronger zooplankton treatments had been maintained in experiments one and two, and if a relatively constant density had been maintained in all enclosures in experiment three. Densities could have been better maintained, by more frequent additions, or removals, of zooplankton.

More frequent maintenance of pH in experiments one and two would also have helped interpretation of results.

2) Most factors cannot be regulated, making it difficult to obtain reproducible results, or to identify the explanation for a varying result.

This is likely to be particularly true with low numbers of replicate treatments, or low intensity treatments, as significant effects may be obscured by variation of other factors.

DeMelo *et al.* (1992) examined the results from enclosure experiments that investigated the importance of top-down control, and found that 53 % of studies produced undecided results. These were due to confounding of the experiments by factors unrelated to the treatments, making it impossible to distinguish, from the observed effects, those that were directly related to the treatments.

For example, in experiment one in Rostherne Mere, the reduction in circulation in the enclosures appears to have been an important factor in determining species composition. This reduction in circulation overrode treatment effects, although it did highlight the importance that light may play during spring in determining the size of the phytoplankton crop.

Confounding factors increase with complexity of the enclosed community. As well as direct predation effects, zooplankton (and fish) may stimulate phytoplankton growth through increased nutrient recycling (Carrillo *et al.*, 1990).

3) Even if the treatment is shown to produce a statistically significant result, the experiment may use unrealistic concentrations of chemical variables or zooplankton densities, with little ecological significance.

The sudden increase in pH in experiment three, in Oak Mere, may have shown statistically important results due to an increase in DIC concentration; however, sudden pH changes in the lake, associated with photosynthesis, may actually be in response to decreases in DIC concentration.

4) Interpretations of the patterns observed in the experiment may be strongly influenced by the time-scale, or spatial scale of the experiment.

In experiment three, in Oak Mere, cyanobacteria may have appeared if the experiment had continued for longer. However, after several weeks in small enclosures, the periphytic community on the sides of the enclosures may significantly

affect the results, by a reduction in nutrient concentrations for example, so the duration of the experiments was restricted.

The enclosure experiments were, however, of some benefit. They indicated that light was of importance in limiting the spring and summer phytoplankton biomass in Rostherne Mere, whilst nutrient concentrations appeared of little importance, as has been suggested previously (Reynolds, 1978b; Reynolds & Bellinger, 1992). They also indicated that grazing may have limited the populations of certain phytoplankton species, possibly even having some limiting effect on cyanobacteria populations. Experiment three indicated that, in Oak Mere, nutrient concentrations alone did not appear to be important in limiting phytoplankton biomass, but may be important in combination with a higher pH. This latter result stresses the usefulness of factorial experiments, which enable interaction effects to be identified.

8.3 Limitation of phytoplankton

The importance of phosphorus in determining phytoplankton biomass in lakes has long been recognised, and was emphasised by several successful models that predicted chlorophyll *a* concentration as a function of total phosphorus concentration in phosphorus-limited lakes (Dillon & Rigler, 1974; Jones & Bachman, 1976; Prepas & Trew, 1983). However, the observation that about 50 % of observed variability in chlorophyll *a* concentrations could not be attributed to nutrient loading, led to the development of the trophic cascade hypothesis (Carpenter *et al.*, 1985). This proposed that predator-

prey interactions, transmitted through food webs, cause variance in phytoplankton biomass at a constant nutrient load. Controversy over the relative importance of nutrients (usually phosphorus), or zooplankton grazing, has since followed. In shallow lakes, grazers are often able to maintain a stock population, within aquatic plant beds, that can potentially control phytoplankton biomass. In deeper lakes, aquatic plant beds tend to be of less significance, so potential control by grazers is limited, and nutrient limitation is generally more important (McQueen, 1990; Moss, 1990).

Examination of the annual mean total phosphorus and chlorophyll *a* concentrations of the four lakes in this study (Table 8.1) reveals the great discrepancy that can exist between nutrient loading and chlorophyll *a* concentrations. Oak Mere and Mere Mere have similar phosphorus concentrations that would classify them as meso-eutrophic lakes (Vollenweider & Kerekes, 1982) yet in terms of chlorophyll *a* concentration, Mere Mere would clearly be classified as a eutrophic lake. Little Mere on the other hand would be classified as hyper-eutrophic in terms of phosphorus and meso-eutrophic in terms of annual mean chlorophyll *a* concentration (Vollenweider & Kerekes, 1982), despite an extremely high peak chlorophyll *a* concentration. These data clearly indicate that, in these four lakes, phosphorus concentrations alone cannot explain the variation in phytoplankton biomass; other limiting factors must be of importance.

During the phytoplankton growth season, *Daphnia* density was greatest in Little Mere (Table 8.1), where, following a fish-kill in summer, large, efficient grazers developed huge

Table 8.1 Summary of the four Cheshire Meres of this study. Ann refers to annual mean, GS to growth season mean (March to October inclusive), Wint to winter mean (November to February inclusive), Min to growth season minimum, and Peak to maximum. Aquatic plant % cover refers to submerged and floating-leaved communities only.

Site	Mean Depth (m)	Aquatic Plants (% cover)	Total *Daphnia* (GS) (l^{-1})	Total P (Ann) ($\mu g\ l^{-1}$)	SRP (Wint) ($\mu g\ l^{-1}$)	SRP (Min) ($\mu g\ l^{-1}$)	DIN (Wint) ($mg\ l^{-1}$)	DIN (Min) ($mg\ l^{-1}$)	C'phyll *a* (Ann) ($\mu g\ l^{-1}$)	C'phyll *a* (Peak) ($\mu g\ l^{-1}$)
Oak Mere	1.6	10	16.8	61	17	<5	0.33	<0.05	7	30
Mere Mere	2.8	30	9.3	54	18	<5	1.01	<0.05	16	70
Little Mere	0.7	45	26.0	1510	746	860	1.91	1.25	11	248
Rostherne Mere	13.6	<5	8.6	439	431	98	0.84	<0.05	16	74

populations. Top-down control by grazing pressure was the dominant limiting factor, and explained the paradox between the very high nutrient concentrations and relatively low annual mean chlorophyll *a* concentration. Following sewage diversion, grazing will remain important if the aquatic plant community provides sufficient refuge from zooplanktivorous fish.

Rostherne Mere had the lowest growth season grazer density (Table 8.1), which may be a result of its abundant fish population (C. Goldspink, pers. comm.) and lack of grazer refuges. Grazing, therefore, did not appear to be of great importance during summer. Neither did phosphorus appear important; sewage inputs and sediment release meant that high phosphorus concentrations remained throughout summer. DIN, on the other hand, declined to very low concentrations by September. For most of the summer, phytoplankton crops may have been determined largely by light, although at times nitrogen may have been important. Because of the sewage diversion, external loading of phosphorus and nitrogen has been reduced. Nitrogen is likely to remain of importance in limiting phytoplankton biomass, although eventually, as internal sources of phosphorus reduce, phosphorus may become important.

Despite much lower phosphorus concentrations in Mere Mere compared with Rostherne Mere, phytoplankton biomass in the two lakes was similar, further supporting the lack of importance of phosphorus in limiting phytoplankton biomass in Rostherne Mere. Grazing did not appear to be of great importance in Mere Mere, despite greater dominance of submerged aquatic plants, compared with Rostherne Mere (Table 8.1). The depletion of DIN to undetectable concentrations

and the predominance of N-fixing cyanobacteria during summer, suggested that nitrogen was an important limiting factor in Mere Mere, although, phosphorus was also depleted to undetectable levels, suggesting it may have been of importance too.

Phosphorus concentrations in Oak Mere were similar to those in Mere Mere, yet chlorophyll *a* concentrations were much lower in Oak Mere, which suggests that the phytoplankton biomass of Oak Mere was not phosphorus-limited. Grazer density was greater in Oak Mere than in Mere Mere, despite lower percentage cover of aquatic plants. This could have been due to differences in fish populations; Mere Mere is known to support a large coarse fish population (M. Sheehan, Mere Golf and Country Club, pers. comm.), whilst the fish population of Oak Mere appears to be low (Mrs Hunter, daughter of lake owner, pers. comm.), possibly because of the very low pH. The lower chlorophyll *a* concentrations of Oak Mere, compared with Mere Mere, may not, however, have just been a response to the greater importance of grazers, but may have been largely due to the much lower DIN concentrations and the low pH present in Oak Mere.

The importance of grazing and nitrogen in determining phytoplankton biomass is supported by the highly significant relationships found between mean growing season *Daphnia* density and mean growing season chlorophyll *a* concentrations in a group of twelve shallow (maximum depth < 3 m) North-West Midland Meres, and winter mean DIN concentrations and mean growing season chlorophyll *a* concentrations in a group of twelve deep (maximum depth > 3 m) North-West Midland Meres (Moss *et al.*, 1992), in which these four lakes were included. The

importance of grazing in the shallow meres could be attested to the greater importance of the aquatic plant community in these lakes compared with deeper lakes. The unusual circumstance of nitrogen-limitation of phytoplankton biomass in the deeper lakes, rather than phosphorus-limitation, appeared to be due to the high annual mean total phosphorus concentrations present in all lakes studied (Table 8.2).

8.4 The North-West Midland Meres - naturally eutrophic ?

The importance of nitrogen over phosphorus, and the "naturally eutrophic" state, have been suggested as being due to the presence of apatite, a phosphorus-rich mineral, in the underlying drift deposits (Reynolds, 1979). However, the detailed nutrient budget made on the Rostherne Mere catchment provided no evidence to support this. The budget suggested that before sewage diversion, groundwater provided only 2 % of the external phosphorus load to the lake, 83 % came from sewage, surface run-off and drainage. Mere Mere and Oak Mere appear to be unaffected by sewage inputs, and so are likely to represent the natural state more closely. The annual mean total phosphorus concentration in both these lakes was not extremely high, and could almost certainly be accounted for by inputs from intensive agriculture and human inputs. Again this provides little evidence supporting a naturally eutrophic state. The latter two lakes had, however, the lowest annual mean total phosphorus concentrations of the twenty four lake basins studied by Moss *et al.* (1992) (Table 8.2) and so cannot be taken as being representative of the series as a whole. The mean winter DIN concentration of Rostherne Mere is fairly low for the

Table 8.2 Annual mean total phosphorus concentrations (μg l^{-1}), winter mean dissolved inorganic nitrogen (DIN) concentration (mg l^{-1}) and total alkalinities (m-equiv. l^{-1}) for twenty four North-West Midland Meres (modified from Moss *et al.*, 1992).

Mere	Total Phosphorus	DIN	Total Alkalinity
Berrington Pool	113	0.72	1.80
Betley	506	1.85	3.93
Betton	113	0.64	2.08
Bomere	67	0.60	0.67
Chapel	1267	0.65	4.68
Cole	400	1.27	1.49
Comber	362	0.90	3.00
Cop	315	2.34	2.95
Crose	214	0.60	3.05
Fenemere	487	2.80	4.76
Hatchmere	85	1.32	2.36
Little	1510	1.91	1.76
Mere	54	1.01	1.51
Oak	61	0.33	0.03
Oss	296	0.15	3.02
Petty Pool	261	1.03	2.35
Quoisley Big	404	1.54	4.69
Quoisley Little	264	2.13	5.02
Rostherne	439	0.84	2.65
Tabley (North basin)	323	3.74	2.45
Tabley (South basin)	326	5.28	2.46
Tabley moat	720	3.87	3.21
Tatton	263	0.75	2.60
White	1456	0.91	1.88

meres as a whole (Table 8.2), suggesting that, in terms of agricultural inputs, many of them are much more seriously polluted. A detailed study of borehole water taken from aquifers in the glacial drift may help decide whether the meres are naturally phosphorus-rich, or not.

The mean annual total phosphorus concentration of the series as a whole is very high compared with other lake districts (Table 8.3). Of similar magnitude to the North-West Midland Meres is a group of lakes in Florida which drain phosphatic rock (Table 8.3: Florida P-rich lakes), supporting the idea that the phosphorus-rich waters are due to apatite, present in the drift deposits of the Shropshire/Cheshire Plain. However, even higher mean annual total phosphorus concentrations, attributed to pollution from agriculture and sewage, have been recorded in the Qu'Appelle Valley lakes in Canada. Evidence that the latter hypothesis is the reason for the eutrophic state of the meres comes from aquatic plant surveys carried out in the region: a comparison between Leighton's (1841) flora of Shropshire and a recent survey of aquatic plants (Wiggington, 1980) reveals that many species have been lost from the meres over the last century, many of which are classified as oligotrophic species (Palmer *et al.*, 1992), such as *Lobelia dortmanna*, lost from five meres, including White Mere, Bomere, and Berrington Pool. Evidence also comes from recent palaeolimnological studies (see Twigger & Haslam, 1991), which indicate that since about 500 BC, major soil erosion into the meres has occurred, associated with agricultural development in the region; from about the fifth century AD, the sediments in the meres have become

Table 8.3 Annual mean total phosphorus concentrations (μg l^{-1}) of the North-West Midland Meres and other lake regions.

Lake Region	Total phosphorus	No. of lakes in study
North-West Midland Meres (1)	338	21
Qu'Appelle Valley Lakes, Canada (2)	460	6
Florida P-rich lakes (3)	290	8
Norfolk Broads (4)	207	12
Sicilian lakes and reservoirs (5)	70	23
Great Masurian Lakes, Poland (6)	69	21
Florida non-P-rich lakes (3)	38	31
Atlantic Region Lakes, Canada (2)	9	18

(1) Data from Moss *et al.* (1992), omitting lakes with known sewage contamination (Chapel Mere, Little Mere, and Rostherne Mere).

(2) Data from Janus & Vollenweider (1981).

(3) See Hutchinson (1957).

(4) Data from Moss (1983).

(5) Data from Calvo *et al.* (1993).

(6) Data from Zdanowski *et al.* (1984).

increasingly organic, most likely associated with further agricultural intensification.

The occurrence of cyanobacterial blooms, recorded at least since the nineteenth century and referred to in the local folklore as "the breaking of the meres" (Phillips, 1884), and records of the phosphorus concentration this century, are the only pieces of evidence cited for the natural eutrophic state of the meres. These, however, may just be a recent (in geological terms) consequence of a supply of nutrients from the long-standing agricultural practices and settlements on the Shropshire/Cheshire Plain, which, in combination with the high alkalinities of the area (Table 8.2), may favour cyanobacteria. Most intensive limnological research has focussed on large, deep lakes, where the effects of agriculture or sewage inputs are likely to be less pronounced than in the small, relatively shallow basins of the meres. It, therefore, seems plausible that the high phosphorus concentrations of the North-West Midland Meres could be attributed to sewage and intensive agriculture. In many of the meres, it is likely that further intensification of agriculture, that has occurred this century (Moss *et al.*, 1992), and a growing population, has exacerbated pollution, and resulted in the extremely high lake phosphorus concentrations present today, and more intense and frequent cyanobacterial blooms.

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Appendix 1: Calculation of evaporation

Calculation of actual evaporation (E_t) first involved the calculation of potential evaporation (PE), which assumes that the soil is always at field capacity. The calculation of PE was carried out, on a monthly basis, using a modified version of the Thornthwaite equation (Shaw, 1988):

$$PE_m = 16.N_m.(10.T_m.I^{-1})^{a} \qquad (mm)$$

where, m is the months of the year

N_m is the monthly adjustment factor related to hours of daylight (see Shaw, 1988)

T_m is the monthly mean temperature (°C)

I is the heat index of the year, given by:

$$I = \sum i_m = \sum (T_m/5)^{1.5} \text{ for } m = Jan \ldots Dec$$

$$a = (6.7 \times 10^{-7}. I^3) - (7.7 \times 10^{-5}. I^2) + (1.8 \times 10^{-2}. I) + 0.49$$

The values of PE_m were then modified to give E_t to take into account the fact that at certain times of the year, when the soil dries out, the vegetation is unable to abstract water from the soil, and the E_t becomes less than the PE. This involves the calculation of the soil moisture deficit (SMD). The values of SMD and E_t vary with soil type and vegetation. Penman (1950) introduced the concept of root constant (RC) that defines the amount of soil moisture (mm depth) that can be extracted from a soil without difficulty by a given

vegetation. The proportions of the different types of vegetation covering the catchment areas, were estimated from the1:25000 Ordnance Survey map. 20 % of the catchment is assumed to have a water table sufficiently close to the root zone that the vegetation will always transpire at the potential rate (Penman, 1950).

The values of actual SMD are taken from the potential-actual relationship of the vegetational type (see Shaw, 1988). When E_t does become less than PE then E_t is given by the change in SMD plus the rainfall, eg. E_t June = SMD June - SMD May + rainfall June.

Table A1.1. Calculation of Thornthwaite potential evaporation for Catchment North of Rostherne Mere

Month	Mean Temp. (°C)	i_m	N_m	PE_m (mm)
Jan 1990	6.5	1.48	0.68	19.6
Feb	7.2	1.73	0.82	26.5
Mar	8.2	2.10	0.98	36.5
Apr	8.0	2.02	1.15	41.7
May	12.7	4.04	1.31	79.0
Jun	13.6	4.49	1.39	90.4
Jul	16.5	5.99	1.36	109.4
Aug	17.6	6.60	1.23	106.2
Sept	12.5	3.95	1.06	62.8
Oct	11.6	3.53	0.88	48.1
Nov	6.7	1.55	0.72	21.5
Dec	3.9	0.69	0.63	10.4
Jan 1991	2.7	0.40	0.68	8.2
Feb	2.1	0.27	0.82	7.5
Mar	7.9	1.99	0.98	38.4
Apr	8.1	2.06	1.15	46.3
May	10.9	3.22	1.31	73.1
Jun	11.8	3.63	1.39	84.7
Jul	17.6	6.60	1.36	128.6
Aug	16.7	6.10	1.23	109.8
Sep	14.7	5.04	1.06	82.2
Oct	10.4	3.00	0.88	46.7
Nov	6.6	1.52	0.72	23.1
Dec	5.3	1.09	0.63	15.9
Jan 1992	3.7	0.64	0.68	10.9
Feb	5.7	1.22	0.82	21.1
Mar	7.5	1.84	0.98	34.1
Apr	8.7	2.30	1.15	47.1
May	13.7	4.54	1.31	88.5
Jun	16.0	5.72	1.39	111.3
Jul	15.9	5.67	1.36	108.2
Aug	14.9	5.14	1.23	91.1

Table A1.2 Calculation of soil moisture deficit (SMD) and actual evaporation (E_t) for Catchment North of Rostherne Mere. All values given are in mm.

					RC 200 mm		RC 75 mm		Catchment	
Month	Rain	PE	Rain-PE	Pot. SMD	SMD	E_t	SMD	E_t	SMD	E_t
Jan 1990	116	20	+96	0	0	20	0	20	0	20
Feb	82	27	+55	0	0	27	0	27	0	27
Mar	27	37	-10	10	10	37	10	37	8	37
Apr	37	42	-5	15	15	42	15	42	12	42
May	25	79	-54	69	69	79	69	79	55	79
Jun	84	90	-6	75	75	90	75	90	60	90
Jul	25	109	-84	159	159	109	113	63	104	86
Aug	71	106	-35	194	194	106	116	74	116	90
Sep	68	63	+5	189	189	63	111	63	112	63
Oct	111	48	+63	136	136	48	48	48	65	48
Nov	65	22	+43	93	93	22	5	22	30	22
Dec	89	10	+79	14	14	10	0	10	4	10
Jan 1991	53	8	+45	0	0	8	0	8	0	8
Feb	29	8	+21	0	0	8	0	8	0	8
Mar	54	38	+16	0	0	38	0	38	0	38
Apr	32	46	-14	14	14	46	14	46	14	46
May	8	73	-65	79	79	73	79	73	79	73
Jun	69	85	-16	95	95	85	95	85	95	85
Jul	49	129	-80	175	175	129	115	69	110	99
Aug	27	110	-83	258	238	90	122	34	132	66
Sep	53	82	-29	287	241	56	125	56	135	61
Oct	70	47	+23	264	218	47	102	47	116	47
Nov	70	23	+47	217	171	23	55	23	79	23
Dec	63	16	+47	170	124	16	8	16	41	16
Jan 1992	45	11	+34	136	90	11	0	11	27	11
Feb	51	21	+30	106	60	21	0	21	18	21
Mar	85	34	+51	55	9	34	0	34	3	34
Apr	53	47	+6	49	3	47	0	47	1	47
May	57	89	-32	81	35	89	32	89	27	89
Jun	32	111	-79	160	114	111	105	105	87	108
Jul	63	108	-45	205	159	108	113	71	104	90
Aug	96	91	+5	200	154	91	108	91	100	91

Table A1.3 Calculation of Thornthwaite potential evaporation for the Oak Mere catchment.

Month	Mean Temp. (°C)	i_m	N_m	PE_m (mm)
Jan 1990	6.1	1.4	0.68	19.4
Feb	7.1	1.7	0.82	27.6
Mar	8.1	2.1	0.98	38.2
Apr	7.6	1.9	1.15	41.7
May	11.9	3.7	1.31	77.9
Jun	13.3	4.3	1.39	93.4
Jul	16.2	5.8	1.36	113.5
Aug	17.3	6.4	1.23	110.3
Sept	11.7	3.6	1.06	61.8
Oct	11.2	3.4	0.88	48.9
Nov	5.7	1.2	0.72	19.0
Dec	3.9	0.7	0.63	11.0
Jan 1991	1.9	0.2	0.68	6.2
Feb	1.7	0.2	0.82	6.7
Mar	7.7	1.9	0.98	36.2
Apr	8.5	2.2	1.15	47.0
May	11.1	3.3	1.31	69.8
Jun	11.6	3.5	1.39	77.4
Jul	17.3	6.4	1.36	113.0
Aug	16.2	5.8	1.23	95.7
Sep	13.9	4.6	1.06	70.8
Oct	10.1	2.9	0.88	42.7
Nov	5.9	1.3	0.72	20.4
Dec	4.5	0.9	0.63	13.6
Jan 1992	3.5	0.6	0.68	10.9
Feb	5.7	1.2	0.82	22.4
Mar	7.2	1.7	0.98	34.7

Table A1.4 Calculation of soil moisture deficit (SMD) and actual evaporation (E_t) for the Oak Mere Catchment. Values given are in mm, values in brackets are estimates based on rainfall data from Manchester Ringway Airport.

					RC 200 mm		RC 75 mm		Catchment		Catchment
Month	Rain	PE	Rain-PE	Pot. SMD	SMD	E_t	SMD	E_t	SMD	E_t	Effective Rainfall
Jan 1990	96	19	77	0	0	19	0	19	0	19	77
Feb	84	28	76	0	0	28	0	28	0	28	76
Mar	16	38	-22	22	22	38	22	38	18	38	-22
Apr	30	42	-12	34	34	42	34	42	27	42	-12
May	25	78	-53	87	87	78	87	78	70	78	-53
Jun	81	93	-12	99	99	93	98	92	79	92	-11
Jul	28	114	-86	185	185	114	116	46	107	73	-45
Aug	(67)	110	-43	228	226	108	119	70	117	86	-19
Sep	(64)	62	2	226	224	62	117	62	115	62	2
Oct	113	49	64	162	160	49	53	49	64	49	64
Nov	54	19	35	127	125	19	18	19	36	19	35
Dec	(85)	11	74	53	51	11	0	11	10	11	74
Jan 1991	49	6	43	10	8	6	0	6	2	6	43
Feb	35	7	28	0	0	7	0	7	0	7	28
Mar	45	36	9	0	0	36	0	36	0	36	9
Apr	(27)	47	-20	20	20	47	20	47	16	47	-20
May	7	70	-63	83	83	70	83	70	66	70	-63
Jun	67	77	-10	93	93	77	93	77	74	77	-10
Jul	53	113	-60	153	153	113	113	73	98	89	-36
Aug	32	96	-64	217	217	96	119	38	115	61	-29
Sep	(48)	71	-23	240	232	63	120	49	118	56	-8
Oct	65	43	22	218	210	43	98	43	101	43	22
Nov	66	20	46	172	164	20	52	20	64	20	46
Dec	26	14	12	160	152	14	40	14	54	14	12
Jan 1992	39	11	28	132	124	11	12	11	32	11	28
Feb	37	22	15	117	109	22	0	22	22	22	15
Mar	(82)	35	46	71	63	35	0	35	13	35	46

Appendix 2: Rostherne Mere bird roost data

Table A2. Numbers of birds per night. Values for 1991 and 1992 are monthly means, those for 1992 are monthly maximums. Monthly loading to Rostherne Mere is shown, calculated from the figures of gull nights (see section 2.2.7 for further details).

Date	Black-headed Gull (no./night)	Common Gull (no./night)	Black-headed Gull load (kg)	Common Gull load (kg)	Total load (kg)
Jan '90	6100	400	2.84	0.26	3.10
Feb	8500	200	3.57	0.12	3.69
Mar	6200	500	2.88	0.33	3.21
Apr	400	0	0.18		0.18
Aug	2100	0	0.98		0.98
Sep	2400	0	1.08		1.08
Oct	4000	0	1.86		1.86
Nov	10200	200	4.59	0.13	4.72
Dec	8300	400	3.86	0.26	4.08
1990			21.84	1.10	22.94
Jan '91	9300	500	4.32	0.33	4.65
Feb	10000	0	4.20		4.20
Mar	2800	0	1.30		1.30
Aug	600	0	0.28		0.28
Sep	1500	0	0.68		0.68
Oct	5600	100	2.60	0.07	2.67
Nov	8000	100	3.60	0.06	3.66
Dec	5800	300	2.70	0.20	2.90
1991			19.68	0.66	20.34
Jan '92	6500	500	3.02	0.33	3.35
Feb	6500	400	2.83	0.24	3.07
Mar	3200	0	1.49		1.49
Apr	4000	0	1.80		1.80

Appendix 3: Physical and chemical data

KEY

		Units
pH		
Chloride	(Cl)	mg l^{-1}
Nitrate-nitrogen	(NO3)	mg l^{-1}
Ammonium-nitrogen	(NH4)	µg l^{-1}
Dissolved inorganic nitrogen	(DIN)	mg l^{-1}
Silicate-silicon	(SiO2)	mg l^{-1}
Soluble reactive phosphorus	(SRP)	µg l^{-1}
Total soluble phosphorus	(TSP)	µg l^{-1}
Total phosphorus	(TP)	µg l^{-1}
Phenolphthalein alkalinity	(PAlk)	m-equiv. l^{-1}
Total alkalinity	(TAlk)	m-equiv. l^{-1}
Chlorophyll *a*	(Chla)	µg l^{-1}
Carotenoids	(Caro)	µspu l^{-1}
Absorbance ratio 480 nm:663 nm	(480:663)	
Absorbance ratio 430 nm:410 nm	(430:410)	
Water level	(WatLev)	m
Secchi depth	(Secchi)	m
Flow rate	(Flow)	m^3 s^{-1}

Appendix 3. Oak Mere

Date	pH	Cl	NO3	NH4	DIN	SiO2	SRP	TSP	TP	PAlk	TAlk
10.1.90		20.4				1.70	58				
25.1.90		18.9	0.26			1.80	49	90	94		
7.2.90		20.4	0.27	80	0.35	1.70	48	90			
21.2.90		18.8	0.31	66	0.38	1.80	44	80	92	0.00	0.06
7.3.90		10.4	0.31	58	0.37	1.40	48		107	0.00	0.05
21.3.90		22.5	0.35	110	0.46	1.50	37	76	85	0.00	0.05
4.4.90		20.4	0.33	0	0.33	1.20	38	78	81	0.00	0.08
18.4.90	6.4	22.2	0.30	8	0.31	1.00	26	76	120	0.00	0.05
2.5.90	6.6	20.6	0.13	28	0.16	0.60	8	47	84	0.00	0.10
16.5.90	6.9	25.0	0.00	0	0.00	0.90	5	46	80	0.00	0.04
29.5.90	6.9	25.0	0.10	0	0.10	1.00	4	33	61	0.00	0.04
12.6.90	5.7	22.7	0.03	0	0.03	0.90	22	79	107	0.00	0.04
27.6.90	6.4	20.8	0.05	57	0.11	1.00	14	48	67	0.00	0.04
11.7.90	6.7	20.6	0.02	49	0.07	1.10	14	35	48	0.00	0.04
25.7.90	5.8	25.0	0.00	0	0.00	1.10	6	18	47	0.00	0.02
8.8.90	5.6	25.0	0.01	7	0.02	1.40	17	41	75	0.00	0.04
21.8.90	6.3	25.0	0.05	29	0.08	0.75	18	51	60	0.00	0.02
6.9.90	6.6	25.0	0.00	63	0.06	0.91	14	23	63	0.00	0.03
24.9.90	6.4	22.7	0.10	6	0.11	1.18	8	23	54	0.00	0.04
9.10.90	6.5	24.7	0.01	29	0.03	0.57	9	29	95	0.00	0.03
22.10.90	6.6	23.4	0.09	106	0.20	0.54	16	39	67	0.00	0.04
6.11.90	6.2	24.5	0.10	93	0.19	0.71	25	41	60	0.00	0.06
20.11.90	6.2	22.7	0.18	102	0.28	0.42	20	35	54	0.00	0.02
5.12.90	5.8	22.7	0.17	107	0.28	0.53	20	39	85	0.00	0.02
7.1.91	5.6	22.4	0.32	87	0.41	0.54	15	36	63	0.00	0.04
22.1.91	5.5	22.7	0.34	94	0.43		28	34	52	0.00	0.02
5.2.91	5.2	20.6	0.43	87	0.52		12	33	26	0.00	0.02
19.2.91	5.3	22.4	0.24	114	0.35	0.26	12	29	43	0.00	0.02
5.3.91	5.2	40.8	0.31	0	0.31	0.41	0	15	48	0.00	0.03
19.3.91	5.5	50.0	0.13	15	0.14	0.13	1	12	58	0.00	0.02
2.4.91	5.7	22.4	0.22	0	0.22	0.40	6	27	63	0.00	0.07
16.4.91	5.8	44.9	0.01	0	0.01	0.34	2	12	64	0.00	0.04
30.4.91	5.5	26.5	0.00	0	0.00	0.54	0	12	71	0.00	0.03
14.5.91	5.8	22.4	0.02	0	0.02	0.22	5			0.00	0.06
27.5.91	5.3	22.7	0.03	0	0.03	0.23	1	31	30	0.00	0.02
11.6.91	5.4	24.5	0.02	0	0.02	0.08	0	36	76	0.00	0.06
25.6.91	5.2	22.0	0.02	19	0.04	0.06	0	0	37	0.00	0.01
9.7.91	5.0	24.5	0.01	0	0.01	0.24	0	12	66	0.00	0.03
22.7.91	5.0	22.4	0.01	136	0.15	0.37	8	21	48	0.00	0.03
6.8.91	4.9	20.4	0.09	101	0.19	0.21	13	32	50	0.00	0.02
19.8.91		23.4	0.10	131	0.23	0.34	1	12	55	0.00	0.02
9.9.91	4.9	25.0	0.09	64	0.15	0.47	5	18	48	0.00	0.02
23.9.91	5.1	24.5	0.00	17	0.02	0.48	4	10	52	0.00	0.06
9.10.91	5.1	26.1	0.04	32	0.07	0.98	7	10	35	0.00	0.04
22.10.91	5.0		0.06	28	0.09		8	22	40	0.00	0.04
5.11.91	5.1	24.2	0.09	93	0.18	1.12	17	26	66	0.00	0.02
19.11.91	5.5	24.5	0.09	154	0.24	0.80	23	47	54	0.00	0.00
3.12.91	5.3	20.0	0.17	177	0.35	0.76	22	24	57	0.00	0.04
18.12.91	4.8	24.2	0.19	151	0.34	0.77	19		99	0.00	0.02
9.1.92	5.1	23.5	0.28	108	0.39		10	21	77	0.00	0.04
21.1.92	4.9	21.4	0.24	128	0.37	0.83	18	29	93	0.00	0.02
3.2.92	4.7	24.0	0.25	141	0.39	0.73	6	34	37	0.00	0.00
18.2.92	4.9	46.6	0.25	117	0.37		22	45	54	0.00	0.00
3.3.92	5.0	20.0	0.18	1	0.18	0.59	3	12	82	0.00	0.00
18.3.92	4.9	18.7	0.21	8	0.22	0.55	18	46	65	0.00	0.04
1.4.92	4.6	21.8	0.16			0.56	7	21	47	0.00	0.01
28.58											

Appendix 3. Oak Mere

Date	Chla	Caro	480:663	430:410	WatLev	Secchi
10.1.90					-0.13	1.60
25.1.90					-0.11	2.10
7.2.90					-0.05	1.50
21.2.90	5	6	1.26	0.97	-0.02	1.80
7.3.90	4	5	1.37	1.00	0.00	1.80
21.3.90	2	5	3.43	0.86	-0.03	1.50
4.4.90	6	8	1.62	0.98	-0.06	1.80
18.4.90	6	10	1.82	0.91	-0.09	1.80
2.5.90	28	25	0.99	1.23	-0.11	1.20
16.5.90	30	37	1.36	1.14	-0.14	1.10
29.5.90	8	13	1.73	1.20	-0.19	1.40
12.6.90	5	8	1.91	0.81	-0.20	1.90
27.6.90	18	4	0.25	0.88	-0.22	1.90
11.7.90	2	5	2.40	0.90	-0.25	1.90
25.7.90	7	12	1.80	1.00	-0.32	1.70
8.8.90	5	8	1.95	0.87	-0.29	1.80
21.8.90	4	7	1.90	0.80	-0.23	1.80
6.9.90	6	9	1.70	0.90	-0.25	2.10
24.9.90	16	18	1.21	0.99	-0.30	2.10
9.10.90	2	6	3.10	0.80	-0.29	2.70
22.10.90	2	4	1.90	0.90	-0.31	2.40
6.11.90	2	4	2.00	0.90	-0.27	3.50
20.11.90	2	4	2.00	0.90	-0.23	3.00
5.12.90	1	3	3.50	0.70	-0.26	3.30
7.1.91	6	7	1.28	0.80	-0.20	1.50
22.1.91			1.26	0.82	-0.19	
5.2.91			1.22	0.98	-0.21	
19.2.91	0	1	3.00	0.80	-0.23	
5.3.91	5	6	1.40	1.00	-0.22	1.40
19.3.91	15	18	1.29	1.09	-0.21	1.10
2.4.91	12	15	1.39	1.08	-0.24	1.00
16.4.91	10	16	1.80	1.10	-0.26	0.80
30.4.91	7	12	2.10	1.05	-0.28	0.80
14.5.91	7	5	0.80	0.90	-0.32	1.40
27.5.91	12	15	1.39	1.09	-0.37	2.30
11.6.91	8	13	1.70	0.95	-0.39	1.40
25.6.91	4	10	3.20	1.00	-0.39	2.00
9.7.91	3	6	2.10	0.90	-0.42	1.70
22.7.91	4	9	2.60	1.00	-0.47	3.50
6.8.91	3	5	2.20	0.90	-0.49	3.40
19.8.91	7	14	2.30	1.00	-0.54	1.90
9.9.91	4	8	2.10	1.10	-0.61	3.00
23.9.91	10	23	1.50	1.10	-0.64	1.80
9.10.91	8	13	1.80	1.10	-0.63	1.50
22.10.91	11	19	1.90	1.10	-0.64	1.60
5.11.91	7	14	2.20	0.70	-0.59	1.00
19.11.91	0	6	17.00	0.90	-0.58	1.00
3.12.91	5	9	2.00	0.90	-0.60	1.50
18.12.91	9	15	1.80	0.90	-0.60	
9.1.92	8	12	1.70	0.90	-0.54	1.40
21.1.92	6	8	1.60	0.90	-0.57	
3.2.92	4	5	1.50	0.90	-0.59	1.90
18.2.92	2	3	2.00	1.00	-0.59	
3.3.92	8	13	1.80	1.00	-0.59	1.40
18.3.92	17	17	1.10	1.10	-0.57	1.00
1.4.92	10	9	1.00	1.10	-0.58	1.00
28.58					-0.67	

Appendix 3. Inflow MM

Date	pH	Cl	NO3	NH4	DIN	SiO2	SRP	TSP	TP	PAlk	TAlk	Flow
10.1.90		59.2				4.2	86					
25.1.90		90.5	2.72			4.1	53	58	342			
7.2.90		55.1	2.29	275	2.56	4.1	44	66	144			
21.2.90		163.5		219		4.9	56	145	215	0.00	1.20	0.029
7.3.90		70.3	2.12	233	2.35	4.6	81	147	176	0.00	1.35	0.022
21.3.90		57.1	2.13	428	2.56	5.1	104	129	178	0.00	1.78	0.018
4.4.90		51.0	1.42	437	1.86	4.5	112	129	183	0.00	1.73	0.015
18.4.90		52.5	1.29	352	1.64	4.6	119	212	278	0.00	1.78	0.014
2.5.90		51.6	1.70	119	1.82	3.7	111	164	244	0.00	2.25	
16.5.90		45.8	0.97	112	1.08	4.2	69	116	323	0.00	2.00	0.015
29.5.90		54.0	2.59	153	2.74	2.0	67	124	154	0.00	2.70	0.006
12.6.90		54.0	1.05	397	1.45	4.3	164	245	365	0.00	2.60	0.000
27.6.90		50.0	0.83	254	1.08	4.1	154	260	323	0.00	2.75	0.004
11.7.90		54.0	0.90	388	1.29	2.5	95	99	234	0.00	2.78	0.008
25.7.90		54.2	0.92	108	1.03	1.0	188	216	369	0.25	2.55	0.001
8.8.90												0.000
21.8.90		45.8	0.97	320	1.29	4.5	100	145	177	0.00	1.25	0.135
6.9.90		45.8	0.69	176	0.87	3.1	222	216	330	0.15	2.53	0.004
24.9.90		33.0	0.75	408	1.16	3.3	108	152	336	0.00	1.05	0.044
9.10.90		55.7	1.98	190	2.17	5.3	43	63	100	0.00	1.28	0.018
22.10.90		55.3	0.76	402	1.16	4.7	98	104	153	0.00	2.08	0.001
6.11.90		63.3	5.01	202	5.21	6.3	34	96	74	0.00	1.08	0.008
20.11.90		49.5	4.55	236	4.79	4.9	20	38	102	0.00	0.45	0.157
5.12.90		61.9	3.25	243	3.49	5.4	40	64	78	0.00	1.45	0.018
7.1.91		77.6	3.86	186	4.05	4.4	26	39	58	0.00	0.75	0.070
22.1.91		70.1	4.37	167	4.54	4.4	35	64	69	0.00	1.05	
5.2.91		76.3	4.87	146	5.02	5.0	28	62	53	0.00	1.48	
19.2.91		69.4	2.91	188	3.10	4.6	36	66	69	0.00	1.30	
5.3.91		93.9	3.67	120	3.79	4.3	33	52	190	0.00	1.10	0.048
19.3.91		64.6	4.14	69	4.21	4.0	39	76	290	0.00	1.20	0.083
2.4.91		75.5	3.16	490	3.65	3.9	98	122	195	0.00	1.80	0.027
16.4.91		71.4	2.24	23	2.26	3.0	38	47	103	0.00	1.88	
30.4.91		49.0	2.37	219	2.59	4.4	49	66	122	0.00	1.18	0.030
14.5.91		61.2	2.23	275	2.50	3.1	55			0.00	1.90	0.007
27.5.91												
11.6.91		57.1	1.03	706	1.74	3.1	69	127	277	0.15	2.85	0.004
25.6.91		40.0	0.86	182	1.04	3.9	56	66	167	0.00	1.55	0.019
9.7.91		55.1	0.89	431	1.32	5.2	93	119	223	0.00	2.15	0.007
22.7.91		57.1	0.01	2616	2.63	5.4	230	252	439	0.00	2.80	0.003
6.8.91		46.9	0.51	393	0.90	3.1	152	186	321	0.08	2.23	0.003
19.8.91		53.6	0.53	898	1.43	3.3	140	154	348	0.00	2.35	0.001
9.9.91												0.000
23.9.91	7.4	46.9	0.05	1191	1.24	2.1	260	563		0.00	3.45	0.000
9.10.91		50.0	0.39	204	0.59	3.6	111	152	209	0.00	2.45	0.000
22.10.91		82.5	0.24	657	0.90	3.7	90	143	432	0.00	2.25	0.002
5.11.91		66.7	1.01	166	1.18		25	41	51	0.00	1.10	0.009
19.11.91		102.0	2.59	220	2.81	5.6	25	41		0.00	1.08	0.242
3.12.91			2.36	357	2.72	5.1	29	46	61	0.00	1.48	0.000
18.12.91		210.1	1.13	679	1.81	4.9	59	92	116	0.00	1.60	0.003
9.1.92		62.8	4.53	277	4.81	5.1				0.00	1.45	0.043
21.1.92		73.8	3.57	184	3.75	5.6	32	35	42	0.00	1.33	0.009
3.2.92										0.00		0.011
18.2.92		209.7	3.32	364	3.68	5.0	40	45	130	0.00	1.80	0.025
3.3.92		80.0	3.11	227	3.34	4.3	34	65	117	0.00	1.02	0.033
18.3.92		711.8	3.70	118	3.82	4.6	42	89	148	0.00	1.10	0.035
1.4.92		63.4	3.67	117	3.79	4.0	37	65	74	0.00	1.25	0.018

Appendix 3. Mere Mere

Date	pH	Cl	NO3	NH4	DIN	SiO2	SRP	TSP	TP	PAlk	TAlk
10.1.90		53.1				1.9	14			0.00	1.25
25.1.90		54.7	1.15			2.1	0	14	68	0.00	1.25
7.2.90		55.1	1.45	5	1.46	2.4	6	22	74	0.00	1.25
21.2.90		56.3	1.59	0	1.59	2.6	4	23	76	0.00	1.15
7.3.90		72.9	1.69	0	1.69	2.7	7	37	92	0.00	1.23
21.3.90	7.7	57.1	1.63	46	1.68	2.8	0	19	52	0.00	1.18
4.4.90		57.1	0.96	20	0.98	2.2	6	19	54	0.00	1.20
18.4.90	8.3	58.6	1.12	0	1.12	0.3	3	25	59	0.00	1.28
2.5.90	8.1	57.7	1.04	0	1.04	0.0	2	14	67	0.00	1.28
16.5.90	7.8	58.3	0.89	0	0.89	0.4	0	17	46	0.00	1.28
29.5.90	8.5	58.3	0.90	0	0.90	0.4	1	20	85	0.00	1.40
12.6.90	8.1	57.7	0.42	0	0.42	0.4	5	24	152	0.00	1.38
27.6.90	8.9	60.4	0.16	0	0.16	0.4	14	20	74	0.05	1.40
11.7.90	8.5	57.7	0.08	6	0.09	0.2	4	13	77	0.00	1.50
25.7.90	9.4	60.4	0.00	0	0.00	0.5	1	5	79	0.18	1.48
8.8.90	8.5	60.4	0.00	0	0.00	0.8	3	20	109	0.10	1.65
21.8.90	7.9	58.3	0.05	0	0.05	0.8	1	14	71	0.00	1.60
6.9.90	7.9	60.4	0.02	0	0.02	1.0	0	15	82	0.00	1.65
24.9.90	7.7	57.7	0.05	266	0.32	1.5	23	30	136	0.00	1.80
9.10.90	7.9	57.7	0.12	259	0.38	0.6	15	25	82	0.00	1.75
22.10.90	7.7	61.7	0.22	203	0.42	0.2	5	29	81	0.00	1.73
6.11.90	7.6	57.1	0.56	197	0.76	0.9	20	29	84	0.00	1.65
20.11.90	7.4	57.7	0.85	192	1.04	0.9	13	21	60	0.00	1.55
5.12.90	7.7	57.7	0.79	180	0.97	1.3	13	36	55	0.00	1.45
7.1.91	7.3	65.3	2.12	194	2.31	1.7	14	28	39	0.00	1.30
22.1.91	7.4	61.9	2.17	147	2.32	1.9	15	35	53	0.00	1.20
5.2.91	7.4	68.0	2.03	86	2.12	2.3	5	29	37	0.00	1.25
19.2.91	7.6	67.0	1.73	35	1.76	1.7	4	27	43	0.00	1.18
5.3.91	7.6	77.6	2.45	0	2.45	1.6	2	19	51	0.00	1.13
19.3.91	7.9	79.2	1.85	0	1.85	0.7	1	17	37	0.00	1.13
2.4.91	7.7	73.5	1.42	0	1.42	0.6	2	17	68	0.00	1.30
16.4.91	7.5	75.5	1.47	0	1.47	0.4	1	11	35	0.00	1.20
30.4.91	7.8	77.6	1.34	3	1.34	0.5	0	20	40	0.00	1.20
14.5.91	7.8	77.6	0.97	62	1.03	0.4	3			0.00	1.55
27.5.91	7.7	76.3	0.92	72	0.99	0.6	6	30	58	0.00	1.28
11.6.91	7.7	77.6	0.63	27	0.66	0.5	0	49	56	0.25	1.65
25.6.91	7.8	74.0	0.63	0	0.63	0.6	1	0	27	0.00	1.30
9.7.91	8.0	73.5	0.43	12	0.44	0.7	0	15	35	0.00	1.40
22.7.91	8.9	77.6	0.00	0	0.00	0.8	5	22		0.25	1.43
6.8.91	9.1	73.5	0.03	14	0.04	0.5	0	13	80	0.23	1.38
19.8.91	8.4	74.2	0.06	73	0.13	0.9	2	17	72	0.00	1.30
9.9.91	8.2	75.0	0.00	20	0.02	0.3	2	24	58	0.00	1.55
23.9.91	7.7	75.5	0.00	16	0.02	0.5	2	5	90	0.00	
9.10.91	7.7	78.3	0.04	232	0.27	1.0	9	32	90	0.00	
22.10.91	7.7	74.2	0.16	173	0.33	0.0	6	11	69	0.00	1.75
5.11.91	7.3	74.7	0.12	142	0.26	0.0	13	22		0.00	1.65
19.11.91	7.7	77.5	0.25	179	0.43	0.6	14			0.00	2.00
3.12.91	7.7	72.0	0.37	157	0.53	0.8	11	21	32	0.00	1.70
18.12.91	7.8	74.7	0.37	167	0.54	0.5	21	20	35	0.00	1.70
9.1.92	7.6	74.5	1.11	230	1.34	1.0	24		40	0.00	1.45
21.1.92	7.5	73.8	1.43	169	1.60	1.3	23		45	0.00	1.43
3.2.92	7.0	80.0	1.34	163	1.50	1.4	12	50	56	0.00	1.40
18.2.92	7.5	81.6	2.13	218	2.35		22	28	70	0.00	1.90
3.3.92	7.8	84.0	1.24	4	1.24	1.5	3	37	57	0.00	1.26
18.3.92	8.1	78.1	1.44	0	1.44	1.2	0	47	62	0.10	1.30
1.4.92	7.8	73.3	1.90	51	1.95	1.1	0	19	20	0.00	1.25
14.4.92	7.8	72.0	2.00	18	2.02	1.0	0	36	45	0.00	2.20
28.4.92	7.8	74.0	1.13	5	1.13	0.8	5	4	24	0.00	1.80

Appendix 3. Mere Mere

Date	Chla	Caro	480:663	430:410	WatLev	Secchi
10.1.90						
25.1.90						
7.2.90					-0.30	
21.2.90	31.20	41	1.50	1.30	-0.29	
7.3.90	34.80	45	1.40	1.30	-0.29	
21.3.90	10.10	18	1.60	1.10	-0.27	1.5
4.4.90	13.60	22	1.70	1.21	-0.27	1.5
18.4.90	34.50	53	1.70	1.30	-0.27	1.2
2.5.90	4.80	9	2.10	1.25	-0.25	2.2
16.5.90	4.80	13	2.90	1.00	-0.23	3.0
29.5.90	17.40	25	1.60	1.30	-0.16	1.9
12.6.90	26.60	43	1.80	1.23	-0.19	1.7
27.6.90	34.50	58	1.80	1.30	-0.19	1.2
11.7.90	44.20	80	2.00	1.30	-0.18	0.9
25.7.90	47.70	76	1.70	1.30	-0.13	0.8
8.8.90	65.10	92	1.60	1.30	-0.09	0.6
21.8.90	33.90	45	1.50	1.30	-0.18	1.2
6.9.90	26.40	43	1.80	1.30	-0.17	1.0
24.9.90	36.50	51	1.50	1.24	-0.20	1.5
9.10.90	27.30	32	1.29	1.24	-0.25	1.8
22.10.90	34.30	31	1.00	1.19	-0.23	1.5
6.11.90	9.00	12	1.50	1.10	-0.30	1.9
20.11.90	4.40	7	1.70	1.00	-0.40	2.2
5.12.90	3.10	9	3.10	1.00	-0.26	2.6
7.1.91	3.50	7	2.10	0.90	-0.30	1.6
22.1.91	2.40	4	1.70	1.00	-0.30	
5.2.91	7.48	10	1.40	1.17	-0.29	
19.2.91	11.44	15	1.40	1.22	-0.30	
5.3.91	23.10	32	1.50	1.30	-0.30	1.8
19.3.91	21.30	30	1.50	1.24	-0.30	1.5
2.4.91	27.50	33	1.33	1.22	-0.28	1.4
16.4.91	14.00	19	1.50	1.23	-0.27	1.9
30.4.91	11.00	19	1.90	1.16	-0.27	2.0
14.5.91	0.00	3	8.00	0.80	-0.26	3.1
27.5.91	8.00	14	1.80	1.00	-0.23	3.0
11.6.91	12.00	19	1.70	1.10	-0.22	2.2
25.6.91	13.00	22	1.80	1.20	-0.28	2.5
9.7.91	16.00	24	1.60	1.16	-0.29	2.0
22.7.91	62.00	85	1.50	1.29	-0.24	1.0
6.8.91	75.00	106	1.60	1.30	-0.20	0.7
19.8.91	28.00	37	1.50	1.19		1.0
9.9.91	24.00	34	1.60	1.25	-0.12	1.4
23.9.91	43.00	45	1.20	1.20	-0.11	0.9
9.10.91	18.00	30	1.80	1.10	-0.16	1.6
22.10.91	21.00	28	1.50	1.16	-0.17	1.9
5.11.91	13.00	23	2.00	1.00	-0.22	1.9
19.11.91	0.00	6		1.20	-0.34	2.5
3.12.91	6.00	10	1.90	0.90	-0.39	3.8
18.12.91	0.00	5	14.00	0.80	-0.30	
9.1.92	1.00	4	3.70	0.90	-0.31	3.0
21.1.92	0.00	2	7.00	0.80	-0.28	
3.2.92	2.00	4	2.00	0.90	-0.28	
18.2.92	4.00	8	2.30	1.10	-0.29	2.6
3.3.92	14.00	19	1.50	1.10	-0.29	2.0
18.3.92	9.00	14	1.70	1.10	-0.30	
1.4.92	8.00	8	1.10	1.10	-0.28	1.8
14.4.92	10.00	15	1.70	1.10	-0.30	1.6
28.4.92	3.00	4	1.50	1.10	-0.27	2.5

Appendix 3. Little Mere

Date	pH	Cl	NO3	NH4	DIN	SiO2	SRP	TSP	TP	PAlk	TAlk
10.1.90		49.0				2.1	352			0.00	1.75
25.1.90		54.7	0.45			2.3	470	357	673	0.00	1.50
7.2.90		53.1	0.75	1270	2.02	2.5	272	372	548	0.00	1.25
21.2.90		56.3	1.10	503	1.60	1.9	211	282	430	0.00	1.30
7.3.90		75.5	0.97	611	1.58	2.8	309	427	562	0.00	1.30
21.3.90	9.3	59.2	0.65	0	6.50	0.8	540	623	943	0.18	1.38
4.4.90		57.1	0.40	68	4.68	0.6	882	1008	1252	0.05	1.38
18.4.90	9.4	60.6	0.33	36	3.66	0.5	980	1254	1866	0.05	1.50
2.5.90	8.7	59.8	0.41	707	1.12	1.2		604	931	0.00	1.60
16.5.90	7.5	60.4	0.16	4080	4.24	1.9	2255	2349	2390	0.00	1.88
29.5.90	10.1	66.7	0.53	0	5.30	2.5	660	741	1552	0.55	1.60
12.6.90		59.8	0.14	267	4.07	3.1	2843	3232	4759	0.15	1.55
27.6.90	7.8	54.2	0.09	1497	1.59	4.1	2291	2020		0.00	1.75
11.7.90	7.9	55.7	0.11	3007	3.12	3.4	2635	3203	4057	0.00	1.98
25.7.90	7.4	60.4	0.19	5758	5.95	4.4	3362	3742	3874	0.00	2.20
8.8.90	7.6	60.4	0.15	7988	8.13	5.2	4744	5441	5341	0.00	2.30
21.8.90	8.1	54.2	0.26	8493	8.75	4.6	4378	4556	4593	0.00	2.30
6.9.90	7.7	56.3	0.05	8809	8.86	5.2	5072	4546	4485	0.00	2.45
24.9.90	7.5	51.5	0.11	9575	9.69	5.0	4737	5393	5189	0.00	2.45
9.10.90	7.8	51.5	0.10	8785	8.89	3.8	3399	3787	3803	0.00	2.30
22.10.90	7.6	53.2	0.06	8061	8.12	3.3	3227	3307	3368	0.00	2.25
6.11.90	7.6	55.1	0.45			2.2	1657	1693	1578	0.00	1.85
20.11.90	7.3	51.5	0.75	2369	3.12	1.9	750	907	888	0.00	1.60
5.12.90	7.3	55.7	0.46	1941	2.40	1.9	609	624	580	0.00	1.75
7.1.91	7.5	67.3	1.43	816	2.25	2.1	196	280	311	0.00	1.40
22.1.91											
5.2.91	7.4	70.1	0.90	2016	2.92	2.7	703	795		0.00	1.55
19.2.91	7.4	71.0	0.57	1425	2.00	2.1	511	556	608	0.00	1.45
5.3.91	7.7	73.5	0.58	2334	2.91	2.2	727	798	847	0.00	1.45
19.3.91	7.8	75.0	0.61	1873	2.48	1.4	553	612	627	0.00	1.38
2.4.91	7.8	75.5	0.30	1932	2.23	1.4	688	761	777	0.00	1.55
16.4.91	7.6	75.5	0.35	2624	2.97	1.7	1176	1288	1317	0.00	1.58
30.4.91	7.5	69.4	0.24	4834	5.07	2.1	2082	2231	2143	0.00	1.85
14.5.91	7.6	73.5	0.25	5802	6.05	1.9	2646			0.00	2.10
27.5.91	9.0	74.2	0.58	3433	4.01	2.0	2035	2163	2485	0.15	1.80
11.6.91	7.4	73.5	0.13	2473	2.60	3.0	2451	2717	2720	0.03	1.78
25.6.91	7.4	64.0	0.12	4861	4.98	2.9	3107	3445	3459	0.00	1.98
9.7.91	7.4	67.3	0.12	2928	3.05		1754	1919	1912	0.00	1.70
22.7.91	7.4	73.5	0.06	4123	4.18	2.5	1598	1729	1774	0.00	1.75
6.8.91	7.2	71.4	0.17	1593	1.76	2.7	1196	1280	1384	0.00	1.55
19.8.91	7.5	74.2	0.09	2166	2.26	2.9	1306	1288	1464	0.00	1.55
9.9.91	7.5	79.2	0.12	1376	1.50	3.8	1551	1483	1657	0.00	1.65
23.9.91	7.3	75.5	0.01	1245	1.26	3.9	857	707	1140	0.00	
9.10.91	7.0	78.3	0.12	1937	2.06	4.5	1277	1101	1586	0.00	
22.10.91	7.2	76.3	0.09	1998	2.09	3.4	1197	1448		0.00	1.83
5.11.91	6.9	70.7	0.09	1440	1.53	4.6		1396		0.00	1.70
19.11.91	7.2	73.4	0.22	1453	1.67	3.6	1307		1112	0.00	1.98
3.12.91	7.3	72.0	0.43	845	1.28	2.8	825		851	0.00	2.13
18.12.91	7.4	72.7	0.29	636	0.93	1.6	383			0.00	1.68
9.1.92	7.6	70.6	0.48	214	0.69	1.6	51		62	0.00	1.40
21.1.92	7.5	71.8	0.95	242	1.19	1.6	78	146	173	0.00	1.45
3.2.92	7.0	74.0	0.63	238	0.87	1.3	105	146	152	0.00	1.35
18.2.92	7.6	71.8		90			50		94	0.00	1.60
3.3.92	8.7	76.0	0.78	6	0.79	0.3	11	11	150	0.12	1.22
18.3.92	7.9	72.0	0.86	44	0.90	0.7	13	33	60	0.00	1.30
1.4.92	7.5	73.3	1.07	147	1.22	0.9	28	20	40	0.00	1.25

Appendix 3. Little Mere

Date	Chla	Caro	480:663	430:410
10.1.90				
25.1.90				
7.2.90				
21.2.90	31	43	1.54	1.28
7.3.90	25	36	1.59	1.23
21.3.90	296	418	1.55	1.16
4.4.90	251	347	1.52	1.23
18.4.90	355	436	1.35	1.28
2.5.90	68	74	1.19	1.23
16.5.90	22	32	1.60	1.23
29.5.90	70	91	1.43	1.30
12.6.90	92	140	1.67	1.26
27.6.90	32	37	1.28	1.18
11.7.90	27	42	1.70	1.10
25.7.90	2	6	4.00	0.90
8.8.90	1	5	4.50	0.90
21.8.90	5	9	2.00	1.10
6.9.90	13	18	1.50	1.10
24.9.90	4	6	1.50	0.90
9.10.90	2	6	3.60	0.80
22.10.90	2	6	3.80	0.80
6.11.90	0	3	15.00	0.90
20.11.90	0	0		0.67
5.12.90	0	1		0.85
7.1.91	1	6	6.20	0.90
22.1.91				
5.2.91	16	19	1.35	1.28
19.2.91	23	28	1.32	1.27
5.3.91	14	21	1.60	1.20
19.3.91	12	20	1.90	1.10
2.4.91	3	9	3.10	0.96
16.4.91	3	11	3.50	0.90
30.4.91	4	16	4.10	1.00
14.5.91	5	8	2.00	1.10
27.5.91	141	167	1.30	1.31
11.6.91	3	8	3.20	1.00
25.6.91	3	9	3.10	0.90
9.7.91	1	6	5.30	0.80
22.7.91	13	15	1.29	1.00
6.8.91	6	13	2.40	1.00
19.8.91	0	2	6.00	0.90
9.9.91	7	10	1.70	1.10
23.9.91	4	10	2.70	0.90
9.10.91	3	6	2.30	0.90
22.10.91	0	5	14.00	0.80
5.11.91	2	9	4.70	0.80
19.11.91	0	11		0.90
3.12.91	0	3		0.80
18.12.91	0	5		0.80
9.1.92	3	8	3.10	0.90
21.1.92	3	6	2.40	0.90
3.2.92	5	7	1.50	1.10
18.2.92	8	12	1.70	1.18
3.3.92	58	79	1.50	1.25
18.3.92	11	17	1.70	1.08
1.4.92	1	5	4.70	0.88

Appendix 3 Inflow RM

Date	pH	Cl	NO3	NH4	DIN	SiO2	SRP	TSP	TP	PAlk	TAlk	Flow
10.1.90												
25.1.90		56.8	2.69			4.10	308	403	1380			
7.2.90		40.8	2.00	825	2.83	4.10	270	348	1100			
21.2.90		50.0		153		4.00	100	131	264	0.00	2.18	
7.3.90		65.1	2.11	65	2.18	3.40	115		266	0.00	2.25	0.099
21.3.90		44.9	1.89	58	1.95	3.30	133	165	361	0.00	2.85	0.071
4.4.90		44.9	0.98	119	1.10	3.20	173	160	348	0.00	3.00	0.058
18.4.90		44.4	1.55	160	1.71	3.50	165	233	562	0.00	3.28	0.050
2.5.90		41.2	1.66	123	1.78	4.00	248	370	344	0.00	3.45	0.047
16.5.90		43.8	1.51	531	2.04	4.30	356	406	471	0.00	3.43	0.053
29.5.90		41.7	1.96	78	2.04	4.60	250	264	341	0.00	3.70	0.044
12.6.90		39.2	1.53	48	1.58	4.90	412	449	684	0.00	3.50	0.041
27.6.90		39.6	1.74	182	1.92	5.50	289	355	433	0.00	3.68	0.040
11.7.90		39.2	1.88	104	1.98	4.10	183	235	519	0.05	3.50	0.051
25.7.90		35.4	1.98	146	2.13	4.60	145	160	212	0.13	3.60	0.028
8.8.90		37.5	2.40	157	2.56	5.10	133	167	230	0.15	4.30	0.034
21.8.90		41.7	1.33	1285	2.62	4.40	411	443	566	0.00	3.10	0.073
6.9.90		39.6	1.48	404	1.88	4.90	170	150	273	0.00	3.70	0.059
24.9.90		33.0	1.82	1415	3.24	3.40	369	472	3299	0.00	2.20	0.211
9.10.90		45.4	2.37	1476	3.85	4.10	874	944	1017	0.00	3.15	0.065
22.10.90		42.6	2.54	335	2.88	4.30	524	541	624	0.00	3.28	0.057
6.11.90		44.9	2.03	1210	3.24	4.10	572	686	718	0.00	2.60	0.055
19.11.90		47.4	6.42	419	6.84	3.30	215	285	398	0.00	1.90	0.321
5.12.90		47.4	2.35	438	2.79	3.70	139	149		0.10	2.80	0.078
7.1.91		59.2	3.63	442	4.07	3.20	88	127	226	0.00	1.95	0.174
22.1.91		66.0	4.44	415	4.86	3.30	166	201	296	0.00	2.35	0.099
5.2.91		49.5	3.23	560	3.79	4.20	206	238	447	0.00	2.85	0.072
19.2.91		49.0	2.61	605	3.22	3.90	214	260	382	0.00	2.80	0.066
5.3.91		61.2	3.99	561	4.55	3.50	204	236	463	0.00	2.33	0.099
19.3.91		56.3	4.37	294	4.66	2.70	168	199	424	0.00	2.13	0.144
2.4.91		51.0	3.20	564	3.76	3.20	287	330	598	0.00	2.78	0.077
16.4.91		44.9	1.92	98	2.01	3.40	170	229	355	0.00	3.23	0.048
29.4.91		40.8	1.89	142	2.03	4.10	185	206	348	0.05	3.33	0.055
14.5.91		42.9	1.83	298	2.13	3.90	369			0.00	3.35	0.034
27.5.91		43.3	1.79	198	1.99	4.20	282	294	449	0.10	3.40	0.044
11.6.91		42.9	1.68	146	1.83	4.60	137	151	283	0.20	3.65	0.044
25.6.91		42.0	1.49	578	2.07	4.40	592	694	885	0.00	3.10	0.054
9.7.91		46.9	1.46	181	1.64	4.00	316	358	456	0.00	3.15	0.066
22.7.91		42.9	1.42	215	1.64	5.30	196	200	343	0.00	3.55	0.040
6.8.91		38.8	1.68	117	1.80	4.90	95	109	342	0.30	3.70	0.047
19.8.91		41.2	1.80	100	1.90	5.20	101	106	224	0.00	3.50	0.042
9.9.91		37.5	1.98	93	2.07	5.10	46	51	176	0.00	3.90	0.033
23.9.91	8.1	36.7	2.15	155	2.31	4.80	42	27	221	0.00	5.15	0.030
9.10.91		41.3		166		5.50	44	58	129	0.20	4.75	0.042
22.10.91		37.1	1.57	107	1.68	4.20	49	68		0.00	3.85	0.038
5.11.91		46.5	1.40	220	1.62	5.10	71	94	116	0.00	3.28	0.073
19.11.91		65.3	4.84	426	5.27	4.50	125			0.08	3.43	0.082
3.12.91		44.0	2.59	165	2.76	4.20	68	81	155	0.00	3.72	0.057
18.12.91		82.8	1.62	1317	2.94	4.00	412	610	1004	0.00	3.18	0.104
9.1.92		62.8	2.58	178	2.76	3.00	41	97	131	0.00	1.95	0.172
21.1.92		48.5	2.54	121	2.66	4.00	41	39	204	0.08	2.93	0.057
3.2.92		80.0	1.87	262	2.13	4.10	26	64	78	0.30	2.95	0.075
18.2.92		71.8	4.99	450	5.44	4.20	59	79	369	0.30		0.085
3.3.92		60.0	5.15	162	5.31	3.10	31		238	0.00	2.18	0.173
18.3.92		56.2	2.49	202	2.69	2.90	18	74	185	0.30	2.20	0.109
1.4.92	7.8	55.4	2.79	51	2.84	3.00	35	25	104	0.15	2.40	0.084

Appendix 3 Spring RM

Date	pH	Cl	NO3	NH4	DIN	SiO2	SRP	TSP	TP	PAlk	TAlk
2.5.90	7.8	37.1	0.06	72	0.13	5.9	13	16	37	0.00	4.10
16.5.90		35.4	0.04	93	0.13	5.2	12	32	92	0.00	4.10
29.5.90		37.5	0.14	70	0.21	5.3	8	13	39	0.00	4.10
12.6.90		39.2	0.06	69	0.13	5.0	31	35	81	0.00	4.10
27.6.90	8.0	43.8	0.06	128	0.19	5.5	20	17	173	0.00	4.15
11.7.90		37.1	0.06	106	0.17	4.0	38	46	32	0.08	4.03
25.7.90		37.5	0.00	95	0.10	4.4	15	8	68	0.03	3.83
8.8.90		37.5	0.07	82	0.15	5.2	13	15	41	0.10	4.25
21.8.90		37.5	0.10	103	0.20	4.8	15	32	25	0.00	3.95
6.9.90		37.5	0.03	99	0.13	5.2	12		22	0.00	4.05
24.9.90		41.2	0.16	92	0.25	5.0	20	25	65	0.00	3.55
9.10.90	8.1	37.1	0.05	108	0.16	4.5	18	23	25	0.00	3.93
22.10.90		38.3	0.07	78	0.15	4.3	9	12	29	0.10	4.08
6.11.90		36.7	0.28	94	0.37	5.4	14	16	35	0.00	4.00
20.11.90		41.2		97		4.9	24	34	45	0.00	3.20
5.12.90	8.0	37.1	0.08	86	0.17	5.1	8		50	0.10	3.80
7.1.91		34.7	0.46	79	0.54	4.8	6	12	36	0.00	3.70
22.1.91		35.1	0.33	89	0.42	4.8	9	20	37	0.00	3.95
5.2.91	8.1	39.2	0.34	96	0.44	5.4	9	10	34	0.00	4.00
19.2.91		37.0	0.35	71	0.42	4.9	12	16	30	0.00	3.90
5.3.91		38.8	1.04	67	1.11	5.1	7	33	24	0.00	3.70
19.3.91		37.5	1.59	91	1.68	4.9	10	21	61	0.00	3.53
2.4.91	8.2	38.8	0.22	103	0.32	4.8	12	32	82	0.13	3.85
16.4.91		36.7	0.06	88	0.15	5.0	16	26	53	0.00	4.00
30.4.91		34.7	0.11	71	0.18	5.4	9	14	35	0.35	3.70
13.5.91	8.0	36.7	0.05	94	0.14	5.1	10			0.00	3.98
27.5.91		37.1	0.09	98	0.19	4.8	6	4	30	0.10	4.03
11.6.91		36.7	0.09	86	0.18	4.9	10	34	40	0.20	4.15
25.6.91		36.0	0.11	75	0.19	4.9	14	0	55	0.00	4.05
9.7.91		36.7	0.07	80	0.15	4.7	9	6	21	0.00	4.05
22.7.91		40.8	0.01	86	0.10	5.1	15	16	38	0.00	4.10
6.8.91		36.7	0.06	70	0.13	5.3	7	16	37	0.10	3.35
19.8.91		37.1	0.08	66	0.15	5.5	6	9	23	0.00	3.90
9.9.91		39.6	0.05	90	0.14	5.2	11	13	34	0.00	4.00
23.9.91	7.8	36.7	0.04	94	0.13	4.8	1	3	23	0.00	
9.10.91		39.1	0.03	43	0.07	5.4	4	0	23	0.15	5.25
22.10.91		37.1	0.09	45	0.14	4.3	6	33		0.00	3.95
5.11.91		36.4		81		4.7	11		22	0.00	4.05
19.11.91		38.8	0.33	126	0.46	5.2	10			0.23	5.00
3.12.91		36.0	0.13	77	0.21	4.6	8	5	24	0.00	4.40
18.12.91		36.4	0.12	123	0.24	5.0	33		43	0.18	4.40
9.1.92	7.5	43.1	0.84	53	0.89	5.0	6	22	34	0.30	3.60
21.1.92		36.9	0.12	55	0.18	5.7	6	22	21	0.23	4.25
3.2.92		24.0	0.10	58	0.16	5.4	8	8	7	0.80	4.05
18.2.92											
3.3.92		44.0	0.94	32	0.97	5.2	8	32	34	0.00	3.78
18.3.92		37.5	1.32	72	1.39	5.1	0	0	21	0.10	3.80
1.4.92	7.6	37.6	0.85	59	0.91	5.2	16	14	21	0.35	3.90
14.4.92		40.0	0.06	41	0.10	4.5	0	29	39	0.80	
28.4.92	7.6	36.0	1.36	20	1.38	5.3	14	2	3	0.30	4.00
12.5.92		40.0	0.04	28	0.07		7	11	77	0.10	4.00

Appendix 3 Rostherne Mere

Date	pH	Cl	NO3	NH4	DIN	SiO2	SRP	TSP	TP	PAlk	TAlk
10.1.90		40.8				2.00	344				
25.1.90											
7.2.90		40.8	0.87	50	0.92	2.00	378	376	410	0.00	
21.2.90		41.7		0			371	380	408	0.00	2.20
7.3.90		54.7	0.92	23	0.94	1.70	380		419	0.03	2.20
21.3.90	7.6	42.9	1.02	0	1.02	1.50	344	360	353	0.03	2.20
4.4.90		40.8	0.59	0	0.59	0.90	360	390	384	0.00	2.20
18.4.90	8.3	40.4	0.88	27	0.91	0.30	370	453	445	0.00	2.20
27.4.90											
2.5.90	8.3	43.3	0.95	30	0.98	0.30	369	380	390	0.03	2.30
16.5.90	8.4	43.8	1.06	0	1.06	0.30	331	359	398	0.05	2.30
29.5.90	9.1	45.8	0.93	0	0.93	0.50	258	271	466	0.30	2.60
12.6.90	9.0	43.3	0.89	32	0.92	0.50	476	505	615	0.18	2.40
27.6.90		37.5	0.77	75	0.85	0.90	233	274	304	0.35	2.45
11.7.90	8.4	45.4	0.69	86	0.78	0.60	293	365	352	0.13	2.35
25.7.90	9.3	43.8	0.66	38	0.70	0.70	217	243	303	0.28	2.33
8.8.90	9.5	45.8	0.27	19	0.29	1.05	145	180	273	0.30	2.25
21.8.90	9.3	45.8	0.19	7	0.20	0.90	98	115	169	0.30	2.05
6.9.90	9.4	45.8	0.00	24	0.02	1.20	110	116	183	0.45	2.05
24.9.90	9.1	43.3	0.21	12	0.22	1.50	202	234	348	0.25	2.15
9.10.90	9.0	43.3	0.13	9	0.14	0.99	222	251	339	0.20	2.30
22.10.90	9.0	44.7	0.25	13	0.26	1.12	236	247	324	0.28	2.25
6.11.90	8.6	44.9	0.48	112	0.59	1.42	290	340	465	0.10	2.40
20.11.90	7.9	45.4	0.69	289	0.98	1.35	374	414	440	0.00	2.25
5.12.90	7.9	45.4	0.43	373	0.80	1.45	409	442	425	0.05	2.40
7.1.91	8.0	42.9	0.65	373	1.02	1.55	402	418	422	0.00	2.30
22.1.91	8.0	41.2	1.48	226	1.71	1.71	390	393	401	0.00	2.30
5.2.91	7.8	43.3	1.43	16	1.45	2.00	385	431	417	0.00	2.18
19.2.91	8.0	45.0	1.29	0	1.29	1.86	397	422	425	0.00	2.20
5.3.91	8.0	44.9	1.03	0	1.03	1.84	417	434	438	0.00	2.20
19.3.91	8.2	47.9	1.19	0	1.19	1.79	401	427	418	0.00	2.20
2.4.91	8.1	44.9	1.89	0	1.89	1.67	391	392	442	0.03	2.33
16.4.91	8.5	46.9	1.08	3	1.09	0.97	370	340	433	0.03	2.25
30.4.91	8.4	40.8	0.93	0	0.93	0.96	360	338	392	0.10	2.23
14.5.91	8.2	46.9	0.77	49	0.82	0.76	370			0.00	2.28
27.5.91	8.5	47.4	0.96	18	0.98	0.86	326	305	357	0.10	2.30
11.6.91	8.6	44.9	0.83	29	0.86	0.66	312	338	429	0.15	2.25
25.6.91	8.7	40.0	1.21	16	1.23	0.72	302	313	357	0.10	2.33
9.7.91	8.8	44.9	1.14	25	1.16	0.46	319	313	356	0.18	2.33
22.7.91	8.9	46.9	0.68	0	0.68	1.12	268	306	336	0.18	2.43
6.8.91		46.9	0.10	1	0.10	1.00	160	205	319	0.70	2.50
19.8.91	9.7	45.4	0.06	5	0.06	1.92	162	184	305	0.70	3.15
9.9.91	9.7	47.9	0.03	20	0.05	1.49	134	146	238	1.33	3.88
23.9.91	9.6	44.9	0.00	94	0.09	1.39	193	203	257	0.90	3.30
9.10.91	9.3	45.7	0.13	0	0.13	1.84	245	291	380	0.95	4.15
22.10.91	8.7	47.4	0.26	52	0.31	1.08	301	391	453	0.55	3.35
5.11.91	8.4	36.4	0.23	231	0.46	2.73	355	360	488	0.20	3.18
19.11.91	8.1	46.9	0.23	607	0.84	2.11	610	646	847	0.18	3.20
3.12.91	7.9	44.0	0.34	543	0.88	2.09	426	416	462	0.00	2.80
18.12.91	7.9	46.5	0.37	537	0.91	2.27	486	581	696	0.13	2.68
9.1.92	7.5	51.0	0.88	165	1.04	2.51	453	532	530	0.00	2.50
21.1.92	7.7	40.8	0.89	0	0.89	2.26	510	719	861	0.00	2.50
3.2.92	7.6		0.74	0	0.74	2.33	492	515		0.20	2.45
18.2.92	7.7	50.5	1.04	22	1.06		555		643	0.40	2.90
3.3.92	7.8	44.0	0.87	52	0.92	1.99	477	612	744	0.00	
18.3.92	8.3	62.5	1.44	100	1.54	2.95	505	726	829	0.40	2.70
1.4.92	8.0	45.5	1.37	93	1.47	2.73	451	453	480	0.10	2.35

Appendix 3 Rostherne Mere

Date	Chla	Caro	480:663	430:410	WatLev	Secchi
10.1.90					0.96	5.0
25.1.90						
7.2.90					1.05	2.1
21.2.90	3	5	1.80	1.11	0.98	2.8
7.3.90	4	5	1.40	1.15	0.90	2.8
21.3.90	8	12	1.60	1.19	0.76	2.6
4.4.90	11	17	1.70	1.19	0.72	3.0
18.4.90	15	19	1.40	1.23	0.70	2.6
27.4.90						
2.5.90	1	3	4.30	1.04	0.66	6.0
16.5.90	8	15	2.10	1.12	0.66	3.5
29.5.90	43	45	1.20	1.28	0.64	1.1
12.6.90	25	37	1.60	1.19	0.67	1.4
27.6.90	8	12	1.70	1.19	0.70	3.2
11.7.90	7		1.70	1.10	0.70	3.2
25.7.90	25	40	1.70	1.26	0.66	1.3
8.8.90	47	65	1.50	1.25	0.61	1.0
21.8.90	35	49	1.50	1.28	0.69	1.3
6.9.90	41	65	1.80	1.30	0.71	1.0
24.9.90	71	94	1.50	1.30	0.77	1.0
9.10.90	33	63	2.10	1.35	0.86	1.1
22.10.90	18	30	1.90	1.23	0.87	1.3
6.11.90	11	26	2.50	1.24	1.06	1.3
20.11.90	5	10	2.20	1.00	1.20	1.6
5.12.90	0	0			1.06	4.5
7.1.91	0	2			1.10	1.8
22.1.91	1	5			0.95	
5.2.91	0	1			0.82	
19.2.91	0	0			0.77	
5.3.91	0	2	4.50	1.00	0.82	2.2
19.3.91	2	3	2.40	1.10	0.86	2.8
2.4.91	5	8	1.80	1.17	0.80	3.1
16.4.91	0	13		1.38	0.74	2.1
30.4.91	5	10	2.00	1.18	0.69	3.9
14.5.91	0	1	5.00	0.80	0.70	8.2
27.5.91	10	14	1.50	1.04	0.69	4.5
11.6.91	21	24	1.20	1.16	0.69	2.3
25.6.91	17	22	1.40	1.23		2.8
9.7.91	18	22	1.40	1.14	0.80	
22.7.91	22	29	1.40	1.00	0.77	2.7
6.8.91	69	97	1.60	1.34	0.74	1.0
19.8.91	77	93	1.30	1.34		1.0
9.9.91	35	66	2.10	1.30		1.9
23.9.91	43	72	1.90	1.30	0.65	1.2
9.10.91	35	69	2.20	1.17		0.9
22.10.91	25	49	2.00	1.28	0.73	1.1
5.11.91	22	52	2.70	1.10		1.0
19.11.91	1	10	10.30	1.04	0.86	1.7
3.12.91	0	3		0.90	0.87	3.5
18.12.91	0	5	15.00	0.80	0.86	2.5
9.1.92	2	7	3.50	0.90	1.10	
21.1.92	0	2		0.70	0.93	3.4
3.2.92	0	2	6.00	0.80	0.81	3.5
18.2.92	0	2	7.00	1.00	0.83	3.6
3.3.92	3	9	2.90	0.90	0.82	3.5
18.3.92	4	9	2.40	0.94	0.86	3.6
1.4.92	2	5	3.20	0.95	0.87	4.2

Appendix 3 Outflow RM

Date	pH	Cl	NO3	NH4	DIN	SiO2	SRP	TSP	TP	PAlk	TAlk	Flow
10.1.90												
25.1.90		44.2	1.32			3.3	252	307	600	0.00		
7.2.90		38.8	0.95	52	1.00	3.1	320	342	497	0.00		
21.2.90		41.7	0.85	0	0.85	2.2	348	358	383	0.00	2.15	
7.3.90		54.7	0.90	13	0.91	1.7	344	405	497	0.03	2.10	0.293
21.3.90		42.9	0.94	290	1.23	1.1	310	319	366	0.15	2.23	0.151
4.4.90		42.9	0.53	0	0.53	0.7	332	342	348	0.05	2.20	0.108
18.4.90		42.4	0.70	36	0.74	0.3	353	410	401	0.05	2.25	0.106
2.5.90		43.3	0.97	0	0.97	0.3	350	374	361	0.10	2.33	0.069
16.5.90		43.8	0.85	0	0.85	0.4	302	331	475	0.18	2.35	0.060
29.5.90		41.7	1.02	151	1.17	0.4	280	292	340	0.15	2.50	0.052
12.6.90		43.3	0.67	770	1.44	0.8	650	642	801	0.05	2.53	0.072
27.6.90		43.8	0.71	266	0.98	1.1	296	269	277	0.05	2.45	0.081
11.7.90		41.2	0.65	120	0.77	0.7	293	330	377	0.08	2.50	0.071
25.7.90		43.8	0.39	40	0.43	0.9	190	277	549	0.35	2.50	0.061
8.8.90		43.8	0.19	31	0.22	1.0	177	227	324	0.40	2.40	0.048
21.8.90		45.8	0.60	20	0.62	1.3	129	140	193	0.10	2.00	0.067
6.9.90		41.7	0.04	15	0.06	1.4	143	147	226	0.20	2.05	0.067
24.9.90		43.3	1.90	106	2.01	2.1	237	280	436	0.00	1.90	0.093
9.10.90		45.4	0.40	45	0.45	1.2	225	250	405	0.05	2.28	0.081
22.10.90		44.7	0.35	33	0.38	1.2	243	246	322	0.20	2.30	0.145
6.11.90		44.9	0.94	102	1.04	2.0	232	280	319	0.00	2.15	0.078
19.11.90		43.3	3.41	133	3.54	2.4	229	261	289	0.00	1.90	0.297
5.12.90		41.2	0.64	193	0.83	1.6	354	350	366	0.05	2.40	0.151
7.1.91		44.9	1.18	218	1.40	2.0	345	364	371	0.00	2.25	0.376
22.1.91		45.4	1.37	152	1.52	1.8	375	376	417	0.00	2.20	0.262
5.2.91		45.4	0.80	30	0.83	2.1	359	389	409	0.00	2.23	0.240
19.2.91		49.0	1.44	21	1.46	1.9	366	377	432	0.00	2.23	0.163
5.3.91		44.9	1.45	20	1.47	1.9	347	350	403	0.00	2.20	0.208
19.3.91		47.9	1.69	32	1.72	1.9	311	325	368	0.00	2.10	0.288
2.4.91		44.9	1.46	29	1.49	1.3	356	385	419	0.03	2.38	0.154
16.4.91		44.9	1.01	9	1.02	0.6	338	367	397	0.13	2.28	0.121
30.4.91		46.9	0.88	0	0.88	0.6	339	348	371	0.10	2.15	0.133
14.5.91		44.9	0.95	57	1.01	0.6	356			0.08	2.18	0.101
27.5.91		45.4	0.98	36	1.02	0.9	341	330	406	0.10	2.33	0.089
11.6.91		46.9	0.77	45	1.22	0.7	312	434	448	0.10	2.48	0.063
25.6.91		44.0	1.37	103	1.47	1.1	316	344	413	0.00	2.33	0.081
9.7.91		44.9	0.79	60	0.85	0.8	304	341	346	0.00	2.40	0.142
22.7.91		49.0	0.87	84	0.95	0.9	298	312	366	0.00	2.55	0.139
6.8.91		44.9	0.20	55	0.26	1.7	217	232	330	0.45	2.05	0.104
19.8.91		45.4	0.10	39	0.14	2.0	192	216	321		2.35	0.062
9.9.91		45.8	0.07	29	0.10	1.6	133	154	196	1.48	3.98	0.076
23.9.91	9.3	46.9	0.03	35	0.07	1.6	188	121	232	0.80	3.30	0.070
9.10.91		52.2	0.19	24	0.21	2.5	258	283	393	0.40	3.25	0.077
22.10.91		47.4	0.16	19	0.18	1.2	309	391	644	0.23	3.15	0.066
5.11.91		46.5		83		2.0	318	345	571	0.00	2.45	0.075
19.11.91		53.0	1.83	288	2.12	2.8	577	601	854	0.00	2.93	0.135
3.12.91		48.0	1.12	240	1.36	2.2	399	393	476	0.00	2.74	0.112
18.12.91		60.6	0.93	257	1.19	2.6	433	553	658	0.00	2.65	0.131
9.1.92		51.0	1.53	48	1.58	2.9	371	417	471	0.00	2.35	0.184
21.1.92		46.6	0.81	20	0.83	2.6	490	851	850	0.00	2.53	0.151
3.2.92			0.90	0	0.90	2.4	445	488	451	0.20	2.50	
18.2.92		50.5	1.68	51	1.73	2.5	514		750	0.30	2.70	0.126
3.3.92		52.0	0.96	2	0.96	2.6	393	473	641	0.00		0.213
18.3.92		50.0	2.34	37	2.38	2.8	415	580	632	0.40	2.70	0.222
1.4.92	7.9	45.5	1.68	19	1.70	2.3	410	304	453	0.10	2.45	0.212

Appendix 4: Phytoplankton and zooplankton data

Phytoplankton taxa were recorded as number per ml. Algal numbers were recorded as either cells, filaments, or colonies, as appropriate to the normal morphology, except for *Actinastrum*, *Scenedesmus*, *Asterionella*, *Diatoma*, and *Tabellaria*, for which cell numbers were counted. Zooplankton taxa were recorded as numbers per litre.

Table A4.1 Phytoplankton taxa recorded during this study. Presence indicated by '+'.

Taxon		Oak Mere (OM)	Mere Mere (MM)	Little Mere (LM)	Rostherne Mere (RM)
Chlorophyta					
Actinastrum sp.	(Act)				+
Ankistrodesmus falcatus (Corda) Ralfs	(Anki)	+	+	+	+
Ankyra judayi (G. M. Sm.) Fott	(Anky)	+	+	+	+
Botryococcus braunni Kütz.	(Botry)	+			
Chlamydomonas spp.	(Chlam)		+	+	+
Chlorella spp.	(Chlor)				+
Closterium spp.	(Clos)		+	+	+
Coelastrum spp.	(Coela)	+	+	+	
Dictyosphaerium sp.	(Dict)		+		
Elakatothrix gelatinosa Wille	(Elak)	+	+	+	+
Eudorina sp.	(Eud)			+	
Gloeocystis sp.	(Gloe)	+		+	
Micractinium sp.	(Micra)			+	
Oocystis sp.	(Oocy)		+	+	+
Pandorina sp.	(Pan)		+		+
Pediastrum spp.	(Ped)		+	+	+
Planktosphaeria sp.	(Pla)			+	
Scenedesmus spp.	(Scen)	+	+	+	+
Selenastrum sp.	(Sel)		+		
Sphaerocystis sp.	(Sph)	+	+		
Staurastrum spp.	(Staur)	+			+
Tetraedron spp.	(Tet)		+	+	+
Volvox sp.	(Vol)	+	+	+	
Euglenophyta					
Euglena sp.	(Eugl)			+	+
Phacus sp.	(Phac)		+	+	+
Trachelomonas sp.	(Trac)		+	+	+
Cryptophyta					
Cryptomonas spp.	(Crypt)	+	+	+	+
Rhodomonas sp.	(Rhod)	+	+	+	+
Unidentified flagellates					
small unidentified flagellates	(μ Flag)	+	+	+	+
Flagellate 1	(Flag1)	+			
Flagellate 2	(Flag2)	+	+		
Pyrrophyta: Dinophyceae (dinoflagellates)					
Ceratium hirundinella (O. F. Müll.) Schrank	(Cer)		+		+
Gymnodinium sp.	(Gym)	+	+	+	
Peridinium sp.	(Per)		+		+
Unidentified dinoflagellate	(UDin)		+		
Chrysophyta: Chrysophyceae					
Dinobryon sp.	(Din)		+		

Table A4.1 continued.

Taxon	Abbrev.	Oak Mere (OM)	Mere Mere (MM)	Little Mere (LM)	Rostherne Mere (RM)
Chrysophyta: Bacillariophyceae (diatoms)					
Achnanthes sp.	(Ach)			+	
Amphora sp.	(Amp)			+	+
Asterionella formosa Hass.	(Ast)	+	+	+	+
Aulacoseira granulata (Ehrenb.) Simonsen (= *Melosira granulata* (Ehrenb.) Ralfs.)	(Au.gr)		+	+	+
Aulacoseira subarctica (O. Muller) E. Y. Haworth, *comb. nov.* (= *Melosira italica* ssp. *subarctica* O. Muller)	(Au.su)		+		
Aulacoseira sp.	(Au)	+			
Diatoma elongatum Agardh	(Dia)		+	+	
Fragillaria crotonensis Kitton	(Frag)		+	+	+
Gomphonema sp.	(Gom)			+	+
Navicula spp.	(Nav)		+	+	+
Nitzschia spp.	(Nit)			+	
Pinnularia spp.	(Pin)	+		+	+
Stephanodiscus hantzschii Grun.	(S.han)		+	+	+
Stephanodiscus neoastrea Hackansson & Hickel	(S.neo)		+	+	+
Surirella sp.	(Sur)	+			
Synedra acus Kutz.	(Sy.ac)		+		+
Synedra ulna (Nitzsch) Ehrenb.	(Sy.ul)	+	+	+	+
Tabellaria sp.	(Tab)	+			
Unidentified centric	(Cen)		+	+	+
Cyanobacteria					
Anabaena spp.	(Ana)		+	+	+
Aphanizomenon flos-aquae Ralfs *ex* Born. *et* Flah.	(Aphan)	+	+	+	+
Coelosphaerium naegelianum Unger	(Coelo)		+	+	+
Coelosphaerium sp.	(Coelo)	+			
Microcystis aeruginosa Kutz. emend. Elenkin	(Mic)				+
Planktothrix agardhii (Gom.) Anagn. et Kom. (= *Oscillatoria agardhii* Gom.)	(Plank)		+	+	+
Unidentified Chroococcaceae	(Chroo)	+			+

Table A4.2 Zooplankton taxa recorded in this study. Presence indicated by '+'.

Taxon		Oak Mere (OM)	Mere Mere (MM)	Little Mere (LM)	Rostherne Mere (RM)
Cladocera:					
Bosmina longirostris (O. F. Müller) s. str.	(Bos.lo)		+	+	+
Bosmina coregoni var. *obtusirostris* (Sars)	(Bos.ob)	+			
Ceriodaphnia dubia Richard	(Cer.du)		+		
Ceriodaphnia sp.	(Cerio)	+		+	
Chydorus sphaericus (O. F. Müller)	(Chy.sp)				+
Chydorus sp.	(Chyd)	+	+	+	
Daphnia cucullata Sars	(D.cuc)	+	+	+	+
Daphnia longispina aggregate	(D.lon)	+	+	+	+
Daphnia magna Straus	(D.mag)			+	
Daphnia pulex (De Geer)	(D.pul)	+	+	+	+
Diaphanosoma brachyurum Lieven	(Diaph)	+	+	+	+
Leptodora kindtil (Focke)	(Lepto)	+	+		+
Calanoid copepods:					
Diaptomus gracilis Sars	(Di.gra)	+	+	+	+
Cyclopoid copepods:					
Unidentified cyclopoids	(Cyclo)	+	+	+	+

Plate A4.1a *Aulacoseira granulata* (Ehrenb.) Simonsen, Mere Mere 9/10/90. Scale bar = 0.58 µm.

Plate A4.1b *Aulacoseira subarctica* (O. Müller) E. Y. Haworth, *comb. nov.*, Mere Mere 9/10/90. Scale bar = 0.625 µm.

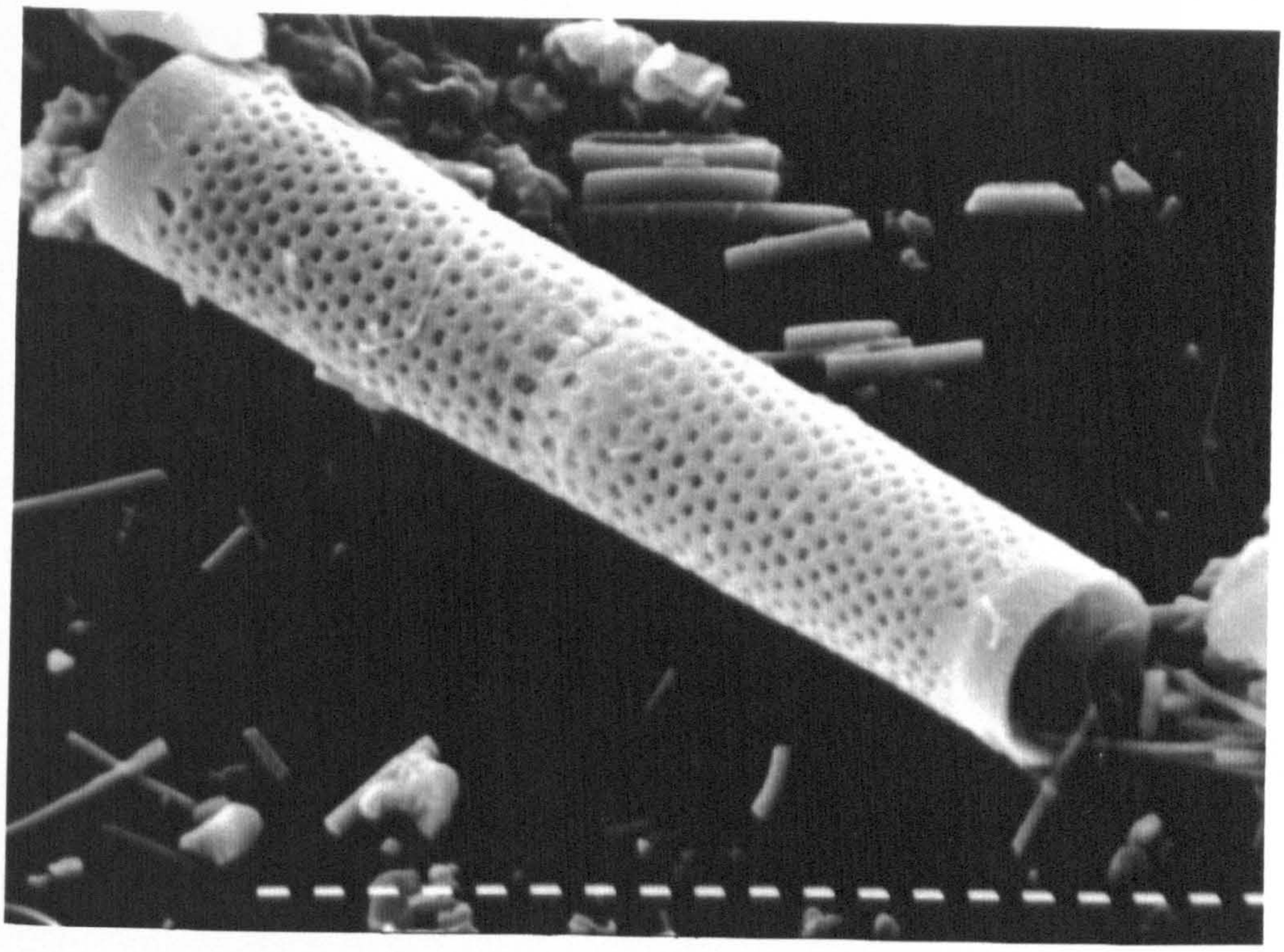
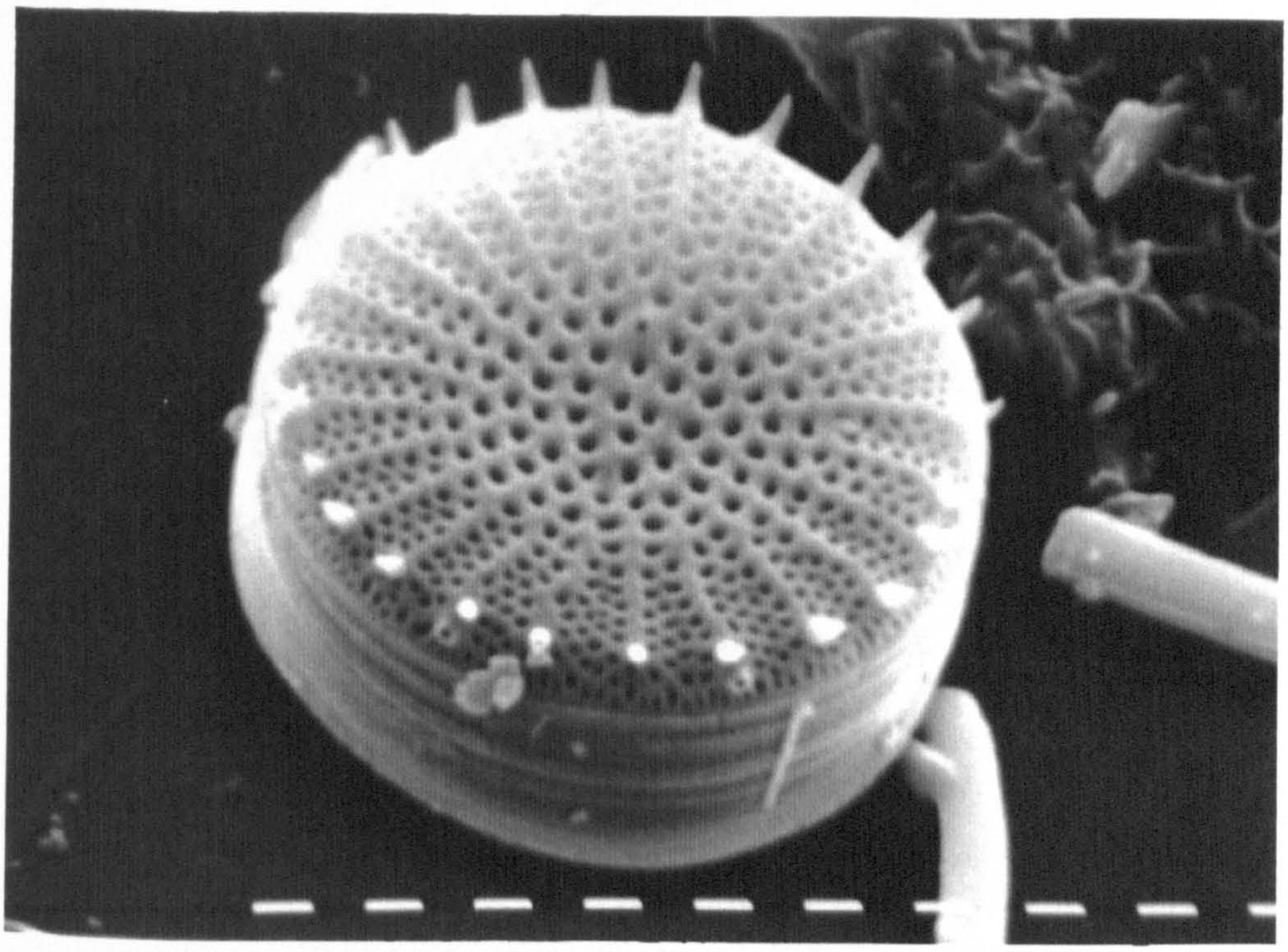
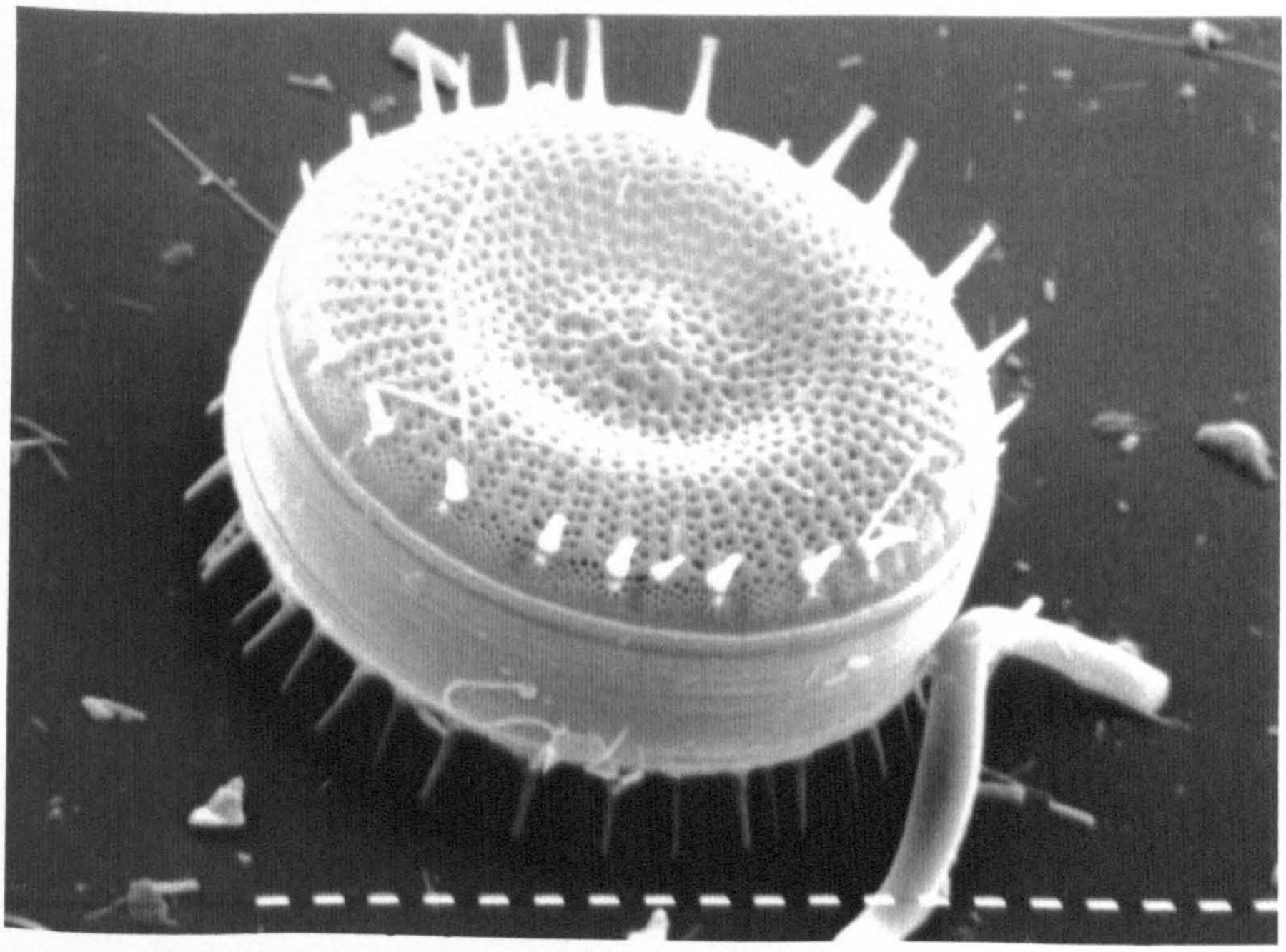


Plate A4.2a *Stephanodiscus hantzschii* Grun.,
Little Mere 27/5/91. Scale bar = 0.625 µm.

Plate A4.2b *Stephanodiscus neoastrea* Hackansson & Hickel,
Rostherne Mere 18/4/90. Scale bar = 1 µm.





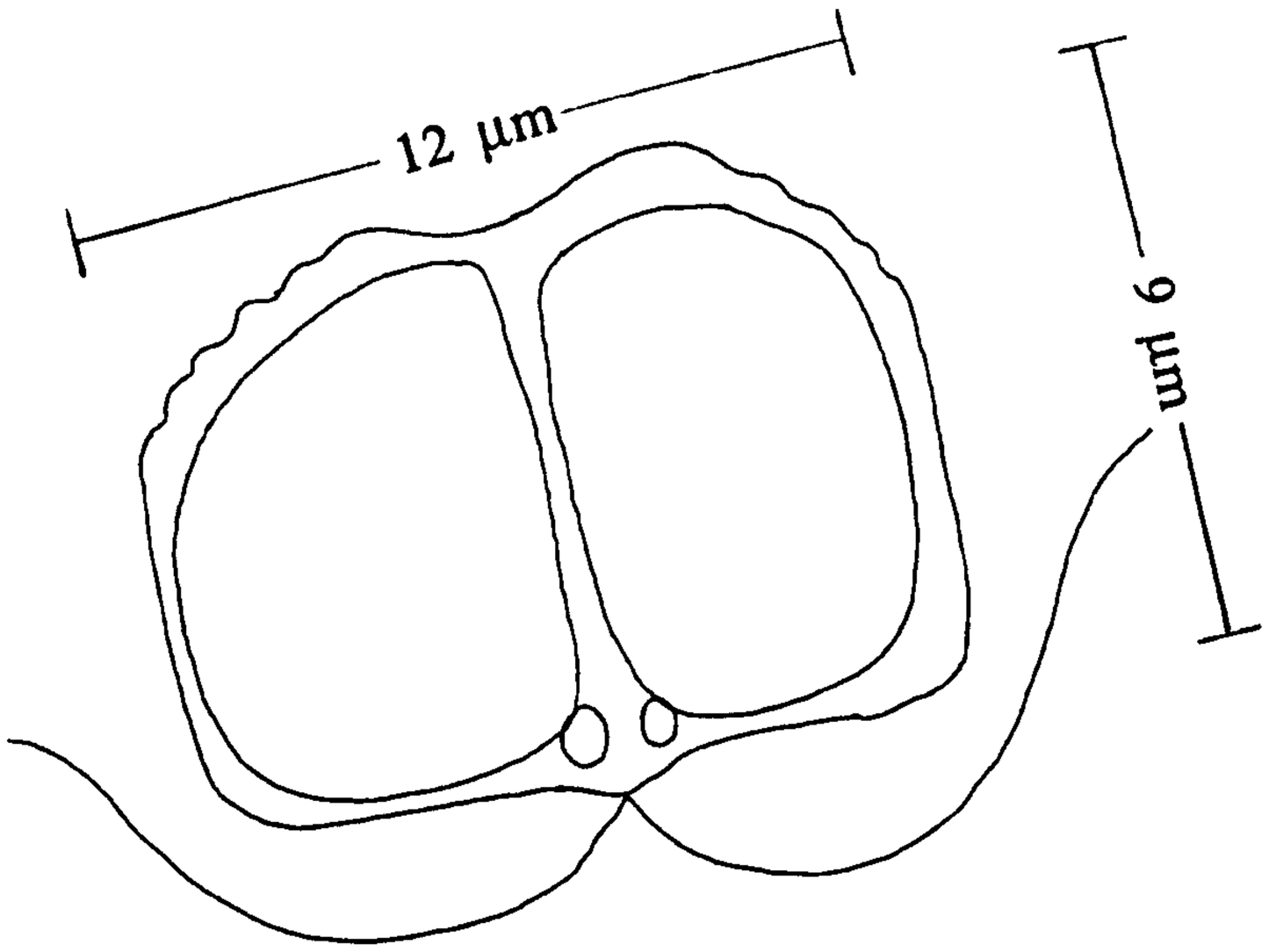


Fig. A4.1a Flagellate 1, Oak Mere 18/2/92

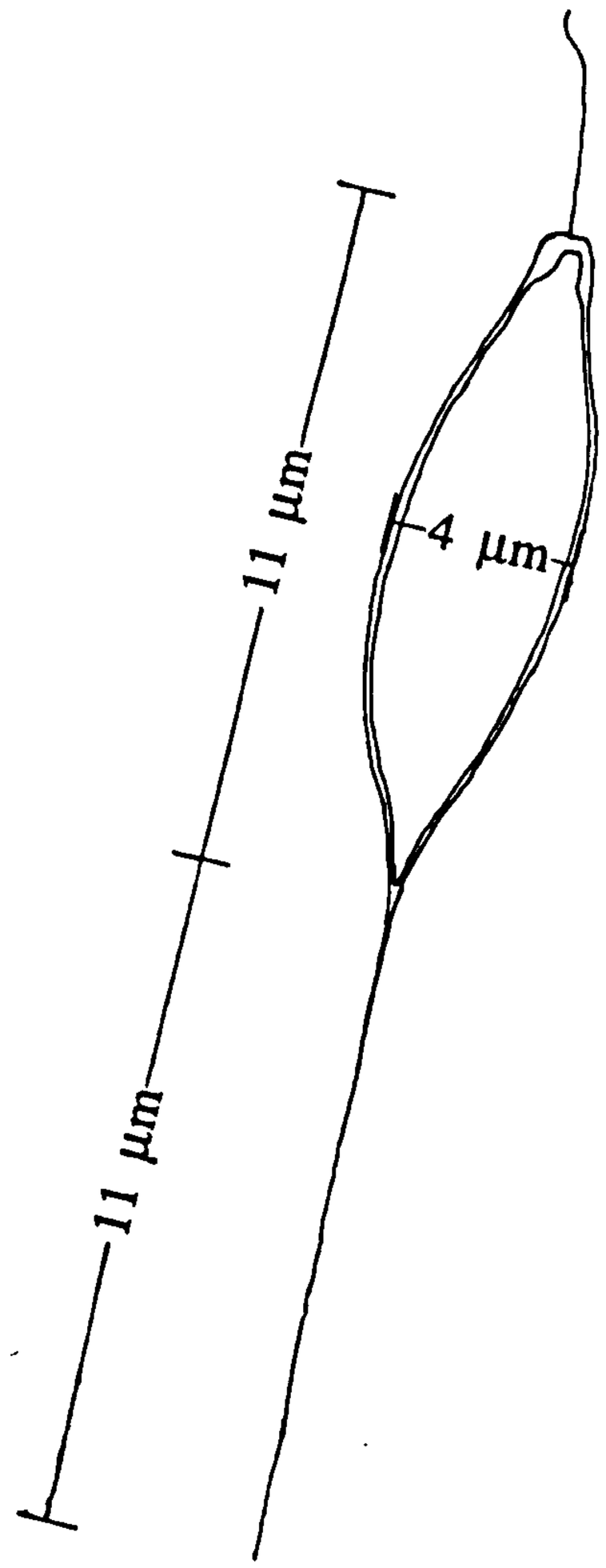


Fig. A4.1b Flagellate 2, Mere Mere 18/2/92

Appendix 4. OM Chlorophyta

Date	Anki	Anky	Botry	Coela	Elak	Gloe	Scen	Sph	Staur
10.1.90	343	0	0	0	0	0	0	0	0
25.1.90	164	0	0	0	0	0	0	0	0
7.2.90	93	0	0	0	0	0	0	0	0
21.2.90	101	0	0	0	0	0	0	0	0
7.3.90	164	0	0	0	0	0	0	0	0
21.3.90	214	13	0	0	0	0	0	0	0
4.4.90	161	0	0	0	0	0	0	0	0
18.4.90	811	0	0	0	0	0	0	0	0
2.5.90	72377	0	0	0	0	0	0	0	0
16.5.90	402097	0	0	0	0	0	0	0	0
29.5.90	151724	0	0	0	0	0	0	0	0
12.6.90	2078	0	0	0	0	0	0	0	0
27.6.90	45	0	0	0	0	0	0	0	0
11.7.90	54	0	0	0	0	0	0	0	0
25.7.90	0	0	13	0	0	0	0	228	0
8.8.90	161	0	0	0	275	0	27	94	0
21.8.90	94	0	0	0	389	0	54	27	0
6.9.90	22	0	0	0	0	0	0	0	0
24.9.90	0	0	0	0	0	0	0	0	0
9.10.90	0	0	48	0	0	0	0	0	0
22.10.90	36	0	0	0	0	0	29	0	0
6.11.90	11	0	0	0	0	0	0	0	0
20.11.90	26	0	0	0	0	0	0	0	0
5.12.90	15	0	0	0	0	0	0	0	0
21.12.90	22	0	4	0	0	0	0	0	0
7.1.91	52	0	122	0	0	0	0	0	4
22.1.91	52	0	0	0	0	0	22	0	0
5.2.91	15	0	0	0	0	0	0	0	0
19.2.91	37	0	0	0	0	0	0	0	0
5.3.91	145	0	61	0	0	0	45	0	0
19.3.91	45	0	22	0	0	0	0	0	0
2.4.91	0	0	5	0	0	0	10	0	0
16.4.91	0	0	0	0	0	0	0	0	0
30.4.91	0	0	22	0	0	0	0	0	0
14.5.91	0	0	0	0	0	0	0	0	0
27.5.91	0	0	0	0	882	0	0	1184	0
11.6.91	0	0	0	0	3083	0	0	3954	0
25.6.91	0	0	67	0	5428	0	0	12331	0
9.7.91	0	0	22	0	3284	0	89	67	0
22.7.91	0	0	22	7	491	0	0	0	0
6.8.91	0	0	305	0	60	0	0	0	0
19.8.91	0	0	938	0	4825	0	0	0	0
9.9.91	45	0	892	0	4685	134	0	134	0
23.9.91	0	0	536	0	21043	0	0	0	0
9.10.91	831	4021	751	214	0	0	0	0	0
22.10.91	1206	5361	456	0	0	0	0	0	0
5.11.91	891	80	469	13	0	0	0	0	0
19.11.91	894	0	331	0	0	0	0	0	0
3.12.91	413	0	469	0	11	0	0	0	0
18.12.91	412	0	694	0	5	0	0	0	0
9.1.92	278	0	397	0	0	0	0	0	0
21.1.92	0	0	328	0	0	0	0	0	0
3.2.92	0	0	266	0	0	0	0	0	0
18.2.92	10	0	248	0	0	0	0	0	0
3.3.92	345	0	153	0	0	0	0	0	0
18.3.92	0	0	380	0	0	0	89	0	0
1.4.92	0	0	45	0	0	0	0	0	0

Appendix 4. OM Cyanobacteria, Cryptophyta, Pyrrophyta, and Bacillariophyceae

Date	Chroo	Crypt	Rhod	µ Flag	Flag1	Flag2	Gym	Ast	Au	Cen	Pin	Sy.ul	Tab
10.1.90	0	15	819	0	0	0	0	0	0	0	0	0	0
25.1.90	0	7	648	0	0	15	0	0	15	0	0	0	0
7.2.90	0	37	518	7	0	134	0	4	4	0	0	0	0
21.2.90	0	26	127	0	0	164	0	0	0	0	0	0	0
7.3.90	0	45	320	0	0	231	0	30	7	4	0	0	0
21.3.90	0	74	67	0	0	40	0	322	0	0	0	0	13
4.4.90	0	60	40	0	0	20	0	469	0	0	0	0	0
18.4.90	0	7	402	369	0	40	0	13	0	0	0	0	27
2.5.90	0	0	0	0	0	0	0	0	0	0	0	0	0
16.5.90	0	0	0	0	0	0	0	0	0	0	0	0	0
29.5.90	0	0	536	0	0	0	0	0	0	0	0	0	0
12.6.90	0	0	45	22	0	0	0	0	0	0	0	0	0
27.6.90	0	0	11	0	2616	0	0	0	0	0	0	0	0
11.7.90	0	0	122	0	0	94	0	0	0	0	0	0	0
25.7.90	0	0	389	0	0	0	1166	0	0	0	0	0	0
8.8.90	0	0	54	0	0	147	536	0	0	0	0	13	0
21.8.90	0	40	308	0	0	0	0	0	0	0	0	13	0
6.9.90	0	0	581	0	0	22	27	0	0	0	15	0	0
24.9.90	0	73	6824	0	0	0	73	0	0	0	0	0	0
9.10.90	0	0	6824	0	0	0	0	0	0	0	0	0	0
22.10.90	0	0	319	0	0	0	0	0	0	0	0	0	0
6.11.90	0	0	93	0	0	0	0	0	0	0	0	0	0
20.11.90	0	0	197	0	0	7	30	0	0	0	0	0	0
5.12.90	0	0	186	0	0	15	7	0	0	0	0	0	0
21.12.90	0	4	127	4	0	15	4	0	0	0	0	0	0
7.1.91	638000	0	186	669	0	122	0	0	0	0	0	0	0
22.1.91	0	0	208	0	0	514	7	0	7	0	0	0	0
5.2.91	0	0	0	0	0	294	0	0	0	0	0	11	0
19.2.91	0	37	15	0	0	1169	0	0	0	0	0	0	0
5.3.91	400000	34	45	487	0	0	0	0	11	0	0	11	0
19.3.91	2000000	0	45	0	0	22	0	0	0	0	0	0	0
2.4.91	1883000	60	0	0	0	0	0	0	0	0	0	0	0
16.4.91	1125000	0	0	0	0	0	0	0	0	0	0	0	0
30.4.91	920000	0	0	0	1274	0	0	0	0	0	0	0	0
14.5.91	0	0	0	0	5027	0	4290	0	67	268	0	0	0
27.5.91	908000	0	0	0	268	0	0	0	0	0	0	0	0
11.6.91	494000	0	0	0	0	0	0	0	0	0	0	0	0
25.6.91	0	0	0	0	0	0	0	0	0	0	0	0	0
9.7.91	0	0	0	0	0	0	0	0	0	0	0	0	0
22.7.91	0	0	0	0	0	0	0	0	0	0	0	0	0
6.8.91	0	7	0	0	0	0	0	0	0	0	0	0	0
19.8.91	0	45	0	0	0	0	0	0	0	0	0	0	0
9.9.91	0	45	0	0	0	0	0	0	0	0	0	0	0
23.9.91	0	0	0	0	0	0	0	0	0	0	0	0	0
9.10.91	0	27	0	0	0	0	0	0	0	0	0	0	0
22.10.91	0	0	0	0	0	0	0	0	0	0	0	0	0
5.11.91	0	13	0	0	0	0	0	0	0	0	0	0	0
19.11.91	0	9	0	0	0	0	0	0	0	0	0	0	0
3.12.91	0	34	0	0	0	0	0	0	0	0	0	0	0
18.12.91	0	124	0	0	14	0	0	0	0	0	0	0	0
9.1.92	0	72	0	0	0	0	0	0	0	0	0	0	0
21.1.92	0	90	0	13	0	0	0	0	0	0	0	0	0
3.2.92	0	47	0	2	7	0	2	0	0	0	0	0	12
18.2.92	275000	137	0	0	15	0	0	0	0	0	0	0	5
3.3.92	400000	139	0	14	34	0	0	0	0	0	0	0	0
18.3.92	800000	179	0	0	45	0	0	0	0	0	0	0	0
1.4.92	700000	22	0	0	0	0	0	0	0	0	0	0	0

Appendix 4. OM Zooplankton

Date	Bos.ob	Cerio	Chyd	D.cuc	D.agg	D.pul	Diaph	Lepto	Di.gra	Cyclo
21.2.90	0.0	0.0	0.0	0.0	30.3	0.0	0.0	0.0	14.5	0.3
7.3.90	0.0	0.0	0.0	0.0	15.5	0.0	0.0	0.0	8.6	0.6
21.3.90	0.1	0.0	0.0	0.0	2.8	0.0	0.0	0.0	2.0	0.3
4.4.90	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
18.4.90	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	3.8	0.0
2.5.90	0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.0	31.9	0.0
16.5.90	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0	15.8	0.6
29.5.90	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	13.8	0.6
12.6.90	0.0	0.0	0.0	4.4	0.0	1.5	0.0	0.0	7.7	0.0
27.6.90	0.0	0.0	0.0	0.0	0.0	45.6	11.9	0.0	21.9	0.0
11.7.90	0.0	0.0	0.0	3.3	0.0	4.2	2.7	0.0	16.1	0.2
25.7.90	0.0	0.0	0.0	0.0	0.0	13.0	8.0	0.0	8.5	0.0
8.8.90	0.0	0.0	0.0	0.0	0.0	5.8	29.3	0.0	42.5	0.0
21.8.90	0.0	0.0	0.0	0.1	0.0	5.9	1.0	0.0	2.0	0.1
6.9.90	0.0	0.0	0.0	0.0	0.0	23.8	0.4	0.0	11.9	0.0
24.9.90	0.0	0.0	0.0	0.0	0.0	5.3	0.5	0.1	9.0	0.2
9.10.90	0.0	0.0	0.0	0.0	0.0	24.8	0.0	0.0	19.3	0.2
22.10.90	0.0	0.0	0.0	0.0	0.0	29.7	0.0	0.0	12.4	0.0
6.11.90	0.0	0.0	0.0	0.1	0.0	3.7	0.0	0.0	11.6	0.0
20.11.90	0.0	0.0	0.0	0.0	0.0	3.7	0.0	0.0	7.1	0.0
5.12.90	0.0	0.0	0.0	0.0	0.0	1.4	0.0	0.0	7.2	0.0
7.1.91	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	7.4	0.0
5.3.91	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	14.1	0.0
19.3.91	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.8	0.0
2.4.91	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	8.8	0.0
16.4.91	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	0.0
30.4.91	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.2	0.0
14.5.91	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	28.6	0.0
27.5.91	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	20.2	0.0
11.6.91	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	19.9	0.0
25.6.91	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	36.9	0.0
9.7.91	0.0	0.0	0.0	0.0	0.0	0.0	141.2	0.0	57.9	0.0
22.7.91	0.4	0.0	0.0	0.0	0.0	0.0	31.4	0.0	42.4	0.2
6.8.91	0.0	0.0	0.0	0.0	0.0	0.0	83.4	0.0	27.7	0.0
19.8.91	0.0	0.0	0.0	0.0	0.0	0.0	17.7	0.0	3.1	0.0
9.9.91	0.0	0.0	0.0	0.0	0.0	0.0	16.6	0.0	7.6	0.0
23.9.91	0.5	0.0	0.0	0.0	0.0	0.0	24.2	0.0	12.7	0.0
9.10.91	13.6	0.0	0.0	0.0	0.0	0.0	4.3	0.0	19.9	0.0
22.10.91	101.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	29.7	0.3
5.11.91	143.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.5	0.0
19.11.91	193.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.8	0.0
3.12.91	122.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.9	0.0
18.12.91	76.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.3	0.0
9.1.92	29.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.9	0.0
21.1.92	5.1	0.0	0.0	0.2	0.0	0.0	0.0	0.0	1.0	0.1
3.2.92	5.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0
18.2.92	23.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0
3.3.92	21.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.9	0.1
18.3.92	8.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.5	0.0
1.4.92	49.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	11.9	0.2

Appendix 4. MM Chlorophyta

Date	Anki	Anky	Chlam	Clos	Coela	Dict	Elak	Oocy	Pan	Ped	Scen	Sel	Sph	Tet	Vol
10.1.90	0	0	302	0	0	0	0	0	0	0	0	0	0	0	0
7.2.90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7.3.90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21.3.90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4.4.90	737	0	268	402	0	0	0	0	0	0	268	0	0	0	0
18.4.90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2.5.90	22	0	0	11	0	0	112	0	0	0	89	0	0	0	0
16.5.90	0	0	0	22	0	0	0	0	0	0	0	0	0	0	0
29.5.90	182	182	0	0	0	0	0	182	0	0	730	0	0	0	0
12.6.90	0	22	0	22	0	0	0	45	0	0	89	0	45	0	0
27.6.90	365	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11.7.90	0	45	0	0	0	0	45	67	0	0	0	0	22	0	0
25.7.90	182	179	0	0	0	0	0	22	0	0	0	0	0	0	0
8.8.90	0	0	0	0	0	0	0	0	0	0	0	0	22	0	0
21.8.90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6.9.90	0	0	0	22	0	0	22	0	0	0	89	0	0	0	0
24.9.90	0	0	0	0	0	0		0	0	0	0	0	0	0	0
9.10.90	0	0	0	11	0	0	0	32	45	0	134	0	11	0	0
22.10.90	0	0	0	0	0	0	0	0	365	0	0	0	0	0	0
6.11.90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20.11.90	0	0	0	0	0	0	0	0	0	0	188	0	0	0	0
5.12.90	0	0	0	0	0	0	0	0	0	0	134	34	0	0	0
7.1.91	20	0	0	0	0	0	0	0	0	0	40	20	0	0	0
22.1.91	48	0	0	0	0	0	0	0	0	0	22	7	0	0	0
5.2.91	67	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5.3.91	313	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19.3.91	1028	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2.4.91	670	0	0	0	0	0	0	0	0	0	0	67	0	0	0
16.4.91	268	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30.4.91	0	0	0	0	0	0	0	0	0	0	179	0	0	0	0
14.5.91	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0
27.5.91	0	0	0	0	22	0	0	0	0	0	0	0	0	0	15
11.6.91	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25.6.91	179	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9.7.91	45	45	0	89	45	0	0	0	0	0	0	22	0	0	0
22.7.91	67	0	0	17	17	34	17	0	0	0	0	0	0	0	0
6.8.91	0	0	0	0	34	34	0	0	0	0	134	0	0	0	0
20.8.91	0	0	17	0	17	0	0	0	0	0	34	0	0	0	0
9.9.91	0	0	0	0	11	101	22	0	0	0	45	11	0	11	0
23.9.91	0	0	0	0	0	0	218	0	0	0	302	17	0	0	0
9.10.91	0	0	0	0	0	0	22	0	0	0	112	34	0	11	0
22.10.91	0	11	0	45	22	0	11	11	0	0	89	134	0	0	0
5.11.91	0	0	0	45	0	0	0	0	22	0	89	78	0	0	0
19.11.91	0	0	0	22	11	0	0	0	0	0	0	11	0	0	0
3.12.91	0	0	0	0	0	0	0	0	0	0	40	47	0	0	0
18.12.91	6	0	0	0	0	0	28	3	0	0	22	14	0	0	0
9.1.92	0	0	0	0	0	0	6	0	0	0	81	0	0	0	0
21.1.92	6	0	0	0	0	0	6	0	0	0	28	3	0	0	0
3.2.92	8	0	0	0	0	0	0	0	0	0	0	8	0	0	0
18.2.92	22	0	22	0	0	0	0	0	0	0	0	0	0	0	0
3.3.92	156	0	0	0	0	0	0	0	0	0	89	89	0	0	0
18.3.92	380	67	22	0	0	0	0	0	0	0	179	0	0	22	0
1.4.92	547	22	0	0	0	0	78	0	0	0	0	89	0	123	0

Appendix 4. MM Chrysophyta

Date	Din	Ast	Au	Cen	Dia	Frag	Nav	S.han	S.neo	Sy.ac	Sy.ul
10.1.90	0	67	0	0	0	0	0	0	0	0	0
7.2.90	0	0	0	0	0	0	0	0	0	0	0
7.3.90	0	0	0	0	0	0	0	0	0	0	0
21.3.90	0	0	0	0	0	0	0	0	0	0	0
4.4.90	0	11998	67	67	0	268	268	201	0	0	0
18.4.90	0	10401	0	0	0	0	0	0	0	0	0
2.5.90	45	1039	11	0	0	0	0	0	11	0	0
16.5.90	0	0	0	0	0	0	0	0	0	0	0
29.5.90	0	365	0	0	0	0	0	0	0	0	0
12.6.90	45	145	67	0	0	22	0	11	22	0	0
27.6.90	0	0	0	0	182	0	0	182	0	0	0
11.7.90	0	89	89	0	1966	156	0	0	22	0	0
25.7.90	0	0	0	0	89	22	0	0	0	22	0
8.8.90	0	0	0	0	0	0	0	0	0	0	0
21.8.90	0	0	0	0	0	0	0	0	0	0	0
6.9.90	0	0	67	0	22	0	0	22	0	22	0
24.9.90	0	0	0	0	0	0	0	0	0	0	0
9.10.90	0	11	1095	0	0	11	0	0	0	0	905
22.10.90	0	0	0	0	0	0	0	0	0	0	0
6.11.90	0	182	0	0	0	0	0	0	0	0	0
20.11.90	0	27	261	0	0	0	0	0	0	0	20
5.12.90	0	13	255	0	0	0	0	0	0	0	0
7.1.91	0	27	114	0	0	0	0	7	0	0	0
22.1.91	0	101	26	0	4	0	0	11	0	0	0
5.2.91	0	0	0	0	0	0	0	0	0	0	0
5.3.91	0	10231	89	0	0	0	0	402	0	0	0
19.3.91	0	4870	89	0	45	0	0	0	0	0	0
2.4.91	0	7372	0	0	0	0	0	0	0	0	0
16.4.91	0	2323	0	0	0	45	0	0	0	0	0
30.4.91	0	1072	0	0	0	0	0	0	0	0	0
14.5.91	0	23	0	0	0	0	0	0	0	0	0
27.5.91	0	0	0	0	0	0	0	0	0	0	0
11.6.91	0	11	0	0	0	0	0	0	0	0	0
25.6.91	0	179	0	0	0	0	0	0	0	0	0
9.7.91	0	22	290	67	0	0	0	0	22	0	0
22.7.91	0	503	101	117	0	34	0	0	0	0	0
6.8.91	0	302	101	101	0	101	0	0	0	0	34
20.8.91	0	0	285	17	0	67	0	0	0	0	0
9.9.91	0	22	89	0	0	123	0	0	0	11	0
23.9.91	0	0	251	0	0	67	0	17	0	0	0
9.10.91	0	11	324	0	45	34	0	0	0	0	0
22.10.91	0	346	558	0	112	22	0	123	0	45	0
5.11.91	0	212	268	0	693	67	0	168	0	0	0
19.11.91	0	34	101	0	480	56	0	34	0	0	0
3.12.91	0	13	60	0	261	194	0	47	0	0	0
18.12.91	0	6	0	0	8	11	3	20	0	0	0
9.1.92	0	3	17	0	3	0	0	11	0	0	0
21.1.92	0	0	0	0	0	0	0	17	0	0	0
3.2.92	0	0	0	0	0	0	0	17	0	0	0
18.2.92	0	0	0	0	0	0	0	45	22	0	0
3.3.92	0	0	45	0	45	0	0	2770	22	0	0
18.3.92	0	45	67	67	89	0	0	447	0	0	22
1.4.92	0	380	123	0	89	34	0	279	101	0	11

Appendix 4. MM Euglenophyta, Cryptophyta, Pyrrophyta, and Cyanobacteria

Date	Phac	Trac	Crypt	Rhod	µ Flag	Flag2	Cer	Gym	Per	UDin	Ana	Aphan	Coelo	Plank
10.1.90	0	0	67	369	50	0	0	0	0	0	0	117	17	1056
7.2.90	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7.3.90	0	0	0	0	1460	0	0	0	0	0	0	0	0	0
21.3.90	0	0	0	0	0	0	0	0	0	0	0	0	0	182
4.4.90	0	0	402	1072	402	402	0	0	0	0	0	603	0	0
18.4.90	0	0	365	547	2190	0	0	0	0	0	0	0	0	1139
2.5.90	0	0	22	726	949	0	0	0	0	11	11	0	22	0
16.5.90	0	0	0	2323	268	0	0	0	67	0	0	0	22	78
29.5.90	0	0	182	730	0	0	0	0	0	0	0	0	0	22
12.6.90	0	0	972	693	45	0	78	0	22	0	11	0	56	0
27.6.90	0	0	912	365	365	0	0	0	0	0	182	182	365	34
11.7.90	0	0	514	760	0	0	179	0	45	0	715	0	424	0
25.7.90	0	0	0	182	365	0	223	0	0	0	2815	0	938	290
8.8.90	0	0	179	22	45	0	156	0	22	0	2390	402	134	514
21.8.90	0	0	730	0	182	0	182	0	182	0	365	547	0	67
6.9.90	0	0	112	782	268	0	67	0	45	179	45	246	22	365
24.9.90	0	0	365	0	0	0	182	0	0	182	0	182	0	3172
9.10.90	0	0	503	380	11	0	0	0	22	357	11	22	11	0
22.10.90	0	0	182	182	0	0	0	0	0	0	0	0	0	0
6.11.90	0	0	182	0	0	0	0	0	0	0	0	0	0	0
20.11.90	0	0	369	610	0	0	0	0	0	74	0	7	7	47
5.12.90	0	0	114	241	80	0	0	0	0	20	0	0	0	34
7.1.91	0	0	34	214	13	34	0	0	0	27	0	0	0	20
22.1.91	0	0	7	67	7	97	0	0	0	11	0	7	0	15
5.2.91	0	0	89	201	2100	647	0	0	0	0	0	0	0	22
5.3.91	0	0	134	983	894	313	0		0	0	0	45	0	45
19.3.91	0	0	313	2859	402	89	0	0	0	0	0	0	0	89
2.4.91	67	0	0	335	3552	0	0	0	0	0	0	0	0	201
16.4.91	0	0	0	45	5763	0	0	45	0	0	0	0	0	45
30.4.91	0	0	357	938	2949	0	0	0	0	0	0	0	0	268
14.5.91	0	0	112	63	0	0	0	0	112	0	0	0	0	0
27.5.91	0	0	15	432	37	0	30	0	0	30	0	0	0	0
11.6.91	0	22	89	1251	0	0	67	0	0	0	0	0	11	0
25.6.91	0	0	447	1921	0	0	112	0	0	0	0	0	0	0
9.7.91	0	22	1095	357	0	0	67	0	0	0	179	0	67	0
22.7.91	0	0	1508	1173	0	0	84	0	0	0	737	0	268	0
6.8.91	0	0	268	134	0	0	134	0	0	0	3384	34	1106	34
20.8.91	0	0	168	0	0	0	101	0	0	0	1508	0	117	84
9.9.91	0	0	78	101	0	0	101	0	0	145	235	0	123	257
23.9.91	0	0	754	1324	0	0	17	0	0	134	84	0	0	670
9.10.91	0	0	78	357	0	0	0	0	212	0	0	0	101	201
22.10.91	0	0	78	257	0	0	0	0	0	34	0	0	56	34
5.11.91	0	0	101	369	78	0	0	0	0	34	22	0	56	22
19.11.91	0	0	45	223	190	0	0	0	0	11	11	0	0	0
3.12.91	0	0	13	80	201	20	0	0	0	0	0	0	13	7
18.12.91	0	0	6	106	47	0	0	0	0	8	0	0	0	14
9.1.92	0	0	0	151	36	0	0	0	0	0	3	0	17	0
21.1.92	0	0	8	246	36	0	0	0	0	3	0	0	11	8
3.2.92	0	0	8	1005	117	42	0	0	0	0	0	0	8	0
18.2.92	0	0	45	1921	0	938	0	0	0	0	0	0	0	22
3.3.92	0	0	45	1117	134	134	0	0	0	0	0	0	0	0
18.3.92	0	0	89	1340	625	0	0	0	22	0	0	0	0	112
1.4.92	0	0	11	302	101	0	0	0	0	11	34	0	0	168

Appendix 4. MM Zooplankton

Date	Bos.lo	Cer.du	Chyd	D.cuc	D.lon	D.pul	Diaph	Lept	Di.gra	Cyclo
7.3.90	19.7	0.0	0.0	0.0	9.3	0.0	0.0	0.0	22.9	2.5
21.3.90	66.3	0.0	0.0	0.0	18.1	0.0	0.0	0.0	32.1	48.2
18.4.90	0.1	0.0	0.0	0.0	1.3	0.0	0.0	0.0	3.0	1.8
2.5.90	0.0	0.0	0.0	6.0	2.2	0.0	0.0	0.0	13.8	5.6
16.5.90	0.0	0.5	0.0	27.7	1.0	0.0	0.0	0.0	3.6	11.4
29.5.90	0.0	0.0	0.0	5.6	0.0	0.0	0.0	0.0	2.0	0.4
12.6.90	0.0	0.0	0.0	9.1	0.0	0.0	0.0	0.0	30.4	2.6
27.6.90	0.0	0.0	0.0	42.8	0.0	0.0	0.8	0.0	0.8	1.6
11.7.90	0.0	0.0	0.0	7.3	0.0	0.1	0.0	0.0	0.9	0.2
25.7.90	0.0	0.0	0.0	24.5	0.0	0.0	0.5	0.0	0.9	1.9
8.8.90	0.0	0.0	0.0	19.7	0.0	0.0	0.6	0.0	1.1	0.2
21.8.90	0.0	0.0	0.0	49.5	0.0	0.0	3.9	0.0	4.3	9.0
6.9.90	0.0	0.0	0.0	9.6	0.0	0.5	0.0	0.0	1.4	4.1
24.9.90	0.0	0.1	0.0	1.4	0.0	0.3	0.0	0.0	1.5	0.4
9.10.90	0.0	28.2	0.0	25.0	0.0	1.4	0.5	0.0	19.4	8.4
22.10.90	0.0	5.9	0.0	0.4	0.0	1.6	0.1	0.0	2.2	0.1
6.11.90	0.0	0.7	0.0	0.9	0.6	0.2	0.0	0.0	27.5	0.0
20.11.90	0.3	0.8	0.1	1.2	0.3	0.5	0.0	0.0	7.0	0.1
5.12.90	0.1	0.5	0.0	0.7	0.0	0.5	0.0	0.0	14.0	0.0
7.1.91	0.2	0.0	0.0	5.1	1.3	0.0	0.0	0.0	26.7	0.2
5.3.91	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	22.6	3.1
19.3.91	4.7	0.0	0.0	2.5	0.0	0.0	0.0	0.0	30.4	14.6
2.4.91	12.4	0.0	0.0	1.4	0.0	0.5	0.0	0.0	17.6	8.5
16.4.91	2.2	0.0	0.0	0.4	0.0	0.0	0.0	0.0	4.2	0.6
30.4.91	1.9	0.0	0.0	1.4	0.0	0.0	0.0	0.0	7.1	0.2
14.5.91	22.9	1.4	0.0	32.4	0.0	0.0	0.0	0.0	26.5	2.8
27.5.91	2.2	1.8	0.0	6.5	1.5	0.0	0.0	0.0	9.3	11.9
11.6.91	0.0	0.3	0.0	8.8	2.0	0.0	0.0	0.0	10.6	3.5
25.6.91	0.0	0.4	0.0	5.0	23.1	0.0	0.0	0.0	8.0	7.1
9.7.91	0.0	0.0	0.0	41.6	4.8	0.0	0.0	0.4	5.9	14.7
22.7.91	0.1	0.0	0.0	7.1	0.0	0.0	0.2	0.1	2.2	2.4
6.8.91	0.0	0.1	0.0	6.3	0.0	0.0	0.2	0.0	0.7	1.8
19.8.91	0.0	0.2	0.0	10.3	0.0	0.0	0.0	0.0	0.7	0.4
9.9.91	0.0	0.4	0.0	8.6	0.0	0.1	0.1	0.0	0.9	2.1
23.9.91	0.4	0.2	0.0	2.5	0.0	0.0	0.1	0.0	2.0	0.5
9.10.91	5.9	0.1	0.0	6.9	0.0	0.0	3.2	0.0	4.3	1.1
22.10.91	1.4	0.0	0.0	4.2	0.0	0.0	0.1	0.0	3.5	2.1
5.11.91	2.5	1.0	0.0	13.5	0.0	0.0	0.0	0.0	8.0	0.2
19.11.91	2.7	0.4	0.0	7.6	0.0	0.0	0.0	0.0	4.7	0.1
3.12.91	1.5	0.1	0.0	2.1	0.0	0.0	0.0	0.0	2.4	0.0
18.12.91	0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.1	0.0
9.1.92	0.2	0.0	0.0	4.1	0.0	0.0	0.0	0.0	3.6	0.0
21.1.92	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0
3.2.92	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
18.2.92	1.3	0.0	0.0	1.4	0.0	0.0	0.0	0.0	9.0	0.1
3.3.92	0.1	0.0	0.0	0.9	0.0	0.0	0.0	0.0	7.3	1.8
18.3.92	1.7	0.0	0.0	5.4	0.0	0.0	0.0	0.0	17.4	6.0
1.4.92	0.4	0.0	0.0	1.3	0.0	0.0	0.0	0.0	4.1	1.4

Appendix 4. LM Chlorophyta

Date	Anki	Anky	Chlam	Clos	Coela	Elak	Eud	Gloe	Micra	Oocy	Ped	Pla	Scen	Tetr	Vol
10.1.90	0	0	24	0	0	0	0	0	0	0	0	0	0	0	0
7.2.90	0	0	46	0	0	0	0	0	0	0	0	0	49	0	0
21.2.90	30	0	61	34	0	0	0	0	0	0	0	0	182	0	0
7.3.90	0	0	168	0	0	0	0	0	0	0	0	0	0	0	0
21.3.90	402	0	0	0	0	0	0	0	402	0	0	0	0	0	0
4.4.90	1217	0	1217	0	0	243	0	243	0	0	0	1460	0	0	0
18.4.90	6569	0	0	0	0	0	1460	0	0	0	0	3650	2920	0	0
2.5.90	1810	201	201	0	201	0	0	0	0	0	0	0	1609	0	0
16.5.90	0	2011	0	0	15383	0	0	0	0	101	0	0	402	0	0
29.5.90	0	0	0	0	9245	0	0	0	0	0	0	0	0	0	0
12.6.90	0	0	0	0	49634	0	0	0	0	0	0	0	730	0	0
27.6.90	0	0	0	0	2866	0	0	0	0	50	0	0	3066	0	0
11.7.90	0	0	0	0	14537	0	0	0	0	61	0	0	365	0	0
25.7.90	0	0	0	0	85	0	0	0	0	0	0	0	0	0	0
8.8.90	0	0	0	0	24	0	0	0	0	0	0	0	0	0	6
21.8.90	0	0	0	0	6	0	0	0	0	0	0	0	49	0	79
6.9.90	0	0	0	0	12	0	0	0	0	0	0	0	30	0	6
24.9.90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9.10.90	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0
22.10.90	0	0	17	0	0	0	0	0	0	0	0	0	0	0	0
6.11.90	6	0	0	6	0	0	0	0	0	0	0	0	0	0	0
20.11.90	0	0	0	18	48	0	0	0	0	0	0	0	0	0	0
5.12.90	0	0	17	0	0	0	0	0	0	0	0	0	25	0	0
7.1.91	0	0	0	0	0	0	0	0	0	0	0	0	34	0	0
22.1.91	0	0	1206	0	0	0	0	0	0	0	0	0	0	0	0
5.2.91	67	0	9786	0	0	0	0	0	0	0	0	0	0	0	0
19.2.91	0	0	13137	0	0	0	0	0	0	0	0	0	0	0	0
5.3.91	142	852	2859	0	0	0	0	0	0	0	0	0	0	0	0
19.3.91	182	55	182	0	0	0	0	0	0	0	0	0	0	0	0
2.4.91	0	255	0	0	0	0	0	0	0	0	0	0	0	0	0
16.4.91	0	158	0	0	0	0	0	0	0	0	0	0	0	0	0
30.4.91	0	122	12	0	0	0	0	0	0	0	0	0	0	0	0
14.5.91	0	1362	0	0	0	0	0	0	0	0	0	0	0	0	0
27.5.91	0	1825	0	0	0	0	0	0	0	0	0	0	0	0	0
11.6.91	0	182	0	0	0	0	0	0	0	0	0	0	0	0	0
25.6.91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9.7.91	0	134	0	0	0	0	0	0	0	0	0	0	0	0	0
22.7.91	0	1906	0	0	0	0	0	0	0	0	0	0	0	0	0
6.8.91	0	426	0	0	41	0	0	0	0	0	0	0	0	0	0
19.8.91	0	292	0	0	0	0	0	0	0	0	0	0	0	0	0
9.9.91	0	24	0	0	0	0	0	0	0	0	0	0	0	0	0
23.9.91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9.10.91	0	36	18	0	0	0	0	0	0	0	0	0	0	0	0
22.10.91	0	73	0	0	0	0	0	0	0	0	0	0	0	0	0
5.11.91	0	61	12	0	0	0	0	0	0	0	0	0	49	0	0
19.11.91	0	0	0	0	0	0	0	0	0	0	18	0	85	6	0
3.12.91	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0
18.12.91	0	0	0	0	0	4	0	0	0	0	0	0	0	4	0
9.1.92	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0
21.1.92	0	0	0	0	0	0	0	0	0	0	0	0	13	0	0
3.2.92	0	0	107	0	0	0	0	0	0	0	0	0	0	0	0
18.2.92	34	0	67	0	0	0	0	0	0	0	0	0	0	0	0
3.3.92	0	0	0	0	0	0	0	0	0	0	0	0	536	0	0
18.3.92	670	0	34	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 4. LM Bacillariophyceae

Date	Ach	Amp	Ast	Au.gr	Cen	Dia	Frag	Gom	Nav	Nit	Pin	S.han	S.neo	Sy.ul
10.1.90	0	0	0	0	0	0	0	0	0	0	0	0	0	12
7.2.90	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21.2.90	0	0	91	0	0	0	0	30	0	0	0	0	0	0
7.3.90	0	0	134	34	402	0	0	0	0	0	0	0	0	0
21.3.90	0	0	0	0	0	0	0	0	0	0	0	129898	0	0
4.4.90	0	0	487	0	0	0	0	0	0	0	0	21898	0	0
18.4.90	0	0	0	0	0	0	0	0	0	0	0	730	0	0
2.5.90	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16.5.90	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29.5.90	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12.6.90	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27.6.90	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11.7.90	0	0	0	0	0	0	61	0	0	0	0	0	0	0
25.7.90	0	0	0	0	0	0	0	0	0	6	0	0	0	0
8.8.90	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21.8.90	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6.9.90	0	0	0	0	0	0	0	0	6	0	0	0	0	0
24.9.90	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9.10.90	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22.10.90	0	0	0	0	0	0	8	0	34	0	8	0	0	0
6.11.90	0	0	0	0	0	0	0	0	12	0	0	0	0	0
20.11.90	0	0	0	0	0	0	0	0	12	0	0	12	0	0
5.12.90	0	0	0	0	0	0	0	8	17	0	0	0	0	8
7.1.91	0	0	17	0	17	0	0	0	8	0	0	17	0	0
22.1.91	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5.2.91	0	0	0	0	67	0	0	0	0	0	0	0	0	0
19.2.91	0	0	0	0	0	0	0	0	134	0	0	335	0	0
5.3.91	0	0	872	0	0	0	61	0	0	0	0	811	0	0
19.3.91	0	0	588	0	1318	0	0	0	0	41	0	223	0	0
2.4.91	0	12	73	0	0	0	0	0	12	0	0	0	0	0
16.4.91	0	0	0	0	0	12	24	0	0	0	0	0	0	49
30.4.91	0	0	0	0	0	0	0	0	0	0	12	109	0	0
14.5.91	0	0	0	0	0	0	0	0	12	0	0	1679	0	0
27.5.91	0	0	0	0	16423	0	0	0	0	0	0	50364	0	365
11.6.91	0	0	0	0	0	0	0	0	0	0	0	353	0	0
25.6.91	91	0	0	0	0	0	0	36	0	0	0	1515	0	91
9.7.91	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22.7.91	0	0	0	0	0	0	0	0	40	0	0	0	0	0
6.8.91	0	0	81	0	0	0	0	0	0	0	0	0	0	0
19.8.91	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9.9.91	0	0	0	0	0	0	0	0	49	0	0	12	0	0
23.9.91	0	0	0	0	0	0	0	0	12	12	0	0	0	0
9.10.91	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22.10.91	0	0	18	0	0	0	0	6	0	9	0	18	0	0
5.11.91	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19.11.91	0	0	6	0	0	0	6	0	0	0	0	0	0	0
3.12.91	0	6	0	0	0	0	0	0	12	0	0	0	0	0
18.12.91	0	0	0	0	0		0	0	9	0	0	4	0	0
9.1.92	0	0	4	0	0	0	0	4	0	0	0	0	0	0
21.1.92	0	0	0	0	0	0	0	0	34	0	0	13	0	0
3.2.92	0	0	0	0	0	0	0	0	161	0	0	161	0	0
18.2.92	0	0	0	0	0	0	0	0	0	0	0	771	0	0
3.3.92	0	0	0	0	0	0	0	0	134	0	0	26270	0	0
18.3.92	0	0	0	0	0	0	0	0	0	0	0	469	34	0

Appendix 4. LM Euglenophyta, Cryptophyta, Pyrrophyta, and Cyanobacteria

Date	Eugl	Phac	Trac	Crypt	Rhod	µ Flag	Gym	Ana	Aphan	Coelo	Plank
10.1.90	0	0	0	12	24	1448	0	0	207	0	560
7.2.90	0	0	0	137	46	5383	0	0	228	0	867
21.2.90	0	0	0	61	547	2981	0	0	61	0	1095
7.3.90	0	0	0	168	1575	4022	0	0	101	0	1441
21.3.90	0	402	0	1206	5630	4826	0	0	0	402	804
4.4.90	0	0		18978	30900	18735	0	0	0	0	973
18.4.90	0	0	0	19708	11679	12409	0	0	0	0	1460
2.5.90	0	0	0	804	4826	402	0	0	0	0	0
16.5.90	0	0	0	101	0	0	0	0	0	0	0
29.5.90	0	0	0	912	182	0	0	0	0	0	0
12.6.90	0	0	0	0	547	0	0	0	0	0	0
27.6.90	0	0	0	2966	100	100	0	0	0	0	0
11.7.90	0	0	0	0	0	61	0	0	0	0	0
25.7.90	0	0	18	0	0	18	0	0	0	0	6
8.8.90	0	0	0	0	6	0	0	0	0	0	0
21.8.90	0	0	0	0	0	0	0	0	0	0	6
6.9.90	0	0	0	6	49	0	0	0	0	0	0
24.9.90	0	0	0	0	13	0	0	0	0	0	0
9.10.90	0	0	0	8	0	0	0	0	0	0	0
22.10.90	0	0	0	0	8	8	0	0	0	0	0
6.11.90	0	0	0	18	24	18	0	0	0	0	6
20.11.90	0	0	0	18	43	30	0	0	0	0	0
5.12.90	0	0	0	0	0	42	0	0	0	0	8
7.1.91	0	8	0	8	17	67	0	0	0	0	17
22.1.91	0	0	402	0	0	12400	0	0	0	0	0
5.2.91	67	0	0	67	0	4156	0	0	0	0	67
19.2.91	0	0	134	0	134	1005	0	0	0	0	0
5.3.91	0	0	0	142	81	1054	0	0	0	0	162
19.3.91	0	0	0	345	81	527	0	0	0	0	81
2.4.91	0	0	0	24	0	146	0	0	0	0	12
16.4.91	0	0	0	0	0	36	12	0	0	0	0
30.4.91	0	0	0	0	0	12	0	0	0	0	12
14.5.91	0	0	0	0	12	0	0	0	0	0	0
27.5.91	0	0	0	0	0	0	0	0	0	0	0
11.6.91	0	0	0	0	85	146	0	0	0	0	0
25.6.91	0	0	0	0	0	219	0		0	0	36
9.7.91	0	0	0	0	24	24	0	0	0	0	0
22.7.91	0	0	0	41	1318	41	0	0	20	0	0
6.8.91	0	0	0	0	142	101	0	81	41	0	0
19.8.91	0	0	0	24	158	36	0	0	0	0	12
9.9.91	0	0	0	97	49	61	0	12	0	0	12
23.9.91	0	0	0	36	426	36	0	0	0	0	0
9.10.91	0	0	0	0	408	36	0	0	0	0	6
22.10.91	0	0	0	18	1022	36	0	0	0	0	0
5.11.91	0	0	0	12	97	49	0	0	0	0	12
19.11.91	0	0	6	6	73	24	0	0	0	0	0
3.12.91	0	0	12	18	109	12	0	0	0	0	0
18.12.91	0	0	0	4	107	31	0	9	0	0	0
9.1.92	0	0	0	9	223	18	0	4	0	0	4
21.1.92	0	0	0	34	737	7	0	0	0	0	0
3.2.92	0	0	0	0	1850	107	0	0	0	0	0
18.2.92	0	0	0	34	1977	168	0	0	0	0	0
3.3.92	0	0	0	268	1608	402	0	0	0	0	0
18.3.92	0	0	0	235	2245	302	0	0	0	0	0

Appendix 4. LM Zooplankton

Date	Bos.lo	Cerio	Chyd	D.cuc	D.lon	D.mag	D.pul	Diaph	Di.gra	Cyclo
18.4.90	1.0	0.0	0.0	0.0	4.1	0.0	0.0	0.0	0.0	107.5
2.5.90	0.0	0.0	0.0	2.8	249.1	0.0	0.0	0.0	5.5	362.5
16.5.90	0.0	0.0	0.0	0.0	19.1	0.0	0.0	0.0	0.3	28.1
29.5.90	0.0	0.0	0.0	1.7	187.7	0.0	0.0	0.0	3.4	0.0
12.6.90	0.0	0.0	0.0	0.0	14.3	0.0	0.0	0.0	3.8	8.1
27.6.90	0.0	0.0	0.0	1.6	23.8	0.0	0.0	1.6	1.6	187.0
11.7.90	0.0	0.0	0.0	2.6	13.4	14.6	0.0	0.0	0.9	1.6
25.7.90	0.0	0.0	0.0	0.0	6.4	127.1	0.0	0.0	0.0	7.6
8.8.90	0.0	0.0	0.0		0.0	449.2	0.0	0.0	0.0	0.0
21.8.90	0.0	14.3	0.0	0.0	3.2	58.5	0.0	0.0	0.5	1.4
6.9.90	0.0	9.1	0.0	3.5	2.7	7.6	0.0	0.1	0.9	2.7
24.9.90	0.0	0.9	0.0	0.2	5.3	1.0	0.0	0.0	1.5	0.8
9.10.90	0.0	8.0	0.0	0.3	0.0	51.6	12.8	0.0	1.7	1.0
22.10.90	0.0	6.5	0.0	0.5	0.0	0.4	1.7	0.0	2.6	0.7
20.11.90	0.0	0.7	0.0	0.1	3.6	0.0	0.9	0.0	1.0	3.2
5.12.90	0.0	0.0	0.0	0.0	2.4	0.0	0.2	0.0	1.3	1.1
7.1.91	0.0	0.0	0.0	0.5	1.9	0.1	0.4	0.0	3.9	0.7
5.3.91	0.1	0.0	0.0	0.0	1.2	0.0	0.0	0.0	1.8	0.7
19.3.91	0.4	0.0	0.0	0.0	24.8	5.1	1.3	0.0	1.5	23.8
2.4.91	3.8	0.0	0.0	0.0	14.4	2.3	0.0	0.0	7.0	2.8
16.4.91	0.9	0.0	0.0	0.0	2.3	51.6	1.8	0.0	1.8	1.4
30.4.91	0.3	0.0	0.0	0.0	2.3	29.9	0.0	0.0	1.1	1.6
14.5.91	0.0	0.0	0.0	0.0	1.3	25.6	0.0	0.0	1.1	1.1
27.5.91	0.0	0.0	0.0	0.0	1.2	0.7	0.0	0.0	1.2	1.1
11.6.91	0.0	0.0	0.0	2.7	10.2	26.5	3.4	0.0	2.1	99.8
25.6.91	0.0	0.0	0.0	0.9	0.0	36.4	0.0	0.0	1.8	0.9
9.7.91	0.0	0.0	0.0	11.0	0.5	19.5	0.0	0.5	1.0	4.7
22.7.91	0.0	0.0	0.0	0.0	0.0	75.7	0.0	0.0	1.8	0.6
6.8.91	0.0	0.8	0.0	0.7	0.0	3.3	0.0	0.1	0.4	8.3
20.8.91	0.0	2.2	0.0	1.5	2.8	26.7	0.0	0.0	0.0	1.5
9.9.91	0.0	0.1	0.0	1.4	0.7	0.5	0.8	0.0	0.5	0.0
23.9.91	0.0	0.4	0.0	0.2	0.9	1.0	1.0	0.0	0.5	0.1
9.10.91	21.5	0.5	0.0	1.4	0.5	23.9	0.0	27.2	15.8	0.3
22.10.91	0.0	0.0	0.0	0.0	0.8	21.8	0.0	0.0	0.6	0.2
5.11.91	1.5	0.0	0.0	0.7	0.1	3.1	0.0	0.0	1.3	0.1
19.11.91	1.0	0.2	0.0	0.9	0.2	0.5	0.0	0.0	0.8	0.0
3.12.91	0.3	0.0	0.0	0.1	0.9	3.3	0.0	0.0	1.2	0.3
18.12.91	0.0	0.0	0.3	0.0	0.2	0.1	0.2	0.0	0.4	0.0
9.1.92	0.1	0.0	0.0	0.2	0.4	0.6	0.1	0.0	0.7	0.0
21.1.92	0.1	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.3	0.1
3.2.92	0.1	0.0	0.0	0.3	0.1	0.0	0.0	0.0	0.1	0.0
18.2.92	1.5	0.0	0.0	0.5	0.0	0.1	0.0	0.0	2.0	0.0
3.3.92	0.0	0.0	0.0	0.6	0.1	0.1	0.0	0.0	2.3	0.9
18.3.92	1.1	0.1	0.0	17.1	2.0	0.1	0.1	0.0	11.9	9.9
1.4.92	1.0	0.0	0.0	10.9	2.5	0.5	0.0	0.0	2.0	0.2

Appendix 4. RM Chlorophyta

Date	Act	Anki	Anky	Chlam	Chlor	Clos	Elak	Oocy	Pan	Ped	Scen	Staur	Tet
10.1.90	0	18	0	0	0	0	0	0	0	0	2	0	6
7.2.90	73	0	0	0	2153	0	0	0	0	0	0	0	0
21.2.90	0	5	0	0	5	5	0	0	0	0	0	0	0
7.3.90	0	7	4	0	26	0	0	0	0	0	7	0	0
21.3.90	0	18	36	0	0	0	0	0	0	0	36	0	0
4.4.90	0	91	0	0	0	0	0	0	0	0	73	0	0
18.4.90	0	61	0	0	0	0	0	0	0	0	170	0	0
2.5.90	0	63	0	0	0	0	0	0	0	0	0	0	0
16.5.90	0	2263	0	0	0	0	0	0	0	0	0	0	0
29.5.90	0	633	0	0	0	0	0	0	0	0	0	0	0
12.6.90	0	175	0	0	0	0	0	0	0	0	0	0	0
27.6.90	0	84	0	0	0	4	0	0	0	0	15	0	0
25.7.90	0	36	0	0	0	0	0	0	0	0	146	142	0
8.8.90	0	55	0	0	0	0	0	0	0	0	49	164	0
21.8.90	0	122	0	0	0	0	0	0	0	0	29	161	0
6.9.90	0	36	0	0	0	0	0	0	0	7	49	29	0
24.9.90	0	73	0	0	0	0	0	0	0	0	0	0	0
9.10.90	0	0	0	0	0	0	0	0	0	0	58	0	4
22.10.90	0	0	0	0	0	0	0	0	0	0	0	0	0
6.11.90	0	0	0	0	0	0	0	0	0	0	0	0	0
20.11.90	0	0	0	0	0	0	0	0	0	0	0	0	0
5.12.90	0	0	0	0	0	0	0	0	0	0	29	0	0
28.12.90	0	0	0	0	0	0	0	0	0	0	0	0	0
7.1.91	0	7	0	0	0	0	0	0	0	0	0	0	0
5.3.91	0	13	0	0	0	0	0	0	0	0	27	0	0
19.3.91	0	27	0	0	0	0	0	0	0	3	0	0	0
2.4.91	0	9	0	119	0	0	0	0	0	0	36	0	0
16.4.91	0	46	0	265	0	0	0	0	0	0	0	0	0
14.5.91	0	292	0	0	0	0	0	0	0	0	0	0	0
27.5.91	0	0	16	15	0	0	58	0	0	0	0	0	0
11.6.91	0	997	0	917	0	0	0	0	0	0	201	0	0
25.6.91	0	50	0	0	0	0	0	0	0	0	0	0	0
9.7.91	0	0	30	0	0	0	6022	0	0	0	0	76	15
22.7.91	0	152	402	0	0	0	0	61	0	0	0	0	0
6.8.91	0	0	0	0	0	0	0	0	0	0	0	134	0
19.8.91	0	0	0	0	0	0	0	0	0	0	0	268	0
9.9.91	0	0	0	0	0	0	0	0	0	0	0	0	0
23.9.91	0	0	0	0	0	0	0	0	0	0	0	0	0
9.10.91	0	0	0	0	0	0	0	0	0	0	0	0	0
22.10.91	0	0	0	0	0	0	0	0	0	0	0	0	0
5.11.91	0	0	0	0	0	0	0	0	0	0	0	0	0
19.11.91	0	0	0	0	0	0	0	0	0	0	0	0	0
3.12.91	0	0	0	0	0	0	0	0	0	0	0	0	0
18.12.91	0	0	0	0	0	0	0	0	0	0	89	0	0
9.1.92	0	0	0	0	0	0	0	0	0	0	0	0	0
21.1.92	0	7	0	0	0	0	0	0	0	0	30	0	0
3.2.92	0	0	0	0	0	0	0	0	0	0	0	0	0
18.2.92	0	4	0	0	0	0	0	0	0	0	0	0	0
3.3.92	0	22	0	0	0	0	0	0	0	0	0	0	0
18.3.92	0	0	0	0	0	0	0	0	0	0	0	0	0
1.4.92	0	15	0	60	0	0	0	0	15	0	0	0	0

Appendix 4. RM Bacillariophyceae

Date	Amp	Ast	Au.gr	Cen	Frag	Gom	Nav	Pin	S.han	S.neo	Sy.ac	Sy.ul
10.1.90	0	0	0	0	0	0	0	0	0	9	0	0
7.2.90	0	0	0	0	0	0	0	0	0	13	0	0
21.2.90	0	0	0	0	0	0	23	0	0	26	0	0
7.3.90	0	26	0	4	4	0	0	0	88	51	0	0
21.3.90	0	79	0	0	0	0	0	0	1350	119	0	0
4.4.90	0	479	0	0	0	0	0	0	1825	164	18	0
18.4.90	0	681	0	0	0	0	12	0	1496	262	24	0
2.5.90	0	73	0	0	0	0	0	0	250	0	8	0
16.5.90	0	0	0	0	0	0	18	0	55	0	0	0
29.5.90	0	0	0	0	0	0	0	0	0	0	0	0
12.6.90	0	0	0	0	0	0	0	0	0	0	36	0
27.6.90	0	0	0	0	0	0	0	0	0	0	4	0
25.7.90	36	620	0	0	213	0	0	0	0	0	0	0
8.8.90	0	0	0	0	169	0	0	0	0	5	0	0
21.8.90	0	0	0	0	292	0	0	0	0	0	36	0
6.9.90	0	0	0	0	36	0	0	0	0	0	0	0
24.9.90	0	0	0	0	24	0	0	0	0	0	0	0
9.10.90	0	0	0	0	73	0	0	0	0	18	18	0
22.10.90	0	0	0	0	0	0	0	0	0	0	0	0
6.11.90	0	0	0	0	0	0	0	0	0	0	0	0
20.11.90	0	0	0	0	0	24	16	0	0	56	0	0
5.12.90	0	0	0	0	0	0	0	0	0	0	0	0
28.12.90	0	0	0	0	0	0	0	0	0	0	0	0
7.1.91	0	0	0	0	0	0	0	0	0	0	0	0
5.3.91	0	168	7	7	0	0	0	7	0	0	0	7
19.3.91	0	3	0	0	0	0	0	0	255	9	0	0
2.4.91	0	0	119	0	0	27	0	0	3276	48	9	0
16.4.91	0	700	0	0	0	0	0	0	10657	128	0	0
14.5.91	0	22	0	0	0	0	0	0	0	0	0	0
27.5.91	0	0	0	0	0	0	0	0	0	0	0	0
11.6.91	0	0	0	0	0	0	0	0	0	0	0	0
25.6.91	0	0	0	0	0	0	0	0	0	0	0	0
9.7.91	0	365	0	0	0	0	0	0	0	0	0	0
22.7.91	0	0	0	0	0	0	45	0	581	0	0	0
6.8.91	0	0	0	0	0	0	89	0	0	0	0	0
19.8.91	0	0	0	0	0	0	0	0	0	0	0	0
9.9.91	0	0	0	0	0	0	0	0	0	0	0	0
23.9.91	0	0	0	0	0	0	0	0	0	0	0	0
9.10.91	0	0	0	0	0	0	0	0	0	0	0	0
22.10.91	0	0	0	0	0	0	0	0	0	0	0	0
5.11.91	0	0	0	0	0	0	0	0	0	0	0	0
19.11.91	0	0	0	0	0	0	0	0	0	0	0	0
3.12.91	0	0	0	0	0	0	0	0	0	0	0	0
18.12.91	0	0	0	0	0	0	0	0	0	0	0	0
9.1.92	0	0	0	0	0	0	0	0	0	0	0	0
21.1.92	0	0	0	0	0	0	0	0	7	0	0	0
3.2.92	0	0	0	0	0	0	0	0	0	0	0	0
18.2.92	0	0	0	0	0	0	0	0	0	0	0	0
3.3.92	0	0	0	0	0	0	0	0	417	0	0	0
18.3.92	0	0	0	0	0	0	0	0	1876	0	0	0
1.4.92	0	0	0	0	0	0	0	0	74	0	30	0

Appendix 4. RM Euglenophyta, Cryptophyta, and Pyrrophyta

Date	Eugl	Phac	Trac	Crypt	Rhod	µ Flag	Cer	Per
10.1.90	0	0	0	3	2	3	3	0
7.2.90	0	0	0	7	0	164	0	0
21.2.90	0	0	0	2	27	534	0	0
7.3.90	0	0	0	35	84	190	0	2
21.3.90	0	0	0	173	1989	109	0	0
4.4.90	18	0	0	41	255	566	0	55
18.4.90	0	0	0	36	97	426	0	12
2.5.90	0	0	0	44	355	219	3	0
16.5.90	0	0	0	18	602	109	4	0
29.5.90	0	0	0	97	511	0	29	0
12.6.90	0	0	0	15	423	650	0	0
27.6.90	0	0	0	62	405	44	73	0
25.7.90	0	0	0	124	103	24	15	0
8.8.90	0	0	0	27	73	91	18	0
21.8.90	0	0	0	7	584	97	29	0
6.9.90	0	0	0	0	365	73	95	0
24.9.90	0	0	0	0	97	195	95	0
9.10.90	0	0	0	36	18	109	55	0
22.10.90	0	7	0	0	36	139	7	0
6.11.90	0	0	0	7	0	0	0	0
20.11.90	0	0	0	0	40	201	0	0
5.12.90	0	0	0	0	0	73	0	0
28.12.90	0	0	0	51	18	270	0	7
7.1.91	0	0	0	0	7	74	0	0
5.3.91	0	0	0	7	409	174	0	0
19.3.91	0	0	0	100	1925	201	0	9
2.4.91	0	0	0	82	73	392	0	9
16.4.91	0	377	0	140	657	109	0	0
14.5.91	0	0	0	0	88	139	0	0
27.5.91	0	0	0	48	772	434	0	0
11.6.91	0	0	0	50	302	302	0	0
25.6.91	0	0	0	603	4763	547	0	0
9.7.91	0	0	0	1277	776	274	30	30
22.7.91	0	0	0	179	625	134	45	0
6.8.91	0	0	0	45	45	0	45	0
19.8.91	0	0	0	0	0	0	45	0
9.9.91	0	0	0	0	0	0	142	0
23.9.91	0	0	27	0	281	27	74	0
9.10.91	0	0	0	0	13	20	10	0
22.10.91	0	0	0	13	13	0	4	0
5.11.91	0	0	0	0	0	27	3	0
19.11.91	0	0	0	0	0	89	0	0
3.12.91	0	0	0	0	0	22	0	0
18.12.91	0	0	0	0	0	67	0	0
9.1.92	0	0	0	0	0	22	0	0
21.1.92	0	0	0	0	0	30	0	0
3.2.92	0	30	0	0	0	22	0	0
18.2.92	0	0	0	22	52	60	0	4
3.3.92	0	0	0	30	149	97	0	15
18.3.92	0	0	0	89	670	149	0	30
1.4.92	0	0	0	74	1251	104	0	0

Appendix 4. RM Cyanobacteria

Date	Ana	Aphan	Chroo	Coelo	Mic	Plank
10.1.90	0	0	15	15	2	2
7.2.90	0	0	0	0	0	35
21.2.90	0	0	0	0	0	33
7.3.90	0	0	0	4	4	58
21.3.90	36	0	0	0	9	122
4.4.90	0	0	0	0	36	64
18.4.90	0	0	0	0	12	36
2.5.90	3	0	0	0	26	10
16.5.90	131	201	0	0	66	0
29.5.90	3601	358	0	0	51	0
12.6.90	467	0	0	0	22	15
27.6.90	33	0	0	0	29	0
25.7.90	190	0	0	6	201	6
8.8.90	5	0	0	0	839	0
21.8.90	0	0	0	0	1168	0
6.9.90	0	0	0	0	664	0
24.9.90	0	0	0	0	263	7
9.10.90	0	0	0	0	693	0
22.10.90	0	0	0	0	226	4
6.11.90	0	0	0	0	569	0
20.11.90	0	0	40	0	145	0
5.12.90	0	0	0	0	11	0
28.12.90	0	0	0	0	36	4
7.1.91	0	0	0	0	0	0
5.3.91	0	0	0	0	0	0
19.3.91	0	0	0	0	0	0
2.4.91	0	0	0	0	0	0
16.4.91	0	0	0	0	0	0
14.5.91	7	0	0	0	7	0
27.5.91	193	0	0	0	0	0
11.6.91	1307	0	0	0	0	0
25.6.91	1340	0	0	0	0	0
9.7.91	0	0	0	0	3	0
22.7.91	89	89	0	0	134	0
6.8.91	938	849	0	0	313	0
19.8.91	0	223	0	45	938	0
9.9.91	0	0	0	17	184	0
23.9.91	0	0	0	13	174	13
9.10.91	0	0	0	3	77	0
22.10.91	0	0	0	2	67	0
5.11.91	0	0	0	0	114	0
19.11.91	0	0	0	0	39	0
3.12.91	0	0	0	0	7	0
18.12.91	0	0	0	0	4	0
9.1.92	0	0	0	0	0	0
21.1.92	0	0	0	0	0	0
3.2.92	0	0	0	0	0	0
18.2.92	0	0	0	0	0	0
3.3.92	0	0	0	0	0	0
18.3.92	0	0	0	0	0	0
1.4.92	0	0	0	0	0	0

Appendix 4. RM Zooplankton

Date	Bos.lo	Chy.sp	D.cuc	D.lon	D. pul	Diaph	Lept	Di.gra	Cyclo
7.3.90	0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.3	0.1
21.3.90	1.6	0.0	0.0	9.2	0.0	0.0	0.0	9.6	1.7
18.4.90	0.8	0.0	0.0	2.8	0.0	0.0	0.0	5.8	3.1
27.4.90	0.4	0.0	0.0	22.5	0.0	0.0	0.0	13.9	9.3
2.5.90	0.0	0.0	0.4	18.9	0.0	0.0	0.0	9.1	6.6
16.5.90	0.0	0.0	0.0	9.0	0.0	0.0	0.0	14.8	1.4
29.5.90	0.0	0.0	1.7	5.4	0.0	0.0	0.6	23.6	1.0
12.6.90	0.0	0.0	8.2	9.8	0.0	1.7	0.6	14.1	1.1
27.6.90	0.0	0.0	9.4	14.5	0.0	1.5	1.0	17.4	2.5
11.7.90	0.0	0.0	0.0	11.9	0.0	12.8	0.5	17.6	2.6
25.7.90	0.0	0.0	4.1	3.4	0.0	6.2	0.1	5.5	2.0
8.8.90	0.0	0.0	0.8	1.5	0.0	5.0	0.1	5.5	7.1
21.8.90	0.0	0.0	0.4	0.5	0.0	6.2	0.1	4.6	6.4
6.9.90	0.0	0.0	2.0	0.8	0.0	6.6	0.2	2.6	1.3
24.9.90	0.0	0.0	0.1	0.5	0.0	0.7	0.0	2.5	0.3
9.10.90	0.0	0.0	0.4	1.1	0.2	0.6	0.1	5.3	0.5
22.10.90	0.0	0.0	0.2	0.6	0.0	0.4	0.0	5.4	0.5
6.11.90	0.0	0.0	0.0	2.0	0.0	0.2	0.0	5.0	0.2
20.11.90	0.0	0.0	0.4	7.1	0.1	0.0	0.0	3.0	0.4
5.12.90	0.0	0.0	0.0	12.6	0.0	0.0	0.0	3.6	0.6
19.3.91	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.5	0.7
2.4.91	0.3	0.0	0.0	0.6	0.0	0.0	0.0	9.0	2.1
16.4.91	0.1	0.0	0.0	0.5	0.2	0.0	0.0	2.4	1.4
30.4.91	0.2	0.0	0.1	4.8	3.7	0.0	0.0	17.0	7.8
14.5.91	0.0	0.0	0.0	18.1	3.6	0.0	0.0	22.3	3.3
27.5.91	0.4	0.0	5.8	2.7	1.0	0.0	0.0	10.7	0.7
11.6.91	0.0	0.0	3.1	7.1	4.9	0.0	0.1	14.9	1.4
25.6.91	0.0	0.0	0.2	2.7	3.1	0.0	0.2	1.1	0.2
9.7.91	0.0	0.0	0.3	0.0	0.1	0.0	0.0	0.7	16.0
22.7.91	0.0	0.0	1.5	0.6	0.2	0.0	0.2	1.7	4.3
6.8.91	0.0	0.0	1.3	1.6	0.2	0.3	0.1	2.7	4.9
19.8.91	0.0	0.0	0.3	1.3	0.0	0.0	0.0	1.4	2.2
9.9.91	0.0	0.0	1.0	2.0	0.0	0.0	0.0	3.0	1.1
23.9.91	0.0	0.0	21.6	18.2	0.0	0.0	0.0	1.3	0.2
9.10.91	0.0	0.0	13.1	8.3	0.0	0.0	0.0	1.2	0.4
22.10.91	0.0	0.1	2.5	1.9	0.0	0.0	0.0	0.4	0.5
5.11.91	0.0	0.1	1.8	5.0	0.0	0.0	0.0	0.1	0.3
19.11.91	0.0	1.4	1.0	9.0	0.0	0.0	0.0	0.4	0.7
3.12.91	0.0	0.1	5.3	1.9	0.0	0.0	0.0	0.1	0.3
18.12.91	0.0	0.3	0.3	1.2	0.0	0.0	0.0	0.2	0.4
9.1.92	0.0	0.0	0.0	0.7	0.1	0.0	0.0	0.3	0.2
21.1.92	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.1	0.0
3.2.92	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.6	0.1
18.2.92	0.1	0.0	0.0	1.0	0.0	0.0	0.0	0.8	0.1
3.3.92	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.2	0.2
18.3.92	0.1	0.0	0.0	0.7	0.0	0.0	0.0	1.0	0.9
1.4.92	0.0	0.0	0.0	1.4	0.0	0.0	0.0	0.8	0.7