Interactions of phytoplankton, zooplankton and planktonic bacteria in two contrasting lakes

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Abstract

This study investigates the seasonal dynamics of phytoplankton, zooplankton and planktonic bacteria in two contrasting freshwater lakes (Rostherne Mere and Hollingworth Lake, NW England) with particular reference to 'bottom-up' and 'top-down' controls.

Rostherne Mere is a deep (max. depth 31m) monomictic system, with stable stratification during the summer. Hollingworth Lake is a shallow (max. depth 7.5m) polymictic system, with frequent wind-induced mixing events and no stable stratification. Assessment of trophic status showed Rostherne Mere to be highly eutrophic while Hollingworth Lake exhibited mesotrophic and eutrophic characteristics and was therefore classified as meso-eutrophic.

Rostherne Mere shows a distinct phytoplankton seasonal succession; diatoms/cryptomonads $\Rightarrow$ clear-water phase $\Rightarrow$ cyanobacteria / dinoflagellates. Bottom-up and top-down factors varied seasonally with bottom-up control by light (mixing in the isothermal water column keeping cells out of euphotic zone for long periods) and temperature during the winter. The top-down factor of grazing increased in importance during the spring, resulting in a distinct clear-water phase. During the summer low zooplankton numbers reduced the impact of top-down control, and bottom-up factors (light and phosphorus limitation) assumed greater importance. Seasonal succession in Rostherne Mere was predictable, and this was attributed to the predictable monomictic mixing regime.

In contrast, Hollingworth Lake was dominated by various species of diatoms, whose seasonality was indistinct and difficult to predict. This was attributed to frequent wind-induced mixing resulting in a physically unstable system with mixing events rapidly changing conditions in the lake from those favouring one taxa, to those favouring another. Analysis of grazing rates suggests that bottom-up, and not top-down factors are of primary importance throughout the year. However, the unpredictable wind-induced mixing events made determination of particular bottom-up factors influencing seasonality difficult, although mixing depth and the availability of phosphorus and silicon were important.

Herbivorous zooplankton (*Daphnia* and *Bosmina*) showed very similar seasonal dynamics in both lakes, with a large spring peak followed by low numbers over the summer. Bottom-up control by food availability was important during winter, spring and early summer with an increasing food resource leading to increased birth rates and a spring peak in zooplankton numbers. The decline in the spring peak was accompanied by a reduction in available food and decreasing birth rates, again suggesting the zooplankton were controlled by food availability. During the summer high birth rates but low numbers indicated a high mortality rate, suggesting top-down control is responsible for the low summer numbers.

Bacterioplankton dynamics were very different within the two systems. In Rostherne Mere there was strong evidence for bacterioplankton to be controlled by the availability of organic substrates released by the phytoplankton. However, in Hollingworth Lake there was very little evidence from which to draw firm conclusions concerning factors controlling bacterial populations. This was attributed to the frequent and unpredictable wind-induced mixing leading to controls on bacterial numbers changing continually, and hence there was no relationship with any one factor. However, concentrations of phosphorus were at levels at which bacterial growth has been restricted in other systems, suggesting that P-limitation may be important.

Declaration

No portion of the work referred to in this thesis has been submitted in support of an application for another degree or qualification of this or any other institute of learning.

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The Author

The Author has a degree in Applied Physics (BSc Hons, 2.1) and Computing (MSc). An interest in environmental issues led to enrolment on the MSc in Pollution and Environmental Control at Manchester University, during the course of which the author spent three months working on Rostherne Mere. This led to an increasing interest in aquatic ecology, and resulted in the author registering for a PhD, the result of which is the current thesis.

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Thanks must also go to the many MSc students that have worked on the lakes and have assisted in the sampling of both systems and to Gary Porteous, for help with practical matters, and in particular, with the dreaded auto-analyser.

Thanks to English Nature for permission to work on Rostherne Mere, and the staff at Hollingworth Lake water sports centre who transported us around the lake in their powerboats, and sat there patiently while we inserted tubes, buckets, nets and instruments into the water.

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Final thanks must go to my parents, Jean and Denis for lots of things, not least of which was providing me with a home while writing up this thesis. It is to them that this thesis is dedicated.

SECTION A: INTRODUCTION, AIMS AND METHODOLOGY

Chapter 1 Introduction

Freshwater plankton form a diverse association of different organisms including phytoplankton, zooplankton, bacteria, fungi and viruses bound together through intricate trophic relationships, the interactions of which are many and complex. This study investigates three components of the plankton; the phytoplankton, zooplankton (particularly the filter feeding cladocerans *Daphnia* and *Bosmina*) and bacteria. It is concerned with the abiotic and biotic factors that influence them, particularly the extent to which 'bottom-up' (factors promoting growth) and 'top-down' (factors causing loss) processes act upon these components of the biota.

The factors that influence the plankton are many. Factors that promote growth of phytoplankton populations (bottom-up) include nutrients, light, temperature and mixing depth (which is related to stratification). Factors causing loss of phytoplankton populations (top-down) include grazing, sedimentation of cells from the water column and viral attack.

Herbivorous zooplankton populations are also dependent on both bottom-up and top-down processes. This study is particularly concerned with the cladocerans *Daphnia* and *Bosmina* for which the principal factor influencing growth is the availability of a phytoplankton food source. The main cause of loss for the zooplankton community is predation, which can come from fish, or from invertebrate predators such as *Chaoborus*, *Leptodora* and predatory copepods.

Factors promoting bacterial growth are the availability of organic substrates for carbon, often in the form of algal exudates. Other factors are the availability of inorganic nutrients (particularly phosphorus) and temperature. Factors causing loss include predation by zooplankton, and viral attack.

Figure 1.1 is a diagrammatic representation of the factors influencing populations of filter feeding zooplankton (*Daphnia* and *Bosmina*), phytoplankton and bacteria. Although this highly simplified representation does not show all the factors that determine the plankton populations, the diagram does show the principal factors that act upon these components of the plankton. The diagram also shows how the phytoplankton, zooplankton and bacteria interact with each other. For instance, the phytoplankton biomass is subject to losses due to zooplankton grazing, while the phytoplankton biomass in turn influences the bacteria by releasing organic substrates for bacterial growth.

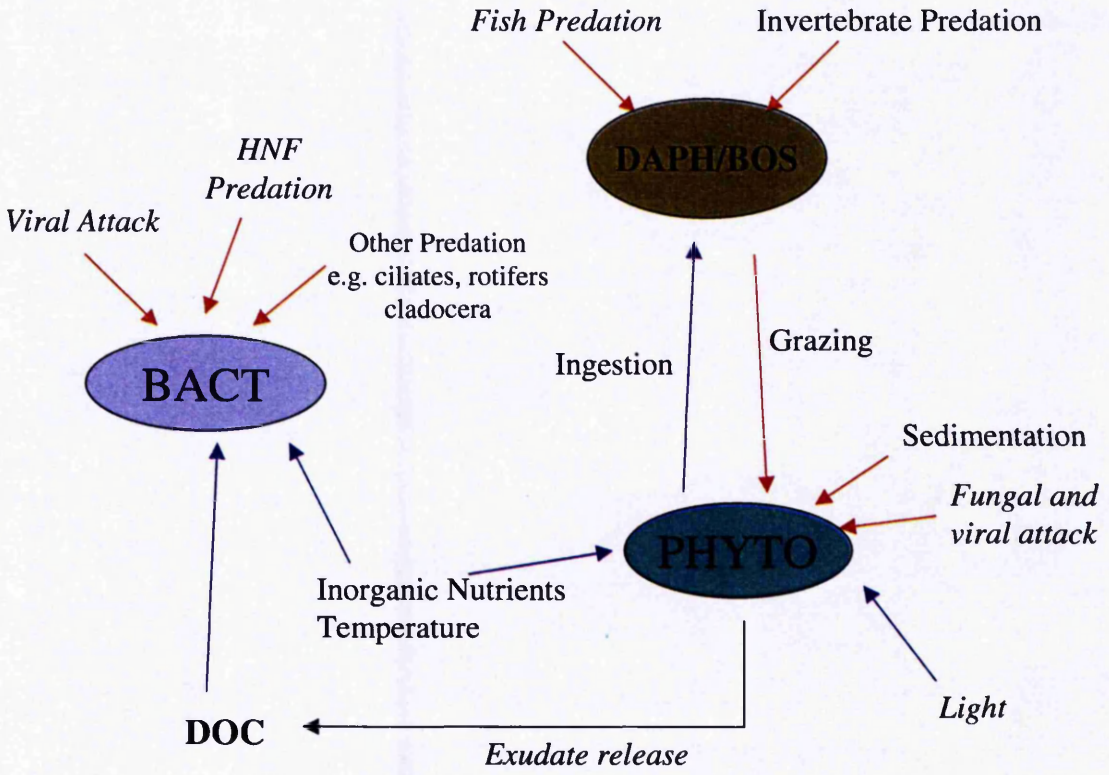


Figure 1.1: Simplified representation of the growth-promoting and loss-causing factors acting on each of the planktonic components under investigation in this study. The diagram also illustrates the inter-relationships between these components. Blue arrows indicate growth-promoting (bottom-up) factors, while red arrows indicate loss-causing (top-down) factors. Factors in italics were not measured in this study, for example the effect of fish predation on zooplankton but are considered when interpreting the results. The large arrow represents release of carbon by phytoplankton, which is often the most important carbon source for bacteria. Abbreviations: PHYTO = phytoplankton, DAPH = *Daphnia* spp., BOS = *Bosmina* spp., BACT = bacteria, HNF = heterotrophic nanoflagellates and DOC = dissolved organic carbon.

The operation of these growth and loss factors, both biotic and abiotic, varies seasonally and gives rise to a seasonal succession of the organisms that make up the plankton. Figure 1.2 is an idealised representation of the seasonal succession of phytoplankton and zooplankton in a eutrophic, stratified lake, and of the abiotic and biotic factors that influence succession of the biota. It can be seen from the diagram that phytoplankton generally show two peaks in biomass, one during spring and a second during summer. During the winter, physical factors (e.g. temperature, light, mixing) are important to the phytoplankton and zooplankton. A reduction in the intensity to which physical factors operate results in an increase in phytoplankton biomass, the decline of which is attributable to grazing, although nutrient limitation may also be important. The decline of the spring zooplankton peak can be attributed to either the bottom-up factor of food limitation (due to the decline of the algal bloom) or the top-down factor of

predation. The reduction in zooplankton numbers leads to reduced grazing pressure on the phytoplankton, which then increase during the summer. During the summer, the phytoplankton may suffer losses due to grazing, and be restricted by nutrient availability. Zooplankton biomass is generally lower than during the spring, and this may be due to food limitation or predation. During the winter, physical factors are again important for both the phytoplankton and the zooplankton. The seasonal dynamics of bacterioplankton is not shown on the diagram, but as bacterioplankton are often limited by the phytoplankton-derived organic growth substrates the seasonal cycle of bacterioplankton is often found to be closely related to phytoplankton biomass.

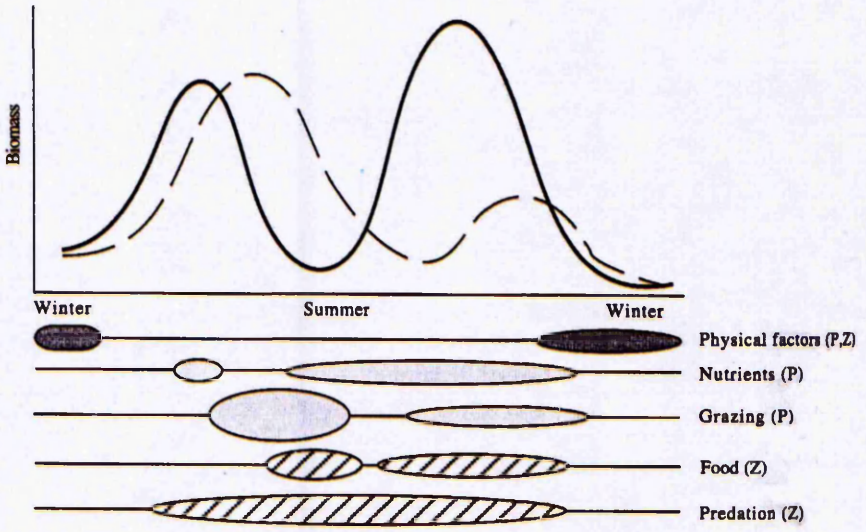


Figure 1.2: Idealised seasonal succession of phytoplankton (solid line) and zooplankton (broken line) in a stratified, eutrophic lake. The bottom panel shows the time when growth and loss factors are important for phytoplankton (P) and zooplankton (Z). The length of the ellipses shows the time over which the factors are important, the width gives an indication of the intensity with which the factors operate. (Diagram taken from Bronmark and Hansson, 1998).

The above description of the factors that influence phytoplankton seasonality is highly simplified, and the situation in a real lake is much more complex. This study investigates the factors that cause the seasonality of phytoplankton, zooplankton and bacteria in two contrasting lake systems, Rostherne Mere and Hollingworth Lake. The overall aim of this study is to examine the interactions between the bacteria, phytoplankton, zooplankton, and physico-chemical parameters; and to determine how these factors change seasonally and so influence the observed seasonality of the plankton. Rostherne Mere has been widely studied, with records of its phytoplankton going back to 1913 (Pearsall, 1923) and continuing throughout the last century. In contrast, the seasonal changes in the plankton of Hollingworth Lake have not been studied. Thus, in the case of Rostherne Mere it is possible to look at a large body of

previous work on the Mere and use this to ask specific questions about the nature of the plankton. In contrast, previous information on the plankton of Hollingworth Lake is very limited. The following discusses previous work carried out on the two systems, areas in which understanding can be improved, and the questions that this study seeks to answer.

1.1 Rostherne Mere

Rostherne Mere is one of a group of more than 60 mainly eutrophic lakes situated on the Shropshire/Cheshire plain. The meres are recognised as a group of freshwaters of national importance (Luther and Rzoska, 1971). They lie in a roughly rectangular area of lowland (<100m asl) measuring about 80km by 60km and are bordered to the north by the River Mersey, and to the south, east and west by the uplands of the Shropshire Hills, the Pennines and the Welsh Marches respectively. The meres have been described as naturally eutrophic (Reynolds and Sinker, 1976) with algal blooms occurring since at least the 19th century (Phillips, 1884). The meres are characterised by high concentrations of phosphorus and low concentrations of nitrogen.

Although they may be naturally eutrophic, there is no doubt that many of the meres are receiving increased nutrient loading due to human activities. The major land use of the plain is agriculture, particularly dairy farming, with an expansion in arable farming in recent decades (Reynolds, 1979), and the use of fertilisers has led to an increase in the nitrogen load to many of the meres. Many meres have also received increased loading of phosphorus due to sewage effluent. Rostherne Mere has been subject to nutrient loading form both of these sources.

Rostherne Mere (53° 21' N, 2° 23'W; National Grid Reference SJ745843) is one of the largest and deepest of the meres with an area of 48.7 ha, a maximum depth of 31m and mean depth of 13.6m, and a volume of 6.64×10^6 m^3 (Woof and Wall, 1984). The mere was formerly part of the private estate of Lord Egerton but is now under the care of English Nature as a National Nature Reserve. Its value for wildlife has led to its designation as both a RAMSAR site and a Site of Special Scientific Interest (SSSI).

The mere has been the subject of a large amount of study, much of which has involved its phytoplankton community, the study of which has a long history. Records of the phytoplankton community go as far back as 1913 (Pearsall, 1923), with subsequent studies including those by Griffiths, (1925), Lind (1944), Belcher and Storey (1968), Reynolds (1978a), and Reynolds and Bellinger (1992). These studies

have shown a change in the seasonal succession in the dominant phytoplankton, with the *Asterionella-Ceratium-Aphanizomenon* succession seen in 1944 giving way to the summer domination of *Microcystis/Ceratium* seen today (Reynolds, 1979). It has been shown from investigations of the sediment remains in the mere that this change occurred fairly abruptly, around 1958 (Livingstone 1979, cited in Reynolds & Bellinger, 1992). In recent years the seasonal succession has been typical of a stratifying eutrophic lake with a vernal diatom phase followed by a clear-water phase, which is then followed by a period of high phytoplankton during the summer, consisting initially of *Aphanizomenon/Anabaena* followed by *Ceratium* and/or *Microcystis* in late summer.

It has been suggested that the change that occurred around 1958 was due to the increased inputs of nutrients to the lake as a result of the establishment in 1910, and subsequent development, of a gull roost (Brinkhurst and Walsh, 1967). Recent work, however has shown this to be unlikely (Carvalho *et al.*, 1995) and it now seems probable that the change is a response to advancing eutrophication, brought about by changing patterns of land use in the surrounding area, in particular the increased used of artificial fertilisers in the surrounding catchment. This may have shifted the mere from a situation where its phytoplankton is limited by nitrogen to one where it is limited by light (Reynolds and Bellinger, 1992), although it has also been argued that nitrogen still remains the limiting factor (Carvalho *et al.*, 1995; Moss *et al.*, 1994, 1997).

Another important source of nutrients, and in particular phosphorus, has been the input of sewage effluent into the mere. In 1935 a sewage works was built that discharged into Little Mere from where it flowed, via Rostherne brook, into Rostherne Mere (Figure 2.1, page 30). This sewage works was overloaded for many years and, in an attempt to reduce the eutrophic nature of the lake (particularly the occurrence of cyanobacterial algal blooms) was finally closed in 1991. A small treatment plant that served Rostherne village (population ~100) and discharged just upstream of Rostherne Mere was also closed in 1991. The sewage from both treatment plants was diverted for treatment elsewhere.

In recent years, both The University of Manchester and the University of Liverpool have been carrying out work on Rostherne Mere. Liverpool University has been concerned with the recovery of the lake following the sewage diversion (Moss *et al.*, 1997, Carvalho *et al.*, 1995). Stephen (1997) also monitored the phytoplankton, zooplankton and nutrients within Rostherne Mere. Rostherne has also been considered

within the wider context of the meres as a whole in relation to the control of phytoplankton crops by top-down and bottom-up mechanisms (Moss *et al.*, 1994).

Much of the work at Manchester University involved the use of x-ray microanalysis to investigate the elemental composition of phytoplankton cells, and how the intracellular concentrations changed in relation to concentrations in the surrounding water (Clay *et al.*, 1991; Sigee and Holland 1997; Sigee *et al.*, 1998; Sigee and Levado, 2000; Krivtsov *et al.*, 2000b). Elemental compositions of bacterial cells within the mere have also been investigated (Booth *et al.*, 1987; Booth, 1988). Data concerning the elemental composition of phytoplankton cells were incorporated into a computer model of the Rostherne ecosystem (Krivtsov *et al.*, 1998; 1999; 2001). The model, known as 'Rostherne' is particularly concerned with the relationship between phytoplankton and nutrient concentrations. Levado (2001) studied the diversity of phytoplankton within Rostherne Mere in relation to depth and season. In addition, a number of MSc projects have been carried out on the Mere (Samsi, 1991; Moriera, 1997; Dean, 1999). Although these projects were restricted to the summer months they nevertheless are a valuable addition to the body of knowledge concerning the mere.

Fish populations within the Mere have also been investigated, including studies by Banks (1970), Goldspink and Goodwin (1979) and Goldspink (1990). The latter two works concentrated on the perch population within the Mere, while the work of Banks was a large survey of the whole fish population including diet, age structure and growth; this showed the population to be mainly perch (*Perca fluviatilis*), roach (*Rutilus rutilus*) pike (*Esox lucius*), of which perch was the most common. Banks stated that the fish population was likely to remain unchanged for the foreseeable future. The fact that no angling is permitted on the Mere and there is no public access makes stocking by fish unlikely and the fish population today is therefore probably much the same as it was at the time of Banks' study.

Although the lake has been the subject of a large amount of study there is much information concerning the operation of the ecosystem that remains unknown. Our understanding of the factors influencing the seasonal dynamics of the phytoplankton, zooplankton and bacteria can all benefit from further study of Rostherne Mere. Section 1.1.1 to Section 1.1.3 briefly discusses the previous work on the Mere as it relates to the components of the plankton under investigation in this study i.e. the phytoplankton, zooplankton and bacteria, and explains how this study aims to build upon and add to this body of knowledge.

1.1.1 Phytoplankton

This study aims to investigate the top-down and bottom-up factors that influence the periodicity of the phytoplankton within Rostherne Mere over the whole growing season. As discussed above, the seasonality of the phytoplankton in Rostherne Mere is well studied. However, three aspects of the seasonality of the phytoplankton within Rostherne Mere are particularly interesting and can benefit from further information – the size of the spring diatom bloom, the causes of the clear-water phase, and the factors influencing the summer phytoplankton maximum.

1.1.1.1 The spring diatom bloom

The first aspect is the factors that contribute to the low size of the spring diatom bloom. When compared to other lakes in the region (Shropshire/Cheshire Meres) the diatom population is small. Reynolds (1978b) monitored Crose Mere, a lake of similar size, and found that maximum spring *Asterionella formosa* populations were in the order of $12x10^3$cells ml^{-1} (approximately 1500 colonies ml^{-1}). This compares to values in Rostherne Mere of approximately 600 colonies ml^{-1} and 7 colonies ml^{-1} in 1996 and 1998 respectively (Krivtsov, 2000a). It may be proposed that the difference is due to silicon limitation; however, winter concentrations of silicon were similar in both lakes at approximately 1.5mg l^{-1}. It has been suggested (Reynolds, 1978b) that the difference is principally due to physical factors, principally the ratio of mixed (Z_m) to euphotic (Z_{eu}) depth, and the onset of stratification. Rostherne Mere is deep (high Z_m/Z_{eu} ratio), and when the lake is isothermally mixed the diatom population will spend a large proportion of the daylight hours outside the euphotic zone, and it is not until mid-March that the day length is long enough (11-12hrs) to support an increase in the diatom population. Crose Mere is shallower than Rostherne Mere and has a lower Z_m/Z_{eu} ratio; therefore, the diatoms within the water column will spend a larger proportion of daylight hours in the euphotic zone, and can start their population increase earlier in the season (during January). It is suggested that the decline of the diatom population (and onset of the clear-water phase) is caused by the onset of stratification, which in both meres occurs in late April/early May, when substantial losses of diatoms occur through sedimentation. Thus, the time available for diatom growth is shorter in Rostherne Mere (mid-March to late-April) than in Crose Mere (January to late-April), and this may account for the smaller size of the final diatom maxima reached in Rostherne Mere. However, other factors may also limit the size of the spring diatom bloom, such as sedimentation losses, grazing, parasitic attack and nitrogen/phosphorus limitation. One

aim of this study is to determine the factors that contribute to the small size of the diatom bloom in Rostherne Mere.

1.1.1.2 The clear-water phase

The second area of phytoplankton periodicity that this study is particularly concerned with is the determination of factors that contribute to the clear-water phase in Rostherne Mere. The spring diatom maximum in Rostherne Mere is immediately followed by rapid decline in numbers of phytoplankton leading to a clear-water phase with low phytoplankton biomass, with chlorophyll-a often falling to $<5\mu g\ l^{-1}$, and high Secchi depths extending to >3.5m (Krivtsov, 2000a).

In many lakes the onset of the clear-water phase is attributed to intense zooplankton grazing reducing the phytoplankton biomass to very low levels, and a number of workers have shown the importance of zooplankton grazing on the onset of the clear-water phase (Jewson *et al.*, 1981; Lampert *et al.*, 1986; Deneke and Nixdorf, 1999). However, the decline in the phytoplankton may be related to other factors such as nutrient limitation, fungal attack or sedimentation of phytoplankton from the water column. Within the context of Rostherne Mere, Reynolds (1978b) implied that the major cause of the clear-water phase may be sedimentation of phytoplankton from the water column. Reynolds and Bellinger (1992) reanalysed previous data on the phytoplankton of Rostherne Mere and also suggested that the clear-water phase is as likely to be due to the settlement of inert suspended particulates following the onset of stratification as it is to grazing. Although sedimentation may be important in some years, recent analysis (Krivtsov, 2000b) of the spring phytoplankton maximum in Rostherne Mere showed that the spring bloom consisted not only of diatoms, which can suffer large sedimentary losses, but also of large numbers of cryptomonads. Cryptomonads have very low losses due to sedimentation (Reynolds and Wiseman, 1992) and the decline of these following the spring maximum suggests that factors other than sedimentation may be responsible for the decrease in phytoplankton biomass. This study aims to investigate the abiotic and biotic factors that contribute to the onset of the clear-water phase in Rostherne Mere. A particular aim is to determine if the grazing rates of the zooplankton are high enough to cause the clear-water phase, as has been shown in other systems, and to determine the importance of other factors such as nutrient limitation and sedimentation.

1.1.1.3 The summer phytoplankton maximum

The third area of particular interest is the determination of the factors that influence the phytoplankton during the summer maximum, particularly the potential top-down influence of grazing and the bottom-up effect of nutrient limitation.

The effect of grazing on the summer phytoplankton community in Rostherne Mere is not known. Moss *et al.*, (1994) grouped 24 meres into deep (>3m) and shallow (<3m), and looked at correlations between chlorophyll-a and *Daphnia* numbers during the growth season (March-October). It was shown that there was a positive correlation among shallow lakes but no correlation for deep lakes and it was proposed *Daphnia* controlled phytoplankton in the shallow lakes but not in the deep lakes. As Rostherne Mere is deep, this suggests that grazing is of minor importance in Rostherne Mere. However, the work did not look at seasonal changes in the influence of grazing, did not look at grazing rates, and did not look at the relative importance of grazing for different phytoplankton species. There is thus a need for an analysis of the summer phytoplankton in Rostherne Mere and the potential impact of grazing upon it.

Also of particular interest is the extent to which the summer phytoplankton may be influenced by the bottom-up factors. It has also been proposed that phytoplankton populations are light-limited (Reynolds and Bellinger, 1992). However, monitoring of Rostherne Mere during the early 1990's showed the lake to be nitrogen limited, with concentrations during the summer falling to undetectable levels (Carvalho *et al.*, 1995; Stephen, 1997). Phosphorus concentrations within the Mere were high, a situation that, as mentioned earlier, may have been exacerbated by the sewage works that until 1991 discharged into the Mere via Blackburns brook. Following the closure of the sewage works it was expected that the levels of phosphorus in the lake would begin to decline, yet in the eighteen months following diversion no change in either phosphorus or biomass was observed (Carvalho *et al.*, 1995). However Moss *et al.*, (1997) noted a slow decline in phosphorus concentrations and it was suggested that in future years the phosphorus concentrations levels will continue to decline and phosphorus may become more important in limiting biomass, leading to a decline in the trophic status of the lake. This study also aims to determine whether the concentrations of phosphorus within the lake have fallen, and the extent to which phosphorus limitation may now be important in the bottom-up control of phytoplankton.

1.1.2 Zooplankton

In contrast to the phytoplankton, the zooplankton of Rostherne Mere has received relatively little attention. In order to understand the functioning of the Rostherne ecosystem it is important to consider the bottom-up effect of food availability on *Daphnia* population dynamics (*Daphnia* is the dominant zooplankton in Rostherne Mere), and the top-down effect of predation on the zooplankton by fish and invertebrates. No study has looked at the population dynamics of the zooplankton within the Mere and the factors that influence it. This study seeks to investigate fluctuations in zooplankton numbers within the mere, monitor changes in population parameters (brood size, birth rate etc) and to use these to determine the extent to which top-down and bottom-up factors influence zooplankton (and particularly *Daphnia*) dynamics.

1.1.3 Bacteria

Planktonic bacteria in Rostherne Mere (excluding the photosynthetic cyanobacteria) have received little attention. The only work carried out on the bacterial populations of Rostherne Mere was that of Booth (Booth *et al.*, 1987; Booth, 1988). Although this work was primarily concerned with the study of the elemental composition of bacteria an estimation of total cell numbers using scanning electron microscopy was made, and this found consistent levels of 10^6 freely suspended cells/ml. No study at Rostherne Mere has investigated dissolved organic carbon (DOC) concentrations, phytoplankton and bacterial biomass for a full annual cycle, and the extent to which phytoplankton, DOC and bacteria are interrelated is not known. This relationship between bacterial numbers and phytoplankton biomass is investigated in this study.

1.2 Hollingworth Lake

Hollingworth Lake (53° 37' N, 2° 05'W; National Grid Reference SO937149) is an artificial lake built in 1804 to supply compensation water to the newly built Rochdale Canal. The lake lies at the base of the Pennines near to the town of Rochdale. The area immediately surrounding the lake consists of smoothly-rounded hills rising to no more than 250m separated by steeply sided valleys. The surrounding land is under low intensity agricultural use.

In 1975 Hollingworth Lake was designated a Country Park by the Countryside Commission. It is currently managed by a Joint Management Committee from Rochdale

Metropolitan Borough Council and North West Water. The lake is situated 171m above sea level, has a surface area of 47 hectares (116 acres), a maximum depth of 7.5m and a volume of $1.25x10^6m^3$. The bottom of the lake is covered by fine, almost colloidal silt, and the shore of the lake consists mostly of steep sided stone embankments, neither of which supports much vegetation. The lake supports a large variety of recreational activities including sailing, fishing, rowing and bird watching.

The main inflow to the lake is Longden End Brook (Figure 2.2, page 31) The outflow from the lake consists of an overflow and from compensation water pumped to the canal from the valve tower. The pumping of compensation water to the canal can often lead to large reductions in the depth of the water

In 1971, the lake was subject to water supply and water quality interest after it was polluted by clay and silt during the construction of the M62 motorway. To settle the clay and silt a coagulant polyamine was used. Following these events the cyanobacteria *Oscillatoria* became abundant and has been present in the lake ever since. It is not known if the appearance of *Oscillatoria* was a consequence of these events or if its appearance was coincidental. In the autumn of 1996, a large bloom of *Oscillatoria agardhii* resulted in a number of lake users falling ill; this led to the temporary closure of the lake to all watersports activities. In autumn 1999, there was another major bloom of *Oscillatoria*, and although it has been present in the lake since then no major bloom has occurred. (Note that the genus *Oscillatoria* has recently been split (Suda *et al.*, 2002; for example *O. agardhii* and *O. redekei* are now *Planktothrix agardhii*, and *Limnothrix redekei*. However, in this study all references to *Oscillatoria* refer to the original, pre-reclassification genus).

In 2001, the University of Manchester was invited to study the lake in order to ascertain the causes of the algal blooms and consider possible restorative measures. However, in order to propose measures to reduce the intensity of algal blooms within the lake an understanding of the functioning of the ecosystem is required, and in particular, the factors influencing the phytoplankton. Yet very little monitoring of the biota of Hollingworth Lake has been carried out. North West Water carried out a fishery survey of the lake, which reported on the fish community and benthic and littoral invertebrates, but did not consider the plankton (Clough, 1979). The first monitoring of the plankton occurred following the algal bloom in autumn 1996 when the Environment agency began to monitor the lake (from 1997 onwards). However, data on the phytoplankton composition of the lake is more limited, with analysis of the

phytoplankton community generally only being carried out in response to a bloom occurrence, and analysis ceasing once the bloom had declined. Furthermore, the data often records phytoplankton by its presence or absence as a dominant species, rather than by counts of individual species. However, the available data does show the lake to be dominated by diatoms, principally of the genera *Tabellaria*, *Aulacoseira*, *Asterionella*, *Cyclotella* and *Synedra*, with occasional dominance of *Oscillatoria*. Selected physico-chemical parameters (pH, BOD, COD, nitrates, ammonia, SRP and suspended solids) were also measured from 1997 until early 2000.

The lack of information on Hollingworth Lake is also reflected in the uncertainty of the lake's trophic state, the earliest reference to which was by Clough (1979), who described the lake as oligotrophic. However, this assessment seems to be based on no particular classification scheme but on a qualitative assessment of the lake's productivity based on macrophyte and phytoplankton abundance. No full assessment of the lakes trophic status was carried out until the study of Hitchen (2001), the monitoring for which (summer, 2001) was carried out in conjunction with the present study. Hitchen classified the lake as mesotrophic according to phytoplankton species but eutrophic based on chlorophyll-a and SRP concentrations. The assessment of trophic status was based on data collected during the summer months only. There is thus a need for an assessment of the current trophic status of the lake based on data collected over a full annual cycle.

It can be seen that there is very little information on the ecology of the lake, a lack of information that this study seeks to address. This is the first study that follows changes in the biota (phytoplankton, bacteria and zooplankton) and abiotic factors (nutrients, temperature etc) over a full seasonal cycle. A number of issues concerning the phytoplankton within the lake are of interest. Firstly, the effect of top-down and bottom-up factors on the phytoplankton, and how these influence seasonal succession; secondly, the possible reasons for the appearance of *Oscillatoria* blooms in some years and not in others; thirdly, as the lake is shallow and subject to strong wind-induced mixing (due to its exposed position), the effect of mixing on phytoplankton periodicity.

There are no previous data on the zooplankton populations within Hollingworth Lake. This study seeks first to determine the fluctuations in these biota, and the factors influencing them with particular emphasis on the influence of the bottom-up effect of food availability, and the top-down effect of predation on the zooplankton population.

There are also no previous data on the bacterial populations within Hollingworth Lake. This study seeks to determine seasonal fluctuations in bacterial numbers and to relate these to possible top-down and bottom-up factors. Of particular interest is the extent to which bacterial population dynamics are related to potential sources of organic substrates i.e. phytoplankton exudates, allochthonous sources of carbon, and other nutrients necessary for growth i.e. phosphorus. Also of interest is the extent to which top-down control of bacterial numbers via zooplankton grazing/predation may be important.

1.3 Aims and Objectives

This study investigates the factors that cause the seasonality of the plankton in two contrasting lake systems, Rostherne Mere and Hollingworth Lake. The overall aim of this study is to examine the interactions between the bacteria, phytoplankton, zooplankton, and physico-chemical parameters; and to determine how these factors change seasonally and so influence the observed seasonality of the plankton. More specifically this study aims to:

1. Characterise the phytoplankton seasonal dynamics and the factors that influence it, for example grazing and nutrient limitation. Specific objectives within the context of Rostherne Mere are to determine the factors that cause the small size of the spring diatom maximum (i.e. is it due to a short growing season?), the factors that influence the onset of the clear-water phase (is it due to increased sedimentation of cells or is grazing important?), and the factors influencing the summer phytoplankton maximum (is it light, nitrogen or phosphorus limited?). Concerning Hollingworth Lake, this aim will provide the first long term analysis of phytoplankton succession and species within the lake, will determine the principal factors that influence phytoplankton seasonal succession (grazing, nutrients, mixing), and provide information concerning the dominance of *Oscillatoria* in recent years.
2. To characterise the seasonal fluctuations in the numbers of zooplankton within both lakes. Specific objectives are to determine the extent to which the population dynamics of zooplankton are influenced by the availability of organic material as a food source, and the extent to which *Daphnia* population dynamics are influenced by top-down predation by invertebrates and fish.
3. To characterise the seasonal fluctuations in bacterial numbers and to determine the factors that influence the seasonality of the bacteria. Specific objectives are

to investigate the importance of the availability of organic substrates and nutrients in regulating bacterial numbers, and the importance of top-down factors such as grazing.

4. To use the data obtained over the sampling period to assess the trophic status of the lakes, and to determine the extent to which the condition of the lake may have changed in recent years. As stated above, the trophic status of Hollingworth Lake is currently uncertain, while that of Rostherne Mere may be undergoing some change since the diversion of sewage. Further information on these points will aid in formulating a strategy for the future monitoring of the lakes.

In the following, each lake is considered in a separate section - Section B is concerned with Rostherne Mere while Section C is concerned with Hollingworth Lake. Both sections consist of a results chapter and a discussion chapter. The structure of the discussion chapters is related to the specific aims of the study (as listed above), with the discussions each divided into four sections coinciding to the four specific aims. A final concluding section (Section D) compares and contrasts the two systems.

However, before the results are presented and discussed it is necessary to describe the methodology employed during the study.

Chapter 2 Materials and Methods

2.1 Sampling Regime

Sampling was carried out over three annual cycles - 2000, 2001 and 2002. Rostherne Mere was sampled during 2000 and 2002, Foot and Mouth disease having prevented access to Rostherne Mere in 2001. Hollingworth Lake was sampled during 2001 and 2002.

Sampling frequency varied between 1 and 3 weeks and was generally higher during periods of intensive change during the summer. On each sampling date, in order to obtain a lake average for the measured parameters, samples were taken from 3 sites. At Rostherne Mere all sites were situated in the deepest part of the lake. Site A had a depth of 31m while sites B and C had depths of approximately 20 and 25m respectively. At Hollingworth Lake samples were also taken at 3 sites, all sites being approximately 7.5m deep.

Table 2.1 summarises the sampling regime at each of the lakes. Figures 2.1 and 2.2 show the positions of the sampling sites.

	Rostherne 2000	Rostherne 2002	Hollingworth 2001	Hollingworth 2002
Sampling Start/End	27th January 2000 - 8th February 2001	17th January - 7th November	10 April - 21st November	30th January - 19th September
Sampling Frequency	Every 3 weeks until 11th May, weekly until 8th of Sep, every 2 weeks until 15th Nov, then monthly	Approx. every 2 weeks	Approx. every 2 weeks	Approx. every 2 weeks
Temp/pH/ Conductivity	Yes	Yes	Yes	Yes
Temp/Oxygen Profiles	Yes, O_2 profiles in July	Yes	Yes	Yes
Nutrients	TP, TDP, SRP, TN, TDN, NO3, NH4, Si	TP, TDP, SRP, TN, TDN, NO3, NH4, Si	TP, TDP, SRP, TN, TDN, NO3, NH4, Si	TP, TDP, SRP, TN, TDN, NO3, NH4, Si
DOC	Yes	Yes	Yes	Yes
Colour	No	Yes	No	Yes
TSS/TOM	Yes	Yes	Yes	Yes
Phytoplankton counts / chlorophyll-a	Yes	Yes	Yes	Yes
Zooplankton counts	Yes	Yes	Yes	Yes
Ciliate counts	Yes	Yes	Yes	Yes
Rotifer counts	No	Yes	No	Yes
Viable Bacteria	Yes	No	Yes	No
Total Bacteria	Yes	Yes	Yes	Yes

Table 2.1: Summary of the sampling carried out at each of the lakes.

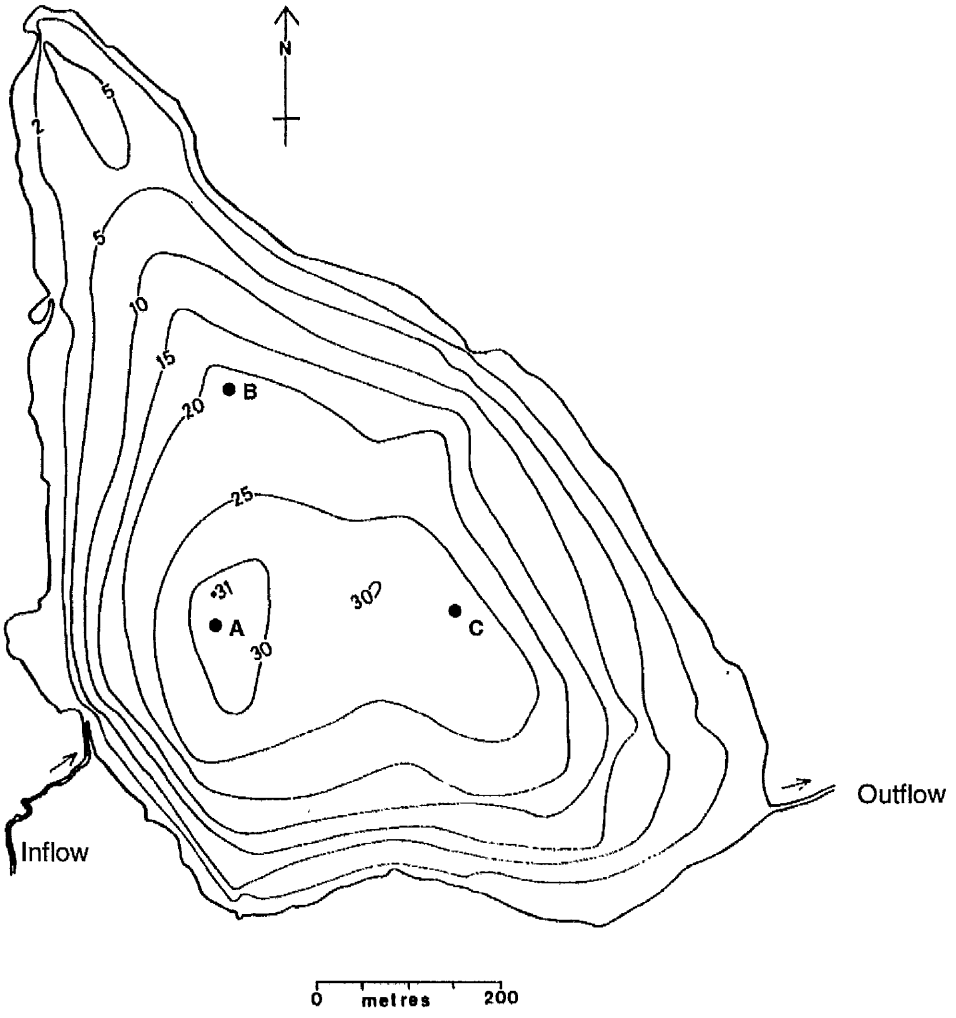


Figure 2.1: Bathymetric map of Rostherne Mere. Depth contours are in metres. A, B and C mark the locations of the sampling sites. Also shown is the main inflow to the lake (Rostherne Brook) and the outflow (Blackburn's Brook). (Map taken from Woof and Wall, 1984).

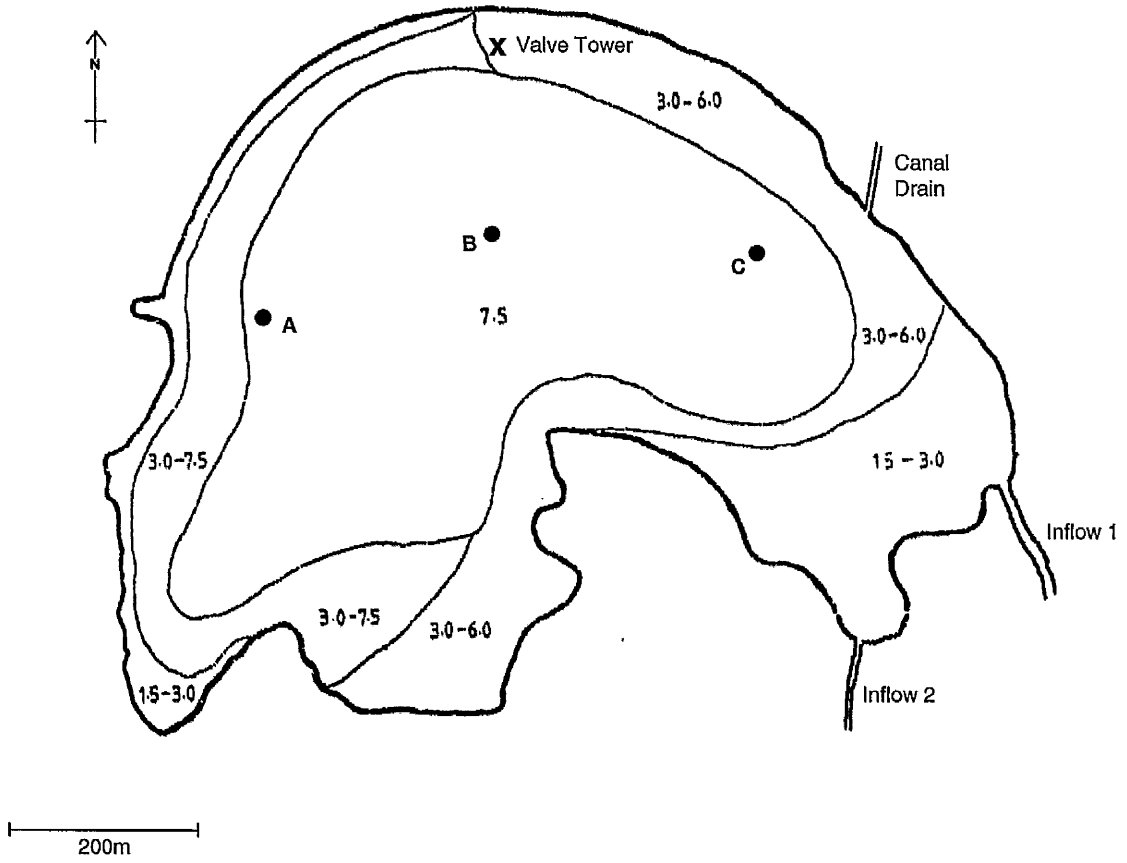


Figure 2.2: Bathymetric map of Hollingworth Lake. Depth contours are in metres. A, B and C mark the locations of the sampling sites. Also shown are the two inflows, Inflow 1 (Longden End Brook) is the main inflow to the lake. The smaller, inflow 2 is unnamed, is of lesser importance, and only flows following high rainfall. The outflow from the lake is principally via the valve tower, however, when the lake is full, overflow water is removed from the lake via the canal drain. (Map taken from Clough, 1979).

2.2 Field Work

2.2.1 Water sampling and Physico-chemical parameters:

2.2.1.1 Depth analysis

Depth profiles of temperature and dissolved oxygen were carried out at the centre of the lake by lowering a Phox (Phox instruments) 62TE meter into the water with a monitoring interval of 1m. Profiles at Rostherne Mere were taken to a depth of 20m. At Hollingworth profiles were taken over 7m, which is the full depth of the water column.

2.2.1.2 Integrated Samples

An integrated water sample was collected at each site by lowering a 5m flexible, weighted polyethylene tube from the surface through to a depth of 5m. The tubing trapped a column of water, which was returned to the surface by retrieving the tubing using a rope attached to its lower end. The sample was then poured into an acid washed polyethylene bucket. The water temperature of the sample was measured using a pHOX 62TE oxygen/temp meter. A pHOX 42E pH meter calibrated at pH 4, 7 and 10 was used for the measurement of pH. Conductivity was measured using a Spectronix conductivity meter.

Two litres of the integrated sample were then placed in a 2 litre polyethylene bottle that had been acid washed for 24 hrs (in 10% HCl) followed by double rinsing in distilled water. This sample was used for the determination of nutrients, chlorophyll-a, organic matter (dissolved organic carbon, carbohydrates, humic acids). The integrated sample was also used for the sampling of phytoplankton, rotifers and bacteria (see below).

The limit of light penetration at each site was measured using a Secchi disk.

2.2.2 Biota Sampling

2.2.2.1 Zooplankton

Cladocerans, copepods and *Chaoborus* larvae were collected by vertical trawls through the water column using a 250μm zooplankton net. A trawl was taken at each site and the zooplankton washed into a bottle and preserved in 4% formaldehyde for later enumeration and identification.

Rotifers were collected by filtering 20 litres of integrated sample through a 63μm micron sieve. The rotifers retained were then washed into a bottle, narcotised with CO_2 and preserved by the addition of 2% formaldehyde.

Ciliates were collected within the iodine preserved phytoplankton sample (see below).

2.2.2.2 Phytoplankton

For phytoplankton (and ciliate) analysis, 250 ml of the integrated sample was placed in a polyethylene bottle and fixed with 1% Lugols iodine solution.

2.2.2.3 Bacteria

For the estimation of bacterial numbers 20ml of the integrated sample was collected in a sterile polyethylene bottle and preserved in 2% Formaldehyde. A further 20ml sample was retained, unpreserved for viable counts.

2.3 Laboratory Analysis

2.3.1 Sample pre-treatment

On return to the laboratory, all samples were stored at 4°C. Separate analysis was carried out on each of the integrated samples collected from sites A, B and C.

2.3.1.1 Nutrients

Immediately on return to the laboratory, 350 ml of integrated sample was filtered through a Whatman 0.45μm cellulose acetate filter. The filtrate was used for the determination of (nitrate-nitrite)-N, total dissolved N, soluble reactive phosphorus, total dissolved phosphorus, ammonia and silicon. One hundred ml of unfiltered water was reserved for the determination of total P and total N.

2.3.1.2 Dissolved organic carbon, total suspended solids (TSS), total organic matter (TOM) and colour

A further 500ml of sample was filtered through an ignited pre-weighed Whatman GF/C filter and 20ml of the filtrate were preserved with the addition of 1% H_2SO_4. This was used for the determination of dissolved organic carbon (DOC). A further 20ml of sample (unpreserved) was used for the measurement of colour. The filter paper was retained and used for the determination of total suspended solids (TSS) and total organic matter (TOM).

2.3.1.3 Chlorophyll-a

For the determination of chlorophyll-a 500 ml of the sample was filtered through a Whatman GF/C filter and the filter paper reserved.

2.3.2 Analysis of Water Chemistry

2.3.2.1 Nutrients

Nitrogen, phosphorus, ammonia and silicon analyses were carried out within 24 hours of the samples being collected and were measured on a SKALAR SansPlus system auto-analyser. Detection limits are given in Table 2.2. For further information on the methods employed by the analyser the reader is referred to Skalar Analytical (1993). For the methods in general see Golterman and Clymo, 1969; Parsons *et al.*, (1984); Mackereth *et al.*, (1989)

Chemical	Detection Limit
Phosphorus (measured as P)	10 μg l^{-1} for 2000/2001 sampling, 1μg l^{-1} for 2002 sampling
Nitrogen (measured as N)	0.01mg l^{-1}
Ammonia (measured as N)	0.01mg l^{-1}
Silicon (measured as Si)	0.01mg l^{-1}
Dissolved Organic Carbon (measured as C)	0.01mg l^{-1}

Table 2.2: Detection limits for the chemical analyses. Throughout this study concentrations of nutrients are presented as elemental concentrations. For example, concentrations of phosphorus are presented as μg l^{-1} of P, not PO_4; concentrations of nitrates are presented as mg l^{-1} of N, not of NO_3; silicon as mg l^{-1} of Si, not of SiO_4. Similarly, ammonium nitrogen is presented as mg l^{-1} of N, and carbon as mg l^{-1} of C.

Phosphorus

For the analysis of phosphorus the autoanalyser uses an automated procedure based on the molybdenum blue method in which ammonium molybdate and potassium antimony tartrate react in an acidic medium with inorganic phosphate to form an antimony phospho-molybdate complex. This complex is reduced to an intensely blue coloured complex, which is measured at 880nm.

In this study soluble reactive phosphorus (SRP), total dissolved phosphorus (TDP), total phosphorus (TP) and total particulate phosphorus (TPP) were determined. Soluble reactive phosphorus is measured on 0.45μm filtered lake water and is a measure of the phosphorus available to phytoplankton (the molybdenum blue method only detects inorganic orthophosphate and does not measure organic phosphorus, thus the measure of SRP is a measure of the inorganic, dissolved orthophosphate). However, the

molybdemum blue method cannot distinguish between dissolved biologically available PO_4 and unavailable colloidal forms that are nevertheless small enough to pass through the 0.45μm filter. Therefore, a measure of dissolved PO_4 using the molybdemum blue may not be a true measure of biologically available P (Reynolds, 1984), hence the use of the term 'soluble reactive phosphorus' (SRP) rather that orthophosphate.

Total dissolved phosphorus is a measure of the phosphorus (inorganic and organic) in the dissolved form i.e. that passes through a 0.45μm filter. Total phosphorus is a measure of the total phosphorus (inorganic and organic) in unfiltered water and includes phosphorus within the phytoplankton, bacteria, detritus etc. as well as dissolved inorganic and organic forms. Total particulate phosphorus was not determined directly but was determined by subtracting the total dissolved phosphorus from the total phosphorus. As organic phosphorus is not detected by the molybdenum blue method the determination of TDP and TP requires the acid digestion of filtered and unfiltered water samples respectively. The digestion procedure converts all forms of phosphorus to orthophosphate.

The digestion method used is based on that used at the FBA Windermere laboratory, and involves a pressure digestion technique with sulphuric acid and potassium persulphate (Mackereth *et al.*, 1989). The sample is then analysed for orthophosphate. The digestion procedure is outlined below:

(i) A strong acid solution was prepared according to the following formula: 300ml sulphuric acid, 700ml distilled water and 4ml nitric acid. (This solution is stable for 3 months under refrigerated conditions).

(ii) 40ml of the sample to be digested was placed in a glass medicine bottle.

(iii) 0.4ml of the strong acid solution and 2/3 of a spatula of potassium persulfate ($K_2S_2O_8$) were added to the water sample and the resulting solution thoroughly shaken until the potassium persulphate had dissolved.

(iv) A blank was made by replacing the 40ml of lake water with 40ml of distilled water and repeating step (iii)

(v) The samples were then autoclaved at 121°C at 20 p.s.i for 30 minutes. The samples were then ready for analysis.

Nitrogen

In this study nitrate/nitrite (NO_x), total dissolved nitrogen (TDN), total nitrogen (TN) and total particulate nitrogen (TPN) were determined. For the analysis of nitrogen the autoanalyser uses a procedure based on the cadmium reaction method in which the sample is reduced from nitrate to nitrite by passing through a column containing granulated copper cadmium. Nitrite (original+reduced NO_3) is then determined by diazotizing with sulfanilamide and coupling with α-naphthylethylenediamine dihydrochloride to form a highly coloured azo dye which is measured at 540 nm. Note that this method does not distinguish between nitrate and nitrite.

Concentrations of NO_x were measured on 0.45μm filtered lake water directly. Total dissolved nitrogen is a measure of the nitrogen (inorganic and organic) in the dissolved form i.e. that passes through a 0.45μm filter. Total nitrogen is a measure of the total nitrogen (inorganic and organic) in unfiltered water and includes nitrogen within the phytoplankton, bacteria, detritus etc., as well as dissolved inorganic and organic forms. Total particulate nitrogen was not determined directly but was determined by subtracting the total dissolved nitrogen from the total nitrogen. The determination of total dissolved nitrogen and total nitrogen requires sample digestion to convert organic nitrogen to nitrate.

The digestion procedure involves the oxidation of the water sample with potassium persulphate under pressure, resulting in the conversion of organic nitrogen to nitrate (Mackereth *et al.*, 1989). The sample is then analysed for nitrate as described above. The digestion procedure is outlined below

(i) A 1.5M solution of NaOH was prepared by dissolving 60g NaOH in 1L distilled water. (This solution is stable for up to 3 months under refrigeration).

(ii) An oxidising reagent was prepared by dissolving 6.0g of potassium persulfate ($K_2S_2O_8$) in 100ml of the NaOH solution. (This solution is stable for up to 8 days under refrigeration).

(iii) 40ml of the water sample to be digested was placed in a glass medicine bottle.

(iv) 6ml of oxidising reagent was added to the sample and mixed by shaking the bottle. Note that this has the effect of diluting the sample resulting in the need to apply a correction factor to the concentration given by the analyser.

(v) A blank was made by replacing the 40ml of lake water with 40ml of distilled water and repeating step (iv)

(vi) The samples were then autoclaved at 121°C at 20 p.s.i for 30 minutes. The samples were then ready for analysis.

Ammonia

For the analysis of ammonia the autoanalyser uses an automated procedure based on the modified Berthelot reaction. Ammonia is chlorinated to monochloroamine, which reacts with salicylate to form aminosalicate. After oxidation and oxidative coupling a green coloured complex is formed, the absorption of which is measured at 660nm. Ammonia was determined by analysing 0.45µm filtered lake water directly.

Silicon

For the analysis of silicon the autoanalyser acidifies the sample and mixes it with ammonium molybdate solution to form molybdosilicic acid, which is then reduced by ascorbic acid to a blue dye, the absorbance of which is measured at 810nm. Silicon was determined by analysing 0.45µm filtered lake water directly.

2.3.2.2 Dissolved Organic Carbon

Dissolved organic carbon (DOC) was measured on a SKALAR SansPlus system autoanalyser. The automated procedure consisted of acidifying the sample and removing the inorganic carbon with nitrogen. Buffered persulphate was then added and the sample irradiated with UV light, following which hydroxylamine was added and the sample passed through a dialyser. The generated CO_2 diffused through a gas permeable silicon membrane and entered a weakly buffered recipient stream of weakly buffered phenolphthalein solution, the colour of which (measured at 550nm) decreases proportionately to the change in pH caused by the absorbed CO_2.

2.3.2.3 Colour

Colour was determined using the method described by Pace and Cole (2002). The absorbance of the water sample at 440nm was measured in a 5cm cell against a distilled water blank and the colour calculated as follows

$$A_{440} = 2.303 \times \left(\frac{absorbance\ at\ 440nm}{0.05m} \right) \qquad \textbf{Equation 1}$$

Colour is expressed as a wavelength specific absorption coefficient (units m^{-1}) and is related to the amount of light absorbing humic material in the water.

2.3.2.4 Total Suspended Solids and Total Organic Matter

These were determined as described by Allen (1989). Total suspended solids were analysed by filtering 500ml of lake water through an ignited (heated to 500°C for three hours) pre-weighed Whatman GF/C filter. The filter was then placed in an oven at 105°C for 24 hours to remove moisture, allowed to cool and weighed. The difference in weight was taken to be the total suspended solids present in the filtered sample. The filter was then heated to 500°C for three hours to remove the organic matter, the further loss in weight being taken as the total organic matter present in the sample.

2.3.3 Biota

2.3.3.1 Zooplankton

Total Biomass

The total dry weight of zooplankton was determined by filtering a full water column trawl through a pre-weighed GF/C filter. The filter was then placed in an oven at 105°C for 24 hours and weighed. The difference in weight gave the total dry weight of zooplankton in the volume trawled. The volume trawled was calculated multiplying the area of the opening of the zooplankton net by the depth of water through which the net was trawled. The volume of trawl was calculated as follows:

$$Volume\ of\ trawl(m^3) = \pi r^2 \times d \qquad \textbf{Equation 2}$$

where:

r = the radius of the opening of the zooplankton net in m (in this study r was 0.15m)

d = the depth through which the net was trawled through (in this study the depth of trawl was 20m for Rostherne Mere and 7m for Hollingworth Lake).

Thus, the dry weight (DW) of zooplankton is given by:

$$Zoo\ DW(mg\,l^{-1}) = \frac{(DW\ of\ zoo + filter(mg)) - (DW\ of\ filter(mg))}{Volume\ of\ trawl(m^3) \times 1000} \qquad \textbf{Equation 3}$$

Counts

Daphnids, calanoids and cyclopoids were counted using a Sedgewick-Rafter Chamber. The preserved zooplankton sample was made up to a known volume (referred to as *x*), the exact volume of which depended on the amount of zooplankton present-the more zooplankton the more it was necessary to dilute the sample. One ml of the sample was then placed in the Sedgewick-Rafter Chamber using a wide bore pipette. The contents of the whole slide were then counted (1ml). During the counts zooplankton were identified into main groups only - daphnids, calanoids and cyclopoids using the keys of Harding and Smith (1974) and Scourfield and Harding (1966).

Numbers per litre were then expressed using the following equation:

$$N^o\,l^{-1} = \frac{Counts\ in\ whole\ SR\ chamber\ i.e.(1ml) \times Vol\ of\ sample\ i.e.\ x(ml)}{Vol\ of\ trawl\ (m^3) \times 1000} \qquad \textbf{Equation 4}$$

where the volume of trawl was calculated using Equation 2. Note that the result of Equation 4 (numbers per litre) assumes that the zooplankton are evenly distributed throughout the depth of the vertical trawl.

Chaoborus larvae were counted in a 5ml Bogorof slide using the preserved sample that was used for the determination of *Daphnia* and copepods. Numbers were expressed per m^3 using the following equation:

$$N^o\, m^{-3} = \frac{Counts\ in\ Bogorof\ slide\ i.e.\ in\ 5ml \times (Vol\ of\ sample\ i.e.\ x\,(ml)/5)}{Vol\ of\ trawl\ (m^3)} \quad \textbf{Equation 5}$$

Rotifers were counted in a Sedgewick-Rafter chamber (note rotifer counts were performed by E. A. Baldwin). The preserved rotifer sample was made up to a known volume (x), the exact volume of which depended on the amount of rotifers present-the more rotifers the more it was necessary to dilute the sample. One ml of the sample was then placed in the Sedgewick-Rafter Chamber using a wide bore pipette. The contents of the whole slide were then counted. Rotifers were identified to at least genus level using Pontin (1978). Numbers per litre were expressed using the following equation:

$$N^o\, l^{-1} = \frac{Counts\ in\ whole\ SR\ chamber\ i.e.(1ml) \times Vol\ of\ sample\ i.e.\ x\,(ml)}{Volume\ of\ water\ filtered\ (litres)} \quad \textbf{Equation 6}$$

where the volume of water filtered was 20 litres (see section 2.2.2.1).

Ciliated protozoa were counted together as a single group, and were counted with the phytoplankton (see section 2.3.3.2).

Zooplankton Population Parameters

The proportion of gravid Cladocera is given by:

$$\%\,gravid = \frac{number\ of\ gravid\ zooplankton\ per\ litre}{total\ number\ of\ zooplankton\ per\ litre} \quad \textbf{Equation 7}$$

Average brood size for the gravid Cladocera were calculated as:

$$Average\ brood\ size = \frac{number\ of\ eggs\ per\ litre}{number\ of\ gravid\ females\ per\ litre} \quad \textbf{Equation 8}$$

Zooplankton birth rates were calculated by the following formula (Lynch, 1982):

$$b = \frac{\ln\left[\left(\frac{C}{N}\right)+1\right]}{D}$$ **Equation 9**

where:

C = the number of eggs per litre

N = the number of zooplankton per litre (in this study the number of adult *Daphnia/Bosmina* was used, rather than total number (George and Reynolds, 1997). It is difficult to distinguish adult and juvenile Cladocera, although only adults bear eggs. Therefore, non egg-bearing *Daphnia/Bosmina* were therefore defined as adults if their size was greater than that of the minimum sized egg-bearing, and hence adult *Daphnia/Bosmina.*

D = the egg development time and is calculated using the equation (Bottrell *et al.*, 1976):

$$\ln D = \ln a + b \ln T + C(\ln T)^2$$

Where T = temperature the zooplankton experience.

and ln a , b and c are defined as in the following table.

Group	ln a	b	c
Daphnidae	3.3956	0.2193	-0.3414
Calanoida	3.9650	-0.4049	-0.1909
Cyclopoida	4.1301	-0.4141	-0.2159

Note that the egg development time will vary depending on the temperature of the water column, which during stratification shows large differences between the epilimnion and hypolimnion. Hence, the positioning of the zooplankton within the water column will affect the egg development time. In this study it was assumed that the zooplankton were evenly distributed within the water column when the lake was isothermal, and T was taken to be the average temperature of the whole water column. During stratification it was assumed that the zooplankton avoided the anoxic hypolimnion (Stewart and Sutherland, 1993) and the average temperature within the epilimnion and thermocline was used.

Zooplankton Filtering Rates

Cladoceran filtering rates were calculated using the following equation (Knoechel and Holtby, 1986)

$$F = 11.695L^{2.480}$$ **Equation 10**

Filtering rates for calanoid copepods were calculated using the following equation (Haney, J. F, 1971, cited Sarnelle, O, 1993)

$$F = 9.44L^{1.133}$$ **Equation 11**

Where F=filtering rate in ml per animal per day

L=Animal body length (mm)

The community filtration rate G, was calculated using the following equation:

$$G = (F_D N_D) + (F_B N_B) + (F_C N_C)$$ **Equation 12**

Where F_D F_B and Fc are the filtering rates of the average *Daphnia*, *Bosmina* and Calanoid copepod, and N_D N_B and N_C are numbers l^{-1} of *Daphnia*, *Bosmina* and calanoid copepods respectively. G can be expressed either as a % of the water volume filtered per day, e.g. 33% day^{-1}, or as a proportion of the water volume filtered per day, e.g. 0.33 day^{-1}. Note that the calculation of community filtration rate depends on the numbers of zooplankton per litre. The numbers per litre calculated according to Equation 4 assumes that the zooplankton were evenly distributed within the water column. However, during stratification the zooplankton may be more numerous in the upper part of the water column as vertical distribution can be restricted by low oxygen conditions in the hypolimnion (Stewart and Sutherland, 1993). Thus, it was assumed that during stratification the total zooplankton population were distributed from the top of the water column to the base of the thermocline. Calculation of numbers per litre, and hence community filtration rate were calculated on this assumption.

Determination of biovolume edible phytoplankton available to *Daphnia* and *Bosmina*

The maximum size of ingested particles for Cladocera was calculated from the following equation (Burns, 1968):

$$S = 22L + 4.87$$ **Equation 13**

Where S=maximum size of particle ingested

L=Animal body length (mm)

2.3.3.2 Phytoplankton

Counts

Analysis was undertaken according to standard methods (Standing Committee of Analysts, 1990). Prior to enumeration the phytoplankton was concentrated by sedimentation. However, to ensure that the cyanobacteria were sedimented it was necessary to collapse their gas vacuoles. This was achieved by dropping the polyethylene bottle containing the fixed iodine sample from a height of 1.5m onto a hard surface. The sudden pressure increase as the bottle strikes the surface serves to collapse the vacuoles. A 1:10 concentration was achieved by placing 250ml of the iodine fixed sample in a measuring cylinder, which was then stored in a darkened area at a fixed temperature for 48 hrs. The top 225ml was then siphoned off using an upturned siphon tip (to reduce the chances of drawing off sedimented cells) leaving a concentrated sample in the remaining 25ml. The concentrated sample was then transferred to a universal tube for storage.

Enumeration of the phytoplankton was carried out by placing a 1mm aliquot of the concentrated iodine sample into a Sedgewick-Rafter Chamber. Twenty squares (enough to count ≈200 cells/colonies of the most common species) were randomly selected and the algae contained therein counted and identified. Algae were identified to genus and sometimes species level using keys (Bellinger, 1992, Belcher & Swale, 1976). Small phytoplankton of <10μm GALD were counted as a group, although the presence of dominant species was noted. The number of cells was then totalled and used to determine the number of cells in 1ml of the original un-concentrated lake water using the following equation.

$$Cells/ml = \frac{N^{o}\ of\ cells\ in\ 1ml\ concentrated\ sample(i.e.total\ in\ 20\ squares \times 50)}{Concentration\ factor}$$

Equation 14

Cell Sizes, Biovolumes and Carbon Content

Cell dimensions were determined using an eyepiece micrometer, the greatest dimension of the cell being recorded as the greatest axial linear dimension (GALD). Biovolumes of phytoplankton were calculated from cell dimensions using the geometrical formulas given by Wetzel and Likens (2000), and by reference to the literature (Stephen, 1997; Reynolds and Bellinger, 1992). Total phytoplankton

biovolumes, and biovolumes for each algal group, were calculated using the following equation:

$$BV\left(\mu m^3\ ml^{-1}\right) = n_1 v_1 + n_2 v_2 .... + n_i v_i \qquad \textbf{Equation 15}$$

Where v_i is the biovolume of a cell, colony or filament of the i^{th} species (as given in Table 2.3) and n_i is the recorded concentration of the i^{th} species (cells, colonies or filaments per ml).

A ratio of cellular organic carbon (pg) to cell volume (μm^3) of 0.21 was used to estimate the cellular organic carbon of phytoplankton (Reynolds, 1984a).

Chlorophyll-a

Determination of chlorophyll-a used the ethanol extraction method described by Jesperson and Christoffersen (1987). Separation of the algae was facilitated by vacuum filtering 500ml of the integrated sample through a Whatman GF/C filter. Pigments were extracted by chopping up the filter paper and placing the pieces into a universal tube to which 10ml of 96% ethanol was added. The universal tubes were then placed in the dark at 4°C for 20 hrs to allow time for the pigments to be fully extracted. The solution was then centrifuged for 10 minutes at 3300 rpm, following which 1ml aliquots of the supernatant was pipetted into non-UVB 1ml quartz cuvettes which was then placed in a Cecil CE 1020 series spectrophotometer. Calculation of the chlorophyll-a concentration was based on the measured absorbance at 665nm corrected for turbidity (750nm). The following equation was used.

$$Chl-a\left(\mu g\, l^{-1}\right) = \frac{V_e \times f \times A}{V_s \times l} \qquad \textbf{Equation 16}$$

Where: V_e = total volume of solvent (ml)

A = Absorbance at 665nm - Absorbance at 750nm

V_s= Total volume of sample filtered (litres)

L = Cell path length (cm)

f=(1/specific extraction coefficient)*1000

where the specific extinction coefficient for chlorophyll-a in ethanol is 83.41 g^{-1} cm^{-1} (Winthermans & Demots, 1965).

	Species	Colony/cell/ filament biovolume (μm^3)	
Bacillariophyceae	*Asterionella formosa*	5040*	1
	Aulacoseira granulata var. angustissima	8500*	1
	Cyclotella sp. (large)	1000	1
	Cyclotella sp. (small)	160	1
	Melosira sp.	16000*	1
	Nitzschia spp.	300	1
	Synedra sp.	600	1
	Stepanodiscus sp.	380	1
	Stephanodiscus rotula	25000	1
	Tabellaria fenestrata	950	1
	Tabellaria fenestrata var. Asterionelloides	7125*	1
Chlorophyceae	*Actinastrum* sp.	1050*	1
	Ankyra sp.	40	1
	Chlamydomonas sp.	100	2
	Chlorella sp.	30	3
	Coelastrum sp.	6500	3
	Dictyosphaerium sp.	1500*	1
	Elakatothrix gelatinosa	170	1
	Monoraphidium sp.	45	1
	Micractinium sp.	1440*	3
	Eudorina sp.	5600*	3
	Pediastrum duplex	16000*	3
	Scenedesmus obliquus	160*	1
	Scenedesmus quadricauda	160*	1
	Sphaerocystis	160*	1
	Staurastrum sp.	3100 (2 semi cells)	2
Cryptophyceae	*Cryptomonas* spp.	1050	1
	Rhodomonas minuta	140	1
Cyanophyceae	*Anabaena* spp.	2165*	2
	Aphanizomenon flos-aquae	1520*	1
	Aphanocapsa sp.	6000*	4
	Gloecapsa spp.	500	1
	Gomphosphaeria sp.	55000*	1, 5
	Microcystis spp.	77117*	2
	Oscillatoria spp.	800	1
	Synechococcus sp.	20	1
Dinophyceae	*Ceratium hirundinella*	41400	2
	Peridinium cinctum	48000	1
	Peridinium sp.	12000	1

Table 2.3: Table of biovolumes for phytoplankton observed during this study. * biovolume for a typical colony or filament ; [1] calculated from the geometrical formulas in Wetzel and Likens (2000) and Willen (1976); [2] taken from Reynolds and Bellinger (1992); [3] taken from Bellinger (1974); [4] taken from Stephen (1997); [5] colony biovolume estimated by multiplying cell volume by the number of cells in an average colony, estimated using the following equation (Reynolds and Jaworski (1978): $\log_{10}$ (Num of cells) = 2.99 log 10 (colony diameter (μm))-2.80

Growth and Loss Rates of the Phytoplankton

In the discussion growth rates and loss rates of selected phytoplankton species are calculated using the following equations. For a full derivation of the equations and further information concerning their use the reader is referred to Reynolds (1984a).

The observed growth rate where (i.e. the exponential growth rate constant, k) was calculated from

$$k = \frac{\left[\ln\left(\frac{N_t}{N_0}\right)\right]}{t_1 - t_0} \qquad \textbf{Equation 17}$$

where N_0 is the initial number of algae at t_0 and N_t is the number at time t_1.

In natural waters, the final N_t reached is net of losses due to grazing, sedimentation, washout, etc, so the exponential growth constant calculated above is actually the growth rate net of losses k_{net}, i.e.:

$$k_{net} = k_{\max} - \left(k_{grazing} + k_{sed} + k_{washout}\right) \qquad \textbf{Equation 18}$$

It can be seen that for a phytoplankton population to decline its losses ($k_{grazing}+k_{sed}+k_{washout}$) must exceed the maximum growth rate k_{max} of the phytoplankton population.

Grazing losses are calculated using the following equation:

$$k_{grazing} = G\phi \qquad \textbf{Equation 19}$$

Where G = the community filtration rate, which is the total volume of water filtered per unit time, expressed as a proportion.

ϕ = the coefficient of selectivity, which is the probability that a particular phytoplankton cell will be ingested and ranges between 0 and 1. Cells that are fully ingestible have a coefficient of 1, those that are completely inedible 0.

Losses through sedimentation can be expressed as the following:

$$K_{sed} = \frac{\left[\ln\left(1 - \left(\frac{V_t}{Z_m}\right)\right)\right]}{t} \qquad \textbf{Equation 20}$$

Where V_t=the terminal sinking velocity of the cells and Z_m is the depth of the upper mixed zone (i.e. the upper isothermal layer in a stratified lake)

Losses due to washout are calculated from

$$k_{washout} = \frac{q}{V}$$ **Equation 21**

where q= outflow volume (m^3 day^{-1})

V= mixed layer volume (m^3)

2.3.3.3 Bacteria

Total counts

The enumeration of total bacteria was carried out using DAPI fluorescent microscopy. The procedure followed was that described by Porter and Feig (1980).

A concentrated DAPI stock solution (5 mg ml^{-1}) was prepared using sterile, 0.2μm filtered, distilled water (stable indefinitely at 0°C). The concentrated DAPI solution was then diluted to 100 μg ml^{-1} (stable for several weeks at 4°C). In the filtering apparatus 20μl of the diluted DAPI solution was added to between 50 and 200μl of sample (depending on the dilution factor required to give approximately 20 counts per field of view when counting) and the volume made up to 8ml with 0.2μm filtered sterile distilled water, giving a final DAPI concentration of 0.2μg ml^{-1}. The sample was then allowed to stand for 5 minutes before being drawn through the filter with a vacuum pump. Samples were filtered onto 0.2μm black Isopore membrane filters. The filter was then removed and a drop of immersion oil placed on the filter and a round 25mm coverslip placed on top. The bacteria were then counted on a fluorescent microscope under UV light at 1000x magnification. The bacterial numbers/unit volume calculated using the following equation (Jones, 1979):

$$n = \left(\frac{X \times A \times d}{a \times V} \right)$$ **Equation 22**

where

X = mean count per graticule area used

A = filtration area of membrane

a = the graticule area

V = volume of sample filtered

d = the dilution factor if applicable

Cell Sizes, Biovolumes and Carbon Content

Mean carbon content of bacteria was taken to be 0.013pg C per cell (quoted by Thompson *et al.*, 1982).

Viable counts

Viable bacterial determinations were undertaken according to the procedures described by Jones (1979). Samples of lake water were filtered through 5μm cellulose acetate filters to remove algal cells and 100μl of the filtrate pipetted (in triplicate) onto petri dishes containing Standard Nutrient Agar (Oxoid). The petri dishes were then incubated for 3 days at 37°C. Aseptic techniques were used throughout. The numbers of colonies were then counted and the numbers scaled up to give viable cells ml^{-1}.

SECTION B: ROSTHERNE MERE

Chapter 3 Results for Rostherne Mere

3.1 Rostherne Mere 2000

The following results are presented in four sections – phytoplankton, physico-chemico parameters, zooplankton and bacteria/dissolved organic carbon. The rationale for the presentation of the results in this order (conventionally physico-chemical parameters are presented first) is that the results are discussed in terms of the top-down and bottom-up influences on the phytoplankton. Phytoplankton is thus presented first, followed by the physico-chemical parameters (bottom-up) and then Section 3.1.3 examines the zooplankton (top-down). Data relating to bacteria are presented at the end in section 3.1.4 as the bacterial populations are dependent on many of the parameters described in the previous three sections, as well as other factors such as dissolved organic carbon and total suspended solids, which are described along with the bacteria.

In the following results, the description of each parameter is referred to in terms of phases, with each phase relating to a stage in the annual succession of the phytoplankton. Phases are defined in terms of phytoplankton biomass (chlorophyll-a), and in relation to the dominance of different taxonomic groups of phytoplankton. For Rostherne Mere in 2000 the year has been split into 6 phases –

Initial winter phase, 27th January - 17th February

Spring phase, 9th March - 20th April

Clear-water phase, 11th May- 24th May

Cryptomonad phase, 31st May-21st June

Summer phase, 28th June - 31st August

Autumn phase, 8th September - 25th October

Winter phase, 15th November - 08th February

The rationale for the selection of these phases will become clear in the following description of the phytoplankton (section 3.1.1).

3.1.1 Phytoplankton

3.1.1.1 Chlorophyll-a and Secchi Depth

Chlorophyll-a and Secchi depth are shown in Figure 3.1. During the spring phase chlorophyll-a increased slightly, reaching a maximum of 10.5μg l^{-1}. There was then a short clear-water phase during May, with low levels of chlorophyll-a (max 7μg l^{-1}) and high Secchi disk transparency (>3m). This was followed by the cryptomonad phase with a substantial peak 75μg l^{-1} during early June (Secchi depth 1.5m), before a short return to conditions similar to that during the clear-water phase (chlorophyll-a 5μg l^{-1}, Secchi depth 3.1m). There then followed an increase in chlorophyll-a concentrations that lasted throughout the summer. Concentrations increased rapidly, reaching a maximum of during late July of 159μg l^{-1} with a Secchi depth of 0.93m. There was a decrease in chlorophyll-a (74μg l^{-1}) during early August before once again increased, reaching a second peak on the 31st of August (chlorophyll-a 127μg l^{-1}, Secchi depth 1.0m). Chlorophyll-a dropped to ≈ 40μg l^{-1} during September (Secchi approximately 1.35m). From October onwards, chlorophyll-a fell, reaching <1μg l^{-1} during December, remaining at this concentration through to November; Secchi depth increasing during this period to reach a maximum of 2.7m in February.

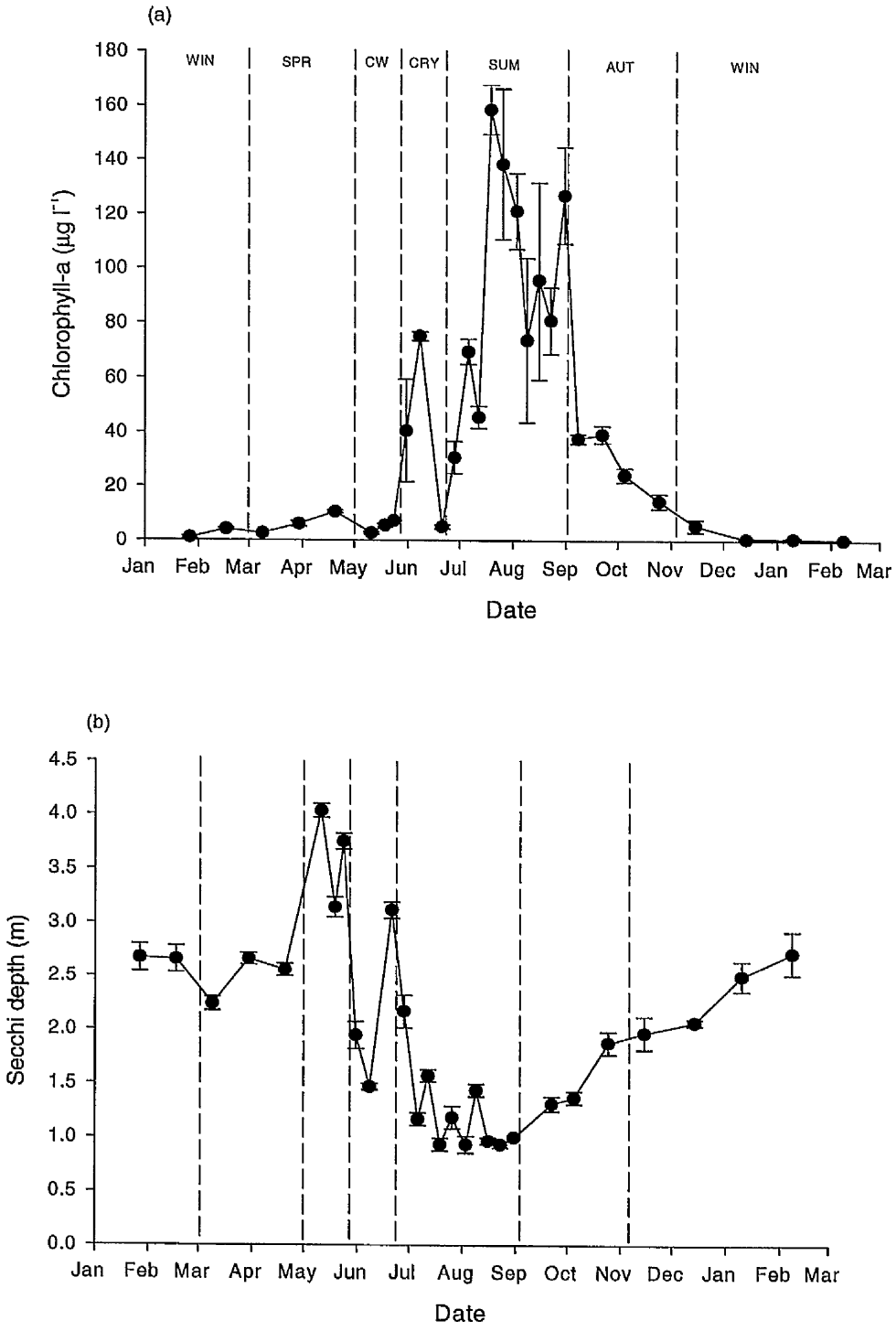


Figure 3.1: Seasonal changes in (a) Chlorophyll-a and (b) Secchi depth in Rostherne Mere 2000. Values are the mean of sites A, B and C. Error bars ±1 SD. (n=3). In some cases error bars are too small to visualise.

3.1.1.2 Major groups

The total algal biovolume and the biovolumes of each algal group are shown in Figure 3.2 to Figure 3.5. Figure 3.2(b) shows the percentage contribution of each algal group to the total biovolume. Figure 3.6 shows the seasonal variation in the biovolume of phytoplankton species considered edible to filter feeding Cladocera. From the biovolumes it can be seen that the phytoplankton showed the following seasonal succession: Diatoms $\Rightarrow$ Clear-water phase $\Rightarrow$ Cryptomonads $\Rightarrow$ Dinoflagellates $\Rightarrow$ Cyanophyceae $\Rightarrow$ Diatoms, with a Chlorophyceae maximum occurring during the dinoflagellate phase. Bacillariophyceae peaked in April ($1.44x10^6\mu m^3\ ml^{-1}$), followed by a large short lived, larger peak in July ($4.67x10^6\mu m^3\ ml^{-1}$), and then a small peak in December ($0.44x10^6\mu m^3\ ml^{-1}$). Cryptomonads peaked in early June ($2.61x10^6\mu m^3\ ml^{-1}$), interrupting the clear-water phase peak, and then oscillated throughout the summer. During the long summer maximum dinoflagellates were dominant during July and August with large peaks in late July (max. $48.1x10^6\mu m^3\ ml^{-1}$) and late August ($40.1x10^6\mu m^3\ ml^{-1}$). Chlorophytes peaked in early August ($3.51x10^6\mu m^3\ ml^{-1}$) while Cyanophyta showed large peaks in late July ($2.38x10^6\mu m^3\ ml^{-1}$) and late August ($3.38x10^6\mu m^3\ ml^{-1}$), with elevated levels through September and October ($\approx 0.8x10^6\mu m^3\ ml^{-1}$). In terms of the major groups of phytoplankton the phases can be described as follows.

Winter: 27th January and 17th February

This phase was dominated by cryptomonads (75% of biovolume), followed by diatoms (96%).

Spring phase: 9th of March - 20th of April

Diatoms were dominant throughout this period, contributing around 90% of the total algal biovolume. Cryptomonads contributed approximately 10% to the total algal biovolume. Chlorophyceae contributed a maximum of 1% while Cyanophyceae and Dinophyceae were absent.

Clear-water phase: 11th of May- 24th of May

Cryptophyceae were dominant at between 36 and 86% with Dinophyceae and Cyanophyceae contributing approximately 30% of the biomass at others times. Very low phytoplankton biomass and high Secchi depths characterized this phase.

Cryptomonad phase 31st of May-21st of June

This may be considered as an interruption to the clear-water phase, with Cryptophyceae again dominant. It is considered a separate phase as Cryptophyceae biomass increased to high levels.

During the peak in chlorophyll-a the phytoplankton was dominated by cryptomonads (>66%). However, by the return to clear-water conditions dinoflagellates were dominant (76%). The combined contribution of the three other groups was never more than ≈ 10% over this period.

Summer phase: 28th June - 31st August

During the summer period dinoflagellates dominated, contributing a minimum of 75% (28th June) of the biovolume and a maximum of 93% (26th of July). The biovolume of the each of the other groups was generally around 2-3% during this time, but on occasion the contribution of individual groups increased to around 10%, for instance the contribution of cyanophytes was approximately 10% on the 6th July, 3rd August and 23rd August, corresponding to the peaks in cyanophyte biovolume. The maximum contribution of diatoms was 13% on the 19th June corresponding to the peak in diatom biovolume; at other times its contribution was <2%. Chlorophytes contribution varied between 1 and 11%, the maximum occurring on 3rd of August, corresponding to the maximum Chlorophyceae biovolume. Cryptomonad biovolume reached 11% on the 28th of June, but generally varied between 0 and 5%.

Autumn phase: 8th September - 25th October

During September the contribution of Dinophyceae had fallen to around 60%, with Cyanophyceae becoming more important, contributing approximately 30% of the total biovolume. Chlorophyceae contributed a maximum of 8%, diatoms 6% and cryptophytes no more than 2%. By the end of the phase, dinoflagellates contributed 0% of the biovolume and cyanophytes approximately 80% of the biovolume

Winter: 15th November - 08th February

In November, cyanophytes contributed approximately 27% of the biovolume, with cryptophytes contributing 24% and chlorophytes 43%. From December onwards diatoms dominated, with > 95% of the biovolume.

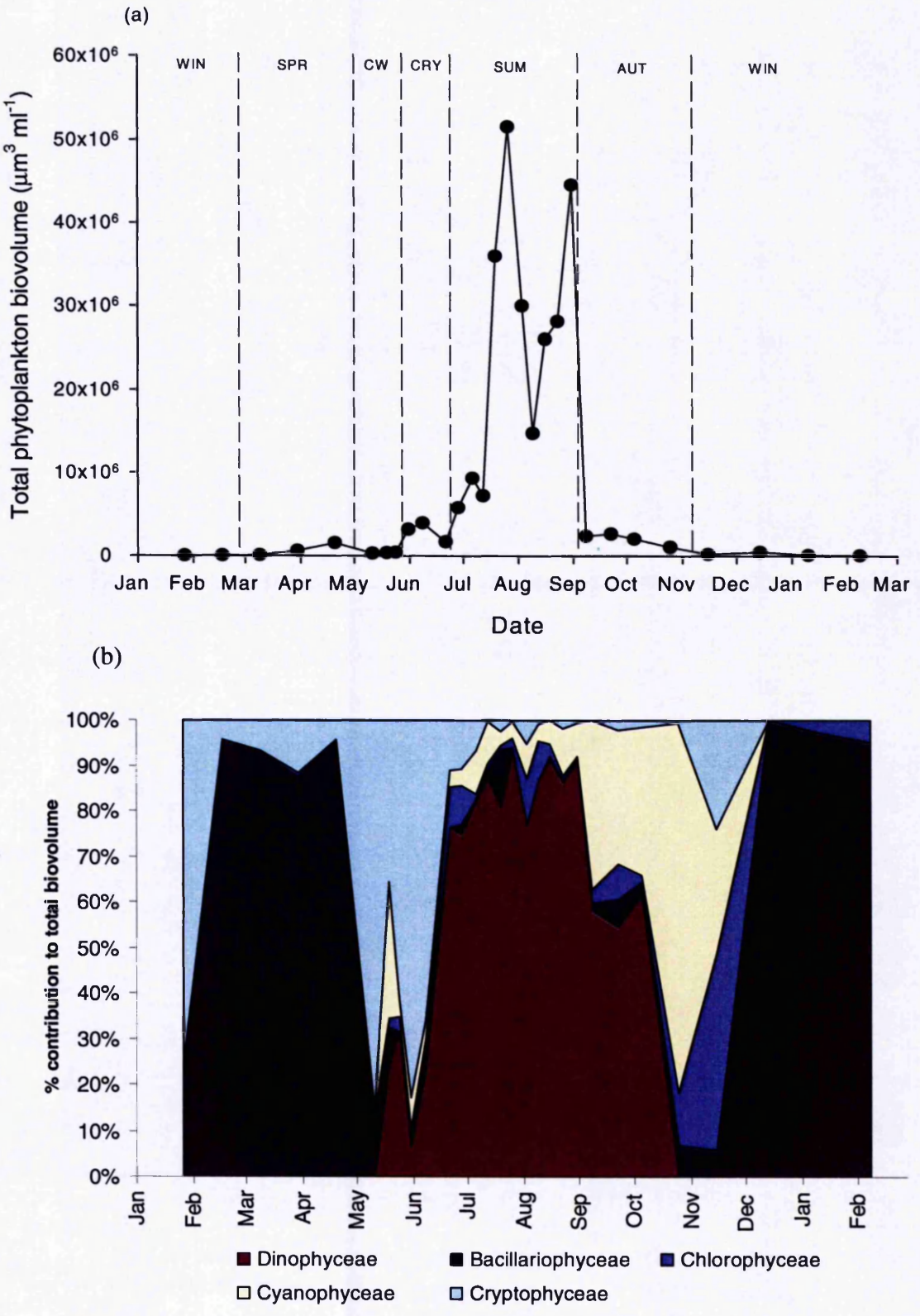


Figure 3.2: Seasonal changes in (a) the biovolume of total phytoplankton and (b) the percentage contribution of each algal group to the total biovolume. Rostherne Mere, 2000.

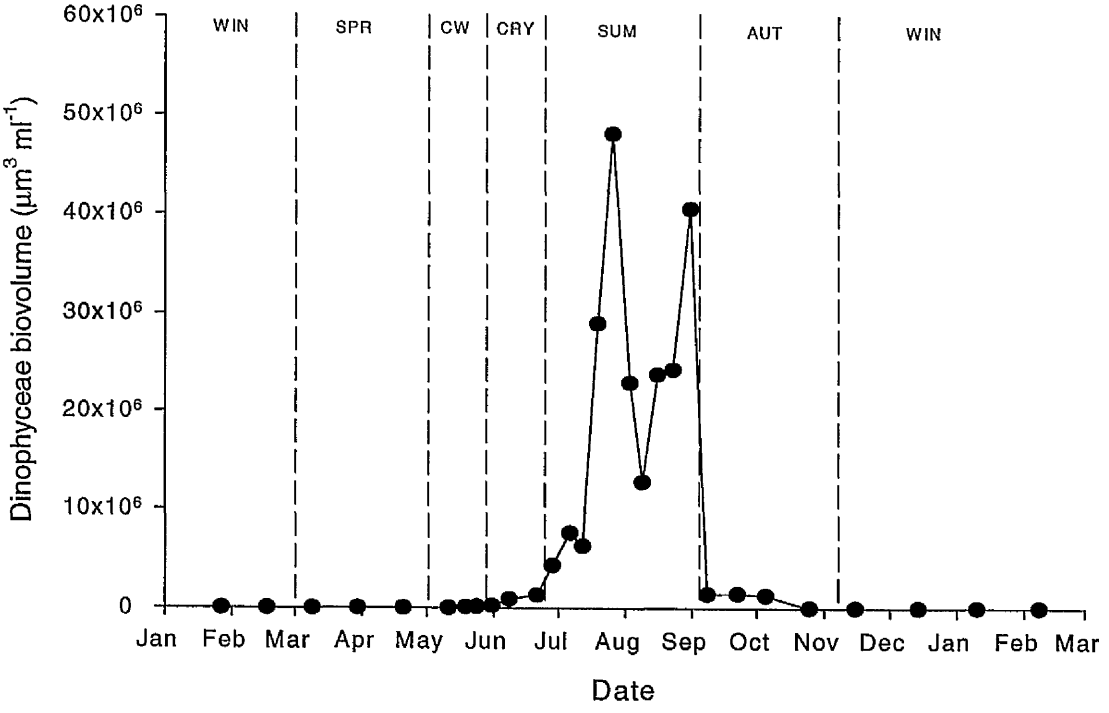


Figure 3.3: Seasonal changes in the biovolume of Dinophyceae in Rostherne Mere, 2000. Biovolumes are calculated using the mean count from integrated samples from sites A, B and C.

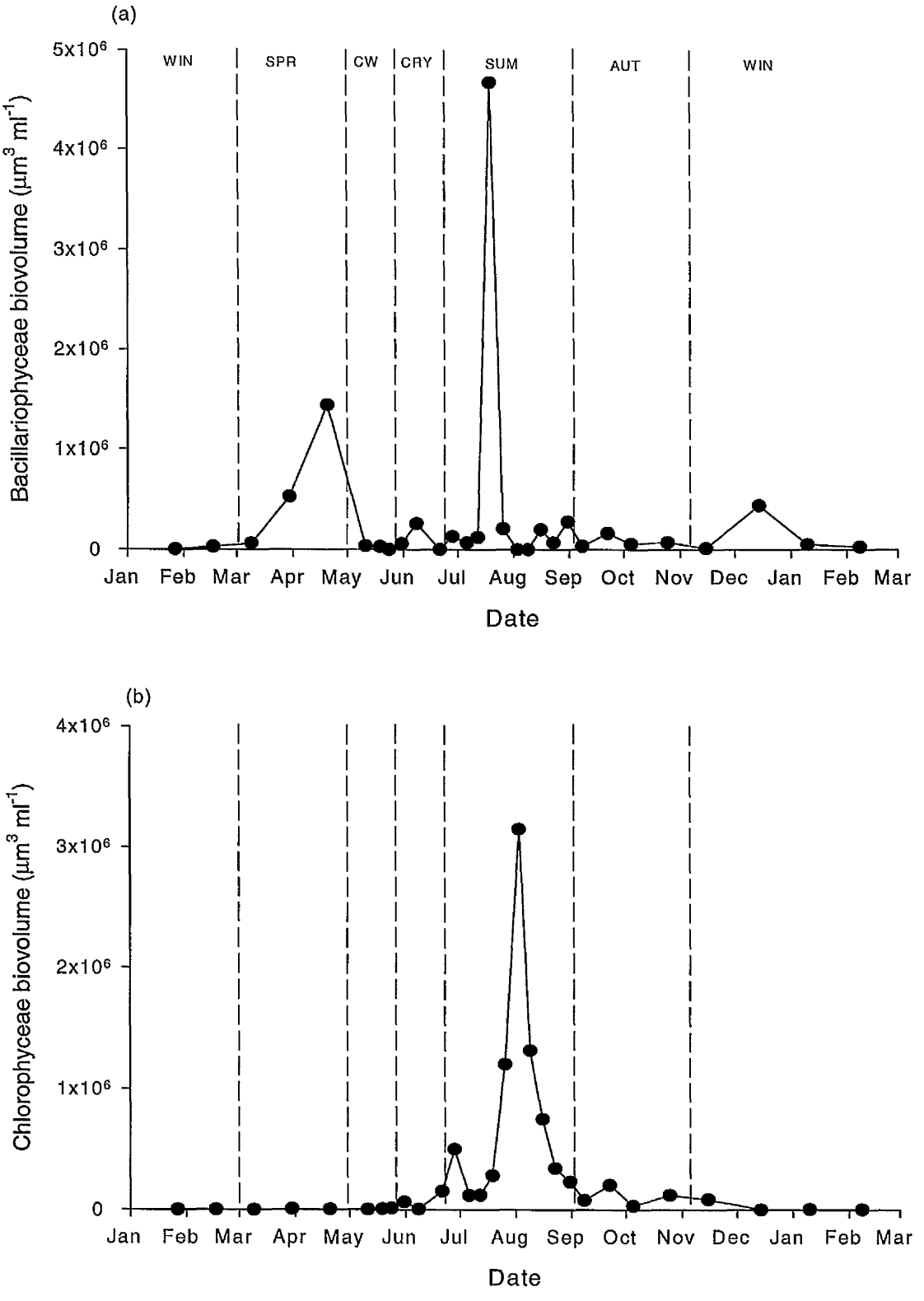


Figure 3.4: Seasonal changes in the biovolume of (a) Bacillariophyceae and (b) Chlorophyceae in Rostherne Mere, 2000. Biovolumes are calculated using the mean count from integrated samples from sites A, B and C.

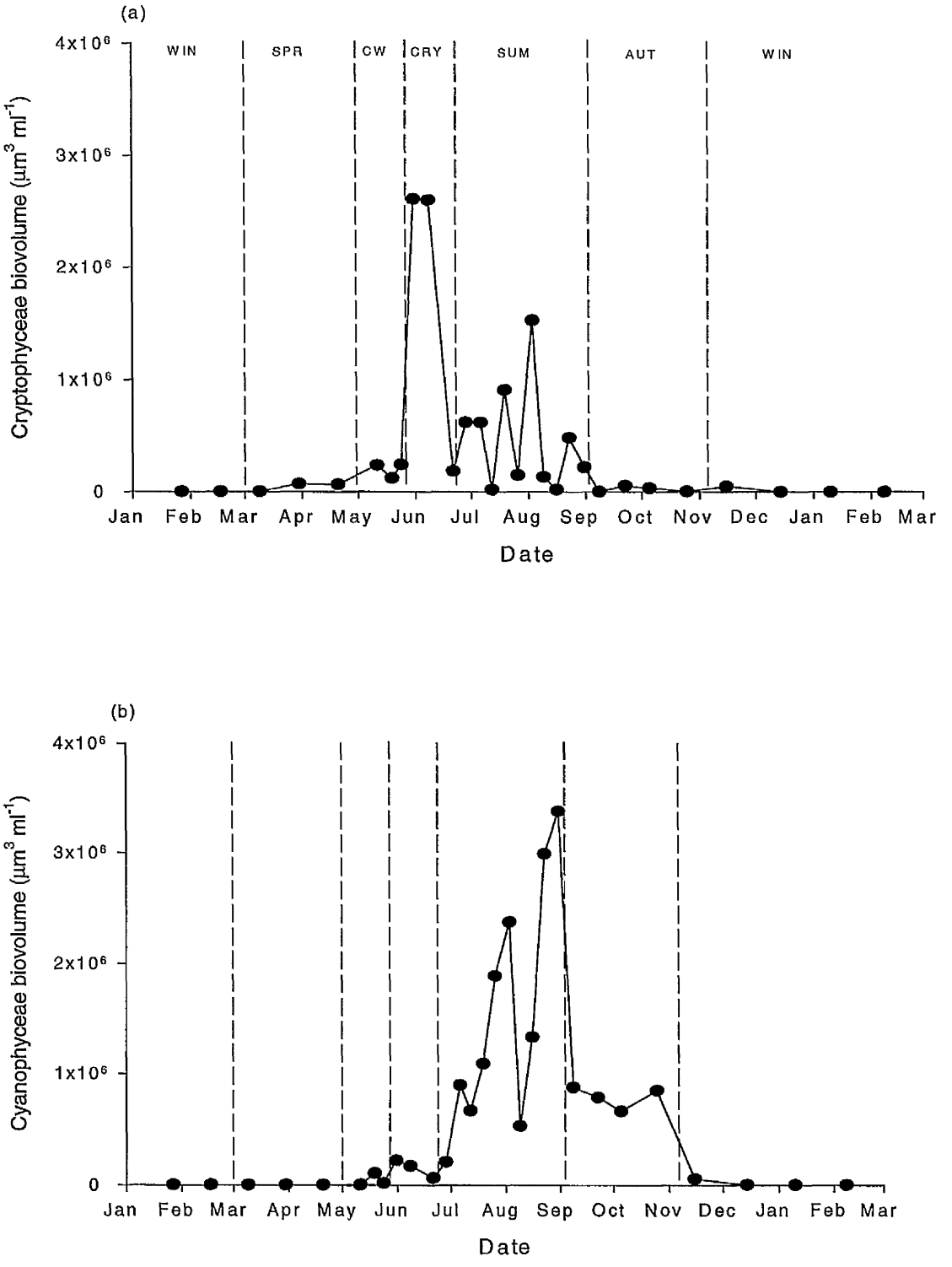


Figure 3.5: Seasonal changes in the biovolume of (a) Cryptophyceae and (b) Cyanophyceae in Rostherne Mere, 2000. Biovolumes are calculated using the mean count from integrated samples from sites A, B and C.

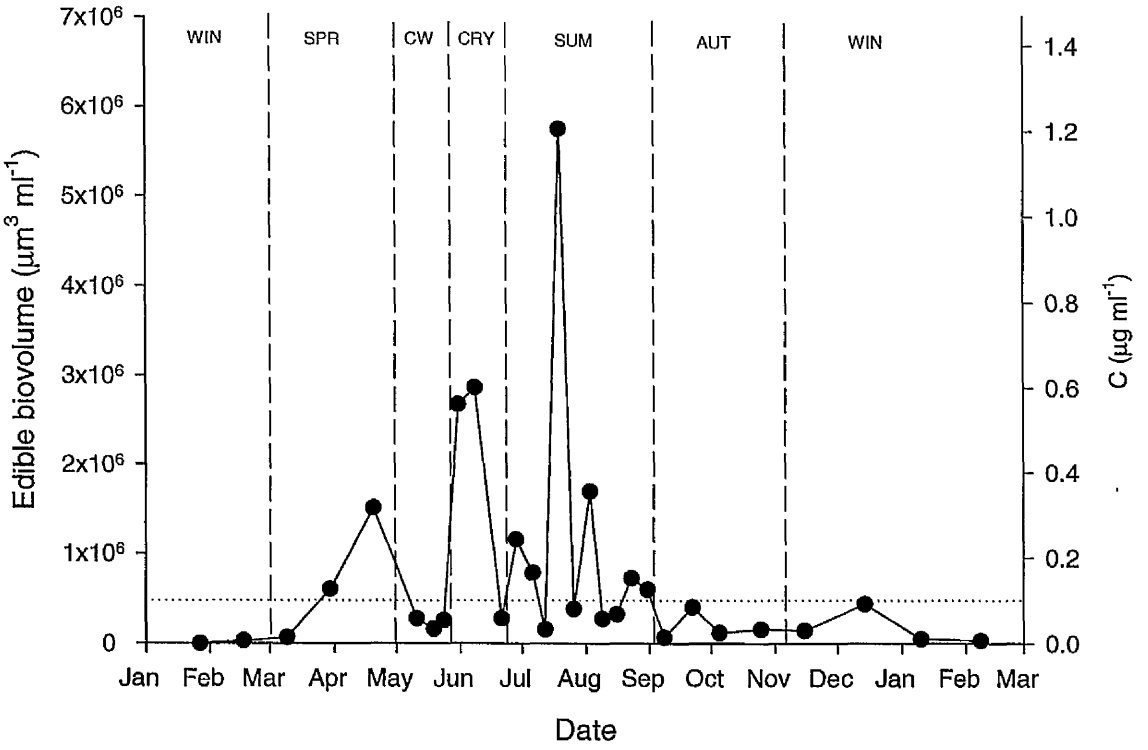


Figure 3.6: Seasonal change in the biovolume of edible phytoplankton species, Rostherne Mere 2000. Edible phytoplankton species include all those whose parameters fall within the size range given by the Burns' equation. Also included are some larger species which evidence suggests can be ingested by *Daphnia*. In the figure above the peak during the spring consists primarily of *Asterionella formosa* and *Stephanodiscus rotula*. The peak during the cryptomonad phase consisted of *Cryptomonas* spp. and *Rhodomonas minuta*. The large peak during the summer was due to *Stephanodiscus hantzschii*. During the rest of the summer, and during the autumn and winter phases the edible phytoplankton consisted of cryptomonads and small Chlorophyceae. The secondary axis shows the edible biovolume expressed as carbon. The horizontal line is the threshold concentration of edible food for *Daphnia*, below which *Daphnia* are food-limited.

3.1.1.3 Phytoplankton Species

Counts of individuals (cells or colonies) are shown in Figure 3.7. to Figure 3.14. Only the main contributors of each group are shown in the figures. Figure 3.7 and Figure 3.8 show changes in the main Bacillariophyceae species, Figure 3.9 shows the Cryptophyceae. Chlorophyceae are shown in Figure 3.10 and Figure 3.11, Cyanophyceae in Figure 3.12 and Figure 3.13 and Dinophyceae in Figure 3.14.

Winter phase: 27th of January and 17th of February

The only phytoplankton present at this time were *Cryptomonas* spp. and *Rhodomonas minuta* (both 1 cell ml^{-1}), *Stephanodiscus rotula* (1 cell ml^{-1} on the 17th of February) and the small *Stephanodiscus minutula* (3 cell ml^{-1}) on the same date.

Spring phase: 9th of March - 20th of April

On the 9th of March, *Stephanodiscus minutula* was the most numerous diatom, present at 28 cells ml^{-1} (having increased from 3 cells ml^{-1} on the 17th of February). Numbers continued to increase, reaching a maximum of 79 cells ml^{-1} on the 30th of March. *Stephanodiscus rotula* increased from 1 cell ml^{-1} on the 17th of February to a maximum of 46 cells ml^{-1} on the 20th of April. *Asterionella* first appeared in the phytoplankton on the 30th of March (4 colonies ml^{-1}) and increased to 53 colonies ml^{-1} on the 20th of April. Within the Bacillariophyceae the much larger size of the *Stephanodiscus rotula* cells led to this species contributing >80% of the diatom biomass on all occasions. The maximum contribution of *Asterionella* was 19% on the 20th of April. The maximum contribution of the small *Stephanodiscus* sp. was 18% on the 9th of March.

Within the Cryptophyceae *Cryptomonas* increased from 1 cell ml^{-1} to a maximum of 42 cells ml^{-1} on the 20th of April. *Rhodomonas* increased from 9 cells ml^{-1} to a maximum of 309 cells ml^{-1} on the 30th of March before dropping to 156 cells on the 20th of April. In terms of biovolume *Cryptomonas* was usually the dominant cryptomonad. An exception was the 30th of March when the *Rhodomonas* peak led to it contributing 61% of the cryptomonad biomass.

Chlorophyceae were very scarce, the only recorded species were *Ankyra* sp. (max 22 cells ml^{-1} on the 20th of April and *Scenedesmus quadricauda* (5 cells ml^{-1} on the 20th of April).

No dinoflagellates or cyanophytes were observed during this phase.

Clear-water phase: 11th of May- 24th of May

All phytoplankton groups were present at this time but in very low numbers. Numbers of diatoms were very low during this phase, at the beginning of which *Asterionella formosa* was present at only 2 cells ml^{-1} and *Stephanodiscus rotula* only 1 cell ml^{-1}.

At the commencement of the phase (11th May) *Cryptomonas* spp. was the most numerous phytoplankton with 222 cells ml^{-1}, remaining at this level throughout the clear-water phase. *Rhodomonas* was less numerous with 36 cells ml^{-1}, but increased to 211 cells ml^{-1} by the 24th May.

The only chlorophyte was *Ankyra* sp., numbers of which increased throughout this phase, from 30 cells ml^{-1} to 333 cells ml^{-1}.

Aphanizomenon was the only cyanophyte present, increasing from 0 to 60 filaments ml^{-1} by the 19th of May.

Dinoflagellates first appeared at this time with *Ceratium* present at 2-3 cells ml^{-1}.

Cryptomonad phase 31st of May-21st of June

Cryptophyceae increased rapidly during this phase. *Cryptomonas* spp. increased from 204 cells at the end of the previous phase (24th of May) to 2148 cells ml^{-1} at the commencement of this phase. Numbers remained high at the peak chlorophyll-a level (June the 8th) at 2301 cells ml^{-1}. *Rhodomonas* also increased rapidly, from 211 cells ml^{-1} at the end of the last phase to 2557 cells ml^{-1} at the start of this phase, followed by a fall to 1331 cells ml^{-1} on the 8th of June. By the 21st (when clear-water conditions returned) numbers of both cryptomonads had dropped dramatically with *Cryptomonas* at 163 cells ml^{-1} and *Rhodomonas* at 107 cells ml^{-1}.

The dinoflagellate *Ceratium hirundinella* increased from 5 to 25 cells ml^{-1} over this period and *Peridinium* sp. first appeared in the plankton at this time, with ≈10 cells ml^{-1} during June.

Within the cyanophytes, *Anabaena* peaked at 60 colonies ml^{-1} on the 8th of June while *Aphanizomenon* decreased from a maximum of 105 filaments ml^{-1} on the 31st of May to 5 cells ml^{-1} at the end of this phase.

Ankyra sp. was the most numerous of the chlorophytes, increasing from 0 to 230 cells ml^{-1} between the 8th and 21st of June. *Scenedesmus quadricauda* reached 30 cells

ml^{-1} on the 8th of June. Diatoms were also present during this period but in very low numbers.

Summer phase: 28th June - 31st August.

Dinophyceae dominated the phytoplankton during the summer phase. Two Dinophyceae species were present, *Peridinium* sp. and *Ceratium hirundinella. Ceratium* was the first to increase, reaching a maximum of 85 cells ml^{-1} on the 6th of July, ending the continuous increase had had begun in the clear-water phase; numbers then dropped to approximately 15cells ml^{-1} before increasing to 85 cells ml^{-1} on the 31st of August. *Peridinium* also continued to increase in numbers during the early part of the summer phase, showing a particularly rapid increase from 118 cells ml^{-1} on the 12th of July to 966 cells ml^{-1} on the 26th July. Numbers then decreased to 253 cells ml^{-1} before increasing to 770 cells ml^{-1} on the 31st of August. *Peridinium* sp. biovolumes dominated *Ceratium* from the 12th of July onwards, with more than 90% of the Dinophyceae biovolume being due to *Peridinium.*

Within the diatoms, the unidentified small pennate diatom increased from 5 cells (28th of June) to a maximum of 170 cells ml^{-1} on the 19th of July. However, the small *Stephanodiscus hantzschii* completely dominated the diatoms at this time, increasing from 160 cells ml^{-1} on the 12th of July to 12000 cells ml^{-1} just one week later, (19th of July) when it contributed 98% of the diatom biomass. By the following week (26th July), *Stephanodiscus* numbers had fallen to 545 cells ml^{-1}, and the small pennate diatom was absent. *Stephanodiscus* showed a further small peak in late August, reaching 730 cells ml^{-1} on the 31st.

The summer phase period also showed a noticeable increase in cyanophytes. *Anabaena flos-aquae,* which first increased during the previous phase, and continued to increase in numbers peaking at 230 colonies ml^{-1} on the 6th of July. It then declined, and was absent from the phytoplankton by August. *Aphanizomenon flos-aquae* increased from 5 filaments ml^{-1} at the start of the phase to a maximum of 1190 filaments ml^{-1} on the 3rd of August; it then declined rapidly to 165 filaments ml^{-1} one week later (9th of August) and continued to fall, reaching 10 filaments ml^{-1} at the close of the phase. *Microcystis* increased during the later half of August, reaching a maximum of 42 colonies ml^{-1} on the 31st of August.

It was during the summer phase that large numbers of chlorophytes first appeared in the plankton, peaking in late July/early August. *Ankyra* sp. peaked at 160 cells ml^{-1} on the 19th of July, before declining to <10 cells ml^{-1} for the remainder of the phase.

Staurastrum also peaked at this time, reaching 40 cells ml^{-1} on the 19th of July, and 30 cells ml^{-1} on the 16th of August. *Micractinium* showed two distinct peaks, 230 cells ml^{-1} on the 26th of July and 120 cells ml^{-1} on the 16th of August. *Eudorina* appeared on the 19th of July with 60 colonies ml^{-1} and then increased to 230 colonies ml^{-1} on the 3rd of August. It then decreased in numbers but remained in the plankton for the rest of the summer phase. *Scenedesmus quadricauda* was present through the summer period, also peaking on the 3rd of August at 255 cells ml^{-1}, and remaining at approximately 90 colonies ml^{-1} for the rest of the summer phase.

Cryptomonads oscillated in numbers during this phase. Both *Rhodomonas* and *Cryptomonas* exhibited four peaks - early July, 19th July, 3rd of August and 23rd of August. The maximum numbers of *Cryptomonas* occurred on the 3rd of August with 1435 cells ml^{-1}, while the maximum of *Rhodomonas* occurred earlier, on the19th July. However, the larger size of *Cryptomonas* meant that it contributed >90% of the Cryptophyceae biomass throughout the summer period.

Autumn phase: 8th September - 25th October

At the end of the previous phase (31st of August) dinoflagellate numbers were 85 cells ml^{-1} for *Ceratium* and 770 cells ml^{-1} for *Peridinium*. By the 8th of September numbers had dropped dramatically, *Ceratium* to 10 cells ml^{-1} and *Peridinium* to 20 cells ml^{-1}. By the end of this phase no dinoflagellates were present.

Within the cyanophyta, *Microcystis* was present at 7-10 colonies ml^{-1}. *Aphanizomenon* was present between 60 and 120 filaments ml^{-1}. In terms of biovolume *Microcystis* contributed approximately 80% of the Cyanophyceae biovolume, *Aphanizomenon* between 10 and 20%.

The chlorophyte *Scenedesmus quadricauda* was present throughout this phase (>50 cells ml^{-1}) reaching a maximum of 140 colonies ml^{-1} on the 5th of October. *Ankyra* was present during October, reaching 90 cells ml^{-1} on the 25th.

Cryptomonad numbers dropped during the autumn phase, *Cryptomonas* from 190 cells ml^{-1} at the end of the summer phase to 0 cells ml^{-1} on the 8th of September and *Rhodomonas* dropped from 160 cells ml^{-1} to 20 cells ml^{-1}. Both genera remained low during this period (*Cryptomonas* maximum was 50 cells ml^{-1}, *Rhodomonas* maximum was 40 cells ml^{-1})

Only small diatoms were present during this phase. *Nitzschia* spp. was present at ≈20 cells ml^{-1}, the *Stephanodiscus minutula* peaking at 380 cells ml^{-1} in the middle of

this phase, and unidentified small pennate diatoms increasing through the phase, reaching a maximum of 80 cells ml^{-1} on the 25th of October.

Winter: 15th November - 08th February

Among the diatoms, *Stephanodiscus hantzschii* (15 cells ml^{-1}) and small pennate diatoms (10 cells ml^{-1}) were present on the 15th of November but declined thereafter. *Stephanodiscus rotula* showed a small peak of 17 cells ml^{-1} in December but was otherwise present at numbers approaching 0 cells ml^{-1}.

With the exception of *Aphanizomenon flos-aquae*, cyanophyceae were absent. The maximum numbers of *Aphanizomenon* was 35 filaments ml^{-1} on the 15th of November, after which it was absent.

Cryptomonads were almost always absent, the exception being 45 *Cryptomonas* cells ml^{-1} on November 15th.

Chlorophyceae were almost completely absent from this phase, while dinoflagellates were completely absent.

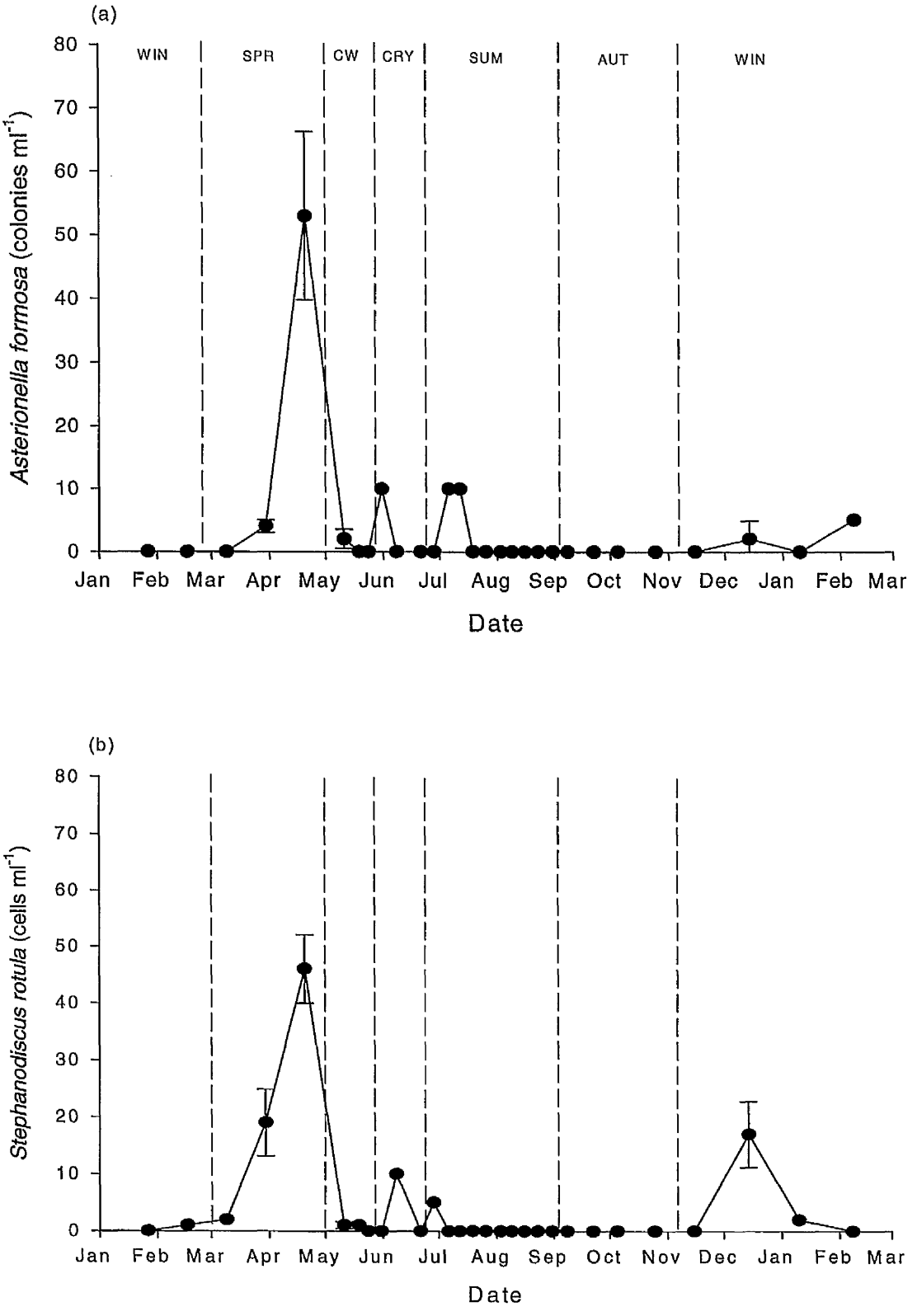


Figure 3.7: Seasonal changes in (a) *Asterionella formosa* and (b) *Stephanodiscus rotula*, Rostherne Mere, 2000. Values are the mean of sites A, B and C. Error bars ±1 SD. (n=3). In some cases error bars are too small to visualise.

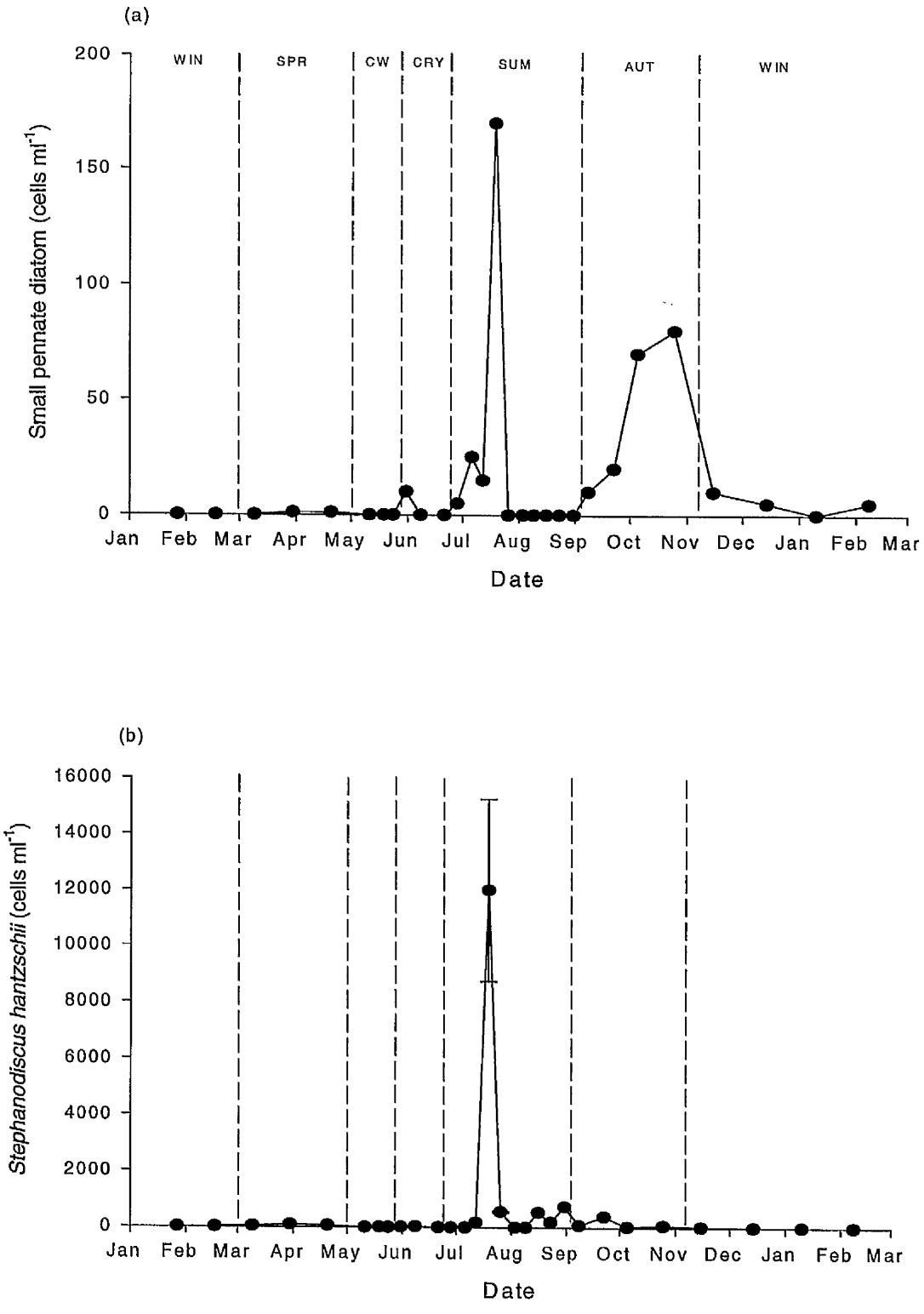


Figure 3.8: Seasonal changes in (a) small unidentified pennate diatoms, counts performed at site A only; and (b) *Stephanodiscus hantzschii*; values are the mean of sites A, B and C, Error bars ±1 SD, (n=3). In some cases error bars are too small to visualise.

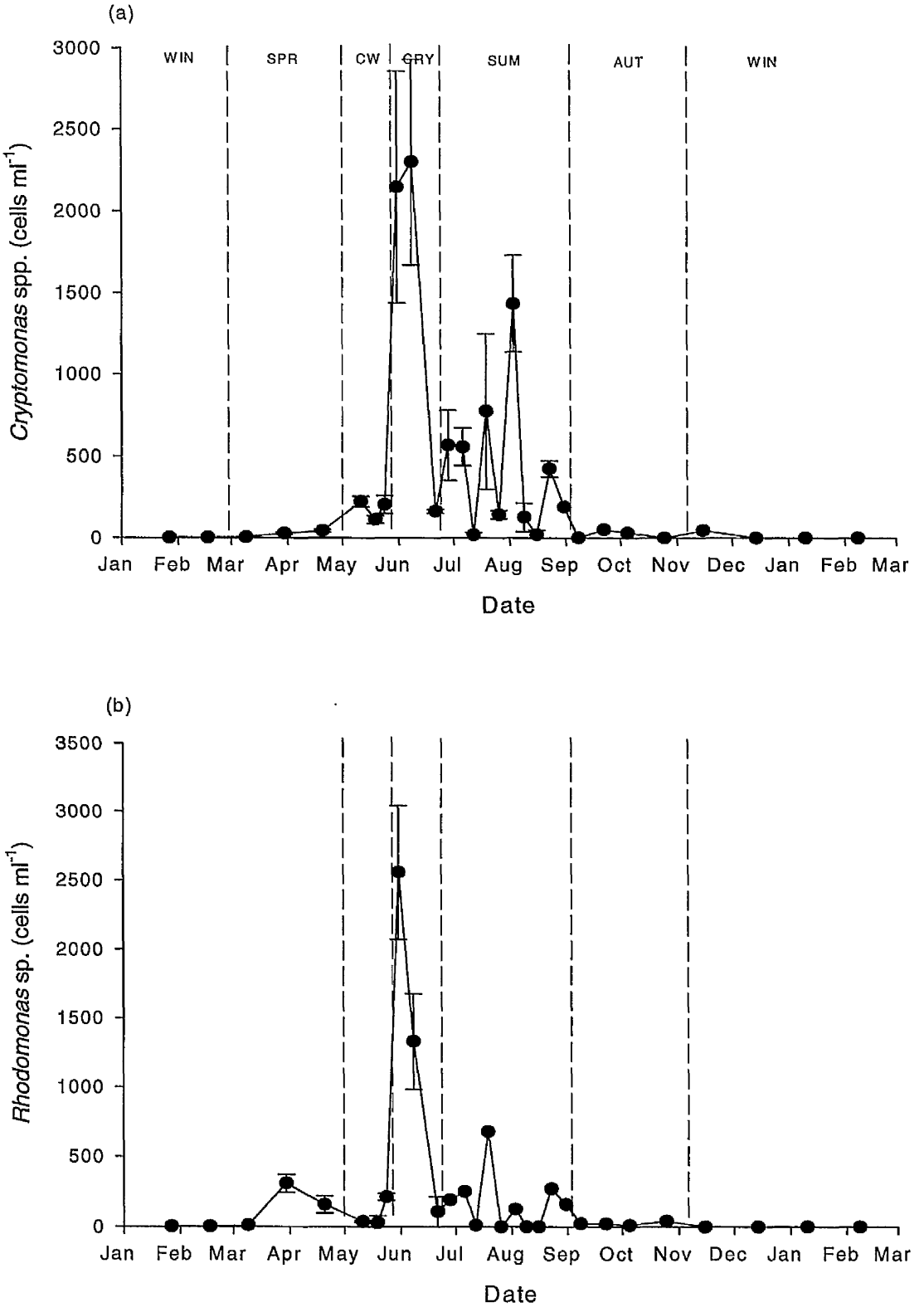


Figure 3.9: Seasonal changes in numbers of (a) *Cryptomonas* spp. and (b) *Rhodomonas* sp. in Rostherne Mere, 2000. Values are the mean of sites A, B and C. Error bars ±1 SD. (n=3). In some cases error bars are too small to visualise.

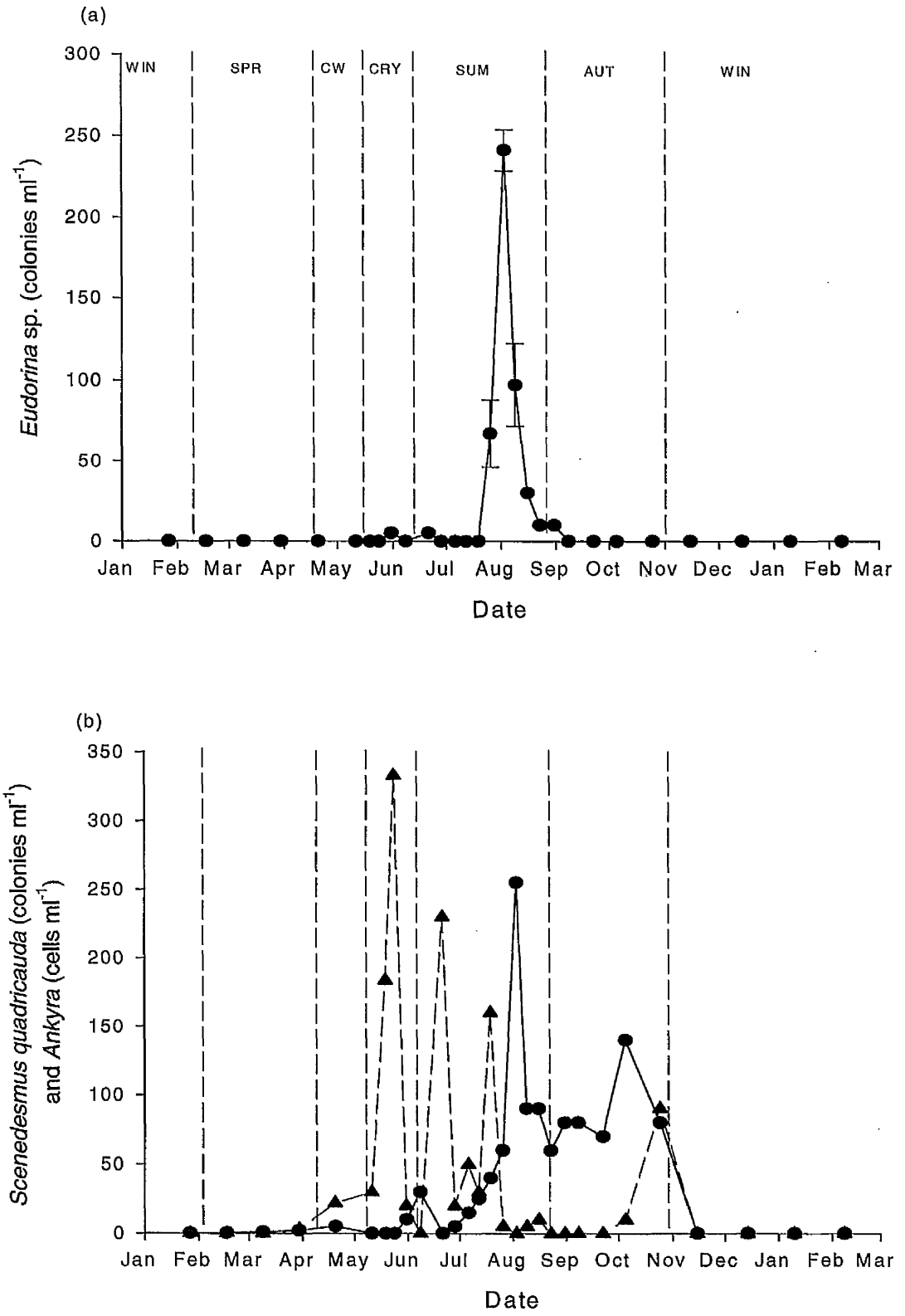


Figure 3.10: Seasonal changes in (a) numbers of *Eudorina* sp. Values are the mean of sites A, B and C, Error bars ±1 SD, (n=3). In some cases error bars are too small to visualise, and (b) *Scenedesmus quadricauda* (•) and *Ankyra* sp. (4), counts performed at site A only.

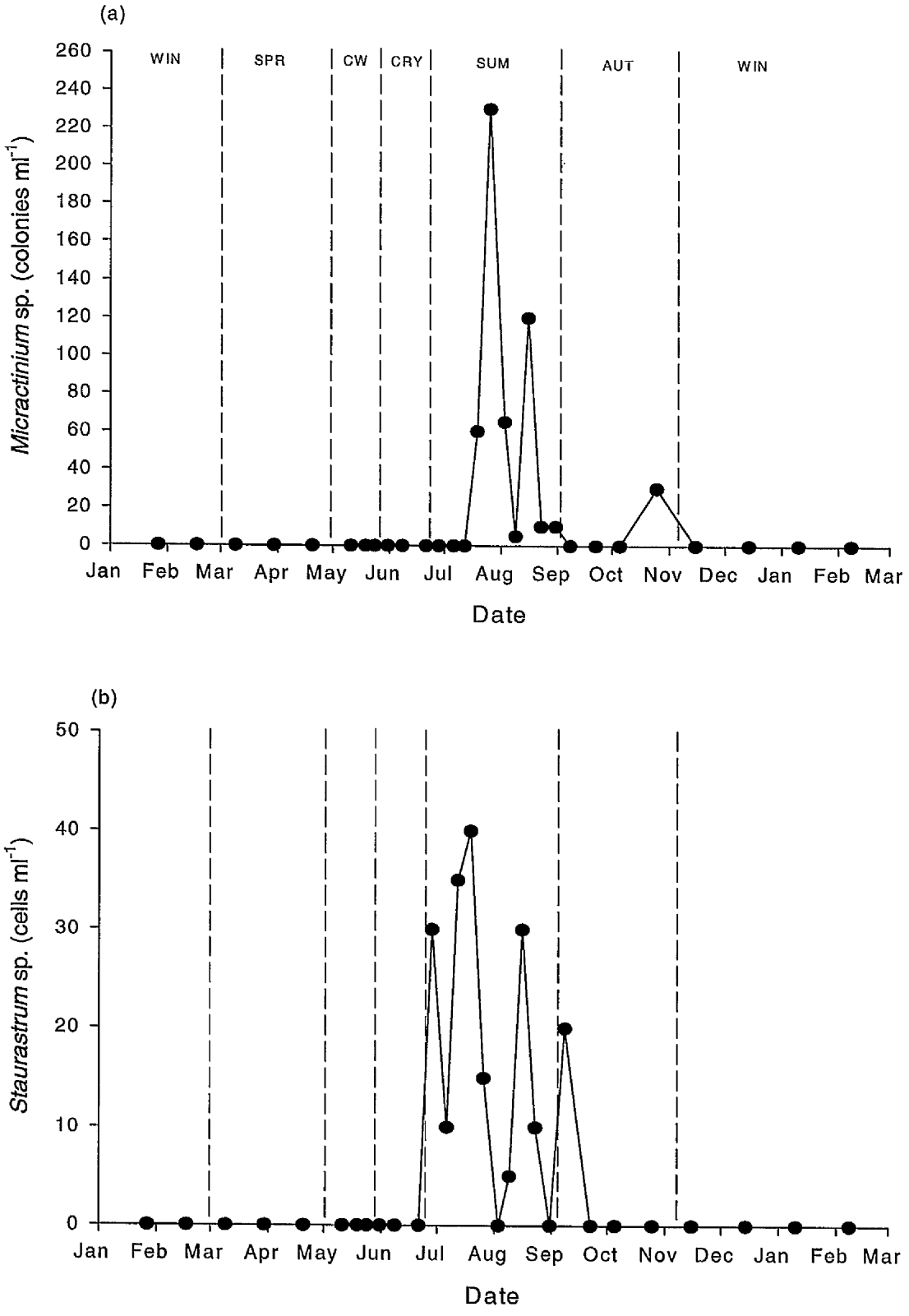


Figure 3.11:Seasonal changes in (a) *Micractinium* sp. and (b) *Staurastrum* sp. in Rostherne Mere, 2000. Counts performed at site A only.

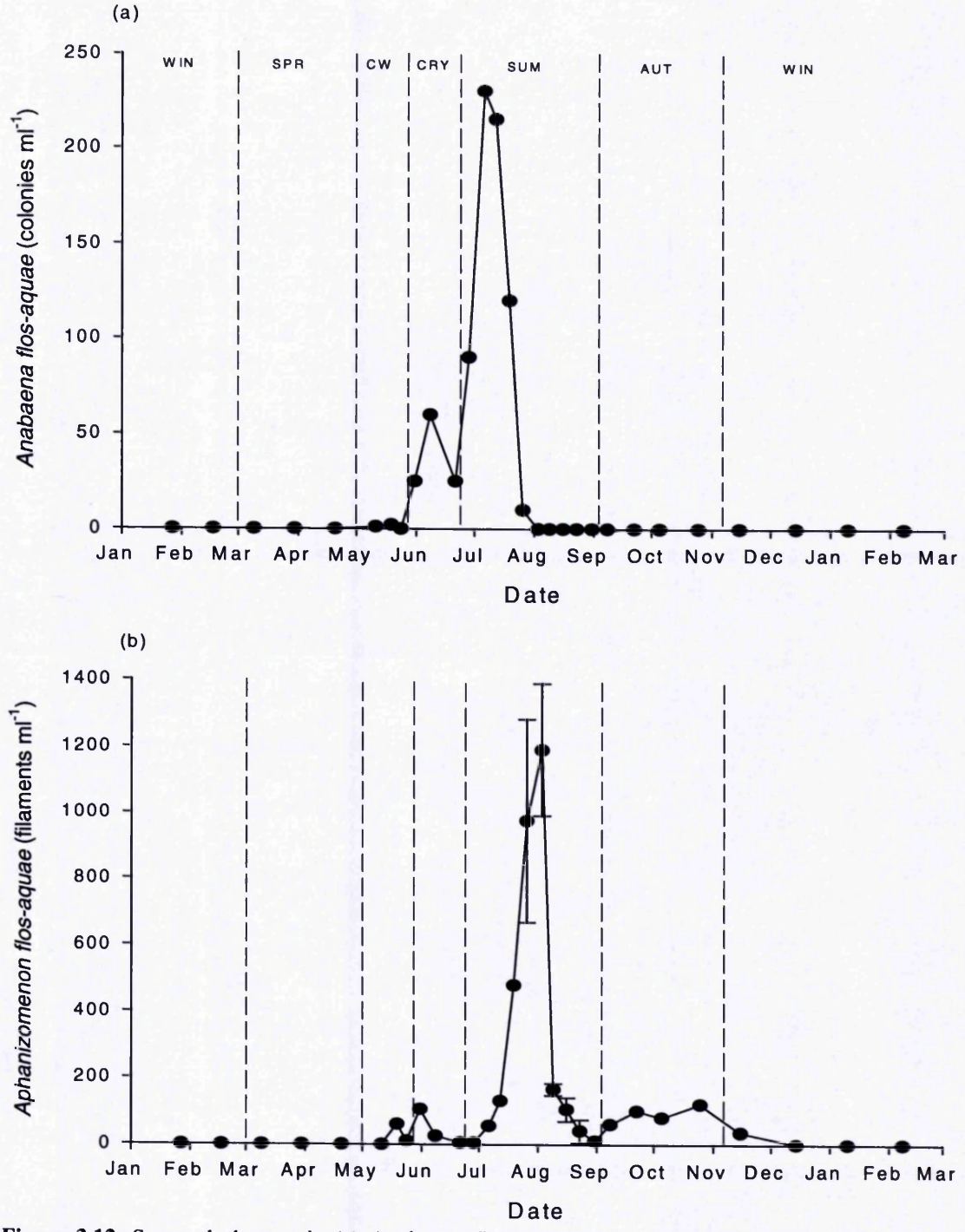


Figure 3.12: Seasonal changes in (a) *Anabaena flos-aquae*, counts performed at site A only and (b) *Aphanizomenon flos-aquae*, Rostherne Mere, 2000; values are the mean of sites A, B and C, Error bars ±1 SD, (n=3). In some cases error bars are too small to visualise.

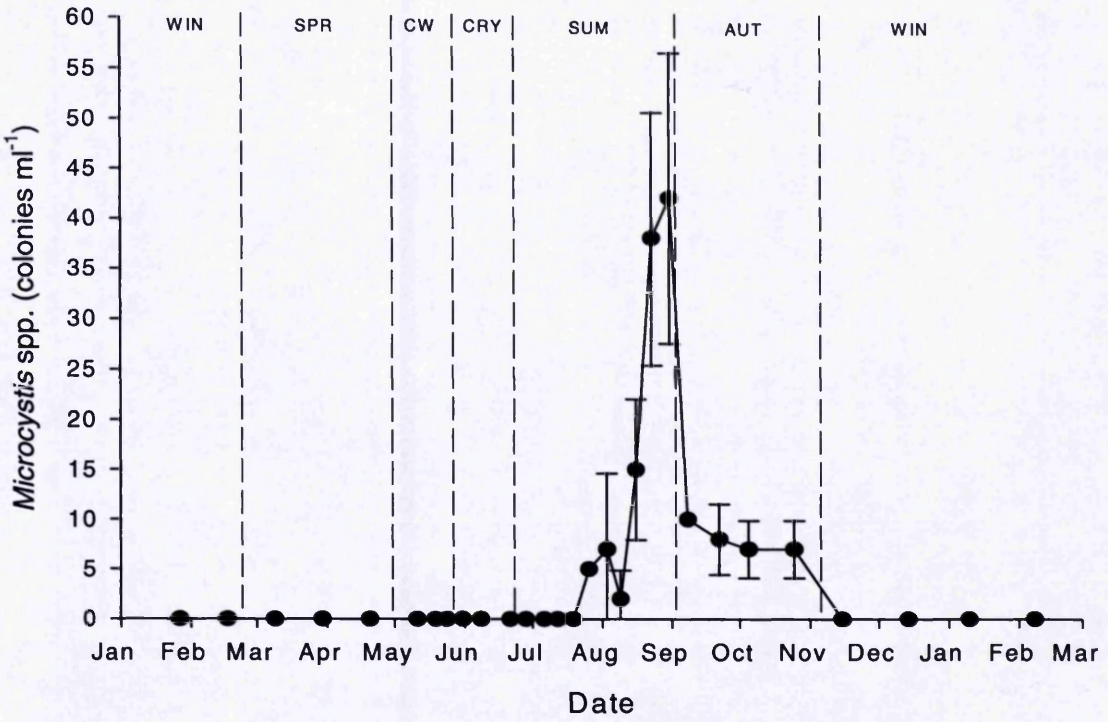


Figure 3.13: Seasonal changes in the numbers of *Microcystis* spp. Colonies in Rostherne Mere, 2000. Values are the mean of sites A, B and C. Error bars ±1 SD. (n=3). In some cases error bars are too small to visualise.

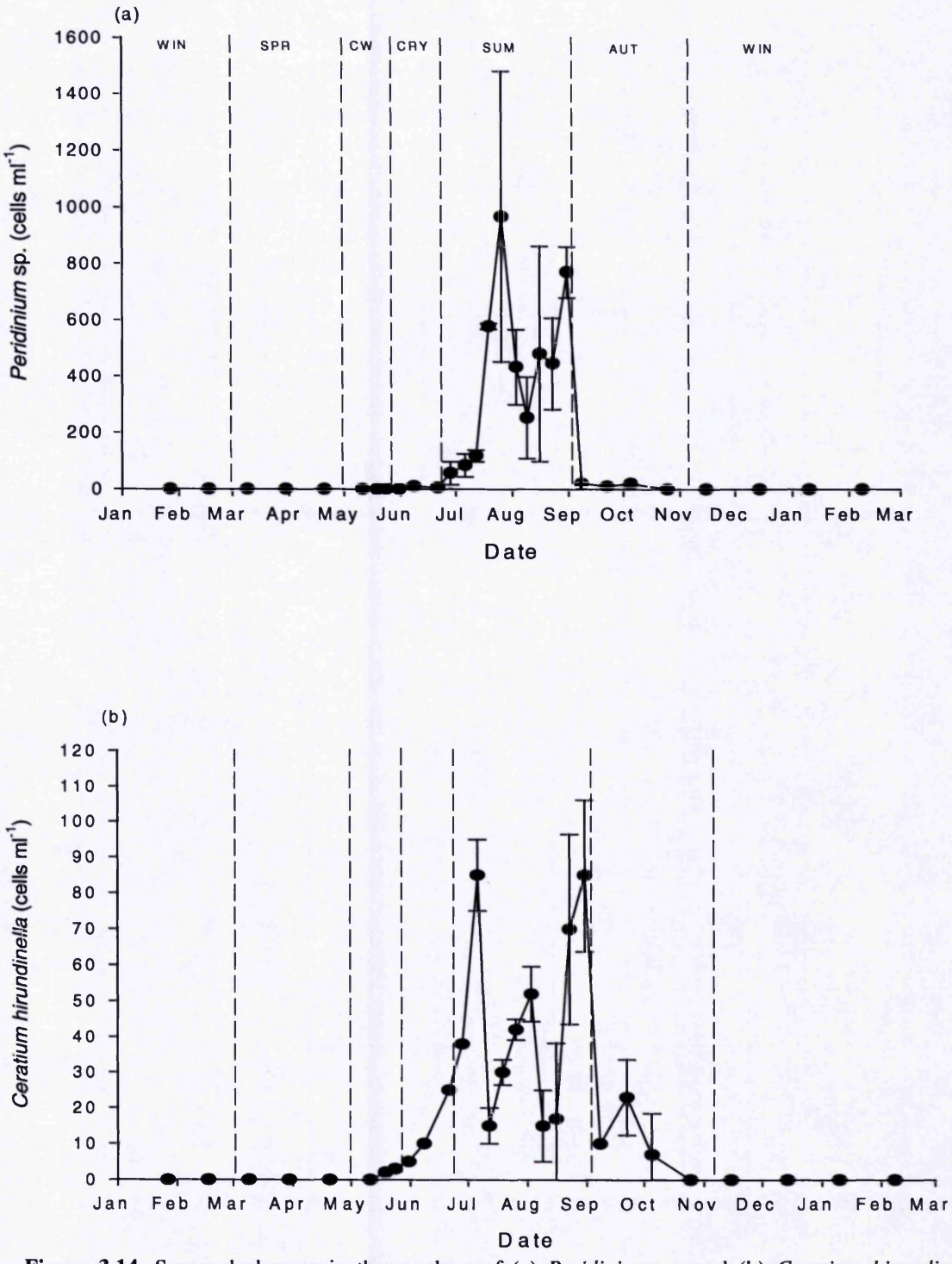


Figure 3.14: Seasonal changes in the numbers of (a) *Peridinium* sp. and (b) *Ceratium hirundinella*, Rostherne Mere, 2000. Values are the mean of sites A, B and C. Error bars ±1 SD. (n=3). In some cases error bars are too small to visualise.

3.1.2 Physico-Chemical Parameters

3.1.2.1 Temperature

Average temperatures for the top 5m of the water column are shown in Figure 3.15. During the initial winter phase and the spring phase temperature steadily increased, from 5.0°C at the commencement of sampling to 9.2°C at the end of the spring phase (20th of April). During the clear-water phase and early cryptomonad phase the temperature had increased to approximately 14.5°C. At the end of the cryptomonad phase the temperature had increased to 19.8°C and remained high during the summer phase, reaching a maximum of 20.1°C on the 23rd of August. During the autumn phase and into the winter phase temperatures declined, reaching a minimum of 4.5°C at the end of sampling.

3.1.2.2 Temperature profiles

Temperature profiles are shown in Figure 3.16 to Figure 3.18. The first temperature profile was taken on the 27th of January, during the initial winter phase, and showed the lake to be fully mixed and isothermal. Profiles taken during the spring phase (9th March, 30th March and 20th of April) show that the lake was isothermal during March, but by April 20th a temperature gradient was observed within the water column, with a temperature difference of 3°C between 0 and 20m. The three profiles taken during the clear-water phase (11th, 19th and 24th of May) show that the lake had stratified. Stratification therefore occurred between the end of the spring phase (20th of April) and start of the clear-water phase (11th May). During the clear-water phase the position of the thermocline fell from between 4 and 7m on 11th of May to between 6 and 8m on the 24th. The profile on the 31st of May was taken during the start of the cryptomonad phase, and shows a thermocline between 7 and 9m. During the summer phase (profiles taken on 12th July, 26th July and 23rd August) the lake remained stratified, with a thermocline between approximately 6 and 10m. During the autumn phase (5th October) the thermocline lay between 9 and 12m. The four profiles taken during the winter phase (25th October, 15th November, 10th January and 8th of February) show that on the 25th of October the thermocline had fallen to between 12 and 13m, which is attributable to the autumn overturn. The profiles taken during the other three months show the lake to be isothermal.

3.1.2.3 Oxygen profiles

Profiles for oxygen saturation were taken during the summer phase (on the 12th and 26th of July) during a period of high phytoplankton biomass. They are shown superimposed on the temperature profiles in Figure 3.17. The 12th of July profile (taken when chlorophyll-a approximately 50μgl^{-1}) shows supersaturated values between 0 and 5m with a maximum of 116% at a depth of 3m. There was a rapid drop between 6 and 7m (from 97% to 47%) below which saturation remained between 40 and 60% to a depth of 16m, and then once again declined, reaching a minimum of 11% at a depth of 20m. The 26th of July profile (taken when chlorophyll-a approximately 140μgl^{-1}) showed supersaturated values from 0-2m, with a maximum of 166% at 1m depth. Values then declined rapidly with 65% at 3m, 40-50% between 4 and 16m (with the exception of 28% saturation at 8 and 9m) before declining to 8% at 20m.

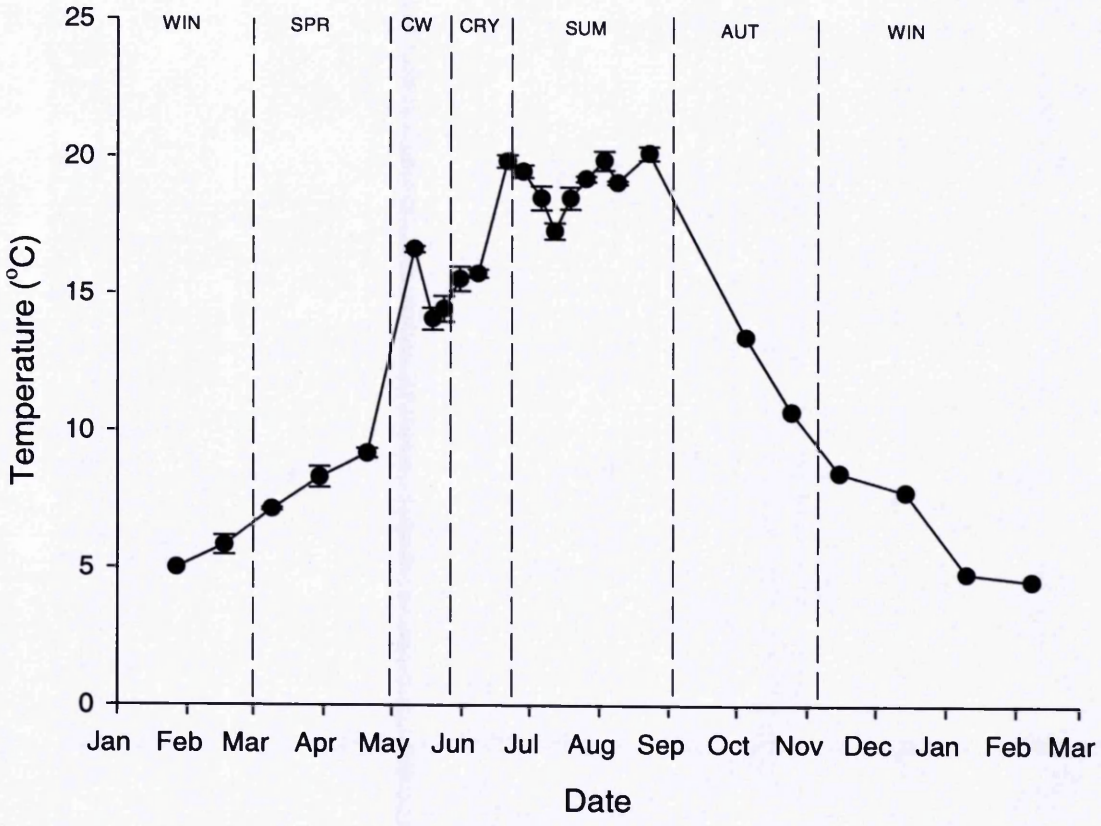


Figure 3.15: Seasonal changes in surface temperature, Rostherne Mere, 2000. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

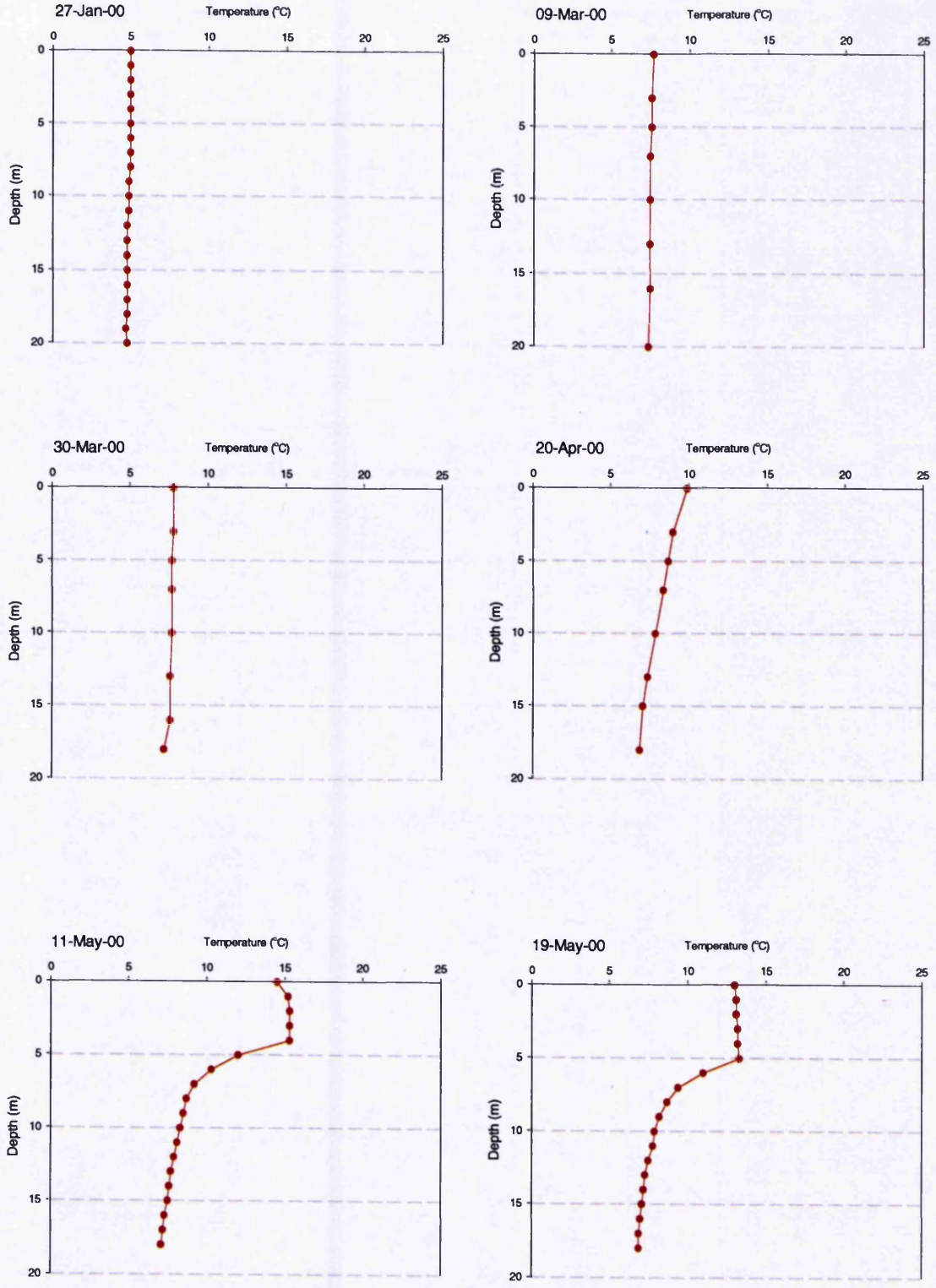


Figure 3.16: Temperature profiles for the 27th of January to 19th of May.

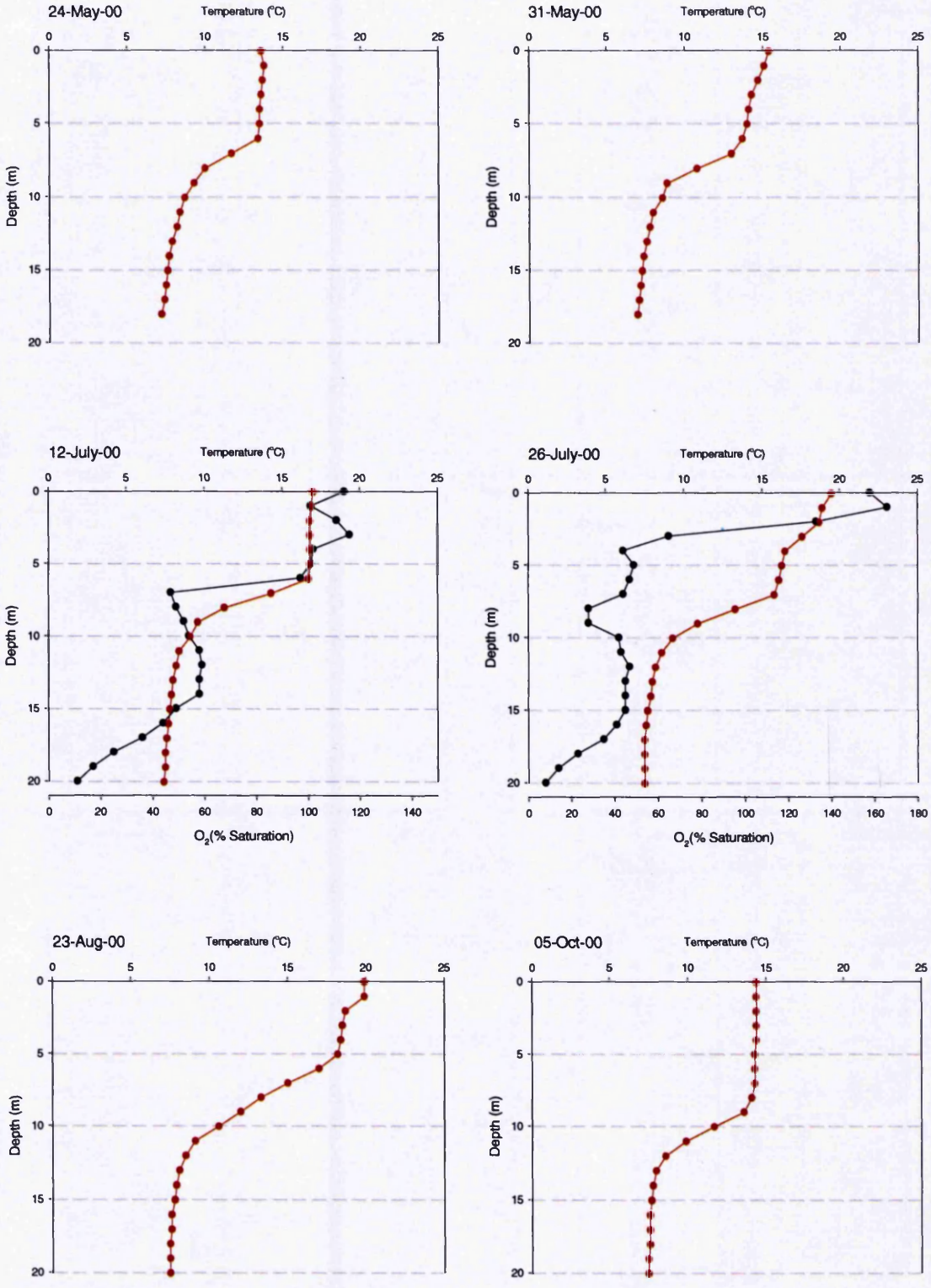


Figure 3.17: Temperature profiles for 24th of May to the 5th of October. Oxygen profiles for the 12th and 26th of July. Temperature (•), oxygen saturation (•).

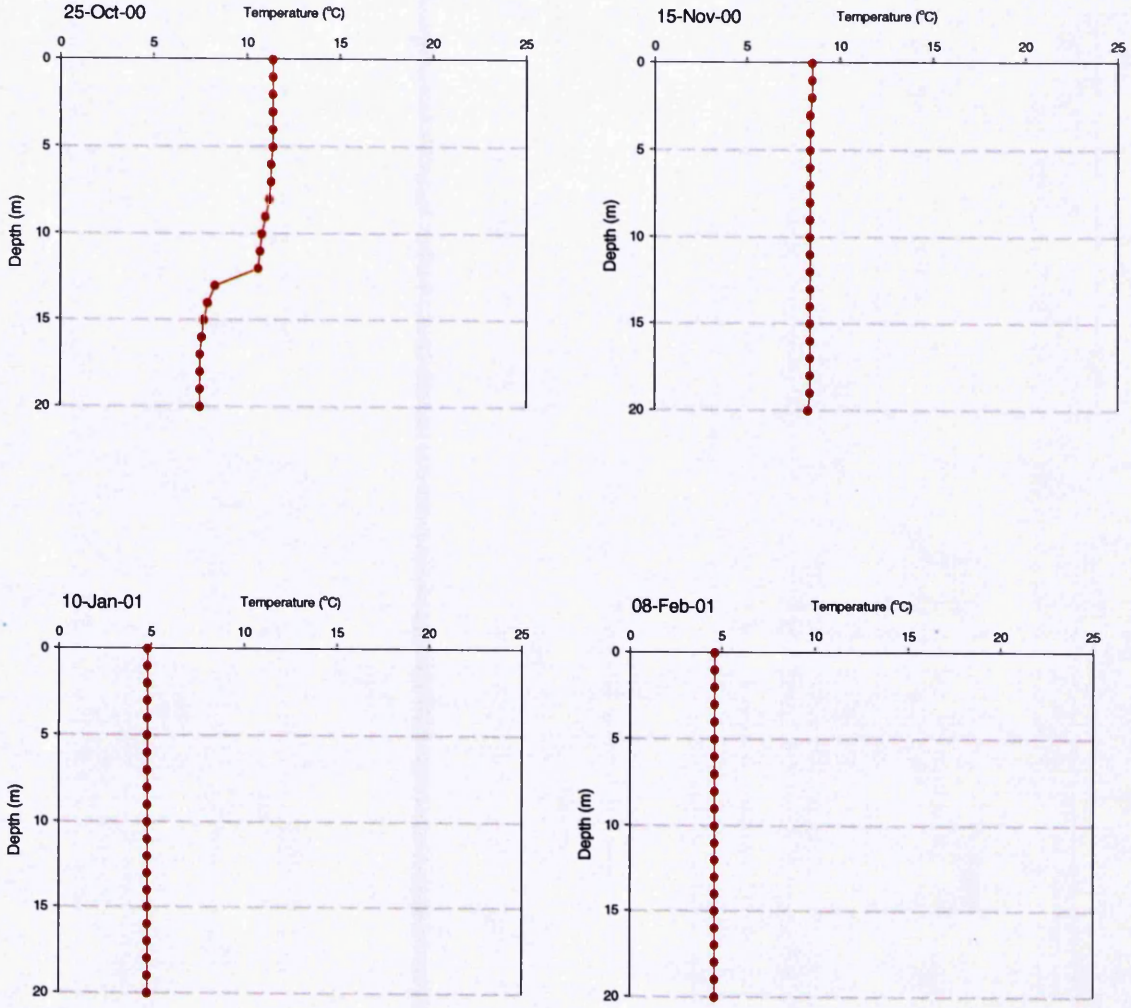


Figure 3.18: Temperature profiles for the 25th of October to the 8th of February 2001.

3.1.2.4 pH

Seasonal variation in pH is shown in Figure 3.19. pH was first measured at the start of the spring phase, during which it was approximately 7.0. During the clear-water phase pH increased from 7 to 8. During the cryptomonad phase pH had increased further, varying between 8.7 and 9.1. pH remained at around 9 during the early summer phase, with a maximum value of 9.3 occurring on the 6th and 19th of July, before dropping to 8.1 at the beginning of August. pH increased slightly towards the end of August (8.6 on the 23rd) before falling during the autumn and winter phases, reaching a minimum of 7.0 in February.

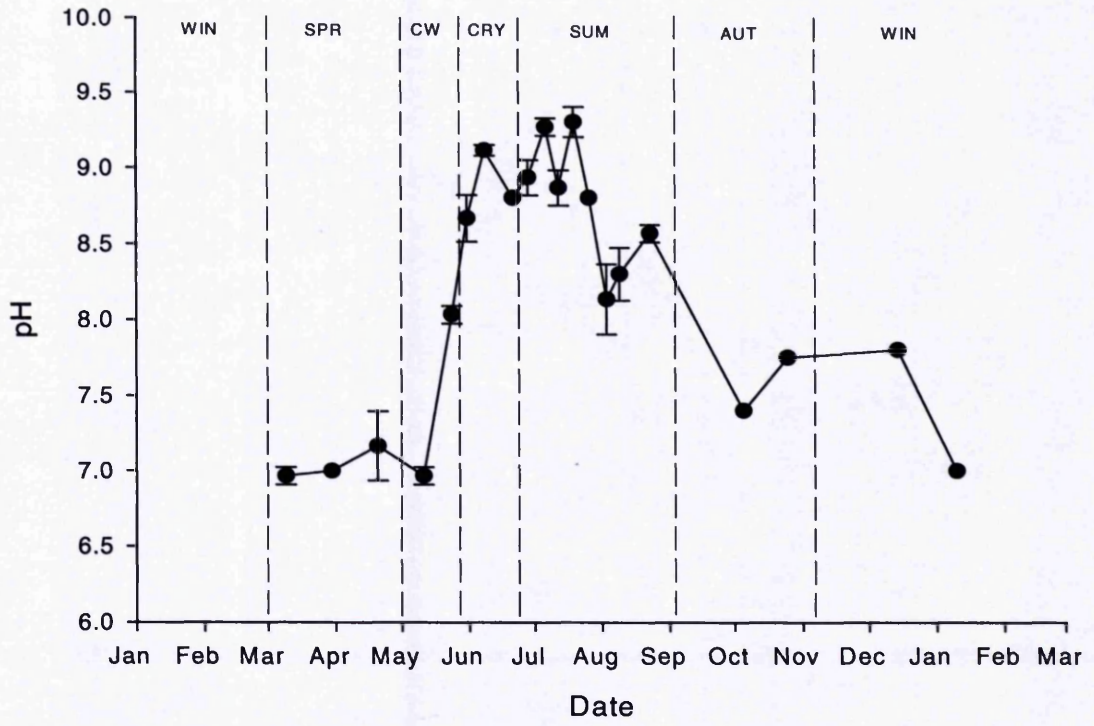


Figure 3.19: Seasonal changes in pH, Rostherne Mere, 2000. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

3.1.2.5 Phosphorus Compounds

Phosphorus (with the exception of particulate P) generally showed high values during winter, an increase to a late spring maximum (April), and a decline to a late July minimum, with concentrations generally remaining low throughout August. During the autumn concentrations increased, leading to winter concentrations similar to those of the preceding winter. Total phosphorus showed a similar pattern but with a late July peak rather than minimum. Extreme vales of nutrients occurred during late July, when algal biomass was at a maximum (note that nutrients were not measured on the 31st of August when biomass peaked for a second time). Particulate phosphorus generally followed the same pattern as chlorophyll-a / total algal biovolume.

Soluble Reactive Phosphorus (SRP)

Soluble reactive phosphorus varied between undetectable and 0.32mg l^{-1} and is shown in Figure 3.20a. Concentrations of SRP were approximately 0.25mg l^{-1} during the initial winter and the early spring phase. Concentrations began to decline from the 30th of March (0.26mg l^{-1}) reaching 0.21mg l^{-1} on the 24th of April, and declined further during the clear-water phase to reach 0.14mg l^{-1}. During the cryptomonad phase concentrations fell from 0.10 to 0.07mg l^{-1}, and remained at approximately this level (0.06mg l^{-1}) during the early part of the summer phase. There was then a rapid drop to 0.01mg l^{-1} on the 19th of July, concentrations remaining ≤0.02mg l^{-1} for the remainder of the summer phase (concentrations undetectable on the 23rd of August). Concentrations of SRP began to increase during the autumn phase, increasing from 0.03mg l^{-1} at the commencement of the phase to reach 0.31mg l^{-1} at the start of the winter phase. In the winter phase concentrations declined, reaching 0.19mg l^{-1} in February 2001.

Total Dissolved Phosphorus (TDP)

Total dissolved phosphorus varied between 0.01mg l^{-1} and 0.34mg l^{-1} and is shown in Figure 3.20b. During the initial winter and the spring phase TDP oscillated between 0.19 and 0.29mg l^{-1}. Concentrations began to decline from the 30th of March, falling from 0.29mg l^{-1} to 0.12mg l^{-1} during the clear-water phase, and then falling further during the cryptomonad phase (from 0.09 to 0.05mg l^{-1}). In the early summer phase TDP concentrations increased to approximately 0.10mg l^{-1} before falling to 0.01mg l^{-1} on the 19th of July, remaining ≤0.02mg l^{-1} during the remainder of the summer period. During the autumn phase TDP concentrations increased, reaching approximately 0.30mg l^{-1} during the winter phase.

Total Phosphorus (TP)

Total Phosphorus (TP) varied between 0.06mg l^{-1} and 0.44mg l^{-1} (Figure 3.21a). During the winter phase concentrations were approximately 0.25mg l^{-1}. During the spring phase TP increased from 0.24mg l^{-1} to a peak on the 30th of March of 0.33mg l^{-1}, following which concentrations began to decline, reaching 0.12mg l^{-1} during the clear-water phase. During the cryptomonad phase concentrations fell from 0.13mg l^{-1} to an annual minimum of 0.06mg l^{-1}. Concentration increased during the early part of the summer phase, reaching approximately 0.25mg l^{-1} on the 19th and 26th of July. During the rest of August values were lower, at around 0.16mg l^{-1}, but increased slightly to approximately 0.20mg l^{-1} during the early autumn phase, and then more rapidly to approximately 0.4mg l^{-1} in December and January samplings, before falling to 0.18 mg l^{-1} in February.

Total Particulate Phosphorus (TPP)

Total particulate phosphorus varied from undetectable to 0.23mg l^{-1} and is shown in Figure 3.21b. A small peak was observed during the spring phase peaking at 0.03mg l^{-1} on the 30th March before declining to undetectable during the clear-water phase. During the cryptomonad phase, concentrations increased to 0.05mg l^{-1} before returning to approximately 0.01 mg l^{-1} at the return of clear-water conditions on the 21st of June. There was a very large increase during the summer phase, reaching 0.23mg l^{-1} on the 19th and 26th of July before falling to 0.14mg l^{-1} for the remainder of this phase. Concentrations fell to 0.08mg l^{-1} during the autumn phase, increased to 0.16mg l^{-1} in the winter phase (Nov and Dec) and then fell to 0.06mg l^{-1} in January.

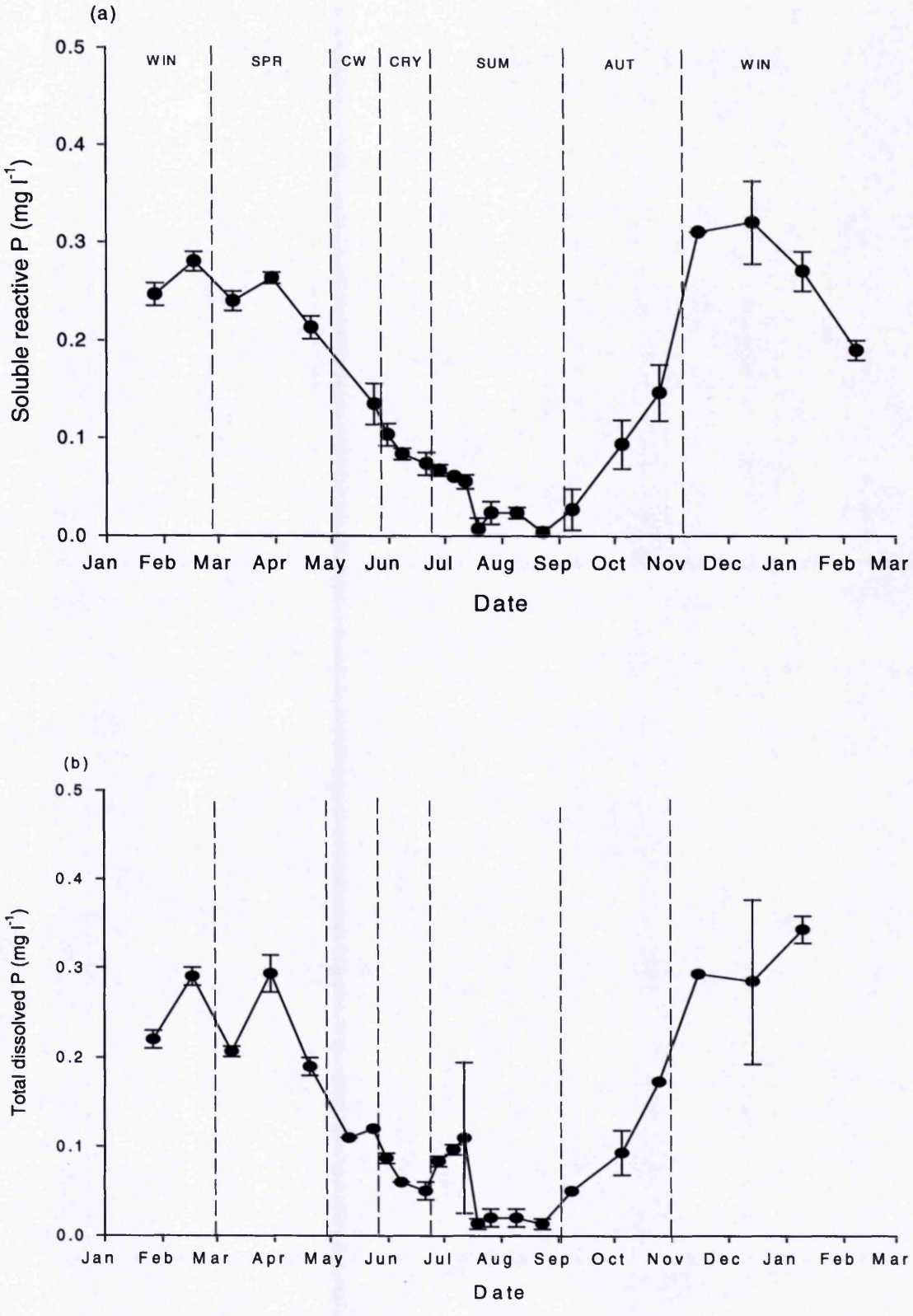


Figure 3.20: Seasonal changes in (a) soluble reactive P and (b) total dissolved P in Rostherne Mere, 2000. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

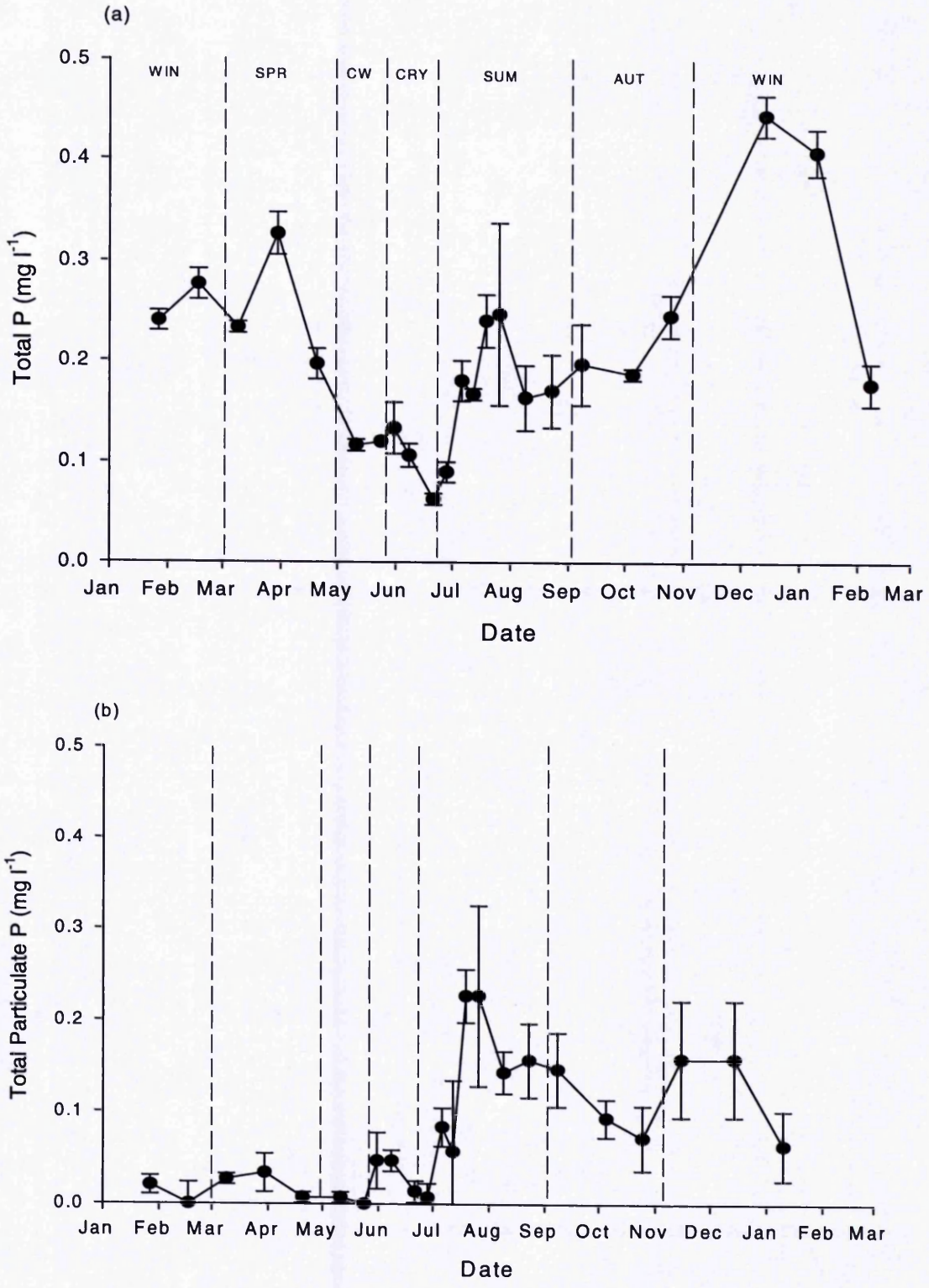


Figure 3.21: Seasonal changes in (a) total P and (b) total particulate P in Rostherne Mere, 2000. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

3.1.2.6 Nitrogen compounds

Nitrogen (with the exception of particulate N) generally showed high values during winter, an increase to a late spring maximum (April), and a decline to a late July minimum, with concentrations generally remaining throughout August. During the autumn concentrations increased, leading to winter concentrations similar to those of the preceding winter. Extreme vales of nutrients occurred during late July, when algal biomass was at a maximum (note that nutrients were not measured on the 31st of August when biomass peaked for a second time). Particulate nitrogen followed the same pattern as chlorophyll-a / total algal biovolume.

Nitrates/Nitrites

NO_3/NO_2 ranged between 0.03 and 1.83mg l^{-1} and is shown in Figure 3.22a. During the initial winter and spring phase concentrations varied between a minimum of 1.53 mg l^{-1} and a maximum of 1.83 mg l^{-1} on the 20th of April. During the clear-water phase concentrations were approximately 1.55 mg l^{-1}, following which concentrations fell to approximately 0.95 mg l^{-1} at the end of the cryptomonad phase and the start of the summer phase. Concentrations dropped rapidly during the early part of the summer phase, reaching approximately 0.1 mg l^{-1} on the 26th of July with concentrations remaining low for the rest of the summer phase, with a minimum of 0.03 mg l^{-1} on the 23rd of August. During the autumn phase and early winter phase concentrations increased, until they remained relatively steady at 1.55 mg l^{-1} from December to February.

Total Dissolved Nitrogen

Total dissolved nitrogen (TDN) showed a similar pattern to total nitrogen. TDN ranged between 0.64 and 2.92 mg l^{-1} (Figure 3.22b). During the initial winter and early spring phase concentrations were approximately 2.2mg l^{-1}, with an increase to 2.92 mg l^{-1} on the 20th of April, following which concentrations declined. By the clear-water phase concentrations had fallen to approximately 2.20mg l^{-1} and fell further during the cryptomonad phase to approximately 1.9mg l^{-1}. Concentrations fell rapidly during the early summer phase and remained between 0.64 and 0.69mg l^{-1} from the 26th July until the end of the summer phase. During the autumn phase and early winter phase concentrations increased, reaching 2.0mg l^{-1} in December.

Total Nitrogen (TN)

Total nitrogen ranged between 0.98mg l^{-1} and 2.97mg l^{-1} (Figure 3.23a). During the initial winter and early spring phase concentrations were approximately 2.3 mg l^{-1}. During the spring phase concentrations increased to 2.97 mg l^{-1} on the 20th of April, following which concentrations declined. During the clear-water phase concentrations had fallen to around 2.30 mg l^{-1}, and fell further during the cryptomonad phase, declining from 2.31 mg l^{-1} to 2.04 mg l^{-1}. Concentrations continued to decline during the summer phase, falling from 1.92 mg l^{-1} on the 28th of June to 1.08 mg l^{-1} on the 9th of August and remained low (≤1.16mg l^{-1}) until the mid-autumn phase. Concentrations then increased, reaching 1.80mg l^{-1} by the end of the autumn phase, and increased further during the winter phase, reaching a maximum of 2.47mg l^{-1} in February.

Total Particulate Nitrogen (TPN)

TPN varied between undetectable and 1.04mg l^{-1} (Figure 3.23b). Concentrations were low (<0.1 mg l^{-1}) during the initial winter phase and the spring phase, the first distinct peak (0.33mg l^{-1}) occurring during the cryptomonad phase, followed by a large peak during the summer phase, with a maximum of 1.04mg l^{-1} on the 26th of July. This larger peak declined during August (no reading was taken on the 31st of August when algal biovolume again peaked). Concentrations declined during the autumn phase to approximately 0.1mg l^{-1} before a slight increase in late winter to approximately 0.25mg l^{-1}.

Ammonia

Ammonia showed no seasonal pattern (Figure 3.24), with values generally less than 0.03 mg l^{-1} throughout the sampling period. Only on two occasions did ammonia exceed 0.3 mg l^{-1}, with values of 0.09 mg l^{-1} on the 21st of June and 0.05 mg l^{-1} on the 8th of September.

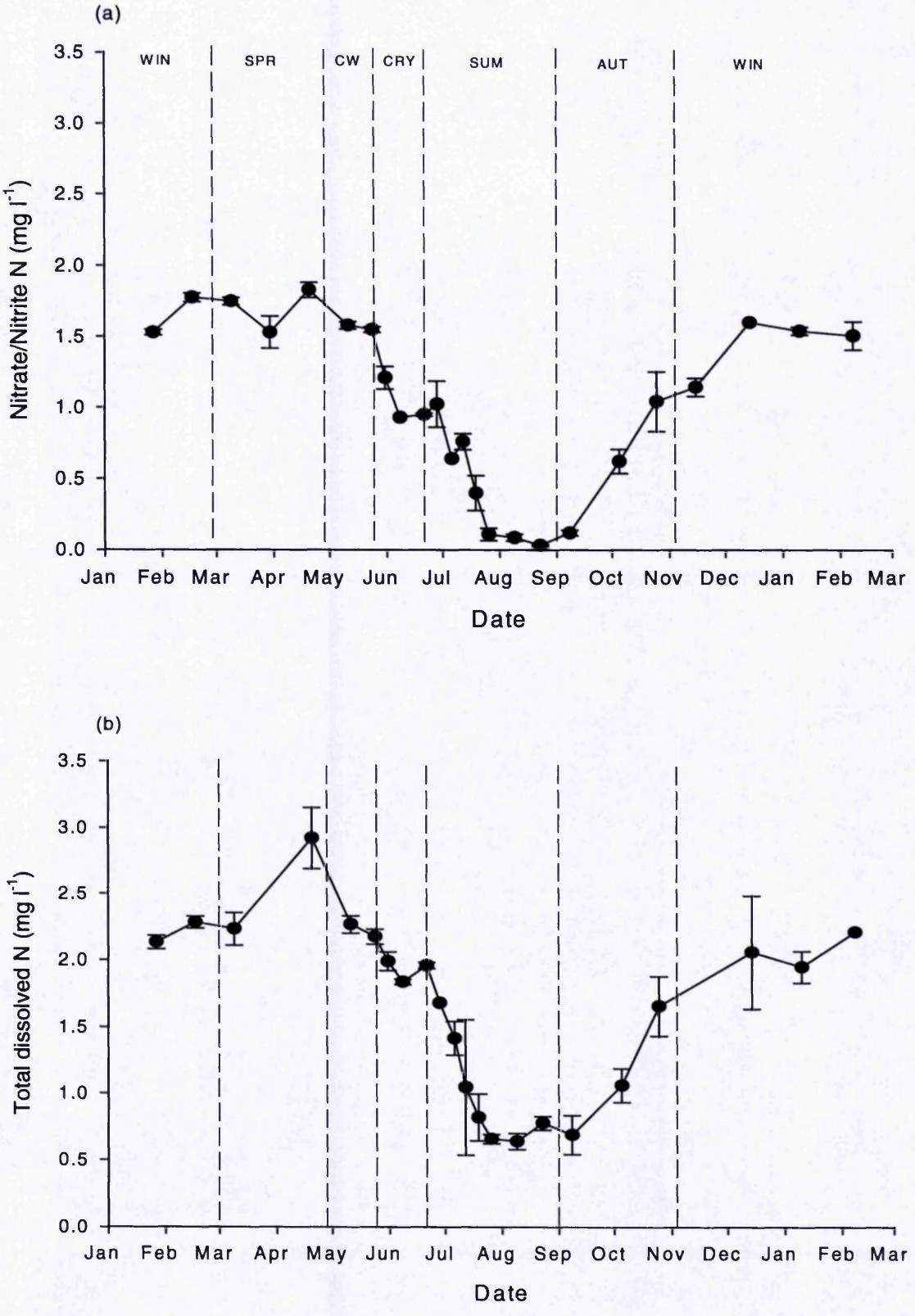


Figure 3.22: Seasonal changes in (a) nitrate/nitrite N and (b) total dissolved N in Rostherne Mere, 2000. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

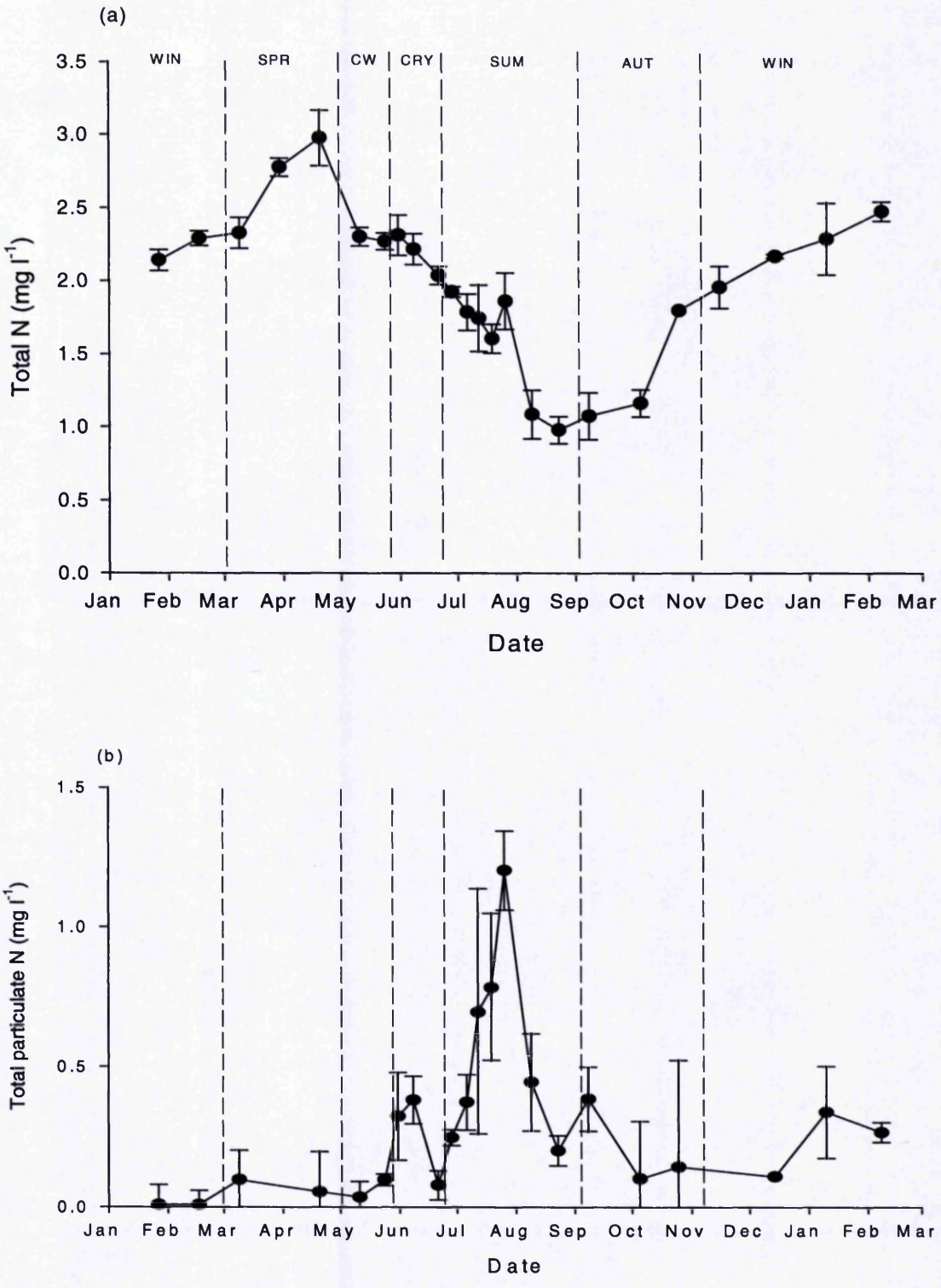


Figure 3.23: Seasonal changes in (a) total N and (b) total particulate N in Rostherne Mere, 2000. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

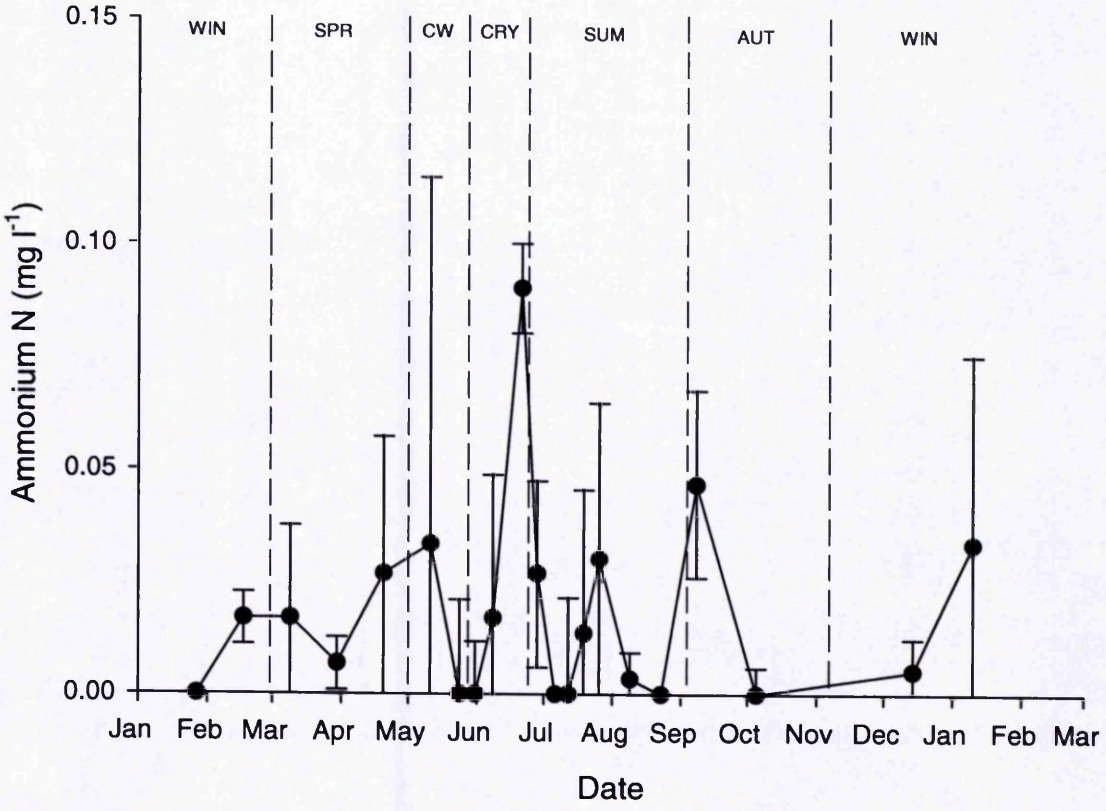


Figure 3.24: Seasonal changes in the concentration of ammonium-N in Rostherne Mere, 2000. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

3.1.2.7 Silicon

Silicon ranged from 0.07 to 2.56mg l^{-1} (Figure 3.25). Concentrations declined slowly during the initial winter phase (from a maximum of 2.51mg l^{-1}) and early spring phase, followed by a more rapid decrease during the late spring phase (1.44 mg l^{-1} on the 20th April) to a minimum of 0.12mg l^{-1} during the clear-water phase. During the remainder of the clear-water phase, the cryptomonad phase and into the beginning of the summer phase concentrations slowly increased, reaching 0.57mg l^{-1} on the 12th of July. On the 19th of July concentrations dropped to 0.07mg l^{-1}, remained low on the 26th of July (0.09mg l^{-1}) and then increased through the remainder of the summer phase, the autumn phase and winter phases, to a maximum of 2.56mg l^{-1} on the 10th of January.

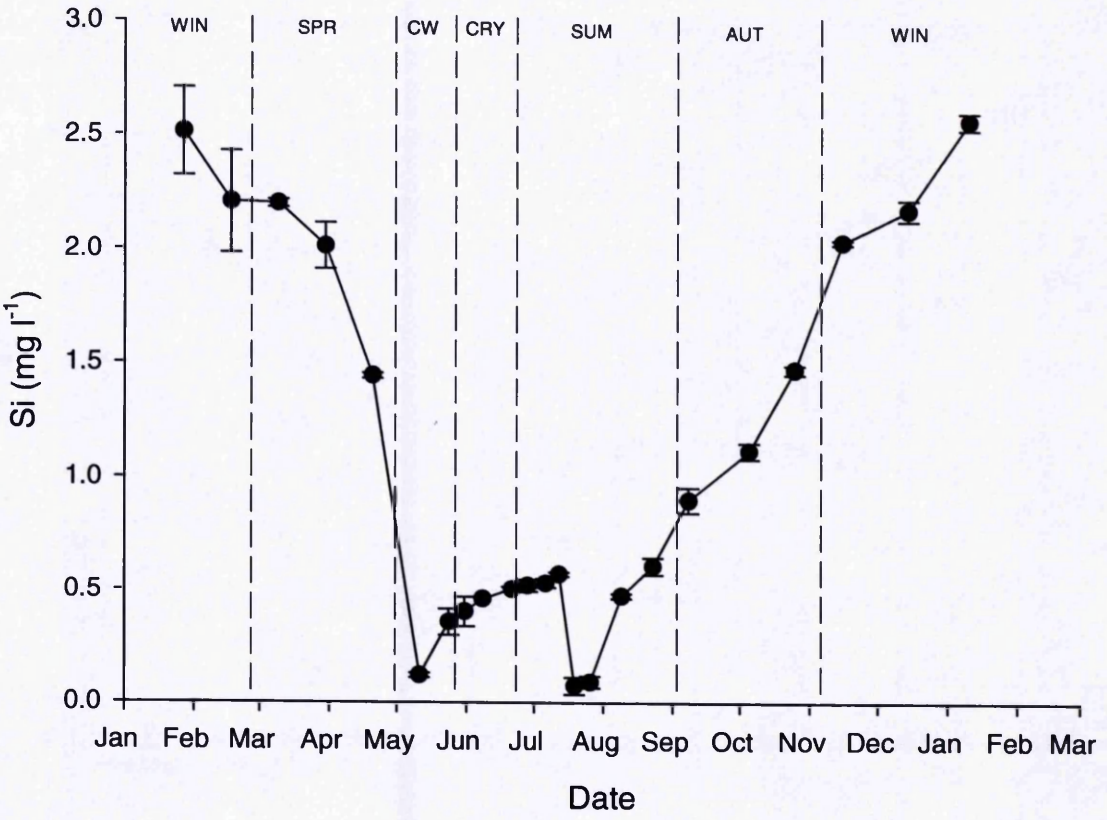


Figure 3.25: Seasonal changes in the concentration of silicon in Rostherne Mere, 2000. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

3.1.3 Zooplankton

3.1.3.1 Zooplankton dry weight.

Seasonal changes in zooplankton dry weight are shown in Figure 3.26. During the initial winter and spring phases zooplankton biomass was approximately 20-30μg l^{-1}, (with the exception of 30th March when it increased to 60μg l^{-1}). During the clear-water phase biomass had increased greatly, during the first two samplings of this phase biomass was approximately 140μg l^{-1}, dropping to approximately 50μg l^{-1} by the end of the clear-water phase and the first sampling during the cryptomonad phase. Dry weight then increased again, reaching a maximum of 154μg l^{-1} at the end of the phase, (when conditions had returned to those pertaining during the clear-water phase). By the start of the summer phase biomass had fallen to approximately 70μg l^{-1}. There was a small peak on the 12th of July (110μg l^{-1}) before falling to a summer minimum of 39μg l^{-1} on the 26th of July. Dry weight increased during the remainder of the summer phase and into the autumn phase, reaching a maximum of 120μg l^{-1} during September, before falling through the remainder of the autumn phase to reach approximately 45μg l^{-1} during the winter phase.

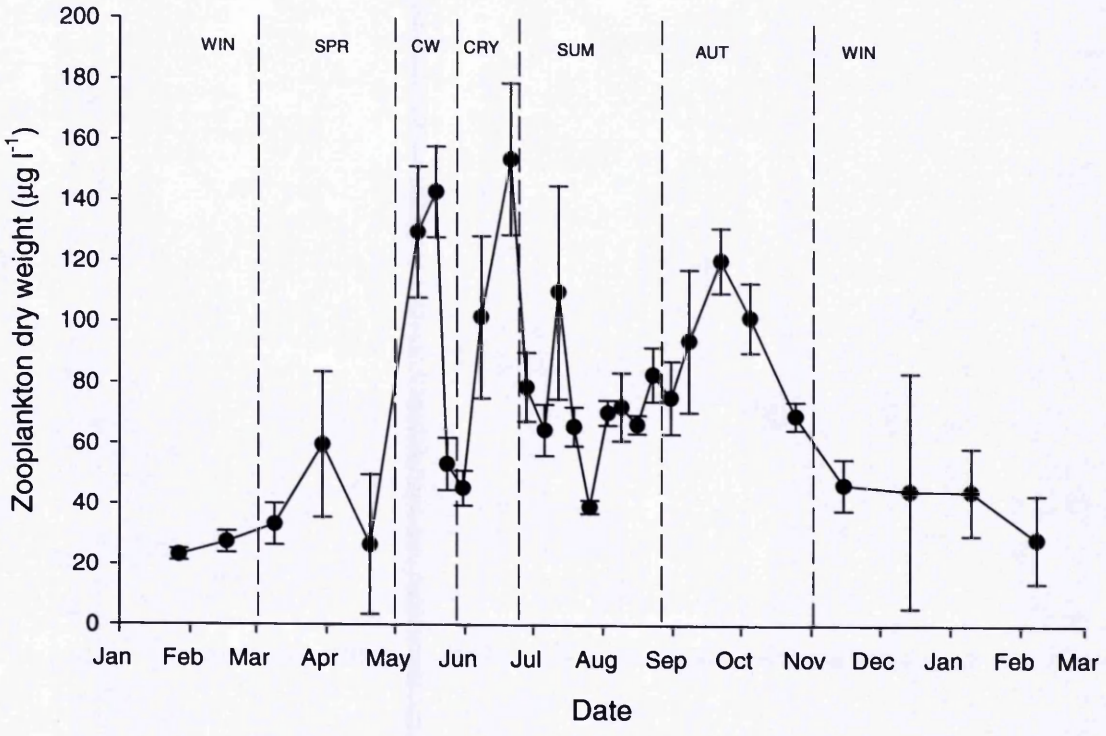


Figure 3.26: Seasonal changes in zooplankton dry weight in Rostherne Mere, 2000. Values are the means of 20m trawls from sites A, B and C. Error bars ±1 SD. (n=3).

3.1.3.2 Zooplankton Population Parameters

Daphnia

Counts

Daphnia populations in 2000 were dominated by *Daphnia longispina. Daphnia* showed three distinct peaks (Figure 3.27a) - during the clear-water phase, the cryptomonad phase, and the winter phase. During the initial winter phase *Daphnia* numbers were low (≤1 *Daphnia* l^{-1}), before increasing slightly during the spring phase to reach a maximum of 2.6 *Daphnia* l^{-1} at the end of the phase. By the clear-water phase numbers had increased rapidly to approximately 9.4 *Daphnia* l^{-1} (11^{th} and 19^{th} of May) before decreasing rapidly to 2.4 *Daphnia* l^{-1} at the end of the phase. Numbers remained low at the beginning of the cryptomonad phase (1.2 *Daphnia* l^{-1}) before increasing during the phase to reach 16.5 *Daphnia* l^{-1} litre on the 21^{st} of June. Both these peaks coincided with maximal Secchi depths. Throughout the summer phase numbers of *Daphnia* averaged 2.4 *Daphnia* l^{-1}, with numbers falling further during the autumn phase, with *Daphnia* present at <1 l^{-1} during October. Following the overturn number peaked at 12.2 *Daphnia* l^{-1} in December, before numbers fell to 1.4 *Daphnia* l^{-1} in February.

Percentage Gravid

The proportion of gravid adult *Daphnia* (i.e. *Daphnia* with eggs) is shown in 3.27b. There were increases at the end of the initial winter phase (71%) and the middle of the spring phase (60%) otherwise % gravid was approximately 20% during these phases. There was a slight increase during the cryptomonad phase (28%) before decreasing <5% at the end of the cryptomonad phase / start of the summer phase, following which values increased to reach an elevated period during July and August, with values generally between 35% and 55%. Values then declined during the autumn phase and overturn until 0% of the *Daphnia* were gravid.

Brood Size

Maximum brood sizes (Figure 3.28a) occurred during the spring phase (7.5 eggs per female) and around the time of the overturn (6-7 eggs per female). A minimum of 1.6 eggs per female was observed during the clear-water phase. At other times, eggs per gravid female varied between 2 and 5.

Birth Rate

Birth rates (Figure 3.28b) were 0.04 during the initial winter phase, increasing to a maximum of 0.13 in the middle of the spring phase (30th of March) and then decreased to reach a minimum during the clear-water phase (0.05). There was a further increase to 0.13 at the start of the cryptomonad phase before falling to 0.04 at the start of the summer phase. During the early summer-phase birth rates increased rapidly, reaching an annual maximum of 0.28 on the 12th of July, remaining >0.20 until the 16th of August/ 19th of July. Birth rates showed a general decline in late august and during the autumn phase, falling to zero in early October. There was then a small increase around the time of the overturn, with a birth rate of 0.15 on October the 25th, before dropping to 0.07 immediately after the overturn, and 0.04 during December. In January and February birth rates were zero. It can be seen that the peaks in *Daphnia* numbers during the clear-water phase, the cryptomonad phase and following the overturn were preceded by elevated birth rates. However, the higher birth rates throughout the summer period, and at the start of the autumn phase were not followed by an increase in *Daphnia* numbers.

Size

Average *Daphnia* body length ranged from 0.99mm to a maximum of 1.49mm (Figure 3.29). Body length was at a minimum during the spring phase (average over phase 1.00mm), increased during the clear-water phase and cryptomonad phase (average 1.20mm) and reached a maximum during the summer phase and early autumn phase (average 1.32mm). The average size then declined reaching 1.14mm during the winter phase. The body length of gravid *Daphnia* was consistently higher (ca. 0.55mm longer) than the average *Daphnia* body length.

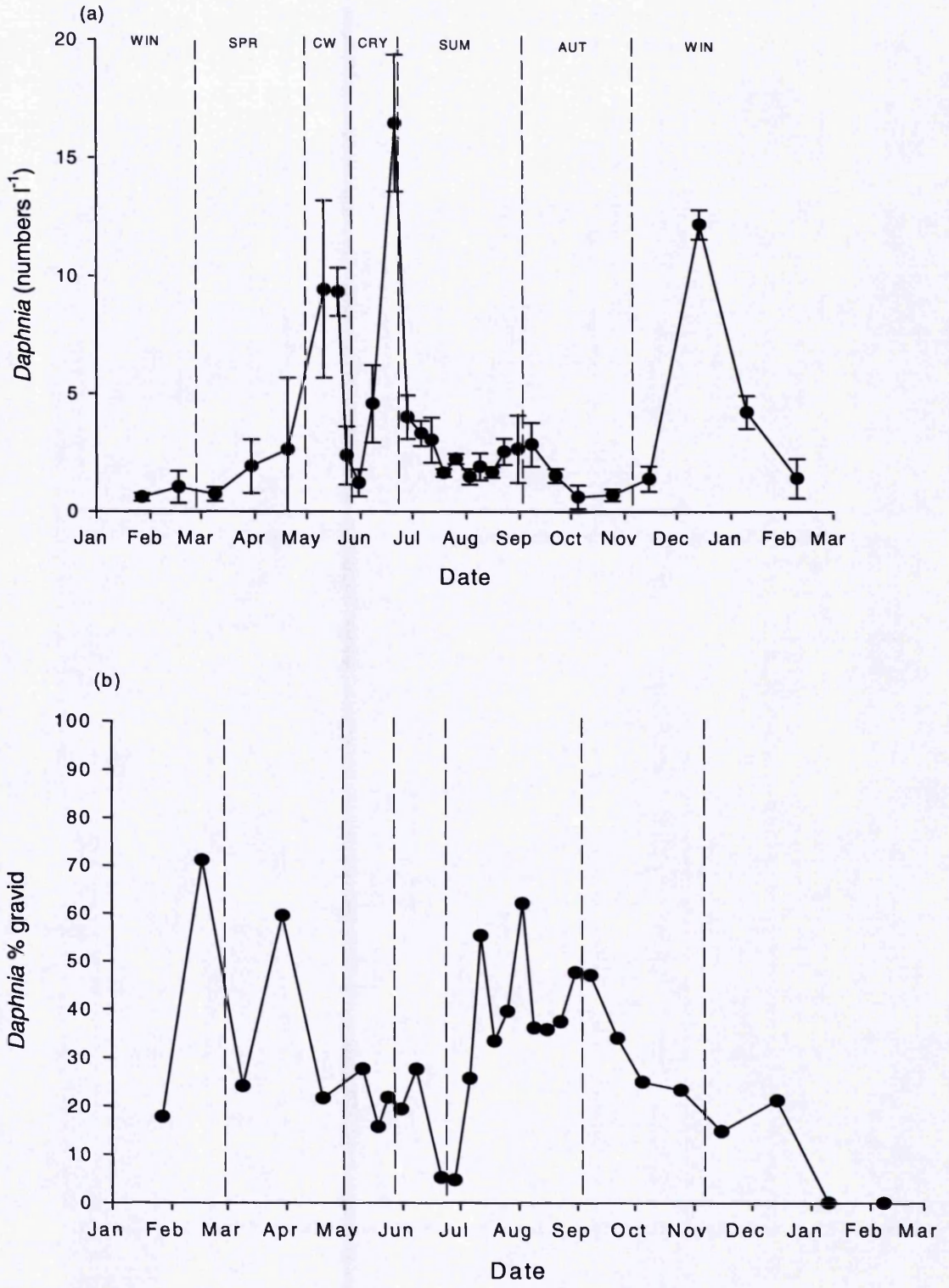


Figure 3.27: Seasonal changes in (a) the numbers of *Daphnia*. Values are the mean of vertical trawls taken from sites A, B and C. Error bars ±1 SD. (n=3). (b) the proportion of gravid adult *Daphnia*, calculated using the sum (sites A, B and C combined) of all gravid *Daphnia* and total *Daphnia* counted during the determination of seasonal changes. Rostherne Mere, 2000.

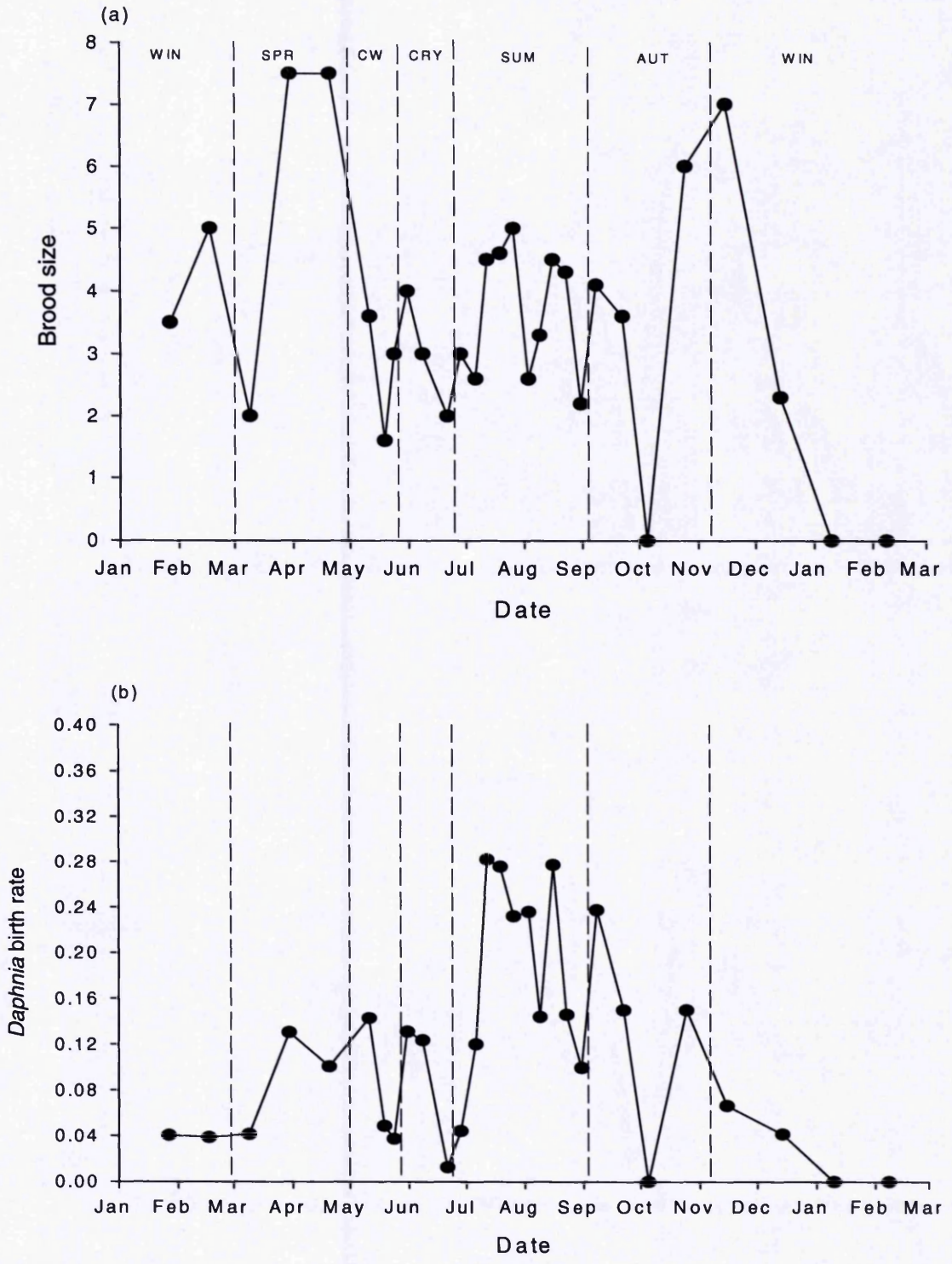


Figure 3.28: Seasonal changes in (a) average brood size of *Daphnia* and (b) the instantaneous birth rate of *Daphnia*. In both cases calculations were based on combined data from all three sites.

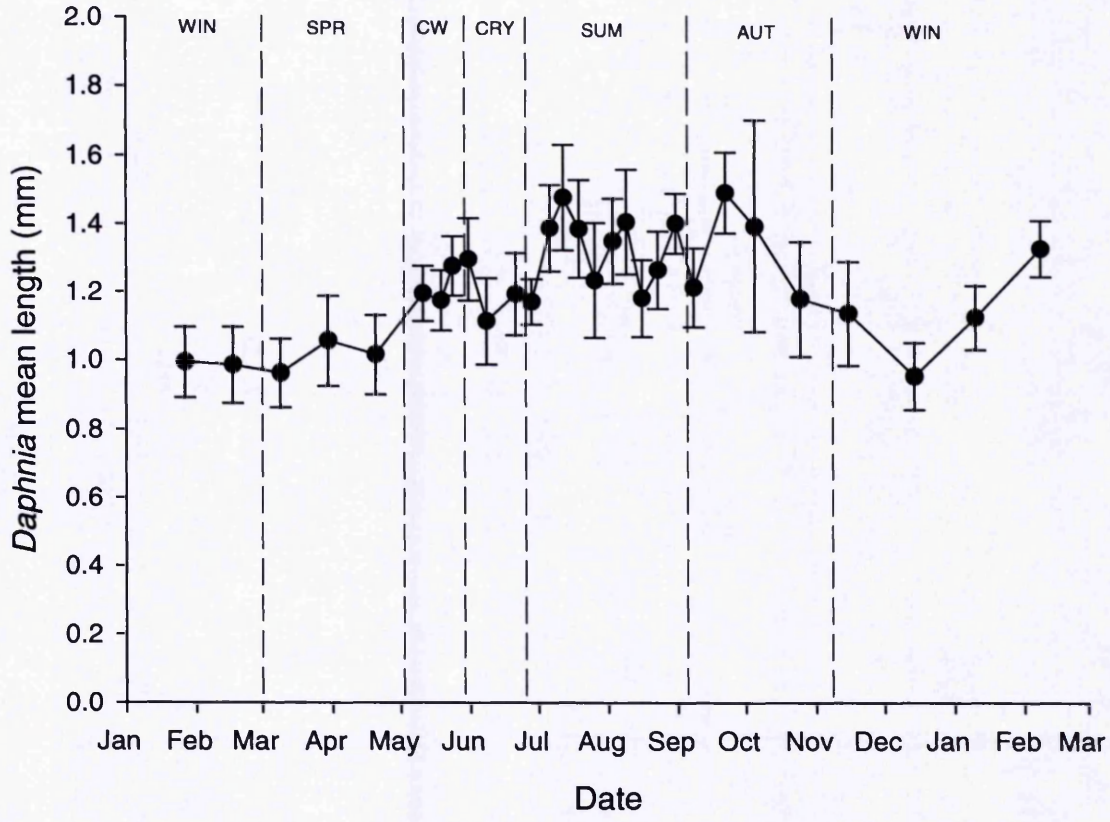


Figure 3.29: Seasonal changes in the average length of *Daphnia* in Rostherne Mere, 2000. Values are the mean lengths of animals randomly selected from sites A, B and C. (n≈40 for each date). Error bars show 95% confidence intervals.

Calanoid Copepods

Counts

Seasonal changes in the number of calanoid copepods are shown in Figure 3.30a. Calanoid copepods increased in numbers during the initial winter and early spring phase, reaching a maximum of 6.1 calanoids l^{-1} in the middle of the spring phase, declining to 2.8 calanoids l^{-1} at the end of the phase. During the early part of the clear-water phase numbers were approximately 4 calanoids l^{-1}, following which numbers declined, reaching a minimum of 0.1 calanoids l^{-1} at the start of the summer phase. Numbers remained at <1 calanoid l^{-1} for the remainder of the summer phase and autumn phase, with an increase to approximately 1.3 calanoids l^{-1} during the winter phase.

Size

Average Calanoid body length varied from 1.05mm to 1.51mm (Figure 3.30b). Mean body length did not show any obvious annual fluctuations. Average length across the whole sampling season was approximately 1.20mm.

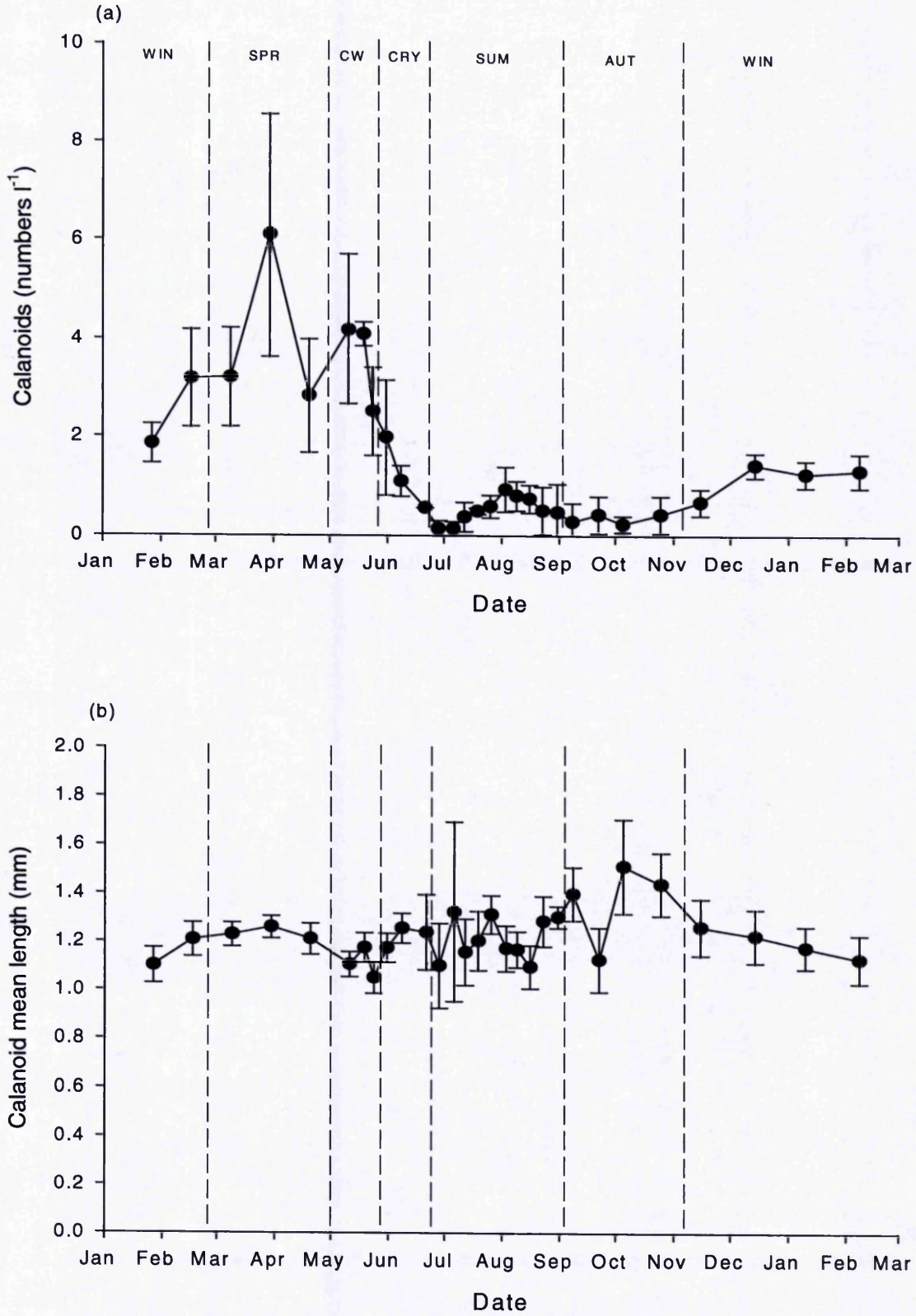


Figure 3.30: (a) Seasonal changes in the numbers of calanoid copepods. Values are the mean of three sites, error bars ±1 SD. (b) Seasonal changes in the mean length of calanoid copepods. Values are the mean lengths of animals randomly selected from sites A, B and C. (n≈40 for each date). Error bars show 95% confidence intervals.

Cyclopoid Copepods

Counts

Cyclopoid copepods showed maximum numbers during the late summer phase and the autumn phase (Figure 3.31a). Numbers were low during the initial winter and spring phase, with the first noticeable increase occurring during the cryptomonad phase, when numbers increased from 2.3 - 7.9 cyclopoids l^{-1}. During the early summer phase numbers were low, with a minimum of 2.8 cyclopoids l^{-1} on the 19th of July. Numbers then increased, with approximately 12 cyclopoids l^{-1} during the whole of August. During the autumn phase cyclopoid numbers increased to annual maximum of 18.4 cyclopoids l^{-1} (early October), before falling to 3.5 cyclopoid l^{-1} at the start of the winter phase. Numbers decreased throughout the winter, reaching a minimum of 0.4 cyclopoids l^{-1} in February.

Size

Average cyclopoid body is shown in Figure 3.31b. Mean body length did not show any obvious annual fluctuations. Average length over the whole sampling season was approximately 1mm.

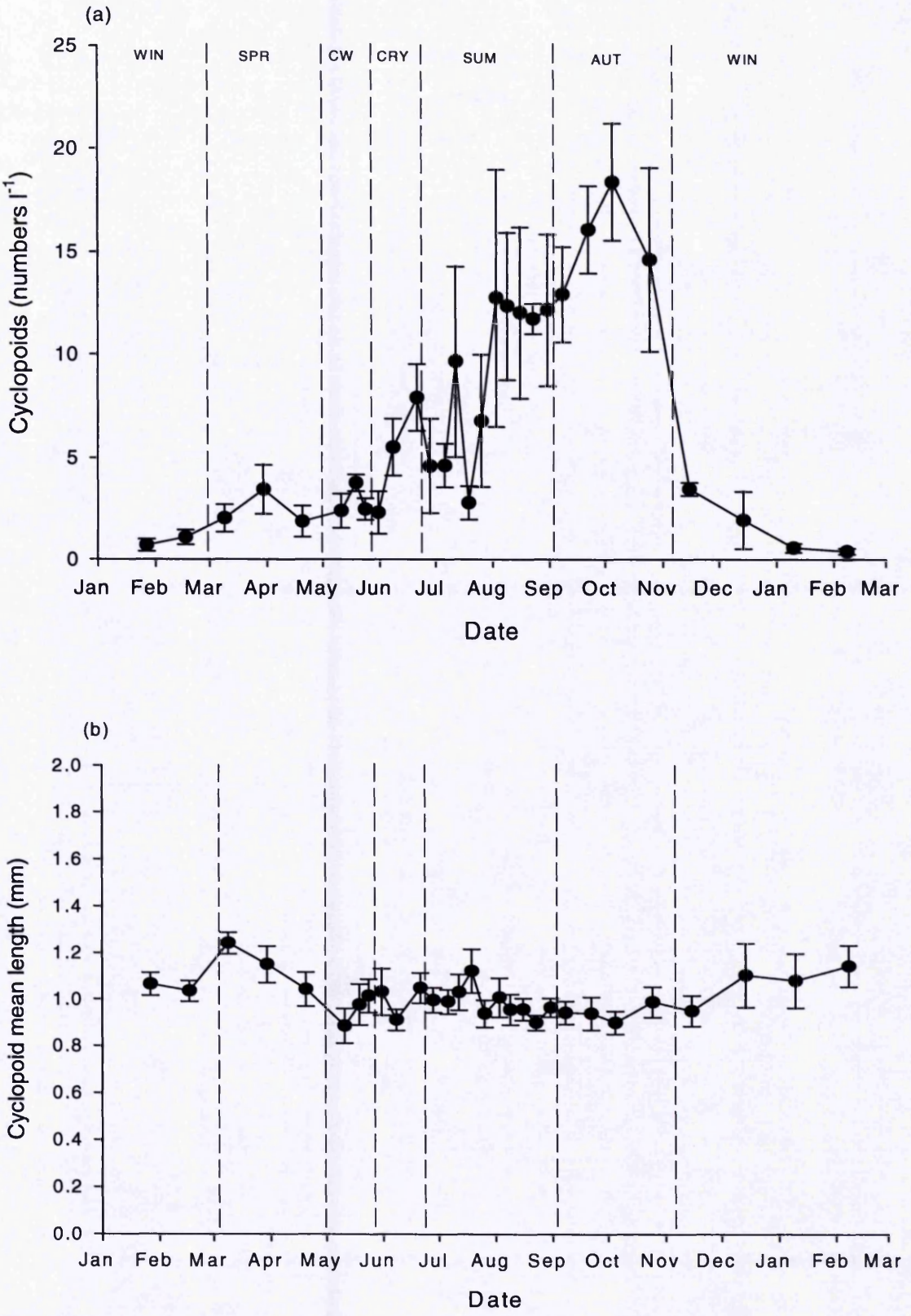


Figure 3.31: (a) Seasonal changes in the number of cyclopoid copepods. Values are the mean of three sites, error bars ±1 SD. and (b) seasonal variation in the mean length of cyclopoid copepods. Values are the mean lengths of animals randomly selected from sites A, B and C. (n≈40 for each date). Error bars show 95% confidence intervals.

Ciliated Protozoa

Numbers of ciliated protozoa are shown in Figure 3.32a. Ciliated protozoa showed a small increase during the spring phase, reaching 14 ml^{-1} on the 20th of April, before falling to 0 ml^{-1} at the start of the clear-water phase. Numbers then increased, peaking at 100 ml^{-1} during the cryptomonad phase (8th of June), before falling back to 0 ml^{-1} at the end of the phase (when condition had returned to those pertaining during the clear-water phase). During the summer phase numbers showed rapid fluctuations, with numbers generally higher during late July and August, with a maximum of 100 ml^{-1} on the 23rd of August, following which numbers fell rapidly, remaining low during the autumn and winter phases.

***Chaoborus* larvae**

Numbers of *Chaoborus* larvae are shown in Figure 3.32b. *Chaoborus* larvae were almost completely absent during the spring and clear-water phase, with maximum numbers during the summer phase and early autumn phase. Numbers first increased during the cryptomonad phase (to 1 *Chaoborus* m^{-3}), and then more rapidly during July, peaking at 10 *Chaoborus* m^{-3} on the 19th of July, with numbers falling to <4 m^{-3} during August. The second substantial peak reached a maximum of 7.7 m^{-3}, numbers then dropping to 0 at the end of the autumn phase, remaining at 0 for the rest of the sampling period.

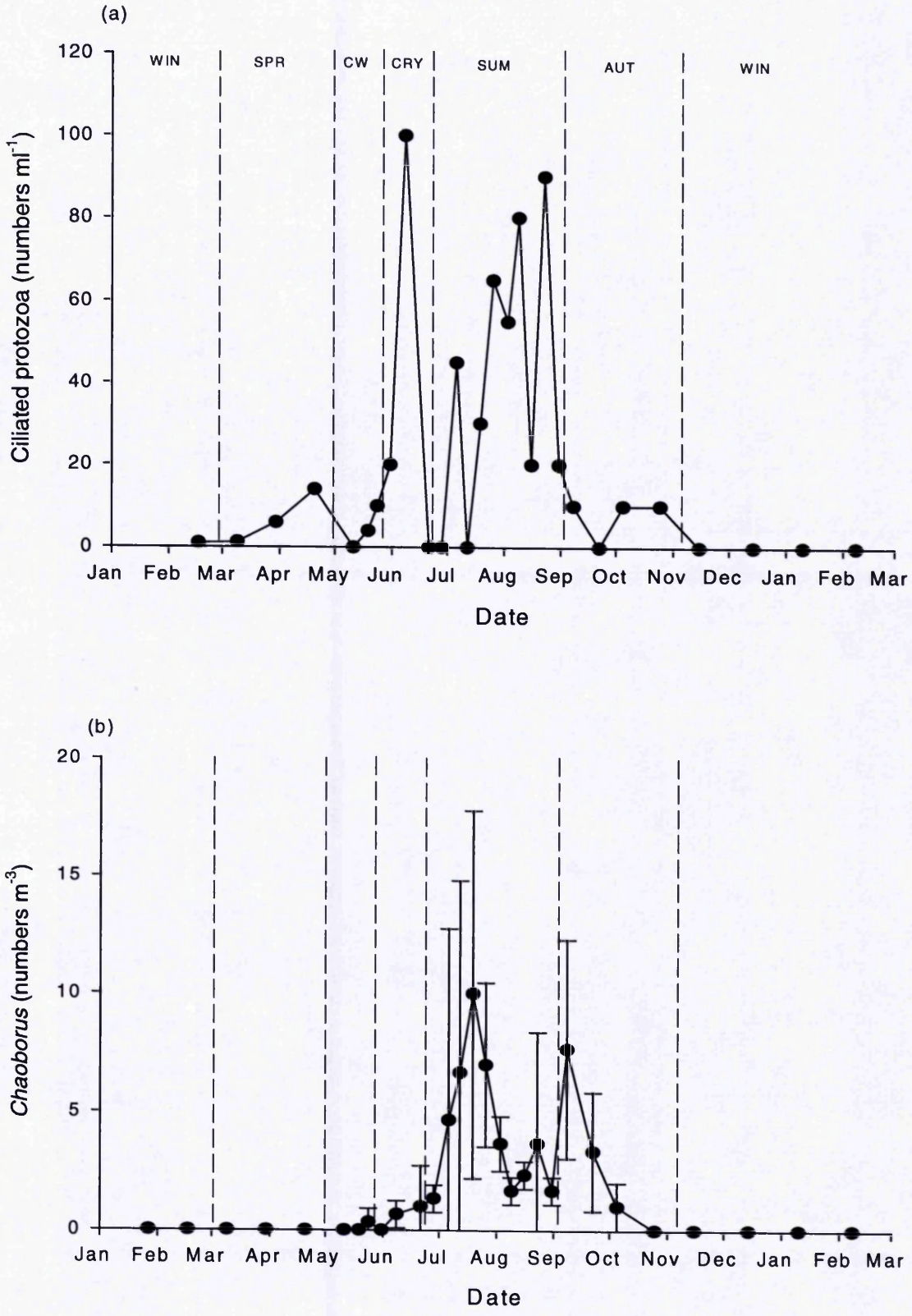


Figure 3.32: Seasonal changes in (a) ciliated protozoa, counts based on site A only and (b) *Chaoborus*, values mean of three sites, error bars ±1SD.

3.1.3.3 Filtering Rate

Total filtering rate (Figure 3.33) (for *Daphnia* and Calanoid copepods combined) varied from a minimum of 3% per day to a maximum of 61% per day. During the winter and early spring phase filtering rate increased from a minimum of 3% to a maximum of 10% per day on the 30th of March, dropping to 7% at the end of the spring phase. The maximum figure occurred when calanoid copepods were at their population maximum, the contribution of calanoids to the total filtering rate being 75% at this time. During the early clear-water phase, (11th and 19th of May) approximately 50% of the water volume was filtered per day, 75% of this being due to *Daphnia*. This had fallen to 15 % at the end of the clear-water phase, and remained low (10%) at the start of the cryptomonad phase. Filtering rate then increased, reaching a maximum of 61% (98% of this filtering rate was due to *Daphnia*), this high filtering rate occurring when conditions had reverted to those found in the clear-water phase. During the summer phase period filtering rates were generally <15%, including during the period of maximum phytoplankton biomass (mid-late July). Filtering rates fell during the early part of the autumn phase, reaching a minimum of 3% at the end of this phase. During the winter phase filtering rates increased, reaching a maximum of 14% in December before dropping to 5% in February 2001.

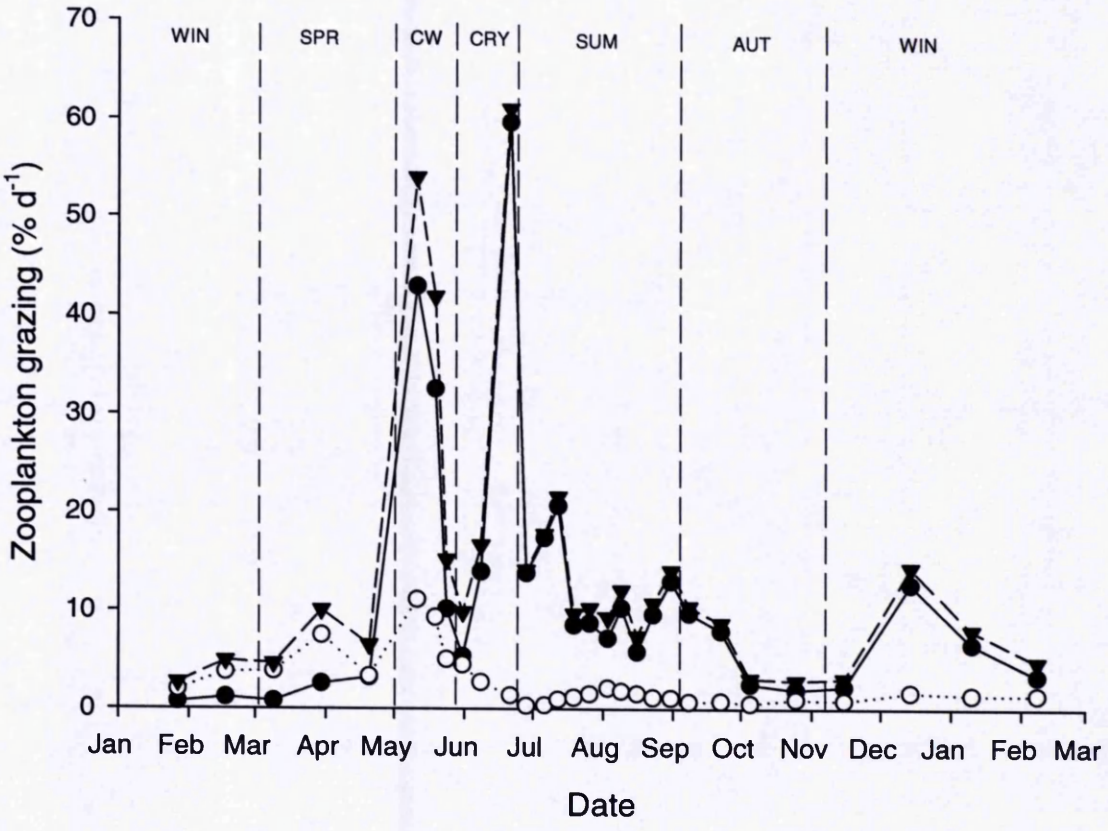


Figure 3.33: Seasonal changes in the filtering rate of *Daphnia* (●), calanoid copepods (○) and both combined (▼), Rostherne Mere 2000.

3.1.4 Bacteria, Dissolved Organic Carbon, TSS and TOM

3.1.4.1 Bacteria

Counts of total bacteria are shown in Figure 3.34a. Numbers ranged from a minimum of $1.97x10^6$ cells ml^{-1} to a maximum of $10.13x10^6$ cells ml^{-1}. During the spring phase numbers increased from $2.66x10^6$ cells ml^{-1} to $6.62x10^6$ cells ml^{-1}. There were then three distinct peaks in bacterial numbers, the first peak occurred during the cryptomonad phase, when numbers peaked at $8.94x10^6$ cells ml^{-1}. Numbers then dropped to approximately $6x10^6$ cells ml^{-1} before increasing to a broad peak, from the 19th July to the 3rd of August, with a maximum of $10.13x10^6$ cells ml^{-1} on the 26th of July. Numbers then dropped to $5.37x10^6$ cells ml^{-1} before increasing to a third peak of $9.63x10^6$ cells ml^{-1} on the 23rd of August, following which numbers fell to $8.08x10^6$ cells ml^{-1} at the end of the summer phase. Numbers dropped throughout the autumn phase, reaching $2.86x10^6$ cells ml^{-1} after the late October overturn, before falling to a minimum of $1.97x10^6$ cells ml^{-1} in January.

3.1.4.2 Viable Bacteria

Counts of viable bacteria varied between 280 CFU ml^{-1} and 3400 CFU ml^{-1} (Figure 3.34b). Viable bacteria were first enumerated during the clear-water phase and numbers did not show any substantial increase until the later half of the summer phase, resulting in a large increase during August and the early autumn phase, reaching a maximum of approximately 3400 CFU ml^{-1} in late September. Numbers then fell to around 1200 CFU ml^{-1} for the rest of the remainder of the phase and into the winter phase.

3.1.4.3 Dissolved Organic Carbon

Seasonal variation in dissolved organic carbon is shown in Figure 3.35. Concentrations ranged from 3.74 mg l^{-1} to 7.02 mg l^{-1}. No distinct seasonal pattern was observed.

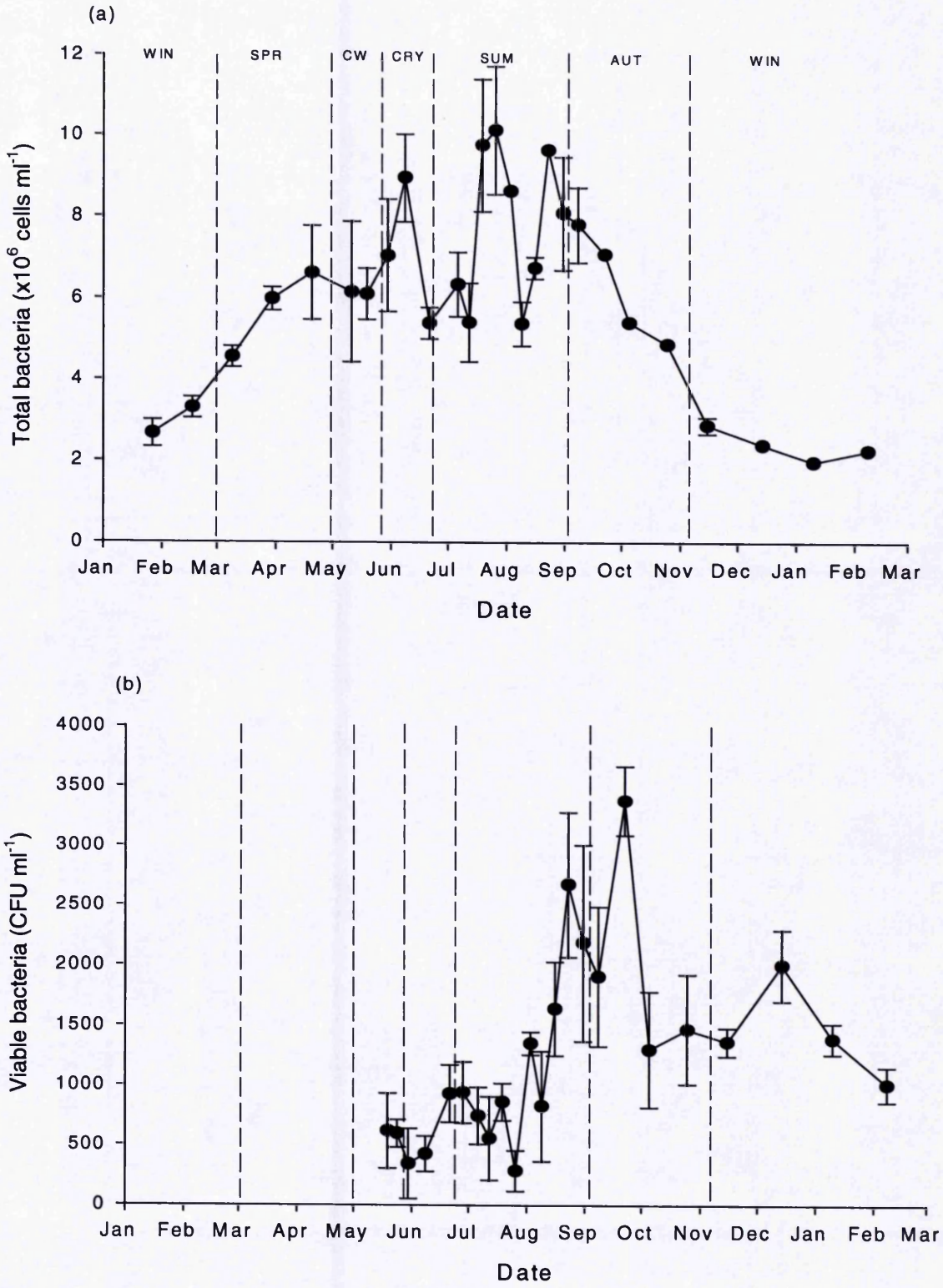


Figure 3.34: Seasonal changes in (a) total bacteria and (b) viable bacteria in Rostherne Mere, 2000. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

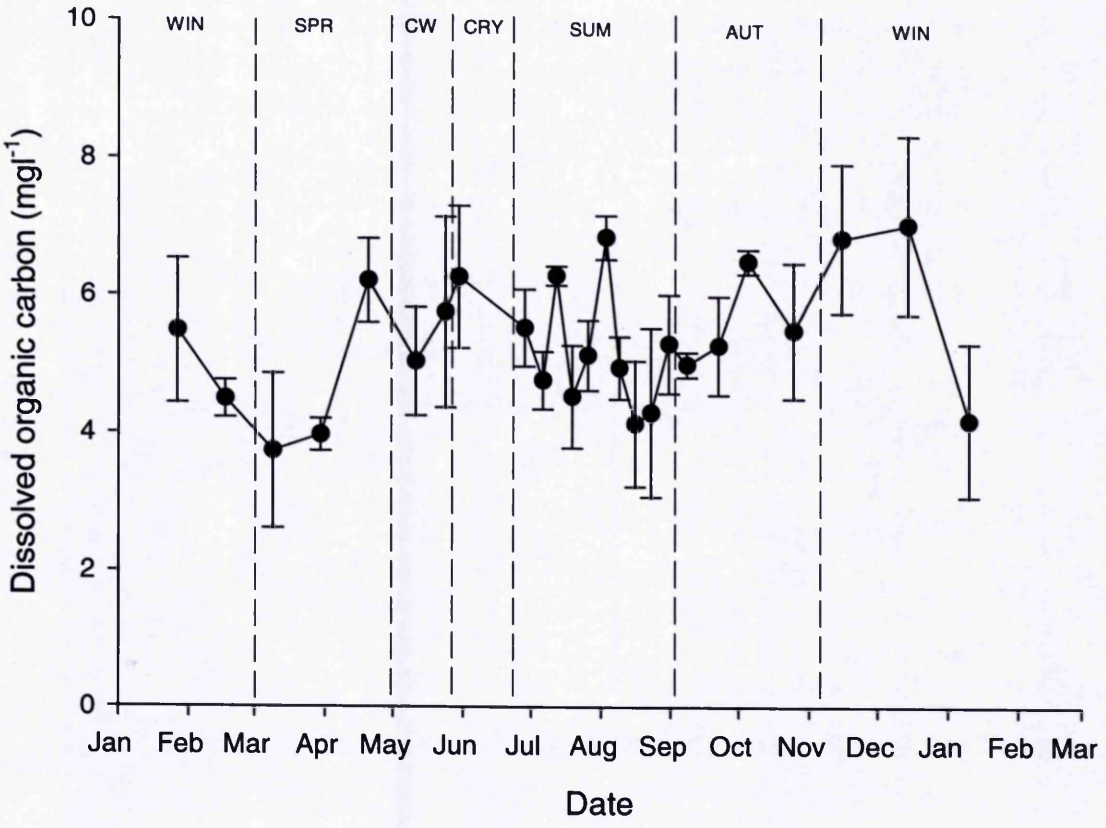


Figure 3.35: Seasonal changes in dissolved organic carbon, Rostherne Mere, 2000. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

3.1.4.4 Total Suspended Solids (TSS) and Total Organic Matter (TOM)

Total suspended solids and total organic matter are shown in Figure 3.36. TSS and TOM showed the same seasonal pattern as chlorophyll-a. During the spring phase TSS increased slightly, reaching a maximum of 4.1mg l^{-1} (TOM 2.3mg l^{-1}). During the clear-water phase TSS fell to 1.7mg l^{-11}, (TOM not recorded) and increased to 5.9mg l^{-1} (TOM 5.1mg l^{-1}) during the cryptomonad phase, before falling back to 2.0 (TOM 1.9 mg l^{-1}) at the phases' end. Concentrations then increased rapidly, reaching a maximum of approximately18 mg l^{-1} on the 19th and 26th of July (TOM max. 16.3 mg l^{-1} on the 26th of July). There was a decrease to 7.9mg l^{-1} (TOM 7.1mg l^{-1}) in early august before a further increase, reaching a second peak of 14.9mg l^{-1} on the 31st of August (TOM 13.3mg l^{-1}). At the start of the autumn phase concentrations had fallen to 7.2mg l^{-1} (TOM 5.7mg l^{-1}) and declined thereafter reaching a minimum of 1.5mg l^{-1} (TOM 1.1 mg l^{-1}) in February.

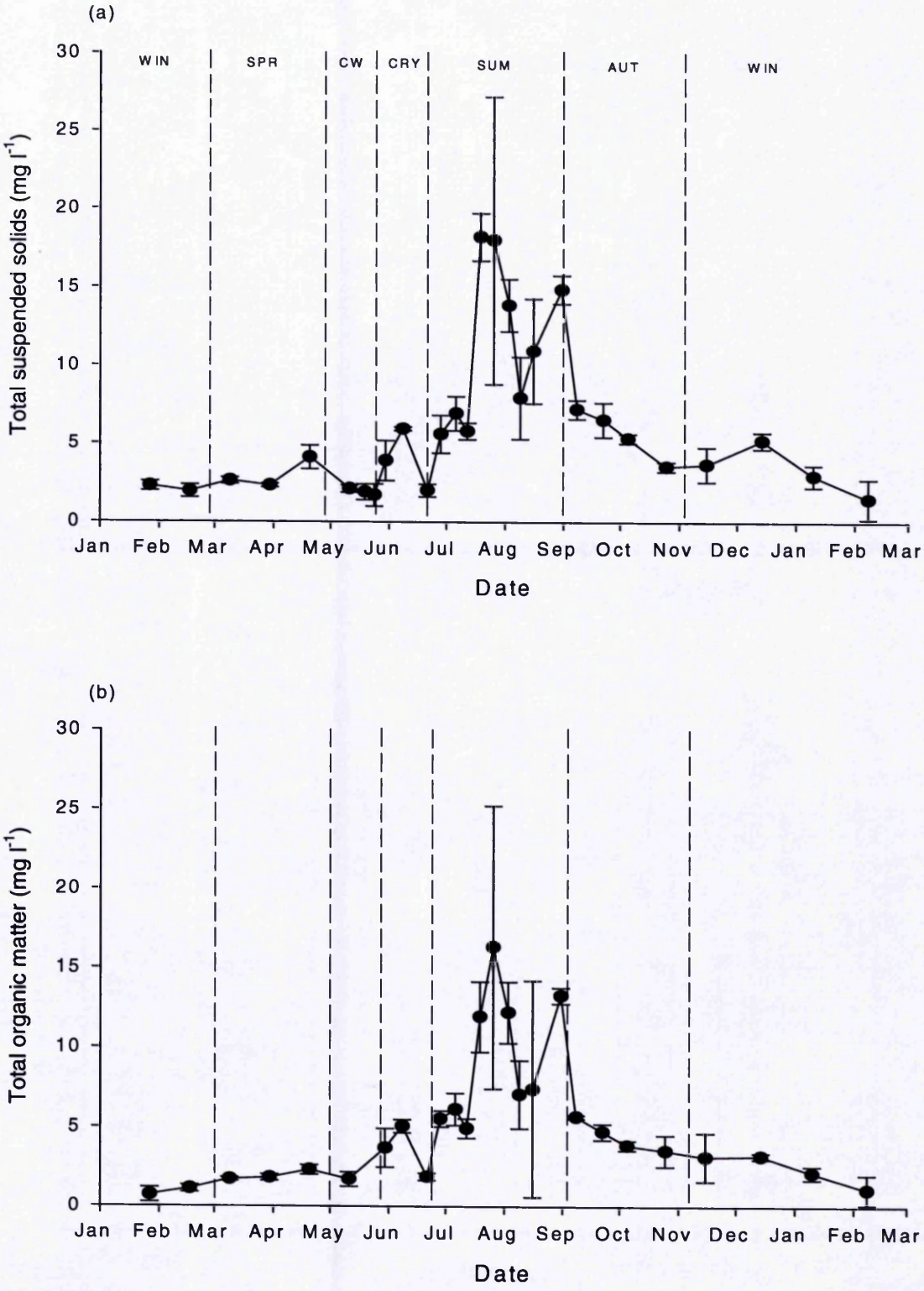


Figure 3.36: Seasonal changes in (a) total suspended solids and (b) total organic matter in Rostherne Mere, 2000. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

3.2 Results for Rostherne Mere, 2002.

For Rostherne 2002 the year has been divided into 5 phases. Phases are defined in terms of phytoplankton biomass (chlorophyll-a), and in relation to the dominance of different taxonomic groups of phytoplankton –

Winter phase, 17th January– 21st March

Spring phase, 3rd April – 2nd May

Clear-water phase, 16th May – 13th June

Summer phase, 27th June- 5th September

Autumn phase, 18th September – 7th November.

3.2.1 Phytoplankton

3.2.1.1 Chlorophyll-a and Secchi Depth

Chlorophyll-a and Secchi disk transparency are shown in Figure 3.37. During the winter phase the concentration of chlorophyll-a was approximately 1μg l^{-1} and the Secchi depth approximately 2m. The concentration of chlorophyll-a increased during the spring phase, from 4.4μg l^{-1} on the 3rd of April, to 60.2μg l^{-1} on the 18th of April (Secchi depth 1.6m). Chlorophyll-a then declined (32.7μg l^{-1} on the final spring phase sampling) to reach <5μg l^{-1} during the clear-water phase (Secchi depth here reached its annual maximum of 5.1m). The clear-water phase was followed by a long broad peak of elevated chlorophyll-a levels rising throughout the summer to reach a maximum of 91.6μg l^{-1} at the start of the autumn phase (September the 18th); during this period Secchi depth fell from 2.1m to a minimum of 0.8m (7th August). At the time of the chlorophyll-a maximum Secchi depth was 1.0m. During the remainder of the autumn phase chlorophyll-a declined to a minimum of 6.1μg l^{-1} in late October (Secchi depth rising to a maximum of 1.9m).

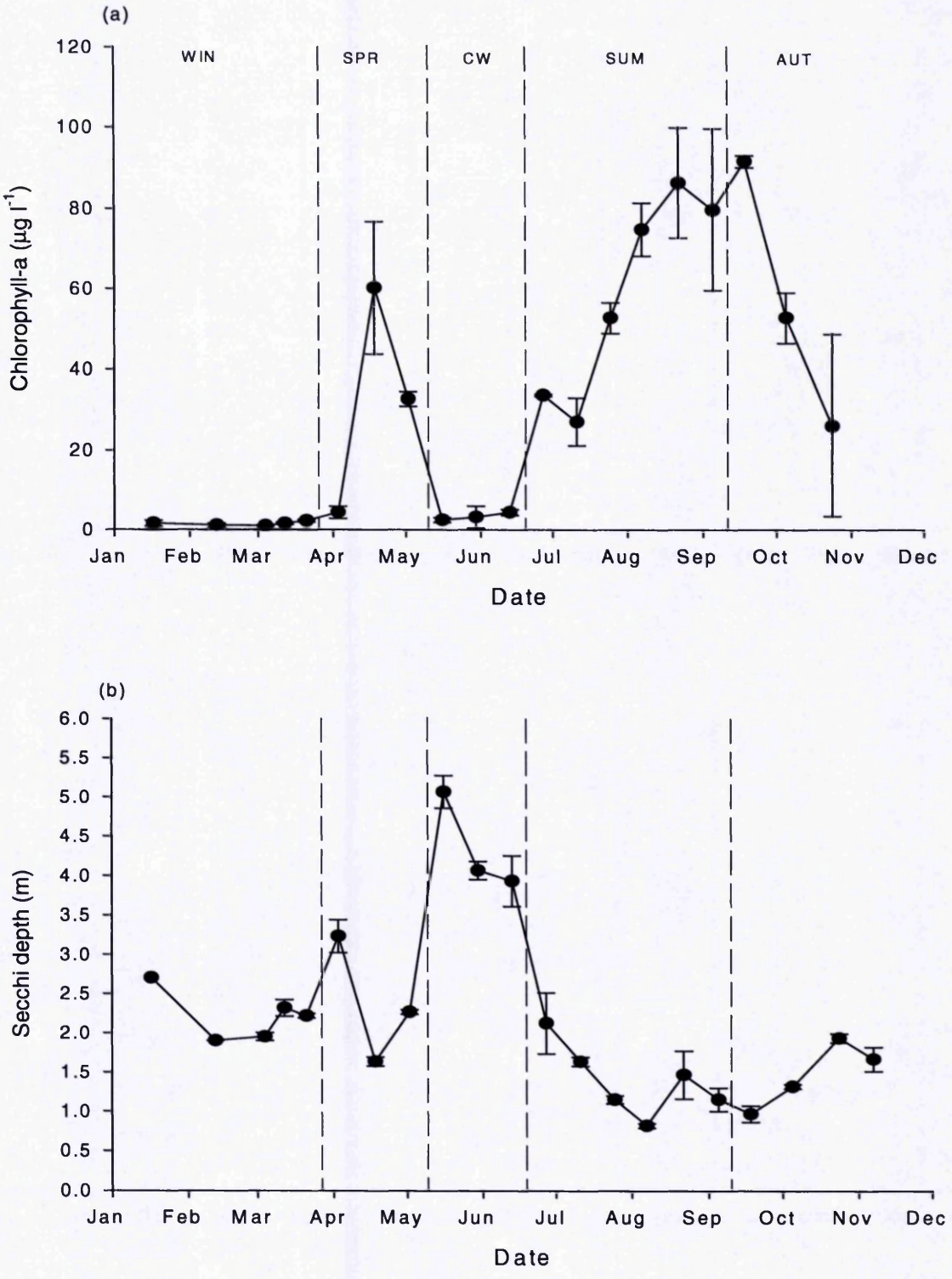


Figure 3.37: Seasonal changes in (a) Chlorophyll-a and (b) Secchi depth in Rostherne Mere, 2002. Values are the mean of sites A, B and C. Error bars ±1 SD. (n=3)

3.2.1.2 Phytoplankton Groups

The total algal biovolume and the biovolumes of each algal group are shown in Figure 3.38 to Figure 3.41. Figure 3.38b shows the percentage contribution of each algal group to the total biovolume Figure 3.42 shows the biovolume of the phytoplankton species considered edible to filter feeding Cladocera. Phytoplankton showed the following seasonal progression: Diatom/Cryptomonad bloom ⇒ Clear-water phase ⇒ Dinophyceae/Chlorophyceae ⇒ Cyanophyceae ⇒ Bacillariophyceae.

The group with the highest biovolume was Cyanophyceae, which showed a broad peak from July to November, peaking at $1.73x10^7$ μm^3 ml^{-1} on the 22nd of August. Bacillariophyceae peaked in April with a biovolume of $2.22x10^6$ μm^3 ml^{-1}, and also in late September/early October with a larger maximum biovolume of $7.74x10^6$ μm^3 ml^{-1}. Cryptophyceae also peaked in April, concurrently with the Bacillariophyceae, and with a similar biovolume ($2.52x10^6$ μm^3 ml^{-1}) and were largely absent at other times. Dinophyceae peaked in late June with a biovolume of $2.76x10^6$ μm^3 ml^{-1} and were absent at other times. Chlorophyceae also showed a large peak in late June/early July with a maximum of $4.21x10^4$ μm^3 ml^{-1}, as well as a small peak in early March of $7.18x10^3$ μm^3 ml^{-1} and were present at other times but in very low numbers. Small phytoplankton (<10μm greatest dimension), which including some unidentified species but was dominated by *Synechococcus* peaked on August 7th with $2.58x10^6$ μm^3 ml^{-1}. In terms of the major groups of phytoplankton the phases can be described as follows:

Winter Phase: 17th January – 21st March

Bacillariophyceae dominated this phase, contributing ca. 90% of the total biovolume. The exception was the 4th of March when Bacillariophyceae contributed 72% (15% Cryptophyceae, 7% small phytoplankton and 6% Chlorophyceae)

Spring Phase: 3rd April - 2nd of May

Bacillariophyceae dominated on the 3rd April and 2nd May, contributing ca. 85% of the total biovolume. Between these dates, on the 18th of May, (the time of the chlorophyll-a peak) Bacillariophyceae contribution dropped to 46% and an increase in cryptomonads led to them contributing 52%. Small phytoplankton (<10μm) and Chlorophyceae contributed a maximum of 7% during this phase. Cyanophyceae and Dinophyceae were almost entirely absent.

Clear-water Phase: 16th of May – 13th of June

Initially, this phase was dominated by cryptomonads, with 83% of the biovolume (cyanophyta contributing 15%). During the middle of the phase Cyanophyceae dominated with 63%, (Cryptophyceae contributing 9% and small phytoplankton 18%). At the end of this phase, Cryptophyceae contributed 50%, Cyanophyceae 29% and Bacillariophyceae 16%.

Summer Phase: 27th of June - 5th of September

Initially this phase was dominated by Dinophyceae with 66% and Cyanophyceae with 24%. For the remainder of this phase Cyanophyceae dominated with ca. 90% and above. The minimum Cyanophyceae contribution of 84% occurred on the 7th of August when small phytoplankton contributed 14% of the biovolume; however, the small phytoplankton was dominated by the cyanophyte *Synechococcus*, so Cyanophyceae may be said to comprise ca. 98% of the biovolume on this date.

Autumn Phase: 18th of September - 7th of November

During the first half of this phase (Sep 18th - 5th October) Cyanophyceae dominance was reduced to ca. 50-60% while that of Bacillariophyceae increased to 35-45%. During the latter half of this phase Cyanophyceae dominance increased to ca. 80%, with small phytoplankton (again dominated by the cyanophyte *Synechococcus*) ca.18%. Bacillariophyceae only contributed 1% of the biovolume at this time.

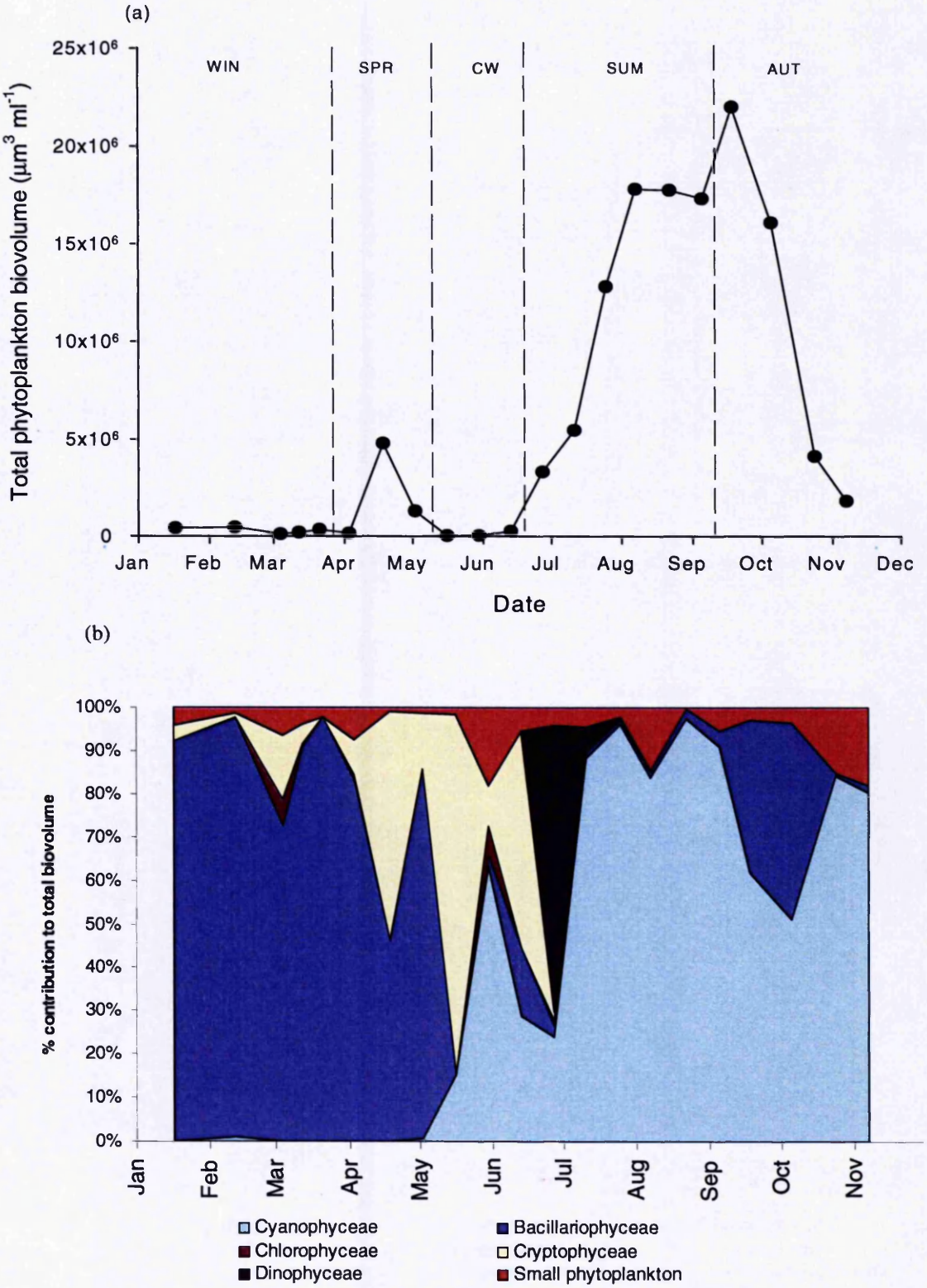


Figure 3.38: Seasonal changes in the (a) the total phytoplankton biovolume and (b) the percentage contribution of each algal group to the total algal biovolume. Rostherne Mere, 2002.

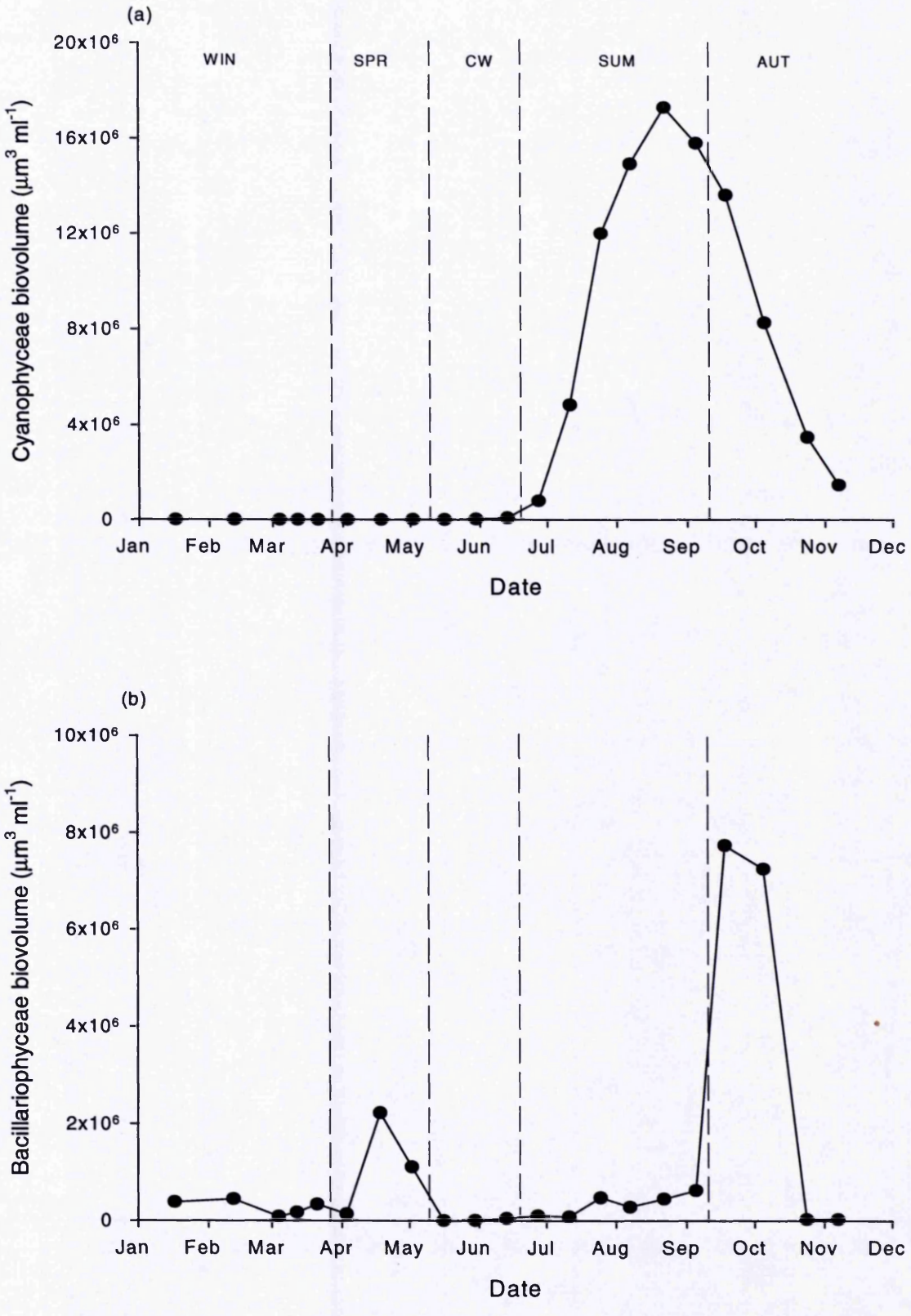


Figure 3.39: Seasonal changes in the biovolume of (a) Cyanophyceae and (b) Bacillariophyceae in Rostherne Mere, 2002. Biovolumes are calculated using the mean count from integrated samples from sites A, B and C.

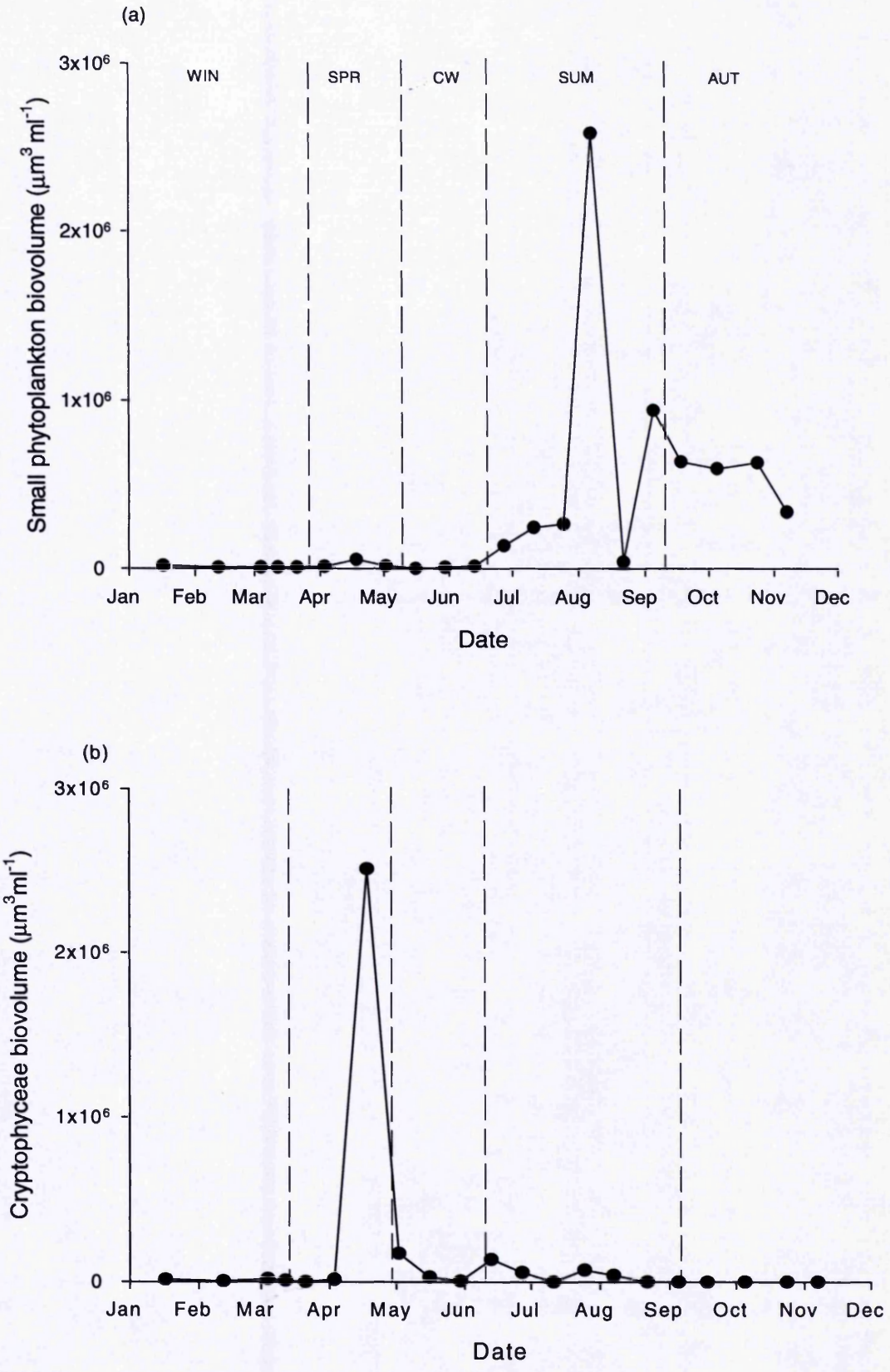


Figure 3.40: Seasonal changes in the biovolume of (a) small phytoplankton (<10µm greatest diameter) including some unidentified forms but dominated by *Synechococcus* and (b) Cryptophyceae in Rostherne Mere, 2002. Biovolumes are calculated using the mean count from integrated samples from sites A, B and C.

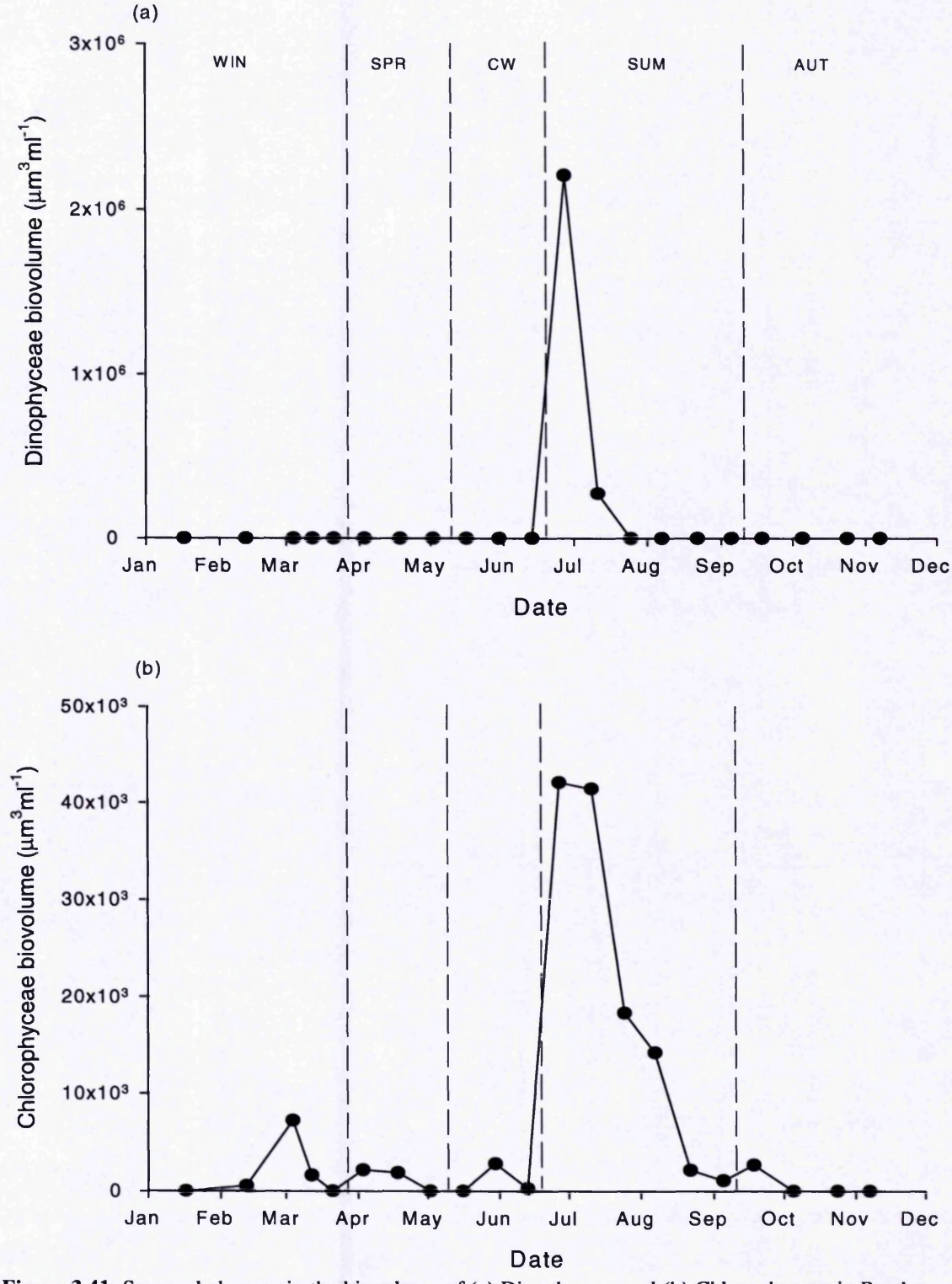


Figure 3.41: Seasonal changes in the biovolume of (a) Dinophyceae and (b) Chlorophyceae in Rostherne Mere, 2002. Biovolumes are calculated using the mean count from integrated samples from sites A, B and C.

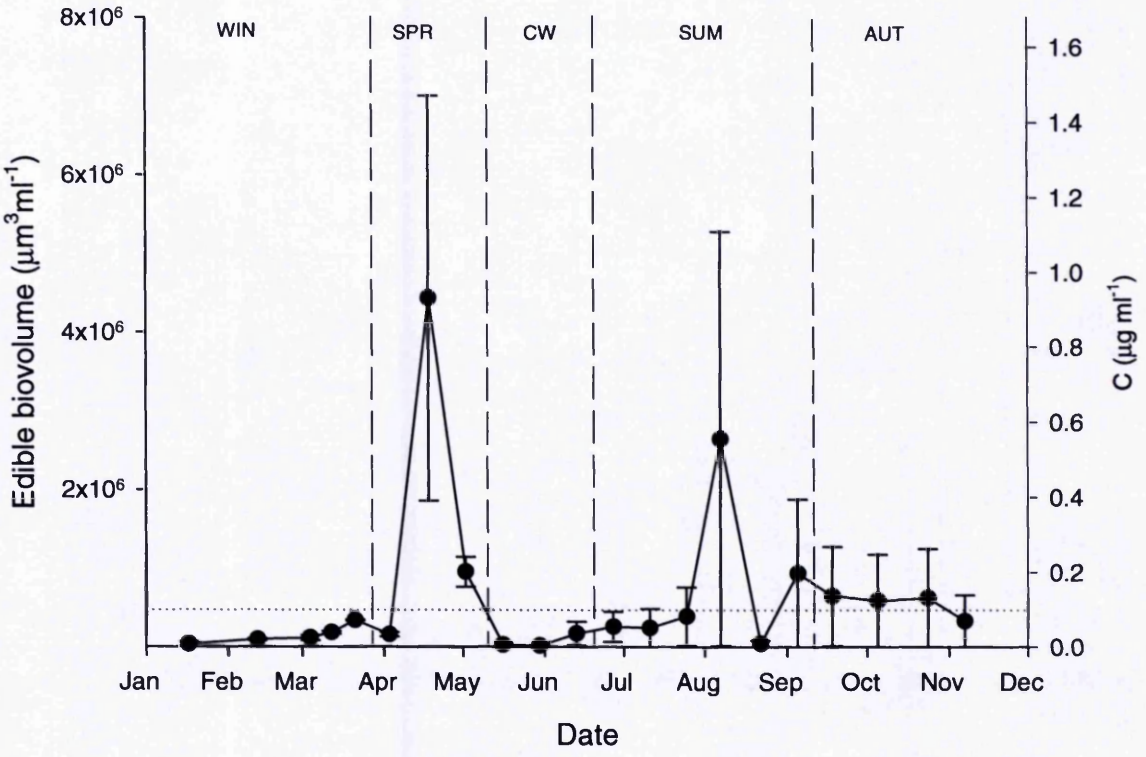


Figure 3.42: Seasonal changes in the biovolume of edible phytoplankton. Edible phytoplankton species include all those whose parameters fall within the size range given by the Burns' equation. Also included are some larger species which evidence suggests can be ingested by *Daphnia*. In the figure above the peak during the spring consists primarily of *Asterionella formosa*, *Cryptomonas* spp. and *Rhodomonas minuta*. The peak during the summer phase consisted of *Synechococcus* sp., as did the 'plateau' during the autumn phase. The secondary axis shows the edible biovolume expressed as carbon. The horizontal line is the threshold concentration of edible food for *Daphnia*, below which *Daphnia* are food limited.

3.2.1.3 Phytoplankton Species

Winter Phase –17th January – 21st March

This period was characterised by the presence of very few phytoplankton. *Cryptomonas* spp. (max. 10 cells ml^{-1}), *Scenedesmus quadricauda* (max. 7 cells ml^{-1}) and *Stephanodiscus rotula* (increasing from 0 to 10 cells ml^{-1} during this phase) were present. *Rhodomonas minuta* were more numerous with a maximum of 77 cells ml^{-1}. Small phytoplankton (<10μm) were present at ca. 300 cells ml^{-1}.

Spring Phase 3rd April – 2nd May

Asterionella formosa peaked during this phase, at 370 colonies ml^{-1} on the 18th of April. *Stephanodiscus rotula* was absent during this phase. *Cryptomonas* spp. and *Rhodomonas minuta* reached their maximum numbers during this phase, both peaking concurrently with *Asterionella formosa*. *Cryptomonas* peaked at 2270 cells ml^{-1} and *Rhodomonas* 940 cells ml^{-1}. No dinoflagellates were present during this phase, and the only cyanophyte was *Aphanizomenon flos-aquae*, with 7 filaments ml^{-1} at the end of this phase. Small phytoplankton (generally unidentified) were present throughout this phase, with numbers generally around 350 cells ml^{-1} during most of the phase, but peaking concurrently with *Asterionella* and the cryptophytes at 2657 cells ml^{-1}on the 18th of April.

Clear-water Phase: 16th of May - 13th of June

Initially only three taxa were recorded: *Cryptomonas* spp. present at 27 cells ml^{-1}, *Aphanizomenon flos-aquae* at 3 filaments ml^{-1} and small phytoplankton at 27 cells ml^{-1}. This was the date when Secchi depth was an annual maximum at 5.1m. By the end of this phase *Rhodomonas* spp. and *Cryptomonas* spp. had increased to 117 and 113 cells ml^{-1} respectively. *Aphanizomenon* increased to 40 filaments ml^{-1} and *Anabaena flos-aquae* first appeared, at 7 colonies ml^{-1}, while small phytoplankton had increased to 727 cells ml^{-1}. In the middle of this phase *Ankyra* spp. and *Scenedesmus* spp. were present at 30 cells ml^{-1} and 10 colonies ml^{-1} respectively.

Summer Bloom: 27th of June - 5th of September

Ceratium hirundinella was the first to peak during this phase, with a maximum of 53 cells ml^{-1} on the 27th of June before rapidly falling to 0 cells ml^{-1}. Within the Bacillariophyceae the small *Stephanodiscus* sp. was the most numerous, increasing rapidly to 983 cells ml^{-1} on the 25th of July, and then falling almost as rapidly, reaching 7 cells ml^{-1} at the end of the phase. *Aulacoseira granulata var. angustissima* increased

from 0 to 80 filaments ml^{-1} during this phase. *Staurastrum* sp. peaked during the early part of this phase, with 13 colonies ml^{-1}. The most numerous green algae was *Scenedesmus* spp. which increased from 0 colonies ml^{-1} to reach 50 colonies ml^{-1} on the 25th of July before declining over the remainder of the phase. Small numbers of *Ankyra* spp. were present at the start of the phase (20 cells ml^{-1}) but decreased to 0 cells ml^{-1} by late July. Cyanophyceae increased in numbers during the summer phase, *Anabaena flos-aquae* was present throughout the phase, reaching a maximum of 457 colonies ml^{-1} on the 25th of July; *Aphanizomenon flos-aquae* peaked later, reaching 143 filaments ml^{-1} on the 7th of August, and was absent thereafter. *Gomphosphaeria* sp. was present throughout the phase, reaching a maximum of 310 colonies ml^{-1} on the 22nd of August, before beginning a decline that would continue throughout the next phase. Within the Cyanophyceae, *Gomphosphaeria* dominated with ca. >90% of the biovolume. Small phytoplankton (<10μm) increased slowly during the early part of the phase before a rapid increase to 129,133 cells ml^{-1} on the 7th of August, fell rapidly to ca. 2000 cells ml^{-1} on the 22nd of August before increasing slightly to 46967 cells ml^{-1} at the end of the phase. The small phytoplankton during this phase was dominated by the Cyanophyte *Synechococcus* sp. *Cryptomonas* spp. was present on three occasions, but in low numbers, with a maximum of 67 cell/ml in late July. *Rhodomonas minuta* was largely absent.

Autumn Phase: 18th of September - 7th of November:

During this phase *Aulacoseira granulata var. angustissima* was present at 997 filaments ml^{-1} on the 18th of September, increasing from just 80 filaments ml^{-1} at the end of the previous phase. Numbers remained high on the next sampling occasion (5th of October) at 937 filaments ml^{-1} before falling to just 3 filaments ml^{-1} for the remainder of the phase. *Gomphosphaeria* sp. declined throughout this phase from 247 to 27 colonies ml^{-1}. The only other cyanophyte present was *Anabaena flos-aquae* at 17 colonies ml^{-1} on the 18th of September. Chlorophytes were largely absent; the only species present was *Scenedesmus* spp. at 17 colonies ml^{-1} on the 18th of September, and absent thereafter. Small phytoplankton (<10μm) were present throughout the phase at ca. 30000 cells ml^{-1} and dominated by *Synechococcus* sp. Cryptophytes and dinoflagellates were absent throughout the phase.

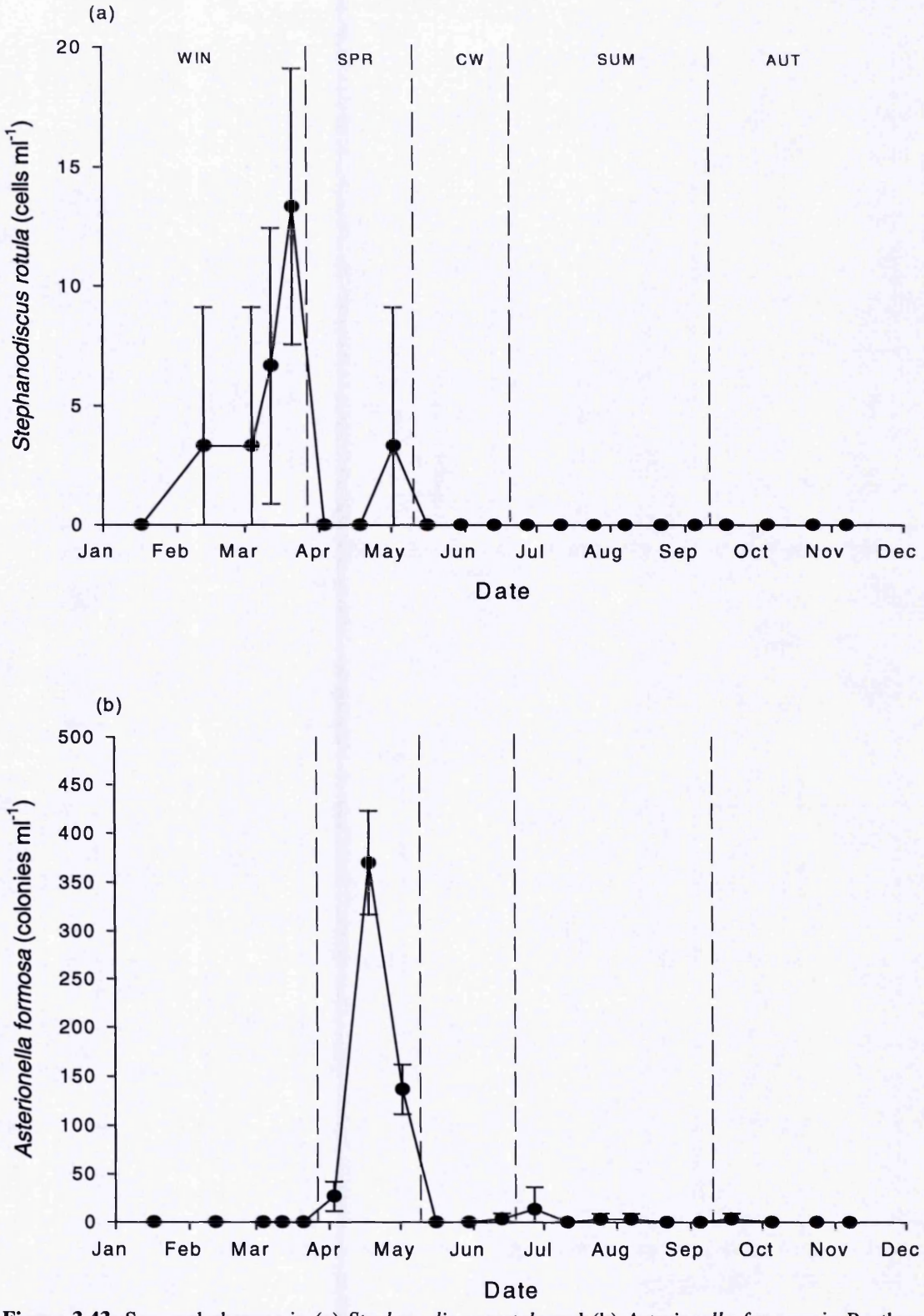


Figure 3.43: Seasonal changes in (a) *Stephanodiscus rotula* and (b) *Asterionella formosa* in Rostherne Mere, 2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

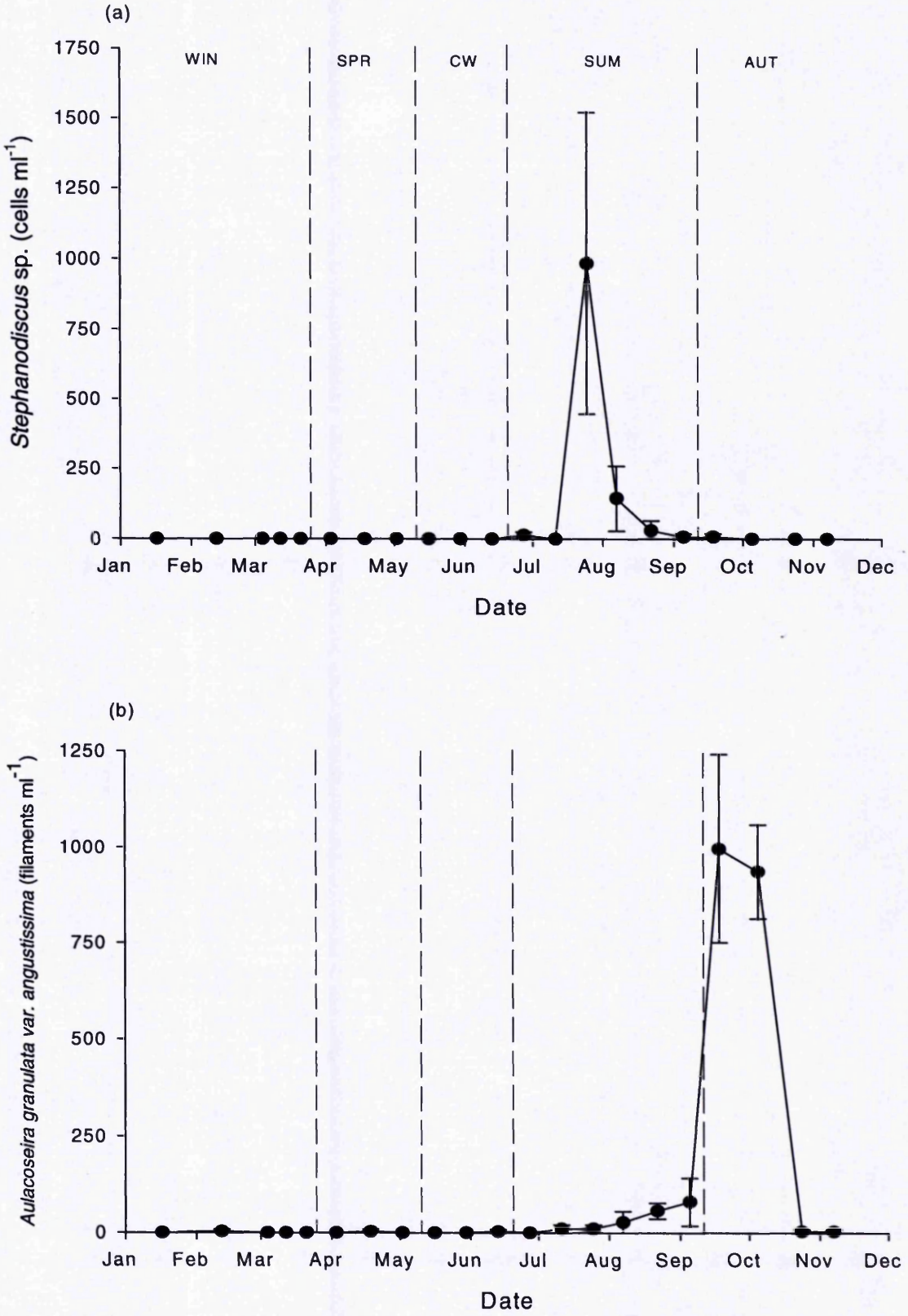


Figure 3.44: Seasonal changes in (a) Small unidentified *Stephanodiscus* sp. (possibly *S. minutula*) and (b) *Aulacoseira granulata var. angustissima*, Rostherne Mere, 2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

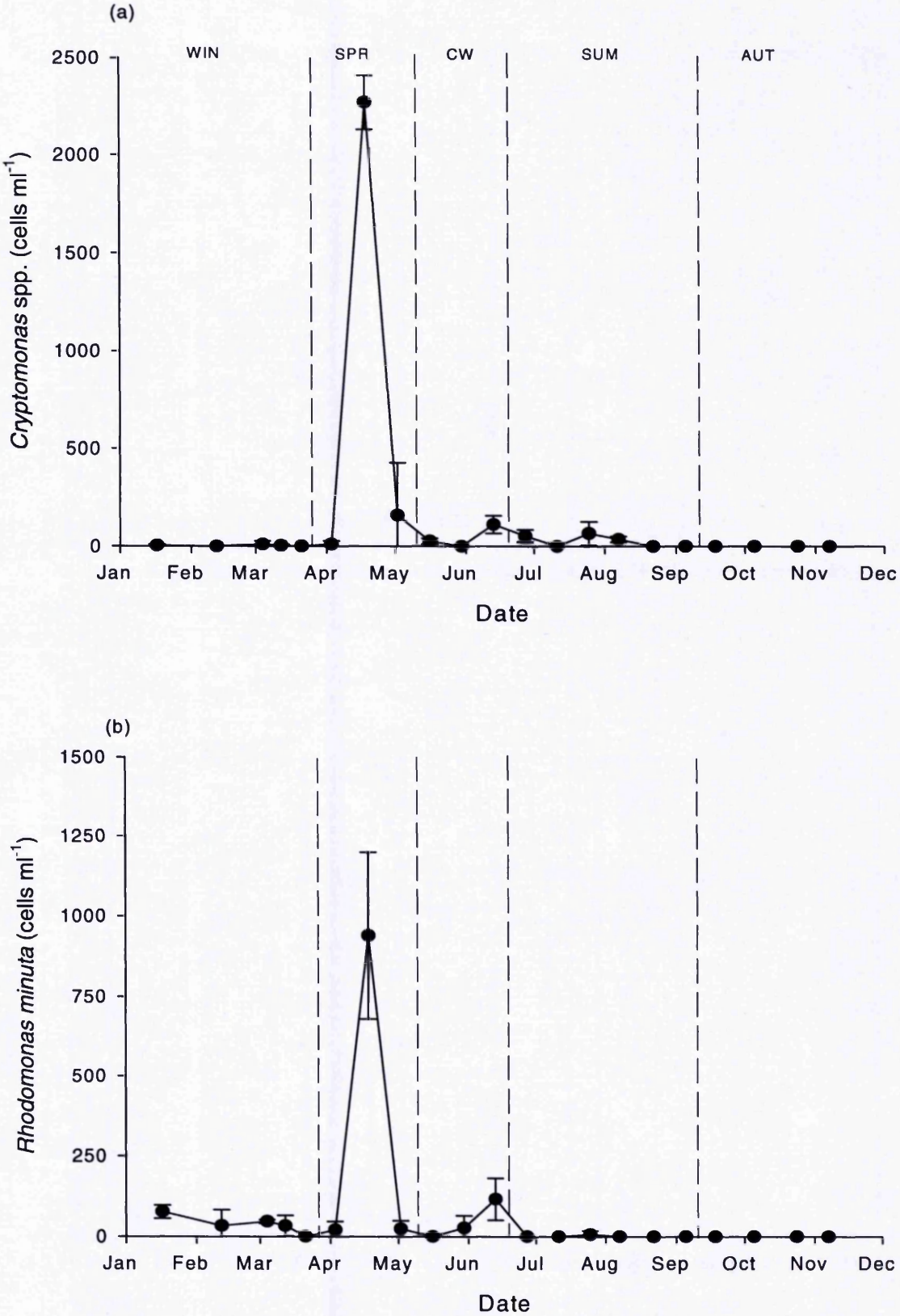


Figure 3.45: Seasonal changes in (a) *Cryptomonas* spp. and (b) *Rhodomonas minuta*, Rostherne Mere, 2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

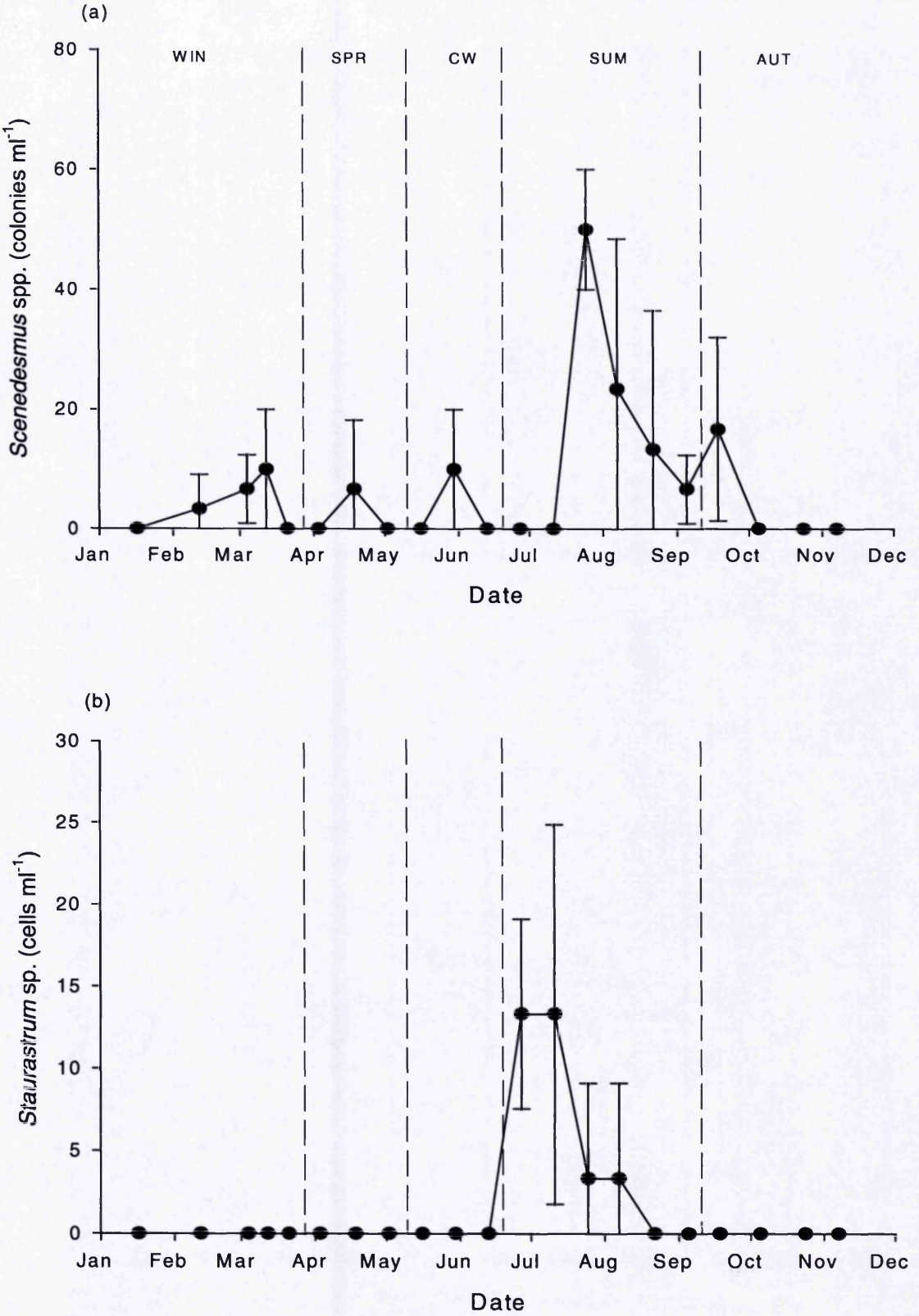


Figure 3.46: Seasonal changes in (a) *Scenedesmus* spp. and (b) *Staurastrum* sp., Rostherne Mere, 2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

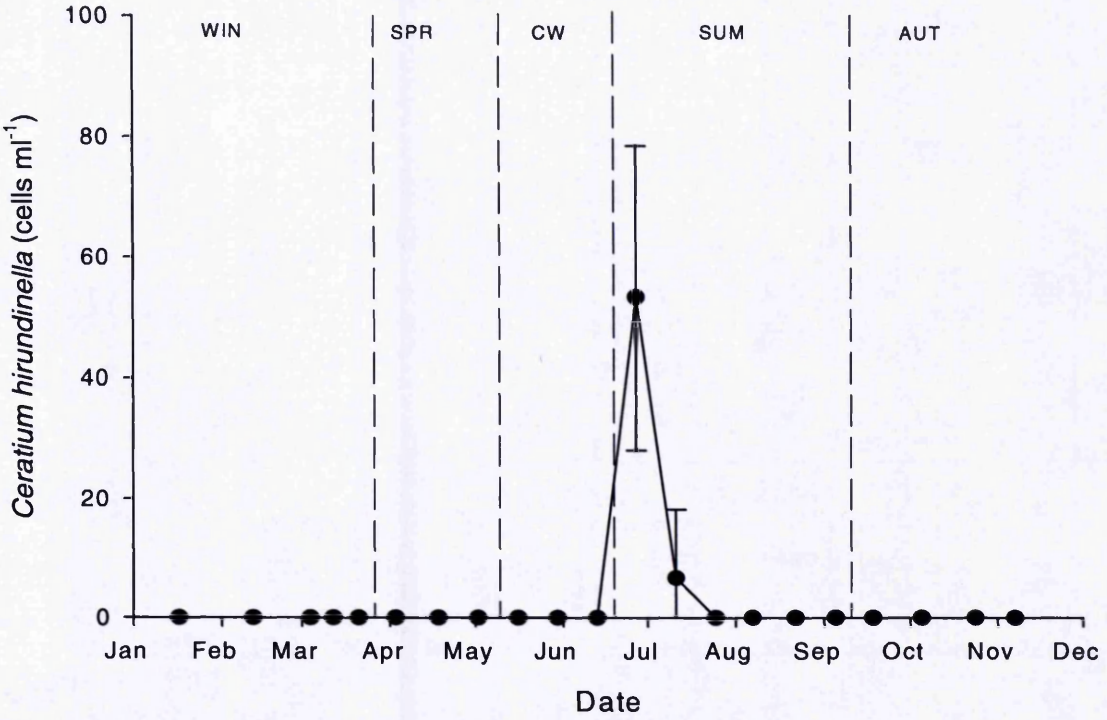


Figure 3.47: Seasonal changes in *Ceratium hirundinella*, Rostherne Mere, 2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

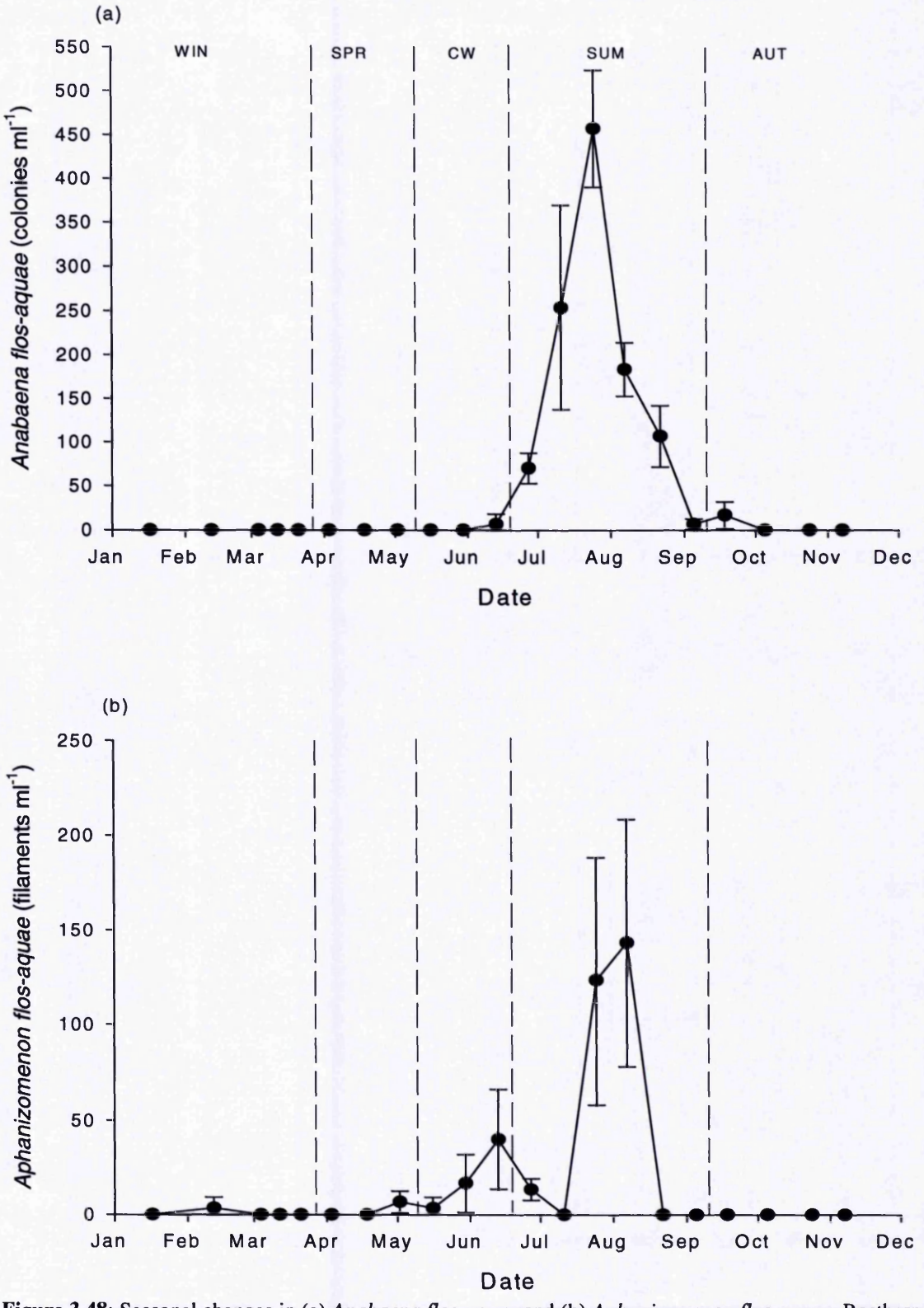


Figure 3.48: Seasonal changes in (a) *Anabaena flos-aquae* and (b) *Aphanizomenon flos-aquae*, Rostherne Mere, 2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

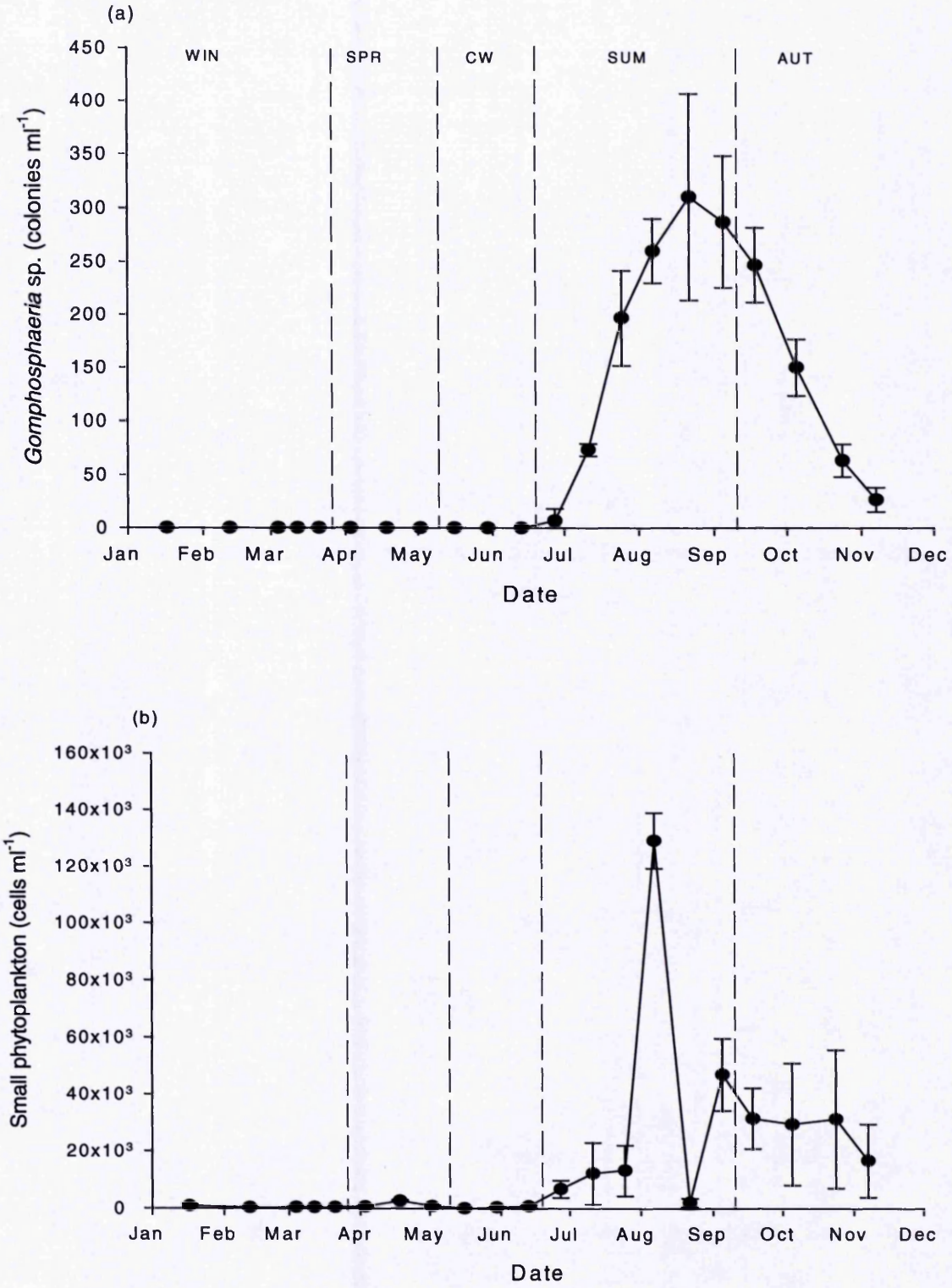


Figure 3.49: Seasonal changes in (a) *Gomphosphaeria* spp. and (b) small phytoplankton (<10µm greatest diameter) which was dominated by *Synechococcus* sp. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

3.2.2 Physico-Chemical Parameters

3.2.2.1 Temperature

Average temperatures for the top 5m of the water column are shown in Figure 3.50. During the winter phase the temperature increased only slightly, from 4.6 to 7.2°C. By the start of the spring phase temperatures had risen to 9.3°C and continued to rise through the clear-water and early summer phases, reaching a maximum of 19.5°C on the 7th of August. Temperatures then declined, reaching 9.9°C on the final sampling trip (7th November).

3.2.2.2 Temperature Profiles

Temperature profiles are shown in Figure 3.51 to Figure 3.54. During the winter phase (until the 21st March) the lake was isothermal. During the spring phase the lake started to undergo stratification, and on the 30th May (mid clear-water phase) the lake was fully stratified, with stratified conditions remaining throughout the summer phase. However, throughout the stratified period the classic stratification profile of a distinct epilimnion, metalimnion, and hypolimnion (as seen during the 2000 sampling) was not observed, the three regions tending to blend into each other (e.g. the profile for the 22nd of August). The lake remained stratified during the early autumn phase, with the depth of the thermocline falling to 14-15m in late October.

3.2.2.3 Oxygen Profiles

Oxygen profiles are shown superimposed on the temperature profiles in Figure 3.51 to Figure 3.54. Oxygen was measured to a depth of 9m from January to May; thereafter oxygen saturation was measured from 0 to 20m depth.

During the winter phase oxygen saturation (to 9m depth) was ca. 80%. At the start of the spring phase oxygen saturation in the top 9m was ca. 95%. There was then a rapid rise in oxygen concentrations on the 18th of April (corresponding with the peak in chlorophyll-a), with values falling from 144% at the surface to 99% at 9m depth. During the clear-water phase concentrations were below saturation, dropping to approximately 70% during the middle of the clear-water phase. On the 13th of June, at the end of the clear-water phase, oxygen concentrations fell continually through the water column, from a maximum of 98% at 1m depth to a minimum of 31% at 19m depth. By the start of the summer phase (27th of June) oxygen concentrations showed a clinograde distribution with values ca. 120% in the top 6m falling rapidly to ca. 60% at

7m before declining to <20% at 18m. During July, August and September a typical clinograde distribution was not observed, instead oxygen concentrations dropped continually throughout the top ca.10 m of the water column with supersaturation only observed at the very top of the water column, generally at 0 - 2 m depth. Below 2m oxygen concentrations dropped rapidly during July, oxygen concentrations dropped to <20% at ca. 17m while during August and September concentrations were <20% at ca. 7-8m depth. At the time of the last sampling of the full water column (late October) oxygen concentrations within the water column returned to a clinograde distribution, with concentrations ca. 65% to a depth of 13m depth before dropping rapidly to <20% at 14m.

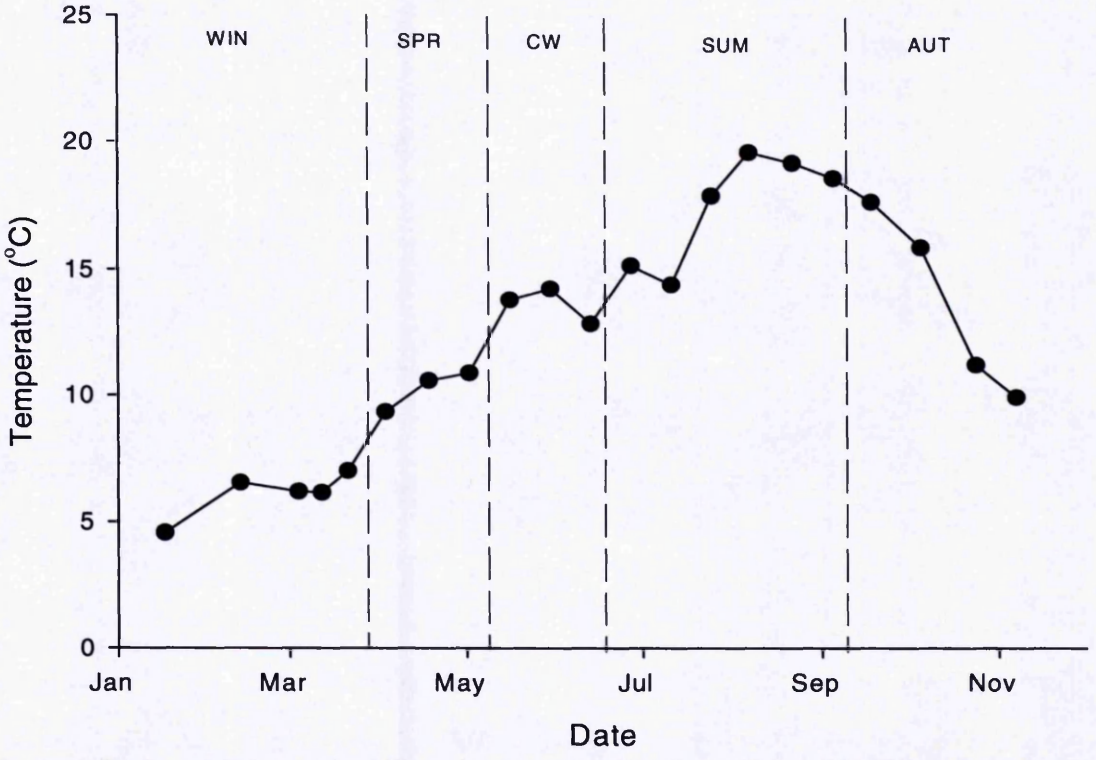


Figure 3.50: Seasonal changes in epilimentic temperature, Rostherne Mere, 2002. Values are the mean of epilimentic values obtained from the depth profile.

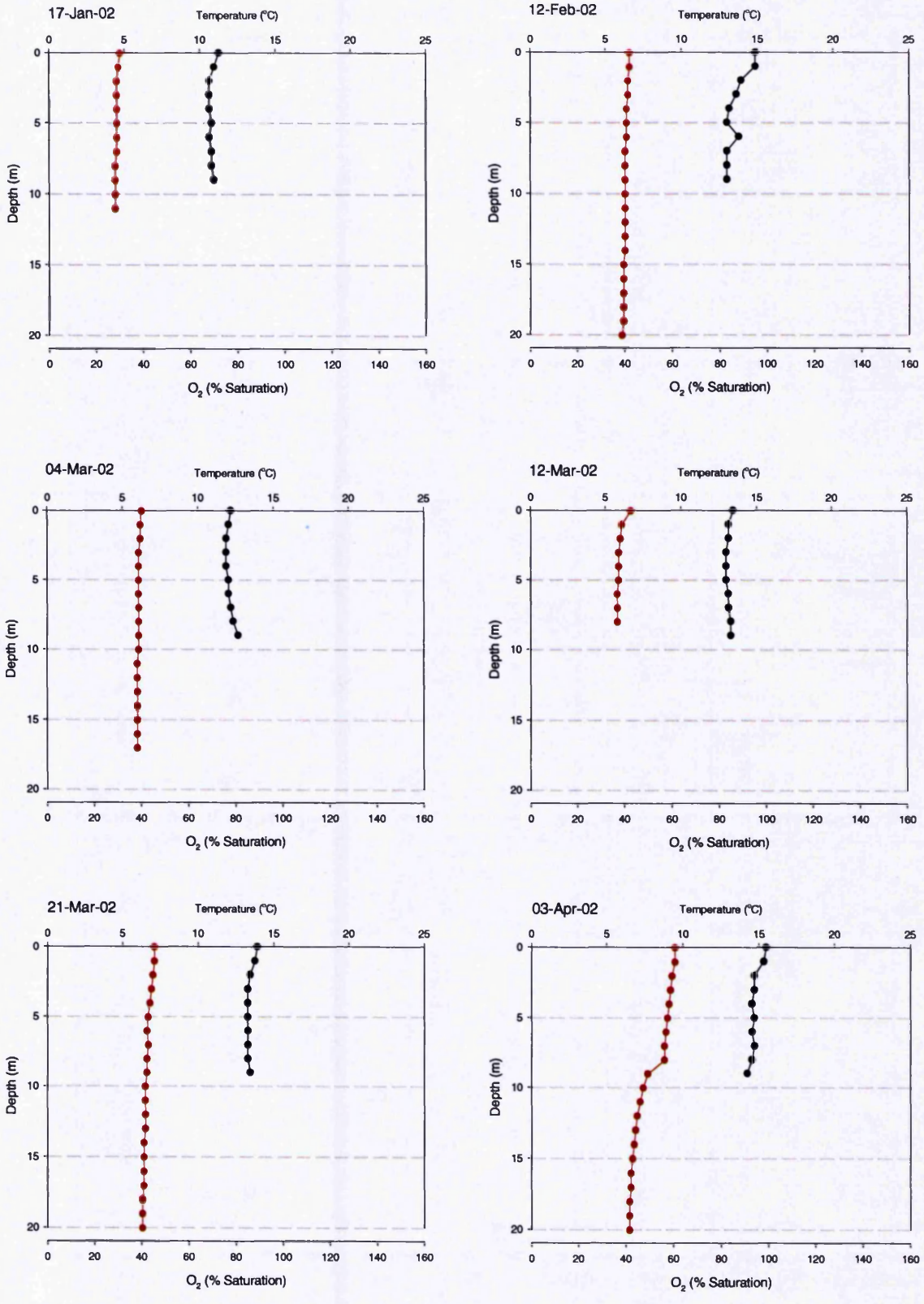


Figure 3.51: Temperature (•) and oxygen profiles (•) for Rostherne Mere, 27th January – 3rd April 2002.

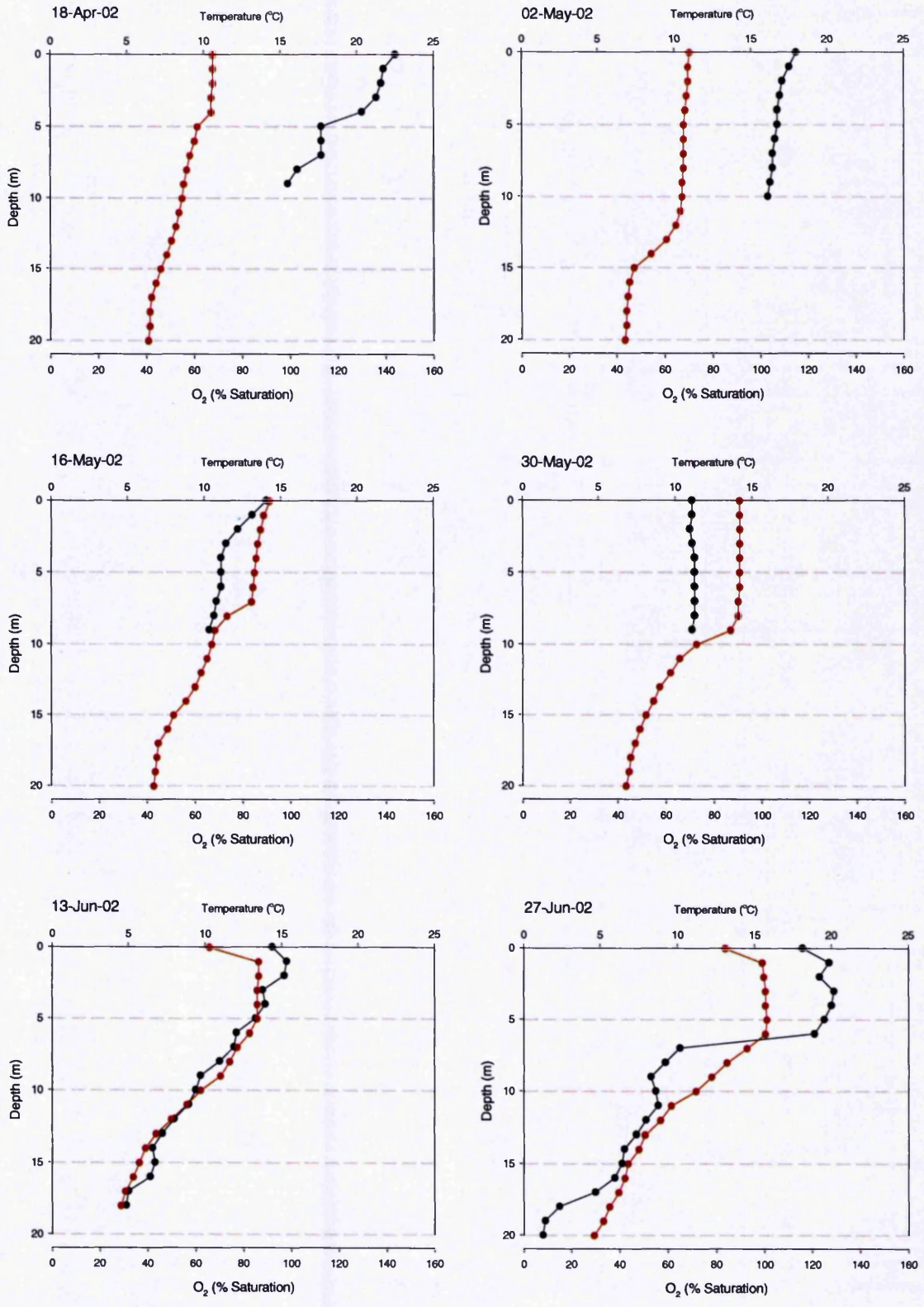


Figure 3.52:. Temperature (•) and oxygen profiles (•) for Rostherne Mere, 18th April – 27th June 2002.

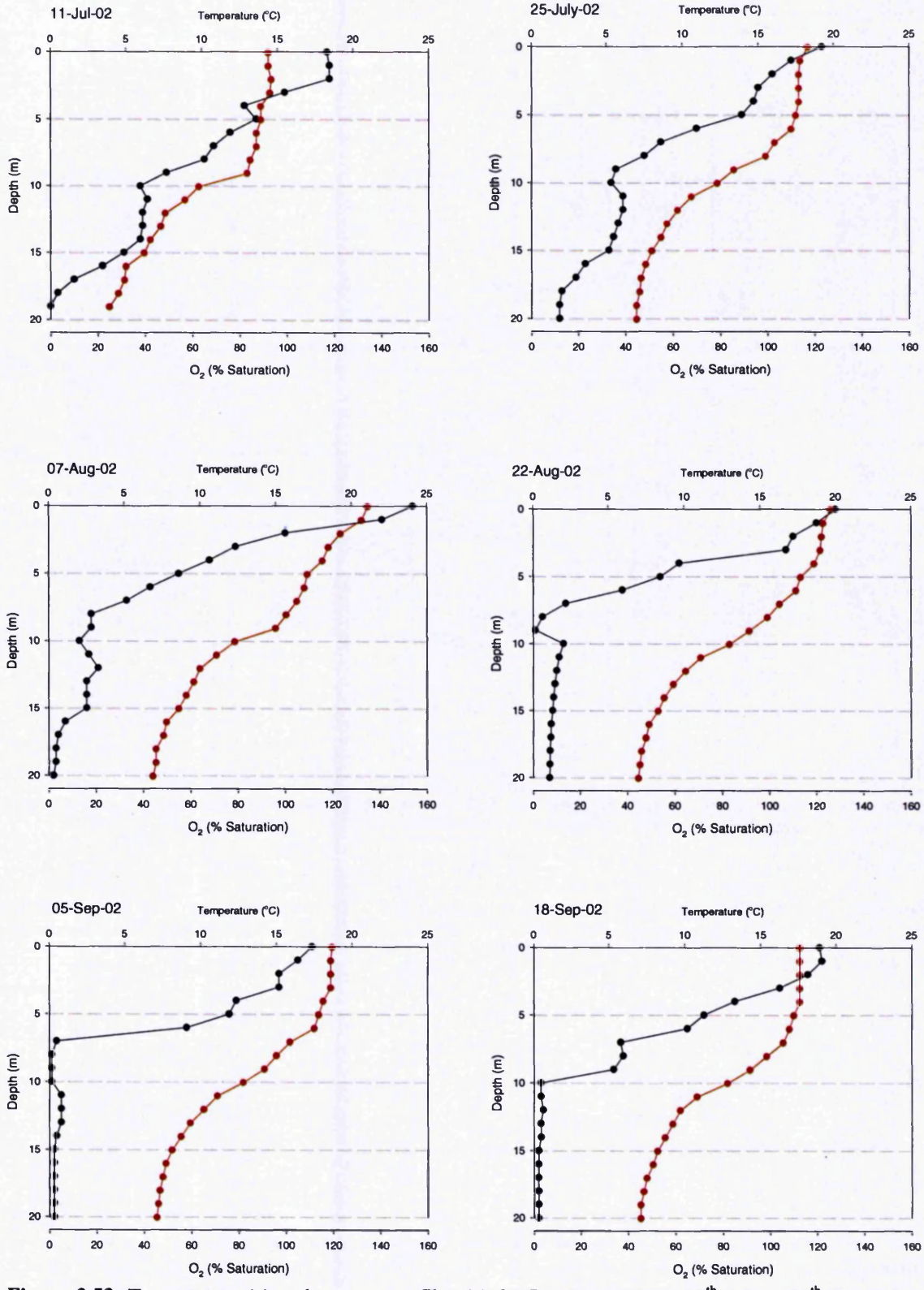
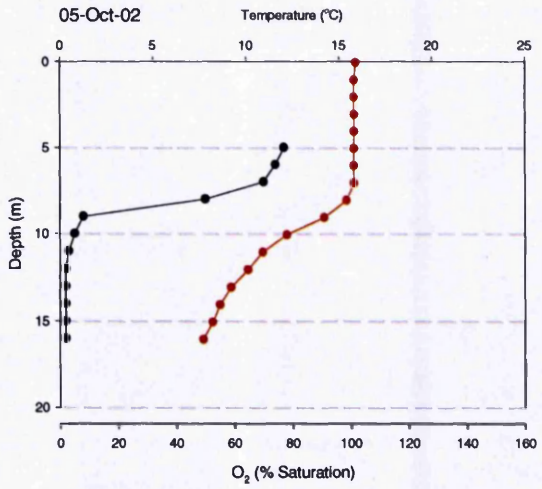
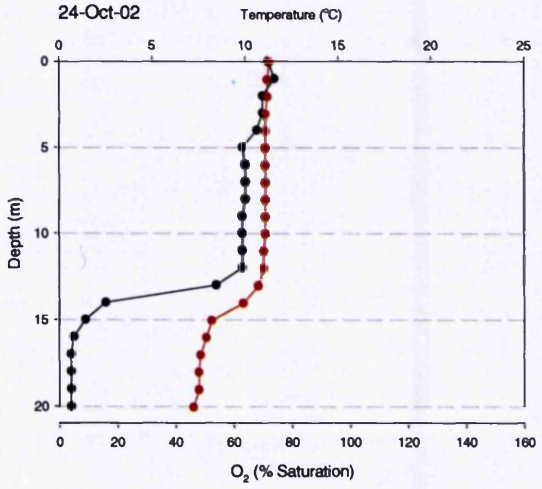


Figure 3.53: Temperature (•) and oxygen profiles (•) for Rostherne Mere, 11th July – 18th September 2002.





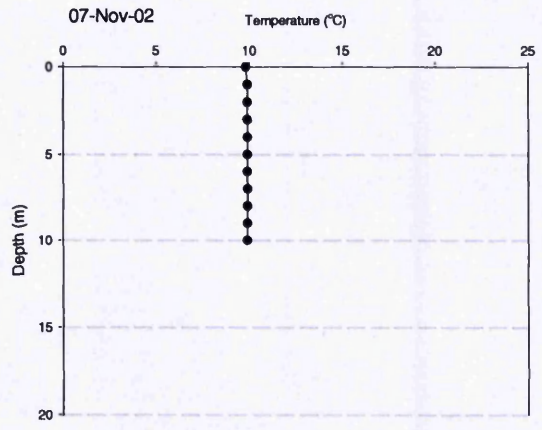


Figure 3.54: Temperature (•) and oxygen profiles (•) for Rostherne Mere, 5th October – 7th November 2002.

3.2.2.4 pH

pH varied between 6.4 and 9.1 and is shown in Figure 3.55a. During the early part of the winter phase pH varied between 7.6 and 8.0 but by the end of the phase it had fallen to 6.4. During the spring phase pH increased to 8.8 during the phytoplankton bloom (18th of April) before falling to 6.7 during the clear-water phase. At the start of the summer phase pH had increased to 7.8, and continued to increase, reaching a maximum of 9.1 on the 7th of August. During the remainder of the summer phase and into the early autumn phase pH remained at approximately 8.8 before declining during the latter half of the autumn phase to reach a minimum of 7.7 on the 25th of October.

3.2.2.5 Conductivity

Conductivity varied between 405µS and 495µS and is shown in Figure 3.55b. During the early winter phase conductivity fell from 421 to 405µS in early May, before increasing to ca. 430µS by the end of the winter phase and during the spring/clear-water phases. At the commencement of the summer phase conductivity increased to 494µS and then declined to approximately 420µS during August. During the autumn phase conductivity increased, reaching a maximum of 489µS in November.

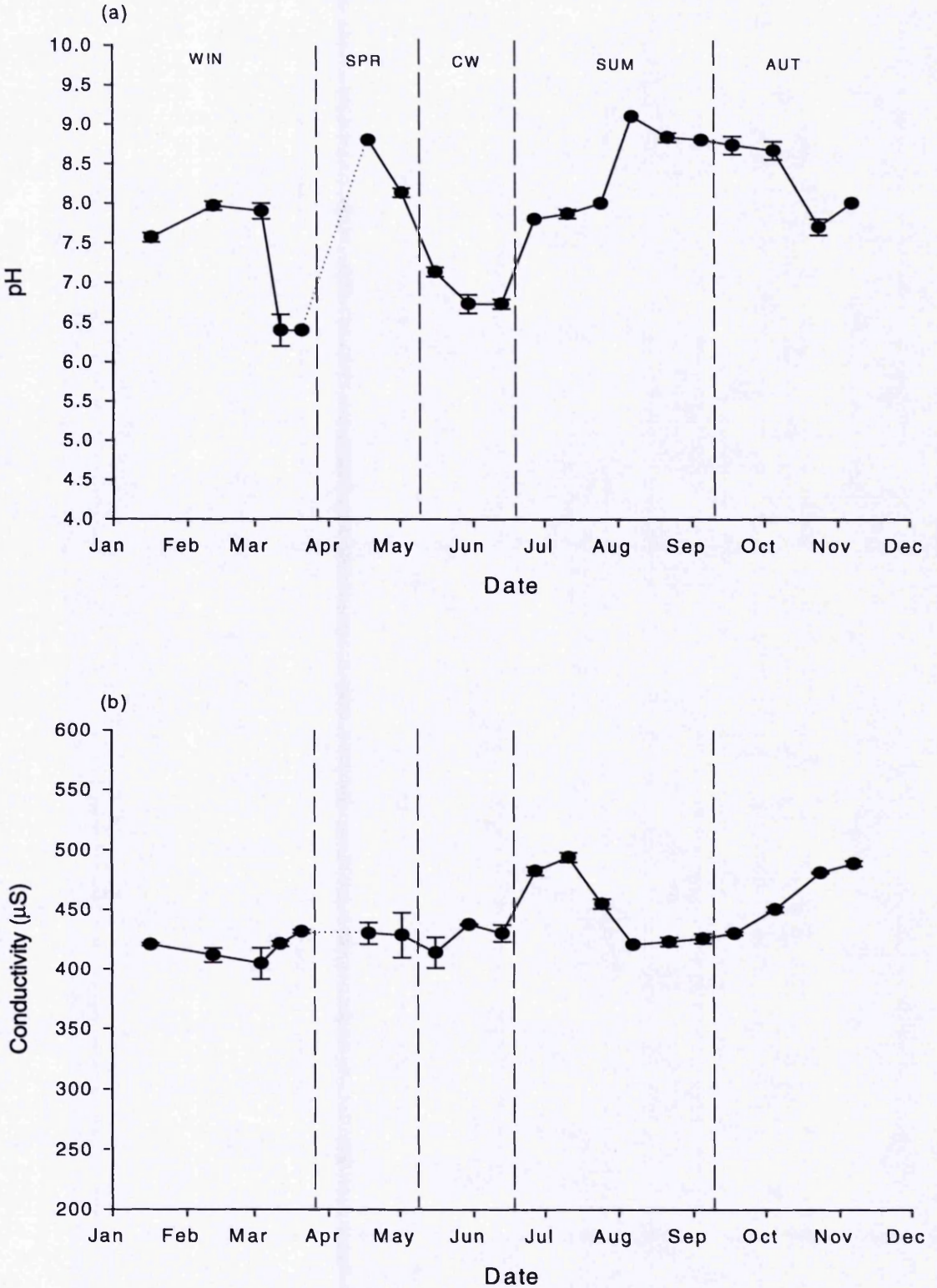


Figure 3.55: Seasonal changes in (a) pH and (b) conductivity in Rostherne Mere, 2002. Due to equipment malfunction no measurement was taken on the 3rd April, the data points either side are therefore joined by a dotted line. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

3.2.2.6 Phosphorus compounds

Soluble Reactive Phosphorus (SRP)

SRP concentrations varied between undetectable and 173µg l^{-1} (Figure 3.56a). During the early winter phase SRP was approximately 170µgl^{-1}, dropping to approximately 145µg l^{-1} during latter part of the phase. During the spring phase SRP declined rapidly to 50µg l^{-1} on the 18th of April (coinciding with the peak of chlorophyll-a). Concentrations then increased to 75µg l^{-1} in the middle of the clear-water phase, following which they declined to a long period of low concentrations during the summer phase, with concentrations <10µg l^{-1} by the 25th of July. Concentrations remained low through to the early part of the autumn phase, and were undetectable on the 5th of October (when the autumn bloom of *Aulacoseira* was at its peak). SRP then increased rapidly to 97µg l^{-1} in early November.

Total Dissolved Phosphorus

TDP concentrations varied from 16µg l^{-1} to 181µg l^{-1} (Figure 3.56b). During the winter phase TDP concentrations were approximately 170µg l^{-1}. Concentrations declined during the spring, reaching 107µg l^{-1} on the 18th April (coinciding with the peak of chlorophyll-a), and then fell to approximately 85µg l^{-1} during the clear-water phase. At the start of the summer phase concentrations had fallen to 43µg l^{-1}, fell further to approximately 20µg l^{-1} in late July and remained at approximately this level through to the early part of the autumn phase (5th October). TDP then increased to 109µg l^{-1} by the final sampling trip.

Total Phosphorus (TP)

TP varied between 77µgl^{-1} and 187µgl^{-1} (Figure 3.57a). During the winter phase and spring phase TP concentrations were approximately 160µgl^{-1}. By the start of the clear-water phase they had fallen to 103µgl^{-1} and fell to 78µgl^{-1} at the end of the phase. During the summer and early autumn phase (until 5th of October) concentrations fluctuated between 80 and 111µgl^{-1}, with an underlying slight increase, before increasing rapidly to 165µgl^{-1} by the final sampling trip.

Total Particulate Phosphorus (TPP)

TPP varied between undetectable and 94µg$l^{-1}$and is shown if Figure 3.57(b). TPP showed a distinct peak of 55µgl^{-1} during the spring phase on the 18th of April,

coinciding with the peak in chlorophyll-a. Concentrations dropped during the clear-water phase, before increasing throughout the summer phase, reaching a peak of ca. $93\mu gl^{-1}$ on the 22nd of August, and again at the start of the autumn phase (18th of September). Concentrations then declined, reaching $55\mu gl^{-1}$ in November.

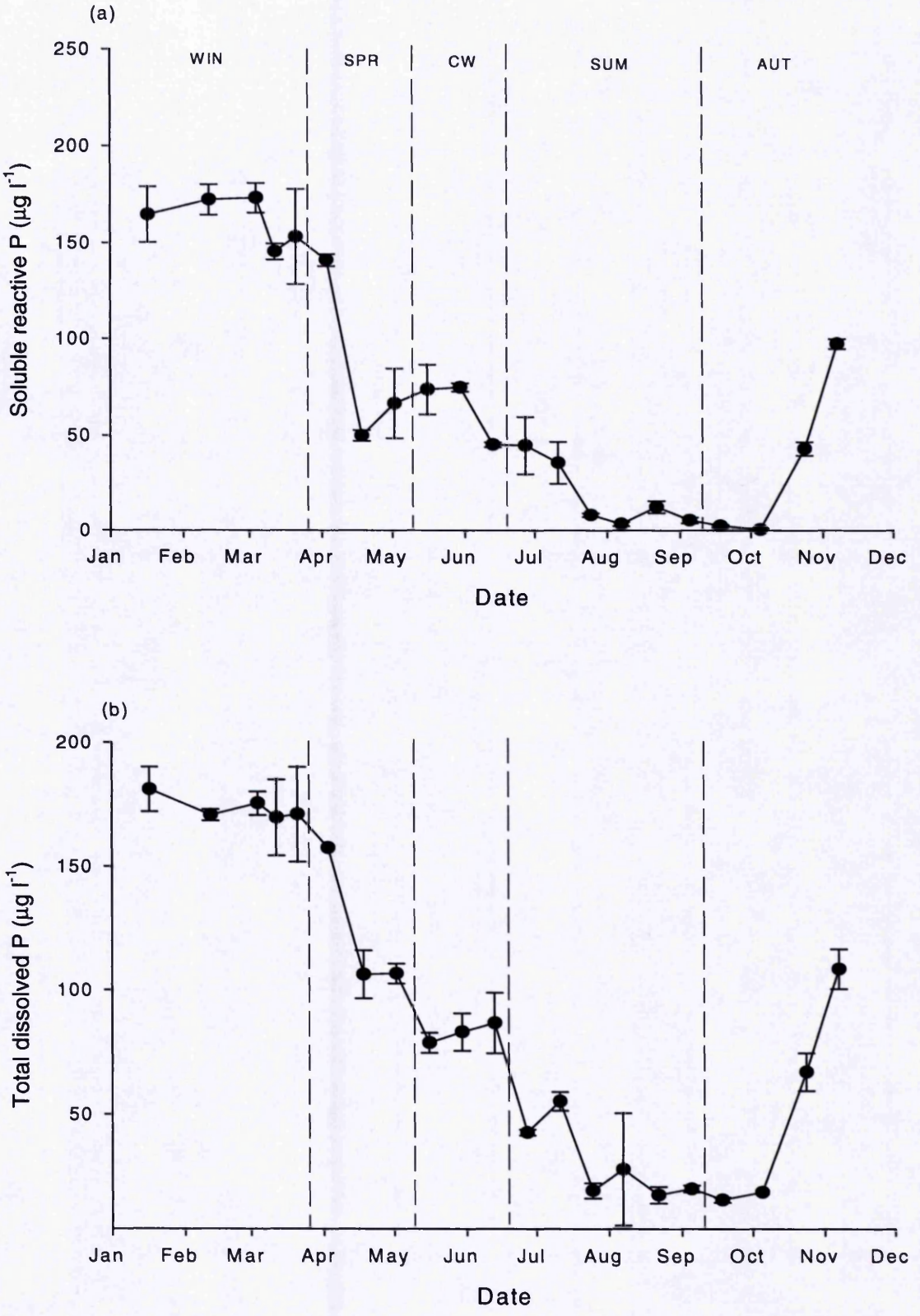


Figure 3.56: Seasonal changes in (a) soluble reactive P and (b) total dissolved P, Rostherne Mere, 2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

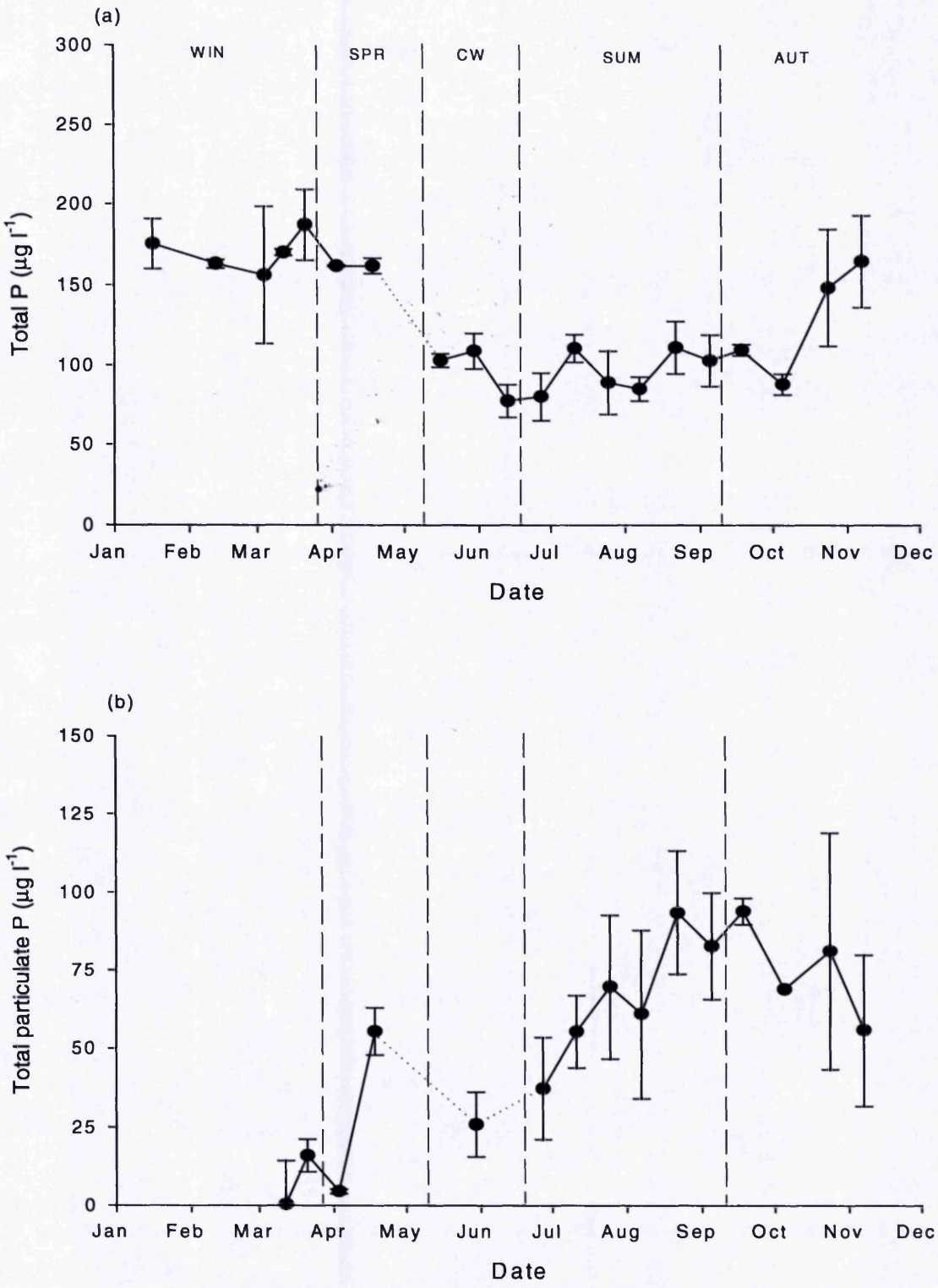


Figure 3.57: Seasonal changes in (a) total P and (b) total particulate P, Rostherne Mere, 2002. Values either side of lost samples are joined by a dotted line. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

3.2.2.7 Nitrates

Nitrates and Nitrites

Nitrates/nitrites varied between 0.15 and 1.92 mgl^{-1} (Figure 3.58a). During the winter phase concentrations increased from 1.51 to reach 1.92mg l^{-1} on the 21st of March. By the 18th of April, when chlorophyll-a had peaked, concentrations had fallen to 1.14mg l^{-1} before increasing to 1.53mg l^{-1} at the commencement of the clear-water phase. During the rest of the clear-water phase and through the summer phase concentrations decreased, reaching a minimum of 0.15mg l^{-1} at the commencement of the autumn phase (18th of September). Concentrations then increased, reaching 0.78mg l^{-1} at the end of sampling.

Total Dissolved Nitrogen (TDN)

TDN varied between 0.91 and 2.57mg l^{-1} and is shown in Figure 3.58b. During the winter phase TDN concentrations increased from 2.01 to 2.57mg l^{-1}. During the spring phase concentrations dropped to 1.96mg l^{-1} (18th of April) and then remained relatively stable at ca. 2.00mg l^{-1} until middle of the clear-water phase. During the rest of the clear-water phase and through the summer phase concentrations decreased, reaching a minimum of 0.91mg l^{-1} at the commencement of the autumn phase (18th of September), followed by an increase to reach 1.66mg l^{-1} at the end of sampling.

Total Nitrogen (TN)

TN varied between 1.64 and 2.66mg l^{-1} and is shown in Figure 3.59a. During the winter and the part of the spring phases TN concentrations were relatively constant at ca. 2.4mg l^{-1}. Concentrations declined from the 18th of April, through the clear-water phase and the early summer phase, reaching a minimum of 1.64mg l^{-1} on the 7th of August. Concentrations increasing during the autumn phase, reaching 2.19mg l^{-1} in November.

Total Particulate Nitrogen (TPN)

TPN varied between undetectable and 0.81mg l^{-1} and is shown in Figure 3.59b. TPN showed a distinct peak of 0.51mg l^{-1} during the spring phase on the 18th of April, coinciding with the peak in chlorophyll-a. Concentrations dropped during the clear-water phase, before increasing throughout the summer phase, reaching a peak of 0.76mg l^{-1} at the end of the phase (5th of September). Concentrations remained at approximately the same level during the autumn phase, before falling to 0.46mg l^{-1} in November.

Ammonia

Ammonium-N varied between undetectable and 0.25mg l^{-1} (Figure 3.60). During the winter phase concentrations ranged between undetectable and 0.07 mg l^{-1} while during the spring phase concentrations fell to undetectable levels (18th April). There was a large increase to 0.25mg l^{-1} at the commencement of the clear-water phase, concentrations then decreasing to 0.10mg l^{-1} by the end of the phase, and continuing to decrease during the early summer phase until concentrations were undetectable from August to October. Concentrations of ammonium-N increased to 0.11mg l^{-1} during November.

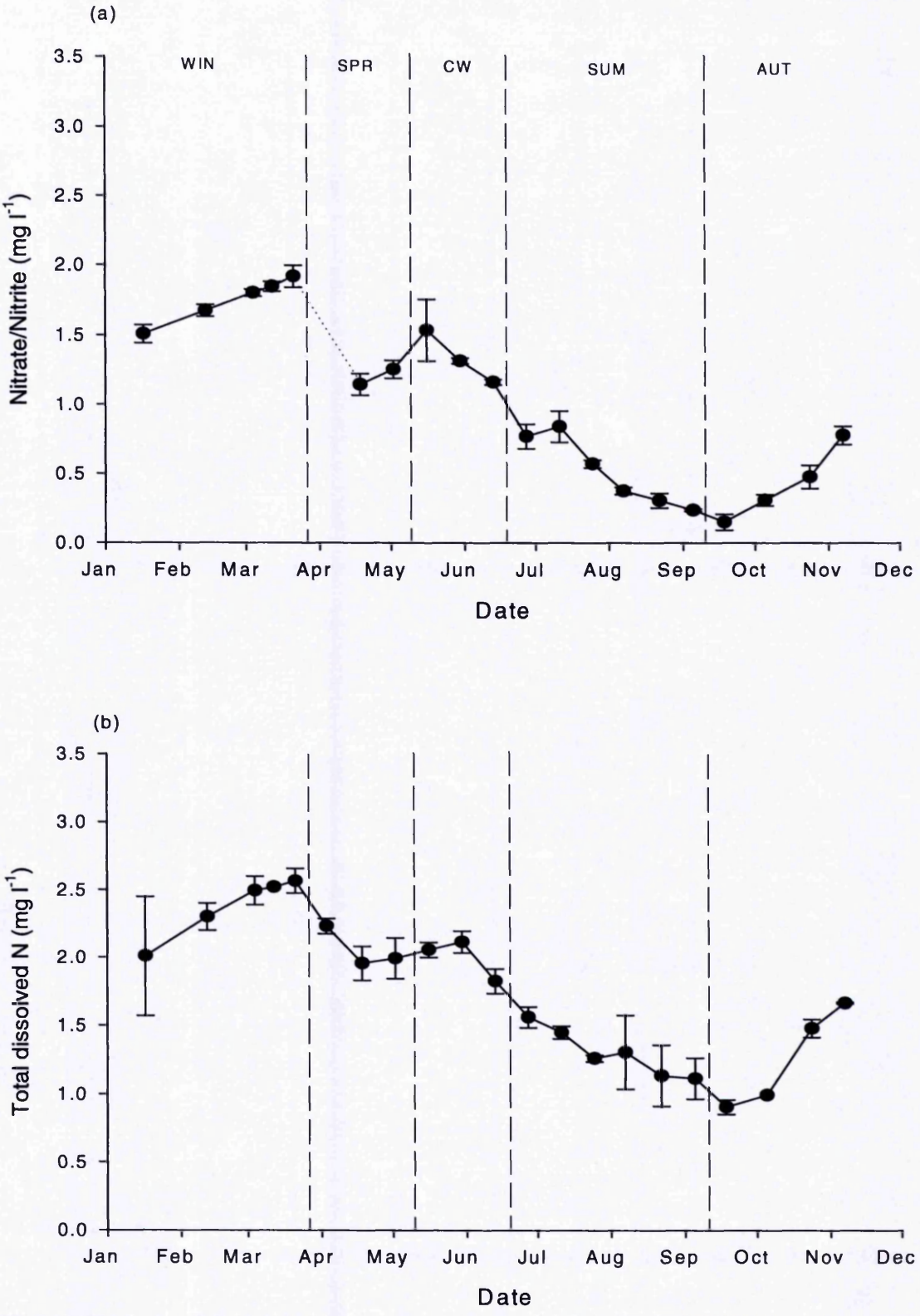


Figure 3.58: Seasonal changes in (a) nitrate/nitrite N and (b) total dissolved N, Rostherne Mere, 2002. The sample for NO_3/NO_2 for the 3rd of April was lost, values either side are joined by a dotted line. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

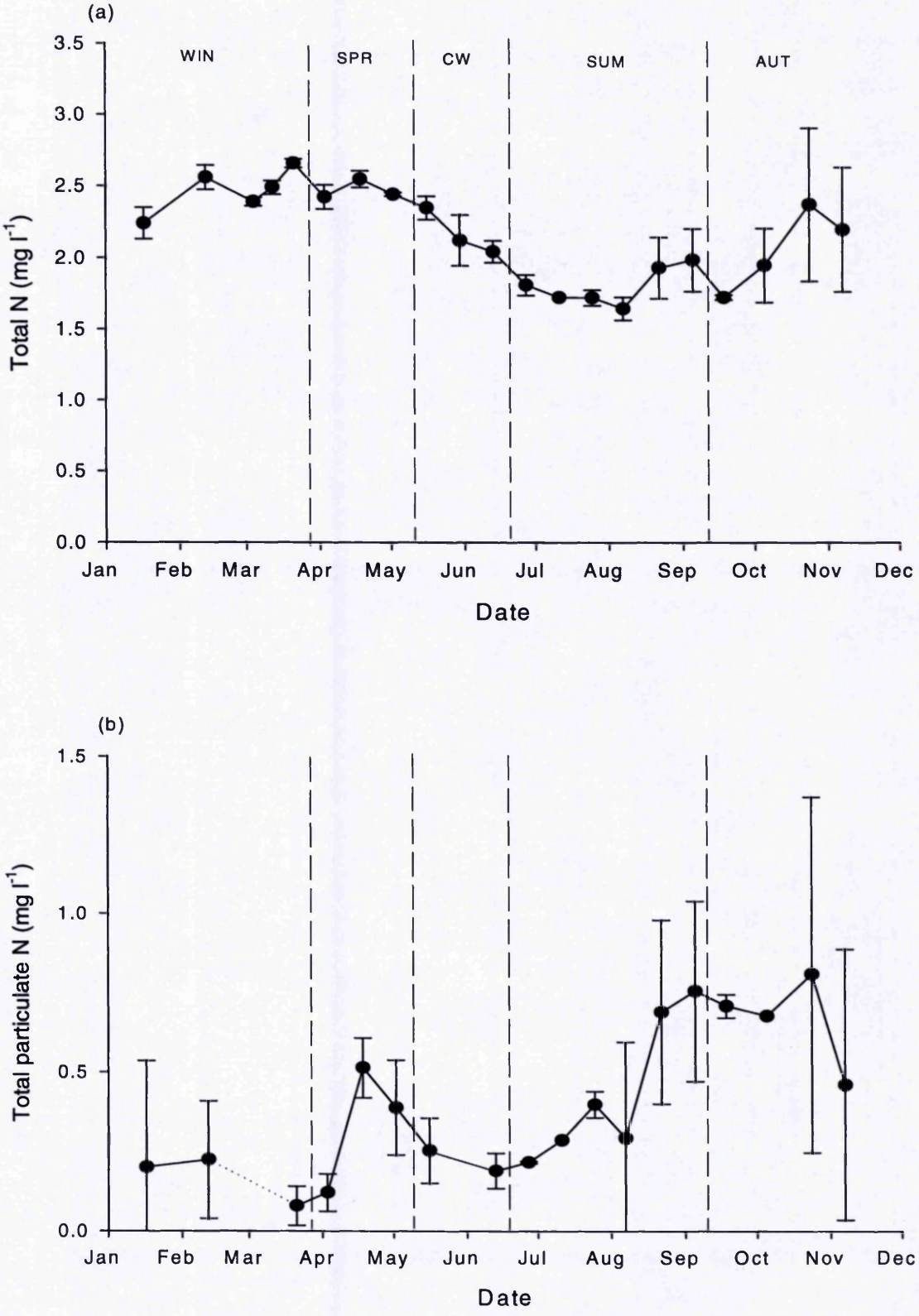


Figure 3.59: Seasonal changes in (a) total N and (b) total particulate N. Rostherne Mere, 2002. Values either side of lost values are joined by a dotted line. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

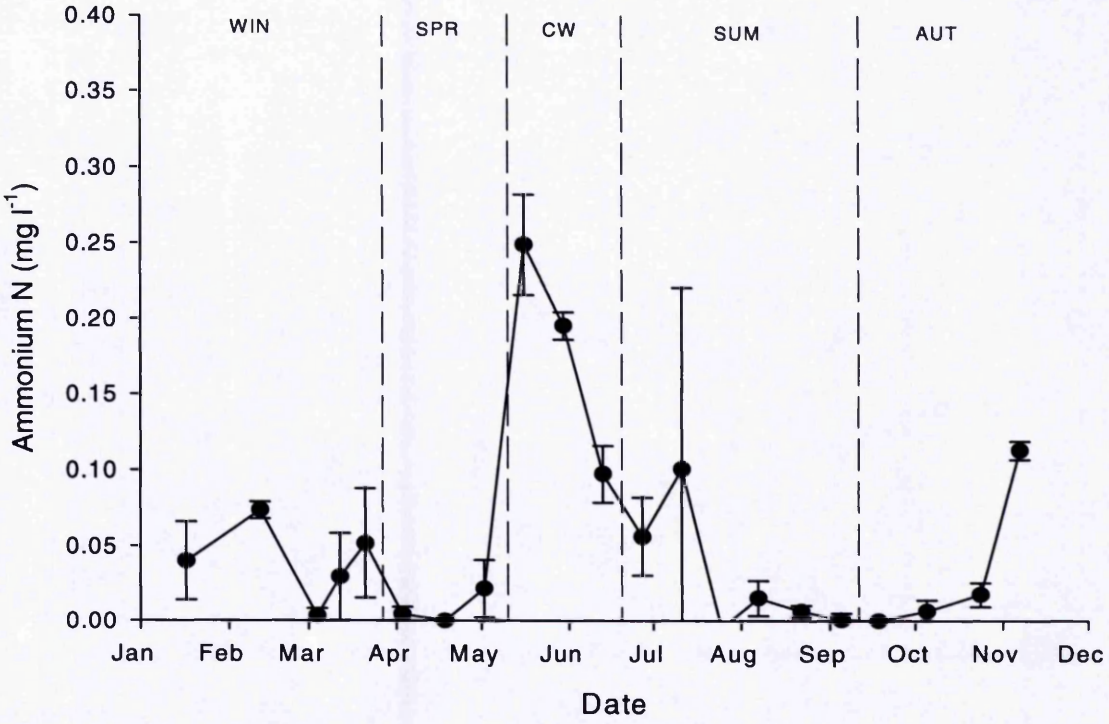


Figure 3.60: Seasonal changes in ammonium N. Rostherne Mere, 2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

3.2.2.8 Silicon

Silicon concentrations varied between 0.07 and 1.97mg l^{-1} (Figure 3.61). During the winter phase concentrations were approximately 1.90 mg l^{-1}, with a maximum concentration of 1.97mg l^{-1} on the 21st of March. Following this, concentrations declined throughout the spring phase and into the clear-water phase, reaching a minimum of 0.68 mg l^{-1} at the end of the clear-water phase (13th of June). Concentrations gradually increased during the summer phase, reaching a maximum of 1.15 mg l^{-1} at the phases end. By the next sampling occasion, (start of the autumn phase and during the *Aulacoseira* bloom) concentrations had fallen to 0.30 mg l^{-1}, falling further to 0.07 mg l^{-1} on the 5th of October. Concentration then rapidly increased, reaching a maximum of 1.46 mg l^{-1} by the end of sampling.

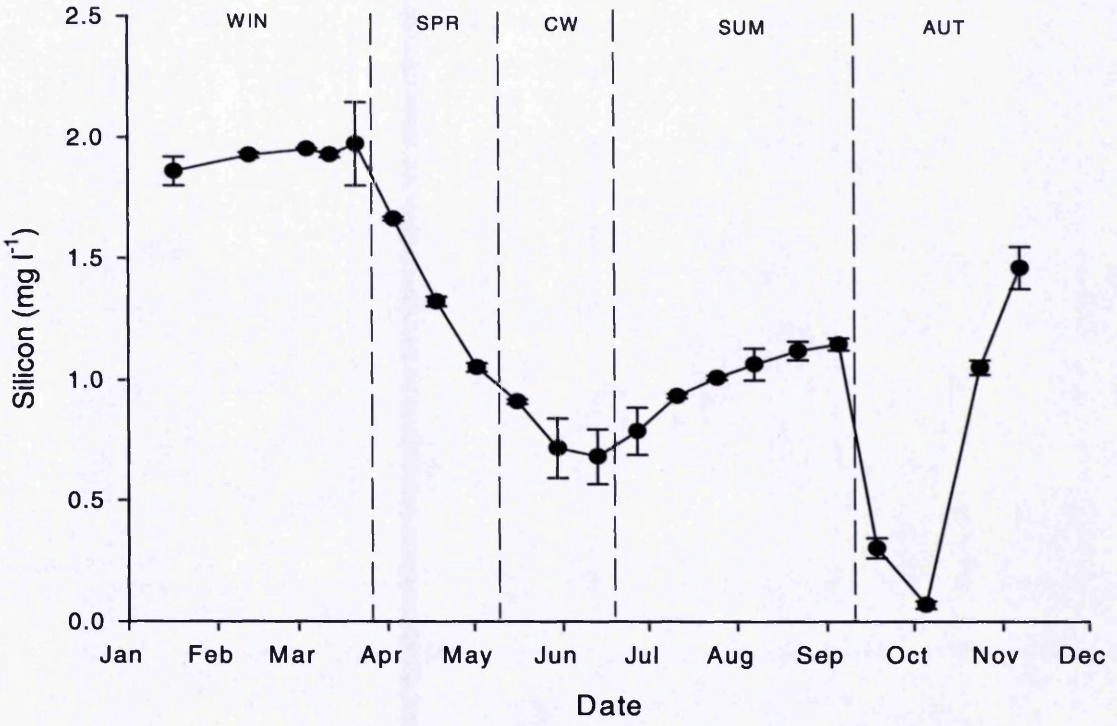


Figure 3.61: Seasonal changes in silicon. Rostherne Mere, 2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

3.2.3 Zooplankton

3.2.3.1 Zooplankton dry weight.

Zooplankton dry weight varied between 13 and 460μg l^{-1} (Figure 3.62). During the winter phase biomass was approximately 20μg l^{-1}. Biomass began to increase during the spring phase, reaching a maximum of 460μg l^{-1}. The peak in zooplankton biomass corresponded with the clear-water phase, with a biomass of 224μg l^{-1} at the beginning of the phase, falling to 79μgl^{-1} at its end. Biomass had increased slightly by the commencement of the summer phase (128μg l^{-1}), but then declined to 38μg l^{-1} at the end of the phase. No values are available for the early part of the autumn phase as the *Aulacoseira* bloom rendered it impossible to separate zooplankton and phytoplankton from the trawl. At the end of the autumn phase biomass was approximately 70μg l^{-1}.

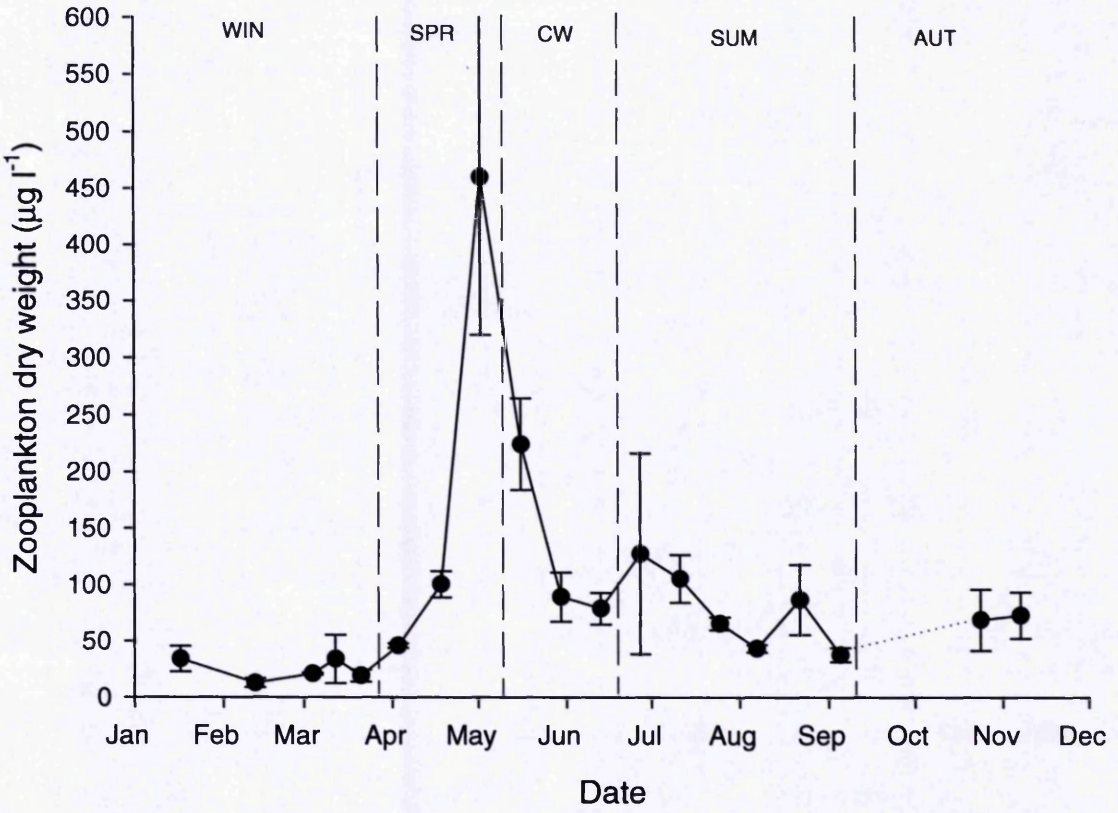


Figure 3.62: Seasonal changes in zooplankton dry weight, Rostherne Mere, 2002. No values are available for the early part of the autumn phase as the *Aulacoseira* bloom rendered it impossible to separate zooplankton and phytoplankton from the trawl. Values are means of 20m vertical trawls taken at sites A, B and C. Error bars ±1 SD. (n=3).

3.2.3.2 Zooplankton Population Parameters

Daphnia

Counts

Daphnia numbers are shown in Figure3.63a. *Daphnia* populations in 2002 were dominated by *Daphnia longispina*, with small numbers of *Daphnia magna* in July and August. *Daphnia* numbers were low during the winter phase (<2 *Daphnia* l^{-1}) and began to increase during the spring phase to a very large peak during the late spring/start of clear-water phase boundary (27.3 *Daphnia* l^{-1} at the commencement of the clear-water phase). Numbers then fell rapidly, to approximately 5 *Daphnia* l^{-1}. Two small peaks were observed during the beginning and end of the summer phase (11.2 and 6.7 *Daphnia* l^{-1} respectively) and a larger peak during the latter part of the autumn phase with 14.7 *Daphnia* l^{-1}, otherwise numbers were between 1 and 3 *Daphnia* l^{-1}.

Percentage Gravid

The proportion of gravid adult *Daphnia* is shown in Figure 3.63b. Maximum values occurred during the spring phase (>30%) before falling to a minimum of 1% during the clear-water phase. During the early summer phase values began to increase, peaking at 46% on the 7th of August. Values remained high into the autumn-phase (30% in early October) before falling to 10% at the end of sampling in early November.

Brood Size

Brood size varied between 0 and 6.3 (Figure 3.64a). During the winter phase from brood size increased from 0 to 2.8. There was a large increase in brood size during the spring phase, increasing from 2.2 at the start of the phase to 6.2 on the 18th of April. Brood size then declined to reach a minimum of 1 during the clear-water phase. At the start of the summer phase brood size had increased to 5.1, fell to 3 during July, before increasing to 3.9 on the 7th of August. At the end of the summer phase brood size was 2.1, increasing to approximately 2.9 during the autumn phase.

Birth Rate

Birth rates (Figure 3.64b) first peaked on the 18th of April (coterminous with the peak in chlorophyll-a) at 0.13, before falling to ca. 0 during the clear-water phase. During the summer phase birth rates peaked at 0.30 on the 7th of August (conterminously with a peak in *Synechococcus*). Birth rates remained at approximately 0.15-0.20 until early October before declining to reach 0.03 at the end of sampling.

Size

Daphnia mean lengths varied between 0.84 and 1.38mm (Figure 3.65), with lengths generally within the range 1.0 - 1.1mm. Maximum vales occurred during the summer phase, with lengths >1.3mm during July.

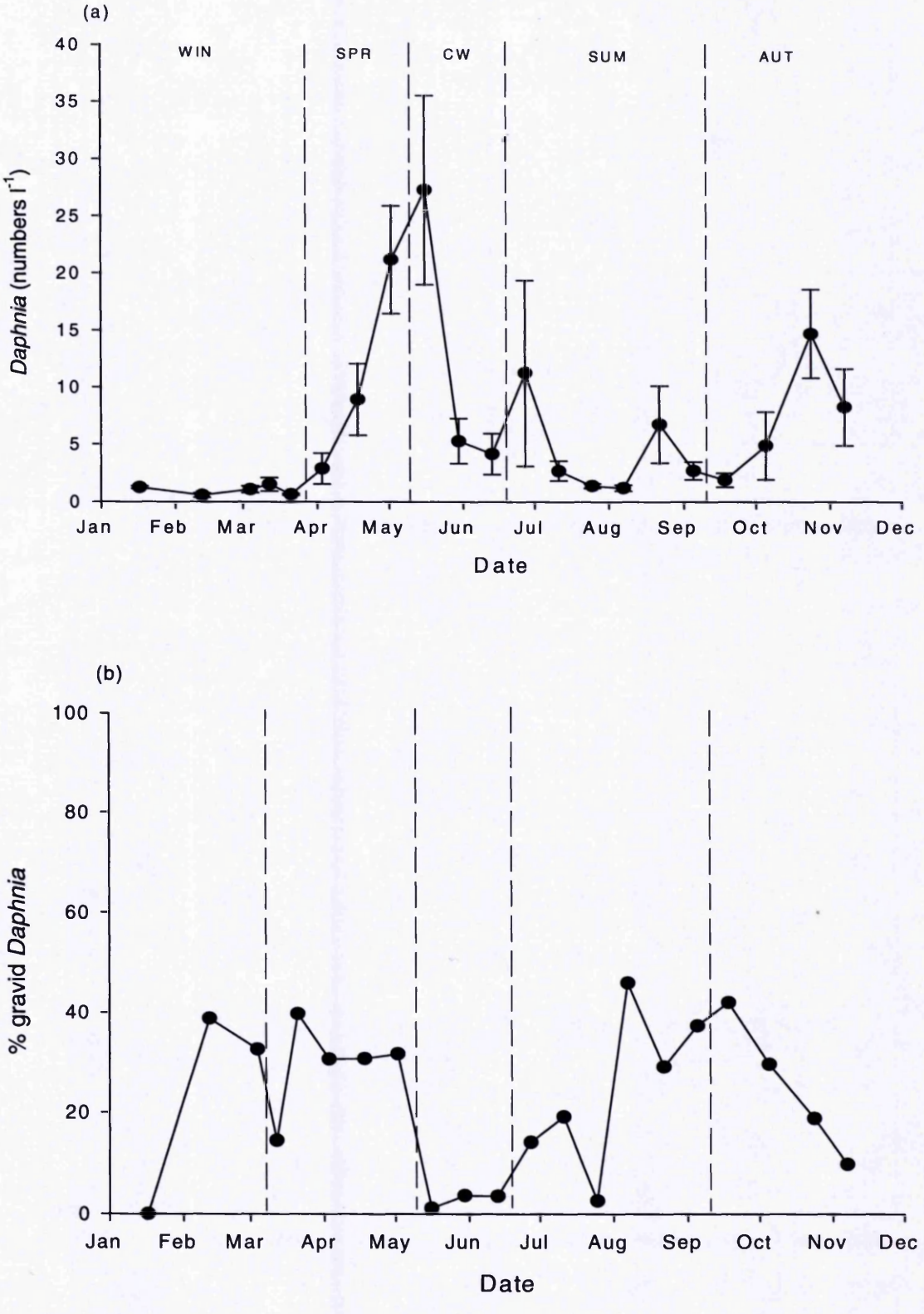


Figure 3.63: Seasonal changes in (a) *Daphnia* numbers. Values are the mean of integrated samples taken from sites A, B and C, error bars ±1 SD. (n=3); and (b) the percentage gravid *Daphnia*, calculated using the sum (sites A, B and C combined) of all gravid *Daphnia* and total *Daphnia*, counted during the determination of seasonal changes. Rostherne Mere, 2000.

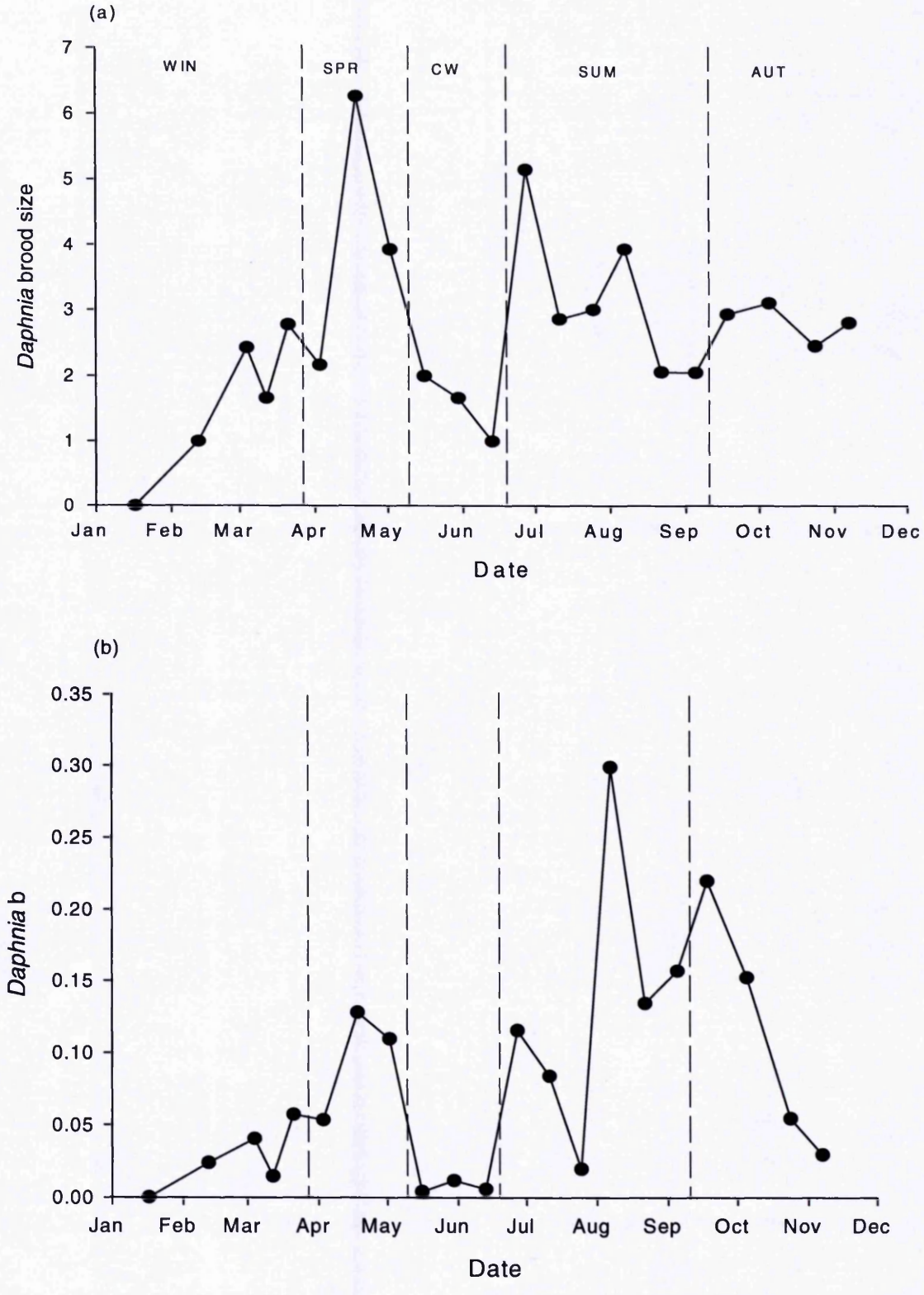


Figure 3.64: Seasonal changes in (a) *Daphnia* brood size and (b) *Daphnia* birth rate, Rostherne Mere, 2002. In both cases calculations were based on combined data from all three sites.

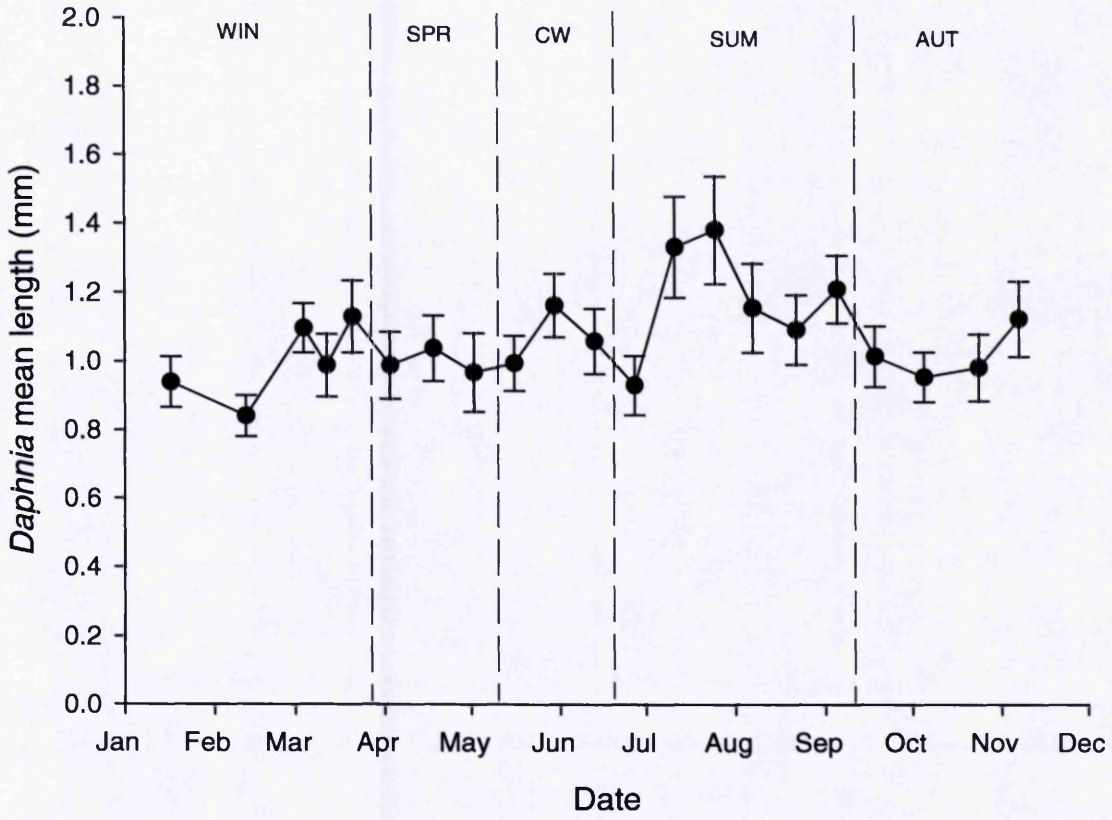


Figure 3.65: Seasonal changes in the mean length of *Daphnia*. Rostherne Mere, 2002. Values are the mean lengths of animals randomly selected from sites A, B and C. (n≈40 for each date). Error bars show 95% confidence intervals.

Calanoid Copepods

Counts

Calanoid copepods were present in very low numbers (Figure3.66a). The maximum number of 2.9 calanoids l^{-1} occurred on two occasions during winter phase, and a further small peak of 2.3 calanoids l^{-1} occurred at the end of the spring phase; otherwise calanoids were present at generally ≤1 calanoid l^{-1} and were absent during the late summer and autumn phases.

Size

Calanoid mean lengths varied between 1.03 and 1.30mm (Figure 3.66b). Lengths increased over the sampling period from approximately 1mm at the commencement of sampling to approximately 1.2mm during the early summer phase (calanoids were absent from middle of the summer phase onwards).

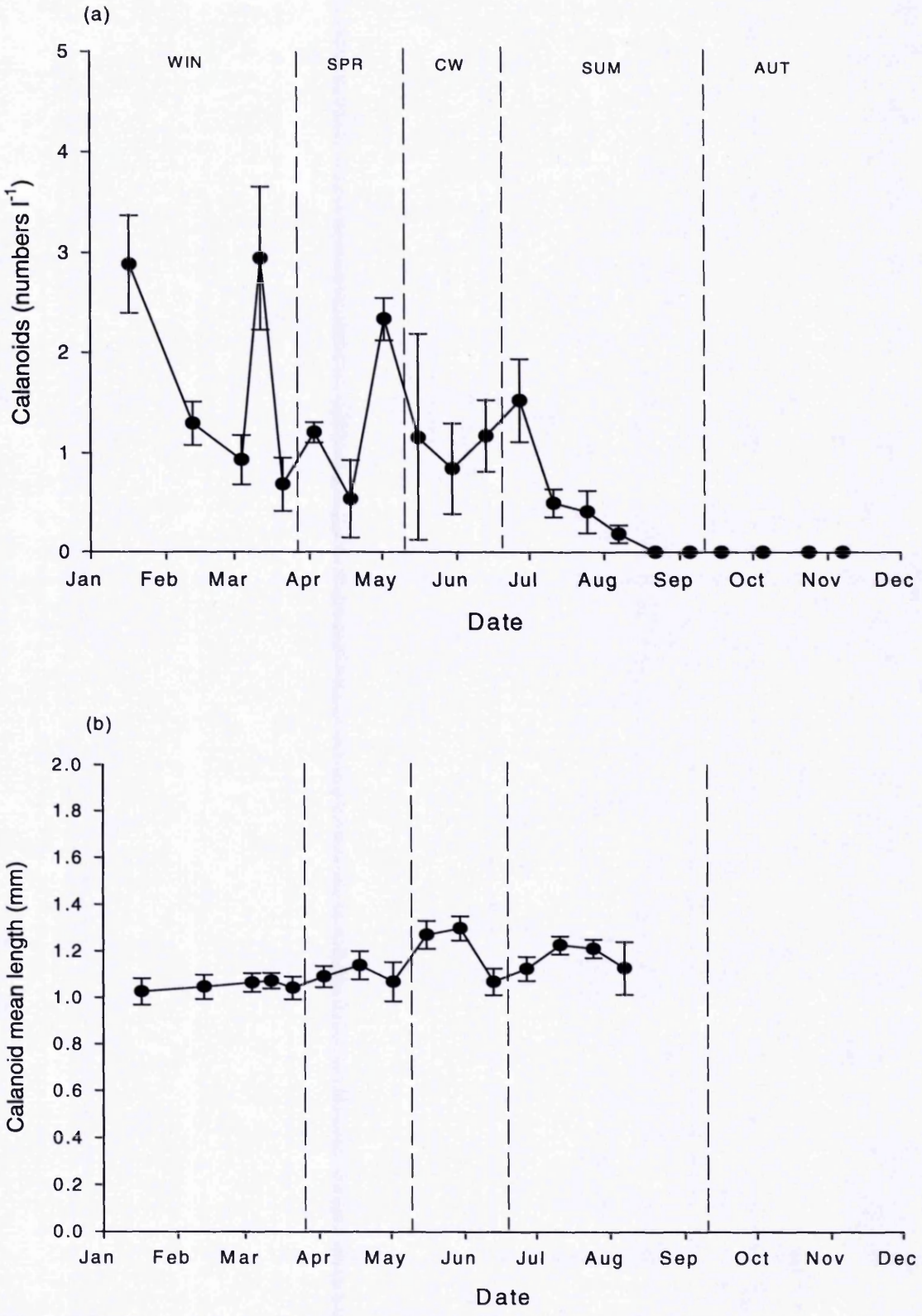


Figure 3.66: Seasonal changes in (a) the number of calanoid copepods. Values are the mean of integrated samples taken from sites A, B and C, error bars ±1 SD. (n=3). and (b) the mean length of calanoid copepods. Values are the mean lengths of animals randomly selected from sites A, B and C. (n≈40 for each date). Error bars show 95% confidence intervals.

Cyclopoid Copepods

Counts

Cyclopoid copepods numbers are shown in Figure 3.67. Cyclopoid copepods were present at ≤ 1 cyclopoid l^{-1} during the winter phase. Numbers began to increase during the spring phase reaching 12.4 cyclopoids l^{-1} either side of the boundary between the spring and clear-water phases. Numbers then fell to approximately 4 l^{-1} during the remainder of the clear-water phase. At the start of the summer phase numbers had increased to 6.8 cyclopoids l^{-1} but declined throughout the remainder of the phase until by its end cyclopoids were only present at 0.1 cyclopoids l^{-1}. Numbers remained at or below this level throughout the autumn phase.

Size

Cyclopoid mean lengths varied from 0.83 to 1.07mm and are shown in Figure 3.67, with lengths generally within the range 0.9 - 1.0mm. Body length showed a slight downward trend over the course of the sampling period.

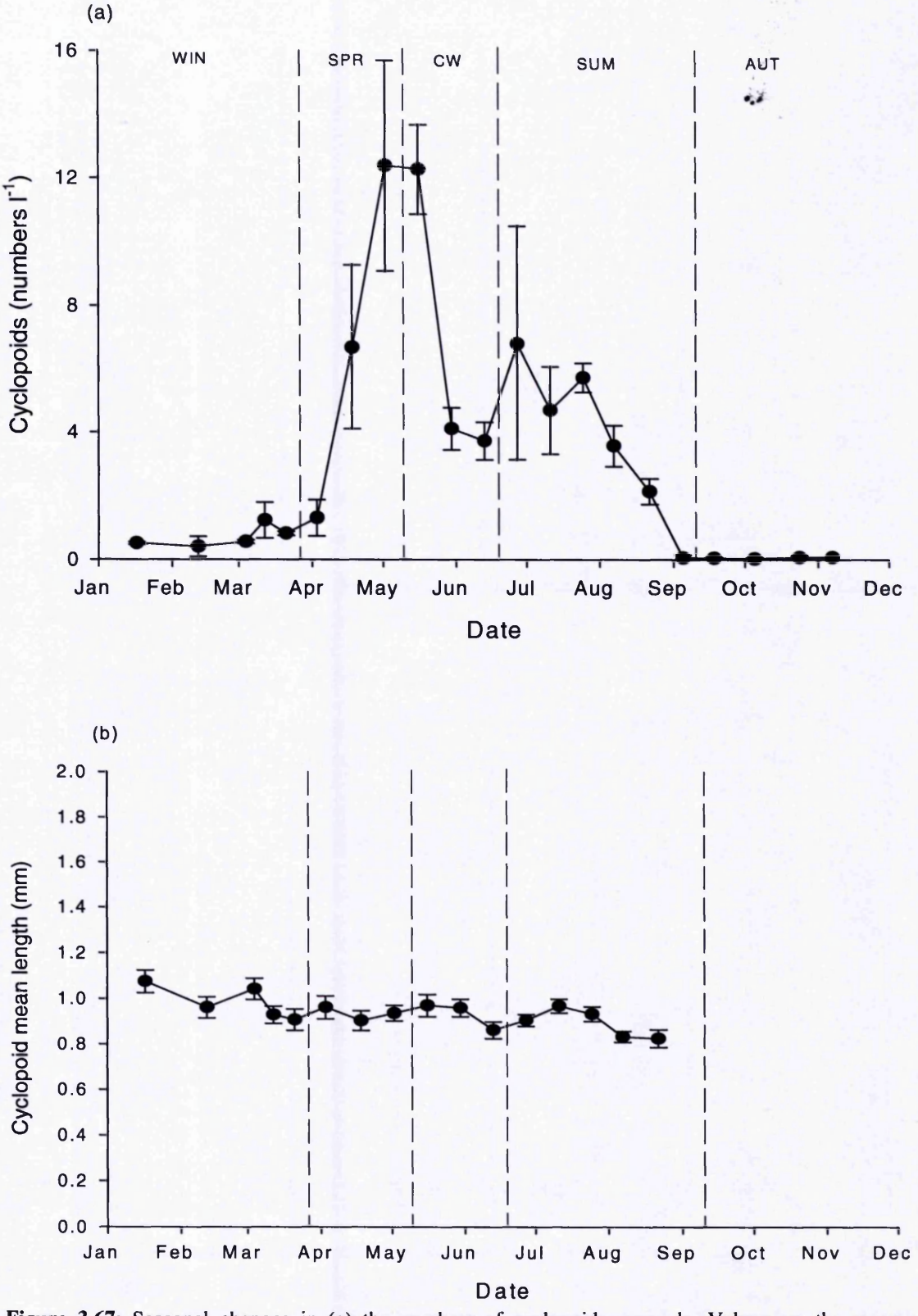


Figure 3.67: Seasonal changes in (a) the numbers of cyclopoid copepods. Values are the mean of integrated samples taken from sites A, B and C, error bars ±1 SD, (n=3). (b) the mean length of cyclopoid copepods. Values are the mean lengths of animals randomly selected from sites A, B and C. (n≈40 for each date). Error bars show 95% confidence intervals.

Rotifers

Seasonal variation in the total number of rotifers is shown in Figure 3.68. Rotifers peaked in spring (612 rotifers l^{-1}), with the increase and subsequent decrease paralleling that of the chlorophyll-a. Numbers were reduced during the clear-water phase (approximately 50 rotifers l^{-1}), followed by a slight increase during the summer phase to reach 150 rotifers l^{-1} in early August.

A number of species were observed. The large spring peak was dominated by *Epiphanes*, (564 *Epiphanes* l^{-1}). During the summer *Keratella quadricauda* and *Keratella cochlearis* dominated.

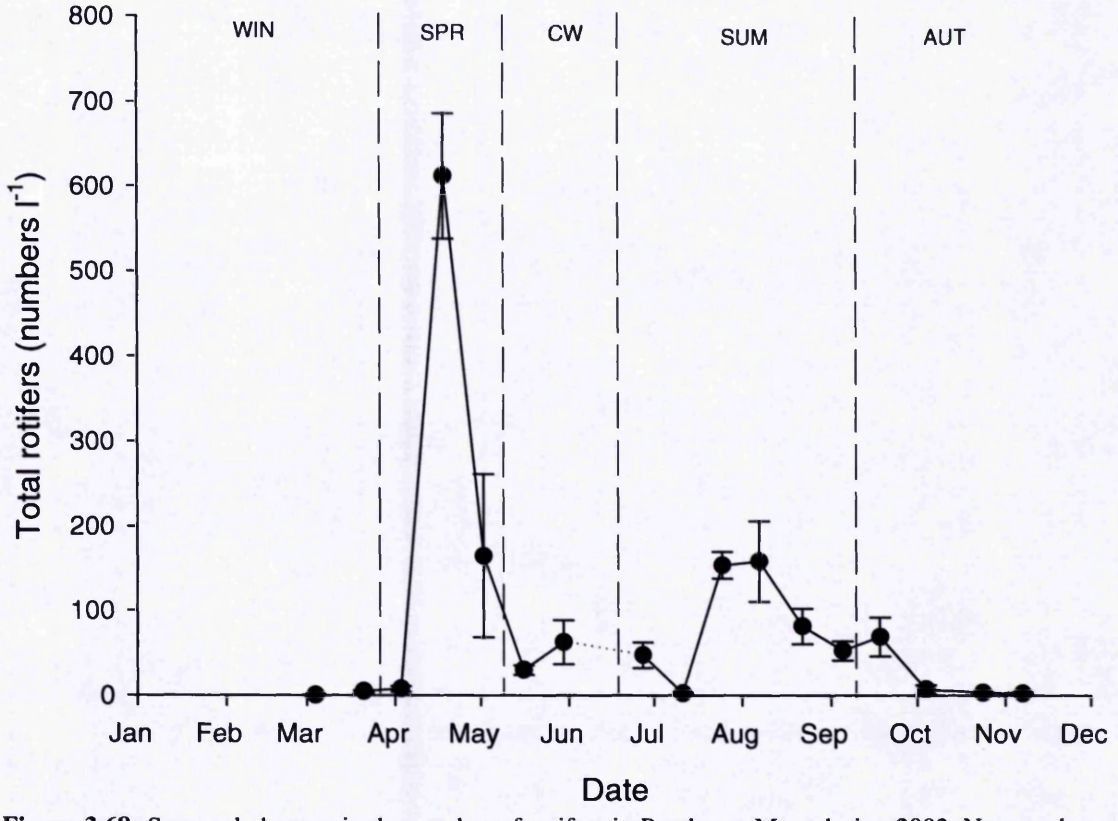


Figure 3.68: Seasonal changes in the number of rotifers in Rostherne Mere during 2002. No sample was taken on the 13th June, values either side are therefore joined by a dotted line. Values are the means from integrated samples taken from each of sites A, B and C. Error bars (±1 SD). (n=3).

Ciliated Protozoa

Seasonal changes in ciliated protozoa are shown in Figure 3.69a. The wide variation exhibited between sites (hence the large error bars) makes it difficult to discern any seasonal trends in the numbers of ciliated protozoa. However, the results do show that numbers of ciliated protozoa were at a minimum during the winter and clear-water phases, with maximum numbers during the spring phases and the early summer phases.

***Chaoborus* larvae**

Chaoborus larvae (Figure 3.69b) were absent from the plankton during the winter, spring and clear-water phases. There was a small increase the start of the summer phase to 15 m^{-3} but numbers remained low (approximately 3 m^{-3}) during July and early August. A large increase in numbers was observed at the end of the summer phase, peaking at 54 m^{-3} on the 5th of September. During the autumn phase numbers were reduced, reaching a minimum of 5 m^{-3} at the end of sampling.

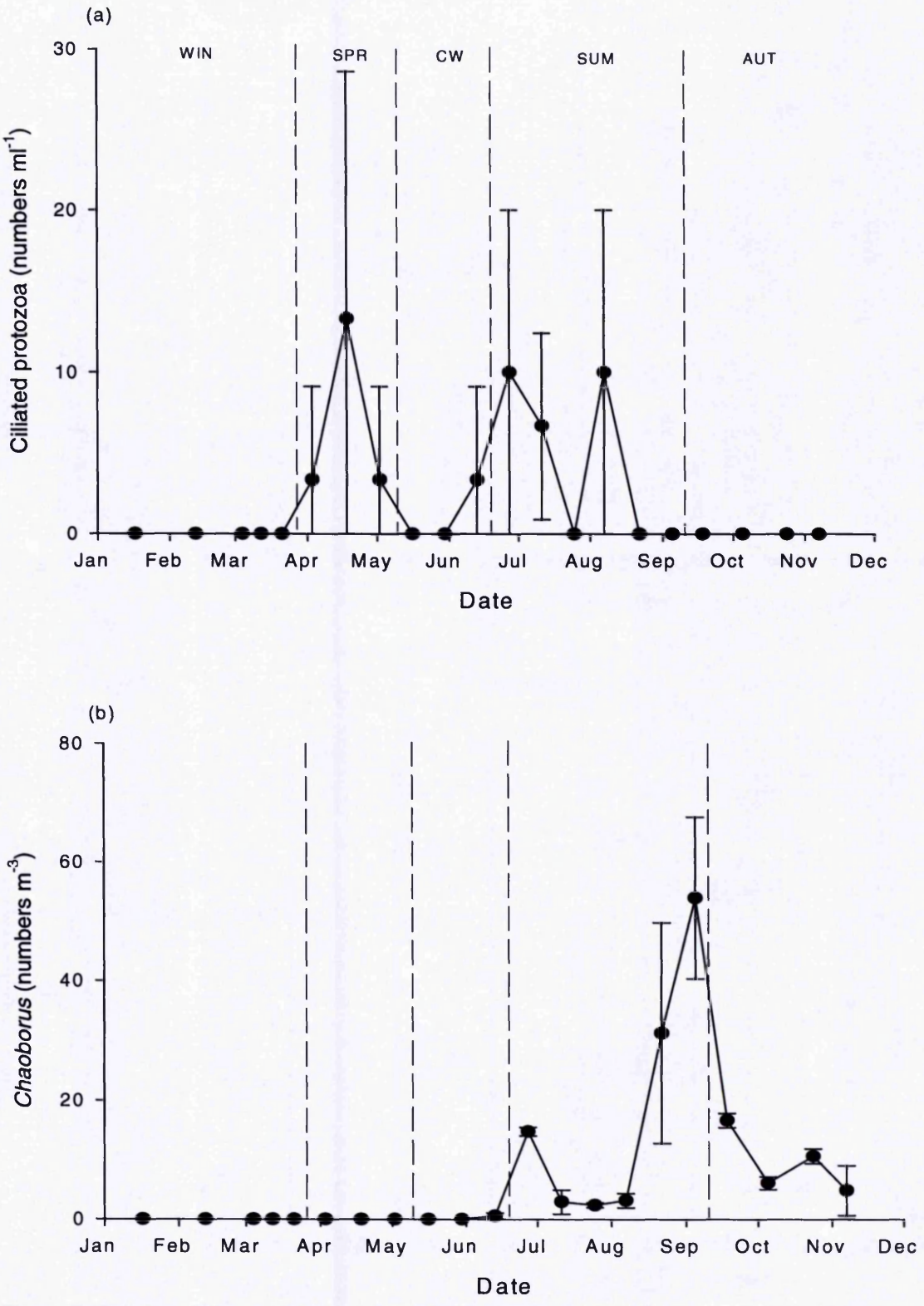


Figure 3.69: Seasonal changes in (a) numbers of ciliated protozoa and (b) numbers of *Chaoborus* larvae in Rostherne Mere, 2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

3.2.3.3 Filtering Rate

Total filtering rate (for *Daphnia* and calanoid copepods combined) varied from a minimum of 2% per day to a maximum of 66% per day. Values were low during the winter phase (≤5%) with a minimum of 2% occurring at the end of the phase (21st of March). Values increased throughout the spring phase, peaking at the beginning of the clear-water phase (66%). Values dropped to 14% by the end of the clear-water phase. During the summer phase filtering rate declined from 25% on the 27th of June to 4% on the 7th of August. There was then an increase to 20% (August 22nd) before filtering rates declined to 5% at the start of the start of the autumn phase, following which they increased to reach approximately 17% towards the end of the autumn phase.

From the late spring phase (18th April) onwards *Daphnia* dominated the filtering rate, contributing between 90 and 100% of the total filtering rate. The maximum contribution of calanoid copepods occurred during the winter and spring phases, when the total filtering rate was <5%. During this time, the contribution of calanoids varied between 28 and 70%.

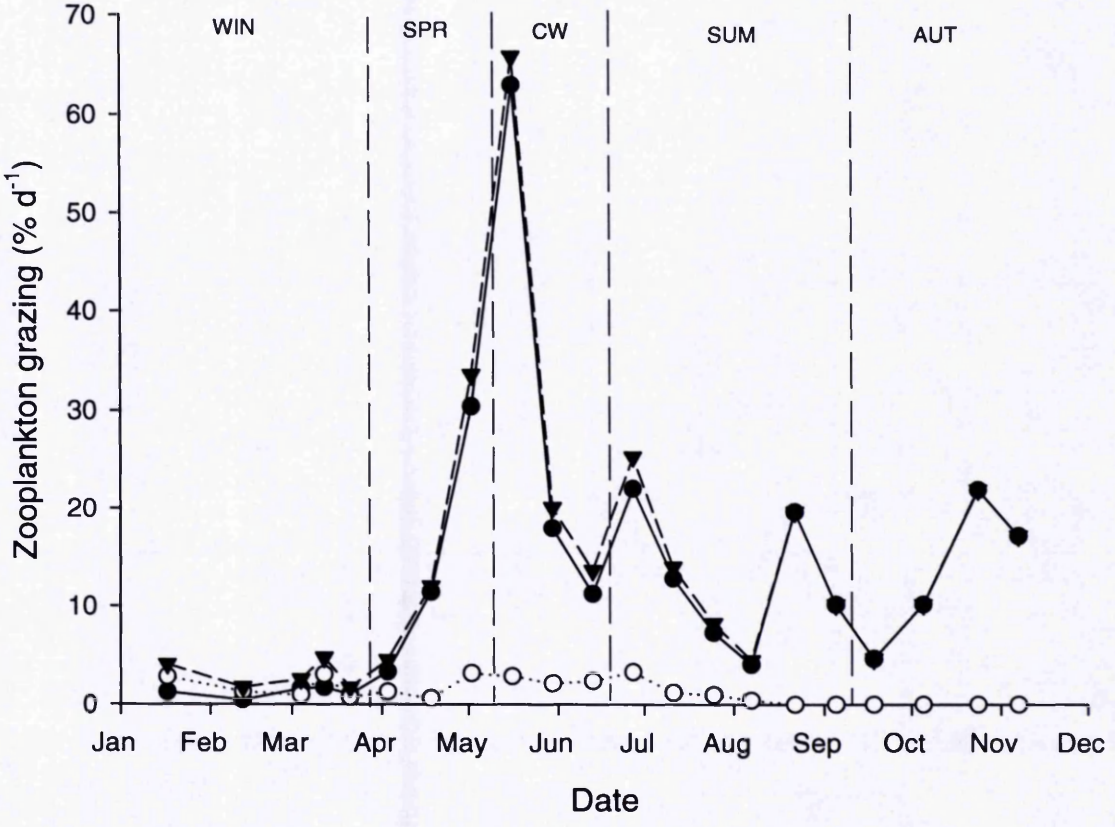


Figure 3.70: Seasonal changes in the filtering rate of *Daphnia* (●), calanoid copepods (○) and both combined (▼), Rostherne Mere 2002.

3.2.3.4 Bacteria, Dissolved Organic Carbon, TSS and TOM

3.2.3.5 Bacteria

Counts of total bacteria are shown in Figure 3.71a. Numbers ranged from a minimum of $2.55x10^6$ cells ml^{-1} to a maximum of $11.13x10^6$ cells ml^{-1} (slightly higher than during 2000). During the winter phase numbers were relatively steady, varying between $2.55x10^6$ cells ml^{-1} and $3.18x10^6$ cells ml^{-1}. There was large during the spring phase, concurrently with the chlorophyll-a peak, reaching $10.25x10^6$ cells ml^{-1} on April the 18th before falling to a minimum of $4.40x10^6$ cells ml^{-1} during the middle of the clear-water phase. Before the end of the clear-water phase, numbers had begun to increase. They continued to increase during the summer phase and peaked at $11.13x10^6$ cells ml^{-1}, numbers remaining at this level from the 11th of July to the 7th of August. This increase and peak in bacterial numbers occurred before the summer increase and peak in chlorophyll-a. When chlorophyll-a reached its maximum (at the end of the summer phase) bacterial numbers had dropped to approximately $8x10^6$ cells ml^{-1}, remaining at this level at the start of the autumn phase, before dropping (concurrently with chlorophyll-a) to a minimum of $3.24x10^6$ cells ml^{-1} by the end of sampling.

It was observed that chlorophyll-a and bacterial numbers were correlated during the whole of 2000, and during the spring and clear-water phase of 2002, however this correlation was not observed during the summer of 2002. As the break down in the chlorophyll-a – bacterial correlation was an important observation it was considered appropriate to carry out a repeat analysis of the sample (site A only) to confirm the results of the first analysis. Figure 3.71(b) shows the results of the repeat analysis, confirming the break down in the chlorophyll – bacterial correlation.

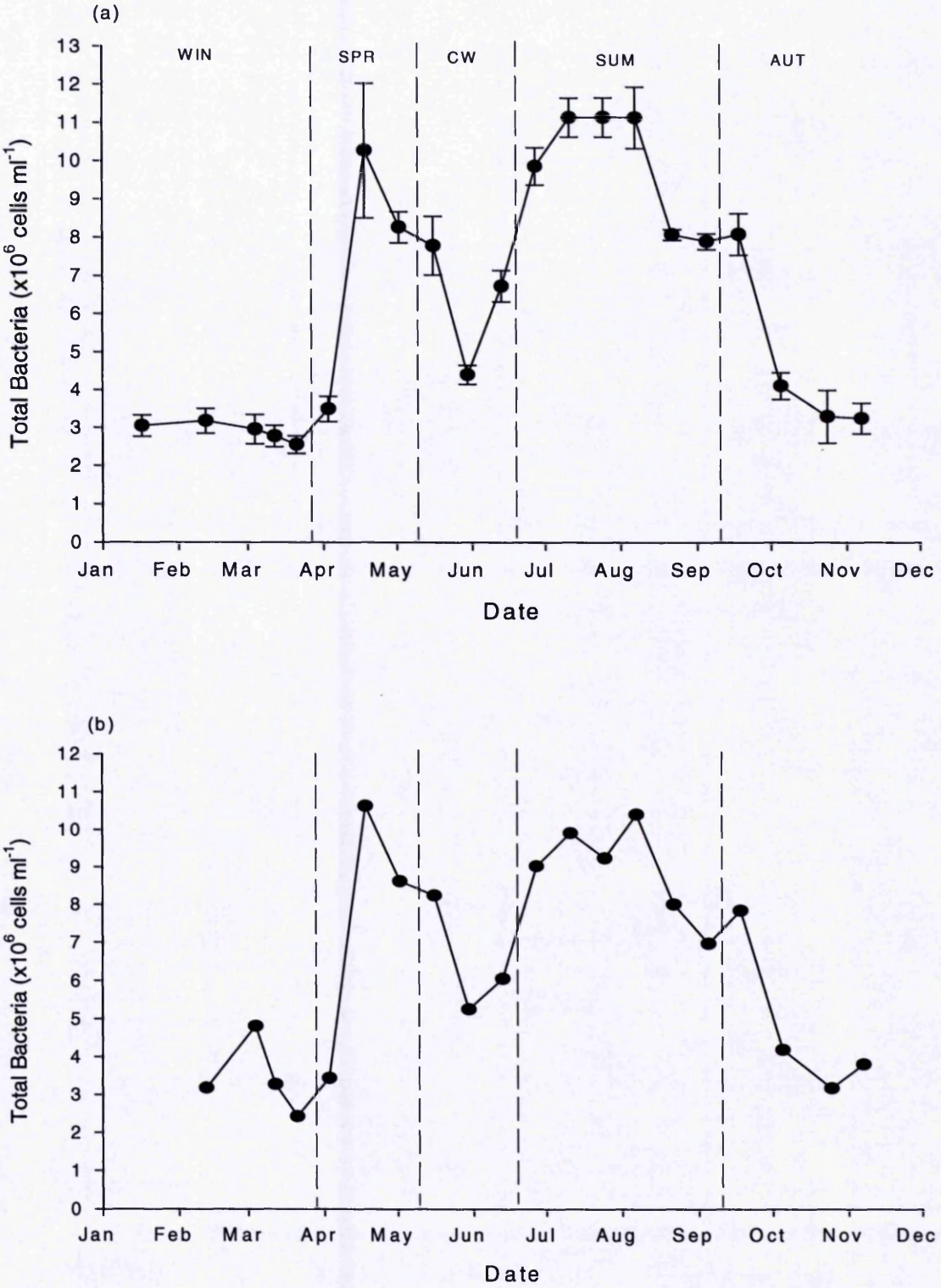


Figure 3.71: Seasonal changes in (a) total bacteria in Rostherne Mere, 2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3) (b) repeat analysis carried out on site A only.

3.2.4 Dissolved Organic Carbon

Seasonal variation in dissolved organic carbon (DOC) is shown in Figure 3.72a. Concentrations ranged from 6.41mg l^{-1} to 9.54mg l^{-1}. No distinct seasonal pattern was observed.

3.2.5 Colour

Seasonal variation in colour is shown in Figure 3.72b. Colour ranged from 2.4 to 9.2 m^{-1}. During the winter phase values were ca. $3m^{-1}$. During the spring bloom there was an increase from 2.4 to $5.1m^{-1}$ coinciding with the peak in chlorophyll-a. Colour then declined to ca. $3m^{-1}$ during the clear-water phase and the beginning of the summer phase. Colour increased during July to $7.1m^{-1}$, declined to $3m^{-1}$ during early August, followed by an increase to $9.2m^{-1}$ on the 18th September (beginning of Autumn phase), before falling to approximately $3.4m^{-1}$ at the end of sampling.

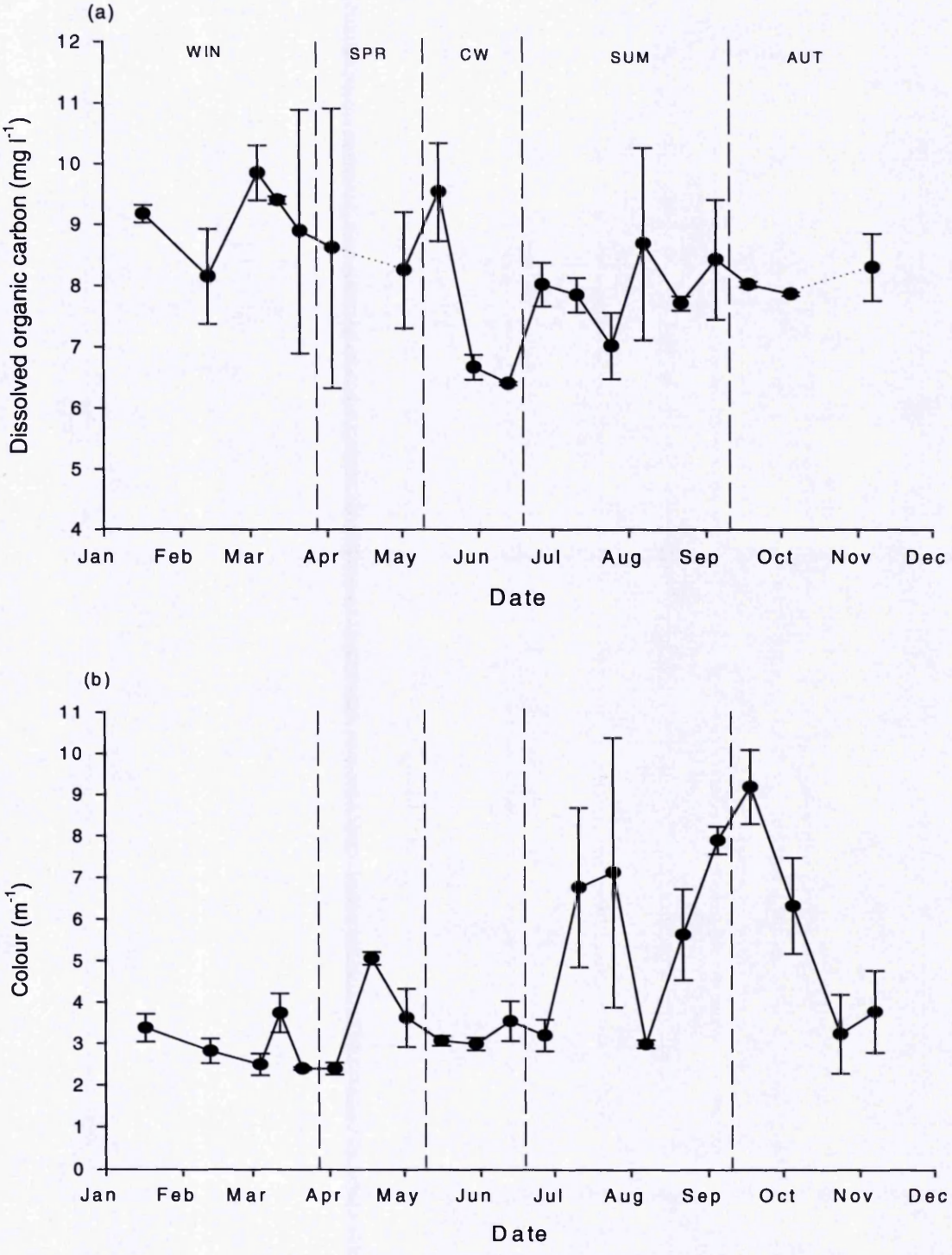


Figure 3.72: Seasonal changes in (a) dissolved organic carbon and (b) colour, Rostherne Mere, 2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3)

3.2.6 Total Suspended Solids and Total Organic Matter

Total suspended solids and total organic matter are shown in Figure 3.73. TSS and TOM showed the same seasonal pattern as chlorophyll-a. During the winter phase TSS fell from approximately 4mg l^{-1} (TOM approximately 2 mg l^{-1}) to approximately 2-3 mg l^{-1} (TOM 1-2 mg l^{-1}). During the spring phase TSS peaked at 6.9 mg l^{-1} on the 18th of April (TOM 5.9 mg l^{-1}) before declining to 1.7 mg l^{-1} during the clear-water phase (TOM 1.5 mg l^{-1}). The clear-water phase was followed by a long broad peak of elevated TSS levels, rising throughout the summer, peaking at 14.8 mg l^{-1} on September the 18th before declining to a minimum of 5 mg l^{-1} (TOM 4.5 mg l^{-1}) at the end of the autumn phase.

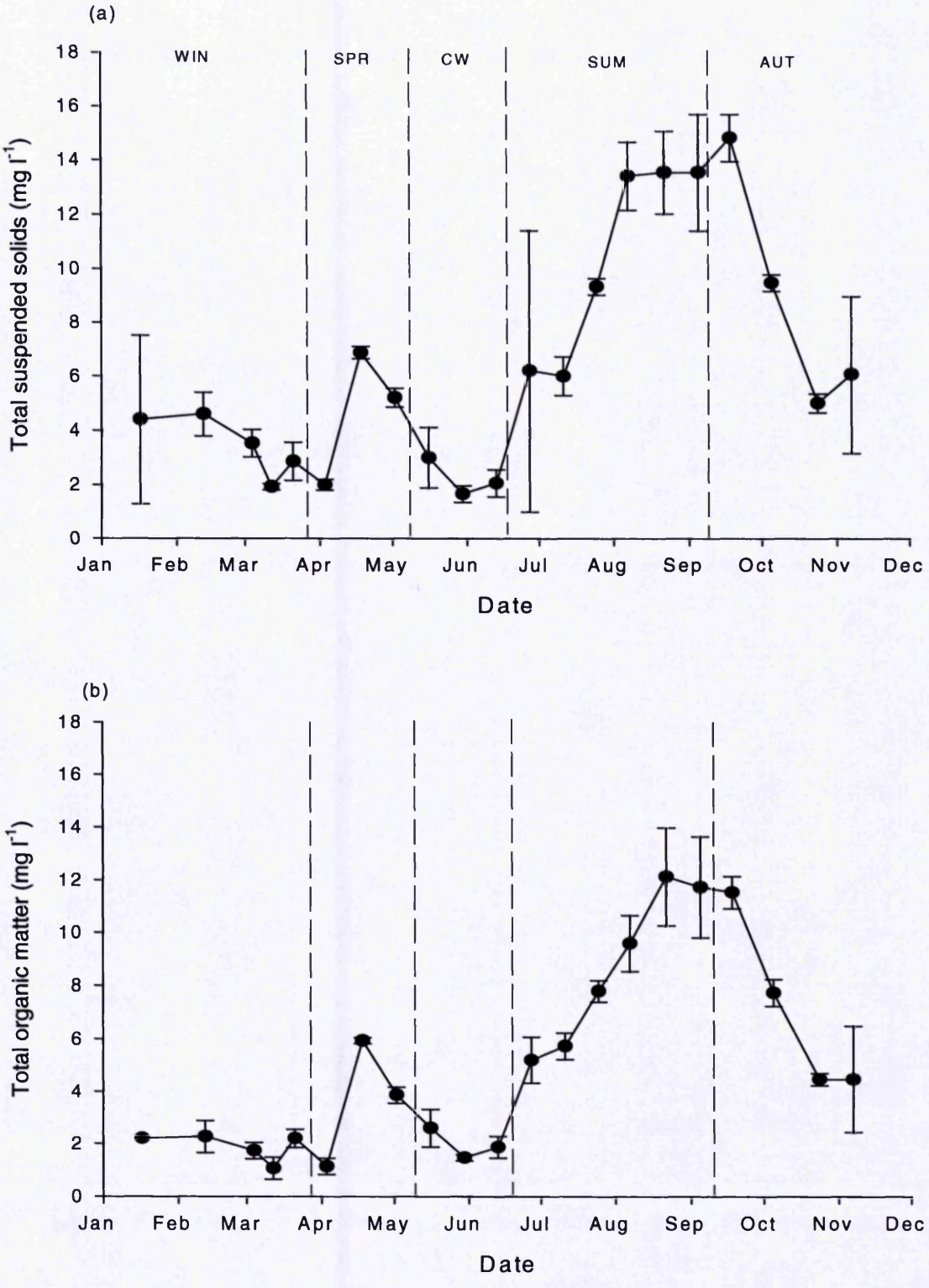


Figure 3.73: Seasonal changes in (a) total suspended solids and (b) total organic matter in Rostherne Mere, 2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

Chapter 4 Discussion for Rostherne Mere

4.1 Phytoplankton Rostherne Mere

The overall aim of this section is to examine seasonal dynamics of the phytoplankton in Rostherne Mere with particular reference to top-down and bottom-up factors, such as grazing and nutrient limitation, that influence the phytoplankton seasonal succession. Of particular interest are the factors influencing the spring diatom bloom and clear-water phase. Also of interest are the factors that influence the summer phytoplankton maximum i.e. is it light, nitrogen or phosphorus-limited, and how important is the impact of zooplankton grazing on the summer phytoplankton biomass.

4.1.1 Early seasonal changes – the spring diatom bloom and clear-water phase

Two questions are particularly important in relation to early seasonal changes:

1. Why is the spring diatom bloom in Rostherne Mere so limited in size? Is it primarily due to a short growing season, or are other factors such as grazing and sedimentation important?
2. What factors contribute to the onset and maintenance of the clear-water phase? Can the decline in diatom populations be attributed to sedimentation in a newly stratified water column, or are other factors such as grazing more important?

4.1.1.1 The Spring Diatom Bloom

The development of the spring diatom bloom, and the reasons for its small size are considered here. One of the most notable observations during this study was that a large quantity of silicon was removed from the water column, yet the observed diatom population was small.

Population Increase in relation to Si uptake

In 2000, the dominant diatoms during the spring period were *Stephanodiscus rotula* and *Asterionella formosa*. Maximum populations were 46 cells ml^{-1} of the former and 53 colonies (approximately 425 cells ml^{-1}) of *Asterionella*, both maxima being observed on the 20th April. The concentration of Si on this date was 1.44 mg l^{-1}, a fall of 0.76mg l^{-1} from the 9th of March, when diatoms were first observed. If *Asterionella formosa* cells have a Si concentration of 65pg Si $cell^{-1}$ and *Stephanodiscus rotula* has a Si content of 0.25pg Si μm^{-3} (Reynolds, 1984a) which, assuming a cell volume of

25000μm^{-3}, gives 6250pg Si cell $^{-1}$ it is possible to estimate the amount of Si the observed diatom population would have removed from the water. An *Asterionella* population of 425 cells ml^{-1} would require 425 cells ml^{-1}x 65pg Si = 0.028μg Si ml^{-1}, while 46 cells of *Stephanodiscus* would require for 46 cells ml^{-1} x 6250pg = 0.287μg Si ml^{-1}, a total of 0.3μg Si ml^{-1}. The observed drop in lake concentrations of Si was 0.76mg l^{-1} (equivalent to 0.76μg ml^{-1}). It can be seen that the observed increase in the diatom population does not account for the loss in Si from the water, in fact it only accounts for approximately 40% of the observed drop in Si.

A similar disparity between observed and theoretical diatom populations occurred in 2002, when Si concentrations fell from 1.97mg l^{-1} on the 21st March to 1.32mg l^{-1} during the *Asterionella* maximum (13th June), a fall of 0.65mg l^{-1}. This is enough to support a population of $10x10^3$ cells ml^{-1} (approximately 1250 colonies ml^{-1}). The maximum observed population was approximately 3000 cells ml^{-1} ($\approx$370 colonies) on the 18th of April, accounting for approximately 30% of the observed drop in Si.

Thus, it can be seen that in both years there is a disparity between the observed diatom population and that predicted from Si uptake. It is possible to calculate the predicted increase in the diatom population from the quantity of silicon removed from the water column. In 2002, the diatom population was dominated by *Asterionella formosa*, with only small numbers of other diatoms present. Hence, it is possible to calculate the *Asterionella* population that would be expected assuming all the Si lost from the water column is incorporated into *Asterionella* cells. The disparity between the observed and predicted populations in 2002 is shown in Figure 4.1. It is evident from the figure that that the observed population is very much lower than that predicted from Si uptake. This is the case on all the sampling occasions during the spring and clear-water phase.

In 2000, it is difficult to treat the data in the same way and determine the predicted diatom population, as both *Stephanodiscus rotula* and *Asterionella formosa* were present. Hence, when making a prediction of diatom numbers based on silicon removed from the water column it is not possible to determine into which species the silicon lost from the water column was incorporated, thus making the prediction of the population increase of these species difficult. Therefore, no graph of observed and predicted populations is presented for 2000.

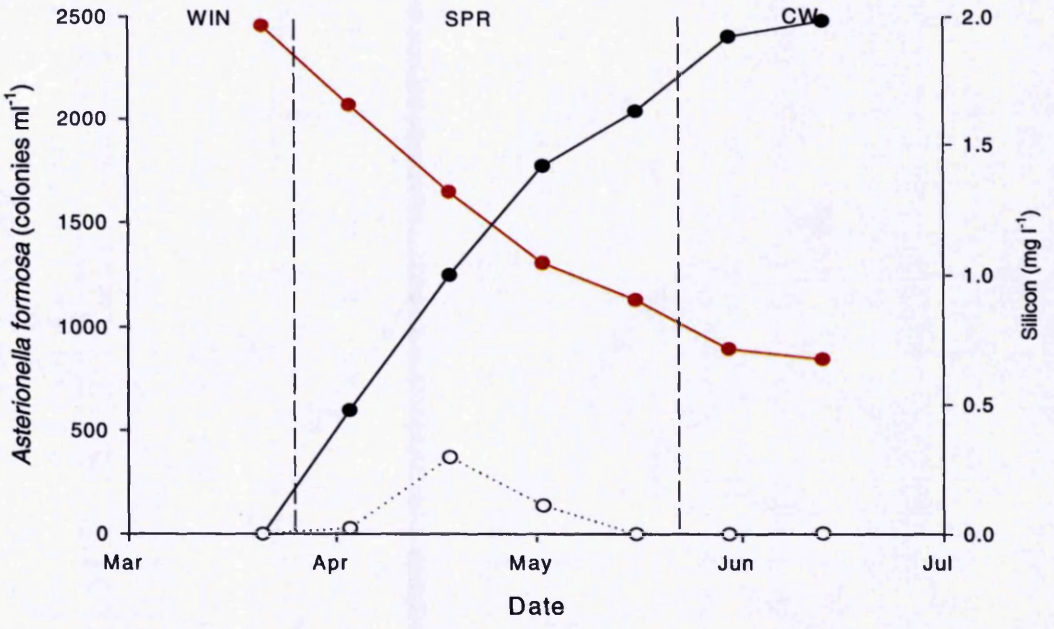


Figure 4.1: Graph to show the discrepancy between the observed population of *Asterionella* (o) and the predicted population (•) calculated according to the loss of Si from the water column (•) for Rostherne Mere in 2002.

Diatom populations in relation to Si uptake in other systems

The above analysis emphasised a disparity between the observed standing crop of diatoms and the depletion of Si within the water column. In lentic systems these are often closely correlated, with the observed standing crop similar to that predicted form Si depletion. In Crose Mere for example (Reynolds, 1978b) the maximum population of *Asterionella* of 12.85×10^3 cells ml^{-1} was associated with a decline in Si concentration of 0.78mg l^{-1}. Assuming cellular Si content of 65pg $cell^{-1}$ (Reynolds, 1997) the observed population maximum would require 0.83mg l^{-1}. In Crose Mere it can be seen that the Si removed from the water column is similar to the Si required to support the observed population.

The same conclusion is reached in terms of a daily Si budget in Crose Mere when allowances are made for an input of Si via daily inflows/runoff and a loss of up to 0.3% of the diatom population each day. The maximum *Asterionella* population is then estimated to be approximately 14.9×10^3 cells ml^{-1}, this numbers of cells would require 0.97mg l^{-1} of Si which is similar to the estimated amount of Si removed from the water column, which is 1.08mg l^{-1}. Close similarity between observed and predicted standing crops has also been observed in many other lentic systems, including Lake Windermere (Lund, 1950), Lough Neagh (Gibson, 1981) and in enclosures situated in Blelham Tarn (Reynolds and Wiseman, 1982).

In Rostherne Mere the discrepancy between the observed and predicted populations suggests either that the sampling greatly underestimates the true diatom population or that the population is subject to high losses, for example by grazing or sedimentation. These possibilities are discussed below.

Reasons for the disparity between observed diatom populations, and populations predicted from Si uptake in Rostherne Mere

Sampling

Sampling may underestimate the true size of the diatom population if there is substantial horizontal and vertical patchiness in the diatom populations. However, horizontal patchiness is unlikely to account for the disparity, as samples were taken from three sites within the lake, and these samples did not produce wide variances in population estimates. Vertical patchiness is another possibility, as samples were taken from the top 5m of the water column; however, diatoms do not migrate within the water column, and in a mixed water column the diatoms should be distributed relatively evenly. Furthermore, for vertical patchiness to underestimate the true diatom populations it would be necessary for the larger proportion of the diatoms to be below 5m depth. Such a distribution which would suggest that the diatoms are falling out of the water column, thus suggesting sedimentation losses rather than sampling as the cause of the disparity between observed and predicted populations.

Infrequent sampling could also be suggested as an explanation as sampling was undertaken either every two or three weeks. For example, there may be a large increase and subsequent decline of the diatom population between sampling visits. However, this is highly unlikely it would still require the diatom population to increase and decrease between each sampling visit of which there were six in 2002 and a similar number in 2000. Furthermore, the losses of the diatom population would still have to explained, again suggesting loss processes are the cause of the disparity between observed and predicted populations.

Potential causal factors that may account for these losses are washout, sedimentation or grazing. When considering the magnitude of the losses quantified below, it is necessary to bear in mind the potential maximum spring growth rate of diatoms, which in the case of *Asterionella* is >0.16 day^{-1} (Reynolds, 1984a). For potential loss factors to contribute to a reduction in the diatom population the combined loss factors must approach the maximum diatom growth rate.

Washout

Washout losses (k_w) are calculated from the discharge per unit time of the outflow divided by the volume of the mixed layer. In spring, the typical discharge from Rostherne Mere is approximately $10000m^3$ day^{-1} (own data, unpublished) and the volume of Rostherne Mere is $6.64x10^6$ m^3 (Woof and Wall, 1984) so the loss rate due to washout when the lake is fully mixed is $10x10^3/6.54x10^6$ which gives a k_w of 0.0015 day^{-1} (using Equation 21, page 47). It can be seen that these losses are very low and may be considered negligible, particularly when compared to the growth rate of *Asterionella* of >0.16 day^{-1}.

Sedimentation

Losses through sedimentation can be approximated using equation 20 (page 46). Estimates of the sinking rate of *Asterionella formosa* are highly variable within the literature; however the sinking rate of healthy, growing colonies is approximately 0.3m d^{-1} (Smayda, 1974; Titman and Kilham, 1976). The mixed depth can be estimated from temperature profiles. Sedimentation losses during the population increase in both years, when the lake was isothermal (mean depth 13.6m), were $k_{sed} \approx 0.02$ day^{-1}. In 2000, the lake had not stratified when the diatom population was at a maximum, so loss rates through sedimentation during the population maximum will be of this level. In 2002, however, the mixed depth was 4m when the diatom population was at a maximum and sedimentation losses would therefore have been ≈ 0.07 day^{-1}. Thus, sedimentation losses may approach half of the growth rate of *Asterionella* during the diatom maximum in 2002 and may therefore cause substantial losses of the diatom population from the water-column. However, although stratification may increase sedimentation losses it will also reduce the mixing depth, the diatoms within the mixed zone will spend a larger proportion of the daylight hours within the photic zone, and this will lead to an increased growth rate of the *Asterionella*. For example Reynolds (1984a) gives a max growth rate of >0.16 day^{-1} during the vernal pre stratified period increasing to >0.40 day^{-1} during the midsummer stratification period. Thus, the increased sedimentation rates due to stratification may be offset to some extent by increased growth rate of the diatoms. Furthermore, stratification was very weak during the diatom maximum (18^{th} April, see Section 3.2.2.2) and sedimentation losses based on a mixed depth of 4m may therefore overestimate sedimentation losses during the peak in diatoms numbers.

In summary, during the increase in the diatom population in both years, and during the maximum in 2000, a large disparity between observed and predicted

populations was observed. As the lake was unstratified during this period, losses (k_{sed}) will have been ≈ 0.02 day^{-1}. Hence sedimentation losses were not high enough to cause substantial losses to a population growing at a rate of >0.16 day^{-1}.

Grazing

If losses due to grazing are to have a significant effect on the phytoplankton populations (i.e. restrict population increase, or cause the population to decrease) then grazing must occur at a rate similar to, or greater than the rate of phytoplankton increase. As zooplankton excrete ingested Si in a particulate, rather than dissolved form (Lampert and Sommer, 1997) the Si in ingested cells would sediment out of the water column. This would result in a depletion of the Si concentration within the water column, and may also result in the small diatom population seen during this study. Losses due to grazing are estimated using $k_{grazing}=G\Phi$. (Equation 19, page 46). In order to calculate $k_{grazing}$ it is necessary to estimate a coefficient of selectivity Φ, for *Asterionella formosa*. Although *Asterionella formosa* colonies are large (ca. 140μm greatest axial linear dimension (GALD)) there is evidence that *Daphnia* can fragment the colonies, and then consume the fragments; Reynolds *et al.*, (1982) give a coefficient of selectivity range of between 0.28 and 1 for this species.

In 2000, filtering rates during the increase in diatom numbers varied between 5 and 10%. With the higher estimate of Φ as 1, maximum losses due to $k_{grazing}$ would be about 0.10 day^{-1}, while if Φ is 0.3 then this gives a $k_{grazing}$ of approximately 0.03 day^{-1}. During the increase in diatom numbers in 2002, filtration rates were 5% on the 3rd of April and 12% on the 18th. Maximum losses due to grazing (with Φ = 1) are therefore 0.12, while with the lower estimate of Φ (= 0.3) $k_{grazing}$ ≈ 0.04.

Thus, if the *Daphnia* are able to ingest *Asterionella* then losses due to grazing are 0.10 – 0.12 during the period when diatoms were increasing. This is close to the value for the maximum growth rate of *Asterionella* (>0.16 day^{-1}), and it is therefore possible that grazing losses will have a major effect on the developing diatom population in Rostherne Mere.

The impact of both grazing and sedimentation on the size of the diatom maximum

The evidence presented above shows that the combined loss rate of diatoms due to sedimentation and grazing were between 0.05 and 0.12 day^{-1} in 2000, and between 0.11 and 0.19 day^{-1} during 2002. As typical maximum growth rates of *Asterionella* during the vernal pre-stratification period are >0.16 day^{-1} these losses may account for a

substantial reduction in the developing diatom population. Thus, combined losses due to grazing and sedimentation during the diatom growth phase may be important in restricting the diatom population in Rostherne Mere.

This analysis suggests that the small size of the spring diatom maximum in Rostherne Mere is not due to the short growing season as suggested by Reynolds (1978b). If the short growing season is the primary influence on diatom population then this would suggest that other losses, such as grazing and sedimentation, are low; and if this is the case then the observed loss of Si from the water column should be commensurate with that observed within the diatom population. However, the above analysis shows that this is not the case. This evidence suggests that the Si is being incorporated into diatom cells, which are then subsequently lost. Furthermore, although the growing season is short, if all the Si lost from the water column was incorporated into *Asterionella formosa* it would support an *Asterionella formosa* population of approximately 2500 colonies ml^{-1}, much higher than the maximum numbers of colonies observed in this study.

4.1.1.2 Clear-water Phase

The diatom maximum in Rostherne Mere is followed by a clear-water phase characterised by low phytoplankton biomass (with chlorophyll-a often falling to <5μg l^{-1}) and Secchi depths extending to >3.5m. Although the onset of the clear-water phase in lakes is typically attributed to grazing (Sommer *et al.*, 1986), in the case of Rostherne Mere it has been suggested that sedimentation is the principal cause of the clear-water phase (Reynolds, 1978b; Reynolds and Bellinger, 1992). The following analysis seeks to quantify losses of the phytoplankton populations during the clear-water phase in order to determine the relative importance of sedimentation and grazing, and to investigate other potential factors such as nutrient limitation.

Potential factors contributing to the onset of the clear-water phase

Washout

During the clear-water phase the lake was stratified. If the depth of the mixed layer is 7m, which is typical for the stratification period, then the volume of the mixed layer is $\approx 2.9 \times 10^6$ then the losses due to washout are $k_{washout}=0.0034$ day^{-1}. In comparison to the growth rate of *Asterionella* of 0.16 day^{-1} it can be seen that these losses are very low and may be considered negligible. Washout therefore has little influence on the onset of the clear-water phase.

Sedimentation

At the commencement of the clear-water phase in 2000 the mixed depth was 4m, estimated losses of *Asterionella* due to sedimentation were therefore ≈0.07 day^{-1}. In 2002 mixed depth was 8m, giving sedimentation losses of ≈0.04 day^{-1}. The maximum growth rate of *Asterionella formosa* during the pre-stratification vernal period is >0.16 day^{-1}, increasing to >0.40 day^{-1} during the mid-stratification period (Reynolds, 1984). It can be seen that sedimentary losses alone cannot exceed the maximum growth rate of *Asterionella formosa,* and are therefore unable to reduce the diatom population to such an extent as to result in the clear-water phase.

Furthermore, the clear-water phase did not only result from a decrease in the spring diatom population, but also a decrease in the spring cryptomonad population. This was particularly evident in 2002 when the decline in cryptomonads paralleled that of *Asterionella formosa.* However, losses of cryptomonads through sedimentation are negligible (Sommer, 1984, Reynolds and Wiseman, 1982) and so the reduction in the cryptomonads must be due to factors other than sedimentation.

Thus, both diatoms and cryptomonad populations decrease during the clear-water phase, yet neither can be accounted for by increased sedimentation. This suggests that sedimentation of particles from the stratified water column, as suggested by Reynolds and Bellinger (1992) cannot be the primary cause of the onset of the clear-water phase.

Grazing

In order to determine the extent to which zooplankton grazing controls phytoplankton populations and causes the clear-water phase, it may be thought that correlation analysis would provide a useful tool. A negative correlation i.e. high zooplankton grazing leading to low phytoplankton numbers, would indicate a significant role for grazing, while a lack of a correlation may be taken as an indication that zooplankton grazing is not important in regulating phytoplankton numbers. Table 4.1 shows a correlation analysis between edible and total biovolume and total filtering rate over the spring and clear-water phases, the period when phytoplankton biomass increased and subsequently decreased to very low levels.

Total filtering rate versus:	Edible biovolume	Total biovolume
2000	ns	ns
2002	ns	ns

Table 4.1: Table to show correlation analysis (Pearson) between edible biovolume and total biovolume against total filtering rate during the spring and clear-water phases. ns - not significant (n=11)

The lack of negative correlation may initially be taken as an indication that zooplankton grazing does not control phytoplankton biomass during the clear-water phase. However, such an assumption is highly misleading, as it assumes that an increasing grazing rate necessarily leads to a decline in phytoplankton populations. In fact, as long as the growth of the phytoplankton population exceeds losses due to grazing, increases in a phytoplankton population can occur in parallel with an increasing zooplankton grazing rate i.e. they can be positively correlated. A parallel increase in both phytoplankton biomass and grazing rate can be seen during the spring phase of 2002 for example. Increasing grazing rates will only cause reductions in the phytoplankton population if the phytoplankton population loss rate from grazing is higher than the rate of population growth. Thus, looking for simple inverse relationships between phytoplankton and zooplankton grazing rates over the period of phytoplankton increase and subsequent decrease is highly simplistic and can be misleading, particularly if periods of phytoplankton population increase are included in the analysis. In order to determine the importance of grazing in the onset of the clear-water phase it is much more important to investigate the relationship between phytoplankton and zooplankton grazing rates during the period of phytoplankton decline.

In both 2000 and 2002, the decline of the phytoplankton population and the initiation of the clear-water phase corresponded with maximum community filtration rates of zooplankton. In 2000, the minimum chlorophyll-a concentration of 2.80µg l^{-1} (Secchi 4.03m) on the 11th of May corresponded with the peak in community grazing rate of 44%. During the clear-water phase a relaxation of grazing to <10% permitted a rapid increase in cryptomonads, producing a chlorophyll-a concentration of 75µg l^{-1} (Secchi 1.47m) before a further increase in grazing to 66% reduced chlorophyll-a to 5µg l^{-1} (Secchi 3.42m). In 2002, the minimum chlorophyll-a concentration of 2.50µg l^{-1} (Secchi 5.1m) on the 16th of May occurred when the grazing rate was 66%. The correspondence of the maximal filtration rate with the minimum chlorophyll-a concentration and the maximum Secchi depth suggests that grazing is a major factor in the onset of the clear-water phase. The rapid increase in cryptomonads in 2000 when

grazing pressure was relaxed (due to a large decline in the *Daphnia* population) also suggests that grazing controls the phytoplankton during the clear-water phase.

This correspondence between maximum grazing rates and minimum phytoplankton biomass suggests grazing is important during the clear-water phase. Further evidence can be gained from a study of grazing rates of the zooplankton. The following quantifies the losses that particular algal groups within the phytoplankton experience due to grazing, and compares these losses to the maximum growth rates of key phytoplankton species. If grazing is higher than the maximum growth rate of the phytoplankton than the decline in phytoplankton populations during the clear-water phase may be attributable to grazing.

Grazing on Diatoms

At the commencement of the clear-water phase in 2000 grazing was 44%, giving a $k_{grazing}$ for *Asterionella formosa* of 0.44 day^{-1} if $\Phi=1$, and if $\Phi=0.3$ then $k_{grazing} \approx 0.13$ day^{-1}. In 2002 grazing at the commencement of the clear-water phase was 66%, therefore losses due to grazing were ≈ 0.66 day^{-1} if $\Phi=1$, with $\Phi=0.3$ losses were 0.20 day^{-1}. In order for grazing to bring about the clear-water phase, losses of phytoplankton to grazing must be greater than the maximum potential growth rate. The maximum growth rate of *Asterionella formosa* during the pre-stratification vernal period is >0.16, increasing to >0.40 during the mid stratification period (i.e. in mid-summer) (Reynolds, 1984a). The growth rates at the onset of the clear-water phase may be expected to be closer to the former estimate, as day length and temperature will both be reduced compared to those pertaining in the mid-summer. The maximum losses due to grazing observed in Rostherne Mere are greater than the maximum growth rate, while the minimum estimates of grazing losses are similar. This again suggests that grazing is important in the onset of the clear-water phase.

Grazing on Cryptomonads

Further evidence for the importance of grazing in the onset of the clear-water phase is provided by changes in the cryptomonad population. Losses of cryptomonads to sedimentation are small (Reynolds and Wiseman, 1982) and the principal loss is grazing (Reynolds *et al.*, 1982). Therefore, it is possible to estimate the maximum rate of growth of cryptomonads from the sum of the net (observed) growth rate and grazing loss rate during the maximum net population increase, and so obtain an estimate of the maximum growth rate at this time i.e. the maximum growth rate is given by

$k_{max}=k_{net}+k_{grazing}$

It is possible to estimate the net growth rate of cryptomonads (k_{net}) (using Equation 17, page 46), and losses due to grazing ($k_{grazing}$) (using Equation 19, page 46) from data obtained during this study. If, when the cryptomonad population subsequently declines, losses due to grazing exceed the maximum growth rate of the cryptomonads, then the decline in the population may be attributed to grazing. During 2000, a large bloom of *Cryptomonas* and *Rhodomonas* occurred during the clear-water phase, when the maximum observed net rate of increase k_{net} was 0.34 day^{-1} for *Cryptomonas* spp., and 0.36 day^{-1} for *Rhodomonas minuta*. Losses due to grazing calculated from the community grazing rate, assuming a coefficient of selectivity of 1 (Reynolds *et al.*, 1982), are 0.14 day^{-1}. Thus, the true rate of growth (k_{max}) for both species was ≈0.50 day^{-1}, which are similar to the values observed during 2002 (see below). These values compare well with literature values for the maximum growth rates of these species during the early stratification period, with *Cryptomonas* >0.61 day^{-1} (Reynolds *et al.*, 1982); maximum growth rates of *Rhodomonas* are not available but net growth rates were ≈0.71 day^{-1} (Reynolds *et al.*, 1982). The *Daphnia* peak that followed the peak in cryptomonads resulted in filtration rates of 62%. It can be seen that the maximum losses due to grazing ($k_{grazing}$) of 0.62 day^{-1} are similar to the maximum growth rate of these species. Thus grazing is high enough to cause the decline in these species and lead to the clear-water phase.

The cryptomonad bloom in 2002 was coterminous with the bloom of *Asterionella formosa*. The maximum observed net rate of growth for both *Cryptomonas* spp. and *Rhodomonas minuta* occurred during April. The maximum net observed growth rates of *Cryptomonas* spp. was 0.36 day^{-1}, for *Rhodomonas minuta* 0.24 day^{-1}. Losses due to grazing at this time were ≈ 0.16 day^{-1}. The estimated maximum growth rates of these species of 0.52 day^{-1} and 0.40 day^{-1} respectively are therefore similar to those observed during 2000. Following the period of maximum observed growth rate the cryptomonad population began to decline. Maximum losses due to grazing during the decline were ≈ 0.50 day^{-1} while at the start of the clear-water phase this had increased to ≈0.66 day^{-1}. It can be seen that losses due to grazing exceed the maximum growth rate of cryptomonads, again suggesting the grazing is a major contribution to the onset of the clear-water phase.

A note on grazing by Rotifers and Ciliates

It should be noted that the above filtration rates did not include rotifers. However, in 2002 (rotifers numbers were not monitored in 2000) the increase and decrease of rotifer numbers paralleled those of *Asterionella* and *Cryptomonas* - peaking together with phytoplankton, and falling to a minimum during the clear-water phase. Thus, rather than contributing to the onset of the clear-water phase rotifer numbers seem to have been reduced in the same manner as diatom and cryptomonad numbers (i.e. via high *Daphnia* grazing rates). Furthermore, even at the maximal rotifer numbers (approximately 600 rotifers l^{-1}) the filtration rate was negligible in comparison to *Daphnia*. For example, if a filtration rate of 0.07 ml day^{-1} per rotifer were assumed (which is the average of the filtration rate for various rotifers given by Pourriot (1977)) the filtration rate of the rotifer population would be approximately 42ml per day, per litre, or 4.2%. During the decline in the spring phytoplankton bloom, and during the clear-water phase, rates were much lower. During the clear-water phase, for example rotifer numbers were approximately 50 rotifers l^{-1}, which using the individual filtration rate of 0.07 ml day^{-1} would give 3.5ml per litre, per day, or less than 1% of the water column.

Ciliated protozoa are also unlikely to have a major impact on the phytoplankton. Ciliated protozoans of the size observed during this study (generally <30μm) graze bacterial sized particles (Wetzel, 2001) and are therefore unlikely to impact on the decline of diatoms and cryptomonads that result in the clear-water phase in Rostherne Mere.

Comparison of grazing to sedimentation during the clear-water phase

As cryptomonads suffer little from sedimentation losses the decline in cryptomonad numbers may be attributed almost exclusively to grazing. Diatoms may also be lost via sedimentation, which has been suggested as the major factor in reducing populations during the clear-water phase (Reynolds and Bellinger, 1992). At the commencement of the clear-water phase in 2000 the mixed depth was 4m, giving estimated losses of *Asterionella* due to sedimentation of 0.07 day^{-1}. Grazing rates were 0.44 day^{-1} if the coefficient of selectivity (Φ) is 1, or 0.13 day^{-1} assuming Φ is 0.3, and it can be seen that grazing losses exceed those through sedimentation even for the lower estimate. Similarly, in 2002 sedimentary losses were 0.04 day^{-1}, again far lower than the losses due to grazing of 0.66 day^{-1} if Φ is 1, or 0.20 day^{-1} if Φ is 0.3. Thus grazing is the most important loss factor for the diatoms during the clear-water phase.

Furthermore, grazing is the only factor that is high enough to exceed the potential maximum growth rate of the diatoms. Of grazing and sedimentation, the low susceptibility of cryptomonads to sedimentation means grazing is the only factor that can account for the loss of the cryptomonad populations.

Although the above analysis shows that grazing is important during the loss of phytoplankton populations both nutrient depletion and parasitism must also be considered.

Nutrient Depletion

In 2000, concentrations of nitrates/nitrites were 1.58mg l^{-1} at the commencement of the clear-water phase while minimum soluble reactive phosphorus (SRP) concentrations were 0.14 mg l^{-1}. In 2002, concentrations at the start of the clear-water phase were 1.53mg l^{-1} for nitrates/nitrites and 74µg l^{-1} for SRP. Limiting concentrations of biologically available N and P are approximately 20µg l^{-1} and 5µg l^{-1} respectively (Ryding and Rast, 1989). The concentrations at the commencement of the clear-water phase are well above the limiting concentrations and so the onset of the clear-water phase cannot be attributed to N or P limitation. The decline in cryptomonads also cannot be attributed to nutrient limitation. However, Si limitation must also be taken into account when considering diatoms. In 2000, Si concentrations at the start of the clear-water phase were 0.12mg l^{-1}, while during 2002 concentrations at the start of the clear-water phase were 0.91mg l^{-1}. The threshold concentration for Si limited growth of *Asterionella formosa* is lower than 0.12mg l^{-1} (Tilman *et al.*, 1981) suggesting that Si limitation did not cause the decline of the diatom during the clear-water phase. Furthermore, the minimum Si concentration of 0.12mg l^{-1} is enough to support the development of a further $1.8x10^3$ *Asterionella formosa* cells ml^{-1}.

Parasitism

Parasitism, particularly by chytrid fungi can be a major factor in the loss of diatom populations (Van Donk, 1983, Sommer, 1987). It is difficult to quantitatively assess the losses due to parasitism but it is possible to estimate qualitatively the importance by looking for signs of parasitism on the cells. Visual inspection of the *Asterionella formosa* cells in both 2000 and 2002 did not show any major parasitic infestation (≈10% of *Asterionella* colonies infected in 2000 and <5% in 2002). Reynolds (1973) found that in Crose Mere chytrid infection caused the population of *Asterionella* to decline when the proportion of infected cells was at 25%. However,

when the proportion of infected cells was 8% no reduction in population was observed. This would suggest that the levels of infection observed during this study are not high enough to cause the decline of the diatom population observed during the clear-water phase.

4.1.2 The period of maximum phytoplankton biomass – Summer Phase in 2000 and the Summer/Autumn phases in 2002

In 2000 the summer phytoplankton biomass was dominated by the dinoflagellates *Peridinium cinctum* and *Ceratium hirundinella*, which generally contributed >80% of the phytoplankton biomass during the summer period. *Peridinium cinctum* was dominant, contributing over 90% of the dinoflagellate biovolume. In 2002 the phytoplankton was dominated by *Gomphosphaeria* which contributed >80% of the phytoplankton biovolume, with a maximum of 97% on the 22nd of August. Both species showed a decline in the population in late summer. The aim of this section is to determine the top-down and bottom-up factors that influence the summer phytoplankton, particularly the rapid decline of the dominant phytoplankton in late summer, and whether this decline can be attributed to grazing, sedimentation or nutrient limitation.

The following assesses the importance of grazing and nutrient limitation each year – *Peridinium* in 2000 and *Gomphosphaeria* in the summer of 2002, and *Aulacoseira* in the autumn of 2002. It then examines other phytoplankton groups that occurred during the summer period.

4.1.2.1 *Peridinium*-The dominant phytoplankton during the summer maximum in 2000

In 2000, *Peridinium* increased during early June, and numbers remained at high levels until the bloom collapsed from 770 cells ml^{-1} on the 31st of August, to 20 cells ml^{-1} on the 8th of September. The decline of summer populations is often attributable to increased mixing during the autumn overturn. However, the decline of the *Peridinium* population occurred well before the overturn, when the lake was still stratified. Hence, increased deep mixing of the population cannot explain the decline in *Peridinium*.

Grazing is also unlikely to account for the collapse in the bloom as grazing rates were low, and *Peridinium* is considered inedible by many authors (Pollingher, 1988). The cells of *Peridinium* were roughly spherical with a diameter of 45μm. The average size of *Daphnia* over the summer phase was 1.31mm, and the maximum size of

particles that could be ingested (according to the Burns' equation) by *Daphnia* of this size is approximately 34μm. It is thus likely that the cells are indeed too large for ingestion by the average *Daphnia*. Gravid *Daphnia* were larger with an average size of 1.65mm, which could ingest particles up to 41μm, while in mid-July the average size of gravid *Daphnia* was 1.8mm, which could ingest cells of ≈45μm. This suggests that some of the *Daphnia* could potentially ingest *Peridinium*, although even if some cells are ingested grazing is unlikely to have any influence on the fluctuations in *Peridinium* numbers. Maximum grazing rates during the increase in *Peridinium* numbers (early July) were ≈ 20%, during the remainder of the summer phase they were ≈10%, as they were when the *Peridinium* declined. Thus, the decline of *Peridinium* did not coincide with any increase in grazing.

Losses of healthy dinoflagellate cells through sedimentation are also likely to be low as cells actively swim, and can maintain themselves within the water column. This of course does not mean that sedimentation of cells does not occur during the population crash at the end of the bloom, when cells have died from other factors such as nutrient limitation, but sedimentation losses of healthy cells is likely to be low.

If sedimentation and grazing are low for *Peridinium*, as argued above, then nutrient limitation may account for the collapse of the bloom. The bloom in *Peridinium* led to SRP concentrations approaching limiting levels of 0.01mg l^{-1} during the peak in chlorophyll-a on the 19th of July. Concentrations then increased slightly to 0.02mg l^{-1} before falling to undetectable on the 23rd of August, immediately before the collapse of the bloom. The reason why no immediate crash in the population occurred following the 19th of July, when concentrations approached limiting values may be due to 'luxury consumption' of phosphorus and the ability of cells to migrate into the upper hypolimnion where nutrients are more plentiful. 'Luxury consumption' of phosphorus (Serruya and Berman, 1975) results in the storage of excess phosphorus within the cells during bloom development, and this is then utilised when external concentrations become limiting. The ability of *Peridinium* to migrate to the hypolimnion may also permit cells to avoid phosphorus limitation. During the maximum phytoplankton biomass in July when SRP approached limiting concentrations, luxury consumption and migration into the hypolimnion may have contributed to the continued high dinoflagellate biomass persisting to the end of August.

The collapse of the dinoflagellate bloom in early September occurred after SRP concentrations had fallen to undetectable levels on August 31st. This suggests that the

collapse of the bloom may have been due to phosphorus limitation. Low phosphorus concentrations during late July and early August may have resulted in the utilisation of the excess 'luxury phosphorus' before SRP concentrations finally fell to undetectable levels on August the 23rd. Although vertical migration may be expected to offset P limitation to some extent, there is evidence that dinoflagellates cannot migrate into anoxic waters. James *et al.* (1992) showed that anoxia in the upper water column restricted the migration of *Ceratium* to the top 3m of the water column, and prevented cells from accessing hypolimnetic phosphorus and this, coupled with low epilimentic P concentrations, led to a decrease in *Ceratium* biomass. Thus, if the upper hypolimnion is anoxic, cells may not be able to access the nutrients within the hypolimnion. In this study, although no oxygen profile was taken in late August there is evidence that oxygen concentrations in Rostherne Mere fall to anoxic levels in late August; in August 2002 for instance anoxic conditions existed below 6m. Thus, when SRP concentrations were undetectable in late August anoxia may have prevented cells accessing hypolimnetic phosphorus, resulting in P limitation and the subsequent decline in the dinoflagellate populations.

Although *Peridinium cinctum* dominated the dinoflagellates and the phytoplankton biomass in general *Ceratium hirundinella* was also present, its fluctuations in numbers generally paralleling those of *Peridinium* but at much lower numbers of <85 cells ml^{-1}. The population dynamics of *C. hirundinella* was therefore likely to be influenced by similar factors.

4.1.2.2 *Gomphosphaeria* and *Aulacoseira* - The dominant phytoplankton during the phytoplankton maximum in 2002

The decline in the *Gomphosphaeria* bloom is also unlikely to be caused by increased mixing during the overturn, as the population declined when the lake was isothermal. Grazing is also unlikely to account for the decline, as grazing during the summer phase was low, declining from ≈25% at the start of the phase to a minimum of 4% on the 7th of August. There was a further increase to ≈20% in late August. Maximum grazing rates were therefore <0.20 day^{-1}, which were not high enough to cause declines in biomass. Furthermore, by virtue of its large size, *Gomphosphaeria* is unlikely to have a high coefficient of selectivity.

Gomphosphaeria may be expected to have a low sedimentation rate as colonial cyanobacteria have gas vacuoles that render the colonies buoyant (Paerl, 1988). Losses of healthy cells through sedimentation are therefore likely to be of limited importance.

As in 2000, it seems that the principal factor influencing phytoplankton growth during 2002 may well have been phosphorus limitation. In 2002, SRP concentration first fell to limiting concentrations in late July and remained limiting throughout August, September and early October.

The continued presence of *Gomphosphaeria* during the summer phase, despite limiting concentrations of phosphorus, may be due to luxury consumption of the element. Blue-green algae frequently become dominant at the same time as nutrient concentrations reach their seasonal minimum (Pearsall, 1932, Lund, 1965). This was observed in this study where the maximum population of *Gomphosphaeria* corresponded with the lowest nutrient concentrations recorded. The ability of *Gomphosphaeria* to survive in conditions of low nutrient availability may be due to the cell quotas of P and N imported during the initial development of the population. It is possible that the decline occurred when all the 'luxury' phosphorus had been utilised. Alternatively, oxygen profiles show anoxic conditions within the lower epilimnion and it is possible that *Gomphosphaeria*, like *Peridinium*, may be restricted in its vertical migration by anoxic conditions, and so be unable to migrate into P-rich waters.

The decline in *Gomphosphaeria* during the autumn did not lead to an immediate decline in chlorophyll-a as the autumn phase saw a rapid increase in the population of *Aulacoseira granulata var. angustissima*. The *Aulacoseira* bloom declined equally rapidly. The low susceptibility of *Aulacoseira* to grazing (due to its long filamentous structure) coupled with low grazing rates during the collapse of the bloom suggests that top-down effects had little influence on the decline of this species. The decline coincided with a fall in SRP to undetectable levels, and Si to 0.07mg l^{-1}, suggesting nutrient limitation may be the cause decline of the *Aulacoseira* bloom.

4.1.2.3 Possible factors regulating other species within Rostherne Mere

Although *Peridinium* and *Gomphosphaeria* dominated during the phytoplankton maximum in Rostherne Mere, other taxa were also present. Grazing may again be presumed to have little influence on these phytoplankton. This is by virtue of the low grazing rates (generally <20%) and by the fact that many of the species may be considered to have a low susceptibility to grazing (by virtue of their maximum dimensions exceeding the feeding gape of *Daphnia*). For example, although there is evidence that small colonies of *Eudorina* and *Microcystis* can be ingested by *Daphnia* spp. the larger, full-sized colonies are too large to be ingested and the coefficient of selectivity for these species will therefore be approaching zero (Reynolds *et al.*, 1982).

Similarly, by virtue of their filamentous nature, the cyanophytes *Anabaena flos-aquae*, *Aphanizomenon flos-aquae* will also have a low susceptibility to grazing.

In addition to the inedible species described above the summer phase of 2000 also saw rapid increases and subsequent decreases in species that may be considered edible on account of their small size; the most notable in terms of numbers and biovolume were *Stephanodiscus hantzschii*, *Scenedesmus* spp. and *Cryptomonas* spp. However, despite these species being edible, grazing rates during the summer are far below those required to reduce populations of theses species. The maximum growth rate of phytoplankton during the summer is generally >0.3 day^{-1} (see Table 17, Reynolds, 1984a). To cause the fluctuations in numbers of these species, as opposed to simply slowing population growth, would require grazing rates >0.30 day^{-1}. However, as discussed above grazing rates were generally <20%, too low to cause a decline in phytoplankton numbers.

For example, the species which reached by far the highest numbers was *Stephanodiscus hantzschii*, which increased from 160 cells ml^{-1} on the 12th of July to 12000 cells ml^{-1} on the 19th of July, giving a net rate of growth >0.60 day^{-1}. There was then a rapid decline to 545 cells ml^{-1} on the 26th of July, with no cells being recorded by the 3rd of August, giving a net rate of decline similar to the net rate of growth (approximately 0.6 day^{-1}). Grazing was 22% on the 12th of July, when the population was increasing. Assuming *S. hantzschii* is susceptible to grazing (by virtue of their small size) and so having a coefficient of selectivity of 1, maximum losses due to grazing would be in the order of 0.22 day^{-1}. During the population decline grazing pressure had reduced to less than that observed during the population increase, falling to a maximum of approximately 0.10 day^{-1}. Grazing losses during the decline are therefore much lower than the potential maximum rate of growth (which must be higher than or equal to the maximum observed net rate of growth of 0.61) and therefore grazing cannot account for the decline in the diatom population. Grazing was also unlikely to account for fluctuations in the populations of other edible phytoplankton during the summer period.

Similarly, when *Scenedesmus* spp. peaked in early August, and *Cryptomonas* spp. fluctuated in numbers during the summer period, peaking at the same time, grazing during August was approximately 5% (max. 10%). Maximum losses due to grazing for the smaller edible species, *Cryptomonas* spp. and *Scenedesmus* spp., which have a coefficient of selectivity approaching 1, would therefore be $k_{grazing} \approx 0.10$ day^{-1}. As with *Stephanodiscus hantzschii* losses due to grazing of <0.10 day^{-1} are too low to cause

the decline in these species which have maximum summer growth rate in excess of 0.50 day^{-1}.

Sedimentation is also unlikely to cause the decline in these species. Sedimentary losses would be low for small cells such as *S. hantzschii.* and *Scenedesmus* spp, while cryptomonads have negligible sedimentary losses (Sommer, 1984). Furthermore, there was no decline in the mixed depth during this period so there should not have been any increase in losses via sedimentation.

If grazing and sedimentation losses are low then fluctuations in the populations of the non-dominant species within Rostherne Mere are again likely to be due to nutrient limitation. For example, the decline of the *Stephanodiscus hantzschii* population described above occurred when concentrations of SRP reached potentially limiting concentrations (0.01mg l^{-1}). Furthermore, diatom biomass was at a maximum while the concentration of Si were also low, at 0.07 mg l^{-1}.

Similarly, the bloom of *Synechococcus* in August 2002 is unlikely to be much affected by grazing or sedimentation. Although its very small size renders it susceptible to ingestion, *Daphnia* and calanoid grazing rates were never more than 20% of the water column. Rotifer grazing rates were also low, at ≤ 1% of the water column (using a figure of 0.07ml day per rotifer which is the average of values given by Pourriot, 1977) even at the maximum population of approximately 150 rotifers l^{-1} during the summer. The small size of *Synechococcus* is also likely to reduce its losses through sedimentation. Thus, *Synechococcus* is likely to be controlled by nutrient availability, particularly as it peaked in August 2002, when SRP concentrations were limiting.

4.1.2.4 Summary of the factors controlling phytoplankton during the summer phase

The evidence presented above shows that during summer zooplankton grazing is not high enough to cause the decline in phytoplankton populations. The reason that grazing has little influence is due to both the low grazing rate of the zooplankton, and the large size of the dominant phytoplankton. Although some of the smaller phytoplankton may be ingested, grazing rates are too low to cause any marked decline in the phytoplankton populations.

Sedimentation is also unlikely to cause any large losses of the phytoplankton as the dominant phytoplankton in both years were large species that can regulate their position in the water-column, and are therefore well suited to stratified conditions.

Concentrations of nutrients suggest that phosphorus limitation may be limiting phytoplankton biomass in the late-summer. However, although Rostherne Mere has previously been shown to be nitrogen limited (Moss *et al.*, 1994, 1997), the evidence from this study now shows the lake to be phosphorus-limited, suggesting that phosphorus or nitrogen concentrations within the lake are changing (this is discussed further in Section 4.4). Thus, phosphorus limitation seems to regulate phytoplankton biomass in late summer.

It has also been suggested that the phytoplankton biomass in Rostherne Mere is light-limited (Reynolds and Bellinger, 1992). It may be that during the early summer period, before nitrates and phosphorus are reduced to limiting concentrations, the phytoplankton is indeed light limited although there is no direct evidence for this from this study. However, the high concentrations of nutrients during the early summer period may free the phytoplankton from nutrient limitation, and as discussed above top-down control by zooplankton is low, as are sedimentation losses. Thus, in the absence of other controls it is possible that the early summer phytoplankton may be limited by the availability of light.

4.1.3 Summary of factors controlling the phytoplankton in Rostherne Mere

It can be seen from the results obtained in 2000 and 2002 that the phytoplankton in Rostherne Mere is subject to different controlling factors over the course of the winter, spring and summer periods. Thus, it is an over-simplification to state that phytoplankton in Rostherne Mere is controlled by light or nutrients, as the controlling factors change seasonally. Table 4.2 shows how the principal factors that control phytoplankton in Rostherne Mere vary seasonally.

Phase	Proposed controlling factors for phytoplankton
Winter	Bottom-up control via deep mixing and short day length restricts diatom growth
Spring bloom	Combination of bottom-up control via deep mixing (as above) and also increasing top-down control by grazing from zooplankton
Clear-water phase	High levels of zooplankton biomass, leads to a high grazing rate and strong top-down control, resulting in very low phytoplankton biomass and high Secchi depths
Summer Early phase	Lack of other controlling factors may suggest that bottom-up control by light limitation may be important in regulating phytoplankton biomass
Summer Late phase	Limiting concentrations of phosphorus suggest bottom-up control of the phytoplankton

Table 4.2: Summary of factors controlling phytoplankton in Rostherne Mere in relation to season, for 2000 and 2002.

4.2 Population dynamics of *Daphnia* in Rostherne Mere

The aim of this section is to determine whether herbivorous zooplankton in Rostherne Mere are regulated primarily by food availability (bottom-up) or predation (top-down), and is divided into sub-sections corresponding to the phases observed within the lake. The first section considers the winter/spring and clear-water phases when *Daphnia* increased from low winter numbers to a peak during the clear-water phase. The second section considers the summer phase, when *Daphnia* numbers were consistently low, and no peaks were observed. This leads onto the Autumn/winter phase, when a further peak in *Daphnia* was observed.

4.2.1 Spring and clear-water phase

4.2.1.1 Influence of food supply on *Daphnia* populations

In 2000, there were two large peaks in zooplankton biomass; the first followed the diatom maximum, with *Daphnia* numbers at ≈ 9 *Daphnia* l^{-1}, while the second followed the cryptomonad bloom, with 16.5 *Daphnia* l^{-1}. In 2002, there was a single peak in zooplankton numbers, occurring after the *Asterionella*/Cryptomonad bloom with numbers reaching a maximum of 27 *Daphnia* l^{-1}. The zooplankton populations then showed a rapid decline during the clear-water phase. Evidence for bottom-up control of zooplankton populations is provided by correlations between food availability and birth rate.

Correlations between food availability and birth rate

An increase in *Daphnia* during the spring is often observed in standing waters and is related to an increase in parthenogenetic reproduction in response to an increase in the availability of edible phytoplankton (Sommer *et al.*, 1986). If the *Daphnia* are food-limited then a positive correlation should be observed between the reproductive rate of *Daphnia* and the availability of edible phytoplankton. A measure of the reproductive rate of the zooplankton is given by the birth rate. A correlation between edible food and *Daphnia* birth rate would suggest the *Daphnia* are controlled by the bottom-up control of food availability (George and Reynolds, 1997). Table 4.3 shows the result of correlation analysis between edible phytoplankton biovolume and birth rate. The correlation between birth rate and the availability of edible food strongly suggests that the zooplankton are controlled by food availability.

Edible phytoplankton biovolume versus	Daphnia birth rate
2000	0.629* (n=11)
2002	0.793** (n=11)

Table 4.3: Correlation analysis (Pearson) between edible phytoplankton biovolume and *Daphnia* birth rate. Correlations carried out from the start of sampling to the end of the cryptomonad phase in 2000, and until the end of the clear-water phase in 2002. * - $P \leq 0.05$, ** - $P \leq 0.01$.

Further evidence for the bottom-up control of zooplankton can be obtained by relating food availability to threshold food concentrations. This is carried out below for the period of increasing *Daphnia* biomass and the period of decreasing *Daphnia* biomass.

Increase in *Daphnia* populations

Evidence for the influence of food availability on zooplankton dynamics can be obtained by comparing the concentration of edible carbon with the threshold food concentration, which is the quantity of ingestible food per volume of lakewater, expressed as carbon ($\mu gC\ ml^{-1}$), below which the animals will starve and die. Various workers have studied *Daphnia* populations and given figures for threshold food concentrations. The threshold concentration varies from species to species; for example, Geller (1985) gave figures of 0.06 $\mu g\ C\ ml^{-1}$ for a population of *D. hyalina* and 0.10 $\mu g\ C\ ml^{-1}$ for *D galeata*. Other studies also suggest that the threshold concentration for *Daphnia* is around 0.10$\mu g\ C\ ml^{-1}$. For instance, Reynolds (1984a) suggests 0.08 $\mu g\ C\ ml^{-1}$, while both Muck and Lampert (1984), and George and Reynolds (1997) suggest a threshold concentration of 0.10 $\mu g\ C\ ml^{-1}$. Reynolds (1997) gives a threshold concentration of 0.05 $\mu g\ C\ ml^{-1}$ for *Daphnia* survival. It should be noted that these figures are independent of the population density of *Daphnia*, and virtually independent of *Daphnia* size and water temperature.

The hypothesis that the spring increase in the *Daphnia* population is a result of increased reproduction due to an increase in the availability of edible phytoplankton (Sommer *et al.*, 1986) is supported by a comparison of the concentration of edible carbon with the threshold concentration given above. In January, February and early March of the 2000 sampling season the quantity of edible carbon was $< 0.014\mu g\ C\ ml^{-1}$ and hence may be considered limiting. It wasn't until the diatom and cryptomonad numbers began to increase on the 30th of March that edible carbon increased to above the limiting concentration, with a concentration of $0.13\mu g\ C\ ml^{-1}$ on the 30th of March, increasing to $0.32\mu g\ C\ ml^{-1}$ on the 20th of April, when chlorophyll-a peaked. The

increase in edible carbon was accompanied by an increase in birth rate from 0.04 in early March to 0.13 on the 30th of March, remaining high (0.10) on the 20th of April. In 2002, edible carbon was ≤0.07μg C ml^{-1} prior to the 18th of April; cryptomonads and *Asterionella* then reached their maximum populations and the concentration of edible carbon increased to 0.9μg C ml^{-1}. These changes were accompanied by an increase in the birth rate from <0.04 in early March to 0.13 on the 18th of April.

In both years, there was a rapid increase in brood size during the spring. In 2000, it increased from 2 in early march to 7.5 on the 30th March and 20th of April and in 2002 from ≈2 to 6.3. Rapid increases in brood size occur when there is a sudden increase in the quantity of edible food, again suggesting *Daphnia* were resource limited at this time (George and Reynolds, 1997).

Decrease in *Daphnia* populations

In both years the *Daphnia* population showed a rapid decrease during the clear-water phase and this is often ascribed to food limitation, with *Daphnia* grazing on the phytoplankton to such an extent that they overgraze their food supply (Sommer *et al.*, 1986). If food limitation is the cause then the decline should be preceded by declining reproductive rates of *Daphnia* brought about by food falling to limiting concentrations. Evidence from both years suggests that this is the case. During the 2000 clear-water phase *Daphnia* numbers were initially >9 *Daphnia* l^{-1}, but fell to 2.4 *Daphnia* l^{-1} by the end of the phase. At the commencement of the clear-water phase in 2000 the quantity of edible food fell to 0.06μg C ml^{-1} with a minimum of 0.034μg C ml^{-1} in the mid-phase. Thus, the food supply during the clear-water phase may be considered limiting according to the threshold concentrations referred to above. The decreased food supply also led to a reduction in both birth rate (<0.05) and brood size (1.6)

During the clear-water phase in 2002, *Daphnia* numbers fell from ≈27 *Daphnia* l^{-1} to ≈ 5 *Daphnia* l^{-1}. Edible food concentrations during the clear-water phase were once again limiting, with concentration initially below 0.006μg C ml^{-1}. Food concentrations were lower than in 2000, and this was reflected in lower birth rates, which were ≤0.01 throughout the phase. Brood size and percentage gravid were also lower. Brood size fell to a minimum of 1, while the proportion of gravid adults, which had been relatively constant at ≈ 30% during the winter and spring fell to <4% during the clear-water phase, with a minimum of 1%, which again suggests food limitation.

Further evidence for the food limitation of spring zooplankton populations in Rostherne Mere is provided by an analysis of the cryptomonad bloom in 2000. This interrupted the clear-water phase, with the increase in cryptomonads occurring when grazing pressure was relaxed due to the decline of the first *Daphnia* peak. The rapid increase in cryptomonads led to edible food concentrations increasing to well above limiting concentration, with ≈0.6μg C ml^{-1} on the 30th of May and 8th of June. Although *Daphnia* numbers were low (< 1.2 *Daphnia* l^{-1}) the increased food concentration led to an increased reproduction, reflected in an increase in the birth rate to ≈0.13 and a brood size of 4. The increased birth rate resulted in an increase in numbers to 16.5 *Daphnia* l^{-1} at the end of the phase. The increased numbers of *Daphnia* reduced the quantity of edible food to limiting concentrations (0.06μg C ml^{-1}) and this was reflected in a decrease in the birth rate and brood size to 0.01 and 2 respectively resulting in a decrease in the *Daphnia* population from 16.5 to 4 *Daphnia* l^{-1} at the start of the summer phase.

The pattern observed in this study is very similar to that observed by Luecke *et al.*, (1990) who studied the clear-water phase in a eutrophic lake. Luecke also found that the *Daphnia* decline coincided with carbon concentrations of edible phytoplankton falling to levels similar to the threshold concentrations, and showed that the number of eggs produced by adult *Daphnia* was reduced when food concentrations were limiting. The decline in *Daphnia* was attributed to a reduction in the availability of food.

There is therefore strong evidence for zooplankton being controlled by bottom up factors during both the 2000 and 2002 spring and clear-water phases. The positive correlation between zooplankton birth rate and edible food concentrations suggests that the *Daphnia* are food limited. Furthermore, the fact that concentrations of edible carbon fell to limiting levels, and that reproductive measures of the *Daphnia* fell to minimum levels when food was limiting provides further evidence that the *Daphnia* are limited by bottom up factors during the spring and clear-water phases. This strongly suggests that the collapse of the *Daphnia* population during the clear-water phase was due to food limitation. However, the top-down factor of predation by fish may also be important.

4.2.1.2 Possible influence of predation on *Daphnia* populations during the clear-water phase

The collapse of the spring *Daphnia* peaks in temperate lakes has been attributed to YOY (young of year fish) predation (Whiteside, 1988; Glicwicz and Pijanowska, 1989). However, Mehner and Thiel (1999) reviewed 18 studies of the impact of 0+ fish on

zooplankton communities and found that control of zooplankton during the spring and early summer was minimal, although significant control of zooplankton communities by 0+ fish was observed during late summer and early autumn. This difference was attributed to the morphological constraints of fish larvae when compared to the improved abilities of the older fish found late in the season. This seasonal pattern of YOY fish predation being low during spring/early summer and increasing in importance during the summer was also found by Romare *et al.*, (1999).

Leuke *et al.*, (1990) also studied the predation impact of fish on zooplankton communities, although this study was based on the feeding of adult fish (*Perca flavescens* and *Coregonus artedii*) rather than juvenile YOY it showed that during the clear-water phase the collapse of the *Daphnia* population could not be attributed to fish predation. However, in July and August fish predation was shown to be responsible for the majority of *Daphnia* mortality. In this case, the seasonal difference was related to temperature, with spring feeding rates of the fish reduced due to low water temperatures. Rudstam *et al.* (1993) also studied the effects of fish predation on zooplankton and found no significant effect of adult fish predation on the *Daphnia* peak during the clear-water phase; it was concluded that the dynamics of the spring *Daphnia* peak was regulated by *Daphnia*-algal interactions rather than by fish predation.

Numbers of potential invertebrate predators (Cyclopoid copepods, *Leptodora*, *Chaoborus*) were also low during the clear-water phase, and no increase in numbers (and so increased predation rates) of these taxa were observed during the decline in *Daphnia* populations. Hence, *Daphnia* mortality was not likely to be caused by invertebrate predation.

Thus, a number of workers have shown that predation both by YOY fish and by adult fish has little influence on the spring peak of *Daphnia* often observed during the clear-water phase. This, combined with the lack of top-down control by invertebrates, and the strong evidence for bottom-up control given above suggests that the spring/clear-water phase *Daphnia* population observed in Rostherne Mere is primarily regulated by the bottom-up control of food availability.

4.2.2 The period of maximum phytoplankton biomass – the summer phase

Numbers of *Daphnia* were continually low during the summer phase of 2000 and 2002, with numbers generally <2 *Daphnia* l^{-1}, with no large zooplankton peaks. Low

numbers of herbivorous zooplankton during the summer phase is often observed in productive lakes despite high phytoplankton biomass, and has been ascribed to both bottom-up and top-down control. Bottom-up control of summer herbivorous zooplankton populations suggests that the high summer biomass of phytoplankton consists of large inedible species, with the biomass of the smaller edible phytoplankton too low to support large populations of zooplankton (Sommer *et al.*, 1986). On the other hand, top-down control suggests that the low numbers are not due to lack of edible food, but to predation of the herbivorous zooplankton by both fish (Luecke *et al.*, 1990) and invertebrate predators such as cyclopoid copepods, *Leptodora* and *Chaoborus* larvae.

4.2.2.1 Influence of food supply on *Daphnia* populations

Evidence from birth rates, brood size and the level of edible food suggest that the low numbers are not due to food limitation. Birth rates were high throughout the summer phase, while brood size was generally >3. The number of gravid adults was generally >40%, again suggesting that food was not limiting.

The concentration of edible carbon was generally above threshold concentrations, although on occasion it did fall below the threshold, suggesting that food limitation may sometimes be important during the summer phase. However, the measure of edible carbon was based on the maximum size of particle that the *Daphnia* can ingest, as given by the Burns' equation (Equation 13, page 42) and from literature evidence for the edibility of some larger species such *Stephanodiscus rotula* and *Asterionella formosa*. *Peridinium*, for example, the dominant phytoplankton during the summer phase was considered inedible. However, subsequent work involving gut analysis of the summer *Daphnia* populations showed that many of the *Daphnia* had ingested *Peridinium* cells. Large *Eudorina* colonies were also observed within *Daphnia* guts, providing further evidence that the *Daphnia* could ingest food particles that are considered inedible when based on the Burns' equation.

Similar considerations apply to other algae. Large numbers of *Aphanizomenon* and *Microcystis* were also observed during the summer-phase, all of which, in this study, have been classified as inedible. However, while the majority of cells or colonies may be unavailable to filter feeding *Daphnia* there is evidence that at least some of the biomass produced may be available as food. Ferguson *et al.* (1982) studied the gut contents of *Daphnia* and found smaller colonies of both *Microcystis*, the size of which were <50μm in diameter. Although smaller than the average size of these species observed in this study (*Microcystis* colonies varied between 40 and 500μm GALD), it

suggests that the *Daphnia* may be able to supplement their diet with smaller *Microcystis* colonies. There is also evidence that filamentous phytoplankton, such as *Aphanizomenon* can be ingested.

The edible food concentrations may therefore be considered the minimum available to the *Daphnia*, as in addition to those species that are considered edible (e.g. *Stephanodiscus hantzschii*, and *Scenedesmus* spp.) the *Daphnia* may be able to supplement their diet with at least some of the larger phytoplankton species.

The lack of a clear distinction between the edible and inedible phytoplankton may explain the lack of correlation between edible biovolume and birth rate, as the measure of edible carbon used in this study may not reflect the quantity of carbon available to the *Daphnia*. If *Daphnia* can eat larger phytoplankton then it may be expected that birth rate would be correlated with total biovolume, yet no correlation was observed. However, the ability to ingest the larger phytoplankton will be dependent on the size of the individual *Daphnia* within the population and the larger phytoplankton will be unavailable to the smaller *Daphnia*. Hence, the birth rate of the smaller *Daphnia* may be influenced more by the biovolume of smaller phytoplankton, while larger *Daphnia* may be influenced by the biovolume of larger species. Because of this, when the birth rate of *Daphnia* is considered as a whole, the correlation with total biovolume may break down.

In 2002 birth rates were also high throughout the summer phases (generally >0.08). Brood size was generally >3 with a high proportion of gravid adults. All these suggest that the zooplankton are not food-limited. However, with the exception of the 7th August and 5th September, when the bloom of *Synechococcus* increased edible carbon levels to well above threshold concentrations, levels of edible carbon were below the threshold, with values ≤0.08µg C ml^{-1}. Despite these low food concentrations, the *Daphnia* did not show any signs of food limitation. However, gut analysis showed that the *Daphnia* were ingesting *Gomphosphaeria*, which by virtue of its large size (colonies ≈100µm diameter) was classed as inedible in this study. The mean size of the *Daphnia* during the summer phase was 1.18mm, which can ingest a particle of approximately 31µm according to the Burns' equation. However, gravid *Daphnia* of approximately 1.25mm in length, which according to Burns should only be able to ingest food particles up to 32µm, were observed with *Gomphosphaeria* colonies of approximately 100µm diameter in their guts. Other workers have also classed cyanobacterial colonies as inedible, Ferguson *et al.*, (1992) considered *Microcystis*

colonies of a similar size to be inedible. It seems that the average sized *Daphnia* during the summer phase can ingest food particles that would generally be considered inedible.

Although edible food concentrations did not correlate with birth rate there is nevertheless evidence that fluctuations in the quantity of edible food affected *Daphnia* birth-rate. The rapid increase in *Synechococcus* on the 7th of August resulted in a rapid increase in birth rate to 0.30 and proportion of gravid adults of 46%. Numbers of *Synechococcus* then declined, with edible carbon falling to below the threshold concentration. Numbers then increased during the late summer phase and into the autumn phase, when edible carbon concentrations were >0.1µg C ml^{-1}. The increased edible carbon resulted in both birth rates and proportion of gravid adults at higher levels than in the summer.

4.2.2.2 Influence of predation on *Daphnia* populations

Evidence from both 2000 and 2002 therefore suggests that food-limitation of the summer *Daphnia* community is unlikely. The possibility that top-down control is important in regulating summer *Daphnia* numbers in Rostherne Mere is discussed below.

The high birth rates observed during the summer-phase did not result in any substantial increase in *Daphnia* numbers. In July 2000 for example, *Daphnia* birth rates were high, with a maximum of 0.28, as was the brood size of the *Daphnia* (max 5). However, this high birth rate did not result in an increase in *Daphnia* numbers, which remained at approximately 2 *Daphnia* l^{-1} during the summer phase. The population increase, r, was therefore approximately 0, suggesting a death rate of a similar level to the birth rate (as d=b-r). Similarly, in 2002 the large increase in birth rate during August (when *Synechococcus* bloomed) to 0.30 only resulted in an increase in *Daphnia* population from 1.2 to 6.7 on the 22nd of August. This also suggests a high *Daphnia* death rate during the summer-phase. As discussed above, the evidence shows that bottom-up control of the *Daphnia* is unlikely, which suggests that the *Daphnia* population during the summer may be controlled by the top-down factor of predation, by either fish or invertebrates.

Fish predation

Fish in Rostherne Mere are represented by perch (*Perca fluviatilis*), roach (*Rutilus rutilus*) pike (*Esox lucius*) (Banks, 1970). Of these, perch is the most common and occurs in large numbers across the lake during the summer months (Goldspink, 1990).

Beside the adult fish there are large numbers of YOY fish present within the Mere, with perch cannibalising these fry during the late summer months. Thus, both juvenile and adult fish may be responsible for predating the zooplankton within Rostherne Mere and preventing any increase in the numbers of *Daphnia* during the summer months. It was discussed above that while fish predation may be of minor importance during the spring the importance of predation by both YOY fish and adult fish increases during the late summer. Mehner and Thiel (1999) reviewed 18 studies of the impact of 0+ fish on zooplankton communities and found that significant control of zooplankton communities by 0+ fish was observed during late summer and early autumn. Romare *et al.,* (1999) also showed control of zooplankton communities by YOY fish during the late summer months. It is known that perch fry are abundant in Rostherne Mere during the summer months (as they are the main component of the diet of adult perch) and they may therefore have a strong effect on summer *Daphnia* numbers. In view of the increase in average *Daphnia* size during the summer months it is interesting to note that 0+ fish often take smaller *Daphnia* which are below the size at which they mature and start carrying eggs (Mehner *et al.*, 1998, Boersma *et al.*, 1996). The preference for smaller prey may be due to the problem of handling the larger prey (Wanzenbock, 1995). Thus, the increase in *Daphnia* size during the summer months is consistent with predation by juvenile fish. This is in contrast to the general view that adult fish predation decreases the size of the zooplankton community through preferential grazing of the larger zooplankton species (Brooks and Dodson, 1965). Furthermore, juvenile percids show a preference for copepods (Guma'a, 1978; Mills *et al.*, 1984), which may explain the very low copepod numbers during 2002; however, this does not explain the increase in copepod numbers during the summer of 2000.

Predation by adult fish may also be important. Luecke *et al.*, (1990) studied the eutrophic Lake Mendota, Wisconsin, and observed a pattern very similar to the situation observed in Rostherne Mere during this study. A spring peak of *Daphnia* was reduced through food limitation, while during the summer period numbers of *Daphnia* remained at low levels throughout the summer months despite high birth rates. Luecke showed that predation by adult fish (perch and cisco (*Coregonus artedii*)) was sufficient to keep *Daphnia* populations at a low level during the summer period.

Hence a similar pattern may be occurring in Rostherne Mere, and the low numbers of *Daphnia* during the summer months (despite a high birth rate) may be due to predation by fish, either adults or juvenile YOY. However, in the absence of any data

on the fish populations during the period of this study the effect of fish predation on the *Daphnia* community cannot be established. However, the low *Daphnia* numbers, despite the high summer birth rate, suggests that the summer *Daphnia* population is being predated and predation by both juvenile and adult fish may be important. However, as discussed in the next section, invertebrate predation may also be significant.

Invertebrate Predation

The increase in average *Daphnia* size during the summer months suggests that the smaller *Daphnia* are being preferentially predated. As invertebrate predation can successfully eliminate smaller zooplankton (Zaret, 1980) this suggests predation by invertebrates may be important.

In 2000, cyclopoid copepods increased in numbers during the summer phase. Cyclopoid copepods may be important in reducing the summer *Daphnia* population as they have been shown to actively predate on *Daphnia*, and show a preference for small *Daphnia* (Gliwicz and Ummana, 1994), and this would account for the observed increase in the size of the summer *Daphnia* population. In 2002 however, numbers of cyclopoid copepods were very low throughout the summer, so are unlikely to be important. Predation on the *Daphnia* could also be due to *Leptodora*. Numbers of *Leptodora* were not quantified during this study, although numbers were low.

Chaoborus larvae were present at Rostherne Mere in both years. In 2000 they were present at a maximum of ≈10 *Chaoborus* m^{-3} and may have been important in predating *Daphnia*. However, they may have been more important during 2002 when *Chaoborus* larvae increased rapidly during the summer phase to reach higher numbers than in 2000, with a maximum of ≈55 *Chaoborus* m^{-3}. In 2002, numbers of *Chaoborus* reached a late summer maximum of 54 individuals m^{-3}. It is important to consider if these numbers of *Chaoborus* are high enough to account for the observed effect on *Daphnia* numbers. It has been estimated that *Chaoborus* account for one crustacean zooplankter per hour (Kajak and Ranke-Rybicka, 1970). In one day they could consume approximately 1300 zooplankters m^{-3} or 1.3 zooplankters l^{-1}. Numbers of *Daphnia* during the summer phase were often <2 *Daphnia* l^{-1} so it is feasible that *Chaoborus* predation may have a strong effect on the summer *Daphnia* population in Rostherne Mere. *Chaoborus* have been shown to selectively predate smaller *Daphnia*, which may explain the increased *Daphnia* body size during the summer. It has also been shown that *Chaoborus* preferentially seek copepods over *Daphnia* (Swuste *et al.*, 1973); the

reduced numbers of summer copepods in 2002 may therefore also be due to the large numbers of *Chaoborus* present, although other factors such as food limitation must also be considered.

4.2.3 Autumn/winter phase

4.2.3.1 Influence of food supply on *Daphnia* populations

In 2000 there was an increase in brood size from 0 in early October to >6 in late October/early November. Birth rate also showed an increase in October, from 0 to 0.15. The increased zooplankton productivity at this time may be responsible for the increased *Daphnia* numbers in December, when numbers increased to ≈12 *Daphnia* l^{-1}. The high brood size and increased birth rate, followed by an increase in *Daphnia* numbers is similar to the spring-phases of both years. However, whereas during the spring phase the increase in zooplankton productivity coincided with an increase in food to above the threshold limiting concentration, the increase in the late autumn occurred when food concentrations were approximately 0.03µg C ml^{-1} less than the threshold concentration. The increased productivity of the *Daphnia* coincided with the enlargement of the epilimnion and the return of isothermal conditions. In Rostherne Mere the end of stratification and epilimnetic enlargement in autumn may lead to a re-establishment of diatom populations, or alternatively to the establishment of volvocales (Reynolds, 1976, 1978a) and these would theoretically provide the food source necessary for the increased *Daphnia* productivity. However, the only species that increased during the end of stratification were the small pennate diatoms, the quantity of which, along with other edible species, were below the threshold concentration required for increased *Daphnia* production. However, as sampling during the late autumn of 2000 was carried out approximately every 3 weeks it is possible that sampling missed a brief increase in diatom numbers that may have provided the necessary food source to facilitate the increase in *Daphnia* birth rate/brood size and numbers. However, despite the lack of any observed increase in the quantity of food for the zooplankton the increased productivity, and increased numbers, of the *Daphnia* suggests the availability of a suitable food source.

Similarly, in 2002, there was also an autumn increase in the numbers of *Daphnia*, peaking in late October. This increase was likely due to a high autumn birth rate resulting from the large numbers of *Synechococcus* present during the autumn phase, giving edible food concentrations of >0.1µg C ml^{-1}.

What is interesting about the autumn/winter rise in *Daphnia* numbers is that the increase actually did occur. During the summer phases there was only minimal increases in *Daphnia* numbers, despite high birth-rates, and this lack of increase was ascribed to predation pressure. The fact that increases in numbers of *Daphnia* did occur during the autumn and winter (despite lower birth rates than during the summer) suggests an autumn reduction in predation. It is not possible to say certainly if this is the case without detailed knowledge of the potential predators. In terms of invertebrate predators, during the autumn numbers of both cyclopoid copepods and *Chaoborus* were reduced, resulting in a decrease in predation on the *Daphnia* from invertebrate predators. Data on the gut contents of perch (Goldspink and Goodwin, 1979) also suggests that fish predation on *Daphnia* may be reduced during the late autumn/winter. Fish predation may also be reduced due to the cold temperatures, Lueke *et al.*, (1990), for example, found that feeding rates of cisco (*Coregonus artedii*) were low at temperatures <12°C, allowing *Daphnia* populations to increase.

4.2.4 Summary of the factors influencing *Daphnia* populations in Rostherne Mere

Table 4.4 summarises the factors influencing *Daphnia* over the annual cycle. It can be seen from the above discussion that the principal factors influencing *Daphnia* population dynamics change over the annual cycle, with *Daphnia* influenced primarily by bottom-up factors of food availability during the spring and clear-water phase, by top-down factors during the summer, and a return to the food availability in autumn/winter.

Phase	Proposed controlling factors for *Daphnia*
Winter/Spring	Bottom-up control of food availability is suggested by an increasing birth rate and brood size of the zooplankton. Further evidence comes from the concentration of edible carbon which increased to above the threshold concentration in parallel with the increase in birth rate / brood size.
Clear-water Phase	Bottom-up control of food availability suggested by decreasing birth rates, indicating low food availability. Further evidence came from the quantity of availability of edible carbon, the fall of which to below the threshold concentration coincided with the decrease in birth rates, leading to a decline in *Daphnia* numbers.
Summer Phytoplankton Maximum	Top-down control strongly suggested by low *Daphnia* numbers despite high birth rates, which suggests a high mortality rate due to predation. Edible food generally above threshold concentrations, although below in early summer 2002. However, gut analysis showed large, generally considered inedible, phytoplankton (*Peridinium*, *Gomphosphaeria*) in guts, suggesting food was not limiting.
Autumn Phase	Bottom-up control suggested by increase in birthrate / brood size, resulting in an increase in *Daphnia* numbers. The increase in *Daphnia* suggests a relaxation in predation pressure when compared to the summer phase, resulting in *Daphnia* being primarily regulated by food availability.

Table 4.4: Summary of the principal factors influencing zooplankton population dynamics in Rostherne Mere during 2000 and 2002.

4.3 Planktonic Bacteria in Rostherne Mere

The aim of this section is to examine seasonal fluctuations in bacterial numbers in Rostherne Mere and to relate these changes to the factors that influence bacterial growth and population size. Bacteria may be limited by bottom-up factors such as the availability of organic substrates and inorganic nutrients (particularly phosphorus), and by environmental parameters such as temperature and light. Factors that may be considered top-down include predation and viral attack.

4.3.1 Measurement of bacterial populations – total counts v viable counts

The measurement of bacterial populations by plating onto media gives a measure of the viable counts. Whatever growth medium is used it will always exert selective pressures for specific bacteria (Jones, 1970) and only a proportion of the bacterial population will therefore grow. The size of this proportion is also influenced by other factors such the incubation time and temperature (Jones, 1979). Because of these limitations, viable counts underestimate natural, heterogeneous, bacterial populations by factors of 10^2-10^5 (Wetzel, 2001). Jones (1977) found that viable counts were approximately 0.25% of the total count. In Rostherne Mere viable counts during 2000 generally underestimated total counts by a factor of 10^3. Because of the problems with viable counts bacterial populations are now estimated by direct microscopic observation which give a much better estimation of the total numbers of bacteria. (Porter and Feig, 1980). In this study, both viable and total counts were determined during 2000, but in 2002 only total counts were performed. In view of the fact that total counts give a much better representation of the numbers of bacteria within the water the following discussion is primarily concerned with total bacteria.

4.3.2 Growth factors and bacterial populations in Rostherne Mere

To prevent repetition, as would occur if each phase was examined separately the discussion below does not look at each phase in turn but considers factors that affect bacteria and how these factors may operate at different times over the seasonal cycle.

4.3.2.1 Sources of organic substrates for bacterial growth

In order to determine that factors that may be important in regulating the populations dynamics of bacteria, correlation analysis was carried out between total bacterial numbers and possible sources of organic growth substrates (Table 4.5)

	Chl-a	DOC	Colour
Bacteria 2000	0.786** (n=26)	ns	nd
Bacteria 2002	0.627** (n=20)	ns	0.488* (n=21)

Table 4.5 Pearson correlations between total bacterial numbers and factors that may potentially limit bacterial numbers. Correlations carried out over whole sampling season. * - $P \leq 0.05$, ** - $P \leq 0.01$, ns- not significant, nd- not done.

Phytoplankton (chlorophyll-a)

There are two main ways in which phytoplankton can provide an organic substrate for bacterial growth. Firstly, phytoplankton can provide an organic substrate for bacterial growth via the release of extracellular dissolved organic compounds, which results in a positive correlation between bacterial growth and algal production (Cole *et al.*, 1988). Alternatively, the phytoplankton can release organic material during cell lysis and death in which case the bacterial peaks occur during periods of algal decline and decomposition (Straskrabova, 1975, cited in Wetzel, 2001). In this case, increases in bacterial populations can follow phytoplankton maxima by many days or weeks (Straskrabova and Komarkova, 1979). No correlation may suggest other factors, for example, nutrient availability or grazing are the primary influence on the bacteria.

Algal exudates

In 2000, bacterial numbers and chlorophyll-a were correlated over the whole season, with fluctuations in bacterial biomass mirroring the changes in phytoplankton biomass. There was no observable phase shift between the peaks of phytoplankton and bacteria, strongly suggesting algal exudates provide the organic substrate for bacterial growth. In 2002, there was a correlation until mid-summer when the correlation broke down, possibly due to other limiting factors (discussed in section 4.3.2.2).

The correlation between phytoplankton biomass and bacterial numbers suggests that the main source of carbon for the bacteria within Rostherne Mere is algal exudates. Various workers have attempted to quantify the importance of algal exudation to bacterial production, with the fraction of bacterial carbon that can be met by algal exudates release varying between 4 and >100% (Riemann *et al.*, 1982; Bell and Kuparinen, 1984). The importance may also be dependent on the productivity of the lake, Cole *et al.*, (1982) for example, showed that algal exudation supported approximately 33% of bacterial production in an oligotrophic lake while Bell *et al.*, (1983) found up to 80% of bacterial production in a eutrophic lake was due to algal exudation. Wetzel (2001) suggests that >95% of the carbon for bacterioplankton can be

provided by algal exudates. On the other hand, Baines and Pace (1991) reviewed a number of studies and suggested that algal exudation generally provides less than half of the bacterial carbon requirements. The gross quantity of algal exudates increases markedly with increasing lake eutrophication (Wetzel, 2001), it may therefore be expected that in the highly eutrophic Rostherne Mere the gross quantity of exudates released into the water column are high. This, and the close correlation between phytoplankton and bacteria suggests that within Rostherne Mere the bacteria are limited by phytoplankton exudation, which is the classic explanation for seasonal variations in bacterial numbers (Cole *et al.*, 1988). However, other sources of carbon may be important; these include organic material released during phytoplankton cell lysis and death.

Cell lysis and death

An important source of carbon for bacterial growth may be by lysis and death of phytoplankton cells (Fuhrman *et al.*, 1980), in which case it may be expected that bacterial abundance would be higher when cells die during the crash of an algal bloom. Increases in bacterial biomass following the collapse of a phytoplankton bloom has been observed in other eutrophic systems, for example Coveney *et al.*, (1977), observed two large bacterial peaks in biomass, which followed the collapse of the spring and summer algal blooms respectively while Hadas and Berman (1998) observed maximum bacterial numbers during the decline of a *Peridinium gatunense* bloom. In this study, cell lysis and death may be expected to be particularly important immediately after the collapse of the large summer phytoplankton blooms. However, no peak of bacteria followed the late summer peak in chlorophyll-a in either 2000 or 2002, which suggests that the DOC released through phytoplankton cell lysis did not result in an increase in bacterial biomass. Nor did any increase in bacterial numbers follow the collapse of the spring bloom. The only increase in bacterial numbers following a decline in phytoplankton was in 2000 when viable counts did show an increase during late August, to reach a maximum of 3.4×10^3 CFU ml^{-1} in late September. In 2002, no increase in bacterial numbers was observed following the collapse of the *Gomphosphaeria* bloom, when bacterial numbers decreased ahead of the decrease in the phytoplankton, however, as will be discussed later, the relationship may have been modified by other limiting factors.

Other autochthonous sources – zooplankton and macrophytes

Bacteria may also utilise other sources of organic material, including that released by grazing zooplankton which have been shown to release dissolved organic matter into the water column through both sloppy feeding (Lampert, 1978) and egestion products (Olsen *et al.*, 1986). Olsen *et al.*, (1986) estimated that approximately 20% of egestion products of cladocerans are released as dissolved compounds that are readily ingested by bacteria. Grazing by rotifers and protozoa may also be presumed to lead to the release of organic compounds. However, no increase in DOC was observed during the period of maximum grazing and zooplankton biomass (i.e. the clear-water phase in this study). It could be argued that the released DOC was rapidly incorporated into the bacteria before it could accumulate in the water column; however, there was no increase in bacterial numbers in 2000, while in 2002 numbers of bacteria fell rapidly during the clear-water phase. Furthermore, no correlation between bacterial numbers and zooplankton filtering rate / zooplankton numbers was observed. Thus although zooplankton in Rostherne Mere may be presumed to release readily utilisable organic material both through 'sloppy feeding' and egestion this does not seem to have any great influence on bacterial dynamics.

Another autochthonous source of organic material is littoral aquatic plants (Hough and Wetzel, 1975). These are most important in small and shallow lakes, where the littoral sources of carbon can exceed those due to phytoplankton. However due to steeply sloping sides and its depth, the littoral zone of Rostherne Mere is restricted to a small area bounding the lake. Within Rostherne Mere the quantity of organic material released by littoral plants is therefore likely to be negligible when compared to the very high biomass of phytoplankton.

Allochthonous sources of carbon

An attempt was made to quantify the quantity of humic material in the lake by measuring the colour of the water (Cuthbert and Giorgio, 1992, Pace and Cole, 2002). It may be expected that DOC in the inflow to the lake would consist primarily of humic material derived form higher plants within the catchment area. However, no correlation between DOC and colour for the inflow was observed. This may be due to the DOC within the inflow consisting of non-humic material; alternatively, the methodology used may not give an accurate measure of humic material within the water. For example, colour was positively correlated with chlorophyll-a, which suggests that the large

phytoplankton biomass within Rostherne Mere interfered with the measurement of colour.

However in view of the high phytoplankton biomass in the Mere, allochthonous sources of DOC are likely to be of low importance in providing organic substrates for bacteria, particularly as the allochthonous DOC is likely to consist of high molecular weight, recalcitrant compounds that are poorly utilised by bacteria.

Seasonal variation in dissolved organic matter

If bacterial growth is dependent on the presence of an organic substrate then a correlation between bacteria and DOC may be expected. However, no correlations with DOC were observed during 2000 and 2002. Nor did DOC show any distinct seasonal pattern in either year, ranging between 4 and 6 mg l^{-1} in summer 2000, and 7 and 8 mg l^{-1} in 2002. The difference between the absolute concentrations during the two years may be due to the different preservation methods of the water samples; in 2000 samples were frozen before analysis, while in 2002 samples were acid preserved. The lack of any obvious seasonal pattern in DOC is typical for lentic water bodies, where seasonal changes are often indistinct, with small ranges (Burney, 1994).

This relatively constant DOC pool suggests it is not utilised by the bacteria, otherwise seasonal variation in DOC would be seen to occur. However, a large proportion of the DOC in lakes is dominated by humic and fulvic acids, derived from the decay of higher plants, and often washed in from the catchment area (Wetzel, 2001). These organic substrates are used at a much slower rate than carbohydrates, proteins and other labile carbon substrates derived from the phytoplankton (Wetzel, 2001). It is possible that the relatively steady pool of DOC observed in Rostherne Mere consists of humic and fulvic acids, which are degraded at a slow rate, and that fluctuations in the numbers of bacteria are related to the availability of rapidly utilisable labile organic compounds released by the phytoplankton. Carbon released by phytoplankton is labile and is rapidly utilised by bacteria (Cole *et al.*, 1982) while much bacterial metabolism is strongly coupled to the availability of labile, rapidly utilisable substrates such as carbohydrates and amino acids, which have high turnover rates. Thus, the indistinct seasonal pattern in DOC may be due to rapid bacterial uptake of labile carbon, and this rapid uptake prevents any accumulation of DOC within the water column. Accumulation of DOC in surface waters may only be expected to occur when bacterial utilisation of carbon is restricted and consumption is unable to match release, due to food web mechanisms controlling growth and biomass of bacteria. Important

mechanisms are predation, nutrient limitation and temperature limitation (Thingstad and Hagstrom, 1997).

4.3.2.2 Other factors influencing bacterial growth

Nutrients

A number of studies have indicated that the bacterioplankton may be restricted by nutrient availability, particularly phosphorus (Coveney and Wetzel, 1992; Watanabe, 1996; Morris and Lewis, 1992). Table 4.6 shows correlations of the nutrient fractions measured in this study with total bacterial numbers.

	SRP	TDP	TPP	TP	NO_x	TDN	TPN	TN
Bacteria 2000	-0.794** (n=20)	-0.808** (n=21)	0.436* (n=26)	-0.498** (n=21)	-0.645** (n=21)	-0.524* (n=19)	0.585** n=19	ns
Bacteria 2002	-0.728** (n=21)	-0.689** (n=21)	ns	-0.676** (n=20)	-0.507* (n=20)	-0.555** (n=21)	ns	-0.648**

Table 4.6 Table to show Pearson correlations between total bacterial numbers and factors that may potentially limit bacterial numbers. * - $P \leq 0.05$, ** - $P \leq 0.01$, (ns- not significant).

It is evident from the table that bacteria correlate with almost all of the nutrient fractions. However, the correlations are likely to be a result of the close correlation between chlorophyll-a and total bacteria, rather than through any cause and effect relationship between bacteria and nutrients (correlations between chlorophyll-a and the nutrient fractions shows the same pattern of correlations). Thus, the correlations between bacteria and nutrients are likely to be indirect, and due to the strong correlation between bacteria and chlorophyll-a, rather than any 'real' relationship between bacteria and the availability of nutrients. Correlation analysis is therefore of limited value in determining possible effects of nutrient limitation on bacterioplankton. To gain an insight into the likely effect of nutrients on the bacterioplankton it is more instructive to look at the absolute values of nutrients, and whether these are at a level at which the bacterioplankton may be nutrient limited.

In the summer of 2002, levels of soluble reactive phosphorus fell to concentrations that are considered limiting for phytoplankton. Levels fell to 3 $\mu g l^{-1}$ on the 7th of August and generally remained less than, or close to this level until October. Bacteria have been shown to have substantially higher phosphorus requirements than phytoplankton (Currie and Kalff, 1984) and it is therefore feasible that bacteria were also phosphorus-limited at this point. Morris and Lewis (1992) showed that P limitation was important in a mesotrophic lake in which both SRP and dissolved organic phosphorus concentrations ranged between 0.2 and 3$\mu g\ l^{-1}$, similar to the minimum

concentrations measured during the summer of 2002. Nutrient limitation may lead to the correlation between chlorophyll-a and bacterial numbers breaking down. The only time that the correlation broke down during this study was during the summer of 2002 when despite the rising concentration of chlorophyll-a, bacterial numbers remained steady before decreasing. Table 4.7 shows the correlations between chlorophyll-a and bacterial numbers in Rostherne Mere during 2002. It can be seen that although there is a positive correlation over the whole sampling season, and during the winter and spring phases, no correlation was found over the summer and autumn phases.

Bacteria	Chlorophyll-a
Whole sampling season	0.627** (n=20)
Winter/spring and clear-water phase	0.797** (n=11)
Summer/Autumn Phase	0.110 ns (n=9)

Table 4.7: Table to show correlations (Pearson) between chlorophyll-a and total bacteria for the whole of 2002; the early part of 2002 (up to the end of the clear-water phase); and during the period of maximum phytoplankton biomass (the summer and autumn phases). * - $P \leq 0.05$, ** - $P \leq 0.01$, (ns- not significant).

The constant bacterial biomass coincided with soluble reactive phosphorus falling to the lowest concentrations recorded in both 2000 and 2002 (3 μgl^{-1} on the 7th of August). It is therefore possible that bacterial numbers were reduced due to phosphorus limitation. However, with the data available it is not possible to say with any certainty whether this is the case. The fall in bacterial numbers may be due to other factors, i.e. grazing or viral attacks which are discussed in section 4.3.3.

Physical parameters – temperature and pH

Total bacterial numbers were positively correlated with temperature in both years. However, the correlation between temperature and bacterial numbers may be indirect. The effect of temperature on metabolism and the physical structure of the environment (stratification) can lead to temperature correlating with factors with which there is no true cause and effect relationship (Morris and Lewis, 1992). Table 4.8 shows correlations analysis between bacteria and temperature.

	Temp
Bacteria 2000	0.769** (n=22)
Bacteria 2002	0.722** (n=21)

Table 4.8: Table to show correlation coefficients (Pearson) between total bacteria and temperature in 2000 and 2002. * - $P \leq 0.05$, ** - $P \leq 0.01$, (ns- not significant).

Although there is evidence that at water temperatures <10-15°C bacterial growth is positively correlated with temperature (Scavia and Laird, 1987, Ochs *et al.*, 1995); at

higher temperatures other factors are important such as the availability of nutrients and particularly organic substrates (Felip *et al.*, 1996). As temperatures during the majority of the growing season in Rostherne Mere were higher than 10-15°C temperature is unlikely to be a major factor in regulating bacterial numbers. Temperature may be expected to be more important during the spring, when water temperatures are low, however there is no evidence for this. For example, during the early part of 2002 (until the end of the clear-water phase), despite temperatures remaining <15°C, there was no correlation between bacteria and temperature. In fact, temperature seemed to have little effect on the bacterial biomass, with the rapid increase and peak in bacterial numbers occurring at approximately 11°C, and correlated closely to changes in chlorophyll-a.

Extremes of pH have been shown to affect bacteria, for example bacterial production is affected by pHs in excess of 10 (Jeppesen *et al.*, 1997). In this study, the pH at Rostherne Mere did not exceed 9.3 and it is therefore unlikely that pH affected bacterial numbers.

4.3.3 Possible losses of bacteria through grazing and viruses

The effect of top-down factors on the bacteria in Rostherne Mere may be low. Wetzel (2001) mentions that growth (i.e. bottom-up factors) of bacterial populations are often evenly balanced by mortality (i.e. top-down factors) and that this often leads to little seasonal variations in bacterial numbers. In Rostherne Mere there were large seasonal variations in bacterial numbers for much of the season, and these seasonal variations were strongly correlated to the bottom-up factor of chlorophyll-a. The fact that the increased bacterial growth rates resulted in increasing bacterioplankton populations suggests that loss factors, such as grazing and viral attack may have a low impact in regulating the fluctuations in bacterial numbers in Rostherne Mere. If top-down factors were more important then seasonal fluctuations in bacterial numbers may be expected to be much less. This is because increased growth rates, due for example to increasing availability of algal exudates, may not lead to increases in numbers due to strong top-down control. Thus, a clear correlation with chlorophyll-a may not be observed. The fact that large seasonal variations in bacterial numbers were observed, as was a strong correlation with chlorophyll-a, suggests that bottom-up factors are of primary importance in regulating bacterial numbers in Rostherne Mere. However top-down factors may be important at certain times in the season, for example, when the correlation between bacteria and chlorophyll-a broke down in the summer of 2002, or during the clear-water phase of that year.

4.3.3.1 Grazing

Bacteria are grazed by cladocerans (Geller and Muller, 1981; Porter *et al.*, 1983, Brandelberger, 1991), ciliated protozoa (Fenchel, 1987), rotifers (Ooms-Wilms *et al.*, 1995) and heterotrophic nanoflagellates (HNF's). It is now recognised that heterotrophic nanoflagellates dominate grazing on bacteria (Sanders *et al.*, 1989, Wetzel, 2001), although at certain times of years the other grazers may be important.

In this study, ciliated protozoa were positively correlated with bacterial numbers suggesting that ciliate numbers are directly related to the availability of a bacterial food supply, and may be feeding on the bacteria. However, ciliate numbers were also positively correlated with chlorophyll-a (Table 4.9).

Correlation of ciliated protozoa with	Bacteria	Chlorophyll-a
2000	0.636** (n=26)	0.648** (n=29)
2002 (spring-clear-water phase only) No correlation observed during summer/autumn phases or overall	0.749** (n=11)	0.905** (n=11)

Table 4.9: Pearson correlations of ciliate protozoa with bacteria and chlorophyll-a. * - $P \leq 0.05$, ** - $P \leq 0.01$, (ns- not significant).

A number of studies have shown a strong positive correlation between ciliates and chlorophyll-a both within, and between lakes (Wiackowski *et al.*, 2001; Beaver, 1982). Ciliates have been shown to feed on both bacteria and phytoplankton (Fenchel, 1987; Finlay *et al.*, 1988). However, ciliated protozoa of the size observed during this study (ca. 30μm) have a range of food particle size of 0.2-1μm (Wetzel, 2001). Thus, although chlorophyll-a and ciliated protozoa correlate, the majority of the phytoplankton biomass is unavailable as food. Bacteria are available as food however, and it is possible that the positive correlation between ciliated protozoa and bacterial numbers is due to a real relationship between ciliates and their bacterial food source. Hence, the correlation between ciliates and chlorophyll-a observed in this study may simply be an indirect one, resulting from the correlation between ciliates and bacteria. However, although ciliated protozoa may be feeding upon the bacteria there was no inverse relationship between bacterial numbers and ciliates (the correlation was positive), which suggests that ciliates had little effect on fluctuations in bacterial numbers.

Rotifer numbers in 2002 were correlated with bacteria numbers (Table 4.10). However, rotifers utilise both bacteria and small algae and the correlation may be an

indirect correlation resulting from the positive correlation between rotifers and chlorophyll-a.

Correlation between Rotifers and Bacteria	
2002 Overall	0.492* (n=17)
2002 (Jan-July)	0.786* (n=7)
2002 (July-Nov)	0.666* (n=10)

Table 4.10: Pearson correlations of rotifers with bacteria. * - $P \leq 0.05$, ** - $P \leq 0.01$, (ns- not significant).

As with ciliated protozoa, even if rotifers are only feeding upon bacteria there was no inverse relationship between bacterial numbers and rotifers (the correlation was positive), which suggests that rotifers had little effect on fluctuations in bacterial numbers. Furthermore, the filtration rate of rotifers was very low, ranging from <1% to a maximum of 4% of the water volume per day (see page 184) giving losses due to grazing of approximately 0.01 day^{-1} and 0.04 day^{-1}. As the potential maximum growth rate of bacteria is >1 day^{-1} (Wetzel, 2001) potential losses from grazing therefore did not reach the levels at which the grazing could cause fluctuations in bacterial numbers.

Grazing of bacteria by cladocerans (e.g. *Daphnia*) generally does not significantly impact on bacterial populations, although it can substantially reduce bacterial populations when their filtering rates are particularly high, as sometimes occurs during the clear-water phase (Wetzel, 2001). In this study, *Daphnia* grazing may have impacted on the bacterial population during the clear-water phase in 2002 when the fall in bacterial numbers paralleled the phytoplankton. Although the reduction in bacterial numbers at this time may have been due to a reduction in the availability of phytoplankton exudates, the reduction in bacterial biomass may also be due to the high grazing pressure, as minimum bacterial numbers corresponded with maximum grazing rates, as well as minimum phytoplankton and rotifer biomass. Thus, the high grazing pressure may have reduced the numbers of all these biota. For the majority of the growing season however, the grazing rate of *Daphnia* was low, and may have little impact on bacterial numbers.

Thus, grazing by ciliates and rotifers seems to have little impact on the fluctuations in bacterial biomass and, with the possible exception of the clear-water phase in 2002, *Daphnia* grazing also seems to have little effect on the fluctuations in bacterial numbers. This is in agreement with other work that has studied the effect of grazing on bacteria. Sanders *et al.*, (1989) studied grazing in the eutrophic Lake Oglethorpe (USA) and found that grazing by rotifers and ciliates accounted for between

3 and 11% of the total grazing on bacteria, while cladocerans accounted for <1%. In Lake Constance (Gude, 1986; Simon *et al.*, 1998a) daphnids accounted for 9-12% of bacterial mortality, while ciliates accounted for between 14 and 19%. In both of these lakes bacterivory was dominated by heterotrophic nanoflagellates, which accounted for 49-81% of the grazing in Lake Oglethorpe and 52-68% of bacterial mortality in Lake Constance. As heterotrophic nanoflagellates were not monitored in this study it is impossible to assess their importance in influencing bacterial dynamics in Rostherne Mere. However, they may be expected to dominate the top-down factor of grazing for the majority of the season.

4.3.3.2 Viruses

Viral-induced mortality of bacteria is well known, and can account for a substantial fraction of the bacterial mortality (Wommack and Colwell, 2000; Hennes and Simon, 1995). For example, over an annual period Simon *et al.*, (1998a, b) estimated viral mortality to range between 1 and 24% of total bacterial mortality. The bacteria within Rostherne Mere will suffer losses through mortality due to viral infection, although the extent to which this occurs cannot be predicted from the data collected during the present study. However, although bacteria will be subject to losses from grazing and viral attack, the positive correlation between bacterial numbers and chlorophyll-a, and the possibility of phosphorus limitation when the correlation broke down suggests bottom-up control is the most important factor in regulating bacterial numbers.

4.3.4 Summary of the factors influencing bacterial dynamics in Rostherne Mere

Table 4.11 summarises the importance of the various factors influencing the bacterioplankton population dynamics in Rostherne Mere. However, unlike the tables summarising the factors affecting phytoplankton and *Daphnia*, which were divided according to phases, Table 4.11 is split into the various factors that may influence bacterioplankton population dynamics. The rationale for this is that factors influencing bacteria did not show any obvious seasonal variation between phases.

Potential abiotic and biotic factors influencing bacterial numbers	Evidence for the importance of the factor upon bacterial numbers
Bottom-up - organic substrates	Strong positive correlation between chlorophyll-a and bacterial numbers suggests bottom-up control, particularly through the availability of algal exudates.
Bottom-up – nutrients, temperature, pH	Break-down of strong correlation between bacterial populations and chlorophyll-a during the summer of 2002 suggests other controlling factors important. Very low concentrations of P, for extended period suggests phosphorus limitation. Other factors of minor importance - pH below levels influencing bacterial growth and temperature generally above that which limits bacterial growth.
Top-down - grazing by Cladocera, rotifers and ciliates	With the exception of the clear-water phase in 2002, when the minimum of bacterial numbers coincided with maximum the *Daphnia* grazing rate, grazing by these taxa is of little significance.
Top-down - grazing by HNF's, and viral attack	Effects of heterotrophic nanoflagellates and viral attack were not investigated in this study. Literature evidence suggests that they are most important top-down factors influencing bacteria, however in this study wide seasonal variation in bacterial numbers and strong coupling to chlorophyll-a suggests that top-down effect of these factors is low.

Table 4.11: The importance of various factors acting upon the bacterial populations in Rostherne Mere during 2000 and 2002.

4.4 Trophic status of Rostherne Mere

The following section examines the current trophic status of Rostherne Mere, and investigates the extent to which nutrient concentrations within the lake have changed in recent years. In the determination of the trophic status of the Mere a number of different methods of classifying trophic status are considered, the Organisation for Economic Cooperation and Development (OECD) scheme, the TGL27885/01 scheme, formerly used in the former German Democratic Republic, and also by an investigation of phytoplankton seasonal succession.

4.4.1 OECD Classification

The Organisation for Economic Cooperation and Development fixed classification system (Ryding and Rast, 1989, after OECD, 1982) classifies lakes according to the maximum and annual mean chlorophyll-a concentrations, the minimum and annual mean Secchi depth transparency and the annual mean total phosphorus concentrations. Table 4.12 shows the boundary values for each trophic classification, and the values of each of the classification parameters obtained during the current study.

Trophic Category	Mean TP ($\mu g\ l^{-1}$)	Mean Chl ($\mu g\ l^{-1}$)	Max Chl ($\mu g\ l^{-1}$)	Mean Secchi (m)	Min Secchi (m)
Ultra-oligotrophic	<4.0	<1.0	<2.5	>12.0	>6.0
Oligotrophic	<10.0	<2.5	<8.0	>6.0	>3.0
Mesotrophic	10-35	2.5-8	8-25	6-3	3-1.5
Eutrophic	35-100	8-25	25-75	3-1.5	1.5-0.7
Hypertrophic	>100	>25	>75	<1.5	<0.7
Rostherne Mere 2000	230 (H)	28 (H)	159 (H)	2.09 (E)	0.93 (E)
Rostherne Mere 2002	136 (H)	32 (H)	92 (H)	2.20 (E)	0.80 (E)

Table 4.12: OECD boundary values for trophic classification system (from Ryding and Rast, 1989, after OECD 1982), with corresponding values for Rostherne Mere in 2000 and 2002. Letters in brackets give the lake classification based on the particular parameter – E=eutrophic and H=hypertrophic.

It is evident from the above that Rostherne Mere is classified as eutrophic according to Secchi depth while it is classified as hypertrophic according to chlorophyll-a and total phosphorus. The lower classification according to Secchi depth may be due to the fact that Secchi depth is very sensitive to biomass changes at low concentrations of algal biomass, but insensitive at high concentrations (Carlson, 1977). Hence, the very high phytoplankton biomass in Rostherne Mere may reduce the accuracy of the classification based on Secchi depth. Thus, according to the OECD

scheme the classification based on TP and chlorophyll-a may be a truer reflection of the trophic state of Rostherne Mere, classifying the lake as hypertrophic.

4.4.2 Classification according to TGL27885/01

A second method of classification is that based on a technical standard originally used in the German Democratic Republic (Ryding and Rast 1989, after Technical Standard, 1982). This scheme is much more detailed than the OECD classification and evaluation of water quality can be based on three classes of criteria, namely hydrographic and territorial criteria; trophic criteria; and salt content/hygienically relevant criteria. The data collected during this study relates to the trophic criteria, and the analysis below is therefore based on this criterion only.

The trophic criteria are based on three subdivisions - oxygen balance, nutrient budget and bioproduction. The oxygen criteria require knowledge of diurnal variations in oxygen saturation, data that was not collected in this study. However, it is possible to classify the lake according to nutrient concentrations and bioproduction parameters.

The classifications according to nutrient budgets uses mean epilimnion values of SRP, TP and DIN during what is referred to as 'the stagnation period in summer' (Ryding and Rast, 1989). The meaning of this is not clear, but in this study it has been interpreted as encompassing the start of the summer phase to the end of October when the autumn overturn occurred. However, the precise nature of the period over which values were averaged does not seem to be critical as the boundaries for each classification are wide. Thus the inclusion of extra sampling points in the averaging process is unlikely to change the classification. Table.4.13 shows the classification boundaries according to this scheme, together with the values obtained in Rostherne Mere during 2000 and 2002.

Trophic Category	TP (mg P l^{-1})	SRP (mg P l^{-1})	DIN (mg N l^{-1})
Oligotrophic	≤0.015	0-0.002	≤0.01
Mesotrophic	≤0.04	0-0.005	≤0.03
Eutrophic	0.04-0.3	0-0.1	≤0.1
Polytrophic	>0.3	>0.1	>0.1
Hypertrophic	>0.5	>0.5	>0.5
Rostherne 2000	0.19 (E)	0.05 (E)	0.48 (H)
Rostherne 2002	0.106 (E)	0.027 (E)	0.54 (H)

Table.4.13: Table to show trophic classification based on total phosphorus (TP), soluble reactive phosphorus (SRP) and dissolved inorganic nitrogen (DIN) according to TGL27885/01. Values are the mean value for epilimnion for the summer stagnation period.

It can be seen that this scheme classifies Rostherne Mere as eutrophic according to phosphorus concentrations, but hypertrophic according to dissolved inorganic nitrogen. The high classification according to nitrogen reflects the high concentration of nitrates within Rostherne Mere. The use of the DIN classification is only if nitrogen is the limiting nutrient, however during this study the limiting nutrient was phosphorus.

Like the OECD classification, the classification scheme according to TGL27885/01 also allows the lake to be classified according to chlorophyll-a and Secchi depth, averaged over the period from April to September. Table 4.14 shows the classification of lakes according to these parameters, together with the values obtained for Rostherne Mere during 2000 and 2002.

Trophic Category	Chlorophyll-a ($\mu g\ l^{-1}$)	Secchi depth (m)
Oligotrophic	≤3	≥6
Mesotrophic	<10	≥4
Eutrophic	10-40	≥1
Polytrophic	40-60	≥0.05
Hypertrophic	>60	<0.5
Rostherne 2000	51 (P)	1.93 (E)
Rostherne 2002	43 (P)	2.3 (E)

Table 4.14: Table to show trophic classification based on chlorophyll-a and Secchi depth according to TGL27885/01. Values are the mean values for the epilimnion from April to September.

The classification based on chlorophyll-a and Secchi depth is similar to that given by the OECD classification, with a higher classification according to chlorophyll-a than Secchi depth. Again, this is likely due to the lack of sensitivity of Secchi depth measurements when chlorophyll-a concentrations are high. The Mere is classified as polytrophic according to chlorophyll-a concentrations, thus agreeing with the hypertrophic classification of the OECD scheme (the OECD scheme does not differentiate between polytrophic and hypertrophic).

A further method of classification according to TGL27885/01 uses zooplankton dry weight, again using epilimnion values averaged over the period from April to September. Table 4.15 shows the boundary values for classification based on zooplankton dry weight.

Trophic Category	Zooplankton (g dry weight m^{-1})	
Oligotrophic	<0.1	
Mesotrophic	<0.3	
Eutrophic	<0.8	
Polytrophic	>0.8	
Hypertrophic	0->0.8	
Rostherne 2000	0.084 (O)[a]	0.23 (M)[b]
Rostherne 2002	0.122 (M)[a]	0.35 (E)[b]

Table 4.15: Table to show trophic classification based on zooplankton dry weight according to TGL27885/01. Values are the mean values for the epilimnion from April to September.

However, the classification based on zooplankton dry weight is problematic for two reasons. The first problem is that the classification requires measurement of the dry weight of zooplankton from within the epilimnion. Zooplankton may undergo diurnal vertical migration within the water column and hence if zooplankton trawls are taken through the epilimnion only, the sample may vary depending on the extent to which zooplankton have migrated out of the epilimnion. During this study zooplankton were monitored by means of deep 20m trawls through the water column, thus changes in zooplankton biomass reflect true changes in biomass, and not those due to zooplankton migration. The first figure (superscript a) gives the zooplankton biomass assuming the zooplankton are evenly distributed throughout the top 20m of the water column i.e. the depth of the trawl. It can be seen that this classifies the lake as oligotrophic in 2000 and mesotrophic in 2002. However, there is no reason to suppose that the zooplankton are evenly distributed within the water column. It is possible that they are concentrated within the epilimnion to avoid low oxygen conditions in the hypolimnion (Stewart and Sutherland, 1993). During the summer in Rostherne Mere the epilimnion extends to a depth of approximately 7m. The second figure given in Table 4.15 (superscript b) is calculated on the assumption that all of the zooplankton taken in a 20m vertical trawl though the water column are within the epilimnion (taking the bottom of the epilimnion to be at approximately 7m depth). It is therefore obtained by multiplying the biomass figure obtained from a 20m trawl by 20/7. Thus, it can be seen from Table 4.15 that even assuming all the zooplankton to be within the epilimnion the lake in 2000 is classified as mesotrophic. In 2002, it is classified as eutrophic, yet the value of 0.35 is close to a mesotrophic classification.

Thus, the use of zooplankton biomass as a classification parameter seems to underestimate the trophic status of Rostherne Mere. This may also be due to the second problem using zooplankton biomass as an index of trophic status, which is that summer zooplankton in Rostherne Mere were subject to strong top-down control, which kept zooplankton biomass at low levels. Hence, the strong top-down control leads to a reduced zooplankton biomass, resulting in an underestimate of the trophic status of the lake. It is therefore recommended that zooplankton should not be considered as a measure of the trophic state of this system.

4.4.3 Classification according to phytoplankton species and succession

Phytoplankton can also be used as an indication of a lakes trophic state. Reynolds (1984a,b) gives seasonal successions for eutrophic and hypertrophic lakes (Figure 4.2). It can be seen that the seasonal succession for a eutrophic system is very similar to that observed in Rostherne Mere, suggesting that the Mere should be classified as eutrophic.

	SPRING	SUMMER		AUTUMN
EUTROPHIC	***Asterionella formosa***	***Eudorina* spp.**	***Anabaena* spp.**	***Ceratium hirundinella***	*Oscillatoria*
	Fragilaria crotonensis	*Pandorina* spp.	***Aphanizomenon flos-aquae***	***Microcystis aeruginosa***	*Asterionella formosa*
	Stephanodiscus rotula	*Volvox* spp.	*Gloeotrichia* spp.	***Gomphosphaeria* spp.**	***Stephanodiscus rotula***
	Stephanodiscus hantzschii	*Ankyra judayi*			
	Ankistrodesmus spp.				
HYPERTROPHIC	*Synedra spp.*	*Monoraphidium* spp.	*Pediastrum* spp.	*Aphanocapsa*
	Stephanodiscus hantzschii	Scenedesmus spp.	*Coelastrum* spp.	*Aphanothece*
	Fragilaria spp.	*Tetrastrum*	*Oocystis* spp.	
	Diatoma	*Crucigenea* spp.		
	Scenedesmus spp.			

Figure 4.2: Generalised seasonal succession for eutrophic and hypertrophic lakes. Adapted from Reynolds, (1984a,b). Species recorded during this study indicated in bold.

However, it should be noted that the eutrophic succession given by Reynolds was largely based on the typical seasonal successions observed in the Shropshire/Cheshire Meres. Thus, the similarity between the Rostherne Mere and typical eutrophic successions is to be expected, as it was based on lakes with similar characteristics to Rostherne Mere, i.e. lowland, eutrophic, stratifying lakes. The sequence is very unlike the succession observed in a hypertrophic system however. Thus, if the lake was classified as hypertrophic, as is suggested by the OECD classification this would lead to

a false indication of the phytoplankton species, and seasonal succession within the Mere. Hence, an analysis of the phytoplankton suggests that the lake is classified as eutrophic.

4.4.4 Classification according to bacteria

It is also possible to classify lakes according to the abundance of planktonic bacteria. There is a strong positive correlation between bacterial abundance and chlorophyll-a, hence by using this relationship it is possible to convert a classification based on Chl to one based on bacteria. For example, Bird and Kalff (1984) observed a strong positive empirical relationship is observed between bacterial numbers and chlorophyll-a, given by the equation:

$$Bacterial\ numbers = 5.911 + 0.763\ \log chl - a$$

where *bacterial numbers* are measured as numbers per millilitre

and *chl-a* is measured in $\mu g\ l^{-1}$

Thus, it is possible to convert the trophic state boundary values of chlorophyll-a in to the corresponding bacterial numbers. Bird and Kalff used the chlorophyll-a based classification of Forsberg and Ryding (1980), together with the regression equation to determine the bacterial numbers corresponding to each trophic category.

Trophic Category		Bacterial numbers ($x10^6$ cells ml^{-1})
Oligotrophic		<1.7
Mesotrophic		1.7-6.5
Eutrophic		≥6.5
Rostherne 2000	Peak	10 (E)
	Summer average	7.6 (E)
Rostherne 2002	Peak	11 (E)
	Summer average	8.9 (E)

Table 4.16: Classification of lakes according to numbers of total bacteria according to Bird and Kalff (1984).

Table 4.16 shows the classification of lakes trophic status according to bacterial numbers. However, there is no indication whether the bacterial numbers represent peak values, annual average values or summer average values. Thus, Table 4.16 shows the

classification of the lake based on peak bacterial numbers, and numbers averaged over the summer period. However, whichever measure is used it can be seen that the numbers of bacteria in Rostherne Mere indicate a eutrophic system.

4.4.5 Summary of information concerning the trophic status of Rostherne Mere

The above discussion considered a number of methods to determine the trophic status of Rostherne Mere, the results of which are summarised in Table 4.17. If the classification according to zooplankton dry weight is omitted (for the reasons outlined above) it can be seen that the lake can be classified as both eutrophic and hypertrophic, depending on the classification scheme used. However, the fact that the phytoplankton succession is characteristic of a eutrophic system, and bears little resemblance to that seen in hypertrophic systems, suggest that a classification of the Mere as hypertrophic would be misleading. This suggests that the TGL27885/01 classification system more accurately reflects trophic status of the Mere. Thus, the evidence gathered during this study suggests that the lake should be classified as eutrophic.

		Mesotrophic	Eutrophic	Hypertrophic
OECD Scheme	P			TP classifies the lake as hypertrophic
	Chl-a			Both mean and maximum chlorophyll-a classifies the lake as hypertrophic
	Secchi		Eutrophic according to both mean and minimum values	
TGL27885/01	P		Both TP and SRP values classify the lake as eutrophic	
	DIN			High concentrations classify the lake as on the polytrophic / hypertropic boundary
	Chl-a		Polytrophic Mean chlorophyll-a (April-September) classifies the lake as intermediate between the upper eutrophic and lower hypertrophic boundaries	
	Secchi		Eutrophic according to April-September average	
Phytoplankton			Seasonal succession typical of a eutrophic system	
Bacteria			Numbers >$6.5x10^6$ suggests eutrophic conditions	
Zooplankton dry weight (TGL27885/01)		Suggests mesotrophic conditions but determination of epilimnion values and top down control makes classification unreliable		

Table 4.17: Summary of the trophic classification of Rostherne Mere based on data collected during 2000 and 2002.

4.4.6 Recent changes in the ecology of the lake

Data collected during this study shows that the late summer phytoplankton in Rostherne Mere was phosphorus-limited. This is in contrast to the accepted view of the lake as nitrogen limited (Carvalho *et al.*, 1995; Moss *et al.,* 1997). The fact that the lake is now phosphorus-limited rather than nitrogen-limited suggests that phosphorus or nitrogen concentrations within the lake are changing. It is instructive to compare the values obtained by Carvalho *et al.* between 1990 and 1993 to those obtained during this study. Between 1990 and 1993 mean annual concentration of SRP varied between 280 and 339μg l^{-1}, whereas during 2000 it had fallen to 170μg l^{-1} while in 2002 it had fallen to 70μg l^{-1}. Total phosphorus also shows a substantial fall with concentrations varying between 375 and 505μg l^{-1} during 1990 and 1993, while in 2000, the mean annual concentration was 230μg l^{-1}. In 2002, concentrations of TP had fallen further, to 136μg l^{-1}. It can be seen that there has been a substantial reduction in the lake phosphorus concentration, causing the Mere to switch from N to P limitation.

The reduction in phosphorus concentrations may be a delayed reaction to the closure of a small sewage works, which, until 1991 discharged into Little Mere from where it entered via Rostherne brook, into Rostherne Mere. A small treatment plant that served Rostherne village (population ~100) and discharged just upstream of Rostherne Mere was also closed in 1991. The sewage from both treatment plants was diverted for treatment elsewhere. Although it was expected that the levels of phosphorus in the lake would begin to decline in the eighteen months following sewage diversion, no change in phosphorus was observed (Carvalho *et al.*, 1995). It was suggested that due to the long residence time of the mere and its large depth, reduction in phosphorus may take up to 50 years and although Moss *et al.,* (1997) noted signs of a slight downward trend in phosphorus it was argued that it would require a very severe fall in phosphorus loading to reach P limitation. Nevertheless, it was suggested that in future years the phosphorus concentrations levels will begin to decline and phosphorus may become more important in limiting biomass. The shift to P limitation indicated in this study suggests that the reduction in the P concentration within the Mere has occurred faster than was initially expected.

There are also indications that the concentrations of nitrates within the Mere have also changed during the last decade. Between 1990 and 1993 total oxidized nitrogen (nitrate and nitrite) varied between 0.51 and 0.71mg l^{-1}. The concentrations recorded in this study show an increase, with a mean concentration of 1.23mg l^{-1} during 2000 and a

mean of 1.10mg l^{-1} during 2002. Thus, the switch to P limitation may not only be due to a decreasing concentration of phosphorus, but also due to increasing concentrations of nitrogen, both of which will result in an increased N:P ratio, increasing the likelihood of P limitation.

Table 4.18 shows the minimum concentrations of both SRP and NO_x in Rostherne Mere, thus giving an indication of which nutrient was limiting. It can be seen that there was a large drop in SRP concentrations between 1993 and 1996, with concentrations remaining low subsequently. It is also evident from the table that although NO_x concentrations were limiting up to 1998, concentrations have not been limiting in recent years.

Year	Minimum concentration of SRP ($\mu g\ l^{-1}$)	Minimum concentration of NO_x ($mg\ l^{-1}$)	Reference
1990-1993	≈70-100	Undetectable	Carvalho *et al.*, (1995) (Estimate of minimum concentrations obtained by inspection of fig.2)
1996	3	Undetectable	Krivtsov (2000a)
1998	Undetectable	Undetectable	Krivtsov (2000a)
1999	5	0.02	Levado (2001)
2000	Undetectable	0.03	
2001	Undetectable	0.04	
2002	Undetectable	0.15	

Table 4.18: Minimum values of SRP and NO_x from 1990 to 2002. Years 2000-2002 are based on data collected in this study. Values for 2001 are based on unpublished values taken on two sampling trips, in late August and early September (foot and mouth disease restricted access to the Mere prior to these dates).

It is notable that the switch to P limitation was accompanied by a switch of the dominant summer phytoplankton from *Ceratium hirundinella* and/or *Microcystis* spp. to *Gomphosphaeria* and *Peridinium*, which has not been previously observed in Rostherne Mere. Although the change in the dominant species may be coincidental, it is also possible that the reduction in phosphorus has altered the nutrient regime of the Mere against *Ceratium* and *Microcystis*. It is not possible to determine the extent to which *Peridinium* and *Gomphosphaeria* is attributable to a change in the nutrients within the Mere without monitoring the lake in future years. However, it is notable that a previous change in the dominant phytoplankton from *Aphanizomenon* dominance to *Microcystis/Ceratium* dominance occurring in the 1960's has been attributed to a

change in the nitrogen budget of the Mere, with the Mere experiencing increased nitrogen load due to the increase in N fertilisers in the surrounding catchment and so altering the N:P ratio in favour of *Microcystis/Ceratium*. It is therefore possible that the reduced P levels will alter the N:P ratio away from *Ceratium* and *Microcystis*, and in favour of other species. However, confirmation of this must wait upon sampling of the Mere in future years.

SECTION C: HOLLINGWORTH LAKE

Chapter 5 Results for Hollingworth Lake, 2001-2002

For the presentation of the data obtained from Hollingworth Lake in 2001 and 2002 the years have been divided into a number of phases.

For the 2001 sampling the phases are:

Spring, 10th April – 23rd May

Summer, 11th June – 28th August

Autumn maximum, 11th September – 9th October

Autumn decline, 24th October – 21st November

For the 2002 sampling the phases are:

Winter, 30th January and 13th of February

Spring, 7th March – 15th May

Early summer, 29th May – 15th July

Late summer, 24th July – 19th September

The rationale for the selection of these phases will become clear in the description of the seasonal changes in chlorophyll-a and total algal biovolume, on which the phases are based.

5.1 Phytoplankton

5.1.1 Chlorophyll-a

Chlorophyll-a data are shown in Figure 5.1a.

Year 2001: Chlorophyll-a varied between 2.7 μg l^{-1} and 34.7 μg l^{-1} during 2001. Concentrations were approximately 10 μg l^{-1} during the spring and early summer (June) phases, increased throughout the remainder of the summer phase, reaching maximum values during the autumn maximum phase (max. 34.7 μg l^{-1}). During the autumn decline concentrations fell rapidly, reaching a minimum of 2.7 μg l^{-1} at the end of sampling.

Year 2002: During 2002 chlorophyll-a varied between 0.7 and 13.5 μg l^{-1}. In contrast to 2001 no large peak of chlorophyll-a was observed. Values were at a minimum during the winter phase (<1.0 μg l^{-1}), increased to 11.4μg l^{-1} at the start of the spring phase, and remained at approximately 7 μg l^{-1} during the remainder the phase. Concentrations

increased to 13.5 μg l^{-1} at the start of the summer phase and then remained between 7.6 μg l^{-1} and 12.6 μg l^{-1} for the remainder of the sampling period.

5.1.2 Secchi Depth

Secchi depth data are shown in Figure 5.1b.

Year 2001: Secchi depth during this period varied between 0.82m and 2.10m. The minimum occurred when chlorophyll-a peaked in the autumn maximum (9th October), while the minimum Secchi depth recorded occurred at the end of the spring phase (23rd of May), when chlorophyll-a was at a near minimum of 5 μg l^{-1}. Although chlorophyll-a was 2.7 μg l^{-1} on the 21st of November no Secchi depth was taken on this date as the disk was Secchi disc was lost during sampling.

Year 2002: Secchi depth during this period varied between 0.80m and 1.98m. The minimum occurred during February, when chlorophyll-a was 1 μg $^{-1}$. The maximum occurred on the 21st of August, when chlorophyll-a was 9.4 μg l^{-1}.

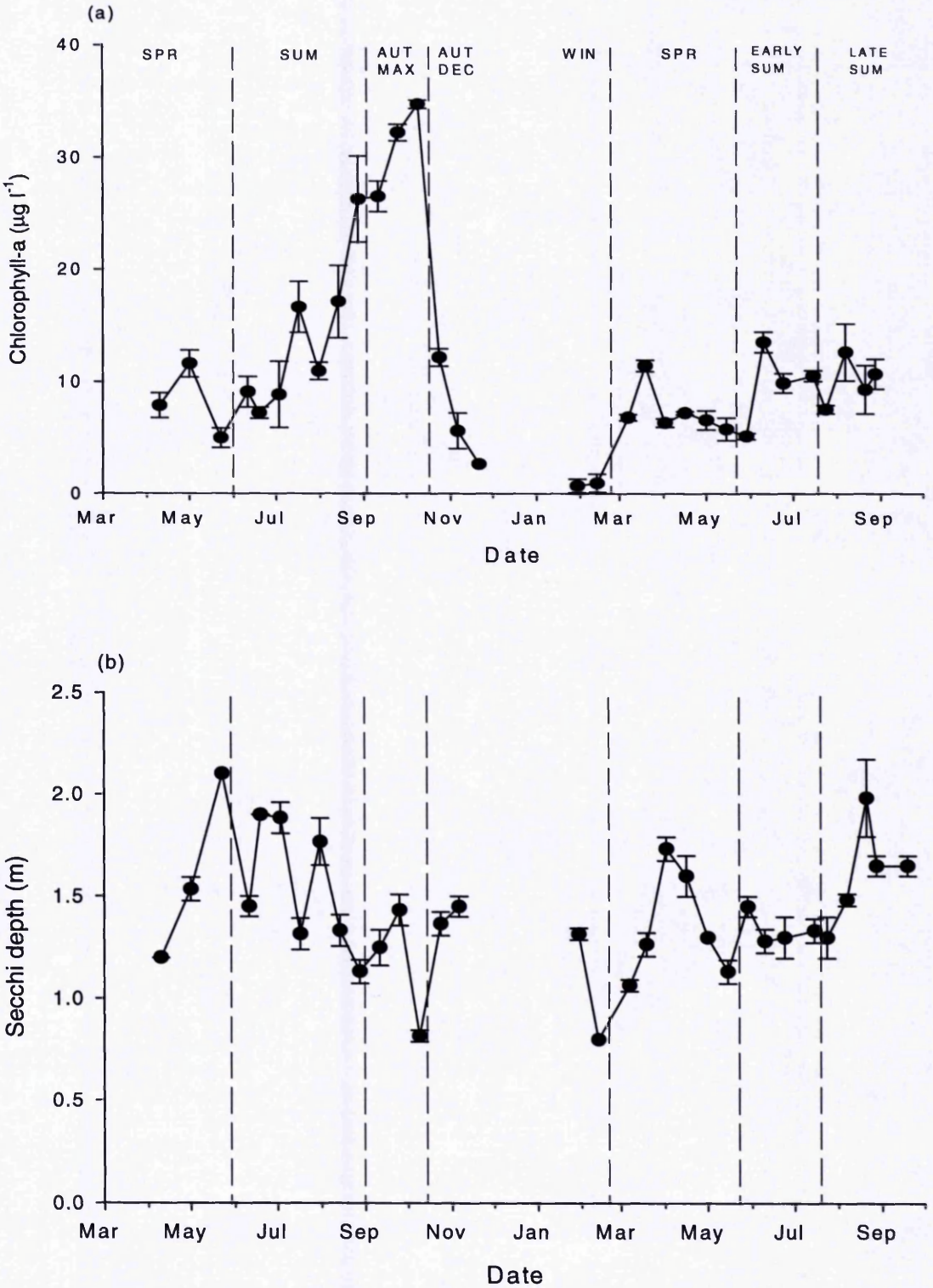


Figure 5.1: Seasonal changes in (a) chlorophyll-a and (b) Secchi depth in Hollingworth Lake 2001-2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

5.1.3 Phytoplankton Groups:

The total algal biovolume and the biovolume of each algal group is shown in Figure 5.2 to Figure 5.6. Figure 5.2b shows the percentage dominance of each algal group to the total biovolume. Figure 5.7 shows the biovolume of those species considered edible to the dominant zooplankton in Hollingworth Lake (*Daphnia* and *Bosmina*).

Bacillariophyceae was by far the dominant group for the majority of the sampling period, the biovolume of which closely followed total biovolume. The correlation between Bacillariophyceae and total biovolume only broke down in late August/September 2002, when Cryptophyceae and Dinophyceae biovolumes were at a maximum. During 2001, Bacillariophyceae biovolume (Figure 5.3a) showed a large peak ($2.15x10^6 \mu m^3\ ml^{-1}$) during the autumn-maximum phase. In 2002, there were two large peaks, the first in the spring phase ($2.57x10^6 \mu m^3\ ml^{-1}$), and the second during the early summer phase ($3.51x10^6 \mu m^3\ ml^{-1}$). Dinophyceae (Figure 5.3b) showed a small increase to $0.22x10^6 \mu m^3\ ml^{-1}$ during the 2001 summer phase, and a large peak of $1.19x10^6 \mu m^3\ ml^{-1}$ in the late summer phase of 2002.

Cryptophyceae biovolumes (Figure 5.4a) were low during 2001, and for the majority of 2002; however there was a large increase during the late summer phase in 2002, with biovolume increasing to $0.44x10^6 \mu m^3\ ml^{-1}$.

Cyanophyceae biovolume (Figure 5.4b) showed two peaks in 2001, $9.13x10^4 \mu m^3\ ml^{-1}$ at the end of the summer phase, and a much larger peak of $0.39x10^6 \mu m^3\ ml^{-1}$ during the late autumn maximum phase. No peaks were observed in 2002.

Chlorophyceae biovolumes (Figure 5.5a) were very low; during 2001 there was an increase in the spring phase followed by oscillations during the summer, reaching a maximum biovolume of $4.79x10^4 \mu m^3\ ml^{-1}$ (these oscillations were almost entirely caused by fluctuations (between 0 and 2 cells ml^{-1}) in the numbers of large colonies of *Pediastrum*). Chrysophyceae (Figure 5.5b) showed a very small peak during the summer phase in 2001 ($3.00x10^3 \mu m^3\ ml^{-1}$) and a larger increase in the late summer phase of 2002, reaching a maximum biovolume of $22.3x10^3 \mu m^3\ ml^{-1}$. Chrysophyceae biovolumes were entirely due to *Dinobryon*.

Small unidentified phytoplankton (<10μm) biovolume was only measured in 2002 and showed fluctuations throughout the sampling period; biovolumes were very low with a maximum of $9.60x10^3 \mu m^3 ml^{-1}$ during the late summer phase.

As there was no consistent seasonal succession of algal groups the phases have been based on changes in total algal biovolume and chlorophyll-a. The phases can be described as follows:

Year 2001

Spring: 10th April – 23rd May

This phase showed a decrease in total biovolume from $1.14x10^6 \mu m^3 ml^{-1}$ to $0.30 x10^6 \mu m^3 ml^{-1}$ reaching the minimum at the end of the phase. During this phase Bacillariophyceae contributed >80% of the biovolume, with Cryptophyceae (max. 12%) and Dinophyceae (max. 5%) contributing the remainder.

Summer: 11th June – 28th August

This phase is characterized by a continuous increase in chlorophyll-a from 9.1μg l^{-1} at the beginning of the phase to 26.3μg l^{-1} at the end. However, interestingly there was no increase in calculated algal biovolumes. During this phase Bacillariophyceae generally contributed >80% of the biovolume. The exception was July when an increase in Dinophyceae biovolume to approximately 25% and Cryptophyceae to 5% reduced the contributed of Bacillariophyceae to 63%.

Autumn maximum: 11th September – 9th of October

This phase was characterized by elevated levels of algal biovolumes (max. $2.17x10^6 \mu m^3 ml^{-1}$) and maximum values of chlorophyll-a (max 34.7μg l^{-1}), with both parameters peaking at the end of the phase. Bacillariophyceae contributed >96% of the biovolume on the first two sampling occasions, reducing to 80% at the end of the phase when there was an increase in the contribution of Cyanophyceae to 16%.

Autumn decline: 24th October – 21st November

At the start of this phase total biovolume had decreased to $0.86x10^6 \mu m^3 ml^{-1}$ and continued to decrease during the remainder of the phase reaching a minimum of $0.11x10^6 \mu m^3 ml^{-1}$ at the phases' end. During this phase Bacillariophyceae contributed >97% of the biovolume.

Year 2002

Winter: 30th January and 13th of February

This phase showed low levels of chlorophyll-a (<1.0μg l^{-1}) and algal biovolume (min. 0.25 x10^6μm^3 ml^{-1}). The contribution of the Bacillariophyceae was >95% during this phase.

Spring: 7th March – 15th May

This phase consisted of a large initial, short-lived peak in biovolume (max. 2.58x10^6μm^3 ml^{-1}) followed by a decrease to a very low level of 0.04 x10^6μm^3 ml^{-1} at the end of the phase (this was the minimum biovolume recorded over the whole 2 year sampling period). Chlorophyll-a showed a similar pattern but with a less pronounced peak early in the phase. The contribution of Bacillariophyceae was >97% during this phase (with the exception of the last sampling date when it dropped to 84% due to an increase in the contribution of Cryptophyceae (9%) and small (<10μm) phytoplankton (7%)

Early Summer: 29th May – 15th July

This phase consists of a short-lived, large peak in algal biovolume (max. 3.52x10^6μm^3 ml^{-1} followed by a rapid decline to 0.42x10^6μm^3 ml^{-1} (chlorophyll-a again showed a similar pattern but with a less pronounced peak). Bacillariophyceae contributed >90% of the total algal biovolume during this phase.

Late Summer: 24th July – 19th September

This phase was characterised by a further increase in phytoplankton biovolume to a maximum of 1.70x10^6μm^3 ml^{-1}. During this phase there was an increase in the biovolume of the other algal groups. The contribution of Cryptophyceae and Dinophyceae were particularly important during this phase. The contribution of Bacillariophyceae was approximately 70% on the first two sampling occasions, dropped rapidly during late August (14% on the 21st of August, 2% on the 28th) and then recovered to 49% at the end of sampling. Cryptophyceae increased from 0% at then start of the phase to 42% on the 21st of August and then declined to 16% at the end of sampling. The contribution of Dinophyceae increased from 25% at the beginning of the phase to 70% on the 28th of August, and then fell to 33% at the end of sampling.

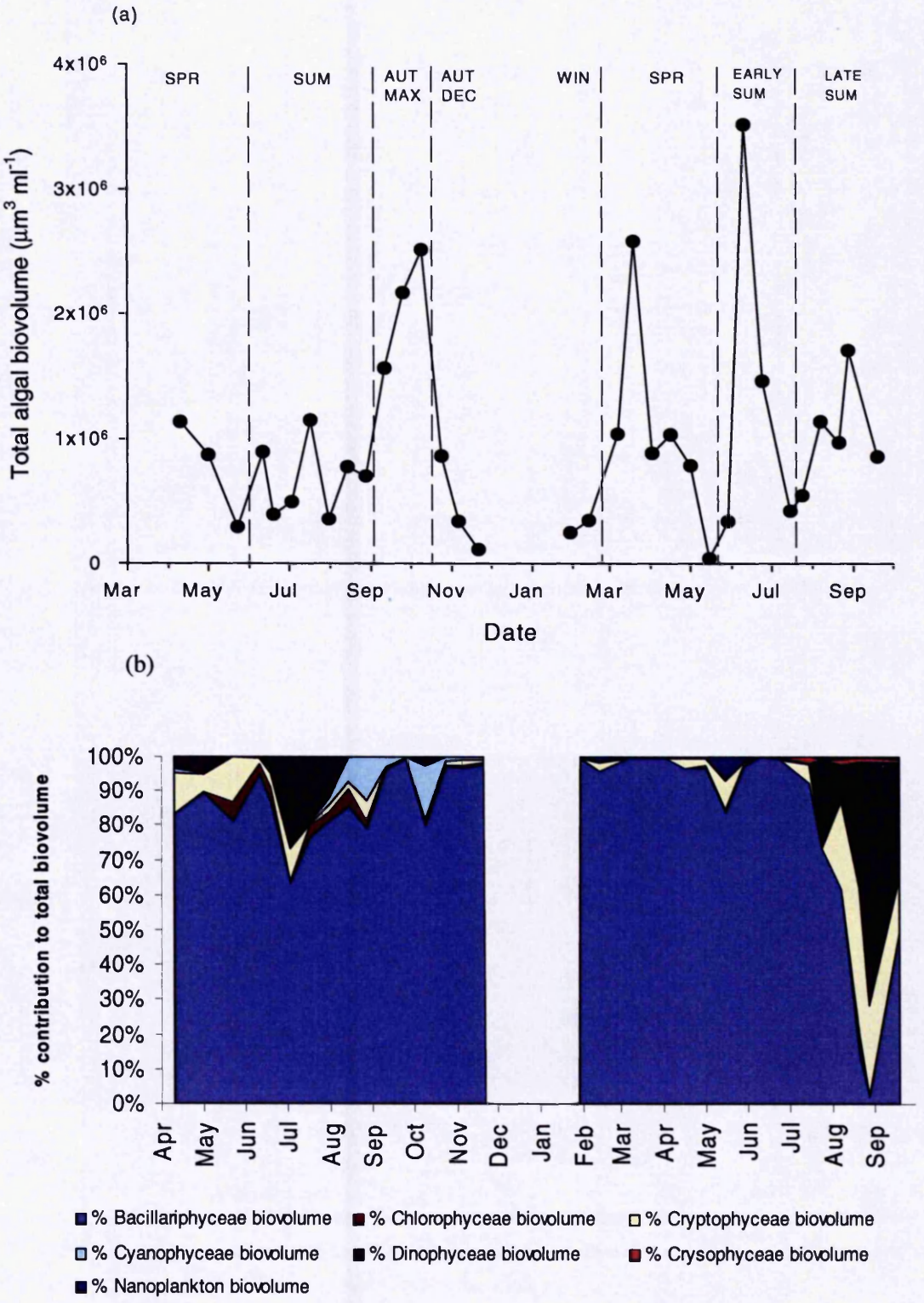


Figure 5.2: Seasonal changes in (a) total algal biovolume and (b) the percentage contribution of each algal group to the total biovolume. Hollingworth Lake 2001-2002.

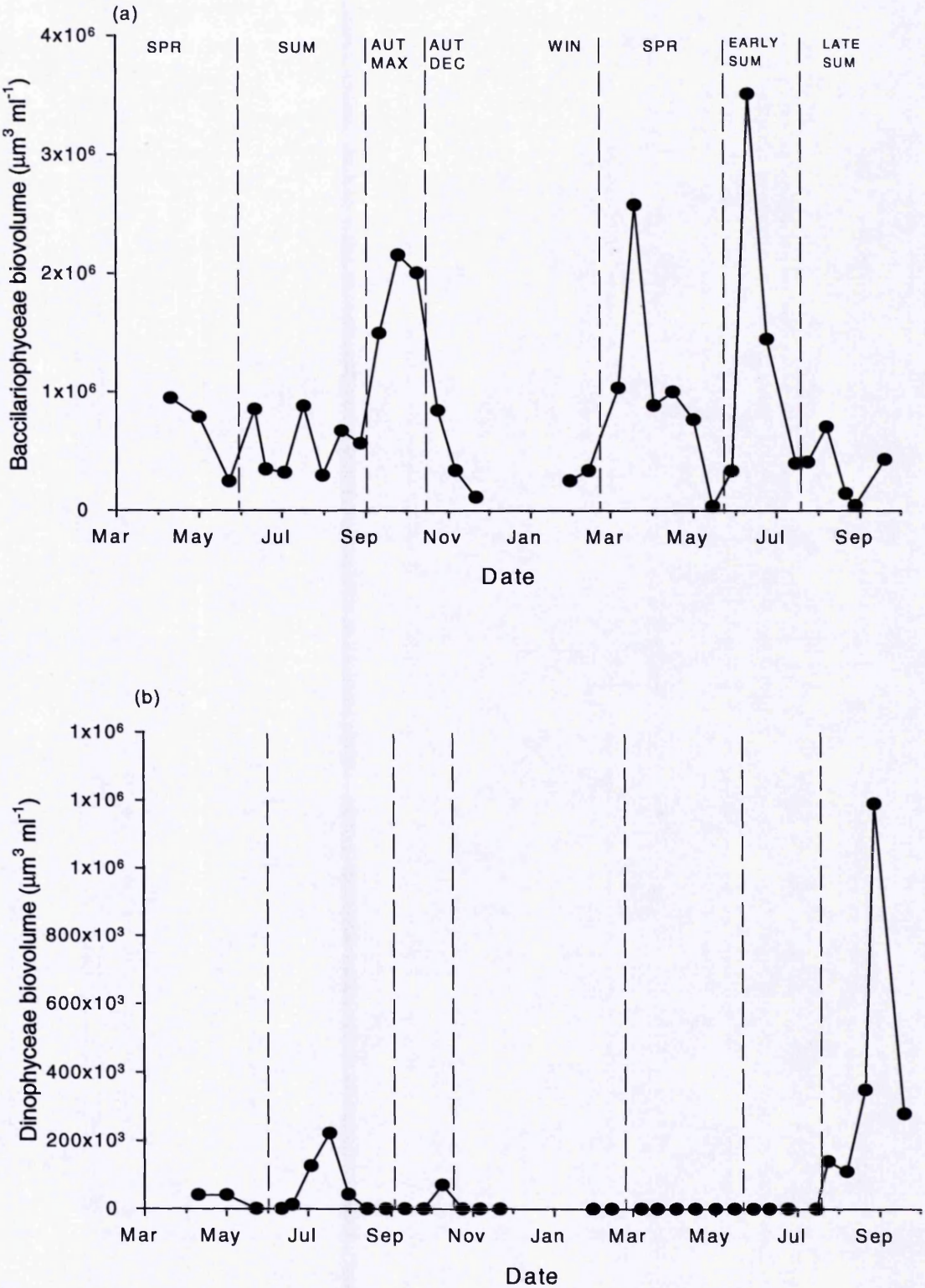


Figure 5.3: Seasonal changes in the biovolume of (a) Bacillariophyceae and (b) Dinophyceae in Hollingworth Lake, 2001-2002. Biovolumes are calculated using the mean count from integrated samples from sites A, B and C.

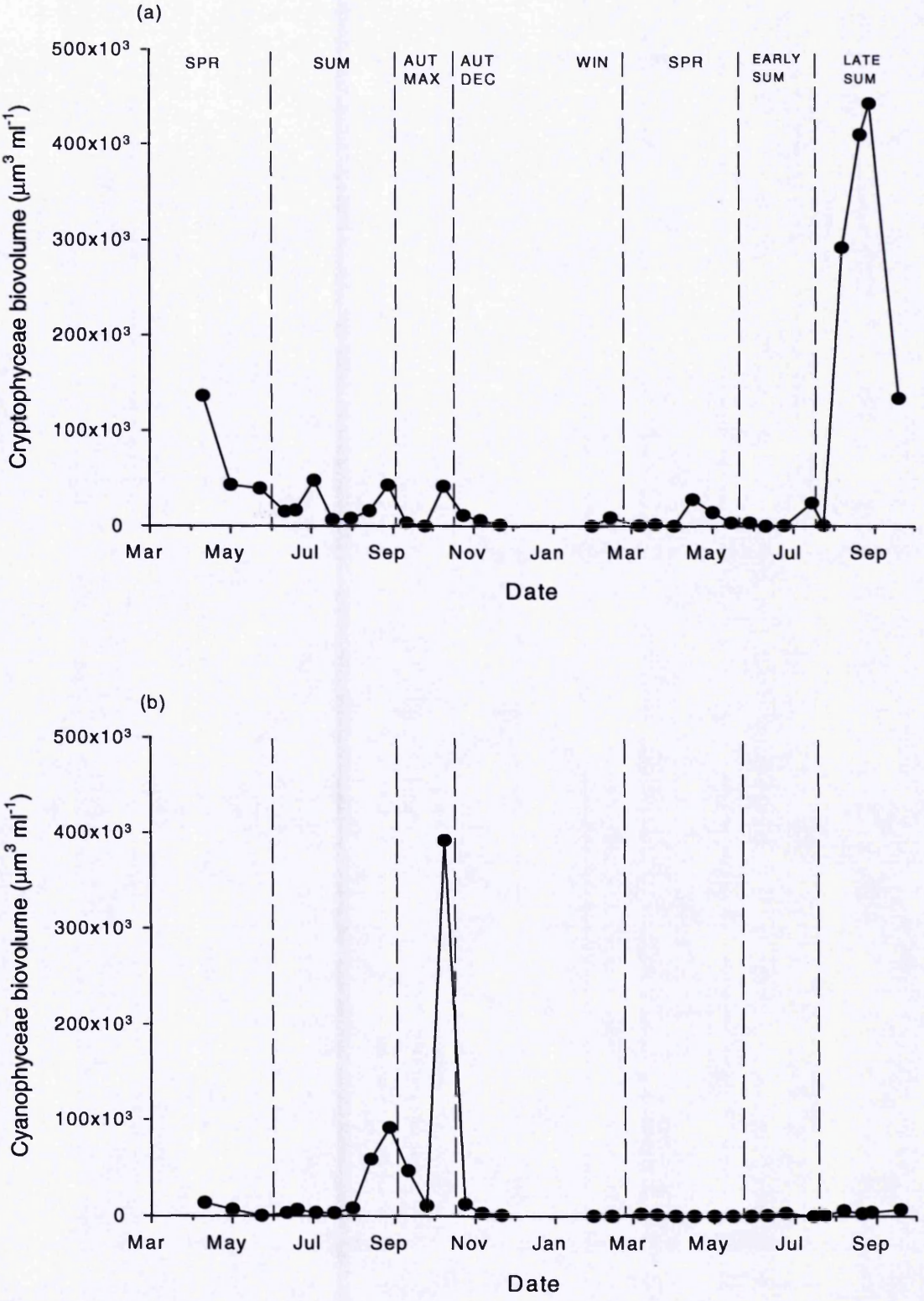


Figure 5.4: Seasonal changes in the biovolume of (a) Cryptophyceae and (b) Cyanophyceae in Hollingworth Lake, 2001-2002. Biovolumes are calculated using the mean count from integrated samples from sites A, B and C.

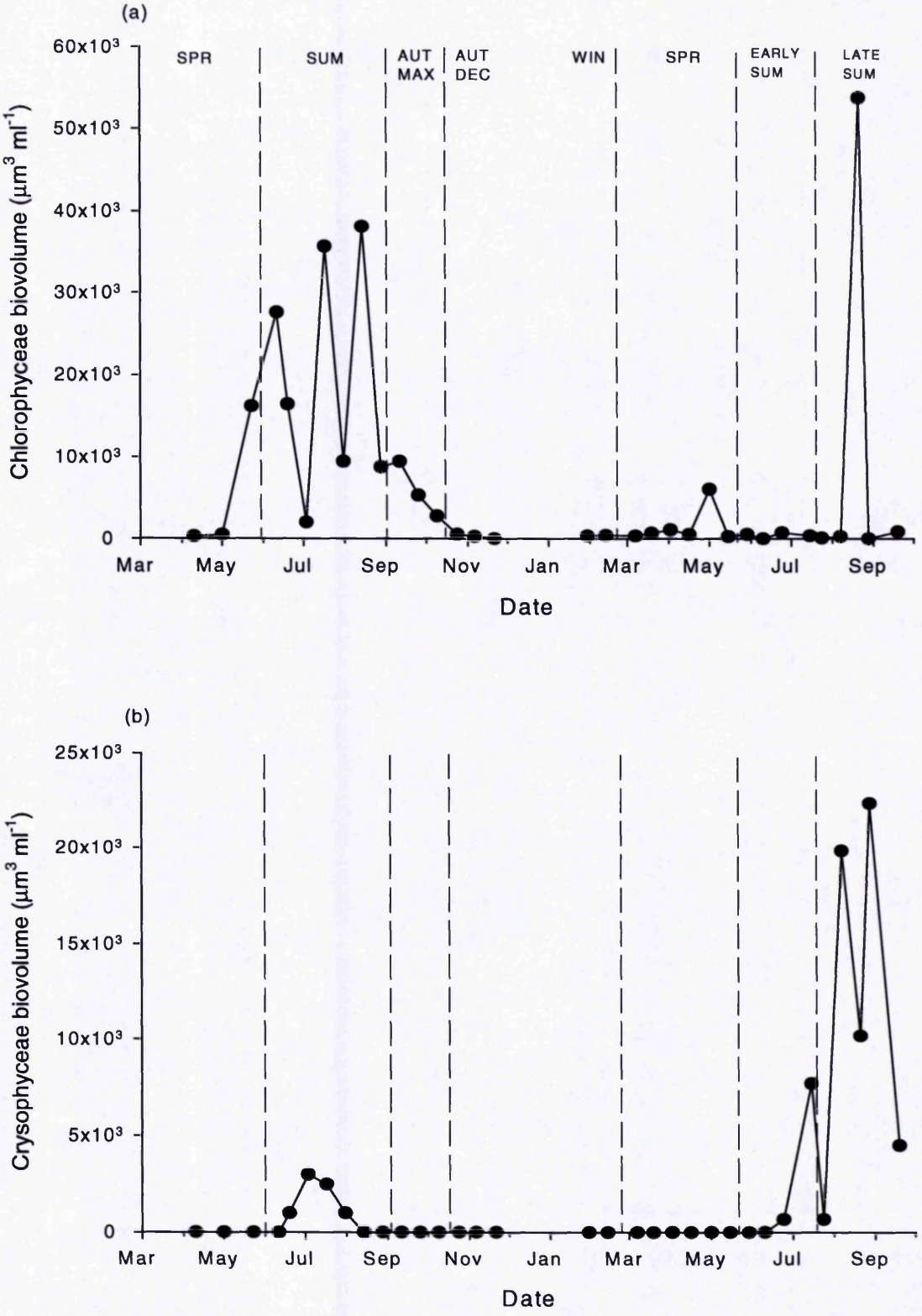


Figure 5.5: Seasonal changes in the biovolume of (a) Chlorophyceae and (b) Chrysophyceae in Hollingworth Lake, 2001-2002. Biovolumes are calculated using the mean count from integrated samples from sites A, B and C.

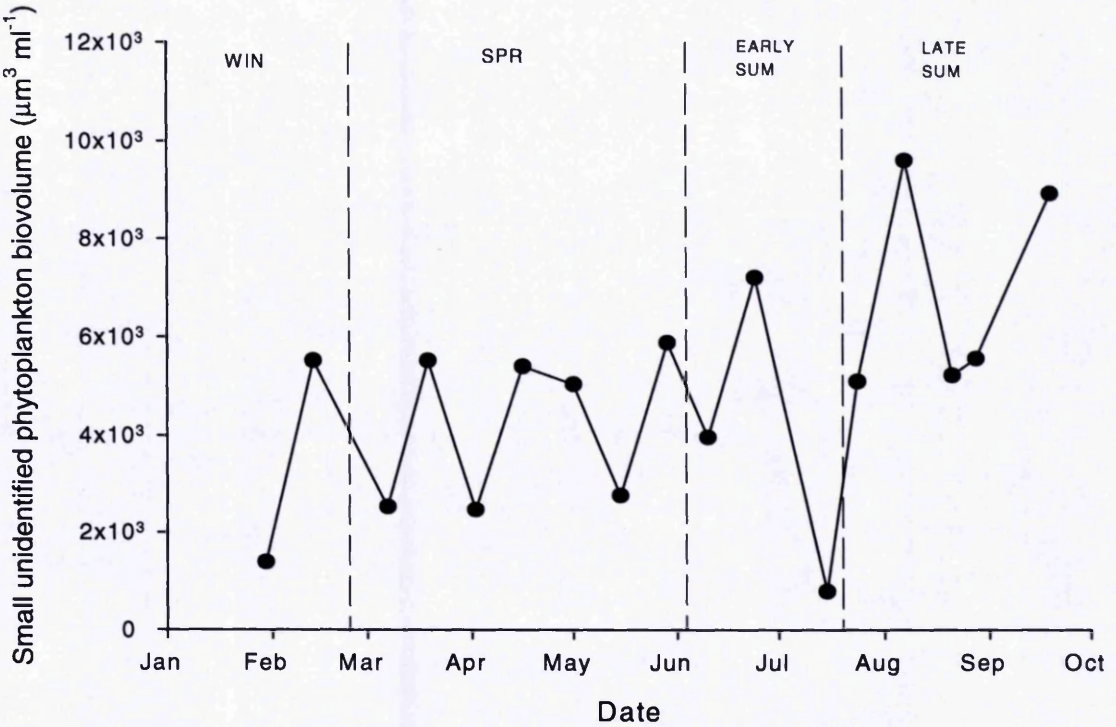


Figure 5.6: Seasonal changes in the biovolume of small unidentified phytoplankton (≈5µm) in Hollingworth Lake, 2001-2002. Biovolumes are calculated using the counts taken from site C only.

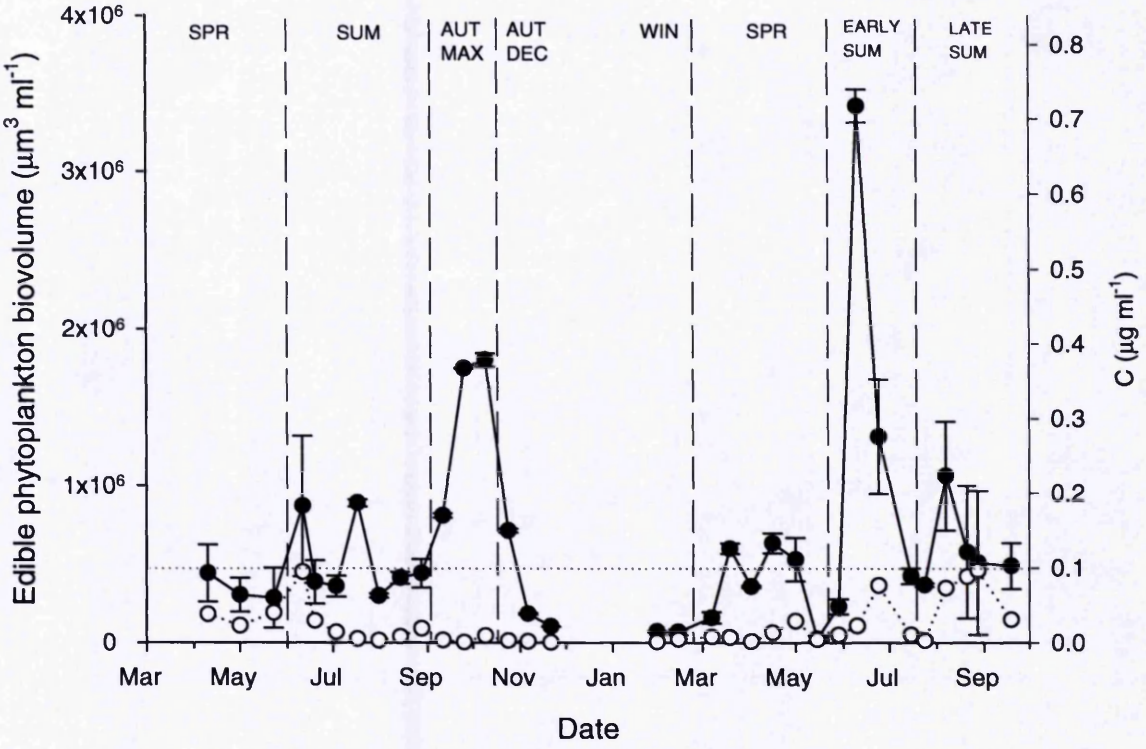


Figure 5.7: Seasonal changes in the biovolume of edible phytoplankton species within Hollingworth Lake 2001-2002. The figure shows those phytoplankton species that are fully edible according to the Burns equation only (o), and the biovolume of those according to the Burns' equation together with colonial species (*Asterionella formosa* and *Tabellaria*) that may be partly edible (•). The rational for the two measures of edible biovolume with become evident in the ensuing discussion. The secondary axis shows the edible biovolume expressed as carbon. The horizontal line is the threshold concentration of edible food for *Daphnia*, below which *Daphnia* are food limited.

5.1.4 Phytoplankton Species

Counts of individuals (cells or colonies) are shown in Figure 5.8 to 5.18. Figure 5.8 to 5.12 show changes in the Bacillariophyceae species, Figure 5.13 and 5.14 the Cyanophyceae. Cryptophyceae are shown in Figure 5.15, Dinophyceae and Chrysophyceae in Figure 5.16, Chlorophyceae in Figure 5.17 and the counts of small (<10μm), largely unidentifiable phytoplankton in Figure 5.18.

Spring Year 2001: 10th April – 23rd May

During this phase there was a decrease in a number of diatom species. *Tabellaria fenestrata* declined form 180 to 12 cells ml^{-1}, *Synedra acus* from 72 to 11 cells ml^{-1}, *Melosira* sp. from 15 to 0 cells ml^{-1}, and *Aulacoseira* from 44 to 0 cells ml^{-1}.

Other diatom species were present in low numbers throughout the phase- *Asterionella formosa*, *Nitzschia* spp. and *Tabellaria fenestrata var. asterionelloides* and the small *Cyclotella* sp. were also present but always at <10cells/colonies ml^{-1}.

Cyclotella showed a different pattern to the other diatoms, increasing from 0 cells ml^{-1} at the start of the phase to 150 cells ml^{-1} at its end (this increase continued into the summer phase, peaking at 429 cells ml^{-1} at the phases commencement).

Other species present during this phase were *Oscillatoria* spp. (decreasing from 17 to 0 filaments ml^{-1} and *Cryptomonas* spp. (decreasing from 80 to 21 cells ml^{-1}) and *Rhodomonas minuta* (decreasing from 652 to 223 cells ml^{-1}). Numbers of other phytoplankton species (*Scenedesmus* spp., *Pediastrum* sp., and *Peridinium* sp.) were very low (<5 cells ml^{-1}).

Summer Year 2001: 11th June – 28th August

Cyclotella sp. decreased from 429 cells ml^{-1} at the start of the phase to approximately 0 cells ml^{-1} in July (July was notable for very low numbers of phytoplankton of all groups) followed by a slight increase to 35 cells ml^{-1} at the end of the phase. *Asterionella formosa* decreased from an early summer maximum of 36 colonies ml^{-1} to 0 colonies ml^{-1} in July and was absent during the remainder of the phase. *Tabellaria fenestrata var. asterionelloides* showed a general increase over the phase, from 31 colonies ml^{-1} at the start to 50 colonies ml^{-1} at the phases end, with a mid phase peak to 117 colonies ml^{-1}. *Aulacoseira* increased in numbers at the end of the phase. Other diatom species were present in very low numbers (generally <5 cells/colonies ml^{-1}).

At the end of this phase there were also increases in the number of cyanophyte species, with maximum numbers at the phases end. *Aphanocapsa* sp. peaked at 35 colonies ml^{-1}, *Oscillatoria* spp. peaked at 35 filaments ml^{-1} and *Gloecapsa* spp. peaked at approximately 15 colonies ml^{-1}.

Ceratium showed a maximum of 5 cells ml^{-1} during the middle of the phase, while *Dinobryon* peaked at 30 cells ml^{-1} at around the same time.

Cryptomonas spp. and *Rhodomonas minuta* were present throughout the phase, but in low numbers (*Cryptomonas* generally <40 cells ml^{-1}, *Rhodomonas* generally <100 cells ml^{-1})

Scenedesmus spp. and *Pediastrum* sp. were present throughout the phase at <5cells/colonies ml^{-1} (with the exception of July 31st when absent)

Autumn maximum Year 2001: 11th September – 9th of October

Cryptomonads, dinoflagellates and *Dinobryon* were present in extremely low numbers or were absent during this phase, as were *Scenedesmus* spp. which decreased from 12 to 0 cells ml^{-1} during the phase The phase was dominated by an increase in *Tabellaria fenestrata var. asterionelloides* which increased from 107 to 247 colonies ml^{-1}. *Oscillatoria* spp. also increased, from 18 to 490 filaments ml^{-1}. *Asterionella formosa* and *Aulacoseira* were both present, both showing maxima of approximately 50 colonies/filaments ml^{-1}. *Synedra* increased from 0 to 7 cells ml^{-1}.

Autumn decline Year 2001: 24th October – 21st November

During the autumn decline there were very few species present. During this phase *Tabellaria fenestrata var. asterionelloides* declined from 98 to 14 colonies ml^{-1}, *Aulacoseira* from 15 to 1 cell ml^{-1}, and *Synedra* from 13 to 0 cells ml^{-1}.

Winter Year 2002: 30th January and 13th of February

There were very low numbers of species during this phase. The only diatom species present at more than 10 cells ml^{-1} were *Nitzschia* and *Synedra* with maximum populations of approximately 20 cells ml^{-1}). Small phytoplankton (<10µm GALD) increased from 230 to 920 cells ml^{-1}.

Spring Year 2002: 7th March – 15th May

The spring phase was dominated by diatom species. No Cyanophyceae, Dinophyceae or Chrysophyceae species were present. Cryptomonads were present at generally < 10 cells ml^{-1} and the only Chlorophyte was *Scenedesmus* at <10 cells ml^{-1}.

Numbers of small, unidentified plankton (<10μm greatest diameter) oscillated between 400 and 100 cells ml^{-1}.

Tabellaria fenestrata peaked in April at approximately 90 cells ml^{-1} and then rapidly declined while *Melosira* sp and *Aulacoseira* both increased rapidly at the beginning of the phase (*Melosira* to 88 filaments ml^{-1}, *Aulacoseira* to 67 filaments ml^{-1}), followed by a rapid decline to be almost completely absent at the phases end. Indeed, by the end of the phase most species were almost absent from the plankton (the exception was *Cyclotella*, present at 10 cells ml^{-1}). The small *Cyclotella* species was at a maximum at the beginning of the phase (190 cells ml^{-1}) and then declined rapidly to be absent from April onwards, while *Cyclotella* peaked towards the end of the phase at 107 cells ml^{-1}. *Asterionella* was present throughout the phase at approximately 100 colonies ml^{-1} (with the exception of the very start and end of the phase when numbers were much lower). *Synedra* and *Nitzschia* were present in low numbers, both species increasing to approximately 15 cells ml^{-1} at the end of the phase

Early Summer Year 2002: 29th May – 15th July

Diatoms dominated this phase. Dinoflagellates were absent, and cryptomonads, cyanophytes and chlorophytes were present in very low numbers only (<5 cells/colonies ml^{-1}). *Dinobryon* was absent during the early part of the phase but increased to 77 cells ml^{-1} by the end of the phase. Numbers of small, generally unidentified phytoplankton, fell to a minimum (130 cells ml^{-1}) at the end of this phase.

Asterionella increased from 32 colonies ml^{-1} at the start of the phase to 632 colonies ml^{-1} on the next sampling occasion (10th June) and then rapidly decline to 12 coloniess ml^{-1} by the next sampling. *Cyclotella* sp. and *Tabellaria fenestrata var. asterionelloides* both showed peaks on the 24th of June, *Tabellaria* reaching 125 colonies ml^{-1} and *Cyclotella* 355 cells ml^{-1}.

Late Summer Year 2002: 24th July – 19th September

This was the only phase when diatoms did not dominate although by the end of the phase there are indications that diatom species were beginning to increase, while species from other groups are beginning to decrease.

Of the diatom species *Tabellaria fenestrata var. asterionelloides* peaked early in the phase, at 97 colonies ml^{-1}, declined during August and then increased slightly in numbers to 30 colonies ml^{-1} by the end of sampling. *Asterionella* also increased in

numbers towards the end of sampling, reaching 25 colonies ml^{-1} (it was absent at the start of the phase); other diatom species were absent or present in very low numbers.

Ceratium hirundinella increased from 3 cells ml^{-1} at the start of the phase to peak at 28 cells ml^{-1} on the 28th of August, then falling to 7 cells ml^{-1} at the end of sampling. *Dinobryon* also increased in numbers during this phase, with a maximum of 233 cells ml^{-1}, falling to 45 cells ml^{-1} at the end of sampling. Cryptophyceae also increased during this phase; *Rhodomonas minuta* increased from 10 cells ml^{-1} at the start of the phase to 1727 cells ml^{-1} on the 28th of August, falling to 227 by the end of sampling. *Cryptomonas* spp. increased from 0 cells ml^{-1} to approximately 300 cells ml^{-1} throughout August, falling to 110 cells ml^{-1} at the end of sampling.

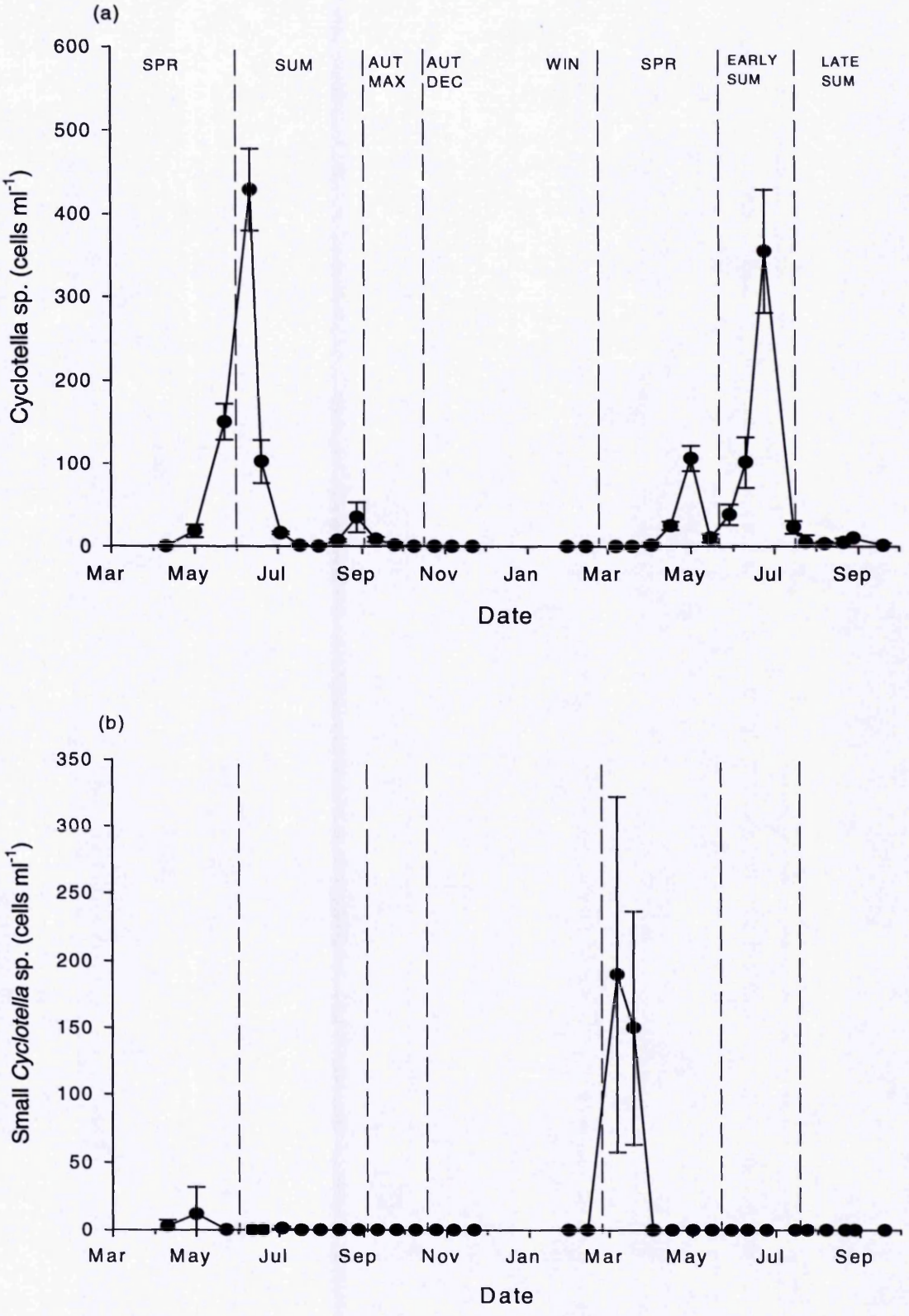


Figure 5.8: Seasonal changes in (a) *Cyclotella* sp. and (b) small *Cyclotella* sp. in Hollingworth Lake 2001-2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

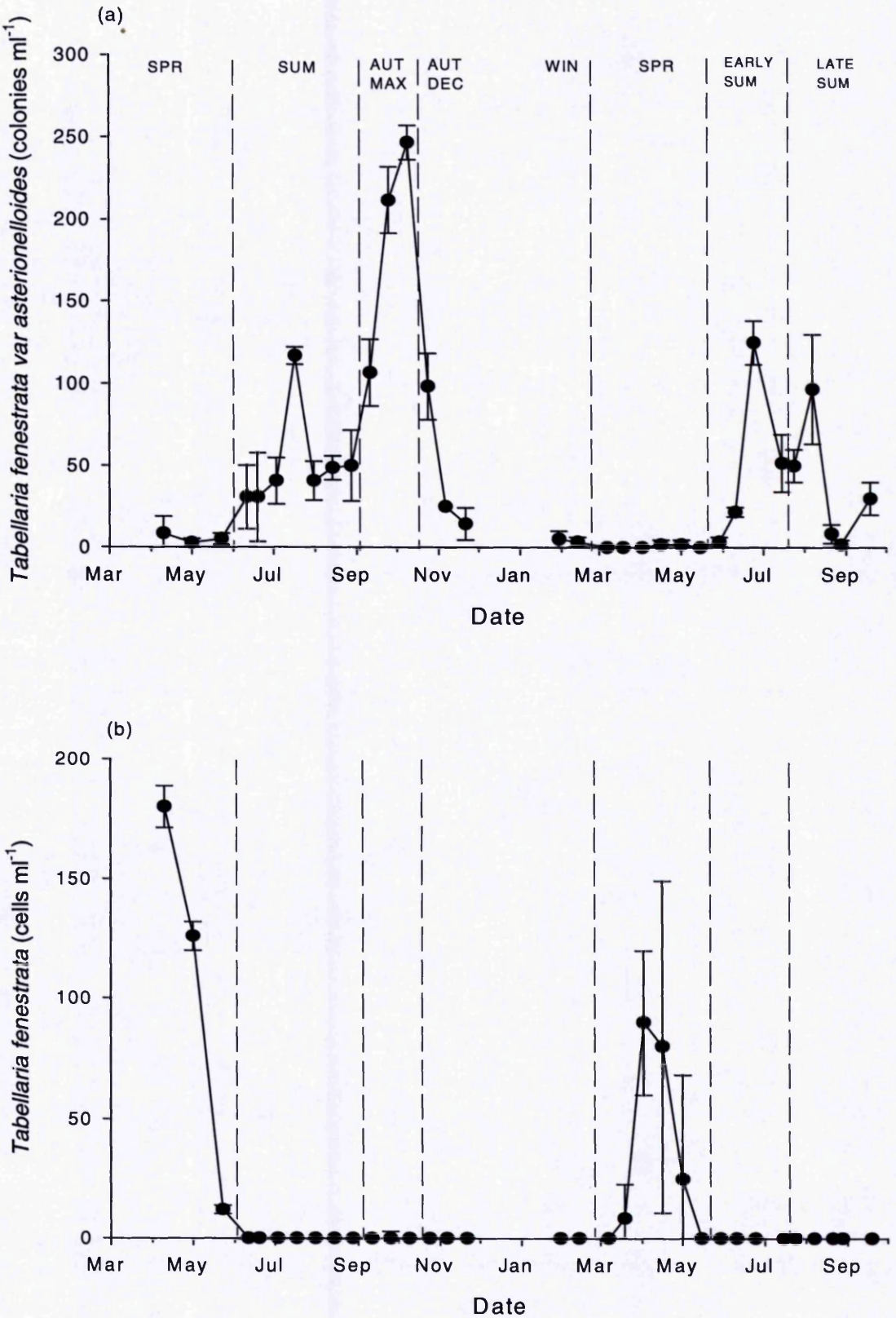


Figure 5.9: Seasonal changes in (a) *Tabellaria fenestrata var. asterionelloides* and (b) *Tabellaria fenestrata* in Hollingworth Lake 2001-2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

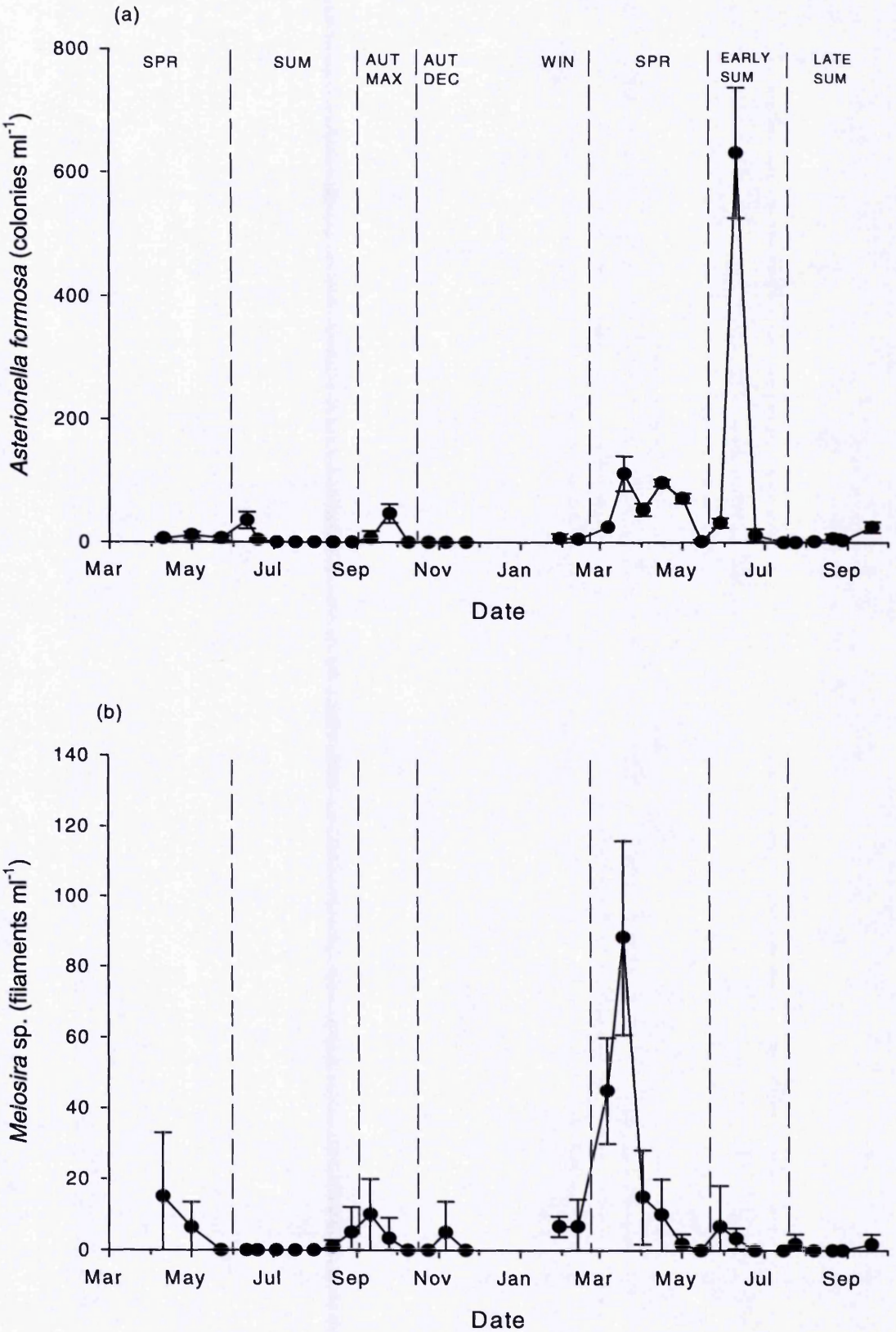


Figure 5.10: Seasonal changes in (a) *Asterionella formosa* and (b) *Melosira* sp. in Hollingworth Lake 2001-2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

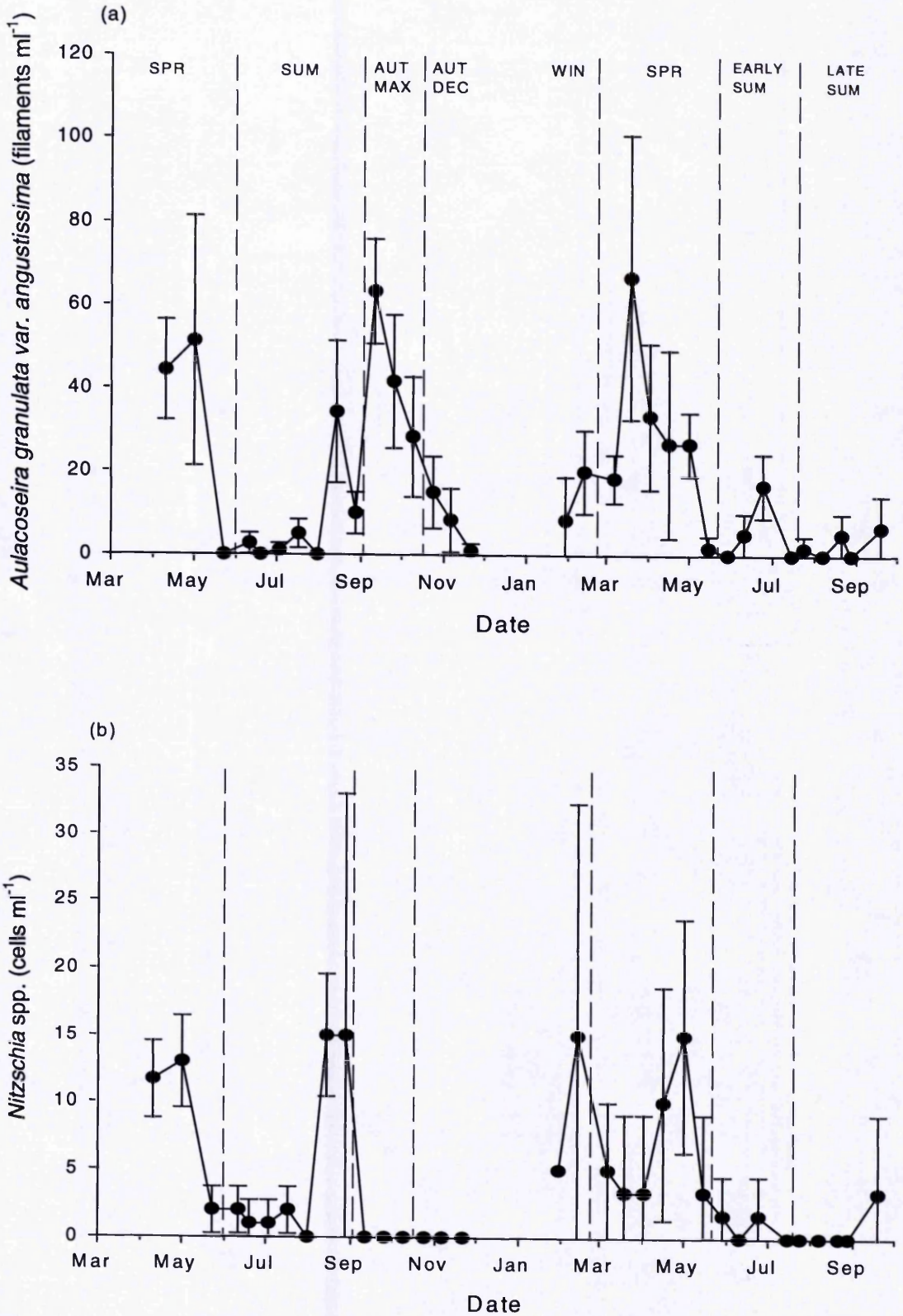


Figure 5.11: Seasonal changes in (a) *Aulacoseira granulata var. angustissima* and (b) *Nitzschia* spp. in Hollingworth Lake 2001-2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

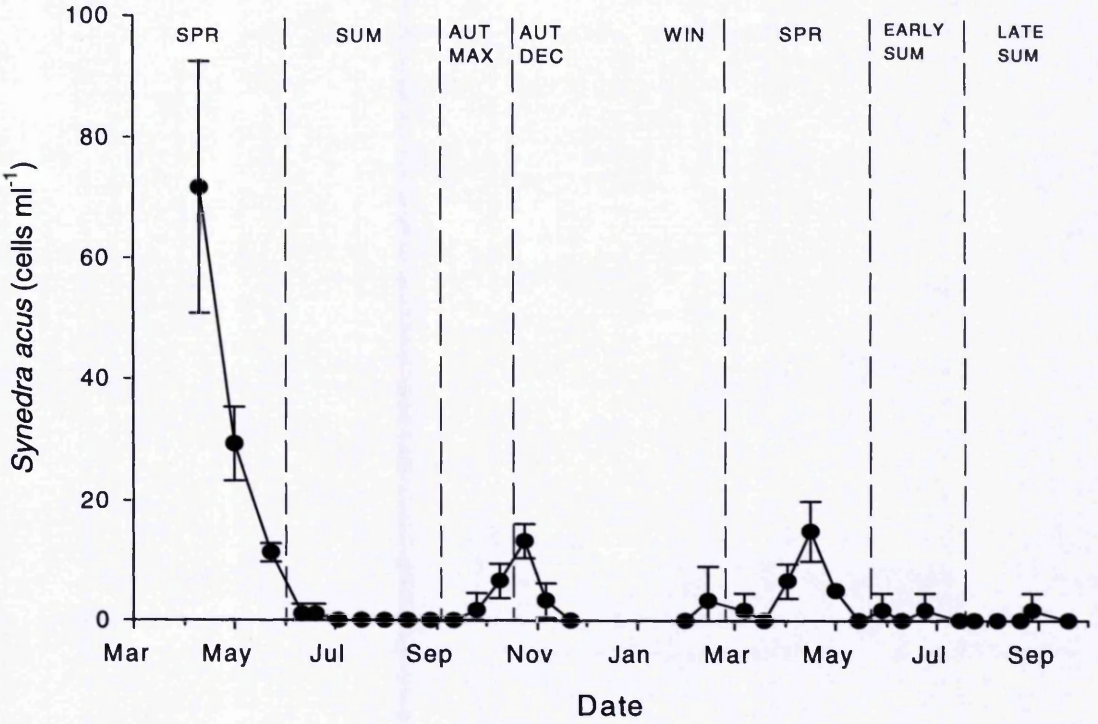


Figure 5.12: Seasonal changes of *Synedra acus* in Hollingworth Lake 2001-2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

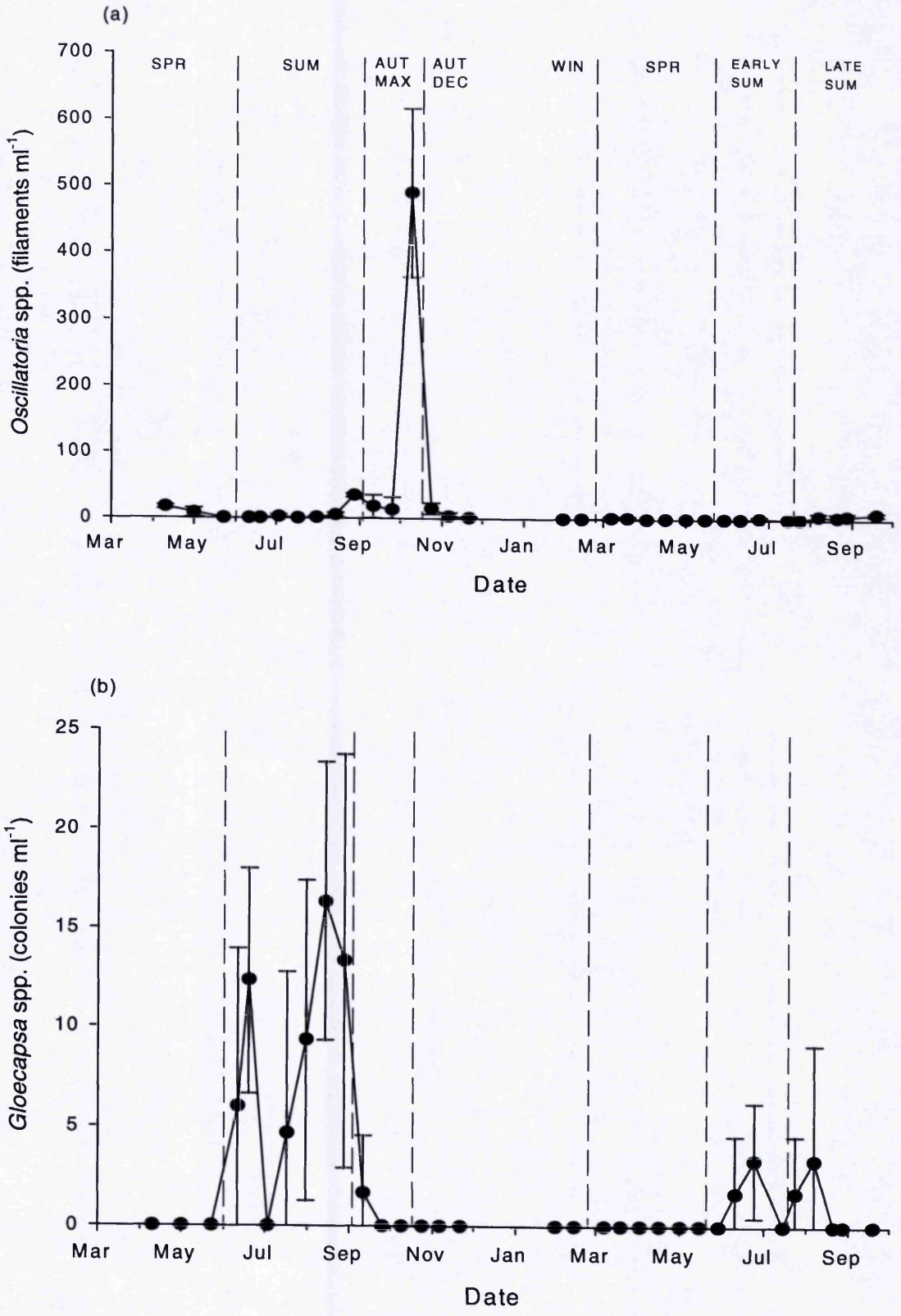


Figure 5.13: Seasonal changes in (a) *Oscillatoria* spp. and (b) *Gloecapsa* sp. in Hollingworth Lake 2001-2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

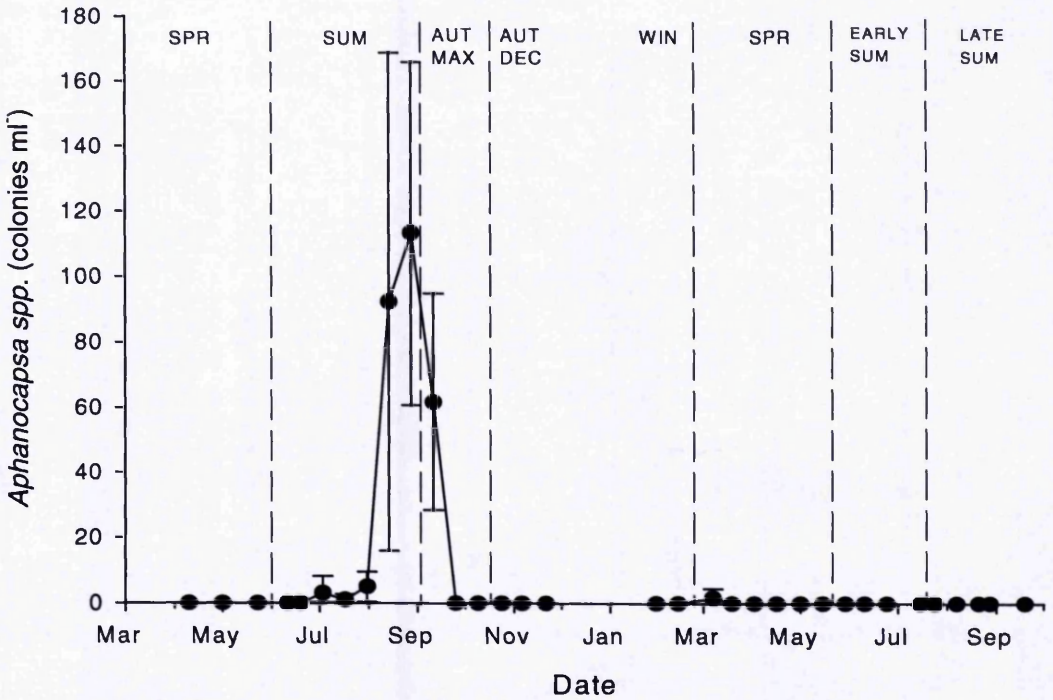


Figure 5.14: Seasonal changes in the numbers of *Aphanocapsa* sp. colonies in Hollingworth Lake, 2001-2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

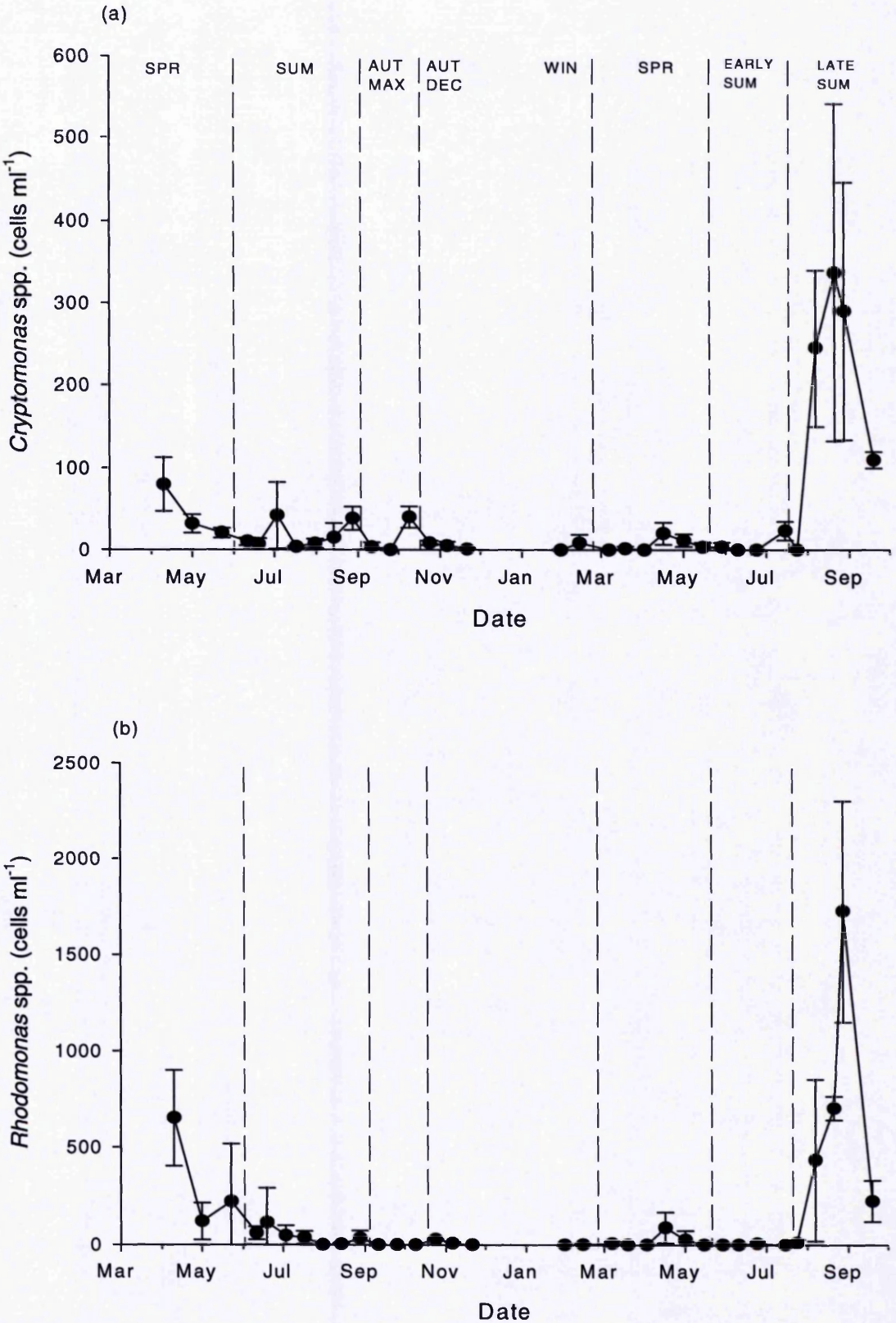


Figure 5.15: Seasonal changes in (a) *Cryptomonas* spp. and (b) *Rhodomonas minuta* in Hollingworth Lake 2001-2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

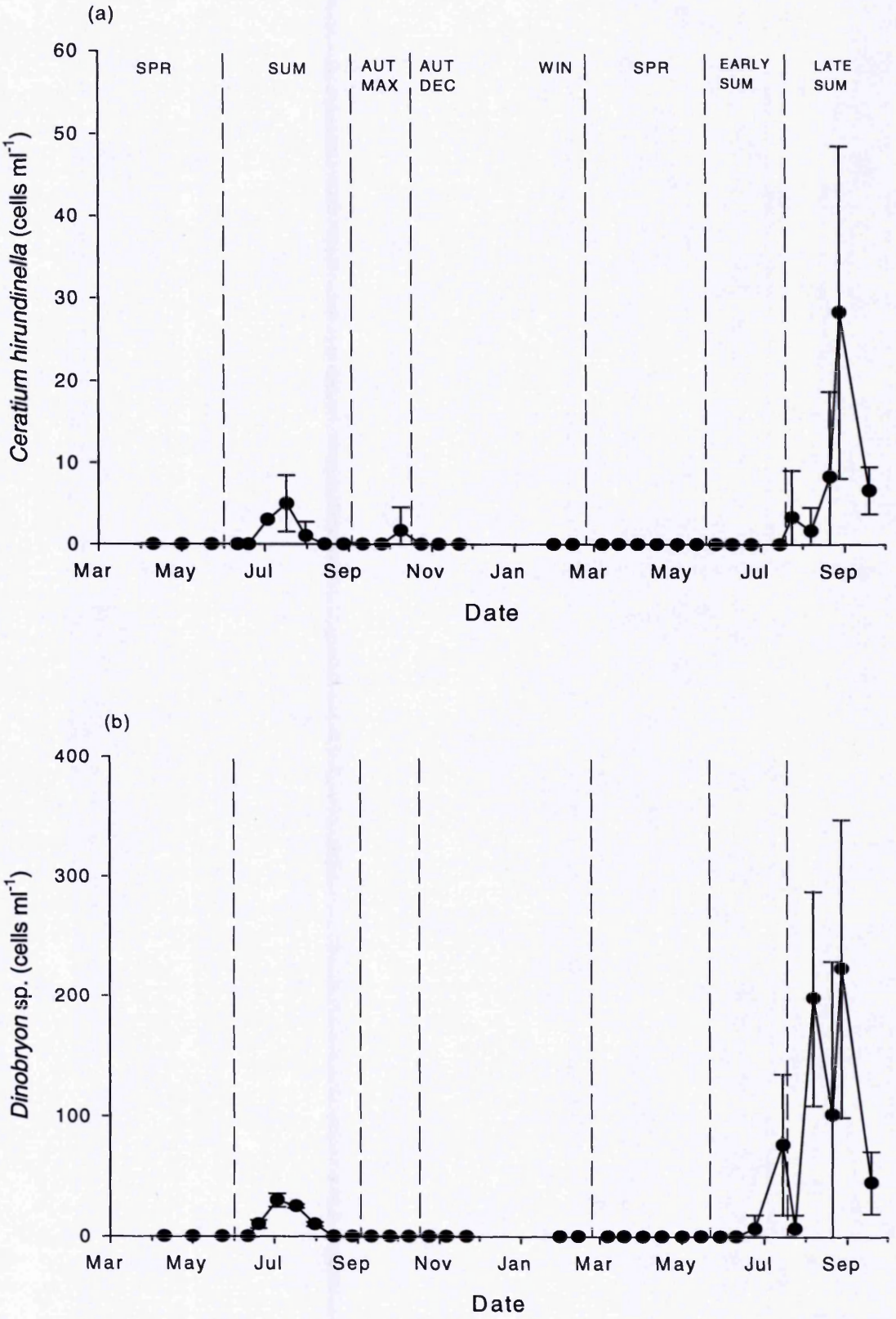


Figure 5.16: Seasonal changes in (a) *Ceratium hirundinella* and (b) *Dinobryon* sp. in Hollingworth Lake 2001-2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

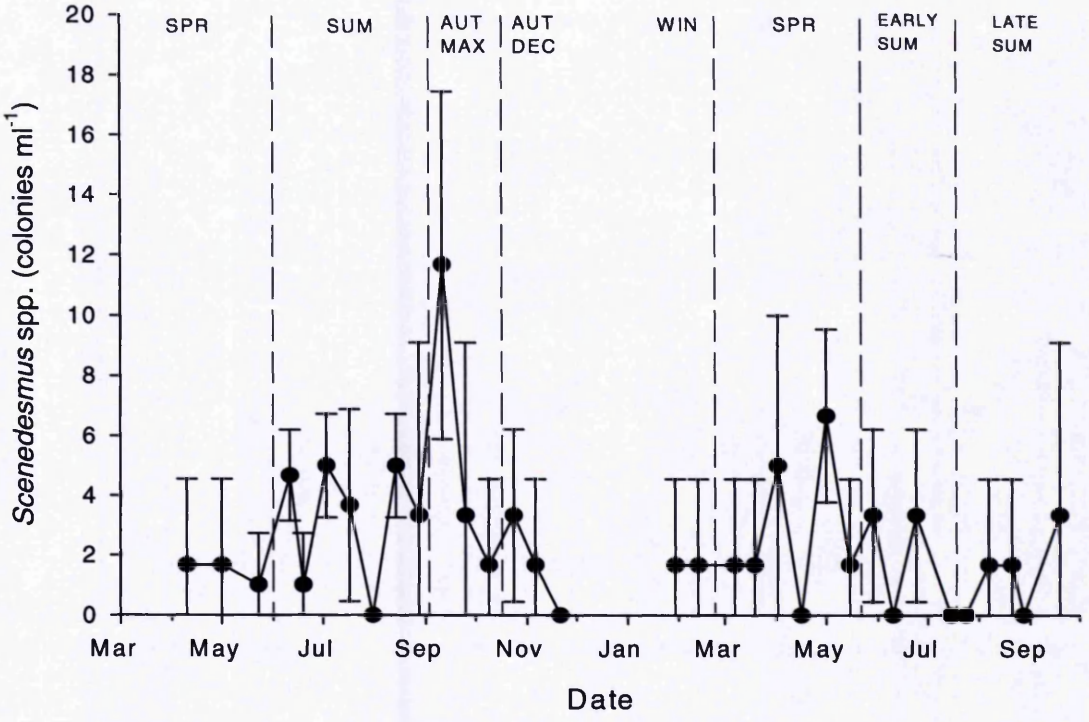


Figure 5.17: Seasonal changes in *Scenedesmus* spp. in Hollingworth Lake 2001-2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3)

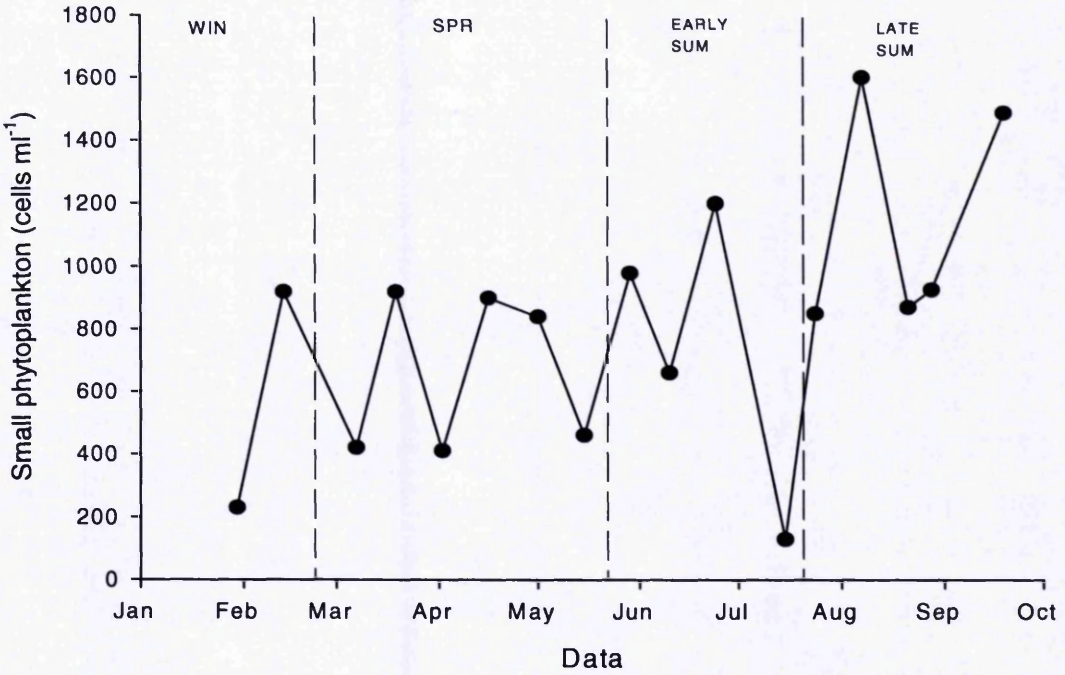


Figure 5.18: Seasonal changes in the number of small plankton (<10μm GALD) in Hollingworth Lake 2002. Values are counts from an integrated sample taken from the centre of the lake (Site C).

5.2 Physico-chemical Parameters

5.2.1 Temperature

Year 2001: At the commencement of sampling on the 10th of April the average temperature of the water column was 6.7°C. Temperatures then increased through the spring phase, reaching a maximum of 19.0°C in the late summer phase (31st of July). Temperatures remained high for the remainder of the summer phase before falling during the autumn phases to a minimum of 6.8°C at the end of sampling.

Year 2002: During the winter phase and early spring phase (until the 19th of March) the temperature of the water column varied between 5.2 and 6.6°C. Temperatures then increased, reaching a maximum of 18.2°C during the summer phase (7th of August), before declining to 15.5°C at the end of sampling.

5.2.2 Temperature profiles

For the sake of completeness, profiles for all sampling occasions are given, thus allowing inspection of profiles for any sampling date of choice. However, this leads to a large numbers of figures, many of them showing similar profiles. The reader is therefore referred to the profiles on particular dates, when the profiles showed features of particular interest. Profiles for 2001 are shown in Figure 5.20 to Figure 5.22. Those for 2002 are shown in Figure 5.23 to Figure 5.25.

Year 2001: During 2001 the lake was generally isothermal although stratification was observed on the 23rd of April and 3rd of July. However, on both occasions windy conditions returned the lake to isothermal by the next sampling occasion.

Year 2002: During the winter, spring and the start of the summer phases the lake was isothermal. On the 15th of July the lake was stratified, but this had broken down by the next sampling occasion (24th July). During August the lake did not stratify although temperature gradients between the top and bottom of the water column were observed. By the end of sampling (September) the lake was isothermal.

5.2.3 Oxygen Profiles

Oxygen profiles for 2001 and 2002 are shown superimposed on the temperature profiles. It can be seen that on the majority of sampling occasion there was little variation in oxygen concentration within the water column, with concentrations typically approximately 90%. However, during the period of high phytoplankton

biomass in September 2001 oxygen saturation was >100%. On some occasions oxygen saturation fell towards the bottom of the water column (see for example 28th August, 2001, 24th July 2002 and 28th August 2002).

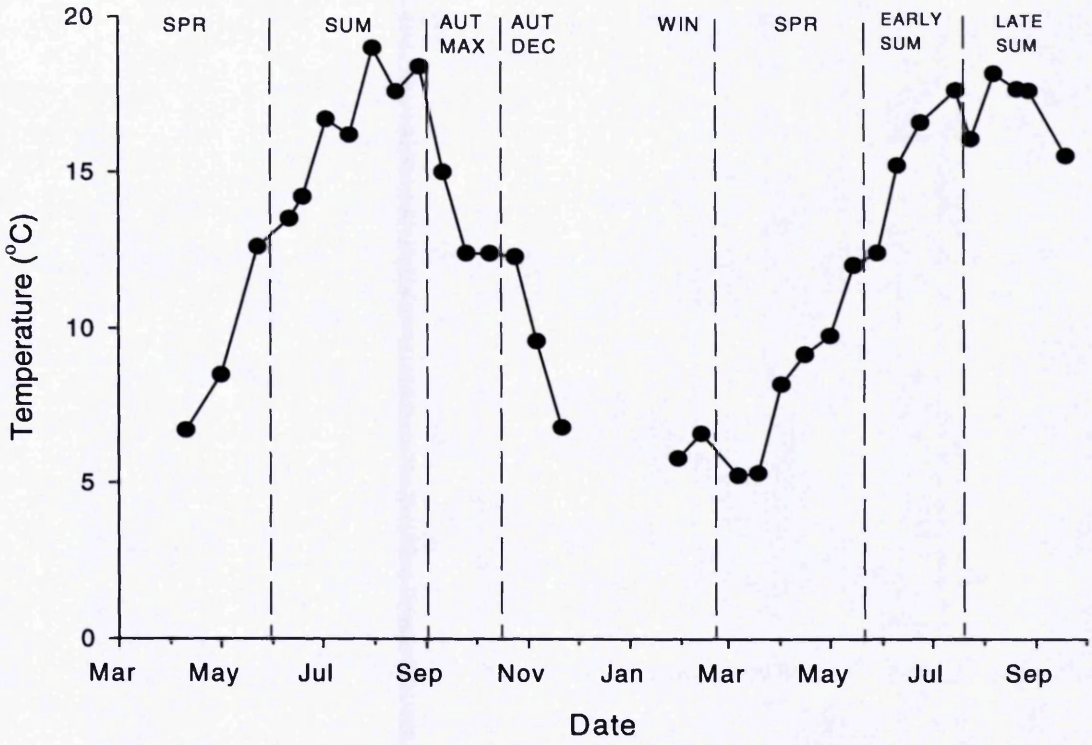


Figure 5.19: Seasonal change in the average temperature of the water column, Hollingworth Lake, 2001-2002. Values calculated from the mean of the water column values, obtained from the depth profile.

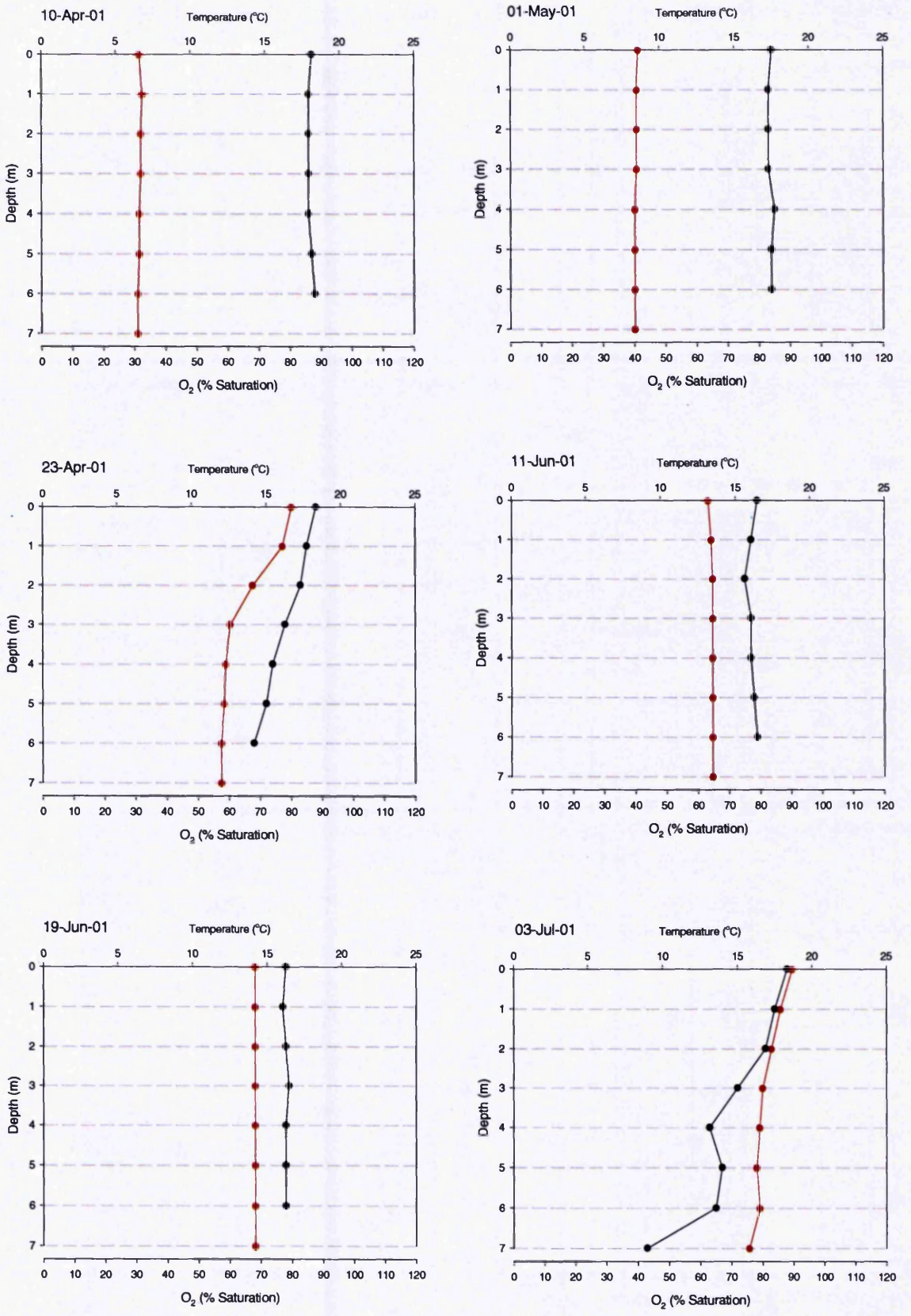


Figure 5.20: Temperature (•) and oxygen (•) profiles for 10th of April to the 3rd of July, Hollingworth Lake, 2001.

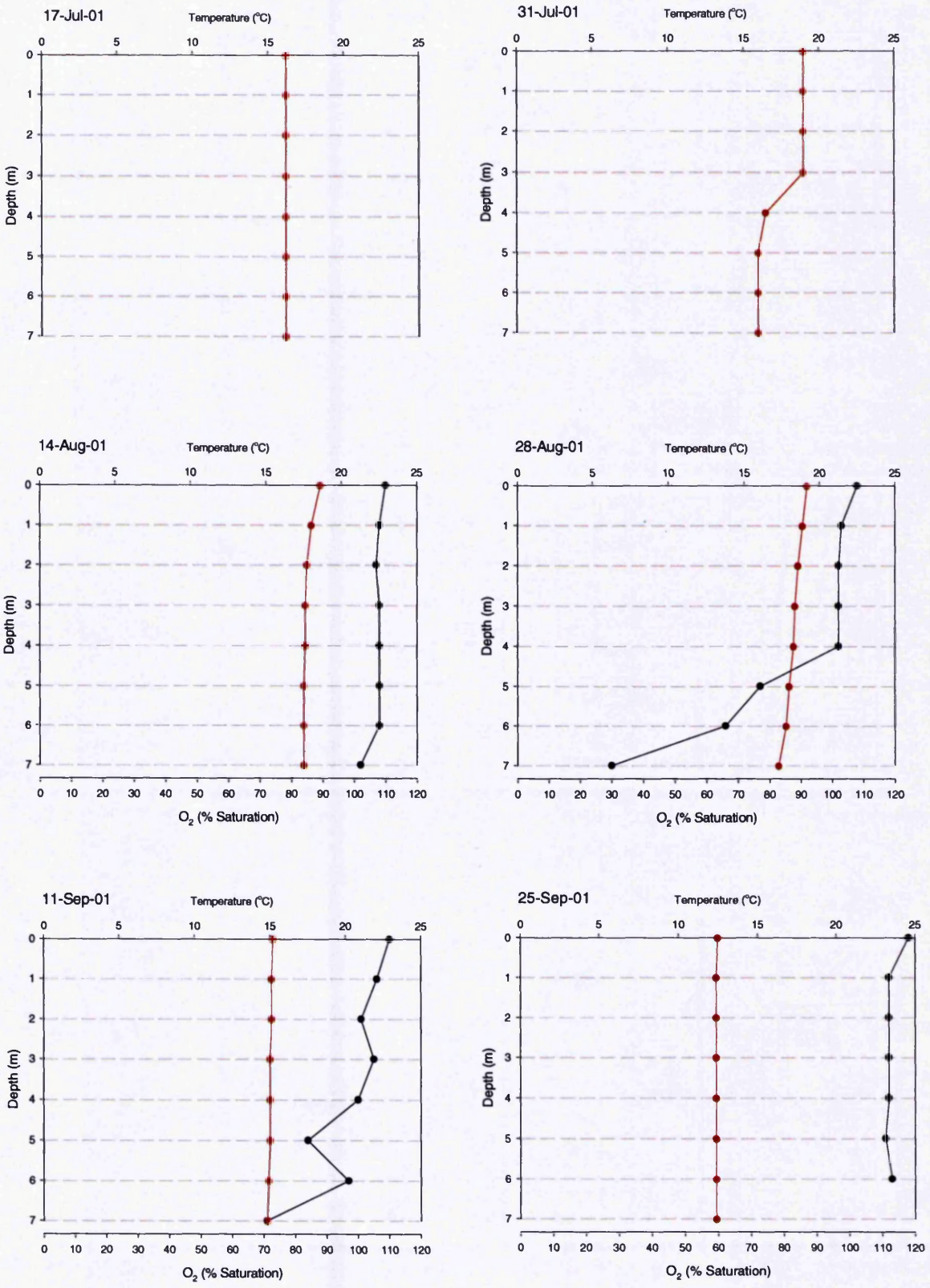


Figure 5.21: Temperature (•) and oxygen (•) profiles for 17th of July to the 25th of September, Hollingworth Lake, 2001.

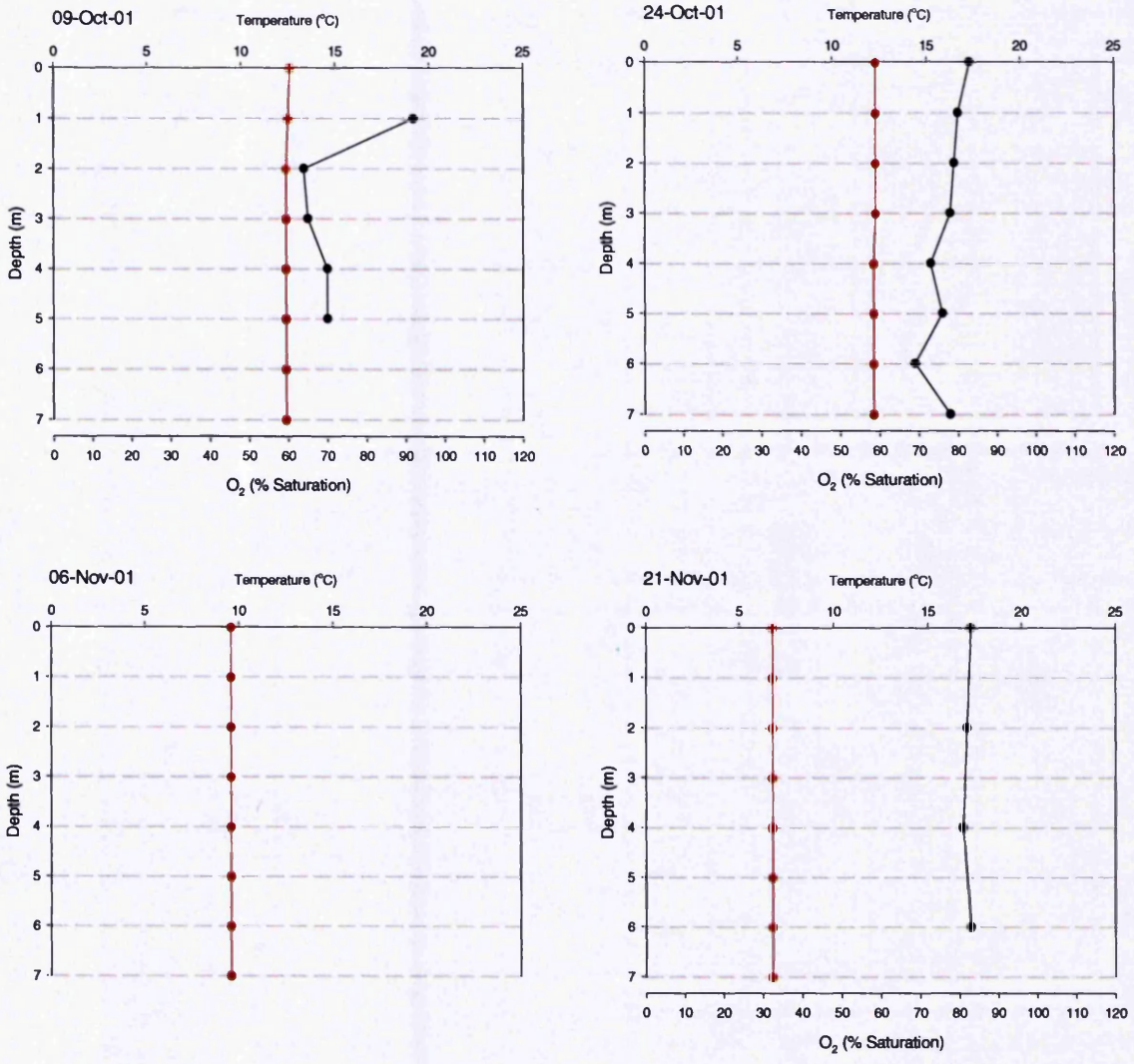


Figure 5.22: Temperature (•) and oxygen (•) profiles for 09th of October to the 21st of November, Hollingworth Lake, 2001.

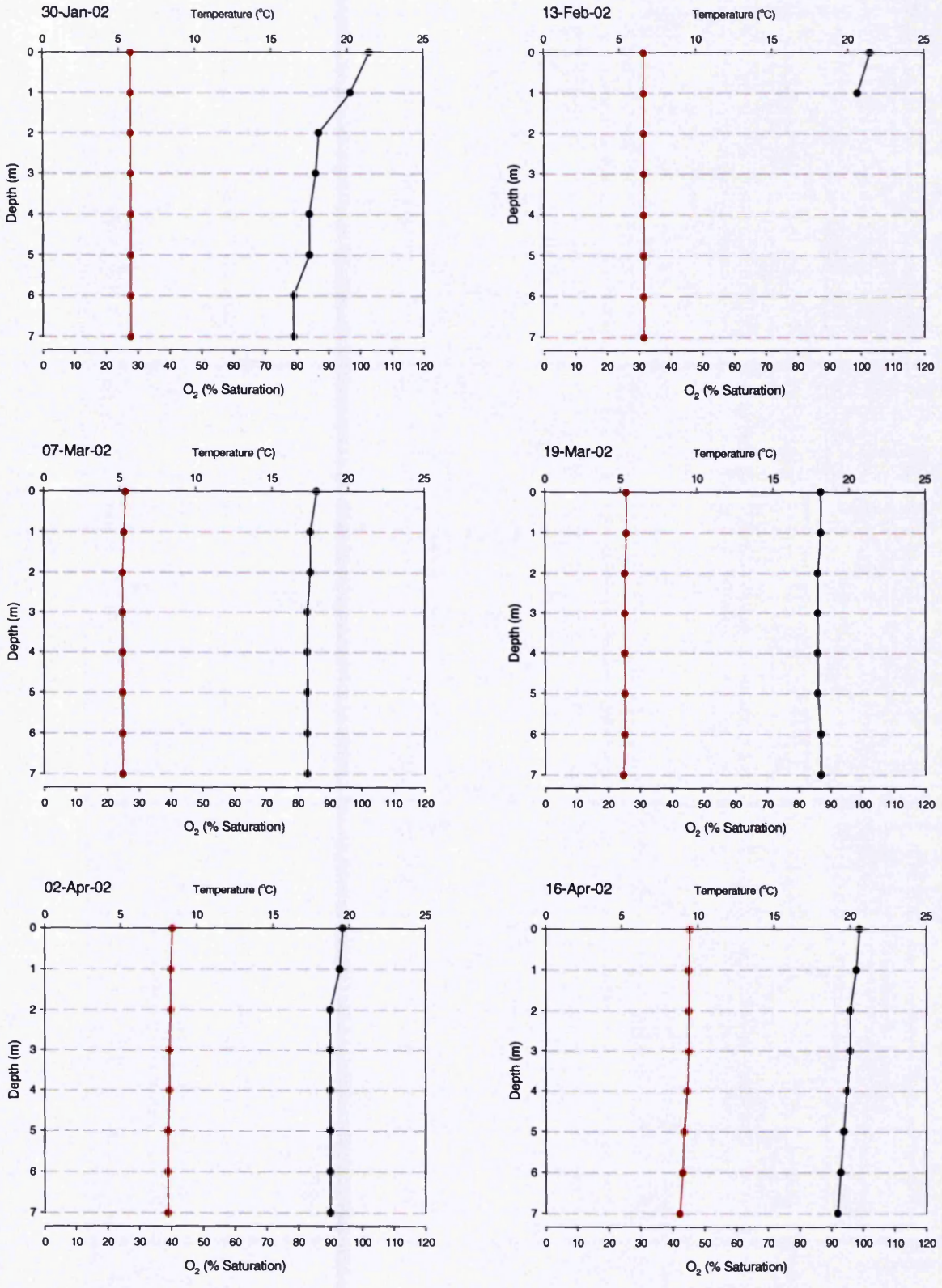


Figure 5.23: Temperature (•) and oxygen (•) profiles for 30th of January to the 16th of April, Hollingworth Lake, 2002.

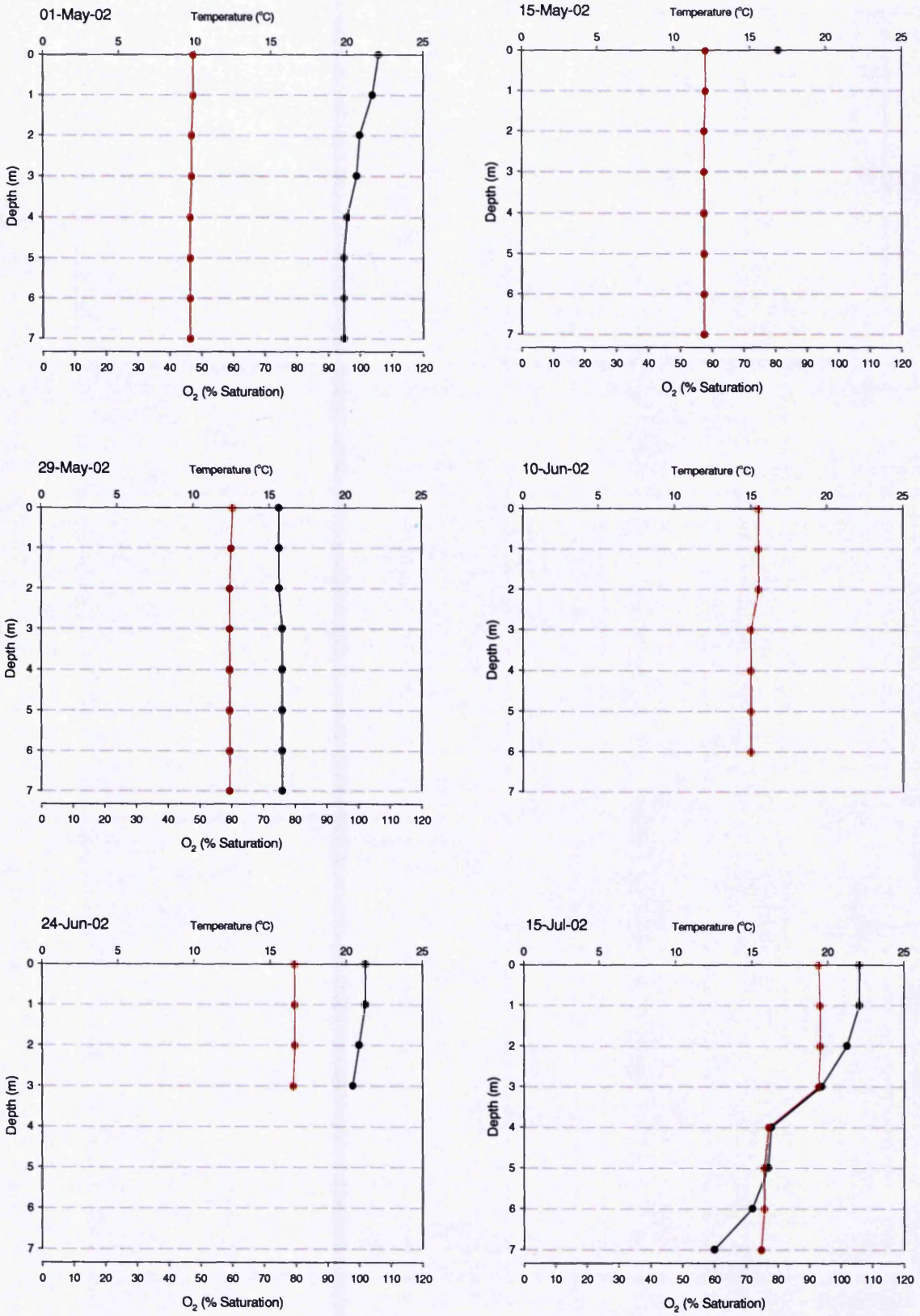


Figure 5.24: Temperature (•) and oxygen (•) profiles for 1st of May to the 15th of July, Hollingworth Lake, 2002.

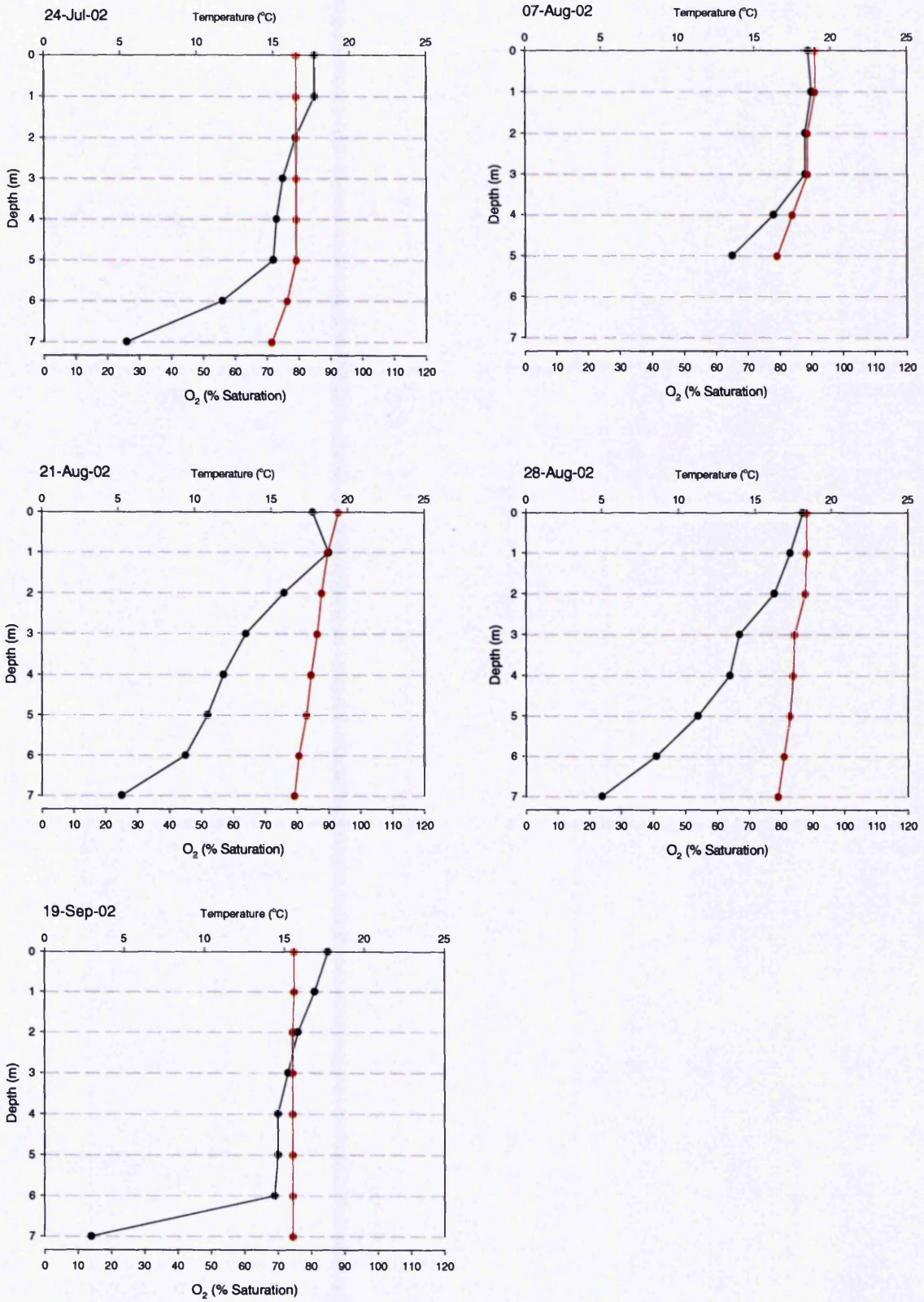


Figure 5.25: Temperature (•) and oxygen (•) profiles for 24th of July to the 19th of September, Hollingworth Lake, 2002

5.2.4 pH

Seasonal variation of pH is shown in Figure 5.26a. During 2001 pH varied between 6.2 and 7.3 while during 2002 pH varied between 6.2 and 7.8.

Year 2001: During the spring and early part of the summer phase (June) pH was approximately 6.2 but increased to approximately 7.0 for the remainder of the summer phase. Values were lower during the autumn maximum (6.3) but increased to a maximum of 7.3 during the autumn decline.

Year 2002: pH dropped from 7.3 in the winter phase to 6.2 in the early spring phase (19th March). By the middle of the spring phase (16th of April) pH had increased to 7.1. It then decreased to 6.4 at the end of the spring phase, before an increase during the summer phase to reach a maximum of 7.8 in late June/mid July before a slight fall to 7.4 by the end of sampling.

5.2.5 Conductivity

Seasonal variation in conductivity is shown in Figure 5.26b. In 2001 conductivity varied between 180 and 238µS while in 2002 conductivity varied between 203 and 234µS.

Year 2001: Conductivity was relatively steady during the spring and early summer phases, varying between 215 and 230µS throughout spring and summer and the first two samplings of the autumn maximum. Thereafter conductivity dropped to 180-190µS.

Year 2002: At the commencement of sampling (winter phase) conductivity was 234µS. It then dropped to remain at approximately 206µS during the spring phase and start of the early summer phase. It then increased to approximately 230µS on the 24th of June/15th July before dropping during August to reach a value of approximately 210µS in late August/September.

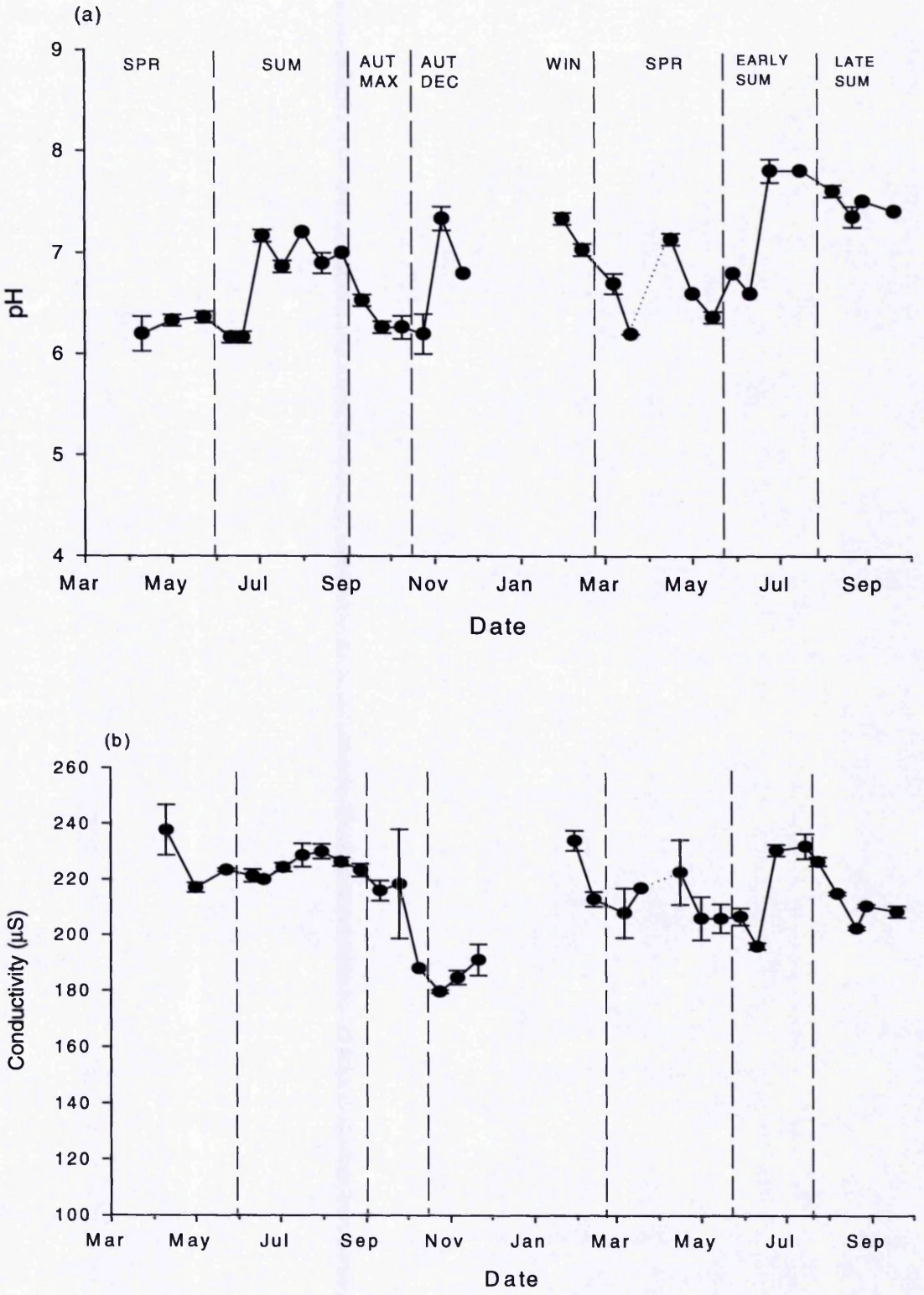


Figure 5.26: Seasonal change in (a) pH and (b) conductivity in Hollingworth Lake, 2001-2002. Due to equipment malfunction no measurement was taken on the 2nd of April. Data points either side of the missing value are therefore joined with a dotted line. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

5.2.6 Phosphorus

5.2.6.1 Soluble reactive phosphorus (SRP)

Seasonal variation in soluble reactive phosphorus is shown in Figure 5.27a.

Year 2001: During the spring phase P increased from 7 to 20μgl^{-1} before falling to undetectable at the beginning of summer phase (11th of June). Concentrations remained low before peaking at 95μgl^{-1} on the 17th of July, then fell to 3μgl^{-1} on July 31st before increasing to a further peak of 33μgl^{-1} on the 14th of August. Concentrations were undetectable at the end of the summer phase and through both the autumn maximum and autumn decline phases.

Year 2002: No large peaks in SRP were observed in 2002. During the winter phase concentrations were approximately 10μgl^{-1}. Spring phase concentrations were lower, varying between 2 and 6μgl^{-1} while during the majority of the summer phases concentrations were undetectable.

5.2.6.2 Total Dissolved Phosphorus (TDP)

Seasonal variation in total dissolved phosphorus is shown in Figure 5.27b.

Year 2001: With the exception of a large peak during the summer phase (127μgl^{-1} on the 17th of July falling to 70μgl^{-1} on the 31st). TDP concentrations were approximately 20μgl^{-1} throughout 2001.

Year 2002: In 2002 no peaks of TDP were observed, concentrations being approximately 10μgl^{-1} throughout the sampling period.

5.2.6.3 Total Phosphorus (TP)

Seasonal variation in total phosphorus is shown in Figure 5.28a.

Year 2001: During the spring total phosphorus fell from 67 to 27$\mu g\ l^{-1}$, remained at approximately 20$\mu g\ l^{-1}$ during the early summer phase (June). There followed a large peak on the 17th of July at 143$\mu g\ l^{-1}$, following which concentrations fell to approximately 30$\mu g\ l^{-1}$ by the end of the summer phase. During autumn maximum phase TP increased to 57μgl^{-1}, before decreasing to 19μgl^{-1} during the autumn decline.

Year 2002: TP showed no large peaks during 2002. Values were approximately 20μgl^{-1} but with increases to 40-50μgl^{-1} on two occasions during the spring phase (19th March, 1st May) and summer phase (10th June, 24th July).

5.2.6.4 Total Particulate Phosphorus (TPP)

TPP is calculated from the difference between TP and TDP so any error in the estimation of these parameters is compounded when TPP is estimated. Hence, determinations of TPP are subject to large errors. Seasonal variation in total particulate phosphorus is shown in Figure 5.28b.

Year 2001: In 2001 the baseline concentration of TPP was approximately $20\mu gl^{-1}$. Concentrations were particularly high during the spring phase (declining from $63\mu g\ l^{-1}$ to $10\mu g\ l^{-1}$), with a further peak during the autumn-maximum phase ($37\mu g\ l^{-1}$), before falling during the autumn decline.

Year 2002: In 2002 TPP concentrations during the winter and early spring were approximately $20\mu g\ l^{-1}$, with peaks in TPP to approximately $30\text{-}40\mu gl^{-1}$ occurring (concurrently with peaks in total phosphorus) during the spring phase (19th March, 1st May) and summer phase (10th June, 24th July).

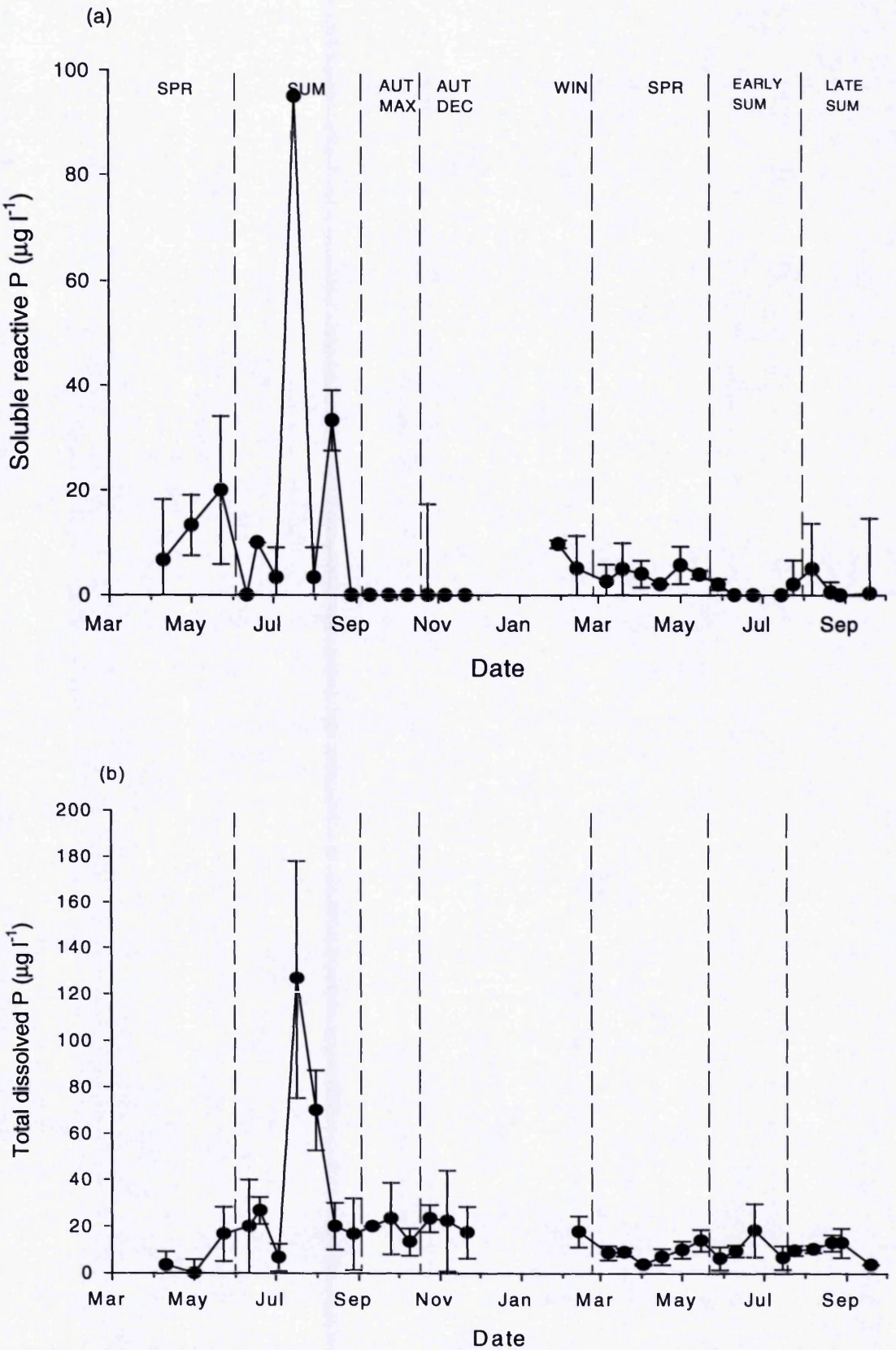


Figure 5.27: Seasonal change in (a) soluble reactive P and (b) total dissolved P, Hollingworth Lake, 2001-2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

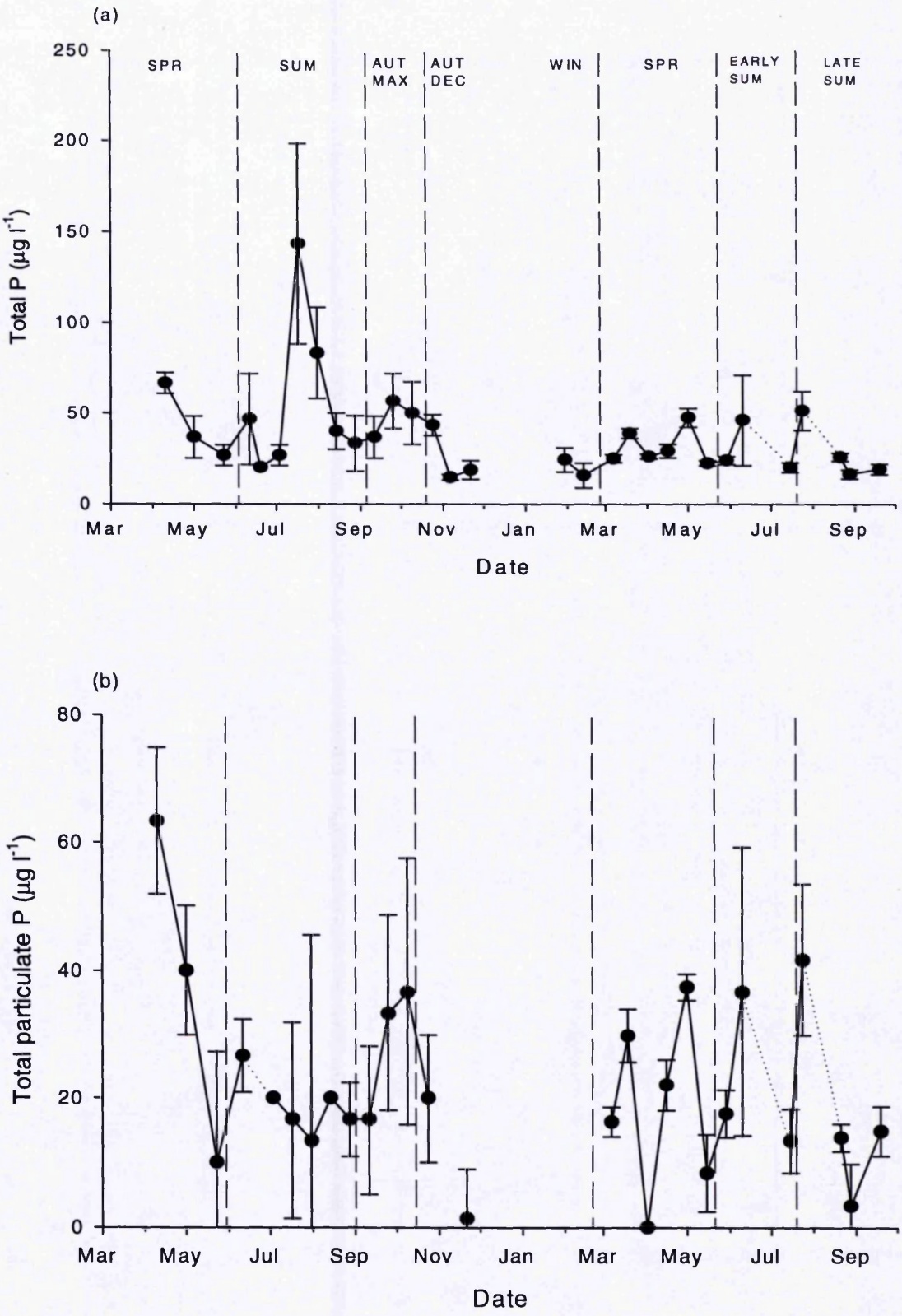


Figure 5.28: Seasonal change in (a) total P and (b) total particulate P, Hollingworth Lake, 2001-2002. Values either side of missing values are joined by a dotted line. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

5.2.7 Nitrogen compounds

5.2.7.1 Nitrates and Nitrites

Seasonal variation in nitrates/nitrites is shown in Figure 5.29a.

Year 2001: During the spring nitrates/nitrites were approximately 0.40mg l^{-1}, with a peak value of 0.48mg l^{-1} on the 1st of May, following which concentrations fell gradually until mid-July, reaching 0.36mg l^{-1}, and then more rapidly, reaching 0.04 mg l^{-1} at the end of the summer phase (August the 28th). During the autumn maximum concentrations remained at approximately this level, reaching a minimum of 0.02mg l^{-1} at the start of the autumn decline, before increasing to 0.1mg l^{-1} at the end of sampling.

Year 2002: Winter concentrations were approximately 0.45mgl^{-1} and increased rapidly during the early spring phase to reach a maximum of 0.85mgl^{-1} on the 2nd of April. Concentrations fell during the remainder of the spring phase, reaching a minimum 0.30mgl^{-1} at the commencement of the summer phase. There was a gradual fall in concentrations during the early summer, reaching a minimum of 0.18mgl^{-1} on the 24th of July. Concentrations then increased to approximately 0.30mgl^{-1} during August and September.

5.2.7.2 Total Dissolved Nitrogen (TDN)

Seasonal variation in total dissolved nitrogen is shown in Figure 5.28b.

Year 2001: During the spring phase TDN was approximately 0.60 mg l^{-1}, increasing to 1.10mg l^{-1} at the start of the summer phase. During the remainder of the summer phase concentrations fell, reaching a minimum of 0.08mg l^{-1} during the autumn maximum. Concentrations then increased, reaching a maximum of 0.75mg l^{-1} by the end of sampling (21st of November).

Year 2002: During the winter and at the start of the spring phase concentrations were approximately 0.90mg l^{-1}. Concentrations fell during the spring phase, reaching a minimum of 0.41mg l^{-1} at the phases' end, but by the start of the summer phase concentrations had increased to approximately 0.72mg l^{-1}. On the 15th July concentrations had reached a summer phase minimum of 0.42mg l^{-1}, after which concentrations increased to 0.59mg l^{-1} at the end of sampling.

5.2.7.3 Total Nitrogen (TN)

Seasonal variation in total nitrogen is shown in Figure 5.30a.

Year 2001: During the spring phase concentrations were ca. 0.75 mg l^{-1}, increasing to 1.10mg l^{-1} at the start of the summer phase. During the remainder of the summer phase concentrations fell, reaching a minimum of 0.44mg l^{-1} on the 14th of August, and remained low during the autumn-maximum phase. During the autumn decline concentrations increased to 1.00mg l^{-1}.

Year 2002: During the winter phase concentrations peaked at 1.4mg l^{-1} (February), following which they declined to reach a minimum of 0.65mg l^{-1} in early spring (2nd April). Concentrations then increased to approximately 0.90mg l^{-1} during the late spring phase and early summer phase before decreasing again to a mid-summer minimum of 0.63mg l^{-1} (15th July), following which concentrations remained low until the end of sampling (between 0.65 and 0.78mg l^{-1}).

5.2.7.4 Total Particulate Nitrogen (TPN)

TPN is calculated from the difference between TN and TDN so any error in the estimation of these parameters is compounded when TPN is estimated. Hence, determinations of TNN are subject to large errors. Seasonal variation in total particulate nitrogen is shown in Figure 5.30b.

Year 2001: A broad in TPN occurs during the late summer/autumn maximum phases, coinciding with the peak in chlorophyll-a, reaching a maximum of 0.34mg l^{-1} during the autumn maximum.

Year 2002: During 2002 the baseline concentration of TPN was approximately 0.20mg l^{-1} with two peaks of ca. 0.45mg l^{-1} on the 13th of February and 15th May.

5.2.7.5 Ammonia

Seasonal variation in ammonia is shown in Figure 5.31.

Year 2001: Concentrations were highest during the summer phase (max 0.08mg l^{-1}), fell to undetectable during the autumn maximum, and then increased during the autumn decline to 0.07mg l^{-1}.

Year 2002: Concentrations were at a maximum during the winter (0.07mg l^{-1}), reached minimum values during the spring (undetectable), and increased during the late summer (max. 0.05mg l^{-1}).

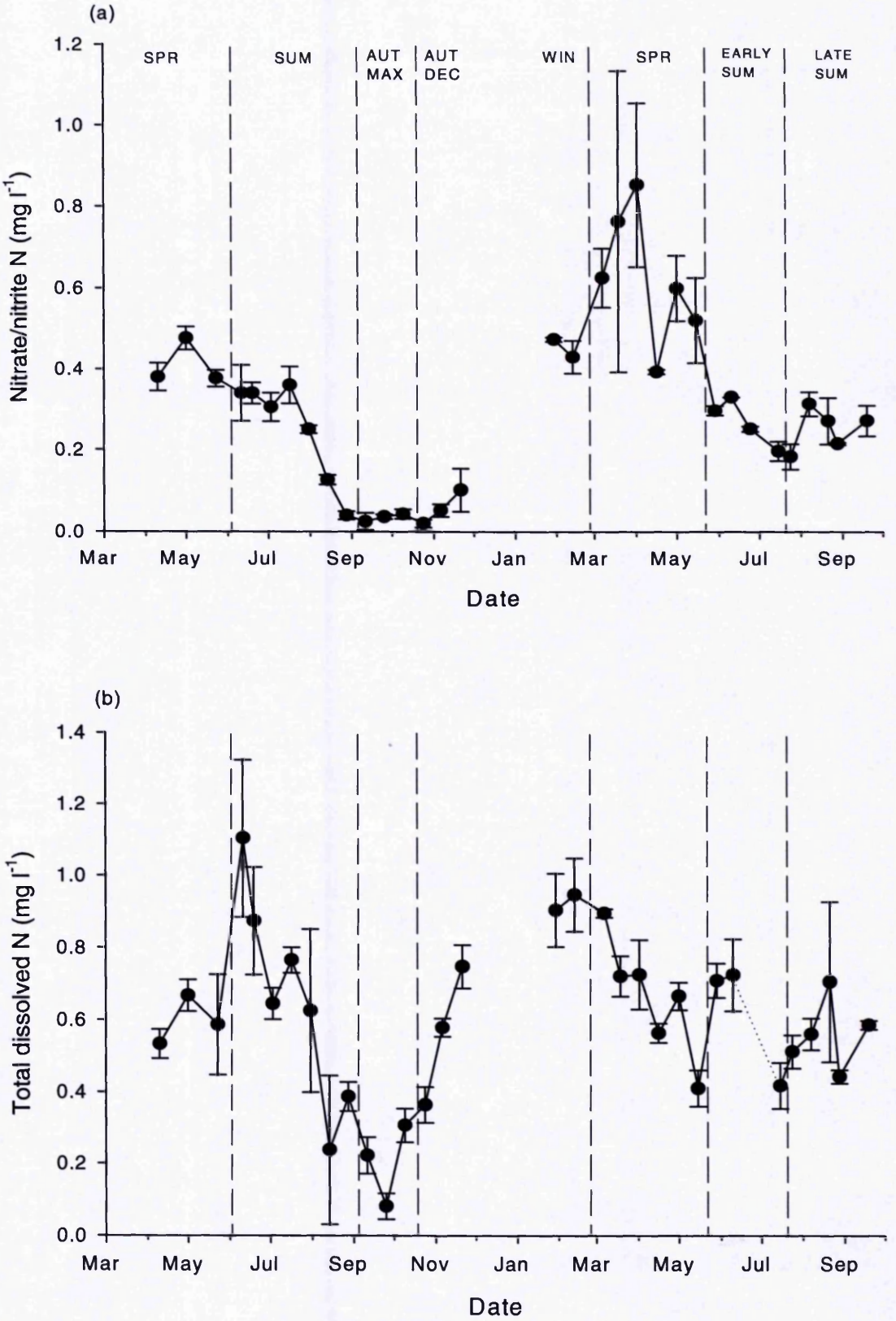


Figure 5.29: Seasonal change in (a) nitrate/nitrite N and (b) total dissolved N, Hollingworth Lake, 2001-2002. Values either side of missing values are joined by a dotted line. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

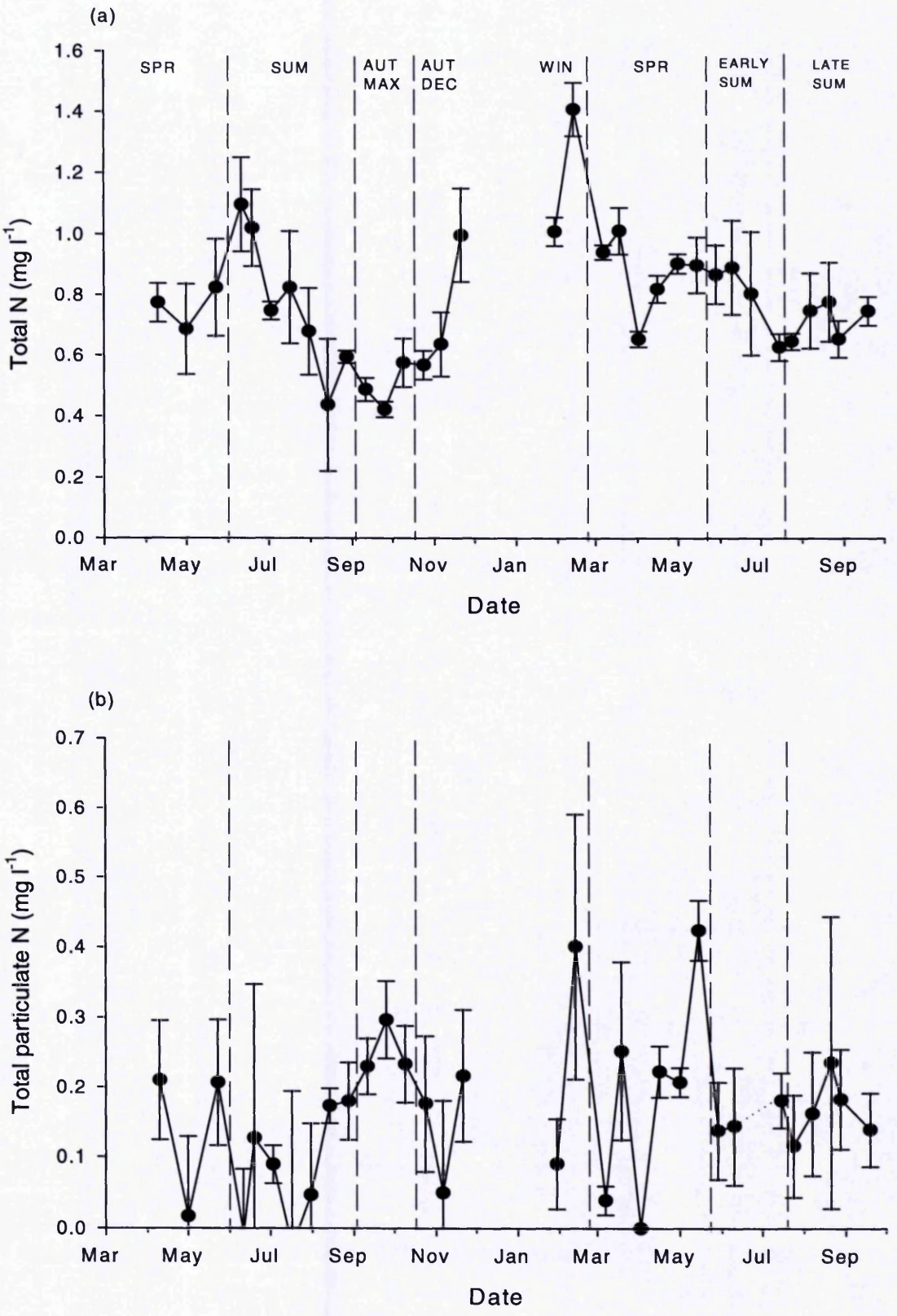


Figure 5.30: Seasonal change in (a) total N and (b) total particulate N, Hollingworth Lake, 2001-2002. Values either side of missing values are joined by a dotted line. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3)

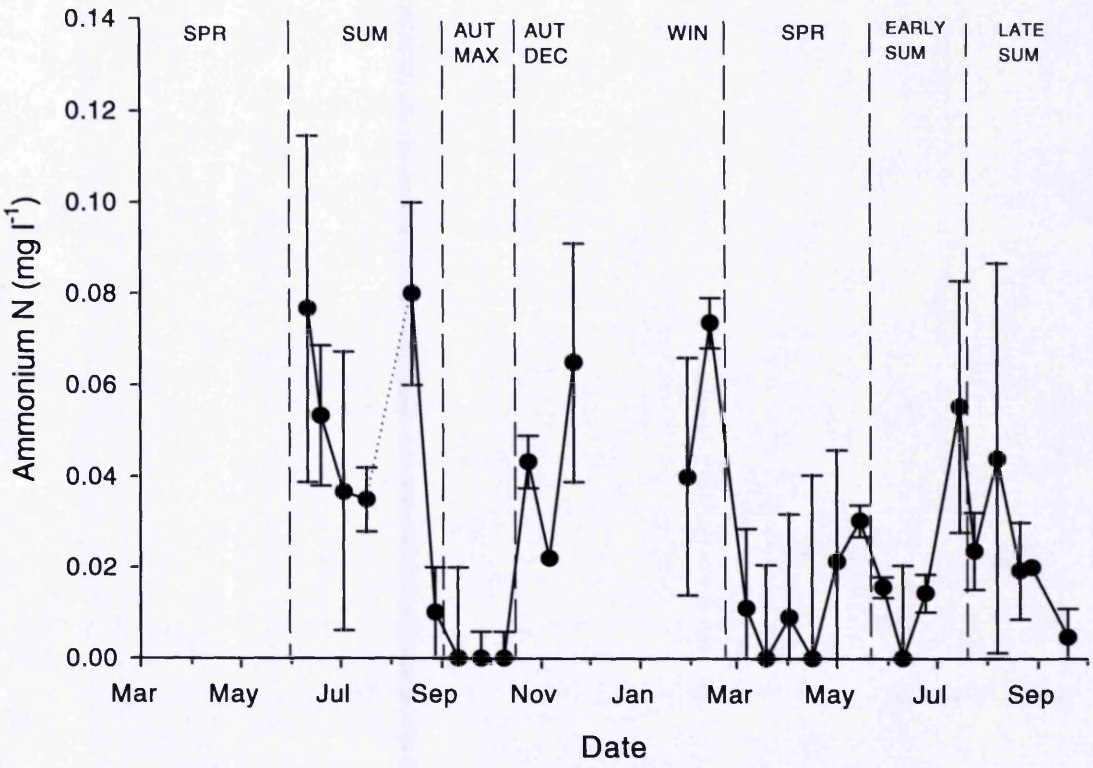


Figure 5.31: Seasonal change in ammonium-N, Hollingworth Lake, 2001-2002. Values either side of missing values are joined by a dotted line. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3)

5.2.8 Silicon

Seasonal changes in silicon concentrations are shown in Figure 5.32.

Year 2001: At the commencement of sampling (10th of April) the concentration of silicon was 2.10 mg l^{-1}. Concentrations fell rapidly to reach 0.13 mg l^{-1} at the start of the summer (11th of June), with summer concentrations remaining at approximately 0.15 mg l^{-1} (with a slight increase in mid-august to 0.33 mg l^{-1}). Concentrations decreased to an annual minimum of 0.07 mgl^{-1} during the autumn maximum phase, following which concentrations increased rapidly, reaching 1.71 mg l^{-1} on the 6th of December.

Year 2002: At the end of the winter phase silicon was 2.15 mg l^{-1} Values again dropped rapidly during the spring, from 2.18 mg l^{-1} on the 7th of March to 1.15 mg l^{-1} on the 15th of May. Concentrations continued to drop during the early summer phase, from 1.01 mg l^{-1} on the 29th of May to undetectable on the 24th of June, remaining undetectable through to the 24th of July. Concentrations began to increase in during the late summer phase, reaching 0.64 mg l^{-1} at the end of sampling.

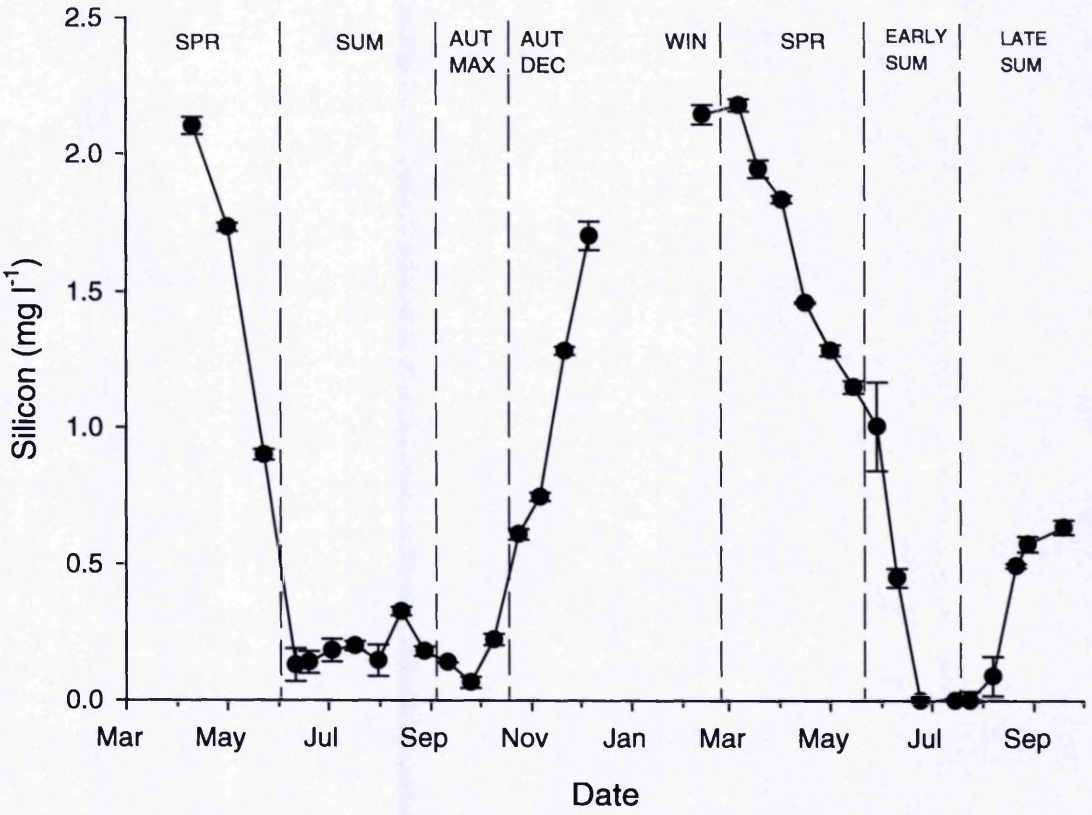


Figure 5.32: Seasonal change in silicon concentrations, Hollingworth Lake, 2001-2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

5.3 Zooplankton

5.3.1 Zooplankton dry weight

Zooplankton dry weight is shown in Figure 5.33.

Year 2001: On the first two sampling occasions during the spring period zooplankton dry weight was approximately 30μg l^{-1}. This was followed by a large peak across the spring/summer phase boundary with dry to increasing during late spring until it reached a maximum of 282 μg l^{-1} in the early summer phase (19th of June). Dry weight then rapidly declined, reaching an annual minimum of 7μg l^{-1} on the 31st of July. Dry weight then began to increase, increasing through both the autumn maximum and autumn decline phases to reach 93.7μg l^{-1} in November.

Year 2002: In 2002 zooplankton dry weight also showed a late spring/early summer peak. Dry weight was low during the winter phase, with values approximately 15μg l^{-1} and began to increase during the spring phase, gradually until mid-April, and more rapidly thereafter, reaching a peak of 228μg l^{-1} at the commencement of the summer phase. During the early summer phase dry weight decreased to a minimum of 60μg l^{-1} at the phases' end (mid-July), before increasing to a 122μg l^{-1} in late August. Dry weight then fell to 45μg l^{-1} by the end of sampling.

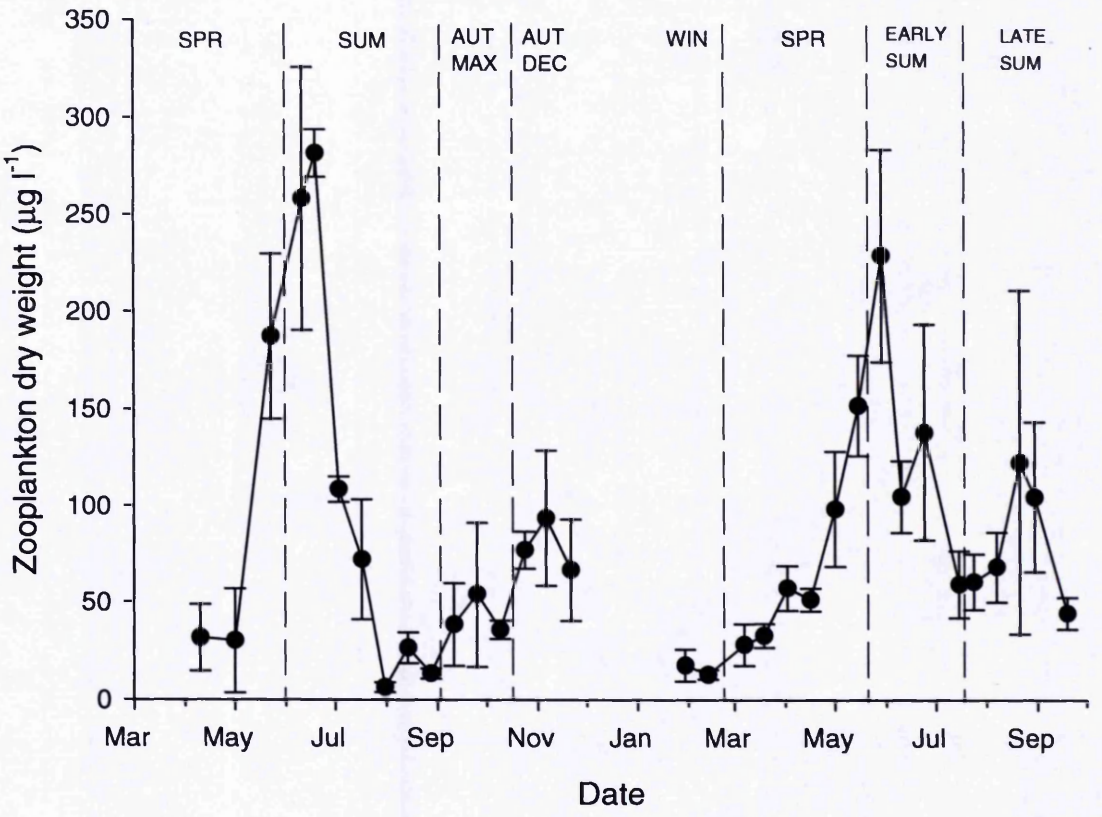


Figure 5.33: Seasonal changes in zooplankton dry weight, Hollingworth Lake, 2001-2002. Values are means of full water column trawls taken at sites A, B and C. Error bars ±1 SD. (n=3).

Zooplankton Population Parameters

5.3.1.1 *Daphnia*

Counts

Seasonal change in the numbers of *Daphnia* is shown in Figure 5.34a. The *Daphnia* populations in Hollingworth Lake were dominated by *Daphnia cucculata.*

Year 2001: On the first two sampling occasions during the spring period *Daphnia* were present at approximately 0.5 *Daphnia* l^{-1}. This was followed by a peak in numbers early in the summer phase, with numbers beginning to increase during late spring until they reached a maximum of 30.9 *Daphnia* l^{-1} in the early summer phase (19th of June). Numbers then rapidly declined, reaching a minimum of 1.4 *Daphnia* l^{-1} during the middle of the summer phase (31st of July). Note that on this date all four zooplankton groups exhibited a minimum. During the remainder of the summer phase numbers increased slightly, resulting in a small peak in the middle of the autumn maximum. Numbers remained between 9.1 and 15.0 *Daphnia* l^{-1} until the final sampling occasion, when numbers had fallen to 5.9 *Daphnia* l^{-1}.

Year 2002: In 2002 *Daphnia* numbers also showed a late spring/early summer peak. Numbers were low (ca. 0.1 *Daphnia* l^{-1}) during the winter and the early spring phase and began to increase slightly during April, followed by a much more rapid increase during May, reaching a peak of 39.8 *Daphnia* l^{-1} at the start of the early summer phase. Numbers then dropped, reaching 8.4 *Daphnia* l^{-1} on the at the end of the early summer phase (24th of July). There was a further increase in numbers during the late summer phase, reaching 19.6 *Daphnia* l^{-1} on the 21st of August

Percentage Gravid

Seasonal changes in the proportion of gravid *Daphnia* are shown in Figure 5.34b.

Year 2001: Percentage gravid *Daphnia* were elevated during the spring phase (max 26% on the 1st of May), fell to low levels in the early summer phase (6% in June) and then increased with elevated values (40-50%) lasting throughout the remainder of the summer phase (although there was a fall to 15% on the 31st of July). During the autumn maximum and autumn decline phases values declines to reach a minimum of 2%.

Year 2002: During the winter phase were high (maximum 50%), falling to 14% at the commencement of the spring phase (these values for the early part of the season must be treated with caution, as due to the low numbers of *Daphnia* present at this time they are based on a low n-number). On the 19th March the percentage of gravid *Daphnia* was 43%, following which it declined to 27% by the end of the spring phase and continued to fall during the early summer phase to reach a minimum of 7% at the end of the early summer phase. With the exception of the final sampling occasion (30%), percentage gravid remained at <15% for the remainder of sampling.

Brood Size

Seasonal changes in the average brood size of gravid *Daphnia* are shown in Figure 5.35a. In both years average brood size was at a maximum during the spring phase.

Year 2001: Brood size was at a maximum at the commencement of sampling with an average of 5. During the remainder of the spring phase this had fallen to approximately 3.3, and by the start of the summer phase had fallen further to a minimum of 1.6 (19th June). There was a very slight increase to approximately 2 during the later part of the summer phase, followed by a fall to 1.0 by the end of sampling.

Year 2002: During the winter phase brood size was low (<1). During the spring phase there was an increase in average brood size, leading to a long period when the brood size was approximately 5 (2nd April–1st of May). There was then a decrease with brood size approximately 1.2 at the start of the early summer phase. A slight increase followed to 2.0 on the 15th of July, following which brood size was approximately 1.5 until the end of sampling.

Birth Rate

Seasonal change in the *Daphnia* birth rate is shown in Figure 5.35b.

Year 2001: *Daphnia* birth rate increased during the spring phase from 0.04 to 0.08, fell to low levels at the start of the summer phase (0.02 in June) and then increased to reach maximum values of approximately 0.22 on the 14th and 28th August. During the autumn maximum and autumn decline values fell, to reach a minimum of 0.00 at the end of sampling.

Year 2002: During the winter phase *Daphnia* birth rate was approximately 0.03. During the spring phase there was an increase from 0.01 at the start of the phase to a

mid-phase maximum of 0.12 (16th of April), followed by a decline to 0.02 at the start of the early summer phase. During the summer phase there was a slight increase to 0.07 on the 7th of August, followed by a fall to 0.03 on the 21st of August. There was then an increase in birth rate, reaching 0.10 at the end of sampling.

Size

Average *Daphnia* body size is shown in Figure 5.36. Mean body size varied between 0.70mm and 0.97mm. Average length over the whole sampling period was 0.82mm. The only noticeable change in mean length occurred during 2001, when mean length increased from 0.76mm during the spring phase to 0.97mm during the early summer phase, with values returning to 0.76mm at the end of July.

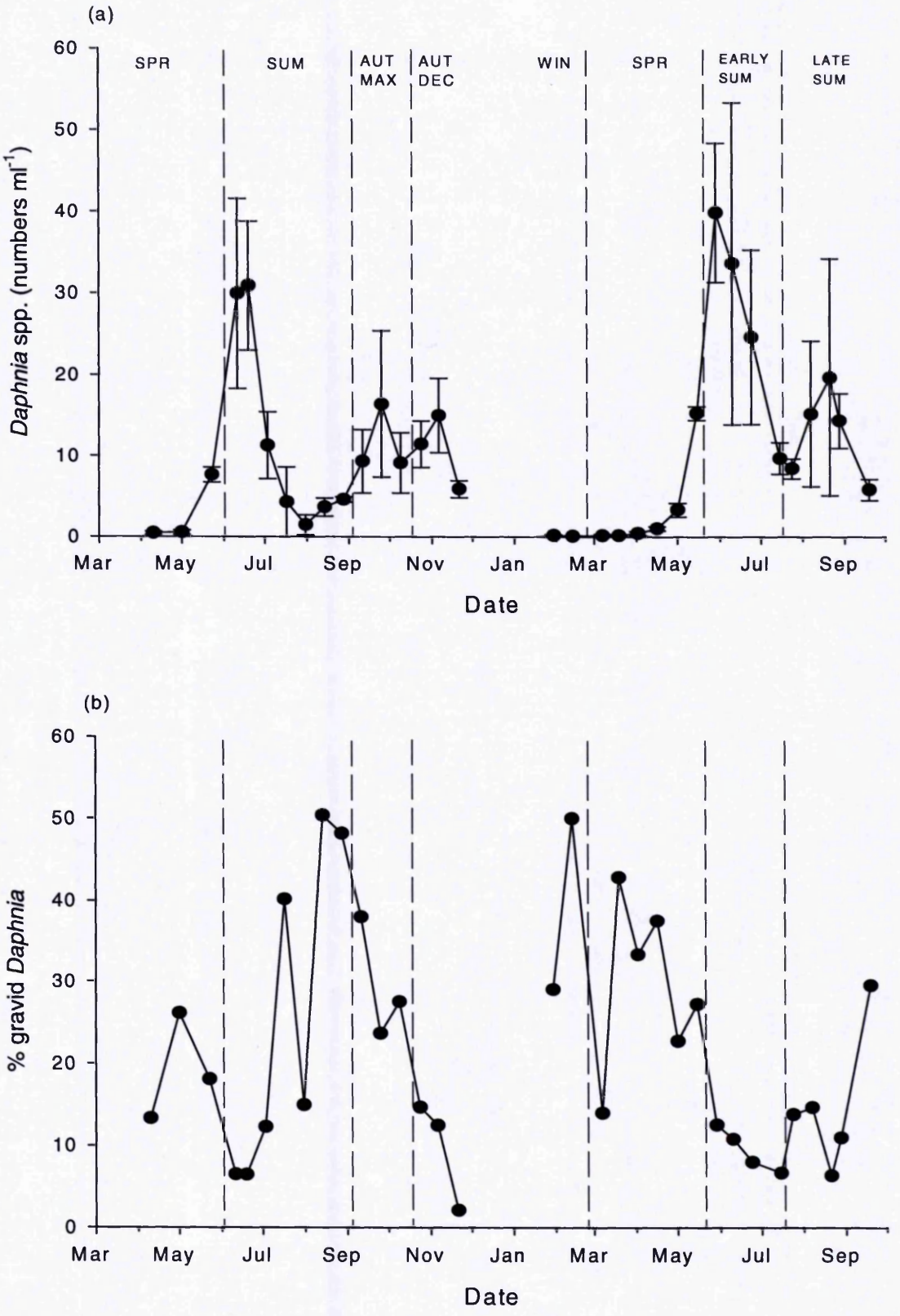


Figure 5.34: Seasonal changes in (a) the numbers of *Daphnia*. Values are the mean of vertical trawls taken from sites A, B and C. Error bars ±1 SD. (n=3). (b) proportion of gravid adult *Daphnia*, calculated using the sum (sites A, B and C combined) of all gravid *Daphnia* and total *Daphnia* counted during the determination of seasonal changes in Hollingworth Lake, 2001-2002.

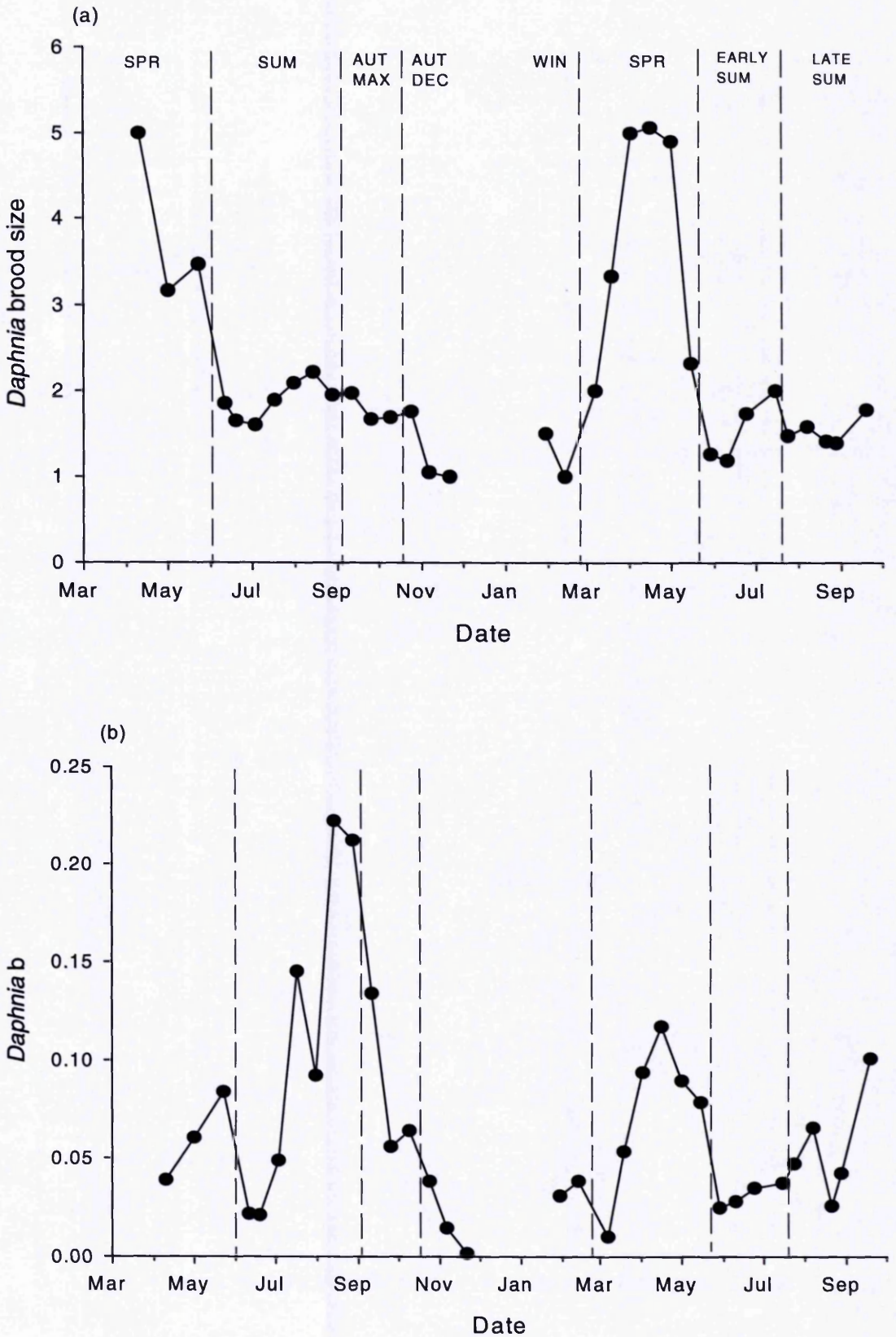


Figure 5.35: Seasonal changes in (a) average brood size of *Daphnia* and (b) the instantaneous birth rate of *Daphnia*, Hollingworth Lake, 2001-2002. In both cases calculations were based on combined data from all three sites.

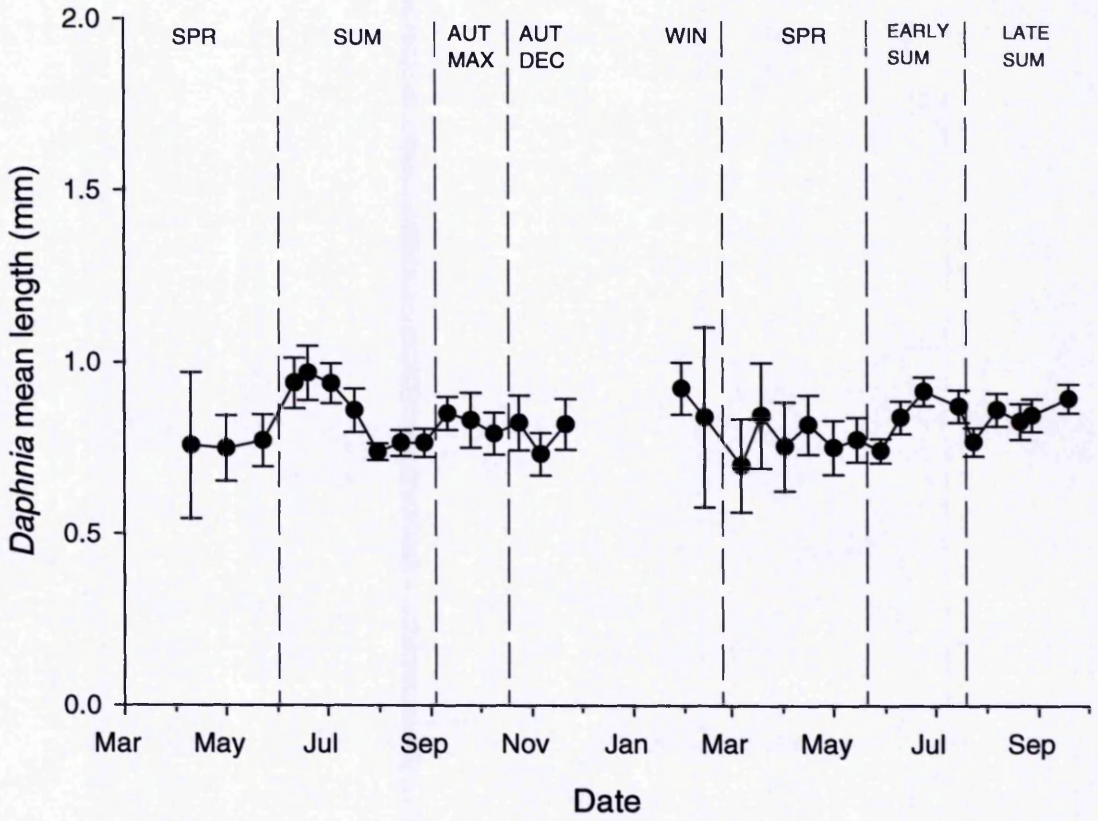


Figure 5.36: Seasonal changes in the average length of *Daphnia* in Hollingworth Lake, 2001-2002. Values are the mean lengths of animals randomly selected from sites A, B and C. Error bars show 95% confidence intervals.

5.3.1.2 *Bosmina*

Counts

Seasonal change in the numbers of *Bosmina* is shown in Figure 5.37a.

Year 2001: On the first two sampling occasions during the spring phase *Bosmina* were present at approximately 1 *Bosmina* l^{-1}. Numbers began to increase during late spring until they reached 6.8 *Bosmina* l^{-1} at the start of the summer phase (19th of June). Numbers then rapidly declined to a minimum of 0.2 *Bosmina* l^{-1} on the 31st of July. During the remainder of the summer phase, and through the autumn maximum phase numbers remained low (<1 *Bosmina* l^{-1}), but increased during the autumn decline to reach 9.8 *Bosmina* l^{-1}.

Year 2002: During the winter and early spring phase numbers were low (<1 *Bosmina* l^{-1}). Numbers began to increase in April (slightly before the *Daphnia* increase), reaching a peak of 29.6 *Bosmina* l^{-1} at the end of the spring phase (before the maximum of *Daphnia* numbers). During the early summer phase numbers fell rapidly, reaching 1.3 *Bosmina* l^{-1} on June 28th. There was then a gradual increase in numbers, reaching 7.1 *Bosmina* l^{-1} by the end of sampling.

Percentage Gravid

Seasonal changes in the proportion of gravid *Bosmina* are shown in Figure 5.37b.

Year 2001: The percentage gravid *Bosmina* were elevated during the spring phase (max 70% on the 1st of May), fell to low levels at the start of the summer phase (11% on the 19th June). It then increased to a long period of elevated values (>70%) lasting throughout the remainder of the summer phase and into the start of the autumn maximum phase, during which the proportion of gravid *Bosmina* began to decline, reaching a minimum of 13% at the end of sampling.

Year 2002: At the commencement of sampling (winter phase) the % gravid *Bosmina* was 13%. There was an increase to approximately 40% either side of the winter/spring phase boundary, before a fall to 21% in March. During the remainder of the spring phase values increased, peaking at 62% on the 31st of May. This was followed by a rapid decline to a minimum (1%) at the commencement of the early summer phase. There was then an increase to approximately 50% in mid-late July, a fall to approximately 28% at the start of the late summer phase (early-mid August), followed by an increase to approximately 60%.

Brood Size

Seasonal changes in the average brood size of gravid *Bosmina* are shown in Figure 5.38a. In both years average brood size was at a maximum during the spring phase.

Year 2001: The maximum brood sizes occurred during the spring phase (max 4.4 on May 1st) following which the average brood size fell to reach a minimum at the start of the summer phase (1.3 on the 19th of June). There was then a slight increase through the remainder of the summer phase and autumn maximum, peaking at 2.7 at the end of the autumn maximum phase. During the autumn decline brood size fell to reach 1.1 at the end of sampling.

Year 2002: At the commencement of sampling (winter phase) brood size was 1, following which it increased to reach a mid-spring phase peak of 2.9 on the 2nd of April. During late spring brood size decreased, reaching approximately 1 either side of the spring/summer phase border. There was a slight increase to 1.9 by the end of the early summer phase, following which average brood size was approximately 1.5.

Birth Rate

Seasonal change in *Bosmina* birth rate is shown in Figure 5.38b. Changes in *Bosmina* birth rates followed a similar pattern to *Daphnia* birth rates.

Year 2001: During the spring phase *Bosmina* birth rates increased from 0.04 to 0.11, fell to low levels at the start of the summer phase (0.02 on 19th June) and then increased to reach maximum values of approximately 0.18 on the 31st of July and remaining high throughout August. During the autumn maximum values declined (approximately 0.09 at the phases' end), with a further fall during the autumn decline, reaching a minimum of approximately 0.01 at the end of sampling.

Year 2002: Birth rates were low during the winter phase and early spring phase ($\leq$0.02), increased to 0.06 towards the end of the spring phase and then declined to reach $\leq$0.01 on either side of the spring/summer phase boundary. There was an increase during the early summer phase to a maximum of 0.12 on the 15th of July followed by a decline to 0.06 in early August. There was then an increase to approximately 0.09 at the end of sampling.

Sizes

Mean *Bosmina* length over the sampling period is shown in Figure 5.39. Values varied from 0.37mm to 0.53mm, with an average length of 0.42mm over the whole sampling period. A possible seasonal change was a decrease in mean length from 0.53mm at the start of the 2001 spring phase to approximately 0.37mm at the end of the summer phase, and a difference in mean size between the early (approximately 0.50mm) and late (approximately 0.38mm) spring phase in 2002.

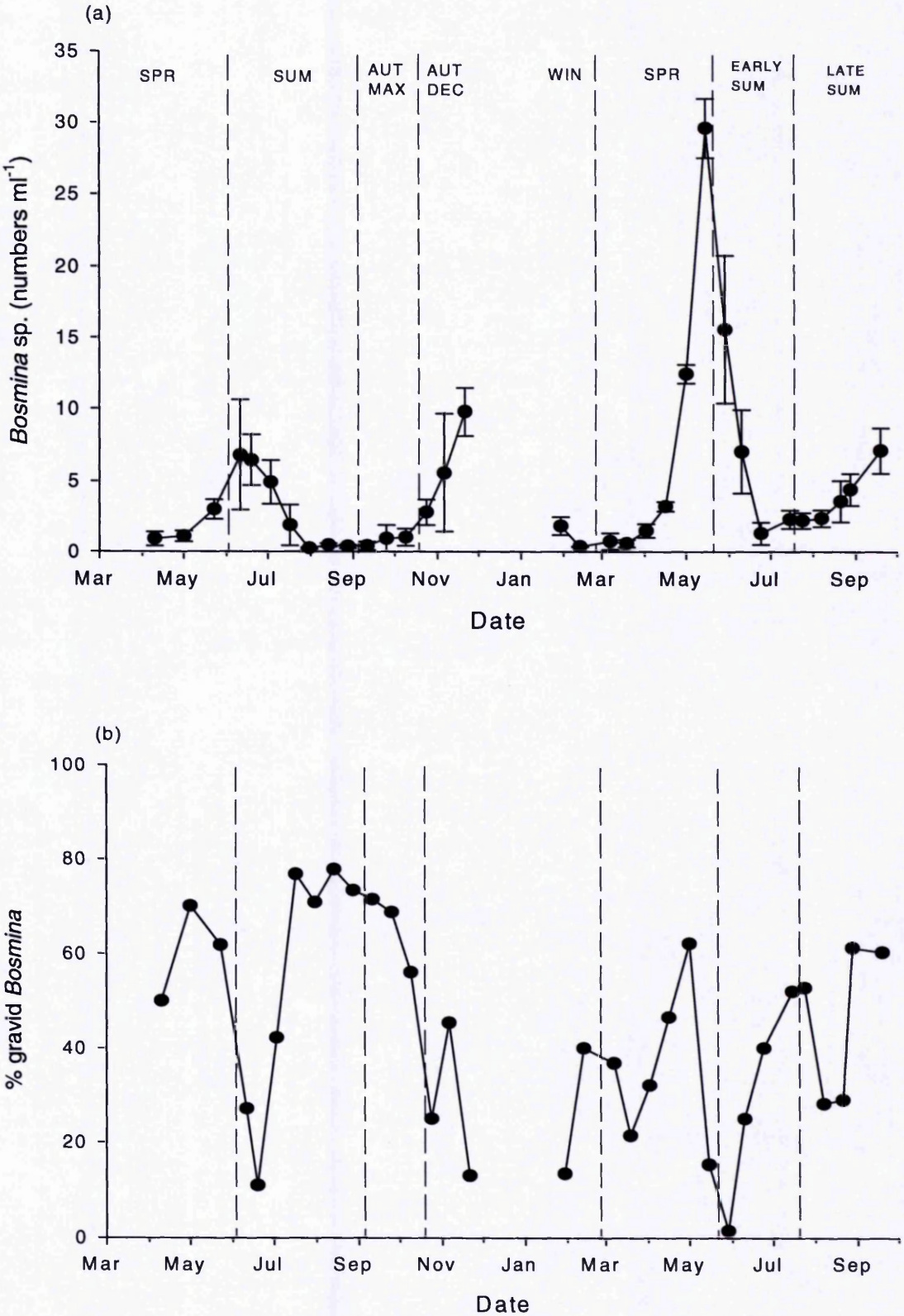


Figure 5.37: Seasonal changes in (a) the numbers of *Bosmina*. Values are the mean of vertical trawls taken from sites A, B and C. Error bars ±1 SD. (n=3). (b) proportion of gravid adult *Bosmina*, calculated using the sum (sites A, B and C combined) of all gravid *Bosmina* and total *Bosmina* counted during the determination of seasonal changes. Hollingworth Lake, 2001-2002.

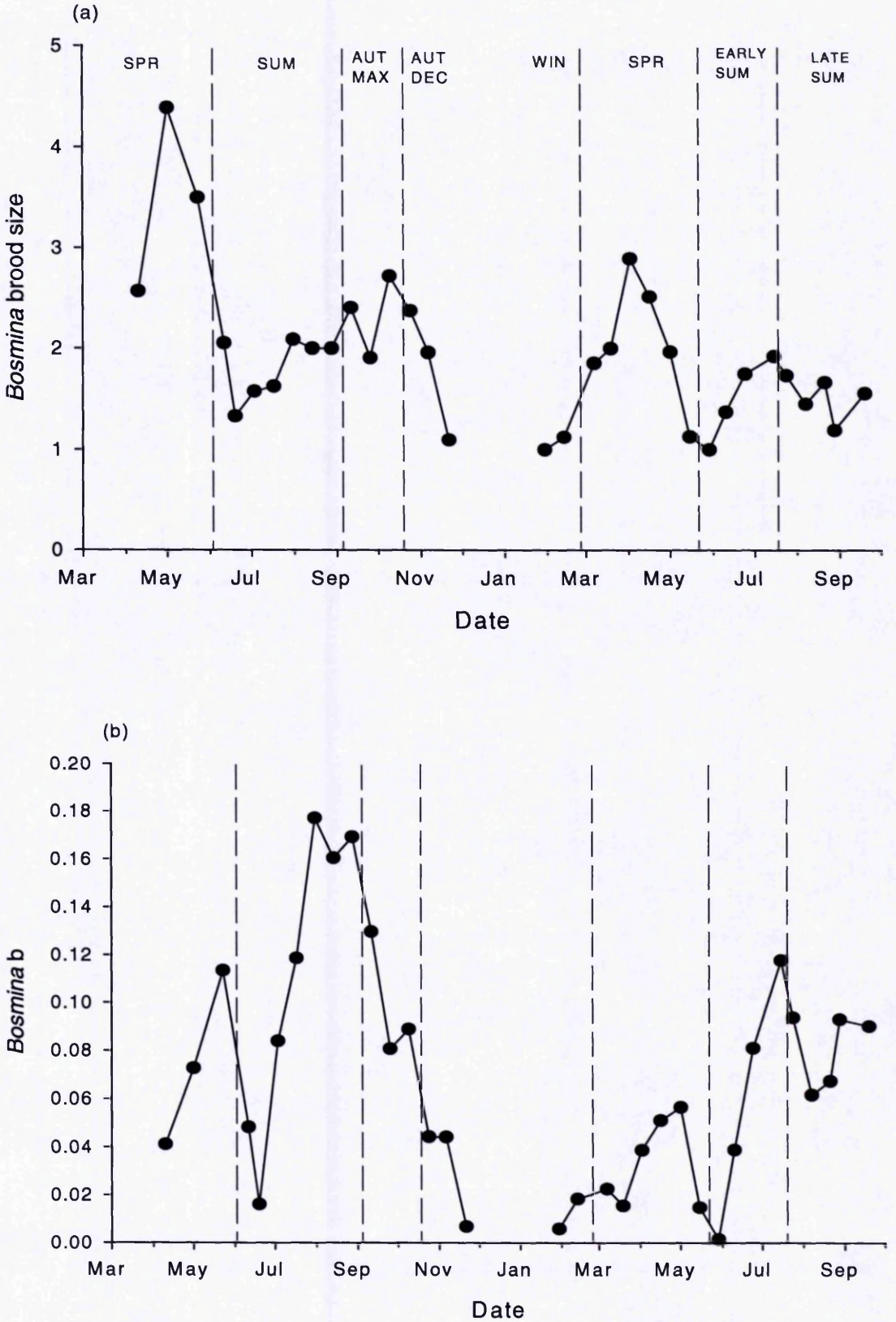


Figure 5.38: Seasonal changes in (a) average brood size of *Bosmina* and (b) the instantaneous birth rate of *Bosmina*, Hollingworth Lake, 2001-2002. In both cases calculations were based on combined data from all three sites.

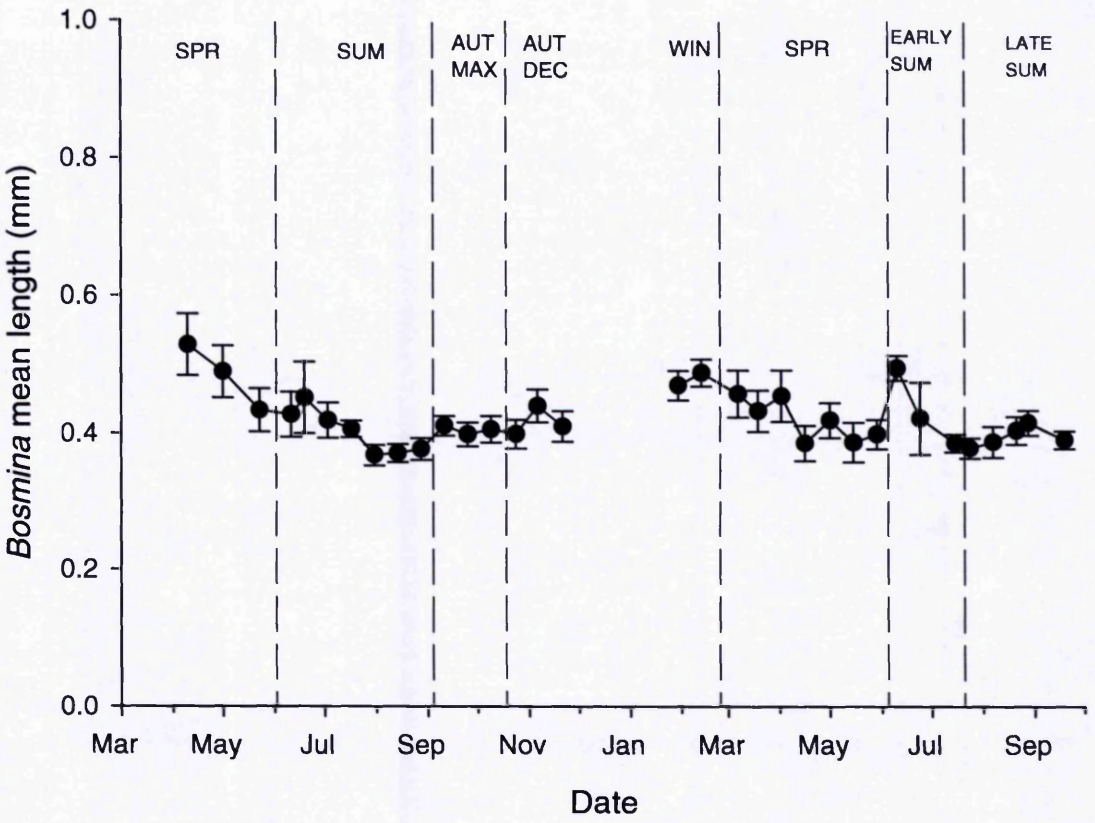


Figure 5.39: Seasonal changes in the average length of *Bosmina* in Hollingworth Lake, 2001-2002. Values are the mean lengths of animals randomly selected from sites A, B and C. Error bars show 95% confidence intervals.

5.3.1.3 Calanoid Copepods

Counts

Seasonal changes in the numbers of calanoid copepods are shown in Figure 5.40a. Numbers were low in both 2001 and 2002, with numbers never exceeding 3.9 calanoids l^{-1}.

Year 2001: During the first two samplings during the spring phase numbers were low (<1 calanoid l^{-1}). Numbers began to increase during the late spring, reaching maximum numbers at the start of the summer phase (max. 3.9 calanoids l^{-1} on the 3rd of July). Numbers then dropped rapidly, reaching 0.4 calanoids l^{-1} by the 31st of July, remaining at <1calanoid l^{-1} throughout the remainder of the summer and autumn maximum phases, before increasing slightly to 1.2 calanoids l^{-1} during the autumn decline

Year 2002: During the winter phase numbers were approximately 0.5 calanoids l^{-1}. During the early spring phase numbers increased slightly to reach a maximum of 3.6 calanoids l^{-1} at the commencement of the early summer phase. Numbers then decreased to reach 1.3 calanoids l^{-1} at the early/late summer phase boundary, following which numbers increased to reach a second late summer peak of 3.5 calanoids l^{-1} on the 28th of August. By the end of sampling number had fallen to 2.1 calanoids l^{-1}.

Size

Calanoid mean length varied between 0.88 and 1.19mm and is shown in Figure 5.40b. Average length over the whole sampling period was 1.03mm. The only noticeable change was an increase in mean length between the winter and middle of the spring phase in 2002, when mean length increased from approximately 0.96 to 1.22mm.

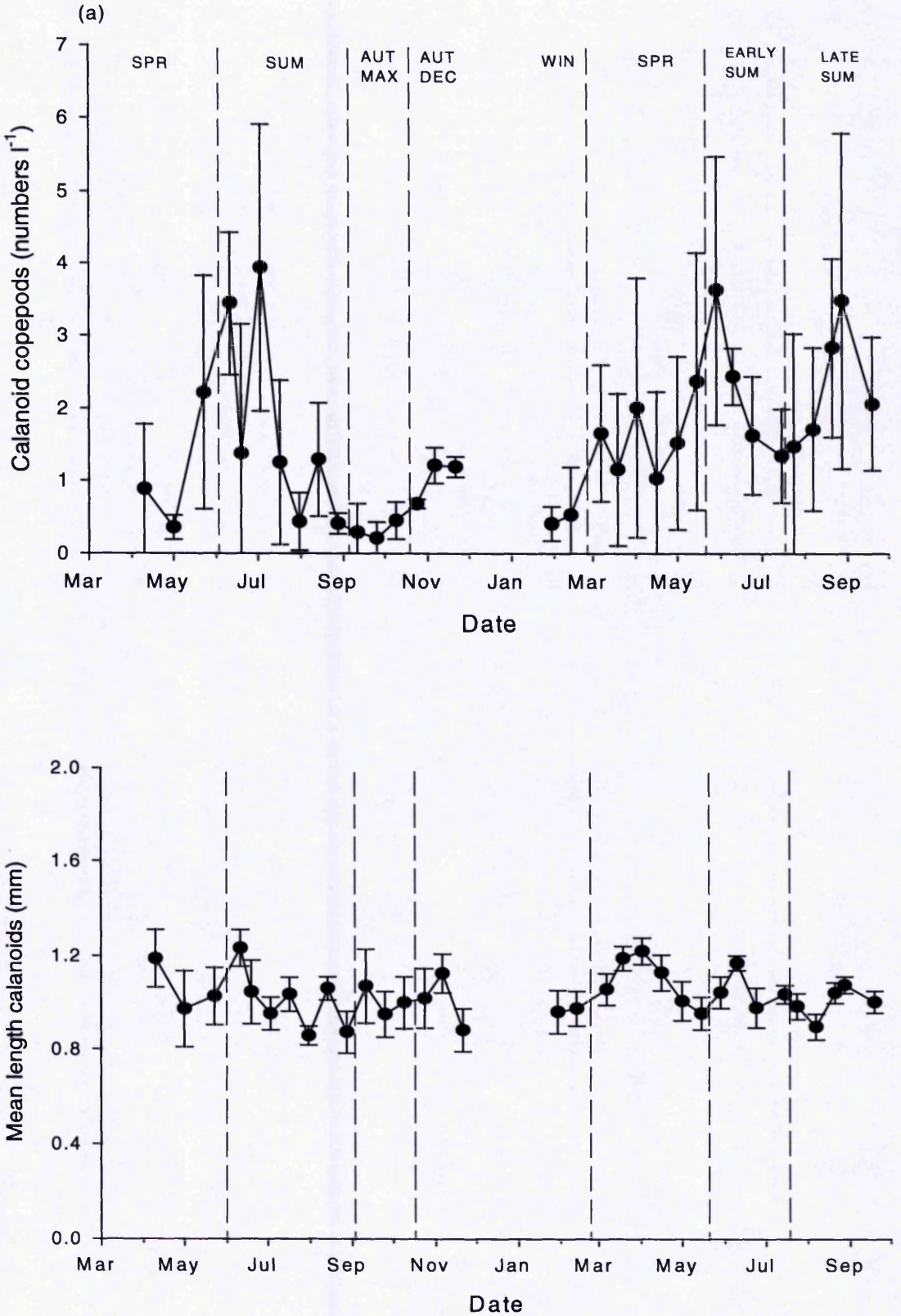


Figure 5.40: (a) Seasonal changes in the numbers of calanoid copepods. Values are the mean of three sites. Error bars ±1 SD. (b) Seasonal changes in the mean length of calanoid copepods. Values are the mean lengths of animals randomly selected from sites A, B and C. (n≈40 for each date). Error bars show 95% confidence intervals.

5.3.1.4 Cyclopoid Copepods

Counts

Year 2001: Cyclopoid copepods (Figure 5.41a) increased from 2.1 cyclopoids l^{-1} at the commencement of sampling to reach a peak of 8.6 cyclopoids l^{-1} at the end of the spring phase. During the summer phase numbers decreased, reaching a minimum of 0 cyclopoids l^{-1} on the 31st of July. Numbers remained low for the remainder of the summer phase (<1 cyclopoid l^{-1}), increased slightly during the autumn maximum (approximately 1.5 cyclopoids l^{-1}), and then exhibited a second peak in numbers at the beginning of the autumn decline (4.5 cyclopoids l^{-1}), following which numbers declined to reach 1.5 cyclopoids l^{-1} at the end of sampling.

Year 2002: At the commencement of sampling (winter phase) numbers were 0.4 cyclopoids l^{-1} following which they increased throughout the spring phase to reach a maximum of approximately 4.2 cyclopoids l^{-1} at the end of the spring phase/start of the summer phase. Numbers then fell to approximately 2 cyclopoids l^{-1} before increasing during the late summer phase to reach a peak of 5.7 cyclopoids l^{-1} on August the 31st. By the end of sampling numbers had fallen to 3.1 cyclopoids l^{-1}.

Size

Cyclopoid mean length varied between 0.63 and 1.30mm and is shown Figure 5.41b. Average length over the whole sampling period was 0.87mm. Mean lengths of cyclopoid copepods showed more variation than the other zooplankton groups.

Year 2001: Mean length increased from 0.96mm at the commencement of sampling (spring phase) to peak at 1.30mm on the 19th of June (summer phase). During the remainder of the summer phase average length decreased, reaching a minimum of 0.87mm at the phases' end. Mean length remained low during the autumn maximum, but increased during the autumn decline phase to reach 0.87mm at the end of sampling.

Year 2002: During 2002 mean length was approximately 0.80mm. Exceptions were a peak in early spring (approximately 1.01mm) and a further peak in early summer (approximately 1.16mm).

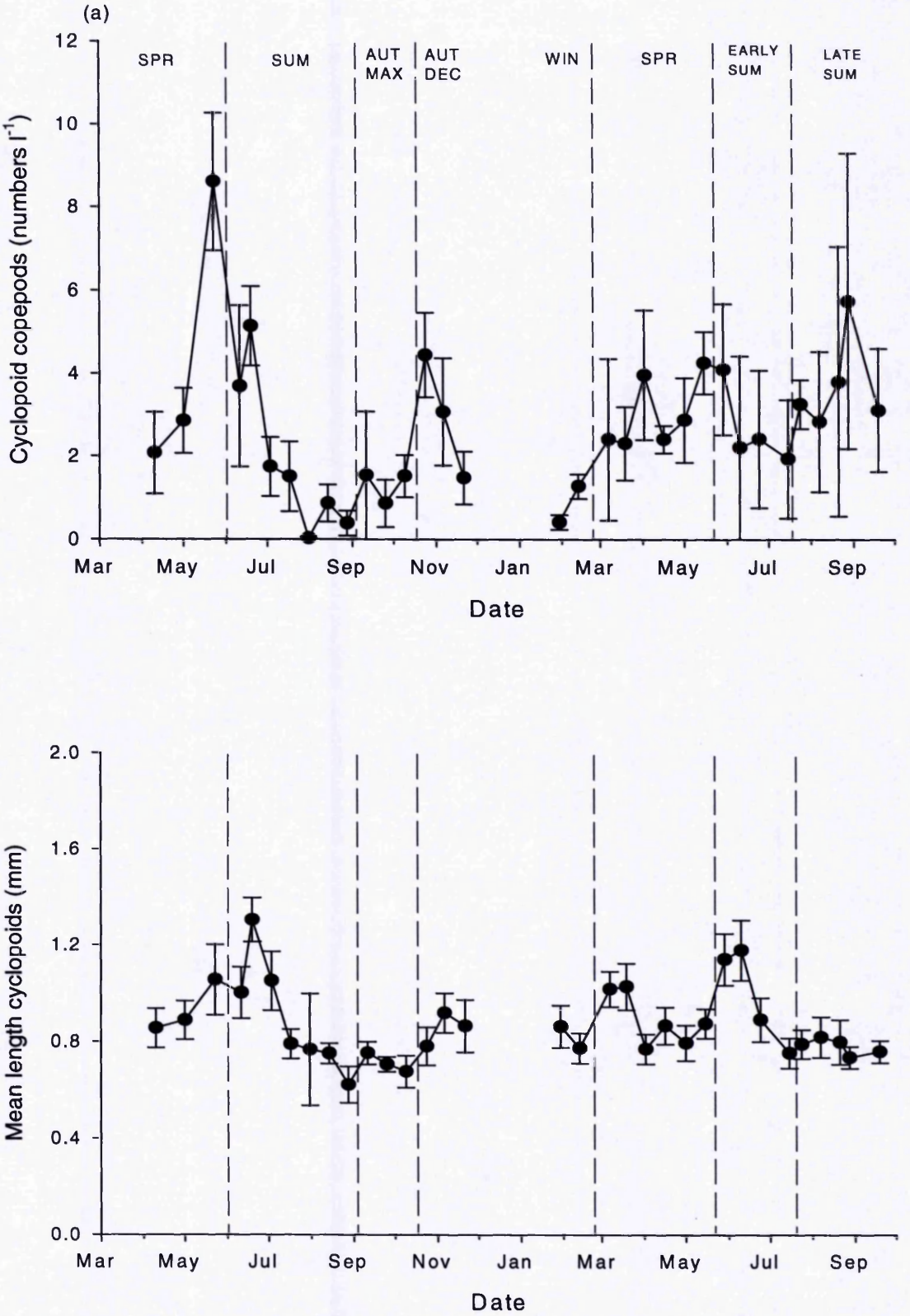


Figure 5.41: (a) Seasonal changes in the numbers of cyclopoid copepods. Values are the mean of three sites. Error bars ±1 SD. (b) Seasonal changes in the mean length of cyclopoid copepods. Values are the mean lengths of animals randomly selected from sites A, B and C. (n≈40 for each date). Error bars show 95% confidence intervals.

5.3.1.5 Rotifers

Seasonal change in the number of rotifers is shown in Figure 5.42 and Figure 5.43. Rotifers numbers were monitored in 2002 only.

Year 2002: Two species showed short lived peaks during the spring phase, *Pompholyx* increased during the middle of the phase, to 48 animals l^{-1}, while *Brachionus* showed a much larger peak at the end of the phase, to 630 animals l^{-1}. Both genera were absent during other phases.

Polyathra were present throughout the sampling period. Numbers were low during winter and spring (generally <5 animals l^{-1}), showed a small increase in the early-summer phase to 23 animals l^{-1} followed by a decline to low numbers (<2 animals l^{-1}) at the start of the late-summer phase. Numbers remained low until a large increase at the end of the phase, numbers increasing to 57 animals ml^{-1} at the end of sampling.

Keratella cochlearis and *Keratella longispina* showed similar patterns with *Keratella cochlearis* reached the highest numbers. *K. cochlearis* showed a small increase in the winter phase to 12 animals l^{-1} followed by a decline to <5 animals l^{-1} during the early spring phase. Numbers increased during the latter part of the spring phase to 13 animals l^{-1} before falling to <1 animal l^{-1} during the early-summer phase. During the late-summer phase numbers were high at the beginning at 18 animals l^{-1}, dropped to approximately 6 animals l^{-1} in late August before a large increase to 38 animals l^{-1} at the end of sampling. *K. longispina* showed a similar pattern, with a late spring maximum of 12 animals l^{-1} in the late spring phase, 18 animals l^{-1} at the beginning of the late summer phase and a maximum of 22 animals l^{-1} at the end of sampling.

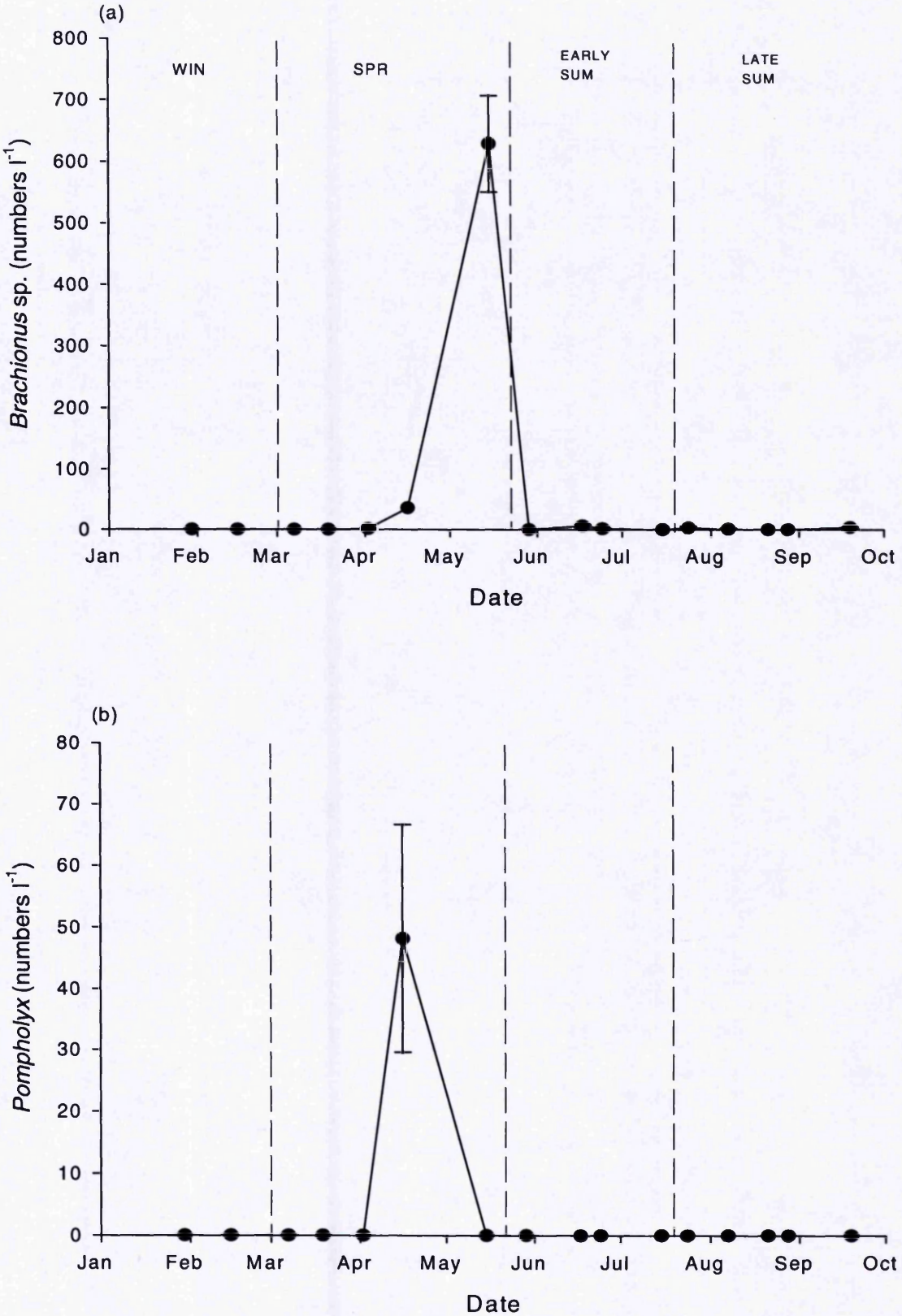


Figure 5.42: Seasonal change in the numbers of rotifers in Hollingworth Lake, 2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

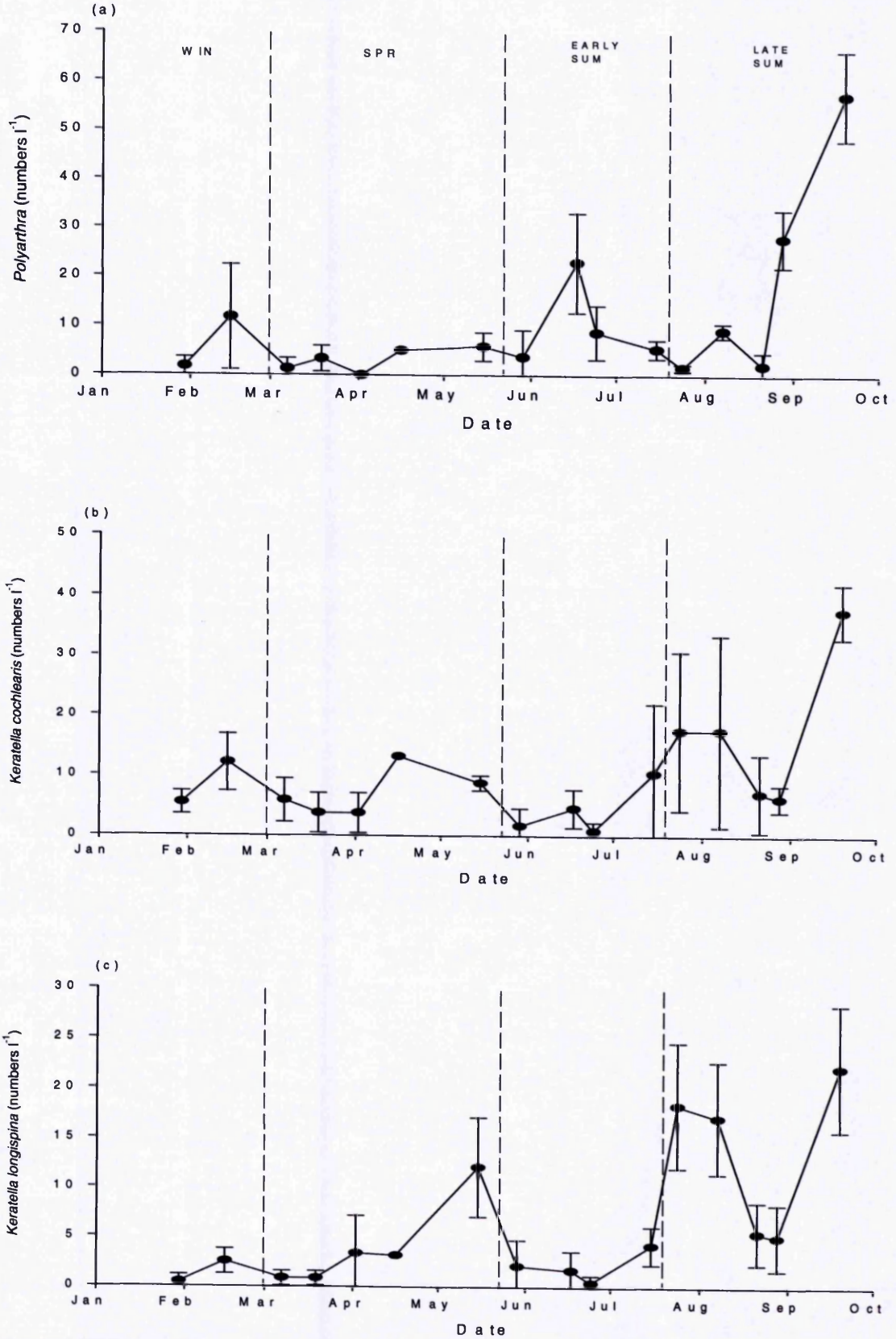


Figure 5.43: Seasonal change in the numbers of rotifers in Hollingworth Lake, 2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

5.3.1.6 Ciliated Protozoa

Seasonal change in the numbers of ciliated protozoa is shown in Figure 5.44. Ciliated protozoa were counted as a group and no separation into genera/species was made.

Year 2001: Numbers dropped during the spring phase (from 17 to 1 protozoa ml^{-1}) and then increased during the summer phase, peaking at the end of the phase at 20 protozoa ml^{-1}. Numbers were low (<5 protozoa ml^{-1}) during the autumn maximum and autumn decline.

Year 2002: Numbers were low during the winter and spring phase (<5 protozoa ml^{-1}), increased during the early-summer phase to 13 protozoa ml^{-1}, and decreased to <5 protozoa ml^{-1} during the late summer phase, with the exception of an isolated peak of 13 protozoa ml^{-1} at the end of August.

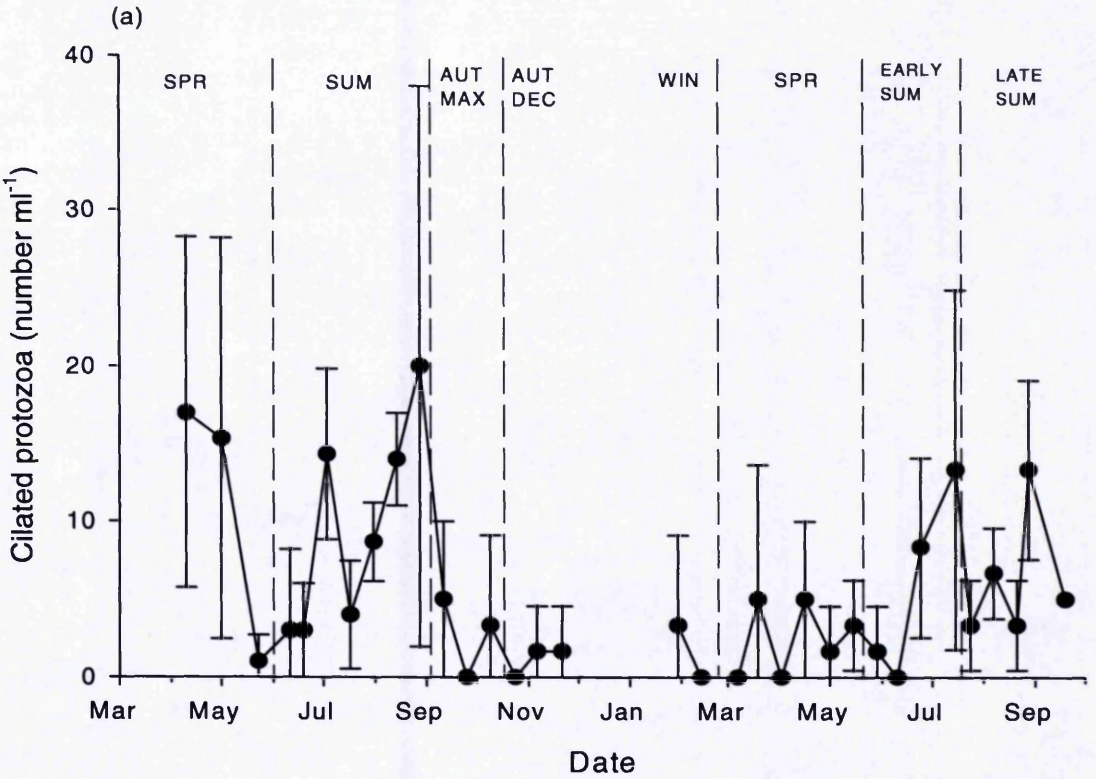


Figure 5.44: Seasonal changes in the number of ciliated protozoa in Hollingworth Lake, 2001-2002. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

5.3.2 Filtering Rates of Zooplankton

Seasonal change in zooplankton filtering rate is shown in Figure 5.45.

Year 2001: On the first two sampling occasions during the spring period the total filtering rate was low (<2% d^{-1}). This was followed by a large peak during the early summer phase, with filtering rate beginning to increase during late spring until it reached a maximum of 37% d^{-1} at the start of the summer phase (11th and 19th of June). Filtering rate then rapidly declined, reaching a minimum of 1% d^{-1} on the 31st of July. During the remainder of the summer phase filtering rate increase slightly, reaching a small peak in the middle of the autumn maximum (13% d^{-1}). Filtering rate remained between 7 and 12% d^{-1} until the final sampling occasion, when it had fallen to 4% d^{-1}. The filtering rate was dominated by the contribution of *Daphnia*, which was generally >80% of the total filtering rate. The maximum contribution of *Bosmina* and calanoids occurred during the early summer phase, contributing a maximum filtering rate of 3 and 4% d^{-1} respectively.

Year 2002: In 2002 filtering rate showed a late early summer peak. Filtering rates were low during the winter phase, with values approximately 1% d^{-1}, and began to increase during the spring phase, gradually until mid-April, and more rapidly thereafter. A peak of 31% d^{-1} occurred at the commencement of the early summer phase, remained high during the remainder of the phase, and then decreased to 7% at the start of the late summer phase. There was an increase to approximately 18% d^{-1} in late August followed by a fall to 9% by the end of sampling. The total filtering rate was again dominated by *Daphnia* which generally contributed >80% of the total filtering rate. The maximum filtering rate of *Bosmina* occurred at the end of the spring phase, when it filtered 10% d^{-1}, 50% of the total. The maximum filtering rate of calanoid copepods was 4% d^{-1} in the early summer phase, approximately 12% of the total.

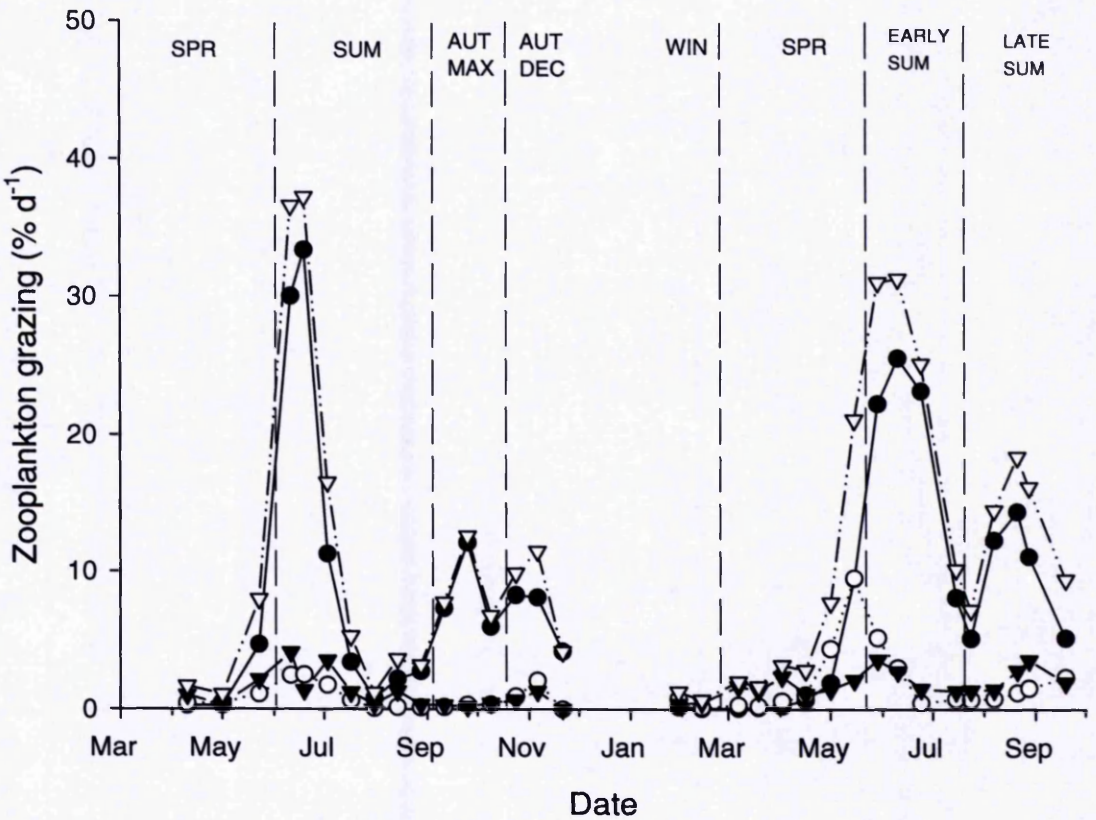


Figure 5.45: Seasonal changes in the filtering rate of *Daphnia* (•), *Bosmina* (o), calanoid copepods (▼) and the filtering rate for all three combined (▽), Hollingworth Lake, 2001-2002.

5.4 Bacteria, Dissolved Organic Carbon and Colour

5.4.1 Total Bacteria

Counts of total bacteria are shown in Figure 5.46a.

Year 2001: On the first two sampling occasions during the spring phase, bacteria were present at approximately $4.0x10^6$ cells ml^{-1}. This was followed by a peak in numbers early in the summer phase, with numbers beginning to increase during late spring until they reached a maximum of $7.80x10^6$ cells ml^{-1} during the early part of the summer phase (until mid-July). Numbers then declined, reaching a minimum of $5.25x10^6$ cells ml^{-1} at the end of the summer phase. Numbers increased to approximately $6.80x10^6$ cells ml^{-1} during the autumn maximum, before falling during the autumn decline (min. $4.23x10^6$ cells ml^{-1}).

Year 2002: Numbers were low during the winter and early spring phase at approximately $4.20x10^6$ cells ml^{-1} and then increased to peak at $8.82x10^6$ cells ml^{-1} at the end of the phase. Numbers declined during the early summer phase to $4.37x10^6$ cells ml^{-1}. There was a slight increase during the late-summer phase, with numbers falling at the phases' end to a minimum of $3.91x10^6$ cells ml^{-1}.

5.4.2 Viable Bacteria

Numbers of viable bacteria for 2001 is shown in Figure 5.46b. Numbers of viable bacteria were not monitored in 2002.

Year 2001: During the spring viable bacteria were between 1.4 and $1.9x10^3$ CFU ml^{-1}. During the summer-phase numbers decreased to $0.21x10^6$ CFU ml^{-1} in mid-July, followed by a rapid increase to $3.9x10^6$ CFU ml^{-1} in late July. Numbers then fell to reach a minimum of $0.66x10^6$ CFU ml^{-1} during the autumn maximum phase, followed by a slight increase to $1.83x10^6$ CFU ml^{-1} during the autumn decline phase.

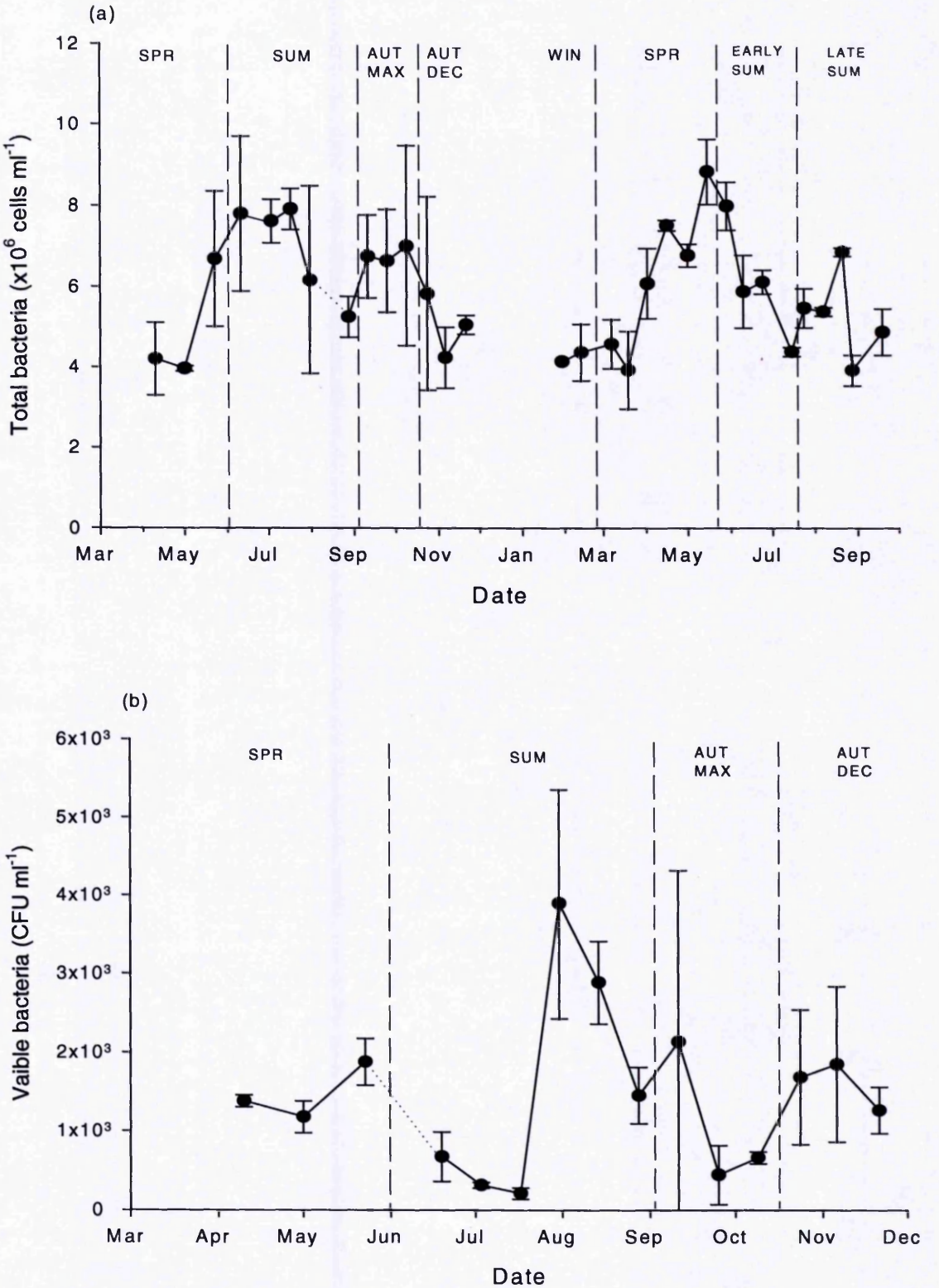


Figure 5.46: Seasonal changes in (a) total bacteria in Hollingworth Lake, 2001-2002 and (b) viable bacteria in Hollingworth Lake, 2001. Where values are missing a dotted line is used to join points on either side of the missing value. Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

5.4.3 Dissolved Organic Carbon (DOC)

Seasonal variation in DOC is shown in Figure 5.47a.

Year 2001: DOC was approximately 2.2mg l^{-1} during the spring phase. During the other phases DOC showed an increase, from 2.4mg l^{-1} at the start of the summer phase, to 3.6mg l^{-1} at the end of the autumn decline phase.

Year 2002: DOC showed a decline during the spring phase, from 3.02mg l^{-1} during the winter phase to 1.46 mg l^{-1} at the start of the early-summer phase. During the remainder of this phase DOC increased, reaching 3.60 mg l^{-1} at the phases' end. During the late-summer phase DOC remained at approximately this level.

5.4.4 Colour

Seasonal variation in colour for 2002 is shown in Figure 5.47b.

Year 2002: Colour declined during the spring from 3.3 to 1.9 m^{-1} by mid-April. There was an increase during the early-summer phase to 2.9m^{-1}, followed by a decrease to 1.5m^{-1} at the early-summer/late-summer phase boundary. For the remainder of the sampling period colour was approximately 2.5m^{-1}.

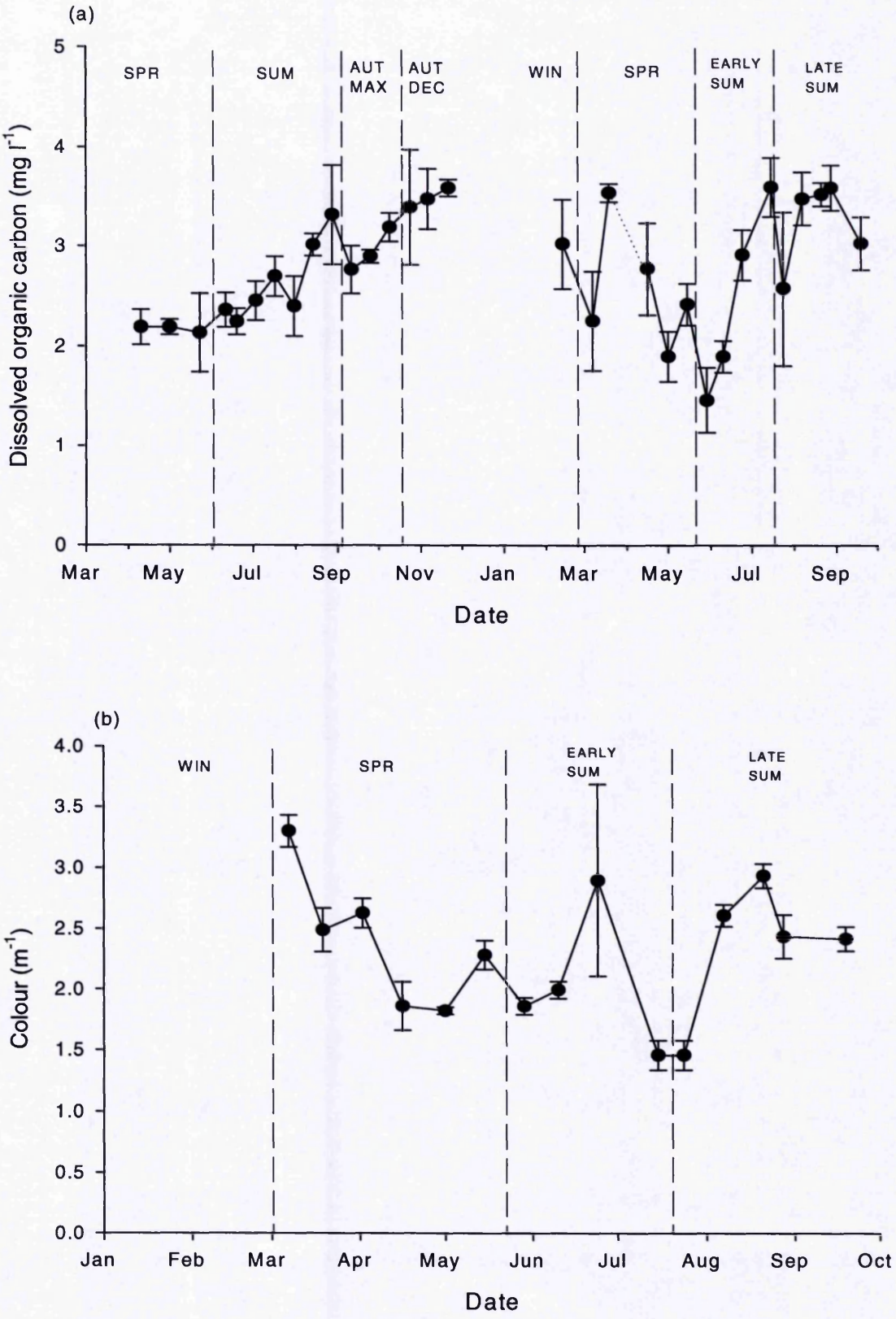


Figure 5.47: Seasonal changes in (a) dissolved organic matter, Hollingworth Lake 2001-2002 and (b) colour, Hollingworth Lake, 2002. Where values are missing a dotted line is used to join points on either side of the missing value Values are the mean of integrated samples taken from sites A, B and C. Error bars ±1 SD. (n=3).

5.4.5 TSS and TOM

TSS and TOM showed similar seasonal changes, but the changes in TOM were much less pronounced than for TSS. Seasonal variation in TSS and TOM is shown in Figure 5.48.

Year 2001: TSS declined during spring from 4mg l^{-1} (TOM 2.5 mg l^{-1}) to 1.4mg l^{-1} (TOM 1.0mg l^{-1}). At the start of the summer phase TSS had increased to 4.9mg l^{-1} (TOM 2.6mg l^{-1}) and remained high at 4.3 - 5mg l^{-1} (TOM 2.0mg l^{-1}) until it decline to a summer phase minimum of 2.7mg l^{-1} (TOM 1.66mg l^{-1}) at the end of July. There was then an increase, reaching 5.1mg l^{-1} (TOM 3.0mg l^{-1}) at the end of the phase and continued to increase during the autumn maximum phase, peaking at 8.3mg l^{-1} (TOM 3.7mg l^{-1}) at the end of the phase. During the autumn decline TSS had fallen to approximately 4.0mg l^{-1} (TOM 2.1 mg l^{-1}).

Year 2002: At the start of sampling (winter phase) TSS was 3.9mg l^{-1} (TOM 1.5mg l^{-1}). This was followed by a very high peak in February of 11.1 mg l^{-1} (TOM 3.8 mg l^{-1}) (as this was an extremely windy day the high value may attributed to suspension of the sediment). Values then declined to reach approximately 3.5 mg l^{-1} (TOM 1.3 mg l^{-1}) in the middle of the spring phase. There was then an increase to approximately 6-7 mg l^{-1} (TSS 2.5 mg l^{-1}) over the spring/early summer phase boundary before declining to 3-4 mg l^{-1} (TOM 2-2.5 mg l^{-1}) during the late summer phase.

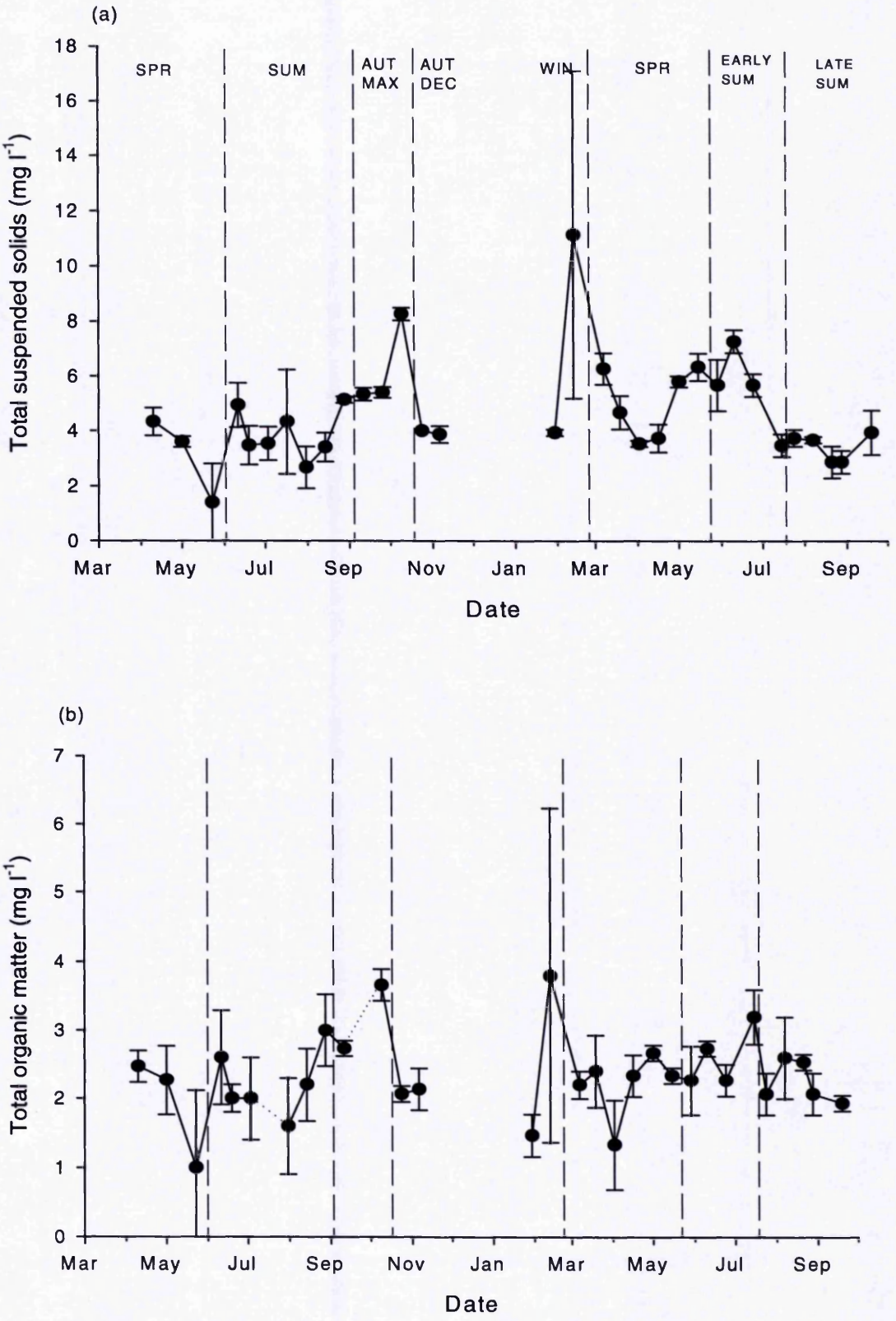


Figure 5.48: Seasonal changes in (a) total suspended solids and (b) total organic matter in Hollingworth Lake, 2001-2002. Where values are missing a dotted line is used to join points on either side of the missing value Values are the mean of integrated samples taken from sites A, B and C. Error bars±1 SD. (n=3).

Chapter 6 Discussion: Hollingworth Lake

6.1 Phytoplankton populations and seasonal changes

The objective of this section is to establish which factors influence the seasonal dynamics of the phytoplankton in Hollingworth Lake. Of particular interest is whether loss factors, such as washout and grazing are high enough to account for the observed decline in certain phytoplankton species and thereby influence seasonal succession. Also of interest is the extent to which bottom-up factors such as nutrient availability may influence phytoplankton seasonal succession.

Seasonal changes within the phytoplankton in Rostherne Mere were considered in relation to the different phases, and the differing impact of grazing, sedimentation and nutrient limitation (Chapter 4). It was shown that these factors operate to differing extents depending on the season, and the operation of these factors led to distinct 'phases' over the full annual cycle. In Hollingworth Lake distinct phases were not so clearly observed as the phytoplankton was generally dominated by diatoms throughout the year. However, some changes in the phytoplankton were observed. In both years there was a decline in both numbers and biomass of diatoms during the spring and a summer increase in diatoms. In summer 2001, *Tabellaria* dominated, reaching a maximum in the early autumn, before rapidly declining. During the early summer of 2002 there was a rapid increase in *Asterionella formosa*, which declined equally rapidly, leading to very low diatom biomass during the late-summer phase.

Seasonal changes in the phytoplankton at Hollingworth Lake can be considered in relation to physical loss factors (washout, sedimentation), grazing and nutrient limitation.

6.1.1 Physical Loss Factors – Washout and Sedimentation

Two factors, sedimentation and losses through washout, showed little variation over the course of the growing season and may therefore be expected to have little impact on the phytoplankton periodicity.

6.1.1.1 Washout

Losses can be estimated from the discharge of water from Hollingworth Lake via the valve tower, which is the main outflow. Summer discharge (between May and September) in Hollingworth Lake is often at $20x10^3$ m^3 day^{-1} (Hitchen, 2001). The volume of the lake is approximately $1.25x10^6$ m^3 and maximum losses due to washout

would therefore be ≈0.016 day^{-1} (using equation 21, page 47). When considering the likely impact of washout on summer phytoplankton populations, and whether such washout can account for the observed fluctuations in phytoplankton numbers it is necessary to consider the losses in relation to the potential growth rate of the phytoplankton. If the loss rate exceeds the potential maximum growth rate of the phytoplankton then declines in phytoplankton populations may be due to the particular loss factor. However, the potential maximum growth rates of phytoplankton in natural conditions are often >0.30 day^{-1} (see table 17 in Reynolds, 1984a). For example, *Asterionella formosa* which showed a rapid increase in numbers during summer 2001, followed by a equally rapid decrease, has a potential growth rate during the spring of >0.16 day^{-1}, while in the summer the maximum growth rate is >0.40 day^{-1}. It can be seen that a loss rate due to washout of ≈0.016 day^{-1} is not high enough to cause the observed decline in the *Asterionella* population, even at the lower rate of growth.

6.1.1.2 Sedimentation

It an unstratified lake such as Hollingworth Lake it is difficult to estimate sedimentary losses of healthy phytoplankton. The lack of summer stratification suggests that the lake is continually mixed, and the exposed position of the lake means that it is likely to be subject to long periods of wind disturbance. Cells that sediment out from the water column may therefore be regularly entrained within, and returned to the water column. Furthermore, the equation used (equation 20, page 46) to estimate sedimentary losses is based on only one mixing event per unit time (i.e. one complete mixing of the water column per day), which in a very well mixed lake such as Hollingworth Lake may be an underestimate. For these reasons estimated sedimentary losses of phytoplankton in Hollingworth Lake may be considered the maximum that are likely to occur. An estimate of the magnitude of phytoplankton loss from the water column in Hollingworth Lake can be obtained using *Asterionella formosa* as an example. The sinking rate of healthy growing colonies is approximately 0.3m d^{-1} (Smayda, 1974; Titman and Kilham, 1976) and the mixed depth of Hollingworth Lake is the same as the depth of the water column (due to lack of stratification) and is approximately 7m. Using these figures and Equation 20 (page 46) an estimate of sinking losses due to sedimentation is in the order of ≈0.04 day^{-1}. Although sedimentary losses are greater than those due to washout they are well below the potential maximum growth rate of *Asterionella formosa*, and are therefore not high enough to cause the observed decline of this alga in the summer of 2002. Similarly, the loss rates are below the potential maximum growth

rates of *Tabellaria fenestrata var. asterionelloides* (spring growth rate >0.13 day^{-1}, summer growth rate >0.34 day^{-1}, (Reynolds, 1984a)) and are not able to account for the rapid decrease in *Tabellaria* numbers observed during the autumn decline phase in 2001.

However, sinking losses may increase during periods of stratification. The water column was stratified in July of both years; however, the stratification was short-lived (observed on a single sampling occasion only) and did not correspond to any large decline in diatoms. The spring decline in diatom numbers for instance, did not occur when the lake was stratified, nor did the decline of the two major diatom blooms, that of *Tabellaria fenestrata var. asterionelloides* in 2001 and *Asterionella formosa* in 2002.

6.1.2 Grazing

The above analysis suggests that sedimentation and washout cannot account for the decline in phytoplankton. Even if the losses are combined they do not approach the level necessary to cause declines in phytoplankton species. Another possible cause of the decline in certain species may be grazing. However, correlation analysis (Table 6.1) provides no evidence that increases in zooplankton grazing rate caused decreases in phytoplankton biomass, as the only significant correlations were positive.

Total filtering rate versus:	Total phyto biovolume	Edible phyto biovolume (as predicted by the Burns' equation)	Edible phyto biovolume (including partly edible colonial phytoplankton such as *Asterionella*)
2001	ns	0.585*	ns
2002	ns	ns	0.546*

Table 6.1: Correlation (Pearson) between total filtering rate (*Daphnia, Bosmina* and Calanoids) and phytoplankton biovolume (both total and edible). * - $P \leq 0.05$, (ns- not significant). (n=16).

However, there are other methods by which the impact of zooplankton grazing on phytoplankton populations can be assessed. The following considers the potential impact of grazing in relation to phytoplankton edibility, by an analysis of zooplankton grazing rates, and by comparing phytoplankton grazing losses to growth rates.

6.1.2.1 Phytoplankton size and edibility

The impact of grazing on the phytoplankton in Hollingworth Lake is dependent on the filtration rate of the zooplankton and the susceptibility of the phytoplankton species to grazing. The dominant phytoplankton species were *Tabellaria fenestrata, Synedra acus, Melosira* sp., *Asterionella formosa, Cyclotella* spp. *Aulacoseira granulata var. angustissima* and *Nitzschia* spp. According to Equation 13 (page 42) the maximum size of particle that can be ingested by an average *Daphnia* within Hollingworth Lake

(length 0.82mm) is 20-25μm, while that of the average *Bosmina* (length 0.42mm) is approximately 15μm. Thus, the only species that may be readily ingested are *Cyclotella* spp. *Nitzschia* spp., *Cryptomonas* spp. and *Rhodomonas minuta.*

The other (generally dominant) species formed large filaments, or stellate colonies whose largest dimension was well above the theoretical maximum size according to the Burns' equation and may therefore be expected to be little influenced by grazing. However, there is evidence to suggest that *Daphnia* can ingest some large algal species (which should be inedible according to the Burns' equation). Nadin-Hurley & Duncan (1976) showed that flexible filaments of *Tribonema* of up to 225μm were observed in *Daphnia magna* guts, while those in *Daphnia hyalina* were up to 120μm. Ferguson *et al.,* (1982) also studied *Daphnia hyalina* and noted that *Oscillatoria* filaments were observed within the guts, although only filaments of <100um were ingested. The average size of the filamentous phytoplankton in Hollingworth Lake (for example *Aulacoseira, Melosira*) was generally >200μm which suggests that these species will not be ingested by the zooplankton. Stellate colonies may be ingested, the maximum dimension of *Asterionella* for example should theoretically render it unsusceptible to grazing although there is evidence that the colonies can be ingested, possibly by fragmenting the colonies into smaller, edible pieces (Reynolds *et al.* 1982). Presumably, *Tabellaria* can also be broken up and ingested. The zooplankton may therefore be able to ingest some of the larger phytoplankton. However, the ability of the Cladocera to ingest these species is greatly reduced when compared to species that fall within the size range predicted by the Burns' equation. For example Reynolds *et al.*, (1982) gives selectivity coefficients for small species such as *Cryptomonas* and *Ankyra* of 1, the large colonial *Microcystis* 0, while *Asterionella* formosa was given a range of 0.28 to 1.0. Thus, in view of the large size of the dominant phytoplankton (large filamentous and colonial species) the selectivity coefficient for the dominant species found in Hollingworth will be substantially less than 1, and have low susceptibility to grazing. Furthermore, the susceptibility of the phytoplankton to grazing may also be reduced due to the small average size of the *Daphnia* and *Bosmina* in Hollingworth Lake. These species may have more difficulty than larger *Daphnia* in ingesting large filamentous and stellate colonies such as *Asterionella*, and this may further reduce the susceptibility of the dominant phytoplankton to grazing.

Thus, analysis of the size of the phytoplankton, and the theoretical maximum size of ingestible particles available to *Daphnia* suggests that the effect of grazing on the large, dominant phytoplankton in Hollingworth Lake may be low.

6.1.2.2 Analysis of zooplankton grazing rates

Further information for the effects of grazing can be obtained by an analysis of grazing rates, and changes in phytoplankton populations, particularly during the spring decline, and the decline of the 2001 *Tabellaria* maximum and the 2002 *Asterionella* maximum.

Spring Decline

Analysis of the data suggests that grazing had little effect on the spring decline of the phytoplankton. In 2001 *Tabellaria fenestrata* and *Synedra acus* numbers decreased during the early spring phase, although it is difficult to attribute this to grazing, as grazing rates during the decline were very low at <2% of the water column filtered per day. Expressed in terms of the losses due to grazing ($k_{grazing}$), (see Equation 19, page 46) this would give a loss of 0.02 day^{-1}, assuming that the phytoplankton were highly susceptible to grazing (i.e. $\Phi=1$). These losses are approximately equal to those due to washout and sedimentary losses which as discussed above are well below the maximum potential growth rates of the phytoplankton. Even at the period of minimum phytoplankton biomass the filtering rate had only increased to 8%, ($k_{grazing} \approx 0.08$ day^{-1}). Thus, the losses due to grazing are below the level required for grazing to cause the spring decrease in phytoplankton. This is the case when the phytoplankton are considered to be fully susceptible to grazing (i.e. $\Phi=1$). However, in view of the filamentous nature of many of the phytoplankton species, and the small size of the zooplankton the true value of Φ is likely to be significantly less than 1, thus reducing the effects of grazing on the spring phytoplankton decline still further. Filtering rates reached a maximum of 37% during the spring/summer phase border, due to an increase in zooplankton numbers. At first glance this may imply that the increased filtering rate may cause the decline of the spring phytoplankton bloom, as the maximum grazing losses would be 0.37 day^{-1}. This is above the typical spring growth rate of *Asterionella formosa* for example, which is one of the species that exhibited a spring decline. However, closer examination shows that the increased filtering rate occurred during the early part of the summer phase, following the spring decrease in phytoplankton. As

mentioned above, the filtering rate during the actual decline of the phytoplankton decline was much less, at 2%.

In 2002, a spring biomass minimum occurred during mid-May when grazing rates were 21%. Thus grazing during the phytoplankton minimum was much higher than in 2001, and grazing may be expected to have more impact on the spring decline. However the decline in phytoplankton began in mid-March and occurred when filtering rates were ≈3%, thus losses due to grazing during the decline would be ≈0.03 day^{-1} assuming Φ=1. However, among those species that declined from March onwards were the large filamentous *Aulacoseira* and *Melosira*, and the colonial 'chain' of *Tabellaria fenestrata*, species that may be considered to have low susceptibility to grazing. Thus, during the decline of these species the losses due to grazing may be considered to be lower than the figure of 0.03 day^{-1}. This is again well below the figure required for grazing to exceed the potential growth rate of the phytoplankton and so cause the decline. *Aulacoseira granulata* for instance has a maximum summer growth rate in excess of 0.43 day^{-1} (Sommer, 1981). However, the spring growth rate is likely to be lower (due to reduced temperature and shorter day length) which assuming a spring growth rate similar to other diatoms would be in the order of 0.15 day^{-1} (Reynolds, 1984a). Thus grazing losses cannot account for the decline in phytoplankton during the spring bloom. Further evidence that the decline of the 2002 spring phytoplankton was not due to grazing can be obtained by studying the summer phase in 2002. In the early part of this phase, *Asterionella* maintained a rapid rate of increase when grazing pressure was at an annual maximum of 31%. If *Asterionella* can maintain a population increase under this high grazing pressure then the lower grazing pressure at the end of the spring phase should not be able to cause the observed reduction in the spring *Asterionella formosa* population. Furthermore, the other species that decline during the spring – *Tabellaria fenestrata*, *Aulacoseira*, *Melosira* sp. may be considered no more susceptible to grazing than *Asterionella formosa*. Thus, if *Asterionella* can maintain an increase despite high grazing pressure, other less susceptible diatom species should certainly be able to maintain their own growth. Thus, there is little evidence to suggest that the decline of the spring phytoplankton populations may be due to grazing.

Summer Phase

During the summer of 2001 the dominant phytoplankton was *Tabellaria fenestrata var. asterionelloides*. Reynolds (1984a) gives net growth rates for this species of 0.13 day^{-1} during the pre-stratification period and 0.33 day^{-1} during the mid-summer

stratification period, and as these are net growth rates (i.e. after losses) maximum growth rates must be higher than these figures. Although summer grazing rates were 37% at the beginning of the summer, they rapidly fell to <5%. Filtering rates remained at <5% during the remainder of the summer, during which time *Tabellaria* numbers slowly increased. During the rapid increase in *Tabellaria* numbers filtering rates were approximately 10%, remaining at this level during the rapid decrease in numbers during the autumn-decline phase. Thus even assuming that *Tabellaria* are readily ingested by the *Daphnia* and *Bosmina* (i.e. a coefficient of selectivity of 1) the maximum loss rate through grazing during the summer phase would be $k_{grazing} \approx 0.05$ day^{-1} increasing to ≈ 0.10 day^{-1} during the rapid increase in early autumn. Losses due to grazing during the period of *Tabellaria* increase are therefore well below the maximum growth rate of the species. Furthermore, the rapid increase in numbers during the late summer/early autumn occurred when filtering rates had actual increased not decreased (10% as compared to 5% in mid-summer) suggesting that grazing did not have a major effect in regulating *Tabellaria* numbers. Nor does grazing seem to have a major effect during the autumn-decline phase, when *Tabellaria* numbers rapidly dropped. In order to attribute this decline to grazing a rapid increase in grazing rates would be required, with grazing rates exceeding the maximum growth rates. However, during the decline grazing rates remained at approximately 10%, the same level of grazing pressure under which *Tabellaria* rapidly increased during the autumn maximum. Thus grazing cannot account for the autumn decline in *Tabellaria*. Add in the fact that the coefficient of selectivity of *Tabellaria* may actually be much lower than 1, then the impact of grazing is reduced further. This evidence suggests that the fluctuations in *Tabellaria* numbers cannot be attributed to grazing.

Further evidence for the low impact of grazing on the phytoplankton can be obtained from a study of the early summer phase in 2002. *Asterionella formosa* showed a rapid increase at the beginning of the phase, increasing from 32 to 632 colonies ml^{-1} between the 29th May and 10th June, a net growth rate of $k_{net} \approx 0.25$ day^{-1}, (Using Equation 17, page 46) before rapidly declining to 12 colonies ml^{-1} by the 24th of June and decline of $k_{net} \approx -0.28$ day^{-1}. Maximum grazing rates of ≈31% occurred on the 29th of May and 10th of June, when *Asterionella formosa* growth rate was at a maximum. Losses due to grazing, assuming that *Asterionella* colonies are fully ingestible, would therefore be ≈ 0.31 day^{-1}. The true growth rate of the *Asterionella formosa* would therefore be approximately 0.55 day^{-1} (assuming other losses are negligible). For the

decline to be attributable to grazing, the losses due to grazing must be higher than this true growth rate, however during the *Asterionella* decline grazing rates had actually declined slightly to 25%, giving losses due to grazing of ≈0.25 day^{-1}, much lower than the estimated true growth rate. Thus, even assuming *Asterionella* to be highly susceptible to grazing the evidence suggests that grazing rates were not high enough to cause the decline.

Although the above argues that grazing has little impact on the periodicity of the dominant phytoplankton this is not to say that grazing has no effect at all. Smaller species such as *Cyclotella* may still be subjected to losses through grazing. In 2001, for example the summer phase was characterised by an initial peak of *Cyclotella*. The increase in *Cyclotella* began at the end of the spring phase, when grazing was <10%. The net rate of growth during spring was approximately 0.1 day^{-1}, when the maximum grazing rate was approximately –0.1 day^{-1} (assuming that the coefficient of selectivity for *Cyclotella* spp. is 1 by virtue of its small size (<20μm)). The maximum growth rate was therefore ≈0.2 day^{-1} (again assuming other losses are negligible). When numbers peaked at the beginning of the summer phase on the 11th of June, and during the subsequent decline grazing rates were 37%, giving grazing losses ($k_{grazing}$) of 0.37 day^{-1}. Grazing losses during the early summer phase were therefore high enough to cause the decline in *Cyclotella* sp. Losses due to washout and sedimentation will be of a similar magnitude to those given in the discussion of the clear-water phase, i.e. 0.016 and 0.04 day^{-1} respectively, and are therefore unlikely to cause the decline. Thus it is possible (although by no means proven) that grazing can be important in regulating numbers of the smaller phytoplankton in Hollingworth Lake.

It should be noted that the filtering rates quoted above are concerned with the community filtration rate due to *Daphnia*, *Bosmina* and Calanoid copepods, and does not include the contribution of rotifers. However, numbers of rotifers (measured in 2002 only) were generally low at about 20 rotifers l^{-1}, (mainly *Keratella* spp.) although on one sampling occasion in late spring numbers did reach 600 *Brachionus* l^{-1}. Taking a *Brachionus* filtration rate of 0.08 ml day^{-1} per rotifer (Halbach and Halbach-Keup, 1974, cited in Reynolds, 1984a) gives 48 ml filtered, per litre, per day or approximately 5%. Thus, even at peak of rotifer numbers (which was on one sampling occasion only) only ≈5% of the water column is filtered. Furthermore, Starkweather *et al.*, (1979) give much lower filtration rates for *Brachionus*, ranging between 0.007-0.017 ml day^{-1}, so the figure of 5% given above may be an overestimate. At other times of the season, if a

filtration rate of 0.07 ml day^{-1} per rotifer is assumed (which is the average of the filtration rate for various rotifers given by Pourriot (1977)) the filtration rate of the rotifer population would be approximately 1.4ml filtered per litre, per day, or 0.1%. It can be seen from these figure that the impact of rotifers on the phytoplankton is likely to be negligible when compared to the filtration rate of the Cladocera and calanoid copepods.

Ciliated protozoa are also unlikely to have a major impact on the phytoplankton. Ciliated protozoans of the size observed during this study (generally <30μm) graze bacterial sized particles (Wetzel, 2001) and are therefore unlikely to impact on the major phytoplankton species within Hollingworth Lake.

Thus the evidence is that the large diatom species that dominate the plankton in Hollingworth Lake are little effected by grazing. If grazing, sedimentation and washout only play a minor role in regulating phytoplankton periodicity in Hollingworth Lake then availability of nutrients may be important.

6.1.3 Nutrient Limitation

Declines of phytoplankton species may be due to nutrient limitation. However, during the spring decline in 2001 there was no evidence of nutrients falling to limiting concentrations. Nitrates were approximately 0.40mg l^{-1}, SRP 20μg l^{-1} and silicon 0.90 mg l^{-1}. In 2002, silicon concentrations on the 15th of May were far from limiting, at 1.15 mg l^{-1}, as was biologically available nitrogen, which was >0.50 mg l^{-1}. Although SRP concentrations were limiting (<5μg l^{-1}) when the diatom population declined, they were higher than the concentrations at the beginning of the summer phase, when there was a large increase in diatoms (particularly *Asterionella formosa*) despite SRP being undetectable.

During the summer, concentrations of SRP were particularly low and were close to limiting or undetectable. Silicon concentrations were also low, in 2001 concentrations were <0.2mg l^{-1} during the summer and early autumn of 2001, while in 2002 concentrations were undetectable during the late summer. However there was no evidence of a decline in phytoplankton species coinciding with nutrients falling to limiting concentrations. In fact, concentrations of SRP were often at limiting concentrations during increases in phytoplankton species, as well as subsequent decreases. For example, during both the rapid increase and decrease of *Asterionella*

formosa during 2002 concentrations of SRP were undetectable. Hence, there is little evidence to confirm that nutrient limitation causes declines of phytoplankton species.

6.1.4 Seasonal succession of phytoplankton in Hollingworth Lake

The above looked at factors that may cause declines of phytoplankton species in Hollingworth Lake, and so influence seasonal succession. However, there was little evidence for the succession of algal groups being due to any of the factors discussed above. The phytoplankton succession may therefore be due to other factors, such as changes in nutrient ratios and mixing. The following discussion considers the factors that cause the dominance of diatoms in Hollingworth Lake, the factors that may cause the succession between different diatom species, and those that influence the succession between diatoms and other algal groups.

Dominance and seasonal succession of diatom species

The limiting concentrations of SRP for long periods of the growing season helps explain the dominance of diatoms in Hollingworth Lake. A large number of studies have shown that diatoms are extremely good competitors for phosphorus (Tilman and Kiesling, 1984; Sommer, 1983). In P-limited steady state competition experiments only Si limitation could prevent diatoms from outcompeting cyanobacteria (Holm and Armstrong, 1981). Diatoms have also been shown to outcompete green algae at high Si:P ratios (Sommer, 1985). The nutrient concentrations in Hollingworth Lake, i.e. high silicon and low SRP are therefore ideal for the continuing dominance of diatoms, as was observed for the majority of the sampling. It is interesting to note that the only time when the phytoplankton was not dominated by diatoms was in the late-summer phase of 2002, when silicon concentrations were undetectable.

However diatom species also vary in their optimal Si:P ratios, and in their ability to grow at limiting concentrations of Si and SRP (Tilman, 1977, 1981). Thus changes in the Si:P ratio may favour one diatom over another, and this may cause the succession between different species observed in Hollingworth Lake. It may also cause succession to other algal groups, such as the autumn blooms of *Oscillatoria* sometimes observed in Hollingworth Lake.

Mixing conditions within Hollingworth Lake are also likely to favour diatoms over other algae. As the lake rarely stratifies the mixed depth over the whole season rarely changes, and is commensurate with the depth of the lake i.e. 7m. Mixing also leads to large amounts of suspended particulate matter being entrained within the water

column, hence Secchi depths are low. If Secchi depths are low then the euphotic depth, (which is the lower limit of the euphotic zone in which photosynthesis is possible), will also be low. Euphotic depth can be approximated to 1.7 Z_s (Reynolds, 1984a) where Z_s is the Secchi depth. In Hollingworth Lake the Secchi depth generally varied between 1 and 2m, suggesting maximum euphotic depths Z_{eu} of 3.4m, while the average euphotic depth would be ≈ 1.6m. It can be seen that the mixed depth will therefore regularly exceed the euphotic depth, the ratio of Z_m/Z_{eu} in Hollingworth lake will therefore be high, and the phytoplankton will therefore spend a large proportion of the daylight hours mixed out of the euphotic zone and so unable to photosynthesise. Diatoms have lower minimum light requirements than other algae (Sommer, 1988), and can therefore grow at higher Z_m/Z_{eu} ratios, hence the mixing conditions and high turbidity of the lake will favour diatoms over other algae. That the lake is fully mixed is also advantageous to diatoms in other ways. Nutrients, including silicon, will be returned to the water column facilitating diatom growth and, as described above, the mixing of the full water column will reduce losses of diatoms through sedimentation.

Although a distinct seasonal succession of different algal groups was not observed, seasonal changes within the dominant diatom species were observed. The reason for the dominance of a particular diatom species over another may to be due to mixing and nutrient concentrations. Diatom species are likely to vary in their requirements for light, and have differing optima for ratio of Z_m/Z_{eu}, and will be dependent on the day length; in addition, different species have differing temperature optima (Tilman *et al.*, 1981). Thus, the selection of any particular diatom species over a potential competitor will depend on a number of factors, including light, temperature and nutrients, all of which will vary over the growing season. Thus, the wax and wane of diatoms species within Hollingworth Lake will depend on a combination of a number of factors, the combined effect of which give the competitive advantage to one species at the expense of the others. Because of the polymictic nature of the lake such factors can change rapidly are it is therefore very difficult to predict what factors will be operating at any particular point in the season and hence which particular diatom species will be favoured.

6.1.4.2 Factors that may lead to a succession of *Oscillatoria* in some years

In the recent past *Oscillatoria* has dominated the late summer/early autumn phytoplankton in some, but not all years. Particularly large blooms occurred in 1996 and 1999 (Hitchen, 2001). The dominance of *Oscillatoria* is also seen in other exposed,

shallow lakes such as Lough Neagh in Northern Ireland (Gibson *et al.*, 1971) and Drontermeer and Wolderwijd in the Netherlands (Berger, 1975). No large bloom was observed during this study but a slight increase occurred in late August 2001, followed by a larger short-lived peak in October. Within the cyanobacteria, *Oscillatoria* spp. is better adapted to turbulent conditions than other genera as it can still maintain growth even if the mixing depth Z_m exceeds Z_{eu} (Harper, 1992). The ability of *Oscillatoria* to grow in turbulent conditions may explain why *Oscillatoria* and not other cyanobacteria such as *Microcystis* are observed within the lake. *Oscillatoria* spp. is also able to achieve its maximum rates of growth at relatively low nutrient availabilities (van Liere, 1979 cited in Reynolds, 1984a), enabling it to grow at the low phosphorus concentrations found within Hollingworth Lake, where conditions are often undetectable.

Conditions within Hollingworth Lake therefore suggest that *Oscillatoria* should be successful, however it only succeeds diatoms as the dominant phytoplankton in some years, and not in others. The reason for the dominance of *Oscillatoria* in some years, and diatoms in others may be related to nutrient concentrations and the mixing regime within the lake. As mentioned above, cyanobacteria can only out-compete diatoms when silicon is limiting. Thus in years when silicon within the lake remains above limiting concentrations, cyanobacteria may be out-competed by diatoms. Mixing is also likely to be important, as although both diatoms and *Oscillatoria* are adapted to turbulent conditions, they are likely to have different optima of Z_{mix}/Z_{eu}. Therefore, a change in the ratio through for example, stratification may change the ratio from favouring *Oscillatoria* as opposed to diatoms and vice versa.

Thus, the succession between diatoms and *Oscillatoria* is dependent on the same factors that regulate the succession of different diatom species, particularly mixing depth and nutrient levels. Because of the polymictic nature of the lake such factors can change rapidly are it is therefore very difficult to predict what factors will be operating at any particular point in the season, or how the operation of these factors will vary from year to year. The rapidly changing conditions within the lake make it difficult to determine the precise factors that result in a particular algal group or species dominating the phytoplankton. For example, during this study Dinophyceae dominated the plankton during the late-summer phase in 2002, although the precise reason for the dominance by this algal group is difficult to determine.

6.1.4.3 Predictability of the seasonal succession in Hollingworth Lake

The polymictic nature of the lake is a major factor in the absence of any clear seasonal succession. In many lakes, including Rostherne Mere, growth and loss factors vary seasonally in a predictable manner, and this gives rise to a distinct seasonal succession. For example, diatoms give way to the clear-water phase, which in turn gives way to Cyanophyceae/Dinophyceae. In Hollingworth Lake the regular mixing of the lake means that conditions remain similar seasonally, and there is a less distinct and predictable seasonal succession. It is interesting to compare the phytoplankton seasonal succession of Hollingworth Lake with the typical seasonal successions for lakes of varying trophic status as given by Reynolds (1984a, 1984b). Figure 6.1 shows the sequence for a typical stratifying mesotrophic lake.

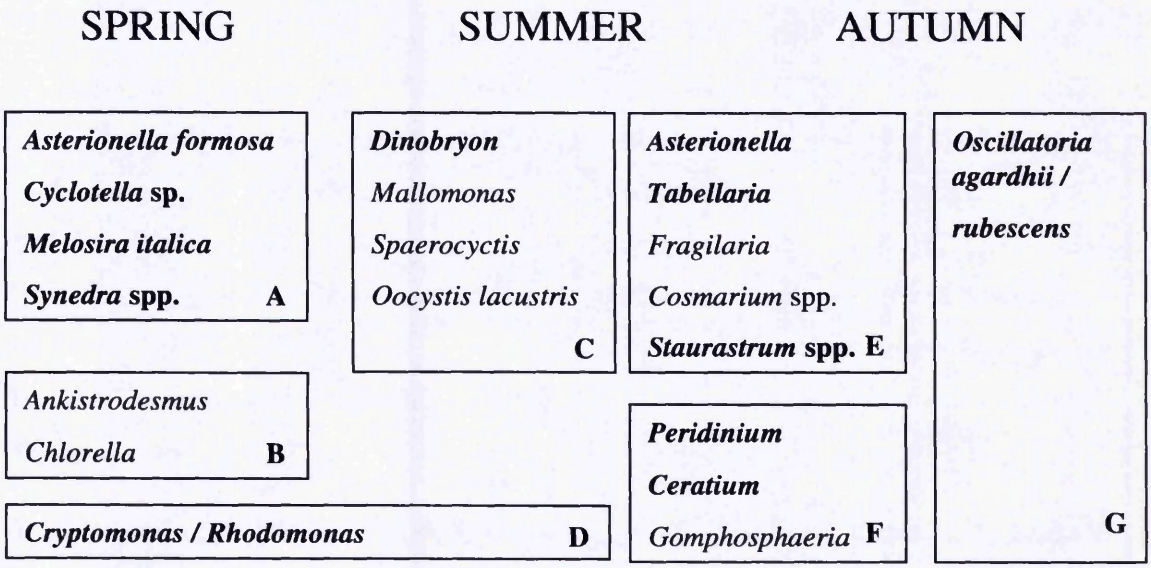


Figure 6.1: Seasonal succession for a typical stratifying mesotrophic lake, compiled from Reynolds (1984a, 1984b). The boxes group together phytoplankton assemblages that are often found together. A typical seasonal succession will follow one or other of the horizontal progressions. Species recorded during this study indicated in bold.

It can be seen that the majority of the dominant phytoplankton species in Hollingworth Lake are represented within the various assemblages within the mesotrophic succession. In terms of seasonal succession, in 2001 the phytoplankton seasonal succession followed the succession A⇒E, while in 2002 it followed A⇒E⇒F. In years when there is an autumn *Oscillatoria* bloom the sequence may consist of A⇒E⇒G. Thus, although there is a seasonal succession, it is not as distinct as observed in Rostherne Mere, and the succession did not follow a simple horizontal progression, dominance by assemblage C for example was not seen, and the phytoplankton was dominated by assemblages A and E. Furthermore, there seems to be little year-to-year

similarity in the plankton seasonal succession. In 1999, there was an autumn bloom of *Oscillatoria*, in 2001 the phytoplankton was dominated by diatoms throughout the sampling period, while in 2002 the phytoplankton diatom dominance was replaced by dinoflagellate dominance. Also, whereas the sequence observed in Rostherne Mere i.e. diatoms/cryptomonads⇒ clear-water phase⇒ cyanobacteria / dinoflagellates could be related to the top-down and bottom-up factors, i.e. grazing, low summer nutrient concentrations, it is difficult to relate the succession in Hollingworth Lake to bottom-up and top-down factors operating within the lake.

Many of these facts may be attributed to the frequent wind-induced mixing in Hollingworth Lake. This results in a much less physically stable system, with mixing events rapidly changing conditions in the lake from those favouring one phytoplankton group/species, to conditions favouring another, for example via the return of nutrients to the water column, or through altering the euphotic depth/mixing depth ratio. However, the occurrence and timing of these mixing events in Hollingworth Lake is unpredictable, leading to difficulty in predicting the seasonal succession of phytoplankton. This unpredictability is typical of shallow, polymictic lakes, for example a study of the shallow eutrophic, non-stratifying Loch Leven (Bailey-Watts, 1978) found a lack of seasonality in phytoplankton succession, which was attributed to the to regular, unpredictable, mixing events. Seasonal succession in Hollingworth Lake is similarly unpredictable.

6.1.5 Summary of factors influencing the phytoplankton in Hollingworth Lake

It can be seen that the seasonal succession within Hollingworth Lake is unpredictable and that the factors that influence the phytoplankton succession are unclear, uncertainties that can be related to the unpredictability of mixing within the lake. Mixing events are likely to result in rapid changes in the factors influencing the phytoplankton, for example, nutrient limitation, mixing depth (and hence light) can all change in an unpredictable manner. For these reasons it is not possible to relate the seasonal succession to top-down and bottom-up effects, as was done for Rostherne Mere (Section 4.1.3). However, it seems likely that bottom-up factors (nutrients, mixing and light) take precedence over the top-down factor of grazing which the analysis above suggests as only having a minor impact on phytoplankton seasonal succession in Hollingworth Lake.

6.2 Population dynamics of *Daphnia* and *Bosmina*

The herbivorous zooplankton in Hollingworth lake principally consisted of *Daphnia cucculata* and *Bosmina* sp. Calanoid copepods were present, but in low numbers. The aim of this section is to examine whether herbivorous zooplankton (particularly *Daphnia* and *Bosmina*) in Hollingworth Lake are regulated primarily by bottom-up (Section 6.2.1) or top-down controls (Section 6.2.2). Factors contributing to the decline of the spring peak of these organisms, and the low summer numbers are of particular interest.

6.2.1 Bottom up influences on the zooplankton – the response of *Daphnia* to a changing food supply

The effect of food availability on the zooplankton can be assessed by calculating the quantity of edible carbon available to the zooplankton, and comparing it to the threshold concentration required for zooplankton growth and reproduction, which is approximately 0.08-1.0 μg C ml^{-1} (Reynolds, 1984a; Muck and Lampert, 1984; George and Reynolds, 1997). However, in order to do this it is necessary to identify the principal food source of the zooplankton. The principal food of *Daphnia* and *Bosmina* may be the small 'edible', readily digested phytoplankton i.e. phytoplankton within the size limits predicted by the Burns' equation; it may include both the 'edible' fraction and also the stellate colonies of *Asterionella* and *Tabellaria*, for which there is evidence that some cladocerans can fragment colonies prior to ingestion. It may be the total phytoplankton, or it may be the bacteria. Zooplankton may also be feeding on all three groups of organisms – 'edible' phytoplankton, 'larger' phytoplankton and planktonic bacteria.

In order to gain an insight into which of these food fractions provide the principal food for the zooplankton three types of analysis were carried out: correlations between potential food sources and zooplankton population parameters, assessment of food availability and analysis of reproductive parameters.

6.2.1.1 Zooplankton/phytoplankton correlations

Correlations were carried out between the potential food sources and the zooplankton population parameters (total population, birth rate, brood size and the proportion of gravid adults). Table 6.2 shows a correlation matrix between the reproductive parameters and the various food fractions. George and Reynolds (1997)

showed that these parameters correlate positively to an increase in the availability of zooplankton food. However, correlations carried out from the data obtained at Hollingworth Lake are inconclusive. It can be seen that only six correlations are significant. Brood size showed no correlations with any food resources. The proportion of gravid adults correlated only with edible biovolume in 2002, however this is unlikely to be biologically significant, as it is difficult to see why increases in 'edible' phytoplankton could have a negative impact on zooplankton reproduction. If edible phytoplankton are grouped with those species that may only be partially edible (i.e. the colonial *Tabellaria* and *Asterionella*) then only *Daphnia* numbers in 2002 correlate. Birth rate of both *Daphnia* and *Bosmina* was positively correlated with bacterial numbers in 2001, which may suggest a relationship; however, in 2002 no relationship of potential food resources was seen either with bacteria, or with total phytoplankton biovolume or 'edible' phytoplankton biovolume.

Correlations with *Daphnia* and *Bosmina* numbers were also inconclusive, showing both negative (*Bosmina* and total biovolume) and positive (*Daphnia* and edible including colonies and *Bosmina* and bacterial numbers in 2002).

	2001				2002			
	'Edible' biovolume	'Edible' inc colonies	Total phyto biovolume	Bacterial numbers	'Edible' biovolume	'Edible' inc. colonies	Total phyto biovolume	Bacterial numbers
Daphnia numbers	ns	ns	ns	ns	ns	0.522 * (n=17)	ns	ns
Daphnia B/Rate	ns	ns	ns	0.511 * (n=16)	ns	ns	ns	ns
Daphnia Brood Size	ns	ns	ns	ns	ns	ns	ns	ns
Daphnia % Gravid	ns	ns	ns	ns	-0.521 * (n=17)	ns	ns	ns
Bosmina numbers	ns	ns	-0.515 * (n=16)	ns	ns	ns	ns	0.670 ** (n=17)
Bosmina B/Rate	ns	ns	ns	0.507 * (n=16)	ns	ns	ns	ns
Bosmina Brood size	ns	ns	ns	ns	ns	ns	ns	ns
Bos % Gravid	ns	ns	ns	ns	ns	ns	ns	ns

Table 6.2: Correlation matrix to show correlations (Pearson) between zooplankton reproductive parameters and potential zooplankton food resource. Correlations were carries out over the whole annual cycle in each year. * - $P \leq 0.05$, ** - $P \leq 0.01$, (ns- not significant)

It can be seen that the results of the correlation analysis are inconsistent, both between years, and within a single year, and it is therefore difficult to draw any meaningful conclusions concerning zooplankton food sources from the results. However, a lack of a correlation does not necessarily mean a lack of a relationship. Correlations, or lack of them, can often be misleading due to other interfering factors and this may be the case with the data obtained from Hollingworth Lake. For instance, it may be that the *Daphnia* and *Bosmina* feed to some extent on all the fractions, and that

the extent to which they feed on each fraction varies seasonally. This may mask any simple relationship between one particular food source and zooplankton reproductive rate, and thus make it difficult to make any firm conclusions concerning the food source of the *Daphnia* and *Bosmina* using correlation analysis. It is therefore necessary to consider other evidence when attempting to determine the food sources of the zooplankton. In the discussion below the evidence for the zooplankton feeding on each food fraction is considered, as is the ability of each fraction to meet the nutritional needs of the zooplankton. This will give an indication of the extent to which the zooplankton are controlled by the bottom up factor of food availability. The effect of food availability is then considered in relation to the population dynamics of the zooplankton, and in particular the decline of the spring zooplankton maximum, and the continuing low numbers of *Daphnia* and *Bosmina* during the summer.

6.2.1.2 Assessment of the availability of food to the zooplankton

Evidence for *Daphnia* and *Bosmina* feeding on the 'edible' phytoplankton

It was argued in section 6.1.2.1 that the majority of the phytoplankton species within Hollingworth Lake have low grazing susceptibilities and that the only species that are readily 'edible' are *Cyclotella* sp. *Nitzschia* spp, *Cryptomonas* spp and *Rhodomonas minuta*. However, if this is the case then the quantity of edible food remained well below the threshold concentration of 0.08-1.0 μg C ml^{-1} for the majority of the sampling season, including periods when the reproductive rate of the *Daphnia* was high. For example during spring 2002 the average *Daphnia* brood size increased from ≈1 during the winter to reach a maximum of approximately 5 on the 2nd of April. Rapid increases in brood size occur when there is a sudden increase in the quantity of edible food (George and Reynolds, 1997). However, in this study the increase in brood size occurred when edible food concentrations remained well below the threshold concentration, with concentrations at <0.01μg C ml^{-1}. In 2001 although sampling was not undertaken until brood size was already exhibiting a spring maximum the quantity of 'edible' carbon was again well below the threshold concentration, with values of <0.04μg C ml^{-1}. Thus if small, readily ingestible 'edible' phytoplankton are the only food available to the zooplankton during the spring the quantity of available carbon would suggest that the zooplankton were food limited; however, the reproductive response of the zooplankton suggests non-limiting food concentrations.

'Edible' food concentrations were also low during the rest of the sampling period. During the summer and autumn of 2001 edible carbon was less than 0.01µg C ml^{-1}, including the period of maximum birth rate and percentage of gravid adults in August. In 2002, 'edible' carbon was also low, only exceeding the theoretical threshold of approximately 0.08 to 0.10µg C ml^{-1} during the late-summer phase of 2002, when there was a rise in the numbers of cryptomonads. Considering that the carbon content of 'edible' phytoplankton was below the threshold concentration for zooplankton growth and reproduction for long periods of the season it is unsurprising that 'edible' biovolume did not correlate with any of the reproductive parameters i.e. birth rate, proportion of gravid adults or brood size.

It can be seen that for much of the season the quantity of small phytoplankton cannot provide enough edible carbon to satisfy even the minimum concentration required for survival, never mind the high reproduction during for example the spring, and in August 2001. It is therefore necessary to assume that in addition to the small 'edible' phytoplankton the *Daphnia* are also ingesting the larger phytoplankton or bacteria. These possibilities are considered below.

Evidence for *Daphnia* and Bosmina feeding on 'inedible' in addition to 'edible' phytoplankton

It was argued previously that the phytoplankton species dominating the phytoplankton in Hollingworth Lake were little affected by grazing, and that this was due to the phytoplankton species having a low susceptibility to grazing, and also due to a low zooplankton grazing rate. However, it does not follow that these phytoplankton species are completely inedible to the zooplankton, and so not available as food. For instance, although the average filament length of *Aulacoseira* and *Melosira* was >200µm and may be considered inedible smaller filaments may have been available to the zooplankton. Furthermore, despite the low susceptibility of stellate colonies such as *Asterionella*, some of the colonies may have been ingested. Thus, during periods when large phytoplankton species dominated it may have been possible for the zooplankton to ingest a small proportion of the phytoplankton biomass (e.g. small filaments), thus avoiding food limitation. If this were the case then zooplankton reproductive parameters would be expected to increase as the biomass of these larger species increased. In the summer of 2001 *Tabellaria* was dominant and increased over the summer and the birth rates of *Daphnia* and *Bosmina* also increased, possibly suggesting that the *Daphnia* and *Bosmina* were feeding on a proportion of the *Tabellaria* biomass. However, when

Tabellaria exhibited its maximum rate of increase in early autumn the birth rate actually showed a sharp decline, suggesting that the increase in *Tabellaria* biomass had no positive effect on zooplankton reproduction. Similarly, although the early summer of 2002 there was a large increase in *Asterionella* no increase in birth rate, proportion of gravid adults, or brood size was observed. Thus, as with 'edible biovolume' it is not possible to relate changes in the reproductive parameters of the zooplankton to any fluctuations in total phytoplankton biovolume.

Evidence for *Daphnia* and *Bosmina* feeding on Bacteria

Another possibility is that the cladocerans are ingesting bacterial cells. *Daphnia cucculata* has been shown to have very fine filter-mesh sizes from 0.23 to 0.45μm (Geller and Muller, 1981). As the cell size of natural bacteria range from 0.2 to 2μm (Straskrabova and Sorokin, 1972) *Daphnia cucculata* should be able to utilise the majority of bacteria cells. *Bosmina* is also able to feed upon bacteria (Porter *et al.*, 1983) The edible carbon content within the bacterial fraction was almost continually at or near the threshold concentration for *Daphnia*, with values between 0.08 and 0.10 μg C ml^{-1}. Hence, if the *Daphnia* and *Bosmina* are ingesting bacteria as well as the small 'edible' phytoplankton species then it is unlikely that food will fall below limiting concentrations. Correlation analysis showed a positive correlation between both *Daphnia* and *Bosmina* birth rate and bacterial biovolume in 2001 suggesting that bacteria may be a major food source of the zooplankton. This, together with the fact that these species have been shown to be bacterial feeders suggests utilisation of bacteria may be important. However, no relationship between bacteria and Cladocera was observed in 2002 so the evidence is not conclusive.

6.2.1.3 Zooplankton reproductive parameters and population size

The above section attempted to determine the extent of bottom-up control by assessing the availability of food for the zooplankton. However, this was inconclusive, and it is therefore difficult to relate food concentration to the threshold food concentration below which zooplankton starve and die, and so determine the extent of bottom up control. However, it is possible to gain an insight into the likely effect of bottom up control on food limitation by looking at the reproductive parameters of the zooplankton, not in relation to the availability of a particular food source as was carried out above, but in relation to the numbers of zooplankton. For instance, if the zooplankton have a high birth rate, this would suggest an adequate food source.

Effect of food limitation on the spring zooplankton maximum

In both 2000 and 2001, an increase in *Daphnia* and *Bosmina* occurred during the spring. A spring increase in zoooplankton is often observed in standing waters and is related to an increase through parthenogenetic reproduction in response to an increase in the availability of edible phytoplankton (Sommer *et al.*, 1986). In both 2001 and 2002 an increase in reproductive rate can be seen from the increase in brood size, which showed a maximum during March and April. Rapid increases in brood size occur when there is an increase in the availability of edible food (George and Reynolds, 1997), which suggests that during early spring the *Daphnia* and *Bosmina* were ingesting food in excess of the threshold concentration. The increased reproductive rate led to increases in the numbers of both *Daphnia* and *Bosmina*, which peaked in late May/early June before declining to low levels in June/July.

The decrease in the spring zooplankton peak has been attributed to the bottom-up effect of a decline in the available food, leading to starvation and death of the zooplankton (Sommer *et al.*, 1986; Luecke *et al.*, 1990). One way to assess this would be to measure the carbon available to the zooplankton; however, as was discussed above the lack of certainty concerning the zooplankton food source makes it impossible to assess the carbon available to the zooplankton, and whether it had fallen below threshold concentrations. However, a decreasing birth rate would also suggest low food availability, and if the spring decrease in zooplankton numbers followed a decrease in birth rates then this would suggest that the decline in the spring peak was caused by a decline in the available food. In this study, low birth rates (approximately 0.02-0.03) occurred at the start of the summer phase, around the time when the spring phytoplankton had declined and phytoplankton biovolume was at a minimum. This suggests that a reduction in food may be responsible for the reduced zooplankton numbers. However, in both years the minimum birth rate occurred after the phytoplankton biovolume was at a minimum, and when phytoplankton biomass were increasing. Furthermore, the decline in zooplankton numbers occurred when birth rates were actually increasing. However, the fact that birth rates did decrease towards the end of spring, before the decline in zooplankton, suggests that a reduction in food availability may have played a part in the decline of the spring bloom. However, the fact that the low birth rates occurred during an increase in phytoplankton biomass, and the fact that the zooplankton decline occurred at a time of increasing birth rates suggest that other factors, such as predation may also be important.

Effect of food limitation on the low summer numbers of *Daphnia* and *Bosmina*

The increase in birth rates during the spring zooplankton decline continued during the remainder of the summer. With the exception of *Daphnia* birth rates during the summer of 2002 birth rates increased to higher levels than those observed during the spring. However, despite high summer birth rates, no large summer increase of zooplankton was observed. This suggests that during the summer the main control of zooplankton numbers may be predation, rather than food availability. An exception may be during the summer of 2002. During this period, *Daphnia* birth rate was less than it was during the spring, and much less than the values reached during the summer of 2001 suggesting that during the summer the availability of food was lower than at these other times. The low numbers of *Daphnia* during the summer of 2002 may therefore be due to low food levels. However, during the summer of 2002 *Bosmina* numbers were also low, remaining at ≈2 *Bosmina* l^{-1}, yet the birth rate of *Bosmina* during the summer was double than that observed during the spring when the maximum *Bosmina* population was ≈30 *Bosmina* l^{-1}. Thus, a doubling of the birth rate during the summer resulted in a population of less than 10% of that observed during spring. The disparity between the birth rate and the population increase suggests that the *Bosmina* were subject to high mortality due to predation. If *Bosmina* suffered losses through predation during the summer of 2002, it seems likely that the *Daphnia* population would also suffer predation. Thus, despite the low birth rate of the *Daphnia* during the summer of 2002 suggesting low food levels, it seems likely that the low numbers are also due to predation.

6.2.2 Effect of predation on *Daphnia* and *Bosmina* population dynamics

Predation on the zooplankton can be due to fish, including both adult fish and fish fry, and invertebrates such as *Chaoborus*, *Leptodora* and cyclopoid copepods. No attempt to monitor the predation impact of fish and predatory zooplankton upon the *Daphnia* and *Bosmina* populations has been made in this study. However, by investigating the literature on fish and predatory zooplankton predation it is possible to suggest how predation may impact on the zooplankton populations in Hollingworth Lake.

6.2.2.1 Fish Predation

Although fish were not monitored during this investigation, a study that ran concurrently did investigate the fish populations in Hollingworth Lake and showed the fish population to consist of perch (*Perca fluviatilis*), bream (*Abramis brama*), roach (*Rutilus rutilus*), ruffe (*Acerina cernua*) and pike (*Esox lucius*), (E. A. Baldwin, *pers. com.*) of which roach was the most numerous. All of these fish include stages that feed wholly or partly on the zooplankton. Predation may therefore come from young of year (YOY) fish, also referred to as 0+, which are fish in their first year, and from adult fish.

Mehner and Thiel (1999) reviewed 19 studies of the impact of 0+ fish on zooplankton communities and found that the evidence for the control of zooplankton during the spring and early summer (when fish were in larval stages of development) was equivocal, but that the evidence for control during late summer and autumn was much stronger. However, some studies (Keast, 1980; Cryer *et al.*, 1986; Whiteside, 1988) have concluded that predation by fish larvae may be important during the spring, particularly if the zooplankton consists of small cladocerans such as *Bosmina*. The zooplankton species within Hollingworth Lake were *Bosmina* (length ≈0.42mm) and the small-bodied cladoceran *Daphnia cucculata* (length ≈0.80mm) so the small size of the zooplankton may render it more susceptible to predation by fish larvae. Evidence from the studies of Baldwin shows that perch were hatching in late April and early May, while the first roach larvae were found in the lake during mid-June, prior to the decline in zooplankton numbers. It is therefore possible that predation by newly hatched larval fish may cause the spring decline in *Daphnia* and *Bosmina*. However, without more detailed knowledge of the numbers of fry and their feeding rate on the zooplankton it is impossible to determine with any confidence the impact of YOY fish predation on the spring peak.

Predation by adult fish may also be important. The fish population is dominated by roach, which is zooplanktivorous, and it may be the case that the feeding rate of the roach population increases as the weather becomes warmer during the spring. Lueke *et al.*, for example, found that feeding rates of cisco (*Coregonus artedii*) were low at temperatures <12°C, allowing spring *Daphnia* populations to increase; feeding rates of the fish then increased with increasing temperature. It is possible that in Hollingworth Lake low water temperatures during the spring could result in low predation by adult fish, allowing an increase in zooplankton numbers. Increasing water temperatures during the early summer may have resulted in an increased feeding rate, thus reducing

the spring zooplankton bloom. However, without further data on fish populations within the lake this idea can only remain as informed speculation.

The continuing low numbers of zooplankton during the summer months may also be due to fish predation. The impact of fish predation often increases during the summer months, as the YOY fish reach a larger size, resulting in a larger mouth gape and better ability to detect and consume prey items (Mehner and Thiel, 1999). As mentioned above, Mehner and Thiel (1999) reviewed 18 studies of the impact of 0+ fish on zooplankton communities and found that significant control of zooplankton communities by 0+ fish was observed during late summer and early autumn. Although they found the evidence for zooplankton control during the spring to be inconclusive, the evidence for YOY fish predation impacting on summer zooplankton was much stronger. Other studies have also shown that predation by adult fish can also control summer zooplankton communities (Luecke *et al.*, 1990). It is therefore possible that fish predation is keeping summer zooplankton numbers low in Hollingworth Lake.

6.2.2.2 Invertebrate Predation

Predation by invertebrates may also be important in reducing the numbers of *Daphnia*. Numbers of *Leptodora* and *Chaoborus* were consistently low, and may be presumed to have a small effect on the *Daphnia* community. Cyclopoid copepods were also present, with numbers during the summer phase varying between 1 and 2 cyclopoids l^{-1}. The small size of the zooplankton within Hollingworth Lake may render them susceptible to cyclopoid predation. Gliwicz and Ummana (1994) calculated feeding rates of a cyclopoid copepod (*Acanthocyclops*) on various species of *Daphnia* and showed that the small-bodied species were more vulnerable to predation than large bodied forms, with *Daphnia cucculata* calculated to have a predatory induced *Daphnia* death rate of between 0.4 and 0.7 day^{-1}, which is higher than cladoceran birth rates observed during this study. Although feeding rates were measured under experimental conditions it suggests that copepod predation can have an important effect on *Daphnia* numbers in natural systems. Gliwicz and Ummana did not investigate feeding rates of cyclopoids on *Bosmina*. However, in view of the small size of *Bosmina* within Hollingworth (smaller than *D. cucculata*) it is unlikely that predation-induced death rate of *Bosmina* will be much lower than that of *D. cucculata*.

If predation by cyclopoid copepods was important in reducing *Daphnia* numbers an increase in cyclopoid numbers, resulting in an increased predation rate, would be expected to be observed during the spring *Daphnia/Bosmina* decline, with numbers

remaining high during the summer. However, the only large increase in cyclopoid numbers occurred during the spring of 2001, prior to the decrease in *Daphnia/Bosmina* numbers. Furthermore, during the decline of the *Daphnia* and *Bosmina* numbers of cyclopoid copepods also declined and no increases in cyclopoid numbers were observed. Thus, the reduction in the spring zooplankton peak cannot be attributed to increase grazing by cyclopoids. In fact, the parallel decrease of *Daphnia*, *Bosmina* and cyclopoid copepods suggests that the population decrease of all three taxa was caused by the same causal factors. It is also interesting to note that cyclopoid copepods numbers were also reduced during the summer months, again suggesting that similar factors are reducing the numbers of cyclopoid copepods and the Cladocera during the summer phase. This, together with that fact that numbers of the other predatory zooplankton species *Leptodora* and *Chaoborus* were low suggests that predatory zooplankton are unlikely to be responsible for the collapse of the spring zooplankton peak, and the low summer numbers.

Thus, during the summer the high zooplankton birth rates and low numbers suggest a high mortality through predation. Of these predatory controls the albeit limited evidence suggests that predation by fish will be more important than that of invertebrates.

6.2.3 Summary of factors influencing seasonal population dynamics of the Cladocera within Hollingworth Lake

Table 6.3 summarises the evidence for the operation of controls on numbers Cladocera within Hollingworth Lake. It can be seen that there is evidence for a switch between bottom-up control in the spring, when zooplankton numbers peaked but the evidence for top-down control increases towards the summer period.

Cladoceran population dynamics	**Evidence for top-down and bottom-up control**
Winter/ increasing numbers during spring	Increasing brood size and birth rate during spring suggests an increasing food supply and that the population increase of the Cladocera is limited by the bottom-up control of food availability It is difficult to determine the quantity of edible carbon available to the zooplankton during this period, as there is no clear evidence as to the food source of the cladocera.
Decline of the Spring Peak	Possibly due to combination of both top-down and bottom-up control. Declining birth rates suggest bottom-up control is a possible cause of decline of spring peak. However, minimum birth rates occurred after phytoplankton biomass minimum so evidence not clear. Top-down control also suggested by decline in Cladocera numbers when birth rates increasing, suggesting top-down control. Small size of Cladocera may render them vulnerable to predation by 0+ fish, which may also play a part in reducing the spring peak. Again, it is not possible to use the quantity of edible carbon available to the zooplankton as further evidence for bottom up control as there is no clear evidence of food resource of the cladocera.
Low Summer Numbers	High birth rates suggest food availability not primary factor influencing numbers of cladocera, although again no evidence is available from edible carbon. Top-down control strongly suggested by low *Daphnia* numbers despite high birth rates, which suggests a high mortality rate due to predation. Fish are likely to be the major predator.

Table 6.3 Summary of the principal factors influencing zooplankton population dynamics in Rostherne Mere.

6.3 Planktonic Bacteria in Hollingworth Lake

The aim of this section is to consider the seasonal fluctuations in bacterial numbers within Hollingworth Lake and to relate these fluctuations to the various factors that influence bacterioplankton. The bottom-up (growth) factor that typically limited bacterioplankton growth is the availability of organic substrates, often via release by phytoplankton (Cole *et al.*, 1988); however, numbers can also be limited by temperature (Scavia and Laird, 1987; Felip *et al.*, 1996; Simon and Wunsch, 1998) and by inorganic nutrient availability (Coveney and Wetzel, 1992; Watanabe, 1996, Morris and Lewis, 1992).

6.3.1 Influence of bottom-up factors on bacterioplankton in Hollingworth Lake

In order to show which factors may be important in regulating the populations dynamics of bacteria correlation analysis was carried out between total bacterial numbers and possible sources of organic growth substrates (Table 6.4), and also between temperature and inorganic nutrient fractions (Table 6.5).

Total Bacteria versus:	Chl-a	DOC	TSS	TOM	Colour
2001	ns	ns	ns	ns	ns
2002	ns	-0.559* (n=15)	ns	ns	ns

Table 6.4: Pearson correlations between total bacterial numbers and factors that may potentially limit bacterial numbers. * - $P \leq 0.05$. (ns- not significant).

Total Bacteria versus:	Temp	SRP	TDP	TP	NO_x	TDN	TN
2001	0.613* (n=14)	ns	ns	ns	ns	ns	ns
2002	ns	ns	ns	ns	ns	ns	ns

Table 6.5: Pearson correlations between total bacterial numbers and factors that may potentially limit bacterial numbers. * - $P \leq 0.05$. (ns- not significant).

It can be seen from the tables that only two significant correlations were observed, that between temperature and bacterial numbers in 2001, and a negative correlation between bacterial numbers and DOC in 2002. As organic carbon provides the growth substrate for the bacteria it is unlikely that a negative correlation between DOC and bacterial numbers represents a real relationship. The correlation with temperature in 2001 may suggest a relationship however. The correlation analysis therefore provides limited information on the factors that may be important in regulating bacterial

numbers. The following discussion looks at each of the potential controlling factors, and through a careful analysis of the data and by reference to the literature, attempts to shed some light on the factors that may be important in regulating bacterial numbers in Hollingworth Lake.

6.3.1.1 Organic substrates – chlorophyll-a, humic acids, TSS and TOM

The main factor regulating bacterial growth is often organic substrates released by phytoplankton (Cole *et al.*, 1988), resulting in a positive correlation between bacterial growth and algal production. This increased growth can lead to an increase in bacterial numbers, leading to a positive correlation with chlorophyll-a (as was observed in Rostherne Mere).

No correlation between chlorophyll-a and bacterial numbers was observed in Hollingworth Lake, however. The lack of correlation may be due to the low phytoplankton biomass in Hollingworth Lake resulting in low exudates release by the phytoplankton. The reduced organic substrates from the phytoplankton may lead to a greater reliance on non-algal sources of carbon, for example, macrophytes, or allochthonous sources such as humic acids. DOC release by macrophytes may be considered negligible, as Hollingworth Lake has extremely few macrophytes. Allochthonous sources of carbon may be important however. Bacterioplankton growth and productivity are sometimes correlated with inputs of allochthonous DOC rather than phytoplankton productivity (Wetzel and Otsuki, 1974; Laybourne-Parry *et al.*, 1994). Allochthonous DOC often consists of humic material, which although utilised less efficiently than simple organic substrates (Wetzel, 2001), can be used for bacterial growth (Tranvik, 1990). An attempt was made to determine the levels of humic acids in the lake by measuring colour during 2002. Colour is a relative measure of the brown colour of lake water and reflects the content of light absorbing, primarily humic material in the water (Cuthbert and Giorgio, 1992, Pace and Cole, 2002). As Hollingworth Lake has low phytoplankton biomass it may be expected that allochthonous humic material would make up a high proportion of the DOC pool, particularly as the catchment of the main inflow to the lake consists of peat moorland. However, there was no correlation between DOC and colour. The lack of correlation may be due to the unreliability of the measurement of colour (see page 210) or alternatively, the majority of the DOC within Hollingworth may indeed be non-humic. There was also no evidence for a relationship between bacterial numbers and colour, which suggests that the bacteria are not primarily using humic material as the principal growth material.

The bacteria may of course be utilising both autochthonous and allochthonous sources of organic carbon, in which case the dissolved organic carbon (DOC) measured in this study (which includes both the autochthonous and allochthonous sources) may be expected to correlate with bacteria. However no correlation with DOC was observed.

Due to the shallowness and frequent wind-induced mixing, Hollingworth Lake has a high proportion of non-algal material suspended in the water column. Sediment re-suspension may return detrital carbon to the water column and this may constitute a significant source of bacterial carbon at certain times of the year (McKinley and Wetzel, 1979). However, detrital carbon will have been included within the measurement of DOC, and as mentioned above there was no evidence of a relationship between DOC and bacterial numbers. The case for the bacteria relying on re-suspended detrital carbon is therefore not proved.

Re-suspension of the sediments would however lead to an increase in total suspended solids (TSS) within the water column. Thus, if the bacteria were influenced by re-suspended detrital carbon then a correlation between bacterial numbers and TSS may occur; however there was no correlation. However, the TSS may include both inorganic material as well as organic material. Hence, an attempt was made to measure particulate organic carbon within the water column. POC was correlated with phytoplankton biomass however, suggesting that despite sediment re-suspension, the majority of particulate organic carbon within the water column was of algal origin. Again, there was no correlation between POC and bacterial numbers.

6.3.1.2 Other bottom-up factors regulating bacterial growth – nutrients, temperature and pH

Although the availability of organic substrate is often considered to the primary restraint on bacterial growth, a number of studies have indicated that the bacterioplankton may be restricted by inorganic nutrient availability. Although nitrogen limits bacterial growth in marine systems (Moriarty and Bell, 1993), in freshwater systems the limiting nutrient is usually phosphorus (Coveney and Wetzel, 1992; Watanabe, 1996; Morris and Lewis, 1992). Phosphorus limitation is particularly important in humic lakes, where the high level of allochthonous carbon relieves the bacteria of their dependence on autochthonous carbon and leads to limitation by phosphorus (Jansson *et al.*, 2001) and also, due to the low nutrient concentrations, oligotrophic systems (Chrzanowski, *et al.*, 1995). During this study no relationship between SRP concentrations and bacterial numbers was observed in either year,

however this does not mean that low nutrient levels are not a major influence on bacterial populations within the lake. The concentrations of phosphorus in Hollingworth Lake were often very low, with undetectable concentration for long periods of the growing season. Thus, phosphorus may have an important bottom-up effect on bacterial populations within the lake. Morris and Lewis (1992) showed that P limitation was important in a mesotrophic lake in which SRP and dissolved organic phosphorus concentrations both ranged between 0.2 and 3μg l^{-1}. In Hollingworth lake during 2001 concentrations of SRP oscillated between >10μg l^{-1} and undetectable during the summer, and were undetectable throughout the autumn. In 2002 spring levels of SRP were <5μg l^{-1} while during the summer were undetectable. Thus for long periods of the growing season the bacteria may have been phosphorus-limited which may explain the lack of correlation between organic substrates and bacterial numbers.

Temperature has been shown to regulate bacterial growth (Scavia and Laird, 1987; Felip *et al.*, 1996) and by implication bacterial numbers. The correlation between temperature and bacterial numbers observed in 2001 may therefore be indicative of real relationship. However, these studies found that growth was only correlated with temperatures at less than 10°C and at higher temperatures other factors such as nutrients and organic substrates are more important. Temperatures in Hollingworth Lake exceeded 10°C during the summer and early autumn and it therefore unlikely to regulate bacterial growth and numbers in Hollingworth Lake for the majority of the growing season. Furthermore, correlations with temperature are often misleading, as temperature has a positive effect on metabolism in general, and can produce statistically significant correlations between variables that have no true cause and effect relationship (Morris and Lewis, 1992).

Extremes of pH have been shown to affect bacteria, with production affected by pH values in excess of 10 (Jeppesen *et al.*, 1997). In this study the pH at Hollingworth Lake generally varied between 6 and 7, and the maximum reached was 7.8. It is therefore unlikely that pH affected bacterial numbers.

6.3.1.3 Summary of bottom-up factors in Hollingworth Lake

It can be seen form the above that there is little evidence for any clear relationship with any of the potential sources of organic substrates required for bacterial growth, or with any of the other potential growth factors, although the low levels of phosphorus suggests that P-limitation may be important in regulating bacterial numbers. The lack of

correlations may be due to the factors influencing the bacterioplankton changing seasonally, with different combinations of controlling factors operating at different times. This may obscure any simple relationship with any one factor. Alternatively, the lack of correlation may reflect the fact that bacterial numbers, and not bacterial growth rates, were monitored in this study. Bacterial numbers reflect the cumulative effects of growth and loss. Therefore, although bacterial growth may indeed be limited by one of the sources of organic substrates measured above if loss rates are high then an increase in bacterial growth may not result in any increase in bacterial numbers. For example, Wetzel (2001) mentions that growth (i.e. bottom-up factors) of bacterial populations are often evenly balanced by mortality (i.e. top-down factors) and that this often leads to little seasonal variations in bacterial numbers. Thus, an increase in growth does not necessarily result in an increase in numbers. The lack of correlation between bacterial numbers and any bottom up factor in Hollingworth Lake may therefore reflect the fact that top-down factors cause substantial losses of the bacteria population. Therefore, bacterial growth may indeed be limited by the availability of organically released carbon from phytoplankton, yet if there are significant top-down factors causing mortality of the growing population then no increase in population would be observed, resulting in no correlation between bacterial numbers and chlorophyll-a. In order to test this hypothesis however, it is necessary to measure bacterial growth rates, which is beyond the scope of this study. However, it is possible to look at the top-down factors that influence the bacterioplankton, and make some suggestions as to how they may operate in Hollingworth Lake.

6.3.2 Possible losses of bacteria through grazing and viruses

It was mentioned above that bacterial numbers, as measured in this study, reflect the cumulative effects of growth and loss and the lack of a correlation between bacterial numbers and possible controlling factors may be due to loss top-down factors keeping bacterial numbers low. Losses can occur through grazing by cladocerans (Brandelberger, 1991), ciliated protozoa (Fenchel, 1987), rotifers (Ooms-Wilms *et al.*, 1995) and heterotrophic nanoflagellates (Sanders *et al.*, 1989, Wetzel, 2001) and through viral attack (Wommack and Colwell, 2000). In this study cladoceran filtering rate was monitored, and ciliate and rotifers numbers. Table 6.6 shows correlation analysis of these parameters with bacterial numbers.

Total Bacteria versus:	Filtering rate (due to cladocerans and calanoid copepods)	Ciliated protozoa numbers	Rotifer numbers
2001	ns	ns	-
2002	0.496* (n=17)	ns	0.554 * (n=16)

Table 6.6: Pearson correlations between total bacterial numbers and top-down factors that may potentially limit bacterial numbers. * - $P \leq 0.05$, ** - $P \leq 0.01$, (ns- not significant).

There was positive correlation between total filtration rate and bacterial numbers in 2002, although no correlation was observed in 2001. If Cladocera were significantly impacting on bacterial numbers then a negative correlation between cladoceran filtering rate and bacterial numbers mayd be expected as the higher the filtering rate the more the bacterial population would be reduced. However, a positive correlation was observed suggesting that Cladocera do not impact on bacterial numbers. Furthermore, the filtration rate of the Cladocera is unlikely to have any great impact on bacterial numbers. The potential maximum growth rate of bacteria is >1 day^{-1} (Wetzel, 2001), which is much greater than the potential losses due to grazing, which (as the filtering rate was often <10%) were <0.1 day^{-1}. Only during the spring did the filtering rate increase to >30% (0.3 day^{-1}). Potential losses from grazing therefore did not reach the levels at which the grazing could cause fluctuations in bacterial numbers.

There was a positive relationship between rotifer numbers and bacterial numbers, which suggests that rotifers may be feeding upon bacteria. However, it is unlikely that rotifers have a major impact on bacterial numbers as no negative relationship between rotifer numbers and bacteria numbers were observed which suggests that increases in rotifers did not cause any significant reductions in bacterial numbers. Furthermore, as was calculated in Section 6.1.2.2 the grazing rate of Rotifers was generally low, at approximately 0.1% of the water column filtered per day, which would give a grazing loss rate of ≈0.01 day^{-1}. As with the cladocera, these grazing rates are well below the levels at which the grazing could cause fluctuations in bacterial numbers.

There was no relationship between ciliated protozoa and bacterial numbers, which suggests that ciliates have a low impact on bacterial numbers. This is confirmed by an analysis of the filtration rate of the ciliated protozoa, which can be calculated by using the clearance rate of a typical ciliate, and the size of the ciliate population. Taking 10^{-5} ml h^{-1} as clearance rate for a typical ciliate feeding on bacteria (middle of the range given by Wetzel, 2001), and 20 ciliates ml^{-1} (20,000 l^{-1}) which was the maximum population observed in Hollingworth Lake, would give a filtration volume of 20000x10^{-}

^{5}x24 or 4.8ml per litre, per day. However, over the majority of the annual cycle ciliate numbers were <5 ciliates ml^{-1}, which would give a filtration rate of <1.2ml per day for the majority of the annual cycle. Thus grazing rate of the total ciliate population is low, and typically 1% of the water volume, giving a loss due to grazing of the bacterial population of only 0.01 day^{-1}. Again, this is far below the rate required for grazing to cause fluctuations in bacterial numbers. For these reasons ciliates are unlikely to have any significant impact on phytoplankton populations within Hollingworth Lake.

This suggests that grazing by cladocera, rotifers and ciliates have a low impact on bacterial numbers in Hollingworth Lake. This is in agreement with other work on the effect of grazing on bacteria. Sanders *et al.*, (1989) studied grazing in the eutrophic Lake Oglethorpe (USA) and found that grazing by rotifers and ciliates accounted for between 3 and 11% of the total grazing on bacteria, while cladocerans accounted for <1%, in Lake Constance daphnids accounted for 9-12% of bacterial mortality, while ciliates accounted for between 14 and 19% (Gude, 1986; Simon *et al.*, 1998a,b).

If cladoceran, rotifer and ciliate grazing have little impact on bacterial numbers in Hollingworth Lake, and the bacteria are indeed subject to a high rate of loss, then two factors that were not monitored in this study may be important – grazing by heterotrophic nanoflagellates and viral-induced mortality.

Heterotrophic nanoflagellates are often the major predators of bacteria. In the studies of Gude and Simon mentioned above bacterivory in both of the lakes was dominated by heterotrophic nanoflagellates (HNF's), which accounted for 49-81% of the grazing in Lake Oglethorpe and 52-68% of bacterial mortality in Lake Constance. Thus if grazing is a significant top-down factor on bacteria in Hollingworth Lake then it is likely to be dominated by heterotrophic nanoflagellates.

Grazing is not the only important top-down factor inducing bacterial mortality. Viral induced mortality of bacteria can account for a substantial fraction of the bacterial mortality (Wommack and Colwell, 2000). Simon *et al.* (1998a, b) for example estimated viral mortality to range between 1 and 24% of the total bacterial mortality. The influence of viral mortality on the bacterial population in Hollingworth Lake is therefore likely to be important.

6.3.3 Summary of factors influencing bacterioplankton in Hollingworth Lake

There is very little evidence from which to make firm conclusions concerning factors controlling bacterioplankton populations in Hollingworth Lake. In terms of bottom-up factors there this study could not detect a clear relationship with any source of organic substrate, or with any other factor such as phosphorus. In common with the phytoplankton, the lack of any observable relationship with growth factors may be related to disturbance, as the frequent mixing of Hollingworth Lake may lead to the factors influencing the bacterial numbers changing in an unpredictable manner, thus no relationship iss observed with any one factor. However, the low levels of phosphorus in Hollingworth Lake suggest that phosphorus may be an important limiting factor.

The lack of a clear relationship with bottom-up factors may also be due to strong top-down control. Bacteria may be strongly influenced by the top-down effect of factors that were not monitored during this study, such as grazing by HNF's and high bacterial mortality due to viruses. The operation of these factors may mean that increased growth rates of the bacterioplankton due to increases in organic substrates, may not result in increased bacterial numbers. Hence, a positive relationship between bacterial numbers and chlorophyll-a for example may be obscured. Further research is required to determine the extent to which top-down factors influence the bacterioplankton dynamics in Hollingworth Lake.

6.4 Trophic status of Hollingworth Lake

Very little previous monitoring of Hollingworth Lake has been carried out and there is little information concerning the trophic nature of the lake, the earliest reference to which was by Clough (1979), in an internal fisheries report for the water supply company, which described the lake as oligotrophic. However, this assessment seems to be based on no particular classification scheme but on a qualitative assessment of the lake's productivity based on macrophyte and phytoplankton abundance. No further assessment of the lake's trophic status was carried out until the study of Hitchen (2001), the monitoring for which (during the summer of 2001) was carried out in conjunction with the present study. Hitchen classified the lake as mesotrophic; however, this assessment was based on data collected during the summer months only. There is thus a need for an assessment of the current trophic status of the lake based on data collected over a full annual cycle. The following uses a number of methods with which to determine the trophic status of the lake.

6.4.1 OECD Classification

The Organisation for Economic Cooperation and Development fixed classification system (OECD, 1982) classifies lakes according to the maximum and annual mean chlorophyll-a concentrations, the minimum and annual mean Secchi depth transparency and the annual mean total phosphorus concentrations. Table 6.7 shows the boundary values for each trophic classification, and the values of each of the classification parameters obtained during the current study.

Trophic Category	Mean TP ($\mu g\ l^{-1}$)	Mean Chl ($\mu g\ l^{-1}$)	Max Chl ($\mu g\ l^{-1}$)	Mean Secchi (m)	Min Secchi (m)
Ultra-oligotrophic	<4.0	<1.0	<2.5	>12.0	>6.0
Oligotrophic	<10.0	<2.5	<8.0	>6.0	>3.0
Mesotrophic	10-35	2.5-8	8-25	6-3	3-1.5
Eutrophic	35-100	8-25	25-75	3-1.5	1.5-0.7
Hypertrophic	>100	>25	>75	<1.5	<0.7
Hollingworth 2001	46 (E)	15 (E)	35 (E)	1.46 (H)	0.82 (E)
Hollingworth 2002	29 (M)	8 (M/E)	14 (M)	1.39 (H)	0.80 (E)

Table 6.7: OECD boundary values for trophic classification system (from Ryding and Rast, 1989, after OECD 1982), with corresponding values for Hollingworth Lake in 2001 and 2002. Letters in brackets give the lake classification based on the particular parameter: M=mesotrophic, E=eutrophic and H=hypertrophic. Mean values are the average over one annual cycle.

It can be seen that according to the above classification scheme the trophic status of the lake differed between the two years sampled. In 2001, the classification due to TP and chlorophyll-a concentrations is eutrophic, while the classification based on Secchi depth is hypertrophic and eutrophic. In 2002, the lake can be classified as mesotrophic according to TP and chlorophyll-a, while the classification according to Secchi depth is again eutrophic and hypertrophic.

However, in the case of Hollingworth Lake the classification arising from Secchi depth measurements is unreliable. There is usually an inverse relationship between Secchi depth and chlorophyll-a, hence Secchi depth gives a measure of the phytoplankton biomass in a lake and hence the trophic status. However, in Hollingworth Lake there is no relationship between Secchi depth and chlorophyll-a although there was a strong inverse relationship with total suspended solids (Table 6.8)

Secchi depth versus:	**Chlorophyll-a**	**TSS**
2001-2002	-0.277 ns (n=31)	-0.798** (n=32)

Table 6.8: Table to show correlations between Secchi depth and chlorophyll-a, and Secchi depth and total suspended solids (TSS) in Hollingworth Lake. Correlations carried out using data from both years combined. * - $P \leq 0.05$, ** - $P \leq 0.01$, (ns- not significant).

The lack of a correlation is due to frequent mixing events leading to large quantities of material being re-suspended from the sediment and entrained in the water column. Thus, the low Secchi depth reflects the large suspended solid in the water column and not chlorophyll-a. Therefore, Secchi depth does not give a true measure of trophic state of this system.

The classification must therefore be based on total phosphorus and chlorophyll-a. It can be seen that using these parameters in 2001 the lake falls within the boundary values for eutrophic, while in 2002 the lake falls within the mesotrophic classification.

6.4.2 Classification according to TGL27885/01

A further method of identifying a lake's trophic status is the technical standard TGL27885/01, originally used in the German Democratic Republic (Ryding and Rast, 1989). Table.6.9 shows the classification scheme, together with the values obtained during this study. The scheme requires average values of nutrients in the epilimnion during the 'summer stagnation period'. In Hollingworth Lake it is difficult to determine the stagnation period, particularly as the lake does not stratify or show any periods of sustained high phytoplankton biomass. The values give in Table.6.9 are the average values over the period from June-September. As with the OECD scheme the lake is

classified as eutrophic in 2001. However, the classification in 2002 classifies the lake as oligotrophic according to SRP, but mesotrophic according to TP. The classification according to dissolved inorganic nitrogen is polytrophic in both years, however this classification is only valid if the lake is nitrogen limited (Hollingworth is P-limited).

Trophic Category	SRP (mg P l^{-1})	TP (mg P l^{-1})	DIN (mg N l^{-1})
Oligotrophic	0-0.002	≤0.015	≤0.01
Mesotrophic	0-0.005	≤0.04	≤0.03
Eutrophic	0-0.1	0.04-0.3	≤0.1
Polytrophic	>0.1	>0.3	>0.1
Hypertrophic	>0.5	>0.5	>0.5
Hollingworth 2001	0.016 (E)	0.054 (E)	0.20 (P)
Hollingworth 2002	0.001 (O)	0.029 (M)	0.26 (P)

Table.6.9: Table to show trophic classification based on total phosphorus (TP), soluble reactive phosphorus (SRP) and dissolved inorganic nitrogen (DIN) according to TGL27885/01. Values are the average taken over all sampling occasions

Like the OECD classification, the TGL27885/01 classification scheme also allows lakes to be classified according to chlorophyll-a and Secchi depth, averaged over the period from April to September. Table 6.10 shows the classification of classification scheme according to these parameters, together with the values obtained for Hollingworth Lake during 2000 and 2002.

Trophic Category	Chlorophyll-a (μg l^{-1})	Secchi depth (m)
Oligotrophic	≤3	≥6
Mesotrophic	<10	≥4
Eutrophic	10-40	≥1
Polytrophic	40-60	≥0.05
Hypertrophic	>60	<0.5
Hollingworth 2001	15 (E)	1.53 (E)
Hollingworth 2002	9 (M)	1.48 (E)

Table 6.10: Table to show trophic classification based on chlorophyll-a and Secchi depth according to TGL27885/01. Values are the mean values for the epilimnion from April to September.

As with the OECD scheme, the classification according to Secchi depth is likely to be unreliable due to the large amount of non-algal particulate matter in Hollingworth

Lake. According to the concentrations of chlorophyll-a the trophic status of the lake is again eutrophic in 2001 and mesotrophic in 2002.

A further method of classification according to TGL27885/01 uses zooplankton dry weight, again using epilimnion values averaged over the period from April to September. Table 6.11 shows the boundary values for classification based on zooplankton dry weight.

Trophic Category	Zooplankton (g dry weight m^{-3})
Oligotrophic	<0.1
Mesotrophic	<0.3
Eutrophic	<0.8
Polytrophic	>0.8
Hypertrophic	0->0.8
Hollingworth 2001	0.09 (O)
Hollingworth 2002	0.10 (O/M)

Table 6.11: Table to show trophic classification based on zooplankton dry weight according to TGL27885/01. Values are the mean values for the epilimnion from April to September.

The problems with using zooplankton as a measure of a lakes trophic status were discussed earlier in relation to Rostherne Mere (Section 4.4.2). When considering the zooplankton biomass values obtained in Hollingworth Lake the problem of determining epilimnion values is not relevant, as trawls were taken though the entire, fully mixed water column. However, the classification according to zooplankton again seems to greatly underestimate the trophic status of Hollingworth Lake. The possible explanation for the discrepancy is that the summer the zooplankton population in Hollingworth Lake were subject to strong top-down control, which kept the zooplankton biomass at low levels. Hence, the strong top-down control leads to a reduced zooplankton biomass, resulting in an underestimate of the trophic status of the lake.

6.4.3 Classification according to phytoplankton species and succession

The presence of particular phytoplankton species can be used as an indication of a lakes trophic status. The most dominant species in Hollingworth Lake were *Asterionella formosa*, *Tabellaria fenestrata var. asterionelloides*, *Cyclotella*, *Melosira* sp. and *Aulacoseira granulata var. angustissima*. When diatoms did not dominate the phytoplankton (late-summer phase 2002) *Ceratium hirundinella* was the dominant

phytoplankter, with smaller numbers of *Dinobryon*. Table 6.12 shows the dominant phytoplankton taxa found within Hollingworth Lake, together with the trophic state the species presence indicates according to the lists of Rosen (1981) Harper (1992) and Mason (1996).

Species	Rosen (1981)	Harper (1992)	Mason (1996)
Asterionella formosa	O/M	E	E
Aulacoseira granulata var. angustissima	E	E*	E*
Cyclotella	O	O/M	M
Melosira sp.	Species vary between O-E	M	E*
Tabellaria fenestrata var. asterionelloides	O/M	O	M
Ceratium hirundinella	M/E	M	M
Dinobryon	O/M	O	O
Oscillatoria	E	nl	nl

Table 6.12: Principal phytoplankton species found within Hollingworth Lake during this study, together with the trophic state that the species indicated according to various authors. * indicates that the list refers to the genus *Melosira* as being indicative of eutrophic conditions i.e. it does not distinguish between *Melosira* species, nor is it clear is the reference to *Melosira* includes *Aulacoseira* (formerly *Melosira*) *granulata*. nl indicates that the species is not listed.

It can be seen from the table that the phytoplankton taxa present within Hollingworth Lake are indicative of all trophic states. Thus, the use of indicator species is inconclusive in determining the trophic status of Hollingworth Lake. However, a comparison of the seasonal succession seen in Hollingworth Lake with the typical seasonal successions described by Reynolds (1984a, 1984b) show that the phytoplankton in Hollingworth Lake closely resembles that of a mesotrophic system (Figure 6.2).

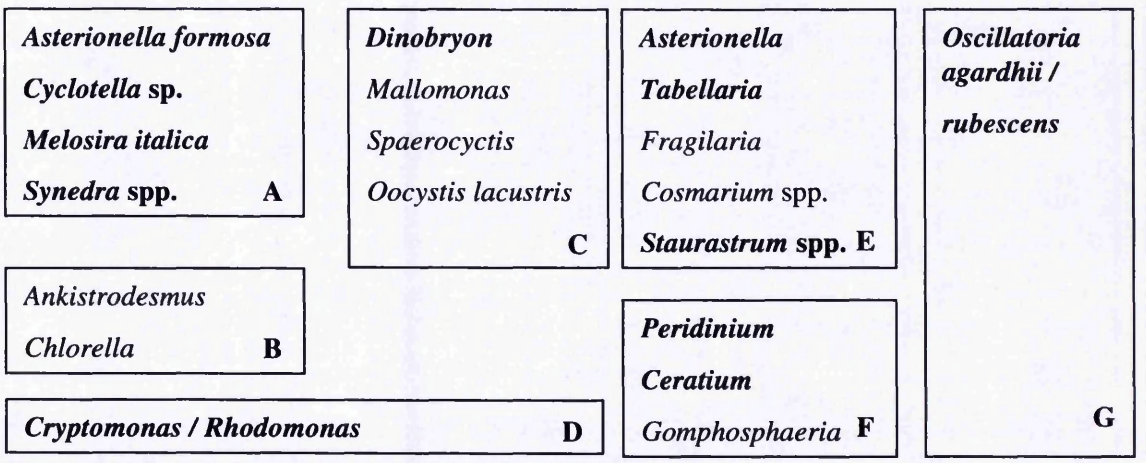


Figure 6.2: Seasonal succession for a typical stratifying mesotrophic lake, compiled from Reynolds (1984a, 1984b). The boxes group together phytoplankton assemblages that are often found together. A typical seasonal succession will follow one or other of the horizontal progressions. Species recorded during this study indicated in bold.

6.4.4 Classification according to bacteria

Lakes can also be classified according to the bacterial populations (Bird and Kalff, 1984). Table 6.13 shows the boundary values of bacterial numbers for each trophic state. However, in the paper by Bird and Kalff no indication of whether these numbers represent peaks values, annual mean, or summer mean values is given, it is simply states that an oligotrophic lake for example 'should contain' $<1.7 \times 10^6$ cells ml^{-1}. Thus, Table 6.13 shows figures for both peak values and summer average values for bacterial numbers in Hollingworth Lake.

Trophic Category		Bacterial numbers ($x10^6$ cells ml^{-1})
Oligotrophic		<1.7
Mesotrophic		1.7-6.5
Eutrophic		≥6.5
Hollingworth 2001	Peak	7.9 (E)
	Summer average	6.9 (E)
Hollingworth 2002	Peak	7.8 (E)
	Summer average	5.7 (M)

Table 6.13: Table to show classification of lakes according to bacteria (Bird and Kalff, 1984), together with the annual peak bacterial numbers, and summer average bacterial numbers in Hollingworth Lake, 2001-2002.

It can be seen that peak bacterial numbers are within the eutrophic classification band. However, if summer average values are taken then the lake is classified as eutrophic in 2001 and mesotrophic in 2002, which agrees with the other classifications which suggest that the trophic state of the lake differed in the two years sampled i.e. eutrophic in 2001 and mesotrophic in 2002.

6.4.5 Previous information on the trophic status of Hollingworth Lake

It is very difficult to assess the trophic state of Hollingworth Lake in years before this study. As mentioned above Clough (1979) suggested that the lake was oligotrophic, although Clough did not give any indication on what this classification was based. The accuracy of this assessment of the lake as oligotrophic is therefore subject to some doubt.

The only other source of information concerning the previous state of the lake is data collected by the environment agency during the period from 1997-2000 (data originally unpublished, but reproduced in Hitchen, (2001)). In terms of assessing the lakes previous trophic state the data on SRP and chlorophyll-a is the most useful.

The EA data concerning chlorophyll-a is very limited, as analysis was only carried out in response to the occurrence of a bloom, with analysis ceasing once the bloom had declined. Thus, there is no data concentring chlorophyll-a over a full annual cycle. However, it is possible to use the chlorophyll-a measurements collected by the environment agency during the autumn (at the time of maximum chlorophyll-a) of 1999 and 2000 to estimate the trophic status using the OECD classification system. During these years, chlorophyll-a samples were taken from the surface and at a depth of 5m. Table 6.14 shows the maximum chlorophyll-a concentrations in these years.

	Max Chl ($\mu g\ l^{-1}$) in 1999	Max Chl ($\mu g\ l^{-1}$) in 2000
Surface	18 (E)	140 (H)
5m depth	18 (E)	39 (E)

Table 6.14: Maximum chlorophyll-a concentration recorded by the Environment Agency during the autumn period of 1999 and 2000. Values are given for samples collected from the surface, and from a depth of approximately 5m.

The 1999 surface sample may be misleading as it may have included floating, surface scum. This sample classifies the lake as hypertrophic according to the OECD classification system. Samples collected from 5m depth are probably more indicative of the concentrations of chlorophyll-a within the water column and these classify the lake

the concentrations of chlorophyll-a within the water column and these classify the lake as eutrophic. Thus, past data on chlorophyll-a concentration suggests that the lake is classified as eutrophic, in agreement with the classification based on the data collected in 2001.

The Environment Agency also collected data on phosphorus concentrations within the lake from 1997 to 2000, with data collected over full annual cycles. Figure 6.3 shows the mean annual values of SRP for the period 1997-2002. It can be seen that the there may be a suggestion that concentrations have been falling in recent years.

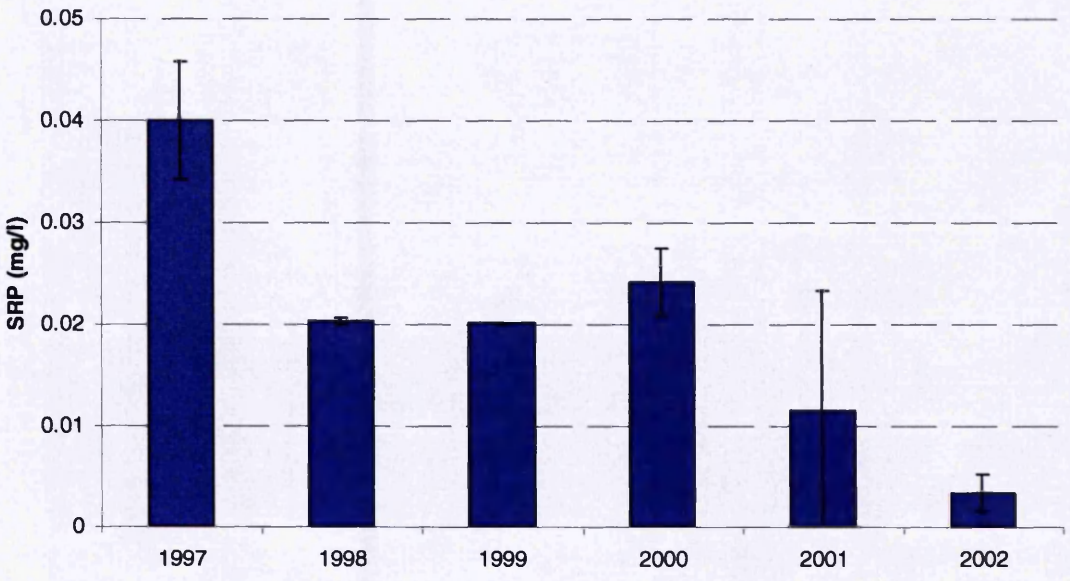


Figure 6.3: Mean annual values for SRP for the EA data (1997-2000), and for data collected during this study (2001-2002). Samples for EA data taken from surface water near the overflow (i.e. close to site C in this study) Error bars represent 95% confidence limits.

It is not possible to use the EA data to determine the lake's trophic status in the years 1997-2000, however, as only concentrations of orthophosphate were measured and it is not possible to apply the EA data to the OECD classification scheme (which uses total phosphorus). However, it is possible to use the TGL27885/01 scheme, which assesses trophic status according to the mean epilimnion SRP concentrations over the 'summer stagnation period'. Mean summer values of SRP for the years 1997 to 2000 are similar to the annual averages displayed in the figure and fall within the range 0.005-0.1 mg l^{-1} that classifies the lake as eutrophic.

6.4.6 Summary of information concerning the trophic status of Hollingworth Lake

A summary of the results of the analysis of the trophic state of Hollingworth Lake is shown in Table 6.15.

		2001	2002
OECD Scheme	**P**	EUTROPHIC	MESOTROPHIC
	Chlorophyll-a	EUTROPHIC	MESOTROPHIC
	Secchi*	Mean Secchi depth classifies lake as hypertrophic, min. Secchi depth classifies the lake as eutrophic	
TGL27885/01	**P**	Both SRP and TP concentrations classify lake as EUTROPHIC	TP concentrations classify lake as MESOTROPHIC, SRP as OLIGOTROPHIC
	DIN	POLYTROPHIC	
	Chlorophyll-a	EUTROPHIC	MESOTROPHIC
	Secchi*	Eutrophic	Eutrophic
Phytoplankton species		Species indicative of all trophic states i.e. OLIGOTROPHIC, MESOTROPHIC, EUTROPHIC	
Phytoplankton seasonal succession		Seasonal succession, typical of that found in MESOTROPHIC systems	
Bacteria		Peak values and summer average EUTROPHIC	Peak value EUTROPHIC, summer average MESOTROPHIC
Zooplankton dry weight (TGL27885/01)		Suggests oligotrophic conditions but top down control makes classification unreliable	

Table 6.15: Summary of the trophic classification of Hollingworth Lake.

If the classifications according to Secchi depth and zooplankton dry weight are discounted (due to the problems outlined above) then it can be seen that according to phosphorus and chlorophyll-a the lake is classified as eutrophic in 2001 and mesotrophic in 2002. However, the phytoplankton seasonal succession indicates mesotrophic conditions in both years. The lake therefore exhibits characteristics of both mesotrophic and eutrophic classifications; it is therefore recommended that the lake be classified as meso-eutrophic.

The mesotrophic classification in 2002 may reflect a change in the trophic nature of the lake through a reduction in phosphorus concentrations. However, it may merely reflect an atypical year, and bear no relation to any long-term change in the character of the lake. Only by monitoring in future years can any long-term trends be distinguished.

SECTION D: SUMMARY AND CONCLUSIONS

Chapter 7 General Discussion

7.1 Comparison of the physicochemical parameters and productivity of the two systems

This study looked at two ecosystems, the first of which, Rostherne Mere, is a well-studied eutrophic system, while the second, Hollingworth Lake has been subject to much less examination. Monitoring was first carried out on Rostherne Mere in 2000 and on choosing Hollingworth Lake as the other system to be studied (in 2001), it was considered that the outbreak of recent *Oscillatoria* blooms were also indicative of a highly productive eutrophic system. It was felt that Hollingworth would therefore provide an interesting comparison to Rostherne Mere, particularly as the lakes varied in depth (Hollingworth Lake max. depth 7.5m, Rostherne Mere max. depth 31m). However, this study shows that the differences between the two systems were larger than anticipated. This can be seen in Table 7.1, which shows a comparison of the physicochemical parameters of the two systems. It is evident that despite the occurrence of recent algal blooms, Hollingworth Lake was much less productive than Rostherne Mere, as Rostherne Mere is classed as a highly eutrophic system while Hollingworth Lake is meso-eutrophic. The difference in productivity is evident from the differing levels of nutrients in the two systems. Rostherne Mere had higher concentrations of both phosphorus and nitrogen, with phosphorus as the limiting nutrient in both systems. In neither system did nitrogen fall to limiting concentrations. Levels of silicon were similar in both systems.

The lakes not only differ in productivity, but also in terms of the physical nature of the two systems, particularly with respect to the degree of wind-induced mixing of the water column. Rostherne Mere is a deep, monomictic system, with stable summer stratification, while Hollingworth Lake is a shallow, polymictic, and non-stratifying system. Thus, the principal difference between the lakes is in relation to the mixing regimes, and productivity.

	Rostherne Mere	Hollingworth Lake
Morphometry	Surface area 48.7 ha Volume 6.64×10^6 m^3 Max depth 31m	Surface area 47 ha Volume 1.25×10^6 m^3 Max depth 7.5m
Trophic status	Highly eutrophic	Meso-eutrophic
Mixing	Monomictic	Polymictic
Stratification	Stratified during the summer period	Non-stratifying
Phosphorus	High concentrations Annual means TP 136 and 230µg l^{-1} SRP concentrations falling to limiting in late summer only	Low concentrations Annual means TP 29 and 46µg l^{-1} SRP concentrations often limiting for long periods of the summer and autumn
Nitrates	TN annual means 1.98 and 2.14 mg l^{-1} Do not fall to limiting concentrations.	TN annual means 0.71 and 0.85mg l^{-1} Do not fall to limiting concentrations.
Silicon	Max winter concentrations ≈ 2.56 and 1.97 mg l^{-1}	Max winter concentrations ≈ 2.10 and 2.15 mg l^{-1}

Table 7.1: Comparison of physicochemical properties of Rostherne Mere and Hollingworth Lake. Annual means and maximum values are given for the two years of study.

7.2 Comparison of the plankton of the two systems

Table 7.2 shows the principal differences between the plankton of the two systems. The two systems differ in their plankton, including phytoplankton species composition, and phytoplankton seasonal succession. The two systems also differ in the relationship between phytoplankton biomass numbers of planktonic bacteria. The only similarity is within the zooplankton, where both systems exhibited a spring peak in zooplankton followed by low summer numbers. The following compares the plankton of the two systems and relates it to the trophic status of the systems and the mixing regime within the lakes.

	Rostherne Mere	Hollingworth Lake
Phytoplankton succession	Regular, predictable seasonal succession, typical of eutrophic conditions	Irregular succession, unpredictable. Similar to the typical seasonal succession for mesotrophic conditions
Chlorophyll-a	Very high, max concentrations 159 and 92 $\mu g\ l^{-1}$ in 2000 and 2002 respectively	Low, max concentrations 35 and 14 $\mu g\ l^{-1}$ in 2001 and 2002 respectively
Secchi Depth	Varies from to <1m during peaks in algal biomass to 5m during the clear-water phase. Significantly correlated with chlorophyll-a	Continuously low, due to suspended non-algal particulate matter in the water column. No correlation with chlorophyll-a
Zooplankton succession	Spring peak in zooplankton biomass. Low summer numbers	Spring peak in zooplankton biomass. Low summer numbers
Bacteria succession	Closely correlated with fluctuations in phytoplankton numbers	Relationship with other factors unclear. Possibly limited by phosphorus availability.

Table 7.2: Comparison of phytoplankton, zooplankton and bacterioplankton populations within Rostherne Mere and Hollingworth Lake.

7.2.1 Phytoplankton

Different trophic status and levels of nutrients in the two lakes leads to differences in the overall levels of phytoplankton biomass, and in the seasonal succession. The phytoplankton species composition in Hollingworth Lake was typical of a mesotrophic system while that of Rostherne Mere was typical of a eutrophic system.

Both the taxa present within the lakes and the level of biomass are dependent on the nutrient status of the systems. It is well known that increasing concentrations of nutrients lead to increasing phytoplankton biomass. Sakamoto (1966) showed a close positive relationship between mean chlorophyll content and both total phosphorus and total nitrogen. Dillon and Rigler (1974) also found a positive relationship between spring total phosphorus and average summer chlorophyll-a. Thus, the difference in phytoplankton biomass between the two systems is to be expected.

The difference between the phytoplankton taxa between the two systems can also be attributed to trophic status. The same algal taxa occur in lakes of similar trophic status but taxa differ between lakes of different trophic status (Harper, 1992). Hence, the use of phytoplankton in the trophic classification of lakes, as carried out in this study (see Section 4.4.3, page 223 and Section 6.4.3, page 347).

In addition to nutrient effects, wind-induced mixing of the water column also contributed to phytoplankton differences between the two lakes.

7.2.1.1 Effect of mixing on the seasonal succession of the phytoplankton

An area in which the two systems differed significantly was in the degree of predictability of the seasonal succession. In Rostherne Mere there was a distinct seasonal succession with different algal groups succeeding each other. The sequence observed in this study was diatoms/cryptomonads $\Rightarrow$ clear-water phase $\Rightarrow$ cyanobacteria / dinoflagellates. This sequence is very similar to the sequence observed in recent years and it suggests that the phytoplankton succession in Rostherne Mere is predictable. This predictability may well be related to the predictability of the mixing events within the Mere, with stratification occurring during late spring/early summer and persisting until the autumn overturn. Thus, conditions favour diatoms in the spring, while the onset of stratification favours species that can regulate their position within the water column and survive at low nutrient concentrations (as nutrients are lost from the euphotic zone due to sedimentation of material). Thus stable summer stratification leads to a predictable succession of different algal groups.

Mixing is also important in determining the phytoplankton succession in Hollingworth Lake. However, whereas the mixing regime in Rostherne Mere was stable and predictable that in Hollingworth Lake was much less so, and this gave rise to a variable seasonal succession. This is evident during this study, when in 2001 diatoms dominated throughout the sampling period, while in 2002 dinoflagellates were dominant in late summer, and in the fact that in some years (1996 and 1999) *Oscillatoria* dominated in the autumn while in other years no such dominance of this cyanobacterium was observed. This is likely to be due to the frequent wind-induced mixing in Hollingworth Lake resulting in a much less physically stable system. Mixing events rapidly change conditions in the lake from those favouring one phytoplankton group/species, to conditions favouring another, for example via the return of nutrients to the water column, or through altering the euphotic depth/mixing depth ratio. In Hollingworth Lake the mixed conditions also favour diatoms for much of the season by keeping the Z_m/Z_{eu} ratio high, and preventing the sedimentation of diatoms. The occurrence and timing of these mixing events in Hollingworth Lake is unpredictable, as it is dependent on the wind speed and direction, leading to difficulties in predicting the seasonal succession of phytoplankton. This unpredictability is often observed in shallow, polymictic lakes. For example, a study of the shallow eutrophic, non-

stratifying Loch Leven (Bailey-Watts, 1978) also found a lack of seasonality in phytoplankton succession which was attributed to the regular unpredictable, mixing events. Sommer *et al.*, (1986) looked at 24 lakes, reservoirs and ponds, of which three were non-stratifying shallow lakes. It was found that the non-stratifying shallow lakes had unpredictable seasonal successions, which was attributed to wind-induced mixing. It was observed that the succession was disrupted more often, and hence it was less predictable, in lakes exposed to strong wind action. The seasonal succession in Hollingworth Lake is similarly unpredictable.

7.2.2 Comparison of the zooplankton populations within the two systems

As the phytoplankton showed very different seasonal successions, it may be predicted that the herbivorous zooplankton would be subject to differing bottom-up control. This may in turn be expected to lead to different zooplankton population dynamics in the two systems. However, zooplankton showed very similar dynamics in both systems, with a large spring peak followed by a decline to low numbers in early summer, with low numbers continuing throughout the summer months.

The similarity in the zooplankton dynamics between the two systems seems to derive from very similar seasonal variation in top-down and bottom-up factors acting upon the zooplankton. Early in the spring the zooplankton in both systems was resource controlled – with low numbers and birth rates. Increasing spring levels of phytoplankton allowed the zooplankton to increase their birth rate. In both systems, the increasing birth rate was due largely to a rapid increase in brood size. The decline in the spring zooplankton peak was observed in both systems. In Rostherne Mere there was strong evidence for the decline in the zooplankton peak being due to bottom-up factors – i.e. a reduction in food availability. In Rostherne Mere the decline coincided with a reduction in the quantity of edible food to below the threshold concentration, and also a reduction in reproductive parameters; both of these pieces of evidence indicate food limitation. In Hollingworth Lake the zooplankton peak also declined during early summer, however the evidence for this being due to bottom-up control is not as strong as in Rostherne Mere. The difficulty in determining the zooplankton food source in Hollingworth Lake made the comparison of available food with threshold concentrations difficult. Evidence on bottom-up control in this system must therefore be based on zooplankton reproductive parameters, and the decline in birth rates at the time that the zooplankton population declined. Thus, the evidence from both systems suggests that bottom-up

factors are important during the winter spring and early summer. However, the use of zooplankton reproductive parameters as an index of food availability suggests that bottom-up control is of secondary importance in both systems during the summer months. The high birth rates and low zooplankton numbers suggests a high mortality rate, and this suggests that top-down control of the zooplankton populations is important in both systems. Thus, despite the different nature of the two systems the factors that regulate the zooplankton populations appear to be very similar.

7.2.3 Comparison of the bacteria within the two systems

The bacterial dynamics within the two systems were very different. In Rostherne Mere, there was strong evidence for the bacterioplankton to be controlled by the availability of organic substrates released by phytoplankton. However, in Hollingworth Lake there is very little evidence from which to make any firm conclusions concerning factors controlling bacterioplankton populations. This may again be related to mixing, as the frequent mixing of Hollingworth Lake may lead to the factors influencing the bacterial numbers changing continually, resulting in no relationship with any one factor. However, bacteria may also have been influenced by the different productivity of the systems. Hollingworth Lake has much lower levels of phosphorus, with undetectable concentrations for long periods of the summer; thus, the lower productivity of Hollingworth Lake may mean that phosphorus may be the factor that principally limits bacteria in Hollingworth Lake, and for that reason no relationship with chlorophyll-a is observed.

7.2.4 Other differences between the two lakes

The above considerations on differences in the two lakes showed that the differences between the lakes could largely be related to differences in productivity and mixing processes within the lakes. However, during the course of this study it has also become evident that the lakes differ in other respects, which although not specifically related to the aims of this study, are nevertheless of interest. These are the nature of the algal blooms that occur within the lakes, and the conservation and amenity value of the two ecosystems.

7.2.4.1 Conservation and amenity value of the lakes

A comparison of the value of the two systems for nature conservation and amenity is interesting. Rostherne Mere is important in terms of nature conservation, and this has resulted in its designation as a RAMSAR site, a SSSI and a NNR. The importance of

the system however led to a restriction on public access thus reducing its amenity value. Hollingworth Lake is also important in terms of nature conservation and although its status is rather less than Rostherne Mere it is important regionally. In 1978 the Nature Conservancy Council surveyed the reservoirs of the mid-Pennine area and showed Hollingworth Lake to be the richest site in terms of water birds. However, it is as a recreational facility that Hollingworth Lake is of greatest value. Whereas public access is restricted to Rostherne Mere, recreational use is promoted at Hollingworth Lake. There is an activity centre upon the lake, with facilities for sailing, windsurfing and canoeing. There is also a rowing and sailing club, and a sea cadet centre. The public can also hire boats and embark on organised cruises around the lake. There is also a visitor centre, cafes and picnic areas, as well as a walk-way around the lakes perimeter.

7.2.4.2 Nature of the algal blooms within the lakes

Rostherne Mere is an example of an ecosystem in which the eutrophic nature, and the related occurrence of blooms of cyanobacteria, is a natural phenomenon. Paleolimnological studies on some of the west midland meres have shown that cyanophytes have been abundant in the lake for 6000 years (McGowan, 1997 cited in Moss, 1998). The long history of bloom formation in the meres suggest that the presence of blooms may not be as a direct result of anthropogenic eutrophication but may in fact be the 'natural' condition of the Mere. In contrast, the occurrence of algal blooms in Hollingworth Lake is likely to be due to human interference. The lake was polluted by clay and silt during the building of the M62 motorway in 1971 and 1972, and a coagulant polyamine was used to settle this material. It was following these events that *Oscillatoria* became abundant in the lake. Thus, the presence of algal blooms in Hollingworth Lake appears to be due to human interference.

In view of the long history of blooms on Rostherne Mere the elimination of water blooms may not be considered a desirable management objective. It would be better to reduce the nitrogen loading to the lake and return it to a condition that may be more representative of its natural state, or at least to its state in the early part of last century, before the intensification of agriculture greatly increased the nitrogen load to the lake. This would lead to dominance by blooms of N-fixing cyanobacteria.

In contrast, the blooms within Hollingworth Lake appear to be of anthropogenic origin, and in view of this, and particularly in view of the high amenity value of Hollingworth Lake, the reduction in algal blooms must be a priority in the future management of the lake.

7.3 Concluding remarks

In conclusion, this study has considered the factors regulating the plankton in two very different systems, one a highly eutrophic monomictic system, and the other a polymictic meso-eutrophic system. The differences between the systems can largely be attributed to the two principal differences between the lakes - their productivity, and the degree of wind-induced mixing.

The lakes also differed in the extent to which they had been studied. Rostherne Mere has a long history of study, with records of the phytoplankton going back to 1914 (Pearsall, 1923). However, despite this large body of work there were a number of areas in which understanding could benefit from further study, for example in the factors that influence the phytoplankton, zooplankton and bacteria, and the current status of the nutrient regime within the Mere. It is hoped that the results of this study will increase the understanding of the factors that regulate the plankton in Rostherne Mere, and add new and valuable information to the existing body of work concerning this ecosystem.

In the case of Hollingworth Lake the work contained within this thesis is the first in-depth study of the plankton community within that system. It is hoped that this investigation will provide the foundation on which future studies of this ecosystem can be based. It is also hoped that this study will help in the understanding of the nature of the plankton within similar systems, and of shallow, polymictic lakes in general.

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