Whole lake and mesocosm studies on the role of nutrients and zooplankton grazing in a system of shallow and deep lakes

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Abstract

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There is a controversy about the relative importance of determination of phytoplankton crops in lakes by bottom-up (nutrients and physical factors) control and top-down (zooplankton grazing) control. Both factors might act together to control the phytoplankton community in a lake. With increasing depth, availability of nutrients that are usually supplied by external loading (usually N & P) appears to be of greater importance. Grazers appear to control the phytoplankton community in shallow, plant dominated lakes where internal nutrient loading seems to be an important source.

Generally, shallow lakes show more evidence of top-down control of phytoplankton, deep lakes of bottom-up control. Control of external nutrient loading of eutrophic deep lakes is an accepted approach for restoration, but not for shallow lakes due to observed prolonged resilience. Through regular monitoring of water chemistry, phytoplankton and zooplankton communities, this study examined the impact of sewage effluent diversion on Little Mere and the downstream Rostherne Mere. Mere Mere, upstream to Little Mere, was not affected by sewage effluent and acts as a comparator. Rostherne Mere, a eutrophic deep lake, and Little Mere, a hypertrophic shallow one, appear to challenge conventional wisdom because diversion of sewage effluent from Little Mere has shown rapid, major changes but in Rostherne Mere, phosphorus concentrations have decreased little and there has been no change in the chlorophyll a concentration four years after effluent diversion. Nitrogen appears to be the limiting factor of the phytoplankton community in Rostherne Mere. No clear limiting factor could be identified in Mere Mere, although nitrogen appears to be of greater importance than phosphorus and a recent decline of the DIN due to inconstancy of nitrogen loading to Mere Mere from its catchment may have caused severe nitrogen limitation of its phytoplankton community.

To predict future ecosystem changes in Little Mere following effluent diversion, experimental manipulations of the lake community were carried out in mesocosms. Little Mere has provided strong evidence for the existence of alternative stable states over a wide range of nutrient concentrations. The lake had clear water at extremely high nutrient concentrations prior to effluent diversion, with very high densities of large body-sized grazers with very low fish predation. Following sewage effluent diversion, the nutrient concentrations significantly declined, the oxygen concentrations rose, and in turn fish predation increased. The high density of large body-sized grazers shifted to one of relatively smaller body-sized animals but the clear water state has been maintained. This is probably due to provision of refuges for the grazers by large nymphaeid stands (also found prior to diversion). In mesocosms, in the absence of the plant refuges, increased chlorophyll a concentration and decreased large grazer

densities highlighted the significance of macrophyte stands and their buffering mechanisms in stabilizing a clear water state.

Compared with the observed effectiveness of water lilies for sheltering grazers against fish predation, in Little Mere and elsewhere, submerged plants were less effective when tested in a mesocosm experiment. The degree to which they were effective may depend on creation of pH conditions which inhibit fish feeding.

In Little Mere, since 1991, there have been great decreases in nutrient concentrations and expansion of the total macrophyte coverage, largely by submerged plants since 1993. The grazer community of Little Mere has also responded to this latter change with a decline in daphnids and an increase in densities of weed-associated grazers. The reasons for disappearance of the open water daphnids are not clear, but factors linked with habitat complexity of the submerged plants might have interfered with the feeding of open water grazers.

The presence of large densities of the open water grazers was the apparent main buffer mechanism of the clear water state until 1994. The lake has, so far, maintained its clear water in the absence of these grazers. Thus, new buffer mechanisms appear to operate to stabilize the ecosystem. Though little is known about grazing efficiency of the weed-associated grazers on phytoplankton, they might play a significant role. The expansion of the rooted macrophyte stand might also be important for the low chlorophyll a concentrations, perhaps due to uptake of nitrogen by the plant biomass. The N:P ratio in the lake water hints at possible nitrogen-limitation of the phytoplankton community. In the presence of the current large macrophyte stands, Little Mere appears to have shifted from its previous top-down controlled clear water state to a bottom-up controlled clear water state.

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Chapter 1: Introduction

1.1 Introduction

1.1.1 Eutrophication

During the latter half of this century, there has been increasing concern over the increasing nutrient status, or eutrophication, of many lakes because the eutrophication of temperate lakes leads to increase in algal biomass (including potentially toxic cyanophytes) and changes in community structure. As a result much research has focused on factors that may limit phytoplankton populations (Pearsall, 1932; Hutchinson, 1957; Rosen, 1981; Vollenweider and Kerekes, 1981) and numerous investigators have used algal species composition to characterize lake trophic states (Järnefelt, 1952; Rawson, 1956; Rott, 1984). Cyanophyta appear to be common algal taxa associated with poor water quality in eutrophic deep lakes and are recognized as a major water quality problem worldwide (Reynolds and Walsby, 1975). Several competing hypotheses have been proposed to explain seasonal and geographical incidence of cyanophytes. One proposed hypothesis is high water temperature (Jackson, 1964; Robarts & Zohary; 1984). In general, cyanophytes have higher temperature optima than chlorophytes and diatoms and their water blooms occur during summer and in tropical lakes. Laboratory evidence by Tilman & Kiesling (1984) and Tilman *et al.* (1981) has supported the validity of the hypothesis. Data largely from physiological studies of individual cyanophytes have suggested a low light hypothesis (Reynolds, 1976; Mur *et al.* 1978) that low light availability in the water column favours the growth of cyanophytes over other algae. The low N:P hypothesis has been investigated more thoroughly than the first two. It has been

suggested that low N:P ratios in the nutrient supply favour cyanophytes over other algae because they are good competitors for N (Schindler, 1977, Barica *et al.* 1980, Smith, 1983; Stockner & Hyatt, 1984). A further proposed hypothesis is the role of buoyancy (Reynolds, 1976) which gives advantage to vacuolate cyanophytes in moving to where conditions favour them. Lastly there is the low CO_2/high pH hypothesis. Shapiro (1973a; 1973b) found that cyanophytes become dominant over chlorophytes at high pH values, indicating that the algae are efficient in deriving carbon from very low CO_2 concentrations (King, 1970). Further studies by Shapiro & Wright (1984) and Shapiro (1990a) have shown the significance of the hypothesis for cyanophyte dominance. These suggested hypotheses form a base line to understand the mechanisms for controlling cyanophyte problems of water bodies but are generally results of intensive studies on large, deep lakes. More recently a great deal of research has been carried out in shallow lakes, where the significance of zooplankton grazing has become apparent for controlling algal crops (Shapiro *et al.* 1975; Leah *et al.* 1980; Moss *et al.* 1994), though not necessarily cyanophytes.

1.1.2 Control of phytoplankton

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) (DeMelo *et al.* 1992; Agusti *et al.* 1992; Carpenter & Kitchell, 1992). It has become generally accepted that both influences may operate depending on the trophic status of lakes and other factors such as depth (McQueen & Post, 1986; McQueen, 1990;

Moss *et al.* 1994).

Wide acceptance of the importance of nutrient concentrations in water quality deterioration has resulted in much interest in external nutrient loading control. The isolation of lakes from external nutrient loading is thus often considered to be the first and the main step to reverse adverse effects of eutrophication (Björk, 1985; Hosper & Meijer, 1986; van Liere, 1986; Sas, 1989). It has been effective in deep lakes (Edmondson, 1970; Edmondson & Lehman, 1981) probably due to more pronounced effects of nutrients in deep lakes. Decreased external nutrient loading is likely to be generally successful in eutrophic deep lakes but not necessarily in all (Bengtsson *et al.* 1975; Carvalho *et al.* in press). The scenario in shallow lakes, after external nutrient reduction, has been one of almost complete resilience or long delayed recovery (Sas, 1989; Marsden, 1989; Søndergaard, 1989). Homeostatic control mechanisms, largely trophic interactions (involving fish/zooplankton and other invertebrates) have had an important role in resilience of eutrophic shallow lakes (Benndorf, 1987; Scheffer, 1989; Jeppesen, *et al.* 1991 Meijer *et al.* 1990; Phillips *et al.* 1994; Breukelaar *et al.* 1994). However, release of phosphorus from the sediment appears to be a factor in many shallow lakes (Sas, 1989; Søndergaard, 1989; Søndergaard, *et al.* 1990; Jeppesen *et al.* 1990a; van Liere & Gulati, 1992; Jeppesen *et al.* 1991; Bales *et al.* 1993; Perrow *et al.* 1994; Moss *et al.* 1995). Flushing rates of water bodies are important for recovery because under such high flushing rates, fast reduction in concentrations of limiting nutrients (dilution) has been recorded (Cooke *et al.* 1986; Jagtman *et al.* 1992).

Release of P and N from the sediments appears to be widely significant (Sinke, 1992) but a general model has not yet been constructed that will predict the rate of release. A variety of mechanisms have been shown to be important for controlling phosphorus release from lake sediments, including the sediment iron content and oxygen conditions (Mortimer, 1941; 1942). Total Fe:TP ratios have been proved to be a very important factor in P release from the sediments of Danish lakes (Jensen *et al.* 1992; Søndergaard, *et al.* 1993). Formation of H_2S has been shown to inactivate Fe absorption capacity (Boström *et al.* 1988). Increased temperature, pH and resusupension of sediment are also able to enhance sediment release (Boström *et al.* 1982; Jensen and Andersen, 1992). Bioturbation of sediment by bottom feeders, benthivorous fish and invertebrates have been shown to increase release of phosphorus significantly (Meijer *et al.* 1990; Horppilo & Kairesalo, 1990; Phillips *et al.* 1994).

1.1.3 Top-down and bottom-up control

Lakes systems consist of numerous components, which are not linked through a unidirectional flow of influence from nutrients to phytoplankton to zooplankton and finally to the fish. This is probably the main reason for failure of external nutrient loading reduction to restore eutrophicated shallow lakes. Thus, many studies have focused on the profound effects of top level consumers, such as fish, on lower levels of the aquatic community in addition to external nutrient control. The experimental work by Shapiro *et al.* (1975) led to many subsequent studies of what he called biomanipulation and which is generally regarded as a feasible technique in aquatic management in addition to nutrient

control, specifically for the control of algal biomass through the trophic pyramid (Benndorf, 1987). This top-down effect is also termed cascading trophic interaction (Carpenter *et al.* 1985). Most approaches have focused on removal of zooplanktivorous fish to stimulate zooplankton populations to increase grazing pressure on phytoplankton (Leah *et al.* 1980; Shapiro & Wright, 1984; McQueen *et al.* 1986; Hosper, 1989; Irvine *et al.* 1989; van Donk *et al.* 1990a; Søndergaard, *et al.* 1990; van Donk *et al.* 1990b; Meijer *et al.* 1989; Hosper & Jagtman, 1990; Meijer *et al.* 1990; Moss, 1992a; Hosper & Meijer, 1993; Carvalho, 1994). Some studies have involved a reduction of zooplanktivorous fish biomass by piscivore stocking (Hergenrader, 1983; Carpenter *et al.* 1987; Carpenter *et al.* 1995). Despite the apparent potential of piscivore manipulation, there may be drawbacks to this approach in that improved water quality will only be possible when zooplanktivore yields are reduced to such low levels that the piscivore can not be maintained (McQueen, 1990). The combined effect of both reduction of external nutrient loading and biomanipulation of the fish community have been successful in reducing phytoplankton populations and creating clear-water in many shallow lakes. The short-term results of these food-web manipulations are encouraging, but there is still much controversy on the long-term stability of the clear-water state. Signs of deterioration of water quality of manipulated shallow lakes have already been recorded (Perrow *et al.* 1994; Meijer *et al.* 1994) hinting at possible return to a turbid-water state which might be associated with a lack of macrophytes and the significant key-role they may play in maintaining clear water in shallow lakes.

1.1.4 Alternative stable states

Turbid water with phytoplankton dominance (or suspended sediment) and a clear-water state with strong macrophyte dominance seem to be alternative stable states in shallow eutrophic lakes (Scheffer 1989; 1990; Moss 1990; 1991). These two states have been reported from different geographical regions and appear to fulfil the requirements of alternative stable states (Balls *et al.* 1989; Irvine *et al.* 1990a; Hosper, 1989; Scheffer *et al.* 1993; Carvalho, 1994; Beklioglu & Moss, 1995; Beklioglu & Moss, in preparation; Moss, 1995). Two alternative stable states or bistability of shallow lakes was suggested by Scheffer (1989; 1990) and Moss (1990; 1991) and this idea was based on observation that restoration of turbid eutrophic lakes by means of nutrient reduction seems often to be prevented by ecological feedback mechanisms. Moreover the clear state also possesses a number of stabilizing feedback mechanisms. The negative effect of aquatic macrophytes on turbidity has been one of the reasons to expect alternative stable states in freshwater systems. Scheffer (1990) has modelled alternative equilibria in shallow systems from the following assumptions: 1. Algal growth enhances turbidity, and increases with enrichment, whereas over the range of relatively high nutrient levels to which attention is restricted, nutrient limitation is of minor importance to macrophytes; 2. Vegetation has negative effects on turbidity. Mechanisms proposed for stabilising the clear water state by macrophytes include the provision of refuges against predation pressure for phytoplankton grazers (Timms & Moss, 1984), similar linkages for periphyton grazers (Leah *et al.* 1978), allelopathy (Elankovitch & Wooten, 1989; van Vierssen *et al.* 1994), reduction of resusupension of bottom material (Boström *et al.* 1982), nutrient limitation of

phytoplankton through nitrogen uptake by the plants or denitrification by the microorganisms associated with them (van Donk *et al.* 1993; Ozimek *et al.* 1990), provision of spawning grounds and refuge against cannibalization for piscivorous fish like pike, which in turn decrease zooplanktivorous and benthivorous fish density (Grimm, 1989; Grimm & Backx, 1990). We must be also aware of switch mechanisms, which cause the change from one state to another and through which the stabilizing buffer mechanisms of either state are exceeded. Early explanation of the switch to the turbid state was simply by progressive external loading that would increase the growth of periphyton and phytoplankton and steadily shade out the plants (Phillips *et al.* 1978). However, Balls *et al.* (1989) tested this hypothesis by adding nutrients to plant-dominated experimental ponds but found no increase in phytoplankton biomass, There is a general understanding that switches from clear to turbid are associated with high nutrient availability but the phenomenon has yet to be fully quantified. Brőnmark & Weiser (1992) have explained the switch to a turbid state by catastrophic disturbance events such as winterkill or summerkill of a top predator in the fish community resulting in increased zooplanktivores. This has been recorded elsewhere (Casselman & Harvey, 1975). The model has been based on presumed importance of predation pressure by top predators in the macrophyte-dominated state. Predation by piscivores should cascade down and reduce planktivorous fish numbers, in turn increasing phytoplankton grazers, and benthivorous fish numbers thereby decreasing predation pressure on grazing benthic invertebrates (such as snails which effectively graze on epiphytes). An increased benthivorous density (tench), in an enclosure experiment resulted in increased epiphyton through reduced density of

snails and in turn reduced growth rate of the dominating submerged macrophyte (see Brőnmark & Weiser, 1992). Grazing by birds has been shown to damage macrophytes and might be important for macrophyte loss and a switch to turbid conditions (Moss, 1990). The disappearance of submerged plants increases nutrient concentrations from previous stores in macrophytes (Irvine *et al.* 1989) which may then become available for phytoplankton. Low grazing pressure from zooplankton (due to lack of refuges or lack of piscivorous pressure on planktivores), may allow rapid increase in phytoplankton biomass.

There are several examples of such alternative states in nature (Drake, 1989) but understanding of the shallow lakes system is probably greater than that of many others. The theoretical possibility that ecosystems have more than one equilibrium has been discussed extensively (May, 1977). Drake (1989) has explained recurrent existence of alternative community states under different conditions in terms of assembly mechanics, much like fitting together the pieces of a puzzle, where the rules of assembly are implicit in the relative shapes of the pieces. Species composition may act as a switch, turning the intransitivity 'on' or 'off' and affecting the period of various states. He concluded that disturbance and the frequency of its occurrence in relation to species composition may well create pivotal points in community assembly. Diamond's and Gilpin's (1982) study has shown the patterns of species coexistence among communities in New Guinea provides insight into assembly mechanisms. Cole (1973) found alternative stable combinations of ant species under different assembly scenarios. These are some examples of where assembly mechanics produce alternative states in ecosystems.

The provision of refuges against fish predation pressure for phytoplankton grazers in macrophyte beds appears to be an important buffering mechanism of the clear water state. Thus, to have better insight into how refuges work would help our approaches to control eutrophication. The idea of plants as refuges was introduced by Timms & Moss (1984). They showed the efficiency of floating-leaved plants, (water lilies), for sheltering *Daphnia* in the presence of fish but subsequent works have shown that fish are not excluded from plant beds (Serafy & Harrell, 1993; Venugopal & Winfield, 1993). The efficiency of floating-leaved plants for sheltering of open-water grazers has been recorded in several other shallow lakes (Carvalho, 1994; Moss *et al.* 1994). Contrary to the efficiency of floating-leaved plants for sheltering *Daphnia*, avoidance of *Ceratophyllum demersum* by *Daphnia longispina* was found by Dorgelo & Heykoop (1985) and was attributed to photosynthetic activity of the plant. Disappearance of *Daphnia* but presence of large numbers of weed-associated zooplankton species were recorded in *C. demersum* beds (Irvine *et al.* 1990b). Recent experiments in a shallow lake suggested that lilies do act as refuges for *Daphnia hyalina* against perch feeding but that the density of lilies is very important (Moss & Kornijow, in preparation) and in a second experiment, submerged beds of *Potamogeton berchtoldii* were less effective as refuges against perch predation for *Daphnia* but refuge effects were nonetheless present (Beklioglu & Moss in preparation). This difference between floating-leaved plants and submerged plants for sheltering open water zooplankton might be explained by their different physical and chemical effects on the associated water (Carpenter & Lodge, 1986; Frodge *et al.* 1990; Jones *et al.* in press).

The phase hypothesis of Moss (1991) and Moss *et al.* 1995 (Fig.1.1) summarizes ecosystem development in shallow lake communities undergoing eutrophication. In this model, Phase 1 reflects a near pristine state in which low nutrient loadings limit the phytoplankton crops, whilst low-growing macrophyte species, for example many charophytes, derive their nutrient from sedimentary sources and are not inhibited by phytoplankton competition. Grazing by zooplankton may be considerable but not crucial to the survival of plant dominance. With increasing nutrient loading (Phase 2), zooplankton grazing becomes more important as the potential for phytoplankton growth increases. The macrophytes provide refuges, the water remains clear and predators such as pike and perch continue to limit number of zooplanktivorous and benthivorous fish. Under these conditions, the low growing plants of Phase 1 are replaced by more competitive tall growing species (e.g. *Potamogeton* spp, *Nuphar lutea*, *Myriophyllum spicatum*, *Ceratophyllum demersum*), capable of surviving occasional periods of phytoplankton-induced water turbidity due to the position of their leaves closer to the water surface. The Phase 2 community is clearly less stable than Phase 1 and it may be replaced by an alternative Phase 3, dominated by phytoplankton and from which macrophytes are lost. In this phase zooplanktivorous fish are able to remove the larger, more effective zooplankton grazers and the phytoplankton is able to take advantage of the available nutrient supply. Loss of macrophytes may include various forms of damage to plants themselves (e.g. mechanical destruction, grazing by exotic vertebrate herbivores such as coypu, Canada geese or common carp) or damage to zooplankton grazer community by pesticide run-off (Stansfield *et al.* 1989), or greatly increased salinity

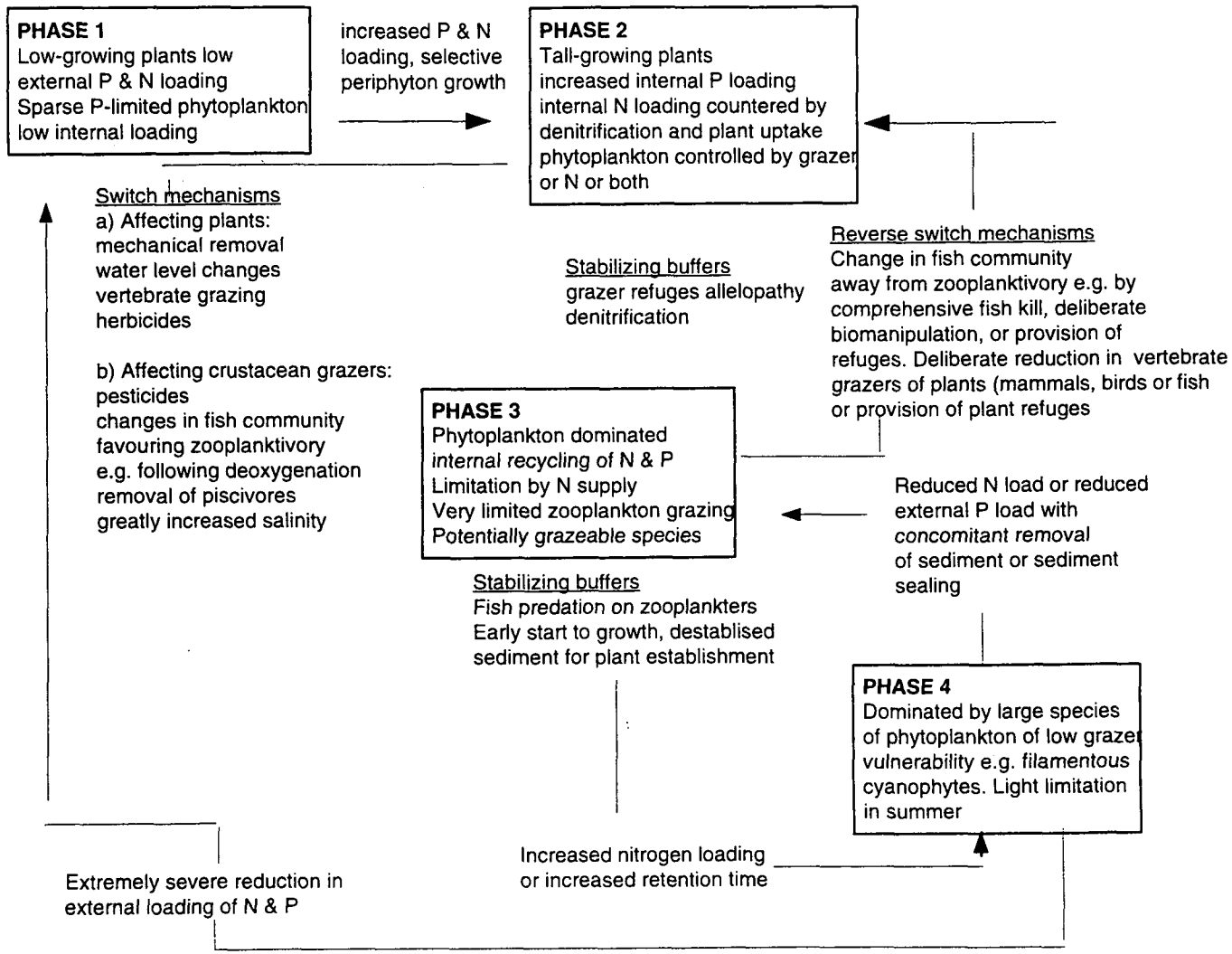

Fig.1.1 A model of changes with eutrophication in shallow, initially macrophyte-dominated lakes. (Moss *et al.* 1995).

(Bales *et al.* 1993). Plant-dominated (Phase 2) or phytoplankton-dominated (Phase 3) systems can exist as alternative stable states over wide range of nutrients (Scheffer *et al.* 1993 see above). In addition, higher nutrient concentrations or other circumstances such as reduced flushing may lead to the production of poorly grazeble phytoplankters such as cyanophytes or gelatinous chlorophytes as observed in shallow eutrophic Danish lakes (Jensen *et al.* 1994). This constitutes Phase 4. This thesis is concerned with a group of eutrophic lakes, and their potential restoration, in the North-West Midlands of the U.K.

1.2 The study area

The North-West Midland Meres are a large association of lakes that lie on the Shropshire-Cheshire-Staffordshire plain (Fig 1.2). There are over sixty lakes exceeding 1 ha in area in this lowland drift plain, which was mostly laid down on the retreat of the last (Devensian) glaciation, about 13000 years ago. Most of the meres 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 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, 1978) in contrast to the more oligotrophic lakes of the Cumbrian Lake District, and some of them are reported to have supported cyanophyte blooms at least since the nineteenth century (Phillips, 1884). However records from the nineteenth century (Leighton, 1841)

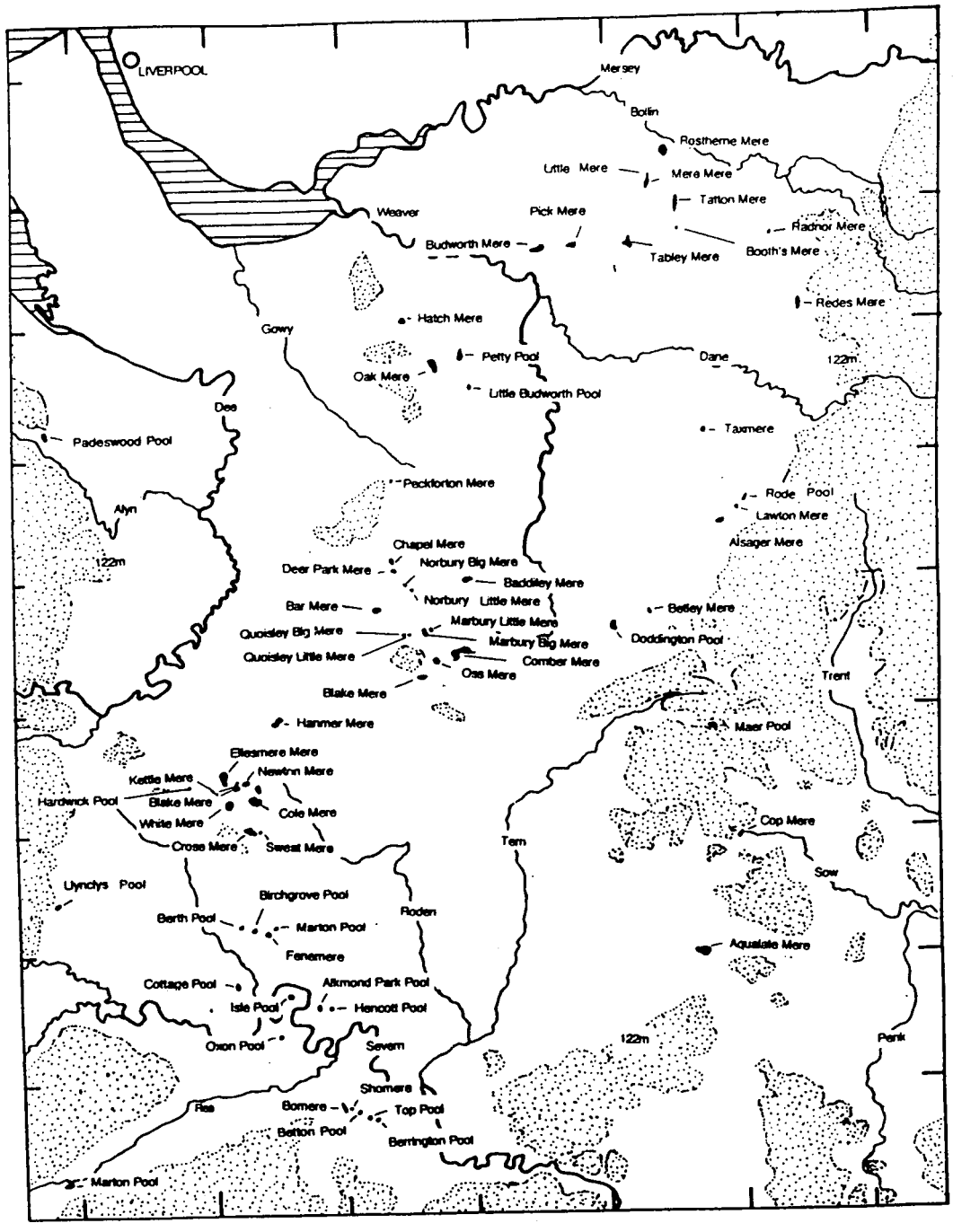

Fig.1.2 The North-West Midland Meres.

also reveal that plants, such as *Lobelia dortmanna*, a species characteristics 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) and he suggested that, relative to algal growth requirements, nitrogen appeared to be scarcer than phosphorus, but, because of apparently natural nutrient-rich water in the meres, the phytoplankton biomass may be light-limited, rather than nutrient-limited. The total phosphorus mass balance of Rostherne Mere, the deepest eutrophic Cheshire mere, has shown no evidence, however, to suggest that phosphorus sources are naturally derived (Carvalho *et al.* in press). A recent study (Moss *et al.* 1994) of a group of deep lakes, including Rostherne Mere and Mere Mere, and group of shallow lakes, including Little Mere (main site for this thesis), revealed that growth season chlorophyll a concentrations were significantly correlated with winter nitrogen loading in the deep lakes, but that in the shallow lakes they were significantly inversely correlated with zooplankton grazer density. There have been studies of the seasonal periodicity of the water chemistry (Grimshaw & Hudson, 1970; Reynolds, 1971), phytoplankton populations, (Pearsall, 1923; Lind, 1944; Belcher & Storey, 1968; Reynolds, 1973; 1978a; Reynolds & Bellinger, 1992), and zooplankton populations (Galliford, 1954; Reynolds, 1978b) in a few meres. But until recently no intensive study of these three aspects was carried out simultaneously (Carvalho, 1993, Moss *et al.* 1994)

1.3. Approaches

General monitoring of water chemistry, phytoplankton and zooplankton communities of lakes is crucial to understand links between nutrients, algae and zooplankton but it is not comprehensive enough to explain operating forces. To gain a better insight into how top-down and bottom-up forces operate in lakes, the following approaches have been used:

1) Laboratory experiments: these are considered to be inappropriate to understand food-web interactions as phytoplankton and zooplankton communities generally do not survive for a long time in a small culture flask. Conditions in a laboratory environment are artificial and do not fully include impacts on a lake ecosystem such as weather and hydrology and rarely reproduce light intensity, daylight and temperature. It is not easy to create replicated laboratory containers which include algae, zooplankton, fish and macrophytes with all the possible environmental effects of a lake system.

2) Large-scale enclosures or whole lake experiments: Large-scale enclosure experiments are more suitable in that the enclosed community has a greater chance of being representative of that of the lake, if edge effects are reduced. Carrying out the experiments in situ also allows presence of factors not taken into account in a laboratory experiment and resembles the situation in the lake more closely. However, as a result of the size and cost of enclosures, and the time involved in sampling many variables and analysing results, replication has to be limited. Alternatively, large-scale enclosures or whole-lake studies may remove problems with spatial scale and heterogeneity associated with enclosure experiments (Frost *et al.* 1988), but they frequently lack reference or adequate control treatments (Hulbert, 1984; Carpenter, 1988).

3) Medium-scale enclosures or mesocosms: Enclosures are not perfect mimics of a lake environment. Circulation within them might be inhibited and edge effects are greater than in the lake. Nutrient loading from the catchment and from the sediment may be excluded in closed enclosures (Gerhart & Likens, 1975), or the full impacts of predation may not be experienced (Carpenter & Kitchell, 1988). Carpenter and Kitchell have criticized enclosure studies by suggesting that small-scale, in-situ, enclosures are not at appropriate size scales to determine true causal pathways and are therefore inadequate for assessing patterns in community-wide behaviour (Kitchell, 1988; Carpenter, 1988). Short running time is another limitation to in-situ enclosure experiments. Frost *et al.* (1988) suggested that complex interactions in which fish are able influence phytoplankton indirectly through increasing zooplankton mortality, require a long time to become manifested. Nevertheless, freshwater communities are ideal for such experiments as populations large enough to be sampled repeatedly can be enclosed. Factors (predation and resources) can be easily be manipulated and replication of treatments is easily possible. Factorial experiments enable effects of more than one factor to be analyzed simultaneously, saving time, effort and money. Also factorial analysis can test interactions among factors. Despite all the discussed disadvantages of small-scale enclosure experiments, they are compromises between whole-lake experiments, where replication is impossible, and the more artificial conditions of the laboratory.

1.4 Aims of the study

This study was carried out on three Cheshire meres which are Mere Mere, Little Mere

and Rostherne Mere (Fig.1.3).

The study focused on how the ecosystem of Little Mere changed following sewage effluent diversion and tested hypotheses about control of events in the water column through top-down process:

- that grazing by zooplankton determines the size and nature of the phytoplankton community.
- that the fish community determines the zooplankton community.
- that diversion of effluent would lead to cyanophyte-dominated turbid-water.
- that internal nutrient loading from the sediment would be a major determinant of events in the lake following effluent diversion.
- that the existing macrophyte-dominated clear-water was an alternative stable state to phytoplankton-dominated turbid-water and was stabilized by provision of refuges for the zooplankton against fish predation

Even closely timed observations are often insufficient to comprehend ecosystem development. Therefore, the hypotheses were tested by carrying out relatively small-scale, in-situ, enclosure experiments. The fish stock of the lake was determined, and also diurnal behaviour of the zooplankton community in different sub-habitats was studied. The study also included biweekly background monitoring of the Mere Mere, Little Mere and Rostherne Mere system for water chemistry, phytoplankton and zooplankton communities to assess the changes in the shallow lake, Little Mere, and the deep lake, Rostherne Mere,

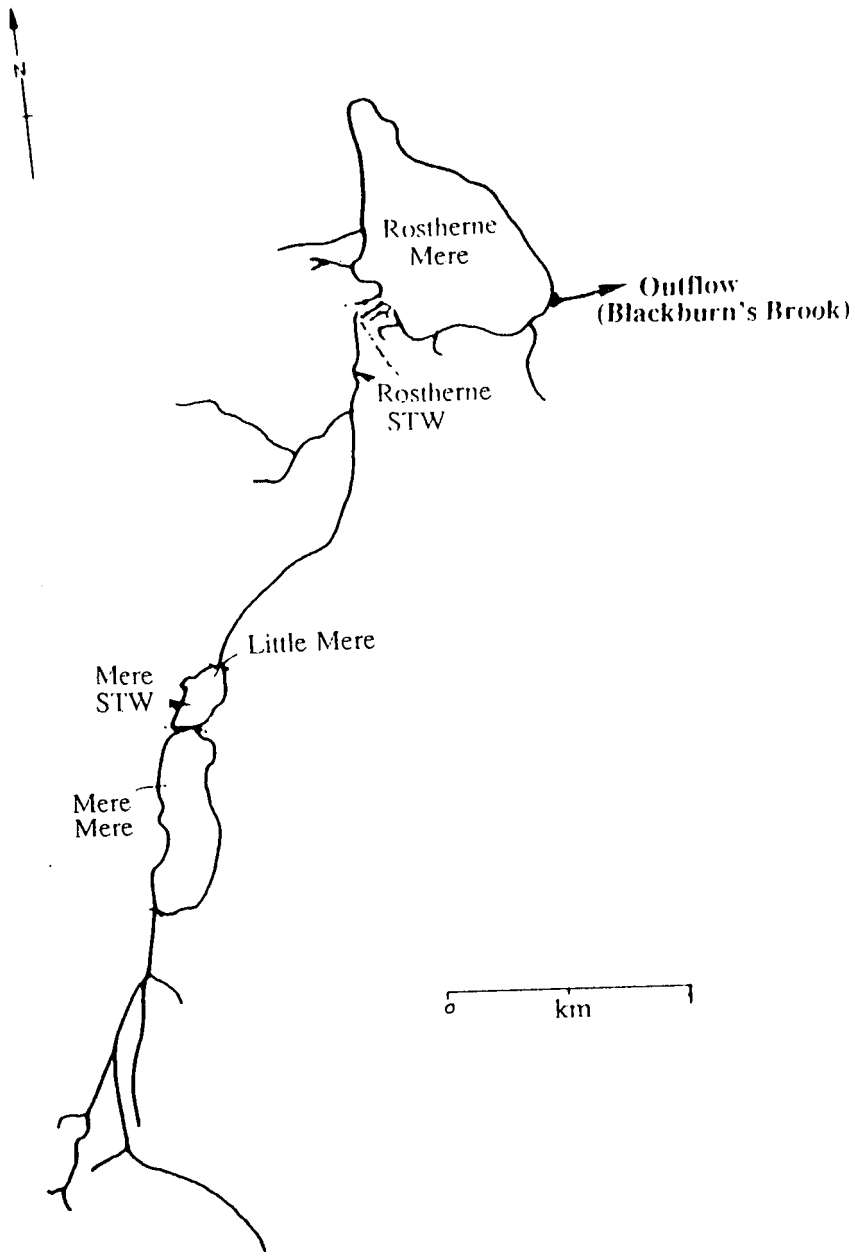

Fig.1.3 Mere Mere, Little Mere and Rostherne Mere which are connected by the Rostherne Brook. Inputs of sewage effluent are also indicated.

which lies downstream of it, following sewage effluent diversion. Data from the pre-diversion period and three years post-diversion enabled a better insight of the system. Detailed water and nutrient budgets were made for Little 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: Water chemistry of Mere Mere, Little Mere and Rostherne Mere

2.1. Introduction

Eutrophication remains one of the most important problems of water quality. Undoubtedly, the main cause is a high loading of phosphorus and nitrogen, which in lakes eventually lead to high algal biomass and the collapse of interactions in many parts of the food-web leading to further deterioration of water quality. Despite recognition of the importance of both nitrogen and phosphorus in controlling eutrophication, phosphorus has been widely accepted as the limiting nutrient to phytoplankton crop-size (Schindler, 1977; Dillon & Rigler, 1974; Smith, 1983). Therefore, lake restoration techniques have traditionally focused on reduction in external phosphorus loading. This has proved effective in some cases (Edmondson, 1970; Edmondson & Lehman, 1981), but not in others (Bengtsson *et al.* 1975). Following the external nutrient reduction, it is generally accepted that shallow lakes are more resilient to recovery than deep lakes (Bengtsson *et al.* 1975; Sas 1989; Jeppesen *et al.* 1991). This resilience to change is partly due to homeostatic mechanisms involving the fish/zooplankton community (Scheffer 1989; Breukelaar *et al.* 1994; Phillips *et al.* 1994), but release of phosphorus from the sediment is also major factor (Boström *et al.* 1982; Marsden 1989; Søndergaard *et al.* 1990; Moss *et al.* 1995).

Rostherne Mere belongs to a group of lakes, the North-West Midland Meres, that have been described as being naturally eutrophic (Reynolds & Sinker, 1976). This is believed to be due to deposits of apatite, a phosphorus-rich mineral, present in the glacial drift deposits that cover much of the region (Reynolds, 1979). If the

phosphorus load is primarily derived from apatite deposits, control of anthropogenic nutrient loads from the catchment is unlikely to result in major changes in the lakes. However, following a consensus view that phosphorus control is the best strategy for lake restoration, sewage from a treatment works that discharged into Little Mere, a small, macrophyte-dominated shallow lake just upstream of Rostherne Mere, was diverted out of the system. Low quality effluent had caused near anoxia and fish reduction in Little Mere (Carvalho, 1994). The sewage effluent was diverted in June 1991, along with that from a smaller sewage treatment works that also discharged into the catchment, for treatment elsewhere.

A detailed monitoring programme for water chemistry, and the phytoplankton and zooplankton communities was used to assess the present state of the meres and to make predictions of the impact of the sewage diversion on the shallow Little Mere, and the deep Rostherne Mere. Mere Mere which lies upstream of Little Mere, was considered as a control lake. The detailed study began in January 1990, the first two years of data being collected by L. Carvalho and was continued by me until April 1994. In this chapter, data from 1990 to 1994 were used to assess the seasonality of nutrients in the system before and after the sewage effluent diversion.

2.1.2 Site description

Mere Mere, Little Mere and Rostherne Mere form of a series of lakes connected by Rostherne Brook (Fig 1.3). Rostherne Brook rises on Tabley Moss and flows into the south-west end of Mere Mere. Water enters Little Mere from Mere Mere over a concrete sluice and flows out over another sluice at the northern end of Little Mere. For a long period in the summer, when the water level in both lakes drops, water

stops flowing over the sluices. Rostherne Brook enters Rostherne Mere 2 km below Little Mere. 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 flows into the River Mersey and Manchester Ship Canal near Warrington.

There are several other short streams, springs, and transitory drainage ditches that flow into Rostherne Mere.

Mere Mere (National grid reference SJ 733 828) (Plate 2.1, Fig.2.1) has one of the most diverse aquatic floras of the North-West Midland Meres. Mere Mere was designated as an SSSI in 1985 because of its diverse aquatic plants. Its catchment area is mainly mixed farmland and woodland. The golf course of Mere Golf and Country Club borders the southern and western sides of the lake. Private housing lines the eastern side of the lake, whose eastern fringe has been largely changed by artificial banks, jetties and gardens. There is not much recreational use of the lake except limited angling and rowing. There is also a golf driving range into the lake.

Little Mere (National grid reference SJ 733 828) (Plate 2.2, Fig. 2.1) is a shallow lake, with an abundant plant community which covers over 75 % of the lake surface area. The flora is not as diverse as in Mere Mere. From sediment cores it appears to be a relatively new lake, and most likely man-made. The catchment area consists of golf-course, agricultural land, and woodland. The lake is surrounded partly by private housing and mixed woodland. There was a sewage treatment works (Mere S.T.W.) situated on its banks (Fig. 1.3) that was diverted in 1991. The basins of Mere Mere

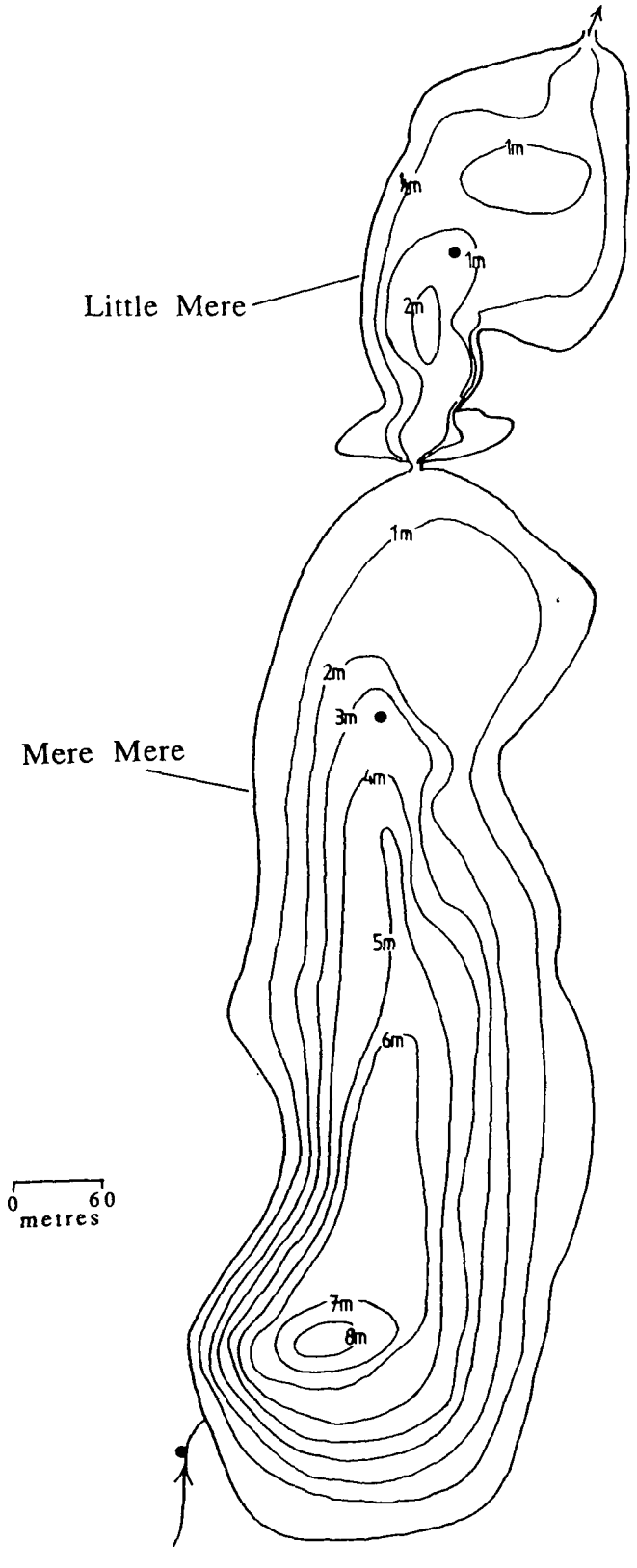

Fig.2.1 Bathymetric map of Mere Mere (surveyed June 1992) and Little Mere (surveyed April 1992). Depths shown are in metres. Solid round symbols (●) indicate the sampling points in this study.

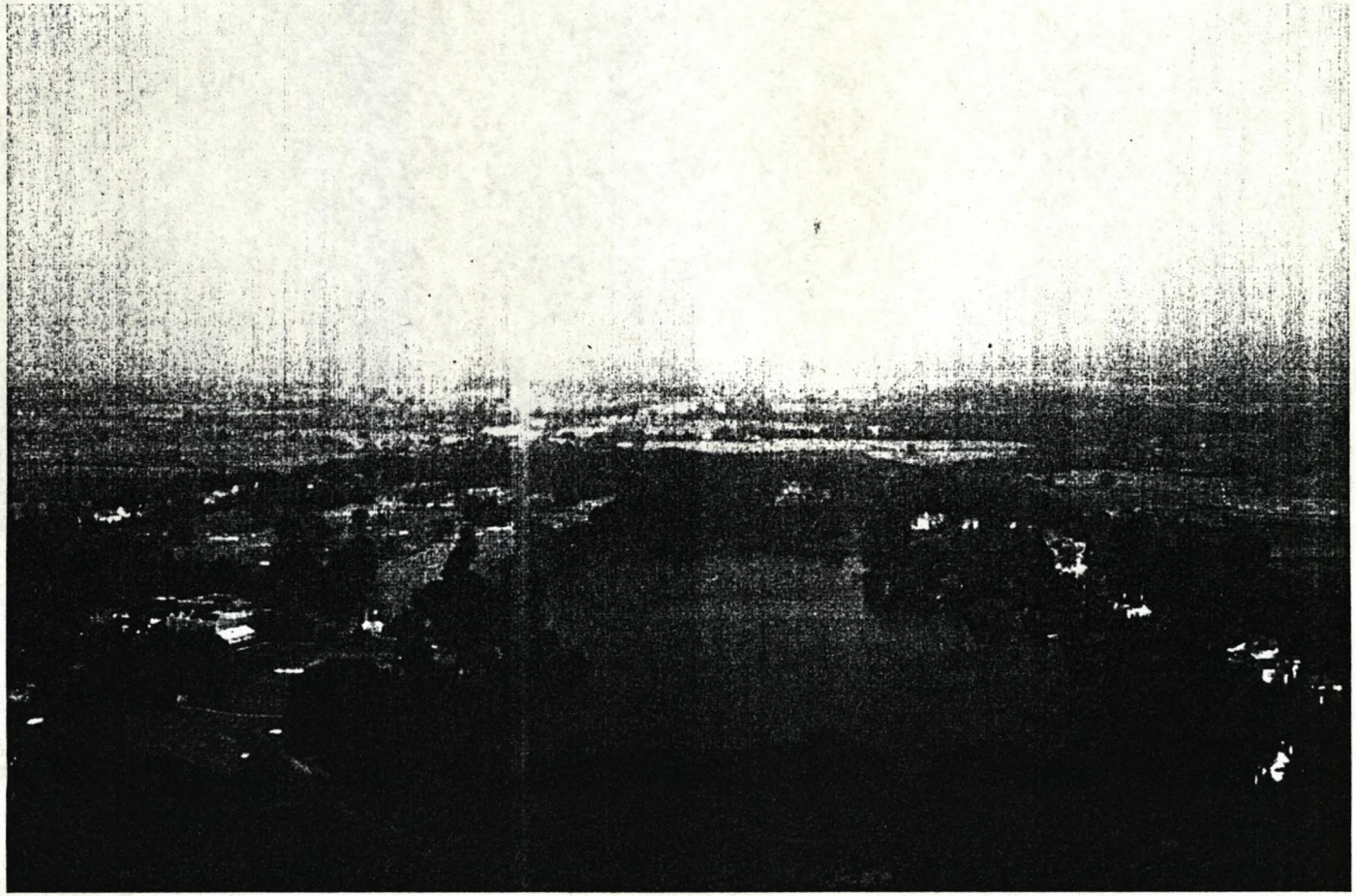

Plate 2.1 Aerial view of Mere Mere, with Golf and Country Club. (photographed May 1992).

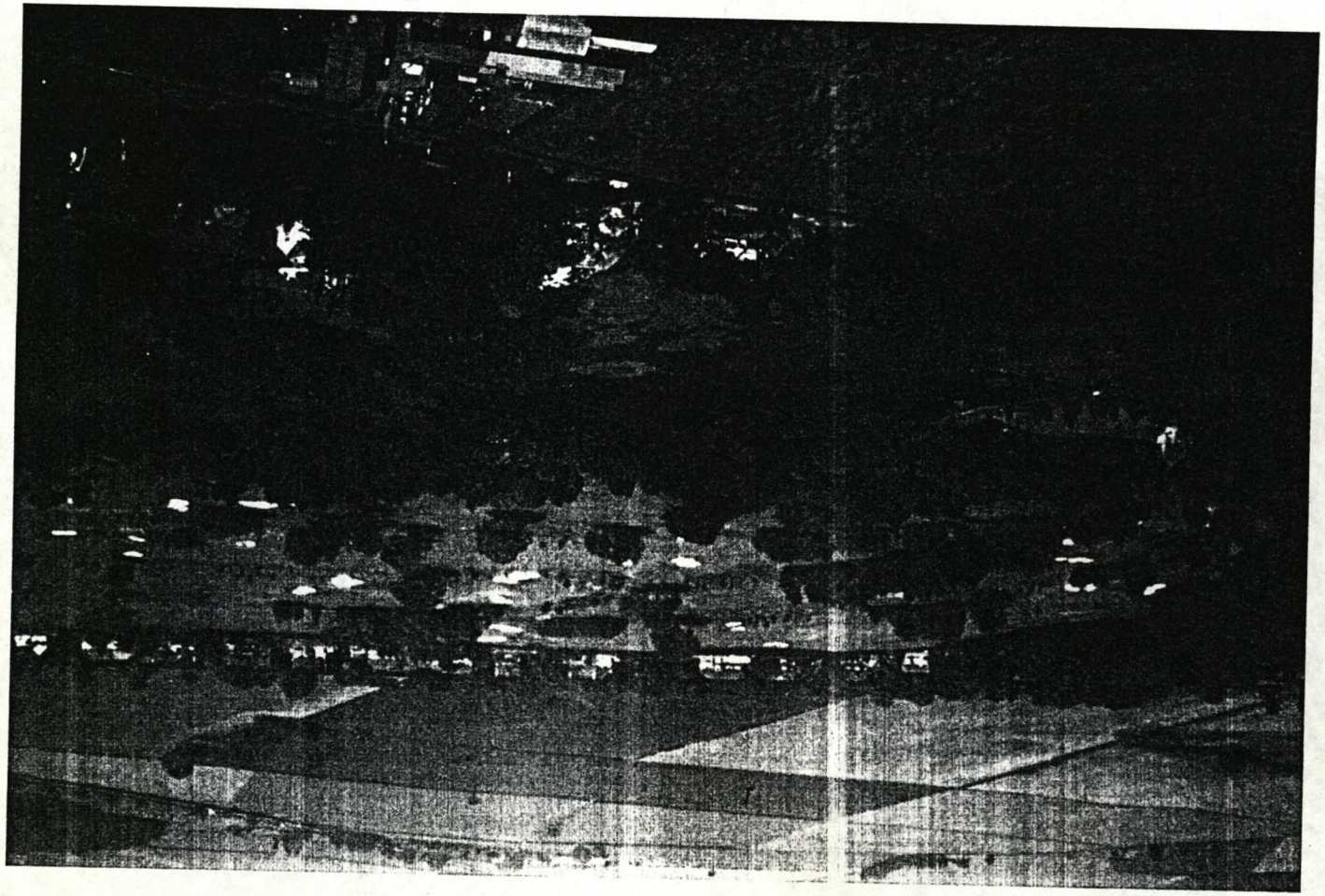

Plate 2.2 Aerial view of Little Mere, showing coverage of water lilies (photographed May 1992).

and Little Mere 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).

Rostherne Mere (National Grid reference SJ 745 844) (Plate 2.3, Fig 2.2) is the deepest and one of the largest of the North-West Midland Meres. Rostherne Mere is a grade 1 SSSI and became a National Nature Reserve in 1961. It is listed under the Ramsar Convention as a wetland of international importance as it is an important site for wintering wildfowl. There is no public access to the lake so as 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 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 lakes and their catchments are shown in Table 2.1.

2.1.3. Background to the study

Mere Mere and Little Mere have received very little limnological attention in the past. The phytoplankton of Mere Mere has been studied on three occasions (discussed in Chapter 3), but there are no past water chemistry data neither for Mere Mere or Little Mere.

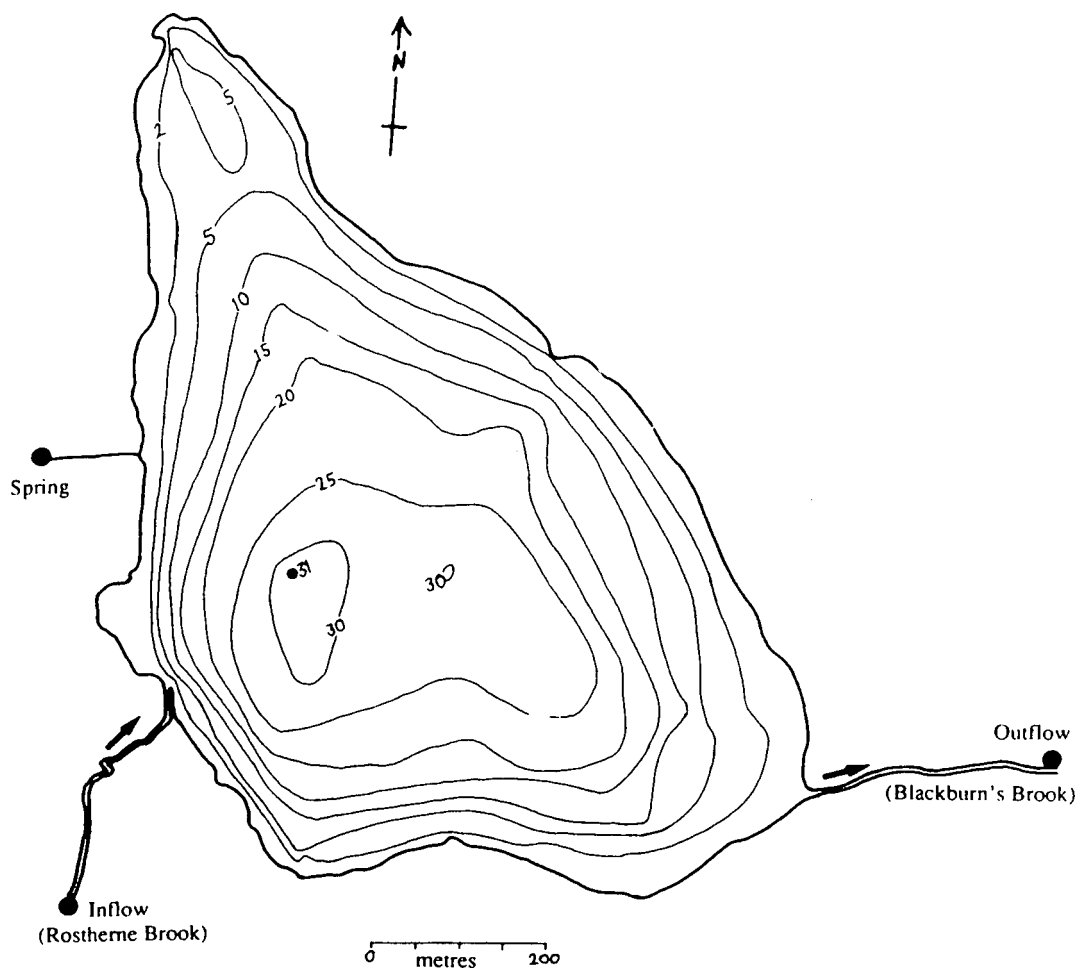

Fig.2.2 Bathymetric map of Rostherne Mere (taken from Woof and Wall 1984). Depths shown are in metres. Solid round symbols (●) indicate the sampling points in this study.

Plate 2.3 Aerial view of Rostherne Mere, with Rostherne village in the foreground (photographed May 1992).

Table 2.1 Details of Mere Mere, Little Mere and Rostherne Mere and their catchments.

	Mere Mere	Little Mere	Rostherne Mere
Geographical co-ordinates	53 20' N 2° 24' W	53 20' N 2° 24' W	53 20' N 2° 23' W
Altitude (m a.s.l.)	51	50	21
Surface area (ha.)	15.5	2.8	48.7
Maximum depth (m)	8.0	2.6	31
Mean depth (m)	2.8	0.7	13.6
Volume (m^3)	4.4×10^5	2.1×10^4	6.6×10^6
Catchment area (ha)	310	351	940
Time taken to displace the lake volume (year)	0.8-9.5	0.03-0.4	1.6-1.8

In contrast with the other meres, Rostherne Mere has had much limnological attention in the past. The phytoplankton of Rostherne Mere has been studied on many occasions (discussed in chapter 3). Chemical analyses of the water of Rostherne Mere have previously been carried out by Tattersall & Coward (1914), Gorham (1957), Grimshaw & Hudson (1970), and the North West Water Authority (N.W.W.A.) (1983). Unfortunately, (Gorham, 1957) pre-1960 data of nitrogen and phosphorus are unlikely to be accurate because only a single winter sampling was taken and the samples were stored for a long period before analysis. The first reliable data are from the study by Grimshaw & Hudson (1970) in which phosphate was never undetectable, the minimum concentration recorded being 100 $\mu g\ l^{-1}$, but nitrate concentrations were undetectable near the end of the summer. Nitrogen has been suggested as being an important limiting nutrient in Rostherne Mere pre-1960 (Reynolds, 1978a), and is still considered to be the limiting nutrient in many other deep North-West Midland Meres (Moss *et al.* 1994).

The sewage treatment works (S.T.W.) at Little Mere was 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. Sewage entering it was diverted on June 25 1991 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. 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 and phosphate and ammonium were in such excess that considerable

quantities passed through the outflow into Rostherne Brook (NWWA, 1983). The other S.T.W. was situated in the catchment of Rostherne Mere and was an important phosphorus point source for Rostherne Mere. It was closed in 1991 with the intention of reducing phytoplankton crop-size in Rostherne Mere (NWWA, 1983).

2.2 Methods

2.2.1 Physical factors and water chemistry

Water samples were collected at fortnightly intervals from October 1990 to March 1994. Lake samples for Mere Mere and Rostherne Mere were taken from the top 4 m, at the middle of the lake using a weighted polyethylene hose pipe. Because of the shallow, unstratified nature of Little Mere, samples were taken using a 1 m long plastic tube at the middle of the lake. Samples were transferred into acid-washed 1-litre pyrex bottles. Water temperature and dissolved oxygen concentrations were measured, in the afternoon, using a WTW oxygen meter. Water samples were also taken from Rostherne Brook just upstream of Mere Mere (Inflow Mere Mere), from Rostherne Brook just upstream of Rostherne Mere (Inflow Rostherne Mere) at the sites shown in figure 2.1 and 2.2 Water samples were also taken from the Harper's Bank spring inflow to Rostherne Mere, and the outflow of Rostherne Mere was also sampled.

Chemical analyses were carried out on return to the laboratory and on the following day. Table 2.2 gives a list of 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 the day of sampling laboratory using a Corning 250 pH meter and Jenway 4010 conductivity meter.

2.2.2 Chlorophyll a and carotenoids

A measured volume of water was filtered through a 4.5 cm diameter GF/C filter. The

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 Chapter 2 and 3	± 5 %

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 centrifuged at 4000 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 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 2.1:

$$Chlorophyll\ a\ (\mu g l^{-1}) = \frac{110\ .\ Absorbance\ (663)}{V} \qquad (2.1)$$

Where V = volume of water filtered in litres.

Carotenoid concentrations were calculated from the absorbance at 480 nm (Richards with Thompson, 1952) as in equation 2.2:

$$Carotenoids\ (mspu\ l^{-1}) = \frac{100\ .\ Absorbance\ (480)}{V} \qquad (2.2)$$

2.2.3. Bathymetric survey

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

2.3. Results

Detailed physical and chemical data recorded for Mere Mere, Little Mere and Rostherne Mere can be found in Appendix 1.

2.3.1 Mere Mere

Temperature (Fig. 2.3a) increased in spring and summer from winter zero values under ice cover (Dec 1992, Jan & Nov 1993 & Feb 1994), reaching 21.3 °C during August 1992. There was no evidence of stratification in the top 2 m, but during calm periods of summer it certainly occurred at greater depths. There was no particular seasonal pattern of dissolved oxygen (Fig. 2.3b). There was a decrease of percentage saturation of dissolved oxygen with depth during summer.

There were no clear trends in annual mean concentrations of soluble reactive phosphorus (SRP) and total phosphorus (TP) (Table 2.3, Fig. 2.4a). The highest concentrations of SRP were found during winter months and never exceeded 50 $\mu g\ l^{-1}$, whilst from February to September concentrations were almost always undetectable. There was no significant correlation between inflow Mere Mere and the lake SRP concentrations ($p>0.25$, $n=99$). The fact that the highest SRP concentrations of inflow Mere Mere were found during summer months (April to September) and the lowest concentrations in the winter months (Fig. 2.5a). There was no clear seasonality of total phosphorus concentrations in Mere Mere (Fig 2. 4a), and the concentrations ranged from 16 to 255 $\mu g\ l^{-1}$. The inflow TP concentrations showed a similar pattern to the SRP concentrations in the inflow (Fig 2.5a). There was a significant correlation between the lake TP and the inflow TP ($r^2= 0.39$ $p<0.0001$, $n=95$).

Table 2.3. Mean annual values (± 1 SD) of soluble reactive and total phosphorus (SRP & TP), dissolved inorganic nitrogen (DIN), ammonium-nitrogen (NH_4-N), and total oxidised nitrogen (TON:nitrate+nitrite), and phytoplankton chlorophyll a, in Mere Mere and its inflow, Rostherne Mere and its main inflow, and Little Mere, between 1990 and 1993, comparisons of the variables between before diversion (10.1.1990 to 11.6.1991) and after diversion (25.6.1991 to 21.12.1993) by t-test; symbols *P<0.05, **P<0.01, ***P<0.001 and NS: no significance.

Sites		1990	1991	1992	1993	t-test
Mere Mere	SRP ($\mu g\ l^{-1}$)	7±7	21±10	14±15	12±11	*
	TP ($\mu g\ l^{-1}$)	80±25	55±20	70±55	95±70	NS
	DIN ($mg\ l^{-1}$)	0.76±0.58	0.93±0.81	0.93±0.74	0.55±.50	* * *
	NH_4($\mu g\ l^{-1}$)	62±98	72±77	53±57	47±58	NS
	TON($mg\ l^{-1}$)	0.7±0.58	0.85±0.8	0.88±0.7	0.51±.49	* * *
	C'phyll a($\mu g\ l^{-1}$)	24±16	18±18	19±16	34±36	NS
Little Mere	SRP ($\mu g\ l^{-1}$)	1950±1670	1250±792	259±314	62±51	* * *
	TP ($\mu g\ l^{-1}$)	2245±1755	1420±875	410±400	185±200	* * *
	DIN ($mg\ l^{-1}$)	3.81±3.36	2.6±1.4	0.67±0.49	0.33±0.4	* * *
	NH_4($\mu g\ l^{-1}$)	3390±3450	2230±1430	276±401	80±96	* * *
	TON($mg\ l^{-1}$)	0.42±0.36	0.32±0.26	0.39±043	0.25±.38	NS
	C'phyll a($\mu g\ l^{-1}$)	59±103	11±28	6±10	17±16	* * *
Rostherne	SRP ($\mu g\ l^{-1}$)	296±99	339±107	333±175	280±108	NS
Mere	TP ($\mu g\ l^{-1}$)	373±95	420±125	505±240	400±220	NS
	DIN ($mg\ l^{-1}$)	0.66±0.33	0.86±0.50	0.82±0.5	0.59±.23	*
	NH_4($\mu g\ l^{-1}$)	55±95	115±190	119±125	86±150	NS
	TON($mg\ l^{-1}$)	0.61±0.33	0.71±0.50	0.7±0.51	0.51±.20	*
	C'phyll a($\mu g\ l^{-1}$)	20±19	16±22	13±16	14±16	NS
Inflow	SRP ($\mu g\ l^{-1}$)	96±50	77±65	96±110	47±20	NS
Mere Mere	TP ($\mu g\ l^{-1}$)	220±100	170±110	185±170	180±151	NS
	DIN ($mg\ l^{-1}$)	2.10±1.22	2.41±1.30	2.30±1.20	1.69±.84	* *
	NH_4($\mu g\ l^{-1}$)	269±110	440±570	432±515	162±142	NS
	TON($mg\ l^{-1}$)	1.85±1.22	1.97±1.62	1.88±1.44	1.53±.80	* *
Inflow	SRP ($\mu g\ l^{-1}$)	284±179	185±132	72±45	52±33	* * *
Rostherne	TP ($\mu g\ l^{-1}$)	590±655	380±215	190±110	150±90	* * *
Mere	DIN ($mg\ l^{-1}$)	2.54±1.18	4.20±0.74	2.40±1.11	1.42±.73	* * *
	NH_4($\mu g\ l^{-1}$)	440±475	325±270	144±112	119±176	* * *
	TON($mg\ l^{-1}$)	2.10±1.08	2.44±1.10	2.2±01	1.30±.70	* *

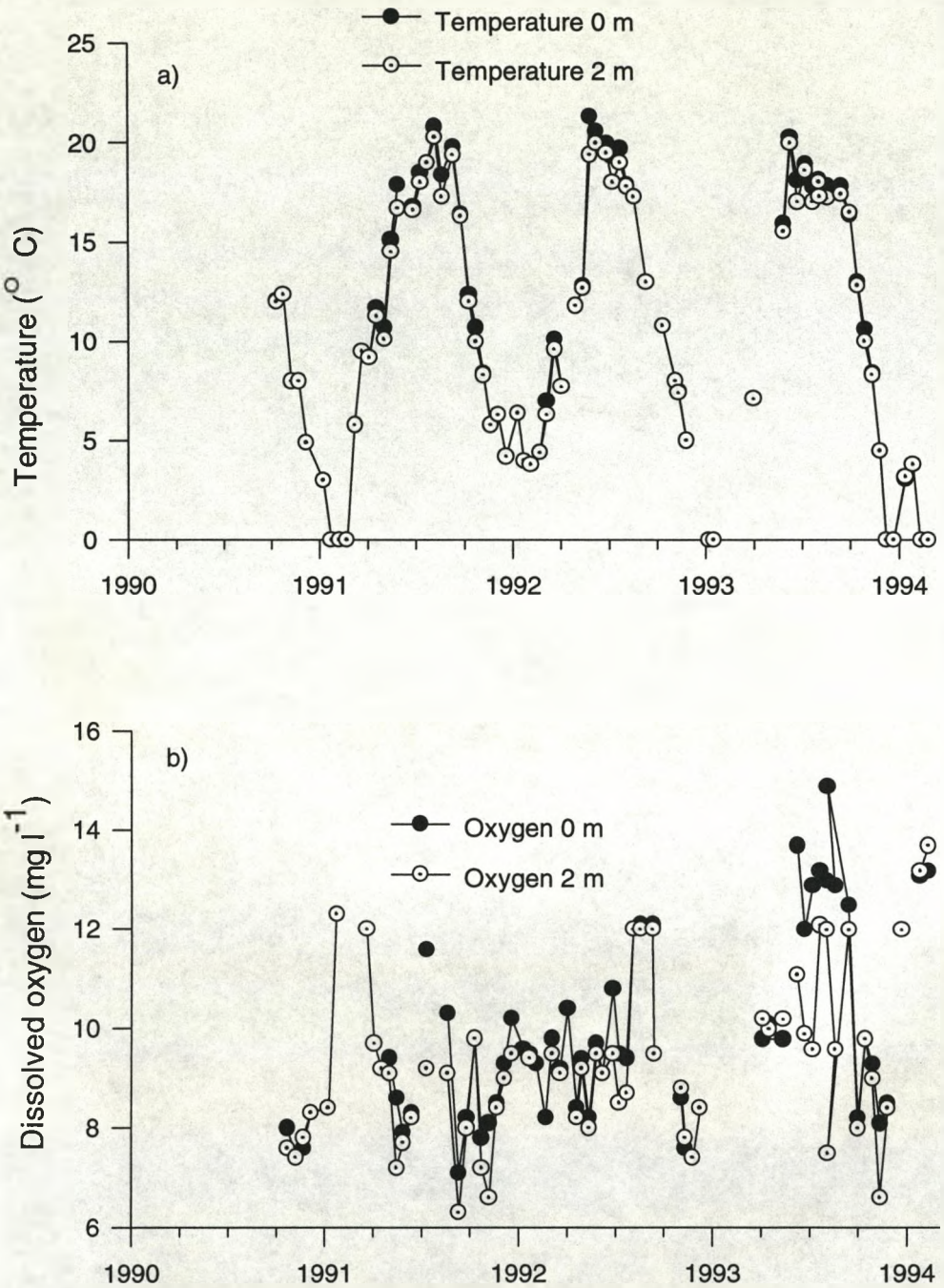

Fig. 2.3 Seasonality of a) temperature at the surface (0 m) and at 2 m. depth, and b) dissolved oxygen at the surface (0 m) and at 2 m depth in Mere Mere between 1990 and 1994 (first three months data of 1994 were used).

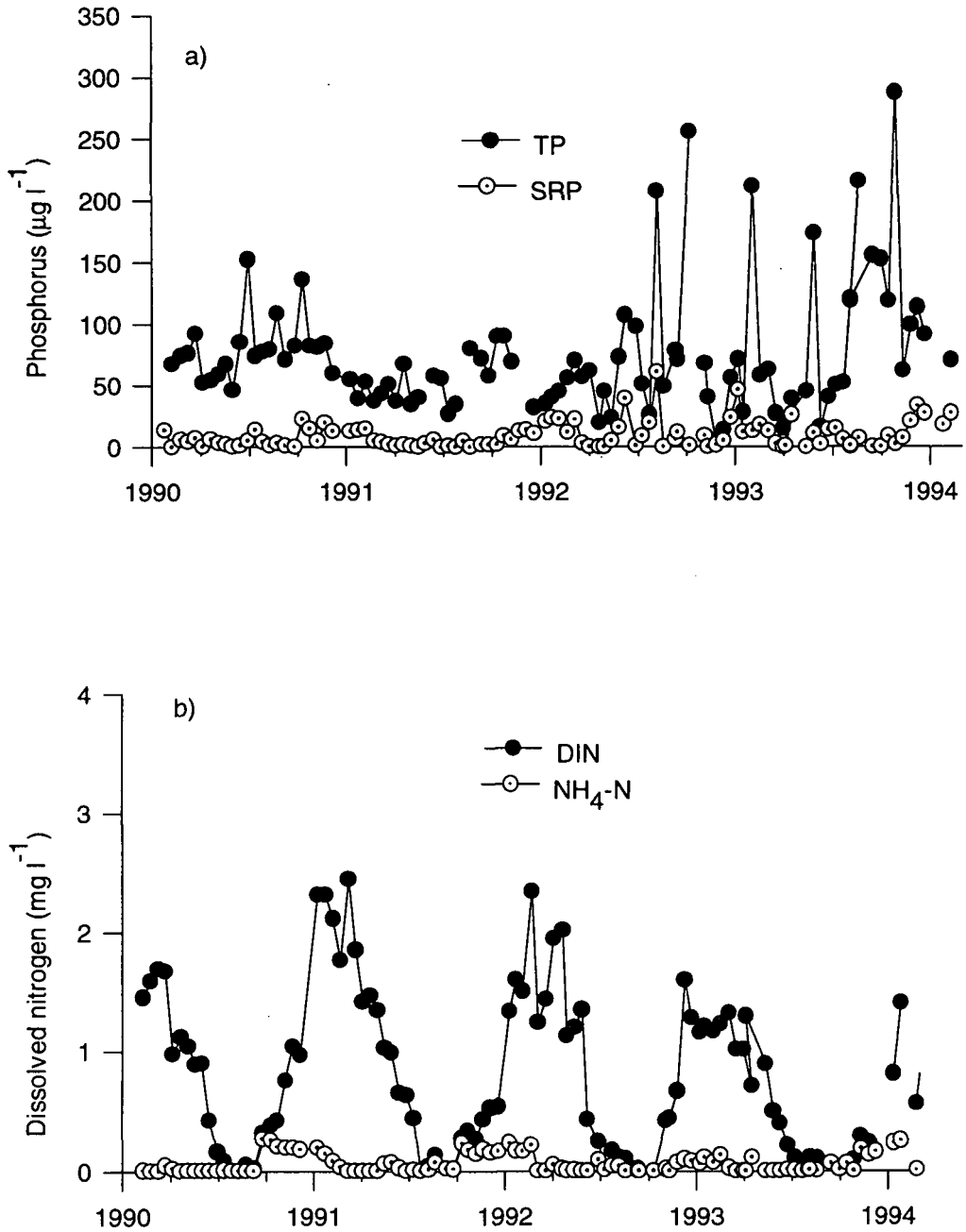

Fig. 2.4 Changes in concentrations of a) total phosphorus (TP) and soluable reactive phosphorus (SRP) b) dissolved inorganic nitrogen (DIN) and ammonium-nitrogen (NH_4-N) in Mere Mere, between 1990 and 1994 (first three months data of 1994 were used).

Dissolved inorganic nitrogen (DIN) (Fig 2.4b) showed clear seasonality over the four-year data set. Maximum concentrations were recorded in the winter months: March 1991, February 1992, December 1993 and January 1994 (2.45 mg l^{-1}, 2.35 mg l^{-1}, 1.33 mg l^{-1} and 1.41 mg l^{-1} respectively). The concentrations declined to undetectable levels by July in all years. The DIN concentration of inflow Mere Mere showed the same seasonal pattern (Fig. 2.5b), increasing in winter and decreasing in summer so that the lake and the inflow concentrations were significantly correlated (r^2=0.694 $p<0.0001$, n=98).There was a marked decrease in the DIN concentrations of the lake in 1993 and 1994. This is probably due to lower loading of DIN from the inflow, where the concentrations of DIN were markedly lower in 1993 and 1994 than in the previous years. Ammonium-nitrogen (NH_4-N) concentrations showed slightly different seasonality with minima in spring and summer (0 µg l^{-1} for all the years) (Fig. 2.4b) The concentrations sharply increased in autumn and stayed high in winter. Recorded maximum concentrations were 266 µg l^{-1} in Sep 1990, 232 µg l^{-1} in Oct 1991, 154 µg l^{-1} in Dec 1992, 185 µg l^{-1} in Nov 1992 and 250 µg l^{-1} in 1994. There was no significant correlation between the lake NH_4-N concentrations and the inflow NH_4-N concentrations ($p<0.25$, n=99) (Fig. 2.5b). The lake NH_4-N concentrations showed significant correlation with the lake SRP concentrations (r^2=0.45, $p<0.0001$, n=99) (Fig. 2.6a). The concentration maxima in autumn and winter are probably partly due to mixing of the hypolimnion water as well as greater leaching from the land compared with summer.

Nitrate-nitrogen (Fig. 2.6b) had a similar seasonality with the DIN in as much as concentration maxima were recorded in winter (2.45 mg l^{-1} 1991, 2.13 mg l^{-1} 1992, 1.30 mg l^{-1}, 1993 and 1.16 mgl^{-1} 1994) and minima in summer (0 mg l^{-1} for all the

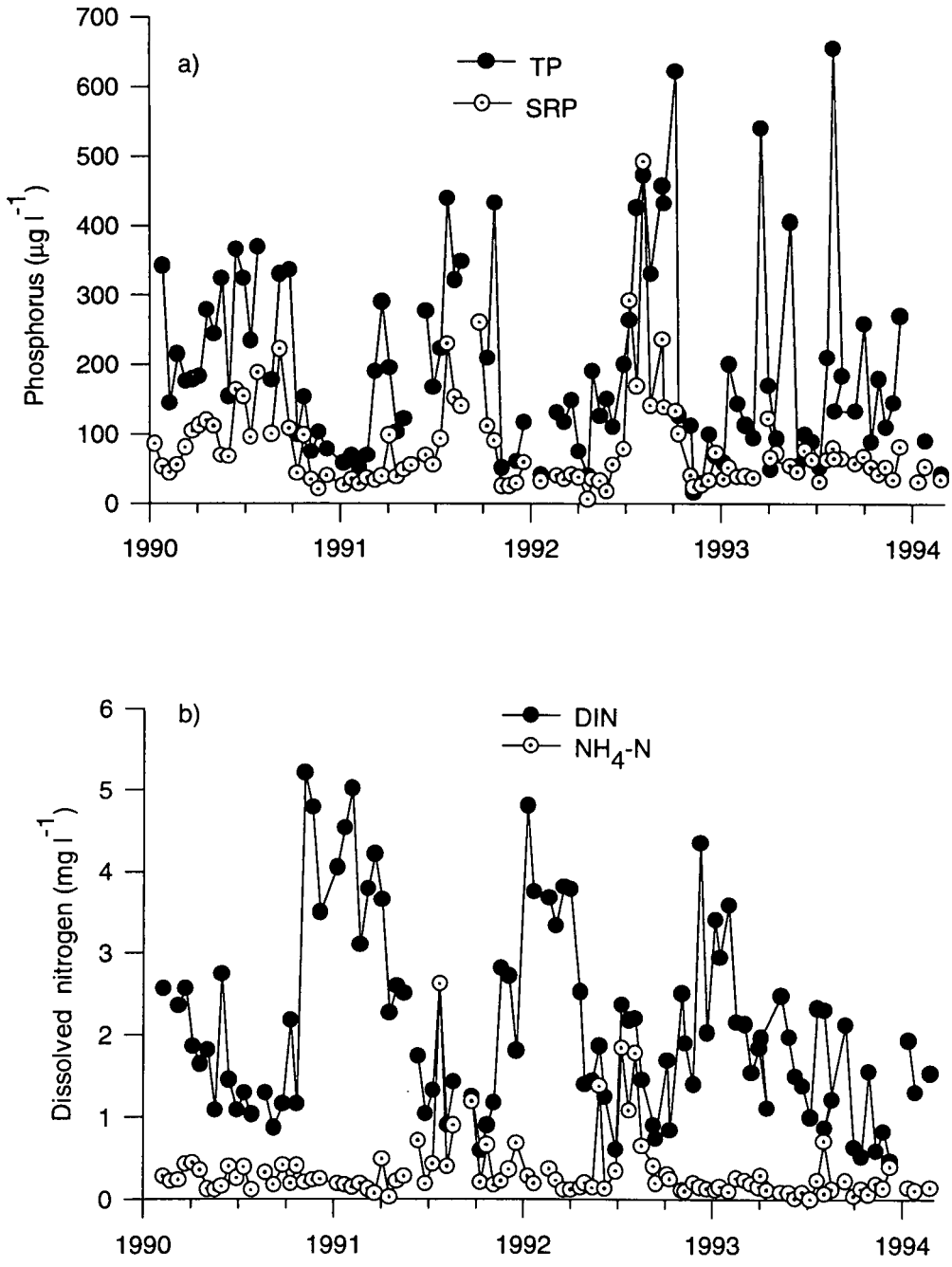

Fig. 2.5 Changes in concentrations of a) total phosphorus (TP) and soluble reactive phosphorus (SRP) b) dissolved inorganic nitrogen (DIN) and ammonium-nitrogen (NH_4-N), in inflow Mere Mere, between 1990 and 1994 (first three months data of 1994 were used).

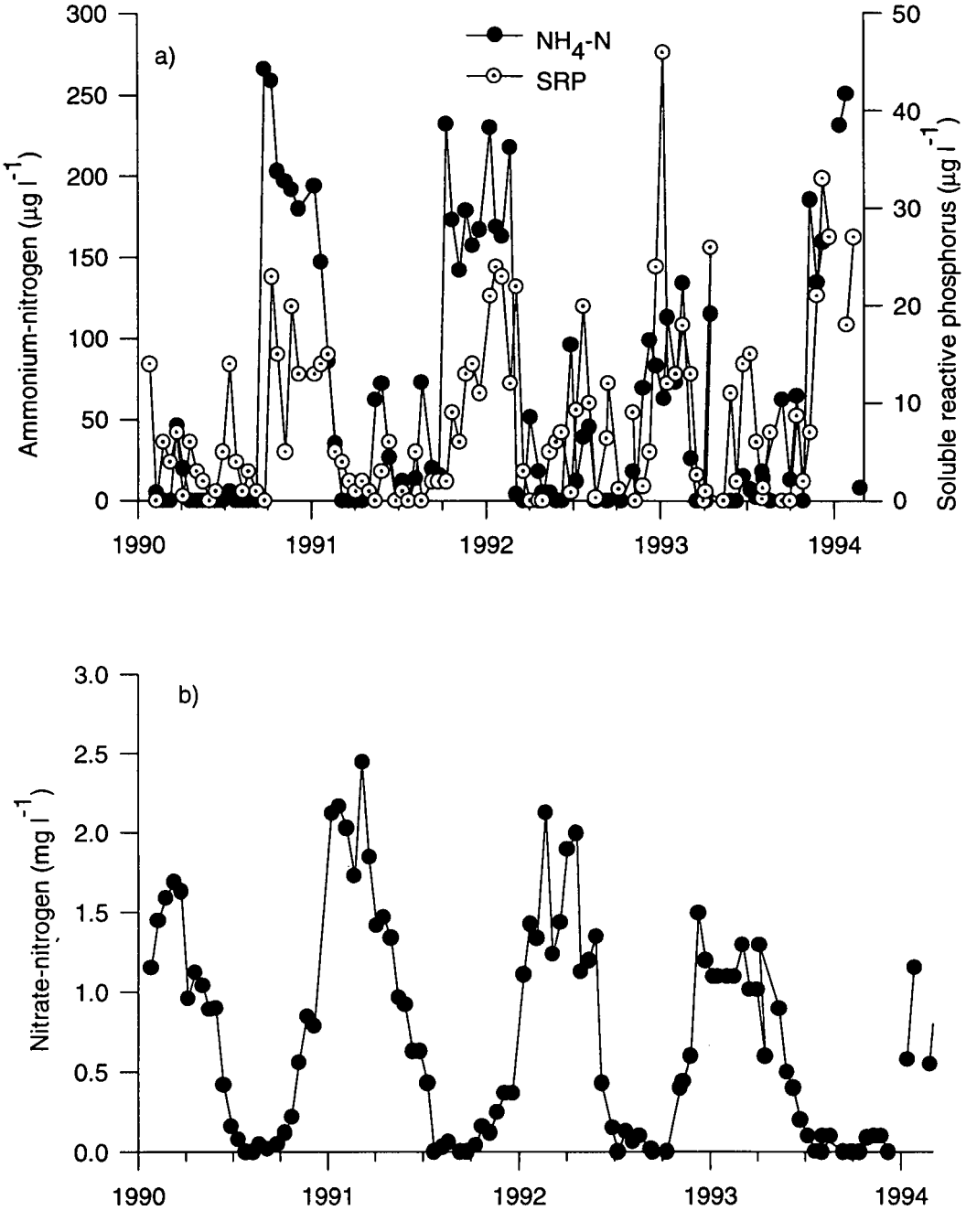

Fig. 2.6 Changes in concentrations of a) ammonium-nitrogen (NH_4-N) and soluble reactive phosphorus (SRP) b) nitrate-nitrogen ($N0_3$-N), in Mere Mere between 1990 and 1994 (first three months data of 1994 were used).

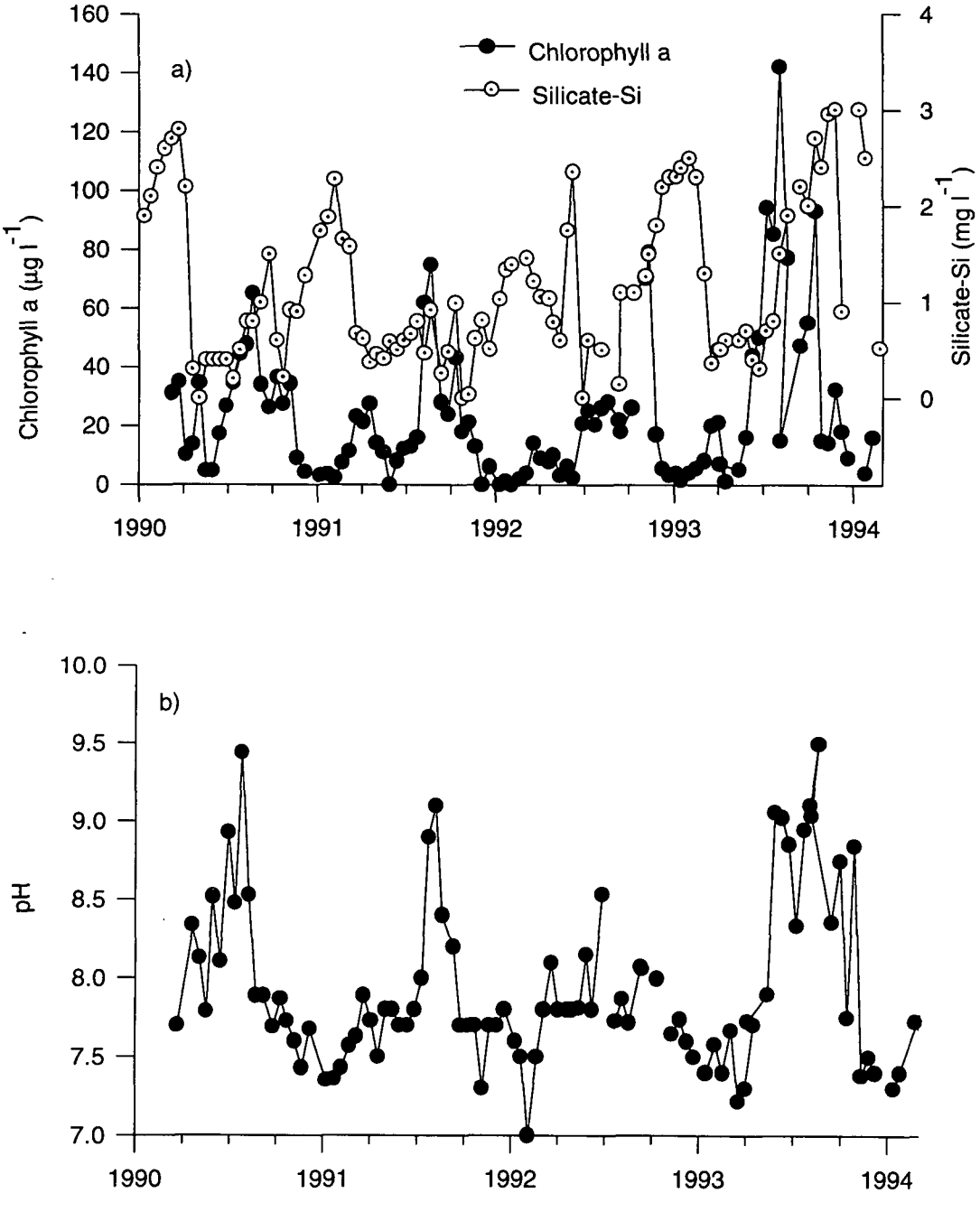

Fig. 2.7 Changes in concentrations of a) chlorophyll a and silicate-silicon (silicate-Si) and b) pH, in Mere Mere, between 1990 and 1994 (first three months data of 1994 were used).

years).

Silicate-silicon concentrations (Fig. 2.7a) showed minima in spring and autumn, declining to undetectable levels during May 1990, October 1991, September 1992, May 1993 and March 1994.

pH showed a clear seasonal pattern with minima in winter (7.3 in 1991, 7.0 in 1992, 7.4 in 1993 and 7.4 in 1994) and maxima in summer (9.4 1990, 9.1 1991, 8.5 1992 and 9.5 1993) (Fig. 2.7b). pH was strongly correlated with chlorophyll a concentrations (r^2=0.658, p<0.0001, n=95) (Fig. 2.7a). The concentration maxima of chlorophyll a were recorded in summer except 1992. They were 65 μg l^{-1} in August 1990, 75 μg l^{-1} in August 1991, 70 μg l^{-1} in November 1992 and 142 μg l^{-1} in July 1993.

2.3.2 Little Mere

Dissolved oxygen concentrations (measured at midday) (Fig. 2.9a) were very low before sewage effluent diversion. 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 increased to 18 mg l^{-1} which was closely related with high chlorophyll a (r^2=0.99, p<0.0001, n=99). Since September 1991 O_2 levels have been higher than before diversion. Recorded dissolved oxygen concentration maxima for summer 1992 and 1993 were 11.8 mg l^{-1} and 12 mg l^{-1}, and recorded dissolved oxygen concentration minima for summer 1992 and 1993 were 1.8 mg l^{-1} and 7.8 mg l^{-1} respectively.

Following the sewage effluent diversion in 1991, Little Mere showed a very clear

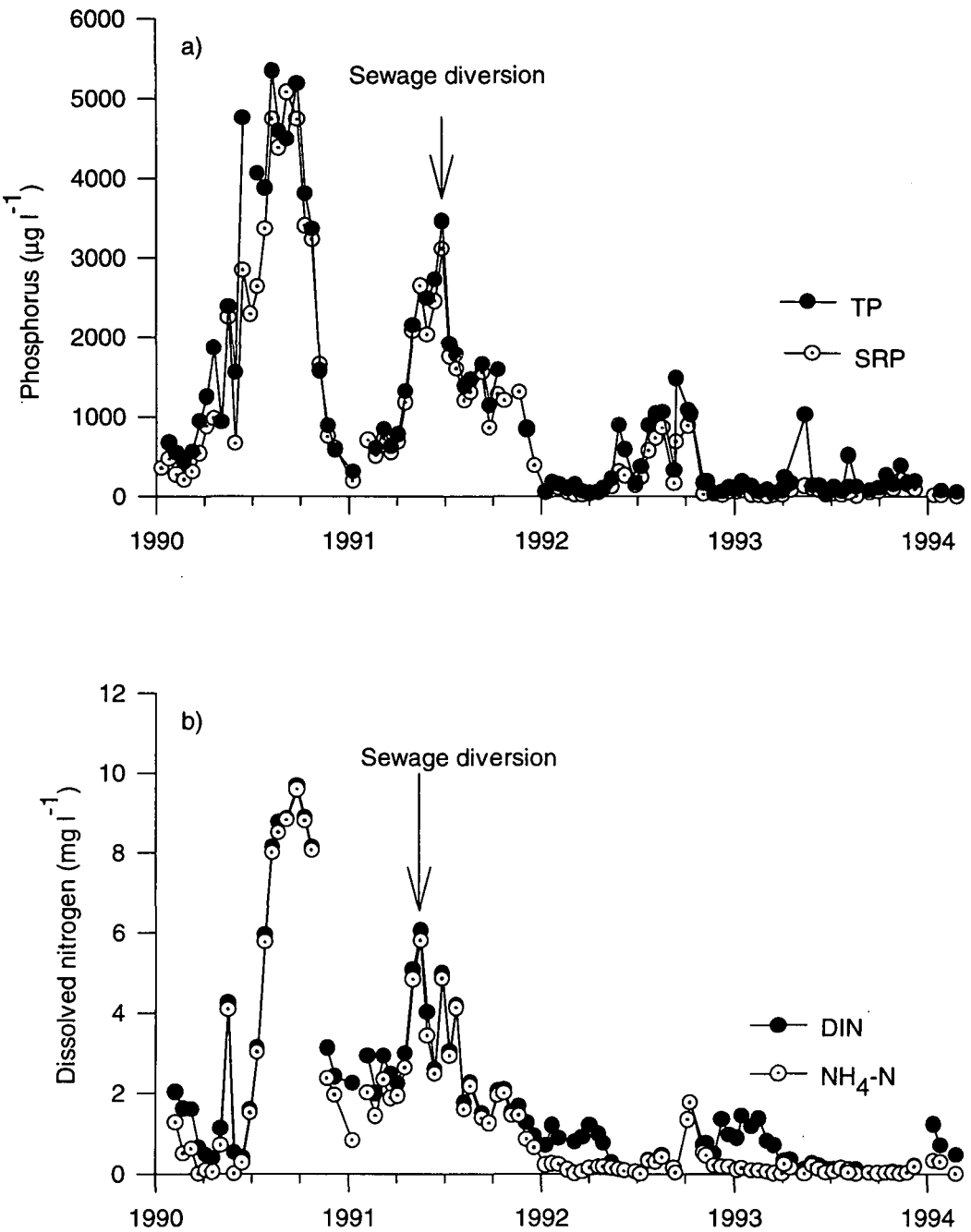

Fig. 2.8 Changes in concentrations of a) total phosphorus (TP) and soluble reactive phosphorus (SRP), and b)dissolved inorganic nitrogen (DIN) and ammonium-nitrogen (NH_4-N), in Little Mere, between 1990 and 1994 (first three months data of 1994 were used).

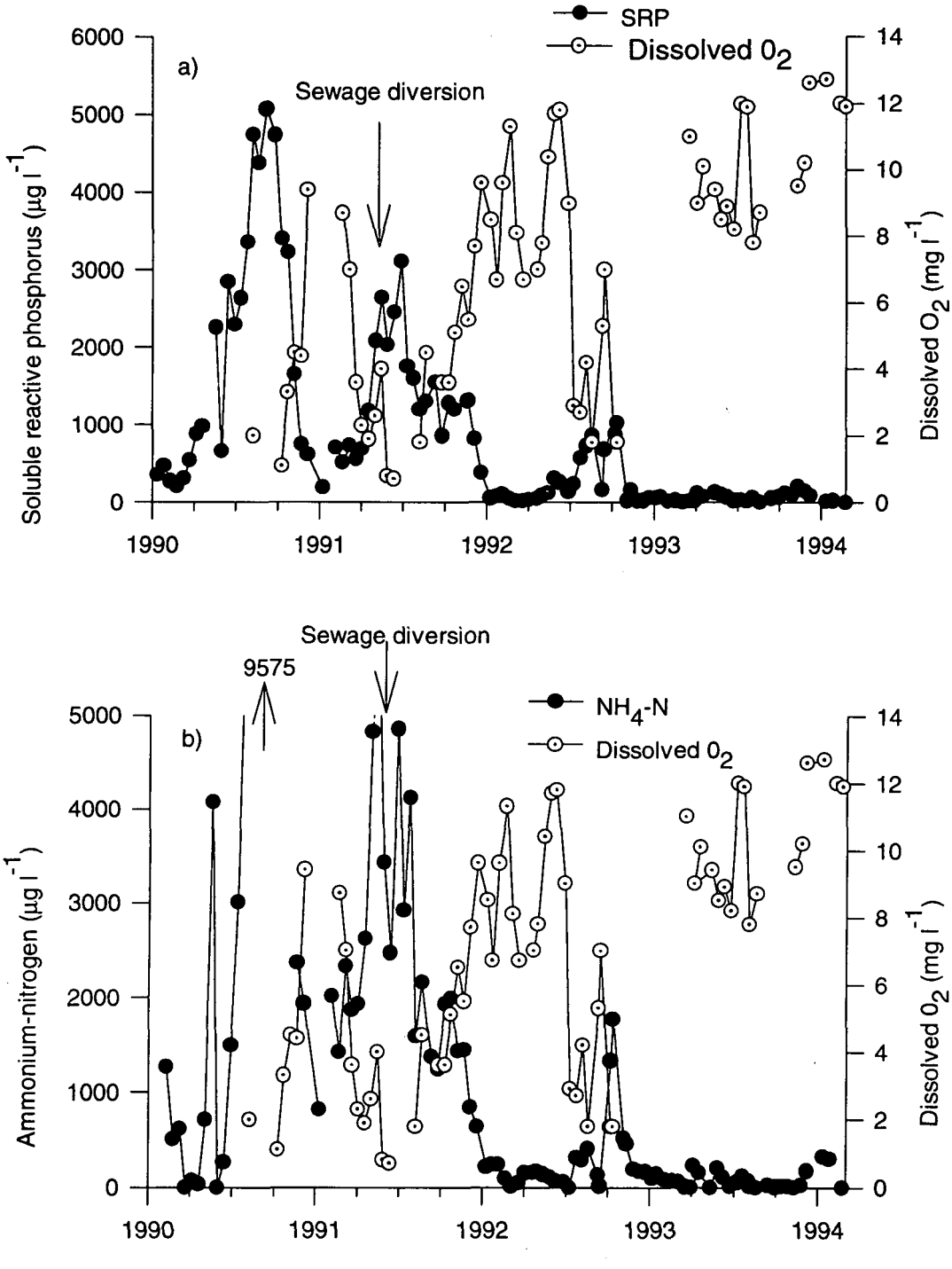

Fig. 2.9 Changes in concentrations of a) soluble reactive phosphorus (SRP) and dissolved oxygen and b) ammonium-nitrogen (NH_4-N) and dissolved oxygen in Little Mere, between 1990 and 1994 (first three months data of 1994 were used).

declining trend of SRP and TP (Fig. 2.8a). Extremely high concentrations of both were recorded in June 1990 (5.1 mg l^{-1} and 5.2 mg l^{-1} respectively). The concentrations have steadily declined from summer 1991 so that SRP concentration maxima were 3.1 mg l^{-1} in June 1991, 1.1 mg l^{-1} in August 1992 and 0.126 mg l^{-1} May 1993, and TP concentration maxima were 3.5 mg l-1 in June 1991, 1.5 mg l^{-1} in September 1992 and 0.512 in August 1993.

DIN and ammonium-nitrogen showed a similar pattern to those of SRP and TP. Following the effluent diversion their concentrations declined several fold (Fig. 2.8b). Pre-diversion concentration maxima of 9.7 mg l^{-1} DIN and 9.58 mg l^{-1} NH_4-N were recorded in summer 1990. The concentrations have steadily declined from early summer 1991 and the seasonality of the concentrations has shifted from summer maxima to autumn and winter maxima. After diversion, recorded concentration maxima of DIN were 1.77 mg l^{-1} in Oct 1992, 1.37 mg l^{-1} in Feb 1993 and 1.22 mg l^{-1} in Jan 1994. Recorded NH_4-N concentration maxima were 0.45 mg l^{-1} in Dec 1992, 0.23 mg l^{-1} in April 1993 and 0.320 mg l^{-1} in Jan 1994.

Nitrate-nitrogen concentrations were inversely correlated with NH_4-N concentrations (r^2=0.2 $p \leq 0.025$, n=101). Following the effluent diversion there was an increase in nitrate-nitrogen contribution to DIN and a decrease in NH_4-N contribution (Fig 2.10a). This was probably ultimately because of an increase in dissolved oxygen concentrations. Whilst nitrate-nitrogen concentrations were significantly correlated with dissolved oxygen concentrations (r^2=0.3, $p \leq 0.001$, n=101), NH_4-N concentrations were inversely correlated with dissolved oxygen concentrations (r^2=0.5, $p<0.0001$, n=101).

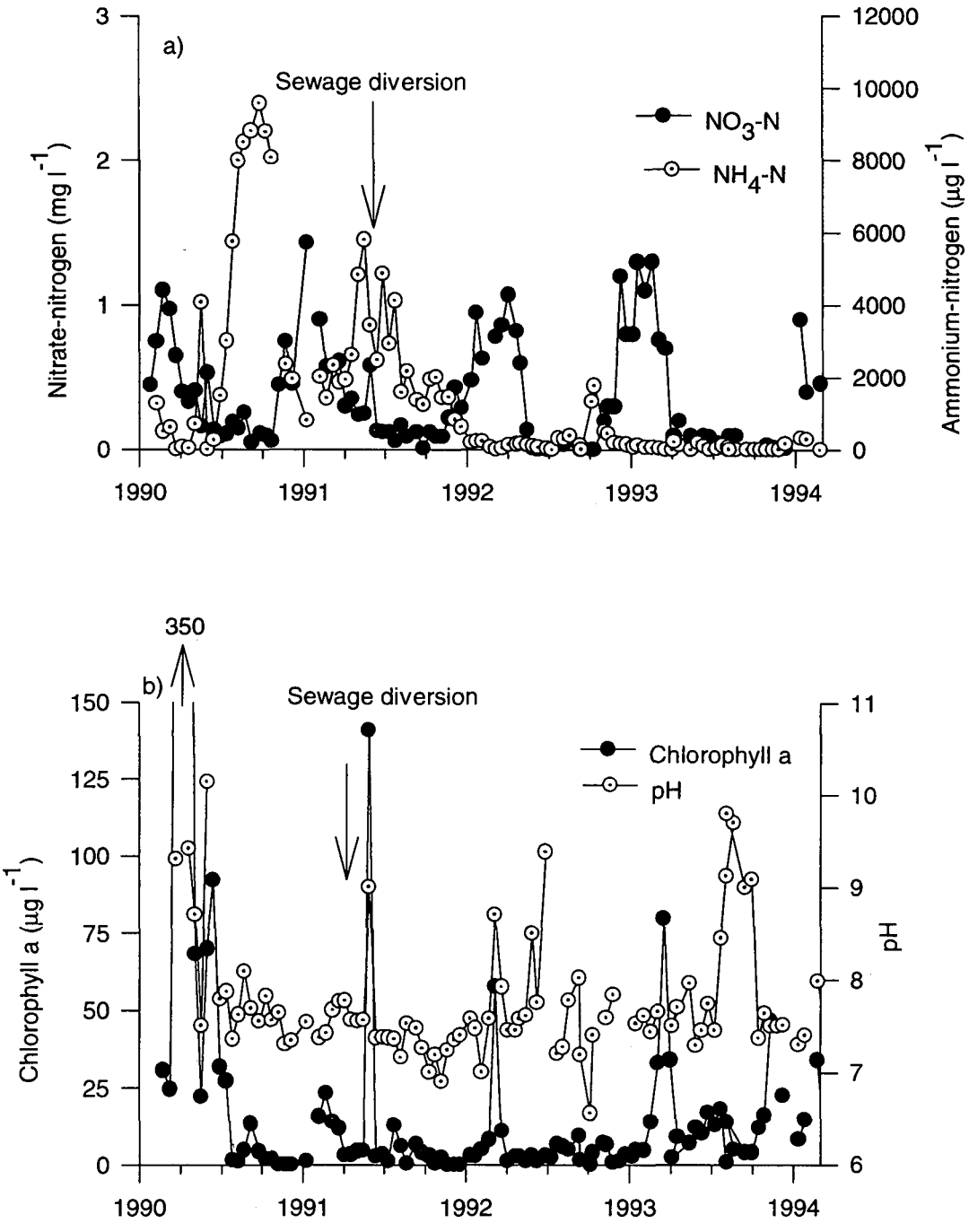

Fig. 2.10 Changes in concentrations of a) nitrate-nitrogen (NO_3-N) and ammonium-nitrogen (NH_4-N) and b)chlorophyll a and pH. in Little Mere between 1990 and 1994 (first three months data of 1994 were used).

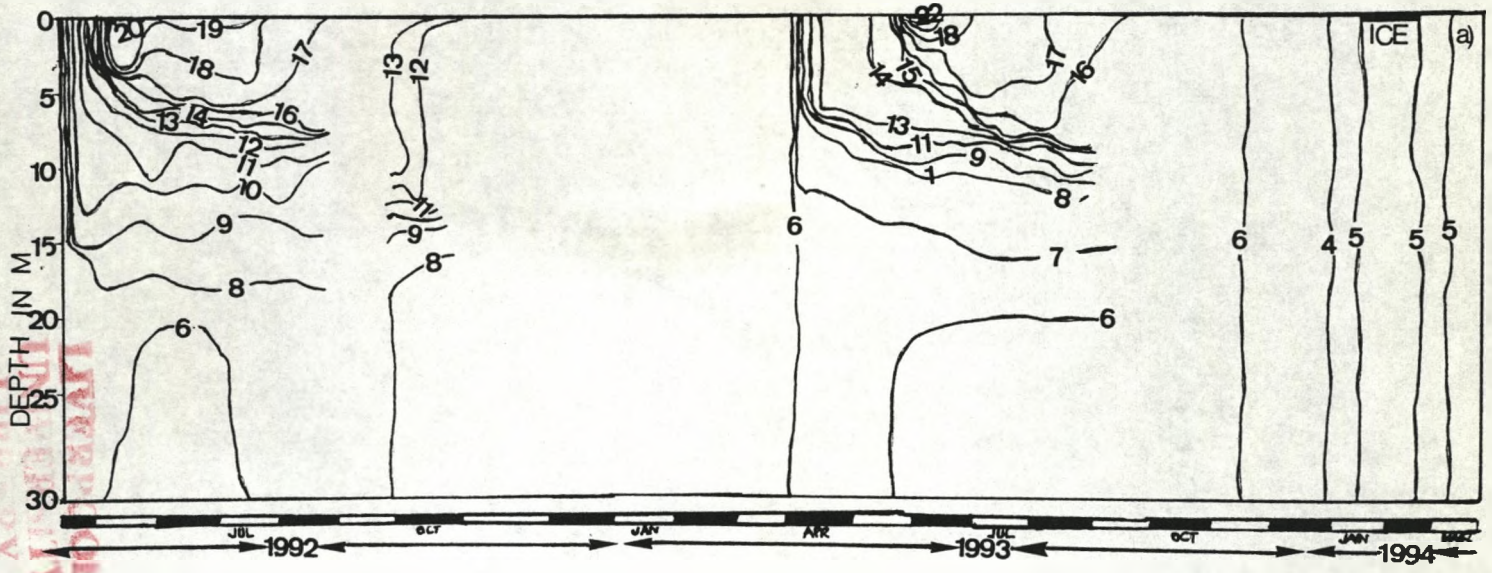

Fig.2.11a Depth-time diagrams for temperature (° C) in Rostherne Mere, from May 1992 to April 1994.

Fig.2.11b Depth-time diagrams for dissolved oxygen (mg l^{-1}) in Rostherne Mere, from May 1992 to April 1994.

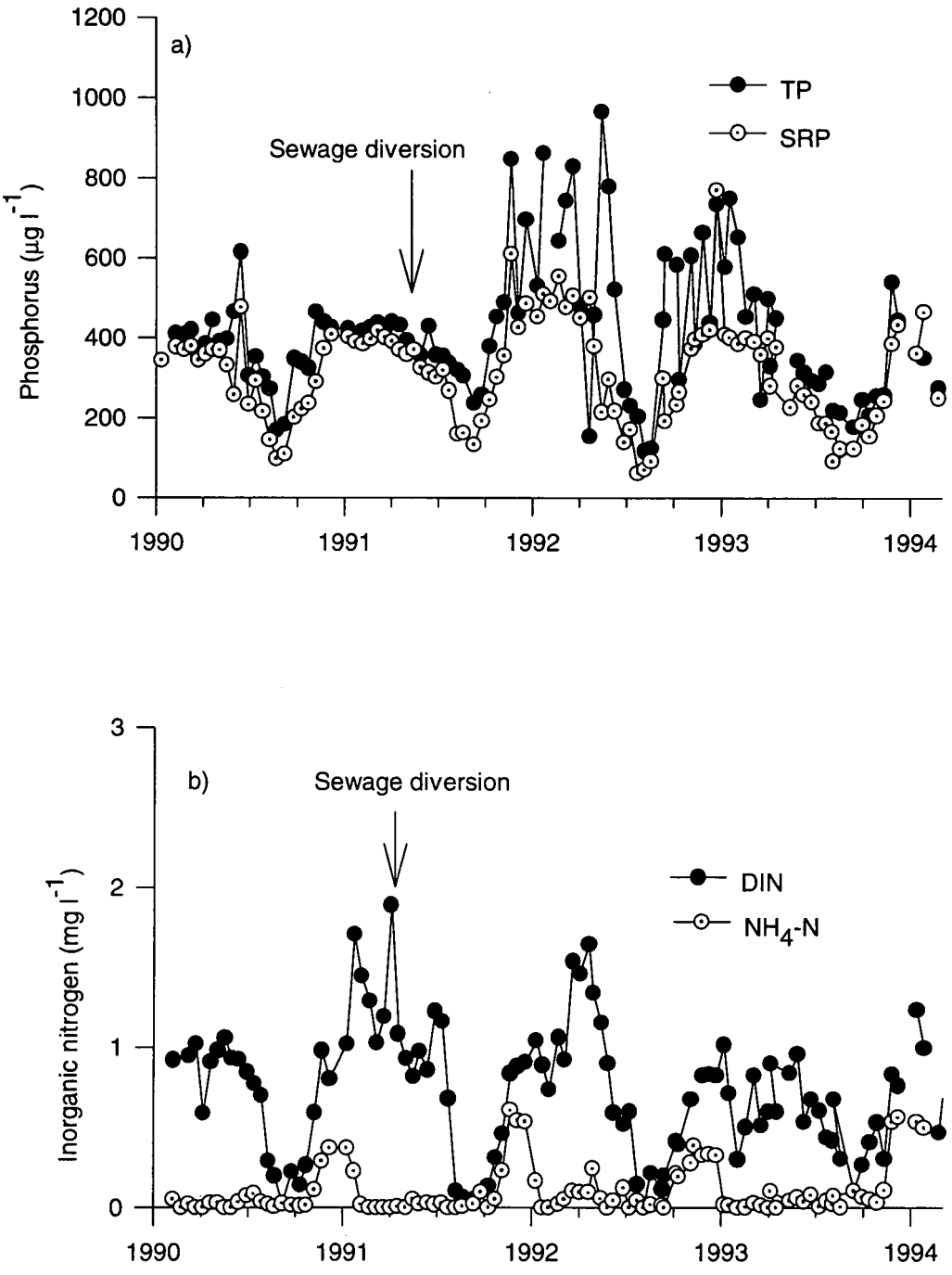

Fig. 2.12 Changes in concentrations of a) total phosphorus (TP) and soluble reactive phosphorus (SRP), b)dissolved inorganic nitrogen (DIN) and ammonium-nitrogen (NH_4-N) in Rostherne Mere, between 1990 and 1994 (first three months data of 1994

Both SRP and NH_4-N concentrations were directly related to each other (r^2=0.92, p<0.0001, n=101), and there was an inverse relationship for both of them with dissolved oxygen concentrations (SRP, r^2=0.54, p<0.0001, n=101; NH_4-N r^2=0.5, p<0.0001, n=101) (Fig. 2.9a and b).

pH was generally in the range 7-8, showing increases in the spring closely related with increase in chlorophyll a concentrations (r^2=0.48, p<0.0001, n=91) (Fig. 2.10b). Over four years data, the highest chlorophyll a concentrations were found in spring (354 µg l^{-1} 1990; 141 µg l^{-1} 1991; 60 µg l^{-1} 1992; 80 µg l^{-1} 1993) and were followed by very low summer concentrations despite the existence of a huge nutrient potential for algal growth. In summer 1993, the concentrations were slightly higher than the previous years.

2.3.3 Rostherne Mere

Fig.2.11 show the temperature and dissolved oxygen stratification over the period of study (May, 1992 to March, 1994). Temperature stratification sets in during May, though it was difficult to be clear about how long it lasted due to lack of data in autumn 1992 and 1993. In 1990 and 1991 it lasted untill the end of October (Carvalho, 1993). The development of stratification coincided with the development of a deoxygenated hypolimnium, for the rest of the year the lake was well mixed (Fig.2.11a and b).

Fig.2.12a shows the seasonality of total phosphorus and soluble reactive phosphorus in Rostherne Mere. There were no clear differences in the concentrations before and

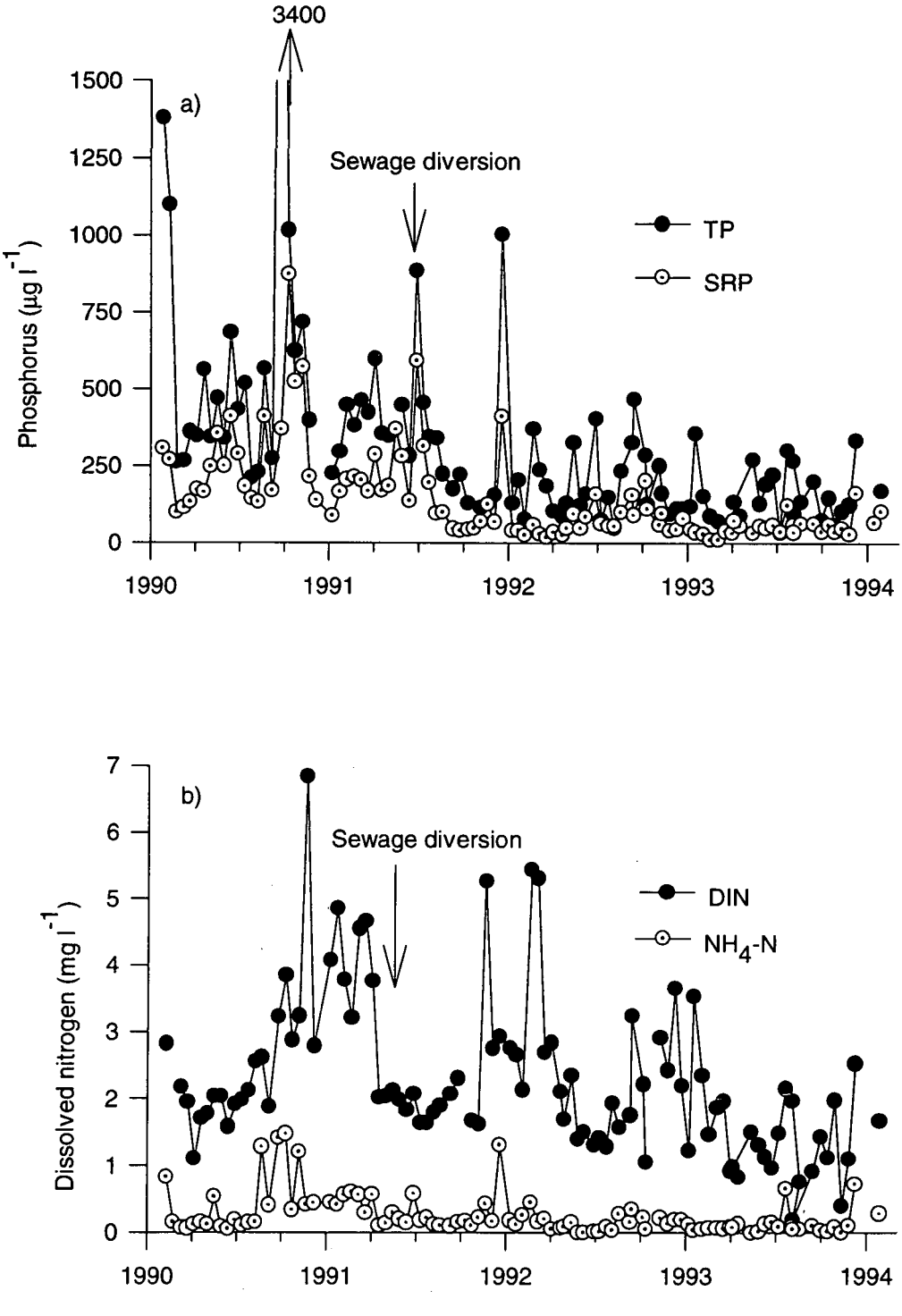

Fig. 2.13 Changes in concentration of a) total phosphorus and soluble reactive phosphorus (SRP), b) dissolved inorganic nitrogen (DIN) and ammonium-nitrogen (NH_4-N) in inflow Rostherne Mere, between 1990 and 1994 (first three months data of 1994 were used).

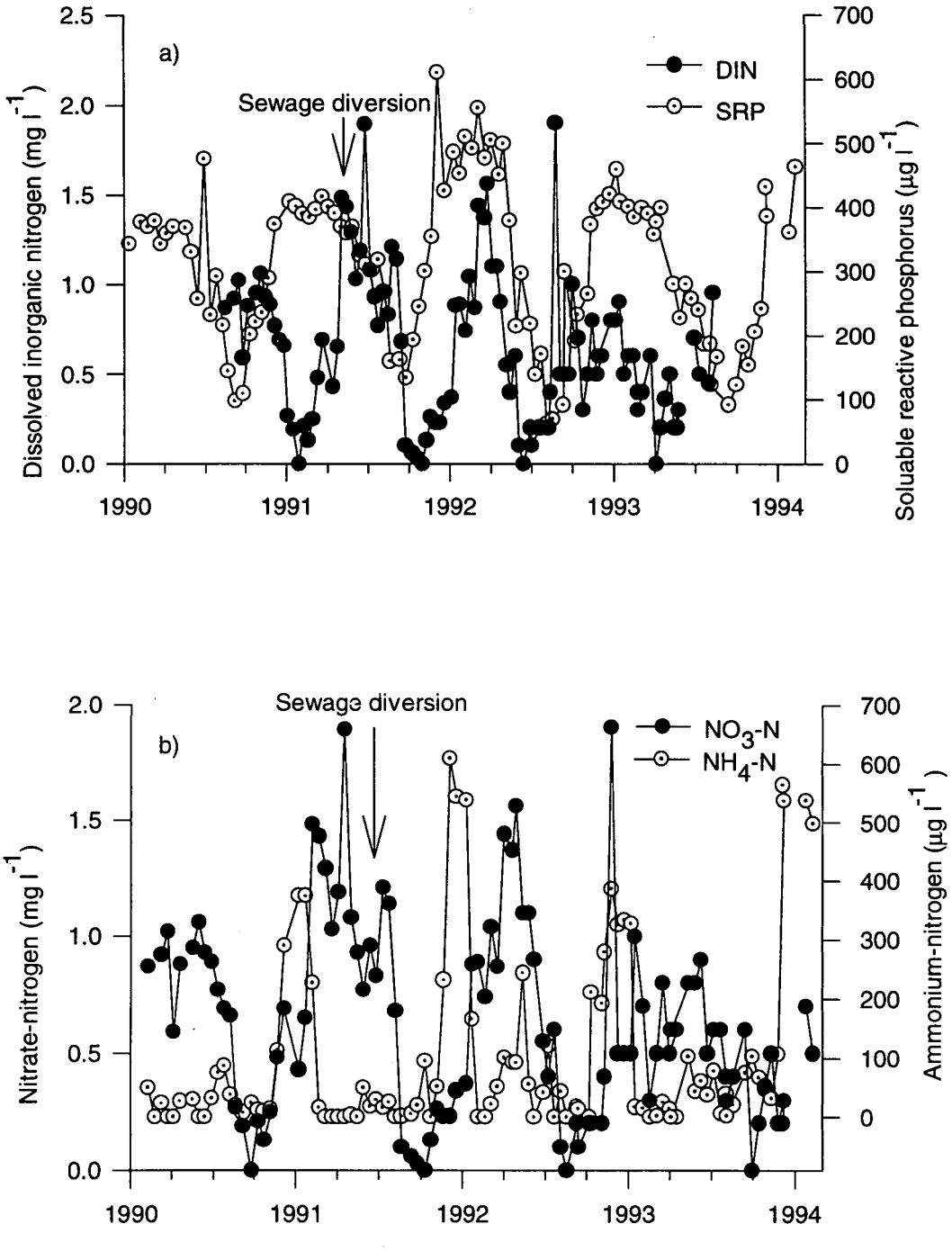

Fig. 2.14 Changes in concentrations of a) dissolved inorganic nitrogen (DIN) soluble reactive phosphorus, b) nitrate-nitrogen (NO_3-N) and ammonium-nitrogen (NH_4-N), in Rostherne Mere, between 1990 and 1994 (first three months data of 1994 were used).

after effluent diversion. The concentration maxima of TP and SRP were found in winter and the minima during summer. In summer decrease in the epilimnion SRP was correlated with the summer increase in chlorophyll a (r^2=0.45, p<0.005, n=35). Though depletion of TP and SRP occurred during the summer, their concentrations never reached low concentrations (relative to the concentrations in most eutrophic lakes); the minima recorded were 117 μg l^{-1} and 70 μg l^{-1} respectively in August 1992.

The concentrations of DIN significantly decreased after effluent but ammonium-nitrogen like those for of TP and SRP showed no clear trend of decrease before and after effluent diversion (Fig. 2.12b). DIN showed a very similar pattern to that of SRP (r^2=0.64, p<0.0001, n=102) (Fig. 2.14a). Concentration maxima were recorded in winter and the minima during the summer of each year. The depletion of DIN in the epilimnion was correlated with the summer increase in chlorophyll a (r^2=0.68, p<0.0001, n=35). In contrast to summer SRP concentrations, DIN concentrations declined to very low levels during the summer of each year. There were sharp increases in ammonium-nitrogen concentrations around October/November of each year, when stratification broke down. Two forms of nitrogen were analyzed (Fig. 2.14b); nitrate-nitrogen was dominant and its concentration declined clearly following the effluent diversion.

Over the four years studied, there was a clear declining trend in the phosphorus concentrations of inflow Rostherne Mere (Fig. 2.13a). For the first two years of the study concentrations of TP and SRP were very high. Recorded concentration maxima were 3299 μg l^{-1} and 874 μg l^{-1} respectively in 1990; 885 μg l^{-1} and 592 μg l^{-1} respectively in 1991. Following the effluent diversion, concentrations sharply declined

and 161 μg l^{-1} and 64 μg l^{-1} respectively in 1993.

DIN concentrations of inflow Rostherne Mere declined following the effluent diversion. The recorded winter maximum before diversion was 6.84 mg l^{-1} in 1990 and after diversion maxima were 5.27 mg l^{-1} 1991; 3.67 mg l^{-1} 1992 and 2.53 mg l^{-1} 1993 (Fig. 2.13b). Ammonium-nitrogen concentrations showed a similar trend in that before diversion the winter maximum concentration was 1.476 mg l^{-1} 1990, and after diversion winter maxima were 1.317 mg l^{-1} 1991; 0.214 mg l^{-1} 1992 and 0.151 mg l^{-1} 1993.

Silicate-silicon concentrations (Fig. 2.15a) showed marked seasonality with late spring/early summer minima (0.3 mg l^{-1} in 1990; 0.46 mg l^{-1} in 1991; 0 mg l^{-1} in 1992 and 0.3 mg l^{-1} in 1993) and winter maxima (≥ 2 mg l^{-1}). pH (Fig.2.15a) also showed a marked seasonality, with summer maxima (9.5, 1990; 9.7, 1991; 9.5, 1992 and 9.7, 1993) and winter minima (7.8, 1991; 7.5, 1992; 7.5, 1993 and 7.7, 1994).

Chlorophyll a concentrations in Rostherne Mere (Fig. 2.15b) increased in spring, early summer and mid-late summer. The concentration maxima were 71 μg l^{-1}, 1990; 77 μg l^{-1} 1992; 55, μg l^{-1} 1993; 68 μg l^{-1} 1993. Chlorophyll was often undetectable over the winter period. Chlorophyll a was closely correlated with pH (r^2=0.78, p<0.0001, n=91) and inversely correlated with secchi depth (r^2=0.65, p<0.0001, n=90) (Fig.2.15b).

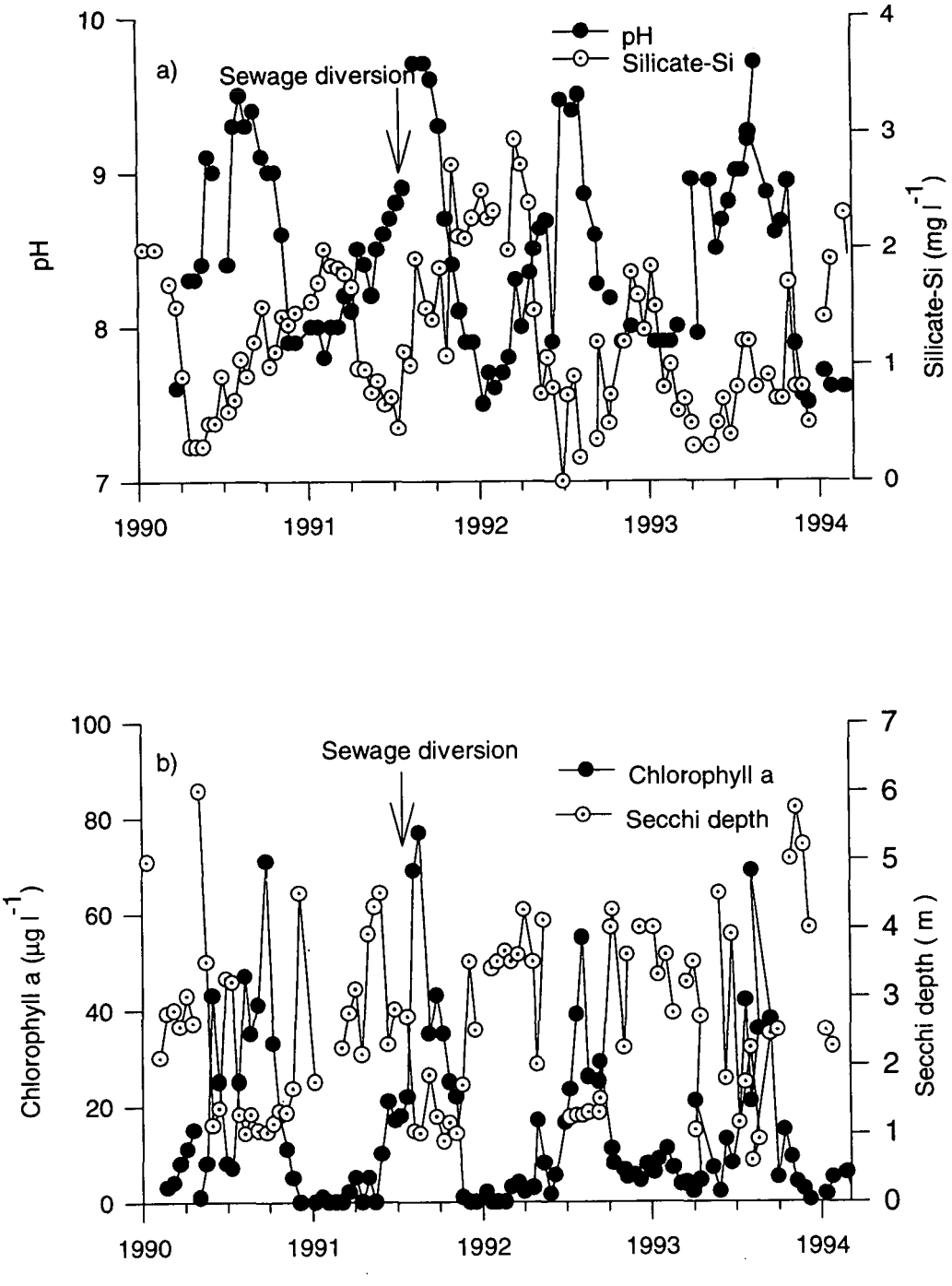

Fig.2.15 Changes in concentrations of a) silicate-silicon (silicate-Si) and pH, b) chlorophyll a and secchi depth, in Rostherne Mere between 1990 and 1994 (first three months data of 1994 were used).

2.4. Discussion

The seasonality of nutrient concentrations in the three meres reveals that, following sewage diversion, nutrient concentrations in Little Mere were dramatically reduced. Phosphorus concentrations were still higher than upstream in Mere Mere which was unaffected by sewage effluent, but DIN concentrations declined to values lower than those in Mere Mere. Rostherne Mere, however, showed no sign of recovery in phosphorus concentrations, despite the significant reduction in the concentrations in inflow Rostherne Mere.

Although inflow Mere Mere was unaffected by sewage effluent, there were significant declining trends in the concentrations of DIN and TON in inflow Mere Mere after sewage diversion in Little Mere (Table 2.3). This suggests a relative inconstancy of nitrogen loads delivered to the system from the catchment. The same significant declining trend of DIN and TON was observed in Mere Mere (Table 2.3). Annual mean DIN and TON concentrations were 0.76 mg l^{-1} and 0.70 mg l^{-1} respectively in 1990 and 0.55 mg l^{-1} 0.51 mg l^{-1} respectively in 1993 (Table 2.3). Mere Mere showed clear seasonality of DIN, with a peak during winter/spring declining to undetectable values by July. Ammonium-nitrogen concentrations were low, indicating that most DIN was in the form of total oxidised nitrogen (TON), although there were sharp rises in ammonium concentrations during autumn. Significant decreased loading of DIN and TON from inflow Mere Mere probably caused significant decrease in those nutrient concentrations in the lake. There were no clear trends in annual mean concentrations of ammonium-nitrogen which were 0.062 mg l^{-1} in 1990 and 0.055 mg l^{-1} in 1993. Mere Mere had much lower phosphorus concentrations than the other two meres. Despite relative uniformity of phosphorus loading to Mere Mere from inflow Mere

Mere over the four years studied, SRP concentration significantly increased from 7 μg l^{-1} in 1990 to 12 μg l^{-1} TP in 1993 in Mere Mere (Table 2.3). There was no significant change in annual mean concentrations of TP which were 80 μg l^{-1} in 1990 and 95 μg l^{-1} 1993 (Table 2.3).

Following the sewage diversion, nutrient concentrations in Little Mere were dramatically reduced (Table 2.3). Annual mean SRP and TP concentrations declined from 1951 μg l^{-1} and 2245 respectively in 1990, before diversion to 62 μg l^{-1} and 185 μg l^{-1} respectively in 1993, after diversion (Table 2.3). Little Mere again showed a very clear declining trend over the study period with annual mean ammonium-nitrogen and DIN concentrations 3.14 mg l^{-1} and 3.82 mg l^{-1} respectively in 1990, before diversion and 0.08 mg l^{-1} and 0.37 mg l^{-1} respectively in 1993, after diversion. In Little Mere, however, phosphorus concentrations remained, following diversion of sewage, higher than upstream in Mere Mere which was not affected by sewage effluent. However DIN concentrations declined to values lower than those in Mere Mere. Although reduction in external nutrient loading, as a method to improve water quality, has been ineffective in many shallow lakes, mainly due to internal nutrient loading (Sas 1989; Jeppesen *et al.*1991), there has, in Little Mere, been a very fast response to the external nutrient reduction (see Chapter 4).This has resulted in a marked reduction in nutrient concentrations following the sewage diversion. Progressive increase in dissolved oxygen concentration from near anoxic (Fig. 2.9) following the effluent diversion, might have played an important role in reducing internal loading which was probably a main nutrient source to the lake in summer (Chapters 4, and 6). In Little Mere the existence of dense plants beds might have also made an important contribution to the decrease in nutrients through buffering

mechanisms such as increased denitrification (Reddy *et al.* 1989; van Donk *et al.* 1993) and the luxury uptake of nutrients by macrophyte (Balls *et al.* 1989; Ozimek *et al.*1990) as discussed in Chapters 4, 5, 6 and 7.

Rostherne Mere, however, showed no sign of recovery in phosphorus concentrations, despite the large significant reductions in the concentrations of Inflow Rostherne Mere. In the first two years of the study concentrations were particularly high when water was flowing out of Little Mere. The annual mean TP and SRP concentrations declined significantly from 590 μg l^{-1} and 284 μg l^{-1} respectively in 1990 to 151 μg l^{-1} and 52 μg l^{-1} respectively in 1993 (Table 2.3). Reduction in DIN concentration of Inflow Rostherne Mere was significant between before and after diversion, and the concentration declined from 2.54 mg l^{-1} in 1990 to 1.44 mg l^{-1} in 1993 (Table 2.3). It is too early say if this represent a real decline or merely an annual fluctuation. There was also a declining trend in the ammonium-nitrogen concentrations which were significantly different before and after sewage diversion but the same structure must apply. The annual mean concentration declined from 440 μg l^{-1} in 1990 to 120 μg l^{-1} in 1993 (Table 2.3). Comparisons of the nutrient concentrations in Rostherne Mere before and after effluent diversion highlighted no significant response of SRP and TP concentrations over the study period; annual mean concentrations were 296 μg l^{-1} and 375 μg l^{-1} respectively in 1990, before sewage diversion and 280 μg l^{-1} and 400 μg l^{-1} respectively in 1993, after diversion. In contrast to the lake phosphorus concentrations, the phosphorus outflow concentration from Rostherne Mere increased slightly, which suggested the presence of internal nutrient loading as a major nutrient source to the lake (Carvalho *et al.* in press). Phosphorus concentrations have been shown to build up in the summer in the hypolimnion, and appear to be derived from the sediment

(Grimshaw & Hudson, 1970). It therefore appears probable that large internal sources of phosphorus were responsible for the lack of any significant change in the concentrations of Rostherne Mere, following the sewage effluent diversion. Despite the significant reduction of phosphorus loading from inflow Rostherne Mere following the sewage diversion, the concentration did not decrease in the lake. There was significant decrease in DIN and TON in Rostherne Mere as observed in inflow Mere Mere. Annual mean concentrations were 0.66 mg l^{-1} and 0.61 mg l^{-1} respectively in 1990 before diversion compared with 0.59 mg l^{-1} and 0.51 mg l^{-1} respectively in 1993 after diversion. Regression analyses were carried out on inflow Mere Mere concentrations of DIN and TON with time to examine whether the decline in these nutrient concentrations is part of erratic change or a consistent decrease. Decrease in DIN and TON concentrations of inflow Mere Mere were significantly dependent on elapsed time (r^2=0.062, p=0.013, n=97 for DIN and r^2=0.0522, p=0.02, n=98 for TON) (Fig. 2.16 a,b). Therefore the decreasing trend of these nutrient concentrations in Rostherne Mere is most likely attributable to the decreasing trend of them in inflow Mere Mere, reflecting the nature of agricultural catchment which is the main external source to the system rather than to sewage diversion. There was no significant change in concentration of ammonium-nitrogen before and after diversion (Table 2.3) in Rostherne Mere. Contribution of ammonium-nitrogen was small in proportion even before diversion. Some ammonium may be derived from breakdown of stratification and internal loading but is probably only a minor source of supply on an annual basis.

Chlorophyll a concentrations in the three meres studied were complexly related to the lakes' supply of nutrients. In Mere Mere, the annual mean concentrations were similar from 1990-1992. Although there was an slight increase in 1993 there was no

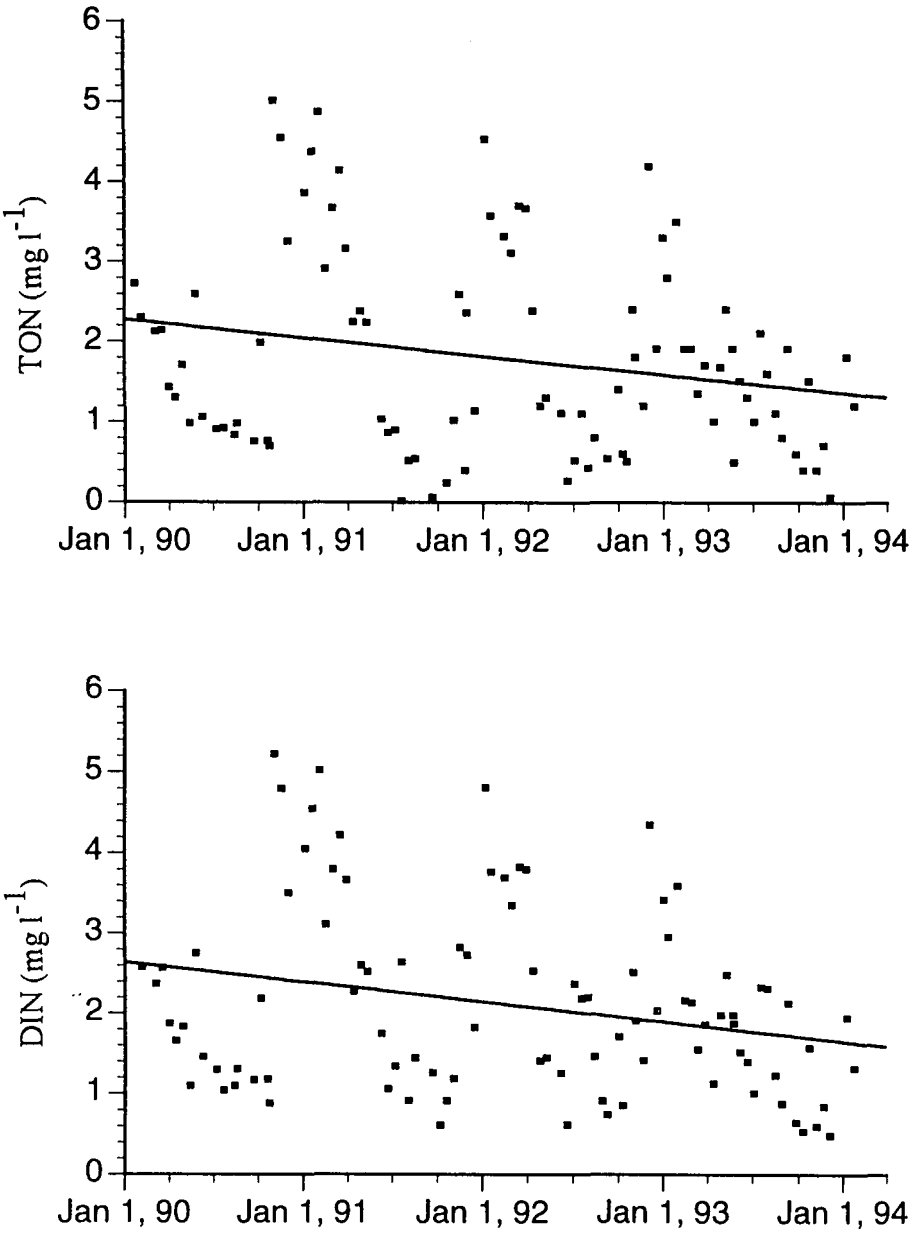

Fig.2.16 Relationship between a) TON concentrations and b) DIN concentrations and time after the start of the study (monthly) in inflow Mere Mere

significant difference between before and after sewage effluent diversion. Annual mean concentrations were 14-24 μg l^{-1} during 1990-1992 and 34 μg l^{-1} in 1993 (Table 2.3). Little Mere showed a clear declining trend over the study period with annual mean concentrations declining from 59 μg l^{-1} in 1990, to 6 μg l^{-1} in 1992, and increasing slightly to 17 μg l^{-1} in 1993. Values were significantly different before and after sewage diversion (Table 2.3). The paradox of Little Mere having higher nutrient but lower chlorophyll a concentrations than Mere Mere involves grazer activity (Carvalho, 1994; Chapter 3) and the existence of large and denser macrophyte stands following the effluent diversion (Chapters 8). Annual mean concentrations declined slightly in Rostherne Mere from 20 μg l^{-1} in 1990, to 14 μg l^{-1} in 1993 (Table 2.3) though there is little suggestion of real declining trend, and the difference was not significant before and after diversion (Table 2.3). Reynolds & Bellinger (1992) believe that the phytoplankton biomass in Rostherne Mere is light-limited, but a recent study (Moss *et al.* 1994) of a group of deep lakes in this region, including Rostherne Mere, revealed that growth season chlorophyll a concentrations were significantly correlated with winter nitrogen loading. The small but insignificant declining trend in chlorophyll a concentration is consistent with the declining trend of DIN concentration. Regression analysis revealed that the chlorophyll a concentration was significantly dependent on the DIN concentration (r^2=0.43, F=71 p>> 0.0001, n=97). The fact that Rostherne Mere appears to be close to a state where nitrogen limits phytoplankton biomass. By late summer DIN concentrations declined to almost undetectable values and this is consistent with dominance then of N-fixing cyanophytes (Chapter 3).

2.4.1. Conclusion

Annual changes of the nutrient concentrations in the three meres reveal that in Little

Mere, diversion of sewage effluent has had a marked and immediate effect. Clear reductions in nutrient concentrations (along with other factors: dense macrophyte stands and grazer activity) have led to a consequent reduction in chlorophyll a concentrations. In Rostherne Mere, however, there has been little effect on either nutrient or chlorophyll a concentrations. Lake restoration techniques for deep lakes have traditionally focused on reductions in external phosphorus loading, but phosphorus control may not be an effective measure for restoration of Rostherne Mere. Rostherne Mere is not unique in this as it may be true for many deep North West Midland Meres, which differ from many other lakes in the fact that control of nitrogen sources would appear to be a more effective strategy for restoration. The reason for this is not clear. There is yet little evidence to suggest that phosphorus sources are naturally derived from phosphorus-rich minerals in the drift which forms the surface geology of their catchments. It appears more probable that it is the result of relatively large diffuse nutrient sources and internal sources, which may be significant in many of the basins of this region (Carvalho *et al.* in press).

Chapter 3: Phytoplankton and zooplankton communities of Mere Mere, Little Mere and Rostherne Mere

3.1. Introduction

Phytoplankton community structure has been a focus of study for many decades (Pearsall, 1923; 1932; Hutchinson, 1967; Lund, 1961; Reynolds, 1973; Porter, 1977). Especially, rapid eutrophication of surface waters and deterioration of water quality have increased research on the factors controlling the biomass and photosynthetic activity of phytoplankton (Reynolds & Walsby, 1975; Schindler, 1977; Schindler and Brunskill, 1972 Smith, 1979; Vollenweider & Kerekes, 1981; Rhee & Gotham 1980). Clear differences exist in algal species composition, both between lakes and within a single lake over time. If we can determine the ecological factors which lead to nuisance algae, like Cyanophyta, in lakes, then it should be possible to develop rational water management strategies. However, there is a controversy about the relative importance of determination of phytoplankton crops in lakes by bottom-up control or by top-down. The importance of availability of nutrients (generally P and N) in determining growth has widely been shown (Rhee, 1978; Dillon & Rigler, 1974; Smith, 1983; 1985). There have also been many studies that have supplied evidence of the effects of piscivorous fish on freshwater community structure and productivity through the in influence on the abundance of planktivorous fish and in turn the abundance and productivity of zooplankton and phytoplankton. (Shapiro & Wright, 1984; Carpenter *et al.* 1985; McQueen, 1990; van Donk; *et al.* 1989; Meijer *et al.* 1990; Hosper & Meijer, 1993). Both factors might act together to control phytoplankton community in a lake. The phytoplankton community structure of deep lakes appears to be controlled largely by availability of nutrients, which are usually supplied by external nutrient loading, and physical factors (bottom-up control), though

in spring grazing by filter-feeders may override these and create clear water (Lampert *et al.* 1986; Arndt & Nixdorf, 1991). Later in the year, feeding by young-of-the-year fish or lack of appropriate food may cause collapse of zooplankton populations and availability of nutrients and physical factors may then take over control of phytoplankton community structure (Reynolds, 1971). Shallow, plant-dominated lakes are usually rich in nutrients because of fertile catchments and partly because of internal loading of nutrients from sediment (Sas, 1989; Søndergaard, 1989; Søndergaard *et al.* 1993). The open water of such lakes may be clear in summer and phytoplankton crops very small in relation to the growth potential set by the availability of nutrients (Jeppesen *et al.* 1991). In such macrophyte-dominated lakes, grazers appears to control the phytoplankton community throughout summer, the plants providing refuge for large cladoceran populations despite an abundance of planktivorous fish (Timms & Moss, 1984).

Generally, shallow lakes then, show more evidence of top-down control of phytoplankton, deep lakes of bottom-up control. Control of external nutrient loading of eutrophic deep lakes is an accepted approach to restoration; biomanipulation is becoming widely used in shallow lakes. Rostherne Mere, a eutrophic deep lake, and Little Mere, a hypertrophic shallow lake, are appear to be exceptions to these general rules because diversion of sewage effluent from Little Mere, upstream of Rostherne Mere has shown major effects in Little Mere but not in Rostherne Mere (Chapter 2; Carvalho *et al.* in press). The shallow lake, Little Mere responded very rapidly (Chapter 2; Carvalho *et al.* in press) though resilience to the measure taken was expected because of internal loading from the sediment.

In this chapter, changes in the phytoplankton and zooplankton communities of Little Mere and Rostherne Mere are examined. Over four years of data were used to investigate the impact of effluent diversion on phytoplankton and zooplankton communities. Mere Mere, upstream to Little Mere, was not affected by sewage effluent and acts as a comparator.

3.2. Background to the study

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* (O.F Műll) and a variety of chlorophytes and cyanophytes. There has been no previous study of the zooplankton of Mere Mere. Little Mere has not received any limnological attention in the past.

Descriptive accounts of the phytoplankton assemblages of Rostherne Mere for 1912 (Pearsall, 1923), 1922 (Griffith, 1925), 1941-1943 (Lind, 1944), 1962-1963 (David, 1963), 1963-1966 (Belcher & Storey, 1968), and 1967-1989 (Booth, 1988: Reynolds, 1978a; Reynolds & Bellinger, 1992) comprise an important long-term phytoplankton data set (Elliot, 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 recent dominance by the cyanophyte *Microcystis aeruginosa* Kutz. emend. Elenkin.

Livingstone's (1979) investigation of the stratigraphic records of the sediment confirmed that the recent shift to *Microcystis* occurred around 1958. Nelms (1984)

confirmed, through diatom stratigraphy, that there was a shift in the diatom community around the same time. Reynolds (1979) suggested that the change was due to a further increase in the mere's nutrient concentration through increased use of synthetic fertilisers, which have been heavily used since the 1950's (Hood, 1982), and could have shifted Rostherne Mere from a state where nitrogen was limiting to a state where the phytoplankton populations are limited by light rather than nutrients (Reynolds & Bellinger, 1992).

3.2 Methods

3.2.1 Phytoplankton and zooplankton

Phytoplankton and zooplankton samples were collected at the same times and places as those for chemical analysis. Phytoplankton samples from Mere Mere were collected from the top 3 m using a plastic hosepipe. In Little Mere, phytoplankton samples were taken with a 1-m long plastic tube sampler. Samples from the upper 4 m of the water column of Rostherne Mere were taken for phytoplankton. Samples were preserved within a hour by addition of Lugol's iodine solution (Vollenweider, 1969). Phytoplankton was counted under an inverted microscope (Wild M40) at a magnification of 400 x. The commonest species was counted to a precision of ±20%; the other dominant species were counted to a precision of at least ±50% (Lund *et al.* 1958). Identification was carried out to genus, or species, where possible, with the aid of standard works (Bourrelly, 1966; 1968; 1970; Hustedt, 1942; Prescott, 1962). Biovolumes were determined from measurement of linear dimensions of ten preserved cells of each taxon, using formulae for the appropriate geometric shapes (Wetzel and Likens, 1991). Biovolume density of each species (μm^3 ml^{-1}) was determined by multiplying average cell volume by cell population density. Community biovolume density was obtained by summing biovolume densities of all species present. Volumes of taxa recorded in this study are given in Appendix 2 (Table A2.2).

Zooplankton samples from Mere Mere were collected by vertical tows from 3 m to the surface using a 63 μm mesh-size, nylon phytoplankton net. In Little Mere, 10 l of water were taken using the tube sampler from the entire water column and filtered through the phytoplankton net. Zooplankton samples from Rostherne Mere were collected by vertical tows from 7.5 m to the surface using the phytoplankton 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 most common 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; Pontin, 1978).

3.2.2 Chlorophyll a, carotenoids, and pigment ratios

For chlorophyll a and carotenoids methods, see Chapter 2. The ratios of absorbance at 480 nm to that at 663 nm, and that at 430 nm to that at 410 nm were calculated. These ratios together may give indications of intense grazing activity, nitrogen deficiency and physiological state of the phytoplankton (Watson and Osborne, 1979). A high value for the ratio A480:A663 (>1.2) may indicate nitrogen deficiency or may indicate resuspension of mud containing decaying algae or plants, since carotenoids are more resistant to decay than is chlorophyll a. An indication of whether a high value of A480:A663 indicates nitrogen deficiency or decomposition (by grazing or resusupension of mud) is given by the ratio A430:A410. For undecomposed chlorophyll a (even in nitrogen deficient conditions) the ratio A430:A410 ratio has a value of 1.2 or more. For partly or completely degraded chlorophyll a the A430:A410 ratio often falls below 1.0 (Moss, 1967; Moss, 1969).

3.3 Results

3.3.1. Phytoplankton and zooplankton of Mere Mere

Chlorophyll a concentrations increased (see Chapter 2; Fig 2.7a) in spring, summer and autumn. The spring increase in chlorophyll a concentration was largely due to the diatom *Asterionella formosa* Hass. in 1990 and 1991 but in 1992 the spring increases in chlorophyll a concentration and biovolume of *Asterionella formosa* were much lower than in the previous two years (Fig. 3.1b). There was a decrease in contribution of *Asterionella formosa* to the spring diatom peak in 1993. The spring 1993 diatom peak was largely due to *Aulacoseira* sp. and this shift continued in spring 1994. *Cryptomonas spp.* and *Rhodomonas minuta* Lewis contributed to the spring increase in chlorophyll a concentrations but to a lesser extent than the diatoms throughout the study (Fig. 3.1a).

The summer increase in phytoplankton biomass from June to September was principally due to the cyanophytes *Anabaena* spp., *Coelosphaerium naegelianum* Unger and *Planktothrix agardhii* (Gom.) Anagn. et Kom. (Fig. 3.2a) and the dinoflagellates, *Ceratium hirundinella* and *Peridinium* sp. (Fig.3.2b). *Cryptomonas* spp. and *Rhodomonas minuta* were also present with varying total biovolumes throughout the study (Fig. 3.1a). Biovolume of Chlorophyta did not make an important contribution to the summer phytoplankton community. *Chlamydomonas* spp. and *Micractinium pusillum* Fresenius were the dominant chlorophyte species though their biovolumes were low throughout the study period (Fig. 3.1c).

In Mere Mere, there was an important change in both species composition and the contribution of the species to total phytoplankton biomass. In 1990 and 1991,

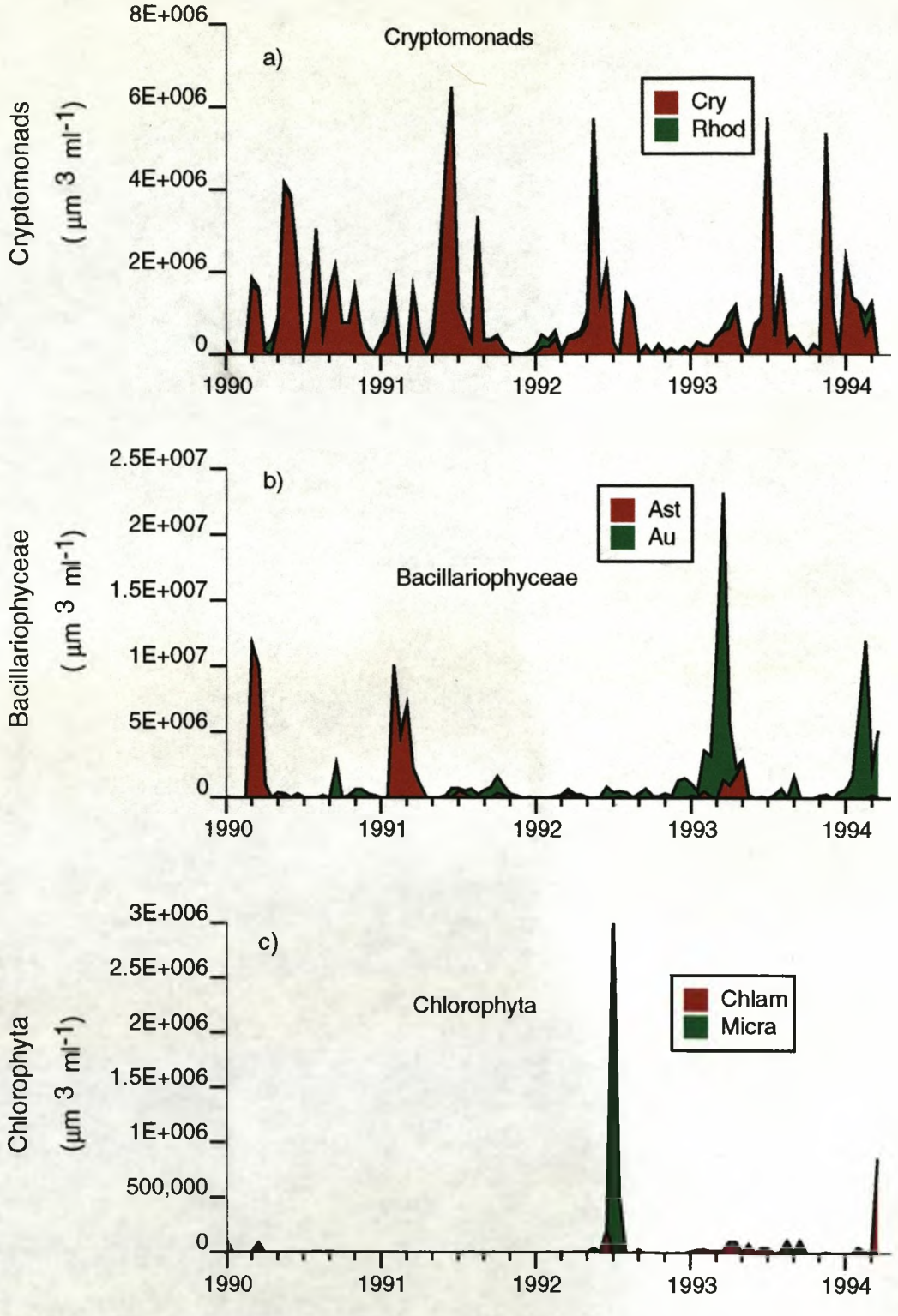

Fig. 3.1 Changes in biovolumes of a) Cryptomonads b) Bacillariophyceae and c) Chlorophyta in Mere Mere, between 1990 and1994 (First three months data of 1994 used). Cry: *Cryptomonas* spp., Rhod: *Rhodomonas minuta,* Ast: *Asterionella formosa*, Au: *Aulacoseira* sp., Chlam: *Chlamydomonas* sp., Micra: *Micractinum pusillum.*

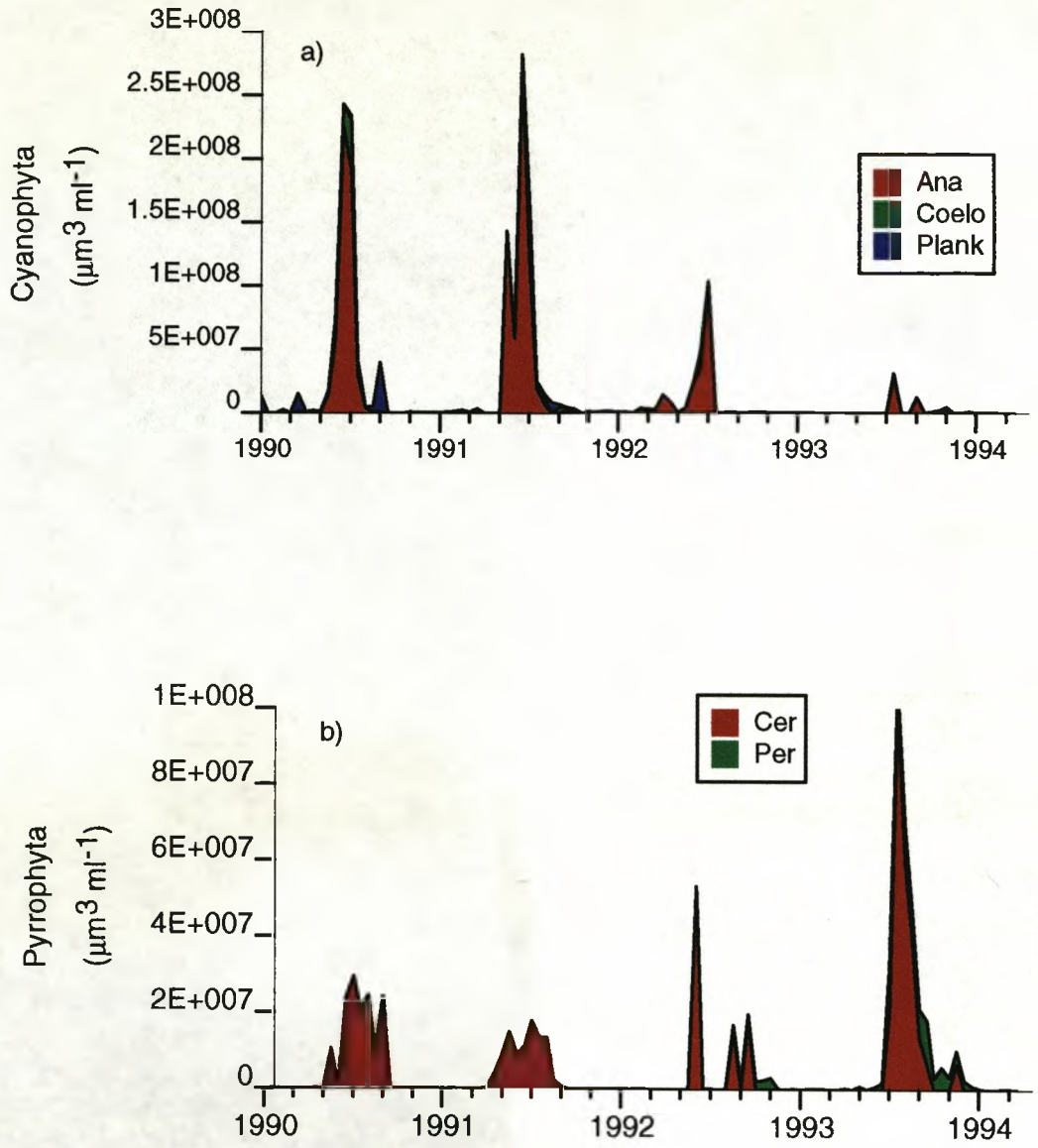

Fig. 3.2 Changes in biovolume of a) Cyanophyta and b) Pyrrophyta in Mere Mere between 1990 and 1994 (first three months data of 1994 used). Ana: *Anabaena* sp., Coelo: *Coelosphaerium naegelianum* , Plank: *Planktothrix agardhii*, Cer: *Ceratium hirundinella* , and Per: *Peridinium* sp..

cyanophytes predominated in the total phytoplankton biomass largely with *Coelosphaerium naegelianum* (24.5%) and *Planktothrix agardhii* (20.7%) in 1990 (Fig.3.3a) In 1991, it was largely *Anabaena* spp. (73.9%) (Fig.3.3b). *Ceratium hirundinella* was dominant in 1990 (41%) though its biovolume decreased in 1991 (9.6%). Though *Asterionella formosa* dominated the spring phytoplankton biomass, its contribution to total phytoplankton biomass was low in 1990 & 1991. There was a shift in dominant diatom species from *Asterionella formosa* to *Aulacoseira* sp. in 1992 (Fig. 3.3c) though *Aulacoseira* sp. did not make a major contribution to the total phytoplankton biomass (1.5%). *Anabaena* spp. (Cyanophyta) and the dinoflagellate, *Ceratium hirundinella* dominated the total phytoplankton biomass (54% and 27% respectively) in 1992. In 1993, the contribution of *Anabaena* spp. to the total biomass decreased (8.8%), whilst the contribution of *Ceratium hirundinella* to the total biomass increased greatly (52.5%). Domination by *Aulacoseira* sp. of the diatom community continued, though its biovolume was low (1.5%) as in the previous year. The cryptomonads, *Cryptomonas* sp. and *Rhodomonas minuta* were present through the study period with varying biovolumes (Fig. 3.3d).

Cladoceran grazers of Mere Mere were represented by large-bodied species (*Daphnia longispina* aggregate) (Fig.3.4a) and small-bodied species (*Daphnia cuculata* Sars, *Bosmina longirostris* (O.F.Műller) and *Ceriodaphnia* spp.) during the study period (Fig.3.4b). The small Cladocera were much more abundant with a series of peaks throughout the spring and summer. Early summer peaks were principally due to *Bosmina* and those in mid to late summer to *D.cucullata*. Large Cladocera (*D. longispina*) density was low throughout the study. The copepods (Fig.3.2c) were most abundant in spring and autumn. *Diaptomus gracilis* Sars reached a peak in March and

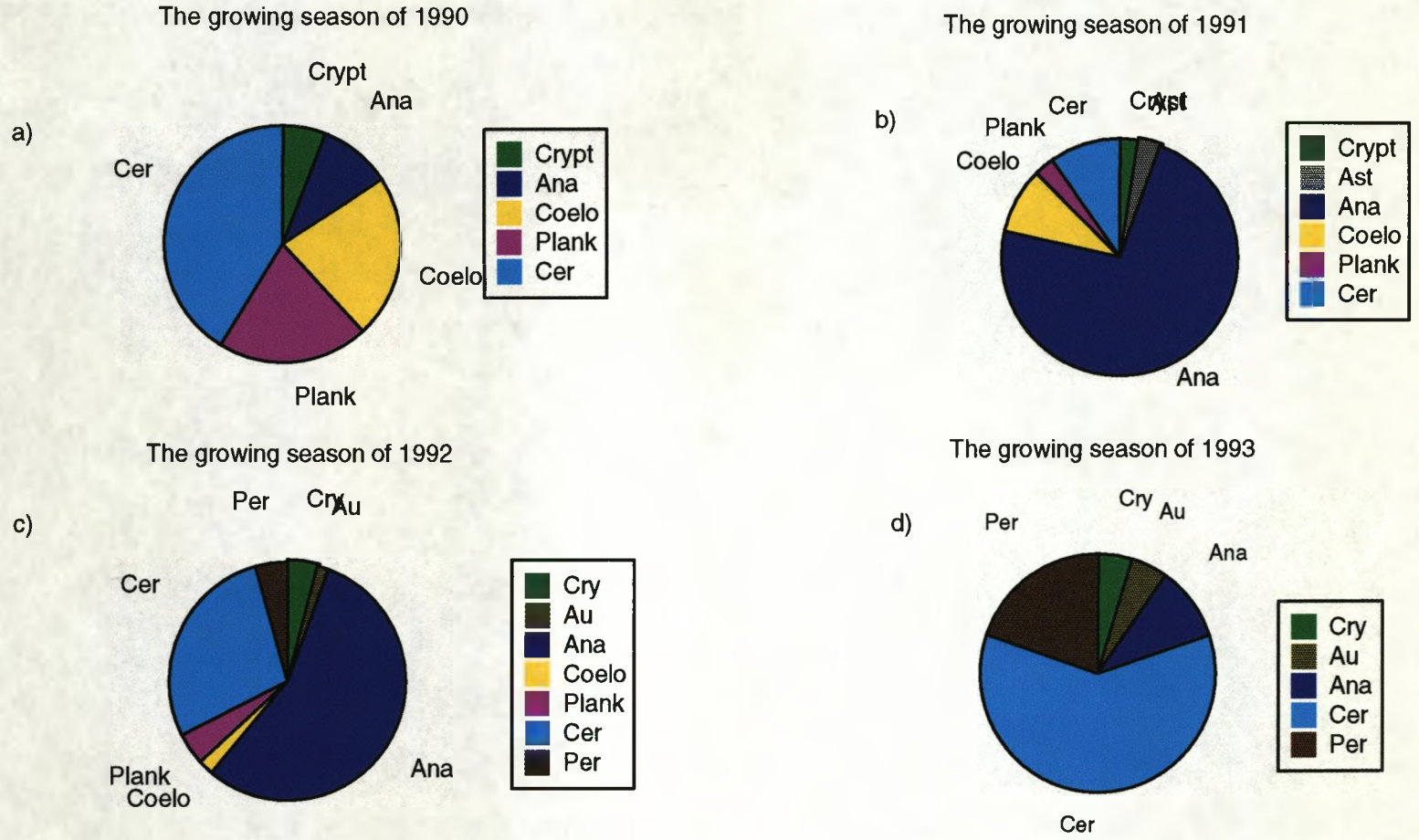

Fig. 3.3 Changes in total phytoplankton biovolumes in the growing season (March to October) of a) 1990, b) 1991, c) 1992 and d) 1993 in Mere Mere (Ana: *Anabaena* sp., Ast: *Asterionella formosa*, Au: *Aulacoseira* sp., Cer: *Ceratium hirundinella,* Coelo: *Coelosphaerium naegelianum* , Cry: *Cryptomonas* spp. Per:*Peridinium* sp. and Plank : *Planktothrix agardhii*).

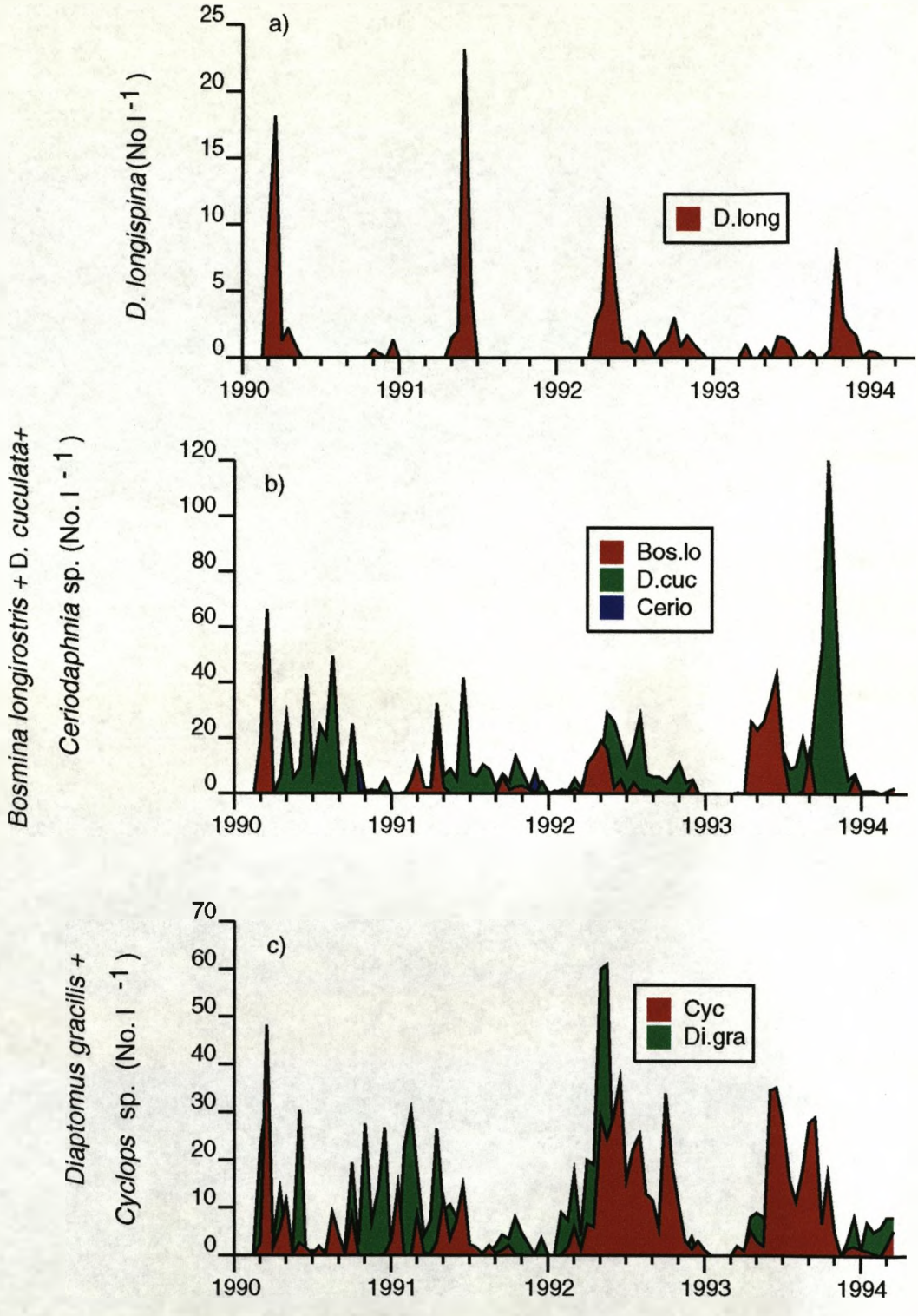

Fig.3.4. Changes in density of a) *D. longispina*, b) *D.cuculata, Bosmina longirostris* and *Ceriodaphnia* spp. in Mere Mere between 1990 and 1994 (first three months data of 1994 used).

November through the four years. *Cyclops* spp. also showed spring peaks in March and summer peaks in July and August. Nauplii were not included in calculations of copepods density.

The zooplankton community of Mere Mere did not show major inter-annual changes during the study period (Fig. 3.5). The small-bodied cladocerans, *Daphnia cuculata* and *Bosmina longirostris* were the predominant cladoceran grazers. They contributed (to the total numbers in the zooplankton community in the growing seasons of the study period) 35.8% and 13.8 % in 1990, 30.5% and 12.2% in 1991, 24.4 % and 8.7 % in 1992, and 42.1 % and 19.8 % in 1993 respectively. The contribution of *Ceriodaphnia* spp. was negligible with the highest value (5.5 %) in 1990 (Fig. 3.5a). The densities of the large-bodied cladoceran, *Daphnia longispina*, were low with the highest contribution (6.5 %) in the growing season of 1991 (Fig. 3.5b). The densities of copepods, *Diaptomus gracilis* and *Cyclops* spp. made an important contribution to the total zooplankton density throughout the study (Fig. 3.5).

Multiple regression analyses were carried out to examine which factors may have been responsible for changes in the phytoplankton community in the diatom-dominated spring period and the cyanophyte and the dinoflagellate dominated summer community. Multiple regression analysis of spring (March to April) chlorophyll a concentration against DIN, SRP, silicate concentrations and Cladocera densities (which included *Daphnia longispina*, *Daphnia cuculata*, *Bosmina longirostris* and *Ceriodaphnia* spp.) (Table 3.1) showed no significant relationships. However, analysis of summer (June to September) chlorophyll a concentrations against DIN and SRP concentrations and Cladocera densities (Table 3.1) showed significant relationships

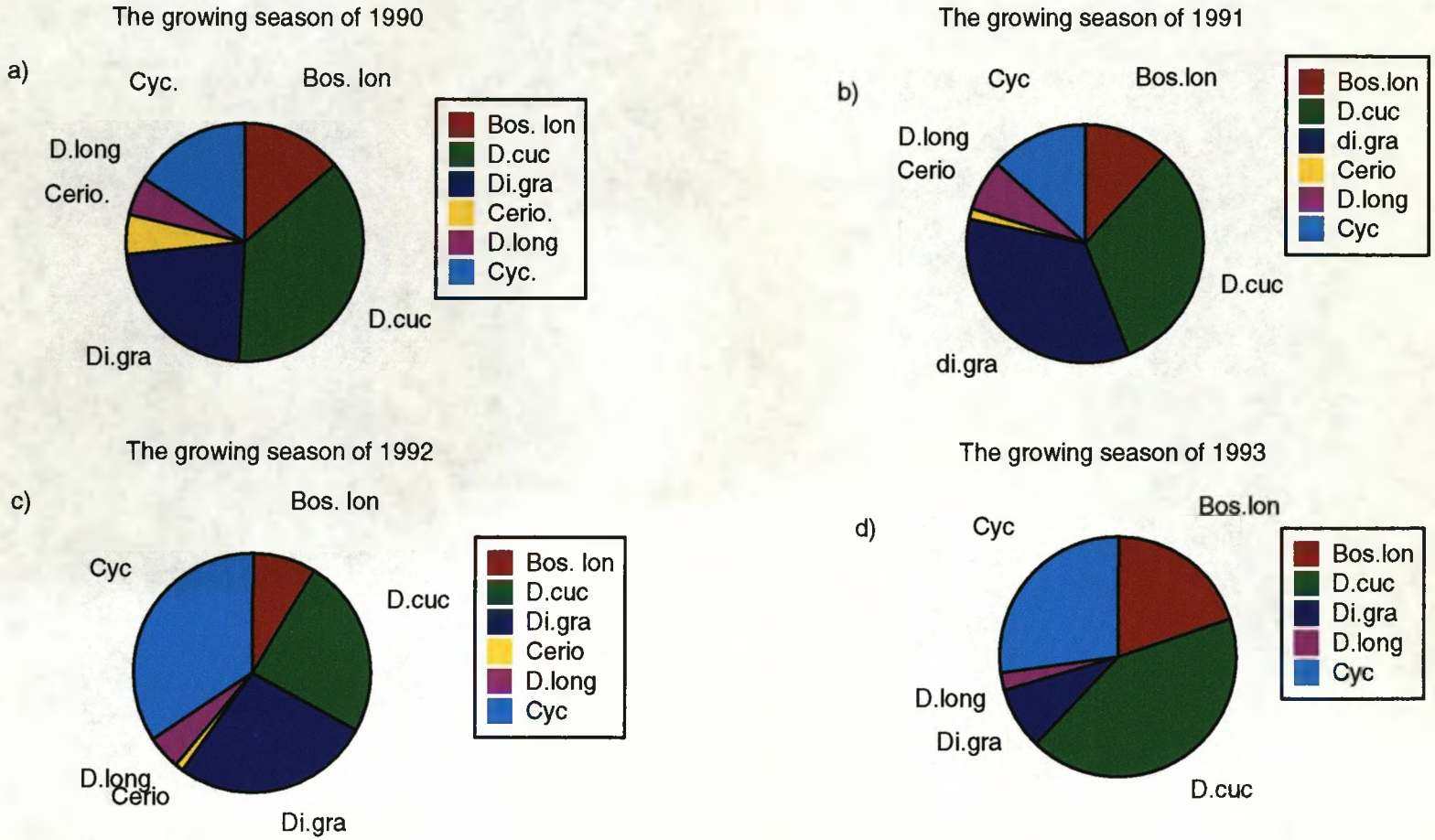

Fig. 3.5 Changes in total zooplankton density in the growing seasons (March to October) of a) 1990, b)1991 c) 1992 and d) 1993 in Mere Mere. Bos.lon:*Bosmina longirostris*, Cer: *Ceriodaphnia* sp., Cyc: *Cyclops* sp., Di.gra: *Diatomus gracilis,* D.cuc: *Daphnia cuculata* and D.long: *Daphnia longispina* .

Table 3.1 Result of multiple regression analyses on spring (March to April for Mere Mere and April to mid May for Rostherne Mere) and summer (June to September for Mere Mere and late May to September for Rostherne Mere) chlorophyll a concentrations, between 1990 and 1993.

	Chlorophyll a	Partial F	r^2	probability
	versus: DIN	0.49		P>0.5
Mere Mere	SRP	0.97		P>0.6
spring	Silicate	1.29		P>0.07
	Herbivores	1.57		P>0.1
	Total	2.65	0.44	P>0.08
	Chlorophyll a			
Mere Mere	versus: DIN	3.59		0.005>P>0.001
summer	SRP	0.8		P>0.3
	Herbivores	0.4		P>0.7
	Total	3.5	0.27	0.02<P<0.03
	Chlorophyll a			
	versus: DIN	0.06		P<1
Rostherne Mere	SRP	0.8		P>0.4
spring	Silicate	0.08		P<1
	Herbivores	2.2		P>0.5
	Total	1.8	0.42	P>0.1
	Chlorophyll a			
Rostherne Mere	versus: DIN	4.11		P<0.0001
summer	SRP	0.8		P>0.5
	Herbivores	2.2		P<0.05
	Total	11.67	0.55	P<0.0001

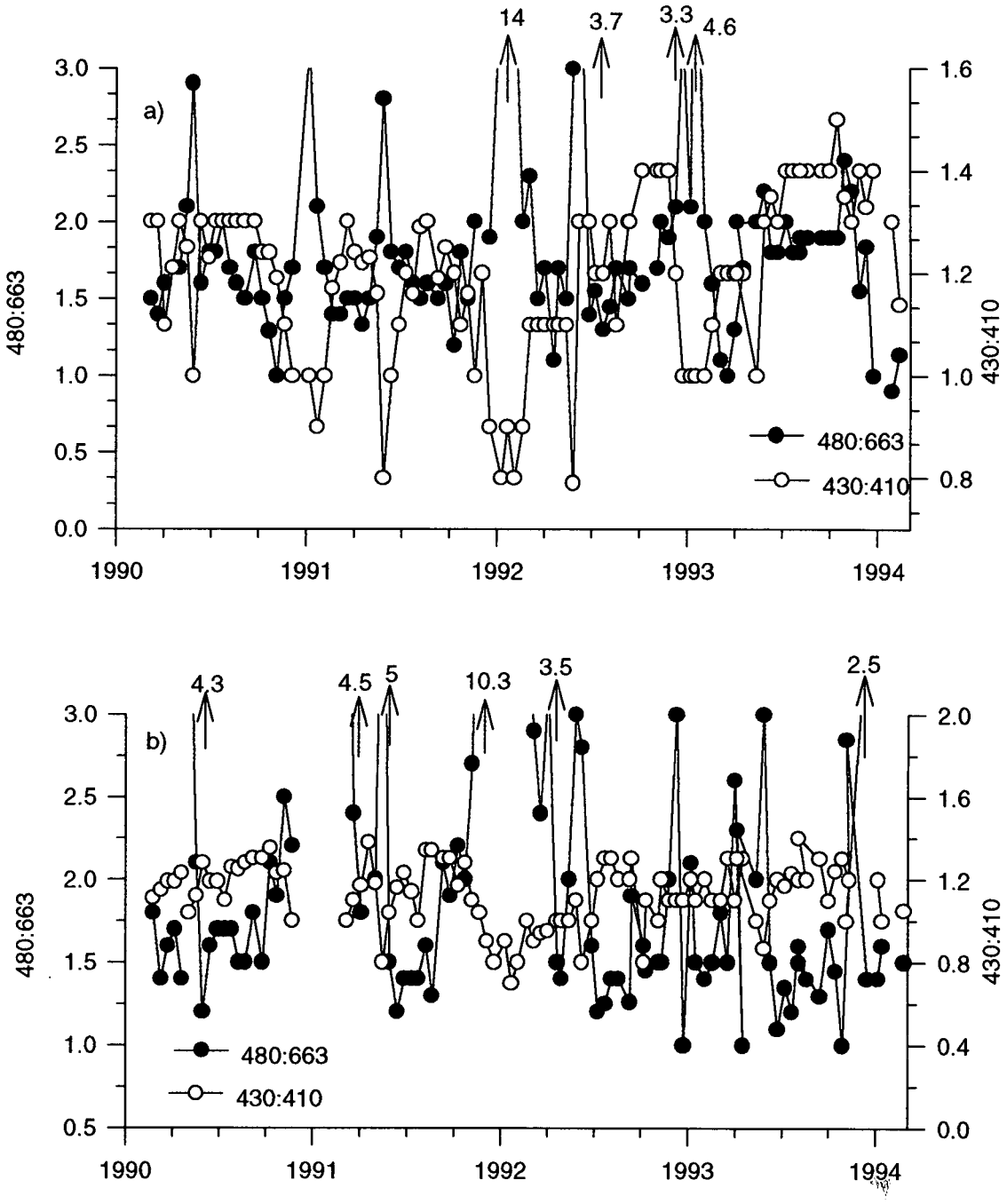

Fig. 3.6 Seasonality of the ratio of carotenoid pigments to chlorophyll a (ratio of absorbance at 480 nm: 663 nm and the ratio of the absorbance at 430 nm: 410 nm). a) in Mere Mere and b) in Rostherne Mere, between 1990 and 1994 (first three months data of 1994 used).

(r^2=0.27, 0.01 < p<0.03). DIN appeared to be of greatest importance.

The ratio of carotenoid pigments to chlorophyll a (A480:663) was >1.3 throughout most of the study period (Fig. 3.6a). A430:410 ratio was <1.2 during winter, but during spring and summer the A430:410 ratio was >1.2 (Fig.3.6a).

3.3.2 Phytoplankton and zooplankton of Little Mere

There were sharp increases in chlorophyll a concentrations (see Chapter 2, Fig. 2.10b) during spring though the spring increase was much higher pre-diversion than post-diversion. In spring 1990, a huge phytoplankton biomass developed with the diatom *Stephanodiscus hantzschii* Grun, the cryptomonads *Cryptomonas* spp. and *Rhodomonas minuta* (Fig.3.7a,b) and the cyanophytes *Planktothrix agardhii* and *Coelosphaerium naegelianum* (Fig.3.8a). In the early summer of 1990 there was an increase in green algae (*Planktosphaeria* sp. and *Coelastrum* sp.) (Fig.3.7c). The spring increase in phytoplankton biomass developed later, and to a lesser extent, in 1991, 1992 and 1993 compared with 1990. In spring 1993 there was a shift in the dominant diatom species from *Stephanodiscus hantzschii* to *Aulacoseira* sp. which was also recorded in spring 1994 (Fig.3.7b). There was a large spring increase in cryptomonad biomass in 1993 (Fig.3.7a).

The phytoplankton crops in the summers of the various years were similar with very low biomass. The only algae of any importance during the 1990 and 1991 summers was the large, grazer resistant *Volvox* sp. which was visibly present in late summer, but had little impact on chlorophyll a concentrations or algal biovolumes. Cryptomonads, (*Cryptomonas* spp. and *Rhodomonas minuta)* were present with

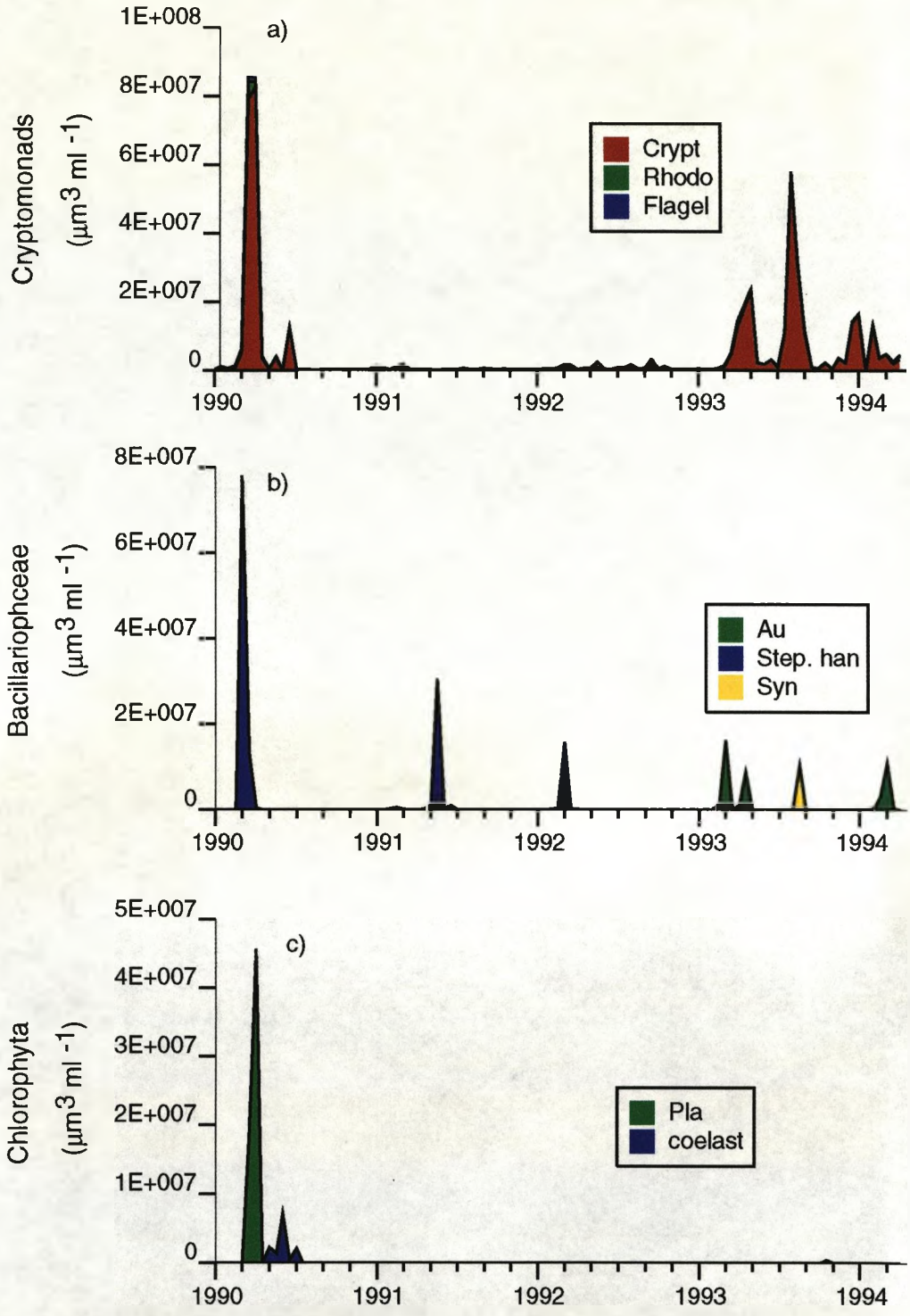

Fig. 3.7 Changes in biovolume of a) Cryptomonads, b) Bacillariophyceae and c) Chlorophyta in Little Mere, between 1990 and 1994 (first three months data of 1994 used). Crypt:*Cryptomonas* spp., Rhodo:*Rhodomonas minuta*, Flagel:Unidentifed small flagellate, Au:*Aulacoseira* sp., Step. han:*Stephanodiscus hantzchii*, Syn:*Synedraulna*, Pla: *Planktosphaeria* sp.Coelast: *Coelastrum* sp..

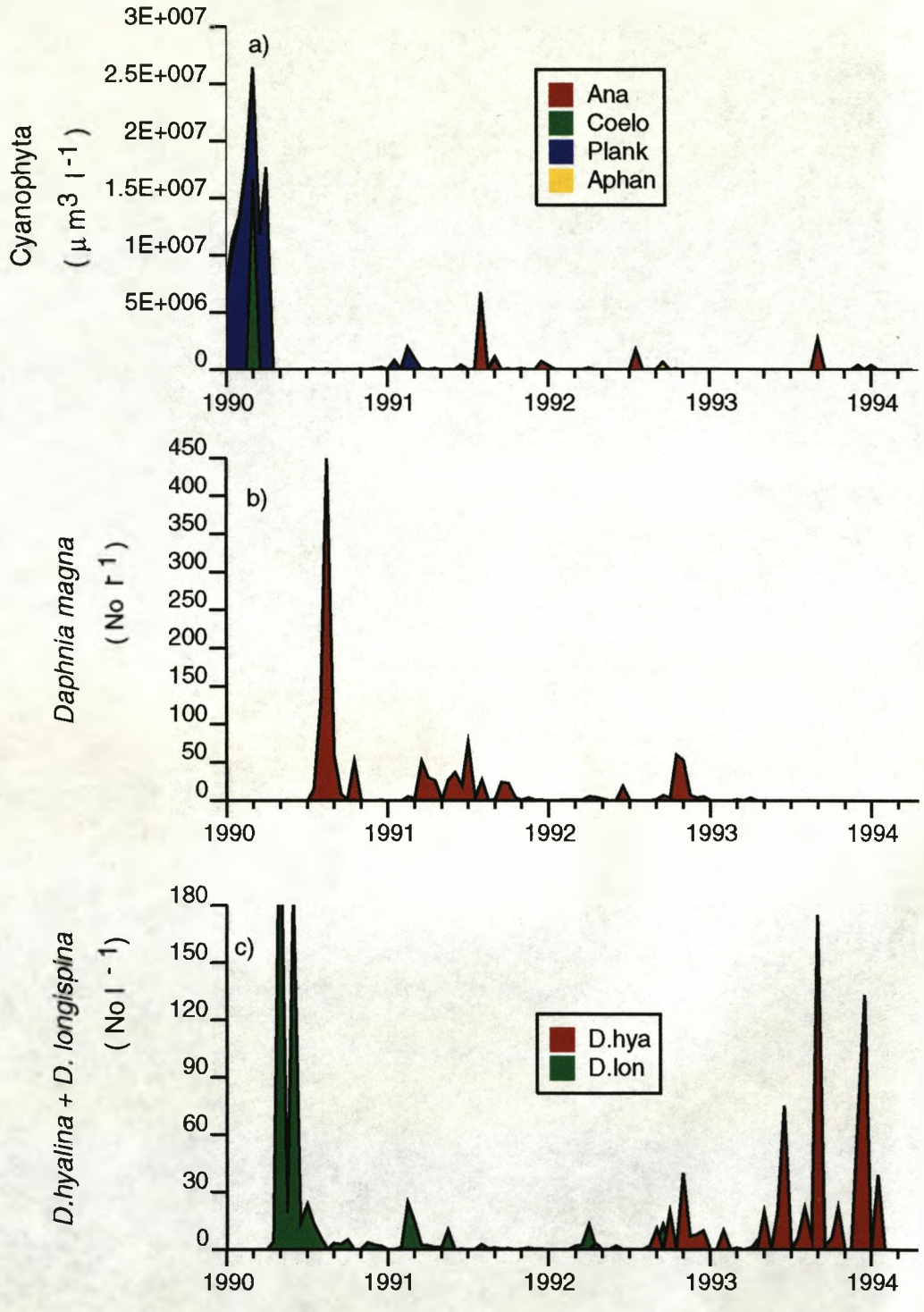

Fig. 3.8 Changes in biovolume of a) Cyanophyta and density of b) *Daphnia magna* and c) *D. hyalina* and *Daphnia longispina* in Little Mere, between 1990 and 1994 (first three months data of 1994 used) Ana: *Anabaena* sp., Coelo: *Coelosphaerium naegelianum*, Plank : *Planktothrix agardhii*, Aphan: *Aphanizomenon flos-aquae*).

varying biovolumes in the summer phytoplankton community through the study period.

There was a change between the pre-diversion and post-diversion phytoplankton communities in Little Mere. The highest phytoplankton biomass was observed in the growing season of 1990 (Fig.3.9a) The biovolume of cryptomonads dominated the phytoplankton community, largely with *Cryptomonas* sp. (41.8%). The diatom, *Stephanodiscus hantzschii* was the second predominant species with 20.4% of the total phytoplankton biomass. The only prominent contribution of chlorophytes was recorded in 1990, and was due to *Planktosphaeria* sp. (19.5%). For the rest of the study period Chlorophyta biovolume was negligible. The dominant cyanophyte species were *Planktothrix agardhii* (12.6%) and *Coelosphaerium naegelianum* (3.7%). In 1991 the phytoplankton biomass was lower than in the previous year and *Stephanodiscus hantzschii* dominated the total phytoplankton biomass (65.7%) (Fig.3.9b). The cyanophyte, *Planktothrix agardhii* was prominent in 1991 but with a lesser contribution (10.4%). *Anabaena* sp., in contrast to other cyanophytes in Little Mere, grew through the summers with varying biomass and its highest contribution was observed in 1991 (16.9%). There was a major decrease in *Cryptomonas* spp to (7%) in 1991. The species composition of the growing season of 1992 was similar to the previous year (Fig.3.9c) but the contribution of Cryptomonads to the total phytoplankton biomass increased to 43%. In 1993, there was a major change in the dominant diatom species by which *Aulacoseira* sp replaced *Stephanodiscus hantzschii,* though its contribution was not high (2.5%) The phytoplankton biomass was largely dominated by *Cryptomonas* spp (94.8%) (Fig.3.9d).

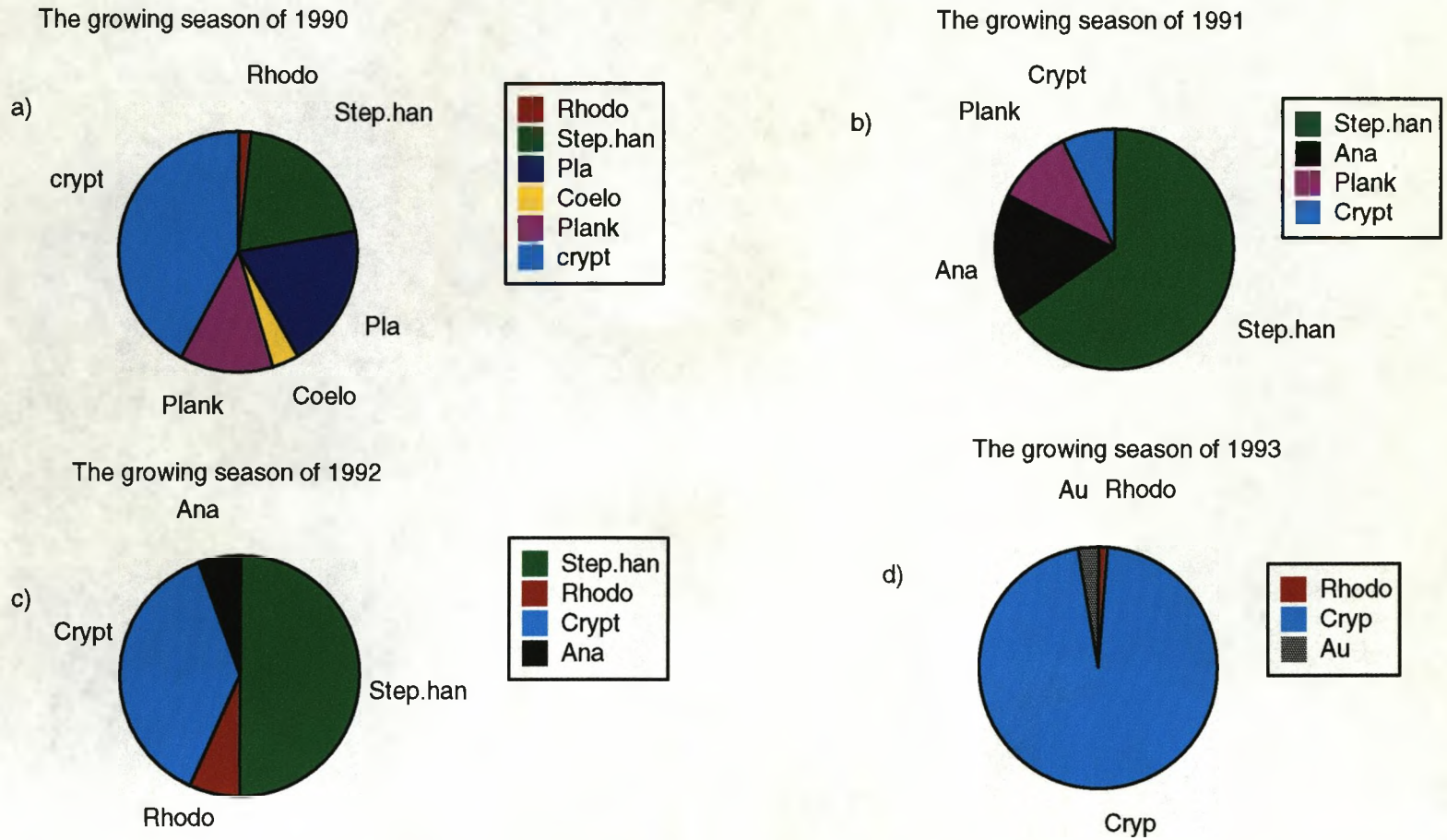

Fig. 3.9 Changes in total phytoplankton biovolume of the growing season (March to October) of a) 1990, b) 1991, c) 1992 and d) 1993 in Little Mere. Ana; *Anabaena* sp., Au: *Aulacoseira* sp., Coelo: *Coelosphaerium naegelianum*, Crypt: *Cryptomonas* spp., Pla: *Planktosphaeria* sp., Plank: *Planktothrix agardhii*, Rhodo: *Rhodomonas minuta*, Step.han: *Stephanodiscus hantzschii*.

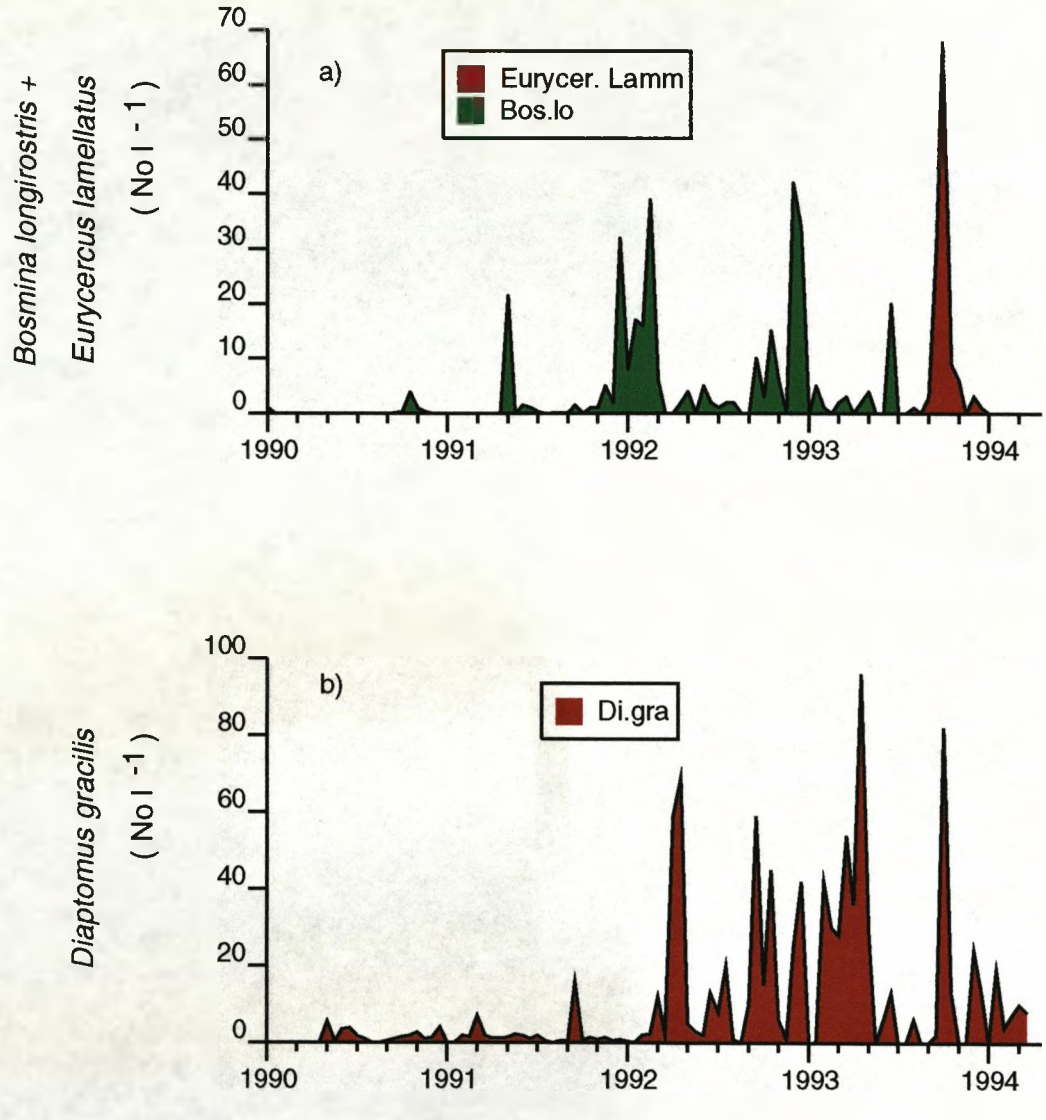

Fig. 3.10 Changes in density of a) *Bosmina longirostris* and *Eurycercus lamellatus*, and b) *Diaptomus gracilis* in Little Mere between 1990 and 1994 (four months data of 1994 used).

The zooplankton grazers are separated into two groups, the large bodied *Daphnia magna* Straus (Fig.3.8b) and other Cladocera. The latter group was dominated numerically by *Daphnia longispina*, *D. hyalina* Leydig (Fig.3.8c) *Bosmina longirostris* and *Eurycercus lammellatus* (O.F Műll) (Fig 3.10a). In 1990 and 1991 *D. magna* and *D.longispina* dominated the zooplankton community. In both years *Daphnia magna* was unusually bright red and because of its large size (growing up to 5 mm) it was clearly visible in the water. Their contributions to the total density of zooplankton were 56.3% and 41.9% respectively in 1990 (Fig. 3.11a). The total zooplankton density was much lower in 1991 than 1990 (Fig.3.11), *D. magna* and *D.longispina* were the dominant species (72.9% and 13.3% respectively). *Bosmina longirostris* was much more prominent than previously (5.4%) in 1991 (Fig.3.11b). In 1992 there was a major change in the zooplankton community. The contribution of *D. magna* and *D.longispina* was lower than in the previous years (21.5% and 6.9% respectively). *D. hyalina* was observed in the zooplankton community for the first time with a contribution to the total biomass of 10.8%. There was also an increase in contribution of *Bosmina longirostris* to 13.8% (Fig. 3.11c). In 1993, the shift from *D. magna* and *D.longispina* to *D.hyalina* was much more prominent than in the previous year and *D.hyalina* predominated (45.3%) (Fig. 3.11d). *D. magna* was not recorded and density of *D.longispina* was very low. Weed-bed associated Cladocera, including *Eurycercus lammellatus* were recorded for first time with an important contribution to the community (12.9%).

Linear regression analysis was carried out to examine the importance of *Daphnia* density for controlling chlorophyll a. Linear regression analysis of the study period chlorophyll a against *Daphnia* showed no significant relationships (Fig.3.12), though

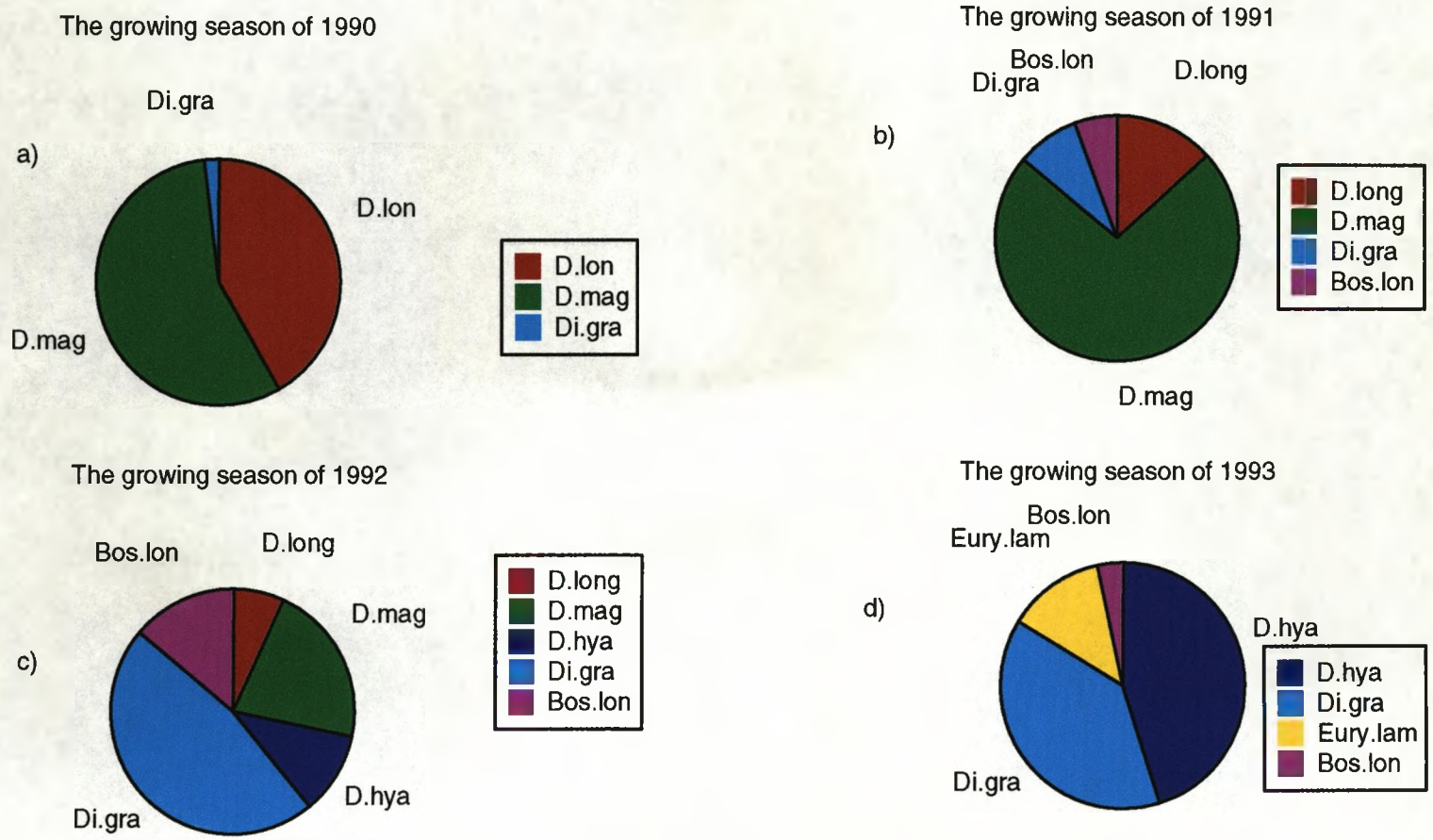

Fig. 3.11 Changes in total zooplankton density in the growing season (March to October) of a) 1990, b) 1991, c) 1992 and d) 1993 in Little Mere. Bos.lon*Bosmina longirostris*, Eury.lam: *Eurycercus lammellatus*, D.long: *Daphnia longispina*, D.hya: *Daphnia hyalina*, D.mag: *Daphnia magna*, and D.gra: *Diaptomus gracilis*).

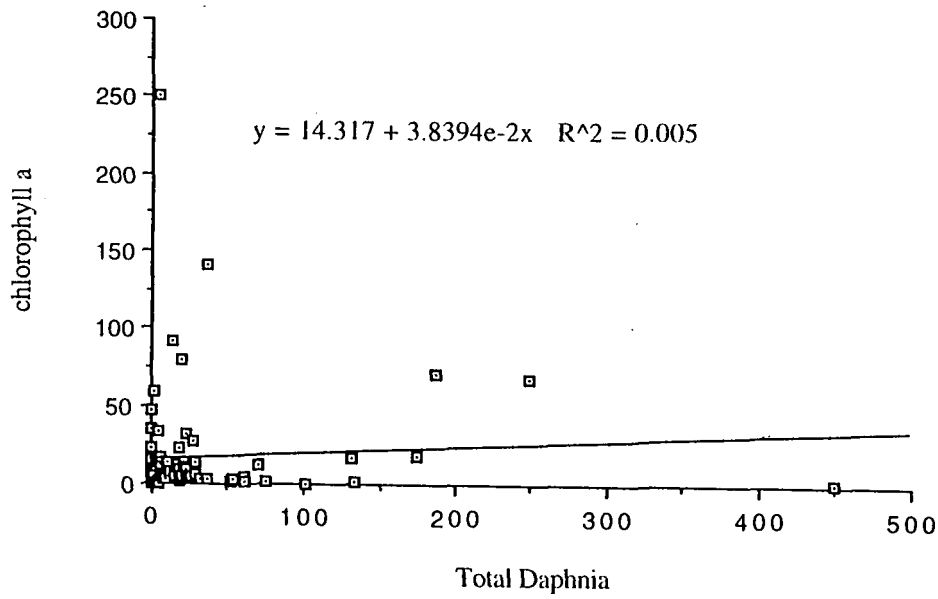

Fig. 3.12 The relationship between total Daphnia and chlorophyll a in Little Mere between1990 and 1994 (first three months data of 1994 used)

for much of the summer the water was clear and nutrient rich and *Daphnia* was abundant.

3.3.3 Phytoplankton and zooplankton of Rostherne Mere

The spring increase in chlorophyll a was largely due to the diatoms, *Stephanodiscus hantzschii* in 1990, 1991 and 1992 (Fig. 3.13b) In 1993, there was a shift from *Stephanodiscus hantzschii* dominance to joint *Aulacoseira* sp.-*Stephanodiscus hantzschii* dominance with *Stephanodiscus hantzschii* biovolume lower than in previous years. In 1994, the shift was much clearer than a year before. *Stephanodiscus hantzschii* was not recorded in the spring diatom peak. The spring diatom peak coincided with the spring decline in silicate concentrations (see Chapter 2). Cryptomonads, *Cryptophyta* sp, *Rhodomonas minuta* and some other flagellates contributed to the spring phytoplankton biomass throughout the study period (Fig. 3.13a). An early summer increase was principally due to filamentous cyanophytes, *Anabaena* sp.. There was a brief exception to this in 1992 when *Anabaena* sp was negligible (Fig.3.14a). The mid-late summer increase was due to the colonial cyanophyte *Microcystis aeruginosa*. However, there was no mid-late summer increase of *Microcystis aeruginosa* in 1993. The dinoflagellate, *Ceratium hirundinella*, showed its biovolume maximum in late summer throughout the study (Fig.3.14b). In 1992 there was a big increase in biovolume of *Ceratium hirundinella* which coincided with low *Anabaena* sp.. The increase in abundance of *Aulacoseira* sp continued, with a greater biovolume than in the spring peak throughout summer 1992 and 1993. In Rostherne Mere, biovolumes of Chlorophyta were negligible with *Chlamydomonas* spp, *Elakatothrix gelatinosa* Wille and *Planktospheria gelatinosa* Aut. recorded with varying biovolumes (Fig.3.13c).

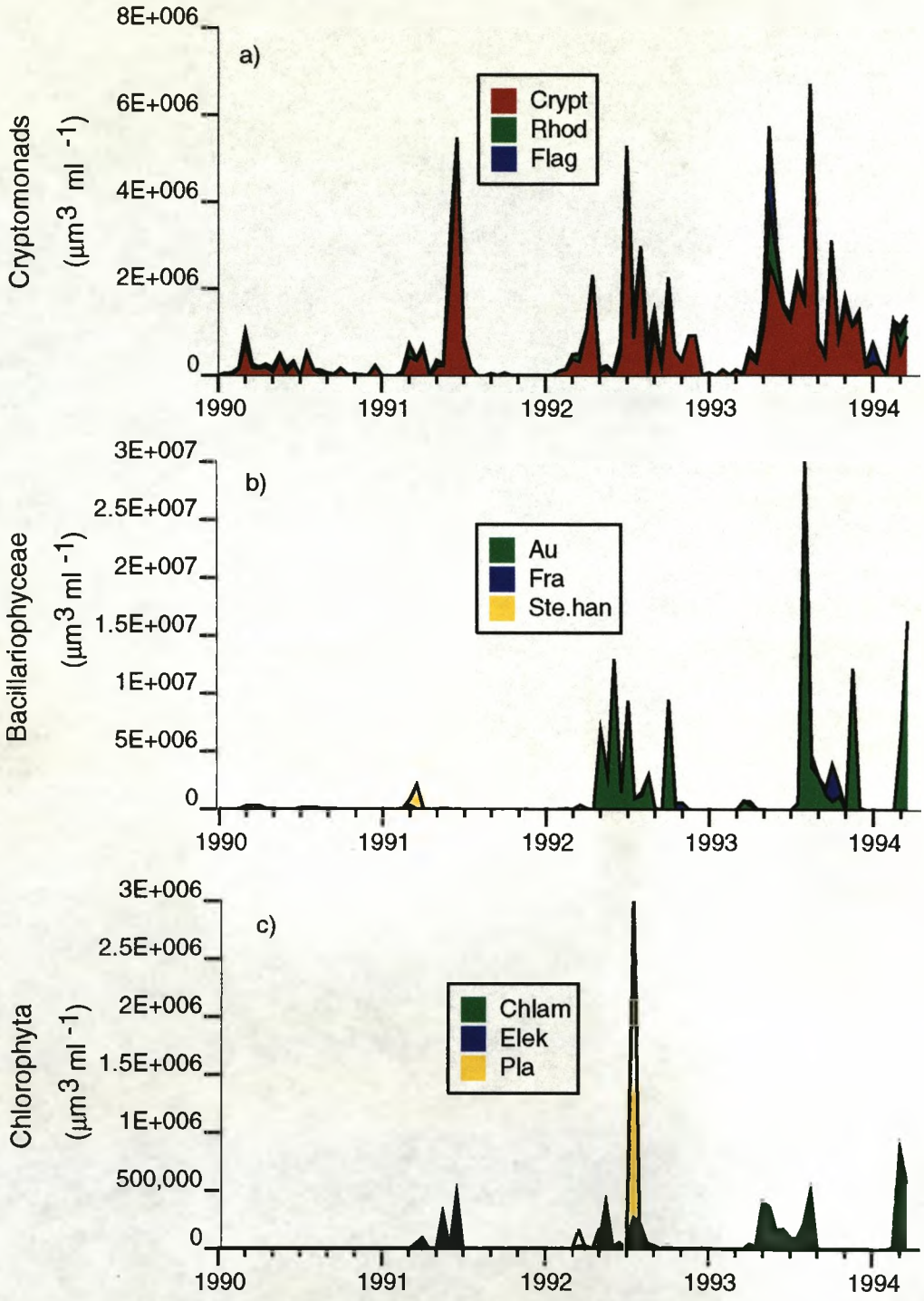

Fig. 3.13 Changes in biovolume of a) Cryptomonads, b) Bacillariophyceae and c) Chlorophyta, in Rostherne Mere, between 1990 and 1994 (first three months data of 1994 used). Crypt: *Cryptomonas* spp., Rhod: *Rhodomonas minuta*, Flag: unidentified flagellates, Chlam: *Chlamydomonas* sp., Elek: *Elakatothrix gelatinosa*, Pla: *Planktospheria gelatinosa*, Au: *Aulacoseira* sp., Fra: *Fragilaria* sp., Ste.han: *Stephanodiscus hantzschii*.

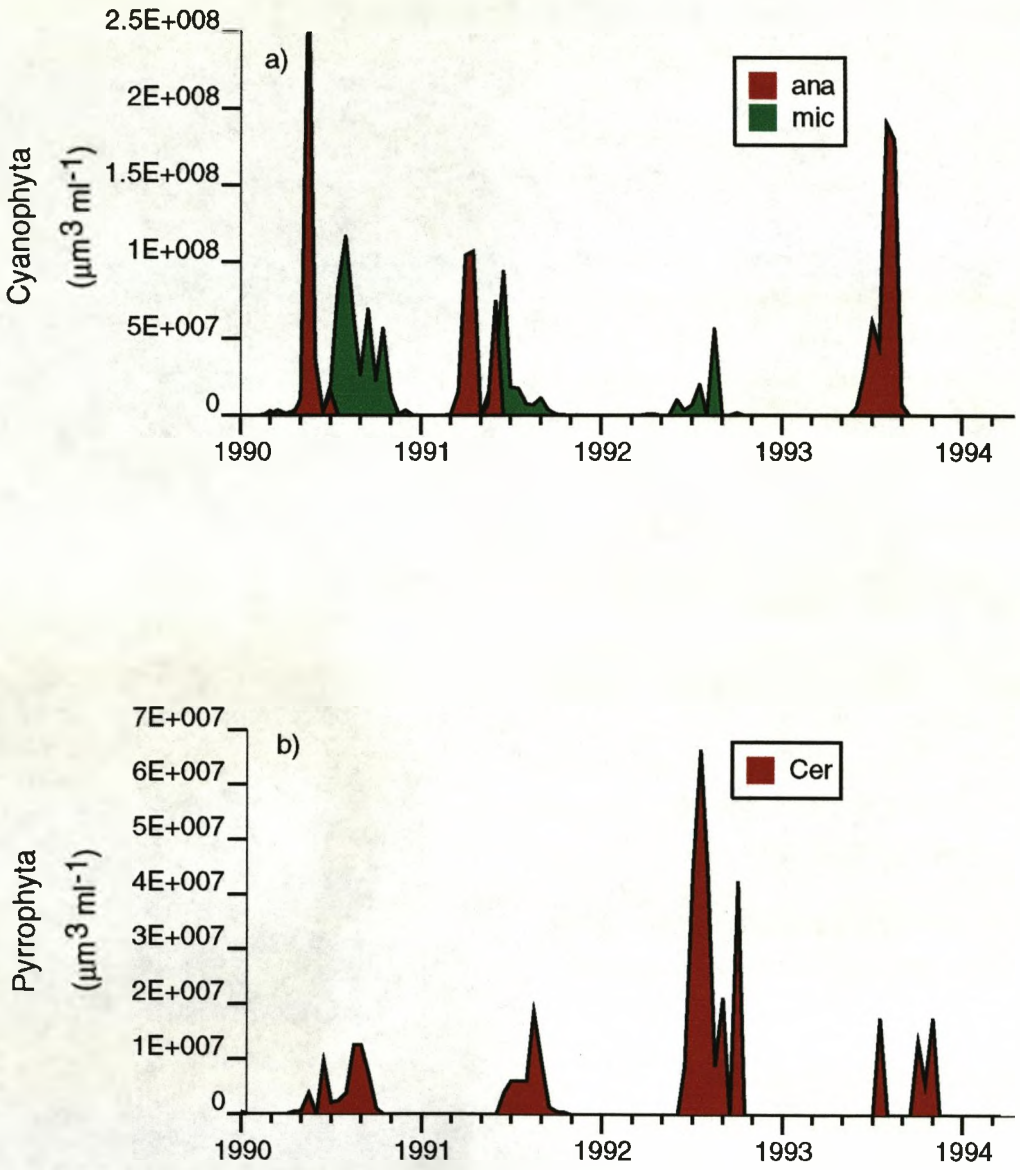

Fig. 3.14 Changes in biovolume of a) Cyanophyta, b) Pyrrophyta in Rostherne Mere, between 1990 and 1994 (first three months data of 1994 used). Ana: *Anabena* sp., Mic: *Microcystis aeruginosa*, Cer: *Ceratium hirundinalla*.

Biovolumes of the cyanophytes, *Microcystis aeruginosa, Anabaena* sp. and the dinoflagellate, *Ceratium hirundinella* dominated the total phytoplankton biomass of the growing seasons (June to September) of 1990 and 1991(Fig. 3.15a,b). Their contributions were 52.8%, 40% and 6.3% respectively in 1990 and 36.3%, 52.9% and 8.93% respectively in 1991. There was a major change in the growth season of 1992 when the contribution of *Anabaena* sp to the total phytoplankton biomass was replaced by *Ceratium hirundinella* (51.3%) (Fig. 3.15c). The biovolume of *Microcystis aeruginosa* was prominent (34.4%) as in previous years. *Aulacoseira* sp. became the dominant diatom species with a greater contribution (10.4%) to the total phytoplankton biovolume than *Stephanodiscus hantzschii.* In 1993, *Anabaena* sp dominated the phytoplankton biomass (75.5%) as in the first two years of the study period (Fig.3.15d). The biovolume of *Microcystis aeruginosa* in 1993 was the lowest recorded (1.46%) throughout the study. The contribution of *Ceratium hirundinella* was similar to first two years of the study (7.9%). *Aulacoseira* sp dominance continued as in the as previous year (10.9%).

The prominent zooplankton species of Rostherne Mere throughout the study period were the large-bodied cladoceran grazer, *Daphnia longispina* (Fig.3.16a), the small-bodied cladoceran grazers, *D.cuculata* (Fig.3.16a), *Bosmina longirostris* and *Chydorus* sp. (Fig.3.16b), and the copepod, *Diaptomus gracilis* (Fig.3.16c). Both large and small-bodied cladocerans showed a very similar seasonality, though the large-bodied species was generally more abundant. Densities were greatest in the spring and early and mid summer and declined during late summer. In autumn the densities briefly increased. *Diaptomus gracilis* showed a similar seasonality to that of the Cladocera, with peak

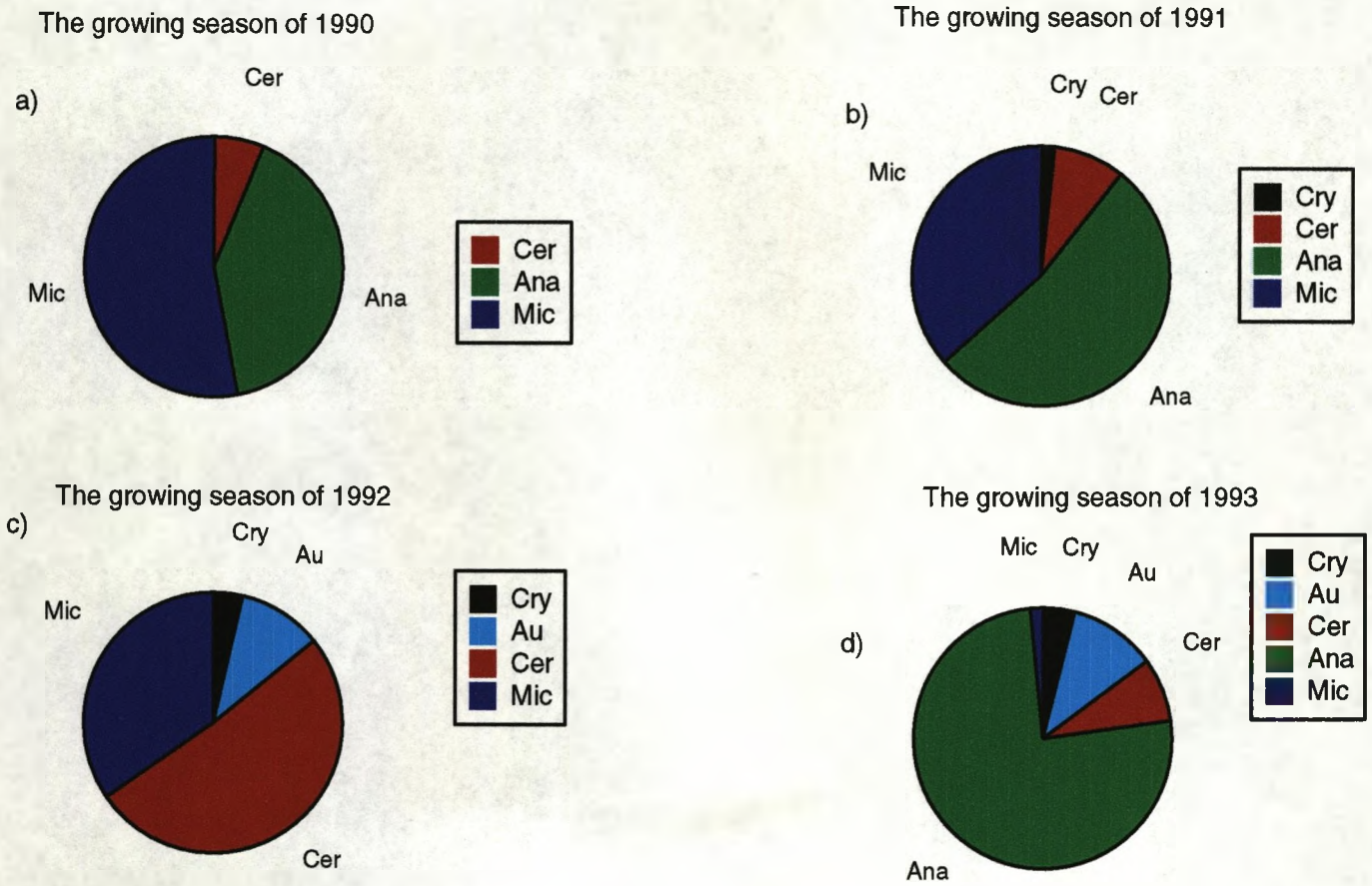

Fig. 3.15 Changes in total phytoplankton biovolume in the growing season (March to October) of a) 1990, b) 1991, c) 1992 and d) 1993 in Rostherne Mere (Ana:*Anabaena* sp., Au:*Aulacoseira* sp., Cer: *Ceratium hirundinella* , Cry: *Cryptomonas* sp., Mic: *Microcystis aeruginosa*).

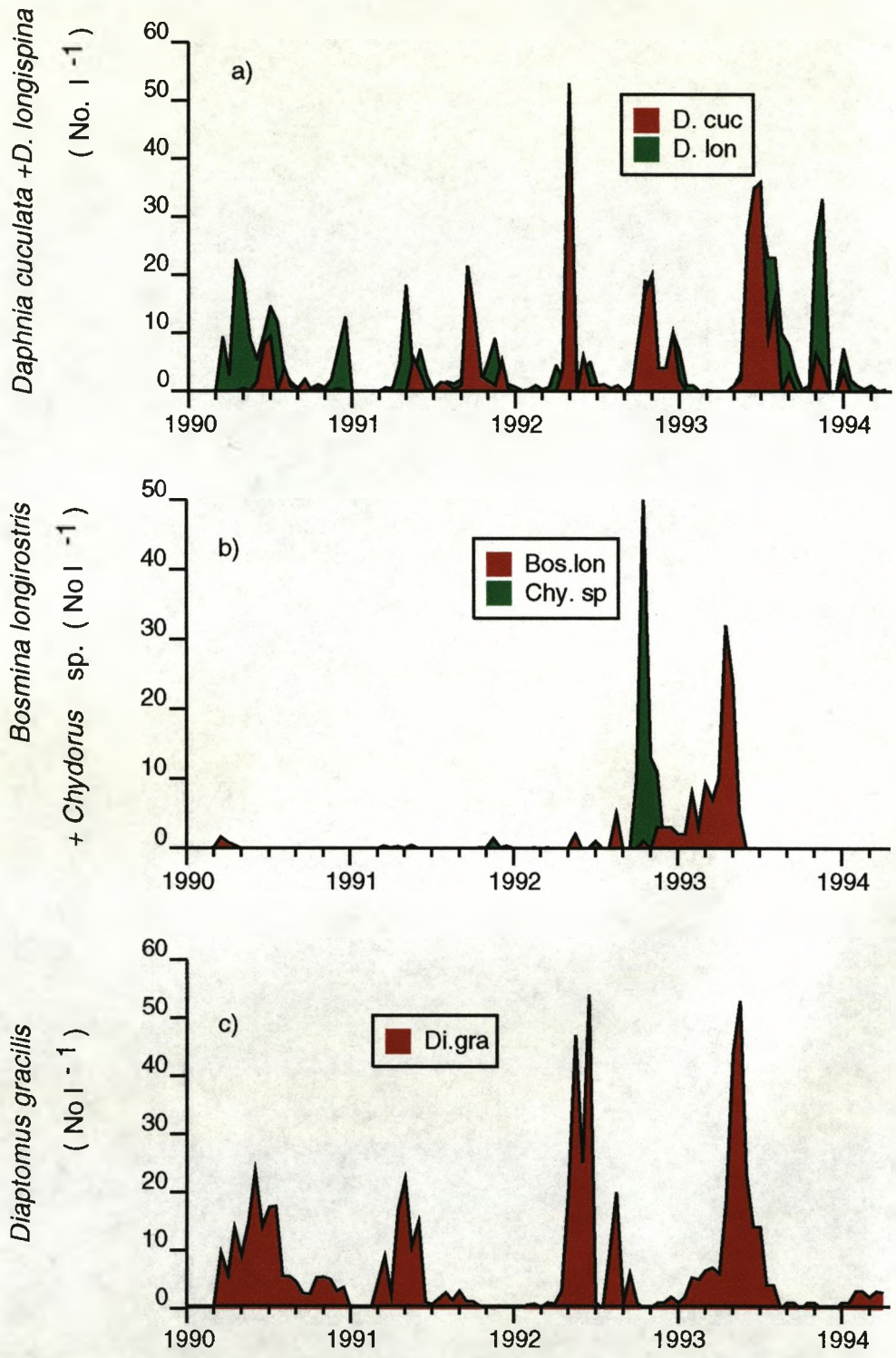

Fig. 3.16 Changes in densities of a) *D.cuculata* and *D. longispina, b) Bosmina longirostris* and *Chydorus* sp., and c) *Diaptomus gracilis* in Rostherne Mere, between 1990 and 1994 (first three months data of 1994 used).

densities in the spring and mid and early summer.

Daphnia longispina was predominant throughout the study with a numerical contribution to the total zooplankton community in the growing seasons of the study period of 40.8% 1990, 32.5% 1991, 20.7% 1992 and 34.4% 1993 (Fig.3.17a,b,c and d). *D.cuculata* and *Bosmina longirostris* were the prominent species of small-bodied cladoceran grazers which were largely dominated by *D.cuculata* throughout the study period. Their contributions to the total zooplankton density were 9.2% and 1% in 1990, 23.4% and 0.8% in 1991, 23% and 1.6% in 1992, and 22.3% and 12.5% in 1993 respectively. *Chydorus* sp. was occasionally observed with a peak of its density (16.25%) in 1992 (Fig.3.17c) *Diaptomus gracilis* was the prominent copepod and made an important contribution to total zooplankton community. Its contributions throughout the study period were 52.3% in 1990, 43.3% in 1991, 38.4 in 1992 and 30.7 % in 1993 (Fig. 3.17a,b,c and d).

Multiple regression analysis of summer chlorophyll a concentrations (April to mid-May) DIN, SRP and silicate concentrations and herbivore densities showed no significant relationships (Table 3.1). Multiple regression analysis of summer chlorophyll a concentrations (June to September) against DIN and SRP concentrations and herbivore densities (which included *Daphnia longispina*, *D.cuculata*, *Bosmina longirostris* and *Chydorus* sp.) showed a highly significant relationship (Table 3.1); DIN appeared to be of greatest importance. Linear regression analysis of DIN against chlorophyll a concentrations showed that this was a negative relationship, chlorophyll a concentrations increasing as DIN concentrations decreased (r^2=0.464, F=26.8, P< 0.00001, n=33). Herbivores were the next important factor in the multiple regression

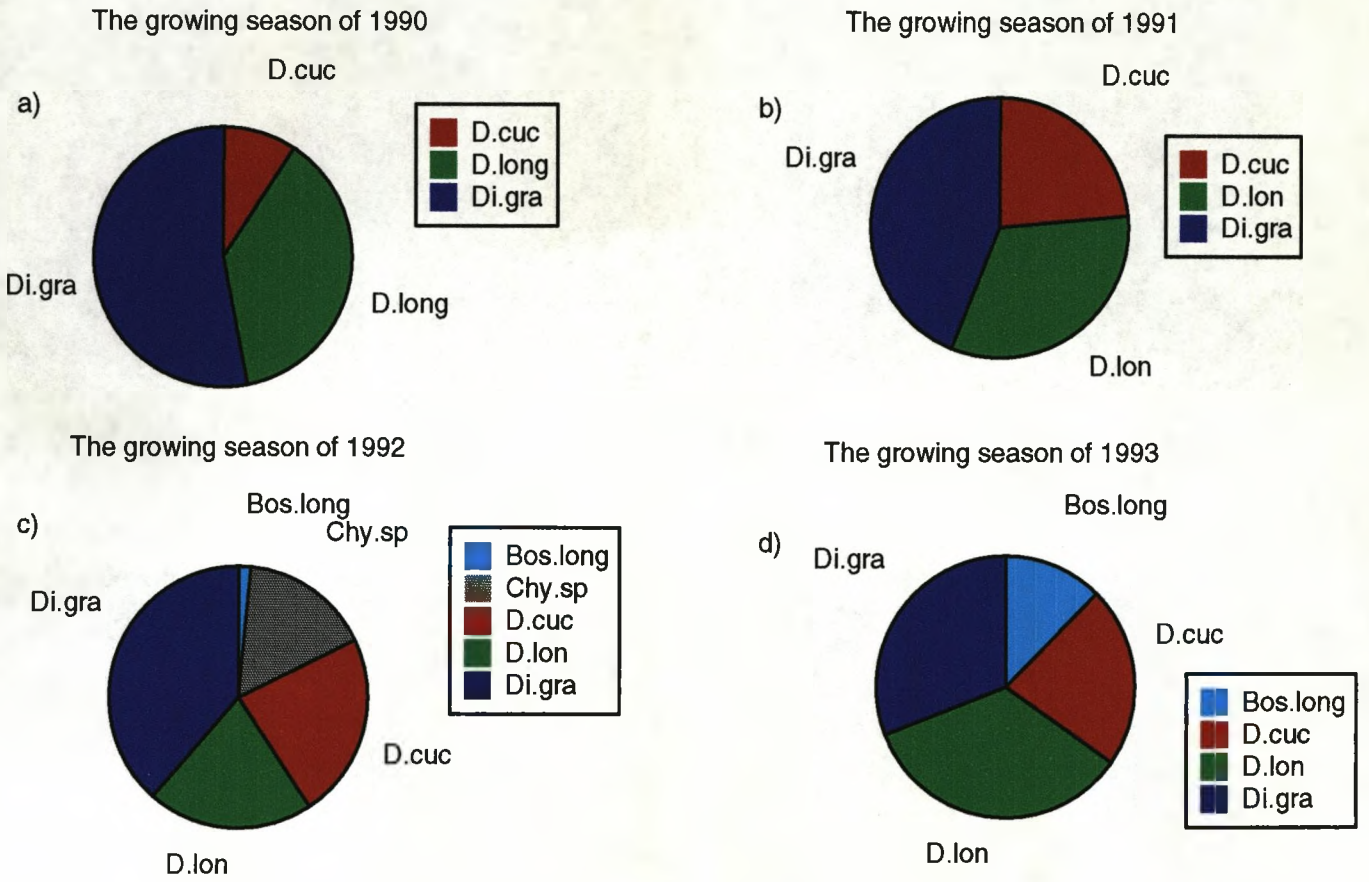

Fig. 3.17 Changes in total zooplankton density in the growing season (March to October) of a) 1990, b) 1991, c) 1992 and d) 1993 in Rostherne Mere. Bos. long: *Bosmina longirostris*, Chy sp: *Chydorus* sp., D.lon: *Daphnia longispina* , D.cuc: *Daphnia cuculata* and Di.gra: *Diaptomus gracilis* .

analysis (Table 3.1).

The ratio of carotenoid pigments to chlorophyll a pigments (A480:663) was >1.3 throughout most of the study period. For long periods the ratio of A430:410 was <1.2, but during the summer moths the ratio of A430:410 was >1.2 (Fig. 3.6b).

3.4. Discussion

3.4.1. Mere Mere

In Mere Mere the spring increase in chlorophyll a was largely due to diatoms and was closely correlated with a depletion of silicate to undetectable concentrations (r^2=0.38, P<0.001 n=19). This depletion might also have caused a decline in the diatom peak (Lund, 1950; Kilham, 1971; Sommer & Stabel, 1983) though losses might have been increased by the high density of grazers present during spring (Lampert *et al.* 1986). *Asterionella formosa* was dominant for the first three years of the study. In 1992 the spring increase in chlorophyll a and biovolume of *Asterionella formosa* were much lower than in the previous years. The contribution of *Asterionella formosa* to the spring diatom peak decreased in 1993 and it was largely replaced by *Aulacoseira* sp.. This shift continued in spring 1994. Though *Asterionella* and *Aulacoseira* are both apparently favoured by high Si:P ratios (Tilman *et al.* 1982) *Asterionella formosa* has high requirements with respect to silicate but very low requirements with respect to phosphorus (Tilman *et al.* 1982). There was no significant decrease in total phosphorus concentrations in Mere Mere throughout the study period (Chapter 2; Carvalho *et al.* in press). To check possible effects of any change in wind strength (reflecting mixing intensity) on this shift, one-way ANOVA was carried out on summer wind strength (June-September; km hr^{-1}) but revealed no significant change between the years (F=2.75, P>0.05). It is not clear what favoured *Aulacoseira* dominance over *Asterionella formosa* and whether the shift is permanent.

Multiple regression analysis of spring (March to April) chlorophyll a concentrations against DIN, SRP and silicate concentrations and Cladocera densities (Table 3.1) showed no significant relationships. However, analysis of summer (June to September)

chlorophyll a concentrations against DIN and SRP concentrations and Cladocera densities (Table 3.1) showed significant relationship (r^2=0.27, 0.02<P<0.03). DIN appeared to be of greatest importance. This might indicate a limitation of phytoplankton biomass by DIN because DIN did decline to undetectable, or very low, concentrations during July and August in 1990, June, July and August in 1991, July and September in 1992 and July, August and September in 1993 (Chapter 2; Carvalho *et al.* in press). Though SRP decreased to relatively low values for the lake, it was always absolutely abundant and the relatively high P:N ratio may have favoured the growth of the nitrogen-fixing cyanophyte *Anabaena* (Nalewajko & Lean, 1978; Rhee, 1978; Smith, 1983). The dinoflagellates *Ceratium* and *Peridinium* may have low nutrient requirements, due to their lower growth rates (Pollingher, 1988) and may also have been favoured by these conditions. During summer except in 1993, *Anabaena* dominated the phytoplankton community along with *Ceratium* and *Peridinium*. Reynolds and Walsby (1975) and Horne (1979) note that numerous factors may be involved in the ecological success of Cyanophyta. One proposed explanation for their dominance is that low nitrogen to phosphorus (N:P) ratios in the nutrient supply favour vacuolate, nitrogen-fixing Cyanophyta over other types of algae (Schindler 1977; Flett *et al.* 1980). There was a significant declining trend of DIN and TON in Mere Mere after sewage effluent diversion in Little Mere, though this must be coincidental as inflow Mere Mere was not affected by sewage effluent (Chapter 2; Carvalho *et al.* in press). This inconstancy of nitrogen loading to Mere Mere from the catchment may have decreased the N:P ratio and resulted in an increase of nitrogen-fixing *Anabaena* dominance, but wide interspecies variations have been found in optimum N:P ratios of different cyanophyte species (Reynolds, 1984). Thus, a given species seasonal succession may not necessarily illustrate the generalization. The

decrease in *Anabaena* sp. biovolume in 1993 coincided with an increase in biovolume of the dinoflagellate, *Ceratium hirundinella* which is able to move to deeper layers and tap hypolimnion nutrient sources (Reynolds, 1976). Also grazer-resistance, because of their cell size and their hard cell wall structure, might have favoured *Ceratium hirundinella* (Nicholls *et al.* 1980). Vacuolate cyanophytes also appear to move to deeper water and tap hypolimnetic nutrients (Ganf & Oliver, 1982). The decrease in *Anabaena* sp. biovolume in 1993 did not appear to be related to water temperature and neither the wind strength nor the air temperature changed ($F=2.75$, $P>0.05$; $F=0.34$, $P=0.8$ respectively).

Grazing pressure did not appear to be of great importance for controlling the phytoplankton community through summer in Mere Mere (Table 3.1). In Mere Mere, small cladocerans, were predominant, early summer peaks being principally due to *Bosmina* and those in summer to *D.cuculata*. There was more than a two fold increase in the density of *D.cuculata* in 1993 which coincided with the decrease in *Anabaena* sp. biovolume. The suitability of cyanophytes as a food source for herbivorous zooplankton has been much discussed. De Bernardi *et al.* (1981) found that fecundity, reproduction and population growth of three species of *Daphnia* (*D.hyalina*, *D.cuculata* and *D.obtusa* Kurz.) on cyanophytes were similar to those obtained with similar densities of green algae. They concluded that, in general, the small zooplankters are less mechanically influenced by the presence of filaments or colonies of cyanophytes than are the large ones (De Bernardi *et al.* 1981; De Bernardi & Giussani, 1990). The increase in *D.cuculata* density might have been important in the decrease of *Anabaena* biovolume, though simple regression of summer (June to September) 1993 *Anabaena* biovolume against *D.cuculata* density showed no

significant relationship. Thus, it is not clear that the decrease in *Anabaena* sp. biovolume is permanent or just an annual fluctuation. The reason for the increase in *D.cuculata* density is not clear either because no data exist on fish populations of Mere Mere. The large cladoceran, *D.longispina*, density was low throughout summer and this might be due to indigestibility of the available phytoplankton biomass as a food source (Bucka and Zurek, 1992) and it is being less efficient of handling the cyanophyte as a food source (Richman & Dodson, 1983; Gliwicz, 1980; 1990a). Fish predation may also account for the low density of large Cladocera.

More evidence of possible nitrogen deficiency in control of phytoplankton crops in Mere Mere comes from the ratio of carotenoid pigments to chlorophyll a (A480:663), which was >1.3 throughout most of the study period, indicating that the phytoplankton community may have been nitrogen deficient. However, in winter the A430:410 ratio was <1.2 which suggests that the high A480:663 ratio may have been due to resuspended sediment or grazing effects. But during the spring and summer months the A430:410 ratio was >1.2 whilst the A480:A663 ratios remained high. This suggests that the phytoplankton crop was nitrogen deficient. The presence of a large population of nitrogen-fixing cyanophytes, during these months, is also an indication of nitrogen deficiency (Schindler, 1977). Moss *et al.* (1994) 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 >3m) North-West Midland Meres (including Mere Mere), which suggests that nitrogen may be the limiting factor of phytoplankton crop-size in many lakes of this area. Thus during summer, nitrogen appeared to be the factor most likely to be limiting the phytoplankton biomass. The phytoplankton periodicity in Mere Mere has changed little from previous studies (Griffiths, 1925; David, 1963;

Belcher & Storey, 1968). *Ceratium* is still abundant during summer. However, *Microcystis*, which was observed in the two earliest studies, was not observed in the present study, or the previous one (Belcher & Storey, 1968). The nitrogen-fixing cyanophyte *Anabaena* has become much more abundant. An exception to this was observed in 1993, but it is not clear that whether it was a consistent decrease or just an annual change.

3.4.2. Little Mere

According to observed relationships between lake phosphorus concentrations and chlorophyll a concentrations (Dillon & Rigler, 1974), Little Mere showed a huge potential for phytoplankton growth, though to a lesser but still considerable extent following the sewage effluent diversion. The lake had a brief spring increase in diatoms, and small flagellates, and cyanophytes in 1990, as is common in many temperate lakes (Hutchinson 1967). This is often followed by a spring "clear water" phase because of large densities of filter feeders (Lampert *et al.* 1986). 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 the summers of the study period. The summer clear water phase was almost certainly due to high densities of grazers, in particular the large bodied *Daphnia magna* and later *D.hyalina.*

In Little Mere, there has been a considerable change in water chemistry following sewage effluent diversion in June 1991 which in turn has been associated with great changes in both the phytoplankton community and the zooplankton community. Little Mere showed a significant declining trend of annual mean chlorophyll a concentrations

over the study period (59µg l^{-1} in 1990 to 6 µg l^{-1} in 1992 increasing slightly to 17 µg l^{-1} in 1993) (Chapter 2; Carvalho *et al.* in press). Chlorophyll a concentrations were mostly due to the spring increase in phytoplankton community though the spring increases were much lower and with different species contributions after sewage effluent diversion. Before the effluent diversion, the biggest contribution to chlorophyll a concentrations was from spring peak of *Stephanodiscus hantzchii.* There was major shift from *Stephanodiscus hantzchii* to *Aulacosira* sp., two years after the effluent diversion in 1993 which continued in spring 1994. *Stephanodiscus hantzchii* is a typical of very eutrophic conditions (Anderson *et al.* 1990) and it is a species associated with low Si:P ratios (Lund, 1950; Tilman *et al.* 1982). Following the sewage effluent diversion, TP concentrations decreased over ten fold (2245 µg l^{-1} in 1990 to 185 µg l^{-1} in 1993) (Chapter 2; Carvalho *et al.* in press); in return Si:P increased from 1.97 to 11.27. *Aulacosira* sp. is a mesotrophic plankton form (Anderson, 1989; Anderson, 1990) associated with high Si:P ratios (Lund, 1950; Tilman *et al.* 1982). Thus, the major decrease in TP concentrations increased the Si:P ratios, and in turn this may have resulted the shift of dominant diatom species from *Stephanodiscus hantzchii* to *Aulacosira* sp. However, a similar shift occurred in Mere Mere, where there has been no input of sewage effluent nor major change following diversion of it, so other factors may have been involved.

Cyanophytes were near absent from Little Mere throughout the study period, except in spring 1990 with filamentous *Planktothrix agardhii, Aphanizomenon flos-aquae* and the colonial *Coelosphaerium naegelianum* to a lesser extent in 1991. The cyanophytes disappeared in the spring at the same time as *Daphnia magna* density increased. Throughout summer the large daphnid densities were very high and the cyanophyte,

Anabaena sp. biovolume was very low. Though controversy surrounds the suitability of Cyanophyta as a food source for zooplankton because of production of toxic chemicals (Nizan *et al.* 1986), poor assimilation (Arnold, 1971), and mechanical interference (Gliwicz, 1990a; Hartman, 1985), a wide range of examples is available confirming a general pattern of cyanophyte reduction after fish removal and the consequent increase in filter-feeding zooplankton (van Donk *et al.* 1989; Jeppesen *et al.* 1990b). Another explanation for the absence of Cyanophyta in Little Mere during the summer might be growth conditions which disfavoured them. The presence of inocula from the upstream Mere Mere and the lake's very low flushing rate in summer might be expected to favour, in Little Mere, the large and slow growing cyanophytes over small algae with high growth rate. However, the presence of high free-CO_2 concentrations due to a large contact area with organic sediments enriched with organic matter from the sewage effluent, may have mitigated against cyanophytes. Cyanophyta are believed to be favoured over other algal types by low free-CO_2 (Shapiro 1990a). The role of CO_2 for cyanophytes in Little Mere was checked in experimental enclosures with increasing pH values (giving low free-CO_2 concentrations). Lack of cyanophytes in the lake does not seem to be function of CO_2 or high pH (Chapter 7, Beklioglu & Moss, 1995).

Before the 1991 diversion of effluent from Little Mere, its zooplankton community was dominated by large body-sized *D.magna* and to a lesser extent by *D.longispina.* Individuals of *D.magna* were bright red due to the presence of hemoglobin, which is produced in response to low levels of dissolved oxygen (Carvalho, 1984). The pigmentation increases their vulnerability to visual predation by fish (Kerfoot, 1980) and along with their large size (growing up to 5 mm.) and the clear water conditions,

D.magna would have been very susceptible to fish predation. Evidently there was little fish predation on the zooplankton community, though fish could move into the lake from Mere Mere upstream (Carvalho, 1994). The quality of the sewage effluent was such as to deoxygenate the water to near anoxia (Chapter 2; Carvalho, 1994; Carvalho *et al.* in press). The low concentrations of dissolved oxygen along with extremely high ammonium concentrations are likely to have resulted in fish-kills. Thus, the large body-sized *D.magna* thrived with lack of predation pressure.

After June 1991, when the sewage effluent was diverted elsewhere, dissolved oxygen concentrations rose (Carvalho *et al.* in press). Fish, predominantly perch, *Perca fluviatilis* L., moved in from upstream (Chapter 8). Although the density of the large grazers, *D.magna* decreased, clear-water was maintained despite the presence of mainly juvenile perch predation pressure, probably because of the presence large stands of macrophytes including nymphaeids, *Potamogeton berchtoldii* Fieber and *Elodea canadensis* Michaux. Aquatic plants provide refuges in which large populations of grazer Cladocera may be sustained and coexist with zooplanktivorous fish populations (Timms & Moss, 1984). In 1993 there was a switch from *D.magna* to *D.hyalina*, probably due to increased predation pressure of fish or less favourable conditions for *D.magna* abundance. *D.hyalina* was prominent, and there was an increase in its density in 1993 which might be due to increase in the total macrophyte coverage, largely by *Potamogeton berchtoldii*. Experiments with changed plant densities and presence or absence of perch in enclosures in Little Mere have shown reduction in numbers of *D.hyalina* at high plant densities in the presence or absence of perch (Moss & Kornijow, in preparation). *D.hyalina* may thus have concentrated to a greater extent in the remaining open water, but the diurnal sampling in summer

1994 showed near absent density of *D.hyalina* (Chapter, 8) that was consistent with its general density in the lake throughout summer 1994 (D. Stephen, unpublished data). Because of the increase in the aquatic plant stand, weed-bed associated zooplankters largely *Eurycercus lamellatus* with lesser densities of *Simocephalus* spp. and *Sida crystallina* became more prominent. The densities of weed-bed associated cladocerans were low, which might be due to the nature of the sampling station, open water, and an inappropriate sampling technique. Samples taken from the weed-bed, at the same time as those for phytoplankton and zooplankton, contained higher densities of these zooplankters (Chapter 6, 7 and 8) and there was a significant increase in the weed-associated zooplankters densities in 1994 that the diurnal sampling in summer 1994 showed that they have become more prominent (Chapter 8).

Linear regression analysis was carried out to examine the relationship between the density of *Daphnia* and chlorophyll a in Little Mere but showed no significant relationship. Clearly the phytoplankton community of Little Mere was not nutrient-limited because the concentrations of SRP and DIN were extremely high prior to the effluent diversion (1925 $\mu g\ l^{-1}$ and 3.81 $mg\ l^{-1}$ respectively in 1990) and though their concentrations significantly decreased following the effluent diversion (62 $\mu g\ l^{-1}$ and 0.33 $mg\ l^{-1}$ respectively in 1993) they remained substantial (Chapter 2; Carvalho *et al.* in press) and were high enough to support a large growth potential for algae. The possible explanation for the low phytoplankton crop was more likely related to the huge *Daphnia* density. The scatter graph (Fig.3.12) showed a cluster of points around the origin because throughout the study chlorophyll a concentrations were near zero at very high *Daphnia* densities. This might have masked the significance of actual

grazing pressure of *Daphnia*. Maintenance of high *Daphnia* densities at low phytoplankton crops was most likely due to availability of alternative food sources. Some *Daphnia* species with fine-mesh filters like *D.magna* and *D.hyalina* are capable of utilizing bacteria and detritus as a food source (Geller & Muller, 1981; Brendelberger, 1991). The ability of the dominant *Daphnia* to eat bacteria and detritus may have maintained their densities high enough in Little Mere to make them independent of phytoplankton which they would otherwise graze when available.

Following the diversion of sewage effluent in 1991, Little Mere has so far maintained high density of grazers, clear water, and the macrophyte-dominated conditions found prior to diversion and attributed to lack of fish through deoxygenation. Fish, perch in particular, have recolonized Little Mere in considerable numbers but did not prevented the development of large *Daphnia hyalina* populations untill 1994 that its density decreased. Recently, the zooplankton community of the lake has been largely dominated by the weed-associated grazers and the clear water has been maintained so far (see Chapter 8). Although the lake retained a huge potential for algal growth this remained negligible in summer. Recovery of the fish population could have shifted the lake to a phytoplankton-dominated phase from its current clear-water phase, but so far this has not happened. As Scheffer *et al.* (1993) suggest, turbid-water is not a just function of high nutrient loading. Turbid-water with phytoplankton dominance and clear water with macrophyte dominance seem to be alternative stable states in shallow eutrophic lakes. Little Mere has strong macrophyte stands whose total surface coverage increased following the effluent diversion (Chapter 8). Large macrophyte stands may help maintain low phytoplankton crops directly through luxury nutrient uptake (Ozimek *et al.* 1990). This might have played an important role in the lake

though there are no data available on luxury nutrient uptake. Provision of refuges to large filter-feeding *Daphnia* by macrophytes against fish predation (Timms & Moss, 1984) may have had an important role in maintaining the clear-water. So far the changes in the lake have corresponded with Scheffer's *et al.* (1993) suggestion of a clear-water state with macrophyte dominance as an alternative stable state in shallow eutrophic lakes.

In future, a possible further expansion of the present macrophyte stands might shift the lake's current zooplankton community, largely open-water genera like *Daphnia*, to loosely or firmly plant- associated genera like *Simocephalus*, *Sida* and *Eurycercus*, which have already become more prominent. Probably because open-water genera like *Daphnia* seems to need some sediment contact or because the dense weed-beds seem to be less favourable (Moss & Kornijow, in preparation), *Daphnia* declined irrespective of fish predation. In addition, further expansion of rooted macrophyte stands might shift the phytoplankton to nutrient limitation, possibly nitrogen. Plants have free access to sedimentary nutrients through their roots (Denny, 1972) but phytoplankton does not. Thus, the phytoplankton community of Little Mere might become both nutrient and grazer-limited depending on the extent of macrophyte expansion (Chapter 4).

3.4.3. Rostherne Mere

The documented record of direct observations on the phytoplankton of Rostherne Mere, which dates from 1912 (Pearsall, 1923), has been recognized as an important long term data set (Elliott, 1990) though it is not an uninterrupted sequence. It testifies to the long-standing eutrophic character of the lake. Reynolds (1978a) suggests that

light most likely limits the spring phytoplankton crop. Rostherne Mere is deep and when the water column is isothermally mixed, phytoplankton must spend large parts of the day in low-light conditions. Seasonal data showed that grazing pressure may also be important in limiting the size of the spring phytoplankton crop, and for a spring clear-water phase as observed elsewhere (Arndt & Nixdorf, 1991). Multiple regression analysis of spring chlorophyll a concentrations (April to May) against DIN, SRP, and silicate concentrations and herbivore densities (Cladocera and *Diaptomus*) however showed no significance. The spring peak of chlorophyll a of Rostherne Mere was largely of diatoms along with cryptomonads. There was shift from *Stephanodiscus hantzschii* to *Aulacoseira* sp. in 1993 and the shift was prominent in 1994. The reason for the shift was not related to the Si:P ratios of the lake because the Si:P ratios were not different before and after effluent diversion (mean Si:P:3.4, before effluent diversion and mean Si:P: 3.1 after effluent diversion). In 1992 and 1993, *Aulacoseira* sp.was present throughout summer and made an important contribution to the total phytoplankton biovolume. Although diatoms are often favoured by lack of thermal stratification (Hutchinson, 1967), diatom species may remain dominant in summer (Reynolds, 1978a; 1979). There have been some occasions when diatom dominance was recorded is summer in Rostherne for example Mere *Aulacoseira granulata* in August, 1968 and *Stephanodiscus hantzschii* in August, 1986 (Reynolds & Belinger, 1992). These were attributed to early breakdown of stratification (Reynolds, 1973) but *Aulacoseira* sp. abundance throughout summer 1992 and 1993 did not appear to be attributable to breakdown of the thermal stratification (Fig.2.11a, Chapter 2), though it is difficult to be certain because of lack of temperature data in September, 1992 and the end of August, September and October in 1993.

The summer phytoplankton community of Rostherne Mere was dominated by potentially nitrogen-fixing *Anabaena* in June and July and *Microcystis* along with *Ceratium* for the rest of summer and autumn (within an exception to this in 1993). Multiple regression analysis of summer chlorophyll a concentrations (June to September) against DIN and SRP concentrations and herbivore densities showed a highly significant relationship. DIN appeared to be of greatest importance in controlling summer phytoplankton crops. In fact, DIN declined to very low concentrations during August and September throughout the study. There was a significant decreasing trend of DIN and TON concentrations in Rostherne Mere following effluent diversion but this trend occurred also in Mere Mere, above the former effluent input (Chapter 2, Carvalho *et al.* in press). However, if any nutrient was limiting the summer phytoplankton crop, it appears most likely to have been nitrogen. Herbivores were the next most significantly important factor in the multiple regression analysis. Limitation of many summer phytoplankton species, including *Anabaena*, *Aphanizomenon* and *Cyclotella*, by increased zooplankton densities was found in an enclosure experiments in Rostherne Mere (Carvalho, 1993).

The ratio of carotenoid pigments to chlorophyll a pigments (A480:663) was >1.3 throughout most of the period time indicating that 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 resuspensed sediment. The A430:A410 the ratio was >1.2 during June, August, and September, which suggests that the high A480:663 ratios during these months were due to nitrogen deficiency. The presence of large populations of nitrogen-fixing algae may be an indication of nitrogen deficiency also (Schindler, 1977).

However, in Rostherne Mere, in 1990, the potentially nitrogen-fixing *Anabaena*, dominated in early summer from May to June, before major depletion of DIN occurred. In 1991, *Anabaena* was observed again abundant in June, pre-DIN depletion, but also increased during the period of DIN depletion. *Microcystis* was the phytoplankter most abundant 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 sources in the hypolimnion, which have been shown to build up in Rostherne Mere during times of thermal stratification (Grimshaw & Hudson, 1970). Why *Anabaena* should have developed earlier than *Microcystis* and failed to dominate over summer (except in 1993) was not clear. Reynolds & Bellinger (1992) suggest that *Anabaena* grows and develops well at temperatures marginally below those preferred by *Microcystis*, and dominates only in years when the development of *Microcystis* and *Ceratium* is delayed due to cooler conditions. With some water temperature data missing from both summer 1992 and 1993 it was difficult to interpret any change in the temperatures but temperatures appeared to be slightly lower in summer 1993 than in the previous year (Chapter, 2) especially than in summer 1990 and 1991 (Carvalho, 1993). The *Anabaena* abundance during severe DIN depletion months, July to September in 1993 might be due to summer 1993 being cooler than in previous years (Chapter 2) but *Ceratium* did grow well in summer 1993 though *Ceratium* and *Microcystis* have similar temperature preferences. The decreasing trend of DIN and TON concentrations following the sewage effluent diversion might have caused even more serious nitrogen deficiency than previously. This was supported by A480:4663 ratios which were >1.2 and increased up to 2.5. Nitrogen deficiency thus appeared to have had an important role in favouring nitrogen-fixing *Anabaena* over *Microcystis*

in 1993.

A recent publication (Reynolds & Bellinger, 1992) has detailed a change in the phytoplankton community from the early surveys of Pearsall and Lind. The latter observed a diatom - *Ceratium* - *Aphanizomenon* or *Coelosphaerium* sequence, which has given way to a cycle where there is a brief spring diatom peak, followed by a major summer growth of *Microcystis* and *Ceratium* (Belcher & Storey, 1968; Reynolds & Bellinger, 1992). The only clear difference is the rise in dominance of *Microcystis* (never common in the five years covered by early surveys but abundant in 14 out of 23 of the summers of more recent surveys (1962-1989)). This increase in abundance of *Microcystis* was confirmed in a study of algal remains in the sediment (Livingstone, 1979). *Anabaena* was sparse in the early studies; *Coelosphaerium* was common in the earlier surveys, but has been sparse in all later surveys.

This study confirms rise of *Anabaena* and abundance of *Microcystis* and decline of *Coelosphaerium.* Reynolds (1979), Nelms (1984) and Reynolds & Bellinger (1992) have all described the changes as suggesting that the lake has changed to a state where the populations are light-limited, not nitrogen-limited any more. The theory was supported by the increase in abundance of the non-nitrogen fixing cyanophyte, *Microcystis*, although this species has been shown to migrate vertically 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) and its dominance in 1993, and the significant decrease in DIN and TON concentrations would suggest that nitrogen-limitation might have controlled the phytoplankton community more severely than in the previous years.

Chapter 4: Water and nutrient budgets and direct measurements of internal release rates in Little Mere

4.1. Introduction

Eutrophication of water bodies is a biological reaction to nutrient enrichment, the eventual consequence of which is development of primary production to nuisance levels and deterioration of water quality. The phosphorus concentration of water bodies has been widely accepted as the most likely limiting factor of phytoplankton crop-size (Schindler, 1977; Schindler & Comita, 1972; Reynolds, 1984). The isolation of lakes from external phosphorus loading is thus often considered to be the first step in reversing the undesirable effects of eutrophication (Sas, 1989) and has proved effective in deep lakes (Edmondson, 1970). This is probably because deep lakes show more evidence of bottom-up control so that limitation of external nutrient loading is more likely to be successful in eutrophic deep lakes but not necessarily in others (Bengtsson *et al.* 1975; Carvalho *et al.* in press; Chapter 2). In shallow lakes, responses to successful reduction in external nutrient loading have been resilience or long delay of recovery (Marsden, 1989; Jeppesen *et al.* 1991). This has been attributed to homeostatic control mechanisms, largely trophic interactions including fish-zooplankton and other invertebrates, in the water body (Benndorf, 1987; 1990; Shapiro, 1990b) and most importantly to internal release of phosphorus. It has also been shown that flushing rates of water bodies are important and that enhanced flushing can improve eutrophic lakes through reduction in the concentration of the limiting nutrients (dilution) (Cooke *et al.* 1986)

Phosphorus release from lake sediments is facilitated by a variety of mechanisms (Boström *et al.* 1988). Early studies largely focused on redox conditions at the sediment-water interface. Special attention was given to the sediment iron content and oxygen conditions. Under aerobic conditions, ferric iron (Fe^{+3}) immobilises sediment P and the process is reversed under low redox potential, when ferric iron is reduced to ferrous iron (Fe^{+2}) and releases sediment P into the overlying water (Mortimer, 1941 and 1942). The redox potential of sediment and its iron content are considered to be very important in eutrophic Danish lakes for internal P release (Jeppesen *et al.* 1991; Søndergaard *et al.* 1993) which is greatly reduced when the Fe:P ratio is higher than 15-20 (by weight) (Jensen *et al.* 1992)

With growing attention to controlling internal nutrient loading, many other potential controlling factors have been recognised in different lakes. It has been shown that H_2S inactivates iron through FeS formation and reduces P absorption (Boström *et al.* 1988). High concentrations of NO_3 appear to inhibit sediment P-release through buffering sediment redox potential (Andersen, 1982). Increased temperature lowers redox potential through stimulating mineralization of organically bound P and results in the release of P (Jensen and Andersen, 1992) Resuspension of sediment and high pH are also able to enhance sediment release rates (Boström *et al.* 1982). Bottom feeders, both fish and invertebrates have been shown to increase release of phosphorus significantly through bioturbation (Benndorf, 1990). Macrophytes provide habitats for bottom feeders, and aquatic plants may therefore indirectly increase P-release. More directly macrophytes increase sedimentation (Barko *et al.* 1991), stimulate

mineralization (Carignan, 1985) and increase pH (Serafy & Harrell, 1993; Frodge *et al.* 1990) all of which may increase sediment P-release. The effectiveness of these controlling factors varies among water bodies depending on the history of eutrophication, and on physical, chemical and trophic interactions.

In this study the impact of diversion of sewage effluent in Little Mere was investigated by the determination of water, TP and DIN budgets for a year prior to effluent diversion (1990/1991) and three years following effluent diversion (1991/92, 1992/93 and 1993/94). Initially long delayed recovery was anticipated but nutrient concentrations largely decreased (Carvalho *et al.* in press; Chapter 2). TP and DIN mass balances were constructed to assess the changes in nutrient concentration pre-and post-diversion. Internal release of nutrients was measured in intact sediment cores sampled from five different sites at control and ambient temperatures to understand the importance of the sediment for nutrient concentrations in the lake.

4.2. Methods

4.2.1. Water budget

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

$$outflow = inputs - evaporation \pm \partial\, lakevolume \quad \text{equation (4.1)}$$

Fig 4.1 shows the sub-catchment divisions used to calculate the budget for Little Mere: inflow from the total Mere Mere catchment (520.5 ha.) was named as catchment 1 and includes the catchment of the inflows stream to Mere Mere (inflow Mere Mere, 310 ha). The immediate surrounds to the lake plus the lake itself (a further 210.5 ha) as well. The immediate Little Mere catchment (38 ha.) was named as catchment 2. The outflow volume was calculated from direct rainfall over the catchment 1 and catchment 2 (catchment 2 included Little Mere) (561.3 ha.), corrected for actual evapotranspiration. The catchment areas were measured from the 1:25000 Ordnance Survey map.

A water budget was calculated monthly from spring 1990-spring 1994. Annual budgets and a total budget for the whole study period were calculated.

Four inputs were calculated:

1. Inflow from Mere Mere catchment (catchment 1), calculated from the rainfall over

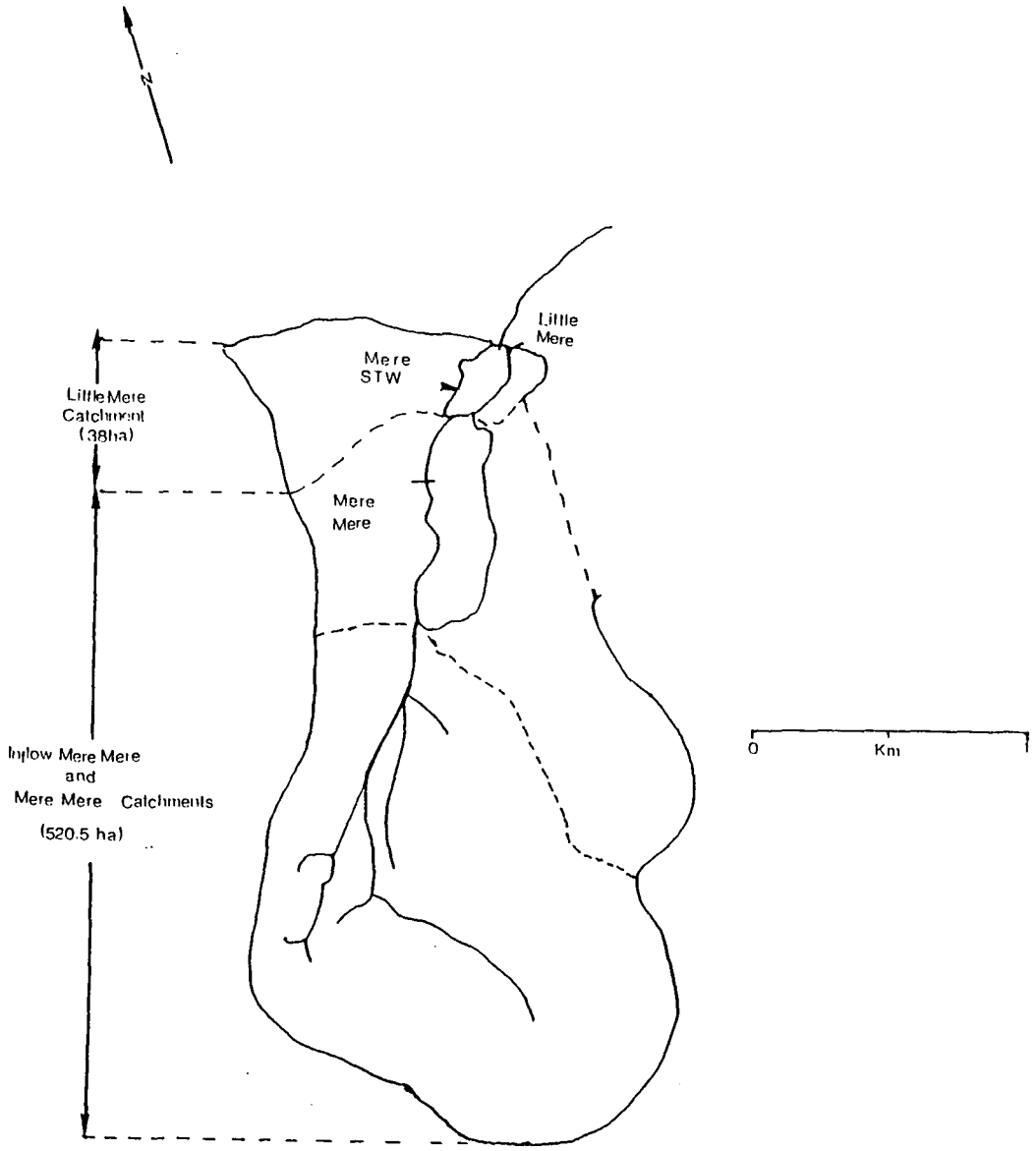

Fig.4.1 Inflow Mere Mere and Mere Mere catchment (catchment1) and Little Mere catchment (catchment 2). The major divisions are shown by dotted lines. Inputs of sewage effluent are also indicated.

this area, corrected for actual evapotranspiration.

2. Inflow from Little Mere catchment (catchment 2), calculated from the rainfall over this area, corrected for actual evapotranspiration.

3. Direct rainfall on the lake surface.

4. Flow from the Sewage Treatment Works between February 1990- July 1991 (NWWA, 1983), calculated from the dry weather flow rate of 0.3 Ml d^{-1} which was measured by dilution gauging, although this is subject to a large source of error.

Mean monthly rainfall (Monthly Weather Report, 1990;1991;1992;1993 and 1994) was recorded by the Meteorological Office at Manchester Ringway Airport, 4 miles south of Little Mere. Actual evapotranspiration, from the mean of 1961-1990 actual evapotranspiration measurements for the area, was used to calculate run off from the land surface. The actual evapotranspiration data of the area were supplied by the Meteorological Office (MORECS). The used mean actual evapotransporation data are given in Appendix 3 (Table A3.1).

Water level measurements were taken every two weeks from a marked point at the sluice. Changes in lake volume were calculated by multiplying the change in lake level by the surface area of the lake.

From the volume of water flowing out of Little Mere (V_{out}) per unit time (t), and the volume of the lake (V_{lake}), a theoretical flushing rate (p) can be calculated: (Vollenweider, 1975)

$$p = \left(\frac{V_{out}}{V_{lake}}\right) . t^{-1}$$ equation (4.2)

4.2.2 Nutrient budgets

There are various sources of both phosphorus and nitrogen to Little Mere. These include effluent from the STW, field drainage, direct rainfall and internal loading in the lake. Budgets for total phosphorus (TP) and dissolved inorganic nitrogen (DIN) were calculated. As in the water budget an equation can be constructed to balance the processes for a given period:

$$output = external\ inputs \pm internal\ sources/sinks - \partial\ lake$$

equation (4.3)

where:

Output = (concentration x volume) of the outflow

δLake = the change in nutrient quantity in the whole lake water volume

Four categories of external inputs were quantified:

catchment 1 via run-off and drainage

catchment 2 via run-off and drainage

Direct sewage effluent to the lake from the STW

Direct rainfall

Loading from catchment 1 through Mere Mere via run-off and drainage was estimated by multiplying the estimated volume of water entering from this source by the monthly mean nutrient concentrations in Mere Mere which was monitored every two weeks throughout the study. This was appropriate as major changes in nutrient concentrations from those entering by the stream may take place within the lake

system. Loading from the catchment of Little Mere (catchment 2) via run-off and drainage was estimated by multiplying the estimated volume of water entering by the monthly mean nutrient concentration of the inflow to Mere Mere. This stream was monitored every two weeks throughout the study and drains an area with a very similar land usage to Catchment Little Mere.

Estimates of sewage effluent loading to Little Mere of phosphate, nitrate and ammonium were 2 kg d^{-1}, 3 kg d^{-1} and 3 kg d^{-1} respectively (NWWA, 1983).

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 appears in agreement with NO_3-N figures from Aldergrove, Northern England (Soderlund *et al.* 1985) of 0.035 mg l^{-1}. These values PO_4-P and DIN (0.06 mg l^{-1} and 0.05 mg l^{-1} respectively) were then used to calculate the rainfall loading.

4.2.3 Internal loading

Intact sediment cores with overlying water were collected monthly (between 14th April 1993 to 8th March 1994) in extruded acrylic tubes (length 50 cm, diameter 6.9 cm) using a pole corer. Care was taken to minimise disturbance during transport. On each occasion two replicates were taken from each of five stations which were numbered 1, 2, 3, 4 and 5 (Fig 8.7). The macrophyte densities of the stations varied so that two of the stations (1 and 2) were in water lily beds (covered by mainly

Nuphar lutea and patches of *Nymphaea alba*). Station 3 was open-water in early summer 1993 and later in the summer largely covered by *Potamogeton berchtoldii*. The remaining two stations (4 and 5) had patches of *Elodea canadensis* and *Potamogeton berchtoldii* whose stands largely increased in the late summer. On return to the laboratory the height of the overlying water in each core was measured. A sample amount of water was carefully taken for analyses from each core using a thin plastic tube without disturbance of the sediment (see below). The cores were wrapped in aluminium foil to exclude light from the core sides. One core from each station was then placed in a water bath at tap-water temperature (ambient temperature) and the rest of the cores were incubated in a incubator at 20 °C (control temperature) and the cores were incubated overnight (a typical incubation period was approximately 16 hours). The next day overlying water samples were taken from the cores to be analyzed.

The following analyses were carried out on samples taken before and after incubation: Soluble reactive phosphorus (SRP), total phosphorus (TP), ammonium-nitrogen (NH_4-N), nitrate plus nitrite-nitrogen (NO_3 and NO_2-N). Methods are given in Chapter 2.

4.2.4 Calculation of release rate

$$release\ rate\ (mg\ m^{-2}\ day^{-1}) = \frac{C.H.1000.24}{i} \quad \text{equation (4.4)}$$

where:

C(mg l^{-1})= is the differences in concentrations between the start and end of the

incubation.

H= height of overlying water in m

i= incubation in hours

4.2.5 Statistical analysis

The internal release rate results were analyzed using two-way ANOVA in the following way:

- comparison of the release rates at the standard control temperature versus ambient temperature over the sampling dates (14.4.93 to 8.3.1994).

- comparison of release rates results (measured at ambient temperature) between the stations over the sampling periods.

4.3 Results

4.3.1 Water budget

Table 4.1 shows the results of the water budget. The percentage contributions of the four inputs in terms of the total input volume are shown in brackets. The volume lost from the lake surface through evaporation is also shown as a percentage of the total inputs.

Catchment 1 was clearly the most important of the measured inputs, contributing 87 % in July 1990-June 1991 before effluent diversion, and 92 % in July 1991-June 1992, 91% in July 1992-June 1993 and 92% in July 1993-June 1994 after effluent diversion. Catchment 2 and the input from the S.T.W made the second biggest contribution to the total inputs and were 6.4% and 6% respectively before effluent diversion. After the effluent diversion, contribution of catchment 2 was about 6%. Direct rainfall made a very small contribution to the water budget (0.94%, 1.2%, 1% and 1 % respectively over the budget periods). Though overall direct rainfall contribution was insignificant, when there was no run-off from either catchment, the rainfall was the only water source to the lake after the sewage effluent diversion.

Although overall evaporation from the lake surface was an insignificant sink for the budget periods 1%, 1.2%, 0.9% and 0.8 % in 1990/91, 1991/92, 1992/93 and 1993/94 respectively, evaporation occasionally became a significant sink when the evaporation was greater than rainfall, especially after sewage effluent diversion.

Table 4.1 Water budget of Little Mere between 22.2.90 to 13.6.94. Values are given in $10^4 m^3$, except δV which are in m^3. Figures in brackets indicate the percentage contribution in relation to the total input volume for the corresponding period.

Budget Period	day	Catchment1	Catch-ment 2	STW	Direct rainfall	total input	Evapo-ration	out-flow	δV lake	Flushing rate(yr^{-1})
Feb 90	29	34.2 (90)	2.5 (6.6)	0.9 (2.3)	0.23 (0.6)	37.8	0.05 (01)	36.9	140	221
Mar 90	31	0	0	0.9 (92)	0.77 (8)	1	0.1 (10)	0	-210	0
Apr 90	30	0	0	0.9 (90)	0.1 (10)	1	0.2 (15)	0	0	0
May 90	31	0	0	0.93 (93)	0.07 (7)	1	0.2 (22)	0	-280	0
Jun 90	30	7.9 (79)	0.6 (6)	0.9 (9.4)	0.23 (2.4)	9.6	0.2 (2)	8.5	210	49
Jul 90	31	0	0	0.93 (93)	0.07 (7)	1	0.2 (17)	0	-70	0
Aug 90	31	5.31 (79)	0.4 (6)	0.93 (14)	0.07 (1)	6.7	0.2 (3)	5.7	210	32
Sept 90	30	13.3 (87)	1 (6.3)	0.9 (6)	0.2 (1)	1.5	0.1 (0.8)	14.3	280	83
Oct 90	31	43.2 (91)	3.2 (6.6)	0.93 (2)	0.3 (0.7)	47.6	0.08 (0.2)	46.6	280	261
Nov 90	30	25 (90)	1.8 (7)	0.9 (3)	0.2 (0.7)	27.6.	0.05 (0.2)	26.6	140	154
Dec 90	31	40 (91)	2.9 (7)	0.93 (2)	0.25 (0.6)	44	0.04 (0.2)	43	700	241
Jan 91	31	20.8 (89)	1.5 (7)	0.93 (4)	0.15 (0.6)	23.4	0.04 (0.6)	22.5	-280	126
Feb 91	28	6.3 (82)	0.5 (6)	0.84 (11)	0.08 (1)	7.7	0.5 (0.6)	6.8	-560	42
Mar 91	31	9.2 (84)	0.7 (6)	0.93 (9)	0.15 (1.4)	11	0.1 (1)	10	140	56
Apr 91	30	0	0	0.9 (91)	0.09 (9)	0.98	0.15 (15)	0	-560	0
May 91	31	0	0	0.93 (98)	0.02 (2.4)	0.95	0.22 (2)	0	-170	0
Jun 91	30	0.31 (22)	0.02 (2)	0.9 (63)	0.2 (14)	1.4	0.2 (13)	0.3	0	2
Jul 91	31	0	0	-	0.14 (100)	0.14	0.2 (134)	0	-140	0
Aug 91	31	0	0	-	0.08 (100)	0.08	0.2 (224)	0	-140	0
Sept 91	30	5.5 (91)	0.4 (6.6)	-	0.15 (2.5)	6	0.1 (2)	5.9	280	34
Oct 91	31	22 (92)	1.6 (7)	-	0.2 (1)	23.8	0.08 (0.3)	23.7	140	132
Nov 91	30	27.6 (93)	2 (7)	-	0.2 (1)	29.8	0.05 (0.2)	29.7	120	172
Dec 91	31	26.6 (93)	1.9 (7)	-	0.18 (0.6)	28.7	0.04 (0.1)	28.7	-560	161
Jan 92	31	16.7 (93)	1.2 (7)	-	0.13 (0.7)	18	0.04 (0.2)	18	330	101
Feb 92	29	17.8 (93)	1.3 (7)	-	0.14 (0.7)	19.1	0.5 (0.3)	19.1	170	115
Mar 92	31	25.5 (92)	1.9 (7)	-	0.24 (0.9)	27.6	0.1 (0.4)	27.5	260	154
Apr 92	30	0	0	-	0.15 (100)	0.15	0.2 (101)	0	-990	0
May 92	31	0	0	-	0.16 (100)	0.16	0.2 (138)	0	-280	0
Jun 92	30	0	0	-	0.09 (100)	0.09	0.2 (213)	0	0	0
Jul 92	31	0	0	-	0.18 (100)	0.18	0.2 (101)	0	280	0
Aug 92	31	18.1 (93)	1.3 (7)	-	0.3 (1.4)	19.7	0.2 (1)	19.5	1540	109
Sept 92	30	9.3 (91)	0.7 (7)	-	0.2 (2)	10.2	0.1 (1)	10	-999	58
Oct 92	31	48.5 (93)	3.5 (7)	-	0.34 (0.6)	52.3	0.08 (0.2)	52.3	280	292
Nov 92	30	53.6 (93)	3.9 (7)	-	0.34 (0.6)	57.8	0.05 (0.1)	57.8	560	334

Dec 92	31	30.9 (93)	2.3 (7)	-	0.2 (0.6)	33.4	0.04 (0.1)	33.3	840	187
Jan 93	31	34 (93)	2.5 (7)	-	0.2 (0.6)	36.8	0.04 (0.1)	36.7	280	206
Feb 93	29	0	0	-	0.04 (100)	0.04	0.05 (127)	0	-900	0
Mar 93	31	0	0	-	0.03 (100)	0.03	0.1 (347)	0	-588	0
Apr 93	30	7.7 (91)	0.6 (7)	-	0.2 (2)	8.5	0.1 (2)	8.3	28	48
May 93	31	0	0	-	0.17 (100)	0.17	0.2 (113)	0	-140	0
Jun 93	30	0	0	-	0.17 (100)	0.17	0.2 (0.8)	0	-540	0
Jul 93	31	20.5 (92)	1.5 (6.7)	-	0.3 (1.3)	22.2	0.2 (2)	22	364	124
Aug 93	31	9.4 (91)	0.7 (6.6)	-	0.2 (2.3)	10.3	0.1 (1.7)	10.1	-140	57
Sept 93	30	6.2 (91)	0.5 (6.6)	-	0.15 (2.3)	6.8	0.1 (1.8)	6.8	-140	39
Oct 93	31	13.3 (92)	1 (6.7)	-	0.15 (1)	14.4	0.08 (0.5)	14.3	168	80
Nov 93	30	12.4 (92)	0.9 (6.7)	-	0.12 (0.9)	13.4	0.05 (0.4)	13.4	448	77
Dec 93	31	78.9 (93)	5.8 (6.8)	-	0.45 (0.5)	85.1	0.04 (.04)	85	560	477
Jan 94	31	40.3 (93)	2.9 (7)	-	0.25 (0.6)	43.5	0.04 (.08)	43.4	0	244
Feb 94	28	12 (92)	0.9 (6.7)	-	0.1 (0.9)	13	0.04 (0.4)	12.9	280	80
Mar 94	31	32.3 (93)	2.4 (6.8)	-	0.28 (0.8)	35	0.1 (0.3)	34.8	140	195
Apr 94	30	8 (91)	0.6 (6.6)	-	0.2 (2)	8.7	0.15 (1.7)	8.6	120	44
May 94	31	0	0	-	0.07 (100)	0.07	0.22 (301)	0	-560	0
Jun 94	30	0	0	-	0.1 (100)	0.1	0.2 (177)	0	-400	0
Jul 90-June 91	365	163 (87)	12 (6.4)	10.9 (6)	1.8 (0.94)	187	1.9 (1)	175.8	110	83.7
Jul 91-June 92	366	142 (92)	10.3(6.7)	-	1.8 (1.2)	154	1.9 (1.2)	152.7	-986	72.5
Jul 92-Jun 93	366	193 (91)	14.8 (7)	-	2.3 (1)	210	1.9 (0.9)	218	160	104
Jul 93 - Jun 94	365	233.2 (92)	17 (6.7)	-	2.4 (1)	253	1.9 (0.8)	251	148	119
Jul 90-June 94	1462	731 (91)	54.1(6.7)	10.9 (1.4)	8.3 (1)	804	7.6 (0.9)	790	94	91

The flushing rate fluctuated throughout the year, the lowest value being 0 yr^{-1} recorded during the spring and early summer. February and March 1993 when there was no outflow due to the lake being ice-covered. The highest flushing rates recorded during the autumn and the winter months were 261 yr^{-1} during Jul 1990-Jun 1991, 172 yr^{-1} during Jul 1991-Jun 1992, 334 yr^{-1} during Jul 1992-Jun 1993 and 477 yr^{-1} during Jul 1992-Jun 1994.

Table 4.1 also gives figures for the whole period of study, showing that the four inputs, catchment 1, Catchment 2, STW and direct rainfall contributed on average 91 %, 6 %, 1.4 % and 1% respectively. It also shows that direct evaporation from the lake was responsible for the loss of about 0.8 % of these total inputs.

4.3.2 Total phosphorus budget

Table 4.2 shows the results of total phosphorus budget. Annual budgets for before (Jul 90-Jun 91) and after (Jul 91-Jun 92, Jul 92-Jun 93 and Jul 93-Jun 94) sewage diversion are shown.

The inputs, in terms of percentage of total external inputs, from catchment 1, catchment 2, STW and direct rainfall were 1.4 %, 0.2 %, 98 % and 0.014 % respectively before diversion. After effluent diversion, percentage contributions of catchment 1, catchment 2 and direct rainfall were 83 %, 15 % and 0.59 % respectively in Jul 91-Jun 92, 81 %, 18 % and 1 % respectively in Jul 92-Jun 93 and 89 %, 10 % and 0.9 % respectively in Jul 93-Jun 94.

Mere STW was clearly the major source of phosphorus before diversion with an annual input of 730 kg and catchment 1 was the next largest phosphorus source with 10.7 kg annual contribution. Contributions of catchment 2 and direct rainfall were low with 1.53 kg and 0.105 kg respectively.

Following effluent diversion, catchment 1 became the main external source to the lake with annual inputs of 7.9 kg, 13 kg and 23.6 kg respectively and catchment 2 made the second biggest contribution with 1.43 kg, 2.9 kg and 2.5 kg respectively. These contributions were mainly in the winter months. During the early summer and summer months their contributions became either negligible or zero when evaporation was greater than rainfall. There was an increase in the contributions of both catchments 1 and 2 during 92/93 and 93/94 probably because of those periods being wetter than the previous two periods and thus giving increased loading from the catchments. Direct rainfall added about 0.15 kg annually, which was negligible. However during the dry period the only external phosphorus input to the lake was from direct rainfall.

The large reduction in the total external inputs to the lake in 1991 was clearly reflected in the decrease of outflow export following the effluent diversion. The annual outflow export was 341 kg before diversion and in the three budget periods following the diversion decreased to 125.6 kg, 105 kg and 25.2 kg respectively.

A negative result from the balance indicates sedimentation > sediment release. This was very considerable with 405 kg annual sedimentation during 90/91 before effluent

Table 4.2 Total phosporus budget of Little Mere between 22.2.90 and 13.6.94. Values are given in kg. Figures in brackets represents % contribution of total inputs for a given period. Balance represents amount of P lost to or released from the sediment.

Budget Period	Day	Catchment 1	Catchment 2	STW	Direct rainfall	Total inputs	outflow	δP lake	Balance
Feb 90	29	2.6 (4.2)	0.85 (1.4)	58 (94)	0.014 (0.02)	61.5	18	-0.39	-44
Mar 90	31	0	0	62 (99.8)	0.05 (0.08)	62.1	0	0.55	-62
Apr 90	30	0	0	60 (99.9)	0.006 (0.008)	60.1	0	1.7	-58
May 90	31	0	0	62 (99.2)	0.004 (0.008)	62.04	0	0.13	+62
Jun 90	30	1.1 (1.8)	0.2 (0.3)	60 (98)	0.014 (0.02)	61.31	41	6.6	-14
Jul 90	31	0	0	62 (99.9)	0.004 (0.007)	62.04	0	-1.7	-63.7
Aug 90	31	0.5 (0.8)	0.07 (0.1)	62 (98)	0.004 (0.007)	63.2	29	2.1	-39.1
Sept 90	30	1.5 (2.4)	0.34 (0.55)	60 (96.7)	0.01 (0.02)	62	69	-0.27	+6.7
Oct 90	31	3.5 (5)	0.4 (0.6)	62 (93.9)	0.02 (0.03)	66	167	-2.6	+98.4
Nov 90	30	1.4 (2)	0.16 (0.3)	60 (96.7)	0.011 (0.02)	62	32	-4.8	-35
Dec 90	31	2.2 (3.4)	0.23 (0.4)	62 (96.3)	0.014 (0.02)	64.4	25	-1.5	-41
Jan 91	31	0.96 (1.5)	0.1 (0.2)	62 (98.4)	0.009 (0.01)	63	7	-0.6	-57
Feb 91	28	0.25 (0.4)	0.03 (0.05)	56 (99.6)	0.005 (0.009)	56.3	4.1	0.06	-52.1
Mar 91	31	0.4 (0.6)	0.2 (0.3)	62 (99)	0.009 (0.01)	62.6	7.3	0.3	-55
Apr 91	30	0	0	60 (99.9)	0.005 (0.009)	60.1	0	1.42	-59
May 91	31	0	0	62 (99.9)	0.002 (0.007)	62	0	2.3	-60
Jun 91	30	0.013 (1)	.005 (0.008)	60 (99.9)	0.012 (0.02)	60	1	1.27	-58
Jul 91	31	0	0	-	0.008 (100)	0.008	0	-2.6	-2.7
Aug 91	31	0	0	-	0.005 (100)	0.005	0	-0.9	-0.9
Sept 91	30	0.4 (75)	0.12 (23)	-	0.009 (1.7)	0.53	8.2	-0.05	+8
Oct 91	31	1.74 (75.6)	0.51 (22)	-	0.012 (0.5)	2.3	38	0.4	+36.1
Nov 91	30	2.2 (95)	0.1 (4.3)	-	0.012 (0.5)	2.31	48	-1.2	+44.5
Dec 91	31	0.9 (81)	0.2 (18)	-	0.01 (0.9)	1.11	24.4	-0.3	+23
Jan 92	31	0.71 (92)	0.05 (7)	-	0.008 (1)	0.77	2.11	-1.5	-0.11
Feb 92	29	1.1 (84)	0.2 (15)	-	0.009 (0.7)	1.31	2.4	0.01	+1.1
Mar 92	31	0.84 (76)	0.25 (23)	-	0.014 (1.3)	1.1	2.5	-0.04	+1.4
Apr 92	30	0	0	-	0.009 (100)	0.009	0	-0.08	-0.17
May 92	31	0	0	-	0.01 (100)	0.01	0	1.02	+1.01
Jun 92	30	0	0	-	0.006 (100)	0.005	0	-0.4	-0.05
Jul 92	31	0	0	-	0.011 (100)	0.01	0	-0.5	-0.51
Aug 92	31	1.14 (67)	0.53 (31)	-	0.02 (1.2)	2.7	14.2	0.9	+13.4

Sept 92	30	1.25 (78)	0.3 (18.8)	-	0.01 (0.6)	1.6	9.8	-0.3	+8
Oct 92	31	4.5 (77)	1.32 (22)	-	0.02 (0.3)	5.84	61	0.33	+56
Nov 92	30	0.37 (62)	0.2 (33)	-	0.02 (3.3)	0.6	11.4	-1.8	+9
Dec 92	31	1.87 (89)	0.19 (9)	-	0.012 (0.6)	2.1	2.9	-0.2	+0.6
Jan 93	31	3.6 (92)	0.32 (8)	-	0.013 (0.3)	2.8	4.5	0.12	+1.82
Feb 93	29	0	0	-	0.002 (100)	0.002	0	-0.1	-0.1
Mar 93	31	0	0	-	0.002 (100)	0.002	0	-0.06	-0.06
Apr 93	30	0.12 (70)	0.04 (24)	-	0.011 (6)	0.71	1.6	0.3	+1.2
May 93	31	0	0	-	0.01 (100)	0.01	0	0.8	+0.79
Jun 93	30	0	0	-	0.01 (100)	0.01	0	-1	-1
Jul 93	31	2.94 (91.7)	0.2 (8)	-	0.02 (0.7)	2.54	1.6	0.02	-0.92
Aug 93	31	1.59 (87)	0.22 (18)	-	0.04 (0.7)	1.82	2	0.34	+0.52
Sept 93	30	0.84 (91)	0.07 (8)	-	0.009 (1)	0.92	0.43	-0.33	-0.82
Oct 93	31	2.17 (94)	0.13 (5)	-	0.009 (0.4)	2.31	2.9	0.24	+0.83
Nov 93	30	1.1 (89)	0.13 (10)	-	0.007 (0.6)	1.24	3.2	0.2	+1.98
Dec 93	31	8.83 (92)	0.73 (8)	-	0.03 (0.3)	9.6	8	-0.2	-1.8
Jan 94	31	2.8 (77)	0.8 (22)	-	0.02 (0.6)	3.62	3.4	-0.23	-0.4
Feb 94	28	0.7 (93)	0.04 (5)	-	0.006 (0.8)	0.75	0.97	-0.04	+0.18
Mar 94	31	2.11 (91)	0.18 (8)	-	0.016 (0.7)	2.31	2.1	-0.02	-0.2
Apr 94	30	0.54 (92)	0.04 (7)	-	0.012 (2)	0.59	0.58	0.005	-0.005
May 94	31	0	0	-	0.005 (100)	0.005	0	-0.05	-0.009
Jun 94	30	0	0	-	0.007 (100)	0.007	0	0.003	-0.04
Jul 90 - June 91	365	10.71 (1.4)	1.53 (0.2)	730 (98)	0.105 (0.014)	742.3	341	-4	-405
Jul 91 - June 92	366	7.89 (83)	1.43 (15)	-	0.11 (0.59)	9.5	125.6	-5.23	+111
Jul 92 - Jun 93	366	13 (81)	2.9 (18)	-	0.141 (0.8)	16	105	-1.9	+87
Jul 93 - Jun 94	365	23.6 (89)	2.58 (10)	-	0.233 (0.8)	26.4	25.2	-0.02	-1.2

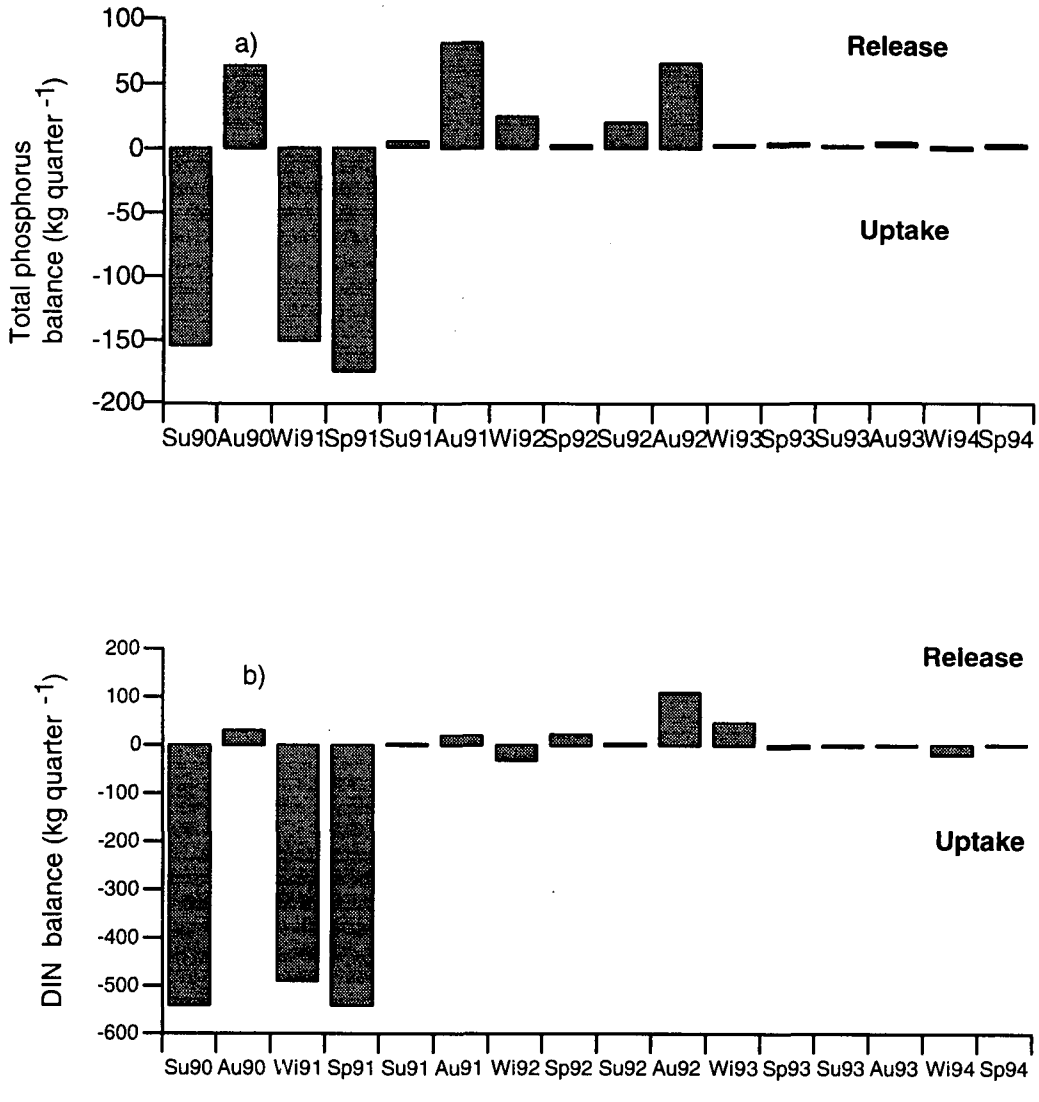

Fig 4.2 Quarterly variation in total phosphorus and DIN balance in Little Mere from July 1990 to June 1994 (kg quarter l^{-1}).
The calculations are based on total phosphorus and DIN budgets (Wi:winter, Au:autumn, Sp:spring and Su:summer).

diversion. (Fig. 4.2a). Following effluent diversion, in the first two years, the balances were positive suggesting that internal phosphorus release from the sediment became an important source to the lake, but the internal phosphorus loading to the lake decreased from 111.2 kg in 1991/92, to 87 kg in 1992/93 and in 93/94 the sediment again became a sink with 1.1 kg lost to it (Fig. 4.2a).

4.3.3 Dissolved inorganic nitrogen budget

Table 4.3 shows the results of the DIN budget. Annual budgets for before (Jul 90- Jun 91) and after (Jul 91- Jun 92, Jul 92- Jun 93 and Jul 93- Jun 94) sewage diversion are shown.

The inputs, in terms of percentage of the total external inputs, from catchment 1, catchment 2 and Mere STW were 6.8%, 1.6%, 91.6% respectively, before diversion. Direct rainfall inputs were negligible. Mere STW was clearly the most important source of DIN from these inputs with an annual 2190 kg contribution. In the three DIN budget periods following diversion of the sewage effluent, catchment 1 became the largest source of DIN to the lake with annual percentages about 82%, though there was a slight decrease in DIN loading from catchment in the periods after diversion. Catchment 2 was the second biggest source to the lake with annual percentage contribution about 17% after the diversion. Although the annual loadings from catchment 2 were lower than from catchment 1, loading from catchment 2 increased in August, September, October and November 1992 and 1993.

Table 4.3 DIN budget of Little Mere between 22.2.90 and 13.6.94. Values are given in kg. Figures in brackets represent % contribution of total inputs for given period.

Budget Period	Days	Catchment 1	Catchment 2	STW	Direct rainfall	Total inputs	out-flow	δDIN lake	Balance
Feb 90	29	52.2 (22.4)	6.4 (12.7)	174 (75)	0.012 (0.005)	233	66.8	0.7	-166
Mar 90	31	0	0	186 (99)	0.004 (0.002)	186	0	-1.5	-188
Apr 90	30	0	0	180 (99)	0.005 (0.003)	180	0	-1.5	-182
May 90	31	0	0	186 (99)	0.004 (0.002)	186	0	4.1	-182
Jun 90	30	2.3 (1.3)	0.73 (0.4)	180 (99)	0.012 (0.007)	183	8.5	-2	-177
Jul 90	31	0	0	186 (99)	0.004 (0.002)	186	0	7.4	-179
Aug 90	31	1.3 (0.7)	0.54 (0.3)	186 (99)	0.004 (0.002)	187.8	48.5	8.2	-131
Sept 90	30	2.2 (1.2)	1 (0.55)	180 (98.3)	0.01 (0.005)	183.2	133	1.7	-49
Oct 90	31	17.3 (8.3)	5.3 (2.5)	186 (89)	0.02 (0.01)	208.6	396	-1.6	+186
Nov 90	30	22.2 (11)	9 (4.3)	180 (85)	0.009 (0.004)	211.2	69	-12.4	-155
Dec 90	31	38.7 (17)	10.2 (4.3)	186 (79)	0.012 (0.005)	235	103	-0.4	-132
Jan 91	31	48.2 (20)	6.5 (2.7)	186 (77)	0.008 (0.003)	241	50	-0.33	-192
Feb 91	28	12.2 (6.6)	2.3 (1.3)	168 (92)	0.004 (0.002)	183	17	0.43	-166
Mar 91	31	20 (9.6)	2.7 (1.3)	186 (89)	0.008 (0.004)	209	27	0.52	-181
Apr 91	30	0	0	180 (99.9)	0.005 (0.003)	180	0	1.54	-178
May 91	31	0	0	186 (99.9)	0.001 (0.007)	186	0	3.4	-182
Jun 91	30	0.2 (0.1)	0.03 (0.02)	180 (99.8)	0.01 (0.006)	180.3	1.3	-2.6	-182
Jul 91	31	0	0	-	0.007 (100)	0.007	0	-0.4	-0.4
Aug 91	31	0	0	-	0.004 (100)	0.004	0	-3.44	-3.4
Sept 91	30	0.6 (54)	0.1 (45)	-	0.08 (0.13)	1.11	8.1	-1.3	+6.2
Oct 91	31	6.64 (83)	1.2 (15)	-	0.01 (0.07)	8	49.1	1.4	+4.8
Nov 91	30	9.5 (70)	4 (39.6)	-	0.01 (0.05)	13.5	48	-1	+15
Dec 91	31	14 (76)	4.4 (23.9)	-	0.009 (0.05)	18.4	32	-1.1	+13
Jan 92	31	24.5 (82.4)	5.2 (17.5)	-	0.007 (0.02)	29.7	17	-0.3	-13
Feb 92	29	34.2 (87.7)	4.8 (12.3)	-	0.007 (0.002)	39	9.3	-1	-31
Mar 92	31	38.1 (85)	6.7 (14.8)	-	0.012 (0.03)	45	23	0.8	-21
Apr 92	30	0	0	-	0.008 (100)	0.008	0	0.3	+0.3
May 92	31	0	0	-	0.008 (100)	0.008	0	-1.7	-1.71
Jun 92	30	0	0	-	0.005 (100)	0.005	0	-0.3	-0.31
Jul 92	31	0	0	-	0.009 (100)	0.009	0	0.23	+0.22
Aug 92	31	1.92 (44.3)	2.4 (55.4)	-	0.013 (0.3)	4.33	8	0.5	+4.2

Sept 92	30	0.1 (14)	0.6 (84)	-	0.009 (1.2)	0.71	0.8	-0.7	-0.61
Oct 92	31	0.5 (5)	4.5 (94)	-	0.017 (0.4)	4.8	81	3.1	80
Nov 92	30	31.3 (80)	7.6 (19.5)	-	0.017 (0.4)	38.9	42.4	-1.9	6
Dec 92	31	50 (87.4)	7.2 (12.6)	-	0.01 (0.02)	57.21	38.6	1.06	-18
Jan 93	31	63.4 (89)	7.9 (11)	-	0.01 (0.02)	71.3	43	0.008	-28.3
Feb 93	29	0	0	-	0.002 (100)	0.002	0	0.23	+0.02
Mar 93	31	0	0	-	0.002 (100)	0.002	0	-1.6	-1.6
Apr 93	30	5.5 (86.3)	0.86 (13.5)	-	0.01 (0.2)	6.4	2.8	-0.4	-4
May 93	31	0	0	-	0.009 (100)	0.009	0	-0.4	-0.4
Jun 93	30	0	0	-	0.009 (100)	0.009	0	-0.04	-0.05
Jul 93	31	1.04 (29.7)	2.49 (71)	-	0.014 (0.4)	3.5	2.7	-0.07	-0.9
Aug 93	31	0.75 (42.6)	1 (56.8)	-	0.01 (0.6)	1.8	1	-0.05	-0.8
Sept 93	30	0.23 (17)	1.1 (82)	-	0.008 (0.6)	1.34	0.06	-0.18	-1.5
Oct 93	31	0.81 (4.5)	1 (54.9)	-	0.008 (0.6)	1.82	0.4	0.1	-1.5
Nov 93	30	0.25 (27.7)	0.64 (71)	-	0.006 (0.7)	0.9	0.3	-0.07	-0.7
Dec 93	31	11.8 (81.3)	2.7 (18.6)	-	0.023 (0.2)	14.5	16	-0.05	1.8
Jan 94	31	45 (88.7)	5.7 (11.2)	-	0.013 (0.03)	50.71	42	1.63	-7.1
Feb 94	28	14.4 (91.6)	1.3 (8.3)	-	0.006 (0.04)	16.71	6	-1.04	-11
Mar 94	31	21.3 (85.2)	3.46 (13.8)	-	0.014 (0.06)	25	22.2	0.4	-2.4
Apr 94	30	5.6 (83.5)	1.1 (16)	-	0.01 (0.15)	6.71	7.9	0.08	1.27
May 94	31	0	0	-	0.004 (100)	0.004	0	-0.01	-0.02
Jun 94	30	0	0	-	0.005 (100)	0.005	0	0.008	-0.004
Jul 90 - June 91	365	162.2 (6.8)	37.5 (1.6)	2190 (91.6)	0.095 (0.004)	2391	845	5.86	-1541
Jul 91 - June 92	366	128 (82)	27 (17.4)	-	0.167 (0.06)	155	187	-8	+23.5
Jul 92 - Jun 93	366	125 (82)	31 (17)	-	0.12 (0.06)	184	217	0.2	+33.5
Jul 93 - Jun 94	365	101 (82.3)	21 (17)	-	0.12 (0.09)	122	99	1.77	-21.2

Although direct rainfall provided the smallest contribution to the DIN budget, on average 0.13 kg annually, during the dry periods in early summer and summer, direct rainfall was the only DIN source to the lake following the effluent diversion.

DIN concentrations in the lake generally decreased in summer and increased in winter and whilst in the summer periods the lake DIN was largely NH_4-N during the winters it was largely NO_3 -N.

The output DIN concentrations decreased greatly from 845 kg annually before effluent diversion to 186.5 kg, 217 kg and 99 kg respectively annually in the three annual DIN budget periods following the effluent diversion.

The DIN budget can not provide information on sedimentation/internal release as there are additional unmeasured 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 and conversion of DIN to organic forms of nitrogen. To obtain a more accurate picture of internal sources and sinks of DIN a total nitrogen budget would have to be calculated. Taking these omissions into account, the DIN budget evaluation has to be done carefully. There was clearly a net loss or conversion of DIN before effluent diversion with 1541 kg lost annually (Fig.4.2b). In the two years following effluent diversion there was a net increase perhaps from internal loading of ammonium. In 93/94 there was a small net loss of 21.2 kg (Fig.4.2b).

4.3.4 Direct measurement of internal release rates

Table 4.4 shows the mean values with standard deviations of sediment release rates ($mg/m^2/day$) of the variables at a standard temperature of 20 °C, and measured at ambient temperature (under running tap water). The rates were measured monthly for a year (14.4.1993 - 8.3.1994).

Two-way ANOVA revealed highly significant effect of temperature on the release rates of SRP, TP and NH_4-N (P=0.001, P=0.02 and P=0.006 respectively) (Table 4.5) which were greater at the standard temperature (20°C) (Fig 4.3 a, b and c). The sampling dates had significant effects on the release rates of these variables at the control temperature (P=0.003, P=0.002 and P=0.003 respectively) such that the release rates increased during summer months (June, July and August) (Fig 4.3 a, b and c). There was an exception to this in October when the release rates of these variables increased. The uptake rate of NO_3-N was only measured an four occasions because the lake NO_3-N concentrations were insignificant throughout the summer months. Although the uptake rate of NO_3-N was significantly different between the sampling dates (P=0.005) there was no significant effect of the different temperatures (P=0.6) (Table 4.5) (Fig. 4.4). There was uptake by the sediment in March 1994 and in April 1993 but a low release rate on 13.5.93 and 19.6.993.

Two-way ANOVA revealed no significant effect of different plant stands (different stations) on SRP, TP, NH_4-N release rates and NO_3-N uptake rate (P=0.3, P=0.5, P=0.3 and P=0.7 respectively) (Table 4.5). The sampling dates were significant for

Table 4.4 Mean values with standard deviations of sediment release rates (mg/m^2/day) of the variables measured monthly for a year in Little Mere, *measured only on four occasions (14.4.1993, 13.5.93, 19.6.93 and 8.3.1994).

	SRP	TP	NH_4-N	NO_3-N*
Mean standard temperature	43±7	83±23	96±11	-21±11
Mean ambient temperature	20±6	38±12	48±13	-21±13
Ambient station1	4±4	15±16	44±13	-46±32
Ambient station2	34±20	64±25	40±13	12±43
Ambient station3	12±11	36±23	46±13	-25±34
Ambient station4	18±10	17±34	47±12	-28±24
Ambient station5	30±14	54±30	55±14	-20±21

Table 4.5 Comparisions of measured release rates (mg/m^2/day) against, temperature sampling date (temperatures: control versus ambient) and at different stations against sampling dates in Little Mere following two-way ANOVA.

	SRP	TP	NH_4-N	NO_3-N
Sampling date	** (P=0.003)	** (P=0.002)	** (P=0.003)	** (P=0.005)
temperatures (ambient vs control)	*** (P=0.001)	* (P=0.02)	** (P=0.006)	NS (P=0.6)
Sampling date (ambient temp)	** (P=0.005)	* (P=0.03)	NS (P=0.1)	NS (P=0.2)
Stations (ambient temp)	NS (P=0.3)	NS (P=0.5)	NS (P=0.3)	NS (P=0.7)

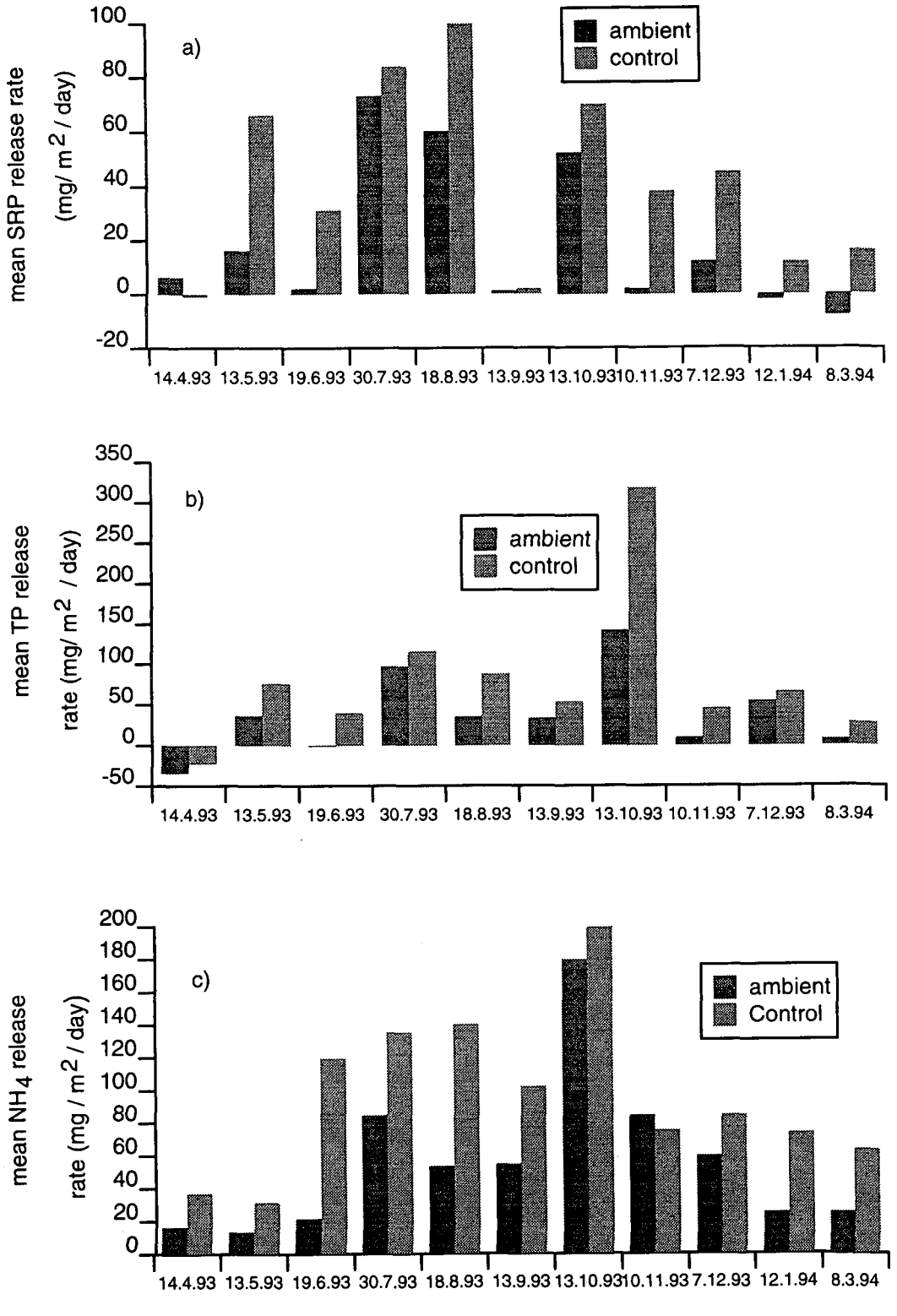

Fig.4.3 Mean measured sediment release rates of a) SRP, b) TP and c) NH_4 at ambient and control temperatures in Little Mere between April 1993 to March 1994 on a monthly sampling frequency.

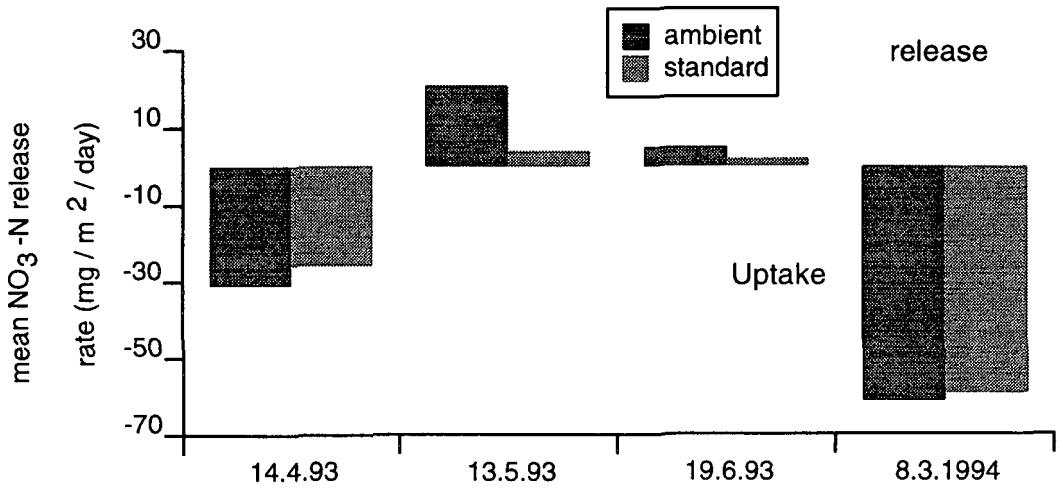

Fig.4.4 Mean measured sediment exchange rate of NO_3 -N at ambient and control temperatures in Little Mere on four sampling occasions.

SRP and TP release rates (P=0.005 and P=0.03 respectively) at ambient temperature but not for NH_4-N and NO_3-N (P=0.1 and P=0.2 respectively) (Table 4.5). The release rates of SRP and TP greatly increased in July and August and decreased in September. There was an increase in both SRP and TP release rates in October. The release rates were low for the rest of the year, and negative in March 1994 for SRP and April 1993 for TP suggesting a net uptake.

4.4 Discussion

4.4.1 Water budget

The water budget showed that over four years, catchment 1, catchment 2, and direct rainfall contributed on average, 92 %, 6% and 1% respectively. The water budget calculations included a year budget (1990/91) before effluent diversion when STW effluent contributed 6% to the water budget. Despite the percentage contributions of the different sources remaining roughly the same over the four annual budgets, the period 1991/92 was much drier than previous and later periods. The 1993/94 period was the wettest. Use of long-term mean values for actual evapotranspiration over the area and specific annual total rainfall may have created some errors in water budget calculations. Calculation of water flow to Little Mere from Mere Mere was based on estimates of rainfall and evaporation over the catchment of Mere Mere and the lake itself which might have underestimated the water flow to the lake over summer (when evaporation exceeded rainfall). In reality periods of no flow might have been shorter. During winter, water flow to the lake might have been overestimated for the same reason. Before effluent diversion, contribution from the STW to the water budget was based on dry weather flow rate (0.3 Ml day^{-1}) and thus underestimates the contribution in wet months.

Clearly, however, catchment 1 is the major source of water to the lake over the four annual water budget periods. When evaporation was greater than direct rainfall, there was no flow from either Catchment 1 or catchment 2, and the only water source to the lake was direct rainfall over the lake though its overall contribution was insignificant

(1%). The budget also showed that direct evaporation was responsible for the loss of about 0.9% of these total inputs an amount almost equal to the amount of direct rainfall over the lake surface.

As 98 % of the inputs to Little Mere were due to surface run-off and drainage, the flushing rate will show a seasonality corresponding to these inputs, hence the lowest flushing rate, (zero) was in the summer months due to greater evapotranspiration rates in these months. The highest flushing rate was recorded in the wettest period, 1993/94.

4.4.2 Total phosphorus budget

The STW was initially by far the most significant of the external sources of phosphorus to the lake. In the annual budget period prior to sewage diversion it accounted for 98% (730 kg) of the external sources (Table 4.2). Calculation of annual load from the STW was based on the North West Water Authority (NWWA) (1983) measurement of 2 kg day^{-1}. There is probably some error associated with the measurement because the value was based on a single measurement of dry weather flow. Assuming 1 person contributes 0.77 kg of total phosphorus per year (Moss *et al.* 1988), the annual load into Little Mere ought to have been 2553 kg because the STW served 3315 people before it was shut down. This figure is much greater than the NWWA estimate. Prior to sewage diversion the annual lake mean TP concentration was 2245 μg l^{-1} (the lake TP content was 47 kg) and the mean flushing rate was 84 times per year. A requirement for a total load of 47 x 84 is this indicated (3948 kg). This is rather greater than the 2553 estimated and much greater than that

measured by NWWA. Loadings from Catchment 1, catchment 2 and direct rainfall were relatively insignificant in their contributions compared to the STW prior to effluent diversion (Table 4.2) whatever estimate is made for STW contribution.

In years following diversion of the sewage effluent, catchment 1 became the most significant external source and accounted for 8 kg, 13 and 23.6 kg respectively (Table 4.2). The lowest TP loading to the lake from Mere Mere and its catchment was recorded during 1991/92 probably due to 1991/92 being the driest period over the four years. The highest external load was recorded in 1993/94 which was the wettest period. Throughout the study period there was no significant change in TP concentrations in Mere Mere (Carvalho *et al.* in press; Chapter 2). Therefore, the increase in TP loading was probably related to random variation in the annual rainfall. The loading from the Little Mere catchment (catchment 2) became the second biggest source to the lake with 1.4 kg, 2.9 kg and 2.5 kg respectively (Table 4.2) following effluent diversion. The loading increased in 1992/93 because during the same period there was a significant increase in TP concentrations of inflow Mere Mere (Carvalho *et al.* in press; Chapter 2) which were used in calculating loadings from catchment 2. The contribution from direct rainfall was insignificant over the budget periods

A long period of resilience in phosphorus concentrations was anticipated in Little Mere, from previous studies elsewhere which have shown small response to reduction of external nutrient loading. This resilience to change, partly due to homeostatic mechanisms involving fish and zooplankton (Scheffer, 1989; Jeppesen *et al.* 1991;

Phillips *et al.* 1994), but also release of phosphorus from the sediment, appears to be a major factor in many shallow eutrophic lakes (Boström *et al.* 1982; Sas, 1989; Marsden 1989; Hosper, 1989; Søndergaard, 1989; Jeppesen *et al.* 1991; Bales *et al.* 1993; Perrow *et al.* 1994). Little Mere, however, rapidly responded to reduction in external nutrient loading and the TP concentrations decreased greatly following effluent diversion (Carvalho *et al.* in press; Chapter 2). Balancing the pre-diversion TP budget revealed that there was a net loss to the sediment of 405 kg (at least). The post-diversion budgets (1991/92 and 1992/93) show net gains from the sediment of 111 kg and 87 kg respectively and a small loss to the sediment of 1.1 kg in 1993/94. Mechanisms which play an important role in internal release and independent measures of the release rates of nutrients in Little Mere are discussed below.

The resilience of lakes depends on their nature and previous history. Oligotrophic lakes will respond slowly to increasing load but rapidly to decreasing load as long as perturbation is brief (Vollenweider & Kerekes, 1982). Lakes with a long previous eutrophication history, as in Little Mere (over fifty years sewage discharge), are suggested to have lost resilience, and are presumed to respond much more slowly to comparable load reduction (Janus & Vollenweider, 1984). Following the received wisdom, delayed recovery of Little Mere was anticipated. The relative residence time of TP was calculated for prior to the effluent diversion (1990/91) and after effluent diversion (1991/92, 1992/93 and 1993/94) as:

$$\tau_p/\tau_w = \frac{\dfrac{\text{Standing stock phosphorus in lake (in mg)}}{\text{yearly supply of phosphorus to lake (in mg.year}^{-1})}}{\dfrac{\text{lake volume (in m}^3)}{\text{yearly water discharge (in m}^3 \text{ . year}^{-1})}}$$

(equation 4.5) (Janus & Vollenweider, 1984).

The relative residence times of TP in Little Mere for the budget periods were 0.053, 22.8, 5.6 and 0.96 respectively. If the substance is dissolved and no reaction takes place, its relative residence time is 1 and the substance is conservative. If, on the other hand, the substance is removed from the water column by absorption, sedimentation, etc., its relative residence time will drop below 1. In cases where internal loading occurs, the relative residence time is greater than 1 (Janus & Vollenweider, 1984). In Little Mere before effluent diversion, TP was largely lost to the water probably by sedimentation. For two years following the effluent diversion, the relative residence time of TP suggested that internal loading occurred as found from balancing the TP budget. During the 1993/94 period, relative residence time was less than one indicating loss to the sediment. This might be due to further expansion of the existing plant stands in the lake (Chapter 8) It has been shown that macrophyte stands increase sedimentation rate (Boers *et al.* 1991). To assess major factors determining the relative residence time of TP, a regression analysis of the relative residence time of TP against flushing rate, total external TP load and chlorophyll a was carried out for the four budget periods. The flushing rate explained 44% of the variation in relative residence time of TP. The total external load of TP to the lake explained 23% of the variation, and chlorophyll a only explained 15% of the variation. It thus seems that the high

flushing rate of Little Mere may have been the main controlling factor behind fast recovery though some caution is needed because of some autocorrelation due to the flushing rate being used in the relative residence time calculation. Especially during 1992/93 and 1993/94 with higher flushing rates, due to wetter weather. TP might have been washed out rather than returned to the sediment resulting in decreased lake concentration. Cooke *et al.* (1986) found that, of the mechanisms induced by flushing, dilution gave the most pronounced effect in recovery of Green Lake and Moses Lake in the USA. Another example is from The Netherlands, where the flushing of Veluwemeer, eutrophic shallow lake, led to water quality improvement with significantly decreased P concentrations and cyanophyte biovolumes (Jagtman *et al.* 1992). Lakes with low flushing rates tend to have accumulated nutrient, released from the sediment following diversion of external nutrient sources, and this delays recovery (Marsden, 1989; van Liere *et al.* 1990). One drawback of diversion of nutrient rich point sources, i.e. inflow streams, from low-flushed shallow lakes to reduce nutrient loading is that this may affect water levels, reduce flushing and increase the accumulation of released nutrient (Marsden, 1989; van Liere *et al.* 1990). There may also be changes in the phytoplankton population toward slow-growing groups/species such as Cyanophyta (Moss *et al.* 1991). Contrary to the fast recovery of the rapidly flushed Little Mere, many shallow Danish lakes, even with fast-flushing, seem to have a long recovery period (Jeppesen *et al.* 1991) due to large amounts of phosphorus accumulated in the sediment relative to the lake area (Søndergaard *et al.* 1993). The iron:phosphorus ratio appears to be an important factor for controlling phosphorus release, which is suppressed when the ratio (by weight) is higher than 15 to 20 in

shallow Danish lakes (1990; Jensen *et al.* 1992). However, in eutrophic shallow lakes of the Norfolk Broads, the highest release rates were associated with high total sediment Fe:P ratios (Phillips *et al.* 1994). Thus, the mechanisms which govern recovery following external nutrient diversion appear to vary between lakes.

4.4.3 Dissolved inorganic nitrogen budget

As with phosphorus, Mere STW was by far the most significant of the external sources of DIN to the lake. Mere STW accounted for 2190 kg (92%) in the annual period prior to sewage diversion and the contributions from catchments 1, and 2 were insignificant (6.8% and 1.6% respectively) (Table 4.3). In the years following diversion, catchment 1 became the most significant external DIN load to the lake (82%) and catchment 2 was second most important with 17%. Despite relatively steady percentage contributions over three annual budget periods, loadings from catchment 1 and catchment 2 (in kg) varied. The lowest loads from the catchments were recorded in 1993/94, which was the wettest period during the study and when DIN concentrations significantly decreased in Mere Mere and inflow Mere Mere (Carvalho *et al.* in press; Chapter 2). The DIN loads increased during the winter months and decreased during the summer months. The load of direct rainfall was insignificant and accounted for less than 1% during the study.

As total nitrogen was not measured, a budget only for DIN (nitrate, nitrite and ammonium) could be calculated. Particulate and dissolved organic nitrogen loading were not accounted for, which could severely underestimate the total nitrogen load to

the lake. It has been 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 (Johnes & Burt, 1991). Holden and Caines (1974) found on average about 32% of nitrogen in sewage effluent was in an organic form. DIN therefore probably only accounts for, at most, two thirds of the total nitrogen load to the lake. Taking into account the weakness of a DIN budget for overall estimation of nitrogen, there was pre-diversion major loss of combined nitrogen, perhaps due to sediment denitrification. In the two annual periods following the effluent diversion, ammonium loading from the sediment might have been important probably due to very low dissolved oxygen concentration (Carvalho *et al.* inpress and Chapter 2). There was then a DIN loss to the sediment probably due to increase in dissolved oxygen concentrations (Carvalho *et al.* inpress and Chapter 2) and expansion of the macrophyte stands. It has been shown that macrophytes can increase dissolved oxygen concentration and nitrification and in turn increase overall denitrification in freshwater bodies (Reddy *et al.* 1989; Christensen *et al.* 1990).

4.4.4 Impact of sewage diversion on Little Mere

The response of lakes to a decrease in external nutrient loading varies. Often reduction of external nutrient loading does not immediately lead to a reduction in nutrient concentrations in the lake, and, therefore, to no reduction in phytoplankton biomass. This has been the general scenario in many eutrophic shallow lakes. The resilience of the lake to change may depend on factors such as flushing rate, internal release from the sediment, chemistry of the sediment and the biological community (Jeppesen *et*

al. 1991). Opposite to this expectation, tremendous recovery of Little Mere has been observed in less than three years following sewage diversion when the concentration of nutrients greatly decreased (Carvalho *et al.* in press and Chapter 2). The phytoplankton community has been dominated by fast-growing, potentially grazeable groups with low chlorophyll a concentrations (Chapter 3). The submerged macrophyte stand has expanded and almost covered the lake (Chapter 8). The pre-diversion clear-water phase has been maintained so far.

Cyanophytes were formerly scarce in the lake and remain so, though in summer 1993, a small increase of *Anabaena* sp. biovolume was recorded (Chapter 3). Whether it was a sign of nitrogen limitation and in turn of future cyanophyte increase or just an annual variation in the lake's phytoplankton community is not yet known. Two questions need to be answered to predict what change in phytoplankton biomass might eventually occur, following the reduction in loading:

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

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

The relationship between loading and lake nutrient concentration can not be established without taking into account sedimentation and flushing (Dillon, 1975). This leads to the prediction of mean lake total phosphorus concentration from load by an empirical equation 6 (Vollenweider & Kerekes, 1981). Assuming that similar factors are important in the relationship between DIN loading and mean DIN concentrations,

this equation can be used to predict future mean lake concentrations of DIN and TP:

$$[M]_{lake} = \frac{[M]_i}{(1+\sqrt{R})} \qquad \text{equation (4.6)}$$

where,

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

$[M]_i$= mean inflow concentration of nutrient

R=mean residence time of water (yr^{-1})

For Little Mere, after diversion, 1993/94 period:

$[P]_i$=mean annual inflow concentration of TP

=annual load of TP / annual inflow volume of water

=26.4 kg yr^{-1} / 253 x 10^4 m^3 yr^{-1}

= 0.01 mg l^{-1}

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

=annual load of DIN / annual inflow volume of water

=183.7 kg yr^{-1} / 253 x 10^4 m^3 yr^{-1}

=0.073 mg l^{-1}

R=volume of Little Mere / annual volume of outflow

= 2.1 x 10^4 m^3 / 251 x 10^4 m^3 yr^{-1}

= 0.0084 yr

therefore using equation 4.6

$[P]_{lake}$ = 0.01/ (1 + $\sqrt{0.0083}$)

= 0.0092 mg l^{-1}

= 9.2 µg l^{-1}

$[DIN]_{lake}$= 0.073 / (1+$\sqrt{}$0.0083)

= 0.067 mg l^{-1}

= 67 µg l^{-1}

N:P = 0.067:0.0092

= 7.3:1

This ratio uses the predicted value of total P, and not orthophosphate-P, and that of DIN rather than TN so the real ratio ought to be higher that this perhaps by a factor of 1.5-2.0 (see above). Forsberg *et al.* (1978) suggested that if the ratio N:P= <9-10:1, the phytoplankton yield was determined primarily by nitrogen. Smith (1979) found this ratio <13 for nitrogen limitation. Therefore, the phytoplankton of Little Mere could (just) show signs of nitrogen limitation. In Little Mere, prior to sewage effluent diversion and in the years following effluent diversion, the phytoplankton community of the lake was grazer-limited (by large body-sized cladocerans, first *Daphnia magna* and later largely with *D.hyalina*) (Chapter 3). Although the nutrient concentrations have greatly decreased, they are high enough to a support high phytoplankton crop (Carvalho *et al.* in press; Chapter 2). Recently, the zooplankton community has shifted to loosely or firmly plant-associated species with a large expansion of the macrophyte stands. Therefore, zooplankton grazing pressure may have weakened. The expansion of rooted macrophyte stands might have had an important role in shifting the phytoplankton to nutrient limitation. From the predicted nutrient concentrations of the lake, the N:P ratio hints at possible nitrogen-limitation of the phytoplankton community. A possible future scenario of nitrogen-fixing cyanophyte dominance in the lake might not be likely, however, because of a number of negative feedback

mechanisms: submerged macrophytes can reduce the growth of the phytoplankton through luxury uptake of nutrients (Ozimek *et al.* 1990; van Donk *et al.* 1993) including P as well as N. Plants have free access to sedimentary nutrients through their roots (Denny, 1972). Another mechanism is release of allelopathic substances by macrophytes (Wium-Anderson, 1987; van Vierssen *et al.* 1994). In addition, the flushing rates of the lake seem to be generally too high, depending on the rainfall, to support slow-growing nitrogen-fixing cyanophytes (Moss *et al.* 1991) though this is not the case in late summer.

4.4.5 Internal nutrient loading

The release rates of TP, SRP and NH_4 measured at control (20 °C) and ambient temperature showed significant increase at the control temperature. It has been shown that temperature increase stimulates mineralization of organically bound P and a lowering of the redox potential, which may result in the release of Fe-bound P. Jensen and Andersen (1992) found temperature alone accounted for 70% of the seasonal release in three out of four Danish lakes. Though the control temperature was kept constant, the results suggest some seasonal variation. This is probably because of increased biological activity or organic load on the sediment surface which might have enhanced the control temperature effect in summer. The release rates of these nutrients were significantly higher in June-August than in the rest of the year at ambient temperatures probably because of increased temperature, increased metabolic activity of microorganisms and increased oxygen consumption of sediment dwellers which decreased redox potential and stimulated release of Fe-bound P (Kamp-Nielsen, 1974;

Fleischer, 1978). One exception to this was observed in October when the release rates of these nutrients were very high. The highest release rates of TP and NH_4-N were recorded, probably due to senescence of macrophytes, at the end of the growing season. Macrophytes take up P and N from both sediment and overlying water through roots and leaves which then provide a potential pathway for nutrient mobilization and consequent release into the overlying water, either through release from healthy plants or from senescing plant tissues. It appears that healthy plants do not release significant amounts (McRoy *et al.* 1972; Gabrielson,1977; Moeller *et al.* 1988), but that senescent macrophytes release a major part of their P and N into the overlying water (Kistritz, 1978; Lansers & Frey, 1980). The contribution from senescing plants probably supplies a high load of labile matter to the sediment surface thus altering the sediment chemistry which may ultimately lead to phosphate release (Moss *et al.* 1990). Decomposition of plants may also contribute a significant load to the nutrient pool in the water column (Malthus *et al.* 1990). This may have contributed to the presence of early (February) peaks of diatoms in 1993 and 1994 in Little Mere (Chapter 3).

The sediment uptake rate of NO_3-N was only measured on four occasions because NO_3-N concentrations were undetectable in summer in Little Mere. The different temperatures did not have a significant effect on the release rates, but sampling dates did. In spring (8.3.1994 and 14.4.93) NO_3-N was largely taken up by the sediment (or denitrified by it) but in early summer, May and June 1993, there was a release from the sediment. The sediment uptake in spring might be due to a sharper diffusion gradient arising from lower interstitial concentrations than the overlying water (Stumm

& Leckie, 1971), and the release into the overlying water in early summer months may have been due to the same reason operating in the opposite direction. Microbial activity in the sediment and in the water have also been shown to be an important determining factor in NO_3-N movement (Kamp-Nielsen, 1974). Thus, during the early summer increased microbial activity might have increased NO_3-N transfer, through mineralization, to the overlying water.

The different sites (stations) did not have significant effects on the release rates of these nutrients measured at ambient temperature, probably because all the sites were covered with macrophytes later in summer when the highest concentrations of nutrients were released from the sediment. Station 2 was open water in early summer but was later covered by *Potamogeton berchtoldii*. Thus, there being no open water site for the experiment in summer might have masked an effect of macrophytes on internal release, though the sites were covered by different macrophyte stands. It has been shown that macrophytes are capable of nutrient uptake through roots and shoots (Carignan and Kalff, 1980; Denny, 1972), but the potential depletion of sediment phosphorus and nitrogen by macrophytes is likely to be balanced by other processes. The sedimentation rate within plant beds is greater than in open water and plants stabilize sediments (Barko *et al.* 1991; Carignan, 1985). Macrophytes are known to alter the sediment and overlying water chemistry (Carpenter & Lodge, 1983). In aquatic plant beds, extremes of dissolved oxygen and pH have been recorded (Frodge *et al.* 1990; Serafy & Harrell, 1993; Jones *et al.* in press). High pH values stimulate release of nutrients from the sediment (Boström *et al.* 1982), though nutrient release

been largely associated with anoxia. Under aerobic conditions, substantial amounts of nutrient release have been recorded (Jensen & Anderson, 1992). Invertebrates, through bioturbation have been shown to increase significantly the release of phosphorus from sediment (Phillips *et al.* 1994). Therefore macrophytes may indirectly increase P-release by providing habitat for invertebrates. In Little Mere and the upstream Mere Mere Stephen *et al.* (1996) has found a significantly higher SRP release and NO_3 uptake in the presence of plants in summer and this may be attributed to increasing sedimentation, enhanced mineralization, elevated pH and invertebrate activity. Sampling date significantly affected release rates of SRP and TP such that the highest rates were recorded in July and August. This may have depended largely on temperature. In October, the rates also increased probably because of loading from senescing plants.

Mean release rates of SRP, TP, NH_4-N and NO_3-N based on direct measurements were calculated for the whole lake for the whole sampling period (337 days) and were 189 kg, 359 kg, 434 kg and -198 kg respectively. The rates obtained from balancing the TP and DIN budgets were 0.18 kg and 17.2 kg respectively for the same period. The measured rates of TP (359) and DIN (434-198=236 kg) in laboratory conditions were thus much higher than the budget values. This may be linked with the very high flushing rates of Little Mere which may create a very different environment at the sediment surface than was present in the experimental tubes (Cooke *et al.* 1986; Jagtman *et al.* 1992). The nutrient concentrations used for the TP and DIN budgets

concentrations in the lake. Probably some errors were also associated with the laboratory release rates measured. When overlying water was sampled, concentration gradients were probably changed and the sediment might have been disturbed. During incubation, tap-water (ambient) temperature was probably higher than in the lake water due to warming between the lake source and the tap. Using sediment cores from plant beds without intact plants, is also unlikely to take into account the full impact of the plants. Though macrophytes indirectly stimulate P release, they deplete N and P in the overlying water and the sediment. Aquatic macrophytes also enhance denitrification through decreasing oxygen concentrations at the base of the beds and in turn by daytime oxygenation also increase nitrification. This was also the qualitative conclusion of the laboratory experiment. Balancing the budget for DIN showed loss of DIN to the sediment in 1993/94. This loss is probably due to a large expansion of the macrophyte stands and net denitrification. There are, of course, uncertainties in the mass balance budget, especially in the use of long-term average meterological data but because of all the possible disadvantages created in laboratory conditions, it seems likely that these have overestimated the release rates.

The balancing of the TP and DIN budgets showed high release of these nutrients a year following effluent diversion but the rates greatly decreased in the 1992/93 and 1993/94 periods probably because of changes in the nature of the sediment surface and because these periods were wetter than previous ones leading to faster flushing of the lake water. Also increases in dissolved oxygen concentrations in the lake, following the effluent diversion, might have reduced the release rates. Another possibility is that

the P pool in the sediment had declined through previous release and washout. It has been shown that a higher external P-loading may not necessarily result in increased accumulation of P in the sediment because the percentage of P retained in lakes is also related to hydraulic retention time and generally increases with increasing hydraulic retention time (Janus & Vollenweider, 1984; Dillon & Rigler, 1974). To be able to assess the possibility of a low P-pool in the sediment the phosphorus content of the sediment both organic and inorganic (Fe-bound P, Ca-bound P) should be measured. Measurements of the total iron :TP ratio may also explain some the interactions in the sediment.

4.4.6 Conclusion

In shallow lakes, diversion of external nutrient loads alone has generally been ineffective as a restoration measure owing to internal loading along with other biological homeostatic mechanisms (Sas, 1989; Jeppesen *et al.* 1991; Phillips *et al.* 1994). Despite the anticipation of resilience in Little Mere, the lake has shown a fast response in chemistry and recovery of oxygen concentrations and fish community following effluent diversion (Carvalho *et al.* in press; Chapter 2 and 8). The TP budget suggests that there was release of TP from the sediment for two years following the effluent diversion though the release rates decreased and there was uptake in 1993/94. The decrease in internal release of TP might have been related to the increase of flushing rates in the last two years of the period. The flushing rate of the lake explained 44% variation in the relative residence time of TP (though there is a degree of autocorrelation in this), and also the large increase in dissolved oxygen

concentrations might have reduced the release rate. The duration of net annual sediment release in manipulated lakes is sometimes relatively short, (i.e not more than five years (Sas, 1989) and Little Mere appears to fit this expectation. However, the laboratory release rate measurements showed the existence of a potential important release from the sediment contrary to the budget result. This is probably because of the severe difference in conditions between the laboratory and the lake.

The pre-diversion clear-water state of Little Mere was maintained following the effluent diversion. The macrophyte stands expanded, largely with submerged plants (Chapter 8). The phytoplankton populations of the lake were probably grazer-limited, pre and post-diversion. The predicted concentrations of P and N and the N:P ratios showed possible nitrogen-limitation of the algal crop. The large decrease in nutrient concentrations and the expansion of the macrophyte stand might now shift the lake to a nitrogen-limited state. A potential nitrogen-fixing cyanophyte dominance in the lake may not be realised because of the negative feed-backs that are imposed on phytoplankton community by the macrophyte stands and high flushing rate of the lake (see Chapters 6, 7 and 8).

Lake restoration techniques for deep lakes have traditionally focused on reduction in external P loading. This has proved effective in some cases, (Edmondson, 1970; Sas & Vermij, 1987). Following the conventional wisdom on lake restoration, the aim of sewage effluent diversion from Little Mere was to restore the downstream deep lake, Rostherne Mere, which is eutrophic with cyanophyte blooms. Following sewage

effluent diversion, Rostherne Mere has shown little reduction in phosphorus, and none in chlorophyll a concentrations, despite large reductions in nutrient concentration in its main inflow following those in Little Mere (Carvalho *et al.* in press; Chapter 2). The expected recovery time for Rostherne Mere by dilution is up to fifty years (Carvalho *et al.* in press). Little Mere has shown fast recovery in three years following diversion of sewage effluent. Simple dilution appears to have been very important in the fast recovery of Little Mere along with its expanding macrophyte stands.

Chapter 5: The effects of the increasing fish densities and the sediment on water chemistry, phytoplankton and zooplankton communites in mesocosms in Little Mere in 1992

5.1 Introduction

Previous monitoring of Little Mere has emphasized that as in other freshwaters, the phytoplankton crop is not only controlled by 'bottom-up' mechanisms (Schindler & Comita, 1972; Schindler, 1977; Smith, 1983), but also by 'top-down' mechanisms (Leah *et al.* 1980; Shapiro & Wright, 1984; Carpenter *et al.* 1985; Gulati, 1990; Meijer *et al.* 1990; Carvalho, 1994; Moss *et al.* 1994). Increasing concern about eutrophication has focused attention on nutrient supply as a regulator of lake productivity, with well established regressions of phytoplankton chlorophyll a and phosphorus concentrations (Vollenweider, 1976), though inverse relationships also exist between zooplankton numbers and phytoplankton chlorophyll a (McCauley & Briand, 1979). Certainly, however, nutrient supply can explain the potential crop (Dillon & Rigler, 1974) though this potential may not always be fully realised.

To control eutrophication of freshwaters by reducing external nutrient loads has been tried as a technique, though there are few fully successful examples such as Lake Washington (Edmondson, 1970; Edmondson & Lehman,1981). More often there has been short-term success or a complete failure (Bengtsson *et al.* 1975; Bjőrk, 1985). Attempts are often hindered by resilience through internal nutrient loading (Sas, 1989; Søndergaard *et al.* 1989; Marsden, 1989 Jeppesen *et al.* 1991) and also there are some water bodies to which nutrient reduction can not be applied because of geographical, economical, political and technical reasons. There are some well-studied examples oft he probable inapplicability of external nutrient reduction, like Rostherne Mere. Three

years following sewage effluent diversion there is no sign of recovery (Carvalho *et al* in press; Chapter 2). In the north-west Midland Meres where phosphorus sources may be naturally derived from phosphorus-rich mineral deposits in the catchment (Reynolds 1979). In Lake Zwemlust, the Netherlands, restorative techniques, including sediment dredging to reduce internal nutrient loading and application of herbicides have been attempted to improve the water quality, but without success. In this lake, nutrient reduction was not possible, because the lake receives nutrient-rich seepage (van Donk *et al.* 1989). The potential use of external nutrient reduction seems to be less widespread than formerly anticipated for many lakes. Thus, other techniques need to be used often in addition to nutrient control to ensure water quality improvement. Top-down control or food web manipulation offers some help. A variety of examples shows the success of top-down control of phytoplankton crops by large Cladocera, especially *Daphnia* spp. (Shapiro & Wright, 1984; Timms & Moss, 1984; van Donk *et al.* 1990; Hosper & Meijer, 1993). This is often established by manipulation of the fish community to increase zooplankton density, because abundance of plankivorous fish can cause major reduction in large filter feeders (Zaret, 1980; Gulati, 1989; Søndergaard *et al.* 1990) which in turn may affect the phytoplankton. There are some spectacular short-term results from several small lakes (Meijer *et al.* 1989; Hosper & Jagtman, 1990; Moss, 1992a). But there are drawbacks to this technique, posed by the difficulties of fishing-out large water bodies or the alternative addition of fish predators (Benndorf, 1990). If the initial biomanipulation is weak, for example only partial removal of fish, effects may be minimal (McQueen, 1990), and even the most intensive fish removal operation is never complete and is costly. The short-term results of these food web manipulations are encouraging. However it is unclear whether in the long term the manipulated system will return to the initial turbid condition or stay

in a new, clear state (Benndorf, 1990). As shown from the five-year results of four manipulation cases from The Netherlands and Denmark, none of the cases studied has returned to a permanently turbid state, yet deterioration in summer and other signs of instability are observed (Meijer *et al.* 1994) and similar signs of instability were observed in manipulated shallow eutrophic broads (the Norfolk Broads) (Perrow *et al.* 1994).

None of the above discussed approaches to improve water quality is usually successful alone. The problem needs tackling widely, taking into account the whole system rather than just the symptoms of the problem to ensure permanent of improvement. The existence of bi-stability theory (multiple stable states) in shallow eutrophic lakes would offer significant possibilities for restoration (Scheffer 1989; Moss, 1990; 1991). Over a range of nutrient concentrations, shallow lakes can have two alternative equilibria: clear water dominated by macrophytes and a turbid state with high algal biomass, and these two alternative states seem to be stable (Moss, 1990; Scheffer, 1990; Scheffer *et al* 1993). Thus the success of biomanipulation seems to be closely related to an increase of transparency long enough after biomanipulation to allow strong development of vegetation in the following years (van Donk *et al.* 1990; Meijer *et al.* 1990). Under strongly developed vegetation, recruitment of the remaining fish is good; increasing numbers of young planktivorous fish in the following years can exert a huge predation pressure on zooplankton. Nonetheless, the lakes can maintain clear water because of the stabilizing effects of vegetation (Balls *et al.* 1989; Scheffer *et al.* 1993; Moss *et al.* 1994; Carvalho, 1994). The system appears to be able to resist the effects of eutrophication through a variety of macrophyte-induced buffering mechanisms, which include reducing nutrient levels (Ozimek *et al.* 1990; van Donk

et al. 1993), provision of refuges against fish predation for grazers (Timms & Moss, 1984), forming spawning grounds and refuges against cannibalism for piscivorous fish like pike (Grimm, 1989) and prevention of resuspension of the sediment by wind and benthivorous fish (Meijer *et al.* 1990). The role of aquatic vegetation in lake restoration is therefore predominantly a stabilizing one. Thus, success of these techniques, which have been used to improve water quality, depends on establishment of strong and diverse macrophyte stands.

Little Mere has had a clear water state at very high available inorganic phosphate-phosphorus and ammonium-nitrogen concentrations (several milligrams per litre), with large stands of aquatic vegetation, and with very low dissolved-oxygen concentrations because of proportionally large amounts of sewage effluent which were directly discharged into the lake (Carvalho, 1994) (See Chapters 2, 3 and 4 for the details).

There seemed to be several ways in which the ecosystem might develop as the effects of the previous effluent declined. This experiment was designed to predict the effects of progressive reoxidation of the sediment surface and decline of release of nutrients from it coupled with expected recolonization of fish as oxygen concentrations increased. Two different types of enclosures were used- some enclosures open to the sediment surface and others sealed (closed) from it - at four different fish densities. Open enclosures were used to reflect the present lake (in 1992 when the experiment was done) with its highly reduced sediment surface and closed enclosures to anticipate the future lake when the sediment surface might become less reduced as labile organic matter derived from the former effluent decomposes. In both cases increasing fish predation on zooplankters must be expected. We hypothesised that the presence of

reduced sediment would supply sufficient nutrient loading to permit build-up of very large phytoplankton crops in the presence of fish but that the release of carbon dioxide from the sediment would mitigate against a significant cyanophytes component. In turn we hypothesised that the future, oxidized sediment with lower CO_2 release would allow pH to rise and favour cyanophyte, in water that would remain relatively nutrient rich.

5.2 Methods

5.2.1 Design and apparatus

The experiment was carried out between 17th July and 13th August 1992, in twenty-four polyethylene enclosures. Each enclosure consisted of thin, (125 μm wall thickness) clear and colourless polyethylene film formed into two kinds of mesocosms referred to as open and closed enclosures. The closed enclosures were sealed at the bottom and open to the atmosphere at the top, and the open enclosures were open to the both sediment and atmosphere. The diameter was 1 m and the depth was 1.5 m, yielding a volume of 1100 L. The enclosures were placed in middle of the lake, where the depth was 1 m and were filled with water pumped from a depth of 0.5 m. They were suspended from a wooden raft, anchored to the bottom and floated with air-filled plastic bottles, which kept the open ends of the enclosures 0.3 m above the water surface so as to prevent exchange with the lake water. The placement of the treatments was randomised within the wooden frames.

The experimental design was 2x4 factorial with two types of enclosures and four different fish densities. Half of the enclosures were open to the sediment representing the present situation of the lake water, and the remainder of the enclosures were

closed to the sediment to simulate the future lake water in which the sediment surface is predicted to become oxidised and less active in release of nutrients. Roach (*Rutilis rutilis* (L)), 8-11 cm total length, were caught by seining in the Shropshire Union Canal and immediately placed in appropriate enclosures at four different population sizes, 0 fish, 1, 3, and 4 fish per enclosure. Each treatment was carried out in triplicate, making a total of twenty-four enclosures.

5.2.2 Sampling methods

The first sample was taken immediately after the treatments had been initiated. Sampling of the enclosures was carried out each week from the entire water column in the enclosures. Before sampling, the water in the enclosures was mixed using an oar, with care being taken not to disturb the sediment surface. Methods for the water chemistry were described in Chapter 2, except where detailed below.

Free- CO_2 concentrations were calculated according to Mackereth *et al.* (1978).

The methods for phytoplankton and zooplankton samples were described in Chapter 3, except where detailed below.

Body (carapace) lengths of *Daphnia magna* were measured (100 x magnification) to assess change in biomass, using linear regressions relating lengths (mm) with dry weight (µg) (Bottrell *et al.* 1976) when W is weight, L is length, and a is a constant:

$$LnW = Lna + bLnL \qquad \text{equation (5.1)}$$

5.2.3. Statistical analyses

The effects of treatments on water chemistry, phytoplankton and zooplankton populations were assessed using two-way ANOVA with repeated measures (Winer, 1971). All analyses were carried out using the Statistical Analyses System General Linear Model (GLM) routine (SAS Institute Inc, 1988.). All dates except the initial sampling date were used in the analyses. To check for normality in the data, plots of fitted values in the ANOVA model against error terms were examined; when there was a noticeable heterogeneity of error variance, log transformations were employed. To determine whether initial conditions were similar among the groups of enclosures to be used as treatments, one-way ANOVA was performed.

5.3. Results

5.3.1 Initial status of enclosures

One-way analyses of variance on the initial chlorophyll a concentration, cyanophyte, chlorophyte and diatom biovolume concentrations and population densities of *Daphnia magna, D. hyalina* and *Bosmina longirostris* revealed no significant differences among enclosures.

Because of punctures in three of the polyethylene enclosures during the experiment, one of the closed and two of open enclosures were omitted from subsequent analyses. All the other enclosures remained intact throughout. The fish survived in both open and closed enclosures except for a few which died and were quickly replaced with the similar-sized ones. The densities were maintained at the intended levels by checking regularly during the experiment.

5.3.2 Response of chemical variables

Table 5.1 shows mean values ± S.D. of variables measured in the experiment and Table 5.2 the results of repeated measures of two-way ANOVA. The sediment had significant effects on SRP, NH_4-N, dissolved-O_2 and free-CO_2 concentrations and pH (P=0.0001, P=0.0001, P=0.0001, p=0.035 and P=0.0001 respectively) (Table 5.2). Whilst concentrations of SRP, NH_4-N and free-CO_2 increased significantly in the presence of sediment (open enclosures) (Fig.5.1a, b and Fig.5.2a respectively) the concentration of dissolved-O_2 and pH decreased significantly in open enclosures (Fig.5.1c and 2b respectively). The mean values of SRP, NH_4-N, free-CO_2, dissolved-O_2 and pH for open enclosures were 764 $\mu g\ l^{-1}$, 204 $\mu g\ l^{-1}$, 0.202 $\mu g\ l^{-1}$, 5.3 $mg\ l^{-1}$ and 7.53 respectively, and the mean concentrations for closed enclosures were 573 $\mu g\ l^{-1}$,

Table 5.1. Mean values with standard deviations for variables measured across all dates in an experiment carried out in enclosures in Little Mere, in summer 1992 (algal biovolumes are given in ten thousand of $\mu m^3 ml^{-1}$).

	Closed Enclosures				Open enclosures			
	0	1	2	4	0	1	3	4
	n=3	n=3	n=3	n=2	n=3	n=3	n=3	n=1
Chlorophyll a ($\mu g\ l^{-1}$)	2.1±1.5	6±5	15±9	21±12	12±6	12±4	27±14	31±18
Soluble R. P. ($\mu g\ l^{-1}$)	562±22	583±76	575±98	571±89	778±55	777±52	762±60	693±47
NH_4-N ($\mu g\ l^{-1}$)	30±21	25±34	86±129	88±116	233±56	193±90	191±94	190±83
Free-CO_2 ($\mu g\ l^{-1}$)	0.08±0.04	0.08±0.03	0.07±0.03	0.08±0.02	0.1±0.03	0.13±0.04	0.12±0.03	0.11±0.04
Dissolved-O_2 ($\mu g\ l^{-1}$)	8.6±1.6	8.7±2.7	8.7±1.9	8.4±1.7	5.5±2.3	5.7±2.7	5.9±2	6.4±2.5
pH	7.7±0.2	7.8±0.3	7.8±0.2	7.7±0.1	7.5±0.1	7.5±0.1	7.5±0.1	7.6±0.2
Cyanophyta	0.1±0.4	5±9	15±24	6±16	0±0	0.5±1.9	1±2	0±0
Chlorophyta	0.6±0.6	7.5±8	17±18	24±17	12±11	5±3	17±16	19±20
Chlamydomonas spp	0.2±0.4	0.3±0.4	1.3±0.9	1.6±2	8.7±10	2.7±2	9.7±15	6.1±6.5
Oocystis spp	0±0	1.9±2.9	2.6±3	3.2±3.5	0±0	0.3±1.2	0.3±1.1	0±0
Cryptophyta	59±40	88±102	143±227	178±311	19±19	60±182	228±455	178±146
C. ovata	49±38	77±103	127±229	174±310	15±19	56±183	219± 446	167±154
R. minuta	10±7.8	2.9±3	6±9	3.2±3	4±7	3±4	8.8±13	11±11
Bacillariophyta	8.7±7.6	141±253	160±322	88±80	57±49	44±33	71±55	185±194
S. ulna	4.2±5.7	7.3±9	9±7.7	6.3±5	16±25	21±30	35±41	38±38
A. granulata	1.6±4.2	130±253	140±321	75±73	7.8±26	0±0	4.8±7.8	1.8±3.7
N. palaea	1.5±4.1	2.6±3.4	4±4	1.3±0.9	23±22	19±22	22±41	88±128
Unidentified Flag.	8±10	26±41	83±177	164±272	9±5	6±8	11±18	16±18
D. magna ($ind.l^{-1}$)	22±28	14±19	0.5±0.9	4.9±12	51±70	7±5	28±42	3±2
D. magna ($\mu g\ l^{-1}$)	5629±12831	3065±5466	10±19	934±2584	31076±63821	18920±6100	12079±22772	113±134
D.hyalina ($ind.l^{-1}$)	4.3±6	17±18	7.3±9.5	8±8.8	47±33	177±165	34±44	33±35
Ceriodaphnia spp ($ind.l^{-1}$)	2±4	13±22	41±73	66±75	7±10	11±11	17±18	66±72
B. longirostris ($ind.l^{-1}$)	6.2±18	6±9	15±26	9±9	6±18	1±2	3±4	16±5
Cyclops spp ($ind.l^{-1}$)	41±43	47±28	107±64	88±61	41±34	47±34	186±139	187±110

Table 5.2. Summary of the effects of sediment, fish and sediment-fish interaction on the water chemistry, algal biovolume and zooplankton density in a series of enclosures in Little Mere in summer 1992 following repeated measures of 2-way ANOVA .Symbols *P<0.05;**P<0.01; ***P<0.001; NS=no significance. +,- signs show the direction of the effects with exposure to the sediment and fish density.

	Sediment	fish	fish/sediment interaction
Chlorophyll a($\mu g\ l^{-1}$)	+ ***	+ ***	+ *
Soluble reactive P($\mu g\ l^{-1}$)	+ ***	NS	NS
NH_4-N ($\mu g\ l^{-1}$)	+ ***	NS	+ *
Free-$C0_2$ ($\mu g\ l^{-1}$)	+ **	NS	NS
Dissolved-0_2 ($\mu g\ l^{-1}$)	- **	NS	NS
Cyanophyta ($\mu m^3 ml^{-1}$)	- *	+ **	+/- *
Chlorophyta($\mu m^3 ml^{-1}$)	NS	+ *	NS
Chlamydomonas spp ($\mu m^3 ml^{-1}$)	- ***	+ **	NS
Oocystis spp($\mu m^3 ml^{-1}$)	+ ***	NS	NS
Cryptophyta ($\mu m^3 ml^{-1}$)	NS	NS	NS
Cryptomonas ovata ($\mu m^3 ml^{-1}$)	NS	NS	NS
Rhodomonas minuta ($\mu m^3 ml^{-1}$)	NS	NS	NS
Bacillariophyta ($\mu m^3 ml^{-1}$)	NS	+ **	NS
Synedra ulna ($\mu m^3 ml^{-1}$)	- ***	+ **	+ *
Aulacoseira granulata ($\mu m^3 ml^{-1}$)	- ***	+ **	NS
Nitzschia palaea ($\mu m^3 ml^{-1}$)	+ ***	+ ***	+ ***
Unidentifed flagellate($\mu m^3 ml^{-1}$)	- **	+ *	NS
Daphnia magna ($ind.l^{-1}$)	NS	- *	NS
Daphnia magna ($\mu g\ l^{-1}$)	+ *	- **	NS
Daphnia hyalina ($ind.l^{-1}$)	+ **	- **	+/- *
Ceriodaphnia spp.($ind.l^{-1}$)	NS	+ ***	NS
Bosmina longirostris ($ind.l^{-1}$)	NS	+ ***	NS
Cyclops spp.($ind.l^{-1}$)	+ **	+ ***	+ *

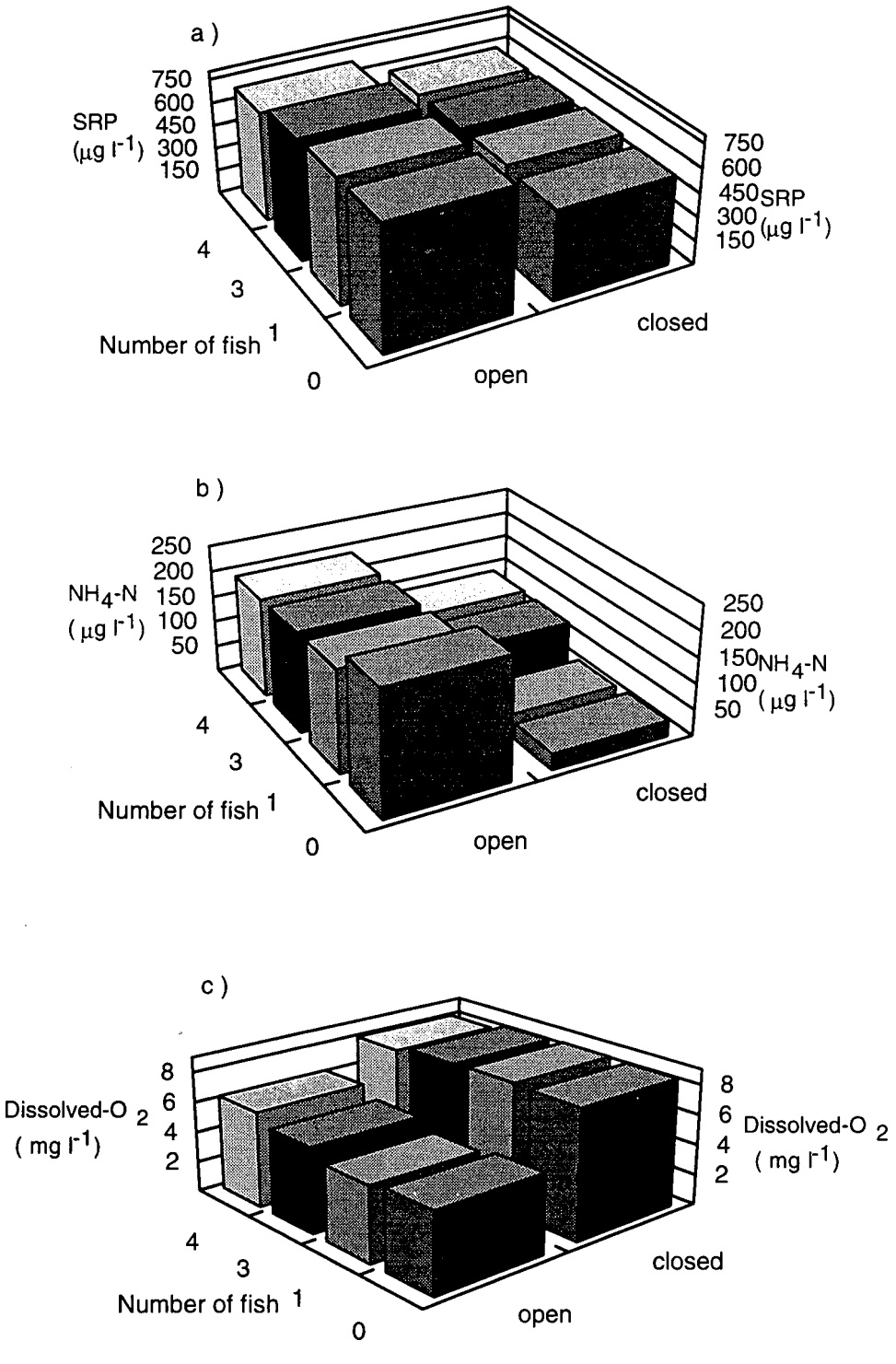

Fig.5.1 The effects of exposure to sediment (open) and isolation from sediment (closed), and increasing density of fish added on the concentrations of a) soluble reactive phosphorus b) ammonium-nitrogen and c) dissolved-oxygen in an experiment carried out in Little Mere in summer 1992.

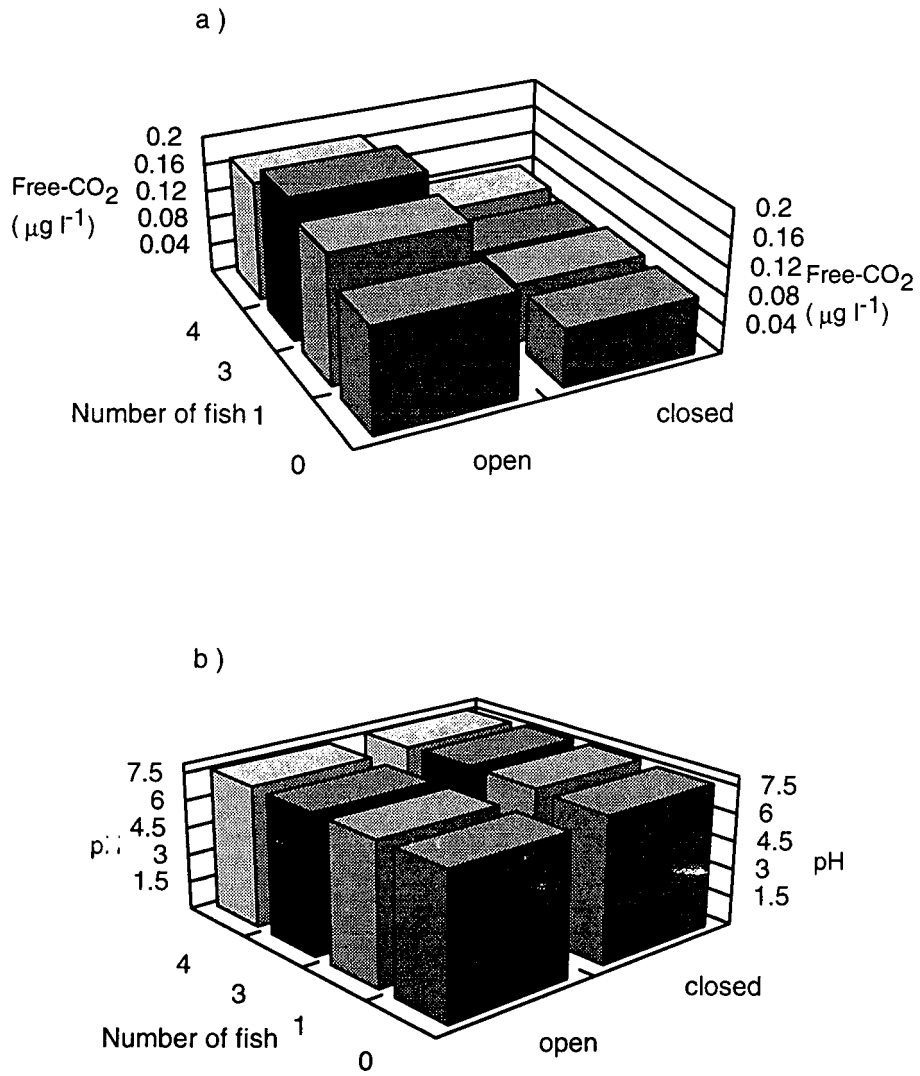

Fig 5.2 The effects of exposure to sediment (open) and isolation from sediment (closed), and increasing density of fish added on concentration of a) free-carbon dioxide and b) pH in an experiment carried out in Little Mere in summer 1992.

54 μg l^{-1}, 0.11 μg l^{-1}, 8.44 mg l^{-1} and 7.74 respectively. Increasing fish densities had no significant effects on SRP, NH_4-N, dissolved-O_2, free-CO_2 concentrations and pH (P=0.150, P=0.34, P=0.57, P=0.787 and P= 0.089 respectively). The interaction effects of presence of the sediment and fish were significant for NH_4-N and pH (P=0.04 and P=0.0004 respectively) but not significant for SRP, dissolved-O_2 or free-CO_2 (P=0.17, P=0.17 and P=0.92 respectively) (Table 5.2).

5.3.3 Response of chlorophyll a and phytoplankton biovolumes

Repeated measures of ANOVA performed on chlorophyll a concentrations revealed highly significant effects of the presence of sediment, increasing fish densities and the interaction of the sediment and fish (P=0.0001, P=0.0001 and P=0.022 respectively) (Table 5.2). Concentrations increased in both open and closed treatments with increasing fish densities, especially in open enclosures. The mean concentrations in closed enclosures at 0, 1, 3 and 4 fish densities were 2 μg l^{-1}, 6.3 μg l^{-1}, 14.4 μg l^{-1} and 21.2 μg l^{-1} respectively, and the mean concentrations in open enclosures at 0, 1, 3 and 4 fish densities were 12.4 μg l^{-1}, 11.4 μg l^{-1} 27 μg l^{-1} and 31 μg l^{-1} respectively (Fig. 5.3a).

Cyanophytes, though present, were not dominant among the phytoplankton community at any time during the experiment. The presence of sediment, increasing fish densities and interaction of sediment and fish had significant effects on cyanophyte biovolume (P=0.002, P=0.01 and P=0.025 respectively) (Table 5.2). Whilst its biovolume decreased significantly in the presence of sediment, there was an increase with increasing fish densities, except in four-fish enclosures (Fig.5.3c). The mean concentrations in open enclosures with increasing fish densities were 0 μm^3 m l^{-1}, 5660

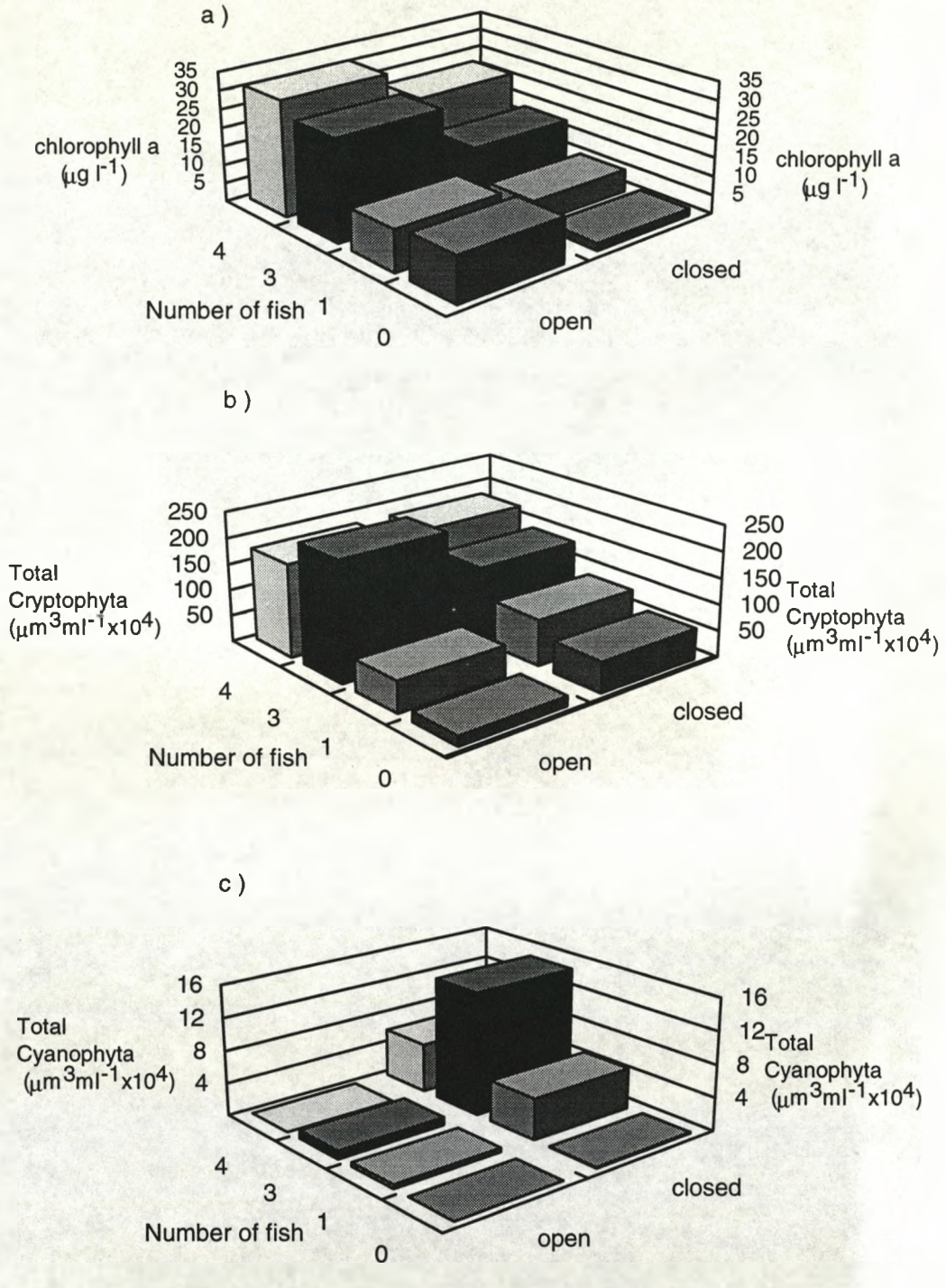

Fig.5.3 The effects of exposure to sediment (open) and isolation from sediment (closed), and increasing density of fish on a) chlorophyll a concentration and biovolumes of b) total Cryptophyta and c) total Cyanophyta in an experiment carried out in Little Mere in summer 1992.

μm^3 ml^{-1}, 9570 μm^3 ml^{-1} and 0 μm^3 m l^{-1} respectively, and the mean concentrations for closed enclosures with increasing fish densities were 1400 μm^3 ml^{-1}, 50000 μm^3 m l^{-1}, 151000 μm^3 ml^{-1} and 62200 μm^3 ml^{-1} respectively. *Anabaena* sp, *Aphanizomenon flos-aquae* and *Oscillatoria* sp. were the species of Cyanophyta variously present.

Chlorophytes were not predominant phytoplankters either in the presence or absence of sediment during the experiment. Repeated measures of two-way ANOVA performed on Chlorophyta biovolume revealed no significant increase with the presence or absence of sediment (P=0.78). Whilst increasing fish densities significantly increased chlorophyte biovolume, the interaction effect of sediment and fish had no significant effect on (P=0.025 and P=0.36 respectively) (Table 5.2) (Fig. 5.4a). The mean concentrations for closed enclosures with increasing fish densities were 6700 μm^3 ml^{-1}, 74600 μm^3 ml^{-1}, 173000 μm^3 ml^{-1} and 238000 μm^3 ml^{-1} respectively, and the mean concentrations for open enclosures at 0, 1, 3 and 4 fish densities were 123000 μm^3 ml^{-1}, 49400 μm^3 ml^{-1}, 166000 μm^3 ml^{-1} and 194000 μm^3 ml^{-1} respectively. In all enclosures the increase in Chlorophyta biovolume was mainly in *Chlamydomonas* spp. and *Oocystis* spp. Repeated measures of two-way ANOVA employed on these species revealed significant effects of the presence of sediment on the biovolume of these species (P=0.001 and P=0.006 respectively) (Table 5.2). Whilst the biovolume of *Chlamydomonas* spp. was higher in open enclosures than in closed enclosures, the opposite was the case for *Oocystis* spp. Whilst increasing fish density had significant effects on biovolume of *Chlamydomonas* spp. (P=0.013), it did not have a significant effect on biovolume of *Oocystis* spp. (P=0.143). (Fig. 5.4b and 4c) Interaction of sediment and fish was not significant for either *Chlamydomonas* spp. or *Oocystis*

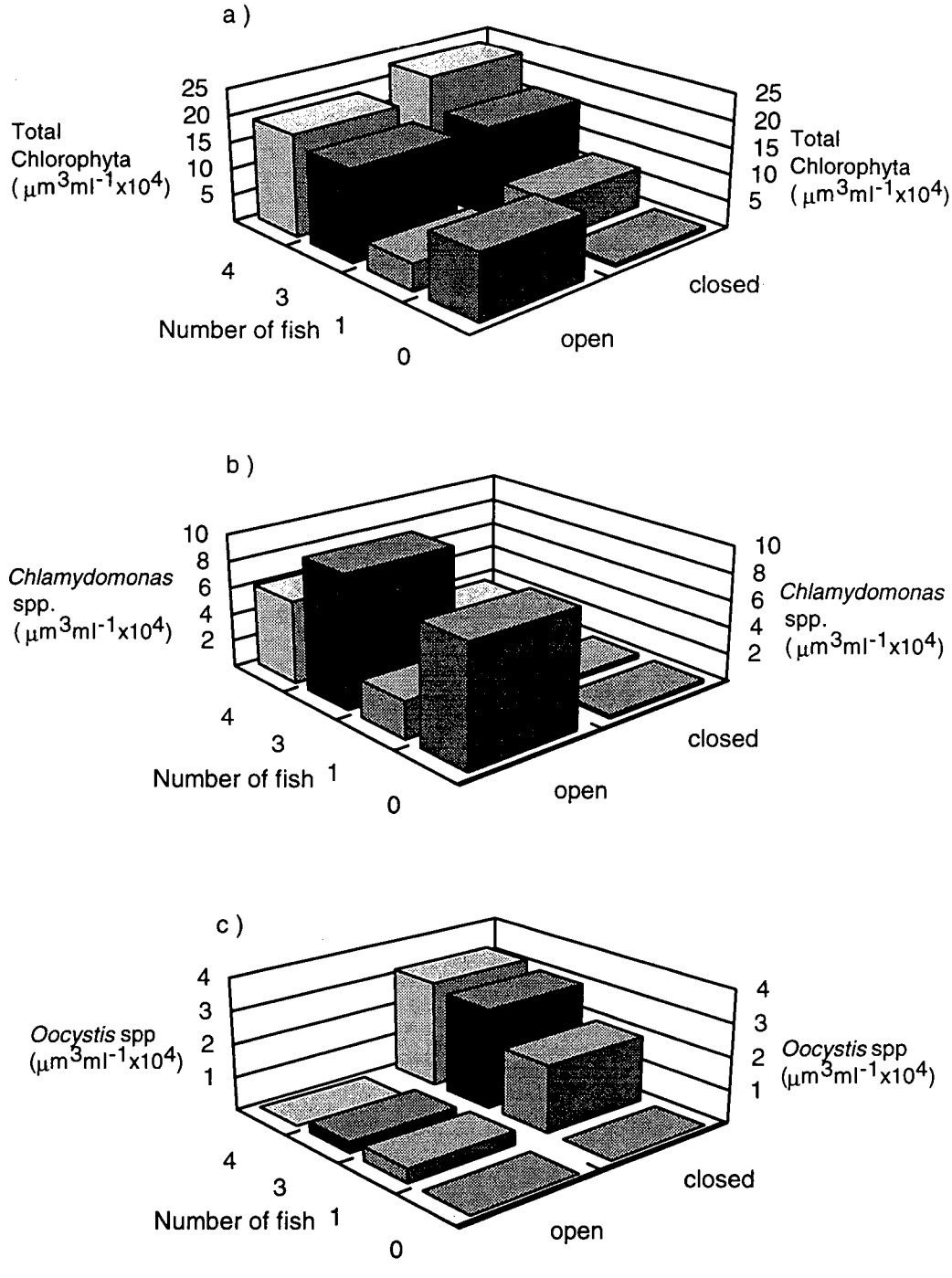

Fig. 5.4 The effects of exposure to sediment (open) and isolation from sediment (closed), and increasing density of fish on biovolumes of a) total Chlorophyta b) *Chlaymodomonas* spp. and c) *Oocystis* spp. in an experiment carried out in Little Mere in summer 1992.

spp. (P=0.078 and P=0.24 respectively) (Table 5.1).

The biovolume of Cryptophyta co-dominated (with diatoms) the phytoplankton community regardless of the presence or absence of sediment. Repeated measures of two-way ANOVA revealed no significant effects of either the sediment, fish or interaction of sediment and fish treatments on the biovolume of Cryptophyta (P= 0.96, P=0.304 and P=0.88 respectively) (Table 5.2) (Fig. 5.3b). Cryptophyta were mainly represented by *Cryptomonas ovata* and *Rhodomonas minuta.* Repeated measures of two-way ANOVA revealed the same pattern for these species in that none of the treatments were significant for either *Cryptomonas ovata* (P=0.92, P=0.34 and P=0.88 respectively) or *Rhodomonas minuta* (P=0.49, P=0.2 and P=0.85 respectively).

Diatoms were the predominant phytoplankters throughout the experiment regardless of the presence or absence of sediment. Repeated measures of two-way ANOVA revealed no significant effect of the presence of sediment on diatom biovolume (P=0.1). The effect of increasing fish densities and the interaction effect of sediment and fish significantly increased diatom biovolume (P=0.005 and P=0.018 respectively) (Table 5.2) (Fig. 5.5a). The biovolumes of *Synedra ulna*, *Nitzschia palaea* and *Aulacoseira granulata* made the biggest contribution to diatom biovolume and repeated measures of two-way ANOVA revealed significant effects of the presence of sediment on these species' biovolume (P=0.0001, P=0.0001 and P=0.0002 respectively). Increasing fish densities significantly increased the biovolume of these species (P=0.006, P=0.001 and P=0.01 respectively) (Table 5.2). Whilst biovolumes of *Synedra ulna* and *Nitzschia palaea* dominated in the open enclosures with increasing fish densities, the biovolume of *Aulacoseira granulata* dominated the closed

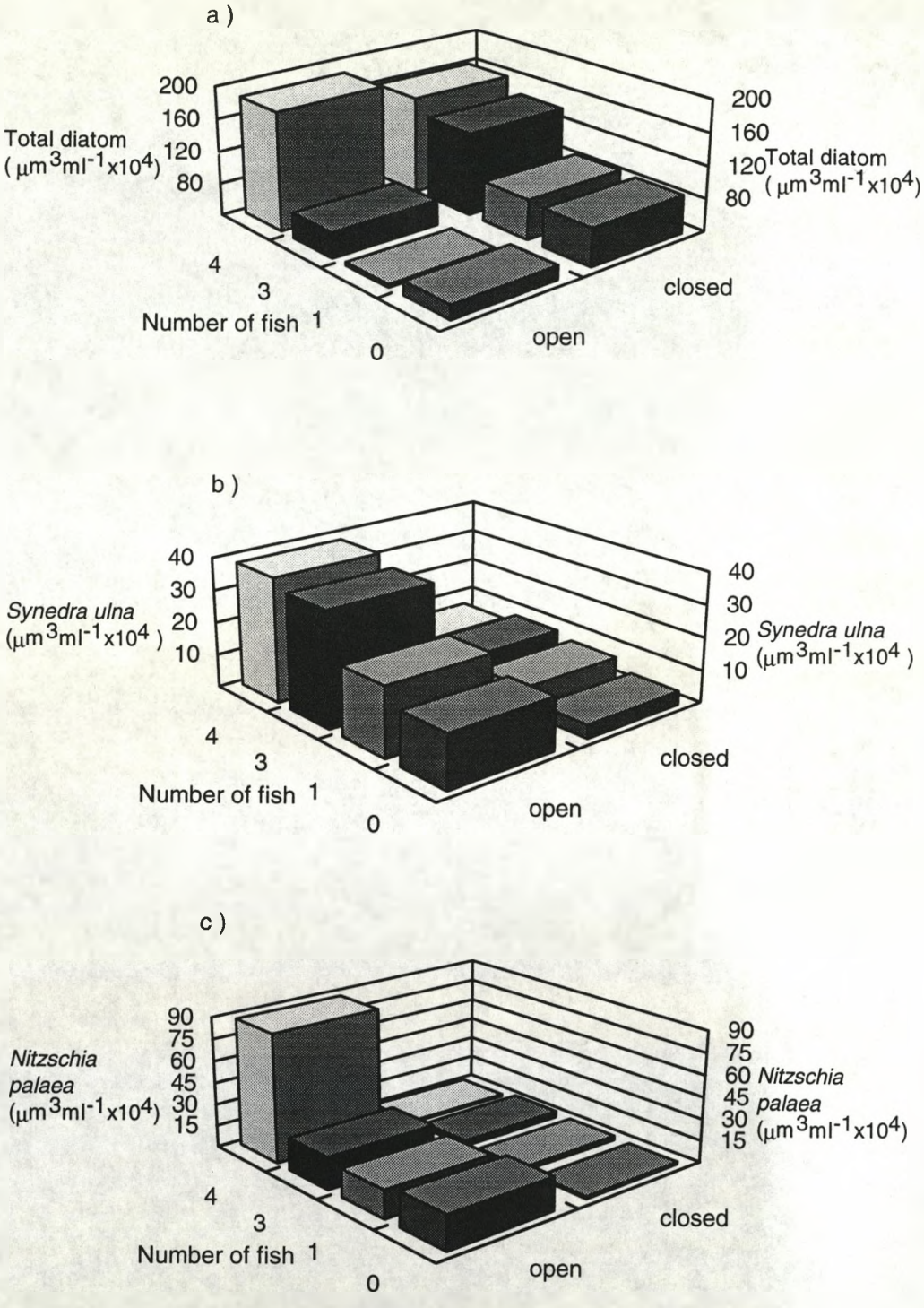

Fig.5.5 The effects of exposure to sediment (open) and isolation from sediment (closed), and increasing density of fish on biovolumes of a) total diatoms, b) *Synedra ulna* and c) *Nitzschia palaea* in an experiment carried out in Little Mere in summer 1992.

enclosures (Fig. 5.5b, 5c and 6a respectively). The interaction effects of sediment and fish were significant for *Synedra ulna,* and *Nitzschia palaea* (P=0.039 and P=0.001 respectively) but not significant for *Aulacoseira granulata* (P=0.16). Different diatom species thus reacted to the presence of sediment in different ways.

Repeated measures of two-way ANOVA performed on unidentified flagellates, showed that the presence of sediment and increasing fish densities significantly changed the biovolume of these organisms (p=0.002 and p=0.02 respectively) (Table 5.2) (Fig 5.6b).The biovolume of unidentified flagellates was significantly higher in the closed enclosures than in the open enclosures. The mean values in closed enclosures with increasing fish densities were 78000 μm^3 ml^{-1}, 263000 μm^3 ml^{-1}, 831000 μm^3 ml^{-1} and 1640000 μm^3 ml^{-1} respectively, and the mean values for the open enclosures at 0, 1, 3 and 4 fish densities were 37100 μm^3 ml^{-1}, 62200 μm^3 ml^{-1}, 112000 μm^3 ml^{-1} and 158000 μm^3 ml^{-1} respectively. The interaction of sediment and fish had no significant effect on biovolume of unidentified flagellates. (P=0.056).

In summary (Table 5.3), the effects of the presence or absence of sediment on percentage biovolume of the main phytoplankton groups during the experiment were that Cyanophyta, though not predominant, were significantly more abundant in the closed enclosures than the open enclosures. Chlorophyta did not dominate in the phytoplankton community either and were unaffected by the presence or absence of sediment. The biovolumes of Cryptophyta and diatoms were predominant in the phytoplankton communities of both the open and closed enclosures but the sediment treatment did not significantly change their biovolumes. The biovolume of unidentified flagellates made an important contribution to the phytoplankton community in the

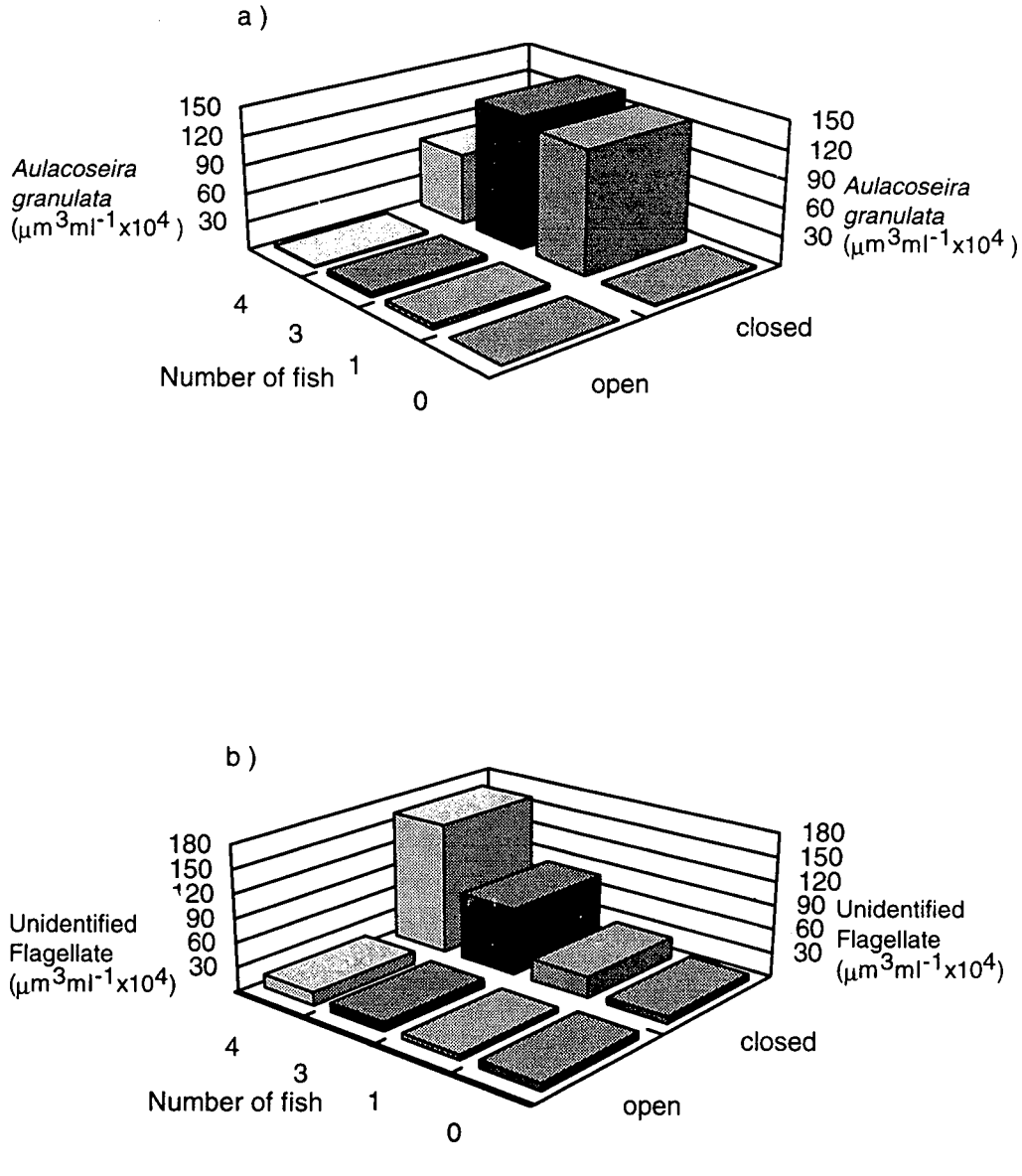

Fig.5.6 The effects of exposure to sediment (open) and isolation from sediment (closed), and increasing density of fish added on biovolumes of a) *Aulacoseira granulata* and b) Unidendified flagellates in an experiment carried out in Little Mere in summer 1992.

Table 5.3. Composition of the phytoplankton community (Mean % of total biovolume ± S.D.) in closed and open enclosures in an experiment carried out in Little Mere in summer 1992.

	Closed enclosures	Open enclosures
Cyanophyta	2.3±2.6	0.22±0.4
Chlorophyta	3.8±2.5	6.1±3.5
Cryptophyta	38±31	55±72
Bacillariophyta	35±37	35±21
Unidentified flagellate	21±26	4±3.2

Table 5.4. Comparision of *Daphnia magna* density, in open water and within water lily beds in Little Mere (Data based on three summer 1992 samplings, n:12).

	Open water	**Refuge**	**t-test comparison**
D. magna (ind.l^{-1})	6±10	69±27	***

*** P< 0.001

closed enclosures but was significantly decreased in the open enclosures.

5.3.4 Response of the zooplankton community

Several zooplankton species responded to the treatments (Table 5.2). In all treatments filter-feeding cladocerans dominated, including *Daphnia magna, D. hyalina, Bosmina longirostris* and *Ceriodaphnia* spp. The only copepods were *Cyclops* spp.

D.magna was the most abundant filter feeder. Repeated measures of two-way ANOVA were performed on both its density and biomass. Whilst the presence of sediment had no significant effect on *D.magna* density (P=0.159), its biomass significantly increased in the open enclosures (P=0.038). With increasing fish densities, both the density and the biomass of *D. magna* significantly decreased (P=0.044 and P=0.015 respectively). The interaction effects of the sediment and fish were not significant for either *D. magna* density or *D.magna* biomass (P=0.24 and P=0.80 respectively) (Table 5.2).Mean values in the closed enclosures for *D. magna* density with increasing fish densities were 22 ind. l^{-1}, 14 ind. l^{-1}, 1 ind. l^{-1} and 5 ind. l^{-1} respectively. In the open enclosures mean values for *D. magna* density with increasing fish densities were 51 ind. l^{-1}, 7 ind.l^{-1}, 28 ind. l^{-1} and 3 ind. l^{-1} respectively (Fig. 5.7a). The closed-enclosures mean values for *D. magna* biomass with increasing fish densities were 6400 μg l^{-1}, 3100 μg l^{-1}, 11 μg l^{-1} and 934 μg l^{-1} respectively, and the open enclosures mean values for *D. magna* biomass at 0, 1, 3 and 4 fish densities were 31000 μg l^{-1}, 19000 μg l^{-1}, 12000 μg l^{-1} and 114 μg l^{-1} respectively (Fig. 5.7b).

Other cladocerans which responded significantly to the treatments were *D. hyalina, Bosmina* spp. and *Ceriodaphnia*. Density of *D. hyalina* significantly changed with

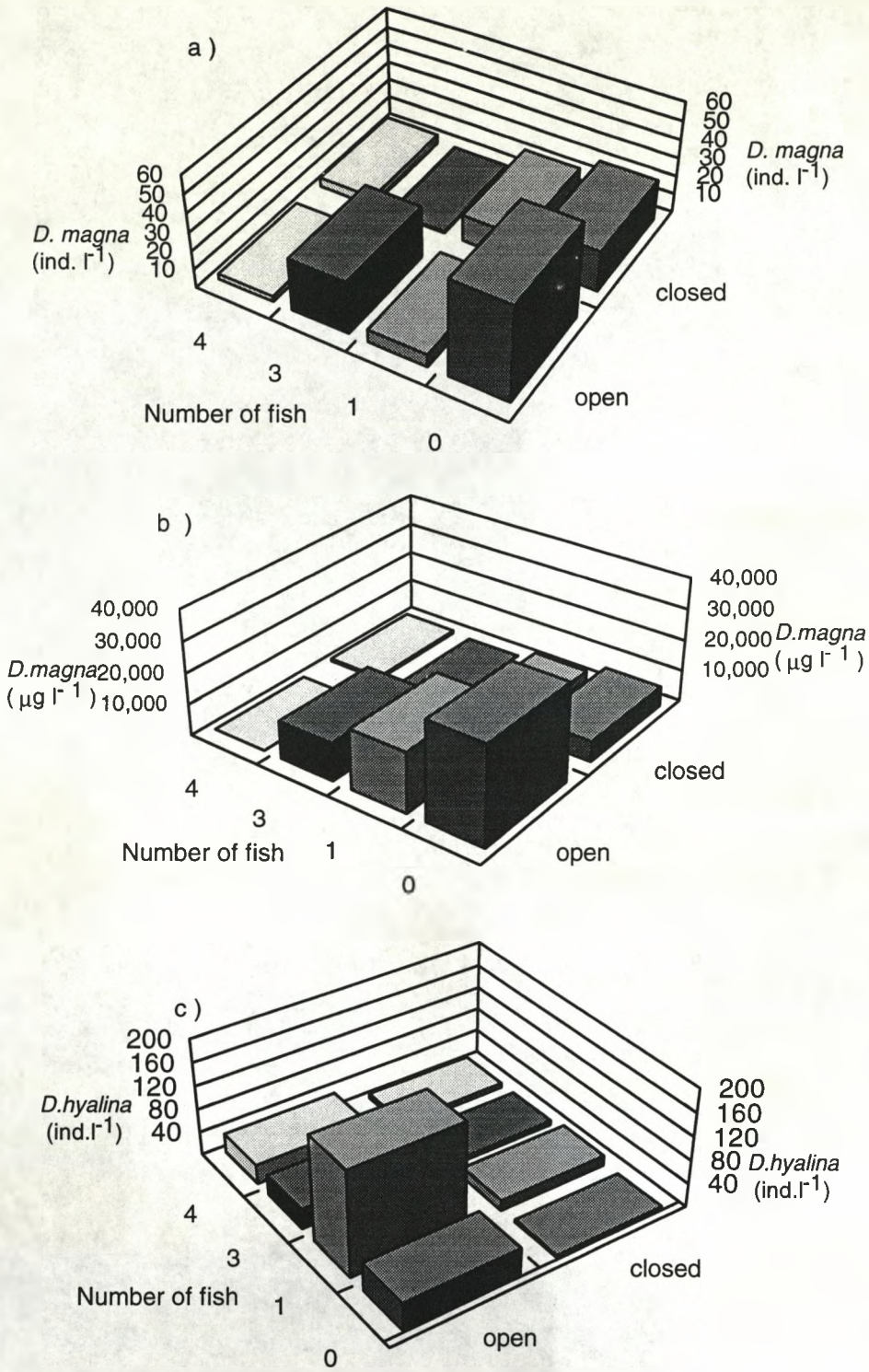

Fig.5.7 The effects of exposure to sediment (open) and isolation from sediment (closed), and increasing density of fish added on density of a) *Daphnia magna*, biomass of b) *Daphnia magna* and density of c) *Daphnia hyalina* in an experimentcarried out in Little Mere in summer 1992

presence of sediment, increasing fish densities and the interaction effect of sediment and fish (P=0.004, P=0.012 and P=0.03 respectively) (Table 5.2). Whilst density of *D. hyalina* significantly increased with sediment treatment, its density significantly decreased with increasing fish densities (Fig 5.7c). The closed enclosure mean values for *D. hyalina* with increasing fish densities were 5 ind. l^{-1}, 17 ind. l^{-1}, 7 ind. l^{-1} and 8 ind. l^{-1} respectively, and the mean values of *D. hyalina* in the open enclosures at 0, 1, 3 and 4 fish densities were 47 ind. l^{-1}, 177 ind. l^{-1}, 34 ind. l^{-1} and 33 ind. l^{-1} respectively. The presence of the sediment had no significant effect on *Bosmina* spp. and *Ceriodaphnia* spp. numbers (P=0.327 and P=0.44 respectively). With increasing fish densities, densities of these species significantly increased (P=0.006 and P=0.002). The interaction effect of sediment and fish was not significant for either *Bosmina* spp. or *Ceriodaphnia* spp (Table 5.2). The mean values of *Bosmina* spp. in the closed enclosures with increasing fish densities were 6 ind. l^{-1}, 6 ind. l^{-1}, 15 ind. l^{-1} and 9 ind. l^{-1} respectively, and the mean values in the open enclosures with increasing fish densities were 6 ind. l^{-1}, 1 ind. l^{-1}, 4 ind. l^{-1} and 16 ind. l^{-1} respectively (Fig 5.8b). *Ceriodaphnia* spp. mean values in the closed enclosures with increasing fish densities were 2 ind. l^{-1}, 13 ind. l^{-1}, 41 ind. l^{-1} and 66 ind. l^{-1} respectively, and the mean values in the open enclosures with increasing fish densities were 7 ind. l^{-1}, 11 ind. l^{-1}, 17 ind. l^{-1} and 66 ind. l^{-1} respectively (Fig 5.8a).

Repeated measures of two-way ANOVA revealed that density of *Cyclops* spp. significantly increased with the presence of sediment, increasing fish densities and the interaction effect of sediment and fish (P=0.002, P=0.0001 and P=0.013 respectively) (Table 5.2). The mean densities of *Cyclops* spp. in the closed enclosures with increasing fish densities were 41 ind. l^{-1}, 47 ind. l^{-1}, 107 ind. l^{-1} and 88 ind. l^{-1}

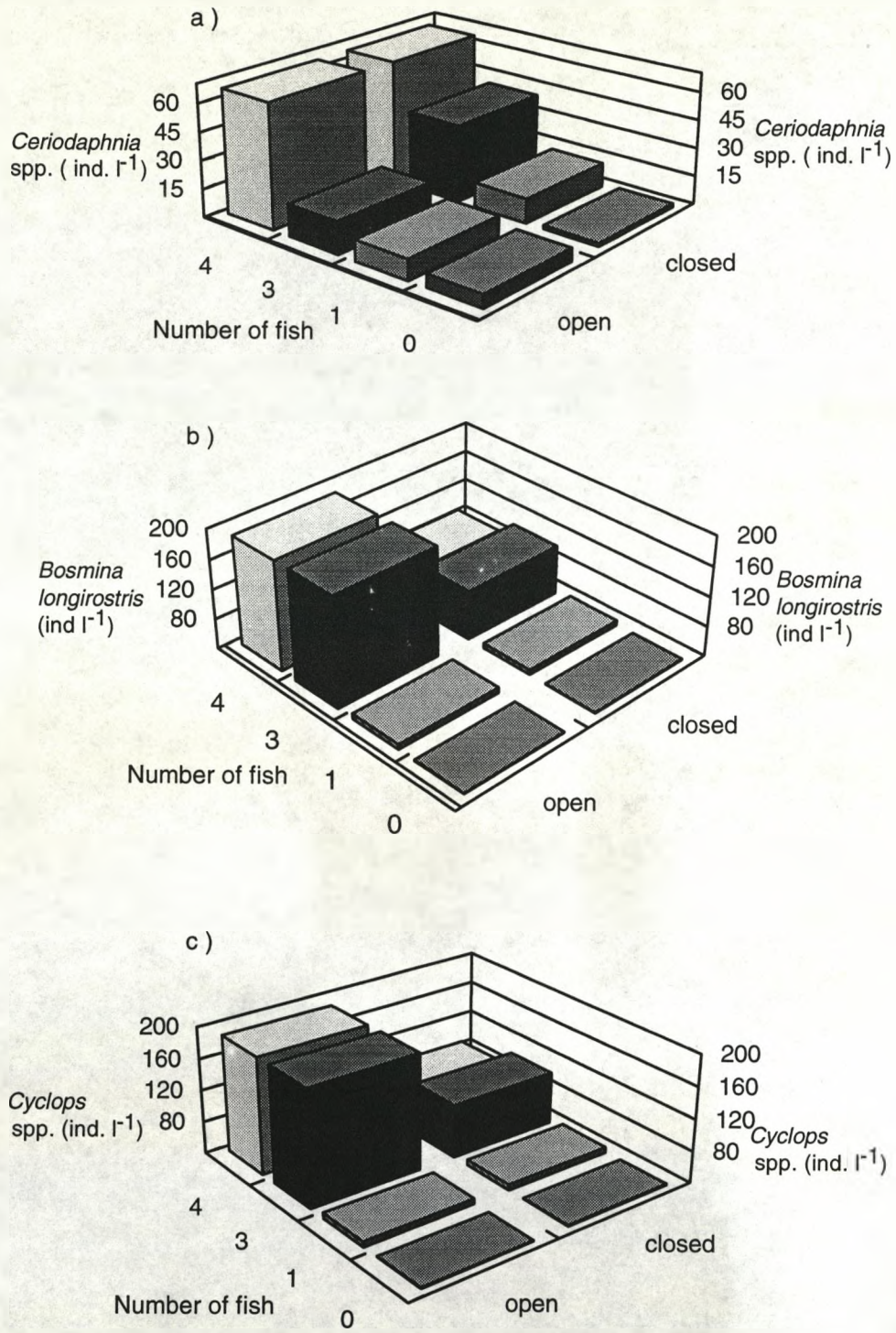

Fig.5.8 The effects of exposure to sediment (open) and isolation from sediment (closed), and increasing density of fish added on densities of a) *Ceriodaphnia* spp., b) *Bosmina longirostris* and c) *Cyclops* spp. in an experiment carried out in Little Mere in summer 1992.

respectively, and the mean values in the open enclosures with increasing fish densities were 41 ind. l^{-1}, 46 ind. l^{-1}, 186 ind. l^{-1} and 187 ind. l^{-1} respectively (Fig 5.8c).

5.4. Discussion

The results of this enclosure experiment can be discussed in the frame of the hypotheses which were initially put forward. These were that the presence of sediment would result in increasing nutrient concentrations; that increasing fish density would increase the biomass of phytoplankton with an increasing cyanophyte dominance through removal of *Daphnia* grazing and might lead to a phytoplankton-dominated turbid phase.

The highly reduced sediment surface was probably the main nutrient source in the lake water following the sewage effluent diversion especially during summer when the inflow dries up. Enclosures open to the sediment surface showed increased concentrations of SRP, NH_4 free- CO_2 and decreased concentrations of dissolved-O_2 and of pH. The low dissolved-O_2 is likely to have promoted the release of phosphate from the sediment (Mortimer, 1941; 1942; Boström *et al.* 1982) and denitrification of nitrate to ammonium (Mortimer, 1941; 1942) thus nitrate is virtually absent from the lake in summers (Chapter 2). Free-CO_2 concentrations were much higher in the open enclosures than in the closed ones because of the existence of a large contact area of organic sediment, relative to the depth and water volume and because organic matter from the previous sewage effluent could fuel bacterial respiration and release abundant free-CO_2. In many lakes control of external nutrient loading has not necessarily led to reduction in lake nutrient concentrations (Sas, 1989; Jeppesen *et al.* 1991) because of internal loading. Internal nutrient loading was a major feature of Little Mere as reflected by a considerable reduction in concentrations of SRP and NH_4 in the closed enclosures. Monitoring of the lake over four years has shown drastic reductions in mean annual SRP and NH_4 concentrations before and three years after the effluent

diversion. Values were 1951 μg l^{-1} and 440 μg l^{-1} respectively in 1990 before diversion and 62 μg l^{-1} and 120 μg l^{-1} in 1993 after diversion (Carvalho *et al.* in press). Partly this is due to the effluent diversion but dissolved-O_2 concentration has begun to increase, suggesting that release from the sediment is also declining .

Increasing fish density increased the biomass of the phytoplankton community. A significant increase in chlorophyll a concentration was recorded in both open and closed enclosures with increasing fish density, probably due to reduced zooplankton grazing pressure. Inclusion of the sediment surface in open enclosures led to greater increases in chlorophyll a concentration than in closed enclosures. The greater increase in chlorophyll a concentrations in open enclosures might be due to resuspension of a large supply of benthic-living algae from the sediment. The biggest contributor to the diatom community of open enclosures, was *Nitzschia palaea* which is a sediment-living algae and was significantly more abundant in open enclosures than closed ones. Another reason might be the nitrogen limitation. The ammonium concentrations in closed enclosures were far lower than in the open ones and might have had an important role in controlling the algal growth in closed enclosures. The N:P ratio of a water body can give an indication of which of these nutrients is likely to be limiting algal cells require elements in relatively fixed proportions though there is some variation between algae (Rhee & Gotham, 1980). The ratios of NH_4:SRP showed indications of nitrogen limitation in closed enclosures. Many diatom species are superior phosphorus competitors but they are inferior competitors for nitrogen compared with natural co-occurring species of green and blue-green algae (Tilman *et al.* 1986) Thus, lower availability of nitrogen and the absence of a supply of sediment-living algae might explain the lower chlorophyll a concentrations in closed enclosures

compared to open enclosures.

Differences in the percentage composition of the phytoplankton community suggest that biovolumes of cryptophytes and diatoms were not affected in Little Mere by the presence of sediment. They were equally present in both open and closed enclosures where they dominated the algal community. Nor was increasing fish density a key factor in controlling cryptophytes. Lack of grazer effects on cryptophytes might be due to high growth rates of algae compensating for grazing losses. Although the overall effect of exposure to sediment was not significant for the biovolume of diatoms, each species responded differently. The different responses of the diatom species may be explained by differences in species-specific nutrient requirements. Different diatoms are favoured by different Si:P ratios (Tilman *et al.* 1986; Kilham, 1971). This ratio is likely to have differed in open and closed enclosures. Pennate diatoms, like *Synedra* and *Nitzschia* (Tilman *et al.* 1982), are favoured by high Si:P ratios which may have been generated by the presence of sediment in this experiment though the opposite is more likely to be true. *Nitzschia palaea* is typically a sediment-living diatom and its population may have come from the availability of suitable inoculum in the sediment. *Aulacoseira granulata* is considered to be a poor competitor at low N,P or CO_2 concentrations (Talling, 1976; Tilman *et al.* 1986) but its biovolume was reduced in the presence of sediment and relatively high values of these variables. Reduced grazing pressure on diatoms at increasing fish densities resulted in an increase in its biovolume. It is probably edible to large cladocerans (Balls, 1986).

The remaining large contribution to the algal community in closed enclosures was by unidentified flagellates whose abundance was greatly reduced in the presence of the

sediment. The reasons for this are not clear.

Shallow lakes and ponds, particularly those that are organically rich, like Little Mere, tend to favour green algae (King, 1970). Jensen *et al.* (1994) have suggested increasing dominance of Chlorophyta in shallow hypertrophic lakes with increasing availability of nutrients and carbon dioxide released from the sediments. They also suggested that high growth rates make Chlorophyta superior competitors even when nutrients are low and pH is high. The present chlorophyte results are not consistent these earlier findings in that the contribution of Chlorophyta to the algal community in the experiment was small and not affected by the presence or absence of the sediment, despite the differences in response of the dominant chlorophytan species. In the experiment carried out in summer 1993 with increased pH (Chapter 7, Beklioglu & Moss, 1995), there was chlorophytan dominance especially in untreated lake water and at high pH (pH 11). This might suggest that the reason for increasing Chlorophyta dominance in eutrophicating lakes must be more complex in that supply of nutrients from the sediments was prevented during the experiment and carbon dioxide concentrations were maintained at very low values (Chapter 7; Beklioglu & Moss, 1995). Because they are small, edible and generally readily grazed, there was an increasing chlorophytan biovolume with increasing fish density, except for *Oocystis* spp. which was not affected by increasing fish density. The presence of a gelatinous envelope might make *Oocystis* spp. grazer resistant (Porter, 1975).

Cyanophytes were not predominant in the algal community. Although there were inocula from upstream Mere Mere, cyanophytes were unimportant in Little Mere, disappearing in the spring at the same time as the increase in zooplankton density,

perhaps due to the high grazing pressure (Carvalho, 1994) in the absence of fish. This has been recorded elsewhere (Jeppesen *et al.* 1990a). Cyanophytes decreased in the open enclosures compared with the closed. This might be attributed to presence of high free-CO_2 concentrations. Shapiro (1990a) concluded that cyanophytes tend to be favoured over other algal groups by low free-CO_2 concentrations because they have more efficient CO_2-concentrating mechanisms (Raven 1985) among other reasons. In Little Mere, elevated pH in an enclosure experiment, despite the presence of ample inocula and other favourable conditions for cyanophytes (low N:P ratio, very low flushing rate etc.), resulted in no predominance of cyanophyte. On the contrary their biovolume was significantly reduced at high pH values (pH 10 and pH 11) (Chapter 7; Beklioglu & Moss, 1995) as also in hypertrophic Danish Lakes (Jensen *et al.* 1994). The reason for this might be sought in the complexity of water bodies which confound generalisations based on simple cause and effect relationships. Increasing fish density led to an increase in biovolume of cyanophytes suggesting that they may have been grazed in the absence of fish. There is much controversy about the suitability of cyanophytes as food for zooplankton. They have been shown to affect growth and mortality of grazers by producing toxic chemicals (Nizan *et al.* 1986), by being poorly assimilated (Arnold, 1971) and by inhibiting feeding on co-occurring foods (Fulton, 1988). Despite this, it has been found that large *Daphnia* can control population growth of filamentous blue-green algae in nutrient-rich lake water (Jeppesen *et al.* 1990a). This also appears to have occurred in the open water of Little Mere (Carvalho, 1994).

Increasing fish density decreased the density of *Daphnia* as recorded elsewhere (Gulati, 1990) in both open and closed enclosures. Density of both *D. magna, D.*

hyalina and biomass of *D. magna* were greatly reduced by increasing fish density. Both species are large enough to be taken easily by planktivorous fish. Both in the lake water and the enclosures *D. magna*, was the most abundant species, with its large body-size and bright red colour, probably due to presence of haemoglobin, which is produced in response to low dissolved oxygen (Carvalho, 1984). This pigmentation increases vulnerability to visual predation by fish (Kerfoot, 1980) and along with their large body size, *D. magna* must have been very easy prey for roach in the enclosures. Relative decrease in biomass of *D. magna* and density of *D. hyalina* in the closed enclosures might be due to reduced food concentration because some *Daphnia* species also feed on bacteria on derived from sediment (Brendelberger, 1991). At low food levels *Daphnia* may lose weight and reduce its filtering rate (Gliwicz, 1990b).

Other, smaller, filter feeding zooplankters (*Ceriodaphnia* spp. and *Bosmina longirostris*) showed conventional increases with increasing fish density as proposed by the size-efficiency hypothesis (Brooks and Dodson, 1965).

5.4.1 Conclusion

In Little Mere, despite the improvement of water quality following the sewage effluent diversion, concentrations of SRP and NH_4-N remained high and concentration maxima were found during summer probably because of low dissolved-oxygen concentrations due to large populations of bacteria deoxygenating the sediment surface. Anaerobic conditions promoted release of P from the sediment and also denitrification (Chapter 4). These trends were also observed in open enclosures. Four years after the sewage effluent diversion, Little Mere has shown considerable reduction in nutrient concentrations (Carvalho *et al.* in press) as was observed in closed enclosures.

Dissolved-oxygen concentration has been gradually increasing in Little Mere and this has led to fish recolonization, which was simulated in the enclosures by introducing fish. Fishing operations in the lake early in 1993 caught 11 roach 17 perch 2 tench. Fishing later in 1993 showed that fish (predominantly perch) had moved in large numbers from the upstream Mere Mere (Chapter 8). The combination of residual high nutrient concentrations and high fish populations might be expected to result in high algal crops through reduction of grazing pressure by *Daphnia*, as was found in the experiment. There has been no cyanophyte dominance in the lake so far nor was there in the enclosure experiment. Increased pH in an enclosure experiment in Little Mere in summer 1993 showed that the lack of cyanophytes was not related to high free-CO_2 (Chapter 7; Beklioglu & Moss, 1995). However, other algae grew well in the enclosures with the increasing fish density. Thus, recovery of the fish population might shift the lake to a phytoplankton dominated-phase from its previous clear-water phase, through breakdown of cladoceran buffering mechanisms. Eventually, reduced nutrient concentrations following completion of decomposition of organic matter at the sediment surface might result in a return to nutrient limitation of algal growth as is the case in upstream Mere Mere. There was some evidence of reduced chlorophyll a in the closed enclosures due to shortage of nitrogen. In such a shallow lake, however nutrients are always likely to be plentiful as all sediment surfaces release nutrients to some extent. This, however is the possible scenario that can be drawn from the experimental results.

But what the experiment did not take into account was the existence of large stands of macrophytes. Little Mere has large stands of macrophytes (Chapter, 8). Having open enclosures in the experiment, without macrophytes, illustrated by comparison the

important functions of aquatic vegetation for high water quality, and offered evidence for Moss (1991) and Scheffer's *et al.* (1993) theory of the presence of alternative stable clear-water and turbid water states at high nutrient concentrations in shallow lakes. Although the lake had a huge potential for algal growth, which was shown in open enclosures in the absence of the macrophytes and presence of fish, in the lake water algal growth was negligible. As Scheffer *et al.* (1993) suggested, turbid-water is not a just function of high nutrient loading. Both reduction of external nutrient loading and manipulation of fish community have been successful in reducing phytoplankton populations and creating clear-water and even allowing the growth of macrophytes in many shallow lakes (Perrow *et al.* 1994; Meijer *et al.* 1994). Turbid-water states with phytoplankton dominance and a clear-water states with macrophyte dominance seem to be alternative stable states in shallow eutrophic lakes and the presence of strong and diverse macrophyte stands plays a key role in maintaining the water quality. Macrophyte-dominated lakes appear to be able to resist the effects of increased nutrient loading and stabilize a clear-water state through several mechanisms. Provision of refuges for grazers against predation by fish, (Timms & Moss, 1984, Balls *et al.* 1989, Irvine *et al.* 1989; Moss, 1991) is one possibility. This may have played an important role in the stability of clear-water in Little Mere. The importance of aquatic plants as refuges for high populations of *Daphnia* was shown in Little Mere by comparison of *D. magna* counts from open water and from within water-lily beds (Table 5.4). The number of *D. magna* was significantly higher in water-lily beds than in open water. Macrophytes are resilient to changes in nutrient loading (Balls *et al.* 1989) and also help maintain low phytoplankton standing crops directly through luxury nutrient uptake and competition for nutrients (Ozimek *et al.* 1990). In summer 1993 luxury nutrient uptake by macrophytes played an important

role in Little Mere (Chapter 6). Recovery of the lake's fish population, largely with perch but also pike, probably due to provision of suitable habitat for spawning (Grimm, 1989), is another very important buffer mechanism of macrophytes for piscivorous fish may maintain the zooplanktivorous fish population at reduced levels. Another suggested stabilizing function of macrophytes is allelopathy (van Vierssen *et al.* 1994) which might have had an important role in Little Mere though this was not examined. In Little Mere, abundance of cyanophytes does not seem to be function of either nutrients or low-free-CO_2/high pH as was demonstrated in the 1993 pH experiment (Chapter 7; Beklioglu & Moss, 1995). Thus, the lake may have been held in a clear-water state with high nutrient concentrations because of the presence of these buffering mechanisms of macrophytes in the lake. A switch to cyanophyte-dominated turbid water seems at present to be unlikely, unless some unexpected effects take place.

A possible future scenario for Little Mere might thus be clear-water, maintained at high, though perhaps decreasing, nutrient concentrations, due to the presence of large stands of macrophytes and their manifold stabilizing mechanisms - provision of refuges for *Daphnia* in the presence of fish, luxury uptake of nutrients, providing suitable habitat for top-predators such as pike and through other possible mechanisms.

The results of the experiment suggest that macrophyte-dominated clear water is an alternative stable state to turbid water despite high nutrient concentrations. Presence of strong and diverse macrophyte stands has a key role in restoring eutrophic shallow lakes at various nutrient concentrations. Therefore, more studies are needed to understand the growth of macrophytes and the reasons why macrophytes sometimes

collapse after their regrowth, following improvement measures which includes reduction of external nutrient loading and food-web manipulation.

Chapter 6: The effects of increasing densities of the fish, the sediment and the plant on water chemistry, phytoplankton and zooplankton communities in mesocosms in Little Mere in 1993

6.1 Introduction

Hypertrophic shallow lakes with severe algal blooms do not usually respond instantaneously to a decrease in nutrient loading (Mardsen, 1989; Moss *et al.* 1989; Jeppesen *et al.* 1990b). The reasons for resilience in maintenance of the existing state are different from lake to lake and depend for example, on the lake morphology, or sometimes counter-active environmental changes. In Lake Enäjärvi, Finland, the sedimentary record indicates that the lake nutrient balance had deteriorated due to lowering of the lake water level in 1928 despite measures taken to reduce phosphorus level (Salonen *et al.* 1993). The previous condition of the water body in terms of nutrient concentrations, the structure of food web and the degree of nutrient reduction may also be important. Food web structure may hamper recovery through the feeding strategies of the more abundant fish species, which are generally zooplanktivorous, and benthivorous fish which may disturb the bottom of eutrophic lakes (Grimm, 1989). Most importantly, lack of macrophytes seems to play an important role in resistance to recovery through a major reduction or complete loss of piscivorous fish, because of lack of spawning environment (Grimm & Backx, 1990). This major reduction in top predators may result in an increase in planktivorous and benthivorous fish which causes further deterioration of water quality through increase in nutrient concentrations by resuspension of sediment and declines in filter-feeding grazers, which in turn may result in an increase in algal biomass. The overall result is a continuation of turbid water with a lower chance of creating an appropriate environment for redevelopment of vigorous vegetation. Many shallow lakes in Europe have lost their vegetation through eutrophication. The reason for loss of macrophyte

stands seem to be more complex than simple shading out by algae as nutrient loading increases (Balls *et al.* 1989). Moss suggested (1991) that nutrient increase is important for loss of the phase 1 (short growing plants) which seem to be more vulnerable to the nutrient loadings. The phase 2 (taller-growing plants) seem to be able to resist further increase in loading without being replaced by phytoplankton (Balls *et al.* 1989). Tall-plant dominated systems appear to be buffered against such changes through several mechanisms (see Fig.1.1) (Irvine *et al.* 1989; Moss, 1990).

The turbid-state characterized by high algal biomass, like the clear-state dominated by aquatic plants, seems to be very stable and resistant to external changes suggesting the existence of two alternative stable states (Scheffer, 1990, Moss, 1990) in nutrient rich shallow lakes. This has important implications for the possibilities of restoring eutrophic lakes. Nutrient reduction alone may result in little recovery even if the nutrient level is considerably reduced. In such cases restoration needs be catalysed by additional measures to bring the ecosystem to the alternative clear-water state (Scheffer *et al.* 1993, Hosper & Meijer, 1993). This may be achieved by food-web manipulation (Shapiro *et al.* 1975).

Although changes are still occurring, four years of monitoring, along with the results of enclosure experiments in Little Mere, indicate a continuing stability of the clear-water state which has persisted from the time prior to sewage effluent diversion (Chapter 2, 3, 4, 5 and 7). Despite still relatively high nutrient concentrations and an invasion of planktivorous fish, large plant stands persist (Chapter 8). It is uncertain, however, whether the lake will stay clear in the future. Short-term enclosure experiments might not mimic the long-term development of the lake, but they help to

explain some of the changes in the whole system. In the present (1993) enclosure experiment I have examined the possibility for future stability of the clear-water phase with its large macrophyte stands, recovering fish populations and decreasing but still high nutrient concentrations following the effluent diversion (Carvalho *et al.* in press; Chapter 8).

The experimental design was based on the similar predictions to those the previous year's (1992) experiment that the effect of progressive reoxidation of the sediment surface would be the decline of release of nutrients and carbon dioxide from it. Two different types of enclosures were used- some open to the sediment surface and some sealed (closed) from it- at three different fish densities. However in the 1993 experiment, open enclosures with macrophyte stands were used to reflect the current state of the lake with its increased plant growth. Closed enclosures were used to anticipate the future lake when the sediment surface is predicted to become increasingly less active in nutrient regeneration and to provide a macrophyte-free control. Increasing fish predation on zooplankters was expected in closed enclosures which also lacked macrophytes. In open enclosures, I hypothesised that fish predation would be weakened by the availability of the macrophyte refuges. I hypothesised that despite progressive reoxidation, the sediment surface would still be the main nutrient source for the lake through internal nutrient loading especially in summer when the inflow dries up. The sediment surface would thus supply potential for a high phytoplankton crop but this potential might not be fully realised due to the presence of the macrophytes in open enclosures where there would be lower phytoplankton crops. In turn I hypothesised that the future, oxidized sediment with lower CO_2 release would allow pH to rise and favour cyanophytes in water that would remain relatively

nutrient rich.

6.2. Methods

6.2.1 Design and apparatus

The experiment was carried out between 12 July and 10 August 1993, in eighteen polyethylene enclosures. The features of enclosures and the design of the experiment were the same as in the previous year's experiment and were described in Chapter 5.

The experimental design was 2x3 factorial with 2 types of enclosures and three different fish densities. Half of the enclosures were open to the sediment representing the present situation of the lake water, and the other half the enclosures were closed to the sediment to simulate the future lake water in which the sediment surface is predicted to become oxidised and less active in release of nutrients. Perch (*Perca fluviatilis* L.), 10-12 cm total length, were caught by seining in Little Mere and immediately placed in appropriate enclosures at three different population sizes, 0 fish, 2, and 4 fish per enclosure. Each treatment was carried out in triplicate, making a total of eighteen enclosures. The enclosures were placed randomly within a wooden frame in the middle of the lake, where the summer 1992 experiment had been carried out. In summer 1993, however, the area was mainly covered by *Potamogeton berchtoldii*. Thus, the open enclosures had high densities of the macrophyte which were not present in the previous's year experiment.

6.2.2 Sampling methods

The sampling methods used were the same as in the previous's year experiment

described in Chapter 5. In addition, soon after the experiment had finished, the plants of the open enclosures were harvested and kept in separate plastic bags before being dried at 100 °C and weighed.

The methods for water chemistry were described in Chapter 2 and the methods for phytoplankton and zooplankton sampling were described in Chapter 3.

6.2.3 Statistical analyses

The methods for the statistical analyses were described in Chapter 5.

6.3. Results

6.3.1 Initial status of enclosures

Repeated measures of one-way of ANOVA on the initial chlorophyll a, SRP and NH_4 concentrations revealed no significant differences. Biovolume of cyanophytes, chlorophytes and diatoms were not significantly different among the enclosures either. Repeated measures of one-way ANOVA also performed on densities of *D.hyalina* and *Polyphemus pediculus* revealed no significant differences among the enclosures.

The enclosures remained intact throughout the experiment. The fish survived in both open and closed enclosures except for a few which died and were quickly replaced with the similar-sized ones.

6.32 Response of chemical variables

Table 6.1 shows mean values ± S.D. of variables measured in the experiment and Table 6.2 the results of repeated measures of two-way ANOVA. Repeated measures of two-way ANOVA performed on the water chemistry showed that the presence of the sediment had no significant effects on SRP, NH_4-N, free-CO_2 or pH (P=0.94, P=0.94, P=0.69 and P=0.47 respectively) (Table 6.2). Increasing fish densities significantly decreased the concentrations of SRP and NH_4-N (P=0.05 and P=0.04 respectively). Neither free-CO_2 concentration nor pH were changed with increasing fish densities (P=0.69 and P=0.47 respectively) (Table 6.2). The interaction effects of presence of the sediment and increasing densities of fish were not significant for any of these chemical variables (P= 0.061, P=0.31, P=0.08 and P=0.09 respectively) (Table 6.2) (Fig 6.1a, 1b, 2a and 2b). Whilst the concentration of dissolved O_2 significantly decreased in the presence of sediment (open enclosures) and there were significant

Table 6.1. Mean values with standard deviations for variables measured across all dates in an experiment carried out in enclosures in Little Mere, Cheshire in summer 1993. Algal volumes are given in ten thousands of $\mu m^3 l^{-1}$.

	Closed Enclosures			Open enclosures		
	0 n=3	2 n=3	4 n=3	0 n=3	2 n=3	4 n=3
Chlorophyll a ($\mu g\ l^{-1}$)	5.2±5	54±64	57±44	6±4	7±7	23±18
Soluble R. P. ($\mu g\ l^{-1}$)	103±117	20±45	6± 9	68±79	37±23	28±13
NH_4-N ($\mu g\ l^{-1}$)	348±498	60±114	74±102	300±708	193±593	17±20
Free-CO_2 ($\mu g\ l^{-1}$)	0.04±0.05	0.006±0.007	0.004±0.006	0.02±0.02	0.01±0.02	0.03±0.03
Dissolved-O_2 ($\mu g\ l^{-1}$)	8.3±2.1	9.3±2.1	9.6±1.4	8.3±2.1	9±0.9	6±.3
pH	8.3±0.6	8.9±0.6	9±0.4	8.8±0.8	8.6±0.6	8.4±0.7
Cyanophyta ($\mu m^3 ml^{-1}$)	7±23	24±76	27±71	4±12	3±7.6	0.5±0.8
Chlorophyta ($\mu m^3 ml^{-1}$)	67±118	306±429	904±871	13±16	9.5±11	42±65
Chlamydomonas spp($\mu m^3 ml^{-1}$)	15±32	16±20	70±104	9.5±10	7.9±10	23±36
Cryptophyta ($\mu m^3 ml^{-1}$)	133±203	100±169	258±81	62±80	68±82	109±150
Cryptomonas ovata ($\mu m^3 ml^{-1}$)	71±113	74±114	214±256	47±61	40±53	98± 142
Rodomonas minuta ($\mu m^3 ml^{-1}$)	62±167	27±35	45±41	16±26	29±43	19±121
Bacillariophyta ($\mu m^3 ml^{-1}$)	78±129	150±270	265±416	53±134	20±21	245±287
Aulacoseira granulata($\mu m^3 ml^{-1}$)	43±84	72±187	101±183	5.3±16	0±0	38±71
Nitzschia palaea ($\mu m^3 ml^{-1}$)	7.8±20	6.8±14	2.7±4.4	45±134	8.3±9.6	48±63
Unidentified Flag. ($\mu m^3 ml^{-1}$)	120±307	271±442	41±59	2.8±4.8	8.2±14	5±7.9
Daphnia hyalina ($ind.l^{-1}$)	85±112	4±4	4.3±12	57±65	24±21	8±12
Daphnia cuculata ($ind.l^{-1}$)	17±17	8±20	4 ±6	9±11	3 ±3	1±2
Polyphemus pediculus ($ind.l^{-1}$)	66±89	129±141	104±119	22±24	48±55	32±43
Ceriodaphnia spp ($ind.l^{-1}$)	27±69	66±156	91±169	3±3	25±37	54±83
Bosmina longirostris ($ind.l^{-1}$)	2±18	6±10	64±106	1±1	0.3±1	3±8
Cyclops spp ($ind.l^{-1}$)	11±7	44±73	99±124	36±42	47±36	106±117
Chydorus ovalis ($ind.l^{-1}$)	0.2 ±0.6	2.1±5	0.1±0.3	5.2±12	9±12	17±25
Eurycercus lamellatus ($ind.l^{-1}$)	7.3±11	6±13	1±3	5±4	9±14	13±17
Simocephalus spp ($ind.l^{-1}$)	0.2±0.6	3±7	0±0	12±15	6±9	6±10
Sida crystallina ($ind.l^{-1}$)	0.1±0.3	0.2±0.6	0.2±0.6	3± 4	5.3±10	7±6

Table 6.2. Summary of the effects of sediment, fish and sediment-fish interaction on the water chemistry, algal biovolume and zooplankton density in a series of enclosures in Little Mere in summer 1993 following repeated measures of 2-way ANOVA. Symbols *P<0.05;**P<0.01; ***P<0.001; NS=no significance. +,- signs show the direction of the effects with exposure to or decrease with exposure to sediment fish density.

	Sediment	fish	fish/sediment interaction
Chlorophyll a ($\mu g\ l^{-1}$)	- **	+ ***	+/- **
Soluble reactive P($\mu g\ l^{-1}$)	NS	- *	NS
NH_4-N ($\mu g\ l^{-1}$)	NS	- *	NS
Dissolved-0_2 ($\mu g\ l^{-1}$)	- **	NS	- *
Free-$C0_2$ ($\mu g\ l^{-1}$)	NS	NS	NS
pH	NS	NS	NS
Cyanophyta ($\mu m^3 ml^{-1}$)	NS	NS	NS
Chlorophyta ($\mu m^3 ml^{-1}$)	- ***	NS	NS
Chlamydomonas spp ($\mu m^3 ml^{-1}$)	NS	+ *	NS
Cryptophyta ($\mu m^3 ml^{-1}$)	- **	+ **	+/- *
Crytomonas ovata ($\mu m^3 ml^{-1}$)	- *	+ *	NS
Rhodomonas minuta ($\mu m^3 ml^{-1}$)	NS	NS	NS
Bacillariophyta ($\mu m^3 ml^{-1}$)	NS	+ *	NS
Aulacoseira granulata ($\mu m^3 ml^{-1}$)	- *	NS	NS
Nitzschia palaea ($\mu m^3 ml^{-1}$)	+ **	NS	NS
Unidentifed flag. ($\mu m^3 ml^{-1}$)	- **	NS	NS
Daphnia hyalina ($ind.l^{-1}$)	- **	- ***	NS
Daphnia cuculata ($ind.l^{-1}$)	NS	- **	NS
Polyphemus pediculus ($ind.l^{-1}$)	- **	NS	NS
Ceriodaphnia spp.($ind.l^{-1}$)	NS	+ ***	NS
Bosmina longirostris ($ind.l^{-1}$)	- ***	+ ***	NS
Cyclops spp.($ind.l^{-1}$)	NS	NS	NS
Chydorus ovalis ($ind.l^{-1}$)	+ ***	NS	NS
Eurycercus lamellatus ($ind.l^{-1}$)	+ **	NS	NS
Simocephalus spp.($ind.l^{-1}$)	+ **	NS	NS
Sida crystallina ($ind.l^{-1}$)	+ ***	NS	NS

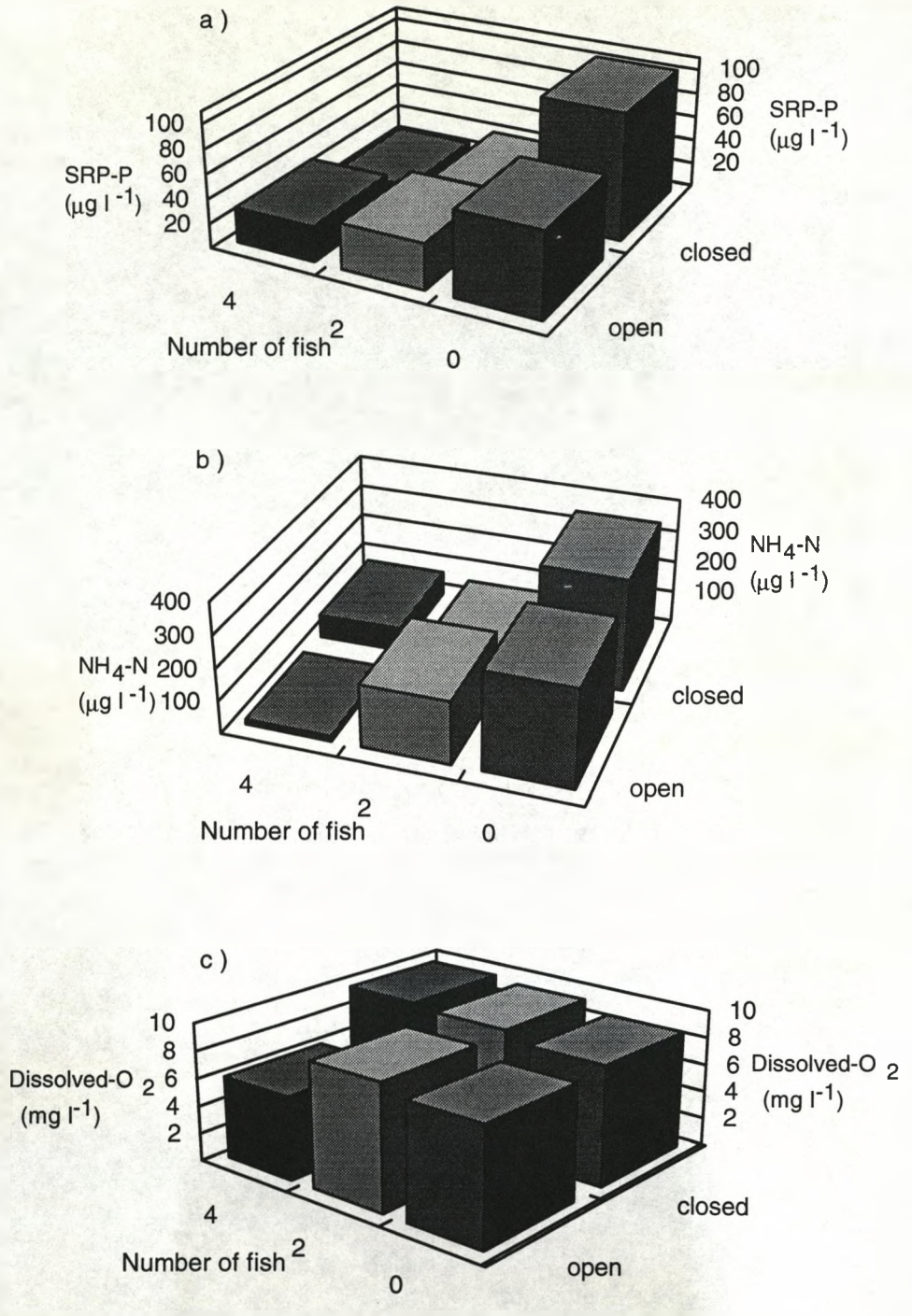

Fig.6.1 The effects of exposure to sediment and the presence of plant (open) and isolation from sediment and the plant (closed) and increasing density of fish added on the concnetrations of a) soluble reactive phosphorus, b) ammonium-nitrogen and c) dissolved-oxygen in an experiment carried out in Little Mere in summer 1993.

interaction effects of the presence of sediment and fish (P=0.013 and P=0.02 respectively), increasing fish densities had no significant effect (P=0.11) (Table 6.2) (Fig. 6.1c).

6.3.3 Response of chlorophyll a and phytoplankton biovolumes

Repeated measures of ANOVA performed on chlorophyll a concentrations revealed highly significant effects of the presence of sediment, increasing fish densities and the interaction of the sediment and fish (P=0.005, P=0.0002 and P=0.01 respectively) (Table 6.2). Whilst the concentration of chlorophyll a increased greatly with increasing fish densities, the concentrations of chlorophyll a were significantly reduced in the presence of the sediment. The mean chlorophyll a concentrations of closed enclosures at 0, 2 and 4 fish densities were 5 $\mu g\ l^{-1}$, 54 $\mu g\ l^{-1}$ and 57 $\mu g\ l^{-1}$ respectively and the mean concentrations in open enclosures at 0, 2 and 4 fish densities were 6 $\mu g\ l^{-1}$, 7 $\mu g\ l^{-1}$ and 23 $\mu g\ l^{-1}$ (Fig. 6.3a).

Although diatoms were predominant phytoplankters of the open enclosures, repeated measures of two-way ANOVA revealed no significant effects of the presence of sediment or significant interaction effects of the sediment and fish (P=0.34 and P=0.69 respectively). Increasing fish densities significantly increased the diatom biovolume (P=0.04) (Table 6.2 and Fig. 6.3c). The mean biovolumes of diatoms for 0, 2 and 4 fish densities were $6.5 \times 10^5\ \mu m^3\ ml^{-1}$, $8.5 \times 10^5\ \mu m^3\ ml^{-1}$ and $2.55 \times 10^6\ \mu m^3\ ml^{-1}$ respectively. The increase in the biovolume of diatoms was mainly due to *Aulacoseira granulata* and *Nitzschia palaea*. Whilst the presence of sediment significantly reduced the biovolume of *Aulacoseira granulata* (P=0.039), it significantly increased the biovolume of *Nitzschia palaea* (P=0.01). Neither the increasing fish density (P=0.33

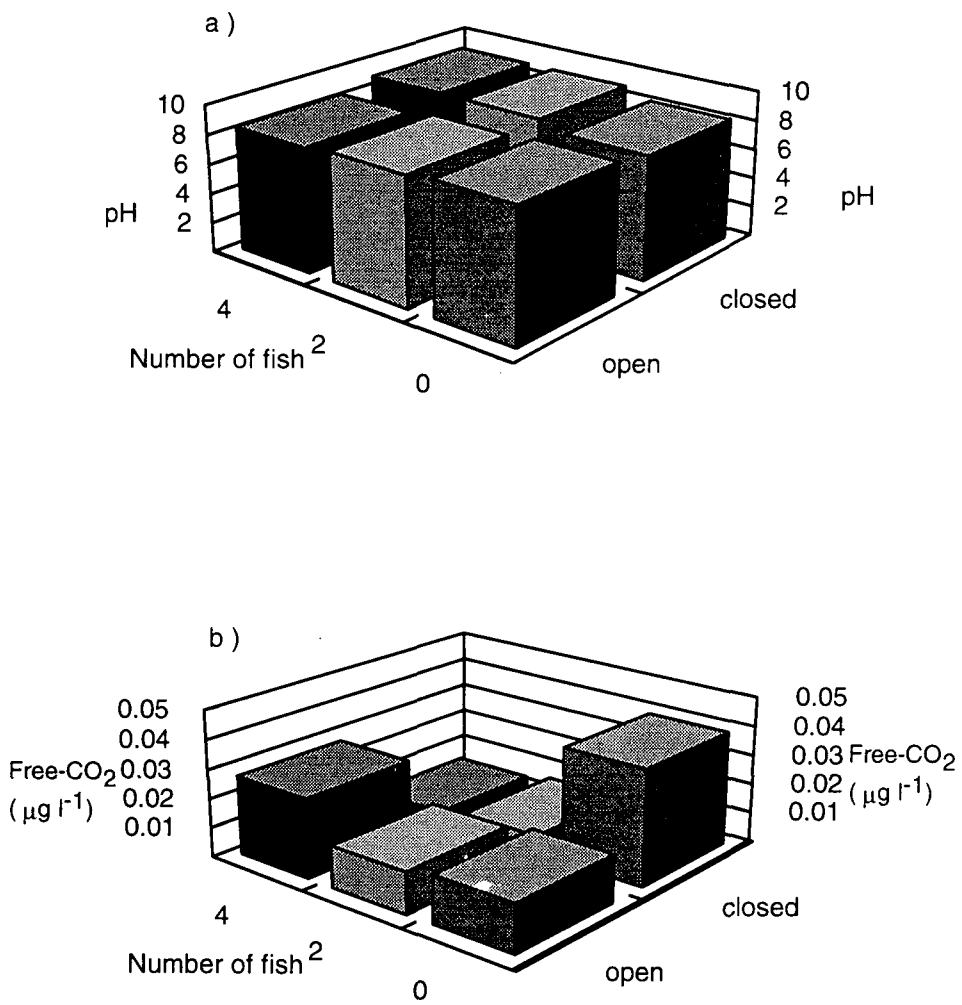

Fig.6.2 The effects of exposure to sediment and the presence of plant (open) and isolation from sediment and the plant (closed), and increasing density of fish added on a) pH and concentration of b) free-carbon dioxide in an experiment carried out in Little Mere in summer 1993.

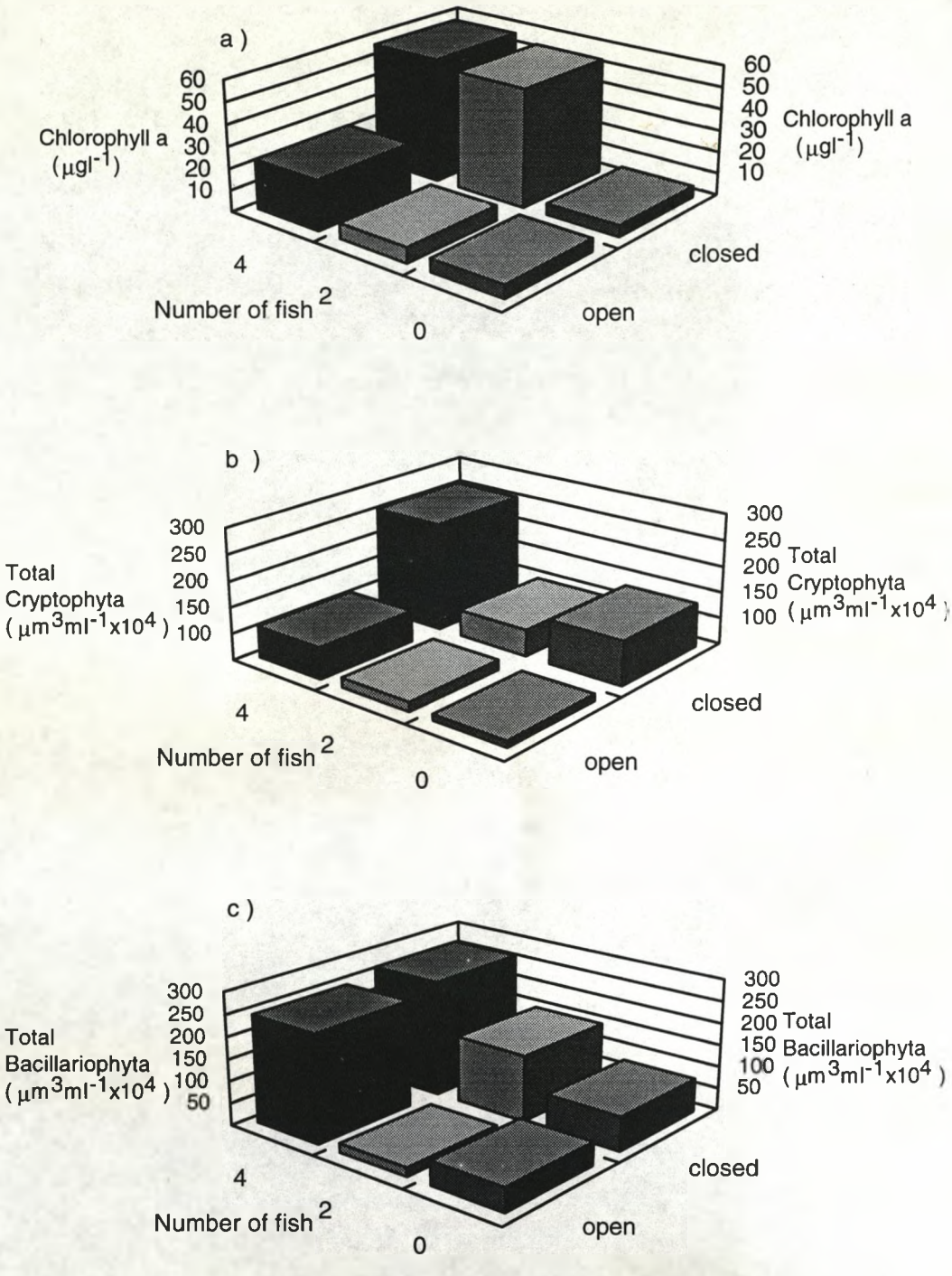

Fig.6.3 The effects of exposure to the sediment and the presence of plant (open), and isolation from sediment the plant (closed) and increasing density of fish added on concentration of a) chlorophyll a,and biovolumes of c) total Cryptophyta and c) total Bacillariophyta, in an experiment carried out in Little Mere in summer 1993.

and P=0.94 respectively) nor the interaction effect of sediment and fish (P=0.94 and P=0.84 respectively) were significant for the biovolume of these species (Table 6.2 and Fig. 6.6a, b).

Chlorophyta were predominant phytoplankters in the absence of sediment (closed enclosures). Repeated measures of two-way ANOVA performed on Chlorophyta biovolume revealed a significant decrease in the presence of sediment (P=0.0005). Neither increasing fish densities nor the interaction effect of sediment and fish had significant effects on the biovolumes of Chlorophyta (P=0.07 and P=0.13 respectively) (Table 6.2 and Fig. 6.4b). The mean biovolumes of Chlorophyta for closed and open enclosures were 4.3 x 10^6 μm^3 ml^{-1} ind 2.2 x 10^5 μm^3 ml^{-1} respectively. In all enclosures the increase in chlorophyte biovolume was mainly in *Chlamydomonas* spp. Repeated measures of two-way ANOVA employed on the species biovolume revealed no significant effects of the presence of sediment on this species' biovolume (P=0.12). Whilst the biovolume of *Chlamydomonas* significantly increased with increasing fish densities (P=0.05), the interaction effect of sediment and fish had no significant effect (P=0.32) (Table 6.2 and Fig. 6.4c)

The biovolume of Cryptophyta was also prominent in the phytoplankton community of closed enclosures, along with that of diatoms. Repeated measures of two-way ANOVA revealed highly significant effects of the presence of sediment, increasing fish densities and interaction of sediment and fish (P=0.006, P=0.05 and P=0.04 respectively) (Table 6.2). Whilst Cryptophyta biovolume significantly decreased with the presence of sediment, it significantly increased with increasing densities of fish. The mean biovolumes in closed enclosures at 0, 2 and 4 fish densities were 1.3 x 10^6

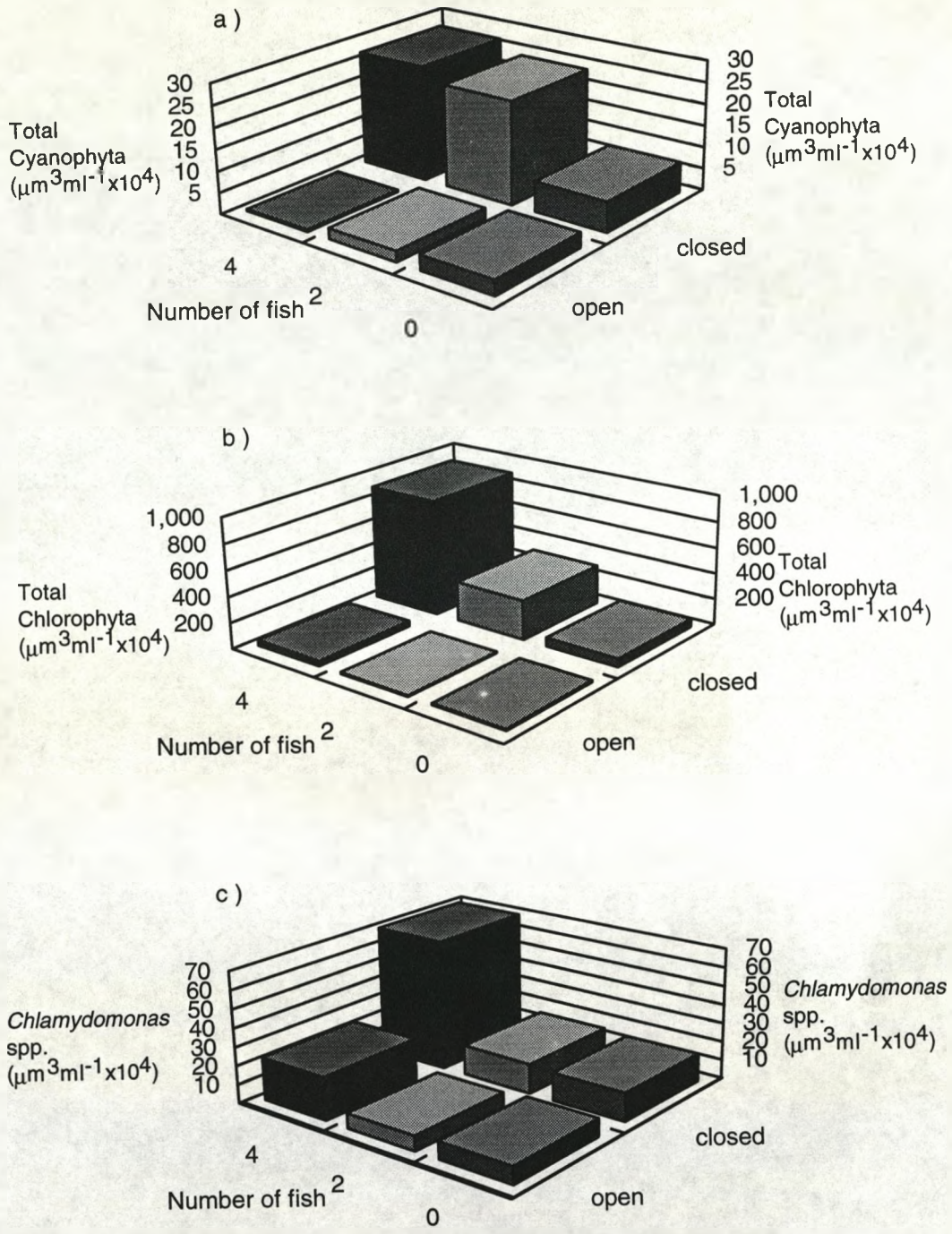

Fig.6.4 The effects of exposure to sediment and the presence of plant (open) and isolation from sediment and the plant (closed), and increasing density of fish added on biovolumes of a) tota Cyanophyta, b) total Chlorophyta and c) *Chlamydomonas* spp., in an experiment carried out in Little Mere in summer 1993.

μm^3 ml^{-1}, 1 x 10^6 μm^3 ml^{-1} and 2.5 x 10^6 μm^3 ml^{-1} respectively, and the mean biovolumes of open enclosures at 0, 2 and 4 fish densities were 6.2 x 10^5 μm^3 ml^{-1}, 6.8 x 10^5 μm^3 ml^{-1} and 1.1 x 10^6 μm^3 ml^{-1} respectively (Fig.6.3b). Cryptophyta were mainly represented by *Cryptomonas ovata* and *Rhodomonas minuta*. In repeated measures of two-way ANOVA performed on these species, biovolume of *Cryptomonas ovata* significantly decreased with the presence of sediment (P=0.05), but its biovolume significantly increased with increasing densities of fish (P=0.02). Interaction of the sediment and fish had no significant effect on biovolume of *Cryptomonas ovata*. None of the treatments were significant for biovolume of *Rhodomonas minuta* (P=0.5, P=0.84 and P=0.07 respectively) (Table 6.2 and Fig. 6.5a,b).

Cyanophyta, though present, were not dominant either in open enclosures or in closed enclosures. Repeated measures of two-way ANOVA revealed that none of the treatments were significant for biovolume of cyanophytes (P=0.109, P=0.74 and P=0.67 respectively) (Table 6.2) (Fig. 6.4a). *Phormidium* sp and *Oscillatoria* sp were the only cyanophyte genera observed.

Repeated measures of two-way ANOVA performed on unidentified flagellates revealed that the presence of sediment significantly decreased the biovolume of these organisms (P=0.003). Neither increasing densities of fish nor the interaction effects of the presence of sediment and fish had significant effects on the biovolume of these organisms (P=0.75 and P=0.09 respectively) (Table 6.2 and Fig. 6.5c). The mean biovolumes of unidentified flagellates for closed and open enclosures were 1.4 x 10^6 μm^3 ml^{-1} and 5.3 x 10^4 μm^3 ml^{-1} respectively.

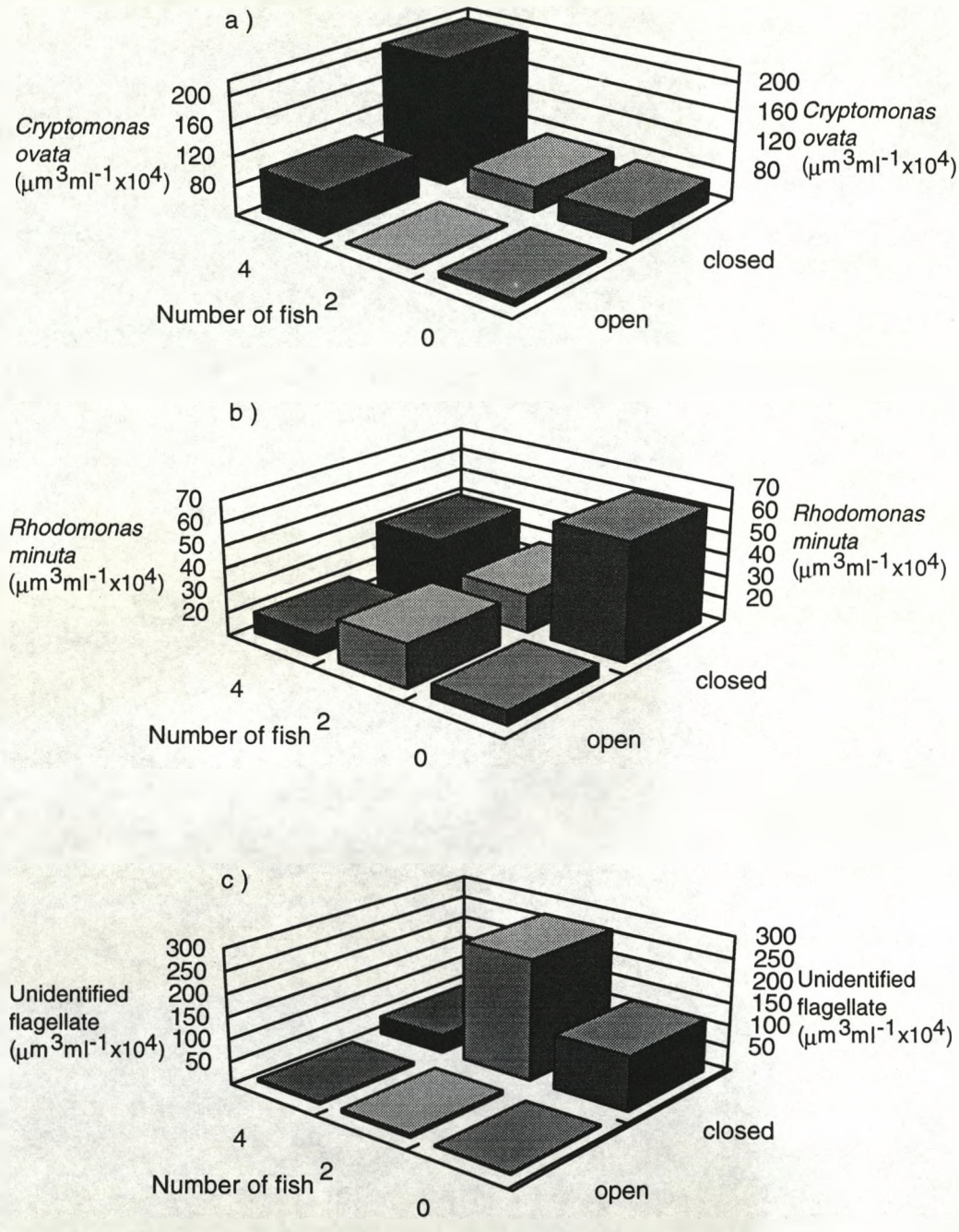

Fig.6.5 The effects of exposure to sediment and the presence of plant (open) and isolation from sediment and the plant (closed), and increasing density of fish added on biovolumes of a) *Cryptomonas ovata*, b) *Rhodomonas minuta* and c) unidentified flagellates in an experiment carried out in Little Mere in summer 1993.

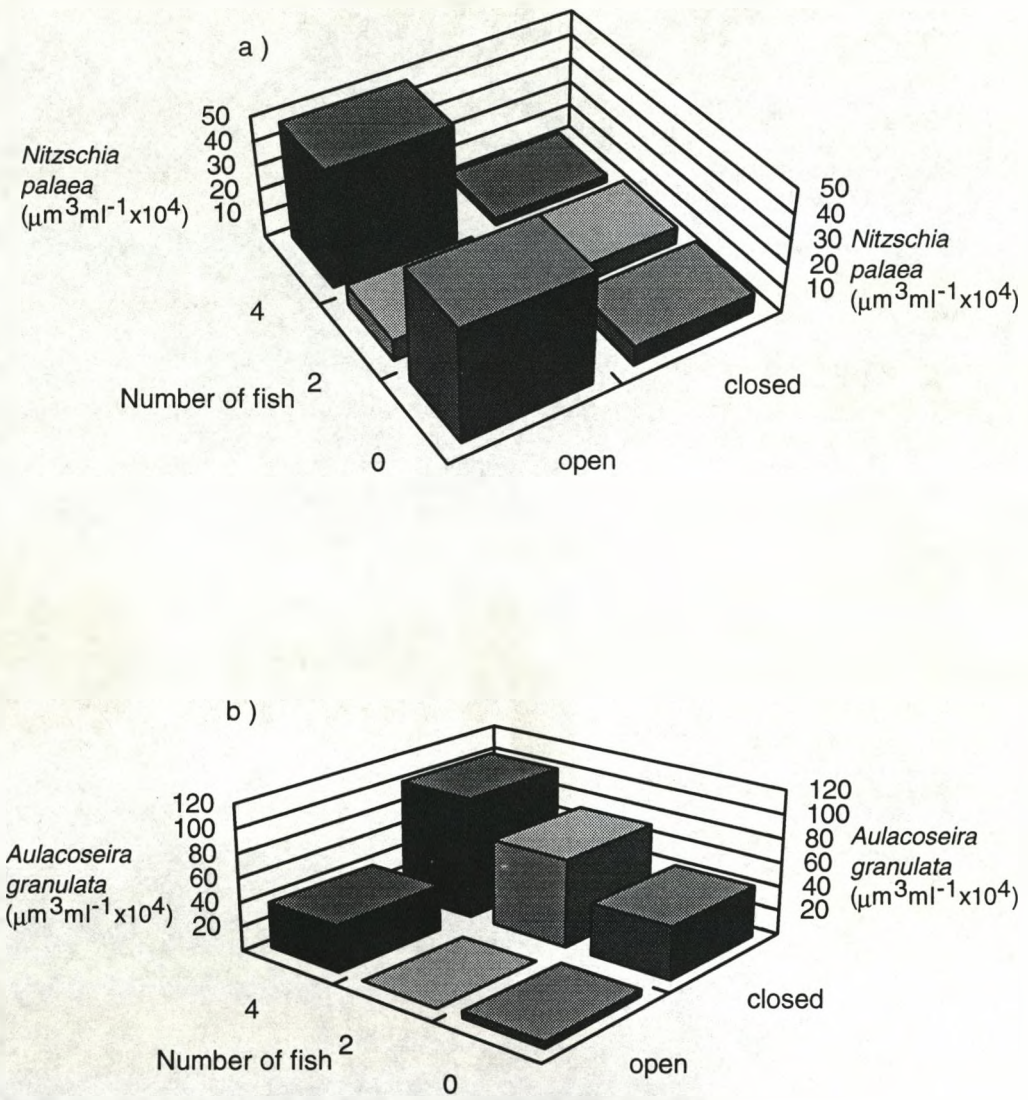

Fig.6.6 The effects of exposure to sediment and the presence of plant (open), and isolation from sediment and the plant (closed) and increasing density of fish added on biovolumes of a)*Nitzschia palaea* and b) *Aulacoseira granulata* in an experiment carried out in Little Mere in summer 1993.

In summary (Table 6.3), the effects of presence or absence of sediment on percentage biovolume of the main phytoplankton groups during the experiment were that Chlorophyta predominated in the algal community of closed enclosures, that their presence decreased significantly in the open enclosures. Biovolume of diatoms and Cryptophyta dominated the algal community of open enclosures but their biovolumes decreased in the closed enclosures. Biovolume of Cyanophyta was not dominant either in the open enclosures or in the closed enclosures. The biovolume of unidentified flagellates made an important contribution to the phytoplankton community of closed enclosures and significantly decreased in the open enclosures.

6.3.4. Response of the zooplankton community

Several zooplankton species responded to the treatments (Table 6.1). Filter feeding cladocerans dominated including *Daphnia hyalina*, *D.cuculata*, *Bosmina longirostris* and *Ceriodaphnia* spp. Weed-bed associated cladocerans including *Chydorus ovalis*, *Eurycercus lamellatus*, *Simocephalus* spp. and *Sida crystallina* also responded to the treatments. The copepods were solely *Cyclops*. Rotifer were rare. *Polyphemus pediculus*, an omnivorous raptorial cladoceran, was abundant in the zooplankton community.

D. hyalina was one of the most abundant filter feeders of both open and closed enclosures. Repeated measures of two-way ANOVA performed on density of *D. hyalina* revealed that both the presence of sediment and increasing density of fish significantly decreased the density of *D. hyalina* (P=0.02 and P=0.0001 respectively) (Table 6.2). The interaction effect of the sediment and fish had no significant effect on its density (P=0.11) (Table 6.2) (Fig. 6.7a). The mean densities for closed

Table 6.3. Composition of the phytoplankton community (Mean % of total biovolume ± S.D.) in closed and open enclosures in an experiment carried out in Little Mere in summer 1993.

	Closed enclosures	Open enclosures
Chlorophyta	46.4±42.5	10±10.9
Cryptophyta	17.9±13.4	37.2±29.1
Bacillariophyta	17.9±19.4	49.3±55
Cyanophyta	2.1±4.0	1±2.2
Unidentified flagellate	15.7±20.7	2.5±2.7

Table 6.4. Means and standard deviations of dry weight of *Potamogeton berchtoldii* in open enclosures in an experiment carried out in Little Mere in summer 1993.

	Control	Two Fish	Four Fish
Potamogeton berchtoldii (g)	97.4 ± 54	67.3 ± 42	130 ±152

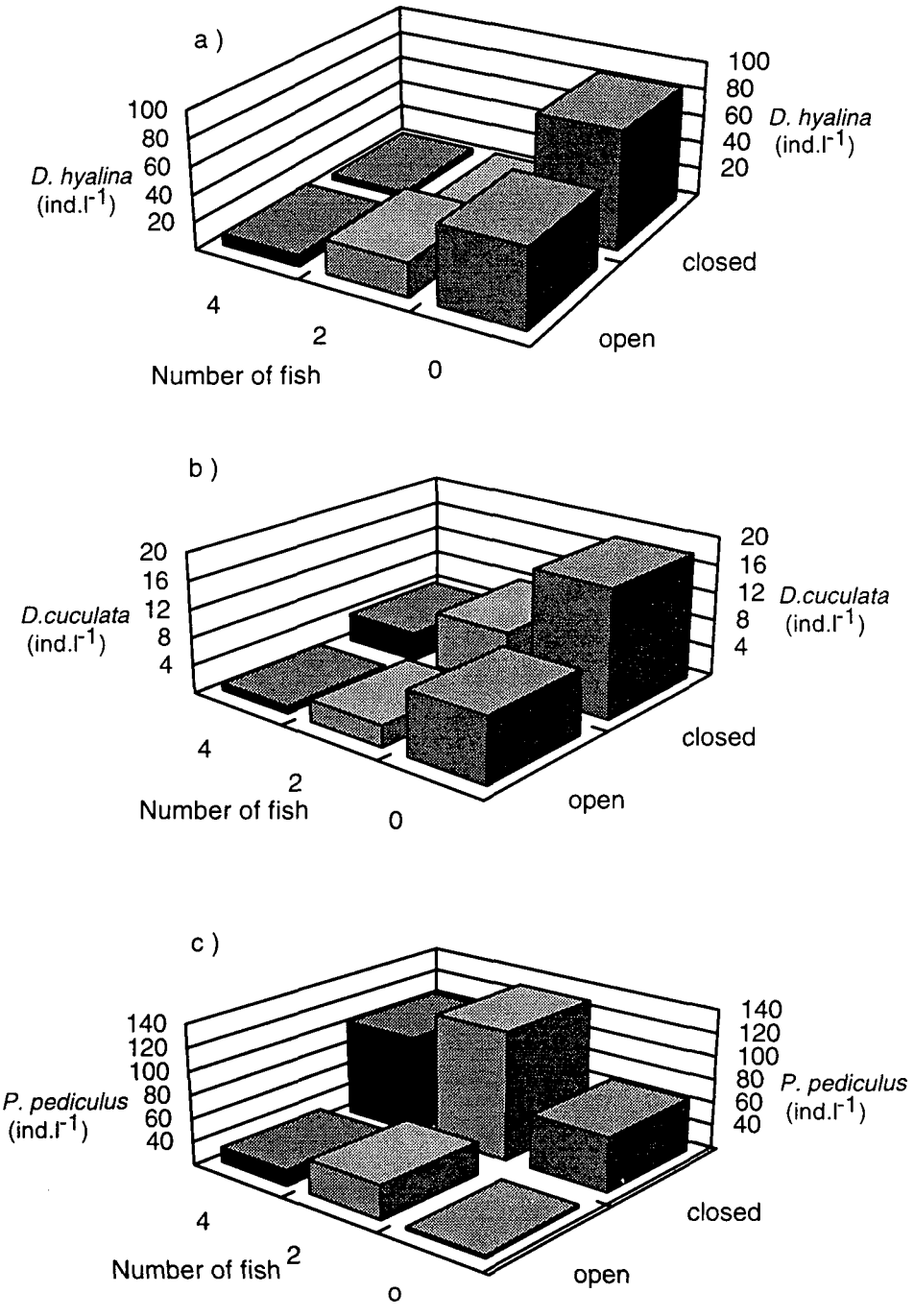

Fig.6.7 The effects of exposure to sediment and the presence of plant (open), and isolation from sediment and the plant (closed) and increasing density of fish added on density of a) *D. hyalina*, b) *D. cuculata* and c) *Polyphemus pediculus* in an experiment carried out in Little Mere in summer 1993.

enclosures at 0, 2 and 4 fish densities were 85 ind. l^{-1}, 4 ind.l^{-1} and 4 ind.l^{-1}. The mean densities for open enclosures at 0, 2 and 4 fish densities were 57 ind.l^{-1}, 24 ind.l^{-1} and 8 ind.l^{-1}.

Repeated measures of two-way ANOVA performed on the density of *D. cuculata.* showed that the presence of sediment and the interaction of effects of sediment and fish were not significant (P=0.18 and P=0.56 respectively), whilst increasing density of fish significantly decreased its density (P=0.01) (Table 6.2) (Fig. 6.7b). The mean densities of *D. cuculata* at 0, 2 and 4 fish densities were 13 ind.l^{-1} , 5 ind.l^{-1} and 3 ind.l^{-1}.

Polyphemus pediculus was an abundant zooplankter, along with *D. hyalina*, throughout the experiment. Repeated measures of two-way ANOVA revealed that its density significantly decreased in the presence of sediment (P=0.001) (Table 6.2). The mean densities for closed and open enclosures were 100 ind.l^{-1} and 34 ind.l^{-1} respectively. Neither the increasing fish densities nor the interaction effect of fish and sediment had significant effects on the density of *Polyphemus pediculus* (P=0.29 and P=0.76 respectively) (Table 6.2 and Fig. 6.7c).

Repeated measures of two-way ANOVA performed on densities of *Bosmina longirostris* and *Ceriodaphnia* spp. showed that the presence of sediment significantly decreased the density of *Bosmina longirostris* (P=0.002), but had no significant effect on the density of *Ceriodaphnia* spp. (P=0.98) (Table 6.2). The densities of both species increased significantly with increasing fish densities (P=0.04 and P=0.02 respectively) (Table 6.2). The interaction effect of the presence or absence of sediment

and fish was significant only for the density of *Bosmina longirostris* (P=0.04) (Table 6.2) (Fig. 6.8a and 8b). The mean densities of *Bosmina longirostris* for closed enclosures at 0, 2 and 4 fish densities were 2 ind.l^{-1}, 6 ind.l^{-1} and 64 ind.l^{-1} respectively; the mean values for open enclosures at 0, 2 and 4 fish densities were 1 ind.l^{-1}, 0.4 ind.l^{-1} and 3 ind.l^{-1} respectively. The mean densities of *Ceriodaphnia* spp. at 0, 2 and 4 fish densities were 15 ind.l^{-1}, 45 ind^{-1} and 73 ind.l^{-1} respectively.

Repeated measures of two-way ANOVA revealed that none of the treatments were significant on the densities of *Cyclops* spp. (P=0.24, P=0.06 and P=0.67 respectively) (Table 6.2).

Many weed-associated cladocerans responded to the treatments. Repeated measures of two-way ANOVA revealed significant effects of the presence of sediment on densities of *Chydorus ovalis*, *Eurycercus lamellatus*, *Simocephalus* spp. and *Sida crystallina*. These species densities greatly increased in open enclosures (P=0.0008, P=0.01, P=0.0004 and P=0.015 respectively) (Table 6.2). Neither increasing densities of fish (P=0.14, P=0.89, P=0.61 and P=0.78 respectively) nor the interaction effects of the presence or absence of sediment and fish (P=0.1, P=0.15, P=0.67 and P=0.65 respectively) were significant for these species densities (Table 6.2 and Fig. 6.8c, 9a, 9b, 9c).

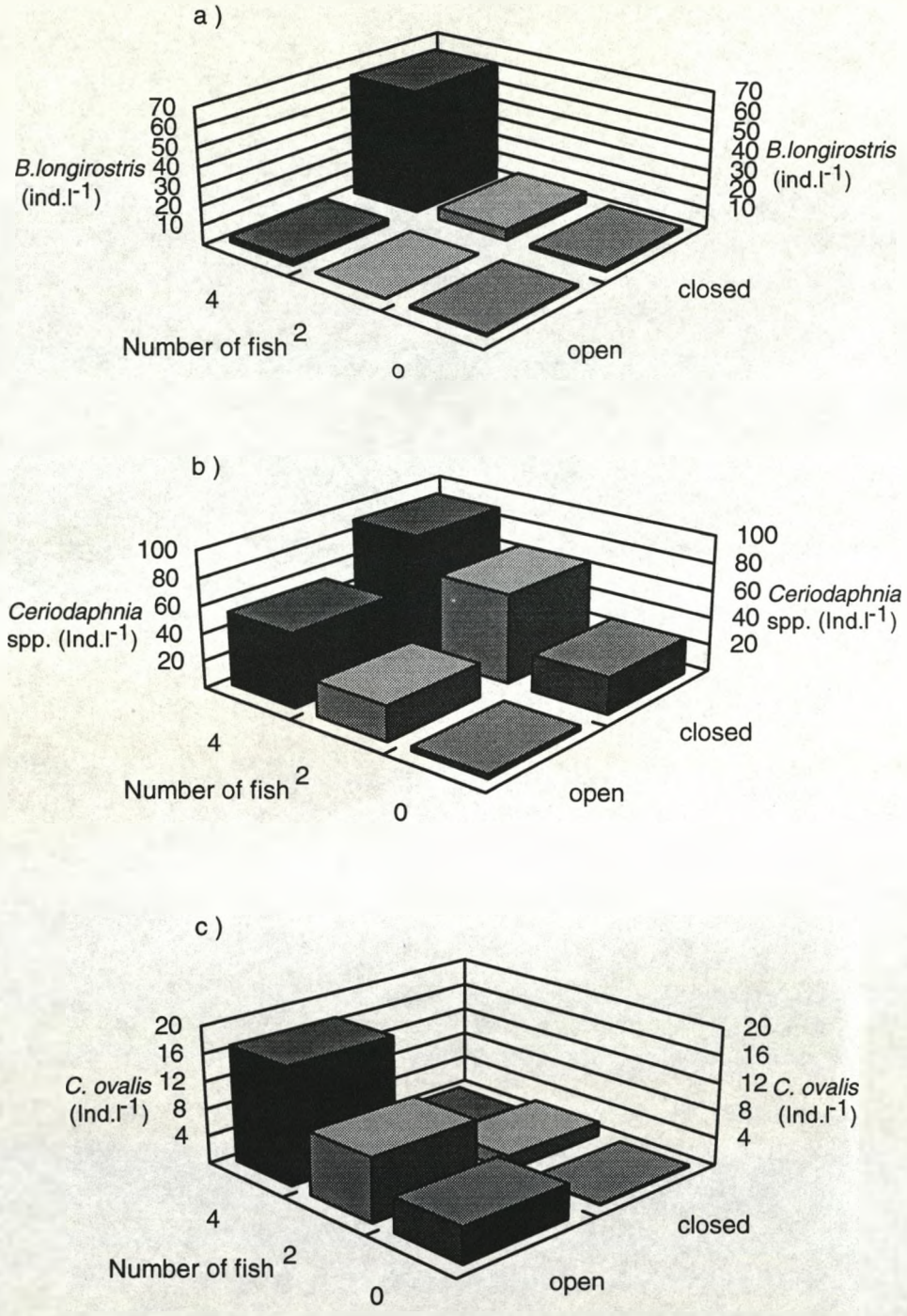

Fig.6.8 The effects of exposure to sediment and the presence of plant (open), and isolation from sediment and the plant (closed) and increasing density of fish added on density of a) *Bosmina longirostris*, b) *Ceriodaphnia* spp. and c) *Chydorus ovalis* in an experiment carried out in Little Mere in summer 1993.

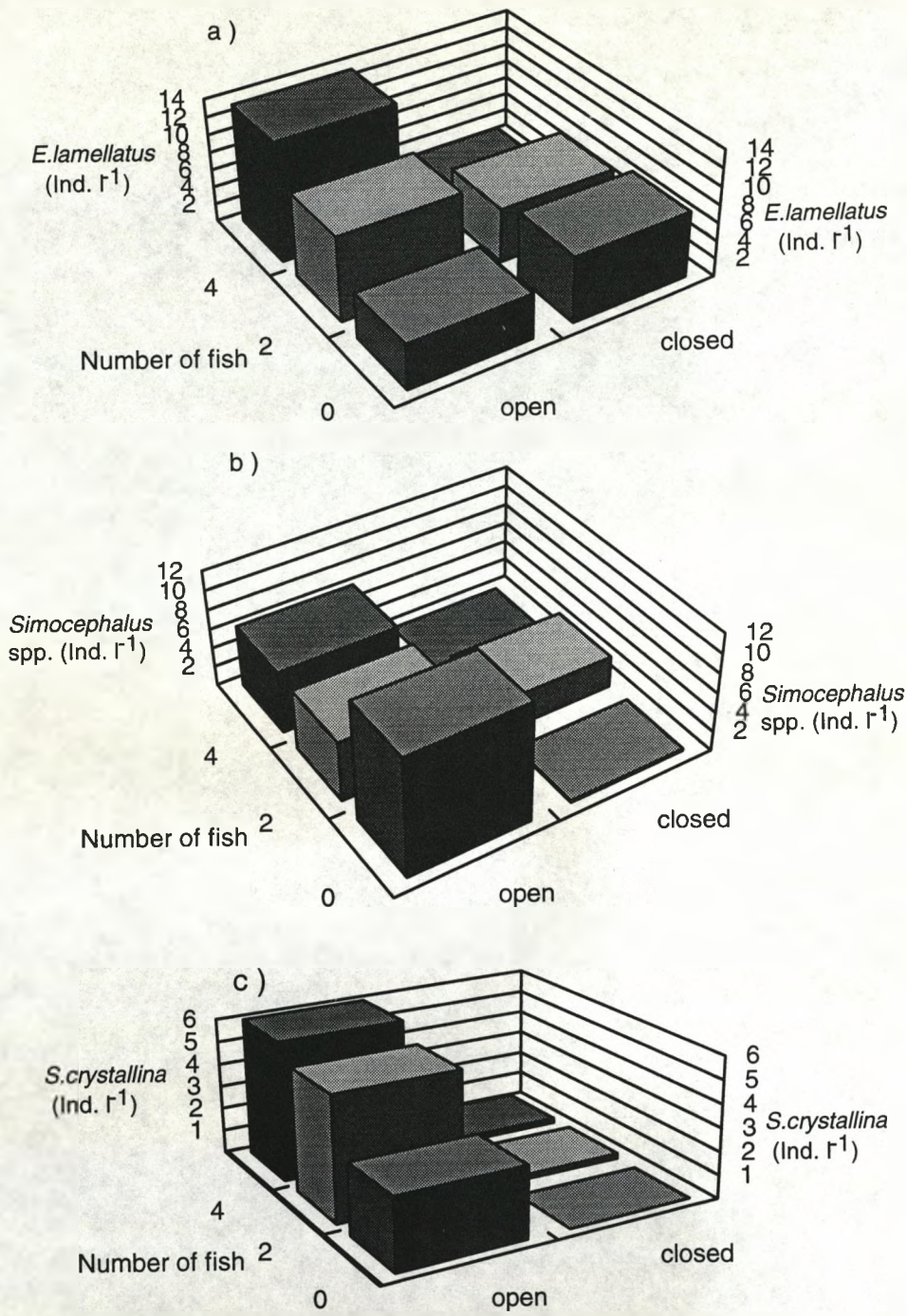

Fig.6.9 The effects of exposure to sediment and the presence of plant (open) and isolation from sediment and the plant (closed). and increasing density of fish added on density of a) *Eurycercus lamellatus*, b) *Simocephalus* spp. and c) *Sida crystallina* in an experiment carried out in Little Mere in summer 1993.

6.4. Discussion

I hypothesised that the sediment surface would be an important nutrient source through internal nutrient loading, though dissolved-oxygen concentrations have been gradually increasing. Contrary to expectation, the presence or absence of sediment in the enclosures did not result in significant differences of SRP and NH_4-N concentrations. The concentrations of these nutrients were much lower than in the previous year. In open enclosures in 1992 there were means of 752 μg l^{-1}, S.D.= 40 for SRP and 200 μg l^{-1}, S.D.=20 for NH_4-N respectively. Thesee were significantly different from the values in 1993, which were 44 μg l^{-1}, S.D.=21 and 170 μg l^{-1}, S.D.=142 respectively. These results suggest considerably lower rates of internal release of these nutrients compared with the previous year. Low dissolved-oxygen concentrations have been shown as important for internal release of phosphate along with pH, temperature and other factors (Boström *et al.* 1982; Jensen & Andersen, 1992). Increase in dissolved-oxygen concentration may have been one of the causes of decreasing internal SRP and NH_4 loading in Little Mere. The mean dissolved-oxygen concentrations (in mg l^{-1}) of open enclosures in 1992 and 1993 were 5.8, S.D.= 0.4 and 7.8, S.D.=1.6 respectively, and the values for the closed enclosures were significantly higher than in the open enclosures in both years. The 2 mg l^{-1} difference in the concentrations during the day should reflect similar differences at night and perhaps at the sediment surface might be strong enough to increase the redox potential and in turn decrease internal loading. However, significant amounts of P may be released from aerobic sediment surfaces of eutrophic shallow temperate lakes (Andersen, 1982; Jensen & Andersen, 1992). If aerobic P release happened in open enclosures, the insignificantly different concentrations of nutrients between open and closed enclosures might be due to the presence of *Potamogeton berchtoldii* biomass

(Table 6.4). The luxury uptake of nutrients by macrophytes has been shown elsewhere (Ozimek *et al.* 1990; van Donk *et al.* 1993). Balls *et al.* (1989) found loss of the nutrients just after and for some days after fertilization in a system of fertilized experimental plant-dominated ponds but not in plant-free ponds. They concluded that presence of intact plant communities was able to buffer strongly the effects of the added nutrients in the ponds. Thus presence of the submerged plants in open enclosures might have been important in decrease of nutrient concentrations. Internal loading may thus have been lower than in the previous year because of progressive increase of dissolved oxygen concentration, and the presence of the plants may have buffered the concentrations to comparable levels between open and closed enclosures. Increased denitrification which has been shown to be high in plant beds (Christensen *et al.*1990; Reddy *et al.* 1989) may also have been involved. These results may ultimately thus be consistent with the previous's year enclosure experiment conclusions that the sediment surface was the main nutrient source for the lake water (Chapter 5).

The reasons why pH and free-CO_2 concentrations were not significantly different between open and closed enclosures might be explained by the phytoplankton dominance (discussed in detail below) in the closed enclosures and the presence of *Potomogeton bertcholdii* in the open enclosures. They might have taken up free-CO_2 equally, and shifted the pH to the similar levels. Large daily and seasonal changes in pH and concentration of free-CO_2 due to phytoplankton growth (Goldman, 1972) and submerged macrophyte photosynthetic activity (Frodge *et al.* 1990, Jones *et al.* in press) have been observed. The great increase in the pH and decrease in the free-CO_2 concentrations compared with the previous year's experiment might be explained by

the continued loss by decomposition of labile organic matter formerly contributed to the sediment from the sewage effluent. In turn reduced bacterial respiration and release of free-CO_2 might be expected.

Although reduction in external nutrient loading, as a method to improve water quality, has been ineffective in many shallow lakes, due to internal nutrient loading and other reasons (Sas 1989, Jeppesen *et al.* 1991), there has, in Little Mere, been a very fast response to the external nutrient reduction. This has resulted in marked reduction in nutrient concentrations following sewage effluent diversion (Carvalho *et al.* in press), and highlights the important role of large stands of macrophytes and their buffering capacities (Moss, 1990; 1991).

I hypothesised that the sediment surface would supply a high nutrient potential for high phytoplankton crops, though it appears this potential may not be realised due to presence of macrophytes in open enclosures. I also hypothesised that increasing fish densities might decrease grazing pressure of cladocerans differently in open and closed enclosures because of provision of refuges in open enclosures. These hypotheses were accepted in that the chlorophyll a concentrations were significantly higher in closed enclosures than in open enclosures. Both open and closed enclosures had similar potential for algal growth in terms of nutrient concentrations which were not significantly different. Thus, according to observed relationships between total phosphorus concentrations and chlorophyll a concentrations (Smith & Shapiro, 1981), chlorophyll a concentrations should have been the same both in open and closed enclosures. However the presence of *Potamogeton berchtoldii*, and its buffering effects, seemed to suppress the potential for phytoplankton growth in open enclosures.

By a number of negative feedback mechanisms, submerged macrophytes can reduce the growth rate of phytoplankton as discussed in Chapters 3 & 5.

I hypothesised (as in the previous experient, Chapter 5) that the future, oxidized sediment resulting in water with lower CO_2 concentrations, and higher pH, in the presence of suitable inocula, would favour cyanophyte predominance over other algae in water that is relatively nutrient rich. This hypothesis was rejected, as previously. In open and closed enclosures, without any significant difference in free-CO_2 concentration between them, the mean values of CO_2 were 0.00036 mmoles l^{-1} and 0.00045 mmoles l^{-1} for closed and open enclosures respectively and these values were well within the suggested limit of free CO_2 for cyanophyte dominance (0.003 mmoles l^{-1}) (King, 1970). In the upstream Mere Mere, summer increase in phytoplankton biomass was principally of cyanophytes, with the biovolumes of it reaching up to 9 x 10^8 μm^3 l^{-1} and a mean free CO_2 concentration of 0.0026 μg l^{-1} - higher than those in the enclosures (Table 6.1). In a series of papers, Moss (1973a; 1973b) suggested that at high pH (8.4-9.9) and above, eutrophic species grow well and among these eutrophic species were several cyanophyte species. In the present experiment, the mean pH values range for closed and open enclosures were 8.7 and 8.6 and were within the suggested range for eutrophic cyanophytes but there was a continued lack of cyanophyte predominance. Thus the explanation for cyanophyte dominance may be more complicated than previously suggested. The lack of cyanophyte predominance in Little Mere might be because the lake has been in a clear-water state with dense macrophytes stands at varying high nutrient levels and seems to be in a stable state as suggested by Moss (1990), Scheffer (1989) and Scheffer *et al.* (1993). In Little Mere, the existence of large macrophyte stands seems to stabilize the clear-water,

cyanophyte-free state despite the presence of a potential for a turbid water state with cyanophyte dominance and may remain so unless disturbed by a strong shock, like mechanical loss of the macrophyte stands.

Where there was increase in algal biomass, reflected in chlorophyll a, it was predominantly by Chlorophyta in closed enclosures with lower predominance of Cryptophyta and Bacillariophyta. For open enclosures, the increase was predominantly due to Bacillariophyta and Cryptophyta (Table 6.3).

Organically rich shallow lakes tend to favour chlorophyte dominance (King, 1970, Jensen *et al.*1994). Chlorophyte contribution to the algal community decreased in open enclosures with the presence of *Potamogeton berchtoldii*. Although algae associated with high pH values (above about 8) either use bicarbonate or can extract CO_2 at very low concentrations (Talling, 1976), not all plants can use bicarbonate or use of it less efficiently because of their bulk. Thus the high pH values found in the enclosures could potentially have given competitive advantage to the chlorophytes over the macrophytes but did not appear to do so. In the previous year's enclosure experiment, chlorophyte biovolume also significantly decreased in the open enclosures which had high free-CO_2 but did not have macrophytes. There were no grazer effects on chlorophytes perhaps due to high growth rates of algae compensating for grazer losses. The species level response of chlorophytes to the treatments was different from the general trend as exemplified by *Chlamydomonas* spp.

Though biovolume of cryptophytes was reduced and diatoms were not affected by the presence of the sediment, both made the biggest contribution to the algal community

of open enclosures, consistent with the previous year's experiment. Both cryptophytes and diatoms thrived at reduced grazer pressure, perhaps due to their being small, edible and generally readily grazed. However the species level responses varied from the general trends for these taxa. Whilst *Cryptomonas ovata* responded similarly to cryptophytes in general to the treatments, *Rhodomonas minuta* responded to none of the treatments, perhaps because of high growth rates compensating for grazing losses. A similar variation was observed for the two most numerous species of diatoms. The species-specific responses of diatoms are sometimes related to the ambient Si:P ratios (Kilham, 1971). There were likely to have been different Si:P ratios in open and closed enclosures but data were not collected for Si. Pennate diatoms are often favoured by high Si:P ratio (Tilman *et al.* 1982) which might have favoured *Nitzschia palaea* in open enclosures but *Nitzschia palaea* is typically a sediment-living diatom and its numbers may have been enhanced by resuspension from the bottom of a rich inoculum available for further growth. *Aulacoseira granulata* is considered to be a poor competitor at low N:P ratios or CO_2 concentrations (Talling, 1976, Tilman *et al.* 1986). However these nutrient concentrations were not significantly different in open and closed enclosures. *Aulacoseira granulata* biovolume was significantly reduced in open enclosures but the reasons for this are not clear.

As in the previous year's experiment, a large contribution to the algal community of closed enclosures was by unidentified flagellates, whose abundance was greatly reduced by the presence of the sediment. The reasons for this are not clear.

I hypothesised that increasing fish predation must be expected to reduce numbers of large cladocerans in closed enclosures, but that in open enclosures fish predation

would be weakened by the availablity of the macrophyte refuges. This hypothesis is partly accepted and partly rejected. Increasing fish predation reduced the density of *D. hyalina* in closed enclosures as expected. but it was also reduced in open enclosures despite the availability of refuges (Table 6.1) though to lesser extent than in the closed enclosures. Timms' & Moss' refuge hypothesis (1984) suggests a much greater refuge effect and this might be because the hypothesis was developed in lakes with dense stands of floating-leaved plants (mainly *Nuphar lutea* (L)). This unexpected significant reduction of *D. hyalina* in the open enclosures despite the presence of submerged plant beds might be explained by differences between floating-leaved plants and submerged plants in terms of structural effects and how they change water chemistry and physics (Carpenter & Lodge, 1986), in turn offering different levels of provision of refuges. Whilst submerged plants increase DO and pH to much higher levels than in open water (Frodge *et al.* 1990), Serafy and Harrell (1993) found no significant avoidance of plant beds by fish species tested to pH 9.52-9.83 when accompanied by 204 to 250 % DO. Floating-leaved plants like water lilies deplete light, and DO (Frodge *et al.* 1990). Fish avoid very low levels of DO depending on the concentrations (Serafyry & Harrell, 1993). The combination of low light and DO might impair feeding of fish in floating-leaved plant beds without necessarily detering their presence (Venugopal & Winfield, 1993), in turn resulting in refuges for large cladocerans. The refuge theory of Timms & Moss (1984) appears to work well with floating leaved plants (Chapters 3, 5 & 8; Moss *et al.* 1994; Carvalho, 1994). However it may not apply to all plant stands and submerged plants may be less capable of protecting open water large cladocerans. This suggestion is supported by the present *D. hyalina* (and *D. cuculata*) findings and by the results of the diurnal samplings in 1993 and 1994 (see Chapter 8) but may be an outcome simply of the small scale

enclosure experiment which may not mimic the whole system. Thus, my assumption about possible potential differences among different plant types for provision of refuges to zooplankton needs further testing.

Polyphemus pediculus was not so abundant in previous years in Little Mere. Recently it has been a predominant zooplankter along with *D.hyalina*. The density of *Polyphemus pediculus* was not changed by fish predation, perhaps because of its rapid movement and considerable visual abilities in helping to avoid attack. But the reasons why this omnivorous raptorial cladoceran significantly decreased in numbers in the presence of sediment are not clear.

The increase in density of *Ceriodaphnia* spp. and *Bosmina longirostris* with increasing fish predation is consistent with the size-efficiency hypothesis (Brooks & Dodson, 1965). But there was a significant reduction in density of *Bosmina longirostris* in the open enclosures. This might suggest that *Bosmina longirostris* is disadvantaged in submerged plant beds compared with open water (see below).

Whilst the abundance of the weed-bed associated cladocerans was not affected by the increasing fish predation, their abundance was significantly reduced in the closed enclosures. These findings might give extra information about the refuge capacity of the submerged plants. *Eurycercus lamellatus*, *Chydorus ovalis*, *Simocephalus* spp. and *Sida crystallina* are typical weed-bed cladocerans (Smirnow & Davis, 1973; Fairchild, 1981). All were more abundant in open enclosures. It is more likely that they gain shelter in weed-beds against fish predation than open water cladocerans like *D.hyalina*.

Comparisons of densities of *D. hyalina*, *Bosmina longirostris*, *Ceriodaphnia* spp. *Eurycercus lamellatus* and *Chydorus ovalis* in open water, within *Nuphar lutea* beds and *Potamogeton berchtoldii* beds in Little Mere are shown in Table 6.5 and are consistent with the findings of the enclosure experiment. Density of *D. hyalina* was significantly different among the locations. The highest densities were found in *Nuphar lutea* (L) beds whilst the density was not significantly different between open water and *Potamogeton berchtoldii* beds suggesting a lesser role of them as *D. hyalina* refuges. The density of *Bosmina longirostris* was not significantly different among the different plant beds but was significantly lower in *Nuphar lutea* (L) beds and *Potamogeton berchtoldii* beds than in open water, as found in the experiment. The density of *Ceriodaphnia* spp. was similar among *Potamogeton berchtoldii* beds and open water and significantly higher in these habitats than in *Nuphar lutea* beds. This result parallels the enclosure experiment results. The density of *Chydorus ovalis* did not differ among the plant beds. This finding is also consistent with the experiment results. The density of *Eurycercus lamellatus* was significantly different between *Nuphar lutea* and *Potamogeton berchtoldii* beds. It was significantly more abundant in *Potamogeton berchtoldii* beds than open water or *Nuphar lutea* beds where its densities were similar. Again this is consistent with the results of the experiment.

6.4 1. Conclusion

Eutrophication of lakes has been hitherto largely considered in terms of nutrients. Though the exact nutrient concentrations are not clear, Jeppesen *et al.* (1991) suggested that 80-150 μg TP l^{-1} is the P-threshold at which macrophyte colonization is feasible. Alternatively clear water can be maintained at concentrations well above this as observed in Little Mere (Chapter 3; Carvalho, 1994). As suggested by Scheffer

Table 6.5. Comparision of densities (Ind. l^{-1}) of *Daphnia hyalina*, *Bosmina longirostris*, *Ceriodaphnia* spp., *Chydorus ovalis* and *Eurycercus lamellatus*, in open water,and within *Nuphar lutea* and *Potamogeton berchtoldii* beds in LittleMere in summer 1993. Results of Fisher's multiple comparisons (based on pairwaise differences between level means): O, open water; N, *Nuphar lutea*; *Potamogeton berchtoldii*. The habitat values are arranged in order of increasing densities from left to right. A common line beneath letters denotes that densities in these habitats were not significantly different (α=0.05) from each other.

	Open water	*Nuphar lutea*	*Potamogeton berchtoldii*	One-way ANOVA	Habitats comparisons		
D.hyalina	4.7±4.5	38±8	7.5±9.9	***	O	P	N
B. longirostris	28±54	0.25±0.5	1±2	NS	N	P	O
Ceriodaphnia spp	90±82	8.8±6.8	65±47	NS	N	P	O
Chydorus ovalis	0.25±0.5	31±16	54±69	NS	O	N	P
E. lamellatus	1.5±1.9	4.2±5	29±29	*	O	N	P

* $P < 0.05$

*** $P < 0.01$

NS: no significance

et al. (1993) & Balls *et al.* (1989) over a wide range of nutrient concentrations, shallow lakes can have a clear state dominated by aquatic plants (phase 2) as well as a turbid state dominated by phytoplankton (phase 3). The findings of this experiment, those of the previous year's experiment and over four years of monitoring of the lake give support to the alternative equilibria hypothesis of Scheffer (1990) & Moss, (1991). Little Mere has provided a good example of a stable, clear-water macrophyte-dominated lake at high nutrient concentrations that have been progressively decreasing. There has been a very rapid recovery of denser and more diverse plant beds following the external nutrient reduction as concentrations of TP and NH_4-N have decreased from several mg l^{-1} to µg l^{-1} levels (Carvalho *et al.* in press; Chapter 2). With a change from near anoxic to progressively increasing dissolved-oxygen concentrations, there has been recolonization of fish, including perch and pike and a shift in the dominant zooplankter from the very large body-sized, bright red *D. magna* to *D. hyalina* (Chapter 3). The water is clear with dense aquatic plant stands, where recruitment of the fish appears successful giving a potentially huge predation pressure on zooplankton. Nevertheless, the lake remains clear, seemingly because of the stabilizing effect of the present macrophyte stands. The system stability is reflected in the insignificant difference in nutrient concentrations between the enclosures but lesser chlorophyll a concentrations in open macrophyte-colonised enclosures than in closed enclosures. Despite the presence of potentially favourable conditions for cyanophytes in the enclosures, they did not develop nor have they in the lake so far (Chapter 3).

In the future, it seems to be less likely that Little Mere will switch to a turbid state than it will stay in its current clear-water state, unless some unexpected 'shock' effect comes into play.

Chapter 7: The effects of pH on interactions among phytoplankton, zooplankton and the fish in mesocosms in Little Mere

7.1 Introduction

Major changes in hydrogen ion concentration clearly have far reaching effects on the communities of low-conductivity, poorly buffered waters. A large literature exists on the problem of recent acidification in upland igneous and metamorphic rock catchments (e.g. Hall *et al.* 1980). Very high hydrogen ion concentrations (pH< about 4.5) cause large reductions in diversity through a variety of mechanisms. Equally, very high pH values in soda lakes (pH>10) create similarly extreme conditions, associated with low diversity (Jenkin, 1936).

In aquatic systems within these extremes, pH receives less attention, being eclipsed perhaps in the interpretation of mechanisms and consequences in such waters by strong influences of nutrient loading and predation. However, there is a myriad of ways in which pH may interact with these agents of acknowledged importance. It determines the speciation of inorganic carbon, leading to differential proportions of free CO_2 and bicarbonate (Hutchinson, 1957), which may influence the specific composition of algal (Moss, 1973a; Peslova *et al.* 1990; Shapiro, 1973a; Talling 1976) and plant (Madsen and Sand-Jensen, 1991) communities; it influences the solubility of trace metals (Stumm & Morgan, 1981). It may determine the behaviour of invertebrates (O'Brien & de Noyelles, 1972; Hansen *et al.* 1991) and the habitat preferences of fish (Serafy & Harrell, 1993). Large changes in diurnal pH associated with the photosynthetic activity of plant beds may produce a mosaic of pH domains within a water body that might determine patterns of predation and zooplankton grazing. Superimposed on these complexities may be pH changes consequent on

longer term changes in a lake following progressive eutrophication or restoration from it. Although there is an increasing literature on the interactions between nutrient loading, zooplankton grazing, and fish predation on zooplankters in determining the operation of plankton-based system, there remain many details to be explained perhaps by factors interacting with these processes. Ultimately this chapter concerns the potential role of pH in these interactions in shallow lakes. It concerns also the potential links between incidence of cyanophytan blooms and the speciation of inorganic carbon mediated through pH both in shallow and deep lakes.

Nowhere is the complexity of community interaction greater than in shallow, macrophyte dominated freshwaters, where the structural complexity is great and where nutrient loads have often changed markedly as a result of eutrophication. Macrophyte-dominated lakes appear to be able to resist the effects of increased nutrient loading through a variety of buffering mechanisms (Balls *et al.* 1989; Irvine *et al.* 1989; Timms & Moss, 1984; Moss, 1991), which include provision of refuges for crustacean grazers of open-water-phytoplankton against predation by fish and allow maintenance of clear water and a suitable light climate for plant growth, despite phosphorus and nitrogen concentrations capable of supporting dense algal populations. Over a similar range of nutrient concentrations, phytoplankton communities can dominate as an alternative stable state with few or no macrophytes and little zooplankton grazing potential (Moss, 1990; Scheffer *et al.* 1993). pH may have a major role to play in influencing the behaviour of both fish and zooplankton, through pH changes induced by plant uptake in macrophyte-dominated lakes and algal uptake in phytoplankton dominated ones. The possible stimulation of cyanophytan growth by increasing pH (Shapiro, 1973a, 1990a) may be particularly germane to the outcome of fish-grazer

phytoplankton interactions.

Many shallow lakes in Europe have lost their macrophyte communities as a result of eutrophication and the process of restoring these communities is proving difficult (Sas, 1989). Reduction of nutrient load alone seems inadequate in most cases and additional measures prove necessary. Collectively these constitute restoration of the buffer mechanisms that stabilise the macrophyte community and often involve manipulation of the fish community (Moss, 1992a). Sometimes they are successful for a time then fail. Current knowledge of the mechanisms is presently inadequate to predict the effects of a given management initiative with any certainty, and this underlines the need to investigate the mechanisms in much greater detail. Furthermore in lake systems of lesser structural complexity there is still considerably uncertainty about the mechanisms that lead to particular types of algal community at high nutrient concentrations for many potentially influential factors also change consequent to the increased nutrient loading and establishment of the symptoms of eutrophication. The reason for the occurrence of large crops of Cyanophyta in some situations but not in others in a case in point.

An opportunity to investigate the interaction of pH with fish predation an zooplankton and on the consequent phytoplankton community has been presented by management carried out. Little Mere was, until 1991, considerably more nutrient-enriched than upstream Mere Mere and still in to some extent (Chapter, 2; Carvalho, *et al.* in press). The water was very clear and there was a flourishing macrophyte community of nymphaeids, *Potamogeton berchtoldii* Fieber and *Elodea canadensis* Michaux (Chapter, 8). The algal growth potential of the water was very high, with milligram

per litre quantities of ammonium and soluble reactive phosphorus. pH values were in the range 7.3 to 9.0, presumably kept lower than the potential created by the fertility of the effluent, by the decomposition of organic matter suspended in it. When phytoplankton algae grew in the spring they were diatoms. *Volvox* and cryptomonads constituted the negligible summer community. Cyanophytes were near absent (Chapter, 3).

After June 1991, although the N and P concentrations fell markedly they remained higher than in Mere Mere. In summer 1993, mean total phosphorus was 253 $\mu g\ l^{-1}$ in Little Mere and 82 $\mu g\ l^{-1}$ in Mere Mere (Chapter, 2). The former Little Mere environment had remained a clear water macrophyte-dominated system because of the absence of fish predation. Now that fish were able to return and that pH was likely to rise as the residual organic matter completed its decomposition, we anticipated an increase in fish predation, reduced grazing and a move in the phytoplankton community towards the cyanophyte dominance of upstream Mere Mere.

In turn we expected the increasing predominance of cyanophytes to disfavour grazer control and events to lead to a breakdown of the buffers that had stabilised the macrophyte community, with consequent phytoplankton dominance. We have taken advantage of the lake situation to examine experimentally how the buffer mechanisms might be operating by creating, in mesocosms, conditions that the literature led us to expect would lead to cyanophyte dominance, and thus to test hypotheses primarily put forward by Shapiro (1990a).

We simulated increasing pH within a high nutrient environment in which we created

conditions of increasing predation on the zooplankters. Specifically we hypothesised that increasing pH would increase the dominance of cyanophytes within the phytoplankton community, that increasing fish predation would increase the biomass of phytoplankton community, with increasing predominance also of cyanophytes; and that number of Daphnia would decline with increasing fish predation, irrespective of pH.

7.2 Methods

7.2.1 Experimental design

The experiment was carried out between 16 June and 10 July 1993, in thirty-six polyethylene enclosures (Fig.7.1). The features of the enclosures and the placement of the enclosures were described in Chapter 5.

The experimental design was 3x4 factorial with different fish densities and raised pH. Four pH values were employed including the lake water pH as a control, pH 9, pH 10 and pH 11. The pH was increased using 1M NaOH, the appropriate initial amount of NaOH being determined by titration of the lake water. In order to maintain the pH at the desired value, a pH check was carried out every other day throughout the experiment using a portable pH-meter and further amounts of NaOH were added if necessary. During this pH adjustment the enclosure water was vigorously mixed with an oar. Perch (*Perca fluviatilis)*, 9-10 cm total length, were caught by seining in Little Mere and immediately placed in appropriate enclosures in three different population densities, 0 fish, 2 and 4 fish per enclosure. Each of the twelve treatments was carried out in triplicate, making up a total of thirty-six enclosures.

Fig.7.1 Experimental enclosures used on Little Mere.

7.2.2. Sampling methods

The methods for water chemistry were described in Chapter 2 and the method for free-CO_2 concentration was described in Chapter 5.

The sampling methods for phytoplankton and zooplankton were described in Chapter 3, except where detailed below.

The demographic responses of *Daphnia hyalina* to increased pH and fish predation treatments were assessed using the egg ratio method (Edmondson, 1971; Paloheimo, 1974). E, the egg ratio (total number of eggs per total number of females) was employed to calculate instantaneous per capita birth rate (b) as:

$$b = \frac{\ln (1 + E)}{D} \qquad \text{equation (7.1)}$$

where D is the time required for eggs to develop, from the time an egg is laid to the time it is released as a free-swimming individual. D is a function of temperature (Downing and Rigler, 1984) and it was calculated by directly measuring egg development time at 15o and extrapolating to other temperatures using a Krogh curve (Edmondson, 1971).

The instaneous per capita rate of increase (r) was estimated from where N_o and N_t , the population sizes at time 0 and time t respectively. The instantaneous per capita death rate (d) was estimated as:

$$r = \frac{\ln_t - \ln_o}{t} \qquad \text{equation (7.2)}$$

r, b and d were calculated for each sampling interval (6-7d).

$$d = b - r \qquad \text{equation (7.3)}$$

7.2.3. Statistical analyses

The statistical analyses were described in Chapter 5.

7.3. Results

7.3.1 Initial status of enclosures

pH values in the enclosures remained close to the adjusted values (± 0.1-0.2 unit) throughout the experiment (Table 7.1 and Fig.7.2a). In all pH 11 enclosures, the fish died soon after introduction and zooplankton and algal growth were negligible until day 20. All fish survived in all other enclosures.

One-way ANOVA performed on the initial chlorophyll a concentrations, cyanophyte, chlorophyte, and diatom biovolumes and population densities of *Daphnia hyalina*, *Polyphemus pediculus* and *Bosmina longirostris* densities revealed no significant differences among the group of enclosures.

Because of punctures made in three of the polyethylene enclosures by a trapped duck during the experiment, two of the pH 10 and one of the pH 11 enclosures were omitted from the subsequent analyses. All other enclosures remained intact throughout.

7.3.3 Response of chemical variables

Table 7.1 shows mean values (± S.D.) of major chemical and biological variables during the experiment. Repeated measures of ANOVA performed on the water chemistry showed that increasing pH, fish densities and pH-fish interactions treatments had no significant effects on the SRP concentration (P=0.06, P=0.5 and P=0.2 respectively), and NH_4-N concentrations (P=0.66, P=0.38 and P=0.19 respectively) (Table 7.2). pH had significant effects on the free-CO_2 concentration (P=0.004) that decreased with increasing pH value, and declined to zero in pH 10 and pH 11 enclosures (Fig.7.2b). Increasing number of fish had no significant effect on the CO_2

Table 7. 1 Mean values with standard deviations for variables measured across all dates in an experiment carried out in enclosures in Little Mere. Cheshire in summer 1993. Algal volumes are given in millions of $\mu m^3 l^{-1}$ and zooplankton in numbers per litre.

pH treatment	Control			pH 9			pH 10			pH 11		
No of perch	0	2	4	0	2	4	0	2	4	0	2	4
No of observation	12	12	12	12	12	12	12	8	8	12	8	12
pH	8.3±0.6	8.9±.6	8.95±.4	9.2±.1	9±0.2	9.1±.2	9.5±0.2	9.9±.3	10.1±.2	11±.2	11±.2	11±.2
C'phyll a ($\mu g\ l^{-1}$)	5.2±4.7	54±64	57±44	7±11	28±15	35±34	4±5	31±43	78±110	1±1	7±8	15±21
Sol react P($\mu g\ l^{-1}$)	103±117	20±45	6±9	44±25	131±220	33±50	28±18	59±54	93±107	127±132	272±265	299±327
NH_4-N ($\mu g\ l^{-1}$)	349±499	60±114	74±102	52±41	266±227	159±265	35±33	146±141	438±748	134±128	271±265	398±388
Free-CO_2(ng l^{-1})	39±47	5.5±7	4±6	2±1	3±1	2.6±1	0	.25±.7	0	0	0	0
Cyanophyta	.07±0.2	.2±.8	.3±.7	.004±.003	1.7±4.4	2.4±4.6	.1±.2	.1±.2	.1±.2	0	0	0
Chlorophyta	.7±1	3±4	9±9	.3±3.6	1.2±.9	2±3	.5±.7	1.9±1.5	7.8±15	.5±1	13±30	2.6±4
Chlorella elipsoidea	.8±.9	.6±1.7	.5±.7	0	.06±.09	.1±.4	.02±.04	.2±.4	5±10	0	0	.3±.7
Gloeocystis major	.03±.06	.2±.4	.03±.1	.002±.003	.01±.04	.01±.03	.001±.002	.07±.02	.01±.01	.01±.01	.09±.01	.23±.37
Cryptophyta	1.3±2	1±1	3±2	4±9	8±16	3±5	4±8	14±25	17±30	.1±.1	.25±.5	.7±1.3
Crytomonas ovata	.7±1	.7±1	2±2	4±8	8±15	2±5	3±7	13±25	16±30	.1±.1	.2±.5	.7±1
Rhodomonas minuta	.01±2	.3±.3	.4±.4	.3±.7	.3±.4	.3±1	.6±.4	2±2	1±2	.01±.02	.01±.01	.002±.005
Bacillariophyta	.8±1	1.5±2.7	2.6±4	.4±.9	.8±.8	.8±.8	.06±.09	.3±.4	.3±.4	.03±.05	.02±.03	.3±.7
Synedra ulna	.02±.05	.02±.05	.09±.2	.2±.4	.1±.4	.2±.3	.03±.03	.2±.3	.2±.4	0	0	0
Aulacoseira gran.	.4±.8	.7±1.9	1±1.8	.04±.01	.4±.7	.6±.1	.01±.17	0	.03±.06	.01±.05	0	0
Daphnia hyalina	85±112	4±4	4.2±11	101±93	34±69	8±6	105±69	181±252	236±333	14±33	4±5	9±24
Polyphemus pedic.	66±89	130±141	104±120	69±84	96±154	157±154	19±24	20±11	20±19	.4±1	.6±1	.9±1
Bosmina longir.	2±3	6±10	64±106	.3±.7	1.3±2.3	13±31	4±10	0	5±11	0	.1±.4	.5±1.4
Ceriodaphnia spp	27±70	66±156	91±169	.3±.8	44±63	41±110	.9±1.8	1.5±1.9	4.7±6.8	0	.1±.35	0
Cyclops spp	11±7	44±73	99±124	7±5	32±77	35±39	9.5±12	8.8±8.8	8.9±15	1.6±2.9	1.3±1.6	.6±1.2

Table 7.2. Summary of the effects of pH, fish and pH/fish interaction on the water chemistry, algal biovolume and zooplankton density in a series of enclosures in Little Mere following repeated measures of 2-way ANOVA.Symbols *P<0.05;**P<0.01; ***P<0.001; NS=no significance . +,- signs show the direction of the effects as increase or decrease with increasing pH or fish density.

	pH	fish	pH/fish interaction
Chlorophyll a(μg l^{-1})	– ***	+ ***	NS
Soluble reactive P(μg l^{-1})	NS	NS	NS
NH_4-N (μg l^{-1})	NS	NS	NS
Free-$C0_2$ (μg l^{-1})	– **	NS	– *
Cyanophyta ($\mu m^3 ml^{-1}$)	– *	NS	NS
Chlorophyta($\mu m^3 ml^{-1}$)	+ ***	+ *	NS
Chlamydomonas spp ($\mu m^3 ml^{-1}$)	+ **	+ **	+ *
Chlorella ellipsoidea($\mu m^3 ml^{-1}$)	+ ***	+ **	NS
Gleocystis major ($\mu m^3 ml^{-1}$)	+ *	+ *	NS
Cryptophyta ($\mu m^3 ml^{-1}$)	+ **	NS	NS
Cryptomonas ovata ($\mu m^3 ml^{-1}$)	+ *	NS	NS
Rhodomonas minuta ($\mu m^3 ml^{-1}$)	+ **	NS	NS
Diatoms ($\mu m^3 ml^{-1}$)	– **	NS	NS
Synedra ulna ($\mu m^3 ml^{-1}$)	– *	NS	NS
Aulacoseira granulata($\mu m^3 ml^{-1}$)	– **	NS	NS
Daphnia hyalina (ind.l^{-1})	+ ***	+/- ***	+/- **
Polyphemus pediculus(ind.l^{-1})	– ***	NS	NS
Ceriodaphnia spp. (ind.l^{-1})	– ***	+ **	NS
Bosmina longirostris(ind.l^{-1})	– **	+ *	NS
Cyclops spp.(ind.l^{-1})	– *	NS	NS

concentration (P=0.07) whilst the interaction of pH and fish significantly decreased the free-CO_2 concentration (P= 0.015) (Table 7.2).

7.3.4. Response of chlorophyll a and phytoplankton biovolumes

Repeated measures of ANOVA, performed on chlorophyll a concentrations, revealed a highly significant effect of increasing pH and fish densities (P= 0.0001, P=0.0002 respectively) (Table 7.2) Concentrations increased especially (Fig. 7.2c) in control, pH 9 and pH 10 enclosures at the highest fish densities. There was a lesser affect at pH 11. The chlorophyll a concentration increased particularly after day 12 for control, pH 9 and pH 10 treatments at two- and four-fish densities giving mean concentrations of 57 $\mu g\ l^{-1}$ 32 $\mu g\ l^{-1}$ and 78 $\mu g\ l^{-1}$. In pH 11 enclosures, chlorophyll a concentration began to increase after day 20, giving a mean of 15 $\mu g\ l^{-1}$. There was a significant decline in chlorophyll a concentration with increasing pH (Fig. 7.2c and Table 7.2). No significant effect interaction effects of pH and fish density were found for chlorophyll a concentration (P=0.52) (Table 7.2).

Cyanophytes, though present, did not dominate the phytoplankton community, either at the start or during the experiment. Increasing pH significantly decreased cyanophyte biovolume (P=0.02) (Table 7.2), The highest biovolume of cyanophytes was found in pH 9 enclosures on day 7 when the overall mean value was 1.4 x $10^6\ \mu m^3\ ml^{-1}$ but, it was a very small percentage (17.3 %) of the total phytoplankton biovolume. Cyanophyta biovolume was very low in control and pH 10 enclosures (1.9 x $10^5 \mu m^3$ ml^{-1} and 1.2 x $10^5\ \mu m^3\ ml^{-1}$ respectively). At pH 11, cyanophytes were not recorded during the experiment (Fig. 7.3a). *Anabena* spp, *Oscillatoria agardhii* and *Microcystis aeruginosa* were the species of Cyanophyta variously present. Fish density and the

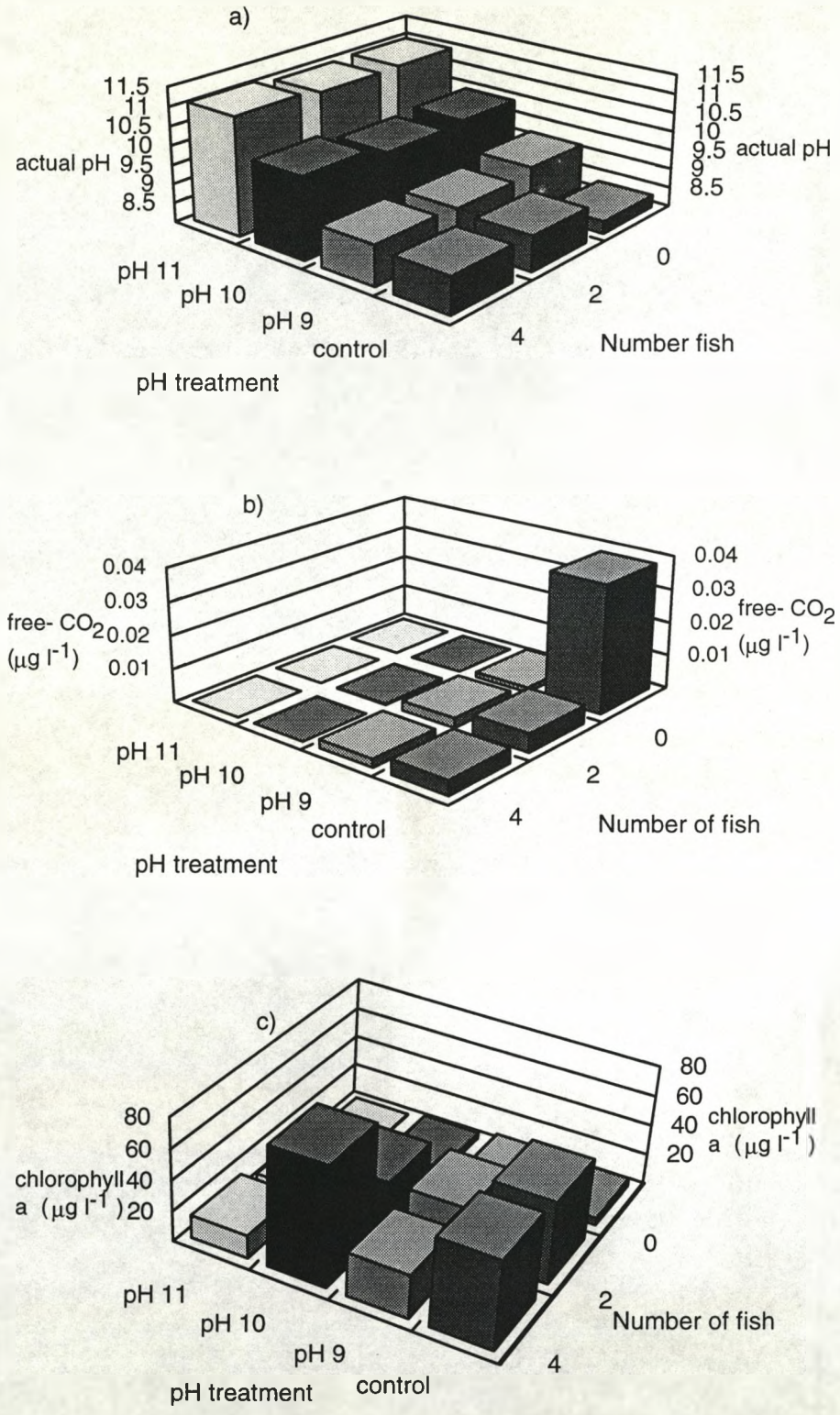

Fig.7.2 The effects of elevated pH and increasing density of fish on a) actual pH, concentrations of b) free-carbondioxide and c) chlorophyll a in an experiment carried out in Little Mere in summer 1993.

pH-fish interaction had no significant effect on the biovolume of cyanophytes (P=0.34 and P=0.34 respectively) (Table 7.2).

Chlorophyta were not predominant phytoplankters at the beginning of the experiment, but their biovolume increased during it. Repeated measures of ANOVA performed on Chlorophyta biovolumes revealed significant increases with increasing pH and fish density (P=0.0002 and P=0.04 respectively) (Table 7.2). After day 7, biovolumes of Chlorophyta increased consistently with increasing pH and fish densities (Fig. 7.3b), the mean values for the control, pH 9 and pH 10 at the highest fish density were 9 x 10^6 μm^3 ml^{-1}, 2.1 x 10^6 μm^3 ml^{-1} and 7.8 x 10^6 μm^3 ml^{-1} respectively. At pH 11 in the four-fish treatment after day 20, the biovolume of Chlorophyta started to increase and reached 1.3 x10^7 μm^3 ml^{-1}, the highest recorded Chlorophyta biovolume. Interaction of pH and fish had no significant effects on biovolumes of Chlorophyta (P=0.11) (Table 7.2). In all treatments the increase in Chlorophyta biovolume was mainly due to *Chlamydomonas* spp, *Chlorella ellipsoidea*, and *Gloeocystis major*. Repeated measures ANOVA employed on these species revealed that their biovolumes were significantly increased with increasing pH (P=0.01, P=0.0005, and P=0.02 respectively) and fish densities (P=0.0035, P=0.003, and P=0.05 respectively). The biovolume of *Chamydomonas* spp showed a greater increase from day 20 in pH 11, four-fish-enclosures than in others (1 x 10^7 μm^3 ml^{-1}). In pH 10, four-fish-enclosures, *Chlorella ellipsoidea* was the most abundant chlorophytan, with a biovolume of 1.4 10^7 μm^3 ml^{-1}, after day 12 which contributed much towards the chlorophyll a concentration of 255 μg l^{-1}, the highest recorded throughout the experiment. The highest biovolume of *Gloeocystis major* was recorded in pH 11, four-fish enclosures after day 20, and was 6.1 x 10^6 μm^3 ml^{-1}. The interaction effects of pH and fish were

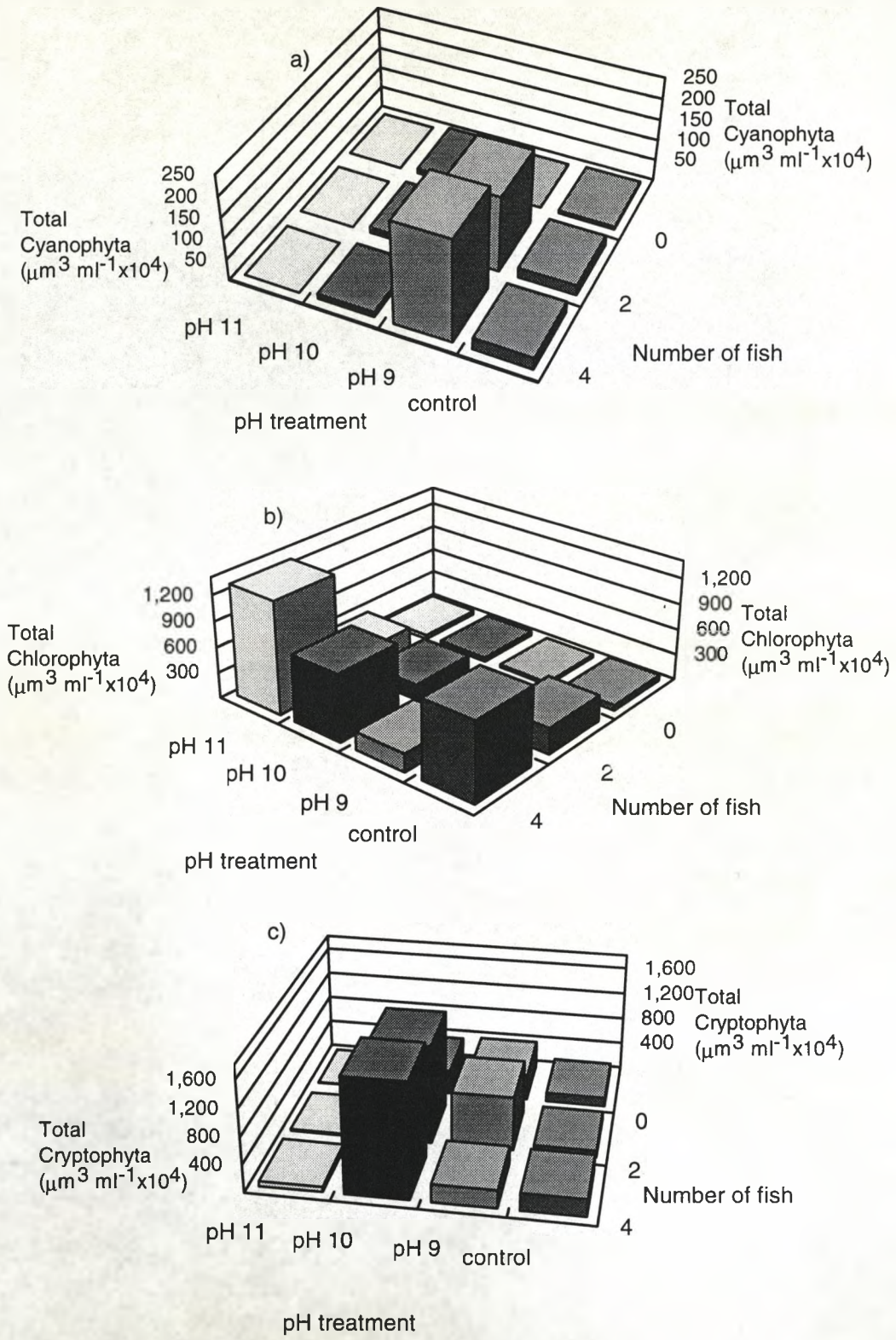

Fig.7.3 The effects of elevated pH and increasing density of fish on biovolumes of a) total cyanophyte, b) total cholorophyte and c) total cryptophyte, in an experiment carried out in Little Mere in summer 1993.

significant for *Chlamydomonas* spp. (P= 0.033) but, not significant for either *Chlorella ellipsoidea* or *Gloeocysts major* (P=0.68 and P=0.5 respectively).

The biovolume of Cryptophyta was proportionately high among of the phytoplankton community from the start of the experiment until day 20. Repeated measures of ANOVA showed a significant change in biovolume with pH whilst increasing fish densities, and the interaction of pH and fish were not significant effect (P=0.01, P=0.31 and P=0.49) (Table 7.2). The increase in Cryptophyta biovolume was greater at pH 9 and pH 10 than in the control and pH 11 (Table 7.1, Fig. 7.3c). The mean biovolume values for control, pH 9, pH 10 and pH 11 were 1.6 x 10^6 μm^3 ml^{-1}, 4.8 x 10^6 μm^3 ml^{-1}, 1 x 10^7 μm^3 ml^{-1} and 3.8 x 10^5 μm^3 ml^{-1} respectively. Cryptophyta were represented largely by *Cryptomonas ovata* and *Rhodomonas minuta*, whose biovolumes significantly increased with increased pH, except at pH 11 (P=0.023 and P=0.004 respectively) (Table 7.2). The mean values of *Cryptomonas ovata* for control, pH 9, pH 10 and pH 11 were 1.2 x 10^6 μm^3 ml^{-1}, 4.5 x 10^6 μm^3 ml^{-1}, 9.4 x 10^6 μm^3 ml^{-1} and 3.7 x 10^5 μm^3 ml^{-1} respectively, and the mean values for *Rhodomonas minuta* were 4.4 x 10^5 μm^3 ml^{-1}, 3.5 x 10^5 μm^3 ml^{-1}, 1 x 10^6 μm^3 ml^{-1} and 5.6 x 10^3 μm^3 ml^{-1} respectively. Increasing fish density did not significantly change these species biovolumes (P=0.34 and P=0.84 respectively), nor were the interaction effects significant (P=0.56 and P=0.63 respectively).

Repeated measures ANOVA revealed that increasing pH had significant negative effects on biovolumes of diatoms (P=0.0002), (Table 7.2, and Fig. 7.4a). The mean diatom biovolumes for the control, pH 9, pH 10 and pH 11 were 1.6 x 10^6 μm^3 ml^{-1} 6.8 x 10^5 μm^3 ml^{-1}, 1.8 x 10^5 μm^3 ml^{-1} and 1.2 x 10^5 μm^3 ml^{-1} respectively. The effect

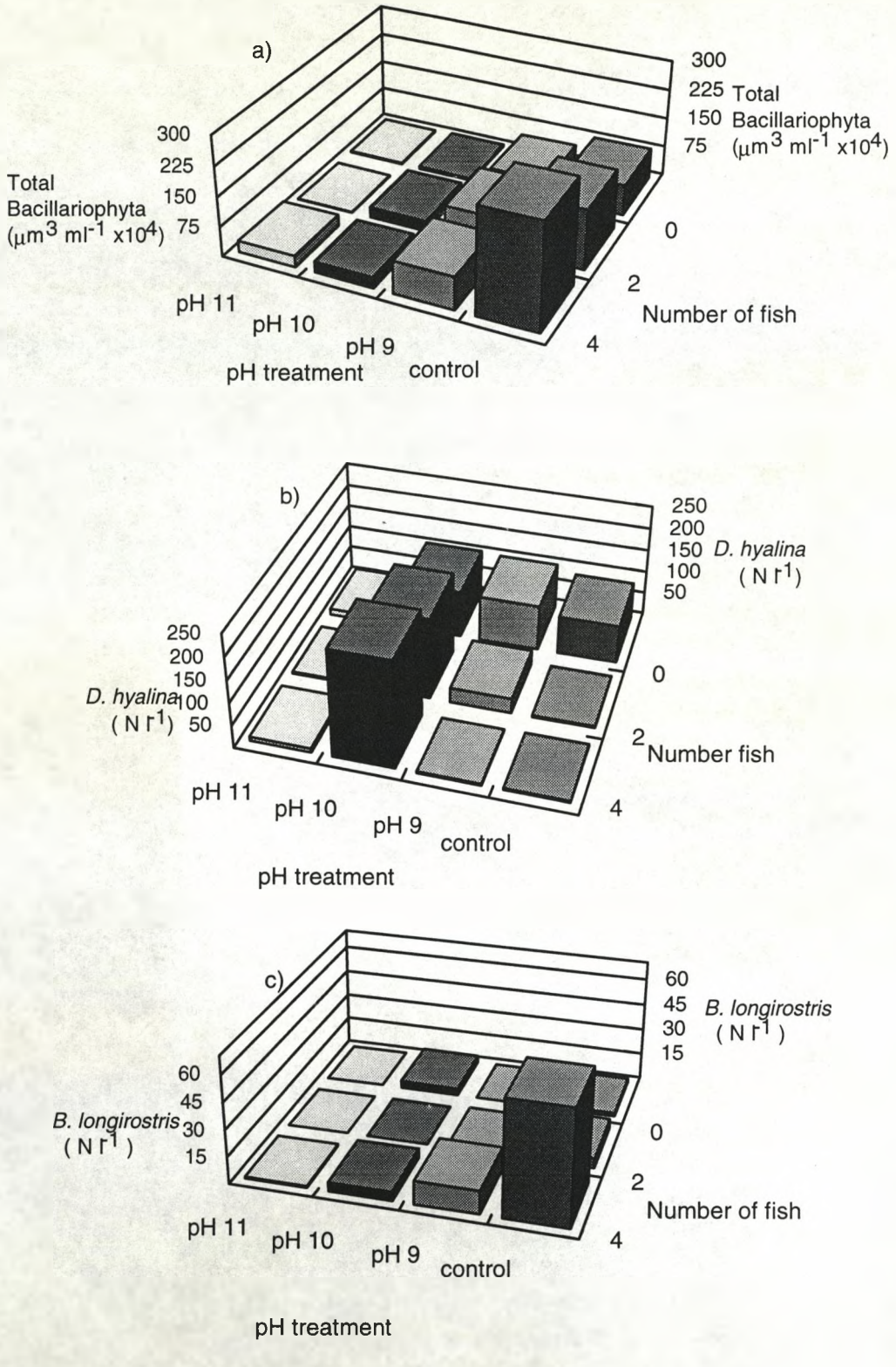

Fig. 7.4 The effects of elevated pH and increasing density of fish on biovolumes of a) total bacillariophyte, densities of b) *Daphnia hyalina* and c) *Bosmina longirostris* in an experiment carried out in Little Mere in summer 1993.

of increasing fish densities on biovolume of diatoms was not significant at the 5% level (p=0.057). The biovolumes of *Synedra ulna* and *Aulacoseira granulata* made the greatest contibution to the total biovolume of diatoms and increasing pH significantly decreased their biovolumes (P=0.022 and P= 0.002 respectively) (Table 7.2). In the control, pH 9 and pH 10 enclosures, biovolumes of *Synedra ulna* were similiar but *Synedra ulna* was absent from pH 11 enclosures. Mean biovolumes were 1.4×10^5 $\mu m^3 ml^{-1}$, 1.6×10^5 $\mu m^3 ml^{-1}$, 1×10^5 $\mu m^3 ml^{-1}$ and 0 respectively. There was a gradual decrease with increasing pH for *Aulacoseira granulata* biovolumes, 7.2×10^5 $\mu m^3 ml^{-1}$, 3.4×10^5 $\mu m^3 ml^{-1}$, 1.2×10^4 $\mu m^3 ml^{-1}$ and 4.9×10^3 $\mu m^3 ml^{-1}$ respectively. Neither the fish density nor the interaction effect of pH and fish density significantly changed biovolumes of *Synedra ulna* (P=0.64 and P=0.76 respectively) or *Aulaciseira granulata* (P=0.30 and P=0.5 respectively).

In summary (Table 7.3), the effects of increasing pH on percentage biovolumes of the main phytoplankton groups were that, throughout the experiment, Cyanophyta, though present, were never prominent. The highest biovolume of Cyanophyta was recorded in pH 9 enclosures, but the biovolume decreased dramatically at pH 10 and declined to 0 in pH 11 enclosures. Chlorophyta were predominant in the control and pH 11. The biovolume of Cryptophyta was also considerable, and high at pH 9 and pH 10, sharply decreased at pH 11. Diatoms were never dominant in the algal community and their biovolume decreased gradually with increasing pH .

7.3.5. Response of zooplankton community

Several zooplankton species responded to the manipulation of pH and fish (Table 7.2). In all treatments the filter feeding component of the cladoceran community mainly

Table 7.3. Composition of the phytoplankton community (Mean % of total biovolume ± S.D.) with increasing pH in experimental enclosures in Little Mere.

	Control	pH 9	pH 10	pH 11
Cyanophyta	2.5±5	17.3±20	0.9±0.6	0
Chlorophyta	55±53	14.7±11	22±27	89.6±92
Cryptophyta	21.2±17	59.5±62	76.2±70	7.8±5
Bacillariophyta	21.3±24	8.5±5	1.3±1.1	2.4±2.8

composed *Daphnia hyalina*, *Bosmina longirostris* and *Ceriodaphina* spp. The copepods were solely Cyclops spp. Rotifers were rare and included *Keratella quadrata* and *Keratalla cochlearis*. *Polyphemus pediculus*, an omnivorous raptorial cladoceran, was abundant in the zooplankton community.

The cladoceran, *Daphnia hyalina*, was the most abundant filter feeder, and probably of greatest importance with respect to grazing pressure. Repeated measures of ANOVA revealed that increasing pH, fish densities and interaction effects of pH and fish treatments all had significant effects on density of *D. hyalina* (P=0.0001, P=0.0001 and P=0.005 respectively) (Table 7.2). With increasing pH, its density increased except at pH 11 where *D. hyalina* was very sparse until day 20. However even though it then increased, it was low relative to the other treatments. The mean values for control, pH 9, pH 10 and pH 11 were 31 ind. l^{-1}, 46 ind. l^{-1}, 164 ind. l^{-1} and 9 ind. l^{-1} respectively (Fig. 7.4b). *D. hyalina* numbers declined severely with increasing fish densities at the lowest pH values. Control enclosures had 84 ind. l^{-1}, 4 ind. l^{-1} and 4.3 ind. l^{-1} respectively for increasing densities of fish and in the pH 9 enclosures were 101 ind. l^{-1}, 33 ind. l^{-1} and 3.8 ind. l^{-1} respectively. In pH 10 enclosures the direction of the effect of increasing fish density on *D. hyalina* was reversed and, the mean densities for 0, 2 and 4 fish enclosures were 105 ind. l^{-1}, 181 ind l^{-1} and 236 ind. l^{-1} respectively. Estimation of instantaneous per capita rate birth rate (b) and death rate (d) for all pH and fish treatments were made of using the egg ratio method (Table 7.4). Repeated measures of ANOVA on population variables of *D. hyalina* (Table 7.4) revealed that, while pH had no significant effect on birth rate (P=0.16), increasing fish densities and the interaction of pH and fish significantly decreased the birth rate in the control and pH 10 enclosures and significantly increased

Table 7.4. Mean (± S.D.) instantaneous birth (b) and death (d) rates (per day) of *Daphnia hyalina* treatments with respect to pH and fish treatments, and the effects of pH, fish and pH-fish interaction on birth and death rates of *D. hyalina* in enclosures at Little Mere. Results of repeated measures of ANOVA are shown as probability values. Symbols: *P<0.05; **P<0.01; ***P<0.001; NS= not significant. +, - signs show the direction of the effects as increase or decrease with increasing pH and fish densities.

	control			pH 9			pH 10					
Number of fish	0	2	4	0	2	4	0	2	4	pH	fish	pH/fish interaction
Birth rate	0.26 ± 0.28	0.33 ± 0.50	0.05 ± 0.02	0.22 ± 0.28	0.20 ± 0.25	0.29 ± 0.32	0.14 ± 0.20	0.15 ± 0.20	0.13 ± 0.14	NS	+/- *	+/- * *
Death rate	0.48 ± 0.2	0.31 ± 0.46	0.2 ± 0.07	0.3 ± 0.31	0.52 ± 0.29	0.32 ± 0.49	0.12 ± 0.21	-0.05 ± 0.17	0.25 ± 0.06	+/- ***	NS	+/- * * *

at pH 9 (P=0.044 and P=0.005 respectively) (Table 7.4). Increasing pH and the interactions of pH and fish density significantly decreased the death rate of *D. hyalina* between the control and pH 10 enclosures. Death rates due to pH and fish interaction increased significantly between the control and pH 9 (P=0.001 and P=0.0004), whilst the increasing fish densities had no overall effect on the death rate of D. hyalina (P=0.82) (Table 7.4). In pH 11 enclosures, after day 22, *D. hyalina* began to increase, resulting in mean denisties of 14 ind. l^{-1}, 4 ind. l^{-1} and 9 ind. l^{-1} respectively in the nominally increasing fish densities, though these were reflected only in the number of corpses present at pH 11.

Other cladocerans that responded significantly to the treatments, were *Bosmina longirostris* (Fig. 7.4c) and *Ceriodaphnia* spp. (Fig. 7.5a). Increasing pH significantly reduced *Bosmina longirostris* and *Ceriodaphina* spp numbers (P=0.003 and P=0.0001 respectively); increasing fish densities significantly increased the densities of these species (P=0.027 and P=0.016 respectively) (Table 7.1, 7.2; Fig. 7.4c, 7.5a). The interaction of pH and fish treatments had no significant effect on densities of these species (P=0.23 and P=0.5 respectively) (Table. 7.2).

Polyphemus pediculus (Fig. 7.5b) was the predominant species in the zooplankton community throughout the experiment. Repeated measures of ANOVA revealed that increasing pH significantly decreased the density of the species (P=0.019) (Table 7.2), the mean densities for the control, pH 9 pH 10 and pH 11 were 100 ind. l^{-1}, 107 ind. l^{-1} 20 ind. l^{-1} and 0.7 ind. l^{-1} respectively (Fig. 7.5b). Increasing fish density, and the interaction of pH and fish had no significant effect on *Polyphemus pediculus*. (P=0.62 and P=0.9 respectively) (Table 7.2).

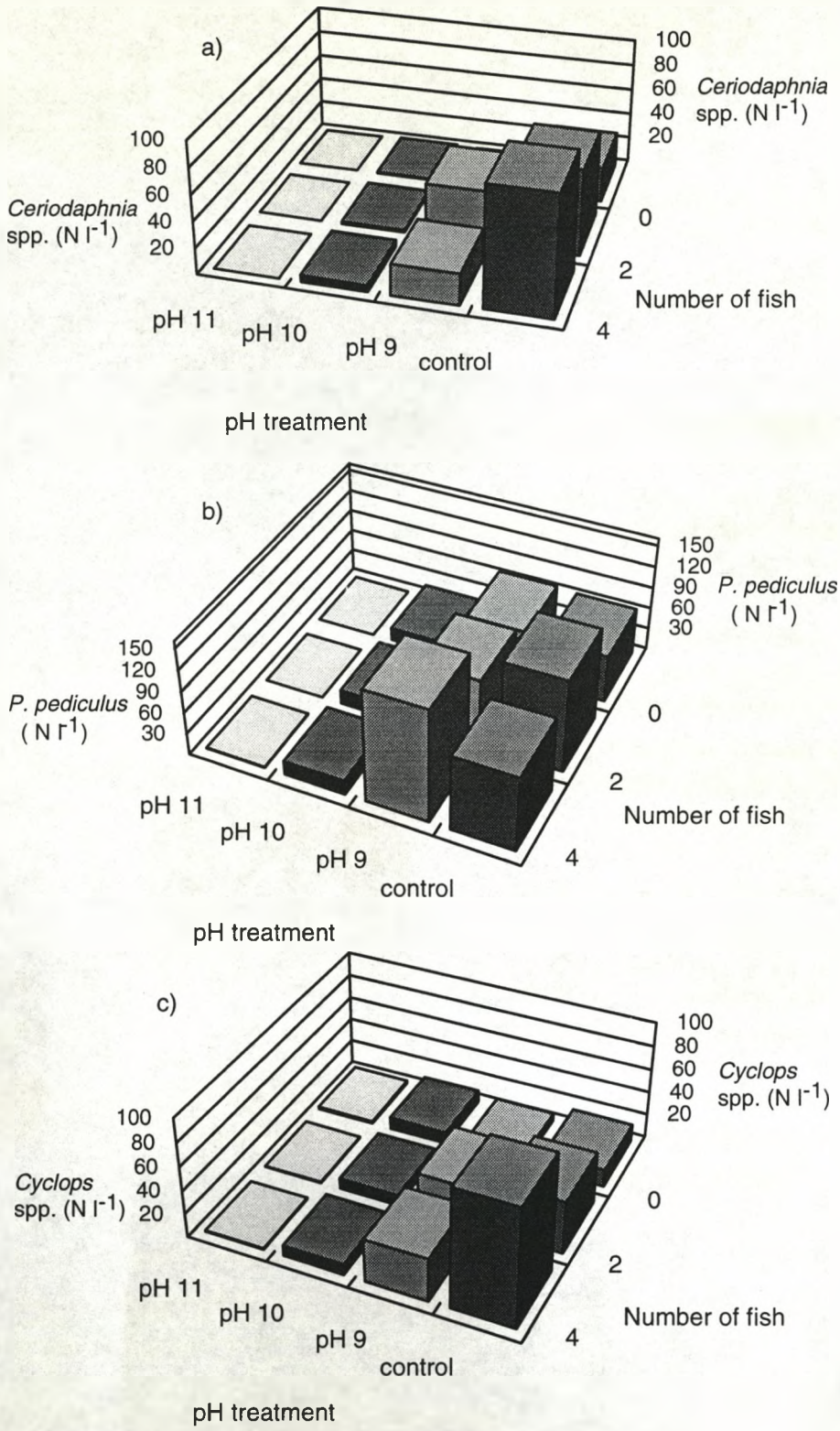

Fig. 7.5. The effects of elevated pH and increasing density of fish on densities of a)*Ceriodaphnia* spp., b) *Polyphemus pediculus* and c) *Cyclops* spp., in an experiment carried out in Little Mere in summer 1993.

Repeated measures of ANOVA performed on the density of *Cyclops* spp. (Fig. 7.5c) revealed that its density was significantly reduced by increasing pH (P=0.05) (Table 7.2). The mean densities for control, pH 9 pH 10 and pH 11 were 51 ind. l^{-1}, 25 ind. l^{-1}, 9 ind. l^{-1} and 1 ind. l^{-1} respectively. Fish density and the interaction between pH and fish did not have significant effects on the density of *Cyclops* spp. (P=0.2 and P=0.44 respectively) (Table 7.2).

7.4 Discussion

The results of the experiment may be discussed in the contexts of the hypotheses initially posed. These were that increasing pH would increase the proportion of cyanophytes in the phytoplankton biomass; that increasing fish density would likewise increase the proportion of cyanophytes in the context of an increasing total phytoplankton biomass; and that numbers of *Daphnia* would decline with increasing fish density irrespective of pH change.

Increasing pH did not result in increasing proportions of cyanophytes and resulted in decreasing total biovolumes of phytoplankton and decreasing concentrations of chlorophyll a. The reason for anticipation of increased amounts of cyanophytes arose from proposals by Shapiro (1990a). Shapiro outlined several current views relating sets of environmental factors to high biomasses of cyanophytes, including increased temperature, low light availability, low nitrogen to phosphorus ratios, ability to move between layers in stratified lakes, low vulnerability to grazing by zooplankters and the ability to thrive at very low carbon dioxide concentrations. In all cases there was evidence of some relationship but the evidence pointed to the latter circumstance, the availability of carbon dioxide, as a master variable with which the others might be directly or secondarily linked. Cyanophytes in general have lower K_s values for carbon dioxide uptake than other algae, demonstrated ability to continue photosynthesis at the high pH values (to 11) found in some highly fertile lakes, lower carbon dioxide compensation points than other algae, and a high ability to concentrate carbon dioxide from low concentrations in the water.

The conditions created in the experimental bags should amply have favoured

cyanophytes. pH values were high, carbon dioxide concentrations were low, the water was supplied with inocula from the upstream lake, Mere Mere where cyanophytes are predominant summer feature and suitable inocula were present over a sufficiently long period for significant populations to have developed. In addition the phosphorus concentrations were high whilst nitrogen was present but appeared in low N:P ratios (Table 7.1). The experiment was conducted at summer temperatures, provision was made for high grazing intensity. Growth of algae in some enclosures resulted in low underwater light intensity. Stratified conditions were not present but there are examples of lakes with dense cyanophyte populations that are unstratified (see Reynolds & Walsby, 1975). Despite all this, cyanophytes remained relatively minor components of algal communities in the bags. There was a small increase at pH 9 where a mean allocation of biomass to cyanophytes of 17.5% was found but there was no trend upwards with pH and much greater proportionate biomasses of cryptophytes (pH 9 and pH 10) and Chlorophyta (control and pH 11) were found. Cyanophyte mean biomass in upstream Mere Mere is at least 100 times greater than that found in the experimental enclosures whilst Mere Mere has pH values and carbon dioxide concentrations spanned by those provided in the enclosures.

There was also no relationship between cyanophyte biomass with fish density and hence it is difficult to see much support for any of the conventional hypotheses concerning factors favouring cyanophytes from the result of this experiment. The experimental results are consistent with events that have transpired in the lake itself. As fish moved in, the expected loss of zooplankton grazing potential had not materialized although there had been a switch from *Daphnia magna* to *Daphnia hyalina*, the water has remained clear, algal populations remain low and submerged

plant populations have thrived. The buffer mechanisms that are purported to stabilize plant-dominated communities (Moss, 1991, Scheffer *et al.* 993) appear to be very effective.

Chlorophyta and Cryptophyte were favoured by pH, the former to pH 11, the latter to pH 10. Chlorophyta were also favoured by increasing fish densities though there were no fish effects on Cryptophytes. Jensen *et al.* (1994) have found increasing dominance of Chlorophyta in shallow hypertrophic lakes (with pH values up to 10.1) and attributed it to high availability of nutrients and carbon dioxide released from the sediments. They suggest that high growth rates make Chlorophyta superior competitors to cyanophytes even when available nutrients are low and pH is high. The present results are consistent with those of the surveys carried out by Jensen *et al.* (1994) but suggest that the reasons for increasing Chlorophyta dominance must be more complex in that supply of nutrients from the sediments was prevented during the experiment and carbon dioxide concentrations were maintained at very low values. Because they are small, edible and generally readily grazed, the increase in chlorophytan representation with increasing fish density (and hence declining grazer density, see below) was not unexpected but the similarly expected trend was not observed in the comparable cryptophytes. Nor was it in the trend of diatom biovolume where there was a strong decline with pH but no effect of fish (though the probability value at 0.057 was close to conventional significance). The apparent lack of grazer effects on cryptophytes and diatoms might be due to high growth rates of algae compensating for grazer losses but they may be due to subtle changes in feeding behaviour of zooplankters at high pH. At pH 10 especially, large numbers of *Daphnia* were associated with large biomasses of edible algae, suggesting that feeding rates were in

some way impaired by high pH. One of the few significant interaction effects detected was on *Daphnia* abundance.

Total phytoplankton biomass, predicted to increase with fish abundance, indeed did so but declined with increasing pH. The former effect might be expected from the very large literature that now links decline in large filter-feeding Cladocera with increases in zooplanktivorous fish but the links here are clearly more complex. *Daphnia* was the main filter feeder and did decrease with fish number in the controls and at pH 9. It increased in number with increasing fish density at pH 10 and its numbers collapsed, as did the fish, at pH 11. The increase at pH 10 was not associated with major changes in birth or death rates and must be attributed, since all the fish survived, to changes in fish feeding behaviour at this potentially stressful high pH. Serafy & Harrell (1993) found that three species of shallow water fish [banded killifish (*Fundulus diaphanus*), bluegill (*Lepomis macrochirus*), and juvenile striped bass (*Morone saxatilis*, Walbaum)] avoided pH values exceeding pH 9.5. Although *Daphnia hyalina* clearly thrived at pH 10, and indeed increased with pH up to pH 11, other, smaller, filter feeding zooplankters (*Ceriodaphnia* sp and *Bosmina longirostris*) showed conventional increases with fish density at all pH values in which fish survived but both significantly declined with pH.

Previous studies (Bogatova, 1962; Walter, 1969) have shown a generally deterious effect of high pH on Cladocera but with some species specificity. *Ceriodaphnia reticulata* survivorship markedly declined between pH 10.5 to pH 11 in experiments carried out in ponds in New York State and in the laboratory (O'Brien & De Noyelles 1972) and the effect was apparently directly linked with pH. In experiments in

enclosures, from which fish were excluded, in a Danish Lake, Hansen *et al.* (1991) found that over the pH range, 9.0 to 10.6, numbers of *Daphnia longispina*, *Bosmina longirostris* and *Chydorus sphaericus* significantly decreased, whilst those of *Daphnia magna*, *Cyclops vicinus* and *Cyclops strenuus* were unaffected. Walter, (1969) found pH 11 to be toxic to both *Daphnia pulex* and *D. magna*, whilst Bogatova, (1962) found lethal limits between pH 10.6 to 11 for various Chydoridae. The marked reduction in Cladocera at pH 11 in the present experiment is consistent with an upper limit of about 10.5 to 11 for Cladocera in general. Below this there seems to be differential tolerance with considerable ability of *Daphnia* species to survive and increase at pH 10 and somewhat above. In Hansen's *et al.* (1991) experiments, although *Daphnia longispina* was less abundant at pH 10.6 than in controls at pH 9 and below, it still reached population densities of up to 110 animals per litre. At such densities it must have been actively feeding, as *Daphnia hyalina* must have been at pH 10 in the present experiment. There thus seems evidence that at pH values above 9.5 or 10, fish activity may be impaired though they survived whilst the activity of large filter feeding Cladocera may continue to pH values about one unit higher.

In the present experiment, numbers of *Cyclops* spp. decreased with pH as did those of the raptorial cladoceran, *Polyphemus pediculus*, which was very abundant in the enclosures. Neither taxon was significantly affected by fish, presumably because of their rapid movements and, in the latter case, considerable visual abilities in helping to avoid attack.

Thus the first hypothesis posed - that increasing pH would increase the proportion of cyanophytes in the phytoplankton-was rejected; the second - that increasing fish

density would increase the biomass of phytoplankton - was supported though its rider, that there would be an increasing proportion of cyanophytes in this biomass, was not; and the third hypothesis - that *Daphnia* would decline with increasing fish density, irrespective of pH - was rejected. *Daphnia* became abundant at pH 10 irrespective of the number of fish. What are the implications of these results in the understanding of processes that go on in shallow lakes and in the restoration of them?

First it would seem wise to stop generalising about whole algal groups such as the cyanophytes and to accept that simple, single cause and effect relationships are unlikely to be helpful in explaining the functioning of complex systems. Shapiro's (1990a) superficially very convincing arguments were based largely on reductionist studies of single species under laboratory conditions and though the magnitude of K_s values and the like undoubtedly reflects real properties of the algae, their relevance under ecosystem conditions is perhaps hidden under the effects of more powerful environmental factors. In this experiment there was every reason for an upsurge of cyanophytes; but it simply did not happen, for reasons that we do not know. Such reasons can only be adduced from more complex field experiments. However, experiments that cross classify even two major factors with graded treatments and even minimal replication are costly and logistically complex. This one involved 36 enclosures. Manipulation of a third factor at three levels with the same replication would increase this to 108. Some comfort may be drawn from the comparative shortage of interaction effects between pH and fish density. However, one of these effects concerned the numbers of *Daphnia hyalina*, an organism representative of a key link in shallow lakes.

Daphnia spp. are important phytoplankton grazers and may control the algal crops in shallow lakes (Moss *et al.* 1994). They appear to be one of the important buffers that maintain clear water and a suitable environment for submerged macrophytes in waters that are often nutrient rich and capable of supporting large algal crops (Moss, 1990; 1991; Scheffer *et al.* 1993). Other Cladocera present in plant beds may also be important (Moss *et al.* 1995) though they have been little investigated. Their absence through predation in waters that have lost their macrophyte communities seems to be an important factor in stabilising the then established phytoplankton crops so that biomanipulation is consequently necessary for reestablishment of plants (Moss, 1992a). pH may have an important role in operation of these functions.

In these experiments, pH values of 10 and 11 had important differential effects on both *Daphnia* and perch. At pH 10 *Daphnia* was abundant and perch survived but did not consume it. The fish died at pH 11 and *Daphnia* was greatly reduced in numbers. pH values in the region of 10.5 to 11 have been recorded elsewhere as lethal to various species of Cladocera, whilst some e.g. *Daphnia magna* (Hansen *et al.* 1991) are unaffected at least at pH 10.6. In and around plant beds, in the afternoon, pH values may easily rise to such values (Shutte & Elseworth, 1954; Mizuno, 1961; Stangenberg-Oporowska, 1966; Walter, 1969; O'Brien & De Noyelles, 1972) and potentially contribute to a discouragement of fish predation and an enhancement of refuge role of macrophyte beds for grazing Cladocera (Timms & Moss, 1984). Serafy & Harrell (1993) did not find that fish avoided macrophyte beds in a species rich-North American shallow lake but the pH values recorded were less than 10. Small differences in the pH at these general levels represent very large changes in ion concentrations. Venugopal & Winfield (1993) also found no reduction in the incidence

of juvenile cyprinid fish within weed beds compared with open water in a hypertrophic pond and argue against the refuge function proposed by Timms & Moss (1984). However, if increased pH within the beds affects fish feeding behaviour, it would be possible to reconcile the separate evidence of large populations of Cladocera which build up in the plant beds, access of fish to the beds and the increased growth rates of fish in weedy lakes as a result of the fish feeding in the open water on cladocerans drifting out of the beds.

In macrophyte-dominated systems the pH increase generated by macrophyte photosynthesis may be muted by the carbon dioxide generated by decomposition at the bases of plant beds. This may also be true in phytoplankton dominated shallow lakes but perhaps to a lesser extent as much of the produced biomass is washed out of the lake rather than accumulated on the bottom. In such circumstances pH values may rise marginally higher to the point where pH becomes lethal to most cladoceran species and may eliminate the possibilities of much grazing even where fish are absent or not feeding. The ponds of O'Brien & De Noyelles, (1972) would appear to be in this category as are sewage oxidation ponds (Verduin, 1971). Talling, (1976) lists several large lakes in which values above 10 have been recorded. Such conditions are more likely however in shallow waters in lowland catchments with high populations and intensive agriculture. Where pH does rise to such values as a result of phytoplankton photosynthesis, it may act as an additional factor buffering the maintenance of the phytoplankton-dominated state.

The course of events in Little Mere following the diversion of sewage effluent in 1991 was, by 1993, one of maintenance of the grazer-maintained, clear water, macrophyte-

dominated conditions found prior to diversion and attributed to lack of fish through deoxygenation. Fish, perch in particular, colonised the Mere in considerable numbers but had not prevented the development of substantial *Daphnia hyalina* populations. We attribute this to the refuge role played by the plants for the water remained extremely nutrient rich as a result of release of phosphate and ammonium from the sediment. The results of the enclosure experiments reported here support this interpretation, for increasing fish densities in the absence of macrophyte refuges in the enclosures led to markedly increased phytoplankton crops. They also hint that the increased pH predicted from the expansion of the plant beds that has so far occurred will help maintain plant dominance rather than result, with the operation of other factors, in an increasing predominance of cyanophytes. But the complexity of species specific effects such as the differential effects of pH on *Daphnia hyalina* and other zooplankters advise caution in far reaching prediction.

Chapter 8: Diurnal sampling of some water chemistry variables and zooplankton in Little Mere in 1993 and 1994

8.1. Introduction

Many taxa of both marine and freshwater zooplankton perform diel vertical migrations (Hutchinson, 1967). The normal pattern is an evening ascent and a morning descent, though some exceptions have been recorded (Bayly, 1986). The presence of diurnal vertical migration in so many taxa suggests that it has some adaptive value (Lampert, 1989) which has been explained by several competing hypotheses, for example: metabolic and demographic advantages (Swift, 1976); and resource related diurnal migration (Stich & Lampert, 1984). Probably the strongest argument in favour of demographic advantage though predation-avoidance has been provided by Gliwicz (1986). He found a clear relationship between the amplitude of diurnal vertical migration and the period for which the lake had had a fish population in various lakes of the Tatra mountains.

This behavioural defense of planktonic herbivores appears to avoid fish predation pressure through exploitation of physical and chemical factors as refuges in deep lakes. The most commonplace defensive behaviour of planktonic animals is to move to safer habitats in deep strata where low light intensity does not allow planktivorous fish to feed efficiently during the daytime (Zaret & Suffern, 1976; Confer *et al.* 1978). Taking visual refuge appears to be one of the most important defense mechanisms in Peter Lake, where removal of the visual refuge by alum treatment resulted in disappearance of *Daphnia pulex* which was previously abundant in the presence of

high rainbow trout density (Kitchell & Kitchell, 1980). Another potential refuge need by diurnally migrating *Daphnia* is low oxygen concentrations which are tolerated by zooplankton but in which fish can not survive continuously (Prepas & Rigler, 1978; Summerfelt, 1981; Burns & Mitchell, 1980). Diurnal shift to safer but cooler hypolimnetic habitats to use low temperature as refuge (Dawidowicz & Loose, 1992) is also widely used by zooplankton. In deep lakes, diurnal vertical migration of zooplankters to lower light, DO and temperature refuges appear to be efficient defense strategies to protect against fish predation (Lampert & Taylor, 1985; Dini & Carpenter, 1992).

Contrary to studies on deep lakes and their open-water cladoceran defense strategies, little is known about potential similar defense strategies of cladocerans against fish predation in shallow lakes. Stands of macrophytes, however, have been shown to act as refuges for large *Daphnia* in the presence of planktivorous fish (Crowder & Cooper, 1982; Timms & Moss, 1984). The study of Timms & Moss (1984) suggested that large-bodied, open-water grazers move horizontally out of the plant beds in darkness to feed on the phytoplankton crop. In the 1993 diurnal sampling described below, this suggestion was investigated.

Timms' & Moss' (1984) study also showed the efficiency of water lilies for sheltering *Daphnia* and this has been recorded in several other shallow lakes (Carvalho, 1994; Moss *et al.* 1994; Beklioglu & Moss, in preparation). Contrary to the efficiency of floating-leaved plants for sheltering *Daphnia*, avoidance of *Ceratophyllum demersum*

by *Daphnia longispina* was found (Dorgelo & Heykoop, 1985) and attributed to photosynthetic activity of the plant. The disappearance of *Daphnia* and increased weed-associated zooplankters were recorded in *C. demersum* beds (Irvine *et al.* 1990b). We hypothesised that floating-leaved plants are more effective than submerged plants for providing refuges to open-water Cladocera against fish predation because floating-leaved macrophytes and submerged plants have very different physical and chemical effects on the associated water depending on daily intensity of photosynthesis and respiration (Carpenter & Lodge, 1986; Frodge *et al.* 1990). No avoidance of macrophytes by fish has been recorded (Serafy & Harrell, 1993; Venugopal & Winfield, 1993). Thus, the intensity of changes created in floating-leaved plant beds during day time might be severe enough to impair feeding of fish and in turn provide predation-free habitat to zooplankton, just as large zooplankters in stratified lakes use deeper hypolimnetic water as a refuge against fish predation.

Little attention has been paid to loosely or firmly weed-associated zooplankters of shallow lakes and the littoral zone of deep lakes, though within submerged plant beds a wide range of invertebrates species is found, including the herbivorous filter-feeders *Simocephalus* species and *Sida crystallina* (Quade, 1968; Smirnow & Davis, 1973). Most studies on zooplankton communities within submerged plant beds have tended to be descriptive (Smyly, 1952; Whiteside, 1970; 1974) with a few exceptions (Szlauer, 1962; Fairchild, 1981; Irvine *et al.* 1990b). Fairchild (1981) found no diurnal migration of weed-associated *Simocephalus* and *Sida* which hardly moved from the submerged plant beds during day and night. However, *Chydorus* and *Eurycercus*

lamellatus showed clear diurnal migration in that they stayed in the plant beds during day time and moved up to the water surface at night (Szlauer, 1962; Fairchild, 1981). We hypothesised that submerged plants would be safer refuges to weed-associated zooplankters due to their evolutionary adaptations to the plant beds but not to open-water zooplankters because the physical and chemical changes in the associated water may not be severe enough to impair feeding of fish.

To have a better understanding of interactions between zooplankton and fish in macrophyte beds would allow us to improve control of eutrophication. We took advantage of the current dense stands of floating-leaved plants, and the submerged plant, *Potamogeton berchtoldii*, in Little Mere, to examine possible diurnal migration of both open-water and weed-associated zooplankters and the efficiency of both macrophytes for sheltering cladocerans against fish predation in relation to chemical and physical changes in the associated water created by the plants. Data are also given in this chapter a fish communities and plant communities.

8.2. Method

8.2.1 Diurnal sampling in 1993

Diurnal sampling of zooplankton and chlorophyll a was carried out on 14th/15th August 1993 in Little Mere. Five sampling stations were chosen among the present macrophyte communities and the open water of the lake. Two of the sampling stations were densely covered by water lilies *(Nymphaea* alba and *Nuphar lutea*). Two other stations were in open water, though one of them had a very small patch of *Elodea canadensis.* The last station had a medium density stand of *Potamogeton berchtoldii* and there was a small patch of *Elodea canadensis* as well.

Samples were taken from the stations at 10:00 hr, 15:30 hr, 20:30 hr, 01:30 hr and 06:00 hr BST. The weather was warm but not very bright and relatively calm. For zooplankton sampling, 10 l of water were taken using a tube sampler from each station. The method for zooplankton sampling was described in Chapter 3. For chlorophyll a 300 ml water sample was taken using a tube sampler and the method was described in Chapter 2.

8.2.2 Diurnal sampling in 1994

Diurnal sampling of zooplankton, chlorophyll a, alkalinity, temperature, dissolved oxygen and pH was carried out on 12/13 August 1994. Five sampling stations were chosen, as in the previous year, but the macrophyte density and communities were different as the lake had changed. Two of the sampling stations were densely covered by water lilies (*Nymphaea alba* and *Nuphar lutea*) as in the previous year. The total

coverage of macrophytes was greater in 1994 than in the previous year and the open water station was only nominal and had a substantial patch of *Elodea canadensis* in the bottom. The last two stations were densely covered by *Potamogeton berchtoldii* and some filamentous algae were present.

Samples were taken at 10:30 hr, 13:00 hr, 15:00 hr, 19:30 hr, 00:00 hr and 08:00 hr. The weather was warm but not sunny, and there were spells of rain and wind. Sampling of zooplankton and chlorophyll a was carried out as described above. Temperature and dissolved oxygen concentrations were measured using a WTW oxygen-meter to precision of ± 1%. Free-CO_2 and total alkalinity were determined according to Mackereth *et al.* (1978). For pH measurement, small water samples were collected from the surface, mid-depth and bottom of the each station with a remote sampler consisting of a 60 cm^3 hypodermic syringe without a needle, attached to a long, stiff graduated pole. The water was transferred into a 30 ml beaker with minimum disturbance and the pH measured with a 3050/3070 Jenway field pH meter.

8.2.3 Fishing

Fishing of the lake was carried out on three occasions in January 1993, June 1993 and November 1993 in the same locations. A micro-mesh seine net was used (25 m long, 2 m deep, 2.5 mm mesh-size). Length of fish caught was measured from snout to the base of the tail fork.

8.2.4 Aquatic plants survey

Aquatic plants were surveyed in August 1993. Sampling was carried out from a boat using a grapnel and a Petersen grab. Aquatic plants were identified using Haslam, Sinker & Wolseley (1975). Percentage cover of submerged and floating-leaved communities was estimated from a weighed photocopied image of the vegetation map.

8.3. Results

8.3.1 Diurnal sampling in 1993

Table 8.1 shows mean values (± S.D.) of chlorophyll a and zooplankton densities. Two-way ANOVA performed on chlorophyll a concentrations showed that whilst the habitats had significant effects on the concentrations (P=0.02) (Table 8.2), sampling time and interaction of sampling time and the habitats had no significant effect on the chlorophyll a concentrations (P=0.7 and P=0.7 respectively). The highest concentrations of chlorophyll a were found associated with *Potamogeton berchtoldii* and the lowest were in the lily beds (Fig.8.1a). Two-way ANOVA performed on zooplankton densities, revealed significant effects of the habitats on densities of *D.hyalina*, *Bosmina longirostris* and *Ceriodaphnia* sp. (P=0.0018, P=0.007 and P=0.034 respectively) (Table 8.2). No significant effects of sampling time on the densities of these species were found (P=0.18, P=0.1 and P=0.17 respectively) (Table 8.2). Whilst the interaction effect of sampling time and habitat revealed a significant effect on density of *D.hyalina* (P=0.004), no significant effect of the interaction was found on the densities of *Bosmina longirostris* and that of *Ceriodaphnia* sp. (P=0.76 and P=0.44 respectively) (Table 8.2). Whilst the highest densities of *D.hyalina* were recorded in lily beds, *Bosmina longirostris* had its highest density in *Potamogeton berchtoldii* beds and *Ceriodaphnia* sp. was in the open water. Whilst the lowest densities of *D.hyalina* were in *Potamogeton berchtoldii* beds, those of *Bosmina longirostris* and *Ceriodaphnia* sp. were in lily beds (Fig 8.2 a,b and c). Two-way ANOVA employed on densities of *Eurycercus lamellatus*, *Chydorus* sp, *Polyphemus pediculus*, *Simocephalus* sp., *Cyclops*+nauplii and rotifers showed that the sampling time, the habitats and the interaction effects of the sampling time and the habitats had

Table 8.1 Mean values (±SD) of chlorophyll a concentrations and zooplankton densities at the different stations in diurnal sampling on 14th/15th August 1993 in Little Mere (n=5).

	Water lily (Station1)	Water lily (Station 2)	open-water (Station 3)	open-water (Station 5)	*P.berchtolldi* (Station 4)
Chlorophyll a (μg l^{-1})	13±3	8.7±1	12±2	20±8	16±2
D.hyalina (ind.l^{-1})	75±15	51±18	12±5	33±12	6±3
B.longirostris (ind.l^{-1})	1.4±0.7	2.2±1.4	58±4	113±41	124±33
Ceriodaphnia sp.(ind.l^{-1})	9.4±2	11±4	49±16	210±82	144±48
P.pediculus (ind.l^{-1})	2±0.6	0.4±0.2	0±0	1±1	0±0
E.lamellatus (ind.l^{-1})	14±3	31±15	17±3	28±15	2±2
Chydorus sp. (ind.l^{-1})	33±7	12±2	3±0.5	21±9	2±2
Simocephalus sp.(ind.l^{-1})	1.2±0.5	1.2±0.8	4±1.4	6±2.5	6±5
Cyclops+nauplii (ind.l^{-1})	120±61	67±14	104±8	88±31	169±57
Rotifers (ind.l^{-1})	5±3	4.6±0.6	7±4	6±6	9±4

Table 8.2 Summary of effects of the sampling time, the different habitats and the time-habitats interaction on the chlorophyll a concentrations and zooplankton densities in diurnal sampling on14th/15th August 1993 in Little Mere following two-way ANOVA. Symbols *P<0.05, **P<0.01, ***P<0.01 and NS: no significance.

	Time	Habitats	Interactions
Chlorophyll a (μg l^{-1})	NS	*	NS
D.hyalina (ind l^{-1})	NS	* * *	*
Bosmina longirostris (ind l^{-1})	NS	* *	NS
Ceriodaphnia (ind l^{-1})	NS	*	NS
Polyphemus pediculus (ind l^{-1})	NS	NS	NS
Eurycercus lamellatus (ind l^{-1})	NS	NS	NS
Chydorus sp. (ind l^{-1})	NS	NS	NS
Simocephalus sp. (ind l^{-1})	NS	NS	NS
Cyclops + nauplii (ind l^{-1})	NS	NS	NS
Rotifers (nd l^{-1})	NS	NS	NS

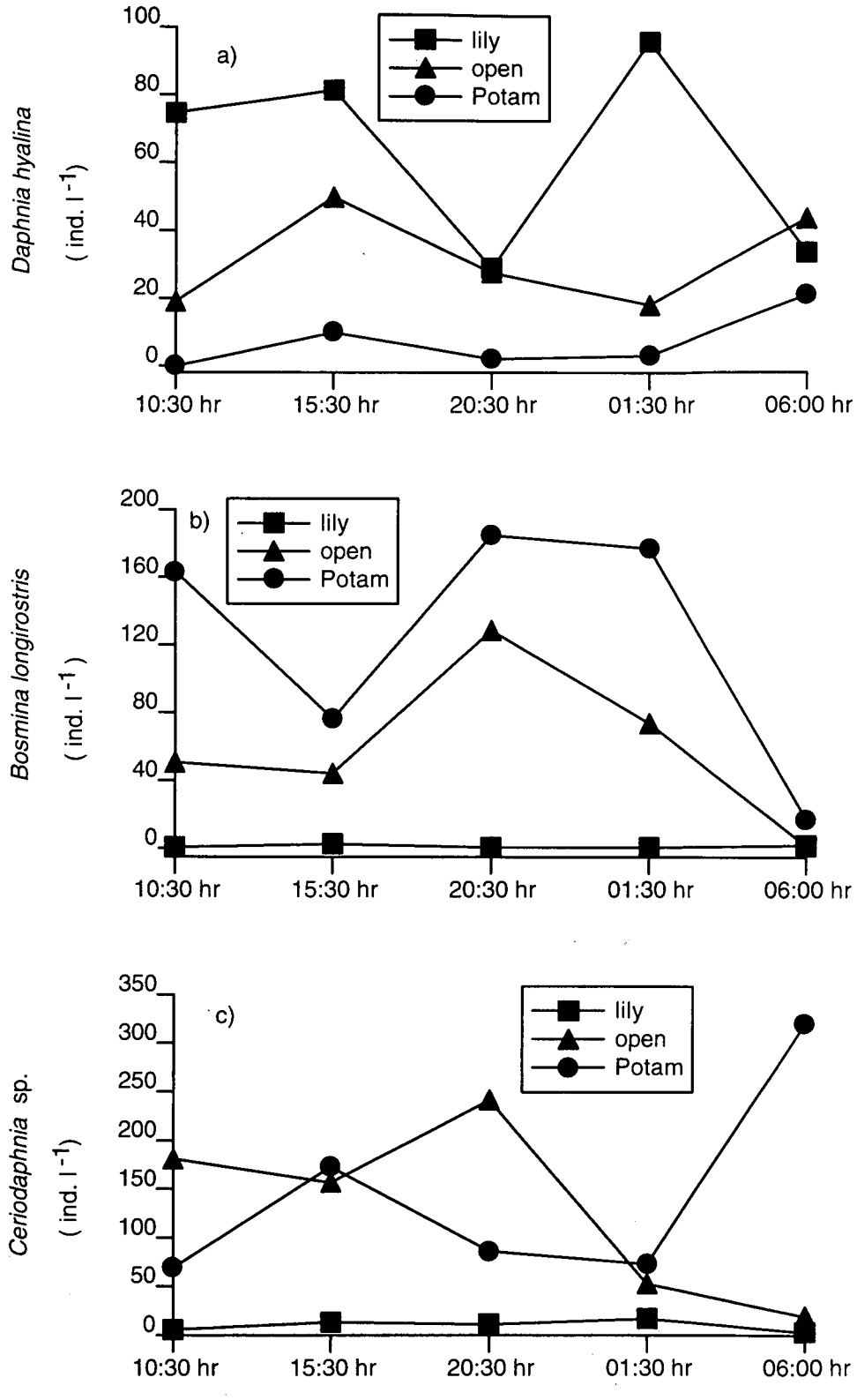

Fig. 8.2 Changes in densities of a) *Daphnia hyalina*, b) *Bosmina longirostris* and c) *Ceriodaphnia* sp. in diurnal sampling on 14th/15th August 1993 in Little Mere.

time, the habitats and the interaction effects of the sampling time and the habitats had no significant effects (Table 8.2).

8.3.1 Diurnal sampling in 1994

Table 8.3 shows mean values (± S.D.) of water chemistry, chlorophyll a and zooplankton densities.Two-way ANOVA performed on the water chemistry and chlorophyll a showed that the different habitats had significant effects on chlorophyll a concentrations, dissolved oxygen, free-CO_2 and pH ($P<0.001$, $P=0.0012$, $P<0.001$ and $P<0.001$ respectively) (Table 8.4). The sampling time had a significant effect only on dissolved oxygen concentrations ($P=0.02$) whilst the interaction between sampling time and habitats had significant effects on the chlorophyll a concentrations, free-CO_2 and pH ($P=0.005$, $P=0.04$ and $P=0.02$ respectively) (Table 8.4). There was no significant interaction effect on the dissolved oxygen concentrations ($P=0.09$) (Table 8.4). The highest concentrations of chlorophyll a were found in the lily beds. The concentrations of chlorophyll a were similarly low both in *Potamogeton berchtoldii* beds and the open water (Fig 8.1b). The dissolved oxygen concentrations reached their highest values in the afternoon and gradually decreased in the evening to the lowest values at the midnight in all three habitats. The highest dissolved oxygen concentrations were found in *Potamogeton berchtoldii* beds and the lowest values were recorded in the lily beds (Fig 8.3 a). In the lily beds, the highest free-CO_2 concentrations and the lowest pH values were recorded and the opposite was found in *Potamogeton berchtoldii* beds as free-CO_2 concentration is closely related to pH values (Fig.8.3 b and c).

Table 8.3 Mean values (±SD) of water chemistry, chlorophyll a concentrations and zooplankton densities at the different stations in diurnal sampling on 12th/ 13th August 1994 in Little Mere (n=6).

	Water lily (Station1)	Water lily (Station 2)	open-water (Station 3)	*P.berchtolldi* (Station 4)	*P.berchtolldi* (Station 5)
Chlorophyll a ($\mu g\ l^{-1}$)	63±6	63±7	28±4	32±3	30±3
Dissolved-oxygen(mgl^{-1})	2.4±0.4	2.7±0.4	4.4±0.4	4±0.4	5±0.8
Free- CO_2($\mu g\ l^{-1}$)	0.87±0.1	0.77±0.4	0.5±0.08	0.34±0.005	0.1±0.04
pH	6.9±0.06	7±0.05	7.2±0.09	7.4±0.009	7.8±0.1
B.longirostris($ind.l^{-1}$)	42±19	83±20	32±7	36±26	16±5
Ceriodaphnia sp.($ind.l^{-1}$)	1114±446	1073±106	185±52	192±36	366±99
E.lamellatus ($ind.l^{-1}$)	3±2	4±0.8	0.8±0.3	55±19	49±12
Chydorus sp. ($ind.l^{-1}$)	6±3	2.3±1.5	0.5±0.3	179±62	41±9
P. pediculus (ind.l-1)	35±25	305±94	22±4.2	4.8±2.2	1.5±1.1
Simocephalus sp.($ind.l^{-1}$)	1.6±1.1	3.2±1.2	0.2±0.2	204±91	102±41
D.brachyurum ($ind.l^{-1}$)	144±57	82±16	4±1	0.6±0.4	0±0
Cyclops+nauplii ($ind.l^{-1}$)	259±59	230±39	108±21	333±85	261±57
Rotifers ($ind.l^{-1}$)	52±18	54±14	24±8	32±14	57±12

Table 8.4 Summary of effects of the sampling time, the different habitats and the time- habitats interaction on the water chemistry, chlorophyll a concentration and zooplankton densities in diurnal sampling on 12th/13th August 1994 in Little Mere following two-way ANOVA. Symbols*P<0.05, **P<0.01, ***P<0.01 and NS: no significance.

	Time	Habitats	Interaction
Chlorophyll a ($\mu g\ l^{-1}$)	NS	* * *	* *
Dissolved-oxygen ($mg\ l^{-1}$)	*	* *	NS
Free-CO_2 ($\mu g\ l^{-1}$)	NS	* * *	*
pH	NS	* * *	*
Bosmina longirostris ($ind.l^{-1}$)	NS	NS	NS
Ceriodaphnia sp. ($ind.l^{-1}$)	NS	* * *	*
Eurycercus lamellatus ($ind.l^{-1}$)	NS	* * *	*
Chydorus sp. ($ind.l^{-1}$)	NS	* *	NS
Polyphemus pediculus ($ind.l^{-1}$)	NS	*	NS
Simocephalus vetulus ($ind.l^{-1}$)	NS	* *	NS
Diaphanosoma brachyurum ($ind.l^{-1}$)	NS	* * *	NS
Cyclops s_{L} + nauplii ($ind.l^{-1}$)	NS	*	*
Rotifers ($ind.l^{-1}$)	NS	NS	NS

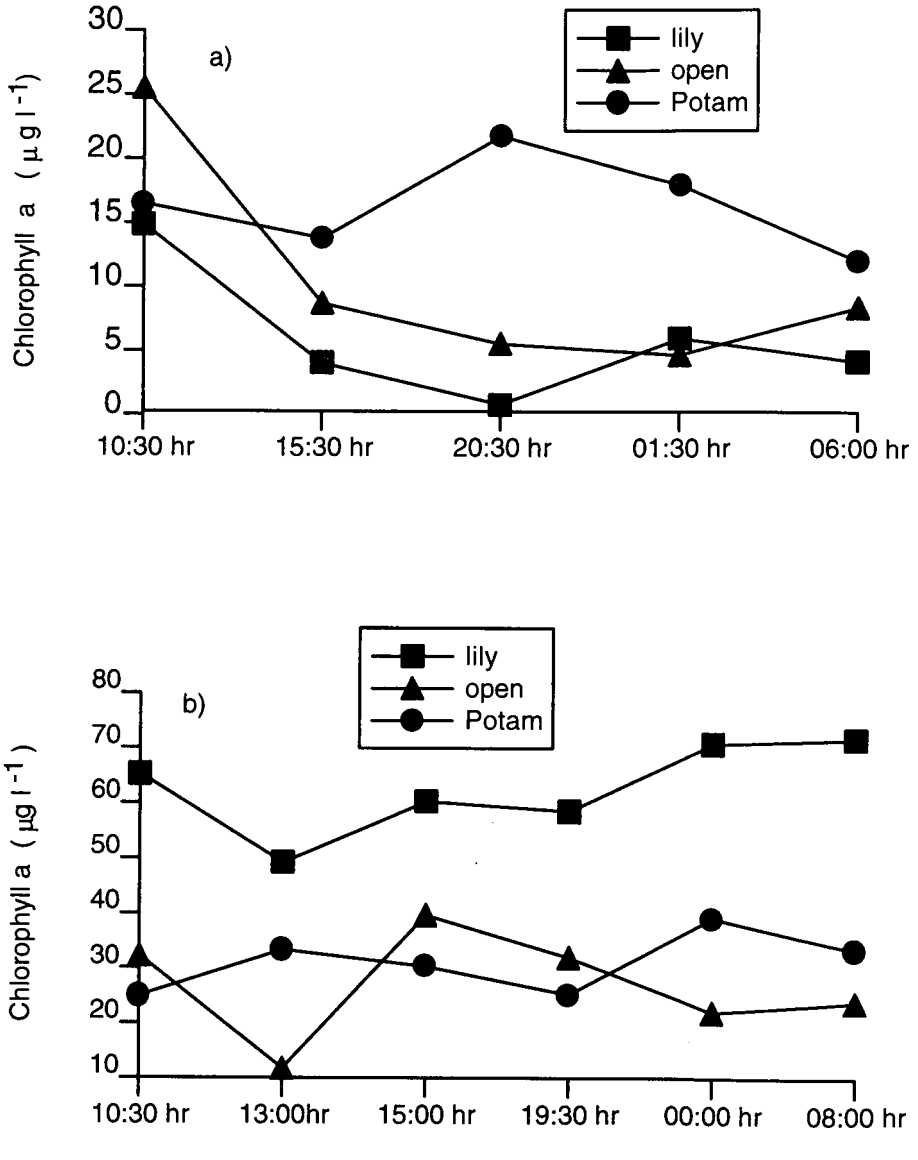

Fig. 8.1 Changes in concentrations of chlorophyll a in diurnal samplings a) on 14th/15th August 1993 and b) on 12th/13th August 1994 in Little Mere.

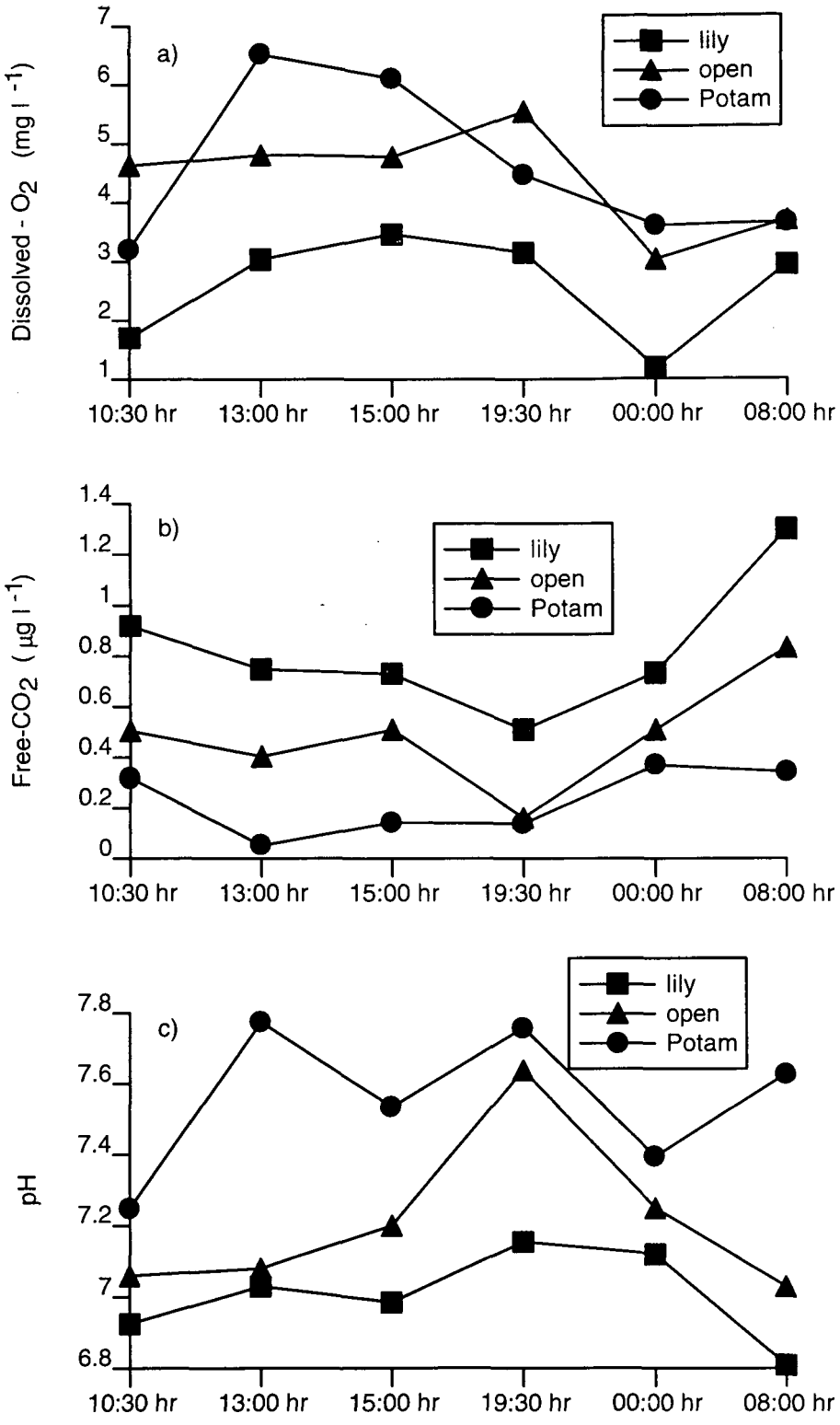

Fig. 8.3 Changes in concentrations of a) dissolved-oxygen, b) free- carbondioxide and c) pH in diurnal sampling on 12th/13th August in 1994 in Little Mere.

Two-way ANOVA performed on the densities of the dominant zooplankton species revealed significant effects of the different habitats on densities of *Ceriodaphnia* sp, *Eurycercus lamellatus*, *Chydorus* sp., *Polyphemus pediculus*, *Simocephalus vetulus*, *Diaphanosoma brachuyrum* and *Cyclops*+nauplii (P=0.002, P<0.001, P=0.003, P=0.0014, P=0.0044, P=0.001 and P=0.045 respectively) (Table 8.4). Whilst the sampling time had no significant effects on any of these zooplankton species, the interaction effect of sampling time and the habitats was significant on densities of *Ceriodaphnia* sp, *Eurycercus lamellatus* and *Cyclops* + nauplii (P=0.042, P=0.034 and P=0.02 respectively) (Table 8.4). Densities of *Ceriodaphnia* sp, *Diaphanosoma brachyurum* and *Polyphemus pediculus* showed similar trends among the different habitats with their highest densities recorded in the lily beds, and their lower densities in both open water and *Potamogeton berchtoldii* beds (Fig 8.4 a, b, and c). The highest densities of the weed-bed associated zooplankters, *Eurycercus lamellatus*, *Chydorus* sp. and *Simocephalus vetulus* were recorded in *Potamogeton berchtoldii* beds but their densities were near zero in the lily beds and the open water (Fig. 8.5 a,b and c). Though two-way ANOVA did not reveal a significant effect of sampling time, the densities of *Eurycercus lamellatus*, *Chydorus* sp. and *Simocephalus vetulus* showed a similar trend throughout the 24 hr with their densities gradually increasing from the first sampling (10:30 hr) in the morning and to the highest densities in the afternoon at 15:00 hr followed by a gradual decrease to the lowest values at midnight. One-way ANOVA was carried out to examine the effect of sampling time on the densities of *Eurycercus lamellatus*, *Chydorus* sp. and *Simocephalus vetulus* in the *Potamogeton berchtoldii* beds and revealed a significant effect of sampling time on

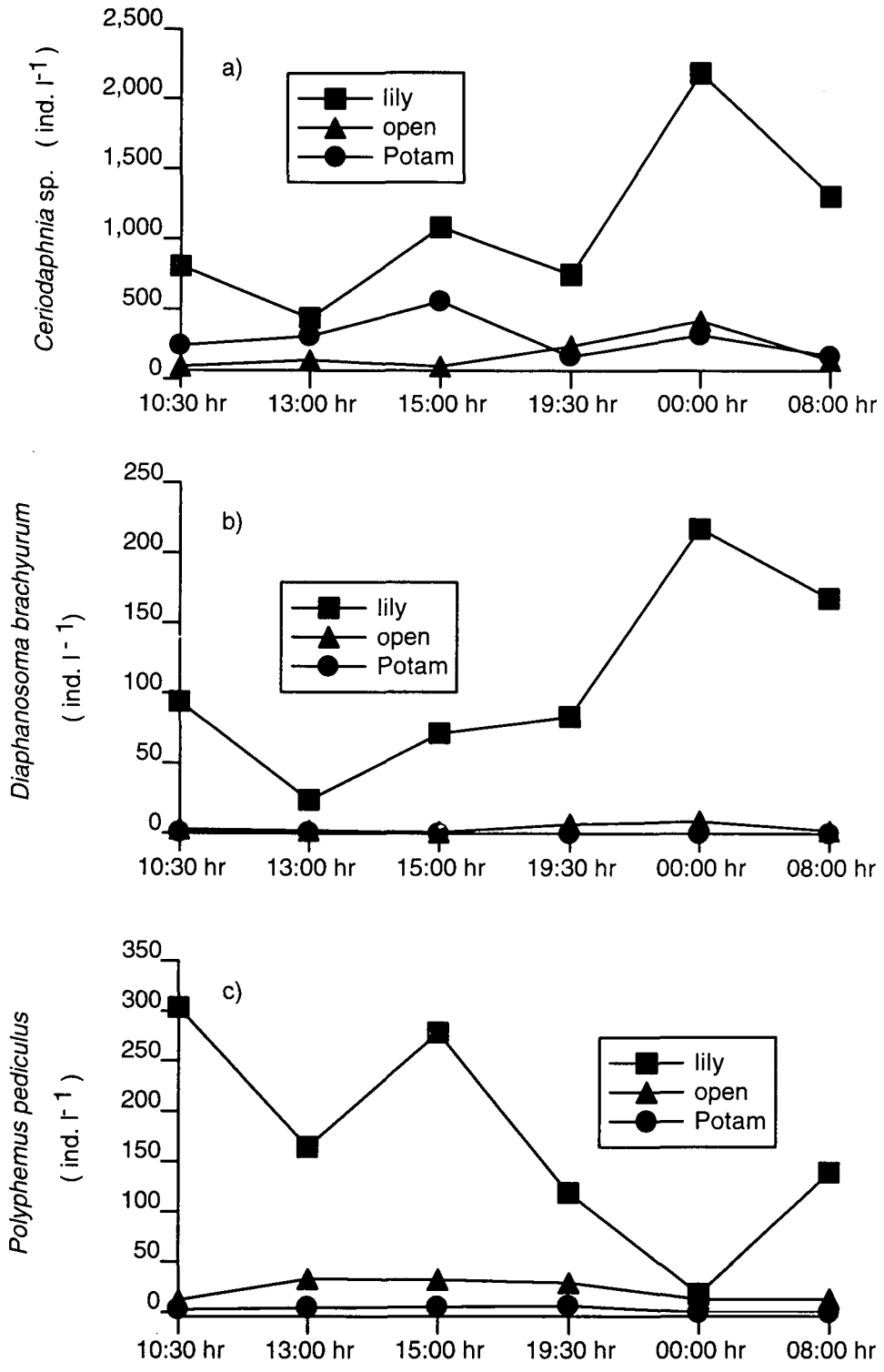

Fig.8.4 Changes in densities of a) *Ceriodaphnia* sp., b) *Diaphanosoma brachyurum* and c) *Polyphemus pediculus* in diurnal sampling on 12th/13th August 1994 in Little Mere.

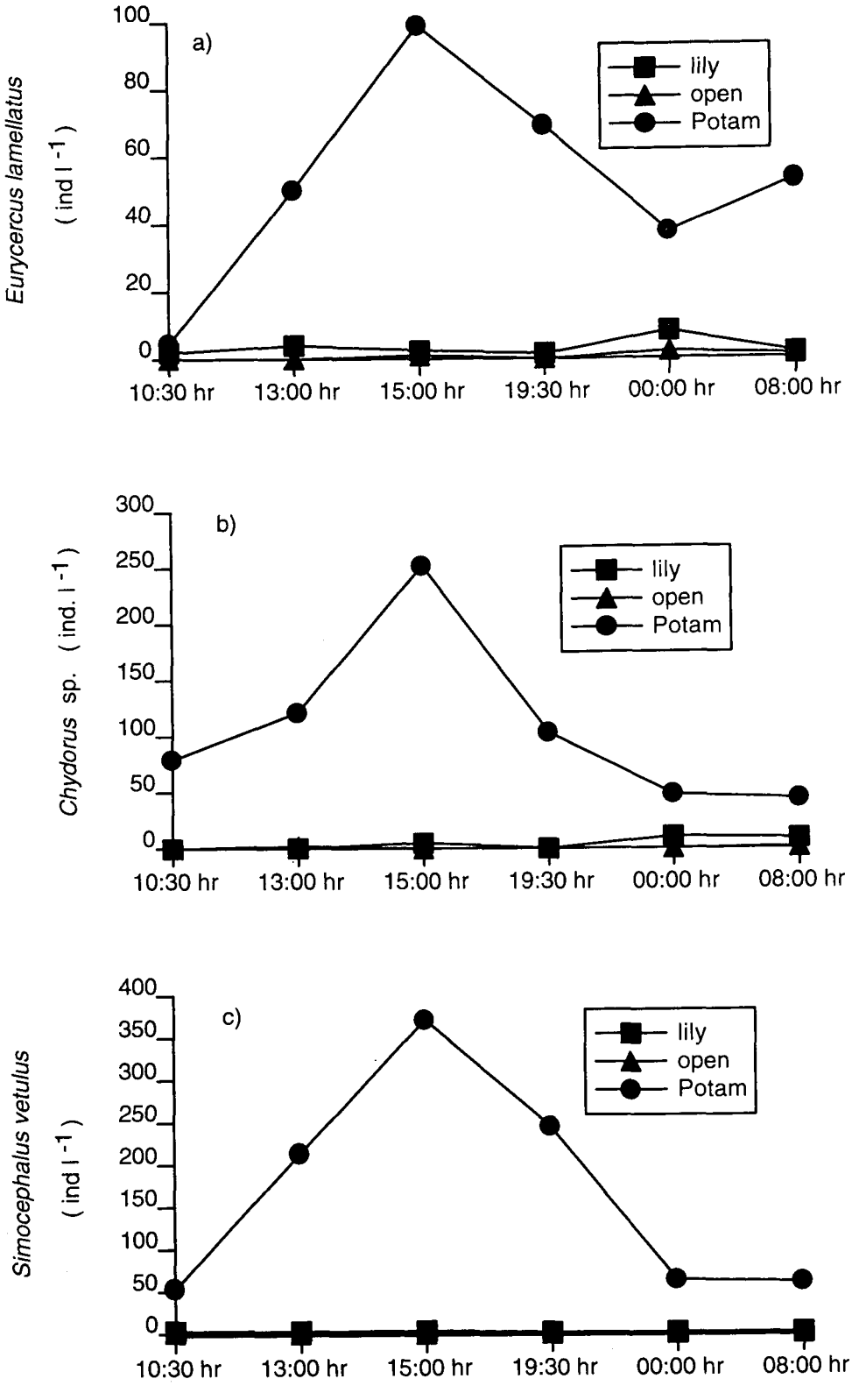

Fig. 8.5 Changes in densities of a) *Eurycercus lamellatus,* b) *Chydorus* sp. and c) *Simocephalus vetulus* in diurnal sampling on 12th/13th August 1994 in Little Mere.

the densities of these weed-bed zooplankters (F=6.24, P=0.0023; F=11.79, P=0.006 and F=9.3, P=0.0058 respectively). *Cyclops* + nauplii were favoured in the *Potamogeton berchtoldii* beds where the highest densities were recorded, and their densities were lower in the open water than in the lily beds (Fig. 8.6).

8.3.3 Fish

Perch, *Perca fluviatilis* L. largely predominated in the fish community of Little Mere on the three sampling occasions with 17, 99 and 19 perch caught (in January, July and November 1993 respectively) (Table 8.5). Number of roach (*Rutilis rutilis* L.) was higher in January 1993 than in July and November 1993 (11, 1 and 1 respectively) (Table 8.5). Populations of tench (*Tinca tinca* L.) and pike (*Esox lucius* L.) were near absent in Little Mere. Two tench fry were caught in January 1993 and 1 pike in November 1993.

8.3.4 Aquatic plants

The aquatic plant community (Fig. 8.7 & Plate 8.1) was well developed in the clear water and included extensive beds of floating- leaved, water-lilies (*Nuphar lutea* (L.) Smith and *Nymphaea alba* L. which covered about 33.8 % of the lake area. There was a large expansion of the submerged plant, *Potamogeton berchtoldii* Fiber between 1992 and 1993 when it covered 41 % of the lake area. The other dominant submerged species was *Elodea canadensis* Michaux. Small patches of *Nitella* sp. and *Callitriche* sp. were recorded.

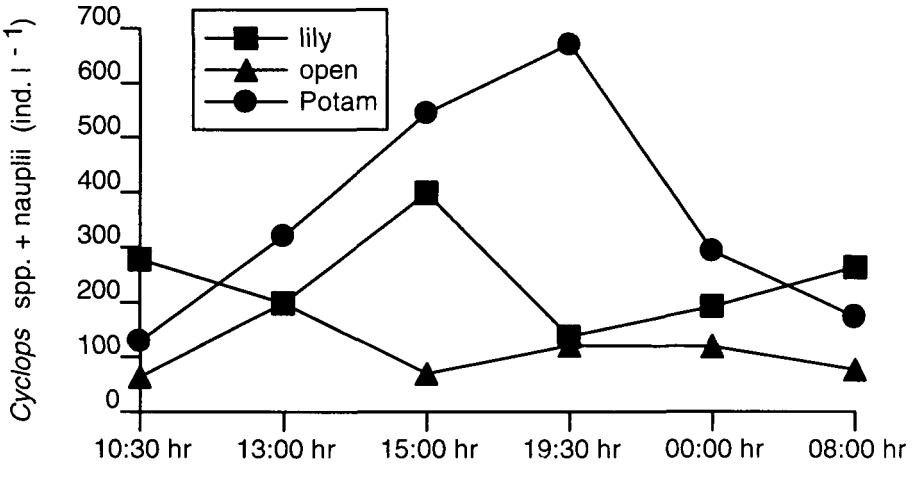

Fig. 8.6 Changes in densities of *Cyclops*+nauplii in diurnal sampling on 12th/13th August 1994 in Little Mere.

Table 8.5 Details of fish caught on three occasions in 1993 in Little Mere (μ:mean body lengths (±SD) and are given in cm).

	Roach (*Rutilis rutilis* L.)	Perch (*Perca fluvialitis* L.)	Tench (*Tinca tinca* L.)	Pike (*Esox lucius* L.)
January 1993 *	11 (μ=7.06±0.3)	17 (μ=18±0.3)	2 (μ=3.15±0.2)	2 (μ=51.5±4)
July 1993	1 (μ=15.3)	99 (μ=14.9±0.1)	-	-
November 1993	1 (μ=18.5)	19 (μ=17.1±0.3)	-	1 (μ=22)

* fish were caught in three sweeps of micromesh seine net on each occasion .

Plate 8.1 View across Little Mere, showing dense plant stands (photographed July 1993).

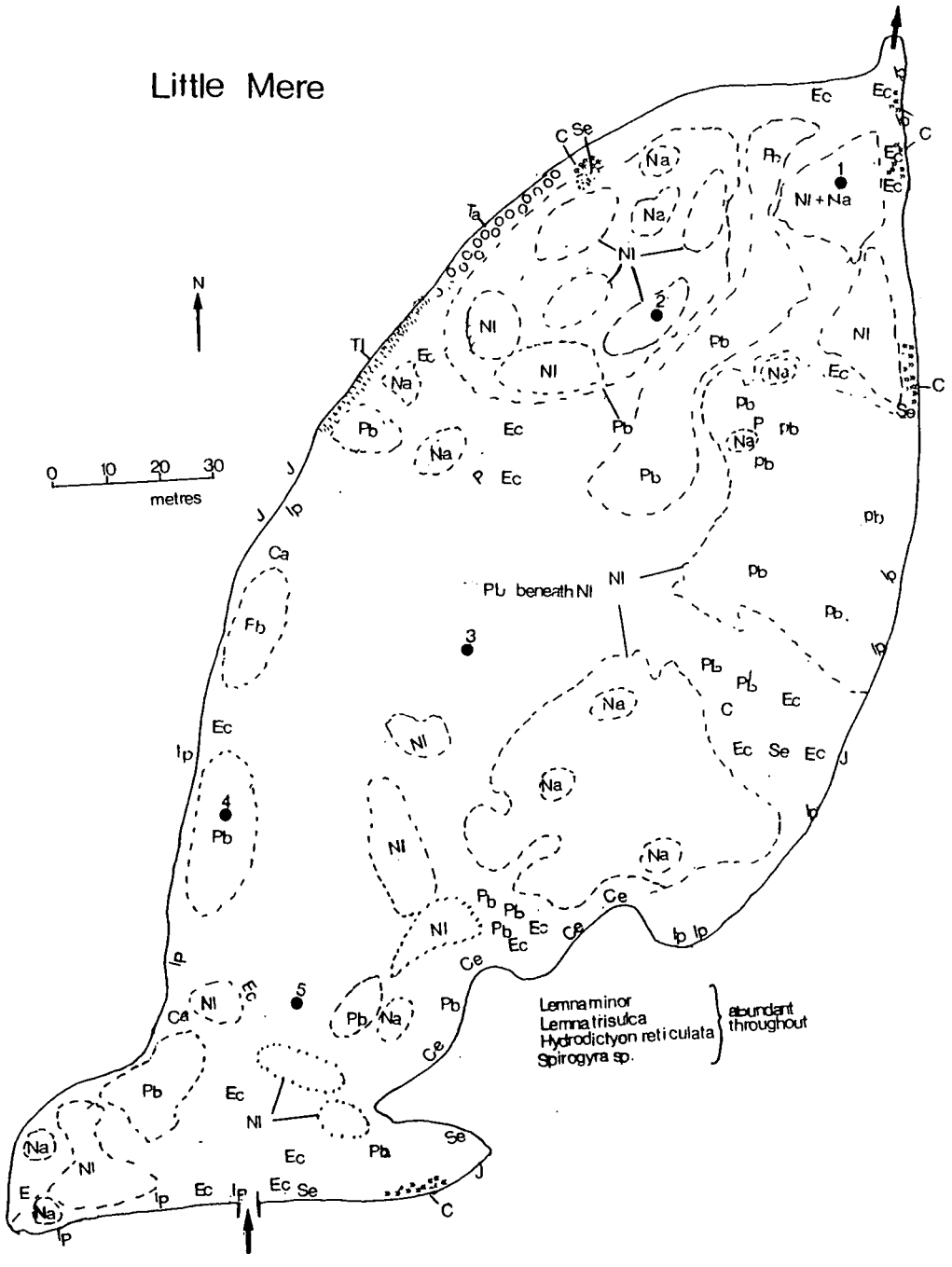

Fig.8.7 Aquatic plant survey of Little Mere (carried out in July 1993. Solid round symbols (●) indicate the sampling points in this study.

Key to Vegetation Map

Ec *Elodea canadensis*

Ca *Callitriche hermaphroditica*

Pb *Potomageton berchtoldii*

Nl *Nuphar lutea*

Na *Nymphaea alba*

Ip *Iris pseudacorus*

J *Juncus* spp

Ta *Typha angustifolia*

Tl *Typha latifolia*

Se *Sparganium erectum*

C *Carex* spp

8.4 Discussion

8.4.1 Diurnal sampling in 1993

The chlorophyll a concentrations were significantly lower in the lily beds where the highest *D.hyalina* densities were recorded. The effectiveness of grazing pressure of large filter-feeding *Daphnia* on phytoplankton crops has been recorded elsewhere (Shapiro, 1988; van Donk *et al.* 1989; Vanni & Findlay, 1990). Thus, the presence of high *D.hyalina* density was probably very important in decreasing the chlorophyll a concentrations to near zero in the lily beds. In the lily-beds, the presence of high density of *Daphnia hyalina* did not seem to be a function of absence of potential fish predation because perch had strongly recolonized the lake, and the presence of substantial fish populations has been recorded in lily beds in small shallow lakes elsewhere (Venugopal and Winfield, 1993). In Little Mere, the floating-leaved water lilies appeared to be more efficient at provision of refuges for *Daphnia hyalina* than the submerged, *Potamogeton berchtoldii,* where the lowest *Daphnia hyalina* density was recorded. Though in the 1993 diurnal sampling no physical and chemical variables were sampled, the reasons why the lily-bed was more efficient at harbouring *Daphnia hyalina* might be due to differences between floating-leaved plants and submerged plants in terms of structural effects or how they change associated chemistry and physical conditions (Carpenter & Lodge, 1986).

The density of *Daphnia hyalina* decreased at 20:30 hr at night in the lily beds but it reached its peak density at 01:30 hr. Thus, there was a little evidence to support the data of Timms & Moss (1984) that cladocerans move out from refugia at night to

graze in open water. Taking into account the possibility that many zooplanktivorous fish are capable of preying efficiently on large-cladocerans in virtual darkness by using cues other than vision (Townsend & Risebrow, 1982), the finding of this diurnal study may not be surprising. The results are in accordance with findings of Irvine, (1987) and Perrow & Stansfield (1994). However in some shallow Danish lakes, a large decrease in *Daphnia* abundance in the littoral zone at night was found (Lauridsen *et al.* 1995).

The densities both of *Ceriodaphnia* sp. and *Bosmina longirostris* were near zero in the lily beds but high with varying densities both in the open-water and *Potamogeton berchtoldii* bed. *Ceriodaphnia* sp. and *Bosmina longirostris* might have been disadvantaged by the presence of high *Daphnia hyalina* density in the lily beds perhaps due to competition for food, because the lowest chlorophyll a concentrations were recorded in the lily beds. *Ceriodaphnia* sp and *Bosmina* appear to be less efficient grazers on phytoplankton crops than *Daphnia hyalina* (Brooks & Dodson, 1965; Zaret, 1980). The chlorophyll a concentrations were higher in the open-water and the submerged plant beds where *Ceriodaphnia* sp. and *Bosmina* densities were high, though the chlorophyll a concentration of the open-water was slightly lower than that in the submerged plant beds. The insignificant densities of weed-bed associated *Eurycercus lamellatus*, *Chydorus* sp. and *Simocephalus* sp. would also have restricted the potential grazing pressure on phytoplankton crops in the *Potamogeton berchtoldii* bed.

8.4.2. Diurnal Sampling in 1994

Frodge *et al.* (1990) suggested that floated-leaved plants and submerged plants are

very different in terms of creating different physical and chemical environments in water bodies. The dissolved oxygen concentrations and pH were significantly different between the habitats with much lower values in the lily beds than in the open water and the submerged plant beds. This might be due to floating-leaved plants like lilies forming a layer on top of the water surface, creating a physical barrier between the surface water and the atmosphere, restricting oxygen diffusion inwards and carbon dioxide diffusion outwards Though light was not measured, it was likely to have been relatively low in the lily beds. Free-CO_2 concentrations were higher in the lily beds as expected from the lower pH values (Goldman, 1972; Raven, 1985). In dense surface canopies of submerged plants, very high dissolved oxygen concentrations (> 30 mg l^{-1}) and pH values (pH > 10) have been recorded, which were much higher than in the open water (Frodge *et al.* 1990). Localized large pH and dissolved oxygen concentration fluctuations have been observed elsewhere in submerged plant beds (Jones *et al.* in press) depending on intensity of respiration and photosynthetic activity. In this study, dissolved oxygen concentrations and pH values did not increase as much as values elsewhere probably because of cloudy and partly rainy weather conditions on the sampling day, which might have caused low photosynthetic activity. However, significantly higher dissolved oxygen concentrations and pH values were recorded in *Potamogeton berchtoldii* beds than in the open water and in the water lily beds throughout 24 hrs. The mean dissolved oxygen concentrations of the lily beds were 2.4 to 2.7 mg l^{-1}. Summerfelt (1981) suggested that 3 mg l^{-1} would be critically low for typical planktivores. Thus, the recorded values of dissolved oxygen concentrations are likely to have impaired the feeding of fish in the lily beds. However, in *Potamogeton berchtoldii* beds, the oxygen concentrations were high enough not to have detrimental effects on the feeding of fish throughout 24 hrs. In 1994 there was

higher chlorophyll a concentration in the lily beds in contrast to the previous year. The reasons why chlorophyll a concentration increased especially in the lily beds may have been related to changes in the zooplankton community structure (discussed below).

The zooplankton community of Little Mere has shown great changes from the bright red, large body-sized *D.magna* to *D.hyalina* following sewage effluent diversion (Chapter 3), and to near absence of *D. hyalina* in summer 1994 (D.Stephen, unpublished data). The density of *D.hyalina* was negligible in this study, consistent with its general density in the lake throughout summer 1994. The reason why density of *D.hyalina* has decreased to near absent may not be explained by the existence of fish predation because the lake has had prominent water lily stands which provide refuges to the large filter-feeding cladocerans. The efficiency of provision of refuges by the water lily stand was great enough to maintain high densities of large cladocerans in previous years (Chapter 3, 5 and 6) as observed in the previous year's diurnal sampling. The total surface coverage of macrophyte stands of Little Mere has greatly expanded, largely with *Potamogeton berchtoldii,* following the effluent diversion and the total surface coverage was larger in summer 1994 than in the previous years. This might offer an explanation for disappearance of *D.hyalina,* probably because open-water genera like *Daphnia* seem to need some sediment contact (Moss & Kornijow, in preparation). *Daphnia* can use bacteria and organic matter derived from sediment as a food sources (Brendelberg, 1991) and it has been shown experimentally that food-limitation may cause extinction of larger cladoceran species (Gliwicz, 1985). However this cannot be the entire explanation because substantial *Daphnia* populations may exist in deep lakes. Factors linked with dense physical habitat structures, like interference of zooplankton filtering appendages by detrital

material trapped by submerged plant fronds may be equally important. Reduction of *Daphnia* abundance and increase of weed-associated zooplankton in submerged plant beds has been recorded elsewhere (Dorgelo & Heykoop, 1985; Irvine *et al.* 1990b).

D.hyalina was largely replaced by small open-water cladocerans, *Ceriodaphnia*, *Diaphanosoma brachyurum*, and the omnivorous raptorial cladoceran *Polyphemus pediculus*. Densities of *Ceriodaphnia*, *Diaphanosoma brachyurum* and *Polyphemus pediculus* were significantly higher in the water lily beds than in the open water and the submerged plant beds. Neither *Ceriodaphnia* nor *Diaphanosoma brachyurum* showed signs of moving out of the lily beds at night, their greater densities were recorded at 00:00 hr. Probably *Ceriodaphnia* and *Diaphanosoma brachyurum* might have become easy prey to fish in the absence of *Daphnia hyalina*. It has been shown in Lake Cahora Bassa that *D. lumholzi* was the preferable prey to the fish due to its large size, but when it disappeared, the smaller *Ceriodaphnia* became desirable prey and the fish predation drove *Ceriodaphnia* to very low densities. Lastly, the even smaller and less opaque *Diaphanosoma* became undetectable in the lake (Gliwicz, 1994). In weed beds, high densities of *Polyphemus pediculus* have been recorded elsewhere (Smyly, 1952; Smirnow & Davis, 1973) consistent with the high densities of *Polyphemus pediculus* found here. Its density decreased at night so *Polyphemus pediculus* might have moved out the lily beds though significant effect was not shown. Despite this, the highest chlorophyll a concentrations were found in the lily beds in contrast to the previous year. This might be due to the small cladocerans being less efficient at grazing phytoplankton crops than large cladocerans like *Daphnia,* as grazing efficiency is a function of body size (Brooks & Dodson, 1965).

Large submerged plant-associated cladocerans like *Simocephalus* and *Eurycercus,* whose densities were much higher in *Potamogeton berchtoldii* beds than in the previous year, may have been responsible for reducing the phytoplankton crop in this habitat. Though two-way ANOVA did not reveal an overall significant effect of sampling time, the densities of these plant-associated species appeared to increase gradually toward the afternoon and decrease to the lowest densities at night, one-way ANOVA revealed a significant effect of time on these species in this habitat. The reason why these species had peak numbers in the afternoon is not clear. Fish predation might have increased in the late afternoon and Schriver *et al.* (1995) found increased fish predation during the day in a *Potamogeton pusillus* bed. During the night the fish migrated out from the bed. The animals harboured in the beds might be numerous enough to replace the populations at high densities in the adjacent water during the next day or *Eurycercus lamellatus*, *Chydorus* sp. and *Simocephalus vetulus* might have moved to the bottom or attached to the plant stems to avoid fish predation. In submerged plant beds, low night densities of *Eurycercus lamellatus* (Szlauer, 1962) and *Chydorus* sp. (Fairchild, 1981; Whiteside & Williams, 1975) have been recorded elsewhere. Both *Sida* and *Simocephalus* share the same adaptation of attaching to aquatic plants and filter feeding. *Sida* was rarely found away from plant surface (Fairchild, 1981). A similar pattern might be expected for *Simocephalus* but in this study its abundance largely decreased at night. Detailed research on plant bed associated zooplankton and fish interactions are needed.

We hypothesised that floating-leaved plants are better for sheltering open water cladocerans due physical and chemical conditions they create in the associated water and this was accepted. The water lily beds (*Nuphar lutea* and *Nymphaea alba*)

appeared to play an important role in harbouring and maintaining high densities of the open water cladocerans against fish predation in Little Mere as suggested by Timms' and Moss' (1984) refuge theory, perhaps by depleting dissolved oxygen and cutting off light to an extent dependent on the density of the plant surface canopy (Frodge *et al.* 1990) as very low dissolved oxygen concentrations were recorded in this study. This might impair feeding of fish in dense stands of floating-leaved lilies without necessarily affecting abundance of fish (Venugopal & Winfield, 1993). We hypothesised that submerged plants are more efficient for sheltering loosely or firmly plant bed-associated zooplankters but not open water zooplankters and this appears to be the case. The submerged *Potamogeton berchtoldii* appeared to be efficient at sheltering loosely or firmly plant bed-associated zooplankters but not the open water zooplankters in Little Mere. The reason why submerged plants are less efficient in harbouring open water zooplankters might be due to the plant-bed environment being unfavourable. Serafy and Harrell (1993) observed avoidance behaviour by fish in water above pH 9.5, but an increase in pH is usually associated with increase in dissolved oxygen in dense submerged-plant beds. The highest pH and dissolved oxygen values recorded in this study were found in such beds. Serafy and Harrell (1993) also found a lack of significant avoidance response by the fish tested at pH 9.52 to 9.83 when accompanied by 204 to 250 % dissolved oxygen concentrations and this was supported by their field results. Fish apparently benefit from the increased oxygen levels, which counterbalance the adverse effects of high pH, perhaps allowing them to feed on open water cladocerans in submerged plant beds. Thus detailed studies are necessary to understand the difference between floating-leaved and submerged plants in terms of their effects on the associated water chemistry and in turn provision of refuges and the effectiveness of submerged plants for harbouring of

Cladocera against fish predation.

8.4.3 Fish

In Little Mere, the fish population was previously very low and probably near absent such that 1990 and in December 1991, no fish were caught in three sweeps of the micromesh seine net. Because sewage effluent deoxygenated the water to near anoxia (Chapter 2; Carvalho *et al.* in press) the low dissolved oxygen concentrations are likely to have resulted in kills of fish moving in from upstream Mere Mere. Following sewage effluent diversion, dissolved oxygen concentrations greatly increased (Chapter 2; Carvalho *et al.* in press). Fish, predominantly perch, moved in from upstream Mere Mere. Perch has appeared to out-compete roach probably because of further expansion of the submerged macrophytes in Little Mere. Submerged macrophytes appear to be greater mechanical obstacles to roach than to perch which then has a competitive advantage over cyprinids (Diehl, 1988; Lammens *et al.* 1990; Persson, 1993).

Chapter 9: Overview

9.1. Importance of shallow lakes

Shallow water bodies are likely to be more productive than deep ones because of the increased possibilities of recycling of regenerated nutrients from the sediment and bottom waters and because of the contributions made by extensive beds of aquatic plants which occupy relatively very small proportional areas in the littoral zones of deep lakes (Moss, 1988). The presence of extensive aquatic plant beds in shallow lakes might be the key element of their productivity and their rich species diversity because aquatic plant beds of shallow lakes supply diverse habitats to wildlife such as spawning and living habitats for fish, invertebrates and waterfowl. Thus, it should not be surprising that plant-dominated shallow water bodies are among the greatest producers of organic matter per unit area of the world's ecosystems (Wetzel, 1975). Evaluation of annual net productivity of plant communities of different ecosystems shows that approximate organic productivity (mt. d.w. ha^{-1} yr^{-1}) of tropical and temperate freshwater emergent macrophytes accounts for the highest productivity with 78 and 38 respectively whilst lake phytoplankton accounts only for 2 (Westlake, 1965). Their treasures were widely recognized by indigenous peoples whose lifestyles strongly depended on such aquatic habitats for drinking water, inland fisheries, wildlife as food, rearing livestock and use of wetland products like reed (Reader, 1988). With increasing human population, increasing technological sophistication and decreasing connectedness of human beings with natural systems there have developed threats to freshwater bodies that lead to an increased phosphorus loading in particular from sewage treatment works, discharge of raw sewage (including that from farm

animals and from fish farms), run-off of nitrates from intensively arable catchments, alteration of natural hydrologies for irrigation water, and the drainage of wetlands (Moss, 1992b). In consequence, in shallow lakes, phytoplankton dominance has often replaced former extensive macrophytes with reduction in invertebrate and fish diversity as well as loss of plants which may have reduced the conservation and aesthetic values of such lakes. In deep lakes, the parallel process has been an increase in phytoplankton growth from a low trophic state to a modest one (Moss, 1990). Despite the great significance of shallow lakes, unfortunately most syntheses have been concerned solely with phytoplankton production, and the fringing and bottom plant communities have been ignored for lack of data. Probably also traditional limnological approaches to lake systems as unidirectionally linked flows of influence from nutrients to the phytoplankton have played an important role in maintaining relative ignorance of plant-dominated shallow lakes.

9.2. Bistability of shallow lakes

We have a more sophisticated understanding than formerly of the changes that occur in shallow lakes during eutrophication. Our current knowledge is probably reasonably comprehensive enough to see that changes in the system are not linear with increased nutrient loading. There seem to be alternative states of clear water and aquatic plant dominance versus turbid water and phytoplankton dominance (Balls *et al.* 1989; Moss, 1989; 1990; Scheffer, 1990; Scheffer *et al.* 1993). Existence of each state is possible over a range of nutrient loadings or concentrations (Meijer *et al.* 1994). A high potential impact of plants on maintenances of clear water and decrease of vegetation

with turbidity are important in the existence of this bistability. Therefore, the phenomenon of alternative clear and turbid stable states is expected to be restricted to shallow lakes, where a major part of the water body can be occupied by plants (Scheffer *et al.* 1993). Each state is buffered into stability by several mechanisms and also change from one state to another is caused by switch mechanisms (see Chapter 1, 4, 5, 7). Some shallow lakes might be expected to show a bistability of states depending on their history of response to disturbance or changes in external factors other than nutrients. The current literature on shallow lakes does indeed provide several observations of these phenomena. A good example is the Great Linford sand and gravel pit complex in England. The site has 14 lakes excavated over the past 40 years. Some were dry-dug, other were wet-dug. The digging method appears to have a great impact on turbidity. Dry-dug ones retain clear water with rich vegetation, while wet-dug ones stay in a turbid state for some decades because of high loading of fine silt (Giles, 1987). In 1987, part of the fish stock was removed from some turbid ones and led to a reduction of turbidity, whilst large weed beds quickly developed (Wright & Phillips, 1992). The former turbid lakes have remained in a clear state so far, supporting the view that the clear and turbid states are alternative stable states with different buffering and switch mechanisms. Another example is from the Norfolk Broadland, England. Hoveton Great Broad and Hudsons Bay are freely interconnected shallow basins. Fish can move between them and they receive river water daily as a result of physical tides from the effluent-rich River Bure. Hudsons Bay has a large bed of nymphaeids, Hoveton Great Broad has very few aquatic plants and contains phytoplankton-dominated open water. In Hudsons Bay, the open water is maintained

extremely clear, in the growth season of the nymphaeids, by zooplankton, finding refuges in the plant beds from fish predation. This appears to buffer the clear water state (Timms & Moss, 1984). A further example is from the south of Sweden, where two shallow, moderately eutrophic lakes, Takern and Krankesjön have shifted several times between a clear water state with abundant submerged plants, and a turbid state with high phytoplankton densities, over the past 40-50 years, without considerable changes in the external nutrient loading. In both lakes, water level fluctuations were the most common mechanism causing shifts, affecting submerged macrophytes either through changes in light availability or through catastrophic events such as drying-out or mechanical damage by ice movement (Blindow *et al.* 1993). Lastly, an interesting example from the Netherlands shows the two contrasting states can coexist within a lake. The turbid shallow lakes Wolderwijd and Veluwemeer have had large areas of clear water during the summer 1993. The clear water areas coincide with submerged plant stands dominated by *Chara contraria* A. Braun ex Kűtzing (Scheffer *et al.* 1994). Though obviously these observations fit the theory, and the alternative stable state hypothesis appears to be valid so far, long-term data are needed to gain better insight into how buffer and switch mechanisms operate for the successful control of eutrophication.

9.3. Significance of Little Mere in providing evidence for the alternative state hypothesis

Little Mere had clear water at extremely high nutrient concentrations prior to effluent diversion, with very high densities of large body-sized *D.magna* and to lesser extent

D. longispina with very low fish predation due to the low quality of the sewage effluent (see Chapter 3). One might ask that if the sewage effluent had been higher quality and had not deoxygenated the water to near anoxia and had thus not caused fish-kills, or if fish predation had been high, could Little Mere have had turbid water?. The answer might seem to be positive, as it was observed in the summer 1992 enclosure experiment that introduction of fish with increasing densities resulted in increased chlorophyll a concentrations both in the presence and absence of sediment (Beklioglu & Moss, in preparation; Chapter 5). But the answer is more likely to be no, because what this speculation and the experiment did not take into account, was existence of large stands of water lilies and their buffering mechanisms. Provision of refuges for grazers against fish predation by macrophytes is one possible important role in Little Mere. Comparison of *D.magna* counts from open water and from water lily beds (Table 5.4) showed significantly higher *D.magna* in water lily beds than in open water. The possible answer to the imaginary question would again be no, had the grazer population even been dominated by the smaller body-sized *D.hyalina,* as observed in the lake after fish recolonization. Following effluent diversion, nutrient concentrations significantly declined and dissolved oxygen concentration rose (Carvalho *et al.* in press; Chapter 2), and fish, perch in particular, recolonized (Chapter 8). Little Mere has so far maintained its clear water state with large macrophyte stands as found prior to diversion. Other suggested buffering mechanisms of macrophytes (See Chapters 4 and 5 for details) might have also been important for maintaining the clear water along with provision of refuges but apart from the possible effects of high pH in the beds, these were not examined in this study. The results of

this study have provided strong evidence for the existence of a plant-dominated state over a wide range of nutrient concentrations. Also the study suggests a need for vigorous buffering mechanisms associated with macrophytes to stabilize the system in the clear water state when fish are present. Reduction of fish populations (biomanipulation) has been successful in several turbid shallow lakes in enforcing a switch to clear water (Meijer *et al.* 1990; Søndergaard *et al.* 1990). But without development of strong macrophyte stands, deterioration of water quality of manipulated lakes has been observed and attributed to lack of strong macrophyte stands and their buffering mechanisms (Meijer *et al.* 1994).

9.4. Differential effectiveness of Nymphaeids and submerged macrophytes as refuges against fish predation

The idea of plants as refuges was introduced by Timms & Moss (1984) who found large densities of large-bodied cladocerans in extensive water lily beds and in the open water at night. The presumption was that fish remained out of the lily beds which thus allowed cladoceran populations to build up in the absence of fish predation. However, recent studies have shown that fish are not excluded from plant beds (Serafy & Harrell, 1993; Venugopal & Winfield, 1993). Contrary to the observed effectiveness of water lilies in Little Mere and elsewhere for sheltering *Daphnia*, the results of an enclosure experiment, with increasing densities of fish and the absence or presence *Potamogeton berchtoldii* at densities averaging 125 g dry wt m^{-2} in open enclosures, have shown a less effective refuge effect of *Potamogeton berchtoldii* for sheltering *D. hyalina*. Densities of *D. hyalina* significantly decreased in the presence

of fish in the plant enclosures as observed also in the closed (plant-less) enclosures though their numbers were higher in the open plant enclosures than the closed, plant-less enclosures (Beklioglu & Moss, in preparation, Chapter 6, Table 6.1). These results suggest that a refuge effect may be present within a *Potamogeton berchtoldii* bed, though perhaps not greatly effective. In the presence of plants (the open enclosures) the abundance of weed-associated cladocerans was not affected by increasing fish predation, whilst their abundance was significantly reduced in the absence of plants (closed enclosures). Thus, *Potamogeton berchtoldii* appears to provide more effective refuges to weed-associated grazers than open water grazers (Chapter 6, Table 6.1). The findings of the experiment were supported by comparison of the densities of open-water grazers with the densities of weed-associated grazers from open water, lily beds and *Potamogeton berchtoldii* beds during sampling throughout the summer of 1993 (Chapter 6, Table. 6.5). This differential effectiveness between water lilies and the submerged plants for sheltering grazers was attributed to their different physical and chemical effects on the associated water (Frodge *et al.* 1990; Serafy & Harrell, 1993; see Chapters 6 & 8 for details). This assumption was supported by the findings of the 1994 diurnal sampling that dissolved oxygen concentrations and pH were significantly higher in *Potamogeton berchtoldii* beds than the water lily beds though the values were not as high as recorded elsewhere (probably due to the weather conditions of the sampling day) (Chapter 8). Thus, one might expect impaired feeding of fish in a water lily bed due to very low dissolved oxygen concentrations and low light due to leaf canopy formation on water surface (Frodge *et al.* 1990). Less detrimental effects on fish feeding of high pH when accompanied by high dissolved oxygen concentrations

might also be expected, as no avoidance of macrophytes by fish was recorded under such conditions (Serafy & Harrell, 1993).

9.5. New model for role of *Daphnia*

The grazer community of Little Mere has greatly changed from the bright red, large body-sized *D.magna* in 1991-2 to *D.hyalina* in 1993 with increasing fish predation following the effluent diversion in 1991 (Chapter 3). The density of *D.hyalina* was subsequently found to be negligible during the diurnal sampling in 1994 (Chapter 8). This was consistent with its general density in the lake throughout summer 1994 (D. Stephen, unpublished data). Though the reason for disappearance of *Daphnia* is not clear, the existence of fish predation may not be the explanation because the lake has continued to have prominent water lily stands (33.8% of the total lake area, see Chapter 8) which have provided potential refuges to the large grazers. The provision of refuges by the water lily stand was efficient enough to maintain high densities of large cladocerans in previous years (Chapter 3, 5 and 6). The increase in total surface coverage of macrophyte stands largely with *Potamogeton berchtoldii*, and the greater total coverage in 1994 than in previous years, might be an explanation for disappearance of *D.hyalina*. It has been shown in Little Mere, in netting enclosures, that *Daphnia* populations were disfavoured by increasing densities of the water lily in the absence of fish whilst their densities remained high at the low and medium plant densities in fishless enclosures (Moss & Kornijow, in preparation). They suggested that open-water genera like *Daphnia* seem to need some sediment contact. Thus, factors linked with habitat complexity of *Potamogeton berchtoldii* might have

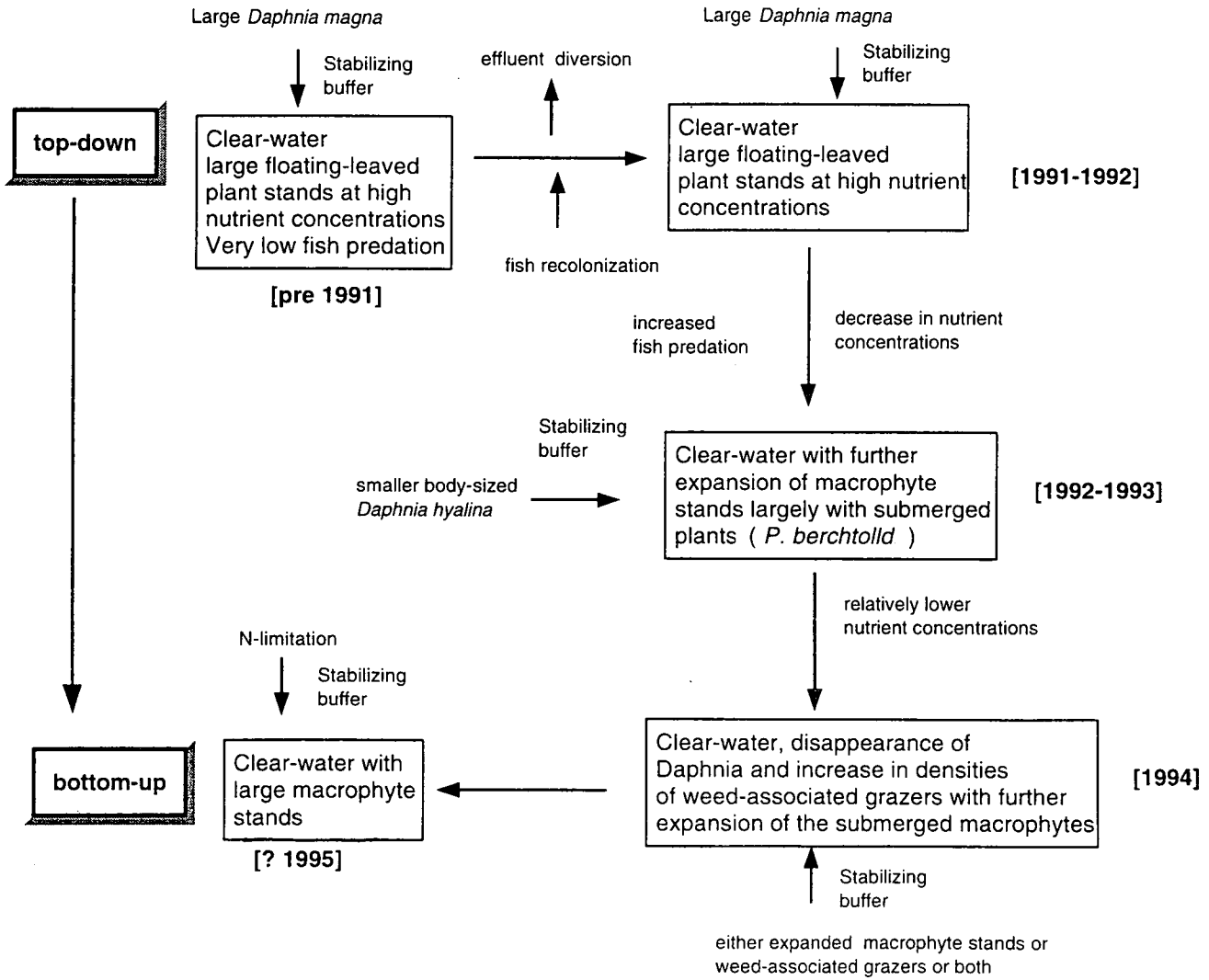

Fig. 9.1. Ecosystem development in Little Mere between 1990 to 1994.

interfered with *Daphnia* feeding activity and disfavoured their dominance. Reduction of *Daphnia* abundance and increase of weed-associated zooplankton in submerged plant beds has been recorded elsewhere (Irvine *et al.* 1990b).

The presence of large densities of *Daphnia* was apparently the main buffer mechanism to stabilize macrophyte-dominated clear-water in Little Mere until 1994. In the absence of *Daphnia*, the lake has maintained its previous clear-water state. It appears that new buffer mechanisms are in operation for stabilizing the macrophyte-dominated clear water phase. Though little is known about the grazing efficiency of weed-bed associated cladocerans on phytoplankton crops, they may have played an important role in maintaining the clear-water in the lake. The expansion of rooted macrophyte stands might have also been important for the low phytoplankton chlorophyll a concentrations as well. Rooted plants have free access to sedimentary nutrients through their roots (Denny, 1972). *Elodea nuttallii* (Planchon) St.John, for example, stored up 86 % of the available N and 80 % of the available P and acted as sink both for N and P and maintained a clear water state in Lake Zwemlust (van Donk *et al.* 1993). From the predicted nutrient concentrations of the lake, the N:P ratio hints at possible nitrogen-limitation of the phytoplankton community (Chapter 4). If the expanded macrophyte stands of the lake remain high or further expansion happens, the lake might become nitrogen-limited. Thus, Little Mere may shift from its previous and probably presently top-down controlled state to a bottom-up controlled state (Fig.9.1).

9.6. Suggestions for future studies

9.6.1. Testing the validity of macrophyte-dominated alternative state

So far, the evidence (see above) has suggested that the macrophyte-dominated clear-water state is an alternative to the turbid water in Little Mere. To test the validity of this, one might divide the lake into two separate unmixing compartments such that, in one compartment, all the plant stands are cleared out, whilst the other maintains its plant stands. The hypothesis would be that the cleared compartment would become turbid, though there might be a drawback to this experiment because in the plant-less compartment, the bacteria on the sediment surface might be still important for N loss through denitrification and may maintain clear water through nitrogen limitation .

9.6.2 Testing the efficiency of the submerged plants for sheltering both open water and weed- associated grazers

The evidence suggested that the submerged plants might not be fully effective for sheltering open water grazers in Little Mere. To test the refuge potential of the submerged plants at different densities, one might carry out an experiment in netting enclosures at three different densities of the plant, low, medium and high, with presence and absence of juvenile cyprinid or percid fish. The effect of the plants should be closely followed by sampling for pH, dissolved oxygen, temperature, alkalinity and light to construct a possible relation between the plant biomass and its possible effect on associated water and on the states of the phytoplankton and zooplankton communities.

9.6.3 Testing the effectiveness of the present macrophyte stands and cladoceran grazers for maintaining the clear water

We need to know more about the effects of plant type and density and the chemical conditions within the beds to make sure that the well established phenomenon of clear water in association with plant beds is really a function of Cladocera or of a plant-generated competition for nitrogen with the phytoplankton. To test this one would carry out enclosure experiments in plant beds with the presence and absence of grazers. This is currently being done in Little Mere.

9.6.4. Testing the grazing efficiency of weed-associated cladocerans on phytoplankton crops

Little is known about this and some laboratory grazing experiments need carrying out to understand species-specific grazing efficiency of different cladoceran genera perhaps by using radioactive labelling methods.

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Appendix 1: Physical and chemical data

KEY

		Units
pH		
Chloride	(Cl)	mg l^{-1}
Nitrate-nitrogen	(NO_3)	mg l^{-1}
Ammonium-nitrogen	(NH_4)	µg l^{-1}
Dissolved inorganic nitrogen	(DIN)	mg l^{-1}
Silicate-silicon	(SiO_2)	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)	cm
Secchi depth	(Secchi)	m
Flow rate	(Flow)	m^3 s^{-1}

Appendix 1. Inflow Mere Mere

Date	pH	Cl	NO3	NH4	DIN	SiO2	SRP	TSP	TP
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	2.565	4.1	44	66	144
21.2.90		163.5		219		4.9	56	145	215
7.3.90		70.3	2.12	233	2.353	4.6	81	147	176
21.3.90		57.1	2.13	428	2.558	5.1	104	129	178
4.4.90		51	1.42	437	1.857	4.5	112	129	183
18.4.90		52.5	1.29	352	1.642	4.6	119	212	278
2.5.90		51.6	1.7	119	1.819	3.7	111	164	244
16.5.90		45.8	0.97	112	1.082	4.2	69	116	323
29.5.90		54	2.59	153	2.743	2	67	124	154
12.6.90		54	1.05	397	1.447	4.3	164	245	365
27.6.90		50	0.83	254	1.084	4.1	154	260	323
11.7.90		54	0.9	388	1.288	2.5	95	99	234
25.7.90		54.2	0.92	108	1.028	1	188	216	369
8.8.90									
21.8.90		45.8	0.97	320	1.29	4.5	100	145	177
6.9.90		45.8	0.69	176	0.866	3.1	222	216	330
24.9.90		33	0.75	408	1.158	3.3	108	152	336
9.10.90		55.7	1.98	190	2.17	5.3	43	63	100
22.10.90		55.3	0.76	402	1.162	4.7	98	104	153
6.11.90		63.3	5.01	202	5.212	6.3	34	96	74
20.11.90		49.5	4.55	236	4.786	4.9	20	38	102
5.12.90		61.9	3.25	243	3.493	5.4	40	64	78
7.1.91		77.6	3.86	186	4.046	4.4	26	39	58
22.1.91		70.1	4.37	167	4.537	4.4	35	64	69
5.2.91		76.3	4.87	146	5.016	5	28	62	53
19.2.91		69.4	2.91	188	3.098	4.6	36	66	69
5.3.91		93.9	3.67	120	3.79	4.3	33	52	190
19.3.91		64.6	4.14	69	4.209	4	39	76	290
2.4.91		75.5	3.16	490	3.65	3.9	98	122	195
16.4.91		71.4	2.24	23	2.263	3	38	47	103
30.4.91		49	2.37	219	2.589	4.4	49	66	122
14.5.91		61.2	2.23	275	2.505	3.1	55		
27.5.91									
11.6.91		57.1	1.03	706	1.736	3.1	69	127	277
25.6.91		40	0.86	182	1.042	3.9	56	66	167
9.7.91		55.1	0.89	431	1.321	5.2	93	119	223
22.7.91		57.1	0.01	2616	2.626	5.4	230	252	439
6.8.91		46.9	0.51	393	0.903	3.1	152	186	321
19.8.91		53.6	0.53	898	1.428	3.3	140	154	348
9.9.91									
23.9.91	7.4	46.9	0.05	1191	1.241	2.1	260	563	
9.10.91		50	0.39	204	0.594	3.6	111	152	209
22.10.91		82.5	0.24	657	0.897	3.7	90	143	432
5.11.91		66.7	1.01	166	1.176		25	41	51
19.11.91		102	2.59	220	2.81	5.6	25	41	
3.12.91			2.36	357	2.717	5.1	29	46	61
18.12.91		210.1	1.13	679	1.809	4.9	59	92	116
9.1.92		62.8	4.53	277	4.807	5.1			
21.1.92		73.8	3.57	184	3.754	5.6	32	35	42
3.2.92									

Appendix 1. Inflow Mere Mere

Date	pH	Cl	NO3	NH4	DIN	SiO2	SRP	TSP	TP
18.2.92		209.7	3.32	364	3.684	5	40	45	130
3.3.92		80	3.11	227	3.337	4.3	34	65	117
18.3.92		711.8	3.7	118	3.818	4.6	42	89	148
1.4.92		63.4	3.67	117	3.787	4	37	65	74
14.4.92		71	2.38	144	2.524	3.54	6	35	40.2
28.4.92		76	1.2	193	1.393	3.44	34	38	189.4
12.5.92		52	1.3	138	1.438	3.2	32	53	125
26.5.93		60	0.49	1377	1.867		17	45	149
9.6.92		56	1.11	131	1.241	5	56	39	109
23.6.92			0.26	344	0.604		78	37	199
7.7.92		52	0.52	1842	2.362	1.4	291	80	263
21.7.92		48	1.1	1080	2.18	3	168	101	424
4.8.92		48	0.42	1780	2.2		490	446	471
17.8.92		52	0.8	652	1.452	2.8	140	161	329
1.9.92		48	0.5	401	0.901	3	235	334	455
12.9.92		48	0.54	196	0.736	4.4	137	370	430
5.10.92		48	1.4	298	1.698		132	141	620
13.10.92		44	0.6	246	0.846	7	100	0	126
3.11.92		42	2.4	108	2.508		40	62	111
9.11.92		40	1.8	102	1.902	5.4	23	0	15
24.11.92		44	1.2	203	1.403	5.6	26	3	29
8.12.92		44	4.2	148	4.348	4.2	33	61	99
22.12.92		44	1.9	132	2.032	4.9	73	67	67
6.1.93		44	3.3	109	3.409	5.5	35	7	58
15.1.93	7	48	2.8	148	2.948	5.4	51	16	199
2.2.93	7	52	3.5	92	3.592	5.1	38	88	142
16.2.93	7.33	48	1.9	255	2.155	5.3	39	46	112
2.3.93	7.11	48	1.9	235	2.135	5	36	157	94
15.3.93	7.05	56	1.35	192	1.542	4.5		256	538
29.3.93	7.2		1.7	149	1.849	3.9	121	89	169
15.4.93	7.2		1	115	1.115	4.5	72	14	93
30.4.93	7.3	63	1.68	289	1.969	4	65	28	48
11.5.93	7.5	64	2.4	79	2.479	3.3	54	235	403
25.5.93	8.1		1.9	75	1.975	2.8	45	0	54
8.6.93	7.9	54	1.5	5	1.505	4	76	36	99
22.6.93	7.4	64	1.3	85	1.385	5.6	62	49	89
6.7.93	8.2	51	1	0	1	3.1	31	33	52
20.7.93	7	42	2.1	228	2.328	5.9	62	94	209
2.8.93	7	45	1.6	707	2.307	5.2	79	373	653
18.8.93	7.5	48	1.1	119	1.219	5.8	64	86	182
31.8.93	9.1		0.8	72	0.872		64	102	132
13.9.93	7	43	1.9	226	2.126	4.4	57	79	132
29.9.93	9.06	48	0.6	39	0.639	4.8	67	78	257
13.10.93	7		0.4	122	0.522	6.2	52	75	89
27.10.93	7.3	51	1.5	62	1.562	4.7	41	39	178
10.11.93	6.8	55	0.4	185	0.585	6.2	52	80	109
24.11.93		46	0.7	134	0.834	6.8	34	52	144
7.12.93	6.5	48	0.06	416	0.476	3	82	123	269
21.12.93									
12.1.94	6.7	55	1.8	143	1.943	4.2	31		
26.1.94	6.4	48	1.2	107	1.307	4.2	53	71	90
9.2.94									

Appendix 1. Inflow Mere Mere

Date	pH	Cl	NO3	NH4	DIN	SiO2	SRP	TSP	TP
22.2.94	6.9	72	1.4	104	1.5	4.7	35	43	43
8.3.94	7	68	1.5	0	1.5	4.9	31	44	44
21.3.94	6.5	92	1.33	108	1.43		38	65	106

Appendix 1. Inflow Mere Mere

Date	PAlk	TAlk	Flow
10.1.90			
25.1.90			
7.2.90			
21.2.90	0	1.2	0.0286
7.3.90	0	1.35	0.0225
21.3.90	0	1.78	0.0183
4.4.90	0	1.73	0.0152
18.4.90	0	1.78	0.0145
2.5.90	0	2.25	
16.5.90	0	2	0.0148
29.5.90	0	2.7	0.0059
12.6.90	0	2.6	0
27.6.90	0	2.75	0.0039
11.7.90	0	2.78	0.0085
25.7.90	0.25	2.55	0.001
8.8.90			0
21.8.90	0	1.25	0.1348
6.9.90	0.15	2.53	0.0042
24.9.90	0	1.05	0.0442
9.10.90	0	1.28	0.0177
22.10.90	0	2.08	0.001
6.11.90	0	1.08	0.0076
20.11.90	0	0.45	0.1572
5.12.90	0	1.45	0.0178
7.1.91	0	0.75	0.0703
22.1.91	0	1.05	
5.2.91	0	1.48	
19.2.91	0	1.3	
5.3.91	0	1.1	0.0483
19.3.91	0	1.2	0.083
2.4.91	0	1.8	0.0266
16.4.91	0	1.88	
30.4.91	0	1.18	0.0296
14.5.91	0	1.9	0.0066
27.5.91			
11.6.91	0.15	2.85	0.0041
25.6.91	0	1.55	0.0186
9.7.91	0	2.15	0.00666
22.7.91	0	2.8	0.00252
6.8.91	0.08	2.23	0.00341
19.8.91	0	2.35	0.00125
9.9.91			0
23.9.91	0	3.45	0
9.10.91	0	2.45	0
22.10.91	0	2.25	0.00172
5.11.91	0	1.1	0.00941
19.11.91	0	1.08	0.24151
3.12.91	0	1.48	0
18.12.91	0	1.6	0.00302
9.1.92	0	1.45	0.04281
21.1.92	0	1.33	0.00856
3.2.92	0		0.01066

Appendix 1. Inflow Mere Mere

Date	PAlk	TAlk	Flow
18.2.92	0	1.8	0.0248
3.3.92	0	1.02	0.03287
18 3.92	0	1.1	0.03471
1.4.92	0	1.25	0.01793
14.4.92	0	1.3	0.014
28.4.92	0	1.1	0.017
12.5.92	0	1.7	0.019
26.5.93	0.1	2.4	0.0016
9.6.92	0.05	2.1	0.0055
23.6.92	0.03	2.4	
7.7.92	0	2.8	0.0018
21.7.92	0.1	2.1	0.00091
4.8.92	0	2.7	0.0015
17.8.92	0	2.2	0.0036
1.9.92	0	1.9	0.0044
12.9.92	0.05	1.05	
5.10.92	0	0.08	0.039
13.10.92	0	1.6	0.0044
3.11.92	0	1	0.0056
9.11.92	0	0.7	0.0144
24.11.92	0	0.5	
8.12.92	0	0.6	0.053
22.12.92	0	0.8	0.015
6.1.93	0	1.4	
15.1.93	0	0.9	0.0475
2.2.93	0	1.15	
16.2.93	0	1.55	0.0227
2.3.93	0	1.5	0.0116
15.3.93	0	1.8	0.0017
29.3.93	0	1.9	0.01
15.4.93	0	1.5	
30.4.93	0	1.9	0.0058
11.5.93	0	2.4	
25.5.93	0.2	2.6	0.0052
8.6.93	0.4	2.4	0.0048
22.6.93	0	2	0.0056
6.7.93	0.2	2.7	0.0032
20.7.93	0	1.5	0.00174
2.8.93	0	2.8	0.001
18.8.93	0	1.9	0.00674
31.8.93	0.4	2.6	0.0047
13.9.93	0	2	0.0106
29.9.93	0.3	2.2	0.002
13.10.93	0	1.7	0.0066
27.10.93	0	1.4	0.007
10.11.93	0	1.65	0.0165
24.11.93	0	1.7	0.023
7.12.93	0	1.1	0.262
21.12.93			
12.1.94			0.042
26.1.94	0	0.85	0.052
9.2.94			

Appendix 1. Inflow Mere Mere

Date	PAlk	TAlk	Flow
22.2.94	0	1.8	0.025
8.3.94	0	1.6	0.0184
21.3.94	0	1	0.034

Appendix 1. Mere Mere

Date	pH	Cl	NO3	NH4	DIN	SiO2	SRP	TSP	TP	PAlk
10.1.90		53.1				1.9	14			0
25.1.90		54.7	1.15			2.1	0	14	68	0
7.2.90		55.1	1.45	5	1.455	2.4	6	22	74	0
21.2.90		56.3	1.59	0	1.59	2.6	4	23	76	0
7.3.90		72.9	1.69	0	1.69	2.7	7	37	92	0
21.3.90	7.7	57.1	1.63	46	1.676	2.8	0.5	19	52	0
4.4.90		57.1	0.96	20	0.98	2.2	6	19	54	0
18.4.90	8.34	58.6	1.12	0	1.12	0.3	3	25	59	0
2.5.90	8.13	57.7	1.04	0	1.04	0	2	14	67	0
16.5.90	7.79	58.3	0.89	0	0.89	0.4	0	17	46	0
29.5.90	8.52	58.3	0.9	0	0.9	0.4	1	20	85	0
12.6.90	8.11	57.7	0.42	0	0.42	0.4	5	24	152	0
27.6.90	8.93	60.4	0.16	0	0.16	0.4	14	20	74	0.05
11.7.90	8.48	57.7	0.08	6	0.086	0.2	4	13	77	0
25.7.90	9.44	60.4	0	0	0	0.5	1	5	79	0.18
8.8.90	8.53	60.4	0	0	0	0.8	3	20	109	0.1
21.8.90	7.89	58.3	0.05	0	0.05	0.8	1	14	71	0
6.9.90	7.89	60.4	0.02	0	0.02	1	0	15	82	0
24.9.90	7.69	57.7	0.05	266	0.316	1.5	23	30	136	0
9.10.90	7.87	57.7	0.12	259	0.379	0.6	15	25	82	0
22.10.90	7.73	61.7	0.22	203	0.423	0.22	5	29	81	0
6.11.90	7.6	57.1	0.56	197	0.757	0.92	20	29	84	0
20.11.90	7.43	57.7	0.85	192	1.042	0.9	13	21	60	0
5.12.90	7.68	57.7	0.79	180	0.97	1.28	13	36	55	0
7.1.91	7.35	65.3	2.12	194	2.314	1.74	14	28	39	0
22.1.91	7.36	61.9	2.17	147	2.317	1.89	15	35	53	0
5.2.91	7.43	68	2.03	86	2.116	2.28	5	29	37	0
19.2.91	7.57	67	1.73	35	1.765	1.66	4	27	43	0
5.3.91	7.63	77.6	2.45	0	2.45	1.58	2	19	51	0
19.3.91	7.89	79.2	1.85	0	1.85	0.67	1	17	37	0
2.4.91	7.73	73.5	1.42	0	1.42	0.62	2	17	68	0
16.4.91	7.5	75.5	1.47	0	1.47	0.37	1	11	35	0
30.4.91	7.8	77.6	1.34	3	1.343	0.46	0	20	40	0
14.5.91	7.8	77.6	0.97	62	1.032	0.41	3			0
27.5.91	7.7	76.3	0.92	72	0.992	0.59	6	30	58	0
11.6.91	7.7	77.6	0.63	27	0.657	0.5	0	49	56	0.25
25.6.91	7.8	74	0.63	0	0.63	0.6	1	0	27	0
9.7.91	8	73.5	0.43	12	0.442	0.67	0	15	35	0
22.7.91	8.9	77.6	0	0	0	0.8	5	22		0.25
6.8.91	9.1	73.5	0.03	14	0.044	0.47	0	13	80	0.23
19.8.91	8.4	74.2	0.06	73	0.133	0.92	2	17	72	0
9.9.91	8.2	75	0	20	0.02	0.26	2	24	58	0
23.9.91	7.7	75.5	0	16	0.016	0.48	2	5	90	0
9.10.91	7.7	78.3	0.04	232	0.272	0.99	9	32	90	0
22.10.91	7.7	74.2	0.16	173	0.333	0	6	11	69	0
5.11.91	7.3	74.7	0.12	142	0.262	0.04	13	22		0
19.11.91	7.7	77.5	0.25	179	0.429	0.62	14			0
3.12.91	7.7	72	0.37	157	0.527	0.81	11	21	32	0
18.12.91	7.8	74.7	0.37	167	0.537	0.51	21	20	35	0
9.1.92	7.6	74.5	1.11	230	1.34	1.03	24		40	0
21.1.92	7.5	73.8	1.43	169	1.599	1.34	23		45	0
3.2.92	7	80	1.34	163	1.503	1.39	12	50	56	0
18.2.92	7.5	81.6	2.13	218	2.348		22	28	70	0
3.3.92	7.8	84	1.24	4	1.244	1.46	3	37	57	0

Appendix 1. Mere Mere

Date	pH	Cl	NO3	NH4	DIN	SiO2	SRP	TSP	TP	PAlk
18.3.92	8.1	78.1	1.44	0	1.44	1.22	0	47	62	0.1
1.4.92	7.8	73.3	1.9	51	1.951	1.06	0	19	20	0
14.4.92	7.8	72	2	18	2.018	1.04	0	36	45	0
28.4.92	7.8	74	1.13	5	1.135	0.79	5	4	24	0
12.5.92	7.81	70	1.2	5.2	1.2052	0.6	16	5.3	73	0
26.5.92	8.15	68	1.35	0	1.35	1.75	39	86	107	0.1
9.6.92	7.8	68	0.43	0	0.43	2.36	0.9	15	98	0.05
23.6.92	8.54	70	0.15	96	0.246	0	9.3	9.3	51	0.1
7.7.92		72	0	12	0.012	0.6	20	0	26	0
21.7.92	7.73	70	0.13	39	0.169		61	76	207	0.1
4.8.92	7.87	76	0.067	45	0.112	0.5	0.3	0	49	0
17.8.92	7.72	74	0.1	0.2	0.1002		6.4	15	78	0.1
1.9.92	8.08	68	0.02	0	0.02	0.14	12	26	71	0.1
12.9.92	8.06	68	0	0	0	1.1	1.2	27	255	0.15
5.10.92										
13.10.92	8	68	0	0	0	1.1	9	0	68	0.05
3.11.92		68	0.4	18	0.418	1.27	0	16	40	0
9.11.92	7.65	76	0.44	0	0.44	1.5	1.5	0	5	0
24.11.92	7.74	74	0.6	69	0.669	1.8	5	0	14	0.1
8.12.92	7.6	72	1.5	99	1.599	2.2	24	38	56	0
22.12.92	7.5	66	1.2	83	1.283	2.3	46	31	71	0
6.1.93		68	1.1	63	1.163	2.31	12	0.5	28	0
18.1.93	7.4	68	1.1	113	1.213	2.4	13	8	211	0
2.2.93	7.58	64	1.1	73	1.173	2.5	18	17	58	0
16.2.93	7.4	68	1.1	134	1.234	2.3	13	41	63	0
2.3.93	7.67	68	1.3	26	1.326	1.3	2.7	19	27	0
15.3.93	7.22	68	1.02	0.07	1.02007	0.36	0	4	15	0
29.3.93	7.3	68	1.02	0	1.02	0.5	26	26	39	0
15.4.93	7.71		0.6	115	0.715	0.6	1	0	23	0
30.4.93	7.73	64	1.3	0	1.3	0.5	0	10	45	0
11.5.93	7.9	68	0.9	0	0.9	0.6	11	148	173	0
25.5.93	9.06	68	0.5	0	0.5	0.7	2	0	16	0.2
8.6.93	9.03	67	0.4	0	0.4	0.4	14	17	40	0.2
22.6.93	8.86	65	0.2	15	0.215	0.3	15	13	50	0.2
6.7.93	8.34	65	0.1	7	0.107	0.7	6	8	52	0.1
20.7.93	8.95	61	0.006	2	0.008	0.8	0.2	18	118	0.15
2.8.93	9.11		0	18	0.018	1.5	7	32	215	0.05
18.8.93	9.5	59	0.1	0	0.1	1.9	1.3	33	120	0.3
31.8.93	9.04	61	0.1	14	0.114		0	34	155	0.2
13.9.93	8.36	63	0	62	0.062	2.2	0	97	152	0.1
29.9.93	8.75	60	0	13	0.013	2	8.7	35	118	0.15
13.10.93	7.75	61	0	64	0.064	2.7	2	21	287	0.1
27.10.93	8.85	63	0.09	0	0.09	2.4	7	32	62	0.15
10.11.93	7.38	59	0.1	185	0.285	2.95	21	45	99	0
24.11.93		62	0.1	134	0.234	3	33		144	0.1
7.12.93	7.4	64	0	159	0.159	1	27		91	0.1
21.12.93										
12.1.94	7.3	63	0.58	231	0.811	3	18			0.05
26.1.94	7.4	64	1.16	250	1.41	2.5	27	45	70	0
9.2.94										
22.2.94	7.73	62	0.55	8	0.55	0.52	10	29	51	0.1
8.3.94	7.63	64	1.13	0	1.13	0.5	5	36	45	0
21.3.94	7.29	65	0.54	0	0.54	1.8	4	26	50	0

Appendix 1. Mere Mere

Date	TAlk	Chla	Caro	480:663	430:410	WatLev	Secchi
10.1.90	1.25						
25.1.90	1.25						
7.2.90	1.25					30	1.07
21.2.90	1.15	31.2	41.2	1.5	1.3	29	0.86
7.3.90	1.23	34.8	45.4	1.4	1.3	29	0.9
21.3.90	1.18	10.1	17.8	1.6	1.1	27	1.52
4.4.90	1.2	13.6	22	1.7	1.21	27	1.52
18.4.90	1.28	34.5	53.4	1.7	1.3	27	1.21
2.5.90	1.28	4.8	9.2	2.1	1.25	25	2.18
16.5.90	1.28	4.8	12.8	2.9	1	23	3.05
29.5.90	1.4	17.4	25.2	1.6	1.3	16	1.9
12.6.90	1.38	26.6	42.6	1.8	1.23	19	1.68
27.6.90	1.4	34.5	57.8	1.8	1.3	19	1.22
11.7.90	1.5	44.2	80	2	1.3	18	0.92
25.7.90	1.48	47.7	76	1.7	1.3	13	0.79
8.8.90	1.65	65.1	92	1.6	1.3	9	0.62
21.8.90	1.6	33.9	45	1.5	1.3	18	1.16
6.9.90	1.65	26.4	42.6	1.8	1.3	17	1.02
24.9.90	1.8	36.5	51	1.5	1.24	20	1.51
9.10.90	1.75	27.3	32	1.29	1.24	25	1.84
22.10.90	1.73	34.3	31.2	1	1.19	23	1.5
6.11.90	1.65	9	12	1.5	1.1	30	1.87
20.11.90	1.55	4.4	6.6	1.7	1	40	2.2
5.12.90	1.45	3.1	8.8	3.1	1	26	2.6
7.1.91	1.3	3.5	6.8	2.1	0.9	30	1.6
22.1.91	1.2	2.4	3.8	1.7	1	30	
5.2.91	1.25	7.48	9.6	1.4	1.17	29	
19.2.91	1.18	11.44	14.8	1.4	1.22	30	
5.3.91	1.13	23.1	32.2	1.5	1.3	30	1.75
19.3.91	1.13	21.3	29.6	1.5	1.24	30	1.5
2.4.91	1.3	27.5	33.2	1.33	1.22	28	1.45
16.4.91	1.2	14	19	1.5	1.23	27	1.9
30.4.91	1.2	11	19	1.9	1.16	27	2
14.5.91	1.55	0	3	8	0.8	26	3.15
27.5.91	1.28	8	14	1.8	1	23	3
11.6.91	1.65	12	19	1.7	1.1	22	2.25
25.6.91	1.3	13	22	1.8	1.2	28	2.5
9.7.91	1.4	16	24	1.6	1.16	29	2.05
22.7.91	1.43	62	85	1.5	1.29	24	1
6.8.91	1.38	75	106	1.6	1.3	20	0.7
19.8.91	1.3	28	37	1.5	1.19		1
9.9.91	1.55	24	34	1.6	1.25	12	1.45
23.9.91		43	45	1.2	1.2	11	0.95
9.10.91		18	30	1.8	1.1	16	1.6
22.10.91	1.75	21	28	1.5	1.16	17	1.9
5.11.91	1.65	13	23	2	1	22	1.95
19.11.91	2	0	6		1.2	34	2.45
3.12.91	1.7	6	10	1.9	0.9	39	3.75
18.12.91	1.7	0	5	14	0.8	30	
9.1.92	1.45	1	4	3.7	0.9	31	3
21.1.92	1.43	0	2	7	0.8	28	
3.2.92	1.4	2	4	2	0.9	28	
18.2.92	1.9	4	8	2.3	1.1	29	2.6
3.3.92	1.26	14	19	1.5	1.1	29	2.05

Appendix 1. Mere Mere

Date	TAlk	Chla	Caro	480:663	430:410	WatLev	Secchi
18.3.92	1.3	9	14	1.7	1.1	30	
1.4.92	1.25	8	8	1.1	1.1	28	1.8
14.4.92	2.2	10	15	1.7	1.1	30	1.65
28.4.92	1.8	3	4	1.5	1.1	27	2.5
12.5.92	1	6.4	17.6	3	0.79	29	2.41
26.5.92	1.9	2.2	8.3	4.2	1.3	24	2.28
9.6.92	1.25	20.9	27.3	1.4	1.3	27.5	1.4
23.6.92	1.2	25	35	1.55	1.2	22	1
7.7.92	1	20.5	25	1.3	1.2	18	1.2
21.7.92	1.7	26	34	1.45	1.3	18	1.05
4.8.92	1.5	28	42	1.7	1.1	28	0.97
17.8.92	1.9	22	31	1.5	1.3	21	1.25
1.9.92	1.5	18	27	1.7	1.3		
12.9.92	1.4	26	39	1.6	1.4		
5.10.92						27	1.5
13.10.92	2	70.4	111	1.7	1.4	28	1.6
3.11.92	1.9	79	150	2	1.4		1.6
9.11.92	1.9	17	30	1.9	1.4	34	2
24.11.92	1.3	5.5	10.6	2.1	1.2	35.5	2.5
8.12.92	1.3	3.3	10	3.3	1	23	1.5
22.12.92	1.2	4	7.6	2.1	1		
6.1.93	1.3	1.8	7.6	4.6	1		
18.1.93	1.6	4	8	2	1	27	2
2.2.93	1.4	5.5	8	1.6	1.1	28	1.5
16.2.93	1.35	8	8	1.1	1.2		
2.3.93	1.3	20	17	1	1.2	29	1.24
15.3.93	1.2	21	24	1.3	1.2	28	1.5
29.3.93	1.2	1	21	1.7	1.2	29	1.4
15.4.93	1.25	7	12	2	1.2		
30.4.93	0.8	5	9	2	1	30	2.05
11.5.93	1.4	16	35	2.2	1.3	39	2
25.5.93	1.4	44	72	1.8	1.35	25	2.5
8.6.93	1.2	50	83	1.8	1.3	25	1.6
22.6.93	1.4	94	167	2	1.4	24	0.56
6.7.93	1.1	85	146	1.8	1.4	30	0.64
20.7.93	1.75	142	239	1.8	1.4	27	0.88
2.8.93	2.05	77	136	1.9	1.4	22	1.15
18.8.93	1.7	15	26	1.9	1.4	29	1.4
31.8.93	1.6	47	79	1.9	1.4	26	0.85
13.9.93	1.7	55	94	1.9	1.4	27	1.36
29.9.93	2.2	93	163	1.9	1.5	28	1
13.10.93	1.7	15	33	2.4	1.35	28.5	1.4
27.10.93	2.3	14	28	2.2	1.3	27	1.16
10.11.93	2	32	45	1.55	1.4	27	1.18
24.11.93	2	18	31	2.9	1	29	1.65
7.12.93	1.8	8.8	8	1	1.4	32	1.74
21.12.93						31	1.75
12.1.94	1.05	4	3	1	1.3		
26.1.94	1	16	16.6	1.2	1.2	33.5	1.5
9.2.94							
22.2.94	1.5	12.5	14	1.3	1.1	31.5	1.66
8.3.94	1.4	1.8	0.6	0.7	1.2	32	1.6
21.3.94	1.25	9	9	1.1	1.1	32	1.5

Appendix 1. Little Mere

Date	pH	Cl	NO3	NH4	DIN	SiO2	SRP	TSP	TP	PAlk
10.1.90		49				2.1	352			0
25.1.90		54.7	0.45			2.3	470	357	673	0
7.2.90		53.1	0.75	1270	2.02	2.5	272	372	548	0
21.2.90		56.3	1.1	503	1.603	1.9	211	282	430	0
7.3.90		75.5	0.97	611	1.581	2.8	309	427	562	0
21.3.90	9.3	59.2	0.65	0	0.65	0.75	540	623	943	0.18
4.4.90		57.1	0.4	68	0.468	0.55	882	1008	1252	0.05
18.4.90	9.41	60.6	0.33	36	0.366	0.53	980	1254	1866	0.05
2.5.90	8.7	59.8	0.41	707	1.117	1.21		604	931	0
16.5.90	7.5	60.4	0.16	4080	4.24	1.89	2255	2349	2390	0
29.5.90	10.14	66.7	0.53	0	0.53	2.5	660	741	1552	0.55
12.6.90		59.8	0.14	267	0.407	3.12	2843	3232	4759	0.15
27.6.90	7.79	54.2	0.09	1497	1.587	4.1	2291	2020		0
11.7.90	7.87	55.7	0.11	3007	3.117	3.4	2635	3203	4057	0
25.7.90	7.36	60.4	0.19	5758	5.948	4.4	3362	3742	3874	0
8.8.90	7.62	60.4	0.15	7988	8.138	5.2	4744	5441	5341	0
21.8.90	8.09	54.2	0.26	8493	8.753	4.6	4378	4556	4593	0
6.9.90	7.69	56.3	0.05	8809	8.859	5.2	5072	4546	4485	0
24.9.90	7.55	51.5	0.11	9575	9.685	5	4737	5393	5189	0
9.10.90	7.82	51.5	0.1	8785	8.885	3.8	3399	3787	3803	0
22.10.90	7.56	53.2	0.06	8061	8.121	3.3	3227	3307	3368	0
6.11.90	7.64	55.1	0.45			2.25	1657	1693	1578	0
20.11.90	7.3	51.5	0.75	2369	3.119	1.88	750	907	888	0
5.12.90	7.34	55.7	0.46	1941	2.401	1.9	609	624	580	0
7.1.91	7.54	67.3	1.43	816	2.246	2.08	196	280	311	0
22.1.91										
5.2.91	7.37	70.1	0.9	2016	2.916	2.68	703	795		0
19.2.91	7.42	71	0.57	1425	1.995	2.13	511	556	608	0
5.3.91	7.67	73.5	0.58	2334	2.914	2.23	727	798	847	0
19.3.91	7.76	75	0.61	1873	2.483	1.4	553	612	627	0
2.4.91	7.77	75.5	0.3	1932	2.232	1.42	688	761	777	0
16.4.91	7.56	75.5	0.35	2624	2.974	1.66	1176	1288	1317	0
30.4.91	7.55	69.4	0.24	4834	5.074	2.08	2082	2231	2143	0
14.5.91	7.56	73.5	0.25	5802	6.052	1.94	2646			0
27.5.91	9	74.2	0.58	3433	4.013	2.03	2035	2163	2485	0.15
11.6.91	7.37	73.5	0.13	2473	2.603	3.05	2451	2717	2720	0.03
25.6.91	7.38	64	0.12	4861	4.981	2.86	3107	3445	3459	0
9.7.91	7.37	67.3	0.12	2928	3.048		1754	1919	1912	0
22.7.91	7.36	73.5	0.06	4123	4.183	2.45	1598	1729	1774	0
6.8.91	7.16	71.4	0.17	1593	1.763	2.68	1196	1280	1384	0
19.8.91	7.53	74.2	0.09	2166	2.256	2.88	1306	1288	1464	0
9.9.91	7.48	79.2	0.12	1376	1.496	3.77	1551	1483	1657	0
23.9.91	7.26	75.5	0.01	1245	1.255	3.92	857	707	1140	0
9.10.91	7	78.3	0.12	1937	2.057	4.47	1277	1101	1586	0
22.10.91	7.19	76.3	0.09	1998	2.088	3.39	1197	1448		0
5.11.91	6.9	70.7	0.09	1440	1.53	4.62		1398		0
19.11.91	7.24	73.4	0.22	1453	1.673	3.6	1307			0
3.12.91	7.35	72	0.43	845	1.275	2.81	825		851	0
18.12.91	7.4	72.7	0.29	636	0.926	1.57	383			0
9.1.92	7.58	70.6	0.48	214	0.694	1.6	51		62	0
21.1.92	7.47	71.8	0.95	242	1.192	1.62	78	146	173	0
3.2.92	7	74	0.63	238	0.868	1.28	105	146	152	0
18.2.92	7.58	71.8		90			50		94	0
3.3.92	8.7	76	0.78	6	0.786	0.34	11	11	150	0.12

Appendix 1. Little Mere

Date	pH	Cl	NO3	NH4	DIN	SiO2	SRP	TSP	TP	PAlk
18.3.92	7.92	72	0.86	44	0.904	0.67	13	33	60	0
1.4.92	7.45	73.3	1.07	147	1.217	0.9	28	20	40	0
14.4.92	7.45	76	0.82	158	0.978	0.87	40	32	58	0
28.4.92	7.58	72	0.6	162	0.762	0.89	83	67	103	0
12.5.92	7.61	68	0.14	136	0.276	0.22	122	220	220	0
26.5.92	8.5	72	0.01	101	0.111	0.27	311	531	892	0.1
9.6.92	7.75	68	0.005	69	0.074	2.27	258	231	585	0.1
23.6.92	9.38	72	0.002	56	0.058	0.77	139	44	160	0.1
7.7.92		72	0.002	0	0.002	3	238	121	365	0
21.7.92	7.2	74	0.04	312	0.352	3.4	570	652	891	0
4.8.92	7.27	72	0.04	287	0.327	5.5	726	368	1030	0
17.8.92	7.78	74	0.07	400	0.47		855	720	1050	0.05
1.9.92	8.02	76	0.007	129	0.136	2.5	164	160	323	0.15
12.9.92	7.19	82	0	14	0.014	0.326	680	159	1475	0.25
5.10.92	6.56	76	0	1334	1.334	2.8	882	478	1079	0
13.10.92	7.4	68	0	1774	1.774	2.8	1024	100	1034	0
3.11.92		75	0.2	516	0.716	1.4	25	128	170	0
9.11.92	7.59	72	0.3	453	0.753	1.8	162	41	187	0
24.11.92	7.84	64	0.3	194	0.494	1.7	26	11	45	0.1
8.12.92			1.2	162	1.362	2	23	53	62	0
22.12.92		67	0.8	159	0.959	2.2	59	51	110	0
6.1.93		64	0.8	92	0.892	2.5	61	69	85	1
18.1.93	7.53	67	1.3	137	1.437	2.4	78	35	197	0
2.2.93	7.61	65	1.1	80	1.18	2.3	20	28	125	0
16.2.93	7.44	64	1.3	69	1.369	2	24	28	63	0
2.3.93	7.65	68	0.76	54	0.814	1.8	5.4	23	88	0
15.3.93		68	0.7	0.08	0.7	0.9	20	0	38	0
29.3.93			0	0	0	0.5	19	7	66	0
15.4.93	7.7		0.2	151	0.351	0.8	73	68	167	0
30.4.93	7.5	63	0.1	227	0.327	1	124	130	240	0
11.5.93	7.96	72	0.1	0	0.1	1	126	848	1017	0
25.5.93	7.29		0.04	205	0.245	1.8	95	23	137	0
8.6.93	7.45	71	0.1	105	0.205	1.8	70	108	127	0.1
22.6.93	7.74	66	0.09	13	0.103	1.5	22	24	30	0
6.7.93	7.45	63	0.05	50	0.1	1.7	37	102	116	0
20.7.93	8.45	57	0.02	121	0.141	1.2	18	44	62	0
2.8.93	9.13	59	0	67	0.067	0.9	53	409	512	0.05
18.8.93	9.78	79	0.1	0	0.1	1.9	1.3	91	120	0.3
31.8.93	9.73		0.1	16	0.116		43	79	124	0.45
13.9.93	9	65	0	17	0.017	1.4	53	31	75	0.2
29.9.93	9.09	80	0	2	0.002	0.4	67	81	101	0.3
13.10.93	7.37		0	11	0.011	2.4	119	140	260	0.1
27.10.93	7.64	67	0.03	12	0.042	2.1	95	122	144	0
10.11.93	7.5	78	0.02	0	0.02	2.8	201	247	380	0
24.11.93	7.5	68	0	23	0.023	3	145	93	180	0.1
7.12.93	7.2	60	0.01	172	0.182	0.8	91	146	188	0.1
21.12.93										
12.1.94	7.3	65	0.9	320	1.22	3	12			0.1
26.1.94	7.4	76	0.4	297	0.697	2.4	24	48	79	0
9.2.94										
22.2.94	7.99	64	0.46	0	0.46	0.57	6	34	62	0.1
8.3.94	7.56	62	0.55	0	0.55	0.85	0.5	24	76	0
21.3.94	7.29	60	0.69	32	0.693	0.88	2	21	45	0

Appendix 1. Little Mere

Date	TAlk	Chla	Caro	480:663	430:410	WatLev
10.1.90	1.75					
25.1.90	1.5					
7.2.90	1.25					36
21.2.90	1.3	30.6	42.8	1.54	1.28	36.5
7.3.90	1.3	24.6	35.6	1.59	1.23	37
21.3.90	1.38	295.9	417.8	1.55	1.16	37
4.4.90	1.38	251.2	347.2	1.52	1.23	37
18.4.90	1.5	354.6	435.6	1.35	1.28	36.5
2.5.90	1.6	68.2	74	1.19	1.23	37
16.5.90	1.88	22.2	32.4	1.6	1.23	38.5
29.5.90	1.6	70	91.2	1.43	1.3	38
12.6.90	1.55	92.2	139.8	1.67	1.26	38
27.6.90	1.75	31.7	37	1.28	1.18	37.5
11.7.90	1.98	27.3	41.8	1.7	1.1	38
25.7.90	2.2	1.5	5.6	4	0.9	38.5
8.8.90	2.3	1.3	5.4	4.5	0.9	37
21.8.90	2.3	4.8	9	2	1.1	37
6.9.90	2.45	13.4	18.2	1.5	1.1	36
24.9.90	2.45	4.4	6.2	1.5	0.9	36
9.10.90	2.3	2	6.4	3.6	0.8	35
22.10.90	2.25	1.8	6	3.8	0.8	35
6.11.90	1.85	0.2	3	15	0.9	34
20.11.90	1.6	0	0.4		0.67	34
5.12.90	1.75	0	1		0.85	32
7.1.91	1.4	1.1	6.2	6.2	0.9	33
22.1.91						35
5.2.91	1.55	15.6	19.2	1.35	1.28	35
19.2.91	1.45	23.3	28	1.32	1.27	34.5
5.3.91	1.45	14.1	20.8	1.6	1.2	36
19.3.91	1.45	11.9	20.2	1.9	11.1	37
2.4.91	1.38	3.1	8.8	3.1	0.96	36.5
16.4.91	1.55	3.3	10.6	3.5	0.9	37
30.4.91	1.58	4.4	16.3	4.1	1	37
14.5.91	1.85	4.6	8.4	2	1.1	36.5
27.5.91	2.1	141	167.2	1.3	1.31	36.5
11.6.91	1.8	2.6	7.6	3.2	1	38
25.6.91	1.78	3.3	9.2	3.1	0.9	38
9.7.91	1.98	1.3	6.4	5.3	0.8	39
22.7.91	1.7	12.8	15	1.29	1	38
6.8.91	1.75	6.2	13.2	2.4	1	37
19.8.91	1.55	0.4	2.4	6	0.9	38
9.9.91	1.55	6.6	10.3	1.7	1.1	41
23.9.91	1.65	4	10	2.7	0.9	43
9.10.91		2.9	6	2.3	0.9	38
22.10.91		0.4	4.7	14	0.8	37
5.11.91	1.7	2.2	9.3	4.7	0.8	36
19.11.91	1.98	0	11.3		0.9	40
3.12.91	2.13	0	3		0.8	37
18.12.91	1.68	0	4.7		0.8	35
9.1.92	1.4	2.9	8.3	3.1	0.9	32.5
21.1.92	1.45	2.9	6.3	2.4	0.9	35
3.2.92	1.35	5.1	7	1.5	1.1	38
18.2.92	1.6	8.1	12.3	1.7	1.18	38
3.3.92	1.22	57.9	79.3	1.5	1.25	37

Appendix 1. Little Mere

Date	TAlk	Chla	Caro	480:663	430:410	WatLev
18.3.92	1.3	11	17.3	1.7	1.08	35
1.4.92	1.25	1.1	4.7	4.7	0.88	36
14.4.92	2.6	2.6	5.3	2.28	0.97	37.5
28.4.92	1.1	2.6	0.7	0.285	1.2	39
12.5.92	1.4	1.2	13.2	12	0.9	38
26.5.92	0.9	2.9	0.3	0.13	1	36
9.6.92	1.5	1.46	4.6	3.5	1	37
23.6.92	1.9	2.9	8	3	1	
7.7.92	2.1	2.2	33	0.2	1	38
21.7.92	1.6	6.6	6.6	1	1.22	32
4.8.92	1.8	5.9	7	1.3	1	33
17.8.92	1.3	5.1	8.6	1.9	1	37
1.9.92	1.75	9.5	11.6	1.3	1	
12.9.92	1.65	1.5	5	3.7	1	
5.10.92	1.4	0.3	17.6	5.3	0.8	36
13.10.92	1.8	4	9.6	2.6	3.8	37
3.11.92	2	7.3	2.7	1.4	1.2	
9.11.92	1.8	6.6	13	2.2	1.3	31
24.11.92	1.4	0.7	4.6	7	1	30
8.12.92	1.5	1.1	9.6	9.6	0.8	32
22.12.92	1.3	3.3	3.3	1	1	33
6.1.93	1.3	2.6	7	1	1	32
18.1.93	1.3	4.8	10	2	2	34
2.2.93	1.3	4.8	7.6	1.7	1	34
16.2.93	1.3	14	17	1.3	1.2	34
2.3.93	1.3	33	45	1.5	1.3	36.5
15.3.93	1.3	80	80	1.1	1.3	38
29.3.93	1.4	34	41	1.3	1.2	36
15.4.93	1.4	9	13	1.6	1.2	
30.4.93	1.3	2.2	6	3	0.7	34
11.5.93	1.4	7	8.7	1.4	1	37
25.5.93	1.55	12.1	36	3	1.1	38
8.6.93	1.2	10.3	13	1.4	1.1	38.6
22.6.93	1.25	17	19	1.2	1.25	37
6.7.93	1.2	13	16	1.4	1.1	38.5
20.7.93	1.3	18	28	1.6	1.28	38
2.8.93	1.15	0.7	4.6	7	0.6	
18.8.93	1.8	5	10	2.1	1.1	36
31.8.93	1.4	14	17	1.4	1.3	37
13.9.93	1.55	4	7	2.2	1.1	36
29.9.93	1.1	4	8	2	1.2	37
13.10.93	1.7	12	26	2.2	1.3	36.2
27.10.93	2	16	13	0.9	1.2	36
10.11.93	1.95	47	38	0.88	1.3	36
24.11.93	2.1					34
7.12.93	1.8	22.7	16.3	0.8	1.4	34
21.12.93						
12.1.94	1.4	8.4	2.3	1.7	1.3	35
26.1.94	1.35	14.6	12	0.9	1.1	36
9.2.94						
22.2.94	1.4	34	38	1.4	1.3	33
8.3.94	1.35	11	11.6	1.1	1.2	34
21.3.94	1.25	18	18	1.1	1.2	36

Appendix 1. Inflow Rostherne Mere

Date	pH	Cl	NO3	NH4	DIN	SiO2	SRP	TSP	TP
10.1.90									
25.1.90		56.8	2.69			4.1	308	403	1380
7.2.90		40.8	2	825	2.825	4.1	270	348	1100
21.2.90		50		153		4	100	131	264
7.3.90		65.1	2.11	65	2.175	3.4	115		266
21.3.90		44.9	1.89	58	1.948	3.3	133	165	361
4.4.90		44.9	0.98	119	1.099	3.2	173	160	348
18.4.90		44.4	1.55	160	1.71	3.5	165	233	562
2.5.90		41.2	1.66	123	1.783	4	248	370	344
16.5.90		43.8	1.51	531	2.041	4.3	356	406	471
29.5.90		41.7	1.96	78	2.038	4.6	250	264	341
12.6.90		39.2	1.53	48	1.578	4.9	412	449	684
27.6.90		39.6	1.74	182	1.922	5.5	289	355	433
11.7.90		39.2	1.88	104	1.984	4.1	183	235	519
25.7.90		35.4	1.98	146	2.126	4.6	145	160	212
8.8.90		37.5	2.4	157	2.557	5.1	133	167	230
21.8.90		41.7	1.33	1285	2.615	4.4	411	443	566
6.9.90		39.6	1.48	404	1.884	4.9	170	150	273
24.9.90		33	1.82	1415	3.235	3.4	369	472	3299
9.10.90		45.4	2.37	1476	3.846	4.1	874	944	1017
22.10.90		42.6	2.54	335	2.875	4.3	524	541	624
6.11.90		44.9	2.03	1210	3.24	4.1	572	686	718
19.11.90		47.4	6.42	419	6.839	3.3	215	285	398
5.12.90		47.4	2.35	438	2.788	3.7	139	149	
7.1.91		59.2	3.63	442	4.072	3.2	88	127	226
22.1.91		66	4.44	415	4.855	3.3	166	201	296
5.2.91		49.5	3.23	560	3.79	4.2	206	238	447
19.2.91		49	2.61	605	3.215	3.9	214	260	382
5.3.91		61.2	3.99	561	4.551	3.5	204	236	463
19.3.91		56.3	4.37	294	4.664	2.7	168	199	424
2.4.91		51	3.2	564	3.764	3.2	287	330	598
16.4.91		44.9	1.92	98	2.018	3.4	170	229	355
29.4.91		40.8	1.89	142	2.032	4.1	185	206	348
14.5.91		42.9	1.83	298	2.128	3.9	369		
27.5.91		43.3	1.79	198	1.988	4.2	282	294	449
11.6.91		42.9	1.68	146	1.826	4.6	137	151	283
25.6.91		42	1.49	578	2.068	4.4	592	694	885
9.7.91		46.9	1.46	181	1.641	4	316	358	456
22.7.91		42.9	1.42	215	1.635	5.3	196	200	343
6.8.91		38.8	1.68	117	1.797	4.9	95	109	342
19.8.91		41.2	1.8	100	1.9	5.2	101	106	224
9.9.91		37.5	1.98	93	2.073	5.1	46	51	176
23.9.91	8.1	36.7	2.15	155	2.305	4.8	42	27	221
9.10.91		41.3		166		5.5	44	58	129
22.10.91		37.1	1.57	107	1.677	4.2	49	68	
5.11.91		46.5	1.4	220	1.62	5.1	71	94	116
19.11.91		65.3	4.84	426	5.266	4.5	125		
3.12.91		44	2.59	165	2.755	4.2	68	81	155
18.12.91		82.8	1.62	1317	2.937	4	412	610	1004
9.1.92		62.8	2.58	178	2.758	3	41	97	131
21.1.92		48.5	2.54	121	2.661	4	41	39	204
3.2.92		80	1.87	262	2.132	4.1	26	64	78
18.2.92		71.8	4.99	450	5.44	4.2	59	79	369
3.3.92		60	5.15	162	5.312	3.1	31		238

Appendix 1. Inflow Rostherne Mere

Date	pH	Cl	NO3	NH4	DIN	SiO2	SRP	TSP	TP
18.3.92		56.2	2.49	202	2.692	2.9	18	74	185
1.4.92	7.8	55.4	2.79	51	2.841	3	35	25	104
14.4.92		49	2.04	64	2.104	3.05	25	70	84
28.4.92	7.8	46	1.6	90	1.69	3.67	48	61	128
12.5.92		48	2.2	145	2.345	3.4	94	148	326
26.5.93		36	1.4	0	1.4	4.5	49	97	123
9.6.92		40	1.5	0	1.5	4.7	86	48	158
23.6.92		42	1.3	12	1.312	3.8	158	213	403
7.7.92		36	1.4	8	1.408	4.6	62	11	74
21.7.92		36	1.2	86	1.286	5.3	55	39	149
4.8.92	7.9	36	1.9	31	1.931	4.9	54	12	47
17.8.92	7.8	38	1.3	273	1.573	4.6	101	114	233
1.9.92	8.12	36	1.6	153	1.753	5	156	181	325
12.9.92		36	2.9	341	3.241	5.1	91	256	467
5.10.92		40	2	220	2.22	4.7	202	200	284
13.10.92	7.9	40	1	53	1.053	4.4	111	0	125
3.11.92		40				3.5	60	198	250
9.11.92	7.5	40	2.7	214	2.914	3.2	96	48	161
24.11.92	7.9	46	2.3	126	2.426	2.6	40	26	93
8.12.92			3.48	185	3.665	3	45	50	110
22.12.92		68	2	187	2.187	3.4	79	40	112
6.1.93		72	1.1	124	1.224	3.96	45	37	118
15.1.93	7.7	64	3.5	36	3.536	3.3	35	45	356
2.2.93	7.7	64	2.3	54	2.354	3.2	29	97	153
16.2.93	7.8	64	1.4	61	1.461	3.5	10	41	87
2.3.93	8	68	1.8	65	1.865	3.6	12	0	70
15.3.93			1.9	59	1.959	4	39	0	36
29.3.93			0.84	84	0.924	4	32	19	52
15.4.93	7.8		0.7	128	0.828	3.8	55	0	89
30.4.93	8	41	0.9	74	0.974	3.6	72	75	133
11.5.93	8.1	38	1.5	0	1.5	4.4	32	194	271
25.5.93	8		1.3	15	1.315	5.5	54	90	128
8.6.93	7.9	42	1	128	1.128	5	49	61	191
22.6.93	8	42	0.8	160	0.96	3.9	57	56	220
6.7.93	8	36	1.4	87	1.487	5.1	38	6	35
20.7.93	7.8	40	1.5	651	2.151	3.6	123	161	301
2.8.93	8	45	1.9	74	1.974	4.9	58	74	265
18.8.93	7.9	48	0.7	52	0.752	3.7	64	85	132
31.8.93	8		0.13	57	0.187		35	42	97
13.9.93	7.8	39	0.8	108	0.908	5	64	14	200
29.9.93	8	34	1.4	36	1.436	5.8	38	32	75
13.10.93	7.7		1.1	15	1.115	4	59	74	146
27.10.93	8.1	37	1.9	76	1.976	5.5	36	36	57
10.11.93	7.6	36	0.4	0	0.4	5.1	49	50	102
24.11.93	7.7	40	1	102	1.102	5.3	31	0	124
7.12.93	7.3	48	1.8	729	2.529	2.5	162	209	332
21.12.93									
12.1.94	7.2	80	1.2	451	1.63	3.5	66		
26.1.94	7.4	52	1.4	276	1.67	3.2	104	106	171
9.2.94									
22.2.94									
8.3.94	7.7	54	2.1	9	2.1	2.6	23	51	85
21.3.94	7.4	54	2.4	49	2.44	2.6	40	41	75

Appendix 1. Inflow Rostherne Mere

Date	PAlk	TAlk	Flow
10.1.90			
25.1.90			
7.2.90			
21.2.90	0	2.18	
7.3.90	0	2.25	0.099
21.3.90	0	2.85	0.071
4.4.90	0	3	0.058
18.4.90	0	3.28	0.05
2.5.90	0	3.45	0.047
16.5.90	0	3.43	0.053
29.5.90	0	3.7	0.044
12.6.90	0	3.5	0.041
27.6.90	0	3.68	0.04
11.7.90	0.05	3.5	0.051
25.7.90	0.13	3.6	0.028
8.8.90	0.15	4.3	0.034
21.8.90	0	3.1	0.073
6.9.90	0	3.7	0.059
24.9.90	0	2.2	0.211
9.10.90	0	3.15	0.065
22.10.90	0	3.28	0.057
6.11.90	0	2.6	0.055
19.11.90	0	1.9	0.321
5.12.90	0.1	2.8	0.078
7.1.91	0	1.95	0.174
22.1.91	0	2.35	0.099
5.2.91	0	2.85	0.072
19.2.91	0	2.8	0.066
5.3.91	0	2.33	0.099
19.3.91	0	2.13	0.144
2.4.91	0	2.78	0.077
16.4.91	0	3.23	0.048
29.4.91	0.05	3.33	0.055
14.5.91	0	3.35	0.034
27.5.91	0.1	3.4	0.044
11.6.91	0.2	3.65	0.044
25.6.91	0	3.1	0.054
9.7.91	0	3.15	0.066
22.7.91	0	3.55	0.04
6.8.91	0.3	3.7	0.047
19.8.91	0	3.5	0.042
9.9.91	0	3.9	0.033
23.9.91	0	5.15	0.03
9.10.91	0.2	4.75	0.042
22.10.91	0	3.85	0.038
5.11.91	0	3.28	0.073
19.11.91	0.08	3.43	0.082
3.12.91	0	3.72	0.057
18.12.91	0	3.18	0.104
9.1.92	0	1.95	0.172
21.1.92	0.08	2.93	0.057
3.2.92	0.3	2.95	0.075
18.2.92	0.3		0.085
3.3.92	0	2.18	0.173

Appendix 1. Inflow Rostherne Mere

Date	PAlk	TAlk	Flow
18.3.92	0.3	2.2	0.109
1.4.92	0.15	2.4	0.084
14.4.92	0.3	4.5	0.0638
28.4.92	0.2	3.9	0.0559
12.5.92	0.1	3.9	0.077
26.5.93	0.25	3.95	0.0232
9.6.92	0.35	3.35	0.025
23.6.92	0.05	4.05	0.0324
7.7.92	0.3	3.9	
21.7.92	0.5	4	0.0538
4.8.92	0.2	3.9	0.051
17.8.92	0.15	3.25	0.03
1.9.92	0.3	3.6	
12.9.92	0.2	3.1	
5.10.92	0.3	3.8	0.103
13.10.92	0.4	3.3	0.0442
3.11.92	0	2.5	0.7597
9.11.92	0	2.2	0.163
24.11.92	0.1	1.8	0.284
8.12.92	0	1.85	0.2008
22.12.92	0	1.85	0.087
6.1.93	0	2	0.0794
15.1.93	0.2	2.1	0.1179
2.2.93	0.2	2	0.0472
16.2.93	0.1	2.5	0.0558
2.3.93	0.2	2.7	0.0666
15.3.93	0.1	3.1	0.1166
29.3.93	0.2	3.85	0.0635
15.4.93	0.05	3.5	0.083
30.4.93	0.4	3.7	0.129
11.5.93	0.3	3.8	
25.5.93	0.02	3.5	0.068
8.6.93	0.6	3.6	0.0334
22.6.93	0.2	3.1	0.059
6.7.93	0.3	3.6	0.085
20.7.93	0	2.7	0.057
2.8.93	0.2	3.5	
18.8.93	1.1	3.7	0.0631
31.8.93	0.35	3.9	0.0189
13.9.93	0.35	3.75	0.0341
29.9.93	0.15	3.75	0.076
13.10.93	0.2	2.9	0.08
27.10.93	0.15	3.7	0.0348
10.11.93	0.2	3.65	0.079
24.11.93	0.3	3.5	0.082
7.12.93	0.1	1.9	0.093
21.12.93			
12.1.94	0.1	1.95	0.118
26.1.94	0	1.3	0.14
9.2.94			
22.2.94			
8.3.94	0.1	2.45	0.108
21.3.94	0.1	2.3	0.123

Appendix 1. Spring Rostherne Mere

Date	pH	Cl	NO3	NH4	DIN	SiO2	SRP	TSP	TP	PAlk	TAlk
2.5.90	7.8	37.1	0.06	72	0.132	5.9	13	16	37	0	4.1
16.5.90		35.4	0.04	93	0.13	5.2	12	32	92	0	4.1
29.5.90		37.5	0.14	70	0.21	5.3	8	13	39	0	4.1
12.6.90		39.2	0.06	69	0.13	5	31	35	81	0	4.1
27.6.90	8	43.8	0.06	128	0.19	5.5	20	17	173	0	4.15
11.7.90		37.1	0.06	106	0.17	4	38	46	32	0.08	4.03
25.7.90		37.5	0	95	0.1	4.4	15	8	68	0.03	3.83
8.8.90		37.5	0.07	82	0.15	5.2	13	15	41	0.1	4.25
21.8.90		37.5	0.1	103	0.2	4.8	15	32	25	0	3.95
6.9.90		37.5	0.03	99	0.13	5.2	12		22	0	4.05
24.9.90		41.2	0.16	92	0.25	5	20	25	65	0	3.55
9.10.90	8.1	37.1	0.05	108	0.16	4.5	18	23	25	0	3.93
22.10.90		38.3	0.07	78	0.15	4.3	9	12	29	0.1	4.08
6.11.90		36.7	0.28	94	0.37	5.4	14	16	35	0	4
20.11.90		41.2		97		4.9	24	34	45	0	3.2
5.12.90	8	37.1	0.08	86	0.17	5.1	8		50	0.1	3.8
7.1.91		34.7	0.46	79	0.54	4.8	6	12	36	0	3.7
22.1.91		35.1	0.33	89	0.42	4.8	9	20	37	0	3.95
5.2.91	8.1	39.2	0.34	96	0.44	5.4	9	10	34	0	4
19.2.91		37	0.35	71	0.42	4.9	12	16	30	0	3.9
5.3.91		38.8	1.04	67	1.11	5.1	7	33	24	0	3.7
19.3.91		37.5	1.59	91	1.68	4.9	10	21	61	0	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	16	26	53	0	4
30.4.91		34.7	0.11	71	0.18	5.4	9	14	35	0.35	3.7
13.5.91	8	36.7	0.05	94	0.14	5.1	10			0	3.98
27.5.91		37.1	0.09	98	0.19	4.8	6	4	30	0.1	4.03
11.6.91		36.7	0.09	86	0.18	4.9	10	34	40	0.2	4.15
25.6.91		36	0.11	75	0.19	4.9	14	0	55	0	4.05
9.7.91		36.7	0.07	80	0.15	4.7	9	6	21	0	4.05
22.7.91		40.8	0.01	86	0.1	5.1	15	16	38	0	4.1
6.8.91		36.7	0.06	70	0.13	5.3	7	16	37	0.1	3.35
19.8.91		37.1	0.08	66	0.15	5.5	6	9	23	0	3.9
9.9.91		39.6	0.05	90	0.14	5.2	11	13	34	0	4
23.9.91	7.8	36.7	0.04	94	0.13	4.8	1	3	23	0	
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	3.95
5.11.91		36.4		81		4.7	11		22	0	4.05
19.11.91		38.8	0.33	126	0.46	5.2	10			0.23	5
3.12.91		36	0.13	77	0.21	4.6	8	5	24	0	4.4
18.12.91		36.4	0.12	123	0.24	5	33		43	0.18	4.4
9.1.92	7.5	43.1	0.84	53	0.89	5	6	22	34	0.3	3.6
21.1.92		36.9	0.12	55	0.18	5.7	6	22	21	0.23	4.25
3.2.92		24	0.1	58	0.16	5.4	8	8	7	0.8	4.05
18.2.92											
3.3.92		44	0.94	32	0.97	5.2	8	32	34	0	3.78
18.3.92		37.5	1.32	72	1.39	5.1	0	0	21	0.1	3.8
1.4.92	7.6	37.6	0.85	59	0.91	5.2	16	14	21	0.35	3.9
14.4.92		40	0.06	41	0.1	4.5	0	29	39	0.8	
28.4.92	7.6	36	1.36	20	1.38	5.3	14	2	3	0.3	4

Appendix 1. Spring Rostherne Mere

Date	pH	Cl	NO3	NH4	DIN	SiO2	SRP	TSP	TP	PAlk	TAlk
12.5.92		40	0.04	28	0.068		7	11	77	0.1	4
26.5.92		40	0.04	0	0.04	4.5	14	40	57	0.25	4.25
9.6.92	7.8	38	0.2	0	0.2	5.4	0	13	23	0.5	3.9
23.6.92			0.06	42	0.7	4.9	8	0	47	0.1	4.1
7.7.92		38	0.15	0	0.15	5.1	52	0	53	0.2	4
21.7.92											
4.8.92	7.7	34	0.04	56	0.096	7.8	24	0	39	0.3	3.9
17.8.92	7.7	38	0.2	50	0.25	7.7	9	0	9	0.2	3.9
1.9.92	8	36	0.08	33	0.041	5.3	31	16	37	0.3	3.8
12.9.92	7.2	36	0.1	49	0.16		80	0	144	0.6	4
5.10.92	7.1	38	0.2	47	0.25	5.3	47	0	60	0.4	3.9
13.10.92	7.8	36	0.1	18	0.12		20	2.6	27	0.3	3.8
3.11.92		36	1	20	1.02	4.9	1	9	39	0	3.4
9.11.92	7.7	36	3.3	44	3.34	5	7	0	9	0	2.3
24.11.92	8	38	2	28	2.03	5.7	3	0	42	0.2	3.4
8.12.92		38	1.9	40	1.94	5.5	20	31	48	0.3	3.3
22.12.92		36	0.7	31	0.73	5.3	17	16	31	0.25	2.45
6.1.93		38	0.9	7	0.9	5.3	23	23	51	0	3.7
16.1.93	7.8	36	1.5	10	1.51	5.3	14	24	210	0.2	3.6
2.2.93	7.7	40	0.6	17	0.62	5.4	6	0	37	0.4	3.6
16.2.93	7.8	36	0.1	31	0.131	4.7	10	8	18	0.3	3.8
2.3.93	7.9	36	0.14	64	0.204	5	0	0	7	0.3	3.6
15.3.93		36	0.1	52	0.152	5.5	14	0	16	0.3	4.1
29.3.93			0	56	0.056	5	7	0	0	0.25	3.35
15.4.93	7.9		0.09		0.09	4.3	21	36	57	0.25	3.85
30.4.93	7.8	31	0.08	220	0.3	5	0	0	0	0.4	5.4
11.5.93	7.9	40	0.2	15	0.22	5	10	108	121	0.25	3.95
25.5.93	7.8		0.2	25	0.13	6	9	0	9	0.4	3.9
8.6.93	7.8	38	0	50	0.05	6	22	13	8	0.5	3.3
22.6.93	7.9	40	0.1	44	0.144	5	14	6	0	0.35	3.95
6.7.93	7.8	36	0.11	55	0.165	5	10	2	25	0.3	4.3
20.7.93	7.8	34	0.06	105	0.165	5.5	13	0	27	0.2	34
2.8.93	7.7	39	0	66	0.066	5.9	6	27	49	0.05	3.8
18.8.93	7.8	36	0.2	66	0.27	5.6	11	0	18	0.05	3.9
31.8.93	7.7		0.1	146	0.246		0	8	21	0.1	3.95
13.9.93	7.6	35	0.1	83	0.183	5.6	63	57	229	0.05	3.85
29.9.93	7.7	34	0.08	40	0.12	6	17	16	29	0.2	3.8
13.10.93	7.7		0.16	70	0.23	5.3	2	13	22	0.4	3.85
27.10.93	7.9	37	0.2	53	0.25	6.1	10	0	13	0.2	4
10.11.93	7.6	36	0.08	45	0.13	5.5	7	3	11	0.35	3.95
24.11.93	7.7	36	0.1	185	0.29	6.2	6	0	21	0.3	4.15
7.12.93	7.3	40	1	316	1.32	4.4	108	233	397	0.2	3.5
21.12.93											
12.1.94	7.4	40	1.5	188	1.69	5.6	44			0.3	3.35
26.1.94	7.9	40	0.6	265	0.87	5.3	154	168	228	0	3.25
9.2.94											
22.2.94	7.6	36	0	65	0.065	5.2	7	15	31	0.25	4.05
8.3.94	7.6	40	0.11	46	0.16	5.6	14	36	44	0.3	3.85
21.3.94	7.4	32	0.5		0.5	5.7	10	10	49	0.3	3.45

Appendix 1. Rostherne Mere

Date	pH	Cl	N03	DIN	NH4	DIN	SiO2	SRP	TSP	TP	PAlk
10.1.90		40.8					2	344			
25.1.90											
7.2.90		40.8	0.87	0.92	50	0.92	2	378	376	410	0
21.2.90		41.7			0			371	380	408	0
7.3.90		54.7	0.92	0.943	23	0.943	1.7	380		419	0.03
21.3.90	7.6	42.9	1.02	1.02	0	1.02	1.5	344	360	353	0.03
4.4.90		40.8	0.59	0.59	0	0.59	0.9	360	390	384	0
18.4.90	8.3	40.4	0.88	0.907	27	0.907	0.3	370	453	445	0
27.4.90											
2.5.90	8.3	43.3	0.95	0.98	30	0.98	0.3	369	380	390	0.03
16.5.90	8.4	43.8	1.06	1.06	0	1.06	0.3	331	359	398	0.05
29.5.90	9.1	45.8	0.93	0.93	0	0.93	0.5	258	271	466	0.3
12.6.90	9	43.3	0.89	0.922	32	0.922	0.5	476	505	615	0.18
27.6.90		37.5	0.77	0.845	75	0.845	0.9	233	274	304	0.35
11.7.90	8.4	45.4	0.69	0.776	86	0.776	0.6	293	365	352	0.13
25.7.90	9.3	43.8	0.66	0.698	38	0.698	0.7	217	243	303	0.28
8.8.90	9.5	45.8	0.27	0.289	19	0.289	1.05	145	180	273	0.3
21.8.90	9.3	45.8	0.19	0.197	7	0.197	0.9	98	115	169	0.3
6.9.90	9.4	45.8	0	0.024	24	0.024	1.2	110	116	183	0.45
24.9.90	9.1	43.3	0.21	0.222	12	0.222	1.5	202	234	348	0.25
9.10.90	9	43.3	0.13	0.139	9	0.139	0.99	222	251	339	0.2
22.10.90	9	44.7	0.25	0.263	13	0.263	1.12	236	247	324	0.28
6.11.90	8.6	44.9	0.48	0.592	112	0.592	1.42	290	340	465	0.1
20.11.90	7.9	45.4	0.69	0.979	289	0.979	1.35	374	414	440	0
5.12.90	7.9	45.4	0.43	0.803	373	0.803	1.45	409	442	425	0.05
7.1.91	8	42.9	0.65	1.023	373	1.023	1.55	402	418	422	0
22.1.91	8	41.2	1.48	1.706	226	1.706	1.71	390	393	401	0
5.2.91	7.8	43.3	1.43	1.446	16	1.446	2	385	431	417	0
19.2.91	8	45	1.29	1.29	0	1.29	1.86	397	422	425	0
5.3.91	8	44.9	1.03	1.03	0	1.03	1.84	417	434	438	0
19.3.91	8.2	47.9	1.19	1.19	0	1.19	1.79	401	427	418	0
2.4.91	8.1	44.9	1.89	1.89	0	1.89	1.67	391	392	442	0.03
16.4.91	8.5	46.9	1.08	1.083	3	1.083	0.97	370	340	433	0.03
30.4.91	8.4	40.8	0.93	0.93	0	0.93	0.96	360	338	392	0.1
14.5.91	8.2	46.9	0.77	0.819	49	0.819	0.76	370			0
27.5.91	8.5	47.4	0.96	0.978	18	0.978	0.86	326	305	357	0.1
11.6.91	8.6	44.9	0.83	0.859	29	0.859	0.66	312	338	429	0.15
25.6.91	8.7	40	1.21	1.226	16	1.226	0.72	302	313	357	0.1
9.7.91	8.8	44.9	1.14	1.165	25	1.165	0.46	319	313	356	0.18
22.7.91	8.9	46.9	0.68	0.68	0	0.68	1.12	268	306	336	0.18
6.8.91		46.9	0.1	0.101	1	0.101	1	160	205	319	0.7
19.8.91	9.7	45.4	0.06	0.065	5	0.065	1.92	162	184	305	0.7
9.9.91	9.7	47.9	0.03	0.05	20	0.05	1.49	134	146	238	1.33
23.9.91	9.6	44.9	0	0.094	94	0.094	1.39	193	203	257	0.9
9.10.91	9.3	45.7	0.13	0.13	0	0.13	1.84	245	291	380	0.95
22.10.91	8.7	47.4	0.26	0.312	52	0.312	1.08	301	391	453	0.55
5.11.91	8.4	36.4	0.23	0.461	231	0.461	2.73	355	360	488	0.2
19.11.91	8.1	46.9	0.23	0.837	607	0.837	2.11	610	646	847	0.18
3.12.91	7.9	44	0.34	0.883	543	0.883	2.09	426	416	462	0
18.12.91	7.9	46.5	0.37	0.907	537	0.907	2.27	486	581	696	0.13
9.1.92	7.5	51	0.88	1.045	165	1.045	2.51	453	532	530	0
21.1.92	7.7	40.8	0.89	0.89	0	0.89	2.26	510	719	861	0
3.2.92	7.6		0.74	0.74	0	0.74	2.33	492	515		0.2
18.2.92	7.7	50.5	1.04	1.062	22	1.062		555		643	0.4

Appendix 1. Rostherne Mere

Date	pH	Cl	N03	DIN	NH4	DIN	SiO2	SRP	TSP	TP	PAlk
3.3.92	7.8	44	0.87	0.922	52	0.922	1.99	477	612	744	0
18.3.92	8.3	62.5	1.44	1.54	100	1.54	2.95	505	726	829	0.4
1.4.92	8	45.5	1.37	1.463	93	1.463	2.73	451	453	480	0.1
14.4.92	8.35	48	1.56	1.65	92	1.65	2.4	500	130	155	0.4
28.4.92	8.5	46	1.1	1.343	243	1.343	1.47	379	410	458	0.25
12.5.92	8.63	44	1.1	1.155	55	1.155	0.75	215	612	965	0.3
26.5.92	8.68	40	0.9	0.9	0	0.9	1.06	297	458	779	0.3
9.6.92	7.9	48	0.55	0.592	42	0.592	0.8	218	186	522	0.2
23.6.92	9.47	40	0.4	0.52	120	0.52	0	139	137	271	0.6
7.7.92		52	0.6	0.6	0	0.6	0.74	171	70	231	0.9
21.7.92	9.4	40	0.1	0.143	43	0.143	0.9	62	126	205	0.6
4.8.92	9.5	44	0	0	0	0	0.2	70	13	117	0.8
17.8.92	8.86	44	0.2	0.217	17	0.217		92	52	124	0.4
1.9.92	8.59	48	0.1	0.114	14	0.114	0.36	300	377	446	0.3
12.9.92	8.27	46	0.2	0.2	0	0.2	1.2	192	453	610	0.3
5.10.92		44	0.2	0.411	211	0.411	0.5	233	252	584	0.7
13.10.92	8.18	44	0.2	0.392	192	0.392	0.74	265	87	296	0.7
3.11.92		44	0.4	0.678	278	0.678	1.2	373	265	606	0
9.11.92	7.9	44	1.9		386		1.2	397		384	0.1
24.11.92	8	40	0.5	0.825	325	0.825	1.8	408	283	663	0.2
8.12.92			0.5	0.832	332	0.832	1.6	421	161	439	0.1
22.12.92		40	0.5	0.826	326	0.826	1.3	770	323	734	0.1
6.1.93		44	1	1.017	17	1.017	1.85	409	320	578	0
15.1.93	7.9	44	0.7	0.715	15	0.715	1.5	401	707	1213	0.2
2.2.93	7.9	44	0.3	0.3	0	0.3	0.8	385	254	651	0.3
16.2.93	7.9	44	0.5	0.502	2	0.502	1	399	226	453	0.05
2.3.93	8	48	0.8	0.825	25	0.825	0.6	390	138	510	0.2
15.3.93		48	0.5	0.514	14	0.514	0.7	358	171	247	0.2
29.3.93			0.6	0.6	0	0.6	0.5	399	238	497	0.1
15.4.93	7.95		0.6	0.6	0	0.6		377	160	449	0.1
30.4.93	8.95	43	0.8	0.903	103	0.903	0.3	280	197	330	0.3
11.5.93	8.94	44	0.8	0.844	44	0.844	0.3	227			0.3
25.5.93	8.5		0.9	0.961	61	0.961	0.5	280	193	343	0.3
8.6.93	8.68	48	0.5	0.538	38	0.538	0.7	258	275	312	0.2
22.6.93	8.8	48	0.6	0.678	78	0.678	0.4	240	269	294	0.3
6.7.93	9	43	0.6	0.606	6	0.606	0.8	186	250	284	0.5
20.7.93	9	42	0.4	0.439	39	0.439	1.2	187	245	313	0.3
2.8.93	9.2	42	0.4	0.421	21	0.421	1.2	166	844		0.4
18.8.93	9.7		0.3	0.302	2	0.302	0.8	123	138	214	0.7
31.8.93	9.25		0.6	0.675	75	0.675		92	118	220	0.5
13.9.93	8.86	43	0	0.103	103	0.103	0.9	123	50	177	0.4
29.9.93	8.6	43	0.2	0.267	67	0.267	0.7	183	165	246	0.35
13.10.93	8.67		0.36	0.408	48	0.408	0.7	154	92	208	0.2
27.10.93	8.93	45	0.5	0.532	32	0.532	1.7	206	220	254	0.2
10.11.93	7.88	48	0.2	0.306	106	0.306	0.8	242	249	256	0.15
24.11.93	7.55	46	0.3	0.836	536	0.836	0.8	386	350	540	0.15
7.12.93	7.5	44	0.2	0.763	563	0.763	0.5	432	445	445	0.25
21.12.94											
12.1.94	7.7	44	0.7	1.237	537	1.237	1.4	361			0.3
26.1.94	7.6	46	0.5	0.997	497	0.997	1.9	464	332	349	0.15
9.2.94											
22.2.94	7.6	44	0.45	0.472	22	0.472	2.3	250	306	274	0.15
8.3.94	7.7	44	0.95	0.95	0	0.95	1.5	344	361	197	0.15
21.3.94	7.7	44	1	1.01	8	1.01	1.6	328	323	348	0.15

Appendix 1. Rostherne Mere

Date	TAlk	Chla	Caro	480:663	430:410	WatLev	Secchi
10.1.90						96	4.96
25.1.90							
7.2.90						105	2.1
21.2.90	2.2	3	5	1.8	1.11	98	2.75
7.3.90	2.2	4	5	1.4	1.15	90	2.79
21.3.90	2.2	8	12	1.6	1.19	78	2.56
4.4.90	2.2	11	17	1.7	1.19	72	3
18.4.90	2.2	15	19	1.4	1.23	70	2.6
27.4.90							
2.5.90	2.3	1	3	4.3	1.04	66	6
16.5.90	2.3	8	15	2.1	1.12	66	3.5
29.5.90	2.6	43	45	1.2	1.28	64	1.12
12.6.90	2.4	25	37	1.6	1.19	67	1.36
27.6.90	2.45	8	12	1.7	1.19	70	3.25
11.7.90	2.35	7		1.7	1.1	70	3.2
25.7.90	2.33	25	40	1.7	1.26	66	1.28
8.8.90	2.25	47	65	1.5	1.25	61	1
21.8.90	2.05	35	49	1.5	1.28	69	1.28
6.9.90	2.05	41	65	1.8	1.3	71	1.04
24.9.90	2.15	71	94	1.5	1.3	77	1.01
9.10.90	2.3	33	63	2.1	1.35	86	1.14
22.10.90	2.25	18	30	1.9	1.23	87	1.33
6.11.90	2.4	11	26	2.5	1.24	106	1.3
20.11.90	2.25	5	10	2.2	1	120	1.65
5.12.90	2.4	0	0			106	4.5
7.1.91	2.3	0	2			110	1.75
22.1.91	2.3	1	5			95	
5.2.91	2.18	0	1			82	
19.2.91	2.2	0	0			77	
5.3.91	2.2	0	2	4.5	1	82	2.25
19.3.91	2.2	2	3	2.4	1.1	86	2.75
2.4.91	2.33	5	8	1.8	1.17	80	3.1
16.4.91	2.25	0	13		1 38	74	2.15
30.4.91	2.23	5	10	2	1.18	69	3.9
14.5.91	2.28	0	1	5	0.8	70	8.15
27.5.91	2.3	10	14	1.5	1.04	69	4.5
11.6.91	2.25	21	24	1.2	1.16	69	2.3
25.6.91	2.33	17	22	1.4	1.23		2.8
9.7.91	2.33	18	22	1.4	1.14	80	
22.7.91	2.43	22	29	1.4	1	77	2.7
6.8.91	2.5	69	97	1.6	1.34	74	1.03
19.8.91	3.15	77	93	1.3	1.34	72	1
9.9.91	3.88	35	66	2.1	1.3		1.85
23.9.91	3.3	43	72	1.9	1.3	65	1.24
9.10.91	4.15	35	69	2.2	1.17		0.88
22.10.91	3.35	25	49	2	1.28	73	1.15
5.11.91	3.18	22	52	2.7	1.1		1
19.11.91	3.2	1	10	10.3	1.04	86	1.7
3.12.91	2.8	0	3		0.9	87	3.5
18.12.91	2.68	0	5	15	0.8	86	2.5
9.1.92	2.5	2	7	3.5	0.9	110	
21.1.92	2.5	0	2		0.7	93	3.4
3.2.92	2.45	0	2	6	0.8	81	3.5
18.2.92	2.9	0	2	7	1	83	3.65

Appendix 1. Rostherne Mere

Date	TAlk	Chla	Caro	480:663	430:410	WatLev	Secchi
3.3.92		3	9	2.9	0.9	82	3.5
18.3.92	2.7	4	9	2.4	0.94	86	3.6
1.4.92	2.35	2	5	3.2	0.95	87	4.25
14.4.92	3	2.9	4	1.5	1	74	3.5
28.4.92	2.6	17	54	1.4	1	74	2
12.5.92	2.5	8.1	15	2	1	72	4.1
26.5.92	2.5	1.5	4	3	1.1	66	
9.6.92	1.9	5.5	1.4	2.8	0.8	65	
23.6.92	2.5	16.5	24	1.6	1		
7.7.92	2.5	23.4	26	1.2	1.2		
21.7.92	2.6	39	45	1.25	1.3	60	1.25
4.8.92	2.5	55	69	1.4	1.3	60	1.25
17.8.92	1.9	26	32	1.4	1.2	68	1.3
1.9.92	2	25	28	1.26	1.2	69	1.3
12.9.92	2.1	29	34	1.9	1.3	70	1.5
5.10.92	2.2	11	16	1.6	0.8	75	4
13.10.92	2.7	8	10.6	1.45	1.1		4.25
3.11.92	2.1	6.6	9	1.5	1	96	2.25
9.11.92	2.2	5	7	1.5	1.2	97	3.6
24.11.92	2.1	5.5	10	2	1.1	98	
8.12.92	2.05	4.4	12	3	1.1	120	4
22.12.92	2.1	7.7	8	1	1.1	130	
6.1.93	2.2	6.2	12	2.1	1.2		4
15.1.93	2.2	8.8	12	1.5	1.1	89	3.3
2.2.93	2.3	11	14	1.4	1.2	90	3.6
16.2.93	2.25	7	9	1.5	1.1	88	2.75
2.3.93	2.2	3.6	6	1.8	1.1	80	
15.3.93	2.3	4	2	0.5	1.3	76	3.2
29.3.93	2.2	2.2	5	2.6	1.1	71	3.5
15.4.93	2.3	4.4	4	1	1.3		2.7
30.4.93	2.3	21	44	2.3	1.3	74	1.04
11.5.93		7	13	2	1		
25.5.93	2.3	2	6.6	11	0.87	66	4.5
8.6.93	2.1	13	17	1.5	1.1	64	1.8
22.6.93	2.5	8	8	1.1	1.2		3.9
6.7.93	2.5	16.5	20	1.35	1.17	65	1.15
20.7.93	2.5	42	46	1.2	1.23	72	1.74
2.8.93	2.6	21	30	1.6	1.2	73	2.25
18.8.93	2.5	36	44	1.4	1.2	78	0.91
31.8.93	2.35	69	93	1.5	1.4	78	0.6
13.9.93	2.25	38	34	1.3	1.3	76	2.45
29.9.93	2.45	5	8	1.7	1.1	76	2.5
13.10.93	2.3	15	20	1.45	1.24	84	
27.10.93	2.2	9.2	8	1	1.3	80	5
10.11.93	2.35	4	7.6	2	1.2	76	5.75
24.11.93	2.4	2.6	6.6	2.85	1	80	5
7.12.93	2.55	0.4	1.6	0.3	2.5	86	4
21.12.94							
12.1.94	2.45	1.5	3.6	0.6	1	99	2.5
26.1.94	2.45	5	6.2	1.4	1.2	96	2.27
9.2.94							
22.2.94	2.35	6	7.6	1.5	1.05	86	
8.3.94	2.35	0	6.6	0	1.1	90	4
21.3.94	2.2	4	8	2	1.1	88	2.27

Appendix 1. Outflow Rostherne Mere

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		
7.2.90		38.8	0.95	52	1	3.1	320	342	497	0		
21.2.90		41.7	0.85	0	0.85	2.2	348	358	383	0	2.15	
7.3.90		54.7	0.9	13	0.91	1.7	344	405	497	0.03	2.1	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	2.2	0.108
18.4.90		42.4	0.7	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	0.1	2.33	0.069
16.5.90		43.8	0.85	0	0.85	0.4	302	331	475	0.18	2.35	0.06
29.5.90		41.7	1.02	151	1.17	0.4	280	292	340	0.15	2.5	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	2.5	0.071
25.7.90		43.8	0.39	40	0.43	0.9	190	277	549	0.35	2.5	0.061
8.8.90		43.8	0.19	31	0.22	1	177	227	324	0.4	2.4	0.048
21.8.90		45.8	0.6	20	0.62	1.3	129	140	193	0.1	2	0.067
6.9.90		41.7	0.04	15	0.06	1.4	143	147	226	0.2	2.05	0.067
24.9.90		43.3	1.9	106	2.01	2.1	237	280	436	0	1.9	0.093
9.10.90		45.4	0.4	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	0.2	2.3	0.145
6.11.90		44.9	0.94	102	1.04	2	232	280	319	0	2.15	0.078
19.11.90		43.3	3.41	133	3.54	2.4	229	261	289	0	1.9	0.297
5.12.90		41.2	0.64	193	0.83	1.6	354	350	366	0.05	2.4	0.151
7.1.91		44.9	1.18	218	1.4	2	345	364	371	0	2.25	0.376
22.1.91		45.4	1.37	152	1.52	1.8	375	376	417	0	2.2	0.262
5.2.91		45.4	0.8	30	0.83	2.1	359	389	409	0	2.23	0.24
19.2.91		49	1.44	21	1.46	1.9	366	377	432	0	2.23	0.163
5.3.91		44.9	1.45	20	1.47	1.9	347	350	403	0	2.2	0.208
19.3.91		47.9	1.69	32	1.72	1.9	311	325	368	0	2.1	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	0.1	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	0.1	2.33	0.089
11.6.91		46.9	0.77	45	1.22	0.7	312	434	448	0.1	2.48	0.063
25.6.91		44	1.37	103	1.47	1.1	316	344	413	0	2.33	0.081
9.7.91		44.9	0.79	60	0.85	0.8	304	341	346	0	2.4	0.142
22.7.91		49	0.87	84	0.95	0.9	298	312	366	0	2.55	0.139
6.8.91		44.9	0.2	55	0.26	1.7	217	232	330	0.45	2.05	0.104
19.8.91		45.4	0.1	39	0.14	2	192	216	321		2.35	0.062
9.9.91		45.8	0.07	29	0.1	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	0.8	3.3	0.07
9.10.91		52.2	0.19	24	0.21	2.5	258	283	393	0.4	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	318	345	571	0	2.45	0.075
19.11.91		53	1.83	288	2.12	2.8	577	601	854	0	2.93	0.135
3.12.91		48	1.12	240	1.36	2.2	399	393	476	0	2.74	0.112
18.12.91		60.6	0.93	257	1.19	2.6	433	553	658	0	2.65	0.131
9.1.92		51	1.53	48	1.58	2.9	371	417	471	0	2.35	0.184
21.1.92		46.6	0.81	20	0.83	2.6	490	851	850	0	2.53	0.151
3.2.92			0.9	0	0.9	2.4	445	488	451	0.2	2.5	
18.2.92		50.5	1.68	51	1.73	2.5	514		750	0.3	2.7	0.126
3.3.92		52	0.96	2	0.96	2.6	393	473	641	0		0.213

Appendix 1. Outflow Rostherne Mere

Date	pH	Cl	NO3	NH4	DIN	SiO2	SRP	TSP	TP	PAlk	TAlk	Flow
18.3.92		50	2.34	37	2.38	2.8	415	580	632	0.4	2.7	0.222
1.4.92	7.9	45.5	1.68	19	1.7	2.3	410	304	453	0.1	2.45	0.212
14.4.92		40	1.4	57	1.5	1.75	430	74	141	0.4	2.7	0.031
28.4.92	8.87	46	1.38	59	1.44	0.86	347	347	334	0.15	2.35	0.1808
12.5.92		44	0.57	50	0.62	0.55	189	514	831	0.1	2.3	0.1027
26.5.93		52	0.6	0	0.6	0.5	298	479	804	0.25	2.45	0.12
9.6.92	7.85	48	0.5	0	0.5	1	186	216	539	0.2	2.3	0.05
23.6.92		40	0.47	99	0.57	0	116	126	280	0.4	2.6	0.045
7.7.92		48	0.4	25	0.43	0.9	70	112	142	0.4	2.4	0.054
21.7.92		44	0.1	89	0.19	1	71	74	174	0.6	2.7	0.061
4.8.92	8.95	48	0.06	114	0.174	0.5	41	50	55	0.5	3.1	0.0398
17.8.92												
1.9.92	8.46	44	0.15	27	0.18	0.6	315	398	423	0.3	2	0.02
12.9.92	7.24	46	1.3	61	1.36	1.7	200	480	622	0.2	2.2	0.059
5.10.92	7.2	44	0.6	88	0.69	0.9	224	266	587	0.15	2.55	0.07
13.10.92	7.91	48	0.5	109	0.61	0.64	280	200	354	0.1	2.1	0.046
3.11.92		44	0.7	241	0.94	1.3	292	290	543	0	2.2	0.0326
9.11.92	7.67	40	0.6	209	0.81	2.1	275	119	273	0	2.2	1.651
24.11.92	7.86	44	0.9	240	1.14	1.8	284	260	573	0.1	2.2	0.0756
8.12.92			1	162	1.2	1.9	370	140	485	0.1	2.45	0.2126
22.12.92		44	0.6	161	0.76	1.4	628	290	559	0.3	2.3	0.3761
6.1.93		40	1.3	0	1.3	1.4	389	382	501	0	2.1	0.0786
15.1.93	7.84	44	1.1	15	1.12	1	365	45	219	0.2	2.3	0.2059
2.2.93	7.9	44	1.4	0	1.4	0.8	347	372	685	0.2	2.2	0.1924
16.2.93	7.8	44	0.84	0	0.84	0.5	356	193	387	0.15	2.35	0.0657
2.3.93	7.9	44	1.1	504	1.6	0.7	347	96	474	0.2	2.3	0.139
15.3.93		48	1	31	1.03	0.67	327	176	237	0.2	2.1	0.1085
29.3.93			0.6	8	0.61	0.6	376	221	488	0.2	2.2	0.123
15.4.93	8		1	17	1.02	1	358	38	388	0.1	2.3	0.09
30.4.93	8.9	44	0.9	30	0.93	0.3	272	211	394	0.3	2.3	0.12
11.5.93	8.64	48	1.2	25	1.23	0.4	241			0.2	2.2	0.134
25.5.93	8	46	1.2	5	1.21	0.5	267	172	319	0.2	2.1	0.109
8.6.93	8.75		0.6	142	0.742	1	225	269	375	0.25	2.25	0.078
22.6.93	8.5	44	0.4	67	0.47	0.6	247	275	303	0.2	2.3	0.047
6.7.93	8.67	44	0.7	82	0.782	1	219	260	264	0.3	2.6	0.098
20.7.93	8.2	42	0.5	52	0.55	1.6	197	252	356	0.1	2.4	0.079
2.8.93	8.45	48	0.5	61	0.56	1.4	195	689	980	0.2	2.6	0.089
18.8.93	9.36	48	0.4	42	0.44	1	137	168	289	0.5	2.5	0.067
31.8.93	8.8		0.3	59	0.36		127	153	195	0.25	2.45	0.059
13.9.93	7.91	47	0.3	53	0.35	2.3	148	131	257	0.2	2.45	0.048
29.9.93	7.9	46	0.1	58	0.16	0.5	189	166	251	0.1	2.2	0.061
13.10.93	8.1		0.8	61	0.86	1.1	178	202	307	0.15	2.15	0.099
27.10.93	7.9	47	0.73	77	0.81	1.8	212	227	267	0.1	2.45	0.109
10.11.93	7.28	44	0.2	130	0.33	1.2	224	257	283	0.2	2.3	0.12
24.11.93	7.4	44	0.4	423	0.82	1	384	468	612	0.2	2.05	0.094
7.12.93	6.97	44	0.8	187	0.99	2	203	273	325	0.1	2.05	0.11
21.12.93												
12.1.94	7.4	48	0.67	292	0.96	1.7	291			0.2	2.25	0.17
26.1.94	7.1	44	0.8	204	1	2.1	349	255	289	0.1	2.15	0.165
9.2.94												
22.2.94	7.5	46	0.36	1	0.36	1.4	390	250	331	0.2	2.5	0.123
8.3.94	7.7	44	0.6	0	0.6	1.6	307	307	341	0.3	2.4	0.106
21.3.94	7.8	44	1.5	0	1.5	1.9	287	287	311	0.2	2.2	0.087

Table A2.1 Phytoplankton taxa recorded during the study. Presence indicated by '+'. Phytoplankton taxa are given in density (No ml^{-1}).

Taxon		Mere Mere	Little Mere	Rostherne Mere
Chlorophyta				
Actinastrum sp.	(Act)			+
Ankistrodesmus falcatus (Corda) Ralfs	(Anki)	+	+	+
Ankyra judayi (G.M.Sm.) Fott	(Anky)	+	+	+
Chlamydomonas spp.	(Chlam)	+	+	+
Chlorella spp.	(Chlor)			+
Chlorogonium elangatum Dang	(Chloro)	+	+	
Closterium spp.	(Clos)	+	+	+
Coelastrum spp.	(Coela)	+	+	
Cosmorium sp.	(Cos)		+	
Dictyosphaerium pulchellum Wood	(Dict)	+		
Elakatothrix gelatinosa Wille	(Elak)	+	+	+
Eudorina elegans Ehrenberg	(Eud)		+	
Gleocystis sp.	(Gloe)		+	
Micractinium sp.	(Micra)		+	
Oocystis sp.	(Oocy)	+	+	+
Pandorina morum (Muell.) Bory	(Pan)			+
Pediastrum spp.	(Ped)	+	+	+
Scenedesmus spp.	(Scen)	+	+	+
Selenastrum sp.	(Sel)	+	+	+
Sphaerocystis sp.	(Sph)	+		
Shroderia sp.	(Schr)		+	+
Staurastrum sp.	(Staur)			+
Tetraedron sp.	(Tet)	+	+	+
Volvox sp.	(Vol)	+	+	
Euglenophyta				
Euglena sp.	(Eugl)	+	+	+

Phacus sp.	(Phac)	+	+	+
Trachelomonas sp.	(Trac)	+	+	+
Cryptophyta				
Cryptomonas spp.	(Crypt)	+	+	+
Rhodomonas minuta Lewis	(Rhod)	+	+	+
Unidentified flagellate				
Flagellate	(μFlag)	+	+	+
Pyrrophyta: Dinophyceae (Dinoflagellates)				
Ceratium hirundinella (O. F. Műll.) Schrank	(Cer)	+		+
Gymnodinium sp.	(Gym)	+	+	
Peridinium sp.	(Per)	+		+
Unidentified dinoflagellate	(UDin)			
Chrysophyta: Chrysophyceae				
Dinobryon sp.	(Din)	+		
Chrysophyta: Bacillariophyceae				
Achnanthes sp.	(Ach)		+	
Amphora sp.	(Amp)		+	+
Asterionella formosa Hass.	(Ast)	+	+	+
Aulacoseira granulata (Ehrenb.) Simonsen (=*Melosira granulata* (Ehrenb.) Ralfs.)	(Au.gr)	+	+	+
Aulacoseira subartica (O. Műller) E.Y. Haworth, comb. nov. (=*Melosira italica* ssp. subarctica O. Műller)	(Au.su)	+		
Diatoma elongatum Agardh	(Dia)	+	+	
Fragilaria 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)	+	+	+
Synedra acus Kutz.	(Sy.ac)	+		+
Synedra ulna (Nitzsch) Ehrenb.	(Sy.ul)	+	+	+
Unidentified centric	(Cen)	+	+	+
Cyanophyta				
Anabaena spp.	(Ana)	+	+	+
Aphanizomenon flos-aquae Ralfs *ex* Born. et Flah.	(Aphan)	+	+	+
Coelosphaerium naegelianum Unger	(Coelo)	+	+	+
Microcystis aeruginosa Kutz. emend. Elenkin	(Mic)			+
Planktothrix agardhii (Gom) Anagn. *et* Kom. (=*Oscillatoria agardhii* Gom.)	(Plank)	+	+	+

Table A2.2 Volumes (μm^3) of taxa recorded in this study.

	Volume
Chlorophyta	
Chlamydomonas sp. (cell)	343
Chlorellaalipsoidea (cell)	151
Coelastrum sp. (cell)	145
Elakatothrix sp. (cell)	80
Gleocystis major (cell)	311
Micractinum pusillum (cell)	2424
Oocystis sp. (colony)	707
Planktosphaeria sp. (colony)	12514
Cryptophyta	
Cryptomonas spp. (cell)	2610
Rhodomonas minuta (cell)	151
Pyrrophyta:Dinophyceae (Dinoflagellate)	
Ceratium hirundinella (cell)	43740
Peridium sp. (cell)	2346
Unidentified falgellates	
Unidentified flagellates (cell)	170
Bacillariophycea (diatoms)	
Asterionella formosa (cell)	950
Aulacoseira sp. (cell)	856
Aulacoseira granulata (cell)	847
Fragillaria sp. (cell)	623
Nitzschia palaea (cell)	108
Synedra ulna (cell)	10260
Stephanodiscus hantzschii (cell)	400
Cyanophyta	
Anabaena sp. (mean filament)	3970
Aphanizomenon flos-aquae (mean filament)	4170
Coelosphaerium nagelianum (cell)	45
Microcystis aeruginosa (mean colony)	4960
Plankttothrix agardhi (/mm length)	39360

Table A2.3 Zooplankton taxa recorded in the study. Presence indicated by '+' and are given in density (No ml^{-1}).

Taxon		Mere Mere	Little Mere	Rostherne Mere
Cladocera:				
Bosmina longirostris (O.F. Műller) s. str.	(Bos.lo)	+	+	+
Ceriodaphnia coregoni var. obtusirostris (Sars)	(Cer.du)	+		
Ceriodaphnia sp.	(Cerio)		+	
Chydorus sphaericus (O.F. Műller)	(Chy.sp)			+
Chydorus sp.	(Chyd)	+	+	
Daphnia cuculata Sars.	(D.cuc)	+	+	
Daphnia longispina aggregate	(D.long)	+	+	+
Daphnia magna Straus	(D.mag)		+	
Daphina hyalina Leydig	(D.hya)		+	
Daphnia pulex (De Geer)	(D.pul)	+	+	+
Diaphanosoma brachyurum Lieven	(Diap)	+	+	+
Leptodora kindtii (Focke)	(Lepto)			+
Polyphemus pediculus (L.)	(P.ped)		+	
Eurycercus lamellatus (O.F. Műller)	(E.lam)		+	
Sida crystallina (O.F. Műller)	(S.cry)		+	
Simocephalus sp.	(Sim)		+	
Scapholebris mucronata (O.F. Műller)	(S.muc)		+	
Calanoid copepods:				
Diaptomus gracilis Sars	(Di.gra)	+	+	+
Cyclopoid copepods:				
Cyclops spp.	(Cyclo)	+	+	+
Nauplii	(Nau)		+	+
Rotifera:				
total rotifers	(Rot)		+	+

Appendix 2. Mere Mere Chlorophyta

date	Anki	Anky	Chlam	Clos	Coela	Dict	Elak	Oocy	Pan	Ped
10.1.90	0	0	302	24	0	0	0	0	0	0
7.2.90	0	0	0	0	0	0	0	0	0	0
7.3.90	0	0	0	0	0	0	0	0	0	0
21.3.90	0	0	0	0	0	0	0	0	0	0
4.4.90	737	0	268	402	0	0	0	0	0	0
18.4.90	0	0	0	0	0	0	0	0	0	0
2.5.90	22	0	0	11	0	0	112	0	0	0
16.5.90	0	0	0	22	0	0	0	0	0	0
29.5.90	0	182	0	0	0	0	0	182	0	0
12.6.90	0	22	0	22	0	0	0	45	0	0
27.6.90	365	0	0	0	0	0	0	0	0	0
11.7.90	0	0	0	0	0	0	0	67	0	0
25.7.90	182	179	0	0	0	0	0	22	0	0
8.8.90	0	0	0	0	0	0	0	0	0	0
21.8.90	0	0	0	0	0	0	0	0	0	0
6.9.90	0	0	0	22	0	0	22	0	0	0
24.9.90	0	0	0	0	0	0	0	0	0	0
9.10.90	0	0	0	11	0	36	0	32	45	0
22.10.90	0	0	0	0	0	0	0	0	365	0
6.11.90	0	0	0	0	0	0	0	0	0	0
20.11.90	0	0	0	0	0	0	0	0	0	6
5.12.90	0	0	0	0	0	0	0	0	0	0
7.1.91	20	0	0	0	0	0	0	0	0	0
22.1.91	48	0	0	0	0	0	0	0	0	0
5.2.91	67	0	0	0	0	0	0	0	0	0
5.3.91	313	0	0	0	0	0	0	0	0	0
19.3.91	1028	0	0	0	0	0	0	0	0	0
2.4.91	670	0	0	0	0	0	0	0	0	0
16.4.91	268	0	0	0	0	0	0	0	0	0
30.4.91	0	0	0	0	0	0	0	0	0	0
14.5.91	0	0	0	0	0	0	0	0	0	0
27.5.91	0	0	0	0	22	0	0	0	0	0
11.6.91	22	0	0	0	0	0	0	0	0	0
25.6.91	179	0	0	0	0	0	0	0	0	0
9.7.91	45	45	0	89	45	0	0	0	0	0
22.7.91	67	0	0	17	17	68	17	0	0	0
6.8.91	0	0	0	0	34	68	0	0	0	0
19.8.91	0	0	17	0	17	0	0	0	0	0
9.9.91	0	0	0	0	11	201	22	0	0	0
23.9.91	0	0	0	0	0	0	218	0	0	0
9.10.91	0	0	0	0	0	0	22	0	0	0
22.10.91	0	11	0	45	22	0	11	11	0	0
5.11.91	0	0	0	45	0	0	0	0	22	0
19.11.91	0	0	0	22	11	0	0	0	0	0
3.12.91	0	0	0	0	0	0	0	0	0	0
18.12.91	6	0	6	0	0	0	28	3	0	0
9.1.92	0	0	0	0	0	0	6	0	0	0
21.1.92	6	0	0	0	0	0	6	0	0	0
3.2.92	8	0	0	0	0	0	0	0	0	0

Appendix 2. Mere Mere Chlorophyta

date	Anki	Anky	Chlam	Clos	Coela	Dict	Elak	Oocy	Pan	Ped
18.2.92	22	0	22	0	0	0	0	0	0	0
3.3.92	156	0	0	0	0	0	0	0	0	0
18.3.92	380	67	22	0	0	0	0	0	0	0
1.4.92	547	22	0	0	0	0	78	0	0	0
14.4.92	146	0	12	0	0	0	0	0	0	0
28.4.92	40	0	13	0	0	0	0	0	0	27
12.5.92	12	0	24	12	0	0	0	0	0	0
26.5.92	13	0	27	0	13	0	13	27	0	0
9.6.92	442	0	0	0	0	0	0	40	0	0
23.6.92	0	0	600	100	0	251	0	200	0	0
7.7.92	0	0	22	402	120	67	112	204	0	0
21.7.92	0	0	67	0	600	0	0	168	0	67
4.8.92	34	0	0	0	1640	0	34	67	0	34
17.8.92	45	0	0	0	89	0	0	0	0	22
1.9.92	0	0	89	0	156	0	0	0	0	22
10.9.92	0	0	0	0	0	0	0	0	0	0
15.9.92	0	0	0	0	22	0	0	0	0	0
5.10.92	0	0	0	0	112	0	0	0	0	22
13.10.92	0	0	0	0	0	0	0	0	0	0
3.11.92	0	0	0	0	0	0	0	0	0	0
24.11.92	0	0	17	0	0	0	0	0	0	0
8.12.92	17	0	0	0	0	0	0	0	0	0
22.12.92	13	0	40	0	0	0	0	0	0	0
6.1.93	27	0	94	0	0	0	0	0	0	0
18.1.93	0	0	112	0	0	0	0	0	0	0
2.2.93	22	0	67	0	0	0	0	0	0	0
16.2.93	112	0	67	0	0	0	0	0	0	0
2.3.93	134	0	65	0	0	0	0	0	0	0
15.3.93	938	0	313	0	0	0	0	0	0	0
29.3.93	654	0	302	0	0	0	0	0	0	0
15.4.93	754	0	0	0	0	0	0	0	0	0
30.4.93	0	0	251	0	0	0	0	0	0	0
11.5.93	0	0	0	0	0	0	0	0	0	0
25.5.93	0	0	151	0	0	0	0	0	0	0
8.6.93	0	0	151	0	0	0	0	0	0	0
22.6.93	0	0	0	0	0	0	0	0	0	0
6.7.93	0	0	50	0	0	0	0	452	0	50
20.7.93	0	0	0	151	0	0	0	403	0	101
2.8.93	0	0	0	0	0	0	0	0	0	0
18.8.93	0	0	0	0	0	0	0	0	0	50
31.8.93	50	0	0	0	0	0	0	0	0	0
13.9.93	0	0	0	0	25	0	0	0	0	0
29.9.93	0	0	0	0	50	0	0	0	0	0
13.10.93	0	0	25	0	75	0	0	0	0	0
27.10.93	50	0	0	0	75	0	0	101	0	0
10.11.93	25	0	0	0	25	0	0	0	0	0
24.11.93	0	0	0	0	0	0	0	0	0	0
7.12.93	0	0	0	0	101	0	0	0	0	0
12.1.94	40	0	161	0	40	0	0	0	0	0

Appendix 2. Mere Mere Chlorophyta

date	Anki	Anky	Chlam	Clos	Coela	Dict	Elak	Oocy	Pan	Ped
26.1.94	27	0	54	27	0	0	0	0	0	0
8.3.94	442	0	0	0	0	0	0	0	0	0
21.3.94	1984	0	2574	0	0	0	0	0	0	0

Appendix 2. Mere Mere Chlorophyta

date	Scen	Sel	Sph	Tet	Vol	Pla	Micra	Chlo
10.1.90	0	0	0	0	0	0	0	0
7.2.90	0	0	0	0	0	0	0	0
7.3.90	0	0	0	0	0	0	0	0
21.3.90	0	0	0	0	0	0	0	0
4.4.90	268	0	0	0	0	0	0	0
18.4.90	0	0	0	0	0	0	0	0
2.5.90	89	0	0	0	0	0	0	0
16.5.90	0	0	0	0	0	0	0	0
29.5.90	730	0	0	0	0	0	0	0
12.6.90	89	0	45	0	0	0	0	0
27.6.90	0	0	0	0	0	0	0	0
11.7.90	0	0	22	0	0	0	0	0
25.7.90	0	0	0	0	0	0	0	0
8.8.90	0	0	22	0	0	0	6	0
21.8.90	0	0	0	0	0	0	0	0
6.9.90	89	0	0	0	0	0	6	0
24.9.90	0	0	0	0	0	0	0	0
9.10.90	134	0	11	0	0	0	0	0
22.10.90	0	0	0	0	0	0	0	0
6.11.90	0	0	0	0	0	0	0	0
20.11.90	188	0	0	0	0	0	0	0
5.12.90	134	34	0	0	0	0	0	0
7.1.91	40	20	0	0	0	0	0	0
22.1.91	22	7	0	0	0	0	0	0
5.2.91	0	0	0	0	0	0	0	0
5.3.91	0	0	0	0	0	0	0	0
19.3.91	0	0	0	0	0	0	0	0
2.4.91	0	67	0	0	0	0	0	0
16.4.91	0	0	0	0	0	0	0	0
30.4.91	179	0	0	0	0	0	0	0
14.5.91	0	0	11	0	0	0	0	0
27.5.91	0	0	0	0	15	0	0	0
11.6.91	0	0	0	0	0	0	0	0
25.6.91	0	0	0	0	0	0	0	0
9.7.91	22	0	0	0	0	0	0	0
22.7.91	0	0	0	0	0	0	0	0
6.8.91	134	0	0	0	0	0	0	0
19.8.91	34	0	0	0	0	0	0	0
9.9.91	45	11	0	11	0	0	0	0
23.9.91	302	17	0	0	0	0	0	0
9.10.91	112	34	0	11	0	0	0	0
22.10.91	89	134	0	0	0	0	0	0
5.11.91	89	78	0	0	0	0	0	0
19.11.91	0	11	0	0	0	0	0	0
3.12.91	40	47	0	0	0	0	0	0
18.12.91	22	14	0	0	0	0	0	0
9.1.92	81	0	0	0	0	0	0	0
21.1.92	28	3	0	0	0	0	0	0
3.2.92	0	8	0	0	0	0	0	0

Appendix 2. Mere Mere Chlorophyta

date	Scen	Sel	Sph	Tet	Vol	Pla	Micra	Chlo
18.2.92	0	0	0	0	0	0	0	0
3.3.92	89	89	0	0	0	0	0	0
18.3.92	179	0	0	22	0	0	0	0
1.4.92	0	89	0	123	0	0	0	0
14.4.92	49	12	0	0	0	0	0	0
28.4.92	0	13	0	27	0	0	0	0
12.5.92	0	0	0	0	0	12	0	0
26.5.92	0	54	0	40	0	0	13	0
9.6.92	0	61	0	0	0	0	0	0
23.6.92	151	101	0	251	0	0	0	0
7.7.92	22	491	0	67	0	0	1290	0
21.7.92	167	201	0	0	0	0	201	0
4.8.92	0	0	0	0	0	0	0	0
17.8.92	67	0	0	0	0	0	0	0
1.9.92	45	0	0	0	0	0	0	0
10.9.92	0	0	0	0	0	0	0	0
15.9.92	22	22	0	0	0	0	0	0
5.10.92	22	0	0	0	0	0	0	0
13.10.92	45	0	0	0	0	0	0	0
3.11.92	0	0	0	0	0	0	0	0
24.11.92	67	17	0	0	0	0	0	0
8.12.92	204	50	0	0	0	0	0	0
22.12.92	0	13	0	0	0	0	0	0
6.1.93	0	0	0	0	0	0	0	0
18.1.93	0	0	0	0	0	0	0	0
2.2.93	89	0	0	0	0	0	0	0
16.2.93	22	67	0	0	0	0	0	0
2.3.93	0	101	0	0	0	0	0	0
15.3.93	200	290	0	0	0	0	0	0
29.3.93	1256	151	0	0	0	0	0	0
15.4.93	1910	151	0	0	0	0	0	0
30.4.93	0	50	0	0	0	0	0	1508
11.5.93	0	0	0	0	0	0	0	0
25.5.93	0	0	0	0	0	0	0	0
8.6.93	0	0	0	0	0	0	0	0
22.6.93	0	0	0	0	0	0	0	0
6.7.93	202	0	0	0	0	0	0	0
20.7.93	203	0	0	0	0	0	50	0
2.8.93	402	50	0	0	0	0	0	0
18.8.93	101	50	0	50	0	0	50	0
31.8.93	203	0	0	0	0	0	0	0
13.9.93	0	0	0	0	0	0	0	0
29.9.93	203	0	0	0	0	0	0	0
13.10.93	0	0	0	0	0	0	0	0
27.10.93	102	0	0	0	0	0	0	0
10.11.93	0	0	0	0	0	0	0	0
24.11.93	50	0	0	0	0	0	0	0
7.12.93	0	0	0	0	0	0	0	0
12.1.94	161	0	0	0	0	0	0	0

Appendix 2. Mere Mere Chlorophyta

date	Scen	Sel	Sph	Tet	Vol	Pla	Micra	Chlo
26.1.94	54	0	0	0	0	0	0	0
8.3.94	0	0	0	0	0	0	0	0
21.3.94	0	0	0	0	0	0	0	0

Appendix 2. Mere Mere Chrysophyta

Date	Din	Ast	Au	Cen	Dia	Frag	Nav	S.han	S.rot	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

Appendix 2. Mere Mere Chrysophyta

Date	Din	Ast	Au	Cen	Dia	Frag	Nav	S.han	S.rot	Sy.ac	Sy.ul
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
14.4.92	0	73	97	49	0	13	0	73	0	0	0
28.4.92	0	121	54	54	0	0	0	27	0	0	0
12.5.92	0	12	12	0	0	0	0	0	0	0	0
26.5.92	0	0	0	27	0	0	0	54	0	0	0
9.6.92	0	0	40	0	0	0	0	0	0	0	0
23.6.92	0	0	352	655	0	351	0	151	0	0	50
7.7.92	0	0	178	268	0	100	0	0	0	0	0
21.7.92	0	100	168	0	0	34	0	34	0	0	34
4.8.92	0	0	168	168	0	200	0	0	0	0	34
17.8.92	0	0	22	67	0	1631	45	0	0	0	0
1.9.92	0	0	134	22	0	782	0	22	0	0	0
10.9.92	0	0	300	0	0	0	0	0	0	0	0
15.9.92	0	0	67	45	0	402	0	0	0	0	0
5.10.92	0	0	45	45	0	0	0	0	0	0	0
13.10.92	0	0	134	0	0	0	0	45	0	0	0
3.11.92	0	0	67	67	0	0	0	0	0	0	0
24.11.92	0	0	553	0	0	22	0	0	0	0	0
8.12.92	0	24	636	17	0	0	0	0	0	0	0
22.12.92	0	161	403	13	0	0	0	0	0	0	0
6.1.93	0	107	161	13	0	0	0	0	0	0	0
18.1.93	0	491	1340	0	0	0	22	0	0	0	0
2.2.93	0	112	1320	0	0	0	0	0	0	0	0
16.2.93	0	0	4959	0	0	0	0	0	0	0	45
2.3.93	0	1407	9373	0	0	302	0	0	0	0	0
15.3.93	0	983	2033	179	0	67	0	0	0	0	50
29.3.93	0	1760	251	100							50
15.4.93	0	2865	50	0	0	0	0	0	0	0	101
30.4.93	0	0	100	50	0	0	0	0	0	0	50
11.5.93	0	0	0	0	0	0	0	0	0	0	0
25.5.93	0	101	0	0	0	250	0	75	0	0	0
8.6.93	0	0	0	0	0	4072	0	50	0	0	0
22.6.93	0	0	101	202	0	4072	0	101	0	0	0
6.7.93	0	0	302	0	0	953	0	0	0	0	0
20.7.93	0	0	0	0	0	0	0	50	0	0	0
2.8.93	0	0	704	0	0	0	0	0	0	0	0
18.8.93	0	0	0	0	0	251	0	0	0	0	0
31.8.93	0	0	0	0	0	0	0	0	0	0	0
13.9.93	0	0	0	0	0	0	0	0	0	0	0
29.9.93	0	50	75	0	0	277	25	0	0	0	0
13.10.93	0	50	101	101	0	327	0	0	0	0	0
27.10.93	0	0	0	0	0	0	0	0	0	0	0
10.11.93	0	0	201	0	0	0	0	0	0	0	0
24.11.93	0	0	277	50	0	251	50	50	0	0	0
7.12.93	0	25	679	251	0	327	25	0	0	0	0
12.1.94	0	0	2693	0	0	0	0	0	0	0	20

Appendix 2. Mere Mere Chrysophyta

Date	Din	Ast	Au	Cen	Dia	Frag	Nav	S.han	S.rot	Sy.ac	Sy.ul
26.1.94	0	0	5138	0	0	0	0	0	0	0	0
8.3.94	0	241	885	6154	0	0	51	40	0	0	0
21.3.94	0	109	2145	695	0	0	0	0	0	0	0

Appendix 2. Mere Mere Euglenophyta, Cryptophyta, Pyrrophyta and Cyanophyta

Date	Phac	Trac	Crypt	Rhod	µFlag	Cer	Gym	Per	UDin	Ana
10.1.90	0	0	67	369	50	0	0	0	0	0
7.2.90	0	0	0	0	0	0	0	0	0	0
7.3.90	0	0	0	0	1460	0	0	0	0	0
21.3.90	0	0	0	0	0	0	0	0	0	0
4.4.90	0	0	402	1072	402	0	0	0	0	0
18.4.90	0	0	365	547	2190	0	0	0	0	0
2.5.90	0	0	22	726	949	0	0	0	11	11
16.5.90	0	0	0	2323	268	0	0	67	0	0
29.5.90	0	0	182	730	0	0	0	0	0	0
12.6.90	0	0	972	693	45	78	0	22	0	11
27.6.90	0	0	912	365	365	0	0	0	0	182
11.7.90	0	0	514	760	0	179	0	45	0	715
25.7.90	0	0	0	182	365	223	0	0	0	2815
8.8.90	0	0	179	22	45	156	0	22	0	2390
21.8.90	0	0	730	0	182	182	0	182	0	365
6.9.90	0	0	112	782	268	67	0	45	179	45
24.9.90	0	0	365	0	0	182	0	0	182	0
9.10.90	0	0	503	380	11	0	0	22	357	11
22.10.90	0	0	182	182	0	0	0	0	0	0
6.11.90	0	0	182	0	0	0	0	0	0	0
20.11.90	0	0	369	610	0	0	0	0	74	0
5.12.90	0	0	114	241	80	0	0	0	20	0
7.1.91	0	0	34	214	13	0	0	0	27	0
22.1.91	0	0	7	67	7	0	0	0	11	0
5.2.91	0	0	89	201	2100	0	0	0	0	0
5.3.91	0	0	134	983	894	0		0	0	0
19.3.91	0	0	313	2859	402	0	0	0	0	0
2.4.91	67	0	0	335	3552	0	0	0	0	0
16.4.91	0	0	0	45	5763	0	45	0	0	0
30.4.91	0	0	357	938	2949	0	0	0	0	0
14.5.91	0	0	112	63	0	0	0	112	0	0
27.5.91	0	0	15	432	37	30	0	0	30	0
11.6.91	0	22	89	1251	0	67	0	0	0	0
25.6.91	0	0	447	1921	0	112	0	0	0	0
9.7.91	0	22	1095	357	0	67	0	0	0	179
22.7.91	0	0	1508	1173	0	84	0	0	0	737
6.8.91	0	0	268	134	0	134	0	0	0	3384
20.8.91	0	0	168	0	0	101	0	0	0	1508
9.9.91	0	0	78	101	0	101	0	0	145	235
23.9.91	0	0	754	1324	0	17	0	0	134	84
9.10.91	0	0	78	357	0	0	0	212	0	0
22.10.91	0	0	78	257	0	0	0	0	34	0
5.11.91	0	0	101	369	78	0	0	0	34	22
19.11.91	0	0	45	223	190	0	0	0	11	11
3.12.91	0	0	13	80	201	0	0	0	0	0
18.12.91	0	0	6	106	47	0	0	0	8	0
9.1.92	0	0	0	151	36	0	0	0	0	3
21.1.92	0	0	8	246	36	0	0	0	3	0
3.2.92	0	0	8	1005	117	0	0	0	0	0
18.2.92	0	0	45	1921	0	0	0	0	0	0
3.3.92	0	0	45	1117	134	0	0	0	0	0
18.3.92	0	0	89	1340	625	0	0	22	0	0

Appendix 2. Mere Mere Euglenophyta, Cryptophyta, Pyrrophyta and Cyanophyta

Date	Phac	Trac	Crypt	Rhod	µFlag	Cer	Gym	Per	UDin	Ana
1.4.92	0	0	11	302	101	0	0	0	11	34
14.4.92	0	0	85	365	134	0	0	0	0	12
28.4.92	0	0	94	603	134	0	0	0	0	27
12.5.92	12	0	109	608	219	0	0	0	0	170
26.5.92	13	13	174	1836	375	0	0	0	0	94
9.6.92	0	0	925	12265	241	0	0	0	0	0
23.6.92	0	0	302	50	2011	402	202	0	0	50
7.7.92	0	167	514	0	0	0	67	22	0	290
21.7.92	0	167	67	0	610	0	134	34	0	436
4.8.92	0	34	0	0	0	0	0	0	0	1273
17.8.92	0	134	346	45	1877	0	0	67	0	0
1.9.92	0	156	268	89	1564	112		871	0	0
10.9.92	0	0	0	67	0	0	0	573	0	17
15.9.92	0	134	45	156	983	134	0	782	0	0
5.10.92	0	134	0	67	313	0	0	872	0	0
13.10.92	0	89	45	313	1184	0	0	961	0	0
3.11.92	0	89	0	201	201	0	0	1250	0	0
24.11.92	0	67	24	201	503	0	0	50	0	0
8.12.92	0	50	0	134	251	0	0	0	0	0
22.12.92	0	0	40	121	402	0	0	54	0	0
6.1.93	0	0	13	27	487	0	0	0	0	0
18.1.93	0	45	67	45	268	0	0	22	0	0
2.2.93	0	0	45	89	201	0	0	22	0	0
16.2.93	0	0	45	22	201	0	0	67	0	0
2.3.93	0	67	101	268	637	0	0	0	0	0
15.3.93	0	0	134	402	2049	0	0	0	0	0
29.3.93	0	250	150	2212	5681	0	0	100	0	0
15.4.93	0	101	252	855	1961	0	0	0	0	0
30.4.93	0	151	50	402	1709	0	0	302	0	0
11.5.93	0	0	0	0	0	0	0	0	0	0
25.5.93	0	0	151	603	126	0	0	251	0	0
8.6.93	0	0	202	202	855	0	0	654	0	0
22.6.93	0	302	1357	402	3821	151	0	5329	0	0
6.7.93	0	452	101	203	3368	754	0	2715	0	0
20.7.93	0	402	4562	352	905	452	0	4072	0	353
2.8.93	0	1910	50	754	603	302	0	3519	0	0
18.8.93	0	553	101	50	1759	101	0	3318	0	0
31.8.93	0	151	50	101	302	50	0	4926	0	151
13.9.93	0	176	0	0	402	0	0	1207	0	0
29.9.93	0	251	50	215	277	0	0	2439	0	0
13.10.93	0	126	27	0	277	0	0	1282	0	0
27.10.93	0	352	1282	0	427	50	0	1483	0	0
10.11.93	0	251	251	50	779	0	0	955	0	0
24.11.93	0	126	25	0	654	0	0	402	0	0
7.12.93	0	327	553	75	905	0	0	101	0	0
12.1.94	0	302	322	181	844	0	0	0	0	0
26.1.94	0	134	295	188	992	0	0	0	0	0
8.3.94	0	402	120	3017	2293	0	0	40	0	0
21.3.94	0	349	215	2417	1475	0	0	27	0	0

Appendix 2. Mere Mere Euglenophyta, Cryptophyta, Pyrrophyta and Cyanophyta

Date	Aphan	Coelo	Plank	Mic
10.1.90	117	17	1056	0
7.2.90	0	0	0	0
7.3.90	0	0	0	0
21.3.90	0	0	182	0
4.4.90	603	0	0	0
18.4.90	0	0	1139	0
2.5.90	0	22	0	0
16.5.90	0	22	78	0
29.5.90	0	0	22	0
12.6.90	0	56	0	0
27.6.90	182	365	34	0
11.7.90	0	424	0	0
25.7.90	0	938	290	0
8.8.90	402	134	514	0
21.8.90	547	0	67	0
6.9.90	246	22	365	0
24.9.90	182	0	3172	0
9.10.90	22	11	0	0
22.10.90	0	0	0	0
6.11.90	0	0	0	0
20.11.90	7	7	47	0
5.12.90	0	0	34	0
7.1.91	0	0	20	0
22.1.91	7	0	15	0
5.2.91	0	0	22	0
5.3.91	45	0	45	0
19.3.91	0	0	89	0
2.4.91	0	0	201	0
16.4.91	0	0	45	0
30.4.91	0	0	268	0
14.5.91	0	0	0	0
27.5.91	0	0	0	0
11.6.91	0	11	0	0
25.6.91	0	0	0	0
9.7.91	0	67	0	0
22.7.91	0	268	0	0
6.8.91	34	1106	34	0
20.8.91	0	117	84	0
9.9.91	0	123	257	0
23.9.91	0	0	670	0
9.10.91	0	101	201	0
22.10.91	0	56	34	0
5.11.91	0	56	22	0
19.11.91	0	0	0	0
3.12.91	0	13	7	0
18.12.91	0	0	14	0
9.1.92	0	17	0	0
21.1.92	0	11	8	0
3.2.92	0	8	0	0
18.2.92	0	0	22	0
3.3.92	0	0	0	0
18.3.92	0	0	58	0

Appendix 2. Mere Mere Euglenophyta, Cryptophyta, Pyrrophyta and Cyanophyta

Date	Aphan	Coelo	Plank	Mic
1.4.92	0	0	168	0
14.4.92	122	0	12	0
28.4.92	195	0	0	0
12.5.92	195	0	0	0
26.5.92	228	0	0	0
9.6.92	2654	0	0	0
23.6.92	7289	0	0	0
7.7.92	0	134	626	0
21.7.92	0	22	33	0
4.8.92	0	0	0	302
17.8.92	22	0	0	0
1.9.92	0	0	0	0
10.9.92	0	0	0	0
15.9.92	0	0	0	0
5.10.92	0	0	67	0
13.10.92	0	0	134	0
3.11.92	0	0	0	0
24.11.92	17	0	0	0
8.12.92	17	0	0	0
22.12.92	0	0	0	0
6.1.93	0	0	0	0
18.1.93	0	0	0	0
2.2.93	0	0	0	0
16.2.93	0	0	0	0
2.3.93	0	0	0	0
15.3.93	0	0	0	0
29.3.93	0	0	0	0
15.4.93	0	0	0	0
30.4.93	0	0	0	0
11.5.93	0	0	0	0
25.5.93	0	0	0	0
8.6.93	0	0	0	0
22.6.93	0	0	0	0
6.7.93	150	50	0	50
20.7.93	253	0	0	50
2.8.93	101	0	0	0
18.8.93	101	0	0	50
31.8.93	50	0	0	50
13.9.93	0	0	50	0
29.9.93	0	0	151	0
13.10.93	0	0	377	0
27.10.93	0	0	0	0
10.11.93	0	0	0	0
24.11.93	0	0	50	50
7.12.93	0	0	0	0
12.1.94	0	0	0	0
26.1.94	0	0	0	0
8.3.94	0	0	0	0
21.3.94	0	0	0	0

Appendix 2. Mere Mere Zooplankton

Date	Bos.lo	Cer.du	Chyd	D.cuc	D.long	D.pul	Diaph
7.3.90	19.7	0	0	0	9.3	0	0
21.3.90	66.3	0	0	0	18.1	0	0
18.4.90	0.1	0	0	0	1.3	0	0
2.5.90	0	0	0	6	2.2	0	0
16.5.90	0	0.5	0	27.7	1	0	0
29.5.90	0	0	0	5.6	0	0	0.6
12.6.90	0	0	0	9.1	0	0	0
27.6.90	0	0	0	42.8	0	0.5	0
11.7.90	0	2	0	7.3	0	0.3	0
25.7.90	0	1	0	24.5	0	1.4	0.5
8.8.90	0	0	0	19.7	0	1.6	0.1
21.8.90	0	2	0	49.5	0	0.2	0
6.9.90	0	2	0.1	9.6	0	0.5	0
24.9.90	0	6	0	1.4	0	0.5	0
9.10.90	0	8	0	25	0	0	0
22.10.90	0	11	0	0.4	0	0	0
6.11.90	0	0.7	0	0.9	0.6	0	0
20.11.90	0.3	0	0	1.2	0.3	0.5	0
5.12.90	0.1	0	0	0.7	0	0	0
7.1.91	0.2	0	0	5.1	1.3	0	0
5.3.91	0	0	0	0.5	0	0	0
19.3.91	4.7	0	0	2.5	0	0	0
2.4.91	12.4	0	0	1.4	0	0	0
16.4.91	2.2	0	0	0.4	0	0	0.2
30.4.91	1.9	0	0	1.4	0	0	0.2
14.5.91	22.9	0	0	32.4	0	0.1	0
27.5.91	2.2	0	0	6.5	1.5	0	0.1
11.6.91	0	0	0	8.8	2	0	0.1
25.6.91	0	0	0	5	23.1	0	3.2
9.7.91	0	0	0	41.6	4.8	0	0.1
22.7.91	0.1	0	0	7.1	0	0	0
6.8.91	0	0	0	6.3	0	0	0
20.8.91	0	0	0	10.3	0	0	0
9.9.91	0	0	0	8.6	0	0	0
23.9.91	0.4	0	0	2.5	0	0	0
9.10.91	5.9	0.5	0	6.9	0	0	0
22.10.91	1.4	0	0	4.2	0	0	0
5.11.91	2.5	0	0	13.5	0	0	0
19.11.91	2.7	0	0	7.6	0	0	0
3.12.91	1.5	1	0	2.1	0	0	0
18.12.91	0.1	8	0	0.1	0	0	0
9.1.92	0.2	0	0	4.1	0	0	0
21.1.92	0.6	0	0	0	0	0	0
3.2.92	0	1	0	0.1	0	0	0
18.2.92	1.3	0	0	1.4	0	0	0
3.3.92	0.1	0	0	0.9	0	0	0.4
18.3.92	1.7	0	0	5.4	0	0	0
1.4.92	0.4	0	0	1.3	0	0	3
14.4.92	11	0	0	10.8	2.8	0	0.3
28.4.92	14	0	0	14	4.1	0.3	0.1
12.5.92	19	0	0	12	12	0.4	0
26.5.92	16	0	0	29	5.4	0	0

Appendix 2. Mere Mere Zooplankton

Date	Bos.lo	Cer.du	Chyd	D.cuc	D.long	D.pul	Diaph
9.6.92	2	0	0	26	1.13	0	0
23.6.92	5	0	0	18	1.2	0	0
7.7.92	0	0	0	10	0.44	0.3	0
21.7.92	4	0	0	17	2	2	0
4.8.92	1	0.7	0	28	1.2	0	0
17.8.92	1	0.2	0	7	0.2	0	0
1.9.92	0	0	0	6	1	0	0
10.9.92	1	2.6	0	6	1.4	0	0
15.9.92	0	0.5	0	3.8	3	0	0
5.10.92	0	2.8	0	7.2	0.84	0	0
13.10.92	0	3.7	0	11	1.7	0	0
3.11.92	0	4.5	0	4	1	0	0
24.11.92	4	0.2	0	5	0.5	0	0
8.12.92	0	0	0	0	0	0	0
22.12.92	0	0	0	0	0	0	0
6.1.93	0	0	0	0	0	0	0
18.1.93	0	0	0	0	0	0	0
2.2.93	0	0	0	0	0	0	0
16.2.93	0	0	0	0	0	0	0
2.3.93	0	0.5	0	0	1	0	0.6
15.3.93	0	0	0	0	0	0	0.8
29.3.93	26	0	0	4	0	0	2.7
15.4.93	23	0.5	0	3	0.8	0	0.2
30.4.93	26	0	0	4	0	0	0
11.5.93	34	0	0	19	1.6	0	0
25.5.93	43	0	0	15	1.5	0	0
8.6.93	13	0	0	15	1	0.7	0
22.6.93	0	0	0	9	0	0.2	0
6.7.93	0	0	0	10	0	0	0
20.7.93	1	0	0	20	0.5	0	0
2.8.93	15	4	0	8	0	0	0
18.8.93	0	0.5	0	32	0	0	0
31.8.93	0	0.34	0	5	0	0	0
13.9.93	2	0	0	7	0	0	0
29.9.93	0	0	0	53	0.58	0	0
13.10.93	0	0	0	120	8.2	0	0
27.10.93	0	0.34	0	5	1.7	0	0
10.11.93	6	0	0	7	0	0	0
24.11.93	1	0	0	1	0.5	0	0
7.12.93	0	0.2	0	1	0.43	0	0
12.1.94	0	0	0	1	0	0	0
26.1.94	0	0	0	0	0	0	0
8.3.94	1	0	0	0	0	0	0.1
21.3.94	2	0	0	0	0	0	0

Appendix 2. Mere Mere Zooplankton

Date	Lept	Di.gra	Cyclo
7.3.90	0	22.9	2.5
21.3.90	0	32.1	48.2
18.4.90	0	3	1.8
2.5.90	0	13.8	5.6
16.5.90	0	3.6	11.4
29.5.90	0	2	0.4
12.6.90	0	30.4	2.6
27.6.90	0	0.8	1.6
11.7.90	0	0.9	0.2
25.7.90	0	0.9	1.9
8.8.90	0	1.1	0.2
21.8.90	0	4.3	9
6.9.90	0	1.4	4.1
24.9.90	0	1.5	0.4
9.10.90	0	19.4	8.4
22.10.90	0	2.2	0.1
6.11.90	0	27.5	0
20.11.90	0	7	0.1
5.12.90	0	14	0
7.1.91	0	26.7	0.2
5.3.91	0	22.6	3.1
19.3.91	0.4	30.4	14.6
2.4.91	0.1	17.6	8.5
16.4.91	0	4.2	0.6
30.4.91	0	7.1	0.2
14.5.91	0	26.5	2.8
27.5.91	0	9.3	11.9
11.6.91	0	10.6	3.5
25.6.91	0	8	7.1
9.7.91	0	5.9	14.7
22.7.91	0	2.2	2.4
6.8.91	0	0.7	1.8
20.8.91	0	0.7	0.4
9.9.91	0	0.9	2.1
23.9.91	0	2	0.5
9.10.91	0	4.3	1.1
22.10.91	0	3.5	2.1
5.11.91	0	8	0.2
19.11.91	0	4.7	0.1
3.12.91	0	2.4	0
18.12.91	0	0.1	0
9.1.92	0	3.6	0
21.1.92	0	0.1	0
3.2.92	0	0	0
18.2.92	0	9	0.1
3.3.92	0	7.3	1.8
18.3.92	0	17.4	6
1.4.92	0	4.1	1.4
14.4.92	0	20	6.6
28.4.92	0	19	6
12.5.92	0	60	29
26.5.92	0	61	24.5

Appendix 2. Mere Mere Zooplankton

Date	Lept	Di.gra	Cyclo
9.6.92	0	17	28.8
23.6.92	0	8	37
7.7.92	0	5	15.9
21.7.92	0	7	22.3
4.8.92	0	3	25.3
17.8.92	0	1	13
1.9.92	0	2	11.7
10.9.92	0	1	5.8
15.9.92	0	1	34
5.10.92	0	1	18.4
13.10.92	0	1	10.8
3.11.92	0	1	3.1
24.11.92	0	4	1.4
8.12.92	0	0	3
22.12.92	0	0	1.2
6.1.93	0	0	0
18.1.93	0	0	0
2.2.93	0	0	0
16.2.93	0	0	0
2.3.93	0	0	2
15.3.93	0	0	1
29.3.93	0	8	5.3
15.4.93	0	9	3
30.4.93	0	8	2
11.5.93	0	6	34.7
25.5.93	0	7	35.2
8.6.93	0	7	28
22.6.93	0	1	16
6.7.93	0	1	11.4
20.7.93	0	2	17.9
2.8.93	0	1	28
18.8.93	0	3	29
31.8.93	0	3	1.6
13.9.93	0	3	2
29.9.93	0	4	6.7
13.10.93	0	8	17
27.10.93	0	3	1.6
10.11.93	0	8	2
24.11.93	0	1	1.4
7.12.93	0	7	1
12.1.94	0	5	0.5
26.1.94	0	6	0
8.3.94	0	8	2.3
21.3.94	0	8	5.3

Appendix 2. Little Mere Chlorophyta

Date	Anki	Anky	Chlam	Clos	Coela	Elak	Eud	Gloe	Micra
10.1.90	0	0	24	0	0	0	0	0	0
7.2.90	0	0	46	0	0	0	0	0	0
21.2.90	30	0	61	34	0	0	0	0	0
7.3.90	0	0	168	0	0	0	0	0	0
21.3.90	402	0	0	0	0	0	0	0	402
4.4.90	1217	0	1217	0	0	243	0	243	0
18.4.90	6569	0	0	0	0	0	1460	0	0
2.5.90	1810	201	201	0	201	0	0	0	0
16.5.90	0	2011	0	0	15383	0	0	0	0
29.5.90	0	0	0	0	9245	0	0	0	0
12.6.90	0	0	0	0	49634	0	0	0	0
27.6.90	0	0	0	0	2866	0	0	0	0
11.7.90	0	0	0	0	14537	0	0	0	0
25.7.90	0	0	0	0	85	0	0	0	0
8.8.90	0	0	0	0	24	0	0	0	0
21.8.90	0	0	0	0	6	0	0	0	0
6.9.90	0	0	0	0	12	0	0	0	0
24.9.90	0	0	0	0	0	0	0	0	0
9.10.90	0	0	0	0	8	0	0	0	0
22.10.90	0	0	17	0	0	0	0	0	0
6.11.90	6	0	0	6	0	0	0	0	0
20.11.90	0	0	0	18	48	0	0	0	0
5.12.90	0	0	17	0	0	0	0	0	0
7.1.91	0	0	0	0	0	0	0	0	0
22.1.91	0	0	1206	0	0	0	0	0	0
5.2.91	67	0	9786	0	0	0	0	0	0
19.2.91	0	0	13137	0	0	0	0	0	0
5.3.91	142	852	2859	0	0	0	0	0	0
19.3.91	182	55	182	0	0	0	0	0	0
2.4.91	0	255	0	0	0	0	0	0	0
16.4.91	0	158	0	0	0	0	0	0	0
30.4.91	0	122	12	0	0	0	0	0	0
14.5.91	0	1362	0	0	0	0	0	0	0
27.5.91	0	1825	0	0	0	0	0	0	0
11.6.91	0	182	0	0	0	0	0	0	0
25.6.91	0	0	0	0	0	0	0	0	0
9.7.91	0	134	0	0	0	0	0	0	0
22.7.91	0	1906	0	0	0	0	0	0	0
6.8.91	0	426	0	0	41	0	0	0	0
19.8.91	0	292	0	0	0	0	0	0	0
9.9.91	0	24	0	0	0	0	0	0	0
23.9.91	0	0	0	0	0	0	0	0	0
9.10.91	0	36	18	0	0	0	0	0	0
22.10.91	0	73	0	0	0	0	0	0	0
5.11.91	0	61	12	0	0	0	0	0	0
19.11.91	0	0	0	0	0	0	0	0	0
3.12.91	0	6	0	0	0	0	0	0	0
18.12.91	0	0	0	0	0	4	0	0	0
9.1.92	0	0	7	0	0	0	0	0	0

Appendix 2. Little Mere Chlorophyta

Date	Anki	Anky	Chlam	Clos	Coela	Elak	Eud	Gloe	Micra
21.1.92	0	0	0	0	0	0	0	0	0
3.2.92	0	0	107	0	0	0	0	0	0
16.2.92	34	0	67	0	0	0	0	0	0
3.3.92	0	0	0	0	0	0	0	0	0
18.3.92	670	0	34	0	0	0	0	0	0
1.4.92	50	0	10	0	0	0	10	0	0
14.4.92	429	0	40	0	0	0	0	0	0
28.4.92	27	0	0	0	0	0	0	0	0
12.5.92	13	0	61	13	0	0	0	0	0
26.5.92	710	0	80	0	0	0	0	0	0
9.6.92	147	0	938	0	0	0	0	0	0
23.6.92	0	0	60	0	0	0	0	0	0
7.7.92	0	0	0	44	0	67	0	0	44
21.7.92	67	0	0	0	0	0	0	0	0
4.8.92	1430	0	0	0	0	0	0	0	0
17.8.92	1340	0	0	0	0	0	0	0	0
1.9.92	0	0	0	0	0	0	0	0	0
10.9.92	0	0	0	0	0	0	0	0	0
15.9.92	0	0	0	0	0	0	0	0	0
5.10.92	0	0	0	0	0	0	0	0	0
13.10.92	0	0	0	0	0	0	0	0	0
3.11.92	0	0	0	0	0	0	0	0	0
24.11.92	0	0	35	0	0	0	0	0	0
8.12.92	13	0	13	0	0	0	0	0	0
22.12.92	0	0	0	0	13	0	0	0	0
6.1.93	0	0	898	0	0	0	0	0	0
18.1.93	0	0	134	0	0	0	0	0	0
2.2.93	67	0	335	0	0	0	0	0	0
16.2.93	402	0	100	0	0	0	0	0	0
2.3.93	1909	0	101	0	0	0	0	0	0
15.3.93	11562	0	402	0	0	0	0	0	0
29.3.93	1106	0	352	201	0	0	0	0	0
15.4.93	0	0	0	0	0	0	0	0	0
30.4.93	0	0	34	0	0	0	0	0	0
11.5.93	0	0	436	0	0	0	34	0	0
25.5.93	0	0	0	0	0	0	0	0	0
8.6.93	0	0	100	0	0	0	0	0	0
22.6.93	201	0	603	0	0	0	0	0	0
6.7.93	0	0	50	0	0	0	0	0	0
20.7.93	0	0	67	0	0	0	0	0	0
2.8.93	0	0	156	0	0	0	0	0	0
18.8.93	0	0	0	0	0	0	0	22	0
31.8.93	0	0	302	0	67	0	0	0	0
13.9.93	0	0	0	0	0	0	0	0	0
29.9.93	0	0	46	0	0	0	0	0	0
13.10.93	0	0	0	0	0	0	0	0	0
27.10.93	0	0	0	0	0	0	0	0	0
10.11.93	0	0	0	0	0	0	0	0	0
24.11.93	503	0	67	67	0	0	0	0	0

Appendix 2. Little Mere Chlorophyta

Date	Anki	Anky	Chlam	Clos	Coela	Elak	Eud	Gloe	Micra
7.12.93	0	0	67	0	0	0	0	0	0
12.1.94	536	0	67	112	0	0	0	0	0
26.1.94	0	0	267	0	0	0	0	0	0
8.3.94	9315	0	536	0	0	0	0	0	0
21.3.94	838	0	1776	67	0	0	0	0	0

Appendix 2. Little Mere Chlorophyta

Date	Oocy	Ped	Pla	Scen	Tetr	Vol	Chlo	Staur	Sel	Chlor
10.1.90	0	0	0	0	0	0	0	0	0	0
7.2.90	0	0	0	49	0	0	0	0	0	0
21.2.90	0	0	0	182	0	0	0	0	0	0
7.3.90	0	0	0	0	0	0	0	0	0	0
21.3.90	0	0	0	0	0	0	0	0	0	0
4.4.90	0	0	1460	0	0	0	0	0	0	0
18.4.90	0	0	3650	2920	0	0	0	0	0	0
2.5.90	0	0	0	1609	0	0	0	0	0	0
16.5.90	101	0	0	402	0	0	0	0	0	0
29.5.90	0	0	0	0	0	0	0	0	0	0
12.6.90	0	0	0	730	0	0	0	0	0	0
27.6.90	50	0	0	3066	0	0	0	0	0	0
11.7.90	61	0	0	365	0	0	0	0	0	0
25.7.90	0	0	0	0	0	0	0	0	0	0
8.8.90	0	0	0	0	0	6	0	0	0	0
21.8.90	0	0	0	49	0	79	0	0	0	0
6.9.90	0	0	0	30	0	6	0	0	0	0
24.9.90	0	0	0	0	0	0	0	0	0	0
9.10.90	0	0	0	0	0	0	0	0	0	0
22.10.90	0	0	0	0	0	0	0	0	0	0
6.11.90	0	0	0	0	0	0	0	0	0	0
20.11.90	0	0	0	0	0	0	0	0	0	0
5.12.90	0	0	0	25	0	0	0	0	0	0
7.1.91	0	0	0	34	0	0	0	0	0	0
22.1.91	0	0	0	0	0	0	0	0	0	0
5.2.91	0	0	0	0	0	0	0	0	0	0
19.2.91	0	0	0	0	0	0	0	0	0	0
5.3.91	0	0	0	0	0	0	0	0	0	0
19.3.91	0	0	0	0	0	0	0	0	0	0
2.4.91	0	0	0	0	0	0	0	0	0	0
16.4.91	0	0	0	0	0	0	0	0	0	0
30.4.91	0	0	0	0	0	0	0	0	0	0
14.5.91	0	0	0	0	0	0	0	0	0	0
27.5.91	0	0	0	0	0	0	0	0	0	0
11.6.91	0	0	0	0	0	0	0	0	0	0
25.6.91	0	0	0	0	0	0	0	0	0	0
9.7.91	0	0	0	0	0	0	0	0	0	0
22.7.91	0	0	0	0	0	0	0	0	0	0
6.8.91	0	0	0	0	0	0	0	0	0	0
19.8.91	0	0	0	0	0	0	0	0	0	0
9.9.91	0	0	0	0	0	0	0	0	0	0
23.9.91	0	0	0	0	0	0	0	0	0	0
9.10.91	0	0	0	0	0	0	0	0	0	0
22.10.91	0	0	0	0	0	0	0	0	0	0
5.11.91	0	0	0	49	0	0	0	0	0	0
19.11.91	0	18	0	85	6	0	0	0	0	0
3.12.91	0	0	0	0	0	0	0	0	0	0
18.12.91	0	0	0	0	4	0	0	0	0	0
9.1.92	0	0	0	0	0	0	0	0	0	0

Appendix 2. Little Mere Chlorophyta

Date	Oocy	Ped	Pla	Scen	Tetr	Vol	Chlo	Staur	Sel	Chlor
21.1.92	0	0	0	13	0	0	0	0	0	0
3.2.92	0	0	0	0	0	0	0	0	0	0
18.2.92	0	0	0	0	0	0	0	0	0	0
3.3.92	0	0	0	536	0	0	0	0	0	0
18.3.92	0	0	0	0	0	0	0	0	0	0
1.4.92	0	0	0	0	0	0	30	0	0	0
14.4.92	0	0	0	13	0	0	429	0	0	0
28.4.92	0	0	0	0	0	0	0	0	0	0
12.5.92	0	0	0	0	0	0	0	0	0	0
26.5.92	0	0	0	0	0	0	0	0	0	0
9.6.92	0	0	0	0	0	0	0	0	0	0
23.6.92	0	0	0	0	0	0	0	0	0	0
7.7.92	22	0	0	44	0	0	0	44	201	0
21.7.92	0	0	0	0	0	0	0	0	0	0
4.8.92	0	0	0	0	0	0	0	0	0	0
17.8.92	0	0	0	0	0	0	0	0	0	0
1.9.92	0	0	0	0	0	0	0	0	0	0
10.9.92	0	0	0	13	0	0	0	0	0	0
15.9.92	0	0	0	0	0	0	0	0	0	0
5.10.92	0	0	0	0	0	0	0	0	0	0
13.10.92	0	0	0	0	0	0	0	0	0	0
3.11.92	0	0	0	0	0	0	0	0	0	0
24.11.92	0	0	0	0	0	0	0	0	0	0
8.12.92	0	0	0	0	0	0	0	0	0	0
22.12.92	0	0	0	0	0	0	0	0	0	0
6.1.93	0	0	0	0	0	0	0	0	0	0
18.1.93	0	0	0	26	0	0	0	0	0	0
2.2.93	0	0	0	0	0	0	0	0	67	0
16.2.93	0	0	0	136	0	0	0	0	34	0
2.3.93	0	0	0	0	0	0	0	0	0	0
15.3.93	0	0	0	1005	0	0	0	0	101	0
29.3.93	0	0	0	250	0	0	0	0	302	0
15.4.93	0	0	0	34	0	0	0	0	34	132
30.4.93	0	0	0	0	0	0	0	0	0	0
11.5.93	0	0	0	0	0	0	34	0	0	0
25.5.93	0	0	0	0	0	0	0	0	0	0
8.6.93	0	0	0	0	0	0	235	0	0	34
22.6.93	0	0	0	0	0	0	0	0	0	0
6.7.93	50	0	0	0	0	0	0	0	0	151
20.7.93	0	0	0	0	34	0	0	0	0	134
2.8.93	0	0	0	0	0	0	0	0	0	45
18.8.93	0	0	0	0	223	0	0	0	0	67
31.8.93	136	0	34	136	0	0	0	0	0	0
13.9.93	0	0	0	0	0	0	0	0	0	45
29.9.93	0	0	0	0	0	0	0	0	0	223
13.10.93	0	0	0	0	0	0	0	0	0	0
27.10.93	0	0	0	0	0	0	0	0	0	0
10.11.93	0	0	0	0	0	0	469	0	0	0
24.11.93	0	0	0	0	0	0	369	0	0	0

Appendix 2. Little Mere Chlorophyta

Date	Oocy	Ped	Pla	Scen	Tetr	Vol	Chlo	Staur	Sel	Chlor
7.12.93	0	0	0	0	0	0	168	0	0	0
12.1.94	0	0	0	0	0	0	0	0	0	0
26.1.94	0	0	0	0	0	0	0	0	0	67
8.3.94	0	0	0	268	0	0	0	0	0	201
21.3.94	0	0	0	201	0	0	0	0	0	2278

Appendix 2. Little Mere Chlorophyta

Date	Shro	Cos	Dict
10.1.90	0	0	10
7.2.90	0	0	0
21.2.90	0	0	0
7.3.90	0	0	0
21.3.90	0	0	0
4.4.90	0	0	0
18.4.90	0	0	0
2.5.90	0	0	0
16.5.90	0	0	0
29.5.90	0	0	0
12.6.90	0	0	0
27.6.90	0	0	0
11.7.90	0	0	0
25.7.90	0	0	0
8.8.90	0	0	0
21.8.90	0	0	0
6.9.90	0	0	0
24.9.90	0	0	0
9.10.90	0	0	0
22.10.90	0	0	0
6.11.90	0	0	0
20.11.90	0	0	0
5.12.90	0	0	0
7.1.91	0	0	0
22.1.91	0	0	0
5.2.91	0	0	0
19.2.91	0	0	0
5.3.91	0	0	0
19.3.91	0	0	0
2.4.91	0	0	0
16.4.91	0	0	0
30.4.91	0	0	0
14.5.91	0	0	0
27.5.91	0	0	0
11.6.91	0	0	0
25.6.91	0	0	0
9.7.91	0	0	0
22.7.91	0	0	0
6.8.91	0	0	0
19.8.91	0	0	0
9.9.91	0	0	0
23.9.91	0	0	0
9.10.91	0	0	0
22.10.91	0	0	0
5.11.91	0	0	0
19.11.91	0	0	0
3.12.91	0	0	0
18.12.91	0	0	0
9.1.92	0	0	0

Appendix 2. Little Mere Chlorophyta

Date	Shro	Cos	Dict
21.1.92	0	0	0
3.2.92	0	0	0
18.2.92	0	0	0
3.3.92	0	0	0
18.3.92	0	0	0
1.4.92	0	0	0
14.4.92	0	0	0
28.4.92	0	0	0
12.5.92	0	0	0
26.5.92	0	0	0
9.6.92	0	0	0
23.6.92	0	0	0
7.7.92	0	0	0
21.7.92	0	0	0
4.8.92	0	0	0
17.8.92	0	0	0
1.9.92	0	0	0
10.9.92	0	0	0
15.9.92	0	0	0
5.10.92	0	0	0
13.10.92	0	0	0
3.11.92	0	0	0
24.11.92	0	0	0
8.12.92	0	0	0
22.12.92	0	0	0
6.1.93	0	0	0
18.1.93	0	0	0
2.2.93	0	0	0
16.2.93	0	0	0
2.3.93	0	0	0
15.3.93	0	0	0
29.3.93	0	0	0
15.4.93	0	0	0
30.4.93	0	0	0
11.5.93	1541	0	0
25.5.93	0	0	0
8.6.93	503	0	0
22.6.93	50	0	0
6.7.93	0	0	0
20.7.93	22	0	0
2.8.93	0	0	0
18.8.93	0	0	0
31.8.93	0	536	0
13.9.93	0	0	0
29.9.93	0	0	0
13.10.93	0	0	0
27.10.93	0	0	0
10.11.93	0	0	0
24.11.93	0	0	0

Appendix 2. Little Mere Chlorophyta

Date	Shro	Cos	Dict
7.12.93	0	0	0
12.1.94	0	0	22
26.1.94	0	0	0
8.3.94	0	0	0
21.3.94	0	0	0

Appendix 2. Little Mere Bacillariophyceae

Date	Ach	Amp	Ast	Au.gr	Cen	Dia	Frag	Gom	Nav	Nit
10.1.90	0	0	0	0	0	0	0	0	0	0
7.2.90	0	0	0	0	0	0	0	0	0	0
21.2.90	0	0	91	0	0	0	0	30	0	0
7.3.90	0	0	134	34	402	0	0	0	0	0
21.3.90	0	0	0	0	0	0	0	0	0	0
4.4.90	0	0	487	0	0	0	0	0	0	0
18.4.90	0	0	0	0	0	0	0	0	0	0
2.5.90	0	0	0	0	0	0	0	0	0	0
16.5.90	0	0	0	0	0	0	0	0	0	0
29.5.90	0	0	0	0	0	0	0	0	0	0
12.6.90	0	0	0	0	0	0	0	0	0	0
27.6.90	0	0	0	0	0	0	0	0	0	0
11.7.90	0	0	0	0	0	0	61	0	0	0
25.7.90	0	0	0	0	0	0	0	0	0	6
8.8.90	0	0	0	0	0	0	0	0	0	0
21.8.90	0	0	0	0	0	0	0	0	0	0
6.9.90	0	0	0	0	0	0	0	0	6	0
24.9.90	0	0	0	0	0	0	0	0	0	0
9.10.90	0	0	0	0	0	0	0	0	0	0
22.10.90	0	0	0	0	0	0	8	0	34	0
6.11.90	0	0	0	0	0	0	0	0	12	0
20.11.90	0	0	0	0	0	0	0	0	12	0
5.12.90	0	0	0	0	0	0	0	8	17	0
7.1.91	0	0	17	0	17	0	0	0	8	0
22.1.91	0	0	0	0	0	0	0	0	0	0
5.2.91	0	0	0	0	67	0	0	0	0	0
19.2.91	0	0	0	0	0	0	0	0	134	0
5.3.91	0	0	872	0	0	0	61	0	0	0
19.3.91	0	0	588	0	1318	0	0	0	0	41
2.4.91	0	12	73	0	0	0	0	0	12	0
16.4.91	0	0	0	0	0	12	24	0	0	0
30.4.91	0	0		0	0	0	0	0	0	0
14.5.91	0	0	0	0	0	0	0	0	12	0
27.5.91	0	0	0	0	16423	0	0	0	0	0
11.6.91	0	0	0	0	0	0	0	0	0	0
25.6.91	91	0	0	0	0	0	0	36	0	0
9.7.91	0	0	0	0	0	0	0	0	0	0
22.7.91	0	0	0	0	0	0	0	0	40	0
6.8.91	0	0	81	0	0	0	0	0	0	0
19.8.91	0	0	0	0	0	0	0	0	0	0
9.9.91	0	0	0	0	0	0	0	0	49	0
23.9.91	0	0	0	0	0	0	0	0	12	12
9.10.91	0			0	0	0	0	0	0	0
22.10.91	0		18	0	0	0	0	6	0	9
5.11.91	0			0	0	0	0	0	0	0
19.11.91	0	0	6	0	0	0	6	0	0	0
3.12.91	0	6	0	0	0	0	0	0	12	0
18.12.91	0	0	0	0	0		0	0	9	0
9.1.92	0	0	4	0	0	0	0	4	0	0

Appendix 2. Little Mere Bacillariophyceae

Date	Ach	Amp	Ast	Au.gr	Cen	Dia	Frag	Gom	Nav	Nit
21.1.92	0	0	0	0	0	0	0	0	34	0
3.2.92	0	0		0	0	0	0	0	161	0
18.2.92		0		0	0	0	0	0	0	0
3.3.92	0	0	0	0	0	0	0	0	134	0
18.3.92		0		0	0	0	0	0	0	0
1.4.92	0	0	0	0	0	0	10	0	0	0
14.4.92	0	0	0	0	0	0	0	0	13	0
28.4.92	0	0	0	0	0	0	0	0	13	0
12.5.92	0	0	85	0	0	0	85	0	13	0
26.5.92	0	0	0	0	0	0	13	0	0	0
9.6.92	0	0	0	0	0	0	0	0	0	0
23.6.92	0	0	0	0	0	0	20	0	20	0
7.7.92	0	0	0	0	0	0	20	0	0	0
21.7.92	0	0	0	0	0	0	0	0	0	0
4.8.92	0	0	0	0	0	0	0	0	0	84
17.8.92	0	0	0	0	0	0	0	0	0	134
1.9.92	0	0	0	0	0	0	0	0	0	13
10.9.92	0	0	0	13	13	0	0	0	26	26
15.9.92	0	0	0	0	0	0	0	0	0	0
5.10.92	0	0	0	0	0	0	0	0	0	13
13.10.92	0	0	0	13	0	0	0	0	13	0
3.11.92	0	0	0	0	27	0	0	0	0	0
24.11.92	0	0	0	34	0	0	0	0	0	0
8.12.92	0	0	50	0	0	0	0	0	0	0
22.12.92	0	0	26	52	13	0	0	0	0	0
6.1.93	0	0	0	0	0	0	0	0	67	0
18.1.93	0	0	13	649	0	0	0	0	67	0
2.2.93	0	0	442	6968	0	0	0	0	0	0
16.2.93	0	0	0	0	34	0	0	0	0	0
2.3.93	0	0	202	303	0	0	0	0	0	0
15.3.93	0	0	0	2626	0	0	0	0	0	101
29.3.93	0	0	250	0	0	0	0	0	0	0
15.4.93	0	0	21	0	0	0	0	0	0	0
30.4.93	0	0	0	0	0	0	0	0	0	0
11.5.93	0	0	0	0	0	0	0	0	0	0
25.5.93	0	0	0	0	0	0	0	0	0	0
8.6.93	0	0	0	0	0	0	67	0	0	0
22.6.93	0	0	0	0	0	0	0	0	0	0
6.7.93	0	0	0	0	0	0	0	0	0	151
20.7.93	0	0	0	0	0	0	0	0	34	67
2.8.93	0	0	0	0	0	0	314	0	0	134
18.8.93	0	0	0	0	0	0	0	112	0	0
31.8.93	0	0	0	0	0	0	0	0	0	0
13.9.93	0	0	0	0	0	0	0	22	0	0
29.9.93	0	0	0	0	0	0	0	626	0	134
13.10.93	0	0	0	0	0	0	0	0	0	0
27.10.93	0	0	0	0	0	0	67	0	34	0
10.11.93	0	0	0	0	0	0	0	0	0	0
24.11.93	0	0	0	0	0	0	0	0	0	0

Appendix 2. Little Mere Bacillariophyceae

Date	Ach	Amp	Ast	Au.gr	Cen	Dia	Frag	Gom	Nav	Nit
7.12.93	0	0	0	68	0	0	0	0	34	0
12.1.94	0	0	0	1251	0	0	0	176	44	0
26.1.94	0	0	0	4691	838	0	0	67	67	0
8.3.94	0	0	2145	134	0	0	0	0	0	34
21.3.94	0	0	0	0	0	0	0	0	0	89

Appendix 2. Little Mere Bacillariophyceae

Date	Pin	S.han	S.rot	Sy.ul
10.1.90	0	0	0	12
7.2.90	0	0	0	0
21.2.90	0	0	0	0
7.3.90	0	0	0	0
21.3.90	0	129898	0	0
4.4.90	0	21898	0	0
18.4.90	0	730	0	0
2.5.90	0	0	0	0
16.5.90	0	0	0	0
29.5.90	0	0	0	0
12.6.90	0	0	0	0
27.6.90	0	0	0	0
11.7.90	0	0	0	0
25.7.90	0	0	0	0
8.8.90	0	0	0	0
21.8.90	0	0	0	0
6.9.90	0	0	0	0
24.9.90	0	0	0	0
9.10.90	0	0	0	0
22.10.90	8	0	0	0
6.11.90	0	0	0	0
20.11.90	0	12	0	0
5.12.90	0	0	0	8
7.1.91	0	17	0	0
22.1.91	0	0	0	0
5.2.91	0	0	0	0
19.2.91	0	335	0	0
5.3.91	0	811	0	0
19.3.91	0	223	0	0
2.4.91	0	0	0	0
16.4.91	0	0	0	49
30.4.91	12	109	0	0
14.5.91	0	1679	0	0
27.5.91	0	50364	0	365
11.6.91	0	353	0	0
25.6.91	0	1515	0	91
9.7.91	0	0	0	0
22.7.91	0	0	0	0
6.8.91	0	0	0	0
19.8.91	0	0	0	0
9.9.91	0	12	0	0
23.9.91	0	0	0	0
9.10.91	0	0	0	0
22.10.91	0	18	0	0
5.11.91	0	0	0	0
19.11.91	0		0	0
3.12.91	0	0	0	0
18.12.91	0	4	0	0
9.1.92	0	0	0	0

Appendix 2. Little Mere Bacillariophyceae

Date	Pin	S.han	S.rot	Sy.ul
21.1.92	0	13	0	0
3.2.92	0	161	0	0
18.2.92	0	771	0	0
3.3.92	0	26270	0	0
18.3.92	0	469	34	0
1.4.92	0	160	0	0
14.4.92	0	0	0	13
28.4.92	0	0	0	0
12.5.92	0	13	0	0
26.5.92	0	0	0	13
9.6.92	0	0	0	0
23.6.92	0	0	0	0
7.7.92	0	22	0	0
21.7.92	0	0	0	0
4.8.92	0	0	0	0
17.8.92	0	0	0	0
1.9.92	0	0	0	0
10.9.92	0	0	0	0
15.9.92	0	0	0	0
5.10.92	0	0	0	0
13.10.92	0	0	0	0
3.11.92	0	0	0	0
24.11.92	0	0	0	50
8.12.92	0	0	0	0
22.12.92	0	0	0	0
6.1.93	0	0	0	0
18.1.93	0	0	0	0
2.2.93	0	0	0	67
16.2.93	0	0	0	0
2.3.93	0	601	0	0
15.3.93	0	265	0	302
29.3.93	0	0	0	0
15.4.93	0	0	0	0
30.4.93	0	0	0	0
11.5.93	0	0	0	0
25.5.93	0	0	0	0
8.6.93	0	0	0	0
22.6.93	0	0	0	0
6.7.93	0	0	0	13720
20.7.93	0	0	0	0
2.8.93	0	0	0	0
18.8.93	0	0	0	0
31.8.93	0	0	0	0
13.9.93	0	0	0	0
29.9.93	0	0	0	0
13.10.93	0	0	0	0
27.10.93	0	0	0	0
10.11.93	0	0	0	0
24.11.93	0	0	0	0

Appendix 2. Little Mere Bacillariophyceae

Date	Pin	S.han	S.rot	Sy.ul
7.12.93	0	0	0	0
12.1.94	0	0	0	0
26.1.94	0	0	0	0
8.3.94	0	0	0	0
21.3.94	0	0	0	0

Appendix 2. Little Mere Euglenophyta, Cryptophyta, Pyrrophyta and Cyanophyta

Date	Eug	Phac	Trac	Crypt	Rhod	µFlag	Cer	Gym	Ana	Aphan	Coelo
10.1.90	0	0	0	12	24	1448	0	0	0	207	0
7.2.90	0	0	0	137	46	5383	0	0	0	228	0
21.2.90	0	0	0	61	547	2981	0	0	0	61	0
7.3.90	0	0	0	168	1575	4022	0	0	0	101	0
21.3.90	0	402	0	1206	5630	4826	0	0	0	0	402
4.4.90	0	0		18978	30900	18735	0	0	0	0	0
18.4.90	0	0	0	19708	11679	12409	0	0	0	0	0
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	0
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	0
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	0
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	0
7.1.91	0	8	0	8	17	67	0	0	0	0	0
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	0
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	0
19.3.91	0	0	0	345	81	527	0	0	0	0	0
2.4.91	0	0	0	24	0	146	0	0	0	0	0
16.4.91	0	0	0	0	0	36	0	12	0	0	0
30.4.91	0	0	0	0	0	12	0	0	0	0	0
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	0
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	0	20	0
6.8.91	0	0	0	0	142	101	0	0	81	41	0
19.8.91	0	0	0	24	158	36	0	0	0	0	0
9.9.91	0	0	0	97	49	61	0	0	12	0	0
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	0
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	0
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	0	9	0	0
9.1.92	0	0	0	9	223	18	0	0	4	0	0

Appendix 2. Little Mere Euglenophyta, Cryptophyta, Pyrrophyta and Cyanophyta

Date	Eug	Phac	Trac	Crypt	Rhod	µFlag	Cer	Gym	Ana	Aphan	Coelo
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
1.4.92	0	10	0	0	0	30	0	10	0	40	0
14.4.92	13	0	40	94	67	0	0	0	0	0	0
28.4.92	0	0	0	94	134	0	0	0	0	0	0
12.5.92	13	0	0	523	61	40	0	0	0	0	0
26.5.92	0	0	0	40	322	67	0	0	0	0	0
9.6.92	0	0	0	13	295	0	0	0	0	0	0
23.6.92	0	0	0	0	4281	60	0	0	0	0	0
7.7.92	0	0	0	112	0	223	0	44	22	0	0
21.7.92	0	0	0	334	290	0	0	0	0	0	0
4.8.92	0	0	268	0	1251	268	0	34	0	0	0
17.8.92	22	0	22	67	1294	0	0	0	0	0	0
1.9.92	0	0	0	710	107	54	0	0	308	0	0
10.9.92	0	0	13	40	13	54	0	81	0	0	0
15.9.92	0	0	40	215	0	174	0	0	0	13	0
5.10.92	0	0	13	27	40	0	0	0	0	0	0
13.10.92	0	0	0	0	0	54	0	0	0	0	0
3.11.92	0	0	13	13	94	241	0	40	0	0	0
24.11.92	0	0	17	0	35	687	0	17	0	0	0
8.12.92	0	0	0	40	201	134	0	0	0	0	0
22.12.92	0	0	0	13	94	134	0	0	0	0	0
6.1.93	0	0	0	13	134	509	0	0	0	0	0
18.1.93	0	0	0	94	107	362	0	0	0	0	0
2.2.93	0	0	67	235	670	905	0	0	0	0	0
16.2.93	0	67	0	1107	972	3116	0	0	0	0	0
2.3.93	0	0	303	3000	1910	17695	0	101	0	0	0
15.3.93	0	0	202	4307	503	10054	0	0	0	0	0
29.3.93	0	0	0	5580	654	3720	0	50	0	0	0
15.4.93	202	0	0	500	101	2279	0	67	0	0	0
30.4.93	0	0	0	404	34	302	0	0	0	0	0
11.5.93	0	0	0	737	268	134	0	0	0	0	0
25.5.93	0	0	0	168	2513	737	0	0	0	0	0
8.6.93	168	0	0	2647	67	693	0	0	0	0	0
22.6.93	0	0	503	13774	905	603	0	0	0	0	0
6.7.93	0	0	0	7239	4826	5077	0	0	0	0	0
20.7.93	0	0	168	2614	2513	309	0	503	34	0	0
2.8.93	0	0	22	201	424	0	0	0	0	0	0
18.8.93	22	0	0	89	246	1720	0	134	0	0	0
31.8.93	0	0	0	503	235	503	0	0	0	0	0
13.9.93	0	0	0	99	134	45	0	0	0	0	0
29.9.93	0	0	0	827	581	157	0	0	0	0	0
13.10.93	17	0	101	536	17	0	0	888	0	0	0
27.10.93	0	0	0	3385	369	268	0	34	0	0	0
10.11.93	0	0	0	3854	1441	905	0	0	0	0	0
24.11.93	0	0	0	0	0	0	0	0	0	0	0

Appendix 2. Little Mere Euglenophyta, Cryptophyta, Pyrrophyta and Cyanophyta

Date	Eug	Phac	Trac	Crypt	Rhod	µFlag	Cer	Gym	Ana	Aphan	Coelo
7.12.93	0	0	134	3083	1541	704	0	0	0	0	0
12.1.94	0	0	223	871	314	536	0	22	0	0	0
26.1.94	34	0	301	1072	469	1340	0	0	0	0	0
8.3.94	0	0	134	469	1407	2815	0	0	0	0	0
21.3.94	0	0	268	734	6534	1668	0	34	0	0	0

Appendix 2. Little Mere Euglenophyta, Cryptophyta, Pyrrophyta and Cyanophyta

Date	Mic	Plank
10.1.90	0	560
7.2.90	0	867
21.2.90	0	1095
7.3.90	0	1441
21.3.90	0	804
4.4.90	0	973
18.4.90	0	1460
2.5.90	0	0
16.5.90	0	0
29.5.90	0	0
12.6.90	0	0
27.6.90	0	0
11.7.90	0	0
25.7.90	0	6
8.8.90	0	0
21.8.90	0	6
6.9.90	0	0
24.9.90	0	0
9.10.90	0	0
22.10.90	0	0
6.11.90	0	6
20.11.90	0	0
5.12.90	0	8
7.1.91	0	17
22.1.91	0	0
5.2.91	0	67
19.2.91	0	0
5.3.91	0	162
19.3.91	0	81
2.4.91	0	12
16.4.91	0	0
30.4.91	0	12
14.5.91	0	0
27.5.91	0	0
11.6.91	0	0
25.6.91	0	36
9.7.91	0	0
22.7.91	0	0
6.8.91	0	0
19.8.91	0	12
9.9.91	0	12
23.9.91	0	0
9.10.91	0	6
22.10.91	0	0
5.11.91	0	12
19.11.91	0	0
3.12.91	0	0
18.12.91	0	0
9.1.92	0	4

Appendix 2. Little Mere Euglenophyta, Cryptophyta, Pyrrophyta and Cyanophyta

Date	Mic	Plank
21.1.92	0	0
3.2.92	0	0
18.2.92	0	0
3.3.92	0	0
18.3.92	0	0
1.4.92	0	0
14.4.92	0	0
28.4.92	0	0
12.5.92	0	0
26.5.92	0	0
9.6.92	0	0
23.6.92	0	0
7.7.92	0	0
21.7.92	0	0
4.8.92	0	0
17.8.92	0	0
1.9.92	0	0
10.9.92	0	0
15.9.92	0	0
5.10.92	0	0
13.10.92	0	0
3.11.92	0	0
24.11.92	0	0
8.12.92	13	0
22.12.92	0	0
6.1.93	0	0
18.1.93	0	0
2.^.93	0	0
16.2.93	0	0
2.3.93	0	0
15.3.93	0	0
29.3.93	0	0
15.4.93	0	0
30.4.93	0	0
11.5.93	0	0
25.5.93	0	0
8.6.93	0	0
22.6.93	0	0
6.7.93	0	0
20.7.93	0	0
2.8.93	0	0
18.8.93	0	0
31.8.93	0	0
13.9.93	0	0
29.9.93	0	0
13.10.93	17	34
27.10.93	0	0
10.11.93	0	34
24.11.93	0	0

Appendix 2. Little Mere Euglenophyta, Cryptophyta, Pyrrophyta and Cyanophyta

Date	Mic	Plank
7.12.93	0	0
12.1.94	0	0
26.1.94	0	0
8.3.94	0	0
21.3.94	0	0

Appendix 2. Little Mere Zooplankton

Date	Bos.lo	Cerio	Chyd	D.cuc	D.lon	D.mag	D.hya	D.pul	P.ped	Diaph
18.4.90	1	0	0	0	4.1	0	0	0	0	0
2.5.90	0	0	0	2.8	249.1	0	0	0	0	0
16.5.90	0	0	0	0	19.1	0	0	0	0	0
29.5.90	0	0	0	1.7	187.7	0	0	0	0	0
12.6.90	0	0	0	0	14.3	0	0	0	0	0
27.6.90	0	0	0	1.6	23.8	0	0	0	0	1.6
11.7.90	0	0	0	2.6	13.4	14.6	0	0	0	0
25.7.90	0	0	0	0	6.4	127.1	0	0	0	0
8.8.90	0	0	0		0	449.2	0	0	0	0
21.8.90	0	14.3	0	0	3.2	58.5	0	0	0	0
6.9.90	0	9.1	0	3.5	2.7	7.6	0	0	0	0.1
24.9.90	0	0.9	0	0.2	5.3	1	0	0	0	0
9.10.90	0	8	0	0.3	0	51.6	0	12.8	0	0
22.10.90	0	6.5	0	0.5	0	0.4	0	1.7	0	0
20.11.90	0	0.7	0	0.1	3.6	0	0	0.9	0	0
5.12.90	0	0	0	0	2.4	0	0	0.2	0	0
7.1.91	0	0	0	0.5	1.9	0.1	0	0.4	0	0
5.3.91	0.1	0	0	0	1.2	0	0	0	0	0
19.3.91	0.4	0	0	0	24.8	5.1	0	1.3	0	0
2.4.91	3.8	0	0	0	14.4	2.3	0	0	0	0
16.4.91	0.9	0	0	0	2.3	51.6	0	1.8	0	0
30.4.91	0.3	0	0	0	2.3	29.9	0	0	0	0
14.5.91	0	0	0	0	1.3	25.6	0	0	0	0
27.5.91	0	0	0	0	1.2	0.7	0	0	0	0
11.6.91	0	0	0	2.7	10.2	26.5	0	3.4	0	0
25.6.91	0	0	0	0.9	0	36.4	0	0	0	0
9.7.91	0	0	0	11	0.5	19.5	0	0	0	0.5
22.7.91	0	0	0	0	0	75.7	0	0	0	0
6.8.91	0	0.8	0	0.7	0	3.3	0	0	0	0.1
20.8.91	0	2.2	0	1.5	2.8	26.7	0	0	0	0
9.9.91	0	0.1	0	1.4	0.7	0.5	0	0.8	0	0
23.9.91	0	0.4	0	0.2	0.9	1	0	1	0	0
9.10.91	21.5	0.5	0	1.4	0.5	23.9	0	0	0	27.2
22.10.91	0	0	0	0	0.8	21.8	0	0	0	0
5.11.91	1.5	0	0	0.7	0.1	3.1	0	0	0	0
19.11.91	1	0.2	0	0.9	0.2	0.5	0	0	0	0
3.12.91	0.3	0	0	0.1	0.9	3.3	0	0	0	0
18.12.91	0	0	0.3	0	0.2	0.1	0	0.2	0	0
9.1.92	0.1	0	0	0.2	0.4	0.6	0	0.1	0	0
21.1.92	0.1	0	0	0	0.1	0	0	0	0	0
3.2.92	0.1	0	0	0.3	0.1	0	0	0	0	0
18.2.92	1.5	0	0	0.5	0	0.1	0	0	0	0
3.3.92	0	0	0	0.6	0.1	0.1	0	0	0	0
18.3.92	1.1	0.1	0	17.1	2	0.1	0	0.1	0	0
1.4.92	1	0	0	10.9	2.5	0.5	0	0	0	0
14.4.92	5	0	1	20	13	5	0	34	0	0
28.4.92	2	0	0	1	1	4	3	0	0	0
12.5.92	32	5	0	0	0	2	0	0	0	0
26.5.92	8	0	0	0	0	0	0	0	0	3
9.6.92	17	0	0	0	2	0	0	0	0	2
23.6.92	16	0	0	0	0	18	0	0	0	0
7.7.92	39	0	0	7	0	0	0	0	0	0

Appendix 2. Little Mere Zooplankton

Date	Bos.lo	Cerio	Chyd	D.cuc	D.lon	D.mag	D.hya	D.pul	P.ped	Diaph
21.7.92	6	0	0	8	0	0	0	0	0	0
4.8.92	0	0	0	10	0	0	0	0	0	0
17.8.92	0	0	0	0	0	0	2	0	0	0
1.9.92	2	2	0	11	4	1	11	4	0	0
10.9.92	4	0	1	20	13	6	0	34	0	0
15.9.92	0	0	0	0	0	3	20	0	0	1
5.10.92	5	8	0	0	2	60	0	0	0	0
13.10.92	2	6	0	22	9	52	40	0	0	0
3.11.92	1	3	0	5	7	6	7	3	0	0
24.11.92	2	5	0	14	1	3	8	0	0	0
8.12.92	2	2	0	25	0	5	10	0	0	0
22.12.92	0	0	0	0	0	0	0	0	0	0
6.1.93	0	0	0	0	0	0	0	0	0	0
18.1.93	10	0	0	2	0	0	10	2	0	0
2.2.93	3	0	0	4	0	0	0	1	0	0
16.2.93	15	0	0	4	0	1	1	1	0	0
2.3.93	6	0	0	0	0	0	0	0	0	0
15.3.93	0	6	0	8	0	3	1	0	0	0
29.3.93	42	0	0	0	5	0	0	0	0	0
15.4.93	34	0	2	0	0	0	20	0	0	0
30.4.93	0	0	0	0	0	0	0	0	0	0
11.5.93	5	0	0	0	0	0	19	0	0	0
25.5.93	1	0	0	0	0	0	75	0	0	0
8.6.93	0	0	0	0	0	0	0	0	0	0
22.6.93	2	0	0	0	0	0	6	0	0	0
6.7.93	3	0	0	0	0	0	22	0	1	0
20.7.93	0	1	0	0	0	0	6	0	0	0
2.8.93	2	2	0	0	0	0	175	3	10	2
18.8.93	4	112	36	0	0	0	2	0	0	0
31.8.93	0	99	157	0	0	0	6	10	3	1
13.9.93	0	20	20	0	0	0	22	0	0	0
29.9.93	20	0	5	0	0	0	0	0	0	1
13.10.93	0	0	0	0	0	0	0	0	0	0
27.10.93	0	8	0	0	0	0	70	0	0	0
10.11.93	0	0	0	0	0	0	133	0	0	0
24.11.93	0	0	0	0	0	0	0	0	0	0
7.12.93	0	0	0	0	0	0	39	0	0	0
12.1.94	1	0	0	0	0	0	0	0	0	0
26.1.94	0	0	0	0	0	0	0	0	0	0
8.3.94	0	0	0	0	0	0	0	0	0	0
21.3.94	0	0	0	0	0	0	0	0	0	0

Appendix 2. Little Mere Zooplankton

Date	E.Lam	S.muc	S.cry	Sim	Di.gra	Cyclo	Nau	Rot
18.4.90	0	0	0	0	0	107.5	0	0
2.5.90	0	0	0	0	5.5	362.5	0	0
16.5.90	0	0	0	0	0.3	28.1	0	0
29.5.90	0	0	0	0	3.4	0	0	0
12.6.90	0	0	0	0	3.8	8.1	0	0
27.6.90	0	0	0	0	1.6	187	0	0
11.7.90	0	0	0	0	0.9	1.6	0	0
25.7.90	0	0	0	0	0	7.6	0	0
8.8.90	0	0	0	0	0	0	0	0
21.8.90	0	0	0	0	0.5	1.4	0	0
6.9.90	0	0	0	0	0.9	2.7	0	0
24.9.90	0	0	0	0	1.5	0.8	0	0
9.10.90	0	0	0	0	1.7	1	0	0
22.10.90	0	0	0	0	2.6	0.7	0	0
20.11.90	0	0	0	0	1	3.2	0	0
5.12.90	0	0	0	0	1.3	1.1	0	0
7.1.91	0	0	0	0	3.9	0.7	0	0
5.3.91	0	0	0	0	1.8	0.7	0	0
19.3.91	0	0	0	0	1.5	23.8	0	0
2.4.91	0	0	0	0	7	2.8	0	0
16.4.91	0	0	0	0	1.8	1.4	0	0
30.4.91	0	0	0	0	1.1	1.6	0	0
14.5.91	0	0	0	0	1.1	1.1	0	0
27.5.91	0	0	0	0	1.2	1.1	0	0
11.6.91	0	0	0	0	2.1	99.8	0	0
25.6.91	0	0	0	0	1.8	0.9	0	0
9.7.91	0	0	0	0	1	4.7	0	0
22.7.91	0	0	0	0	1.8	0.6	0	0
6.8.91	0	0	0	0	0.4	8.3	0	0
20.8.91	0	0	0	0	0	1.5	0	0
9.9.91	0	0	0	0	0.5	0	0	0
23.9.91	0	0	0	0	0.5	0.1	0	0
9.10.91	0	0	0	0	15.8	0.3	0	0
22.10.91	0	0	0	0	0.6	0.2	0	0
5.11.91	0	0	0	0	1.3	0.1	0	0
19.11.91	0	0	0	0	0.8	0	0	0
3.12.91	0	0	0	0	1.2	0.3	0	0
18.12.91	0	0	0	0	0.4	0	0	0
9.1.92	0	0	0	0	0.7	0	0	0
21.1.92	0	0	0	0	0.3	0.1	0	0
3.2.92	0	0	0	0	0.1	0	0	0
18.2.92	0	0	0	0	2	0	0	0
3.3.92	0	0	0	0	2.3	0.9	0	0
18.3.92	0	0	0	0	11.9	9.9	0	0
1.4.92	0	0	0	0	2	0.2	0	65
14.4.92	0	0	0	0	59	131	40	51
28.4.92	0	0	0	0	69	1	5	29
12.5.92	0	0	0	0	5	43	63	20
26.5.92	0	0	0	0	3	20	6	24
9.6.92	0	0	0	0	2	1	5	178
23.6.92	0	0	0	0	13	17	2	0
7.7.92	0	0	0	0	8	7	25	155

Appendix 2. Little Mere Zooplankton

Date	E.Lam	S.muc	S.cry	Sim	Di.gra	Cyclo	Nau	Rot
21.7.92	0	0	0	0	20	30	20	88
4.8.92	0	0	0	0	1	3	2	27
17.8.92	0	0	0	0	0	0		253
1.9.92	0	0	0	0	10	14	4	217
10.9.92	0	0	0	0	59	131	40	51
15.9.92	0	0	0	0	15	1	7	91
5.10.92	0	0	0	0	45	15	14	118
13.10.92	0	0	0	0	6	14	28	92
3.11.92	0	0	0	0	1	1	3	12
24.11.92	0	0	0	0	25	0	14	128
8.12.92	0	0	0	0	42	32	20	81
22.12.92	0	0	0	0	0	0		0
6.1.93	0	0	0	0	0	0		0
18.1.93	0	0	0	0	42	3	33	90
2.2.93	0	0	0	0	30	3	23	165
16.2.93	0	0	0	0	28	2	80	133
2.3.93	0	0	0	0	54	1	80	154
15.3.93	0	0	0	0	36	20	25	118
29.3.93	0	0	0	0	96	25	110	760
15.4.93	0	0	0	0	29	52	63	1240
30.4.93	0	0	0	0	0	0		0
11.5.93	0	0	0	0	6	27	2	0
25.5.93	0	0	0	0	13	17	2	0
8.6.93	0	0	0	0	0	0		0
22.6.93	0	0	0	0	0	3	5	0
6.7.93	1	0	0	0	6	99		2
20.7.93	0	0	0	0	0	20		2
2.8.93	3	0	0	0	0	63	175	10
18.8.93	31	5	4	0	2	179	29	123
31.8.93	68	4	0	4	82	139	125	100
13.9.93	9	0	0	19	13	52	1	0
29.9.93	6	2	0	5	0	8		0
13.10.93	0	0	0	0	0	0		10
27.10.93	3	0	0	0	24	27	41	325
10.11.93	1	0	0	0	13	68	51	93
24.11.93	0	0	0	0	0	0		
7.12.93	0	0	0	0	19	94	48	15
12.1.94	0	0	0	0	4	4	40	62
26.1.94	0	0	0	0	7	5	42	40
8.3.94	0	0	0	0	10	20	53	21
21.3.94	0	0	0	0	8	30	97	66

Appendix 2. Rostherne Mere Chlorophyta

Date	Act	Anki	Anky	Chlam	Chlor	Clos	Coela	Elak	Mic	Oocy	Pan	Ped
10.1.90	0	18	0	0	0	0	0	0	0	0	0	0
7.2.90	73	0	0	0	2153	0	0	0	0	0	0	0
21.2.90	0	5	0	0	6	5	0	0	0	0	0	0
7.3.90	0	7	4	0	26	0	0	0	0	0	0	0
21.3.90	0	18	36	0	0	0	0	0	0	0	0	0
4.4.90	0	91	0	0	0	0	0	0	0	0	0	0
18.4.90	0	61	0	0	0	0	0	0	0	0	0	0
2.5.90	0	63	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
29.5.90	0	633	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
27.6.90	0	84	0	0	0	4	0	0	0	0	0	0
25.7.90	0	36	0	0	0	0	0	0	0	0	0	0
8.8.90	0	55	0	0	0	0	0	0	0	0	0	0
21.8.90	0	122	0	0	0	0	0	0	0	0	0	0
6.9.90	0	36	0	0	0	0	0	0	0	0	0	7
24.9.90	0	73	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
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	0	0	0	0	0	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	7	0	0	0	0	0	0	0	0	0	0
5.3.91	0	13	0	0	0	0	0	0	0	0	0	0
19.3.91	0	27	0	0	0	0	0	0	0	0	0	3
2.4.91	0	9	0	119	0	0	0	0	0	0	0	0
16.4.91	0	46	0	265	0	0	0	0	0	0	0	0
14.5.91	0	202	0	0	0	0	0	0	0	0	0	0
27.5.91	0	0	16	15	0	0	0	58	0	0	0	0
11.6.91	0	997	0	917	0	0	0	0	0	0	0	0
25.6.91	0	50	0	0	0	0	0	0	0	0	0	0
9.7.91	0	0	30	0	0	0	0	6022	0	0	0	0
22.7.91	0	152	402	0	0	0	0	0	0	61	0	0
6.8.91	0	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
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	7	0	0	0	0	0	0	0	0	0	0
3.2.92	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
3.3.92	0	22	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

Appendix 2. Rostherne Mere Chlorophyta

Date	Act	Anki	Anky	Chlam	Chlor	Clos	Coela	Elak	Mic	Oocy	Pan	Ped
1.4.92	0	15	0	60	0	0	0	0	13	0	15	0
14.4.92	0	13	0	67	0	0	0	0	0	0	0	0
28.4.92	0	0	0	0	13	0	0	0	0	0	0	0
12.5.92	0	0	0	61	61	170	0	0	0	0	0	0
26.5.92	0	134	0	1786	13	0	0	13	0	27	0	0
9.6.92	0	496	0	53	0	0	0	0	0	0	0	0
23.6.92	0	44	0	156	0	0	0	0	0	0	0	0
7.7.92	0	22	0	0	0	0		0	0	0	0	0
21.7.92	0	50	0	765	0	0	0	0	151	50	150	0
4.8.92	0	0	0	637	0	0	0	0	0	35	0	35
17.8.92	0	67	0	134	0	0	67	0	134	0	0	0
1.9.92	0	0	0	80	0	80	0	0	0	0	0	0
10.9.92	0	84	0	0	0	0	0	0	0	0	0	0
15.9.92	0	80	0	80	0	0	0	0	40	27	0	0
5.10.92	0	15	0	0	0	0	0	0	0	0	0	0
13.10.92	0	15	0	0	0	0	0	0	0	0	0	0
3.11.92	0	0	0	0	0	17	0	0	0	0	0	0
24.11.92	0	0	0	0	0	0	0	0	0	0	0	0
8.12.92	0	13	0	27	0	0	0	0	0	0	0	0
22.12.92	0	0	0	0	0	0	0	0	0	0	0	0
6.1.93	0	0	0	0	0	0	0	0	0	0	0	0
18.1.93	0	0	0	13	0	0	0	0	0	0	0	0
2.2.93	0	0	0	13	0	0	0	0	0	0	0	0
16.2.93	0	0	0	0	0	0	0	0	0	0	0	0
2.3.93	0	0	0	0	0	0	0	0	0	0	0	0
15.3.93	0	13	0	134	0	0	0	0	0	0	0	0
29.3.93	0	67	0	67	0	0	0	0	0	0	0	0
15.4.93	0	402	0	1207	0	0	0	0	0	0	0	0
30.4.93	0	1541	0	1072	0	0	0	0	0	0	0	67
11.5.93	0	1921	0	492	0	0	0	0	0	0	0	0
25.5.93	0	0	0	523	0	0	0	0	0	0	0	0
8.6.93	0	34	0	302	0	0	0	0	0	168	0	0
22.6.93	0	0	0	268	0	0	0	0	0	0	0	34
6.7.93	0	0	0	628	0	0	0	0	0	0	0	223
20.7.93	0	0	0	1474	0	0	0	0	0	45	0	0
2.8.93	0	17	0	33	0	0	0	0	0	134	0	0
18.8.93	0	134	0	0	0	0	0	0	0	0	0	34
31.8.93	0	67	0	0	0	0	0	0	0	0	0	34
13.9.93	0	0	0	0	0	0	0	0	0	0	0	0
29.9.93	0	0	0	0	0	0	0	0	0	0	0	0
13.10.93	0	0	0	22	0	0	0	0	0	0	0	0
27.10.93	0	0	0	0	0	0	0	0	0	0	0	0
10.11.93	0	0	0	0	0	0	0	0	0	0	0	0
24.11.93	0	0	0	0	0	0	0	0	0	0	0	0
7.12.93	0	0	0	0	0	0	0	0	0	0	0	0
12.1.94	0	0	0	0	0	0	0	0	0	0	0	0
26.1.94	0	27	0	54	0	27	0	0	0	0	0	0
8.3.94	0	1442	0	2574	0	0	0	0	0	0	0	0
21.3.94	0	1984	0	1662	0	0	0	0	0	0	0	0

Appendix 2. Rostherne Mere Chlorophyta

Date	Pla	Scen	Staur	Tet	Schr
10.1.90	0	2	0	6	0
7.2.90	0	0	0	0	0
21.2.90	0	0	0	0	0
7.3.90	0	7	0	0	0
21.3.90	0	36	0	0	0
4.4.90	0	73	0	0	0
18.4.90	0	170	0	0	0
2.5.90	0	0	0	0	0
16.5.90	0	0	0	0	0
29.5.90	0	0	0	0	0
12.6.90	0	0	0	0	0
27.6.90	0	15	0	0	0
25.7.90	0	146	142	0	0
8.8.90	0	49	164	0	0
21.8.90	0	29	161	0	0
6.9.90	0	49	29	0	0
24.9.90	0	0	0	0	0
9.10.90	0	58	0	4	0
22.10.90	0	0	0	0	0
6.11.90	0	0	0	0	0
20.11.90	0	0	0	0	0
5.12.90	0	29	0	0	0
28.12.90	0	0	0	0	0
7.1.91	0	0	0	0	0
5.3.91	0	27	0	0	0
19.3.91	0	0	0	0	0
2.4.91	0	36	0	0	0
16.4.91	0	0	0	0	0
14.5.91	0	0	0	0	0
27.5.91	0	0	0	0	0
11.6.91	0	201	0	0	0
25.6.91	0	0	0	0	0
9.7.91	0	0	76	15	0
22.7.91	0	0	0	0	0
6.8.91	0	0	134	0	0
19.8.91	0	0	268	0	0
9.9.91	0	0	0	0	0
23.9.91	0	0	0	0	0
9.10.91	0	0	0	0	0
22.10.91	0	0	0	0	0
5.11.91	0	0	0	0	0
19.11.91	0	0	0	0	0
3.12.91	0	0	0	0	0
18.12.91	0	89	0	0	0
9.1.92	0	0	0	0	0
21.1.92	0	30	0	0	0
3.2.92	0	0	0	0	0
18.2.92	0	0	0	0	0
3.3.92	0	0	0	0	0
18.3.92	0	0	0	0	0

Appendix 2. Rostherne Mere Chlorophyta

Date	Pla	Scen	Staur	Tet	Schr
1.4.92	13	0	0	0	0
14.4.92	0	0	0	0	0
28.4.92	0	0	0	0	0
12.5.92	13	0	0	0	0
26.5.92	13	0	0	0	13
9.6.92	0	13	0	0	13
23.6.92	0	0	0	246	0
7.7.92	0	67	938	313	0
21.7.92	251	201	803	0	0
4.8.92	0	335	168	0	0
17.8.92	0	470	67	0	0
1.9.92	0	282	40	0	0
10.9.92	0	0	0	0	0
15.9.92	0	40	121	0	0
5.10.92	0	0	0	0	0
13.10.92	0	0	0	0	0
3.11.92	0	0	0	0	0
24.11.92	0	0	0	0	0
8.12.92	0	0	0	0	0
22.12.92	0	0	0	0	0
6.1.93	0	0	0	0	0
18.1.93	0	0	0	0	0
2.2.93	0	0	0	0	0
16.2.93	0	0	0	0	0
2.3.93	0	0	0	0	0
15.3.93	0	0	0	0	0
29.3.93	0	67	0	0	0
15.4.93	0	101	0	0	0
30.4.93	0	268	0	0	0
11.5.93	0	179	0	0	0
25.5.93	0	0	0	0	40
8.6.93	0	134	0	0	168
22.6.93	0	0	0	0	67
6.7.93	0	0	0	0	45
20.7.93	17	0	0	0	447
2.8.93	0	0	0	0	85
18.8.93	0	134	0	0	0
31.8.93	0	0	0	0	22
13.9.93	0	0	0	0	0
29.9.93	0	0	0	0	22
13.10.93	0	0	0	0	0
27.10.93	0	0	0	0	0
10.11.93	0	0	0	0	0
24.11.93	0	0	0	0	0
7.12.93	0	0	0	0	0
12.1.94	0	0	0	0	0
26.1.94	0	54	0	0	0
8.3.94	0	0	0	0	0
21.3.94	0	0	0	0	0

Appendix 2. Rostherne Mere Bacillariophyceae

Date	Amp	Ast	Au.gr	Cen	Frag	Gom	Nav	Pin	S.han	S.rot	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	46	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

Appendix 2. Rostherne Mere Bacillariophyceae

Date	Amp	Ast	Au.gr	Cen	Frag	Gom	Nav	Pin	S.han	S.rot	Sy.ac	Sy.ul
1.4.92	0	0	0	0	0	0	0	0	74	0	30	0
14.4.92	0	13	0	13	0	0	0	0	0	0	0	13
28.4.92	0	1334	13	54	0	0	0	0	54	0	0	0
12.5.92	0	0	0	12	0	0	0	0	0	0	0	0
26.5.92	0	27	0	0	107	54	0	0	13	0	0	0
9.6.92	0	0	0	0	0	0	0	0	0	0	0	0
23.6.92	0	0	2950	0	0	0	0	0	0	0	0	44
7.7.92	0	0	1259	0	0	0	0	0	0	0	0	829
21.7.92	0	0	5580	0	0	0	0	0	0	0	0	302
4.8.92	0	0	603	0	0	0	0	0	0	0	0	370
17.8.92	0	0	3954	0	268	0	67	0	0	0	0	0
1.9.92	0	0	402	0	0	0	80	0	0	0	0	0
10.9.92	0	0	503	0	503	0	0	0	0	0	0	0
15.9.92	0	0	1245	0	121	0	40	0	0	0	0	0
5.10.92	0	0	43	0	27	0	0	0	0	0	0	0
13.10.92	0	0	0	0	0	0	0	0	0	0	0	0
3.11.92	0	0	4060	0	0	0	0	0	50	0	0	0
24.11.92	0	0	0	0	938	0	0	0	50	0	0	0
8.12.92	0	0	0	0	884	0	0	0	67	0	0	0
22.12.92	0	0	0	0	0	0	13	0	40	0	0	0
6.1.93	0	0	0	0	0	0	0	0	54	0	0	0
18.1.93	0	0	0	0	0	0	0	0	362	0	0	0
2.2.93	0	0	0	0	0	0	13	0	482	0	0	0
16.2.93	0	0	0	0	0	0	0	0	121	0	0	0
2.3.93	0	0	154	0	0	0	0	0	89	0	0	0
15.3.93	0	0	0	0	0	0	0	0	0	0	0	0
29.3.93	0	0	0	0	0	0	0	0	0	0	0	0
15.4.93	0	0	301	0	0	0	0	0	0	0	0	0
30.4.93	0	0	0	0	409	0	0	0	0	0	0	0
11.5.93	0	0	0	0	0	0	0	0	0	0	0	0
25.5.93	0	0	0	0	0	0	60	0	0	0	0	0
8.6.93	0	0	0	0	0	0	0	0	0	0	0	0
22.6.93	0	0	0	0	0	0	0	0	0	0	0	0
6.7.93	0	45	0	0	0	0	0	0	0	0	0	0
20.7.93	0	0	0	0	0	0	0	0	0	0	0	0
2.8.93	0	117	238	0	0	0	0	0	0	0	0	0
18.8.93	0	0	12566	0	1307	0	0	0	34	0	0	0
31.8.93	0	0	1575	0	1676	0	0	0	0	0	0	0
13.9.93	0	0	1208	0	44	0	0	0	0	0	0	0
29.9.93	0	0	581	0	804	0	0	0	0	0	0	0
13.10.93	0	536	302	0	5127	0	0	0	0	0	0	34
27.10.93	0	514	495	0	1474	0	0	0	0	0	0	22
10.11.93	0	89	0	0	0	0	0	0	0	0	0	0
24.11.93	0	178	0	0	0	0	0	0	0	0	0	0
7.12.93	0	40	0	0	241	0	60	0	0	0	0	20
12.1.94	0	0	0	0	0	0	0	0	0	0	0	0
26.1.94	0	0	5229	0	0	0	0	0	0	0	0	0
8.3.94	0	241	6989	0	0	0	80	0	40	0	0	0
21.3.94	0	1019	2835	0	0	0	0	0	0	0	0	0

Appendix 2. Euglenophyta, Cryptophyta, Pyrrophyta and Cyanophyta

Date	Eugl	Phac	Trac	Crypt	Rhod	µ Flag	Cer	Per	Ana	Aphan	Chroo
10.1.90	0	0	0	3	2	3	3	0	0	0	15
7.2.90	0	0	0	7	0	164	0	0	0	0	0
21.2.90	0	0	0	2	27	534	0	0	0	0	0
7.3.90	0	0	0	35	84	190	0	2	0	0	0
21.3.90	0	0	0	173	1989	109	0	0	36	0	0
4.4.90	18	0	0	41	255	566	0	55	0	0	0
18.4.90	0	0	0	36	97	426	0	12	0	0	0
2.5.90	0	0	0	44	355	219	3	0	3	0	0
16.5.90	0	0	0	18	602	109	4	0	131	201	0
29.5.90	0	0	0	97	511	0	29	0	3601	358	0
12.6.90	0	0	0	15	423	650	0	0	467	0	0
27.6.90	0	0	0	62	405	44	73	0	33	0	0
25.7.90	0	0	0	124	103	24	15	0	190	0	0
8.8.90	0	0	0	27	73	91	18	0	5	0	0
21.8.90	0	0	0	7	584	97	29	0	0	0	0
6.9.90	0	0	0	0	365	73	95	0	0	0	0
24.9.90	0	0	0	0	97	195	95	0	0	0	0
9.10.90	0	0	0	36	18	109	55	0	0	0	0
22.10.90	0	7	0	0	36	139	7	0	0	0	0
6.11.90	0	0	0	7	0	0	0	0	0	0	0
20.11.90	0	0	0	0	40	201	0	0	0	0	40
5.12.90	0	0	0	0	0	73	0	0	0	0	0
28.12.90	0	0	0	51	18	270	0	7	0	0	0
7.1.91	0	0	0	0	7	74	0	0	0	0	0
5.3.91	0	0	0	7	409	174	0	0	0	0	0
19.3.91	0	0	0	100	1925	201	0	9	0	0	0
2.4.91	0	0	0	82	73	392	0	9	0	0	0
16.4.91	0	377	0	140	657	109	0	0	0	0	0
14.5.91	0	0	0	0	88	139	0	0	7	0	0
27.5.91	0	0	0	48	772	434	0	0	193	0	0
11.6.91	0	0	0	50	302	302	0	0	1307	0	0
25.6.91	0	0	0	603	4763	547	0	0	1340	0	0
9.7.91	0	0	0	1277	776	274	30	30	0	0	0
22.7.91	0	0	0	179	625	134	45	0	89	89	0
6.8.91	0	0	0	45	45	0	45	0	938	849	0
19.8.91	0	0	0	0	0	0	45	0	0	223	0
9.9.91	0	0	0	0	0	0	142	0	0	0	0
23.9.91	0	0	27	0	281	27	74	0	0	0	0
9.10.91	0	0	0	0	13	20	10	0	0	0	0
22.10.91	0	0	0	13	13	0	4	0	0	0	0
5.11.91	0	0	0	0	0	27	3	0	0	0	0
19.11.91	0	0	0	0	0	89	0	0	0	0	0
3.12.91	0	0	0	0	0	22	0	0	0	0	0
18.12.91	0	0	0	0	0	67	0	0	0	0	0
9.1.92	0	0	0	0	0	22	0	0	0	0	0
21.1.92	0	0	0	0	0	30	0	0	0	0	0
3.2.92	0	30	0	0	0	22	0	0	0	0	0
18.2.92	0	0	0	22	52	60	0	4	0	0	0
3.3.92	0	0	0	30	149	97	0	15	0	0	0
18.3.92	0	0	0	89	670	149	0	30	0	0	0

Appendix 2. Euglenophyta, Cryptophyta, Pyrrophyta and Cyanophyta

Date	Eugl	Phac	Trac	Crypt	Rhod	µ Flag	Cer	Per	Ana	Aphan	Chroo
1.4.92	0	0	0	74	1251	104	0	13	0	0	0
14.4.92	0	0	0	248	189	40	0	40	0	0	0
28.4.92	0	0	0	550	94	0	0	0	0	0	0
12.5.92	0	0	0	12	827	61	0	0	0	0	0
26.5.92	0	0	0	40	442	0	0	0	13	158	0
9.6.92	0	0	0	0	536	40	0	0	13	0	0
23.6.92	0	156	22	112	1251	983	67	0	0	0	0
7.7.92	0	0	22	1251	380	89	335	0	0	0	0
21.7.92	0	0	0	201	2916	855	503	0	0	0	0
4.8.92	0	0	0	700	302	168	335	0	0	0	0
17.8.92	0	0	201	0	134	9048	67	67	0	0	0
1.9.92	0	80	80	241	1890	2695	161	0	0	0	0
10.9.92	0	0	0	50	17	771	0	17	0	0	0
15.9.92	0	0	80	402	2011	3459	322	40	0	0	0
5.10.92	0	0	0	134	0	43	0	0	0	0	0
13.10.92	0	0	0	80	0	27	0	0	0	0	0
3.11.92	0	0	0	218	0	17	0	0	0	0	0
24.11.92	0	0	17	215	0	101	0	0	0	0	0
8.12.92	0	0	13	0	0	54	0	0	0	0	0
22.12.92	0	0	0	13	13	94	0	0	0	0	0
6.1.93	0	0	0	0	0	0	0	0	0	0	0
18.1.93	0	0	0	27	0	107	0	0	0	0	0
2.2.93	0	0	0	0	0	67	0	0	0	0	0
16.2.93	0	0	0	27	54	0	0	40	0	0	0
2.3.93	0	0	0	0	67	474	0	89	0	0	0
15.3.93	0	0	0	107	898	281	0	13	0	0	0
29.3.93	0	0	0	67	704	0	0	0	0	0	0
15.4.93	0	0	0	251	2865	1609	0	0	0	0	0
30.4.93	0	0	0	603	8375	24321	0	0	0	0	0
11.5.93	0	0	89	492	4468	3232	0	0	0	0	0
25.5.93	0	0	0	362	603	261	0	0	0	0	0
8.6.93	0	0	34	302	402	1039	0	0	0	0	0
22.6.93	0	0	0	503	1206	268	134	0	67	0	0
6.7.93	447	0	0	402	45	223	0	268	357	0	0
20.7.93	0	0	0	1519	1519	1474	0	0	760	0	0
2.8.93	0	0	0	184	84	453	0	17	565	0	0
18.8.93	0	0	168	101	307	603	0	804	2379	335	0
31.8.93	0	0	34	670	335	3116	101	670	2245	0	0
13.9.93	0	0	22	201	67	648	44	156	89	22	0
29.9.93	0	0	0	380	246	2390	134	114	0	0	0
13.10.93	0	0	34	268	101	302	0	201	0	0	0
27.10.93	22	0	22	313	626	827	0	22	0	0	0
10.11.93	0	0	0	44	178	245	0	22	0	0	0
24.11.93	0	0	0	67	22	5741	0	0	0	0	0
7.12.93	0	0	0	60	60	221	0	0	0	0	0
12.1.94	0	0	0	0	0	0	0	0	0	0	0
26.1.94	0	0	134	295	188	27	0	0	0	0	0
8.3.94	0	40	402	120	3017	2293	0	40	0	0	0
21.3.94	0	0	349	215	2413	1475	0	27	0	0	0

Appendix 2. Euglenophyta, Cryptophyta, Pyrrophyta and Cyanophyta

Date	Coelo	Mic	Plank
10.1.90	15	2	2
7.2.90	0	0	35
21.2.90	0	0	33
7.3.90	4	4	58
21.3.90	0	9	122
4.4.90	0	36	64
18.4.90	0	12	36
2.5.90	0	26	10
16.5.90	0	66	0
29.5.90	0	51	0
12.6.90	0	22	15
27.6.90	0	29	0
25.7.90	6	201	6
8.8.90	0	839	0
21.8.90	0	1168	0
6.9.90	0	664	0
24.9.90	0	263	7
9.10.90	0	693	0
22.10.90	0	226	4
6.11.90	0	569	0
20.11.90	0	145	0
5.12.90	0	11	0
28.12.90	0	36	4
7.1.91	0	0	0
5.3.91	0	0	0
19.3.91	0	0	0
2.4.91	0	0	0
16.4.91	0	0	0
14.5.91	0	7	0
27.5.91	0	0	0
11.6.91	0	0	0
25.6.91	0	0	0
9.7.91	0	3	0
22.7.91	0	134	0
6.8.91	0	313	0
19.8.91	45	938	0
9.9.91	17	184	0
23.9.91	13	174	13
9.10.91	3	77	0
22.10.91	2	67	0
5.11.91	0	114	0
19.11.91	0	39	0
3.12.91	0	7	0
18.12.91	0	4	0
9.1.92	0	0	0
21.1.92	0	0	0
3.2.92	0	0	0
18.2.92	0	0	0
3.3.92	0	0	0
18.3.92	0	0	0

Appendix 2. Euglenophyta, Cryptophyta, Pyrrophyta and Cyanophyta

Date	Coelo	Mic	Plank
1.4.92	0	0	0
14.4.92	0	0	0
28.4.92	0	0	0
12.5.92	0	0	0
26.5.92	0	0	0
9.6.92	0	0	0
23.6.92	0	0	0
7.7.92	0	0	0
21.7.92	0	100	0
4.8.92	0	35	0
17.8.92	0	67	0
1.9.92	0	201	0
10.9.92	0	0	0
15.9.92	0	563	0
5.10.92	0	0	0
13.10.92	0	0	0
3.11.92	0	17	0
24.11.92	0	0	0
8.12.92	0	0	0
22.12.92	0	0	0
6.1.93	0	0	0
18.1.93	0	0	0
2.2.93	0	0	0
16.2.93	0	0	0
2.3.93	0	0	0
15.3.93	0	0	0
29.3.93	0	0	0
15.4.93	0	0	0
30.4.93	0	0	0
11.5.93	0	0	0
25.5.93	0	0	0
8.6.93	0	0	0
22.6.93	0	0	0
6.7.93	0	0	0
20.7.93	0	0	0
2.8.93	151	67	0
18.8.93	201	0	0
31.8.93	67	0	0
13.9.93	22	0	0
29.9.93	0	0	0
13.10.93	22	0	0
27.10.93	34	0	0
10.11.93	0	0	0
24.11.93	0	0	0
7.12.93	0	0	0
12.1.94	0	0	0
26.1.94	0	0	0
8.3.94	0	0	0
21.3.94	0	0	0

Appendix 2. Rostherne Mere Zooplankton

Date	D. cuc	D. lon	D. pul	Diaph	Bos.lo	Chy. sp	Lepto
7.3.90	0	0	0	0	0	0	0
21.3.90	0	0	0	0	0	0	0
18.4.90	0	0	0	0	0	0	0
27.4.90	0	0	0	0	0	0	0
2.5.90	0	0.1	0	0	0.1	0	0
16.5.90	0	9.2	0	0	1.6	0	0
29.5.90	0	2.8	0	0	0.8	0	0.6
12.6.90	0	22.5	0	1.7	0.4	0	0.6
27.6.90	0.4	18.9	0	1.5	0	0	1
11.7.90	0	9	0	12.8	0	0	0.5
25.7.90	1.7	5.4	0	6.2	0	0	0.1
8.8.90	8.2	9.8	0	5	0	0	0.1
21.8.90	9.4	14.5	0	6.2	0	0	0.1
6.9.90	0	11.9	0	6.6	0	0	0.2
24.9.90	4.1	3.4	0	0.7	0	0	0
9.10.90	0.8	1.5	0.2	0.6	0	0	0.1
22.10.90	0.4	0.5	0	0.4	0	0	0.04
6.11.90	2	0.8	0	0.2	0	0	0
20.11.90	0.1	0.5	0.1	0	0	0	0
5.12.90	0.4	1.1	0	0	0	0	0
19.3.91	0.2	0.6	0	0	0	0	0
2.4.91	0.04	2	0	0	0	0	0
16.4.91	0.4	7.1	0.2	0	0	0	0
30.4.91	0	12.6	3.7	0	0	0	0
14.5.91	0	0	3.6	0	0	0	0
27.5.91	0	0	1	0	0	0	0
11.6.91	0	0	4.9	0	0	0	0.1
25.6.91	0	0	3.1	0.03	0	0	0.2
9.7.91	0	0.03	0.1	0	0.03	0	0
22.7.91	0	0.6	0.2	0	0.3	0	0.2
6.8.91	0	0.5	0.2	0.3	0.1	0	0.1
19.8.91	0.1	4.8	0	0.02	0.2	0	0.02
9.9.91	0	18.1	0	0	0	0	0
23.9.91	5.8	2.7	0	0	0.4	0	0
9.10.91	3.1	7.1	0	0	0	0	0
22.10.91	0.2	2.7	0	0	0	0	0
5.11.91	0.3	0	0	0	0	0	0
19.11.91	1.5	0.6	0	0	0	0	0
3.12.91	1.3	1.6	0	0	0	0	0
18.12.91	0.3	1.3	0	0	0	0	0
9.1.92	1	2	0.1	0	0	0	0
21.1.92	21.6	18.2	0.02	0	0	0	0
3.2.92	13.1	8.3	0	0	0	0	0
18.2.92	2.5	1.9	0	0	0	0.1	0
3.3.92	1.8	5	0	0	0.04	0.1	0
18.3.92	1	9	0	0	0	1.4	0
1.4.92	5.3	1.9	0.1	0	0	0.1	0
14.4.92	0.3	1.2	0	1	0	0.3	0
28.4.92	0	0.7	0	0	0	0.03	0
12.5.92	0	0.1	0	0	0.01	0.01	0
26.5.92	0.02	0.3	0	0	0	0	0
9.6.92	0	1	9	0	0.1	0	0

Appendix 2. Rostherne Mere Zooplankton

Date	D. cuc	D. lon	D. pul	Diaph	Bos.lo	Chy. sp	Lepto
23.6.92	0	0.3	0	0	0.01	0	0
7.7.92	0	0.7	0	0	0.1	0.01	0
21.7.92	0	4.4	1	0	0	0	0
4.8.92	4	2	0	0	0	0	0
17.8.92	53	38	0	0	0	0	2
1.9.92	0	3	2	0	2	1	0
15.9.92	6	4	0	0	0	0	0
5.10.92	1	5	0	0	0	0	0
13.10.92	1	1	0	0	0	1	0
3.11.92	1.2	0.5	0	0	0	0	0
24.11.92	0.5	0	0	0	0	0	0
8.12.92	1	1	1	0	5	5	0
22.12.92	0	0	0	0	0	0	0
6.1.93	0	1	0	0	0	0	0
18.1.93	8.3	5	0	0	0	10	0
2.2.93	17	19	0	0	1	50	0
16.2.93	20	18	0	0	0	13	0
2.3.93	4	3	0	0	3	11	0
15.3.93	4	3	0	0	3	0	0
29.3.93	10	10	0	0	3	0	0
15.4.93	2	7	0	0	2	0	0
30.4.93	0	1	0	0	2	0	0
11.5.93	0	1	0	0	8	0	0
25.5.93	0	0	0	0	3	0	0
8.6.93	0.2	0	0	0	9.3	0	0
22.6.93	0	0	0	0	7	0	0
6.7.93	0	0	0	0	10	0	0
20.7.93	0	0	0	0	32	0	6
27.7.93	1	1	0	0	24	0	0
2.8.93	2	3	0	0	5	0	0
18.8.93	27	21	0	0	0	0	0
31.8.93	35	32	0	0	0	0	0
13.9.93	36	30	0	0	0	0	0
29.9.93	9.4	23	0	0	0	0	0
13.10.93	16	23	0	0	0	0	0
27.10.93	0	10	0	0	0	0	0
10.11.93	3	8	0	0	0	0	0
24.11.93	0	3	0	0	0	0	0
7.12.93	0	0.3	0	0	0	0	0
12.1.94	0	1	0	0	0	0	0
26.1.94	6.4	26	0	0	0	0	0
21.3.94	4	33	0	0	0	0	0

Appendix 2. Rostherne Mere Zooplankton

Date	Di.gra	Cyclo	Nau	Rot
7.3.90	0.3	0.1	0	0
21.3.90	9.6	1.7	0	0
18.4.90	5.8	3.1	0	0
27.4.90	13.9	9.3	0	0
2.5.90	9.1	6.6	0	0
16.5.90	14.8	1.4	0	0
29.5.90	23.6	1	0	0
12.6.90	14.1	1.1	0	0
27.6.90	17.4	2.5	0	0
11.7.90	17.6	2.6	0	0
25.7.90	5.5	2	0	0
8.8.90	5.5	7.1	0	0
21.8.90	4.6	6.4	0	0
6.9.90	2.6	1.3	0	0
24.9.90	2.5	0.3	0	0
9.10.90	5.3	0.5	0	0
22.10.90	5.4	0.5	0	0
6.11.90	5	0.2	0	0
20.11.90	3	0.4	0	0
5.12.90	3.6	0.6	0	0
19.3.91	4.5	0.7	0	0
2.4.91	9	2.1	0	0
16.4.91	2.4	1.4	0	0
30.4.91	17	7.8	0	0
14.5.91	22.3	3.3	0	0
27.5.91	10.7	0.7	0	0
11.6.91	14.9	1.4	0	0
25.6.91	1.1	0.2	0	0
9.7.91	0.7	16	0	0
22.7.91	1.7	4.3	0	0
6.8.91	2.7	4.9	0	0
19.8.91	1.4	2.2	0	0
9.9.91	3	1.1	0	0
23.9.91	1.3	0.2	0	0
9.10.91	1.2	0.4	0	0
22.10.91	0.4	0.5	0	0
5.11.91	0.1	0.3	0	0
19.11.91	0.4	0.7	0	0
3.12.91	0.1	0.3	0	0
18.12.91	0.2	0.4	0	0
9.1.92	0.3	0.2	0	0
21.1.92	0.1	0.03	0	0
3.2.92	0.6	0.1	0	0
18.2.92	0.8	0.1	0	0
3.3.92	0.2	0.2	0	0
18.3.92	1	0.9	0	0
1.4.92	0.8	0.7	0	0
14.4.92	14	19	0	0
28.4.92	85	49	0	0
12.5.92	214	13	231	250
26.5.92	104	43	0	0
9.6.92	223	12	16	27

Appendix 2. Rostherne Mere Zooplankton

Date	Di.gra	Cyclo	Nau	Rot
23.6.92	1	12	11	19
7.7.92	2	7	14	36
21.7.92	38	168	62	104
4.8.92	76	354	199	0
17.8.92	3	31	21	4
1.9.92	27	270	4	15
15.9.92	4	310	18	56
5.10.92	1	212	11	11
13.10.92	1	101	50	22
3.11.92	3	61	43	26
24.11.92	3	32	40	84
8.12.92	7	40	16	1
22.12.92	3	23	7	42
6.1.93	8	20	11	16
18.1.93	8	20	11	16
2.2.93	20	5	21	12
16.2.93	27	10	24	0
2.3.93	39	12	19	0
15.3.93	22	33	10	8
29.3.93	80	47	9	48
15.4.93	302	67	2	80
30.4.93	220	101	19	62
11.5.93	98	330	0	20
25.5.93	57	66	80	117
8.6.93	0	0	0	0
22.6.93	16	103	46	73
6.7.93	8	140	38	33
20.7.93	1	64	6	14
27.7.93	3	20	5	33
2.8.93	7	74	12	36
18.8.93	3	74	16	42
31.8.93	3	37	9	87
13.9.93	7	336	41	400
29.9.93	2	117	0	0
13.10.93	0	0	0	0
27.10.93	0	0	0	0
10.11.93	3	8	3	105
24.11.93	3	8	13	65
7.12.93	11	20	10	45
12.1.94	8	6	10	110
26.1.94	7	7	18	33
21.3.94	12	11	6	8

Table A3.1 Monthly mean (1961-1990) actual evapotranspiration data for the area (MORECS).

Month	Actual evapotranspiration
January	13.4
February	16.6
March	36.4
April	53.6
May	78.7
June	68.5
July	63.3
August	61.3
September	42.8
October	27.7
November	17.4
December	12.3